Factors Affecting Germination of Conidia of *Podosphaera clandestina* on Leaves and Fruit of Sweet Cherry

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Accepted for publication 30 July 1991 (submitted for electronic processing).

ABSTRACT

Grove, G. G., and Boal, R. J. 1991. Factors affecting germination of conidia of *Podosphaera clandestina* on leaves and fruit of sweet cherry. Phytopathology 81:1513-1518.

The effects of temperature and vapor pressure deficit on germination of conidia of *Podosphaera clandestina* on sweet cherry foliage were determined under controlled conditions. Germination occurred at vapor pressure deficits between 0 and 851 Pa and increased with decreasing vapor pressure deficit. Germination occurred at 15–30 C during 8-h incubation periods and 10–30 C during 16- and 24-h incubation periods. The optimum temperature for germination after 16 h of incubation was 25 C, but after 24 h, shifted downward to 20 C. After 24 h, germination exceeded 50% under optimum conditions of 0 Pa at 20 C. At 20 C, germination decreased from 51% at 0 Pa to 29% at 466 Pa. After 24 h, germ tube length was greatest at 25 C and was not affected significantly by increasing vapor pressure deficit. Germination on immature (green) fruit increased with incubation time and decreased vapor pressure deficit (e.g., at 0 Pa germination ranged from 8% after 8 h to 48% after 24 h). Germination on ripening fruit was lower than on green fruit and was suppressed by increasing soluble solid concentrations (e.g., at 0 Pa the mean proportion of conidia germinated equaled 26% and 2% on fruit with soluble solid concentrations of 7–14.9% and ≥15%, respectively. Multiple regression equations using temperature and vapor pressure deficit, and temperature, vapor pressure deficit, and incubation time as independent variables adequately described germination on foliage and green fruit, respectively. Multiple regression equations using vapor pressure deficit and fruit soluble solid content adequately described germination on maturing fruit.

Additional keywords: *Prunis avium*, quantitative epidemiology.

Epidemics of powdery mildew on sweet cherry (*Prunus avium* (L.) L.), caused by *Podosphaera clandestina* (Wallr.:Fr.) Lév., have occurred in Washington in recent years (9). In 1986 and 1987, Washington growers reported severe financial losses due to fruit infections that were apparently hastened by moist weather in May and June. Many growers reported the rejection of entire crops, destined for fresh market sale, due to infection by the fungus.

Powdery mildew affects foliage and less commonly fruit. The fungus overwinters as cleistothecia on the orchard floor, in tree crotches, and in bark crevices (9). Rains during April and early May promote ascospore release and primary infection (9). Primary mildew colonies first appear in late April to early May, with secondary infections of foliage continuing over the next 6–8 wk preceding harvest. The developing mildew colonies are more prevalent during moist years and are a potential source of secondary inoculum that may infect the fruit. The highest fruit losses occur in orchards where foliar mildew is prevalent during the latter 4–6 wk of fruit development. Fruit infections have traditionally been associated with rain showers that occur several days before harvest. However, outbreaks of fruit mildew after these rains are inconsistent, even when foliar mildew is prevalent. Many growers apply fungicides after these rains and still experience a large fruit loss. Mildew symptoms typically appear on ripe fruit within several days of a rain shower. The incubation period for foliar symptoms however is 7–10 days at 15–25 C (G. G. Grove, *unpublished*), which may indicate that fruit infection is occurring when fruit is less mature, and the moist weather is actually promoting sporulation and the appearance of mildew, rather than initiating the infection per se.

The purposes of this study were to determine some of the factors conducive to secondary infection, specifically: temperature and moisture requirements for germination of conidia on foliage and the effects of fruit soluble solid content and vapor pressure deficit on germination of conidia on fruit.

MATERIALS AND METHODS

Germination of conidia on foliage. *Inoculum production and harvest.* Because numerous attempts to maintain single-conidial isolates of *P. clandestina* for extended periods of time on sweet cherry trees or cherry seedlings have been unsuccessful (G. G. Grove, *unpublished*), conidia derived from a composite of isolates were used for germination studies (7,25,28). Overwintered cleistothecia were used as a primary inoculum source. During each year of the study, 10 overwintered, infested leaves bearing numerous cleistothecia were retrieved from the orchard floor of a 0.8-ha block of 35-year-old sweet cherry trees (cv. Bing) at bud burst. Each leaf was hand-macerated, placed in a plastic centrifuge tube containing 15 ml of sterile distilled water, and vortexed at high speed for 60 s. Suspensions were then combined in a flask, mixed by shaking for 60 s, and filtered in 15-ml aliquots over 10-cm-diameter filter paper disks. Each filter paper disk was then inverted over a sweet cherry seedling (cv. Bing × Van) grown, inoculated, and incubated as previously described (9). After colony establishment, a camel's-hair brush was used to distribute the conidia from a single seedling onto young leaves emerging from 2-year-old cherry trees (cv. Bing) that had grown in a 1:1:1 (v:v:v) silt loam/sand/peat mixture for 10–14 days. Trees were placed on a greenhouse bench contained in a greenhouse isolation room and were incubated 7–10 days at 20–24 C with a 16-h photoperiod. The greenhouse isolation room was isolated from other rooms by several physical (glass) barriers and by positive airflow. Subsequent conidia were brushed onto the apical leaves emerging from 20 freshly planted cherry trees. Relative humidity in the room was maintained above 85% with mist from room humidifiers and by daily saturation of the sand-filled greenhouse benches on which the trees were placed. Inoculation of freshly planted trees was performed at weekly intervals.

All inoculations were done with conidia from colonies 12–14 days old. Infected trees were shaken vigorously 24 h before harvest to remove any stale conidia (10,20). Conidia were harvested by positioning three to four infected leaves (located near stem apices) over a 0.45-mm filter contained in a vacuum filtration funnel (Gelman Inc., Ann Arbor, MI) that was, in turn, connected to an operating vacuum pump. Stem apices were gently shaken.

Inoculation and incubation. Detached leaf culture (28) was used to determine the effects of temperature and vapor pressure deficit on germination of *P. clandestina* conidia on foliage. Young, emergent but unexpanded leaves were obtained from mildew-free trees (cv. Bing) grown in a second isolation room similar to that described above. The room was separated from other rooms by several physical (glass) barriers and by positive airflow. Tree foliage was syringed with tap water every 24 h to minimize the development of mildew (G. G. Grove, *unpublished*). Terminal leaves that had not fully expanded (i.e., the angle between lamina at either side of the midvein did not exceed 45 degrees) were removed from trees. Leaf petioles were immediately placed into micropipette tips containing 1 ml of sterile distilled water. Leaf laminae were rinsed once with sterile distilled water, gently shaken, and allowed to air-dry for about 1 h in a fume hood. Leaves were inoculated by brushing freshly harvested conidia onto the lower leaf surfaces with a camel's-hair brush. Only leaf undersides were inoculated as preliminary experiments revealed that conidial germination was low on adaxial leaf surfaces (G. G. Grove, *unpublished*).

For each temperature tested, four inoculated leaves were placed in each of four 0.5-L glass jars containing 100 ml of various solutions of anhydrous glycerol and sterile distilled water mixed at proportions calculated to result in relative humidities of 80, 90, 95, and 100% (4,5,11,21,22,26). The humidities corresponded to vapor pressure deficits ranging from 0 to 239, 0 to 346, 0 to 466, 0 to 638, and 0 to 851 Pa at 10, 15, 20, 25, and 30 C, respectively. Jars were covered with plastic petri plate tops each coated on the inside with high-vacuum silicone grease. Tops were secured with large rubber bands. Abaxial leaf surfaces were kept 1–2 cm above the surface of humidifying solutions by placing the pipette tips through openings in small 0.5-cm mesh wire screens and tilting them so that the angle of the leaf petiole was about 30 degrees relative to the surface of the solution. Each incubation jar was sealed in a polyethylene bag and placed in a cylindrical petri plate sterilization can. The four cans were placed in a controlled temperature circulating water bath and incubated 8, 16, or 24 h at 10, 15, 20, 25, or 30 C. The order of temperatures tested was random. Temperature within the incubation chambers was maintained to ±0.2 C. The experiments were designed as a two-factor (temperature and vapor pressure deficit) experiment with four observations in each treatment. Temperature and relative humidity within each incubation chamber were continuously monitored with sensors (Vaisala HMP-123Y sensors, Vaisala Inc., Warburn, MA) inserted into the chambers through a small rubber grommet lining a circular opening in each petri plate top. Leaf wetness within the chambers was continuously monitored with self-constructed miniature printed-circuit leaf wetness sensors electrically similar to Campbell Scientific model 237 (P. D. Campbell, *personal communication*). Sensors were connected to a CR-21X Datalogger (Campbell Scientific, Logan, UT). At the conclusion of the respective incubation periods, leaves were removed from containers, and their abaxial surfaces were sampled using collodion membranes (7,28). Membranes were placed in several drops of lactophenol on glass slides and observed at ×160. At least 250 conidia were counted on the membrane samples from each leaf. The total number of conidia and the proportion of those germinated were recorded. A conidium was considered germinated when the germ tube length exceeded the width of the spore (12,15). For the 24-h incubation periods, the germ tube lengths of about 25 conidia per leaf were measured with an ocular micrometer. Each experiment was conducted twice.

Germination of conidia on fruit. All fruit were harvested from 50-year-old sweet cherry trees (cv. Bing) at the Tree Fruit Research and Extension Center, Columbia View Research Plot, Orondo, WA. Fungicides were not applied at any time to source trees. Green fruit were harvested from trees on 29–31 May 1989 and 1990, to determine the effects of incubation time and vapor pressure deficit on germination. Fruit were rinsed once with sterile distilled water, allowed to dry for 1 h in a fume hood, and inoculated with conidia as described previously for leaves. Fruit were placed on metal screens and incubated in the aforementioned chambers for 8, 16, or 24 h at 239, 120, 59, or 0 Pa at 20 C. The order of incubation times tested was random. Four fruit were subjected to each vapor pressure deficit. At the conclusion of the incubation period, epidermal peels were taken and prepared for microscopic examination as described above. The proportion of germinated conidia on each fruit was determined as described above.

In 1989 and 1990, fruit at varying stages of maturity were harvested periodically during the latter 3 wk of June to determine the effect of vapor pressure deficit and fruit soluble solid concentration on germination. After harvest, fruit were rinsed with sterile distilled water, allowed to dry, and then inoculated as described previously. Four inoculated fruit were placed in each incubation container and incubated 24 h at vapor pressure deficits of 239, 120, 59, and 0 Pa at 20 C. Fruit surfaces were sampled as described previously, and the proportion of germinated conidia was determined. After sampling, several drops of juice from each fruit were placed on the prism of a refractometer and the percentage of soluble solids was determined at 20 C.

Data analyses. *Germination of conidia on leaves.* Relative humidity values from each chamber were converted to vapor pressure deficit according to formulae given by other workers (24,27). Data from the different incubation times were analyzed separately. All analyses were conducted using Minitab Data Analysis Software (Minitab, Inc., State College, PA). Regression analysis was used to determine the influence of temperature (T) and vapor pressure deficit (V) on the proportion of conidia germinated (Y). Because Y was a proportion, and to stabilize variances, it was transformed using the arcsin (inverse sine or angular) transformation (18). Unless otherwise stated, Y in the following text represents the transformed value (i.e., arcsin proportion of conidia germinated). To minimize the effects of multicollinearity, temperature was expressed as deviations from the mean temperature before raising to quadratic or cubic terms (18) or before cross-multiplication with V. All possible combinations of T, V, T^2, T^3, TV, T^2V, and T^3V were evaluated for significance of regression coefficients, coefficients of determination (R^2), coefficient of determination adjusted for degrees of freedom (R_a^2), standard error (s), and pattern and distribution of residuals (14,17-18). Each analysis was done on the two trials (within each incubation period) separately, and then on the pooled data. An F test was conducted to determine whether the results from the two trials were significantly different (17) and to determine if pooling the data was warranted.

To determine the effect of temperature and vapor pressure deficit on germ tube length, the logarithm (base 10) of length (μm) was regressed on all possible combinations of T, V, and TV. Each analysis was done on the two trials separately, and then on the combined data. An F test was conducted to determine whether the results from the two trials were significantly different (17) and to determine if pooling the data was warranted.

Germination of conidia on fruit. Regression analysis was used to determine the effects of incubation time (I) and vapor pressure deficit (V) on the proportion of conidia germinated on green unripe fruit, and vapor pressure deficit and percentage of soluble solids (S) on germination on colored, ripening fruit. In the case of green fruit, Y was regressed on all possible combinations of I, V, and IV. The regressions were done on each trial separately, and then on the combined data. Equations were evaluated as described above. An F test was conducted to determine whether the results from the two trials were significantly different and to determine if pooling the data was warranted.

With colored, maturing fruit, Y was regressed on all possible combinations of V, S, and VS. Equations were evaluated as described above. The regressions were done on each trial sepa-

rately, and then on the combined data. An F test was conducted to determine if the results from the two trials were significantly different and to determine if pooling the data was warranted.

RESULTS

Germination of conidia on leaves. In general, germination increased with increasing temperature and with decreasing vapor pressure deficit, except at 10 C, at which the influence of vapor pressure deficit was less pronounced. Germination occurred at 15–30 C after 8 h and at 10–30 C after 16 and 24 h. During 8-h incubation periods, germination increased with increasing temperature and occurred at vapor pressure deficits between 0 and 851 Pa (Fig. 1). At 0 Pa, germination ranged from 4% at 15 C to 9% at 30 C. At 20–30 C, germination decreased with increasing vapor pressure deficit (e.g., at 30 C, germination decreased from 9% at 0 Pa to 6% at 851 Pa at 30 C.)

The F test ($F = 0.9$) indicated that the results of the two trials were not significantly different ($P > 0.05$). Therefore, the data were pooled, and the equation:

$$Y = 0.27 + 0.0066T - 0.00011V \quad (1)$$

described germination with R^2, R_a^2, and s equal to 0.52, 0.51, and 0.031, respectively. All regression coefficients were significant at $P < 0.001$. Residual patterns were random and normally distributed.

During 16-h incubation periods, germination occurred between 10 and 30 C and increased with decreasing vapor pressure deficit (Fig. 2A). At 0 Pa, values ranged from 5% at 10 C to 32% and 39% at 20 and 25 C, respectively. At the optimum temperature of 25 C, germination ranged from 18% at 638 Pa to 39% at 0 Pa. At the other temperatures, similar general increases in germination with decreased vapor pressure deficit were also observed. At 0 Pa at 30 C, a large proportion of conidia had lysed; wetness sensors indicated leaf wetness under those conditions. Therefore, observations from that treatment were omitted from the statistical analysis.

The F test ($F = 1.57$) indicated that the results of the two trials were not significantly different from each other ($P > 0.05$). Therefore, the data were pooled, and the equation:

$$Y = 0.55 + 0.025T - 0.00034V - 0.0023T^2 - 0.00013T^3 + 0.0000022T^2V \quad (2)$$

described germination with R^2, R_a^2, and s equal to 0.92, 0.92, and 0.038, respectively. All regression coefficients were significant at $P < 0.001$. Residual patterns were random and normally distributed. The equation was used to generate the response surface presented in Figure 2B.

After 24-h incubation periods, germination was highest at 0 Pa at 20 C; germination under those conditions exceeded 50% (Fig. 3A). Germination at 0 Pa ranged from 10% at 10 C to 51% at 20 C. At 15–30 C, germination increased with decreasing vapor pressure deficit (e.g., at the optimum temperature of 20 C, germination was 29% at 466 Pa and increased to 42, 46, and 51% at 239, 120, and 0 Pa, respectively). At 10 C, germination ranged from 10% at 0 Pa to 12% at 239 Pa. Lysed conidia were observed at 0 Pa at 30 C; wetness sensors indicated leaf wetness under those conditions. Therefore, observations from that datum point were omitted from the statistical analysis.

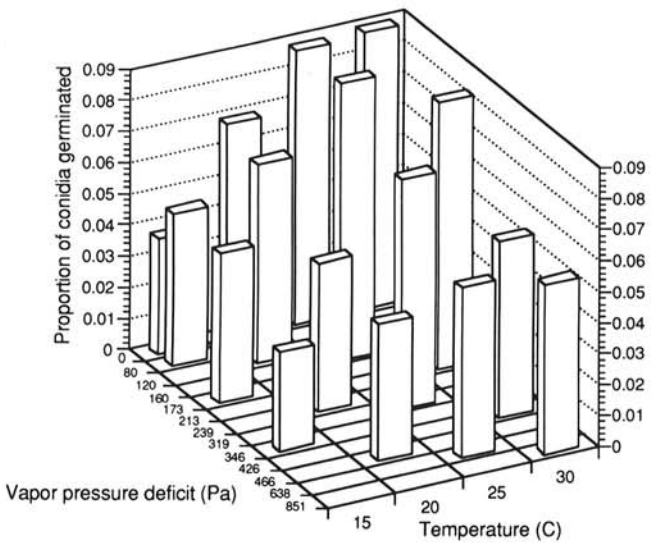

Fig. 1. Effects of temperature (C) and vapor pressure deficit (Pa) on germination of *Podosphaera clandestina* conidia on leaves of sweet cherry during 8-h incubation periods at four constant temperatures and at several vapor pressure deficits. Leaves were inoculated with conidia, incubated, and then sampled with collodion membranes. Because the F test indicated that results of two trials of the experiment were not significantly different, each datum bar represents the mean germination proportion of eight observations (four observations per trial) at each temperature and vapor pressure deficit treatment.

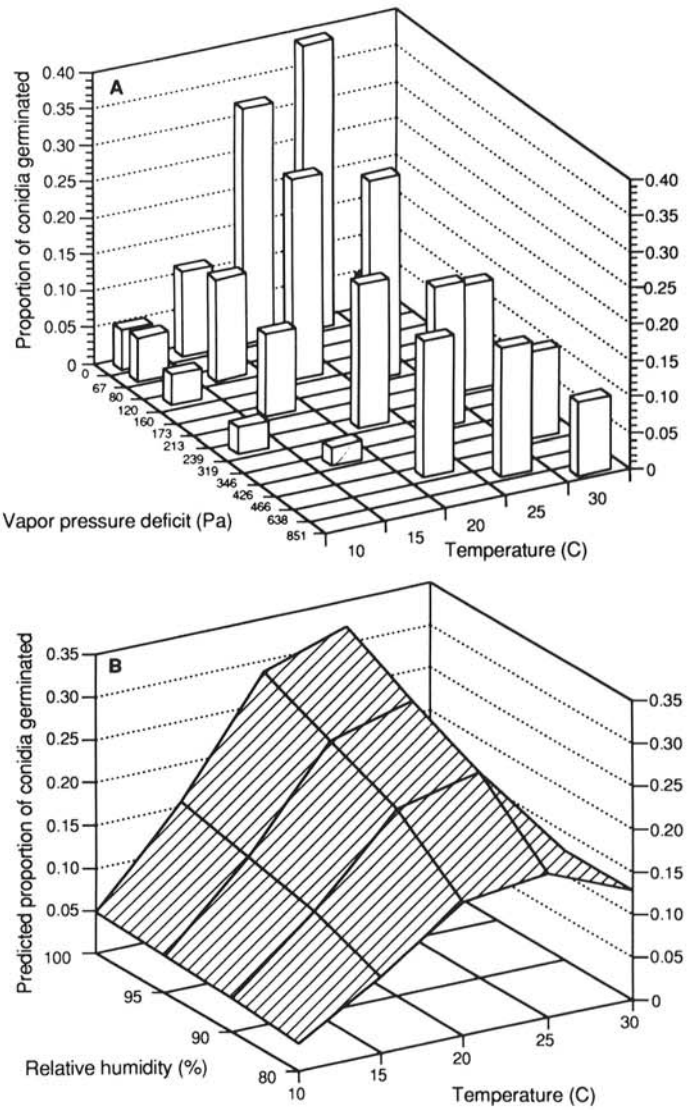

Fig. 2. Effect of temperature (C) and vapor pressure deficit (Pa) on **A,** observed and **B,** predicted germination of *Podosphaera clandestina* conidia on leaves of sweet cherry during 16-h incubation periods at five constant temperatures and at several vapor pressure deficits. Leaves were inoculated with conidia, incubated, and then sampled with collodion membranes. Because the F test indicated that results of two trials of the experiment were not significantly different, each datum bar in A represents the mean germination proportion of eight observations (four observations per trial) at each temperature and vapor pressure deficit treatment. Response surface (B) was generated using Equation 2 with parameters from the pooled data.

The F test ($F = 1.01$) indicated that the results of the two trials were not significantly different from each other ($P > 0.05$). Therefore, the data were pooled, and the equation:

$$Y = 0.77 + 0.0094T - 0.00051V - 0.0029T^2 + 0.000098T^3 + 0.0000020T^2V \quad (3)$$

described germination with R^2, R^2_a, and s equal to 0.91, 0.91, 0.048, respectively. All regression coefficients were significant at $P < 0.001$. Residual patterns were random and normally distributed. The equation was used to generate the response surface presented in Figure 3B.

In general, germ tube length increased as temperature increased up to 25 C (e.g., at 0 Pa lengths of 30, 30, 75, and 131 mm were recorded at 10, 15, 20, and 25 C, respectively (Fig. 4). Increasing vapor pressure deficit had little effect on length at 10–25 C (e.g., at 25 C, lengths of 125, 127, 139, and 131 mm at 638, 319, 160, and 0 Pa, respectively, were recorded). However, at 30 C, length decreased from 100 to 51 mm as vapor pressure deficit increased from 426 to 851 Pa.

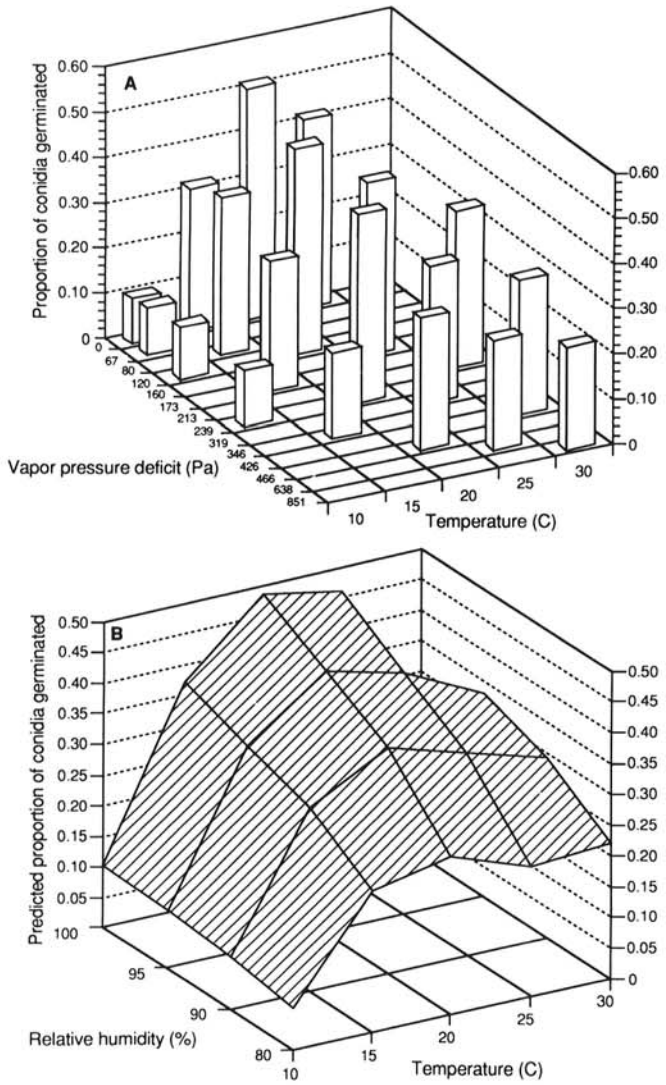

Fig. 3. Effect of temperature and vapor pressure deficit (Pa) on **A,** observed and **B,** predicted germination of *Podosphaera clandestina* conidia on leaves of sweet cherry during 24-h incubation periods at five constant temperatures and at several vapor pressure deficits. Leaves were inoculated with conidia, incubated, and then sampled with collodion membranes. Because the F test indicated that results of two trials of the experiment were not significantly different, each datum bar represents the mean germination proportion of eight observations (four observations per trial) at each temperature and vapor pressure deficit treatment. Response surface (B) was generated using Equation 3 with parameters from the pooled data.

The F test ($F = 0.10$) indicated that the results from the two trials were not significantly different from each other ($P > 0.05$). Therefore, the data were pooled, and the equation:

$$Y = 1.72 + 0.042T \quad (4)$$

(in which $Y = \log_{10}$ [germ tube length]) described germ tube lengths with R^2 and s equal to 0.81 and 0.1252, respectively. Regression coefficients were significant at $P < 0.001$. When Y was regressed on either V or TV alone, the results were insignificant ($P < 0.05$).

Germination of conidia on fruit. In general, the proportion of conidia germinated was higher on green, immature fruit than on softer, ripening fruit. On green fruit, germination usually increased with increased incubation time and decreasing vapor pressure deficit (Fig. 5). At 0 Pa, germination ranged from 2

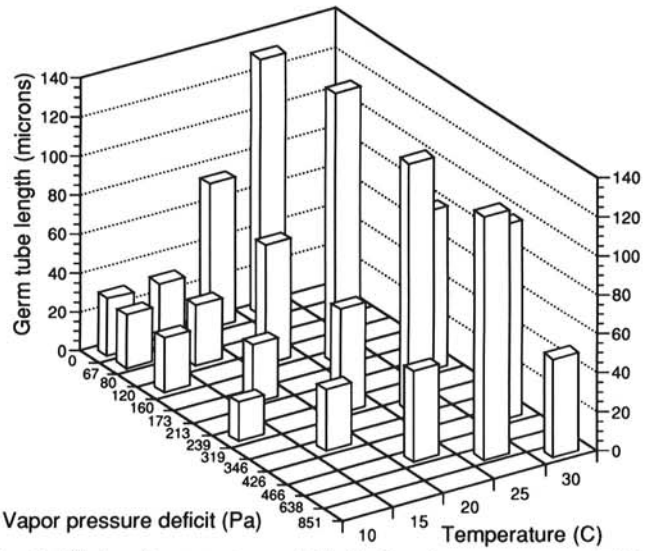

Fig. 4. Effects of temperatures of 10–30 C and vapor pressure deficits of 0–851 Pa on germ tube length of *Podosphaera clandestina* conidia on sweet cherry leaves during 24-h incubation periods. Because the F test indicated that results of the two trials of the experiment were not significantly different, each datum bar represents the mean value of both trials of the experiment and the mean germ tube length of about 50 observations (25 observations per trial) at each temperature and vapor pressure deficit treatment.

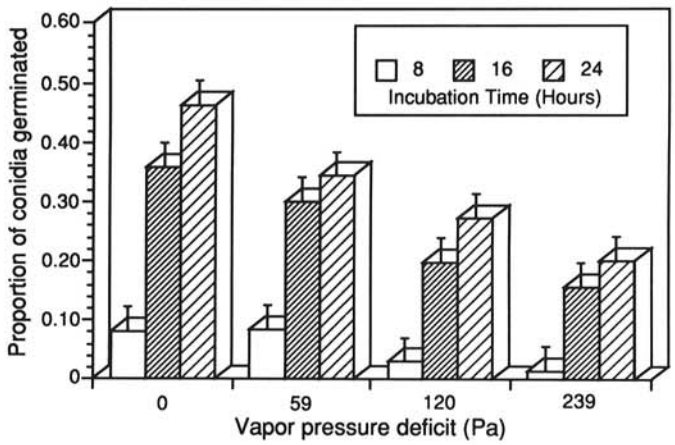

Fig. 5. Effects of vapor pressure deficits between 0 and 239 Pa at 20 C and incubation time (h) on germination of *Podosphaera clandestina* conidia on immature (green) fruit of sweet cherry at 20 C. Fruit were inoculated with conidia, incubated, and then sampled with collodion membranes. Because the F test indicated that results of two trials of the experiment were not significantly different, each datum bar represents the mean germination proportion of eight observations (four observations per trial) at each temperature and vapor pressure deficit treatment. Bars represent standard error.

to 13%, 10 to 48%, and 33 to 67% after 8-, 16-, and 24-h incubation periods, respectively. Germination after 24 h ranged from 13 to 36%, 1 to 31%, and 9 to 20% at 59, 120, and 239 Pa, respectively. The general decrease in germination with increased vapor pressure deficit was also observed at the shorter incubation periods.

The F test ($F = 0.77$) indicated that the results of the two trials on green fruit were not significantly different ($P > 0.05$). Therefore, the data were pooled and the equation:

$$Y = 0.14 - 0.00098V + 0.025I \quad (5)$$

described germination with R^2, R^2_a, and s equal to 0.73, 0.72, and 0.12, respectively. All regression coefficients were significant at $P < 0.001$. Residual patterns were random and normally distributed.

On more mature fruit, germination in general decreased with increasing vapor pressure deficit and soluble solids (Fig. 6). A noticeable decrease in germination occurred as soluble solid concentrations exceeded 15% (e.g., at 0 Pa the mean percentage of germination on fruit with soluble solid concentrations of 7–15% was about 26%). Conversely, on fruit with ≥15% soluble solids, the mean germination equaled 2%. In 1989, germination ranged from 8 to 59%, 9 to 43%, 8 to 21%, and 2 to 28% at vapor pressure deficits of 0, 59, 120, and 239 Pa, respectively, on fruit with soluble solid concentrations ≤15%. On fruit with >15% soluble solids, germination ranged from 0 to 30%, 0 to 5%, 0 to 8%, and 0 to 5% at 0, 59, 120, and 239 Pa, respectively. In 1990, germination ranged from 0 to 20% and 0 to 11% on fruit with soluble solid concentrations ≤15% or ≥15%, respectively.

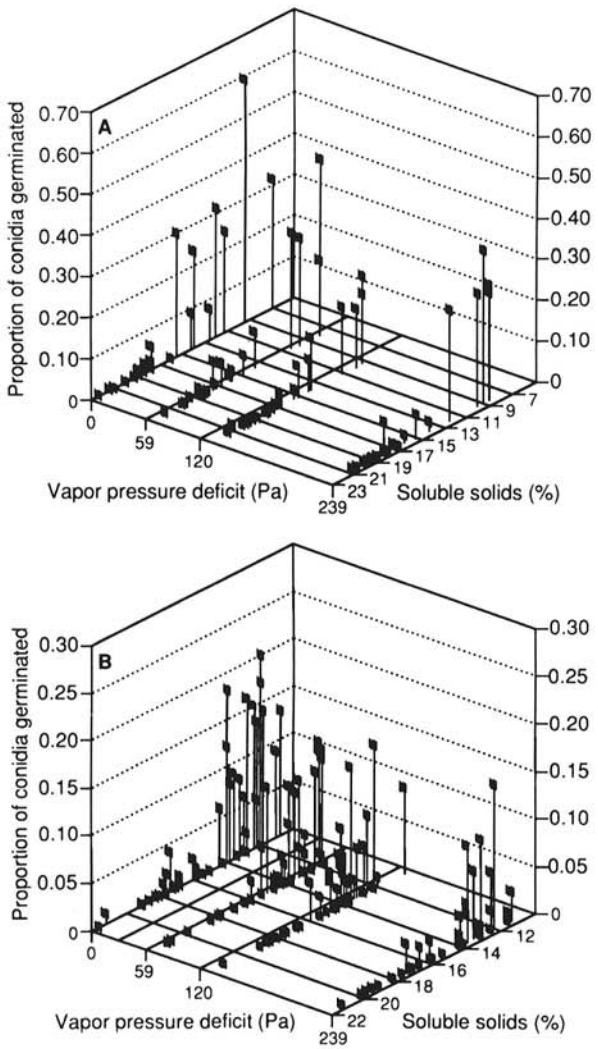

Fig. 6. Effects of vapor pressure deficits between 0 and 239 Pa at 20 C and fruit soluble solid content (%) on germination of *Podosphaera clandestina* conidia on maturing fruit of sweet cherry in 1989 (A) and 1990 (B). Fruit were inoculated with conidia, incubated, and then sampled with collodion membranes.

Regressing germination on the percentage of soluble solid concentration alone accounted for about 80% ($R^2 = 0.787$) and 50% ($R^2 = 0.484$) of the variability in 1989 and 1990 germination proportions, respectively. However, the F test ($F = 20.8$) indicated that the results from the two trials were significantly different ($P < 0.05$). The equations:

$$Y\,(1989) = 1.05 - 0.051S - 0.00031V \quad (6)$$

$$Y\,(1990) = 0.96 - 0.050S - 0.0025V + 0.016SV \quad (7)$$

described the respective 1989 and 1990 data with R^2 values equal to 0.80 ($R^2_a = 0.80$) and 0.64 ($R^2_a = 0.62$). All regression coefficients were significant at $P < 0.05$.

DISCUSSION

Temperature and vapor pressure deficit had significant effects on the germination of *P. clandestina* conidia on sweet cherry foliage. During longer incubation periods, temperature and vapor pressure deficit accounted for about 90% of the variability in the proportion of conidia germinated on foliage. On immature (green) fruit, incubation time and vapor pressure deficit accounted for more than 70% of the observed germination variation. On more mature fruit, vapor pressure deficit, fruit soluble solid concentrations, and their interactions (1990 studies only) accounted for more than 60% of the variation in observed germination proportions. The results of the 1989 and 1990 trials on maturing fruit were significantly different. This was possibly due to the range of soluble solid concentrations tested; soluble solid concentrations ranged from 7 to 22% and 10 to 24% in 1989 and 1990, respectively.

The effects of temperature, relative humidity, and/or vapor pressure deficit on germination of conidia have been reported for a number of powdery mildews, and vary within the Erysiphaceae (1–3,6–8,10,12,13,15,16,19,20,23-25,28,29). As a group, the optimum temperature for germination and growth is about 21 C (24). Optimum temperatures of 21 C have been reported for *Sphaerotheca macularis* on strawberry (20), 21–27 C for *S. pannosa* on peach (28), 20 C for *Erysiphe graminis* (15), 24 C for *E. polygoni* on red clover (25), and 18 C and 26 C for *E. cichoracearum* on lettuce and cucumber, respectively (23,24). The optimum germination temperatures for *P. clandestina* were 25 C and 20 C after incubation periods of 16 and 24 h, respectively. Similar downward shifts in the temperature response (with increased incubation time) have been reported for *S. pannosa* (13) and *E. cichoracearum* (23). The 20 C optimum temperature after 24 h was similar to the 18–20 C optima reported for germination of *P. clandestina* conidia on hawthorn leaves (12), and the 20 C reported for germination of *P. leucotricha* conidia on apple leaves (6).

As reported for *E. graminis* (15), germ tube elongation by *P. clandestina* on sweet cherry was favored by temperatures slightly higher than those for germination. However, in contrast to their findings, and to those of Nour (19), vapor pressure deficit did not have a significant effect on germ tube growth at the vapor pressure deficits tested in our study. At each temperature tested between 10 and 25 C, germ tube lengths were similar among the vapor pressure deficits tested. However, at 30 C, germ tube length decreased from 100 to 51 mm as vapor pressure deficit increased from 426 to 851 Pa. At the lower temperatures, the effects of vapor pressure deficit perhaps would have been more apparent at lower relative humidities.

Schnathorst (24), using vapor pressure deficit as a measure of moisture stress, classified the powdery mildews based on their conidial germination response to vapor pressure deficit: those that germinate only at low vapor pressure deficits; those that germinate optimally at low vapor pressure deficits, with a small proportion of conidia that will germinate at high vapor pressure

deficits; and those that germinate well over a wide range of vapor pressure deficits. Although extensive experiments on the effect of high vapor pressure deficits on germination of *P. clandestina* conidia have not been conducted, we have observed reduced germination at vapor pressure deficits as high as 1.9 and 3.4 kPa at 20 and 30 C, respectively (G. G. Grove, *unpublished*). Commensurately, germination of conidia increased as vapor pressure deficit decreased indicating that *P. clandestina* probably has affinities with Schnathorst's second group. Various reports have indicated that the negative influence of increasing vapor pressure deficit on germination is less pronounced at lower temperatures (3,15,20). In our studies, this was apparent at 10 C at which germination proportions were similar over the range of vapor pressure deficits tested.

On foliage and green fruit, germination rates were relatively low after 8-h incubation periods, but increased substantially after 16 and 24 h. In the absence of rain, orchard atmospheric humidities in eastern Washington can range from 20 to 30% during the day to 60 to 70% for several hours at night. During years when showers are absent or infrequent, foliar mildew incidence and severity are lower and fruit mildew is absent. It is possible that the increased mildew severity during moist years may be due in part to rain showers extending periods of lower vapor pressure deficit, which are conducive to conidial germination and the initiation of the infection process.

Delp (7) reported reduced infection of grape fruit by *Uncinula necator* when sugar contents were >8%. Conidia of *P. clandestina* germinated in the highest proportions on green fruit. Germination on ripening fruit was inversely correlated with increasing concentration of soluble solids; germination was negligible at soluble solid concentrations >15%. The average fruit soluble solids content of eastern Washington Bing cherries typically exceeds 15% 10–14 days before harvest. In 1990, for example, the mean soluble solid concentration was 14.9% on 13 June and increased to 19.7% on 27 June, several days before harvest. This raises interesting questions regarding the phenological timing and control of fruit infection. Powdery mildew becomes evident on fruit only when rains occur near harvest. As conidial germination during this time is negligible, it is unlikely that high-moisture conditions promote infection, but instead may promote fungal sporulation on previously infected fruit and thus the development of visible mildew on the fruit surface. Although the precise time of fruit infection was not demonstrated in this study, results indicate that the initiation of fruit infection is most likely to occur when fruit is immature. The effectiveness of the common practice of applying fungicides in response to rain immediately before harvest (when concentrations of fruit soluble solids are high) is therefore questionable unless the fungicide is an antisporulant. However, a fungicide application during this time could be useful during years when fruit of widely variant stages of maturity are present within the orchard. More effective disease control could probably be accomplished by minimizing foliar mildew and thus reducing the amount of secondary inoculum available for infection of the fruit, and by protecting immature fruit with fungicides to suppress infection.

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