PHYTOPHTHORA ROOT ROT OF CAULIFLOWERS

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INTRODUCTION

A destructive root rot of cauliflower (Brassica oleracea L. var. botrytis L.) occurs during the winter in certain coastal regions of California (10), mainly in low or poorly drained spots in heavy soils that are subject to waterlogging during irrigation or rainy periods. Considerable losses as a result of this disease have been observed in all varieties in the San Francisco Bay section. The disease has also been found near Colma, Half Moon Bay, and Salinas. Other naturally infected hosts are cabbage (B. oleracea L. var. capitata L.), Brussels sprouts (B. oleracea L. var. gemmifera DC.), and hybrid cineraria (Senecio cruentus DC.) grown in a lath house at Salinas. J. B. Kendrick isolated the fungus from diseased stock or gilliflower (Mathiola incana R. Br. var. annua Voss) collected in Solano County in January 1934.

The disease is caused by Phytophthora megasperma Drechsler.

SYMPTOMS

The disease is characterized by a reddish discoloration of the older leaves followed by a sudden wilting of all the older leaves, which fall prostrate to the ground (fig. 1), leaving the head or curd exposed. The curd is not noticeably discolored but becomes tough and rubbery and is unmarketable. Plants of all ages are susceptible.

The lower end of the taproot, often along with the underground part of the stem, is badly rotted (fig. 2), and infected plants may be pulled from the soil with little effort. The cortex of the taproot and lateral roots is softened and water-soaked (fig. 2, B), usually sloughs off, and remains in the soil when the plant is pulled. The woody cylinder or stele is discolored and often frayed at the lower end (fig. 2, A). About the upper edge of the diseased part of the root there may be callus formation in the cortex (fig. 2, A), and numerous adventitious roots are sometimes produced (fig. 2, C). The upper margin of the diseased tissues of the cortex, stele, and pith is marked by a blackened zone. The infected pith is often collapsed, with resultant cavities.

In earlier stages of infection, lateral cankers are found in the cortex of the root, but in plants that show leaf symptoms the entire root and part of the underground stem are usually involved. Externally, the

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3 Reference is made by number (italic) to Literature Cited, p. 692.
diseased tissues may be Isabella color, sepia, or black; internally, ivory yellow to sepia of Ridgway (9).

Typically, the reddish discoloration of the older leaves consists of a broad, marginal band with interveinal extensions toward the midrib, the upper surface being Pompeian red to neutral red, the lower surface Vernonia purple.

THE CAUSAL FUNGUS, PHYTOPHTHORA MEGASPERMA

The fungus is readily isolated by planting tissue fragments taken from the margin of the lesion in malt-extract agar (7). The same fungus was obtained from diseased cauliflower plants collected in various localities and from cabbage, Brussels sprouts, stocks, and cineraria hybrids. It is found only in the root system and underground portions of the stem.

Freehand cross and longitudinal sections of naturally infected roots were stained with fast green and Magdala red. The fungus is intercellular. Drechsler (4) observed the mycelium of *P. megasperma* to be intercellular, and Dowson (3) found an abundant intercellular mycelium in decaying carrots.

The fungus grows rapidly on the ordinary culture media. On oatmeal agar it produces short, tufted aerial growth which gives the surface a somewhat mealy appearance. Sexual spores develop early and very abundantly on this medium. Transfers of isolates of *Phytophthora megasperma* from hollyhock, the type culture of Drechsler (4), stock, cabbage, cauliflower, cineraria, and of a culture (host not specified) which was sent to the Centraalbureau voor Schimmelcultures,
Baarn, Netherlands, by Ashby, behave similarly in cultural characters and spore production. Oogonia and oospores from oatmeal-agar cultures vary somewhat in size, as shown in table 1.

Table 1.—Diameter of oogonia and oospores of Phytophthora megasperma from various sources

<table>
<thead>
<tr>
<th>Source</th>
<th>Oogonial diameters</th>
<th>Oospore diameters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Limits</td>
<td>Average</td>
</tr>
<tr>
<td>Cauliflower:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>32-43.2</td>
<td>38.2</td>
</tr>
<tr>
<td>2</td>
<td>32-46.0</td>
<td>38.4</td>
</tr>
<tr>
<td>Stock:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>30-48</td>
<td>42.8</td>
</tr>
<tr>
<td>2</td>
<td>32-50</td>
<td>42.0</td>
</tr>
<tr>
<td>Cabbage</td>
<td>32-43.6</td>
<td>38.0</td>
</tr>
<tr>
<td>Hollyhock</td>
<td>39-52</td>
<td>42.6</td>
</tr>
<tr>
<td>Ashby culture</td>
<td>32-47.2</td>
<td>41.6</td>
</tr>
<tr>
<td>Cineraria</td>
<td>31-41.7</td>
<td>35.9</td>
</tr>
</tbody>
</table>
The size of the oogonia and oospores is affected by temperature, smaller spores developing at temperatures near the maximum, and by the culture medium, those produced on moist corn meal being smaller than those produced on oatmeal agar. Oogonia and oospores produced in liquid media are generally slightly smaller than those produced on solid media. The size of the oogonia and oospores is, therefore, subject to variation. However, all observed are sufficiently larger than those of *Phytophthora cactorum* to permit ready separation of cultures of the two species. The oogonia of *P. megasperma* are thin-walled, usually spherical or subspherical, with a short, rather slender stalk (pl. 1), while those of *P. cactorum* are inflated in the region enclosing the oospore and taper to form a broad funnel-shaped stalk. The latter type often appears in cultures of *P. megasperma* but is not typical of the species. The oogonia of *P. syringae* and *P. hibernalis* resemble those of *P. cactorum*. The oospores of *P. megasperma* occur singly in the oogonia, almost filling them (pl. 1, C–G); the oospore wall is smooth, thick, lemon yellow to straw color. Germination was not observed.

The antheridia of *Phytophthora megasperma* are preponderantly paragynous in type (pl. 1, B–G), yet variable proportions of them are amphigynous (pl. 1, H). The latter type is produced more frequently in liquid than on solid media, and in many cases the oogonia and oospores are smaller than those with paragynous antheridia. In all cultures examined the paragynous greatly outnumbered the amphigynous antheridia. None of the latter was found in oatmeal-agar cultures of some of the isolates. The antheridia may be borne on different or the same hyphae on which the oogonia develop; sometimes the antheridia develop on a short branch originating on the same hypha and only a few microns from the point of attachment of the stalk of the oogonium.

Sporangia do not develop on the solid media used, and but very scantily in liquids. A few appeared on hyphae grown 4 days in pea broth and transferred to sterile distilled water, as suggested by Rands (8) in 1922 and more recently by Leonian (6). They were obpyriform with a broad rounded base, nonpapillate, but with a thin refringent layer at the apex, resembling those described by Drechsler (4). They measured 41.6 to 56 by 28 to 40 microns, averaging 49.4 by 33.6 microns. Zoospore development and discharge were observed. Attempts to induce sporangium development by flooding cultures on Difco and unfiltered corn-meal agar and lima-bean agar with sterile distilled water and by transferring hyphae from oatmeal-agar cultures to Petri's solution and a nonsterile soil suspension were not successful.

The temperature relations of the cauliflower fungus are similar to those of the other isolates of the species, as indicated by the results of plate tests in which Difco corn-meal agar was used.

Of the other species with paragynous antheridia *Phytophthora hibernalis* and *P. syringae* cannot tolerate the high temperatures at which *P. megasperma* grows well. The temperature relations of *P. cactorum* are similar to those of *P. megasperma*.

The species appears to be quite distinct, and is one of the most easily recognized because of its large sexual spores which are produced early and profusely. It was not included in the key for the identifica-
Phytophthora Root Rot of Cauliflower

A, Young oogonium without antheridium.  B, Unfertilized oogonium and antheridium.  C, Fertilized oogonium with developing oospore.  D-G, Oogonium with oospores in various stages of development, as indicated by the thickening of the walls of the oospores, the antheridia in B-G being paragynous.  H, Oogonium with amphigynous antheridium.

PHYTOPHTHORA MEGASPERMA DRESCHLER.  X 465.
tion of species published by Tucker (11, p. 190) in 1931, which may now be emended as follows:

B. Widely spreading growth on malt-extract agar and ordinary agar media after 6 days at 20° C.
   1. Oogonia developing promptly (within 2 weeks) and abundantly on oatmeal agar or steamed corn meal.
      Antheridia predominantly paragynous.
      a. Growth on corn-meal agar after 4 days at 28° C.
         (1) Average diameter of oospores (oatmeal-agar cultures) exceeding 30 microns. 
           \[ P. megasperma. \]
      
      (2) Average diameter of oospores less than 30 microns. 
           \[ P. cactorum. \]
      
      b. No growth on corn-meal agar after 4 days at 28° C. 
         \[ P. syringae. \]

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\text{TABLE 2.—Diameter of mycelial growth of Phytophthora megasperma from various sources after exposure for 96 hours at different temperatures in plate tests}
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<table>
<thead>
<tr>
<th>Source</th>
<th>Diameter of mycelial growth after 96 hours at—</th>
<th></th>
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<tbody>
<tr>
<td></td>
<td>20° C.</td>
<td>25° C.</td>
<td>30° C.</td>
</tr>
<tr>
<td>Cauliflower:</td>
<td>Millimeters</td>
<td>Millimeters</td>
<td>Millimeters</td>
</tr>
<tr>
<td>1</td>
<td>25</td>
<td>25</td>
<td>18</td>
</tr>
<tr>
<td>2</td>
<td>30</td>
<td>38</td>
<td>33</td>
</tr>
<tr>
<td>Stock:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>38</td>
<td>40</td>
<td>21</td>
</tr>
<tr>
<td>2</td>
<td>33</td>
<td>40</td>
<td>21</td>
</tr>
<tr>
<td>Cabbage</td>
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<td>Hollyhock</td>
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<tr>
<td>Ashby culture</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Cineraria</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

1 No growth at 35° C.

Since the isolation and description of \[ Phytophthora megasperma \] by Drechsler (4) in 1931 as the cause of a crown rot of the hollyhock in the District of Columbia, the species has been found widely distributed and attacking hosts not closely related. Cairns and Muskett (1, 2) in 1933 reported the isolation of the species from potato tubers affected by a pink rot in Northern Ireland, and its identification by Ashby. Fawcett (5) in 1933 reported the isolation of the same species, also identified by Ashby, from citrus roots in California. Dowson (3) obtained the fungus in Tasmania, from the roots of carrots growing in a reclaimed bog during an abnormally wet season, under conditions resembling those prevailing in fields where the species causes a root rot of cauliflower in California. It is worthy of note that Cairns and Muskett (2) emphasize the importance of soil drainage “sufficiently good to prevent the land from becoming unduly wet in times of heavy rainfall” as a means of preventing pink rot of potatoes caused, at least occasionally, by \[ P. megasperma. \]

INOCULATIONS IN WATERLOGGED SOIL

Attempts to cause infection of potted cauliflower plants in the greenhouse, by adding inoculum to the soil and watering the plants heavily, were unsuccessful, even when the roots were wounded by needle pricks. Typical infection occurred on unwounded roots, how-
ever, when the pots were set in about 4 inches of water in buckets and incubated outdoors in tests made during February to May. The incubation period was about 3 weeks.

Inoculum was prepared by growing the fungus isolated from cauliflower on sterilized, moistened, cracked wheat and adding this to the soil in 6-inch pots, each containing a young cauliflower plant growing in autoclaved soil. On January 7, 12 potted plants of the February variety of cauliflower were slightly wounded by pricking the taproot with a sterilized needle. After the inoculum had been added to the soil, the pots were placed in buckets out of doors. The temperature varied from 14° to 20° C. On February 10, 10 of the inoculated plants showed typical wilting and reddening of the leaves, while the 6 noninoculated controls remained healthy. The fungus was reisolated from each of the 10 infected plants.

On March 8, 1935, 15 potted cauliflower plants with six leaves were inoculated without wounding the roots and placed in buckets of water along with five noninoculated controls. On March 26, all of the inoculated plants were infected, and the fungus was reisolated from 12 plants. The controls remained healthy in spite of the waterlogged condition of the soil. Another set of 15 plants was similarly inoculated on March 15, and on April 9 all were infected. The cortical tissues were completely softened and were readily sloughed off from the central cylinder. The fungus was reisolated from these plants. The five noninoculated controls remained healthy. Similar results were obtained in a set of 20 plants inoculated with the reisolated fungus on May 8. On May 24, 19 were infected and the fungus was reisolated from 18 roots. The five noninoculated controls were healthy.

EXPERIMENTAL HOST RANGE

By the use of the inoculation method that provided waterlogged soil, the fungus isolated from cauliflower proved to be pathogenic to stock (Mathiola incana var. annua) and wallflower (Cheiranthus cheiri L.).

On March 8, 1935, 15 potted stock plants in the six-leaf stage were inoculated without wounding the roots and placed in buckets of water along with 5 control pots. On April 19, 13 of the inoculated plants were infected, and the fungus was reisolated from each. The five controls remained healthy. A repetition of the test was made on May 10 with a culture reisolated from stock, and by June 2, 7 of the 10 inoculated stock plants were infected, and the fungus was reisolated. The four controls remained healthy.

On April 6, 20 potted wallflower plants were inoculated and placed in buckets of water along with 5 noninoculated control pots. On April 27 all of the inoculated plants were infected, and the fungus was reisolated from 16. The controls remained healthy. On June 7, 20 wallflower plants were inoculated with a culture reisolated from infected wallflower plants and on July 8, 12 were infected. The fungus was recovered in culture. The noninoculated controls remained healthy.

Ripe fruits of tomato Lycopersicum esculentum Mill. var. commune Bailey) were successfully infected. Inoculations were made by placing a small square of inoculum from an agar culture of the fungus
on the unbroken surface and keeping this moist with absorbent cotton under an inverted preparation dish. On January 15, 1936, four fruits were inoculated with a 6-day-old agar plate culture. On January 24, water-soaked lesions had formed measuring 5.0 by 7.0, 6.0 by 4.0, 5.0 by 4.0, and 5.0 by 5.0 cm. The two fruits used as controls remained healthy. The fungus was reisolated from all infected fruits. With the reisolated fungus, four tomato fruits were inoculated on January 30. Two fruits were infected on February 2 and the fungus was reisolated.

On March 5, 1936, eight cineraria plants in the six-leaf stage were inoculated without wounding the roots, and six noninoculated plants were used as controls. On March 22 five of the inoculated plants were infected and the fungus was reisolated from each, while the controls remained healthy.

Attempts to infect unwounded fruits of bell or sweet pepper (Capsicum frutescens L. var. grossum (Bailey)) and Early White Bush Scallop and Zucchini pumpkins (Cucurbita pepo L.), potato tubers (Solanum tuberosum L.), and roots of garden beet (Beta vulgaris L.), turnip (Brassica rapa L.), hollyhock (Althea rosea Cav.), cotton (Gossypium hirsutum L. var. Acala), Chinese hibiscus (Hibiscus rosa-sinensis L.), and carrot (Daucus carota L. var. sativa DC.) were unsuccessful. Dowson (3), using an isolation from rotted carrots, was unable to secure infection through unwounded surfaces. Potato tubers inoculated by placing mycelium and oospores in a small slit about 4 mm deep were invaded by the isolate from cineraria and by Ashby's culture. The type of infection was similar to that resulting from infection by numerous species of Phytophthora, the infected tissues becoming pink on exposure to the air. The isolates from stock, cabbage, hollyhock, and cineraria did not cause infection. Similarly, inoculated apple fruits were infected by all isolates, with the development of a light brown, mealy type of decay.

**SUMMARY**

A root rot of cauliflower, caused by *Phytophthora megasperma* Drechsler, is responsible for losses in the winter cauliflower crop in the coastal districts of California. The disease occurs only where the soil has become waterlogged.

The disease also occurs on cabbage, Brussels sprouts, cineraria, and stock.

The outer leaves of infected cauliflower plants show a reddish discoloration and later the plants wilt rather suddenly. Affected plants are easily pulled, and the basal end of the taproot is found to be rotted to such an extent that the cortex usually sloughs off.

The cauliflower fungus is described and compared with isolates from certain other hosts.

Infection was obtained by adding the fungus to the soil of potted cauliflower plants and incubating them outdoors in buckets containing water about 4 inches deep. The incubation period was about 3 weeks. Infection was also obtained on stock, cineraria, and wallflower plants and on ripe tomato fruits. Attempts to infect certain other unwounded vegetables were unsuccessful.
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