of a succulent terminal part. Anthracnose can be controlled out-of-doors by spraying with bordeaux mixture or other good fungicides, such as zineb, ferbam, lime-sulfur, or wettable sulfur. In the greenhouse, one can control it simply by keeping the foliage dry.

AMONG THE OTHER DISEASES of snapdragons are:

POWDERY MILDEW (*Oidium* species) has been confined to greenhouse-grown snapdragons in the United States. It is characterized by white powdery growth on both leaf surfaces and occasionally on young stems. It can be controlled by sulfur dust or a wettable sulfur spray plus a suitable spreader to insure complete coverage.

DOWNY MILDEW (*Peronospora antirrhini*) is most common on seedlings, on which it causes a characteristic paling and downward marginal curvature of affected leaves. The terminal-shoot growth is checked and the disease can cause the death of all aerial parts. The fungus sporulates on the lower surface of leaves as a white, sparse downy growth.

ROOT KNOT (*Meloidogyne* species) is evidenced as gall-like swellings on the roots. This nematode disease is controlled by soil sterilization.

STEM ROT AND WILT (*Phytophthora cactorum*) is characterized by a girdling of the stem at the root level, followed by wilting and death. The disease can be controlled by soil sterilization.

W. D. MCCLELLAN, *a native of California, studied plant pathology at the University of California and Cornell University. He was on the staff of the University of Maryland and the Bureau of Plant Industry, Soils, and Agricultural Engineering before he became director of research for the Mid-State Chemical Supply Co. at Lindsay, Calif., in 1951.*

Fusarium Wilt of China Aster

Kenneth F. Baker

The fusarium wilt disease—stem rot, black stem, aster wilt—caused by *Fusarium oxysporum* f. *callistephi*, is generally the most serious disease of China aster (*Callistephus chinensis*) in commercial and home-yard plantings over most of the world.

The China aster was introduced from China into France about 1731 and into the United States before 1800. Commercial aster culture had developed in this country by 1890. The first definite report of fusarium wilt was made by B. T. Galloway from several places in northeastern United States in 1896, but it probably was present and unnoticed before then. The fungus was widely distributed during the next 25 years, probably with the seed.

In many places it is the factor that determines whether asters can be successfully grown. Soil once infested with the fungus is essentially ruined for growing asters. Growers in California, therefore, avoid land that is known ever to have been used for the crop. Some home gardeners have found asters so unreliable because of disease that they are replacing them with zinnias.

Losses result from three phases of the disease: Damping-off of the seedlings at any time from emergence to time of transplanting; the typical wilt of mature plants; and the decay of flowers in storage. Wilt of mature plants usually causes the greatest loss, but damping-off is important because seedlings fre-

quently are infected in the seedbed and fail to show the disease until much later, when they have already infested the land with the fungus.

THE SYMPTOMS of fusarium wilt may appear at any stage of plant growth. Following emergence, seedlings may fall over from damping-off caused by the fungus. The warmer the soil (up to about 80° F.) and the greater the soil infestation, the sooner that will occur. The stems of tiny seedlings may rot near the soil surface and the cotyledons wither. Symptoms may be delayed at lower soil temperatures or lesser soil infestation, or with somewhat resistant plants.

Diseased seedlings about 2 inches high may show nothing more specific than the death and browning of basal leaves, stunted plant growth, drooping of leaves during the heat of the day, and perhaps poor green color. The typical diseased plant 4 inches or more high has a black streak up one side of the stem, and all leaves originating from the streak are dead. A single branch may be killed.

Plants grown in heavily infested soil or at high soil temperatures, however, usually have dead leaves on a blackened stem base, and do not have unilateral development. In a dry climate, as in southern California, such stems may be harder and woodier than those of healthy plants. In a humid area that symptom may be lacking, but just above soil level there is often a pink crust consisting of masses of mycelium and spores of the fungus. The roots usually have few or no rotted areas unless they are growing in very wet soil. When infected stems are cut longitudinally, one can see brown or black streaks that extend upward through the woody tissues. The black color of the basal stem may extend into the pith.

All those symptoms do not necessarily appear in any one plant, but most of them may be observed in a large planting. The one-sided development, the black streak in the stem, and the pink spore mass at soil level are the most dependable symptoms.

Other diseases may be confused with fusarium wilt.

Verticillium wilt causes much the same symptoms but lacks the pink basal spore layer.

Phytophthora root rot may cause death of tops, but the roots are then discolored and decayed, whereas fusarium wilt plants have nearly clean roots.

Phomopsis stem canker in humid areas causes a basal stem canker, in which tiny black fungus fruiting bodies are seen; the pink spore crust, the one-sided development, and dark streaks in the wood are lacking.

A stem rot caused by *Fusarium roseum* produces pink spore crusts on the cankers, but it does not extend up one side of the stem nor become vascular. Symptoms progress from outside inward, in contrast to wilt that develops outwardly from the inner tissues.

The spotted wilt virus causes dead tan areas in leaves and brown surface blotches on stems. Although symptoms may be unilateral, no black streak or pink spore crust is produced.

Root aphids sometimes cause wilting of the plants, but can be recognized by the insects on the roots.

Stem miners can produce wilting of aster plants in California. The tiny tunnels formed in the pith differentiate this trouble from fusarium wilt.

Flowers produced on plants infected by *Fusarium* under cool conditions may not show obvious external symptoms. The fungus has been found by W. C. Snyder to grow out from infected stems of such flowers and cause them to decay in warm storage.

The host range of the pathogen of fusarium wilt is not known to include plants other than China aster, nor does it even include all varieties of the single species, *Callistephus chinensis*. Varietal differences in susceptibility have been noted by many workers.

Resistant varieties have been developed several times, only to be lost when introduced into commerce. After

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1925, efforts to develop resistant varieties by selection on heavily infested land were conducted by L. O. Kunkel at Yonkers, N. Y., L. R. Jones and R. S. Riker at Madison, Wis., E. R. Honeywell in Indiana, and D. J. MacLeod at Fredrickton, New Brunswick.

Mr. Kunkel's selections were turned over to Jones and Riker, who supplied material to seed companies in California and Illinois in a cooperative arrangement from 1929 to 1932.

The resistant varieties first offered to the trade in 1931 were American Branching Mary Semple, A. B. Azure Blue, Ostrich Feather Deep Rose, Crego Deep Rose, Royal Azure Blue, and Heart of France. More recently, P. E. Tilford at Wooster, Ohio (1940–42) and K. F. Baker at Los Angeles (1940–44) selected resistant plants under more favorable conditions for elimination of susceptible plants.

In the latter instance, only 0.75 percent of 78,000 plants of nearly 100 varieties survived in 1942, while 38.3 percent of 13,500 plants grown from 1942 selections survived in 1943. We have considerable evidence that satisfactory resistance can be obtained in three to five selection generations in heavily infested warm soil. Mr. Tilford's selections were marketed by the Ohio Florists' Association until 1950, when they were discontinued. Mr. Baker's selections were released to several seed companies.

Despite those and other efforts, one seedsman wrote in 1948: "Asters today are at their lowest ebb . . . for petalage and susceptibility to stem rot. Little is usually done except order 'rot resistant' strains, and regardless of where they come from, all too frequently they are disappointing."

Resistance was lost through one or more of the following factors:

(1) Making single-plant selections for flower type under conditions of very low wilt losses and correspondingly great risk of selecting susceptible plants. Selections thus made in commercial seed fields where soil was either poorly infested or too cool for severe wilt have lost resistance in a single generation.

(2) Planting in cool or poorly infested soil in all or in most years. Resistance to this disease is not stable or homozygous, and continuous selection is necessary to maintain it. The variable low percentage of natural crossing among even highly double varieties in seed fields contributes to this instability.

(3) Expense of maintaining resistance, which involves special procedures and single-plant lines. To develop or maintain resistant lines one must be able to sacrifice plants and seed yield. That in turn means more costly seed. Resistance consequently is basically an economic problem.

(4) Use of alternative plants, such as zinnia, in home yards and the disinfestation of soil and seed in commercial plantings have reduced the demand for resistant varieties.

The China aster is peculiar among hosts of wilt Fusaria in that it is the sole representative of the host genus and probably was developed from plants cultivated from antiquity by the Chinese. Indeed, it is not certain that the true wild progenitor is even represented in herbaria. It is possible that the full complement of potential resistance factors of the genus is not represented in the present commercial aster, and that if such factors were incorporated into commercial varieties a stable high-level resistance could be maintained.

Present commercial resistance seems to be best explained as the result of more than one genetic factor, perhaps several, which may be cumulative in effect. There is no correlation between resistance and flower color, but single varieties such as Single Chinensis and Rainbow types often, but not always, are quite resistant.

THE CAUSAL FUNGUS is *Fusarium oxysporum* f. *callistephi*. Other Fusaria (*F. roseum*, *F. lateritium*, *F. solani*, and *F. episphaeria*) have also been suggested as

causal, but it is now known that some of them (*F. roseum* in particular) produce stem decay under moist conditions, rather than a vascular wilt of China aster. In earlier literature the wilt *Fusarium* has gone under such names (now synonyms of *F. oxysporum* f. *callistephi*) as *F. conglutinans* var. *callistephi* and *F. conglutinans* var. *majus*. Likewise the existence of several strains of forma *callistephi* has been postulated in explanation of the "breakdown of resistance" in commercial varieties since 1930. The assumption here that the level of resistance of aster varieties has not changed since 1930 is unwarranted, however.

Riker and Jones in 1935 presented evidence for the existence in Indiana and Japan of fungus strains of greater virulence to aster than those from Germany, Canada, and other sections of this country. It is not known, however, whether they were dealing with a greater *degree* of virulence or with a different *type* of pathogenicity.

Different isolates of the aster wilt *Fusarium*, as well as those from other hosts, are known to vary from weakly to strongly parasitic. In practice this affects severity of injury but not the host range, because a plant truly resistant to a virulent isolate under the most favorable conditions will not be susceptible under any circumstances. This differs greatly from *type* of pathogenicity (selective pathogenicity), in which the parasite has the ability to attack a new host, or against which a new set of genetic factors is necessary for resistance. This latter situation is clearly known among vascular Fusaria in garden pea and tomato, but is thought to be uncommon.

Because of the great importance of environment in the occurrence of aster wilt, the fact that no completely resistant aster varieties have been developed, the fact that verticillium wilt has not always been differentiated from that due to *Fusarium*, and the uncertainty that the tests of Riker and Jones were conducted with maximum soil infestation and optimum temperature, it is considered that evidence is still lacking for differing types of pathogenicity in forma *callistephi*. The selections directly or indirectly derived from those developed in Wisconsin proved highly resistant in field tests in California, Illinois, Maine, New York, the District of Columbia, New Brunswick, England, Sweden, Tasmania, and Germany, and were partially resistant in South Africa and Indiana. The selections developed at the University of California (Los Angeles) were highly resistant in various places in California, New York, Connecticut, Indiana, and Illinois, the only places where they were tested.

THE LIFE HISTORY of the fungus is similar to that of other wilt Fusaria. The organism persists in the soil, even in the absence of aster plants, for many years and reduces the usefulness of the land for the crop. The disease potential may decline after 5 years, but it builds up rapidly with return of the crop. The fungus is carried from place to place on tools and workmen's shoes, in irrigation water, and perhaps with soil particles by the wind.

Conidia formed on the stems are sticky and probably not airborne, although readily spread by water. These spores can germinate at once or remain alive under dry conditions for several months. The fungus can persist in plant refuse as dormant, thick-walled chlamydospores and be spread through the medium of the compost pile. These spores are more resistant to drying, heat, and fungicides than are the conidia or mycelium. The fungus also is commonly distributed with transplants from the seedbeds, where it may or may not have had time to produce disease. An infested seedbed may therefore introduce the disease to several fields or home yards.

The more delicate type of spore (conidium) is carried on the surface of the seeds. Presumably it gets there

during threshing operations, either from dust or from the pink masses on stem bases. Spores are also carried on debris mixed with the seed. Whether a crop grown from contaminated seed will show wilt depends in part on soil temperature; it may do so at 77° F. but appear tardily or not at all at 60°. In either case the soil becomes infested. The fungus establishes most readily in soil freed (*i. e.*, pasteurized) of other competitive organisms, and will produce heaviest losses in such soil. This seed-borne fungus is initially most destructive in steamed soil under warm conditions, and is thus most rapidly damaging in glass houses and seedbeds.

Plants are susceptible to infection at any time from germination to maturity. Infection generally occurs through uninjured roots, but inoculations may be made into stem wounds. Infection in most instances is between the cells of the root cap and between the epidermal cells in the region of elongation.

In susceptible plants the fungus develops copiously in the xylem of the root, from which it spreads upward through the xylem of the stems. From the xylem it may spread outward into phloem and cortex in roots or stems. Stem cankers thus arise in moist, warm weather. In resistant plants there is little development of mycelium in the root tip, and it remains localized, though still alive, in tiny lesions. Resistance is of the physiological type, as in cabbage and tomato fusarium wilts, rather than of the morphological type. It is reported that lower losses result from seeding in place than from transplanting, but the results in all instances may have been due to higher soil temperature in the seedbed than in the field, rather than to transplanting injuries.

The damage to the plant results from toxins formed in the water-conducting tissues and carried to the leaves and stems, where cells are injured or killed. Insufficient mycelium is formed to block the xylem vessels and interfere seriously with water movement.

ENVIRONMENTAL CONDITIONS are important in determining the severity of the disease. Soil temperature is of such significance as to determine largely whether the disease occurs or not. Thus A. B. Jackson found in 1927 that parallel series in naturally infested soil at 63°–68° F. and 68°–77° developed 12.5 and 100 percent wilt, respectively. The optimum for growth of the fungus in culture is about 80°–86°, and no growth is produced at 39° or 95°. No symptoms other than slight loss of weight develop on asters grown in infested soil at 54°. Slight wilt develops at 61°. The optimum for wilt is about 80°, and the maximum is 90°.

Thus, even in heavily infested soil at about 55°, plants will sustain little loss from fusarium wilt, and only in heavily infested soil will symptoms develop at about 60°. On the other hand, lightly infested soil (such as clean soil planted with infested seed) will produce wilt plants if temperatures are 77° to 80°. To a certain extent, then, temperature and amount of fungus in the soil are interchangeable factors—an increase of one will offset a decrease of the other.

A certain length of time is required for wilt symptoms to appear. The lower the soil temperature or soil infestation, the longer that interval will be. Other things being equal, the shorter the exposure to heavily infested warm soil, the less will be the disease. However, winter planting of asters in coastal California has led to excessive losses from botrytis gray mold and rhizoctonia stem rot. The losses in a given field grown continuously to asters will vary greatly from year to year, depending on soil temperatures. Asters grown in the cool soils along the coast of California consistently have less wilt than those grown in the warm soils of the interior valleys of that State and are undesirable for a wilt-selection program.

A new commercial area planted to asters normally may pass through several stages. In the first year scattered diseased plants will appear through the field, their number depending on whether spread is restricted by seed sown in place and whether infected transplants were used and on the prevailing soil temperatures. The next year the disease will appear more uniformly through the field; if the soil is warm, severe losses may occur. By the third season a profitable crop will be produced only if the soil remains very cool. Usually the venture is then abandoned as uneconomic.

THE CONTROL of fusarium wilt is made difficult by the unavailability of commercial asters of high resistance, although advertisements may claim the contrary. Should truly resistant varieties again become available they would provide the ideal solution for home-yard and commercial plantings. In the meantime some benefit may be gained by using seed saved from the few plants surviving in heavily infested warm soil.

The protection of uninfested soil from introduction of the wilt fungus is highly important. Treatment of seed is essential in this, but one should recognize that it is done to protect the soil from infestation from the seed, rather than the seedling from the soil-borne fungus.

The best treatment at present is a mercuric chloride (corrosive sublimate) soak. A glass jar is filled about one-third full of seed and filled up with corrosive sublimate (1 to 1,000, or one 7½-grain tablet per pint of water), unheated and without any spreading agent. The lid is replaced and the seed intermittently shaken for 30 minutes. Then the fungicide is poured out through a cheesecloth held over the top of the jar. Three separate changes of water are used in rinsing. The jar is shaken each time. The seed is then spread out to dry in a warm place. The treatment lowers germination somewhat, particularly of seed whose cracked coats permit the mercury to reach the embyro. Heating the solution above room temperature is highly injurious. W. O. Gloyer found that seed treatment permitted the growing of asters in the same field in New York for five consecutive years without wilt.

To avoid infestation of land it is further necessary to prevent carrying the fungus on tools, machinery, shoes, and such. Formaldehyde solution (1 part commercial formaldehyde in 15 parts of water), may be prepared for dipping infested tools, for applying to shoes, and for spraying machinery before it is used on clean land.

Once soil becomes infested, three courses are open if resistant lines are not available: It may be abandoned for asters; it may be used once every five or more years for this crop, being rotated with any other in the interim; the soil may be steamed or treated chemically to free it of the organism.

The third is imperative for seedbeds as a routine procedure. If steam is used, the soil should be heated to at least 180° F. and held at this level for 30 minutes. A formaldehyde drench (diluted 1 to 40) has been recommended; enough of it is applied to penetrate the soil to at least an 18-inch level. The soil is covered with canvas for 2 days, and then aerated for at least a week before planting.

Old infected plant parts, in which the fungus can survive for at least a year, should be burned. They should never be used in a compost pile unless it is to be steamed before use.

Because of the restrictive effect of cool soil on the occurrence of wilt, losses may be reduced by shading if shading keeps soil temperatures near 60° F.

KENNETH F. BAKER, *a plant pathologist in the California Agricultural Experiment Station, Los Angeles, has been engaged in studies on diseases of floricultural crops for more than 15 years. He has conducted pathological investigations in Washington, Wisconsin, Nebraska, Hawaii, New York, and California.*