Biological Control of Ergot by Fusarium

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ABSTRACT

Fungal hyperparasites of *Claviceps purpurea* were examined as potential biological control agents for ergot of wheat. The most virulent hyperparasites of ergot from a worldwide collection were certain cultivars of *Fusarium roseum*. The pathogenicity of isolates was tested under both glasshouse and field conditions. Promising strains were reisolated from glasshouse-infected ergot sclerotia and screened with regard to their toxicity and host-parasite relations. As a result of both field and clinical tests, a clone of

F. roseum 'Sambucinum' was determined to be a highly effective biological control agent of ergot. Breakdown of ergotamine by this clone to psychotropically inert substances was observed: neither rabbits nor rats displayed deleterious effects after administration of 5 mg equivalent- or 10 mg equivalent per kg body wt of hyperparasite-digested ergotamine, respectively, during tests for subacute toxicity.

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Ergotism and its causal agent Claviceps purpurea have drawn the interest of farmers, scientists, and physicians alike for over 300 yr; many of the great plagues in Europe from the Dark Ages to the Industrial Revolution stemmed from ergot poisoning. With better disease control methods in the 20th century, attention has focused on the pharmaceutical use of ergot alkaloids. Ergot of rye is an invaluable source of several therapeutic drugs for the treatment of migraine headache, hypertension, and lingering childbirth. Moreover, interest in the psychiatric use of LSD (d-lysergic acid diethylamide) and its abuse as a hallucinogenic drug should stimulate research on the use of ergot alkaloid derivatives.

Through a better understanding of the epidemiology of ergot, certain control methods were developed for common wheat varieties which work reasonably well during years of average rainfall. Use of clean seed, burning stubble and chaff, deep-plowing of post-harvest fields combined with mowing perennial grasses on field borders help to control ergot, but during very wet growing seasons these control measures break down. The use of gas burners on post-harvest fields has provided excellent control (7), but this practice has received serious setbacks from anti-pollution legislation. With the possibility of widespread use of hybrid wheats, in which the F₁ male sterile contracts ergot much more readily than does rye (18), the future prospects of controlling this fungus look bleak. For these reasons, biological control of C. purpurea was investigated.

Only one biological control agent has been reported (13), and the number of possible control agents of ergot appear to be sparse. Considering the abundance of nutrients in the honeydew and the sclerotium of Claviceps, fewer saprophytes and parasites have been reported on ergots than might be expected. Undoubtedly Claviceps spp. have evolved certain defense mechanisms which have allowed their worldwide distribution and freedom from most of the common hyphomycetes. A number of microorganisms are able to circumvent these defenses and are considered here as possible control agents for C. purpurea.

A species of Epicoccum (Cerebella Ces.) attacks the

sphacelial stage of some ergot fungi (20). Although an invasion of the sphacelium by Epicoccum stops the development of the sclerotium and curbs disease spread, there are no reports of Epicoccum successfully parasitizing ergots of rye or wheat. Gloeotinia temulenta is thought to be associated with C. purpurea (M. Noble Personal Communication), but either the hyperparasite or the complex may be responsible for certain toxic properties of rye grain (17). Although hyphae of this hyperparasite can be detected in the cortical tissue of ergot sclerotia, G. temulenta appears to be only weakly pathogenic. Moreover, a serious further difficulty in its use as a control agent lies in the fact that it causes a blind seed disease in cereals (8). A bacterium, Leuconostoc mesenteroides, reportedly competes successfully with C. purpurea for host sucrose (14), producing a large amount of capsular dextran which causes the sphacelium to be sloughed off. Although L. mesenteroides was not used in our pathogenicity tests on ergot, this and other bacteria with sucrase activity should be studied for possible use as control agents. Other more obscure hyperparasites of ergot such as Barya (16) and Cordyceps (12) are also potential control agents.

Field observations of ergot led to the conclusion that certain fusaria would likely be the best biological control agents of *C. purpurea*. *Fusarium* spp. have been frequently reported as contaminants of ergot, but the identity of these fusaria and their pathogenicity toward ergot have not hitherto been determined. In the present study, numerous ergot contaminants were collected, and the pathogenicity and specific identities of many of the *Fusarium* isolates were resolved. Because of the worldwide distribution and the apparent pathogenicity of the fungi in these collections, it was hoped that a fair appraisal of their ability to control ergot could be made.

A microbial control agent for ergot should possess as many of the following characteristics as possible: (i) a capacity to rapidly infest and destroy sphacelial and sclerotial thalli; (ii) ability to produce a large number of propagules (high secondary infection rate); (iii) inability to damage the cereal plant; (iv) inability to produce substances toxic to mammals either from ergot alkaloids

TABLE 1. Origin and capacity of Fusarium roseum isolates to infect ergot

Fusarium roseum	Origin	Host of ergot	Disease ratings ^a		Percent germination of ergot sclerotia ^b	
isolates			Misted	Not misted	Field inoculation	Slant inoculation
'Sambucinum' clones						
R13a	California, USA	Poa	2	1	0 (84)	0 (93)
R13b	Louisiana, USA	Axonopus	2	0	•••	79 (93)
R13c	California, USA	Lolium	3	1	0 (84)	0 (93)
R13d	Costa Rica	Paspalum	1	0		. A. 2
R13e	Texas, USA	Paspalum	1	0	***	•••
'Gibbosum' clones						
R15a	France	Triticum	2	0		84 (93)
R15b	England	Spartina	2	0	****	75 (93)
R15c	France	Lolium	1	0	***	98 (93)
R15d	Norway	Elymus	1	0		12.00
R15e	France	Lolium	2	0	•••	***

Disease ratings on a 0-3 scale with a rating of 3 being most severe; plants grown in a glasshouse.

^hPercent germination of healthy controls in parentheses. Sclerotia collected from field following natural infestation; other sclerotia dipped in spore suspension (slant inoculation) prior to cold treatment.

or de novo; (v) capacity to degrade ergot alkaloids to biologically inactive substances. The first three characteristics can be used as criteria in the selection of most fungal biological control agents, while the fourth and fifth would apply mainly to ergot. Other fungal associations in which toxins are either produced or destroyed may also be assessed in a similar manner.

MATERIALS AND METHODS.—Claviceps purpurea (Fr.) Tul. (strain R-56) was maintained in its parasitic state on svaloff fluorex rye, Secale cereale L. (10). The hyperparasitic fusaria listed in Table 1 were originally isolated on a selective medium (15). After each strain was tested for pathogenicity on R-56 ergot, it was maintained on potato-dextrose agar (PDA). Strain R-13c was grown on PDA in 15.2-cm (6-inch) diam petri dishes, and when orange sporodochia formed, the conidia were harvested and lyophilized in 10% instant powdered milk (Co-op brand) in thick-walled tubes. These tubes were sealed under vacuum and stored at 5 C.

Pathogenicity tests on ergot.—To assess the extent of pathogenicity of each clone, two separate tests were employed under glasshouse conditions. The first test was designed to determine the extent of damage inflicted on the asexual stage of the ergot. A heavy spore suspension of the hyperparasite was sprayed onto the sphacelial stage of R-56. The average relative humidity (RH) during the day was 60% with a range of 40 to 80%. At night the RH was approximately 80%, and some of the plants were misted with a fogging unit. The temp ranged from 28 to 32 C during the day, and was maintained at 19 Cat night. If, under these conditions, the sphacelial stage was destroyed and no sclerotia developed, the hyperparasite clone received a rating of 1 (Table 1). A rating of 2 was given if, in addition, it was able to attack the new unpigmented pseudoparenchyma at the base of the sclerotium. The clone received a rating of 3 if it could also penetrate and colonize the mature, pigmented sclerotia. After symptom development, the causal agent was reisolated, this time from dissected host mycelium representing an uncontaminated infection court. The extent

colonization of the sclerotia was determined by microscopic examination of freeze-sectioned material under a Zeiss phase-contrast microscope.

Another means for assessing pathogenicity was based on the percent reduction of ascostromata from infected sclerotia (Table 1). Germination of both field-infected and healthy ergot sclerotia was brought about by an alternating cold temp technique. In each test, 50 sclerotia (strain R-56) were first placed in wet sand inside crystalizing dishes and exposed to fluctuating temp of 0 and 10 C on a diurnal cycle of 12 h each for 2 mo, after which they were allowed to germinate at 19 C. In a similar experiment, dishes containing 100 smaller sclerotia, collected in Oregon on *Lolium multiflorum* Lam., were inoculated with conidia from an agar slope immediately prior to the above germination scheme.

The most pathogenic clone, R-13c, was used in field trials to test its suitability as a commercial biological control agent. In the first part of a two-part study, the ergot and its Fusarium parasite were grown under standard summer conditions in Berkeley, California, using furrow irrigation, while in the second part, they were grown using sprinkler irrigation. The summers in Berkeley are cool and dry, and the sclerotia of *Clavicens* develop only in areas where there is sprinkler irrigation. When ergot was inoculated onto rye (Secale cereale L.) growing in furrow-irrigated plots (3.6 \times 11.0 m), the honeydew stage developed in approximately 0.2% of the florets. Half of the plot was sprayed with a 10⁻⁴ dilution (v/w) of lyophilized R-13c conidia which yields approximately 600 conidia per ml. The same test was repeated using sprinkler irrigation for 1.0 h before sunset and 1.0 h after sunrise; this regime was necessary for eventual sclerotium production by all strains of C. purpurea tested.

Secondary infection.—A subjective evaluation of propagule formation was made from the size of the sporodochial mass produced in glasshouse trials. In field tests, the number of healthy and diseased thalli of Claviceps was recorded weekly. The weekly increase in

number of diseased thalli was used to determine the rate of secondary infection.

Pathogenicity tests on cereal.—The hyperparasite was also tested for pathogenicity on wheat and rye. The capacity of clone R-13c to attack pre-emergence seedlings was tested by sowing infested seeds in both sandy and clay soils. Newly germinated California spring wheat (Triticum aestivum L.) seedlings were dipped into sterile distilled water suspensions containing 3×10^5 conidia/ml, after which 1,000 seedlings of each were sown in 40-cm diam pots of soil at 16, 21, 27, and 32 C. Simultaneous tests were run with F. roseum f. sp. cerealis 'Graminearum' and 'Culmorum', clones R-1b and R-2b, respectively.

Damage by Fusarium to developing seeds during field tests was also examined. The wt and quality of the rye grain were compared in treated and nontreated Claviceps-infested plots. After the ergot was floated off in 20% brine, the rye seed was dried and weighed.

Alkaloid degradation and bioassays.—To test whether certain ergot hyperparasites were capable of degrading known ergot alkaloids to either biologically active or inactive products, culture extracts were analyzed both by thin-layer chromatography, and by biological assays. Fusaria were first grown in defined media containing low nitrogen. Ergotamine tartrate (0.1% w/v) was then added to late log-phase cultures grown in the dark. The types of degradation products accumulated were used as a measure of each strain's ability to break down ergot alkaloids. The defined medium consisted of: 10 g glucose, 0.1 g asparagine, 0.1 g NaH₂PO₄, 5.0 mg cystine, and 1.0 ml Barthelot's trace element solution, brought to 1.0 liter with glass distilled water. The medium was passed through a prewashed sterile Millipore filter (0.22 µm). Fungi (5 \times 10² spores/ μ l of medium) were grown in 250ml Erlenmeyer flasks containing 50 ml of medium, shaken on a New Brunswick rotary shaker for 10 days at 180 rpm with a 2.5-cm eccentric throw. All harvesting and extraction procedures were carried out under a yellow safe-light.

Cultures were centrifuged at 12,000 g for 10 min. The mycelial pellet was washed and recentrifuged in distilled water. Washings were combined with the culture broth supernatant. The mycelium, moistened with 5.0% tartaric acid, was ruptured in a French Press and extracted in 80% aqueous acetone. When the acetone was evaporated, the aqueous solution was added to the broth and washings. The resulting solution was brought to pH 8.5 with a saturated sodium carbonate solution and extracted four times with equal volumes of chloroform. By this procedure, amides of lysergic acid were extracted and were then concd by evaporation of the chloroform under vacuum. A small portion of the extract was spotted on Brinkman 0.2 mm, MN silica gel N-HR thin-layer chromatography plates. The alkaloids were separated in chloroform-methanol (9:1, v/v) and detected with 1.0% p-dimethylaminobenzaldehyde in concd hydrochloric acid (22).

The remaining portions of each chloroform extract were partitioned into 0.05% aqueous tartaric acid, brought to pH 6.0 with sodium bicarbonate, and injected into New Zealand male rabbits to test for the presence of LSD-like substances which cause a hyperthermic

TABLE 2. Infection of wheat seedlings by Fusarium roseuma

Temp		Percen		
	Clone R1b	Clone R2b	Clone R13c	Distilled water
16	30 (76)°	70 (74)	0 (89)	0 (88)
21	50 (45)	75 (65)	0 (90)	0 (92)
27	36 (58)	21 (72)	0 (92)	0 (91)
32	5 (90)	2 (89)	0 (91)	0 (93)

"Fusarium roseum f. sp. cerealis (R1b and R2b), F. roseum 'Sambucinum' (R13c).

^hPercent of diseased seedlings 2 wk following inoculation and germination.

Percent germination given in parentheses.

response (19). The samples were injected (2 mg ergotamine tartrate equivalents per kg body wt) into the ear vein in 0.9% sodium chloride. The rectal temp were recorded at 20 min intervals. The chloroform-extracted broths were neutralized with tartaric acid and incorporated into the feed of rabbits that were tested for the above temp response. To insure minimal variation in control temp, the thermometers were inserted to the same depth in the rectum during each measurement and no feed was offered up to or during 12 h prior to injection or offering of 5.0 g of test feed. Lyophilized culture broth was incorporated into rat feed (10 mg ergotamine tartrate equivalents / kg body wt per day) for a period of 30 days.

RESULTS.—Identification of fungi.—Collections of suspected hyperparasites of Claviceps were made from Sept 1969 to Nov 1971. Each sclerotium or sphacelium was inspected for necrosis brought about by foreign molds; isolates were made only from ergots exhibiting definite damage. These fungi are listed in Table 1. The suspected hyperparasites were identified according to the system of Snyder and Hansen (21); the European isolates were all Fusarium roseum 'Gibbosum', one brown pigmented clone (R-15c) and four red-pigmented clones.

The American isolates were all identified as F. roseum 'Sambucinum'. A clone of the latter cultivar, found parasitizing ergot of Poa annua in Berkeley, effectively controlled the ergot during certain months of the year. During the early spring (late February to early April), the honeydew stage of C. purpurea is prominent on Poa heads after intermittent spring rains. During mid- and late spring the dry, warm climate necessitates sprinkler irrigation and periodic mowing, both of which cause a serious outbreak of ergot. In the wake of this outbreak, the Fusarium hyperparasite becomes epidemic and results in nearly total eradication of the pest. An intensive search for sclerotia revealed only a few, and then only in areas on high ground. A similar situation was observed in San Francisco's Golden Gate Park.

Pathogenicity tests.—Each Fusarium isolate was tested for its pathogenicity towards C. purpurea. Under glasshouse conditions, even the most virulent strains were only moderately pathogenic (Table 1). With a dry glasshouse environment, conditions were suboptimal for sclerotium production and probably inhibitory to colonizing molds. Under misting conditions, a much broader range of pathogenicity was observed. Under alternating wet and dry conditions, orange sporodochia were apparent after 1 wk, usually becoming pronounced after several weeks. After each pathogenicity test was

completed, an attempt was made to reisolate the pathogen. In each test, the isolate was identical to the original clone collected in nature.

Many of the larger sclerotia were not wholly consumed by the fusaria. It was of interest, therefore, to know if this uninfected pseudoparenchyma was capable of giving rise to ascostromata after a simulated overwintering condition in the laboratory. As can be seen from Table 1, the lack of germination was consistent in all sclerotia infected by clones 13a and 13c. In most cases, sclerotia that had small basally situated lesions were entirely consumed by the time stromata were initiated in healthy sclerotia. A few sclerotia from diseased lots that were apparently healthy prior to the cold treatment, remained so if they were not in direct contact with infected ones. The only contact between sclerotia was through the moist sand; it is not known whether they would have germinated had they not been finally overrun by hyphae from nearby diseased sclerotia. Other Fusarium clones were not as aggressive as the above two.

From these data, clone R-13c appeared to be the most aggressive pathogen of *C. purpurea*. This strain was then tested for its ability to control ergot of rye in the field. When the ergot was in its honeydew stage, it was inoculated with an aerosol of *Fusarium* spores. Neither the orange sporodochia of R-13c nor the sclerotia appeared on the plants in furrow-irrigated plots.

When sprinkler irrigation was employed, both the parasite and hyperparasite developed normally. Within 1 wk after inoculation of the young sphacelia, orange sporodochia could be seen in the test plot. After 2 wk the test plot had 2.2 infections of Fusarium per 10³ florets (0.22%) as judged by the presence of orange sporodochia. At the end of the 3rd wk there was 0.34% infection. The infection rate decreased drastically thereafter; within 1 mo there was only 0.35% infection. Sclerotia began to appear 3 wk following inoculation, and their occurrence reached a peak in the 4th wk. Only 3.1 sclerotia per 104 florets (0.031%) developed in the test plot. Out of these, 1.7 sclerotia per 10⁴ florets were apparently healthy. From these data, the apparent control was about 95%, assuming the number of orange sporodochia plus the sclerotia represented the total number of *Claviceps* infections.

In the control plot, only 2.0 orange sporodochia per 10⁵ florets (0.002%) were noted. Hyperparasitism was observed mainly in areas bordering the test plot. Because of the elusive nature of the sphacelial stage, an assessment of the rate of ergot infection at this point was not attempted. However, the final amount of ergot, which probably includes both primary and secondary infections, was 0.51%. If these data were used to calculate control of ergot in the test plot, the apparent percentage of control would be 97%.

Effect of hyperparasite on cereal.—The rye was reaped, threshed, and winnowed by hand. A sedimentation method was used with a 20% sodium chloride solution to separate the ergot from the seed. After washing and drying, seed lots were weighed. Seed from both the test-and the control plots weighed 707 kg/m³ (54.5 lb. per bu). The test plot yielded 3,263 kg/hectare (48.5 bushels per acre) whereas the control plot yielded 3,203 kg/hectare (47.6 bushels per acre). Several subjective tests uncovered no differences in quality between grain on hyperparasitized and healthy heads except for an

occasional punky sclerotium in the test grain. Microscopic examination of the ergot-hyperparasite interface revealed that the hyperparasite did not invade healthy plant tissue.

Fusarium roseum 'Sambucinum' is considered to be a saprophyte; only occasionally has the organism been reported as pathogenic, and in these cases it may have been present as a secondary pathogen, speculation which may well explain reports of F. roseum 'Sambucinum' as a root rot of cereals (3). As a precautionary measure, pathogenicity tests were done with clone R-13c on wheat seedlings in comparison with F. roseum f. sp. cerealis 'Graminearum' and 'Culmorum'. In Table 2 the damage appears most severe at 21 C; the latter two clones damaged all of the plants tested, while the former showed no aboveground symptoms of pathogenicity. The only noticeable belowground symptoms were some browning of the coleoptile sheath by clone R-13c.

Toxicology.—The possibility of the production of more toxic products as a result of mold action on ergot alkaloids was examined. The alkaloid salt, ergotamine tartrate, was used as a substrate because its base is one of the more prominent active alkaloids in *C. purpurea*. Ergotamine was also considered a likely suspect for degradation to psychotropically active substances (5) such as *d*-lysergic acid ethylamide, a chemical known for its hallucinogenic activity (9).

Basic chloroform extracts from cultures containing fusaria grown on ergotamine tartrate were investigated by use of thin-layer chromatography (TLC). Most of the fusaria tested demonstrated a significant capacity to degrade ergotamine as indicated by the increased number of van Urk's positive spots on developed TLC plates; no attempt was made in the present study to identify these spots. However, most preparations revealed green spots when separated by TLC, which suggested the presence of clavine alkaloids. Some preparations contained one to several major breakdown products (blue spots) while others appeared to have a multiplicity of products.

When considering the history of ergotism, the need for screening against the production of a more highly toxic principle like LSD becomes apparent. Ergot grown in a dry climate or nonmoldy ergot has not been shown to be hallucinogenic, while numerous reports cite hallucinogenic symptoms during very wet years, periods in which certain molds can readily colonize ergot sclerotia (1, 2, 6). The rabbit hyperthermia assay was used to test for the presence of such psychotropic compounds. None of the fusaria tested caused an increase above 0.3 C in the rectal temp after an intravenous injection of the digested ergotamine. Neither the neutralized aqueous phase of the ergotamine digest, nor the unadulerated digest would elicit a hyperthermic response when incorporated into rabbit feed. On the other hand, 12.5 μ g of d-lysergic acid diethylamide caused nearly a 1.7-C temp rise either alone or in combination with ergotamine digests. These results indicate that one or more hallucinogenic indole derivatives are absent from these mold digests of ergotamine. In order to test for conversion of all of the naturally occurring ergot alkaloids, a great many strains of ergot would have to be grown and analyzed under special conditions, a work that is currently in progress.

Culture digests incorporated into rat feed were tested for their subacute toxicity over a period of 30 days. During the feeding sequence and the month following, no symptoms of overt toxicity were noticed, and all of the test animals appeared normal and healthy. Control rats fed undigested ergotamine lost portions of their tails after the first 2 wk of feeding, a common symptom of ergotism in rats and mice.

DISCUSSION.—The chemical control of plant pests is much more widely practiced than is biological control. The use of parasitic fungi to control pests is essentially impracticable due to several epidemiological problems. Of the three major factors limiting the successful spread, colonization, and ultimate destruction of most harmful plants and animals by their respective fungal parasites, climate often ranks highest. Most insects and weeds and many foliar plant parasites are considerably more tolerant to drier environments than their prospective control agents. Rust and powdery mildew fungi are tolerant of lower moisture levels than are their respective Darluca and Ampelomyces (Ciccinobolus) hyperparasites. In the case of Claviceps and its Fusarium parasite, both the pest and the control agent need high moisture. Whenever climatic conditions favor sclerotium development, the hyperparasite can occur as well.

When other factors are right for biological control to occur naturally, the problem of population dynamics plays a key role. When the host population is high, the control agent is favored, and conversely, a low host population disfavors the control agent. This problem can be circumvented by artificial application of the control agent; the number of propagules can be made high enough to get complete control of the host, if other factors are optimal. A low ergot population was used for the present study since 1% sclerotia in grain may be economically damaging. The Fusarium in this case was able to almost completely control the ergot with the use of a rather inexpensive spray at a relatively low concn. The secondary spread of the hyperparasite was also quite effective, although it is unknown whether the Fusarium macroconidia were spread principally by water splash or by insects. Insects such as the green blow fly, Lucilia sericata (Meigen), and the spotted cucumber beetle. Diabrotica undécimpunctata hówardi Baker, became unusually numerous after the ergot began producing honeydew.

An ideal control agent not only inhibits the host's propagative system, but is eradicative as well. Although the fusaria in this study were eradicative, they did permit some host propagation since entry by the control agent occurs only after the ovary has parted from the rachilla and honeydew formation has begun. The *Fusarium* hyperparasite is an effective biocontrol agent because of its rapid colonization of the sphacelium and probable codissemination with *Claviceps* conidia.

Highly aggressive hyperparasites are often pathogenic on the higher plant. Although *F. roseum* is generally considered saprophytic to higher plants, certain cultivars are notorious secondary pathogens as is the case with snapdragon rust and its *F. roseum* hyperparasite (4). Fortunately, clone R-13c does not have this kind of relationship with the cereal hosts of *Claviceps*. Since this clone causes neither a root rot nor a head disease, it would appear that the previous reports of pathogenicity on cereals concern other clones of *F. roseum* 'Sambucinum' or clones of secondary colonizers of diseased tissues.

Ergot sclerotia with lesions containing *F. oxysporum* were received from East Germany, and preliminary glasshouse trials indicated that this *Fusarium* species is also a hyperparasite of ergot (R. L. Mower, *unpublished*). However, it has not been evaluated as a biological control agent.

While F. roseum 'Sambucinum' clone R-13c is an excellent biological control agent by several criteria, rigorous toxicological and pathological tests should be carried out on experimental animals before extensive field tests are begun. Several Fusarium spp. have been implicated in serious poisonings of mammals (11); thus, members of this genus should be examined thoroughly before being used as biological control agents for plant diseases. Preliminary toxicological studies indicate that strain R-13c exhibits no real subacute mammalian toxicity. However, toxins leading to organ degeneration or cancers would not have been detected with procedures used in this study.

Another key factor concerning the usefulness of a hyperparasite of *Claviceps* is the matter of ergot toxicity where there is concern for the possible production of an LSD-like compound during parasitism of sclerotia. The results of culture experiments demonstrate that most fusaria isolated from ergot are able to degrade ergotamine to presumably smaller less toxic compounds in defined media. Although these results point to a possible danger of *d*-lysergic acid ethylamide production during parasitism, they indicate that the hyperparasite is capable of detoxification of probably many, if not all, ergot alkaloids. Thus, the outlook for *Fusarium* as a biological control agent for ergot appears bright.

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