Letter to the Editor

Root Camouflage and Disease Control

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Biocontrol research on rhizosphere-specialized microorganisms is heavily influenced by the idea that successful biological control agents must extensively colonize the rhizosphere. Indeed, this ability to colonize the rhizosphere, often called rhizosphere competence, is a notable feature of many microorganisms that are effective biocontrol agents. Although rhizosphere competence is often encountered among root-specialized microbes, other evidence suggests that the use of microorganisms from nonrhizosphere soil may offer advantages over rhizosphere specialists as biological control agents.

Bacteria are numerically more abundant on plant roots than in root-free soil, a phenomenon known as the "rhizosphere effect" (3,7,8,25–27,30,31). There also are significant qualitative differences between bacteria isolated from rhizosphere and nonrhizosphere soils. Lochhead and colleagues (10–16,23,29,33,34,36) showed that gram-negative, motile, pigmented, and short rod-shaped bacteria are more abundant in the rhizosphere than in nonrhizosphere soil and that rhizosphere bacteria are more likely than soil bacteria to grow in culture on rich media. The relationships between these qualitative aspects of the rhizosphere effect and plant disease have been addressed by a number of researchers. Table 1 lists all the studies of which we are aware that relate both rhizosphere and soil microbial communities to plant disease incidence or severity.

In this letter, we introduce the idea of "root camouflage" for microbial control of root diseases. By root camouflage, we mean that roots with rhizosphere microbial communities more similar to the microbial community in the surrounding soil (a reduced rhizosphere effect) may be less attractive to pathogens. We draw on both our own work on biological control and on literature concerning interactions between rhizosphere and soil microbial communities and disease resistance, soil amendments, and disease-conducive and -suppressive soils.

***Bacillus cereus* UW85 and biological control.** *Bacillus cereus* UW85 is an effective biological control agent for damping-off diseases of legumes (4). UW85 was isolated from alfalfa roots, but in most of its physiological characteristics (i.e., carbon source utilization, extracellular enzyme production, and antibiotic resistances), it is more similar to bacteria isolated from bulk soil than to those isolated from the rhizosphere of soybeans (2). Such similarities are depicted in Figure 1 in which we compared UW85's ability to produce ammonia and sequester calcium from broth culture with numerous rhizosphere and bulk soil strains of *B. cereus.* Soil and root strains were easily differentiated even within the species, and although isolated from roots, UW85 more closely resembled *B. cereus* strains from soil than strains from roots.

Coating soybean seeds with UW85 can have a large impact on the bacterial community that subsequently develops in the rhizosphere, even when UW85 does not persist in large numbers (2). We conducted three field experiments comparing the bacterial communities found in bulk soil with those occurring in the rhizosphere of soybeans grown from nontreated or UW85-coated seeds. Although no significant community size differences were detected, bacteria from the control soybean rhizospheres were able to utilize significantly more simple carbon sources than were bacteria isolated from the nonrhizosphere soil. This difference reflects a qualitative manifestation of the rhizosphere effect. Bacteria isolated from roots of plants grown from seeds coated with UW85 were intermediate in their carbon source-utilization patterns as compared to bacteria isolated from nonrhizosphere soil and nontreated plants. Thus, although the efficacy of UW85 in biological control (4) and the effects of UW85 on reducing the rhizosphere effect (2) have not yet been tested in the same experiment, they may be linked.

Resistant and susceptible cultivars. Timonin, Lochhead, and West worked during the 1940s with cultivars of flax and tobacco that varied in resistance to Fusarium wilt and black root rot, respectively. They found that roots of susceptible cultivars supported higher densities of in vitro-culturable bacteria, among which were proportionally more gram-negative, short, rod-shaped bacteria (31), more gelatin liquefiers, and more nitrate reducers compared to roots of resistant cultivars (10,16). Bacteria cultured from rhizospheres also were more likely than those from bulk soil to be stimulated by amino acid nitrogen and growth factors. Moreover, the percentage of strains isolated from rhizospheres of resistant cultivars that was stimulated by amino acids, growth factors, or yeast extract was nearly always intermediate between those bacteria from rhizospheres of susceptible cultivars and from soil (35). Later, Strzelczyk (28) and Peterson et al (20) found similar results on the same crops for different nutritional groups of bacteria and fungi. In these systems, resistant cultivars of flax and tobacco showed weaker qualitative and quantitative rhizosphere effects than did the susceptible controls.

Additional studies indicated that rhizosphere communities on disease-resistant cultivars were more similar to the microbial communities in the surrounding soil than were those of the susceptible varieties. Cultivars of banana resistant to Panama disease exhibited weaker quantitative rhizosphere effects than did susceptible varieties in the absence of disease, but results were variable in the presence of disease (5,21). With the exception of fungal populations, Neal et al (18,19) showed that the rhizosphere effect was stronger in wheat cultivars susceptible to common root rot than in resistant cultivars. Substitution of specific chromosome pairs that conferred disease resistance from the resistant cultivar into the genome of the susceptible cultivar was correlated with a change in the rhizosphere microflora of the substitution line to resemble the microflora of the resistant donor parent. Substitution of chromosome pairs that did not confer resistance also did not alter the rhizosphere community. Another example demonstrating the relationship between resistance and the rhizosphere effect is seen in the work of Miller et al (17) who examined resistant and susceptible cultivars of maize (to *Fusarium*), *Poa* (to *Dreschlera*), and wheat (to acidity). They found that resistance was associated with a weaker rhizosphere effect for both fungal pathogens, but no correlation was established for the effects of acidity on various acid-resistant and -susceptible cultivars of wheat.

TABLE 1. Summary of studies that provide data on both soil and rhizosphere microbial communities and plant disease incidence or severity

Disease	Presence[a]	Comparisons	Measurements	Results	Ref.[b]
Fusarium wilt of flax	−	Resist./suscept. cvs.	No. of bacteria, actinomycetes, fungi	Higher R/S[c] on suscept. cv.	31
Fusarium wilt of flax	?	Resist./suscept. cvs.	No. of bacteria, actinomycetes, fungi	Higher R/S on suscept. cv.	16
Fusarium wilt of flax	?	Resist./suscept. cvs.	No. of bacteria	Higher R/S on suscept. cv.	10
Fusarium wilt of flax	−	Resist./suscept. cvs.	No. of bacteria, fungi	Soil < resist. < suscept.	20
Black root rot of tobacco	−	Resist./suscept. cvs.	No. of bacteria, actinomycetes, fungi	Higher R/S on suscept. cv.	31
Black root rot of tobacco	?	Resist./suscept. cvs.	No. of bacteria, actinomycetes, fungi	Higher R/S on suscept. cv.	16
Black root rot of tobacco	?	Resist./suscept. cvs.	No. of bacteria	Higher R/S on suscept. cv.	10
Strawberry root-rot	+	Cover crops, manure	No. of bacteria	R/S proportional to disease severity	6
Panama disease of banana	?	Resist./suscept. cvs.	No. of bacteria	R/S of 2 resist. cvs. intermediate to 2 suscept. cvs.	5
Panama disease of banana	+/−	Resist./suscept. cvs.	No of bacteria, spore-forming bacilli actinomycetes, fungi	R/S of resist. cvs. < R/S of suscept. cvs. for all disease (−); variable disease (+)	21
Common root rot of wheat	−	Resist./suscept. cvs.	No. of bacteria	Soil < resist. < suscept.	18
Common root rot of wheat	−	Resist./suscept. cvs.	No. of fungi	Soil < suscept. < resist.	18
Damping-off of pea and cucumber	+	Compost	Microbial biomass	Higher in compost-amended, disease-suppressive soil than conducive soil[d]	1
Fusarium wilt of flax	?	Resist./suscept. cvs.	Morphological groups	Soil - resist. - suscept.[e] (4/4 groups)	16
Fusarium wilt of flax	?	Resist./suscept. cvs.	Morphological groups	(Soil <> resist.) - suscept.[f] (8/8 groups)	10
Black root rot of tobacco	?	Resist./suscept. cvs.	Morphological groups	Soil - resist. - suscept. (4/4 groups)	16
Black root rot of tobacco	?	Resist./suscept. cvs.	Morphological groups	(Soil <> resist.) - suscept. (7/8 groups)	10
Fusarium wilt of flax	?	Resist./suscept. cvs.	Nutritional groups[g]	Soil - resist. - suscept. (3/3 groups)	16
Fusarium wilt of flax	?	Resist./suscept. cvs.	Nutritional groups	(Soil <> resist.) - suscept. (7/10 groups)	36
Fusarium wilt of flax	?	Resist./suscept. cvs.	Nutritional groups of bacteria	Soil - resist. - suscept. (5/5 groups)	28
Fusarium wilt of flax	?	Resist./suscept. cvs.	Nutritional groups of streptomycetes	Soil - resist. - suscept. (3/5 groups)	28
Fusarium wilt of flax	?	Resist./suscept. cvs.	Nutritional groups of fungi	Soil - resist. - suscept. (4/5 groups)	28
Black root rot of tobacco	?	Resist./suscept. cvs.	Nutritional groups	Soil - resist. - suscept. (3/3 groups)	16
Black root rot of tobacco	?	Resist./suscept. cvs.	Nutritional groups	(Soil <> resist.) - suscept. (8/10 groups)	36
Black root rot of tobacco	?	Resist./suscept. cvs.	Nutritional groups of bacteria	Soil - resist. - suscept. (5/5 groups)	28
Black root rot of tobacco	?	Resist./suscept. cvs.	Nutritional groups of streptomycetes	Soil - resist. - suscept. (4/5 groups)	28
Black root rot of tobacco	?	Resist./suscept. cvs.	Nutritional groups of fungi	Soil - resist. - suscept. (5/5 groups)	28
Common root rot of wheat	−	Resist./suscept. cvs.	Nutritional groups	(Soil <> resist.) - suscept. (4/5 groups)	18
Fusarium wilt of flax	−	Resist./suscept. cvs.	Physiol. groups-rhizosphere[h]	Soil - resist. - suscept. (4/4 groups)	20
Fusarium wilt of flax	−	Resist./suscept. cvs.	Physiol. groups-rhizoplane	Soil - resist. - suscept. (2/4 groups)	20
Fusarium wilt of flax	?	Resist./suscept. cvs.	Physiol. groups	(Soil <> resist.) - suscept. (4/7 groups)	10
Black root rot of tobacco	?	Resist./suscept. cvs.	Physiol. groups	(Soil <> resist.) - suscept. (5/7 groups)	10
Common root rot of wheat	−	Resist./suscept. cvs.	Physiol. groups[i]	Soil - resist. - suscept. (3/4 groups)	18
Common root rot of wheat	−	Resist./suscept. cvs.	Physiol. groups[j]	Soil < resist. < suscept.	19
Strawberry root-rot	+	Root-rot/healthy soil	BBI[k]	Root-rot soil < healthy soil	35
Strawberry root-rot	−	Rhizo./healthy soil	BBI	Healthy soil < rhizosphere	35
Strawberry root-rot	+	Cover crops, manure	BBI	R/S proportional to disease severity	6
Tomato root-rot	+	Fumigants, steam	BBI	R/S and disease reduced for all treatments	9
Mn-deficiency disease of oats	+	Resist./suscept. cvs.	BBI	R/S greater in resist. cv.	32
Potato scab	+	Cover crops	BBI	R/S lower in scab-reducing traits	22
Fusarium root rot of maize	?	Resist./suscept. cvs.	Taxonomic groups[l]	(Soil <> resist.) - suscept.[m]	17
Dreschlera on *Poa*	?	Resist./suscept. cvs.	Taxonomic groups	(Soil <> resist.) - suscept. (4/4 groups)	17
Acidity toxicity on wheat	−	Resist./suscept. cvs.	Taxonomic groups	Variable	17
Common root rot of wheat	−	Resist./suscept. cvs.	%bacteria antagonistic to pathogen	Suscept. < soil < resist.	18

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[a] Disease present (+), absent (−), or not reported (?).

[b] Reference.

[c] Rhizosphere/Soil ratio.

[d] Although root microbial biomass was not determined, evidence from many other studies indicates that there are more bacteria on roots than in bulk soil; this should result in a lower R/S in compost-treated soil, which also suppresses damping-off.

[e] Response for resistant cultivar was intermediate to responses of soil and susceptible cultivar for all groups.

[f] Resistant cultivar intermediate to soil and susceptible cultivar or more extreme than soil.

[g] Nutritional groups of bacteria (unless otherwise specified) based on requirements for amino acids, growth factors, and yeast extract.

[h] Physiological groups of bacteria based on methylene blue reduction, acid or gas from glucose, and ammonification.

[i] Ammonifiers, nitrate reducers, and aerobic sporeformers respond as indicated, starch hydrolyzers do not.

[j] Total bacteria and cellulolytic, pectinolytic, amylolytic, and ammonifying groups.

[k] Bacterial Balance Index = (percent require cysteine + percent require other amino acids + percent require vitamins) − (percent gram-negative, nonfluorescent growth on basal medium).

[l] Percentage of total bacteria that are *Bacillus* spores, fluorescent pseudomonads, total pseudomonads, coryneform bacteria, and actinomycetes.

[m] Three/four groups at 23 days after planting (DAP) 4/5 at 38 DAP, and 2/4 at 52 DAP by percentage of total; 3/5, 6/6, 5/5 groups by population density.

Disease-conducive versus -suppressive soils. Another line of evidence suggesting a qualitative relationship that differentiates soil and rhizosphere bacterial communities is West and Lochhead's "Bacterial Balance Index" (BBI) (36). The BBI was developed to characterize the bacteria from soils associated with high levels of strawberry root rot ("root-rot" soil) compared with those from soils in which plants did not become infected ("healthy" soil). Bacteria with requirements for exogenous cysteine, amino acids, vitamins, or their combinations (nutrient-requiring bacteria) were more abundant in "healthy" soils, whereas gram-negative, nonfluorescent bacteria that grew on minimal medium were associated with root-rot soil. The BBI was defined as the difference between the percentage of bacterial strains categorized as nutrient requiring and the percentage of strains categorized in the minimal medium-competent group. Healthy soils had a more positive BBI than did root-rot soils, such that the differential between rhizosphere bacterial communities (which had strongly positive BBIs) and healthy soils was smaller than the difference between the rhizosphere bacterial communities and root-rot soils. In this system, disease severity was greatest when the rhizosphere bacterial communities were most different from the surrounding soil. Again, this suggests that a stronger rhizosphere effect is associated with more disease.

Cultural and chemical control. In an investigation of the effects of cover crops and of steam pasteurization on root rot, Hildebrand and West (6) showed that strawberry root-rot was most severe when the rhizosphere BBI was most different from that of the surrounding soil. Additionally, they demonstrated that treatments that reduced disease severity also tended to narrow the difference between the rhizosphere and soil BBIs. For example, chemical treatments and steam pasteurization reduced the difference between the soil and rhizosphere BBIs and reduced disease incidence in root rot of greenhouse-grown tomatoes (9). Likewise, the incorporation of cover crops that reduced potato scab also reduced the difference between root and soil BBIs (22). Chen et al (1) found higher microbial biomass in compost-amended soils that suppressed *Pythium*-caused damping-off than in the disease-conducive soil, which suggests that the rhizosphere communities have a microbial density more similar to disease-suppressive soil than to disease-conducive soil. However, they made no direct determinations of the status of the rhizosphere community. Each of these studies suggests that altering the soil microflora to reduce disease incidence also reduced the difference between the soil and rhizosphere microbial communities.

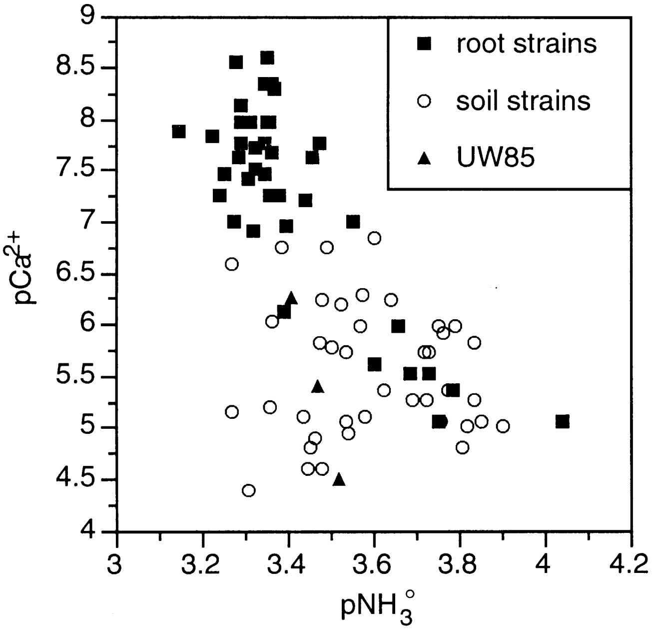

Fig. 1. Biological control agent *Bacillus cereus* UW85 shows behavior more similar to *B. cereus* strains from root-free soil than to strains from roots of soybeans. Cultures were grown in shaken Trypticase soy broth (0.05 recommended strength) for 41 h. Concentration of ammoniacal-N was measured colorimetrically and activity of NH_3° was calculated based on solution pH. Activity of Ca^{2+} was measured with a calcium-specific microelectrode. Chemical activities are expressed as −log(activity) (smaller numbers indicate higher activity). Uninoculated broth was $pNH_3^\circ = 5.4$ and $pCa^{2+} = 4.9$.

Rouse and Baker (24) showed that cellulose amendment to soil reduced the slope of inoculum density-disease incidence curves for *Rhizoctonia solani* on radishes. They suggested that nitrogen normally available in the rhizosphere is important for stimulating fungal propagules to germinate, and the greater soil microbial activity induced by cellulose limits the supply of nitrogen to the rhizoplane. However, increased soil microbial populations and activity also would reduce the differential in microbial abundances between rhizosphere and bulk soil. Neither microbial abundance nor nitrogen availability were measured in this study, so the two possibilities cannot be evaluated, but the rhizosphere microorganisms certainly modify the nutrient environment in the rhizosphere, and modifications that make the root less apparent to pathogens in the soil are consistent with the camouflage effect.

Exceptions in the literature. The only case we know of in which the difference between the rhizosphere and soil BBI was greater for resistant than for susceptible cultivars was for manganese-deficiency disease of oats, which is associated with an overabundance of Mn-oxidizing bacteria in the rhizosphere of plants grown in Mn-deficient soils (32). The Mn-oxidizing bacteria are apparently not associated with roots that are not Mn-deficient, and perhaps the "root-like" rhizospheres of the resistant varieties are unsuitable for the growth of these bacteria.

Summary. Taken together, the information in the literature and the experiments with UW85 suggest a correlation between microbially camouflaged roots and disease suppression. Studies of plant disease resistance, suppressive soils, the addition of a biological control agent, and soil amendments each indicate that a reduction in plant disease incidence or severity is strongly correlated with a reduction in the rhizosphere effect. Both numbers and types of microorganisms associated with plant roots in disease-suppressive situations are more similar to surrounding soil than they are in disease-permissive situations.

This correlation suggests a new approach to developing management systems for root diseases. Biological control agents that are not rhizosphere specialists may aid in developing rhizosphere communities more similar to communities in surrounding soil than would be expected on nontreated plants. Such microbes might best be found by screening microorganisms isolated from bulk soil or habitats other than plant roots. Breeding for plants with characteristics that lead to a weak rhizosphere effect (i.e., reduced root exudation) may be useful in developing disease-resistant cultivars. Perhaps most promising is the use of cultural practices such as green manuring or composting that change the soil microbial community to more closely resemble the communities usually associated with plant roots. Further experimental data are needed to determine whether root camouflage is important in avoiding host detection by pathogens, whether plant- or microorganism-associated features are important characteristics of the system, and whether particular aspects of root camouflage (i.e., the presence or absence of certain microbial species or root exudates in the rhizosphere) are related to disease suppression.

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