

The risks of hospitality

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Received: 3 March 2011 / Accepted: 3 March 2011 / Published online: 18 March 2011
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Cellular integrity is essential, because the chemical gradients necessary to sustain life would otherwise be subdued by entropy. No wonder that, already, the earliest life-forms have developed mechanisms to defend their integrity against invaders. However, there are two occasions where cells have to adopt a softer approach towards integrity: first, when a cell has to take up molecules or other cells to support its own metabolism (endocytosis in its variants); second, when two cells of the same species fuse to initiate sexual propagation. Whereas the uptake of food is perfectly compatible with defence, the defence machinery has to be quelled or at least modulated during sexual fusion in such a way that the DNA of the (male) “guest” is not damaged. This evolutionary reasoning already illustrates that any fusion or perforation at the outer membrane must be under the control of specific signals. Many pathogens have developed, during an evolutionary arms race with their hosts, means to manipulate this signalling to circumvent or suppress defence by so called effectors (Jones and Dangl 2006), which allows them to remodel the plasma membrane and to penetrate into the host cell without killing it. It is rather unlikely that these so called biotrophic pathogens have invented such a complex manipulation de novo—they probably just usurped a signal cascade that already functioned in the host cell in a different context: to downregulate defence during sexual fusion. Two contributions in the current issue provide surprising details of haustoria formation that link sexuality with defence.

The work by Guan et al. (2011) in the current issue investigates resistance of the Chinese wild *Vitis pseudoreticulata* against powdery mildew (*Uncinula necator*). This biotrophic fungus penetrates into the epidermal cell and forms a haustorium which allows the invader to profit from the metabolism of the host. From the comparison of the resistant with a susceptible host genotype, they identified a glyoxal oxidase that is upregulated in the resistant host and localized in the apoplast. The function of this enzyme in plants is unclear; in wood-degrading fungi where it was originally discovered, glyoxal oxidase is secreted and seems to support the degradation process by generating hydroxy peroxides. The induction of glyoxal oxidase in the resistant *V. pseudoreticulata* might thus be either adaptive in nature or just a byproduct of defence. To test this, Guan et al. (2011) overexpressed the glyoxal oxidase in the susceptible host by agroinfiltration into young leaves that were subsequently infected with powdery mildew. They observed delayed and even partially arrested colonization in those leaf areas, where the transgene was expressed. Thus, the induction of glyoxal oxidase is sufficient to confer resistance to powdery mildew probably through the generation of extracellular reactive oxygen species that seem to suppress haustoria formation.

The work by Hiratsuka and Terasaka (2011) in the current issue describes haustoria formation in a completely different context. The pollen tubes of many gymnosperms (that represent an evolutionary precursor of “modern” angiosperm pollen tubes) are branched. Some of these branches do not convey sperms, but penetrate into the extracellular matrix of the female nucellus acting as haustoria that support the male gametophyte during the often several months between pollination and sperm delivery. The transmitting tissue in the style secretes specific arabinogalactan proteins that guide pollen tube

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growth and seem to be even incorporated into the pollen tube walls (Qin et al. 2007). Interestingly, extracellular reactive oxygen species play a role in this process; however, on the part of the “guest”, a tip-localized NADPH oxidase generates reactive oxygen species that are required to sustain pollen-tube growth (Potocký et al. 2007). Investigating the branched pollen tubes in *Pinus densiflora*, Hiratsuka and Terasaka (2011) provide evidence that some branches act indeed as haustoria that extract material from the nucellar cells. Stimulated by pollination, starch grains were synthesized in nucellar cells, but were degraded when the pollen tube penetrated into the nucellus. The nucellar cells undergoing programmed cell death produced electron-dense vacuoles displaying autophagic structures that were then transferred as vesicles into the pollen tube after passage through the extracellular matrix. Thus, the interaction of a biotrophic pathogen with a susceptible angiosperm host recapitulates certain aspects of the interactive devel-

opmental programme observed in pollen tube/nucellus interaction in gymnosperms.

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