Chapter 15
Beneficial Rhizobacteria Induce Plant Growth: Mapping Signaling Networks in *Arabidopsis*

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15.1 Agricultural Impact of Plant Growth-Promoting Rhizobacteria

Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil microorganisms that colonize roots and stimulate shoot and root growth. Such bacteria have been applied to a wide range of agricultural crops for the purpose of growth enhancement, including increased seed emergence, plant weight, and crop yields (Kloepper et al. 1991). For example, emergence increases of 10–40% result for canola when seeds are coated with PGPR before planting, and plant weight of tuber-treated potatoes increases by 80% on average by midseason (Kloepper et al. 1980). Yield increases between 10 and 20% with PGPR applications have also been documented for several other agricultural crops (Kloepper et al. 1991).

Plant-PGPR associations are mediated through an exchange of chemical metabolites. Root exudates provide energy-rich organic acids that are metabolized within hours by soil microorganisms (Jones et al. 2003) while specialized microbes generate an array of biologically active compounds that elicit plant growth promotion (Kloepper et al. 1999; Ryu et al. 2003; Paré et al. 2005). Widely accepted mechanisms for plant growth promotion by PGPR include bacterial synthesis of plant hormones (Loper and Schroth 1986; Timmusk et al. 1999; MacDonald et al. 1986), breakdown of plant produced ethylene (Glick et al. 1999), and increased mineral availability in the soil by bacterial produced siderophores (Lin et al. 1983).

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G. Witzany (ed.), *Biocommunication in Soil Microorganisms*, Soil Biology 23,
DOI 10.1007/978-3-642-14512-4_15,

15.2 Low-Molecular Weight Bacterial Signals

To differentiate between bacterial-defined signaling and bacterial mimicry of plant signaling, often times by nonvolatile components such as hormone production and siderophores, blends of volatile organic chemicals (VOCs) emitted from specific strains of PGPR, in the absence of physical contact with plant roots, have been assayed for growth induction in the model plant *Arabidopsis* (Ryu et al. 2003). Of the several PGPR strains assayed, two species *Bacillus subtilis* GB03 and *B. amyloliquefaciens* IN937a elicited plant growth via volatile emissions. To provide a comprehensive chemical profile of bacterial volatiles emitted from these biologically active strains, headspace solid phase micro extraction (SPME) coupled with software extraction of overlapping GC-separated components was employed (Farag et al. 2006). Thirty eight volatile metabolites from GB03 and IN937a were characterized. Most of the identified compounds were branched-chain alcohols released from IN937a, at much higher levels than in GB03. Principal component analysis clearly separated GB03 from IN937a, with GB03 producing higher amounts of 3-methyl-1-butanol, 2-methyl-1-butanol, and butane-1-methoxy-3-methyl. The branched-chain alcohols share a similar functional motif to that of 2,3-butanediol and may afford alternative structural patterns for elicitors from bacterial sources.

15.3 Probing Bacterial-Mediated Plant Growth Signaling Pathways

To elucidate signaling networks involved in growth promotion via PGPR VOCs, a series of mutant lines were tested (Ryu et al. 2003). Enhanced total leaf surface area was observed from exposure to GB03 VOCs for mutant lines ethylene insensitive (*etr*1), auxin-transporter-deficient and ethylene insensitive (*eir*1), gibberellic acid-insensitive (*gai*2), and brassinosteroid-insensitive (*cbb*1) mutants, thereby negating the essential involvement of brassinosteroid-, gibberellic acid-, or ethylene-signaling in the activation of growth promotion by VOCs. Considering that the auxin efflux carrier EIR1 (also known as AGR and AtPIN2) is a root-specific protein (Luschnig et al. 1998; Sieberer et al. 2000), a mutation in this auxin transporter (*eir1*) does not necessarily affect basipetal auxin transport or auxin action in leaves. Therefore, participation of auxin in VOC-induced growth promotion cannot be excluded. The cytokinin receptor-deficient (*cre*1) and cytokinin- and ethylene-insensitive (*ein*2) mutants were also tested and exhibited no growth promotion with exposure to GB03 VOCs. Although the function of EIN2 has not been clearly resolved, *ein2* mutants have been recovered in screens for *Arabidopsis* mutants resistant to auxin transport inhibitors, cytokinins, or abscisic acid and in screens for delayed senescence (Alonso et al. 1999), implicating auxin, cytokinin, and/or abscisic acid as possible mediators of growth promotion by GB03 VOCs.

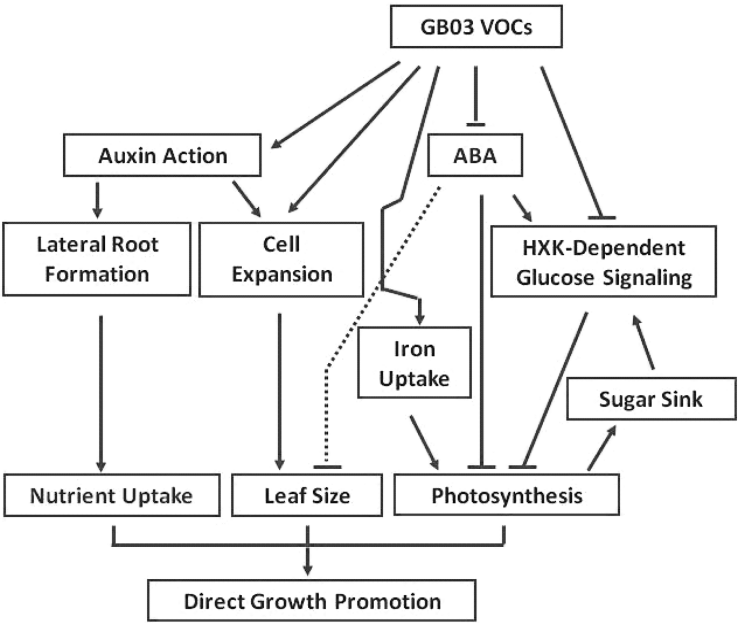

Fig. 15.1 Integrated mechanistic links for growth promotion in *Arabidopsis* by *Bacillus subtilis* (GB03) volatile emissions. *Arrows* and *blocked lines* indicate up- and down-regulated pathways, respectively; *unbroken lines* represent direct experimental evidence while *dotted lines* are proposed responses. Abbreviations: *VOCs* volatile organic chemicals, *ABA* abscisic acid, *HXK* hexokinase. See text for appropriate references

15.3.1 Bacterial Regulation of Auxin Synthesis, Transport, and Distribution in Planta

To directly probe how PGPR VOCs trigger growth in plants, RNA transcript levels of *Arabidopsis* seedlings exposed to *B. subtilus* (GB03) were examined using oligonucleotide microarrays (Zhang et al. 2007). In screening over 26,000 protein-coded transcripts, a group of approximately 600 differentially expressed genes related to cell wall modifications, primary and secondary metabolism, stress responses, hormone regulation, and other expressed proteins were identified. Transcriptional and histochemical data indicate that VOCs from the PGPR strain GB03 trigger growth promotion in *Arabidopsis* by regulating auxin homeostasis. Specifically, gene expression for auxin synthesis was up-regulated in aerial regions of GB03-exposed plants; auxin accumulation decreased in leaves and increased in roots with GB03 exposure as revealed in a transgenic DR5::GUS marker line for auxin accumulation (Ulmasov et al. 1997), suggesting activation of basipetal auxin transport. Application of the auxin transport inhibitor 1-naphthylphthalamic acid (NPA) restricted auxin accumulation to sites of synthesis (Keller et al. 2004),

thereby preventing GB03-mediated decreases in shoot auxin levels as well as thwarting GB03-mediated growth promotion.

Although the role auxin plays in controlling leaf expansion remains unclear, increased auxin levels have been reported to have negative effects on leaf expansion. *Arabidopsis* mutants *sur1* and *sur2* that overproduce auxin have reduced leaf expansion (Boerjan et al. 1995). Transgenic petunia (*Petunia hybrida*), which overproduces auxin, develops leaves that are epinastic as well as smaller and narrower than wild-type plants (Klee et al. 1987). And application of exogenous auxin to bean (*Phaseolus vulgaris*) and *Arabidopsis* leaf blades inhibits long-term blade elongation (Keller et al. 2004). Auxin transport inhibition by NPA application to petioles traps auxin within the leaf and selectively increases leaf auxin content thereby inhibited leaf growth (Keller et al. 2004). On the other hand, low auxin concentrations drive cell elongation, cell enlargement, and cell differentiation in tobacco cell culture (Winicur et al. 1998; Zazimalova et al. 1995). Although NPA-induced reduction of plant growth due to a nonspecific response such as diminished plant perception of VOCs and/or downstream interference of critical nonauxin signaling pathways cannot be ruled out, the spatial and temporal redistribution of auxin observed with GB03 VOCs as well as exogenous NPA treatment demonstratively implicates auxin participation in plant growth promotion (Zhang et al. 2007).

15.3.2 Transcriptional Regulation of Cell Wall Rigidity by GB03

In addition, microarray data revealed coordinated regulation of cell wall loosening enzymes that implicated cell expansion with GB03 exposure, which was confirmed by comparative cytological measurements. Genes differentially regulated with exposure to GB03 emissions and associated with cell wall modifications were examined for possible regulatory control of cell enlargement. The induction of a group of pectin-related genes, including pectin methylesterase inhibitor, pectinase, and pectate lyase (Zhang et al. 2007) suggested that cell-wall loosening contributes to cell expansion. Pectins, a mixture of heterogeneous, branched, and highly hydrated polysaccharides rich in D-galacturonic acid, are thought to perform several cell-wall functions including determination of wall porosity, provide charged surfaces that can modulate wall pH and ion balance, and serve as recognition molecules that alert plant cells to the presence of symbiotic organisms, pathogens, and insects (Buchanan et al. 2000). Pectin methylesterases hydrolyze methyl ester of pectins and thus create free carboxyl groups that can link with Ca^{2+} ions and stabilize two polygalacturonan (PGA) chains, thereby making the pectic network more rigid. Moreover, binding of GalA units in PGA to Ca^{2+} results in calcium pectate, which is the cementing substance for cell adhesion. Besides the action of cell wall reassembly enzymes, enzymes involved in the biosynthesis of cell walls also seemed to be altered. UDP-glucose 4-epimerase is involved in channeling UDP-D-galactose into cell wall polymers and was down-regulated with plant exposure to GB03 VOCs. Mutation in *UGE4* has been reported to

weaken cell structure as observed with a dramatic bulging of root epidermal cells (Schiefelbein and Somerville 1990; Baskin et al. 1992).

Traditional models of rhizobacterial-stimulated plant growth promotion suggest that soil microbes produce auxin and/or other phytohormones that drive plant growth promotion (Loper and Schroth 1986; Timmusk et al. 1999; MacDonald et al. 1986; Glick et al. 1999; Lin et al. 1983); however, in the case of biologically active bacterial VOCs, blends of volatile chemicals devoid of traditional auxins can trigger plant growth promotion mediated by auxin synthesis and transport *in planta* (Zhang et al. 2007). This observation that bacterial VOCs devoid of auxin or other known plant hormones regulate auxin homeostasis, and cell expansion provides a new paradigm as to how rhizobacteria promote plant growth.

15.3.3 GB03 Volatile Organic Compounds Elevate Plant Energy Acquisition

Although cell wall loosening in combination with increase water uptake can explain short-term leaf expansion, an increase in energy uptake seems necessary for sustained growth promotion. In measuring photosynthetic efficiency with plant exposure to GB03 volatiles, it was observed that photosynthetic capacity is augmented in *Arabidopsis* by increasing photosynthetic efficiency and chlorophyll content (Zhang et al. 2008b). Mechanistic studies revealed an elevation of sugar accumulation as well as the suppression of classic glucose signaling responses, including hypocotyl elongation and seed germination, with exposure to GB03. Compared with wild-type plants, two *Arabidopsis* mutants defective in hexokinase-dependent sugar signaling exhibited increased photosynthetic capacity, which is not further enhanced with GB03 exposure. Overlap in sugar/ABA sensing is observed in GB03-exposed plants, with a reduction of ABA biosynthetic transcripts as well as downstream metabolite levels in leaves. Moreover, exogenous ABA abrogates GB03-triggered increases in photosynthetic efficiency and chlorophyll content. These results demonstrate that certain rhizobacteria elevate photosynthesis through the modulation of endogenous sugar/ABA signaling and establish a regulatory role for soil microbes in plant acquisition of energy.

GB03 enhances *Arabidopsis* photosynthetic capacity by improving the efficiency of the conversion of light energy, as well as by enhancing the photosynthetic apparatus, as evidenced by increases in photosynthetic efficiency and chlorophyll content, respectively (Zhang et al. 2008b). Consistent with elevated photosynthesis, transcripts of genes encoding chloroplast proteins known to be associated with photosynthesis are up-regulated with GB03 exposure (Zhang et al. 2007). A plastic partition separating bacteria from the plant excludes the possibility that GB03 represses the glucose inhibition of hypocotyl elongation or of germination through competition for plant sugar uptake. Moreover, the higher hexose level in GB03-exposed plants establishes that GB03 attenuates glucose inhibitory effects through the repression of sugar signaling, rather than by lowering sugar accumulation.

Furthermore, studies using *Arabidopsis* mutants defective in hexokinase-dependent sugar signaling (Zhang et al. 2008b) indicate that GB03 augments photosynthesis through repressing hexokinase-dependent, rather than hexokinase-independent, sugar signaling. Glucose signaling largely overlaps with ABA signal transduction, as revealed by the fact that *Arabidopsis* ABA synthesis (aba) and ABA insensitive (abi) mutants are, to varying degrees, sugar-sensing mutants (Rolland et al. 2006; Smeekens 2000). Therefore, the reduction of ABA levels explains the repressed glucose signaling in GB03-exposed plants. Although ABA initiates various protective responses in plants upon biotic or abiotic stress (Finkelstein et al. 2002), ABA can also suspend the postgerminative growth of seedlings, representing an early developmental checkpoint (Lopez-Molina et al. 2001). Genetic and biochemical studies have provided enzymatic information for ABA biosynthesis, which is subject to complex regulation during plant development and in response to abiotic stresses (Finkelstein et al. 2002; Nambara and Marion-Poll 2005; Xiong and Zhu 2002). Results of transcriptional studies show that GB03 reduces plant ABA production (Zhang et al. 2008b). The future identification of cis-elements for ABA synthesis genes, and their respective transcriptional factors, will assist in the elucidation of how GB03 regulates ABA levels in plants.

An additional observation in employing the split-plate Petri dish assay is that bacterial emissions are sufficient to regulate observed photosynthetic changes (Zhang et al. 2008b). Volatiles from a nongrowth-promoting Escherichia coli strain DH5a failed to augment photosynthetic efficiency via a nonspecific microbial signal, such as the generation of elevated CO_2.

15.3.4 GB03 Regulates Iron Assimilation Independent of Metal Chelation

With the photosynthetic complex being one of the most iron-enriched cellular systems in nature with over 20 atoms per complex, photosynthetic activity is highly sensitive to the availability of iron (Spiller and Terry 1980; Sandmann 1985; Behrenfeld et al. 1996). With mounting evidence that GB03 plays a signaling role in activating growth responses in plants, the question arises as to whether such soil microbes regulate iron assimilation. Indeed GB03 activates the plant's own iron acquisition machinery to increase assimilation of metal ions in *Arabidopsis* (Zhang et al. 2009). Mechanistic studies reveal that GB03 transcriptionally upregulates the Fe-deficiency-induced transcription factor 1 (FIT1), which is necessary for GB03-induction of ferric reductase FRO2 and the iron transporter IRT1. In addition, GB03 causes acidification of the rhizosphere by enhancing root proton release and by direct bacterial acidification, thereby facilitating iron mobility. As a result, GB03-exposed plants have elevated endogenous iron levels as well as increased photosynthetic capacity compared with water-treated controls. In contrast, loss-of-function fit1-2 mutants are compromised in terms of enhanced iron assimilation and photosynthetic efficiency triggered by GB03.

Given the importance of iron homeostasis in plant growth and development, a highly orchestrated series of root localized and shoot-borne signals have been characterized that tightly control the production of proteins involved in Fe^{3+}-chelate reductase activity and Fe^{2+} uptake, although initiation of these signals remains elusive (Romera et al. 1992; Grusak 1995; Schmidt and Schuck 1996; Curie and Briat 2003; Vert et al. 2003). GB03-triggered induction of IRT1 and FRO2 gene is not observable in the fit1 mutant, suggesting that FIT1 mediates regulation of IRT1 and FRO2 by GB03. Since FIT1 itself is iron-regulated (Colangelo and Guerinot 2004), an iron sensor upstream of FIT1 would be predicted. Characterization of activating signals in GB03 VOCs that stimulate acquisition of iron by plants may well reveal insights into early regulatory steps in plant iron uptake and homeostasis.

15.4 GB03 Volatile Organic Compounds Augment *Arabidopsis* Reproductive Success

While utilizing Petri-dish grown *Arabidopsis* seedlings has proven to be an effective model system to mechanistically probe early growth responses activated by volatiles from beneficial bacteria (Fig. 15.1) (Zhang et al. 2007, 2008a), an examination of long-term growth promotion by PGPR volatiles requires expanded growth conditions. Closed Magenta boxes (75 × 75 × 100 mm) coupled together as pairs by a plastic collar and containing solid growth medium allow for long-term plant exposure to GB03 VOCs that resulted in sustained growth promotion compared with water controls in *Arabidopsis* (Xie et al. 2009). Persistent GB03 signaling appears to be necessary and sufficient as indicated by the loss of enhanced growth when GB03 is withdrawn early in plant development. In addition to larger root mass (Zhang et al. 2007), greater rosette number likely contributes to the significantly higher fresh and dry weight numbers (Xie et al. 2009). Although flowering time was delayed with sustained GB03 exposure, seed set as a metric of reproductive success was significantly increased compared with water controls at a 10-week harvest period.

15.5 Induced Growth Promotion Beyond the Model Plant

Bacterial volatiles emitted by GB03 significantly increase biomass and essential oil production in laboratory-grown sweet basil (*Ocimum basilicum*) (Banchio et al. 2009). Because plant volatiles are utilized for flavor enhancement in foods as well as for natural defense against herbivore pests, how bacterial-induced plant growth promotion influences essential oil production on a fresh weight basis is of particular interest in the growing of commercial spices.

For field applications, GB03 is thought to survive on seeds until planted and then uses seed exudates during seed germination, directionally multiplying to reach young roots, and maintaining a robust population in the presence of field crops via plant–microbial interactions (Kloepper et al. 2004). The minimum bacterial density in the soil for triggering observable plant responses is ca. 10^4 colony forming units (cfu)/root. GB03 can maintain soil populations of 10^5 cfu/root for over 60 days after planting; negative plant development effects are not observed with bacterial populations as high as 10^{10} cfu/root (Kokalis-Burelle et al. 2006). The inoculum in Petri dish bioassays for VOC-mediated growth promotion contains ca. 10^7 cfu.

Acknowledgments This research was partially supported by the Robert Welch Foundation (D-1478) and the ACS/Frasch Foundation for Chemical Research.

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