

Vegetative Compatibility Among Races of *Fusarium oxysporum* f. sp. *cubense*

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ABSTRACT

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Isolates of *Fusarium oxysporum* f. sp. *cubense* (incitant of Panama disease of *Musa* and *Heliconia* spp.), collected from Australia, the Canary Islands, the Comores Islands, Honduras, Jamaica, Malaysia, the Philippines, South Africa, Taiwan, and the United States were characterized for vegetative compatibility by using nitrogen metabolism mutants. Isolates belonged to race 1, 2, or 4 or were of unknown race. Eleven vegetative compatibility groups (VCGs) were identified among the 96 isolates in this collection. In general, there was a good correlation between VCG and race among isolates for which race was known. Six VCGs were composed of isolates of only a single race and five were composed of isolates representing two different races. Race 4 isolates belonged to at least three different VCGs, indicating genetic diversity among strains of this race. The use of representative strains from these VCGs is suggested when banana selections are screened for resistance to race 4 or other variants of this pathogen. The use of vegetative compatibility to characterize isolates of unknown race is discussed.

Additional keywords: Cavendish, Fusarium wilt of banana, *nit* mutants

Fusarium wilt or Panama disease of *Musa* and *Heliconia* spp. is considered one of the most destructive plant diseases (18). Currently, four races of the pathogen, *Fusarium oxysporum* Schlecht. f. sp. *cubense* (E. F. Smith) Snyder & Hans. (FOC), that cause the disease are recognized worldwide (20,23). Race 1 occurs in most banana-growing regions and was responsible for decimating the large commercial plantations of the cultivar Gros Michel in tropical America during the early 1900s (18,19). Silk, Apple, Lady Finger, and [Taiwan] Latundan are other commonly grown cultivars that are susceptible to race 1 (20,23; R. H. Stover, *personal communication*). Race 2 isolates are virulent on Bluggoe and closely related plantains (20,23). Race 3, described by Waite (25) in 1963 in Honduras as being pathogenic to *Heliconia* spp., apparently is rare or no longer exists in Central America (R. H. Stover, *personal communication*). At this time, race 4 is known to occur in the following areas of the Eastern Hemisphere: Canary Islands; Mindanao Province, Philippines; Queensland, Australia; South Africa; and Taiwan (20,23). The wide host range of race 4 includes all of the above plus the widely used and important dessert bananas of the Cavendish group (20,23). Cavendish cultivars are resistant to races 1, 2, and 3 and have generally replaced Gros Michel

as the bananas grown for world commerce (19). Race 4 has caused concern in a trade that depends on a commercially acceptable banana cultivar with resistance to Panama disease (20,23).

In a recent article on banana breeding, Stover and Buddenhagen (20) discussed strategies for developing an acceptable replacement for Cavendish bananas that would have resistance to race 4. Ignorance of the genetics that govern virulence among different strains of race 4 was cited as an obstacle to this goal. It is possible that race 4, as well as other races, from different geographic regions has different genes for virulence (20,23). For example, Stover and Buddenhagen (20) reported indirect evidence for differences in virulence among race 1 strains from the Caribbean on the IC2 banana selection. Although such variability would have important implications regarding the selection and screening of resistant material, it has not been investigated. Work identifying and characterizing genetic diversity in this pathogen is needed.

No sexual stage is known for *F. oxysporum*. Consequently, heterokaryosis may play an important role in determining genetic diversity in different populations of this fungus (16). Heterokaryosis was first described in FOC by Buxton (3).

Isolates that form heterokaryons with each other are vegetatively compatible, and those that are compatible compose a vegetative compatibility group, or VCG (16). Because vegetatively incompatible isolates do not form heterokaryons, the potential for genetic interactions between such isolates is limited. Isolates in the same VCG often share common biological,

physiological, and pathological attributes (5).

Recently, Puhalla (16) characterized isolates from 13 different formae speciales of *F. oxysporum* on the basis of vegetative compatibility. Subsequent work by others has identified two patterns among formae speciales of *F. oxysporum*: Isolates within a VCG either all belong to the same race (2,8,9) or belong to more than one race (9,11). The former pattern may be useful when identification of isolates of *F. oxysporum* to race by conventional means is desirable but impractical because of time or space constraints, and both patterns may provide some insight into the possible origins and genetic diversity of races of various formae speciales.

Characterization of FOC isolates to race is difficult. Race of a given isolate is normally determined by evaluating disease reactions in the field; clean corms of differential cultivars are planted in infested soil and disease is scored 2-9 mo later (24). Race determinations are expensive and time-consuming, and results may be equivocal because of variability inherent in growing conditions at a given location and/or in planting material used in a given study (20,23). Furthermore, regulatory restrictions in a given location (e.g., Florida) may not allow work with quarantined isolates to be conducted in the field. Of the difficulties in screening banana selections for resistance to Panama disease (and by analogy the difficulties in determining race of a given FOC isolate) Stover and Buddenhagen (20) have written: "The problem of realistic screening has many facets, and for a soil-borne pathogen such as *Fusarium oxysporum* and a large perennial plant such as banana, it is especially difficult." Laboratory procedures that could expedite race identification would provide valuable information about this pathosystem.

In his work describing vegetative compatibility in *F. oxysporum*, Puhalla (16) placed an isolate of FOC from Australia in VCG 0120. In subsequent work with a collection of 11 FOC isolates from Australia, Honduras, Taiwan, and the Philippines, Correll and Leslie (7) described four additional VCGs (0121, 0122, 0123, and 0124). The present work expands on these results by examining 85 additional FOC isolates from the above countries plus the Canary Islands, the Comores Islands, Jamaica, Malaysia, South Africa, and the United States

(Florida) for vegetative compatibility. In particular, race 4 isolates from all regions of the world reporting this race to date were included in this study. Portions of this work were published previously (7,15).

MATERIALS AND METHODS

A worldwide collection of FOC isolates was obtained from individuals or culture collections (Table 1); we relied on the donors for the race designations. Isolates were characterized for vegetative compatibility using Puhalla's technique (16), as described below.

Generation of *nit* mutants. Single-conidium isolates were grown on two agar media, each containing 15 g/L of KClO₃: KMM, a mineral salts medium containing sucrose and L-asparagine, and KPS, containing potato broth and sucrose (16). Growth of most isolates was reduced and appressed to the surface of both media. After 1–3 wk, however, chlorate-resistant sectors (putative *nit* mutants) arose from colonies on KMM and KPS. Sectors had a fluffy, aerial morphology and a rapid growth rate compared with the wild-type portions of a colony. The yields of mutants were considerably higher on KPS than on KMM. Therefore, KMM was used only in preliminary portions of this work. Also, because of a relative insensitivity to chlorate, recovery of mutants for many race 4 isolates was easier on KPS containing 25 or 45 g/L instead of 15 g/L of KClO₃. *Nit* mutants were identified by their thin expansive growth on Puhalla's (16) minimal medium (MM), which contains nitrate as a sole source of nitrogen.

Complementation of *nit* mutants and determination of vegetative compatibility. For each isolate, all *nit* mutants were paired in random combinations on MM. Those *nit* mutants able to complement one another (as a result of heterokaryon formation) formed a line of wild-type growth where the two colonies came in contact.

In early portions of this study, different *nit* mutants able to complement one another were arbitrarily designated A through E. Complementary *nit* mutants from each isolate were used as testers to determine vegetative compatibility among other isolates. Incompatible reactions between the *nit* mutants of different isolates were retested with other *nit* mutants of those isolates in order to verify that the isolates were indeed vegetatively incompatible. Pairs that formed weak or questionable heterokaryons were retested on MM containing 5% activated charcoal; complementation between some *nit* mutant pairs was more evident on this medium than on nonamended MM. Charcoal was incorporated in media used in previous studies on heterokaryosis in other plant pathogens (1,10).

In later portions of this study, the physiology of certain *nit* mutant testers was determined as previously described by Correll et al (6), who have used NitM mutants as reliable testers for a given VCG. Therefore, NitM mutants were identified among previously generated *nit* mutants to help clarify questionable

complementation reactions. Also, a *nit* mutant from an isolate representing each VCG identified in the present study was paired with a physiologically distinct *nit* mutant from a strain in each VCG described by Correll et al (6) to verify that each VCG in the present work was distinct.

Table 1. Vegetative compatibility groups (VCGs) among isolates of *Fusarium oxysporum* f. sp. *cubense*

Race ^x	Isolate ^y	<i>Musa</i> spp. cultivar	Source ^z	Origin
VCG 0120				
?	15638	?	a	Malaysia
1	34661	Highgate	a	Honduras
1	3S1	Highgate	i	Honduras
4?	O-1219	Mons	c	Queensland, Australia
?	O-1220	Mons	c	Queensland, Australia
1	O-1222	Mons	c	Queensland, Australia
4?	22410	Cavendish	g	Wamuran, Qld., Australia
4?	22411	Cavendish	g	Wamuran, Qld., Australia
?	22424	Lady Finger	g	Moorina, Qld., Australia
4?	22425	Cavendish	g	Wamuran, Qld., Australia
4	F9127	Grande Naine	g	South Africa
4	F9131	Cavendish	g	South Africa
4	T4	Cavendish	f	Taiwan
4	A2	Mons mari	f	Australia
4	A3	Mons mari	f	Australia
4?	C1	Cavendish	f	Canary Islands
4?	C2	Cavendish	f	Canary Islands
4?	NB	Cavendish	f	Natal, South Africa
4?	NH	Williams	f	Natal, South Africa
4?	NW	Williams	f	Natal, South Africa
4?	TL	Williams	f	East Transvaal, South Africa
4?	TM	Williams	f	East Transvaal, South Africa
4?	TH	Williams	f	East Transvaal, South Africa
4?	NL	Cavendish	f	Natal, South Africa
4?	TP	Williams	f	East Transvaal, South Africa
4	ADJ1	Dwarf Cavendish	d	Adeje, Canary Islands
4	ADJ2	Dwarf Cavendish	d	Adeje, Canary Islands
4	BUE1	Dwarf Cavendish	d	Buenavista, Canary Islands
4	BUE2	Dwarf Cavendish	d	Buenavista, Canary Islands
4	GAL1	Dwarf Cavendish	d	Las Galletas, Canary Islands
4	GAL2	Dwarf Cavendish	d	Las Galletas, Canary Islands
4	IC1	Dwarf Cavendish	d	Icod de los Vinos, Canary Islands
4	IC2	Dwarf Cavendish	d	Icod de los Vinos, Canary Islands
4	ORT1	Dwarf Cavendish	d	La Orotava, Canary Islands
4	ORT2	Dwarf Cavendish	d	La Orotava, Canary Islands
4	PAJ1	Dwarf Cavendish	d	Pajalillos, Canary Islands
4	PAJ2	Dwarf Cavendish	d	Pajalillos, Canary Islands
VCG 0121				
4	T3	Cavendish	f	Taiwan
4	F9130	Cavendish	g	Taiwan
4?	GM	Gros Michel	h	Taiwan
4	ML	Cavendish	h	Taiwan
4	TBR	Cavendish	h	Taiwan
4	SKC	Cavendish	h	Taiwan
4	H1	Cavendish	e	Taiwan
?	O-1124	?	c	Taiwan
VCG 0122				
4	P18	Cavendish	h	Philippines
4	P79	Cavendish	h	Philippines
4	LAP	Cavendish	h	Philippines
2	SABA	Saba	h	Philippines

(continued on next page)

^xRace designation provided by donor of isolate: ? = race unknown, ? combined with number = probable race.

^yAccession number provided by donor.

^za = American Type Culture Collection, Rockville, MD; b = author (RCP); c = Fusarium Research Center, Pennsylvania State University, University Park; d = Julio Hernandez Hernandez, Tenerife, Canary Islands; e = S.-C. Hwang, Taiwan Banana Research Institute, Pingtung, Republic of China; f = Barry Manicom, Nelspruit, South Africa; g = Ken Pegg, Brisbane, Australia; h = Shirley Nash Smith, Alameda, CA; i = R. H. Stover, La Lima, Honduras; j = IFRA, Montpellier, France (via R. H. Stover).

Table 1. (continued from preceding page)

Race ^x	Isolate ^y	<i>Musa</i> spp. cultivar	Source ^z	Origin
VCG 0123				
2?	DAVAO	Silk	h	Philippines
1	F9129	Latundan	g	Taiwan
1	T1	Gros Michel	f	Taiwan
VCG 0124				
2	BLUG	Bluggoe	h	Honduras
?	S?	Tetraploid 1242	i	Bodles, Jamaica
?	O-1224	Mons	c	Queensland, Australia
2	18773	?	a	?
VCG 0125				
1	A1	Lady Finger	f	Australia
1	A4	Lady Finger	f	Australia
1	8606	Lady Finger	g	Currumbin, Qld., Australia
1	8610	Lady Finger	g	Murwillumbah, N.S.W., Australia
1	8611	Lady Finger	g	Currumbin, Qld., Australia
1	8624	Lady Finger	g	Currumbin, Qld., Australia
1	8625	Lady Finger	g	Currumbin, Qld., Australia
1	22468	Lady Finger	g	Tomewin, Qld., Australia
1	22479	Ducasse	g	Bowen, Qld., Australia
?	N5448	Lady Finger	g	Bli Bli, Qld., Australia
?	22417	Lady Finger	g	Rocksberg, Qld., Australia
4?	22541	Cavendish	g	Byron Bay, N.S.W., Australia
1	O-1223	Mons	c	Queensland, Australia
?	1S?	Williams	i	Bodles, Jamaica
VCG 0126				
1	S1	Highgate	i	Honduras
1	STMZ	Maqueno	i	Honduras
1	4S1	Maqueno	i	Honduras
1	5S1	Maqueno	i	Honduras
VCG 0127				
1?	NJ	Butter	f	Natal, South Africa
VCG 0128				
2	22993	Bluggoe	g	South Johnstone, Qld., Australia
2	22994	Bluggoe	g	South Johnstone, Qld., Australia
?	A47	Bluggoe	j	Comores Islands
VCG 0129				
4?	N5331	Cavendish	g	Yandina, Qld., Australia
4?	N5354	Cavendish	g	Yandina, Qld., Australia
4?	N5443	Cavendish	g	Doonan, Qld., Australia
4?	8604	Cavendish	g	North Arm, Qld., Australia
4?	8622	Cavendish	g	North Arm, Qld., Australia
4?	8627	Cavendish	g	North Arm, Qld., Australia
4?	22402	Cavendish	g	Wamuran, Qld., Australia
?	22507	Lady Finger	g	Queensland, Australia
1	O-1221	Mons	c	Queensland, Australia
VCG 01210				
1?	A1-1	Apple	b	Florida, United States
1?	A2-1	Apple	b	Florida, United States
1?	A3-1	Apple	b	Florida, United States
1?	A4-1	Apple	b	Florida, United States
1?	A10	Apple	b	Florida, United States
1?	A14	Apple	b	Florida, United States
1?	F2	Apple	b	Florida, United States
1?	F3	Apple	b	Florida, United States
1?	F4	Apple	b	Florida, United States

RESULTS AND DISCUSSION

Eleven VCGs were identified among the 96 isolates of FOC included in this study. Donors supplied the race designations of 50 of these isolates but were unsure of or did not know the race of the remaining 46 isolates (Table 1). Among the former isolates, there was a good, although not absolute, correlation between VCG and race. VCGs 0121, 0126, 0127, and 0128 contained isolates from a single race, whereas VCGs 0120 and 0122 each contained isolates belonging to two different races. The remaining VCGs—0123, 0124, 0125, 0129, and 01210—contained isolates of

unknown race or possibly two different races. After further study of vegetative compatibility in FOC, it may be possible to determine the race identity of isolates of FOC by characterizing them for vegetative compatibility. Correll et al (8) have demonstrated the utility of such an approach for *F. o. f. sp. apii* (R. Nelson & Sherb.) Snyder & Hans.

It is possible that some of the isolates responsible for the less than complete correlation between VCG and race are mislabeled with regard to race. For example, isolates O-1221 and O-1222 from the Fusarium Research Center are listed as race 1 isolates even though the

host they were isolated from was Mons, a Cavendish cultivar. Because Cavendish cultivars are susceptible to race 4 but not to race 1, it is possible that these are actually race 4 isolates. Likewise, the Silk cultivar that DAVAO in VCG 0123 was isolated from is a host for race 1, not race 2. Although it is outside the scope of the present work, race characterizations should be repeated for these and other isolates in this collection.

Recently, Sun and Su (24) reported characterizing three isolates of FOC for race by testing them on tissue culture explants of differential cultivars of banana in growth chambers. In their work, disease reactions were obtained 2–4 wk after inoculation; one race 4 isolate wilted Cavendish (race 4 differential) explants, whereas two race 1 isolates wilted Cocos (race 1 differential) explants but not Cavendish. One of us has recently observed race 4 isolates (A2, C1, NB, and 22425 in Table 1), but not race 1 isolates (8606 and 22479) causing wilt on explants of a Cavendish cultivar (Grande Naine) in preliminary studies in growth chambers (Ploetz, unpublished). Although these results corroborate some of those of Sun and Su (24), additional work with explants of race 1, 2, and 4 differentials needs to be conducted before the reliability of this technique can be ascertained. It is possible that disease reactions with explants in growth chambers may differ from those obtained with rhizomes in the field (R. H. Stover, personal communication).

Our results with VCGs containing race 4 or putative race 4 isolates may have relevance to the origins of this race in Cavendish plantations of the Eastern Hemisphere. Panama disease on Cavendish cultivars was first noted in 1932 in the Orotava Valley on Tenerife in the Canary Islands (4); race 4-type virulence was not reported in southeast Asia until 1967 in south Taiwan (22). Although it is not clear from subsequent reports of race 4-type virulence in other banana-growing regions (20,21,23) whether the pathogen(s) responsible for these outbreaks originated in the Canary Islands, Taiwan, or other areas, it is tempting to speculate on these origins based on the present work. All race 4 isolates from the Canary Islands in the present study are in VCG 0120; ADJ1, ADJ2, BUE1, BUE2, GAL1, GAL2, IC1, IC2, ORT1, ORT2, PAJ1, and PAJ2 are all from various locations on Tenerife, and ORT1 and ORT2 are from the Orotava Valley. It is possible that other isolates in VCG 0120 from Australia, Honduras, South Africa, and Taiwan originated in Tenerife. An alternative origin for isolates in VCG 0120 is Southeast Asia. Isolate 15638 in VCG 0120 was recovered in Malaysia, the probable center of origin for the Cavendish group and related bananas (17). It is possible that members of this

VCG coevolved with bananas in this region and were subsequently distributed to other banana-growing regions on rhizomes used as propagation material. Race 4 isolates in VCGs 0121, 0122, and 0129 may have originated independently of those in VCG 0120 in Taiwan, the Philippines, and Australia, respectively. However, additional work characterizing these and other race 4 isolates for traits other than vegetative compatibility (e.g., virulence on putatively resistant selections, isozyme polymorphisms [2], and restriction fragment length polymorphisms of total [14], mitochondrial [12], or plasmid DNA [13]) will be needed before the origins and relatedness of members of these VCGs can be more fully addressed.

Su et al (23) described differences in growth on modified Komada's medium among race 4 isolates from Taiwan, Australia, the Canary Islands, and the Philippines. The present work documents genetic differences in this race on the basis of vegetative compatibility. Differences in virulence may also exist among race 4 isolates. Work identifying pathogenic variability among race 4 isolates is needed before intelligent decisions can be made about screening new banana clones for resistance to Panama disease.

Six of the VCGs described in the present study (0121, 0122, 0126, 0127, 0129, and 01210) were each represented by isolates from only one country (Table 1); e.g., all isolates in VCG 0129 were from Australia. Although the distribution of isolates in each of these VCGs appears to be limited, it is possible that future work may add isolates from different countries to some of these groups, resulting in the more cosmopolitan representation observed in VCGs 0120, 0123, 0124, 0125, and 0128, each of which has members from more than one country. One of the means by which FOC is disseminated is through the movement of infested rhizomes (17,18). It is possible

that the international transport of infested rhizomes is responsible for the widespread occurrences of VCGs 0120, 0123, 0124, 0125, and 0128 and that stricter quarantines may be needed to stop the spread of race 4 or other important variants of this pathogen in the future.

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