THE HOST-PARASITE RELATIONSHIP IN SUSCEPTIBLE CANTALOUPS, RESISTANT CANTALOUPS AND CUCUMBERS INOCULATED WITH *Fusarium* *bulbigenum* (Cke. and Mass.) var. *niveum* Wr. f. 2.

- By -

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INTRODUCTION

Fusarium wilts are among the most important diseases of cultivated plants. A serious wilt of cantaloups (*Cucumis melo* L.) is caused by *Fusarium bulbigenum* (Cke. and Mass.) var. *niveum* Wr. form 2. This disease has been described by Leach, and Leach and Currence (4, 6).

The host-parasite relationship in various plants subject to attack by vascular Fusaria has been investigated (1, 2, 11, 14, 16, 18, 20, 22, 23, 24), but the only study of the histology of cantaloups infected with Fusarium wilt is a brief discussion by Leach and Currence (6). Yoshii (22, 23, 24) and Wilson (20) studied the relationship between host and parasite in susceptible and resistant varieties and strains of watermelons infected with Fusarium wilt. The watermelon pathogen is a "form" of *F. bulbigenum* var. *niveum* Wr. and can be distinguished from the cantaloup "form" only on the basis of pathogenicity (3, 4, 6, 15, 21).

The most satisfactory method of controlling wilt diseases has been the development and use of resistant varieties. No significant resistance to Fusarium wilt was found by Leach and Currence (5, 6) in any of the netted skinned varieties of *Cucumis melo*, but resistance was found in smooth skinned types. Highly resistant strains of netted skinned melons have since been obtained by hybridization, but those so far produced have not been entirely satisfactory from the commercial point of view.

While resistant varieties of various plants may not develop typical symptoms of the disease, they may be invaded to some extent by the wilt Fusaria. This has been observed in watermelons by Wilson (20), in cabbage by Smith and Walker (14) and Anderson and Walker (1), in peas by Schroeder and Walker (11) and Virgin and Walker (18), in flax by Tisdale

(16), and in other plants by various workers. The relationship between parasite and host in resistant cantaloups has not been investigated previously.

Cucumbers, which are closely related to cantaloups, were not affected by the cantaloup wilt Fusarium in tests conducted by Leach and Currence (6). However, Porter (10) was able to isolate F. bulbigenum var. niveum capable of infecting watermelons from supposedly immune citron vines.

In as much as preliminary trials showed that F. bulbigenum var. niveum f. 2 can be isolated from tissues of resistant cantaloups and cucumbers inoculated with that fungus, it was considered worthwhile to investigate further the responses of susceptible and resistant cantaloups and of cucumbers to inoculation. The purpose of this work was to study comparatively the host-parasite relationship in these three plants.

MATERIALS AND METHODS

Source of Seed

The susceptible cantaloup plants used throughout this work were all raised from a single lot of commercial seed of the variety Hales Best No. 36. The resistant cantaloups were grown chiefly from seeds of strain 11-38, which was provided by Dr. T. M. Currence of the University of Minnesota. This strain originated at the Iowa Agricultural Experiment Station from a cross between Honey Ball and Sugar Rock, and was homozygous for wilt resistance. Another resistant strain used to a limited extent was known as P. B. No. 13. This strain was furnished by Dr. H. M. Munger of the Department of Plant Breeding at Cornell University. The cucumbers were of the variety Early Fortune.

Source of Inoculum

The culture of Fusarium used in this study was designated A-122-1-1-1. It was the third successive single microconidial isolate from a culture isolated from a wilted cantaloup plant from Anne Arundel County, Maryland. The original isolation was made by Dr. Mark Woods on July 10, 1938 and identified as Fusarium bulbigenum var. niveum f. 2. Culture A-122-1-1-1 was somewhat more virulent but identical in pathogenicity with a culture of Fusarium bulbigenum var. niveum f. 2 from Minnesota which it resembled closely in morphological and cultural characteristics.

The inoculum used throughout the study[1] was prepared in the following manner. The fungus was grown on 50 c.c. of a liquid medium[2] in 125 c.c. Erlenmeyer flasks. After approximately 30 days incubation at 28° C. the liquid cultures were filtered, and the fungus mat from each flask was ground in a Waring Blendor with 100 c.c. of tap water. The resulting milky suspension of spores and mycelial fragments was used without further dilution.

Culture and Inoculation of Plants

For the penetration studies seeds were surface sterilized with one percent calcium hypochlorite solution and germinated at room temperature on filter paper moistened with sterile nutrient solution in petri dishes.

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[1] A spore suspension was used to inoculate seedling roots in the penetration studies.

[2] Richard's modified solution: Sucrose, 50 gm.; potassium nitrate, 10 gm.; dihydrogen potassium phosphate, 5 gm.; magnesium sulfate, 2.5 gm.; water, 1,000 c.c.

When the radicles were 1 to 3 cm. long, they were inoculated either by dipping them into a suspension of spores from the surface of an agar culture of the wilt Fusarium or by pouring a few drops of the spore suspension over them. At intervals after inoculation portions of the living roots were mounted in tap water on a microscope slide under a cover slip supported by strips of paraffin to prevent crushing and examined under the oil immersion lens of the microscope.

In order to study the effect of the wilt Fusarium on seed germination and the development of seedlings, seeds were planted in sterilized sand in earthenware bulb pans in the greenhouse and inoculated by pouring 100 c.c. of the inoculum over the seeds in each bulb pan before the sand was firmed over them. The sand was kept moist with tap water until the first plants began to appear and thereafter was moistened with nutrient solution.[1]

For studies on the gross and histological effects of the fungus on older plants, seeds were germinated in flats of sand in the greenhouse and inoculated by dipping the roots of selected, uniform plants into a beaker of the inoculum just before transplanting into 4 inch pots of sterilized sand. The plants were fed with 100 c.c. of nutrient solution per pot each day. A number of experiments were run so as to have a complete picture of the symptom sequence and a wide range of material for histological study.

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[1] A 3 salt nutrient solution was used: $Ca(NO_3)_2 \cdot 4H_2O$, .005 mols per liter; KH_2PO_4, .0025 mols per liter; $MgSO_4 \cdot 7H_2O$, .0025 mols per liter. This solution was supplemented by the addition of approximately: 0.11 p.p.m. Mn., 0.02 p.p.m. Zn., 0.02 p.p.m. Cu., 0.12 p.p.m. B. Iron was supplied as ferric tartrate at the rate of 1 c.c. of a 0.5% solution per liter of nutrient solution.

Seeds of susceptible cantaloups and of cucumbers for the experiment with grafted plants were planted directly in 2 gallon crocks of sand. The plants were fed with nutrient solution by a drip system which delivered approximately 1 liter of solution per day per crock (9). When the plants were 40 days old they were approach grafted. The graft union was made in the second to fourth internode and the union wrapped with parafilm (Plate I). When union was established, approximately 15 days, the undesired root system and the opposite shoot system were severed. Eighteen cantaloup plants on cucumber roots, and eighteen cucumber plants on cantaloup roots, an equal number of cantaloup plants on cantaloup roots and cucumber plants on cucumber roots were prepared in this manner. Such plants grew normally and set and matured fruits if they were not killed by the disease. Five days after severing the undesired root and shoot systems the sand was brushed aside to expose a portion of the root system, and the plants were inoculated by pouring 10 c.c. of the inoculum directly onto the exposed roots. Ungrafted cantaloup and cucumber plants growing under the same conditions were similarly inoculated at the same time.

Reisolation of the Fungus

The location of the fungus in inoculated plants was determined by plating out portions of tissue on acidified Wellman's agar.[1] Tissues selected for culturing were washed in running water and surface sterilized

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[1] Wellman's agar: proteose peptone 5.0 g., dihydrogen potassium phosphate 0.5 g., magnesium sulfate 0.5 g., maltose 15.0 g., ferrous sulfate 0.03 g., agar 12.0 g., water 1,000.00 c.c. It was acidified by adding 3 drops of 20% lactic acid per 15 c.c. of medium after autoclaving.

by immersion for 20 minutes in 1 percent calcium hypochlorite solution.

Histological Materials

Tissues adjacent to areas which yielded the wilt Fusarium were selected and fixed either in formol-acetic-alcohol, Navaschin's solution or Helley's solution. They were dehydrated by the short butyl alcohol series and embedded in Tissuemat. Sections were cut 15 or 18 microns thick on a rotary microtome and stained with safranine and fast green. The counts of tyloses in the vessels and some of the effects on the cytoplasm and the development of necrotic areas in the pith and cortex were observed in fresh tissues. These were sectioned on the sliding microtome at approximately 150 to 200 microns and examined without staining.

RESULTS

External Symptoms

Seedlings

The germination of seeds of cantaloups and cucumbers was little affected when the seeds were inoculated at the time they were planted in sand, but the seedlings were attacked very soon after germination. Many of the seedlings of both the susceptible and resistant cantaloups were attacked severely and died within a few days. The Fusarium caused root-rot and damping-off. A few persisted as long as two weeks but were subnormal in size and appearance (TABLE 1). The root systems were necrotic with some of the lateral roots completely rotted away. There were brown lesions near the peg in some cases. The hypocotyl was sometimes cracked, and the cotyledons were yellowed with narrow necrotic strips at the mar-

TABLE 1. Effect of inoculation with *Fusarium bulbigenum* var. *niveum* f. 2 on emergence and stand of seedlings.

	Percent emergence		Percent of plants surviving two weeks after first seedling emerged	
	Check	Inoculated	Check	Inoculated
Susceptible Cantaloup	73.7	70.8	100.0	12.9
Resistant Cantaloup	40.0	34.7	96.7	30.8
Cucumber	60.0	68.0	100.0	91.2

gins. The inoculated cucumber seedlings, however, were indistinguishable from their uninoculated checks except that a few of them had narrow necrotic strips at the margins of the cotyledons. The wilt Fusarium was consistently isolated from all parts of the susceptible and resistant cantaloups but in only half the cases from the lower hypocotyl and once from the cotyledons of cucumbers (TABLE 2).

Older Plants

When older plants were inoculated by the root dipping technique, symptoms developed in a definite sequence. The time between inoculation and appearance of the first symptoms varied from 5 to 13 days in experiments in which plants ranged in age from 18 to 38 days.

In general the course of the disease was shorter in the greenhouse than in the field, and the symptoms occurred much as follows: First, the leaves of susceptible cantaloups began to yellow, followed in from one to three days by cupping of the upper leaf (Plate II, Fig. 5). The leaves began to wither and die from the base of the plant upward. Within 5 to 6 days after the first yellowing, all of the leaves except those enclosing the terminal bud were usually dead. Sometimes necrotic streaks with gummy exudations appeared, the entire stem having a yellowish translucent appearance. The plants were usually dead within 7 to 10 days after the appearance of the first symptom (Plate III, Fig. 9). None of the susceptible cantaloups survived. Stunting was characteristic of inoculated plants.

The earliest symptoms in resistant cantaloups were usually two to five days later in appearing. In general the sequence of symptoms was similar, but extended over a longer period (Plate III, Figs. 10, 11). The

TABLE 2. Results of reisolation of *Fusarium bulbigenum* var. *niveum* f. 2 from inoculated seedlings two weeks after emergence.

	Base of hypocotyl						Upper hypocotyl						Cotyledons					
	Plant number						Plant number						Plant number					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Susceptible Cantaloup	f	f	f	f	f	f	f	f	f	f	f	f	0	f	f	c	f	0
Resistant Cantaloup	f	f	f	f	f	f	c	f	f	f	f	f	0	f	f	0	0	f
Cucumber	0	0	f	0	f	f	0	0	0	0	0	0	c	0	0	0	f	0

f - Fusarium reisolated
0 - Sterile
c - Contaminated

inoculated plants died, with an occasional notable exception when development of the disease would cease and a plant would remain alive but stunted for a long period of time (Plate IV, Figs. 13, 14, 15). Stunting of growth was a characteristic response of resistant plants. The cupping of the first expanding leaf below the growing point was less striking than in the susceptible variety (Plate II, Fig. 6).

In inoculated cucumber plants the sequence of symptoms characteristic of cantaloups did not develop. In general the plants were not stunted (Plate III, Fig. 12). However, a striking and characteristic vein clearing of the young leaves, never observed in uninoculated checks, did occur in most of the inoculated cucumber plants (Plate II, Figs. 7, 8). In some cases it was accompanied by a slight cupping of the leaf. Vein clearing appeared about the same time after inoculation as the cupping of the young leaves of inoculated susceptible cantaloups. It was a transient condition persisting for only a few days. A few of the lower leaves of inoculated plants usually turned yellow and died, but no conditions developed which prevented the plants from growing normally and setting fruits.

Inoculated roots were flaccid, more or less discolored and necrotic in contrast with the white, turgid, uninoculated ones. Resistant cantaloup roots were more severely affected than those of cucumbers but not so severely affected as those of susceptible cantaloups (TABLE 3). Roots of inoculated susceptible cantaloups were more discolored than those of resistant cantaloups and of cucumbers. The former showed evidence of a generalized infection,while in the latter the greatest amount of necrosis had occurred on the lower part of the tap root. In many cases it had rotted away leaving only a sharp pointed stub just below the

TABLE 3. Appearance of roots two weeks after inoculation with <u>Fusarium</u> <u>bulbigenum</u> var. <u>niveum</u> f. 2.

	Susceptible Cantaloup	Resistant Cantaloup	Cucumber
Extent of infection	General	Principally the tap root	Tap root and older laterals
Tap root	Necrotic but intact	Partly rotted away	Partly rotted away
Branch roots	Undergoing soft rot or stunted	Rotting or discolored	Rotting or discolored
Adventitious roots	Few; stunted	Few to many; stunted to normal	Many; much elongated

peg region. Only a few stunted adventitious roots formed on susceptible cantaloups. They were more abundant on resistant cantaloups, and on cucumbers were so abundant and long that the total mass of roots on the inoculated plants was almost as great as on the uninoculated checks (Plate V, Figs. 16, 17, 18).

In order to trace the progress of the fungus, a total of 1021 platings were made on nutrient agar of tissues from various parts of the plants grown in the experiments. The wilt Fusarium was recovered from some part of practically all of the inoculated plants, but was not recovered from uninoculated checks. It has been determined that Fusarium bulbigenum var. niveum f. 2. grows not only in the tissues of susceptible cantaloups, but also in those of resistant cantaloups, and cucumbers. However, the extent of the invasion varies. For example, when the disease had progressed in the young susceptible cantaloups of 4 to 6 internodes to the point where the lower leaves were dead and the upper ones were beginning to wilt, the Fusarium ordinarily could be isolated from all of the internodes and from the petioles of the leaves as well as from the roots and hypocotyl, but was not isolated from tissues of the true leaves. However, from resistant cantaloups the Fusarium could be isolated only from the roots, hypocotyl and second internode. In fact, the fungus was rarely recovered from tissues above the second internode of resistant plants regardless of the duration of infection or the severity of symptoms. In comparable cucumbers it was not recovered from tissues above the cotyledonary node, and was often confined to the roots and the base of the hypocotyl.

In older susceptible cantaloups the highest point at which the pathogen was ever recovered was the 25th internode, approximately 145 cm. from the crown. The plant from which this isolation was made was seeded

May 13th, inoculated July 1st and the culture made on August 10th. It was setting fruits and showing distinct symptoms of infection. The fungus was rather commonly isolated from the 14th or 15th internodes of similar plants.

Grafted Plants

This experiment was undertaken to determine whether cantaloup and cucumber plants growing on roots of the opposite species would respond to inoculation with *Fusarium bulbigenum* var. *niveum* f. 2 differently from the plants on their own root systems, and whether the shoots of one species would affect the susceptibility of roots of the other species. For this purpose four types of grafted plants were prepared: Cantaloup-on-cantaloup, cucumber-on-cucumber, cantaloup-on-cucumber, and cucumber-on-cantaloup. The cantaloup-on-cantaloup grafts behaved identically with ungrafted cantaloups. None of the cucumber-on-cucumber plants developed symptoms of the disease. In the cucumber-on-cantaloup grafts, the cantaloup root stocks apparently became infected about as readily as ungrafted cantaloup plants, while the scions did not develop symptoms of the disease. Symptoms typical of Fusarium wilt did not develop on the cantaloup-on-cucumber plants. The response of each type of grafted plant will be described separately.

CANTALOUP-ON-CANTALOUP: The first symptoms appeared 10 to 16 days after inoculation and none of them escaped infection. Elongated necrotic lesions appeared on the stems both above and below the graft unions. Drops of dark amber to reddish gum were exuded from the necrotic lesions and from lateral cracks on the stems. Infection usually occurred at the side of the root system where the inoculation was made. One or more of the larger lateral roots on this side was dark brown in color and more or less necrotic (Plate VI, Fig. 19). The tap root was necrotic at and above the base of these laterals. Except for an occasional spot, the rest of the root system was white and healthy in appearance.

> CUCUMBER-ON-CUCUMBER: All grew normally and set fruit. The roots bore no necrotic lesions.
>
> CUCUMBER-ON-CANTALOUP: Within 10 to 15 days after inoculation the root stocks developed characteristic symptoms such as yellowing of the leaves and necrotic streaks with gummy exudations. The leaves at the tips of runners of the stock were up-turned at the margins. Elongated necrotic lesions rarely extended beyond the graft union into the first internode of the cucumber scion. The leaves of the scions withered and died from the apex toward the base as infection of the root stock progressed. The stems remained green for some time after the death of the leaves, the last parts of the stem to wither being those internodes adjacent to the nodes bearing fruit. Some of the fruits became watersoaked near the stem and exuded drops of reddish gummy material.
>
> CANTALOUP-ON-CUCUMBER: The cucumber tissue adjacent to and just below the graft union generally was watersoaked in appearance and olive green in color. In a few cases narrow watersoaked strips extended up into the lower internodes of the cantaloup scion. The root systems were generally white, turgid and free of lesions, but in 3 cases there was slight necrosis of the base of the hypocotyl.

May (8) obtained similar results when he inoculated reciprocal grafts between resistant and susceptible tomatoes with the tomato wilt Fusarium.

The extent of invasion in the cantaloup and cucumber portions of the inoculated grafted plants was determined by plating out sections of tissue for recovery of the wilt Fusarium (TABLE 4). Adjacent sections were examined histologically and are described later.

Development of the Pathogen

Young Roots

When seedling roots of susceptible cantaloup ,of resistant cantaloup and of cucumber inoculated with a spore suspension were examined microscopically, no differences were observed in the method of penetration or in the number of hyphae which penetrated the roots. Twelve hours after

TABLE 4. Recovery of _Fusarium bulbigenum_ var. _niveum_ f. 2 from inoculated grafted plants.

Grafted plants	Kind of tissue	Number platings	Typical cultures	Percent
Cantaloup-on-cantaloup	Cantaloup	125	77	61.6
Cucumber-on-cucumber	Cucumber	55	2*	3.6
Cucumber-on-cantaloup	Cantaloup	31	17	54.8
	Cucumber	72	12	16.6
	Both	103	29	28.1
Cantaloup-on-cucumber	Cantaloup	45	6	13.3
	Cucumber	57	2	3.5
	Both	102	8	7.8

* One of these was from the tap root of one plant and the other was from the base of the hypocotyl of another.

inoculation, germinating spores could be seen on and near the roots and a number of hyphae were growing over the surface. Twenty-four hours after inoculation abundant hyphae could be observed. Most of them remained appressed to the surface of the root and followed the uneven contour closely (Plate VII, Fig. 20, B). In one case a hypha was so tightly wrapped around a root hair that it distorted the shape of the cell (Plate VII, Fig. 20, A). The greatest concentrations of hyphae were at the region of collapsing root hairs and at the root cap. The number of hyphae on the roots continued to increase until they were so abundant between 72 and 96 hours after inoculation that it was difficult to follow the course of the individual filaments and almost impossible to observe penetration. At this time conidiophores bearing microconidia were sometimes seen. The earliest penetrations were observed 12 hours after inoculation. The greatest frequency of penetration occurred in the region of collapsing root hair cells, but some penetrations were found between this region and the root tip. The hyphal tips penetrated between the epidermal cells of the host, often at the junction of 3 cells, but sometimes between two cells (Plate VIII, Fig. 21).

The fungus seemed to encounter little resistance from the host cells, as the hypha was rarely bent or swollen at the point of entry. Occasionally, however, there was a swelling in the hypha at the surface of the root with the portion of the hypha which passed between the cells being somewhat smaller in diameter. The walls of the host cells were sometimes pushed slightly aside by the penetrating hypha. In some cases the hypha penetrated between cells which appeared perfectly normal. Usually, however, one or more of the cells adjacent to the penetrating hypha was either dead, cytoplasm coagulated, or in a low state of vitality, as indicated by granulation and vacuolation of the cytoplasm either without cyclosis or with cyclosis at a reduced or uneven rate. When a few of the roots were treated with a 0.0025 percent solution of neutral red, the stain failed to accumulate in the vacuoles of the cells adjacent to the hyphae. In two cases it accumulated in the cell walls at the point of intercellular penetration.

By adjusting the focus of the microscope the course of the penetrating hyphae could be followed into the tissue. In some cases the hyphae remained intercellular, but in others they could be seen to become intracellular by direct penetration of the walls of cortical cells. In these cases the hyphae were swollen on either side of the wall and the portion which passed through the wall was smaller in diameter than the normal hyphae (Plate VIII, Fig. 21 and Plate IX, Fig. 23). The penetrating hypha was often bent or twisted, and the wall of the host cell was sometimes locally displaced as if the fungus were exerting pressure to accomplish penetration.

In no case was direct penetration of the wall of living epidermal or root hair cells observed. However, several cases of direct penetration of the walls of dead root hair cells were seen, and one case each of direct penetration of the cell wall of a dead epidermal cell and of a dead detached root cap cell was observed (Plate VII, Fig. 20 and Plate VIII, Fig. 21, A).

The fungus hyphae grew in great abundance over the root cap and ramified throughout the spaces between the loose root cap cells. The cytoplasm of the meristematic root tip cells is so dense that it was impossible to see hyphae between them in whole roots, and it was thought that meristematic penetration did not occur until it was observed in the inoculated roots after fixing, sectioning and staining. In these stained mounts several cases of intercellular penetration in the root tip of susceptible cantaloups were observed (Plate IX, Fig. 22), and one case was seen in a cucumber root. Intercellular penetration of the root tip meristem of the resistant cantaloups has not been seen.

After the fungus had penetrated between epidermal cells, it branched repeatedly and ramified throughout the cortical tissue of the young roots of susceptible cantaloups (Plate IX, Fig. 24 and Plate X, Fig. 25). The fungus then proceeded both intercellularly and intracellularly, tending to become more intracellular as it approached the stele. The endodermis apparently does not constitute a barrier to the radial progress of the hyphae as many of them made their way into the stelar tissues. The protoxylem vessels were penetrated directly, the hyphae passing through the thin vessel wall between the spiral or annular thickenings (Plate XI, Fig. 27). Within the vessels the fungus grew both up and down, sometimes following the contours of the walls, sometimes crossing the lumen and frequently producing lateral branches (Plate XII, Fig. 30). A hyphal tip often passed between the thickenings out of the vessel (Plate XI, Fig. 28) into the adjacent parenchymatous cells of the stele, entered another vessel by way of a pit or reinvaded the cortex. Phloem cells were also invaded although to a lesser extent than xylem and cortical cells. Strands of the fungus were sometimes seen in the newly differentiated vascular elements, suggesting that infection may have occurred from hyphae which penetrated the root tip rather than from those entering farther back along the root. Anastomosis of hyphae within vessels or in the cells of cortical tissue was sometimes observed (Plate VII, Fig. 20, D).

The fungus ramified much less extensively in the resistant cantaloup and cucumber roots than in the susceptible cantaloups (Plate X, Fig. 26). The greater part of the hyphae which penetrated in the region of the root hairs remained confined to the outer layers of the cortical cells, and those hyphae which did penetrate the cortex radially tended to be intercellular rather than intracellular. Invasion of stelar tissues by hyphae from the cortex was not observed. However, many of the protoxylem and metaxylem elements in the inoculated roots contained the fungus (Plate XII, Fig. 29). By comparison with the situation in vessels of the susceptible cantaloups, the hyphae in these vessels were less abundant, they branched less frequently, more rarely passed from vessel to vessel, seldom attacked other stelar tissues and were never observed to reinvade the cortex. These vessels may have been invaded during differentiation by hyphae which penetrated between cells of the root tip.

Young Hypocotyls

In susceptible cantaloup seedlings the quantity of fungus present in vessels of the hypocotyl was often greater than in vessels of the root. As in the seedling roots all types of xylem elements were invaded. The fungus could be seen passing from one vessel to another and ramifying throughout the adjacent cells. Upward growth of the fungus occurred within the vessels rather than in the cortical tissue, but at intervals some of the hyphae grew out of the bundle into areas of the cortex. Young phloem cells were also sometimes invaded. Intercellular and intracellular hyphae ramified throughout small isolated areas in the outer layers of the cortex so as to suggest that infection had occurred by direct penetration of the epidermis rather than from infected bundles, but no actual penetrations of the hypocotyl from the exterior were observed.

Hyphae were rare in the epidermal and outer cortical cells of hypocotyls of similar seedlings of resistant cantaloups. Neither spores nor hyphae could be found in the vascular tissues or in the adjacent cells of the cortex or pith. Certain other histological symptoms of infection, however, which will be described later, were in evidence in these tissues.

The Fusarium was not recovered from platings of sections of the hypocotyl of comparable cucumber seedlings, and hyphae were not observed on slides prepared from adjacent sections of the hypocotyls. Cells of these tissues appeared normal.

Fungus hyphae could not be demonstrated histologically in the cotyledons of any of the plants even though it was isolated from tissues adjacent to the sections fixed. It is probable that the cultures may have developed from a few spores or hyphae embedded in the collapsed areas at the margins of the cotyledons. These areas stained so deeply that details within them could not be determined accurately.

Older Roots

When the roots of susceptible cantaloups (one to 3 months old) in which secondary growth had taken place were examined, the hyphae of the wilt Fusarium were found in all of the tissues but were most abundant in the xylem. All types of cells were invaded. The hyphae grew both laterally and transversely through the vessels, and passed from vessel to vessel by way of the pits and across the lumina of the smaller elements and xylem parenchyma cells. In many bundles hardly a cell could be found which did not contain some hyphae. The hyphae often coiled about inside the cells, but sometimes passed directly through them. Intercellular as well as intracellular hyphae were present. In some bundles practically all of the larger vessels contained hyphae, while in others none at all or only those near the center of the stele were involved. Some of the hyphae remained appressed to the vessel walls; others crossed back and forth across the lumina (Plate XIII, Fig. 32). In some cases the vessels were almost completely plugged. Both macroconidia and microconidia formed abundantly in the vessels (Plate XI, Fig. 28 and Plate XIV, Fig. 33). In some sections isolated conidia were seen in a vessel in which no hyphae could be found. This might indicate that they had been formed on hyphae farther down in the vessel and had been carried upward in the transpiration stream. Hyphae ramified intercellularly and intracellularly into the parenchyma cells of the pericyclic rays sometimes becoming abundant in this tissue. Less frequently it invaded the phloem, tending to remain intercellular rather than intracellular. In a few sections hyphae could be seen in the pericyclic cells outside the secondary phloem.

In comparable roots of resistant cantaloups most of the same tissues were involved, the principal difference being in the amount of fungus present. Fewer hyphae were found in the larger vessels and they remained more closely appressed to the walls rarely forming a mass in the lumen. There was less ramification from vessel to vessel, thus fewer of the other xylem cells were invaded. Microconidia formed less abundantly than in the susceptible host, and macroconidia were not observed. The ray cells were less frequently invaded, and no hyphae were seen in the phloem or in the layers of pericyclic cells outside the secondary phloem.

The hyphae were confined to the larger vessels and adjacent parenchyma cells of the primary xylem in comparable roots of cucumbers, except in a few sections where they were also present in pericyclic cells just inside the periderm. The latter tissue may have been invaded from the exterior before formation of the periderm was completed or from infected cortical cells farther down along the root. There was no evidence of the fungus in vessels of the secondary xylem or in the phloem. The rays were not invaded. The hyphae in these roots differed from those in cantaloup roots in that their cytoplasm appeared less dense, stained less deeply, their walls appeared thinner and they contained fewer septations.

Older Hypocotyls and Stems

The cells of practically any tissue of the hypocotyls and stems of susceptible cantaloups may be invaded by the wilt Fusarium. Thick hyphae extended upward through the vessels of the hypocotyl (Plate XV, Fig. 35) and on into the stem, in some cases continuing even into the young protoxylem elements in the internode just below the terminal bud. Some of the larger vessels were plugged with hyphae, and many of the smaller elements were tightly packed with parallel filaments or with masses of microspores. A network of hyphae ramified throughout the xylem parenchyma. The mycelium became enormously abundant in the parenchyma cells surrounding the bundles and in the parenchyma of the pith, especially the large cells at the limits of the pith cavity (Plate XIII, Fig. 31). In rare cases the upward progress of the fungus appeared to have been more rapid in the pith cells than in the vascular system, as patches of severely infected pith cells could be seen in cross sections in which no hyphae were to be found in the xylem. An interesting type of intercellular ramification of hyphae between parenchyma cells was observed in living sections of stem tissue. Hyphae usually penetrated the cell walls directly or passed between cells in the relatively large intercellular spaces. However, occasionally mycelial branches forced their way between cell walls which fitted together tightly. These hyphae were much flattened and distorted with many short irregular branches. They may best be described as "dendroid" in appearance. Upon reaching an intercellular space they resumed their normal shape. The relative abundance and the radial ramification of the fungus decreased progressively from the hypocotyl toward the upper limits of invasion in the stems until in the uppermost invaded internode only one or two thick, unbranched, parallel hyphae could be seen in the lumina of the protoxylem elements.

In the hypocotyls of resistant cantaloup plants hyphae occurred sparsely in the larger vessels and in the xylem cells immediately adjacent to them, but were not observed in other tissues. Adventitious roots arising from the hypocotyls were infected, and the distribution of the fungus was the same as in the primary and secondary roots previously described. Invasion of the vessels of the hypocotyl from infected adventitious roots was observed. The hyphae in these vessels were in short fragments rather than in long continuous filaments. They absorbed the stain irregularly and their cell walls were indistinct. Hyphal fragments embedded in floccular material were also seen in sections of living tissues. These observations suggest that the fungus was undergoing disintegration within the vessels of the resistant host. Hyphae were not seen in sections of the resistant cantaloup stem above the cotyledonary node.

In the cucumber plants the fungus could not be demonstrated histologically above the base of the hypocotyls (Plate XV, Fig. 36) or in any of the tissues of the stems. Adventitious roots from the hypocotyl, however, were infected, the hyphae following the vessels of the root as it passed through the tissues of the hypocotyl. Both hyphae and microconidia were found in vessels of these roots very near to the point where they made contact with the vessels of the hypocotyl.

Grafted Plants

In the grafted plants the occurrence of the fungus was dependent upon the response of the root stock. The scion did not affect the occurrence of the hyphae in the stock. The distribution of the fungus in cantaloup grafted on cantaloup was the same as in ungrafted plants. As in ungrafted cucumbers no hyphae were observed in the hypocotyls and stems of cucumber grafted on cucumber root stocks. In cucumber-on-cantaloup grafts hyphae were abundant in xylem and parenchyma of cantaloup root stocks and usually more abundant in the cantaloup side of the graft union than in the cucumber side. A few of the cucumber vessels contained hyphae which extended for a short distance up into the scion. The parenchyma of the cucumbers immediately above the union was invaded, but the fungus was not seen in either the cucumber stocks or in the cantaloup scions in grafted plants of that type.

Host Responses

Several distinct types of responses on the part of host cells to invasion by Fusarium bulbigenum var. niveum f. 2 have been observed. The most striking of these occur in the xylem.

A characteristic internal symptom of infected susceptible cantaloups is the dark brown color of the vascular bundles of the roots and stems. The discoloration was less intense in infected resistant cantaloups, and except in the roots was rarely observed in inoculated cucumbers. Vascular discoloration results from an accumulation in the tissues of a gummy material similar to that exuded from necrotic lesions on the stems of infected susceptible cantaloup plants. This material stained red in safranine. Examination of stained sections of root and stem tissue revealed that it was apparently excreted by the host cells in the invaded bundles. Appearing first as droplets at the pits, it coalesced to line the walls of the vessels (Plate XIV, Fig. 34) and in extreme cases increased until it plugged the entire vessel. Hyphae of the Fusarium were sometimes coated with it. Although these gum-like occlusions often formed in vessels containing hyphae, they were observed somewhat more frequently in adjacent vessels in which the fungus did not occur. This type of occlusion occurred in the vessels of resistant cantaloups with approximately the same frequency as in susceptible cantaloups, but less frequently in the vessels of inoculated cucumbers (Plate XV, Fig. 36). In all three hosts it usually extended beyond the upper limits of invasion. Vessels containing these gum-like deposits were very rarely observed in uninoculated plants.

Two other types of abnormal material occurred in the vessels of inoculated plants. One of these was a floccular substance which was whitish in unstained tissues and appeared blue-green after staining with safranine and fast green. It sometimes surrounded mycelial fragments in the vessels of resistant cantaloups. The other was a highly refractive granular material which took on a red to purple color when stained in the same dyes. Either of these materials sometimes partly or completely filled the lumen of a vessel but they did not occur together in the same vessel. They were absent in many infected bundles and usually involved only a few of the vessels of a bundle in which they did occur. Both occurred frequently in vessels of inoculated susceptible and resistant cantaloups but rarely in cucumbers. The floccular material is more characteristic of the resistant than of the susceptible cantaloups.

Tyloses, intrusions of bladder-like projections of adjacent parenchymatous cells through the pits of walls of vessels, are characteristic of Cucurbitaceous plants (25). Their significance is not known, but they occurred more frequently in inoculated resistant and susceptible cantaloups and cucumbers than in uninoculated checks, (TABLE 5). Tyloses sometimes developed in vessels containing hyphae but more frequently in uninvaded vessels of the same bundle. They often occurred in such abundance as to fill completely the lumen of the vessel. In inoculated cantaloups and more rarely in inoculated cucumbers minute droplets of the gum-like material previously mentioned accumulated on the surface of the tyloses giving them a strikingly beaded appearance (Plate XVI, Fig. 37). The tyloses usually contained a nucleus as well as cytoplasm and were ordinarily thin walled (Plate XVI, Fig. 38). Occasionally, however, the walls developed secondary thickenings. These were laid down in a scalariform pattern and they stained red in safranine (Plate XVI, Fig. 39).

The cytoplasm and cell walls of parenchyma cells in sections of living infected tissue, even in areas not actually invaded by the fungus, were light brown to yellowish in color in contrast to the almost colorless cytoplasm and cell walls of healthy plants. Discoloration was less intense in stems of resistant than in susceptible cantaloups and almost absent in cucumber stems, but there was little difference in the roots of the three hosts.

Chloroplasts in the stems of the plants studied occurred in a few layers of cells just beneath the epidermis and also in certain of the parenchyma cells surrounding the bundles. In healthy plants they were a

TABLE 5. Comparison of the frequency of occurrence of tyloses in vessels of inoculated and uninoculated plants.

	Root		Hypocotyl		2nd. Internode	
	Number cross sections examined	Average number vessels containing tyloses per cross section	Number cross sections examined	Average number vessels containing tyloses per cross section	Number cross sections examined	Average number vessels containing tyloses per cross section
SUSCEPTIBLE CANTALOUP						
Uninoculated	50	0.56	50	0	50	0
Inoculated	90	1.94	90	1.05	90	0.33
RESISTANT CANTALOUP						
Uninoculated	50	0.40	50	0.16	50	0.14
Inoculated	90	1.45	100	1.42	100	0.58
CUCUMBER						
Uninoculated	50	0.96	50	0.86	50	0.50
Inoculated	70	0.87	80	1.13	80	1.43

brilliant green, while in inoculated ones they varied from light green to yellow. Starch grains were rather evenly distributed throughout the parenchyma of healthy plants. In inoculated plants the starch grains were smaller, less abundant, and more or less confined to areas adjacent to the bundles. The effect on both the chloroplasts and stored starch was greatest in inoculated susceptible cantaloups, less marked in the resistant ones and almost imperceptible in inoculated cucumbers.

The cytoplasm of cells in invaded areas of the roots appeared denser and more granular than in uninfected areas or healthy roots. In fixed tissues, especially those of resistant cantaloups and cucumbers, two types of abnormal responses to staining were observed. One of these was a failure of differential staining, the fungus hyphae, the cell walls of the host and the cytoplasm and nuclei all staining reddish-purple in safranine and fast green. This was especially common in areas where breakdown of host cells had taken place. The other was the absorption of safranine by walls of some of the parenchyma cells near the limits of invasion. In some cases it appeared that a diffuse material in or on the cell walls had absorbed the red stain. Both of these responses occurred less commonly in infected susceptible cantaloups.

It was observed occasionally that the cytoplasm of uninvaded parenchyma cells accumulated on the cell walls adjacent to the cells containing hyphae.

Two types of pathological responses of parenchyma cells at some distance from invaded areas have been noted. The first and most frequent of these was the formation of numerous small vacuoles in the cytoplasm (Plate XVII, Fig. 40). This type of cell occurred most frequently in roots and stems of susceptible cantaloups, less frequently in resistant cantaloups and only rarely in the roots of cucumbers. In the second type, which was seen principally in sections of living tissues of inoculated resistant cantaloups, rarely in susceptible cantaloups and which was not observed in cucumbers, spherical globules of a highly refractive material appeared in the cytoplasm. They varied from about the size of nuclei in cells containing only a few to minute droplets in cells containing many. Starch grains and other cell inclusions tended to gather at the surface of the larger ones.

In severely infected stems of susceptible cantaloups, groups of cells disintegrated to form necrotic pockets which were sometimes lined or partially filled with the red staining gum-like material (Plate XV, Fig. 35). Sometimes the inner margin of the pith cavity was lined with gum. Narrow necrotic strips radiated from the infected cavity toward the margins of the hypocotyl (Plate XVIII, Fig. 41). When these reached the surface, a lateral crack from which gummy material was exuded formed on the surface of the hypocotyl. Necrotic streaks on the hypocotyls and stems were formed by the enlargement of necrotic areas in the cortical or pericyclic parenchyma (Plate XVIII, Fig. 42). These parenchyma cells had been invaded by hyphae from the infected bundles.

The response of the host cells to inoculation in grafted plants was dependent upon the extent of invasion and abundance of the fungus in the tissues. All responses of cantaloup-on-cantaloup and cucumber-on-cucumber grafts were indistinguishable from those of ungrafted plants. The cantaloup stocks of cucumber-on-cantaloup grafts showed all the histological symptoms characteristic of cantaloups. Discoloration of some of the vascular bundles of the cucumber scion within and just above the graft union usually occurred. A narrow layer of gum-like material often lined the vessels above the upper limits of fungus invasion. In the reciprocal grafts discoloration of the vascular bundles of the cucumber stocks was rare, but a slight discoloration of the xylem of the cantaloup scions usually occurred even where the bundles of the stocks appeared normal in color.

DISCUSSION

Resistant cantaloups differed from susceptible cantaloups in their gross and histological responses to inoculation with _F_. _bulbigenum_ var. _niveum_ f. 2 in degree rather than in kind. Cucumbers, however, did not develop typical symptoms of the disease and were not killed by the pathogen even though many of their internal responses resembled those of resistant cantaloups.

Failure of the resistant cantaloups to demonstrate a higher degree of resistance to the wilt Fusarium in these experiments may be due in part to the method of inoculation or to the virulence of the strain of Fusarium used as inoculum. The root dipping technique is a drastic one, and it is unlikely that plants would ever come in contact with such a mass of inoculum in the field even under the most sever conditions of infestation. Even in the susceptible cantaloups the disease developed more rapidly and the plants were killed sooner than would be expected in the field. In many vascular Fusaria new strains may arise as sectors on artificial media or as dissociants in the soil. These strains vary widely in virulence. Sleeth (13) found that his more virulent strains of the watermelon wilt pathogen attacked both resistant and susceptible watermelons, while the less virulent strains attacked only the susceptible varieties. It is possible that the strain of Fusarium used in these experiments may have been sufficiently more virulent than those to which the resistant cantaloups were exposed during the development of the variety as to account for their behavior in the present experiments. If the vein clearing described in the inoculated cucumbers was a result of the drastic type of inoculation or of the particular strain of Fusarium used, it seems possible that it might not occur under field conditions.

The differences in the responses of the three types of plants to inoculation with the wilt Fusarium were not the result of the failure of the organism to gain entrance into the primary tissues, since it was observed that penetration proceeds in essentially the same manner in all three plants. The ability of Fusaria to penetrate the young root tissues of resistant and susceptible varieties with equal ease has been observed in watermelons (20), in cabbage (1), in peas (11, 18) and in flax (16). Valleau and Johnson (17) have shown that seedling tissues of a number of plants demonstrated very little specific resistance to attack even when inoculated with Fusaria isolated from widely unrelated hosts. Tisdale (16) found that F. conglutinans could penetrate seedling roots of flax, and that F. lini was evidently able to penetrate those of cabbage as they were killed by it in tube cultures. F. conglutinans, F. lycopersici and F. lini were all able to penetrate the outer layers of cells of watermelon roots (20). Hence the penetration of root tissues of resistant cantaloups and cucumbers by the cantaloup wilt Fusarium cannot be considered unusual.

It was demonstrated in the vessels of the roots of all three hosts that the differences in the response of older plants did not result from failure of the Fusarium to invade their vascular systems. It was also observed that no anatomical differences could explain the variations in method and in extent of invasion of stelar tissues of the three hosts. This is not uncommon as Walker (19), after discussing types of resistance due to cell membranes and to interaction of the protoplasts of invader and host, concludes that ". . . There are many cases in which the pathogen invades the resistant host but does not proceed beyond the early stages; however, neither cell membrance nor cell protoplast reactions have been discerned as accounting for the resistance phenomenon." He states that Fusarium wilts best illustrate cases of this type. The fungus was less abundant in the resistant cantaloup and cucumber roots than in those of the susceptible cantaloups. In this respect also, the situation is similar to that in cabbage yellows (14) and near wilt of peas (18).

In view of the relatively small amount of fungus found in the resistant cantaloup plants as compared with the susceptible plants, the severity of their symptoms and their death might seem surprising were it not for the findings of Linford (7). He showed that in pea wilt even a small amount of Fusarium inserted into a wound in the shoot of a resistant plant was sufficient to produce symptoms of the disease even though the inoculum did not grow to any appreciable extent in the resistant tissues.

No type of host cell response was observed with sufficient frequency or consistency in the resistant cantaloups or in cucumbers to account for their resistance. More gum-like material in proportion to the amount of fungus present was found in vessels of the resistant cantaloups, but not in cucumbers. In the susceptible plants the gum-like material apparently did not impede the growth of the fungus and probably did not do so in the resistant plants. Tyloses may represent a rather common response to infection with Fusaria. Sleeth (12) found them more abundantly in watermelons infected by Fusarium wilt than in healthy plants. Wilson (20) made the same observation. Fahmy (2) found them also in wilted cotton. In this study they have been observed more frequently in vessels of inoculated plants than in their uninoculated checks. They are probably not concerned in resistance as they occurred with approximately equal frequency in all three types of inoculated hosts. Wilson (20) regards tyloses as responses of living cells injured by either toxic, metabolic or enzymatic products of the wilt pathogen.

Microconidia which form abundantly in the vessels of roots and stems of susceptible cantaloups probably may be carried upward in the transpiration stream to establish new loci of infection. This has been shown by Yoshii (23) to occur in watermelons. They also appear, but less abundantly, in the vessels of the roots and of adventitious roots arising from the hypocotyls of resistant cantaloups and cucumbers. Whether they are able to establish new loci of infection in these hosts has not been demonstrated, but they probably would be capable of germinating on suitable media. This might explain the isolation of the fungus from tissues in which it could not be demonstrated histologically. Smith and Walker (14) were able to isolate Fusarium from resistant cabbage tissues in which the fungus could not be seen. It may also explain the isolation of Fusarium in 13.3 percent of the cases from cantaloup scions and in only 3.5 percent of the cases from cucumber root stocks of inoculated cantaloup-on-cucumber grafts.

The inoculated seedlings of susceptible and resistant cantaloups behaved almost identically. Wilson (20) found this to be the case in watermelons, and he concluded that apparently no well developed defense mechanism had time to develop and function in the early seedling stage. The results of the present experiments lead to the conclusion that, in the development of wilt resistant varieties of cantaloups, greenhouse indexing in the seedling stage should not be depended upon to give a true picture of the probable performance of the plants under field conditions. Moreover, the isolation of the Fusarium from a plant is not a criterion of its susceptibility to cantaloup wilt, since in these experiments the pathogen was recovered readily from both homozygous resistant cantaloups and from cucumbers.

In so far as it could be determined by histological means, it appears that the behavior of the resistant cantaloups could be attributed not only to a slower rate of development of the fungus in their tissues, but also that their cells were less susceptible to any toxic substance or metabolic by-products which might be produced by the fungus or by interaction between the fungus and host cells. In various other plants subject to Fusarium wilts the investigators have attributed the failure of the fungus to grow in the resistant plants to the presence in their tissues of a postulated inhibitory or antagonistic substance (1, 14, 18). If such a substance were present in resistant cantaloups, it must be concluded that it was not able to prevent the production of many of the symptoms of wilt even when only a small amount of the fungus was present. The failure of inoculated cucumber seedlings to succumb, and the absence of typical internal and external symptoms of cantaloup wilt in older cucumbers which contained almost as much Fusarium as the resistant cantaloups, indicates that they have a greater degree of resistance and suggests that they may possess a different type of resistance from that of the resistant cantaloups. The graft experiment yielded evidence similar to that obtained by May (8) with grafted resistant and susceptible tomatoes. It indicated that whatever is responsible for the reduced rate of development of the fungus in cucumbers is resident in their tissues and is not transferred through a graft union to the cantaloup portion of the plants. This is shown by the failure of the fungus to develop extensively in cucumber scions on inoculated cantaloup roots, together with the fact that it could be isolated more frequently from the cantaloup scion than from the cucumber root stocks of cantaloup-on-cucumber grafts.

SUMMARY

When seeds of susceptible cantaloups, resistant cantaloups and cucumbers were germinated in sand inoculated with *Fusarium bulbigenum* (Cke. and Mass.) var. *niveum* Wr. f. 2, the seedlings of resistant cantaloups were almost as severely affected by the fungus as those of susceptible cantaloups. Cucumber seedlings were unaffected. The fungus could be reisolated from all three types of plants.

When older plants were inoculated by a root dipping technique, resistant cantaloups developed symptoms similar to those on susceptible cantaloups and died, with the exception of an occasional plant which remained alive but much stunted. Cucumber plants did not develop symptoms characteristic of cantaloup wilt and were not killed. It was shown by cultural methods that the Fusarium extended farther up into susceptible plants than in resistant plants and was confined to the roots and hypocotyls of cucumbers.

The seedling roots of all three types of plants were penetrated with equal ease and frequency. The vascular systems of all three were invaded. The Fusarium grew more abundantly in the vascular system and the invasion was more extensive in susceptible cantaloups than in resistant cantaloups or cucumbers. Resistant cantaloups demonstrated more of the internal symptoms of infection than did cucumbers. In an experiment with reciprocal grafts between cantaloups and cucumbers the susceptibility of root stocks was not affected by that of the scions. Cucumber scions were not extensively invaded by hyphae from the susceptible cantaloup root stocks and the Fusarium was reisolated more frequently from cantaloup scions than from the cucumber root stocks in grafted plants of that combination.

The responses of resistant cantaloups to inoculation differed from those of susceptible cantaloups in degree rather than in kind. There was some evidence that cucumbers possess a different type of resistance from that of resistant cantaloups.

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PLATES

PLATE I

The process of grafting cantaloups and cucumbers.

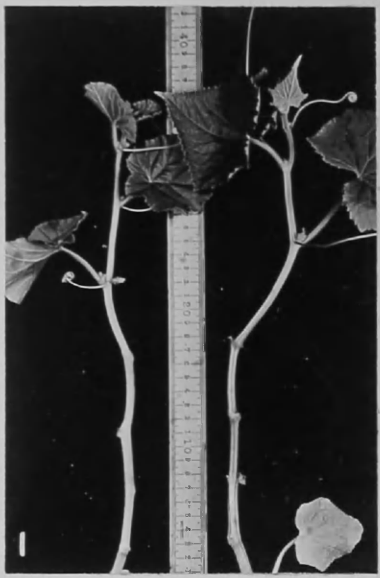
Figure 1. Prepared for grafting by removal of lower leaves.

Figure 2. Graft incisions made.

Figure 3. Fitting the graft union together.

Figure 4. Wrapping the graft union with parafilm.

PLATE I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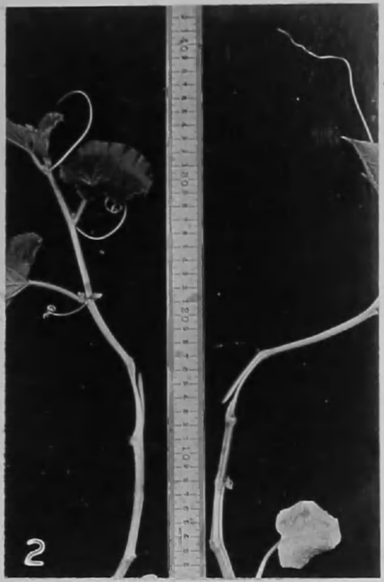
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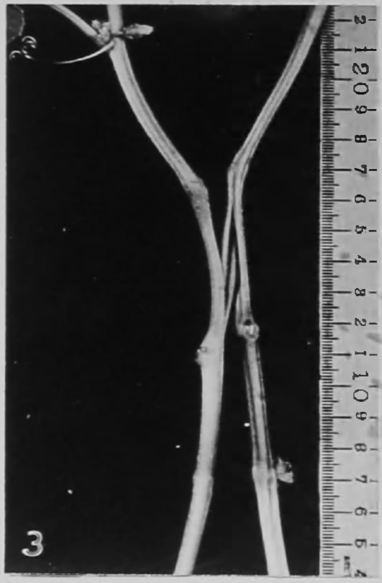
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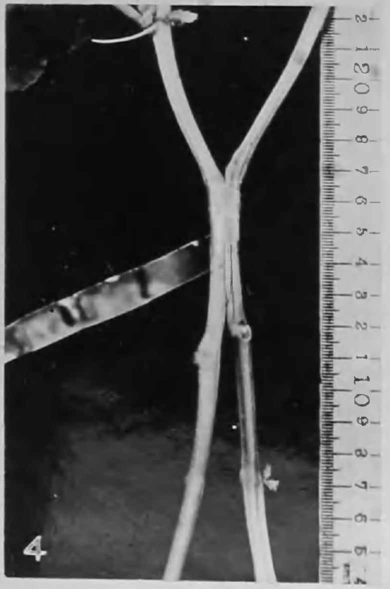
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PLATE II

Leaf symptoms on young susceptible and resistant cantaloup and cucumber plants inoculated with Fusarium bulbigenum var. niveum f. 2. Healthy plant (right), inoculated plant (left), except in Figure 8.

Figure 5.	Susceptible cantaloups; typical curling of margin of uppermost leaf.
Figure 6.	Resistant cantaloups. Curling of upper leaf less striking than in susceptible variety.
Figure 7.	Tips of young cucumber plants. Note vein clearing of one of the leaves.
Figure 8.	Enlarged single leaf of cucumber showing vein clearing.

PLATE II


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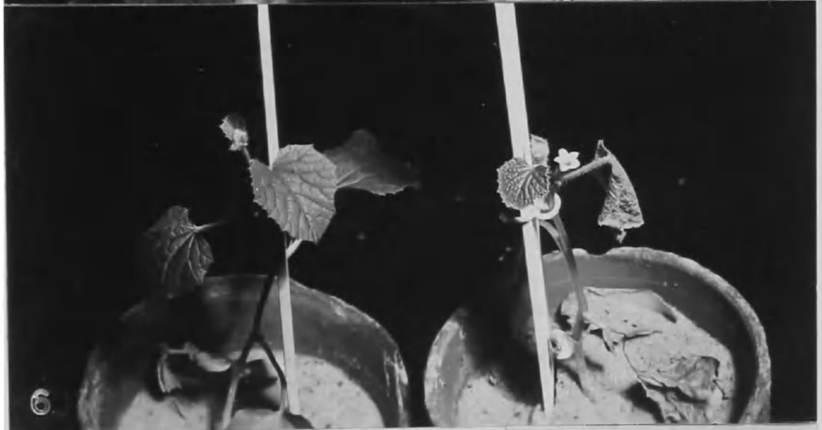
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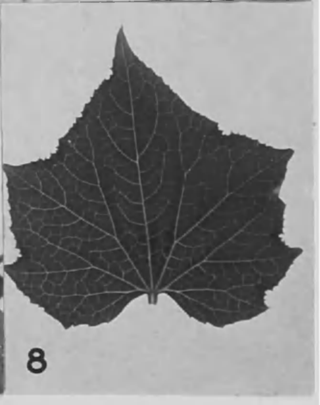
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PLATE III

Comparison of three uninoculated plants (left) and three inoculated plants (right) eight days after inoculation by the root dipping technique. Susceptible and resistant cantaloups are showing severe symptoms of infection; cucumbers are indistinguishable from the uninoculated checks.

Figure 9. Susceptible cantaloups.

Figure 10. Resistant cantaloups (P. B. # 13).

Figure 11. Resistant cantaloups (11-38).

Figure 12. Cucumbers.

PLATE III


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PLATE IV

Comparison of uninoculated resistant cantaloups (left) and inoculated resistant plants (right) which survived inoculation but remained stunted. All other inoculated plants in the same series died.

Figure 13. Resistant cantaloup (11-38) two months after inoculation.

Figure 14. Resistant cantaloups (P. B. # 13) three weeks after inoculation.

Figure 15. Resistant cantaloups (11-38) three weeks after inoculation.

PLATE IV


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PLATE V

Comparison of inoculated (right) and uninoculated (left) root systems two weeks after inoculation. Roots selected to show range of variation.

Figure 16. Susceptible cantaloups.

Figure 17. Resistant cantaloups.

Figure 18. Cucumbers.

PLATE V


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PLATE VI

Figure 19. Cantaloup root from one of the grafted plants. Notice discoloration of some of the lateral roots. The tap root and hypocotyl above are also discolored.

PLATE VI

PLATE VII

Figure 20. Relationship of Fusarium to the young roots. X 580.

A. Hypha from germinating macroconidium of Fusarium tightly wrapped around a cucumber root hair.

B. and B'. A cucumber root showing hyphae tightly appressed to the surface.

C. and C'. A seedling root of cantaloup showing hypha penetrating intercellularly.

D. Anastomosis of hyphae and penetration into and between reticulate vessels in young susceptible cantaloup root.

E. Direct penetration of the cell wall of a collapsed root hair of susceptible cantaloup.

PLATE VII

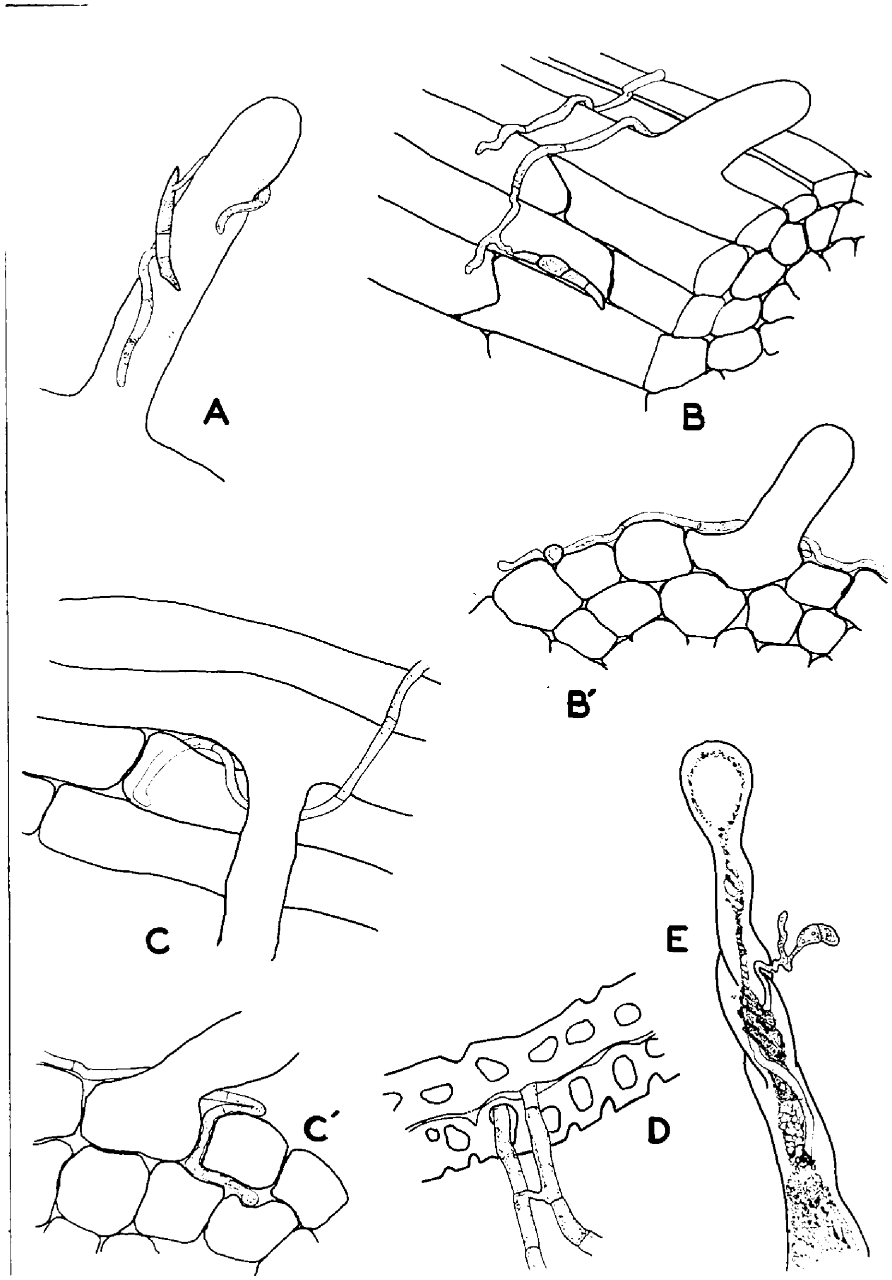


PLATE VIII

Figure 21. Penetration of the young roots by hyphae of the wilt Fusarium. X 1140

A. Direct penetration of wall of a dead epidermal cell of susceptible cantaloup.

B. Two hyphae penetrating between epidermal cells of susceptible cantaloup root.

C. Intercellular penetration of cucumber root.

D. Hypha penetrating intercellularly and becoming intracellular in young root of resistant cantaloup.

PLATE VIII

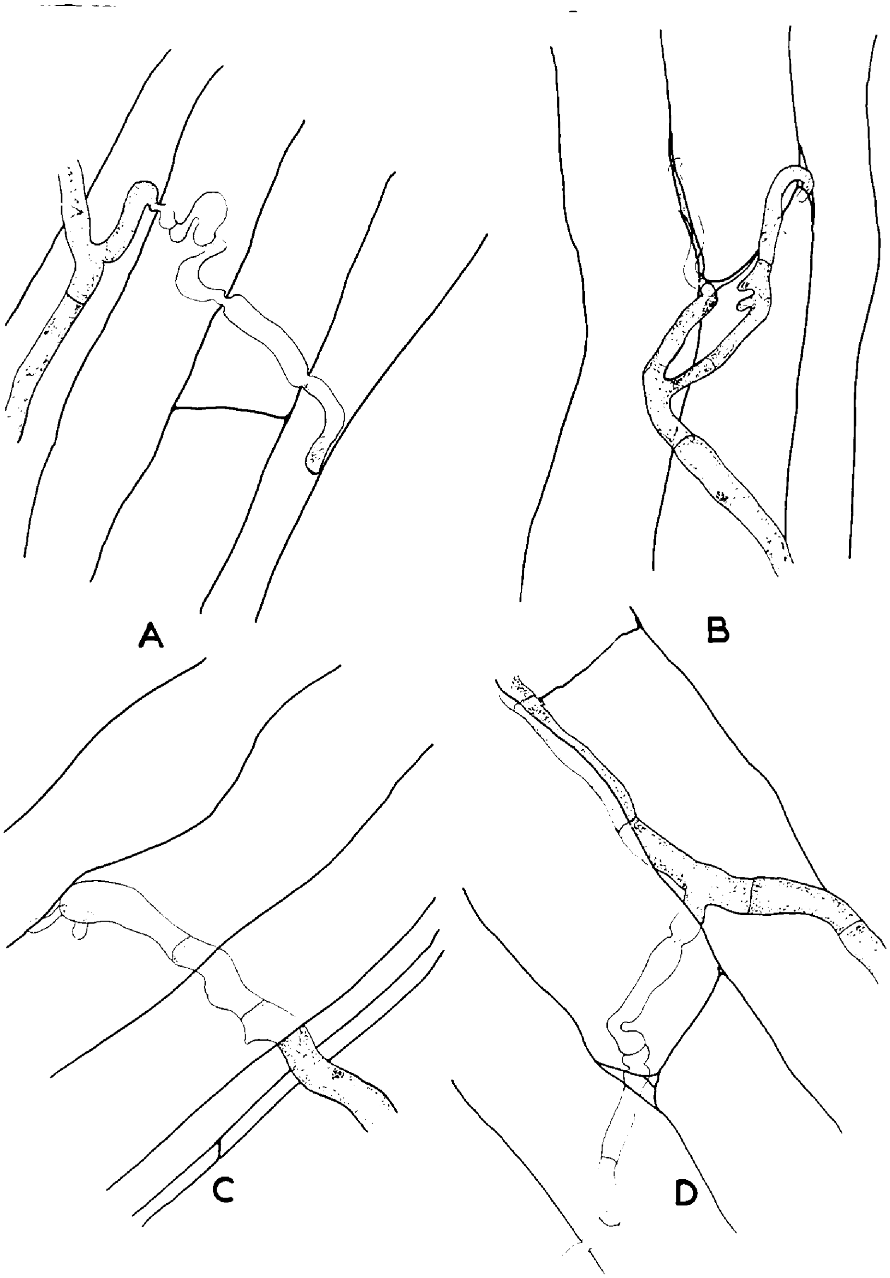


PLATE IX

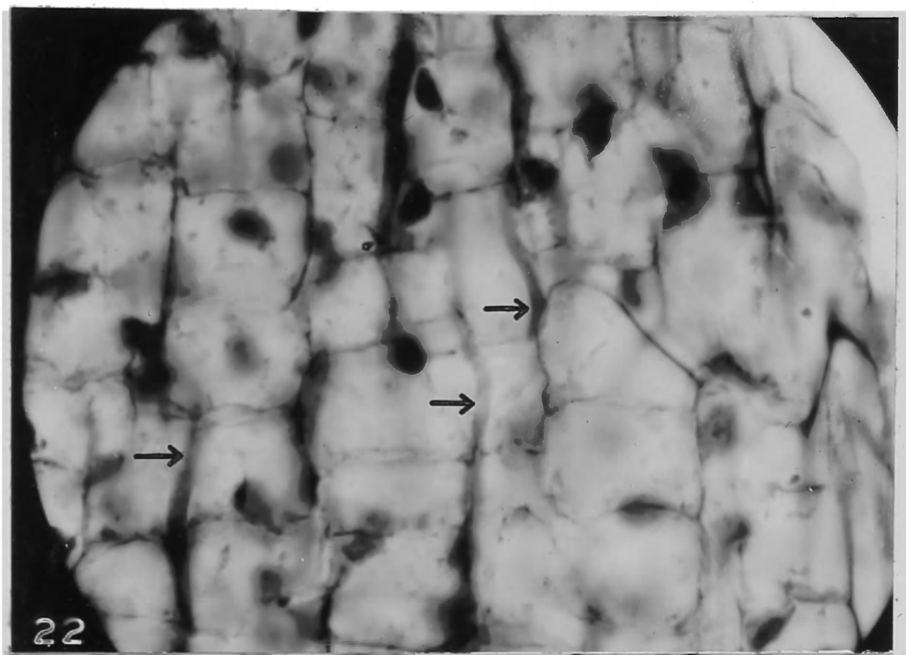
Hyphae of the Fusarium in the tissues of susceptible cantaloups.

Figure 22. Intercellular hyphae in root tip at points indicated by arrows. X 1140.

Figure 23. Intercellular hypha becoming intracellular in the cortex at point indicated by arrow. X 1140.

Figure 24. Hyphae penetrating intercellularly between epidermal cells of young root at points indicated by arrows. X 480

PLATE IX



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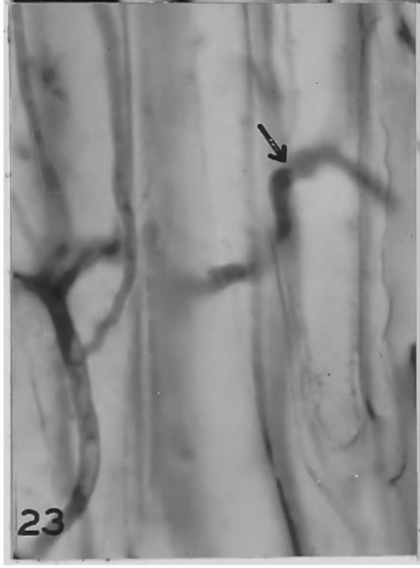

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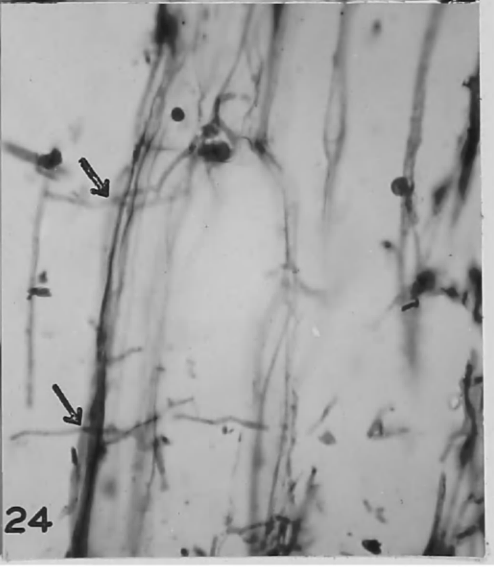

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PLATE X

Ramification of hyphae in the cortex of young roots. X 480.

Figure 25.	Section of young root of susceptible cantaloup showing abundant hyphae in the tissue.
Figure 26.	Section of young root of cucumber. Hyphae are less abundant than in the susceptible cantaloup.

PLATE X

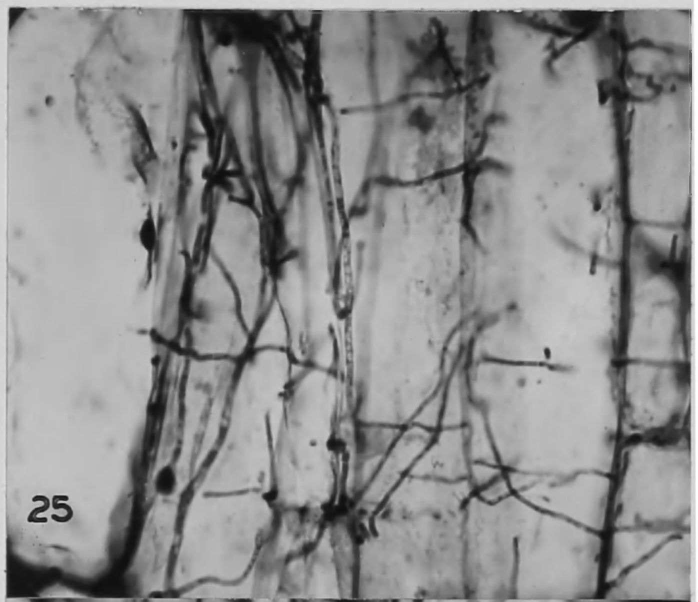
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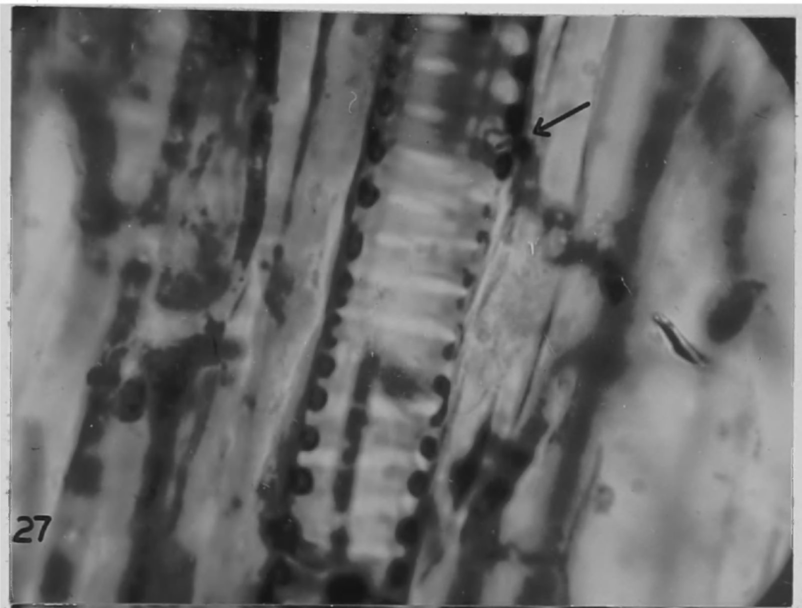
PLATE XI

Invasion of the xylem in susceptible cantaloup roots. X 1140.

Figure 27. Hyphal tip penetrating between the secondary thickenings in the wall of a vessel at point indicated by arrow.

Figure 28. Hyphae in vessels and adjacent tissues. Hyphal tip passing out between secondary thickenings of vessel wall at point indicated by arrow. Microconidia in one of the vessels indicated by "M".

PLATE XI



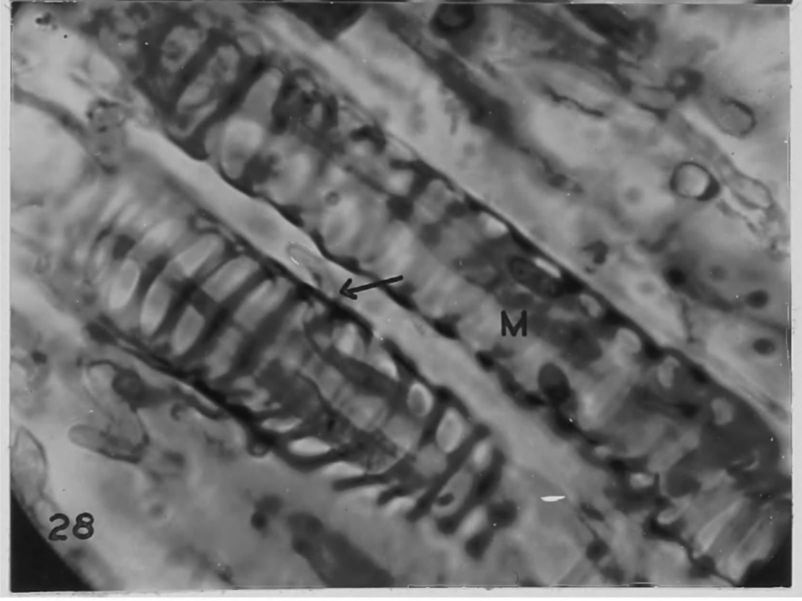


PLATE XII

Hyphae in the vessels of resistant and susceptible cantaloup roots. X 480.

Figure 29. Single thick hypha in a vessel of a resistant cantaloup root.

Figure 30. Hyphae in protoxylem vessel and in cortex of young susceptible cantaloup root, indicated by arrows.

PLATE XII

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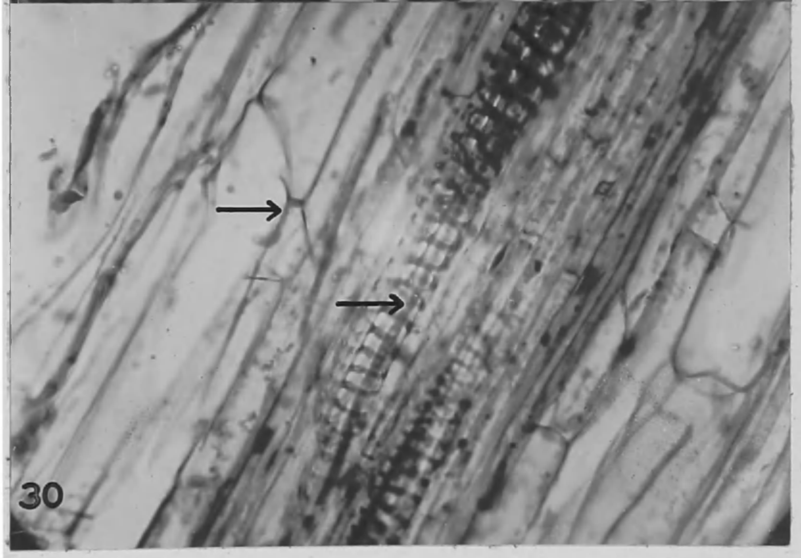

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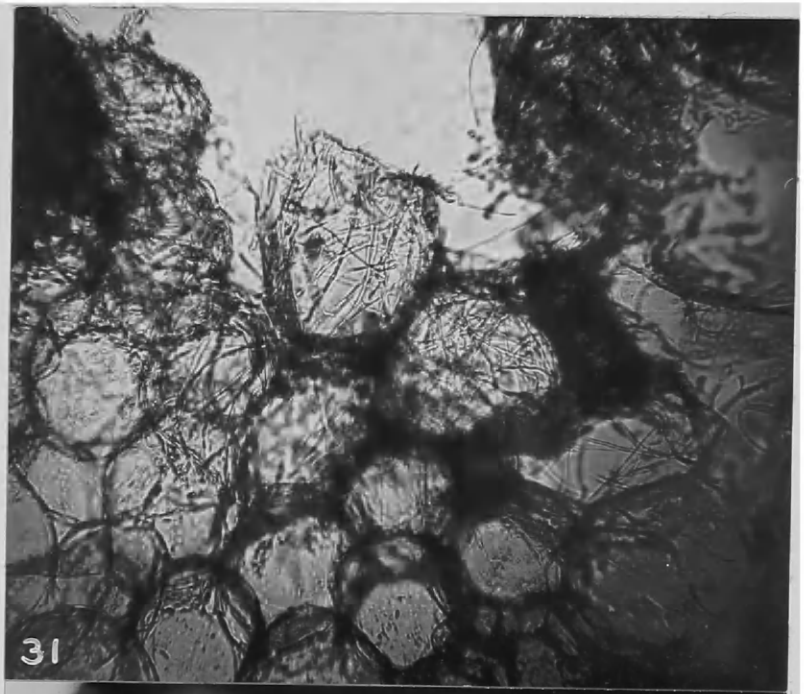
PLATE XIII

Hand sections of unfixed susceptible cantaloup tissue. X 136.

Figure 31. Hyphae in the parenchyma cells at the margin of the pith cavity in the hypocotyl.

Figure 32. Hyphae in the lumina of infected vessels in the hypocotyl.

PLATE XIII



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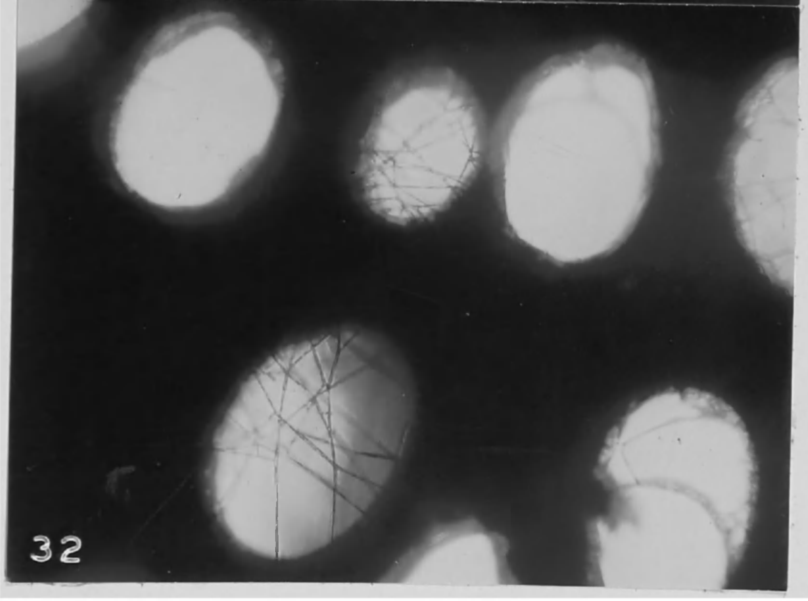

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PLATE XIV

Vessels in susceptible cantaloups. X 480.

Figure 33. Macroconidia in a vessel.

Figure 34. Gummy material partly lining the wall of a vessel. Notice that the material accumulates as droplets at the pits of the vessel wall.

PLATE XIV

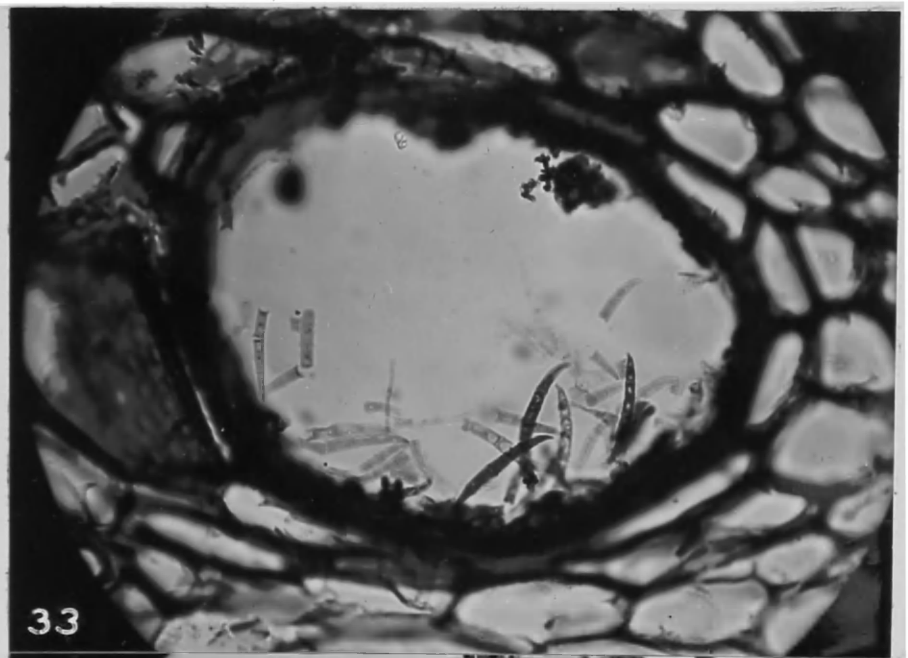

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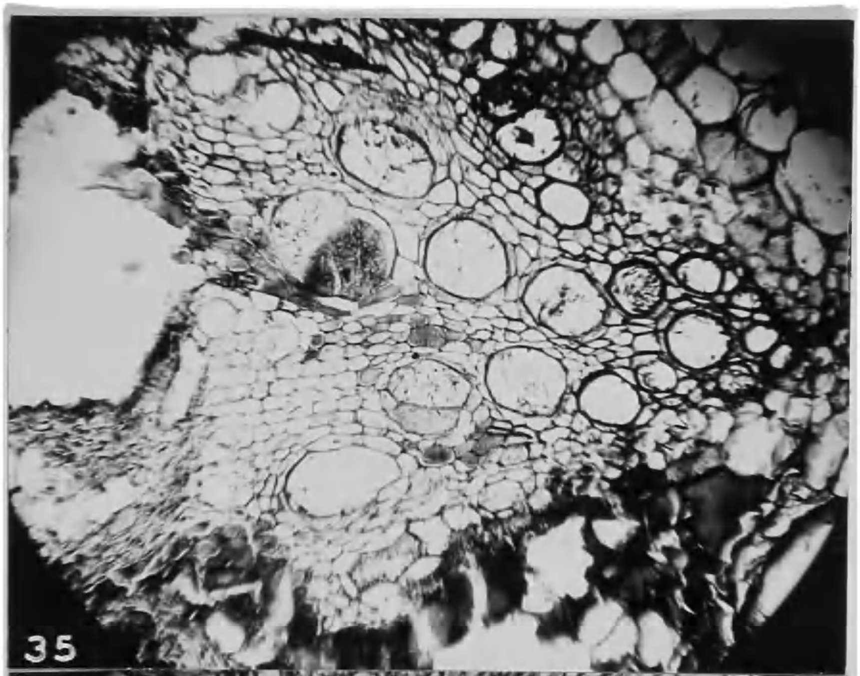
PLATE XV

Comparison of vascular infection in inoculated susceptible cantaloups and cucumbers. X 112.

Figure 35. Cross section of an infected vascular bundle at the base of the hypocotyl of a susceptible cantaloup. Notice hyphae in the vessels, vessels lined with gummy material (upper center) and necrotic cavities (left and lower right). The cavities are lined with gummy material and some of the cells are filled with it.

Figure 36. Cross section of a vascular bundle in the base of the hypocotyl of an inoculated cucumber. Notice that the few hyphae present are confined to the metaxylem elements of the primary xylem (below and to the right of center). The walls of these vessels are lined with gummy material. A necrotic cavity has started to form (lower center).

PLATE XV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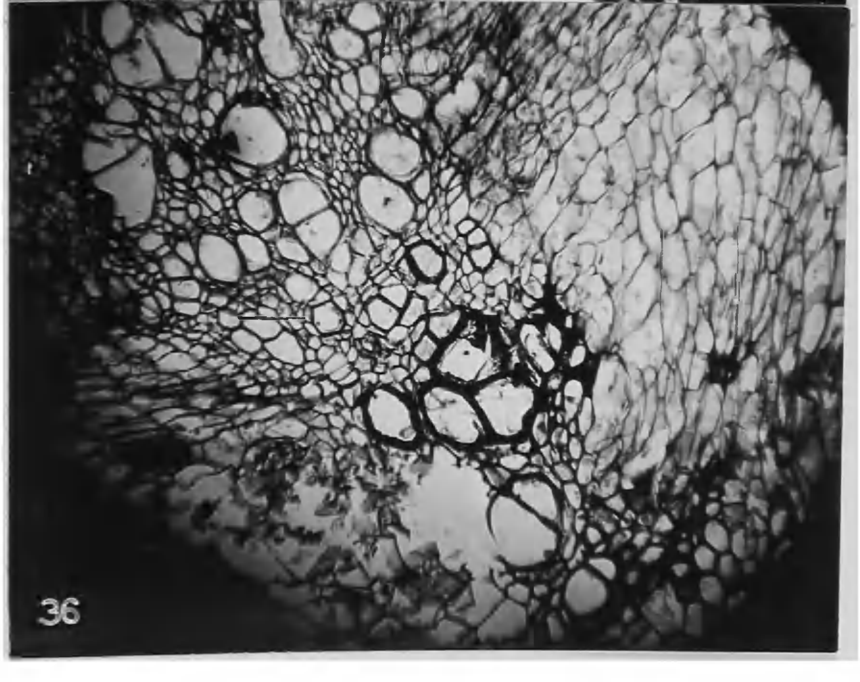
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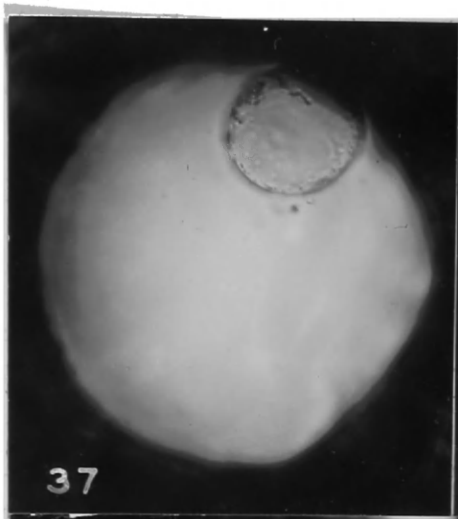
PLATE XVI

Tyloses in xylem vessels of susceptible cantaloup.

Figure 37.	Droplets of gummy material have accumulated on the surface of the tylose giving it a beaded appearance. X 580.
Figure 38.	Group of four typical thin walled tyloses in a vessel. X 580.
Figure 39.	Scalariform secondary thickenings in the walls of a tylose. X 480.

PLATE XVI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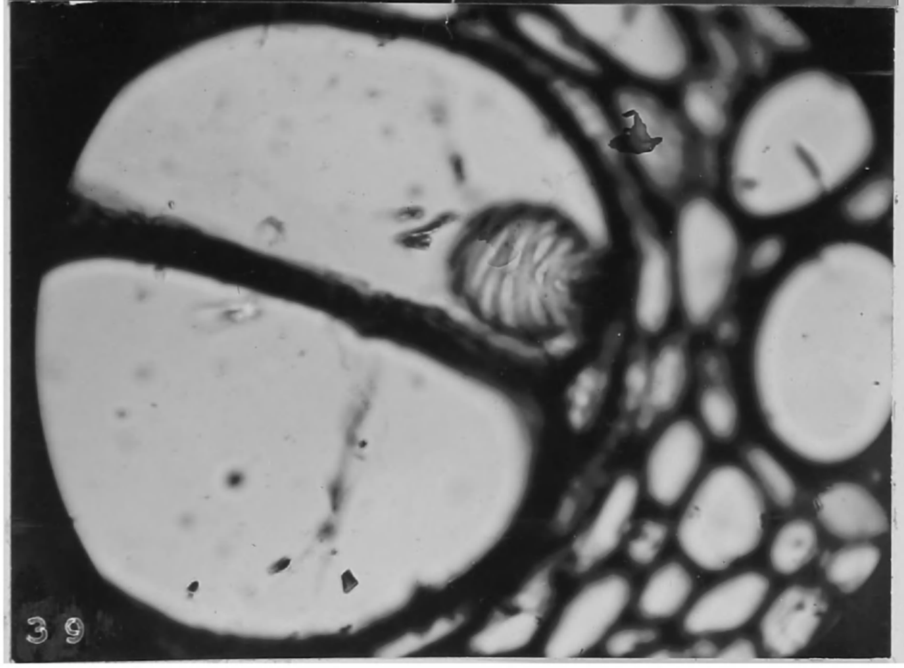
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PLATE XVII

Figure 40. Single parenchyma cell of an inoculated susceptible cantaloup stem showing numerous small vacuoles in the cytoplasm. This condition was typical of cells adjacent to infected areas. X 480.

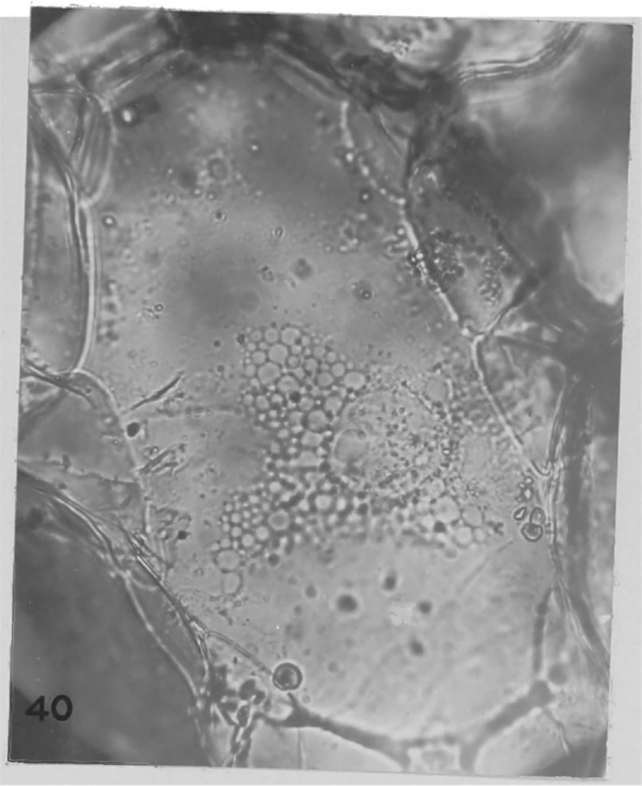

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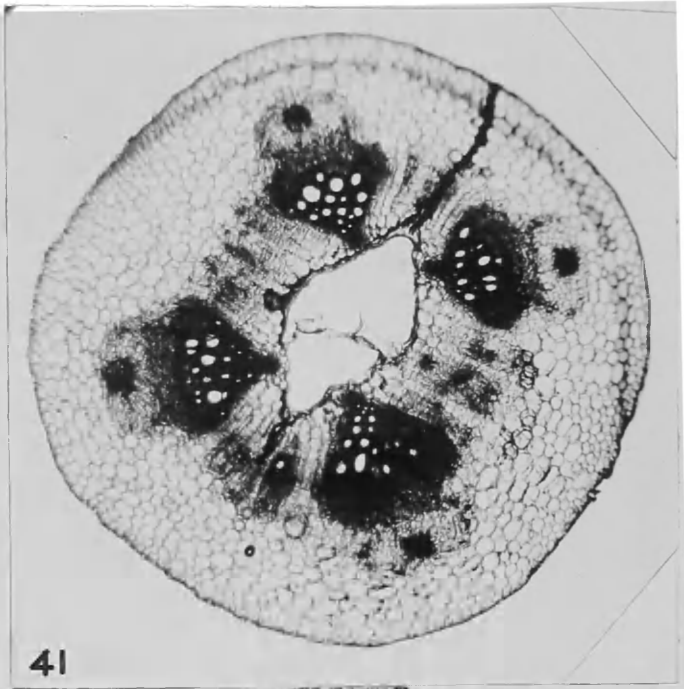
PLATE XVIII

Origin of cracks and necrotic streaks on the hypocotyls of infected cantaloup plants. X 15.

Figure 41.	Pith cavity lined with gummy material and strip of gum filled cells radiating to surface. At the opposite side of the cavity a short strip extends part of the way toward the surface.
Figure 42.	Hyphae have invaded the parenchyma adjacent to the lower bundle in the photograph and infection has extended to the surface to form a necrotic streak.

PLATE XVIII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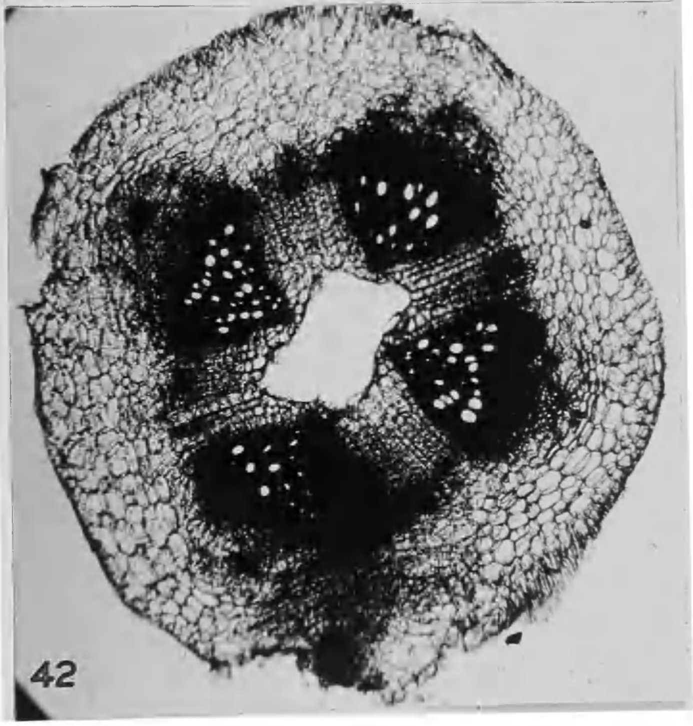
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