Fusarium Wilt of Susceptible and Resistant Tomato Isolines: Host Colonization

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ABSTRACT

The effect of the site of inoculation and inoculum concentration on disease development (as expressed by killing, stunting, vascular browning, and colonization) was investigated in susceptible and resistant host isolines. No killing, a nearly constant amount of vascular browning, and no stunting were observed in the resistant host inoculated with 5×10^6, 5×10^4, 5×10^3, and 5×10^2 spores/ml. The susceptible host, however, showed progressive sensitivity as the inoculum concentration increased.

In both host cultivars, the amount of mycelial colonization of the hosts decreased as the distance from the point of inoculation increased, even though there was nearly systemic distribution of fungus spores through the axis xylary system. Furthermore, the site of inoculation greatly affected the extent to which the host was colonized by the pathogen. Both the susceptible and resistant hosts showed increased resistance to colonization as the site of inoculation moved up the plant axis. It was concluded that two morphologically distinct zones, tissue above the cotyledonary node and tissue below the cotyledonary node, should be considered separately in comparative physiological or biochemical studies of susceptibility and resistance to *Fusarium* wilt of tomato. Phytopathology 61:834-840.

Additional key words: primary xylem; *Fusarium oxysporum* f. sp. *lycopersici,* race 1.

Fusarium oxysporum f. sp. *lycopersici* (Sacc.) Snyd. & Hans. spores were distributed throughout the main axis xylary system following the inoculation of stem cuttings (8). The rate of spore distribution and their distribution pattern, appeared to be the same for both susceptible and resistant isolines. However, no studies were made of the fate of either the spores or the plant after the spores became widely distributed in the xylem.

Studies by Beckman et al. (1, 2) on the nature of resistance to *Fusarium* in banana indicate that the major factors protecting the resistant plant are its ability to trap spores in the root xylem vessels and to seal off infected vessels from further invasion by the pathogen. Other investigations on tomato indicate that biochemical factors are of major importance in protecting the tomato plant from *Fusarium* infection (4, 5, 7, 11).

Scheffer & Walker (10) showed that resistant tomato plants retain their resistance when inoculated by placing stem cuttings directly into a *Fusarium* spore suspension. This, considered with reports (8, 9) that spores are widely distributed in the stem with this type of inoculation, indicates that the blockage mechanism, as operative in bananas, is ineffective as a resistant factor in *Fusarium* wilt of tomato stem cuttings. The objectives of this study were to determine if there were differences in the degree and sites of colonization of susceptible and resistant isolines of tomato inoculated by the cut stem technique with *F. oxysporum* f. sp. *lycopersici.*

MATERIALS AND METHODS.—*Host and pathogen.*—The materials and cultural methods for the host and pathogen have been described earlier (8). Briefly, the host material consisted of two cultivars of tomato, *Lycopersicon esculentum* Mill., wilt-susceptible Improved Pearson, and wilt-resistant Pearson VF_{11}. The two cultivars are isolines of one another. Plants were grown in a sterile soil-vermiculite mixture (3:1) in the greenhouse and fertilized with soluble 20-20-20 fertilizer solution as part of the watering regime. Plant age was measured from the time of seeding. Greenhouse temperature for all experiments was about 27 C.

The pathogen, *F. oxysporum* f. sp. *lycopersici,* Race 1, was originally obtained from the American Type Culture Collection (ATCC No. 16417). Spores for inoculum were harvested from 1-week-old shake cultures produced from a lyophilized subculture of the ATCC isolate. Inoculum was prepared by adding washed spores to sterile distilled water and by adjusting the concentration with the aid of a hemocytometer. Inoculations were made 2 cm below the cotyledonary node unless otherwise stated. The inoculation period was 30 min.

Effects of inoculum concentration.—In each of the following three experiments, 40 test and 10 control plants (25 days old) of each cultivar were divided into five equal groups and the plants prepared for inoculation as previously described (8). Four groups of each cultivar were inoculated with 5×10^6, 5×10^4, 5×10^3, or 5×10^2 spores/ml; the fifth group (controls) was treated with water. After inoculation, the cuttings were placed in sterile soil:vermiculite (3:1) and held in a mist chamber for 3 days. The plants were then placed on a greenhouse bench until sampled. The experiments were repeated 3 or more times. The mycelium production experiment was repeated 12 times for plants inoculated with 5×10^4 spores/ml and 4 times for plants inoculated with the other inoculum levels.

1) *Killing and stunting.*—Twenty days after inoculation, the number of plants of each cultivar that were killed as a result of inoculation at the various inoculum concentrations was determined. From the plants that survived, the number showing distinct stunting (less

than 80% of the size of the controls) was determined.

2) *Mycelium distribution.*—Twenty days after inoculation, the main axis of the plants was sectioned at 1-cm intervals from the point of inoculation. The sections were examined microscopically and the degree of colonization was estimated. The degree of colonization was rated on a scale from 0-4: 0 = no mycelium; 1 = less than 25% of the primary xylem vessels contain mycelium; 2 = 25-50% of the primary xylem vessels contain mycelium; 3 = 50-75% of the primary xylem vessels contain mycelium; 4 = 75-100% of the primary xylem vessels contain mycelium. Plants that were killed as a result of infection were also rated 4.

3) *Extent of vascular browning.*—This experiment was designed to determine how far from the point of inoculation (using the four inoculum concentrations given earlier) vascular browning could be detected. The plants were sampled 20 days after inoculation. Sections were cut at 1-cm intervals along the main axis. The sections were examined microscopically for the presence of browned vessels; and the section containing browned vessels farthest removed from the site of inoculation was recorded. No attempt was made to rate the amount of browning.

Effect of the site of inoculation on the degree of colonization and vascular browning.—Thirty 25-day-old plants were prepared for inoculation as described earlier (8). The plants were divided into three groups of 10 plants of each cultivar. One group was transversely cut through the hypocotyl 2 cm below the cotyledonary node. The second group was transversely cut through the cotyledonary node. The third group was transversely cut through the stem 2 cm above the cotyledonary node. The plants were then inoculated with a suspension of 5×10^4 spores/ml. After inoculation, the cuttings were placed in sterile soil:vermiculite (3:1) and held in a mist chamber for 3 days. The plants were placed on a greenhouse bench and sampled 15 days after inoculation. Five transverse sections were cut from the main axis at 1-cm intervals from the point of inoculation. The degree of colonization in each section was microscopically estimated and rated according to the parameters given in the previous part of this paper.

The number of plants that showed vascular browning in the various sections was also determined microscopically. No attempt was made to estimate the amount of browning. The experiment was repeated 4 times with 10 plants of each cultivar for each inoculation site. Controls consisted of 10 plants of each cultivar similarly treated but placed in sterile water instead of the spore suspension.

Spore lysis.—An attempt was made to determine if the spores transported to the upper portions of the stem, particularly the resistant stem, were lysed. Twenty 25-day-old plants of each cultivar were prepared for inoculation as described earlier (8). The plants were inoculated with a suspension of 5×10^4 spores/ml through a transverse cut 2 cm below the cotyledonary node. Ten inoculated plants of each cultivar were sampled immediately to determine spore transport distance. The other 10 inoculated plants of each cultivar were placed in sterile soil:vermiculite mix (3:1), held in a mist chamber for 3 days, then placed on a greenhouse bench. These plants were sampled 10 days after inoculation.

Sampling consisted of surface sterilization of the main axis and the aseptic removal of a 1-cm section of stem tissue taken between 2-3 cm above the cotyledonary node. The sampled stem tissue was cut into three discs and placed on acidified potato-dextrose agar (PDA) (8). The plated tissue was incubated at 28 C for 1 week to determine if viable *Fusarium* spores were present. The stem tissue immediately below the sampled area was examined for the presence of mycelium. Only plants in which mycelium was not observed immediately below the sampled area were considered valid for the spore lysis study. The absence of mycelium should indicate that subsequent growth of the fungus from the sampled tissue sections came from spores and not mycelium colonizing the tissue at the time of sampling. The experiment was repeated 3 times with 10 plants of each cultivar. Noninoculated controls were similarly treated.

RESULTS.—*Effect of inoculum concentration.*—1) *Killing and stunting.*—The effect of four inoculum concentrations: A, 5×10^6; B, 5×10^4; C, 5×10^3; and D, 5×10^2 spores/ml on the per cent kill that occurs from such inoculations is presented in Fig. 1. Regardless of the inoculum concentration, the resistant plant (R) retained its resistance, and no killing was observed. The susceptible plant (S), however, did show increased susceptibility to increased inoculum concentrations. The susceptible cultivar inoculated with 5×10^2 spores/ml showed 100% survival. If observations of survival had been made beyond 20 days after inoculation, it is probable that some killing of susceptible plants also would have occurred with inoculum concentrations of 5×10^2 spores/ml.

Figure 2 shows the per cent of the susceptible (S) and resistant (R) plants that were stunted as a result of inoculation at A, 5×10^6; B, 5×10^4; C, 5×10^3; and D, 5×10^2 spores/ml. Plants less than 80% of the size of the controls were considered stunted. Growth of the resistant cultivar (R) was apparently not affected by the inoculum levels used in the study, as no stunting was observed; however, the susceptible cultivar (S) was progressively affected as the inoculum level was increased.

2) *Mycelium distribution.*—Figure 3 shows the average estimates of the degree of colonization at the various positions on the axis of plants inoculated with 5×10^6, 5×10^4, 5×10^3, and 5×10^2 spores/ml. With each inoculum concentration, the amount of mycelium decreases as the distance from the site of inoculation increases. In general, the decreases in the amount of mycelium (i.e., the difference between the degree of colonization at one level and the degree at the levels above it) is inversely related to the inoculum concentration. In no instance was mycelium observed in the resistant stem further than 4 cm above the cotyledonary node. Indeed, mycelium was rarely observed in the

resistant stem beyond 1 cm above the cotyledonary node. In the susceptible plant, however, mycelium was frequently observed at 7 cm above the cotyledonary node, although it was usually not abundant at that level in the stem.

3) *Extent of vascular browning.*—The average distance that browning of the vascular bundles extended from the point of inoculation in both susceptible (S) and resistant (R) plants inoculated at A, 5×10^6; B, 5×10^4; C, 5×10^3; and D, 5×10^2 spores/ml is shown in Fig. 4. In the susceptible cultivar, there was a direct relationship between the extent of browning and the inoculum concentration. The extent of browning in the resistant cultivar was comparable at all inoculum concentrations.

Effect of the site of inoculation.—The effect of three sites of inoculation (2 cm below the cotyledonary node, at the cotyledonary node, and 2 cm above the cotyledonary node) on the degree of colonization observed at different positions on the axis, and the number of plants showing vascular browning at those positions, is illustrated in Fig. 5. The colonization (indicated by the area under the curve) observed in the susceptible plant was greater than that observed in the resistant plant inoculated at the same position. This relationship does not hold for comparing susceptible plants inoculated at one site with resistant plants inoculated at another site. The degree of colonization at any position on the axis of the susceptible plant was always greater than that observed at the same position in the resistant plant. This relationship holds for comparing susceptible and resistant plants inoculated at the same or different sites. For instance, the rating of the degree of colonization at position 3 on the axis of resistant plants inoculated 2 cm below the cotyledonary node was 0; the colonization rating at the same position on the axis of susceptible plants inoculated at the same site was 0.37. By contrast, the degree of colonization at position 3 on the axis of susceptible plants inoculated at the cotyledonary node was 0.35; the colonization rating at position 3 on the axis of susceptible plants inoculated 2 cm above the cotyledonary node was 0.47.

Figure 5 also shows that the amount of mycelium decreases as the distance from the inoculation site increases. Both cultivars followed this pattern at each inoculation site. It is interesting to note that the mycelium extinction point (location on the axis with 0 mycelium rating) for resistant plants was found closer to the inoculation site as the site of inoculation was moved up the axis. For example, the mycelium extinction point in resistant plants inoculated 2 cm below the cotyledonary node was 5 cm from the inoculation site; in resistant plants inoculated at the cotyledonary node, the extinction point was 4 cm from the site of inoculation; in resistant plants inoculated 2 cm above the cotyledonary node, the extinction point was 3 cm from the inoculation site. Although the extinction point was not observed in the susceptible cultivar, it appears that a similar relationship would occur.

Since only the first 5 cm from the point of inoculation was examined, the extinction point for susceptible plants inoculated at the various sites was not observed. However, assuming that the observed values of the degree of colonization in the first 5 cm of the susceptible plant fall along a straight line, a prediction of the extinction point based on the line of best fit (method of least squares) was made; for comparative purposes similar calculations were made for the resistant plant (Table 1). The similarity between the observed and calculated mycelium extinction points for resistant plants indicates that there was a linear decrease in the amount of mycelium from the point of inoculation. In susceptible plants inoculated 2 cm below the cotyledonary node, the mycelium extinction point was calculated to be 5.7 cm from the site of inoculation. The extinction point should have been observed at 4.9 and 4.7 cm from the site of inoculation in plants inoculated at the cotyledonary node and 2 cm above the cotyledonary node, respectively.

Using the line of best fit for the degree of colonization curves in Fig. 5, it was possible to make a simple determination of the area under each curve. The areas were then used to calculate ratios to demonstrate an increase in resistance in both cultivars as the site of inoculation moved up the axis (Table 2); the larger the ratio, the greater the resistance. In addition, the table shows that resistance is increasing in the resistant cultivar faster than in the susceptible cultivar (compare the ratios of Items 1, 2, 3, with 4, 5, 6, Table 2).

Plants used to determine the amount of mycelium at different positions on the axis were also examined for vascular browning. The per cent of plants that had vascular browning at the various positions on the plant axis is shown (Fig. 5). More vascular browning was observed in susceptible than in resistant plants; the amount of browning decreased as the distance from the site of inoculation increased; less browning occurred as the site of inoculation was moved up the axis. Vascular browning extended beyond the mycelium extinction point except in plants inoculated 2 cm below the cotyledonary node.

Spore lysis.—The purpose of sampling the stem and

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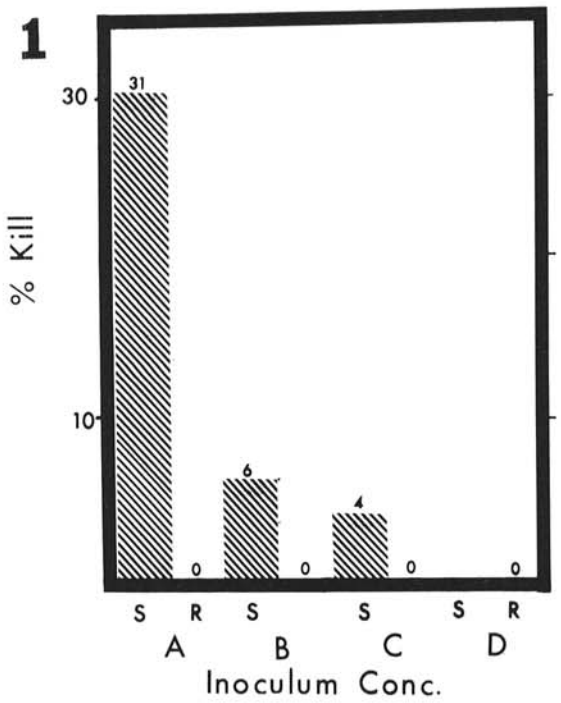
Fig. 1-4. Twenty-five-day-old wilt-susceptible (S), Improved Pearson, and wilt-resistant (R), Pearson VF_{11}, tomato isolines inoculated with *Fusarium oxysporum* f. sp. *lycopersici* spores through the main axis 2 cm below the cotyledonary node. Aqueous spore suspensions of (A), 5×10^6; (B), 5×10^4; (C), 5×10^3; and (D), 5×10^2 spores/ml were used as inoculum. Data collected 20 days after inoculation. **1)** The effect of the four inoculum concentrations on the per cent of host plants killed. **2)** The effect of the four inoculum concentrations on the per cent of plants stunted. Plants less than 80% of the size of the controls were considered stunted. **3)** The effect of the four inoculum concentrations on the extent of colonization of the host. The degree of colonization was estimated microscopically in transverse section taken at 1-cm intervals along the main axis of the host. **4)** The effect of the four inoculum concentrations on the distance vascular browning extended from the point of inoculation. Transverse sections at 1-cm intervals along the main axis were examined microscopically.


1
% Kill
30
10
31
6
4
0
0
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S R S S S R
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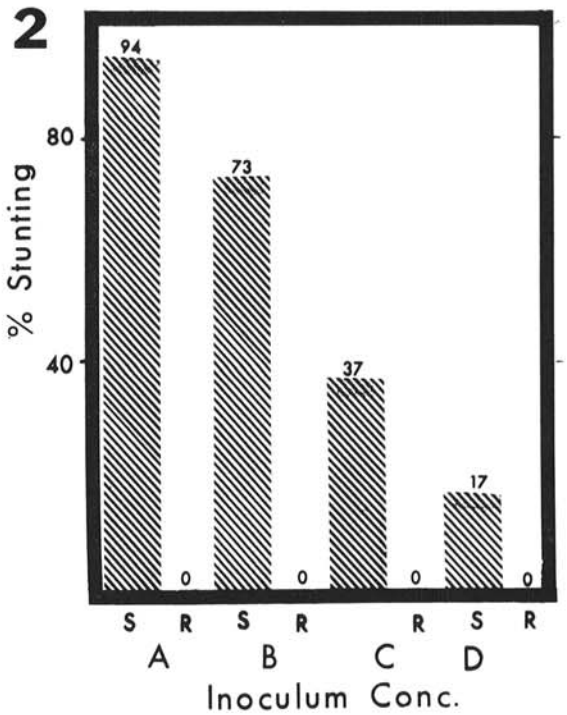
Inoculum Conc.


2
% Stunting
80
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94
73
37
17
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S R S R R S R
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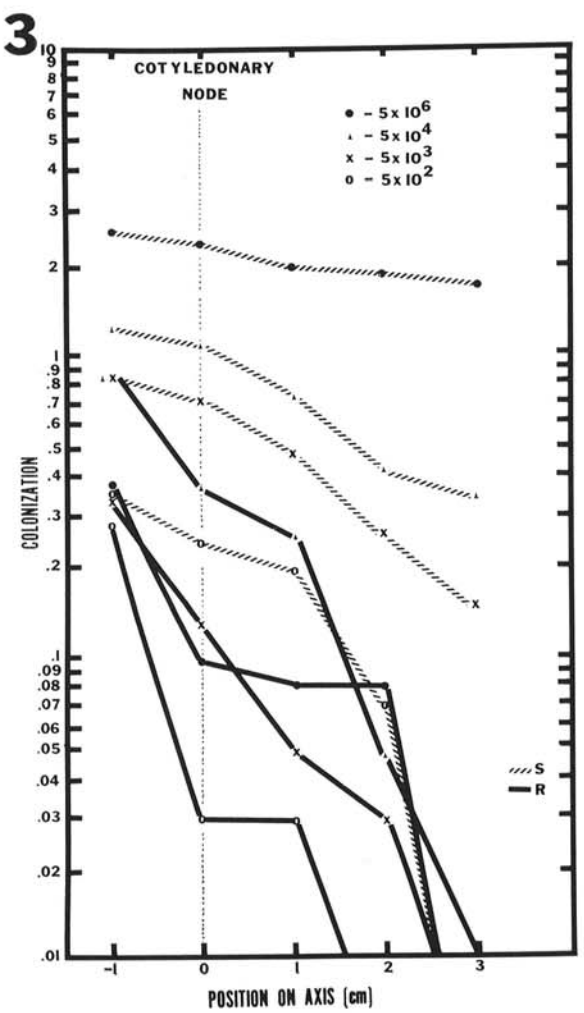
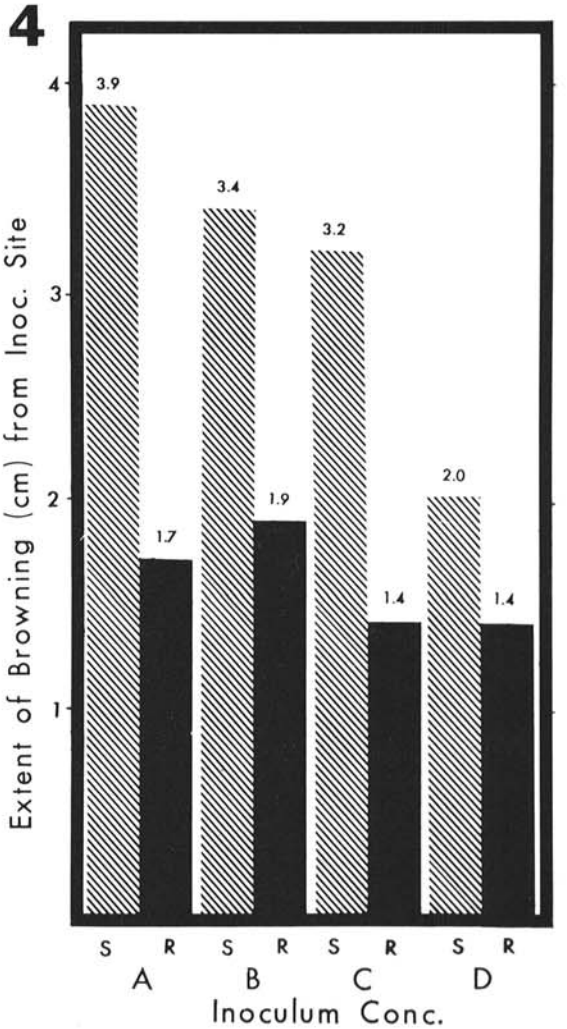

3
COTYLEDONARY NODE
● - 5x10^6
▲ - 5x10^4
x - 5x10^3
o - 5x10^2
COLONIZATION
S
R
POSITION ON AXIS (cm)


4
Extent of Browning (cm) from Inoc. Site
4
3
2
1
3.9
1.7
3.4
1.9
3.2
1.4
2.0
1.4
S R S R S R S R
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Inoculum Conc.

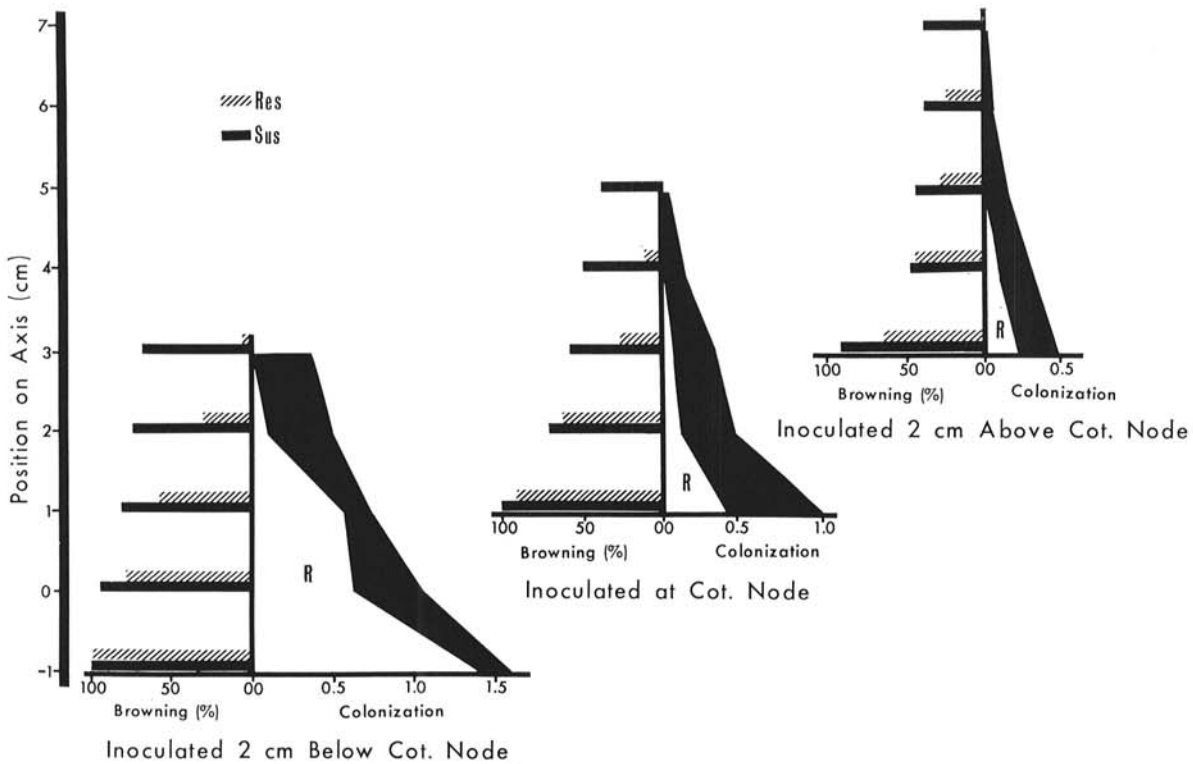

Fig. 5. The effect of the site of inoculation on host colonization and vascular browning. Wilt-susceptible, Improved Pearson (S), and wilt-resistant, Pearson VF_{11} (R), isolines of tomato were inoculated with *Fusarium oxysporum* f. sp. *lycopersici* (5×10^4 spores/ml) through a transverse cut 2 cm below the cotyledonary node, at the cotyledonary node, and 2 cm above the cotyledonary node, 25 days after planting. Fifteen days after inoculation, sections cut from various positions on the plant axis were examined to determine the degree of colonization at that position, and also to determine the per cent of sections that showed vascular browning. The ordinate represents the plant axis; the position at which sections were cut are in reference to the cotyledonary node (0); —1 and 1 indicate 1 cm below and above the cotyledonary node, respectively. The abscissa, repeated for each inoculation site, contains two scales. To the left of 00 is represented the per cent of plants showing vascular browning at the position indicated by the ordinate; to the right of 00 is the estimate of the degree of colonization at the position indicated by the ordinate.

plating sections immediately after inoculation was to determine if the spores were transported to a level 2-3 cm above the cotyledonary node. Previous studies (8) indicated that spores should be transported that distance and that noticeable lysis does not occur during the time required to sample the tissue.

Transverse sections cut 2-3 cm above the cotyledonary node 10 days after inoculation produced excellent *F. oxysporum* f. sp. *lycopersici* growth when plated on PDA. This leads us to conclude either that noticeable lysis did not occur within 10 days after inoculation, or, if lysis did occur, the mycelium in the lower part of the axis sporulated and the newly formed spores were transported to the area sampled. The ability of *F. oxysporum* f. sp. *lycopersici* mycelium to sporulate in the vessels of the tomato plant is documented (Fig. 6); thus, a positive, but erroneous, spore viability test could have been obtained 10 days after inoculation.

TABLE 1. Calculated and observed distance (cm) from the site of inoculation with *Fusarium oxysporum* f. sp. *lycopersici* to the point where 0 mycelium rating occurs (mycelium extinction point) in Improved Pearson, susceptible (S), and Pearson VF_{11}, resistant (R), tomato isolines

	$Y = mx + C$[a]		Distance (cm) of extinction point from inoculation site			
			Calculated		Observed	
Site of inoculation	S	R	S	R	S	R
2 cm Below cot. node	$-0.31 \times +1.5$	$-0.33 \times +1.21$	5.7	4.7		5
At cot. node	$-0.22 \times +0.85$	$-0.12 \times +0.31$	4.9	4.0		4
2 cm Above cot. node	$-0.12 \times +0.45$	$-0.12 \times +0.19$	4.7	3.0		3

[a] The values for the equation $Y = mx + C$ were derived from the line of best fit (method of least squares) for the observed data. Inoculations were made at measured distances from the cotyledonary (cot.) node.

TABLE 2. Ratios of the degree of colonization by *Fusarium oxysporum* f. sp. *lycopersici* in Improved Pearson, susceptible (S), and Pearson VF_{11}, resistant (R), tomato isolines inoculated at the same and different positions on the plant axis

Item	Numerator/Denominator	A_1/A_2[b]	$A_1 + A_2$	Ratio
1.	S, inoculated 2 cm below cot.[a] / S, inoculated 2 cm below cot.	285/285		1.0
2.	S, inoculated 2 cm below cot. / S, inoculated at cotyledon	285/134	419	2.1
3.	S, inoculated 2 cm below cot. / S, inoculated 2 cm above cot.	285/66	351	4.3
4.	R, inoculated 2 cm below cot. / R, inoculated 2 cm below cot.	171/171		1.0
5.	R, inoculated 2 cm below cot. / R, inoculated at cotyledon	171/36	207	4.8
6.	R, inoculated 2 cm below cot. / R, inoculated 2 cm above cot.	171/16	187	10.7
7.	S, inoculated 2 cm below cot. / R, inoculated 2 cm below cot.	285/171	456	1.7
8.	S, inoculated 2 cm above cot. / R, inoculated 2 cm above cot.	66/16	82	4.1

[a] Inoculations were made at measured distances from the cotyledonary node (cot.).
[b] A_1 and A_2 are arbitrary units of the areas under the curves calculated from the line of best fit for the observed data.

DISCUSSION.—If *Fusarium* wilt-susceptible and -resistant tomato cultivars are compared on the basis of the extent to which the plants are colonized by the invading pathogen, our data seem to indicate that a paradox exists. Depending upon the site of inoculation, resistant plants may approach the level of susceptibility of susceptible plants, and vice versa. When both the susceptible and resistant cultivars are inoculated below the cotyledonary node, the degree of colonization of the resistant plants approaches that of the susceptible plants (indicated by a ratio of 1.7, Table 2, item 7). When inoculations were made above the cotyledonary node, both cultivars were colonized to a much lesser extent (indicated by the lower values of $A_1 + A_2$, Table 2) than when inoculations were made below the cotyledonary node. Thus, susceptibility is manifest in both cultivars, but to a greater extent in the susceptible, when inoculations are made below the cotyledonary node; and resistance is expressed in both cultivars, but to a greater extent in the resistant, when inoculations are made above the cotyledonary node. Consequently, two morphological zones, tissue above the cotyledonary node in resistant plants and tissue below the cotyledonary node in susceptible plants should be emphasized in comparative studies of susceptibility and resistance of tomato to *Fusarium* wilt.

Blackhurst & Wood (3) observed a situation similar to that reported here while working on the susceptibility and resistance of tomato to *Verticillium* wilt. They found that the main axis and petioles of the susceptible plants were nearly systemically colonized by the pathogen; however, the resistant cultivar was free of the pathogen in the upper petioles. Apparently, something was interfering with the growth of the pathogen into the resistant petioles. Dimond & Edgington (6) and Scheffer & Walker (9) point out that the cause of wilt is more a result of dysfunction in the petioles than in the stem. This may explain why the extensive colonization we observed in the lower axis of the resistant plant was not tantamount to wilt.

In effect, the data reported here and previously (8) dictate a particular direction for our future studies on *Fusarium* wilt of tomato. Previous studies convinced us that *F. oxysporum* f. sp. *lycopersici* spores can be widely distributed throughout the primary xylem when plants are inoculated through a transverse cut in the plant axis. This, considered with the estimates of the degree of colonization and the apparent absence of spore lysis, leads us to conclude that the spores trans-

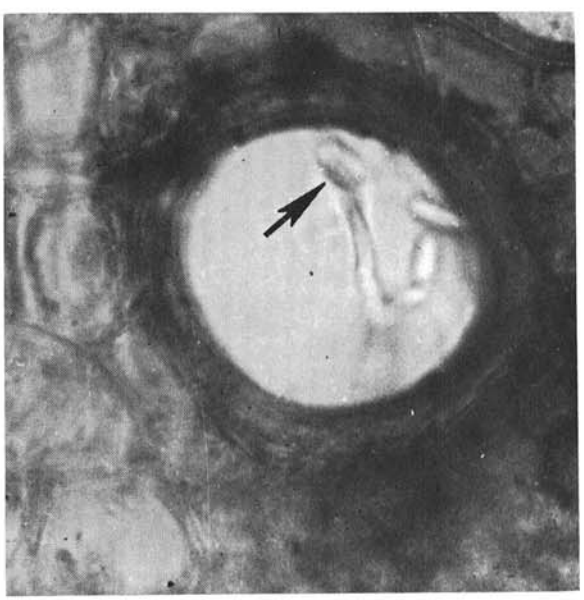

Fig. 6. *Fusarium oxysporum* f. sp. *lycopersici* mycelium sporulating (arrow) in a vessel of the susceptible tomato, Improved Pearson, 5 cm from the point of inoculation and 20 days after inoculation.

ported to the upper portions of the axis, although perhaps not lysed, do not germinate or grow as well as in the lower portions of the axis. This is particularly true of the resistant cultivar.

The task immediately ahead is to determine what factor(s) is responsible for retarding the germination of spores or growth of mycelium in the axis tissue above the cotyledonary node. If the factor is a naturally occurring compound whose effectiveness is determined by concentration, then we would expect to find the highest effective concentration in the upper portion of the resistant plant axis and a lower concentration in the upper portion of the susceptible plant axis. The lowest concentration should be found in the susceptible plant tissue below the cotyledonary node.

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