Article Addendum

Chemical Signal as a Rapid Long-Distance Information Messenger After Local Wounding of a Plant?

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KEY WORDS

tobacco, local burning, systemic response, hydraulic surge, electrical signal, abscisic acid, jasmonic acid

ABBREVIATIONS

ABA abscisic acid
JA jasmonic acid

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Addendum to:

Electrical and Chemical Signals Involved in Short-Term Systemic Photosynthetic Responses of Tobacco Plants to Local Burning

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ABSTRACT

A series of works have described an important role of chemical signaling compounds in generation of the stress response of plants in both the wounded and distant undamaged plant tissues. However, pure chemical signals are often not considered in the fast (minutes) long-distance signaling (systemic response) because of their slow propagation speed. Physical signals (electrical and hydraulic) or a combination of the physical and chemical signals (hydraulic dispersal of solutes) have been proposed as possible linkers of the local wound and the rapid systemic response. We have recently demonstrated an evidence for involvement of chemical compounds (jasmonic and abscisic acids) in the rapid (within 1 hour) inhibition of photosynthetic rate and stomata conductance in distant undamaged tobacco leaves after local burning. The aim of this addendum is to discuss plausible mechanisms of a rapid long-distance chemical signaling and the putative interactions between the physical and chemical signals leading to the fast systemic response.

Plants have evolved an amazingly complex system of defence-related strategies to protect themselves upon local wounding.¹⁻⁷ Important characteristics of self-defence responses of plants are their velocity and ubiquity. Indeed, fast (minutes to hours) responses to injurious factors have been detected in the site of injury and in distant regions (systemic response) in various plants.⁸⁻¹¹ These findings suggest that a signal generated by an attack to one leaf is transmitted through a whole plant. Several kinds of chemical^{3,6} and physical¹² signals induced by local wounding and even their combination¹³ have been implicated. However, a little is known about the interactions of these signals and about the mechanisms of initiation of the short-term systemic responses.

We have used a model system—tobacco plants exposed to the local burning—to study the signals involved in rapid wound responses of photosynthetic apparatus.¹⁴ Local burning of an upper leaf of a tobacco plant induced rapid changes in surface electrical potential (within seconds) and a pronounced fast decline in the stomatal conductance, CO₂ assimilation and transpiration (within minutes) in the basipetal direction (Fig. 1). Moreover, we have detected a fast (within minutes) transient increase in levels of endogenous abscisic acid (ABA) followed by a huge rapid rise in endogenous jasmonic acid (JA) in the leaf below the burned one. ABA and jasmonates are known to be involved in signaling pathways leading to stomatal closure and downregulation of photosynthesis.^{15,16} Increases in ABA and/or JA levels have only previously been detected in remote untreated tissues several hours after local wounding^{8,9} suggesting that chemical signals are too slow to induce rapid systemic response. Previous works have reported that fast physical (electrical) signals play an essential role in short-term systemic photosynthetic responses.^{11,17} However, a several-minutes delayed stomata closing response after the initiation of electrical potential changes has been reported in *Mimosa*¹⁸ and in our case in tobacco¹⁴ plants. Therefore, the guard cell deflation is most likely triggered not only by the electrical signal, but also by indirect factors. Based on close correlations, our results now provide a new evidence for the idea that chemical signals (ABA and mainly JA) participate in mediating the short-term systemic photosynthetic responses to local burning in tobacco plants.

The question is how do the physical (electrical and/or hydraulic) and chemical signals act? They may independently induce specific elements of systemic responses. However, they are more likely to act in a coordinated, interactive fashion. In this scenario (see Fig. 1), within first minutes after the local burning, hydraulic surge transmitted basipetally and acropetally through the xylem would transport chemicals released at the wound site (hydraulic dispersal¹⁹) and evoke changes in the ion fluxes in surrounding living cells leading to the local electrical activity.^{12,13} The hypothesis of hydraulic dispersal is

Figure 1. The model of putative signalling pathways leading to the rapid systemic responses of tobacco plants to local burning. Hypothetical (dashed lines) local responses, generation of signals and transport processes and detected (full line) systemic responses are demonstrated. For details see the text.

supported by our preliminary experiments with the fluorescent dye Rhodamine B applied on cut petiole of the upper leaf of tobacco plants showing that solutes can be rapidly transported (within minutes) basipetally following wounding.

The rapid kinetics and transient character of ABA accumulation¹⁴ suggest that the main transport mechanism is the hydraulic dispersal in xylem. The participation of ABA in the generation of systemic electrical activity and/or vice versa cannot be ruled out.^{8,20}

A rapid hydraulically driven transport of chemicals in the xylem of wounded plant in a reversed (basipetal) direction^{19,21} to transpiration stream is not generally accepted. Exposing of leaves of undamaged plants to radioactive labelled molecules to determine the speed of chemical signal transport could be misrepresent, because hydraulic signal is not generated in undamaged plants and then the detected transport speed is too slow. Moreover, previous work²² demonstrated that neither the mass flow itself, nor the associated pressure changes induce the systemic response (the proteinase inhibitor activity). Thus, the efficacy of chemical agents in rapid systemic signaling seems to depend on transport by the mass flows associated with hydraulic signals.¹⁹

However, hydraulic dispersal acts only for minutes, until all water released at the wound site is exhausted.²¹ A requirement for hydraulic dispersal of any solute is its presence in the wounded tissue at the time of wounding.¹⁹ Detected slower kinetics of JA accumulation than in the case of ABA and the huge rise of JA levels¹⁴ indicate a systemic accumulation of JA also by some additional processes.

Does additional JA accumulation result from de-novo synthesis in undamaged leaves as a response to physical signal or does it result from a JA transport from the wounded leaves? In the longer time-frame the phloem transport²³ should also be considered. Experiments

with tomato plants have shown that de novo JA synthesis in distant leaves is not required for the systemic response and that biosynthesis of JA at the wound site is necessary for the generation of a systemic signal.⁷ Indeed, a short-term increase in endogenous concentrations of JA has been detected in wounded tissue in *Nicotiana sylvestris*⁹ and rice.¹⁰

However, a rapid burst in the systemic JA accumulation found in our experiments¹⁴ would implicate an ultra-rapid and extreme JA accumulation at the wound site before its transport. The systemic JA accumulation (within 1 hour¹⁴) preceded the generation of enzymes involved in the JA biosynthesis in the wounded leaf.

Thus, several processes are suggested to play a role in the ultra-rapid and huge JA accumulation:

- (1) initiation of JA accumulation by preexisting enzymes,²⁴
- (2) fast release of free JA from its storage pools in cells (e.g., JA-conjugates²⁵),
- (3) direct uptake of elicitors (JA) by the phloem of the wounded leaf and exchange between the xylem and phloem as a consequence of severe wounds,²⁶
- (4) the mass flow (containing remaining JA) driven mainly acropetally in the xylem by transpiration after damping the hydraulic surge,²¹
- (5) JA accumulation evoked by the fast transmitting physical (electrical or hydraulic) signal that leads to imbalances in ion fluxes,^{8,12,27}
- (6) JA accumulation (and subsequent transport) directly in the phloem, where JA biosynthetic enzymes are located (at least in tomato²⁴),
- (7) volatile chemical compounds (methyl ester of JA) spreading in the surrounding air of wounded leaf could serve as signaling molecules and sources of JA.^{25,28}

The relevance of the above mentioned mechanisms should be checked by further research. Complex quantitative and kinetic analysis of JA and ABA content, levels of its biosynthetic derivatives (also volatiles in the surrounding air) and simultaneous physical signal detection in wounded and distant unwounded tissues would fill the remaining void about their role and interactions in the wound signal transduction networks. In addition, a suppression of other signaling pathways with similar transport kinetics (e.g., volatile compounds transmission, systemin and oligosaccharides generation and/or transport, using mutant plants) would be useful.

Substantial similarity between the rapid physical (electrical) signaling in animal nervous system compared with the physical (electrical) signaling in plants has already been reported.^{29,30} Interaction of chemical and electrical signals is the process well documented for post-synaptic events in animals. Our data now strengthen the role of chemical signals next to the role of physical signals in plants in the rapid systemic wound response; such a role of chemicals in plants was often underestimated up to now.

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