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TITLE

Information processing and distributed computation in plant organs

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ABSTRACT

The molecular networks plant cells evolved to tune their development in response to the environment are becoming increasingly well understood. Much less is known about how these programs function within the multicellular context of organs, and the impact this spatial embedding has on emergent decision-making. To address these questions, organ scale information processing may be viewed as a distributed computation. This perspective provides the opportunity to investigate whether the computational control principles identified in engineered information processing systems also apply to plant development. Examples of distributed computing underlying plant development are presented, and support the presence of shared mechanisms of information processing across these domains. The co-investigation of computation across plant biology and computer science can provide novel insight into the principles of plant development and suggest novel algorithms for use in distributed computing.

Genetic networks and plant development

The development of plants is intricately linked to their environment [1]. The ability to respond to, remember, and predict the environment enhances adaptive fitness [2, 3]. Constraints in plant motility increase the selective pressures leading to the emergence of these traits.

Plants perceive a wide variety of external signals including gravity, temperature, external gas composition, water abundance, both light quality and intensity, and many others [4]. Receptors and sensory systems have been described at a molecular level for most of these signals, which has been achieved through a combination of genetic screens and biochemical assays [5-8]. While details of these molecular events continue to be uncovered at increasingly greater detail within cells, how they are embedded and operate within the multicellular context of plant organs is only beginning to be understood.

Within complex tissues, different cell types have distinct gene expression profiles [9], conferring both unique identity and function [10]. Examples of individual cell types controlling organ-level responses through the control of hormone responses have been provided, including gibberellin-mediated root elongation [11], root growth towards water [12], and leaf expansion [13]. These examples demonstrate a division of labour in hormone response across cell types, while the functional significance of this compartmentalization is less clear. The impact spatially embedding gene expression programs across the multicellular context of plant organs has on the control of plant development remains a knowledge gap. The mechanisms by which plants process information may only be partially explained by molecular level networks alone.

In this Opinion, the impact of embedding genetic networks into multicellular organs on environmental information processing is examined. By viewing organs as distributed information processing systems, we may begin to understand the relative contribution of genetic and cellular networks in plant development. Experimental evidence supporting the use of this framework is provided, and enables an enhanced understanding of environmental information processing at the cellular level within plant organs.

Environmental information processing and developmental transitions in plants

Behaviour in plants is manifest at the level of morphological and developmental changes [14]. Two of the most important transitions in the plant life cycle include the termination of seed dormancy, and induction of flowering [15, 16]. These determine where and when plants are established, and the time they reproduce, respectively. The timing of these decisions is intricately linked to the environment to optimize plant fitness. Genetic programs that mediate the timing of developmental transitions in response to environmental inputs have been uncovered previously [17, 18]. This detailed understanding of genetically-encoded components and their interactions that underpin environmental information processing has provided a step-change in our understanding of plant development at the molecular scale.

The ability of the constituent cells of plant organs to collectively process environmental information represents an additional level of complexity present in multicellular organisms. To better understand the integrated nature of the organ scale, a computational perspective of information processing in plant organs may be useful. In considering this approach, it is important to note that computers are not limited to the modern incarnation of hardware with which we are most familiar [19], but rather represent a broader class of information processing systems which includes diverse biological media [20].

A computational perspective of plant development

By viewing plants as information processing systems, we can apply the associated formalized language to describe the distinct aspects of this process:

Inputs are the environmental signals that plants perceive from the environment that have relevant developmental consequences.

Outputs can be developmental transitions, such as that from vegetative growth to the commencement of reproduction (flowering), or the termination of seed dormancy and induction of germination. This is a system level property emerging from the collective behaviour of cell populations, as opposed to the activities of individual cells.

The notion of a genetic program is term broadly used in scientific literature (see Glossary). This represents the genetically-encoded molecular components and their interactions that mediate plant development and responses to the environment. In the

context of information processing in this analogy, genetic programs are the ***software*** plants employ. It is at this molecular level within individual cells that we currently have the greatest level of understanding.

In order to run software, a hardware substrate is required. A single cell is sufficient to provide the necessary hardware. In the context of multicellular plants, cells do not operate in isolation, and their ***hardware*** includes the collection of cells that make up organs.

The body plan of the plant organ is therefore the multicellular template upon which molecular processes take place. Algorithms encoded by the genome to perform calculations act within the constraints provided by these cellular templates. Genetically-encoded patterning processes create cell arrangements [21, 22], and are often distinct from those that process environmental information.

Plant organs as distributed information processing systems

An innovation in computational information processing system architecture is that of "distributed computation" [23]. Rather than having a single Central Processing Unit (CPU) perform all calculations, tasks are distributed across a series of interconnected processors that individually perform calculations and communicate their results to one another (Fig. 1a). A common goal and final output is achieved by passing messages, representing the results of their calculations through a process termed "aggregation", enabling the integration of individual computational outputs.

There are several advantages to employing a distributed architecture. This strategy confers robustness to the failure and errors in individual components by having redundancy through a collective population of interconnected communicating processors [19, 23]. Computational capacity is also increased by chaining together multiple identical processors, and aggregating results. This enables the reuse of the same components, removing the need for the creation of novel designs, in order to enhance the abilities of a system.

A further advantage of a distributed architecture is increased computational adaptability. By changing either the rate at which processors communicate their results with one another, or the circuit (structure of their connections) [24], the outputs of the system can

be changed. In this way, the same hardware may be used in different ways to generate a broader spectrum of outputs.

Distributed cellular architectures in plant organs

As in computational systems, information processing in biology also relies on message passing [25]. Many systems in biology process information in a distributed manner at different scales. Individuals in communities can represent the computational units, as in ant colonies [26, 27] or bacterial colonies [28], to perform calculations that collectively optimize the completion of tasks. Within tissues, individual cells may contribute towards the collective processing of information, such as in neuronal systems [29].

Multicellular plant organs can also be viewed as distributed information processing systems [14]. Individual cells act as processors running genetically-encoded programs, and are connected to one another through shared cell walls. Cellular level outputs of these calculations come in the form of developmentally significant signalling molecules (e.g. ions, hormones, peptides, mRNAs, miRNAs, proteins), representing the mobile elements of cellular computation (Fig. 1b). These molecules move to neighbouring cells by cytoplasmic connections named plasmodesmata (PD) [30], through specific transporters, or through the intercellular space, termed the apoplast. This in turn leads to a global output in the form of a developmental transition, and results from the collective computations of individual cells through collective decision-making (See Glossary).

Within an organ, computations therefore take place across different scales, including within cells and across tissues. Outputs from single cells include the developmentally significant mobile molecular agents mentioned above (Fig. 1c), and organ scale computation is the emergent decision to undergo tissue scale transitions (Fig. 1d). Organ scale computation therefore bridges complexity across the molecular and cellular scales.

The advantages conferred to computational systems by distributed architectures also apply to plants. Robustness to failure in organs allows for individual cells failing to perform their function as may happen through herbivory, or defective cellular machinery.

In such instances, plants are still capable of timing their transitions appropriately owing to this redundancy, and the loss of an individual cell is not fatal for the organism.

A lattice-like topology of uniform cellular connectivity most closely satisfies robustness criteria for a spatially constrained system, such as a plant organ [31]. In this configuration, communication between cells across the system is slower due to the absence of shortcuts that facilitate connectivity at a distance. As a result, the robust nature of such a configuration comes at the cost of speed in system-wide information transfer.

An alternative topology may be one where connectivity is non-uniform, leading to the emergence of cells which link many other cells together. In this instance, global communication efficiency is enhanced due to there being fewer steps to be traversed between all cells in an organ, resulting in faster system-wide communication. This enhanced transfer rate comes at the cost of robustness, should those select privileged cells which connect others together undergo a failure. The impact of these contrasting topologies on collective decision-making in plant organs remains unclear.

Additional advantages to a distributed architecture may also translate to plant organs. Enhanced computational capacities are conferred to plant organs by being distributed, and are discussed in more detail below with respect to the timing of both flowering and seed germination.

What does it mean to be distributed as a plant?

Plants make sophisticated calculations to optimize the timing of their developmental transitions in response to the environment. The timescales by which plants make decisions relative to animals are much slower, and on a comparative basis, may favour accuracy over speed. In this regard, robustness is more important than runtime. As a result, plants may not be short of computational capacity, but rather strive towards achieving precision in the optimization of their fitness. In this sense, the lattice-like structure of their organs conferring robustness at the cost of speed is well suited to this class of organism.

Conversely, the ability to transform complex inputs into meaningful outputs, such as the use of variable temperatures to stimulate flowering [32] and the breaking of seed

dormancy [33], provide additional adaptive advantages. Increasing computational capacities in plants therefore lend themselves to enhanced adaptive fitness and the colonization of novel niches.

Beyond this teleological explanation, there are additional advantages to being distributed as a plant on a macro scale. If an entire organ is eliminated due to mechanical or biotic stress, the plant can continue to function. In turn having additional cells provides additional functional redundancy using the information processing framework described.

Cellular level distributed computation in plants

Our understanding of the spatial distribution of genetic programs across plant organs has been enhanced by recent advances in imaging [34, 35] and computational image analysis [36]. This has enabled global single cell analyses of organ-scale cell architecture, and the simultaneous quantification of genetic programs within individual cells [37]. In this way the spatial distribution and abundance of genetically encoded components can be quantified in individual cells across whole organs, providing key insight into the spatial embedding of information processing components.

A role for distributed design in the control of whole plant behaviour has been considered previously [1, 38]. Below we examine information processing at the cellular level using this architecture.

Distributed control of optimized gas exchange in leaves

Decision-making typically involves minimizing the impact of trade-offs to optimize the timing of choices. In the case of the control of gas exchange in leaves, an optimization between the exchange of CO_2 and loss of water is managed through the control of stomatal aperture [39]. A challenge in this regard is the co-ordination of the populations of stomata present across an individual leaf. In a seminal study, the co-ordinated spatial behaviour of stomatal opening was investigated in cocklebur (*Xanthium strumarium*) [40]. Patchy sectors of stomatal behavior was observed across the surface of the leaf in this species, and likened to a distributed computation. In this regard, localized co-

ordination gave rise to a population level behavior in patches of cells (Figure 2a). The nature of the mobile aggregation agent in this example remains unknown.

Optimization in plant decision-making

Two major decisions in the life cycle of plants include the developmental transitions of the breaking of seed dormancy and induction of flowering [15]. In both cases, an optimization trading off a balance between speed and accuracy takes place. Being too slow to transition runs the risk of missing out on favourable environmental conditions and being outcompeted, while transitioning too early may lead to compromised individual fitness in unfavourable conditions. In the context of animal behaviour, this speed accuracy trade-off is referred to as Fitts Law [41].

In the face of variable environmental conditions, optimizing this tradeoff becomes increasingly challenging. Distributed cellular architectures are used in both the control of flowering and seed dormancy to optimize the timing of these decisions, as outlined below.

Distributed control of flowering time in response to cold

The induction of flowering in many species is initiated by sustained periods of low temperature, a process termed vernalization. The control of cold-induced flowering in arabidopsis (*Arabidopsis thaliana*) is principally controlled by the repressor gene *FLOWERING LOCUS C* (*FLC*) through temperature-mediated epigenetic silencing [3, 42]. Following a critical period of cold, a stable and mitotically heritable silencing occurs, providing memory storage in this system.

Microscopic examination of the spatial distribution of *FLC*-silenced cells in response to cold revealed an all-or-nothing pattern of *FLC* promoter activity in individual cells [42, 43] (Figure 2b). Each cell is therefore performing a “digital” registration of cold through their chromatin state. In the context of an organ, this series of integrated distributed switches provides the possibility for rich behaviours, including both a temperature averaging mechanism and system robustness, thus increasing the computational capacity of the system. The mechanism by which the aggregation step is performed has yet to be demonstrated, and represents a calculation known as the majority problem,

whereby rules that recognize the state of the majority are invoked [44]. This algorithm in plants may include a critical message passing algorithm or a spatial averaging mechanism. Mobile genetic elements controlling flowering time have been described previously including *FLOWERING LOCUS T* [45], and provide a plausible mobile agent mediating this aggregation step.

The use of a single bit epigenetic encoding mechanism represents a minimization of information content in this system. This removes the need for the production of complex molecules and the need to discriminate between their molecular concentrations, such as in thresholding mechanisms [46]. The use of such simplified messages therefore results in a reduction of energy cost to perform this computation.

Distributed computation of alternating temperatures in the control of seed dormancy

The breaking of seed dormancy determines where and when plants are established [47]. Like in the case of flowering, the input of low temperatures lead to an output in the form of the breaking of seed dormancy [48]. The antagonistically acting hormones abscisic acid (ABA) and gibberellic acid (GA) underpin the decision to germinate [49], and is proposed to follow a ratio-based thresholding mechanism [46, 50].

Microscopic examination of the signaling components for each of these hormones revealed they are enriched within the cells of the dormant embryo radicle [33]. Responses to ABA and GA were however not found to be manifest in the same cells, but did overlap with the synthesis and degradation genes for each of these hormone metabolic pathways. This represents a distributed architecture whereby spatially separated response centres control hormone abundance through their feedback onto hormone metabolism gene expression, and communicate by hormone movement (Figure 2c).

The presence of mutually inhibiting, spatially separated response centres is also present in human motor movement decision-making in the form of the basal ganglia-cerebellum-cortex loop [51, 52]. Here it is thought that the spatial separation introduces a time delay, enabling noisy inputs to be filtered and optimizing decision-making.

While this topological configuration is shared between both *Arabidopsis* seeds and the human brain, seeds do not filter noise from variable temperature inputs, but preferentially utilize them [53]. The spatial separation of hormone response centres is required in order for this processing of alternating temperatures to occur [33], demonstrating the need for the distribution of genetic components across the embryo body plan to perform this computation. The spatial embedding of this genetic program across the body plan of the dormant embryo therefore increases the computational capacity of a dormant *Arabidopsis* seed.

Recent work has also demonstrated that flowering time is also stimulated by alternating temperatures [32]. In light of there being greater daily fluctuations in daily temperature in the autumn and spring, this temperature processing mechanism may provide a means of predicting the onset of changing seasons.

Connectionist approaches to information processing

The cells that make up plant organs provide the multicellular templates upon which information from the environment is processed. Genetically-encoded patterning processes lead to the construction of these cellular arrangements that shape and constrain organ function following structure-function relationships [54].

With a view of a plant organ as a distributed information processing system, the way in which cells are organized and communicate represents the multicellular circuitry of information processing.

Networks are a useful means of abstraction, providing a discrete methodology to understand how interactions between components give rise to system-wide properties and behaviours [55]. Mapping networks of cells with a view to understanding information processing has been performed previously in the *C. elegans* nervous system [56] with a view to understanding the information processing capacity of the nervous system in this worm. The topological analysis of this “connectome” of interacting neurons has provided functional insight into the role of individual cells [57, 58].

Unlike animals, plants lack a nervous systems, but still perform computations using the cells which make up their organs [59]. Understanding global cellular connectivity in plants therefore provides the opportunity to understand the principles of communication

and computation within these organs. Information is aggregated across an organ following the body plan, making cellular patterning analogous to a circuit. Mapping cellular connectivity following connectionist approaches therefore provides wiring diagrams of potential molecular information exchange across plant organs [60].

The use of measures that identify optimized routes of information flow across cellular interaction networks based on traversing shortest paths was sufficient to predict the bulk flow of small molecules at single cell resolution in the *Arabidopsis* hypocotyl [61]. Specifically, the atrichoblast epidermal cell type lies upon shorter paths then their neighbouring trichoblast cells, and preferentially transports small molecules [62]. The use of a connectome in plant organs is therefore capable of predicting global intercellular communication, and function, at single cell resolution. While the relationship between cell organization and information processing remains poorly understood, this provides a discrete framework to further investigate these relationships.

Intercellular communication dynamics and information processing

In light of intercellular interaction and communication underpinning distributed computation in plant organs, understanding the topology of these arrangements is central to revealing the control of their computations. Due to the combination of the constraints of mechanics and cellular packing, topological complexity in plant organs constrained, and lattice-like in nature. This is in stark contrast to that of neurons, which are highly branched and elongated cells that are not subject to these impediments. Resulting from this are long tailed distributions of the number of neighbours cells have in the nervous system, which are not observed in plant organ connectomes (Figure 3a).

While cells within plant organs cannot move with respect to one another, they do have the ability to change whether or not they communicate. The two principal ways in which plant cells communicate is through transporters, and PD [63]. Transporters can be present or absent, active or inactive, providing a controllable means of intercellular communication. PD can also modulate cell-to-cell communication by modulating their aperture and distribution [64, 65].

PD aperture is dynamically controlled across plant development and in response to biotic and abiotic stresses [66, 67]. These dynamic changes in functional cellular

connectivity result in alterations to the cellular circuitry of the organ (Figure 3b). In light of the limited topologies plants can generate in the creation of their organs, this provides a means of topologically rewiring intercellular circuitry to dynamically generate new topologies and novel potential information processing circuits, transcending the constraints imposed by cellular topology.

This is analogous to specialized distributed computational circuits called Field-Programmable Gate Arrays (FPGAs) [68]. These distributed circuits can be dynamically re-configured to perform specialized tasks on demand, and are used by exploratory satellites due to the extended time scales of their lifetimes and unpredictability of the calculations that may need to be performed once released.

Preliminary evidence for plant organs implementing a similar mechanism as FPGAs to facilitate an increased palette of responses to the environment has been reported previously. In the shoot apical meristem (SAM) from both birch and poplar, low temperatures have been reported to promote PD opening [66, 67]. Subgroups of cells in the *Arabidopsis* SAM are also symplastically linked together following day length-mediated flowering signals, leading to the formation of symplastic domains [69]. A functional role for the reorganization of cellular connectivity in the SAM remains unclear [70]. A recent study demonstrated a PD-mediated gating mechanism controlling ABA-mediated photoperiodic induction of the SAM in hybrid aspen trees [71]. In this example, closed PD block growth-promoting signals until the decision to break bud dormancy is reached, demonstrating a role for intercellular communication in environmental information processing.

PD aperture dynamics may increase computational complexity, and therefore, adaptability in plants following the principles of distributed computation.

The second way distributed systems can change outputs is by altering the aggregation rate. This can also be achieved by altering transporter abundance or activity, or PD aperture and abundance. Evidence that an aggregation rate can impact the timing of outputs in plants is provided by the study of *Arabidopsis* seed dormancy. Increasing the rate which the ABA and GA response centres communicate by overexpressing the ABA/GA transporter *NPF3* [72] made seeds more sensitive to alternating cold and warm temperatures [33].

A role for aggregation rates impacting outputs in biological systems has also been demonstrated using red harvester ants, where the rate at which workers interact impacts decision-making with regards to which task an individual performs [73]. This control principle of engineered distributed computation is therefore transferrable to multiple biological contexts, enabling the modification of the timing of biological outputs simply by modulating communication rates and not the underlying program.

PD may be capable of achieving both modes of altering organ scale outputs. The abundance and aperture of these pores can modulate both aggregation rates and the symplastic topology of the organ.

Collective decision-making in plant organs

In plants, a single specialized master cell does not make decisions on behalf of the rest of an organ [14, 59]. Organ-scale decision-making occurs in a distributed fashion, and emerges from the collective states of individual cells (see Collective decision-making, Glossary).

The application of the control principles of distributed computation lends itself nicely to better understanding how collective decision-making may occur in plants. Individual cells that make up plant organs perform calculations in a largely asynchronous manner, such as in the case of *FLC* cold registration (Figure 2b). A singular collective decision to commence flowering is thought to be reached when a critical number of cells have *FLC* silenced [43]. Given that all cells are not synchronized, and are reaching the end of their computation at different times (the silencing of *FLC*), a gap between cellular and organ scales needs to be bridged in order for flowering to be induced. The algorithm that is employed to solve this majority voting problem in the SAM has not yet been identified.

The field of biologically-inspired computation makes use of algorithms identified in natural systems to solve problems in the technological domain [24]. Examples of this include the development of anti-virus software based on non-self-recognition principles from the human immune system [74], ant colony behaviour to optimize business [75] and an algorithm used by *Drosophila* to categorize smells to perform similarity searches [76]. Understanding the algorithms utilized by plants in collective decision-making may

prove useful in the computer science domain, especially in light of the asynchronous nature of these computations [77].

Concluding remarks

Understanding the principles of computation in the context of multicellular plant organs addresses a gap in understanding how molecular interactions scale up to adaptive behaviours in complex organisms (see Outstanding Questions). A distributed computation perspective of plant development further enables biological researchers to engage with the expanding field of computation in biology [78]. Plants are a very well suited system to investigate and engineer multicellular distributed computation in light of cellular immobility and the ability to manipulate individual cell types. Collectively this may lead to the identification of novel algorithms for use in the computational domain using biology-inspired designs [79]. This perspective can also lead to the development of the next generation of crop species with enhanced environmental response and predictive capacities. Knowledge gaps as to how cellular organization and communication influences the outputs of genetic programs need to be filled before these complex multicellular systems can be reliably and predictably reprogrammed.

Finally, while statements regarding the “intelligence” of plants remain difficult to make, information processing provides a well-defined and quantifiable field that is generalizable across diverse domains, ranging from plant biology to computer science.

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FIGURE LEGENDS

Figure 1. Comparison of distributed computing architectures in (a) engineered information processing systems, and (b) multicellular plant tissue. (a) In a computational configuration, the outputs of computation from individual processors are communicated to other processors as indicated by arrows. (b) In plant tissue, small molecules which are generated as the outputs of cellular computation are moved to neighbouring cells, and in turn influencing their cellular activity. (c) Schematic illustrating single cell computation and the molecular nature of the outputs. (d) Schematic of organ scale computation and the output of a developmental transition following collective decision-making.

Figure 2. Examples of distributed computations in plant organs. (a) Co-ordinated activity of stomata aperture across a lead surface. Schematic illustrates changes in the distribution of chlorophyll fluorescence over time with red showing increased and green decreased signal, indicative of stomatal aperture. Based on [40]. (b) Digital registration of cold in the cells of the *Arabidopsis* SAM. The grid represents cells in the SAM and the presence of a blue dot the activity of the *FLC* promoter. Following cold exposure, individual cells either do or do not have promoter activity. Based on [43]. (c) Optical section of a dormant *Arabidopsis* embryo indicated the separate cellular locations of ABA and GA responses. Arrows indicate the movement of both hormones between response centres. Based on [33].

Figure 3. Topological features of multicellular assemblies. (a) Comparison of the relative distribution of degree (number of neighbours a cell has) in each an *Arabidopsis* hypocotyl [61] and the *C. elegans* nervous system [56]. (b) Schematic illustrating dynamics topological rearrangements in a plant organ. Nodes represent cells and blue edges physical associations between cells that are communicating. Grey edges highlight regions of the tissue that are topological isolated from other cells, such as in the context of symplastic domains.

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