

## Vegetative compatibility of an isolate of *Verticillium dahliae* pathogenic to both tomato and pepper

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An isolate of *Verticillium dahliae* Vdp-4, pathogenic to both tomato and pepper (tomato-pepper pathotype), was examined for its vegetative compatibility with testers of the Japanese vegetative compatibility group (subgroups J1, J2, and J3). Seven isolates of *V. dahliae* from the same field as Vdp-4 in Misato, Nagano Pref. and two isolates from Hokkaido were separately determined as either tomato pathotype (B) or pepper pathotype (C). Isolate 5922 previously reported as tomato-pepper pathotype was also examined. Compatible *nit1* and NitM mutants were obtained from all isolates except for isolates Vdp-3 and Vdt-10. The isolate of tomato-pepper pathotype Vdp-4 showed a strong reaction with VCGJ1 and J3 and was thus assigned to J3. Seven of these isolates showed compatibility and were assigned into three provisional subgroups. The isolate 5922 was self-incompatible.

Key Words—genetics; *nit*; tomato-pepper pathotype; VCG; *Verticillium dahliae*.

*Verticillium dahliae* Kleb. shows a broad host range (Chen, 1994; Rijkers et al., 1992; Strausbaugh, 1993; Subbarao et al., 1995), but particular host specificity was exceptionally recorded for isolates from Brussels sprouts and mint (Isaac, 1957; Nelson, 1947). Specificity of *Verticillium* wilt of pepper (*Capsicum annuum* L.) has been argued by several researchers. Kendrick and Middleton (1959) established an inoculation method with controlled soil temperature and found that *Verticillium* wilt of pepper appeared at lower temperatures than those affecting tomato. Their isolates pathogenic to pepper were not pathogenic to tomato in the inoculation test. On the contrary, Bewley (1922) reported that an isolate pathogenic to tomato was also pathogenic to pepper as well as cotton, cucumber, eggplant, snapdragon, sycamore (*Acer* sp.), and elm. Therefore, isolates of *V. dahliae* pathogenic to pepper were differentiated in their pathogenicity to tomato, that is, some isolates were pathogenic to pepper but not to tomato and others were pathogenic to both pepper and tomato.

In Japan, Iijima (1983) demonstrated that isolates of *V. dahliae* could be classified into two groups based on their pathogenicity to tomato. However, for a long time no isolate which was pathogenic to both tomato and pepper was obtained from fields in Japan (Iijima, 1983). Horiuchi et al. (1990) classified isolates into four groups: eggplant pathotype, tomato pathotype, pepper pathotype, and crucifera pathotype. Isolates of pepper patho-

type did not show pathogenicity to tomato in the artificial inoculation (Wakatabe et al., 1997). Nor did tomato pathotype show pathogenicity to pepper in the artificial inoculation (Nagao et al., 1997; Wakatabe et al., 1997). In 1991, four isolates of *V. dahliae* were obtained from diseased peppers in a field in Nagano Pref. and one of the isolates was pathogenic to both tomato and pepper. The appearance of the tomato-pepper pathotype was briefly reported (Oshima et al., 1993). Results of pathogenicity test and the effect of soil temperature on *Verticillium* wilt of pepper will be precisely described elsewhere (Oshima et al., unpublished).

Genetical relatedness in fungi is estimated by their ability to form hyphal anastomoses. Fungal strains that anastomose and form heterokaryons with each other are regarded as vegetatively compatible and are assigned to a single vegetative compatibility group (VCG) (Bayman and Cotty, 1991; Brooker et al., 1991; Correll et al., 1987, 1988; Kuhlman and Bhattacharyya, 1984; Leslie, 1993; Puhalla, 1985). *Verticillium dahliae* was genetically classified into four VC groups using nitrate nonutilizing (*nit*) mutants (Joaquim and Rowe, 1990, 1991; Strausbaugh et al., 1992; Strausbaugh, 1993). Japanese isolates of *V. dahliae* comprised a VCG including three subgroups (J1, J2 and J3) distinguished by the strength of heterokaryon (Wakatabe et al., 1997). There was a good relationship between pathogenicity to tomato and vegetative compatibility. Origin of *V. dahliae* race-2 was examined by auxotrophic mutants (O'Garro and Clarkson, 1988) and their result suggested

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that each race-2 isolate coincidentally emerged from a local population of *V. dahliae* race-1. For Japanese isolates of race-2, all race-2 isolates examined were vegetatively compatible with subgroup J2 (Nagao et al., 1997). Therefore vegetative compatibility is a useful method to trace the origin of a new pathotype by comparing it with the known VCG including subgroups.

In this study, we examined the vegetative compatibility relationship of the tomato-pepper pathotype with testers of the Japanese vegetative compatibility groups. A part of this study was previously reported (Nagao et al., 1995).

## Materials and Methods

**Isolates** Origin of isolates of *V. dahliae* examined in this study are listed in Table 1. Most of the isolates were obtained from the same field in Misato, Nagano Pref. Isolates Vdt-10 and Vdt-12 were obtained from a distant area of Nagano Pref. An isolate previously reported as tomato-pepper pathotype 5922 was also examined (Iijima, 1983).

Six *nit* tester isolates (*nit1* and NitM) were combined with the field isolates. Each pair of isolates represented the subgroup provisionally designated as J1, J2, and J3 depending upon their compatible reactions (Wakatabe et al., 1997).

**Recovery and characterization of *nit* mutants** *Nit* mutants were generated according to a modified method of Puhalla (1985). Procedures for *nit* mutants were conducted as previously reported (Wakatabe et al., 1997).

**Complementation tests** Pairings were conducted by placing two mycelial blocks of *nit1* and/or NitM mutants 15 mm apart on MM in 90-mm Petri dishes. The plates

were kept at 25°C for 20 d. Stable complementary heterokaryons were evident by the formation of wild-type growth at the mycelial interface between two *nit* mutants. As previously described (Wakatabe et al., 1997), the most stable *nit1* and NitM mutants which gave the strongest reactions were chosen as testers for each isolate. A cellophane barrier was placed between paired *nit* mutants to examine cross-feeding.

**Criteria for vegetative compatibility** The criteria for vegetative compatibility were evaluated as previously described (Wakatabe et al., 1997). Pairings of *nit1* and NitM mutants from each isolate showed wild-type growth greater than 5 mm in width, which was scored as a positive reaction (++). When an evident line of microsclerotia formed at the mycelial junction of both mutants, but this line developed only slightly (<5 mm), this reaction was considered weak complementation (+). In other cases, growth was limited to a few small clumps of mycelia and/or microsclerotia along the interface between *nit* mutants. These limited reactions were scored as (-). No reaction between the mutants was scored as (N). Only strongly (++) reacting isolates were used to assign VCGs.

## Results

**Recovery of *nit* mutants** Frequencies of chlorate-resistant sectors were very variable (Table 2). Ratios of *nit* mutants in totally isolated sectors were not affected by frequency of chlorate-resistant sectors, i.e., in Vdp-4 the ratio of generated sectors was 141.7% and that of *nit* sectors was 20.6%, whereas in Vdt-9 the ratios were 76.9 and 47.5%. Three phenotypically characterized *nit* mutants were obtained, i.e., *nit1*, NitM, and *nit2*.

Table 1. Source and pathogenicity of Japanese isolates of *Verticillium dahliae*.

Isolate	Host origin	Place <sup>a)</sup>	Year	Pathotype <sup>b)</sup>
Vdp-4	Pepper ( <i>Capsicum annuum</i> L. var. <i>grossum</i> Sendt.)	1	1991	B+C <sup>c)</sup>
Vdp-1	Pepper	1	1991	C
Vdp-2	Pepper	1	1991	C
Vdp-3	Pepper	1	1991	C
Vdb-6	Tomato ( <i>Lycopersicon esculentum</i> Mill.)	1	unknown	B
Vdt-6	Tomato	1	1992	B
Vdt-7	Tomato	1	1992	B
Vdt-9	Tomato	1	1992	B
Vdt-10	Tomato	2	1991	B
Vdt-12	Tomato	2	1991	B
5922	Unknown	3	unknown	B+C <sup>d)</sup>

a) 1=Misato, Nagano Pref.; 2=Higashi-Kagura, Hokkaido; 3=Fungal collection in Tsukuba Univ.

b) Horiuchi et al. (1990) proposed four pathogenicity groups. A, pathogenic to eggplant and Chinese cabbage; B, pathogenic to tomato, eggplant, and Chinese cabbage; C, pathogenic to pepper, eggplant, and Chinese cabbage; D, pathogenic to Chinese cabbage.

c) Oshima et al. (1993) reported new pathotype.

d) Iijima (1983) reported new pathotype in culture collection of Tsukuba Univ.

Both *nit1* and NitM were obtained except for Vdp-3 and Vdt-10. *Nit2* appeared in all isolates except Vdp-1, Vdt-10, and Vdb-6. All *nit* mutants generated were *nit1* in Vdt-10.

**Vegetative compatibility group** Both *nit1* and NitM mutants were generated from 9 of the 11 isolates of *V. dahliae*. However, 5922 was self-incompatible. Mycelia of *nit* mutants of 5922 were autolysed on MM 21 d after incubation. Autolyses were occurred despite of hyphal conjugation.

We investigated compatibility of these eight isolates with the testers of Japanese VCG (Table 3). Vdp-4 and Vdp-2 were compatible with testers of subgroups J1 and J3. Vdp-1 showed a strong reaction with all testers of VCGJ except SM312. Vdb-6, Vdt-6, Vdt-7, Vdt-9 and Vdt-12 showed strong reactions with testers of subgroup J2. However, in Vdt-12, a strong reaction was also observed with one of the testers of subgroup J3 (AC406). Vdb-6 slightly reacted with one of the testers of subgroup J3 (AC406). From these results, Vdp-4 and Vdp-2 were assigned to VCG J3, Vdp-1 was assigned to subgroup J1, and the remaining five isolates were assigned to subgroup J2.

Compatibility among these isolates of *V. dahliae* was tested (Table 4). Compatibility reactions were comparable with the reactions paired with VCGJ testers. There was no exceptional reaction among Vdp-4 and isolates assigned to subgroup J2.

## Discussion

Isolates of *V. dahliae* obtained from diseased peppers in the same field in Nagano Pref. were assigned to different vegetative compatibility subgroups (Table 3). The isolate of new pathotype, Vdp-4, was assigned to subgroup J3. Vdp-1 was assigned to subgroup J1, and Vdp-2 to

subgroup J3. Isolates of pepper pathotype, Vdp-1 and Vdp-2, were placed in subgroups J1 and J3, respectively. Vdp-3 was self-incompatible. In our previous study, isolates of pepper pathotype and eggplant pathotype were found to be assigned to either subgroup J1 or J3. However, most of isolates of pepper pathotype were assigned to subgroup J1. Isolate SM312, pepper pathotype, was solely compatible with subgroup J3 (Wakatabe et al., 1997). The isolate of the new pathotype, tomato-pepper pathotype, was compatible with subgroup J3 (Table 3). As described above, the pepper pathotype assigned to subgroup J3 was considered to be exceptional. We examined four isolates of tomato pathotype which were obtained from the same field in Nagano Pref. These isolates were assigned to subgroup J2 and vegetative compatibility test with Vdp-4 showed no reaction (Table 4). There was no exceptional reaction between Vdp-4 and isolates assigned to subgroup J2. Previously, we reported weak reactions among the isolates of subgroup J2 and subgroup J3 and interpreted these as indicating a distance in the evolutionary relationship (Wakatabe et al., 1997). However, in this experiment, no reaction was observed between the tomato-pepper isolate and the isolates of subgroup J2. It is suggested that the degree of vegetative compatibility of this tomato-pepper isolate to subgroup J2 may have weakened.

Pathotypes of *V. dahliae* correlate with VCGs (Corsini et al., 1985; Joaquim and Rowe, 1991; Strausbaugh et al., 1992) and the subgroups of VCG4 exhibit different degrees of virulence (Joaquim and Rowe, 1991). Ten subgroups in VCG4 existed in California isolates (Strausbaugh et al., 1992), and nine subgroups in VCG4 were also recognized in Idaho isolates, in which there was gradient from the highly virulent subgroup 4A strains to the less virulent subgroups 4A/B and 4B strains (Straus-

Table 2. Results of *nit* mutant generation and ratio of *nit* mutant phenotypes of Japanese isolates of *Verticillium dahliae*.

Isolate	No. of colonies inoculated on MMC	No. of generated sectors (%) <sup>a)</sup>	No. of <i>nit</i> sectors (%) <sup>b)</sup>	Phenotypes of <i>nit</i> (%) <sup>c)</sup>			
				<i>nit1</i>	NitM	<i>nit2</i>	else
Vdp-4	24	34(141.7)	7(20.6)	57.1	28.6	14.3	0.0
Vdp-1	16	20 (12.5)	10(50.0)	20.0	30.0	0.0	50.0
Vdp-2	16	8 (50.0)	5(62.5)	20.0	40.0	40.0	0.0
Vdp-3	20	0 (0.0) <sup>d)</sup>	—	—	—	—	—
Vdb-6	40	32 (80.0)	10(13.3)	70.0	20.0	0.0	10.0
Vdt-6	80	96(120.0)	28(29.1)	53.6	7.1	7.1	32.2
Vdt-7	28	38(135.7)	22(57.9)	68.2	18.2	13.6	0.0
Vdt-9	52	40 (76.9)	19(47.5)	31.5	26.3	21.1	21.1
Vdt-10	52	67(128.8)	27(40.3)	100.0	0.0	0.0	0.0
Vdt-12	16	13 (81.3)	8(61.5)	50.0	25.0	25.0	0.0
5922	20	45(225.0)	10(22.2)	40.0	40.0	20.0	0.0

a) Number of generated sectors on MMC (percentage=total generated sectors/total inoculated colonies on MMC).

b) Number of *nit* sectors determined (percentage=total determined *nit* ssectors/total generated sectors).

c) *Nit3* mutant was not generated.

d) No *nit* mutant was generated.

Table 3. Results of pairings of *nit1* (1) and Nit M (M) among isolates of *Verticillium dahliae*.

VCG		J1		J1		J2		J2		J3		J3	
Mutant		84023		22720		ST1		LE103		AC406		SM312	
		25	8	11	1	18	28	30	13	14	18	27	30
		(1)	(M)	(1)	(M)	(1)	(M)	(1)	(M)	(1)	(M)	(1)	(M)
Vdp-4	3 [ <i>nit1</i> ]	N	++	N	++	N	N	N	-	+	++	+	++
	16 [NitM]	-	-	++	++	N	N	N	-	++	++	++	N
Vdp-1	6 [ <i>nit1</i> ]	-	+	++	++	N	N	+	+	+	+	N	N
	17 [NitM]	++	++	++	++	++	++	+	+	++	++	N	N
Vdp-2	8 [ <i>nit1</i> ]	-	++	N	+	N	N	N	N	N	++	N	N
	5 [NitM]	+	+	-	+	N	N	N	-	++	++	N	N
Vdb-6	21 [ <i>nit1</i> ]	N	N	-	-	N	+	N	++	-	+	N	N
	31 [NitM]	N	-	-	-	N	N	+	++	-	+	N	N
Vdt-6	23 [ <i>nit1</i> ]	N	N	N	-	N	+	N	++	N	N	N	N
	27 [NitM]	N	N	-	++	++	+	++	N	-	-	-	-
Vdt-7	40 [ <i>nit1</i> ]	N	N	N	N	N	++	N	++			N	N
	53 [NitM]	N	N	N	N	++	++	++	++			N	N
Vdt-9	10 [ <i>nit1</i> ]	+	-	N	-	++	++	++	N	N	N	N	N
	7 [NitM]	-	N	-	N	++	N	++	++	-	-	-	N
Vdt-12	8 [ <i>nit1</i> ]	N	N	N	+	N	++	N	+	N	N	N	N
	6 [NitM]	N	N	N	N	N	N	++	+	++	-	N	N

++: thick, wild-type growth and more than 5 mm width of complementation line; +: slightly complemental line of less than 5 mm; -: sparsely limited formation of complementary colonies; N: no reaction.

Table 4. Results of pairings of *nit1* (1) and NitM (M) among Japanese isolates of *Verticillium dahliae*.

Mutant		Vdp-1		Vdp-2		Vdb-6		Vdp-6		Vdp-7		Vdp-9		Vdp-10		Vdp-12	
		17	6	5	8	21	31	27	23	40	53	10	7	10		8	6
		(1)	(M)	(1)	(M)	(1)	(M)	(1)	(M)	(1)	(M)	(1)	(M)	(1)		(1)	(M)
Vdp-4	3 [ <i>nit1</i> ]	++	++	+	+	N	N	N	N	N	N	N	N	N		N	N
	16 [NitM]	N	-	N	N	N	N	N	N	N	N	N	N	N		N	N
Vdp-1	17 [ <i>nit1</i> ]			N	N	+	N	+	+	N	N	++	++			++	++
	6 [NitM]			N	N	N	N	N	N	N	N	N	N			N	N
Vdp-2	5 [ <i>nit1</i> ]					N	N	N	N	N	N	N	N	N		N	N
	8 [NitM]					N	N	N	N	N	N	N	N	N		N	N
Vdp-6	21 [ <i>nit1</i> ]							+	N	N	+	N	-	N		N	N
	31 [NitM]							+	+	++	N	N	+	N		-	+
Vdt-6	27 [ <i>nit1</i> ]											+	+				
	23 [NitM]											++	++				
Vdt-7	40 [ <i>nit1</i> ]											++	++				
	53 [NitM]											++	++				
Vdt-9	10 [ <i>nit1</i> ]													+		-	++
	7 [NitM]													+		+	N

++: thick, wild-type growth and more than 5 mm width of complementation line; +: slightly complemental line of less than 5 mm; -: sparsely limited formation of complementary colonies; N: no reaction.

baugh, 1993). On the contrary, the unique strong reaction of Japanese isolates of *V. dahliae* race-2 with subgroup J2 suggested the further genetical isolation from subgroups J1 and J3 with regards to vegetative compatibility (Nagao et al., 1997). This new pathotype, tomato-pepper pathotype, and *V. dahliae* race-2 tend to have specific pathogenicity and limited vegetative compatibility reactions.

A diversity of vegetative compatibility subgroups exists in Misato field, Nagano Pref. A relationship between the locality and VC subgroups was not found, as reported previously (Wakatabe et al., 1997).

Japanese isolates of *Verticillium* spp. have been analyzed using random amplified polymorphic DNA (RAPD) (Koike et al., 1995, 1996, 1997). In these studies, RAPD group of tomato-pepper isolate (Vdp-4) was significantly different from those of isolates of tomato pathotype. Vdp-4 clustered with either the isolates of non-tomato pathotype (Koike et al., 1996) or those of pepper pathotype (Koike et al., 1995). These results suggest that tomato-pepper pathotype was sorted into the nontomato pathotype at the molecular level and may support the compatibility of tomato-pepper pathotype with VCG J1 and J3. Further molecular study is needed to trace the relationship between the pathogenicity differentiation and vegetative compatibility.

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