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Understanding and exploiting plant beneficial microbes

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After a century of incremental research, technological advances, coupled with a need for sustainable crop yield increases, have reinvigorated the study of beneficial plant–microbe interactions with attention focused on how microbiomes alter plant phenotypes. We review recent advances in plant microbiome research, and describe potential applications for increasing crop productivity. The phylogenetic diversity of plant microbiomes is increasingly well characterized, and their functional diversity is becoming more accessible. Large culture collections are available for controlled experimentation, with more to come. Genetic resources are being brought to bear on questions of microbiome function. We expect that microbial amendments of varying complexities will expose rules governing beneficial plant–microbe interactions contributing to plant growth promotion and disease resistance, enabling more sustainable agriculture.

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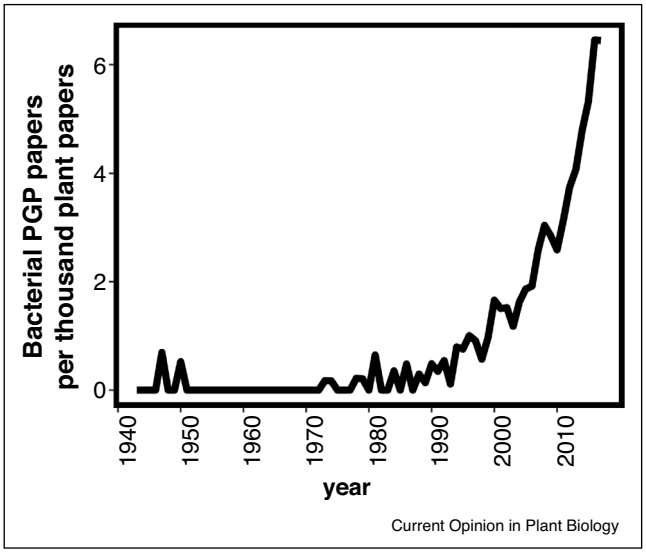
Introduction

The manipulation of soil microbiomes to optimize crop productivity is an ancient practice; records can be traced to ~300 BC [1]. It is interesting to note that although soil microbiomes are now touted as a cornerstone of the next green revolution [2•], the first commercial bioinoculant, 'nitrogin', was patented in 1896 [3], during the golden age of microbiology and preceding the Haber–Bosch process by 15 years. Currently, the Organic Materials Review Institute (OMRI) lists 174 products under the category of 'microbial inoculants' and 274 products under the category 'microbial products', either as crop fertilizers or as crop management tools. The number of publications associated with plant growth promoting (PGP) microbes, has been growing exponentially since the 1990s (Figure 1). Few, if any, of these are associated with mechanistic studies or modes of action; exceptions being biological nitrogen fixation by rhizobia on legumes [4], and auxin [5] or ACC-deaminase [6] -mediated phytostimulation. However, the lack of broad host ranges and variable field efficacy have sharply limited their widespread deployment. We therefore need to forge a deeper understanding of (a) the mechanisms governing microbial invasion and persistence into standing heterogeneous communities in diverse locations, soils and hosts; and (b) the genetics, in both partners, that drives colonization and delivery of plant phenotypes by microbes. The advent of culture-independent microbial ecology, powered by development of high-throughput analytic technologies, has enabled increasingly systematic study of the plant-associated ecological context in which microbial inoculants could be applied; and of mechanisms of plant control over colonization by beneficial microbes. However, novel approaches are needed in order to bridge current gaps between plant-productivity phenotypes and understanding of the underlying mechanisms [7–9].

Screening of large isolate collections

The limited taxonomy of plant-associated microbes, compared with the vast diversity of soil microorganisms [9–11], suggests that plants are a highly selective microbial niche and thus that general rules may be inferred for plant colonization by microbes. Shotgun metagenomics to compare plant-associated microbiome functions can be used to search for plant colonization markers [12,13]; this can be complemented by read-binning and assembly of bacterial genomes from plant-associated environments [14]. However, metagenomic datasets from different rhizospheres exhibit little overlap in plant-enriched functions [13,15]. On the other hand, plant-associated microbiomes contain a relatively high cultivable fraction of microbes, particularly bacteria [16•,17–19]. It is therefore feasible in plant microbiome research to mitigate the limitations of culture independent methods by generating and studying taxonomically and functionally representative culture collections from plant-associated

Figure 1



The number of articles about bacterial plant growth promotion per year per thousand plant-related papers, found in the PubMed database, using the search term ((“plant development”[MeSH Terms] OR (“plant”[All Fields] AND “development”[All Fields]) OR “plant development”[All Fields] OR (“plant”[All Fields] AND “growth”[All Fields]) OR “plant growth”[All Fields]) AND promoting[All Fields] AND (“microbiology”[Subheading] OR “microbiology”[All Fields] OR “bacteria”[All Fields] OR “bacteria”[MeSH Terms])) OR ((“plant development”[MeSH Terms] OR (“plant”[All Fields] AND “development”[All Fields]) OR “plant development”[All Fields] OR (“plant”[All Fields] AND “growth”[All Fields]) OR “plant growth”[All Fields]) AND promoting[All Fields] AND rhizobacteria[All Fields]).

habitats. Returning to culture-dependent microbial surveys allows the construction of increasingly complex experimental ecology systems for understanding plant–microbe interactions, while providing material for the discovery of potential PGP inoculants. Large-scale isolation, genome sequencing and functional screening efforts are underway in both academic and industrial settings (http://news.monsanto.com/press-release/corporate/novozymes-and-monsanto-complete-closing-bioag-alliance). The definition of large scale, in fact, has changed rapidly from hundreds [16•] to tens of thousands [20] of strains. Recent plant-associated bacterial and fungal isolate collections (summarized in Table 1) are derived from sugarcane [20]; grapevine [21–23]; potato [24]; tomato [25]; eucalyptus [25]; rice [26,27]; ancient wheat ancestors [19]; lettuce [28]; Arabidopsis [16•,29]; poplar [29]; and from plants growing in an arsenic-contaminated soils [30•]. The increasing volume of isolate collections will tax existing repositories; yet the genomic diversity contained in the bacterial isolates that are being obtained is not nearing saturation [16•]. Mechanisms to curate, share and standardize metadata for strains from these collections are needed.

While ongoing attempts exist to screen isolates in the field (see Supplementary Table 1 summarizes of recent PGP experiments in laboratory and field settings), the most common approach is to utilize a pre-screening strategy to select candidate strains for further analysis. Pre-screening strategies include *in vitro* screening for known PGP-related activities such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase [31], phosphate solubilization [32], nitrogen fixation [33], or enhancement of plant immune system function [34,35•,36]. Of the 1151 bacterial strains screened in [21,22,27,29], 332 strains solubilized phosphate, 229 strains produced auxin; ACC deaminase activity was found in 85 of 729 strains and bacterial nitrogen fixation was measured in 54 of 229 strains. These screening methods, however, are more likely to confirm the known, rather than to discover novel mechanism of PGP. Furthermore, none of these traits are actually correlated with the magnitude of PGP. Thus the suite of PGP traits that are commonly tested does not predict plant-associated phenotypes, and suggests that untapped mechanisms await discovery.

Genome sequencing of strain collections (Figure 2) [16•,37•] might provide a richer screening tool for sets of PGP traits that could be readily detected in genomes [38]. For example, the presence of minimal *Nif* and full *Phn* gene cassettes and genes required for indole acetic acid (IAA) production corresponded to the respective phenotypes in *Paenibacillus polymixa* genomes, albeit at variable levels [39]. This indicates that identification of appropriate genomic markers and screening of genome collections might provide a faster and less labor-intensive alternative to physiological screening, while also providing the opportunity for the discovery of correlated and novel PGP-associated genes.

Ecological considerations for plant beneficial function of microbes in the field

Ultimately, beneficial phenotypes will need to be operative in the field. A successful microbial inoculant has to invade and persist in the context of indigenous microbes and local abiotic conditions in variable settings, and to establish a compatible interaction with the host that includes molecular détente with the plant immune system. Studies of successional dynamics of plant microbiota suggest that upon emergence, initial seed microbiomes rapidly give way to different, soil-derived communities that are still changing days following emergence [40]. Throughout the growing season, this soil-derived community undergoes continuous succession in both above-ground [41,42] and below-ground [43•] fractions of the plant. Thus, even if PGP inoculants colonize the plant initially, their persistence over time is not guaranteed. Measuring persistence of bacterial inoculants in soil poses technical difficulties, as the inoculant needs to be identified from within a complex community. Heterologous bacterial inoculants can persist in soil for