Behavior of a Wild-Type and Two Mutant Strains of *Colletotrichum gloeosporioides* f. sp. *aeschyromene* on Northern Jointvetch in the Field

Y. Luo and D. O. TeBeest, Research Associate and Professor, Department of Plant Pathology, University of Arkansas, Fayetteville 72701

ABSTRACT

Luo, Y., and TeBeest, D. O. 1998. Behavior of a wild-type and two mutant strains of *Colletotrichum gloeosporioides* f. sp. *aeschyromene* on northern jointvetch in the field. Plant Dis. 82:374-379.

The fungus *Colletotrichum gloeosporioides* f. sp. *aeschyromene* causes an anthracnose on *Aeschynomene virginica* and has been used as a biological control agent to control this weed in the United States. The population dynamics of a wild-type strain (3-1-3) and two mutant strains of 3-1-3 of *C. gloeosporioides* f. sp. *aeschyromene*, a benomyl-resistant strain (B21) and nitrate-nonutilizing strain (Nit A), were studied in field tests on northern jointvetch in 1994 and 1995 to determine how the strains interacted on infected plants under field conditions. Plants were co-inoculated with strains 3-1-3 and B21, strains 3-1-3 and Nit A, and strains 3-1-3, B21, and Nit A at equal and unequal initial proportions. Plants were grown and maintained under flooded conditions in small wading pools. In co-inoculation of plants with 3-1-3 and B21 from equal initial proportions, the population of 3-1-3 increased slightly until it reached a proportion of 60 to 70%, whereas the population density of B21 reached 30 to 40% at the end of growing season. From unequal initial proportions, the population density of B21 decreased from 90 to about 50%, whereas the 3-1-3 increased from 10 to 50%. The population density of 3-1-3 increased from an equal initial proportion and was significantly greater than that of Nit A on every sampling time. From unequal initial proportions, the population density of 3-1-3 increased from 10 to 90%, whereas that of Nit A declined. In co-inoculation of plants with the three strains, the population density of 3-1-3 was significantly greater than those of the mutant strains at every sampling time. The proportions of mutant strains within the total population of *C. gloeosporioides* f. sp. *aeschyromene* on plants varied according to the test conditions and the number and types of strains co-inoculated.

Additional keywords: autecology, competition, epidemiology, mycoherbicide, synecology

The fungal plant pathogen *Colletotrichum gloeosporioides* f. sp. *aeschyromene* (Penz.) Penz. & Sacc. is used as a commercial mycoherbicide, COLLEGO (Encore Technologies, Minnetonka, MN), in rice and soybean fields to control northern jointvetch, *Aeschynomene virginica* (L.) BSP (4,7), a weed that interferes with harvesting of rice (*Oryza sativa* L.) and reduces crop value. Many aspects of the disease caused by this fungus have been studied extensively. The fungus overwinters on host debris and seeds and is dispersed by wind-driven rain, tree frogs, and insects (19,22-27).

Little is known about the behavior of individual strains, including the commer-

cialized strain, of this fungus in the field, or how mutant or genetically engineered strains compete with wild-type strains when released in the fields. Mutant strains may be useful in studies to answer the above questions. Benomyl-resistant and nitrate-nonutilizing strains of this fungus were less competitive than a wild-type strain in greenhouse experiments (28) in which benomyl-resistant and nitrate-nonutilizing strains of *C. gloeosporioides* f. sp. *aeschyromene* did not persist in a mixed population of several strains of the fungus. Mechanisms explaining the observed differences were not reported, nor were similar tests conducted in the field. Recently, Luo and TeBeest (16) observed differences in the infectivity of mutant and wild-type strains, including those used by Yang and TeBeest (28), on northern jointvetch seedlings inoculated and incubated under controlled conditions.

The objective of this study was to determine the competitiveness of wild-type and mutant strains of *C. gloeosporioides* f. sp. *aeschyromene* in the field. The information is necessary to predict the consequences when strains with different fitness and competitiveness, such as wild-type, mutant, or genetically engineered strains, are released.

MATERIALS AND METHODS

Source and growth of northern jointvetch plants. Seeds of northern jointvetch, collected from field-grown plants, were germinated on moistened filter paper in petri dishes at 28°C for 24 h. Seedlings were planted in vermiculite in jiffy pots (Hummert International, Earth City, MO) 57 by 57 by 57 mm deep and grown for 10 days at 28°C. After 10 days, healthy seedlings were transplanted into soil in paper cups (525 ml capacity) and were grown for 4 to 5 weeks under greenhouse conditions (25 to 30°C, 15 h day-light).

Strains of *C. gloeosporioides* f. sp. *aeschyromene*. A wild-type strain, 3-1-3, and two mutant strains, a benomyl-resistant strain (B21) and a nitrate-nonutilizing strain (Nit A), were used in this study. B21 was generated by ethyl methanesulfonate mutagenesis of parental strain 3-1-3 of *C. gloeosporioides* f. sp. *aeschyromene* (21). B21 can grow on YPSS medium (4 g yeast extract, 15 g soluble starch, 1 g K₂HPO₄, 16 g agar) amended to contain 25 µg/ml benomyl, whereas the wild-type strain 3-1-3 cannot. Nit A was obtained by growing 3-1-3 on minimal medium amended with potassium chlorate (6). Nit A grows very sparsely on minimal medium (6), whereas strain 3-1-3 grows as a dense colony. All three strains were maintained on Torula agar (TA) medium (28) and inoculum was prepared from spores obtained from TA cultures. The strains are preserved in cryo-storage at the University of Arkansas in the Department of Plant Pathology.

Experimental design. Replicated competition experiments with three treatments were conducted in 1994 and 1995. In treatment A, plants were co-inoculated with 3-1-3 and B21; in treatment B, with 3-1-3 and Nit A; and in treatment C, with 3-1-3, B21, and Nit A. Each treatment was replicated twice. Ten plastic wading pools (1.22 m in diameter by 0.45 m deep) were used for each replicate. In these tests, one pool was placed in the center and nine pools were placed in rows (3 pools in one of 3 rows at approximately 120° intervals between two rows). The distance between any two pools within each row was approximately 1 m. The pools were buried to a depth of 30 cm and partially filled with soil. All pools were then filled with water. Ten 5-week-old plants grown in soil as described above were transplanted into each pool.

Corresponding author: D. O. TeBeest
E-mail: dtebeest@comp.uark.edu

The publication of this paper was approved by the Director of the Arkansas Agricultural Experiment Station, manuscript no.97006. The research was supported in-part by a grant from the USDA, No. 92-34195-7162.

Accepted for publication 12 November 1997.

Publication no. D-1998-0206-01R
© 1998 The American Phytopathological Society

In 1995, two additional treatments, D and E, were used to test competition between 3-1-3 and B21 and between 3-1-3 and Nit A, respectively. An initial ratio of 1:9 for inoculations with the wild-type and mutant strains, respectively, was used for each treatment. Six pools were used for each of two replicates of each treatment. One pool was placed in the center and the other five pools were placed in a circle around the central pool at 72° intervals. The distance between the central pool and each pool in the circle was 2 m. Ten plants were placed in each pool. Procedures for controlled inoculations are described in the following section.

Co-inoculation of northern jointvetch plants. Inoculations were made 10 days after transplanting. Tips of sterilized wooden toothpicks were infested with spores of *C. gloeosporioides* f. sp. *aeschynomene* by insertion into TA cultures. Infested toothpicks were used to puncture plant stems to cause infections. In treatments A and B, a plant of each pool was selected arbitrarily and inoculated once with each strain. In treatment C, a plant of each pool was inoculated once with each of the three strains. Thus, the initial ratios of lesions were as follows: 3-1-3:B21 at 1:1 in treatment A; 3-1-3:Nit A at 1:1 in treatment B; and 3-1-3:B21:Nit A at 1:1:1 in treatment C. In treatments D and E in 1995, the initial ratio of lesions was 1:9 for 3-1-3:B21 or 3-1-3:Nit A. In these treatments, one arbitrarily selected plant was inoculated with 3-1-3 only, whereas the other nine plants were each inoculated once with B21 (treatment D) or Nit A (treatment E). Visual inspection of inoculated plants confirmed that each inoculation produced one lesion at the inoculation site. Overhead irrigation was repeatedly used (about four times a week when no rain occurred) during the experiments to maintain water levels in the pools and to disperse the pathogen.

Sampling procedure. Lesions were sampled approximately every 10 days beginning about 20 days after inoculation. At each sampling time, 3- by 3-mm pieces of diseased tissues were excised from the edges of approximately 150 to 200 lesions for each replicate of each treatment. A lesion was sampled only once during the season. Samples were immediately placed in sterile test tubes, sealed, and placed on ice until they were taken to the laboratory. Samples not used immediately were stored at 4°C for 3 to 5 days.

Plant replacement. Dead plants caused by disease in the pools were replaced with healthy plants during all experiments on an as-needed basis. Healthy replacement plants were grown and maintained in a greenhouse and were approximately the same size as the remaining plants in the pools.

Isolation and identification of strains. Excised lesion tissues were placed in 0.5% sodium hypochlorite solution for 3 to 5

min and washed three times with sterilized distilled water. In preliminary experiments, over 97% of the samples treated in this manner produced colonies of *C. gloeosporioides* f. sp. *aeschynomene*.

After surface sterilization, tissues were placed and cultured on selective media to differentiate the strains found in each lesion. Samples collected from plants in treatments A and D were cultured on YPSS medium amended with 25 µg/ml benomyl, 12.5 µg/ml chlortetracycline, and 30 µg/ml streptomycin.

The samples collected from plants in treatments B and E were incubated on YPSS medium (containing 12.5 ppm chlortetracycline and 30 ppm streptomycin) at 28°C for 2 days. Hyphal tips from the leading margins of each colony from all excised lesions were transferred to minimal NO₃ medium (6) to further characterize the presence of the Nit A strain. These strains were easily identified on minimal NO₃ medium; the wild-type strain (3-1-3) produced an expansive aerial colony, whereas the Nit A strain produced a sparse colony (Fig. 1).

The samples from plants in treatment C were incubated on YPSS medium containing chlortetracycline and streptomycin at 28°C for 2 days. After 2 days, hyphal tips from the leading margins of all colo-

nies were transferred to minimal medium and cultured for 2 more days. The three strains were identified from three different colony types on minimal medium. Strain 3-1-3 produced a dense colony, Nit A, a sparse colony, and strain B21, a small dense colony with a hyaline edge (Fig. 1).

Data analysis. The proportion of either wild-type or mutant strains isolated from the sampled lesions at each sampling time was calculated by division of the number of lesions from which each strain was isolated by the total number of lesions sampled for each replicate of each treatment. The data shown are the proportions of strains at each sampling date and are averages for each treatment. The chi-square test (10) was used in data analysis. For each sampling time, the significant differences in average proportions of number of lesions between two (treatment A and B) or among three (treatment C) strains were determined with χ^2 values calculated for the number of lesions isolated for each strain (10).

Weather data from 1994 and 1995, including daily temperature and rainfall, were collected from a weather station maintained by the Department of Horticulture at the University of Arkansas and located approximately 1 kilometer from the experimental plots.

Fig. 1. Cultural characteristics of colonies of wild-type, benomyl-resistant, and nitrate-nonutilizing strains of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on minimal media (6). (A) Typical colony of strain 3-1-3, (B) typical colony of the nitrate-nonutilizing strain Nit A, and (C) typical colony of benomyl-resistant strain B21.

RESULTS

Co-inoculation of northern jointvetch plants with a wild-type and a benomyl-resistant strain. The results of these experiments differed only slightly between the 1994 and 1995 tests (Fig. 2A,B). There

was a decrease in the proportion of lesions from which isolate 3-1-3 was reisolated on August 13 that appeared to be temporary and possibly due to sampling procedures.

In general, from an initial proportion of 50% for both strains, the proportion of

lesions from which 3-1-3 was isolated increased slightly at each sampling time until it reached a frequency of about 60 to 70% of all of the recoveries made in September of both years.

In the tests in which the two strains were inoculated on plants in unequal proportions, the proportion of lesions from which the wild-type strain was isolated remained nearly constant at a frequency of 0.2 for 4 weeks, then gradually increased to slightly above 0.4 by the end of the experiment in mid-September (Fig. 2C).

The mean percentage of reisolation of the wild-type strain (3-1-3) was significantly greater than that of reisolation of the benomyl resistant strain at six sampling times in 1994 (Fig. 2A) and 1995 (Fig. 2B), but only once, on 11 August 1995, in the treatment in which the initial population of the benomyl resistant strain was nine times greater than the initial population of the wild-type strain.

Co-inoculation of northern jointvetch with a wild-type and a nitrate-nonutilizing strain. The proportion of the Nit A strain within the total population of sampled lesions declined with respect to that of the wild-type strain (Fig. 3A,B). Only relatively minor differences were noted in tests conducted in 1994 and 1995, and variances in proportions at which each strain was reisolated from randomly collected new lesions for most of the sampling times in the 2-year study appeared to be small.

On plants on which the strains 3-1-3 and Nit A were co-inoculated in equal proportions in 1994 and 1995 (Fig. 3A,B), the proportion of the lesions from which the Nit A strain was reisolated decreased rapidly over time from 50 to less than 10% by September of each year. By the end of the growing season, the frequency of recovery of the Nit A strain from lesions was only about 8%, whereas the 3-1-3 strain was recovered from about 92% of the lesions (Fig. 3A). The ratio of decline of the population of Nit A appeared to be constant, even though it was more rapid and earlier in 1995 than in 1994 (Fig. 3B). In 1995, the population of Nit A declined from 50 to less than 10% in only 2 to 3 weeks and remained at less than 10% of the population for the rest of the season.

In the experiment in which the initial population ratio of 3-1-3 to Nit A was 1:9, the frequency at which Nit A was reisolated declined over time (Fig. 3) at a rate very similar to the rate of decline observed for Nit A in the experiments in which the initial proportions were equal. Recovery of Nit A from lesions declined rapidly from 90 to approximately 30% during the first few weeks, then declined more slowly to less than 10% in mid-September. Although the population of Nit A was very small in each of the two replicates in this experiment, this strain could still be found in lesions at the end of season. Statistically,

Fig. 2. Changes in the populations of wild-type (3-1-3) and benomyl-resistant (B21) strains of *Colletotrichum gloeosporioides* f. sp. *aescynomene* on northern jointvetch in field experiments conducted in 1994 (A) and 1995 (B). Individual plants were mechanically inoculated to establish an initial ratio of the strains 3-1-3:B21 of 1:1 (A and B) and 3-1-3:B21 of 1:9 (C) at the beginning of each season. At each sampling time, 150 to 200 lesions were collected, surface sterilized, and placed on selective media to determine the proportion of reisolations for each strain.

the mean proportion of the reisolation of the wild-type strain was significantly greater than the average recovery of the nitrate non-utilizing strain on every sampling time (Fig. 3A,B).

Co-inoculation of northern jointvetch with a wild-type, a benomyl-resistant, and a nitrate-nonutilizing strain. The wild-type strain was isolated from an increasingly greater proportion of lesions with time, eventually reaching a frequency of 90% by mid-September of both years. In 1994, the frequency at which 3-1-3 was isolated from randomly collected lesions increased from 33 to about 90% in 4 to 5 weeks (Fig. 4A). The frequency at which the two mutant strains were reisolated from lesions declined steadily from 33 to less than 10% in 1994. By the end of the season, the frequency at which B21 was reisolated from lesions was 3%, while the frequency at which Nit A was isolated from lesions was 7%.

In 1995, the frequency at which 3-1-3 was isolated from lesions increased from 33 to 90% in about 4 weeks. As in 1994, the frequency at which both mutant strains were reisolated declined steadily over time (Fig. 4B). By mid-September, fewer than 7% of the reisolations were identified as one of the two mutant strains remained. As in 1994, although the populations of the two mutant strains were small, both mutant strains could still be reisolated. The mean percentage of reisolation of the wild-type strain was always greater than either mutant strain over two years (Fig. 4A,B).

DISCUSSION

The results of our experiment were similar to results obtained from previous studies in greenhouse microcosms in which the proportion of mutant strains decreased to about 10% by the end of 10 generations (28). In our study, the population of B21 remained relatively high in both 1994 and 1995. The B21 strain is competitive with the 3-1-3 strain, since it is capable of maintaining a population at an equilibrium frequency near 0.5 of the total population. It is interesting that this frequency was approximated regardless of the initializing populations in these experiments. We have previously shown that the infection efficiency (number of lesions per plant) was greater for B21 than for 3-1-3 at 28°C (16). This might explain why B21 maintained a relatively high proportion of the total population under the conditions encountered in the field, although it eventually declined to constitute only 30 to 40% of the population.

Recovery of Nit A from new lesions declined rapidly over time. In previous studies, Nit A produced significantly fewer lesions on northern jointvetch than 3-1-3 (16), and the number of lesions caused by Nit A was significantly reduced by temperature changes during the infection stages (Y. Luo and D. O.

TeBeest, unpublished data). Taken together, these greenhouse, growth chamber, and field studies suggest that infection efficiency may be an important infection component governing epidemics caused by this fungus.

Differences in population dynamics and competition patterns of strains of *C. gloeosporioides* f. sp. *aeschynomene* between the 2 years of experiments were observed. Variation of weather may be the possible reason. Daytime temperatures

Fig. 3. Changes in the populations of wild-type (3-1-3) and nitrate nonutilizing (Nit A) strains of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on northern jointvetch in field experiments conducted in 1994 (A) and 1995 (B). Individual plants were mechanically inoculated to establish an initial ratio of the two strains 3-1-3:Nit A of 1:1 (A and B) and 3-1-3:Nit A of 1:9 (C) at the beginning of each season. At each sampling time, about 150 to 200 lesions were collected, surface sterilized, and placed on selective media to determine the percentage for each strain.

were significantly higher in July and August of 1995 than in 1994. The number of days in which the average temperatures exceeded 28°C (the optimal temperature for *C. gloeosporioides* f. sp. *aeschynomene* growth; 16,19) was 7 days in July 1995, compared with only 3 days in July 1994; and 15 days in August 1995 compared with 0 days in August 1994. There were differences between years in precipitation as well. Precipitation in July and August of 1995 was only 71 and 29% of that in July and August of 1994, respectively. A previous study (Y. Luo and D. O. TeBeest, unpublished data) also demonstrated that mutant strains were sensitive to temperature changes in infection compared with wild-type strain. This may partially explain the field experimental results.

Little is known about the long-term survival of wild-type strains of *C. gloeosporioides* f. sp. *aeschynomene* in nature (20). The overwintering survival

rate of 3-1-3 is higher than that of the two mutant isolates described here (Y. Luo and D. O. TeBeest, unpublished data). As previously suggested, long-term testing under conditions unsuitable for infection is needed (14).

Adee et al. (1) studied competition between *Pyrenophora tritici-repentis* and *Septoria nodorum* in wheat leaves and found that the de Wit replacement series is a useful tool for quantitative examination of competitive interactions between plant pathogens. Our experiments were conducted as replacement series also, and the results can be explained in several ways. First, the competition for infection sites between wild-type and introduced strains may be an important factor in the changes in frequency at which the strains were found over time. However, this seems unlikely because plants were not totally covered with lesions during these experiments. Second, significant reductions in

the general fitness of mutant strains and in several of the infection components were previously demonstrated (16). Third, environmental conditions may play an important but unseen role in our experiments, influencing factors or processes involved in interactions between strains (Y. Luo and D. O. TeBeest, unpublished data).

The competitiveness of an isolate or strain of a pathogen reflects its general fitness to cause disease in the physical, chemical, and biological environments into which it is placed (15). Several studies concerning the competition and population dynamics of fungicide-sensitive and fungicide-resistant strains of fungal pathogens have been reported (8,11,14,17,18). Dovas et al. (8) tested the competitiveness of benomyl-resistant strains of *Cercospora beticola* in the field and reported that the relative proportion of the resistant strain increased after application of benomyl. Kadish and Cohen (11,12) reported that, in the absence of metalaxyl, metalaxyl-resistant strains increased in the population from 10 to 100% after 8 to 10 sporulation cycles. Kadish et al. (13) reported that the lesions induced by resistant isolates were significantly larger than those induced by sensitive isolates, although no differences in sporulation or infection efficiency were found between resistant or sensitive isolates. On the other hand, Al-Mughrabi and Gray (3) found that isolates of *Erysiphe graminis* f. sp. *tritici* resistant to triadimefon were less fit than sensitive strains in the absence of triadimefon. There is little information on the population dynamics of strains of *Colletotrichum gloeosporioides* with which to compare our data. Agostini and Timmer (2) have studied the dynamics of two strains on citrus in Florida, a slow-growing orange (SGO) strain and a fast-growing gray (FGG) strain. They found that the SGO strain reached high population densities on flower petals during bloom, and the propagule densities of the FGG strain were relatively stable throughout the year. However, the number of propagules recovered in leaf washes declined to nearly 0 in 30 days for both strains, although both strains still could be isolated from leaf pieces. Chakraborty and Billard (5) quantitatively described the relationship between weather conditions and spread and infection of healthy seedlings of *Stylosanthes scabra* by *C. gloeosporioides*. Infection was generally associated with rainfall. Infection of northern jointvetch seedlings is also generally associated with dispersal of spores by rainfall (25).

Population dynamics of bacterial strains also have been studied. Egel et al. (9) studied the dynamics of three strains of *Xanthomonas campestris* on Swingle citrumelo and grapefruit and found that the highly aggressive strain (*X. campestris citrumelo*) on Swingle most consistently produced the highest bacterial populations

Fig. 4. Changes in the populations of wild-type (3-1-3), benomyl-resistant (B21), and nitrate-nonutilizing (Nit A) strains of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on northern jointvetch in field experiments conducted in 1994 (A) and 1995 (B). Individual plants were mechanically inoculated to establish the initial ratio of populations of the three strains 3-1-3:B21:Nit A of 1:1:1 at the beginning of the growing season. At each sampling time, 150 to 200 sampled lesions were collected, surface sterilized, and placed on selective media to determine the proportion of each strain within the population.

and the largest lesions compared with other strains. In general, strains with higher fitness characteristics remained at higher levels in a population.

Because it is relatively difficult to study population dynamics of pathogens in the field, it is often necessary to obtain information describing the infection components of a pathogen under precisely controlled environmental conditions. The information could be used to predict the behavior of strains with different fitness when released into the field. The effects on biological control of weeds with these strains can also be evaluated, such as how and when certain levels of initial population of the pathogen can be used for weed control according to the fitness of the corresponding strain. Simulations based on empirical data collected in the laboratory and validated by comparison to field data may prove feasible. With refined and appropriate methodologies, the population dynamics of an engineered strain after release in the field could possibly be studied before even small-scale controlled releases are made.

LITERATURE CITED

1. Adee, S. R., Pfender, W. F., and Hartnett, D. C. 1990. Competition between *Pyrenophora tritici-repentis* and *Septoria nodorum* in the wheat leaf as measured with de Wit replacement series. *Phytopathology* 80:1177-1182.
2. Agostini, J. P., and Timmer, L. W. 1994. Population dynamics and survival of strains of *Colletotrichum gloeosporioides* on citrus in Florida. *Phytopathology* 84:420-425.
3. Al-Mughrabi, K. I., and Gray, A. B. 1995. Competition between triadimefon-sensitive and triadimefon-resistant isolates of *Erysiphe graminis* f. sp. *tritici*. *Plant Dis.* 79:709-712.
4. Bowers, R. C. 1986. Commercialization of Collego—An industrialist's view. *Weed Sci.* 34 (Suppl.):24-25.
5. Chakraborty, S., and Billard, L. 1995. Quantitative relationships between *Colletotrichum gloeosporioides* infection of *Stylosanthes scabra* and weather under field conditions. *Plant Pathol.* 44:63-72.
6. Correll, J. C., Klittich, C. J. R., and Leslie, J. F. 1987. Mutants of *Fusarium oxysporum* and their use in vegetative compatibility tests. *Phytopathology* 77:1640-1646.
7. Daniel, J. T., Templeton, G. E., Smith, R. J. Jr., and Fox, W. T. 1969. Biological control of northern jointvetch in rice with an endemic fungal disease. *Weed Sci.* 21:303-307.
8. Doivas, C., Skylakakis, G., and Georgopoulos, S. G. 1976. The adaptability of the benomyl-resistant population of *Cercospora beticola* in northern Greece. *Phytopathology* 66:1452-1456.
9. Egel, D. S., Graham, J. H., and Riley, T. D. 1991. Population dynamics of strains of *Xanthomonas campestris* differing in aggressiveness on Swingle citrumelo and grapefruit. *Phytopathology* 81:666-671.
10. Gomez, K. A., and Gomez, A. A. 1984. Statistical procedures for agricultural research. John Wiley & Sons, New York.
11. Kadish, D., and Cohen, Y. 1988. Competition between metalaxyl-sensitive and metalaxyl-resistant isolates of *Phytophthora infestans* in the absence of metalaxyl. *Plant Pathol.* 37:558-564.
12. Kadish, D., and Cohen, Y. 1989. Population dynamics of metalaxyl-sensitive and metalaxyl-resistant isolates of *Phytophthora infestans* in untreated crops of potato. *Plant Pathol.* 38:271-276.
13. Kadish, D., Grinberger, M., and Cohen, Y. 1990. Fitness of metalaxyl-sensitive and metalaxyl-resistant isolates of *Phytophthora infestans* on susceptible and resistant potato cultivars. *Phytopathology* 80:200-205.
14. Lalancette, N., Hickey, K. D. and Cole, H., Jr. 1987. Parasitic fitness and intrastain diversity of benomyl-sensitive and benomyl-resistant subpopulations of *Venturia inaequalis*. *Phytopathology* 77:1600-06.
15. Lenski, R. E. 1992. Relative fitness: Its estimation and its significance for environmental applications of microorganisms. Pages 183-198 in: *Microbial Ecology: Principles, Methods, and Applications*. M. A. Levin, R. J. Seidler, and M. Rogul, eds. McGraw-Hill, Inc. New York.
16. Luo, Y., and TeBeest D. O. 1997. Infection components of wild-type and mutant isolates of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on northern jointvetch. *Plant Dis.* 81:404-409.
17. McGee, D. C., and Zuck, M. G. 1981. Competition between benomyl-resistant and sensitive strains of *Venturia inaequalis* on apple seedlings. *Phytopathology* 71:529-532.
18. Ruppel, E. G. 1975. Biology of benomyl-tolerant strains of *Cercospora beticola* from sugar beet. *Phytopathology* 65:785-789.
19. TeBeest, D. O., Templeton, G. E., and Smith, R. J. Jr. 1978. Temperature and moisture requirements for development of anthracnose on northern jointvetch. *Phytopathology* 68:389-393.
20. TeBeest, D. O. 1982. Survival of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* in rice irrigation water and soil. *Plant Dis.* 66:469-472.
21. TeBeest, D. O. 1984. Induction of tolerance to benomyl in *Colletotrichum gloeosporioides* f. sp. *aeschynomene* by ethyl methanesulfonate. *Phytopathology* 74:864.
22. TeBeest, D. O. 1988. Additions to the host range of *Colletotrichum gloeosporioides* f. sp. *aeschynomene*. *Plant Dis.* 72:16-18.
23. TeBeest, D. O. 1991. Ecology and epidemiology of fungal plant pathogens studied as biological control agents of weeds. Pages 97-114 in: *Microbial Control of Weeds*. D. O. TeBeest, ed. Chapman and Hall, New York.
24. Weidemann, G. J., TeBeest, D. O., and Cartwright, R. D. 1988. Host specificity of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* and *C. truncatum* in the Leguminosae. *Phytopathology* 78:986-990.
25. Yang, X. B., and TeBeest D. O. 1992. Rain dispersal of *Colletotrichum gloeosporioides* under simulated rice field conditions. *Phytopathology* 82:1219-1222.
26. Yang, X. B., and TeBeest, D. O. 1992. Green tree frogs as vectors of *Colletotrichum gloeosporioides*. *Plant Dis.* 76:1266-1269.
27. Yang, X. B., and TeBeest, D. O. 1994. Distribution and grasshopper transmission of northern jointvetch anthracnose in rice. *Plant Dis.* 78:130-133.
28. Yang, X. B., and TeBeest, D. O. 1995. Competitiveness of mutant and wild-type isolates of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on northern jointvetch. *Phytopathology* 85:705-710.