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1 **Harnessing rhizosphere microbiomes for drought resilient crop production**

2

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10

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12

13 Key words: root exudates, root traits, microbiome, rhizosphere, plant-soil communication,
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15

16 Short title: Harnessing rhizosphere microbiomes

17

18 Single sentence summary: Mechanistic and field understanding of plant-microbiome interactions is
19 crucial for securing food production under drought

20

21

22 **Root-associated microbes can improve plant growth, and offer potential to increase crop**
23 **resilience to future drought. While our understanding of the complex feedbacks between**
24 **plant and microbial responses to drought is advancing, most of our knowledge comes from**
25 **non-crop plants in controlled experiments. Here, we describe a framework for quantifying**
26 **relationships between plant and microbial traits, and we propose that future research**
27 **efforts should explicitly focus on food crops and include longer-term experiments under**
28 **field conditions. Overall, we highlight that an improved mechanistic understanding of the**
29 **complex feedbacks between plants and microbes during, and particularly after, drought -**
30 **through integrating ecology with plant, microbiome and molecular approaches - is central to**
31 **making crop production more resilient to our future climate.**

32

33

34 Interactions between plants and soil organisms are crucial for the functioning of terrestrial
35 ecosystems and their response to a changing climate (1, 2). Plants and soil organisms interact via a
36 variety of different mechanisms. Plants fuel the soil food web through their belowground carbon
37 (C) inputs, in the form of leaf and root litter, and root exudates. While soil microbes are the primary
38 decomposers of these C inputs, their biomass supports the existence of higher trophic levels, and in
39 turn, organisms from these higher trophic levels, such as Collembola and nematodes, stimulate the
40 activity of soil microbes. Together, the activities of these organisms release nutrients for plant
41 growth, and determine the balance between C respiration and stabilisation in the soil. But these
42 organisms also interact directly with plants in the rhizosphere, for example through feeding on, or
43 infecting roots, through forming symbiotic relationships such as mycorrhizae, or through
44 promoting plant growth through phytohormone production or reducing plant stress signalling. It is
45 well known that different plant species or genotypes can select for different soil communities (3).
46 These selective pressures are especially strong in the rhizosphere - the area around the roots that is
47 directly influenced by root processes and that is the home of the rhizosphere microbiome. Recent
48 studies suggest a pivotal role for root exudates in selecting the rhizosphere microbiome, and that
49 selecting a favourable rhizosphere microbiome via altering root exudation patterns might open up
50 new opportunities to increase plant performance, with particular benefits for crop production (4).

51
52 In many regions of the world, the frequency and duration of drought spells is predicted to increase,
53 significantly threatening global crop yields (5). Much recent research effort is focused on
54 harnessing rhizosphere microbial communities for making food production more sustainable (6-8),
55 and emerging evidence shows that these microbiomes might also alleviate plant drought stress (9-
56 11). However, despite an increased understanding of the mechanisms through which plants select
57 their rhizosphere microbiomes, and the subsequent feedbacks of these microbiomes to plant
58 growth and fitness, our understanding of these mechanisms under drought is still limited.
59 Moreover, our understanding of the response of soil microbial communities to drought, and the
60 implications for crop response to drought, is hampered by the fact that very little of our knowledge
61 comes from studying how soil microbes modify plant response to drought and, of those that do,
62 only a modest proportion focus on crop plants (Fig. S1). Here we argue that an increased
63 understanding of the complex feedbacks between plants and microbes during, and after, drought,
64 will pave the way for harnessing the rhizosphere microbiome to increase the resilience of crop
65 production to drought.

66

67 **Microbial drought response and the consequences for plant drought tolerance**

68 Drought is probably the abiotic stress that has the most dramatic effect on soil biota (12). In addition
69 to osmotic stress, drought increases soil heterogeneity, limits nutrient mobility and access, and
70 increases soil oxygen, often inducing a strong decrease in microbial biomass (13, 14). On short time
71 scales, the resistance of microorganisms to this drastic alteration in environmental conditions is
72 determined by specific “response traits” that protect against desiccation, like the presence of a thick
73 peptidoglycan cell wall in monoderm taxa, osmolyte production, sporulation, and dormancy (Fig. 1;
74 15–18). These traits have co-evolved convergently in diverse organisms, notably in fungi and Gram-
75 positive bacteria, in particular *Actinomycetes* (19). These organisms are described as stress-tolerant
76 strategists according to the recently proposed Y-A-S theory (high yield – resource acquisition – stress
77 tolerance; 20). This, and other frameworks, suggest a connection between drought response and
78 effect traits (generally defined as determining the effect on ecosystem functioning of the microbial
79 drought response, though here we focus on the effect of microbes on plant performance under
80 drought, Fig. 1). However, to date there is little evidence of this coupling between microbial drought
81 tolerance mechanisms and those functional traits that affect plant performance under drought.

82

83 While much research has focused on elucidating the microbial traits responsible for drought
84 tolerance, accumulating evidence suggests that the indirect effects via plants can outweigh the direct
85 effects of drought on microbial communities (21, 22). Root exudates are an important pathway of
86 plant-microbial communication: they provide C for microbial growth, but also facilitate direct
87 communication between plants and microbes via signalling molecules and phytohormones. Drought
88 can affect the quantity and quality of root exudates (21), and a recent study showed that the drought
89 history of root exudates was a stronger driver of the microbial respiration induced by those root
90 exudates than the drought history of the soil and its microbial communities (22). On longer
91 timescales, drought-induced shifts in plant growth and abundance seem to be more important than
92 direct effects of drought for altering soil microbial community composition, potentially through
93 altered root exudation (4). These indirect effects of drought can induce a drastic modification of the
94 effect traits in microbial communities that are involved in basic metabolic processes. Altered rates
95 and composition of root exudation can trigger increased microbial mineralisation of nutrients, thus
96 affecting plant recovery from drought (4), but longer-term changes in microbial communities have
97 also shown to affect the fitness of subsequent plant generations under drought (9). Thus, these
98 changes in microbial communities have the potential to affect ecosystem carbon and nitrogen cycling
99 (22). Indeed, drought has been shown to increase the frequency of effect traits related to carbon and

100 nitrogen acquisition in fungi as well as in bacteria (23, 24), which can feed back to plant performance
101 under drought and during recovery after drought. On longer timescales, compositional changes in
102 microbial communities, together with eco-evolutionary feedbacks between plants and microbes,
103 horizontal gene transfer, and adaptation, can determine future drought responses of the plant-
104 microbe holobiont (25; Fig. 1, Table 1, Table 2).

105
106 Despite their hypothesised link, the correlation between microbial drought response traits, and
107 microbial effect traits that confer an increased drought tolerance or faster recovery to plants (Fig. 1
108 arrow 4, Table 1), has rarely been verified. One exception is arbuscular mycorrhizal fungi (AMF,
109 specifically *Glomeromycota*), which can increase in abundance under drought (26, 27, but see 28) and
110 confer drought tolerance to their host plant by enhancing antioxidant enzyme activity, thereby
111 reducing oxidative stress and promoting better water use efficiency and greater biomass (8, 27).
112 Similarly, the enrichment of *Streptomyces* under drought has been evidenced to play a subsequent
113 role in the drought-tolerance of plants (18, 29). Still, many of the microbial effect traits proposed as
114 beneficial are common and shared across many microbial taxa, raising questions on their specific
115 mode-of-action (30). Moreover, despite widespread claims of efficacy of inoculation with plant
116 growth promoting rhizobacteria (PGPRs) under laboratory conditions, we were unable to find
117 studies demonstrating attribution of the beneficial effect to the specific selected trait, and there is
118 limited evidence of inoculation success and subsequent benefits for plant growth under drought in
119 field settings. Thus, understanding the mechanisms through which soil microbes affect plant drought
120 tolerance and recovery, and their relevance and applicability under realistic field conditions, offers
121 much potential for making crop production systems more resilient to drought.

122 123 **We need a mechanistic understanding of the feedbacks between plant and microbial** 124 **response to drought**

125 There is increasing interest in manipulating host-microbiome interactions through adding bacteria
126 (probiotics) in a range of systems and in gut-microbe systems in particular. Guts have strong
127 mechanistic parallels with the rhizosphere environment (31) and studies in humans provide proof
128 of concept that manipulation of very specific feedbacks is possible with probiotics. For example,
129 trials in babies have demonstrated microbiome invasion by a probiotic without major disruption of
130 community structure, resulting in very specific activation of glycerol-3-phosphate (G3P) uptake
131 genes by that community (32). Microbiome expression of G3P uptake genes has also been
132 demonstrated as a critical response to drought in soy (17), while in sorghum it is thought to allow

133 uptake and metabolisation of G3P secreted by the host plant, enabling preferential root-
134 colonisation by monoderm bacteria which then aide in drought tolerance (18). While probiotic
135 manipulation may be effective (32), having identified such a specific pathway, crops, unlike human
136 systems, are open to host engineering for adjusting that pathway (33). In addition, in humans,
137 applying key small molecules (prebiotics) has been shown to have a host effect via the microbiome
138 (34). For example, butyrate, a short chain fatty acid, is an important molecule for interactions
139 within the gut microbiome, as it is, for anaerobic soil systems (35). While there is little existing
140 evidence of efficacy such small molecule treatments in agricultural systems (36), the fundamental
141 parallels between gut-microbiome and plant-microbiome interactions might inform targeted
142 research into manipulating rhizosphere microbiome drought effect traits.

143
144 Plants themselves produce diverse small molecules in the rhizosphere. These primary and
145 secondary metabolites, including volatiles, can be critical during stress (37, 38). For instance, in the
146 early stages of drought, oak tree secondary metabolites play an important role in signaling to the
147 rhizosphere; primary metabolites may serve a greater purpose during recovery (39). Interestingly,
148 many of the drought responsive microbial metabolites described in this study act as precursors of
149 immune phytohormones (such as phenylalanine, which is a precursor to salicylic acid (SA)
150 biosynthesis and other stress-responsive secondary metabolites; 40), along with increased
151 concentrations of abscisic acid (ABA). ABA plays a central role in drought tolerance in crops (41)
152 and has long been understood to be present in the rhizosphere (42) where it is actively metabolised
153 by rhizosphere bacteria and may be involved in helping plants tailor their rhizosphere microbial
154 communities (43). The fact that ABA-induced sugar accumulation is the primary mechanism of
155 drought tolerance in liverworts, ancestors to land-plants (44), also indicates that this is a highly
156 conserved drought response pathway. Thus, engineering its activity to generate more drought
157 resistant crops is promising (41). Furthermore, genes responsive to the immune hormones SA and
158 jasmonic acid (JA) are downregulated in sorghum during drought (28). As SA related exudation
159 signals are instrumental in allowing both systemic resistance and the plant-mediated development
160 of a rhizosphere specific microbiome (45, 46) this is another potentially malleable pathway for
161 influencing a drought-protective rhizosphere microbiome. However, manipulating the central plant
162 metabolism, especially concerning immune phytohormones such as ABA, could result in
163 undesirable outcomes, such as altered disease resistance (as is the case with ABA overexpressing
164 mutants of Arabidopsis, which experience increased susceptibility to the biotrophic pathogen
165 *Dickeya dadantii*; 47).

166

167 Novel metagenomic approaches and high-resolution measurements in controlled experiments will
168 improve our understanding of the production and role of drought responsive metabolites. These
169 methods need to be employed not just during drought, where ultimately plant-microbial
170 communication breaks down as the drought continues (3) but also after drought, when a fast
171 sequence of physiological changes in both plant and microbes creates rapid feedback between
172 plants and their microbiome (Fig. 3; 4). Moreover, many of these interactions may be highly context
173 dependent. For example, investing in protective cell walls requires significant allocation of
174 resources to build these structures, which trades-off with growth rates and competitiveness under
175 resource-rich conditions; thus, this strategy might be selected against in agricultural soils (48).
176 Similarly, plant cues via root exudation that stimulate microbial release of nutrients for plant
177 regrowth after drought might either not happen or not play a role in nutrient-rich agricultural soils,
178 where sufficient nutrients are available for plant (re)growth. Furthermore, nutrient-rich soils might
179 increase the vulnerability of drought-stressed plants to pathogens that increase under drought (49),
180 might select for inherently drought-sensitive plants and microbiomes (50, 51) and reduce the
181 benefits and root colonisation of AMF (52). Much of our understanding of plant-microbial
182 interactions under drought comes from non-crop species (Fig. S1), while crop species are selected
183 for traits that might inherently compromise drought resistance and beneficial interactions with
184 rhizosphere microbiomes (53, 54). Therefore, manipulating the rhizosphere microbiome via
185 introducing the selective traits into crops, or via inoculating soils with either probiotics or
186 prebiotics, is likely to be more successful when paralleled by other measures to increase the
187 sustainability of agro-ecosystems (6).

188

189 **Putting our knowledge to work**

190 Understanding the full extent of interactions between plants and microbes, and how these are
191 affected over time under conditions of drought, will open many new research avenues to improve
192 plant resilience to moisture stress. Efforts should focus on crop plants, and be pursued in
193 combination with management approaches such as minimum tillage and maintenance of plant
194 cover, to enhance soil organic matter and soil moisture retention. To promote plant drought
195 resistance, given the uncertainties over bio-inoculant usefulness, we emphasise here the
196 importance of manipulating plant traits to enhance both the drought resistance of beneficial
197 microbes, as well as promoting specific beneficial plant-microbe interactions. Such manipulations
198 could include diversifying crops in time and space (intercropping), cultivar selection, or

199 manipulation through breeding or new methodologies for localised gene editing (e.g. CRISPR; 55).
200 More generally, calls for more advanced non-invasive phenotyping of the plant root soil system (56)
201 need to consider microbial phenotypes and interactions with plants, and the large body of
202 knowledge on beneficial microbial traits identified in the bioinoculant literature needs to be
203 extended, incorporating ecological and evolutionary studies, to identify in-field mechanisms by
204 which rhizosphere microbes extend the plant phenotype under periods of drought and subsequent
205 recovery (Fig. 2).

206

207 **Conclusion**

208 Increasing our mechanistic, as well as our real-world, understanding of microbe-plant interactions
209 under drought offers huge potential for increasing the resilience of crop production to drought.
210 Here, we have outlined promising avenues to increase our understanding of the complex feedbacks
211 between plant and microbial responses to drought, and argue that our research efforts will now
212 need to focus on crop plants and be tested under realistic field conditions. Understanding the role
213 of plant-microbe interactions during drought recovery, and in response to recurring droughts, is
214 necessary if we are to harness these interactions not just for increasing crop resilience to drought,
215 but also for maximising crop yields, building soil carbon and optimising soil nutrient cycling.

216

217

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423

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428 **Author contributions**

429 All authors conceived the idea for the manuscript. FTdV led the writing of the manuscript, with
430 inputs from all authors.

431

432 **Competing interests**

433 There are no competing interests

434

435 **Data and materials availability**

436 All data is available in the supplementary materials

437

438 **Supplementary Materials**

439 Figure S1

440 Data S1

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442

443 **Tables**

444

445 **Table 1 Microbial community response and effect traits during drought**

Response or effect	Trait	Description	Has this been observed in the field?	References
Response	Cell wall architecture	Monoderm (gram positive) increase relative to diderms - thicker cell walls mean increased resistance to water stress.	Field	Xu <i>et al.</i> 2018 (17)
Response	Morphology, filamentous hyphae	In certain fungi access to spatially separated sources of water during drought through production of filamentous structures. This may aide host or increase pathogenic fungi.	Field	Francisco <i>et al.</i> 2019 (57)
Response	Sporulation	Protective spore production can promote persistence in the soil in certain species during extreme drought. Drought itself reduces the ability to sporulate.	Field, observational.	Naylor <i>et al.</i> 2017 (58)
Response and effect	EPS/ Biofilm	Production of an EPS matrix in mixed microbial communities generates an environment that is more osmotically stable during drought	CE	Khan & Bano 2019 (59)
Response and effect	Osmoprotection	Production of osmolytes by microbes and stimulation of osmolyte production in the roots via microbially derived signals impart a more stable osmotic environment during drought stress	CE Field	Vurukonda <i>et al.</i> 2016 (60)
Effect	Root elongation via IAA	Bacteria produce auxins (IAA) and gibberellins during drought which act as growth stimulators, altering root morphology for greater water acquisition	CE	Jochum <i>et al.</i> 2019 (61)
Effect	antimicrobial / allelopathy	Certain PGPM promote their own survival and potentially limit the growth of pathogens by producing allelopathic and antimicrobial molecules	Field, observational	Bouskill <i>et al.</i> 2016 (23)
Effect	Antioxidant production	Drought leads to oxidative stress and internal cell damage. This can be directly mitigated by certain PGPM which produce antioxidants, such as glutamic and aspartic acids, and ROS degrading enzymes such as superoxide dismutase.	Field, observational	Chiaperro <i>et al.</i> 2019 (62)

Effect	ABA augmentation	Direct production, and stimulation, of the phytohormone ABA allows a greater drought stress response through holistic reorchestration of water use (Table S2).	CE	Vurukonda <i>et al.</i> 2016 (63)
Effect	Nutrient acquisition via enzymes	Greater C and N scavenging enzyme production during drought can provide access to limited resources which are less available during drought	Field	Bouskill <i>et al.</i> 2016 (23)

446 EPS exopolysaccharide matrix; IAA indole acetic acid; ABA abscisic acid; PGPR plant growth promoting microorganisms; ROS
447 reactive oxygen species; CE controlled environment

448

449 **Table 2 Plant response and effect traits during drought**

Response or Effect	Trait	Description	Has this been observed in the field?	References
Response	Transpiration and water use decreased	Through changes in hormonal signalling, inducing stomatal closure, water loss is decreased. Increased cuticular wax deposition aides in foliar water retention.	Field	Moshelion <i>et al.</i> 2014 (64)
Response	Osmoprotective physiology favoured	Induced changes in antioxidant physiology to protect plants from oxidative stress	Field	Szabados & Saviouré, 2010 (65)
Response	Root hydraulic conductance increases	Aquaporin expression increases during drought. Dehydrin production promotes an osmotically stable environment.	Field	Eldhuset <i>et al.</i> 2013 (66)
Response	Development limited	Photosynthetic activity decreases, foliar growth stops, root shoot ratio increases.	Field	Lipiec <i>et al.</i> 2013 (67)
Effect	Changes in root exudation chemistry	This occurs as both quantity and composition of root exudates are responsive to drought. Different compositions are likely to influence a root microbiome that is more conducive to drought tolerance	CE	De Vries <i>et al.</i> 2019 (22); Williams and de Vries 2020 (4)
Effect	Increased mucilage production	More mucilage excretion around the roots helps to create a more osmotically positive environment.	CE	Ahmed <i>et al.</i> 2014 (68)
Effect	Altered soil C flux	Changes in soil C deposition, as well as its degradation and feedback into the atmosphere during drought.	CE	van der Molen <i>et al.</i> 2011 (69)

450 CE - controlled environment

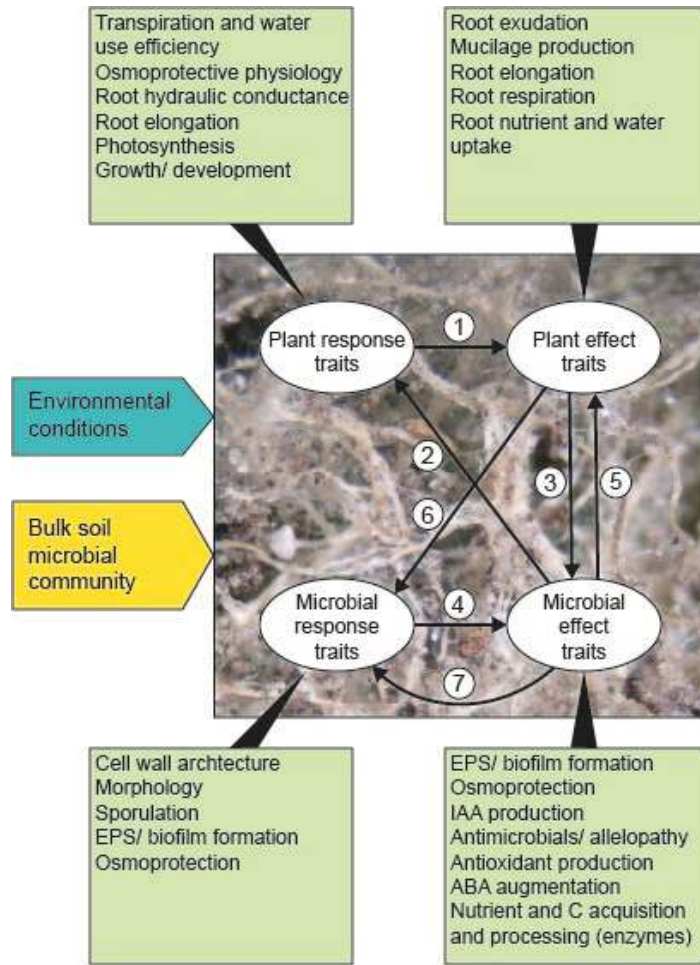
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454 **Figures**

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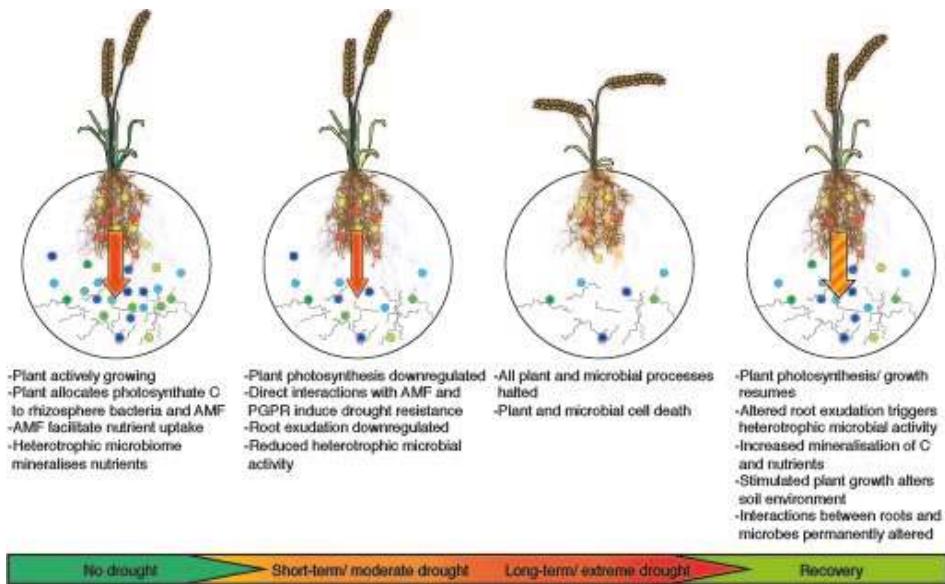


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457 **Figure 1. Relationships between plant drought response and effect traits, and microbial**
458 **drought response and effect traits.** Drought response traits determine the direct response of
459 plants and microbes to drought, and these traits have a hypothesised link with drought effect traits
460 (arrows 1 and 4), which determine the effect of drought on the plant. Plant and microbial effects
461 traits can feedback to each other (arrows 3 and 5) and determine plant and microbial response to
462 drought (arrows 2 and 6). Microbial effect traits can also feed back to influence microbial response
463 to drought (arrow 7). All traits are affected by environmental conditions and bulk soil microbial
464 communities. Morphology refers to filamentous hyphal growth of fungi. EPS is exopolysaccharide,
465 ABA is abscisic acid, IAA is indole acetic acid. References for the traits included here can be found in
466 Tables 1 and 2.

467

468



469

470 **Figure 2. Hypothesised alterations in plant-microbial interactions during and after drought.**

471 During drought, direct interactions with PGPR and AMF induce plant drought tolerance, but these

472 interactions break down under severe or continuing drought. After drought, different plant-

473 microbial interactions are assembled, with the potential of affecting future plant and soil response

474 to drought.

Supplementary Materials for

Harnessing rhizosphere microbiomes for drought resilient crop production

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This PDF file includes:

Fig. S1
Caption for Data S1

Other Supplementary Materials for this manuscript include the following:

Data S1

Fig. S1.

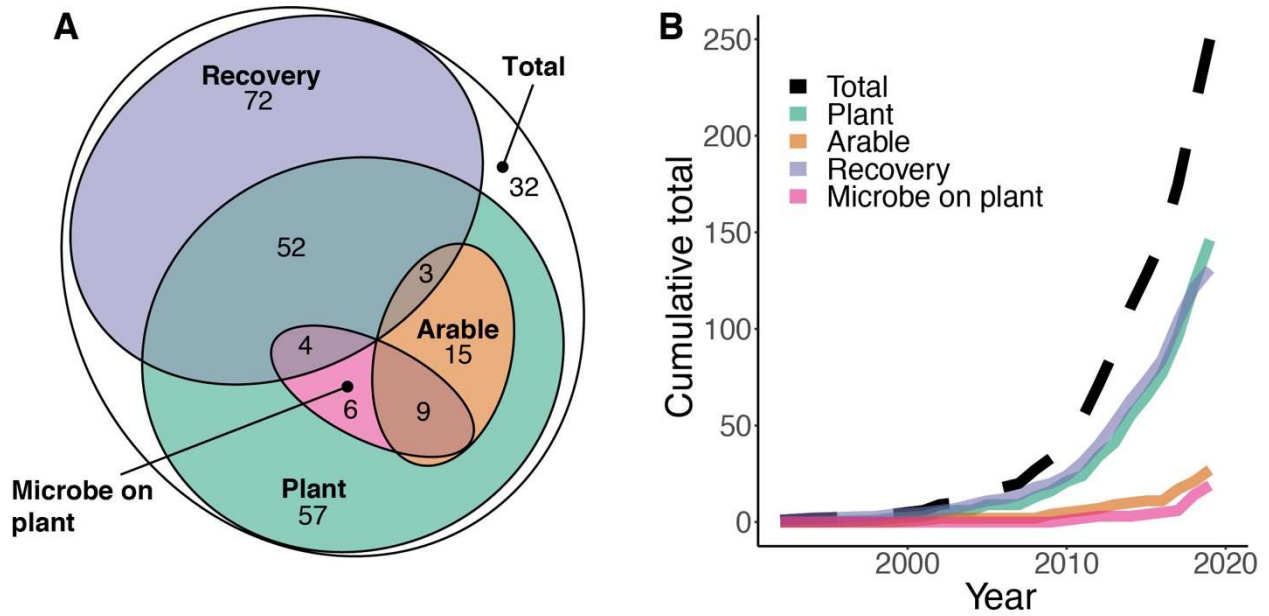


Figure S1. Effects of drought on soil microbial communities: the literature. Two hundred and fifty papers dealing with drought and soil microbial communities ('Total') were classified by whether they involved plants ('Plant'), whether they included recovery from drought ('Recovery'), whether they used an arable plant or crop ('Arable'), and whether they specifically considered the effect of soil microbes on plant drought response ('Microbe on plant'). **A** Euler diagram of all papers, showing that no papers tested the effect of microbes on an arable plant through recovery from drought. **B** The recent large growth in relevant papers has largely ignored arable systems and microbes on plants. Papers were identified using Web of Science and at least one of the following four search terms: drought effects soil (fungal OR bacterial) microbial; drought effects soil "microbial community"; (drying OR drying-rewetting OR dry-wet) effects soil (fungal OR bacterial) microbial; (drying or drying-rewetting OR dry-wet) effects soil "microbial community". Full list of papers is available as Data S1.

Data S1. (separate file)

File containing all papers used for Fig. S1, as extracted from Web of Science with the search terms specified in Fig. S1.