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The 'root-brain' hypothesis of Charles and Francis Darwin

Revival after more than 125 years

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This year celebrates the 200th anniversary of the birth of Charles Darwin, best known for his theory of evolution summarized in *On the Origin of Species*. Less well known is that, in the second half of his life, Darwin's major scientific focus turned towards plants. He wrote several books on plants, the next-to-last of which, *The Power of Movement of Plants*, published together with his son Francis, opened plants to a new view. Here we amplify the final sentence of this book in which the Darwins proposed that: "It is hardly an exaggeration to say that the tip of the radicle thus endowed [with sensitivity] and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements." This sentence conveys two important messages: first, that the root apex may be considered to be a 'brain-like' organ endowed with a sensitivity which controls its navigation through soil; second, that the root apex represents the anterior end of the plant body. In this article, we discuss both these statements.

Introduction

Recent advances in plant molecular biology, cellular biology, electrophysiology and ecology, unmask plants as sensory and communicative organisms, characterized by active, problem-solving behavior.¹⁻⁶ This new view of plants is considered controversial by several plant scientists.⁷ At the heart of this problem is a failure to appreciate different living time-scales: plants generally do not move from the spot where they first became rooted, whereas animals are constantly changing their location. Nevertheless, both animals and plants show movements of their organs; but, as mentioned, these take place at greatly different rates. Present day results,⁸⁻¹³ however, are increasingly coming to show that, in contrast with the classical view, plants are definitely not passive automatic organisms. On the contrary,

they possess a sensory-based cognition which leads to behavior, decisions and even displays of prototypic intelligence.^{4,12}

Charles and Francis Darwin and their Revolutionary Biology

Charles Darwin's interest in plants resulted in the publication of several books from 1862 up to 1880.¹⁴⁻¹⁷ Whereas the period 1835–1849 was dominated by geological studies and the collecting of facts that found their way into *On the Origin of Species*, the second half of Darwin's scientific activities (1850–1882) was dominated by botany (reviewed in ref. 18). One of his last books, entitled *The Power of Movements in Plants*,¹⁷ is a record of the numerous experiments which Charles Darwin performed together with his son Francis. It represents a breakthrough in plant biology. In this revolutionary book, the Darwins departed from the classical and still dominant view of plants as organisms which had no need of movements that were based on sensory perceptions or a brain-like organ.^{1,5,16,19} Plants were revealed to live in a veritable whirl of activities—but at their own slow pace—in which plant parts (leaves, roots, tendrils) continually made rhythmic, and even diurnal, nastic, tropic and nutational movements. But these observations were not accepted by the leading botanists of the time, especially the eminent plant physiologist, Julius Sachs.^{14,16,20,21} He castigated the Darwins for being amateurs who performed careless experiments and obtained misleading results.^{14,20,21} The heaviest criticism fell on the Darwins' root decapping experiments made in relation to root growth and tropisms.^{16,21} It turned out, however, that it was Sachs, not the Darwins, who was maladroit. Sachs, or in fact his assistant Emil Detlefsen, removed root caps badly and his roots showed strong wounding effects.^{17,21} In our own experiments, the growth of decapped maize roots was even quicker after decapping than before.²² However, these roots did not accomplish any gravitropism; they grew ageotropically according to their initial orientation.²² One can consider the acceleration of root growth as an escape tropism. In soil, a root apex is easily the victim of both biotic and abiotic insults. Therefore, the speeding up of the growth of such affected roots with damaged caps, but also showing the earliest stages of cap regeneration,²³ might be considered to be an adaptive trait that contributes to a plant's ecological success.

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Box 1. The Last Paragraph from the *Power of Movements in Plants*:¹⁷ We believe that there is no structure in plants more wonderful, as far as its functions are concerned, than the tip of the radicle. If the tip be lightly pressed or burnt or cut, it transmits an influence to the upper adjoining part, causing it to bend away from the affected side; and, what is more surprising, the tip can distinguish between a slightly harder and softer object, by which it is simultaneously pressed on opposite sides. If, however, the radicle is pressed by a similar object a little above the tip, the pressed part does not transmit any influence to the more distant parts, but bends abruptly towards the object. If the tip perceives the air to be moister on one side than on the other, it likewise transmits an influence to the upper adjoining part, which bends towards the source of moisture. When the tip is excited by light (though in the case of radicles this was ascertained in only a single instance) the adjoining part bends from the light; but when excited by gravitation the same part bends towards the centre of gravity. In almost every case we can clearly perceive the final purpose or advantage of the several movements. Two, or perhaps more, of the exciting causes often act simultaneously on the tip, and one conquers the other, no doubt in accordance with its importance for the life of the plant. The course pursued by the radicle in penetrating the ground must be determined by the tip; hence it has acquired such diverse kinds of sensitivities. It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body; receiving impressions from the sense-organs, and directing the several movements.

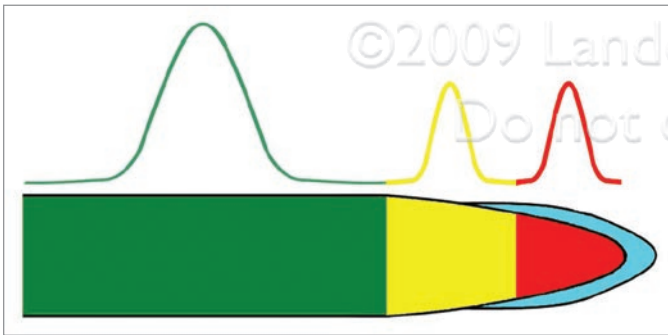


Figure 1. Schematic depiction of idealized three root apex zones (meristem in red, transition zone in yellow, elongation region in green) and idealized peaks of cellular activities (mitotic in red, synaptic in yellow, cell elongation in green) characteristic for these zones.

The Darwins' 'Root-Brain' Hypothesis

The most controversial of the Darwins' propositions is that roots behave as do lower animals with their apex seated at the *anterior* pole of the plant body where it acts as a *brain-like organ* (Box 1).¹⁶ This so-called 'Root-Brain' hypothesis^{16,19} has been forgotten, or ignored, for more than 125 years until we revived it a few years ago.^{1,19,24} Our interest in this Darwinian 'phyto-cerebrated' view of plants emerged from a long-term interest in roots, their growth and their tropisms. The numerous data and results which we review here are clearly not compatible with the classical concept of plants which places them outside the realm of cognitive, animated, animal living systems—a view which traces back to Aristotle.²¹

Recent Support for the Darwins' 'Root-Brain' Hypothesis

Transition zone as 'brain-like' command centre. In 1990, we reported upon a unique zone within the root apex of maize which is interpolated between the apical meristem and the elongation region (Fig. 1).²⁵ It is very interesting to remark that the Darwins concluded that the 1.0–1.5-mm region from the root tip is the most sensitive zone (see page 192 in ref. 17). In the contemporary literature, this root apex zone was at first termed 'postmitotic isodiametric zone',^{25–28} Later, it was renamed as the 'distal elongation zone',²⁹ and later still as the 'transition zone'.^{27,30,31} Recently, the term 'basal meristem' has been used for this same zone.^{32–34} However, as we have confirmed for maize roots, and also for root apices of *Arabidopsis thaliana*,³⁵ rapid cell elongation, the hallmark for the elongation region (Fig. 1), starts just at the basal border of the transition zone.^{25–27} Moreover, cell divisions are an exceptional occurrence in this zone. Therefore, 'transition zone' appears to be the most suitable name for this unique portion of root apex. In future, terms 'command centre'²⁴ or 'cognitive centre,' might prove even better.

Plant synapses: actin-based adhesion domains specialized for cell-cell communication. In 1997, we discovered that the transition zone of the root plays a unique role in the continual development of the actin cytoskeleton as the cells within the root are gradually displaced from apex to base by their own growth and division.³⁶ From a perinuclear F-actin network with no particular orientation and which is characteristic of meristematic cells, is fabricated a system of prominent actin bundles in the form of inverted conical arrays which contact perpendicularly and then align in parallel with the transverse cross-walls where they proceed to reassemble as dense meshworks of F-actin.^{36–38} This bundled arrangement of the actin filaments is characteristic for cells of the elongation zone. The transition between the two mentioned aspects of actin organization takes place in the transition zone. At the time of our first observations it was not clear why dense F-actin meshworks should localize at the non-growing cross-wall domains in the elongation zone, particularly when, in many eukaryotic cells, such F-actin meshworks are markers of actively growing cell-boundary domains.^{31,39–41} Subsequent studies revealed the underlying cytoplasm of the non-growing cross-wall domain to be specialized for high rates of vesicle recycling based on a system of endocytosis and secretory endosomes. This breakthrough was enabled by making use of the fungal inhibitor, brefeldin A (BFA), which blocks all secretion within eukaryotic cells but leaves endocytosis active and unaffected.⁴² As a consequence, all recycling proteins and molecules accumulate rapidly within the cytoplasm, appearing as large roundish BFA-induced compartments.^{42–45} Such compartments were mainly formed in cells of the transition zone of BFA-treated maize roots, indicating the presence there of endocytic structures. Together with the specialized actin/myosin adhesion sites that link the cell cross-wall with the cytoskeleton,⁴⁶ the endosomes could contribute to a system of cell-cell communication along the cell files which extend from the tip of the root to its base.

Plant synapses: from endocytic recycling to auxin secretion. One of the first proteins shown to be involved in the local polarized recycling of membranes within cells of root apices was the auxin efflux carrier, PIN1.^{43,46,47} Later, other PIN proteins of the auxin efflux carrier family were also shown to accomplish polarized endocytosis and vesicular recycling.⁴⁸⁻⁵¹ Interestingly, the classical inhibitors of auxin transport, such as TIBA and NPA, were revealed to be inhibitors of these two processes.^{47,52-55} These data explain the sensitivity of polar auxin transport to BFA, as well as to monensin:⁵⁶ both agents inhibit secretion of auxin at the cellular cross walls.

In 2002, we reported that, besides PINs and several other transporter proteins,⁵⁷ cell wall epitopes such as pectins cross-linked with boron, calcium and xyloglucans, also underwent endocytosis-mediated recycling at the cross-walls.^{43,44,58,59} Both the PIN molecules and the internalized cell wall molecules obviously participate in the same endosomal pathways since it has been found that these molecules colocalize with the vesicles that form after BFA treatment.⁵⁹⁻⁶¹ Moreover, in both control and BFA-exposed root cells, the endosomes and endocytic vesicles are enriched with auxin, as visualized by fluorescently labeled auxin-specific antibody.^{54,60} This finding suggests that PIN efflux carriers transport auxin into both the endosomes and the endocytic recycling vesicles, the interiors of which topologically correspond to extracellular space (Fig. 2). Auxin is then released from the vesicle into this extracellular space under the cell wall via a secretion event (see below). Importantly, these endosomes/vesicles are also enriched, as is the extracellular space, with calcium and cell-wall pectins cross-linked with calcium and boron, as well as with xyloglucans.⁵⁹⁻⁶¹ Finally, both the extracellular space and the endosomal/vesicular interior have acidic pH values. This means that, as predicted by the chemiosmotic theory on the basis of pH gradients across membranes, auxin will leak out of endosomes/vesicles and the PIN efflux carriers will then counterbalance this process. Thus, the secretory model for auxin transport across cellular boundaries is not in conflict with the chemiosmotic theory: it just adds another layer of complexity to it owing to the active contribution of endosomes to this process (Fig. 2). The secretory auxin transport model also explains several recently published data incompatible with the model which considers PIN efflux activity as occurring at the plasma membrane only. First, it easily explains why there is no evident coupling between the presence of PINs at the plasma membrane and auxin transport capacity.^{54,55,63,64} Second, it predicts that there should be a close correlation between rates of auxin transport and rates of vesicle recycling, a datum which has been reported recently.^{55,65-67} Third, it can explain why the auxin molecule, although small enough to do so, does not diffuse through the plasmodesmata: this is because PIN-equipped vesicles and endosomes can effectively remove all free auxin molecules from the vicinity of plasmodesmal orifices (Fig. 2).

Plant synapses as gravity-sensing domains: ‘synaptic auxin secretion’ hypothesis. There are several other mysteries and paradoxes⁶⁸ which can be explained by the secretory model, but which are difficult to reconcile with the classical chemiosmotic model.⁶⁸ First, polar auxin transport is oriented along the gravity

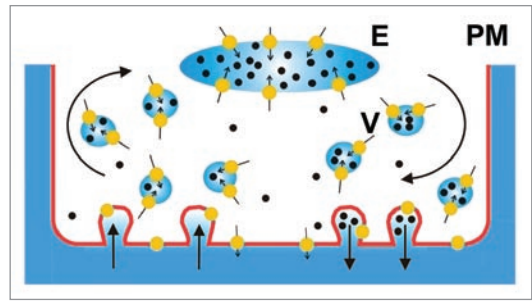


Figure 2. Secretory chemiosmotic model of the polar auxin transport. Hypothetical root cell from the transition zone is shown secreting auxin towards the root apex. Auxin is shown as black dots. PIN1 (yellow dots with arrows) transport auxin into endosomes (E) and endocytic recycling vesicles (V) which then release auxin after fusion with the plasma membrane (red line). Importantly, endosomal and vesicle interior corresponds to the cell wall not only topologically but also with respect of cell wall pectins, high calcium levels and acidic pH. Plasma Membrane (PM) is shown in red, extracellular space and endosome (E) interior is shown in blue.

vector. This necessitates the existence of some mass-sensitive feature of the auxin transport process.⁶² Protoplasmic pressure is experienced in the physically lower portion of plant cells by higher plasma membrane tension (strain)—this strain is relieved by the addition of membrane via vesicular fusions which lead to secretion—i.e., the liberation of vesicular contents. Second, the secretory model^{22,62-65,68} can incorporate a gravity-mediated feature; it manifests, after cellular reorientation with respect to the gravity vector, as a stimulation of auxin secretion^{62,68,69} in response to the gravity-induced increase in tension-load upon the plasma membrane brought about by pressure from a gravity-directed protoplasmic load.^{22,68} Hence, a gravity/auxin-induced growth differential follows. Interestingly, a similar mechanical principle based on plasma membrane tension (strain) regulates vesicle recycling and activities at *Drosophila* neuromuscular synapses.⁶⁹

Besides enabling the gravity-mediated polarisation of auxin transport, the root synapses might themselves act as gravisensing devices.^{22,68} This would explain cases of graviperception at sites remote from the root cap,⁷⁰⁻⁷² in zones whose cells lack sedimentable organelles. Furthermore, analogous synaptic cross walls would explain the gravisensing shown by Characean internodal cells. These cells lack sedimentable organelles and are known to accomplish their gravisensing at their cellular cross-walls.^{73,74}

The ‘Synaptic Auxin Secretion’ hypothesis^{22,62,68} is, perhaps, similar to the gravitational pressure model of Mark Staves and Randy Wayne,⁷²⁻⁷⁴ but with many of the molecular details now made explicit. It should not, however, be viewed as an alternative to the well known ‘Starch Statolith’ hypothesis which is based on amyloplast sedimentation.^{75,76} Rather, the gravity-mediated ‘Synaptic Auxin Secretion’ hypothesis has many elements which allow unification of these seemingly disparate models. In the root cap statocytes, too, gravistimulation redistributes auxin efflux within these sensory cells.⁷⁷ Thus, according to this hypothetical perspective, sedimenting statoliths increase the protoplasmic load (or strain) upon the plasma membrane at the lower part of the cell,

Box 2. Shoot tropisms: positive phototropism, negative phototropism, thigmotropism, shade-avoidance thigmotropism, parasitic host tropism. **Root tropisms:** positive phototropism, negative phototropism, positive oxytropism, positive hydrotropism, chemotropism, thigmo-tropism, traumatotropism, thermotropism, rheotropism, electrotropism, magnetotropism, parasitic host tropism, stress escape tropism, stress avoidance tropism.

thus altering the polarity of 'synaptic auxin secretion'. Thus, this type of secretion is sensitive to any repositioning of a cell within a gravity vector field. Due to this feature, plant synapses may couple the sensory and motoric systems into the adaptive root tropisms.

Root Tropisms: From Sensory Systems to Motoric Systems

Growing root apices are well-known to screen the numerous abiotic and biotic parameters of their environment and to respond to them with either positive or negative tropisms.⁷⁸⁻⁸⁰ Sensory areas are typically at the apices of organs whereas the responsive motoric areas are located basally which implicates long-distance transmission of sensory signals. This, in effect, is an animal-like sensory-motoric circuit which allows adaptive behavior,⁷⁹ and it was remarked upon for the first time by Charles and Francis Darwin in *The Power of Movements in Plants*.¹⁷ Contemporary plant science cites this book quite often, but usually in relation to its historical contribution to shoot phototropism and auxin biology.⁸¹ Surprisingly, the Darwins' experiments with roots, which cover a large part of this book¹⁷ and which culminated in their statement about the brain-like root apices seated at the anterior pole of the plant body (in fact, this statement is contained in the last sentence of the book), had not been mentioned in the literature until 2005 when the 'Root-Brain' hypothesis (Box 1), as well as several related topics,⁸² were discussed at the first symposium on plant neurobiology held in Florence.^{1,19}

Interestingly, the 'astonishing' Darwinian hypothesis of a 'Root Brain' is slowly penetrating mainstream molecular plant biology, as evidenced from the introduction to meeting report from a Keystone Symposium on plant sensing, response and adaptation to the environment.⁸³

Ethylene-based root crawling underlies root searching, avoidance and escape behavior. One often overlooked feature of root tropisms is that they are supported by two bending zones: one initiated in the transition zone, the other occupying the central part of the elongation region. The two zones can bend independently of each other, but they are obviously coordinated and ethylene is essential for this motoric coordination.^{22,84-87} The result is that intact growing root apices can, under appropriate circumstances, perform crawling-like searching movements^{22,86} which closely resemble the type of behavior of a lower animal. The root cap is essential for these crawling movements.^{22,85-87} All this is in accordance with data and concepts of the Darwins' 'Root-Brain' hypothesis.^{16,17,19} On page 196 of their book, they note that the way the root movements are coordinated is admirably perfect.¹⁷

The most extensively studied root tropism (for an overview of all known tropisms, see Box 2) is gravitropism. Despite

expenditure of many man-hours of experimental research, this tropism is far from being completely understood. The putative receptor(s) remain elusive, and both the signal transduction pathway and the information-processing network await full characterization. Another root tropism, which can be traced back to *The Power of Movements in Plants*,¹⁷ is negative phototropism. In fact, one of the first experimental studies published on negative phototropism of roots is a paper published by Francis Darwin alone, in 1880.⁸⁸ With the discovery of receptors such as the blue-light receptor, PHOT1, the signal transduction pathway of this tropism has become one of the best known in plants. PHOT1 localizes to the plant-root synapses in the root transition zone,⁸⁹ indicating that auxin-secreting sensory synapses unify portions of the separate networks of gravi- and phototropism. Root hydrotropism⁹⁰ has also had a long history of study¹⁷ and is now a maturing field for the further understanding of sensory-motoric circuits in plants. We will not discuss here any of the other tropisms listed in Box 2: Gladys Cassab has adequately summarized these topics recently.⁹⁰

It is important to mention briefly two further important aspects of the aforementioned tropisms. First, the cells/organs of perception are always distant from the cells/organs accomplishing the respective motoric adaptive responses. This signal transmission phenomenon was extensively discussed by the Darwins.¹⁷ Second, root apices monitor and integrate numerous parameters simultaneously and then 'translate' these sensory 'experiences' into complex motoric responses. Analysis of informational networks will eventually show the means by which roots are able to compute an appropriate growth response.

Escape Tropism of Illuminated Roots: Stress Situation for the Whole Seedling

More often than not, roots live in darkness. If dark-grown roots are illuminated, they perform a negative phototropism, apparently in an attempt to escape to a dark environment. Illumination of Arabidopsis roots is associated with a speeding-up of root growth, further supporting the idea of an escape response.⁹¹ Similar avoidance tropisms of growing roots have been reported also for salt stress⁹² and aluminium toxicity.⁹³ Surprisingly, it is common laboratory practice to grow Arabidopsis seedlings in transparent Petri dishes and to expose them to light-dark cycling. The light phase would be perceived by the roots as a stress and would induce an escape tropism. It is well known that stress perceived at one site is rapidly communicated through the whole plant body. Thus, seedlings with illuminated roots are stressed generally. Similarly, all data obtained from living roots via light-based in vivo microscopy should be interpreted with caution. For instance, the PIN proteins which export auxin from root cells show different localisations depending on whether roots are grown in light or darkness.⁹¹ Salt stress and aluminium toxicity also induce avoidance tropism via targeting PIN2 localisation and stability.^{63,92} Therefore, we urge plant scientists to keep living roots in darkness and bring them into the light only when necessary.

Neurobiological View of the Plant Body Solves the Recently Introduced ‘Schizophrenic’ Apical-Basal Dichotomy

There has recently been controversy about cell, organ and plant polarity. It was initiated by plant biologists studying polar auxin transport.⁹⁴ Plant anatomy treats shoots and roots as equals in terms of their polarity.⁹⁴ The organ apex is always regarded as one pole, and the base of that organ as the other pole. Thus, each organ is bi-polar. This reflects the usual view which is to separate, conceptually, root and shoot organs; polarity is then defined by reference to the respective apical meristem of the root or shoot, and by an anatomically defined root-shoot transition zone between them. But a slightly different view of bi-polarity emerges if the whole plant is considered as one unit, which logically it is. In this alternative view, it is enough to emphasise this unity by recalling that the taproot of the seedling is a continuation of the embryonic root, and the plumule is the continuation of the embryonic shoot; root and shoot branches are the branched parts of a unitary plant body. Now, however, in certain quarters of recent plant cell biology, it has been assumed that the shoot apex is the apical pole and that the root apex marks the basal pole of a plant.⁹⁴ Thus, a rather serious semantic problem arises because the cell pole facing the root apex should then not be termed apical, but basal.⁹⁵ To most people who have worked with roots this is a schizophrenic situation. The writings of Charles and Francis Darwin present a solution: they proposed, as already mentioned, that the root apex represents the anterior end of the plant body. They reached this conclusion in the last sentence of ‘The Power of Movements in Plants’ (Box 1),¹⁷ and it was based on an analogy between roots and lower animals. Now, all non-plant multicellular organisms have their anterior pole specialized for the uptake of nutrients and for the possession of sensory and brain-like organs. The opposite pole—the posterior pole—is specialized by the expression of sexual organs, excretory apparatuses and motility.¹ Although the Darwins did not discuss this issue further, this observation from the lower animals fits nicely with the plant body, too:^{1,21} the posterior pole of the plant body generates not only flowers with their sexual organs, but also gas-exchanging stomata and motile, nutating stems bearing nutating leaves and tendrils. Our proposal for polarity ignores any root/shoot transition structure and views the plant in its wholeness and follows the analogy between animals and plants. Roots are therefore anterior and shoots are posterior. This is essentially a phyto-neurobiological view of the plant body, with a plant-specific ‘head’ and a ‘brain’ at the plant’s anterior end.^{1,19} It does provide, however, a remedy for the potentially ‘schizophrenic’ situation raised by confused notions of plant polarity. It follows that a cross wall at the end of a cell which faces the root apex is an anterior wall, and a cross wall at the other end of the cell is a posterior wall. This anterior/posterior polarity totally encompasses all root and shoot cells.

A novel idea, and one in accord with the Darwins’ ‘Root-Brain’ hypothesis (Box 1), is that plants are evidently anchored in the soil by their ‘heads’, exposing their sexual organs to the air and to prospective pollinators.²¹

Bose’s Unity of Life and Ockham’s Razor Updated

There is another important aspect of the phyto-neurobiological view which needs to be opened. In keeping with Charles Darwin’s theory of common descent of all organisms, a unification of animals/humans and plants according to their body polarity is possible and thereby removes from view the Aristotelian dichotomy^{1,21} between plant and animal organisms, an axiom of classical biology which has posed a serious problem in the understanding of the logic of evolution and the nature of biological systems. The common descent of all organisms is the central pillar of Charles Darwin’s theory of evolution and, as pledged by Sir Jagadish Chandra Bose,^{96,97} the unity of life implied thereby is a revelation of both beauty and simplicity. By the same token, the existence of a plant neurobiology harmonises with the neurobiology of animals. At the same time, it fills an obvious gap in the all-embracing ‘Living Systems Theory’ of JG Miller.^{19,98}

Recently, the plant neurobiology initiative has been criticized for not fulfilling the simplicity required of a ‘true’ theory—that is, one which would allow it to escape the strictures of Ockham’s razor.⁹⁹ However, we would argue that there is no problem, and that, if anything, the opposite is the case: plant neurobiology is a necessary proposition in the argument for the unity of life. This is a simpler view than the proposition of a dichotomy between plant and animal forms²¹ and may have been found passable by William of Ockham. Besides, as shown, plant neurobiology neatly closes the gap between animals/humans and plants.^{1,21,98}

Finally, we would like to remark in this respect upon Sydney Brenner’s ‘Ockham’s Broom’ principle¹⁰⁰ which is used to sweep under the carpet all inconvenient facts in the interests of saving a favored interpretation against unpalatable and messy reality.^{100,101} Ockham’s Broom explains the tendency to jealously retain long-standing dogmas in science past their expiry date, and perhaps it tells us something also about the fierce resistance to the current plant neurobiology initiative.⁷

Outlook: Complex Social Life of Plant Roots

Recent advances in chemical ecology reveal the astonishing communicative complexity of higher plants as exemplified by the battery of volatile substances which they produce and sense in order to share with other organisms information about their physiological state.¹⁰²⁻¹⁰⁹ The next surprise is that plants recognize self from non-self;¹⁰⁹ and roots even secrete signaling exudates which mediate kin recognition.^{10,11} Finally, plants are also capable of a type of plant-specific cognition,^{3,110} suggesting that communicative and identity-recognition systems are used, as they are in animal and human societies, to improve the fitness of plants and so further their evolution. Moreover, both animals and plants are non-automatic, decision-based organisms. Should Charles and Francis Darwin have witnessed these unprecedented discoveries, they would surely have been pleased by them.

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References

- Baluška F, Hlavacka A, Mancuso S, Barlow PW. Neurobiological view of plants and their body plan. In: *Communication in Plants: Neuronal Aspects of Plant Life*. Baluška F, Mancuso S, Volkmann D, (eds.), Springer Verlag, Berlin—Heidelberg—New York 2006; 19-35.
- Brenner ED, Stahlberg R, Mancuso S, Vivanco J, Baluška F, Van Volkenburgh E. Plant neurobiology: an integrated view of plant signaling. *Trends Plant Sci* 2006; 11:413-9.
- Calvo Garzón F, Keijzer F. Cognition in plants. In: *Plant-Environment Interactions from Behavioural Perspective*. Baluška F, (ed.), Springer Verlag, Berlin; Heidelberg; New York 2009; 247-66.
- Trewavas A. Plant intelligence. *Naturwissenschaften* 2005; 92:401-13.
- Trewavas A. Response to Alpi et al.: Plant neurobiology—all metaphors have value. *Trends Plant Sci* 2007; 12:231-3.
- Baluška F, Mancuso S. Plant neurobiology: From stimulus perception to adaptive behavior of plants, via integrated chemical and electrical signaling. *Plant Signal Behav* 2009; 4:475-6.
- Alpi A, Amrhein N, Bertl A, Blatt MR, Blumwald E, Cervone F, et al. Plant neurobiology: no brain, no gain? *Trends Plant Sci* 2007; 12:135-6.
- Tapken D, Hollmann M. *Arabidopsis thaliana* glutamate receptor ion channel function demonstrated by ion pore transplantation. *J Mol Biol* 2008; 383:36-48.
- Masi E, Ciszak M, Stefano G, Renna L, Azzarello E, Pandolfi C, et al. Spatio-temporal dynamics of the electrical network activity in the root apex: A multi-electrode array (MEA) study. *Proc Natl Acad Sci USA* 2008; 106:4048-53.
- Karban R, Shiojiri K. Self-recognition affects plant communication and defense. *Ecol Letts* 2009; 12:502-6.
- Biedrzycki ML, Jilany TA, Dudley SA, Bais HP. Root exudates mediate kin recognition in plants. *Commun Integr Biol* 2010; 3:In press.
- Trewavas A. Plant intelligence. *Naturwissenschaften* 2005; 92:401-13.
- Trewavas A. What is plant behaviour? *Plant Cell Environ* 2009; 32:606-16.
- Ayres P. The Aliveness of Plants: the Darwins at the Dawn of Plant Sciences. Pickering & Chatto, London 2008.
- Kutschera U, Briggs WR. From Charles Darwin's botanical country-house studies to modern plant physiology. *Plant Biol* 2009; 11:785-95.
- Kutschera U, Nicklas KJ. Evolutionary plant physiology: Charles Darwin's forgotten synthesis. *Naturwissenschaften* 2009; 96:1339-54.
- Darwin CR. (assisted by Darwin F.) *The Power of Movements in Plants*. 1880; John Murray, London (<http://darwin-online.org.uk/>).
- Penny D. Charles Darwin as a theoretical biologist in the mechanistic tradition. *Trends Evol Biol* 2009; 1:e1.
- Barlow PW. Charles Darwin and the plant root apex: closing the gap in Living Systems Theory as applied to plants. In: *Communication in Plants: Neuronal Aspects of Plant Life*. Baluška F, Mancuso S, Volkmann D, (eds.), Springer, Berlin—Heidelberg—New York 2006; 37-51.
- Heslop Harrison J. Darwin and the movement of plants: a retrospect. In: Skoog F, (ed.), *Plant Growth Substances* 1979, Springer Verlag 1980; 3-14.
- Baluška F, Mancuso S. Plants and animals: convergent evolution in action? In: *Plant-Environment Interactions from Behavioural Perspective*, Baluška F, (ed.), Springer Verlag, Berlin—Heidelberg—New York 2009; 285-301.
- Baluška F, Schlicht M, Wan Y-L, Burbach C, Volkmann D. Intracellular domains and polarity in root apices: from synaptic domains to plant neurobiology. *Nova Acta Leopold* 2009; 96:103-22.
- Barlow PW. Regeneration of the cap of primary roots of *Zea mays*. *New Phytol* 1974; 73:937-54.
- Baluška F, Mancuso S, Volkmann D, Barlow PW. Root apices as plant command centres: the unique 'brain-like' status of the root apex transition zone. *Biologia* 2004; 59(Suppl 13):9-17.
- Baluška F, Kubica Š, Hauskrecht M. Postmitotic 'isodiametric' cell growth in the maize root apex. *Planta* 1990; 181:269-74.
- Baluška F, Barlow PW, Kubica Š. Importance of the post-mitotic 'isodiametric' growth (PIG) region for growth and development of roots. *Plant and Soil* 1994; 167:31-42.
- Baluška F, Volkmann D, Barlow PW. Specialized zones of development in roots: view from the cellular level. *Plant Physiol* 112:3-4.
- Ishikawa H, Evans ML. Induction of curvature in maize roots by calcium or by thigmostimulation: role of the postmitotic isodiametric growth zone. *Plant Physiol* 1993; 100:762-8.
- Ishikawa H, Evans ML. The role of the distal elongation zone in the response of maize roots to auxin and gravity. *Plant Physiol* 1993; 102:1203-10.
- Baluška F, Vitha S, Barlow PW, Volkmann D. Rearrangements of F-actin arrays in growing cells of intact maize root apex tissues: a major developmental switch occurs in the postmitotic transition region. *Eur J Cell Biol* 1997; 72:113-21.
- Baluška F, Volkmann D, Barlow PW. A polarity crossroad in the transition growth zone of maize root apices: cytoskeletal and developmental implications. *J Plant Growth Regul* 2001; 20:170-81.
- De Smet I, Tetsumura T, De Rybel B, Frey NF, Laplace L, Casimiro I, et al. Auxin-dependent regulation of lateral root positioning in the basal meristem of *Arabidopsis*. *Development* 2007; 134:681-90.
- De Smet I, Jürgens G. Patterning the axis in plants—auxin in control. *Curr Opin Genet Dev* 2007; 17:337-43.
- Péret B, De Rybel B, Casimiro I, Benková E, Swarup R, Laplace L, et al. *Arabidopsis* lateral root development: an emerging story. *Trends Plant Sci* 2009; 14:399-408.
- Verbelen J-P, De Cnodder T, Le J, Vissenberg K, Baluška F. The root apex of *Arabidopsis thaliana* consists of four distinct zones of cellular activities: meristematic zone, transition zone, fast elongation zone and growth terminating zone. *Plant Signal Behav* 2006; 1:296-304.
- Baluška F, Hlavacka A. Plant forms come to age: something special about cross-walls. *New Phytol* 2005; 168:499-503.
- Volkmann D, Baluška F. The actin cytoskeleton in plants: from transport networks to signaling networks. *Microsc Res Tech* 1999; 47:135-54.
- Baluška F, Barlow PW, Volkmann D. Actin and myosin VIII in developing root cells. In: *Actin: A Dynamic Framework for Multiple Plant Cell Functions*. Staiger CJ, Baluška F, Volkmann D, Barlow PW, (eds.), Kluwer Academic Publishers, Dordrecht, The Netherlands 2000; 457-76.
- Baluška F, Volkmann D, Barlow PW. Actin-based domains of the 'cell periphery complex' and their associations with polarized 'cell bodies' in higher plants. *Plant Biol* 2000; 2:253-67.
- Barlow PW, Baluška F. Cytoskeletal perspectives on root growth and morphogenesis. *Annu Rev Plant Physiol Plant Mol Biol* 2000; 51:289-322.
- Baluška F, Wojtaszek P, Volkmann D, Barlow PW. The architecture of polarized cell growth: the unique status of elongating plant cells. *BioEssays* 2003; 25:569-76.
- Nebenführ A, Ritzenthaler C, Robinson DG, Brefeldin A: deciphering an enigmatic inhibitor of secretion. *Plant Physiol* 2002; 130:1102-8.
- Baluška F, Hlavacka A, Šamaj J, Palme K, Robinson DG, Matoh T, et al. F-actin-dependent endocytosis of cell wall pectins in meristematic root cells: insights from brefeldin A-induced compartments. *Plant Physiol* 2002; 130:422-31.
- Hause G, Šamaj J, Menzel D, Baluška F. Fine structural analysis of brefeldin A-induced compartment formation after high-pressure freeze fixation of maize root epidermis: Compound exocytosis resembling cell plate formation during cytokinesis. *Plant Signal Behav* 2006; 1:134-9.
- Robinson DG, Langhans M, Saint-Jore-Dupas C, Hawes C. BFA effects are tissue and not just plant specific. *Trends Plant Sci* 2008; 13:405-8.
- Baluška F, Šamaj J, Wojtaszek P, Volkmann D, Menzel D. Cytoskeleton—plasma membrane—cell wall continuum in plants: emerging links revisited. *Plant Physiol* 2003; 133:482-91.
- Geldner N, Friml J, Stierhof YD, Jürgens G, Palme K. Auxin transport inhibitors block PIN1 cycling and vesicle trafficking. *Nature* 2001; 413:425-8.
- Teale WD, Paponov IA, Palme K. Auxin in action: signalling, transport and the control of plant growth and development. *Nat Rev Mol Cell Biol* 2006; 7:847-59.
- Palme K, Dovzhenko A, Ditengou FA. Auxin transport and gravitational research: perspectives. *Protoplasma* 2006; 229:175-81.
- Kleine-Vehn J, Friml J. Polar targeting and endocytic recycling in auxin-dependent plant development. *Annu Rev Cell Dev Biol* 2008; 24:447-73.
- Petrásek J, Friml J. Auxin transport routes in plant development. *Development* 2009; 136:2675-88.
- Dhonukshe P, Grigoriev I, Fischer R, Tominaga M, Robinson DG, Hasek J, et al. Auxin transport inhibitors impair vesicle motility and actin cytoskeleton dynamics in diverse eukaryotes. *Proc Natl Acad Sci USA* 2008; 105:4489-94.
- Mancuso S, Marras AM, Volker M, Baluška F. Non-invasive and continuous recordings of auxin fluxes in intact root apex with a carbon-nanotube-modified and self-referencing microelectrode. *Anal Biochem* 2005; 341:344-51.
- Schlicht M, Strnad M, Scanlon MJ, Mancuso S, Hochholdinger F, Palme K, et al. Auxin immunolocalization implicates vesicular neurotransmitter-like mode of polar auxin transport in root apices. *Plant Signal Behav* 2006; 1:122-33.
- Mancuso S, Marras AM, Mugnai S, Schlicht M, Zarsky V, Li G, et al. Phospholipase D ζ 2 drives vesicular secretion of auxin for its polar cell-cell transport in the transition zone of the root apex. *Plant Signal Behav* 2007; 2:240-4.
- Wilkinson S, Morris DA. Targeting of auxin carriers to the plasma membrane: effects of monensin on transmembrane auxin transport in *Cucurbita pepo* L. tissue. *Planta* 1994; 193:194-202.
- Fuji K, Miwa K, Fujiwara T. The intracellular transport of transporters: membrane trafficking of mineral transporters. *Curr Opin Plant Biol* 2009; 12:In press.
- Baluška F, Liners F, Hlavacka A, Schlicht M, Van Cutsem P, McCurdy D, et al. Cell wall pectins and xyloglucans are internalized into dividing root cells and accumulate within cell plates during cytokinesis. *Protoplasma* 2005; 225:141-55.
- Dhonukshe P, Baluška F, Schlicht M, Hlavacka A, Šamaj J, Friml J, et al. Endocytosis of cell surface material mediates cell plate formation during plant cytokinesis. *Dev Cell* 2006; 10:137-50.
- Šamaj J, Baluška F, Voigt B, Schlicht M, Volkmann D, Menzel D. Endocytosis, actin cytoskeleton and signalling. *Plant Physiol* 2004; 135:1150-61.

61. Šamaj J, Read ND, Volkmann D, Menzel D, Baluška F. The endocytic network in plants. *Trends Cell Biol* 2005; 15:425-33.
62. Baluška F, Volkmann D, Menzel D. Plant synapses: actin-based adhesion domains for cell-to-cell communication. *Trends Plant Sci* 2005; 10:106-11.
63. Shen H, Hou NY, Schlicht M, Wan Y, Mancuso S, Baluška F. Aluminium toxicity targets PIN2 in Arabidopsis root apices: Effects on PIN2 endocytosis, vesicular recycling and polar auxin transport. *Chin Sci Bull* 2008; 53:2480-7.
64. Baluška F, Schlicht M, Volkmann D, Mancuso S. Vesicular secretion of auxin: Evidences and implications. *Plant Signal Behav* 2008; 3:254-6.
65. Li G, Xue HW. Arabidopsis PLDzeta2 regulates vesicle trafficking and is required for auxin response. *Plant Cell* 2007; 19:281-95.
66. Yang X, Song L, Xue HW. Membrane steroid binding protein 1 (MSBP1) stimulates tropism by regulating vesicle trafficking and auxin redistribution. *Mol Plant* 2008; 1:1077-88.
67. Wang Y, Lin WH, Chen X, Xue HW. The role of Arabidopsis 5PTase13 in root gravitropism through modulation of vesicle trafficking. *Cell Res* 2009; 19:1191-204.
68. Baluška F, Barlow PW, Volkmann D, Mancuso S. Gravity related paradoxes in plants: plant neurobiology provides the means for their resolution. In: *Biosemiotics in Transdisciplinary Context, Proceedings of the Gathering in Biosemiotics 6*, Salzburg 2006, Witzany G, (ed.), Umweg, Helsinki 2007; 9-35.
69. Siechen S, Yang S, Chiba A, Saif T. Mechanical tension contributes to clustering of neurotransmitter vesicles at presynaptic terminals. *Proc Natl Acad Sci USA* 2009; 106:12611-6.
70. Wolverson C, Mullen JL, Ishikawa H, Evans ML. Root gravitropism in response to a signal originating outside of the cap. *Planta* 2002; 153-7.
71. Mancuso S, Barlow PW, Volkmann D, Baluška F. Actin turnover-mediated gravity response in maize root apices: gravitropism of decapped roots implicates gravisensing outside of the root cap. *Plant Signal Behav* 2006; 1:52-8.
72. Staves MP, Wayne R, Leopold AC. The effect of the external medium on the gravitropic curvature of rice (*Oryza sativa*, Poaceae) roots. *Am J Bot* 1997; 84:1522-9.
73. Wayne R, Staves MP, Leopold AC. The contribution of the extracellular matrix to gravisensing in characian cells. *J Cell Sci* 1992; 101:611-23.
74. Staves MP. Cytoplasmic streaming and gravity sensing in Chara internodal cells. *Planta* 1997; 203:79-84.
75. Nemeč B. Über die Art der Wahrnehmung des Schwerkraftreizes bei den Pflanzen. *Ber dtsh bot Ges* 1900; 18:241-5.
76. Sack F. Plastids and gravitropic sensing. *Planta* 1997; 203:63-8.
77. Friml J, Wisniewska J, Benková E, Mendgen K, Palme K. Lateral relocation of auxin efflux regulator PIN3 mediates tropism in Arabidopsis. *Nature* 2002; 415:806-9.
78. Gilroy S. Plant tropisms. *Curr Biol* 2008; 18:275-7.
79. Hodges A. Root decisions. *Plant Cell Environ* 2009; 32:628-40.
80. Monshausen GB, Gilroy S. The exploring root-root growth responses to local environmental conditions. *Curr Opin Plant Biol* 2009; 12: 766-72.
81. Whippe CW, Hangarter RP. Phototropism: bending towards enlightenment. *Plant Cell* 2006; 18:1110-9.
82. Baluška F, Mancuso S, Volkmann D. *Communication in Plants: Neuronal Aspects of Plant Life*. Springer Verlag, Berlin; Heidelberg; New York 2006.
83. Jiménez-Gómez JM, Maloof JN. Plant research accelerates along the (bio)informatics superhighway: symposium on plant sensing, response and adaptation to the environment. *EMBO Rep* 2009; 10:568-72.
84. Wolverson C, Ishikawa H, Evans ML. The kinetics of root gravitropism: dual motors and sensors. *J Plant Growth Regul* 2002; 21:102-12.
85. Edelmann HG, Roth U. Gravitropic plant growth regulation and ethylene: an unsought cardinal coordinate for a disused model. *Protoplasma* 2006; 229:183-91.
86. Hahn A, Firn R, Edelmann HG. Interacting signal transduction chains in gravity-stimulated maize roots. *Signal Transduct* 2006; 6:449-55.
87. Hahn A, Zimmermann R, Wanke D, Harter K, Edelmann HG. The root cap determines ethylene-dependent growth and development in maize roots. *Mol Plant* 2008; 1:359-67.
88. Darwin F. Über das Wachstum negativ heliotropischer Wurzeln im Licht und im Finster. *Arbeiten des Botanisches Instituts in Würzburg* 1880; 2:521-8.
89. Wan Y, Eisinger W, Ehrhardt D, Baluška F, Briggs W. The subcellular localization and blue-light-induced movement of phototropin 1-GFP in etiolated seedlings of *Arabidopsis thaliana*. *Mol Plant* 2008; 1:103-17.
90. Cassab G. Other tropisms and their relationship to gravitropism. In: *Plant Tropisms*. Gilroy S, Masson PH, (eds.), Blackwell Publishing Ltd 2008; 123-39.
91. Laxmi A, Pan J, Morsy M, Chen R. Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in *Arabidopsis thaliana*. *PLoS ONE* 2008; 3:1510.
92. Li X, Zhang WS. Salt-avoidance tropism in *Arabidopsis thaliana*. *Plant Signal Behav* 2008; 3:351-3.
93. Hawes MC, Gunawardena U, Miyasaka SC, Zhao X. The role of root border cells in plant defence. *Trends Plant Sci* 2000; 5:123-33.
94. Baluška F, Barlow P, Baskin T, Chen R, Feldman L, Forde BG, et al. What is apical and what is basal in plant root development? *Trends Plant Sci* 2005; 10:409-11.
95. Friml J, Benfey P, Benková E, Bennett M, Berleth T, Geldner N, et al. Apical-basal polarity: why plant cells don't stand on their heads. *Trends Plant Sci* 2005; 11:12-4.
96. Bose JC. Unity of life. Presidential Address at the 13th Indian Science Congress, Lahore, 1927; Reprinted in the *Everyman's Science* 2004; 34:206-23.
97. Shepherd VA. From semi-conductors to the rhythms of sensitive plants: the research of J.C. Bose. *Cell Mol Biol* 2005; 51:607-19.
98. Barlow PW. Reflections on 'plant neurobiology'. *BioSystems* 2008; 92:132-47.
99. Struik PC, Yin X, Meinke H. Plant neurobiology and green plant intelligence: science, metaphors and nonsense. *J Sci Food Agric* 2008; 88:363-70.
100. Brenner S. In theory. *Curr Biol* 1997; 7:202.
101. Robertson M. Ockham's broom. *J Biol* 2009; 8:79.
102. Bruin J, Dicke M. Chemical information transfer between wounded and unwounded plants: backing up the future. *Biochem Syst Ecol* 2001; 29:1103-13.
103. Pierik R, Whitelam GC, Voeseek LA, de Kroon H, Visser EJ. Canopy studies on ethylene-insensitive tobacco identify ethylene as a novel element in blue light and plant-plant signalling. *Plant J* 2004; 38:310-9.
104. Karban R, Shiojiri K, Huntzinger M, McCall AC. Damage-induced resistance in sagebrush: volatiles are key to intra- and interplant communication. *Ecology* 2006; 87:922-30.
105. Arimura G, Matsui K, Takabayashi J. Chemical and molecular ecology of herbivore-induced plant volatiles: proximate factors and their ultimate functions. *Plant Cell Physiol* 2009; 50:911-23.
106. Dicke M, van Loon JJ, Soler R. Chemical complexity of volatiles from plants induced by multiple attack. *Nat Chem Biol* 2009; 5:317-24.
107. Baluška F. (ed). *Plant-Environment Interactions: From Sensory Plant Biology to Active Plant Behavior*. Springer Verlag, Berlin—Heidelberg—New York.
108. Heil M, Karban R. Explaining evolution of plant communication by airborne signals. *Trends Ecol Evol* 2009; In press.
109. Gruntman M, Novoplansky A. Physiologically mediated self/non-self discrimination in roots. *Proc Natl Acad Sci USA* 2004; 101:3863-7.
110. Calvo Garzon F. The quest for cognition in plant neurobiology. *Plant Signal Behav* 2007; 2:208-11.