VEGETATIVE COMPATIBILITY GROUPS OF *VERTICILLIUM DAHLIAE* ISOLATES FROM WEEDS IN POTATO FIELDS

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SUMMARY

Fifteen species of weedy plants were collected from potato fields between July and September 2006 in Erzurum (Turkey). In total, 21 isolates of *Verticillium dahliae* were obtained from *Cirsium arvense, Convolvulus arvensis, Chenopodium album, Polygonum lapathifolium* and *Sinapis arvensis*. Of these, 15 were isolated from *C. arvense*, and one or two isolates from the other weed species. This is the first report of *V. dahliae* isolated from these weed species in Turkey. All isolates from weeds were assigned to vegetative compatibility groups (VCGs) using nitrate-nonutilizing (*nit*) mutants. Two VCGs were found and identified as VCG 2B (11 isolates) and VCG 4A (10 isolates) by using tester isolates of known VCGs. Pathogenicity of *V. dahliae* isolates was tested on potato by the root-dip method. Both VCG 2B and VCG 4A isolates from weeds were pathogenic to potato.

Key words: *Verticillium dahliae*, weeds, vegetative compatibility groups, *nit* mutants, pathogenicity on potato.

INTRODUCTION

Verticillium wilt, caused by *Verticillium dahliae* Kleb., is an important disease of potato (*Solanum tuberosum* L.) and many other crops worldwide (Pegg and Brady, 2002). Many weed species have also been reported as hosts of *V. dahliae* (Vargas-Machuca *et al*., 1987; Waipara *et al*., 1997; Pegg and Brady, 2002; Ligoxigakis *et al*., 2002; Camele *et al*., 2005; Vallad *et al*., 2005). In Turkey, the pathogen has been isolated from *Amaranthus viridis* L., *Datura* sp., *Erigeron* sp. and *Xanthium strumarium* L. (Kocatürk and Karcılıoglu, 1979). Recent studies indicate that *V. dahliae* also was found to be widely distributed on potato fields in Erzurum (Turkey), where more than 5,000 ha of potatoes are planted annually (Dane, 2007).

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The identification of vegetative compatibility groups (VCGs) proved to be a powerful tool in determining fungal genetic structure of *V. dahliae*, an anamorphic fungus with no known sexual stage. By using nitrate-nonutilizing (*nit*) mutants, four major VCGs (VCG 1, VCG 2, VCG 3 and VCG 4) of *V. dahliae* have been reported. VCG 2 and 4 have been further divided into subgroups (2A and 2B, 4A and 4B, respectively) based on differential interactions between isolates (Joaquim and Rowe, 1990; 1991). VCGs 2A, 2B, 4A, 4B and 4A/B have been detected among *V. dahliae* isolates from potato plants (Joaquim and Rowe, 1991; Strausbaugh, 1993; Korolev *et al*., 2000; Tsror *et al*., 2001; Zeise and Von Tiedemann, 2002). In Erzurum, Verticillium wilt of potato is mainly caused by *V. dahliae* VCG 2B and VCG 4A (Dane, 2007).

The objective of this research was to determine VCG diversity of *V. dahliae* isolates obtained from weeds in potato fields and to investigate the pathogenicity of these isolates to potato.

MATERIALS AND METHODS

Isolation of *V. dahliae* from weed species. Fifteen weed species from potato fields were surveyed between July and September 2006. One to ten plants of each weed species showing wilt symptoms, or symptomless plants, were collected from each field. In total, 11 fields were sampled from Askale (one field), Center (5 fields), Köprüköy (one field) and Pasinler (4 fields) districts located in the Erzurum province of eastern Anatolia. Askale is located 53 km west of Center; Pasinler and Köprüköy are located 40 and 58 km east of Center, respectively.

Weed plants were washed with tap water, then two stem sections (1.5-cm long) from each plant (~1 and 10-cm above soil level) were excised. Tissue sections were surface disinfected with 0.5% sodium hypochlorite for 1 min, rinsed with sterile distilled water, dried on sterile filter paper and placed on water agar (WA, 2%) amended with 100 mg l^{-1} streptomycin sulfate in Petri plates. Plates were incubated at 24°C in the dark for 5-7 days until verticillately branched conidiophores formed around the stem sections. Emerging fungi were subcul-

tured on potato dextrose agar (PDA). Single-spore isolates of *V. dahliae* were obtained, identified as described (Hawksworth and Talboys, 1970; Goud *et al*., 2003), and maintained on PDA medium in tubes at 10°C.

Generation and characterization of *nit* mutants. *Nit* mutants of *V. dahliae* were generated on cornmeal agar with 0.02% glucose amended with 3% potassium chlorate (CMC) as described by Korolev and Katan (1997). Mycelial discs (5 mm diameter) of fungal isolates were removed from the margin of actively growing colonies and placed on CMC in six to eight separate points in 9 cm diameter Petri plates. Plates were incubated in the dark at 24ºC for 2-4 weeks. Chlorate-resistant sectors were transferred to Czapex-Dox Agar (CDA) plates. Sectors that grew on CDA as thin expansive colonies with no aerial mycelium were considered *nit* mutants. CDA amended with sodium nitrite (0.5 g l^{-1}) or hypoxanthine (0.2 g l^{-1}) was used for partial phenotyping of the *nit* mutants (Correll *et al*., 1987). Mutants that grew profusely on sodium nitrite and hypoxanthine were classified as *nit*1, whereas mutants that grew profusely on sodium nitrite but sparsely on hypoxanthine were classified as *nit*M.

Vegetative compatibility grouping. All *nit* mutants obtained in this study were paired with *nit* mutants of VCG tester isolates of *V. dahliae*. A set of VCG tester isolates [VCG 1 (T9), VCG 2A (PH), VCG 2B (115), VCG 3 (70-21), VCG 4A (BB) and VCG 4B (S-39 *nit*1, MT *nit*M)] was provided by R.C. Rowe (Department of Plant Pathology, Ohio State University, Wooster, OH, USA). Phenotypically distinct mutants were placed 1.5 cm apart on CDA in 9 cm diameter Petri plates and incubated at 24ºC for 2-4 weeks. Complementation was evident by the development of prototrophic growth where two mutant colonies met and formed a stable heterokaryon (Bao *et al*., 1998). The degree of complementation was ranked as follows: (+) = dense prototrophic growth, (+/-) = small microsclerotial dots with or without a little aerial mycelium, (-) = prototrophic growth absent or inconspicuous (Korolev *et al*., 2000). Each pairing was repeated at least twice. When mutants of two isolates formed a heterokaryon, their parents were assigned to the same VCG.

Pathogenicity to potato of *V. dahliae* isolates from weed species. Pathogenicity of *V. dahliae* isolates from weed species was determined on potato plants (cv. Marfona) by the root-dip method. This cultivar has been grown in Erzurum for nearly twenty years. Surface-disinfected potato tubers (1 min in 0.5% sodium hypochlorite followed by rinsing in sterile distilled water) were planted in 15 cm diameter pots containing sterile soil mix of topsoil and sand (1:1, v/v) in a growth chamber. After 3-5 weeks, 10 to 20 cm tall plants were selected for inoculation (Joaquim and Rowe, 1991). Two isolates from each weed species and VCG having more than one isolate were randomly selected for inoculation (10 total). The isolates were grown on PDA at 24°C in the dark for 7-10 days. Conidia were washed off the agar surface with sterile distilled water, and the inoculum density adjusted to 10^6 conidia ml^{-1} with a hemacytometer (Strausbaugh, 1993). Potato plants were uprooted from the soil mix, rinsed in sterile distilled water, and dipped in a conidial suspension for 30 min. Inoculated plants were transplanted in 15 cm diameter pots containing sterile soil mix. Control plants were dipped in sterile distilled water before transplanting. Plants were grown in a growth chamber at 22°C under a 16 h photoperiod. A completely randomized design with three replicate pots per isolate was used. Sixty days after inoculation, disease severity was rated on a scale 0-3 (0= no symptoms, 1= vascular discoloration without apparent leaf symptoms, 2= vascular discoloration with leaf-wilt symptoms, 3= dead plant) according to Bao *et al*. (1998). After disease evaluations, small sections from all above-ground parts (stem, petiole and leaf) of each plant were surface-disinfected and placed on WA to determine the presence of *V. dahliae*. Statistical analysis was performed by SAS Software (SAS Institute, USA). The General Linear Models procedure was used to test effects at the 0.05 level of probability and means were compared by *t* test.

Table 1. Isolation of *Verticillium dahliae* from weed species collected from potato fields in Erzurum.

Weed species	Fields infected / Fields sampled	Location[(a)]				
		Askale	Center	Köprüköy	Pasinler	Total
Chenopodium album	1/8	1/10	0/41	0/5	0/21	1/77
Cirsium arvense	7/10	3/5	5/45	0/10	7/30	15/90
Convolvulus arvensis	1/11	0/10	1/51	0/10	0/30	1/101
Polygonum lapathifolium	1/1	0/0	0/0	0/0	2/10	2/10
Sinapis arvensis	1/2	0/0	0/9	0/0	2/5	2/14

[(a)] Number of plants infected by *V. dahliae*/total number of examined plants.

RESULTS

Isolates of *V. dahliae* from weed species. Fifteen weed species were collected from potato fields in Erzurum between July and September 2006: *Amaranthus retroflexus* L., *Anchusa arvensis* (L.) Bieb*., Avena fatua* L*., Centaurea depressa* Bieb., *Chenopodium album* L*., Cirsium arvense* (L.) Scop*., Convolvulus arvensis* L*., Euphorbia* spp*., Hibiscus trionum* L., *Lallemantia canesces* (L.) Fish. et C. A. Mey*., Linum bienne* Mill., *Malva grandfolia* C. Morr*., Polygonum lapathifolium* L., *Sinapis arvensis* L. and *Tragopogon buphthalmoides* (DC.) Boiss.

Twenty one isolates of *V. dahliae* were obtained from five weed species in 3 districts (Table 1). The pathogen was not isolated from Köprüköy district. Of these isolates, 15 were isolated from *C. arvense* (Asteraceae), one from *C. album* (Chenopodiaceae) and *C.s arvensis* (Convolvulaceae), and two from *P. lapathifolium* (Polygonaceae) and *S. arvensis* (Brassicaceae). Five isolates (OC2, OC5, CA2, CA3 and PA4) from *C. arvense* and one isolate (OE8) from *C. album* were obtained from the middle of stems; the other isolates were obtained from the base of stems. According to our observations, *C. arvense* showed wilt symptoms in the fields.

Generation and characterization of *nit* mutants. In total, 74 *nit* mutants were obtained from the 21 *V. dahliae* isolates, ranging from 1 to 6 mutants per isolate. *Nit* mutants were identified based on their phenotype; 59 (80%) mutants were classified as *nit*1 and the remainder as *nit*M (Table 2). Three isolates produced both types of mutants, 15 the *nit*1 type mutant, and three the *nit*M type mutant only. No *nit*3 mutants were recovered.

Table 2. Complementation between *nit* mutants derived from *Verticillium dahliae* isolates from weed species and testers of previously described VCGs.

Weed species	Isolates	Location	Number of *nit* mutants			Reference tester isolates[a]						VCGs[b]
			*nit*1	*nit*M	Total	1	2A	2B	3	4A	4B	
Chenopodium album	OE8	Askale	2	1	3	-	-	+	-	-	-	2B
	OC1	Askale	0	2	2	-	-	+	-	-	-	2B
	OC2	Askale	1	0	1	-	-	+	-	-	-	2B
	OC5	Askale	3	0	3	-	-	+	-	-	-	2B
	PT2	Center	4	0	4	-	-	-	-	+	+/-	4A
	CA2	Center	4	0	4	-	-	+	-	-	-	2B
	CA3	Center	4	0	4	-	-	+	-	-	-	2B
	SA5	Center	1	0	1	-	-	+	-	-	-	2B
Cirsium arvense	BA8	Center	6	0	6	-	-	+	-	-	-	2B
	CA4	Pasinler	4	2	6	-	-	+	-	-	-	2B
	EA4	Pasinler	2	0	2	-	-	-	-	+	+/-	4A
	EA5	Pasinler	4	0	4	-	-	-	-	+	+/-	4A
	EA6	Pasinler	3	0	3	-	-	-	-	+	+/-	4A
	PA2	Pasinler	4	0	4	-	-	+	-	-	-	2B
	PA3	Pasinler	4	0	4	-	-	-	-	+	+/-	4A
	PA4	Pasinler	0	4	4	-	-	-	-	+	+/-	4A
Convolvulus arvensis	BC6	Center	1	3	4	-	-	+	-	-	-	2B
Polygonum lapathifolium	EF3	Pasinler	5	0	5	-	-	-	-	+	+/-	4A
	EF4	Pasinler	5	0	5	-	-	-	-	+	+/-	4A
Sinapis arvensis	ED3	Pasinler	0	3	3	-	-	-	-	+	+/-	4A
	ED5	Pasinler	2	0	2	-	-	-	-	+	+/-	4A

[a] The degree of complementation was ranked as follows: (+) = dense prototrophic growth, (+/-) = small microsclerotial dots with or without a little aerial mycelium, (-) = prototrophic growth absent or inconspicuous (Korolev *et al*., 2000).
[b] Vegetative compatibility groups of *V. dahliae* isolates from weeds.

Table 3. Pathogenicity of *Verticillium dahliae* isolates from weed species on potato cv. Marfona.

VCGs[a]	Isolates	Source of isolate	Disease severity[b]	Plant colonization[c]		
				Stem	Petiole	Leaf
VCG 2B	OE8	*Chenopodium album*	1.6	2/3	2/3	0/3
	CA3	*Cirsium arvense*	2.3	2/3	2/3	0/2
	OC2	*Cirsium arvense*	2.0	3/3	2/3	0/3
	BC6	*Convolvulus arvensis*	1.6	3/3	1/3	0/3
VCG 4A	PT2	*Cirsium arvense*	2.3	3/3	3/3	0/3
	EA5	*Cirsium arvense*	2.0	3/3	2/3	1/3
	EF3	*Polygonum lapathifolium*	2.0	3/3	3/3	3/3
	EF4	*Polygonum lapathifolium*	2.0	3/3	2/3	1/3
	ED3	*Sinapis arvensis*	2.3	3/3	3/3	0/3
	ED5	*Sinapis arvensis*	1.6	3/3	3/3	1/3

[a] Vegetative compatibility groups of *V. dahliae* isolates from weeds.
[b] Disease severity was on a scale of 0-3; 0= no symptoms, 1= vascular discoloration without apparent leaf symptoms, 2= vascular discoloration with leaf-wilt symptoms, 3= dead plant (Bao *et al*., 1998).
[c] Number of plants colonized by *V. dahliae* / total number of examined plants.

Vegetative compatibility grouping. After complementation with tester isolates of known VCGs, 11 isolates were assigned to VCG 2B, and 10 to VCG 4A (Table 2). Isolates assigned to VCG 2 showed strong complementation only with tester isolates of VCG 2B. Cross-reactions occurred between isolates VCG 4 from weeds and tester isolates of VCG 4 (subgroups A and B), VCG 4 isolates showed strong complementation with tester isolate of VCG 4A, but all were also weakly compatible with tester isolate of VCG 4B. Both VCG 2B (9 isolates) and VCG 4A (6 isolates) came from *C. arvense*, VCG 2B from *C. album* (1 isolate) and *C. arvensis* (1 isolate) only, and VCG 4A from *P. lapathifolium* (2 isolates) and *S. arvensis* (2 isolates) only.

Pathogenicity to potato of *V. dahliae* isolates from weed species. The pathogenicity of ten isolates obtained from five weed species, representing VCG 2B and VCG 4A, was assessed on potato plants. Sixty days after inoculation, all isolates were pathogenic to potato with various levels of aggressiveness (Table 3). Disease severity ranged from 1.6 to 2.3. There were not statistically significant differences ($F_{3,30}$=0.56, P=0.8167) between VCG 2B and 4A isolates on disease severity. Control plants showed no disease symptoms. *V. dahliae* was recovered from all the inoculated plants but not from control plants.

DISCUSSION

V. dahliae isolates were obtained from *C. album*, *C. arvense*, *C. arvensis*, *P. lapathifolium* and *S. arvensis* in this study which, in addition to *A. retroflexus* and *S. viridis* (L.) P. Beauv., are the most common weed species in Erzurum's potato fields (Zengin and Güncan, 1993). *C. album*, *C. arvense*, *C. arvensis* and *S. arvensis* have been reported in previous studies as hosts of *V. dahliae* in natural environments (Waipara *et al*., 1997; Ligoxigakis *et al*., 2002). To our knowledge, *V. dahliae* was isolated for the first time from *P. lapathifolium* in this study. This is also the first report of *V. dahliae* isolated from these weed species in Turkey.

The genetic diversity among *V. dahliae* isolates was determined. Two phenotypic classes of *nit* mutants were identified among 74 mutants; 80% of these mutants were characterized as *nit*1, and 20% as *nit*M. Similar frequencies of *nit*1 and *nit*M classes were found for *V. dahliae* from various hosts including potato (Bao *et al*., 1998; Zeise and Von Tiedemann, 2001; Dane, 2007). In this study, 21 *V. dahliae* isolates most of which collected from *C. arvense* were classified as VCG 2B and VCG 4A. In a study from Erzurum, *V. dahliae* isolates from potato plants had also been assigned to VCG 2B and VCG 4A (Dane, 2007).

Pathogenicity tests showed that isolates of VCG 2B and VCG 4A from weed species were pathogenic to a focal cultivar of potato, and there was no difference between the isolates for disease severity. Disease severity of *V. dahliae* isolates from potato plants in Erzurum ranged from 1.5 to 2.8 for VCG 2B isolates and from 2.0 to 2.5 for VCG 4A isolates (Dane, 2007). However, VCG 4A isolates were more virulent on potato than VCGs 2, 4B and 4A/B isolates (Joaquim and Rowe, 1991; Strausbaugh, 1993). In another research, symptom severity was significantly higher in potato plantlets inoculated with VCG 4B than VCG 2A and VCG 2B (Tsror *et al*., 2001). The susceptibility of potato to isolates of *V. dahliae* that were obtained from weeds raises concerns about the potential of weed species to act as a reservoir of *V. dahliae* in Erzurum potato production areas. Several other studies have reported that weed species are an important source of *V. dahliae* (Busch *et al*., 1978; Johnson *et al*., 1980; Vargas-Machuca *et al*., 1987; Pegg and Brady, 2002; Ligoxigakis *et al*., 2002; Vallad *et al*., 2005).

Of the 21 *V. dahliae* isolates, 71% were isolated from *C. arvense*, and one or two from other weed species. Of these, *C. arvense* and *C. arvensis* are perennials; *C.album*, *S. arvensis* and *P. lapathifolium* are annuals. *C. arvense* usually showed external wilt symptoms in the field, contrary to other weeds hosting of *V. dahliae*, that frequently show no external symptoms (Vargas-Machuca *et al*., 1987; Pegg and Brady, 2002). As mentioned above, VCGs and pathogenicity of *V. dahliae* from weeds in potato fields were similar to those obtained from potato plants in Erzurum. In addition, the largest number of isolates was collected from *C. arvense* in three districts, confirming its importance as a reservoir of the pathogen in Erzurum. Based on these results, it can be concluded that weeds might be important in the survival and increase of inoculum of *V. dahliae* in the field where the fungus survives as microsclerotia in the soil and in crop residues for many years (Pegg and Brady, 2002). Moreover, one study has reported that formation of microsclerotia in senescent tissues of infected weeds could be an important factor in the failure of rotation programs to control *V. dahliae* effectively (Johnson *et al*., 1980). Infected perennial weed tissues are also very important, because the pathogen could be easily maintained between growth seasons. The results of this study show that some of the common weeds (especially *C. arvense*) in potato fields can act as hosts of *V. dahliae* and potentially play important role in its survival.

ACKNOWLEDGEMENTS

We are grateful to Professor Hüseyin Zengin (Department of Plant Protection, Faculty of Agriculture, Atatürk University, 25240 Erzurum, Turkey) for identification of weed species.

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Received February 2, 2009
Accepted June 3, 2009