

Information Processing and Distributed Computation in Plant Organs

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1 **TITLE**

2 Information processing and distributed computation in plant organs

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13 **ABSTRACT**

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

26

27

28

29 **Genetic networks and plant development**

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

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

42 Within complex tissues, different cell types have distinct gene expression profiles [9],
43 conferring both unique identity and function [10]. Examples of individual cell types
44 controlling organ-level responses through the control of hormone responses have been
45 provided, including gibberellin-mediated root elongation [11], root growth towards water
46 [12], and leaf expansion [13]. These examples demonstrate a division of labour in
47 hormone response across cell types, while the functional significance of this
48 compartmentalization is less clear. The impact spatially embedding gene expression
49 programs across the multicellular context of plant organs has on the control of plant
50 development remains a knowledge gap. The mechanisms by which plants process
51 information may only be partially explained by molecular level networks alone.

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

58

59 **Environmental information processing and developmental transitions in plants**

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

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

78

79 **A computational perspective of plant development**

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

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

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

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

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

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

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

103

104 **Plant organs as distributed information processing systems**

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

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

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

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

124

125 **Distributed cellular architectures in plant organs**

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

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

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

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

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

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

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

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

171

172 **What does it mean to be distributed as a plant?**

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

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

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

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

191

192 **Cellular level distributed computation in plants**

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

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

203

204 **Distributed control of optimized gas exchange in leaves**

205 Decision-making typically involves minimizing the impact of trade-offs to optimize the
206 timing of choices. In the case of the control of gas exchange in leaves, an optimization
207 between the exchange of CO₂ and loss of water is managed through the control of
208 stomatal aperture [39]. A challenge in this regard is the co-ordination of the populations
209 of stomata present across an individual leaf. In a seminal study, the co-ordinated spatial
210 behaviour of stomatal opening was investigated in cocklebur (*Xanthium strumarium*)
211 [40]. Patchy sectors of stomatal behavior was observed across the surface of the leaf in
212 this species, and likened to a distributed computation. In this regard, localized co-

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

215

216 **Optimization in plant decision-making**

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

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

228

229 **Distributed control of flowering time in response to cold**

230 The induction of flowering in many species is initiated by sustained periods of low
231 temperature, a process termed vernalization. The control of cold-induced flowering in
232 arabidopsis (*Arabidopsis thaliana*) is principally controlled by the repressor gene
233 *FLOWERING LOCUS C (FLC)* through temperature-mediated epigenetic silencing [3,
234 42]. Following a critical period of cold, a stable and mitotically heritable silencing occurs,
235 providing memory storage in this system.

236 Microscopic examination of the spatial distribution of *FLC*-silenced cells in response to
237 cold revealed an all-or-nothing pattern of *FLC* promoter activity in individual cells [42,
238 43] (Figure 2b). Each cell is therefore performing a “digital” registration of cold through
239 their chromatin state. In the context of an organ, this series of integrated distributed
240 switches provides the possibility for rich behaviours, including both a temperature
241 averaging mechanism and system robustness, thus increasing the computational
242 capacity of the system. The mechanism by which the aggregation step is performed has
243 yet to be demonstrated, and represents a calculation known as the majority problem,

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

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

254

255 **Distributed computation of alternating temperatures in the control of seed** 256 **dormancy**

257 The breaking of seed dormancy determines where and when plants are established
258 [47]. Like in the case of flowering, the input of low temperatures lead to an output in the
259 form of the breaking of seed dormancy [48]. The antagonistically acting hormones
260 abscisic acid (ABA) and gibberellic acid (GA) underpin the decision to germinate [49],
261 and is proposed to follow a ratio-based thresholding mechanism [46, 50].

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

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

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

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

286

287 **Connectionist approaches to information processing**

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

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

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

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

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

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

318

319 **Intercellular communication dynamics and information processing**

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

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

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

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

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

346 Preliminary evidence for plant organs implementing a similar mechanism as FPGAs to
347 facilitate an increased palette of responses to the environment has been reported
348 previously. In the shoot apical meristem (SAM) from both birch and poplar, low
349 temperatures have been reported to promote PD opening [66, 67]. Subgroups of cells in
350 the *Arabidopsis* SAM are also symplastically linked together following day length-
351 mediated flowering signals, leading to the formation of symplastic domains [69]. A
352 functional role for the reorganization of cellular connectivity in the SAM remains unclear
353 [70]. A recent study demonstrated a PD-mediated gating mechanism controlling ABA-
354 mediated photoperiodic induction of the SAM in hybrid aspen trees [71]. In this example,
355 closed PD block growth-promoting signals until the decision to break bud dormancy is
356 reached, demonstrating a role for intercellular communication in environmental
357 information processing.

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

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

367 A role for aggregation rates impacting outputs in biological systems has also been
368 demonstrated using red harvester ants, where the rate at which workers interact
369 impacts decision-making with regards to which task an individual performs [73]. This
370 control principle of engineered distributed computation is therefore transferrable to
371 multiple biological contexts, enabling the modification of the timing of biological outputs
372 simply by modulating communication rates and not the underlying program.
373 PD may be capable of achieving both modes of altering organ scale outputs. The
374 abundance and aperture of these pores can modulate both aggregation rates and the
375 symplastic topology of the organ.

376

377 **Collective decision-making in plant organs**

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

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

391 The field of biologically-inspired computation makes use of algorithms identified in
392 natural systems to solve problems in the technological domain [24]. Examples of this
393 include the development of anti-virus software based on non-self-recognition principles
394 from the human immune system [74], ant colony behaviour to optimize business [75]
395 and an algorithm used by *Drosophila* to categorize smells to perform similarity searches
396 [76]. Understanding the algorithms utilized by plants in collective decision-making may

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

399

400 **Concluding remarks**

401 Understanding the principles of computation in the context of multicellular plant organs
402 addresses a gap in understanding how molecular interactions scale up to adaptive
403 behaviours in complex organisms (see Outstanding Questions). A distributed
404 computation perspective of plant development further enables biological researchers to
405 engage with the expanding field of computation in biology [78]. Plants are a very well
406 suited system to investigate and engineer multicellular distributed computation in light of
407 cellular immobility and the ability to manipulate individual cell types. Collectively this
408 may lead to the identification of novel algorithms for use in the computational domain
409 using biology-inspired designs [79]. This perspective can also lead to the development
410 of the next generation of crop species with enhanced environmental response and
411 predictive capacities. Knowledge gaps as to how cellular organization and
412 communication influences the outputs of genetic programs need to be filled before
413 these complex multicellular systems can be reliably and predictably reprogrammed.
414 Finally, while statements regarding the “intelligence” of plants remain difficult to make,
415 information processing provides a well-defined and quantifiable field that is
416 generalizable across diverse domains, ranging from plant biology to computer science.

417

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424

425 **FIGURE LEGENDS**

426

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

436
437 **Figure 2.** Examples of distributed computations in plant organs. (a) Co-ordinated
438 activity of stomata aperture across a leaf surface. Schematic illustrates changes in the
439 distribution of chlorophyll fluorescence over time with red showing increased and green
440 decreased signal, indicative of stomatal aperture. Based on [40]. (b) Digital registration
441 of cold in the cells of the *Arabidopsis* SAM. The grid represents cells in the SAM and the
442 presence of a blue dot the activity of the *FLC* promoter. Following cold exposure,
443 individual cells either do or do not have promoter activity. Based on [43]. (c) Optical
444 section of a dormant *Arabidopsis* embryo indicated the separate cellular locations of
445 ABA and GA responses. Arrows indicate the movement of both hormones between
446 response centres. Based on [33].

447
448 **Figure 3.** Topological features of multicellular assemblies. (a) Comparison of the
449 relative distribution of degree (number of neighbours a cell has) in each an *Arabidopsis*
450 hypocotyl [61] and the *C. elegans* nervous system [56]. (b) Schematic illustrating
451 dynamics topological rearrangements in a plant organ. Nodes represent cells and blue
452 edges physical associations between cells that are communicating. Grey edges
453 highlight regions of the tissue that are topological isolated from other cells, such as in
454 the context of symplastic domains.

455
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