Fusarium oxysporum f. sp. niveum Race 2: A Highly Aggressive Race New to the United States

R. D. MARTYN, Associate Professor, Department of Plant Pathology and Microbiology and Texas Agricultural Experiment Station, Texas A&M University, College Station 77843

ABSTRACT

Martyn, R. D. 1987. Fusarium oxysporum f. sp. niveum race 2: A highly aggressive race new to the United States. Plant Disease 71: 233-236.

In 1981, an isolate of Fusarium oxysporum f. sp. niveum was isolated from a wilted watermelon plant in south central Texas that was highly aggressive toward several highly wilt-resistant watermelon cultivars. A second highly aggressive isolate was obtained in 1984 from the seed coat of a commercial lot of hybrid watermelon seed grown in north central Texas. Both isolates were highly aggressive in greenhouse tests, causing a mean of 90% wilt of all 17 watermelon cultivars tested, 10 of which are considered highly wilt-resistant. Comparisons with isolates of races 0, 1, and 2 (sensu Cirulli) indicated that the Texas isolates were identical to race 2, first described in Israel in 1973.

Fusarium wilt of watermelon (Citrullus lanatus (Thunb.) Natsum. & Nakai) caused by Fusarium oxysporum (Schlecht.) f. sp. niveum (F. o. f. sp. niveum) (E. F. Sm.) Snyd. & Hans. was first described by Smith (23,24) in 1894 from South Carolina and Georgia. The pathogen is now well established throughout the watermelon-growing regions of the world. In many areas, it is a

Texas Agricultural Experiment Station Journal Series No. TA21720.

Accepted for publication 29 September 1986 (submitted for electronic processing).

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

© 1987 The American Phytopathological Society

limiting factor in production. Where Fusarium wilt has been controlled, it has primarily been with the use of wiltresistant cultivars. Orton (17) developed the first wilt-resistant watermelon cultivar, Conqueror; however, it was not entirely satisfactory as a commercial type, and its resistance was lost or appreciably decreased when it was introduced into new areas such as Oregon and Iowa (22). Sleeth (22) was perhaps the first to investigate the possible existence of physiologic strains (races) of F. o. f. sp. niveum. He examined 23 "isolants" from seven states and indicated that they ranged in virulence from avirulent to highly virulent and were therefore different pathogenic strains (22). Reid (21) examined 99 isolates and separated them into a number of cultural races but into only two pathogenic races. McKeen (11) examined several isolates of F. o. f. sp.

niveum from Canada, and on the basis of timing of the wilt symptom and final percentage of wilt, he concluded that there were three distinct strains differing widely in virulence.

In 1963, Crall (4) reported two physiologic races in Florida: one that only caused wilting in susceptible cultivars and one that caused 100% wilting in susceptible cultivars and some wilting in moderately resistant cultivars such as Charleston Gray and Summit. From 1949 to 1959, Armstrong and Armstrong (1) tested 17 isolates from South Carolina to determine if different races were present. They later included Crall's two races from Florida (4) and concluded that differences in virulence existed among the isolates, but there was insufficient evidence to distinguish them as races. Following the genetic model for wilt resistance proposed by Henderson et al (6), Cirulli (3) classified F. o. f. sp. niveum isolates from Italy into two pathogenic groups: race 0 and race 1. Netzer and Dishon (15) and Netzer (13) reported the existence of a third race in Israel that was highly pathogenic to many cultivars with moderate or high wilt resistance. On the basis of their tests and following the nomenclature suggested by Cirulli (3), they designated the Israeli isolate as race 2. An isolate with similar pathogenicity was also found in Greece (13) and in Turkey (Fantino and Zengen, 1974, cited in 13).

In 1985, Martyn (9) reported a highly aggressive race of F. o. f. sp. niveum in Texas. Pathogenicity toward a number of moderately and highly wilt-resistant cultivars suggested the Texas isolate was similar to race 2, although no race number designation was assigned. The purpose of the present study was to compare two Texas isolates of F. o. f. sp. niveum with the Israeli race 2 along with the two races from Florida (races 0 and 1) and one from South Carolina (race 1) to determine if race 2 sensu Cirulli was present in the United States.

MATERIALS AND METHODS

Source of isolates. Two Texas isolates of F. o. f. sp. niveum were used. One (TX-X1D) was originally isolated by R. J

McLaughlin from the lower stem of a wilted plant of an unknown cultivar from Frio County (south central Texas) in 1981. The second isolate (TX-HC3-13B) was collected by R. D. Martyn in 1984 from the seed coat of a hybrid seedless watermelon seed lot produced in north central Texas. Each isolate was singlespored, tested initially for pathogenicity on a susceptible cultivar, and stored in soil-culture tubes (12). Race 2 (IS-59) was obtained from D. Netzer, Volcani Center, Bet Dagan, Israel, Isolates FL-60-3A(11) and FL-64-2(M59-1), races 0 and 1, respectively, were obtained from J. M. Crall, University of Florida, Agricultural Research Center, Leesburg. A second isolate of race 1 (ATCC 18467) was purchased from the American Type

Table 1. Percent wilt of watermelon cultivars inoculated with different isolates of Fusarium oxysporum f. sp. niveum (experiment 1)²

| | Isola | Cultivar mean | | |
|------------------|------------|---------------|-----------------|--|
| Cultivar | ATCC 18467 | TX-X1D | of all isolates | |
| Black Diamond | 100 a | 100 a | 100 a | |
| Sugar Baby | 80 a | 100 a | 90 ab | |
| Jubilee | 70 a | 67 a | 68 abc | |
| Charleston Gray | 27 a | 40 a | 36 c | |
| Calhoun Gray | 13 a | 52 b | 32 c | |
| Crimson Sweet | 13 a | 100 b | 56 abc | |
| Dixielee | 7 a | 95 b | 51 bc | |
| Treatment mean | | | | |
| of all cultivars | 44 a | 79 b | | |

²Inoculum level: 1×10^5 microconidia per milliliter. Percentage figures are the means of five replicated pots (five plants per pot) and are rounded to the nearest whole number. Numbers across a row followed by the same letter are not significantly different (P = 0.05) according to Fisher's LSD test. Statistical analysis and mean separation based on arc sine-transformed and weighted data. Statistical letters for cultivar mean separation (down column) have not been included except for the cultivar means of all isolates. All control plants (isolate = water) were rated 0% wilt and data are not included in the table.

Table 2. Percent wilt of watermelon cultivars inoculated with different isolates of Fusarium oxysporum f. sp. niveum (experiment 2)^z

| | | Cultivar mean of all | | | |
|-------------------------------|------------|-------------------------|------------|----------|--|
| Cultivar | ATCC 18467 | TX-X1D | TX-HC3-13B | isolates | |
| Black Diamond | 100 a | 100 a | 100 a | 100 a | |
| Black-Seeded Chilean | 100 a | 100 a | 100 a | 100 a | |
| Jubilee | 93 a | 100 a | 93 a | 95 ab | |
| Charleston Gray | 80 a | 93 ab | 100 b | 91 abc | |
| Charleston Gray 133 | 100 a | 60 b | 93 ab | 84 abc | |
| Peacock | 53 a | 93 ь | 93 ab | 80 bc | |
| Crimson Sweet | 43 a | 100 b | 100 b | 81 abc | |
| Sugarlee | 30 a | 100 b | 93 b | 74 bc | |
| Dixielee | 13 a | 100 b | 100 b | 71 bc | |
| Summit | 13 a | 87 b | 100 b | 67 c | |
| Royal Sweet | 13 a | 87 ь | 100 b | 67 c | |
| Royal Charleston | 27 a | 100 b | 100 b | 76 bc | |
| Royal Jubilee | 20 a | 93 b | 100 b | 71 bc | |
| All Sweet | 7 a | 100 b | 100 b | 69 c | |
| Calhoun Gray | 0 a | 100 b | 100 b | 67 c | |
| Citrullus colocynthis (Texas) | 92 a | 93 a | 87 a | 91 abc | |
| Treatment mean | | | | | |
| of all cultivars | 49 a | 94 b | 98 b | | |

²Inoculum level: 1×10^6 microconidia per milliliter. Percentage figures are the means of five replicated pots (three plants per pot) and are rounded to the nearest whole number. Numbers across a row followed by the same letter are not significantly different (P = 0.05) according to Fisher's LSD test. Statistical analysis and mean separation based on arc sine-transformed and weighted data. Statistical letters for cultivar mean separation (down column) have not been included except for the cultivar means of all isolates. All control plants (isolate = water) were rated 0% wilt and data are not included in the table.

Culture Collection (ATCC), Beltsville, MD. This isolate originated from South Carolina and was deposited with ATCC by G. M. Armstrong. All isolates were single-spored when received, increased, and stored in soil-culture tubes.

Method of inoculation. Unless stated otherwise, all plant inoculations were performed as follows: An active culture of each isolate was obtained by placing several soil granules from a soil-tube culture into a liquid mineral salts medium (5) and incubated on a rotary shaker (100 rpm) at 25 ± 2 C for 48-72 hr under continuous fluorescent light. The cultures were filtered through eight layers of sterile cheesecloth under aseptic conditions, and the predominantly microconidial suspensions were adjusted to either 1×10^5 or 1×10^6 microconidia per milliliter with sterile, deionized water. Captan-treated seeds of watermelon cultivars were obtained from commercial suppliers and planted in flats containing a vermiculite-perlite mix (1:1, v/v). Seed of the Egyptian cultivar Giza was supplied by Mr. Hamza, I.N.R.A.T., Tunis, Tunisia. When the first true leaf was evident (about 2 wk after planting), the seedlings were uprooted and the roots washed under a stream of gently flowing water. Seedlings were root-dipped into the respective inocula for 10-15 sec, swirled several times, and transplanted into 15-cm pots (three or four seedlings per pot) containing a coarse sand-peatvermiculite soil mix (4:1:1, v/v). Depending on the experiment, there were either five or seven replicated pots per treatment and the inoculum level was either 1×10^5 or 1×10^6 microconidia per milliliter. Control inoculations were made by root-dipping seedlings into sterile water or diluted, sterile mineral salts medium. All plants were maintained in the greenhouse and fertilized regularly after 1 wk with 10-20-10 NPK (twothirds-strength Miracle Gro) in the irrigation water. Percent wilt of plants was recorded weekly, and final percentage figures were reported for 3 or 4 wk.

Three evaluations of the Texas isolates were made. The first (experiment 1) was conducted in March 1983 and was the original cultivar-screening test of isolate TX-X1D. The second test (experiment 2) was conducted in March 1985, when an isolate of F. o. f. sp. niveum (TX-HC3-13B) was obtained from watermelon seed. In September 1985, a third test (experiment 3) was conducted in which the two Texas isolates were compared with identified races of F. o. f. sp. niveum from other areas, including race 2 from Israel.

RESULTS

The TX-X1D isolate was significantly (P = 0.05) more aggressive than ATCC 18467 toward three cultivars: Calhoun Gray, Crimson Sweet, and Dixielee (Table 1). These three cultivars are considered highly wilt resistant to the common isolates of F. o. f. sp. niveum, thus the 52, 100, and 95% wilt, respectively, caused by TX-X1D was the first indication of a possible new race. The small amount of wilt exhibited in Calhoun Gray (13%), Crimson Sweet (13%), and Dixielee (7%) with the ATCC 18467 isolate is consistent with earlier results using the same inoculum level (1× 10⁵ microconidia per milliliter) (10). When each cultivar was analyzed statistically across both isolates, the isolates clearly separated into two distinct reactions (Table 1). The ATCC 18467 isolate caused a mean of 44% wilt of all cultivars, whereas the TX-X1D isolate caused a mean of 79% wilt of all cultivars.

In the second test, the seed isolate was compared with TX-X1D and ATCC 18467. The inoculum level was increased 10-fold to 1×10^6 microconidia per milliliter, and more cultivars were tested. The two Texas isolates reacted similarly to each other on each cultivar, and the mean percentage of wilt for all cultivars was the same (Table 2). There was an increase in percentage of wilt caused by the increase in inoculum level from 1 × 10^5 to 1×10^6 microconidia per milliliter on the moderately and highly wiltresistant cultivars with the Texas isolates. Increasing the inoculum level of race 1 (ATCC 18467) resulted in an higher wilt percentage only in the slightly resistant and moderately resistant cultivars Jubilee and Charleston Gray. This is consistent with earlier results (10). Both Texas isolates clearly separated as distinct strains from the ATCC 18467 isolate: they caused a mean of 94 and 98% wilt on all cultivars compared with a mean of

49% wilt induced by ATCC 18467.

Comparisons of wilt percentages caused by the Texas isolates with those caused by the Israeli race 2 (IS-59) (experiment 3) on 17 cultivars suggest that they are identical (Table 3). As with other tests with these isolates, no cultivar was identified as either moderately or highly resistant (≥50% wilt) to race 2. Several cultivars showed less wilt than others when inoculated with the same isolate (i.e., Charleston Gray and Crimson Sweet) but were not significantly different from the others (P = 0.05)(Table 3). Again, each of the race 2 isolates was distinct from the other isolates, resulting in a mean of 90% wilt for all cultivars.

The two isolates of race 1, FL-64-2(M59-1) and ATCC 18467, reacted similarly when the means of all cultivars were compared, 36 and 32% wilting, respectively, but there were clear differences between the two isolates on individual cultivars (Table 3). Specifically, the cultivars All Sweet, Dixielee, Summit, and Sugarlee were only moderately resistant to the Florida isolate of race 1 [FL-64-2(M59-1)] but highly resistant to the South Carolina isolate of race 1 (ATCC 18467). Similarly, Charleston Gray 133 reacted differently to the two isolates of race 1.

There were also clear differences between race 0 and race 1. FL-60-3A(11) was pathogenic only to highly susceptible cultivars, which carry no resistance genes, and clearly avirulent on all other moderately or highly wilt-resistant cultivars tested. This was not the case with either isolate of race 1.

DISCUSSION

The results of this work document the existence of a highly aggressive race of F. o. f. sp. niveum in the United States. On the basis of comparison with the Israeli isolate of race 2, it is concluded that the Texas isolates are race 2. The extent of the distribution of this race in Texas or the United States is not known; however, its occurrence in south Texas and north central Texas suggests that it may be widespread in Texas. Recently, a third isolate of race 2 was confirmed from wilted plants (cultivar Jubilee) grown in northwest Texas (South Plains) near the New Mexico border. At present, no other state has reported the occurrence of race 2. Answers to the questions as to how and when race 2 arrived in Texas are lacking. The original isolation of race 2 in Texas was in 1981, only 7 yr after it was identified in Israel (13). It is most probable that a population of race 2 existed in Texas before 1981, because reports from farmers and extension agents during the late 1970s indicated higher than usual incidences of watermelon wilt.

The significance of this new race in Texas is potentially great. Texas produces almost 25% (24,000 ha) of the nation's watermelons. Although Fusarium wilt has been a long-standing problem to Texas watermelon production, it has generally been kept in check with wilt-resistant cultivars. Many cultivars have high wilt resistance to the common isolates of race 1 (i.e., Calhoun Gray, Crimson Sweet, Dixielee, and Sugarlee) (10), but none of these is resistant to race 2. Additionally, several hybrid watermelons (i.e., Royal Sweet and

Table 3. Percent wilt of watermelon cultivars inoculated with different isolates of Fusarium oxysporum f. sp. niveum (experiment 3)2

| | Isolate | | | | | | Cultivar |
|----------------------|--------------------------|----------------------------|------------------------|------------------------|--------------------|-------------------|-------------------------|
| Cultivar | FL-60-3A(11) (race 0) | FL-64-2(M59-1) (race 1) | ATCC 18467 (race 1) | TX-HC3-13B (race 2) | TX-X1D (race 2) | IS-59 (race 2) | mean of all isolates |
| Black-Seeded Chilean | 96 a | 86 a | 100 a | 96 a | 100 a | 100 a | 96 a |
| Black Diamond | 79 a | 96 a | 100 a | 100 a | 96 a | 96 a | 95 ab |
| Giza | 92 a | 93 a | 96 a | 89 a | 100 a | 96 a | 94 ab |
| Sugar Baby | 56 a | 50 a | 81 a | 96 a | 96 a | 100 a | 80 bc |
| Jubilee | 27 a | 54 ab | 86 b | 81 b | 93 b | 89 ь | 72 cd |
| All Sweet | 0 a | 46 b | 11 a | 100 c | 96 с | 100 c | 59 de |
| Dixielee | 0 a | 56 b | 4 a | 100 c | 96 с | 100 c | 59 de |
| Summit | 0 a | 55 b | 0 a | 90 c | 95 c | 100 c | 57 def |
| Sugarlee | 0 a | 56 b | 7 a | 89 с | 96 с | 92 c | 57 def |
| Royal Sweet | 0 a | 0 a | 4 a | 96 b | 92 b | 89 ь | 47 fgh |
| Charleston Gray 133 | 4 a | 0 a | 36 b | 88 c | 68 bc | 86 c | 47 fgh |
| Royal Jubilee | 0 a | 8 a | 0 a | 93 b | 85 b | 89 ь | 46 fgh |
| Royal Charleston | 0 a | 8 a | 4 a | 86 b | 96 b | 79 b | 46 fgh |
| Smokylee | 0 a | 0 a | 0 a | 95 b | 90 ь | 86 b | 45 fgh |
| Calhoun Gray | 4 a | 4 a | 0 a | 89 b | 89 b | 79 b | 44 gh |
| Charleston Gray | 0 a | 0 a | 18 a | 71 b | 71 b | 79 b | 41 h |
| Crimson Sweet | 0 a | 4 a | 4 a | 75 b | 88 b | 68 b | 40 h |
| Treatment mean | | | | | | | |
| of all cultivars | 21 a | 36 b | 32 ab | 90 с | 91 c | 90 с | |

Inoculum level: 1×10^6 microconidia per milliliter. Percentage figures are the means of seven replicated pots (four plants per pot) and are rounded to the nearest whole number. Numbers across a row followed by the same letter are not significantly different (P = 0.05) according to Fisher's LSD test. Statistical analysis and mean separation based on arc sine-transformed and weighted data. Statistical letters for cultivar mean separation (down column) have not been included except for the cultivar means of all isolates. All control plants (isolate = water) were rated 0% wilt and data are not included in the table.

Royal Jubilee) are becoming increasingly popular because of their wilt resistance. These too, however, are susceptible to the newly described race 2.

Resistance to Fusarium wilt was initially believed to be inherited as a recessive trait (18,20). Bennett (2), concluded that resistance was probably dependent on several factors (genes). Later studies (6,16,26), however, indicated that wilt resistance is controlled by a single dominant gene. Netzer (14) suggested that a nonspecific, polygenic resistance may be effective against race 2.

The status of the search for resistance to race 2 currently is not very encouraging. Netzer (14) screened 65 cultivars of domestic watermelon (C. lanatus), 138 Citrullus spp. accessions, a wild species of C. colocynthis common in Israel, and two wild species native to equatorial Africa (C. rehmii and C. ecirrhosus) for resistance to F. o. f. sp. niveum race 2. None of these cultivars or lines expressed resistance to race 2 when tested in the seedling stage. In the present study, a Texas selection of C. colocynthis was also susceptible to both race 1 and race 2.

A second significant finding is the detection of race 2 on commercial seed. Isolate TX-HC3-13B was obtained from the seed coat of a commercial seed lot of hybrid seedless watermelon and therefore has potential importance in the dissemination of this new race. F. o. f. sp. niveum is known to be externally seedborne (7,19,25). Porter (19) demonstrated a 3% infection level of commercial seed obtained from three southern states: Texas, Georgia, and Florida. In the present study, only one isolate of race 2 was obtained from a sample of 100 seeds; therefore, the infection level was $\leq 1\%$. Seeds sampled from other lots were negative for F. o. f. sp. niveum.

A secondary objective of this study was to evaluate watermelon cultivars in an effort to determine which one(s) would serve as the best differentials for separating races of F. o. f. sp. niveum. Cirulli (3) reported that Sugar Baby, Charleston Gray, and Calhoun Gray would separate races 0 and 1, with Charleston Gray being the key intermediate cultivar resistant to race 0 and susceptible to race 1. In our study,

depending on which isolate of race 1 was used. Charleston Gray was either susceptible or resistant (Table 3) and thus may not be the best differential cultivar. When each cultivar was analyzed statistically across all isolates, no one cultivar stood out as a clear choice for the intermediate reaction. Cultivars highly susceptible to all three races were easily identified (Black Diamond, Black-Seeded Chilean, Giza, and Sugar Baby), and cultivars highly resistant to race 0 and both isolates of race 1 were identified (Royal Sweet, Royal Jubilee, Royal Charleston, Smokylee, Calhoun Gray, and Crimson Sweet), but no cultivar was resistant to race 0 and susceptible to both isolates of race 1.

It may be that to separate isolates of F. o. f. sp. niveum into races will require more than several cultivars and the use of more than one isolate of known races to guard against differences in populations of the fungus. It is also necessary that defined inoculum levels and methods be adopted, because resistance is known to be affected by pathogen inoculum density (10) and inoculation method (8).

ACKNOWLEDGMENTS

I wish to thank R. J. McLaughlin, M. Meyer, and J. P. McEntee for technical assistance. I also thank the following companies for graciously supplying seed used in this study: Asgrow Seed Co., Burrel Seed Co., Northrup King Seed Co., ARCO Seed Co., and PetoSeed Co.

LITERATURE CITED

- Armstrong, G. M., and Armstrong, J. K. 1978. Formae speciales and races of Fusarium oxysporum causing wilts of the Cucurbitaceae. Phytopathology 68:19-28.
- Bennett, L. S. 1936. Studies on the inheritance of resistance to wilt (Fusarium niveum) in watermelon. J. Agric. Res. 53:295-306.
- Cirulli, M. 1972. Variation of pathogenicity in Fusarium oxysporum f.sp. niveum and resistance in watermelon cultivars. Pages 491-500 in: Actas Congr. Un. Fitopatol. Mediterr. Oeiras, 3rd.
- Crall, J. M. 1963. Physiologic specialization in Fusarium oxysporum f. niveum. (Abstr.) Phytopathology 53:873.
- Esposito, R., and Fletcher, A. M. 1961. The relationship of pteridine biosynthesis to the action of copper 8-hydroxy-quinolate on fungal spores. Arch. Biochem. Biophys. 93:369-376.
- Henderson, W. R., Jenkins, S. F., Jr., and Rawlings, J. O. 1970. The inheritance of Fusarium wilt resistance in watermelon, Citrullus lanatus (Thunb.) Mansf. J. Am. Soc. Hortic. Sci. 95:276-282.
- Fulton, H. R., and Winston, J. R. 1915.
 Watermelon wilt spread by contaminated seed.

- Pages 48-51 in: Biennial Report. N.C. Agric. Exp. Stn.
- Latin, R. X., and Snell, S. J. 1986. Comparison of methods for inoculation of muskmelon with Fusarium oxysporum f.sp. melonis. Plant Dis. 70:297-300.
- Martyn, R. D. 1985. An aggressive race of Fusarium oxysporum f. sp. niveum new to the United States. Plant Dis. 69:1007.
- Martyn, R. D., and McLaughlin, R. J. 1983. Effects of inoculum concentration on the apparent resistance of watermelons to Fusarium oxysporum f. sp. niveum. Plant Dis. 67:493-495.
- McKeen, C. D. 1951. Investigations of Fusarium wilt of muskmelons and watermelons in southwestern Ontario. Sci. Agric. 31:413-423.
- McKeen, C. D., and Wensley, R. N. 1961. Longevity of Fusarium oxysporum in soil culture. Science 134:1528-1529.
- Netzer, D. 1976. Physiological races and soil population level of Fusarium wilt of watermelon. Phytoparasitica 4:131-136.
- Netzer, D. 1983. Inheritance of resistance to Fusarium oxysporum in watermelon and cotton; mechanism of resistance in cotton. Pages 137-142 in: La Selection des Plantes. Bordeaux, France. Les Colloques de l'INRA 11.
- Netzer, D., and Dishon, I. 1973. Screening for resistance and physiological specialization of Fusarium oxysporum in watermelon and muskmelon. Abstr. 941 in: Int. Congr. Plant Pathol., 2nd. Minneapolis, MN.
- Netzer, D., and Weintall, C. H. 1980. Inheritance
 of resistance in watermelon to race 1 of
 Fusarium oxysporum f. sp. niveum. Plant Dis.
 64:853-854.
- Orton, W. A. 1917. Watermelon diseases. U.S. Dep. Agric. Farmers Bull. 821. 18 pp.
- Orton, W. A. 1907. On methods of breeding for disease resistance. Proc. Soc. Hortic. Sci. 5:28.
- Porter, D. R. 1928. Infection studies with watermelon wilt caused by *Fusiarum niveum* EFS. Pages 347-368 in: Iowa Agric. Exp. Stn. Res. Bull. 112.
- Porter, D. R., and Melhus, I. E. 1932. The pathogenicity of Fusarium niveum EFS and the development of wilt-resistant strains of Citrullus vulgaris Schrad. Iowa Agric. Exp. Stn. Res. Bull. 149, 184 pp.
- 21. Reid, J. 1958. Studies on the fusaria which cause wilt in melons. I. The occurrence and distribution of races of the muskmelon and watermelon fusaria and a histological study of the colonization of muskmelon plants susceptible or resistant to Fusarium wilt. Can. J. Bot. 36:393-410.
- Sleeth, B. 1934. Fusarium niveum, the cause of watermelon wilt. Pages 3-23 in: W.V. Agric. Exp. Stn. Bull. 257.
- 23. Smith, E. F. 1894. The watermelon disease of the South. Proc. Am. Adv. Sci. 43:289-290.
- Smith, E. F. 1899. Wilt disease of cotton, watermelon, and cowpea (*Neocosmospora* nov. gen.). U.S. Dep. Agric. Bull. 17. 73 pp.
- Taubenhaus, J. J. 1935. Seeds of watermelon and okra as possible carriers of Fusarium wilt. Phytopathology 25:969.
- Welch, A., and Melhus, I. E. 1942. Wilt resistance in F₁ hybrid watermelons. Phytopathology 32:181-182.