Role of Deleterious Rhizobacteria as Minor Pathogens in Reducing Crop Growth

T. V. Suslow and M. N. Schroth

Former graduate student and professor, Department of Plant Pathology, University of California, Berkeley 94720.
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ABSTRACT

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Various strains of root-colonizing bacteria were pathogenic on sugar beet seedlings and were termed deleterious rhizobacteria (DRB). These DRB were a major component of the bacterial microflora of field-grown sugar beet roots. Pelleting DRB on sugar beet seed, at populations of 10^6 colony-forming units per seed, caused reduced seed germination, root distortions, root lesions, reduced root elongation, increased infection by root-colonizing fungi, and significantly decreased plant growth. These effects were observed in sterile polyester seed growth pouches containing Hoagland's solution, in U.C. soil mix, and in field soil. Reductions in fresh and dry weight of sugar beet tops up to 48% ($P = 0.05$) were obtained with some strains. The genera of DRB that were tentatively identified included: *Enterobacter, Klebsiella, Citrobacter, Flavobacterium, Achromobacter,* and *Arthrobacter.* Three fluorescent *Pseudomonas* spp. were identified as similar to *Pseudomonas cichorii* and *Pseudomonas viridiflava.* Colonization of roots by DRB was determined by marking strains for resistance to rifampicin (rif) and nalidixic acid (nal) and reisolating on King's medium B amended with the two antibiotics. Resistant rif-nal strains of DRB were reisolated from all lesions and areas of root distortion on inoculated plants. Coinoculation of sugar beet seed with strains of plant growth-promoting rhizobacteria (PGPR) and DRB resulted in inhibition of DRB colonization of roots and increased plant growth compared to inoculation with DRB alone. The mode of action of PGPR in increasing plant growth was in part related to the inhibition of DRB.

Control of parasitic and nonparasitic microbes not widely recognized as plant pathogens has been suggested by several workers (4,6,8,10,18,19) as a major contributing factor for plant growth increases achieved following soil and seed fumigation or the use of certain antagonists. Seedborne and soilborne strains of *Bacillus* sp. induced seed decay, reduced germination, reduced hypocotyl and radicle elongation, and stunted seedling plants of soybean under extreme environmental conditions in both greenhouse and field trials (4,16,17,23,24). *Streptomyces* spp. and *Pseudomonas* spp. also were implicated in plant growth reductions (5,20) and in deleterious synergistic interactions with root-infecting fungi (28). These reports strongly suggest that some components of the saprophytic bacterial soil microflora can, under certain environmental or growth conditions, produce substances that reduce germination and growth of seedling plants.

During our study on plant growth-promoting rhizobacteria (PGPR) (25,26) we commonly isolated other root-colonizing bacteria that were deleterious to seed germination and seedling growth. In this article we call them deleterious rhizobacteria (DRB).

Although the mechanisms by which PGPR enhance plant growth have not been fully elucidated, their role in beneficially altering the composition of rhizosphere and rhizoplane microbial populations (sensu Garrett [11]) appears to be an important factor (13–15, 25–27). High populations of PGPR on roots reduced root colonization by other endemic bacterial and fungal rhizosphere components, many of which were suspected of being infectious and/or toxigenic to roots.

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The data presented in this article show that various DRB, not previously recognized as plant pathogens, reduce the growth of sugar beet seedlings. Evidence also is presented that plant growth enhancement by PGPR seed treatment is related to inhibition of and reduced root colonization by DRB.

MATERIALS AND METHODS

Isolation of deleterious rhizosphere bacteria. Strains of DRB were isolated from the rhizospheres of seedlings and mature sugar beets collected from commercial fields throughout California. Three sections of secondary roots, ~20 cm in length, were removed from beet plants and placed in test tubes containing 10 ml of an autoclaved 0.1 M $MgSO_4$ solution. Tubes containing the root samples were transported from the field on ice until isolations were made. Isolations by dilution series plating on King's medium B (KB) were completed either the same day or the following morning. Pathogenicity tests were done by pelleting each isolate on sugar beet seed (cultivar USH 10) in a methylcellulose or xanthan gum-talc carrier (27) and planting in greenhouse pot tests. Ten seeds coated with one of each bacterial isolate were planted per 15-cm-diameter clay pot and then thinned to three seedlings after development of the first true leaves. Preliminary observations were made at this time. At least 15 pots were used per treatment. Isolates were tested in the various soils from which they were originally obtained and in Shafter sandy loam (9,27).

Bacterial strains that caused statistically significant seedling growth reductions in the various field soils were designated as DRB. Fourteen strains of DRB were characterized to genus by using standard determinative tests (7) in conjunction with API 20E diagnostic strips (Analytab Products, 200 Express Street, Plainview, NY 11803). Growth reductions were evaluated as fresh and/or dry weight of roots, shoots, or whole plants 30 days after germination. Thirteen representative strains of DRB were retested in greenhouse trials planted in Shafter sandy loam soil. Ten wooden flats with 14 seedlings per flat were used for each isolate of DRB. Shoots, excised at the point just below the cotyledon attachment, were harvested at day 25 and the total dry weight of shoots in each flat was determined.

Effects of DRB and PGPR on root development in sterile seed growth pouches. Sugar beet seed inoculated with DRB or PGPR were placed in a sterile cellulose acetate growth container (DiSPo® Growth Pouches, American Scientific Products, Sunnyvale, CA 94086) to study their colonization and its effect on plant growth. Sugar beet seeds, cultivar USH11B, were surfaced sterilized with 0.5% sodium hypochlorite prior to soaking them with agitation in a suspension containing 10^7 colony forming units (cfu) of PGPR strains $RV3_{RN}$, $B4_{RN}$, or $SH52_{RN}$, or DRB strains Wasco 4_{RN}, $MtCa7_{RN}$, or $7SR1_{RN}$ per milliliter for 30 min. The strains of DRB and PGPR were marked for resistance for rifampicin (rif) and nalidixic acid (nal) (rif-nal) to facilitate selective reisolation (26). Ten seeds of each treatment were placed in autoclaved growth pouches containing 15 ml of 0.25% Hoagland's solution. Seed pouches were placed at ambient temperatures (25 C) under Gro-Lux lights (8,700 lux, A. Hummert Seed Co., 2746 Chouteau Ave., St. Louis, MO 63103). Each treatment was replicated four times. Seed germination, bacterial population, root length, and lateral root measurements were taken at day 10. Bacterial colonization of roots was measured by dilution plating on KB amended with rif and nal. Final concentrations of rif and nal were 100 μg/ml (active ingredient) added after autoclaving and partial cooling of the KB medium.

Effect of DRB on sugar beet growth in U.C. soil mix. Sugar beet seeds were pelleted individually with one of seven strains of DRB or PGPR strain SH5, at populations averaging 2.1×10^6 cfu per seed, and planted in U.C. mix (2) in greenhouse trials. Ten seeds were planted per pot and then thinned to three seedlings after development of the first true leaves. Seven pots were planted for each treatment and arranged in a randomized complete block design. Plant tops were harvested as described above, 30 days after emergence.

Antibiosis in vitro by PGPR toward deleterious rhizobacteria (DRB). Three strains of PGPR (RV3, B4, and SH5) used in sugar beet field trials (27) were tested in vitro for antibiosis to 16 DRB. PGPR were spotted on KB and incubated for 24 hr at 28 C. Suspensions of each DRB strain, approximately 10^8 cfu/ml, were prepared and sprayed over the PGPR colonies. After 24 hr of incubation, cultures were evaluated and strains with zones of inhibition greater than 5.0 mm were judged as positive for in vitro antibiosis.

Effect of PGPR treatment on DRB colonization and plant growth effects. Sugar beet seeds were inoculated with bacteria as described previously to determine the effect of coinoculation of PGPR and DRB strains on plant growth. Inoculations were made with suspensions of DRB strains Wasco 4_{RN}, $MtCa7_{RN}$, or $7SR1_{RN}$ pm seed singly, or with suspensions of SH5 and each DRB strain in combination. Aqueous suspensions were prepared at populations of 10:1 PGPR to DRB (10^8 cfu/ml:10^7 cfu/ml). Populations of DRB were tested singly by placing seed in suspensions containing 10^7 cfu/ml. Ten seeds were placed in seed pouches with four replications per treatment. Light and temperature conditions were as described previously. Population samples were taken from 1-cm root segments of 10 seedlings. Dilution plating was done on KB rif-nal for strains Wasco 4_{RN}, $MtCa7_{RN}$, and $7SR1_{RN}$ and unamended KB for strain SH5.

In greenhouse tests, PGPR strains were coinoculated on surface-sterilized sugar beet seed with a mixture of eight DRB to determine whether plant growth reductions and other deleterious effects could be prevented. Seed was pelleted with either a DRB alone, DRB and PGPR strain SH5, RV3, or B4 in combination, or an aqueous control. Populations of PGPR and DRB on seed were approximately 10^8 cfu per seed and 10^4 cfu per seed, respectively. Pots were planted, as described, in U.C. mix with six replications per treatment. Fresh top weight was determined at day 14 for two trials and day 35 for one trial.

Prevalence of DRB in commercial sugar beet fields. Roots of field-grown sugar beets were surveyed for the prevalence of DRB. Strains of 16 predominant morphologically distinct bacterial colonies obtainable by dilution series plating on KB were selected at random by isolation from the rhizosphere of sugar beets taken from each of four commercial fields in California (26). The 64 isolates selected were tested on sugar beets in a sandy loam soil for separation into neutral, deleterious, or beneficial plant growth effects. Seed was pelleted with each strain and planted in three wooden flats per isolate. The emerged plants were thinned to 24 seedlings per flat after development of the first true leaves. Shoots were harvested at day 35. Tests were repeated twice with all isolates.

Effect of DRB on root-colonizing fungi. The effect of high populations of DRB on colonization of roots by soil fungi was quantified by using Huisman's root plating technique (12). Sugar beet seeds were inoculated with a mixture of eight strains of DRB as described, planted in Woodland sandy clay soil, and placed in the greenhouse. Other treatments were a mixture of PGPR strains (SH5, B4, and RV3) and fungicide-treated control (commercially treated with Lesan, PCNB, and lindane). Ten plants were harvested at day 25 and the roots for each treatment were pooled after initial washings in hexa-metaphosphate and Tergitol 7 anionic (12) and three final washings in sterilized distilled water. Root segments without visible lesions, ranging from 3 to 7 cm, were aligned on cellophane extract agar (12) along a series of scaled lines totaling 40 cm drawn on the bottom of each petri dish. Eight plates were prepared for each treatment. Roots were observed for developing fungal colonies for 20 consecutive days. Counts of total root-colonizing fungi and total *Pythium* spp. colonization were made. Hyphae suspected of being *Pythium* spp. were removed from media by hyphal tipping and transferred to oatmeal agar for identification.

RESULTS

Isolation and detection of DRB. Strains of rhizosphere bacteria that caused statistically significant growth reductions of sugar beets in greenhouse trials were readily isolated from roots of both seedling and mature beets (Table 1). DRB strains were obtained

from all commercial sugar beet fields sampled in various regions in California. Table 1 presents results of a representative sample of greenhouse trials using field soil showing typical plant growth reductions of sugar beet caused by inoculation of seed with DRB. Not all strains or replications are presented. Plant growth reductions ranged from 21 to 47% (significant at either $P = 0.05$ or 0.01) in dry weight of shoots as compared to untreated controls. Sugar beet seedlings affected by DRB were observed to have poor root growth, reduced height, reduced cotyledon development, root distortions and chlorosis.

Identification of DRB. Characterization by the use of AP120E determinative tests and 95 additional physiological and nutritional tests (7) tentatively placed strains of deleterious rhizobacteria in the genera *Enterobacter, Klebsiella, Citrobacter, Flavobacterium, Achromobacter,* and *Arthrobacter.* Three stains, 7SR8, 7SR1, and SB24, were identified as fluorescent *Pseudomonas* spp. similar to *Pseudomonas cichorii* or *Pseudomonas viridiflava.* Complete characterization has not been possible as DRB strains are highly variable and do not closely align with described taxonomic species.

Effect of DRB on root development in seed pouches. Three DRB strains, MtCa7$_{RN}$, Wasco 4$_{RN}$, and 7SR1$_{RN}$, caused statistically significant reductions in root length, up to 36%, in autoclaved seed pouches as compared to untreated seed or seed treated with strains of PGPR (Table 2). DRB strains MtCa7$_{RN}$ and Wasco 4$_{RN}$ also significantly reduced lateral root development as compared to untreated controls and PGPR strain RV3$_{RN}$. Germination of DRB-treated seed was delayed at day 5 by up to 50% with MtCa7$_{RN}$. Final emergence at day 10 was higher for all DRB strains than at day 5, but late-emerging plants never developed elongating roots. DRB strains caused obvious stunting, browning, and distortion of roots, and poor root hair development compared to untreated controls and those of seedlings grown from PGPR-treated seed. Isolations from 25 areas of root browning were in all cases associated with high population densities of DRB.

Colonization of roots by DRB and PGPR occurred in seed pouches from seed treated with an aqueous suspension of each strain prior to planting. Fluorescent pseudomonad strains B4$_{RN}$, SH5$_{RN}$, RV3$_{RN}$, and 7SR1$_{RN}$ (DRB strain) attained much greater population densities on roots, ranging from 5.2×10^5 to 7.1×10^6 cfu/cm, than DRB strains Wasco 4$_{RN}$, 2.0×10^4 cfu/ml, or MtCa7$_{RN}$, 3.8×10^4 cfu/cm (Table 2). All 1-cm segments along the root from root tip to an area of lateral root development were colonized to approximately the same level in seed pouches.

Effect of DRB on sugar beet growth in U.C. mix. Selected strains of DRB caused significant weight reductions of seedling sugar beets in U.C. mix (Table 3). Reductions in fresh weight of tops up to 48% were obtained ($P = 0.01$). In the sterilized U.C. mix, PGPR had no significant effect on plant growth. As in seed pouches, root browning and growth distortions were observed with DRB strains MtCa7 and Wasco 4. This study was repeated twice with similar results.

In vitro antibiosis by PGPR towards DRB. PGPR strains RV3, B4, and SH5 caused in vitro antibiosis on KB media towards 12 of the 18 DRB strains used in greenhouse trials. Four strains of DRB not sensitive to PGPR antibiosis were also flourescent *Pseudomonas* spp. The other two were not identified. In all cases, viable populations of DRB were recovered from the zone of inhibition when transferred to fresh media.

PGPR reduce DRB colonization of sugar beet roots. PGPR strain SH5 inhibited the colonization of DRB on sugar beet roots and significantly reduced their deleterious effects on root length development. SH5 reached populations ranging from 1.8×10^5 cfu/cm to 3.2×10^5 cfu/cm on plant roots with DRB strains Wasco 4$_{RN}$, MtCa7$_{RN}$, or 7SR1$_{RN}$. Populations of each DRB strain were reduced, when inoculated simultaneously with SH5, ranging from undetectable (less than 10^2 cfu/cm) to 2.3×10^3 cfu/cm compared to populations ranging from 2.7×10^3 cfu/cm to 4.9×10^4 cfu/cm when inoculated alone. Seed treatment with DRB plus PGPR SH5 significantly ($P = 0.01$) increased root length up to 81% compared to seed treated only with DRB.

Mean differences of root length for DRB-treated seed ranged from 4.4 to 5.7 cm as compared to PGPR or untreated controls ($LSD_{P=0.01} = 2.0$). Mean root length of seed coinoculated with DRB strains and SH5$_{RN}$ were not significantly different from untreated controls or SH5$_{RN}$ alone. Measurements of root length were taken from four replications of 10 roots each. Tests were repeated twice with similar results. Some root distortions were

TABLE 1. Effect of deleterious rhizosphere bacteria (DRB) on plant growth in field soil

DRB strains	Mean dry weight of plant tops (g)[a]	Decrease (%) vs control[b]
Nontreated control[c]	12.5	
Shf6	9.8	21.6*
7SR13	9.2	26.4*
7SR2	9.2	26.4*
7SR4	8.8	29.6*
B2	8.4	32.8*
7SR1	8.2	34.4*
7SR10	7.7	38.4*
Wasco6	7.6	39.2*
Wasco5	7.5	40.0**
LP2	7.2	42.4**
SHT6	7.2	42.4**
Wasco4	6.9	44.8**
MtCa14	6.6	47.2**

[a] Plantings were in Shafter sandy loam with 24 seedlings per flat and 10 flats per treatment. Tops harvested at 25 days after germination.
[b] $P = 0.05$(*) or 0.01(**).
[c] Untreated control seeds were soaked in sterile distilled water prior to planting. Treated seed was soaked in bacterial suspensions of 10^8 colony-forming units (cfu) per milliliter for 30 min prior to planting.

TABLE 2. Effect of treating sugar beet seed with strains of deleterious rhizobacteria (DRB) or plant growth-promoting rhizobacteria (PGPR) on germination, root length, and lateral root formation in growth pouches

Treatment	Germination at day 5 (%)	Population[y] (cfu × 10^4/cm)	Mean length of primary root (cm)[z]	Avg no. of lateral roots/root[z]
DRB				
MtCa7$_{RN}$	40	3.8	5.6 b	0.0 b
Wasco 4$_{RN}$	56	2.0	6.9 b	0.2 b
7SR1$_{RN}$	53	62.0	7.0 b	0.5 a
Sterile untreated Control	80	0.0	8.7 a	1.0 a
PGPR				
B4$_{RN}$	73	52.0	9.5 a	1.4 a
SH52$_{RN}$	80	61.0	9.9 a	0.9 a
RV3$_{RN}$	73	710.0	10.3 c	4.0 c
LSD ($P = 0.05$)			1.3	0.63

[y] Populations of rhizobacteria measured on King's B amended with 100 μg/ml rifampicin and 100 μg/ml nalidixic acid. cfu = colony-forming units.
[z] Numbers followed by a different letter are significantly different from controls, $P = 0.05$. Numbers represent averages of 10 seeds per replication with four replications per treatment. Tests were repeated twice with similar results.

observed for DRB-treated and PGPR+DRB-treated plants as described previously.

Interaction between PGPR and DRB on plant growth in U.C. mix. PGPR strains B4, SH5, and RV3 significantly increased sugar beet growth in U.C. mix, when coinoculated with a mixture of eight DRB strains, as compared to plants inoculated with DRB alone. Plant growth increases ranged from 50 to 97% ($P = 0.05$) as compared to DRB-treated plants and from 5 to 39% above untreated controls. Inoculation of seed with DRB alone at populations of 10^4 cfu/seed caused a 30% reduction in sugar beet seedling growth.

Prevalence of DRB in commercial sugar beet fields. Deleterious rhizobacteria were more prevalent on the roots of sugar beets taken from commercial fields than PGPR. Of the 64 isolates tested, approximately 26% caused statistically significant growth reductions as compared to untreated controls, while only 2% increased plant growth. The majority (72%) of rhizosphere bacteria had no significant or observable effect on sugar beet growth as compared to controls.

Sugar beet seed treated with a mixture of 12 strains of DRB had significantly greater fungal colonization per centimeter of root than fungicide (Lesan or PCNB)-treated seed and PGPR-treated seed (Table 4). The total number of *Pythium* spp. colonizing roots was 262% higher on DRB-treated roots than fungicide-treated roots and 130% higher than on PGPR-treated roots.

DISCUSSION

These studies indicate that the root microflora of sugar beet include bacterial components deleterious to root growth and overall plant vigor. Increased fungal colonization of roots from bacterially treated plants indicate that DRB may either increase the susceptibility of roots to colonization by certain fungi or stimulate the fungi to colonize them. When acting in toto, DRB may be as important as many recognized root pathogens in reducing yields. The effects of DRB as a limiting factor in crop growth has probably eluded detection in the past because of their widespread occurrence in soils and uniform presence on roots. In this study, they were detected at relatively high frequencies and were part of the normal root microflora of field-grown sugar beets. The DRB identified belong to a number of different genera and families such as *Pseudomonas,* the Enterobacteriaceae, and the Corynebacteriaceae and should be considered "minor pathogens," sensu Salt (21).

The effects of DRB on roots such as root lesions or browning, distortions, reduced root hair development, or increased colonization by soil fungi are subtle and can easily escape notice, especially in field conditions. The overall effects on early growth and final yield, however, can be substantial. In bacterization trials with PGPR strains RV3, B4, and SH5, seedling growth and mature root yield increases averaged 45 and 13%, respectively, above untreated seed in the absence of observable major root-pathogen control (26,27). Isolations from roots sampled from those field trials and results presented here indicate that this increased growth was caused, in part, by reductions in colonization by DRB and root colonizing fungi.

Seed treatment with PGPR reduced or prevented root colonization by DRB and negated their plant growth reducing effects. Inhibiting DRB colonization could benefit plant growth by preventing the elaboration of toxic compounds or metabolites released during their growth (3). The action of toxic compounds on roots may be related to the increase in root-fungi infections following seed treatment with DRB. In related work (26), PGPR also significantly reduced root colonization by a number of fungi in field tests. Reduced root-fungi colonization by PGPR treatment may occur indirectly by minimizing synergistic interactions of DRB with root fungi. Thus, PGPR seed treatment appears to temporarily alter the population composition of the root microflora, as would occur with soil fumigation (1), favoring optimum plant growth.

The mechanisms by which PGPR effect change in the rhizosphere microflora, whether direct or indirect, are not fully understood. Van Vuurde et al (29) claimed that only a small percentage of the total available root surface is colonized after emergence. Microbial growth on the root during the first 8 days was generally restricted to specific sites along epidermal cell junctions and areas of lateral root emergence. The ability of the rapidly growing PGPR to be more active than DRB in competition for these available sites on the root is a likely mechanism for reducing DRB effects and subsequent fungal infections. The production of biostatic compounds, such as pseudobactin (14,15), at these sites and throughout the rhizosphere would also inhibit deleterious microflora and result in plant growth increases.

The presence of oxidase-negative fluorescent pseudomonads on the roots of sugar beets as part of the normal microflora is of particular interest because this group is generally pathogenic to plants causing an assortment of different diseases. *Pseudomonas* isolates SB24 and 7SR1 were among the most detrimental strains tested, causing root browning, root distortions, and severe stunting. Schneider and Grogan (22) also isolated oxidase-negative fluorescent pseudomonads from the roots of sugar beets as well as other crop and weed plants. This group of bacteria, closely related to *Pseudomonas syringae,* may produce toxins while colonizing roots which reduce plant growth without obvious cell damage. The role of these and other DRB requires further investigation. Results of these studies, along with those of similar investigations of other plants, indicate that DRB are ubiquitous and common to all root systems. They probably, in time, will be recognized as a significant pathogenic group that contributes to limiting plant growth and yield and influences host-pathogen interactions at the root surface.

TABLE 3. Effect of rhizobacteria (DRB) on plant growth in U.C. mix

DRB strains	Mean weight of three seedlings (g)[y]	Change (%) vs control
Untreated control	15.1 a	...
PGPR		
SH5[z]	16.3 a	+8.0
DRB		
7SR4	12.2 a	−19.2
MtCa14	11.5 b	−24.0
WASCO 9	10.8 b	−28.4
BX	9.6 b	−36.4
MtCa7	9.5 b	−37.0
7SR13	8.0 b	−47.0
Wasco 4	7.8 b	−48.3
LSD		
$P = 0.05$	3.4	
$P = 0.01$	4.6	

[y] Averages are from three seedlings per replication with seven replications per treatment. Plants were harvested 30 days after germination.
[z] Plant growth-promoting rhizobacteria (PGPR) strain SH5 was used as a non-DRB treatment for comparison to DRB rhizobacteria. Numbers followed by a different letter are significantly different, $P = 0.05$

TABLE 4. Comparison of fungicide or rhizobacterial seed treatment effects on fungal colonization of sugar beet roots

Treatment	Mean no. colonies per 40-cm root[w]	Mean *Pythium* spp. per 40 cm root	Change (%) colonies per 40 cm
DRB[x] Mix	63.5 a	14.7 a	
Fungicide[y] treated control	33.7 b	3.5 b	−43.0
PGPR[z] Mix	26.2 b	5.5 b	−55.7

[w] Averages are from six plates per treatment, 40 cm of root per plate. Root samples were pooled from six individual seedlings planted in Woodland sandy clay.
[x] Deleterious rhizobacteria (DRB).
[y] Fungicide-treated seeds were commercially treated with a combination of Lesan, PCNB, and lindane. Numbers followed by a different letter are significantly different, $P = 0.05$.
[z] Plant growth-promoting rhizobacteria (PGPR).

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