HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 17 | JANUARY, 1947 | NUMBER 6

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SNAPDRAGON downy mildew, caused by *Peronospora antirrhini* Schroet., has been recorded only on *Antirrhinum orontium*, a wild species of Europe, and on *Antirrhinum majus*, the cultivated snapdragon. Kenneth F. Baker[3] found this mildew on *Antirrhinum nuttallianum* at Otay Lake, San Diego County, California, in 1941. All varieties of snapdragon inoculated by the writer, or observed under conditions of heavy natural infection, have been susceptible. Murphy (*13*)[4] indicates that dark-colored varieties are the most susceptible. In a heavy natural infection at Guadalupe, California, in 1940, breeding lines with dark, waxy foliage had fewer infected plants than light-colored ones.

Peronospora antirrhini was first reported on *Antirrhinum orontium* in 1874 (*15*) from Germany, on this same species in Switzerland in 1907 (*10*), and in Denmark in 1913 (*12*). It is not recorded to have caused commercial damage until 1936, when Murphy (*13*) in Ireland reported it to be severe on nursery seedlings of cultivated snapdragons. It has since been found in England (*1, 7, 8*), New South Wales (*2*), California (*9*), Pennsylvania (*11*), and Oklahoma (*14*). McWhorter[5] found the disease at Portland, Oregon, in the spring of 1944. Snapdragon mildew was first observed by the writer on May 25, 1938, on specimens brought in by a nurseryman near Hayward. By 1940 it not only was severe throughout the San Francisco Bay district, but also had appeared in southern California.

IMPORTANCE OF THE DISEASE

Snapdragon downy mildew has been principally a seedling disease of nursery plants. Systemically infected plants are unsalable. They are unsuitable for planting because they generally fail to grow and finally die. Losses have varied from none to all plants in a given planting. The standard practice in the San Francisco Bay area is to plant about 1,000 snapdragon seeds per flat, and later to transplant the resulting seedlings at the rate of 100 to 120 seedlings per flat. The plants are sold in the second flats within a few days to a few weeks after transplanting. If more than about 10 plants per flat show systemic infection, the entire flat is usually discarded. One nursery in Oakland discarded its entire stock of 600 flats of snapdragons at one time because of downy mildew infection. In 1940–1942 the infection was so generally destructive in southern California that it was impossible to obtain healthy seedlings. At a seed farm at Guadalupe, 90 to 95 per cent of the plants in 1,400 flats were lost because of mildew in January, 1940, and at a nursery in Los Angeles about 1,000 flats were discarded because of mildew in 1942. Murphy (*13*) and Green (*7, 8*) also indicate extensive nursery losses in Ireland and England.

Losses may also occur on greenhouse plants grown for cut flowers, but the writer has little information on how severe this may be.

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[3] All observations in southern California are those of Kenneth F. Baker, Associate Professor of Plant Pathology, and Associate Plant Pathologist in the Experiment Station.

[4] Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

[5] F. P. McWhorter of Oregon State College, in a personal communication to the author dated December 10, 1945.

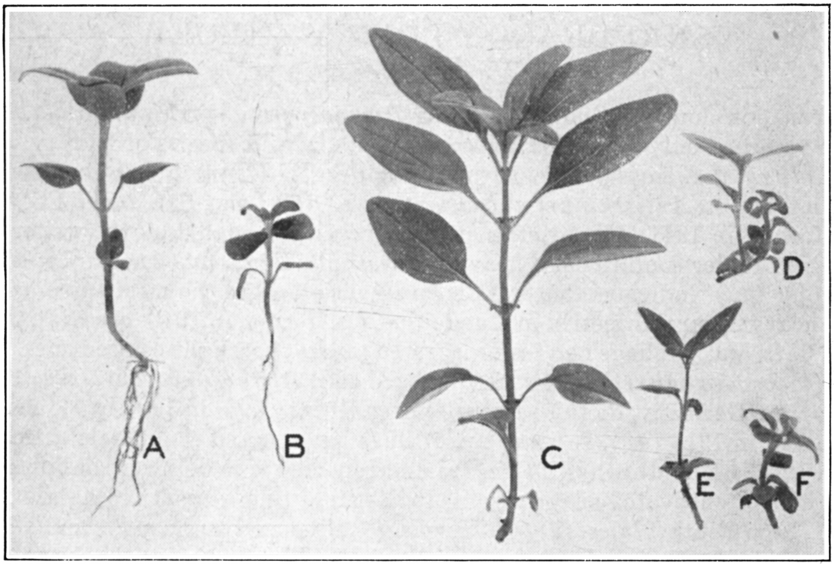

Fig. 1.—Symptoms of systematic infection of downy mildew on seedling snapdragons. *A*, healthy noninoculated plant; *B*, inoculated. *A* and *B* were the same age and size at time of inoculation on February 21, 1940; photographed March 7, fourteen days after inoculation. *C*, healthy noninoculated plant; *D, E, F*, inoculated; *C, D, E, F* were the same age and size at time of inoculation on February 1, 1940; *C, D, E, F*, photographed March 26, fifty-three days after inoculation; *D* shows recovery by growth of a lateral noninfected shoot; *E* shows recovery by growth of a terminal healthy shoot; and *F* shows no recovery.

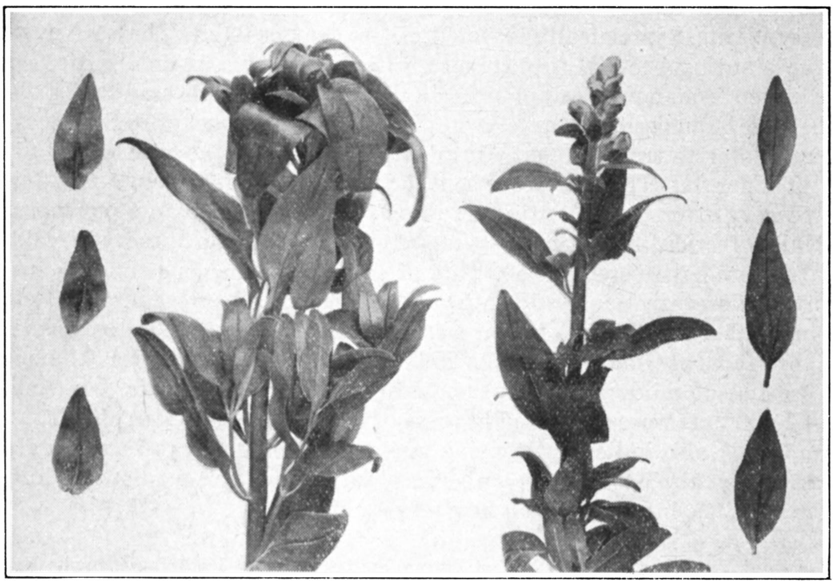

Fig. 2.—Symptoms of systemic infection of downy mildew on snapdragons grown in the greenhouse for cut flowers; plant and individual leaves on right are healthy; plant and individual leaves on left show systemic infection. Systemically infected plants are shorter than normal; leaves show basal infection. Photographed January 29, 1942.

SYMPTOMS

The most important infections of downy mildew on snapdragons are systemic and the symptoms are characteristic of systemic infections of other downy mildew diseases. On seedling plants there is a downward curling of the leaves, a reduction in the size of the leaves and of the plants, and the infected leaves are paler green than normal. On seedlings, downy mildew causes a stunting or killing which progresses from the top of the plant down to the soil surface; it is thus readily distinguished from the common damping-off of seedlings which kills the plants from the taproot in the soil up to the soil surface. Symptoms may appear from the time when the plant has two cotyledons and continue to appear until the plants are about 6 inches tall (fig. 1). They may appear again on the growing points of plants, 1 to 4 feet tall, which are coming into flower (fig. 2). On these large plants, there is a rosetting of the growing points. It is not suggested that plants between these specified stages of growth are immune, but infection has not been observed on them by the writer. Furthermore, in the writer's inoculation tests, systemic infection has not occurred on plants inoculated when they are more than about 4 inches tall. Unfavorable environmental factors may well have contributed to these failures. Local (nonsystemic) infections of leaves are common but are rarely destructive. They consist of pale rounded areas up to 15 millimeters in diameter with smooth diffuse margins.

The disease is rare in garden or field plantings, but on May 24, C. M. Tompkins found the disease severe on seedling plants grown outdoors at Colma under conditions of overhead sprinkling irrigation but in a growing season without rain for several previous weeks.

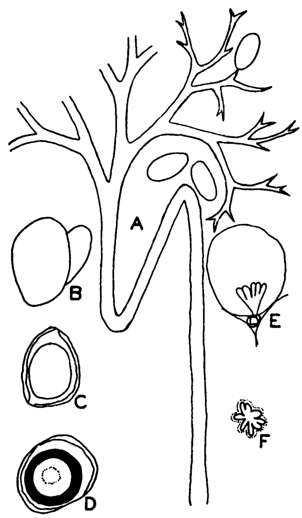

Fig. 3.—*Peronospora antirrhini: A*, portion of sporangiophore, showing attached and detached sporangia (the sporangiophore is illustrater as bent in order to reduce the size of the illustration); *B*, early stage in oöspore formation with antheridium on side of oögonium; *C*, later stage, oöspore formed; *D*, mature oöspore enclosed in oögonium; *E*, branched intracellular haustorium in host cell and intercellular hypha; and *F*, surface view of haustorium indicating protoplasmic sheath.

ETIOLOGY

Snapdragon downy mildew is caused by *Peronospora antirrhini* Schroet.—a typical downy mildew. Sporangiophores and sporangia (conidiophores and conidia) are borne principally on the lower leaf surface, but also in abundance on the stems and upper surface of the leaves of young succulent plants. Sporangiophores emerge through the stomatal openings, are 350 to 704μ long, dichotomously branched, with 27 to 140 ultimate branches, each bearing an ovoid sporangium. Sporangia are 14–17 by 21–29μ and have been observed to germinate by a germ tube only. The internal intercellular mycelium bears intracellular haustoria with 4 to 8 fingerlike branches, similar to those of

Pseudoperonospora on cucumber and hop, and not seen previously on any member of the genus *Peronospora* observed by the writer. Oöspores 30 to 33μ in diameter in oögonia 43–52μ in diameter are produced in great abundance in the cortex and pith of systemically infected seedlings. Green (*8*) indicates that in England oöspores were very rare in living plants, but in the writer's material they have been more numerous than in any other downy mildew examined.

The morphologic features of *Peronospora antirrhini* are indicated in figure 3. Quantitative differences in the writer's description and illustrations from the descriptions and illustrations of other observers (*3, 6, 8, 14*) are not considered of any taxonomic significance. The branched haustoria are considered the most useful character in distinguishing this from most other species of *Peronospora.*

The shortest period in which symptoms have appeared in controlled tests has been 4 days after inoculation.

EPIDEMIOLOGY

Snapdragon downy mildew, like most other downy mildews, appears to be favored by low temperatures and high humidity. In one test, leaves from systemically infected plants placed in moist chambers and incubated at a range of temperatures failed to sporulate at 7° C and below, sporulated luxuriantly at 13° and moderately at 19° but not at 22° or above. In one test of the effect of temperature on spore germination, sporangia in drops of water on slides in petri dish moist chambers germinated as follows: at 1°, 0; 4°, 0; 7°, 11 per cent; 10°, 65 per cent; 13°, 37 per cent; 16°, 26 per cent; 19°, 0; and at 22°, 0. No tests of the effect of temperature on infection under controlled conditions have been performed, but greenhouse inoculations of plants during the winter and early spring months have been successful while inoculations during the hotter summer months have been distinctly less so. On the basis of the limited information available, the writer believes the optimum temperature for snapdragon downy mildew is about 10° C.

In the San Francisco Bay region, snapdragon seedlings are grown principally from February to May in unheated greenhouses as bedding plants for sale, and it is under these conditions that downy mildew has been so destructive. A maximum-minimum thermometer placed in one such greenhouse from February 24 to April 2, 1940, and reset every day showed a minimum temperature ranging from 40° to 50° F (4° to 10° C) and averaged 44° F (7° C); while the maximum temperature ranged from 61° to 95° F (16° to 35° C) and averaged 74° F (23° C). The luxuriant development and active spread of downy mildew in greenhouse culture, more active according to the writer's observation than in outdoor culture, indicates that rain plays little necessary part in the epidemiology of this disease.

In southern California, on the other hand, snapdragon seedlings are grown principally under lath or cloth, or outdoors, and the disease is severe under these conditions. Epidemics there are associated with dark, foggy, humid, and rainy weather.

Environmental conditions during the incubation period (from inoculation until the pathogen establishes nutritive relations with the host) are undoubtedly most critical in determining the amount of infection. Dry seedling plants in pots were dusted with dry sporangia and placed in a variety of environments for 24 hours and then returned to a heated greenhouse where the amount of systemic infection was recorded 15 days after inoculation. No water was applied to the leaves in any case. The percentages of systemic infection in four trials with inoculations in varying environments, made January 21–28, 1942, with an average of 9 plants per treatment in each trial were as follows:

	Per cent
Moist chamber in heated greenhouse, about 20°C	54
Open bench in heated greenhouse, about 20°C	7
Moist chamber in unheated greenhouse, 7°–15°C	100
Open bench in unheated greenhouse, 7°–15°C	52
Open bench in unheated greenhouse, and with electric fan directed on plants to reduce humidity, 7°–15°C	0

Environmental conditions following the incubation period are probably less important than those during incubation. Plants which had been inoculated and held in a moist chamber overnight were placed in the following contrasting environments: a heated greenhouse with the temperature about 20° C, natural outdoor environment, an unheated greenhouse, and a lathhouse. In two tests, with an average of 12 plants in each environment in each test, the average percentages of systemic infection in the environments listed were 47, 24, 74, and 40 respectively—least, therefore, in the plants left out of doors.

The writer believes that considerable infection in commercial greenhouses is traceable to the contamination of healthy plants in the process of transplanting. Workers contaminate their hands with sporangia by handling infected plants which may or may not show distinct symptoms, and unknowingly transfer these sporangia to healthy plants. On two occasions heavy infection appeared in flats about a week after transplanting.

CONTROL BY SANITATION AND VENTILATION

As snapdragon downy mildew does not yet occur in most regions, its control in these regions by exclusion would appear in order. The most likely method by which the disease could move long distances would appear to be by oöspores in the seed. The sequence of occurrence in Ireland in 1936 (*13*), England in 1937 (*1*), California in 1938 (*9*), New South Wales in 1941 (*2*), Oregon in 1944, Pennsylvania in 1945 (*11*), and Oklahoma in 1945 (*14*) would seem to depend on some such mode of primary distribution. Since oöspores from seedling infections would seem to have little chance of getting into the seed, whereas oöspores in terminal infections of flowering plants could easily contaminate the seed, it would appear that this latter type of infection may be more common than recorded. In a disease-free district it would seem to be a wise precaution not to use seed from diseased areas, if this is possible. Within regions where the disease already occurs, local exclusion, such as avoiding carrying infectious material from an infested to a noninfested nursery, would appear worth while.

Oöspores in infected seedlings which die and disintegrate can readily contaminate the soil in which they are grown, and it would appear logical to expect that this contaminated soil might be an important source of primary infection. Attempts to eradicate the disease by destroying infected plants are reported by Murphy (*13*), Green (*8*), and Harris (*9*). Those by the latter two were apparently unsuccessful. Two nurserymen have told the writer of their attempts to control the disease by disposing of all snapdragon plants, but the disease reappeared next year. On the other hand, at one seed farm at Guadalupe the sterilization of the soil used for snapdragon seedlings was associated with reduced downy mildew infection for two years. Some nurseries have escaped the disease without any specific precautionary measures.

Where the disease occurs in greenhouses, control by manipulation of environment would seem a definite possibility. Practices which reduce the humidity at the plant surfaces should reduce infection. During the course of greenhouse studies of the disease for two seasons, the writer's plants grown in a heated greenhouse never became infected naturally, though infected plants were frequently close to them. When such plants were heavily dusted with spores, however, 3 out of 16 plants became infected in one test but none became infected in three other tests. Exposing inoculated plants to an air current from an electric fan entirely prevented infection of plants in an unheated greenhouse, though similar plants not exposed to the fan showed 52 per cent infection. This method of control by air movement would appear practical.

CONTROL WITH FUNGICIDES

The success with paradichlorobenzene for the control of tobacco downy mildew (*5*) suggested its use for snapdragon downy mildew. To treat with paradichlorobenzene, frames 23 × 14 × 3 inches (the same size as the flats to be treated) and covered with two layers of cheesecloth on the upper side, were placed over the test flats of plants, and the desired amount of medium paradichlorobenzene crystals was scattered over the surface of the cheesecloth. The entire flats and frames were then covered tightly with oilcloth to confine the fumes overnight, and the oilcloth and frame removed in the morning. Dosages ranged from 0.5 to 2.5 grams paradichlorobenzene per flat and this treatment was repeated every second or third night. Treatments were applied at 5 to 6 p.m. and the treated flats were uncovered about 8 a.m. next morning. In all instances flats of heavily infected plants were placed among the test flats to insure an adequate amount of inoculum but the plants were not artificially inoculated. The results of four tests at two nurseries, presented in table 1, indicate effective control, but with crop injury at dosages of 2 grams or more per flat. Even in the absence of localized necrotic injury this treatment stunted the plants somewhat and on warm nights severe injury sometimes resulted. It is likely that nightly applications with the lower dosages would have been more successful but this type of treatment was not considered practical by either nurserymen or the writer.

Hydrogen sulfide diluted with air or vapors from dilute lime-sulfur was relatively ineffective in eradicating snapdragon downy mildew (*16*), and these vapor mixtures could be used to kill rust infections without killing the downy mildew in the same plants (*17*).

Spray and dust treatments appear more adaptable to nursery practice than vapor treatments, and a variety of sprays and dusts were tried. In some tests healthy plants were treated with the test fungicides and artificially inoculated within 24 hours. Rosin lime-sulfur (*19*) and cuprous oxide cottonseed oil were tested more thoroughly than other sprays. Rosin lime-sulfur was prepared by adding the required amount of rosin soap and then the required amount of concentrated lime-sulfur to the required amount of water. For example, to prepare 100 cc of 0.5 per cent rosin lime-sulfur, 99 cc of water was first added to a container, then 0.5 cc of rosin soap, and then 0.5 cc lime-sulfur and the whole agitated. Rosin soap was prepared by heating together 14 parts by weight of water, 5 parts of rosin, and 1 part of potassium hydroxide. Results of four trials with a series of dosages of rosin lime-sulfur and cuprous oxide cottonseed oil were analyzed by dosage response methods (*4*).

TABLE 1

CONTROL OF SNAPDRAGON DOWNY MILDEW IN COMMERCIAL NURSERIES WITH PARADICHLOROBENZENE CRYSTALS

Grams of paradichlorobenzene at each treatment	Number of plants counted	Per cent of plants showing systemic infection	Plant injury from paradichlorobenzene
0.0	1,355	53.0	None
0.5	73	22.0	None
1.0	376	22.0	None
1.5	374	18.0	Trace
2.0	444	0.7	Moderate
2.5	176	1.5	Severe

The dosage for 95 per cent control was about 0.3 per cent rosin soap plus 0.3 per cent lime-sulfur for the first mixture and 0.17 per cent cuprous oxide plus 0.17 per cent self-emulsifying cottonseed oil for the second mixture. The curve slopes (mortality probits per log. dose) as determined for data showing between 50 and 100 per cent control was 2.9 for the rosin lime-sulfur and 3.5 for the cuprous oxide mixture. The same and higher concentrations of lime-sulfur and cuprous oxide without the rosin soap or cottonseed oil supplements were less effective. Other spray mixtures tried, and the corresponding percentages of infection resulting, were as follows: 1 per cent bordeaux, 25 per cent; 0.2 per cent bordeaux plus 0.05 per cent glyceryl alkyl resin, 0; 1 per cent burgundy, 0; 0.1 per cent copper sulfate plus 1 per cent rosin soap, 0; 2 per cent of a proprietary copper ammonium carbonate solution containing 2 per cent copper, 25; and 0.03 per cent ferric dimethyl dithiocarbonate (Fermate) plus 0.05 per cent glyceryl alkyl resin, 0.

If effective, dusts are more acceptable to growers than sprays. In tests of methods of evaluating sulfur dust for the control of five downy mildew diseases, sulfur was more consistently effective against snapdragon mildew than against the downy mildews of hop, cucumber, onion, or lettuce (*18*). In six trials in which snapdragon infection in the controls averaged 86 per cent, sulfur dust entirely prevented infection in three trials, but 22, 65, and 100 per cent infection occurred on sulfured plants in three other trials. The cause of these discrepancies is not known, but it may be related to the washing off of the sulfur in the normal practice of watering. Experiment has clearly shown that sulfur dust applied to snapdragons can be so effectively removed by washing the plants with a water spray that the sulfured washed plants can be readily infected with downy mildew or rust. Other dusts tested and the percentage of infection associated with their use were: pure cuprous oxide, 0; copper lime dust, 30 per cent; a dust consisting of 10 per cent cuprous oxide plus 10 per cent iron oxide plus 80 per cent filler, 40 per cent; and a dust consisting of 50 per cent sulfur plus 5 per cent basic copper sulfate plus 10 per cent iron oxide plus 35 per cent filler, 43 per cent.

The spray (rosin lime-sulfur) and dust (sulfur) which appeared most promising at the time were compared in a test in which different groups of

TABLE 2

CONTROL OF SNAPDRAGON DOWNY MILDEW IN COMMERCIAL NURSERIES WITH SPRAYS AND DUSTS

Treatment	Per cent infection		
	Applications every 8 days, Nov. 21 to Jan. 24	Applications every 3 days, April 9 to 25	Applications every 3 days, April 12 to May 3
Control	80	80	59
0.2 per cent cuprous oxide plus 0.2 per cent emulsified cottonseed oil	..	29	3
0.2 per cent bordeaux plus 0.05 per cent glyceryl alkyl resin	13	..	..
0.5 per cent rosin soap plus 0.5 per cent lime-sulfur	11	26	0.5
Sulfur dust	76	4	1.0
Dust consisting of 10 per cent cuprous oxide, 10 per cent iron oxide, and 80 per cent filler	..	55	11
Dust consisting of 50 per cent sulfur, 5 per cent basic copper sulfate, 10 per cent iron oxide, and 35 per cent filler	32	..	..

plants were treated separately with the test fungicides at intervals of three days (all being treated the first day of the test), appropriate checks were maintained, and all were exposed to conditions of heavy natural inoculation in a cool unheated greenhouse. The test was started December 27, 1940, and results were recorded January 22, 1941. The checks showed 92 per cent infection, the rosin lime-sulfur series showed 0, 2, 7, and 15 per cent infection on plants treated every 3, 6, 9, and 12 days, respectively, and the sulfur-dust series showed 59, 32, 27, and 39 per cent infection in a similar series. It is obvious that the spray was much more pronounced in its protective action than the dust.

In addition to the spray and dust trials in the experimental greenhouses, trials of sprays and dusts were made in commercial nurseries. As sources of inoculum, flats of heavily infected plants were maintained close to the test flats. Treatments were applied every 3 to 8 days, starting when the seedlings were coming through the soil or about that time. Results of three typical tests are given in table 2. In these, as in other tests of this type not reported, no treatment ever gave perfect control though with most treatments disease control was marked, and the results might be considered commercially satisfactory. Rosin lime-sulfur spray, with an average of 82 per cent control, was perhaps the best treatment; but sulfur dust at 3-day intervals was a close rival.

CONTROL BY RESISTANT VARIETIES

One seed company in southern California attempted to develop mildew-resistant snapdragons but the attempt was abandoned in favor of fungicidal control with rosin lime-sulfur. The possibility that seed produced by plants which recovered from systemic infection (fig. 1) might produce seedlings carrying factors for resistance was investigated. Seed was saved from 2 plants which had recovered by sending out healthy shoots from the systemically infected growing point. In the first trial, 27 seedlings from such seed were inoculated and all became systemically infected. This line of investigation was therefore discontinued.

SUMMARY

Snapdragon downy mildew, a relatively new disease of restricted world distribution, has been severe on nursery seedlings in the San Francisco Bay area since 1938, and in southern California since 1939. Only *Antirrhinum orontium, A. majus,* and *A. nuttallianum* are known to be affected.

In a suitable environment, symptoms may appear in as little as 4 days after inoculation. Symptoms of systemic infection consist of a down curling, paling, and rosetting of the leaves and a stunting of the plant. Local infections, which are of little importance, cause the formation of pale-green areas with diffuse margins. Recovery from systemic infection is frequently manifested by the formation of noninfected shoots from systemically infected plants. On plants about to come into flower a rosetting of the growing point occurs.

The causal organism *Peronospora antirrhini* has dichotomously branched sporangiophores and branched haustoria and produces oöspores in abundance in the cortex of systemically infected plants. Germination of the sporangia is by a germ tube. The optimum temperature for the causal organism is about 10° C. High humidity is necessary for infection.

Control by forced air circulation, by the vapor from paradichlorobenzene crystals, by sulfur dust, and by rosin lime-sulfur and other sprays has been demonstrated. The first and last of these treatments are considered most practical in localities where the disease has become established.

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