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Systemic signaling in response to wounding and pathogens

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Plants possess systemic signaling networks that allow the perception of local stresses to be translated into plant-wide responses. Although information can be propagated via a variety of molecules such as hormones and RNAs moving within the bulk flow of the phloem or in the transpiration stream, the vasculature also appears to be a major pathway whereby extremely rapid signals move bi-directionally throughout the plant. In these cases, the movement mechanisms are not dependent on redistribution through bulk flow. For example, self-reinforcing systems based around changes in Ca^{2+} and reactive oxygen species, coupled to parallel electrical signaling events appear able to generate waves of information that can propagate at hundreds of μm/s. These signals then elicit distant responses that prime the plant for a more effective defense or stress response in unchallenged tissues. Although ion channels, Ca^{2+}, reactive oxygen species and associated molecular machineries, such as the NADPH oxidases, have been identified as likely important players in this propagation system, the precise nature of these signaling networks remains to be defined. Critically, whether different stimuli are using the same rapid, systemic signaling network, or whether multiple, parallel pathways for signal propagation are operating to trigger specific systemic outputs remains a key open question.

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Introduction

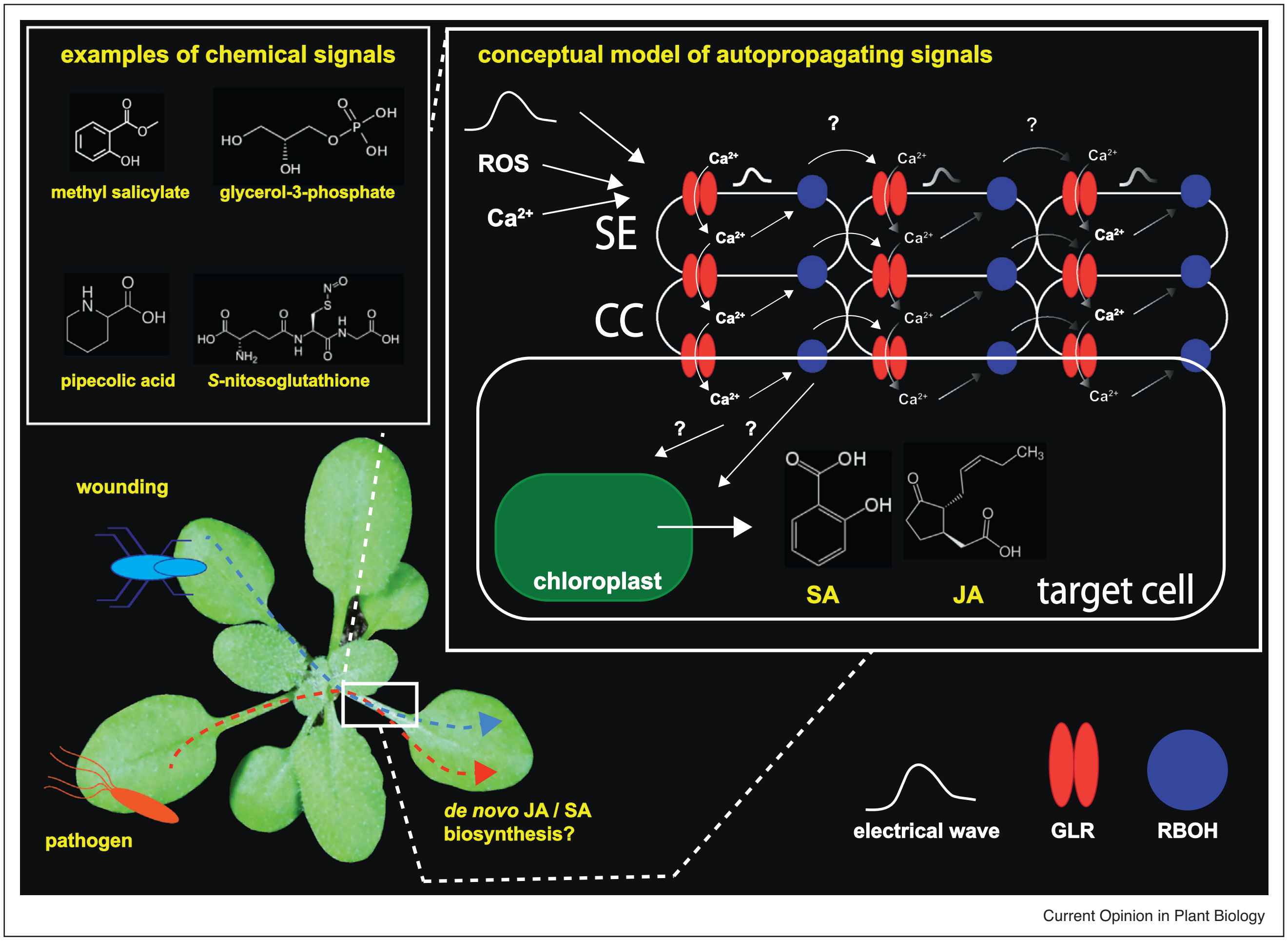
Biologists have long known that plants show the ability to perceive events locally and then translate them into distant, often plant-wide reactions. Such systemic plant responses are classified into broad categories based on the triggering stimulus: systemic acquired resistance (SAR) to pathogens (reviewed in [1]), systemic wound responses (SWR) to damage and herbivory (reviewed in [2]) and systemic acquired acclimation (SAA) to abiotic stresses (reviewed in [3]). The theme behind these plant-wide response networks is that the signals generated by a local stimulus lead to distant parts adapting more efficiently to subsequent stresses of the same (or often of different) nature. For SAR, this effect can translate into the mounting of a more rapid and efficient defense response [4,5] and for SAA, local stressing of one leaf can lead to the ability to withstand high levels of for example, light and heat stress in other leaves (e.g., [6,7]). Such changes can even be passed from generation to generation, providing a significant advantage to the ‘primed’ offspring [8–10] and potentially even to those offspring’s own progeny [8]. In the case of SAR, these transgenerational effects are likely being mediated via a salicylic acid (SA)-dependent epigenetic mechanism centered on RNA-directed DNA methylation [11].

For a localized stress to trigger such long-range responses requires signaling networks that integrate activities across the entire plant body. The cells of the vascular system are emerging as likely central conduits for such rapid, long-distance information exchange. Indeed, the vasculature has long been recognized as an information superhighway, providing systemic interconnection between distant organs to coordinate physiology and development. This long-range signaling is thought to be accomplished through the exchange of a host of signals ranging from proteins and RNAs to hormones and metabolites carried by the flow of the transpiration and translocation streams [12,13]. However, we are only now just beginning to understand the makeup of a parallel machinery that uses signals such as reactive oxygen species (ROS), Ca^{2+} and electrical changes that is also likely using the vasculature to propagate stress-related information throughout the plant at speeds of hundreds of μm/s (Figure 1).

Information flow: RNAs, proteins and metabolites

A wide spectrum of potential signaling molecules have been seen moving in the vasculature ranging from hormones and metabolites to proteins and RNAs (reviewed in [12,14]) that all have the potential to be carrying systemic information. The challenge now is to define specific information-carrying molecules from those caught up in the mass transit from, for example, source to sink [15•] and from those that may represent the cellular debris of the developmental transition from

Figure 1



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Local stresses such as leaf wounding or pathogen infection can elicit long-distance signals that propagate through the vasculature to affect defense responses in distal leaves. In local leaves, production of a structurally diverse set of chemical signals (e.g. methyl salicylate, G3P, pipecolic acid, *S*-nitosoglutathione, jasmonic acid, salicylic acid) occurs. These signals can then potentially be: (1) transmitted to distal leaves through the vasculature, or other symplastic transport mechanisms, or (2) trigger downstream long-range signaling networks. Auto-propagating signals (e.g. electrical waves, calcium waves, and ROS waves) can rapidly move to distal leaves to induce systemic response such as *de novo* synthesis of defense compounds (e.g. jasmonic acid for wounding/herbivory and salicylic acid for biotrophic pathogen infection). These waves of information likely work in a self-reinforcing manner, by which membrane depolarization through gating of plasma membrane ion channels may activate further plasma membrane calcium channels in a feed-forward loop. The GLR family of channels appears important in this network but their precise role(s) remain to be defined. Increased cytosolic calcium can in turn activate RBOHs through binding to the N-terminal EF hands on this enzyme, increasing ROS, leading to further ion channel gating and so wave propagation. A major unanswered question at present, is how far this model can be applied to the conducting cells of the phloem.

proto-phloem, with its full array of cellular components, to the much reduced architecture of the mature sieve element. Recently, for RNAs, a structural motif that may define motility within the vasculature has been reported, providing hints toward a mechanism for specificity and potentially for specific information flow. Thus, endogenous plant mRNAs containing tRNA-like structures (TLS) have been seen to be preferentially trafficked through the phloem [16•]. mRNAs that are not normally seen in the phloem could be engineered to be transported once this TLS 'stem-bulge-stem-loop' structure had been added. Positive stranded RNA viruses also appear to use TLS-like motifs to potentiate their transit through the phloem. At first glance, this type of movement seems like it should be limited to the source to sink bulk flow of the translocation stream. Yet, grafting experiments have shown long-distance RNA movement that does not simply mirror these source–sink relationships (e.g., [17]), implying an alternative motility machinery. The possibility that plants possess such a multi-directional macromolecule transport system that permeates the plant body and carries a specific subset of information carrying molecules may sound unlikely. However, the PIN, AUX/LAX, ABCB system driving polar auxin movements (reviewed