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PLANT-ASSOCIATED BACTERIA:
SURVEY, MOLECULAR PHYLOGENY,
GENOMICS AND RECENT ADVANCES

Abstract. Bacteria that associate with plants are diverse in the habitats they occupy, their phylogeny, and their effects on plant and environmental health. The spermosphere, rhizosphere, phyllosphere, vascular tissue and endophytic regions offer distinctive habitats for bacteria. The phylogenetic diversity of bacteria in these habitats extends across the Bacterial and Archaeal Domains; however, bacteria that are known phytosymbionts or phytopathogens are classified into only four Bacterial phyla, the Cyanobacteria, Proteobacteria, Firmicutes, and Actinobacteria. Most plant-associated prokaryotes are commensals that have no detectable effect on plant growth or physiology; these are found primarily on plant surfaces. Mutualistic bacteria include the legume symbionts, Frankia, and cyanobacterial symbionts, which form nitrogen-fixing symbioses, as well as associative nitrogen-fixing bacteria and plant growth-promoting rhizobacteria, which can enhance plant growth directly by increasing nutrient availability or producing plant growth-enhancing products, and indirectly by biologically controlling plant diseases. Phytopathogenic bacteria are diverse in the symptoms they induce as well as in their invasion strategies, mechanisms of pathogenesis, culturability, and even genome structure and fluidity. Other organisms that can detrimentally influence plant health are the ice nucleating bacteria, bacteria that overproduce plant growth regulators, and the deleterious rhizobacteria, which can help control weeds. Effects of plant-associated bacteria on environmental health include contributions to the remediation of soilborne pollutants, the decomposition of organic matter, and soil aggregation. Recent advances in genomic sequencing, functional genomics, and microbial ecology are dramatically changing our research approaches to these organisms and the questions we can address about their biology and their interactions with plants.

1. INTRODUCTION

Bacteria that associate with plants are diverse in their ability to affect plant health, their genotypic and phenotypic characteristics, and their phylogeny. These bacteria are typically members of complex microbial communities, with only a few establishing pure clonal populations within a plant. Although the majority of research on plant-associated bacteria has focused on phytopathogens and diazotrophic (nitrogen-fixing) phytosymbionts, interest in the diversity of organisms associated with plants has increased as the tools to assess diversity have advanced. It is clear that many plant-associated microbes, even those that comprise only a small proportion of a community, can have functions that are of agricultural or environmental importance. Technical advances in microbial ecology and genomics have been paralleled by advances in our understanding of the structure and dynamics of these microbial communities and in the molecular basis of plant-microbe and microbe-microbe interactions. The aim of this book is to provide comprehensive coverage of all types of bacteria that are found in association with plants.
Prokaryotes, and primarily members of the Bacterial Domain, are the numerically dominant component of most microbial communities on plants. These prokaryotes, collectively referred to as bacteria, can attain densities as high as $10^9$ cells per gram of plant tissue of roots based on culturing, and $10^{10}$ cells per g based on cultivation-independent methods. The eukaryotic microflora can include filamentous fungi, yeasts, algae, protozoa, and nematodes, but usually at densities many orders of magnitude lower than the prokaryotes. For example, the rhizosphere may contain, in culturable numbers per gram of root, $10^5$-$10^7$ non-actinomycetous bacteria, $10^7$ actinomycetes, $10^5$-$10^6$ fungi, $10^3$ algae and $10^2$-$10^3$ protozoa. Bacteriophage and viruses can also be members of these communities and, although the populations in the rhizosphere have not been extensively examined, they have been found at densities as high as $10^8$ to $10^9$ per gram of soil (Ashelford et al., 2003; Williamson et al., 2005). Although many interesting interactions occur within these communities, and some are being exploited for the control of plant pathogens, this chapter is focused exclusively on the associations between bacteria and their plant hosts.

2. Plants as habitats for bacteria

Plants offer a wide range of habitats that support microbial growth. These include sites that are moist and rich in nutrients, and thus ideal for fostering bacterial growth, as well as sites that are nutrient-poor or exposed to stressful environmental conditions. The surfaces of seeds, roots, leaves, and fruits often harbor large, diverse bacterial communities, whereas blossoms, stems, vascular tissue, and the intercellular spaces within plant tissues often are free of microorganisms or support only limited bacterial communities.

2.1. The spermosphere

The spermosphere is the zone that is influenced by a seed; it often extends 1 to 10 mm from the seed surface. Nutrients that support microorganisms are released when the seed imbibes, with nutrient release being greatest from the embryo end, i.e., the end closest to the emerging radicle, and from seeds that are cracked or damaged. Bacteria that establish populations on seeds can colonize roots as they emerge.

2.1.2. The rhizosphere

The rhizosphere is the zone that is influenced by the root, although experimentally it is often defined as the soil adhering to the root. Root growth changes the physical and chemical properties of the soil, including the mineral and organic content, the