

Introduction



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Overview: biotic signalling for smart pest management

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Biotic signalling refers to species or phylogenetic-clade-specific signals that elicit adaptive and acceptable responses within and among organisms. It is not only the molecular basis of the ecological relationships among different species, such as parasitism, symbiosis and predation, but also serves as ideal targets that can be used to manipulate these ecological relationships. This concept was proposed by a group of scientists from the Chinese Academy of Sciences (CAS) and actively pursued in a five-year research project in 2014 funded by the CAS (\$40 million), entitled 'Decoding biotic interactions and mechanism for target management of agricultural pests'. The multi-disciplinary project aimed at a systematic investigation of the intra-species and inter-species and interactions via biotic signalling, with the ultimate goal being the development of novel methods to manage the pest insects and diseases. We hereby propose a topic 'Biotic signalling sheds light on smart pest control' as a theme issue for the *Philosophical Transactions of the Royal Society B*. It contains a total of 18 reviews and research articles under the topic of signalling manipulation for pest management. Unravelling these complex interactions among plants, microbial pathogens and insects holds promise for developing novel strategies to protect crop plants without compromising agricultural productivity and environmental health.

This article is part of the theme issue 'Biotic signalling sheds light on smart pest management'.

1. Introduction

The production of enough and safe food to feed the global population is a constant challenge facing human kind. Based on the data from the Food and Agriculture Organization, the number of undernourished people increased from 777 million in 2015 to 815 million in 2016, affecting 11 per cent of the global population [1]. Besides abiotic causes of crop losses, global food security is threatened by harmful organisms—animal pests (insects, mites, nematodes, rodents, etc.), microbial pathogens (viruses, bacteria, fungi, chromista) and weeds, collectively termed pests in agriculture. The pest insects, pathogenic microbes and other pests often become devastating organisms, resulting in disasters for world's agriculture production. Throughout human history, plant diseases and insect pest plagues have frequently resulted in massive decline of populations and cause violent upheavals to society. Even today, pest insects and plant diseases generally result in 10–30% loss of crop yields in the world annually, even though various approaches have been actively applied for crop protection. Modern science and technologies in agriculture have significantly promoted the quality and efficiency of crop production. Widespread use of fertilizers, pesticides, herbicides, antibiotics and plant hormones is pivotal in securing crop yields and contributes to feed over 7 billion people on the earth. At present, pest control relies heavily on pesticides, which means pesticides provide the mainstay of crop protection. Pesticide use, including but not limited to insecticides, fungicides, bactericides and herbicides, topped 3.83 billion kilograms worldwide in 2012. Among them, China accounted for 47% (1.81

billion kilograms) and USA accounted for 11% (0.41 billion kilograms) [2]. These pesticides target the basic metabolism, physiological and biochemical pathways and nerve receptors of pests and microbial organisms. The main pesticide targets are often homologous to their human and animal homologues, having proverbial, negative effects on human and other animal health. Abuse of pesticides results in pesticide resistance, biodiversity loss, farmland and environmental pollution. But, interactions between climate change, crops and pests are complex, and the extent to which crop pests and pathogens have altered their latitudinal ranges in response to global warming [3]. Therefore, alternative theories and methods for pest management in agricultural settings have been the subject of increasing interest by researchers, farmers and broader public in recent decades owing to increased awareness of the risk that pesticides pose to the human health environment. Meanwhile, there is an urgent need to develop creative and environment-friendly strategies to effectively control these pest organisms for sustainable agriculture.

In ecosystems, organisms dynamically interact with living communities and the non-living components of their environment. The interacting organisms regulate flux of energy and matter cycles through the food chain in the ecosystem. However, the information flow linking different species at different trophic levels is more complex and specific. Therefore, urgent demands for sustainable agriculture count on a better understanding of interactions of organisms, especially interactions between plants and other organisms from molecules to ecosystem levels. In the past three decades, scientists have made considerable progress in understanding the delicate relationship between plants and other organisms, establishing the notion that communication among species in communities is mainly mediated by biotic signalling, including physical signalling, pheromones, kairomones, hormones, metabolites, peptides, proteins and RNAs. For example, insects can use a vibration signal and pheromones to communicate and aggregate conspecific individuals; plant secondary metabolites play key roles in defence against the infection or attacks by insects, fungi, bacteria, viruses and other herbivores. Plants also sense chemical signals released from the attackers and respond appropriately. On the other side, pests and pathogens manipulate host defences by secreting virulence factors, some of which are directly injected into plant cells. Instead of being passive victims in these interactions, plants recognize and respond to both conserved and variable pathogen elicitors to defend themselves. In addition, vector-borne pathogens have become a major cause of emerging diseases of crop plants. Insect vectors have the ability to bridge spatial and ecologic gaps between pathogens (especially virus) and plants, and thus increase the infection opportunities. Small adaptations of a pathogen to an insect vector may have significant effects on the transmission rate and pathogen dispersal. But, insect pests can also be infected and killed by a variety of entomopathogenic fungi, bacteria and viruses. Recently, scientists revealed multiple functions of symbiotic microorganisms in their hosts. Unravelling these complex biotic interactions among plants, insects and microbial pathogens holds promise for sustainable agriculture. Undoubtedly, cooperation of scientists from different disciplines is necessary to tackle these complex questions and develop new strategies to protect crops without compromising environmental health.

The last few decades have seen a growing appreciation of the myriad ways in which plants directly and indirectly interact with such organisms, either by inter- or intra-species interactions or cross-kingdom interactions, all orchestrated by biotic signalling. The biotic signalling belongs to a main category of the information flow in ecosystem. Biotic signalling refers to species or phylogenetic-clade-specific signals that elicit adaptive and acceptable responses within and among organisms. It is not only the molecular basis of the ecological relationships among different species, such as parasitism, symbiosis and predation, but also serves as ideal targets that can be used to manipulate these ecological relationships. The relationship and interactions in intra- or inter-species have been successfully exploited in pest management. Push–pull technology is a well-known strategy for controlling agricultural pests by using repellent ‘push’ plants and trap ‘pull’ plants [4]. For example, cereal crops like maize or sorghum are often infested by stem borers. Grasses planted around the perimeter of the crop attract and trap the pests, whereas other plants, like *Desmodium*, planted between the rows of maize, repel the pests and control the stemborers [5]. Even, the simultaneous use of a repellent (push) and attractant-baited traps (pull) is highly effective in reducing house entry by malaria mosquitoes [6]. The use of artificial vibrational noise allowed prevention of the mate recognition and localization mediated by vibrational signals in the grapevine pest *Scaphoideus titanus* [7]. Phytopathogenic bacteria belonging to Xanthomonadaceae produce mediate-chain fatty acids named diffusible factor (DSF) to act as cell–cell communication signals [8]. DSF elicits innate immune responses in host plants [9], and scientists have exploited this by ectopic expression of enzymes producing DSF in tobacco and sweet orange to successfully engineer disease resistance to the bacterial pathogens [10]. These results suggest that manipulation of the quorum-sensing signalling of pathogens is a promising approach to promote plant disease resistance.

We not only manipulate the behaviour of pests and natural enemies through specific interaction and the relationship of intra- and inter-species but also administer unique genes, proteins and pathways of plants and pests to control the pest outbreaks based on signal reception, transduction and cascade in cell and molecular levels. This concept was proposed by a group of scientists from the Chinese Academy of Sciences (CAS) and actively pursued in a five-year research project in 2014 funded by the CAS (\$40 million), entitled ‘Decoding biotic interactions and mechanism for target management of agricultural pests’. The multi-disciplinary project aimed at a systematic investigation of the intra-species and inter-species and interactions via biotic signalling, with the ultimate goal being the development of innovative methods to manage the pest insects and diseases. Efforts from this research consortium have made great progress in this fascinating area, including the study of the molecular basis of phase change in locusts, dissection of protein complexes of plant immune receptors and signal transduction of innate immune responses, identification of microbial receptors of plant chemicals or hormones and molecular interactions among plant-vector-virus in nature. These advances have been published in top-tier academic journals such as *Science*, *Cell Host Microbe*, *Nature Plants*, *Nature Biotechnology*, *Nature Communications*, *Proceedings of the National Academy of Sciences of the United States of America*, *Molecular Cell*, *Plant Cell*, *Cell Reports* and *PLoS Pathogens*. In

addition, the project has resulted in the development of a number of new biotechniques for plant disease control. For example, genome editing of the *mlo* alleles in wheat created disease-resistant wheat plants [11], and understanding of the RNA transfer between cotton and pathogenic fungi facilitated breeding of disease-resistant cotton plants [12].

In the light of the complexity of the signalling networks that were rapidly uncovered, combined with the complex datasets associated with genomics research and result in emergence of novel manipulation strategies of pest insects and diseases from this project, we hereby propose a topic 'Biotic signalling sheds light on smart pest control' as a theme issue for the *Philosophical Transactions of the Royal Society B*. The theme issue contains a total of 18 reviews and research articles under the topic of signalling manipulation for pest management.

Plant innate immunity recognizes potential invading pathogens and triggers successful defences using sophisticated mechanisms. Recognition of diverse microbial pathogens by host plants relies on pattern recognition receptors (PRRs) at the cell surface and is crucial for plant disease resistance. PRRs trigger immune responses upon perception of microbial or endogenous molecular patterns released during infection, and pattern-triggered immunity has been a centre piece of plant innate immunity studies. Zhou *et al.* highlighted recent advances in early signalling mechanisms, particularly the tight regulation of major components of receptor complexes and signalling relay from receptor kinases to downstream cellular responses [13]. How pathogenic bacteria sense host plant and plant-associated stimuli remains unknown. Wang *et al.* reviewed the progress of their elegant studies [14]. In the causative agent of black rot disease of crucifer, *Xanthomonas campestris* *pv.* *campestris*, they identified histidine kinases to monitor the signals of iron depletion of the host plant, a quorum-sensing signal, and interestingly, a plant hormone-cytokinin [15–17]. The results of these studies give insight into our understanding on the inter-kingdom communications between eukaryotes and prokaryotes. To counter the host immune system, pathogens have evolved diverse strategies to suppress host immunity. miRNA-like small RNAs (milRNAs) have recently been identified in several fungi with unknown function. Jin *et al.* identified a milRNA (VdmilR1) in *Verticillium dahliae*, a soil-borne fungal pathogen responsible for devastating wilt diseases in many crops. They found that an RNaseIII domain-containing protein, VdR3, rather than canonical DCL (Dicer-like) proteins, participates in VdmilR1 biogenesis. VdmilR1 targets a hypothetical protein coding gene, *VdHy1*, at the 3'UTR for transcriptional repression through increased histone H3K9 methylation of *VdHy1*. *VdHy1* is essential for fungal virulence. Their data uncover a non-canonical pathway for VdmilR1 biogenesis and an epigenetic mechanism for VdmilR1 in regulating the virulence target gene [18].

The identification and use of broad-spectrum resistance genes are considered to be one of the most economical/cost-saving and effective methods to control diseases. Rice blast caused by *Magnaporthe oryzae* (*M. oryzae*) is the most destructive disease in rice. Xie *et al.* isolated a new blast R locus *Pizh* in the variety ZH11 containing nine tandemly arranged nucleotide-binding leucine-rich repeat (NLR) genes, of which only *Pizh-1* and *Pizh-2* are expressed to confer strong blast resistance. *Pizh-1* acts as a sensor NLR, whereas *Pizh-2* functions as a helper NLR. *Pizh-1* interacts with *Pizh-2* to form an NLR complex to execute disease resistance, thus providing not only a

new molecular tool for rice disease resistance breeding but also deep insight into NLR association and function in plant immunity [19].

Recent advances have elucidated the biosynthetic pathway for gossypol and related sesquiterpenes, which are major phytoalexins in cotton plants. Among the six newly identified intermediates, one (8-hydroxy-7-keto- δ -cadinene) has an α , β -unsaturated carbonyl group and stimulates the expression of a large number of pathogenesis-related genes, despite the fact that it deteriorates plant resistance to diseases. This paradoxical effect implies that the gossypol pathway may have evolved step by step in the family of *Malvaceae* [20]. Reactive oxygen species (ROS) also play important roles in the defence response of host plant against various pathogens. However, the contribution of ROS to parasite's pathogenicity remains largely unexplored. Zhang *et al.* report that transcriptional regulation of the ROS pathway, in combination with the insulin signalling pathway, increased the pathogenicity of invasive species *Bursaphelenchus xylophilus*. They concluded that the destructive pathogenicity of *B. xylophilus* to pines is partly owing to its upregulated fecundity caused by the insulin signalling pathway associated with the ROS pathway and H₂O₂ oxidative stress. These findings lead us towards a better understanding of pathogenic mechanisms in plant–pathogen interactions and evolution of invasive species [21]. Insect feeding on maize induces defence-related responses in specific regions of the insect-attacked leaf, as well as in undamaged leaves. These findings shed a light on the spatial regulation of induced resistance to insect herbivores and will help to develop herbivore-resistant maize cultivars [22]. The pea leafminer, *Liriomyza huidobrensis*, is a detrimentally agricultural insect pest worldwide. Because of its high resistance and resurgence to chemical sprays, the management of this pest calls for new control strategies. Ge *et al.* found that female-puncture-induced plant volatiles, but not insect-derived chemical cues, attract both sexes of adult leafminers to mating sites. In addition, these volatiles increase the mating success of leafminers by promoting vibrational communication between the sexes. This study opens a new avenue for the combined use of plant volatiles and acoustic signals for trapping control of agromyzid flies [23].

Diseases caused by plant viruses seriously restrict the yield and quality of major crops, such as rice, wheat, corn, potatoes and vegetables. About 1100 plant viruses have been reported in the world. Although plants are non-mobile, plant viruses can spread from plants to plants across wide geographical locations, and around 80% of viruses are transmitted by insect mediators. Host plant-mediated interactions between viruses and insects play vital roles in the population dynamics of insect mediators and the epidemiology of plant virus diseases. Exploring the complex biological relationship between plant hosts, viruses and mediator insects is essential for future design of effective and sustainable strategies to control the major virus diseases. Lu *et al.* found that Rice black streaked dwarf virus (RBSDV) infection suppresses the protein kinase C activity of the insect mediator *Laodelphax striatellus* (small brown planthopper). This new finding sheds light on the special function of RBSDV coat protein during virus transmission and infection, and contributes to our knowledge on the mechanisms controlling RBSDV transmission through *L. striatellus* [24]. Cellular receptor determines the cell type that a virus invades; however, no insect receptor for arbovirus has been characterized. Huo *et al.* demonstrated that a plant arbovirus

hitchhikes a well-defined insect ligand–receptor interaction pathway to achieve its cell entry, representing an undescribed mechanism for arbovirus to invade vector cells [25]. Salivary effector proteins present in viruliferous insects play an important role in the tripartite interaction. Cui *et al.* found that Armet, an effector protein of aphids, induced a four-fold increase in salicylic acid (SA) accumulation by regulating the expression of *SAMT* and *SABP2*, two genes associated with SA metabolism. The results suggest that Armet causes plants to make a pathogen-resistance decision and reflect a novel tripartite insect–plant–pathogen interaction [26]. Wang *et al.* conducted a functional genomics screening of whitefly salivary effectors and found that *Bemisia tabaci* salivary protein 9 (Bsp9) interacts with WKRY33, a vital regulator of plant innate immunity, to suppress resistance against whitefly [27]. Besides working as the vectors for transmitting viral pathogens, insects are also the hosts of bacterial symbionts. Whether bacterial symbionts directly interact with the virus and mediate its transmission has been poorly understood. Wu *et al.* showed that rice dwarf virus (RDV), a plant reovirus, moves with the two obligate bacterial symbionts *Sulcia* and *Nasuia* from the haemolymph into the oocytes of female rice leafhopper vectors through direct interactions between viral outer capsid proteins and the outer membrane proteins of bacteria. Thus, this new finding reveals that RDV, *Sulcia* and *Nasuia* have formed complex tripartite interactions during their joint transovarial transmission to next insect generations, and provides novel insights into the development of efficient approaches to attenuate viral epidemics by targeting symbiont-mediated maternal transmission mechanisms [28].

Genetic engineering has proved to be one of the most effective and sustainable ways to improve the crop resistance to diseases and pest insects. Crop lines expressing active insecticidal cry genes from the bacterium *Bacillus thuringiensis* (Bt) have been developed to achieve efficient control of insect pests. Recently, one of the research hot spots in insect Bt resistance is the mutation identification of Bt toxin receptors that recognize insect/Bt-associated molecular patterns. Xiao *et al.* systematically reviewed the advances in interaction between insect and Bt toxin, with special reference to variation in the toxin-activated process, mutation genes of the toxin receptors and changes in the immune system of insect. Study on the insect Bt resistance mechanism can expand our understanding of a relationship between Bt crops and their target pests, navigate for developing new-generation Bt crop, and promote sustainable application of Bt technology in agriculture [29]. In the past several years, genome editing technology has revolutionized biology through enabling targeted modifications to DNA/RNA within living cells. Yin and Qiu reviewed the recent developments of genome editing technology and its application for crop disease and pest resistance. They also

discussed challenges and opportunities for using genome editing technology for sustainable agriculture [30].

Biological pest control is a promising approach that is safe to human beings and without pollution of the environment. Baculoviruses are insect-specific viruses that have been extensively used as biological agents for pest control. Wang and Hu reviewed versatile mechanisms exploited by baculoviruses to overcome diverse host barriers to establish successful primary- and systemic infection, as well as to finely regulate host physiology and behaviour for optimal virus replication and dispersal. These advances promote the improvement of baculoviral pesticides [31]. Entomopathogenic fungi represent another promising class of bio-insecticides for insect pest control. Fungal formation of the infection structure appressorium is a hallmark of host recognition to initiate the penetration process of host cuticles. A group of appressorium-specific proteins containing the DUF3129 domain with unknown function(s) have been identified with virulence contributions from different fungal pathogens. Huang *et al.* report the identification of seven DUF3129 domain-containing genes in the insect pathogen *Metarhizium robertsii*. They found that Ste12-like transcription factor jointly regulated these genes at the appressorium formation stage. Protein localization assay revealed that these proteins are present on the surface of lipid droplets. Loss-of-function studies indicated that six of seven genes are required for fungal virulence against insect hosts by mediating the degradation of cellular lipid droplets to generate turgor pressure for insect cuticle penetration. The findings of this study advance the understanding of the function of DUF3129 proteins that are widely distributed in different fungi [32]. Besides the entomopathogenic fungi and viruses, nematophagous microbes are natural enemies of nematodes and potential biocontrol agents against plant-parasitic nematodes. Liang *et al.* reviewed the advances in signalling of the nematode–pathogen interactions, including attraction, recognition, morphological development induction of the pathogens, as well as the defence of the nematodes with their innate immune system. Understanding these molecular actions during microbial infections is crucial for developing of high efficient bionematicides [33].

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