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

Jay Ram Lamichhane, Martin Barbetti, Martin Chilvers, Abhay Pandey, Christian Steinberg

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2   Jay Ram Lamichhane[1]*, Martin J. Barbetti[2], Martin I. Chilvers[3], Abhay K. Pandey[4], Christian Steinberg[5]

3   [1]INRAE, Université Fédérale de Toulouse, UMR AGIR, F-31326 Castanet-Tolosan Cedex, France

4   [2]School of Agriculture and Environment and the UWA Institute of Agriculture, University of Western

5   Australia, Western Australia 6009, Australia

6   [3]Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing, MI 48824, USA

7   [4]Department of Mycology & Microbiology, Tea Research Association, North Bengal Regional R & D Center,

8   Nagrakata-735225, West Bengal, India

9   [5] Agroécologie, INRAE Institut Agro, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon,

10   France

11

12   *For correspondence: jay-ram.lamichhane@inrae.fr; Tel: 0033 561285250; ORCID: 0000-0001-9780-0941

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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

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Root exudates: complex organic substances relased in the rhizosphere

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

Root exudates: a hidden arsenal for plant defense?

Root exudates can directly recruit, repel, stimulate, inhibit, or kill other rhizosphere organisms including detrimental ones **(Table 1)**. Phytopathogenic fungi and oomycetes are attracted by trophic sources constituted by root exudates or by signal molecules indicating the presence of a host plant of interest. To counteract infection and defend themselves against phytopathogens, plants, through their root exudates, release an arsenal of metabolites into the rhizosphere [31]. The nature and relative abundance of 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	*Bacillus amyloliquefaciens/Fusarium oxysporum* f. sp. *cubense*	Fusarium wilt	[32]
Common bean	Isoflavone phytoalexins	*Phytophthora sojae*	Phytophthora root rot	[33]
Legumes	Phenolic acids and flavonoids	*Fusarium oxysporum* f. sp. *cubense*	Fusarium wilt	[34]
Maize	Lipopeptides	*Bacillus amyloliquefaciens/Fusarium graminearum*	Maize stalk rot	[35]
Panax notoginseng	Cinnamic acid, 2-dodecenoic acid, and 12-oxo-phytodienoic acid	*Burkholderia* sp. B36	Root rot	[36]
Potato onion	Not determined	*Plasmodiophora brassicae*	Chinese cabbage clubroot	[37]
Rapeseed	Antimicrobial compounds	*Phytophthora parasitica* var. *nicotianae*	Tobacco black shank disease	[38]
Tomato	Extracellular vesicles	*Fusarium oxysporum, Botrytis cinerea* and *Alternaria alternata*	Soil-borne	[39]
Tomato	Carbohydrate exudate	*Trichoderma atroviride/Phytophthora cinnamomi*	Phytophthora root rot	[40]
Tomato	Organic compounds	*Bacillus amyloliquefaciens/Ralstonia solanacearum*	Bacteria wilt	[41]
Tomato	Volatile organic compounds	*Trichoderma harzianum/Fusarium oxysporum* f. sp. *lycopersici*	Fusarium wilt	[42]
Maize and soybean intercropping	Phenolic acids	*Phytophthora sojae*	Phytophthora root rot	[43]
Potato	Organic compounds	*Spongospora subterranea*	Powdery scab	[44]
Wheat/faba bean intercropping	Phenolic acids, organic acids, amino acids and sugars	*Fusarium oxysporum* f. sp. *fabae*	Faba bean fusarium wilt	[45]
Wheat/watermelon intercropping	Not determined	*Fusarium oxysporum* f. sp. *niveum*	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. amyloliquefaciens* 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].

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].

Dealing with knowledge gaps: root exudates and soil-borne disease complexes under changing 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.

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

- Most studies focused on specific pathosystems for a specific cropping season, entailing only one host plant and a beneficial or harmful organism. This is not consistent with reality where inter-species and/or inter-kingdom interactions occurring among a myriad of organisms shape semi-quantitative changes in composition of root exudates. Indeed, there is increasing evidence that soil-borne diseases are primarily caused not by individual species but by pathogenic complexes [65–68] where each pathogen within a soilborne complex is differentially affected by environment, with the complexity of soilborne pathogens x environment interactions highlighted by the multifaceted and contrasting interactions such as those associated with temperature and moisture [62]. The unpredictable and ever-changing proportions of different pathogens within complexes across seasons and locations further increases this complexity [63]. In addition, synergistic and/or antagonistic interactions occur not only between soil-borne pathogens but also between soil-borne pathogens and other beneficial and/or commensal organisms constituting the soil microbiome. The latter plays a positive role in the soil food web as well as in soil and plant health since the bulk of the plant microbiome is concentrated belowground at the plant root-soil interface.

- Most studies generally focused on a single cropping or natural ecosystem with a unique, yet often undefined, set of environmental (e.g., soil, host) characteristics, missing the opportunity to assess the advantages/disadvantages of different host(s), soil type, soil amendments, tillage and cropping systems to define the most beneficial future scenarios. While such a systemic approach is difficult to implement locally, an increasing number of meta-analyses make it possible to combine field observations and experimental results conducted under contrasted conditions that helps determine the most favorable biotic and abiotic parameters to plant health [69–71].

- It remains unknown whether beneficial and soil-borne pathogens use the same or different root exudate molecules to proliferate in the rhizosphere of diverse plant species because a taxon,

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

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

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

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

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

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

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

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

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

Concluding remarks and future perspectives

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

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

Acknowledgements

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Glossary

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

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

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

- 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.

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

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

- 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.

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

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

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

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

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

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

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

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

- 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.

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

- Soil-borne pathogens: microorganisms surviving and operating in the soil at least during part of their lives infecting healthy plants belowground.
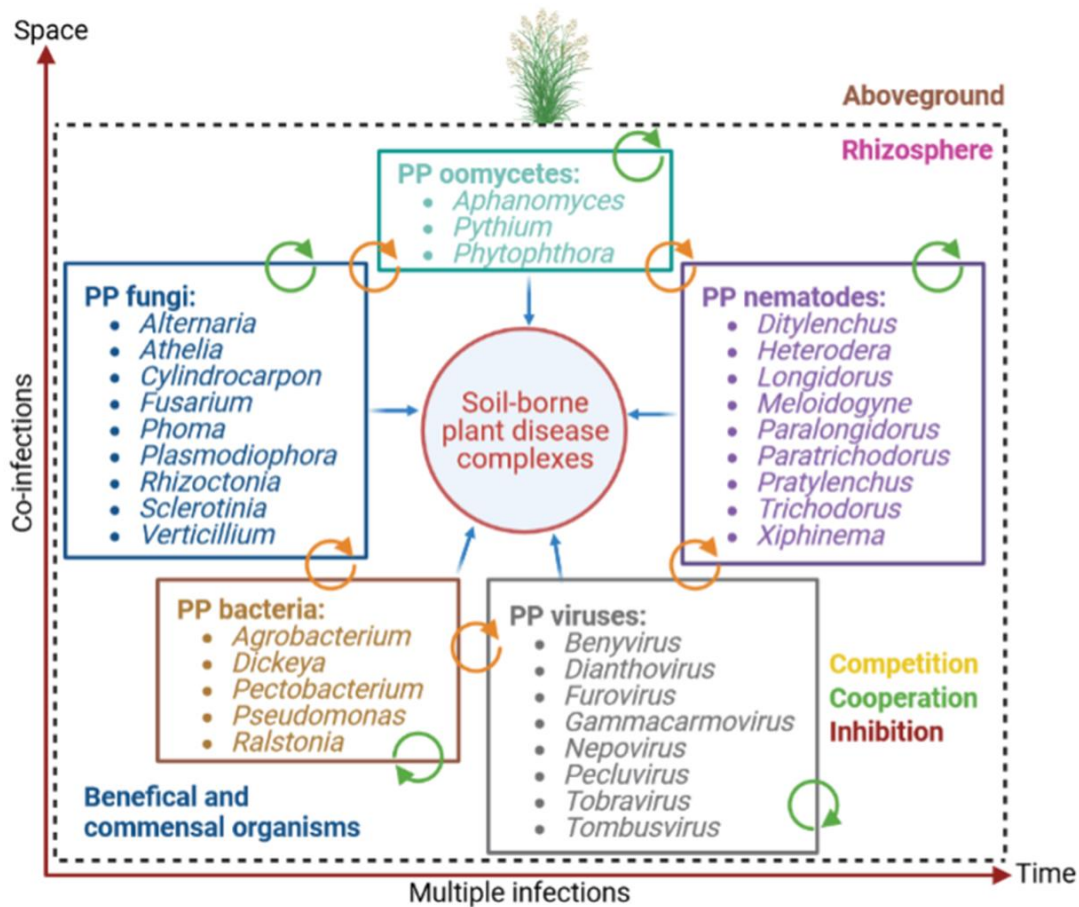
- Soil-borne disease complexes: diseases resulting from the contributions of multiple soil-borne pathogens that attack plants either simultaneously or at different time points.

- Soil food web: a complex living system represented by the community of organisms living all or part of their lives in the soil in interaction among them.

- Soil microbiota/microbiome: Dynamic community of microorganisms (microbiota) or their DNA (microbiome) within the soil. Although often used interchangeably, microbiota includes living microorganisms while microbiome refers to the living and dead microorganims represented by their DNA as well as the functional potential of the microbiota.

- Strigolactones: a group of chemical compounds produced by plant roots.

- Trophic sources: feeding and nutrition sources.

- Vesicles: membrane-bound organelles that transport material within or outside the cell.

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

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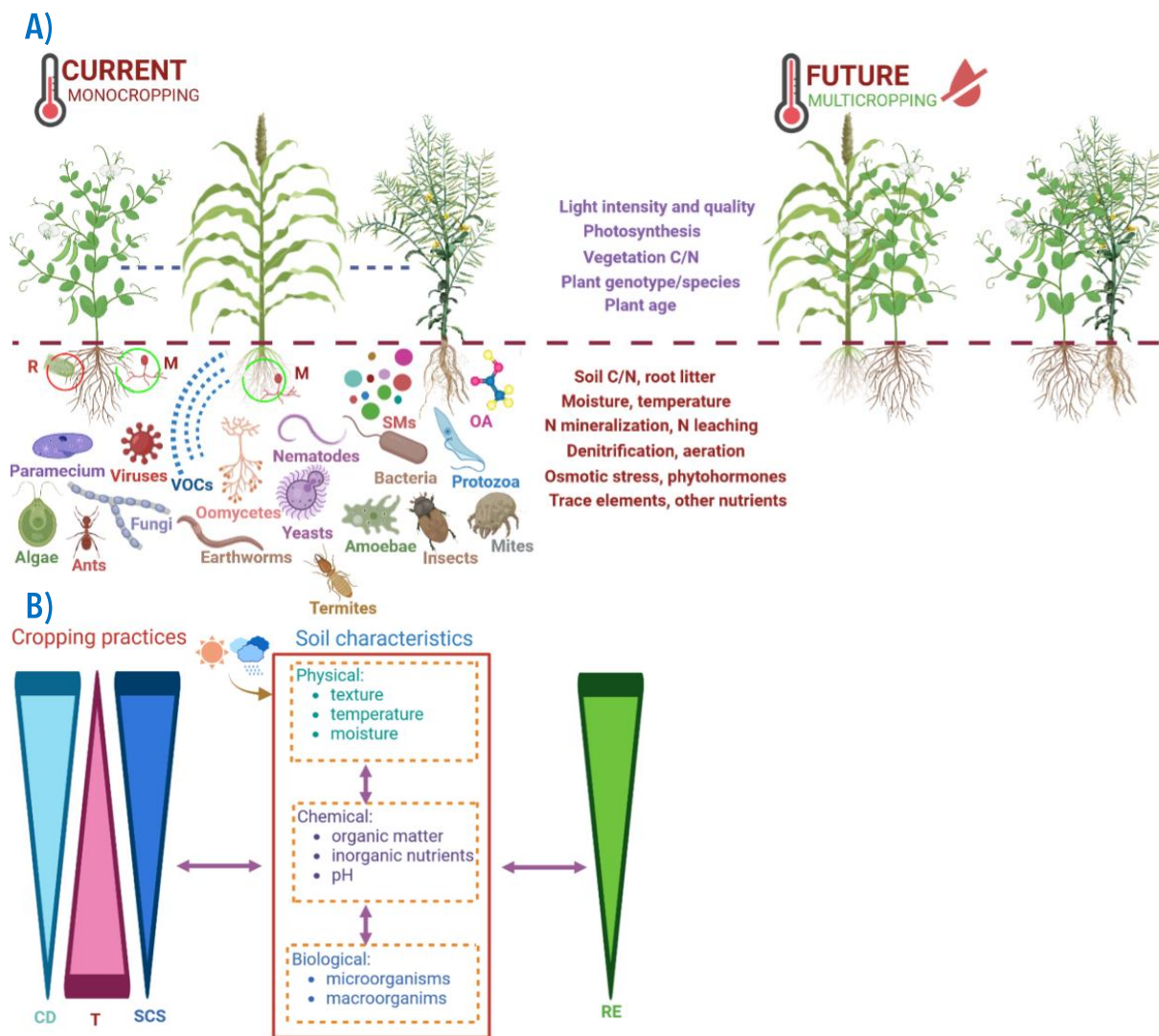
Figure 2. Schematic representation of key above- and below-ground factors affecting the root exudation process (a) and a hypothetical overview of key cropping practices that may affect the root exudation process in interaction with soil and climate (b). Unlike some available knowledge about the effect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