Plant roots: autopoietic and cognitive constructions

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Abstract: Many facets reflecting the autopoietic process of Life and Living can be found in plant roots at many levels relevant to their organisation, from cells to ecosystems. At each level, there are sub-processes dedicated to both the auto-reproduction and the self-maintenance of that level, these processes being contained within a boundary appropriate for that level. Auto-reproduction and self-maintenance unite with a third sub-process, cognition, and provide the basis of a coherent multi-levelled programme of root-research.

Keywords: autopoiesis, cognition, living systems, roots, self-maintenance

Introduction

During the last decade, root research, supported by innovative gene and metabolomic technologies (Mochida and Shinozaki 2010), has exhibited a resurgence; moreover, a sense of urgency now attends the quest for a better understanding of the radicular 'hidden half' of plants. No doubt some of the impetus for the new activity in root research also derives from the uncertain future of Earth's flora and fauna in the face of human population pressures, climatic change and soil degradation. Appreciation of the fundamental biological and ecological connectedness of organisms is therefore an imperative, and this, in turn, requires that attention should be paid to the signs and communicational pathways that enable the coherence of living systems (Barlow 2007). Also, some older topics, such as allelopathy (in modern times placed on a reliable footing by Hans Molisch, 1937), have emerged into the spotlight (Bais et al. 2006), recognised by epithets such as 'chemical signalling between plants' (Tomilov et al. 2006), 'kin recognition' (Dudley and File 2007), and so on, placed within the titles of the cognate publications.

The properties of roots in terms of their structure and metabolism, as well as their responses to passing perturbations of their various *modi vivendi*, are of great interest not only to the biologists who study them, but also to a wider public for whom news of such research contribute a backcloth to scientific literacy. Moreover, the fact that plants and their roots sense the materiality of their immediate environment, and that some of these materials may be the product of other plants, has led to the notion that plants (and maybe their individual roots also) are cognitive, and even 'intelligent', entities (Trewavas 2003, Calvo and Keijzer 2009). However, for many root biologists, cognition and intelligence are perhaps unfamiliar themes within their spheres of interest. One aim of the present article, therefore, is to draw attention to these two concepts in order that they may inform, and even become integrated with, the more traditional areas of root biology. The notion of cognition (Calvo and Keijzer 2009) is particularly intriguing because it is linked with the question of what it means to be 'Living' (Maturana and Varela 1980). The possibility of 'cognitive roots' therefore endows these organs with a special significance which projects them to the question lying at the heart of biology: 'What is Life?' Given that the 'Santiago Theory of Cognition' (Maturana and Varela 1980) proposes that cognition does not provide a representation of an independently existing and observable world, but is more concerned with the continual *bringing forth of a world* through the process of Living. A second aim, therefore, is to explore, if we can, this question of Life and Living from the perspective of plants and their roots. Moreover, when the vast volume of research topics and the results gained from roots are considered together, it seems that just about every aspect summed up in the concept of a 'Living System' is evident and ideally represented in plants, and especially in their roots (Miller 1978, Barlow 1999). Roots are thus potential paradigms for studying the entire range of Living processes; and they can also help answer the biologic-philosophical question of what it means to be alive.

Roots as mirrors of Life

In considering the above questions concerning, specifically, of what Living processes consist and how they could be identified in plant roots, it is interesting to encounter the following sentence: "Life is a cyclic process that produces the components that in turn self-organize in the process itself, and all within a boundary of its own making" (Bitbol and Luisi 2004, p. 99). Or, in another, later formulation of the same theme: "A living system is a system capable of self-reproduction and self-maintenance through a regenerative network of processes which take place within a boundary of its own making and regenerates itself through cognitive or adaptive interactions with the medium" (Damiano and Luisi 2010, p. 149). To those sensitised to root science, it might very well seem that what is being referred to in the two quotations is a plant root, albeit one of unspecifiable origin. But, actually, the system to which the quotations are linked is more abstract and concerns the processes which support Life itself. Nevertheless, can it be said that the essentials of Life and its continuing existence are somehow evident within a root? This conundrum presented itself to the philosopher of existentialism, J-P Sartre, for whom contemplation of a chestnut tree root was a revelation: "I was in the municipal park just now. The root of the chestnut tree plunged into the ground just beneath my bench ... I was sitting alone in front of that black knotty mass, which was utterly crude and frightened me. And then I had this revelation. It took my breath away. Never, until these last few days, had I suspected what it meant to 'exist'. Usually existence hides itself. It is there, around us, in us, it is us... there was just one word in my head, the word 'to be' ... And without formulating anything clearly, I understood that I had found the key to existence... to my own life." (Sartre 1963; pp. 182, 185). The key-word that is absent from the above quotations and opinions of PL Luisi and colleagues, and which also summarises what, for Sartre, it meant to exist, is the word 'autopoiesis' (from the Greek *auto – αυτό,* for self , and *poiesis – ποίησις,* for creation or production). An understanding of autopoiesis brings clarification to biology and to the nature of Life and Living.

In the present exploration of roots and Life in relation to autopoiesis, the process is as originally conceived by Varela et al. (1974) and Maturana and Varela (1980). The term 'autopoiesis' refers to a system which organises, maintains, and recreates itself (Bitbol and Luisi 2004, Damiano and Luisi 2010). Life is an autopoietic phenomenon and, thus, a living root – any root – continually re-creates Life, for it, too, is an autopoietic system existing at the organisational level of the organ (see below) as well as being part of a further autopoietic system which is associated with the level of the plant organism. Although the philosopher, Henri Bergson, warned that "The intellect is characterised by a natural inability to comprehend life" (Bergson 1911, p.165), autopoiesis and the example of the root as an autopoietic organ do provide a portal through which a glimpse is given of how Life and Living proceed as systems of continuing construction and becoming.

A third aim of the present paper is to link the autopoietic aspect of roots with the notion of cognition for, as Bitbol and Luisi (2004, p. 101) have proposed, the aspect of cognition relevant here is that which concerns the "local environmental conditions for maintaining an *operationally closed autopoietic system*" (my italics). Living systems are cognitive systems (Maturana and Varela 1980); and, seemingly, cognitive systems are alive (Heschl 1990, Stewart 1996).

Levels of organisation

Before tackling the problem of how to join what some would regard as metaphysical speculations on Life and autopoiesis with the more practical issues of root research, it is necessary to distinguish briefly the levels of biological organisation from which these topics may be viewed. Many would agree that, in their totality, biological systems are hierarchical constructions (where the so-called 'levels of organisation' are of different scale and complexity, and are 'nested' within each other) as opposed to being heterarchical (where organisational units are of similar importance and are connected 'horizontally'). An appreciation of hierarchical levels is important because it forms an orientation which investigators can use in interpretating knowledge of biological phenomena gained from experimental results and observations.

To grasp the meaning of a 'level' of biological organisation, we can turn to JG Miller's 'Living Systems Theory' where it is proposed that each level is comprised of, and is supported by, a canonical set of 20 sub-systems (Miller 1978). A description given by JG Miller of the characteristics of a level and how it might be defined can be found at the following URL: http://www.panarchy.org/miller/livingsystems.html. In terms of their sub-system structure, levels are self-similar: the 20 sub-systems supporting a biological system at reference level *n* are the same in their operation, though differing in their components, to those supporting systems at levels *n*+1 and *n*-1. Sub-systems of any level devolve into three groups with distinctive functions: one for regulating the reproduction of the level in question, another for processing matter and energy, and a third for processing matter-energy and information (Miller

1978, Miller and Miller 1992). The ways in which sub-systems interact within a given level is the grist for the mill of systems research (Kitano 2002, Barabási and Oltvai 2004): probably, the sub-systems function without a central control but are subject to the structural determinism inherent to the level in question. In the text which follows, it will become evident that many of the ideas pertaining to autopoiesis and cognition (see Bitbol and Luisi 2004) complement the sub-systems proposed by Living Systems Theory (Miller and Miller 1992, 1995).

For a discussion of the relationship between roots and autopoiesis, it is sufficient to consider four levels of organisation, the cell, the root organ, the metamer, and the root–shoot organism (Fig. 1); a fifth level, comprised of roots in relation to their ecosystem, is considered only when relevant. The cell or, more precisely, the 'cell body' (Baluška et al. 2004), is generally considered to be the fundamental unit, if not of Life, at least of biological growth and development. The demonstrable totipotency of zygotic and somatic cells indicates that from one such cell-body the whole organism can be developed. The cell itself is regarded, in the terminology of autopoiesis (Maturana 2000), as either a 'single Unity' or a 'composite Unity', depending on whether or not one wishes to include for consideration the putative endosymbiotic status of cellular organelles. The root–shoot organism is comprised of cell-constituted root- and shoot-organ units, or 'metamers' (Barlow 1994a). However, it is the organ level, as exemplified by the root, which is the main focus in the remainder of this article.

One of the general principles underlying the structuring of the organisational hierarchy is that each level is, as it were, striving to extract energy of progressively higher quality from the organisational level above: cells acquire carbohydrates from organs (leaves), organs capture photons from sunlight, and organisms are embedded and integrated within a noospheric world or cosmos (Barlow et al. 2010).
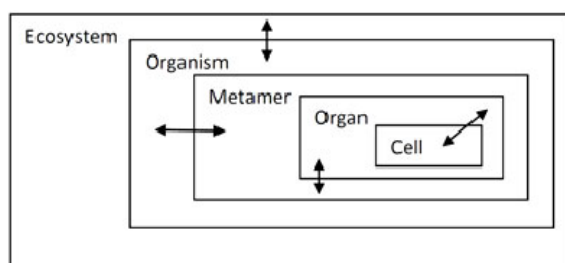
Fig. 1. A scheme of plant organisation which views plant construction as a nested hierarchy of different 'levels' (the levels named in the scheme are indicated by the various boxes nested one within another). There is two-way communication (↔) between levels, from level *n* to level *n*+1 and vice versa, by means of signs and signals appropriate to each level.

Another principle relevant to Life and autopoiesis is the necessity of perceiving and capturing, via cognition, moments of instability in the 'environment' of a given level, and of utilising the resulting internal perturbations as starting points for adaptation: that is, cognition becomes the means of modifying the surrounding environmental conditions of Living in relation to the unceasing autopoietic process.

Autopoiesis

An autopoietic system is possessed of three essential features: auto-reproduction, an auto-constructed boundary, and a self-maintained metabolism; cognition enters as a fourth feature (Bitbol and Luisi 2004). All these features will be discussed below; and all are, in one way or another, components of Miller's Living Systems Theory (Miller 1978).

Auto-reproduction

Auto-reproduction and self-organisation lie at the heart of autopoiesis. From the point of view of cellular reproduction and its theoretical and analytical representation, the development of L-systems (Lindenmayer 1975) and of interactionless double-wall map (dwM0) L-systems in particular (Lück et al. 1988), have allowed the generation of a range of cellular maps which are analogues of observable biological cellular patterns on the apices of plants and elsewhere. Many of these maps indicate that auto-reproduction is a property shared not only by <u>cells</u> but also by particular privileged <u>patterned groups of cells</u>. The latter patterns are precursors for the production (which appears as an auto-reproduction) of <u>organs</u>. Auto-reproduction is hereby expressed through the repetitive and patterned branching of organ axes. For roots, the rhizotaxy of lateral roots along their supporting axis is an example of auto-generated patterning. Another example is seen in the phyllotaxy of leaves and buds, in the case of shoots (Barlow and Lück 2007). It, too, is characterised by a patterned production of new and repeating portions of the vegetative axis, these being known as metamers or modules (Barlow 1994a). It is as though there is a reproducer of organogenesis (axis branching) which is intimately associated with, and even dependent upon, a particular group of cells arranged in a distinctive pattern. This privileged group can be given the term 'generative centre'. The development of a generative centre is dependent upon the auto-reproduction of one or more stem cells or structural initials (Barlow 1994b) which bear a particular structural quality or 'state' (Terpstra and Heidstra 2009). Thus, the notional outputs of dwM0L-system algorithms relate to one of the three biological features of autopoiesis –

auto-reproduction: and it is this last-mentioned feature which, when supported by the complete set of biological sub-systems, sustains and propagates Life.

The auto-reproductive feature inherent to L-system algorithms, as applied by Barlow et al. (2000, 2004a), relates both to individual stem cells <u>and</u> to the generative centres of plant roots. Also inherent to the algorithms is the production of new cell boundaries, or cell walls. All these mentioned items are abstractions, though there must also be biological analogues of the notional cells and walls derived from the algorithm and its starting conditions. Both cellular and generative-centre auto-reproduction conform with the 'reproducer' sub-system of Living Systems Theory, which is associated with each level of biological organisation. Thus, the 'reproducer' identifies with the generative centre at the organ level, and with the cell body at the cellular level.

To provide a little more detail, a dwM0L-system, S_{5-5}, was applied to a notional 3-sided cell b (Fig. 2). This cell b is an analogue of a 3-sided structural initial, or apical cell; such a cell is characteristic of root and shoot apices of certain ferns. The operation of system S_{5-5} was found to produce a sequence of notional cells which faithfully reproduce the spiral patterns of actual biological cells observable upon the apices of roots and shoots of the fern, *Psilotum nudum* (Barlow et al. 2000, 2004a, Barlow and Lück 2004).

From the viewpoint of autopoiesis, two important events occur during the operation of system S_{5-5}. The first is that not only does cell b give rise to 3-, 4-, and 5-sided cellular products, but it also re-produces itself, thus concluding a cell-production cycle. Moreover, the steps in the cell production cycles are recurrent: after a defined number of steps, the initial b-cell state is recovered and the production cycle of its already-existing polygonal-cell descendents continues (Fig. 2). Thus, in accordance with the autopoietic principle, the biological analogue of L-system S_{5-5} operating within the b cell at the apex of *Psilotum*, can be said to be a self-reproducing system. A second noteworthy event is that a new 3-sided cell, a, is produced, after a definite number of steps have been accomplished by one of the descendents of the 3-sided
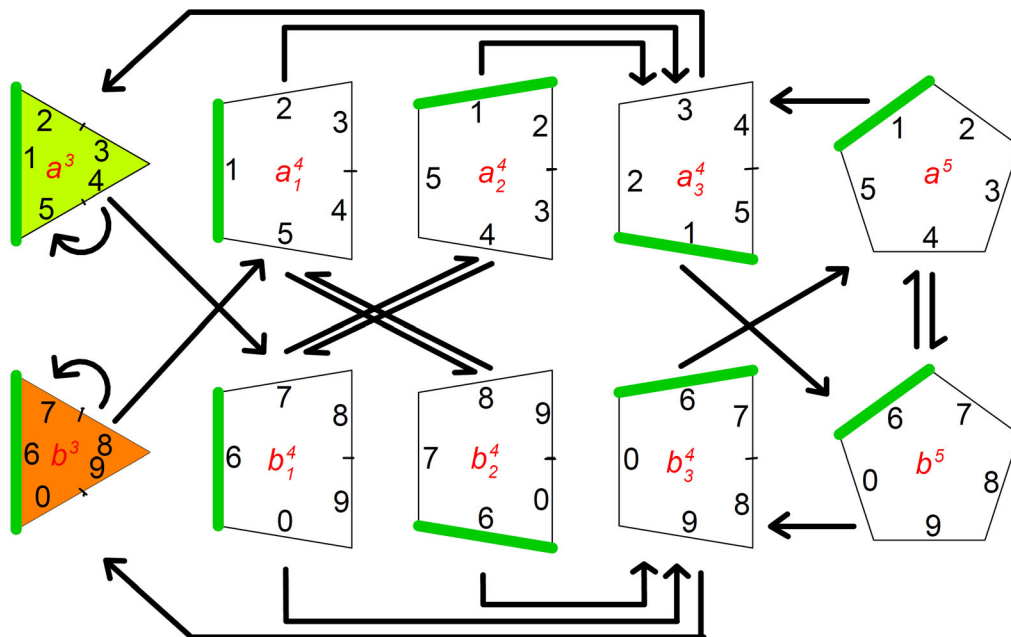
Fig. 2. Partial representation of the operation of dwM0L-system S_{5-5}. There are 10 types (states) of cells with three different shapes due to the number of walls. In this scheme, all cells derive from an auto-reproductive 3-sided initial (orange) cell, b^3, and lead to the production of a new 3-sided cell, a^3, (shown in light green) which is also auto-reproductive. Arrows indicate the transitions between cell states. Transitions occur simultaneously at each time-step. Walls are numbered according to their own state. The site of insertion of a new division wall is indicated by a fleck (⌐). The most recently inserted division walls are coloured dark green. Cells are labelled (red script) according to their state, the superscript numeral referring to the number of walls, and subscript numeral referring to the order in which the cell was produced with respect to its origin from the b^3 initial at time-step 1. The whole cell group constitutes an auto-reproductive, self-maintaining generative centre. (Adapted from Barlow et al. 2000)

cell *b*. Then, in accordance with the operation of system S$_{5-5}$, cell *a* proceeds to repeat the same sequence of cell production as does cell *b*, except that the handedness of its cell productions is the contrary to those from cell *b*. This feature of the notional cellular system agrees with the biological system (Barlow and Lück 2004). The similarity between the L-system mode of cell production and that observed in the biological material is strong. Both cellular systems, notional and biological, are auto-reproducing: hence, they fulfil one feature of an autopoietic system. Moreover, the systems are deterministic in the sense that an event, or state transition, has only one outcome. This theme of determinism will be returned to elsewhere in our discussion. It should also be remarked that the auto-reproductive property of the cellular map formed by system S$_{5-5}$ (and others dwL-systems) is conferred upon it by rules which govern the change in state of the walls at each time-step. The importance of the boundary properties of cells and organs for their autopoiesis will also be mentioned later.

Both the notional and the biological cellular systems derived from dwM0L-system S$_{5-5}$ are two-dimensional. Hence, only the anticlinal cell productions are considered. All newly produced cells grow unless otherwise instructed to do so (this is an important option for morphogenesis and contributes to axis branching, as has already been discussed (Barlow et al. 2004a)), and their productions are continually interpolated into an expanding 'skin' of the apex. The third dimension for cell production involves cells divisions which are periclinal. New cells are produced towards either the interior of the organ or to its exterior, giving rise to cap tissue (if a root), or to leaves (if a shoot). These periclinal divisions are not specified by the L-system algorithm S$_{5-5}$, however; their three-dimensional representation requires the more complex L-systems of 'cellworks' (Lück and Lück 1996).

The roots of higher plants (angiosperms) also contain auto-productive generative centres which account for axis branching, often in an acropetal sequence. However, it is not an external epidermal layer which is involved (as in *Psilotum*) but is, instead, the pericycle, this being the external layer of the vascular cylinder or plerome (usage of the latter term, even though it is less familiar, will be retained here). Each new pericyclic generative centre arises at a particular distance from the root apex determined by the number of division cycles λ associated with the descendents of the plerome stem cells (functional initials) (Barlow and Lück 2008). Because the new axes are also potentially self-producing, they are able to generate, after periclinal divisions and a 90° switch in growth polarity of a selected group of cells (Barlow

et al. 2004b, Szymanowska-Pułka and Nakielski 2010), a ramified root system. Importantly, the pericycle layer of the parental root and one of its new generative centres enter into each daughter root (see Byrne et al. 1977). Thus, it is the pericycle which ramifies; it continues to be an unbroken cell layer, drawing into it a new plerome formed from the auto-produced generative centre, thereby extending the physical span of what is, in effect, a single root organ with many ramifications.

The pericycle is the auto-reproductive component of an autopoietic root axis: it produces new generative centres which create new pleromes of the next order of branching and hence perpetuates the pericyclic cell type. Although this process is commonly thought of as lateral root production, it should not be forgotten that the endodermis of the parental root contributes to the newly-formed cap of any new lateral root. In this regard, the generative centre derived by auto-reproduction in the pericycle appears to stimulate, by some type of induction process, the development of a cap structure from the overlying endodermis of the periblem (Barlow et al. 2004b). Recent evidence on lateral root formation (de Smet et al. 2007) suggests that, for a short while, the apex of the young primordium leaks auxin, which is derived from the vascular tissue within the parental plerome, and it is this auxin which induces the endodermal cell divisions that accompany new cap production. The new root cap is an ephemeral structure, however, and is replaced by one developed from a calyptrogen concurrently with the emergence of the new root from the parental axis. Modelling studies, using auxin fluxes and relative cellular sensitivities as variables, have been helpful in defining the requirements for deterministic generative-centre auto-reproduction in the pericycle (Lukas et al. 2008).

Not all plant tissues are autopoietic; the plerome is one such tissue, as we have seen. Other tissues, even though derived from their own set of functional initials, are apparently denied the power to auto-reproduce. Take, for example, the case of the peripheral root cap. The fate of the component protodermal cells is to be sloughed from the root apex as part of the outer peripheral cap complex. The processes effecting this involve cell separation, cytolysis, and possibly cell death (Wenzel et al. 2001). Depending on the species, peripheral cap cells peel away from the apex either as single cells or as rafts of cells. The importance of this is that the detached cells form a lubricating layer which assists the passage of the root tip through mechanically-resistant soil (Iijima et al. 2004) and they also provide nutritious material for the surrounding microbe population. Although the maturing and mature cells of both peripheral cap and the central cap columella are important as sensory or

perceptive tissues, they contrast with autopoietic tissue. How and where, then, comes about this distinction between root tissues – those which are dedicated to self-perpetuation and those to self-annihilation? What we have termed as being structural and functional initials are probably strongly imprinted (Sang et al. 2009, Terpstra and Heidstra 2009) with elements that control their destiny.

The autopoietic principle also operates at a level of plant organisation higher than the organism. At this higher level, the autopoietic system perpetuates itself by means of both genets, which express gametic syngamy for the initiation of a new autopoietic cycle, and ramets, which express asexually-reproducing, autopoietic propagules. An introduction to the meaning and usage of the terms 'genet' and 'ramet' can be found in, e.g., Eriksson (1993).

Self-maintenance

No plant or root lives in an unchanging environment: due to transient instabilities, there is a constant cycle of sensation and response between the units at each level of the organisational hierarchy and their respective environment. The responses evoked are fairly specific to each level and have been considered to fall into two categories: short-term plastic responses and longer-term regenerative responses (Barlow 1993). They are manifestations of each level's capacity for self-maintenance, or homeostasis (Table 1).

One area where self-maintenance is of crucial importance is that of the generation of form, for it is out of form that function arises. In the case of roots, form is dependent upon the means by which the isotropic growth expressed by the stem cells

(structural initials) is diverted towards anisotropic growth, this being is a feature of their histogenetic stem-cell descendents (functional initials). Emerging from this isotropic/anisotropic transformation is the cylindrical form that characterises all growing root apices. Although this is a simplistic view of root growth, it was from the straightforward mensuration of cell growth that the discovery of the 'transition zone' was made (Baluška et al. 1996, 2010). This zone 'master-minds' the rapid cell elongation needed to respond adequately and commensurately to perturbations sensed by the root in relation to its unstable external environment.

A methodology employed to model the change from isotropy to anisotropy during rhizogenesis is one derived from growth tensors (Hejnowicz 1989, Szymanowska-Pułka 2007). Paraboloidal tensors have mostly been used in this situation. They are constructed on the basis of the orthogonal intersections between files of cells, their anticlines and their periclines. The tensor parameters accordingly specify the velocities with which these intersections move apart along the anticlinal/periclinal principal directions of growth thereby defining a morphogenetic space within a boundary structure. A given root-growth tensor is, in effect, an analogue of a boundary-enclosed metabolic system which includes the activities of the auxin-transporting PIN proteins (see Baluška et al. 2010), and which supports the autopoietic system of the plerome as well as the growth of the remaining zones of the root apex.

The establishment of a growth tensor field within and around the few stem cells which constitute a generative centre of a root has been examined theoretically (Szymanowska-Pułka 2007), thereby illuminating the modes of initiation and the subse-

Table 1. Plastic and regenerative responses to perturbations which exemplify the self-maintenance of different levels of plant organisation, with emphasis on roots (Modified from Barlow 1993)

Level	Self-maintenance response		Perturbation
	Plastic	Regenerative	
Community	Ecokinesis*	Succession	Fire, vegetation clearance
Organism	Genetic and epigenetic variants, genotrophs	Compensatory growth	Rich or poor nutrient patches, toxins
Organ	Neoformations, 'plastic' organ forms	Tropisms, cell divisions with organ regeneration	Reorientation within gravity vector, browsing by animals
Cell	Hypertrophy	Cellular repair, division	Wounding, chemical inhibitors

*Ecokinesis was a term used in Barlow (1993) to indicate changing floristic patterns in relation to a perturbation (say periods of higher summer temperature).

quent growth of root apices within an embryo or a primordium (Szymanowska-Pułka and Nakielski 2010). Unlike the products of an auto-reproductive L-system, however, a growth tensor cannot replicate itself and, hence, cannot develop a new tensor which would support the production of a daughter root. The replication of a tensorial focus, where anticlines and periclines converge, can come about only if the tensor is re-aligned to collocate with a new cellular generative centre. However, it might be possible to align the growth tensor so that it could cooperate with the biological–cellular analogue of certain of the already mentioned L-systems which develop the cellular framework of the root. The tensor expresses itself through the expansion of cell walls; and it is the link between cell wall area, cell volume and cell body replication and division which determines the creation of new walls and, hence, enables the self-maintaining property of the tensor.

Occasionally, departures from stable root growth can be deduced from anatomical preparations of roots where they take the form of minor alterations to the planes of cell division. These lead, for example, to breaks in the root–cap junction with accompanying intrusions of new cells into the cap from localised origins in the epidermis and cortex. However, more major developmental alterations of internal behaviour are evidenced by switches in meristem construction – for example, the change-over from a 'closed'-type to an 'open'-type of meristem, an occurrence which seems to be a natural accompaniment of root growth (Heimsch and Seago 2008). Both these anatomical variations can be attributed to a 'wandering' of the focal point of some biological analogue of the root growth tensor. In the first case mentioned (breaks in the cap junction), the wandering could be occurring in lateral or rotational directions with respect to the root axis (Nakielski 1997). In the second case, of changes of meristem construction, the closed-to-open change in meristem type may be evidence of a large-scale wandering of the tensor analogue, even to the extent of its departure from the vectorial map of the root's interior; but it is more likely that the change is due to breakdown in the self-maintenance of the tensor analogue itself. The new, 'open'-type meristem then becomes destined to a final determinate phase of growth, ending with the abolition of a meristem and the cessation of root elongation (Chapman et al. 2003).

In a further case of axial tensorial wandering, a back-and-forth direction was inferred from the periodic activation and deactivation of the quiescent centre coupled with phases of root-cap tissue renewal at the apices of cultured roots of mutant, gibberellin-deficient tomato roots (Nakielski and Barlow 1995). The process appeared to be self-correcting since the overall growth and form of the roots did not change even though details of its cell production did so. In fact, a similar sequence of cap renewal is found at the tips of newly forming roots. For example, in a germinating tap root, the cap which had been formed in the embryogenic, pre-germination phase of root ontogeny is replaced by a cap newly formed from the apex of the post-germination root, the old cap being pushed off the root tip as germination is completed. In certain cases, though, there is no new cap formation, and the apex remains cap-less (Richardson 1955).

Internal movements of the growth tensor may theoretically account for some types of physical root movements, such as micro-nutations, and even, perhaps, for the small deviations from rectilinear tip growth which occur when roots grow through soil (Nakashima et al. 2008). Whether such micro-movements are spontaneous – i.e., outcomes of random events – or induced by sensitivity to some property of the soil, is not known. Mutation, such as the *agt* mutation in maize roots (Abeysekara and McCully 1993), as well as those factors which regulate root-looping (Hahn et al. 2006), can amplify these small growth deviations. In these cases, the growth elements of the cells appear to have become more sensitive to, or the roots have become more cognisant of, perturbations external to its boundary. However, such self-correcting movements imposed on rectilinear growth have not been explored in much detail. In the case of autotropisms, putative tensor alignments may be influenced by a higher-level system of regulation (Barlow 1992).

Boundary

The auto-reproductive and self-maintaining processes of autopoiesis require a space for their action (Varela and Frenk 1987), and this space requires a boundary for its definition. The boundary defines, and is defined by, the range of activities which can be accomplished at a given organisational level, be they chemical reactions within a single cell, or between groups of cells in a generative zone, or the morphogenetic correlations between buds within the crown of a tree. The properties of the boundary also define the shape and form of the constructions produced by autopoiesis at each organisational level and, hence, define the identity assigned to them by anatomists and morphologists. Indeed, it might be too easy to ignore the importance of biological boundaries, believing them simply to be like fences which either include or exclude wandering materials. A boundary, as Beloussov et al. (1997) and Beloussov and Grabovsky (2007) have argued, may possess organisational properties which determine the fate of the entire biological system. In plant development, the external

boundary at the proembryonic stage is clearly a determinant of cell fate (Vroemen et al. 2003). Properties of the boundary are also encapsulated in the dwM0L-systems discussed earlier.

A boundary is expressed at three levels of organisation in the context of the autopoietic root – the cell, the plerome (as a component of the root organ), and the entire root (as part of the metamer unit of an organism). Each one of these boundaries bears on the principle of autopoiesis (Bitbol and Luisi 2004). The boundary is, moreover, a component sub-system of Living Systems Theory (Miller 1978).

Cell

According to a new view of cells posited in 'Cell-Body Theory' (Baluška et al. 2004), the boundary of the plant cell is its peripheral cytoplasm and the surrounding cellulosic wall. The peripheral cytoplasm is believed to have been derived during the course of eons of evolutionary time, when endosymbiosis was an important event in cell phylogeny, from a 'host' organism which engulfed a 'guest' cell which provided a cell body. The two components of the endosymbiotic cell then possessed two different cytoskeletal systems: actin filaments and microtubules, respectively. Together, these cytoskeletal units define some of the structural/functional properties of the cell, such as its cytonuclear ratio as well as the means of auto-productive and self-assembling cell-boundary formation, as seen when wall or outer membrane are stripped off and naked cytoplasm thereby displays the ability to regenerate these boundary items (see Baluška et al. 2004 for references). Evidently, in this last-mentioned example, boundary formation conforms to the autopoietic principle at the cellular level in that it is self-assembled from materials already present within the system of the damaged cell. And in the same manner as the extracellular matrix of animal tissues, the cell-wall and peripheral-complex extend as a continuum throughout the plant organism. Plant cell walls can probably transmit signals of a chemical or physical nature to and from the interior of the cells which they enclose; and, collectively, the intercellular spaces between walls permit the transmission of light and gases throughout the plant.

Plerome

Unlike boundaries of the cell and of the organism, the boundary pericycle of the plerome does not have thickened walls and is physically relatively weak in comparison with not only the osmotic potentials enclosed within it but also the boundaries particular to other levels of the plant. Fortunately, the endodermis on the external surface of the pericycle affords it additional structural support. Actually, endodermis and pericycle can be considered as coeval lineages since they trace back to a common progenitor cell (Di Laurenzio et al. 1996). Endodermis is also the site where endogenous gibberellin regulates the extension rate of the root (Ubeda-Tomás et al. 2009) and it has also been proposed to be an electrical-insulating structure (Barlow 2009) in much the way that myelin insulates animal neurons.

Root

Every root is part of a metamer, a unitary component of whole-plant construction (Barlow 1994a). Following the formation of a zygote and proembryo, a root (plerome + periblem + dermatogen + calyptrogen) develops as a branch unit from the apical (suspensor) end of the embryonic hypocotyl. Embryogeny proposes that root periblem is in continuity with the outer tissues of the stem, and that the root epidermis (dermatogen) is part of an unbroken skin which covers the whole root–shoot organism. Calyptrogen arises from its own set of initials as a covering to the structural initials (stem cells) of the root. So, calyptrogen, too, stands on a dermal boundary at the extreme apex of the root.

A feature of many roots, especially those of the Gramineae, is that the cells external to the plerome are not long-lived. The periblem and dermatogen disintegrate and the component cells are set free when cell growth ceases (Troughton 1962, Spaeth and Cortes 1995). Once within the soil, they participate in the formation of a rhizosphere into which microbes, and microfauna also, make their entry. Thus, the boundary of the root is a zone in which periblem merges with its external environment. Holistically – that is, from a perspective which simultaneously takes account of each organisational level – the boundary of the root is elevated, conceptually, to be a living, rhizospheric element embedded within the next higher organisational level, that of the plant community. The rhizosphere is a metabolic structure within that higher level, one of whose other autopoietic components (assuming the plants therein to be dioecious) is the reproductive pair (Barlow 1999). Thus, one might go so far as to regard the periblem and dermatogen as potential components of the rhizosphere rather than limited to being components of the root. In fact, the pericyclic/endodermal boundary of the root plerome is akin to the epidermal boundary of the stem for, although these two zones with their different tissues are not known to be in anatomical continuity (though they might become so after the shedding of periblem), the extension of both their boundaries are regulated by complex molecules – gibberellin and brassinosteroid, repectively (Savaldi-Goldstein et al. 2007).

It has been argued (Bitbol and Luisi 2004) that a definition of 'Living', in the sense of the operation of a fundamental 'unit of Life', incorporates the principle of autopoiesis. However, not all autopoietic systems are living – see, for example, the fascinating Belousov –Zhabotinsky (BZ) chemical reaction (Zaikin and Zhabotinsky 1970, Maselko and Showalter 1989; see also http://heracles.chem.wvu.edu/gallery.html). It may be asked: Why is this reaction considered as non-living? Or, put another way: What is missing from a non-living autopoietic system such as the BZ reaction, which would bring it alive? A boundary would contribute to the latter task; but not just any boundary; it would have to be a boundary created and maintained by the system itself! Once again, the root can claim to be an analogue of the ideal elemental autopoietic system – an encapsulation of Life and of existence itself, just as J-P Sartre, in the quotation given earlier in the Introduction, had realised. Autopoiesis perpetuates the generation of boundaries: from that of the cell-body to that of the organism, which itself produces the principal boundaries that enclose egg and sperm bodies (ovary and sporogenous cells, respectively), and thence to the boundaries that enclose zygotic cell bodies.

Cognition

So far, we have considered roots as organs possessed of autopoiesis. An intrinsic feature of autopoiesis is the faculty of cognition (Maturana and Varela 1980), for it is the means by which the autopoietic process of Life itself is sustained and advanced. Moreover, roots are positioned on the plant so that they can 'cognise' the plant's underground semiosphere. It is not in any sense frivolous to speak of the 'root brain' (Barlow 2006, Baluška et al. 2009) and to make analogy between a 'swarm' of root tips within a root system and the collective sensory apparatuses of insect swarms and other animal groups.

Two definitions of cognition are (a) 'the mental process or faculty by which knowledge is acquired', and (b) 'that which comes to be known through perception'. Because 'knowledge' has been mentioned in definition (a), its own definition is needed: 'the sum or range of what has been perceived or discovered' (Universal Dictionary 1987). These three dictionary definitions come handed down as consensus, and probably anthropocentric, statements. Nevertheless, the two definitions of 'cognition' would apply to plants if the word 'mental' (in definition (a)) were removed. Expanding the definition of cognition so that it can have a general meaning, mention should be made of an act of reception, in the interior of the organism or within a unit at some other level, of a significant sensation, which has been initiated by an act of perception. The perceived sensation is transformed into a material able to interact with the current metabolic or behavioural states, and of affecting thereby some change which leads to a response – i.e., leads to a new, but nevertheless temporary, behavioural state.

Usually, cognition is spoken of as though it were predominantly a human faculty and applied to just one level of organisation (the organismal). In theory, it is quite legitimate to consider cognition as it might feature at other levels and also in individuals of other species, those of plants, in particular. And even though species of plants and animals (and microbes) have characteristics which set them apart from each other and also install them within separate taxonomic kingdoms, animals and plants possess the same hierarchical organisational levels. If it is accepted that a property of all living systems is that their levels are supported by similar sub-systems, even though these sub-systems work with different degrees of intensity, in particular those concerned with matter-information processing (Barlow 2010), then this would mean that the plant kingdom, also, is filled with organisms which are cognitive. In fact, according to 'The Santiago Theory of Cognition', developed by Maturana and Varela (1980), living systems are cognitive systems, and living, is a process of cognition which applies irrespective of the presence and intervention of a nervous system (Maturana 2000). Therefore, we should ask: What types of sensations are perceived and then internally translocated and transformed by plant organisms for their process of autopoiesis? Do perceptions occur at different levels of organisation? And how do these events relate to cognition as defined previously? Naturally, answers to these questions are dependent upon observation: that is, they depend upon cognitive processes which are already operating in a human observer, and this may introduce some bias or subjectivity into observational interpretation. What are observed are usually alterations in an organism's behaviour, and these changes can manifest at various levels in a reference plant. Sometimes, clues to the changes can be gained from observation of neighbouring plant units, especially if neighbouring rhizospheres make contact. Any change might point to cognition occurring within an even higher level – that of the ecosystem. And in this respect, cognition ranges from that triggered by auto-toxicity, which often leads to feeble growth (Singh 1999), to the discrimination between kin and non-kin (Dudley and File 2007), to intimate co-operative interactions due to root-grafting (Graham and Bormann 1966).

Cognition feeds the autopoietic process with impulses for change (for a summary, see Lyon 2006). Generally, the basis of cognition is a perturbation that

can be sensed and registered by an internal steady-state pattern of self-maintaining metabolism. Then, if perturbation leads to a behavioural change in state which is advantageous for self-maintenance, the processes effecting this state-change may be selected and assimilated by epigenetic and/or genetic means (reproducer sub-system). Hence, cognition can assist adaptation. At the same time, change in a behavioural state may modify the surrounding environment, e.g., lead to the secretion, by the reference organism, of materials into its rhizosphere which subsequently modify the behaviour of neighbouring organisms. Even within the rhizosphere and ecosphere, it seems that there is a strict interplay of sensing and response, leading to the belief that here, too, at this level, there is structural determinism (Gómez et al. 2010), and that this feature may extend to those genetic and phenotypic adaptations, realised in time, which are usually referred to as evidence of 'evolution' (Edelmann and Denton 2007).

Because biological organisation is based upon the principle of a hierarchy built of nested levels (Fig. 1), sensations, perturbations and cognition, could theoretically be recorded at each separate level within this nesting. Then, there could be communication between levels, so that behavioural manifestations at one level, say of level n, could impinge upon, and be perceived at, a lower level, n-1 (Barlow 1993). However, it seems less likely that the converse occurs – that an entity of level n can comprehend totally an entity of a higher level, n+1, due to limitations of the former level's information-processing sub-systems.

Mention was made earlier concerning the determinism of cell division patterns in apical meristems as revealed by analogous division systems operated by L-system algorithms. In fact, determinism of auto-productions is, at the same time, a means of self-maintenance, as shown by the autopoietic cellular generative centres, for example. Indeterminism, by contrast, appears to be an inconceivable guideline for development, especially for the maintenance of Life, and would seem incompatible with autopoiesis. Similarly, indeterminism in the cognitive process would lead to chaotic and even pathological patterns of behaviour and, wherever these occur could possibly be evidence of a breakdown in the self-maintaining metabolic aspect of autopoiesis. So, as proposed elsewhere (Barlow 2010) with respect to plant behaviour and cognition, deterministic transitions from state to state, at a chosen level, would be more comprehensible within the context of plant activities at all levels.

In an earlier discussion (Barlow 2010), behavioural state changes were coordinated and represented within the framework of Petri Nets (very simply described by Pinney et al. 2003). These Nets are useful analogues of behaviour because not only is it possible to build closed, self-maintaining Nets, but their use also makes it possible to see how prototypic 'decisions' can be made. Essentially, decisions concern the resolution of choices between alternative pathways which, in the biological situation, could be the cognitive responses leading to, or converging upon, undecidable pathways and alternative end-points. Resolution of such conflicts can take place only when some additional state or a new pathway, becomes available to the existing Net, thus facilitating the attainment of a new end-point and the restoration of the original Net structure. Adaptations involve a systematic re-structuring of the Net.

The biological and internal analogue of the Petri Net is a set of signal-processing sub-systems. Their operation is deterministic because they themselves compose, and are also parts of an auto-constructed system. Chemistry brings coherence to the sub-systems and confers upon them a dynamic dimension; and it has been argued by Kováč (2006) that chemistry is a basis for cognition. Furthermore, according to Maturana (2000), whatever arises in a structure-determined system is a consequence of its dynamics. Nothing external to it can specify what happens in it, but only triggers a change in its structure, and that this change, too, is determined by the pre-existing structure or state. Biological structural determinism is well represented by the methodology of Petri Net proposed earlier for cognition in plants (Barlow 2010). Importantly, in a Petri Net there is no material 'flow' of information but only a set of pre-determined state-changes which arise out of the structure and nature of the Net itself and a set of pre-conditions to which the firing of a state-change responds. At many levels in the organism, however, there can be resonances to a perturbation: as Lyon (2006) comments, how an organism behaves resonates down to the internal molecular dynamics and, likewise, molecular interactions amplify into behaviour at the organism level.

There is also a place for memory in arriving at cognitive end-points (Barlow 2010). A trace, or memory, of a previously cognised event, has a material basis. Providing it is not erased with the passage of time, this material, because it is now available to a signal-processing pathway, can serve as a pre-condition for a response pathway already determined within the organism. Memory traces of many past perceptions and responses also initiate what might be called 'stores of knowledge'. Here we arrive at a difficult topic because the usual corollary of 'knowledge' is the act of its application in order to operate some process or other. Application of 'knowledge', especially if it leads to an advantageous result, is usually considered to be a display of

'intelligence'. From the perspective of animal behaviour, intelligent acts may be thought of as being the result of certain conscious choices in the employment of outside agencies, such as tools (Barlow 2010); in plants, however, these types of choices might be questioned if consciousness is denied to them, as was averred by Bergson (1911, p. 111). In fact, Bergson (ibid.) claimed that the level of consciousness of an organism is proportionate to its power to move *freely* (Bergson's italics), which might in turn be paralleled with the degree of its cognitive activity. However, if 'knowledge' is considered to be the sum of many stored and retrievable memory traces, then what is called 'intelligence' would be the outcome of a deterministic set of Petri-Net-like transitions, enabled by retrieved memory traces acting as pre-conditions for change, which then lead to a variety of equally determinate end-point states.

Concluding remarks

It is easy to overlook, or take for granted, that plant roots display a range of properties which make up a set of characteristics essential for the sustenance of Life on Earth. While root gravitropism was at one time regarded as a paradigm for the study of differential growth and auxin action, the time is ripe now for roots themselves to be considered as paradigms for studying the cell, organ and metamer levels of plant organisation as well as for uncovering the deep structures of the Life process itself. In both cases, an additional and important adjunct for expanding our understanding is the topic of cognition, imported into plant sciences from animal psychology and neural sciences. Interestingly, this knowledge also runs in reverse, as consideration of the role that natural plant products play in the behavioural and neurological states of animals has shown (Hagen et al. 2009). Together with the concepts of auto-reproduction and self-maintenance, the concept of cognition binds together root studies into a purposive whole (which itself is perhaps autopoietic), and establishes these studies as a coherent and holistic discipline.

Acknowledgement

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