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Dispersal of rice sheath blight fungus, *Rhizoctonia solani* AG-1(IA), and subsequent disease development in paddy fields, from survey of vegetative compatibility groups

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The rice sheath blight fungus, *Rhizoctonia solani* AG-1(IA), was isolated from surface soil and stubble in the pretransplanting season (early March) and from sheath blight lesions on plants at the maturing stage (late September) in two paddy fields (TW and TM: 8 a). Isolates were classified into vegetative compatibility groups (VCG) based on the formation of a barrage zone (or interaction zone) at the colony interface between isolates on paired cultures. In field TW surveyed in 1991 and 1992, 128–142 isolates obtained in the pretransplanting season and 82–85 isolates from lesions on mature plants were classified into 27–29 and 28–30 VCGs, respectively. Seven to 10 VCGs (26–35%) were common between both samples, and of 30 VCGs from mature plants 12 (40%) survived the winter 1991/1992 and recovered from stubble and/or soil. In field TM in 1992, 111 isolates in the pretransplanting season and 99 from mature plants were divided into 18 and 14 VCGs, respectively. Seven (39%) out of 18 VCGs in the pretransplanting season were recovered again from mature plants. Occurence of common VCGs throughout the year indicated that ca. one third of VCGs found in the pretransplanting season caused sheath blight on rice plants about 6 mo later in the same field. Further, it was shown that about the same rate of VCGs which had caused disease overwintered on stubble and/or surface soil until the following pretransplanting season.

Key Words——dispersal; paddy field; *Rhizoctonia solani* AG-1(IA); vegetative compatibility groups.

Sheath blight caused by *Rhizoctonia solani* AG-1(IA) is a major disease of rice plants and occurs wherever rice plants are grown in Japan, Southeast Asia, and the United States (Nonaka et al., 1979b; Lee and Rush, 1983; Ou, 1984). *Rhizoctonia solani* AG-1(IA) survives in paddy fields generally in the form of sclerotia produced on the surface of leaf sheaths, which fall into rice hills more frequently than onto soil surfaces (Yamaguchi et al., 1971; Hori, 1991). After overwintering, the buoyant sclerotia are dispersed by irrigation water (Hashiba et al., 1972) and infect newly transplanted plants to cause sheath blight.

Recently, the field population of *R. solani* has been found to consist of many subgroups based on anastomosis affinity between field isolates within an anastomosis group, e.g., AG-1, AG-2-2, and AG-8 (Ogoshi and Ui, 1983; Nishimura and Sugimoto, 1985; MacNish et al., 1993; Inagaki and Kawabuchi, 1995). Furthermore, in *Athelia (Sclerotium) rolfsii*, *Leucostoma persoonii*, and *Leucocytospora kunzei*, as well as *R. solani* (Punja and Grogan, 1983; Proffer and Hart, 1988; Adams et al., 1990), subgroups within a species or anastomosis group were identified on the basis of the formation of a barrage zone (interaction zone or demarcation line) at the interface between paired colonies of different isolates (Adams and Roth, 1967; Sonoda, 1982; Shew and Melton, 1995). Such subgroups based on barrage zone formation are called vegetative compatibility groups (VCGs). In the present study, VCGs of *R. solani* AG-1(IA) were qualitatively surveyed to understand the dynamics of this pathogen in paddy fields, especially its dispersal and the subsequent outbreak of sheath blight.

Materials and Methods

Collection of soil, stubble and sheath blight lesions Two paddy fields (TW and TM: ca. 8 are) were selected in Togo near Nagoya City as sites for collection of rice stubble, soil samples and sheath blight lesions. Forty plots were set up at intervals of 4.5–5.0 m in the fields. Before transplanting of rice seedlings, early March, 2 rice stubble 5–10 cm high and 200 g of soil samples from about 400 cm^2 of soil surface were collected from each plot of field TW in 1991 and 1992 and field TM in 1992. These were air-dried for 3 wk at room temperature (10–20°C) and kept at 5°C until fungal isolation. Isolates obtained from stubble and soil were combined and treated as those in the pretransplanting season or as those from stubble and/or soil. In addition, a maximum of 10 culms of diseased plants with sheath blight lesions were collected from each plot at the mature stage of rice plants in late September. Each collection plot for diseased plants contained 15–20 hills.

Fungal isolation A modified soil-sieving method was

employed for soil samples (Ogura, 1984). Each 200-g sample of soil was thoroughly crushed, immersed in 1,000 ml of distilled water, blended for 30 s and passed through a 65 mesh sieve (Tyler: 0.210 mm pore size) to collect plant residues. This process was repeated 5 times. The residue was washed 5 times in distilled water, surface disinfected in 1% sodium hypochlorite solution for 3–4 min, and placed on water agar (WA) containing 50 μg/ml streptomycin in 9-cm Petri dishes. After 2–7 d of incubation at 28°C, newly developing hyphal segments were transferred to potato sucrose agar (PSA). Withered stubble stems were cut into 1-cm segments and washed 4–5 times in distilled water. One hundred segments in both samples were then used to isolate *R. solani* AG-1(IA) by the method mentioned above. The fungus was isolated from sheath blight lesions in the same way. Each lesion was cut into 2 pieces, and 1–10 lesions per plot were used for isolation. Isolates from the three isolation sources (soil, stubble and lesions) were identified as *R. solani* AG-1(IA) by both anastomosis affinity with a tester isolate (I-5201) on WA and cultural characteristics on PSA.

Determination of vegetative compatibility groups Preliminary cultural experiments for barrage zone formation gave the same results irrespective of the type of medium used, i.e., corn meal agar, malt extract agar (modified), oatmeal agar, PSA, and Richard agar (modified; Tuite, 1969), and PSA was used routinely. Five small disks, each from PSA culture plates of different isolates of *R. solani* AG-1(IA), were placed at about 2 cm apart on PSA plates and incubated at 28°C for 5–14 d. Isolates that grew together and failed to show a barrage reaction at the colony junction were classified as the same VCGs, whereas isolates exhibiting a barrage reaction were classified into different VCGs. The number of VCGs within a plot was initially determined, and constituent VCGs were compared between plots. The differences between plots or isolation sources were surveyed using a representative isolate of each VCG. Each VCG received a unique serial number, regardless of the isolation source within a field: e.g., VCG 25 from stubble and/or soil and from lesions in 1991 and VCG 25 from stubble and/or soil in 1992 (field TW) are the same VCGs. Furthermore, VCGs repeatedly detected in the same field were shown using * in Figs. 2, 3. For instance, VCGs 7*, 15**, and 25*** in field TW indicate that VCGs 7, 15, and 25 were detected 2, 3, and 4 times, respectively, out of 4 times of fungal isolation, i.e., the isolation from stubble and/or soil in 1991, from lesions in 1991, from stubble and/or soil in 1992, and from lesion in 1992. Tests were repeated 2 to 5 times with two replicate plates.

Results

Formation of barrage zone A barrage zone was observed along contact lines of colonies from different isolates, but not between colonies of the same isolates (Fig. 1). Mycelial growth was meager in the barrage zones, and dead fused cells defined as imperfect fusions (Ogoshi, 1976) were observed microscopically. Barrage zones differed in width and extent of pigmentaion according to the combination of isolates.

Number of isolates and VCGs In both fields TW and TM, *R. solani* (IA) was isolated more frequently from soil than from stubble, and was obtained from lesions collected in 30–32 plots (75–80%) out of 40 surveyed (Table 1). The number of isolates obtained from field TW in 1991 and 1992 amounted to 210 and 227, belonging to 49 and 48 VCGs, respectively. A total of 210 isolates belonging to 25 VCGs were obtained from field TM in 1992. Several VCGs were common to different sources.

Distribution of VCGs Regardless of isolation source, only a small number of VCGs were ubiquitous, the majority being restricted (Table 2): 97 (61%) of total of 160 VCGs detected were found to occur in a single plot, and 19 (12%) were widespread, occuring in more than 5 plots. Field distribution of VCGs from stubble and soil are combined in the same figure, as shown in Figs. 2 and 3. VCGs 4 (1991) and 2 (1992) in field TW (Fig. 2) and VCG 1 in field TM (Fig. 3), each from stubble and/or soil, as well as VCG 1 in field TM from lesions were detected in 19-22 plots, equivalent to about one half of total plots in each field. Many VCGs, such as VCGs 13, 18, 19, 25 and 27 from stubble and/or soil and VCG 48 from lesions

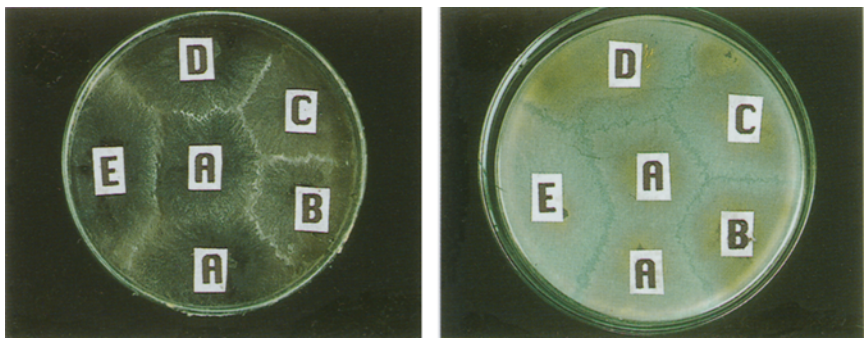

Fig. 1. Paired culture between field isolates of *Rhizoctonia solani* AG-1 (IA) on PSA, viewed from the obverse (left) and the reverse of the plate (right).
Barrage zones (or interaction zones) were observed between center (isolate A) and all surrounding isolates (B–E) except one (A). The reverse side of the PSA plate is more suitable for observation of barrage zones than obverse.

Table 1. Number of isolates and VCGs of *Rhizoctonia solani* AG-1(IA) from three isolation sources, stubble, soil surface and sheath blight lesions, collected in two paddy fields in different seasons of 1991 and 1992.

Paddy field	Yr	Sampling time[a]	Isolation source	The number of		
				Plots infested[b]	Isolates	VCGs
TW	1991	Early March	Stubble	19	49	11
		do.	Soil	27	79	21 (29)[d]
		Late September	Lesion	32	82	30
		Total		40[c]	210	49[e]
	1992	Early March	Stubble	10	17	8
		do.	Soil	29	125	25 (27)[d]
		Late September	Lesion	30	85	28
		Total		40[c]	227	48[e]
TM	1992	Early March	Stubble	5	11	5
		do.	Soil	29	100	18 (18)[d]
		Late September	Lesion	31	99	14
		Total		40[c]	210	25[e]

a) Soil samples and stubble were collected in the pretransplanting season (early March), while sheath blight lesions were collected at the mature stage of rice plants (late September).
b) The number of plots where the pathogen was detected.
c) Number of plots surveyed was 40.
d) Total of stubble and soil VCGs. VCGs common to both sources are counted only once.
e) VCGs common to all sources are counted only once.

Table 2. Distribution ranges of VCGs of *Rhizoctonia solani* AG-1(IA) from three isolation sources collected in two paddy fields in different seasons of 1991 and 1992.

Paddy field	Yr	Isolation source	Number of plots								Total
			1	2	3	4	5	6–10	11–15	16–20	
TW	1991	Stubble	8[a]	1	0	0	0	2	0	0	11
		Soil	11	5	2	1	0	1	1	0	21
		Lesion	20	5	1	1	1	1	1	0	30
	1992	Stubble	7	0	0	0	1	0	0	0	8
		Soil	15	3	4	1	1	0	0	1	25
		Lesion	19	4	2	0	1	2	0	0	28
TM	1992	Stubble	3	1	1	0	0	0	0	0	5
		Soil	10	4	1	0	0	1	1	1	18
		Lesion	5	5	0	1	0	2	0	1	14
Total		Stubble	18	2	1	0	1	2	0	0	24
		Soil	35	13	7	2	1	2	2	2	64
		Lesion	44	14	3	2	2	5	1	1	72

a) Number of VCGs.

in field TW (1991), were found to be distributed in neighboring plots, although some VCGs, e.g., VCGs 15 from stubble and/or soil and 43 from lesions in TW field (1991), were present in distant plots within a field.

Presence of the same VCGs in different isolation sources or between years Several VCGs were detected repeatedly in different sources and years. In field TW, 32 (1991) and 33 VCGs (1992) from both stubble and soil contained the same 3 (VCGs 2, 4, and 8) and 6 VCGs (VCGs 2, 7, 25, 45, 48, and 51), respectively. Twenty-three VCGs from both stubble and soil in field TM also contained the same 5 VCGs (VCGs 1, 2, 3, 4, and 5), equal to the total number of VCGs from stubble. Therefore, in the pretransplanting season, the total number of VCGs exclusive of the common groups was 29 (1991) and 27 (1992) in field TW, and 18 (1992) in field TM.

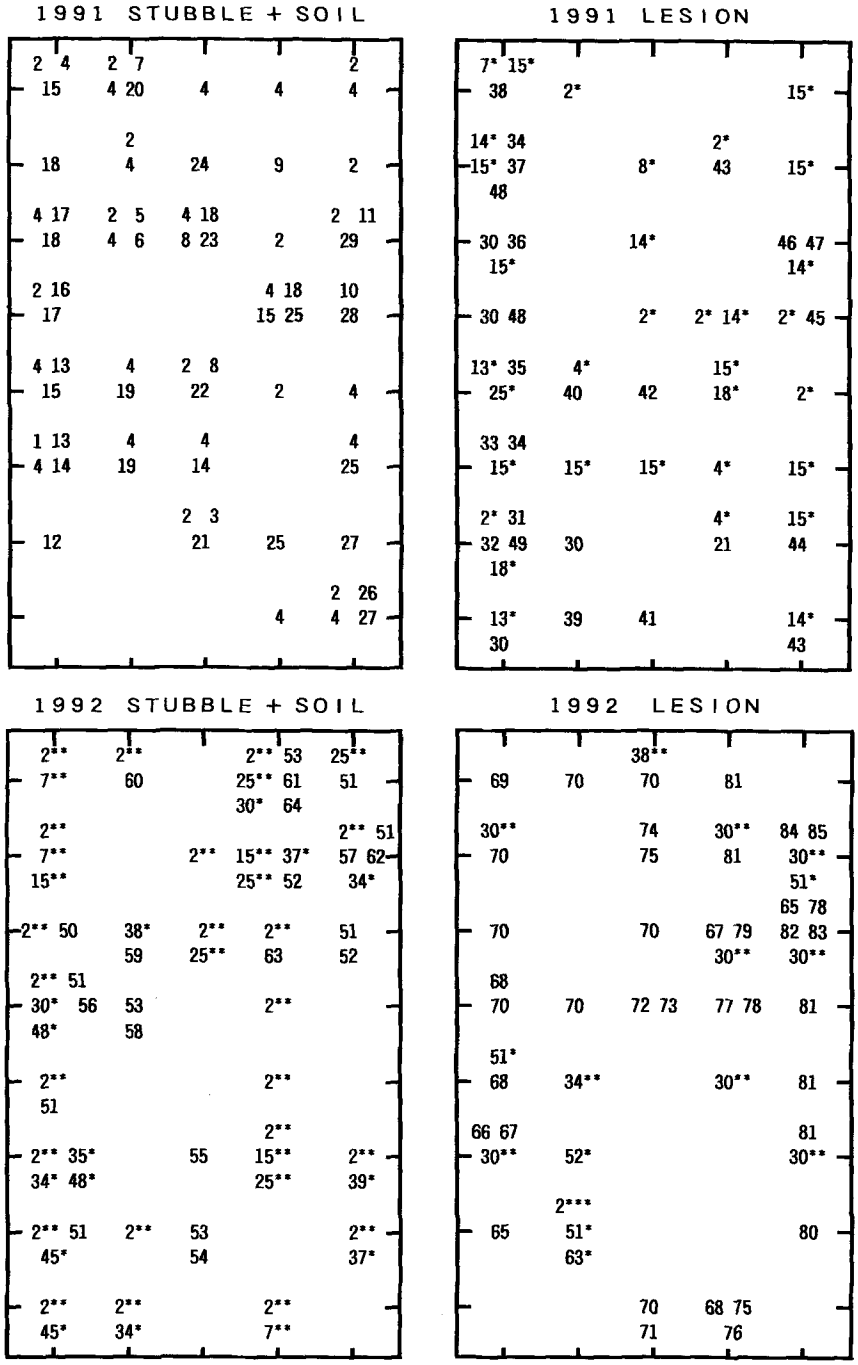

Fig. 2. Distribution of VCGs of *Rhizoctonia solani* AG-1 (IA) from three isolation sources collected in fields TW in 1991 and 1992. VCGs from stubble and/or soil are shown in a single figure. VCG with *, ** and *** mean those which were detected 2, 3, and 4 times, respectively, out of 4 times of fungal isolation, i.e., 1: isolation from stubble and/or soil in 1991, 2: do. from sheath blight lesions in 1991, 3: do. from stubble and/or soil in 1992, and 4: do. from sheath blight lesions in 1992.

Ten VCGs (35%; VCGs 2, 4, 7, 8, 13, 14, 15, 18, 21, and 25) out of 29 and 7 VCGs (26%; VCGs 2, 30, 34, 38, 51, 52, and 63) out of 27 from stubble and/or soil caused sheath blight in 1991 and 1992, respectively, in field TW (Fig. 4). Twelve VCGs (40%; VCGs 2, 7, 15, 25, 30, 34, 35, 37, 38, 39, 45, and 48) out of 30 from lesions survived the winter 1991/1992 in the stubble and/or soil. In field TM, 7 VCGs (39%; VCGs 1, 2, 4, 9, 10, 13, and 15) out of 18 observed in the pretransplanting season were found again from lesions. These VCGs with one to three asteriks, as shown in Figs. 2, 3, were found in 27 (84%), 13 (45%), and 28 plots (90%) out of 32 (field TW, 1991), 29 (TW, 1992), and 31 plots (TM, 1992) infested, respectively. Six VCGs among 7 (field

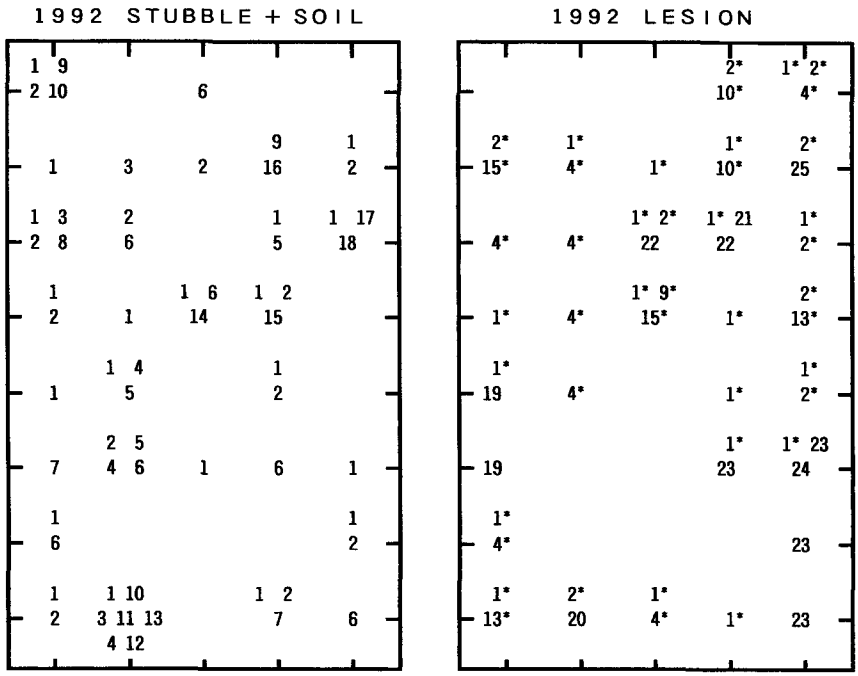

Fig. 3. Distribution of VCGs of *Rhizoctonia solani* AG-1 (IA) from three isolation sources collected in field TM in 1992. See Fig. 2.

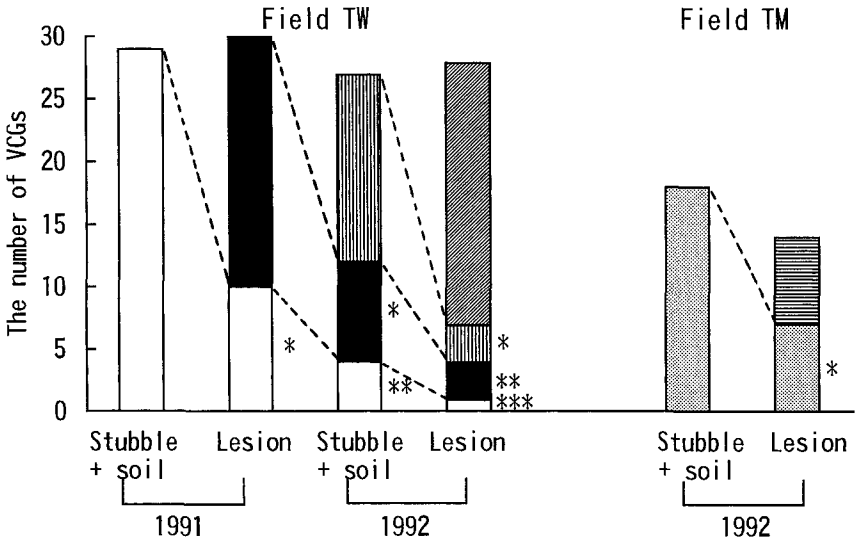

Fig. 4. Presence of the same VCGs of *Rhizoctonia solani* AG-I (IA) in different isolation sources and in different years. Thirty VCGs drawn in white, for instance, from stubble and/or soil in field TW (1991) contain 10 VCGs that were again detected from lesions ca. 6 mo later. See Figs. 2, 3.

TW: VCGs 2 and 4 in 1991, and VCGs 2 and 51 in 1992; field TM: VCGs 1, 2, and 6) obtained in 6 or more plots in the pretransplanting season were also detected from lesions.

In 1991 and 1992 in field TW, 12 (40%) out of 30 VCGs from lesions in 1991 were the same as 12 (44%) with * and ** out of 27 VCGs in 1992-pretransplanting season, and these 12 VCGs were found in 25 plots (86%) out of 29 infested plots in the 1992 pretransplanting season. Most of the same VCGs did not differ greatly in distribution between the two seasons within a yr, and between seasons in consecutive yr, with several notable exceptions: VCGs 4 and 15 (field TW, 1991), VCGs 2 and 30 (TW, 1992) and VCGs 2, 15, and 25 (TW, 1991-1992).

Discusssion

Vegetative compatibility means that isolates within a species are able to fuse without the death of cells and to

exchange nuclei and cytoplasmic materials (Anagnostakis, 1977). The vegetative compatibility system has been applied to study the dynamics of some tree pathogens in the field (Anagnostakis, 1977; Adams et al., 1990). The present study demonstrated the existence of abundant subgroups within an anastomosis group, as already shown by Ogoshi and Ui (1983), who focussed on subgroups from lesions. By this approach, I demonstrated that ca. one third (26–39%) of total VCGs present in stubble and/or soil caused sheath blight lesions within the same yr and that 40% (12 out of 30 VCGs) overwintered in the stubble and/or soil. These results suggest that sclerotia formed on rice plants survive without living host tissues until the following transplanting season, then cause sheath blight about 6 mo later in paddy fields. It was also recognized that sheath blight is caused not only by *R. solani* AG-1(IA) sclerotia native to the field but also by newly introduced sclerotia or by the transplanting seedlings that contain fungal propagules (Kadowaki and Isota, 1993). However, the ratio of appearence of the same VCGs in different yr or from different sources seems to vary considerably depending on the yr and the field. Thus, VCGs varied in the time of dectection, e.g., from the pretransplanting season to the mature stage of rice plants, or from the latter to the former season of the following yr. In *R. oryzae* Ryker et Gooch, which causes rice bordered sheath spot, strains detected for 2–9 yr and for only 1 yr in paddy fields are distinct in their virulence to mature rice plants (Inagaki, 1996). *Rhizoctonia solani* AG-1(IA) has been found to vary in cultural and pathological features (Hashiba et al., 1974; Nonaka et al., 1979a; Ou, 1984; Hori, 1991). Further studies should reveal the relationship between these parameters and detection periods as well as their range of distribution in paddy fields, as mentioned later.

Individual subgroups based on anastomosis compatibility (a-c groups, clones or strains) are known to exist in a limited area of the field in *R. solani* AG-1 (clone: Ogoshi and Ui, 1983), AG-2-2 IIIB (strain: Inagaki et al., 1994), and *Sclerotium oryzae-sativae* (strain: *Rhizoctonia oryzae-sativae*; Inagaki and Isomura, 1992), which cause rice sclerotial diseases, and *R. solani* AG-2-2 (a-c group: Nishimura and Sugimoto, 1985), which causes sugar beet root rot. In the present study of *R. solani* AG-1(IA), 80% of total VCGs from sheath blight lesions were limited to within two plots and 60% of them were recovered in only one plot. There were no discernible differences in these ratios between lesion VCGs and stubble or soil ones. However, some VCGs were distributed over 12 to 22 plots, equivalent to one quarter to one half of the area of the field. Wide distribution of clones (a–c groups or strains) within a field has also been reported in *R. solani* AG-1 and AG-2-2, which causes rice sclerotial diseases (Ogoshi and Ui, 1983; Inagaki et al., 1994), but it is scarcely refered in pathogens of upland crops, such as AG-2-2 causing sugar root rot (Ogoshi and Ui, 1983; Nishimura and Sugimoto, 1985), and AG-3 causing potato black scurf (Ogoshi and Ui, 1983). Formation of basidiospores of *R. solani* AG-2-2 on sugar beets are partly concerned with diversity and dispersal of VCGs of the pathogen in the fields (Naito, 1998), while AG-1 is not known well enough for the role of basidiospores in sheath blight development in paddy fields.

It is considerably difficult to elucidate explicitly the dynamics of *R. solani* AG-1(IA) in paddy fields because fungal isolation sources, e.g., rice leaf sheath, stubble, soil, etc., are inevitably different in shape, sample size, sampling sites within a field. Examination of vegetative compatibility groups is one effective way to study dynamics of *R. solani* AG-1(IA) within a single year or in consecutive yr. It is useful in tracing even genetically highly related strains distributed over geographically distant places (Punja and Grogan, 1983; Proffer and Hart, 1988; MacNish et al., 1993; Matsumoto et al., 1995). On the other hand, a survey of sclerotial density in rice hills and surface soil is another way to elucidate dynamics of this fungus. Combined with these methods, therefore, dynamics of *R. solani* AG-1(IA) in paddy fields should become more accurate and desirable.

In conclusion, abundant VCGs of *R. solani* AG-1(IA), possibly due to the frequent influx and efflux of genetically different sclerotia in paddy fields proved to be widely dispersed in fields in the pretransplanting season and to remain in considerable levels until the mature stage of rice plants to cause sheath blight in the same field.

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