Symptomatology and Formation of Microsclerotia in Weeds Inoculated with *Verticillium dahliae* from Cotton

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Langston University Journal Series Paper 79-2 and Oklahoma Agricultural Experiment Station Journal Series Article 3617.
Supported by U.S. Department of Agriculture Science and Education Administration Cooperative Research Grants 416-15-26 and 516-15-90.
Accepted for publication 2 July 1979.

ABSTRACT

JOHNSON, W. M., E. K. JOHNSON, and L. A. BRINKERHOFF. 1980. Symptomatology and formation of microsclerotia in weeds inoculated with *Verticillium dahliae* from cotton. Phytopathology 70:31-35.

Symptomatology and microsclerotial formation were evaluated among 35 weed species inoculated with a defoliating strain of *Verticillium dahliae* isolated from upland cotton. The weed species are of economic importance in cotton production. A wide range of disease reactions was observed (0.0–4.4 on a 0–5 scale). Of 35 species, 19 were infected systemically. In four of the 35, *V. dahliae* was isolated from the proximal region of taproots with no vascular discoloration evident in basal stem areas. Twelve species were highly resistant to the wilt pathogen. Some infected weeds failed to exhibit any external symptoms, but stem tissues had mild to extensive vascular discoloration. The virulence of *V. dahliae* isolates recovered from inoculated weeds varied, but most isolates induced moderate to severe symptoms in susceptible cotton. Development of microsclerotia in senescent tissues of infected weeds could be an important factor in the failure of rotation programs to control the pathogen effectively. This study indicates that weeds can serve as a source of microsclerotia. The data support the need for an effective weed control program as an aid in reducing the incidence of Verticillium wilt.

Additional key words: crop rotation, *Gossypium hirsutum,* pest interactions.

Verticillium wilt of upland cotton (*Gossypium hirsutum* L.) is spreading rapidly throughout the cotton growing areas of the southern and western United States. Today, Verticillium wilt is destructive in all major cotton producing areas and ranks as one of the three most devastating diseases of the crop (4,7). In the 1976 growing season, Verticillium wilt caused the greatest loss of any parasitic disease of cotton in the Unitd States (8).

Although some agronomically adapted cotton cultivars exhibit various levels of resistance to the causal organism, *Verticillium dahliae* Kleb., none posses high levels of resistance (6). Moreover, a breeder may be confronted with the appearance of more virulent strains of the pathogen (18,24).

The importance of this disease and the lack of cultivars with high levels of resistance necessitate continuous efforts to develop effective control measures. A pathogen's persistance and possibly its multiplication on alternative susceptible hosts or symptomless carrier hosts seriously affect control measures, especially those based on rotation.

Some weed species are hosts of *V. dahliae* (5,11,14,20,22,26), but information based on critical evaluations of weed hosts for *V. dahliae* is scarce. Some disease evaluations have been based on a single plant specimen. Because of their importance in the long-term survival of *V. dahliae,* development, if any, of microsclerotia in weed tissue is of importance. The pathogenicity of isolates of *V. dahliae* recovered from weed hosts has not always been reported.

Objectives of this investigation were to critically assess the susceptibility and symptomatology of weeds common in cotton fields to an isolate of *V. dahliae* from cotton, to determine microsclerotia formation in weeds, and to test the virulence of isolates recovered from weed hosts on cotton. A preliminary report on part of this work has been published (17).

MATERIALS AND METHODS

The *V. dahliae* isolate used in this study was obtained from a diseased cotton plant growing in a nursery naturally infested with Verticillium wilt near Stillwater, OK. The isolate was classified as a defoliating strain (24).

Method of plant culture. Seeds of most weed species were germinated in agricultural grade vermiculite and grown until the first true leaves began to emerge. Seedlings were then gently uprooted and separated, and roots were washed free of adhering vermiculite. Seeds of a few species were not available, but seedlings were obtained from their natural habitat. Weed seedlings, whether grown from seed or obtained from natural habitats, were selected for uniformity and then transferred to a complete nutrient solution modified from that of Arnon and Hoagland (2,16). Iron was supplied as ferric EDTA. Nutrient solutions were adjusted to pH 6.8 by use of dilute HCl.

0031-949X/80/01003105/$03.00/0

TABLE 1. Susceptibility of some weed species to a *Verticillium dahliae* isolate from cotton.

Family Common name Botanical name[a]	Reaction type[b]	Change in height[c] (%)	Average disease index rating[d]
Aizoaceae			
Carpetweed			
Mollugo verticillata L.	S	−43.2	3.5
Amaranthaceae			
Palmers pigweed			
Amaranthus palmeri Watts	S	−32.7	1.5
Red root pigweed[e]			
A. retroflexus L.	S	− 3.7	1.3
Chenopodiaceae			
Lamb's-quarters			
Chenopodium album L.	S	−39.2	2.3
Compositae			
Cocklebur			
Xanthium pennsylvanicum Wallr.	R	− 2.1	0.0
Common ragweed			
Ambrosia artemisiifolia L.	R	− 1.0	0.0
Dandelion			
Taraxacum officinale Weber	S	−12.1	1.6
Perennial ragweed			
Ambrosia psilostachya DC	R	+ 2.8	0.0
Prickly lettuce			
Lactuca scariola L.	NS	− 2.5	0.1
Convolvulaceae			
Common morning glory[e]			
Ipomoea purpurea (L.) roth	S	− 9.2	1.8
Ivy leaf morning glory			
I. hederacea (L.) Jacq.	S	−33.9	2.3
Cruciferae			
Shepherd's purse			
Capsella bursa-pastoria (L.) Medic.	S	−28.0	3.2
Virginia pepperweed			
Lepidium virginicum L.	S	−23.2	4.2
Cyperaceae			
Yellow nutsedge[e]			
Cyperus esculentus L.	NS	− 3.5	0.1
Euphorbiaceae			
Copperleaf			
Acalypha virginica L.	NS	− 2.9	0.1
Geraniaceae			
Carolina cranesbill			
Geranium carolinianum L.	S	−17.1	3.7
Gramineae			
Barnyard grass[e]			
Echinochloa crus-galli (L.) Beauv.	R	0.0	0.0
Bermuda grass[e]			
Cynodon dactylon (L.) Pers.	R	−13.9	0.0
Goosegrass			
Eleusine indica (L.) Gaertn.	NS	+ 7.3	0.1
Green foxtail			
Setaria viridis (L.) Beauv.	R	− 0.3	0.0
Labiatae			
Henbit			
Lamium amplexicaule L.	S	−35.3	3.6
Malvaceae			
Flower-of-the-hour			
Hibiscus trionum L.	S	−69.1	4.4
Prickly sida[e]			
Sida spinosa L.	S	−22.1	3.1
Velvet leaf			
Abutilon theophrastii Medic.	R	− 2.3	0.0
Onagraceae			
Evening primrose			
Oenothera laciniata Hill	R	− 2.5	0.0
Oxalidaceae			
Oxalis			
Oxalis stricta L.	R	− 2.6	0.0
Polygonaceae			
Pennsylvania smartweed			
Polygonum pennsylvanicum L.	R	− 2.7	0.0
Portulacaceae			
Common purslane[e]			
Portulaca oleracea L.	S	−60.5	3.6
Solanaceae			
Buffalobur[e]			
Solanum rostratum Dunal.	S	−26.5	2.8
Carolina horsenettle[e]			
S. carolinense L.	S	−37.5	2.9
Ground cherry			
Physalis pumila Nutt.	R	− 4.7	0.0
Jimson weed			
Datura stramonium L.	S	−44.4	3.9
Silverleaf nightshade[e]			
Solanum elaeagnifolium Cav.	S	−33.1	3.0
Smooth ground cherry			
Physalis subglabrata Mack. & Bush.	R	+ 4.9	0.0
Zygophyllaceae			
Puncture vine			
Tribulis terrestris L.	S	−29.8	1.9

[a] Common names generally conform to the Weed Science Society Committee Report on Common Names.

[b] S = systemic, NS = nonsystemic, R = resistant.

[c] $\frac{\text{Mean height of control plants} - \text{mean height of inoculated plants}}{\text{mean height of control plants}} \times 100 =$ percent change in height. Each control mean based on 16 observations and each inoculated mean based on 20 observations.

[d] Rating based on scale of 0–5; 0 = no external symptoms, plant healthy; 1 = no external symptoms, vascular discoloration; 2 = slight leaf chlorosis and/or necrosis involving lower leaves; 3= advanced leaf chlorosis and/or necrosis with some defoliation; 4 = lethal reaction without complete defoliation; and 5 = lethal reaction with complete defoliation.

[e] One of the 10 most troublesome weeds in cotton in the western United States (15).

Tanks designed for controlling root temperature were used in these greenhouse experiments. Each tank contained 18 10-L buckets, and in each bucket four plants were placed individually in 1.5-cm holes in wooden strips attached to the plastic lids. Plants were supported in the holes by nonabsorbent cotton. The tanks were filled with water that was circulated by a motor driven propeller to maintain the root temperature at 21 C, which favors wilt development (1,9,13,23). Continuous forced aeration was provided to roots of all plants by an air pump.

Preparation of inoculum and method of inoculation. A 5-mm sterile cork borer was used to cut plugs from a 14-day-old culture of *V. dahliae* grown on Czapek-Dox agar. Agar plugs then were transferred to a sterile semimicro blending container, and 7 ml of sterile distilled water was added for each plug. The mixture was blended for 45 sec and then 1 ml of fungal suspension was pipetted onto Czapek-Dox agar in 100-mm diameter petri plates. A flattened multilooped transfer needle was used to spread the suspension uniformly over the agar surface. Plates were incubated at 24 C for 4 days, at which time fungal growth was uniform. For plant inoculations, fungal suspensions were prepared by blending for 1 min one plate of the 4-day-old cultures in 100 ml of tapwater. These fungal suspensions, consisting of a mixture of mycelia, microsclerotia, and conidia, were poured into buckets containing nutrient solultion. Final inoculum concentration averaged 1.7×10^4 viable propagules per milliliter of nutrient solution, as determined by dilution plate counts on Czapek-Dox agar. Control plants received comparable amounts of blended agar and water suspensions without the fungus. Each weed species was grown in nine buckets. In each instance, 20 plants (five buckets) were inoculated; the remaining 16 plants (four buckets) served as controls.

Plant evaluation. Disease readings were recorded 4–6 wk after inoculation, depending on the weed species. Plants were examined individually for foliar and vascular symptoms. To confirm presence or absence of the pathogen in plant tissues, four root and four stem sections from each inoculated plant were surface disinfected with 0.5% sodium hypochlorite after momentary wetting with 95% ethyl alcohol. The sections were transferred to Czapek-Dox agar.

Plant heights were recorded for all weed species after disease ratings were determined. Plants were tagged for identification and air-dried for 3–4 wk. Microsclerotial formation in senscent tissues was evaluated by employing a technique described by Brinkerhoff (3).

RESULTS

Weed species exhibited a very wide range of disease reactions. The susceptibility to *V. dahliae* of some weeds reported to be troublesome in cotton production is recorded in Table 1.

Of the 35 species, 19 were infected systemically (the fungus was isolated from root and stem tissue). Some infected weeds did not exhibit any external symptoms but developed mild to extensive internal browning in stem tissues. In four weed species, the pathogen was isolated from the proximal region of the taproot, but no vascular discoloration was evident in the basal stem area. Twelve species were highly resistant to wilt infection.

Several methods of inoculation with *V. dahliae* have been described (5,10,12,16). Different inoculation procedures may exert various influences on the inoculated plants. Injury to the root system may facilitate entry of the pathogen. Root injury did not occur with the inoculation technique used in this investigation.

Symptomatology. Infected plants usually were stunted, and average disease index ratings appeared to be positively correlated with shoot height reductions with some exceptions (Table 2). Root masses were not noticeably reduced (relative to control plants), however, except those of common morning glory (*Ipomoea purpurea* (L.) Roth), ivy leaf morning glory (*I. hederacea* (L.) Jacq.), and Virginia pepperweed (*Lepidium virginicum* L.).

Susceptibility of individual carpetweed plants (*Mollugo verticillata* L.) varied greatly. Inoculated plants generally were either severely attacked or not infected at all. The variation did not necessarily occur between buckets since plants within the same bucket varied. Anthesis occurred earlier in infected plants and flowers were fewer and smaller than those produced by uninfected plants. Infected plants had dropped large numbers of seed onto bucket lids before flowers had opened on uninfected plants.

Buffalobur (*Solanum rostratum* Dunal.) and Carolina horsenettle (*S. carolinense* L.), members of Solanaceae, are prolific weeds that often grow in cotton fields. Infected buffalobur plants exhibited moderate chlorosis with little necrosis, although discoloration was evident in vascular tissue. Flowering was extensive among both inoculated and control plants. Control plants of Carolina horsenettle also bloomed and set seed readily; in contrast, relatively few wilt-infected plants produced flowers but none were actually killed as a result of infection. Flowers were fewer and much smaller on infected plants than on control plants and aborted rapidly after anthesis. Flowers of infected plants did not abort after anthesis in the other weeds. Greenhouse whitefly (*Trialeurodes vaporariorum* Westwood) became a problem only on infected Carolina horsenettle plants. Very few whiteflies were observed on the more vigorously growing control plants, although control and inoculated buckets were located side by side in the same temperature tank.

Infection also influenced floral development in Virginia pepperweed. Flowers of infected plants were smaller and racemes were considerably more compact than those of control plants. Severely infected plants had set and dropped their seed by the time control plants began to flower. Root development of infected plants was also greatly reduced compared with controls.

No external symptoms were observed in inoculated plants of yellow nutsedge (*Cyperus esculentus* L.), but the pathogen was reisolated from root tissue near the crown. Isolations were accomplished with difficulty; the ratio of attempted isolations to successful recoveries was 160:9. The pathogen was not isolated from the base of the stem. Inoculated and control plants did not differ in flowering, root development, or height.

Among the weed species, sequence and severity of disease development in flower-of-the-hour (*Hibiscus trionum* L.) most closely paralleled those in susceptible cotton. Both flower-of-the-hour and cotton are members of the Malvaceae. *V. dahliae* was easily reisolated from both stem and root tissue.

Pathogenicity of isolates. Pathogenicity of 24 isolates of *V. dahliae* (recovered from 11 weed species) to the wilt-susceptible cotton cultivar Stoneville 62 is given in Table 2. The virulence rating for each isolate was based on disease reactions in eight inoculated cotton plants. The method of inoculating cotton plants was the same as described for the weed tests. Only two isolates failed to induce detectable symptoms in Stoneville 62 and could not be reisolated; six isolates induced a moderate level of infection, and 16 isolates caused severe disease symptons.

Formation of microsclerotia. All *V. dahliae* isolates obtained from plant root and/or stem material produced microsclerotia when cultured on Czapek-Dox agar, but the amounts of microsclerotia produced in culture by the different isolates recovered from weeds varied. For example, isolates from yellow nutsedge produced microsclerotia in agar culture but the amount was considerably less than that produced by the original culture. Isolates from copperleaf (*Acalypha virginica* L.) behaved similarly. In sharp contrast, the isolates recovered from flower-of-the-hour and Jimson weed (*Datura stramonium* L.) produced unusually large amounts of microsclerotia in agar culture compared with the original culture.

Development of microsclerotia in senescent host tissues was also evaluated (Table 3). Amounts of microsclerotia varied in senescent

TABLE 2. Relative pathogenicity of 24 isolates of *Verticillium dahliae* isolated from 11 weeds to Stoneville 62 cotton

Source of *Verticillium* isolates	Number of isolates from each source	Disease reaction of inoculated cotton[a]		
		Not infected	Moderately infected	Severely infected
Buffalobur	3	0[b]	1	2
Carolina horsenettle	2	0	0	2
Common morning glory	2	0	1	1
Common purslane	2	0	0	2
Flower-of-the-hour	3	0	0	3
Goosegrass	1	1	0	0
Jimson weed	2	0	0	2
Lamb's-quarters	1	0	1	0
Prickly sida	3	1	0	2
Yellow nutsedge	2	0	2	0
Virginia pepperweed	3	0	1	2

[a] Based on disease evaluation of eight plants per isolate.
[b] Each figure denotes number of isolates inducing the respective disease reaction in cotton.

TABLE 3. Microsclerotia in senescent root and stem tissue of weed species inoculated with *Verticillium dahliae* from cotton

Host	Relative amount of microsclerotia produced[a]	
	In root tissue	In stem tissue
Jimson weed	4.0	4.0
Flower-of-the-hour	3.0	4.0
Buffalobur	3.5	3.0
Common purslane	3.0	4.0
Virginia pepperweed	3.0	2.0
Common morning glory	2.0	1.0
Palmers pigweed	0.5	0.0
Lamb's-quarters	0.5	0.0
Stoneville 62 (check)	4.0	4.0

[a] Based on a 0–4 scale: 0 = no microsclerotia observed, 2 = microsclerotia production moderate, 4 = microsclerotia production very heavy.

tissues of all weeds that were systemically infected. Microsclerotia were also produced in some weeds that were not systemically infected. Relatively few microsclerotia occurred in root tissues of oxalis (*Oxalis stricta* L.), and none were detected in basal stem tissues. Microsclerotial production was also sparse in roots of goosegrass (*Eleusine indica* (L.) Gaertn.) and green foxtail (*Setaria viridis* (L.) Beauf.) but was more abundant in stem sections. Senescent tissue of copperleaf and prickly lettuce (*Lactuca scariola* L.) did not yield microsclerotia. No microsclerotia were observed in any weed species that did not have evidence of infection. Microsclerotia developed abundantly in senescent tissues of Jimson weed and flower-of-the-hour.

DISCUSSION

Most weed species evaluated in this investigation are of economic importance in cotton production in the United States and are common in and around cotton fields (15,19).

In most cases, only one species in a family was evaluated, but three or more species were included in each of four families: Gramineae, Malvaceae, Solanaceae, and Compositae (Table 1). Four species of Gramineae showed little variation in infection levels, with three average disease index ratings of 0.0 and one of 0.1. In the three dicot families, however, the range of reactions was relatively wide. The family Malvaceae includes cotton and flower-of-the-hour, which had the highest disease index rating of any weed species tested (4.4 on a 0–5 scale) but also contains velvet leaf (*Abutilon theopharastii* Medic.), which had a disease index rating of 0.0. In Solanaceae, the disease index range was from 0.0 for both ground cherry (*Physalis pumila* Nutt.) and smooth ground cherry (*P. subglabrata* Mack. & Bush.) to 3.9 for Jimson weed. Three of four species of Compositae rated 0.0 on the disease index scale, although dandelion (*Taraxacum officinale* Weber) received a 1.6 rating. Clearly, family relationships cannot be used to predict susceptibility to *V. dahliae* in these families, and this is probably also true for other families.

Verticillium isolates recovered from inoculated weeds varied somewhat in virulence, but most induced moderate to severe disease symptoms in susceptible cotton. In some weed species in which anthesis occurred during the period between inoculation and disease evaluation, wilt infection markedly affected anthesis and subsequent seed production. When plants are stressed by disease, however, flowering may occur earlier than usual. Two exceptions to this generalization were noted: anthesis occurred at about the same time in both infected and unifected plants of Carolina horsenettle (disease rating = 2.9) and buffalobur (disease rating = 2.8). Flowers of infected Carolina horsenettle plants were smaller and fewer than those of uninfected plants and soon aborted. Floral and seed development of infected buffalobur plants did not appear to differ from that in uninfected plants.

Nonlethal infections increase preference of some insect pests to certain plants (21). Such may have been the case with Carolina horsenettle plants in this study. The greenhouse whitefly was scarce on uninfected plants but abundant on infected plants in adjacent buckets.

As reported by Sherrod and Elliot (25), plants other than dicotyledons may be hosts for *V. dahliae*. In our study, species from two monocot families became infected with the pathogen: goosegrass (Gramineae) and yellow nutsedge (Cyperaceae). Both species yielded microsclerotia in root tissue. Symptomless hosts may be colonized by the pathogen, as demonstrated in goosegrass, yellow nutsedge, and some of the systemically infected weeds. In the field, many infected weeds would be difficult or impossible to differentiate from healthy ones.

Microsclerotia are important in the long-term survival of the pathogen during host-free periods and when conditions are unfavorable for active growth (3); thus development of microsclerotia in weed tissues could be important. This study indicates that weeds can serve as a source of microsclerotia. Relative amounts of microsclerotia produced in stem and root tissue of a given plant were not always similar. If a field is sufficiently infested with a wilt-susceptible winter annual weed such as henbit (*Lamium amplexicaule* L.), the pathogen population could be adequately maintained between summer crops, even if microsclerotia were absent. Henbit is economically important in the production of wheat, which is often recommended as a rotation crop to control Verticillium wilt.

Thus, several weed species growing in and around cotton fields may serve as alternate hosts of *V. dahliae*. Results of studies evaluating crop rotation to control Verticillium will have been inconsistent. The number of viable microsclerotia in soil influences the effectiveness of a rotation program aimed at reducing inoculum density of the pathogen (3,4). We suggest that the formation of microsclerotia, often in large numbers, in senescent tissues of infected weeds, may be an important reason why some rotation programs fail. *V. dahliae* probably can successfully survive any crop rotation sequence if weed control is not effective.

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