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Bacteria with ACC deaminase can promote plant growth and help to feed the world☆

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ABSTRACT

To feed all of the world's people, it is necessary to sustainably increase agricultural productivity. One way to do this is through the increased use of plant growth-promoting bacteria; recently, scientists have developed a more profound understanding of the mechanisms employed by these bacteria to facilitate plant growth. Here, it is argued that the ability of plant growth-promoting bacteria that produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase to lower plant ethylene levels, often a result of various stresses, is a key component in the efficacious functioning of these bacteria. The optimal functioning of these bacteria includes the synergistic interaction between ACC deaminase and both plant and bacterial auxin, indole-3-acetic acid (IAA). These bacteria not only directly promote plant growth, they also protect plants against flooding, drought, salt, flower wilting, metals, organic contaminants, and both bacterial and fungal pathogens. While a considerable amount of both basic and applied work remains to be done before ACC deaminase-producing plant growth-promoting bacteria become a mainstay of plant agriculture, the evidence indicates that with the expected shift from chemicals to soil bacteria, the world is on the verge of a major paradigm shift in plant agriculture.

1. The problem

As a consequence of increases in and environmental damage and worldwide population growth, global food production may soon be insufficient to feed all of the world's people. In this regard, the world's population, which is currently around 7 billion people has been projected to increase to around 10 billion in the next 50 years. To feed all of these individuals it is absolutely essential that agricultural productivity be significantly increased within the next few decades. However, providing sufficient food for an ever-increasing world population is not an easy task; it will require a variety of different strategies and approaches. To produce more food, the world will require (at least initially) more agricultural land; greater use of chemicals including fertilizers, pesticides and herbicides; more farm mechanization; greater use of transgenic crops; and the expanded use of plant growth-promoting microorganisms. Of course, many of the solutions to this problem that will be attempted are not sustainable and will only be effective in the short term. Since we live in a finite world with limited resources, any effective and longer term solutions to providing food for the world (once the population has leveled off) must include sustainable and environmentally friendly biological solutions. To this end, the purposeful use of PGPB in agriculture is an attractive technology to address this problem. While scientists have dramatically increased our knowledge of the mechanisms employed by PGPB in the past 15–20 years (Glick 2012), additional understanding of the fundamental mechanisms employed by these bacteria will likely hasten the acceptance of these organisms as suitable and effective adjuncts to agricultural practice (Reed and Glick 2004). Therefore, of necessity, any efforts to increase the practical use of PGPB must start with a better understanding of how these bacteria promote plant growth.

2. Plant growth-promoting bacteria

Most soils contain an enormous diversity of microorganisms including bacteria, actinomycetes, fungi, algae and protozoa. It has been suggested that a typical gram of soil contains $\sim 9 \times 10^7$ bacteria, 4×10^6 actinomycetes, 2×10^5 fungi, 3×10^4 algae, 5×10^3 protozoa and 3×10^1 nematodes (Alexander 1991). Of course, the numbers of these organisms in any one soil compared to another may vary greatly.

Soil bacteria in particular have the ability to grow rapidly and to utilize a very wide range of different substances as nutrient sources. While many bacteria are dispersed within the soil, often attached to soil particles, many interact with the roots of plants. It is quite common for the concentration of bacteria that is found around the roots of plants, i.e. in the rhizosphere, to be much greater than the

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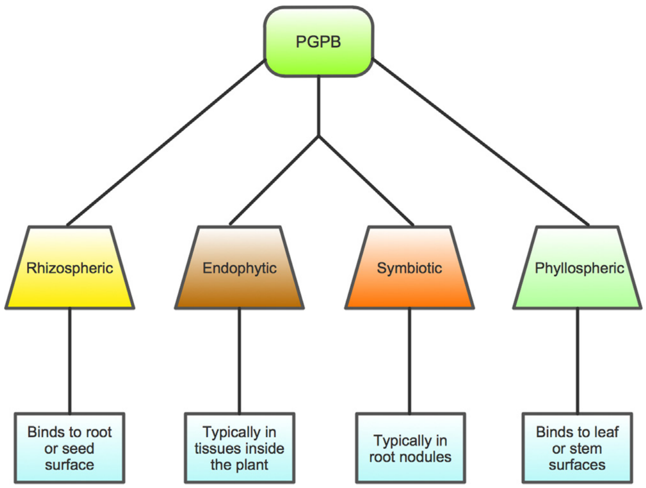

Fig. 1. PGPB includes bacteria that interact with plants in a range of different ways.

bacterial concentration in the rest of the soil (Lynch 1990). The high concentration of bacteria around the roots of plants presumably occurs because of the presence of high levels of nutrients including amino acids, sugars and organic acids that are exuded from the roots of plants, and are then used by rhizosphere bacteria to support their growth and metabolism (Whipps 1990). In this regard, various estimates of the amount of photosynthetically fixed carbon that is exuded by the roots of various plants range from 5% up to around 30%.

The interaction between soil bacteria and plant roots may be classified as being beneficial, harmful or neutral for the plant, and sometimes the effect of a particular bacterium may vary as the soil conditions change (Lynch, 1990). For example, a bacterium that facilitates growth only by providing plants with fixed nitrogen would not provide any benefit to plants when the soil contains large amounts of chemical nitrogen fertilizer. Similarly, bacteria that promote plant growth by decreasing the inhibitory effects of various environmental stresses (abiotic or biotic) are unlikely to have much effect on plant growth when the conditions are optimal (Glick et al. 2007).

Bacteria that facilitate plant growth (Fig. 1) may do so either by binding to the plant's outer surface such as the roots (the rhizosphere) or the leaves (the phyllosphere), or they may inhabit the interior surfaces of the plant forming an endophytic relationship (Hallmann et al. 1997; Sturz et al. 2000; Davison 1988; Kloepper et al. 1989). A bacterial endophyte may be localized in only certain plant tissues such as roots and stems, it may be distributed throughout the plant's tissues, or it may form specific structures such as nodules, depending upon the bacterium and the plant. Endophytic bacteria that form and occupy nodules on specific host plants have previously been called symbiotic bacteria and have been studied extensively (Oldroyd et al. 2011; Wang et al. 2012). These organisms were among the first soil bacteria to be utilized commercially as a biological means of promoting plant growth (Reed and Glick 2004). Plant beneficial soil bacteria, regardless of where they are primarily found on the plant, are now commonly referred to as plant growth-promoting bacteria or PGPB (Bashan and Holguin 1998).

While many different soil bacteria are considered to be plant growth-promoting bacteria, not all strains of a particular bacterial genus and species have the same genetic makeup and metabolic capabilities. Thus for example, some strains of *Pseudomonas fluorescens* may actively promote plant growth while other strains of this species have no measurable effect on plants. This reflects the fact that the so-called core genes that define the fundamental metabolic capabilities of a bacterium are not typically involved in plant growth promotion (Huang et al. 2013).

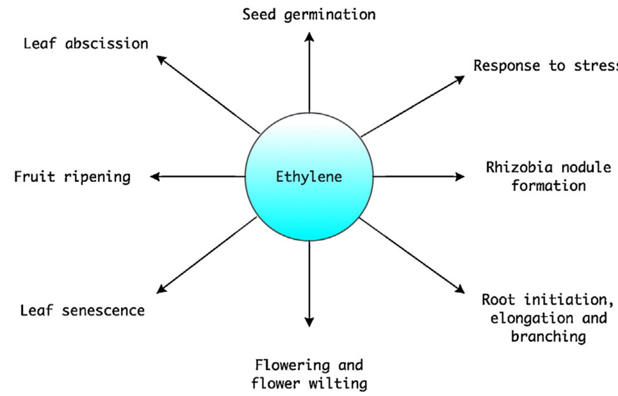

Fig. 2. The phytohormone ethylene affects a large number of different processes in the growth and development of a plant.

Plant growth-promoting bacteria may facilitate plant growth and development either indirectly or directly. Indirect plant growth promotion occurs when these bacteria decrease or prevent some of the deleterious effects of a plant pathogen (usually a fungus) by any of one of several different mechanisms (Glick 2012). The direct promotion of plant growth by plant growth-promoting bacteria generally entails facilitating the acquisition of nutrient resources from the environment including fixed nitrogen, iron and phosphate, or in specifically modulating plant growth by altering plant hormone levels such as auxin, cytokinin and ethylene (Glick 2012).

3. Ethylene and plants

The hormone ethylene, which is found in all higher plants, is an important modulator of normal plant growth and development in plants as well as a key feature in the response of plants to a wide range of stresses (Abeles et al. 1992). Many aspects of the growth of plant tissues such as roots, stems, leaves, flowers and fruits, as well as all stages of plant development are affected by ethylene (Fig. 2). A variety of other plant processes involve ethylene including rhizobia nodulation of legumes (Goodlass and Smith 1979), rooting of cuttings (Li et al. 2005; Mayak et al. 1999; Montero-Calasanz et al. 2013), as well as a plant's interaction with beneficial mycorrhizal fungi (Beyrle 1995; Gamalero et al. 2008).

Within any particular plant, ethylene synthesis is affected by a number of different factors including temperature, light, gravity, nutrition, the presence and level of other plant hormones, and the presence of various types of biological stress to which the plant may be subjected (Abeles et al. 1992). Regarding a plant's response to stress, an increased level of ethylene is typically formed in response to the presence of metals, organic and inorganic chemicals, temperature extremes, too much or too little water, ultraviolet light, insect damage, nematode damage, phytopathogens (both fungi and bacteria), and mechanical wounding (Abeles et al. 1992). One model that describes the synthesis of "stress ethylene" includes the ethylene being synthesized in two peaks (Glick et al. 2007; Pierik et al. 2006; Van Loon et al. 2006). The first ethylene peak is typically only a small fraction of the magnitude of the second peak. This small peak of ethylene, which consumes the existing pool of 1-aminocyclopropane-1-carboxylate (ACC, the precursor of ethylene) in stressed plant tissues, is believed to be responsible for initiating the transcription of genes that encode plant defensive/protective proteins (Robison et al. 2001a). The first ethylene peak is often technically difficult to measure depending upon the sensitivity of the instrumentation that is utilized. The second, much larger, ethylene peak occurs following synthesis by the plant of additional ACC in