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Plastic, inquisitive roots and intelligent plants in the light of some new vistas in plant biology

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Abstract

Metaphors, such as those used in the title of this article, are often useful for the comprehension of specialised topics in plant biology. A brief attempt is made to elucidate one of these metaphors, plant “intelligence”, as it relates to the plastic responses of roots and root systems to their environment. Tropisms and nastic movements of root apices are two expressions of an inherent plasticity of form exhibited by roots. In soil, roots are exposed to multiple stimuli, many of which can potentially elicit such movements. Hence, a key question is how roots respond to and process the different stimuli which simultaneously reach their surfaces. Assuming that roots always use the same site along their length to express their movement responses, and that they also use an auxin-based information-transduction pathway, the most evident choices for the processing of stimuli are that roots either prioritise the various incoming stimuli and respond only to the strongest or they amalgamate stimuli and mount an averaged compromise response to all of them. The proposal that plants may be “intelligent”, especially in respect to their plastic growth responses, is one that draws upon knowledge of this faculty from animal biology. Also implied is that plants and animals are sufficiently similar to share usage of this term “intelligence”. But an alternative view is that plants and animals are sufficiently different and so intelligence is an unfitting term. Following the line of enquiry into creative evolution initiated by Henri Bergson, plants can be viewed differently to animals. The tendency of plants is towards instinctive behaviour rather than intelligent behaviour.

Keywords: Bergson, determinism instinct, memory, plant intelligence, plasticity, root apices, root systems, tropisms

Introduction

Plant organogenesis is a two-track process. One track – an obligate, or constitutive, track – involves the expression of patterns of cell division and cell wall expansion which repeat in successive generations (Barlow & Lück 2004a). The rates of both of the mentioned cellular processes, division and expansion, are governed by the mass of the nuclear genome (Francis et al. 2008). Eventually, from the highly organised cell complexes so produced and contained within extensible organ boundaries, this first track brings about the construction of histological compartments (Barlow 1982a) wherein cellular differentiation takes place in accordance with longitudinal and radial morphogenetic gradients (Bhalerao & Bennett 2003; Müller & Sheen 2008; Benková et al. 2009). These gradients are established first within the early embryo, perhaps by means of chemical diffusion-reaction processes, as proposed by Wardlaw (1953, 1955). Although there is no evidence that denies or affirms this type of reaction process in embryos, it has been shown to occur in xylem elements where it brings about specific distributions of cytoskeletal elements (Tabony 1996). Morphogenetic gradients are then propagated within developing organs via the intercellular movement of differentiation-inducing factors, which would be the basis of homoeogenetic induction (see Motose et al. 2004).

The regulation of this constitutive track is in accordance with a logic embedded in the protoplasmic and cell-wall networks, and which has its origin principally within the nuclear genome (Birnbaum et al. 2003). Also incorporated within the histogenetic and organogenetic programmes are contributions from organelles such as mitochondria and plastids. At the higher level of plant morphogenesis, shoot and root systems are developed by repeated branching events.
analogous to cell reproduction at a lower level of biological organisation (Barlow 1997). Accordingly, root systems are said to be modular (de Kroon et al. 2005) in the sense that each branch root is a module which has been inserted into a pre-existing structure in accordance with definite rules (Barlow & Lück 2008).

Then there is a second track – a facultative or an epigenetic track which is no less rigorous than the first track. It relies on internal epigenetic factors, examples of which are nuclear-DNA-base methylations, acetylations and associations of codons with interference RNA (RNAi) (Bird 2007). Amplification of ribosomal DNA in the so-called genotrophs of flax (Linum usitatissimum) and Nicotiana due to exposure of root systems to high or low levels of PO$_4^-$ is another epigenetic modification (Hill 1965; Durrant 1971). Each of these factors leads to various expressions of developmental and phenotypic plasticity at the whole plant level: processes in which epigenetic regulation comes into play are organ heteroblasty, vernalisation and juvenile/adult vegetative/floral phase transitions (He et al. 2003; Bäurle & Dean 2006; Meijón et al. 2009). Morphological plasticity, in this context, is dependent upon the genotype whose expression can be altered by environmental influences (Brashaw 1965). Plasticity may even extend to cellular events such as cell death, a terminal event developed according to either facultative or obligate pathways of development (Barlow 1982b; Bassham 2007).

Although it may be hard to defend with great confidence the absolute distinction between the two mentioned tracks – feedback inhibition of gene action (Umberger 1956) being one example where both facultative and obligate pathways are integrated at the molecular level – one thing is certain: that development via either track, obligate or facultative, is regulated by internal and external thresholds which have to be overcome if development is to proceed (Barlow & Lück 2004b; Barlow & Powers 2005).

**Roots and root systems**

Roots and root systems show good evidence of two-track development. For example, Erwin Lichtenegger (1983) was perhaps one of the first researchers to propose that the plasticity of root systems found in Nature might be classifiable according to the ecological setting of the plant and, hence, according to physico-chemical properties of soil types. In more recent years, the topic of root and root-system plasticity, especially in relation to plant nutrition, has become a focus of intense research (e.g. Forde & Lorenzo 2001; Wahl et al. 2001; Hodge 2004, 2006, 2009; Zobel et al. 2007), and this has led to the view that plant development comprises not only intrinsic deterministic processes where one or a combination of unique states is a pre-condition for an event but also extrinsic, non-deterministic conditions which impact upon the genotype and thence upon developmental networks which “plasticise” organogenesis. Moreover, it seems that plasticity is intrinsic to a range of developmental processes found in nature, from the molecular level of organisation (even being displayed by allotropic elements such as carbon and sulphur) up to higher order levels. It is as though all aspects of development proceed subject to, or in accordance with, a fractal type of logic, transcending that which pertains to any individual organism (Barlow 1993; Agnati et al. 2009).

A simple definition of phenotypic plasticity is that it is a product of the interaction between genotype and environment (Brashaw 1965; Briggs & Walters 1984); the same could be said of physiological plasticity. The phenomenon of plasticity reminds us that plastic organs, such as roots, are as much processes as they are forms. In the case of a root system, for example, it is not clear whether, given a particular stimulus, the resulting phenotypic response settles around some mean unit of root module, or whether the response enables the production of one particular, determinate type of root module. In the first case, root-system plasticity would involve the expression, in accordance with the regulatory power of the external environment, of a restricted range of modular forms from out of a much broader range of potentially available forms. In the second case, the selection event would evoke one (or maybe more) distinct type of root module. The findings of Varney et al. (1991) and Zobel et al. (2007) tend to correspond with the latter possibility. These authors believed that first-order branch-root diameters fell into a limited number of distributions of root diameters, each with its own particular statistical variation around a mean diameter value, and that these were clustered within a larger overall distribution of diameters. On the basis of this size criterion, different sub-types of roots could be evoked from within the total potential population of determinate branch roots in response to particular environmental conditions. Further support for this conclusion comes from observations on the lengths attained by each root sub-type, some being long roots, others being short roots of determinate length. This finding is, of course, one that is of great interest to those who study the roots of forest trees (Persson 1983; Gower et al. 1992). There may exist, therefore, distinct gene cassettes for modular branch-root development which can be evoked in the course of root-system development. Which cassette out of the overall range of such cassettes actually becomes activated, as already alluded to, upon an environmental feature which commands the overcoming of a particular developmental threshold.

Powerful techniques are now available to explore many of the questions which are raised by the form...
and behaviour within what was, in the past, considered to be the unseen world of roots. An amazing complexity of interactions exists within this world, not only between roots which are related or unrelated by genotype (Biedrzycki et al. 2010) but also between roots and their shoots whose susceptibility to predator attack can be influenced by the roots (Erb et al. 2009). Root behaviour – and behaviour here is defined simply as the temporal sequence of determinist developmental events or states – ultimately affects not only plant reproductive fitness but also plant-species and ecosystem adaptability. Analyses of the various behavioural end-points depend, naturally, upon how well the plastic traits of metabolism (cf. Waisel & Eshel 2002) and form can be identified.

Thresholds

Thresholds regulate the dynamics of plant development (see Barlow & Powers 2005). They are analogous to the activation energies of chemical or enzymic reactions. The crossing of a threshold occurs when a sufficiency of stimulus has been perceived and summed up within the organism during a critical period of time. This idea is the basis of composite developmental units (Powers et al. 2003) such as the “degree-day”, discovered by R.-A. de Réaumur during his investigations of the hatching of insect eggs. The same idea emerged in the early studies of bacterial genetics in relation to enzyme induction (Cohn 1958). Logically, thresholds regulate organogenetic and morphogenetic plasticity. Included in the latter is the familiar process of root gravitropism in which the summation of successive stimuli up to a threshold composite unit of mass, acceleration and time enables the bending response (Volkmann & Tewinkel 1996).

Communication

One feature of a root system is that its individual apices are, on the one hand, autonomous in their response to the external environment but, on the other hand, they communicate information about their internal state to each other (Amzallag 1999; de Kroon et al. 2009) by means of plant hormones (Kuppusamy et al. 2009; Wang et al. 2009). Information may also be conveyed to non-meristematic sites. The channel used in this case may be a rudimentary plant nervous system (Rhodes et al. 1996; Baluška & Mancuso 2007). By this means, for example, a wound response which involves morpho-physiological regeneration can be efficiently instituted. Another means by which a network of root apices may monitor the general state of the plant is via its “pulse” – just as medical practice uses the pulse of blood flow to assess health. It is known that a pressure shock to a plant organ generates a wave of electrical potential along its length (Malone 1996; Rhodes et al. 1996). Moreover, variation in root pressure is a cyclical diurnal event (White 1938) which could lead to communication between apices. Recent work on the topic of root pressure has shown that connections can be made with events in animal neurotransmission (Zholkevich et al. 2007). There may, therefore, be phytoneurological outputs that can reach far-away apices initiated via pressure-induced surges through the super-apoplasm.

Information processing

Tropisms

Roots are inquisitive in so far as they can be induced to respond, sometimes positively, sometimes negatively, to conditions within their physico-chemical environment. Their responses lead them to grow towards patches of soil enriched with aliments and which offer optimal thermal and moisture conditions, as well as to avoid patches of negative quality. These directional movements have been determined by natural selection so that plant fitness is enhanced, and occupation of an optimum environment and ecology is consolidated.

The most evident signals eliciting root growth movements are:

- Gravity (gravitropism)
- Light (phototropism)
- Moisture (hydrotropism)
- Chemical (chemotropism)
- Temperature (thermotropism)
- Touch (thigmotropism)
- Trauma (triatmotropism)
- Water flow (rheotropism)
- Geomagnetic field (magnetotropism)
- Electrical flux (galvanotropism)

Plant roots, therefore, seem to share the same perception of sensations as do animal organisms: the latter perceive their posture (baroreception – equivalent to gravitropism) and also assess the directionality of heat, light, magnetic fields, chemicals and moisture. In addition, roots seem able to “hear”: that is to perceive air-borne or soil-borne vibrations (Takahashi et al. 1992; Jeong et al. 2008). Conversely, maize primary roots sporadically emit noises as they grow (D. Robert, personal communication), possibly due to the cracking of the root cuticle during root elongation (cf. Hofer et al. 1976). Speculatively, these cracking noises might be registered by the auditory apparatuses of insects in the soil and serve as signs of the presence of a root.

Whereas tropisms and nastic movements require differentials of longitudinal, radial and circumferential growth which involve the outer epidermal and cortical portions of the root, another type of growth response utilizes a modification of the longitudinal
extent of the zone of rapid elongation. A shortening of this zone leads to precocious swelling at the root apex as occurs, for example, when a root encounters compacted soil (Materechera et al. 1992). With the exceptions of gravity and light whose stimuli are perceived internally (Iijima et al. 2008; Wan et al. 2008), all other cues are registered at the root surface, or at the surface of the root cap in the case of signals such as soil moisture. All perceived signals are transduced into an input sign interpretable by receptive cytoskeletal and metabolic networks and, finally, this sign is transformed into an output sign that is transduced into a growth response.

**Simultaneous signals**

Many laboratory experiments, using either whole roots or root segments, have examined both the nature of the graviresponse per se and the modifications of this response when some additional stimulus (chemical, thermal, etc.) is also present (Pilet 2002). This second situation is particularly interesting because roots live in soil wherein there is a welter of signals and, hence, potential information. So, an immediate question is: How can roots distinguish between the different signals within this semiosphere (Kull 1998), many of which could be regarded as heralds of stress conditions, and initiate an appropriate response?

To answer such a question, it is necessary to identify both the entry point of the signal (i.e. its zone of perception within or upon the root – for graviperception, see Blancaflor et al. 1998; Wolverton et al. 2002) and the route of the transduced signal to a responsive target zone. It may also be asked whether there is only one set of motoric cells along the length of the root through which all tropic growth differentials are expressed? Or can different signals elicit responses in different root zones? Two, or even three, bending zones have been identified along the length of gravitropic roots (Rufelt 1957; Hoson 1994); and Iversen (1973) and others have shown how, after presenting a gravitational stimulus to a root, a growth differential progresses basipetally from the cap to the elongation zone. Part of this progression may be a reversible growth response due to temporary changes in turgor in the cap, and this precedes an irreversible growth response due to differential cell wall growth in the elongation zone. Alterations to turgor can be sources of electrical change (see Zimmermann & Beckers 1978), the latter being one of the earliest responses to gravisusception in the root cap (Behrens et al. 1985). This physico-chemical response may affect the orientation of auxin movement both within and issuing from the cap.

It is also necessary to clarify the nature of the external tropic stimulus reaching a root apex. For example, responses of roots to touch (thigmotropism) may indeed result from an external pressure stimulus; but they could also be due to a build-up of growth-inhibiting root-cap mucilage and other components around the apex (see Iijima et al. 2000; Semchenko et al. 2008). Therefore, what was supposed to be a thigmotropism might have been confused with a chemotropic response. Related to the touch response is the rheotropism of roots reported in older literature (reviewed by Newcombe 1902). Again, this tropism may have nothing directly to do with touch or the direction of water flow but be the result of a flushing of growth regulatory substances away from the root surface.

The question of how a root distinguishes between the various signals which reach its zones of perception has led to experiments where two signals are presented simultaneously: for example touch and gravity (Massa & Gilroy 2003; Edelmann & Roth 2006), and moisture gradients and gravity (Takahashi et al. 2009). It may be that different signals have different susception times: that is, they accumulate suspected developmental units to reach the threshold that triggers the requisite response at different times; or composite developmental units may be used to mount an “averaged” response. The use of microarrays undoubtedly would be useful in sorting out effects of mixed signals, particularly since minute zones of a root can be analysed in real time following challenge by a stimulus. They have, for example, clarified the molecular response of roots to salt stress (Dinneny et al. 2008). Microarray analyses of the effects of two disparate stress stimuli have also helped dissect the response pathway of simultaneous sensory perceptions (Rizhsky et al. 2004).

Even more complex are cases where root bending results from a combination of gravitational, vibrational and touch stimuli. Migliaccio et al. (2000) concluded that root waving is the result of the meeting between nutational, gravitropic and thigmotropic bending responses (see also Simmons et al. 1995). Using oligonucleotide arrays to search for gene transcripts, Moseyko et al. (2002) detected within gravistimulated roots a substantial number of transcripts known to be elicited by vibration. In the case of a mixed hydrootropic/gravitropic response, the ubiquitous auxin molecule regulates the root’s differential growth in each case (Takahashi et al. 2009). One goal would be to define the pathways of the respective tropic responses, discovering which are held in common and which are unique (see Hahn et al. 2006; Lokerse & Weijers 2009).

The processes at issue are involved in plant decision-making. Interestingly, a model system for such a faculty was discovered years ago by Adler and Tso (1974) in the bacterium *Escherichia coli* and was in relation to positive or negative tactic responses (due to opposing molecular flagellar motor activities).
including by conflicting (attractive or repellent) chemical stimuli. The general idea coupled with suitable material for experimentation could be useful in uncovering the bases for the decisions made by plant roots.

Plant “intelligence”

Active verbs and vivid images are often used when plant biologists speak of their subject – as even noticed by columnists in the popular press (Angier 2009). Purposeful activities are also sometimes imputed to roots: “plans often must be modified to cope with prevailing conditions” (Hodge 2009, p. 628). In considering root-system growth responses, of which plasticities of form and function within a heterogeneous soil environment would be one example, anthropocentric analogies and metaphors have led to the proposition that plants possess some form of “intelligence” and, hence, to the idea that plants show “intelligent”, “purposeful behaviour” (Trewavas 2003, 2005). Here, it seems that the Aristotelian “final cause” (the sake for which things exist) has been confused with the “efficient cause” (that from which change first starts). Moreover, as noted by Cvrková et al. (2009), much of the argumentation about plant intelligence relies upon seductive metaphors. In his exposition of “Living Systems Theory”, J.G. Miller (1978) did not feature “intelligence” as one of the canonical sub-systems necessary for the support of life at various levels of organisation. There is, however, a set of sub-systems that define the processing of information (Miller 1978; Miller & Miller 1995; Barlow 2006, 2008). Deployment of these sub-systems can, in some respects, replace the subjective notions attached to “intelligence” with a more dispassionate view of behaviour and development.

A Petri-net representation

To approach this problem of “intelligence”, the schemata of Figure 1(a)–(c), based on the idea of Petri nets (Petri 1980; Lück & Lück 1991; Barlow 1994), can be used. Briefly, the methodology can be followed taking, first, Figure 1(a). Open circles with labels A–E are empty “places”; all of them represent potential states, either pre-conditional or post-conditional with respect to a future event. The presence of a token (•) indicates the conversion of an empty place to a filled place (Figure 1b), the latter now representing a completed state capable of activating an “event” [1]. In Figure 1(b), for example, states A• and B• are pre-conditions that enable the formation of a new state D• (Figure 1c). After activation of an event, a previously filled place (Figure 1b) becomes an empty place (Figure 1c), and any newly filled post-conditional place (Figure 1c) can now serve as a pre-condition for a further event. Consider a set of places [A• B• D] (Figure 1b) and its directed transition to [A B D•] (Figure 1c). Let us suppose that these places and the associated transitional events reside within root apices of a root system. A sensitive appraisal by the root system of its environment might, however, lead to an alternative scenario (Figure 1d): in some apices, place (state) C• substitutes for state B• (as shown in Figure 1d), thereby enabling an event that leads to the creation of a new state, E• (Figure 1e). If this alternative state E• were now able to ameliorate the plant’s response to an environmental disturbance better than state D•, “intelligence” might then be imputed to the root system because it can appraise the environment and then effect this switch in final states (contrast Figure 1e with Figure 1c). Evidently, to account for the disappearance of pre-condition B• and the presence of pre-condition C•, some information has become available to the apex which has led to the replacement of one state by another. That new information might be either inherent to the root or external to it in the abiotic environment.

Because pre-condition A• is shared by both events (Figure 1b and 1d), whether or not new state E• is preferable to former state D• cannot be resolved by the net shown here. (In fact, the construction of switching points in Petri nets is somewhat involved, and this is not the place to provide a complete net which would show this for the D•/E• switch.) Whether the ability to switch between final states D•/E• is evidence of “intelligence” is debatable. The potentiality to effect the switch is itself a consequence of the construction of the place/event network and is also coupled with the ability of the net to receive and feed additional information into the net (and into its biological analogue). In the end, this seems little different to an optimisation of net design.

The dimorphism of the final states D• and E• and hence the alternative, plastic growth processes in which they participate are the outcomes of variation in the kinetics that govern the rates at which relevant pre-conditional states are generated, at which thresholds are overcome, and then the rates of utilisation of the filled, post-conditional states. Any far-sighted planning of behaviour and the “plastic” modification that follow are simply outcomes of determinate networks of events and places (Lück & Lück 1991). They give evidence of adaptability rather than of intelligence.

The role of the external environment

The role of the external environment can be accommodated in a modification of the schemata in Figure 1. In the now-classical experiments of Drew (1975) on the plastic modification of a barley plant root system in response to localised concentrations of
mineral ions in the surrounding soil, root apices were temporarily exposed to a modified mineral content. After the apices re-emerged into the previously experienced soil–mineral conditions, a change was noticed in the degree of lateral root formation that subsequently formed on the mineral-exposed portion of root (Drew 1975). The ionic conditions in the soil surrounding the apices would be analogous to an empty place $G$, or to a filled place $G\cdot$ (Figure 2a), and places $E\cdot$ or $E$ equate to the status of the lateral roots (Figure 2b and 2c).

Organisms which perceive and then make use of an object in their external environment as a tool are proposed as being intelligent (Gould & Gould 2007). Parasitic plants (e.g. *Cuscuta europaea*) and epiphytes (e.g. *Monstera gigantea*), whose seeds germinate at

Figure 1(a)–(f). Petri-net-style notations for hypothetical state changes within a root apex. (a) Circles are places. A token • within a circle creates a filled place which may represent a state, $A\cdot$ or $C\cdot$ (b, d). Such states now become pre-conditions for events []. When all pre-conditions are fulfilled an event is fired and new states comes into being ($D\cdot$, $E\cdot$) (c, e). A newly filled place is then a potential pre-condition for a further event. States can be self-regenerating (f). Events fire in a pre-determined sequence thus affecting the sequence in which new states arise. Arrows ($\rightarrow$) indicate the direction in which state changes proceed; they do not indicate a flow of information. The box-style enclosure of each scheme indicates that all states and events are enclosed within the internal environment of the root apex.
of herbs or trees, respectively, and whose seedlings then proceed to climb up their support (or host) plants, sense the external environments and use the elements therein as tools to assist their growth (see Strong & Ray 1975 – *Monstera*; Runyon et al. 2006 – *Cuscuta*). This type of behaviour, however, is considered as instinctive rather than intelligent on account of the lack, in the plant, of foresight or reasoning (as there is in animals) of how to use an object, encountered by chance, as a tool to overcome a problem. The pre-conditions that enable such behaviour in both animals and plants lie in a space external to the organism, as shown in Figure 2. The organism internalises a pre-condition offered by external state G – the dark background of a potential support plant, in the case of *Monstera*, a chemical stimulus in the case of *Cuscuta* – thus enabling a climbing event leading to state E.

**An alternative view to intelligence**

To close this brief foray into the question of whether or not plants are intelligent, we should recall what was evident to commentators on this topic, namely, that within the context of plant sciences, the word “intelligence” has been imported from studies of intelligence in animals, and humans in particular; it is, therefore, regarded as a metaphor, a linguistic/cognitive device which can be of help in defining critical issues (Havel 2007; Trewavas 2007) raised by the use of this word. The somewhat apologetic use of single quotation marks indicates not only the novelty but also the uncertainty attached to this idea of intelligence. Affirmation of plant intelligence should require that the organisms which science identifies as “animals” be sufficiently similar to the organisms identified as “plants”. Conversely, to deny intelligence to plants should require that plants and animals are so distinct that the term “intelligence”, in the form by which it is understood in relation to animals, is irrelevant. There would then be no need for metaphors, or for quotation marks. If affirmation of plant–animal similarity is in order, then straightforward affirmative argumentation could be written without qualifying statements or resorting to writing about plants as though they were animals, but not quite.

Although animals and plants were considered by Aristotle to constitute separate categories of living forms, in recent years a view has grown up, evidently stemming from the prevailing ethos of reductionist biology, that plants and animals are sufficiently similar for them to be regarded as two sub-classes within a category of more developed, or derived, life forms. This view is based on the common constituents of animal and plant cells, their metabolic similarities and their dependence upon DNA and RNA. But these are not the only criteria by which differences or similarities of plants and animals should be considered. Animals are mobile, plants are sessile; and with this mobility or its lack comes their respective conscious and unconscious natures.

Living beings are dissipative systems which absorb energy from the environment, create order within themselves, pass disorder to the environment and are autoreproductive (Nicolis & Prigogine 1977). Such systems maintain states far from thermodynamic equilibrium. Another defining feature of living forms is their propensity to make errors in their autoreproductive process which by means of Darwinian natural selection permits them to evolve (Eigen 1971). Life has become clothed within cellular apparatuses which perform these dissipative tasks. Hence, at the lower levels of organisation (e.g. of cells and organs), the supportive sub-systems of plants are similar to those found at analogous levels in animals (Barlow 2006). But cells do not necessarily make the plant or animal (Barlow 1982c). Cells have been developed by life to support and perpetuate that same mysterious principle. As indicated above, the essential nature of plants and animals has to be looked for, not in cells, but in properties at more highly developed levels of organisation. Analogically, intelligence has also to be searched for.
in a new way. Moreover, the faculties of intelligence and intellect have to be differentiated from the faculties of instinct and intuition, though in a living organism both tendencies co-exist.

In discussing intelligence, emphasis was given above to tool-making. Henri Bergson, one of the earliest forerunners of process philosophy, in his major opus “Creative Evolution”, which is still of interest to present-day philosophers of science (e.g. Ansell-Pearson 1999), insisted that “intelligence perfected is the faculty of making and using unorganised instruments” whereas “instinct perfected is a faculty of using and even of constructing organised instruments”; and, further, that “intelligence, considered in what seems to be its original feature, is the faculty of manufacturing artificial objects, especially tools to make tools, and of indefinitely varying the manufacture” (Bergson 1911, pp. 140, 180, 139). During the evolution of living forms, the faculties of instinct and intelligence, which were present as prototypes in the first organisms, have become separated: intelligence achieves its highest perfection in animals, whereas instinct is dominant in plants. “Life manifested by an organism”, says Bergson, “is, in our view, a certain effort to obtain certain things from the material world” (p. 136). Intelligence enabled matter to be transformed into instruments of further action upon matter. Intelligence is the counter-tendency to instinct; and it is the tendency towards instinct that characterises plants. It would, however, be incorrect to adopt an either/or position in this complex question of intelligence/intuition in plants and animals. Each group has its own undeniable and characteristic tendency. Bergson continues: “intelligence illumines present actions and foresees their results.” Can plants foresee results? This ability relies on memory, the rudiments of which appear to be present in plants. But memory, in turn, depends upon an association with past events; to foresee is to project the memory of past experience into a vision of the future.

Memory

Another aspect of the adaptation of roots to their external environment – an environment, or rhizosphere, which they themselves help to create (Griffiths et al. 2007; Somasundaram et al. 2008) – is the faculty of memory. Short-term memory of a physiological type is now recognised in plants, thanks to the work of M. Thellier and his colleagues (Thellier et al. 2000; Tafforeau et al. 2006), and has been discussed by Cvrčková et al. (2009). Long-term memory of another, epigenetic, type, in the form of patterns of DNA methylation (Henderson & Jacobsen 2007; Berger & Chaudhury 2009) and DNA amplification (Cullis 1977), is stored in the nucleus. Epigenetic memory may persist across many generations, following on from the time when the epigenetic state change was first introduced. It is an ontogenetic memory regulating development in ways compatible with the conditions which initiated it. Either type of memory – long- or short-term – cannot be far removed from what has been discovered about “habituation” – the acquired auxin and cytokinin independence of tissues in culture (Meins 1982). Interestingly, both physiological and ontogenetical memories were discussed by Francis Darwin (1908) in his address to the British Association in 1908. Memory was referred to as an “Engram”, or trace of a stimulus, imprinted upon the organism. Nearly 100 years later, Bruce et al. (2007) named these as “stress imprints”, using this term not only to avoid anthropocentric associations linked with the word “memory” but also to avoid giving the impression that plants were cognitive organisms. According to Darwin, Engrams are “causal agencies built up by external conditions which have, or may have, ceased to exist” and which endow living matter with “the power of retaining the residual effect of former stimuli and of giving forth or reproducing under certain conditions an echo of the original stimulus” (Darwin 1908, p. 11). The short-term physiological memory described by Thellier et al. (2000) as well as the longer-term epigenetic memory, consist of just this: the induction, by a stimulus, of some product which not only serves to bring about a response but also does not degrade (or does so only slowly). This product can then be used again and again: its presence is “memo- rised” – in the case of epigenetic memory, over many generations before it decays; and the memory product can become a recurrent pre-condition for an event.

Using again the scheme offered by Figure 1, memory would be evident if, after its induction as a filled place, state B• persisted following the firing of an event for which it was a pre-condition: that is [A• B• D] → [A• B• D•] (Figure 1b and 1f). Then, before the first two states A• B• can recur (as in Figure 1b), the post-condition D• must be removed by some further event for which D• serves as a pre-condition (not shown here). The persistence of state B• enables place A to be relabelled so that [A• B• D•] → [A• B• D] → [A• B• D•] and so on. Thus, there is no need for a repetition of the event which induced state B• in the first instance. State B• is a memory of that initial event, requiring the presence of state A• as a pre-condition for it to be “recalled” and utilised.

Sometimes a memory product facilitates the subsequent firing of an event for which it is a pre-condition. Repetition of a stimulus then either short- enes the delay in eliciting a response or increases its intensity. Memorised responses have been found in
previously nutrient-deficient barley roots in relation to exposure to and uptake of Cl− (Lee 1982) and sulphate (Hawkesford 2003), and in algae as a result of previous exposures to PO4 3− (Wagner et al. 1995). In plants, these memories have their bases in the up-regulation of ion transporters and ion channels, and in the activation of signalling cascades (Ashley et al. 2006). Memories of a previous experience also find their way into responses to wounding: they relate to the up-regulation of specific gene activities (Tafforeau et al. 2006), the products of which had earlier provided the first intimations of memory.

Concluding remarks

The plasticity of plant behaviour – and users of this word “behaviour” surely have in mind notions of sensation and movement, and perhaps even some sort of cognition, on the part of the plant in relation to a teleologically conceived goal – and also the plasticity of plant development, of which root-system growth is one component, have been fundamental to the successful colonisation of land by plants. Behind plasticity lie regulatory processes which range from short-term molecular events (induction and repression of gene activity by feedback inhibition during the course of protein synthesis, for example) to longer-term processes such as the development of ecotypes, a term coined by the Swedish botanist Göte Turesson (1922a, 1922b). With respect to ecotypes, Briggs and Walters (1984) commented upon Turesson’s pioneering work as follows:

His contribution to our understanding of the patterns of variation within species is of very great importance: he demonstrated clearly the widespread occurrence of infraspecific habitat-correlated genetic variation. Adaptation to the environment was sometimes by plastic response, but more frequently it had a genetic basis. Such studies were grouped together under the name of “genecology”. (p. 152)

That plastic response and genetic variation should go side by side in response to the environment is a significant and challenging idea: it is as though the former were a short-term solution to an environmental challenge, whereas the latter were a long-term solution to that same problem; and both contribute to the ability of a plant to “fix” its plastic response in such a way that it becomes integrated into the genotype. Hence, the integrated response should be expressed by later generations of plants as a genetic eco-variant or ecotype. Genotrophic amplification of DNA and the integration of this DNA into the genotype could be one basis for the emergence of a stable eco-variant. Fixation of plasticity could be immedi-ate – within one generation, perhaps. But if so, this would contrast with the Darwinian pathway which relies on both the arising of a genetic variant by mutation and its subsequent natural selection. However, since the direct acquisition and inheritance of acquired characteristics, as envisaged in the early years of the nineteenth century by Jean-Baptiste Lamarck, has by and large been ruled out from established, Darwinian thinking on evolutionary development, it seems necessary to investigate some alternative process whereby the plastic phenocopy or genotroph can be converted into a stable genocopy or genotype. Could it be that environmentally driven epigenetic variation provides the link between the plastic phenotype and the genotype (see Molinier et al. 2006; Akimoto et al. 2007; Damiani 2007; Chinnusamy 2009)? At the least, the search could find a process which, en passant, harmonises the romantic notion of Lamarck with the known possibilities offered by twenty-first-century genetic research.

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Note

1. Intelligence – two definitions from the Oxford English Dictionary are: “The faculty of understanding”; “The action or fact of mentally apprehending something; understanding, knowledge, comprehension (of something)”. Or put more simply, as in the Reader’s Digest Universal Dictionary: “The capacity to acquire and apply knowledge”; “The faculty of thought and reason”.

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