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### ► To cite this version:

Jay Ram Lamichhane, Martin Barbetti, Martin Chilvers, Abhay Pandey, Christian Steinberg. Exploiting root exudates to manage soil-borne disease complexes in a changing climate. Trends in Microbiology, inPress, 32 (1), pp.27-37. 10.1016/j.tim.2023.07.011 . hal-04276892

**HAL Id: hal-04276892**

**<https://hal.inrae.fr/hal-04276892>**

Submitted on 9 Nov 2023

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1 **Exploiting root exudates to manage soil-borne disease complexes in a changing climate**

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13

14 **Running head:** Root exudates and soil-borne disease complexes

15

16 **Abstract**

17 Ongoing climate change will both profoundly impact land-use (e.g. changes in crop species or cultivar and  
18 cropping practices) and abiotic factors (e.g. moisture and temperature), which will in turn alter plant-  
19 microorganism interactions in soils including soil-borne pathogens (i.e. plant pathogenic bacteria, fungi,  
20 oomycetes, viruses and nematodes). These pathogens often cause soil-borne disease complexes, which, due  
21 to their complexity, frequently remain undiagnosed and unmanaged leading to chronic yield and quality  
22 losses. Root exudates are a complex group of organic substances released in the rhizosphere with potential  
23 to recruit, repel, stimulate, inhibit, or kill other organisms including the detrimental ones. An improved  
24 understanding of how root exudates affect inter-species and/or inter-kingdom interactions in the  
25 rhizosphere under ongoing climate change is prerequisite to effectively manage plant-associated microbes  
26 including those causing diseases.

27 **Keywords:** Land-use change, soil-borne pathogens, soil-microbiome, disease suppressiveness

28

29 **Root exudates: complex organic substances released in the rhizosphere**

30 Root exudates are a complex group of organic substances released in the rhizosphere and are mostly soluble  
31 and liquid [1,2]. Root exudates are rich in sugars, amino acids, organic acids, vitamins, nucleosides,  
32 phytosiderophores, phenolic compounds, fatty acids, among others, including some still unidentified  
33 substances [3–6]. Root exudation occurs passively (i.e. by diffusion due to osmotic differences between the  
34 soil solution and root cells) or actively (i.e. by secretion). From 5 to 25% of the photosynthetically fixed  
35 carbon can be released by soil-grown plants as root exudates into the rhizosphere [7–9]. The production of  
36 root exudates is specifically linked to the plant species, their genotypes, the plant growth stages, and the  
37 nearby biotic and abiotic environment [10,11]. Overall, root exudates play an important role in plant growth  
38 by shaping plant-microorganism interactions in the rhizosphere (**Box 1**).

**Box 1. Root exudates as plant growth promoters in the rhizosphere**

The rhizosphere is a 'hot spot' of microbial interactions as rhizodeposits released in solid, liquid or gaseous forms by plant roots are a main food source for microorganisms that constitute a driving force of their population density and activities [3,12–16]. Plants have developed several mechanisms to secrete metabolites into the rhizosphere, including different types of passive and active transports [17]. Each pathway is responsible for the release of different molecules depending on their nature: diffusion releases low molecular weights, ionic channels release carbohydrates and vesicle transport excretes metabolites with high molecular weight stored in vesicles [5]. Active transport mechanisms rely on transporter proteins found in the membranes of root cells that secrete different types of metabolites [17]. Plants can also modify soil pH through changes in root exudate composition, which may increase nutrient availability but also affect pathogenic and beneficial bacteria, fungi, oomycetes, and nematodes [13,18,19].

One of the notable and particularly beneficial effects of root exudates for the plant is their ability to attract bacteria and fungi that stimulate production of compounds promoting plant growth [20–23]. Examples are *Azospirillum lipoferum* and *A. brasilense* releasing phytohormones including auxins favorable to the growth of wheat and maize [24], *Pseudomonas fluorescens* and *P. aeruginosa* promoting the growth of rice by producing indole acetic acid [25], *P. monteilii* releasing gibberellin and salicylic acid, near tomato roots in presence of organic acids and sugars [26]. Root exudation in maize and potato modifies transcriptomic and gene expression responses thereby improving the recruitment of Gram-positive bacteria *Bacillus amyloliquefaciens*, *B. atrophaeus* or *B. mycoides* involved in the plant-growth promotion [27–29]. Likewise, arbuscular mycorrhizal fungi alter root exudation in *Lotus japonicus* to cultivate a beneficial microbiome for plant growth [30].

39

40 **Root exudates: a hidden arsenal for plant defense?**

41 Root exudates can directly recruit, repel, stimulate, inhibit, or kill other rhizosphere organisms including  
42 detrimental ones (**Table 1**). Phytopathogenic fungi and oomycetes are attracted by trophic sources  
43 constituted by root exudates or by signal molecules indicating the presence of a host plant of interest. To  
44 counteract infection and defend themselves against phytopathogens, plants, through their root exudates,  
45 release an arsenal of metabolites into the rhizosphere [31]. The nature and relative abundance of  
46 components in root exudates have a profound effect on shaping the soil microbial communities, including

47 pathogen populations. Some root exudates exhibit antibacterial, antifungal, or nematicidal properties that  
 48 directly or indirectly help the plant in controlling detrimental microorganisms (Table 1).

49 **Table 1.** A non-exhaustive list of references published in the last decade (2014-2023) showing potential of  
 50 root exudates in attracting biocontrol agents and repelling soil-borne pathogens leading to improved  
 51 disease management

Root exudating plant species	Compounds identified in root exudation	Attracted biocontrol agents and/or affected soil-borne pathogens	Disease in question	References
Banana	Phenolic acids	<i>Bacillus amyloliquefaciens</i> / <i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	Fusarium wilt Phytophthora root rot	[32]
Common bean	Isoflavone phytoalexins	<i>Phytophthora sojae</i>		[33]
Legumes	Phenolic acids and flavonoids	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	Fusarium wilt	[34]
Maize	Lipopeptides	<i>Bacillus amyloliquefaciens</i> / <i>Fusarium graminearum</i>	Maize stalk rot	[35]
Panax notoginseng	Cinnamic acid, 2-dodecenoic acid, and 12-oxo-phytodienoic acid	<i>Burkholderia</i> sp. B36	Root rot	[36]
Potato onion	Not determined	<i>Plasmidiophora brassicae</i>	Chinese cabbage clubroot	[37]
Rapeseed	Antimicrobial compounds	<i>Phytophthora parasitica</i> var. <i>nicotianae</i>	Tobacco black shank disease	[38]
Tomato	Extracellular vesicles	<i>Fusarium oxysporum</i> , <i>Botrytis cinerea</i> and <i>Alternaria alternata</i>	Soil-borne	[39]
Tomato	Carbohydrate exudate	<i>Trichoderma atroviride</i> / <i>Phytophthora cinnamomi</i>	Phytophthora root rot	[40]
Tomato	Organic compounds	<i>Bacillus amyloliquefaciens</i> / <i>Ralstonia solanacearum</i>	Bacteria wilt	[41]
Tomato	Volatile organic compounds	<i>Trichoderma harzianum</i> / <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Fusarium wilt	[42]
Maize and soybean intercropping	Phenolic acids	<i>Phytophthora sojae</i>	Phytophthora root rot	[43]
Potato	Organic compounds	<i>Spongospora subterranea</i>	Powdery scab	[44]
Wheat/faba bean intercropping	Phenolic acids, organic acids, amino acids and sugars	<i>Fusarium oxysporum</i> f. sp. <i>fabae</i>	Faba bean fusarium wilt	[45]
Wheat/watermelon intercropping	Not determined	<i>Fusarium oxysporum</i> f. sp. <i>niveum</i>	Fusarium wilt of watermelon	[46]

52

53 There is a long research history about how plant exudates stimulate pathogen development and microbial  
 54 interactions in the rhizosphere (see seminal review by Lockwood [47] and references therein). For instance,  
 55 egg hatching in cyst nematode *Globodera pallida* Stone (Tylenchida: Heteroderidae) is stimulated by host  
 56 plant root exudates rather than by soil microbiota composition [48]. The soil-borne fungal pathogen  
 57 *Fusarium oxysporum* reorients its hyphal growth towards a variety of chemical signals in the presence of root  
 58 exudates produced by the host plant tomato [49]. In the *Arabidopsis thaliana*-*Pseudomonas simiae* WCS417  
 59 model system, the root-specific transcription factor MYB72-dependent coumarin exudation shapes root

60 microbiome assembly to promote plant health [50]. How a beneficial or pathogenic soil-borne organism  
61 draws benefits from root exudates seems also dependent on the soil microbial community composition. For  
62 example, competitive use of root exudates by the soil-borne biocontrol agent *B. amyloliquifaciens* enables it  
63 to control the tomato bacterial wilt pathogen *Ralstonia solanacearum* [41]. However, the types and amounts  
64 of exudates secreted by plant roots are determined both by plant genotypes and environmental factors [51]  
65 and as such will be influenced by seasonal and climate changes. Hence, it is perhaps not surprising that  
66 findings on beneficial or detrimental effects of root exudates on plant health are often inconsistent and  
67 context dependent, warranting further investigations.

68 Infection by phytopathogens triggers the plant's defense reactions. In pea, pisatin, an isoflavonoid that  
69 confers resistance to the plant, is secreted by the plant following attacks by the oomycete *Aphanomyces*  
70 *euteiches*, the causal agent of pea root rot [52]. However, foliar infections also lead to a change in the nature  
71 of root exudates resulting in an increase in plant resistance to both below- and above-ground pathogens  
72 [53]. The strategies and biochemistry implemented by plants to activate the defense mechanisms against  
73 their pathogens via root exudates have been reviewed [17].

#### 74 **Soil-borne pathogens and soil-borne disease complexes**

75 Soil-borne pathogens are characterized by three key traits: i) they infect plants through below-ground  
76 organs; ii) they act as saprotrophs, hemibiotrophs or parasites on roots, stems and/or leaves of herbaceous  
77 or woody plants; and iii) they cause monocyclic, in some cases polyetic and, more rarely, polycyclic diseases.  
78 Soil-borne pathogens are responsible for chronic crop yield and quality losses in agricultural settings, but  
79 also severe decline of natural ecosystems.

80 Effective management of soil-borne diseases is often difficult as the rhizosphere is not directly accessible to  
81 crop protection interventions. Indeed, the soil buffering capacity may protect soil-borne pathogens from  
82 adversities such as heat, drought or cold stresses. In addition, soil-borne pathogens inside infected host  
83 tissue are inaccessible to mycoparasites affecting biocontrol activities. Therefore, favoring root exudation is  
84 an important strategy to recruit microorganisms having potential to containing or suppressing the disease  
85 caused by soil-borne pathogens. This is why the search for new ideotypes and genotypes adapted to the  
86 abiotic stresses triggered by climate change must also take into account the ability of plants to produce  
87 exudates to maintain the interaction with the rhizobiome. This is especially true for managing soil-borne  
88 disease complexes that are caused by a complex interaction among soil-borne pathogens (**Figure 1**). The  
89 order/succession of host infection by each pathogen in a disease complex and its trophic level might affect  
90 the nature of interaction that these pathogens eventually develop during disease occurrence. Overall,  
91 disease complexes are caused by multiple infections, either simultaneous or sequential, leading to  
92 competitive interactions among pathogens involved in an infection process that shapes pathogen  
93 coexistence [54].

#### 94 **Dealing with knowledge gaps: root exudates and soil-borne disease complexes under changing 95 climate**

96 Climate change can have direct and indirect effects on soil-borne disease epidemics, as climate change  
97 affects host susceptibility, the survival of pathogen inoculum, the rate of disease progress and epidemic  
98 duration [55]. The proportion of soil-borne pathogens increases with warming [56] and understanding  
99 factors limiting their propagation is critical in forecasting their impact on human well-being and ecosystem  
100 sustainability under projected climate and land-use change scenarios.

101 While precise consequences of climate change for soil-borne pathogens are difficult to predict, climate  
102 change influence on soil-borne pathogens will be predominantly plant stress mediated, where released root  
103 exudates play a key role in recruitment of microorganisms enhancing or suppressing a disease. For instance,  
104 in the US midwest, climate change results in warmer springs with heavier precipitation events which will  
105 increase plant stress and soil-borne disease epidemics [57–59]. In southern Australia, increased severity of  
106 rhizoctonia diseases [60,61], but decreased severity of some soil-borne oomycete disease epidemics [62] on  
107 field crops, are associated with decreasing growing season rainfall from climate change. In northern France,  
108 the evolution of the pathogen complex responsible for the pea root rot across seasons reveals a  
109 replacement of oomycetes having an optimum of growth and activity in cold and wet periods by  
110 ascomycetes, in particular *Fusarium* sp., having an optimum growth and activity under warmer and dryer  
111 periods [63]. This minor time scale scenario likely indicates the possible evolution of the pathogen  
112 complexes that crops will face under hot and dry weather triggered by climate change. In the last 15 years, a  
113 profound change in drought and rain periods during crop cycles has been reported across traditional  
114 agricultural areas, worldwide [64]. Some of the agricultural areas previously characterized by hot and dry  
115 summers under Mediterranean basin are now experiencing longer rainfall periods during summer. Under  
116 these circumstances, it is important to understand how ongoing climate change will affect the root  
117 exudation process and how all this will influence the rhizobiome. Overall, while several studies focused to  
118 understand the effect of root exudates on beneficial or pathogenic soil-borne organisms, all these studies  
119 have five key limitations.

- 120 • Most studies focused on specific pathosystems for a specific cropping season, entailing only one  
121 host plant and a beneficial or harmful organism. This is not consistent with reality where inter-  
122 species and/or inter-kingdom interactions occurring among a myriad of organisms shape semi-  
123 quantitative changes in composition of root exudates. Indeed, there is increasing evidence that soil-  
124 borne diseases are primarily caused not by individual species but by pathogenic complexes [65–68]  
125 where each pathogen within a soilborne complex is differentially affected by environment, with the  
126 complexity of soilborne pathogens x environment interactions highlighted by the multifaceted and  
127 contrasting interactions such as those associated with temperature and moisture [62]. The  
128 unpredictable and ever-changing proportions of different pathogens within complexes across  
129 seasons and locations further increases this complexity [63]. In addition, synergistic and/or  
130 antagonistic interactions occur not only between soil-borne pathogens but also between soil-borne  
131 pathogens and other beneficial and/or commensal organisms constituting the soil microbiome. The  
132 latter plays a positive role in the soil food web as well as in soil and plant health since the bulk of  
133 the plant microbiome is concentrated belowground at the plant root-soil interface.
- 134 • Most studies generally focused on a single cropping or natural ecosystem with a unique, yet often  
135 undefined, set of environmental (e.g., soil, host) characteristics, missing the opportunity to assess  
136 the advantages/disadvantages of different host(s), soil type, soil amendments, tillage and cropping  
137 systems to define the most beneficial future scenarios. While such a systemic approach is difficult to  
138 implement locally, an increasing number of meta-analyses make it possible to combine field  
139 observations and experimental results conducted under contrasted conditions that helps determine  
140 the most favorable biotic and abiotic parameters to plant health [69–71].
- 141 • It remains unknown whether beneficial and soil-borne pathogens use the same or different root  
142 exudate molecules to proliferate in the rhizosphere of diverse plant species because a taxon,

143 pathogenic for one plant can be beneficial for another by using the same root exudate. Conversely,  
144 the same fungal species such as *Fusarium oxysporum* for example, can harbor pathogenic and non-  
145 pathogenic populations having *quasi*-identical ecological requirements in the same rhizosphere.  
146 Actually, the relative success of soil-borne pathogens and mutualists in their respective association  
147 with plant roots is also affected by the degree of activity of microbes that antagonize or support  
148 them. Such microbe-microbe interactions, mediated via root exudates and microbial-specific  
149 production and perception of molecules, provide important ecosystem services to the plant [72]. In  
150 the case of competition between pathogenic and non-pathogenic populations of *F. oxysporum*, the  
151 outcome of competition in favor of non-pathogenic populations was strongly dependent on the  
152 production of siderophores by a population of fluorescent *Pseudomonas*. The non-pathogenic strain  
153 of *F. oxysporum* is not very susceptible to iron depletion whereas the pathogenic population is  
154 susceptible. The siderophores produced by *Pseudomonas* sp. create iron deficiency creating an  
155 unfavorable environment for the pathogen. The plant therefore, has an interest in promoting the  
156 bacterial population which not only provides it with iron but reduces the pathogenic pressure of *F.*  
157 *oxysporum* [73]. Therefore, it is essential that plants maintain their root exudation potential despite  
158 climate change, which is vital to also maintain high microbial diversity and activity in their  
159 rhizosphere. All this, in turn, will lead to improved root architecture, enhanced nutrient uptake,  
160 promotion of plant growth, activation of induced systemic resistance, and suppression of soil-borne  
161 pathogens and microbes that stimulate induced systemic susceptibility as shown in maize grown  
162 under warm climatic conditions [74]. Another example is the case of fungal pathogens with  
163 hypovirulence-associated mycoviruses that grow endophytically in roots and have shown potential  
164 as microbial biocontrol agents from the mycelial film they form around the root surface and with  
165 masses of hyphae in root cells and/or root intercellular spaces [75]. Similarly, there remains  
166 potential to further explore and exploit non- or weakly-pathogenic strains of important soilborne  
167 pathogens like *Rhizoctonia*. These strains are well adapted to the same ecosystem processes as are  
168 the more pathogenic *Rhizoctonia* strains and colonize roots even in the presence of more  
169 pathogenic strains, increasing seedling emergence and plant size [76,77]. For both these examples,  
170 the observed benefits are likely associated with changes in root exudates, yet this remains  
171 unconfirmed and further investigation is required to explore and exploit their potential for future  
172 management of soilborne diseases and their complexes.

173 • While there is an established link between drought resilience (i.e., climate change) with  
174 endophytes, opportunities to understand and exploit the full array of benefits from endophytes  
175 seem overlooked. For example, the ability of endophytes to make plants such as ryegrass much  
176 more drought-resilient has been demonstrated [78]. Yet, such plants with fungal endophytes will  
177 almost certainly also have greater soilborne-disease-resilience associated with significant changes  
178 in root exudates. For example, the endophyte *Epichloë festucae* var. *lolii* in *Lolium perenne* results  
179 in >80 metabolites being differentially present or genes being expressed in endophyte presence vs  
180 absence plants. Similarly, recent comparative molecular analyses of the diversity of endophytic  
181 fungal communities of a range of plant species showing presence or absence of disease symptoms  
182 revealed that asymptomatic plants harbored a taxa core absent from the symptomatic ones [79].  
183 This raises the question about the potential role of these taxa in plant protection (e.g. antagonism  
184 toward pathogens, stimulation of plant defense reactions) and how we can ensure and boost their  
185 presence under climate change situations. Further research is needed to connect such changes in

186 root exudate chemical composition with ecosystem processes, including recruitment of  
187 endophyte taxa and subsequent effects on soil-borne disease complexes.

188 • Although drought has been reported to affect the quantity and quality of root exudation [80],  
189 drought is only one of the stresses due to climate change and it remains unknown if and how  
190 different stresses generated by ongoing climate change will affect the quantity and composition of  
191 root exudates. This may occur either by modifying soil physical (e.g. soil moisture, temperature) or  
192 chemical (e.g. soil organic matter, pH) parameters as a consequence of changes in soil organic  
193 carbon dynamics, especially in the mid-to long-term. For instance, root exudates alter the  
194 expression of diverse metabolic, transport, regulatory, and stress response genes in rhizosphere  
195 *Pseudomonas* spp. [81]. Despite these complexities and challenges, there are significant, yet  
196 unexploited, opportunities to better understand and then to manipulate the ecosystem  
197 environment towards novel and improved management solutions of soil-borne pathogen  
198 complexes under changing climate conditions [82]. Root exudates form a two-way direct  
199 communication pathway between plants and rhizosphere microbes that likely influences plant  
200 growth and development under fluctuating environments, especially under climate change.  
201 Therefore, a better understanding of the mechanisms of root exudation and microbial metabolite  
202 reception/recognition contributing to future sustainable crop protection is critical.

### 203 **Crop management practices as a key lever to modulate root exudation under climate change?**

204 Climate change is expected to impact land use and cover at various temporal and spatial scales directly and  
205 indirectly by altering disturbance patterns, species distributions, and suitability of land for specific uses [83].  
206 To cope with climate change, multicropping practices that ensure better soil vegetation cover (e.g. relay-,  
207 cover- and inter-cropping) need to be designed, tested and adopted. The current agricultural model is  
208 largely dominated by monocropping while multicropping based on spatio-temporal diversity of crops may  
209 have potential to improve resource use efficiencies and resource complementarities that will help manage  
210 biotic and abiotic stressors in the rhizosphere (**Figure 2a**). For instance, pea is a legume that can fix  
211 atmospheric nitrogen via root symbiotic bacteria and bring some of it to the soil through exudates in the  
212 form of amino acids (e.g. proline, homoserine and alanine) that increase plant tolerance to drought. At the  
213 same time, pea is also able to perform arbuscular mycorrhizal symbiosis that further confers tolerance to  
214 biotic and abiotic stresses. On the other hand, maize cannot fix atmospheric nitrogen in the soil but is  
215 strongly mycorrhizal dependent. In contrast, oilseed rape has neither nitrogen fixing nor mycorrhizal  
216 capacity but it is a glucosinolate-containing plant species characterized by soil-borne pathogen suppressing  
217 ability. Growing these crops in association via multicropping (e.g. cover-, inter- or relay-cropping) may thus  
218 modulate the type and quantity of root exudates in the rhizosphere with the consequent positive impact on  
219 beneficial soil organisms that help mitigate climate change. However, there is paucity of information in this  
220 regard, especially as to whether multicropping of diverse plant species providing different functions has  
221 positive or negative effects on the root exudation process, especially under climate change (e.g. increased  
222 drought events, elevated temperature etc.) that needs further investigation. For example, does planting a  
223 brassica crop (e.g. canola), which is one of the few non-mycorrhizal plant families, with a mycorrhizal crop  
224 (e.g. pea or maize), reduces arbuscular mycorrhizal fungi inoculum?

225 Root exudation is affected by physical, chemical and biological factors including soil water stress,  
226 temperature, light intensity, age, species and genotypes of plant, mineral nutrition, soil microbiome, degree  
227 of anaerobiosis, and application of biologicals and chemicals (**Figure 2a**). Most of these factors can be



228 modulated by management practices that can lead to semi-quantitative changes in composition of root  
229 exudates and consequent inter-species and/or inter-kingdom interactions in the rhizosphere (**Figure 2b**).  
230 We hypothesize that there is a negative relationship between tillage intensity and root exudation as tillage  
231 promotes soil organic carbon oxidation and decomposition and also exposes beneficial microbes to the  
232 external environment thereby creating unfavorable conditions for plant growth and root exudation in a more  
233 later phase; a positive relationship between crop diversification and root exudation as well as soil carbon  
234 storage and root exudation; and a positive or a negative relationship between crop species and root  
235 exudation, depending on plant species and genotypes that needs to be tested. The interactions among soil,  
236 climate and management practices can lead to semi-quantitative changes in composition of root exudates  
237 affecting inter-species and/or inter-kingdom interactions in the rhizosphere. For example, intercropping  
238 management of watermelon/aerobic rice alleviates the *Fusarium oxysporum* f. sp. *niveum* responsible for  
239 watermelon wilt disease, thanks to unidentified component(s) in rice root exudates that suppress pathogen  
240 sporulation and spore germination [84]. Likewise, pea and faba bean root exudates increase and decrease  
241 the *Aphanomyces euteiches* pea root rot severity, respectively [85], thereby suggesting the importance of  
242 multicropping in soil-borne disease management. However, the mechanisms and extent to which plant  
243 genotypes affect the soil microbiome and the consequent soil suppressiveness to diseases remains largely  
244 unknown to date.

245 Management practices that alter secretion of root exudates toward favouring beneficial organisms therefore  
246 play a key role in promoting plant health and ecosystem functioning. However, the potentially important  
247 ecological and environmental impact caused by minor changes in the composition of root exudation should  
248 be studied to avoid possible negative repercussions on non-target soil organisms that are potentially  
249 beneficial to the plant. Key changes due to climate change need a careful consideration to understand how  
250 these events affect root exudation. For instance, Bobille *et al.* [86] showed how amino acids released by pea  
251 roots are altered by a short period of induced drought. Molecules released by root exudates leave an imprint  
252 on the soil that is critical in plant-soil microorganism interactions. Such interactions can help plants to  
253 maintain health by better adapting to their environment.

## 254 **Concluding remarks and future perspectives**

255 Root exudates are key mediators in the interaction between plants and soil microbiota and, as such, they  
256 affect the recruitment of beneficial microorganisms and the establishment of defense reactions against plant  
257 pathogens. Therefore, it is important to exploit the potential of root exudates to more effectively: i) attract  
258 microorganisms directly beneficial to plants *per se* and/or those indirectly benefiting plants through  
259 antagonism to pathogens, ii) increase resistance to abiotic stresses, iii) promote plant growth and health  
260 while reducing the use of fertilizers and synthetic plant protection products within the frame of  
261 agroecological crop protection [87].

262 Recent technological advancement allows collection, identification and characterization of a diverse array of  
263 metabolites present in plant root exudates [88,89]. However, our knowledge is still limited on the: i) role  
264 these root exudate molecules play towards soil organisms (e.g. soil-borne pathogens, beneficial,  
265 commensals); ii) changes in semi-quantitative composition of root exudates in relation to environmental  
266 conditions, especially under climate change; and iii) potential of crop management practices to steer root  
267 exudation processes, especially by promoting increased species diversity and vegetation cover duration.  
268 Medium- to long-term studies focusing on root exudate - crop management interactions are non-existent  
269 but are urgently needed to quantify the role of root exudation on more ecologically-relevant timescales.

270 Recent advancement in molecular and sequencing tools help improve understanding of soil microbiome  
271 taxonomic and functional diversity although there is still need to define more precisely the role and relative  
272 importance of each of the active or latent gene clusters in the rhizosphere. A paradigm shift in research to  
273 understand these complexities is needed. However, this is only possible by shifting focus from mono-  
274 disciplinary to multi- and inter-disciplinary research via greater collaboration between agronomists, soil  
275 microbial ecologists, phytopathologists, soil scientists, and soil chemical ecologists. This will foster  
276 development of new methodologies while strengthening the existing ones in order to elucidate how root  
277 exudates affect inter-species and/or inter-kingdom interactions in the rhizosphere under ongoing climate  
278 change. Finally, this will lead to sustainable and durable management of soil-borne disease complexes  
279 while ensuring ecological functioning across natural or agricultural settings.

## 280 **Acknowledgements**

281 We thank the four anonymous reviewers who provided detailed and constructive comments on an earlier  
282 version of this manuscript that markedly helped increase the quality of this paper. JRL is grateful to Dr.  
283 Timothy C. Paulitz, USDA-ARS, for his thoughtful insights and feedback on an earlier version of this paper. We  
284 apologize for the omission of any relevant articles that have not been cited due to space limitation. JRL is  
285 partly supported by the FAST project (Faisabilité et Evaluation de Systèmes de Cultures Economes en  
286 pesticides en l’Absence répétée de Semences Traitées) funded by the French Agency for Biodiversity, by  
287 credits from the royalty for diffuse pollution, attributed to the funding of the Ecophyto plan.

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482

## Glossary

483

- Allelopathy: biological phenomenon whereby an organism produces one or more biochemical substances that influence the germination, growth, survival and reproduction of other organisms.

484

485

- Chemoattractants: chemical substances causing stimulation, polarization and locomotion of eucariotic or procariotic cells.

486

487

- Commensals: microorganisms that colonize an organism without any positive or negative effects.

488

- Hemibiotrophs: pathogens that keep their host alive while establishing itself within the host tissue, taking up the nutrients with brief biotrophic-like phase prior to switching to a necrotrophic life-style, where it kills the host cells, deriving its nutrients from the dead tissues.

489

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491

- Monocyclic disease: disease having only one life cycle in one year.

492

- Mycoparasites: fungi that are parasitic on other fungal species and grows on their mycelium or fruiting body.

493

494

- Parasites: organisms living on (ectoparasite) or in (endoparasite) other organisms and feeding on the hosts without destroying them as long as their life cycle is not complete.

495

496

- Phytohormones: organic chemicals produced by plants that regulate their growth, development, reproductive processes, longevity, and even death.

497

498

- Phytosiderophores: iron-solubilizing compounds released by plant roots.

499

- Phytotoxins: toxic chemical compounds produced by plants, most often having defense function.

500

- Polyetic disease: disease that continues developing from one growing season to the next.

501

- Polycyclic disease: disease that completes two or more life cycles in one year.

502

- Rhizodeposition: the excretion of inorganic and organic elemental solution from living roots.

503

- Resting spore: spore that remains dormant for a period before germination often to survive adverse environmental conditions.

504

505

- Rhizosphere: the region of the soil directly formed and influenced by the roots and associated microorganisms that are part of the plant microbiota.

506

507

- Root exudates: a suite of substances in the rhizosphere that are secreted by the roots of living plants and microbially modified products of these substances.

508

509

- Saprotroph: organism that feeds and grows on dead organic matter.

510

- Soil-borne pathogens: microorganisms surviving and operating in the soil at least during part of their lives infecting healthy plants belowground.

511

512

- Soil-borne disease complexes: diseases resulting from the contributions of multiple soil-borne pathogens that attack plants either simultaneously or at different time points.

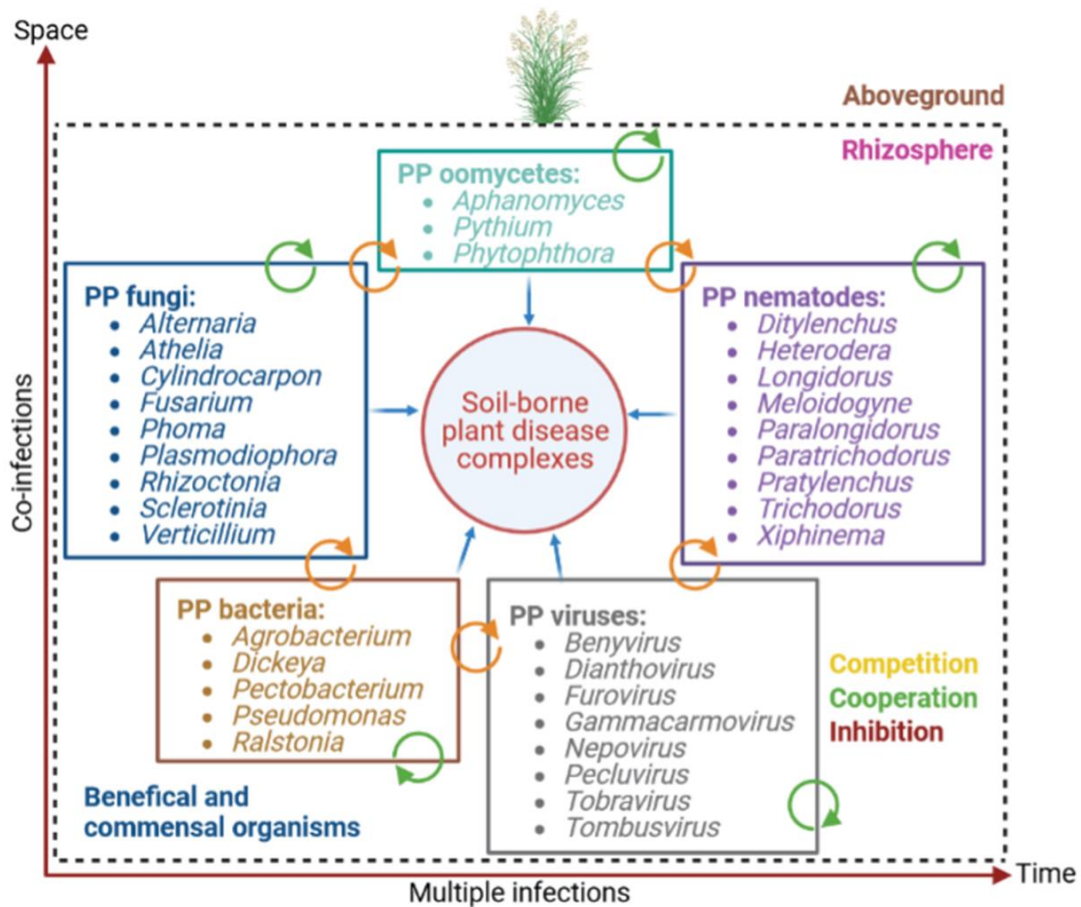
513



- 514 • Soil food web: a complex living system represented by the community of organisms living all or part  
515 of their lives in the soil in interaction among them.
- 516 • Soil microbiota/microbiome: Dynamic community of microorganisms (microbiota) or their DNA  
517 (microbiome) within the soil. Although often used interchangeably, microbiota includes living  
518 microorganisms while microbiome refers to the living and dead microorganisms represented by  
519 their DNA as well as the functional potential of the microbiota.
- 520 • Strigolactones: a group of chemical compounds produced by plant roots.
- 521 • Trophic sources: feeding and nutrition sources.
- 522 • Vesicles: membrane-bound organelles that transport material within or outside the cell.
- 523

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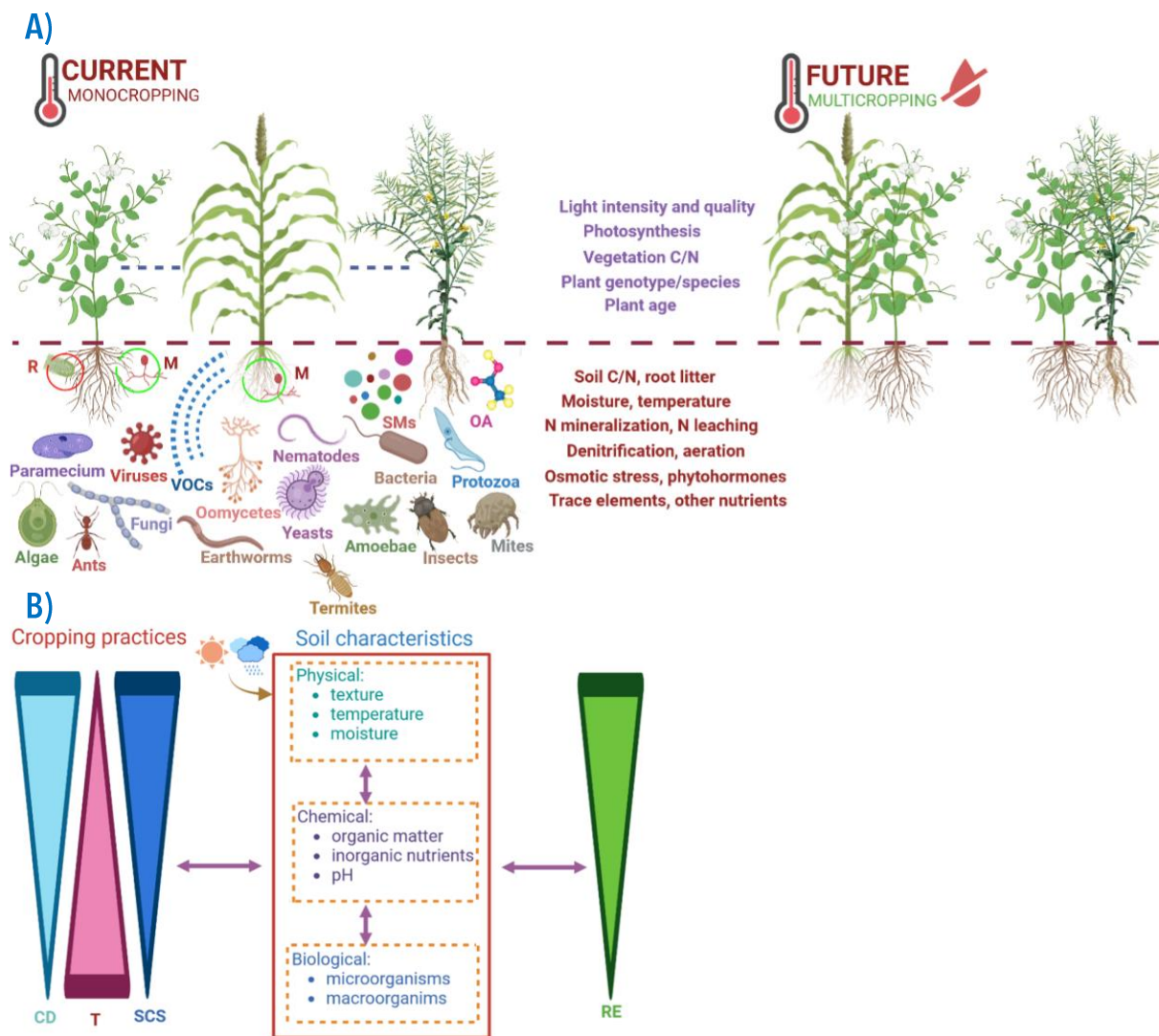


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528 **Figure 1.** Key soil-borne plant pathogenic genera leading to soil-borne disease complexes. A disease  
 529 complex can be caused by inter-species (green circle) and/or inter-kingdom interactions (orange circles)  
 530 among plant pathogenic (PP) organisms in the rhizosphere. The order/succession of host infection by each  
 531 pathogen in a disease complex can be simultaneous or sequential. The severity of a given soil-borne disease  
 532 on a given host due to multi-infection depends on three kinds of interactions (competition, cooperation or  
 533 inhibition) not only among pathogens but also with other soil-dwelling organisms, host and environmental  
 534 conditions (see Figure 3). Soil-borne disease complexes due to soil-borne viruses are vector-mediated and  
 535 most soil-dwelling pathogens including nematodes, fungi and bacteria act as their vector.

536



538

539 **Figure 2.** Schematic representation of key above- and below-ground factors affecting the root exudation  
 540 process (a) and a hypothetical overview of key cropping practices that may affect the root exudation process  
 541 in interaction with soil and climate (b). Unlike some available knowledge about the effect of current  
 542 monocropping systems on the type and quantity of root exudates, there are severe knowledge gaps as to  
 543 whether multicropping systems under future climate change will alter inter-species and/or inter-kingdom  
 544 interactions in the rhizosphere and how all this modulate the quantity and quality (absolute and relative) of  
 545 root exudates, microbial community and functioning and soil suppressiveness to soil-borne pathogens.  
 546 VOCs: volatile organic compounds; R: rhizobia promoting atmospheric nitrogen fixation; M: mycorrhization;  
 547 SMs: secondary metabolites; OA: organic acids; CD: crop spatio-temporal diversification; T: tillage; SCS: soil  
 548 carbon storage; RE: root exudation.