

Toward a systemic view for plant learning: an (eco)physiological perspective.

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Abstract

Herein, we have proposed a concept of plant learning based on some principles of systemic plant ecophysiology. In order to accomplish this task, a framework consisting in basic epistemological assumptions is offered, as well as a cognitive context that underpins the perspective of learning. Accordingly, a number of empirical studies are quoted to illustrate the basic idea presented herein.

*The world is richer than it is possible
to express in any single language.
Ilya Prigogine.*

1) Introduction

In what "world" does it make sense to attribute to plants characteristics common to humans and animals, such as intelligence, learning, decision-making, *etc.*? This rhetorical question can be written in a more orthodox mode: In what scientific paradigm, in Thomas Kuhn's sense, can concepts related to cognition (learning, attention, memory, decision-making, *etc.*) be adequately attributed to plants?

This question is critical because science, as a human enterprise seeking for the knowledge and understanding of the universe, is not deprived of a human view of the world. Despite of the relative objectivity of scientific knowledge, the philosophical perspective of the observer, even unconsciously, has a powerful influence on the whole process of scientific production, from the questions being asked to the interpretation of the observations (empirical data). Therefore, the question if plants are cognitive entities capable to learn, making decisions,

exhibit intelligence, somehow, depends on the scientific perspective of the observer. Obviously, such possibility of understanding on the plants realm must be based on facts, observations of the physical aspects of the plants world, supported by solid scientific theories. Notwithstanding, in the process of the development o new perspectives of the world, analogical thinking and even a little bit of metaphorical inspiration are acceptable and even necessary (Trewavas, 2007). For the philosopher of science Paul Feyerabend (1975), the proliferation of theories is beneficial to science, while uniformity weakens its critical power. Accordingly, the condition of coherence, by virtue of which new hypotheses are necessary to conform to accepted theories, is irrational because it preserves the older, not necessarily the better theory.

In this context, Plant Neurobiology was presented as a proposal of a new science concerning with a more holistic perspective of the plant realm, imputing to them some cognitive attributes (Trewavas, 2003; Brenner et al., 2006; Baluska and Mancuso, 2007; Barlow, 2008; Calvo, 2016). Despite of the welcome criticism from part of plant biology scientific community (Firn, 2004; Alpi et al., 2007; Struik et al., 2008), new ideas and hypothesis are a fundamental condition for the development of science.

Herein, we will focus particularly on the aspects of plant learning. However, to accomplish this task properly, we will explicit the epistemological framework underlying our approach, in order to specifying about what plant model (theoretical representation) we are talking about. Additionally, we need to specify our concept of cognition, in order to clarify the definition of learning and its attributes. Following, we offer a variety of empirical examples to illustrate what we have considered as plant learning.

II) Epistemological framework and the systemic concept of plants

Indeed, we are not totally convinced that the term “neurobiology” is the best option to name the new scientific perspective of the plant realm. It is not because with think that metaphors (if, indeed, is the case of the prefix ‘neuro’) and analogies are not sufficient to support a science, rather because we think the term is actually restrictive to account for the whole complexity of the

phenomena that it have claimed. Overall, the object of study of the science of 'plant neurobiology' is neither the plant itself nor some specific structure or process of the plants; such is in classical human neuroscience. Instead, the object of the study is the relationship plant-environment. Thus, the main problem is to understand how plants survive and develop embedded in a changing world, creating stable communities (physiognomies), and evolving. Regarding the epistemological framework, which will be discussed below, the study of such relational object demands an interdisciplinary, even transdisciplinary, science (Barlow, 2008; Debono, 2013). Accordingly, in the recent manifesto by Paco Calvo (Calvo, 2016) it was proposed the 'hexagon of Plant Neurobiology', showing the relationships among different domains of the human knowledge, representing the interdisciplinary collaborations (philosophy, ecology, (electro)physiology, cellular and molecular biology, biochemistry, evolutionary and developmental biology), supporting Plant Neurobiology studies. Coincidentally, the set of collaborative sciences proposed by Paco (2016) is essentially the same that constitute the classical science of Physiological Plant Ecology (often named Ecophysiology), which was begun early in the 1800's century, with the same object of study: the plant-environment relationship in different scales of organization (Larcher, 1995; Lüttge, 2008).

However, throughout the development of Ecophysiology, concepts related to aspects of plant cognition have not emerged in the theories and hypothesis to explain the plant-environment relationship. Why did it is so? In my opinion, as a Plant Ecophysiologicalist, despite of the intrinsic more holistic perspective, Ecophysiology was born and has grown in the world dominated by the modern scientific paradigm based on both the mechanical principles and the reductionist view. Therefore, although concerning a very complex object of study, the underlying understanding (even unconsciously) that plants are reactive organisms (rote behaviour), instead cognitive systems have been dominant. Additionally, there is a strong and still growing influence of the molecular biology approach, supporting the belief that all biological phenomena can be explained by the processes of low level in the cells; the 'omics' era (Sheth and Thaker, 2014). Nevertheless, concomitant with the development of Plant Neurobiology, there is a solid criticism emerging inside the traditional Plant

Ecophysiology proposing an explicit systemic perspective of this science, even though not attributing cognitive abilities for plants (Lüttge, 2012; Matyssek and Lüttge, 2013; Souza et al., 2016a).

Notwithstanding, recently Souza et al. (2016b) have assumed a link between the 'systemic' plant (eco)physiology and the perspective of plant cognition claimed by Plant Neurobiology. Thus herein, in order to distinguish from the current 'system biology' view, we have assumed a 'systemic' perspective. We think this differentiation necessary because 'system biology', despite a more holistic view of life processes, is restricted to the cellular domain (Sheth and Thaker, 2014) and, thus still reductionist, while the 'systemic' approach is derived from the General System Theory (GST) (von Bertalanffy, 1968) based on principles of multiscaled self-organized systems (Souza et al., 2016b). This approach is not essentially different from the perspective proposed by Barlow (2008) based on the Living System Theory (LST) (Miller, 1978). Actually, the main difference is that LST assume an explicit cybernetics/biosemiotics approach describing any living being, wherever the scale of organization (from single cells to ecosystem), as input-output informational system composed by receptors, decoders and transducers. We are not convinced that such "analogical" simplification (actually a reduction to) to pure informational systems is adequate and sufficient to accounts for the complexity of all living beings, specially the cognitive aspects. One main problem in adopting an informational model of plant cognition is that such approach often falls in a type of "mental" representational cognitive system (Garzón, 2007). As will be discussed later, this is not the unique model for the understanding of plants as cognitive systems. Thus, we have considered more appropriate maintain the original epistemological position set on GST and its derived Complex System Theory (Mitchel, 2009), which offers more possibilities to develop new insights and hypothesis. Moreover, in certain way, LST is included in GST.

Accordingly, we consider plants as non-equilibrium systems, open thermodynamically, in the sense of Nicolis and Prigogine (1977). Therefore, the organization of such systems relying on continuous flows of exchanges of matter,

energy and information with the surrounding environment (Schneider and Kay 1994). Thus, plants must deal with the constant fluctuation of the environmental resources (light energy, water, nutrients) that eventually may constrain or threaten their stability (Souza and Lüttge, 2015). The ability to face the complexity of the environmental changes is particularly critical for sessile organisms such as plants (Trewavas, 2003; Trewavas, 2014).

Because of the limited capacity of locomotion, plants must deal with all sorts of environmental variation in their surroundings. As a result, their stability requires dynamic elements that confer some degree of organizational flexibility. To the set of possible changes in response to external stimuli we call phenotypic plasticity (DeWitt and Scheiner, 2004). Therefore, there is a close correlation between the stability of a system and the plasticity of phenotypic responses for a specific genotype. In essence phenotypic plasticity gives the system the ability to expand its capacities of physiological adjustments (in the case of individuals) or genetic adaptation (in the case of populations). The plasticity, particularly the modulation or control of plasticity, is related to patterns of organization of biological systems, which are characterized by complex networks (Hütt and Lüttge 2005, Souza et al. 2009). Overall, biological systems are essentially complex adaptive systems.

Notwithstanding the environment triggers responses in the organism, the pattern of such responses is determined by the internal dynamics of the system itself. This internal dynamics is integrated in a complex metabolic network that operates out of some rules of interactions. The rules that specify the interactions among the system components are performed using only local information, without reference to a pre-existing global pattern (Camazine et al., 2001). In complex systems, such interactions are typically nonlinear processes based on negative and positive feedback loops. The negative feedback plays a crucial role in maintaining homeostasis of the system, whereas the positive feedback operates propagating and amplifying signals throughout the system. Both processes work together in the formation and stabilization of new patterns of organization, which makes difficult the prediction of their global behaviour (Camazine et al., 2001; Lüttge, 2012). Such a dynamical process of organization,

operating through the different scales of the organization of the system, produces emergent properties and, hence, makes the system as whole non reducible to its components at smaller scales of organization (Souza et al., 2016a)

Besides the complexity inherent to the internal dynamics of the system organization, there is the effect of environmental noise (random fluctuations of physical factors of the environment) that interferes in plant responses to specific environmental factors (Bertolli and Souza, 2013). Indeed, a simple combination between two or more stress factors is capable to change significantly the plant responses (Prasch and Sonnewald, 2015). Henceforth, it is clear the huge challenge for plants survive in such complex world, where simple reactive strategies to solve all sort of constraining faced by plants in theirs environment would be unlikely. According to Trewavas (2003, 2005), only organisms with intelligence (the capacity for solving problems in a efficient way) would be able to supports its organization and, in consequence, maintain the fitness.

Another remarkable characteristic in plants, defining part of their own existence, is the modular structure of their bodies. A module can be considered as a biological entity (an individual, a structure, a process, or a pathway) characterized by more internal than external integration (Bolker, 2000). Overall, modules can be considered as the knots of networks that are connected *via* the edges (different modes of short and long-distance signalling). In hierarchical networks (such as any biological system), networks of finer scales can become knots in networks of higher scales and so on (Lüttge, 2012). In plant biology, de Kroon et al. (2005) use the term module to refer to *“repeated, often semiautonomous, structural and functional units”*. According to de Kroon and collaborators, *“the response of a plant to its environment is the sum of all modular responses to their local conditions plus all interaction effects that are due to integration”*. In other words, taking the definition of plants proposed herein, the responses of plants to environment are emergent properties. Emergence is the inevitable self-organized unfolding of new functions and structures of a system on a higher scalar integrative level (Lüttge, 2012). This is a far-reaching assumption. It is implied from it that, for instance, physiological responses (from

the point of view of the external observer) are emergent properties from the lower organization level (cellular/molecular level), therefore, such responses cannot be accurately inferred from below. In a more clear words: (eco)physiological responses to environmental cues are not reducible to molecular phenomena in a straightforward way, although they have correlation (taking into account that correlation do not imply necessarily causation) (Vitolo et al., 2012; Bertolli et al., 2014; Souza and Lüttge, 2015; Souza et al., 2016a).

Modularity and emergent properties brings, at least, two challenges to the understanding of the plant learning abilities: 1) Who does it is the 'individual' that learns?; and 2) How and where does to observe the learning? Howsoever, both challenges fall in the problem of individuality in plants.

Gilroy and Trewavas (2001) have hold that individuality is a term used to describe sets of structures morphologically similar (cells, tissues or plants) showing unique responses to signals. Overall, the expression of heterogeneous behaviour in a set of similar structures indicates individuality. For instance, the heterogeneity observed in the stomatal responses in a single leaf, indicates that each single stomata respond in a different way under a specific situation and, eventually, a group of single cells can synchronize exhibiting a local collective behaviour (Mott and Buckley, 2000). Analogously, the phenology of trees subjected to different environmental changes may exhibit complex spatiotemporal patterns with likely far-reaching consequences for ecosystem and biosphere functioning and structure (Peñuelas et al., 2004). Therefore, according to Clarke (2012) the individuality in plants is a matter of degree, depending of the hierarchical scale of observation. Some plants, in some circumstances, give us reason to say that modules are individuals, while other plants will exhibit different properties and would be best viewed as having individuality at a higher level.

Thus, somehow, individuality in plants, as modular organisms, depends on the scale of observation chosen by the observer himself, recognizing patterns of responses in groups of similar structures in a certain hierarchical level of organization. Howsoever, plants could be seeing as networked multi-agent systems (Olfati-Saber et al., 2007) insofar the semiautonomous modules,

connected by a complex network of different types of short and long-range signals (Baluska et al., 2006; Baluska (2013), may engender a dynamic of consensus and collaboration, resulting in an expression of higher level individuality; at whole plant level.

A possible explanation for individuality is the occurrence of stochastic processes during development (Gilroy and Trewavas, 2001). The biochemical process underlying cells development (cellular, division, differentiation and growth), in particular the role of the enzymes in biosynthesis, results in a complex nonlinear dynamics, since a single enzyme may function in many interconnected enzymatic pathways. Moreover, the diffusion and the number of signalling molecules (for example, plant hormones) among developing cells follows a complex self-organized non-homogenous dynamics, inducing minimal differences among cells. Nonlinear complex systems, such as cells whole metabolism, are sensitive to small perturbation, mainly under suboptimal conditions. Thereupon, random perturbations tend to become magnified, increasing the differentiation among groups of cells and creating independence from each other (Moller and Swaddle, 1997). Moreover, the complex electrical network, named 'electrome', underpinning cellular activities, shall display a major role on the organism individuality. De Loof (2016) holds that there are not two identical electromes. Each cell has its own electrome that is different from any other cells, even considering two cells derived from mitosis. This is reasonable insofar the daughter cells has different distribution of quantities and types of ionic channels and pumps, as well as different cytoskeleton structure, which coordinate the fluxes of ions generating electrical activity (Debono 2013; De Loof, 2016).

Such "epigenetic noise" allows a variation of responses, from the cell to the population level, to a plethora of environmental cues; thus, individuality forms a basis for phenotypic plasticity (Gilroy and Trewavas, 2001). Plasticity is one of the bases of plant stability, conferring multifunctional regulatory capacity for plants (Souza and Lüttge, 2015).

Finally, in order to defining plant learning both in theoretical and practical terms it is necessary to explicit the concept of cognition that underlies our understanding.

Summarizing,

- 1) learning in plants (as well as other cognitive abilities) shall be considered under the light of a more holistic scientific paradigm, and we thought that the systemic approach accomplish this task. Discussing such likely abilities with the lens of the classical paradigm (mechanist and reductionist) is unfruitful and makes non sense insofar the epistemological bases and the overall understanding on the object of study is radically different;
- 2) plants are open systems, and their entire organization depends upon such openness. Thus, the object of study is the plant-environment system;
- 3) the modularity of plants body organization makes difficult to define a single scale of observation representing the “whole plant”. Therefore, the definition of the individuality itself depends on the observer and upon the contingencies around it;
- 4) individuality is the basis for plasticity and, in turn, forms the basis for plant surviving in a changing environment.

III) A framework for plant cognition

Insofar as learning is one aspect of the cognitive phenomena (the main target in Plant Neurobiology) (Calvo, 2016) and there are different approaches in the cognitive sciences (Gomila and Calvo, 2008), it is worthy to present a general framework, on which we stand a position in order to define “plant learning”.

We think two main aspects are critical to be accounted: 1) the concept of representation (or no representation at all) and 2) the extension that cognition can reach in the natural world (beyond a human capacity).

Classical cognitivism is founded on the perspective of mental representations (Modern Philosophy) and information-processing systems (Artificial Intelligence, Computational Neuroscience). In this traditional approach, the cognitive capabilities of mind are conceived as disembodied and the cognitive phenomena are trivially depended upon environment in a stimulus-response basis. Influenced by the cybernetic approach, the metaphor of the brain as hardware and mind as the software exacerbate the Cartesian dualism on it is based on. Symbol structures are assumed to correspond to real physical structures in the brain and the combinatorial structure of a representation is supposed to have a counterpart in structural relations among physical properties of the brain (Gomila and Calvo, 2008; Richardson et al., 2008). In consequence, usually, cognition is thought as it were predominantly a human faculty and applied to just one level of organisation (the organismal) (Barlow, 2010).

On the other hand, in the *post-cognitivism* cognition is considered not as an abstract computation, instead cognition is viewed as interactive, embodied and embedded. Despite of the many research programs in post-cognitivism, the different approaches takes cognition and behaviour in terms of the dynamical interaction of an embodied system (a real biological organism, for instance) that is linked to the surrounding environment (embodied-embedded nature) (Gomila and Calvo, 2008). This is a major step toward a concept of cognition extensible to plants insofar as plants have a modular (non centralized) body inextricably connected to its environment. Under this perspective, plant is taken as an *individual-coupled-with-its-environment system*, and cognition is rather an emergent and extended self-organizing phenomenon. Centralized processes are not necessary (Garzón, 2007).

Accordingly, the 'Santiago Theory of Cognition' developed by Maturana and Varela (1980) holds that living systems are cognitive systems, and living is a process of cognition, which applies irrespective of the presence, and intervention of a nervous system. The concept of cognition as a basic biological phenomenon is assumed, as a general assumption, by Plant Neurobiologists such as Brenner et al. (2006), Garzón (2007), Barlow (2008, 2010), Gagliano (2015). Garzón and Keijzer (2011) summarize this general standing: "cognition is a biological

phenomenon, and that it exhibits itself as a capability to manipulate the environment in ways that systematically benefit a living organism”.

Thus, at least under the perspective of post-cognitivist, it is reasonable to assume cognition as a property/process extensible to plants. However, it remains the question about what position, representational or non-representational, would be more appropriate for a model of plant cognition?

Broadly, in the perspective of representationalist, cognitive systems are taken as information processors that produce representations, which can exploit them in a purposeful manner; on the other hand, the anti-representationalist framework holds a non-computational way to understand the relationship between an organism and their environment (Calvo, 2016). In order to take a cognitive system as representational, when the processing of representational states marks cognitive activity, Garzón (2007) have proposed two main principles. The principle of dissociation, meaning that a physical representation must stand accessible even when things or events are not available temporally; and the principle of reification, whenever the representational states are clearly identified to a computational role they are supposed to play.

According to Calvo (2016), a problem with applying the representationalist approach to plants is that the perception is the outcome of a logic-like process of inference, because the stimulus is ‘inherently ambiguous’. Recently, an alternative non-representationalist and anti-mechanist view have been revisited: the Gibson’s ecological psychology. Although originally Gibson’s framework (1966) was restricted to animals’ behaviour, his ideas have been extended to plants (Gagliano, 2014; Calvo 2016). Gibson argues that ‘animals’ should not be conceived as machines, and the mechanistic view of the environment as a matter in motion is inappropriate to understand animal behaviour. Instead, Gibson holds that the environment of the animals consists of action possibilities, which he termed *affordances* (Withagen et al., 2012).

Two aspects of the concept of affordance are remarkable: 1) environment itself is meaningful; and 2) environment consists of opportunities for action, i.e., environment is not conceived as a collection of causes, but as a manifold of action possibilities (Withagen et al., 2012). Under the ecological framework, perception is organized around action. Opportunities for action could be

'perceived directly' as interaction with an 'unambiguous environment'. Thus, plants perceive opportunities for behavioural interaction in the form of affordances (Richardson et al., 2008). Affordances are not properties of the phenomenological world that depend upon the state of the observer; rather, they are ecological phenomena that exist in the environment. Thus, environment does not cause behavior, but simply make it possible (Withagen et al., 2012).

At least, two major problems can be considered in the ecological psychology approach: the supposed unambiguity of the environment; and the direct perception. Actually, as we argue before, the natural environment of a plant is very complex with a plethora of stimuli affecting each other in time and space and, thus it is inherently ambiguous. Accordingly, the interaction of the plant with the surrounding has a complex non-linear dynamics, demanding an integration of many ambiguous signals in order to allow the stability of plant organization. This is specially a critical ability for a modular organism (Souza and Lüttge, 2015). For instance, stomatal responses to simultaneous applied opposing environmental factors cannot be predicting from studying one factor at a time. The stimulation induces ambiguous responses those are specie-specific (Merilo et al., 2014).

However, the concept of direct perception is more controversial, because its explanation is flawed. According to Richardson et al. (2008) "solutions, perceptually speaking, emerge out of the interaction between the organism and its local environment". There is no clue how such direct perception takes place. It is a hypothesis hard to be tested empirically.

Moreover, the enormous amounts of empirical data, showing well-known strong correlation between plant physiological changes and abiotic and biotic cues (Atkinson and Urwin, 2012; Jenks and Hasegawa, 2014; Azooz and Ahmad, 2016), indicates that plant metabolism and, overall, plant behavior is inextricably coupled with the environment (Trewavas, 2009a). Indeed, plant responses to changes in environmental conditions involve corresponding changes in the perceptual apparatus of plant cells. Such perceptual apparatus consists in specific membrane receptors for different signals that trigger cascades of signaling transducers that, in turn, regulates the gene expression and the corresponding metabolic changes. Enormous numbers of molecular

connections integrate into a complex self-organized and dynamic network, modulating plant behavior under changing external conditions (Sweetlove and Fernie, 2005; Trewavas, 2005; Lucas et al., 2011).

What we are suggesting is that such metabolic organization, coupled to environmental cues is, indeed, a 'molecular representation' of a corresponding environmental condition. Those 'representations' are, indeed, changes in metabolic network topologies (different arrangements among cellular components) that engender metabolic schemes corresponding to the current status of the cells under certain local conditions. Such schemes can be stored and recalled later in certain circumstances (storage/recall type of memory), eventually changing future plant behavior (Thellier and Lüttge, 2012).

There is no plant physiological response that is not mediated by changes in the perceptual apparatus of the plants. Thus, 'direct perception' is, in our opinion, a misleading and unnecessary concept without correspondence with empirical data from ecophysiological studies.

Notwithstanding the criticism on some aspects of ecological psychology, we agree with the perspective that environment do not cause behavior, but make it possible. The changes expressed by metabolism are not ruled by environment, rather they are emergent responses from the interactions among the networks of different modules in the plant body, integrating and canalizing external information into new states of organization, allowing plant stability. This perspective is consistent with the view of plants as autonomous individuals, instead objects in a mechanistically conceived world.

Summarizing, the concept of 'plant learning' developed below, is conceived on the following cognitive perspective: plants are modular embodied-embedded systems, hierarchically organized, perceiving and acting on the world by manipulating local representations (cellular schemes) and by means of electric ionic waves guided by proteins and feeding back on the same proteins, determining the plasticity of the active signal-transduction pathways, and integrate them globally through short and long-distance signaling processes.

As a consequence of organizational changes in the plant (structural and / or functional), its surrounding environment can be altered, re-feeding the perceptual system of the plant and, eventually, generating new internal schemes

and changes in the respective signaling pathways (Figure 1). However, this process of true feedback between the plant and its environment can occur locally in specific modules. For example, during the development of a tree canopy, different leaves develop in different positions receiving different amounts of light energy with different durations and time interval (sunflecks), creating micro-environments (Watling et al., 1997). On the other hand, the perceptual process can occur in the whole individual, as in controlled experiments with tiny plants of *Arabidopsis thaliana* (Kreps et al., 2002). Whatever the case, a sophisticated system of internal signaling takes place in order to integrate local or global cellular changes (Choi et al., 2016).

Different types of signals, such as hormones, ROS, Ca²⁺ and electrical signals, compose the plant's signaling network (Baluska, 2013; Choi et al., 2016). Increasing strong evidences have demonstrated that electrical signals play central role in both cell-cell and long-distance communication in plants (Baluska et al., 2006; Fromm and Lautner, 2007; Gallé et al., 2015). Electrical signal transmission takes place throughout cellular connections in the symplasmatic phloematic continuum, creating a complex network, similar to a simple neural net (Baluska et al., 2006; Debono, 2013; Choi et al., 2016), engendering the plant electrome (De Loof, 2016). Evidence of synchronization of electrical spikes among different cells, indicating a collective behavior of groups of cells interconnected by the plasmodesmata network, supports the neuroid conduction hypothesis in plants (Masi et al., 2009; Debono, 2013). Recently, Saraiva et al. (2016) have demonstrated that electrome in plants, measured as time series of low voltage variations, can exhibit high complex dynamic patterns (actually, chaotic behavior instead purely white noise). Moreover, the complexity of the electrical signals showed dependence of the environmental stimulation, exhibiting burst of electrical spikes following a power law (i.e. spikes without a characteristic size), suggesting that plant electrome can be critically self-organized (Souza et al. 2017). Such complexity inherent to the signaling network in plants can support a massive informational processing system, enabling plants to process information in order to keep their stability, and learning processes.

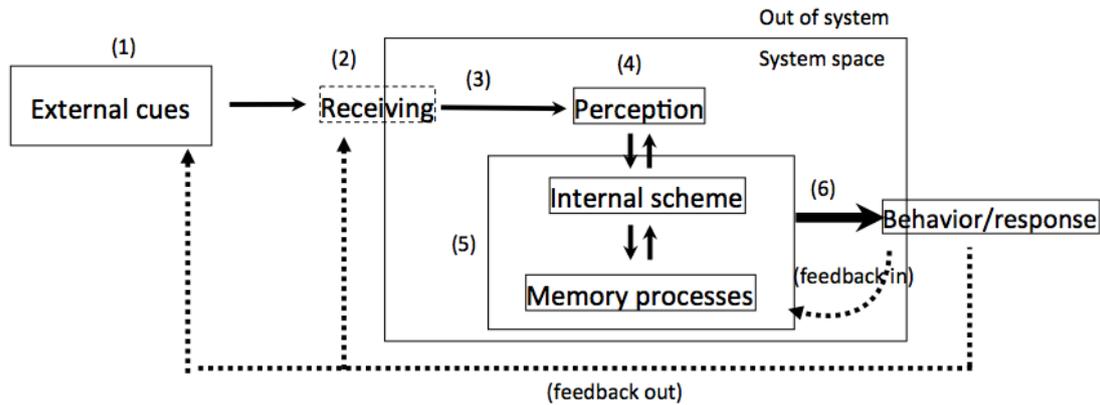


Figure 1 General cognitive model. (1) Environmental factors (both biotic and abiotic); (2) plant membrane receptors (often proteins that recognize specific signals); (3) transducing cascade (often consisting in secondary signals, enzymes and transcriptional factors); (4) network metabolic shaping (including gene expression and further metabolic changes) engendering a cellular scheme; (5) feedbacks between storage and recall metabolic processes (memory); (6) integration processes producing local and/or global new behaviours (plant responses). The responses can modify directly the internal processes (feedback in) and/or affect external environment (feedback out).

III) Concept of learning

As with cognition, there are different possible approaches to an adequate concept of learning in plants. Recently, an interesting and provocative contribution from comparative psychology and behavioural biology provides a scope to discuss possible aspects of learning in plants, based on studies focused in the species *Mimosa pudica*, the sensitive plant (Abramson and Chicas-Mosier, 2016). They have proposed an empirical basis in order to test for associative and non-associative learning. Accordingly, non-associative learning has two categories: habituation and sensitization. Habituation refers to a decrease in responding to a stimulus that is repeatedly presented, while sensitization can be considered the opposite of habituation since it refers to an increase in the frequency or probability of a response. In a recent study with *M. pudica*, Gagliano et al. (2014) showed that the leaf-folding behaviour in response to repeated disturbance exhibited clear persistent habituation, mainly when plants were grown under energetically costly environments.

On the other hand, associative learning has in conditioning its most basic expression, accessed by stimulus-response training experiments (Abramson and Chicas-Mosier, 2016). Gagliano et al. (2016) have tested this hypothesis for plants in a clever set of experiments with *Pisum sativum* (garden pea), emulating the pavlovian empirical approach. By using a Y-maze task, it was showed that, after a period of training, the position of a neutral cue (a fan located in a alternated positions in the arms of the Y-maze), predicting the location of a light source, affected the direction of plant growth, prevailing over innate phototropism.

Despite of some promising empirical data, we are not sure about the ubiquity of such perspective throughout the plant kingdom, as well as on its role for plant living. Actually, maybe the behavioural approach is not consistent with the plants general life stile. According to Trewavas (2014) *“unlike animals, plants are not unitary organisms; they constantly change throughout their development process: we do not deal with the same plant twice”*. The attempts to transpose the framework from the psychology behaviour to the context of plant learning (Abramson and Chicas-Mosier, 2016) present some constrains that, in our opinion, are no suitable for plants living style. First of all, plants do not exhibit movements of their whole bodies (unitary individuals) from one place to another (A-to-B movement), like the free movements of animals. Despite of the different types of tropisms, allowing plants to explore their surroundings, these type of movements are NOT actual free movements. Plants are typically sessile organisms and all sort of evolutionary adaptations match with their life style. Thus, under the point of view of a plant, A-to-B movements simply are not necessary. Even taking the growth of plants as analogous to animals “free movements” in order to adapt experiments from psychology behaviour to test for the different categories of associative and non-associative learning is, somehow, distant form the plant life style in the wild.

Secondly, as we have discussed later, there is the problem of individuality in plants. Plants are not typical unitary individuals. Notwithstanding the many modules communicate each with another by a complex network signalling, allowing some level of integration, each module is semiautonomous and, under certain circumstances, behave like an individual. Furthermore, under natural

conditions, where plants face a enormous complexity of environmental cues in different scales of space and time, the individuality of the modulus are exacerbated (de Kroon et al., 2009). Experiments carried out under very specific and controlled conditions, although they may give some insight into possible behaviours, are far removed from the complex reality of plants (Trewavas, 2003, 2014). Accordingly, Garzón and Keijzer (2011) holds that minimal forms of cognition, be it plant, bacteria or animal, cannot be studied detached from the natural habitat in which they take place; insofar under laboratory conditions the selection pressures are manipulated, affecting the observed behaviour. For instance, the capacity of soybean plants to respond to water deficit was different when plants were grown under environmental controlled conditions (inside a grown chamber) comparing with the plants subjected to same water deficit imposition, but grown under more variable conditions (Bertolli and Souza, 2013). Recently, Vialet-Chabrand et al. (2017) have showed the importance of fluctuation in light on plant photosynthetic acclimation, showing that growing plants under square wave growth conditions ultimately fails to predict plant performance under realistic light regimes.

Therefore, we believe that a more broad and general concept of learning could afford a more suitable framework for the plant learning understanding.

First of all, learning is not an all-or-nothing property; there are levels of learning. The concept of learning levels (L0 to L3) was conceived by Gregory Bateson (Bateson, 1972), insofar as organisms can become responsive to patterns, but then can become recursively responsive to patterns within those patterns. Herein, according to Affifi (2013), we have holds that plants show, at least, the L1 level, which living beings can achieve without a neural circuit: these are the cases in which an entity gives at Time 2 a different response from what it gave at Time 1 to a “similar stimulus”. Cleverly, Bateson holds that the assumption of the repeatable stimulus is critical for the concept of learning, insofar in the wild the existence of exactly the same circumstances in Time 1 and Time 2 is very unlikely. Otherwise, none learning would take place, and all responses fall in the level L0 (when an entity shows minimal change in its response to a repeated item of sensory input).

Whatever, according to Bateson (1972), learning undoubtedly denotes change of some kind, and change denotes process. Therefore, learning is process. Such perspective matches with the concept of learning in Maturana and Varela (1980), where learning is taken as a process that consists in the transformation through experience of the behaviour of an organism. This transformation is an historical process such that each mode of behaviour constitutes the basis over which a new behaviour develops, either through changes in the possible states that may arise in it as a result of interaction, or through changes in the transition rules from state to state. Learning occurs in a manner that, for the observer, the learned behaviour of the organism appears justified from the past, through the incorporation of a representation of the environment (memory) that acts, modifying its present behaviour by recall; notwithstanding this, the system itself functions in the present, and for it learning occurs as an atemporal process of transformation.

Such dependence on the observer claimed by Maturana and Varela is in confluence with the systemic perspective of the nature insofar the observer define the spatial and temporal scale of the observed phenomena and, consequently, define the system itself under observation. A semiotic interpretation of learning (Affifi, 2013), where learning is concerned with changes in sign activity, holds that besides levels of plant learning, in a Bateson's *sensu*, there are also scales of learning, referring to the different spatial and temporal ranges within which learning can be studied (dependence on the observer). Accordingly, there are four major scales in which it is conceivable that plants learn. On the first scale, learning occurs by parts of the plant (modules or individual cells) being regulated by the activity of the plant as a whole. The others levels involve the whole plant as an individual (second scale); learning at the level of population or community (third scale), by processes of plant-plant communication; and the forth scale includes the species scale, through natural selection a species "learns" certain adaptive behaviours. Affifi (2013) have admitted that in the forth scale "learning" takes on a very different sense, no longer associated with anything potentially experiential or phenomenal.

No matter what the scale is, learning is an emergent property from the interactions among elements of the system (or part of it) involving in the

cognitive process. According to Trewavas (2003, 2014), learning process involves construction of networks, such as plasmodesmatal connections among cells, allowing exchange of information among cells through fluxes of proteins, nucleic acids and others smaller molecules, as well as new tissues formation, giving to plants flexibility to changes in their phenotype in a changing environment (phenotypic plasticity). Furthermore, plasticity is also observed experimentally by means of electrical registers of plant tissue activity (Debono, 2013; Souza et al., 2017) generated by ionic fluxes in solution, which are guided by proteins (membranes channels and pumps). Thus, considering that plant tissue is a symplasm that allows the inter-cellular flow of ions and small molecules, engendering a complex electrical network, the learning mechanisms should be looked for in this context, in a similar way as neuroscience.

Spontaneous activity of membrane variation potential is an important property of cerebral cortex that is probably involved in information process and storage (Arcangelis and Herrmann, 2010). Neuronal avalanches in spontaneous spatiotemporal activity were already shown in very few to very large numbers of neuronal assemblages in organotropic cultures of rat cortex slices. The size and duration of avalanches in such neuronal bursts of firing follows a power law distribution with very stable exponents (Beggs and Planz, 2003, 2004). The power law distribution is a signature feature of systems activity under critical state, interpreted in all cases as self-organized criticality (SOC) (Bak,1996; Arcangelis and Herrmann, 2010). Timely, recent results of temporal dynamic of low voltage electrical signals in plant tissues have showed evidence o SOC behaviour. Under different environmental stimuli, Souza et al. (2017) have observed appearance of electrical spikes following a power law. Emergence of SOC is associated with mechanisms of slow energy accumulation and fast energy redistribution, which drives the system to critical state, where avalanches extensions and durations do not have a characteristic size (Bak, 1996; Arcangelis and Herrmann, 2010). The ability of the brain to self-organize connections has been part of theoretical models for learning and verified in real brain activity, where operating in critical level, far from uncorrelated subcritical or too correlated supercritical regime, optimize information management and transmission (Arcangelis and Herrmann, 2010; Beggs and Planz, 2003; Kinouchi

and Copeli, 2006; Eurich et al., 2002). In neuronal models of learning acting in critical state, where a reproduction of physiological mechanisms of neural behaviour is implemented on a network with topological properties similar to brain network, shows how learning and memory can occur in function of different levels of plastic adaptation introduced via non-uniform negative feedback (Arcangelis and Herrmann, 2010). The same model also demonstrate that learning dynamics shows universal properties, independent of the details of the system or the specific task assigned, since slow plastic adaptive parameters is used. The learning process seems to be very sensitive to initial conditions using the model, (Arcangelis and Herrmann, 2010), which may be an indicative of chaotic traits (Schroeder, 1991). Similarly, Saraiva et al. (2016) have showed some empirical evidence that whole plant electrical signals approaches a chaotic dynamic as well.

The conclusions of testing the neuronal model is that systems which acts in critical state response to given inputs in high flexible way, adapting itself more easily to different learning rules and that learning is a collective process dependent on connectivity level and on plastic adaptive strength parameters. The requirement of slow plastic adaptation was confirmed in experimental analysis in humans, showing that learning performance improves when minimal changes occur in functionality network (Shew et. al, 2009). So, the learning process is dependent of plasticity in neurons function and connectivity, what is an example of phenotypic plasticity. Accordingly, based on the evidences of SOC behaviour in plant electrophysiology (Saraiva at al., 2016; Souza et al., 2017) it would be worthy to perform more studies testing the hypothesis that plant learning may be supported by a self-organized electrical network approaching the critical state.

No matter what scale of organization is under consideration, it is clear that some level of phenotypic plasticity is the basis for plant learning. According to Trewavas (2003, 2014) learning involves goals and error-assessment mechanisms that quantify how close the new behaviour approaches that goal (mostly the fitness). Thus, the process of learning requires a continual exchange of information and feedback from the goal to the current behaviour in order to correct current behaviour and direct future more closely towards achieving the

goal, such as is illustrated in feedbacks represented in the model showed in Figure 1. It is equivalent to a trial-and-error process that can be indicated by the presence of robust oscillations in behaviour as the organism continually assesses and makes further correction to behaviour. Stomatal complex oscillations in response to changes in environmental water conditions are a nice example of timely dynamical behaviour (Souza et al., 2004; 2005). Accordingly, phenotypic plasticity allows the error-correcting mechanisms that individual plants use in an attempt to achieve optimal fitness (Trewavas, 2003).

The ability of plant learn can be grasped from acclimation and/or optimization behaviours that allow plant survive and, eventually, maintain or even increase its fitness under certain circumstances. In a working definition proposed by Karban (2015) “learning requires that past events cause chemical changes that influence the sensitivity, speed, or effectiveness of subsequent plant sensing and associated responses”.

In order to holds a clear cut between acclimation and learning, we propose that learning shall consists in phenotypic changes based on memory that, effectively, improves plant responses to similar stimuli experienced in a certain moment in the past and then it was ceased (non longer accessible for the pants). In situations that environmental changes represent a new and permanent condition, the responses of plants are also continuous allowing plant acclimation (according to the Merriam-Webster dictionary, “*acclimation* is the process or result of acclimating; specially: physiological adjustment by an organism to environmental change”). This concept of learning is aligned with our representationalist approach, matching the principle of dissociation proposed by Garzón (2007) that, plus the principle of reification, support the processing of representational states.

Following, we offer a variety of examples to illustrate likely situations that learning could be claimed.

IV) Empirical evidences

Experiencing biotic stimuli

Co-evolution with a range of pathogens and insects has enabled plants to evolve to defend themselves against great part of injurious microbes, insects and others parasites. Plants commonly react to attacks by producing defensive molecules and compounds that are toxic to the aggressor. As a co-evolutionary response, plants acquired the capacity to recognize hostile and virulent pathogens, even at early stages of infection or attack, inducing an appropriate defence response. Such ability involves the capacity to store information (memory) of the experiences of previous interactions with other organism and, then, uses them for improving further responses, a phenomenon known as “priming” by researches studding abiotic stress (Crisp et al., 2016).

The phenomenon of priming is a common topic underlying responses to a range of biotic stresses, wherever previous exposition to some pathogenic organism makes a plant more resistant to future exposure to a stressful event. When a plant is ‘primed’, the information of the priming stimulus is stored until exposure to a triggering stimulus in future; an effect known as ‘memory’ in plant defence (Conrath, 2015; Kandel et al., 2014). Primed plants many times show longer-lasting activation or attenuated repression of defence upon challenge than unprimed plants (Hilker et al., 2015). Defensive traits that can be primed may include, among others, changes in defence-related signalling compounds or processes such as hormones and enzymes, alterations to chromatin, or enhanced presence of pattern-recognition receptors, or defence responses, such as accumulation of phytoalexins, phenolic compounds, reactive oxygen species, glucosinolates, lignin, or plant volatiles induced by herbivory (Balmer et al., 2015). Thus, primed plants show either faster and/or stronger activation of the several defence systems. Therefore, the responses that are induced following attack by either pathogens or insects, facilitates a more rapid response if the stress recurs (Conrath et al. 2006; Ton et al, 2007). It is important because when plants anticipate herbivory, through the perception of indicative signals or by experience of herbivory at their parental generation, plants are physiologically prepared to induce stronger and faster defences upon the anticipated stimuli. Moreover, this strategy may also reduce the possibility of development of counter adaptive strategies by insect herbivores to increased plasticity of induced defence by priming (Zheng and Dicke, 2008). Therefore, plants have

some form of “memory” often termed “stress imprint”, such as a genetic or biochemical modification of a plant that occurs after stress exposure that causes future responses to future stresses to be different.

There are studies on priming in the plant–insect interactions since the first report of defence in maize (Engelberth et al., 2004). Currently, priming research consists in studying priming defence mediated by herbivore-inducible plant volatiles (HIPVs), which are produced and released by the neighbouring plants, or plant parts, under herbivore attack. In literature, a number of experiments have shown that priming effects can last for several days at least. For example, tobacco plants can store information on previous induction for at least 6 days, and in *Arabidopsis* plants, such information can be stored at least 3 days (Goh et al., 2003).

The HIPVs mechanisms are important to plant defence, because they occur many times in the plant life. HIPVs are leaf volatiles [GLVs], terpenoids and other molecules, acting as plant signalling molecules (between and within plant) or attracting natural predators of the herbivores (McCormick et al., 2012). HIPVs can induce or prime defensive responses in neighbouring intact plants or intact plant parts on the same plant. Several volatiles and GLVs produced in response to insect feeding and mechanical damage are capable of priming defences (Heil & Kost, 2006; Choh & Takabayashi, 2006; Kessler et al., 2006; Heil & Silva Bueno, 2007; Frost et al., 2007; Ton et al., 2007; Rodriguez-Saona et al., 2009; Muroi et al., 2011; Peng et al., 2011; Hirao et al., 2012; Li et al., 2012). The primed defences consist of different processes. Accumulation of jasmonic acid (JA), inducing anti-herbivore defences (Engelberth et al., 2004; Frost et al., 2008) and accumulation of linolenic acid, an precursor of JA and GLVs (Frost et al., 2008); increased production of plant secondary metabolites (Kessler et al., 2006; Hirao et al., 2012); increased protease inhibitor activity (Kessler et al., 2006), and enhanced transcription of anti-herbivore defence genes (Ton et al., 2007; Peng et al., 2011). Furthermore, increasing emission of HIPVs and secretion of extra floral nectar, an extra sugar source, attracts predators of plant enemies, such as ants, improving natural plant defences (Heil and Silva Bueno, 2007, Rodriguez-Saona et al., 2009; Muroi et al., 2011; Li et al., 2012; Ton et al., 2007; Peng et al., 2011).

Mechanisms of defence priming in plants are caused by signals that indicate attack by pathogens or herbivores. This include the known “systemic acquired resistance” (SAR), which is triggered by pathogen attack and causes a systemic priming of salicylic acid (SA) that induces defence mechanisms (Jung et al., 2009; Kohler et al., 2002). Another example of stress-indicating priming signals is volatile organic compounds (VOCs), which are release by herbivore-infested plants. Several VOCs can prime JA-dependent defences in plant modules and/or neighbouring plants (Turlings and Ton, 2006; Ton et al. 2007; Heil and Ton, 2008).

Nevertheless, not all priming responses are triggered by adverse signal. For example, plant-beneficial organisms, such as non-pathogenic rhizobacteria and mycorrhizal fungi, can trigger priming that results in an “induced systemic resistance” (ISR) response (van Wees et al., 2008). Priming related to ISR is associated with priming of JA-dependent defences, because is most effective against pathogens that are resistant to JA-inducible defences (Verhagen et al., 2004; Pozo et al., 2008; Ton et al., 2002; van der Ent et al., 2009).

There are many evidences showing that several stress-induced effects in plants can be transmitting to the next generation. Molinier et al. (2006) have observed genomic changes (hyper recombination in the somatic tissue) of plants exposed to UV radiation and flagellin, an elicitor derived from bacteria, as well as in their non treated progeny. The transgenerational stress “imprint” effects were also observed in wild radish (*Raphanus raphanistrum*) responses to herbivore damage by butterfly (*Pieris rapae*), and in plants treated with JA (Agrawal, 2002). Accordingly, the progeny of treated plants were more resistant to herbivory than control plants were. Another study showed that Arabidopsis plants exposed to localized infection by *Pseudomonas syringae* produce progeny more resistant to pathogen (Slaughter et al., 2012). This transgenerational effect is evident in progeny of plants that received repeated infections with *Pseudomonas* (Luna et al., 2012). Rasman et al. (2012) showed that treatment with JA or exposition to insect herbivory make Arabidopsis and tomato produce progeny more resistant against caterpillar feeding. Additionally, some studies reported an enhanced anti-herbivore resistance in plants whose parents experienced previous interaction with herbivores, for instance, in *Raphanus raphnistrum* (Holeski,

2007), *Mimulus guttatus* (Holeski et al., 2012), and in *Taraxacum officinale* (Verhoeven and van Gurp, 2012).

Overall, the different examples above of plant biotic interactions illustrate quite well the ability of plants to grasp environmental information, engendering differing metabolic schemes corresponding with the different stimuli, and improve their responses in future interactions; an actual learning phenomena. Additionally, it is remarkable the possibility of transgenerational memory, improving behaviour of the next generation; an interesting possibility for learning at a population level (Afiffi, 2013).

Experiencing abiotic stimuli

In the literature of abiotic stress the term “acclimation” is equivalent to “priming” in biotic stress studies (Crisp et al., 2016). However, different experimental designs are put together under the same idea of “acclimation”. Many studies on the effects of abiotic factors on plant performance as carried out applying continuous stimulation over a certain period of time, and the plant states are compared before and after stimulation (e.g. Vitolo et al., 2012, Bertolli et al., 2014); while other studies a carried out with subsequent environmental stimuli (e.g. Kron et al. 2008). The type of acclimation that can be seen as learning are those examples whose stimulus is given, then it is cessed for a while, and when applied again it leads to a more efficient response (more rapid and/or more intense). This kind of acclimation is also named as priming, such as for biotic studies. Thus, acclimation that happens continuously and gradually along time cannot be considered (or recognized with) learning if they do not have time interval between stimulus experience cessation and re-stimulation, because it is not possible to verify enhanced performance after an interval (more rapid and/or intense responses). Despite this, we also cannot say that continuous acclimating does not involve learning process at all.

Examples of abiotic priming are scarce compared with biotic priming, because priming concept was consolidated with abiotic stress studies (Conrath et al., 2006). An early example of abiotic stress priming was presented by Knight et al. (1998). Arabidopsis plants pre-exposed to osmotic and oxidative stress

showed improved tolerance to subsequent stimuli compared with control. This behaviour was correlated with different patterns of Ca²⁺ signalling and genetic expression. Similarly, Arabidopsis plants pre-treated with BABA (beta-amino-butyric acid) enhanced activation of plant defence system under post-drought stresses, and in this case “priming” was used to designate such response improvement after an interval of non-stimulating period (Jakab et al., 2005).

This phenomenon have been observed in others species as well. *Arrhenatherum elatius*, for example, displays different performances in response to different previous drought (Walter et al., 2010). *Brassica juncea* L. treated with hydrogen peroxide (H₂O₂) improved drought stress tolerance after 48h (Hossain and Fujita, 2013). There are many other examples using H₂O₂ priming to enhance stress response that can be found in Hossain et al. (2015). Another mustard species (*Brassica campestris* L.) pre-treated with 6°C cold-shock improved seedlings tolerance to salt and drought stress by modulation of antioxidative and glyoxalase system (Hossain et al., 2013a). Heat-shock pre-treatment also improves antioxidative system of plants of same mustard species (*Brassica campestris* L.) when exposed to salt and drought stress (Hossain et al., 2013b). Nitric oxide (NO) is a ubiquitous and important signalling molecule that has shown a priming ability, triggering improved antioxidative responses to salt stress (reviewed in Molassiotis et al., 2010). Low doses of NO, or H₂O₂, applied in rice seedlings allowed higher surviving of green tissues, and higher quantum yield for photosystem II, of plants post-submitted to both salt or heat stress (Uchida et al., 2002). Further examples on abiotic priming can be found in an up-to-date overview by Filippou et al. (2012).

Studies on abiotic priming in seeds have shown long lasting effects persisting during and after germination. This issue is well documented and discussed in reviews by Jisha et al. (2013) and Paparella et al. (2015). A remarkable example of seed priming was presented by Iqbal and Ashraf (2007). Seeds from two different cultivars of wheat were pre-treated with different solutions of CaCl₂, KCl and NaCl then, when the seed were subjected to a saline stress condition, showing a significant increase in tolerance comparing with the seeds without pre-treatment. Similar response was observed with tomato seeds pre-treated

with NaCl, exhibiting higher performance under a subsequent treatment with saline stress, mainly in advanced growth stages (Cayuela et al., 1996).

So far, herein, we clearly identify those examples as a learning process. Accordingly, other environment factors, as temperature, also can induce plant learning. Rice seeds primed with chilling presented less negative effects caused by post-chilling stress after germination, compared with no treated seeds (Hussain et al., 2016a). Another experiment tested how different seed priming stimuli (hydropriming, osmopriming, redox priming, chemical priming, and hormonal priming) could better enhance chilling tolerance in adult plants. Hormonal pre-stimulation with salicylic acid and selenium were efficient to improve plants performance to post-chilling stress (Hussain et al., 2016b). Priming rice seeds of three cultivars with BABA also improved drought and salinity stress tolerance of seedling, mainly in the drought tolerant cultivar Vaisakh and in the salt tolerant cultivar Vyttila (Jisha and Puthur, 2016).

There are several other abiotic examples of priming that are hidden behind “acclimation”, “recovering” or “memory” terminology which could be related with learning (Trewavas, 2005, 2009; Crisp et al., 2016). Anderson et al. (1994), for example, revealed that maize seedlings (a cold intolerant species) treated with 14 °C (a moderate cold) three days before different chilling stimulus degrees showed an improvement in surviving (79% for pre-treated against 22% for non-treated) and development compared with the no treated control plants. The maize pre-treatment with hypoxia improved their survival time in subsequent anoxic incubation (Xia and Saglio, 1992), and mustard seedlings pre-treated with salicylic acid or high temperature (45°C for 1h) improved thermotolerance in subsequent heat-shock of 55°C (Dat et al., 1998).

Many studies on “cross tolerance” or “cross-talk” have been reported (Capiati, et. al, 2006; Mittler, 2006; Pastori and Foyer, 2002; Artetxe et. al, 2002; Mateo et. al, 2004). These are interesting phenomena that show a kind of generalization in plant responses to environment factors, what is one of learning properties (Abramson and Chicas-Mosier, 2016). Generalisation was a learning aspect tested in recent research that investigated learning in plants (Gagliano et al., 2016).

The cellular complex metabolic networks, more specifically the redundancy traits in some metabolic signalling pathways, enabling cross-talk and the consequent cross-tolerance, is an evidence that complex metabolic networks have semantic properties (Witzany, 2006), allowing plants to respond to stimulus in both generalised and specific ways. It is also important emphasize again that in nature, the stimulus from environment never comes alone, what increase the complexity of plant experiences, challenges and capacities (Trewavas, 2003, 2009). Thus, respond to new, ambiguous and unknown stimulus using past experiences can enhance plant performance in natural context, being an advantageous trait of plant life.

V) Concluding remarks

Although, acclimation (or hardening) and learning phenomena both are based on phenotypic plasticity, they implicate in different strategies for surviving and, ultimately, for plant fitness. Under the point of view of the observer, when plants are subjected to continuous environmental stimulus, progressive physiological and morphological changes often takes place in order to reconciles plant organization with the new conditions. However, such changes may consist in very different strategies, depending on the external changes (stimulating or constraining development), ranging from improvements in some traits (e.g. higher water use efficiency, more efficiency in nutrient use) to morpho/physiological constrains, such as lower vital metabolic functions as photosynthesis and reduced growth. On the other hand, without the cessation of the stimulus, and the "imprinting" of memories, which could affect the future behaviour of the plant when subjected to a supposed similar environmental situation or a new situation that involves similar pathways of response (cross-tolerance phenomena), learning abilities are not accessible for the external observer. Furthermore, somehow, the past experiences shall improve the efficiency of future plant responses; otherwise, no learning at all would take place (when the responses are essentially the same) and, eventually, new stressful situations

could cause more extensive damages, decreasing surviving and/or plant fitness.

Another major aspect to access plant learning is the problem of individuality and the scale of observation. As discussed early, insofar plants are modular organisms, consisting of modules with some level of autonomy, under heterogeneous environmental conditions different parts of the plant body can exhibit different behaviours, not necessarily, underpinning learning phenomena. Additionally, a practical problem concerns on what techniques can be used to access plant behaviour. Physiological methods (including molecular ones) are restricted to specific scales of observation, for instance, ranging from the expression of individual genes to the whole canopy carbon assimilation. As argued by Vitolo et al. (2012) and Bertolli et al. (2014), due to the implications of the hierarchical organization of plants (Souza et al., 2016a), there is no a single representative scale of observation.

Thus, how does learning can be accessible for an external observer? Taking the conditions in the definition proposed herein, plant traits representing the integration of the whole plant modules responses, such as biomass and fitness, would be the more reasonable manner to do that reliably. Therefore, the studies in smaller scales (e.g. molecular and cellular), seeking for the understanding of the causes of changes in plant behaviour in upper scales, must be cautious to make inferences and generalizations (Souza et al., 2016a).

Regardless the difficulties to access learning, it has a major and self-evident role in plants life. According to Trewavas (2003, 2005) the necessity for learning rather than rote behaviour relies on the enormous possibilities of environmental factors combinations creating an endless of possible “worlds” for each individual plant. Thus, reactive pre-programed responses are very unlikely to account for all sorts of plant demands in the wild. Accordingly, in order to learning process occurs, cues and signals of the aspects of the environment that are relevant to the learned adaptive response must be available to the organism (*environment invites behaviour*).

However, in some cases, the specific cues required to enable the organism to learn appropriately to their selective environment will not be clearly

available (Brown, 2013). This matches the concept of Sterelny's epistemic differences between two environmental categories (Sterelny, 2003): "transparent" environments (where functional features correspond to reliable perceptual cues) and, more common in the wild, "opaque/translucent" environments (features do not correspond neatly to reliable cues). Thus, in opaque environments, learning may be a more costly process.

Brown (2013) draws attention to the fact the adaptive value of learning to individuals (and pop) is also sensitive to the cost-benefit structure of the world, insofar as plasticity has an intrinsic cost for plants (Kleunen and Fisher, 2005). DeWitt et al. (1998) distinguish some potential costs of phenotypic plasticity: maintenance costs, relative to energetic costs of the sensory and regulatory mechanisms of PF; production costs associated to production of new inducible structures; information acquisition costs (like foraging exploitation of the environment); genetic costs, for instance, when pleiotropic genes conferring adaptive plasticity on a trait also confer negative direct effects on other traits. Thus, learning process, taking place through phenotypic plasticity, is not always adaptive.

Finally, insofar learning can improve both surviving and plant fitness, there is also implications in the population level. Learning allows population to avoid the potential loss of genetic diversity that comes with directional selection, preserving the standing variation in populations (Brown, 2013). Phenotypic plasticity (*underpinning learning process*) can reduce the lethality of the phenotypic variants within a population in the face of environmental changes, allowing higher stability (Souza and Lüttge, 2015). This buffers population from future environmental changes by maintaining their capacity for rapid adaption in future, ultimately, learning can be a source of lineage level robustness and, in consequence, is a source of evolvability (Brown, 2013).

*The major problems in the world are the result
of the difference between how nature
works and the way people think.*

Gregory Bateson

VI) References

- Abramson, CI; Chicas-Mosier, AM. Learning in plants: lessons from *Mimosa pudica*. *Frontiers in Psychology*, 2016. doi: 10.3389/fpsyg.2016.00417
- Affifi, R. Learning plants: semiosis between the parts and the whole. *Biosemiotics*, 6:547-559, 2013.
- Agrawal, A. A. Maternal effects associated with herbivory: mechanisms and consequences of transgenerational induced plant resistance, *Ecology* 83, 3408–3415, 2002.
- Alpi, A. et al. (2007) Plant neurobiology: no brain, no gain? *Trends Plant Sci.* 12, 135–136.
- Artetxe, U.; García-Plazaola, J.I.; Hernández, A.; Becerril, J.M. Low light grown duckweed plants are more protected against the toxicity induced by Zn and Cd. *Plant Physiology and Biochemistry*, 40: 10, p. 859–863, 2002.
- Atkinson, N.J., Urwin, P.E. The interaction of plant biotic and abiotic stresses: from genes to the field. *J Exp Bot* 63:3523-3544, 2012.
- Azooz, MM, Ahmad, P. Plant-environment interaction. Wiley Blackwell, Hoboken, 2016.
- Bak P (1996) *How Nature Works. The Science of Self-Organized Criticality* (Springer, New York).
- Balmer, A; Pastor, V ; Gamir, J ; Flors, V ; Mauch-Mani, B. The ‘prime-ome’: towards a holistic approach to priming. *Trends Plant Sci.* 20, 443–452, 2015.
- Baluska F (ed). Long-distance systemic signalling and communication in plants. Berlin: Springer; 2013.
- Baluska F, Mancuso S (2007) Plant neurobiology as paradigm shift not only in plant sciences. *Plant Sign Behav* 2:205–207.
- Baluska F, Mancuso S, Volkmann D. Communication in plants: neuronal aspects of plant life. 1st ed. Berlin: Springer; 2006.
- Baluska F. (2013) *Long-distance Systemic Signalling and Communication in Plants*. Springer, Berlin.
- Barlow, P. Plant roots: autopoietic and cognitive constructions. *Plant Root* 4:40-52, 2010.

Barlow, P. Reflections on 'plant neurobiology'. *BioSystems* 92:132-147, 2008.

Bateson, G. Steps to an ecology of mind. Jason Aronson Inc., London. 1972.

Beggs JM, Plenz D (2003) Neuronal avalanches in neocortical circuits. *J Neurosci* 23:11167–11177.

Beggs JM, Plenz D (2004) Neuronal avalanches are diverse and precise activity patterns that are stable for many hours in cortical slice cultures. *J Neurosci* 24:5216–5229.

Bertolli, S. C.; Mazzafera, P.; Souza, G. M. Why is it so difficult to identify a single indicator of water stress in plants? A proposal for a multivariate analysis to assess emergent properties. *Plant Biology* 16:578–585 (2014).

Bertolli, SC, Souza, GM. The level of environmental noise affects the physiological performance of *Glycine max* under water deficit. *Theoretical and Experimental Plant Physiology*, 25(1): 36-45, 2013.

Bolker, J.A. (2000) Modularity in development and why it matters to evo-devo. *American Zoologist*, 4,770–776.

Brenner, ED; Stahlberg, R, Mancuso, S; Vivanco, J; Baluska, F; Volkenburgh, EV. Plant neurobiology: an integrated view of plant signalling. *Trends in Plant Science* 11:413-419, 2006.

Brown, RL. Learning, evolvability and exploratory behaviour: extending the evolutionary reach of learning. *Biology and Philosophy*, 28:933-955, 2013.

Calvo, P; Gomila, T. Directions for an embodied cognitive science: toward an integrated approach. In: Calvo, P; Gomila, T (ed.). *Handbook of cognitive science: an embodied approach*. Elsevier, San Diego. pp 1-26, 2008.

Calvo, P. The philosophy of plant neurobiology: a manifesto. *Synthese* 193:1323–1343, 2016.

Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) *Self- organization in biological systems*. Princeton University Press, Princeton, NJ

Capiati, D.A.; País, S.M.; Téllez-Iñón, M.T. Wounding increases salt tolerance in tomato plants: evidence on the participation of calmodulin-like activities in cross-tolerance signalling. *Journal of Experimental Botany*, v. 57:10, p. 2391–2400, 2006. doi:10.1093/jxb/erj212.

Cayuela, E.; Perez-Alfocea, K.; Caro, M.; Bolarin, M.C. Priming of seeds with NaCl induces physiological changes in tomato plants grown under salt stress. *Physiologia Plantarum*, v. 96, p. 231-236, 1996.

Choh, Y. and Takabayashi, J. Herbivore-induced extrafloral nectar production in lima bean plants enhanced by previous exposure to volatiles from infested conspecifics. *Journal of Chemical Ecology*, 32, 2073–2077, 2006.

Choi W, Hilleary R, Swanson SJ, Kim S, Gilroy S (2016) Rapid, long-distance electrical and calcium signalling in plants. *Annu Rev Plant Biol* 67: 287-307.

Clarke, E. Plant Individuality: a solution to the demographer's dilemma. *Biol Philos* 27:321-361, 2012.

Conrath, U ; Beckers, Gjm ; Flors, V ; Garcia-Agustin, P ; Jakab, G ; Mauch, F ; Newman, MA ; Pieterse, Cmj ; Poinssot, B ; Pozo, Mj ; Pugin, A ; Schaffrath, U ; Ton, J ; Wendehenne, D ; Zimmerli, L ; Mauch-Mani, B. Priming: getting ready for battle, *Mol. Plant-Microbe Interact.* 19, 1062–1071, 2006.

Crisp, PA; Ganguly, D; Eichten, SE; Borevitz, JO; Pogson, BJ. Reconsidering plant memory: Intersections between stress recovery, RNA turnover, and epigenetics. *Sci. Adv.* 2016; 2:e1501340

Dat, J.F.; Lopez-Delgado, H.; Foyer.H.; Scott, I.M. Parallel Changes in H₂O₂ and Catalase during Thermotolerance Induced by Salicylic Acid or Heat Acclimation in Mustard Seedlings. *Plant Physiol*, v. 116, p. 1351-1357, 1998.

de Arcangelisa, L; Herrmann, HJ. Learning as a phenomenon occurring in a critical state. *PNAS* 107:3977–3981.

de Kroon H., Huber H., Stuefer J.F., van Groenendael J.M. (2005) A modular concept of phenotypic plasticity in plants. *New Phytologist*, 166, 73–82.

de Kroon, H; Visser, EJW; Huber, H; Mommer, L; Hutchings, MJ. A modular concept of plant foraging behaviour: the interplay between local responses and systemic control. *Plant, Cell and Environment* (2009) 32, 704–712

De Loof A. The cell's self-generated "electrome": The biophysical essence of the immaterial dimension of Life? *Commun& Integr Biol.* 2016;e1197446. doi:10.1080/19420889.2016.1197446.

Debono MW. Dynamic protoneural networks in plants: A new approach of spontaneous extracellular potential variations. *Plant Signal Behav.* 2013;8:6,e24207.doi: 10.4161/psb.24207.

Debono, MW. Perceptive Levels in Plants: A Transdisciplinary Challenge in Living Organism's Plasticity. *Transdisciplinary Journal of Engineering & Science*, 4:21-39, 2013.

DeWitt TJ, Scheiner SM Phenotypic plasticity: functional and conceptual approaches. Oxford University Press, New York, NY, 2004.

DeWitt TJ, Sih A, Wilson DS. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* 13: 77–81, 1998.

Engelberth, J.; Alborn, H. T.; Schmelz, E. A.; Tumlinson, J. H. Airborne signals prime plants against insect herbivore attack. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 1781–1785, 2004.

Eurich CW, Herrmann JM, Ernst UA (2002) Finite-size effects of avalanche dynamics. *Phys Rev E* 66:066137.

Feyerabend, P. *Against method*. NBL, London, 1975.

Filippou, P., Tanou, G., Molassiotis, A.; Fotopoulos, V.. "Plant acclimation to environmental stress using priming agents," in: *Plant Acclimation to Environmental Stress*, eds N. Tuteja and S. S. Gill (Berlin, NY: Springer Science & Business Media), 1–28. 2012.

Firn, R. *Plant Intelligence: an Alternative Point of View*. *Annals of Botany* 93: 345–351, 2004.

Fromm J, Lautner S (2007) Electrical signals and their physiological significance in plants. *Plant Cell and Environ* 30:249–257.

Frost, C. J.; Heidi, M. A.; Carlson, J. E.; De Moraes, C. M.; Mescher, M. C.; Schultz, J. C. Within-plant signaling via volatiles overcomes vascular constraints on systemic signaling and primes response against herbivores. *Ecology Letters*, 10, 490–498, 2007.

Frost, C. J.; Mescher, M. C.; Dervinis, C.; Davis, J. M.; Carlson, J. E.; De Moraes, C. M. Priming defense genes and metabolites in hybrid poplar by the green leaf volatile cis-3-hexenyl acetate. *New Phytologist*, 180, 722–734, 2008.

Gagliano M (2015) In a green frame of mind: perspectives on the behavioural ecology and cognitive nature of plants. *AoB PLANTS* 7:plu075. doi:10.1093/aobpla/plu075

Gagliano, M; Renton, M; Depczynski, M; Mancuso, S. Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia*, 2014. DOI: 10.1007/s00442-013-2873-7

Gagliano, M; Vyazovskiy, VV; Borbeely, AA; Grimonprez, M; Depczynski, M. Learning by association in plants. *Scientific Reports*, 6:38427, 2016. DOI: 10.1038/srep38427

Gallé A, Lautner S, Flexas J, Fromm J (2015) Environmental stimuli and physiological responses: The current view on electrical signalling. *Environ Exp Bot* 114:15-21.

Garzón, FC; Keijzer, F. Plants: adaptive behaviour, root-brains, and minimal cognition. *Adaptive Behaviour*, 19:155-171, 2011.

Garzón, FC. The Quest for Cognition in Plant Neurobiology. *Plant Signaling & Behavior* 2:4, 208-211, 2007.

Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston,

Gilroy, S; Trewavas, A. Signal processing and transduction in plant cells: the end of the beginning? *Nature Reviews | Molecular Cell Biology* 2:307-314, 2001.

Goh, C. H.; Gil Nam, H.; Shin Park, Y. Stress memory in plants: a negative regulation of stomatal response and transient induction of rd22 gene to light in abscisic acid-entrained Arabidopsis plants, *Plant J.* 36, 240–255, 2003.

Heil, M.; Kost, C. Priming of indirect defenses. *Ecology Letters*, 9, 813–817, 2006.

Heil, M.; Silva Bueno, J. C. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 5467–5472, 2007.

Heil, M.; Ton, J. Long-distance signaling in plant defense. *Trends Plant Sci.* 13,264–272, 2008.

Hilker, M. et al. (2015) Priming and memory of stress responses in organisms lacking a nervous system. *Biol. Rev.* Published online August 20, 2015. <http://dx.doi.org/10.1111/brv.12215>

Hirao, T.; Okazawa, A.; Harada, K.; Kobayashi, A.; Muranaka, T.; Kirata, K. Green leaf volatiles enhance methyl jasmonate response in Arabidopsis. *Journal of Bioscience and Bioengineering*, 114, 540–545, 2012.

Holeski, L. M. Within and among generation phenotypic plasticity in trichome density of *Mimulus guttatus*. *Journal of Evolutionary Biology*, 20, 2092–2100, 2007.

Holeski, L. M.; Jander, G.; Agrawal, A. A. Transgenerational defense induction and epigenetic inheritance in plants. *Trends in Ecology and Evolution*, 11, 618–626, 2012.

Hossain, M.A.; Bhattacharjee, S.; Armin, S.M.; Qian, P.; Xin, W.; Li, H.Y.; Burritt, D.J.; Fujita, M.; Tran, L.S.P. Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. *Frontiers in Plant Science*, v.6:420, 2015. Doi: 10.3389/fpls.2015.0042.

Hossain, M.A.; Fujita, M. Hydrogen Peroxide Priming Stimulates Drought Tolerance in Mustard (*Brassica juncea* L.) Seedlings. *Plant Gene and Trait*, v. 4:20, p. 109-123, 2013.

Hossain, M.A.; Mostofa, M.G.; Fujita, M. Cross Protection by Cold-shock to Salinity and Drought Stress-induced Oxidative Stress in Mustard (*Brassica campestris* L.) Seedlings. *Molecular Plant Breeding*, v. 4:7, p. 50-70, 2013.

Hossain, M.A.; Mostofa, M.G.; Fujita, M. Heat-shock positively modulates oxidative protection of salt and drought-stressed mustard (*Brassica campestris* L.) seedlings. *Journal of Plant Science & Molecular Breeding*, 2013. Doi: 10.7243/2050-2389-2-2.

Hussain, S.; Khan, F.; Hussain, H.A.; Nie, L. (2016) Physiological and Biochemical Mechanisms of Seed Priming-Induced Chilling Tolerance in Rice Cultivars. *Front. Plant Sci*, v.7:116, 2016. Doi: 10.3389/fpls.2016.00116.

Hütt M-T, Lüttge U (2005) Network dynamics in plant biology: current progress in historical perspective. *Prog Bot* 66:277–310

Iqbal, M.; Ashraf, M. Seed Preconditioning Modulates Growth, Ionic Relations, and Photosynthetic Capacity in Adult Plants of Hexaploid Wheat under Salt Stress. *Journal of Plant Nutrition*, v. 30, p. 381–396, 2007. Doi: 10.1080/01904160601171330.

Jakab, G.; Ton, J.; Flors, V.; Zimmerli, L.; Me'traux, J.P.; Mauch-Mani, B. Enhancing Arabidopsis Salt and Drought Stress Tolerance by Chemical Priming for Its Abscisic Acid Responses. *Plant Physiology*, v. 139, p. 267–274, 2005.

Jenks, M.A., Hasegawa, P.M. Plant abiotic stress. Wiley Blackwell, Hoboken, 2014.

Jisha, K.C.; Puthur, J.T. Seed Priming with Beta-Amino Butyric Acid Improves Abiotic Stress Tolerance in Rice Seedlings. *Rice Science*, v. 23: 5, p.242-254, 2016.

Jisha, K.C.; Vijayakumari, K.; Puthur, J.T. Seed priming for abiotic stress tolerance: an overview. *Acta Physiol Plant*, v.35, p. 1381–1396, 2013. Doi: 10.1007/s11738-012-1186-5.

Jung, H. W.; Tschaplinski, T. J.; Wang, L.; Glazebrook, J.; Greenberg, J. T. Priming systemic plant immunity RID D-4021-2009. *Science* 324, 89–91, 2009.

Kandel, E ; Dudai, Y ; Mayford, M. The molecular and systems biology of memory. *Cell* 157, 163–186, 2014.

Karban, R. Plant sensing and communication. The University of Chicago Press, Chicago. 2015

Kessler, A.; Halitschke, R.; Diezel, C.; Baldwin, I. T. Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. *Oecologia*, 148, 280–292, 2006.

Kinouchi O, Copelli M (2006) Optimal dynamical range of excitable networks at criticality. *Nat Phys* 2:348–351.

Knight, H.; Brandt, S.; Knight, M.R. A history of stress alters drought calcium signalling pathways in *Arabidopsis*. *The Plant Journal*, v. 16:6, p. 681–687, 1998.

Kohler, A.; Schwindling, S.; Conrath, U. Benzothiadiazole-induced priming for potentiated responses to pathogen infection, wounding, and infiltration of water into leaves requires the NPR1/NIM1 gene in *Arabidopsis*. *Plant Physiol.*128, 1046–1056, 2002.

Kreps, JA; Wu, Y; Chang, H-S; Zhu, T; Wang, X; Harper, JF. Transcriptome Changes for *Arabidopsis* in Response to Salt, Osmotic, and Cold Stress. *Plant Physiology* 130:2129-2141, 2002.

Kron, AP; Souza, GM; Ribeiro, RF. Water deficiency at different developmental stages of glycine max can improve drought tolerance. *Bragantia*, 67:693-699, 2008.

Larcher, W. *Physiological Plant Ecology*. Third edition, 1995, Springer-Verlag, Berlin.

Li, T.; Holopainen, J. K.; Kokko, H.; Tervahauta, A. I.; Blande, J. D. Herbivore-induced aspen volatiles temporally regulate two different indirect defenses in neighbouring plants. *Functional Ecology*, 26, 1176–1185, 2012.

Lucas, M; Laplaze, L; Bennett, MJ. Plant systems biology: network matters. *Plant, Cell and Environment* (2011) doi: 10.1111/j.1365-3040.2010.02273.x

Lüttge U (2012) Modularity and emergence: biology's challenge in understanding life. *Plant Biol* 14:865–871.

Lüttge, U. *Physiological Ecology of Tropical Plants*, 2008. Second edition, Springer-Verlag, Berlin.

MA: Houghton Mifflin.

Masi E, Ciszak M, Stefano G, Renna L, Azzarello E, Pandolfi C, Mugnai S, Baluska F, Arecchi FT, Mancuso S. Spatiotemporal dynamics of the electrical network activity in the root apex. *Proc Natl Acad Sci USA*. 2009;106:4048-4053.doi: 10.1073pnas.0804640106.

Mateo, A.; Mühlenbock, P.; Rustérucchi, C.; Chang, C.C.C.; Miszalski, Z.; Karpinska, B.; Parker, J.E.; Mullineaux, P.M.; Karpinski, S. LESION SIMULATING DISEASE 1 Is Required for Acclimation to Conditions That Promote Excess Excitation Energy. *Plant Physiology*, v. 136:1, p. 2818-2830, 2004. doi: <http://dx.doi.org/10.1104/pp.104.043646>.

Maturana, HR; Varela, FJ. *Autopoiesis and cognition: the realization of the living*. D. Reidel Publishing Company, London. 1980.

Matyssek, R; Lüttge, U (2013) Gaia: The planet holobiont. *Nova Acta Leopoldina* 114(391): 325–344.

McCormick, A.C., Unsicker, S.B. and Gershenzon, J. The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends in Plant Science*, 17, 303–310, 2012.

Merilo, E; Joesaar, I; Brosch, M; Kollist, H. To open or to close: species-specific stomatal responses to simultaneously applied opposing environmental factors. *New Phytologist*, 2014. doi: 10.1111/nph.12667

Miller, J.G., 1978. *Living Systems*. McGraw-Hill Publishing Co., New York.

Mitchell M (2009) *Complexity: a guided tour*. Oxford University Press, New York.

Mittler, R. Abiotic stress, the field environment and stress combination. *TRENDS in Plant Science*, v. 11:1, 2006.

Molinier, J.; Ries, G.; Zipfel, C.; Hohn, B. Transgenerational memory of stress in plants, *Nature* 442, 1046–1049, 2006.

Møller, A.P., Swaddle, J.P., 1997. *Asymmetry, Developmental Stability and Evolution*. Oxford University Press, Oxford.

Mott, K. A.; Buckley, T. N. Patchy stomatal conductance emergent collective behaviour. *Trends Plant Sci.* 5, 258–262 (2000).

Muroi, A.; Ramadan, A.; Nishihara, M.; Yamamoto, M.; Ozawa, R.; Takabayashi, J.; Arimura, G. The composite effect of transgenic plant volatiles for acquired immunity to herbivory caused by inter-plant communications. *PLoS ONE*, 6, e24594, 2011.

Nicolis, G., Prigogine, I., 1989. *Exploring Complexity: An Introduction*. W. H. Freeman, New York.

Olfati-Saber, R; Fax, JA; Murray, RM. Consensus and Cooperation in Networked Multi-Agent Systems. Vol. 95, No. 1, January 2007 | *Proceedings of the IEEE*.

Paparella, S.; Araújo, S.S.; Rossi, G.; Wijayasinghe, M.; Carbonera, D.; Balestrazzi, A. Seed priming: state of the art and new perspectives. *Plant Cell Rep*, 2015. Doi: 10.1007/s00299-015-1784-y. 2015.

Pastori, G.M.; Foyer, C.H. Common Components, Networks, and Pathways of Cross Tolerance to Stress. The Central Role of “Redox” and Abscisic Acid-Mediated Controls. *Plant Physiology*, v. 129:2, p. 460-468, 2002. Doi: <http://dx.doi.org/10.1104/pp.011021>.

Peng, J.; van Loon, J. J. A.; Zheng, S.; Dicke, M. Herbivore-induced volatiles of cabbage (*Brassica oleracea*) prime defense responses in neighboring intact plants. *Plant Biology*, 13, 276–284, 2011.

Peñuelas, J; Filella, I; Zhang, X; Llorens, L; Ogaya, R; Lloret, R; Comas, P; Estiarte, M; Terradas, J. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* (2004) 161 : 837–846.

Pozo, M. J.; Van Der Ent, S.; Van Loon, L. C.; Pieterse, C. M. J. Transcription factor MYC2 is involved in priming for enhanced defence during rhizobacteria-

induced systemic resistance in *Arabidopsis thaliana* RID A-9326-2011. *New Phytol.* 180,511–523, 2008.

Prasch, CM; Sonnewald, U. Signalling events in plants: Stress factors in combination change the picture. *Environmental and Experimental Botany* 114:4–14 (2015)

Rasman, S.; De Vos, M.; Casteel, C. L.; Tian, D.; Halitschke, R.; Sun, J. Y.; Agrawal, A. A.; Felton, G. W.; Jander, G. Herbivory in the previous generation primes plants for enhanced insect resistance. *Plant Physiology*, 158, 854–863, 2012.

Richardson, MJ; Shockley, K; Fajen, BR; Riley, MA; Turvey, MT. *Ecological Psychology: Six Principles for an Embodied–Embedded Approach to Behaviour*. In: Calvo, P; Gomila, T (ed.). *Handbook of cognitive science: an embodied approach*. Elsevier, San Diego. pp. 161-188, 2008.

Rodriguez-Saona, C. R.; Rodriguez-Saona, L. E.; Frost, C. J. Herbivore-induced volatiles in the perennial shrub, *Vaccinium corymbosum*, and their role in inter-branch signaling. *Journal of Chemical Ecology*, 35, 163–175, 2009.

Saraiva GFR, Ferreira AS, Souza GM. Beyond APs and VPs: evidences of chaos and self-organized criticality in electrical signals in plants. 2016; bioRxiv 064790; doi: <https://doi.org/10.1101/064790>.

Schneider, E. D., Kay, J.J., 1994. Life as a manifestation of the second law of thermodynamics. *Mathem. & Comput. Modell.* 19, 25-48.

Schroeder M. (1991) *Fractals, chaos, cower laws: minutes from an infinite paradise*. W.H. Freeman and Company, New York.

Sheth, BP; Thaker, VS (2014) *Plant systems biology: insights, advances and challenges*. *Planta* 240:33–54

Shew WL, Yang H, Petermann T, Roy R, Plenz D (2009) Neuronal avalanches imply max-imum dynamic range in cortical networks at criticality. *J Neurosci* 29:15595–15600.

Slaughter, A.; Daniel, X.; Flors, V.; Luna, E.; Hohn, E.; Mauch-Mani, B. Descendants of primed *Arabidopsis* plants exhibit resistance to biotic stress. *Plant Physiol.*, <http://dx.doi.org/10.1104/pp.111.191593>, 2012.

Souza GM, de Oliveira RF, Cardoso VJM (2004) Temporal dynamics of stomatal conductance of plants under water deficit: can homeostasis be

improved by more complex dynamics. *Arquivos de Biologia e Tecnologia, Curitiba* 47:423–431

Souza GM, Pincus SM, Monteiro JAF (2005) The complexity-stability hypothesis in plant gas exchange under water deficit. *Braz J Plant Physiol* 17:363–373

Souza GM, Ribeiro RV, Prado CHBS, Daminieli DSC, Sato AM, Oliveira MS (2009) Using network connectance and autonomy analyses to uncover patterns of photosynthetic responses in tropical woody species. *Ecological Complexity* 6:15–26

Souza, G. M., Lüttge, U., 2015. Stability as a Phenomenon Emergent from Plasticity Complexity Diversity in Eco-Physiology. *Progr. in Bot.* 76, 211-239.

Souza, GM; Bertolli, SC; Lüttge, U. Hierarchy and Information in a System Approach to Plant Biology: Explaining the irreducibility in plant ecophysiology. *progress in botany. Progress in Botany* 77:167-186, 2016a.

Souza, GM; CHBA; Ribeiro, RV; Barbosa, JPRAD; Gonçalves, AN; Habermann, G. Toward a systemic plant physiology. *Theor. Exp. Plant Physiol.* 28:341–346, 2016b

Souza, GM; Ferreira, AS; Saraiva, GFR; Toledo, GRA. Plant “electrome” can be pushed toward a self-organized critical state by external cues: evidences from a study with soybean seedlings subject to different environmental conditions. *Plant Sig Behav*, 2017. doi: 10.1080/15592324.2017.1290040

Sterelny K (2003) *Thought in a hostile world: the evolution of human cognition.* Wiley-Blackwell, Oxford

Struik, PC; Yin, X; Meinke, H. Plant neurobiology and green plant intelligence: science, metaphors and nonsense. *J Sci Food Agric* 88:363–370, 2008.

Sweetlove, LJ; Fernie, AR. Regulation of metabolic networks: understanding metabolic complexity in the systems biology era. *New Phytologist* (2005) 168: 9–24

Thellier M, Lüttge U (2012) Plant memory: a tentative model. *Plant Biol.* doi:10.1111/j.1438-8677.2012.00674.x

Ton, J. et al. Priming by airborne signals boosts direct and indirect resistance in maize. *Plant J.* 49, 16–26, 2007.

Trewavas A (2003) Aspects of plant intelligence. *Ann Bot* 92:1–20.

Trewavas, A. Green plants as intelligent organisms. *Trends in Plant Science* 10:413-419, 2005.

Trewavas, A. *Plant Behaviour and intelligence*. Oxford University Press, Oxford, 2014.

Trewavas, A. Response to Alpi et al.: Plant neurobiology – all metaphors have value. *Trends in Plant Science* 12:231-233, 2007.

Trewavas, A. What is plant behaviour? *PCE* 32:606-616, 2009.

Turlings, T. C. J.; Ton, J. Exploiting scents of distress: the prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests. *Curr. Opin. Plant Biol.* 9, 421–427, 2006.

Van Kleunen, M; Fisher, M. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* 166: 49–6, 2005.

van Wees, S. C. M.; Van der Ent, S.; Pieterse, C. M. J. Plant immune responses triggered by beneficial microbes RID B-8595-2011 RID A-9326-2011. *Curr. Opin. Plant Biol.* 11, 443–448, 2008.

Verhagen, B. W. M.; Glazebrook, J.; Zhu, T.; Chang, H. S.; van Loon, L. C.; Pieterse, C. M. J. The transcriptome of rhizobacteria-induced systemic resistance in *Arabidopsis*. *Mol. Plant-Microbe Interact.* 17, 895–908, 2004.

Verhoeven, K. J. and van Gurp, T. P. Transgenerational effects of stress exposure on offspring phenotypes in apomictic dandelion. *PLoS ONE*, 7, e38605, 2012.

Vialet-Chabrand, S; Matthews, JSA; Simkin, AJ; Raines, CA; Lawson, T. Importance of fluctuations in light on pant photosynthetic acclimation. *Plant Physiology*, 2017. doi: <http://dx.doi.org/10.1104/pp.16.01767>

Vítolo, HF; Souza, GM; Silveira, JAG. Cross-scale multivariate analysis of physiological responses to high temperature in two tropical crops with C3 and C4 metabolism. *Environmental and Experimental Botany* 80:54–62 (2012)

Von Bertalanffy L (1968) *General system theory*. George Braziller, New York.

Walter, J.; Nagy, L.; Heinb, R.; Rascher, U.; Beierkuhnleinb, C.; Willner, E.; Jentsch, A. Do plants remember drought? Hints towards a drought-memory in grasses. *Environmental and Experimental Botany*, v. 71, p. 34–40, 2011.

Watling, JR; Robinson, SA; Woodrow, IE; Osmond, CB. Responses of Rainforest Understorey Plants to Excess Light during Sunflecks. *Australian Journal of Plant Physiology* 24(1) 17 – 25, 1997.

Withagen, R; Poel, HJ; Araújo, D; Pepping, G-J. Affordances can invite behavior: Reconsidering the relationship between affordances and agency. *New Ideas in Psychology* 30:250-258, 2012.

Witzany, G. Plant Communication from Biosemiotic Perspective. *Plant Signaling & Behavior*, v. 1:4, p. 169-178, 2006.

Xia, J.H.; Saglio, P.H. Efflux as a Mechanism of Hypoxic Acclimation of Maize Root Tips to Anoxia. *Plant Physiol.*, v.

Zheng, S. J. and Dicke, M. Ecological genomics of plant–insect interactions: from gene to community. *Plant Physiology*, 146, 812–817, 2008.