

# Division of Tasks: Defense by the Spatial Separation of Antagonistic Hormone Activities

Kenichi Tsuda\*

Department of Plant Microbe Interactions, Max Planck Institute for Plant Breeding Research, Carl-von-Linne Weg 10, D-50829 Cologne, Germany

\*Corresponding author: E-mail, tsuda@mpipz.mpg.de

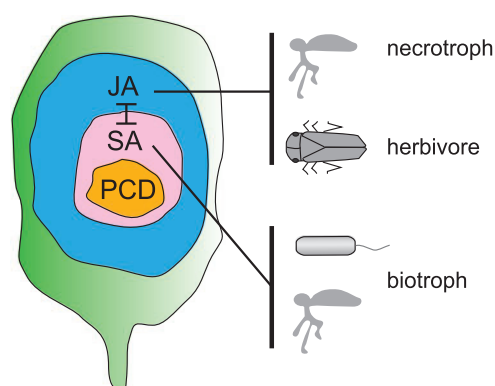
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Phytohormones are signal molecules produced within plants that regulate diverse physiological processes, including defense against pathogens. In particular, salicylic acid (SA) and jasmonate (JA) are major defense-related phytohormones (Berens et al. 2017). In *Arabidopsis thaliana*, SA signaling regulates defense against biotrophic pathogens that feed on living hosts, whereas JA signaling controls defense against insect herbivores and necrotrophic pathogens that actively kill hosts for nutrient acquisition (Glazebrook 2005, Berens et al. 2017). SA and JA signaling pathways inhibit each other and, as a consequence, one gains ascendancy over the other depending on the situation. Therefore, they are not assumed to be highly active at the same time. However, under certain conditions, both SA and JA signaling pathways are simultaneously activated within the same leaf tissue during immunity despite the antagonism. Currently, our knowledge is insufficient to resolve this conundrum.

In this issue, Betsuyaku et al. (2018) provided a simple answer for this problem: SA and JA signaling pathways are active in different adjacent cells, thereby achieving simultaneous activation within the same leaf. The authors generated transgenic *A. thaliana* plants expressing yellow fluorescent protein (YFP) fused to a nuclear localization signal, under the control of the promoters of the SA or JA marker genes *PR1* or *VSP1*, respectively. This set-up allowed them to analyze the activity of these phytohormones and their spatiotemporal dynamics at the single cell level. As a defense stimulant, they employed a strain of the bacterial pathogen *Pseudomonas syringae* (Mindrinos et al. 1994), which is known to trigger simultaneous activation of SA and JA signaling pathways (Spoel et al. 2003, Spoel et al. 2007). Then, they spot-infiltrated this bacterial strain into a leaf and monitored YFP signals around and within the infected spot for >2 d. In this infection mode, cells at the center of the infected spot underwent programmed cell death (PCD) as part of the plant defense response (Mukhtar et al. 2016). Strikingly, SA activity was observed in only several cell layers surrounding the PCD zone. Thus, SA signaling activity is strictly confined to the vicinity of the PCD zone and does not spread. On the other hand, JA signaling was widely but exclusively activated in cell layers outside of the SA active zone. Therefore, the SA and JA signaling pathways are activated in spatially separated domains within the infected leaf in a concentric manner: inner SA and outer JA (Fig. 1).

As is often the case with pioneering studies, the findings of Betsuyaku et al. (2018) have also generated many questions. For instance, how is the concentric pattern of SA and JA activity established? The authors provided a clue for this. They showed that activation of JA signaling precedes activation of SA signaling. This suggests that pre-activation of JA signaling confines the SA active zone to only cell layers between the PCD and JA active zones. How then is this JA active zone formed? Genetic analysis would solve whether the antagonism between SA and JA signaling determines their spatial separation. For instance, spatiotemporal analysis of the SA marker in JA mutants and the JA marker in SA mutants could prove highly valuable. It is also poorly understood how these phytohormones move from cell to cell within a tissue. Thus, understanding the mechanism for intercellular hormone transport would be essential ultimately to comprehend the spatiotemporal dynamics of SA and JA activities.

What is the advantage of spatially separating the activation of these defense pathways? As the authors discussed, cells in the JA active zone would defend themselves against pathogens and insect herbivores that are sensitive to JA-mediated defenses. This has an important implication in natural environments where plants are likely to be exposed to multiple enemies. By this means, defense responsibilities within a leaf are divided between cells that cope



**Fig. 1** Defense by spatial separation of antagonistic hormone activities. Salicylic acid (SA) signaling is activated in the zone (red) surrounding the programmed cell death zone (yellow). Jasmonate (JA) signaling is activated in the zone (blue) outside of the SA active zone. This spatial separation enables the leaf to defend itself against multiple enemies, which may increase the chance of leaf survival in nature.

either with biotrophic pathogens (SA zones) or with necrotrophic pathogens and insects (JA zones). Although the SA zone would be vulnerable to attack by necrotrophs and insects, the JA zone would be protected. Thus, the division of defense tasks into different zones of a leaf might increase the overall chances of survival of the entire tissue (Fig. 1). Some cells, such as meristematic cells, are essential for plants to grow and reproduce; therefore, plants cannot lose them. However, most leaf cells appear dispensable. Therefore, this 'plant zone defense' strategy in leaves may be more affordable for the plant as it saves resources compared with activating both pathways in all cells. Undoubtedly, further research is required to understand the physiological significance and generality of this spatial separation of hormonal defense pathways.

The importance of spatiotemporal information at the cellular level is well recognized in plant development, such as in the maintenance of the shoot apical meristem and organ initiation (Soyars et al. 2016). Betsuyaku et al. (2018) extend this notion by clearly pointing to the importance and necessity of spatiotemporal analysis in the context of plant immunity. Since extensive cross-talk between multiple immune signaling pathways exists, one would expect more publications reporting on tissue-wide spatiotemporal studies in future; these would certainly deepen our understanding of the complex plant immune signaling networks.

## Disclosures

The authors have no conflicts of interest to declare.

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