

Plant growth promotion mediated by bacterial rhizosphere colonizers

JOSEPH W. KLOEPPER¹, ROBERT M. ZABLOTOWICZ, ELIZABETH M. TIPPING and RAN LIFSHITZ

¹*Department of Plant Pathology, Alabama Agricultural Experiment Station, Auburn University, Auburn, AL 36849–5409, USA and Allelix Crop Technologies, 6850 Goreway Drive, Mississauga, Ontario, Canada L4V 1P1*

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Abstract

Plant growth-promoting rhizobacteria (PGPR) represent a diverse subgroup of rhizosphere-colonizing bacteria. PGPR were first described for root crops in the 1970s when the use of antibiotic resistance made possible the monitoring of introduced bacteria in soil. In recent years, the host list of PGPR has grown to include barley, bean, canola (rapeseed), cotton, maize, peanut, rice, vegetables, wheat, and woody species. In addition to increasing crop yields, different strains of PGPR can exert various effects on plants including biological control of soil-borne pathogens, promotion of legume nodulation by nitrogen-fixing rhizobia, and enhancement of seedling emergence rates. Reported mechanisms of action for PGPR have focussed on the indirect mechanisms of siderophore, antibiotic, or hydrogen cyanide production. Such indirect mechanisms reduce the population densities of deleterious microorganisms and thereby result in increased plant growth. Direct growth promotion by PGPR in the absence of deleterious microorganisms has been recently described.

Background and definition of terms

In the last decade, the term “rhizobacteria” has been accepted to describe rhizosphere bacteria which exhibit root colonization (Schroth and Hancock, 1982). Root colonization is a process whereby the bacteria survive inoculation onto seeds or into soil, multiply in the spermosphere in response to seed exudates rich in carbohydrates and amino acids (Kloepper *et al.*, 1985), attach to the root surface, and colonize the developing root system. Hence, rhizobacteria are efficient microbial competitors in the root zone which displace native root-colonizing microorganisms (Kloepper and Schroth, 1981a,b) and which persist through the mid-stages of the host plant ontogeny at population densities of Log 3 to Log 6 cfu/g root fresh weight (Anderson and Guerra, 1985; Bahme *et al.*, 1988; Howie and Echandi, 1983; Kloepper *et al.*, 1980a,b; Polonenko *et al.*, 1987).

In the past few years, the term “rhizosphere colonization” has been suggested as an alternate term to root colonization. While one may argue that the choice of terms is a matter of semantics, there is also a functional difference. Root colonization applies to those bacteria which are specifically resident in two locations—the outside of root surfaces and the internal areas of roots (endocolonizers). Rhizosphere colonization denotes a larger ecological niche encompassing root colonization and including bacterial populations which are not attached to the root, but which are in close proximity. The term “PGPR” for “plant growth-promoting rhizobacteria” was first coined in 1978 (Kloepper and Schroth, 1978) to describe a subset of rhizobacteria which induce increased plant growth after inoculation onto seeds. The first reports documenting plant growth and yield increases with PGPR involved root crop hosts such as potato (Burr *et al.*, 1978; Geels and Schippers, 1983; Howie and Echandi,

1983; Kloepper *et al.*, 1980a; Vransy and Fiker, 1984), radish (Kloepper and Schroth, 1978), and sugarbeet (Suslow and Schroth, 1982).

Work on mechanisms for growth promotion by these PGPR indicated that the strains increased growth indirectly by changing the microbial balance in the rhizosphere. Iron-chelating siderophores (Kloepper *et al.*, 1980a,b; Schippers, 1988), antibiotics (Gardner *et al.*, 1984; Weller, 1988), and HCN (Ahl *et al.*, 1986; Stutz *et al.*, 1986) are produced by some PGPR and have been implicated in reductions of plant pathogens and deleterious rhizobacteria. HCN has also been implicated in direct growth promotion by the discovery that certain deleterious rhizobacteria produce HCN, which restricts plant growth, and that these deleterious rhizobacteria are inhibited by some PGPR strains (Schippers, 1988).

New directions

In the past 5 years, PGPR research has continued in three additional directions. First, significant work has been done on "nonroot crops" as hosts and has demonstrated that the majority of crop plants are conducive to PGPR-induced growth promotion. A second area of new direction involves the characterization of *specific* effects of PGPR *i.e.* effects other than yield promotion. These studies have resulted in the designation of two new subclasses of PGPR and have shown that PGPR can also be used as biological control agents. The third area, mode of action work, has revealed that some PGPR strains may promote plant growth directly, *i.e.* in the absence of pathogenic or deleterious microorganisms.

Host range for PGPR

Barley

Iswandi *et al.* (1987) investigated the effect of "rhizopseudomonad" strain 7NSK2, isolated from a hydroponic culture of barley, on barley growth in soil. Dry weight of plants following PGPR treatment was increased from 5 to 20% compared to controls without PGPR.

Bean

A *Pseudomonas putida* strain colonized lateral roots and main roots of bean (*Phaseolus vulgaris* L.) in hydroponic culture (Anderson and Guerra, 1985) and resulted in increased lignin content of roots. Plant weight was increased by treatment with *P. putida* after inoculation with *Fusarium solani* f. sp. *phaseoli*.

Canola (Rapeseed)

The potential for obtaining yield increases on canola (*Brassica campestris* L and *B. napus* L.) with PGPR was reported in 1988 (Kloepper *et al.*). Over 4,000 bacterial strains were collected from root zones and were individually evaluated for growth at 4–14°C, metabolism of seed exudates, chemotaxis toward asparagine, and root colonization; 887 of these strains were tested for growth promotion in greenhouse trials with field soils. Thirty-five strains increased leaf area in two of three repeat tests. Thirteen strains increased yields up to 57% compared to controls in one of two test years. Three strains increased yields by 6–13% compared to controls in two-year, all-site averages. PGPR strains identified in this study included *P. putida*, *P. fluorescens*, *Serratia liquefaciens*, *P. putida* biovar B, and *Arthrobacter citreus*.

Cotton

Two strains of *P. fluorescens*, which were screened for *in vitro* antagonism to plant pathogenic fungi and bacteria, increased height of 4 week-old cotton in greenhouse trials with field soil by 8 and 40% compared to controls (Sakthivel *et al.*, 1986). *Bacillus subtilis* strain A-13 (Broadbent *et al.*, 1977) has shown promise as a PGPR and a biological control agent on cotton (Backman and Turner, 1989; Greenough and Batson, 1989). The strain is manufactured by Abbott Labs and is licensed to Gustafson Corporation for peanut and cotton. The product is sold under the tradename 'Quantum-4000'.

Maize

The U.S. biotechnology company Agracetus (Middleton, Wisconsin) has conducted field evaluations of pseudomonad PGPR on maize for 5 years (A. Paa, personal communication). The strains were selected as growth promoters in

greenhouse trials under various growth conditions where visual growth promotion and increased dry weight of plants were noted. In field trials, the strains colonize roots at average population densities of Log 3 cfu/cm root and induce yield increases of 3 to 3.5 bu/acre compared to controls in all-site, five-year averages.

Peanut

The A-13 strain of *Bacillus subtilis* (Broadbent *et al.*, 1977) was first found to enhance growth of peanut by field work at Auburn University in 1980 (P.A. Backman, personal communication). Further field trials indicated that the strain induced yield increases averaging 14 to 24% compared to controls in a two-year study in Alabama (Clay, 1986) and 6 to 16% in a three-year study in Texas (Jaks *et al.*, 1985). These results prompted the commercialization of the inoculant, as described above in the cotton section.

Further investigations into the ecology and mechanisms of strain A-13 on peanut indicate that, unlike most strains of *Bacillus* spp., A-13 is a root colonizer, according to the definition above. Turner and Backman (1989) reported root colonization of four peanut cultivars by strain A-13 at average population densities of Log 4.3 to Log 4.7 cfu/g root in field trials 140 days after planting. Root colonization was associated with increased overall plant growth, faster growth of roots, and enhanced plant nutrition. Hence, *B. subtilis* strain A-13 is clearly a PGPR.

Rice

Sakthivel *et al.* (1986) isolated *P. fluorescens* strains from rhizospheres of various crop plants and selected strains which demonstrated broad-spectrum *in vitro* antibiosis toward fungal and bacterial pathogens. When coated onto rice seeds planted in pot trials with field soil, four strains induced increases in plant height ranging from 12 to 24% greater than controls.

Vegetables

The effect of several root-colonizing bacteria on vegetables was reported in a binational collaboration (Elad *et al.*, 1987). Seed treatment with bacteria in pot trials increased dry weight two weeks after planting for tomato, pepper, tobacco, cucumber and melon. Work at Allelix

Crop Technologies, a Canadian biotechnology company, has evaluated PGPR, which were initially selected to enhance canola growth, on vegetables (R. Lifshitz, personal communication). Several strains of fluorescent pseudomonads and *Serratia* spp. promoted growth as evidenced by enhanced dry weight of shoots and roots in greenhouse trials with field soil on tomato, cucumber, sweet corn, carrot and celery.

A research team in California investigated the effect of PGPR on celery (M.N. Schroth, personal communication). Thirty root-colonizing bacteria, including some confirmed as PGPR on other crops, were screened directly in the field for growth enhancement of celery in the presence of indigenous *Fusarium oxysporum* f.sp. *apii*. Four strains were selected for use in three follow-up replicated trials. A pronounced genotypic specificity in response to PGPR inoculation was noted. One PGPR strain induced significant increase in early growth (fresh and/or dry weight increases) in all three trials and significant yield increases ranging from 12 to 15% greater than controls in two trials. The same strain had no effect when tested on another cultivar.

Wheat

Several recent reports from four different research groups have confirmed that PGPR can promote growth of wheat. Weller and Cook (1986) found that 17 of 64 bacterial strains isolated from wheat rhizospheres increased growth of wheat in greenhouse trials. In field trials with four strains, significant increases following seed treatment with bacteria were noted in stand, plant height, number of heads and/or grain yield. No PGPR increases occurred in comparison to metalaxyl controls, which suggests that the growth promotion by PGPR resulted from *Pythium* control.

The importance of *Pythium* to the observed growth promotion was confirmed in a subsequent study by Becker and Cook (1988). Approximately 120 of 350 strains, which were isolated from wheat rhizospheres exhibited *in vitro* antibiosis toward *Pythium*. *In vitro* antibiosis was correlated with increased growth of wheat in greenhouse trials with soil naturally infested with *Pythium*. When 10 of these PGPR were tested in

Pythium-free soil (fumigated), no growth promotion was observed.

In another study with wheat, deFreitas and Germida (1989) developed a consistent growth chamber assay for screening PGPR and found 9 strains which consistently promoted plant growth in field soil. These strains increased plant height, root and shoot biomass, and the number of tillers. No symptoms of Pythium were observed in nontreated controls. The role of the plant in wheat growth promotion by PGPR has also been investigated. Significant genotype variation was observed in response to PGPR inoculation (Ålström and Gerhardson, 1988). In another study, 6 of 7 strains of *Bacillus*, which were isolated from rhizospheres of cv 'Katepwa', promoted growth on 'Katepwa' but not on the cultivar 'Neepawa' (Chanway *et al.*, 1988). Hence, cultivar specificity must be considered in analysis of PGPR results.

Woody species

Guayule (*Parthenium argentatum*) in a perennial, semi-desert shrub from which latex is extracted. Two pseudomonad strains isolated from roots increased shoot dry weight in greenhouse trials by four-experiment averages of 17 and 55% respectively (Olsen and Misaghi, 1984). After transplanting to the field, no significant differences occurred in shoot dry weight of plants treated with bacteria compared to controls.

Caesar and Burr (1987) tested 226 strains of rhizosphere bacteria isolated from apple and rosaceous wild hosts for growth promotion of apple seedlings six weeks after seed treatment. Thirteen strains induced significant increases in fresh weight ranging from 23 to 47% greater than controls. Four bacterial strains also induced significant weight increases ranging from 33 to 121% when applied to rootstocks in greenhouse trials.

PGPR have also been reported on citrus (Gardner *et al.*, 1984) as part of a study to determine the effect of 43 bacterial strains isolated from rough lemon roots on growth of lemon and orange seedlings. Both stimulatory and inhibitory effects on plant growth resulted 10 mo. after inoculation, with ranges from +116% to -52% compared to controls.

Specific effects of PGPR

Biological control

The distinction between biological control and growth promotion is vague at best. As listed in the above summary by crop, bacteria which are selected as potential biological control agents based on *in vitro* antibiosis toward pathogens may also increase plant growth. The general area of biological control by bacterial agents was recently reviewed (Weller, 1988), as was the use of rhizobacteria in biological control (Schippers, 1988), and therefore, the discussion here focuses on the use of bacteria, initially selected for growth promotion, as biological control agents.

The first reports of PGPR on potato noted that growth promotion was associated with a reduction of total fungal propagules on the rhizoplane (Klopper and Schroth, 1981b). This suggested that select PGPR could also be used to reduce pathogen populations in the root zone. Some potato PGPR were subsequently shown to reduce populations of the pathogen *Erwinia carotovora* (Klopper, 1983).

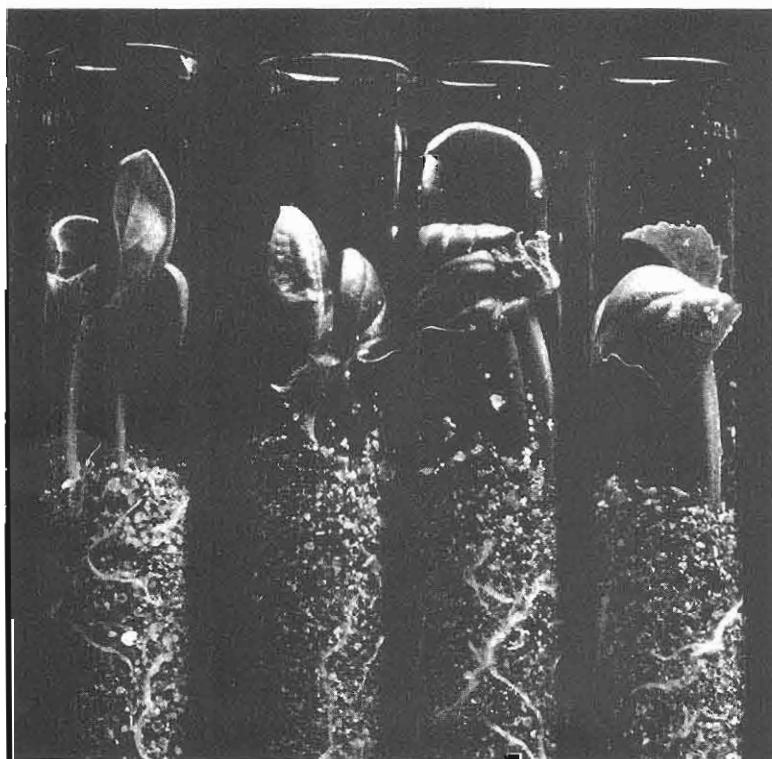
For the past three years, the group at Allelix Crop Technologies Inc has investigated the potential relationship between growth promotion and biological control by evaluating PGPR selected for canola growth promotion in specific disease assays. The disease assays include a sand + vermiculite assay for *Rhizoctonia solani* on canola, a soil assay for Pythium on tomato, cotton, soybean, canola, and whitebean and a sand + vermiculite assay for Pythium on canola and cucumber. In all assays, selected PGPR strains show biological control activity similar to chemical controls, while others have no effect. Some of the PGPR with biocontrol activity show *in vitro* antibiosis toward the pathogen, but others do not.

A representative biocontrol response induced by a PGPR strain in the cucumber/Pythium assay is shown in Figure 1. This strain does not show *in vitro* antibiosis toward Pythium.

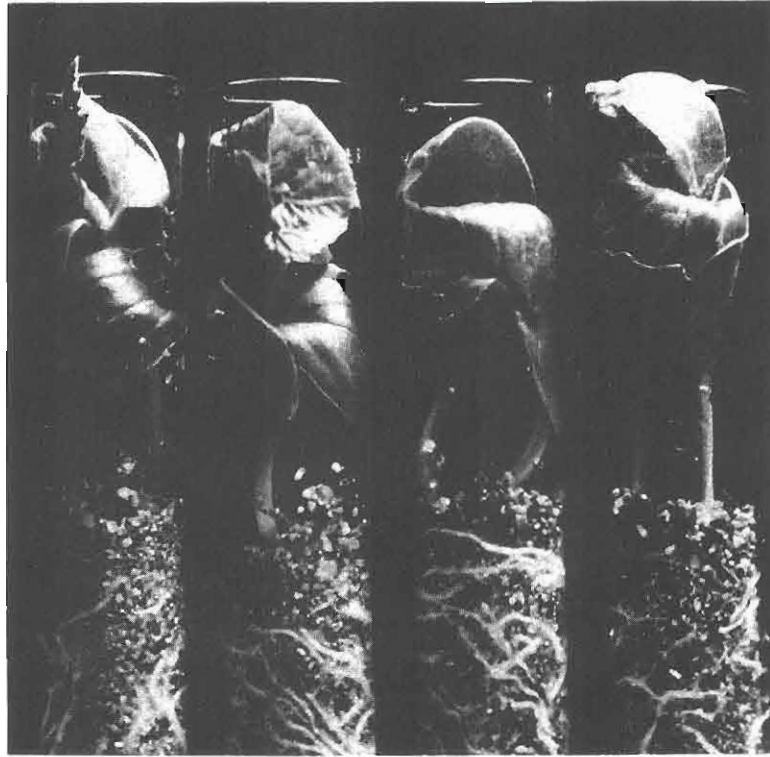
Data from a representative canola/*Rhizoctonia* assay are shown in Figure 2. Controls treated with the pathogen, but not with bacteria, increased stand through day 8 and then declined due to post-emergence damping off. Fungicide-



(a)



(b)



(c)

Fig. 1. Biological control of *Pythium* with PGPR. Representative results from a *Pythium* assay on cucumber are shown. All treatments received *Pythium* inoculum mixed into the sand + vermiculite planting medium. Treatment A is the disease control *i.e.* no other treatment; treatment B is the metalaxyl fungicide control; treatment C received seed inoculation with a PGPR strain at planting time.

treated controls (Vitavax) also increased through day 8 and then declined slightly. Treatment with different PGPR consistently resulted in increased final stand counts and sometimes resulted in control equal to the fungicide.

Further data on biological control by PGPR are shown in Table 1 for whitebean in raw field soil amended with *Pythium* at 100 propagules per gram. Best emergence, final stand, and shoot dry weight resulted from treatment with the metalaxyl control; however, several PGPR strains induced a significant increase in final stand and shoot dry weight compared to the nontreated control.

These examples illustrate that strains selected for growth promotion may also provide protection from plant disease. The work to date suggests that such biocontrol PGPR consist of two groups of strains: those which control disease via antagonism of the pathogen, and those which

control the disease via changing the host plant's susceptibility *e.g.* induced resistance. The identification of this second class of strains affords an opportunity to expand the list of known mechanisms for biological control by bacteria beyond the current mechanisms for antibiosis, competition, and exploitation. For example, a PGPR strain, which produces no *in vitro* antagonism toward a fungal pathogen and yet protects against the disease, is more likely to be operating by changing the host's susceptibility than by inhibiting the pathogen.

Nodulation promotion on legumes

Another specific effect which PGPR can have on plants is to increase the symbiotic nodulation of legumes by nitrogen-fixing rhizobia. Enhanced nodulation of *Phaseolus vulgaris* following inoculation with *Pseudomonas putida* strain M 17 was reported by Grimes and Mount (1984). In

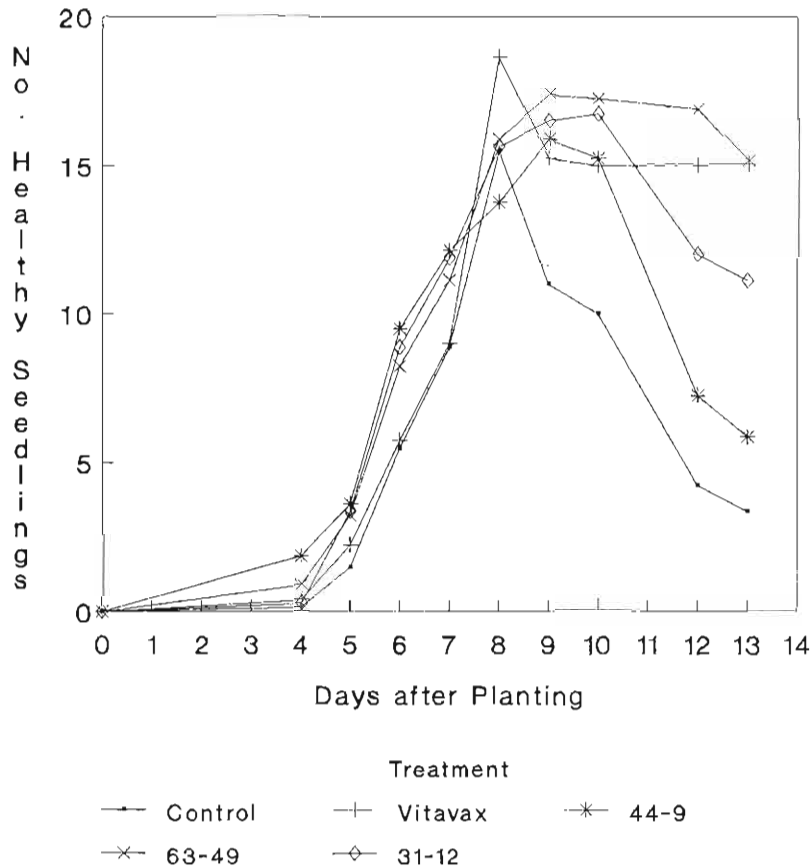


Fig. 2. Biological control of *Rhizoctonia solani* with PGPR. Representative results from a *Rhizoctonia solani* assay on canola are shown. All treatments received *Rhizoctonia* inoculum mixed into the planting medium. Vitavax is the fungicide control. PGPR strains 63-49, 31-12, and 44-9 all gave early protection from damping off, and strain 63-49 resulted in final stands equal to Vitavax.

greenhouse and field trials, treatment with strain induced increased nodulation by *Rhizobium phaseoli*. M 17 is apparently not a PGPR strain, as growth promotion was, with one exception, not observed in greenhouse or field trials.

In another study with soybean (Polonenko *et al.*, 1987), PGPR strains were found generally not to interfere with nodulation by *Bradyrhizobium japonicum* strain 110. Nine of 18 tested root-colonizers significantly increased the weight of nodules in soil. Subsequent work by this group has confirmed that a subset of PGPR strains act as "Nodulation-Promoting Rhizobacteria (NPR)" in coinoculation studies with rhizobia on legumes. Data showing the effect of three NPR strains on nodulation of soybean by native soil rhizobia are shown in Table 2. Aver-

age nodulation from trials at two locations on two cultivars was 19 to 47% greater than controls. Yield was not affected by NPR inoculation in these trials. Mechanisms of nodulation promotion by the NPR strains have not been determined. PGPR strain A-13 (see above sections on cotton and peanut) also shows NPR activity (Turner and Backman, 1989). In field trials with peanut, nodulation was assessed with a 1 to 5 scale for the upper 20 cm of taproot with attached secondary and feeder roots where 1 = no nodules and 5 = 100%. The average nodulation rating for treatment with A-13 + fungicide was 4.3 compared to 3.5 for treatment with the fungicide alone ($LSD_{0.05} = 0.52$). Treatment with A-13 also induced significantly higher levels of nitrogen in leaves as well as yield increases.

Table 1. Screen of plant growth-promoting rhizobacteria strains for biological control of *Pythium ultimum* on whitebean in a soil system^a

Treatment	After planting (DAP)						Final stand	Dry weight per pot ^d		
	4 DAP		7 DAP		13 DAP			No.	%	
	No. ^b	% ^c	No.	%	No.	%				
61-9A	2.0	82	4.3	48*	4.9	29*	5.1	31*	1.22	59*
GR12-2	1.7	55	3.9	34	4.6	21	4.8	23	1.04	36
63-49	1.8	64	4.6	59*	5.2	37*	5.4	38*	1.04	36
2-114	1.9	73	4.8	66*	5.6	47*	5.4	38*	1.04	36
1-102	3.2	191*	5.1	76*	5.5	45*	5.5	41*	1.23	61*
36-43	1.9	73	3.9	34	4.1	8	4.4	13	0.90	18
31-12	1.3	18	3.9	34	4.6	21	4.2	8	0.91	20
G2-8	1.6	45	3.5	21	4.6	21	4.5	15	0.89	17
G20-18	1.9	73	3.8	31	4.8	26	5.0	28*	1.10	44
44-9	1.0	-11	4.0	38*	4.6	21	4.9	26	1.05	37
34-13	2.0	82	4.4	52*	5.1	34*	5.4	38*	1.29	69*
2-68	2.6	136*	4.8	66 ¹	5.5	45*	5.7	46*	1.29	69*
Methylaxyl ^c	4.6	318*	5.7	97*	5.8	53*	5.9	51*	1.50	97*
Pythium control	1.1	-	2.9	-	3.8	-	3.9	-	0.76	-
Nontreated control	1.5	36	3.6	24	4.2	11	4.4	13	1.00	31
LSD $P=0.05$	1.1		1.1		1.1		1.1		0.33	

^a Raw field soil was amended with 100 propagules/g of *Pythium* using cornmeal/sand inoculum;

^b Average number of plants per pot based on 10 replications, each with 6 seeds;

^c Percentage increase over *Pythium* control;

^d Dry Weight (g) of shoot;

^e Apron 70SD seed treatment (350 mg metalazyl and 350 mg thiram ai/kg seed) is the fungicide control.

* Significantly greater than *Pythium* control at $p=0.05$.

Emergence promotion by PGPR

Select PGPR strains were found to enhance emergence of soybean and canola in greenhouse studies with field soils maintained at cold temperatures; the bacteria were termed "Emer-

gence-Promoting Rhizobacteria (EPR)" (Kloeppe *et al.*, 1986). EPR increased the rate of seedling emergence and the final stand in the absence of disease pressure.

Subsequent work at Allelix Crop Technologies

Table 2. Effect of 3 plant growth-promoting rhizobacteria strains on nodule mass and yield of 2 soybean cultivars at two Ontario field locations^a

Treatment	Cultivar maple arrow		Cultivar evans		Average Increase Compared To Control
	Georgetown	Milton	Georgetown	Milton	
<i>Nodule mass (mg/plant)</i>					
G11-32	278 a ^b	166 a	146 ab	240 a	+47%
G2-26	266 a	152 ab	63 c	246 a	+27%
86-64	166 b	154 ab	99 b	247 a	+19%
Control	178 b	109 b	118 ab	154 b	-
<i>Yield (Kg/ha)</i>					
G11-32	3604 a	3415 a	nd ^c	3362 a	-2%
G2-26	3695 a	3636 a	nd	3315 a	+1%
86-64	3654 a	3167 a	nd	3443 a	-5%
Control	3654 a	3352 a	nd	3552 a	-

¹ Values are means of eight replications. All plots received granular peat inoculum of *Bradyrhizobium japonicum* strain 122.

^b Means followed by the same letter do not differ significantly at $P=0.05$.

^c nd = not determined.

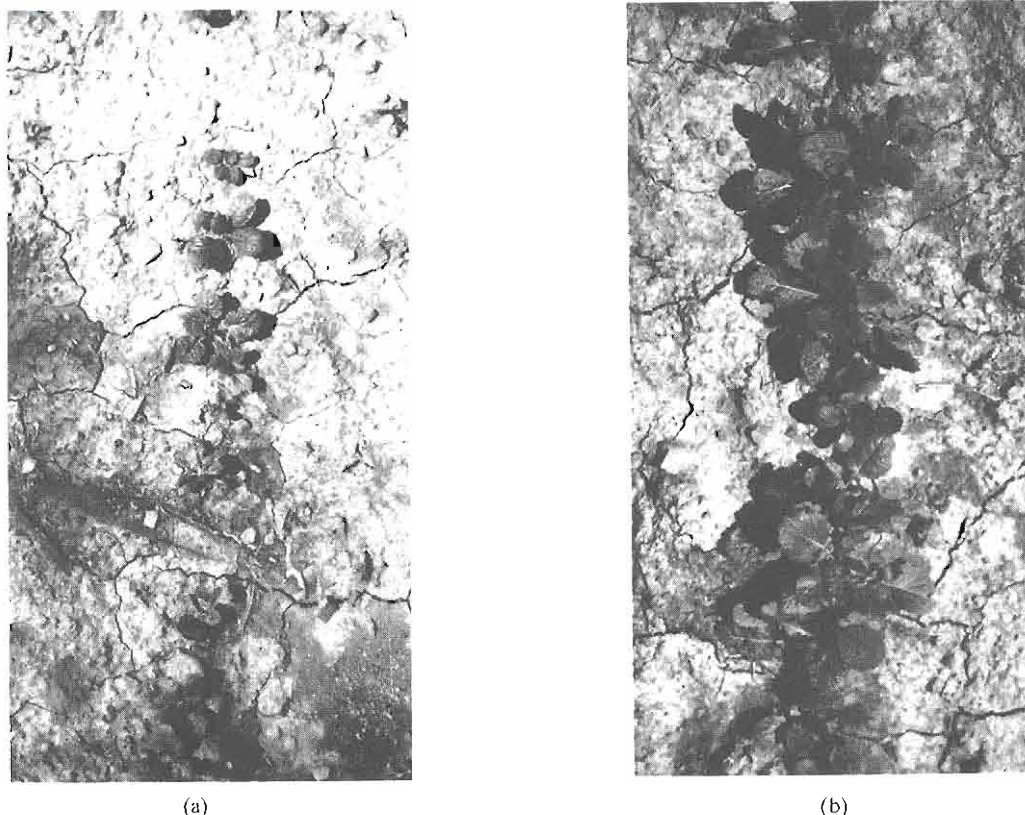


Fig. 3. Promotion of seedling emergence with PGPR. Figure depicts field results on canola. Treatment A is the nontreated control; treatment B received seed inoculation of PGPR.

has confirmed that EPR strains may promote emergence under field conditions. Figure 3 shows a typical field response for canola where seedling emergence rate was increased by treatment with EPR. With canola, the emergence enhancement is associated with an observable increase in leaf area. Increased emergence following inoculation with EPR, which were originally selected for growth-promotion activity on canola or soybean, has been detected with tomato, carrot, wheat, maize, whitebean and alfalfa (R. Lifshitz, personal communication). Two other recent studies have confirmed that select PGPR strains can increase seedling emergence. deFreitas and Germida (1989) found that 7 of 9 PGPR strains tested on wheat decreased emergence in a low fertility field soil; however, 2 strains significantly increased emergence in a high-fertility soil. In field trials with PGPR strain A-13 at three planting dates on peanut, Turner

and Backman (1989) observed significant emergence enhancement at the earliest planting date but not at the subsequent two dates.

Mode of action work

Studies on mechanisms by which PGPR increase growth have focussed on the indirect mechanisms of siderophore, antibiotic, or hydrogen cyanide production and the associated reductions in population densities of deleterious microorganisms in the rhizosphere. In contrast, direct mechanisms are those whereby the PGPR strain exerts the primary effect on the plant without regard to indigenous rhizosphere microflora.

Direct-acting PGPR were described in 1987 (Lifshitz *et al.*) in a study with canola PGPR. A growth pouch assay was developed which allowed evaluation of PGPR strains for root elongation of seedlings under gnotobiotic conditions.

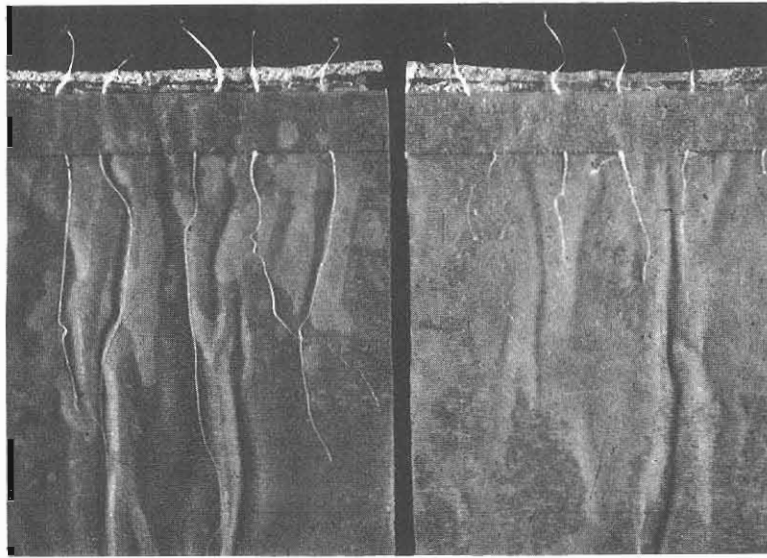


Fig. 4. Direct growth promotion by PGPR. Seeds of canola plants on left were soaked in sterile buffer solution prior to planting. Seeds of plants on right were soaked in PGPR suspension prior to planting. The assay is conducted in sterilized cellophane growth pouches, which are incubated 6 days.

The *P. putida* strain GR12-2 was found to induce consistently a significant elongation of roots compared to controls (Fig. 4). Root elongation was also associated with enhanced shoot height and ^{32}P uptake by roots and shoots. Additional work assessed the direct growth promotion of PGPR from canola in a tube assay using a sterilized mix of sand and vermiculite (Table 3). In this study, EPR strains which increased seedling emergence in field soils retained activity under gnotobiotic conditions. All 6 EPR strains induced a significant ($P = 0.05$) increase in emergence rate and

shoot dry weight of seedlings grown at 16/12 C, while no significant increases resulted from treatment with the fungicide Vitavax.

Direct growth promotion by PGPR was reported by two other groups in 1989. Defago *et al.* (1989) demonstrated that PGPR strain CHAO (Stutz *et al.*, 1989) increased root hair formation in a gnotobiotic assay. deFreitas and Germda (1989) observed that under gnotobiotic conditions, some wheat PGPR induce more lateral root hairs and longer roots compared to controls.

Table 3. Emergence enhancement by plant growth-promoting rhizobacterial on canola in sterilized sand + vermiculite at 16/12°C^a

	5 DAP	6 DAP	7 DAP	8 DAP	9 DAP	10 DAP	11 DAP	12 DAP	Dry weight ^b
Non teated	1	8	15	24	33	35	39	39	111
Vitavax ^c	2	8	12	21	35	39	42	46	89
GR12-2	12	41*	66*	71*	78*	82*	83*	84*	177*
44-9	7	39*	44*	76*	80*	83*	85*	87*	190*
31-12	15	42*	66*	68*	77*	79*	79*	79*	176*
36-43	10	36*	49*	59*	64	65*	66*	69*	160*
61-9A	32*	59*	62*	70*	73*	73*	76*	76*	173*
1-102	20*	40*	47*	49*	64*	68*	69*	74*	156*
L.S.D. ($P = 0.05$)	15	18	17	17	17	18	17	20	42

^a Average percentage emergence, based on 8 replications, each with 20 seeds;

^b Dry weight (g) of shoots;

^c Vitavax RS at 1.26 g ai/kg seed for carbathion and 2.25 g ai/kg seed for thiram.

* Significant increase compared to non-treated control at $P = 0.05$.

Conclusions

Based on the reports summarized above, PGPR research is moving from the descriptive stage to the stage of investigating mechanisms. The descriptive work demonstrated that specific PGPR strains may have diverse beneficial effects on plants, including biological control. Hence, PGPR may be useful components of microbial inoculants for crop improvement and should be included in strategies for increasing crop production.

Early studies on mechanisms suggest that PGPR may produce several different metabolites which stimulate plant growth directly or indirectly. Further elucidation of mechanisms will lay the foundation for understanding and manipulating the genetic control of growth promotion. In addition, details on mechanism will aid efforts to increase consistency of performance by allowing the development of criteria to predict when a plant may benefit from PGPR treatment.

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