Commentary

Regulation of cellulose synthesis – aNOther player in the game?

Cellulose is a central component in plant cell walls. In the primary cell wall (deposited in cells that are still expanding), it is a vital component of the load-bearing network and because of its physical properties is important in determining the orientation of cell expansion. After a period of cell expansion, some cells lay down a thick secondary cell wall inside the primary wall. The secondary cell wall provides plants with the mechanical properties that allow them to stand upright, and is a major component in properly functioning xylem vessels. Cellulose is one of the major components of secondary cell walls. The importance of cellulose in plant cell walls is reflected in it being the world's most abundant biopolymer, with an estimated 180 billion tonnes synthesized annually (Englehardt, 1995). Despite this importance, our understanding of how cellulose is synthesized, and how this synthesis is regulated, is still incomplete. In this issue of *New Phytologist* (pp. 386–396), Correa-Aragunde *et al*. describe how the signalling molecule nitric oxide (NO) modulates cellulose synthesis in tomato (*Solanum lycopersicum*) roots.

Pharmaceutical application of the NO donor sodium nitroprusside (SNP) was used to investigate incorporation of radiolabelled glucose into cellulose. Low (pmolar) concentrations of NO increased incorporation of radiolabelled glucose into the cellulose fraction in roots, whereas higher (nmolar) concentrations reduced incorporation into cellulose. These effects were transient and reversible, as determined by use of an NO scavenger. Microscopic analysis of root structure suggested that these differences were caused by effects on primary cell wall synthesis. Root length was reduced in plants treated with higher concentrations of NO and was accompanied by reduced cortical cell length and an apparent swelling of the root, phenotypes that are frequently observed in Arabidopsis mutants affected in primary cell wall cellulose synthesis. Three different cellulose synthase (CesA) catalytic subunits are generally considered to be required for cellulose synthesis, the three subunits being different in primary and secondary cell walls. Correa-Aragunde *et al*. identified three CesA transcripts from tomato cDNA libraries that are likely to be involved in primary cell wall cellulose synthesis, based on the similarity to three genes involved in this process in potato (*Solanum tuberosum*). The level of transcript of these three genes was slightly reduced by treatment with high concentrations of NO, suggesting that it may be at a transcriptional level that NO affects cellulose synthesis. Nitric oxide signalling in plants is an area in which there is still much to learn, and has been covered in a recent review (Wilson *et al*., 2008). It is clear, however, that NO is important as a signalling molecule in a number of processes in plants, and the description in this issue of its effect on modulating cellulose synthesis adds to a growing list of pathways that are affected by NO.

'It is the organization of multiple glucan chains into microfibrils that is absolutely central to the physical properties that they confer once deposited in the cell wall.'

Cellulose synthesis is central to plant development, but the way in which it is regulated is still unclear and is currently an area of intense research. Cellulose is a simple polymer of unbranched β-1,4-linked glucan chains, with successive glucose residues inverted 180 degrees to form a flat ribbon in which the repeating unit is cellobiose. These parallel chains are then able to form extensive hydrogen bonds between individual glucan chains resulting in crystallization of multiple chains into cellulose microfibrils – insoluble, cable-like structures. It is the organization of multiple glucan chains into microfibrils that is absolutely central to the physical properties that they confer once deposited in the cell wall. This organized structure of the microfibril is a direct result of the organization of the protein complex that synthesizes cellulose. The plasma membrane-bound cellulose synthase complex (CSC) is a large (> 4 MDa) protein complex that includes multiple copies of three different CesA proteins. It is currently not known if there are any other protein components. The CSC can be visualized at the plasma membrane in freeze-fracture electron microscopy as hexameric structures, which gives rise to them being known as rosettes. It is the organization of multiple copies of the three CesA proteins into a defined arrangement that allows the simultaneous synthesis of multiple β-1,4-linked glucan chains in a conformation that allows them to hydrogen bond and crystallize into the functional unit of cellulose, the microfibril (Fig. 1). The three CesAs required are different in primary and secondary cell wall CSCs, and the presence and activity of all three proteins is required for correct cellulose

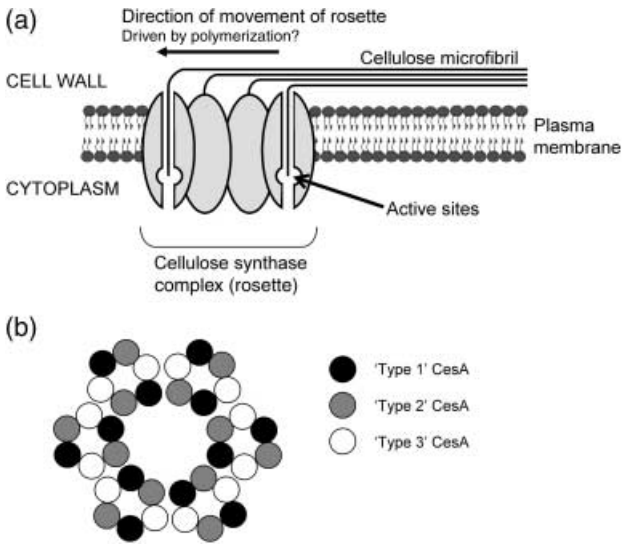

Fig. 1 Model of the cellulose synthase rosette. (a) A 'cross-section' through a rosette is shown, each 'lobe' containing a number of catalytic subunits. The active sites of these subunits are cytosolic, and the extending cellulose microfibril crystallizes as it enters the cell wall. (b) Plan view. Each of the six 'lobes' is predicted to contain multiple copies of three different 'types' of cellulose synthase (CesA) proteins. The exact number of CesA proteins contained within a lobe, their stoichiometry and their specific interactions are currently unknown.

synthesis (Gardiner *et al.*, 2003; Taylor *et al.*, 2003; Desprez *et al.*, 2007; Persson *et al.*, 2007).

Despite the importance of cellulose synthesis to plants, how it is regulated is not well understood. There are a number of different levels at which regulation of cellulose synthesis may occur, and much of our understanding has come from the use of the model plant Arabidopsis. Our current understanding of secondary cell wall cellulose synthesis is more advanced than that of primary cell wall synthesis, mainly because of the fact that plants lacking secondary cell wall cellulose are viable whereas plants lacking primary cell wall cellulose die at a very early stage of development. One consequence of a lack of secondary cell wall cellulose is a collapse of xylem vessels, a result of them being unable to withstand the negative pressure generated by the transpiration stream (Fig. 2) (Turner & Somerville, 1997). In Arabidopsis, a network of transcription factors have been identified that regulate secondary cell wall synthesis in different tissues (for a recent review of genes involved in regulating cellulose synthesis see Taylor, 2008 and references therein). These transcription factors appear to co-ordinately regulate synthesis of all the components of the secondary cell wall (cellulose, lignin and xylan). It is likely, however, that there is a cascade of transcription factors regulating secondary cell wall synthesis, and that further dissection of these networks may identify transcription factors involved in the activation of the individual pathways for the three major secondary cell wall polymers, including cellulose. A second level of regulation is likely to exist in the assembly of the CSC. The CSC is assembled in the endoplasmic reticulum and then transported intact to the plasma membrane. The way in which the three catalytic subunits are assembled into the rosette is currently unknown, but there is clearly a requirement for defined and specific interactions between the subunits, and the organization of such a large protein complex is likely to require the assistance provided by as yet unidentified molecular chaperones.

There is also a requirement for feedback regulation of cellulose synthesis from the cell wall, where the cellulose microfibrils are deposited, and the cytosol, where the catalytic domains of the proteins reside (Fig. 1a). One way in which this signalling across the plasma membrane could occur is by receptor kinases. These proteins, of which there is a diverse family of over 600 in plants, contain an extracellular 'sensing' domain and a linked intracellular kinase domain that can trigger a kinase cascade resulting in phosphorylation of target proteins (for a recent review of cell wall signalling see Humphrey *et al.*, 2007). Phosphorylation sites on the cellulose synthase catalytic subunits have been identified (Nuhse *et al.*, 2004; Taylor, 2007) but the precise role of phosphorylation at these sites has yet to be elucidated.

It is clear that there are multiple levels at which regulation of cellulose synthesis occurs. Despite its central role in plants, our knowledge of how cellulose synthesis is regulated is still very rudimentary and has to date mainly concentrated on developmental regulation. The study by Correa-Aragunde *et al.* in this issue demonstrating that NO affects cellulose synthesis in tomato roots contributes important knowledge on environmental regulation. Resolving some of the unanswered questions about cellulose synthesis is essential if we are to understand fundamental processes in plant development as well as better utilize the vast quantities of sugars contained in plant cell walls as a source of bio-energy to combat global

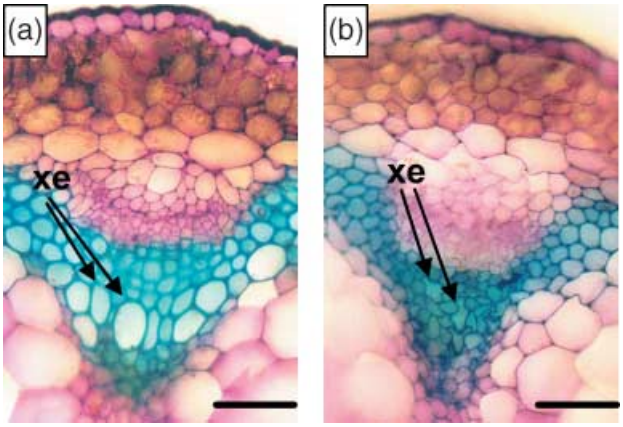

Fig. 2 Arabidopsis stem cross-sections of (a) wild-type and (b) a secondary cell wall cellulose-deficient mutant stained with toluidine blue. xe, xylem elements. Note the collapsed xylem elements in (b). Bars represent 0.05 mm.

climate change. Recent developments have given us hope that one day we may better understand the synthesis of cellulose, and how it is regulated both developmentally and environmentally.

Acknowledgements

NGT is supported by a Royal Society University Research Fellowship.

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Key words: cell wall, cellulose, cellulose synthesis, nitric oxide, plant development, regulation.

Letters

Enchilada redux: how complete is your genome sequence?

In 2004, Jorgensen made a pungent argument for sequencing entire plant genomes, entitled 'Sequencing maize: just sample the salsa or go for the whole enchilada?' (Jorgensen, 2004). For some of us, the genes in the genome *are* the enchilada, and the 80–90% plus of repeats in genomes, like those of maize and barley, amount to eight to nine orders of refried beans. Although we like these refritos more than most, we think that scientists would digest the data better, and produce less gaseous reports, if they mostly concentrated on the genes (as most do). Now, as multiple plant genomes proceed towards completed or draft full-genome status, it seems a timely moment to revisit this issue. Although the question of completeness is largely moot with current technology (no higher eukaryotic genome has been fully sequenced, although the nematode *Caenorhabditis elegans* and rice (IRGSP, 2005) come close), the argument has now shifted to consider what degree of incompleteness is tolerable. We think that this discussion, still somewhat a matter of personal philosophy, needs to continue. However, most importantly, we feel that investigators need to know to what degree the sequence that has been generated and assembled actually approaches completion. We propose here a simple and low-cost method to determine the level of genome sequence completeness, using the *Arabidopsis thaliana* genome as an example.

Back in ancient genome-sequencing days (i.e. 2000), when Arabidopsis provided the first comprehensive plant genome analysis, most sequencing involved clone-by-clone (e.g. BAC-by-BAC) sequencing and assembly across a minimum tiling path (MTP). Some genome projects, like the ongoing maize genome sequence, continue to follow this approach. However, it is now accepted that a certain level of shotgun genome sequence from whole-genomic DNA is a vital adjunct to clone-by-clone approaches, in order to account for

sequences not fully represented in the MTP. This idea had not yet been fully conceived when the Arabidopsis genome was published, so there was no such accompanying data. The participants in the Arabidopsis Genome Initiative (2000) knew that their *c*. 115 Mb assembly of largely contiguous sequence did not cover all of the genome, and they estimated that approx. 10 Mb of DNA had been missed (mostly in pericentromeric, centromeric and ribosomal DNA regions). This estimate appears to have under-represented the true case. By generating a detailed physical map of Arabidopsis centromeres, Hosouchi *et al*. (2002) predicted that > 30 Mb of the genome had not yet been sequenced. By using an unrelated approach (nuclear microfluorescence, with flanking genome size standards (*c*. 100 Mb of *C. elegans* and *c*. 175 Mb of *Drosophila melanogaster*)), Bennett *et al*. (2003) predicted that the Arabidopsis genome in the Columbia ecotype was *c*. 157 Mb, indicating an absence of > 40 Mb of data, or > 25% of the genome! These two techniques have their own issues, however, and might be inaccurate in either direction.

Another approach to determine genome sequence assembly coverage is to compare the results of a whole-genome shotgun sequence analysis with the assembled sequence. If the shotgun sequence data are truly random and present in sufficient quantity, then the percentages of DNA in each sequence type will be exactly identical to their percentages in the full-genome assembly, if it is complete. For instance, if 25% of a genome comprises some specific repeat (as shown by the shotgun analysis), then this repeat should comprise 25% of the completed assembly. In order to test this idea, we sheared, cloned and generated 1583 high-quality random reads from the same source of the Columbia Arabidopsis ecotype that was used for the full-genome sequence, generating *c*. 1.36 Mb of data (Liu, 2005). The sequences of these clones indicated that *c*. 18.3% of the genome contained identified repeats, compared with 7.7% in the Arabidopsis genome sequence assembly that was available in 2005. If one assumes that all of the missed DNA comprises known repeats, then the minimum Arabidopsis genome size can be calculated to be slightly larger than 134 Mb. Of course, some of the missed sequences are likely to be unknown (e.g. low-copy-number and/or centromere-specific) repeats, or even genes. Hence, our prediction is a minimum, but there is no possibility that the genome could be smaller than this size. We therefore predict that the original genome size estimate for Arabidopsis was not too inaccurate, with somewhat over 19 Mb of missed sequence.

As a side benefit, a small additional analysis of the shotgun genome sequence data also allows a prediction to be made of how many genes may have been missed by an assembly. Once again, using Arabidopsis as an example, we found no gene candidates in our data set that were not identified in the Arabidopsis genome sequence. From our reconstruction experiments with known genes, using data with the size distribution present in our 1583 reads, we would have a likelihood of *c*. 66% of identifying genes that are present on these reads. Taking these factors into account, we predict, with a 95% confidence level, that < 250 genes were missed in the Arabidopsis genome-sequencing project, and we have a certainty of > 70% that 100 genes or fewer were missed (Liu, 2005).

Although we believe that our approach provides an ironclad minimum estimate of sequences and genes missing from the Arabidopsis genome assembly, we are also aware that specific biases against the successful cloning of some sequences could skew our analysis. For this reason, sequencing approaches that do not involve cloning (e.g. 454 or Solexa technologies) might provide the most appropriate route to pursue such confirmation.

The ease of generating such an analysis of genome sequence and assembly completion, particularly when most current sequencing projects already contain large dollops of random shotgun sequence data, is difficult to overstate. We propose that such an analysis should be an absolute publication requirement for all future genome-sequencing projects (including those in plants) that describe a 'completed' genome sequence. Although we can, and should, argue about whether we want our genome projects to concentrate on the salsa, enchilada or frijoles, we should all agree that it is necessary to know how much of the feast that we have ordered, and paid for, has been set on the table.

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Key words: *Arabidopsis thaliana*, DNA sequencing, gene discovery, genome finishing, repetitive DNA content, whole-genome shotgun sequence analysis.

Meetings

Plant–microbe and plant–insect interactions meet common grounds

International Conference on Biotic Plant Interactions, Brisbane, Australia, March 2008

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 CO_2 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

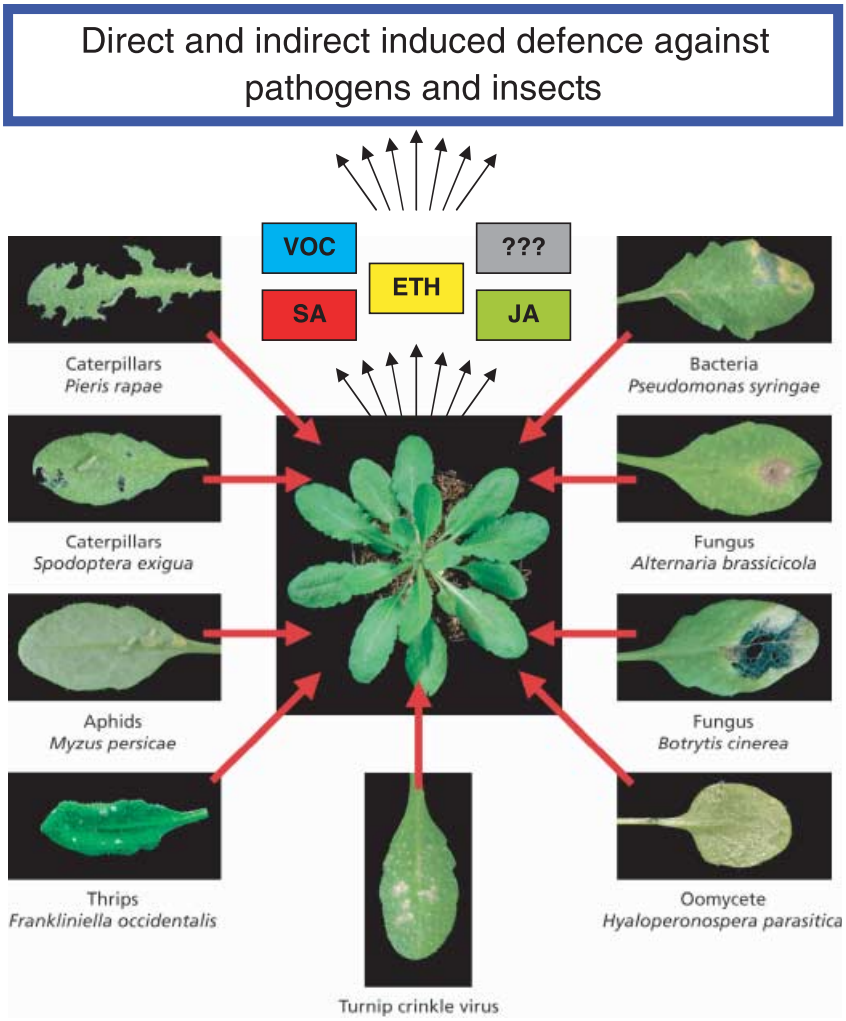

Fig. 1 Representation of the complexity of the plant's induced defence response to pathogens and insect herbivores. The interaction of *Arabidopsis thaliana* with pathogens and insects with different lifestyles or feeding modes results in the production of different defence signal signatures and blends 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,

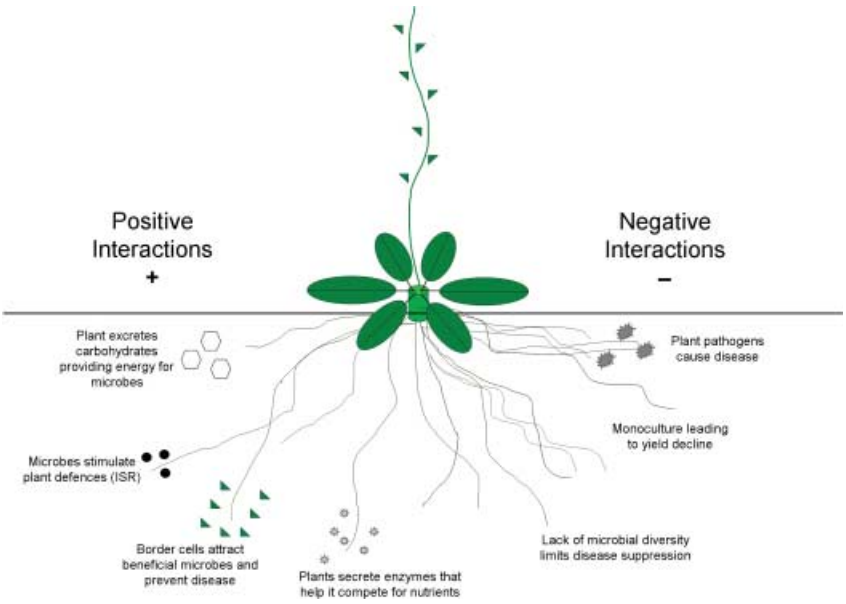

Fig. 2 Examples of root–microbe interactions and rhizosphere biology.

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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Key words: beneficial interactions, biopesticides, biotic plant interactions, ICBPI, microbial communities, plant defence, plant pathology, rhizosphere biology.

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