Opinion Article

Plant intelligence

Why, why not or where?

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The concept of plant intelligence, as proposed by Anthony Trewavas, has raised considerable discussion. However, plant intelligence remains loosely defined; often it is either perceived as practically synonymous to Darwinian fitness, or reduced to a mere decorative metaphor. A more strict view can be taken, emphasizing necessary prerequisites such as memory and learning, which requires clarifying the definition of memory itself. To qualify as memories, traces of past events have to be not only stored, but also actively accessed. We propose a criterion for eliminating false candidates of possible plant intelligence phenomena in this stricter sense: an "intelligent" behavior must involve a component that can be approximated by a plausible algorithmic model involving recourse to stored information about past states of the individual or its environment. Re-evaluation of previously presented examples of plant intelligence shows that only some of them pass our test.

> *"You were hurt?" Kumiko said, looking at the scar.*
> *Sally looked down. "Yeah."*
> *"Why didn't you have it removed?"*
> *"Sometimes it's good to remember."*
> *"Being hurt?"*
> *"Being stupid."*—(W. Gibson: Mona Lisa Overdrive)

Introduction

The concept of plants as intelligent beings is far from new. Already more than 100 years ago, at the heyday of vitalistic biology, the Belgian poet Maurice Maeterlinck describes in his essay on "intelligence of flowers"[1] some of the phenomena used even nowadays to illustrate "intelligent" decision-making in plant ontogeny, in particular the ability of roots to navigate through a complex maze (of a rubbish dump). Re-introduction of this concept into the realm of rigorous contemporary experimental biology, as proposed by Anthony Trewavas several years ago,[2,3] has stimulated a period of lively discussion that has led to further elaboration of the admittedly somewhat controversial original proposal.[4-7]

The initially promising idea unfortunately appears to have been reduced to a mere metaphor nowadays, having possibly partly fallen victim of the heated exchange concerning the program of "plant neurobiology".[8-11] Plant intelligence has become, at best, practically synonymous with Darwinian fitness ("adaptively variable behavior" or "ability of an individual to perform in its environment"); at worst, its defense resorts to collecting other incidents of metaphoric use of the word "intelligence" (such as bacterial, immune, species, artificial, plant *sensu* factory etc., intelligence[6]), or to general arguments about intrinsic value of metaphors in science.[10]

However, while such arguments might make the word socially acceptable, they could be used to support the notion of intelligence in almost any system, not just plants, perhaps up to making the metaphor worthless. If we, for instance, take the notorious textbook example of the lytic versus lysogenic life cycle decision of the lambda phage,[12] depending on the outcome we end up with one intelligent, and thus surviving, lysogenic bacterium, or some ten thousand equally intelligent phages that have successfully outsmarted the bacterium's defenses. But did we gain anything (besides of a bit of fun) by such re-telling of the story?

One may argue that a metaphor remains valuable as long as it provides novel insights and stimulates new research. This, undoubtedly, *is* the case of "plant intelligence", as it has already inspired some mathematical models, though their biological relevance might be questioned.[13,14] Nevertheless, it may be worth trying to delimit plant intelligence in a more restrictive way that would inspire focused experimental study. Here we attempt to formulate "Occam's razor criteria" for recognizing phenomena whose explanation as manifestations of "plant intelligence" is not less parsimonious than alternative hypotheses (reviewed in ref. 15). We then apply our criteria to re-evaluate some previously proposed examples of plant intelligence, and propose some additional candidates that may deserve closer analysis.

Cognition Without Brain

Let us begin with delimiting the central concept of *intelligence*. Since intelligence manifests itself in behavior, it may be appropriate to turn to the founding fathers of ethology, the science of behavior. According to N. Tinbergen,[16] any aspect of behavior can, in principle, be studied from two points of view: (i) functional, focusing on its selective (or survival) value, or (ii) causal, concerned with seeking its mechanistic, ontogenetic or evolutionary (i.e., historical) roots. Inspired by this approach, we can use two sorts of criteria to decide whether an entity (be it a human, a plant, a computer or a hypothetical extra-terrestrial being) can be considered intelligent. First, if this entity "behaves intelligently" (whatsoever this means), it fulfills a *functional* definition of intelligence. Second, if it possesses at least some part of the apparatus known to be required in better known beings for intelligent behavior (e.g., a brain, synapses, action potentials, or anything that can be described as an information-processing network), it matches a *causal* definition of intelligence.

Most of the plant intelligence debate so far revolved around causal delimitations of the phenomenon. Even our current limited mechanistic understanding of the substrate on which more conventional (human) intelligence operates, i.e., the nervous system, has provided inspiring inputs to plant biologists, reflected e.g., in the synapse model of cell to cell communication,[17] or in the birth of the program of plant neurobiology.[8] However, functional aspects seem to be somewhat neglected, the only relevant example so far being application of the (functional) Stenhouse's definition of intelligence as *"adaptively variable behavior within the lifetime of the individual"*[18] (cited in ref. 3). Since, unlike causal analogies, functional definitions allow rigorous testing of the presence or the absence of necessary prerequisites, the functional point of view obviously deserves much deeper elaboration.

Stenhouse's definition may indeed be a good start. Plants display all the necessary "components" of intelligent behavior (assuming that their plastic, flexible development *is* behavior).[19] In particular, they surely do exhibit individual variability and adaptivity (reviewed in refs. 3, 6 and 7). Moreover, they continuously record and evaluate a complex field of external stimuli, forming thereby something which could be described as an "inner representation" or a "cognitive map" of the environment, including information about qualitative and quantitative aspect of light conditions, humidity, temperature and other biotic and abiotic environmental inputs. It is worth noting that some schools of "cognitive science" strive towards explaining (away) not only the human kind of cognition, but ultimately, even the human mind, as "computation on inner (mental) representations" (reviewed in ref. 20); however, we neither want nor need to assume that plants, those "mindless masters",[2] are endowed with a human-like mind.

Nevertheless, any delimitation of the subject of study imposes limits on what can be studied. Stenhouse's definition of intelligence is no exception: if we stick to the conventional meaning of individuality, we have to sacrifice, for instance, phenomena such as "species intelligence" based on epigenetic memory reaching across generations, or emergent "intelligent behavior" taking place on the population level. It may be thus worth examining alternative

functional definitions of intelligence. One such inspiring concept has been proposed by Mia Molvray in an essay on criteria that could be used for recognition of intelligence in a non-human entity.[21] According to her, intelligence is not a quality that is either present or absent. Instead, it can be present to a varying extent, forming a continuum of stages. An absolute minimum is what she calls a *rudimentary intelligence*—basically reducible to the ability to react adaptively to the environment, i.e., *to learn*. Next comes the ability to learn from new stimuli and adapt to changed conditions, and only then the so-called "higher cognitive functions" such as recognition of objects or even self-awareness. (In the context of the plant intelligence debate, we do not need to go beyond rudimentary intelligence).

Unlike Stenhouse's definition, which attributes intelligence to any system that simultaneously exhibits observable behavior (e.g., development), individual variability, and adaptivity (which can be understood as Darwinian fitness, though it may also involve some aspects of learning and memory), Molvray's definition explicitly emphasizes learning. After all, ability to acquire unique and novel experience (and to use this experience in an appropriate manner) is what distinguishes a truly intelligent system from systems such as a washing machine, a fridge or an air-conditioning apparatus (where the "experience" has been provided by a human designer and hard-wired into the appliance), or even from a gravitropic root tip that has acquired a finely tuned error-compensating mechanism from generations of ancestors subjected to natural selection, i.e., also from "outside" of the particular individual (unless we consider the species or population an "individual"). Memory, as a necessary prerequisite of learning, thus gains a central role—and clearly deserves our attention.

False Memories and True Scars

Like intelligence, also memory can be defined either causally or functionally. An example of the former would be e.g., the statement *"Memory is a location where information is stored that is currently being utilized by the operating system, software program, hardware device, and/or the user"*.[22] Obviously, such a concept makes sense only within the narrow field of information processing technology, and we should rather look for a functional definition. A good start could be the definition of memory from the MedTerms medical dictionary: *"Memory is (1) the ability to recover information about past events or knowledge, (2) the process of recovering the information about past events or knowledge, (3) cognitive reconstruction. The brain engages in a remarkable reshuffling process in an attempt to extract what is general and what is particular about each passing moment."*[23] This definition consists of three mutually non-exclusive, and non-synonymous, statements. Understanding it as "logical OR", for now we can safely leave aside point (3), which is obviously anthropocentric and to some extent causal. Nevertheless, it is worth noting that the third part also covers a non-trivial aspect of intelligence—an ability to select relevant things to memorize and recall; but at the moment we are only interested in the ability to recall *anything* at all. Thus, we have to search for situations where an individual actively accesses stored information about its past experience; but how can we recognize that plants do it?

Plants store a wealth of data about their history in the structure of their bodies. Given the permanent character of cell walls, every branch and twig holds information about the past. However, this by no means guarantees that the plant cares—or that it is at least capable of accessing these data. While the density of annual rings on a cross-cut of a branch may provide a dendrologist insight into long-term climatic development, it is highly improbable that this information is accessible to the tree itself. Such "stored information" may be a mere imprint of incidents and accidents of the past, without any informative value for those involved. Whatsoever value we attribute to a pile of dog excrement on the sidewalk, it is rarely that of "memory of the past presence of a dog", unless we are interested in dog ethology. However, traces may be laid down non-accidentally: we may not notice the smell of dog urine on the same sidewalk, while a dog will undoubtedly read a complex message from it. Even accidental imprints of past events may sometimes acquire a memory function—a scar may serve as a reminder of youthful carelessness.

We thus need criteria for distinguishing mere traces of incidents from true accessible (and actively accessed) memories, which also have to be stored *by the studied organism itself*. Let us imagine the trajectory of a river meandering across a landscape, gradually deepening its bed and occasionally changing its path. Albeit the current path of the river does somehow reflect the centuries of erosion, outside of a poetic text we can hardly say that the river actively reflects and interprets its own, or the landscape's, memory of the past: water just flows downhill, erosion just happens, and that's all.

Perhaps one possible hint (though not a decisive criterion) for recognizing true memory may be the presence of functional features typical for systems capable of learning, such as signal amplification, integration of inputs of multiple origins, or responses whose timing, quality or quantity is modified by external inputs. An obvious requirement is also memory trace duration at least comparable with, but preferentially exceeding, that of the original stimulus being memorized (i.e., while the memory does not have to be permanent, it must be lasting). In the absence of a good functional test, we may have to turn also to the causal point of view, i.e., to searching for specialized structures and molecular or physiological mechanisms which appear to possess no conceivable selective value besides the presumed memory function.

To summarize: since memory is a necessary pre-requisite of learning—an essential component of intelligence, we need to examine critically the previously proposed examples of intelligent behavior in plants, and for the sake of certainty discard all cases where involvement of memory cannot be safely inferred. We may even have to give up some potentially relevant phenomena to be sure: what we need are criteria for identification of cases of plant memory and learning that are beyond any doubt.

Science is rooted in making models of the observed phenomena—preferentially formalized (algorithmic), or at worst narrative ones. Thus, given any particular example of seemingly intelligent behavior in plants, we should ask whether we can approximate the observed phenomenon by a biologically plausible model that includes recourse to information about past states of the organism or its part, stored and accessed by the organism. If the answer is no, and especially if we can produce a plausible model that does *not* include retrieval of memories of past events, the example should be discarded. We will further refer to this criterion as "*the memory model test*".

When a "Memory" is Not a Memory

Which of the phenomena previously referred to as examples of intelligent behavior, or at least of learning and memory in plants, will pass our memory model test, and which ones will not? Can we identify any promising candidates at all? The following list does not pretend to be a complete review of all cases that have ever been proposed, rather an overview of representative examples that allow conclusions in one or another direction. Some of the previously reported candidates remain inconclusive, and further examination of them is left to the reader.

Plants, like many (if not all) other living beings, modify their metabolic, regulatory and developmental processes according to the conditions of the environment, including novel stimuli. Convincing examples of gradual adaptation of plants modifying their size and growth rate in the presence of an herbicide (phosfon D) or ether, i.e., compounds they never met before, have been already reviewed.[6] Nevertheless, a change in the organisms' properties per se does not indicate a meaningful adaptation, or even learning. Some human populations are nowadays experiencing abundance of food encountered never before; however, the current epidemics of obesity can hardly be considered a result of learning. Herbicide adaptation (or other metabolic or developmental adaptations) could be similar gratuitous by-products of environmental change, in some cases (such as pathogen or herbivore responses) embraced and fine-tuned by natural selection. We should postpone the decision whether they represent learning or not till we know more about the physiological and molecular mechanisms involved, and till we have convincing evidence that they are indeed adaptive. Increase in leaf size or vegetative biomass does not necessarily correlate with the amount of viable progeny or ability to survive—the widely accepted measures of fitness.[24] However, if we at least suspect that lasting modification of dedicated regulatory circuits, such as e.g., signal transduction pathways, protein phosphorylation switches or transcription factors, plays a specific part in the process of adaptation, we can consider such a process a good candidate for learning, as already proposed.[25]

Not all seemingly convincing examples of "intelligent" plant behavior pass our memory model test. In particular, orientation towards extrinsic cues such as light or gravity can be often described by models that only require perception of, and reaction to, synchronous cues and stimuli, without any reference to the past. Thanks to the impressive models constructed, in particular, by P. Prusinkiewicz and co-workers,[26-29] we have to accept the startling realization that history, if included in the model at all, takes often only the form of constraints carried by the environment (such as e.g., shading by branches or leaves of the developing plant) rather than memory of the developing individual itself. For instance, light-driven morphogenesis of tree crowns, or exploration of patchy environment by foraging clonal plants, can be

convincingly approximated by a model that only requires the individual branches or ramets to avoid collision with congeneric neighbors and to adjust their branching and runner production according to present light conditions.[27] (No "artifical intelligence"—whatsoever it may mean—is involved in these models, produced with the aid of computers incapable of doing anything that has not been programmed into them, and remaining thus, in the context of our discussion, mere "stupid machines").[21]

Alarmingly, the complex pathway of roots through a non-homogenous substrate, this classical example calling for analogies with the maze navigation test of animal intelligence, may fall into the same category. Synchronous perception of gravity, light, mineral nutrient and soil moisture gradients (with the later being constantly modified by activities of the growing root itself) is sufficient to guide a root tip through a rather complex and realistically-looking trajectory.[27] However, it has to be noted that gravitropism, albeit it can be described as a purely synchronous orientation towards an extrinsic gravity vector, apparently involves lasting imprints of the environmental stimulus at least in some plant organs, although it is unclear whether this "memory" is accessed also under natural conditions, or only in some experimental setups.[30] Similarly, the notorious example of dodder host selection (discussed in ref. 3) can be re-told (i.e., narratively modeled) as simple attraction towards synchronous chemical cues produced by the prospective host.

Phenomena dependent on self-nonself recognition, possibly one of the oldest abilities of living beings present already in prokaryotes,[31] have been also quoted to support the notion of plant intelligence.[7] However, distinguishing self from nonself does not need to involve memory—only means for synchronously monitoring bodily continuity are needed. Indeed, abrupt change of plants' behavior towards its detached ramets suggests that integrity of the physical attachment is essential, and that plants do not remember their past relationships. Interesting as it is, self-nonself recognition does not pass the memory model test—and thus it should be left out from the plant intelligence discussion.

A Handful of Candidates

Are there any phenomena left at all that *would* pass our test? Let us leave intelligence aside for now, and look for evidence of memory first. One promising candidate, as long as we attribute individuality also to cells, would be auxin canalization, i.e., gradual tuning of auxin transport across cells and tissues, based on their previous experience and resulting in increased auxin flow in cells that already have transported auxin. This phenomenon, which has been proposed as a major factor determining e.g., the topology of leaf venation (reviewed in ref. 32), can be nowadays explained mechanistically as resulting from re-location of auxin transporters, such as the PIN proteins.[33] Unlike "canalization" of water flow across a landscape facilitated by erosion, auxin canalization depends on *active* participation of transporting cells. Canalization facilitated by transporter regulation and relocation has already been incorporated into mathematical models of vascular differentiation[34] and phyllotaxis.[35] While at least some aspects of these phenomena could be approximated also by models that do not assume canalization (e.g., a simple reaction-diffusion model can generate patterns

surprisingly reminiscent of leaf vasculature or the pattern of organ primordia), the models involving canalization are at least as good (or better), and, more importantly, biologically plausible.

It has to be stressed that development of leaf venation or phyllotaxis are mere pre-programed developmental modules if viewed from the whole organism perspective; to recognize the memory aspect, we have to take cells as individuals. However, memory does exist in plants at least on the cellular level, even by our strict criterion. But can it be found also on the whole plant level? One promising example is the developmental memory represented by reaction of axillar buds of *Scrophularia* cuttings to leaf removal, demonstrated by classical experiments of R. Dostál from the 1960s (reviewed in ref. 3), or later experiments demonstrating specific response of *Bidens* axillar buds to cotyledon injury in decapitated plants.[36,37] Repetition of those experiments using contemporary methodology to follow the processes taking place in the regenerating plants, and possibly on a more "mainstream" and at least somewhat molecularly characterized model, may be a good starting point.

Even more promising may be other phenomena, where we already have a wealth of data (and interpretations thereof) at hand, and which take place in regularly occurring natural situations and/or form an integral part of the plants' life cycle. This cannot be said about response to experimental manipulation such as simultaneous decapitation and piercing of one cotyledon. Namely, developmental decisions, such as vernalization, flowering induction, photomorphogenesis or breaking of seed dormancy depend on long-term integration and evaluation of light or temperature inputs, sometimes recorded and recalled after a time far exceeding the normal duration of the plant's life cycle. For example, *Stellaria* seeds can recall whether they have been imbibed in darkness or in light even after more than a year.[38] Further examples of similar long-term "data collection" have been reviewed in ref. 3.

Mechanistic models of these phenomena are already beginning to emerge. The "memory of winter" involved in seasonally dependent acquisition of flowering competence (vernalization) has been traced down to complex epigenetic regulation of the gene encoding a specific transcription factor (FLC) in Arabidopsis (reviewed in ref. 39). Surprisingly, the target genes appear to be different in grasses, albeit the topology of the whole regulatory network may be analogous.[40] We are also catching first glimpses of the complex web of hormonal and gene expression regulatory pathways controlling seed dormancy (reviewed in ref. 41), as well as the intricate interplay of light-dependent signals such as phytochrome modification, circadian rhythms and phytormonones implicated in light-controlled developmental regulation (reviewed in ref. 42).

Regulation of the saccharide metabolism may provide additional examples of integrating, storing and accessing information on long-term state of the plants' metabolism, including but not limited to the performance of the photosynthetic apparatus. One of the most serious tasks of plant life is achieving balance, over a wide range of environmental conditions, between carbon assimilation in source photosynthetic tissues, and consumption of assimilates in sink tissues and organs resulting in growth and carbon storage. The diurnal rhythm of photosynthesis, moreover, results in a need to put aside a part of assimilates during the day to cover the demands

of both assimilatory and sink tissues during the night (reviewed in ref. 43). Sugar sensing and signaling is an important part of mechanisms orchestrating carbon assimilation, assimilate storage and consumption based on precise sensing and integration of signals on energy balance at different levels.[44] Arabidopsis plants not only tune sugar utilization and growth according to assimilate supply, but they also modulate the deposition of storage carbon (starch) according to "expected" need during the night.[45] Most interestingly, starch mobilization at the night is essentially linear, resulting in nearly complete consumption of the starch reserve during every night. Thus, the plant is apparently able to measure the amount of starch at the end of the day and "anticipate" the length of night. The pattern of assimilation-storage-consumption can be tuned to changes in environmental conditions such as day length or light level in a manner that indicates some kind of memory of previous experience (reviewed in ref. 46). Moreover, the adjustment of enzyme levels includes a two-step reaction—a change in day length results first in a "half-way" transcriptional response that is followed by adequate translational output only upon repeated or lasting environmental stimulation.[47]

Memory is Not (yet) Intelligence: What Next?

Even in this rather unsystematic collection of phenomena we could identify some interesting candidates that at least appear to include memory or learning, i.e., necessary prerequisites of intelligent behavior according to Molvray's functional definition. It has to be stressed that we do not claim that memory (or even learning) and intelligence are synonymous. On the contrary, we feel that we can speak of "intelligent" or "adaptive" behavior only if alternatives are available—in other words, if the memorized information affects some *decisions*. The concept of "decision" may itself, at present, be no less vague (and no less plagued by anthropomorphisms) than those of intelligence or memory, and its more detailed elaboration would thus be obviously desirable. Some of these issues, as well as additional examples, are likely to be covered by articles in the coming special issue of Plant Cell and Environment, devoted to plant behavior (summarized in ref. 19).

Nevertheless, even on the basis of the mere memory criterion we could exclude some phenomena that were promising at the first glance but turned out to be explainable by models not including memory. We do not claim that such memory-less models are correct; we merely suggest that phenomena without clear involvement of memory should be left out from the discussion on plant intelligence until at least some less controversial cases are well characterized. We may have to sacrifice, at least temporarily, some potentially interesting observations for the sake of safety, if we aim to raise the status of plant intelligence from a mere metaphor to an explanatory framework, or (to quote Marcello Barbieri's statement on organic codes[48]), if we are to make plant intelligence *not metaphorical but real*.

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