

Plant synapses: actin-based domains for cell-to-cell communication

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For many years it has been known that plants perform rapid long-distance signalling using classical action potentials that have impacts on diverse processes in plants. Plants also synthesize numerous neuronal molecules and fulfill some criteria for intelligent behaviour. Analysis of recent breakthrough data from ecophysiology studies has revealed that plant roots can discriminate between 'self' and 'non-self'; in animals, this ability to discriminate is dependent on the activities of neuronal synapses. Here, we propose that plant cells establish modes of information exchange between each other that have properties in common with neuronal synapses. Moreover, plants also assemble adhesive contacts that orchestrate cell-to-cell communication between the host cells when challenged with pathogens, parasites and potential symbionts. We propose that these adhesive contacts resemble the immunological synapses found in animals.

Neuronal aspects of plant life: from action potentials to plant intelligence

For many years it has been known that plants are a rich source of neuronally active molecules [1,2]. Moreover, higher plants generate and transmit rapid electrical signals known as action potentials [3]. Action potentials were discovered in plants in 1873 [4,5], at that time the animal brain was still largely unexplored and the cellular basis of neuronal circuits was not yet accepted. The authors of these reports did suggest the nerve-like nature of cell-to-cell communication in plants [6,7], but this suggestion did not receive wide acceptance. On the contrary, this was labelled as pseudoscience and 'doomed' for oblivion [3]. There were two major reasons for this rejection and mystification of plant electrophysiology by mainstream science. First, there is tendency to link the electrophysiology of plants with 'metaphysical' or 'paranormal' phenomena (see Box 1 in Ref. [3]). Second, 'green', non-motile plants are widely considered to be passive organisms that are not in need of rapid electrical long-distance signalling and excitability.

However, analyses of numerous data convincingly suggest that action potentials control important physiological processes such as respiration, photosynthesis, lateral organ movements and unloading of phloem in sink tissues [3], reviewed in Ref. [8]. Plant action potentials

trigger a transient rise in cytoplasmic calcium levels [9], and the rapid transmission of oxidative and nitrosative stress signals between root and shoot apices of *Arabidopsis* appear to be relevant for the spread of systemic signals in the establishment of plant immunity [10]. Recent advances in plant physiology and ecology have revealed that plants might indeed be considered as intelligent organisms [11] showing a complex social life mediated preferentially via their root systems [8,12,13]. Plants receive, store and process large amounts of information about their environment, including information from neighbouring plants and other organisms. Plants use this information for memory-based learning, which allows them to benefit from trial-and-error-guided and experience-driven behaviour [11].

Nevertheless, the absence of both neurons and synapses makes the idea of an information-processing network in excitable plants that is based on nerve-like structures rather unfavorable. However, plant cells do not necessarily need to extend long processes (axons) to contact their neighbours. Most shoot and root cells have characteristic tubular shapes and adhere tightly at their non-growing cross-walls; these cross-walls are traversed by numerous plasmodesmata and constitute the end-poles of the cells [14,15]. Recent advances in our understanding of the processes and molecules driving polar auxin transport have confirmed the long-standing proposition that the end-poles act as platforms for polar auxin transport [15–18]. The cell-to-cell transport of auxin across these end-poles is based on actin-driven endocytosis, endosomal sorting and vesicular recycling [16,17]. All these cellular activities are fundamentally similar to the 'synaptic information processing' seen in animal systems. Moreover, immunofluorescence localization of the actin cytoskeleton has revealed that the non-growing cross-walls involved in the intercellular transport of auxin are enriched in F-actin and plant-specific unconventional class VIII myosin [19]. Because the cross-walls at the end-poles represent unique actin- and pectin-based adhesive domains [15,18], we propose the concept of the 'plant developmental synapse' in which auxin and pectin-derived signalling molecules (Box 1) act as plant-specific transmitters for cell-to-cell communication.

Neuronal molecules in plants

In addition to action potentials, one of the most curious pieces of evidence indicating the existence of cellular activities comparable to those in nerve cells is the presence of neuromodulatory and neuron-specific molecules in plant

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Box 1. Molecules and transmitters of plant synapses

Plants use several evolutionarily ancient molecules crucial for calcium-regulated secretion that are known to be involved in transmitter-mediated cell-to-cell communication at neuronal synapses [8,17,20,45,46]. Moreover, several properties of auxin suggest that it acts as a plant-specific excitatory transmitter in cell-to-cell communication. Exogenously added auxin elicits rapid electric responses in plant cells and induces rapid calcium transients [8]. Exogenous auxin also activates plasma membrane H⁺-ATPase as well as modulating the activities of several other ion channels and initiating wave-like stimulation of the polar transport of auxin along the longitudinal axis of plant organs [8].

Homogalacturonan pectins release bioactive signal molecules called oligogalacturonides (OGAs), which are rapidly transported throughout plant bodies and which have numerous effects on plant growth and physiology, most of which are antagonistic to auxin [47]. Besides their rapid transport through plant tissues, OGAs also exert several properties that suggest that these pectin-derived signalling molecules might act as plant-specific inhibitory transmitters of cell-to-cell communication. Exogenously added OGAs induce depolarization of the plasma membrane, activate a phospholipase C-like enzyme,

release H₂O₂ and rapidly promote transient mobilization of cytoplasmic calcium combined with cytosolic acidification [47]. Moreover, OGAs rapidly induce systemic wound responses (SWR) and systemic acquired resistance (SAR), which rapidly spread throughout the plant body via complex signalling cascades involving and driven by electrical long-distance communication [47].

Besides these plant-specific transmitters, plants possess and use several classical transmitters, receptors and interacting molecules in their rapid cell-to-cell communication that are also present in neuronal tissues. For example, glutamate, ionotropic glutamate receptors, glycine, GABA, *N*-arachidonyl ethanolamine (NAE) anandamide, acetylcholine and ATP [1,8]. Whereas glutamate and glycine were shown to gate Ca⁺-permeable channels in plants, glutamate was reported to rapidly depolarize the plasma membrane in a process mediated by glutamate receptors [8]. Therefore, whereas glutamate might represent an alternative to auxin as a plant excitatory transmitter, GABA seems to act as an inhibitory transmitter in plants, as it does similarly in neurons. For instance, it is well documented that GABA is rapidly produced under diverse stress situations and also that GABA can be transported from cell-to-cell across plant tissues [8].

cells [1,2]. Besides the well known secondary metabolites such as theine, caffeine, nicotine, cocaine, morphine and cannabis, plants also contain several neurotransmitter-like molecules relevant for calcium-regulated exocytosis and vesicle recycling at neuronal synapses [1,8,20,21] (Box 1). Many of the neurotransmitters are derived from, and are also structurally similar to, amino acids. Therefore, it is not surprising that amino acid- and neurotransmitter transporters are highly conserved between animals and plants [22].

The plant synapse: a useful concept?

Soon after the discovery of neurons by Santiago Ramón y Cajal, the concept of the synapse was proposed by Charles Scott Sherrington in 1897 for adhesive sites of neuronal cell-to-cell contacts specialized in communication between neurons. For many years, this concept was reserved solely for neurons. However, current advances in immunology have resulted in general acceptance of the term 'immunological synapse' for cell-to-cell contacts between T cells and antigen-presenting cells (APCs) [23]. Recently, this synaptic concept was extended further by the proposal of a 'virological synapse' to explain the viral cell-to-cell spread across animal tissues [24].

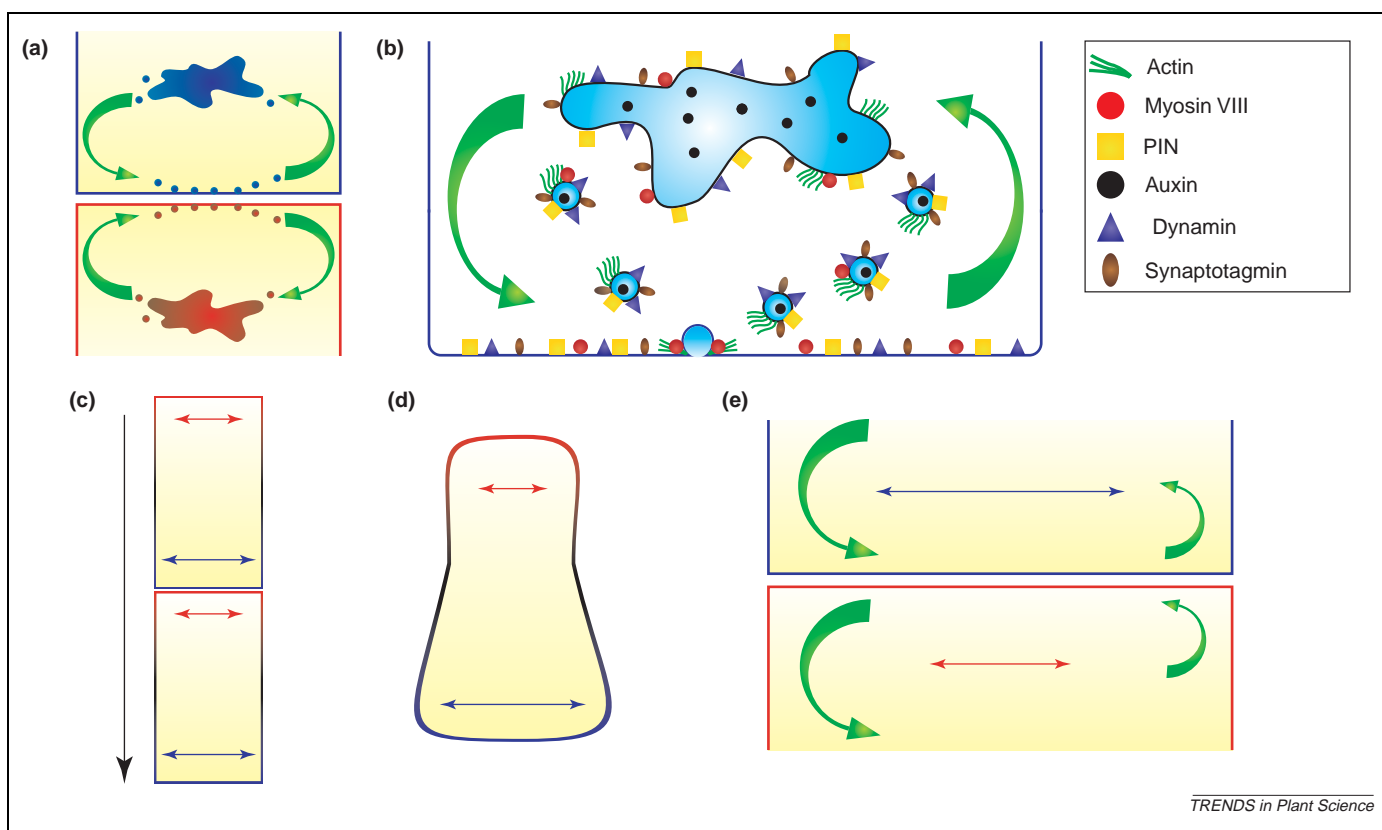
Neuronal molecules and principles of fast excitatory neurotransmission also proved to be useful for explaining the rapid adaptive responses of bone cells to mechanical strain [25,26]. Moreover, the neuronal transmitters GABA and glycine, and their vesicular transporters, are essential for paracrine transmitter interplay in the pancreas [27]. All these findings strongly support the 'conscious cell' concept proposed by Lynn Margulis – that all eukaryotic cells are able to use neuronal principles for controlling their complex behavior in the face of the huge amount of information that cells continuously receive, store and process for making adaptive decisions about their further states and activities [28].

If the term 'synapse' is defined in its broadest sense as a 'stable and asymmetric adhesive domain across which information is relayed by local vesicle recycling' [23], then

the end-poles (cross-walls) of plant cells [14,15] can be considered to represent 'plant synapses' (Figure 1a,b). Plasmodesmata are abundant at plant synapses [15] and are responsible for electrical coupling across plant synapses (reviewed in Ref. [15], see Table 1 in [23] for other types of synapses). In addition, signalling proteins are also found to be enriched at plant synapses [14]. As in the case of the 'immunological synapse' [23], introducing the concept of the 'plant synapse' should prove to be beneficial for the progress of contemporary plant cell biology, which currently lacks any satisfactory explanations for phenomena such as gravisensing and polar transport of auxin (Figure 1c–e). The polar transport of auxin not only mechanistically links gravisensing with the graviresponse of plant organs [29] but also drives bending responses of organs in response to light stimuli, thus shaping the whole plant body [30,31]. In addition, plants are capable of forming cell-to-cell junctions with cells of another organism (plant–fungi–bacteria), which corresponds with the definition for 'immunological synapse'. These specialized cell-to-cell adhesion domains involve the plasma membranes of two organisms opposing each other (Figure 2). Such adhesive domains are sites of active cell-to-cell transport of diverse molecules and metabolites. We propose that they represent 'immunological plant synapses', which might entail plant-specific aspects such as the formation of cell wall appositions called papillae at sites of penetration attempts, haustorial complexes, mycorrhizal arbuscles and tips of rhizobial infection threads (Figure 2).

Polar transport of auxin across the developmental plant synapse

Most of the auxin within the plant body flows down along the gravity vector. Auxin is transported transcellularly from the shoot apex towards the root apex within the stele. At the root cap, this stelar acropetal flow of auxin is redirected into basipetal flow, which takes place in the cortex [30,31]. This transcellular as well as polar transport of auxin is mediated by carriers of the PIN family, which are generally considered to be active at the plasma



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Figure 1. Developmental auxin-transporting plant synapse and its role in gravisensing. (a) In axial plant organs such as roots, cross-walls (synapses) transport auxin from cell-to-cell; the recycling of the putative auxin efflux carrier PIN1 (blue) and the auxin influx carrier AUX1 (red) is essential for this process. (b) Several molecules have been localized to these auxin-transporting plant synapses. (c) Because of gravity force, the protoplast exerts a greater mechanical load on the physical bottom of any cell in axial plant organs (indicated by the larger size of the blue arrow). This asymmetric protoplasmic load is effectively balanced by robust cell walls maintaining tubular cell shapes. (d) The absence of this protective force would result in a distortion of the protoplast shape because of the preferential accumulation of protoplasmic masses at the physical bottom. (e) A differential mechanical load exerted on the plasma membrane domains, which constitute the plant developmental synapse, results in a high plasma membrane tension experienced at the physical bottom, which inevitably facilitates more exocytic events and less endocytic events [42] at the blue (PIN1-enriched) plasma membrane domain, whereas the opposite situation is encountered at the red (AUX1-enriched) domain. This inherently asymmetric nature of plant synapses, encompassing both molecular and physical aspects, results in the polar transport of auxin along the gravity vector.

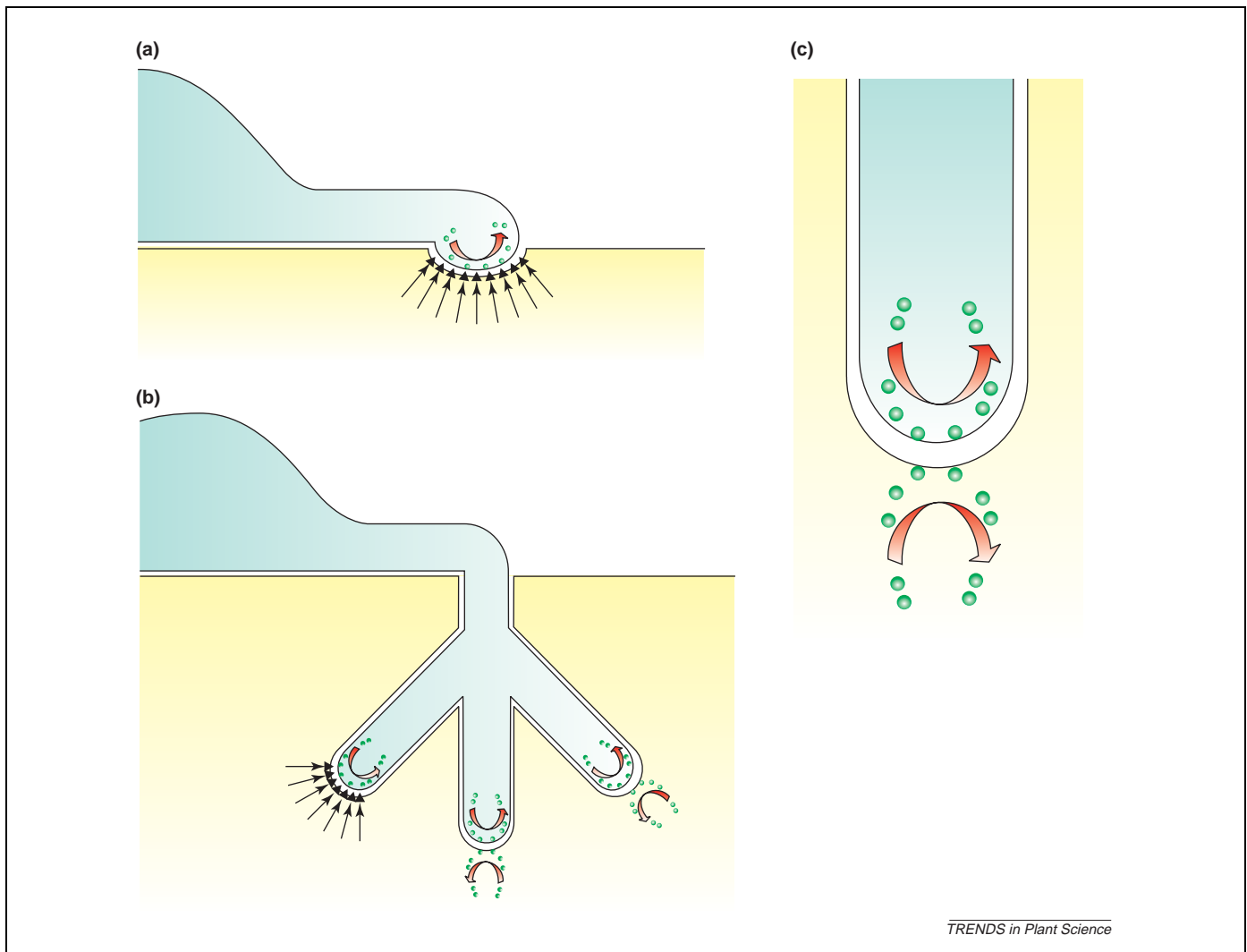
membrane [32]. However, auxin transport inhibitors appear to be general inhibitors of vesicle recycling [33] and their actions can be mimicked by inhibitors of vesicle trafficking [34]. In addition, the powerful inhibitor of secretion, Brefeldin A, as well as pH-mediated inhibition of endosomal activities both inhibit of cell-to-cell transport of auxin. Brefeldin A-induced inhibition of transcellular auxin transport can be observed within a few minutes [35], when most of these putative efflux carriers (e.g. PIN1) are localized to their presumptive site of action: the plasma membrane [16,33]. All this suggests that auxin is not transported directly across the plasma membrane but rather exported from cells via vesicular pathways (Figure 1b), as proposed by several authors [17,34,36]. In this scenario, the auxin efflux carrier PIN1 loads cytoplasmic auxin into endosomes and vesicles [37] derived from these endosomes [16,17]. Subsequently, such auxin-enriched vesicles act as carriers for the quantal release of auxin by means of exocytosis in a neurotransmitter-like mode [15,17]. In accordance with this 'neuronal' concept of auxin export, defects in vesicle trafficking in a myosin XI mutant of *Arabidopsis* are accompanied by failures of the basipetal auxin transport [38].

Neurotransmitter-like cell-to-cell transport of auxin would explain several of the unique abilities of this signalling molecule, which is still generally considered to

be a plant hormone. Auxin is one of the most ancient plant-specific signalling molecules [39] and its mode of action also fulfills criteria of a morphogen [40]. Thus, this small signalling molecule integrates hormonal, morphogen and transmitter functions, which makes studies of auxin extremely complicated. After almost a century of studies, we still have profound problems in explaining the nature of auxin coherently. Transcellular auxin transport is sensitive to light and gravity whereas extracellular auxin initiates the electrical responses of plant cells [8] and acts as a synchronizing signal for cell divisions along cell files [41]. All this raises numerous questions about the signalling nature of auxin – the 'neuronal' view of auxin that we propose here gives us a completely new perspective in tackling these enigmatic issues.

Gravisensing at the plant developmental synapse

It is well known that plant cells are not only excitable but also extremely mechano-sensitive and that they use this inherent property for navigating their growth along the gravity vector. Auxin is essential for inherent coupling graviperception to the growth response; the plant synapse concept might be useful to understand this important aspect of plant cell biology. In contrast to the current concepts of perception–response coupling in gravitational plant biology, the synaptic concept favours the equilibrium



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Figure 2. Immunological plant synapses for cell-to-cell communication between plant host cells and their pathogens, parasites and symbionts. **(a)** Closely apposed plasma membranes of intruder and host cell during a penetration attempt. If the host cell succeeds in effectively forming a papilla then this synaptic cell-to-cell communication is terminated. **(b)** Alternatively, the intruder might penetrate deeply into the host plant cells and then immunological plant synapses support haustorial complexes and mycorrhizal arbuscles. **(c)** During the initiation of a *Rhizobia*-plant symbiosis, bacteria organize infection threads, the tips of which represent immunological plant synapses specialized for transporting bacteria deeply into root tissues.

between exocytosis and endocytosis as being ‘at the heart’ of those mechanisms that underlie the gravity-mediated shaping of plants. Domain-specific local endocytosis and vesicle recycling is determined by the mechanical tension exerted on the plasma membrane (i.e. high tension promotes exocytosis, whereas low tension facilitates endocytosis) [42]. Because the physical load of the whole plant protoplast is lowest at the top and highest at the bottom of tubular plant cells (Figure 1c,d), the plant developmental synapse comprises two plasma membrane faces that differ in their gravity-induced tension-stress: the upper one is under high tension, whereas the lower one is under low tension (Figure 1e). Any deviation of the plant cells from the vertical position will shift the position of the gravi-responsive synaptic domains that secrete auxin out of the cell, and this would then increase the amount of auxin at the new physical bottom. This sequence of events has been recorded in gravistimulated root apices [29,43] and it appears to be a simple way to harmonize the location of plant synapses along the gravity vector. It is also important to note that the low tension of the plasma membrane

at the physical top of a cortical cell is likely to support a high rate of endocytosis because endocytosis can be mechano-sensitive and upregulated in pollen tubes grown under microgravity conditions [44]. This scenario is valid for the acropetal flow of auxin, whereas the basipetal one, which is restricted only to the growing portion of the root apex and which flows against the gravity vector, must be based on more complex phenomena. Last but not least, SNAREs and other highly conserved molecules that drive vesicle trafficking are important for gravisensing and graviresponses in plants [45].

Pathogen, parasite, symbiont – host cell interactions via immunological plant synapses

SNAREs and vesicular trafficking emerge as crucial molecules and processes not only for gravisensing and graviresponses but also for plant responses to pathogen attack as well as for parasitic and symbiotic cell-to-cell interactions [46]. Moreover, the success of the defence mechanisms depends on the ability of the host cells to maintain the adhesive cell wall–plasma membrane domains at

cell-to-cell interaction sites [46]. Thus, the synaptic concept might turn-out to be useful in understanding the molecular mechanisms in these situations too.

Large vesicular structures enriched with H₂O₂, and perhaps other signalling molecules, accumulate at sites of pathogen attack [46] and seem to be crucial for the success of the plant synapse. These pathogen-induced plant synapses (Figure 2) are also the sites of dense F-actin accumulation and they recruit the vesicular trafficking apparatus, effectively polarizing the cytoplasmic architecture [46]. Intriguingly, pectins emerge as plant-specific adhesion molecules and their fragments act not only as pathogen elicitors but also as long-distance signalling molecules with properties antagonistic to auxin [47] (Box 1). This suggests that they might act as inhibitory transmitters of plant synapses. Cell wall pectins are internalized via endocytosis and then co-localize with recycling auxin efflux carriers [48], indicating that pectins and auxin might use the same recycling pathways at plant synapses.

Identification of 'self' through plant synapses?

The plant synapse concept can also help to explain the latest enigma of plant biology – the ability of whole roots to discriminate between 'self'- and 'non-self' neighbours and to adapt their growth and physiology accordingly [13]. Fertile soil is densely packed with root biomass and every root is competing for space and for the limited resources of oxygen, water and mineral nutrients. Roots are able to modulate their growth according to the presence of roots of the same individual and roots of other individuals of the same species, or even of other species [12]. It is a mystery what processes and mechanisms are behind the ability of plant roots to identify 'self' from 'non-self'. A recent breakthrough study discovered that root cuttings from genetically identical plants start to perceive each other as 'non-self' after a short time of separation from the parent body, which suggests that unknown non-genetic processes determine the ability of 'self' and 'non-self' recognition in plants [13]. The concept of the plant synapse might provide a useful framework for explaining this enigma of plant biology because synapses are fundamentally important for 'self and non-self' discrimination at both cellular (immunological synapses) and organismal (neuronal synapses) levels [49].

Conclusions and outlook

Plants assemble and maintain two types of oppositely positioned membrane domains separated by a cell wall that resemble the neuronal and immunological synapses of animal cells. The first one transports auxin and allows the highly plastic development of plants. The activity of this type of so-called developmental plant synapse is modulated by two physical parameters: light and gravity. The second type of plant synapse resembles the immunological synapse of animal cells and allows plants to cope with pathogen and parasite attacks as well as to develop stable symbiotic interactions with *Rhizobia* bacteria and fungal mycorrhiza. We expect the concept of the plant synapse to be useful in explaining unanswered questions about plant cell biology such as the perplexing status of

auxin and the enigmatic nature of its polar transcellular transport along the root–shoot polarity axis guided by gravity and light. Because exogenous auxin exerts rapid electric responses and elicits increases in cytoplasmic calcium levels in plant cells [8], it is conceivable that auxin represents a transmitter of electrical cell-to-cell communication, in addition to its other better-understood roles.

Plant immunological synapses allow cell-to-cell communication between two different organisms, resulting either in the development of pathogen resistance and sensitivity or in the unfolding of complex parasitic and symbiotic interactions. Furthermore, plant synapses might represent the crucial structures that determine the integrity of individual plants by allowing their cells and organs to define and detect 'self' and recognize 'non-self' [13,49]. Last but not least, the plant synapse concept would explain why plants are able to use non-genetic 'public' information [50] transmitted between species boundaries [12,50] for their trial-and-error-navigated and experience-based behaviour [11,12]. Synapses might provide the information platform that confers the integrity and self-consciousness [13,49] to multicellular organisms. All this suggests that plants are much more similar to animals than one would have been willing to believe a few years ago.

To move forward and to bring plant electrophysiology back into the mainstream of plant biology in the form of plant neurobiology, we should focus on crucial molecules such as synaptotagmins [17,20]. The *Arabidopsis* genome expresses six synaptotagmins [20] and our preliminary data using both antibody and green fluorescent protein approaches (Voigt, B., Davletov, B., Craxton, M., Menzel, D. and Baluška, F., unpublished) reveal that they localize to plant synapses in root apices. This gives us hope that plant synapses will also be accessible to the new technologies of plant biology which, when combined with classical electrophysiology, will give us a chance to understand intelligent plants from their neurobiological perspective.

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