Additional Vegetative Compatibility Groups in *Colletotrichum coccodes* Subpopulations from Europe and Israel

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ABSTRACT

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Potato black dot, caused by *Colletotrichum coccodes*, damages tuber quality and may reduce yield. In previous work, four multimember vegetative compatibility groups (VCGs) have been reported. The objectives of the current study were to characterize a population of *C. coccodes* comprised of isolates from Israel and Northern Europe (EU/I) using VCG, and to assess the correlation between VCGs and aggressiveness of isolates on potato. A composite of 176 isolates was collected from symptomatic tissues of potato tubers or stems. A total of 6 (3.4%) isolates were characterized in VCG1; 29 (16.5%), 32 (18.2%), and 7 (4.0%) in VCG 2, 3, and 4, respectively; and 7 (4.0%), 9 (5.1%), 48 (27.3%), and 15 (8.5%) in the newly defined VCG 5, 6, 7, and 8, respectively. Twenty-three isolates (13%) were not assigned to any of the VCGs. Two of the VCGs had a specific geographical distribution: the 9 isolates assigned to VCG6 originated from The Netherlands, and 34 of 38 isolates assigned to VCG7 were from Scotland. Aggressiveness of isolates of a given VCG was examined on potato. VCGs 5 and 6 were comprised of the most aggressive isolates, and VCG1 of the least aggressive. These results could facilitate a more accurate evaluation of damage potential that may be caused by this pathogen.

Additional keywords: black dot, pathogenicity, potato, *Solanum tuberosum*

Colletotrichum coccodes (Wallr.) S.J. Hughes has been reported worldwide on many different hosts. It is primarily found on potato and tomato, causing black dot on potato and anthracnose, respectively. Potato black dot is characterized by the development of small black sclerotia on senescent and dead plant tissue, on decaying roots and stems, and on stolons and daughter tubers, reducing tuber quality and yield (4,16,17). *C. coccodes* lacks a recognized teleomorph, therefore exchange of genetic material among isolates may only occur via the vegetative compatibility system (6,19). Vegetative compatibility refers to the ability of isolates of the same fungal species to undergo mutual hyphal anastomosis and form viable heterokaryons. Strains that are vegetative-compatible are described as members of the same vegetative compatibility group (VCG) (7,11,12,13,15). In

most cases, analysis of VCGs has been based on pairings between complementary nonutilizing nitrate (*nit*) mutants of different isolates, selected using potassium chlorate-containing agar. Compatible isolates, whose complementary *nit* mutants can form stable heterokaryons, are assigned to the same VCG (5,7,13). Vegetatively compatible isolates may form subpopulations that tend to be similar due to a common genetic pool and may have similar pathological and physiological traits that differ from those of isolates that are not assigned to the same VCG (12). Classification of VCGs has been used to study the genetic structure of populations of plant-pathogenic fungi, including *Fusarium oxysporum* (9,15), *Verticillium* spp. (5,7,8,15), and *Colletotrichum* spp. (3,13).

The increasing economic impact of black dot on potato (*Solanum tuberosum*) worldwide has led to an urgent need for studies on *C. coccodes*' population structure. In previous work (13), the occurrence of four multimember VCGs among 110 *C. coccodes* potato isolates originating from Israel, France, and the Netherlands (referred to as EU/I isolates) has been reported. The EU/I-VCG1 consisted of 8 isolates, in which 2 were from Israel, 2

from the Netherlands, and 4 from France. The EU/I-VCG2 was the largest VCG, consisting of 39 isolates, in which 7 were from Israel, 17 from the Netherlands, and 15 from France. The EU/I-VCG3 was the second largest, consisting of 22 isolates, in which 11 were from Israel and 11 from the Netherlands; and the EU/I-VCG4 consisted of 11 isolates, in which 2 were from Israel and 9 from the Netherlands (13). Pathogenicity assays indicated that all isolates were pathogenic to potato, with isolates of EU/I-VCG3 being the most aggressive (13). In a recent study (14), vegetative compatibility of 123 isolates of *C. coccodes* from North America (United States and Canada) originating from potato, tomato, pepper, and mint was tested using *nit* mutants. The North American isolates did not anastomose with previously selected EU/I VCG testers, and therefore new VCG testers (8 isolates) for the North American (NA) population were selected. The 123 isolates from North America were distributed to seven VCGs, at 1.6, 1.6, 4.0, 8.1, 13.8, 19.5, and 36.6%, with 14.6% of the isolates not assigned to any of the seven VCGs (14). A designation system for populations of *C. coccodes* based on their continent source, VCG number, and isolate code was defined (14).

The objectives of the current study were to characterize a population of *C. coccodes* comprised of isolates from Israel and Northern Europe (EU/I) using VCG, and to assess the correlation between VCGs and aggressiveness of isolates on potato.

MATERIALS AND METHODS

Collection of European/Israeli (EU/I) isolates. *C. coccodes* isolates were collected from certified potato seed tuber lots imported to Israel from the Netherlands, Scotland, France, and Germany during the spring seasons of 2002, 2003, and 2004 (Table 1). Israeli isolates were collected from either seed tubers (for the autumn season) or tubers for consumption, and from infected stems collected from 21 different locations in Israel.

All *C. coccodes* isolates were placed on potato dextrose agar (PDA). Plates were incubated at 25°C in the dark for 7 days. Conidia transferred to a medium contain-

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ing 0.2% sorbose, 15% agar, and 100 ppm streptomycin sulfate (SA) were incubated for 24 h at 25°C in the dark. Monoconidial cultures were recovered from each isolate (by micromanipulation) and maintained on Czapek Dox agar (CDA), which contains 0.2% sodium nitrate as a source of nitrogen (Difco, Le Port de Claix, France), at 6°C (10,13).

Selection and characterization of nonutilizing nitrate (*nit*) mutants. *nit* Mutants were generated using previously described techniques (10,15). Water agar chlorate (WAC) medium containing 2% agar, 3% potassium chlorate, and 0.02% glucose was used to select *nit* mutants. Ten mycelial plugs (1 mm) from monoconidial cultures of each isolate were placed on WAC medium and incubated at 25°C in the dark. After 21 days, we transferred growing fringes of samples onto petri plates containing CDA medium and allowed them to grow for 5 days. Colonies with a thin mycelium on CDA were considered *nit* mutants. Phenotyping of *nit1* versus *NitM* mutants was carried out by placing two mycelial plugs of each isolate on both CDA and CDA amended with 0.02% hypoxanthine. Colonies developing after 5 days incubation at 25°C in the dark on CDA supplemented with hypoxanthine with a wild-type phenotype and on CDA with a thin mycelium phenotype, were classified as *nit1/nit3* mutants. Colonies developing on both media as thin mycelia were classified as *NitM* mutants (13).

Complementation tests. Complementation between *nit* mutants was tested on CDA medium containing sodium nitrate as a sole nitrogen source. One mycelial plug (1 mm) of *NitM* and two plugs of *nit1/nit3* mutants were placed 1 cm apart in a triangular pattern (11). Plates were incubated for 14 days at 25°C in the dark. Complementation characterized by prototrophic growth at the contact zone between the two complementary *nit* mutants was usually evident after 7 to 14 days (13).

Preparation of *C. coccodes* inoculum.

Isolates were cultured in 9-cm petri plates containing PDA (Difco) at 25°C for 3 to 4 days. A conidial suspension was prepared by collecting the conidia from colonies' surfaces and filtering through four layers of gauze to separate the mycelium and conidial fractions. Conidial concentration, determined with a hemacytometer, was adjusted to 1×10^5 conidia/ml with sterile distilled water (20).

Inoculation of plantlets. A series of experiments was performed with isolate 138 as a standard in order to assess disease conduciveness in each run. The pathogenicity assays were conducted with potato plantlets (*C. coccodes*-susceptible cv. Desiree obtained by transferring 50-mm-long stem nodes to 15-cm glass tubes containing Murashige and Skoog medium [4.4 g/liter Murashige & Skoog basal medium (Sigma Chemical Co., St Louis, MO), 30 g/liter sucrose, and 8 g/liter agar (Difco) adjusted to pH 5.8] and growing them for 3 weeks at 22°C and 16 h light.) The plantlets were transferred to 50-ml tubes containing 10 ml of perlite and 1/2 strength Hoagland solution (4 ml). After 48 h, eight plantlets for each isolate were inoculated by injection of 0.5 ml of conidial suspension into the perlite. Sterile distilled water (0.5 ml) was added to the control tubes. Plantlets were placed in a growth chamber (25°C, 70% RH, 16 h 100 μ mole photons/m²s) for a period of 2 weeks (20).

Assessment of disease symptoms on plantlets. Symptoms on roots, crown, and shoots were scored 14 days postinoculation on a scale of 0 to 5. For root and crown: 0 = no symptoms; 1 = sparse density of sclerotia; 2 = moderate density; 3 = moderate to severe density; 4 = severe density with moderate rot; 5 = total rot. For shoots: 0 = no symptoms; 1 = chlorosis of lower leaves; 2 = moderate (30 to 50% of leaves) wilt with severe chlorosis; 3 = moderate wilt and necrosis; 4 = severe (>50% of leaves) wilt and necrosis; 5 = dead plantlet (20).

Assessment of stem colonization.

Stems of the inoculated plantlets were surface-sterilized with 10% hypochlorite for 2 min, cut into six 2-mm segments from the base (1 to 4 cm above the crown), the middle (2 to 5 cm), and the top (5 cm to apex) of each stem (for a total of 18 segments), and placed on sorbose agar medium (SA). Plates were placed at 25°C in the dark for 7 days. The number of segments colonized with *C. coccodes* was counted (20). Colonization index was calculated according to the following formula: $I = (Nb \times 2 + Nm \times 4 + Nt \times 6)/N$, where *Nb*, *Nm*, and *Nt* are the number of colonized segments from the base, middle, and top parts of the stem, respectively, and *N* is the total number of tested segments (the numbers of colonized segments from the base, middle, and upper parts were multiplied by the arbitrary factors 2, 4, and 6, respectively, as detection of *C. coccodes* in the upper parts of the stem is considered to reflect a higher level of plant colonization than its detection in the base).

Statistical analyses. Data were analyzed statistically by SAS Software 6.12 (SAS Institute Inc., Cary, NC). The general linear model procedure was used to test the effects of inoculation on stem fungal colonization and sclerotia density at the 0.05 level of probability. Averages of sclerotia density and colonization levels were first calculated for each isolate separately; data from isolates of each VCG were then grouped, and the average values for each VCG calculated. Analysis of variance was followed by mean separation using Tukey-Kramer multiple range test. Data recorded as percentages were arcsine-transformed before analysis. The frequency procedure was used to test the distribution of each VCG across countries, and the distribution of VCGs within a country using χ^2 tests, at $P < 0.05$ and $P < 0.001$, respectively. Correlation coefficients between crown symptoms and shoot symptoms, shoot colonization index, and shoot fresh weight were calcu-

Table 1. Number of *Colletotrichum coccodes* isolates within the vegetative compatibility groups (VCGs) and nonassigned isolates according to their source of origin^a

Source	Year	European-Israeli (EU-I) VCGs								Nonassigned	Total
		1	2	3	4	5	6	7	8		
Israel	2000 ^y	2	7	11	2					14	
	2004	2	2	7	2	4	0	6	3	4	30
The Netherlands	2000	2	17	11	9					12	
	2004	1 ^{*z}	20	22	5	2 [*]	9 [†]	8	12	13	92
France	2000	4	15	0	0					4	
	2004	2	4	2	0	1	0	0	0	2	11
Scotland	2000	ND	ND	ND	ND						
	2004	0	2	0	0	0	0	34 ^{*†}	0	2	38
Germany	2000	ND	ND	ND	ND						
	2004	1	1	1	0	0	0	0	0	2	5
Total	2004	6	29	32	7	7	9	48	15	23	176
		3.4%	16.5%	18.2%	4.0%	4.0%	5.1%	27.3%	8.5%	13.0%	

^a The frequency procedure was used to test the distribution of each VCG across countries and the distribution of VCGs within a country using χ^2 tests.

^y Data from 2000 were obtained in a previous study (13).

^z * Significant differences ($P < 0.001$) within a country (within a row). [†] Significant differences ($P < 0.05$) across countries (within a column). ND = no data.

lated using Origin Software 5.0 (Microcal Origin Inc., Northampton, MA).

RESULTS

Collection of EU/I isolates. In the current study (2002 to 2004), we collected 176 isolates of *C. coccodes* from five geographical sources (Scotland and Germany were added) (Table 1). In our previous report (13), 110 isolates of *C. coccodes* from the Netherlands, Israel, and France, collected during 1998 to 2000, were assigned to four VCGs. The EU/I-VCG1 consisted of 8 isolates, in which 2 were from Israel, 2 from the Netherlands, and 4 from France. The EU/I-VCG2 was the largest VCG, consisting of 39 isolates, in which 7 were from Israel, 17 from the Netherlands, and 15 from France. The EU/I-VCG3 was the second largest, consisting of 22 isolates, in which 11 were from Israel and 11 from the Netherlands; and the EU/I-VCG4 consisted of 11 isolates, of which 2 were from Israel and 9 from the Netherlands. In the present study, out of 176 isolates, 92 were obtained from the Netherlands, 38 from Scotland, 11 from France, 5 from Germany, and 30 from Israel. The major cultivars were Mondial (22%), Nicola (16%), Desiree (10%), and Valor (9%) (data not shown).

Selection and characterization of *nit* mutants. Recovery of *nit* mutants from

WAC medium onto CDA was optimal after 21 days of incubation at 25°C in the dark. On CDA, *nit* mutants appeared as thin mycelia with a greenish pigmentation. The mean frequency of all *nit* mutant sectors was 35% (644 out of 1,823 replicates) (Table 2). Among the mutants, the *nit1/nit3* class made up 85%, while NitM mutants made up 15% of the total number of mutants.

Complementation tests and selection of VCG testers. During the first stages of the research, complementation tests were carried out using the defined tester isolates for the four previously reported VCGs selected during 1998 to 2000 (13). The EU/I testers were isolates #2 and 16 from the EU/I-VCG 1, isolates #3, 12, 13, 18, 24, and 53 from the EU/I-VCG 2, isolates #38 and 138 from the EU/I-VCG 3, and isolates #46, and 49 from the EU/I-VCG 4 (13). New NitM mutants with the ability to anastomose with a larger number of isolates were added to the set of testers, and in some cases replaced previously reported testers (13) that formed heterokaryon in a lower frequency. Isolates that were not assigned to any of the previous four VCGs were tested among themselves. This resulted in the detection of an additional four new multimember VCGs (VCG 5 to 8). The nonassigned isolates collected during the 2000 study were not yet tested with the new VCG testers.

Assignment of EU/I isolates into VCGs. Based on heterokaryon formation with the selected testers, 74 (42%) of the isolates were assigned to four previously reported VCGs, 79 (45%) to four newly detected multimember VCGs (5 to 8), and 23 (13%) of the isolates could not be assigned to any of the groups detected (Table 1). The largest groups in the whole collection were EU/I-VCG2, 3, and 7, comprising 29, 23, and 21% of the total assigned isolates, respectively; EU/I-VCG7 was the largest group among the 176 additional isolates collected during 2002 to 2004. Two of the VCGs had a specific geographical distribution: the nine isolates in EU/I-VCG6 originated exclusively from the Netherlands (Table 1), and 34 of 38 (89%) Scottish isolates were assigned to EU/I-VCG7; out of 48 isolates in this group, 34 (70%), 8 (17%), and 6 (13%) isolates originated from Scotland, the Netherlands, and Israel, respectively (Table 1). Significant differences between VCGs within each country were obtained in isolates originated from the Netherlands and Scotland. The frequency of VCG1 and 5 within the Dutch isolates was significantly ($P < 0.001$) lower than all other VCGs (2, 3, 4, 6, 7, and 8). Within the Scottish isolates, the frequency of VCG7 was significantly higher than VCG2 ($P < 0.001$).

Pathogenicity tests. A subset of 48 isolates, representing eight VCGs, was tested for pathogenicity on potato. A reference isolate #138 (EU/I-VCG3) previously reported (13) was also included in the study. Disease symptoms on the shoot (ranging from 0 to 5) were lowest with isolates from EU/I-VCG1. Shoot weight obtained with EU/I-VCG7 isolates was the highest, the lowest with EU/I-VCG5. Fungal colonization index was significantly higher ($P < 0.05$) in plantlets inoculated with EU/I-VCG5 isolates than with all other VCGs, except for EU/I-VCG6 isolates (Table 3). Although there were no significant differences between VCGs with respect to sclerotia formation on the root and crown, the results showed a similar tendency, where VCG1 isolates had a low

Table 2. Number and frequency of nitrate auxotrophic (*nit*) mutants among the tested isolates of the vegetative compatibility groups (VCGs)

VCG	No. of isolates	Replications ^z	Frequency (%) of <i>nit</i> mutants ^y	
			<i>nit1</i>	NitM
EU/I-1	6	54	14 (73.7%)	5 (26.3%)
EU/I-2	29	283	78 (83.0%)	16 (17.0%)
EU/I-3	32	407	109 (91.1%)	12 (9.9%)
EU/I-4	7	51	24 (77.4%)	7 (22.6%)
EU/I-5	7	34	16 (88.9%)	2 (11.1%)
EU/I-6	9	137	20 (95.2%)	1 (4.8%)
EU/I-7	48	465	154 (87.5%)	22 (12.5%)
EU/I-8	15	147	42 (76.4%)	13 (23.6%)
EU/I nonassigned	23	245	89 (81.7%)	20 (18.3%)
Total	176	1,823	546 (84.8%)	98 (15.2%)

^y Frequency of *nit1* and NitM mutants generated for each VCG out of 10 to 30 replications per isolate.

^z Total number of replications per VCG out of 10 to 30 replications per isolate on water agar chlorate.

Table 3. Aggressiveness of *Colletotrichum coccodes* isolates on potato

VCG	No. tested isolates	Shoot weight (mg)	Symptoms on shoot (0-5)	Sclerotia on root (0-5)	Sclerotia on crown (0-5)	Colonization index (0-4) ^x
Control	...	60.2 a ^y	0	0	0	0
1	4	53.4 ab	0.85 b ^z	2.08 a	1.35 a	0.57 bc
2	8	44.5 ab	1.25 ab	2.12 a	2.10 a	0.55 c
3	6	45.7 ab	1.83 a	2.23 a	2.50 a	0.72 bc
4	6	49.1 ab	1.57 ab	2.33 a	2.09 a	0.58 bc
5	4	34.3 b	2.11 a	2.38 a	2.75 a	1.15 a
6	6	40.9 ab	1.96 a	2.35 a	2.75 a	0.92 ab
7	7	55.0 a	2.18 a	2.06 a	2.08 a	0.6 bc
8	7	46.1 ab	2.10 a	2.46 a	3.04 a	0.84 abc

^x Colonization index was calculated using the following formula: $I = (Nb \times 2 + Nm \times 4 + Nt \times 6)/N$ where *Nb*, *Nm*, and *Nt* are the numbers of infected segments from the base, middle, and top sections of the stems, respectively, and *N* is the total number of tested segments ($N = 18$). For details see Materials and Methods.

^y One-way analysis of variance (ANOVA) was carried out at $P = 0.05$. Means were separated by Tukey-Kramer multiple range tests. Different letters within a column indicate significant differences.

^z All treatments (VCGs) were significantly different from the control (0).

scoring and VCG5 and 8 a high scoring. High positive correlations between crown symptoms and both shoot symptoms (0.8 ; $P = 0.016$) and shoot colonization index (0.74 ; $P = 0.03$) were obtained, as well as a strong negative correlation with shoot fresh weight (-0.77 ; $P = 0.02$).

DISCUSSION

Four new multimember VCGs were detected from 176 isolates of *C. coccodes* recovered from potato. The identification of these new VCGs was made possible by the larger sample size and additional geographical sources (Scotland and Germany). Regional differences in the VCG composition of subpopulations were observed. A significant correlation between geographical origin and VCG was observed for the first time with the Scottish isolates that were assigned almost exclusively to EU/I-VCG7, and with the Dutch isolates, which were the only ones assigned to VCG6. This suggests a possible adaptation of these isolates to the conditions in a specific area. Alternatively, this geographical speciation may be explained by random local mutations, which created a new VCG that had not yet spread to other areas. By monitoring the occurrence of this VCG among the different regions of Northern Europe, the rate of *C. coccodes* spreading can be studied. Regional differences have been previously reported with *Aspergillus flavus*, whereby isolates from Formosa province in Argentina could not be grouped into any of the Córdoba province VCGs and vice versa (except for one atypical VCG) (2). Those two regions differed in their climatic conditions, soil type, crop-sequence history, and latitude, perhaps reflecting adaptation according to different geographic sources (2).

The largest group in the whole collection was EU/I-VCG2, which included 29% (68) of the 286 isolates (Table 1). Isolates from this group were obtained from all source countries (Israel, the Netherlands, France, Germany, and Scotland). In our previous report (13), isolates from France were assigned only to EU/I VCGs 1 and 2. In the current study, an additional two and five French isolates were assigned to EU/I-VCG1 and EU/I-VCG2, respectively, but two more isolates were assigned to EU/I-VCG3 and one to EU/I-VCG5. The absence of French isolates from the other VCGs may be due to the relatively small sample size from this geographical origin.

A significant positive correlation occurred between shoot symptoms and crown symptoms, and a significant negative correlation occurred between crown symptoms and shoot fresh weight. Root symptoms were not significantly correlated with these parameters, suggesting that crown symptoms may be the best measure of aggressiveness. A high level of damage to the crown may result in xylem rot and interrupted water and nutrient flow, caus-

ing death of the plantlet, whereas formation of sclerotia on roots usually occurs close to senescence of the plant and reflects the natural mechanism of fungal survival in soil.

EU/I-VCG5 isolates were the most aggressive and produced the highest stem-colonization levels (Table 3) and lowest shoot weights, whereas isolates of EU/I-VCG1 were the least aggressive (Table 3). When pathogenicity parameters (colonization index, sclerotia on crown, and symptoms on shoot) for EU/I VCGs 1 to 4 were analyzed separately, EU/I-VCG3 was observed as the most aggressive group, confirming our previous report (13). A similar association between VCG and aggressiveness has previously been reported with *Verticillium dahliae*, where VCG4B isolates were more aggressive on potatoes, and VCG2A isolates were more aggressive on tomatoes (18). Also with *F. oxysporum* f. sp. *cucumerinum*, VCG 0186 isolates were significantly less aggressive to cucumber, whereas VCG1-A isolates were significantly more aggressive than other VCGs (1,21). In contrast, no significant differences in mean virulence were observed with isolates from VCG1-B, C, D, E, or F (1).

Differences in VCG aggressiveness may have practical implications, especially for potato crops, in which *C. coccodes* has become an important pathogen. Soil and seed-tuber assays for *C. coccodes* estimate pathogen levels but do not differentiate between VCGs. If VCGs differ in aggressiveness, the presence of the pathogen in the soil or seed tubers does not necessarily indicate its damage potential. Data on the VCG distribution within subpopulations, and on the relative aggressiveness of each VCG, will enable a more accurate evaluation of potential damage and the necessary control measures. Determination of potential aggressiveness on potatoes in *C. coccodes* populations is also important for accurate selection of isolates for screening resistant and tolerant lines in breeding programs.

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