Powdery Mildew of Sweet Cherry: Influence of Temperature and Wetness Duration on Release and Germination of Ascospores of *Podosphaera clandestina*

Gary G. Grove

Assistant plant pathologist, Washington State University Tree Fruit Research and Extension Center, 1100 N. Western Ave., Wenatchee, WA 98801.

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ABSTRACT

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The effects of temperature and wetness duration on release and germination of ascospores of *Podosphaera clandestina*, causal agent of sweet cherry powdery mildew, were determined in controlled-environment studies. Ascospore release occurred in the presence of free water at temperatures between 5 and 30 C and at wetness durations as short as 1 h. Spore release increased rapidly between 2 and 4 h wetness durations, and after 8 h was optimal at 15–20 C. Ascospore release did not occur at relative humidities of 90–100% at 15–25 C; release occurred, however, when cleistothecia previously exposed to high humidities were moistened with water and reincubated at 15 C. A multiple regression equation using temperature and wetness duration as independent variables adequately described ascospore release. Ascospore germination was observed after 8 h at 25 C and after 16 h at 15 and 20 C. Germination was optimal at 25 C, but never exceeded 30%. A multiple regression equation with temperature and wetness duration as independent variables adequately described ascospore germination. Field trapping of ascospores occurred over a range of temperatures at wetness durations as short as 1 h, but generally after 3–4 h. Ascospores were trapped only during periods of wetness initiated by rains exceeding 2.8 mm.

Epidemics of sweet cherry (*Prunus avium* L.) powdery mildew, which in eastern Washington are caused by *Podosphaera clandestina* (Wallr.:Fr.) Lév., have occurred within the state in recent years (7). Cleistothecia of *P. clandestina* were recently shown to be the sole source of primary inoculum for epidemics of the disease (7). Cleistothecia form on infected leaves and overwinter on senescent leaves on the orchard floor or trapped in tree crotches, in partially decomposed leaf litter trapped in tree crotches, and in bark fissures. In spring, leaves are infected by ascospores that are discharged during rain or during wetness periods initiated by rain (7). Mildew colonies resulting from primary infection are generally first observed in late April to early May and are present on leaves of sucker shoots at tree bases, on leaves originating from and positioned close to main scaffold branches, or on leaves positioned near tree crotches. The sporulating primary mildew colonies are a potential source of secondary inoculum for the subsequent foliar infections, the incidence and severity of which increase during the subsequent 6–8 wk fruit development period. Yield losses to the disease are most severe when fruit infection occurs. Commensurately, these losses are most severe in orchards where foliar mildew is prevalent before rains that apparently promote the infection of fruit by conidia.

It is likely that fruit losses could be reduced by lowering the amount of inoculum available for secondary infection (i.e., by adequate control of foliar mildew). During most years, primary mildew is present in the orchard at the time of the initial fungicide application, which is generally made at shuck fall. Subsequent applications are made at 10- to 14-day intervals. During years of high disease pressure, this program fails to result in adequate control of foliar mildew. Lack of control could be due, in part, to the initial application being too late to delay the onset of epidemics. It is possible that an earlier application of fungicide during or soon after conditions conducive to primary infection could prevent infection, delay the onset of epidemics, and subsequently reduce the amount of secondary inoculum available for subsequent infection of foliage and fruit. Other than what was reported previously (7), there is no information on the meteorological factors governing primary infection of cherry by *P. clandestina*. The purposes of this study were to determine the effects of temperature, wetness duration, and relative humidity on ascospore release and germination and to investigate meteorological influences on ascospore release in the orchard.

MATERIALS AND METHODS

Controlled-environment studies. Senescent leaves infected by *P. clandestina* were collected from the floor of a previously described sweet cherry (cv. Bing) orchard near Malaga, WA (7) on 1 April 1988. Trees were at bud burst at the time of leaf collection. Leaves were examined microscopically for the presence of cleistothecia, and 50 leaves with abundant cleistothecia were then selected for use in the temperature-wetness duration experiments. Infested leaves were air dried 24 h on a laboratory bench and then comminuted (while dry) 2 min at high speed in a Waring blender. The resultant leaf powder was then transferred to a polyethylene bag, shaken vigorously for 5 min, and stored in darkness at 3 C.

For each temperature tested, 3.0 g of leaf powder was suspended in 125 ml of sterile distilled water, shaken vigorously, and then vortexed at high speed for 20 s. The suspension was poured over nested 0.047- and 0.120-mm mesh sieves, and washed for 5 min with tap water. The debris collected on the larger sieve was discarded, and the debris collected on the smaller sieve was backwashed into a beaker with 1,500 ml of sterile distilled water. Thirty-milliliter aliquots were filtered onto #2 filter paper contained in a Büchner funnel. Each filter paper disk was attached (with the side bearing cleistothecia facing downward) to the inside of a glass petri plate bottom with a layer of high-vacuum silicone grease and inverted over a single 76- × 50-mm glass slide contained in a petri plate top. Immediately before inversion over glass slides, the filter paper disks were moistened with sterile distilled water delivered by an atomizer. Petri plates were sealed in clear polyethylene bags, placed in an incubator in darkness, and incubated for wetness periods of 1, 2, 4, 8, 16, and 24 h at 5, 10, 15, 20, 25, and 30 C. Two incubators were used for the study. The

incubator used for each temperature and the order of temperatures tested were random. Four replicates of each temperature and wetness duration were sampled. The experiment was designed as a two-factor experiment with four observations in each treatment. Temperatures within each incubator were continuously monitored with thermistors connected to a CR-21 Datalogger (Campbell Scientific, Logan, UT).

After each respective wetness period, four plates were randomly selected from the group, and the glass slides were removed. Immediately after removal from petri plates, a voltmeter was used to detect the presence of free water on slide surfaces. Beginning at the center of the slide, resistance readings were taken with the probe ends 1, 2, 3, and 7 cm, and 1, 2, 3, and 5 cm apart when measuring along the long or short axes of the slide, respectively. Readings ranging from 150 to 450 kΩ were considered wet. Ascospores were then stained by placing several drops of lactophenol on each slide. To avoid washing spores off the slide, one end of each coverslip was placed on the slide while the other end was tilted upward at a 30 degree angle. The tilted end of the coverslip was then gently lowered onto the slide with a needle probe. Three 50- × 25-mm coverslips were used to cover each slide surface. The number of ascospores present and the proportion of those germinated, as well as the number of cleistothecia suspended over each glass slide, were recorded by microscopic observation. A second trial of the experiment was conducted with leaves collected 7 April 1988.

In a second study, leaves collected as described previously were air dried 24 h on a laboratory bench. Leaves were examined for the presence of cleistothecia. Individual leaves bearing numerous cleistothecia were then attached (with the side bearing the most cleistothecia facing downward) to single glass petri plate tops with a layer of silicon grease. Glass slides (76 × 50 mm) were each placed on a metal screen contained in 10- × 9.5-cm (diameter × height) glass dressing jars and positioned about 2.0 cm above the surface of 50-ml solutions of anhydrous glycerol and sterile distilled water mixed in proportions to attain relative humidities of 90, 95, 97.5, and 100% (1,16). Leaves were inverted over slides and the petri plate tops secured to the incubation jars with large rubber bands. Jars were placed in cylindrical petri plate sterilization cans and incubated 24 h at 15, 20, and 25 C in a circulating water bath. Two leaves were used at each temperature and relative humidity point. At the end of the incubation period, slides were prepared for microscopic observation as described and observed for ascospore release and germination. After incubation over humidifying solutions, leaves were moistened to runoff with sterile distilled water delivered from a atomizer and inverted over glass slides as previously described in the temperature and wetness duration experiments. Leaves were incubated 24 h at 15 C. After incubation, the slides were prepared for examination as described previously, and the number of ascospores released was recorded. After observation, a voltmeter was used as described above to detect the presence of free water. The experiment was repeated with leaves collected 7 April 1988. The experiment was designed as a two-factor experiment with two observations in each treatment.

Field studies. Senescent, infected leaves were collected in the same test orchard on 1 October 1987 and 1988 and examined at ×40 for the presence of cleistothecia. About 500 leaves with cleistothecia were placed in a cage consisting of two circular pieces of chicken wire 1.2 and 1.5 m in diameter and 0.3 m in height (Fig. 1) at the Tree Fruit Research and Extension Center (TFREC), Wenatchee, WA. The ends of each respective piece were welded together to form a circle. The smaller piece was placed inside the larger one and fastened with several sections of equally spaced welding rod. Leaves were situated between the two circular pieces. A Burkard volumetric spore trap (Burkard Mfg. Co. Ltd., Rickmansworth, Hertfordshire, UK) was placed on the ground in the center of the 1.2-m-diameter opening inside the cage, adjusted to sample 10 L of air per minute, and operated continuously from 15 March to 1 June. A CR-21X Datalogger positioned 3 m from the cage provided continuous measurements of temperature, relative humidity, and leaf wetness. Sensors connected to the Datalogger were attached to the upper edge of the cage and positioned about 0.5 m above the orchard floor. A National Weather Service weather station 100 m from the trap provided precipitation records. The spore trap impaction tape was retrieved and prepared for microscopic examination as described previously (7).

Data analyses. Because the number of cleistothecia suspended above each glass slide varied from 86 to 343, the number of ascospores on each slide was divided by the number of cleistothecia (divided by 100) suspended above. Spore release (Y) was therefore expressed as the number of ascospores released per 100 cleistothecia. Because Y was expressed as a proportion, and to stabilize variances, it was transformed by 2*arcsin $\sqrt{Y}$ (15). The effects of temperature (T) and wetness duration (W) were evaluated by using a best subsets regression approach. Terms evaluated in the initial analyses were combinations of T, W, TW, T^2, T^3, T^2W, and T^3W. Subsets were initially evaluated for coefficients of determination (R^2), R^2 adjusted for degrees of freedom (R_a^2), and standard errors (s) about the regression curves (12,15). Residual patterns of best subsets were then evaluated for randomness and normality (12,15). Several subsets gave coefficients of determination ranging from 0.60 to 0.70, but residual plots followed a nonrandom pattern. To linearize the relationship between Y and W, W was transformed by $\log_{10}$, and best subsets regressions were performed on all possible combinations of T, $\log_{10}W$, $T(\log_{10}W)$, $T^2(\log_{10}W)$, and $T^3(\log_{10}W)$. Equations were evaluated as previously described. When a suitable regression model was found, an F-test was conducted to determine if results from the two trials were significantly different (14) and to determine if pooling the data was warranted.

Best subsets regression analysis also was used to determine the effects of temperature (T) values of 15–25 C and wetness

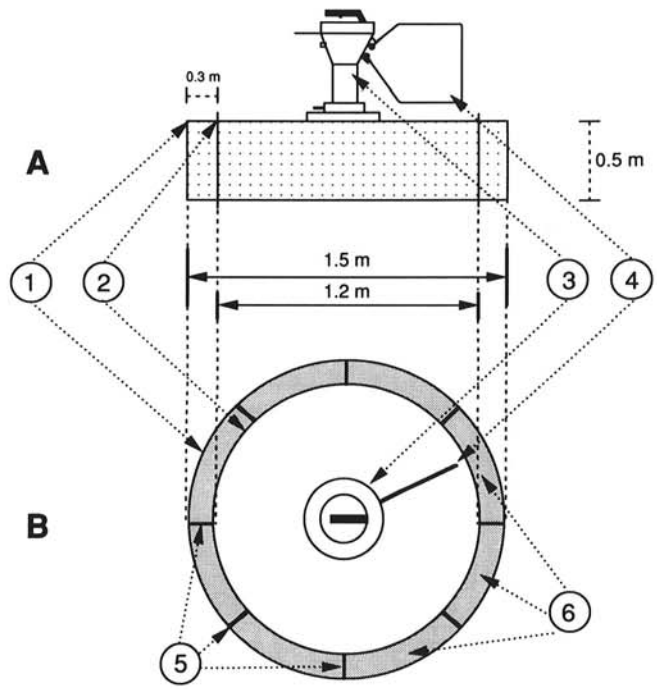

Fig. 1. Side (**A**) and top (**B**) views of cage used for *Podosphaera clandestina* ascospore trapping studies in 1988 and 1989. The circular cage was formed with two pieces of chicken wire 1.2 and 1.5 m in length. The ends of each piece were welded together to form circles. The smaller circular segment (2) was placed inside the larger circular segment (1); the top and bottom of the two segments were fastened together with several pieces of welding rod (5) thus forming a circular semi-rigid cage. A Burkard volumetric spore trap (3) was placed in the center of the enclosed space to allow for free rotation of the spore trap wing (4) and was operated continuously. Senescent sweet cherry (cv. Bing) leaves bearing cleistothecia of *P. clandestina* were placed in the 0.3-m space (6) enclosed by the two circular segments. The lightly stippled area represents cage sides; the darkly stippled area represents enclosed space where leaves were placed.

durations (W) of 8–24 h on the proportion of ascospores germinated (Y). Independent variables evaluated were all possible combinations of T, W, TW, T^2W, and T^3W. Subsets were evaluated as described previously. To determine if pooling the data was warranted, an F-test was conducted to determine if the results of the experiments were significantly different (14). All statistical analyses were conducted with Minitab Data Analysis Software (Minitab Inc., State College, PA).

RESULTS

Controlled-environment studies. The F-test indicated that the results of the two trials were not significantly different ($P < 0.05$, $F = 2.49$), therefore the data were pooled and observed ascospore release proportions are expressed in Figure 2 as the mean of the two trials. Ascospore release occurred at all temperatures tested and at wetness durations as short as 1 h. Ascospores were observed singly or in groups of three to eight. In general, release increased with increasing wetness durations. At 5 C, values ranged from 1.2 ascospores per 100 cleistothecia after 1 h to 21.9 ascospores per 100 cleistothecia after 24 h. At the optimum temperature of 15 C, values ranged from one ascospore per 100 cleistothecia after 1 h to 46.4 ascospores per 100 cleistothecia after 24 h. At 30 C, values increased from 0.3 after 1 h to 10.0 ascospores per 100 cleistothecia after 24 h. The largest increase in spore release occurred between 2 and 4 h wetness durations. Ascospore release did not occur at relative humidities of 90, 95, 97.5, and 100% at any of the temperatures tested. Cleistothecia moistened with water after incubation at high humidity released ascospores. The number of ascospores released per 100 cleistothecia ranged from 42 to 88 (mean: 62.4) and 31 to 94 (mean: 51.5) for trials 1 and 2, respectively.

The equation from the pooled data:

$$Y = 0.084 + 0.108\ T(\log_{10} W) - 0.0033\ T^2(\log_{10} W) \qquad (1)$$

best described ascospore release with R^2, R_a^2, and s equal to 0.80, 0.79, and 0.19, respectively. All estimated parameters were significant at $P < 0.03$. Residual patterns were random and followed a normal distribution. When the predicted Ys were back-transformed, the correlation between observed and back-transformed predicted ascospore per 100 cleistothecia values equaled 0.87. The regression equation was used to generate the response surface presented in Figure 3.

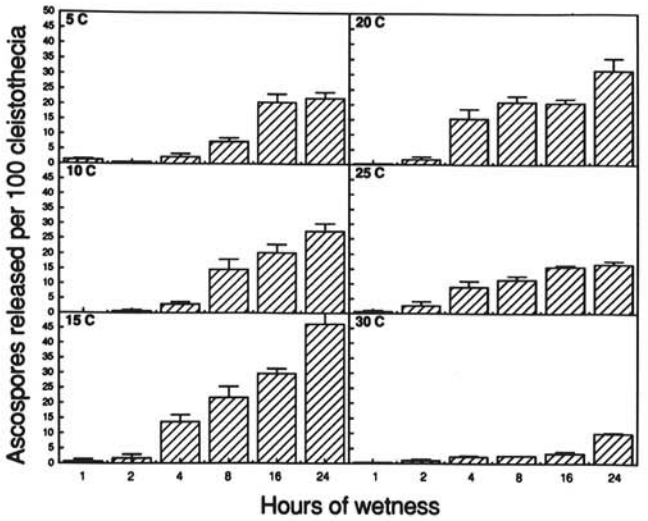

Fig. 2. Effects of temperature (C) and wetness duration (h) on ascospore release (ascospores per 100 cleistothecia) from overwintered cleistothecia of *Podosphaera clandestina* at six temperatures between 5 and 30 C and at six wetness durations between 1 and 24 h. Cleistothecia were collected from the orchard floor in Malaga, WA, and suspended over glass slides. Values given are the means of the two trials. Vertical lines above bars represent standard error.

Ascospore germination. The F-test indicated that the results of the two experiments were not significantly different ($P < 0.05$, $F = 0.37$). Therefore, the observed germination proportions in Figure 4A are expressed as the mean of the two trials. Germination was only observed at 15–25 C. Ascospore germination required an 8-h wetness duration at 25 C, and a 16-h wetness duration at 15 and 20 C. Germination values at 10, 15, and 25 C ranged from 0 to 4.2, 0.8 to 16.4, and 2.7 to 29% at 8–24 h.

The equation from the pooled data:

$$Y = -7.78 + 0.0025\ T^2W \qquad (2)$$

best described ascospore germination with R^2, R_a^2, and s equal to 0.91, 0.90, and 3.4, respectively. When the predicted Ys were back-transformed, the correlation between observed and back-transformed germination proportions equaled 0.95. Predicted germination proportions generated by the equation are presented in Figure 4B.

Resistance measurements taken from each glass slide with a voltmeter indicated the presence of free water on the surface of slides used in all temperature and wetness experiments. Free water was not detected on slides used in relative humidity experiments.

Field studies. Ascospores were trapped during both years of the study and were trapped only during wetness periods initiated by rain. In 1988, five, three, nine, and nine ascospores were trapped during 20-, 8-, 21-, and 10-h wetness periods on 1–2, 17, 21–22, and 27 April, respectively (Fig. 5). Rainfall during the respective periods measured 2.8, 6.9, 9.4, and 3.3 mm. One ascospore was trapped during the second hour of a wetness period, but in general trapping occurred after 3–4 h of wetness. Temperatures at the time ascospores were trapped ranged from 6.5 to 14.3 C. Ascospores were not trapped during 6 days in April when trace amounts of precipitation were recorded. In 1989, 14 and nine ascospores were trapped during 13 and 20 h wetness periods, which occurred on 19–20 and 26–27 April, respectively (Fig. 6). One ascospore was trapped during the initial hour of the latter wetness period, but the remainder were trapped after four or more hours of wetness. Rainfall during the respective wetness periods measured 6.6 and 13.4 mm. Ascospores were not trapped during a period several days after bud burst when 0.8 mm of rain fell; on 28

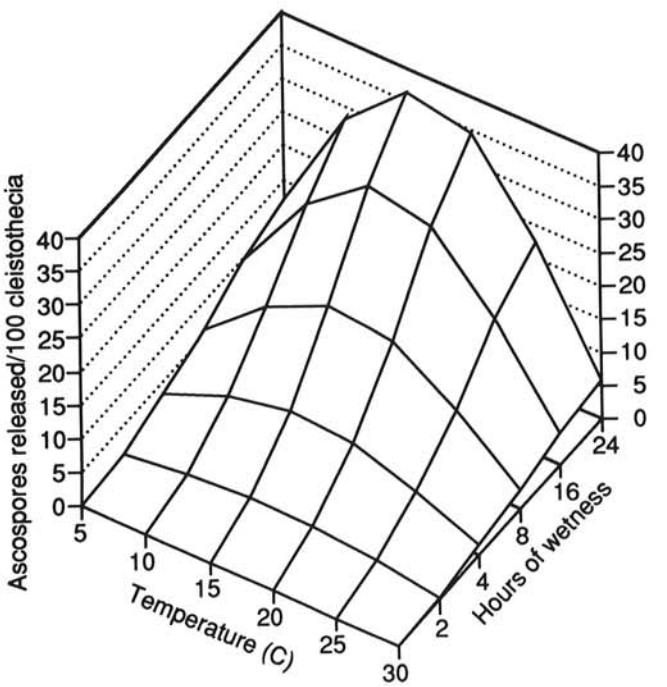

Fig. 3. Effect of temperature (C) and wetness duration (h) on ascospore release (ascospores per 100 cleistothecia) by *Podosphaera clandestina* at six temperatures between 5 and 30 C and at six wetness durations between 1 and 24 h. Response surface was generated using equation 1.

April when rainfall measured 2.04 mm, or during 6 days in April when trace amounts of precipitation were recorded. Temperatures at the time of trapping ranged from 6.2 to 18.4 C. Ascospores were not trapped during May regardless of moisture conditions.

DISCUSSION

Cleistothecia dehisced only when wet in the laboratory, and ascospores were trapped in the field only during rain or during wetness periods initiated by rain. It is apparent from this and previous studies (7) that water is essential for the release of ascospores from overwintered cleistothecia of *P. clandestina* and is additional evidence that free water is an integral component in the epidemiology of powdery mildews with functional sexual stages. Because cleistothecia are the only known source of primary inoculum in eastern Washington (7), free water must be also considered a significant factor in the management of the disease. Ascospores of *P. clandestina* were trapped in the field during rain periods of 2.8 mm or greater at temperatures between 6.2 and 18.4 C. Trapping occurred during the cherry phenophases from bud burst to the onset of full leaf and generally occurred after 4 h or more of wetness. The failure to trap ascospores on four occasions when rainfall measured between 0.25 and 2.8 mm could be due to several factors. Two of the precipitation events initiated wetness durations >3 h; in this case, the failure to trap ascospores could have been due to the airborne inoculum doses being below the 10 spores per cubic meter trapping threshold of the volumetric spore trap. Wetness durations provided by the other two rain events were <1 h in length. In this case, as in the case of trace precipitation events, the failure to trap ascospores could have been due to the insufficient wetting of senescent leaves and bark fissures on which cleistothecia overwinter. Results are

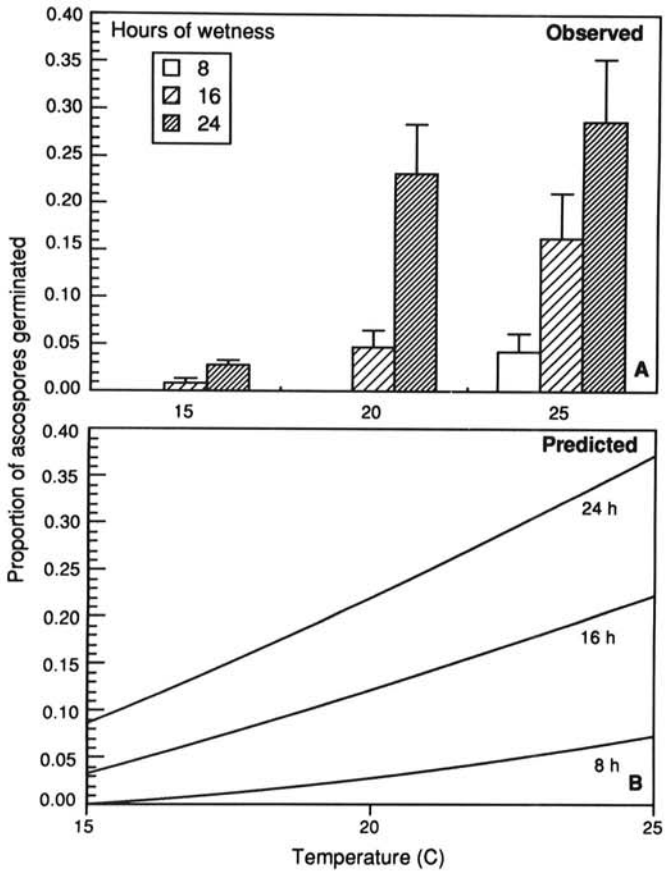

Fig. 4. Effects of temperature (C) and wetness duration (h) on observed (**A**) and predicted (**B**) germination of ascospores of *Podosphaera clandestina*. Cleistothecia were collected from the orchard floor in Malaga, WA, and suspended over glass slides. Values given in **A** are the means of the two trials. Vertical lines above bars in **A** represent standard error of mean.

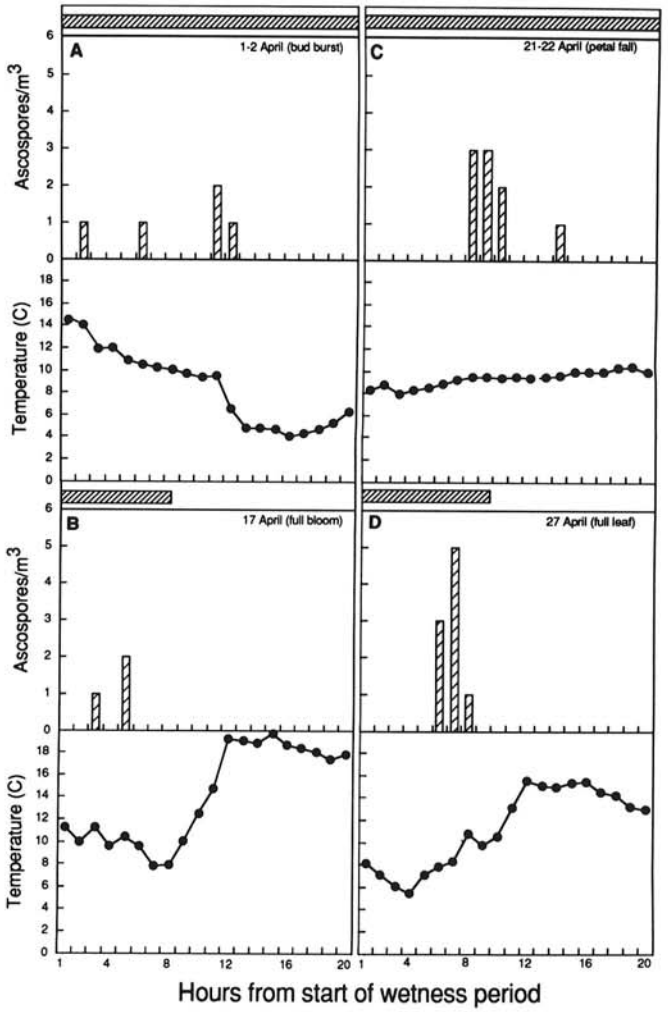

Fig. 5. Release of ascospores of *Podosphaera clandestina* in the field during four wetness periods (**A–D**) 1988. Ascospores were collected by a Burkard volumetric spore trap operated continuously. Horizontal bar above each bar graph indicates length of wetness period; line graphs beneath are temperature values over a 20-h period beginning with the onset of the wetness period.

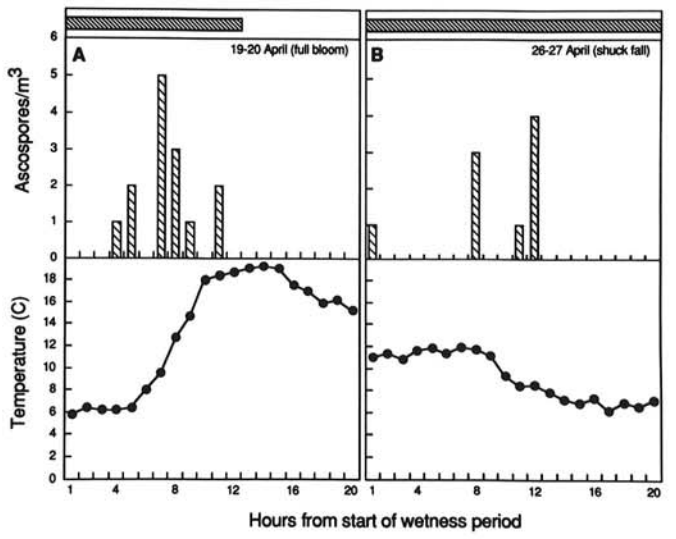

Fig. 6. Release of ascospores of *Podosphaera clandestina* in the field during two wetness periods (**A, B**) in 1989. Ascospores were collected by a Burkard volumetric spore trap operated continuously. Horizontal bar above each bar graph indicates length of wetness period; line graphs beneath are temperature values over a 20-h period beginning with the onset of the wetness period.

similar to those presented by Gadoury and Pearson (5), who reported trapping ascospores of *Uncinula necator* only during or immediately following rains of ≥2.5 mm between the grape phenophases bud burst and bloom.

Irrigation water could also provide moisture conditions necessary for ascospore release. Overtree irrigation is sometimes used for frost protection in eastern Washington when orchard temperatures reach 2 C during the bloom period. The free water provided could meet the moisture requirement necessary for ascospore release and, when temperatures the following day are warm, indirectly promote primary infection. In blocks that use undertree sprinklers or drip irrigation, the first water application is generally applied around the time that initial mildew colonies are evident in the orchard and at the time when ascocarp viability is lower (7). Traditionally, sulfur is used to control cherry powdery mildew. The initial application is generally made at shuck fall (usually about 3 wk after bud burst) during the early stages of secondary inoculum production. During years of intense disease pressure, this fails to provide adequate disease control. The data presented herein indicate that control might be more satisfactory with a more effective fungicide applied according to meteorological variables. Because wetting triggers ascospore release, the application of a fungicide in response to that wetting event may prevent primary infection and thus delay the onset of the epidemic. In this instance, the fungicide of choice would be one with postinfective activity. The rationale for this approach has precedence in the work of Gadoury and Pearson (4,6) for the control of grape powdery mildew in New York.

Ascocarp dehiscence and ascospore release by other fungi of the Erysiphaceae require high relative humidity or free water (2,3,5,7–9,10,13,17,18) and generally can occur during brief exposures to free water. Ascospore discharge from *Erysiphe trina* ascocarps commences within 10 min of wetting (18). Ascocarp dehiscence by *U. necator* (5) and *Sphaerotheca humuli* (11) reportedly occurs at wetness durations as short as 2 h. Release by *Erysiphe cichoracearum* commenced at wetness durations < 6 h (2) and was later demonstrated to be related to the number of hours of incubation in a saturated atmosphere at temperatures above 5 C (3). It was evident in this study that a few ascospores of *P. clandestina* are released within the first hour of wetting, whereas the majority are released after longer periods of wetness. The reason for this is unclear, but could be attributable to the effect of overwintering conditions on the dehiscence potential of the ascocarp or factors affecting discharge of ascospores from asci.

The effects of temperature on release and/or dehiscence varies within the Erysiphaceae. Temperatures of less than 8 C have been reported to reduce ascospore release in *E. cichoracearum* (3) *S. humuli* (11), *Erysiphe graminins* f. sp. *hordei* (13) and *U. necator* (5). Optimum spore release temperatures of 16–20, and 18 C have been reported for *E. graminis* f. sp. *hordei* (13) and *S. humuli* (11). Ascospore release by *E. cicoracearum* (3) was optimal at 20 C, the maximum temperature studied. In *U. necator*, increasing temperature promoted the dehiscence of ascocarps during the first 4 h of wetting (5). Ascospore discharge by *P. clandestina* occurred readily at 5 C, was reduced at 30 C, and occurred optimally at 15–20 C. With *P. clandestina*, as with *E. cichoracearum* (3), it is unclear whether temperature affects the number of ascocarps that dehisce or the number of ascospores that are discharged from the ascus or asci of individual ascocarps of the former and latter, respectively.

Ascospore germination by *P. clandestina* occurred between 15 and 25 C and required longer wetness durations at 15 C than at 20 or 25 C; maximum ascospore germination never exceeded 30%. Ascospores of *S. humuli* germinated optimally at 18 C (11). Moseman and Powers (13) reported germination of *E. graminis* f. sp. *hordei* ascospores between 8 and 24 C with an optimum of 16 C . Although it is not certain if water condensed uniformly on each glass slide in this study, voltmeter readings and the presence of numerous water drops on each slide after removal from incubation chambers indicated that free water and/or high relative humidity does not deleteriously affect *P. clandestina* ascospores as it affects those of *E. trina* (18). Structures similar to those reported for *E. trina*, which were thought to be lysed ascospores, (18) were not observed in this study. Gadoury and Pearson (6) reported *U. necator* ascospore germination only in the presence of free water before April; after April, germination occurred at vapor pressure deficits as high as 1.4 kPa. They also reported increased germination percentages as temperature increased from 10 to 23 C (6).

The temperature and wetness parameters found to be conducive to ascospore release occur commonly in eastern Washington orchards. To optimize the timing of a postinfective fungicide application, additional information on the infection of cherry foliage by the fungus is needed. In preliminary studies under controlled conditions, the optimum temperature for infection of cherry leaves by *P. clandestina* ascospores was 20 C (*unpublished*). Further studies on the effects of temperature and moisture conditions on the infection process, used in conjunction with findings presented herein, may result in fewer, more timely fungicide applications and ultimately improved control of this troublesome disease.

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