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From yogurt to yield: Potential applications of lactic acid bacteria in plant production

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ABSTRACT

Ferments containing lactic acid bacteria (LAB) have been used for decades in agricultural systems to improve soils, control disease and promote plant growth, however, the functional roles of LAB in the phytomicrobiome have yet to be discovered. An understanding of the symbiotic relationship between plants and LAB could be exploited to improve agricultural plant production.

Scientific investigations to validate plant growth promoting properties of LAB are increasing in number and scope. LAB isolated from diverse sources have been shown to be effective biofertilizers, biocontrol agents, biostimulants. As biofertilizers, LAB can improve nutrient availability from compost and other organic material. In fermented food, LAB has served as an effective biocontrol agent; recently LAB have been shown to be effective in the control of a wide variety of fungal and bacterial phytopathogens. As biostimulants, LAB can directly promote plant growth or seed germination, as well as alleviating various abiotic stresses.

In this review, we discuss the history and ecology of plants and LAB, appraise the available information on the use of LAB in improving plant production, and consider the limitations and potential new directions for the use of LAB in plant agriculture.

1. Introduction

Recent advances in plant-microbe interaction research have drawn attention to the importance of microbial communities in promoting plant health and resilience (Smith et al., 2015a; b). Engineering the phytomicrobiome to promote plant growth is a promising strategy for maintaining crop production in the context of a changing climate and growing population. Broadly, plant growth promoting microorganisms (PGPM) promote plant growth by improving nutrient acquisition, acting as biocontrol agents (BCAs), improving the ability of the host plant to withstand biotic and abiotic stress, or by producing compounds that directly stimulate plant growth. Many PGPM promote plant growth through multiple mechanisms simultaneously (Avis et al., 2008).

Plants in nature interact with a diversity of beneficial, pathogenic, and benign microorganisms. Most PGPM research has focused on only a few groups of common symbiotic rhizosphere microorganisms: rhizobia, *Bacillus*, *Pseudomonas* and mycorrhizal fungi (Vessey, 2003). However, the functional roles of other groups of potential PGPMs, including lactic acid bacteria (LAB), have yet to be explored. The as-yet uncharacterized phytomicrobiome is an untapped genetic and metabolic resource that may offer a host of biochemical solutions to pressing agricultural issues.

LAB are ubiquitous members of many plant microbiomes, but little is known about functional interactions between the LAB and their hosts. The gap in our knowledge about LAB-plant interactions stands in contrast to our depth and breadth of knowledge of LAB in food processing. In this review, we appraise the available information on the use of LAB in improving plant production in the context of historical uses of LAB in agriculture and food preservation, and discuss the limitations and potential new directions for the use of LAB in plant agriculture.

LAB are gram positive, facultative anaerobic bacteria that typically reside in substrates rich in carbohydrates, which they ferment into organic acids. The ability of LAB to produce organic acids and other antimicrobial substances has made them indispensable in the preservation of plant and animal-based foods as diverse as sauerkraut, cheese, sausage, sourdough bread and animal silage (de Vuyst and Vandamme, 1994). Furthermore, the efficiency with

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which LAB convert carbohydrates into organic acids has prompted interest in industrial applications of LAB bioreactors used to produce organic acids; especially lactic acid, an important precursor for biodegradable plastics (Konings et al., 2000). The benefits of *Lactobacillus* strains on human health also make them valuable probiotic (Naidu et al., 1999).

The widespread use of LAB in food processing has generated a great deal of knowledge about their physiology and the bioactive compounds they produce (Garsa et al., 2014; de Vuyst and Vandamme, 1994). This usage has also resulted in the designation of LAB as generally regarded as safe (GRAS) and would pose no risks for applications in edible crop production, exempting it from costly and time consuming regulatory approval processes. (Lutz et al., 2012). Moreover, the combined empirical evidence from agriculture paired with a growing body of scientific evidence makes a convincing case for LAB as a new class of PGPM. There is great potential to use LAB as biofertilizers, biocontrol agents and biostimulants to aid in producing food (Fig. 1).

2. History of LAB in agriculture

Proponents of holistic, ecologically-based agricultural systems have long valued LAB, and especially *Lactobacillus* as an agricultural input. *Lactobacillus* is ubiquitous on plants and proliferates quickly when plant tissues are damaged and carbohydrate-rich cell contents are released. The ease of culturing wild lactobacilli without the use of laboratory equipment or microbiological expertise, paired with its ability to preserve, and even improve, the nutritional quality and flavor of foods, have contributed to the widespread use of these microbes by farmers and the general public (Katz, 2008, 2012).

Beginning in the 1930s, when the use of mechanized farm equipment and chemical pesticides and fertilizers was becoming more prevalent, (Martin and Sauerborn, 2013), many alternative agricultural movements, that looked to preindustrial farming practices, were initiated around the world. Many of these alternative agricultural movements adopted LAB, and especially *Lactobacillus,* as an indispensable component of sustainable agriculture, to control pests, condition soils, and stimulate plant growth (Higa, 1991, 2001; Somers et al., 2007; Paulsen et al., 2009).

3. Plant-LAB ecology

To harness the benefits of LAB for improved agricultural production, we must first understand the ecological relationship between plants and LAB, including the ecological niches LAB fill in nature. Plants interact with diverse communities of beneficial, benign, and pathogenic microorganisms in the environment and must be able to distinguish between members of these communities to optimize growth. If the plant-LAB relationship provides an advantage to the plant, this relationship can be promoted or manipulated to improve agricultural production.

Lactobacilli are found in the phyllosphere, endosphere and rhizosphere of many plants. Each of these niches provides distinct challenges to the growth of the LAB. In the phyllosphere, lactobacilli are exposed to a host of stresses including ultraviolet radiation, extremes in water availability, scarce nutrient availability and high redox potential (Mundt and Hammer, 1968; Müller and Seyfarth, 1997). LAB also live inside plants as endophytes, and can survive in seeds (Minervini et al., 2015) and vegetative propagules (Leifert et al., 1994). *Lactobacillus* has been found living as an endophyte in diverse crop plants including sweet corn, cotton, (McInroy and Kloepper, 1991), sugar beet (Jacobs et al., 1985), strawberry fruit (de Melo Pereira et al., 2012) pepper (Shrestha et al., 2014), cucumber (Rzhevskaya et al., 2013), wheat seeds (Baffoni et al., 2015; Minervini et al., 2015) and *Lolium perenne* roots (Gaggìa et al., 2013). The ability of LAB to live in the endosphere of such a diversity of plants suggests an intimate relationship between plants and LAB.

The rhizosphere is defined as the fraction of soil under the direct biochemical influence of root exudates. Plants devote a significant proportion of photosynthetically fixed carbon to root exudates, which include sugars, signaling compounds, enzymes and other chemicals that alter the soil environment to select for particular microbial communities (Bais et al., 2006). This carbohydrate-rich environment would appear to be ideal for LAB, however, organic acids break down quickly in the rhizosphere (Jones, 1998); limiting the ability of LAB to acidify the rhizosphere to their advantage. Although this limitation prevents LAB from being a dominant bacterial group in most soils, diverse LAB strains have been isolated from rhizospheres (Chen et al., 2005; Yanagida et al., 2006; Shrestha et al., 2009a; Ekundayo, 2014). Research on the

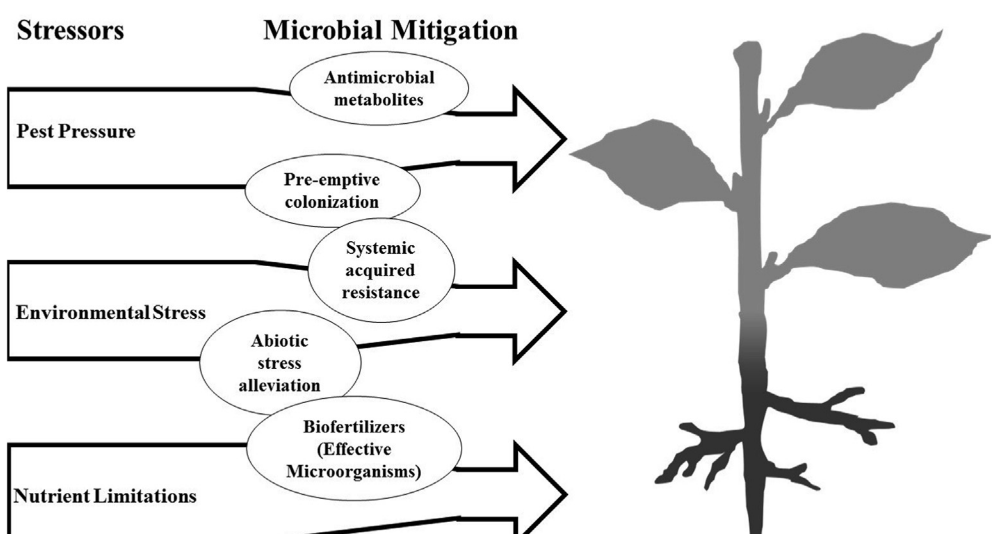

Fig. 1. Mechanisms by which lactic acid bacteria can mitigate stress to plants.