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Abstract: 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.

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26 July 2016

Re: Revision of our review APSOIL-D-16-00199

Dear Prof van Gestel,

Many thanks for your email advising us that our paper may be considered for publication pending major revisions. Please find enclosed our revised article **New frontiers in belowground ecology for plant protection from root-feeding insects**. As you will see this paper has been substantially re-written and developed. Full details of these changes are in our response to reviewers. We are thankful to both reviewers for constructive comments and suggestions.

We are grateful for the extension you provided and very sorry that we were late returning this revision to you.

Please don't hesitate to contact me if I can provide further information.

Yours sincerely

Scott

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Highlights

- Many soil-dwelling herbivores are persistent pests requiring novel control measures
- Increasing knowledge about rhizosphere ecology could provide sustainable solutions
- We review four soil ecological mechanisms that show most scope for pest control
- We assess suitability as management tools and current limitations for application
- Synergies between these mechanisms were apparent and a research agenda is presented

APSOIL-D-16-00199

Detailed Commentary on revisions

Reviewer #1:

This is a mini-review type manuscript authored by ten internationally leading researchers in the field of plant root herbivory and related topics. Reviews are always sought after, by both editors and readers who seek summarized information, and this review could turn into such a sought-after resource. However, I found this review in its present form wanting in several respects. It is not fully developed, it is uneven across sections, it brings concepts, hypotheses and applications into the mix without a good structure. Overall, it is not of the high standard expected from such a high-calibre author team. I recommend major revisions and improvements before acceptance, as detailed below.

DONE: We have taken on board these comments and undertaken a complete re-write, which we comment on in relation to specific points below. We have endeavoured to develop areas more thoroughly and in more detail. As a result, the manuscript is 4,500 words longer and has 80 more citations than the original. We have completely restructured the sections so they have more evenness in length and have a more structured basis.

1) It is not clear how this review differs from recent reviews by the same authors, especially Johnson & Rasmann (2015) and, in the conceptual parts, Rasmann & Agrawal (2008). This needs to be made clearer when the scope of the review is defined. Differences in scope or focus to other, published reviews should also be made clearer (e.g. Chave et al. 2014).

DONE: We agree and make the scope and differences of the review clearer (lines 98-108). The other reviews are about basic ecology of root herbivore interactions with plants and other organisms. While we draw on this information in this review, we adopt an applied perspective by examining how feasible these interactions might be for pest management, what limits application and what needs to be done to remedy this. Chave et al 2014 focusses on plant pathogens, though we recognise there are relevant parallels (which we explain, lines 112-114) and we cite this article on several occassions.

2) In the Introduction (p.3), the global damage caused by these supposedly devastating pests is not impressed upon the reader strongly enough. The corresponding Table 1 is not that convincing either. With due respect to the authors, an average undergraduate thesis on the topic would have a more comprehensive and more up to date table. For instance, the figure cited for root nematodes (a group discussed prominently in the review) is from a 1985 project report, without bibliographic details. Claims of global importance should be supported with global, recent loss estimates or, at least, convincing case studies on selected root pests.

DONE: We have removed Table 1 and opted to provide several case study examples with recent examples of the crop losses. In fact, estimates of losses are quite difficult to make and are usually very specific to certain regions and very quickly become dated. The previous table was an attempt to illustrate the different crops and geographical regions affected by root herbivores; indicated by the legend 'Selected key root herbivores of economic significance'. We have deleted the table and followed the reviewer's suggestion.

3) Figure 1 gives the same impression as the review as a whole: It is not well developed. For instance, the "recommendations" mentioned in the title are not standing out at all. Similarly, what is the function of the "Soil conditions" box in Fig. 1? None of these factors is picked up in the review. Other reviews, not cited by the authors, have covered soil conditions e.g. Erb and Jing (2013). Being text heavy, written out in sentences with small text, this figure is a poor visual representation of any concepts. Perhaps a graphic designer could be employed to produce something visually appealing and scientifically worthy of a critical review? Something scientists and teachers will show and reproduce when discussing root herbivory.

DONE: We have improved the figure by taking the different approach of splitting the research opportunities and priorities (Fig. 1) and potential management outcomes (Fig. 2) into two separate figures. We consider that this makes it much easier to relate to the text, which we now do throughout section 6 using identical headings (lines 493-552), but also distinguishes research opportunities for management opportunities, which were mixed together in the previous figure. It also allows us to explain (lines 485-490) that research needs to be conducted in the context of different soil conditions (to understand what optimises/aggravates these interventions) – Fig. 1 - and how knowing this could help management approaches in terms of what conditions to promote and which should be avoided (lines 490-492) as indicated in Fig. 2.

Splitting the figures has reduced the text (now bigger) which hopefully makes this visually more appealing, as requested.

4) Some sections of the review are particularly poorly developed, one example is section 2) Plant tolerance (pp. 4-5). There is nothing on plant breeding, selection, genetics or the current developments in root phenotyping (e.g. Barah and Bones 2015, Wu and Cheng 2014); all of these are prominent and active areas of research. All named areas should either be covered with good substance, or omitted altogether.

DONE: Lines 115-164. All sections have been expanded and developed. In particular, we now have dedicated section (2.2) for selection, breeding and phenotyping for plant tolerance and a similar section (3.4) for direct defence. In restructuring the paper we introduced a section on plant-soil feedbacks in order to address point 6 about the absence of discussion on root-root interactions but we also considered it important to because interventions of any kind will depend on legacy effects of the soil.

5) The section on silicon in roots (Section 4) is speculative, with the only studies that measured pest attack and silicon in roots being "pers. communications" (p. 7). All other text is from foliar research, which has been reviewed by some of the authors in several other papers. That section should be shortened and, possibly, presented as some sort of outlook or hypotheses-formulating exercise. The authors could also be more specific as to the "crops" (p.7 line 1) they are referring to, presumably Poaceae?

DONE: The section has been greatly reduced (from 2.5 pages to > 1 page) which is now included in the direct resistance section. The work we referred to has now been accepted for publication and we provide the relevant references. We now do not refer to foliar research, except in the context of how silicon might inhibit root herbivore feeding and confirm it is mainly the Poaceae (line 231) that utilise silicon (though other plants like cucurbits do too).

6) The review relies heavily on self-citations. The authors need to be fairer to other researchers and more inclusive of published areas they are not involved in. As a small sample, none of the references cited in this report are included in the manuscript. For instance, root-root interactions are not discussed (Chave et al. 2014), while mycorrhizal fungi have been reviewed more comprehensively by Schouteden et al. (2015).

DONE: By expanding the paper we have increased citations from 103 to 184, which has also increased the diversity of sources. We have cited all of the references supplied by the reviewer. Because we have focussed attention on root-feeding insects specifically, these references offer useful parallels (Chave is concerned with plant diseases and Schouteden with plant parasitic nematodes) where literature concerning root-feeding insects is scarce. We consider it less useful to repeat information given in these reviews, but agree that we should cite these important articles.

7) The manuscript has many small errors and shortcomings that need to be fixed, some examples are:

- The title phrase "rhizosphere ecology" is misleading because most angles covered are not what is generally understood as rhizosphere (i.e. microbial) interactions. See for instance review by Kupferschmied et al. (2013).

DONE: The title is now changed and make it clear elsewhere that we are referring to rhizosphere and surrounding soil and specifically root-feeding insects.

- Abbreviations could be collected, for example in a footnote on the first page, rather than being interspersed in the text.

DONE: Now included as box on page 4.

- If you describe references with phrases such as "more recently" (p.4 line 1), they have to be newer than the one you started with, and certainly not almost 10 years old.

DONE: The ‘more recently’ phrase refers to the ‘more recent development’ of legislation dictating pesticide use than the 2008 reference. We have changed this phrase to ‘Increasingly’ to avoid any misunderstanding (line 79).

- The phrase "in conclusion" (p.13 line 10) appears much too early, with almost 2 pages of text still to come.

DONE: This section has been re-written so does not include this term

- Several references are incomplete, e.g. Ditengou et al. 2015, Popay and Baltus 2001, Sasser and Carter 1985, Seastedt et al. 1989, Turlings et al. 2012.

DONE: These either do not appear in the revised manuscript or have been completed.

Reviewer #2:

In this paper, the authors propose a new strategy, a new concept of rhizosphere ecological interventions to environmentally manage soil herbivores. The paper is well written and neatly organized. However, I differ to call it as a review as it is neither exhaustive nor inclusive of all below ground herbivores. It can be considered as a new 'Opinion' in managing the persistent, soil dwelling herbivores (mostly nematodes) by a judicious integration of plant traits like tolerance/resistance, rhizosphere organisms and soil derived defence through silicon acquisition. I have the following suggestions:

1. Plant parasitic nematodes are very important below ground herbivores. Though they (root-knot and cyst nematodes) have been mentioned as one of the key herbivores of economic significance, nothing is stated on the impact of the proposed strategy on nematode herbivory. A lot many literature is available on nematode suppression by various endophytes and mycorrhiza.

DONE: We agree that it is difficult to exhaustively cover all root pests, particularly because their ecologies differ so much. We make it clear that we are focussing on root-feeding insects (lines 108-112). As discussed above, there are several other reviews that consider plant-parasitic nematodes in this context, which we cite, so we consider this also makes this review distinct and novel.

2. Only four key ecological mechanisms occurring in the rhizosphere viz., plant tolerance, plant resistance, silicon acquisition and deployment of AMF and endophytes are mentioned in this article. What about other soil amendments, other endophytes/PGPRs on root herbivory?

PARTIALLY DONE: We include discussion of PGPRs (lines 331-346) and soil amendments, and specifically plant-soil feedbacks (an entirely new section, 5, lines 423-471). The primary literature concerning root-feeding insects in these areas is scarce so we were reluctant to devote too much text to speculative discussion of these points. We do acknowledge their importance, and also that availability of space and any selective approach will neglect some mechanisms that could play a role in suppression of root-herbivores (line 104-106).

3. Rhizosphere engineering is another key area that is gaining lot of importance (Please see Zhang et al. 2015 Current Opinion in Biotechnology 32: 136-142 & Dessaux et al. 2016. Trends in Plant Science 21: 266-278) and can very well fit into the proposed strategy.

DONE: We cite all of these papers and mention their relevance to the areas discussed. Many thanks for this suggestion.

4. Herbivore induced plant volatiles (HIPV) lead to a cascading of events in the rhizosphere and can even constitute a feedback loop. This is not discussed in details in this review.

DONE: Lines 417-421 provide some discussion of the wider effects of HIPVs on other organisms and trade-offs in the plant.

5. The keywords given are too general and not appropriate. Keywords such as 'insect herbivory', 'root herbivory' etc. may be more ideal.

DONE: We have included more specific words and terms, including those suggested by the reviewer.

REVIEW

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

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Running title: Belowground ecology and root herbivore management

ABSTRACT

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.

Keywords: ecological applications, belowground herbivores, rhizosphere, root-feeding insects, root herbivory, soils

Contents

Abbreviations.

AMF: Arbuscular mycorrhizal fungi; **BX**: benzoxazinoid; **EPN**: Entomopathogenic nematode; **GBCG:** greyback canegrub (*Dermolepida albohirtum*); HTTP: High throughput phenotyping; **JA**: Jasmonic acid; **ODT**: Optimal Defence Theory; **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*)

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 WCR, whose damage and control costs exceed US $1 billion annually in USA (Gray et al., 2009), GBCG 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, VW 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.

2. Plant tolerance

2.1. Root tolerance mechanisms

Plant traits that confer tolerance to herbivory can be expressed before or following herbivore attack, and have the effect of limiting the injury caused to plants following infestation (Stout, 2013), thus reducing the negative impact on productivity and yield. In contrast with plant resistance, a tolerance strategy could provide more durable defence against herbivorous pests as plant traits conferring tolerance are less likely to have adverse effects on herbivore fitness (Weis and Franks, 2006), and therefore are less likely to impose a strong selection pressure on pests to overcome plant tolerance. Mechanisms of herbivore tolerance include changes in photosynthesis and growth, phenology and remobilisation of stored reserves (Tiffin, 2000). For root pests, changes in resource allocation, root growth and vigour have been most widely studied. Diversion of resources belowground following root attack can compensate or even over-compensate for root loss (Quinn and Hall, 1992; Thelen et al., 2005; Ryalls et al., 2013), although this phenomenon is less widely reported for root pests compared to shoot herbivores:, Zvereva & Kozlov (2012) estimated that compensatory growth occurs in about 17% of cases of root herbivore attack, which compares unfavourably with shoot herbivory where compensatory growth is achieved in 35–44% of cases (Hawkes and Sullivan, 2001). An alternative strategy might be to divert resources away from damaged roots towards uninfested tissue (leaves, stems, tubers or healthy roots). Such resource diversion, termed ‘resource sequestration’, has been reported extensively in response to aboveground herbivory (i.e. moving resources to the roots) (Schultz et al., 2013), but there is increasing evidence for resource movement in the opposite direction (i.e. from roots to shoots) following root herbivory. In particular, this has been documented in knapweed (Newingham et al., 2007), tomato (Henkes et al., 2008), potato (Poveda et al., 2010) and maize (Robert et al., 2014). Resource reallocation could allow root investment to be delayed until the threat of attack has passed, a phenomenon that is thought to contribute to tolerance of western corn rootworm in herbivore-tolerant maize (Robert et al., 2015).

2.2. Plant selection, breeding and phenotyping for tolerance

Root and plant vigour can contribute to tolerance of root herbivory and may be a promising approach to combat a wide spectrum of root herbivores. For example, more vigorous plant genotypes mitigated productivity declines in sugarcane infested with GBCG (Allsopp and Cox, 2002) and perennial raspberry infested with VW larvae (Clark et al., 2012). Although tolerance traits such as compensatory growth and root vigour are likely to be controlled by multiple loci, using QTL approaches to identify genetic markers (e.g. for root vigour in raspberry: Graham et al., 2011) could facilitate crop breeding for enhanced plant vigour and ability to withstand herbivore damage without significant loss of yield. In rice, a number of genes associated with root architecture and physiological functions have been identified, and/or cloned, which could be helpful to developing root tolerance to herbivory (Wu and Cheng, 2014).

The rate-limiting step for introgressing novel traits into crops is the ability to conduct high throughput phenotyping (HTP) of root traits in large plant populations (Barah and Bones, 2015), particularly under field conditions. While a range of phenotyping techniques and platforms have been available for some time (e.g. George et al., 2014), non-invasive imaging technologies have been a particular focus of recent research effort (Fahlgren et al., 2015). HTP using imaging could provide a means to identify genotypic differences in response to root stress by using imaging-based indicators of changes in shoot physiology, such as stomatal conductance and water status, leaf pigment composition or photosynthetic activity, that indicate root damage belowground. The utility of plant imaging for HTP of plant-insect interactions is now being recognised (Goggin et al., 2015) and, when combined with other available –omic technologies (Barah and Bones, 2015), this approach offers exciting opportunities for rapid advances in crop improvement for root pest tolerance.

3. Plant resistance via direct defence

Plants resist root herbivory via physical and chemical defences (Rasmann and Agrawal, 2008) that can be constitutive or inducible (van Dam, 2009; Erb et al., 2012). Attributing plant responses specifically to belowground herbivory is challenging to evaluate as it can be confounded with plant responses to wounding and soil micro-organisms. Making the causative link, for example, requires experiments including mechanical damage and insect saliva or saliva ablated insects (Bonaventure, 2012; Acevedo et al., 2015). While only a few studies exist, root responses to herbivory appears to involve modest JA induction, suggesting that roots are sensitive to fine changes in JA levels and/or that other signalling molecules are involved (Erb et al. 2012).

3.1. Physical defences

Root toughness is determined by structural macro-molecules and crystalline deposits such as lignin, cellulose, callose, silicon and calcium oxalate (Arnott, 1966; 1976; Genet et al., 2005; Leroux et al., 2011). Because of the heterogeneous soil environment, roots are amongst the most plastic of plant organs and rapidly allocate structural resources to the roots to allow them to penetrate dense soil and restricted openings (Gregory, 2006). Increasing root toughness in response to herbivory might be an effective defence. Fracture toughness driven by lignin concentration and composition was reported to increase root penetration time by wireworms (Johnson et al., 2010). Root soluble free and conjugated phenolic induction upon leaf herbivory resulted in avoidance behaviour by *D. virgifera* (Erb et al., 2015) and *D. balteata* (Lu et al., 2016) belowground. Callose may also be an interesting candidate for physical resistance, as it was reported to be wound-inducible in the roots of the pea, *Pisum sativum* (Galway and McCully, 1987). Nevertheless, some specialist insects have overcome such physical defenses, as is the case for the sap-sucking grapevine pest, phylloxera, that feed on lignified roots (Powell, 2008).

Root hairs (or trichomes) are specialized cells that play an important role in water and nutrient uptake (Gregory, 2006). They may also provide some physical protection against insect herbivory, potentially by preventing small neonate insects from reaching and penetrating the root epidermis and also providing refugia for the herbivore’s natural enemies (e.g. EPNs). In both these respects, root hairs might have similar functional roles as leaf trichomes aboveground (e.g. Karley et al., 2015).

Few studies have looked at physical defences against root herbivores (Johnson et al., 2010), but mutant plant lines which vary in primary cell wall components or root hair initiation and elongation have been developed (Provan et al., 1997; Cavalier et al., 2008; Nestler et al., 2014). These represent promising research tools to use in behavioral and performance experiments to fill the gap of knowledge.

3.2. Chemical defences

Herbivore feeding on plant tissues involves the release of plant- and insect-derived chemical elicitors and the subsequent activation of genes that underpin reconstruction of the chemical profile inside the plant (Erb et al., 2012). Plant secondary metabolites offer the potential to promote resistance to pests due to toxic, deterrent or anti-feedant effects. Although secondary metabolites with anti-herbivore properties can be present throughout the plant, there is evidence for tissue-localisation in above- or belowground plant parts of some species (Rasmann and Agrawal, 2008; Kabouw et al., 2010; Huber et al., 2015; Johnson et al., 2016). Moreover, tissue accumulation of secondary metabolites can be locally induced by herbivore attack (van Dam and Raaijmakers, 2006; Robert et al., 2012b), though overall this inducibility tends to be lower in roots compared to shoots (Erb et al., 2012). This low inducibility of root secondary metabolites might be explained by their high constitutive concentrations such as for GLS (van Dam et al., 2009) and BXs (Robert et al., 2012c).

Defensive proteins represent a class of inducible metabolites that provide a potential weapon against root herbivores. Erb et al. (2009) suggest that nitrogen consuming defences might have been selected in roots over carbon consuming defences in leaves, as nitrogen acquisition costs might be lower for roots than for leaves (Erb et al., 2009). For example, plant proteinase inhibitors (PIs) were induced in root tissue by the southern corn rootworm (SCR) (Lawrence et al., 2012) and the WCR (Robert et al., 2012b), and PIs were found to act as anti-feedants for adult WCR (Kim and Mullin, 2003), although PI effects on the larval stage remains to be tested. Similarly, strawberry plants transformed with the Cowpea trypsin inhibitor gene supported a lower abundance of root-feeding VW larvae (Graham et al., 2002). However, because many soil dwelling herbivores are specialists, it is likely that they have developed strategies to overcome plant defences. There are numerous examples of plant secondary metabolites that provide effective defence against shoot-feeding insects instead acting as attractants or promoting performance of herbivores belowground. Cabbage root fly (*Delia radicum*) and VW, for example, grew larger on plants with higher concentrations of glucosinolates (GLS) (van Leur et al., 2008) and phenolic acids (Clark et al., 2011; Johnson et al., 2011), respectively. Similarly, WCR larvae tolerate the high concentrations of BX in maize roots and even use them to select the most nutritious tissue (Robert et al., 2012c).

3.3. Defence acquisition from the soil: the example of silicon

Silicon is the second most abundant element in the earth's crust. Although only a fraction of soil silicon is bioavailable as solubilised silicic acid (Gocke et al., 2013), many Poaceae sequester silicon in large quantities (Carey and Fulweiler, 2012), in some species at levels exceeding 10% of plant dry weight (Epstein, 1999). The role of silicon in plant resistance to herbivores has been demonstrated extensively aboveground (Massey et al., 2006; Reynolds et al., 2009). The mechanisms underpinning anti-herbivore effects of silicon aboveground relate to the abrasive nature of silicon-rich bodies (phytoliths) on the leaf surface (Hartley et al., 2015b), which may contribute to the observed reduction in the ability of herbivores to extract nitrogen from plants high in silicon (Massey and Hartley, 2006; Massey and Hartley, 2009). While we are aware of relatively little work examining the response of root herbivores to silicon, GBCG reduced feeding by 68% and relative growth rates were more than three times slower when feeding on sugarcane supplemented with silicon (Frew et al., 2016). The mechanistic basis for this remains to be tested but silicon increases root strength

(Hansen et al., 1976) and such changes in root biomechanical properties have been shown to negatively affect root herbivores (Johnson et al., 2010). Moreover, root-specific phytoliths have been found in roots and tubers (Chandler-Ezell et al., 2006) so the abrasive properties of silicon may play a role in herbivore defence. Silicon is also known to be an inducible defence in response to leaf herbivory (Massey et al., 2007; Reynolds et al., 2009), which has also been observed in at least two grasses subjected to root herbivory by scarab beetles (Power et al., 2016).

3.4. Plant breeding and selection for direct defence

Genomic and molecular breeding techniques are promising because they increase the action and heritability of favourable genes (Moose and Mumm, 2008). Using molecular markers and genetic mapping, for instance, specific alleles can be selected or deleted. One well known example of molecular breeding against root herbivory involved the expression of insecticidal *Bacillus thuringiensis* (Bt) toxins against WCR (for review see Hilder and Boulter, 1999). Bt toxins bind selectively to receptors of the epithelial surface of the larvae midgut and lead to pore formation, cell rupture and septicaemia (Vachon et al., 2012). Despite this, WCR resistance to Bt toxin occurred rapidly in both greenhouse and field experiments (Gassmann et al., 2011; Meihls et al., 2011; Gassmann, 2012). Although there has been no specific attempt to genetically select or manipulate innate belowground direct defences, there has been extensive screening for root herbivore resistant lines in a number of crops. Intensive phenotypic screening for resistant varieties has been conducted for maize (Tollefson, 2007; Bernklau et al., 2010), potato (Parker and Howard, 2001), and Brassicacae (Ellis et al., 1999; Dosdall et al., 2000). Two quantitative trait loci (QTLs), RM-G8 and RM-G4, encoding for resistance against the root maggot were discovered in Brassica (Ekuere et al., 2005) and are promising candidates for breeding of resistant varieties. Genomic and molecular breeding for resistance factors, however, is likely to be associated with physiological costs (e.g.

trade-offs with other defences, primary metabolism, crop quality) and ecological consequences (e.g. untargeted effects, emergence of adapted herbivore species) that need to be carefully evaluated before release.

There is increasing interest in the potential benefits of using silicon in crop protection and silicon is now commonly added to crops in the US, China, Japan, Korea and South East Asian countries (Guntzer et al., 2012). The well-known benefits of silicon for crop growth and resistance to biotic stress have driven the development of commercial silicon supplement products in the UK, the USA, Australia and the Far East, both for turf grasses and cereal crops (Guntzer et al., 2012). Plant breeding and selection may assist such silicon supplementation since there is large variation between and within species in silicon uptake rates (Hodson et al., 2005; Soininen et al., 2013). Much of this variation is believed to reflect genotypic differences in the abundance and efficiency of silicon transporters in roots (Ma and Yamaji, 2006; Ma et al., 2007) and these have been at least partially characterised in a range of crop species (Ma and Yamaji, 2006); 2015), particularly rice (Ma and Yamaji, 2006; Ma et al., 2007), offering the potential to breed for altered silicon uptake in crops. It may not be necessary to use genetic modification to engineer increased silicon uptake. Given that silicon accumulation is known to have a genetic basis, genotyping of lines varying in uptake by mRNA sequencing and genome-wide association studies should allow the identification of candidate genes associated with increased silicon uptake to be used in crop breeding.

Intriguingly we may be able to harness plant mutualists (see section 4 below) to aid in silicon uptake and pest resistance. Both AMF (Kothari et al., 1990) and endophytes (Huitu et al., 2014) have been shown to increase silicon uptake by plants. The mechanisms remain unclear, but recently it has been shown that AMF have the same type of aquaporin transporters used by plants for silicon uptake (Chen et al., 2012), suggesting that AMF may be able to increase silicon levels in plants directly through hyphal uptake.

4. Plant mutualists

4.1. Mycorrhizae, endophytes and PGPR

An increasing number of studies provide evidence that plant symbiotic fungi, such as AMF and endophytes, alter the relationship between plants and herbivorous insects (Hartley and Gange, 2009). AMF mediation of plant-herbivore interactions is highly important as almost 90% of land plants associate with AMF (Smith and Read, 2010) and virtually every plant species has been found to associate with endophytes (Stone et al., 2000). Much previous work has focussed on the impacts of AMF on aboveground herbivores (Bennett et al., 2006), with a significantly smaller proportion looking at how root herbivory is affected, recently reviewed by Johnson and Rasmann (2015). Overall, root AMF colonisation had a negative impact on root herbivore performance; the mechanisms behind these responses remain unclear but given the impact of AMF on plant resource acquisition, they could involve both indirect plant-mediated effects as well as direct physical and/or chemical antagonisms (Johnson and Rasmann, 2015). Schouteden et al. (2015) reviewed AMF impacts on plant parasitic nematodes and proposed a number of mechanisms for how AMF assist plant tolerance and resistance to nematode parasitism. Some of these mechanisms are less likely to apply to insect herbivores, such as competition for infection sites and host nutrients, but others such as ISR and altered patterns of root exudation could explain why root herbivore performance deteriorates on AMF-infected plants (Johnson and Rasmann, 2015). In particular, Schouteden et al. (2015) provide numerous examples of AMF priming defences of plants, especially in terms of upregulation of defence genes, which they suggest could underpin plant defences against plant parasitic nematodes. These could also be effective against root-feeding insects, but this has yet to be empirically demonstrated.

The impacts of endophytes, whether foliar or root colonising, on root herbivores have been even less studied (Hartley and Gange, 2009). The Japanese beetle *Popilla japonica* responded negatively to *Acremonium coenophialum* infected ryegrass (Potter et al., 1992), while *N. lolii* infected ryegrass had no effect (Prestidge and Ball, 1997). Foliar endophytes colonising grasses (Clavicipitaceae (Ascomycota), particularly the genus Neotyphodium), are responsible for the production of alkaloids in their hosts (Reed et al., 2000; Stone et al., 2000) which may affect root herbivores. More recently, endophytes in grasses have been shown to affect plant emissions of VOCs which deterred host plant location by root-feeding *Costelytra zealandica* larvae (Rostás et al., 2015). While focusing on the adult stages (which feed on stems below the soil surface), endophytes also affected host plant location by the African black beetle (*Heteronychus arator*) (Qawasmeh et al., 2015). Endophytes might therefore prove useful in repellence or disruption of adult oviposition of root pests. The effects of endophytes colonising herbaceous species are far less studied than those in grasses, but a recent study demonstrated foliar endophytes elicit similar chemical responses in herbaceous plants to those usually produced following wounding, herbivory and pathogen invasion (Hartley et al., 2015a), though the impacts of these changes on herbivores is unknown.

Plant growth promoting rhizobacteria (PGPR) exert positive effects on plant growth via nutrient fixation (Richardson et al., 2009), phytohormone production (Dobbelaere et al., 2003) and/or activation of systemic resistance pathways (Verhagen et al., 2004; Raaijmakers et al., 2009). Activation of the JA and SA pathways most likely underpin host plant resistance to herbivores (Pineda et al., 2010). PGPR do not increase production of these hormones directly, but appear to prime host plants for attack by initiating these resistance pathways, stopping short of synthesising all products in the pathway (Orrelland and Bennett, 2013). Plants are thus able to respond more rapidly to attack. Unlike AMF, which has received modest attention (Johnson and Rasmann, 2015), the impacts of PGPR on root herbivores are largely unknown but likely to occur given their effects on the JA and SA pathways. Indeed, inoculation of maize plants with the PGPR *Azospirillum brasilense* repelled and decreased the performance of the root herbivore *D. speciosa* (Santos et al., 2014). This particular PGPR is known to significantly alter the secondary metabolite profiles in maize plants (Walker et al., 2011). Other herbivore species with root-feeding larval stages, such as *Acalymma vittatum* and *D. undecimpunctata*, are also negatively affected by PGPR, though these studies used adult insects that feed on foliage rather than the root-feeding larvae (Zehnder et al., 1997a; Zehnder et al., 1997b).

4.2. EPNs

Plants under attack typically increase production of VOCs that can be perceived by predators as information cues for locating their herbivore prey (Poveda et al., 2010), a mechanism termed indirect defence. Roots are no exception, and herbivore damage has been shown to activate the production of VOCs in the soil (Rasmann and Agrawal, 2008). Root volatile exudation can provide information cues for various soil-dwelling organisms such as bacteria, fungi and nematodes or other arthropod species (Johnson and Rasmann, 2015). Such indirect defence mechanisms, especially those involving nematodes, could be implemented in biological control against root pests.

Root feeding insect pest populations are continuously under the threat of soil-dwelling predatory nematodes (i.e. EPNs) (Gaugler and Kaya, 1990; Poinar, 1990). EPNs belong to two families (Heterorhabditidae and Steinernematidae) and include about sixty known species (Ivezic et al., 2009). EPNs predominantly use olfactory cues for successful foraging (Hallem et al., 2011; Rasmann et al., 2012). While inorganic gases (e.g. CO_2) released by roots have been implicated in host location, recent advances have shown that EPNs can integrate other organic volatile root signals, such as caryophyllene in maize, or geijerene and pregeijerene in citrus plants, to forage more efficiently (Rasmann et al., 2005; Ali et al., 2011; Turlings et al., 2012). Although EPN species differ considerably in their behaviour and foraging strategies, they all have an obligate parasitic biology that involves penetration into an arthropod host for successful development and reproduction. They move from host to host as infective juveniles, a resistant form that can survive under adverse conditions for several days to months, even when deprived of food (Kaya and Gaugler, 1993). Once inside the host, they release symbiotic bacteria, which multiply and produce a toxin that causes septicaemia and within days kills the insect pest, which then provides a food source for the nematodes.

4.3 Rhizosphere engineering to enhance plant protection via plant mutualisms

Particularly beneficial AMF strains and/or by management practices to encourage native AMF communities can enhance plant performance (Hamel, 1996). More careful use of agricultural practices that restrict AMF colonisation, such as fertilisation (Smith and Read, 2010), tillage (Karasawa and Takebe, 2012) and biocide application, would encourage AMF colonisation of crops. In addition, for those crops where micropropagation techniques are used, biopriming of plantlets with AMF ensures colonisation and has successfully improved plant performance and protection (Kapoor et al., 2008). The use of endophyte infected plants has already shown promise in perennial ryegrass (*Lolium perenne*) (Popay and Baltus, 2001; Qawasmeh et al., 2015), suggesting that sowing of endophyte infected *L. perenne* seeds in managed grasslands and pastures could mitigate damage by root herbivores. Moreover, we are gaining some insight into how different fermentation and formulation strategies might maximise endophyte establishment (e.g. Lohse et al., 2015), so this knowledge could help this approach. PGPR can also be cultured in the laboratory, and potentially included as a soil amendment (Orrelland and Bennett, 2013). Seed coatings of desirable rhizobia to promote plant growth already occurs, so there is at least the potential to coat seeds with PGPR that increase plant defence and/or tolerance (Orrelland and Bennett, 2013).

Despite the potential benefits of AMF, endophytes and PGPR in the field there is obscurity in their practical application. One of the biggest limitations is that AMF, as obligate symbionts of plants, almost invariably requires large scale cultivation of plants to produce commercial AMF products (Rodriguez and Sanders, 2015). This means that AMF products are time consuming to manufacture and their consistency and quality is difficult to replicate. In addition, the use of current commercial inoculum gives varying results because effects seem to be highly context dependent (Gianinazzi and Vosatka, 2004). A further consideration is that microbes (AMF, endophytes and PGPR) conferring pest resistance might not necessarily be the most competitive and could eventually become displaced by other microbes that offer little or no benefits. Achieving desirable associations to persist may be challenging, particularly for endophytes, which are notoriously difficult to constrain to target plants and whose impacts remain less understood, particularly in herbaceous systems.

Because of the high infectivity potential, the ease of production, formulation, and propagation, EPNs have been considered as biocontrol agents (Lacey et al., 2001). EPNs could be directly applied to seeds while planting, or inoculated in the soil after germination (Shapiro-Ilan et al., 2006; Toepfer et al., 2010a; 2010b). The approach has traditionally suffered two limitations: (1) EPN breeding is still relatively laborious, making EPNs expensive compared with chemical pesticides; (2) inoculation of EPNs in the soil does not automatically result in successful host finding and pest control. Undoubtedly, future breeding programs incorporating EPNs are needed to address these two issues. From a practitioner’s perspective, the first obstacle to overcome is how and when to inoculate EPNs. Several inoculation techniques have been proposed, including irrigation systems and spray equipment that should be adjusted depending on the sensitivity of different EPN strains to mechanical and environmental stressors (Shapiro-Ilan et al., 2006; Toepfer et al., 2010a; 2010b). For instance, while most EPNs can survive relatively high pressures, they are sensitive to UV radiation and desiccation (Shapiro-Ilan et al., 2006). Selective breeding and genetic engineering of crops to enhance or modify VOC signalling (Degenhardt et al., 2003; 2009) could thus be used in combination with EPN strain selection (Hiltpold et al., 2010) for enhanced efficacy in the field. Challenges to this approach remain, however, such as the fact that VOCs such as (*E*)-β-caryophyllene are also attractive to several pests, including WCR and *Spodoptera littoralis* larvae (Robert et al., 2012a). Moreover, engineering plants to produce VOCs may come at a cost to plants in terms of reduced germination, growth and yield (Robert et al., 2013). These side-effects must therefore be evaluated in the field before this approach can be adopted.

5. Soil history and feedbacks

Growing plants strongly alter surrounding soil properties (Philippot et al., 2013). This so-called soil conditioning is mediated through processes involving root exudation, nutrient uptake and root respiration (Philippot et al., 2013). For instance, the release of chemicals into the rhizosphere influences aggregate stabilization (Lynch and Bragg, 1985), pH (Hinsinger et al., 2003; Fageria and Stone, 2006), nutrient availability (Wardle et al., 1999; Lugtenberg and Kamilova, 2009; Sugiyama and Yazaki, 2012) and soil microbial and fungal communities (Harwood et al., 1984; Rangel-Castro et al., 2005; Bais et al., 2006; Haichar et al., 2008; Eilers et al., 2010; Bulgarelli et al., 2012; Neal et al., 2012; Sugiyama and Yazaki, 2012; Oldroyd, 2013; Peiffer et al., 2013). Furthermore, some plant exudates and/or their degradation products can persist in soil for years (Etzerodt et al., 2008). Soil conditioning can also alter the quality and performance of the following plant generations, a mechanism referred to as plant-soil feedback (Bever et al., 1997; Ehrenfeld et al., 2005; Kulmatiski et al., 2008; van der Putten et al., 2013).

Farmers have exploited plant-soil feedbacks for centuries through crop rotation, and scientists recently became interested in their ecological consequences (van der Putten, 1997; Ehrenfeld et al., 2005; van der Putten et al., 2013). For example, plant-soil feedbacks are known to modify interactions between the next generation of plants and their herbivores and even natural enemies of their herbivores. The presence of root herbivores on ragwort plants, for example, changed the performance of the cabbage moth, *Mamestra brassicae*, feeding on the next generation of plants (Kostenko et al., 2012). Specifically, the cabbage moth performed worse on plants grown in soil conditioned by root herbivore infested plants (Kostenko et al., 2012). Furthermore, the presence of root herbivores on the first generation of plants, reduced the adult size and increased the development time of the parasitoid *Microplitis mediator* (Kostenko et al., 2012). The underlying mechanisms of such soil feedbacks remain unclear. Microbes are usually suggested to be the main drivers of soil feedback processes, but changes in soil abiotic conditions might also alter plant defensive responses to root herbivory (see review by Erb and Lu, 2013). The effects of soil feedbacks on root herbivore natural enemies have not yet been considered though it may be useful for pest management strategies.

5.1. Land husbandry to use soil feedbacks for plant protection

Soil feedbacks have long underpinned crop rotation and inter cropping strategies. Soil feedback mechanisms and their effects on plants, herbivore and tritrophic interaction provides the possibility of optimally shaping the physical, chemical and biological properties of the soil for suppression of root herbivores. There has been some consideration of this for managing plant diseases which may have parallels with protection from root herbivores (Chave et al., 2014). In particular, certain crop rotations have been shown to promote beneficial organisms added to the soil, which resulted in greater protection of potato plants from pathogens (Larkin, 2008). In tomato, intercropping has also been used to supress disease (Yu, 1999) and attack by root-knot nematodes (Kumar et al., 2005), via allelopathic root exudates from the intercropped plant. The use of intercropping for suppression of root-feeding insects has not been widely addressed, and where it has this has largely focussed on plant-plant feedbacks rather than plant-soil feedbacks (e.g. Björkman et al., 2008). In that study, glucosinolate concentrations decreased in mixed plant communities, potentially due to plant competition, so this particular planting combination would be unlikely to directly supress root herbivory. Nonetheless, the numerous examples of rotations and intercropping supressing plant pathogens (reviewed by Chave et al., 2014) provides some basis for believing that they could also be effective against root-feeding insects. Engineering soil physical and biochemical properties may also directly alter root herbivore performance, and its interaction with the plant, but still requires a large research effort (Erb and Lu, 2013).

6. Translation: the best opportunities for application

The soil environment is an opaque, tri-phasic medium and has presented significant challenges to understanding how plants interact with the rhizosphere. Ironically, these properties may make this environment more germane to longer term and sustainable manipulation in some cases. In particular, it is a stable environment that is less susceptible to environmental perturbations that frequently disrupt pest control strategies deployed aboveground. Inclement weather, for example, severely disrupts biological and semio-chemical based control strategies aimed at protecting crops aboveground. In contrast, the soil is buffered to some extent from such disturbances and control agents (biological or chemical) will dissipate more slowly and therefore persist for longer.

We set out research opportunities and priorities (Fig. 1) and the potential management outcomes they could deliver (Fig. 2) for the four mechanisms we have considered. As we discuss above, the soil environment offers some advantages for pest management but it also presents a number of challenges. In particular, the prevailing soil conditions are likely to be crucial determinants of the success of rhizosphere intervention. For example, soil water, temperature and porosity are pivotal to the efficacy of EPNs (Barnett and Johnson, 2013), whereas the existing microbial communities of soils will determine the competitive success of inoculated AMF (Hartley and Gange, 2009). We therefore stress that research needs be conducted in the context of variable soil conditions, some of which will be more important than others (Fig. 1). Knowing the optimal soil conditions for each intervention could help inform which management strategy to use to create these optimal conditions and which to avoid (Fig. 2).

6.1. Plant tolerance

Plant tolerance and compensatory root growth should be targeted. The advent of non-invasive HTP to screen large numbers of plant phenotypes to identify those desirable root traits (e.g. vigour) may assist here, particularly when used in conjunction with QTL to identify genetic markers for these traits (Fig. 1). Ultimately, crop lines with known tolerance to root herbivores across a range of soil conditions could be selectively deployed (Fig. 2).

6.2. Direct plant defences

Plant resistance via direct secondary metabolites is a challenging approach simply because insects quickly adapt to such chemicals and there is emerging evidence that several root herbivores actually benefit from their presence (see examples in Johnson and Nielsen, 2012). Avoidance of plant genotypes expressing high concentrations of such secondary metabolites would clearly be beneficial. Wider characterisation of how root defences affect root herbivores would help identify whether secondary metabolites actually had anticipated negative impacts on root herbivores. Where defences were effective, trade-offs for the plant traits (e.g. growth, yield and other defences) must be assessed in addition to whether the root herbivores are likely to become adapted to the defence (Fig. 1). This evidence-based information would be valuable for practitioners for selecting crops and cultivars, particularly in systems and regions that had a history of pest incidence (Fig. 2).

Exploiting silicon-based defences may be easier and less complicated to implement. Identifying plants and plant genotypes with naturally high silicon accumulation under different soil conditions and their effects on root herbivores is a particularly promising line for future research. As discussed, silicon accumulation has a genetic basis, so genotyping of lines by mRNA sequencing and genome-wide association studies could identify candidate genes responsible to high uptake (Fig. 1). The potential exists to both exploit the natural variation in silicon uptake between cultivars, and to engineer crop lines with high uptake rates by over-expressing the main silicon transporter-mediated uptake mechanism. This could be enhanced with silicon fertilisation, particularly in agricultural soils with depleted levels of bioavailable silicon (Fig. 2).

6.3. Exploiting mutualisms

Further controlled and field testing with AMF, endophytes and PGPR is needed to ensure that inoculations persist in the field. Particular strains that confer pest resistance will do better in some soil types than others, so it is likely that context specific products will need to be developed in addition to identifying management strategies (based on experiments with varying different soil conditions) that either promote or adversely affect persistence (Fig. 1). An additional benefit of increasing endophyte and AMF colonisation of crops would be a likely rise in their silicon content (see 6.2), with potential improvements in resistance against root-chewing pest species. Certain crop systems that utilise micro-propagation and biopriming of plantlets seem ideal candidates for inoculation with beneficial microbial strains (Fig. 2).

Further identification of VOC attractants of EPNs, and their incorporation into crop breeding programmes could be particularly promising, especially if highly infective EPN lines and symbiont bacterial strains are used (Johnson and Rasmann, 2015). New research into the encapsulation of EPNs in biocompatible and biodegradable natural polymers would enable slow release of EPNs while ensuring physical protection from adverse soil conditions (Hiltpold et al., 2012; Vemmer and Patel, 2013). These capsules also allow other chemical ingredients to be included, which may lure insects towards the capsules further increasing the efficacy of this approach (Hiltpold et al., 2012). Further, EPNs can work synergistically with entomopathogenic fungi (Ansari et al., 2010), and possibly AMF (Johnson and Rasmann, 2015) (Fig. 1). This research could allow practitioners to apply EPN capsules at the beginning of growing seasons and avoid repeated application of pesticides. Moreover, it may be possible to apply multiple agents to work synergistically to control root herbivores (Fig. 2).

6.4. Plant-soil feedbacks

Transplant experiments have proved very useful for determining patterns in plant-soil feedbacks and could be extended to determine the effects on root herbivores (Fig. 1). Taking into account soil physical, biochemical and biological properties and knowing their impact on the plants that will grow in this medium, will be needed to optimally select species for the crop rotation and inter-cropping. Although the principles of soil feedbacks are already in use, better comprehension will allow the development of more effective crop rotation and/or inter-cropping systems that help maximise negative impacts on root herbivores (Fig. 2).

7. Conclusion

The ‘sledgehammer’ approach of prophylactically applying insecticides to control belowground pests has been particularly damaging to a number of ecosystems (Johnson and Murray, 2008). It is also an approach that is becoming increasingly redundant because of economic and legislative factors, so alternatives are urgently sought. We contend that our increasing understanding of rhizosphere ecology may provide some of these answers by allowing us to manipulate ecological interactions in such a way as to control these extremely damaging plant pests.

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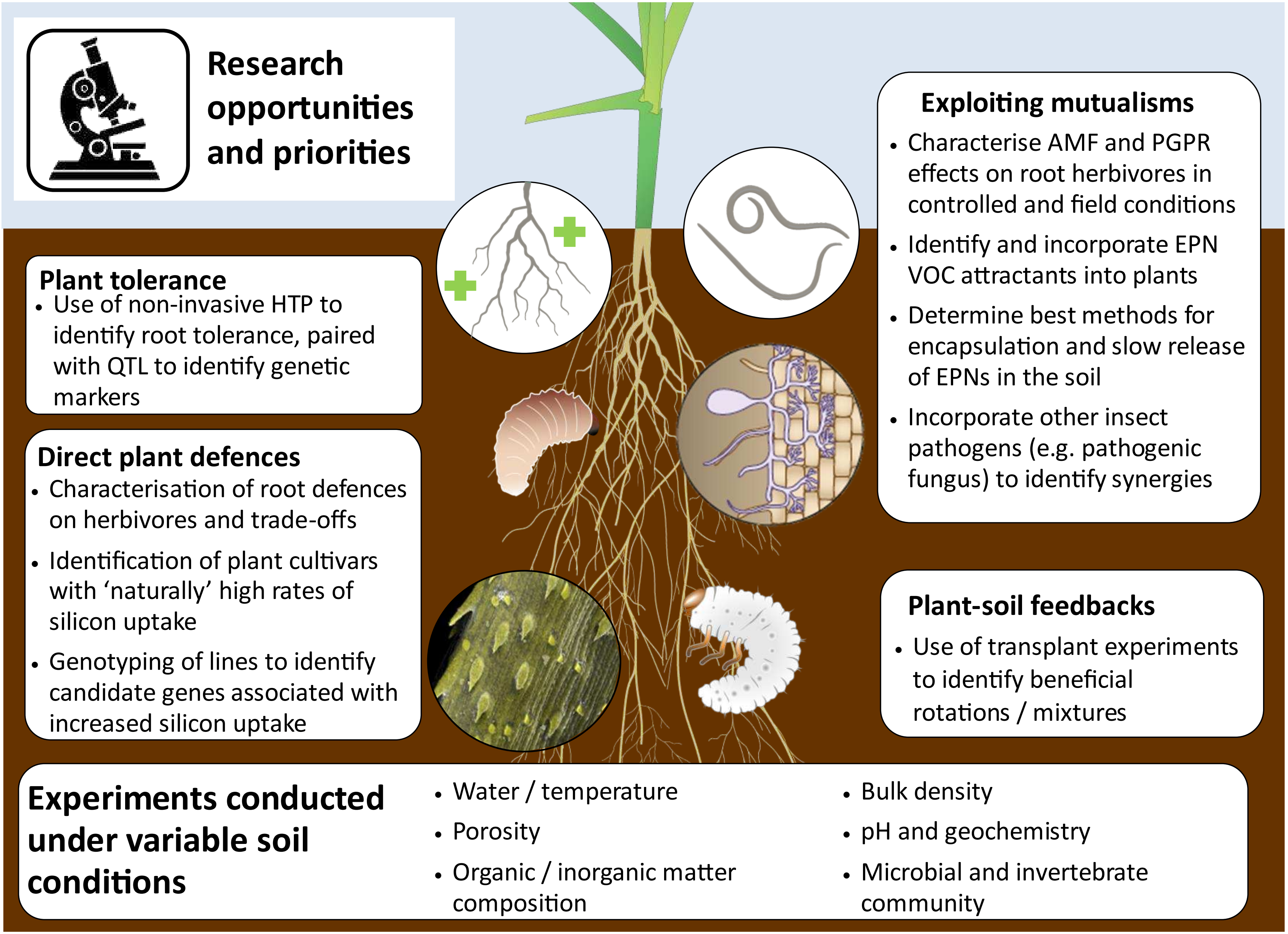
Figure Legends

Fig. 1. Research opportunities and priorities that would help determine the feasibility and optimisation of root herbivore control using plant tolerance, direct defences, plant mutualism and plant-soil feedbacks. Exploring these mechanisms under different soil conditions is particularly important to determine under what circumstances they may be viable and useful for pest control.

Fig. 2. Potential management outcomes for controlling root herbivores using plant tolerance, direct defences, plant mutualism and plant-soil feedbacks.



Research opportunities and priorities

Plant tolerance

- Use of non-invasive HTP to identify root tolerance, paired with QTL to identify genetic markers

Direct plant defences

- Characterisation of root defences on herbivores and trade-offs
- Identification of plant cultivars with ‘naturally’ high rates of silicon uptake
- Genotyping of lines to identify candidate genes associated with increased silicon uptake

Exploiting mutualisms

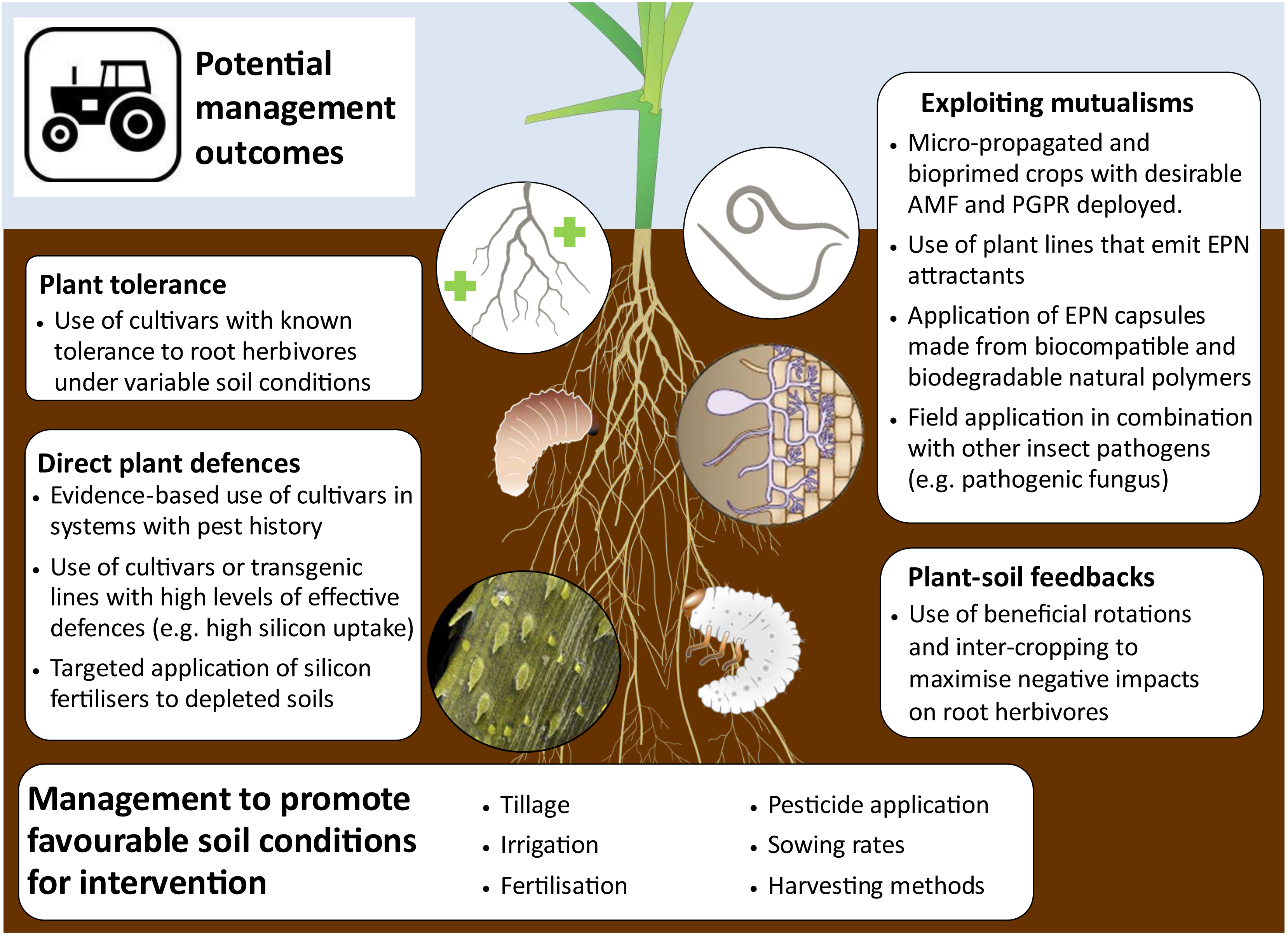
- Characterise AMF and PGPR effects on root herbivores in controlled and field conditions
- Identify and incorporate EPN VOC attractants into plants
- Determine best methods for encapsulation and slow release of EPNs in the soil
- Incorporate other insect pathogens (e.g. pathogenic fungus) to identify synergies

Plant-soil feedbacks

- Use of transplant experiments to identify beneficial rotations / mixtures

Experiments conducted under variable soil conditions

- Water / temperature
- Porosity
- Organic / inorganic matter composition
- Bulk density
- pH and geochemistry
- Microbial and invertebrate community



Potential management outcomes

Plant tolerance

- Use of cultivars with known tolerance to root herbivores under variable soil conditions

Direct plant defences

- Evidence-based use of cultivars in systems with pest history
- Use of cultivars or transgenic lines with high levels of effective defences (e.g. high silicon uptake)
- Targeted application of silicon fertilisers to depleted soils

Exploiting mutualisms

- Micro-propagated and bioprimed crops with desirable AMF and PGPR deployed.
- Use of plant lines that emit EPN attractants
- Application of EPN capsules made from biocompatible and biodegradable natural polymers
- Field application in combination with other insect pathogens (e.g. pathogenic fungus)

Plant-soil feedbacks

- Use of beneficial rotations and inter-cropping to maximise negative impacts on root herbivores

Management to promote favourable soil conditions for intervention

- Tillage
- Irrigation
- Fertilisation
- Pesticide application
- Sowing rates
- Harvesting methods