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Trichothecene Toxin Production by Strains of *Gibberella pulicaris* (*Fusarium sambucinum*) in Liquid Culture and in Potato Tubers

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Fifteen strains of *Gibberella pulicaris* (asexual stage: *Fusarium sambucinum* or *Fusarium sulphureum*) isolated from dry-rotted potato (*Solanum tuberosum*) tubers were tested for trichothecene toxin production in liquid culture and in potato tubers, for pathogenicity on potato tubers, and for ability to form sexual crosses. Fourteen strains were sexually fertile and accumulated 4,15-diacetoxyscirpenol in liquid culture (up to 47 μg of toxin/mg dry weight fungal mass). Most strains were able to rot tuber slices of potato cultivar Russet Burbank and produced 15-monoacetoxyscirpenol and 4,15-diacetoxyscirpenol as well as other minor trichothecenes in infected tubers (up to 5 μg of toxin/g rot fresh weight). These results indicate that production of trichothecene toxins is a common trait of *G. pulicaris* strains isolated from potato tuber dry-rot and that trichothecenes may occur in potatoes naturally infected with this fungus in the field or in storage.

Diacetoxyscirpenol and other trichothecene toxins are produced by a number of *Fusarium* species, including *Gibberella pulicaris* (Fries) Sacc. (asexual stage: *Fusarium sambucinum* Fuckel or *Fusarium sulphureum* Schlecht). The trichothecenes are a closely related group of sesquiterpenes that are potent eukaryotic protein synthesis inhibitors and are associated with a variety of mycotoxicoses in humans and animals (Mararas et al., 1984). *G. pulicaris* is a major cause worldwide of dry-rot of potato tubers (Boyd, 1972; Jeffries et al., 1984). Trichothecene-producing strains of *G. pulicaris* have been isolated as dominant fungal species from rotted potato tubers collected in Germany (Siegfried and Langerfeld, 1978), in France (Lafont et al., 1983), in Poland (Latus et al., 1987), and in a high-incidence area of human esophageal cancer in Iran (Steyn et al., 1978). Despite the widespread occurrence of *G. pulicaris* rot of potato tubers and the documented toxigenicity of strains of *G. pulicaris* isolated from a wide variety of habitats (Marasas et al., 1984; Desjardins and Beremand, 1987), there has been limited study of the ability of *G. pulicaris* to produce trichothecenes in potato tubers. In France, Lafont and co-workers (1983) found several trichothecene toxins in potato tubers naturally and experimentally infected with *G. pulicaris*. In Canada, El-Banna and co-workers (1984) found low concentrations of trichothecenes in potato tubers infected with a strain of *G. pulicaris* that had originally been isolated from potato. We report here the results of a study of 15 single-spored strains of *G. pulicaris* isolated from potato tubers from several widely separated geographic locations, including their trichothecene toxin production in liquid cultures and in potato tubers, their pathogenicity on potato tubers, and their sexual fertility.

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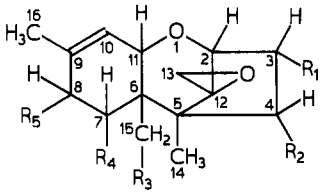
MATERIALS AND METHODS

Source of Strains and Culture Conditions. Strains with the prefix R were identified and supplied by P. Nelson, Fusarium Research Center, The Pennsylvania State University. Strains DAOM 192963, DAOM 192966, and DAOM 196035 were from G. Neish, Biosytematics Research Institute, Agriculture Canada. Strains NRRL 13700 and NRRL 13712 were from A. Murphy, Agriculture Canada. Strains KF-728 and KF-735 were from P. Golinski, Agricultural University of Poznan, Poland. Strain NRRL 13711 was from the author's laboratory, NRRL 13500 from R. Caldwell, University of Wisconsin, and NRRL 13707 from S. Leach, University of Maine. Information on strain identification and habitat was provided by the investigator who supplied the strain. Strain NRRL 13711 was identified by M. Beremand, Northern Regional Research Center. All cultures were reisolated from single spores prior to this study, and the NRRL numbers refer to single-spore strains. Cultures were routinely grown on V-8 juice agar slants (Stevens, 1974) on an alternating 12 h/25 °C light and 12 h/20 °C dark schedule. Cultural characteristics such as pigmentation were based on 10–14-day-old cultures on potato dextrose agar (Nelson et al., 1983). For long-term storage, strains were maintained on V-8 agar slants at 4 °C and as lyophilized conidial suspensions in the Northern Regional Research Center collection (NRRL prefix), Peoria, IL. For all experiments reported here, fresh transfers of the strains were obtained from stock cultures stored at 4 °C.



	R_1	R_2	R_3	R_4	R_5
T-2 Toxin	OH	OAc	OAc	H	$OCOCH_2CH(CH_3)_2$
Neosolaniol	OH	OAc	OAc	H	OH
Diacetoxyscirpenol	OH	OAc	OAc	H	H
Monoacetoxyscirpenol	OH	OH	OAc	H	H

Figure 1.

Procedures for crosses were as previously described (Desjardins and Beremand, 1987). The production of protoperithecia was used as a criterion of femaleness in this study. The tester strains used as females to determine mating characteristics of the field strains were R-6380 (mating type 1,hermaphrodite) and R-5455 (mating type 2, hermaphrodite). A cross was scored as infertile if mature perithecia did not form after four or more attempts.

Analysis of Trichothecene Production in Liquid Culture. Inocula were prepared from strains grown on V-8 agar plates for 7–14 days. Conidia, washed from the surface of the plate with sterile water, were used immediately to inoculate 25 mL of YEPD-5G medium (0.1% yeast extract, 0.1% peptone, 5.0% glucose) (Ueno et al., 1975) at 10^5 conidia/mL in a 50-mL Erlenmyer flask. Cultures were incubated for 7 days at 28 °C on a rotary shaker at 200 rpm. Growth was measured by dry-weight determination of duplicate samples of mycelia collected on preweighed GFA (Whatman) filters. All samples were dried at 80 °C for 24 h before being weighed.

Liquid cultures were assayed for trichothecene toxins by gas–liquid chromatography (GLC) (Beremand and Desjardins, 1988). Following extraction of the whole cultures with two volumes of ethyl acetate, the ethyl acetate layer was passed through a charcoal column (Romer Labs, Inc., Washington., MO), pooled with two subsequent ethyl acetate column washes (10 mL each), and evaporated in vacuo; the residue was resuspended in 1 mL of ethyl acetate. A 50–100-μL aliquot was first evaporated to dryness under nitrogen at 80 °C and then reacted with 100 μL of trimethylsilylating reagent (Tri-Sil/TBT; Pierce Chemical Co., Rockford, IL) at 80 °C for 1 h and finally brought to 1 mL with hexane. Measurements were made in duplicate by flame ionization detection on a Hewlett-Packard gas chromatograph (Model 5890). Trichothecene concentrations were calculated from standard curves generated for each analysis by chromatography of known concentrations of T-2 toxin, neosolaniol, and 4,15-diacetoxyscirpenol standards obtained from Sigma Chemical Co. Structures for these trichothecenes are shown in Figure 1.

Pathogenicity Assays. Tubers of potato cultivar Russet Burbank were obtained from the University of Wisconsin, Lelal Starks Elite Foundation Seed Potato Farm, Rhinelander, WI. Tubers were stored at 4 °C and brought to room temperature several hours prior to use. Slices were prepared aseptically (0.5–0.8-cm thickness and 3-cm diameter) from the medullary tissue of potato tubers. Three tuber slices were placed in a 10-cm plastic Petri dish lined with sterile filter paper moistened with 2 mL of sterile distilled water. Slices were inoculated immediately by placing an inoculum plug (5-mm diameter) mycelial side down at the top edge of each slice. Inoculum plugs were cut from the growing margins of cultures from 1–2 weeks old. All cultures used in each experiment were of equal age. The Petri dishes were sealed in plastic bags and incubated for 6 days at 25 °C in the dark. At the end of each experiment, each group of three tuber slices was weighed. The dark brown, dry-rotted tissue was then removed from each slice with a spatula, and the remaining tuber tissue was weighed. Pathogenicity was determined gravimetrically as grams of tuber rotted. All 15 strains were tested simultaneously in each experiment, and the experiment was repeated three times. Rotted tissue from the three tests of each strain was pooled and frozen at −20 °C for up to 3 weeks. In one experiment 50 g of potato tuber tissue were autoclaved for 20 min prior to infection with strain NRRL 13711 and incubation at 25 °C for 6 days as described above.

Analysis of Toxin Production in Potato Tubers. Rotted tissue obtained from potato tubers inoculated with the 15 strains as described above was thawed, transferred to Erlenmyer flasks, and extracted by shaking twice with ethyl acetate (three volumes per gram fresh weight) overnight at room temperature. The ethyl acetate layer was passed through a charcoal column as described above; the residue was resuspended in 2 mL of ethyl acetate. A volume of extract equivalent to 5 g of fresh weight of potato tissue was removed from each of the 15 samples, except for NRRL 13700 (1 g equiv), NRRL 13712 (2 g equiv), and NRRL 13504 (2.5 g equiv). These aliquots were first evaporated to dryness under nitrogen at 80 °C and then reacted with 100 μL of trimethylsilylating reagent at 80 °C for 1 h. The trimethylsilyl derivatives were analyzed by combined gas chromatography–mass spectroscopy (GC–MS) as previously described (Desjardins et al., 1987). A standard of 15-monoacetoxyscirpenol was supplied by S. Taylor, Northern Regional Research Center. All other standards were obtained from Sigma. The recovery of 4,15-diacetoxyscirpenol was 100% from tuber slices spiked at 50 ng/g of potato fresh weight.

RESULTS AND DISCUSSION

Mating Type and Other Morphological Traits. Although from diverse geographical areas, all strains of *G. pulicaris* isolated from potato were morphologically quite similar and typical of this species as previously described (Nelson et al., 1983). All of the 15 strains produced a diffusable sulfur yellow color, a trait reflected in this species anamorph synonym *F. sulphureum* Schlecht. Although a carmine red undersurface is characteristic of many strains of *G. pulicaris* on potato dextrose agar (Nelson et al., 1983), none of the strains from potato produced red pigments on this medium. Fourteen strains formed fertile crosses with tester strains of *G. pulicaris* (Table I). These results indicate that although they are from widely separated geographic areas, these strains are members of the same species. Eleven strains were of mating type 1 and three of mating type 2; none were self-fertile. Only six of the potato strains produced protoperithecia and were thus females. These distributions of mating types and femaleness in potato strains reflect those previously reported for potato strains in Canada (Gordon, 1954). Potato strains of both mating types were found in the group of strains from Gonbad, Iran (NRRL 13706, NRRL 13703), and in the group from New Brunswick, Canada (NRRL 13700, NRRL 13709), which suggests that the sexual stage may occur naturally even though there have not been any reported occurrences in potato tubers (Gordon, 1954).

Trichothecene Production in Liquid Culture. Diacetoxyscirpenol was detected by GLC of the 15 strains grown for 7 days in a liquid medium in three replicate

Table I. Geographic Origin,[a] Mating Type,[b] Sex, Trichothecene Toxin Production, and Pathogenicity on Potato Tubers of *Gibberalla pulicaris* Strains Isolated from Potato Tubers[c,d]

				liquid cultures		potato tubers						
							trichothecenes,[e] μg/g rotted tissue					
mass culture orig no.	single-spore culture NRRL no.	geographic origin	mating type and sex	dry wt, mg/mL	diacetoxyscirpenol, μg/mg fungal dry wt	pathogenicity, g tuber rotted	DAS	MAS	neo	T-2	HT-2	total
none	13700	New Brunswick, Canada	2 m	4.4 ± 0.8	46.5 ± 19.2	0.8 ± 0.3	tr[g]	–[f]	–	–	–	tr
R-2633	13701	ID, U.S.	1 m	8.3 ± 2.4	31.2 ± 43.8	1.9 ± 1.6	–	–	–	–	–	–
DAOM 192963	13503	Prince Edward Island, Canada	1 m	5.9 ± 1.2	24.7 ± 18.6	6.8 ± 1.9	1.0	4.0	–	–	–	5.0
R-5390	13703	Iran	1 mf	4.1 ± 2.2	21.7 ± 7.2	12.5 ± 6.2	0.6	1.1	–	–	–	1.7
KF 728	13704	Poland	1 m	6.4 ± 1.2	21.3 ± 3.7	14.1 ± 4.6	0.6	2.2	–	–	–	2.8
KF 735	13705	Poland	1 m	5.4 ± 1.9	20.7 ± 6.7	9.2 ± 1.1	0.7	1.3	–	–	–	2.0
R-5389	13706	Iran	2 m	6.4 ± 1.3	17.3 ± 3.1	7.5 ± 2.4	0.7	1.0	–	–	–	1.7
none	13500	WI, U.S.	1 m	7.4 ± 1.8	16.2 ± 2.4	6.4 ± 4.8	0.6	1.7	–	–	–	2.3
none	13707	ME, U.S.	1 m	6.9 ± 1.8	15.1 ± 0.9	4.4 ± 2.5	tr	–	–	–	–	tr
R-6380	13708	Germany	1 mf	5.8 ± 1.8	12.7 ± 1.3	15.7 ± 2.0	0.4	3.6	–	–	–	4.0
DAOM 196035	13709	New Brunswick, Canada	1 m	6.4 ± 1.2	11.6 ± 4.9	12.5 ± 1.9	0.2	+[h]	–	–	–	>0.2
DAOM 192966	13504	Prince Edward Island, Canada	1 mf	7.3 ± 1.5	7.2 ± 5.8	1.6 ± 3.6	0.3	0.4	–	–	–	0.7
R-2882	13710	Australia	2 mf	4.5 ± 1.8	3.2 ± 1.4	7.0 ± 1.5	1.2	1.2	tr	tr	–	2.4
none	13711	CO, U.S.	1 m	7.4 ± 1.7	0.7 ± 1.1	3.1 ± 1.6	0.2	0.2	0.3	0.8	tr	1.5
none	13712	New Brunswick, Canada	not fertile	7.4 ± 0.5	–[f]	1.4 ± 0.7	–	–	–	–	–	–

[a] Data on origin are from the investigator who supplied the strain. [b] Mating type is designated as 1 or 2: (m) means the strain functioned as a male in crosses; (f) means the strain produced protoperithecia. [c] Means and standard deviations for three replicate experiments are given. Experimental details are in Materials and Methods. [d] Pathogenicity is expressed as grams fresh weight rotted of three tuber slices with three replicate tests of each of the 15 strains. The average fresh weight for each group of three slices was approximately 20 g. The pathogenicity was 0 for tuber slice controls inoculated with culture medium. [e] Key: DAS, 4,15-diacetoxyscirpenol; MAS, 15-monoacetoxyscirpenol; neo, neosolaniol; T-2, T-2 toxin; HT-2, HT-2 toxin. [f] None detected. [g] Less than 0.05 μg/g fresh weight. [h] Present but not quantitated.

experiments. The strains are listed in order of their mean 14,15-diacetoxyscirpenol production (with standard deviation) in Table I. Strain NRRL 13711 also produced neosolaniol, acetylneosolaniol, propylneosolaniol, butylneosolaniol (Greenhalgh et al., 1988), and T-2 toxin as minor components. Only strain NRRL 13712 did not produce any detectable trichothecenes in the liquid medium. Diacetoxyscirpenol concentrations ranged from a low mean of 0.7 μg/mg dry weight fungal mass for strain NRRL 13711 to a high mean of 46.5 μg/mg for strain NRRL 13700. Low trichothecene production was not due to poor growth because all strains grew quite well on the test medium (means of from 4.1 to 8.3 mg dry weight/mL of culture). The coefficients of variation in tricothecene level (for the 11 strains producing >10 μg diacetoxyscirpenol/g dry weight) were generally between 10 and 30%, except for strains NRRL 13701 and NRRL 13503 which were highly variable in tricothecene production but not in growth rate.

Pathogenicity on Potato Tubers. The 15 strains of *G. pulicaris* were tested for pathogenicity on tuber slices of cultivar Russet Burbank in three replicate experiments. This cultivar was selected because it is widely grown and has been reported to be highly susceptible to *G. pulicaris* tuber rot (Leach and Webb, 1981). All pathogenic strains produced a dry brown rot with a well-defined edge during 6 days incubation at 25 °C. Mean pathogenicity (standard deviation) of the strains is given in Table I. Coefficients of variation (for the 11 strains rotting more than 10% by weight of tuber) ranged from 12 to 75%. Although all of the strains were originally isolated from potato, some strains (e.g., NRRL 13504, NRRL 13700, NRRL 13701, and NRRL 13712) were weakly or nonpathogenic on cultivar Russet Burbank under our experimental conditions. Others have shown that pathogenicity of *G. pulicaris* can vary among potato cultivars (Boyd, 1972; Leach and Webb, 1981) and with treatment of tubers with sprout inhibitors and various other chemicals (Jeffries et al., 1984). The cultivars of potato from which most of our strains were originally isolated are not known. Strain NRRL 13700, however, which was not pathogenic on cultivar Russet Burbank, was originally isolated from culitvar Fundy. Some strains may also be inherently nonpathogenic and may be able to survive in potato tubers only due to the concurrent presence of other, pathogenic strains.

The only strain (NRRL 13712) that did not produce any detectable 4,15-diacetoxyscirpenol in liquid culture was not pathogenic; however, the correlation between the amount of 4,15-diacetoxyscirpenol in liquid culture and the extent of disease was not significant (correlation coefficient –0.02). For example, strain NRRL 13700, the highest 4,15-diacetoxyscirpenol producer in liquid culture, was not pathogenic, and strain NRRL 13710, a low producer, was of intermediate pathogenicity. In contrast, the ability to produce trichothecenes in liquid culture has been positively correlated with the pathogenicity of *Fusarium graminearum* on wheat (Miller et al., 1981) and *Fusarium sporotrichioides* on parsnip root (Desjardins et al., 1989).

Trichothecene Production in Potato Tubers. Although 15-monoacetoxyscirpenol was not detected in extracts of 15 strains of *G. pulicaris* grown in liquid culture, 15-monoacetoxyscirpenol was detected in all potato extracts where 4,15-diacetoxyscirpenol was detected at more than trace levels (Table I). Concentrations of 15-monoacetoxyscirpenol were equal to or greater than those of 4,15-diacetoxyscirpenol in all strains tested. Scott and Kanhere (P. M. Scott, personal communication, paper presented to Conference on moisissures et levures indesirables en industrie agro-alimentaire, Paris, France, 1987) also detected 15-monoacetoxyscirpenol in one culture of *G. pulicaris* grown on potatoes at 10 °C. Three additional trichothecenes, neosolaniol, T-2 toxin, and HT-2 toxin,

were detected in an extract of potatoes infected with strain NRRL 13711. Neosolaniol and T-2 toxin were also detected in trace amounts in an extract of potatoes infected with strain NRRL 13710.

Diacetoxyscirpenol was the major trichothecene reported to be produced by strains of *G. pulicaris* that were isolated from potatoes in Poland (Latus et al., 1987) and in Iran (Steyn et al., 1978) and were grown on sterilized moist grains. Deoxynivalenol was not detected in extracts of potatoes infected with any of the 15 strains tested in the present study, although it has previously been found along with 4,15-diacetoxyscirpenol and T-2 toxin as a major contaminant in potatoes naturally and experimentally infected with *G. pulicaris* (Lafont et al., 1983; El-Banna et al., 1984). These differences in the trichothecenes produced may result from differences in experimental procedure, such as the use of tuber slices vs whole tubers or the use of high (25 °C) vs low (10 °C) incubation temperatures, or may be due to the use of different strains of the fungus.

The qualitative and quantitative differences observed in this study in trichothecene production by single-spore strains under different culture conditions have been seen in other *Fusarium* species. Pestka et al. (1985) reported that production of 15-acetyldeoxynivalenol and/or deoxynivalenol by *F. graminearum* was highly dependent on conditions of fermentation, including chemical composition of the liquid medium. Miller and co-workers (1983b) have also reported that strains of *F. graminearum* grown on different substrates can vary widely in trichothecene production, both in toxin levels and in particular end products. Since 15-monoacetoxyscirpenol was not detected in liquid culture, its production in infected potato tubers may result from degradation or transformation by potato enzymes. Conversion of 15-acetyldeoxynivalenol to deoxynivalenol and of deoxynivalenol to a variety of as yet unidentified products has been accomplished by incubating pure toxins with maize leaf tissue (Miller et al., 1983a) and wheat cell suspension cultures (Miller and Arnison, 1986). In *G. pulicaris*, further study will be necessary to determine whether 15-monoacetoxyscirpenol is a product of fungal or plant biotransformation or a biosynthetic precursor of 4,15-monoacetoxyscirpenol. A role of potato metabolism in 15-monoacetoxyscirpenol accumulation is supported by the observation that both 15-monoacetoxyscirpenol and 4,15-diacetoxyscirpenol were among the trichothecenes detected following strain NRRL 13711 infection of living potato tubers, but 15-monoacetoxyscirpenol was not detected upon infection of autoclaved tubers even though 4,15-diacetoxyscirpenol and other trichothecenes were present.

Toxicological Significance. *G. pulicaris* is a cosmopolitan soil organism with a wide host range. In addition to its role as a major causative agent of potato storage rot, *G. pulicaris* has been reported as a fruit and storage rot of numerous cultivated plants including tomatoes (Harwig et al., 1979), peanuts (Booth, 1971), and parsnips (Desjardins and Spencer, unpublished material). Losses due to *G. pulicaris* rot of potato tubers are kept to a minimum by chemical control and by the use of less susceptible cultivars, although there are to date few commercially available potato cultivars with a high degree of resistance (Leach and Webb, 1981; Jeffries, 1978). In the absence of these control measures or with adverse weather conditions, disease can be severe as witnessed by epidemics on Prince Edward Island, Canada, in 1946, 1947, and 1960 (Ayers and Ramsay, 1961). The incidence of trichothecene-producing strains of *G. pulicaris* in naturally infected potatoes remains to be studied. In the present study, 12 of the 15 strains (all but NRRL 13706, NRRL 13703, and NRRL 13708) were selected solely on the basis of being cultured from potato tubers, and 11 of these strains were toxigenic on potato tubers. Nine of 12 strains of *G. pulicaris* isolated from rotted tubers in France were toxigenic also (Lafont et al., 1983). The results from these limited samples suggest that trichothecene production is a common trait of strains of *G. pulicaris* from potato tubers.

Information is limited on the occurrence of trichothecenes in potatoes naturally infected with *G. pulicaris* and incubated under low-temperature commercial storage conditions. Dry-rotted market potatoes sampled in France during the winters of 1980–1982 showed contamination with trichothecenes to levels of up to 140 μg/g rotted tissue (Lafont et al., 1983). There is also considerable indirect evidence that trichothecenes could occur in potatoes stored under low-temperature conditions. In vitro, *G. pulicaris* tolerates low temperatures with germination of macroconidia and mycelial growth occurring at 4 °C (Jeffries, 1978). Jeffries (1978), El-Banna et al. (1984), and Leach et al. (1981) have also shown that *G. pulicaris* is able to rot tubers at temperatures as low as 15, 13, or 4 °C. Extracts of potato tubers inoculated with strain R-6380 and incubated at 20, 15, or 6 °C were all highly toxic to brine shrimp, although the specific toxins involved were not identified (Siegfried and Langerfeld, 1978).

Oral administration of trichothecene toxins can cause damage to the gastrointestinal tract and to the hematopoietic and lymphopoietic systems (Marasas et al., 1984). Concentrations of deoxynivalenol lower than 5 μg/g dry weight in experimentally infected grain can affect feed intake and weight gain in swine (Friend et al., 1986). In the present study, trichothecene concentrations of up to 5 μg/g fresh weight were detected in diseased portions of experimentally infected potato tuber slices after 6 days, and far higher concentrations have been detected in whole tubers after several weeks incubation (Lafont et al., 1983). Trichothecenes are quite heat stable (Scott et al., 1983), and the concentration of 4,15-diacetoxyscirpenol in tuber slices experimentally infected with strain NRRL 13708 was not decreased by autoclaving the infected tubers for 30 min. It therefore seems unlikely that trichothecenes would be destroyed by the usual procedures to prepare potatoes for human consumption. Furthermore, visibly unaffected tissue immediately adjacent to dry-rot affected areas of tuber slices experimentally infected with strain NRRL 13708 contained 4,15-diacetoxyscirpenol at 0.1 μg/g fresh weight as compared to 1.8 μg/g fresh weight in visibly rotted tissue. Lafont and co-workers (1983) also detected trichothecenes in apparently healthy tuber tissue adjacent to dry-rotted areas. Therefore, the usual practice of removing rotted parts of slightly diseased tubers may not effectively remove all trichothecene toxins from *Gibberella*-infected potatoes.

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Registry No. 4,15-Diacetoxyscirpenol, 2270-40-8; 15-monoacetoxyscirpenol, 2623-22-5; neosolaniol, 36519-25-2.

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