REVIEW

Harnessing rhizosphere microbiomes for drought-resilient crop production

Franciska T. de Vries[1,2]*, Rob I. Griffiths[3], Christopher G. Knight[1], Oceane Nicolitch[1], Alex Williams[1]

Root-associated microbes can improve plant growth, and they offer the potential to increase crop resilience to future drought. Although our understanding of the complex feedbacks between plant and microbial responses to drought is advancing, most of our knowledge comes from non-crop plants in controlled experiments. We propose that future research efforts should attempt to quantify relationships between plant and microbial traits, explicitly focus on food crops, and include longer-term experiments under field conditions. Overall, we highlight the need for improved mechanistic understanding of the complex feedbacks between plants and microbes during, and particularly after, drought. This requires integrating ecology with plant, microbiome, and molecular approaches and is central to making crop production more resilient to our future climate.

Interactions between plants and soil organisms are crucial for the functioning of terrestrial ecosystems and their response to a changing climate (*1*, *2*). Plants and soil organisms interact by several distinct mechanisms. Plants fuel the soil food web through their belowground carbon (C) inputs—in the form of leaf and root litter—and root exudates. Although soil microbes are the primary decomposers of these C inputs, their biomass supports the existence of higher trophic levels; in turn, organisms from these higher trophic levels, such as Collembola and nematodes, stimulate the activity of soil microbes. Together, the activities of these organisms release nutrients for plant growth and determine the balance between C respiration and stabilization in the soil. But these organisms also interact directly with plants in the rhizosphere by feeding on (or infecting) roots, by forming symbiotic relationships such as mycorrhizae, or by promoting plant growth through phytohormone production or reducing plant stress signaling. It is well known that different plant species or genotypes can select for different soil communities (*3*). These selective pressures are especially strong in the rhizosphere, the area around the roots that is directly influenced by root processes and is the home of the rhizosphere microbiome. Recent studies suggest that root exudates have a pivotal role in selecting the rhizosphere microbiome, and that selecting a favorable rhizosphere microbiome via altering root exudation patterns might open up new opportunities to increase plant performance, with particular benefits for crop production (*4*).

In many regions of the world, the frequency and duration of drought spells is predicted to increase, leading to substantial threats to global crop yields (*5*). Much recent research effort is focused on harnessing rhizosphere microbial communities to make food production more sustainable (*6*–*8*), and emerging evidence shows that plant microbiomes might also alleviate plant drought stress (*9*–*11*). However, despite an increased understanding of the mechanisms through which plants select their rhizosphere microbiome, and the subsequent feedbacks of the microbiome to plant growth and fitness, our understanding of these mechanisms under drought is still limited. Moreover, our understanding of the response of soil microbial communities to drought, and of the implications for crop response to drought, is hampered by the fact that very little of our knowledge comes from studying how soil microbes modify plant response to drought; of those studies that do concern this topic, only a modest proportion focus on crop plants. Here, we argue that an increased understanding of the complex feedbacks between plants and microbes during and after drought will pave the way for harnessing the rhizosphere microbiome to increase the resilience of crop production to drought.

Drought response traits

Drought is probably the abiotic stress that has the strongest effect on soil biota (*12*). In addition to osmotic stress, drought increases soil heterogeneity, limits nutrient mobility and access, and increases soil oxygen, often inducing a strong decrease in microbial biomass (*13*, *14*). On short time scales, the resistance of microorganisms to this drastic alteration in environmental conditions is determined by specific "response traits" that protect against

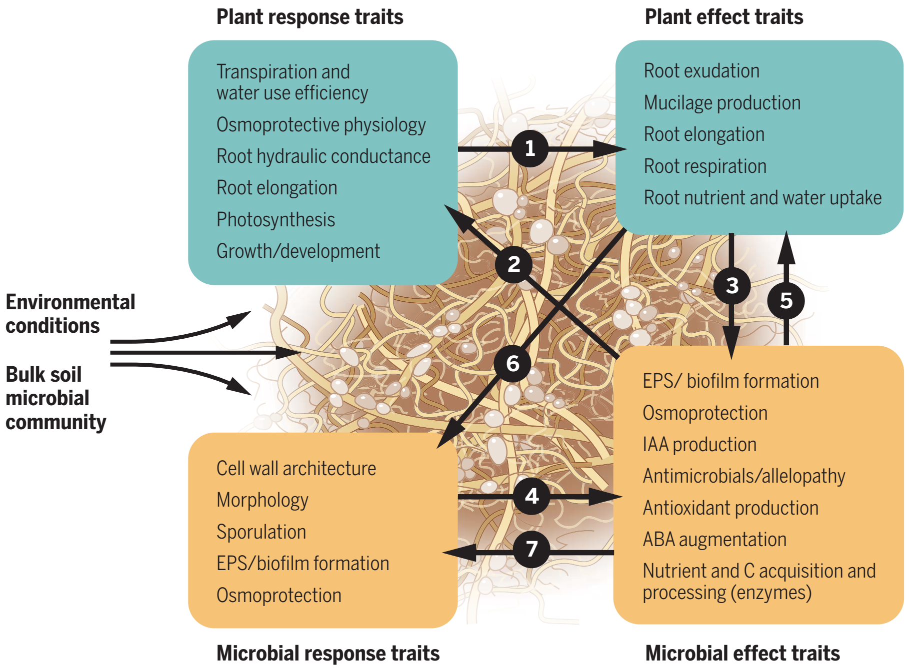

Fig. 1. Relationships among plant and microbial drought response and effect traits. Drought response traits determine the direct response of plants and microbes to drought, and these traits have a hypothesized link with drought effect traits (arrows 1 and 4), which determine the effect of drought on the plant. Plant and microbial effect traits can feed back to each other (arrows 3 and 5) and determine plant and microbial response to drought (arrows 2 and 6). Microbial effect traits can also feed back to influence microbial response to drought (arrow 7). All traits are affected by environmental conditions and bulk soil microbial communities. Morphology refers to filamentous hyphal growth of fungi. EPS, exopolysaccharide; ABA, abscisic acid; IAA, indole acetic acid. Tables 1 and 2 provide references for the traits included here.

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desiccation, such as a thick peptidoglycan cell wall in monoderm (Gram-positive) taxa, osmolyte production, sporulation, and dormancy (Fig. 1) (*15*–*18*). Similar traits have coevolved convergently in diverse organisms, notably in fungi and the Gram-positive bacteria Actinomycetes (*19*). These organisms are described as stress-tolerant strategists according to the recently proposed high yield–resource acquisition–stress tolerance (Y-A-S) theory (*20*). This and other frameworks suggest a connection between drought response and effect traits [generally defined as determining the effect on ecosystem functioning of the microbial drought response, although here we focus on the effect of microbes on plant performance under drought (Fig. 1)]. However, to date there is little evidence of coupling between microbial drought tolerance mechanisms and those functional traits that affect plant performance under drought.

Plant signals

Although much research has focused on elucidating the microbial traits responsible for drought tolerance, accumulating evidence suggests that the indirect effects via plants can outweigh the direct effects of drought on microbial communities (*21*, *22*). Root exudates are an important pathway of plant-microbial communication: They provide photosynthate C for microbial growth, but also facilitate direct communication between plants and microbes via signaling molecules and phytohormones. Drought can affect the quantity and quality of root exudates (*21*). A recent study showed that the drought history of root exudates was a stronger driver of microbial respiration than the drought history of the soil and its microbial communities (*22*). On longer time scales, drought-induced shifts in plant growth and abundance seem to be more important than the direct effects of drought for altering soil microbial community composition mediated by root exudation (*4*). Such indirect effects of drought can modify the effect traits in microbial communities that are involved in basic metabolic processes. Altered rates and composition of root exudation can trigger increased microbial mineralization of nutrients, thus affecting plant recovery from drought (*4*), but longer-term changes in microbial communities have also been shown to affect the fitness of subsequent plant generations under drought (*9*). Thus, these changes in microbial communities have the potential to affect ecosystem carbon and nitrogen cycling (*22*). Indeed, drought has been shown to increase the frequency of effect traits related to carbon and nitrogen acquisition in fungi, as well as in bacteria (*23*, *24*), which can feed back to plant performance under drought and during recovery after drought. On longer time scales, compositional changes in microbial communities, together with eco-evolutionary feedbacks between plants and microbes, horizontal gene transfer, and adaptation, can determine future drought responses of the plant-microbe holobiont (*25*) (Fig. 1 and Tables 1 and 2).

Microbial mechanisms

Despite their hypothesized link, the correlation between microbial drought response traits and microbial effect traits that confer an increased drought tolerance or faster recovery to plants (Fig. 1, arrow 4, and Table 1) has rarely been verified. One exception is arbuscular mycorrhizal fungi (AMF, specifically *Glomeromycota*), which can increase in abundance under drought [(*26*, *27*), but see (*28*)] and confer drought tolerance to their host plant by enhancing antioxidant enzyme activity, thereby reducing oxidative stress and promoting better water use efficiency and greater biomass (*8*, *27*). Similarly, the enrichment of *Streptomyces* under drought has been shown to play a subsequent role in

Table 1. Microbial community response and effect traits during drought. EPS, exopolysaccharide; IAA, indole acetic acid; ABA, abscisic acid; PGPR, plant growth–promoting rhizobacteria; ROS, reactive oxygen species; CE, controlled environment.

Response or effect	Trait	Description	Experimental system in which trait was measured	Reference
Response	Cell wall architecture	Monoderm (Gram-positive) bacteria increase relative to diderms; thicker cell walls mean increased resistance to water stress.	Field	(*17*)
Response	Morphology, filamentous hyphae	In certain fungi, spatially separated sources of water during drought are accessed through production of filamentous structures. This may aid the host plant or increase pathogenic fungi.	Field	(*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	(*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	(*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	(*60*)
Effect	Root elongation via IAA	During drought, bacteria produce auxins (IAA) and gibberellins, which act as growth stimulators, altering root morphology for greater water acquisition.	CE	(*61*)
Effect	Antimicrobial/ allelopathy	Certain PGPR promote their own survival and potentially limit the growth of pathogens by producing allelopathic and antimicrobial molecules.	Field, observational	(*23*)
Effect	Antioxidant production	Drought leads to oxidative stress and internal cell damage. This can be directly mitigated by certain PGPR that produce antioxidants, such as glutamic and aspartic acids, and ROS-degrading enzymes such as superoxide dismutase.	Field, observational	(*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 2).	CE	(*60*)
Effect	Nutrient acquisition via enzymes	Greater C and N scavenging enzyme production during drought can provide access to limited resources that are less available during drought.	Field	(*23*)

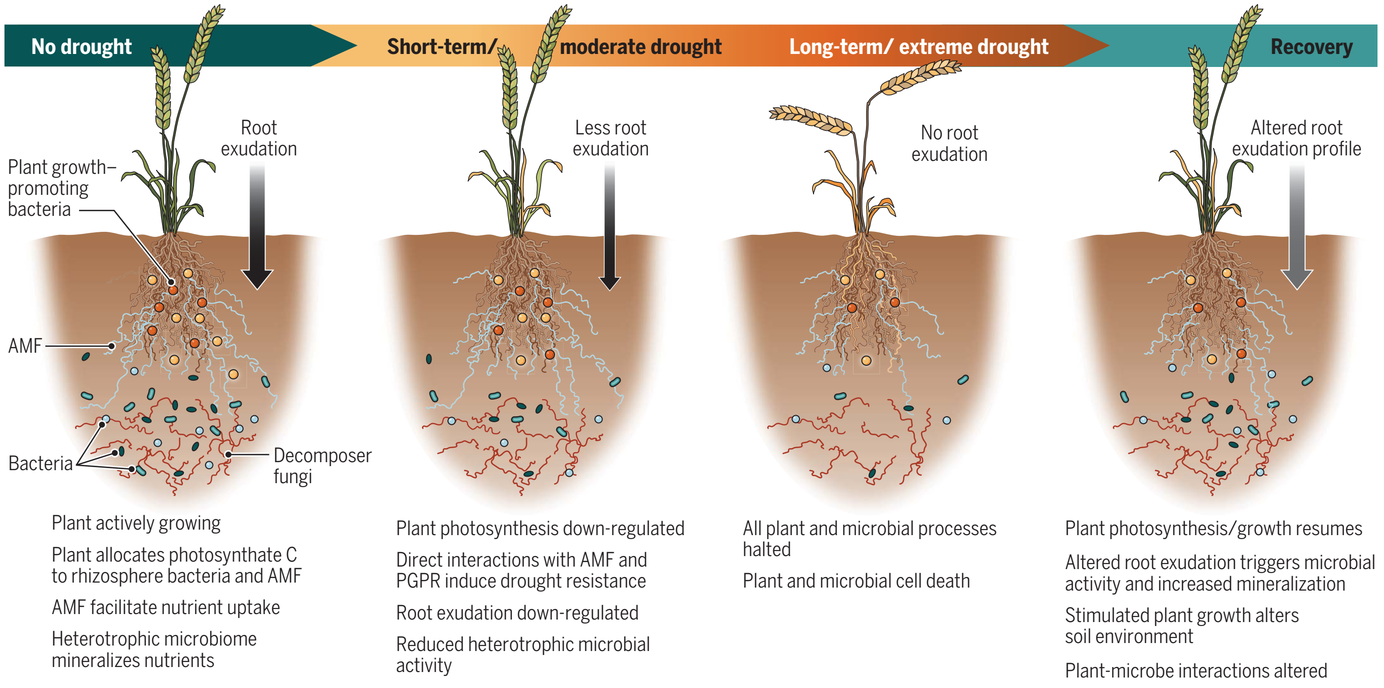

Fig. 2. Hypothesized alterations in plant-microbial interactions during and after drought. During drought, direct interactions with plant growth–promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) induce plant drought tolerance, but these interactions break down under severe or continuing drought. After drought, different plant-microbial interactions are assembled, with the potential of affecting future plant and soil response to drought.

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the drought tolerance of plants (*18*, *29*). Still, many of the microbial effect traits proposed as beneficial are common and shared across many microbial taxa, raising questions about their specific mode of action (*30*). Moreover, despite widespread claims of efficacy of inoculation with plant growth–promoting rhizobacteria (PGPRs) under laboratory conditions, we were unable to find studies demonstrating attribution of the beneficial effect to the specific selected trait, and there is limited evidence of inoculation success and subsequent benefits for plant growth under drought in field settings. Thus, understanding the mechanisms through which soil microbes affect plant drought tolerance and recovery, and their relevance and applicability under realistic field conditions, offers much potential for making crop production systems more resilient to drought.

Probiotics

There is increasing interest in manipulating host-microbiome interactions through adding bacteria (probiotics) in a range of systems, including gut-microbe systems. Guts have strong mechanistic parallels to the rhizosphere environment (*31*), and studies in humans provide proof of concept that manipulation of specific feedbacks is possible with probiotics. For example, trials in babies have shown colonization by a probiotic without major disruption of the resident microbiome, resulting in very specific activation of glycerol-3-phosphate (G3P) uptake genes by that community (*32*). Microbiome expression of G3P uptake genes has also been shown to be a critical response to drought in soy (*17*); in sorghum, it is thought to allow uptake and metabolism of G3P secreted by the host plant, enabling preferential root colonization by monoderm bacteria, which then aid in drought tolerance (*18*). Although the identification of such a specific pathway indicates that probiotic manipulation may be effective (*32*), crops, unlike human systems, are open to host engineering for adjusting that pathway (*33*). In humans, applying key small molecules (prebiotics) has been shown to have a host effect via the microbiome (*34*). For example, butyrate, a short-chain fatty acid, is an important molecule for interactions within the gut microbiome, as well as in anaerobic soil systems (*35*). Although there is little existing evidence of the efficacy of such small-molecule treatments in agricultural systems (*36*), the fundamental parallels between gut-microbiome and plant-microbiome interactions might inform targeted research into manipulating rhizosphere microbiome drought effect traits.

Primary and secondary plant metabolites

Plants themselves produce diverse small molecules in the rhizosphere. These primary and secondary metabolites, including volatiles, can be critical during stress (*37*, *38*). For instance, in the early stages of drought, oak tree secondary metabolites play an important role in signaling to the rhizosphere; primary metabolites may serve a greater purpose during recovery (*39*). Interestingly, many of the drought-responsive microbial metabolites described in (*39*) act as precursors of immune phytohormones [such as phenylalanine, which is a precursor to salicylic acid (SA) biosynthesis and other stress-responsive secondary metabolites (*40*)]. The phytohormone abscisic acid (ABA) was also shown to be strongly induced during drought, although it decreased during recovery (*39*). ABA plays a central role in drought tolerance in crops (*41*) and has long been understood to be present in the rhizosphere (*42*), where it is actively metabolized by rhizosphere bacteria and may be involved in helping plants tailor their rhizosphere microbial communities (*43*). The fact that ABA-induced sugar accumulation is the primary mechanism of drought tolerance in liverworts, ancestors to land plants (*44*), also indicates that this is a highly conserved drought response pathway. Thus, engineering its activity to generate more drought-resistant crops is promising (*41*). Furthermore, genes responsive to the immune hormones SA and jasmonic acid (JA) are down-regulated in sorghum during drought (*28*). Because SA-related exudation signals are instrumental in allowing both systemic resistance and the plant-mediated development of a rhizosphere-specific microbiome (*45*, *46*), this is another potentially malleable pathway for establishing a drought-protective rhizosphere microbiome. However, manipulating the central plant metabolism, especially with respect to immune phytohormones such as ABA, could result in undesirable outcomes, such as altered disease resistance [as is the case

Table 2. Plant response and effect traits during drought. CE, controlled environment.

Response or effect	Trait	Description	Experimental system in which trait was measured	Reference
Response	Transpiration and water use decreased	Through changes in hormonal signaling, inducing stomatal closure, water loss is decreased. Increased cuticular wax deposition aids in foliar water retention.	Field	(*63*)
Response	Osmoprotective physiology favored	Changes in antioxidant physiology are induced to protect plants from oxidative stress.	Field	(*64*)
Response	Root hydraulic conductance increases	Aquaporin expression increases during drought. Dehydrin production promotes an osmotically stable environment.	Field	(*65*)
Response	Development limited	Photosynthetic activity decreases, foliar growth stops, root/shoot ratio increases.	Field	(*66*)
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	(*4*, *22*)
Effect	Increased mucilage production	More mucilage excretion around the roots helps to create a more osmotically positive environment.	CE	(*67*)
Effect	Altered soil C flux	Changes in soil C deposition occur, as well as its degradation and feedback into the atmosphere during drought.	CE	(*68*)

with ABA overexpressing mutants of *Arabidopsis*, which experience increased susceptibility to the biotrophic pathogen *Dickeya dadantii* (*47*)].

Novel metagenomic approaches and high-resolution measurements in controlled experiments will improve our understanding of the production and role of drought-responsive metabolites. These methods need to be used not just during drought, where ultimately plant-microbial communication breaks down as the drought continues (*3*), but also after drought, when a fast sequence of physiological changes in both plants and microbes creates rapid feedback between plants and their microbiome (Fig. 2) (*4*). Moreover, many of these interactions may be highly context-dependent. For example, investing in protective cell walls requires substantial allocation of resources to build these structures, which trades off with growth rates and competitiveness under resource-rich conditions; thus, this strategy might be selected against in agricultural soils (*48*). Similarly, plant cues via root exudation that stimulate microbial release of nutrients for plant regrowth after drought may not occur or may not play a role in nutrient-rich agricultural soils, where sufficient nutrients are available for plant (re)growth. Furthermore, nutrient-rich soils might increase the vulnerability of drought-stressed plants to pathogens that increase under drought (*49*), might select for inherently drought-sensitive plants and microbiomes (*50*, *51*), and may reduce the benefits and root colonization of AMF (*52*). Much of our understanding of plant-microbial interactions under drought comes from noncrop species, whereas crop species are selected for traits that might inherently compromise drought resistance and beneficial interactions with rhizosphere microbiomes (*53*, *54*). Therefore, manipulating the rhizosphere microbiome by introducing the selective traits into crops, or by inoculating soils with either probiotics or prebiotics, is likely to be more successful when paralleled by other measures to increase the sustainability of agro-ecosystems (*6*).

Translational possibilities

Understanding the full extent of interactions between plants and microbes, and how these are affected over time under conditions of drought, will open many new research avenues to improve plant resilience to moisture stress. Efforts should focus on crop plants and be pursued in combination with management approaches, such as minimum tillage and maintenance of plant cover, to enhance soil organic matter and soil moisture retention. To promote plant drought resistance, given the uncertainties over bio-inoculant usefulness, we emphasize the importance of manipulating plant traits to both enhance the drought resistance of beneficial microbes and promote specific beneficial plant-microbe interactions. Such manipulations could include diversifying crops in time and space (intercropping), cultivar selection, or manipulation through breeding or new methodologies for localized gene editing [e.g., CRISPR (*55*)]. More generally, calls for more advanced noninvasive phenotyping of the plant root soil system (*56*) need to consider microbial phenotypes and interactions with plants, and the large body of knowledge on beneficial microbial traits identified in the bioinoculant literature needs to be extended, incorporating ecological and evolutionary studies, to identify in-field mechanisms by which rhizosphere microbes extend the plant phenotype under periods of drought and subsequent recovery (Fig. 2).

Conclusion

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

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ACKNOWLEDGMENTS

Funding: This work was funded by a NERC Discovery Grant (NE/P01206X/1) and a BBSRC David Phillips Fellowship to F.T.d.V. (BB/L02456X/1). **Author contributions:** All authors conceived the idea for the manuscript. F.T.d.V. led the writing of the manuscript with input from all authors. **Competing interests:** There are no competing interests. **Data and materials availability:** Bibliometric analysis is available in (*69*).

10.1126/science.aaz5192

Science

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Science **368** (6488), 270-274.
DOI: 10.1126/science.aaz5192

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