

Recd. Aug. 24, 1939

Vol. 59

AUGUST 1, 1939

No. 3

JOURNAL OF AGRICULTURAL RESEARCH

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Published on the 1st and 15th of each month. This volume will consist of 12 numbers and the contents and index.

Subscription price:

Entire Journal: Domestic, \$3.25 a year (2 volumes)

Foreign, \$4.75 a year (2 volumes)

Single numbers: Domestic, 15 cents

Foreign, 20 cents

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Copies of this number

were first issued

Aug 24, 1929

JOURNAL OF AGRICULTURAL RESEARCH

VOL. 59

WASHINGTON, D. C., AUGUST 1, 1939

No. 3

PHYTOPHTHORA TRUNK CANKER OR COLLAR ROT OF APPLE TREES¹

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INTRODUCTION

Trunk cankers have long been known to cause severe losses of trees in Indiana apple orchards. In some cases the damage has resulted from winter injury, or has been caused by fire blight (*Erwinia amylovora* (Burr.) Comm. S. A. B.). However, the cause of a particular type of destructive canker on the trunks of apple (*Malus sylvestris* Mill.) near the soil line, which occurs primarily on the Grimes Golden variety in Indiana, has not been definitely known. Following a serious epidemic of this type of collar rot in 1933, investigations of the nature of the disease and its control were undertaken. *Phytophthora cactorum* (L. and C.) Shroet. was found to be the causal agent. This paper presents the results of studies of the pathogenicity and physiologic specialization of the causal fungus, resistance and susceptibility of the host, and means of control of the disease.

THE DISEASE

HISTORY

Cankers caused by *Phytophthora cactorum* on the trunks of Grimes Golden trees, described by the writer (3, 5),³ are similar in many respects to collar rot cankers of undetermined or doubtful origin reported by several investigators. As early as 1858 the dying of apple trees as a result of an injury to the bark on the trunk and collar received considerable attention from fruit growers. According to Bradford and Cardinell (7), T. T. Lyon in addressing a meeting of horticulturists at Kalamazoo, Mich. in 1858, advocated the double-working of trees as a means of avoiding winter injury of the tender varieties. They mention that Baldwin, Tompkins King, Roxbury Russet, Rhode Island Greening, Esopus Spitzenburg, Hubbardston, and particularly Grimes Golden have long been listed as susceptible to collar injury. Stewart, Rolfs, and Hall (43), in 1900, described a collar rot of several varieties of apple trees in New York. They mentioned that the Tompkins King variety was so susceptible to attack that the disease was generally known as the king disease. Grossenbacher (17, 18), in 1909 and 1912, reported investigations on the nature of collar rot on apple trees in New York, and presented a review of the literature on this subject. He did not agree with Headden (19, 20) that arsenical poi-

¹ Received for publication November 19, 1938.

² The writer wishes to express his appreciation to Dr. R. M. Caldwell for helpful suggestions in the preparation of the manuscript and to Dr. Laurenz Greene and Prof. J. A. McClintock for their generous cooperation in making available most of the trees that were used for inoculation.

³ Italic numbers in parentheses refer to Literature Cited, p. 182.

soning was the cause of collar rot, but was of the opinion that much of the injury was induced by low winter temperatures. In 1926 Thomas (44) concluded that low winter temperatures caused a root and crown injury on apple trees in New York.

Collar rot of doubtful or unknown origin has been reported frequently. Selby (37), in 1900, in general attributed collar rot of apple trees in Ohio to winter injury. He mentioned that Grimes Golden, Tompkins King, and some other varieties, even in ordinary winters, seem to die on one side of the trunk just above the surface of the ground. Since the injury was not always confined to the south or southwest side of the trees, he expressed some doubt that it resulted entirely from the effects of winter temperatures. In an earlier bulletin (36) he reported that two orchards of 8- to 10-year-old Baldwin trees were ruined by winter freezing in 1881, while Grimes Golden trees under the same circumstances escaped: In 1913 Selby (38) stated that the very serious collar rot of Grimes Golden trees can be largely overcome by using top-grafted rather than root-grafted trees. Later, in 1921, Selby⁴ and in 1922 Thomas,⁵ reported a collar rot of undetermined origin on Grimes Golden and certain other varieties in Ohio. In reply to a question on collar rot, during a meeting in 1900 of the Indiana Horticultural Society, Burton (8, p. 66) stated:

It is quite likely that Mr. Tilson is troubled with what I term Grimes' bark disease. It is very much subject to bark disease, which affects it at the ground or a little above it. I don't know of any other tree so affected * * *

In 1921 Gardner (15) reported one orchard in southern Indiana in which approximately 25 percent of the Grimes Golden trees were affected with a collar rot, the cause of which was unknown. The disease appeared to be particularly serious on trees between 20 and 25 years of age. Anderson (1), in 1917, attributed a collar rot of Grimes Golden in Illinois to winter injury. However, the symptoms which he described are similar to those caused by *Phytophthora cactorum*. In 1918 Anderson (2) stated that collar rot, or Grimes Golden disease, appeared in orchards after the trees were about 10 years old, and frequently developed so rapidly that by the twentieth year, two-thirds of the Grimes trees were dead or in a dying condition. He suggested that double working or high grafting might offer a solution of the trouble. In 1919 collar rot of Grimes Golden trees in Illinois was adjudged to be a physiological condition, since attempts to isolate a causal organism failed (23). Anderson⁶ reported that in 1920 collar rot caused a crop loss of 1 percent in Illinois. Grimes Golden was the principal variety attacked. Anderson stated that the exact cause was unknown, but was probably winter injury.

Hotson (22), in 1920, concluded that most of the collar-rot cankers in the Yakima Valley, Wash., were due to fire blight, though the evidence that he presented was largely circumstantial. He listed a number of causes of collar rot, and stated that in the Yakima Valley comparatively few of the cankers can be traced to winter injury. As in many of the other publications reviewed, no mention was made of varieties affected. Magness (26), in 1929, concluded that low winter temperatures were the main cause of injuries occurring on the base of the trunks and roots of apple trees in Washington. He did not be-

⁴ ANDERSON, H. W. DISEASES OF FRUIT CROPS IN THE UNITED STATES IN 1920. U. S. Bur. Plant Indus., Plant Disease Bull. Sup. 14:1-114. 1921. [Mimeographed.]

⁵ HASKELL, R. J., and WOOD, JESSIE I. DISEASES OF FRUIT AND NUT CROPS IN THE UNITED STATES IN 1921. U. S. Bur. Plant Indus., Plant Disease Bull. Sup. 20:1-138. 1922. [Mimeographed.]

⁶ See footnote 4.

lieve that fire blight, as reported by Hotson (22), was an important contributing factor. A collar rot occurring on 15 varieties of apple trees in Pennsylvania was described by Orton and Adams (29) in 1915. They isolated the fire-blight organism from many of the cankers, and reported that typical cases of collar blight resulted from artificial inoculations into the collar and roots of young apple trees. The Grimes Golden, Baldwin, and York Imperial were listed as very susceptible. Many of the symptoms described were similar to those produced by *Phytophthora cactorum*. Orton and Adams found that trees between 7 and 20 years of age were affected, and that the average age of the trees when first infected was between 12 and 13 years, and that on many of the trees the canker was confined to the bark at the base of the trunk, and showed little advancement in a vertical direction.

Phytophthora cactorum causes cankers on the trunks and branches of many kinds of fruit and nut trees. Osterwalder (30), in 1912, reported the dying of young grafted apple trees in Switzerland, as a result of a killing of the bark near the graft union by *P. omnivora* de Bary, now considered synonymous with *P. cactorum*. Smith and Smith (42), in 1925, described a trunk and crown canker caused by *P. cactorum* and *P. citrophthora* (Smith and Smith) Leonian, on nursery and orchard trees of almond, apricot, cherry, peach, pear, plum, prune, and black walnut in California. A crown and trunk canker of walnut trees in California, caused by *P. cactorum*, was described by Smith and Barrett (40, 41) in 1930. Petri (31), in 1932, observed mycelium of a *Phytophthora* in the necrotic tissues of apple trees having collar rot, in Italy. In 1934 Curzi (10) described a crown rot of peach trees in Italy from which *P. cactorum* was isolated. Dunegan (12), in 1935, described a serious canker disease on the stems of young peach seedlings in Arkansas which was caused by *P. cactorum*. In 1938, Lindquist (25) described a collar rot of 10-year-old apple trees in Argentina from which *P. cactorum* was isolated. Smith (39), in 1937, reported infection on trees and shrubs of 26 plant genera artificially inoculated with a culture of *P. cactorum*. Tucker (46) extensively reviewed the literature and showed that *P. cactorum* is rather generally distributed throughout the temperate zones and parasitizes many different hosts. Tucker (45) and Smith (39) found that cultures of *P. cactorum* were omnivorous.

Tucker (46) has adequately reviewed much of the literature dealing with rots of apple and pear fruit caused by *Phytophthora cactorum*. Rose and Lindegren (34) obtained infection on uninjured pear and apple fruits placed in dishes containing orchard soil which was covered with water. Cooper (9) found that infection of uninjured apple and pear fruits by *P. cactorum* occurred through lenticels, and that zoospores may cause infection. Gardner (16) mentioned that apple fruit rot caused by *P. cactorum* occurred year after year in an orchard at Lafayette, Ind., and that the fungus apparently persists in the soil under the trees. Baines (4, 5) showed that *P. cactorum*, causing fruit rot, may also cause collar rot, and suggested that the growth of the fungus in the fruit may result in its increase in the soil.

OCCURRENCE OF PHYTOPHTHORA COLLAR ROT IN INDIANA ORCHARDS

During 1933 and 1934, years of severe collar rot epidemics in Indiana, apple trees in seven commercial orchards were examined for collar rot infection with respect to varieties and ages of the trees attacked.

In an orchard at Bedford, and in orchards designated as Nos. 1, 3, and 4 at Vincennes (table 1), an excellent opportunity was afforded

TABLE 1.—Occurrence of *Phytophthora trunk cankers* on *Grimes Golden* in 7 Indiana orchards, in 1933 and 1934

Location	Age of tree	Trees healthy	Trees affected		
			Less than ½ girdled	½ to completely girdled	Percentage
Bedford ¹	Years 13	Number 322	Number 3	Number 23	7.0
	18	28	16	26	60.0
Vincennes:					
Orchard No. 1 ²	14	58	4	54	50.0
Orchard No. 2.....	9	300	1	0	.3
	14	141	16	90	43.0
Orchard No. 3 ³	19	216	5	11	7.0
	11	277	2	1	1.0
Orchard No. 4 ⁴	18	49	8	94	68.0
	14	370	175	200	50.0
Bloomfield.....	16	370	5	92	21.0
Evansville.....	13	33	0	37	53.0

¹ No infection occurred in this orchard on 58 Delicious and 70 Winesap trees (18 years old), or on 86 Arkansas, 37 Baldwin, 388 Ben Davis, 185 Jonathan, 87 Maiden Blush, 173 Rome Beauty, 46 Stark, 171 Stayman Winesap, 18 Northern Spy, 25 Tompkins King, 8 Willowtwig, and 417 Winesap trees, which were 24 years old.

² No infection occurred in this orchard on 1,256 trees 14 years old, of the varieties Jonathan, Oldenburg, Rome Beauty, Stayman Winesap, Yellow Transparent, and York Imperial.

³ In this orchard of approximately 3,000 11-, 14-, and 18-year-old trees of the varieties Delicious, Grimes Golden, Jonathan, Oldenburg, Rome Beauty, Stayman Winesap, Yellow Transparent, Winesap, and York Imperial, the disease occurred only on Grimes Golden.

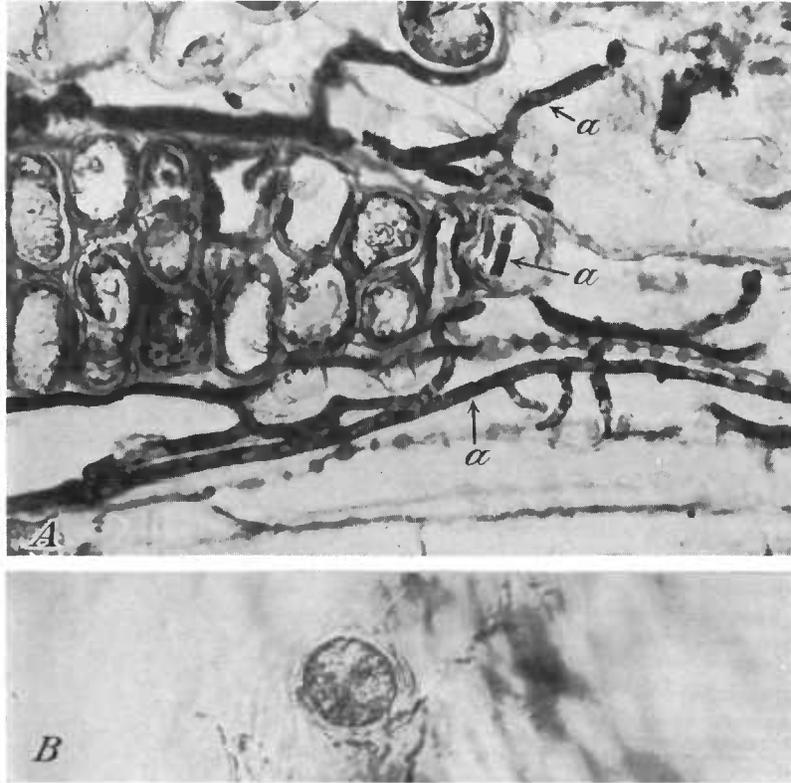
⁴ In this orchard, comprised of 220 acres of bearing trees of the varieties Arkansas, Ben Davis, Delicious, Golden Delicious, Grimes Golden, Jonathan, Maiden Blush, Oldenburg, Rome Beauty, Stayman Winesap, Yellow Transparent, Turley, Winesap, Winter Banana, Willowtwig, and York Imperial, infection, other than on Grimes Golden, occurred only on Rome Beauty, and only a few trees of this variety were infected.

to obtain information on the varieties affected, since in many cases other varieties were interplanted among the infected Grimes Golden trees. In these orchards, although Grimes Golden was severely attacked, no collar-rot cankers of a parasitic nature were observed on trees of the following varieties: Arkansas, Baldwin, Ben Davis, Delicious, Golden Delicious, Jonathan, Maiden Blush, Northern Spy, Oldenburg, Stark, Stayman Winesap, Tompkins King, Willowtwig, Winesap, Winter Banana, Yellow Transparent, and York Imperial. Two Rome Beauty trees affected with cankers which girdled the trunks were found in the orchard designated as No. 4 at Vincennes. The cankers appeared similar to those on Grimes Golden.

In six plantings of Grimes Golden trees, 14 to 18 years old, from 21 to 68 percent of the trees were infected with collar rot (table 1). In one planting of 19-year-old Grimes Golden trees 7 percent were infected. Of two plantings of 13-year-old Grimes Golden trees, one was 7 and the other 53 percent infected. Much less infection, 0.3 and 1 percent, occurred on plantings of Grimes Golden trees 9 and 11 years old, respectively. A discussion of this is presented later in connection with the report of inoculation experiments.

SYMPTOMS

Phytophthora cankers occur mainly on the trunks of the trees, but in later stages may involve the bases of the scaffold branches (fig. 1, C and D). Occasionally, roots near the surface of the ground are invaded. The trunk cankers, frequently irregular in shape, enlarge rapidly in both lateral and vertical directions and may girdle Grimes Golden trees within one season. On double- and high-grafted Grimes



A, Tangential section of infected apple bark showing (a) the intercellular and intracellular mycelium of *Phytophthora cactorum*; B, oospore of *P. cactorum* from infected apple bark. $\times 640$.

Golden, the cankers usually do not extend below the graft union, and consequently may not extend to the soil line (fig. 1, *C*). The first symptom of the disease is a wet, discolored area on the surface of the bark, resulting from an exudation of liquid from the killed bark (fig. 1, *A, c*). Frequently the cankers are well advanced, and the trunks may be completely girdled before any symptoms are noticeable to a casual observer. In later stages of infection, the bark becomes dry and the cankers are delimited by a definite margin. The bark on old cankers becomes cracked, and may pull away from the trunk (fig. 1, *D*). On severely infected trees the fruit ripens early, the foliage in the fall becomes a reddish-bronze color, and premature defoliation occurs (fig. 2, *A*). The affected trees blossom and leaf out the following spring, after which the leaves and fruit on branches directly above the girdled areas on the trunks usually wilt, and the branches die.

The affected bark of active cankers appears brown and water-soaked, and has a strong, fermented odor. Recently infected bark near the margins of enlarging cankers is light brown in color, with a gradual diminution of the brown color toward the healthy tissues (fig. 1, *B, a*). Occasionally, streaks extending 1 to 2 inches beyond the margin of the canker are found near the cambium. Usually the cambium is killed and the sapwood invaded and discolored. The enlargement of the cankers is checked in the fall, presumably by the maturation of the bark tissues. However, cankers which do not girdle trees in one season usually renew activity the following spring at various places on their margins.

PATHOLOGICAL HISTOLOGY

Infected bark from the margins of actively enlarging cankers on the trunks of 13-year-old Grimes Golden trees was fixed, infiltrated with paraffin, and sectioned by the usual method for histological examination. In sections stained in haematoxylin, and aniline blue in picric acid, the mycelium of the fungus, which stained blue, was readily differentiated from the host tissues. An abundance of both intercellular and intracellular coenocytic mycelium was observed in all parts of the infected bark (pl. 1, *A, a*). The infection caused a distinct disorganization of the host-cell protoplast and a break-down of the cell walls, especially of the parenchyma. Mycelium was not observed in advance of the discolored area of affected tissues.

Numerous oospores or chlamydospores, apparently those of *Phytophthora cactorum*, were found in mascerated bark collected in the spring from an overwintering canker produced by artificial inoculation (pl. 1, *B*). No sporangial stage of the fungus on the surface of the cankers was found by macroscopic examination of many cankers.

INFECTIOUS NATURE OF CANKER TISSUE

Early in the investigations, this type of collar rot was demonstrated to be infectious when cankers resulted from inoculations made by inserting pieces of infected bark into the trunks of five healthy Grimes Golden trees 13 years old. Inoculations were made with bark taken from each of five cankers. The inoculations were covered with cheesecloth and grafting wax. Typical cankers, from 5 to 15 cm. in diameter, resulted after 2 weeks from inoculations made with bark from four cankers.

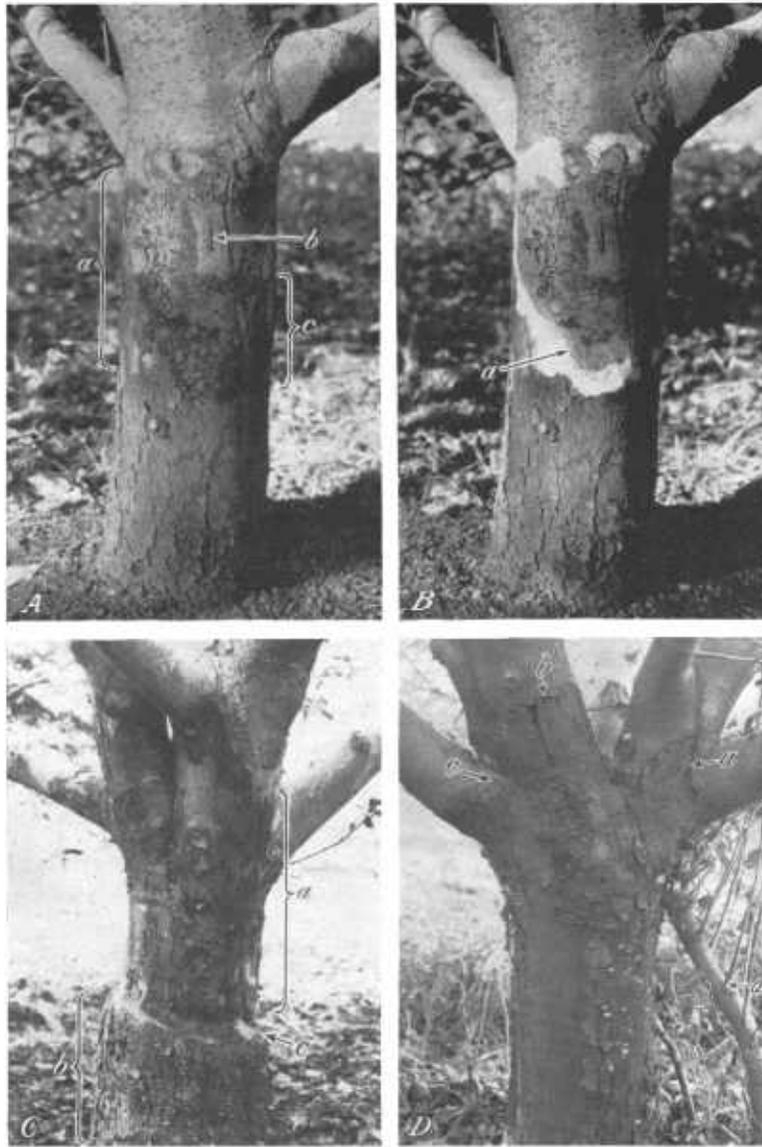


FIGURE 1.—*Phytophthora cactorum* cankers on Grimes Golden trees: *A*, Canker (*a*) on an 11-year-old tree 2 months after inoculation at *b*. The moist dark-colored area (*c*) is the first exterior symptom of the disease. *B*, The same canker as in *A* with the outer bark removed at *a* to show the light-brown, advancing margin of the canker. *C*, Trunk of tree illustrated in Figure 2, *A*. The canker (*a*) was confined to the trunk and bases of the main branches and did not invade the stock (*b*). The graft union (*c*) sharply limited the canker to the Grimes Golden tissues. Healthy light-colored tissue at the margin of the canker has been exposed by removal of the outer bark. *D*, Trunk of a 14-year-old tree girdled by an old canker with infected bark dry, cracked, and invaded by other organisms. The canker did not advance appreciably above the bases of the main branches at *a*, *b*, and *c*, nor infect the inarch (*d*) at the side of the trunk.

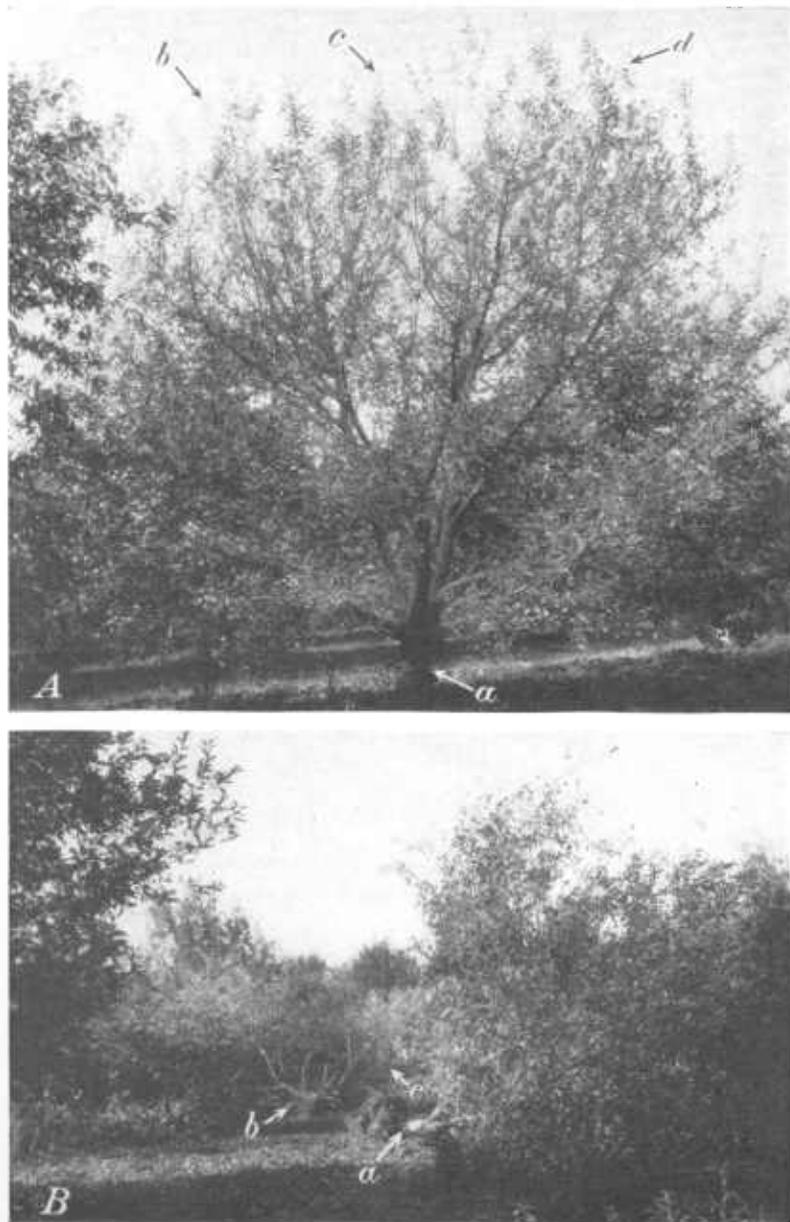


FIGURE 2.—A, 14-year-old, high-grafted Grimes Golden tree with trunk above the graft union (*a*) girdled by *Phytophthora cactorum* (see fig. 1, C). The tree was distinguished by the yellowish-green foliage, becoming reddish at the tips of the upper branches (*b*, *c*, and *d*), and by the partial defoliation. B, 14-year-old Grimes Golden trees (*a*, *b*, and *c*) girdled by *P. cactorum* and pulled up. The roots of 50 similar trees examined, except 1, were healthy.

RELATION OF BACTERIA TO THE DISEASE

Numerous bacterial colonies were obtained from infected bark of 17 trunk cankers of Grimes Golden trees by the dilution-plate method. Bacteria from these cankers were nonpathogenic when inoculated into 14- and 18-year-old Grimes Golden tree trunks, Briarcliff and Premier rose shoots, Rome Beauty and Winesap apple shoots, and Bartlett pear fruits.

Although pathogenic bacteria were not isolated from trunk cankers of Grimes Golden, inoculations were made on this variety with the fire blight organism, *Erwinia amylovora*, in an attempt to produce cankers typical of the collar rot disease. Three cankers less than 3 cm. in diameter, and delimited by cork at their margins, resulted from 12 inoculations made on the trunks of 11 14-year-old and 1 18-year-old Grimes Golden trees on May 11, 1934. Five bark cankers similar to these were also formed around the bases of inoculated succulent shoots which were on the trunks or bases of the first main branches of these trees. The culture of *E. amylovora* used in the inoculations was pathogenic on apple shoots and pear fruits. Obviously the trunk canker disease of Grimes Golden differed greatly from that caused by fire blight.

THE CAUSAL FUNGUS (PHYTOPHTHORA CACTORUM)

ISOLATION

*Phytophthora cactorum*⁷ was consistently isolated from small pieces of infected bark taken from the margins of enlarging cankers. The infected bark tissue was surface-sterilized in a solution of 1:1,000 mercuric chloride, twice rinsed in sterile water, and then plated on potato-dextrose agar. Other fungi, including an undetermined species of *Alternaria*, and a few bacteria, grew from some of the tissue plantings. No infection was obtained when the *alternaria* fungus was inoculated into the bark of the trunk of an 18-year-old Grimes Golden tree. The bacteria which grew from some of the plantings were not typical of *Erwinia amylovora*, and apparently were similar to those obtained by the dilution-plate method mentioned earlier.

During 1934-36, *Phytophthora cactorum* was obtained from 49 of the 64 cankers on the trunks of Grimes Golden trees from which isolation was attempted. The cankers from which the fungus was isolated were collected in 11 orchards in the vicinity of Bedford, Bloomfield, Evansville, Indianapolis, Mitchell, and Vincennes, Ind. All colonies of *P. cactorum* obtained from the 49 cankers, except 1, appeared to be similar in cultural characters on potato 2-percent dextrose agar. From 1 canker both an atypical culture and a typical culture of *P. cactorum* were isolated.

The isolation of *Phytophthora cactorum* from inactive cankers was found difficult by the tissue-planting procedure. However, when apple fruits were inoculated with small pieces of infected bark from the margins of such cankers, a rot frequently developed from which *P. cactorum* was readily isolated. The percentage of inoculations of this type producing infection of the fruits was rather low when the bark was secured from the centers of cankers.

⁷The writer gratefully acknowledges the assistance of Dr. C. M. Tucker in the identification of the culture.

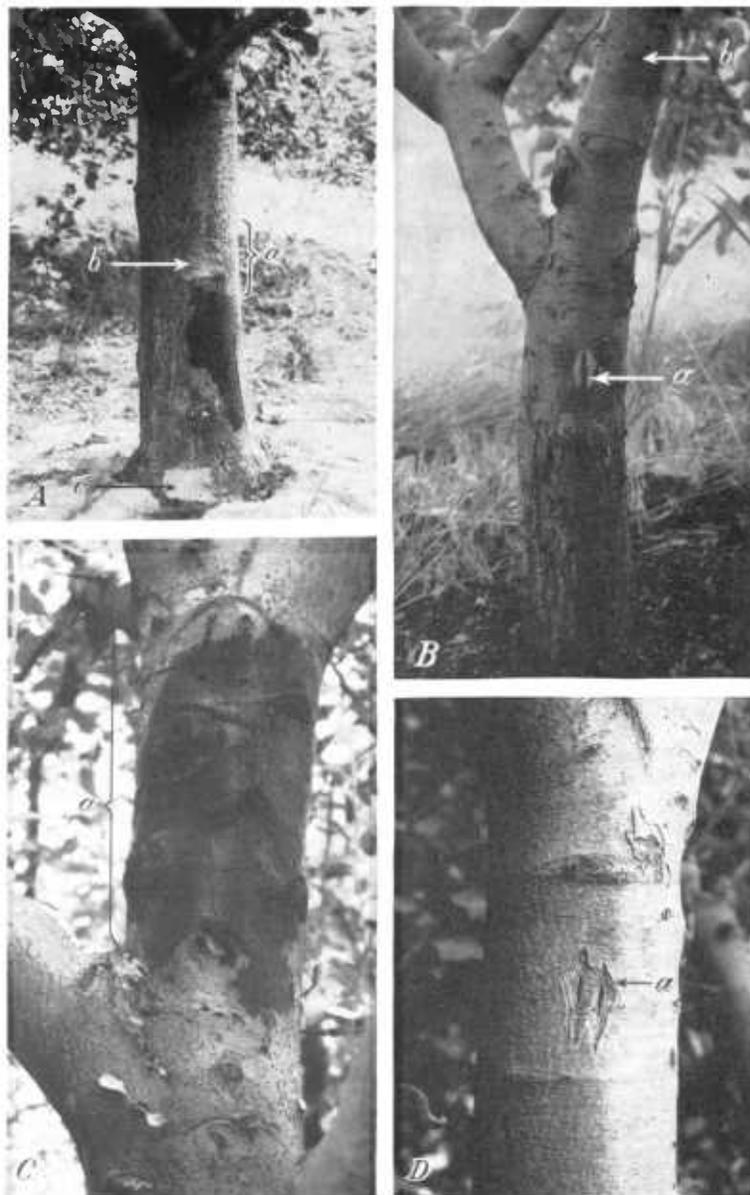


FIGURE 3.—*A*, Infection (*a*) not externally visible on trunk of a 13-year-old Grimes Golden tree 3 weeks after inoculation at (*b*). The wet, discolored area below the canker caused by exudation of a liquid from the infected area is the first external symptom of the disease. No infection resulted from an inoculation (*c*) on the Virginia crab stock. *B*, Inoculation incision (*a*) on a resistant (Jonathan) variety, with outer bark cut away to show the sharp limitation of the disease; check incision (*b*) on branch, which was similar to that on the trunk. *C*, Canker (*a*) produced by artificial inoculation on Grimes Golden branch 15 cm. in diameter. *D*, Slight enlargement at (*a*) of an inoculation incision, which had ceased enlarging and was classified as infection failure, on a Grimes Golden branch 8 cm. in diameter.

Cultures Nos. 1, 3 to 7, 9 to 11, 26, and 27 were severely pathogenic on trees 8 or more years old. Usually the cankers were 20 to 25 cm. in diameter 1 month after inoculation, and showed no evidence of being checked (fig. 1, A, B). In many cases the cankers girdled the 11- to 14-year-old Grimes trees within 3 months after inoculation. *Phytophthora cactorum* was obtained from each of the 32 cankers from which reisolation was attempted. No infection occurred on the 2- to 4-year-old trees, which were inoculated with culture No. 1.

A canker resulted from only one of five inoculations made with culture No. 2, although it was isolated from a canker and was similar in culture to the highly parasitic strains. This canker increased rapidly in size, suggesting that with this culture infection is established with difficulty, although it is capable of developing once established.

TABLE 2.—Pathogenicity of *Phytophthora cactorum* on Grimes Golden trees in Indiana orchards

Source of culture	Culture No.	Year of inoculation	Age of trees	Trees inoculated	Inoculations ¹	
					Total	Producing cankers ²
			Years	Number	Number	Number
Canker.....	1	1935	2	5	8	0
Do.....	1	1936	3	5	8	0
Do.....	1	1937	4	5	8	0
Do.....	1	1938	5	3	6	1
Do.....	1	1935	8	3	3	3
Do.....	1	1934	11	1	2	2
Do.....	1	1936	11	12	15	13
Do.....	1	1935	12	4	4	4
Do.....	1	1934	13	12	14	13
Do.....	1	1935	14	33	33	25
Do.....	1	1934	18	2	8	8
Do.....	1	1935	19	6	13	12
Do.....	1	1935	20	28	29	27
Do.....	1	1935	30	2	6	5
Do.....	2	1935	19	2	5	1
Do.....	3	1936	11	1	2	2
Do.....	3	1935	19	2	5	5
Do.....	4	1935	19	2	5	3
Do.....	5	1935	19	2	5	5
Do.....	6	1935	19	2	5	4
Do.....	7	1935	19	2	5	5
Fruit rot.....	9	1935	19	2	5	4
Do.....	10	1936	11	1	2	1
Do.....	11	1935	19	2	5	4
Soil.....	26	1936	11	2	4	3
Do.....	27	1936	11	2	4	2

¹ No cankers resulted from the 113 check incisions.

² *P. cactorum* was obtained from each of 32 cankers from which reisolation was attempted.

The results of inoculation of the trunks of species of *Prunus*, *Pyrus*, and *Cydonia* with culture No. 1 of *Phytophthora cactorum* are presented in table 3. Two-year-old trees of *Prunus mahaleb* L. (cherry), *P. avium* L. (cherry), *P. americana* Marsh. (plum), and 6-year-old trees of *P. persica* (L.) Batsch. var. Elberta (peach), and 1 tree of *P. domestica* L. var. Reine Claude (plum), 20 years or more old, were highly susceptible to infection by *P. cactorum* (fig. 4, A, B, C). Only one of five 2-year-old trees of *Prunus cerasifera* Ehrh. (plum) became infected. No infection occurred on 2-year-old trees of *Pyrus baccata* L. (apple), *P. coronaria* L. (apple), *P. serotina* Rehd. (pear), and *Cydonia oblonga* Mill. (quince).

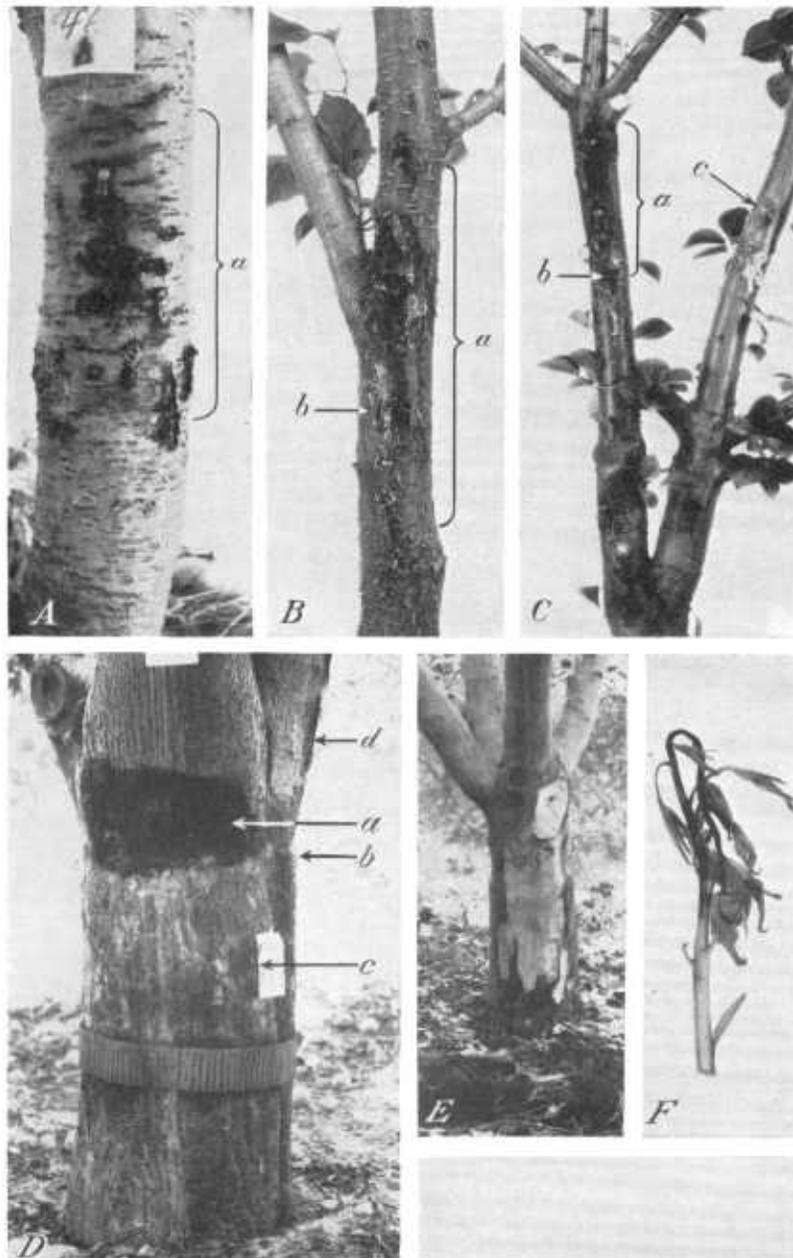


FIGURE 4.—*A*, Canker (*a*) on 6-year-old peach tree (artificial inoculation). *B*, Canker (*a*) on 2-year-old mazzard cherry tree resulting from inoculation at *b*. *C*, Canker (*a*) on 2-year-old mazzard cherry tree resulting from inoculation at *b*; check incision at *c*. *D*, Inoculations on 20-year-old, double-worked Grimes Golden tree producing canker (*a*) on Grimes scion, which extended to graft union (*b*), but no infection from inoculation on Delicious stock (*c*), nor from check incision (*d*) on Grimes scion. *E*, Canker on trunk of 14-year-old Grimes Golden tree treated by scarification and ready for painting with Bordeaux paint. *F*, Infection of peony shoot following artificial inoculation with a virulent culture.

TABLE 3—Results of inoculation of trees of *Prunus*, *Pyrus*, and *Cydonia* species with culture No. 1 of *Phytophthora cactorum*

Species	Age of tree	Trunks inoculated	Cankers produced ¹	Check incisions ²
	Years	Number	Number	Number
<i>Prunus avium</i>	2	5	3	5
<i>Prunus mahaleb</i>	2	5	5	5
<i>Prunus americana</i>	2	5	4	5
<i>Prunus cerasifera</i>	2	5	1	5
<i>Prunus domestica</i>	20	3 ³	2	0
<i>Prunus persica</i>	6	3	3	3
<i>Pyrus baccata</i>	2	5	0	5
<i>Pyrus coronaria</i>	2	5	0	5
<i>Pyrus serotina</i>	2	5	0	5
<i>Cydonia oblonga</i>	2	5	0	5

¹ Apparently pure cultures of *Phytophthora cactorum* were reisolated from cankers on *Prunus avium*, *P. mahaleb*, *P. americana*, and *P. domestica*.

² No infection resulted from the check incisions.

³ Inoculations made on large branches.

No infection resulted from the check incisions during these tests. This fact was considered to justify the practice of not sterilizing the surface of the bark prior to inoculating. The orchards in which the inoculations were made were relatively free from fire-blight and collar-rot infection.

PHYSIOLOGIC SPECIALIZATION

MATERIAL AND METHODS

The inoculations to differentiate physiologic races of the fungus, unless otherwise stated, were made in a 10-year-old orchard of Grimes Golden trees, which contained 1 or 2 trees of each of the 30 other varieties listed in table 5 and footnote 2 of that table. These trees appeared normal, and a week before they were inoculated in July 1936, between 300 and 400 gallons of water were applied under each tree to insure plentiful soil moisture during the experiment. The sources of the 12 cultures of *Phytophthora cactorum* tested are given in table 4. Inoculations were made on the trunk of each tree, except Grimes Golden, with the 10 cultures Nos. 1, 8, and 12 to 19. Each of the 12 cultures was tested on one or more Grimes Golden trees. One check incision on each tree, into which sterile potato-dextrose agar was introduced, remained free from infection during these tests. The inoculations were made as previously described. In addition, inoculations with culture No. 1 were made on 28 varieties, between 12 and 30 years old (footnote 3, table 5). The number of trees available for inoculation was limited because of the danger of killing valuable trees of bearing age.

 TABLE 4.—Cultures of *Phytophthora cactorum* tested for physiologic specialization

Culture No.	Host	Place isolated and year	Collector or source of culture ¹
1	Grimes Golden apple tree.....	Indiana, 1934.....	Writer.
8	do.....	do.....	Do.
12	Apple fruit.....	do.....	Baarn, Netherlands.
13	<i>Lilium candidum</i>	Indiana, 1936.....	E. P. Imie.
14	Lilac.....	Massachusetts, 1929.....	K. S. Chester.
15	Peony.....	Indiana.....	Baarn, Netherlands.
16	Citrus.....	Korea.....	Do.
17	<i>Eriobotrya japonica</i>	Japan.....	T. Tasugi.
18	Snapdragon.....	California, 1932.....	M. P. Harris.
19	<i>Pinus</i> sp.....	do.....	Baarn, Netherlands.
20	Unknown.....	do.....	Do.
21	<i>Lilium dauricum</i>	Japan.....	T. Tasugi.

¹ Cultures Nos. 12 and 14 to 21, inclusive, were received from C. M. Tucker.

TABLE 5.—Pathogenicity and physiologic specialization of cultures of *Phytophthora cactorum* described in table 4 on 10-year-old apple trees, and on flax and peony plants

Culture No. ¹	Source of culture	Virulence of cultures on 7 apple varieties and on flax and peony ²								
		Gano	Grimes Golden	Tompkins King	Northwestern Greening	Rome Beauty	Smoke-house	Stark	Flax	Peony
31	Grimes Golden trees.....	0(2)	3(3); 0(3)	3(1); 0(1)	3(1)	3(1); 0(1)	0(1)	3(1); 0(1)	1(4); 0(6)	3(13); 2(2)
8	Apple fruit.....	3(1); 0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	2(1); 1(6)	3(13); 2(2)
12	Lily.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	1(6); 0(4)	3(13); 2(2)
13	Lily.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	1(6); 0(4)	3(13); 2(2)
14	Lily.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	1(6); 0(4)	3(13); 2(2)
15	Peony.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(2); 1(6); 0(2)	3(7); 2(6); 1(2)
16	Citrus.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(6); 0(8)	3(1); 2(6); 1(6); 0(5)
17	Loquat.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(6); 0(8)	3(1); 2(6); 1(6); 0(5)
18	Loquat.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(6); 0(8)	3(1); 2(6); 1(6); 0(5)
19	Pine.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(6); 0(8)	3(1); 2(6); 1(6); 0(5)
20	Unknown.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(6); 0(8)	3(1); 2(6); 1(6); 0(5)
21	Lily.....	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(6); 0(8)	3(1); 2(6); 1(6); 0(5)

¹No infection resulted from inoculations made with cultures Nos. 1 and 8 to 19, inclusive, on the following 10-year-old trees not included in the table: 1 Arkansas, 2 Baldwin, 2 Ben Davis, 2 Cortland, 2 Delicious, 1 Early Harvest, 2 Golden Delicious, 1 Hubbardston, 1 King David, 1 Lowland Raspberry, 2 McIntosh, 1 Maiden Blush, 1 Northern Spy, 1 Oldenburg, 1 Paragon, 1 Rhode Island Greening, 2 Stayman Winesap, 2 Starking, 1 Wagener, 2 Wealthy, 2 Winesap, 1 Winter Banana, 2 Yellow Transparent, and 1 York Imperial.

²Virulence of the cultures is designated by numerals as follows: Nonpathogenic, 0; slightly virulent, 1; moderately virulent, 2; and extremely virulent, 3. First numeral indicates virulence, and number in parenthesis following virulence figure indicates number of trees or plants so affected.

³Culture No. 1 was also tested on 28 varieties of apple trees from 12 to 30 years old and not reported in the table. Infection resulted on 5 Northwestern Greening and on 1 of

the 3 Rome Beauty trees inoculated. No infection resulted on 10 Arkansas, 1 Baldwin, 2 Bononi, 6 Ben Davis, 14 Delicious, 4 Fernusee, 3 Hibernal, 2 Hubbardston, 5 Jonathan, 7 Lowland Raspberry, 5 McIntosh, 2 Maiden Blush, 1 Miami, 7 Northern Spy, 8 Oldenburg, 3 Red Astrachan, 1 Rhode Island Greening, 5 Stayman Winesap, 1 Tompkins King, 4 Transcendent crab, 2 Virginia crab, 5 Walden, 5 Wagener, 9 Wealthy, 8 Winesap, and 1 Winter Banana. No infection resulted from inoculations in which culture No. 1 was used on the trunks of 2, 3, and 4-year-old trees of the following varieties: Bononi, Black Ben Delicious, Golden Delicious, Golden Sweet, Jonathan, Maiden Blush, McIntosh, Oldenburg, Rome Beauty, Red Rome, Red Delicious, Stayman Winesap, Turley, Wealthy, Winesap, Yellow Transparent, and York Imperial. Four trees of each variety were inoculated twice during consecutive years.

⁴No infection resulted from 5 inoculations on 5 10-year-old trees; 3 cankers resulted from 5 inoculations on 2 10-year-old trees.

Three-week-old flax (Red Wing) plants and peony (Mme. Bou-langer) shoots growing in a greenhouse also were inoculated with the 12 cultures of *Phytophthora cactorum* listed in table 4. A small quantity of mycelium from a culture on potato-dextrose agar was inserted in the stems and covered with a piece of rubber tape. Two groups of 5 plants of flax were grown separately in a greenhouse bench and inoculated with each culture. The tests on peony were conducted in two trials. Five shoots were inoculated in the first trial and 10 in the second. A similar number of check plants treated with sterile potato-dextrose agar instead of inoculum remained free from infection during these tests.

The virulence of the cultures on flax and peony was recorded by assigning values of 0, 1, 2, and 3 to the recognized classes of infection resulting from the inoculations. The value 3 was assigned to the severely infected plants, 0 to the plants not infected, and intermediate values to the plants in the intermediate classes. A virulence of 3 was assigned to the cultures which were pathogenic on the 10-year-old apple trees.

DIFFERENTIAL PATHOGENICITY OF CULTURES

Culture No. 1 isolated from a Grimes Golden trunk was the most widely pathogenic culture on the apple varieties, producing cankers on Grimes Golden, Tompkins King, Northwestern Greening, Rome Beauty, and Stark (table 5). Four other cultures also produced cankers on apple trunks, but differed from culture No. 1 and from one another in the varieties that they infected. Culture 13, from *Lilium candidum* L., was pathogenic on Tompkins King, Rome Beauty, and Stark. Culture 17, from loquat, infected Tompkins King and Smoke-house, being the only culture to infect the latter variety. Culture 14, from lilac, infected only Tompkins King of the 10-year-old trees, but it also infected 19-year-old Grimes Golden in another test. Culture 8, isolated from a Grimes Golden trunk and atypical in growth on media, infected only Gano, and was the only culture to infect this variety. Cultures Nos. 12, 15, 16, 18, and 19 failed to infect any of the above-mentioned seven varieties, which were infected by one or more of the other cultures. Cultures 20 and 21 were nonpathogenic on Grimes Golden. *Phytophthora cactorum* was reisolated from cankers formed by the pathogenic cultures.

Inoculations of flax and peony also brought out differences in pathogenicity of the cultures. Cultures 1, 8, 13, 14, and 17, pathogenic on one or more varieties of apple, were only slightly pathogenic on flax. With the exception of cultures 12 and 15, all of the remaining cultures that were nonpathogenic on apple were highly virulent on flax. All the cultures except No. 15, were highly virulent on peony (fig. 4, F). *Phytophthora cactorum* was reisolated from infected flax and peony plants.

The data presented above are too limited to permit definite classification of races of *Phytophthora cactorum*. However, the writer believes that significant differences in the capacity of cultures of *P. cactorum* to cause collar rot on different apple varieties have been demonstrated.

VARIETAL SUSCEPTIBILITY

TRUNK CANKER

Seven apple varieties were susceptible to phytophthora trunk canker (table 5). The Gano variety was infected by one culture, Grimes Golden by two, Tompkins King by four, Northwestern Greening by one, Rome Beauty by two, Smokehouse by one, and Stark by two. A culture of *Phytophthora cactorum* isolated from peony in 1937, and not included in table 5, was pathogenic on the trunks of 20-year-old Grimes Golden.

No infection resulted on trunks of 10-year-old Arkansas, Baldwin, Ben Davis, Winter Banana, Cortland, Delicious, Oldenburg, Early Harvest, Golden Delicious, Hubbardston, King David, Lowland Raspberry, McIntosh, Maiden Blush, Northern Spy, Paragon, Rhode Island Greening, Stayman Winesap, Starking, Wagener, Wealthy, Winesap, Yellow Transparent, and York Imperial apple trees when inoculated with cultures 1, 8, and 12 to 19. In addition, Benoni, Fameuse, Hibernial, Mann, Red Astrachan, Transcendent crab, Virginia crab, and Walbridge apple trees, 13 to 30 years of age, were resistant to infection by culture No. 1. The inoculations on the trunks from which no infection was recorded, in many cases developed a slight enlargement of the inoculation incision (fig. 3, *B*). In some cases, only one or two inoculations were made with a given culture on a variety. Therefore, final conclusions on the reaction of a variety to a given culture cannot be made from these tests.

ROOT ROT

Cankers near the bases of the trunks of an own-rooted Grimes Golden, 14 years old, and of an 18-year-old Grimes Golden on French crab seedling roots, extended into the large roots. The writer was unable to determine whether the infected roots arose from the Grimes Golden scion of the latter tree. Apparently pure cultures of *Phytophthora cactorum* were isolated from diseased bark from the roots of both trees. The cankers on the roots had definite margins and the infected periderm was brown and soft. In an orchard at Vincennes, 14-year-old Grimes Golden trees severely girdled by phytophthora trunk cankers were pulled with a tractor (fig. 2, *B*). The French crab seedling roots of 49 of these trees were healthy. On 1 tree a large root was decayed by an undetermined organism.

FRUIT ROT

Apple fruits of 29 varieties were inoculated with *Phytophthora cactorum* culture No. 1. Two fruits of each variety were taken from cold storage on November 29, 1935, swabbed with 95-percent alcohol, and inoculated by introducing into a puncture a small quantity of mycelium from a young culture. The inoculations were sealed with petroleum jelly. A check puncture was made on the side of each fruit opposite the inoculation. Each variety was enclosed in a waxed paper bag.

Typical decay was produced by all the inoculations and none by the check punctures. After 1 week the infected areas were between 3.3 and 6.3 cm. in diameter on the Baldwin, Ben Davis, Oldenburg, Fameuse, Grimes Golden, Hubbardston, Jonathan, Tompkins King,

Lowland Raspberry, McIntosh, Maiden Blush, Northern Spy, Northwestern Greening, Rome Beauty, Gallia Beauty, Red Delicious, Rhode Island Greening, Stark, Stayman Winesap, Smokehouse, Yellow Transparent, Turley, Wagener, Winesap, Winter Banana, and York Imperial varieties, between 2.2 and 3.3 cm. on Banks and Golden Delicious, and 1.3 cm. on Arkansas.

FACTORS AFFECTING RESISTANCE AND SUSCEPTIBILITY TO COLLAR ROT

RELATION OF AGE AND VIGOR OF GRIMES GOLDEN TREES TO INFECTION

The trunks of Grimes Golden trees ranging in age from 2 to 30 years were inoculated with culture No. 1 (table 2). The 2-year-old trees were nursery-budded and were inoculated the season that they were replanted. These young trees grew vigorously, and were reinoculated twice during each of the following 3 years. No infection occurred until the fourth year. Then one canker resulted from six inoculations on three 5-year-old trees. The marked resistance of the 2- to 4-year-old trees is difficult to explain. Presumably a similar type of resistance occurred when large scaffold branches of older trees were inoculated, as will be shown later. Typical cankers were produced on the trunks of Grimes Golden trees 8 to 30 years old. All the trees were growing well when inoculated, except two 30-year-old trees and a few 14-year-old trees on poor soil. Typical cankers were obtained on the 30-year-old trees, but the small, slow-growing 14-year-old trees on areas of poor soil appeared to be more resistant to infection than more vigorous trees in the same orchard.

Under conditions of natural infection the disease occurs chiefly on Grimes Golden trees over 13 years of age, as mentioned above. However, Grimes Golden trees 8 and 11 to 13 years of age were easily infected when mycelium of the fungus was introduced into the bark of the trunks. It appeared likely that these younger trees escape infection through the operation of some factors other than internal resistance to the parasite. Therefore, a series of inoculations was made by placing inoculum on the uninjured bark of 11- and 19-year-old trees. Colonies of culture No. 1, grown for 2 weeks on prune-extract medium, were placed on the uninjured surfaces of the trunks of Grimes Golden trees, and covered with moist cheesecloth and heavy wrapping paper for 3 days. Check areas were treated similarly, except that no inoculum was used. From nine inoculations made on six, 19-year-old trees, six cankers developed on four trees. One month after inoculation the cankers were 13 to 25 cm. in diameter and showed no evidence of being checked. The fungus was reisolated from four cankers. No infection resulted from four inoculations and two check treatments made on six 11-year-old trees nor from five check treatments on 19-year-old trees. The results show 19-year-old trees to be susceptible to infection from inoculum placed on the unwounded trunk, and they suggest a structural resistance in 11-year-old trees to infection from such inoculation.

RESISTANCE OF BRANCHES

Cankers caused by natural infection with *Phytophthora cactorum* have never been observed by the writer on scaffold branches. To

determine whether the branches are actually resistant or whether they merely escape infection, inoculations were made during 1935 on both the trunks and branches of 22 varieties ranging in age from 12 to 30 years. Mycelium of culture No. 1 of *P. cactorum* was placed in incisions in the bark, as previously described.

Typical cankers resulted on the trunks of 38 of 46 Grimes Golden trees inoculated (table 6). However, only 3 cankers developed from 70 inoculations on branches. One canker, 20 cm. long, encircled a branch 5 cm. in diameter on a 12-year-old Grimes Golden. The canker was sunken, had a definite margin, and the cambium under most of the canker appeared healthy. *Phytophthora cactorum* was reisolated. A second branch canker, 7 cm. in diameter, occurred on a branch 8 cm. in diameter on a 14-year-old Grimes Golden tree. It was definitely checked in growth and delimited from sound bark. A third canker occurred on a main scaffold branch 15 cm. in diameter on a 19-year-old tree. Two months after inoculation the canker was 35 cm. in diameter and still enlarging (fig. 3, C). No infection occurred on the trunks or branches of the other 21 varieties inoculated except Rome Beauty. A trunk canker resulted from inoculations on 2 Rome Beauty trees. From all the inoculations of branches that were classed as no infection, a slight enlargement of the inoculation wound took place (fig. 3, D).

TABLE 6.—Susceptibility of the branches and trunks of apple trees to infection by *Phytophthora cactorum*, culture No. 1

Variety ¹	Age of trees	Trees inoculated	Trunks infected ²	Inoculations on branches		
				Diameter of branches inoculated	Inoculations	Cankers produced
	Years	Number	Number	Centimeters	Number	Number
Grimes Golden.....	12	4	4	5-7	4	1
	13	4	4	4-7	4	0
	14	33	25	5-10	33	1
	19	2	2	7-15	7	1
	20	1	1	2-15	18	0
	30	1	1	11	1	0
Rome Beauty.....	13	1	1	10	3	0
	13	1	1	5-7	2	0
	30	1	0	12	2	0

¹ No infection resulted from a trunk and branch inoculation on 4 Arkansas, 1 Winter Banana, 2 Baldwin, 1 Benoni, 3 Oldenburg, 6 Fameuse, 3 Hibernial, 2 Hubbardston, 4 Jonathan, 2 Tompkins King, 10 McIntosh, 2 Maiden Blush, 1 Mann, 2 Northern Spy, 1 Rhode Island Greening, 2 Red Astrachan, 5 Stayman Winesap, 2 Wagerer, 9 Wealthy, and 8 Winesap trees, 12 to 30 years of age.

² No infection resulted from 44 check incisions in the trunks.

INTERACTION OF STOCK AND SCION COMPONENTS OF GRAFTED TREES IN RELATION TO RESISTANCE AND SUSCEPTIBILITY

In an effort to avoid trunk cankers, Grimes Golden trees are frequently propagated by grafting the Grimes scion on the stock, 6 or more inches above the soil line, and also by double-working, i. e., by using a second variety to form the base of the trunk onto which the Grimes Golden is grafted. Such trees were used to study the possible effect of stock-scion interaction on the respective susceptibility or resistance of the component parts of the trees to infection by *Phytophthora cactorum*. Fourteen- and twenty-year-old Grimes Golden trees propagated on 13 varieties of stocks, were available for this

test. The Grimes Golden trees, propagated on 5 varieties, had been double-worked in the nursery. The roots of these trees were French crab seedlings. The Grimes Golden scions on 8 varieties of own-rooted stocks had been grafted 8 to 18 inches above the soil line. The roots of the own-rooted stocks were of the same variety as the base of the trunk. Inoculations were made with culture No. 1 near the graft union on the Grimes Golden and also on the stock variety of each tree (fig. 4, D).

Large trunk-cankers were formed on the scion, or Grimes Golden portion, of 56 of the 68 trees inoculated (table 7). Northwestern Greening was the only variety of stock tested that was susceptible, cankers resulting from four of the six inoculations made on four, 20-year-old double-worked trees. No infection occurred from the inoculations on stocks of the varieties Arkansas, Red Astrachan, Delicious, Oldenburg, Fameuse, Hiberna, Lowland Raspberry, Northern Spy, Northern Spy seedling, Transcendent crab, Walbridge, and Wealthy, nor from the check incisions. The downward advance of the cankers on the Grimes Golden bark was checked at the graft union with the resistant stocks. However, when the Grimes Golden was on Northwestern Greening stock, the cankers extended across the graft unions. In this experiment there appeared to be no interaction between the stock and scion which influenced the characteristic resistance or susceptibility of the varieties.

TABLE 7.—Results of inoculations of stock and scion components of the trunks of high- and double-grafted Grimes Golden trees with culture No. 1 of *Phytophthora cactorum*

Varietal composition of the trees ¹		Age of trees	Trees inoculated	Component varieties of trunks inoculated	Inoculations ²	Cankers produced
Intermediate stock	Rootstock					
		Years	Number		Number	Number
Arkansas.....	French crab seedling...	20	8	{Grimes Golden.....	8	7
				{Arkansas.....	8	0
None.....	Red Astrachan.....	14	1	{Grimes Golden.....	1	1
				{Red Astrachan.....	1	0
Delicious.....	French crab seedling...	14	6	{Grimes Golden.....	6	4
				{Delicious.....	5	0
Do.....	do.....	20	10	{Grimes Golden.....	10	9
				{Delicious.....	9	0
None.....	Oldenburg.....	14	6	{Grimes Golden.....	6	3
				{Oldenburg.....	7	0
Do.....	Fameuse.....	14	1	{Grimes Golden.....	1	1
				{Fameuse.....	1	0
Do.....	Hiberna.....	14	3	{Grimes Golden.....	3	3
				{Hiberna.....	3	0
Do.....	Lowland Raspberry....	14	6	{Grimes Golden.....	6	5
				{Lowland Raspberry....	6	0
Northwestern Greening.	French crab seedling...	20	4	{Grimes Golden.....	4	4
				{Northwestern Greening.....	6	4
None.....	Northern Spy.....	14	4	{Grimes Golden.....	4	2
				{Northern Spy.....	4	0
Do.....	Northern Spy seedling.	14	3	{Grimes Golden.....	2	2
				{Northern Spy seedling.	3	0
Do.....	Transcendent crab.....	14	4	{Grimes Golden.....	4	3
				{Transcendent crab.....	4	0
Walbridge.....	French crab seedling...	20	5	{Grimes Golden.....	5	4
				{Walbridge.....	5	0
None.....	Wealthy.....	14	6	{Grimes Golden.....	6	6
				{Wealthy.....	6	0
Do.....	Grimes Golden.....	14	1	{Grimes Golden.....	2	2

¹ Scion always Grimes Golden

² No cankers resulted from 64 check incisions in trunks of Grimes Golden and 2 in trunks of the Arkansas variety.

CONTROL OF THE DISEASE

EFFECT OF HEIGHT OF THE GRAFT UNION ON INFECTION

During 1933 and 1934 collar rot of Grimes Golden appeared to be more prevalent on low-grafted and budded trees than on double-worked trees. Therefore, measurements were made of the height of the graft unions formed between the Grimes scion and the stock, to determine whether collar-rot cankers were more prevalent on trees with low than with high graft unions. These measurements were made in an orchard of 467 double-worked, 16-year-old trees in which 21 percent were killed by *Phytophthora collar rot*.

The height of the graft unions of the diseased and the healthy trees ranged respectively, from 0 to 22 and from 0 to 24 inches above the soil. The mean height of the graft unions of trunk canker-infected trees was 12.4 inches and that of uninfected trees 12.8 inches. Of 354 trees with graft unions 15 inches or less above the soil, 75, or 21 percent, were infected. Of the remaining 113 trees with higher graft unions, 22, or 19 percent, were infected. Within a group of 15 trees having graft unions 20 to 24 inches above the soil 7 were infected. Evidently the propagation of Grimes Golden trees by grafting 15 to 22 inches above the soil is not effective in reducing natural infection with *Phytophthora cactorum*.

Apple growers interviewed, however, are of the opinion that in general less infection occurs on double-worked trees than on regular grafted and budded trees. It may be that in years when *Phytophthora collar-rot* does not occur in epidemic severity, double-worked trees are not so readily infected as low-grafted and budded trees. The use of resistant varieties of apple to form the roots and trunk of the trees, and the grafting of the Grimes Golden variety on these stocks 30 inches or more above the soil, may still be a means of reducing infection from *Phytophthora cactorum*, although no observations have been made of Grimes Golden trees grafted at this height.

BORDEAUX MIXTURE AS A PREVENTATIVE OF COLLAR ROT

The effectiveness of bordeaux mixture as a preventive of collar rot was tested in two orchards. A 16:16:100 bordeaux mixture containing 1 gallon of miscible oil was tested in 1935, and a 30:30:100 bordeaux mixture was tested in 1936 and 1937. The sprays were applied on the trunks of Grimes Golden trees after the dormant period when the apple buds were swelling.

One orchard, at Vincennes, Ind., was 12 years old in 1935. In this orchard the sprays were applied to pairs of tree rows alternating with pairs of unsprayed control rows. There was a total of 151 sprayed and 128 control trees. The other orchard, at Bloomfield, Ind., was 17 years old in 1935. The trees in two-thirds of the rows, comprising 235 trees, were sprayed, while every third row, comprising 135 trees, was left unsprayed as a control. During the years of the test, additional sprays for the control of apple scab and codling moth were applied to all the trees.

Cankers developed from natural infection on 3, 1, and 0.6 percent of the sprayed trees, and on 9, 4, and 0.8 percent of the unsprayed trees in the Vincennes orchard during the years 1935, 1936, and 1937, respectively. In the orchard at Bloomfield, cankers developed on

1, 0, and 0.4 percent of the sprayed trees and on 1, 0, and 1.5 percent of the unsprayed trees, during the years 1935, 1936, and 1937, respectively.

TREATMENT FOR CANKERS BY DECORTICATION

In August 1934, 13 cankers on 14-year-old Grimes Golden trees were treated by decortication. The diseased bark and the healthy bark for 4 cm. beyond the margins of the cankers and the infected and discolored wood beneath the cankers were removed (fig. 4, *E*). The wounds were then painted over with bordeaux-oil paint, as used by Zeller (48). The development of the cankers was permanently checked on 10 trees, while 3 showed slight development in restricted areas.

TREATMENT OF CANKERS WITH ZINC CHLORIDE AND SODIUM ARSENITE SOLUTIONS

The effectiveness of a number of chemical solutions in arresting the development of cankers was tested on Grimes Golden trees from 8 to 25 years old, at Bloomfield, Lafayette, Mitchell, and Vincennes, Ind. The solutions were applied with a brush to the surface of the cankers and to the bark in areas 5 cm. in advance of the cankers. The margins of the cankers when not readily evident were ascertained by probing with a knife, and marked by placing tacks at intervals. In a few treatments with zinc chloride, a thin layer of the outer bark at the advancing margins of cankers was removed with a knife before applying the solution.

Cankers treated with 10-percent copper arsenite in 10-percent ammonium hydroxide, 5- and 10-percent aqueous solutions of sodium arsenite, and Day's (11) solutions containing 43, 53, 64, or 71 percent of zinc chloride in acidified 74-percent alcohol, were not effectively controlled. The cutting away of the outer bark prior to treatment did not improve the effectiveness of the zinc chloride solutions.

Trunk cankers on 93 Grimes Golden trees were treated with a 10-percent solution of sodium arsenite in 50-percent alcohol during the fall of 1935. Only 1 of these cankers showed further enlargement when observed 5 weeks after treatment. Twenty-five untreated cankers continued to enlarge. The cankers were again observed after renewal of growth during the spring. None of the treated cankers showed renewed growth at that time. However, the data on possible renewed growth in the spring is inconclusive, since only 2 of the 25 untreated cankers renewed growth. The failure of the untreated cankers to enlarge in 1936 was an unusual occurrence, possibly associated with the effects of extremely low temperatures during January 1936. Of 13 cankers treated with the alcoholic sodium arsenite solution in 1936, 7 showed continued development 5 weeks after treatment. During 1937, 6 cankers were treated with this solution. Only 1 of these showed renewed activity in a restricted area when examined 6 weeks after treatment and again in 1938. Two untreated cankers continued to enlarge in 1937, and renewed enlargement in 1938. No deleterious effects of the solution on the upper portions of the trees were noticed during a period of 2 years after treatment. The solution was injurious to the bark, but the injury in all cases was confined to the treated area. The callus at the margins of treated cankers appeared to be retarded on a few trees.

DISCUSSION

Collar rot of uncertain origin on Grimes Golden and other varieties of apple has been reported by a number of investigators (15, 23, 37, 43) during the years from 1900 to 1921. The symptoms described in many cases are similar to those of phytophthora collar rot. Furthermore, the varieties Grimes Golden and Thompkins King, often described by earlier workers as especially subject to collar rot, are shown to be most susceptible to phytophthora collar rot in the present work. The writer therefore believes that very likely many of these early reports deal with the phytophthora collar rot disease and that it has been an important cause of loss for many years.

The fact that the cankers in the incipient and actively enlarging stages are not easily detected by casual observation, may account for the failure of earlier workers to detect the causal relation of *Phytophthora cactorum* in the collar rot disease. Infected trees usually do not exhibit prominent symptoms until late in the fall and the second year after infection, at which time the cankers may not be very active. The causal fungus has not been obtained in culture from killed bark which had become dried and pulled away from the wood, and was isolated with difficulty from old cankers which were slightly active or had recently ceased enlarging.

In the physiologic specialization studies a limited number of inoculations were made with each of the 10 cultures tested on 30 varieties of apple trees other than Grimes Golden. Very likely more of the varieties would have been shown to be susceptible to one or more of the cultures had a larger number of inoculations been made. However the writer believes that the apparent differences in pathogenicity and selectivity of host variety exhibited by the cultures cannot be explained entirely on the basis of escape from infection. There is the possibility that the virulence of the cultures is altered with time on artificial media. This may have occurred in the case of culture No. 15, which was isolated from peony. The differences in pathogenicity of all the cultures on the varieties of apple trees, however, cannot be interpreted as traceable to a degeneration of pathogenicity of the cultures, since a number of cultures differing distinctly in pathogenicity were of recent isolation. Thus, cultures Nos. 1 and 8 were isolated in 1934, No. 13 in 1936, No. 14 in 1929, and No. 18 in 1932. Furthermore, cultures Nos. 12, 16, and 18 to 21, inclusive, which were non-pathogenic on 31 varieties of apple trees, were pathogenic on flax and peony plants. Müller (28) has shown that there are also physiologic races of *Phytophthora infestans* (Mont.) De Bary.

Grimes Golden trees, 2 to 4 years old, are resistant to infection even when inoculum is inserted in the bark. However, this resistance in the trunk is lost as the tree matures. Trees of resistant varieties are resistant at all ages. Bearing Grimes Golden trees with rough bark on their trunks are susceptible to infection by inoculum placed both on the surface of the trunk and in incisions in the bark. However, the large branches of bearing Grimes Golden trees are highly resistant to infection when the inoculum is inserted in the bark. The resistance of the large branches may be the same as that possessed by the young trees.

The component varieties of double- and high-graft Grimes Golden trees maintained their own specific reaction toward infection by

Phytophthora cactorum. This is in accord with the results obtained by Bond (6), Leach (24), May (27), Roach (33), and Salmon and Ware (35) in their respective investigations of the interaction of the stock and scion component parts of grafted plants on susceptibility and resistance to specific diseases. On the other hand, Hofmann (21), Richmond (32), and Wormald and Grubb (47) obtained evidence of an altered susceptibility or resistance of the stock and scion parts of grafted plants or their progenies to infection by specific organisms.

The most promising means of controlling the phytophthora collar rot disease of apple trees is the propagation of the susceptible varieties by grafting on desirable varieties of stocks that are resistant to the disease. The graft union of the susceptible variety with the resistant stock probably should be at least 30 inches or more above the soil line. From the standpoint of protection from phytophthora canker and from cold injury to the trunks and crotches of the trees, the more desirable practice would be to graft the susceptible varieties on the main branches of young trees of resistant varieties, after they have become established in the orchard.

Bordeaux mixture applied to the trunks of apple trees was only partly effective in preventing collar-rot infection. Fawcett (13, 14) has recommended scarifying cankers and painting the resulting wounds with bordeaux paste for the control of phytophthora gummosis of citrus trees. He also advocated painting the trunks with bordeaux paste, and the application of a dust of zinc sulphate, copper sulphate, and hydrate lime (12 : 1 : 6) around the bases of young citrus trees, to prevent infection. Curzi (10) recommended decortication of infected tissues and applications of 3 to 5 percent bordeaux mixture as a treatment of phytophthora crown-rot cankers of peach.

SUMMARY

Phytophthora trunk canker, or collar rot, in 1933-34 caused serious losses in apple orchards in Indiana. In six orchards, from 21 to 68 percent of the Grimes Golden trees 14 to 18 years old were infected. In two of these orchards examined each year from 1935 to 1937, annual infection ranged from 0 to 6 percent. Evidence is presented in the review of literature which indicates that loss of Grimes Golden trees from phytophthora collar rot occurred in Indiana as early as 1900.

The disease is not easily detected in its early stages. The first outward symptom is a moist, discolored area on the surface of the bark. The infected bark is dark colored, has a strong fermented odor, and in later stages becomes dry, cracked, and drawn away from the wood. Frequently trees are girdled during one season.

Phytophthora cactorum is shown to be the casual agent of the Grimes Golden collar rot disease. The mycelium of the causal fungus develops both intercellularly and intracellularly, and penetrates all the tissues of the bark. Cultures of *P. cactorum*, pathogenic on apple trees, were isolated from active cankers, diseased fruits, and orchard soil. The fungus was also isolated from sapwood beneath a canker.

Evidence was secured of the existence of physiologic races of *Phytophthora cactorum*, which differ in their ability to infect varieties of apple trees. Certain cultures also differed in degree of virulence on the Grimes Golden variety. The Gano, Grimes Golden, Tompkins

King, Northwestern Greening, Rome Beauty, Smokehouse, and Stark varieties of apple trees were susceptible to one or more physiologic race of *P. cactorum* when artificially inoculated. Certain cultures of *P. cactorum* also were pathogenic on cherry, peach, and plum trees, and on flax and peony shoots. All 29 varieties of apple fruits tested were susceptible to fruit rot when artificially inoculated.

Grimes trees, 2 to 4 years old, were highly resistant both to artificial and to natural inoculation with *Phytophthora cactorum*. Older trees, 8 to 30 years old, were highly susceptible to infection from artificial inoculation. In the field the disease seldom occurs on trees less than 13 years of age. Differences also were found in the ease with which parts of the same tree were infected when inoculated. Trunks of bearing Grimes Golden trees were readily infected, while large branches were only occasionally infected when artificially inoculated.

The component varietal portions of double- and high-grafted Grimes Golden trees retained their specific resistance or susceptibility to *Phytophthora cactorum* unaltered by stock or scion influence.

The practice of grafting Grimes Golden scions on stocks at heights of 15 to 22 inches above the soil was found to be inadequate for the prevention of collar rot infection.

Bordeaux mixtures of the 16:16:100 and 30:30:100 formulae, were found to give partial control of collar rot infection. Day's solutions containing 43, 53, 64, or 71 percent zinc chloride were found to be ineffective in eradicating cankers on Grimes Golden apple trees. A 10-percent solution of sodium arsenite in 50-percent alcohol gave promise of being an effective means of checking the development of established cankers.

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