CellPress
OPEN ACCESS

Trends in
Plant Science

Opinion

Toward uncovering an operating system in plant organs

Gwendolyn V. Davis[1], Tatiana de Souza Moraes[2], Swanand Khanapurkar[3,4], Hannah Dromiack[3,4], Zaki Ahmad[1], Emmanuelle M. Bayer[2], Rishikesh P. Bhalerao[5], Sara I. Walker[3,4,6], and George W. Bassel[1,*]

Molecular motifs can explain information processing within single cells, while how assemblies of cells collectively achieve this remains less well understood. Plant fitness and survival depend upon robust and accurate decision-making in their decentralised multicellular organ systems. Mobile agents, including hormones, metabolites, and RNAs, have a central role in coordinating multicellular collective decision-making, yet mechanisms describing how cell–cell communication scales to organ-level transitions is poorly understood. Here, we explore how unified outputs may emerge in plant organs by distributed information processing across different scales and using different modalities. Mathematical and computational representations of these events are also explored toward understanding how these events take place and are leveraged to manipulate plant development in response to the environment.

Highlights

Tissue-scale multicellular information processing in plants remains poorly understood.

Universal principles of distributed information processing can be applied to plant tissues.

Modelling approaches, including cellular automata and Boolean networks, can be used to understand plant tissue behaviour.

The algorithmic nature of information processing in plants merits further investigation.

Information processing

In a continually changing environment, organisms can make decisions to change their state to enhance their fitness [1]. In the case of plants, these decisions come about in the form of critical developmental transitions, such as flowering, the release from seed dormancy, and the breaking of bud dormancy [2]. The ability to make these decisions in an accurate and robust manner is central to the survival of individuals [3].

An extensive understanding of molecular-scale signalling in plant cells has emerged from decades of genetics research, providing important insight into how cells reach decisions [4–6]. In the case of multicellular organisms, it is not individual cells but rather the collective behaviour of communities of cells that underpin organism fitness [7]. Therefore, the constituent cells of a tissue must act in a coherent manner to fulfil the higher order function of the organ and organism.

While cellular decision-making in plant tissues takes place within individual cells, these decisions are communicated to neighbouring cells through a range of signalling molecules [8]. In this way, the individual decisions that cells make can be coordinated at the organ scale. An example of this is developmental phase transitions (i.e., transition to flowering), which are tissue-scale events mediated by the collective decision of many cells acting together. These processes are distinct from the morphogenetic processes, which lead to the construction of cellular patterning and organ formation [9–11], in that they represent how information is processed within organs after they have been fully formed.

However, the way this is achieved in plants is not well understood; thus, in this opinion piece, we highlight and address this gap in our knowledge and propose ways in which such decision-making might occur.

[1]School of Life Sciences, University of Warwick, Coventry, CV4 7AL, UK
[2]University of Bordeaux, CNRS, Laboratoire de Biogenèse Membranaire, UMR 5200, F-33140 Villenave d'Ornon, France
[3]ASU-SFI Center for Biosocial Complex Systems, Arizona State University, Tempe, AZ 85287, USA
[4]Beyond Center for Fundamental Concepts in Science, Arizona State University, Tempe, AZ 85287, USA
[5]Umeå Plant Science Center, Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, 90183 Umeå, Sweden
[6]School of Earth and Space Exploration, Arizona State University, Tempe, AZ 85287, USA

*Correspondence:
george.bassel@warwick.ac.uk
(G.W. Bassel).

Trends in Plant Science, July 2024, Vol. 29, No. 7 https://doi.org/10.1016/j.tplants.2023.11.006

The problem of decision-making in plants

Plants lack specialised cells, exemplified by the nervous system in animals, that implement centralised control in decision-making. For example, a single cell in a shoot apical meristem (SAM) cannot decide along for the apex to undergo the decision to transition to flower; instead, this is a collective decision between all constituent cells (Figure 1). Therefore, plants have a ‘decentralised’ or ‘distributed’ information-processing architecture [12,13]. How collective decisions can be reached without a **centralised decision-making system** (see Glossary) has been explored in diverse biological systems, but how this is achieved in the cells of plant organs remains less clear.

A computational perspective of information processing in plants

Approaching the question as to how organ-scale information processing and collective emergent decision-making takes place in multicellular plants may benefit from examining other systems in which similar processes occur. One such example is distributed microprocessor-based computing. Although plants are not computers and do not conduct ‘computation’, the potential to understand collective multicellular information processes may be derived from such a comparison.

The nature of inputs and outputs are well defined in computers, and analogous features can be applied to plants. In plants, inputs represent signals from the environment, which are processed and turned into outputs in the form of developmental transitions. It is in the mature structures of plant organs that environmental signals containing relevant information are perceived and processed. The perception and processing of these signals occurs within individual cells across

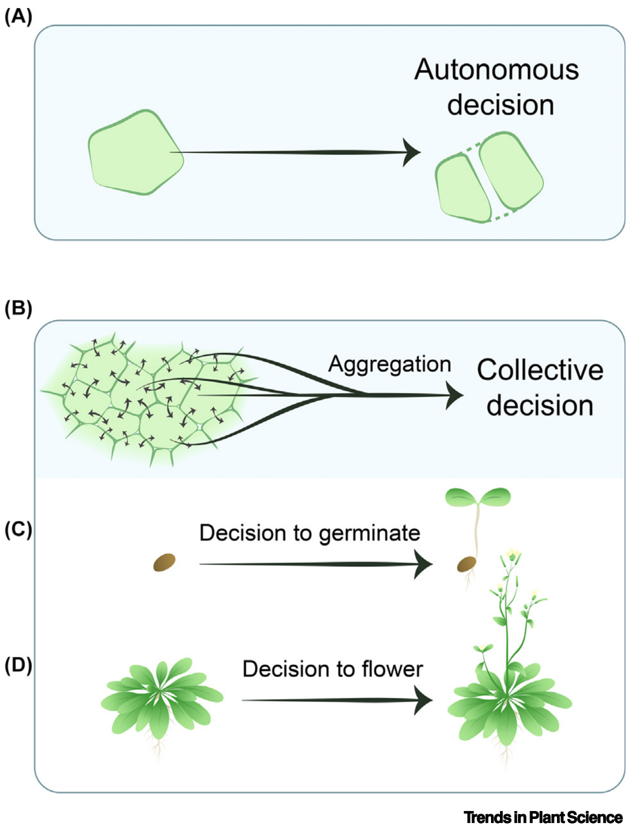


Figure 1. Individual versus collective decision-making in single cells and tissues. (A) A unicellular plant making an autonomous decision, in this example to divide. (B) The collective communication between plant cells in a tissue performing aggregation of mobile information agents leading to a singular collective decision. (C) Collective decision of cells in a seed to break dormancy and germinate. (D) Collective decision of cells in the stem apical meristem (SAM) of a vegetative plant to transition from the vegetative to flowering state.

Glossary

Aggregation: process of integrating the mobile outputs of individual cells in a tissue toward reaching a unified output.

Asynchronous: where the cells in a system do not need to interact with one another at regular intervals or rely upon each other’s existence to function.

Boolean network: modelling framework whereby agents and interactions exist in Boolean states (1 or 0) and follow defined interaction rules.

Cellular Automata (CA): distributed information processing model containing cells in defined states and local interaction rules, which change cell states based on their neighbours during iterative updates.

Centralised decision-making system: system whereby decisions are reached by a single individual leader.

Collective decision-making: process whereby a community of cells each having individual states comes together to generate a single unified state, or decision.

Consensus: agreed final state resulting from the collective information-processing tasks of the cells in a plant tissue.

Decentralised biological system: system whereby no leader is present, and decisions are reached collectively by constituents of the community.

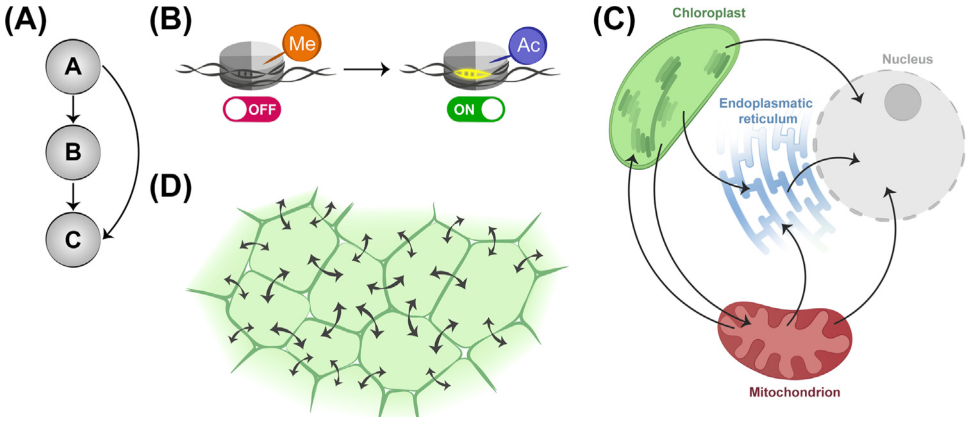


Figure 2. Information processing across different scales. (A) A feed-forward loop motif encoded by a gene regulatory network. (B) Epigenetic marks impacting gene expression. (C) Intracellular communication between organelles in plant cells, illustrating retrograde signalling between the endoplasmic reticulum, mitochondria, chloroplasts, and nucleus. (D) Tissue-scale communication between cells.

a range of scales (Figure 2). However, the distributed nature of multicellular tissues points to the fact that the cells must coordinate toward reaching a unified collective decision to undergo a developmental transition and collective change in cell identity at the organ scale.

Similarly, distributed computing architectures involve the use of multiple processors, which individually perform operations and communicate their outputs to neighbouring processors toward reaching a unified **consensus** output. It is this architecture, which is also widely shared by a range of biological systems, that we explore here in an analogous manner.

Scales of information processing in plants

To explore how decisions in the multicellular organs of plant emerge, the range of scales across which information is processed can be considered (Figure 2), as described below.

Molecular-scale information processing

Within a cell, information is processed across a host of molecular interactions between different classes of molecule. These include gene regulatory networks (GRNs) (protein–DNA interactions) [14,15], biochemical reactions (protein–metabolite–lipid interactions), and chromatin modifications [16] (Figure 2A,B). These small-scale interactions have the capacity to perform logical operations, including AND, NOR, and XOR logic gates [15–18], providing a means to process information and regulate both cellular function and cellular decision-making [19].

Intracellular information processing

Membrane-bound organelles within plant cells can perform distinct functions by acting as discrete compartments, which sequester biochemical and signalling processes. Cellular homeostasis emerges from the function, activity, and interaction between these compartments (Figure 2C). Given their abundance in plant cells, their functions and interactions may also be considered a scale at which distributed information processing takes place. Examples of intraorganelle interactions in plants include the exchange of molecules between mitochondria [20], between chloroplasts via stromules [21], and across different organelles through retrograde signalling [22].

Tissue-scale information processing

The multicellular nature of plant organs makes tissue-scale information processing an emergent property arising from the collective behaviour of individual cell activities [23]. This can be likened to a parallel distributed computation, whereby processes in individual cells reach decisions that lead to the generation of mobile molecular agents, which are communicated to, and influence, neighbouring cells through cell–cell communication (Figure 2D) [13]. In this way, the activities of individual cells are coupled and can lead to a unified organ-scale decision through cell communication.

Classification of information processing in plant organs

To classify the distributed information processing that occurs in multicellular plant organs, a series of classifications and categorisations as to its properties can be applied.

Asynchronous

The biomolecular processes that occur in the individual cells of plant tissues are unlikely to be synchronised (i.e., is **asynchronous**). This is a consequence of the absence of a central regulatory system temporally coordinating molecular activities within individual cells. The circadian clock provides a potential route to the coordination of molecular activities within cells, while the period of this oscillating genetic network has been shown to exhibit heterogeneity across the cells of arabidopsis (*Arabidopsis thaliana*) seedlings [24]. Theoretical work has demonstrated that synchronisation in a distributed computing system is neither essential nor obligatory [25], supporting the plausibility of uncoordinated cellular activity in plants, while reconciling their ability to perform robust decision-making in the absence of this property.

Collective behaviour

The cells within plant tissues are clonal and genetically identical, making their interests aligned and cellular behaviour cooperative as opposed to being competitive. Given these clonal relationships, overlapping interests take precedence over individual cell defectors. Therefore, a bias toward collective behaviour, over individual behaviour, is likely occurring (Figure 1).

Accuracy is favoured over speed

A central trade-off in decision-making is that of speed versus accuracy, as defined by Fitt's Law [26]. A seed that germinates too early in the spring can die from exposure to frost, while germinating too late can lead to being shaded out by competing plants. In light of the timescales across which plants develop, and the largely irreversible nature of the decisions they take, decision-making is likely skewed toward accuracy over speed to support maximal fitness [13]. This skew toward accuracy manifests as different levels of information processing in plant tissues occurring at different timescale, such as in the information processing performed by gene networks within a cell, which occur on a different timescale compared with tissue-level decision-making (Figure 1). The contribution of information processing at different scales toward robust decision-making in plants remains unclear.

Distributed architectures in nature

Distributed decision-making architectures are widespread across living systems. Such systems are found in bacteria, eusocial insects, and group behaviours in animals. Principles of distributed decision-making architectures could also be applied to plants, where the individuals involved in the collective decisions are the individual cells forming a tissue.

Physical states of communities and their impact on information processing

Communities of entities that perform distributed information processing can be viewed as a range of physical states based on their physical state or 'fluidity', referring to the capacity of individuals to interact with other members of the collective within a given context. A spectrum ranging from ‘liquid’ to ‘solid’ states has been proposed [27]. A liquid state refers to a system where the individual agents (cells or individuals) can move freely and interact with any other individual in their community. On the opposite end of the spectrum is a solid state, where agents are locked into place and can only interact with their immediate neighbours.

Examples of ‘liquid’ states include social insect, bird, and fish communities. These individual agents within the collective have the potential to move about and exchange information with all other members by crossing local boundaries, increasing the exchange of information.

By contrast, other systems where individual agents are fixed in place can be considered as existing in a solid state. Plants represent one such system because their cells are stationary within their organs and are fixed to one another through shared cell walls [2]. This architectural limitation, coupled with mechanical constraints of plant cell shape, makes plant organs both ‘solid’ and topologically restricted. The number of neighbouring cells they can communicate and exchange information with is fixed.

Quorum sensing as a means of collective decision-making

One means by which **decentralised biological systems** can reach decisions is through quorum sensing. This describes a process of communication between individuals that allows the sharing of information regarding the density of their population [28]. Extracellular signalling molecules known as autoinducers are produced by individuals at a constant rate, leading to concentrations of these molecules acting as proxies for population density through their detection by other members of the community [29].

Collective behaviours, such as biofilm formation in bacteria, can be triggered when threshold autoinducer concentrations are reached [30]. Quorum sensing can also be used by social insects to decide where to nest, such as in the ant *Temnothorax rugatulus* [31].

Evidence for quorum sensing with populations of plant cells toward **collective decision-making** has yet to be demonstrated. A feed-forward mechanism in the production and transport of the hormone auxin has been proposed as a means to generate new organs [32], suggesting that similar feed-forward thresholding mechanisms have a role in the decision to undergo developmental transitions [33].

However, the way in which quorum sensing works in a plant tissue would be different from a social insect or bacterium owing to the solid state of plant cells versus the liquid states of the insect or bacterial systems. While autoinducers can be released in a liquid system and encountered by agents as they move, they would need to pass from one cell to the next in a solid-state plant organ, resulting in a different form of signal propagation.

Reaching consensus and emergent decision-making

The production of a unified output, or ‘consensus’, in distributed computing is achieved through **aggregation** using an algorithm. The question of how this is achieved in multicellular plant organs remains and underpins the final step implemented by plants to undergo developmental transitions.

In the discussion section describing mathematical models of collective multicellular information processing, we provide plausible approaches that could describe how groups of plant cells reach a unified output and this collective emergent decision.

Mobile molecular elements in plant tissues

A diversity of developmentally instructive mobile molecules has been described to have a role in the previously described information processes in plants [8,34,35]. Phytohormones represent a well-characterised class of such molecules, having established roles in almost all aspects of plant development, and being capable of both short- and long-distance transport [8]. Metabolites, including sugars, would also fit this description, given their capacity to move and impact cellular activity [36]. Ions, including Ca^{2+}, provide another fast-moving means of coordinating cellular behaviour at the tissue and organism scale [37].

Whole proteins and peptides are also capable of being transported between cells to facilitate the processing of inputs from the environment. FLOWERING LOCUS T (FT) is a well-characterised example of this, having a role in the control of both flowering time and bud dormancy [38,39]. Both mRNA and miRNA have been demonstrated to move between plant cells, potentially having a role in tissue-scale information processing [34].

Cell–cell communication in plants

Communication between plant cells occurs through a variety of means, including through membrane-bound transporters, the extracellular space between cells termed the apoplast, and through specialised cytoplasmic channels called plasmodesmata [40] (Figure 3). Plasmodesmata are crucial to communication between cells by allowing molecules, including hormones, peptides, proteins, mRNAs, and miRNAs, to pass between neighbouring cells [41].

The connectivity between cells via plasmodesmata is dynamic, whereby these pores open and close across development and in response to environmental signals [42]. It has been proposed that the neck of the plasmodesmata at the cell wall may be narrowed by the deposition of callose (1,3-β-glucan) in the cell wall adjacent to the opening of the pore through the activity of callose synthase [41,43]. The opening of the pore can be conversely stimulated by the activity of β-1,3-glucanase callose-degrading enzymes.

The dynamic connectivity afforded by the opening and closing of plasmodesmata impacts collective intercellular communication within plant tissues [44–46]. Considering the requirement for cell–cell communication in organ collective decision-making, the modulation of cell connectivity

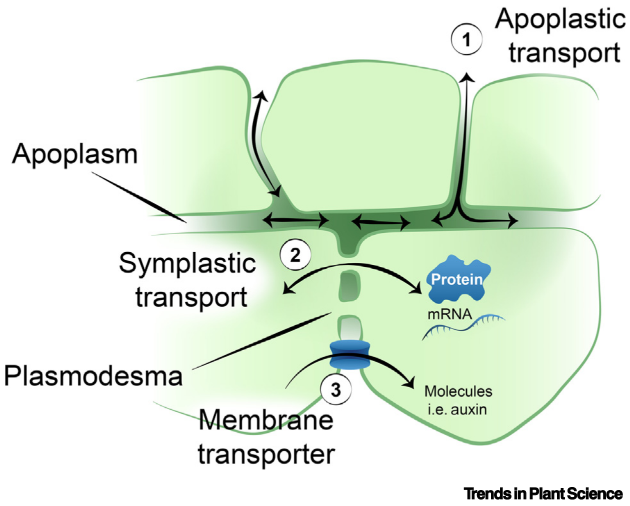


Figure 3. Modes of cellular communication in plant tissues. Apoplastic transport (1) represents the movement of molecules in the space outside of, and between, plant cells. Symplastic transport (2) occurs between cells through the cytoplasmic connections provided by plasmodesmata. Molecular movement between cells (3) can also be mediated by membrane-bound transporters.

through the dynamic gating of plasmodesmata aperture may represent an axis to modulate the processing of environmental information.

Modelling approaches to understand tissue-scale information processing in plants organs

Our understanding of collective emergent decision-making in plant organs remains rudimentary. The algorithmic processes invoked by plant cells to reach unified decisions have yet to be uncovered. The modelling approaches discussed in the following sections in conjunction with experimental parameterisation provide a path toward understanding how this emergent phenomenon occurs.

Modelling collective computation in plants using Cellular Automata

To investigate questions surrounding multicellular information processing in plants, it helps to have a model system that mirrors the 'solid' architecture of these tissues [27]. A class of mathematical models known as **Cellular Automata (CA)** provides such an information-processing framework (Figure 4). CA capture how information is processed in systems with constrained topological interactions following simple local interaction rules [47], as the cells within plant tissues follow.

CA are discrete dynamical systems comprising a collection of abstracted 'cells' arranged on a matrix of a specified size and shape [47]. Each cell can take on one of two possible states, visually depicted as a black or white square, or computationally by '1' or '0' (Figure 4). Each CA is described by a rule, or mathematical function, which defines the state of each cell according to the current state of itself, and the cells in its local neighbourhood. Despite the relative simplicity of CA, they can perform remarkably complex information-processing tasks, which emerge from a relatively simple set of interaction rules between agents. Thus, CA could be a useful modelling approach for understanding decision-making and transitions within a plant tissue in a decentralised manner.

The cells in a CA can represent cellular states within a plant tissue. For example, by assigning a '0' if the cell is not expressing a critical gene, and '1' if it is expressed. Evidence of a cell impacting the state of its neighbour in plant organs has been provided in the context of pattering and cell identity [48], making the updating of cell states based on neighbour states in a CA a plausible information-processing mechanism in plants.

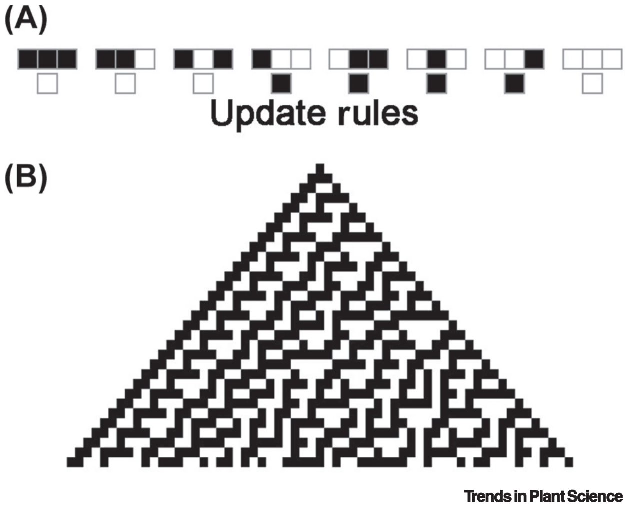


Figure 4. Example of a Cellular Automata (CA) simulation. (A) Update rules by which cell states are changed based on the state of their neighbours. The initial state of a given cell and its two neighbours are shown on the top row, and the resulting state of the middle cell is indicated below. (B) Progressive evolution of cell states moving downward, with each new line representing a time step. The passage of time (down) and the updating of cell states is based on the rule set defined at the top of the figure. Changing these local rule sets in turn impacts the outputs of the CA.

A pertinent example of a CA-based computation for plants is majority voting. This computation determines which state the majority of the cells in a CA are in [49]. This ability to calculate a majority in cellular state provides a potential mechanism toward tissue-scale decision-making in situations where gene expression is progressively regulated in response to environmental inputs [50].

Modelling tissue computation using Boolean networks

A class of models related to CA are **Boolean networks** (BNs) [51]. Here, a network of interactions can be represented graphically in terms of nodes connected by edges. In a BN, those nodes have associated to them a Boolean logic function, which takes as its inputs '0' and '1', and outputs a '0' or '1' as the new state of the node.

BNs have been used previously in plants, particularly to model attractor dynamics in GRNs [52,53]. Models describing the behaviour of stomata guard cells in leaves, which mediate gas exchange in plants, have been described [54]. These have the potential to be extended toward understanding the relationship between GRNs and their embedding within the multicellular context of plant tissues.

Information processing in plant organs

Complex temperature information processing and the control of seed dormancy

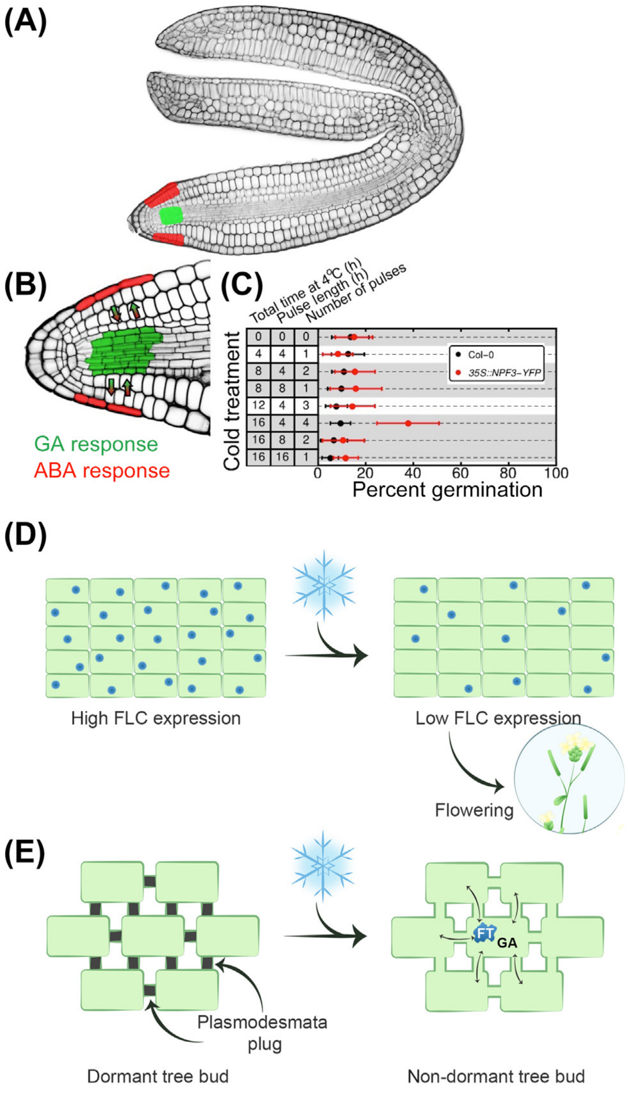
Seeds are how plants move through both time and space, supported by the adaptive trait of dormancy [55]. This is established during development on the mother plant, and is regulated internally by an antagonistic relationship between the hormones abscisic acid (ABA) and gibberellic acid (GA) [56]. The nongerminating dormant state is promoted by ABA. The perception of favourable environmental signals leads to degradation of this hormone and production of the germination-promoting hormone GA [57].

A key environmental input in the control of seed dormancy is temperature. Low temperature breaks dormancy in the seeds of many temperate plant species, signalling the passage of winter. Rather than performing a simple linear accumulation of cold toward the breaking of seed dormancy, seeds perform more complex processing of temperature inputs, showing a preference for alternating warm and cold temperatures [58]. These complex temperature signatures are indicative of spring weather where daily temperatures show greater variability than during the winter [59], helping to promote the timing of germination to these seasons.

The mechanism by which alternating temperatures are processed in seeds was shown to be linked to a decision-making centre in the root tip of the dormant arabidopsis embryo [60] (Figure 5A). Within this tissue, ABA and GA signalling components are enriched in distinct cell types (Figure 5B). This spatial separation enables the processing of alternating temperature inputs to be performed. The rate at which the ABA and GA cells communicate (the aggregation rate) further impacts how seeds use alternating temperatures (Figure 5C). Distributed hormone responses in different cell types of dormant seeds facilitate the harnessing of alternating warm and cold temperatures to break dormancy, representing information processing using a decentralised architecture in plants.

Temperature processing in the control of vernalisation

Vernalisation is the process whereby plants use low temperature, a proxy for the passage of winter, to time the transition from the vegetative state to flowering. A key component of the vernalisation regulatory network is the repressor gene *FLOWERING LOCUS C* (*FLC*) [61]. During cold weather, *FLC* expression in individual cells is epigenetically silenced in an all-or-nothing manner, leading to increased *FLC* silencing as a function of time spent in the cold [50]. This in turn promotes the expression of *FT*, a positive regulator of flowering, in leaves when plants are



Trends in Plant Science

Figure 5. Examples of distributed information processing in plant organs. (A) Control of the decision to break seed dormancy by separate subpopulations of cells in the embryo radicle, which respond to the hormones abscisic acid (ABA) and gibberellic acid (GA), respectively. (B) Movement of ABA and GA between these signalling centres modulates the decision to break dormancy. (C) Altering the rate at which hormones are transported in the *35S::NPF3-YFP* line makes seeds more sensitive to alternating temperatures toward dormancy break [60]. (D) Registration of cold in individual cells through silencing of *FLOWERING LOCUS C* (*FLC*). Progressive exposure to cold leads to all-or-nothing *FLC* expression in individual cells, resulting in a collective emergent decision to transition to flowering. (E) Tissue-scale events underlying the breaking of bud dormancy in hybrid aspen trees. Dormant buds have their plasmodesmata closed. In response to cold, these plasmodesmata open and the hormone GA and FLOWERING LOCUS T (FT) are produced and transported from cell to cell.

exposed to warmer temperatures. The mobile FT protein then moves into the SAM, promoting its transition to flowering.

FLC silencing occurs at an increased rate under fluctuating temperature profile as supposed to constant temperature [59], suggesting complex temperature processing tasks to control both the time to flower and to break seed dormancy. The molecular mechanisms underpinning *FLC* silencing in a single cell are well understood. At the tissue level, the mobile protein FT can silence *FLC* through promotion of the antisense RNA *COOLAIR* [62]. The all-or-nothing nature of the expression of this gene and its coupling to FT movement lends this system to modelling using CA to understand how cellular processes impact tissue-level outputs through local communication (Figure 5D).

Questions related to the collective decision within the cells of the SAM to transition to flower in response to the entry of FT also remain unclear. Dynamic closing and opening of plasmodesmata in the SAM during floral transition have been demonstrated using fluorescent dyes [42], while the functional significance of these intercellular dynamics remains unclear. The possibility remains that the dynamic gating of cell communication (aggregation rate) impacts collective decision-making in the decision to flower, in addition to the decision to break seed dormancy.

Optimisation of gas exchange in leaves via collective behaviour of stomata

Evidence for collective behaviour across groups of cells has been reported in the gas exchange-mediating stomata in plant leaves [63]. A trade-off is present in leaves whereby opening these pores to the environment enables the plant to acquire CO_2, but at the cost of losing water [64]. As such, the opening and closing of stomata needs to be regulated to optimise this trade-off.

Under some conditions, the aperture of stomata are synchronised within patches [65], suggesting that local interactions among decentralised stomata propagate in a coordinated fashion, creating a higher order behaviour. These stomatal collective dynamics were modelled using CA [63]. The internal states of stomata on a virtual leaf surface were dynamically updated (following a CA rule set) based on the current state of the cells, and those of its direct neighbours [63,66]. These simulations showed this behaviour to be indistinguishable from the Gács–Kurdyumov–Levin CA, discretising the rules underlying collective multicellular computation [67]. These results were consistent with a hypothesis of emergent, distributed information processing within plants with regard to the optimisation of gas exchange [63]. More recently, this collective behaviour was likened to a two-layer, adaptive, cellular nonlinear network, providing a novel and powerful approach toward understanding plant adaptive fitness in response to the environment at the tissue level [68].

Breaking of tree bud dormancy in response to low temperature

Another example of collective decision in plants is the release of dormancy and resumption of growth in tree buds (known as bud break). Similar to vernalisation, prolonged exposure to low temperature is required for bud dormancy release. The cells in a dormant bud need to collectively decide when to start to grow in spring in an all-or-nothing manner, with the decision to break dormancy unable to be driven by a single cell. Genetic components and their relationships that govern release of dormancy and subsequent growth are known at the cellular level [69,70], but how these scale into a coordinated and robust resumption of growth by dormancy release remains unknown.

Plasmodesmata in tree buds undergo dynamic modulation from being closed in the dormant state to open as a result of exposure to dormancy breaking low temperature [71] (Figure 5E). During cold exposure, there is a concurrent induction of at least two known mobile growth regulators, FT1 and GA. Both FT1 and GA are known to move from cell to cell via plasmodesmata, while exogenous application of GA to dormant axillary tree buds has been shown to facilitate plasmodesmata opening [72]. The dynamic communication between cells in dormant tree bud cells may provide a level of control in the decision to start growing following decentralised information-processing principles.

Concluding remarks and future perspectives

How the developmental states and identity of individual cells in a plant tissue are turned into a collective organ-level transition remains elusive. While this invariably requires cell communication, the modalities by with the information is integrated into a unified decision remain poorly understood. Here, we provided potential models describing how this might occur, and examples of where these may be applied. While data describing these collective multicellular processes in plants remain sparse, it represents an open area of future research.

Outstanding questions

How do asynchronous collections of plant cells coordinate their behaviour to reach a unified tissue-scale decision?

What is the algorithmic nature of information processing in plant tissues?

To what extent does plant cell communication dynamics impact information processing and decision-making in plant organs?

Understanding the basis of organ-scale information processing and collective decision-making among plant cells could lead to the identification of local rule sets representing the molecular interactions between cells, and how these give rise to emergent behaviours. These local interaction rules can be rationally modulated using synthetic biology tools.

Examples of synthetic multicellular information-processing systems have been developed in bacterial systems [73], while theoretical frameworks for this implementation continue to be developed [74]. Synthetic biological components capable of performing logical operations are being developed in plants [75], paving the way for synthetic distributed computing to be implemented in these rigid biological systems.

Understanding the tissue-level processes that plants use to respond to the environment can provide a powerful means to modulate plant behaviour by leveraging novel higher order processing events underlying complex emergent decision-making. Taking the multicellular context in which genetic programs are executed into account could result in the creation of novel axes to rationally control plant development and create climate-resilient crops (see also Outstanding questions).

Acknowledgments

All authors were supported by Human Frontiers in Science Program research grant RGP0002/2020.

Declaration of interests

None declared by authors.

References

1. Balázsi, G. *et al.* (2011) Cellular decision making and biological noise: from microbes to mammals. *Cell* 144, 910–925
2. Duran-Nebreda, S. and Bassel, G.W. (2019) Plant behaviour in response to the environment: information processing in the solid state. *Philos. Trans. R. Soc. B* 374, 20180370
3. Exposito-Alonso, M. *et al.* (2019) Natural selection on the *Arabidopsis thaliana* genome in present and future climates. *Nature* 573, 126–129
4. Lau, O.S. and Bergmann, D.C. (2012) Stomatal development: a plant's perspective on cell polarity, cell fate transitions and intercellular communication. *Development* 139, 3683–3692
5. Bastow, R. *et al.* (2004) Vernalization requires epigenetic silencing of FLC by histone methylation. *Nature* 427, 164–167
6. Savage, N.S. *et al.* (2008) A mutual support mechanism through intercellular movement of CAPRICE and GLABRA3 can pattern the *Arabidopsis* root epidermis. *PLoS Biol.* 6, e235
7. Michod, R.E. and Roze, D. (2001) Cooperation and conflict in the evolution of multicellularity. *Heredity* 86, 1–7
8. Chaiwanon, J. *et al.* (2016) Information integration and communication in plant growth regulation. *Cell* 164, 1257–1268
9. Smith, R.S. *et al.* (2006) A plausible model of phyllotaxis. *Proc. Natl. Acad. Sci. U. S. A.* 103, 1301–1306
10. Péret, B. *et al.* (2009) *Arabidopsis* lateral root development: an emerging story. *Trends Plant Sci.* 14, 399–408
11. Möller, B. and Weijers, D. (2009) Auxin control of embryo patterning. *Cold Spring Harb. Perspect. Biol.* 1, a001545
12. Gilroy, S. and Trewavas, A. (2001) Signal processing and transduction in plant cells: the end of the beginning? *Nat. Rev. Mol. Cell Biol.* 2, 307–314
13. Bassel, G.W. (2018) Information processing and distributed computation in plant organs. *Trends Plant Sci.* 23, 994–1005
14. Kauffman, S.A. (1969) Metabolic stability and epigenesis in randomly constructed genetic nets. *J. Theor. Biol.* 22, 437–467
15. Shen-Orr, S.S. *et al.* (2002) Network motifs in the transcriptional regulation network of Escherichia coli. *Nat. Genet.* 31, 64–68
16. Prohaska, S.J. *et al.* (2010) Innovation in gene regulation: the case of chromatin computation. *J. Theor. Biol.* 265, 27–44
17. Ben-Hur, A. *et al.* (2004) On probabilistic analog automata. *Theor. Comput. Sci.* 320, 449–464
18. Bryant, B. (2012) Chromatin computation. *PLoS ONE* 7, e35703
19. Kauffman, S. (1971) Gene regulation networks: a theory for their global structure and behaviors. In *Current Topics in Developmental Biology* (6), pp. 145–182
20. Chustecki, J.M. *et al.* (2021) Network analysis of *Arabidopsis* mitochondrial dynamics reveals a resolved tradeoff between physical distribution and social connectivity. *Cell Syst.* 12, 419–431
21. Brunkard, J.O. *et al.* (2015) Chloroplasts extend stromules independently and in response to internal redox signals. *Proc. Natl. Acad. Sci. U. S. A.* 112, 10044–10049
22. Kleine, T. and Leister, D. (2016) Retrograde signaling: organelles go networking. *Biochim. Biophys. Acta (BBA) Bioenerg.* 1857, 1313–1325
23. Trewavas, A. (2009) What is plant behaviour? *Plant Cell Environ.* 32, 606–616
24. Gould, P.D. *et al.* (2018) Coordination of robust single cell rhythms in the *Arabidopsis* circadian clock via spatial waves of gene expression. *eLife* 7, e31700
25. Emek, Y. and Wattenhofer, R. (2013) Stone age distributed computing. In *Proceedings of the 2013 ACM Symposium on Principles of Distributed Computing*, pp. 137–146, ACM
26. Fitts, P.M. (1954) The information capacity of the human motor system in controlling the amplitude of movement. *J. Exp. Psychol.* 47, 381
27. Solé, R. *et al.* (2019) *Liquid Brains, Solid Brains*, The Royal Society
28. Ng, W.-L. and Bassler, B.L. (2009) Bacterial quorum-sensing network architectures. *Annu. Rev. Genet.* 43, 197–222
29. Kaplan, H.B. and Greenberg, E. (1985) Diffusion of autoinducer is involved in regulation of the *Vibrio fischeri* luminescence system. *J. Bacteriol.* 163, 1210–1214
30. Miller, M.B. and Bassler, B.L. (2001) Quorum sensing in bacteria. *Annu. Rev. Microbiol.* 55, 165–199
31. Pratt, S.C. *et al.* (2005) An agent-based model of collective nest choice by the ant *Temnothorax albipennis*. *Anim. Behav.* 70, 1023–1036
32. Bennett, T. *et al.* (2014) Canalization: what the flux? *Trends Genet.* 30, 41–48

33. Bradford, K.J. and Trewavas, A.J. (1994) Sensitivity thresholds and variable time scales in plant hormone action. *Plant Physiol.* 105, 1029
34. Liu, L. and Chen, X. (2018) Intercellular and systemic trafficking of RNAs in plants. *Nat. Plants* 4, 869–878
35. Brunkard, J.O. *et al.* (2015) The cytosol must flow: intercellular transport through plasmodesmata. *Curr. Opin. Cell Biol.* 35, 13–20
36. Chen, L.-Q. *et al.* (2010) Sugar transporters for intercellular exchange and nutrition of pathogens. *Nature* 468, 527–532
37. Toyota, M. *et al.* (2018) Glutamate triggers long-distance, calcium-based plant defense signaling. *Science* 361, 1112–1115
38. Wigge, P.A. *et al.* (2005) Integration of spatial and temporal information during floral induction in *Arabidopsis*. *Science* 309, 1056–1059
39. Nilsson, O. (2022) Winter dormancy in trees. *Curr. Biol.* 32, R630–R634
40. Brunkard, J.O. and Zambryski, P.C. (2017) Plasmodesmata enable multicellularity: new insights into their evolution, biogenesis, and functions in development and immunity. *Curr. Opin. Plant Biol.* 35, 76–83
41. Li, Z.P. *et al.* (2021) Intercellular trafficking via plasmodesmata: molecular layers of complexity. *Cell. Mol. Life Sci.* 78, 799–816
42. Sager, R. and Lee, J.-Y. (2014) Plasmodesmata in integrated cell signalling: insights from development and environmental signals and stresses. *J. Exp. Bot.* 65, 6337–6358
43. Radford, J. *et al.* (1998) Callose deposition at plasmodesmata. *Protoplasma* 201, 30–37
44. Benitez-Alfonso, Y. *et al.* (2013) Symplastic intercellular connectivity regulates lateral root patterning. *Dev. Cell* 26, 136–147
45. Vatén, A. *et al.* (2011) Callose biosynthesis regulates symplastic trafficking during root development. *Dev. Cell* 21, 1144–1155
46. Han, X. *et al.* (2014) Auxin-callose-mediated plasmodesmal gating is essential for tropic auxin gradient formation and signaling. *Dev. Cell* 28, 132–146
47. Wolfram, S. (2002) *A New Kind of Science*, Wolfram Research
48. Cui, H. *et al.* (2007) An evolutionarily conserved mechanism delimiting SHR movement defines a single layer of endodermis in plants. *Science* 316, 421–425
49. Gács, P. (1983) Reliable computation with cellular automata. In *Proceedings of the Fifteenth Annual ACM Symposium on Theory of Computing*, pp. 32–41, ACM
50. Angel, A. *et al.* (2015) Vernalizing cold is registered digitally at FLC. *Proc. Natl. Acad. Sci. U. S. A.* 112, 4146–4151
51. Shmulevich, I. and Kauffman, S.A. (2004) Activities and sensitivities in Boolean network models. *Phys. Rev. Lett.* 93, 048701
52. Bornholdt, S. (2008) Boolean network models of cellular regulation: prospects and limitations. *J. R. Soc. Interface* 5, S85–S94
53. Genoud, T. and Métraux, J.-P. (1999) Crosstalk in plant cell signaling: structure and function of the genetic network. *Trends Plant Sci.* 4, 503–507
54. Li, S. *et al.* (2006) Predicting essential components of signal transduction networks: a dynamic model of guard cell abscisic acid signaling. *PLoS Biol.* 4, e312
55. Bewley, J.D. (1997) Seed germination and dormancy. *Plant Cell* 9, 1055
56. Koornneef, M. *et al.* (1982) The isolation of abscisic acid (ABA) deficient mutants by selection of induced revertants in non-germinating gibberellin sensitive lines of *Arabidopsis thaliana* (L.) Heynh. *Theor. Appl. Genet.* 61, 385–393
57. Holdsworth, M.J. *et al.* (2008) Molecular networks regulating *Arabidopsis* seed maturation, after-ripening, dormancy and germination. *New Phytol.* 179, 33–54
58. Thompson, K. *et al.* (1977) Seed germination in response to diurnal fluctuations of temperature. *Nature* 267, 147–149
59. Hepworth, J. *et al.* (2018) Absence of warmth permits epigenetic memory of winter in *Arabidopsis*. *Nat. Commun.* 9, 1–8
60. Topham, A.T. *et al.* (2017) Temperature variability is integrated by a spatially embedded decision-making center to break dormancy in *Arabidopsis* seeds. *Proc. Natl. Acad. Sci. U. S. A.* 114, 6629–6634
61. Sheldon, C.C. *et al.* (2000) The molecular basis of vernalization: the central role of FLOWERING LOCUS C (FLC). *Proc. Natl. Acad. Sci. U. S. A.* 97, 3753–3758
62. Chen, M. and Penfield, S. (2018) Feedback regulation of COOLAIR expression controls seed dormancy and flowering time. *Science* 360, 1014–1017
63. Peak, D. *et al.* (2004) Evidence for complex, collective dynamics and emergent, distributed computation in plants. *Proc. Natl. Acad. Sci. U. S. A.* 101, 918–922
64. Munemasa, S. *et al.* (2015) Mechanisms of abscisic acid-mediated control of stomatal aperture. *Curr. Opin. Plant Biol.* 28, 154–162
65. Beyschlag, W. and Eckstein, J. (1998) Stomatal patchiness. *Prog. Bot.* 59, 283–298
66. Wolfram, S. (1984) Cellular automata as models of complexity. *Nature* 311, 419–424
67. Gács, P. *et al.* (1978) One-dimensional uniform arrays that wash out finite islands. *Problemy Peredachi Informatsii* 14, 92–96
68. Peak, D. *et al.* (2023) Stomatal patchiness and cellular computing. *Proc. Natl. Acad. Sci. U. S. A.* 120, e2220270120
69. Cooke, J.E. *et al.* (2012) The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant Cell Environ.* 35, 1707–1728
70. Singh, R.K. *et al.* (2018) A genetic network mediating the control of bud break in hybrid aspen. *Nat. Commun.* 9, 4173
71. Tylewicz, S. *et al.* (2018) Photoperiodic control of seasonal growth is mediated by ABA acting on cell-cell communication. *Science* 360, 212–215
72. Rinne, P.L. *et al.* (2011) Chilling of dormant buds hyperinduces FLOWERING LOCUS T and recruits GA-inducible 1, 3-β-glucanases to reopen signal conduits and release dormancy in *Populus*. *Plant Cell* 23, 130–146
73. Regot, S. *et al.* (2011) Distributed biological computation with multicellular engineered networks. *Nature* 469, 207
74. Macía, J. *et al.* (2012) Distributed computation: the new wave of synthetic biology devices. *Trends Biotechnol.* 30, 342–349
75. Brophy, J.A. *et al.* (2022) Synthetic genetic circuits as a means of reprogramming plant roots. *Science* 377, 747–751