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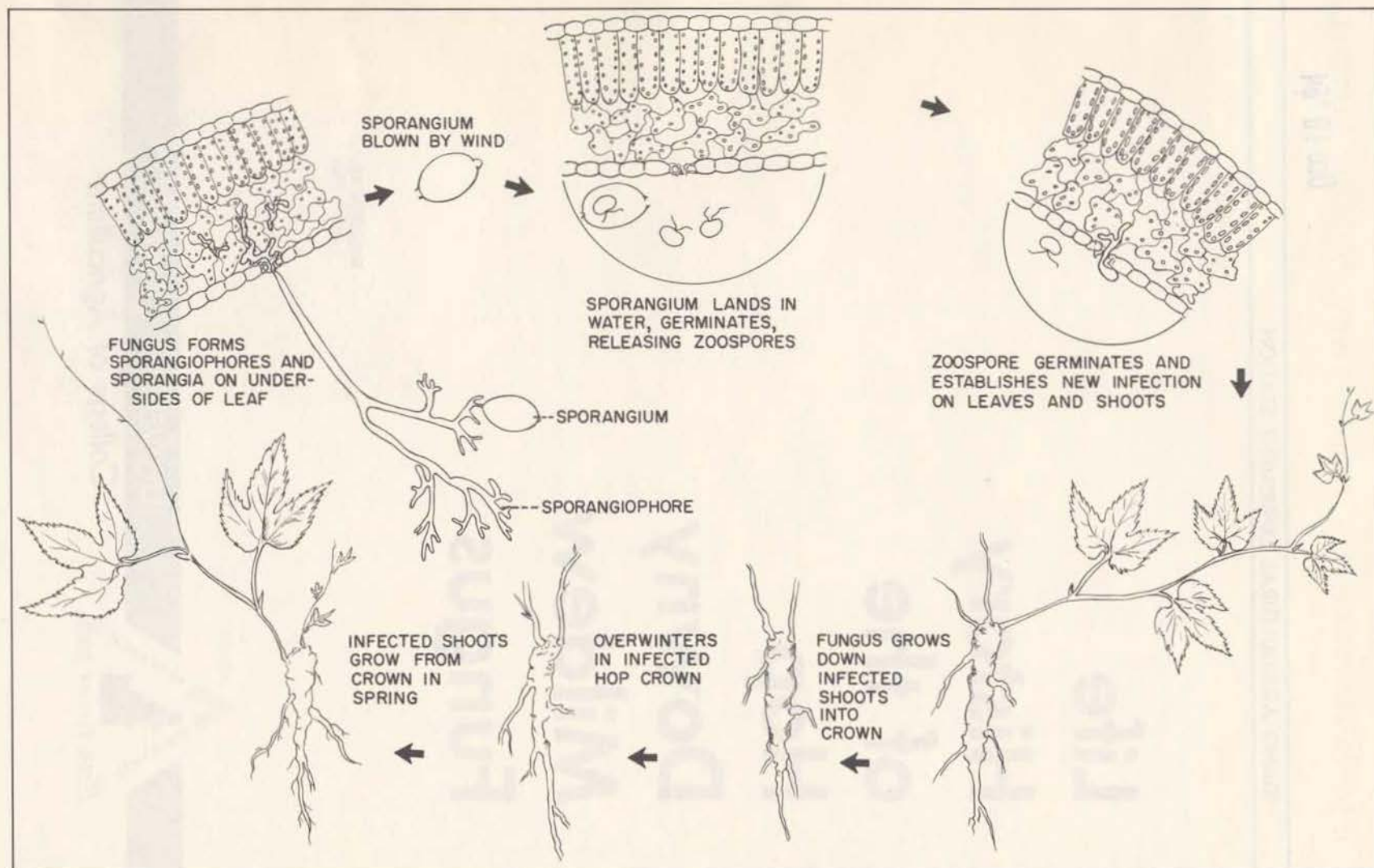
IDAHO AGRICULTURAL EXPERIMENT STATION

Life History of the Hop Downy Mildew Fungus

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Life cycle of the hop downy mildew fungus. The top three drawings showing plant cells and spores are magnified many times.

Life History of the Hop Downy Mildew Fungus

C. B. SKOTLAND AND R. R. ROMANKO¹

INTRODUCTION

Hop downy mildew is a major hop disease problem in most hop growing areas of the world. It was first reported in Japan in 1909 and later in England and Europe. It was recognized in western Washington in 1929. This disease has caused a shift of the major portion of the hop acreage of the United States into desert regions. In spite of the less favorable environment, the hop downy mildew fungus has established itself in the Boise and Yakima Valley hop yards.

Cause

Hop downy mildew disease is caused by a fungus or mold with the scientific name *Pseudoperonospora humuli* (Miyabe and Takahashi) Wilson. Fungi are chlorophyll-less plants that cannot manufacture their own food as green plants do, but must use other plants or animals, living or dead, for food. The hop downy mildew can use only living hop and nettle plants as a source of food.

When hop downy mildew fungus infects a hop plant, usually we see only the results of this infection in the form of stunted shoots, dead crowns, etc. The only time the mildew fungus can be seen with the naked eye is when it produces its reproductive structures on the undersides of infected leaves or on infected stems. These structures cannot be seen if they occur singly. But when thousands of them are massed together, they form a blackish-purple fuzz, hence the name "downy mildew." When this downy growth appears, the mildew becomes "active" or is "working." The only way the mildew fungus can be seen in a diseased plant is to make thin sections of diseased tissue and examine them with a microscope.

The body or thallus of the hop downy mildew fungus consists of thread-like tubes called hyphae. (In some other fungi these thread-like tubes unite to form "mushrooms or toadstools.") The hyphae of the hop downy mildew fungus grow between the cells of the hop plant.

The only parts of the hop downy mildew fungus produced outside of the hop plant are the fruiting structures. This dark "downy fuzz" is the sporangiophores and they bear the reproductive bodies called sporangiospores. The sporangiospores are shaped like a lemon. When the spores are placed in water they germinate and produce tiny swimming spores, called zoospores. The zoospores swim about in the water on the leaf and infect the hop plant.

Another spore that is formed by the hop downy mildew fungus is thick-walled and lives for many years; it is called an oospore. In the Yakima Valley, oospores are rarely formed and at this time are of little importance in the life history of the fungus. They have been found in the Boise Valley in infected hop cones. In such yards they could be a means of overwintering.

LIFE HISTORY AND SYMPTOMS

Winter

The hop downy mildew fungus spends the winter in crowns that were infected in previous years. The drawing shows the life cycle of the fungus. The infected crowns are in various stages of rot, varying from almost completely destroyed to quite sound (figures 1 and 2). Hop downy mildew can be found in most tissues of the hop crown, but is found most often in the white tissue next to the bark. If this tissue has reddish-brown flecks and streaks, it is probably infected with mildew. This should not be confused with



1. Hop crown infected with hop downy mildew.

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2. Healthy hop crown.

the reddish tissue found in the center of most normal hop crowns.

Not only do crowns become infected, but the roots and rhizomes (slip roots) also may become infected (figure 3). These roots will show a reddish-brown discoloration, and since they rarely contain any normal reddish tissue, infected ones can be detected readily.

Quite often, a black rot is found in conjunction with mildew infection. Examination of the area ahead of the black rot should generally reveal a reddish-brown discoloration, characteristic of mildew infection. Black rot symptoms are also associated with hops that have been injured by heptachlor. In both instances, heptachlor and downy mildew weaken the hop plant and secondary fungi enter and produce the black rot.

Spring

As the soil warms in the spring, some of the buds growing from infected crowns will become infected with the downy mildew fungus. As the infected buds grow, the mildew fungus grows with them, causing them to be stunted. These pale yellow-green stunted shoots (figure 4), or "Christ-



3. Hop rhizomes infected with hop downy mildew. The rhizome on the far right is healthy.



4. Hop shoots infected by downy mildew growing from crown.

mas trees," are called "primary spikes." They are the first or the primary sources of infection in the current growing season.

From one to many primary spikes may be found on an infected hill. Only a small portion of the infected crowns produce primary spikes; some may do so one year and not the next, and some infected crowns may never produce primary spikes.

If the spring has been warm and the crowns pruned early, primary spikes will appear as early as the first week of April. When these spikes first appear, they cannot spread mildew, as the mildew has not produced the sporangiospores by which it spreads. This is important, because "spread" can be prevented if these primary spikes are removed before spores are produced. The effectiveness of the control would depend on how thoroughly the spikes were removed.

Primary spikes may reach a length of 20-24 inches before the mildew sporulates on them. Night temperatures are the critical factor in sporulation of the mildew. If a warm night occurs (above 45°F.) the mildew produces downy purplish to black spore masses on the undersides of the leaves of these primary spikes.

Millions of spores are formed on each primary spike. These spores become detached from the primary spikes and are carried by the air currents to leaves and shoots of the same hill and surrounding hills. If water is available in the form of dew or rain, the spores germinate and produce the zoospores. These zoospores produce a small tube which enters the hop plant through natural openings in the epidermis. As soon as this tube enters the hop tissue and becomes established

(within 12 hours), neither weather nor fungicide can prevent the development of the disease.

In 1963, a hop field was observed closely for mildew infection. About 1.9% of the crowns contained primary spikes. It rained periodically for 48 hours. Conditions favored mildew infections, and 75% of the hills had mildew infected shoots. Thus, a small amount of mildew can rapidly develop into a major disease problem when temperature and moisture are favorable.

The fact that mildew is a minor problem in the Upper Ahtanum Valley in Washington is attributed to the cold nights (below 45°F.) which occur in the spring. By the time the weather warms, rain or dew is rare and disease development is slight.

When the mildew spores spread from the primary spikes, new infections occur. The first to appear (7-10 days after infection, depending on the temperature) are the pale yellow angular spots on the leaves (figure 5). If the weather conditions are right, the mildew produces its purplish-black spore masses on these lesions (figure 6). The lesions generally dry up in the arid regions and are of minor importance in the continued development of the disease.

If the growing tip is infected, the tip develops into a "secondary spike" (figure 7). These are bright yellow, stunted, stiff, brittle shoots that



7. The top shoot is an infected primary spike; the middle shoot is an infected secondary spike and the bottom shoot is healthy.

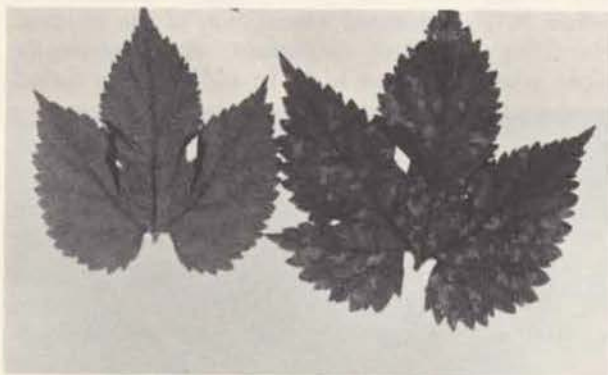
fall away from the string. The leaves are cupped downward. Normal growth occurs below the infected portions.

Unlike primary spikes, secondary spikes may occur on trained shoots, laterals or on basal shoots. Secondary spikes, like primary spikes, produce spores and repeat the infection cycle when temperature and moisture are favorable. New crown infections invariably result from the growth of the mildew organism downward from a secondary spike into the crown.

The mildew fungus is limited in its ability to grow great distances. Its progress is slow under best growing conditions. The further the infected area is from the crown, the less chance there is for mildew to grow back into the crown. It is doubtful if it could grow downward much over 24 inches during a growing season.

Downy mildew infected shoots can be easily confused with shoots stunted by virus (figure 8), zinc deficiency, or frost injury (figure 9). Shoots stunted by virus may have yellow ringspots or lines on them but will not have the bright-yellow cast of infected mildew shoots. Shoots that have been frosted will be stunted but will be green, often quite dark. Shoots stunted by zinc deficiency will be dull yellow and the leaves will be rolled upward instead of downward, and generally the whole plant is affected.

Growers commonly consider a stem that has no hollow center as being infected with mildew.



5. Lesions of downy mildew show on leaf to the right; the left leaf is healthy.



6. Hop downy mildew is sporulating on the hop leaf to the right. The leaf on the left is healthy.

It is true that this does occur with mildew infection, but it also occurs with some of the above-mentioned problems. Anything that stunts the shoot or slows the growth of the shoot will also cause the "solid" stem development.

Summer and fall

Ordinarily, mildew is inactive during late June, July and August. However, in certain years with favorable weather, secondary spikes continue



8. Lateral hop shoot stunted by virus.



9. Frosted hop shoot.

to develop. This may result in a much less common symptom, cone blight. The mildew causes the cone petals to burn brown. Generally, infected cones will be scattered about on the plant and should not be confused with a condition in which all cones on certain plants turn brown.

Quite often, hop vines die late in the season as a result of mildew infection. The base of such a vine will be enlarged (figure 10) and tapered to a very thin point of attachment to the crown. If a wind storm occurs, the vine may break off at the crown.

At other times, the large leaves attached to the main stem turn yellow and die, progressing from bottom to top of vine. Gradually the whole plant turns yellow, often wilts and dies. The cones ripen earlier than those on healthy vines. Other things can also cause this same condition and care must be taken to examine the diseased tissue for evidence of mildew infection before making a diagnosis.

CLIMATE

Some of the weather factors which affect hop downy mildew have been mentioned, but more detail may be desired. For several years, the effects of temperature and humidity have been studied at the Irrigation Experiment Station, Prosser, Wash. Over the years, night temperatures below 40°F. prevented sporulation of the mildew. Humidity was less important, since generally night humidities were high. In addition, the curled



10. Base of hop stem infected with mildew.

up leaf provides high humidities at the leaf surface. Mildew is rare in hop yards near Tampico, Wash., presumably because nights are cool.

The severest mildew problems occur in the lower Yakima Valley and on south slopes of ridges near Sunnyside, Wash. Two factors probably are in operation:

1. The lower valley has a warmer climate, and hops begin growing earlier.
2. More warm nights occur.

Experiments at Prosser, Washington, also have shown that mildew infections can occur in the presence of dew.

CONTROL

The control of hop downy mildew must be directed at the causal fungus and at the points in its life cycle at which a grower has some degree of control. Specifically, control should prevent new infections.

1. *Use clean roots for planting and replanting.* With enough isolation, the use of mildew free planting stock will delay or prevent introducing mildew to a new yard. Since the mildew, as far as we know, overwinters only in the crowns, yards can be replanted with no danger that new infections will come from the soil.

2. *Remove all diseased hills.* The removal of diseased hop crowns will remove the primary sources of mildew spores. The success of this program depends on its thoroughness. Remove crowns showing rot, and hills showing primary spikes.

3. *Remove primary spikes.* Removal of the primary spikes *before* they sporulate will aid materially in reducing infection. This must be done weekly from the time the hops are 8-10 inches tall until (depending on the season) the first week in June in the Yakima Valley to late June in the Boise Valley.

The spikes that are removed quickly dry up and no spores will be produced. If the spikes have spores on them, most of these spores will die in 24 hours in direct sunlight, but will live longer if in shade.

In 1962, mildew was severe in both Washington and Idaho. In Idaho, weekly spike removal alone reduced mildew infections 75% and made control by spraying more effective. In Washington, weekly spike removal in two yards resulted in 9 to 11% of the hills with spikes at the end of May, compared to 21 and 33% hills with spikes in two yards where spikes were not removed weekly. However, by mid-June there was essentially no difference in any of the four yards.

4. *Prune yards as late as possible.* Some control can be achieved by late pruning. Such a

practice would shorten the mildew season for vines selected for training. Hops pruned late in April would not be up until mid-May. Those pruned early in April would have considerable growth by May 1. In general, if growers can get through May with a minor mildew problem, the danger lessens. The weather in June is usually unfavorable for infection. Thus, if one prunes late, instead of a month of probable mildew weather, only 2 weeks are likely.

An example can be found in yards in 1963. The severest mildew occurred in:

1. yards that had a history of mildew
2. those that were not pruned or even touched
3. those in which pruning was done early, when roots were dug to plant new yards.

Other yards with a history of mildew did not suffer. Why? The early pruned yards were well along in growth, with about 5% of the hills showing primary spikes. During the first week of May, 2 days of weather favorable for infection occurred. However, little growth was present in late pruned yards and the primary spikes were not present in these late pruned yards. Consequently, these yards were free of mildew during the critical period and all season long.

The foregoing practices, if implemented carefully and thoroughly, should keep mildew at a low, manageable level. However, with even moderately favorable mildew weather and low incidence of mildew infections, spread can be rapid and the number of infection sites may increase from 2- to 100-fold in 2 weeks. If these conditions should occur, it would be wise to supplement the above practices with the application of fungicidal sprays every week to prevent new infections.

5. *Set up a fungicide spray program.* Since there is no way of really predicting weather favorable to the development of mildew epidemics, it is advisable to spray, before training, just after training, and at 7-10 day intervals thereafter until it becomes apparent that mildew will not be a problem. Consult your county agent for specific recommendations as to fungicides to apply.

GENERAL CONSIDERATIONS

It might be well to discuss the relationship of some of the current general hop growing practices to the incidence of hop downy mildew and other contributing factors.

For a long time, clean training and stripping were performed to control hop diseases and insects. Recently, growers who eliminated these practices found indications of yield increases, as well as much lower production costs. However, omission of these practices may favor downy mildew.

One danger of clean training is that infection may occur with no healthy shoots left to train. It is difficult to evaluate this type of practice, but two approaches can be followed.

One approach, favored by the senior author, is to clean-train initially and then allow the basal shoots to grow, if no mildew infections have occurred before training. If weather has been favorable for infection, it might be wise not to train the field for 7-10 days until the shoots that are infected appear. This practice might save costly retraining. By the time new growth has appeared, the general threat of mildew could be past.

The other possibility, favored by the junior author, is to begin clean training only as a sanitary measure if and after secondary spread has become evident.

The effect of pruning is not certain, but undoubtedly severe pruning does result in death of weaker hills infected with mildew. In two yards inspected in 1963, the overall mildew incidence was 1.9% in one yard and 4.9% in the other. The main difference was that one yard had been carefully checked for poor hills and these were eliminated; in the other yard, the tops had been dragged off and burned back.