
Meetings

Plant–microbe and plant–insect interactions meet common grounds

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Plant–microbe and plant–insect interactions are of global importance for agriculture and of high interest to many plant scientists, microbiologists and entomologists. Traditionally, plant–microbe and plant–insect interactions have been looked at as two separate issues, but in recent years it has become clear that the underlying physiological pathways in plants overlap substantially (Koornneef & Pieterse, 2008). The International Conference on Biotic Plant Interactions (ICBPI; www.uq.edu.au/plants/icbpi/) brought together scientists and students who are interested in plant pathology and in the beneficial interactions of plants with other organisms, including viruses, bacteria, fungi, oomycetes, nematodes, insects and other herbivores. To highlight this, two topics from this year's conference – harmful biotic plant interactions, and the interactions of plants with beneficial microbial communities – are discussed in this article.

'... identifying the overlapping defence mechanisms against pathogen and herbivore attack will reveal new insights into plant function and their responses to environmental pressures ...'

Harmful biotic plant interactions

Plants are sessile organisms that are exposed to a constant barrage of environmental stresses which impact on growth, development and reproduction. Important traits, such as yield and the resistance to biotic stress (e.g. pests and pathogens) and abiotic stress (e.g. ultraviolet light, drought,

salinity, high temperature and nutrient starvation) depend on internal physiological programs and their regulation by signal transduction pathways. Plants are the major source of food and biomaterials worldwide but their production is severely compromised by pathogens that cause disease and reduce yield and quality. The International Panel on Climate Change (IPCC) in their 'AR4 Synthesis report' recently predicted that stresses from climatic extremes will increase and impose significant difficulties, including higher susceptibility to pests and diseases and leading to estimated yield declines of up to 50%. In addition, the impact of climate change on plant defence chemistry, as discussed by Ros Gleadow (Monash University, Victoria, Australia), could reduce the nutritional value of crops, and the anthropogenic increase in CO₂ also compromises plant defence against invasive insects (Zavala *et al.*, 2008). Understanding how plants defend themselves against pathogens and herbivores, and how that may be manipulated, is therefore of critical importance for successful and sustainable agriculture. Boosting the plant's defence system by natural means also means less reliance on environmentally damaging pesticides.

As highlighted by many speakers at the ICBPI, identifying the overlapping defence mechanisms against pathogen and herbivore attack will reveal new insights into plant function and their responses to environmental pressures. It could also potentially lead to the discovery of unifying principles of plant stress tolerance. Currently, there is a worldwide search for genes that can improve crop performance to abiotic and biotic stresses, while plant genetic engineers and breeders increasingly aim towards producing more robust crop plants with reliable yields (rather than just high yields). Indeed, plant scientists have the opportunity to make a real impact, for instance by studying the underlying network of signalling pathways and molecules involved in stress responses and how these regulate both beneficial and harmful biotic interactions. The consequent gain in knowledge is critical in the development of new biotechnological approaches to benefit sustainable agriculture.

Disease resistance in plants is conferred by recognition, signal transduction and defence activation

Pathogen infection and attack by herbivores result in a number of molecular and physiological changes in plants (Fig. 1). The hypersensitive response (HR) is a form of programmed cell-death that is activated by plants after sensing challenge by an

Direct and indirect induced defence against pathogens and insects

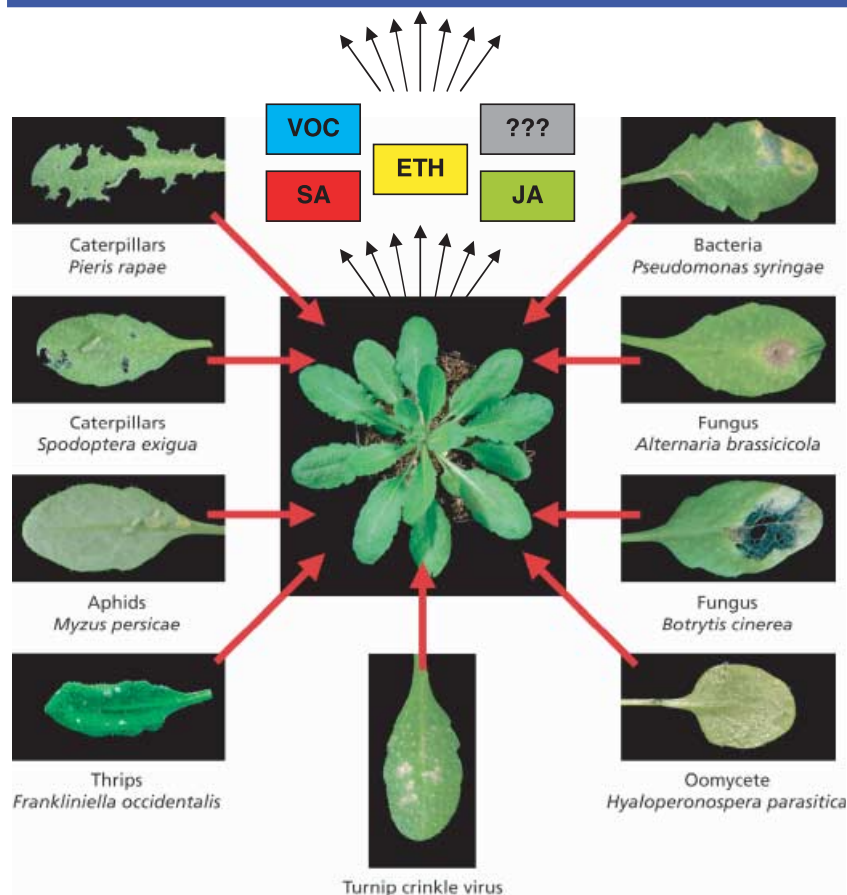


Fig. 1 Representation of the complexity of the plant's induced defence response to pathogens and insect herbivores. The interaction of *Arabidopsis thaliana* with pathogens and insects with different lifestyles or feeding modes results in the production of different defence signal signatures and blends of volatile organic compounds (VOC). Cross-talk between salicylic acid (SA)-, jasmonic acid (JA)- and ethylene (ETH)-dependent signalling pathways shapes the direct induced defence response, while the VOCs play a role in indirect defence.

avirulent pathogen. At the ICBPI the early recognition and signal transduction cascades, triggered by pathogen-associated molecular patterns and leading to resistance, were discussed at the molecular level for several pathogens, including viruses (tobacco mosaic virus), bacteria (*Pseudomonas syringae* and *Xanthomonas oryzae*), fungi (powdery mildews and flux rust), oomycetes (*Phytophthora infestans*) and insects. Shauna Somerville (Energy Bioscience Institute, Berkeley, USA) highlighted in her presentation that the plant cell-wall composition and alterations in this offer a first line of defence. However, in addition, plants also synthesize various signalling molecules, such as salicylic acid (SA), jasmonic acid (JA) and ethylene (ETH), all of which orchestrate a complex and interactive network of signalling pathways (Jones & Dangl, 2006; de Wit, 2007; Koornneef & Pieterse, 2008). As a result, pathogenesis-related (PR) proteins with direct defensive roles often accumulate in both pest/pathogen-challenged and unchallenged (systemic) tissue of the same plant.

Plant defence responses that are most effective against a group of pathogens differ depending on the life style of particular pathogens, which typically either require living cells (biotroph) or dead tissues (necrotroph) for proliferation, but many pathogens also alter their life style during disease progression. In *Arabidopsis*, an intact SA signalling pathway is believed to mediate the resistance to biotrophic pathogens, such as viruses, fungi (e.g. *Erysiphe orontii*), oomycetes (e.g. *Hyaloperonospora parasitica*) and bacteria (e.g. *P. syringae*), whereas the JA–ETH signalling pathway is thought to be necessary for resistance to necrotrophic pathogens, such as the fungus *Botrytis cinerea* and the bacterium *Erwinia carotovora* (Thomma *et al.*, 1998; Rojo *et al.*, 2003). Richard Oliver (Murdoch University, Perth, Australia) alerted researchers to the fact that many crops lack natural resistance genes against necrotrophic pathogens and often produce several toxins that interact with different host-susceptibility gene products. Similarly, as discussed by Corné Pieterse (Utrecht University, the Netherlands) and Karam Singh (CSIRO Plant Industry,

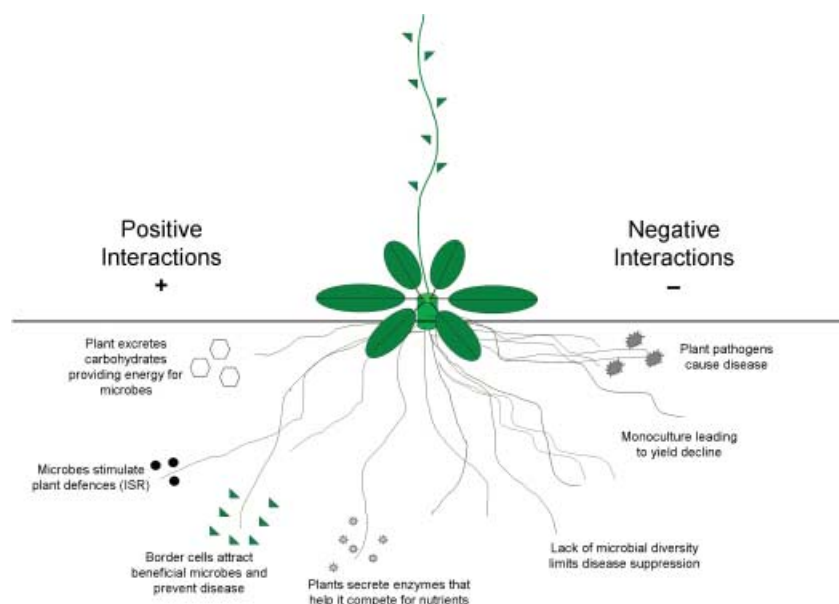


Fig. 2 Examples of root–microbe interactions and rhizosphere biology.

Floreat, Australia), different insects induce very different pathways according to their feeding mechanism and behaviour. For example, phloem-feeding insects, such as aphids and white flies, have been shown to activate the SA pathway, while tissue-chewing insects, such as leaf hoppers and caterpillars, generally activate the JA pathway. Furthermore, different plant volatile organic compounds (VOCs) may attract or repel insects and/or their predators, leading to defence activation in neighbouring plants (Myron Zalucki (University of Queensland, Australia), Alexandre Il-Ichev (Tatura Centre, Victoria, Australia), Kaplan *et al.*, 2008). Kevin Gould (University of Otago, Dunedin, New Zealand) also discussed how red anthocyanin coloration was believed to play a role in the protection of leaves against the ravages of insect herbivores. A new approach for insect resistance, involving plant-mediated insect gene silencing, was presented by Xiao-Ya Chen (Chinese Academy of Sciences, Shanghai, China). He showed how *Arabidopsis* plants that were engineered to produce double-stranded RNA which interferes with a cotton bollworm P450 gene led to stunted larval growth.

For effective defence, plants need to mount a targeted response to pathogen/herbivore invasion which activates only the genes and pathways that are required, whereas others need to be suppressed to conserve resources (Koornneef & Pieterse, 2008). Brigitte Mauch-Mani (Université de Neuchâtel, Switzerland) demonstrated this, showing how priming is a physiological state that may offer these advantages. Priming enables plants to mount different cellular defence responses more strongly or more rapidly when attacked by pathogens or insects or in response to abiotic stress. Priming can also be induced by treatment with natural and synthetic compounds and by beneficial microorganisms (Harman *et al.*, 2004; Beckers & Conrath, 2007). Well known, also at a commercial

level, is the use of some rhizobacteria and antagonistic fungi of the genus *Trichoderma*, as presented by Matteo Lorito (University of Naples, Italy).

Interactions of plants with microbial communities

Plants grown in natural environments are continually exposed to a variety of microorganisms. The complexity of this interaction is most apparent in the region between the plant roots and the soil microbes, and forms part of the plant rhizosphere. Plants co-evolved with soil microbes and have developed numerous and complex ways of managing these interactions. Fossil evidence of early plants suggests that microorganisms such as mycorrhizal fungi were essential for land colonization (Taylor *et al.*, 1995). Some interesting examples of interactions between plants and soil microbes that were discussed at the ICBPI are highlighted in the following section and are illustrated in Fig. 2.

Some interactions are clearly beneficial to the plant: they can improve nutrient availability, protection against diseases, or both. A textbook case is the interaction between legumes and soil rhizobia in specialized root nodules that convert atmospheric nitrogen gas into fertilizer for the plant, as presented by Brent Kaiser (University of Adelaide, Australia) and Peter Gresshoff (University of Queensland, Australia). Similarly, mycorrhizal fungi substantially increase water and nutrient uptake, and also increase resistance to soil pathogens (Pozo & Azcón-Aguilar, 2007) that cause disease on virtually all cultivated species. Kemal Kazan (CSIRO, Plant Industry, Queensland, Australia) considered this in his presentation, focusing on the wilt-causing fungus *Fusarium oxysporum*, a widespread destructive pathogen infecting the roots of a broad range of vegetable, ornamental, field and plantation

crops (e.g. wheat, cotton, tomato and banana). However, the majority of plant–microbe interactions are far more subtle and often involve more than two partners. For example, yield decline occurs when an agricultural crop has been grown as an exclusive monoculture on the same soil over a period of years. The effect manifests as a significant decrease in yields with each progressive season, with losses of more than 30% in crops, such as Australian sugarcane (Ken McGrath, University of Queensland, Australia). Yield decline has a major microbial component, as fumigation of affected soils reverses the decline in biomass yield. The introduction of crop rotation, hence breaking the monoculture lineage, can increase microbial diversity and yield in subsequent seasons (Pankhurst *et al.*, 2005).

Examples of beneficial rhizosphere interactions

Over the last few years, the field of rhizosphere biology has recognized the biological importance of root exudates in mediating interactions with other plants and microbes. Plants constantly secrete a diverse combination of antimicrobial root exudates, which appears to limit the number of microbes that can form a compatible interaction with the plant, resulting in disease (Bais *et al.*, 2005). Surprisingly, plant roots secrete up to 21% (and sometimes more) of all photosynthetically fixed carbon into the rhizosphere through root exudates (Marschner, 1995). Obviously, the plant is gaining a significant benefit to warrant this large energy expense. For example, root-derived antimicrobial exudates from *Arabidopsis* conferred resistance to a wide range of bacterial pathogens, while a pathogen that was resistant to these compounds blocked their synthesis and exudation, resulting in disease (Bais *et al.*, 2005).

Plant roots actively compete for organic nitrogen sources, such as protein. While the plant invests time and energy attempting to manipulate the soil microbiome, the existing microbial population has a marked impact on the growth of the plant. Roots secrete significant amounts of proteases, which facilitate the uptake of organic sources of nitrogen, such as amino acids. Interestingly, plant roots are even able to take up whole proteins, probably via endocytosis, thus actively competing with microbes for organic nitrogen sources (Paungfoo-Lonhienne *et al.*, 2008).

Aside from direct exudation, the roots of some plants can release border cells from the root tips into the rhizosphere during the normal growth process (Vicré *et al.*, 2005). These cells remain alive, being separated from the main plant but acting as agents for the plant's manipulation of the rhizosphere. For example, it has been shown that these cells can produce compounds that can immobilize nematodes, as well as alter the attachment of bacteria to the plant root (Vicré *et al.*, 2005). While it is clear that plant roots and border cells exude many compounds that affect certain microorganisms, very little is known about what effect this has on entire microbial

communities in the rhizosphere. Recently it has been shown that root exudates can vividly change the composition of the soil fungal community (Broeckling *et al.*, 2008).

Some species of the microbial rhizosphere can interact with the plant in a nonpathogenic manner to stimulate the production of plant defence responses. This effect, known as induced systemic resistance (ISR), can provide dramatic increases in resistance to a diverse range of plant pathogens, and has been shown to be effective under agricultural field conditions. Additionally, microbial populations from different soils can alter agronomic performance, resulting in changes in yields for several crops (Watt *et al.*, 2006).

Several presentations given at the ICBPI, including that by Chao-Ying Chen (National Taiwan University, Taiwan), focussed on the occurrence of soils that can actively prevent diseases from infecting pathogens. This rhizospheric effect has recently been investigated more in detail and the so-called 'suppressive soils' have been shown to prevent the infection of many soil-borne pathogens (Borneman & Becker, 2007). It has been demonstrated that a small amount of soil from a suppressive field can be used successfully to 'inoculate' other nonsuppressive fields, transferring this suppressive ability. Suppressive soils have been shown to be effective against many diseases, including *Fusarium* wilt and nematode infestation. The molecular and microbiological basis of this phenomenon has been partially clarified also with the aid of modern functional genomics techniques, including proteomics and metabolomics (Marra *et al.*, 2006). One of the most beneficial outcomes is the selection of superior biocontrol strains, which can then be applied worldwide as bioagents. Highly effective isolates of *Trichoderma*, *Pseudomonas*, *Agrobacterium*, *Bacillus*, *Streptomyces*, *Coniothyrium*, *Azospirillum* and nonpathogenic *Fusarium* species are the active ingredients in over 150 commercial formulations, acting in many cases as both biopesticides and biofertilizers. The global use of these products is beginning to make a significant impact in agriculture by improving yields while alleviating some of the negative effects such as pollution, loss of soil microflora and dependence on pesticides. Although the full potential of the natural germplasm from beneficial rhizospheric agents is far from being fully understood and exploited, it is certainly a tool that could be employed in the future.

The ICBPI meeting in Brisbane clearly demonstrated that plant defences against pathogens and insect herbivores are regulated by a network of interconnecting signalling pathways. The signalling networks that are activated by the plant in response to parasitic and beneficial organisms also overlap, which indicates that the regulation of the adaptive response of the plant is finely balanced between protection against aggressors and acquisition of benefits. Future research on how plants are able to cope with different harmful and beneficial biotic interactions will certainly yield exciting new information that can be utilized for the development of novel crop-protection strategies. The next ICBPI meeting is planned for

2010 in Shanghai and will no doubt provide an interesting update on the current progress being made.

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