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Review

New frontiers in belowground ecology for plant protection from root-feeding insects

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A B S T R A C T

Herbivorous insect pests living in the soil represent a significant challenge to food security given their persistence, the acute damage they cause to plants and the difficulties associated with managing their populations. Ecological research effort into rhizosphere interactions has increased dramatically in the last decade and we are beginning to understand, in particular, the ecology of how plants defend themselves against soil-dwelling pests. In this review, we synthesise information about four key ecological mechanisms occurring in the rhizosphere or surrounding soil that confer plant protection against root herbivores. We focus on root tolerance, root resistance via direct physical and chemical defences, particularly via acquisition of silicon-based plant defences, integration of plant mutualists (microbes and entomopathogenic nematodes, EPNs) and the influence of soil history and feedbacks. Their suitability as management tools, current limitations for their application, and the opportunities for development are evaluated. We identify opportunities for synergy between these aspects of rhizosphere ecology, such as mycorrhizal fungi negatively affecting pests at the root-interface but also increasing plant uptake of silicon, which is also known to reduce herbivory. Finally, we set out research priorities for developing potential novel management strategies.

Contents

Abbreviations: AMF, arbuscular mycorrhizal fungi; BX, benzoxazinoid; EPN, entomopathogenic nematode; GBCG, greyback canegrub (*Dermolepida albohirtum*); GLS, glucosinolates; HTP, high throughput phenotyping; JA, jasmonic acid; PGPR, plant growth promoting rhizobacteria; PI, Proteinase inhibitor; QTL, quantitative trait locus; VOC, volatile organic compound; VW, vine weevil (*Otiorhynchus sulcatus*); WCR, Western corn rootworm (*Diabrotica virgifera virgifera*).

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1. Introduction

It has been estimated that invertebrate pests account for crop losses that would be sufficient to feed more than one billion people (Birch et al., 2011). Global populations are expected to exceed 9.7 billion by 2050 and 11.2 billion by 2100 (UN, 2015). Yet crop productivity has plateaued, so there is an urgent need to reduce crop losses to such pests to ensure food security (Gregory et al., 2009). From a global perspective, soil pests that attack crop roots are amongst the most economically damaging, persistent and difficult to detect and control (Blackshaw and Kerry, 2008). Plant-parasitic nematodes, for instance, inflict annual world-wide crop losses of at least US$80 billion and have received significant research interest because of their economic status (Jones et al., 2013). Root feeding insects include western corn root worm (WCR), *Diabrotica virgifera virgifera*, whose damage and control costs exceed US $1 billion annually in USA (Gray et al., 2009), greyback canegrub (GBCG), *Dermolepida albohirtum*, that cause losses of up to AUD $28 million annually in Australia (Chandler, 2002) and wireworms, whose damage and control costs to the Canadian potato industry approximate CAN $6 million (Agriculture and Agri-Food, 2016). Moreover, in the absence of control measures, vine weevil (VW), *Otiorhynchus sulcatus*, can reach densities of over 300,000 per hectare within three years and reduce raspberry yield by 40–60% (Clark et al., 2012).

Root herbivory can be especially damaging to crops, particularly when combined with abiotic stresses (e.g. drought, which is often exacerbated by damage to roots) (Zvereva and Kozlov, 2012; Erb and Lu, 2013). Plants often cannot tolerate root herbivory to the same extent as they can shoot herbivory, not only because their damage is acute but also because many root-feeding pests are extremely persistent, with damage to plant tissues lasting many months or even years (Johnson et al., 2016). This persistence frequently results in prime agricultural land being taken out of production (Blackshaw and Kerry, 2008). Moreover, because soil pests are cryptic, infestations often go unnoticed and extensive damage to crops then becomes inevitable. Management options are costly and particularly damaging to the environment because practitioners apply insecticides prophylactically, and often unnecessarily, in an attempt to avoid possible losses (Blackshaw and Kerry, 2008). Increasingly, this management option is becoming impractical because of legislation restricting pesticide use (e.g. Nauen et al., 2008), suggesting that control of root-feeding pests may become even more difficult in future.

The extent to which the soil environment is driven by interactions between the plant and soil organisms is becoming increasingly apparent. This represents a significant conceptual advance in ecology and several important breakthroughs have been made, including identifying how plant roots acquire specific microbiomes (Edwards et al., 2015) or how root architecture is sometimes driven by soil microbes (Ditengou et al., 2015). Most recently this has stimulated interest in 'rhizosphere engineering' for promoting plant health and productivity (Zhang et al., 2015; Bender et al., 2016; Dessaux et al., 2016). At the same time, fundamental studies concerning interactions between plants and their root herbivores have gained pace and have been particularly helpful in increasing our understanding of belowground defences (Rasmann and Agrawal, 2008; van Dam, 2009). These defensive interactions are often brokered by a range of microbial (e.g. mycorrhizae) and invertebrate (e.g. nematode) players (Johnson and Rasmann, 2015), in addition to the biogeochemical ecology of the rhizosphere (Erb and Lu, 2013). Some of these ecological insights could now be applied to address a range of management issues, from conservation and climate change mitigation to sustainable pest management.

Using belowground ecology for plant protection from root herbivores, particularly in an integrated way, is a new and challenging frontier and it is therefore timely to synthesise existing knowledge and evaluate problems and prospects for application. In this respect, we differ in our approach to recent articles that examine the basic ecology of such interactions (e.g. Rasmann and Agrawal, 2008; van Dam, 2009; Johnson and Rasmann, 2015). In particular, in this review we strategically examine four aspects which we consider offer most scope for environmental management and regulation of root-feeding insect pests. In making this selection we readily acknowledge that there are ecological mechanisms not explicitly covered in this review that could play a role in management. We assess the suitability of these four mechanisms as management tools, identify what currently limits their application, where the key knowledge gaps are and ultimately what opportunities for development lie ahead. Because the ecologies of insect herbivores and plant-parasitic nematodes differ so much, it's likely that different aspects of belowground ecology will be important for pest control in these two taxa. We therefore focus on insect herbivores and those aspects of belowground ecology we consider to have greatest potential for integrated pest management. We do, however, refer to articles that consider agroecological engineering of the soil for plant protection (e.g. from plant pathogens; Chave et al., 2014) where we feel these are relevant to root-feeding insects.