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Ecological Factors Limiting Epidemics of Hop Downy Mildew in Arid Climates

R. M. Sonoda and J. M. Ogawa

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This study reports on factors affecting the development of hop downy mildew during the dry, hot season in the Sacramento Valley, as well as on factors contributing to the paucity of disease development in apparently favorable conditions. In flood-irrigated commercial hop yards, systemically infected shoots (which can be sources of inoculum) were present until late in the growing season. Dew and guttation fluid appeared on leaves and stems at the base of the plants after irrigation, but only a few lesions developed on the leaves.

Data from Hirst spore traps, used to monitor the concentration of sporangia near systemically infected shoots, indicated a diurnal pattern of sporangial release. Sporangia were released with each sudden lowering of RH under laboratory conditions, and a more rapid lowering resulted in greater release. Sporangial release in the field coincided with RH drop. Most of the sporangia were released in the early morning during evaporation of dew and guttation fluid, and few sporangia were collected in the afternoon, evening, or night.

Longevity of viable sporangia was dependent on RH. Relative humidity below 60 per cent killed sporangia in less than 3 hours. Even in well-irrigated yards the ambient RH remained below 60 per cent for about 10 hours each day; most sporangia do not survive throughout the day in such an environment. A few sporangia do

(Continued inside back cover)

THE AUTHORS:

R. M. Sonoda, formerly a graduate student in the Department of Plant Pathology, University of California, Davis, is now Assistant Professor and Assistant Plant Pathologist in the Institute of Food and Agricultural Science, University of Florida, Agricultural Research Center, Ft. Pierce, Florida.

J. M. Ogawa is Professor of Plant Pathology and Plant Pathologist in the Experiment Station, Davis.

R. M. Sonoda and
J. M. Ogawa

Ecological Factors Limiting Epidemics of Hop Downy Mildew in Arid Climates[1]

INTRODUCTION

HOP DOWNY MILDEW, caused by *Pseudoperonospora humuli* (Miy. and Takah.) Wilson, is not an important disease in dry seasons in Sacramento Valley hop yards, even though inoculum (in the form of sporangia on systemically infected shoots) and free moisture from dew and guttation are present on leaves. Ogawa, Hall, and Koepsell (1967) found occasional secondary infection in Sacramento Valley hop yards during summer months with no rains. Yarwood (1939) reported also that disease did not spread even in the presence of dew in the Sonoma Valley of California. Royle (1970) in England reported little increase of the disease from dew formation.

Skotland (1962) stated that infections are possible in Washington after artificial inoculations followed by nights of heavy dew formation, but his work did not extend beyond this finding. A closely related fungus, *P. cubensis* Berk. and Curt, was reported to cause downy mildew of cucurbits under dry conditions in Massachusetts and New York (Clayton, 1928). Downy mildew disease is also important in some dry coastal areas in Israel (Duvdevani, Reichert, and Palti, 1946) where heavy dew and guttation fluid have provided free moisture.

Hop mildew fungus overwinters in systemically-infected perennial crowns (Skotland, 1961). In California, both healthy and diseased shoots emerge from diseased crowns in late March or early April during frequent rains, and intermittent periods of rain can occur until early June. The disease can spread rapidly, giving rise to angular local lesions on mature leaves and new systemic infection of shoots. Few new infections develop after early June; epidemic of the disease (infecting cones) occurred once in the last 10 years after unseasonal rains in late July and in August.

METHODS AND MATERIALS

The hop *Humulus lupulus* L. variety 'California Cluster' (the only commercially grown variety in the Sacramento Valley) was used in this study. Field studies were conducted in two adjacent commercial hop yards near Sacramento and in a planting on the Davis campus (UCD) during the spring and summer of 1968. No chemicals for mildew control were applied on any of the test plantings. The two commercial yards were flood-irrigated (the form of irriga-

[1] Submitted for publication November 12, 1971.

tion generally used in commercial yards) beginning in early June; yard 1 was irrigated at 2- to 3-week intervals and yard 2 was irrigated every 5 to 6 weeks. The UCD planting was sprinkler-irrigated during the experiment.

Sporangia used as inoculum for the experiments were from (i) sporulating lesions on leaves in the field, (ii) sporulation induced on infected leaves from the field, (iii) infected leaves from potted plants grown in a chamber kept at 20°C 60 per cent RH with 14-hour day induced to sporulate. Sporulation was induced by incubating infected leaves in Petri dishes lined with moistened filter paper (Petri-dish humidity chamber) or in 31 × 23 × 10 cm covered plastic crispers with a false wire-mesh floor beneath to which was added a liter of water (crisper humidity chamber). Incubation temperatures were either 15°C or 25 ± 2°C; leaves were incubated for 16 hours before sporangia developing on them were used.

"Wet" inoculations were made by applying drops of, or atomizing, 1×10^4 to 1×10^5 sporangia per ml suspensions onto the surface inoculated. "Dry" inoculations were made by lightly touching the sporangia-bearing hop leaf surface (lower surface) to the surface to be inoculated.

For *in vitro* germination tests, sporangia were incubated in 0.2 ml of 0.001 M histidine (Sonoda, 1969) in 0.3 ml microbeakers at 15°C to obtain uniform germination. Sporangial suspensions were obtained by placing the histidine solution onto surfaces with sporangia and removing the histidine-sporangia suspension with a Pasteur capillary pipette. Direct observation for germination (zoospore release) was made with a compound microscope at 100X magnification.

Measurements of leaf temperature and RH near the leaf were made with a Leeds Northrup 8662 potentiometer (Schnathorst, 1960). Ambient temperature and RH were measured with an Atkins F01-F46 Relative Humidity gun or with Freiss 7-day hygrothermographs. All times reported are Pacific Daylight Time (PDT).

Hop culture and its effect on survival of inoculum

Certain cultural practices usually followed in commercial yards in California are described because they differ from those followed in other states. Many shoots develop from the crown in late March and early April. In May two young shoots are trained onto each of the two twines from the crown to a trellis 20 feet above the ground, and extra shoots are cut back at this time. When the bines reach the trellis (by the middle or end of June) leaves are stripped from the lower 4 feet and side branches to facilitate harvesting. Although extra shoots are cut periodically from the crown and the crown covered with soil, new shoots emerge rapidly; thus, new shoots are present around the base of the bine throughout the growing season. Cones are harvested from late July to early September.

In spring, growers should remove infected shoots and in severely infected crowns (Ogawa and Hall, 1964). Infected shoots are sometimes removed during cutting of extra shoots, but new systemically infected shoots soon reappear and thus complete elimination of the pathogen is not accomplished.

Frequency of occurrence of systemically infected shoots in a well-irrigated yard (yard 1) was compared to frequency in a seldom-irrigated yard (yard 2) during dry weather; the yards were separated by a 40-foot wide roadway. Systemically infected shoots were observed in both yards in June, although no counts of infected shoots were made. Of 1,500 hills inspected in yard 1, 120 had diseased shoots with viable sporangia on July 11, 125 on July 23, and 15 on August 11. No infected shoots were found on the same days in yard 2, and diseased shoots in this yard began

to dry and die in the middle of June. Apparently, the presence of moisture enhances survival of diseased shoots during the hot dry summer in commercial yards in the Sacramento Valley of California.

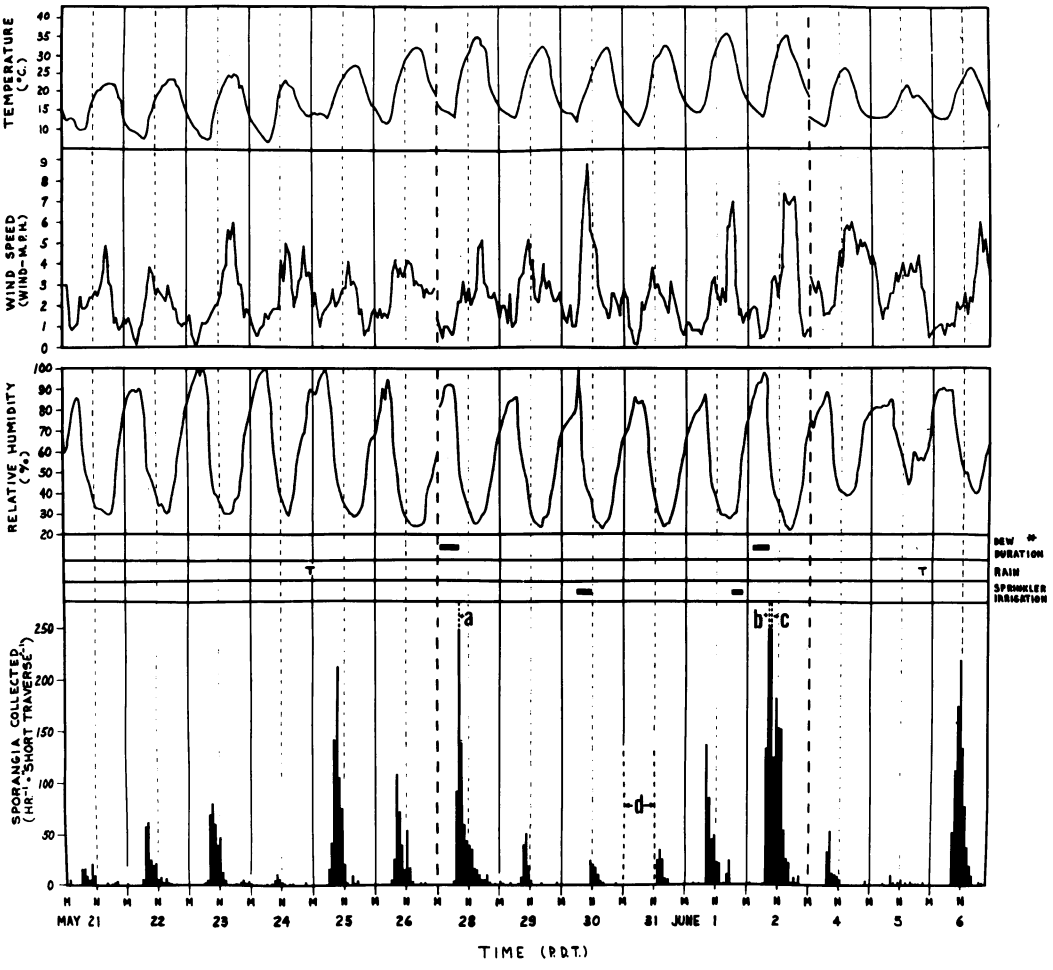

Fig. 1. Pattern of daily sporangial collection and hourly climatological data for 15 days in UCD hop planting. Observations of dew formation or duration were made only on 2 days. Letters a, b, and c refer respectively to 370, 480, and 359 sporangia counted per scan at 100X, perpendicular to the direction of slide movement in the spore trap; at d, equipment failed to operate. M is midnight and N is noon.

RESULTS

Dispersal of sporangia

Diurnal periodicity of sporangial dispersal. To determine if sporangia are released when dew and guttation fluid are present, two Hirst (Hirst, 1952; Hirst, 1953) volumetric spore traps were placed north and south of the UCD planting having numerous

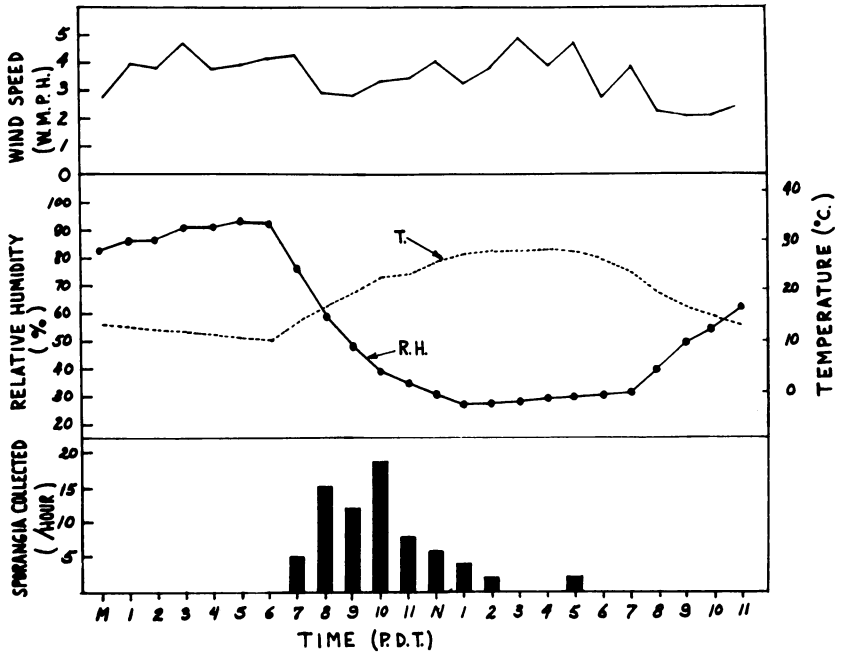

Fig. 2. Pattern of sporangial collection and hourly climatological data for June 11. Sporangia were not collected until RH began to drop, even when relatively high wind-miles per hour occurred beginning at 1:00 a.m.

systemically infected shoots. The traps were immobilized to point toward these sources of inoculum. Orifices of the traps were 45 cm above the ground and about 45 cm from the nearest sporangia-bearing leaf. Temperatures and RH were recorded by a hygrothermograph in a weather shelter on a 4-inch high platform.

Sporangia were collected from May 19 to June 20, by which time most of the systemically-infected shoots had dried up in the UCD planting. Figure 1 shows the pattern of sporangial collected for 15 days. The data presented from May 21 through May 27 are from the north trap which collected more sporangia; after May 27 data are from the south trap. No sporangia were collected during sprinkler irrigation from 5 a.m. to 11 a.m. on May 30 and from 6 p.m. to 10 p.m. on June 1. Sporangia were first collected at about 7 a.m.; the largest number was collected at about 8 a.m. (fig. 1) on 6 days, 9 a.m. on 2 days, 10 a.m. on 1 day, and 11 a.m. on 1 day. The number collected diminished rapidly after the peak and few were collected in the afternoon. On a few days some sporangia were collected up to about 9 p.m. when the RH began to rise again. Royle (1968) in England found a similar diurnal pattern of sporangia collection but observed a usual peak at 10 a.m. Neither overcast or partly cloudy weather nor trace precipitation altered the pattern of collection, although fewer sporangia were collected on days preceding light precipitation. Relatively high wind-speed in the morning before a drop in RH did not increase spore dispersal (fig. 2).

Changes in RH release sporangia. Pinckard (1942) attributed the release of sporangia of *Peronospora tabacina* Adam to the twisting and turning of sporangiophores with changes in RH. Ogawa and Hall (1964) saw similar sporangiophore behavior of *P. humuli* and observed the release of sporangia.

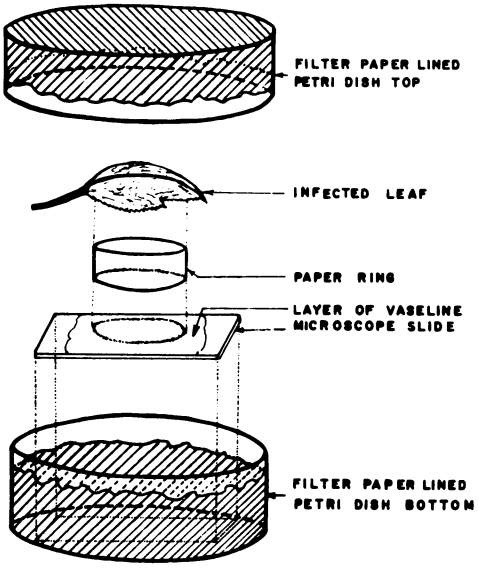

Fig. 3. Apparatus used to determine effect of RH on the release of sporangia. Filter paper wetted with a graded series of glycerol-distilled water solutions produced chambers with different relative humidities.

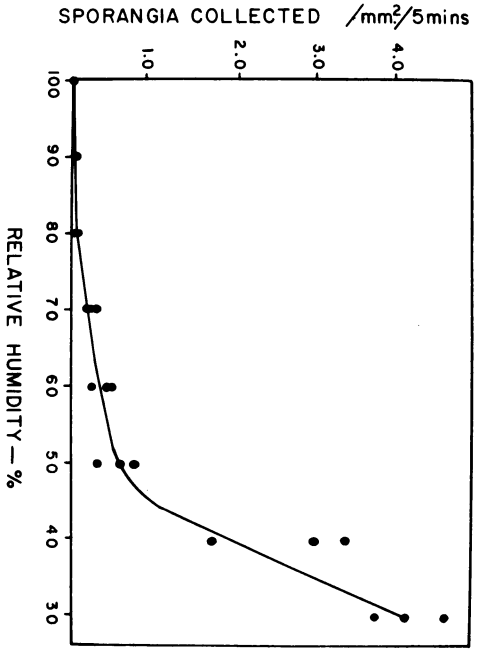

Fig. 4. Sporangia released in chambers with different relative humidities at 24 ± 2°C. Curve shows increase in sporangial release with lower humidity.

The sporangia collection data shown in figure 2 indicate that a change in RH could be the major factor in the release of sporangia.

Petri-dish chambers having RH's ranging from 30 to 90 per cent were made by lining 30-mm-deep dishes with filter paper moistened with varying ratios of glycerol to distilled water (Osborne and Bacon, 1961). Distilled water was used to moisten the filter paper for the 100 per cent RH chamber. Systemically-infected leaves with sporangia on their lower surface were placed on a 5-mm-high paper ring on a vaseline-coated microscope slide within these chambers (fig. 3). Leaves were exposed for 5 minutes in each chamber, starting with the 100 per cent RH chamber. Between exposure in each chamber, leaves were exposed to 100 per cent RH for about 5 minutes.

To avoid counting sporangia released by contact between the paper ring and the sporangia-bearing leaf surface, only sporangia more than 1 mm from the edge of the circle or ellipse formed on the vaseline-coated surface by the ring were counted. The area examined in each case was about 220 mm². The number of sporangia released per unit area per unit time increased with decrease in RH (fig. 4). Results show that a drop in RH even without much air movement can result in release of sporangia.

Downy mildew spread during dry weather. Spread of pathogen from diseased to healthy leaves on shoots on the same crown was shown by collecting leaves two to five nodes below the growing point of untrained shoots and incubating in crisper humidity chambers. Collections from adjacent crowns (5 to 7 feet away) were made to study spread of inoculum. To eliminate contamination from irrigation water, leaves present at irrigation were marked and only leaves formed thereafter were

TABLE 1

SECONDARY SPREAD OF SPORANGIA DURING DRY PERIODS*

Date leaves collected	Number of leaves	Number of leaves with lesions	Total number of sporulating lesions	Preceding irrigation†
		Spread within individual hill		
June 14	23	9	20	June 7
June 21	10	4	17	June 7
June 23	22	7	14	June 21
June 27	10	3	7	June 21
July 11	30	0	0	June 21
July 22	86	26	80	July 16
		Spread one hill removed from source		
June 27	90	21	77	June 21
July 23	60	13	23	July 16

* Leaves picked from yard 1 in Sloughhouse. Only leaves that expanded after preceding irrigation were sampled from hills with "spikes." Leaves incubated in crisper humidity chamber.
† Flood irrigation.

picked. No rain fell during the course of this experiment.

The spread of spores from diseased to healthy leaves within a crown was detected at each sampling during the 5-week period (table 1) except on July 11. The absence of disease on leaves collected on July 11 is attributed to the extreme dryness of the yard which may have prevented spore dispersal or reduced spore viability. The pathogen spread in all directions one hill away from the inoculum source (table 1).

Table 2 shows areas of infection on diseased leaves collected at different degrees of maturity. Lesions were more numerous around leaf margins than in central portions. Free moisture required for germination and infection can come from guttation from hydathodes at the leaf margin, and this could be a reason for more lesions around margins.

TABLE 2

DISTRIBUTION OF LESIONS ON LEAVES OF DIFFERENT AGES OBTAINED FROM A COMMERCIAL HOP YARD UNDER IRRIGATION*

Age of leaf†	Number of leaves‡	Number of lesions and location	
		Marginal	Central
Young	5	18	1
Medium	13	35	11
Old	7	20	6

* Leaves picked on three different days from hills with spikes.
† Young = first expanding leaves; medium leaves = second expanding leaves; old = third or further back.
‡ Only leaves with lesions were counted.

Survival of sporangia

Viability of sporangia on source leaves in the field. Magie (1942) reported that sporangia of *P. humuli* survived for at least 2 weeks on detached systemically-infected source leaves when the leaves were exposed in open dishes in the laboratory. He also reported that some sporangia survived for at least 1 month on source leaves in the field. The latter finding was based on the assumption that the fungus did not sporulate during the month of his observation. In California, sporangia are produced during spring and summer nights when RH is high but not during extremely dry north winds. Maximum temperatures were usually higher and minimum RH lower in California during the host's growing season than in New York (where Magie's studies were conducted).

Sporangia from diseased leaves were collected in 0.001 M histidine in the June and July evenings and then incubated. Many sporangia (table 3) were still viable in the evening even though borne over dry soil on hot dry days. Examination with a microscope showed

TABLE 3

VIABILITY OF SPORANGIA FROM SOURCE LEAVES IN COMMERCIAL YARDS DURING DRY WEATHER

Date and Sampling time		Maximum temperature*	Minimum RH*	Variability in sporangial germination			Condition of soil surface
Date	Time			Number of leaves†	Germination‡	Minimum and maximum	
	pm	*°C*	*per cent*		*per cent*		
June 27	5:30	34	30	5	43	12–87	Moist
June 27	9:00	34	30	5	48	17–95	Moist
July 4	9:00	38	18	2	55	22–86	Dry
July 7	8:30	33.5	20	5	39	14–69	Dry

*Maximum temperature and minimum relative humidity recorded by hygrothermograph in weather shelter within planting.
†Each leaf from a different systemically-infected shoot; three to six samples taken from each leaf.
‡Sporangia germinated in 0.001 M histidine solution.

that most of the sporangia still on the leaves in the evening were detached from sporangiophores. The range in viability was 22 to 86 per cent even when maximum temperature during the day was 38°C.

Effect of RH on the longevity of sporangia. Magie (1942) reported that the sporangia of *P. humuli* ". . . lived only for a few hours when separated from their host plants and dried on glass slides in the laboratory." No record was made of the RH and temperature in his laboratory.

P. humuli sporangia on microscope slides were exposed to different RH's by placing them in Petri dishes lined with filter paper moistened with varying ratios of glycerol to distilled water. The dishes were placed in crispers containing the same ratio of glycerol to distilled water and incubated for varying intervals of time at 25 ± 2°C. After each time interval six lots of sporangia were placed in 0.001 M histidine solution.

The longevity in viability of sporangia decreased with decreasing RH (fig. 5). In the 30 per cent humidity chamber all sporangia were dead within 10 minutes; in the 40 per cent humidity chamber all were dead within 30 minutes. These results are not shown on the graph.

Survival of sporangia on healthy leaves. In the UCD planting, healthy leaves located 6 inches to 2 feet above the ground were "dry" inoculated in the morning on both surfaces with sporangia and then exposed to different weather conditions. Ten to 24 hours after inoculation from 20 to 200 sporangia were collected from each inoculated site and placed in 0.001 M histidine and germinated. Sporangia survived longer on the lower surface than on the upper surface (table 4). Survival on both surfaces was higher under overcast or cloudy days than on clear days.

In commercial yards, healthy leaves on untrained shoots were dry inoculated after dew and guttation fluid had evaporated in the morning (to preclude the possibility of prior infection). Inoculations were made 3 days after an irrigation and again 7 days later. No temperature or RH data are available for the day of the first inoculation; on the second, maximum temperature was 33°C and minimum RH 23 per cent. Dew was observed on inoculated leaves on the mornings following inoculation. Inoculated leaves and uninoculated leaves were harvested on the third day after inoculation and incubated in crisper humidity chambers in the laboratory (25°C ± 2°). No lesions developed on uninoculated leaves after 3 days of incubation, but lesions developed on inoculated leaves (table 5). More lesions developed from inoculations made on

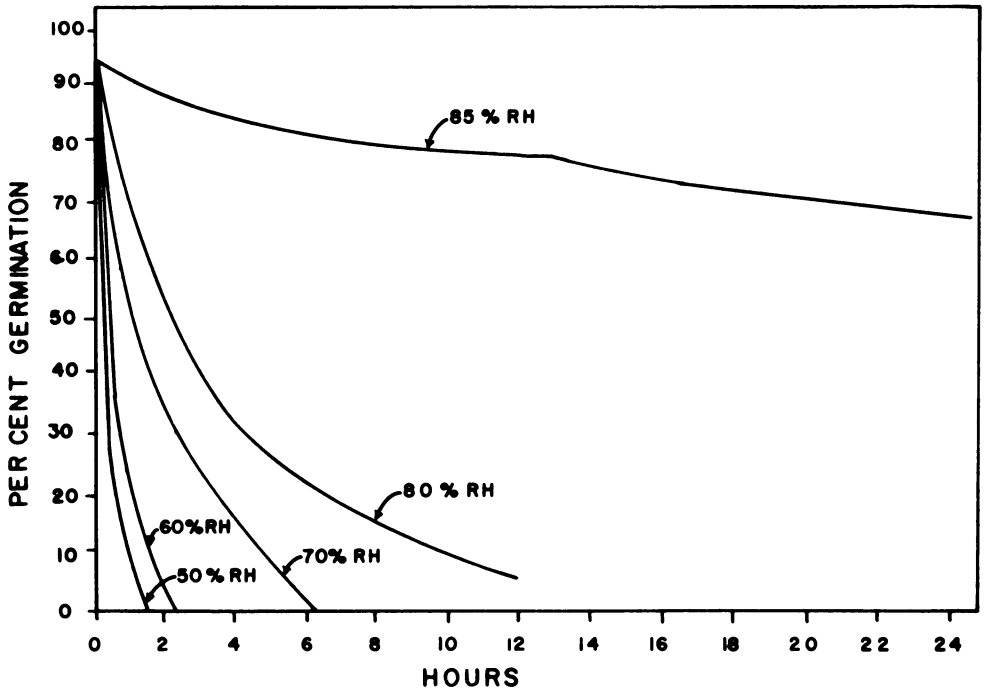

Fig. 5. Longevity in viability of detached sporangia on dry glass slides at different RH's.

the lower surface than from inoculations on the upper surface. Sporangia can survive on both upper and lower surfaces of leaves in yards through unfavorable conditions, and can initiate infections on either surface when conditions become favorable for germination and infection.

In the laboratory, sporangia were dry inoculated on both surfaces of healthy leaves in potted plants. The shades were drawn to reduce the entrance of sunlight. The upper surface of the leaves was exposed to a 200 ft-c intensity light and the lower surface to an intensity of 150 ft-c. The laboratory temperature was 25°C ± 2° and the RH was 30 per cent. Sporangia were also dry inoculated on glass slides exposed to laboratory air. At predetermined intervals, sporangia were collected into 0.001 M histidine and germinated. Again, sporangia survived longer on the lower surface than on the upper surface (fig. 6). Thus lower RH, not direct sunlight, could account for the death of sporangia on the upper leaf surface.

Yarwood and Hazen (1944) using a temperature-depressing method calculated the RH at the lower surface of hop leaves to be 10 per cent higher (61 per cent) than the ambient laboratory air (51 per cent), while the RH on the upper surface was 4 per cent higher than the ambient. Schnathorst's (1960) method based on Frampton and Longree's formula (Frampton and Longree, 1941) was used to calculate the RH near the leaf surface in the present study. The calculated RH at the lower surface was about 72 per cent and that at the upper surface 64 per cent when the laboratory RH was between 52 and 54 per cent (fig. 7) and laboratory temperature was 25°C ± 2°. Thus the RH near the lower surface was higher than the ambient air, which could be the reason for the higher viability of sporangia on this surface.

TABLE 4

SURVIVAL OF SPORANGIA ON UPPER AND LOWER SURFACES OF HEALTHY HOP LEAVES UNDER DIFFERENT WEATHER CONDITIONS*

Type of day	Maximum temperature	Lowest RH	Number of hours sporangia on leaf	Viability	
				Upper	Lower
	°C	*per cent*		*per cent*	
Overcast	23	44	24	22.2	41.4
Scattered clouds	31	38	10	3.6	16.7
Clear—windy	30	28	13	0.2	3.6
Clear—calm	31	25	14	0.2	1.6
Clear—warm	37	24	16	0.0	0.0

* Experiments conducted in experimental plot. Temperature and relative humidity readings from hygrothermograph located in a Stevens screen within plot.

TABLE 5

INFECTION OF LEAVES INOCULATED IN COMMERCIAL HOP YARDS AFTER DEW FORMATION*

Inoculation date and time†		Surface inoculated	Number inoculated		Number infected	
			Leaves	Areas	Leaves	Areas
July 10	9:00 a.m.	Upper	10	30	0	0
		Lower	10	30	1	1
July 18	10:00 a.m.	Upper	11	33	3	6
		Lower	13	39	6	12

* Incubation period: 3 days in the field and 3 days in high humidity chamber.
† Inoculations made after evaporation of free moisture to preclude possible infection occurring on the same morning.

Free moisture required for infection

Minimum wet period required for establishment of infection. Both Magie (1942) and Royle (1970) determined the effect of temperature on the minimum period of free moisture required for infection, but their data were based only on inoculations of the lower surface. Recently, we have reconfirmed the findings of Arens (1929) and Blattny (quoted by Salmon [1928]) that infection can occur through uninjured upper surface and through the epidermis of leaves without stomates (Sonoda, 1969). Sporangial suspensions were placed onto three areas on the lower or upper surface of leaves preincubated for 1 hour at the respective temperatures of incubation. Six leaves, three inoculated on the upper and three on the lower surface from crispers incubated at 12, 15, 18°C were sampled every 30 minutes for 5 hours and dried with a jet of air and re-incubated at 15°C. Leaves incubated at lower temperatures, 3, 6, and 9°C were sampled every hour and treated similarly. The criterion used for infection was sporulation of the fungus on the inoculated areas after 5 to 6 days incubation.

Infections became established about the same time through both surfaces (fig. 8). The only difference was that one-third of the upper surface inoculations resulted in infection while almost all inoculations on the lower surface resulted in infection. The free-moisture requirement data conform more closely to those of Magie (1942) than to those of Royle (1970).

Guttation fluid and its importance as a source of free moisture for infection. The numerous lesions on the margins of hop leaves following irrigation suggested that guttation fluid plays a role

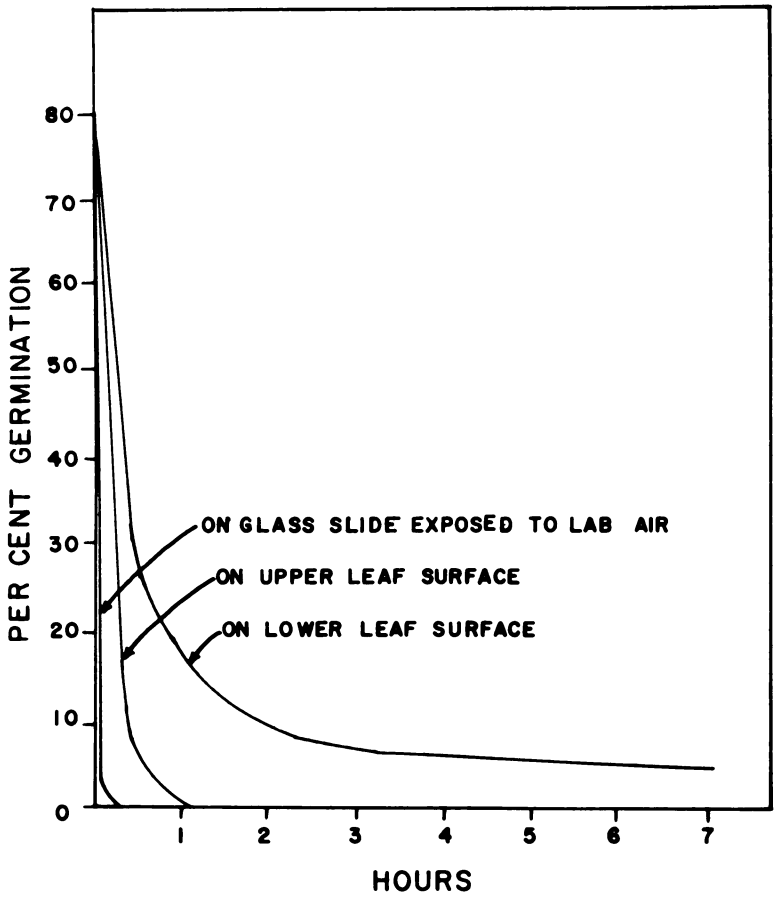

Fig. 6. Longevity (in viability) of "dry-inoculated" sporangia on healthy leaves of potted hop plants under laboratory conditions; temperature 25 ± 2°C; RH 25–30 per cent.

in initiation of infection. Guttation fluid on the upper surface of serration points was observed on leaves in the commercial yards 2 to 3 days after irrigation. Younger leaves had more serration points with guttation fluid. In some cases water drops were randomly distributed on the supper surface, suggesting that the fluid had dripped from one leaf to another. A week after irrigation, guttation fluid was observed on only a few leaves.

After observing that guttation fluid was present up to 11 a.m., leaves with drops of fluid were inoculated by brushing sporangia onto the drops. In yard 1, inoculations were made between 8:15 and 8:45 a.m., 2 days after irrigation and between 7:15 and 7:45 a.m. on the following day on a different set of leaves. Four days later in each case the leaves were harvested and incubated in crisper humidity chambers along with uninoculated leaves collected from plants 10 to 15 feet away from inoculated leaves. No lesions were found on 60 leaves inoculated between 8:15 and 8:45 a.m., while lesions were found on eight of 80 leaves inoculated at 7:15 to 7:45 a.m.

To prove that sporangia can germinate in guttation fluid, sporangia pro-

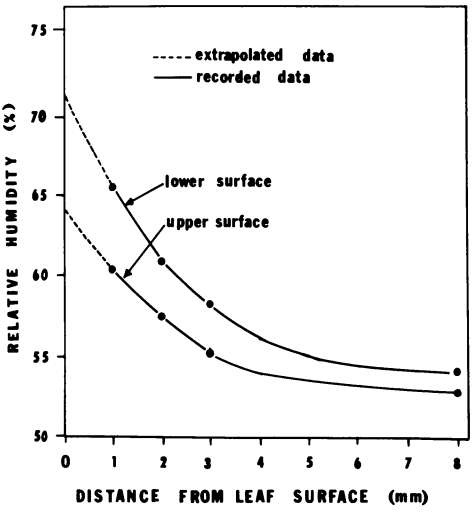

Fig. 7. RH measurements near and at the upper and lower surface of leaves on potted hop plants in the laboratory. Black dots indicate distance of wet- and dry-bulb thermocouple leads from leaf surface.

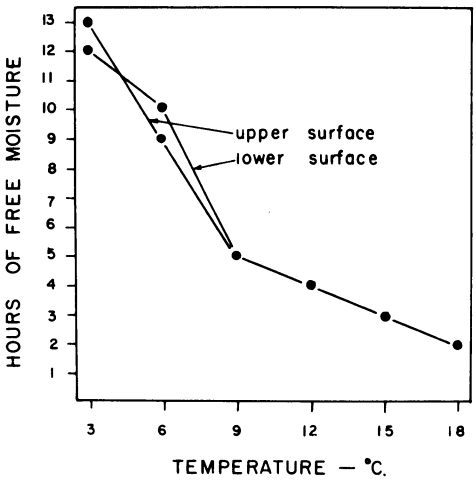

Fig. 8. Curve shows minimum free-moisture time required for infection after inoculation of sporangia on the upper and lower surface of hop leaves.

duced in the field were brushed into microbeakers with guttation fluid. Over 90 per cent of the sporangia produced zoospores, which encysted and formed germ tubes.

Dew and its importance as a source of free moisture for infection. Observations for dew formation and duration were made on 8 nights between May 10 and June 20 in the UCD planting. Initial dew deposit was observed around 1:00 to 3:00 a.m. with the last remnant of free moisture evaporating between 7:00 and 9:00 a.m. Five and a half to seven hours of free moisture occurred during these nights with minimum temperatures ranging from 8 to 14°C. Lower leaves and leaves over moist soil had more dew than leaves over dry soil. There was more dew on upper than on lower surfaces.

Sporangia were dry inoculated onto three areas on the lower surface of 15 leaves in the UCD planting at 10 p.m., before dew formation. There was dew on both leaf surfaces the following morning, and after most of the dew had evaporated (by 7:00 a.m.) inoculated and uninoculated leaves were detached and allowed to air-dry until no moisture was visible. The leaves were then dried with a jet of air to kill sporangia that had not already germinated, and were then incubated in a crisper. Lesions developed in all inoculated areas of the leaves, while no lesions occurred on uninoculated leaves.

Observations of dew formation were not made in commercial yards, but dew was observed until as late as 10:30 a.m. on July 16, 18, and 19 on both leaf surfaces in yard 1 irrigated on July 14. Table 5 data indicate that infection can occur with dew through both upper and lower leaf surfaces in commercial yards.

Effect of high temperature on sporangial germination and lesion development

Rate of sporangial germination affected by pre-incubation exposures to high temperatures. Sporangia in the field can be exposed to high temperatures. Arens (1929) and Zattler (1931) reported that high temperatures increased the time required for sporangial germination but did not give details.

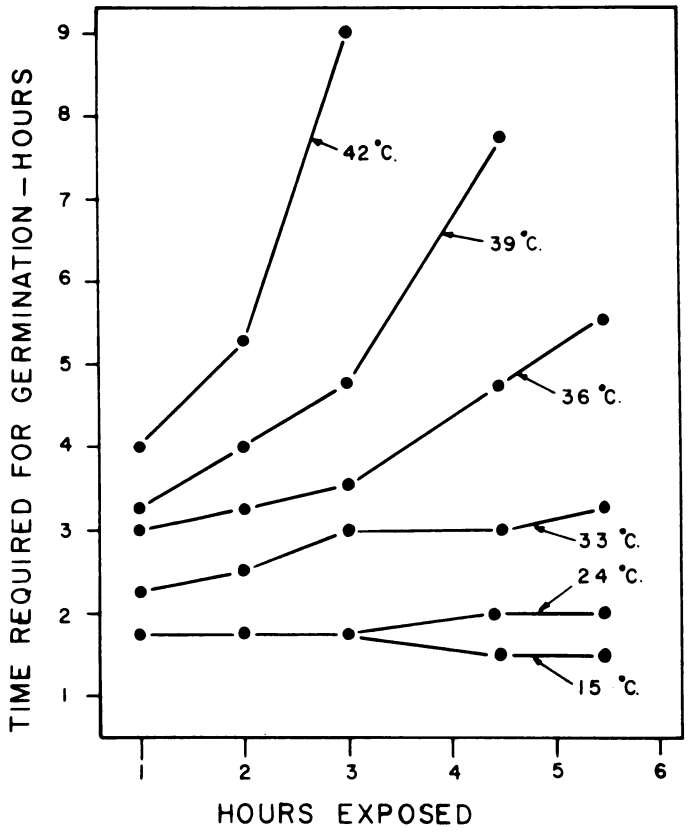

Fig. 9. Effect of preincubation time and temperature on sporangial germination.

Magie (1942) and Zattler (1931) reported that the time required for germination also increased with age.

Fresh sporangia were placed dry on microscope slides in 100 per cent RH Petri-dish chambers. The dishes were put into crisper humidity chambers in incubators set at 15, 33, 36, 39, and 42°C. One set of dishes was incubated at laboratory temperature (25 ± 2°C). Sporangia were removed from the slides with 0.001 M histidine at hourly intervals and incubated at 15°C to determine germination rates.

Exposure to temperatures 33°C and above, as well as longer exposure to these temperatures, increased germination time (fig. 9). The per cent germination was not decreased because over 90 per cent of the sporangia germinated in each case. The time required for germination did not increase on exposure to 15 and 24°C, even when the incubation period for the two temperatures were extended to 4 days at 15°C and 3 days at 24°C.

High temperatures after infection do not inhibit development of lesions. The possibility that paucity of lesions during dry weather resulted from exposure to high day temperatures following nights favorable for infection was investigated. Pairs of leaves in the UCD planting were inoculated with sporangial suspension at 10 p.m., and covered with plastic bags until 5:30 p.m. of the following day to insure infection. The

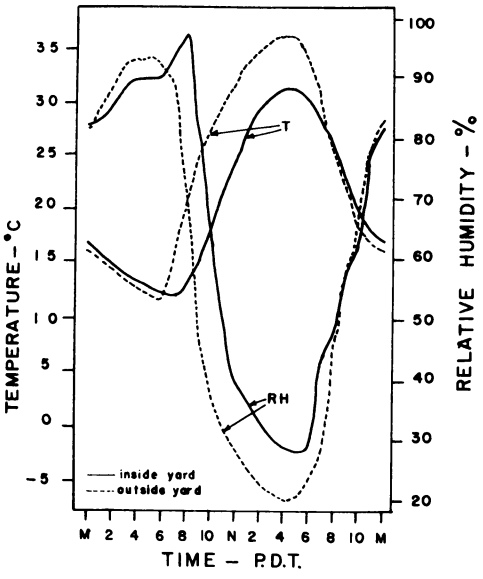

Fig. 10. Average hourly temperature and RH readings inside and outside hop yard 2 for a 2-day period beginning 2 days after irrigation. Data recorded from 9:00 a.m. July 16 to 9:00 a.m. July 23 with a Friess 7-day recording hygrothermograph. M is midnight and N is noon.

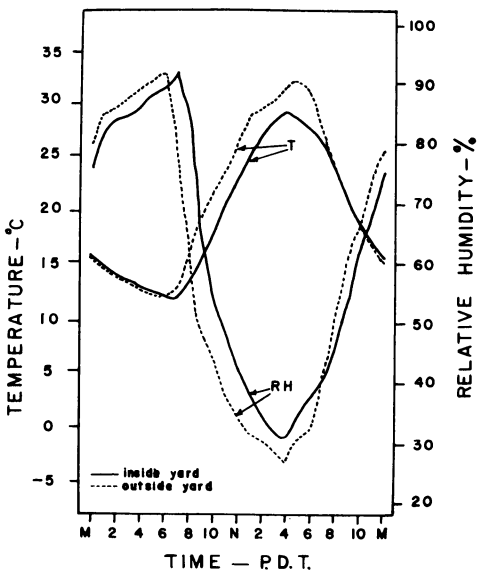

Fig. 11. Average hourly temperature and RH readings inside and outside hop yard 2 for a 6-day period beginning 2 weeks after irrigation. Data recorded from 4:00 p.m. July 31 to 4:00 p.m. August 5 with a Friess 7-day recording hygrothermograph. M is midnight and N is noon.

ambient temperature dropped from 19°C at 10 p.m. to 13°C at 2 a.m. and remained at that level until 5:30 a.m. The highest temperature the following day was 37°C and high temperatures were recorded on subsequent days. One leaf from each pair was detached and incubated at room temperature. There was no significant difference between the number of lesions developing on laboratory-incubated leaves and those left in the field.

Environment inside and outside hop yards during dry weather

Temperature and relative humidities differ between the inside and outside of hop yard. Two hygrothermographs were placed in weather shelters on 4-inch platforms, one inside yard 2 and the other 50 feet away from the yard on a bare soil surface. During a 1-week period (fig. 10) beginning 2 days after an irrigation, the average hourly temperature in the mid-afternoon inside the yard was as much as 10°C cooler than outside; at night temperatures in both areas were about the same. The RH inside the yard was higher than that outside the yard during the day and lower during most of the night. In the early morning hours, however, the RH was higher inside the yard and there was a maximum of a 2-hour delay in RH drop as compared to outside the yard. The same pattern of differences was observed when the yard was drier (fig. 11), although the differences were not as pronounced.

Temperatures of leaves at various heights in sunlight and shade. Leaf and air temperatures in sun and shade were compared. A thermocouple lead from a Leeds Northrup potentiometer coated with white paint to reflect sunlight was inserted through the main lobe of a leaf about 1 cm from the tip, another lead was placed about 5 cm

from the leaf. Leaf temperature recordings were made in yard 1 on July 27, 4 days after an irrigation. The maximum ambient temperature recorded outside the yard was 38.9°C.

Leaf temperatures (table 6) in the sun from 10:30 a.m. through 3:00 p.m. were usually warmer than ambient air. Leaves higher above the ground were cooler than lower leaves and in a few cases cooler than the ambient air in sunlight. Shaded leaves were always cooler, sometimes as much as 4°C, than ambient shade temperature; even during the warmest period of the day, temperature of shaded leaves did not go above 32°C. Most leaves were intermittently in the sun and in the shade. Sporangia deposited on these leaves would be subjected to warm temperatures during some part of the day.

Temperature and RH profiles over wet and dry soils differ. Measurements of RH and temperature were made on August 5 from 3:45 p.m. to 4:15 p.m. when RH was usually the lowest and temperature highest. Over dry soil, air temperature in sun and in shade was warmer near the soil than at higher levels (fig. 12). Over wet soil, air temperature in sunlight was warmer near the soil. Air temperature in the shade did not differ with increasing height (fig. 12). RH was lower with increasing height over moist soil, and higher with increase in height over dry soil. RH over wet soil was higher than that over dry soil, as expected (fig. 13). Leaves near moist soil are in a more moist microclimate than instruments measuring ambient conditions would suggest; over dry soil, the opposite is true.

TABLE 6
SUNLIT AND SHADED HOP LEAF TEMPERATURES ON JULY 27 IN A COMMERCIAL YARD FLOOD-IRRIGATED 5 DAYS PREVIOUSLY

Time	Sunlit leaves			Shaded leaves		
	Height* of leaf	Leaf temperature	Air temperature	Height of leaf	Leaf temperature	Air temperature
	cm	*°C*		*cm*	*°C*	
9:45 a.m.	10	24.0†	23.9†	10	21.3†	23.8†
	—	—	—	10	22.2	24.2
10:30 a.m.	3	32.8	30.0	10	22.3	24.8
	10	26.8	26.8	15	22.8	24.3
	10	29.5	27.8	—	—	—
11:30 a.m.	3	38.0	34.3	8	25.8	27.8
	10	32.1	30.8	10	26.8	30.8
	15	33.1	30.5	—	—	—
	90	31.3	30.6	—	—	—
2:00 p.m.	10	38.0	36.3	5	31.0	33.0
	—	—	—	20	31.3	35.3
	—	—	—	30	30.8	35.0
2:30 p.m.	8	39.3	37.3	—	—	—
	20	39.0	39.5	—	—	—
	30	36.5	35.8	—	—	—
3:00 p.m.	7	40.3	39.0	7	31.7	34.7
	10	37.3	38.5	7	31.8	34.7
	25	36.8	38.0	20	31.8	35.7
5:30 p.m.	3	34.5	33.3	10	27.9	29.8
	10	34.0	35.5	2	28.5	30.8
	30	33.2	34.9	30	27.7	30.9
	45	34.3	35.5	—	—	—
6:30 p.m.‡	—	25.5§	28.1	7	26.5§	28.1
9:00 p.m.‡	—	—	—	10	19.1	19.1

* Height = height of leaf above soil.
† Average of three readings.
‡ 6:30 p.m. = only diffuse light on leaves; 9:00 p.m. = dark.
§ Readings = average of three leaves.

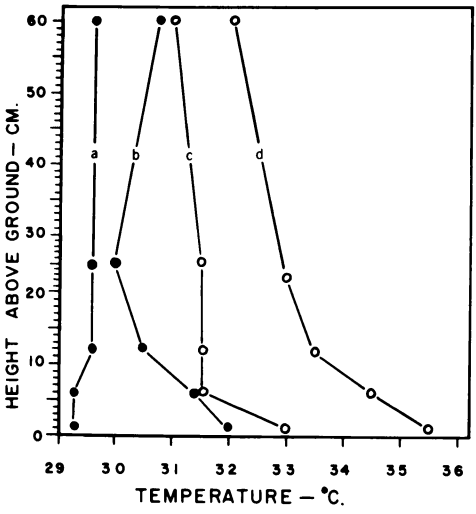

Fig. 12. Temperature profiles above soils irrigated 7 days and 24 days, previously. Temperatures measured with Atkins Model F01–F46 relative humidity gun from 3:45 to 4:15 p.m. on August 5; a: over moist soil in the shade; b: over moist soil in sun; c: over dry soil in the shade; d: over dry soil in sun.

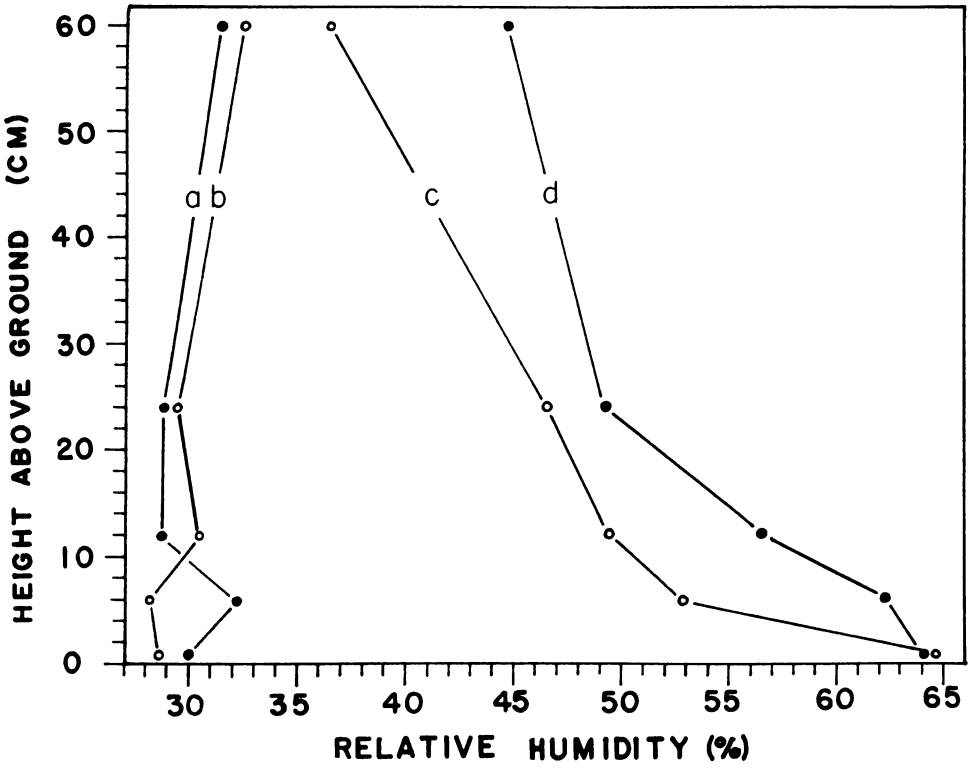

Fig. 13. Relative humidity profiles above soil irrigated 7 days (moist) and 24 days (dry) before measurements. RH determined with Atkins Model F01–F46 relative humidity gun from 3:45 to 4:15 p.m. on August 5; a: over dry soil in sun; b: over dry soil in shade; c: over moist soil in sun; and d: over moist soil in shade.

DISCUSSION

Frequent irrigation during the dry hot summer in Sacramento Valley hop yards favors survival of hop shoots systemically infected with *P. humuli*. In well-irrigated commercial yards, fungal sporulation occurs nightly on infected shoots throughout most of the growing season. For several days after an irrigation in both well-irrigated and dry yards, there was an abundant supply of free moisture in the form of dew and guttation fluid at night. Even under these apparently favorable conditions the increase in incidence of hop downy mildew was nearly nil during dry weather in well-irrigated yards. There was less disease in yards allowed to remain dry for a longer time between irrigations.

Most sporangia in the UCD planting were released beginning at about 7 a.m. Peak collection by the Hirst spore trap occurred about 8 a.m. on most days. Only a few sporangia were collected after 5 p.m. Data from inside commercial yards indicated that sporangia were released beginning at 9 a.m. Ambient RH in both locations decreased rapidly; thus, freshly released sporangia would not be expected to live long after 9 a.m. in the UCD planting and after 11 a.m. in commercial yards. If sporangia are exposed to the environment outside the yard they are quickly killed. In order to survive through the day and to be effective propagules, sporangia must have a RH high enough to allow their survival until the next period of free moisture.

If sporangia are to serve as inoculum for infection on the morning they are released, free moisture must occur concurrently on the leaves for about 2 hours. In both the UCD planting and in commercial yards, sporangial release and dew occurred concurrently for only 1 to 1½ hours. Thus the possibility of infection from fresh sporangia deposited with dew is limited. The possibility of infection in guttation fluid by fresh sporangia in commercial yards was also limited because guttation fluid usually evaporated within 2 hours after the first release of sporangia. When sporangia were inoculated onto leaves with guttation fluid an hour before the expected time of sporangial release no infection occurred, but when inoculations were made 2 hours before expected sporangial release [only] a few lesions developed.

If sporangia on a leaf do not germinate in the morning they are released, a few can survive until the next period favorable for germination and infection, but germination can be delayed because they have been subjected to high temperatures.

In the late afternoon most of the sporangia remaining on source leaves were detached and viability reduced from exposure to higher temperatures. A few of these sporangia may be released from leaves in the evening when ambient RH is rising and becoming favorable for survival. These few sporangia may land on a leaf and initiate infection when dew guttation fluid is present.

Survival of sporangia on source leaves and target leaves may be enhanced by the higher RH near the soil surface over recently irrigated soil. Survival on the lower surface is possible even under fairly dry conditions, but survival on the upper surface probably depends on RH near the leaf surface.

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LITERATURE CITED

ARENS, K.
1929. Untersuchungen uber *Pseudoperonospora humuli* (Miy. u. Takah.) Wilson, den Erreger der neuen Hopfenkrankheit. Phytopath. Z. **1**: 169–93.

CLAYTON, E. C.
1928. Cucumber disease investigations on Long Island. New York State Agr. Expt. Sta. Bul. **558**. 22 p.

DORAN, W. L.
1932. Downy mildew of cucumbers. Massachusetts Agr. Exp. Sta. Bul. **283**. 22 p.

DUVDEVANI, E., I. REICHERT, and J. PALTI.
1946. The development of downy and powdery mildew of cucumbers as related to dew and other environmental factors. Palestine J. Botany, Rehovot Series **5**: 127–51.

FRAMPTON, V. L., and K. LONGREE.
1941. The vapor pressure gradient above a transpiring leaf. Phytopathology **31**: 1040–42.

HIRST, J. M.
1952. An automatic volumetric spore trap. Ann. Appl. Biol. **39**: 257–65.
1953. Changes in atmospheric spore content: diurnal periodicity and the effects of weather. Brit. Mycol. Soc. Trans. **36**: 375–93.

MAGIE, R. O.
1942. The epidemiology and control of downy mildew on hops. New York State Agr. Exp. Sta. Tech. Bul. **267**. 49 p.

OGAWA, J. M., and D. H. HALL.
1964. Epidemiology and control of hop downy mildew in California. Hop Disease Conference, East Malling Research Station and Wye College, England. 5 pp. multilith.

OGAWA, J. M., D. H. HALL, and P. A. KOEPSELL.
1967. Spread of pathogens within crops as affected by life-cycle and environment. p. 247–267. *In* P. H. Gregory and J. L. Monteith (eds.) Airborne Microbes: Seventeenth Symposium of the Society of General Microbiology, Cambridge University Press, London.

OSBORNE, T. S., and J. A BACON.
1961. Two improved and inexpensive systems for moisture stabilization in seeds and other tissues. Plant Physiol. **36**: 309–12.

PINCKARD, J. A.
1942. The mechanism of spore dispersal in *Peronospora tabacina* and certain other downy mildew fungi. Phytopathology **32**: 505–11.

ROYLE, D. J.
1968. Diurnal and seasonal fluctuations in spore concentrations of airborne hop pathogens. Rep. Dep. Hop Res. Wye College for 1967. p. 49–56.
1970. Infection periods in relation to the natural development of hop downy mildew (*Pseudoperonospora humuli*). Ann. Appl. Biol. **66**: 281–91.

SALMON, E. S.
1928. The downy mildew of hop. The Brewers Jour. **1928**: 1–4.

SCHNATHORST, W. C.
1960. Relation of microclimates to the development of powdery mildew of lettuce. Phytopathology **50**: 450–54.

SKOTLAND, C. B.
1961. Infection of hop crown and roots by *Pseudoperonospora humuli* and its relation to the crown and root rot and overwintering of the pathogen. Phytopathology **51**: 241–44.
1962. Factors affecting sporulation and infections by the hop downy mildew fungus, *Pseudoperonospora humuli*. Phytopathology **52**: 153. (Abstract.)

SONODA, R. M.
1969. Ecological studies on the downy mildew of hop. Ph.D. Thesis. University of California, Davis. 183 pp.

YARWOOD, C. E.
1939. Relation of moisture to infection with some downy mildew and rusts. Phytopathology **29**: 933–45.

YARWOOD, C. E., and W. E. HAZEN.
1944. The relative humidity at leaf surfaces. Amer. J. Botany **31**: 129–135.

ZATTLER, F.
1931. Uber die Einflusse von Temperatur und Luftfeuchtigkeit auf Keimung und Fruktifikation von *Pseudoperonospora humuli* und auf das Zustandekommen der Infektion des Hopfens. Phytopath. Z. **3**: 281–302.

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survive on hop leaf surfaces through favorable RH conditions, and they initiate infection during the following dew period. Sporangia survived better on the lower surface than on the upper surface because of higher RH.

Sporangia exposed to temperatures of 36, 39, and 42°C had delayed germination when subsequently placed in environments optimum for germination (temperatures of exposed leaves in the yards occasionally exceed 33°C during the day).

The studies indicate that both inoculum and free moisture are present in the yards and can establish new infections, but that they do not occur concurrently long enough to start epidemics. In the event of summer rains, however, even these few infections can provide sufficient inoculum for an epidemic.

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