Diversity in beauvericin and fusaproliferin production by different populations of *Gibberella fujikuroi* (*Fusarium* section *Liseola*)

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On the basis of the fertility, *G. fujikuroi* has been subdivided into at least six different, genetically distinct, mating populations, termed A – F. We tested members of these mating populations for their ability to produce two recently described toxins, beauvericin and fusaproliferin. Beauvericin was produced in large amounts by isolates belonging to the mating populations B, C, D, and E, whereas isolates of the A and F mating populations produced little, if any, of it. Fusaproliferin was produced by isolates from the D and E, but not by isolates from the A, B, C, and F mating populations. These results support the hypothesis that each mating population in the *Liseola* Section has a characteristic toxicological profile that could be used to differentiate the species of this section.

Keywords: taxonomy, toxin analysis, secondary metabolites.

The *Liseola* section of *Fusarium* encompasses some toxigenic species occurring worldwide on a large range of plants as causual agents of several diseases (Leslie & al., 1990; Elmer & Ferrandino, 1992; Sun & Snyder, 1981). *Fusarium moniliforme* Sheldon, *F. proliferatum* (Matsushima) Nirenberg, and *F. subglutinans* (Wollenw. & Reinking) Nelson, Toussoun & Marasas are the species most commonly described in this section (Nelson & al., 1983), all sharing the same teleomorphic state, *Gibberella fujikuroi* (Sawada) Ito in Ito & K. Kimura (Leslie, 1991). Distinguishing these species using classical morphological criteria is often difficult because the diagnostic characters are often subtle and hard to be seen, such as presence of monophialides and/or polyphialides, production of

microconidia in short chains, long chains or false heads (Nelson & al., 1983). Moreover, some of these features can vary among strains and be significantly influenced by environmental, cultural, and storage conditions.

A method to bypass these difficulties was proposed by Leslie (1991), who used the formation of the sexual stage to distinguish species in the *Liseola* section. In fact, in *Gibberella fujikuroi* six different mating populations, representing different biological species, have been recognized among strains that can be assigned by morphological identification to *F. moniliforme*, *F. proliferatum* and *F. subglutinans* (Hsieh & al., 1977; Klittich & Leslie, 1992; Kuhlmann, 1982; Leslie, 1991). In particular, strains of the A and F mating populations are identical with *F. moniliforme*, strains of the B and E populations correspond with *F. subglutinans*, and strains of the C and D populations can be identified as *F. proliferatum*. Some reports indicate that the different mating populations are isolated preferentially from different hosts (Kuhlmann, 1982; Leslie & al., 1992) and this could be related to their pathogenic potential (Leslie, 1991).

Another approach to differentiate species in *Fusarium* was proposed by Thrane (1989) using the determination of species specific secondary metabolite profiles. For instance, the reported occurrence of different chemotypes in *F. graminearum* which produce different groups of trichothecenes (Ichinoe & Kurata, 1983; Logrieco & al., 1990) was used as a criterion to indicate genetic diversity (Miller & al., 1991). Logrieco & al. (1992) observed a relationship beetween cultural features and toxigenicity in *F. acuminatum* and the correlation observed between molecular data and toxigenicity was used to recognize genetically distinct species within *F. camptoceras* (Logrieco & al., 1993a).

Species in the section *Liseola* have often been reported to produce high levels of several secondary metabolites, such as gibberellic acids (Vesonder, 1981; Marasas, 1984), fusaric acid (Marasas & al., 1984), moniliformin (Marasas & al., 1986), fusarin C (Wiebe & Bjeldanes, 1981), and fumonisins (Nelson & al., 1991; Nelson & al., 1993). Their ability to produce several secondary metabolites has led to the hypothesis that different species may produce different spectra of secondary metabolites (Marasas & al., 1984). Leslie & al. (1992) tested the relationship between mating populations and the ability to produce fumonisin B_1 (FB_1), a well known toxin that causes several animal diseases (Nelson & al., 1993) and is correlated with human esophageal cancer in South Africa (Rheeder & al., 1992). Leslie & al. (1992) found that FB_1 was produced at high levels by members of the A and D mating populations, whereas members of the B, E, and F populations produced low or no levels of the toxin. Moniliformin, which is toxic to experimental animals (Marasas & al., 1984) and has

phytotoxic properties (Cole & al., 1973), was generally reported not to be produced by members of the A mating population, whereas members of the C, D, E, and F mating populations produce high levels of this toxin (Marasas & al., 1986; Marasas, pers. comm.; Plattner & Nelson, 1994). Data on the ability of strains from the B mating populations to produce either toxin are sparse, but it appears that members of this population are able to produce moniliformin, but not FB_1 (Leslie & al., 1992). The known toxin productions and host preferences of the A–F mating populations are summarized in Tab. 1.

Tab. 1. – Relationship beetwen mating populations, preferential host, and toxin production in species of *Fusarium*, *Liseola* section[a].

Mating Population	Anamorph	Preferential Host	Fumonisins[c]	Moniliformin[d]	Beauvericin	Fusaproliferin
A	*F. moniliforme*	maize	[b] +	-	-	-
B	*F. subglutinans*	sugar cane	-	?	+	-
C	*F. proliferatum*	rice	-	+	+	-
D	*F. proliferatum*	various	+	+	+	+
E	*F. subglutinans*	maize	-	+	+	+
F	*F. moniliforme*	sorghum	-	+	-	-

[a] = all data on toxin production are from referenced strains.
[b] + = producing toxin; - = producing no or low level of toxin; ? = no data collected.
[c] = Leslie & al., 1992.
[d] = Marasas & al., 1986; Marasas, pers. comm.

Recently, two toxic metabolites, beauvericin (BEA) (Fig. 1) and a toxin, named fusaproliferin (FUS) (Fig. 2), were reported to be produced by strains in species of the section *Liseola* (Gupta & al., 1991; Moretti & al., 1994; Ritieni & al., 1995a).

Beauvericin is a well known cycloesadepsipeptide first reported to be produced by some entomopathogenic fungi such as *Beauveria bassiana* (Balsamo) Vuill. (Hamill & al., 1969) and *Paecilomyces fumosoroseus* (Wize) Brown & Smith (Bernardini & al., 1975). Beauvericin is highly toxic to insects (Vey & al., 1973; Grove & Pople, 1980; Gupta & al., 1991), and to murine and human cell lines (Ojcius & al., 1991; Macchia & al., 1995). Gupta & al. (1991) detected BEA in an entomopathogenic culture of *F. subglutinans*. More recently, BEA was shown to be produced by several isolates of *F. subglutinans* from maize (Logrieco & al., 1993b; Moretti & al., 1995a) and *F. proliferatum* (Moretti & al.,1994; Plattner & Nelson, 1994; Logrieco & al., 1995),

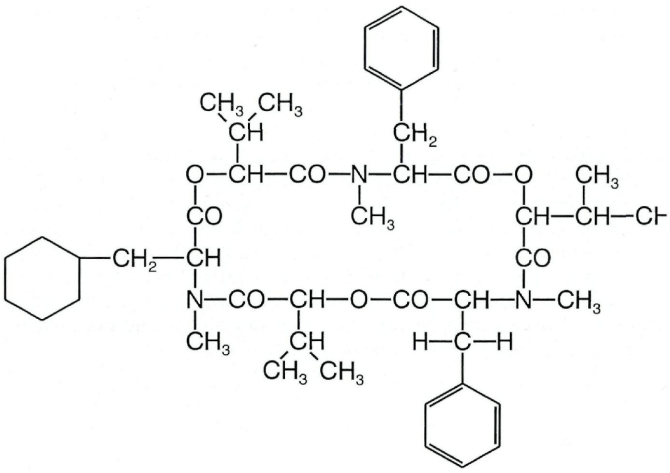

Fig. 1. – Chemical structure of beauvericin.

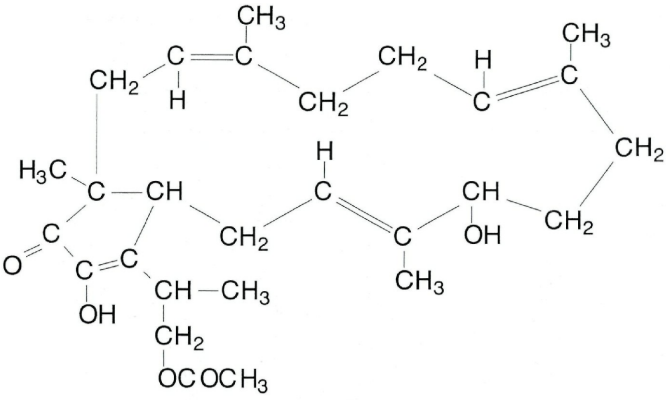

Fig. 2. – Chemical structure of fusaproliferin.

and found as a natural contaminant of maize (Logrieco & al., 1993c; Bottalico & al., 1995). Bottalico & al. (1995) also reported production of BEA by *F. moniliforme* at a very low level.

Fusaproliferin, a new sesterterpene toxic to *A. salina* L. larvae (Ritieni & al., 1995a) and a human B-lymphocyte cell line (A. Logrieco, unpublished), was first purified from cultures of a strain of *F. proliferatum*, isolated from maize ear rot in Northern Italy (Ritieni & al., 1995a). Fusaproliferin was also detected from several maize kernel culture isolates of *F. proliferatum* and *F. subglutinans* from maize (Moretti & al., 1995b), and was found as a natural contaminant of pre-harvest maize kernels (Ritieni & al., 1995b).

Beauvericin and fusaproliferin are extensively produced by some *Fusarium* species in the *Liseola* section and they both are found as natural contaminants of pre-harvest maize. Therefore we decided to investigate the relationship between mating populations and secondary metabolite production by isolates belonging to these biological species, and to use such relationship as another tool for evaluating diversity in the *Liseola* section of *Fusarium*.

Material and methods

Strains

Of the 103 strains examined in this report (Tab. 2), 43 were received from four other investigators. Forty-two were isolated from Italian maize plants showing ear and stalk rot, 6 were isolated from

Tab. 2. – Mating populations, Beauvericin (BEA) and Fusaproliferin (FUS) production by *Fusarium* strains[1].

M.P./ M.T.[2]	ITEM	Other No.	Host	Origin	BEA (µg/g)[1]	FUS (µg/g)[1]
A^+	231		Maize	Italy	ND	ND
A^+	487		Maize	Italy	ND	ND
A^+	504		Maize	Italy	ND	ND
A^-	1495		Maize	Italy	ND	ND
A^-	1497		Maize	Italy	ND	ND
A^+	1501		Maize	Italy	ND	ND
A^-	1502		Maize	Italy	ND	ND
A^+	1510		Maize	Italy	ND	ND
A^-	1511		Maize	Italy	ND	ND
A^-	1512		Maize	Italy	ND	ND
A^-	1744		Maize	Italy	ND	ND
A^+	1745		Maize	Italy	ND	ND
A^+	1746		Maize	Italy	5	ND
A^+	1747		Maize	Italy	5	ND
A^+	1755		Maize	Italy	5	ND
A^-	1757		Maize	Italy	ND	ND
A^-	1758		Maize	Italy	ND	ND
A^-	1759		Maize	Italy	ND	ND
A^-	1773		Maize	Italy	ND	ND

M.P./ M.T.[2]	ITEM	Other No.	Host	Origin	BEA (µg/g)[1]	FUS (µg/g)[1]
A⁻	1774		Maize	Italy	ND	ND
A⁺	1776		Maize	Italy	ND	ND
A⁻	1777		Maize	Italy	ND	ND
A⁻	1758		Maize	Italy	ND	ND
A⁻	1879		Maize	Italy	ND	ND
A⁻	1880		Maize	Italy	ND	ND
A⁻	1881		Maize	Italy	ND	ND
A⁻	1882		Maize	Italy	ND	ND
A⁺	1883		Maize	Italy	ND	ND
A⁻	1884		Maize	Italy	ND	ND
B⁻	1025	B281[4]	Sugar cane	Taiwan	ND	ND
B⁺	1026	B281[4]	Sugar cane	Taiwan	100	ND
C⁻	2146	C1993[4]	Rice	Taiwan	350	ND
C⁺	2147	C1995[4]	Rice	Taiwan	400	ND
?	1767		Rice	Italy	60	ND
?	1768		Rice	Italy	65	ND
?	1769		Rice	Italy	70	ND
?	1771		Rice	Italy	65	ND
?	1772		Rice	Italy	75	ND
D⁺	381		Maize	Italy	20	400
D⁻	382		Maize	Italy	ND	600
D⁻	385		Maize	Italy	5	300
D⁻	497		Maize	Italy	ND	100
D⁺	1269		Wheat	Italy	40	100
D⁻	1298		Wheat	Italy	60	100
D⁺	1300		Wheat	Italy	30	500
D⁻	1301		Wheat	Italy	60	500
D⁺	1313		Wheat	Italy	50	100
D⁺	1475		Asparagus	Italy	90	300
D⁺	1477		Asparagus	Italy	45	250
D⁺	1478		Asparagus	Italy	80	200
D⁺	1479		Asparagus	Italy	55	350
D⁺	1480		Asparagus	Italy	35	175
D⁻	1483		Asparagus	Italy	90	250
D⁺	1484		Asparagus	Italy	75	100
D⁻	1491		Asparagus	Italy	35	300
D⁻	1493		Maize	Italy	30	400
D⁺	1494		Maize	Italy	90	1500
D⁺	1503		Maize	Italy	45	200
D⁻	1493		Maize	Italy	30	400
D⁺	1494		Maize	Italy	90	1500
D⁺	1503		Maize	Italy	45	200
D⁺	1504		Maize	Italy	100	400
D⁻	1505		Maize	Italy	100	600
D⁺	1719		Maize	Italy	100	400
D⁻	1722		Maize	Italy	10	400
D⁺	1724		Maize	Italy	125	ND
D⁻	1725		Maize	Italy	150	500

M.P./ M.T.[2]	ITEM	Other No.	Host	Origin	BEA (µg/g)[1]	FUS (µg/g)[1]
D^-	1726		Maize	Italy	150	600
D^-	1727		Maize	Italy	125	850
D^+	1748		Maize	Italy	150	400
D^+	1749		Maize	Italy	125	800
D^+	1752		Maize	Italy	200	1000
D^-	1761		Maize	Italy	5	500
D^+	1764		Maize	Italy	ND	500
E^-	1029	E990[4]	Maize	USA	ND	1200
E^+	1030	E2192[4]	Maize	USA	ND	1500
E^-	1348	KF163[5]	Maize	Poland	ND	200
E^-	1349	KF195[5]	Maize	Poland	20	100
E^-	1350	KF532[5]	Maize	Poland	100	950
E^-	1351	KF506[5]	Maize	Poland	20	700
E^-	1352	KF201[5]	Maize	Poland	ND	80
E^-	1353	KF241[5]	Maize	Poland	ND	750
E^-	1406	KF242[5]	Maize	Poland	30	150
E^-	1423	KF198[5]	Maize	Poland	200	900
E^-	1428	KF231[5]	Maize	Poland	80	100
E^-	1434	KF534[5]	Maize	Poland	80	850
E^-	1435	KF198[5]	Maize	Poland	100	ND
E^-	1524	IMST86[6]	Maize	Austria	80	80
E^-	1525	RITZ86[6]	Maize	Austria	60	850
E^-	1526	RATT86[6]	Maize	Austria	80	80
E^-	1527	RATT86[6]	Maize	Austria	60	90
E^{-3}	1830	I1B012[7]	Maize	Argentina	ND	130
E^{-3}	1831	I1B014[7]	Maize	Argentina	ND	140
E^{-3}	1832	I1B0003[7]	Maize	Argentina	ND	110
E^{-3}	1833	I1B021[7]	Maize	Argentina	ND	115
E^{-3}	1834	I1B019[7]	Maize	Argentina	ND	120
E^{-3}	1835	I1B013[7]	Maize	Argentina	ND	120
E^{-3}	1837	I5B010[7]	Maize	Argentina	ND	110
F^-	809		Sorghum	Italy	ND	ND
F^-	810		Sorghum	Italy	ND	ND
F^{-+}	811		Sorghum	Italy	ND	ND
F^+	812		Sorghum	Italy	ND	ND
F^-	813		Sorghum	Italy	ND	ND
F^-	814		Sorghum	Italy	ND	ND
F^-	815		Sorghum	Italy	ND	ND
F^-	867		Sorghum	Italy	ND	ND
F^-	869		Sorghum	Italy	ND	ND

[1] Strains were grown on autoclaved maize kernels for 4 weeks at 25 C.
[2] Determined by crossing each strain with standard mating tester strains (Leslie, 1991). M.P. = mating population; M.T. = mating type.
[3] Determined by S. Chulze, Universidad Nacional de Rio Cuarto, Argentina.
[4] = obtained from J. F. Leslie, Kansas State University, Manhatthan, USA.
[5] = obtained from J. Chełkowsky, Institute of Plant Genetics, Polish Academic of sciences, Poznan, Poland.
[6] = obtained from A. Adler, Federal Institute of Agrobiology, Linz, Austria.
[7] = obtained from S. Chulze.

Italian maize-based feeds (Visconti & Doko, 1994), 9 were isolated from sorghum fodder crops showing stem rot in Southern Italy (Basilicata), 8 strains were isolated from diseased Italian asparagus, and 5 strains were isolated from wheat. Following an initial isolation on a modified parachloronitro-benzene medium (Nelson & al., 1983) selective for *Fusarium* species, all cultures were transferred to potato dextrose agar and carnation leaf agar (Nelson & al., 1983) for identification. Selected cultures were initiated from single conidia and stored at 4 C.

Mating tests

All tester strains of the six mating populations (from A to F) were received from J. F. Leslie. Crosses were carried out on Carrot agar (Klittich & Leslie, 1988). All strains in the present study were crossed as male parents to tester strains of all six A-F mating populations. All strains were crossed twice before assigning them to a mating population.

Chemical analyses

The beauvericin standard was purchased from Sigma Chemical Co. (St. Louis, USA). Beauvericin was identified and quantitated by means of high performance thin layer chromatography (HPTLC), and high performance liquid chromatography (HPLC), as described by Logrieco & al. (1993b), with a detection limit of 3 and 1 µg of toxin per g of maize sample, respectively.

The fusaproliferin standard was isolated from maize cultured by *F. proliferatum* ITEM 1494 (Ritieni & al., 1995a). Analysis of fusaproliferin were performed by HPTLC, using methods described by Ritieni & al. (1995a), with a sensitivity of 3 µg of toxin per g of samples.

Results

All fungal strains reported here as members of a mating population, when crossed with the 12 tester strains, were cross-fertile with only with one of them.

The production of BEA and FUS was investigated for 28 strains of the A mating population, 2 of B, 2 of C, 33 of D mating population, 24 of E, and 9 of F. An additional 5 strains of *F. proliferatum* with short conidial chains isolated from rice were also tested (Tab. 2). Usually, these isolates are cross-fertile with the C mating population,

but none of these strains produced fertile perithecia in such crosses. This could be a consequence of the relatively low female fertility of the C testers (Leslie, pers. comm.). We included these strains in this study because they represent an ecologically well-distinguished population.

Beauvericin was produced by strains belonging to 5 of 6 mating populations (F being the exception), but the level of production varied widely. On the other hands, FUS was produced at high levels only by isolates belonging to the D or E mating populations.

Of the 28 strains of mating population A and the 9 strains of mating population F, only 3 strains of the A mating population produced BEA, and then at a very low level (5 µg/g) (Tab. 2). Thus, the level of BEA production is not a good character to distinguish these two populations.

We tested only 2 B strains, and one of them produced a high level of BEA (100 µg/g), whereas the other did not. These data suggest only that both producing and non producing strains are found in this mating population. The B strains we examined are the standard tester strains for this mating population, therefore it could be possible to obtain more information on both their ability to produce BEA and the genetic control of this biosynthetic pathway by analyzing the progeny of a cross between these strains.

The two strains of mating population C tested produced from 350 to 400 µg/g of BEA, and all 5 strains of *F. proliferatum* with short chains also produced from 60 to 70 µg/g BEA. None of these 7 strains produced FUS. Such similarity in toxicological profile between the two groups may indicate that they are closely related even if genetic cross/fertility was not observed.

Among the 33 D mating population strains analyzed, 30 produced some BEA and 27 produced at least 20 µg/g BEA (Tab. 3). These strains were derived from different hosts (asparagus, maize and wheat), but no consistent host-related difference was observed in BEA production, although the strains from maize were, on the average, the best producers.

Twelve of the 24 strains belonging to the E mating population produced BEA in amounts ranging from 20 to 200 µg/g (Tab. 3). This indicates that the BEA *in vitro* production of E mating population members can be variable and influenced by the origin of strains, but additional data are required before any firm conclusion can be made.

Fusaproliferin was produced by most (32/33) strains in the D and 23/24 from the E mating population at levels up to 1,500 µg/g (Tab. 3). None of the isolates of the A, B, C, or F, mating populations produced this toxin (Tab. 2 and Tab. 3).

Tab. 3. – Production of beauvericin and fusaproliferin by mating populations of *Fusarium* species, *Liseola* section.

Mating population	Host	BEA-producing strains / tot. no of strains	BEA Range (µg/g)	FUS-producing strains /tot. no of strains	FUS Range (µg/g)
A	maize	3/28	5	0/28	-
B	sugar cane	1/2	100	0/2	-
C	rice	2/2	350-400	0/2	-
D	asparagus, maize, wheat	30/33	5-200	32/33	100-1500
E	maize	12/24	20-200	23/24	90-1500
F	sorghum	0/9	-	0/9	-

Discussion

Data on BEA and FUS production confirm that there is a significant difference between mating populations with respect to secondary metabolism, as suggested by Leslie & al. (1992). Beauvericin appears to be commonly produced by members of the C, D, and E mating populations, although the production by members of the E population was highly variable. We examined only two members of the C group, but Plattner & Nelson (1994) reported BEA production by a strain designated as a C strain, although fertility data were not presented. They also found that 7 out of 14 *F. proliferatum* strains from rice produced BEA, which is consistent with our observation that BEA was produced by the 5 strains of *F. proliferatum* with short chains that were derived from rice. Thus, it is likely that most members of the C mating population are able of synthesizing significant amounts of BEA. We have, however, not enough data about the B mating population to draw any general conclusions. With respect to the A and F mating populations, it appears that their members synthesize BEA poorly, if at all.

In contrast, fusaproliferin production is useful to distinguish mating populations, since only members of D and E can synthesize this toxin.

Leslie & al. (1992) suggested that fumonisin production could provide a starting point for chemotaxonomy in *Liseola* section. We believe that the differences reported here in the ability to produce FUS and BEA of mating populations support the use of chemotaxonomy in this Section. The differences in toxicological profile could reflect important differences in pathogenicity, natural history and ecology of mating populations. In this respect, the difference between A and D mating populations is of interest. Both mating populations are closely related morphologically (Nelson & al., 1983) and genetically (Ellis, 1988; Peterson & Logrieco, 1991; Xu &

al., 1995), and often are isolated from the same plant host and ecological niche at same time (Leslie & al., 1990; Logrieco & al., 1995), yet they differ significantly in the spectrum of mycotoxins produced.

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