

MICROBIOME

Soil science comes to life

Plants may be getting a little help with their tolerance of drought and heat.

BY ROGER EAST

armers have long tried to improve the chemical and physical condition of their soils, seeking to make more nutrients available to their plants, to retain more moisture in the soil, and to ease the growth of plant roots. But they have typically ignored the role of the teeming diversity of fungi and bacteria in the soil.

Now, however, soil biologists are beginning to understand the significance of the interactions at work in the microbiome surrounding plants' root systems. Recent research has shown, for example, that major food crops can be made dramatically more stress tolerant by transplanting into them various microbiota, such as fungi or bacteria, that colonize other species. There is a clear parallel with medical science, where the myriad microorganisms on our skin and in our gut are now recognized as crucial mediators of a whole range of bodily responses — an understanding that has profoundly changed the way we think about human health.

In agriculture, the drive to eliminate pathogens has encouraged a bazooka approach to the soil microbiome with the widespread use of biocides and fungicides. But the role of the microbiome is too varied and complex for this to be sustainable. "We are standing on a treasure of beneficial microbes, each of them contributing a little bit to plant yield," says Alexandre Jousset, a microbiologist at the University of Göttingen, Germany. "Understanding how these diverse communities help plants to resist adverse situations will open new doors to developing sustainable practices, calling up microbial services that are sleeping in virtually any soil."

STRESS RELIEF

One of the best known of these microbial services involves mycorrhizal fungi, which colonize plant roots and help them penetrate the soil. In the United Kingdom, for instance, the Royal Horticultural Society has approved a mycorrhizal product marketed as Rootgrow, which helps seedlings get established. As the fungi colonize the seedlings' root systems, they send out networks of their own underground filaments, known as hyphae, to cre-

ate what are effectively secondary root systems, improving the plants' access to moisture and nutrients. This is a symbiotic relationship as the

• NATURE.COM More research on this fascinating symbiosis here: go.nature.com/awj6f9 fungi depend on the plants' photosynthesis to deliver the sugars they need to grow.

Root extension is not the only service offered by mycorrhizal fungi. Glomalin, a glycoprotein that the fungi secrete to coat their hyphae, can promote the agglomeration of soil particles, thereby improving moisture retention. But the soil microbiome can do more than enhance basic plant biology — it can alter more nuanced traits too.

Microbiologist Rusty Rodriguez has coined the term 'symbiogenics', or symbiosis-altered genetic expression, to account for the drought tolerance displayed by plants when colonized by certain microorganisms. While working for the US Geological Survey (USGS) in 2002, he found that endophytes (symbionts that reside inside plant tissues) of a particular fungus were present throughout the Dichanthelium lanuginosum (panic grass) plants that grow around hot springs. Plants grown from seed with these endophytes removed lacked their parent plants' heat-tolerant traits - but regained them when the fungi were reintroduced. Rodriguez surmised that the capacity to withstand heat stress was not a genetic adaptation of the plant itself, but rather a characteristic that was expressed only in partnership with the fungus.

This hypothesis was corroborated years later when Rodriguez and colleagues used spores of a fungus from salt-tolerant dune grass plants to colonize rice plants and seeds¹. They saw that the plants' water needs were reduced by up to a half, accompanied by a dramatic increase in growth and seed production. Experiments on wheat produced similarly startling results: plants treated with the fungus from heat-loving panic grass could now tolerate temperatures of up to 70 °C while halving their water requirements.

"We are still trying to work out the mechanisms involved," says Rodriguez. The difficulty is that this is a new way of thinking about plants, as most agronomical research on heat and drought stress is done on plants devoid of a microbiome. "These symbiotic plants are very different. All the obvious things that are meant to happen in plants in such extreme conditions, such as taking up more water or producing certain chemicals, are just not happening."

What is clear, however, is the practical potential. In 2012, Rodriguez left the USGS to focus on his start-up company, Adaptive Symbiotic Technologies, based in Seattle, Washington, which makes agricultural plants symbiotic so they can withstand drought and heat. "All plants get colonized by fungi — they just aren't necessarily the right ones to achieve the results we are seeking," says Rodriguez. In an attempt to find the best fungus for each crop and location, field trials are underway in various parts of the United States to test wheat, maize, barley, rice and soybeans that were grown using seeds coated in fungal spores taken from heat- and salt-resistant plants.

For practical use in agriculture, however, some researchers doubt whether it will be possible to identify the right fungus for the job. One sceptic is molecular biologist Mary Lucero, who, like Rodriguez, has studied the effects of transferring organisms from the microbiome of one plant species to that of another. Her research with Jerry Barrow at New Mexico State University in Las Cruces found that tomatoes, chillies and grasses colonized with endophytes from two species of desert plant showed greater drought tolerance than those without the endophytes². Ultimately, however, Lucero concluded that individual transplants of microorganisms are not the best approach. "There are so many different microbes interacting that it makes a lot more sense to leverage the natural community rather than trying to create any transformation of our own," she says. Lucero is now studying how certain cover crops can encourage the development of a rich diversity of mycorrhizal fungi.

BACTERIAL BENEFITS

Fungal symbiosis is only part of the microbiome picture, however. Studies of bacterial interactions are uncovering further

dimensions. Daniele Daffonchio and colleagues at the University of Milan in Italy and Ain Shams University in Cairo, Egypt, are investigating the ability of capsicum plants to flourish under drought conditions³. When these plants are short of water they develop an enriched population of plant growth-promoting bacteria (PGPBs), which are thought to be attracted to the abundance of nitrogen and other nutrients in the plants' root systems. These PGPBs in turn mediate their host's response to drought, helping to reduce water consumption while increasing metabolic functions. As a result, the plants have up to 40% more biomass and perform more efficient photosynthesis.



Mycorrhizal fungi (white) help plant roots (brown) absorb water and nutrients from the soil.

Daffonchio concludes that plants should not be considered in isolation as single organisms, but rather as meta-organisms - plant plus microbiome — because their symbiotic relationships affect the plant's expression of drought-adaptive genetic characteristics. Another 2013 study⁴ found that seedlings of Arabidopsis thaliana planted in soil previously exposed to A. thaliana grew more vigorously than control samples when faced with drought conditions. Examination of the soil around the roots found higher populations of bacteria from 41 genera, and the researchers concluded that it was the interaction with these bacteria that seemed to reduce the plants' defensive responses to abiotic stress. As well as their increased growth, the plants also exhibited lower expression of several drought-response marker genes. But this came with a price: a higher death rate from drought-related causes.

The right soil bacteria, it seems, could have important implications in an increasingly water-constrained world. "Strains that are capable of optimizing water use could enable savings of 5% of plants' overall requirements," says Daffonchio. The effects may be striking but, as with fungi, the mechanisms are not yet clear. "We don't know what the bacteria are doing to activate the pathways in the plant that reduce water consumption and increase growth," Daffonchio says.

FARMING FOR LIFE

Microorganisms can confer drought tolerance to plants but are themselves not immune to the effects of drought. The drying of the soil can disrupt the diversity of the microbiome and cause microbial biomass to fall by twothirds or more. Soil microorganisms will eventually return to their pre-stress population levels, but any crops planted in the meantime are vulnerable.

Farming techniques for mitigating drought might be as important for their effects on soil biology as for the way they alter its physical characteristics. Kristine Nichols, a soil microbiologist at the US Department of Agriculture in Mandan, North Dakota, thinks that maintaining the microbiome is an important aspect of the use of cover crops, whose benefits are more commonly explained in terms of soil structure, organic matter and chemical balance. By extending photosynthetic time, Nichols says, planting cover crops "makes more carbon available to mycorrhizal fungi for hyphal growth". Similarly, crop rotation, a technique used for centuries to improve the soil, also has a huge effect on microbial populations, and this may underlie the improved plant growth and drought resistance, says Philip Poole, a plant physiologist at the John Innes Centre in Norwich, UK. "We think of things as a triangle of soil structure, microbiome and plant roots, all interacting with one another," he says.

Another approach being encouraged is to minimize tillage. This technique, also known as conservation tillage, not only reduces moisture loss and excessive soil compaction, but also helps to increase microbial biodiversity below the soil surface. Taking this principle further, in zero-tillage farming, the crop residue is left in the field after harvesting and seeds are planted through it into the soil.

Zero tillage can reduce labour, fuel, irrigation and other costs, but it requires more active farm management. Such propositions may struggle to win acceptance, but the holistic view of agricultural ecosystems in which it is rooted is gaining ground. As paradoxical as it seems, soil biologists' growing focus on the microbial world is helping to promote a fresh look at farming on a much larger scale.

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