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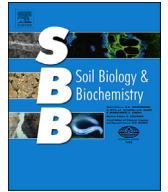**387** PUBLICATIONS   **8,851** CITATIONS

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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.

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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

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
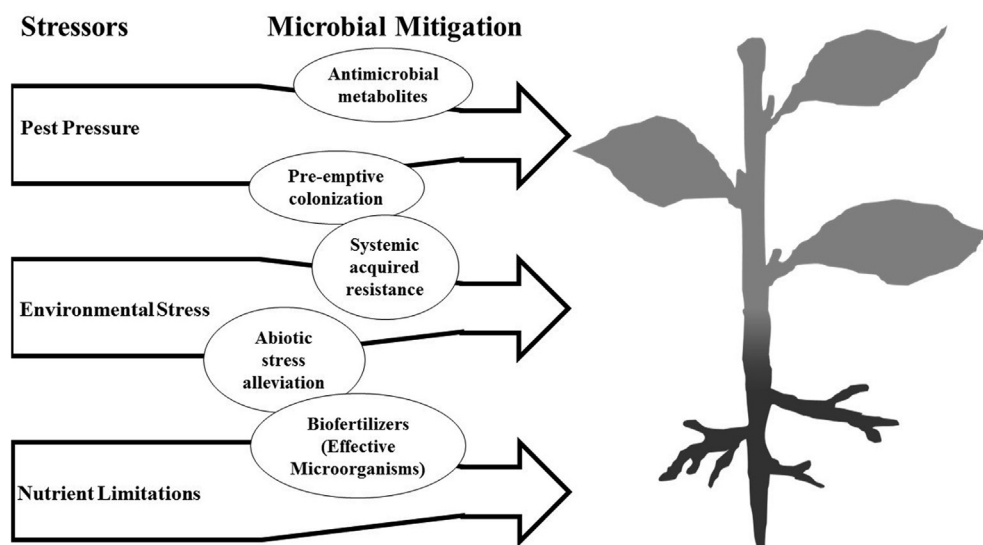

Fig. 1. Mechanisms by which lactic acid bacteria can mitigate stress to plants.

rhizosphere microbiome has shown that microbial communities in the rhizosphere are largely shaped by plant species and age, as well as environmental factors such as temperature and moisture (Grayston et al., 1998). For example, *L. lactis* subsp. *lactis* appears to be a constitutive member of the mulberry microbiome where it is commonly found in the rhizosphere, despite large geographic distances between plants (Chen et al., 2005).

While many soils do not appear to contain large numbers of LAB, they do contain a diversity of LAB, which produce a diverse suite of metabolites (Chen et al., 2005; Yanagida et al., 2006). LAB have been reported to be most numerous in carbon-rich soil environments, such as those under fruit trees or animal agriculture (Yanagida et al., 2005, 2006; Reyes-Escogido et al., 2010), however, a rich diversity of LAB has been isolated from the rhizospheres of olives and desert truffles as well as in desert soils (Fhoula et al., 2013).

Lactobacilli can survive and grow in dry environments with water potentials as low as 15 MPa (Focht and Martin, 1979; Skujinš, 1984) There are also many halotolorant LAB, as is demonstrated by the diversity of LAB in brined fermented foods. LAB often become dominant in mixed cultures by virtue of their ability to acidify their environment to a level that many other microbes cannot survive.

4. LAB as biofertilizers

LAB are one of the major microbial groups responsible for decomposing a variety of organic materials for use in agriculture; they are common in compost (Partanen et al., 2010), silage (MacDonald, 1981), and methogenic anaerobic digestion systems (Li et al., 2011). These waste processing systems generally use indigenous microbial populations, however there have been some attempts to improve these processes by inoculating waste materials with microbial consortia, typically containing LAB.

Effective Microorganisms (EM) consortia are composed of a consortium of yeast, mold fungi, LAB, photosynthetic bacteria, actinomycetes, and others (Higa, 1991). LAB generally becomes the most active and dominant group in mature ferments of EM consortia (Kyan et al., 1999). Analysis of three commercial EM products found that LAB were the most abundant microbial group in the consortia (Ahn et al., 2014).

Compost inoculated with EM have been shown to produce greater yields and increase nutrient uptake for wheat (Hu and Qi, 2010; Hussain et al., 1999), soybean (Javaid and Mahmood, 2010), mung bean (Javaid and Bajwa, 2011) rice (Javaid, 2011) and cotton (Khaliq et al., 2006) than plants grown with non-inoculated composts. Increased productivity in crops treated with EM-inoculated composts versus untreated composts is likely due to hastened decomposition of organic compounds into plant available nutrients. LAB has been shown to solubilize phosphate (Shrestha et al., 2014; Giassi et al., 2016), likely through the production of organic acids. Three strains of LAB isolated from a sugarcane ferment can fix atmospheric nitrogen (Giassi et al., 2016). While LAB appear to have virtually no Fe requirement and have been thought to not produce siderophores (Pandey et al., 1994; Weinberg, 1997), Shrestha et al. (2014) reported three plant growth promoting strains of *Lactobacillus* produced siderophores.

While there have been promising results in many trials with EM, the efficacy of EM has yet to be determined. Many field trials where EM have improved crop yield have been conducted in tropical or subtropical regions, while most trials in temperate regions have not shown any benefit from EM applications (Mayer et al., 2010).

5. LAB as biocontrol

Concerns over the harmful effects many chemical pesticides have on the environment and human health have prompted a search for safer alternatives. Numerous microorganisms have been identified as safe and effective biocontrol agents (BCAs) for bacterial and fungal phytopathogens.

BCAs work through a variety of mechanisms (Compant et al., 2005). There are three known mechanisms by which LAB acts as a biocontrol agent; through the production of antimicrobial compounds (Kao and Frazer, 1966; Tramer, 1966; Trias et al., 2008), reactive oxygen species (Trias et al., 2008) and bacteriocins; by excluding pathogens by pre-emptively colonizing plant tissues vulnerable to infection (Visser and Holzapfel, 1992; Roselló et al., 2013), and by altering the plant immune response (Konappa et al., 2016).

LAB produce a diversity of antimicrobial compounds including antifungal diketopiperazines, hydroxy derivatives of fatty acids, 3-phenyllactate; antibacterial bacteriocins and bacteriocin-like compounds; and general antimicrobials such as organic acids, hydrogen peroxide, pyrrolidone-5-carboxylic acid, diacetyl and reuterin (β-OH-propionic aldehyde) (Stoyanova et al., 2012). It has been proposed that the major mechanism of foliar bacterial pathogen control by LAB is organic acid production (Visser and Holzapfel, 1992) however, with diversity of antimicrobial compounds produced by LAB in mind, it has also been argued that LAB barrage competitor microorganism with a variety of compounds with multiple modes of action (Gupta and Srivastava, 2014; Sangmanee and Hongpattarakere, 2014).

Aside from direct antagonism toward phytopathogens, LAB treatments can alter the response of plant to pathogens, thus improving their innate immunity. Such effect is called systemic acquired resistance (SAR). Hamed et al. (2011) suggested changes to the morphology of tomatoes treated with various *Lactobacillus* strains were evidence of an SAR response, leading to resistance to fungal pathogens. Supporting this theory, tomato seeds treated with *Lactobacillus paracasei* isolated from the tomato rhizosphere produced seedlings that were more resistant to infection by *Ralstonia solanacearum* due to differential expression of defense-related metabolites in treated seedlings (Konappa et al., 2016.

The ability of LAB to control bacterial and fungal phytopathogens of crop plants has been investigated (Table 1). Because, LAB are so ubiquitous in the phyllosphere, LAB were first evaluated as BCAs for foliar phytopathogens (Visser and Holzapfel, 1992), but have been evaluated as BCAs for a variety of bacterial and fungal phytopathogens.

Compost teas fermented with mixed cultures containing *Lactobacillus* have been effective against powdery mildew on a variety of cucurbits (DeBacco, 2011; Naidu et al., 2012). Other compost teas with undefined microbial communities have been effective biocontrols of numerous fungal pathogens (Scheuerell and Mahaffee, 2002; Martin, 2014). It is likely that many compost teas with undefined microbial populations contain a significant proportion of LAB (Ahn et al., 2014), which may have antipathogenic activity. Similarly, milk, whey and other dairy products have often been used as a natural control for powdery mildew (Medeiros et al., 2012) and have been applied to various cucurbits (Ferrandino and Smith, 2007; Bettiol et al., 2008; DeBacco, 2011), grape (Crisp et al., 2006) and greenhouse roses (Wurms et al., 2015). Milk fermented with *Lactobacillus* is an effective control for powdery mildew on melon (Bettiol and Astiarraga, 1998). Furthermore, even uninoculated milk applied to leaves is likely to ferment (Medeiros et al., 2012), leading to a proliferation of LAB and the associated antifungal activity.

6. Lactobacillus and stress amelioration

Climate change and land degradation are expected to make the environment more stressful for plants in many regions. Moreover,

Table 1
Selected lactic acid bacteria biocontrol agents.

Species	Strain	Isolated from	Antagonistic *in vitro*	Crop/Pathogen	Proposed Mechanism	Citation
Lactobacillus plantarum	L1515a	Cucumber pickle	*Xanthomonas campestris, Pseudomonas campestris* and *Erwinia carotova*	Bean & Cucumber/*Pseudomonas campestris*	Organic acids	Visser et al., 1986
Lactobacillus sp.	KLF01	Tomato rhizosphere	*Ralstonia solanacearum, Xanthomonas axonopodis* pv. *citri, X. campestris* pv. *vesicatoria, Erwinia pyrifoliae* and *E. carotovora* subsp. *carotovora, Pectobacterium carotovorum* subsp. *carotovorum*	Tomato/*Ralstonia solanacearum,* Pepper/*Xanthomonas campestris* pv. *vesicatoria,* Chinese Cabbage/*Pectobacterium carotovorum* subsp. *carotovorum*	None	Shrestha et al., 2009a; b
Unidentified LAB	KLC02	Unknown	*Ralstonia solanacearum, Xanthomonas axonopodis* pv. *citri, X. campestris* pv. *vesicatoria, Erwinia pyrifoliae* and *E. carotovora* subsp. *carotovora, Pectobacterium carotovorum* subsp. *carotovorum*	Pepper/*Xanthomonas campestris* pv. *vesicatoria*	None	Shrestha et al., 2009a
Unidentified LAB	KPD03	Unknown	*Ralstonia solanacearum, Xanthomonas axonopodis* pv. *citri, X. campestris* pv. *vesicatoria, Erwinia pyrifoliae* and *E. carotovora* subsp. *carotovora, Pectobacterium carotovorum* subsp. *carotovorum*	Pepper/Xanthomonas campestris pv. Vesicatoria	None	Shrestha et al., 2009a
Lactobacillus plantarum	AF1	Kimchi	*Aspergillus flavus*	Soybean/*Aspergillus flavus*	3,6-bis(2-methylpropyl)-2,5-piperazinedion	Yang and Chang, 2010
Lactobacillus spp.	Unknown	Dairy products	*Fusarium oxysporum*	Tomato/*Fusarium oxysporum*	SAR, antifungal metabolites	Hamed et al., 2011
Lactobacillus plantarum	IMAU10014	Fermented mare milk	*Botrytis cinerea, Alternaria solani, Phytophthora drechsleri, Fusarium oxysporum* and *Glomerella cingulate*	N/A	proteinacious and non-proteinacious antifungal compounds	Wang et al., 2011
Lactobacillus plantarum	C5	Durian fruit	*Streptococcus, Bacillus subtilis, Protous, Klebsilla, E. coli* and *S. aureus*	Pepper seed/*Colletotrichum capsid*	None	Elmabrok and Hussin 2012
Lactobacillus plantarum	G7	Ginger root	*Streptococcus, Bacillus subtilis, Protous, Klebsilla, E. coli* and *S. aureus*	Pepper seed/*Colletotrichum capsid*	None	Elmabrok and Hussin 2012
Unidentified LAB	Unknown	Unknown	*Pythium ultimum*	Cucumber/*Pythium ultimum*	None	Lutz et al., 2012
Lactobacillus plantarum	ONU87	Unknown	*Rhizobium radiobacter*	Carrot & Kalanchoe/*Rhizobium radiobacter*	None	Korotaeva et al., 2013
Lactobacillus paracasei	Unknown	Unknown	*Ralstonia solanacearum*	Tomato/*Ralstonia solanacearum*	None	Murthy et al., 2012
Lactobacillus plantarum	Unknown	Unknown	N/A	Apple & Pear/*Erwinia amylovora*	Preemptive colonization, plantericin	Roselló et al., 2013
Lactobacillus plantarum	SLG17	Unknown	*Fusarium graminearum*	Wheat/*Fusarium graminearum*	Organic acids, plantericin	Baffoni et al., 2015

Table 1 (continued)

Species	Strain	Isolated from	Antagonistic in vitro	Crop/Pathogen	Proposed Mechanism	Citation
Lactobacillus paracasei	Unknown	Unknown	N/A	Tomato/Ralstonia solanacearum	SAR	Konappa et al., 2016

Table 2
Selected lactic acid bacteria biostimulants.

Species	Strain	Isolated from	Crop	Effect	Proposed Mechanism	Citation
Lactobacillus plantarum	IFO 3070	EM-4	Radish	Increased yield	None	Higa and Kinjo, 1991
Lactobacillus acidophilus	Unknown	Dairy products	Tomato	Increased shoot branching, shoot and root growth	None	Hamed et al., 2011
Lactobacillus sp.	Unknown	Dairy products	Tomato	Increased shoot branching, shoot and root growth	None	Hamed et al., 2011
Lactobacillus plantarum	NRRL B-4524	The National Center for Agricultural Utilization Research	Tomato	Increased shoot branching, shoot and root growth	None	Hamed et al., 2011
LAB	Unknown	Agricultural rhizosphere	Tomato	Increased germination rate	None	Lutz et al., 2012
Lactobacillus plantarum	ONU 12	Grape must	Tomato	Increased shoot and root growth	Bacteriogenic metabolites	Limanska et al., 2013
Lactobacillus plantarum	ONU 315, 316	Oyster mushroom surface	Tomato	Increased germination rate, shoot and root growth	Bacteriogenic metabolites	Limanska et al., 2013
Lactobacillus plantarum	ONU 991	Dairy products	Tomato	Increased germination rate, root growth	Bacteriogenic metabolites	Limanska et al., 2013
Lactobacillus acidophilus	WR2	Wheat rhizosphere	Wheat	Increase height and chlorophyll content	Bacteriogenic IAA	Mohite, 2013
Lactobacillus casei	6	Embiko® microbial phytostimulant	Cucumber	Increased germination rate, inhibited seedling growth	None	Rzhevskaya et al., 2014
Lactobacillus lactis	4/6	Embiko® microbial phytostimulant	Cucumber	Increased seedling growth rate	None	Rzhevskaya et al., 2014
Lactobacillus plantarum	20	Embiko® microbial phytostimulant	Cucumber	Increased germination and seedling growth rate	None	Rzhevskaya et al., 2014
Lactobacillus sp.	KLF01	Tomato rhizosphere	Pepper	Increased root length, shoot length, root fresh weight and chlorophyll content	Bacteriogenic IAA, phosphate solubilization	Shrestha et al., 2014
Unidentified LAB	KLC02	Unknown	Pepper	Increased root length, shoot length, root fresh weight and chlorophyll content	Bacteriogenic IAA, phosphate solubilization	Shrestha et al., 2014
Unidentified LAB	KPD03	Unknown	Pepper	Increased root length, shoot length, root fresh weight and chlorophyll content	Bacteriogenic IAA, phosphate solubilization	Shrestha et al., 2014
Lactobacillus plantarum	8P-AZ	Human probiotic	Wheat	Osmotic stress alleviation	Bacteriogenic NO signaling	Yarullina et al., 2014
Lactobacillus plantarum	Unknown	PGPR Corp. (Korea)	Cucumber	Increased growth, nutrient uptake and amino acid content	Increased nutrient availability via succinic acid and lactic acid production	Kang et al., 2015
LAB	BL06	Sugarcane ferment	Citrus seedling	Increased height, stem diameter, dry root and shoot weight	Phosphate solubilization, nitrogen fixation	Giassi et al., 2016
Lactobacillus plantarum	ATCC 9019	Unknown	Swertia chirayita	Salt stress alleviation	Altered plant stress response	Phoboo et al., 2016

increasing food, fiber, and energy demands from a growing population will force more agricultural production onto marginal lands, imposing even more stress on food production globally. Stress alleviation with microbial treatments offers a low-input, low-environmental impact way to sustain food production in a more stressful environment.

Extremophilic microorganisms; those which live in extreme environments, often play an important, or even essential, role in the survival of plants native to harsh environments (Rodriguez and Redman, 2008). The ability of symbiotic microorganisms to alleviate abiotic stresses in their host plant has been well documented. In fact, the effects of many PGPM are only noticeable when plants are subjected to environmental stress (Wang et al., 2012; Subramanian, 2014; Prudent et al., 2015). PGPM can improve the ability of plants to withstand stressful environments by protecting plants from abiotic stresses or by altering the stress response of the plant, thus improving the survival of the entire phytomicrobiome.

Production of reactive oxygen species (ROS) and ethylene are also common plant stress responses. Both aid in responding to and withstanding stress at low concentrations, but are detrimental at higher concentrations. Increasing tissue concentrations of ROS prompts the production of enzymatic and non-enzymatic antioxidants, which scavenge ROS; protecting plants from the harmful oxidizing effects of ROS. Plants will often synthesize osmolytes, such as proline, to regulate cellular osmotic potential in response to a variety of abiotic stresses.

Strains of *Lactobacillus* have been shown to ameliorate abiotic stress in plants (Table 2). Phoboo et al. (2016) found that clones of the medicinal plant, *Swertia chirayita,* that were inoculated with *L. plantarum* (ATCC 9019) were more resilient to salt stress. Plants treated with *L. plantarum* had an altered metabolic response to salt stress. With increasing salt concentrations, treated plants had increased concentrations of proline and decreasing total phenolic concentrations whereas untreated plants had consistently low proline concentrations and consistently high phenolic concentrations across salt concentrations. Treated plants also had decreasing antioxidant activity with increasing salt concentrations except for guaiacol peroxidase, which increased with increasing salt concentrations.

Strains of L. *plantarum* has been shown to produce a variety of polyamines, including putrescene, citrulline and ornithine (Arena and Manca de Nadra, 2001). Bacterial plant growth promotion was observed in a pot experiment in which bean plants were grown in soil inoculated with a polyamine-producing strain of *Streptomyces griseoluteus* (Nassar et al., 2003). While the relationship is not yet elucidated, there appears to be a link between polyamines and plant stress response pathways, including the NO pathway (Yamasaki and Cohen, 2006; Pang et al., 2007; Hussain et al., 2011; Alcázar and Tiburcio, 2014). The ability of LAB to produce polyamines, NO, or other signal molecules may contribute to plant growth stimulation or stress alleviation.

Microbe-associated molecular patterns (MAMPs) are known to change plant response to biotic stresses (Henry et al., 2012) and abiotic stresses and it is likely that MAMPs produced by LAB are responsible for increases resilience of plants treated with LAB. None of these MAMP elicitors for LAB have yet been identified, but the identification of MAMP elicitor compounds could lead to a better understanding of the plant-microbe relationship, as well as enable to purification of active MAMP compounds for use as bioelicitors.

Many of the intricacies of plant stress response networks have yet to be completely understood, but it appears that treatment with LAB can significantly alter plant stress response to the benefit of the plant.

7. LAB as biostimulant

Some plant growth promoting microorganisms produce hormones that can stimulate plant growth (Tsavkelova et al., 2006); however, there is little evidence that bacteriogenic hormones play a significant role in plant growth stimulation by LAB. *L. acidophilus* has been reported to produce cytokinens (Lynch, 1985), and some strains of *Lactobacillus* have been shown to produce indole-3-acetic acid (IAA) (Mohite, 2013; Shrestha et al., 2014; Giassi et al., 2016) while others do not (Kang et al., 2015).

While *Lactobacillus* has been shown to promote growth in diverse crops (Table 2), the underlying mechanisms of this biostimulation remain unclear. There appears to be plant and strain specificity in *Lactobacillus* phytostimulation. Screens of hundreds of *Lactobacillus* strains may only yield a few stimulatory strains (Lutz et al., 2012). Furthermore, different strains of the same *Lactobacillus* species may produce different morphological changes in the same plant (Hamed et al., 2011; Limanska et al., 2013; Rzhevskaya et al., 2014).

Most early EM research did not characterize the activity of individual members of the EM consortium, however, Higa and Kinjo (1991) found that radish had a dose-dependent growth response to varying concentrations of *L. plantarum* cultures, with plants treated with the greatest concentration of culture growing larger than untreated plants. Treatment with the EM consortium can also affect plant growth and development directly. Applications of an EM product containing at least five *Lactobacillus* strains changed the morphology of *Lolium perenne,* to make it less susceptible to mechanical damage associated with turf grass management (Gaggìa et al., 2013). Axel et al. (2012) suggest elucidating the role of LAB in EM by isolating LAB members of the EM consortia to test for bioactivity.

Kang et al. (2015) investigated the effects of three potential members of an EM consortia, *Rhodobacter sphaeroides, Saccharomyces cerevisiae* and *Lactobacillus plantarum* on the growth and development of cucumber. All three microorganisms increased cucumber growth, nutrient uptake and amino acid content. The plant growth stimulation observed for *R. sphaeroides* was attributed to large quantities of IAA, measured in *R. sphaeroides* media filtrate. There was no IAA detected in media filtrate from *L. plantarum*, suggesting it produced another compound that influenced plant growth. In contrast, others have suggested IAA produced by LAB is responsible for plant growth promotion (Mohite, 2013; Shrestha et al., 2014). LAB likely promote plant through diverse environmental-, strain-, and host-dependant mechanisms, which have yet to be elucidated.

8. Limitations and new directions

Some of the major limitations to widespread implementation of PGPMs are developing effective and efficient methods to screen for PGPMs; ensuring PGPMs can survive and have the desired bioactivity in the field environment; and developing effective and efficient formulations for applying PGPMs (Le Mire et al., 2016).

Traditional methods of screening for PGPMs *in vitro* may not be adequate to discover all PGPMs. For example, de Melo Pereira et al. (2012) screened strawberry fruit for potential PGPM endophytes, and, while they found several strain of *L. plantarum,* the only criteria used to identify PGPM were IAA production, N fixation and siderophore production. Along with overlooking strains that may be effective PGPMs, *in vitro* screens may identify strains as good PGPM candidates that do not preform well in the field. In their investigation of LAB as BCAs, Visser and Holzapfel (1992) found there is often there is little correlation between *in vitro* antagonism and practical pathogen control in the field.

As with other PGPMs, a major limitation to the use of LAB in agricultural applications is its ability to survive and produce sufficient quantities of bioactive metabolites in the required environments. Visser and Holzapfel (1992) suggested this could be overcome by isolating or engineering strains that are well suited to the phyllosphere environment; applying cultures with essential nutrients or protective carriers; reapplying cultures to maintain high numbers of viable cells; however, these methods are cumbersome, and time consuming. Using plant growth promoting LAB selectively in environments which are more conducive to its growth; such as fruits, flowers, and highly organic soils, may be another option. This approach has been successful in the control of floral pathogens of rosaceous tree crops (Bonaterra et al., 2013; Martinez et al., 2008; Roselló et al., 2013), and shows great potential in the control of postharvest pathogens (Trias et al., 2008).

Another approach would be to produce bioactive compounds from LAB grown under ideal conditions in bioreactors. Supernatants from LAB bioreactors, or even purified bioactive compounds could then be applied to crops, and the survival of the LAB would not be a concern. Furthermore, some research has shown that excreted metabolites are responsible for the activity of LAB (Omer et al., 2010; Limanska et al., 2015a, b). The strategy of isolating and purifying bacteriogenic bioactive compounds has been successfully employed for the phytostimulatory bacteriocin from *Bacillus thuringiensis* NEB17, thuricin 17 (Gray et al., 2006); and the phytostimulatory lipo-chitooligosaccharide from *Bradyrhizobium japonicum* 532C (Prithiviraj et al., 2003.

Although LAB can survive under harsh environmental conditions, they have complex nutritional requirements for growth. There has been some research into formulating LAB media based in organic wastes from sugar beet (Krzywonos and Eberhard, 2011) and sweet potato processing (Hayek et al., 2013) on an industrial scale, but a consistent LAB medium is needed to improve the sustainability of industrial LAB culture. Higa and Kinjo (1991) suggest that LAB are not as effective as a pure culture and should be applied in a consortium of complimentary microorganisms, such as EM. In the EM framework, the complex nutritional requirements of LAB are satisfied with metabolites from other members of the consortium. In contrast to this view, Giassi et al. (2016) found that inoculation with a pure LAB strain promoted growth, but a mixture of this LAB strain and other PGPBs did not promote plant growth, suggesting inhibitory competition between strains. With this in mind, PGPM consortia must be carefully designed to avoid incompatibility.

LAB strains can improve plant production by improving nutrient availability, acting as a BCA, alleviating biotic and biotic stresses, and directly stimulating plant growth. These plant growth promoting characteristics paired with their long history in food science, and the GRAS status of many LAB, including all lactobacilli, make them particularly well suited for applications in plant production. Despite being a common member of the phytomicrobiome, LAB have been largely overlooked as potential PGPBs. Historical and current research demonstrates a clear potential for LAB as useful, renewable and safe agricultural inputs to improve plant growth. Re-examining uses for such ubiquitous organisms could contribute to solving some of the issues facing food production in the 21st century.

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