

Article Addendum

Do pathogen-specific defense mechanisms contribute to wound-induced resistance in tomato?

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A network of shared intermediates/components and/or common molecular outputs in biotic and abiotic stress signaling has long been known, but the possibility of effective influence between differently triggered stresses (co-protection) is less studied. Recent observations show that wounding induces transient protection in tomato (*Solanum lycopersicum* L.) to four pathogens with a range of lifestyles, locally and systemically. The contribution of ethylene (ET) in basal but also in wound-induced resistance to each pathogen, although dispensable, is demonstrated to be positive (*Botrytis cinerea*, *Phytophthora capsici*) or negative (*Fusarium oxysporum*, *Pseudomonas syringae* pv. *tomato*). Furthermore, the expression of several defense markers is influenced locally and/or systemically by wounding and ET, and might be part of that core of conserved molecular responses whereby an abiotic stress such as wounding imparts co-resistance to biotic stress. In this addendum, we speculate on some of the physiological responses to wounding that might contribute to the modulation of resistance in a more pathogen-specific manner.

The General Adaptation Syndrome in animals is described as a phenomenon by which an organism that has been confronted to a stress becomes “adapted”, i.e., can cope better with a subsequent stressful condition. The same was proposed to happen also in the plant kingdom.¹ In plants, there are several reported examples of cross-protection, but with very few exceptions they concern stresses within homogeneous “classes” (biotic/abiotic; one for all, Systemic Acquired Resistance; SAR)² and not biotic vs abiotic stresses, or vice versa. Instead, there are numerous reports that molecular responses

might overlap above the biotic/abiotic boundary; intuitively, this could underlie cross-protection phenomena. For example, responses to stresses like wounding and pathogen attack share potential coping denominators such as transducers, effectors of resistance, and hormones—among which ethylene—but the possibility of cross-protection was not investigated thoroughly.³⁻⁷ To demonstrate mutual interference between wounding and resistance/susceptibility to pathogens in planta, we tested 4 pathogens with different lifestyles (*Phytophthora capsici*, Pc; *Fusarium oxysporum* f.sp. *lycopersici*, Fol; *Botrytis cinerea*, Bc; *Pseudomonas syringae* pv. *tomato*, Pst) for virulence on WT and ethylene-insensitive tomato plants (Nr) which had been either left unwounded, or root-wounded at different times before inoculation. Our results show that: (i) wounding reduces disease severity transiently (protection peaks in plants wounded 3–7 days before inoculation) independently of the pathosystem, both systemically and locally; (ii) ethylene (ET) contributes to basal resistance either positively (Pc, Bc) or negatively (Pst, Fol); (iii) ET modulates the efficacy of wound-induced protection in accordance with its effect on basal resistance; (iv) wounding induces several markers of defense (PINIIb, PR1b, PR5, PR7 and peroxidase) locally and/or systemically, and ET perception is needed for full induction of all but peroxidase. The description of the general phenomenon of wound-induced resistance at point (i) is important, because it proves that metabolic costs related to wound repair do not generally decrease the plant fitness if pathogen attack follows. The fact that this holds true in four different pathosystems helps to generalize the finding. Again, the reasons behind this common behavior in response to wounding are likely to be in the overlapping molecular responses to the two stresses. This however does not exclude that specific mechanisms, both physiological and morphological, may contribute to the final protective effect against each tested pathogen. In this addendum, we wish to comment more extensively on the two of these pathosystems.

In the case of Pc, one such mechanism could be specifically linked to acquired refractoriness to zoospore attachment (a crucial step in infection); it is striking that disease severity trends—scored as damping off incidence—substantially match the tendency of zoospores to attach to roots. It is well known that zoospores of Oomycetes swim towards roots guided by concentration gradients in exudates and electric fields across membranes. Namely, planonts of

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living-roots pathogens are anodotactic, while zoospores of dead-roots pathogens would be attracted by inward positive fields generated locally by wounding and dying tissues in general. Because the effect on membrane polarity is lost within a few hours from damage, it is not surprising that fresh wounds are most attractive to this kind of zoospores.⁸⁻¹¹ Nothing is known precisely about the sensitivity of Pc zoospores to electric fields, but because it is a wound-attracted (although not wound-dependent) pathogen itself, it would be predicted to be cathodotactic. This is the most likely explanation for the high susceptibility in plants wounded at the time of inoculation [the only exception to the observation at point (i)] and could be tested by performing the same experiments in the presence of fusio-coccin to reverse the electric field around the roots. However, how to explain the reduced tendency to attract zoospores in roots wounded 3–5 days before inoculation compared to unwounded controls? It is unlikely that wounding influences membrane polarity on the long term; the most plausible effect would be rather on abundance or composition of root exudates. In this respect, the role of ET is also quite obscure. In our system, more numerous zoospores invariably encysted on Nr mutant compared to similarly treated WT plants. Either some defensive components are down-represented in the cell walls and/or exudates of ET-insensitive cells, so the success rate of the encystment process is higher, or attractive compounds are more abundant in the same tissues and their exudates. Could one such released metabolite be the ET precursor ACC? It is demonstrated that if the hormone is not perceived, cells upregulate its biosynthetic pathway, however no information is available on the ability of zoospores to use root-exudated ACC as chemiotactic stimulus. This hypothesis is probably worth be tested.

Also in the case of Fol, wounding induces resistance quickly and transitorily. It is known that wounding itself can induce tylosis, which can protect from embolism and vascular diseases while exacerbating wilting symptoms at the same time¹² (G. Tamietti, unpublished observations on tomato roots). However since ET orchestrates and promotes tylosis in response to wounding, at least in grapevine,¹³ this mechanism should not be prevalent in lowering the susceptibility of the ET-insensitive mutant compared to the WT plants. Indeed, it would be worth testing whether tylosis develops in the Nr mutant, and to which extent. As for Pst, the lack of ET perception not only induces higher tolerance to the disease (i.e., lower symptom expression for equal colonization; wilting and senescence are accelerated by ET), but also higher resistance to the pathogen (i.e., lower tissue colonization). To say it differently, these pathogens take advantage of ET action in an unknown physiological mechanism in tomato plants. This is yet another example of the trade-offs between different defense mechanisms being increasingly focused on by biologists interested in signaling and communication at all levels of plant organization.

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