Growth promotion ability of zoysiagrass rhizosphere fungi in consecutive plantings of wheat and soybean

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Several isolates of *Phoma* sp., certain nonsporulating fungi, as well as *Penicillium* and *Trichoderma*, all isolated from zoysiagrass rhizosphere, promoted growth of wheat and soybean under greenhouse conditions. However, the ability of these rhizosphere fungi to enhance plant growth varied with the crop tested. For example, most of the fungi effectively promoted the growth of wheat, whereas only a few fungi were effective on soybean. In consecutive plantings of wheat and soybean grown in soil previously infested with these zoysiagrass rhizosphere fungi, the growth promotion ability of the fungi was lowered. However, addition of fresh potting medium appeared to restore their growth-promotive effects. It appears that the activation of plant growth-promoting fungi in soil might depend on the availability of organic substrates to colonize, as evidenced by the promotion of plant growth.

Key Words——consecutive planting; *Phoma* sp.; plant growth-promotion; potting medium; soybean; wheat; zoysiagrass rhizosphere fungi.

A large number of microorganisms which protect plants against pathogenic microbes and enhance plant growth have been identified. Rhizobacteria, species of *Trichoderma* and *Gliocladium*, and certain sterile fungal isolates have been shown to promote plant growth (Chang et al., 1986; Chanway and Nelson, 1991; Dewan and Sivasithamparam, 1989; Gamliel and Katan, 1991; Hall, 1987; Kleifeld and Chet, 1992; Kloepper et al., 1991; Narita and Suzui, 1991). Nutrients and metabolites released from root systems greatly influence rhizosphere microflora (Bowen, 1991; Miller et al., 1989; Rovira, 1979). Most earlier studies have been concerned with specific nutritional requirements of antagonist organisms in rhizospheres (Gindrat, 1977; Papavizas, 1985), while few have focused on the nutritional requirements of growth-promoting fungal isolates.

Preliminary studies on the growth-promotion ability of some rhizosphere fungi revealed that out of 1399 fungal isolates recovered from rhizospheres of egg plant (*Solanum melongena* L.), chilli (*Capsicum annuum* L.), maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), and zoysiagrass (*Zoysia tenuifolia* (Willd.) Thiele.), 32 isolates from zoysiagrass rhizosphere promoted plant growth in a variety of crops (Hyakumachi, 1994). Certain fungal isolates from zoysiagrass rhizosphere enhanced the growth of wheat and soybean (*Glycine max* (L.) Merr.) plants and increased yield in the greenhouse as well as in the field (Shivanna et al., 1994, 1995). We were interested to determine, under greenhouse conditions, whether plant growth-promoting fungi (PGPF) introduced into soil would also enhance growth in consecutive plantings.

Materials and Methods

Twenty-one zoysiagrass rhizosphere fungal isolates (13 isolates of *Phoma* sp. ('GS' series), 2 isolates of *Penicillium* sp. (isolates E-4 and F-3), and 1 isolate *Trichoderma* sp. (isolate GT2-1), and 5 nonsporulating isolates ('GU' series)), and 3 sterile fungal isolates ('K' series) obtained from wheat rhizosphere, were grown on potato-dextrose agar (PDA) and mass-cultured on autoclaved barley grains (Shivanna et al., 1994). The fungal colonized barley grains were powdered to a mean particle size of 0.5 mm using a dry grinder. The colony forming units (cfu) of powdered inocula used in all experiments ranged between 10^8 and 10^9 cfu/g as determined on PDA.

In the first experiment, plants were grown in soil infested or uninfested with barley grain inocula (BGI) of fungal isolates, then harvested. This was considered as the first planting. In the second experiment, the debris of the first plantings was removed and the same soil, with or without potting medium amendment, was planted with the same type of crop as before. This constituted the second planting.

First planting A soil mixture containing equal volumes of brown loam soil (Gifu University campus, pH 6.5–7.0, total carbon 0.27%, total N 0.048%, total P (P_2O_5) 1.6 mg kg^{-1}, soluble N 0.11%, and soluble P (P_2O_5) 0.022 mg kg^{-1}) and river sand (washed in water and air-dried) was infested with the inoculum (1%, w/w) of the respective fungal isolates and thoroughly mixed. Uninfested soil was also prepared. Soil (3.5 kg) was placed in rectangular pots (26-long × 13-wide × 9.5-height cm) and sown with 10 seeds each of wheat cv. "Haruhikari"

or soybean cv. "Toyosuzu." Soil with 1% (w/w) au-
toclaved, uninfested barley grains were considered as the
treated control. A commercial potting medium, "Star
bed" (containing N, K, and P in the ratio of
200 : 1500 : 200 mg L⁻¹, Kyodohiryo Co. Ltd., Japan),
was placed into pots and sown with seeds of wheat or
soybean to test the effect of fertilization in comparison to
the effect of fungal treatments on growth promotion.
Plants (6 replicates per treatment) were grown in the
greenhouse (85% RH and 25°C) during the spring and
summer of 1992 and 1993. Shoots of five plants in
each pot were harvested after 6 wk and the remaining
five plants were grown until senescence (approximately
10 wk), harvested and discarded.

Second planting Soils used in the first planting were
subsequently dried for 4 wk in the greenhouse during
summer. Soil from six pots of each treatment was
pooled, mixed and sieved (5 mm mesh). This was
referred to as cultivated soil (CS). Only thick primary
roots were discarded, while secondary and lateral roots
were retained in the soil. The CS of each treatment
category was divided into six parts, each of 3000 g.
The CS was amended (CS : autoclaved potting medium,
4 : 1, w/w) or not amended with potting medium to test
the effect of amendment of potting medium on the

growth of subsequent planting. The potting medium-
amended CS was dispensed into three pots, and un-
amended CS was dispensed into three additional pots.
In the experiment in which CS was amended with potting
medium, only CS which already contained inocula of
selected isolates GS7-3,GS8-1,GS8-2,GS8-6,GS14-1,
and GT2 was tested. Some of these isolates were effec-
tive growth promoters of the first planting, while others
were not. The ineffective isolates were included to test
if they could promote the growth of the second planting.
The CS that had received or not received uninfested
barley grain treatment as well as cultivated potting medi-
um also received potting medium amendment. The soil
mixtures were planted with the same crop, either soybe-
an or wheat, as that used for the previous planting.
Plants were grown for 6 wk, in the same greenhouse.
Experiments were conducted two times.

Analysis of plant growth From each replicate pot, five
6-wk-old plants were analyzed for growth promotion.
The shoot lengths were measured and dry biomass was
determined (Shivanna et al., 1994).

Statistical analysis Since the aim of the investigation
was to test the growth-promotion tendency due to fungal
isolates in the subsequent plantings, data of the experi-
ments were arranged as a spilt-plot design with 27 treat-

Table 1. Shoot length and biomass of six-wk-old plants in the first (1) and second (2) plantings of wheat grown in soil infested or uninfested with barley grain inocula of rhizosphere fungal isolates in the greenhouse. Data are the mean of six replications.

Fungal isolates/ treatments	Shoot length (cm)			Dry biomass (mg/plant)		
	1	2	3[a]	1	2	3[a]
E-4	37.6 bc[b]	37.6 ab	—[c]	292 cd	298 c-e	—
GS6-1	41.8 a	37.7 ab	—	329 a-c	429 a	—
GS6-2	41.1 a	39.8 ab	—	338 a-c	319 b-d	—
GS7-3	40.4 ab	38.6 ab	56.9 a	388 a-c	346 a-c	464 a
GS7-4	40.1 ab	37.0 ab	—	337 a-c	380 ab	—
GS8-1	37.6 bc	36.8 b	53.5 ab	317 a-c	255 c-f	434 ab
GS8-2	36.1 cd	40.5 ab	52.9 ab	322 a-c	338 a-c	462 a
GS8-6	41.6 a	40.5 ab	49.6 b	403 a	361 a-c	426 ab
GS10-1	37.0 c	38.2 ab	—	220 de	266 c-f	—
GS12-2	40.2 ab	41.9 a	—	377 a-c	336 a-c	—
GS14-1	32.5 ef	40.5 ab	49.7 b	297 b-d	408 ab	418 ab
GT2-1	32.5 ef	40.5 ab	49.0 b	299 b-d	340 a-c	424 ab
GU21-2	34.0 de	40.8 ab	—	398 ab	219 d-g	—
GU23-3	37.6 bc	37.7 ab	—	313 a-d	302 c-e	—
GU28-1	30.3 fg	38.2 ab	—	290 cd	178 fg	—
K-17	33.0 e	40.0 ab	—	375 a-c	147 g	—
UBG[d]	29.7 g	40.2 ab	43.9 cd	156 ef	358 a-c	390 c
PM[e]	28.3 g	30.5 c	41.3 d	160 ef	200 e-g	327 c
Control	20.1 h	29.9 c	34.4 e	98 f	151 g	199 d
LSD P=0.05	3.4	4.8		100	54	
P=0.01	4.5	6.3		140	74	

a) Growth increase in the second planting due to supplementation of potting medium to cultivated soil.   b) Values
followed by same letters in a column are not significantly different (DMRT, P=0.05).   c) Not tested.   d) Soil amend-
ed with uninfested barley grains.   e) Potting medium.

ments (24 fungal treatments, uninfested barley grain treatment, potting medium, and an untreated control) as main plot factors and two plantings as sub-plot factors. Out of a total of 24 isolates tested, 16 isolates were selected for analysis, since they induced significant growth promotion in at least one of the crops, when tested by the analysis of variance. The replicate trials were tested for homogeneity of variances by Bartlett's test. The data of growth promotion ability of 6 selected isolates in potting medium-amended CS and potting medium-unamended CS of the second plantings were also arranged in a split-plot design to test if the potting medium amendment influences plant growth. The fungal treatments were considered as main plot factors and potting medium amendment conditions as sub-plot factors. The treatment means were separated using Fisher's least significant difference test (LSD, P=0.05, 0.01) or Duncan's new multiple range test (DMRT, P=0.05).

Results

First planting Among 24 fungal isolates tested for growth promotion, 11 isolates increased the length of wheat shoots from 51% to 100% and 5 isolates in-

creased growth greater than 100% compared with untreated control plants. The remaining 8 isolates did not increase growth compared with that of untreated plants. However, 21 isolates increased biomass greater than 100% of control plants. Isolates GS6-1, GS6-2, GS7-3, GS7-4, GS8-6, and GS12-2 increased shoot length by 100% and biomass by 200% over the untreated control (Table 1).

Shoot length of soybean was increased by 10 isolates, up to 25%, but not by the remaining isolates. Four isolates increased the biomass up to 100%, 2 caused 50% increase, and 10 increased the biomass up to 25%. Isolates GS6-4, GS8-2, and GT2-1 increased the shoot length (up to 20%), while E-4, GS10-1, GS10-2, and K-16 were effective in enhancing biomass (up to 50%) (Table 2).

Shoot length and biomass of soybean, and biomass of wheat plants grown in soil which received uninfested barley grains and in potting medium did not differ (P=0.05) from that of plants grown in untreated soil. However, shoot length of wheat in soil treated with uninfested barley grains and in potting medium was high in comparison to that in untreated soil. Uninfested barley grain treatment was not as effective as fungal treatment in causing significant increases in shoot length and bio-

Table 2. Shoot length and biomass of six-wk-old plants in the first (1) and second (2) plantings of soybean grown in soil infested and uninfested with barley grain inocula of rhizosphere fungal isolates in the greenhouse. Data are the mean of six replicates.

Fungal isolates/ treatments	Shoot length (cm)			Dry biomass (mg/plant)		
	1	2	3[a]	1	2	3[a]
E-4	46.1 ef[b]	69.3 gh	—[c]	1025 a	843 a-c	—
GS6-1	48.0 de	98.9 bc	—	839 a-c	764 c-f	—
GS6-2	49.2 cd	78.4 e-g	—	650 d	729 d-f	—
GS6-4	53.2 b	88.6 c-e	—	654 d	893 ab	—
GS7-3	45.9 ef	111.9 a	119.0 a	941 a-c	772 c-f	3502 a
GS7-4	46.3 d-f	98.8 bc	—	796 bc	728 d-f	—
GS8-1	45.9 ef	97.8 b-d	106.3 b	696 d	722 d-f	3226 ab
GS8-2	55.6 a	70.0 gh	88.6 d	793 bc	939 a	2921 b
GS8-6	49.2 cd	87.0 de	99.9 bc	755 c	942 a	2520 c
GS10-1	45.9 ef	83.4 ef	—	977 ab	812 b-e	—
GS10-2	50.8 c	103.6 ab	—	978 ab	776 c-f	—
GS12-2	47.4 d-f	101.3 b	—	708 d	830 b-d	—
GS14-1	45.9 ef	87.6 de	96.3 cd	699 d	495 g	2019 de
GT2-1	53.9 ab	57.3 ij	91.3 cd	677 d	812 b-e	2247 cd
GU26-1	45.9 ef	87.6 de	—	772 c	669 f	—
K-16	45.7 f	74.5 fg	—	1019 a	773 c-f	—
UBG[d]	46.1 ef	62.5 hi	67.0 f	689 d	705 ef	1859 e
PM[e]	47.5 d-f	49.5 jk	76.2 e	652 d	690 f	1789 e
Control	45.9 ef	45.2 k	48.5 g	643 d	464 g	1558 f
LSD P=0.05	8.3	7.9		120	216	
P=0.01	11.0	10.8		170	297	

a) Growth increase in the second planting due to supplementation of potting medium to cultivated soil. b) Values followed by same letters in a column are not significantly different (DMRT, P=0.05). c) Not tested. d) Soil amended with uninfested barley grains. e) Potting medium.

mass, particularly in wheat (Tables 1, 2).

Second planting Seventeen of 24 isolates caused increase of shoot length of wheat up to 50%, and 7 others increased growth up to 25% over untreated control. Nine isolates induced a biomass increase greater than 100%. Seven other isolates increased biomass from 25% to 100%, whereas 8 isolates did not cause any biomass increase (Table 1). Compared with the first planting, the second wheat plantings showed much less increase in shoot length and biomass. The CS containing isolates GS8-2, GS14-1, GT2-1, GU21-2, GU28-1, or K-17 increased shoot length of second plantings (P=0.05). However, the biomass increase (P=0.05) of the second planting was lower in CS containing isolates GS6-1 and GS14-1 than that in the first planting (Table 1).

The shoot length of soybean plants increased more in the second planting than in the first. Six isolates increased shoot length over untreated control plants by more than 100%, while 7 others increased length from 50% to 100%. Eight isolates were ineffective in increasing shoot length. Isolates GS7-3, GS8-1, GS10-2, and GS12-2 increased shoot length by more than 200%. Two isolates (GS8-2 and GS8-6) caused more than 100% increase in biomass, and 12 isolates caused increases between 50% and 100%. Nine isolates failed to cause increase in biomass. Sixteen fungal isolates caused a significant increase of shoot length of the second soybean planting compared with the first planting, but only 5 isolates caused increase (P=0.05) in biomass of the second planting over the first planting. Among these 5 isolates, 3 were highly effective in increasing the biomass only in the second planting (Table 2).

Wheat and soybean plants grown in CS containing uninfested barley grains showed a significant (P=0.05) growth increase over that of untreated control plants. Increase in shoot length and biomass of wheat and soybean due to uninfested barley grains was similar to the increase induced by certain effective PGPF isolates. However, in the case of wheat, uninfested barley grain treatment caused highly significant (P=0.05) increase in shoot length and biomass of the second planting compared with the first planting (Tables 1, 2).

Effect of supplementing cultivated soil with potting medium
Wheat All the selected isolates enhanced the shoot length and biomass of second plantings upon addition of potting medium to CS compared with the potting medium amended-CS of untreated control, CS that had received uninfested barley grain treatment, or cultivated potting medium. The increase in shoot length of the second planting grown in potting medium-amended CS containing selected fungi, over those of potting medium-amended CS control, ranged between 42.4% and 65.4%. Isolates GS7-3, GS8-1 and GS8-2 induced the greatest shoot length increase after supplementing CS with potting medium. Biomass increase in the second planting grown in the potting medium-amended CS containing selected fungi ranged from 110% to 133% over those in the potting medium-amended CS control. The shoot

length of the second crop grown in unamended CS increased slightly over that of the first crop and the addition of potting medium to CS caused a further slight increase of shoot length and biomass (Table 1).

An increase in the plant growth was significantly (P=0.05) greater in the potting medium-amended CS that had received uninfested barley grain treatment over the potting medium-supplemented control; such an increase was not significantly (P=0.05) greater than that induced by certain PGPF isolates. Cultivated potting medium supplemented again with the fresh potting medium was less effective than CS that had received uninfested barley grain treatment in enhancing the shoot length and biomass (Table 1).

Soybean Enhancement of shoot length due to selected fungi in potting medium-amended CS over potting medium-amended CS control ranged between 82.7% and 145.4%. Isolates GS7-3, GS8-1 and GS8-6 caused greater increases. On the other hand, an increase in the biomass of second planting grown in the potting medium-amended CS containing selected fungi over those of potting medium-amended CS control ranged between 29.6% and 124.8%. The isolate GS7-3 was most effective followed by GS8-1 and GS8-6 in decreasing order of efficiency. Isolate GS14-1 induced almost an increase in biomass similar to that of uninfested barley grain treatment inspite of addition of potting medium to CS (Table 2).

A similar tendency of increase of shoot length and biomass due to supplementation of potting medium to CS containing uninfested barley grain treatment or cultivated potting medium or untreated control was observed in soybean, as in case of wheat (Table 2).

Discussion

The growth-promotion ability of rhizosphere fungi varied depending on the type of crop. With wheat, growth was increased by many isolates; but for soybean, fewer isolates were effective. This observation is in agreement with the previous findings (Shivanna et al., 1994, 1995). This difference, also observed in cucumber, tomato, and radish (Hyakumachi, 1994), could be due to their differential ability to colonize roots of crop plants. Most of the zoysiagrass rhizosphere fungal isolates, particularly isolates of *Phoma* sp. were found to be better root colonizers of wheat than of soybean (Shivanna, unpublished). Furthermore, only three of these isolates, all *Phoma* sp., colonized roots of cucumber (Meera et al., 1995). Dewan and Sivasithamparam (1989) also showed that the sterile fungal isolates from rhizospheres of wheat and ryegrass (*Lolium rigidum* L.), which promoted growth of a variety of crop plants, readily colonized roots of cereal crops. In the present study, a weak growth response of soybean plants to rhizosphere fungal isolates in the first planting might be due to a weak colonization ability of fungal isolates on soybean roots.

The growth enhancement of the second planting of soybean compared to the first planting could be due to the interaction between rhizobia and the PGPF isolates.

Root nodules were formed in larger numbers in the second planting of soybean than in the first, and this increase was frequently associated with isolates that enhanced shoot length (data on nodules not shown). The increase in shoot length but not biomass of the second planting of soybean due to fungi could be due to the internodal elongation following increased nitrogen uptake owing to increased production of nodules and nitrogen fixation. The reason for the reduced biomass of the second planting is not well understood, although it could be explained by a "slendering effect" caused by increased nitrogen uptake. In the case of wheat, the increase in shoot length and biomass was more prominent in the first planting than the second planting. This might be related to the dilution of nutrients resulting from the exhaustion of substrate needed for the growth of the fungal isolates as well as for plants in the second planting. The exhaustion of substrate might have led to the decline of PGPF populations in soil. The increased length and biomass of wheat and soybean plants brought about by supplementing cultivated soil with autoclaved potting medium suggests that substrate addition restores PGPF activity. On the other hand, certain isolates which were not effective growth promoters in the first planting became effective in the second. This might be due to their incomplete colonization on substrates and roots in the first planting followed by more complete colonization in the second planting. The growth of such fungi in vitro was also slow (Shivanna et al., unpublished). Thus, although growth-promotion ability differed depending on the crops and PGPF, nutrient and/or substrate content of the soil appears to be very important for the active growth and establishment of PGPF and promotion of plant growth. In fact, Rovira et al. (1990) reported that the type of crop rotation and the method of crop residue management influenced microbial colonization of wheat rhizospheres and crop yield.

Growth promotion of the second planting of soybean and wheat in potting medium-amended CS suggests that the PGPF, particularly *Phoma* sp. and *Trichoderma* sp., compete well for the available substrates on the root surface as well as in the soil. The potting medium might serve as the main source of energy for the reactivation and colonization by the resident PGPF. Possibly, the use of substrates like potting medium can enhance the activity of the beneficial PGPF which have different levels of saprophytic competitive ability. Many biocontrol agents — bacteria (*Bacillus, Enterobacter, Pseudomonas* spp.), fungi (*Trichoderma* and *Gliocladium* spp.), and *Streptomyces* sp. — have been reported to readily colonize composts (Chung and Hoitink, 1990; Hardy and Sivasithamparam, 1991; Hoitink and Fahy, 1986), and thus induce plant growth and decrease losses due to diseases (Mandelbaum and Hadar, 1990). Hoitink et al. (1991) suggested that the use of composts provides opportunities for the natural and induced suppression of diseases and hence good plant growth.

The soil supplemented with uninfested barley grains also resulted in the growth promotion of wheat and soybean plants; and this could be related to the activity of in-digenous microbial population present in the unsterilized soil that might colonize and degrade barley grains and benefit plants. On supplementing potting medium to CS that had received uninfested barley grains, the already established microbes degraded potting medium and further enhanced growth. Our previous study, in which autoclaved uninfested barley grains were added to sterilized nutrient-deficient soil, showed that uninfested barley grain alone can not promote plant growth (Shivanna et al., 1994). On the other hand, plant growth promotion by potting soil alone was considerably less; and the main reason for this could be the loss of microbial activity following the autoclaving of potting medium. However, at the time of the second planting, microbes might have developed in the potting medium and degraded it, resulting in the promotion of plant growth. This, as well as the growth-promotion due to CS that had received fungal treatments and potting medium, suggests that potting medium could become a substrate suitable for the multiplication of microbes.

The possible mechanisms of plant growth promotion due to rhizosphere fungi have been related to the augmented uptake of minerals and ammonia nitrogen by roots following degradation of barley grains by PGPF (Hyakumachi, 1994; Shivanna et al., 1994, 1995) and the suppression of deleterious soilborne microbes by competing for sites of infection (Shivanna et al., 1996) and nutrition with pathogens. Table 3 shows the increased uptake of inorganic minerals by wheat seedlings following their growth in nutrient-depleted soil supplemented with barley grain inocula of certain PGPF. Rovira et al. (1993) have also shown that plant growth promotion caused by rhizosphere microorganisms could be due to the increased absorption of mineral nutrients by plants. Evidence has been obtained for the involvement of certain methanol-soluble active components from culture filtrate and mycelial mat of PGPF in plant growth promotion (Shivanna, 1995). This might suggest that PGPF enhance plant growth by producing certain metabolites during the colonization of roots and substrates.

Table 3. Inorganic components of four-wk-old wheat seedlings grown in brown loam soil supplemented with barley grains colonized with selected zoysiagrass rhizosphere fungal isolates (1.0%, w/w) in the greenhouse.

Fungal treatments	Inorganic components (μg/g)[a, b]					
	Na	Mg	P	K	Ca	Fe
GS8-2	0.29	10.98	26.94	87.10	27.42	0.27
GS10-1	0.12	8.72	21.15	73.20	21.97	3.00
GS12-2	0.36	10.05	26.14	79.48	25.78	6.60
GT2-1	0.24	8.17	17.13	70.53	20.38	0.04
GU23-3	0.00	8.07	17.52	60.90	15.41	0.17
UBG[c]	0.23	9.64	16.65	74.22	24.76	0.78
Control	0.30	9.44	11.76	46.47	22.57	0.68

a) Assayed by inductively coupled plasma atomic emission spectrometry. b) Soil composition as in materials and methods. c) Soil supplemented with uninfested autoclaved barley kernels (1.0%, w/w).

This investigation as well as the previous one (Shivanna et al., 1996) indicates that certain PGPF have saprophytic ability and competitive root colonization ability. Saprophytic ability and competitive root colonization ability are two of the most desired characteristics of an ideal biological control agent. These investigations suggest the potential application of rhizosphere fungi as PGPF as well as biological control agents.

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