Identification of Additional Habitats of Nectria haematococca Mating Population VI

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This research was supported in part by Rockefeller Foundation Grants GA AS 7701 and 75002.

The author thanks J. I. Stein and P. S. Matthews for technical assistance, T. E. Hackett for seeds of Alaskan 2 B, and the investigators who sent cultures of *Fusarium solani*; especially T. Matuo for our original cultures of *Nectria haematococca* mating population VI, T. A. Toussoun and P. E. Nelson who supplied a large number of cultures from the Fusarium Research Center's Collection, and G. E. Harman who sent isolates of *F. solani* obtained from pea.

Accepted for publication 16 May 1978.

ABSTRACT

VANETTEN, H. D. 1978. Identification of additional habitats of Nectria haematococca mating population VI. Phytopathology 68: 1552-1556.

One hundred and fifty-two isolates of *Fusarium solani* were tested for ability to cross with two hermaphroditic isolates of opposite mating type of *Nectria haematococca* mating population VI. Of the 44 isolates which produced a fertile cross, 21 were obtained from diseased pea and at least two isolates were obtained from diseased parts of each of the following plants: chickpea, potato, tuliptree, alfalfa, cottonwood, and sainfoin. Most of the isolates identified as members of mating population VI were tested for virulence on pea. In general, the most virulent isolates on pea originally had been isolated from pea. However, several of the isolates obtained from habitats other than pea were as virulent as or more virulent than some of those from pea. These results indicate that isolates of *N. haematococca* mating population VI pathogenic on pea can be found in a variety of habitats.

Considerable controversy surrounds Fusarium taxonomy at both the species and subspecies levels (1, 7, 24). The confusion regarding the morphological classification of fusaria at the species levels is illustrated by Booth's division of *F. solani* sensu Snyder and Hansen (24) into four species. At the subspecies level a frequently used trinomial is formae speciales in which classification of the isolate is based on pathogenicity (22). The perfect stage (when available) is another way to establish taxonomic relationships. The ability of different isolates to cross readily and produce fertile progeny indicates that they are conspecific. Sexual compatibility also has been proposed as an aid in the identification of formae speciales of *F. solani* (15).

When the perfect stage of *F. solani* has been produced, it has been shown to be *Nectria haematococca* Berk. and Br. (syn. *Hypomyces solani*) (5, 6). Both homothallic and heterothallic isolates of *N. haematococca* have been identified, and among the heterothallic isolates distinct mating populations (MP) exist which do not interbreed (15). Our interest is in MP VI which is the MP that contains members (*F. solani* f. sp. *pisi*) pathogenic on pea. Previous studies have demonstrated that some members of this MP also are pathogens of mulberry (*Morus alba* L.) and ginseng (*Panax ginseng* C. A. Mey) (14). The purposes of this present study were: (i) to identify additional sources (habitats) of *N. haematococca* MP VI and (ii) to evaluate further the relationship between this mating population and pathogenicity on pea.

00032-949X/78/000282$3.00/0
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MATERIALS AND METHODS

Collection and maintenance of isolates.—In addition to the isolates obtained from other investigators, a limited number of isolates were collected from diseased pea or chickpea plants at different localities in New York State. The lower stem and upper root portion of plants bearing lesions characteristic of infections by *F. solani* were washed in running tap water for 6-20 hr. Then the tissue was supported on bent glass rods that had been placed on moistened filter paper in petri dishes. After 24-48 hr, conidia were removed from conidiophores emerging from the infected tissue and transferred to the *Fusarium*-selective medium of Nash and Snyder (16). Hyphal-tip or single-spore isolates were collected from colonies bearing characteristic *Fusarium* macroconidia.

All isolates were assigned a code number and stored in two ways. In the first procedure the isolates were transferred to V-8 juice agar medium [media M-29 (23)] contained in small screw-cap test tubes (1 × 10 cm). The cultures were kept at 24-27 C under fluorescent lighting and/or diffuse sunlight for 1-2 wk and then stored in the dark at 6 C. The *Fusarium* sp. isolates also were stored as lyophilized cultures (25). Fresh transfers of the different isolates were obtained normally from the stock cultures stored at 6 C.

Mating procedure and random ascospore analysis.—Procedures for mating and random ascospore analyses were similar to those described by others (14, 21, 23). Cultures were grown on V-8 juice agar medium in test tubes (15 × 1.5 cm) at 24-27 C under fluorescent lighting and/or diffuse sunlight for 8-14 days. Crosses were made by pouring about 10 ml of a conidial suspension of one

isolate onto the surface of another isolate. After 5-10 min, the spore suspension was decanted, and the fertilized cultures were incubated as above. At periodic intervals during approximately 6 mo the number, color, and fertility of the perithecia were recorded.

For random ascospore analysis, emerging ascospore masses were picked off the ostioles of the perithecia and transferred to about 0.5 ml of water contained in a test tube. The test tube was shaken vigorously (about 200 rpm) for 1-2 hr to help break up the ascospore masses and then the ascospore suspension was plated (about 100-600 spores/plate) on *Neurospora* minimal medium minus biotin (Nm medium) (4). After incubation for 16-20 hr in the dark at 24 C, single germinated ascospores were transferred to slants of Nm medium. A Wild M5 stereomicroscope was routinely used at ×75 to ×200 for identification of germinating ascospores; these could be distinguished readily from germinating macroconidia, but they could not always be easily distinguished from germinating microconidia. In these latter cases the germinating spore was examined under a compound microscope at ×100 to verify the identity of the propagule.

Pathogenicity tests.—Seeds were surfaced sterilized as described previously (17) and plants were grown in steamed soil or sand contained in 11 cm (top diameter) × 10.5 cm clay pots at 28 ± 2 C in a greenhouse or controlled environment chamber. Plants were inoculated by pouring about 25 ml of a $\geq 10^7$/ml conidial suspension into each pot soon after the plants had emerged (7-14 days). Suspensions of conidia were prepared from 5- to 10-day-old cultures grown on PDA or V-8 juice agar media under standard conditions. Two pots were used for each isolate, and noninoculated plants served as controls. Disease development was evaluated 4 wk after inoculation.

The following numbering system was used to code disease development on pea: 11, all plants damped off (five plants/pot); 10, four plants damped off; 9, three plants damped off; 8, two plants damped off; 7, one plant damped off; 6, all plants had stem- or root-girdling lesions >1.5 cm but none damped off; 5, four plants had lesions as in 6; 4, three plants had lesions as in 6; 3, two plants had lesions as in 6; 2, one plant had lesions as in 6; 1, all or some plants had lesions greater than 1 mm but less than 1.5 cm; 0, no lesions on the plants or lesions less than 1 mm. This coding system was used to rank the virulence of the isolates, but the values were not necessarily considered to be an accurate numerical quantitation of disease.

Pedigree of Nectria haematococca MP VI tester isolates.—*Nectria haematococca* MP VI is heterothallic, compatibility being controlled by a pair of factors designated as mating type + or − (14, 18). Independent of mating type, isolates can serve as unisex males (M), unisex females (F), or as hermaphrodites (MF). The tester isolates employed in this study were obtained from a cross of isolate M-37, a colonial phenotype mutant (26), and isolate T-7 (Table 1). Approximately 1 mo after mating, one white perithecium developed on a plate containing about 400 red perithecia. One hundred and two ascospore isolates were collected from the white perithecium and evaluated for growth habit, sex, mating type, perithecium color, and fertility. Two of the ascospore isolates, 6-36 (MF+) and 6-94 (MF−), which were highly interfertile, had the wild-type growth habit, and carried the white perithecial marker, were selected as tester isolates for use in determining the mating characteristics of the field isolates of *F. solani*.

Since all field isolates of MP VI identified previously produce red perithecia, and since perithecium color is determined by the female parent, the color of the perithecia produced in crosses between the tester isolates and the field isolates was used as an aid in determining the sex of the field isolates, as has been done previously with members of MP I (21). The standard means of determining sex by noting the time of perithecium production in reciprocal crosses also was used.

RESULTS

Identification of additional members of Nectria haematococca MP VI—One hundred and fifty-two isolates of *F. solani* were evaluated for ability to cross with isolates 6-36 and 6-94. Forty-four of these isolates produced a fertile cross with one of the tester isolates (Table 1). Three of these (T-4, T-6, T-7) which were obtained from diseased mulberry and were supplied by T. Matuo, have been shown previously to be members of the *N. haematococca* MP VI (14). Fertile crosses also were obtained with 21 isolates obtained from diseased pea and with at least two isolates obtained from the diseased portion of each of the following plants: chickpea (*Cicer arietinum* L.), potato (*Solanum tuberosum* L.), tuliptree (*Liriodendron tulipifera* L.), alfalfa (*Medicago sativa* L.), cottonwood (*Populus deltoides* Marsh.), and sainfoin (*Onobrychis viciifolia*). In addition, one isolate (T-34) collected as a saprophyte was identified as a member of MP VI. Ten other isolates from pea that did not result in fertile crosses either produced sterile perithecia (red) or induced sterile perithecia (white) in one of the tester isolates. Almost all of the remaining isolates of *F. solani* did not induce or support perithecium production. Some of these isolates were obtained from the same sources as those listed above, but most were isolated from diseased portions of a variety of other plant species. This latter group included nine isolates of *F. solani* f. sp. *phaseoli*, 13 isolates of *N. haematococca* MP I, and two isolates each of *N. haematococca* MP V and MP VII.

Pathogenicity on pea.—All the isolates of MP VI that were tested in at least three different experiments for their pathogenicity on peas are listed in order of their virulence in Table 1. In two of the tests the pea cultivar Progress No. 9 (Agway Inc., Syracuse, NY 13201) was used, and in one test the cultivar Alaskan 2B (Asgrow Seed Co., Kalamazoo, MI 49903) was used as host. No noticeable difference in the disease ranking on the two cultivars was observed, and the values reported are the averages obtained from the ratings on both cultivars. Significant differences ($P = 0.05$) among means were determined with Duncan's multiple range test.

In general, the isolates most virulent on pea had been isolated originally from pea but some of the isolates from habitats other than pea (T-126, T-36, T-33, T-6) were as virulent as or more virulent than many of the isolates obtained from pea. Many of the less virulent isolates caused distinct lesions on pea, but because of low levels of disease development in some of the noninoculated controls, it is not known whether the isolates with the

TABLE 1. Source, mating type, sex, and virulence on peas of *Fusarium solani* isolates identified as members of *Nectria haematococca* mating population VI

Isolate code no.	Isolate source: Investigator[v]	Geographic location	Habitat[x]	Sex and mating type[y]	Virulence on peas[z]
T-63	G. E. Harman	NY	Pea	M+	10.8 ± .4 a
T-57	G. E. Harman	NY	Pea	M+	10.7 ± .5 ab
T-55	G. E. Harman	NY	Pea	M+	10.7 ± .5 ab
T-30	J. M. Kraft (RR5)	WA	Pea	M+	10.5 ± .5 ab
T-8	Plant Pathol. Culture Coll., Cornell Univ.		Pea	M+	9.3 ± 2.6 abc
T-126	D. Mathre (5-1)	MT	Sainfoin	M+	8.0 ± 2.3 abcd
T-60A	G. E. Harman	NY	Pea	M+	7.5 ± 3.9 bcde
T-60B	G. E. Harman	NY	Pea	M+	7.2 ± 2.9 cdef
T-54	G. E. Harman	NY	Pea	M+	7.2 ± 2.5 cdef
T-36	FRC[w] (S-131) originally from T. Matuo	Japan	Potato	MF−	7.2 ± 2.2 cdef
T-33	FRC[w] (S-219)	Canada	Cottonwood	MF+	6.8 ± 1.3 cdef
T-6	T. Matuo (SUF II-2)	Japan	Mulberry	MF−	6.7 ± .8 cdef
6-36	See Text			MF+	6.5 ± 3.5 cdef
T-56	G. E. Harman	NY	Pea	M−	6.5 ± 2.6 cdef
T-2	Author	NY	Pea	M−	6.2 ± 3.4 cdef
T-16	Author	NY	Pea	M−	5.6 ± 2.9 defg
T-7	T. Matuo (SUF II-7)	Japan	Mulberry	MF+	5.0 ± 1.7 defgh
T-95	W. Witcher (5)	SC	Tuliptree	MF−	4.7 ± 3.6 efgh
T-27	F. V. Westerlund (507-3 830)	CA	Chickpea	M+	4.5 ± 4.0 efgh
T-3	Author	NY	Pea	M−	4.5 ± 2.6 efgh
T-127	D. Mathre (6-1)	MT	Sainfoin	M+	4.0 ± 2.0 fghi
T-37	FRC[w] (S-60)			MF+	4.0 ± 2.5 fghi
T-29	F. V. Westerlund (507-11 830)	CA	Chickpea	M+	3.8 ± 4.8 fghij
6-94	See text			MF−	3.6 ± 2.9 fghij
T-69	W. Witcher (4)	SC	Tuliptree	M+	2.9 ± 3.8 ghij
T-86	FRC[w] (S-473)		Potato	M−	2.4 ± 3.9 hij
T-31	FRC[w] (S-146) originally from T. Matuo	Japan	Mulberry	MF+	2.3 ± 1.7 hij
T-61	G. E. Harman	NY	Pea	MF−	2.2 ± 2.7 hij
T-53	G. E. Harman	NY	Pea	M−	1.9 ± 2.8 hij
T-32	FRC[w] (S-147) originally from T. Matuo	Japan	Mulberry	M−	1.6 ± 2.4 hij
T-34	FRC[w] (S-190)	Australia	Cooling tower slats	M−	1.5 ± 2.3 ij
T-78	K. T. Leath (918)	PA	Alfalfa	M−	1.4 ± 2.3 ij
T-14	FRC[w] (S-116)		Pea	M−	1.3 ± 1.0 ij
T-76	K. T. Leath (810)	CT	Alfalfa	MF+	1.3 ± 1.1 ij
T-111	W. B. Smyly	IL	Cottonwood	M+	1.0 ± 1.1 ij
T-110	W. B. Smyly	LA	Cottonwood	M+	.8 ± 1.0 ij
T-77	K. T. Leath (906)	PA	Alfalfa	M−	.8 ± .9 j
T-81	FRC[w] (S-174)		Tuliptree	M−	.7 ± .8 j
T-1	Author	NY	Pea	M+	
T-4	T. Matuo (SUF I-9)	Japan	Mulberry	M−	
T-9	Author	NY	Pea	M−	
T-10	Author	NY	Pea	M−	
T-12	Author	NY	Pea	M+	
T-17	Author	NY	Pea	M+	
T-18	Author	NY	Pea	M−	
T-25	Author	NY	Chickpea	M+	

[v]Isolate number used by the investigator that supplied the isolate is given in parentheses.

[w]Abbreviation: FRC = Fusarium Research Center.

[x]Isolates other than T-34, 6-36, and 6-94 were collected from diseased portions of these plants.

[y]Mating type is designated by + or −; M means the isolate functioned as a male, F means the isolate functioned as a female, and MF means the isolate functioned as a hermaphrodite when crossed with 6-36 or 6-94.

[z]Virulence was rated on a 0 to 11 scale, with 11 being the most virulent rating. The means and standard deviations of the virulence ratings of isolates in which at least three virulence tests were run are given. The controls for these experiments had a rating of 1.5 ± 2.1 ij. Means followed by the same letter are not significantly different ($P = 0.05$).

lowest rankings actually were capable of causing disease on pea.

Pathogenicity towards other plant species.—Pathogenicity by MP VI on other hosts was tested to determine if there is pathogenic specialization associated with this MP. All of the isolates listed in Table 1 were tested one time for pathogenicity on common bean, *Phaseolus vulgaris* L. Top Crop (Herbst Brothers Seedmen Inc., Brewster, NY 10509). None of the isolates caused lesions characteristic of those caused by the isolates of *F. solani* f. sp. *phaseoli* used as controls; however, 27 of the isolates produced a hypersensitive type lesion (a lesion < 1 mm) on at least one of the plants 4 wk after inoculation. Several of the isolates obtained from chickpea (T-27, T-29) or sainfoin (T-126, T-127) were pathogenic on the plants from which they were obtained, as previously reported (3, 27). Four isolates (T-7, T-8, T-16, T-33) of *N. haematococca* MP VI were tested for pathogenicity on onion (*Allium cepa* L.), safflower (*Carthamus tinctorius* L.), sweetpea (*Lathyrus odoratus* L.), pepper (*Capsicum frutescens* L.), corn (*Zea mays* L.), cowpea [*Vigna sinensis* (Torner) Savi], mungbean (*Phaseolus aureus* Roxb.), tepary bean (*P. acutifolius* var. *latifolius* Freeman), adzuki bean [*P. angularis* (Wild.) W. F. Wright], urd (*P. mungo* L.), and *Macrostilium atropurpureum*. No disease symptoms were present on any of these plants 4 wk after inoculation.

Interfertility of isolates of Nectria haematococca MP VI.—To demonstrate that the members of MP VI obtained from different types of habitats were an interfertile group, an inheritable morphological trait was passed sequentially from parent to progeny in a selected number of the isolates. Morphological mutants of MP VI with a "spider"(s) type growth habit on Nm medium had been obtained in a previous study (26). Isolates with this growth characteristic can function only as males in a cross (H. D. VanEtten, *unpublished*) and therefore only T-isolates that could function as females were selected for crosses. After each cross, 50-60 ascospores were collected. One ascospore isolate with the spider-type growth characteristic and proper mating type was selected to serve as the male parent in a subsequent cross with another T isolate. Using this procedure and starting with a spider mutant (M-40$^-$), the spider-type growth characteristic was passed through selected T isolates in the following manner: M-40 × T-7 → 4-57(s)+, 4-57 × T-95 → 11-18(s)-, 11-18 × T-76 → spider and wild type progeny. In all cases the spider characteristic was inherited in about a 1:1 ratio, confirming earlier observations (26).

DISCUSSION

Both mating types occur in approximately equal frequency within this sampling of *N. haematococca* MP VI (24+ and 20−, Table 1). Most of the isolates functioned as unisexual males but some were hermaphroditic. None of the isolates behaved as unisexual females (Table 1), although others (14, 18) have identified unisexual females in this MP. Hermaphroditic isolates (T-61, T-76, T-95) of both mating types were found in the group of isolates collected from habitats in the United States. The presence of sexually compatible isolates in the United States and the ease with which the perfect stage can be produced in the laboratory suggest that the perfect stage probably occurs naturally in this country, even though there have not been any reported occurrences. The perfect stage has been found on diseased mulberry in Japan (14). Whether the sexual cycle is important for natural genetic variation is unknown.

Isolates of *N. haematococca* MP VI that can cause disease of pea occur in a variety of habitats and the host range for this MP is broad. Previous studies (3, 12, 14, 27) and the results of this study demonstrate that members of this MP are pathogenic on mulberry, chickpea, ginseng, and sainfoin in addition to pea. One of the isolates collected from tuliptree (T-95) also was pathogenic on that host (W. Witcher, *personal communication*), and other studies (2, 9) have demonstrated that *F. solani* is pathogenic on tuliptree. Whether the particular isolates of MP VI collected from alfalfa and cottonwood are pathogenic on these hosts was not tested but *F. solani* has been reported to be a pathogen on both of these hosts (8, 13). Sukurai and Matuo (19, 20) have reported that *N. haematococca* MP VI (syn. *F. solani* f. sp. *radicicola* race 2) will rot potato tubers. One of the potato isolates (T-36) used in our studies originally came from their collection (Table 1) but we were unable to produce a dry rot in potato tuber with this isolate or with several other isolates of MP VI (T-7, T-8, T-16, T-33) (H. D. VanEtten, *unpublished*). In addition, four isolates of *F. solani* var. 'coeruleum' obtained from G. J. Jellis and reported to cause a dry rot of potato (11) were among the group of isolates which did not result in any perithecia when crossed with our tester isolates of MP VI. Whether or not isolates of *N. haematococca* MP VI can cause the typical dry rot disease of potato needs confirmation.

Although the host range for *N. haematococca* MP VI is broad, pathogenic specialization is associated with the MP and with individual members in the MP. None of the 46 isolates of *F. solani* identified as members of *N. haematococca* MP VI produced root and hypocotyl rot of *P. vulgaris*. In addition, four members of this MP (T-7, T-8, T-16, T-33) lacked pathogenicity under our test conditions on a number of plant species. Since all but three of the 35 isolates originating from pea resulted in fertile or sterile perithecia when crossed with 6-36 or 6-94, pathogenicity on pea may be associated only with members of MP VI. However, other members of this MP are nonpathogenic or weakly virulent on pea (Table 1) (14) while still being pathogenic on other hosts (14).

The fact that not all members of MP VI are pathogenic on pea questions the tendency (15) of equating MP with formae speciales. Since the Code of Botanical Nomenclature does not govern the usage of the forma specialis taxon, there is no recognized authority that establishes the properties or characters an isolate must meet before it can be assigned a forma specialis designation (10). However, pathogenicity on the host from which the forma specialis name was derived would appear to be a prerequisite. Traditionally the forma specialis classification concerns pathogenicity characteristics and not sexual compatibility properties (10). It seems inappropriate to assign an isolate that is nonpathogenic on pea the forma specialis designation *pisi* just because it belongs to the same MP as the pea pathogen.

Attempts to cross our tester isolates of MP VI with a

limited number of members of MP I, V, and VII of *N. haematococca* were not successful. This agrees with previous observations (15, 20) that the different MP are not interfertile. Sexual incompatibility between the different MP implies that they are different species in the biological sense. Apparently morphological differences between the MP are not detectable or are so slight that morphological characters cannot practically serve to delineate them (15, 20) and it may be meritorious to continue usage of the same species name for the different MP. To classify the heterothallic forms of this organism at the subspecies level, a mating population designation may be more appropriate and meaningful than designating formae speciales. Matuo and Snyder (15) have listed the seven known MP of *N. haematococca* and assigned Roman numerals to them according to the chronology of their discovery. Their designation is an appropriate starting point for cataloging the MP of *N. haematococca.*

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