Crosstalk in plant cell signaling: structure and function of the genetic network

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Cell signaling integrates independent stimuli using connections between biochemical pathways. The sensory apparatus can be represented as a network, and the connections between pathways are termed crosstalk. Here, we describe several examples of crosstalk in plant biology. To formalize the network of signal transduction we evaluated the relevance of mechanistic models used in artificial intelligence. Although the perceptron model of neural networking provides a good description of the process, we suggest that Boolean networks should be used as a starting framework. The Boolean network model allows genetic data to be integrated into the logical network of connections deduced from DNA microarray data.

Owing to their sedentary lifestyle, plants have evolved plasticity in metabolism and morphology, which allowed the colonization of diverse environments. To accommodate their metabolism to the surrounding conditions, plant cells integrate different environmental stimuli with internal signals through a parallel processing of information. Signal transduction and amplification has been described in many cases of stimuli sensing, such as hormone, heat, light, salt or pathogen perception. So far, the sequences of the biochemical steps, which are initiated after perception, have been represented by a paradigm of independent cascade events.

However, experimental evidence has shown recently that interactions between signal transduction pathways do exist. Direct connections between specific pathways furnish a rapid and efficient tuning mechanism for optimizing non-cognitive behavior in response to various combinations of stimuli.

Crosstalk connections between pathways, also called interferences or intersections, are widespread in plants, as illustrated by the following examples.

Crosstalk in controlled defense responses

Leaves wounded by insects or by mechanical damage induce the proteinase inhibitor production both locally and systemically[1] (Figs 1 and 2). Transduction of the wound-related signal involves the octadecanoid pathway, and can be mimicked by treatment with jasmonic acid[2]. Salicylic acid is implicated in the perception of pathogen attack in many plant species[3], and inhibits the activation of wound-induced genes elicited by systemin (a systemic wound-peptide signal) and by jasmonic acid (Ref. 4). This inhibition presumably occurs at the level of an enzyme involved in jasmonic acid synthesis. However, in rice, the salicylic acid-analog INA (2,6-dichloroisonicotinic acid) stimulates the expression of genes induced by jasmonic acid in a synergistic manner[5], and reciprocal treatment with jasmonic acid produces a positive regulating effect on the salicylic acid-induced pathway. In *Arabidopsis*, an additional element (CPR6) can modulate the expression of pathogenesis-related (PR) genes via the salicylic acid signal transduction pathway, as well as thionin or defensin genes through the jasmonic acid pathway[6].

Ethylene and jasmonic acid pathways crosstalk

In tobacco, a synergy has been observed between ethylene and methyl jasmonate (Figs 1 and 2) for the induction of two PR genes that code for PR1b and osmotin[7]. In tomato, upon wounding, both ethylene and jasmonic acid are required for the induction of proteinase inhibitor genes[8]. In the case of *Arabidopsis*, ethylene and methyl jasmonate concomitantly induces the expression of a gene coding for an antifungal plant defensin PDF1.2 (Ref. 9), whereas neither substance induces PR1. In *Arabidopsis*, the growth responses controlled by each hormone are independent.

Ethylene and glucose pathways crosstalk

The phytohormone, ethylene, affects many developmental stages of plants, for instance cell elongation, seed germination, fruit ripening and senescence, and is also implicated in biotic[10,11] and abiotic stress perception[8]. Genetic analysis of *Arabidopsis* has unraveled the components involved in ethylene signal transduction[11,12]. The pathway defined by this approach is a system of MAP kinase cascades.

The ethylene precursor 1-aminocyclopropane-1-carboxylic acid can phenocopy many effects of the *gin1* allele identified in a new glucose-insensitive *Arabidopsis* mutant defective in various glucose-specific responses, such as cotyledon expansion and greening, shoot development, floral transition and gene expression[13]. In addition, ethylene antagonizes the glucose signal in the wild type, and the ethylene-insensitive mutants exhibit a glucose hypersensitivity[13]. Thus, the glucose pathway and probably an ethylene-inhibited MAPK cascade interact positively to activate a common branch of signal transduction leading to the control of germination and cotyledon development (Figs 1 and 2). However, modulation of photosynthetic gene repression by sucrose, or control of the ethylene triple-response[13] are not subjected to this interference.

Crosstalk between light signal transduction and pathogenesis-related gene signaling pathway

Crosstalk has been observed between red light and PR-expression-signaling pathways[14]. The *Arabidopsis* light-hypersensitive *psi2* mutant exhibits a light fluence-dependent amplification of salicylic acid-induced PR1a gene expression (T. Genoud *et al*., unpublished; Figs 1–3). To confirm observations that the light signal regulates the sensitivity to salicylic acid, the expression of PR genes was scored in mutants containing no detectable phytochrome A and B proteins. In these plants, expression of PR genes elicited by salicylic acid or benzo-(1,2,3)-thiadiazole-7-carbothioic acid *S*-methyl ester (a salicylic acid-agonist) is strongly reduced and the resistance to *Pseudomonas syringae* pv. *maculicola*, is significantly reduced (T. Genoud *et al*., unpublished). A screen has been set up with a mutagenized population of *psi2* to find plants that are blocked in the crosstalk between the phytochrome pathway and PR induction. This should eventually lead to the identification of a *trans*-signaling element.

Phytochrome signaling crosstalk with cryptochrome signaling

The proportion of blue, red and far-red light in incoming white light is interpreted by the signaling network in different ways. For example, blue light acts synergistically with red light in the activation of the phytochrome pathway, which controls processes such as cotyledon unfolding and cell elongation[15].

Further experiments performed with *Arabidopsis* mutants deficient in one or several photoreceptors have confirmed these physiological observations. The results suggest

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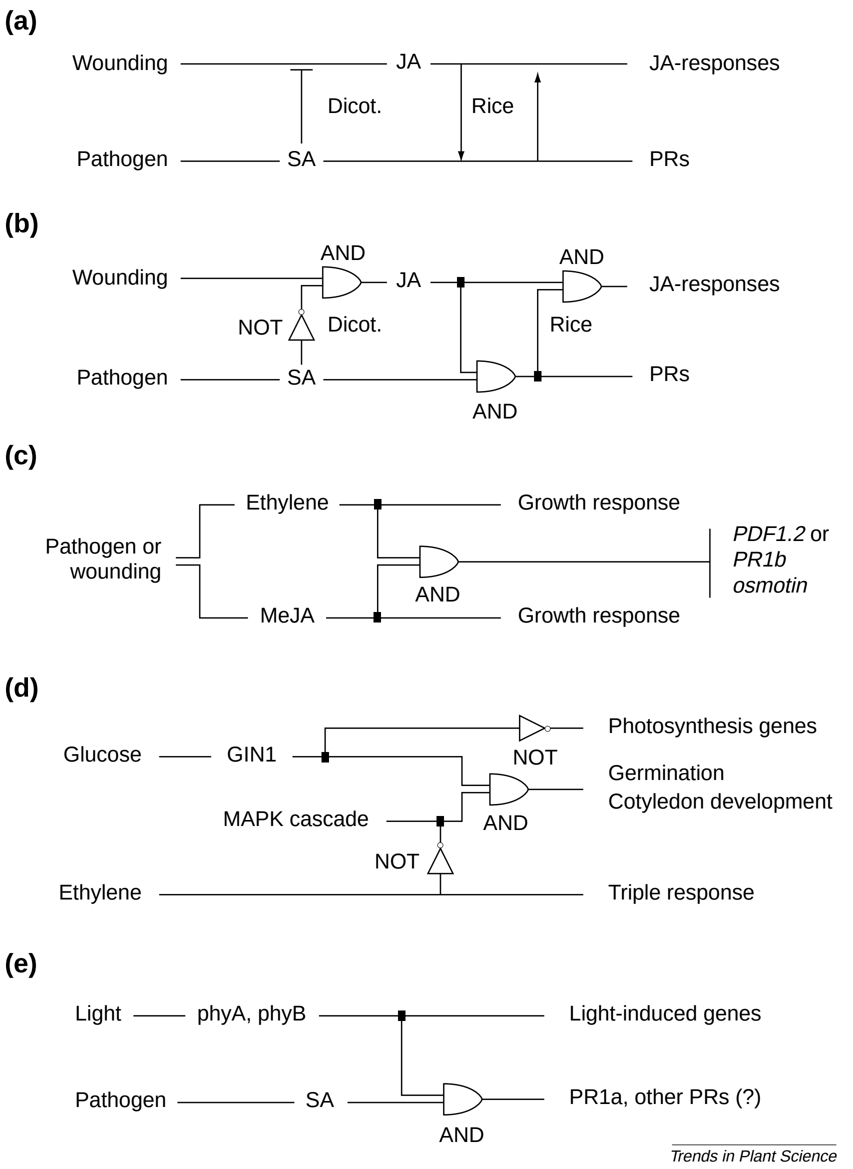

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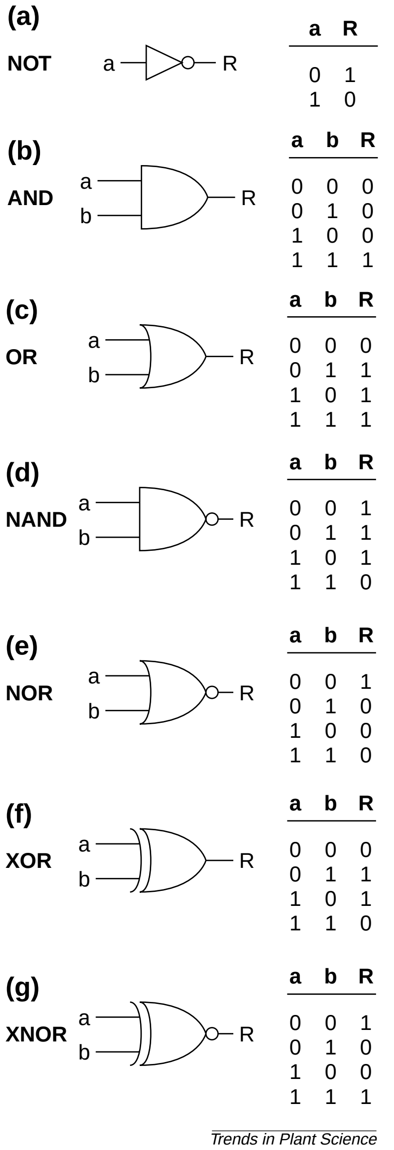
Fig. 1. Schematic representations of some examples of crosstalks between plant signal transduction pathways using Boolean symbols. The crosstalks between the salicylic acid (SA) and jasmonic acid (JA) pathways are represented in intuitive formalism (a) and in a Boolean translation (b) as defined in Fig. 2. (c) Activation of defense-related genes in *Arabidopsis* by the concomitant control of ethylene and methyl jasmonate (MeJA). (d) Crosstalk between ethylene and glucose signaling in *Arabidopsis*. (e) Crosstalk between light and pathogenesis-related (PR) gene signaling. The AND gates combine signals synergetically whereas repressions are represented by a NOT gate connected to an AND gate.



(a) NOT

a	R
0	1
1	0

(b) AND

a	b	R
0	0	0
0	1	0
1	0	0
1	1	1

(c) OR

a	b	R
0	0	0
0	1	1
1	0	1
1	1	1

(d) NAND

a	b	R
0	0	1
0	1	1
1	0	1
1	1	0

(e) NOR

a	b	R
0	0	1
0	1	0
1	0	0
1	1	0

(f) XOR

a	b	R
0	0	0
0	1	1
1	0	1
1	1	0

(g) XNOR

a	b	R
0	0	1
0	1	0
1	0	0
1	1	1

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Fig. 2. Representation of logical gates. Input signals are represented by a and b, the resulting signal leaving the switch is represented by R. Presence or absence of a phenomenologically significant signal is designated by 1 and 0, respectively. Abbreviations: NAND,: not-and; NOR, not-or; XOR, exclusive-or; XNOR, exclusive-not-or.

that the level of active phytochrome strongly modulates the activity of the cry1 photoreceptor[16], whereas the absence of cry1 does not modify the activity of the phytochrome pathway. However, this synergistic effect is conditional[17]: in experiments where blue light is added to a red-light background, under short exposures of blue light, cry1 activity requires phyB. Whereas, under prolonged exposures of blue light, the effects of cry1 and phyB are independent for the control of hypocotyl elongation and cotyledon opening[17]. Using a combination of specific mutants in the photoreceptor phyA, phyB and cry1, it was shown that:

- The blue-light-response mediated by cry1 in blue light is modulated by phyB.
- The effect of phyA and phyB on chlorophyll accumulation in de-etiolated seedlings is modulated by cry1.
- In far-red light, both phyB and cry1 are modulators of the accumulation of anthocyanin controlled by the phyA molecule[18].

Recent results demonstrate that cry1 and phyA photoreceptors interact in a two-hybrid system and that the cry1 molecule is phosphorylated by a phyA-associated kinase activity, indicating that crosstalk probably occurs at the receptors level[19] (Fig. 4).

From the various observations mentioned here, it is inferred that blue and far-red light act antagonistically to modify signaling by phyB. In addition, UV-B and UV-A wavelengths can replace the blue light required for the stimulation of chalcone synthase expression, and a synergism occurs between these UV-pathways and the cry1 signal[20]. These few examples highlight the complexity of light signal processing in plants.

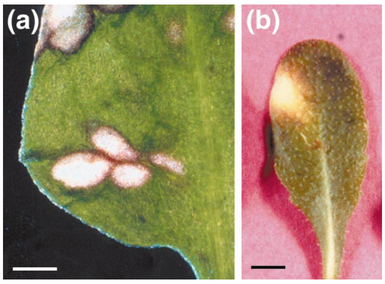

Fig. 3. Lesions in *Arabidopsis* leaves caused by high fluence white light in a light-hypersensitive mutant *psi2* (a), scale bar = 1 mm, and by the bacterium *Pseudomonas syringae* in a wild-type plant (b), scale bar = 2 mm. Both treatments lead to the activation of disease resistance and the corresponding defense genes. The signal transduction pathways initiated by light stimulus and pathogen attack crosstalk synergetically for the subsequent induction of resistance.

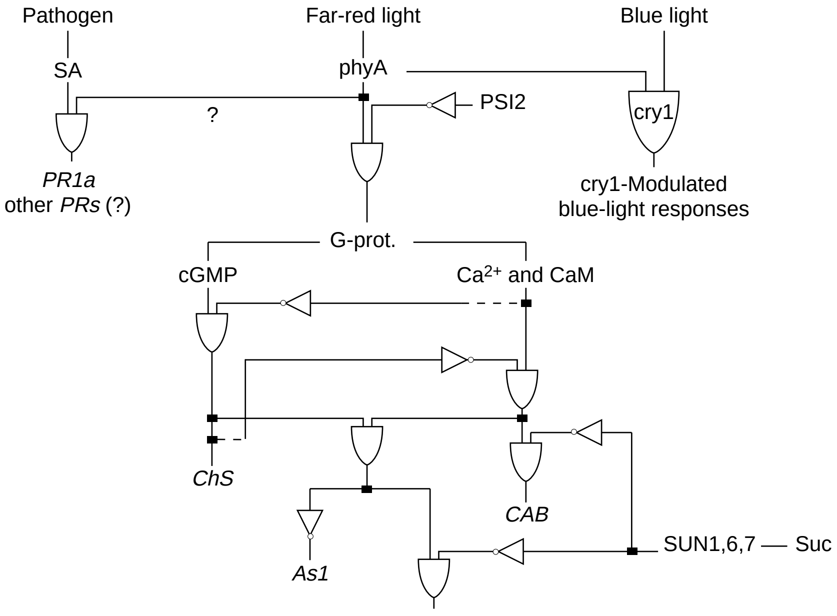

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Fig. 4. Connections and crosstalks within the phyA signaling network. The signal transduction induced by activation of phytochrome A is not fully linear, but divides into at least two subpathways[33,34]. The first events might implicate a trimeric G-protein (Ref. 33). Later, the pathway divides in two branches, one regulated by calcium and calmodulin and the other involving cGMP (Ref. 34). Activation of phyA-controlled genes, such as chalcone synthase (*ChS*), only requires mobilization of the cGMP-controlled pathway, whereas the activation of genes coding for photosystem II components [such as chlorophyll *a/b*-binding protein (CAB)] is controlled by the calcium-modulated branch. A third group of genes [corresponding to components of phytosystem I, such as plastocyanin (*PC*)] is inducible by an adequate combination of both pathway activities, and a fourth [asparagine synthase gene (*AS1*)][35] is repressed by the same combination. A negative reciprocal crossregulation has been found between the cGMP pathway and the calcium pathway[36]. This regulation is timely controlled and only manifested in the presence of high amounts of signaling intermediates. The level of cGMP is also subjected to a desensitization process, which is potentially regulated by a negative feedback loop of the cGMP-activated pathway. The activity of the phytochrome A pathway is regulated near the photoreceptor by the PSI2 protein[14]. Induction of the *PR1a* gene through salicylic acid signaling is probably modulated by the phytochrome signal because an elevated expression of *PR* genes is found in the phytochrome A and B signaling mutant *psi2* under high light intensities[14]. The phyA receptor can phosphorylate the blue-light receptor and therefore modulate the blue-light perception[19]. Sucrose inhibits light-responsive genes via a pathway involving SUN proteins[23]. The broken lines represent pathways that are only active above a certain level of signal.

Crosstalk between sucrose and light signal transduction pathways

In contrast with nitrate reductase or chalcone synthase[21], the phyA-activated genes involved in photosynthesis, such as *CAB*, *RBCS* and *PLASTOCYANIN* (*PC*), are repressed by glucose or sucrose[21,22] (Fig. 4). *PC* expression is upregulated by the phyA pathway (activated by far-red light) and repressed by sucrose, whereas hypocotyl elongation is reduced by both factors. The antagonistic and the positive activity of sucrose on the phyA pathway can be blocked in *Arabidopsis sun* mutants[23]. This uncoupling identifies transduction elements of the sucrose pathway, which are responsible for the interaction with the phyA-controlled light signal transduction pathway (SUN proteins[23]). Such interactions presuppose the existence of common elements integrating the signal converging from both pathways, either additively (for the inhibition of hypocotyl elongation) or substractively (for the activation of *PC* and *CAB* genes). It remains to be determined whether SUN proteins are such elements, or if they simply interact with these elements.

Crosstalk between amino acids and purine metabolism

The various amino acid metabolisms are interconnected, and can be linked up to the purine metabolism[24]. Indeed, *Arabidopsis* plants treated with a histidine biosynthesis inhibitor overexpress genes related to not only histidine biosynthesis but also to aromatic amino acids, to lysine synthesis and, curiously, to purine synthesis[24]. In addition, a reduction in glutamine synthetase activity is observed. As in the case of other eukaryotes[25], a general control system might coordinate metabolite biosynthesis. Such a system would integrate internal as well as environmental signals to modulate the activity of the various metabolite biosynthesis pathway.

Crosstalk in the control of flowering

In *Arabidopsis*, flowering induction is controlled by a complex system of signaling pathways acting in partial redundancy, the signals of which are downstream-integrated by a group of proteins, such as LFY and AP1, which further cooperate additively to confer floral meristem identity (reviewed in Refs 26–28). Multiple opportunities for crosstalk must occur in this system because >80 genes have been found to influence the transition from vegetative to reproductive stage[28]. For example, the time of flowering is influenced by:

- Phytochrome A and B signaling pathways.
- Blue-light receptor pathway.
- Circadian clock.
- Sucrose and gibberellin pathways.

A major challenge will be to functionally characterize these interactions and the corresponding elements forming such a complex network.

Signaling network: a neural network?

From a set of linear and separated signal transduction pathways, the model describing perception and information processing is now shifting towards a network-structured paradigm[29]. As a much higher level of complexity is observed, new models are emerging to account for the properties of living cells. In line with the mechanistic representations adapted from

Table 1. Examples of Boolean gates and logical integration of signals found in plant signal processing[a]

Type of gate	Example	Ref.
AND	See Fig. 1	
OR	CAB gene induction by red or far-red light.	37
NAND	Switch controlling down-regulation of genes involved in vegetative development in the shoot apical meristem or inactivation of a flowering inhibitor in this organ: input information might represent signals controlling the activity of a flowering inhibitor concomitantly (such as LFY and AP1 signals).	28
XOR	Activity of red and far-red light in combination to control cell elongation.	38

[a] The gate types are described in Fig. 2.

research into artificial intelligence, the cell apparatus involved in internal or external signal interpretation can be considered a molecular network. In this more realistic (global) description, the structure of the signaling network resembles a type of neural network called a perceptron[30].

A perceptron is a group of interacting algorithms (neurons) divided into at least three layers: an input layer where the information is entered, an output layer where information is read after processing by the network, and an intermediate layer linking output and input neurons. Information enters the network in the form of sigmoidal or gaussian signals, which are processed by the algorithm-containing neurons to generate new sigmoidal or gaussian signals that will be treated by the next neurons in the 'cascade'. In such networks, fluctuating information is divided into a set of arbitrary components, which is transported and modified by the algorithms through a complex parallel processing.

In the case of a biochemical network, the signal flowing through two molecular neurons can be represented as a pulse of cytoplasmic calcium or a change in the concentration of cyclic nucleotides. The cell's equivalent of a molecular 'neuron' might be, for example, a particular phosphatase activity in the cytoplasm, which is modulated locally and temporally by elevated calcium or cyclic nucleotide concentrations. In this way, the quantitative value or intensity of the calcium signal reaching such a molecular neuron would be translated by the phosphatase-associated 'algorithm' (i.e. the associated transduction rule) in a new signal possessing its own intensity. For example, the generated signal could be the phosphorylation rate of the downstream element.

In perceptrons, one single neuron can integrate two or more different inputs. In the context of cell perception, such integrations are also possible. For example, a phosphatase activity might be modulated by two independent kinases. These two kinases could phosphorylate the enzyme at different sites, both modifications leading to a cumulative and possibly non-linear effect on the phosphatase activity. This implies that a signal-integrating protein molecule can be considered a small computing network.

The ability to 'memorize' sets of conditions is a typical property of neural-like networks[29,30]. In plants, the maintenance of circadian rhythm in darkness is an example of 'memory'[31].

Structure of signaling networks: the Boolean network

Overall, signaling networks are structured like neural networks. However, the use of such a model to identify the molecular components of a signal transduction network would restrict advances in research because information-processing in neural networks is diffusely localized. Thus, for use with a genetic and, consequently, reductionistic approach, a simpler model is needed. A Boolean representation of signaling networks allows for a reductive and rational representation from which experiments can be designed and a certain predictive power gained. Indeed, interfering signals can be considered as 'inputs' reaching a Boolean gate (or switch), and the signal that results from the combination can be defined as the 'output' of such a logical gate[32].

For example, with two inputs, where the value 0 or 1 corresponds to the presence or the absence of a signal, four combinations are possible: 00, 01, 10, 11. In this way, for two signals, 'a' and 'b', converging from different pathways, and possibly modulated by a NOT gate, there are six possible logical operations (Fig. 2, Table 1). These operations are called AND, OR, NAND, NOR, XOR and XNOR, each combining two afferent inputs (a and b) in a single output (R). In signal transduction, the value 0 corresponds to no signal or a low signal and the value 1 indicates that a phenomenological significant signal is passing through the pathway.

Such a Boolean network model can serve as a starting point for a functional description of the network activity. If the signal level is determining, there is the possibility for further investigation of the quantitative 'rule' of signal integration associated with the element by a separate examination. Using a similar procedure, every element of the network could be characterized by a particular algorithm or rule. In the future, assembling these algorithms or rules together in a neural network should lead to a useful simulation of the cell signal transduction apparatus.

Conclusion

An isomorphism between signaling and Boolean networks appears to be emerging. This provides a logical framework that allows a materialistic description of the flow of information in cells. It implies that Boolean switches have a molecular identity, presumably as proteins that are susceptible to various modifications from convergent signals. More detailed information on pathways and crosstalk are needed to fill the gaps in our knowledge concerning signal processing. Molecular characterization of the individual elements of the processing apparatus is a current challenge. Therefore, future work should focus on an extensive characterization of the elements involved in given signaling pathways and those linking these pathways in networks. The use of DNA microarrays to associate signaling networks with gene expression, and genetic approaches based on transgenic plants containing sets of reporter genes, should help in this task. It might be possible to represent signal networks and crosstalk using models that possess good predictive power.

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