

Mating Populations in *Gibberella fujikuroi* (*Fusarium* Section *Liseola*)

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Supported in part by the Kansas Agricultural Experiment Station and by grants from the Kansas State Board of Agriculture (Kansas Corn Commission and Kansas Grain Sorghum Commission), and by the International Sorghum/Millet Collaborative Research Support Program (INTSORMIL) AID/DAN-1254-G-00-0021-00 from the Agency for International Development, Washington, DC.

Contribution 91-221-J from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan.

Accepted for publication 8 February 1991 (submitted for electronic processing).

Fungal isolates belonging to *Fusarium* section *Liseola* are distributed worldwide on a variety of economically important plants including rice (36), maize (20), sorghum (20), mango (38), pine (4), pineapple (33), and sugarcane (23). Additionally, some strains produce significant quantities of secondary metabolites, such as gibberellic acids (30), and mycotoxins, such as moniliformin (22), fusarin C (39), fusaric acid (22), and fumonisins (7). Macroconidial morphology, the most commonly used trait in distinguishing species of *Fusarium*, is not useful for distinguishing the species within the *Liseola* section from one another (24); consequently, some authorities (e.g., 35) have recognized only a single species, usually *F. moniliforme* Sheldon, within this section. More recently, such characteristics as the presence or absence of polyphialides and/or napiforme microconidia, and microconidia in long chains, short chains, or false heads have been used to distinguish the species within this section. Some of these characteristics are sensitive to strain variability and to environmental culture conditions. Using these characteristics, Nelson et al (24) could distinguish four species within this section: *F. anthophilum* (A. Braun) Wollenw., *F. moniliforme*, *F. proliferatum* (Matsushima) Nirenberg, and *F. subglutinans* (Wollenw & Reinking) Nelson, Toussoun & Marasas. Similarly, Nirenberg (25) recognized six species: *F. anthophilum*, *F. fujikuroi* Nirenberg, *F. proliferatum*, *F. sacchari* (Butler) Gams, *F. succisae* (Schröter) Sacc., and *F. verticillioides* (Sacc.) Nirenberg, although these species do not necessarily correspond with those recognized by Nelson et al (24). These differences in nomenclature often have made it difficult for scientists who lack an intense interest in the taxonomy of this group to correctly name strains that are known to be important plant pathogens or to produce economically important secondary metabolites, and have led to significant confusion within the scientific literature.

One possible way around these difficulties is to use the sexual stage to distinguish species. These distinctions usually are based on mating tests and may give rise to either taxonomic or biologic

species, such as those found in *Armillaria* (37) or *Neurospora* (27-29). Whenever techniques similar to this one are used on a large scale, it is important to develop highly fertile tester strains to minimize the number and difficulties associated with strains that do not cross with any of the standard strains. Mating tests are also sensitive to environmental conditions and to naturally occurring mutations that may affect such traits as the number of spores per ascus (12,34), perithecial initiation and pigmentation (1,3), and meiosis and ascus maturation (21).

In *Fusarium* section *Liseola*, Hsieh et al (10) identified three different mating populations termed A, B, and C from corn, sugarcane, and rice, respectively. Crosses were made on many different media, but perithecia were most abundant on V8 juice agar; on Sach's agar + rice straw; and on potato-dextrose agar (PDA) + dried banana leaves, carrot leaves, or rice straw. The number of perithecia produced per cross varied significantly. Within each population, mating was heterothallic and under the control of a single locus with two alleles. Isolation of the mating populations is prezygotic (i.e., sexual diploid zygotes are not formed), and crosses between strains from different mating populations are usually no more fertile than if water alone is used to fertilize the female parent. DuTeau and Leslie (*unpublished*) found no hybridization between the A and a alleles of *N. crassa* Shear & Dodge (8) and any of the standard testers of *Gibberella fujikuroi* (Sawada) Ito in Ito & K. Kimura, even under very low stringency conditions (42 C and 30% formamide). Two preliminary reports of homothallic and heterothallic mating behavior in *F. subglutinans* have been made, but have not been confirmed (18,24). These reports are consistent with mating type switching similar to that reported in *Saccharomyces cerevisiae* Hansen (9) and some other filamentous fungi (26).

Kuhlman (16) extended the work of Hsieh et al (10) to additional strains and, along with Kathariou (11), identified a fourth mating population termed D. Kuhlman (16) assigned each mating population a name as a variety of *G. fujikuroi*: A—var. *moniliformis*, B—var. *subglutinans*, C—var. *fujikuroi*, and D—var. *intermedia*. He could not distinguish these groups as distinct species on morphological grounds because there was too much

overlap between them in the characters that he was using. He provided pairs of testers for each population that produced fertile perithecia in crosses on V8 juice agar or PDA, with or without wheat straw, when one member of the pair was used as the male parent and the other as the female parent. Reciprocal crosses in which the sexual roles were reversed were usually poorly fertile at best and were often sterile. One of Kuhlman's testers for the A group, strain 175, was shown by Correll et al (3) to carry the *hsi1* gene, which results in female sterility and heterokaryon self-incompatibility. These problems with sexual fertility have led to confusion of sexuality with mating type and have made it difficult to screen populations via mating tests.

Since Kuhlman's work, additional studies have shown that the A and D populations can be differentiated on the basis of isozyme analyses (11) and DNA-DNA thermal renaturation experiments (5,6), and mutants have been induced for genetic mapping studies (13,15,31,32) and studies of vegetative compatibility groups (VCGs). Additionally, the field populations described by Leslie et al (20) have been crossed in mating tests with standard testers, and representatives of all four of the known mating populations have been found in the United States (2,17). Also from this work, two additional mating populations, E and F, have been identified but have not yet been formally described (14; Leslie, unpublished).

Depending on the sample, 10–25% of the isolates will not cross with standard testers in mating type tests, and, based on preliminary data, I think it is likely that additional mating populations will be identified. In my laboratory, we have found that carrot agar (13) is usually more effective for making crosses and obtaining large numbers of fertile perithecia than V8 juice agar or carnation leaf agar (24). We also have found that light following fertilization is essential for development of fertile perithecia (13), and that crosses on plates that are sealed with Parafilm or an aqueous condensate are much less fertile than crosses on plates that are not sealed.

With the discovery of additional mating populations have come further taxonomic problems. As a result of Kuhlman's work, at least three different anamorphic species according to Nelson et al (24)—*F. moniliforme*, *F. subglutinans*, and *F. proliferatum*—have the same teleomorph. The E and F populations further complicate this situation because members of both the A and the F populations are *F. moniliforme*, and members of both the B and E populations are *F. subglutinans*. I have crossed standard mating type tester strains with reference cultures obtained from Paul Nelson at Pennsylvania State University, and the results are summarized in Table 1. These results suggest that further work with these fungi is needed to correlate the taxonomic species

TABLE 1. Distribution of strains of *Fusarium* section *Liseola* into different mating populations of *Gibberella fujikuroi*

Strain number ^a	MP MT ^b	Female fertility ^c	Host	Location	Source ^d (and number)	Other source ^d (and number)	Reference
FKMA0102	A ⁺	+	Sorghum	San Joaquin Co., CA	PTS-F80	PEN-M3120	3,11,12,13,15, 17,31,32
FKMA0149	A ⁻	+	Maize	Visalia, CA	PTS-F237	PEN-M3125	11,12,20
FKMA0999	A ⁺	+	Maize	Knightstown, IN	JFL	PEN-M3703	20
FKMA1811	A ⁻	-	PEN-M1068	...	5,17
FKMA2903	A ⁻	+	Maize	Red Spring, NC	JFL	PEN-M3729	1,20
FKMA3823	A ⁻	?	PEN-M1212	WG-12427	24
FKMA3824	A ⁻	?	PEN-M1213	WG-62264	5,24
FKMB0278	B ⁺	+	Sugarcane	Taiwan	PTS-F1251	PEN-M3127	18,19
FKMB0281	B ⁻	+	Sugarcane	Taiwan	PTS-F1254	PEN-M3128	18,19
FKMB3852	B ⁺	+	Progeny from 278 × 281	...	JFL	...	19
FKMB3853	B ⁻	+	Progeny from 278 × 281	...	JFL	...	19
FKMB3820	B ⁻	+	PEN-M942	WG-63342	24
FKMB3821	B ⁻	-	PEN-M943	WG-63448	24
FKMC0596	C ⁻	?	Maize	Cummings, KS	JFL	...	2
FKMC1100	C ⁻	?	Sorghum	Cherokee, KS	JFL	...	2
FKMC1993	C ⁺	+	Rice	...	PEN-M1148	EGK-FSL288	5,16
FKMC1994	C ⁺	+	Rice	...	PEN-M1149	EGK-FSL290	5,16
FKMC1995	C ⁻	-	Rice	...	PEN-M1150	EGK-FSL293	16
FKMC1996	C ⁻	-	Rice	...	PEN-M1151	EGK-FSL294	5,6,16
FKMD0875	D ⁺	+	Sorghum	Beloit, KS	JFL	PEN-M5128	2,19
FKMD1236	D ⁺	?	Sorghum	Holcomb, MS	JFL	PEN-M3838	20
FKMD2892	D ⁻	?	Maize	Carrol, OH	JFL	PEN-M3708	20
FKMD2945	D ⁻	+	Sorghum	Holcomb, MS	JFL	PEN-M3793	20
FKMD2959	D ⁻	-	Tobacco	Fork, SC	JFL	PEN-M3813	20
FKMD3822	D ⁺	?	PEN-M944	WG-10651	24
FKMD3827	D ⁻	?	PEN-M1216	WG-62261	24
FKME0507	E ⁻	-	Maize	Rossville, KS	JFL	PEN-M5119	2,19
FKME0731	E ⁺	-	Maize	Powhattan, KS	JFL	PEN-M5126	2,19
FKME0990	E ⁻	+	Maize	St. Elmo, IN	JFL	PEN-M3696	19,20
FKME2882	E ⁺	+	Maize	St. Elmo, IN	JFL	PEN-M3693	19,20
FKME3809	E ⁺	+	PEN-M845	WG-62275	24
FKME3812	E ⁻	?	PEN-M848	WG-63617	5,24
FKME3813	E ⁺	?	PEN-M849	WG-63619	24
FKME3815	E ⁺	-	PEN-M851	WG-63621	24
FKMF0728	F ⁺	-	Sorghum	Powhattan, KS	JFL	PEN-M5598	14,19
FKMF0966	F ⁻	-	Sorghum	Zeandale, KS	JFL	...	14,19
FKMF1096	F ⁺	-	Sorghum	Brazilton, KS	JFL	PEN-M5139	14,19
FKMF1377	F ⁺	+	Sorghum	WaKeeny, KS	JFL	PEN-M5555	14,19
FKMF1518	F ⁻	+	Progeny from 966 × 1377	...	JFL	...	14,19
FKMF1540	F ⁻	+	Progeny from 966 × 1377	...	JFL	...	14,19

^aStrain number in Kansas State University collection.

^bLetter (A–F) designates mating population (MP); +/– designates mating type (MT).

^c+ = Female fertile; – = female sterile; ? = female fertility unknown.

^dJFL = J. F. Leslie, Dept. of Plant Pathology, Kansas State University, Manhattan; EGK = E. G. Kuhlman, USDA Forest Service, Athens, GA; PEN = P. E. Nelson, Dept. of Plant Pathology, Pennsylvania State University, University Park; PTS = P. T. Spieth, Dept. of Genetics, University of California, Berkeley; WG = W. Gerlach, Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Mikrobiologie, Berlin, Germany.

and mating populations within this group. This correlation is important since different mating populations are found preferentially on different hosts (19), and since these differences may reflect important distinctions related to the pathogenic potential of these organisms.

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