VOICE: A salesman told me that if I sprayed his micronutrient spray on my plants right before cold weather they would be protected from freezing. Is there anything to that at all?

C.J. WEISER: No!

GARY HARTNETT: What about snow-making machines they use on ski slopes. Has this been tried for frost protection in nurseries?

SALLY JOHNSON: Yes, it has been used extensively in British Columbia for frost protection. Several nurseries there are considering buying snow-making equipment because they cannot depend on natural snow for winter freeze protection.

BRUCE BRIGGS: If you had a plant that had been attacked by insects or diseases, or poorly fed and lacking certain micronutrients, wouldn't that plant be more likely to be winter-killed?

C.J. WEISER: A healthy plant, growing well, and going into proper dormancy in the fall will withstand low temperatures best. Withholding nitrogen in late summer to cause growth cessation is good strategy. But I have not seen any experimental evidence that a micronutrient spray just before cold weather will impart any hardiness.

BACTERIZATION OF PLANT PROPAGATION PROPAGULES TO ENHANCE PLANT GROWTH

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INTRODUCTION

Reports have been published recently about the enhanced growth of plants achieved through inoculation of plant propagating propagules with specific kinds of bacteria, a process called "bacterization".

Now, these bacteria have been reported to increase the growth of plants, by as much as 500% over the non-inoculated control plants. The rhizobacteria have been subdivided into three value groups (beneficial, deleterious, and neutral) (30) based on how these bacteria affect the plant.

The purpose of this paper is to describe the bacterization process, provide examples of positive and negative results, list proposed mechanisms of action, evaluate the findings, and discuss some of the theoretical and practical considerations about use of PGPR in plant propagation.

WHAT IS BACTERIZATION?

Bacterizaton is used in this paper to mean the process of growing selected bacterial strains to high populations in laboratory culture media and then adding these bacteria to plant propagules used for propagation (seed, cutting, vegetative parts, bare-rooted plants, etc.) for the purpose of improving plant growth.

Examples of Enhanced Plant Growth Induced by Rhizobacteria. Some amazing growth responses have been reported for plants grown from seed inoculated with PGPR especially in greenhouse trials. Greenhouse soil is often steamed or sterilized, thus removing many of the natural factors that compete with or reduce survival of the PGPR. This system could be an advantage to greenhouse operations that produce bedding and ornamental plants to increase the probability of success with PGPR (1,3).

Certain kinds of plants, such as radish, respond more favorably to PGPR than others, probably because of the relatively short time of maturation for radish plants. However, even woody plants can respond to inoculation with PGPR as evidenced by growth stimulation of rough lemon and sweet orange seedlings (116% greater than the control) (11). A field experiment where almond seedlings were inoculated with *A. rhizogenes* and planted in sandy soil in Israel resulted in about 2 times more leaves per inoculated tree at 120 days, 30% greater stem caliper at 90 days, 43% longer branches at 90 days, and 65% longer branches at 120 days — compared to the noninoculated controls (33).

Since 1975, Schroth and co-workers have established 46 replicated field plots, each testing 3 to 6 different strains of rhizobacteria, to evaluate their ability to increase growth and yield of potatoes, radish, melons, lima beans, lettuce, and sugar beet. In all cases, specific rhizobacteria were isolated and tested which caused statistically significant increases in yield, ranging up to 144% in the case of radish. Other examples of statistically significant yield increases were: potato, 5 to 33% in 12 of 16 plots in CA and ID; sugar beet, 4.4 to 8.4 tons per hectare, with increases in total sugar from 20.7 to 26.9 cwt per hectare in 6 of 8 plots; radish, a short-growth period crop, exhibited spectacular increases of 60 to 144% in root weight in 7 trials.

Bacteria tested on seedpieces of a variety of potato cultivars grown in the field at three different locations in North Carolina gave significant yield increases of 1.17 to 1.37 over controls at two of the three sites (13).

Research in Czechoslovakia (37) also showed a growth and

yield increase from potato plants inoculated with rhizosphere bacteria. Again, results from greenhouse pot experiments were the most dramatic compared to field experiments. Potted tuber pieces inoculated with PGPR produced young potato plants that were 111% larger than the controls; seedpieces inoculated and planted to the field caused 4 to 30% improvement in plant growth and tuber yield.

Examples of Growth Reduction Caused by Rhizobacteria. As noted earlier, not all rhizobacteria are beneficial to plant growth (40). Reports from nearly every study of beneficial rhizobacteria have indicated that they commonly find, simultaneously, bacteria that are deleterious to plant growth. Only 2 to 5% of the bacteria isolated from the roots of plants in California caused a positive plant growth response, compared to 8 to 15% that were deleterious, causing stunting, root necrosis, and decreased stand counts (30). In Czechoslovakia, potato growth was retarded by as much as 66% below the controls (37). Even the "good guys" (PGPR) can enhance growth of one plant species but actually retard growth of another species (39).

Most bacterial strains tested on citrus seedlings and budlings in Florida were growth-inhibiting (causing up to 52% growth reduction) compared to the few that were stimulatory (11).

Deleterious rhizobacteria are not widely recognized as being in the same category as the "major" plant pathogens, but they may act as "minor" pathogens and retard plant growth. Control of these pathogens and other known parasites has been suggested (35) as a major contributing factor for the plant growth increases achieved following soil fumigation, chemical seed treatment, or use of certain antagonists for biological disease control.

Variable Results from Use of Rhizobacteria. Nearly all of the studies mentioned above also indicate that results from use of PGPR can be variable from one site to another, among different host species, or from one year to another, especially when the experiments are performed in the field.

The reasons for the frequent variability (6, 25, 27) in these experiments are not clear. The variability is often ascribed to changes in the activity of the rhizobacterium strain over time. The effect of bacterization is also dependent on the size of inoculum, which may be a reflection of the amount of growth-active substances produced by the strain (14).

Obviously, the rhizobacteria must function in a complex environment which is ever changing, and it is not surprising that variability is observed among data from bacterization ex-

periments. Indeed, it is impressive that we observe the uniformity that has been reported given the complexity of the experimental system! Our task is to gain a greater understanding of this system so that we can reduce this variability and manipulate it to the benefit of plant production.

GENERA OF BENEFICIAL AND DELETERIOUS RHIZOBACTERIA

Beneficial Rhizobacteria. Taxonomically, most of the rhizobacteria whether beneficial or deleterious fall into the *Pseudomonas fluorescens* — *P. putida* group (11, 13, 18, 22, 34). They typically produce a water-soluble fluorescent pigment which appear to play an important role in binding to iron in the soil and at the root surface to make it unavailable to the pathogens. Since iron is an essential element required by microbes to grow, the iron-deficient pathogens are unable to attack the plant, which results in protection and better growth.

Other genera of rhizobacteria have been reported occasionally as beneficial and include: *Agrobacterium* (26, 28, 33), *Azotobacter* (27), *Bacillus* (3, 28), and *Streptomyces* (8, 30). Undoubtedly there are other beneficial rhizobacteria yet to be identified.

Deleterious Rhizobacteria. At least seven genera of "deleterious rhizobacteria" (35) have been tentatively identified: *Enterobacter, Klebsiella, Citrobacter, Flavobacterium, Achromobacter, Arthrobacter,* and *Pseudomonas.* Other researchers have implicated *Bacillus* and *Streptomyces* spp. as agents that cause plant growth reductions (3, 5, 9).

POSSIBLE MECHANISMS BY WHICH BENEFICIAL RHIZOBACTERIA STIMULATE PLANT GROWTH

No single hypothesis has been accepted to explain the phenomenon by which bacteria stimulate plant growth; rather there may be two or more mechanisms that function together or at different times during changes in the environment and life history of the plant and bacterium. The following list includes potential mechanisms by which the beneficial rhizobacteria stimulate seed germination and/or plant growth:

Production of Growth Regulators. Bacteria, such as the pseudomonads, may increase plant growth by producing gibberellin-like compounds that are adsorbed by the roots (4, 10). Fifteen percent of the beneficial bacteria in another test (24) produced a different growth hormone (in vitro) — indole-3-acetic acid (IAA) but these IAA producing strains caused root deformities and decreased root elongation when applied to sugar beets.

Mineralization. The term "bacterial fertilizers" has been

used to describe the application of living bacteria to seeds, roots, or soil to improve crop yield, supposedly via a fertilizer effect. In Europe and the Soviet Union, bacterial preparations of *Rhizobium* are called "nitragen" (7). The Soviet agriculturalists applied other bacterial fertilizers such as "azotobacterin" (nitrogen fixers) prepared from *Azotobacter* spp. and "phosphobacterin" (for solubilization of phosphate rock) prepared from *Bacillus megaterium* var. *phosphaticum*. More than 35 million hectares of land were reportedly treated with these bacteria in Russia with reports of 10 to 20% increases in production for 50 to 70% of the crops tested (9). However, these reports have been criticized for the lack of good statistical design and analysis, thus throwing suspicion upon the claims of increased crop production.

It is difficult to measure whether the stimulated plant growth comes from a fertilizer response or displacement of undesirable rhizosphere microorganisms by the beneficial rhizobacteria or both (2).

Biological Protection of Roots. It is likely that one of the major mechanisms by which beneficial rhizobacteria aid plant growth is by displacement from the root of harmful microorganisms, either through exclusion from selected niches, substrate competition, or production of antibiotics or other biologically active substances that are toxic to these harmful microbes (19, 20, 32, 34). Many of the plant growth promoting rhizobacteria (PGPR) that have been studied were initially selected on the basis of inhibiting the growth of pathogens such as *Erwinia carotovora* (13, 18, 19, 22, 34), *E. stewartii* (11), and *Fusarium* (1, 11, 31, 38) in an *in vitro* plate assay.

If the PGPR are to exert a physiological and/or protective effect on plant growth they must obviously be able to actively colonize the root system rather than be passively adsorbed to the root surface. Binding experiments (15) and use of antibiotic resistant mutants of PGPR (17) all demonstrate that the successful PGPR do aggressively colonize the roots.

The data suggest that these PGPR are functioning much like biological disease control agents. As Cook and Baker (8) point out, plant growth responses are to be expected when the roots and rootlets are maintained in a state of health necessary for uptake of nutrients and synthesis of growth factors for the tops.

Other Mechanisms. The biological diversity observed in nature makes it obvious that there must be other mechanisms by which PGPR function to enhance plant growth. These new mechanisms will likely be discovered or identified at some point in the future if we but keep our minds open to other possibilities.

FINDING AND TESTING BENEFICIAL RHIZOBACTERIA
(PGPR)

Most of the PGPR have been isolated from the roots of plants (11, 13, 16, 34). Typically, the bacteria are isolated, purified, and tested in vitro for antibiosis against some known plant pathogen. Most of the strains that have ultimately proven to be good PGPR also produced antibiotics against a wide spectrum of organisms in vitro. However, antibiotic production in vitro was also common to many of the rhizobacteria which never showed any efficacy in greenhouse or field tests. Conversely, some strains have proven to be effective PGPR, but they did not produce antibiotics in vitro. Strains that show antibiotic activity or enhance plant growth are inoculated to plant propagules and tested for their ability to enhance plant growth in comparative pot tests with uninoculated controls. Strains that show PGPR characteristics are then tested in the field. Since only about 2 to 5% of the strains isolated from the root system provide a positive growth response (30), one must test a large number of strains.

FACTORS AFFECTING THE EFFICIENCY OF PGPR

Based on the literature reports, there are certain conditions that accentuate the growth promoting ability of beneficial rhizobacteria. For example, plants inoculated with PGPR in greenhouse studies typically show markedly greater growth responses than the same treatments in the field (2, 3, 11, 13, 17, 23, 34).

The best plant responses to PGPR usually occurred when high populations of rhizobacteria were applied to the seed (21, 34, 37). Vrany and Fiker (37) also observed that bacterized potato plants produced better than the controls when grown under shortened photoperiods (less than 12 hr). Even the presence of different kinds of fungi in the root environment can influence the way plants respond to bacterization (31).

In addition to specificity of the PGPR for particular crop species or cultivars (2, 13, 39), there appears to be a specificity of PGPR for certain soils. Strain SH5 increased sugar beet yields in several California test sites but failed to do so in two consecutive years in Idaho.

HOW AND WHEN TO APPLY PGPR

Beneficial rhizobacteria have been applied to seeds or vegetative propagules in various ways: liquid suspension and gels (34), as a soil drench (11,12), as a powder formulation (21), or in peat — but one of the best methods to enhance survival and activity, especially when seed were planted in dry soil, occurred with PGPR-pelleted seed (34).

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Placing the PGPR directly on the seed or plant parts in high numbers, and under conditions favorable for maximum colonization, gives them a competitive advantage over the other rhizosphere microbes. PGPR can be applied to seed or plant parts anytime before planting, but care should be taken to protect the treated propagules from excess desiccation, sunlight, heat, or anything else that would kill or dilute the viable concentration of rhizobacteria before they are planted. The planting site should be prepared well. Irrigation of dry soil after planting may be needed to help maintain a high population of PGPR.

Suslow and Schroth (34) discuss the various alternatives of treating seed, describe in detail the kinds of materials tested as bacterial preservatives and adhesives, and provide data of shelf life of the rhizobacteria pelleted on seed.

SUMMARY AND CONCLUSIONS

Bacterization Works With a Variety of Plants. Plant growth promoting rhizobacteria (PGPR) have been shown to increase the growth of both herbaceous and woody types of plants. The kinds of plants reported to respond positively to PGPR include vegetables, cereals, row crops, floral crops, citrus, almond, olive, and apple trees. PGPR can be applied to seeds, cuttings, bare-rooted seedlings, and as a soil drench over roots of potted plants.

Greenhouse vs. Field. The largest growth responses from applications of PGPR to plant propagules were observed when the plants were grown under greenhouse conditions. Results from field tests were not as pronounced as those from greenhouse studies and may vary from one planting site to another. The correlation between results from greenhouse and field tests was generally low.

Beneficial and Harmful Bacteria. Beneficial rhizobacteria have been isolated from all of the plants examined and from all soil types tested, regardless of whether the soils were disease-suppressive or nonsuppressive. Of the bacteria isolated from roots, only about 2 to 5% enhanced plant growth, whereas 8 to 15% were deleterious and caused stunting, root necrosis, or reduced stands.

Inoculum Concentration and Colonizing Ability Important. The concentration of bacteria applied to the plant propagule is very important; application of high concentrations usually resulted in the best growth promotion and yield. Equally important is the ability of the PGPR to colonize the root system and to survive in high numbers (near 10^5 per cm of root) during the growing season.

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Mixtures of PGPR More Effective. In some experiments, mixtures of two or more PGPR caused greater yield increases than a single strain, perhaps due to each strain colonizing a different preferential site on the root of one being more active at any time than another during maturation of the plant.

Selecting PGPR Based on Antibiotic Production vs. Growth Enhancement. Antibiotics are produced *in vitro* by most of the rhizobacteria (including the PGPR) against a wide array of microorganisms. However, some nonproducers were also efficacious as PGPR. Antibiotic production *per se*, therefore, is not the best criterion for selecting a candidate PGPR. Rather it has been suggested that the most effective strains have been selected on the basis of a plant growth response.

Reasons for Failure of PGPR. Lack of establishment of the PGPR on the root appears to be the most common reason for failure of the PGPR to increase plant growth, which probably is due to the poor condition of the inoculum on the bacterized seed or soil dryness at planting time. Use of dry formulations of PGPR or seed pelletized with PGPR resulted in better survival of the bacteria on seed than when aqueous suspensions of PGPR were used.

CONCLUSIONS

There are some striking reports of plant growth promotion following application of beneficial rhizobacteria to plant propagules, which indicates that the phenomenon is real. Variability between tests (especially in the field) is a nagging problem that has not been eliminated. The factors contributing to this variability are poorly understood or unknown, and commercialization of the PGPR will probably be slowed until this variability is reduced and the expected yield benefits become more predictable. At present it would appear that the use of PGPR is still promising but in a juvenile stage of development. Perhaps the best approach would be to concentrate on developing a PGPR *system for such things as greenhouse-produced crops*, plantlets produced via tissue culture, and bedding plant transplants. Such a system would have fewer variables to contend with and opportunities of modifying the environment to aid the PGPR. In any case, it appears that development of these bacteria into a reliable commercial product is still a few years away, and that it will require considerable research and funds to develop a good predictable system.

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CUSTOM SEED PREPARATION FOR OPTIMUM CONIFER PRODUCTION

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I would first like to describe how we test and stratify conifer seed at Brown Seed Company and then discuss some of the different methods which can be used for handling the more difficult species.

The germination possible for a seed lot is determined by the basic soundness of the seed and the care given that seed during collection, processing, and storage. After the seed comes out of freezer storage we then attempt to design or "customize" our treatment procedures for each lot to obtain this maximum possible germination.

SEED TESTING

In order for any program of so-called custom stratification to work, the seed handler needs as much information as possible about the seed lot. This includes:

1. *Purity Test.* This test determines the percentage of pure seed in a sample. For container sowing the seed should be as clean as possible and handpicking is available to bring the seed to 100% purity. A purity test is also necessary to calculate with accuracy the amount of seed needed for sowing.

2. *Seed Count.* The seed count determines the number of seeds found in a pound or gram of pure seed in a lot. The number of seeds/lb. can vary widely within a species and this information is essential to calculating seed needs.

3. *Standard Germination Test.* This test compares the actual germination of chilled with non-chilled seed. The results are especially useful if two different chill periods are used (Table 1). Besides being the best tool for deciding the optimum period of stratification, the standard germination test will also usually indicate if a customer is likely to have mold problems with his seed.