



Trees harness the power of microbes to survive climate change

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Microorganisms are the most abundant and diverse taxa on Earth. They have the ability to tolerate extreme environments, catalyze a range of metabolic functions, and rapidly evolve in response to changing environmental conditions. Imagine if plants and animals could harness these powers. In fact, microorganisms confer numerous benefits to plants and animals. For example, microorganisms in the mammalian gut improve nutrition, reduce susceptibility to disease, and even alter host behavior (1). Some of the most complex microbiomes are found in soils, where they are responsible for nutrient cycling, crop yield, and carbon sequestration (2). In some cases, soil microbes can even rescue plants from the negative consequences of climate change (3). If plants and animals can build associations with specific microbial members that maximize benefits, then harnessing microbial powers may provide rapid and efficient solutions to the challenges resulting from global change.

In PNAS, Gehring et al. (4) show that the relationship between soil microbial communities and plants is not a fortunate coincidence. Instead, some pinyon pine genotypes form associations with different belowground ectomycorrhizal fungal (EMF) communities that help them contend with drought. These EMF communities were responsible for the observed difference in drought tolerance between host tree genotypes. Because these microbial communities are, at least partially, under plant genetic control, EMF community composition is an extended phenotype of the host tree and potentially a mode of adaptation to the increased drought stress pinyon pines face in a changing climate. Given the vast array of biogeochemical and metabolic functions in the microbial arsenal, if similarly tight linkages occur between diverse soil bacterial and fungal communities and host plant genotypes, then host plants may possess a powerful tactic for adapting to environmental change.

Gehring et al. (4) provide important advances for the idea that host-associated microbial communities may underlie adaptation (5). They piece together evidence showing that the pinyon pine genotypes

differ in their EMF microbial associates (even when they are grown in the same soil), and that these divergent EMF communities influence host performance and fitness in response to drought. Such findings support the view that plant-associated microbiomes represent a heritable extended phenotype of the host genome, that microbial communities influence fitness, and that the host traits controlling these associations can serve as adaptations to changing environments (Fig. 1). Although genetically based differences in plant colonization by microbial partners are well known in other symbioses (e.g., refs. 6, 7), rarely are connections between specific plant-controlled symbiotic associations and fitness made. This critical link is necessary to show that these associations are adaptive. Gehring et al. (4) establish this link, between host-determined EMF communities and host fitness variation, by carefully building evidence from a combination of long-term observational field studies, manipulative greenhouse studies, and microbial community sequencing. They characterize EMF communities associated with drought-tolerant and drought-sensitive trees in both the field and greenhouse, while demonstrating how those microbial communities influence tree fitness responses to drought.

While the work of Gehring et al. (4) would be impressive in any system, it is especially noteworthy because they work on a dominant and important tree species. Furthermore, the patterns observed in manipulative greenhouse experiments were bolstered by reanalysis of field observations of tree growth and soil microbial community responses to a 10-y drought, demonstrating that the fitness effects observed in controlled manipulative greenhouse experiments play out in a more complex natural setting. Sequencing allowed Gehring et al. (4) to provide convincing evidence that the observed differences in plant drought tolerance were driven by the capacity of plant genotypes to condition different EMF communities.

The mutualistic association between plants and EMF communities is an ancient symbiosis in which

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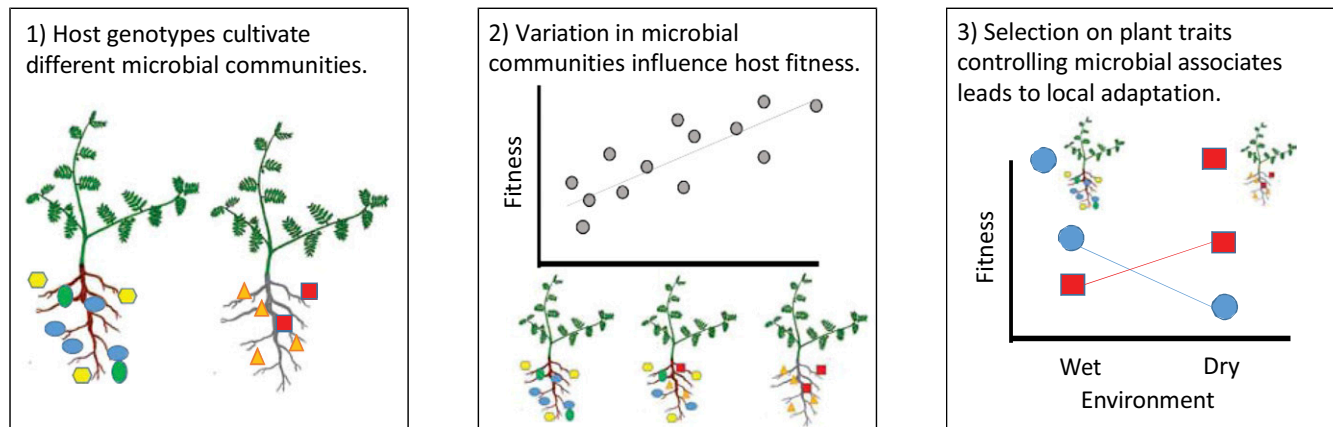


Fig. 1. Diverse belowground microbial communities can facilitate host adaptation if there is intraspecific genetic variation in host traits that mediate interactions with microbes and influence microbial community assembly (i.e., if the microbial community is a heritable extended phenotype of the host plant) (panel 1) and if host genotypes differ in fitness because microbial communities differentially influence host fitness (i.e., if the host traits controlling interactions with microbes are under selection) (panel 2). Panel 2 represents a traditional selection gradient analysis, where the trait of interest is the microbial community supported by the host (i.e., microbial community composition is an extended phenotype of the host). If traits mediating interactions with microbes are the key adaptation, then the fitness–host relationship shown in panel 2 will only be apparent in the presence of microbes. In sterilized conditions, host fitness will not be correlated with the microbial communities they are known to associate with. As a result of this microbe-mediated selection, a classic pattern of local adaptation should result when hosts are grown in association with microbes (panel 3), but no pattern of local adaptation will be observed when hosts are grown under sterile conditions. Illustrations courtesy of S. Magnoli.

hosts provide fixed carbon (from photosynthesis) to their root symbionts in exchange for increased nutrient acquisition via the fungus. However, EMF species can provide other benefits (e.g., stress tolerance) and can vary widely in the levels of host benefits provided (8). Gehring et al. (4) found that drought-tolerant genotypes were colonized by EMF species in the genus *Geospora* at much higher rates. Indeed, even drought-intolerant individuals that had higher colonization by *Geospora* showed higher drought tolerance compared with other drought-intolerant individuals that failed to form associations with *Geospora*. In the absence of EMF species (when soil was sterile), differences between tree genotypes in drought tolerance disappeared.

Since Darwin, evolutionary biologists and ecologists have fixated on adaptations. Here, the adaptation is not a spectacular morphological innovation; rather, it is a cryptic difference in how plants associate with tiny, underground fungi on their roots. Several things remain a mystery, including whether the underlying plant traits controlling these adaptive interactions with microbes are chemical, morphological, or even phenological in nature, although one might hypothesize that the genes and chemical signaling traits underlying interactions with mycorrhizae are involved. Similarly, what is the general importance of plant-associated soil microbes to drought adaptation? In the pinyon pine system, the fact that genotypic variation in drought tolerance was only observed in the presence of microbes suggests that the ability of a plant to associate with a specific microbial community was the primary, if not sole, driver of drought tolerance. In other systems, however, are microbes equally important compared with other putative plant adaptations to drought, such as advanced flowering time, waxy and pubescent leaves, C4 and CAM (Crassulacean acid metabolism) photosynthetic pathways, and deep or tuberous roots?

Arguments have long been made that particular microbial symbioses such as mitochondria or ancient arbuscular mycorrhizae, represent key evolutionary innovations during the history of life, leading to the evolution of eukaryotes ~2 billion y ago and colonization of land by plants ~400 million y ago, respectively. Perhaps similar arguments will someday be made about the more nimble, diverse microbial populations that occupy every habitat and every organism on Earth. Studies such as the one by Gehring et al. (4) illustrate the potential evolutionary importance of plant symbionts such as EMF species. Given that plant genotypes also influence diverse soil bacterial and fungal communities that perform a plethora of metabolic and biogeochemical functions (9, 10), the adaptive potential of host traits underlying plant–microbe interactions could be extensive. Gehring et al. (4) also stimulate many new questions at the intersection of emerging fields in the biological sciences. For example, perhaps the wealth of knowledge on plant–microbe interactions at the biochemical level and, more recently, at the genomic level can someday inform our understanding of global change ecology and lead to better models of plant community responses to climate change. Perhaps the recognition that genotypes vary in their associations with aboveground and belowground microorganisms will change how we breed agronomic crops to feed the planet in the face of the global changes dominating the Anthropocene. Like the functions and capabilities performed by the vast diversity of microorganisms living belowground, the possibilities may be endless.

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