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Growth Enhancement of *shrunken-2* (*sh2*) Sweet Corn by *Trichoderma harzianum* 1295-22: Effect of Environmental Stress

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Abstract. **Sweet corn (*Zea mays* L.) varieties carrying the *sh2* gene are in high demand, but such varieties have poor stress tolerance, especially during plant establishment. *Trichoderma harzianum* Rifai strain 1295-22 is a biocontrol fungus developed to provide season-long colonization of crop roots. It has the potential to reduce root rot and increase root growth. In the absence of detectable disease, colonization by *Trichoderma* increased root and shoot growth by an average of 66%. The enhancement was not uniform among the plants. Low- and intermediate-vigor plants were larger in the presence of *Trichoderma*, but high-vigor plants were not further enhanced by the fungus. Seeds that were subjected to oxidative stress with 0.05% NaOCl had much-reduced vigor; subsequent treatment with *Trichoderma* fully restored vigor. This result indicates that the damage caused by hypochlorite is specifically repaired by *Trichoderma*. Treatment of imbibed but unemerged seeds with cold (5/10 °C night/day) for varying periods reduced subsequent growth. Plants with *Trichoderma*-colonized roots were 70% larger at all durations of cold treatment. The absence of interaction indicates the growth reduction due to cold and the growth enhancement due to *Trichoderma* are by different mechanisms. Allelopathic reduction in root growth by rye was mimicked by applying benzoxazolinone to the soil. *Trichoderma*-colonized roots grew faster, but the characteristic shortening of the radicle still occurred. There was no interaction between *Trichoderma* and allelopathy, indicating that these two treatments affect growth by independent mechanisms. The different ways that growth was enhanced by *Trichoderma* lead us to propose that this fungus acts, in part, by reversing injurious oxidation of lipids and membrane proteins. Root growth is markedly enhanced by colonization with *Trichoderma harzianum*. This enhancement can restore some stress-induced growth reduction and may directly reverse oxidative injury.**

The fungus *Trichoderma harzianum* Rifai has long been studied as a biological control organism against a wide range of soilborne pathogens. In addition, colonization with this fungus can promote plant growth (Chang et al., 1986; Kleifeld and Chet, 1992; Windham et al., 1986, 1989), but the mechanism of this growth promotion is unknown. The growth-promoting effect could be a valuable property of the fungus when used with horticultural crops that have weak seedling growth.

Commercial use of beneficial fungi has been limited by inconsistent colonization of crop root systems, but recent advances have produced a strain that achieves strong colonization (Stasz et al., 1988). The colonization of roots by naturally occurring strains of *Trichoderma* may be transitory and localized depending on the host plant, the growing conditions, and competing microbes (Deacon, 1994). This variability has made its development into an effective biocontrol agent difficult. Only a few strains of this fungus can effectively colonize root surfaces (Harman et al., 1989). Most notably, consistently strong colonization is obtained in a variety of conditions with strain 1295-22, which was bred for its high rhizosphere competence and high production of enzymes important in mycoparasitism (Sivan and Harman, 1991).

In horticultural crops, valuable postharvest and horticultural traits may be detrimental to growth. One such trait is the desirable sweetness and shelf life in sweet corn varieties homozygous for the *sh2* gene. Production of such varieties is difficult due to low seed quality, emergence, and seedling vigor (Parera et al., 1996; Styer et al., 1980). These weaknesses are related to the small carbohydrate reserves, the high sugar content, and the leaky pericarp of the kernel, causing a high degree of disease susceptibility. Furthermore, the kernels are easily colonized by pathogenic fungi while they are drying, causing the seedlings to be highly infested with disease organisms as well. *Shrunken-2* sweet corn production would be easier if seedling vigor could be increased so that the plants grew uniformly and produced harvestable ears. The growth-enhancing effect of *Trichoderma*, combined with the protection from root diseases, may increase this vigor.

To take advantage of the beneficial fungus to mitigate inherent seedling weaknesses in horticultural crops, the nature of the growth enhancement must be better known. This investigation describes the nature of the increase in growth and the effect of *Trichoderma* on the growth reduction associated with three stresses commonly experienced by seedlings: oxidative injury, low temperature, and allelopathy. The experiments were designed to determine whether *Trichoderma* colonization affects growth at the same physiological sites as the three stresses.

Materials and Methods

Plant growth. Plants of 'Supersweet Jubilee' sweet corn (Rogers Seed Co., Boise, Idaho) were grown in the greenhouse with supplemental lighting (500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from metal halide lights). The growing medium was a sandy loam soil (Arkport series), with soluble fertilizer (Peters Professional 20–20–20 with micronutrients, Grace Sierra Horticultural Products Co., Milpitas, Calif.) added supplying (in mg) 5N–2.2P–4.7K per container per

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week. Two container types were used, depending on the experiment. Plastic pots (15 cm high, 15 cm in diameter; Kord Products, Bramlea, Ont.) were filled with 1.1 L of soil, planted with five seeds, and thinned to three plants. Plants for analyzing the root system architecture were grown in acrylic boxes, 2 cm thick, 25 cm wide, and 40 cm deep, that held 2 L of soil. These were planted with three seeds and thinned to one plant. Supersweet Jubilee was chosen because it exemplifies the vigor problems found in *sh2* varieties (He and Burris, 1992; S. Marshall, personal communication)

***Trichoderma harzianum* SEED TREATMENT.** Seeds were treated with a suspension of spores in 5% Polyox sticker (Union Carbide, Danbury, Conn.) to deposit 5×10^6 colony-forming units (cfu) per seed. The spores were from prototype fermentations of commercially produced *Trichoderma harzianum* strain 1295-22 (T-22 Soilguard, Bioworks Inc., Geneva, N.Y.). Colonization was confirmed in each experiment by dilution plating homogenized root samples on *Trichoderma* selective medium as described by Smith et al. (1990). Colonization of inoculated roots was between 10^5 and 10^7 cfu/g. Uninoculated roots were at or below the detection limit of 10^3 cfu/g.

PATHOGEN DETERMINATION. Mesocotyls from plants in the oxidation experiment were sampled at harvest and plated on acid potato dextrose agar, and the resulting colonies were identified by a microbiologist who routinely makes these identifications. Individual plants were scored as either infected or free of pathogens in four classes: *Fusarium*, *Pythium*, other fungi, and bacteria.

GROWTH MEASUREMENTS. Several measures of plant growth were used to determine the nature of growth enhancement. All measurements were made after 21 d of growth. Plant height was measured as the distance from the soil surface to the extended longest leaf. Height was highly correlated with shoot dry mass under comparable growing conditions and the same growth period (height = 40 cm + 0.41 cm·mg^{-1} × mass (mg) ; $r^2 = 0.80$). Root dry mass and shoot dry mass were measured for each pot of three plants after drying at 80 °C for 3 d in a forced-air drying oven. The growth enhancement of roots and shoots by *Trichoderma* in the absence of stress was measured in nine experiments with twelve pots of three plants receiving each treatment.

The root system architecture was analyzed by removing intact root systems from the thin acrylic boxes. A board with stainless-steel nails in a uniform 1-cm grid was pressed into the soil to hold the roots in place, after which the soil was gently washed off. The roots were photographed while in their original orientation. Soil exploration was measured from the photographs as the proportion of the 975 1-cm squares that contained roots. Root-length density was determined from the photograph by measuring the root length in each of the 975 cells and dividing by the soil volume. Maximum root length was measured in the allelopathy experiment as described below. Each treatment was applied to 12 plants.

OXIDATIVE INJURY. In experiments testing the oxidative effects of hypochlorite, the seeds were treated for 15 min at room temperature in 0.05% NaOCl, rinsed three times in tap water, and air dried (Parera and Cantliffe, 1991). Each treatment consisted of 12 pots of 3 plants. The plant height was measured at 21 d to permit nondestructive growth measurement.

COLD TREATMENT. For applying cold treatments, seeds were sown in pots with each treatment consisting of 12 pots of 3 plants. The seeds were allowed to imbibe for 1 d at 20 to 25 °C. They were then transferred to a growth chamber (model E15; Conviron Inc., Winnipeg, Man.) at a diurnal temperature cycle of 12 h each at 5 and 10 °C. No lights were used because the seedlings did not emerge during the cold period. After the cold treatment, the pots were returned to the greenhouse and grown as described above. To provide all the plants with the same greenhouse conditions, the planting was staggered so that all the cold-treated plants were returned to the greenhouse at the same time as the unchilled controls, which had imbibed for 1 d. The plants were harvested 20 d later to result in 21 d of growth, not including the cold treatment. Four different cold exposure times were used: 1, 3, 5, and 7 d. A control and two cold treatments were done at a time due to limited growth chamber space. This protocol was repeated four times so that each exposure time was tested twice.

ALLELOPATHY. Soil was mixed with 2,3-benzoxazolinone (Sigma) at 300 mg·kg^{-1}. This is the precursor of the primary allelopathic compound in rye residue (Barnes and Putnam, 1987). In preliminary experiments, 300 mg·kg^{-1} was found to reduce shoot growth by ≈30%. The conversion of benzoxazolinone (BOA) to the active 2,2′-oxo-1,1′-azobenzene occurred in <24 h, and was monitored by the appearance of yellow color in the methanol extract (Nair et al., 1990). After the conversion, the soil was placed in root boxes and seeds were planted as described above. Each treatment consisted of six pots of three plants. The rooting depth was affected by the allelopathic treatment, so in these experiments the root-system length was also measured as the distance from the mesocotyl to the apex of the longest root when the washed root system was allowed to hang freely.

SOIL STEAMING. In experiments testing the effect of soilborne pathogens, the soil was treated with live steam until the internal temperature reached 105 °C. After cooling, the soil was used in the same manner as controls.

STATISTICS. The experiments testing the effect of the three stresses on growth were designed as a 2×2 factorial of *Trichoderma* and stress as the two factors. These were analyzed by analysis of variance, with a positive interaction being evidence that *Trichoderma* counteracted the stress and no interaction indicating that *Trichoderma* only caused general enhancement of growth. Single-factor comparisons were made using Student's *t* test. In all experiments the containers were randomized on the greenhouse bench. In each experiment there were 12 pots or root boxes per

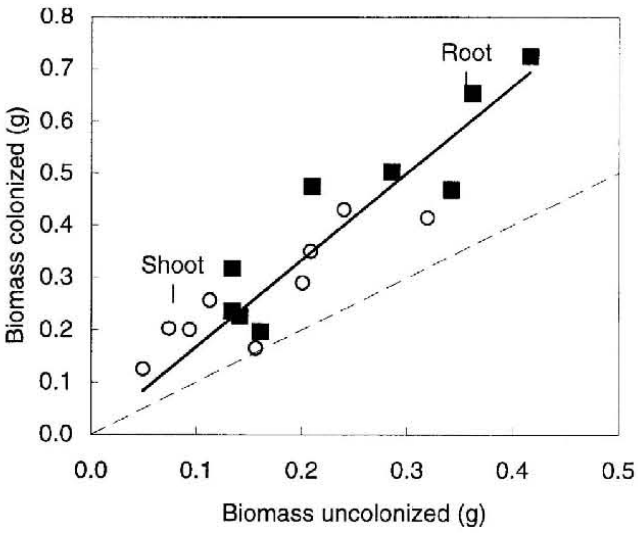

Fig. 1. Effect of *Trichoderma* colonization on root and shoot growth of sweet corn. The dry mass of roots and shoots was measured after 21 d of growth in the greenhouse. Each point is the result from one repetition consisting of 12 pots of each treatment, with three plants per pot. The differences in growth among the repetitions was primarily the result of differing light intensity and daylength. The symbols are for roots (■) and shoots (○). The dashed line shows unity slope, indicating equal sizes. The solid line is the combined regression line for roots and shoots: Colonized-plant biomass = 1.66 × uncolonized-plant biomass.

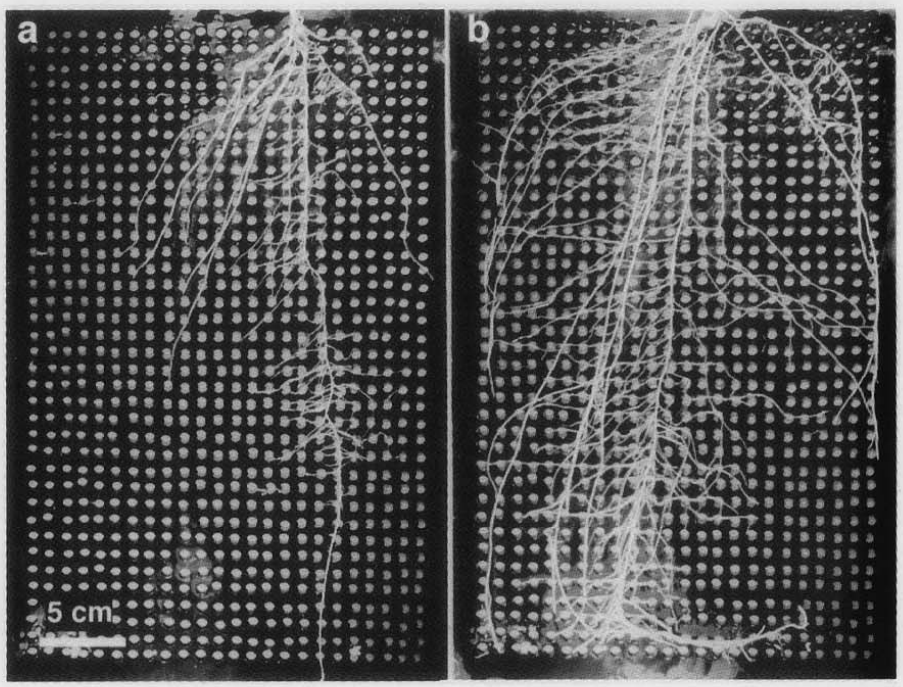

Fig. 2. Enhancement of root growth with *Trichoderma* colonization. (**a**) Control, (**b**) colonized with *Trichoderma*. These were the median plants from one experiment. The soil was washed away while the intact root system was held in place with a pin board. The small circles mark the corners of the 1-cm^2 cells used to quantify soil exploration.

treatment, except in the allelopathy experiments where there were 6. The effect of colonization on growth was analyzed by linear regression with a 0 intercept to estimate the slope. The effect of colonization on individual plant growth was assessed with simple correlation analysis. The size distributions were compared using the Kolmogoroff-Smirnoff test (Siegel, 1956) because a means test is insufficient to demonstrate differences when only part of the population is responding to the treatment (Fisher, 1935).

Results

Growth was markedly increased in sweet corn plants in which the roots were colonized by *Trichoderma harzianum* strain 1295-22. The growth of roots and shoots was similarly enhanced and the effect was consistent in nine replications (Fig. 1). The amount of growth enhancement with colonization was calculated as the slope of the regression line with a 0 intercept. The roots of the colonized plants weighed 170% of uncolonized controls ($r^2 = 0.77$) and the shoots weighed 168% ($r^2 = 0.63$). Over all nine experiments, the mean total dry mass of colonized plants was 0.69 g and of control plants was 0.40 g. The growth response of the whole population was the same whether growing conditions resulted in slow or rapid growth.

Root growth was evaluated as biomass and as soil exploration to determine whether colonization affected root architecture. Exploration of the soil was measured as the proportion of 1-cm^2 cells in the root box that contained roots (Fig. 2). Soil exploration depends on the biomass of the roots and on the distribution of root growth and the amount of branching. The ability of the root system to take up water and nutrients is measured more accurately by soil exploration than by biomass. The soil exploration value was closely related to the root length density (RLD), a parameter that can be used to compare these results with other experiments on root growth. Both soil exploration and RLD were measured in 10 root systems. The relationship was linear over the range of plant sizes in this experiment, with RLD = 2.58 cm·cm^{-3} × soil exploration ($r^2 = 0.97$).

The typical increase in root growth was substantial (Fig. 2), with the greater amount of branch roots at 3 weeks especially noteworthy. The soil exploration by colonized roots was increased by 20%, 94%, 109%, and 130% in four repetitions of the experiment (all increases significant at $P < 0.01$).

Oxidative stress. Treatment of the seeds with dilute hypochlorite to cause oxidation injury resulted in considerably reduced vigor. Subsequent colonization with *Trichoderma* completely restored the vigor of these seedlings (Table 1). Hypochlorite and *Trichoderma* significantly changed the size distributions compared to untreated seedlings (Fig. 3), making them smaller and larger, respectively ($P < 0.05$ using the Kolomogoroff-Smirnov test). *Trichoderma* changed seedling-size distribution of hypochlorite-treated seeds ($P < 0.01$) so that it was the same as seedlings that had been treated only with *Trichoderma*. The effect of hypochlorite and *Trichoderma* treatment on seedling vigor occurred mainly in the moderately vigorous seedlings. In contrast, the strongest seedlings in each group performed similarly.

Cold stress. A cold treatment was applied to reduce vigor

Table 1. Growth response of supersweet corn seedlings to *Trichoderma* (*Tricho*) colonization following vigor-reducing stresses.

Stress	Growth response[z]	Treatment				Statistical significance of effects		
		Control	*Tricho*	Stressed	Stressed and *Tricho*	*Tricho*	Stress	Interaction
Oxidation[y]	Shoot dry mass (g)	0.68	0.82	0.41	0.84	***	**	***
Cold[x]	Root dry mass (g)	0.33	0.42	0.09	0.10	*	**	NS
Allelopathy[w]	Radicle length (cm)	15.1	21.5	2.8	5.4	*	***	NS
	Max root length (cm)	20.5	27.3	10.8	13.3	**	***	NS

[NS,*,**,***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
[z] Growth measured at 21 d.
[y] Treated for 15 min with 0.05% NaOCl before seed imbibition.
[x] Treated for 5 d at 5/10 °C after seed imbibition.
[w] Treated with 300 mg·kg^{-1} benzoxazolinone (BOA) in soil.

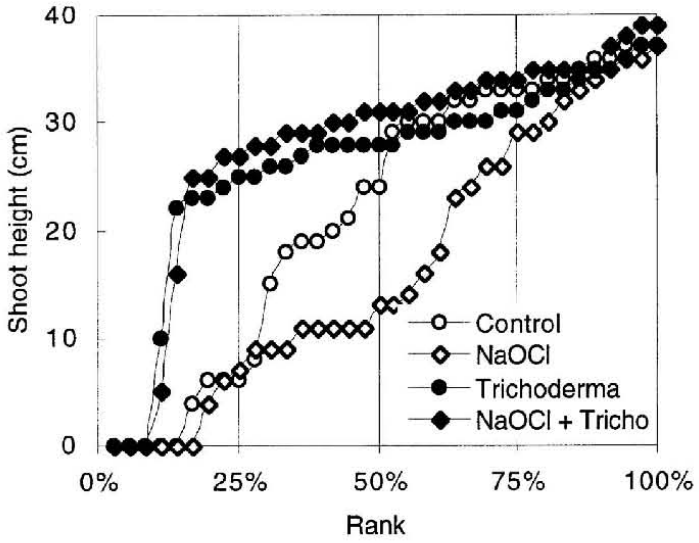

Fig. 3. Distribution of sweet corn plant size as affected by hypochlorite treatment and *Trichoderma* colonization. The shoot height was measured after 21 d of growth in pots. Hypochlorite and *Trichoderma* treatments affected primarily intermediate-vigor seedlings. High-vigor seeds were not further enhanced by *Trichoderma* colonization.

before active *Trichoderma* growth but to avoid imbibitional chilling injury. In a representative test with an intermediate cold exposure of 5 d (Table 1), root biomass was reduced by the cold treatment and increased by *Trichoderma*. At all intensities of cold treatment, there was greater growth in *Trichoderma*-treated plants, but there was no interaction between cold and *Trichoderma* (Fig. 4). If the cold injury were specifically reversed, an interaction would be expected. Colonized plants would be less sensitive to intermediate stresses that cause only lesions that can be reversed by the metabolic action of the fungus. Nevertheless, *Trichoderma*-colonized seedlings grew better after cold stress. Even though *Trichoderma* does not grow well at <15 °C, a growth enhancement resulted even after substantial cold treatment.

Allelopathic stress. Soil treated with BOA resulted in truncated roots with the same biomass as roots grown in the absence of BOA. *Trichoderma* increased the biomass growth (dry mass gain) by 52% (0.08 g; $F = 10.8$, $P < 0.01$) with no BOA effect ($F = 0.2^{ns}$).

Allelopathic stress did have a dramatic effect on root architecture. In root boxes, the average soil exploration of uncolonized plants was reduced from 18% to 8% by BOA ($t = 2.7$, $P < 0.02$). *Trichoderma* increased the elongation growth resulting in a large effect of BOA on the root system length (Table 1). The radicle apex died quickly in the BOA-treated soil, with compensatory growth in branch roots (Fig. 5). These branch-root apices also died relatively quickly, resulting in early higher-order branching as adventitious roots were initiated. The root systems had almost no radicle and a short, highly branched root system whether or not they were colonized by *Trichoderma*.

Pathogens. Even though there was no evidence of root rot, the observed growth enhancement could be due to the control of minor pathogens by *Trichoderma*. If so, controlling pathogens by other means would have the same effect as *Trichoderma*, with no further effect by also adding *Trichoderma*. Controlling soilborne pathogens by steaming the soil did not improve growth. There was no significant effect of steaming ($F = 1.6^{ns}$), and *Trichoderma* enhanced growth the same regardless of steaming ($F = 5.12$, $P < 0.05$; interaction $F = 0.3^{ns}$). In addition, root-box experiments were conducted with steamed and unsteamed soil. The mean root biomass was the same in both: without *Trichoderma* it was 0.155 and 0.145 g, respectively, and with *Trichoderma* it was 0.23 and 0.22 g. Neither of these experiments supports the hypothesis that growth enhancement was primarily through pathogen suppression.

Controlling pathogens by surface sterilizing the seeds likewise did not mimic the growth enhancement caused by *Trichoderma* (Fig. 3). To distinguish the detrimental effect of hypochlorite on seedling vigor from that of pathogens, the mesocotyl of each plant was plated and scored for *Fusarium*, *Pythium*, other fungi, and bacteria. The mean shoot biomass of infected plants was the same as that of uninfected plants (0.227 vs. 0.225 g, pooled $s = 0.125$, $n = 125$ $t = 0.2^{ns}$), indicating that size variation was not explained by disease organisms. While none of these is a definitive test for disease, the results indicate that the growth enhancement associated with *Trichoderma* colonization was more likely to be due to an interaction with the plant than to control of minor pathogens.

Discussion

Trichoderma colonization of sweet corn roots consistently enhanced the growth of both roots and shoots. While the mean growth was greater in colonized plants, the enhancement was mainly the result of a restoration of vigor in reduced-vigor plants. In these plants, the root growth was enhanced by increasing the

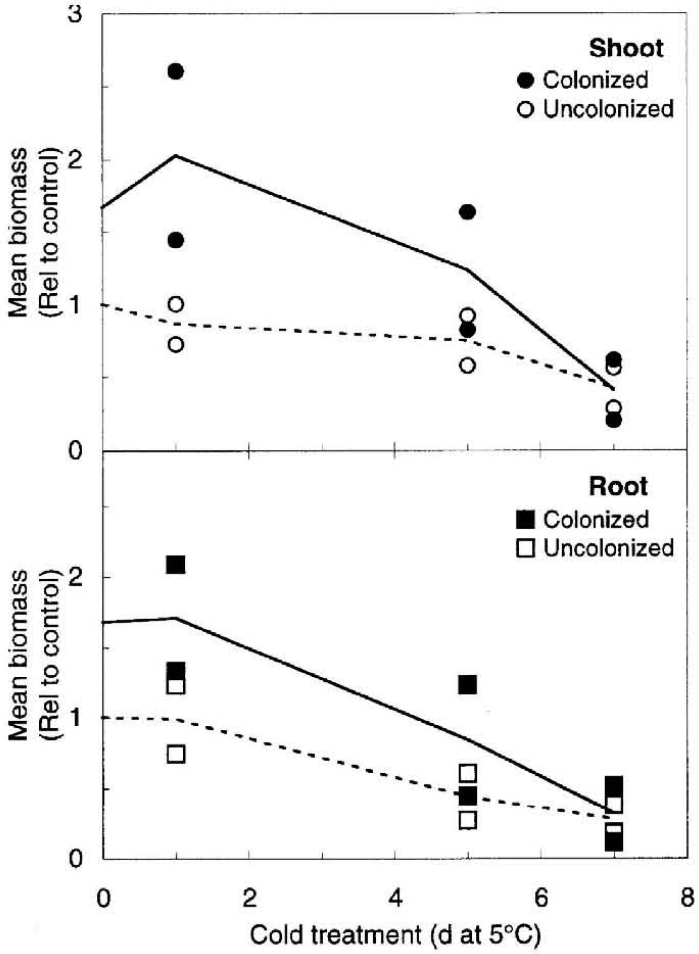

Fig 4. Effect of increasing duration of cold stress on root and shoot growth. Pots were placed in the cold (5/10 °C night/day) for various periods after the seeds had imbibed. The plants subsequently were grown in the greenhouse at 20/25 °C (night/day). Each point represents the root dry mass of one set of 12 pots divided by the dry mass of a contemporaneous unchilled, uncolonized control.

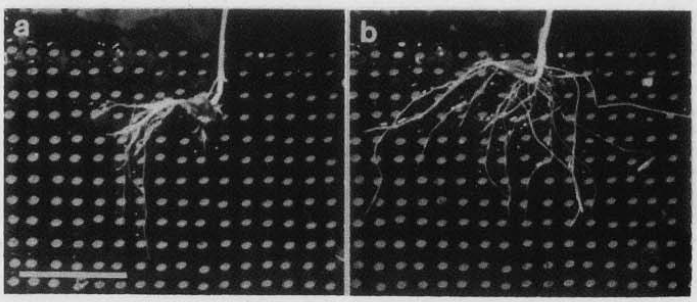

Fig. 5. Root system development in soil containing the active allelopathic agent from rye. (**a**) Benzoxazolinone (BOA) alone, (**b**) BOA and *Trichoderma*. Plants were grown for 21 d in root boxes as in Fig. 3, but the soil was supplemented with 300 mg·kg^{-1} BOA. Scale bar is 5 cm. Growth without BOA is shown in Fig. 2 at the same scale.

biomass and the amount of branching. The branch roots are the primary site of nutrient uptake, so the colonized seedlings are apparently able to begin taking up substantial amounts of mineral nutrients in the soil sooner than uncolonized seedlings. This mechanism is also consistent with the similar growth enhancement in shoots as in the colonized roots.

Within a population, the weaker plants responded the most to colonization. But when the growth of the whole population was reduced by stress, the response did not become greater. The shoot growth responded nearly as much as did root growth, but, with *Trichoderma* colonizing only the roots, enhanced shoot growth reflects the greater nutrient uptake by the root system of the colonized plants. This pattern suggests that the effect of colonization is not a uniform increase in vigor, but a reversal of some metabolic injury that slows the growth of the weaker plants. Growth limitations from other causes are not affected.

Oxidative stress. The proportion of high-vigor seedlings was reduced by treatment with hypochlorite, an oxidizing agent. In one population of seeds, hypochlorite treatment reduced the proportion of high vigor plants (>60% of largest plant) from 60% to 40%. With *Trichoderma* colonization, 85% of the hypochlorite-treated plants had high vigor. Thus, the vigor that was lost during hypochlorite treatment was subsequently restored by the fungus. Again, low-vigor seedlings were revitalized by colonization; there was no effect on high-vigor seedlings or on the proportion of nongerminating seeds. These results are consistent with *Trichoderma*'s reversing the injury caused by hypochlorite.

The reversal of hypochlorite injury could provide a clue to the mechanism of growth enhancement by *Trichoderma.* There are many injurious oxidative reactions caused by hypochlorite (Abdul-Baki, 1979; Sauer and Burroughs, 1986; Schraufstaetter et al., 1990), but of most interest is the peroxidation of membrane lipids, a reaction that can be prevented by the metabolic activity of the fungus. A reason to expect that this strain of *Trichoderma* creates such conditions is that it is resistant to fungicides that act through lipid peroxidation. There are two classes of these fungicides: the dicarboximides and the aromatic hydrocarbons (Edlich and Lyr, 1992; Lyr, 1988). *Trichoderma* is insensitive to both types: the dicarboximide iprodione (Harman et al., 1996), and to the aromatic hydrocarbon chloroneb (G.E. Harman and T. Stasz, unpublished data). In contrast, naturally occurring strains of *Trichoderma*, which are less effective biocontrol agents, are sensitive to iprodione (Kay and Stewart, 1994). Thus, we propose that an important mechanism of growth enhancement by this strain of *Trichoderma harzianum* is that it actively prevents, and possibly reverses, injurious and vigor-reducing peroxidation of membrane lipids and proteins.

Cold stress. Stresses that reduce growth by other mechanisms were not reversed by *Trichoderma* colonization. The growth of stressed plants was enhanced by *Trichoderma*, but only in the same proportion as in unstressed plants. Cold stress was applied in a way that causes injury primarily by accelerated respiration that would occur before active colonization (Stewart et al., 1990); thus, it reduces the amount of seed reserves available for growth. In cold-stressed plants, the amount of growth enhancement was consistent over a wide range of stress intensity, from 1 d of cold, which had little effect, to 7 d, which nearly killed the plants.

Allelopathic stress. The allelopathic agent reduced the root length and soil exploration rather than the biomass. The active allelopathic chemical is toxic to meristematic tissue (Barnes and Putnam, 1987). Killing the meristems caused the roots to be shorter, but the toxicity was not affected by *Trichoderma* colonization. *Trichoderma* caused the BOA-treated roots to grow slightly longer. The greater length could be due either to a faster growth rate or longer survival of the meristem. In all of our experiments, the presence of *Trichoderma* increased the growth rate, and that alone can account for the difference in length. If it does, the meristems die just as quickly, and *Trichoderma* does not neutralize the allelopathic toxicity.

Colonization by *Trichoderma* increased root elongation in the BOA-treated plants, but the pattern of short-lived root apices caused most of the roots to develop near the seed. This root architecture left most of the soil volume unexplored. As a consequence, the plants will be more likely to experience water and nutrient stress even with *Trichoderma,* although that was not realized in these short-term experiments.

Alternative mechanisms. There are two alternatives to the proposed hypothesis of reversal of peroxidation as the mechanism of growth enhancement by *Trichoderma.* First is a growth regulator produced by the fungus that accelerates cell elongation in the root tips, as has been proposed by Windham et al. (1986). If the effect of colonization was a growth-regulator mediated increase in root growth, the enhancement should have been greatest in the most-vigorous seedlings, but there was little enhancement of those seedlings. There should also have been a compensatory decrease in shoot growth as the growth regulator reallocated resources to the roots. There was no such shift in resource allocation, rather a net increase in biomass accumulation in roots and shoots. Furthermore, the growth increase is independent of auxin regulation of the growth rate (Blanchard and Björkman, 1996).

A second alternative is a variation of the disease-suppressive action of *Trichoderma*. In that alternative, *Trichoderma* suppresses minor pathogens through competition and mycoparasitism; that suppression results in increased growth, even though there is no detectable disease in either treatment. Several nondefinitive tests were made to assess whether microbial inhibition of growth was relieved by displacement by *Trichoderma.* Suppression of the microbial flora increased the *Trichoderma* enhancement. Also, there was no relationship between the presence of fungal pathogens and bacteria with plant growth. Both of these results are arguments against the microbial inhibition hypothesis.

The large population of *Trichoderma* is likely to displace other components of the rhizosphere microflora, and this alteration can result in stronger root growth (Whipps and Lynch, 1986). It is difficult to rule out this possibility because normal corn root growth depends on an appropriate rhizosphere flora (Watt et al., 1994). Although the composition of that flora is not well defined, altering its composition and abundance is likely to affect root growth by affecting its growth supporting functions.

The strain of *T. harzianum* used in this study can control a wide

range of fungal pathogens, including *Pythium*, *Rhizoctonia*, *Fusarium*, and *Botrytis* spp. (Datnoff et al., 1995; Harman et al., 1989). This ability, coupled with its strong rhizosphere competence, permits it to control root diseases in field situations (Datnoff et al., 1995; Venette and Gross, 1991). Heretofore, we had considered that enhanced growth in field situations occurred primarily as a consequence of root protection against pathogenic or other deleterious microflora. However, this study indicates that this strain protects roots and also enhances plant growth through direct effects upon the plant's physiology.

Conclusion

Growth was enhanced by *Trichoderma* colonization even after stress treatments that reduced seedling growth. The growth enhancement of low-vigor plants suggests that colonization reverses or limits the damage that causes low vigor. Cold treatments and allelopathic inhibition from the chemical benzoxazolinone inhibited growth, but the proportional enhancement by *Trichoderma* was about the same at all stress intensities. The lack of interaction between stress and *Trichoderma* suggests that the mechanisms are independent rather than specific mitigation of the injury caused by stress. These results demonstrate the potential for a rhizosphere-competent fungus to enhance plant growth in the absence of disease and to improve the performance of *sh2* sweet corn seedlings, even when they have been enervated by certain environmental stresses.

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