

Causes and consequences of a conserved bacterial root microbiome response to drought stress

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Plant-associated microbial communities contribute to host fitness, and perturbations in the plant microbiome can have a major impact on plant health. Drought has recently been shown to lead to enrichment of monoderm bacteria within the roots of many plant species across many environments. However, the underlying causes of this shift, and the consequences for plant fitness, remain largely unexplored. We present the hypotheses that drought-induced shifts in plant metabolism may be responsible for the observed monoderm enrichment, and that increased monoderm abundance may promote increased drought tolerance in the host. Finally, we discuss how these recent discoveries may inform ongoing efforts to use microbially mediated strategies to improve crop productivity.

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Introduction

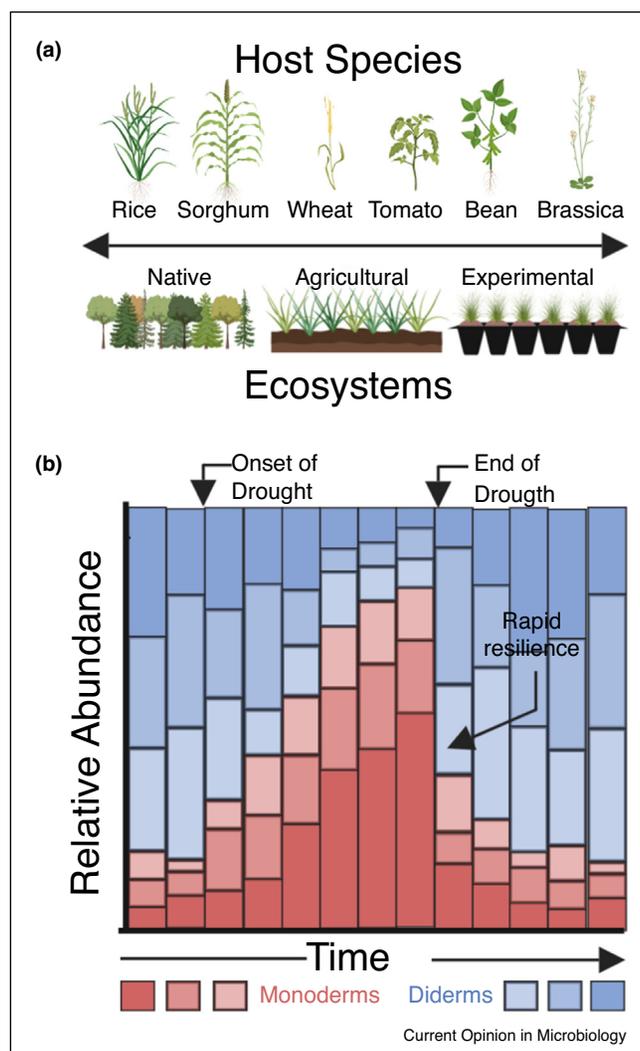
Water is an essential ingredient for life, necessary for basic cellular function in both micro and macroorganisms. Despite this necessity, water availability in most terrestrial ecosystems follows a periodic ebb and flow as a result of weather patterns and climatic variability [1]. When water becomes unavailable for extended periods of time, organisms must undergo adaptive changes to survive [2,3] and these shifts can lead to altered ecosystem function and dynamics [4]. As a potential example of this, recent research has shown that periods of drought substantially impact the composition and activity of plant root-associated bacterial communities in a pattern that is strikingly conserved across host species and sites [5^{**},6^{**},7^{**},8^{**},9^{**}]. While the underlying causes of this phenomenon remain largely unresolved, data from these early studies may offer hints at molecular mechanisms that

are involved. Here we will explore several intriguing features of the drought-induced restructuring of the bacterial root microbiome, and present potential links to plant metabolism at play in this process. We will discuss briefly the potential for the observed drought-enriched lineages to benefit their hosts, and conclude with a discussion of possible methods for manipulating this enrichment phenomenon for improved agricultural productivity.

Drought driven differential development of the root microbiome

Collectively, the suite of recent research that demonstrates drought's impact on the bacterial root microbiome helps illustrate three interesting properties of the observed restructuring [6^{**},7^{**},8^{**},9^{**},10]. First, this enrichment is highly conserved across many different plant hosts and ecosystems (Figure 1a), including monocots and dicot plant species, as well as native ecosystems, agricultural fields, and lab-based experimental systems [5^{**},6^{**},7^{**},8^{**},9^{**}]. Second, unlike some other environmentally driven shifts in the microbiome [11], the pattern of compositional shifts that drought provokes exhibits strong phylogenetic signal, with entire phyla of bacteria responding roughly in unison [5^{**},7^{**},8^{**},9^{**},12]. The predominant feature of this pattern is a near universal enrichment of monoderm (or Gram positive) bacteria, and a depletion of most diderm (or Gram negative) lineages (Figure 1b). Lastly, the observed shifts are greatest within the plant root, intermediate within the rhizosphere and least in the surrounding soil [5^{**},6^{**},8^{**}]. Monoderms are well known to be more tolerant of desiccation than diderms within the soil environment [13], due to their thicker cell walls and the ability of some monoderms to sporulate [1]. However, the observation that monoderm enrichment is greatest in the plant-associated fraction suggests that the enrichment described here is driven at least in part by an interaction within the plant root rather than solely by the monoderm's ability to withstand dry environments. In support of this, comparative analyses of drought-induced changes in bacterial composition in bare soils and soils containing vegetation found significant shifts in community composition by irrigation treatment in vegetated soils, but no such shifts in bare soils, suggesting that primary responses of soil bacterial communities were mediated through responses to the plant community, rather than direct response to changes in abiotic conditions [12]. Taken together, these properties suggest that enrichment of monoderms within the root system during drought is likely an ancient and ubiquitous phenomenon and point to an underlying cause that is

Figure 1



(a) Drought induces a shift in root microbiome composition that is conserved across many plant species, and ecosystems. (b) This shift is characterized by a near universal enrichment in monoderm lineages that increases as drought progresses, with a corresponding depletion in diderm lineages. At the end of drought treatment, the root microbiome has been shown to be capable of rapidly returning to a diderm-dominated state. The shades of red and blue within the diagram represent distinct taxonomic lineages belonging to monoderm or diderm groups.

controlled by plant and microbial traits that evolved deep within the tree of life.

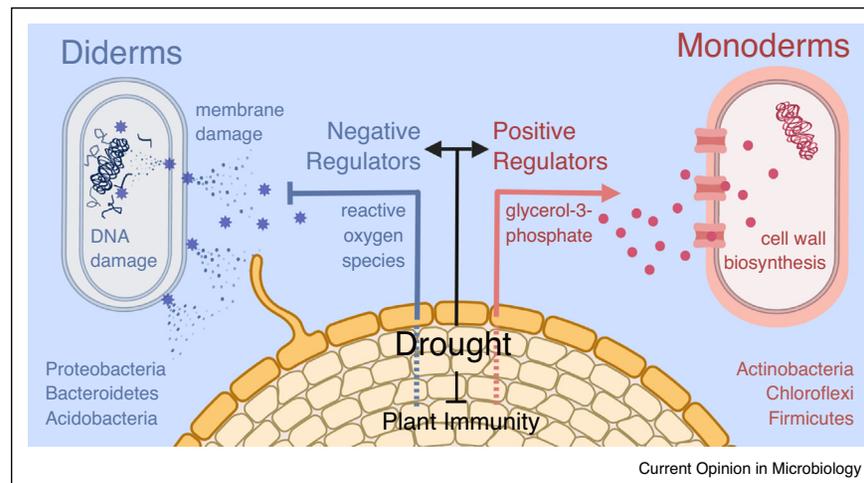
Three additional features of the observed monoderm enrichment patterns offer clues as to the identity of these underlying plant and microbial traits. First, rewatering of drought stressed roots allows for a return to a normal pattern of microbiome development (Figure 1b). This resilience in bacterial composition towards a state typical of watered conditions can occur within one to two weeks [8^{**}], which suggests that the underlying molecular causes

of this enrichment should also respond quickly to the rewatering event. It has been suggested that such mechanisms might be linked to plant metabolism, which can shift rapidly [14], rather than slow responding phenotypic traits, like changes in root architecture or growth habit [15]. In support of this hypothesis, a growing body of evidence suggests that plant-produced metabolites have the ability to significantly shape microbiome composition and activity [16^{**},17,18].

A second clue as to the traits governing these patterns can be found in lineages that represent exceptions to the overall trend of monoderm enrichment. Monoderm bacterial lineages differ from diderms in that they have only a single lipid membrane and have as their outer surface a thick peptidoglycan cell wall [19,20]. Several taxa within monoderms and diderms that have atypical patterns of enrichment or depletion as compared to close relatives are reported to have unusual cell wall architecture based on a survey of previous studies, such as alterations in peptidoglycan structure or the presence of additional cell wall layers [13]. Collectively, the evidence described above suggests that enrichment is driven in part by properties of the bacterial cell wall, and may be linked to shifts in plant metabolism.

A third and final clue as to the traits that drive the observed enrichment may be found in an exploration of shifts in relative and absolute abundance patterns. The observed relative enrichment in monoderm lineages during drought stress could in fact be driven either by increases in their absolute abundance, by decreases in the absolute abundance of diderm taxa, or a combination of both. Interestingly, measurements of absolute changes in monoderm abundance within drought-stressed roots have produced contradictory results, depending on the study [5^{**},8^{**},21]. During mild drought treatments, monoderms have been observed to increase in both relative and absolute abundance in field based experiments [5^{**}], and individual monoderms grown in lab-based mono-association with sorghum have been shown to increase in absolute abundance during drought as well [8^{**}]. However, during a more severe drought, all bacteria were observed to decrease in absolute abundance, though diderm lineages were more negatively impacted than monoderm lineages [8^{**}]. It has been hypothesized [8^{**}] that this inconsistency may be due to the cumulative action of both positive and negative plant-produced regulators of microbial growth (Figure 2), resulting in a multi-tier selection process that changes dynamically with time or drought severity. In this example of 'carrot and stick' manipulation of the root microbiome [22], drought-induced shifts in plant metabolism within the root produce both factors that stimulate monoderm growth, and factors which lead to decreased abundance of the entire bacterial population, perhaps with greater effect on diderm lineages.

Figure 2



Drought provokes changes in plant metabolism that may positively and negatively impact bacterial growth within the root. Glycerol-3-phosphate production by the plant, and uptake by monoderms, may offer a competitive growth advantage of drought-enriched lineages. Oxidative stress induced by ROS production in the plant may generally suppress bacterial growth, with greater negative impact on diderms. Drought-induced repression of immune response may be tied to ROS, G3P, and overall enrichment processes.

Molecular mechanisms at play during monoderm enrichment

Among classes of compounds that could promote monoderm growth, plant-produced carbohydrates and amino acids are strong candidates. They are well known components of root exudates and have been shown to support the growth of rhizobacteria [17]. Additionally, recent work in plant-associated microbiomes has identified correlations between the abundance of monoderm lineages (Actinobacteria, Chloroflexi, and Firmicutes) and specific amino sugars and sugar alcohols, and shown that diderm lineages were correlated with a distinct set of compounds, including polysaccharides and glycoside hydrolases [23]. Additionally, metabolomics of the drought stressed root has revealed marked increases in the production of many carbohydrates, including xylose and glucose, and amino acids, such as proline, threonine and asparagine [8^{**}]. Metatranscriptome analysis of the corresponding drought-stressed rhizosphere has revealed increases in the activity of bacterial transporters of many of these same compounds [8^{**}]. One metabolite of particular interest is the glycolysis intermediate glycerol-3-phosphate (G3P); ABC transporters of G3P are among the most upregulated monoderm gene products in the drought-stressed rhizosphere, and sorghum roots have been shown to produce significantly more G3P during drought stress [8^{**}] (Figure 2). At present, whether G3P levels also increase in the roots of other drought stressed plants remains to be tested; however, it is interesting to note that bacteria can use G3P to produce teichoic acid, a precursor necessary for peptidoglycan biosynthesis and cell wall formation [24]. As a

consequence of their much thicker cell walls, monoderms likely have an increased metabolic demand for G3P [25], making plant produced G3P a comparatively more valuable resource for them. Collectively, these data suggest that drought—induced production of specific plant compounds and differential expression of correlated bacterial transporters may lead to competitive growth advantages for monoderms.

A distinct set of drought-induced factors may negatively impact bacterial growth. Certainly the decrease in available water within the soil and root is itself likely to reduce overall bacterial growth [26]. Another potential negative regulator of microbial growth lies in reactive oxygen species (ROS). ROS can be produced at high levels within plant tissue during periods of drought and may serve as a part of a systemic stress signaling mechanism [27,28] (Figure 2), although the specific role of ROS in stress response is tissue and ROS-species specific, and much better understood within the context of leaf biology than root biology [29]. It has been observed in drought-treated maize that ROS are produced at increased levels within the root apoplast, the intercellular space where most bacterial endophytes reside [30]. Recently, it has been demonstrated that monoderm and diderm lineages respond differently to ROS stress, with ROS treatment leading to a greater decrease in cellular fitness in diderms, likely due to lipid peroxidation of their outer membrane [31]. Additionally, ROS have a very short half-life, on the order of milliseconds [32], and upon rewatering ROS activity and presence within the root can be expected to decrease rapidly [33]. Collectively, these characteristics

of ROS induction under drought fit the profile of a potential drought-induced negative regulator of bacterial fitness that could preferentially lead to monoderm enrichment.

It is worth noting that drought-induced changes in plant immunity may also play a role in shaping bacterial community structure. Plants regulate immunity in part through the activity of the phytohormone, salicylic acid (SA). The drought-induced phytohormone ABA has recently been shown to act antagonistically to SA-mediated immune signaling [34,35], and plants exposed to abiotic stress often exhibit reduced immune function [11,36,37] (Figure 2). SA has also been shown to play a significant role in shaping plant microbiome composition [38], and it stands to reason that compromised immune function that results from response to drought stress may impact root microbiome composition. In accordance with this, recent work has shown that in the phyllosphere, molecular components that balance host abiotic and biotic stress responses play a key role in establishing bacterial communities that reside there [39]. Indeed, it has been suggested that the fine-tuning of immunity may represent a key mechanism employed by plants for manipulating the microbiome in response to various environmental stresses [11,40**]. Interestingly, recent connections have been made between leaf immune response and a systemic stress signaling module that involves both G3P and ROS [41**,42]. However, whether similar links exist in the context of root biology, and what relationships they have with abiotic stress remain to be seen. Taken together, the above results suggest the intriguing possibility that the observed shifts in bacterial community composition under drought may be tied to changes in immune response, or a related stress-signaling network, within the host.

Consequences for crop fitness

Given the importance of the microbiome for plant health, it is reasonable to hypothesize that the large restructuring of the bacterial root microbiome under drought stress may have a significant impact on host fitness. Indeed, two recent studies have found evidence that the monoderm genus *Streptomyces*, which is enriched within the root under drought to exceptionally high levels, is associated with improved fitness under drought stress. Fitzpatrick *et al.* observed a correlation between levels of *Streptomyces* colonization within the roots of 30 angiosperm species and overall drought tolerance as measured by plant biomass [9**]. Additionally, colonization of gnotobiotically grown sorghum seedlings with two different *Streptomyces* isolates resulted in improved root biomass, but only under drought conditions [8**]. Other work has found that inoculation with a broad collection of soil-borne microbes has the ability to improve plant performance under drought, but not control conditions [40**]. These results suggest that manipulating the root microbiome could be used to further improve crop fitness under drought. However, it is important to note that plant fitness is

driven not only by bacteria in the root microbiome, but also by fungi and other eukaryotic microorganisms, and understanding root microbiome dynamics benefits from considering cross kingdom interactions [43,44]. Though several studies have shown that bacterial communities may be more sensitive to drought stress than fungal communities [45], given their importance for plant health, future work aimed at understanding drought's impact on the root microbiome and host fitness would do well to expand its experimental scope to include eukaryotic community members.

The concept of using microbial products, or biologicals, for improving crop fitness under abiotic stress has been growing in popularity, though progress in implementation has been slowed by fundamental challenges. One such a challenge is that persistence of biological amendments within the agroecosystem is often low, even over short developmental time spans [46,47]. In the context of drought, this may in part be due to the fact that many biologicals which have been demonstrated to benefit the host under controlled experimental conditions [48–50] represent taxa which are now known to likely be depleted within the root microbiome under drought stress [5**,6**,8**]. Future efforts to develop drought-tolerance inducing biologicals could avoid this pitfall by focusing screening efforts on monoderm lineages, which increase to high abundance and activity during drought stress and may be easily coated on a seed in spore form.

A likely additional cause of low persistence is that application of biologicals typically represents an introduction of foreign microbes into established microbial ecosystems. Research has demonstrated that organisms that have co-evolved together within an environment are more well-suited to survive and cope in that environment [51], as they consist of member organisms that, together, are more robust to environmental challenges [52]. Future work could circumvent this central issue by focusing on adding simplified synthetic communities of organisms that work well together to support stable microbiome establishment and persistence and desired phenotypic outcomes [53]. Alternatively, it may be feasible to modulate existing community structure within the native microbial ecosystem rather than on introducing foreign microbes. Towards this end, alteration of the microbiome structure through targeted metagenome editing with CRISPR/Cas9 represents an intriguing option; however, methods of CRISPR delivery, targeting and integration will need to be developed and validated [52]. As an alternative, provoking changes in plant metabolism could allow for indirect control over microbiome structure, without the need for inoculation. As suggested by the research described above, many simple drought induced compounds, including sugars and amino acids, may be partially responsible for monoderm enrichment [8**,23], and direct application of these compounds or use of hosts

engineered with inducible delivery systems for these metabolites, could allow for programmable enrichment at the onset of, or even prior, to drought stress.

Conclusion

The primary purpose of the plant root is the uptake of water and nutrients from the surrounding soil. When water becomes scarce, the root system must adapt in order for the plant to survive. This adaptation can involve many changes, including altered development, shifts in metabolism, and, we know now, a restructuring of the root microbiome. As plant fitness is interconnected with the composition and activity of the phytobiome [54–56], we can expect that the strong and conserved restructuring of the root microbiome under drought stress may have profound consequences for host health. For this reason, an improved understanding of the causes and consequences of the drought-induced shifts in the root associated microbial landscape has the potential to help guide and inform efforts to improve crop fitness in the face of increasing incidence and severity of drought stress that faces agroecosystems in the coming century [57–59].

Conflict of interest statement

Nothing declared.

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- Presents evidence that molecular mechanisms that guide plant regulation of biotic and abiotic stress response are intimately tied to microbiome assembly or maintenance. Establishes additional link between plant immunity and modulation of microbiome structure.