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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.

**WESTERN SYDNEY**  
UNIVERSITY



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Hawkesbury Institute  
for the Environment

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 Johnson

---

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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 occasions.

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.

R E V I E W

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

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Running title: Belowground ecology and root herbivore management

1 **ABSTRACT**

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

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

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## 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*)

## 53 1. Introduction

54 It has been estimated that invertebrate pests account for crop losses that would be sufficient to  
55 feed more than one billion people (Birch et al., 2011). Global populations are expected to exceed  
56 9.7 billion by 2050 and 11.2 billion by 2100 (UN, 2015). Yet crop productivity has plateaued, so  
57 there is an urgent need to reduce crop losses to such pests to ensure food security (Gregory et al.,  
58 2009). From a global perspective, soil pests that attack crop roots are amongst the most  
59 economically damaging, persistent and difficult to detect and control (Blackshaw and Kerry, 2008).  
60 Plant-parasitic nematodes, for instance, inflict annual world-wide crop losses of at least US\$80  
61 billion and have received significant research interest because of their economic status (Jones et al.,  
62 2013). Root feeding insects include WCR, whose damage and control costs exceed US \$1 billion  
63 annually in USA (Gray et al., 2009), GBCG that cause losses of up to AUD \$28 million annually in  
64 Australia (Chandler, 2002) and wireworms, whose damage and control costs to the Canadian  
65 potato industry approximate CAN \$6 million (Agriculture and Agri-Food 2016). Moreover, in the  
66 absence of control measures, VW can reach densities of over 300,000 per hectare within three years  
67 and reduce raspberry yield by 40-60% (Clark et al., 2012).

68  
69 Root herbivory can be especially damaging to crops, particularly when combined with abiotic  
70 stresses (e.g. drought, which is often exacerbated by damage to roots) (Zvereva and Kozlov, 2012;  
71 Erb and Lu, 2013). Plants often cannot tolerate root herbivory to the same extent as they can shoot  
72 herbivory, not only because their damage is acute but also because many root-feeding pests are

73 extremely persistent, with damage to plant tissues lasting many months or even years (Johnson et  
74 al., 2016). This persistence frequently results in prime agricultural land being taken out of  
75 production (Blackshaw and Kerry, 2008). Moreover, because soil pests are cryptic, infestations often  
76 go unnoticed and extensive damage to crops then becomes inevitable. Management options are  
77 costly and particularly damaging to the environment because practitioners apply insecticides  
78 prophylactically, and often unnecessarily, in an attempt to avoid possible losses (Blackshaw and  
79 Kerry, 2008). Increasingly, this management option is becoming impractical because of legislation  
80 restricting pesticide use (e.g. Nauen et al., 2008), suggesting that control of root-feeding pests may  
81 become even more difficult in future.

82

83 The extent to which the soil environment is driven by interactions between the plant and soil  
84 organisms is becoming increasingly apparent. This represents a significant conceptual advance in  
85 ecology and several important breakthroughs have been made, including identifying how plant  
86 roots acquire specific microbiomes (Edwards et al., 2015) or how root architecture is sometimes  
87 driven by soil microbes (Ditengou et al., 2015). Most recently this has stimulated interest in  
88 'rhizosphere engineering' for promoting plant health and productivity (Zhang et al., 2015; Bender  
89 et al., 2016; Dessaux et al., 2016). At the same time, fundamental studies concerning interactions  
90 between plants and their root herbivores have gained pace and have been particularly helpful in  
91 increasing our understanding of belowground defences (Rasmann and Agrawal, 2008; van Dam,  
92 2009). These defensive interactions are often brokered by a range of microbial (e.g. mycorrhizae)  
93 and invertebrate (e.g. nematode) players (Johnson and Rasmann, 2015), in addition to the  
94 biogeochemical ecology of the rhizosphere (Erb and Lu, 2013). Some of these ecological insights  
95 could now be applied to address a range of management issues, from conservation and climate  
96 change mitigation to sustainable pest management.

97

98 Using belowground ecology for plant protection from root herbivores, particularly in an integrated  
99 way, is a new and challenging frontier and it is therefore timely to synthesise existing knowledge  
100 and evaluate problems and prospects for application. In this respect, we differ in our approach to  
101 recent articles that examine the basic ecology of such interactions (e.g. Rasmann and Agrawal,  
102 2008; van Dam, 2009; Johnson and Rasmann, 2015). In particular, in this review we strategically  
103 examine four aspects which we consider offer most scope for environmental management and  
104 regulation of root-feeding insect pests. In making this selection we readily acknowledge that there  
105 are ecological mechanisms not explicitly covered in this review that could play a role in  
106 management. We assess the suitability of these four mechanisms as management tools, identify  
107 what currently limits their application, where the key knowledge gaps are and ultimately what  
108 opportunities for development lie ahead. Because the ecologies of insect herbivores and plant-  
109 parasitic nematodes differ so much, it's likely that different aspects of belowground ecology will be  
110 important for pest control in these two taxa. We therefore focus on insect herbivores and those  
111 aspects of belowground ecology we consider to have greatest potential for integrated pest  
112 management. We do, however, refer to articles that consider agroecological engineering of the soil  
113 for plant protection (e.g. from plant pathogens; Chave et al., 2014) where we feel these are relevant  
114 to root-feeding insects.

## 115 **2. Plant tolerance**

### 116 *2.1. Root tolerance mechanisms*

117 Plant traits that confer tolerance to herbivory can be expressed before or following herbivore  
118 attack, and have the effect of limiting the injury caused to plants following infestation (Stout, 2013),  
119 thus reducing the negative impact on productivity and yield. In contrast with plant resistance, a  
120 tolerance strategy could provide more durable defence against herbivorous pests as plant traits  
121 conferring tolerance are less likely to have adverse effects on herbivore fitness (Weis and Franks,

122 2006), and therefore are less likely to impose a strong selection pressure on pests to overcome  
123 plant tolerance. Mechanisms of herbivore tolerance include changes in photosynthesis and growth,  
124 phenology and remobilisation of stored reserves (Tiffin, 2000). For root pests, changes in resource  
125 allocation, root growth and vigour have been most widely studied. Diversion of resources  
126 belowground following root attack can compensate or even over-compensate for root loss (Quinn  
127 and Hall, 1992; Thelen et al., 2005; Ryalls et al., 2013), although this phenomenon is less widely  
128 reported for root pests compared to shoot herbivores; Zvereva & Kozlov (2012) estimated that  
129 compensatory growth occurs in about 17% of cases of root herbivore attack, which compares  
130 unfavourably with shoot herbivory where compensatory growth is achieved in 35–44% of cases  
131 (Hawkes and Sullivan, 2001). An alternative strategy might be to divert resources away from  
132 damaged roots towards uninfested tissue (leaves, stems, tubers or healthy roots). Such resource  
133 diversion, termed 'resource sequestration', has been reported extensively in response to  
134 aboveground herbivory (i.e. moving resources to the roots) (Schultz et al., 2013), but there is  
135 increasing evidence for resource movement in the opposite direction (i.e. from roots to shoots)  
136 following root herbivory. In particular, this has been documented in knapweed (Newingham et al.,  
137 2007), tomato (Henkes et al., 2008), potato (Poveda et al., 2010) and maize (Robert et al., 2014).  
138 Resource reallocation could allow root investment to be delayed until the threat of attack has  
139 passed, a phenomenon that is thought to contribute to tolerance of western corn rootworm in  
140 herbivore-tolerant maize (Robert et al., 2015).

## 141 *2.2. Plant selection, breeding and phenotyping for tolerance*

142 Root and plant vigour can contribute to tolerance of root herbivory and may be a promising  
143 approach to combat a wide spectrum of root herbivores. For example, more vigorous plant  
144 genotypes mitigated productivity declines in sugarcane infested with GBCG (Allsopp and Cox,  
145 2002) and perennial raspberry infested with VW larvae (Clark et al., 2012). Although tolerance traits



146 such as compensatory growth and root vigour are likely to be controlled by multiple loci, using QTL  
147 approaches to identify genetic markers (e.g. for root vigour in raspberry: Graham et al., 2011) could  
148 facilitate crop breeding for enhanced plant vigour and ability to withstand herbivore damage  
149 without significant loss of yield. In rice, a number of genes associated with root architecture and  
150 physiological functions have been identified, and/or cloned, which could be helpful to developing  
151 root tolerance to herbivory (Wu and Cheng, 2014).

152

153 The rate-limiting step for introgressing novel traits into crops is the ability to conduct high  
154 throughput phenotyping (HTP) of root traits in large plant populations (Barah and Bones, 2015),  
155 particularly under field conditions. While a range of phenotyping techniques and platforms have  
156 been available for some time (e.g. George et al., 2014), non-invasive imaging technologies have  
157 been a particular focus of recent research effort (Fahlgren et al., 2015). HTP using imaging could  
158 provide a means to identify genotypic differences in response to root stress by using imaging-  
159 based indicators of changes in shoot physiology, such as stomatal conductance and water status,  
160 leaf pigment composition or photosynthetic activity, that indicate root damage belowground. The  
161 utility of plant imaging for HTP of plant-insect interactions is now being recognised (Goggin et al.,  
162 2015) and, when combined with other available –omic technologies (Barah and Bones, 2015), this  
163 approach offers exciting opportunities for rapid advances in crop improvement for root pest  
164 tolerance.

### 165 **3. Plant resistance via direct defence**

166 Plants resist root herbivory via physical and chemical defences (Rasmann and Agrawal, 2008) that  
167 can be constitutive or inducible (van Dam, 2009; Erb et al., 2012). Attributing plant responses  
168 specifically to belowground herbivory is challenging to evaluate as it can be confounded with plant  
169 responses to wounding and soil micro-organisms. Making the causative link, for example, requires

170 experiments including mechanical damage and insect saliva or saliva ablated insects (Bonaventure,  
171 2012; Acevedo et al., 2015). While only a few studies exist, root responses to herbivory appears to  
172 involve modest JA induction, suggesting that roots are sensitive to fine changes in JA levels and/or  
173 that other signalling molecules are involved (Erb et al. 2012).

### 174 3.1. Physical defences

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

188 Root hairs (or trichomes) are specialized cells that play an important role in water and nutrient  
189 uptake (Gregory, 2006). They may also provide some physical protection against insect herbivory,  
190 potentially by preventing small neonate insects from reaching and penetrating the root epidermis  
191 and also providing refugia for the herbivore's natural enemies (e.g. EPNs). In both these respects,  
192 root hairs might have similar functional roles as leaf trichomes aboveground (e.g. Karley et al.,  
193 2015).

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

### 199 *3.2. Chemical defences*

200 Herbivore feeding on plant tissues involves the release of plant- and insect-derived chemical  
201 elicitors and the subsequent activation of genes that underpin reconstruction of the chemical  
202 profile inside the plant (Erb et al., 2012). Plant secondary metabolites offer the potential to promote  
203 resistance to pests due to toxic, deterrent or anti-feedant effects. Although secondary metabolites  
204 with anti-herbivore properties can be present throughout the plant, there is evidence for tissue-  
205 localisation in above- or belowground plant parts of some species (Rasmann and Agrawal, 2008;  
206 Kabouw et al., 2010; Huber et al., 2015; Johnson et al., 2016). Moreover, tissue accumulation of  
207 secondary metabolites can be locally induced by herbivore attack (van Dam and Raaijmakers, 2006;  
208 Robert et al., 2012b), though overall this inducibility tends to be lower in roots compared to shoots  
209 (Erb et al., 2012). This low inducibility of root secondary metabolites might be explained by their  
210 high constitutive concentrations such as for GLS (van Dam et al., 2009) and BXs (Robert et al.,  
211 2012c).

212

213 Defensive proteins represent a class of inducible metabolites that provide a potential weapon  
214 against root herbivores. Erb et al. (2009) suggest that nitrogen consuming defences might have  
215 been selected in roots over carbon consuming defences in leaves, as nitrogen acquisition costs  
216 might be lower for roots than for leaves (Erb et al., 2009). For example, plant proteinase inhibitors  
217 (PIs) were induced in root tissue by the southern corn rootworm (SCR) (Lawrence et al., 2012) and

218 the WCR (Robert et al., 2012b), and PIs were found to act as anti-feedants for adult WCR (Kim and  
219 Mullin, 2003), although PI effects on the larval stage remains to be tested. Similarly, strawberry  
220 plants transformed with the Cowpea trypsin inhibitor gene supported a lower abundance of root-  
221 feeding VW larvae (Graham et al., 2002). However, because many soil dwelling herbivores are  
222 specialists, it is likely that they have developed strategies to overcome plant defences. There are  
223 numerous examples of plant secondary metabolites that provide effective defence against shoot-  
224 feeding insects instead acting as attractants or promoting performance of herbivores belowground.  
225 Cabbage root fly (*Delia radicum*) and VW, for example, grew larger on plants with higher  
226 concentrations of glucosinolates (GLS) (van Leur et al., 2008) and phenolic acids (Clark et al., 2011;  
227 Johnson et al., 2011), respectively. Similarly, WCR larvae tolerate the high concentrations of BX in  
228 maize roots and even use them to select the most nutritious tissue (Robert et al., 2012c).

### 229 3.3. Defence acquisition from the soil: the example of silicon

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

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

248

#### 249 *3.4. Plant breeding and selection for direct defence*

250 Genomic and molecular breeding techniques are promising because they increase the action and  
251 heritability of favourable genes (Moose and Mumm, 2008). Using molecular markers and genetic  
252 mapping, for instance, specific alleles can be selected or deleted. One well known example of  
253 molecular breeding against root herbivory involved the expression of insecticidal *Bacillus*  
254 *thuringiensis* (Bt) toxins against WCR (for review see Hilder and Boulter, 1999). Bt toxins bind  
255 selectively to receptors of the epithelial surface of the larvae midgut and lead to pore formation,  
256 cell rupture and septicaemia (Vachon et al., 2012). Despite this, WCR resistance to Bt toxin occurred  
257 rapidly in both greenhouse and field experiments (Gassmann et al., 2011; Meihls et al., 2011;  
258 Gassmann, 2012). Although there has been no specific attempt to genetically select or manipulate  
259 innate belowground direct defences, there has been extensive screening for root herbivore  
260 resistant lines in a number of crops. Intensive phenotypic screening for resistant varieties has been  
261 conducted for maize (Tollefson, 2007; Bernklau et al., 2010), potato (Parker and Howard, 2001), and  
262 Brassicaceae (Ellis et al., 1999; Dossdall et al., 2000). Two quantitative trait loci (QTLs), RM-G8 and  
263 RM-G4, encoding for resistance against the root maggot were discovered in Brassica (Ekuere et al.,  
264 2005) and are promising candidates for breeding of resistant varieties. Genomic and molecular  
265 breeding for resistance factors, however, is likely to be associated with physiological costs (e.g.

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

269  
270 There is increasing interest in the potential benefits of using silicon in crop protection and silicon is  
271 now commonly added to crops in the US, China, Japan, Korea and South East Asian countries  
272 (Guntzer et al., 2012). The well-known benefits of silicon for crop growth and resistance to biotic  
273 stress have driven the development of commercial silicon supplement products in the UK, the USA,  
274 Australia and the Far East, both for turf grasses and cereal crops (Guntzer et al., 2012). Plant  
275 breeding and selection may assist such silicon supplementation since there is large variation  
276 between and within species in silicon uptake rates (Hodson et al., 2005; Soininen et al., 2013). Much  
277 of this variation is believed to reflect genotypic differences in the abundance and efficiency of  
278 silicon transporters in roots (Ma and Yamaji, 2006; Ma et al., 2007) and these have been at least  
279 partially characterised in a range of crop species (Ma and Yamaji, 2006); 2015), particularly rice (Ma  
280 and Yamaji, 2006; Ma et al., 2007), offering the potential to breed for altered silicon uptake in  
281 crops. It may not be necessary to use genetic modification to engineer increased silicon uptake.  
282 Given that silicon accumulation is known to have a genetic basis, genotyping of lines varying in  
283 uptake by mRNA sequencing and genome-wide association studies should allow the identification  
284 of candidate genes associated with increased silicon uptake to be used in crop breeding.

285

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

290 uptake (Chen et al., 2012), suggesting that AMF may be able to increase silicon levels in plants  
291 directly through hyphal uptake.

## 292 **4. Plant mutualists**

### 293 *4.1. Mycorrhizae, endophytes and PGPR*

294 An increasing number of studies provide evidence that plant symbiotic fungi, such as AMF and  
295 endophytes, alter the relationship between plants and herbivorous insects (Hartley and Gange,  
296 2009). AMF mediation of plant-herbivore interactions is highly important as almost 90% of land  
297 plants associate with AMF (Smith and Read, 2010) and virtually every plant species has been found  
298 to associate with endophytes (Stone et al., 2000). Much previous work has focussed on the impacts  
299 of AMF on aboveground herbivores (Bennett et al., 2006), with a significantly smaller proportion  
300 looking at how root herbivory is affected, recently reviewed by Johnson and Rasmann (2015).  
301 Overall, root AMF colonisation had a negative impact on root herbivore performance; the  
302 mechanisms behind these responses remain unclear but given the impact of AMF on plant  
303 resource acquisition, they could involve both indirect plant-mediated effects as well as direct  
304 physical and/or chemical antagonisms (Johnson and Rasmann, 2015). Schouteden et al. (2015)  
305 reviewed AMF impacts on plant parasitic nematodes and proposed a number of mechanisms for  
306 how AMF assist plant tolerance and resistance to nematode parasitism. Some of these mechanisms  
307 are less likely to apply to insect herbivores, such as competition for infection sites and host  
308 nutrients, but others such as ISR and altered patterns of root exudation could explain why root  
309 herbivore performance deteriorates on AMF-infected plants (Johnson and Rasmann, 2015). In  
310 particular, Schouteden et al. (2015) provide numerous examples of AMF priming defences of plants,  
311 especially in terms of upregulation of defence genes, which they suggest could underpin plant  
312 defences against plant parasitic nematodes. These could also be effective against root-feeding  
313 insects, but this has yet to be empirically demonstrated.

314

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

330

331 Plant growth promoting rhizobacteria (PGPR) exert positive effects on plant growth via nutrient  
332 fixation (Richardson et al., 2009), phytohormone production (Dobbelaere et al., 2003) and/or  
333 activation of systemic resistance pathways (Verhagen et al., 2004; Raaijmakers et al., 2009).  
334 Activation of the JA and SA pathways most likely underpin host plant resistance to herbivores  
335 (Pineda et al., 2010). PGPR do not increase production of these hormones directly, but appear to  
336 prime host plants for attack by initiating these resistance pathways, stopping short of synthesising  
337 all products in the pathway (Orrelland and Bennett, 2013). Plants are thus able to respond more  
338 rapidly to attack. Unlike AMF, which has received modest attention (Johnson and Rasmann, 2015),



339 the impacts of PGPR on root herbivores are largely unknown but likely to occur given their effects  
340 on the JA and SA pathways. Indeed, inoculation of maize plants with the PGPR *Azospirillum*  
341 *brasilense* repelled and decreased the performance of the root herbivore *D. speciosa* (Santos et al.,  
342 2014). This particular PGPR is known to significantly alter the secondary metabolite profiles in  
343 maize plants (Walker et al., 2011). Other herbivore species with root-feeding larval stages, such as  
344 *Acalymma vittatum* and *D. undecimpunctata*, are also negatively affected by PGPR, though these  
345 studies used adult insects that feed on foliage rather than the root-feeding larvae (Zehnder et al.,  
346 1997a; Zehnder et al., 1997b).

#### 347 4.2. EPNs

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

356

357 Root feeding insect pest populations are continuously under the threat of soil-dwelling predatory  
358 nematodes (i.e. EPNs) (Gaugler and Kaya, 1990; Poinar, 1990). EPNs belong to two families  
359 (Heterorhabditidae and Steinernematidae) and include about sixty known species (Ivezic et al.,  
360 2009). EPNs predominantly use olfactory cues for successful foraging (Hallem et al., 2011; Rasmann  
361 et al., 2012). While inorganic gases (e.g. CO<sub>2</sub>) released by roots have been implicated in host  
362 location, recent advances have shown that EPNs can integrate other organic volatile root signals,

363 such as caryophyllene in maize, or geijerene and pregeijerene in citrus plants, to forage more  
364 efficiently (Rasmann et al., 2005; Ali et al., 2011; Turlings et al., 2012). Although EPN species differ  
365 considerably in their behaviour and foraging strategies, they all have an obligate parasitic biology  
366 that involves penetration into an arthropod host for successful development and reproduction.  
367 They move from host to host as infective juveniles, a resistant form that can survive under adverse  
368 conditions for several days to months, even when deprived of food (Kaya and Gaugler, 1993). Once  
369 inside the host, they release symbiotic bacteria, which multiply and produce a toxin that causes  
370 septicaemia and within days kills the insect pest, which then provides a food source for the  
371 nematodes.

#### 372 *4.3 Rhizosphere engineering to enhance plant protection via plant mutualisms*

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

386 rhizobia to promote plant growth already occurs, so there is at least the potential to coat seeds  
387 with PGPR that increase plant defence and/or tolerance (Orrelland and Bennett, 2013).

388

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

401

402 Because of the high infectivity potential, the ease of production, formulation, and propagation,  
403 EPNs have been considered as biocontrol agents (Lacey et al., 2001). EPNs could be directly applied  
404 to seeds while planting, or inoculated in the soil after germination (Shapiro-Ilan et al., 2006;  
405 Toepfer et al., 2010a; 2010b). The approach has traditionally suffered two limitations: (1) EPN  
406 breeding is still relatively laborious, making EPNs expensive compared with chemical pesticides; (2)  
407 inoculation of EPNs in the soil does not automatically result in successful host finding and pest  
408 control. Undoubtedly, future breeding programs incorporating EPNs are needed to address these  
409 two issues. From a practitioner's perspective, the first obstacle to overcome is how and when to  
410 inoculate EPNs. Several inoculation techniques have been proposed, including irrigation systems

411 and spray equipment that should be adjusted depending on the sensitivity of different EPN strains  
412 to mechanical and environmental stressors (Shapiro-Ilan et al., 2006; Toepfer et al., 2010a; 2010b).  
413 For instance, while most EPNs can survive relatively high pressures, they are sensitive to UV  
414 radiation and desiccation (Shapiro-Ilan et al., 2006). Selective breeding and genetic engineering of  
415 crops to enhance or modify VOC signalling (Degenhardt et al., 2003; 2009) could thus be used in  
416 combination with EPN strain selection (Hiltpold et al., 2010) for enhanced efficacy in the field.  
417 Challenges to this approach remain, however, such as the fact that VOCs such as (*E*)- $\beta$ -  
418 caryophyllene are also attractive to several pests, including WCR and *Spodoptera littoralis* larvae  
419 (Robert et al., 2012a). Moreover, engineering plants to produce VOCs may come at a cost to plants  
420 in terms of reduced germination, growth and yield (Robert et al., 2013). These side-effects must  
421 therefore be evaluated in the field before this approach can be adopted.

422

## 423 **5. Soil history and feedbacks**

424 Growing plants strongly alter surrounding soil properties (Philippot et al., 2013). This so-called soil  
425 conditioning is mediated through processes involving root exudation, nutrient uptake and root  
426 respiration (Philippot et al., 2013). For instance, the release of chemicals into the rhizosphere  
427 influences aggregate stabilization (Lynch and Bragg, 1985), pH (Hinsinger et al., 2003; Fageria and  
428 Stone, 2006), nutrient availability (Wardle et al., 1999; Lugtenberg and Kamilova, 2009; Sugiyama  
429 and Yazaki, 2012) and soil microbial and fungal communities (Harwood et al., 1984; Rangel-Castro  
430 et al., 2005; Bais et al., 2006; Haichar et al., 2008; Eilers et al., 2010; Bulgarelli et al., 2012; Neal et al.,  
431 2012; Sugiyama and Yazaki, 2012; Oldroyd, 2013; Peiffer et al., 2013). Furthermore, some plant  
432 exudates and/or their degradation products can persist in soil for years (Etzerodt et al., 2008). Soil  
433 conditioning can also alter the quality and performance of the following plant generations, a

434 mechanism referred to as plant-soil feedback (Bever et al., 1997; Ehrenfeld et al., 2005; Kulmatiski et  
435 al., 2008; van der Putten et al., 2013).

436

437 Farmers have exploited plant-soil feedbacks for centuries through crop rotation, and scientists  
438 recently became interested in their ecological consequences (van der Putten, 1997; Ehrenfeld et al.,  
439 2005; van der Putten et al., 2013). For example, plant-soil feedbacks are known to modify  
440 interactions between the next generation of plants and their herbivores and even natural enemies  
441 of their herbivores. The presence of root herbivores on ragwort plants, for example, changed the  
442 performance of the cabbage moth, *Mamestra brassicae*, feeding on the next generation of plants  
443 (Kostenko et al., 2012). Specifically, the cabbage moth performed worse on plants grown in soil  
444 conditioned by root herbivore infested plants (Kostenko et al., 2012). Furthermore, the presence of  
445 root herbivores on the first generation of plants, reduced the adult size and increased the  
446 development time of the parasitoid *Microplitis mediator* (Kostenko et al., 2012). The underlying  
447 mechanisms of such soil feedbacks remain unclear. Microbes are usually suggested to be the main  
448 drivers of soil feedback processes, but changes in soil abiotic conditions might also alter plant  
449 defensive responses to root herbivory (see review by Erb and Lu, 2013). The effects of soil  
450 feedbacks on root herbivore natural enemies have not yet been considered though it may be  
451 useful for pest management strategies.

452

### 453 *5.1. Land husbandry to use soil feedbacks for plant protection*

454 Soil feedbacks have long underpinned crop rotation and inter cropping strategies. Soil feedback  
455 mechanisms and their effects on plants, herbivore and tritrophic interaction provides the possibility  
456 of optimally shaping the physical, chemical and biological properties of the soil for suppression of  
457 root herbivores. There has been some consideration of this for managing plant diseases which may

458 have parallels with protection from root herbivores (Chave et al., 2014). In particular, certain crop  
459 rotations have been shown to promote beneficial organisms added to the soil, which resulted in  
460 greater protection of potato plants from pathogens (Larkin, 2008). In tomato, intercropping has  
461 also been used to suppress disease (Yu, 1999) and attack by root-knot nematodes (Kumar et al.,  
462 2005), via allelopathic root exudates from the intercropped plant. The use of intercropping for  
463 suppression of root-feeding insects has not been widely addressed, and where it has this has  
464 largely focussed on plant-plant feedbacks rather than plant-soil feedbacks (e.g. Björkman et al.,  
465 2008). In that study, glucosinolate concentrations decreased in mixed plant communities,  
466 potentially due to plant competition, so this particular planting combination would be unlikely to  
467 directly suppress root herbivory. Nonetheless, the numerous examples of rotations and  
468 intercropping suppressing plant pathogens (reviewed by Chave et al., 2014) provides some basis for  
469 believing that they could also be effective against root-feeding insects. Engineering soil physical  
470 and biochemical properties may also directly alter root herbivore performance, and its interaction  
471 with the plant, but still requires a large research effort (Erb and Lu, 2013).

## 472 **6. Translation: the best opportunities for application**

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

481

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

#### 493 *6.1. Plant tolerance*

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

499

#### 500 *6.2. Direct plant defences*

501 Plant resistance via direct secondary metabolites is a challenging approach simply because insects  
502 quickly adapt to such chemicals and there is emerging evidence that several root herbivores  
503 actually benefit from their presence (see examples in Johnson and Nielsen, 2012). Avoidance of  
504 plant genotypes expressing high concentrations of such secondary metabolites would clearly be  
505 beneficial. Wider characterisation of how root defences affect root herbivores would help identify

506 whether secondary metabolites actually had anticipated negative impacts on root herbivores.  
507 Where defences were effective, trade-offs for the plant traits (e.g. growth, yield and other defences)  
508 must be assessed in addition to whether the root herbivores are likely to become adapted to the  
509 defence (Fig. 1). This evidence-based information would be valuable for practitioners for selecting  
510 crops and cultivars, particularly in systems and regions that had a history of pest incidence (Fig. 2).  
511  
512 Exploiting silicon-based defences may be easier and less complicated to implement. Identifying  
513 plants and plant genotypes with naturally high silicon accumulation under different soil conditions  
514 and their effects on root herbivores is a particularly promising line for future research. As discussed,  
515 silicon accumulation has a genetic basis, so genotyping of lines by mRNA sequencing and  
516 genome-wide association studies could identify candidate genes responsible to high uptake (Fig.  
517 1). The potential exists to both exploit the natural variation in silicon uptake between cultivars, and  
518 to engineer crop lines with high uptake rates by over-expressing the main silicon transporter-  
519 mediated uptake mechanism. This could be enhanced with silicon fertilisation, particularly in  
520 agricultural soils with depleted levels of bioavailable silicon (Fig. 2).

521

### 522 *6.3. Exploiting mutualisms*

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



530 systems that utilise micro-propagation and biopriming of plantlets seem ideal candidates for  
531 inoculation with beneficial microbial strains (Fig. 2).

532

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

#### 545 *6.4. Plant-soil feedbacks*

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

553 **7. Conclusion**

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

560

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566 **References**

567 Acevedo, F.E., Rivera-Vega, L.J., Chung, S.H., Ray, S. and Felton, G.W., 2015. Cues from chewing  
568 insects - the intersection of DAMPs, HAMPs, MAMPs and effectors. *Curr. Opin. Plant Biol.*  
569 26, 80-86.

570 Agriculture\_and\_Agri-Food\_Canada, 2016. New pest management practices for the control of  
571 wireworm. [http://www.agr.gc.ca/eng/news/science-of-agricultural-innovation/new-pest-](http://www.agr.gc.ca/eng/news/science-of-agricultural-innovation/new-pest-management-practices-for-the-control-of-wireworm/?id=1454519421585)  
572 [management-practices-for-the-control-of-wireworm/?id=1454519421585:](http://www.agr.gc.ca/eng/news/science-of-agricultural-innovation/new-pest-management-practices-for-the-control-of-wireworm/?id=1454519421585)  
573 [http://www.agr.gc.ca/eng/news/science-of-agricultural-innovation/new-pest-management-](http://www.agr.gc.ca/eng/news/science-of-agricultural-innovation/new-pest-management-practices-for-the-control-of-wireworm/?id=1454519421585)  
574 [practices-for-the-control-of-wireworm/?id=1454519421585](http://www.agr.gc.ca/eng/news/science-of-agricultural-innovation/new-pest-management-practices-for-the-control-of-wireworm/?id=1454519421585). Accessed 6 June 2016.

575 Ali, J.G., Alborn, H.T. and Stelinski, L.L., 2011. Constitutive and induced subterranean plant volatiles  
576 attract both entomopathogenic and plant parasitic nematodes. *J. Ecol.* 99, 26–35.

- 577 Allsopp, P.G. and Cox, M.C., 2002. Sugarcane clones vary in their resistance to sugarcane  
578 whitegrubs. *Aust. J. Agric. Res.* 53, 1111-1136.
- 579 Ansari, M.A., Shah, F.A. and Butt, T.M., 2010. The entomopathogenic nematode *Steinernema*  
580 *kraussei* and *Metarhizium anisopliae* work synergistically in controlling overwintering larvae  
581 of the black vine weevil, *Otiorhynchus sulcatus*, in strawberry growbags. *Biocontrol Sci.*  
582 *Techn.* 20, 99-105.
- 583 Arnott, H.J., 1966. Studies of calcification in plants. in: Fleisch, H., Blackwood, J.H. and Owen, M.  
584 (Eds.), *Third European symposium on calcified tissues*. Springer-Verlag, New York, USA. pp.  
585 152-157.
- 586 Arnott, H.J., 1976. Calcification in higher plants. in: Watabe, N. and Wilbur, K.M. (Eds.), *The*  
587 *mechanisms of mineralization in the invertebrates and plants*. University of South Carolina  
588 Press, Columbia, SC, USA. pp. 55-78.
- 589 Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S. and Vivanco, J.M., 2006. The role of root exudates in  
590 rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* 57, 233-266.
- 591 Barah, P. and Bones, A.M., 2015. Multidimensional approaches for studying plant defence against  
592 insects: from ecology to omics and synthetic biology. *J. Exp. Bot.* 66, 479-493.
- 593 Barnett, K. and Johnson, S.N., 2013. Living in the soil matrix: abiotic factors affecting root  
594 herbivores. *Adv. Insect Physiol.* 45, 1-52.
- 595 Bender, S.F., Wagg, C. and van der Heijden, M.G.A., 2016. An underground revolution: biodiversity  
596 and soil ecological engineering for agricultural sustainability. *Trends Ecol. Env.* 31, 440-452.
- 597 Bennett, A.E., Alers-Garcia, J. and Bever, J.D., 2006. Three-way interactions among mutualistic  
598 mycorrhizal fungi, plants, and plant enemies: hypotheses and synthesis. *Am. Nat.* 167, 141-  
599 152.
- 600 Bernklau, E.J., Hibbard, B.E. and Bjostad, L.B., 2010. Antixenosis in maize reduces feeding by western  
601 corn rootworm larvae (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 103, 2052-2060.

602 Bever, J.D., Westover, K.M. and Antonovics, J., 1997. Incorporating the soil community into plant  
603 population dynamics: the utility of the feedback approach. *J. Ecol.* 85, 561-573.

604 Birch, A.N.E., Begg, G.S. and Squire, G.R., 2011. How agro-ecological research helps to address food  
605 security issues under new IPM and pesticide reduction policies for global crop production  
606 systems. *J. Exp. Bot.* 62, 3251-3261.

607 Björkman, M., Hopkins, R.J. and Rämert, B., 2008. Combined effect of intercropping and turnip root  
608 fly (*Delia floralis*) larval feeding on the glucosinolate concentrations in cabbage roots and  
609 foliage. *J. Chem. Ecol.* 34, 1368-1376.

610 Blackshaw, R.P. and Kerry, B.R., 2008. Root herbivory in agricultural ecosystems. in: Johnson, S.N.  
611 and Murray, P.J. (Eds.), *Root Feeders - an ecosystem perspective*. CABI, Wallingford, UK. pp.  
612 35-53.

613 Bonaventure, G., 2012. Perception of insect feeding by plants. *Plant Biol.* 14, 872-880.

614 Bulgarelli, D., Rott, M., Schlaeppli, K., van Themaat, E.V.L., Ahmadinejad, N., Assenza, F., Rauf, P.,  
615 Huettel, B., Reinhardt, R., Schmelzer, E., Peplies, J., Gloeckner, F.O., Amann, R., Eickhorst, T.  
616 and Schulze-Lefert, P., 2012. Revealing structure and assembly cues for *Arabidopsis* root-  
617 inhabiting bacterial microbiota. *Nature.* 488, 91-95.

618 Carey, J.C. and Fulweiler, R.W., 2012. The terrestrial silica pump. *Plos One.* 7, e52932.

619 Cavalier, D.M., Lerouxel, O., Neumetzler, L., Yamauchi, K., Reinecke, A., Freshour, G., Zobotina, O.A.,  
620 Hahn, M.G., Burgert, I., Pauly, M., Raikhel, N.V. and Keegstra, K., 2008. Disrupting two  
621 *Arabidopsis thaliana* xylosyltransferase genes results in plants deficient in xyloglucan, a  
622 major primary cell wall component. *Plant Cell.* 20, 1519-1537.

623 Chandler-Ezell, K., Pearsall, D.M. and Zeidler, J.A., 2006. Root and tuber phytoliths and starch grains  
624 document manioc (*Manihot esculenta*), arrowroot (*Maranta arundinacea*), and lleren  
625 (*Calathea* sp.) at the Real Alto site, Ecuador. *Econ. Bot.* 60, 103-120.

- 626 Chandler, K.J. 2002. Strategies to control greyback canegrub in early harvested ratoon crops: SRDC  
627 final report: project IPB001. Sugar Research Australia, QLD, Australia.
- 628 Chave, M., Tchamitchian, M. and Ozier-Lafontaine, H., 2014. Agroecological engineering to  
629 biocontrol soil pests for crop health. *Agroecological engineering to biocontrol soil pests for*  
630 *crop health.* 14, 269-297.
- 631 Chen, X., Li, H., Chan, W.F., Wu, C., Wu, F., Wu, S. and Wong, M.H., 2012. Arsenite transporters  
632 expression in rice (*Oryza sativa* L.) associated with arbuscular mycorrhizal fungi (AMF)  
633 colonization under different levels of arsenite stress. *Chemosphere.* 89, 1248-1254.
- 634 Clark, K.E., Hartley, S.E. and Johnson, S.N., 2011. Does mother know best? The preference-  
635 performance hypothesis and parent-offspring conflict in aboveground-belowground  
636 herbivore life cycles. *Ecol. Entomol.* 36, 117-124.
- 637 Clark, K.E., Hartley, S.E., Brennan, R.M., Jennings, S.N., McMenemy, L.S., McNicol, J.W., Mitchell, C.  
638 and Johnson, S.N., 2012. Effects of cultivar and egg density on a colonizing vine weevil  
639 (*Otiorhynchus sulcatus*) population and its impacts on red raspberry growth and yield. *Crop*  
640 *Prot.* 32, 76-82.
- 641 Degenhardt, J., Gershenzon, J., Baldwin, I.T. and Kessler, A., 2003. Attracting friends to feast on foes:  
642 engineering terpene emission to make crop plants more attractive to herbivore enemies.  
643 *Curr. Opin. Biotech.* 14, 169-176.
- 644 Degenhardt, J., Hiltbold, I., Kollner, T.G., Frey, M., Gierl, A., Gershenzon, J., Hibbard, B.E., Ellersieck,  
645 M.R. and Turlings, T.C.J., 2009. Restoring a maize root signal that attracts insect-killing  
646 nematodes to control a major pest. *Proc. Natl. Acad. Sci. U.S.A.* 106, 13213-13218.
- 647 Dessaux, Y., Grandclement, C. and Faure, D., 2016. Engineering the Rhizosphere. *Engineering the*  
648 *Rhizosphere.* 21, 266-278.

649 Ditengou, F.A., Mueller, A., Rosenkranz, M., Felten, J., Lasok, H., van Doorn, M.M., Legue, V., Palme,  
650 K., Schnitzler, J.-P. and Polle, A., 2015. Volatile signalling by sesquiterpenes from  
651 ectomycorrhizal fungi reprogrammes root architecture. *Nat. Commun.* 6, article 6279.

652 Dobbelaere, S., Vanderleyden, J. and Okon, Y., 2003. Plant growth-promoting effects of diazotrophs  
653 in the rhizosphere. *Crit. Rev. Plant Sci.* 22, 107-149.

654 Dossall, L.M., Good, A., Keddie, B.A., Ekuere, U. and Stringam, G., 2000. Identification and evaluation  
655 of root maggot (*Delia* spp.) (Diptera : Anthomyiidae) resistance within Brassicaceae. *Crop*  
656 *Prot.* 19, 247-253.

657 Edwards, J., Johnson, C., Santos-Medellin, C., Lurie, E., Podishetty, N.K., Bhatnagar, S., Eisen, J.A. and  
658 Sundaresan, V., 2015. Structure, variation, and assembly of the root-associated microbiomes  
659 of rice. *Proc. Natl. Acad. Sci. U.S.A.* 112, E911-E920.

660 Ehrenfeld, J.G., Ravit, B. and Elgersma, K., 2005. Feedback in the plant-soil system. *Annu. Rev.*  
661 *Environ. Resour.* 30, 75-115.

662 Eilers, K.G., Lauber, C.L., Knight, R. and Fierer, N., 2010. Shifts in bacterial community structure  
663 associated with inputs of low molecular weight carbon compounds to soil. *Soil Biol.*  
664 *Biochem.* 42, 896-903.

665 Ekuere, U.U., Dossall, L.M., Hills, M., Keddie, A.B., Kott, L. and Good, A., 2005. Identification,  
666 mapping, and economic evaluation of QTLs encoding root maggot resistance in Brassica.  
667 *Crop Sci.* 45, 371-378.

668 Ellis, P.R., Pink, D.A.C., Barber, N.E. and Mead, A., 1999. Identification of high levels of resistance to  
669 cabbage root fly, *Delia radicum*, in wild Brassica species. *Euphytica.* 110, 207-214.

670 Epstein, E., 1999. Silicon. *Annu Rev Plant Physiol. and Plant Molec. Biol.* 50, 641-664.

671 Erb, M., Lenk, C., Degenhardt, J. and Turlings, T.C.J., 2009. The underestimated role of roots in  
672 defense against leaf attackers. *Trends Plant Sci.* 14, 653-659.

673 Erb, M., Glauser, G. and Robert, C.A.M., 2012. Induced immunity against belowground insect  
674 herbivores- activation of defenses in the absence of a jasmonate burst. *J. Chem. Ecol.* 38,  
675 629–640.

676 Erb, M. and Lu, J., 2013. Soil abiotic factors influence interactions between belowground herbivores  
677 and plant roots. *J. Exp. Bot.* 64, 1295–1303.

678 Erb, M., Robert, C.A.M., Marti, G., Lu, J., Doyen, G.R., Villard, N., Barriere, Y., French, B.W., Wolfender,  
679 J.L., Turlings, T.C.J. and Gershenson, J., 2015. A physiological and behavioral mechanism for  
680 leaf herbivore-induced systemic root resistance. *Plant Physiol.* 169, 2884-2894.

681 Etzerodt, T., Mortensen, A.G. and Fomsgaard, I.S., 2008. Transformation kinetics of 6-  
682 methoxybenzoxazolin-2-one in soil. *J. Environ. Sci. Health Part B-Pestic. Contam. Agric.*  
683 *Wastes.* 43, 1-7.

684 Fageria, N.K. and Stone, L.F., 2006. Physical, chemical, and biological changes in the rhizosphere  
685 and nutrient availability. *J. Plant Nutr.* 29, 1327-1356.

686 Fahlgren, N., Gehan, M.A. and Baxter, I., 2015. Lights, camera, action: high-throughput plant  
687 phenotyping is ready for a close-up. *Curr. Opin. Plant Biol.* 24, 93-99.

688 Frew, A., Powell, J.R., Sallam, N., Allsopp, P.G. and Johnson, S.N., 2016. Trade-offs between silicon  
689 and phenolic defences may explain enhanced performance of root herbivores on phenolic-  
690 rich plants. *J. Chem Ecol.* *In Press.*

691 Galway, M.E. and McCully, M.E., 1987. The time course of the induction of callose in wounded pea  
692 roots. *Protoplasma.* 139, 77-91.

693 Gassmann, A.J., Petzold-Maxwell, J.L., Keweshan, R.S. and Dunbar, M.W., 2011. Field-evolved  
694 resistance to Bt maize by western corn rootworm. *PLoS One.* 6.

695 Gassmann, A.J., 2012. Field-evolved resistance to Bt maize by western corn rootworm: predictions  
696 from the laboratory and effects in the field. *J. Invertebr. Pathol.* 110, 287-293.

697 Gaugler, R. and Kaya, H.K., 1990. *Entomopathogenic Nematodes in Biological Control*. CRC Press,  
698 Boca Raton, Florida, USA.

699 Genet, M., Stokes, A., Salin, F., Mickovski, S., Fourcaud, T., Dumail, J.F. and van Beek, R., 2005. The  
700 influence of cellulose content on tensile strength in tree roots. *Plant Soil*. 278, 1-9.

701 George, T., Hawes, C., Newton, A., McKenzie, B., Hallett, P. and Valentine, T., 2014. Field  
702 phenotyping and long-term platforms to characterise how crop genotypes interact with soil  
703 processes and the environment. *Agronomy*. 4, 242.

704 Gianinazzi, S. and Vosatka, M., 2004. Inoculum of arbuscular mycorrhizal fungi for production  
705 systems: science meets business. *Canadian J. Bot.* 82, 1264-1271.

706 Gocke, M., Liang, W., Sommer, M. and Kuzyakov, Y., 2013. Silicon uptake by wheat: effects of Si  
707 pools and pH. *J. Plant Nutr. Soil Sc.* 176, 551-560.

708 Goggin, F.L., Lorence, A. and Topp, C.N., 2015. Applying high-throughput phenotyping to plant-  
709 insect interactions: picturing more resistant crops. *Curr. Opin. Plant Biol.* 9, 69-76.

710 Graham, J., Gordon, S.C., Smith, K., McNicol, R.J. and McNicol, J.W., 2002. The effect of the Cowpea  
711 trypsin inhibitor in strawberry on damage by vine weevil under field conditions. *J. Hortic.*  
712 *Sci. Biotech.* 77, 33-40.

713 Graham, J., Hackett, C.A., Smith, K., Woodhead, M., MacKenzie, K., Tierney, I., Cooke, D., Bayer, M.  
714 and Jennings, N., 2011. Towards an understanding of the nature of resistance to  
715 *Phytophthora* root rot in red raspberry. *Theor. Appl. Genet.* 123, 585-601.

716 Gray, M.E., Sappington, T.W., Miller, N.J., Moeser, J. and Bohn, M.O., 2009. Adaptation and  
717 Invasiveness of Western Corn Rootworm: Intensifying Research on a Worsening Pest. *Annu.*  
718 *Rev. Entomol.* 54, 303-321.

719 Gregory, P.J., 2006. *Plant roots - growth, activity and interaction with soils*. Blackwell Publishing,  
720 Oxford, UK.



721 Gregory, P.J., Johnson, S.N., Newton, A.C. and Ingram, J.S.I., 2009. Integrating pests and pathogens  
722 into the climate change/food security debate. *J Exp. Bot.* 60, 2827–2838.

723 Guntzer, F., Keller, C. and Meunier, J.D., 2012. Benefits of plant silicon for crops: a review. *Agron.*  
724 *Sust. Dev.* 32, 201-213.

725 Haichar, F.Z., Marol, C., Berge, O., Rangel-Castro, J.I., Prosser, J.I., Balesdent, J., Heulin, T. and  
726 Achouak, W., 2008. Plant host habitat and root exudates shape soil bacterial community  
727 structure. *ISME J.* 2, 1221-1230.

728 Hallem, E.A., Dillman, A.R., Hong, A.V., Zhang, Y.J., Yano, J.M., DeMarco, S.F. and Sternberg, P.W.,  
729 2011. A sensory code for host seeking in parasitic nematodes. *Curr. Biol.* 21, 377-383.

730 Hamel, C., 1996. Prospects and problems pertaining to the management of arbuscular mycorrhizae  
731 in agriculture. *Agr. Ecosyst. Environ.* 60, 197-210.

732 Hansen, D.J., Dayanandan, P., Kaufman, P.B. and Brotherson, J.D., 1976. Ecological adaptations of  
733 salt-marsh grass, *Distichlis spicata* (Gramineae) and environmental factors affecting its  
734 growth and distribution. *Am. J. Bot.* 63, 635-650.

735 Hartley, S.E. and Gange, A.C., 2009. Impacts of plant symbiotic fungi on insect herbivores:  
736 mutualism in a multitrophic context. *Annu. Rev. Entomol.* 54, 323–342.

737 Hartley, S.E., Eschen, R., Horwood, J.M., Gange, A.C. and Hill, E.M., 2015a. Infection by a foliar  
738 endophyte elicits novel arabidopside-based plant defence reactions in its host, *Cirsium*  
739 *arvense*. *New Phytol.* 205, 816-827.

740 Hartley, S.E., Fitt, R.N., McLamon, E.L. and Wade, R.N., 2015b. Defending the leaf surface: intra- and  
741 inter-specific differences in silicon deposition in grasses in response to damage and silicon  
742 supply. *Front. Plant. Sci.* 6.

743 Harwood, C.S., Rivelli, M. and Ornston, L.N., 1984. Aromatic-acids are chemoattractants for  
744 *Pseudomonas putida*. *J. Bacteriol.* 160, 622-628.

745 Hawkes, C.V. and Sullivan, J.J., 2001. The impact of herbivory on plants in different resource  
746 conditions: a meta-analysis. *Ecology*. 82, 2045–2058.

747 Henkes, G.J., Thorpe, M.R., Minchin, P.E.H., Schurr, U. and Roese, U.S.R., 2008. Jasmonic acid  
748 treatment to part of the root system is consistent with simulated leaf herbivory, diverting  
749 recently assimilated carbon towards untreated roots within an hour. *Plant Cell Environ.* 31,  
750 1229-1236.

751 Hilder, V.A. and Boulter, D., 1999. Genetic engineering of crop plants for insect resistance - a critical  
752 review. *Crop Prot.* 18, 177-191.

753 Hiltbold, I., Baroni, M., Toepfer, S., Kuhlmann, U. and Turlings, T.C.J., 2010. Selection of  
754 entomopathogenic nematodes for enhanced responsiveness to a volatile root signal helps  
755 to control a major root pest. *J. Exp. Biol.* 213, 2417–2423.

756 Hiltbold, I., Hibbard, B.E., French, B.W. and Turlings, T.C.J., 2012. Capsules containing  
757 entomopathogenic nematodes as a Trojan horse approach to control the western corn  
758 rootworm. *Plant Soil.* 358, 10-24.

759 Hinsinger, P., Plassard, C., Tang, C.X. and Jaillard, B., 2003. Origins of root-mediated pH changes in  
760 the rhizosphere and their responses to environmental constraints: a review. *Plant Soil.* 248,  
761 43-59.

762 Hodson, M.J., White, P.J., Mead, A. and Broadley, M.R., 2005. Phylogenetic variation in the silicon  
763 composition of plants. *Ann. Bot-London.* 96, 1027-1046.

764 Huber, M., Triebwasser-Freese, D., Reichelt, M., Heiling, S., Paetz, C., Chandran, J.N., Bartram, S.,  
765 Schneider, B., Gershenzon, J. and Erb, M., 2015. Identification, quantification, spatiotemporal  
766 distribution and genetic variation of major latex secondary metabolites in the common  
767 dandelion (*Taraxacum officinale* agg.). *Phytochemistry.* 115, 89-98.

768 Huitu, O., Forbes, K., Helander, M., Julkunen-Tiitto, R., Lambin, X., Saikkonen, K., Stuart, P., Sulkama,  
769 S. and Hartley, S.E., 2014. Silicon, endophytes and secondary metabolites as grass defenses  
770 against mammalian herbivores. *Front. Plant Sci.* 5, 478.

771 Ivezic, M., Raspudic, E., Brmez, M., Majic, I., Brkic, I., Tollefson, J.J., Bohn, M., Hibbard, B.E. and Simic,  
772 D., 2009. A review of resistance breeding options targeting western corn rootworm  
773 (*Diabrotica virgifera virgifera* LeConte). *Agric. Forest Entomol.* 11, 307-311.

774 Johnson, S.N. and Murray, P.J. (Eds.), 2008. *Root Feeders - an ecosystem perspective*. CABI,  
775 Wallingford, UK.

776 Johnson, S.N., Hallett, P.D., Gillespie, T.L. and Halpin, C., 2010. Belowground herbivory and root  
777 toughness: a potential model system using lignin-modified tobacco. *Physiol. Entomol.* 35,  
778 186–191.

779 Johnson, S.N., Barton, A.T., Clark, K.E., Gregory, P.J., McMenemy, L.S. and Hancock, R.D., 2011.  
780 Elevated atmospheric carbon dioxide impairs the performance of root-feeding vine weevils  
781 by modifying root growth and secondary metabolites. *Global Change Biol.* 17, 688–695.

782 Johnson, S.N. and Nielsen, U.N., 2012. Foraging in the dark - chemically mediated host plant  
783 location by belowground insect herbivores *J. Chem. Ecol.* 38, 604–614.

784 Johnson, S.N. and Rasmann, S., 2015. Root-feeding insects and their interactions with organisms in  
785 the rhizosphere. *Annu. Rev. Entomol.* 60, 517-535.

786 Johnson, S.N., Erb, M. and Hartley, S.E., 2016. Roots under attack: contrasting plant responses to  
787 below- and aboveground insect herbivory. *New Phytol.* 210, 413-418.

788 Jones, J.T., Haegeman, A., Danchin, E.G.J., Gaur, H.S., Helder, J., Jones, M.G.K., Kikuchi, T., Manzanilla-  
789 Lopez, R., Palomares-Rius, J.E., Wesemael, W.M.L. and Perry, R.N., 2013. Top 10 plant-  
790 parasitic nematodes in molecular plant pathology. *Mol. Plant Pathol.* 14, 946-961.

791 Kabouw, P., Biere, A., van der Putten, W.H. and van Dam, N.M., 2010. Intra-specific differences in  
792 root and shoot glucosinolate profiles among white cabbage (*Brassica oleracea* var. capitata)  
793 cultivars. J. Agric. Food Chem. 58, 411-417.

794 Kapoor, R., Sharma, D. and Bhatnagar, A.K., 2008. Arbuscular mycorrhizae in micropropagation  
795 systems and their potential applications. Sci. Hortic-Amsterdam. 116, 227-239.

796 Karasawa, T. and Takebe, M., 2012. Temporal or spatial arrangements of cover crops to promote  
797 arbuscular mycorrhizal colonization and P uptake of upland crops grown after  
798 nonmycorrhizal crops. Plant Soil. 353, 355-366.

799 Karley, A.J., Mitchell, C., Brookes, C., McNicol, J.W., O'Neill, T., Roberts, H., Graham, J. and Johnson,  
800 S.N., 2015. Exploiting physical defence traits for crop protection: leaf trichomes of *Rubus*  
801 *idaeus* have deterrent effects on spider mites but not aphids. Ann. Appl. Biol. 168, 159-172.

802 Kaya, H.K. and Gaugler, R., 1993. Entomopathogenic nematodes. Annu. Rev. Entomol. 38, 181-206.

803 Kim, J.H. and Mullin, C.A., 2003. Antifeedant effects of proteinase inhibitors on feeding behaviors of  
804 adult western corn rootworm (*Diabrotica virgifera virgifera*). J. Chem. Ecol. 29, 795-810.

805 Kostenko, O., van de Voorde, T.F.J., Mulder, P.P.J., Van der Putten, W.H. and Bezemer, T.M., 2012.  
806 Legacy effects of aboveground-belowground interactions. Ecol. Lett. 15, 813-821.

807 Kothari, S.K., Marschner, H. and Romheld, V., 1990. Direct and indirect effects of va mycorrhizal  
808 fungi and rhizosphere microorganisms on acquisition of mineral nutrients by maize (*Zea*  
809 *mays* L.) in a calcareous soil. New Phytol. 116, 637-645.

810 Kulmatiski, A., Beard, K.H., Stevens, J.R. and Cobbold, S.M., 2008. Plant-soil feedbacks: a meta-  
811 analytical review. Ecol. Lett. 11, 980-992.

812 Kumar, N., Krishnappa, K., Reddy, B., Ravichandra, N. and K, K., 2005. Intercropping for the  
813 management of root-knot nematode, *Meloidogyne incognita* in vegetable-based cropping  
814 systems. Ind. J. Nematol. 35, 46-49.

815 Lacey, L.A., Frutos, R., Kaya, H.K. and Vail, P., 2001. Insect pathogens as biological control agents: do  
816 they have a future? *Biol. Control.* 21, 230-248.

817 Larkin, R.P., 2008. Relative effects of biological amendments and crop rotations on soil microbial  
818 communities and soilborne diseases of potato. *Soil Biol. Biochem.* 40, 1341-1351.

819 Lawrence, S.D., Novak, N.G., El Kayal, W., Ju, C.J.T. and Cooke, J.E.K., 2012. Root herbivory: molecular  
820 analysis of the maize transcriptome upon infestation by Southern corn rootworm,  
821 *Diabrotica undecimpunctata* Howardi. *Physiol. Plant.* 144, 303-319.

822 Leroux, O., Leroux, F., Bagniewska-Zadworna, A., Knox, J.P., Claeys, M., Bals, S. and Viane, R.L.L.,  
823 2011. Ultrastructure and composition of cell wall appositions in the roots of *Asplenium*  
824 (Polypodiales). *Micron.* 42, 863-870.

825 Lohse, R., Jakobs-Schoenwandt, D., Vidal, S. and Patel, A.V., 2015. Evaluation of new fermentation  
826 and formulation strategies for a high endophytic establishment of *Beauveria bassiana* in  
827 oilseed rape plants. *Biol. Control.* 88, 26-36.

828 Lu, J., Robert, C.A.M., Lou, Y.G. and Erb, M., 2016. A conserved pattern in plant-mediated  
829 interactions between herbivores. *Ecol. Evol.* 6, 1032-1040.

830 Lugtenberg, B. and Kamilova, F., 2009. Plant-growth-promoting rhizobacteria. *Annu. Rev. Microbiol.*  
831 63, 541-556.

832 Lynch, J.M. and Bragg, E., 1985. Microorganisms and soil aggregate stability. *Adv. Soil Sci.* 2, 133-  
833 171.

834 Ma, J.F. and Yamaji, N., 2006. Silicon uptake and accumulation in higher plants. *Trends Plant Sci.* 11,  
835 392-397.

836 Ma, J.F., Yamaji, N., Mitani, N., Tamai, K., Konishi, S., Fujiwara, T., Katsuhara, M. and Yano, M., 2007.  
837 An efflux transporter of silicon in rice. *Nature.* 448, 209-212.

838 Massey, F.P., Ennos, A.R. and Hartley, S.E., 2006. Silica in grasses as a defence against insect  
839 herbivores: contrasting effects on folivores and a phloem feeder. *J. Anim. Ecol.* 75, 595-603.

840 Massey, F.P. and Hartley, S.E., 2006. Experimental demonstration of the antiherbivore effects of  
841 silica in grasses: impacts on foliage digestibility and vole growth rates. *P. Roy. Soc. B-Biol.*  
842 *Sci.* 273, 2299-2304.

843 Massey, F.P., Ennos, A.R. and Hartley, S.E., 2007. Herbivore specific induction of silica-based plant  
844 defences. *Oecologia.* 152, 677-683.

845 Massey, F.P. and Hartley, S.E., 2009. Physical defences wear you down: progressive and irreversible  
846 impacts of silica on insect herbivores. *J. Anim. Ecol.* 78, 281-291.

847 Meihls, L.N., Higdon, M.L., Ellersieck, M. and Hibbard, B.E., 2011. Selection for resistance to mCry3A-  
848 expressing transgenic corn in western corn rootworm. *J. Econ. Entomol.* 104, 1045-1054.

849 Moose, S.P. and Mumm, R.H., 2008. Molecular plant breeding as the foundation for 21st century  
850 crop improvement. *Plant Physiol.* 147, 969-977.

851 Nauen, R., Leadbeater, A. and Thompson, A., 2008. Proposal on the revision of EU directive 91/414.  
852 *Outlooks Pest Management.* 19, 150-151.

853 Neal, A.L., Ahmad, S., Gordon-Weeks, R. and Ton, J., 2012. Benzoxazinoids in root exudates of maize  
854 attract *Pseudomonas putida* to the rhizosphere. *PloS One.* 7, e35498.

855 Nestler, J., Liu, S.Z., Wen, T.J., Paschold, A., Marcon, C., Tang, H.M., Li, D.L., Li, L., Meeley, R.B., Sakai,  
856 H., Bruce, W., Schnable, P.S. and Hochholdinger, F., 2014. Roothairless5, which functions in  
857 maize (*Zea mays* L.) root hair initiation and elongation encodes a monocot-specific NADPH  
858 oxidase. *Plant J.* 79, 729-740.

859 Newingham, B.A., Callaway, R.M. and BassiriRad, H., 2007. Allocating nitrogen away from a  
860 herbivore: a novel compensatory response to root herbivory. *Oecologia.* 153, 913-920.

861 Oldroyd, G.E.D., 2013. Speak, friend, and enter: signalling systems that promote beneficial symbiotic  
862 associations in plants. *Nat. Rev. Microbiol.* 11, 252-263.

863 Orrelland, P. and Bennett, A.E., 2013. How can we exploit above-belowground interactions to assist  
864 in addressing the challenges of food security? *Front. Plant Sci.* 4.

865 Parker, W.E. and Howard, J.J., 2001. The biology and management of wireworms (*Agriotes* spp.) on  
866 potato with particular reference to the UK. *Agric. Forest. Entomol.* 3, 85–98.

867 Peiffer, J.A., Spor, A., Koren, O., Jin, Z., Tringe, S.G., Dangl, J.L., Buckler, E.S. and Ley, R.E., 2013.  
868 Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proc.*  
869 *Natl. Acad. Sci. U.S.A.* 110, 6548-6553.

870 Philippot, L., Raaijmakers, J.M., Lemanceau, P. and van der Putten, W.H., 2013. Going back to the  
871 roots: the microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.* 11, 789-799.

872 Pineda, A., Zheng, S.-J., van Loon, J.J.A., Pieterse, C.M.J. and Dicke, M., 2010. Helping plants to deal  
873 with insects: the role of beneficial soil-borne microbes. *Trends Plant Sci.* 15, 507-514.

874 Poinar, G.O., 1990. Taxonomy and Biology of Steneirneimataidae and Herorhabditidae. in: Gaugler, R.  
875 and Kaya, H.K. (Eds.), *Entomopathogenic Nematodes in Biological Control*. CRC, Boca Raton,  
876 FL, USA. pp. 23-61.

877 Popay, A. and Baltus, J., 2001. Black beetle damage to perennial ryegrass infected with AR1  
878 endophyte. *Proc. NZ Grassland Assoc.* 63, 267-272.

879 Potter, D.A., Patterson, C.G. and Redmond, C.T., 1992. Influence of turfgrass species and tall fescue  
880 endophyte on feeding ecology of Japanese-beetle and southern masked chafer grubs  
881 (Coleoptera, Scarabaeidae). *J. Econ. Entomol.* 85, 900-909.

882 Poveda, K., Gomez Jimenez, M.I. and Kessler, A., 2010. The enemy as ally: herbivore-induced  
883 increase in crop yield. *Ecol. Appl.* 20, 1787-1793.

884 Powell, K.S., 2008. Grape phylloxera: an overview. in: Johnson, S.N. and Murray, P.J. (Eds.), *Root*  
885 *Feeders - an ecosystem perspective*. CABI, Wallingford, UK. pp. 96–114.

886 Power, S.A., Barnett, K.L., Ochoa-Huesco, R., Facey, S.L., Gibson-Forty, E., V-J, Hartley, S.E., Nielsen,  
887 U.N., Tissue, D.T. and Johnson, S.N., 2016. DRI-Grass: a new experimental platform for  
888 addressing grassland ecosystem responses to future precipitation scenarios in south-east  
889 Australia. *Front. Plant Sci.* Accepted.

890 Prestidge, R.A. and Ball, O.J.P., 1997. A catch 22: The utilization of endophytic fungi for pest  
891 management. in: Gange, A.C. and Brown, V.K. (Eds.), *Multitrophic Interactions in Terrestrial*  
892 *Systems*. Blackwell, Oxford, UK. pp. 171-192.

893 Provan, G.J., Scobbie, L. and Chesson, A., 1997. Characterisation of lignin from CAD and OMT  
894 deficient Bm mutants of maize. *J. Sci. Food Agric.* 73, 133-142.

895 Qawasmeh, A., Raman, A. and Wheatley, W., 2015. Volatiles in perennial ryegrass infected with  
896 strains of endophytic fungus: impact on African black beetle host selection. *J. Appl.*  
897 *Entomol.* 139, 94-104.

898 Quinn, M.A. and Hall, M.H., 1992. Compensatory response of a legume root-nodule system to  
899 nodule herbivory by *Sitona hispidulus*. *Entomol. Exp. Appl.* 64, 167–176.

900 Raaijmakers, J.M., Paulitz, T.C., Steinberg, C., Alabouvette, C. and Moenne-Loccoz, Y., 2009. The  
901 rhizosphere: a playground and battlefield for soilborne pathogens and beneficial  
902 microorganisms. *Plant Soil.* 321, 341-361.

903 Rangel-Castro, J.I., Killham, K., Ostle, N., Nicol, G.W., Anderson, I.C., Scrimgeour, C.M., Ineson, P.,  
904 Meharg, A. and Prosser, J.I., 2005. Stable isotope probing analysis of the influence of liming  
905 on root exudate utilization by soil microorganisms. *Environ. Microbiol.* 7, 828-838.

906 Rasmann, S., Köllner, T.G., Degenhardt, J., Hiltbold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J. and  
907 Turlings, T.C.J., 2005. Recruitment of entomopathogenic nematodes by insect-damaged  
908 maize roots. *Nature.* 434, 732–737.

909 Rasmann, S. and Agrawal, A.A., 2008. In defense of roots: a research agenda for studying plant  
910 resistance to belowground herbivory. *Plant Physiol.* 146, 875–880.

911 Rasmann, S., Ali, J., Helder, J. and van der Putten, W., 2012. Ecology and evolution of soil nematode  
912 chemotaxis. *J. Chem. Ecol.*, 1-14.

913 Reed, K.F.M., Leonforte, A., Cunningham, P.J., Walsh, J.R., Allen, D.I., Johnstone, G.R. and Kearney, G.,  
914 2000. Incidence of ryegrass endophyte (*Neotyphodium lolii*) and diversity of associated



915 alkaloid concentrations among naturalised populations of perennial ryegrass (*Lolium*  
916 *perenne* L.). Aust. J. Agr. Res. 51, 569-578.

917 Reynolds, O.L., Keeping, M.G. and Meyer, J.H., 2009. Silicon-augmented resistance of plants to  
918 herbivorous insects: a review. Ann. Appl. Biol. 155, 171–186.

919 Richardson, A.E., Barea, J.M., McNeill, A.M. and Prigent-Combaret, C., 2009. Acquisition of  
920 phosphorus and nitrogen in the rhizosphere and plant growth promotion by  
921 microorganisms. Plant Soil. 321, 305-339.

922 Robert, C.A.M., Erb, M., Duployer, M., Zwahlen, C., Doyen, G.R. and Turlings, T.C., 2012a. Herbivore-  
923 induced plant volatiles mediate host selection by a root herbivore. New Phytol. 194, 1061–  
924 1069.

925 Robert, C.A.M., Erb, M., Hibbard, B.E., French, B.W., Zwahlen, C. and Turlings, T.C.J., 2012b. A  
926 specialist root herbivore reduces plant resistance and uses an induced plant volatile to  
927 aggregate in a density-dependent manner. Funct. Ecol. 26, 1429–1440.

928 Robert, C.A.M., Veyrat, N., Glauser, G., Marti, G., Doyen, G.R., Villard, N., Gaillard, M., Köllner, T.,  
929 Giron, D., Body, M., Babst, B., Ferrieri, R., Turlings, T.C.J. and Erb, M., 2012c. A specialist root  
930 herbivore exploits defensive metabolites to locate nutritious tissues. Ecol. Lett. 15, 55–64.

931 Robert, C.A.M., Erb, M., Hiltbold, I., Hibbard, B.E., Gaillard, M.D.P., Bilat, J., Degenhardt, J., Cambet-  
932 Petit-Jean, X., Turlings, T.C.J. and Zwahlen, C., 2013. Genetically engineered maize plants  
933 reveal distinct costs and benefits of constitutive volatile emissions in the field. Plant  
934 Biotechnol. J. 11, 628–639.

935 Robert, C.A.M., Ferrieri, R.A., Schirmer, S., Babst, B.A., Schueller, M.J., Machado, R.A.R., Arce, C.C.M.,  
936 Hibbard, B.E., Gershenzon, J., Turlings, T.C.J. and Erb, M., 2014. Induced carbon reallocation  
937 and compensatory growth as root herbivore tolerance mechanisms. Plant Cell Environ. 37,  
938 2613-2622.

939 Robert, C.A.M., Schirmer, S., Barry, J., French, B.W., Hibbard, B.E. and Gershenzon, J., 2015.  
940 Belowground herbivore tolerance involves delayed overcompensatory root regrowth in  
941 maize. *Entomol. Exp. Appl.* 157, 113-120.

942 Rodriguez, A. and Sanders, I.R., 2015. The role of community and population ecology in applying  
943 mycorrhizal fungi for improved food security. *ISME J.* 9, 1053-1061.

944 Rostás, M., Cripps, M.G. and Silcock, P., 2015. Aboveground endophyte affects root volatile  
945 emission and host plant selection of a belowground insect. *Oecologia.* 177, 487-497.

946 Ryalls, J.M.W., Riegler, M., Moore, B.D., Lopaticki, G. and Johnson, S.N., 2013. Effects of elevated  
947 temperature and CO<sub>2</sub> on aboveground-belowground systems: a case study with plants,  
948 their mutualistic bacteria and root/shoot herbivores. *Front. Plant Sci.* 4: 445.

949 Santos, F., Penaflor, M., Pare, P.W., Sanches, P.A., Kamiya, A.C., Tonelli, M., Nardi, C. and Bento,  
950 J.M.S., 2014. A novel interaction between plant-beneficial rhizobacteria and roots:  
951 Colonization induces corn resistance against the root herbivore *Diabrotica speciosa*. *PLoS*  
952 *One.* 9.

953 Schouteden, N., De Waele, D., Panis, B. and Vos, C.M., 2015. Arbuscular mycorrhizal fungi for the  
954 biocontrol of plant-parasitic nematodes: a review of the mechanisms involved. *Front.*  
955 *Microbiol.* 6.

956 Schultz, J.C., Appel, H.M., Ferrieri, A.P. and Arnold, T.M., 2013. Flexible resource allocation during  
957 plant defense responses. *Front. Plant Sci.* 4, 324.

958 Shapiro-Ilan, D.I., Gouge, D.H., Piggott, S.J. and Fife, J.P., 2006. Application technology and  
959 environmental considerations for use of entomopathogenic nematodes in biological  
960 control. *Biol. Control.* 38, 124-133.

961 Smith, S.E. and Read, D.J., 2010. *Mycorrhizal Symbiosis*. Academic Press, London, UK.

962 Soininen, E.M., Brathen, K.A., Jurdado, J.G.H., Reidinger, S. and Hartley, S.E., 2013. More than  
963 herbivory: levels of silica-based defences in grasses vary with plant species, genotype and  
964 location. *Oikos*. 122, 30-41.

965 Stone, J.K., Bacon, C.W. and White, J.F., 2000. An overview of endophytic microbes: Endophytism  
966 defined. in: Bacon, C.W. and White, J.F. (Eds.), *Microbial Endophytes*. Dekker, New York, USA.  
967 pp. 3-29.

968 Stout, M.J., 2013. Reevaluating the conceptual framework for applied research on host-plant  
969 resistance. *Insect Sci.* 20, 263-272.

970 Sugiyama, A. and Yazaki, K., 2012. Root exudates of legume plants and their involvement in  
971 interactions with soil microbes. in: Vivanco, M.J. and Baluška, F. (Eds.), *Secretions and*  
972 *Exudates in Biological Systems*. Springer Berlin Heidelberg, Berlin, Heidelberg. pp. 27-48.

973 Thelen, G.C., Vivanco, J.M., Newingham, B., Good, W., Bais, H.P., Landres, P., Caesar, A. and Callaway,  
974 R.M., 2005. Insect herbivory stimulates allelopathic exudation by an invasive plant and the  
975 suppression of natives. *Ecol. Lett.* 8, 209-217.

976 Tiffin, P., 2000. Mechanisms of tolerance to herbivore damage: what do we know? *Evol. Ecol.* 14,  
977 523-536.

978 Toepfer, S., Burger, R., Ehlers, R.U., Peters, A. and Kuhlmann, U., 2010a. Controlling western corn  
979 rootworm larvae with entomopathogenic nematodes: effect of application techniques on  
980 plant-scale efficacy. *J. Appl. Entomol.* 134, 467-480.

981 Toepfer, S., Hatala-Zseller, I., Ehlers, R.-U., Peters, A. and Kuhlmann, U., 2010b. The effect of  
982 application techniques on field-scale efficacy: can the use of entomopathogenic nematodes  
983 reduce damage by western corn rootworm larvae? *Agr. Forest Entomol.* 12, 389-402.

984 Tollefson, J.J., 2007. Evaluating maize for resistance to *Diabrotica virgifera virgifera* leconte  
985 (Coleoptera : Chrysomelidae). *Maydica*. 52, 311-318.

986 Turlings, T., Hiltbold, I. and Rasmann, S., 2012. The importance of root-produced volatiles as  
987 foraging cues for entomopathogenic nematodes. *Plant Soil*. 358, 47-56.

988 UN, 2015. *World Population Prospects: The 2015 Revision, Volume I: Comprehensive Tables*  
989 (ST/ESA/SER.A/379). Population Division of the Department of Economic and Social Affairs  
990 of the United Nations Secretariat. New York, USA.

991 Vachon, V., Laprade, R. and Schwartz, J.L., 2012. Current models of the mode of action of *Bacillus*  
992 *thuringiensis* insecticidal crystal proteins: a critical review. *J. Invertebr. Pathol.* 111, 1-12.

993 van Dam, N.M. and Raaijmakers, C.E., 2006. Local and systemic induced responses to cabbage root  
994 fly larvae (*Delia radicum*) in *Brassica nigra* and *B. oleracea*. *Chemoecology*. 16, 17-24.

995 van Dam, N.M., 2009. Belowground herbivory and plant defenses. *Annu. Rev. Ecol. S.* 40, 373–391.

996 van Dam, N.M., Tytgat, T.O.G. and Kirkegaard, J.A., 2009. Root and shoot glucosinolates: a  
997 comparison of their diversity, function and interactions in natural and managed ecosystems.  
998 *Phytochem. Rev.* 8, 171–186.

999 van der Putten, W.H., 1997. Plant-soil feedback as a selective force. *Trends Ecol. Evol.* 12, 169-170.

1000 van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P.,  
1001 Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J. and  
1002 Wardle, D.A., 2013. Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.*  
1003 101, 265-276.

1004 van Leur, H., Raaijmakers, C.E. and van Dam, N.M., 2008. Reciprocal interactions between the  
1005 cabbage root fly (*Delia radicum*) and two glucosinolate phenotypes of *Barbarea vulgaris*.  
1006 *Entomol. Exp. Appl.* 128, 312–322.

1007 Vemmer, M. and Patel, A.V., 2013. Review of encapsulation methods suitable for microbial  
1008 biological control agents. *Biol. Control.* 67, 380-389.

1009 Verhagen, B.W.M., Glazebrook, J., Zhu, T., Chang, H.S., van Loon, L.C. and Pieterse, C.M.J., 2004. The  
1010 transcriptome of rhizobacteria-induced systemic resistance in *Arabidopsis*. *Mol. Plant-  
1011 Microbe Interact.* 17, 895-908.

1012 Walker, V., Bertrand, C., Bellvert, F., Moenne-Loccoz, Y., Bally, R. and Comte, G., 2011. Host plant  
1013 secondary metabolite profiling shows a complex, strain-dependent response of maize to  
1014 plant growth-promoting rhizobacteria of the genus *Azospirillum*. *New Phytol.* 189, 494-506.

1015 Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N.  
1016 and Ghani, A., 1999. Plant removals in perennial grassland: vegetation dynamics,  
1017 decomposers, soil biodiversity, and ecosystem properties. *Ecol. Monogr.* 69, 535-568.

1018 Weis, A.E. and Franks, S.J., 2006. Herbivory tolerance and coevolution: an alternative to the arms  
1019 race? *New Phytol.* 170, 423-425.

1020 Wu, W. and Cheng, S., 2014. Root genetic research, an opportunity and challenge to rice  
1021 improvement. *Field Crop Res.* 165, 111-124.

1022 Yu, J.Q., 1999. Allelopathic suppression of *Pseudomonas solanacearum* infection of tomato  
1023 (*Lycopersicon esculentum*) in a tomato-Chinese chive (*Allium tuberosum*) intercropping  
1024 system. *J. Chem. Ecol.* 25, 2409-2417.

1025 Zehnder, G., Kloepper, J., Tuzun, S., Yao, C.B., Wei, G., Chambliss, O. and Shelby, R., 1997a. Insect  
1026 feeding on cucumber mediated by rhizobacteria-induced plant resistance. *Entomol. Exp.  
1027 Appl.* 83, 81-85.

1028 Zehnder, G., Kloepper, J., Yao, C.B. and Wei, G., 1997b. Induction of systemic resistance in cucumber  
1029 against cucumber beetles (Coleoptera: Chrysomelidae) by plant growth-promoting  
1030 rhizobacteria. *J. Econ. Entomol.* 90, 391-396.

1031 Zhang, Y., Ruyter-Spira, C. and Bouwmeester, H.J., 2015. Engineering the plant rhizosphere. *Curr.  
1032 Opin. Biotechnol.* 32, 136-142.

1033 Zvereva, E.L. and Kozlov, M.V., 2012. Sources of variation in plant responses to belowground insect  
1034 herbivory: a meta-analysis. *Oecologia*. 169, 441–452.

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1052 **Figure Legends**

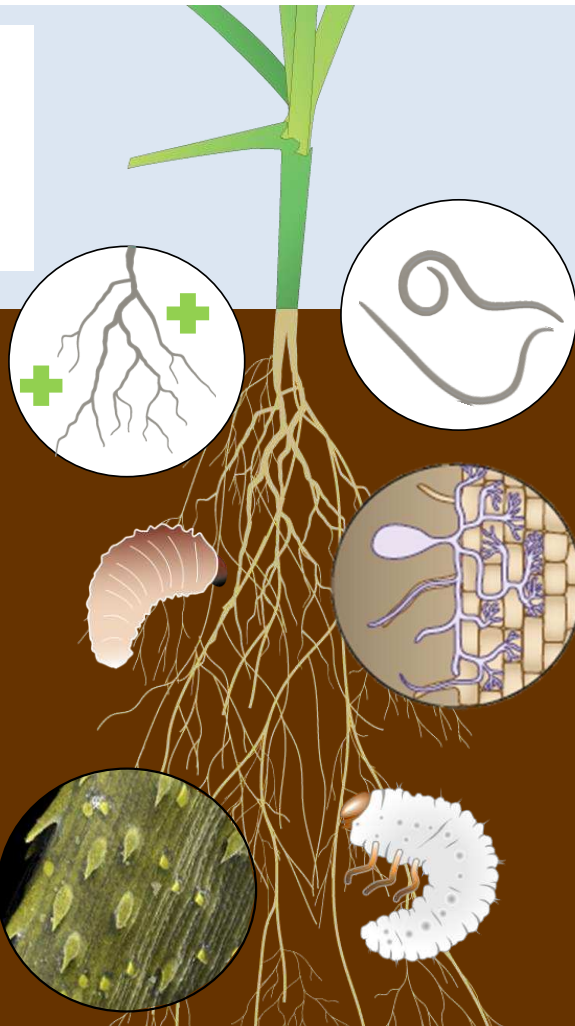
1053 **Fig. 1.** Research opportunities and priorities that would help determine the feasibility and  
1054 optimisation of root herbivore control using plant tolerance, direct defences, plant mutualism and  
1055 plant-soil feedbacks. Exploring these mechanisms under different soil conditions is particularly  
1056 important to determine under what circumstances they may be viable and useful for pest control.

1057

1058 **Fig. 2.** Potential management outcomes for controlling root herbivores using plant tolerance,  
1059 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

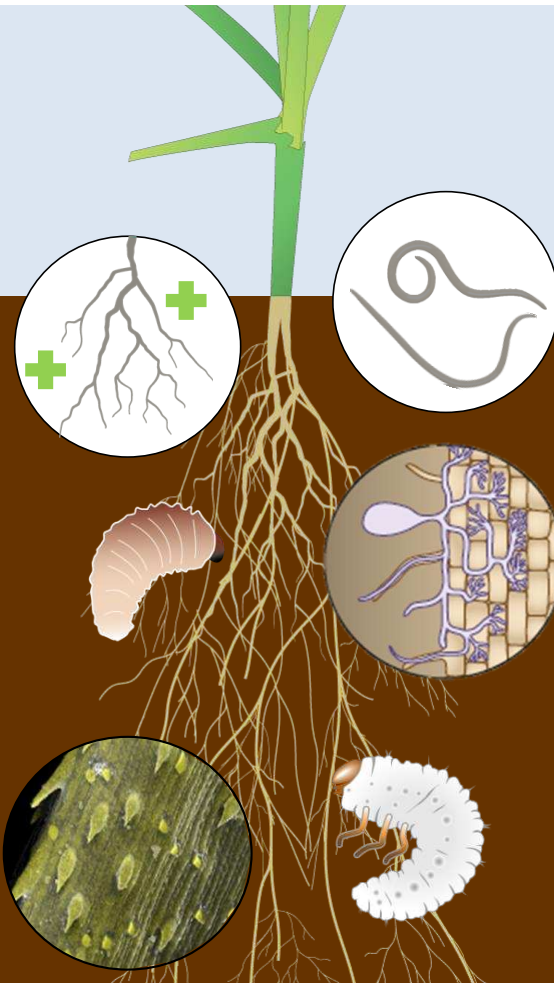
- Use of cultivars with known tolerance to root herbivores under variable soil conditions

### 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

### Management to promote favourable soil conditions for intervention

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



### Exploiting mutualisms

- Micro-propagated and bioprimered 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