APPLIED AND ENVIRONMENTAL MICROBIOLOGY, May 2002, p. 2101–2105 Vol. 68, No. 5
0099-2240/02/$04.00+0 DOI: 10.1128/AEM.68.5.2101–2105.2002

Production of Fumonisin Analogs by *Fusarium* Species

John P. Rheeder,* Walter F. O. Marasas, and Hester F. Vismer

PROMEC Unit, Medical Research Council, 7505 Tygerberg, South Africa

The fumonisins, a family of food-borne carcinogenic mycotoxins, were first isolated in 1988 (21) from cultures of *Fusarium verticillioides* (Sacc.) Nirenberg (previously known as *Fusarium moniliforme* Sheldon). During the same year, the structures of the fumonisins were elucidated (6) and fumonisin B_1 was shown to cause equine leukoencephalomalacia (34). There have been numerous publications dealing with this group of novel, carcinogenic mycotoxins, and comprehensive reviews of different aspects of the fumonisins are available (20, 22, 23, 24, 35, 36, 37, 41, 43, 46, 52, 55, 60, 61, 66). Due to the widespread occurrence of the fumonisins in maize, a dietary staple in many countries, the carcinogenic risk of fumonisins to humans was evaluated by the International Agency for Research on Cancer in 1993, and the toxins produced by *F. moniliforme* were evaluated as "Group 2B carcinogens," i.e., probably carcinogenic to humans (24). This review focuses on the *Fusarium* species that produce fumonisins and the fumonisin analogs produced by each of these species.

FUMONISIN ANALOGS

The 28 fumonisin analogs that have been characterized since 1988 can be separated into four main groups, identified as the fumonisin A, B, C, and P series (Fig. 1 and Table 1). The fumonisin B (FB) analogs, comprising toxicologically important FB_1, FB_2, and FB_3, are the most abundant naturally occurring fumonisins, with FB_1 predominating and usually being found at the highest levels (36). FB_1 typically accounts for 70 to 80% of the total fumonisins produced, while FB_2 usually makes up 15 to 25% and FB_3 usually makes up from 3 to 8% when cultured on corn or rice or in liquid medium (7, 39, 40). Apart from the FB series, some of the other analogs may occur in naturally contaminated maize at relatively low levels (<5% of the total fumonisins present) (48). These lesser-known fumonisin analogs are not detected with most analytical techniques due to the derivatization process, but they can be detected with the use of liquid chromatography-mass spectrometry with electrospray ionization (49).

FUMONISIN PRODUCERS

Fifteen *Fusarium* species have been reported to produce fumonisins (Table 2). Eight of these are in the Section *Liseola*, i.e., *F. verticillioides*, mating population A (MP-A) in the *Gibberella fujikuroi* species complex (6, 8, 9, 10, 11, 14, 15, 17, 18, 21, 25, 28, 29, 30, 31, 32, 45, 46, 48, 49, 50, 57, 58, 62, 68, 70); *F. sacchari* (Butler) W. Gams MP-B (29); *F. fujikuroi* Nirenberg MP-C (16); *F. proliferatum* (Matsushima) Nirenberg MP-D (4, 10, 14, 16, 25, 29, 32, 47, 49, 51, 53, 62, 70, 72); *F. subglutinans* (Wollenw. et Reinking) Nelson, Toussoun, et Marasas MP-E (29); *F. subglutinans* sensu lato, isolated from teosinte seed, representing a potentially new biological species within the *G. fujikuroi* species complex (19); *F. thapsinum* Klittich, Leslie, Nelson, et Marasas MP-F (26, 30, 45); *F. anthophilum* (A. Braun) Wollenw. (12, 51); and *F. globosum* Rheeder, Marasas, et Nelson (69). Another five species fall within the proposed Section *Dlaminia* (27) (closely related to Section *Liseola*), i.e., *F. nygamai* Burgess et Trimboli MP-G (32, 48, 49, 51, 70); *F. dlamini* Marasas, Nelson, et Toussoun (51); and *F. napiforme* Marasas, Nelson, et Rabie (51). Trace amounts of fumonisin were detected in culture material of two newly described species, i.e., *F. andiyazi* Marasas, Rheeder, Lamprecht, Zeller, et Leslie; and *F. pseudonygamai* Nirenberg et O'Donnell (J. F. Leslie, unpublished data). The remaining two fumonisin-producing *Fusarium* species are one species in Section *Elegans*, i.e., *F. oxysporum* Schlecht. emend. Snyd. et Hans. (2, 64, 65) and one in Section *Arthrosporiella*, i.e., *F. polyphialidicum* Marasas, Nelson, Toussoun, et Van Wyk (1). Reports that certain strains of *F. oxysporum* var. *redolens* (2) and *F. polyphialidicum* (1) produce fumonisins need to be confirmed by taxonomic verification of the strains in question as well as by verification of the fumonisins produced.

The only fungus that does not belong to the genus *Fusarium* that has been reported to produce fumonisins (FB_1, FB_2, and FB_3) in culture is *Alternaria alternata* (Fr.) Keissler f. sp. *lycopersici* (3, 13, 44).

The relative production of FB_1, FB_2, and FB_3 by different *Fusarium* species is briefly summarized in Table 2. The most important producers of fumonisins are *F. verticillioides* and *F. proliferatum* because of their overall high levels of production, wide geographical distribution, frequent occurrence on maize, and association with known animal mycotoxicoses (62, 63). With the exception of *F. verticillioides* and *F. proliferatum*, less than 50% of isolates of other fumonisin-producing *Fusarium* species may produce fumonisins at various levels (51).

NON-FUMONISIN PRODUCERS

Several *Fusarium* species have been reported as non-fumonisin producers, but in most cases only a few isolates per species have been analyzed. These *Fusarium* species are *F. acuminatum* Ell. et Ev. (25, 70); *F. annulatum* Bugnicourt (51); *F. avenaceum* (Fr.) Sacc. (70); *F. beomiforme* Nelson, Toussoun, et Burgess (51); *F. camptoceras* (Wollenw. et Reinking) emend. Marasas et Logrieco (25, 70); *F. circinatum* Nirenberg et O'Donnell (= *F. subglutinans* f. sp. *pini*) MP-H (19); *F. compactum* (Wollenw.) Gordon (70); *F. concolor* Reinking (56); *F. crookwellense* Burgess, Nelson, et Toussoun (= *F.*

* Corresponding author. Mailing address: Medical Research Council, PROMEC Unit, P.O. Box 19070, 7505 Tygerberg, South Africa. Phone: 27-21-938-0299. Fax: 27-21-938-0260. E-mail address: john.rheeder@mrc.ac.za.

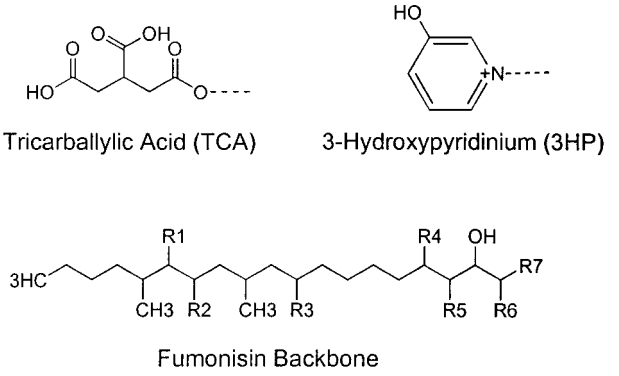

FIG. 1. Basic structure of fumonisin (see Table 1 for a list of known fumonisin analogs and the positions of R side chains).

cerealis [Cooke] Sacc.) (56); *F. culmorum* (W. G. Smith) Sacc. (56); *F. decemcellulare* Brick (70); *F. dimerum* Penzig (25); *F. equiseti* (Corda) Sacc. (25, 70); *F. graminearum* Schwabe (teleomorph: *G. zeae* [Schwabe] Petch) (56, 70); *F. lateritium* Nees (70); *F. longipes* Wollenw. et Reinking (70); *F. poae* (Peck) Wollenw. (70); *F. pseudograminearum* O'Donnell et Aoki (= *F. graminearum* Group 1) (56, 70); *F. reticulatum* Mont. (70); *F. sambucinum* Fuckel (56, 70); *F. scirpi* Lambotte et Fautr. (70); *F. semitectum* Berk. et Rav. (= *F. pallidoroseum* [Cooke] Sacc.) (25, 56, 70); *F. solani* (Mart.) Appel et Wollenw. emend. Snyder et Hansen (25, 70); *F. sporotrichioides* Sherb. (70); *F. succisae* (Schröter) Sacc. (51); and *F. tricinctum* (Corda) Sacc. (70).

FUMONISIN PRODUCTION BY *F. VERTICILLIOIDES*

Most isolates of *F. verticillioides* have the ability to produce fumonisins. Some of the highest FB_1 levels produced by this species have been reported with isolates from South Africa (17,900 mg kg^{-1}) (5), China (10,200 mg kg^{-1}) (72), and Argentina (8,160 mg kg^{-1}) (67). Although a few *F. verticillioides* isolates from Nepal (50) do not produce any fumonisin, other isolates from the same region have been reported to produce FB_1 at levels of up to 6,400 mg kg^{-1} (16, 50). Several isolates of this species from Southeast Asia (42) produce fumonisins at low levels, with a maximum of 147 mg kg^{-1}, whereas some isolates from Australia (50) produced only trace quantities of FB_1.

F. verticillioides strain MRC 826 (= FRC M-1325, accession number at the Fusarium Research Center, Pennsylvania State University, Pa.), which was isolated in 1975 from maize in an area of high incidence of human esophageal cancer in the Transkei region of the Eastern Cape Province, South Africa (33), and from which the fumonisins were first isolated and characterized (21), has been used to produce fumonisins in numerous studies all over the world. "It has been the most thoroughly studied strain of *F. moniliforme* and consequently much of our knowledge of *F. moniliforme* toxicity is attributable to experiments using MRC 826 as a model" (71).

TABLE 1. Fumonisin analogs

Analog	Side chains to fumonisin backbone[a]							Reference[b]
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	
FA_1	TCA	TCA	OH	OH	H	$NHCOCH_3$	CH_3	6
FA_2	TCA	TCA	H	OH	H	$NHCOCH_3$	CH_3	6
FA_3	TCA	TCA	OH	H	H	$NHCOCH_3$	CH_3	49
$PHFA_{3a}$	TCA	OH	OH	H	H	$NHCOCH_3$	CH_3	59
$PHFA_{3b}$	OH	TCA	OH	H	H	$NHCOCH_3$	CH_3	59
HFA_3	OH	OH	OH	H	H	$NHCOCH_3$	CH_3	59
FAK_1	=O	TCA	OH	OH	H	$NHCOCH_3$	CH_3	47
FBK_1	=O	TCA	OH	OH	H	NH_2	CH_3	49
FB_1	TCA	TCA	OH	OH	H	NH_2	CH_3	21
Iso-FB_1	TCA	TCA	OH	H	OH	NH_2	CH_3	31
$PHFB_{1a}$	TCA	OH	OH	OH	H	NH_2	CH_3	68
$PHFB_{1b}$	OH	TCA	OH	OH	H	NH_2	CH_3	68
HFB_1	OH	OH	OH	OH	H	NH_2	CH_3	59
FB_2	TCA	TCA	H	OH	H	NH_2	CH_3	21
FB_3	TCA	TCA	OH	H	H	NH_2	CH_3	11
FB_4	TCA	TCA	H	H	H	NH_2	CH_3	11
FB_5[c]								49
FC_1	TCA	TCA	OH	OH	H	NH_2	H	8
N-acetyl-FC_1	TCA	TCA	OH	OH	H	$NHCOCH_3$	H	65
Iso-FC_1	TCA	TCA	OH	H	OH	NH_2	H	65
N-acetyl-iso-FC_1	TCA	TCA	OH	H	OH	$NHCOCH_3$	H	65
OH-FC_1	TCA	TCA	OH	OH	OH	NH_2	H	64
N-acetyl-OH-FC_1	TCA	TCA	OH	OH	OH	$NHCOCH_3$	H	65
FC_3	TCA	TCA	OH	H	H	NH_2	H	64
FC_4	TCA	TCA	H	H	H	NH_2	H	58
FP_1	TCA	TCA	OH	OH	H	3HP	CH_3	48
FP_2	TCA	TCA	H	OH	H	3HP	CH_3	48
FP_3	TCA	TCA	OH	H	H	3HP	CH_3	48

[a] See Fig. 1 for the structure of the fumonisin backbone and the positions of the R side chains. TCA, tricarballylic acid.
[b] Cited references are the first publications dealing with the analogs in question.
[c] Hexahydroxyalkyl backbone; exact structure unknown at present.

TABLE 2. Fumonisin-producing *Fusarium* species, analogs produced, and the maximum yields of FB_1, FB_2, and FB_3 reported for each species

Fusarium sp.	Fumonisin analog(s)	Reference(s)[a]	Maximum fumonisin level (mg kg^{-1}) for:			Reference(s)[b]
			FB_1	FB_2	FB_3	
Section *Liseola*						
F. verticillioides MP-A	$FA_{1–3}$, $FB_{1–5}$, iso-FB_1, FAK_1, FBK_1, $FC_{1,4}$, $FP_{1–3}$, $PH_{1a–b}$	5, 6, 8, 9, 10, 11, 15, 17, 21, 25, 30, 31, 32, 45, 48, 49, 57, 58, 68, 70	17,900	3,000	2,300	5, 30, 70
F. sacchari MP-B	FB_1	29	21	NT[c]	NT	29
F. fujikuroi MP-C	FB_1	16	7	NT	NT	16
F. proliferatum MP-D	$FA_{1–3}$, $FB_{1–5}$, FAK_1, FBK_1, FC_1, $FP_{1–3}$, $PH_{1a–b}$	10, 14, 16, 25, 32, 47, 49, 51, 53, 62, 70	31,000	17,000	5,700	10, 53
F. subglutinans MP-E	FB_1	29	150	NT	NT	29
F. subglutinans MP-?[d]	FB_1	19	230	NT	NT	19
F. thapsinum MP-F	$FB_{1–3}$	26, 30, 45	30	5	5	30
F. anthophilum	$FB_{1–2}$	12, 51	610	35	NT	12, 51
F. globosum	$FB_{1–3}$	69	330	4	24	69
Section *Dlaminia*						
F. nygamai MP-G	$FA_{1–3}$, $FB_{1–5}$, FAK_1, FBK_1, FC_1, FP_1, PH_{1a-b}	32, 48, 49, 51, 70	7,200	530	140	51, 70
F. dlamini	FB_1	51	82	NT	NT	51
F. napiforme	FB_1	51	480	NT	NT	51
F. pseudonygamai	$FB_{1–2}$	31	Tr[e]	Tr	NT	31
F. andiyazi	FB_1	31	Tr	ND[f]	NT	31
Section *Elegans*						
F. oxysporum	$FC_{1,3–4}$, *N*-acetyl-FC_1, iso-FC_1, *N*-acetyl-iso-FC_1, OH-FC_1, *N*-acetyl-OH-FC_1	64, 65	NT	NT	NT	
F. oxysporum var. *redolens*	$FB_{1–3}$	2	300	6	0.9	2
Section *Arthrosporiella*						
F. polyphialidicum	FB_1	1	500	NT	NT	1

[a] References to the analogs produced by each *Fusarium* species.
[b] References to the maximum FB_1, FB_2, and FB_3 yields in culture. Where more than one reference is cited, the maximum levels for FB_1, FB_2, and FB_3 are summarized from multiple reports.
[c] NT, not tested.
[d] *F. subglutinans* senso lato. These strains were nonfertile with tester strains of mating populations B, E, and H within the *G. fujikuroi* species complex (19).
[e] Tr, trace amounts (1 to 4 ng g^{-1}) were detected.
[f] ND, not detected (<1 ng g^{-1}).

The highest yield of FB_1 (17,900 mg kg^{-1}) by *F. verticillioides* was obtained from whole maize kernels as culture material, with *F. verticillioides* MRC 826 as inoculum, incubated at 20°C in the dark for 13 weeks (5). The highest yield of FB_1 that has been reported for a *Fusarium* species was obtained with a maize isolate of *F. proliferatum* (no accession number given) from Spain cultured on whole maize (31,000 mg kg^{-1}) (10). This isolate also produced the highest published yield of FB_2 (17,000 mg kg^{-1}). *F. proliferatum* M-6284, cultured on whole yellow maize, produced the highest reported yield of FB_3 (5,700 mg kg^{-1}) (53).

CONCLUSION

Numerous studies have provided valuable data on the toxicology of purified fumonisins of the FB series, yet the search continues for other toxic fumonisin analogs which may also pose a health risk to humans and animals. Maize and maize-based products have been the main focus of fumonisin research due to the widespread contamination of this food source by relatively high levels of FB_1, FB_2, and FB_3. As additional and new *Fusarium* species with various fumonisin-producing capabilities are described from other agriculturally important crops, such as sorghum (38) and millet (54), it becomes necessary to determine whether fumonisins also occur in these crops and, if so, to determine which analogs occur and at what levels.

ACKNOWLEDGMENTS

We thank past and present staff members of the PROMEC Unit and our South African and international collaborators.

We thank the Medical Research Council of South Africa for their continued financial support.

REFERENCES

1. **Abbas, H. K., and C. M. Ocamb.** 1995. First report of production of fumonisin B_1 by *Fusarium polyphialicum* collected from seeds of *Pinus strobus.* Plant Dis. **79:**642.
2. **Abbas, H. K., C. M. Ocamb, W. Xie, C. J. Mirocha, and W. T. Shier.** 1995. First report of fumonisin B_1, B_2 and B_3 production by *Fusarium oxysporum* var. *redolens*. Plant Dis. **79:**968.
3. **Abbas, H. K., and R. T. Riley.** 1996. The presence and phytotoxicity of fumonisins and AAL-toxin in *Alternaria alternata*. Toxicon **34:**133–136.
4. **Abbas, H. K., R. D. Cartwright, W. Xie, C. J. Mirocha, J. L. Richard, T. J. Dvorak, G. L. Sciumbato, and W. T. Shier.** 1999. Mycotoxin production by *Fusarium proliferatum* isolates from rice with *Fusarium* sheath rot disease. Mycopathologia **147:**97–104.
5. **Alberts, J. F., W. C. A. Gelderblom, P. G. Thiel, W. F. O. Marasas, D. J. Van Schalkwyk, and Y. Behrend.** 1990. Effects of temperature and incubation period on the production of fumonisin B_1 by *Fusarium moniliforme*. Appl. Environ. Microbiol. **56:**1729–1733.

6. **Bezuidenhout, S. C., W. C. A. Gelderblom, C. P. Gorst-Allman, R. M. Horak, W. F. O. Marasas, G. Spiteller, and R. Vleggaar.** 1988. Structure elucidation of the fumonisins, mycotoxins from *Fusarium moniliforme*. J. Chem. Soc. Chem. Commun. **1988:**743–745.
7. **Branham, B. E., and R. D. Plattner.** 1993. Alanine is a precursor in the biosynthesis of fumonisin B_1 by *Fusarium moniliforme*. Mycopathologia **124:** 99–104.
8. **Branham, B. E., and R. D. Plattner.** 1993. Isolation and characterization of a new fumonisin from liquid cultures of *Fusarium moniliforme*. J. Nat. Prod. **56:**1630–1633.
9. **Cabañes, F. J., M. L. Abarca, M. R. Bragulat, and G. Castellá.** 1993. High incidence of fumonisin-producing strains of *Fusarium moniliforme* isolated in Spain, p. 293–296. *In* K. A. Scudamore (ed.), Occurrence and significance of mycotoxins. Central Science Laboratory, Slough, United Kingdom.
10. **Castellá, G., M. R. Bragulat, and F. J. Cabañes.** 1999. Fumonisin production by *Fusarium* species isolated from cereals and feeds in Spain. J. Food Prot. **62:**811–813.
11. **Cawood, M. E., W. C. A. Gelderblom, R. Vleggaar, Y. Behrend, P. G. Thiel, and W. F. O. Marasas.** 1991. Isolation of the fumonisin mycotoxins—a quantitative approach. J. Agric. Food Chem. **39:**1958–1962.
12. **Chelkowski, J., and H. Lew.** 1992. *Fusarium* species of *Liseola* Section—occurrence in cereals and ability to produce fumonisins. Microbiologie Aliments Nutr. **10:**49–53.
13. **Chen, J. P., C. J. Mirocha, W. Xie, L. Hogge, and D. Olson.** 1992. Production of the mycotoxin fumonisin B_1 by *Alternaria alternata* f. sp. lycopersici. Appl. Environ. Microbiol. **58:**3928–3931.
14. **Chulze, S. N., M. L. Ramirez, M. Pascale, and A. Visconti.** 1998. Fumonisin production by and mating populations of Fusarium section *Liseola* isolates from maize in Argentina. Mycol. Res. **102:**141–144.
15. **Desjardins, A. E., R. D. Plattner, and P. E. Nelson.** 1994. Fumonisin production and other traits of *Fusarium moniliforme* strains from maize in northeast Mexico. Appl. Environ. Microbiol. **60:**1695–1697.
16. **Desjardins, A. E., H. K. Manandhar, R. D. Plattner, G. G. Manandhar, S. M. Poling, and C. M. Maragos.** 2000. *Fusarium* species from Nepalese rice and production of mycotoxins and gibberellic acid by selected species. Appl. Environ. Microbiol. **66:**1020–1025.
17. **Desjardins, A. E., G. Manandhar, R. D. Plattner, C. M. Maragos, K. Shrestha, and S. P. McCormick.** 2000. Occurrence of *Fusarium* species and mycotoxins in Nepalese maize and wheat and the effect of traditional processing methods on mycotoxin levels. J. Agric. Food Chem. **48:**1377–1383.
18. **Desjardins, A. E., and R. D. Plattner.** 2000. Fumonisin B_1-nonproducing strains of *Fusarium verticillioides* cause maize (*Zea mays*) ear infection and ear rot. J. Agric. Food Chem. **48:**5773–5780.
19. **Desjardins, A. E., R. D. Plattner, and T. R. Gordon.** 2000. *Gibberella fujikuroi* mating population A and *Fusarium subglutinans* from teosinte species and maize from Mexico and Central America. Mycol. Res. **104:**865–872.
20. **Dutton, M. F.** 1996. Fumonisins, mycotoxins of increasing importance: their nature and their effects. Pharmacol. Ther. **70:**137–161.
21. **Gelderblom, W. C. A., K. Jaskiewicz, W. F. O. Marasas, P. G. Thiel, M. J. Horak, R. Vleggaar, and N. P. J. Kriek.** 1988. Fumonisins—novel mycotoxins with cancer promoting activity produced by *Fusarium moniliforme*. Appl. Environ. Microbiol. **54:**1806–1811.
22. **Gelderblom, W. C. A., W. F. O. Marasas, R. Vleggaar, P. G. Thiel, and M. E. Cawood.** 1992. Fumonisins: isolation, chemical characterization and biological effects. Mycopathologia **117:**11–16.
23. **Gelderblom, W. C. A., S. D. Snyman, S. Abel, S. Lebepe-Mazur, C. M. Smuts, L. Van der Westhuizen, W. F. O. Marasas, T. C. Victor, S. Knasmüller, and W. Huber.** 1996. Hepatotoxicity and carcinogenicity of the fumonisins in rats. A review regarding mechanistic implications for establishing risk in humans, p. 279–296. *In* L. S. Jackson, J. W. DeVries, and L. B. Bullerman (ed.), Fumonisins in food. Plenum Press, New York, N.Y.
24. **International Agency for Research on Cancer.** 1993. Toxins derived from *Fusarium moniliforme*: fumonisins B_1 and B_2 and Fusarin C, p. 445–466. *In* IARC Monographs on the evaluation of the carcinogenic risks to humans: some naturally occurring substances: food items and constituents, heterocyclic aromatic amines and mycotoxins, vol. 56. International Agency for Research on Cancer, Lyon, France.
25. **Jimenez, M. T., T. Huerta, and R. Mateo.** 1997. Mycotoxin production by *Fusarium* species isolated from bananas. Appl. Environ. Microbiol. **63:**364–369.
26. **Klittich, C. J. R., J. F. Leslie, P. E. Nelson, and W. F. O. Marasas.** 1997. *Fusarium thapsinum* (*Gibberella thapsina*): a new species in section Liseola from sorghum. Mycologia **89:**643–652.
27. **Kwasna, H., J. Chelkowski, and P. Zajkowski.** 1991. Flora Polska, vol. 22. Grzyby (Mycota). Polska Akademia Nauk, Instytut Botaniki, Warsaw, Poland.
28. **Leslie, J. F., F. J. Doe, R. D. Plattner, D. D. Shackelford, and J. Jonz.** 1992. Fumonisin B_1 production and vegetative compatibility of strains from *Gibberella fujikuroi* mating population 'A' (*Fusarium moniliforme*). Mycopathologia **117**:37–45.
29. **Leslie, J. F., R. D. Plattner, A. E. Desjardins, and C. J. R. Klittich.** 1992. Fumonisin B_1 production by strains from different mating populations of *Gibberella fujikuroi* (*Fusarium* Section *Liseola*). Phytopathology **82:**341–345.
30. **Leslie, J. F., W. F. O. Marasas, G. S. Shephard, E. W. Sydenham, S. Stockenström, and P. G. Thiel.** 1996. Duckling toxicity and the production of fumonisin and moniliformin by isolates in the A and F mating populations of *Gibberella fujikuroi* (*Fusarium moniliforme*). Appl. Environ. Microbiol. **62:** 1182–1187.
31. **MacKenzie, S. E., M. E. Savard, B. A. Blackwell, J. D. Miller, and J. W. ApSimon.** 1998. Isolation of a new fumonisin from *Fusarium moniliforme* grown in liquid culture. J. Nat. Prod. **61:**367–369.
32. **Magnoli, C. E., M. A. Saenz, S. M. Chiacchiera, and A. M. Dalcero.** 1999. Natural occurrence of *Fusarium* species and fumonisin-production by toxigenic strains from poultry feeds in Argentina. Mycopathologia **145:**35–41.
33. **Marasas, W. F. O., P. E. Nelson, and T. A. Toussoun.** 1984. Toxigenic *Fusarium* species. Identity and mycotoxicology. Pennsylvania State University Press, University Park, Pa.
34. **Marasas, W. F. O., T. S. Kellerman, W. C. A. Gelderblom, J. A. W. Coetzer, P. G. Thiel, and J. J. Van der Lugt.** 1988. Leukoencephalomalacia in a horse induced by fumonisin B_1 isolated from *Fusarium moniliforme.* Onderstepoort J. Vet. Res. **55:**197–203.
35. **Marasas, W. F. O.** 1995. Fumonisins: their implications for human and animal health. Nat. Toxins **3:**93–198.
36. **Marasas, W. F. O.** 1996. Fumonisins: history, worldwide occurrence and impact, p. 1–17. *In* L. S. Jackson, J. W. DeVries, and L. B. Bullerman (ed.), Fumonisins in food. Plenum Press, New York, N.Y.
37. **Marasas, W. F. O.** 1997. Risk assessment of fumonisins produced by *Fusarium moniliforme* in corn. Proceedings of the Fifth European *Fusarium* Seminar, Szeged, Hungary. Cereal Res. Comm. **25:**399–406.
38. **Marasas, W. F. O., J. P. Rheeder, S. C. Lamprecht, K. A. Zeller, and J. F. Leslie.** 2001. *Fusarium andiyazi* sp. nov., a new species from sorghum. Mycologia **93:**1203–1210.
39. **Marín, S., V. Sanchis, and N. Magan.** 1995. Water activity, temperature, and pH effects on growth of *Fusarium moniliforme* and *Fusarium proliferatum* isolates from maize. Can. J. Microbiol. **41:**1063–1070.
40. **Marín, S., V. Sanchis, I. Vinas, R. Canela, and N. Magan.** 1995. Effect of water activity and temperature on growth and fumonisin B_1 and B_2 production by *Fusarium proliferatum* and *F. moniliforme* in grain. Lett. Appl. Microbiol. **21:**298–301.
41. **Merrill, A. H., E. Wang, D. G. Gilchrist, and R. T. Riley.** 1993. Fumonisins and other inhibitors of *de novo* sphingolipid biosynthesis. Adv. Lipid Res. **26:**215–234.
42. **Miller, J. D., M. E. Savard, A. Sibilia, S. Rapior, A. D. Hocking, and J. J. Pitt.** 1993. Production of fumonisins and fusarins by *Fusarium moniliforme* from Southeast Asia. Mycologia **85:**385–391.
43. **Miller, J. D.** 1995. Fungi and mycotoxins in grain: implications for stored product research. J. Stored Prod. Res. **31:**1–16.
44. **Mirocha, C. J., T. Chen, W. Xie, Y. Xu, H. K. Abbas, and L. R. Hogge.** 1996. Biosynthesis of fumonisin and AAL derivatives by *Alternaria* and *Fusarium* in laboratory culture. Adv. Exp. Med. Biol. **392:**213–224.
45. **Moretti, A., G. A. Bennett, A. Logrieco, A. Bottalico, and M. N. Beremand.** 1995. Fertility of *Fusarium moniliforme* from maize and sorghum related to fumonisin production in Italy. Mycopathologia **131:**25–29.
46. **Munkvold, G. P., and A. E. Desjardins.** 1997. Fumonisins in maize. Can we reduce their occurrence? Plant Dis. **81:**556–565.
47. **Musser, S. M., R. M. Eppley, and E. P. Mazzola.** 1995. Identification of an n-acetyl keto derivative of fumonisin B_1 in corn cultures of *Fusarium proliferatum*. J. Nat. Prod. **58:**1392–1397.
48. **Musser, S. M., M. L. Gay, and E. P. Mazzola.** 1996. Identification of a new series of fumonisins containing 3-hydroxypyridine. J. Nat. Prod. **59:**970–972.
49. **Musser, S. M., and R. D. Plattner.** 1997. Fumonisin composition in cultures of *Fusarium moniliforme*, *Fusarium proliferatum*, and *Fusarium nygamai*. J. Agric. Food Chem. **45:**1169–1173.
50. **Nelson, P. E., R. D. Plattner, D. D. Shackelford, and A. E. Desjardins.** 1991. Production of fumonisins by *Fusarium moniliforme* strains from various substrates and geographic areas. Appl. Environ. Microbiol. **57:**2410–2412.
51. **Nelson, P. E., R. D. Plattner, D. D. Shackelford, and A. E. Desjardins.** 1992. Fumonisin B_1 production by *Fusarium* species other than *F. moniliforme* in Section *Liseola* and by some related species. Appl. Environ. Microbiol. **58:**984–989.
52. **Nelson, P. E., A. E. Desjardins, and R. D. Plattner.** 1993. Fumonisins, mycotoxins produced by *Fusarium* species: biology, chemistry and significance. Annu. Rev. Phytopathol. **31:**233–252.
53. **Nelson, P. E., J. H. Juba, P. F. Ross, and L. G. Rice.** 1994. Fumonisin production by *Fusarium* species on solid substrates. J. Assoc. Off. Anal. Chem. **77:**522–524.
54. **Nirenberg, H. I., and K. O'Donnell.** 1998. New *Fusarium* species and combinations within the *Gibberella fujikuroi* species complex. Mycologia **90:**434–458.
55. **Norred, W. P.** 1993. Fumonisins—mycotoxins produced by *Fusarium moniliforme*. J. Toxicol. Environ. Health **38:**309–328.
56. **Norred, W. P., C. W. Bacon, R. T. Riley, K. A. Voss, and F. I. Meredith.** 1999.

Screening of fungal species for fumonisin production and fumonisin-like disruption of sphingolipid biosynthesis. Mycopathologia **146:**91–98.
57. **Plattner, R. D., D. Weisleder, D. D. Shackelford, R. Peterson, and R. G. Powell.** 1992. A new fumonisin from solid cultures of *Fusarium moniliforme*. Mycopathologia **117:**23–28.
58. **Plattner, R. D.** 1995. Detection of fumonisins produced in *Fusarium moniliforme* cultures by HPLC with electrospray MS and evaporative light scattering detectors. Nat. Toxins **3:**294–298.
59. **Poling, S. M., and R. D. Plattner.** 1999. Rapid purification of fumonisins and their hydrolysis products with solid-phase extraction columns. J. Agric. Food Chem. **47:**2344–2349.
60. **Riley, R. T., W. P. Norred, and C. W. Bacon.** 1993. Fungal toxins in foods: recent concerns. Annu. Rev. Nutr. **13:**167–289.
61. **Riley, R. T., K. A. Voss, W. P. Norred, R. P. Sharma, E. Wang, and A. H. Merrill.** 1998. Fumonisins: mechanism of mycotoxicity. Rev. Méd. Vét. **149:** 617–626.
62. **Ross, P. F., P. E. Nelson, J. L. Richard, G. D. Osweiler, L. G. Rice, R. D. Plattner, and T. M. Wilson.** 1990. Production of fumonisins by *Fusarium moniliforme* and *Fusarium proliferatum* isolates associated with equine leukoencephalomalacia and pulmonary edema syndrome in swine. Appl. Environ. Microbiol. **56:**3225–3226.
63. **Ross, P. F., R. G. Rice, G. D. Osweiler, P. E. Nelson, J. L. Richard, and T. M. Wilson.** 1992. A review and update of animal toxicoses associated with fumonisin-contaminated feeds and production of fumonisins by *Fusarium* isolates. Mycopathologia **117:**109–114.
64. **Seo, J.-A., J.-C. Kim, and Y.-W. Lee.** 1996. Isolation and characterization of two new type C fumonisins produced by *Fusarium oxysporum*. J. Nat. Prod. **59:**1003–1005.
65. **Seo, J.-A., J.-C. Kim, and Y.-W. Lee.** 1999. N-acetyl derivatives of type C fumonisins produced by *Fusarium oxysporum*. J. Nat. Prod. **62:**355–357.
66. **Shephard, G. S., P. G. Thiel, S. Stockenström, and E. W. Sydenham.** 1996. Worldwide survey of fumonisin contamination of foods and feeds. J. Assoc. Off. Anal. Chem. **79:**671–687.
67. **Sydenham, E. W., G. S. Shephard, P. G. Thiel, W. F. O. Marasas, J. P. Rheeder, C. E. Peralta Sanhueza, H. H. L. Gonzalez, and S. L. Resnik.** 1993. Fumonisins in Argentinian field trial corn. J. Agric. Food Chem. **41:**891–895.
68. **Sydenham, E. W., P. G. Thiel, G. S. Shephard, K. R. Koch, and T. Hutton.** 1995. Preparation and isolation of the partially hydrolysed moiety of fumonisin B_1. J. Agric. Food Chem. **43:**2400–2405.
69. **Sydenham, E. W., G. S. Shephard, S. Stockenström, J. P. Rheeder, W. F. O. Marasas, and M. J. Van der Merwe.** 1997. Production of fumonisin B analogues and related compounds by *Fusarium globosum*, a newly described species from corn. J. Agric. Food Chem. **45:**4004–4010.
70. **Thiel, P. G., W. F. O. Marasas, E. W. Sydenham, G. S. Shephard, W. C. A. Gelderblom, and J. J. Nieuwenhuis.** 1991. Survey of fumonisin production by *Fusarium* species. Appl. Environ. Microbiol. **57:**1089–1093.
71. **Voss, K. A.** 1990. Toxins from *Fusarium moniliforme*, a common fungus in corn. Vet. Hum. Toxicol. **32**(Suppl.)**:**57–63.
72. **Yoshizawa, T., A. Yamashita, and Y. Luo.** 1994. Fumonisin occurrence in corn from high- and low-risk areas for human esophageal cancer in China. Appl. Environ. Microbiol. **60:**1626–1629.