

# Analysis of Factors Affecting Latent Infection and Sporulation of *Monilinia fructicola* on Prune Fruit

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## ABSTRACT

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Two studies were conducted to determine the effects of water content (WC) on sporulation on thinned fruit and the effects of wetness duration, inoculum density, and temperature on secondary infection of prune fruit by *Monilinia fructicola*, the main causal pathogen of brown rot in California. In the first study, sporulation intensity and duration of sporulation of the pathogen were tested on inoculated thinned fruit with five levels (67.2, 53.8, 40.3, 26.9, and 13.4%) of WC. Regression analyses showed that both sporulation intensity and duration of sporulation increased as WC of thinned fruit increased. The predicted difference in duration of sporulation between fruit with 13.4 and 67.2% WC was about 3 days. In the second study, three inoculum concentrations (8,000, 16,000, and 24,000 conidia per milliliter) of *M. fructicola* were atomized onto prune fruit on trees in an orchard. Inoculated fruit and shoots were covered with plastic bags to maintain wetness duration for 4, 8, 12, or 16 h. An overnight freezing and incubation technique was used after harvest to determine the proportion of fruit with latent infection. Regression analysis demonstrated that inoculum concentration and wetness duration were significant factors affecting secondary infection. Temperature was less important. Increased inoculum concentration and wetness duration increased the percentage of fruit with latent infections. Increased temperature decreased the percentage of fruit with latent infections.

Additional keywords: epidemiology, *Prunus domestica*, quiescent infection, stone fruit

Brown rot, caused by *Monilinia fructicola* (G. Wint.) Honey, is a destructive disease of stone fruit (*Prunus* spp.) (1,3,14,22). Ascospores or conidia produced from mummies infected by *M. fructicola* serve as inoculum sources that cause blossom blight in the spring (3,14,21). These primary infections can provide inoculum for latent infection of fruit (6,12,12,23). Non-abscised, aborted fruit in trees and thinned fruit on the orchard floor are important sources of secondary inoculum for fruit brown rot (1,14,18). The significance of thinned fruit as a source of secondary inoculum in California nectarine orchards was also confirmed (10). Infected thinned fruit on the floor served as a source of spores that cause secondary infection, and sporulation of *M. fructicola* on these fruit was significantly correlated with the severity of preharvest and postharvest brown rot (8,10). Cultural practices in orchards, especially irrigation and management of thinned fruit, may affect water content (WC) and decomposition of thinned fruit. Estimation of inoculum potential from thinned fruit could be used to

guide disease control. Information on how sporulation relates to WC of thinned fruit is needed to devise control strategies and reduce secondary infection. Appropriate cultural practices in orchards that affect thinned fruit and their WC might be implemented to reduce secondary inoculum.

Under favorable conditions, conidia of *M. fructicola* are dispersed in the air (13), deposited on the fruit surface, and cause infection (2,4,5,15,19). Inoculum concentration and environment serve as important factors affecting secondary infection. Effects of temperature and wetness duration on infection of fresh or harvested stone fruits have been reported (2,4,19). Biggs and Northover (2) found that the optimum temperatures and wetness durations were 20 to 22.5°C and 18 h for infection of cherry fruit, and 22.5 to 25°C and 12 h for infection of peach fruit. Inoculum concentration significantly affected brown rot development on detached cherry (18), nectarine, and peach fruits (11). However, little information is available about effects of these factors on brown rot development of fruit on trees. Since the physiological conditions between detached fruit and fruit on trees are different, finding out how fruit infection on trees relates to different environments is important for estimating inoculum potential and predicting disease development in the field.

If the inoculum potential from thinned fruit could be determined based on the WC of these fruit, then the risk of secondary

infection could be more precisely predicted using the relationship between inoculum availability and predicted temperature and wetness duration. The objectives of this study were (i) to determine the effect of WC of thinned, infected prune fruit on sporulation of *M. fructicola*, and (ii) to define the effects of inoculum concentration, wetness duration, and temperature on secondary infection of prune fruit.

## MATERIALS AND METHODS

**Effects of WC on sporulation of *M. fructicola* on thinned fruit.** An isolate of *M. fructicola* collected from a prune orchard at the Kearney Agricultural Center, University of California in Parlier, was used in this study. This isolate was cultured on potato dextrose agar (PDA) amended with a 25% vol/vol lactic acid (2.6 ml/liter). Cultures were incubated at 23 ± 2°C for 5 days in the dark. Conidia of *M. fructicola* were harvested by pouring 3 ml sterile distilled water in each Petri dish, and the spore concentration was adjusted to 1,000 conidia per milliliter using a hemacytometer.

Immature fruit were collected from a prune orchard at Kearney Agricultural Center. The experiments were conducted from July to August 1999, and fruit stages were from late embryo growth to first harvest (20). Fifteen green prune fruit (cv. French) of different sizes (13.5 ± 3.4 g, 39.2 ± 4.4 mm length and 27.1 ± 1.9 mm diameter) were arbitrarily selected to determine the dry weight of fruit. Each fruit was weighed fresh and then dried at 65°C for about 3 days to stabilize the weight. The average percentage of dry fruit weight over the fresh fruit weight from the 15 fruit was 32.8 ± 1.1%. This value was used to calculate the water content of fruit for subsequent experiments.

Fresh prune fruit collected from the same orchard were surface-disinfected with 0.525% sodium hypochlorite (10% commercial bleach) for 3 min and rinsed with sterile distilled water five times. To initiate latent infections, a sterile nail was used to make a wound (3 mm diameter and 2 mm depth) on the surface of each fruit, and a 30- $\mu$ l drop of spore suspension (1,000 conidia per milliliter) was placed on each wound. The inoculated fruit were placed on waxed wire screens in sterile plastic containers (40 × 24 × 12 cm) and 200 ml water was added to the container to increase humidity and facilitate infection. Containers with the fruit were incubated at

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23°C for 2 days to establish latent infection, then fruit were removed from the containers and placed into an open wooden frame box (44 × 35.5 cm) on paper towels to dry under ambient outdoor conditions (about 6 to 8 h/day under direct sunlight). No further development of brown rot was apparent on the fruit. Five of these fruit were arbitrarily selected and individually weighed daily to determine WC loss. The percentage WC of fresh fruit was 67.2%. When the average WC of the selected five fruit reached 53.8, 40.3, 26.9, and 13.4% (corresponding to 80, 60, 40, and 20% of the WC of fresh fruit, respectively), 35 fruit with each corresponding WC were collected and surface-disinfected with 0.525% sodium hypochlorite for 5 min, rinsed with sterile distilled water five times, placed on waxed wire screens in sterile plastic containers, and incubated at 23°C and 98% relative humidity for the following experiments. Inoculated fresh fruit (without drying) were used to represent the fruit with 67.2% WC.

The day when at least 50% of the 35 fruit showed sporulation was used as the starting date of sporulation for each WC/drying time treatment. At that time, five fruit covered with spores were chosen for testing sporulation intensity. All spores were washed from the five fruit with sterile distilled water 1 day prior to quantifying sporulation. After washing, fruit were incubated for one more day, and the new spores formed were washed into 200 ml distilled water using a paintbrush. The resulting spore suspension was shaken at 180 osc/min for 10 min to break chains of spores and the number of spores of *M. fructicola* for each of the five fruit was determined using a hemacytometer. Sporulation measurements on the same five fruit

were repeated 2 and 5 days after sporulation began.

From the remaining 30 fruit, those showing at least 25% surface area covered with sporodochia producing spores were recorded daily as fruit with sporulation. Following daily observation, spores were brushed off the fruit and the fruit were returned to the plastic container and incubated until no new conidiophores were visually observed. Each experiment lasted about 10 to 12 days. The fruit used in each experiment were at the same growth stage. The experiment was conducted four times.

Treatments were arranged in a randomized complete block design (7). Average sporulation intensity per fruit per day was calculated from the two measurements for each tested fruit. Analysis of variance was conducted to determine the significance of variance in sporulation from experiments as blocks and from WC of thinned fruit as the treatments. The interaction between these two factors was used as an error. The ANOVA procedure of SAS (Version 7.0, SAS Institute, Cary, NC) was used in this analysis. Average sporulation intensity calculated from five sub-samples for each experiment was used in regression of sporulation on WC by using the computer software SigmaPlot (version 5.0, SPSS inc., Richmond, CA).

In each experiment, the duration of sporulation for each WC was determined as days from the sporulation starting date through the day when 90% of fruit stopped producing spores. This duration of sporulation was determined for each WC in each experiment and was linearly regressed on WC of thinned fruit using the REG procedure of SAS. To describe the dynamic process of sporulation, the proportion of fruit with sporulation of *M. fructicola* over

the corresponding days after incubation was used to obtain a linear regression equation for each WC using the REG procedure of SAS. Homogeneity of regression coefficients between any two regressions was tested (7).

**Effects of wetness duration, inoculum concentration, and temperature on latent infection of prune fruit.** Inoculum was prepared as described previously. Spore concentrations used in this study were adjusted to 8,000, 16,000, and 24,000 conidia per milliliter. A total of 500 ml spore suspension was made from each of the three concentrations.

A split-plot design was used in this study. Inoculations were conducted in a prune (cv. French) orchard at the Kearney Agricultural Center in July when fruit were between late embryo growth and first harvest (20). The fruit size was similar to those of the above study. Branches of prune trees with 20 to 30 fruit were uniformly sprayed with 30 ml spore suspension of each concentration using a hand-held sprayer (ACE Hardware Corporation, Oak Brook, IL). Immediately after inoculation, each branch was closed tightly in a 1.5-mil transparent plastic bag to maintain high relative humidity around the inoculated branch. The three inoculum concentrations were applied to different branches of the same tree with enough distance between them to protect from cross contamination. A non-inoculated control was established by spraying 30 ml sterile distilled water on a branch of a separate tree.

For each experiment, inoculation was conducted at about 2000 PST. Four treatments consisting of wetness durations of 4, 8, 12, and 16 h were accomplished by uncovering the plastic bags at 0000, 0400, 0800, and 1200 PST, respectively, on each of four inoculated trees. Fruit normally dried within 15 to 20 minutes after bags were removed. Three branches served as sub-samples for each inoculum concentration and each wetness duration, and one sample of water-inoculated control for each wetness duration was used in each experiment. To prevent high temperature in the inoculated bags caused by sunlight, the plastic bags for treatments of 16-h wetness duration were covered with paper bags (30.4 × 17.3 × 36.2 cm) from 0800 PST until completion of the wetness duration. A data logger (ONSET Company, Pocasset, MA) was used to record hourly temperature outside but close to the bags during each experiment. However, the temperatures measured were probably a few degrees lower than those inside the bags. At the end of each wetness duration, the plastic bags were removed and the inoculated branches were marked. No natural dew was observed during the experiments. Five experiments were conducted using similar methodology. Hourly temperatures during the wetness duration for each inoculation are shown in Figure 1.

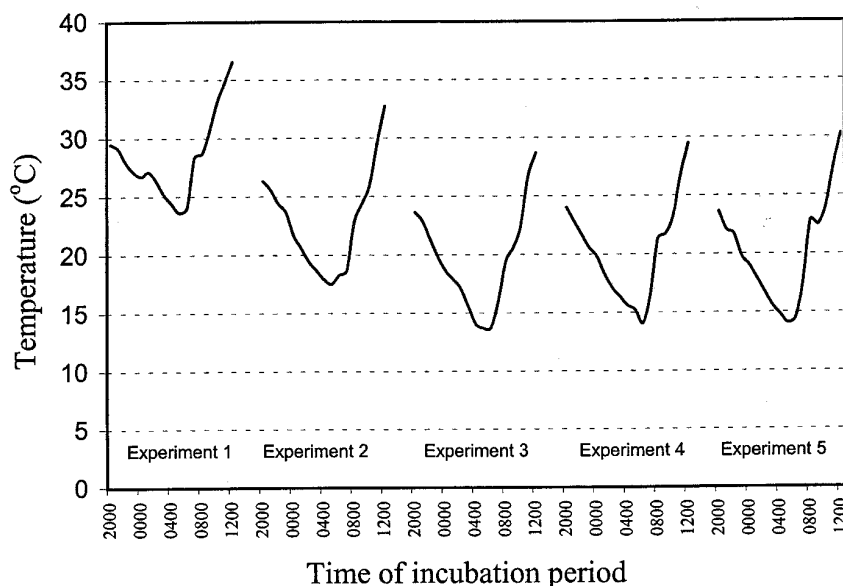


Fig. 1. Temperatures during inoculation of prune fruit on trees with *Monilinia fructicola* in an orchard at Kearney Agricultural Center, University of California, Parlier (five separate experiments).

At commercial harvest time in August, inoculated fruit showing no disease were harvested separately for each treatment combination of inoculum density and wetness duration. The overnight freezing incubation technique (16,17) was used to determine the proportion of fruit with latent infections. Fruit were surface-sterilized in a chlorine solution (32 ml of 0.525% sodium hypochlorite, 32 ml 95% ETOH, and 0.01 ml surfactant Tween 20 in 2 liters water) for 5 min. The fruit were then washed with sterile distilled water five times and placed on a waxed wire screen in a plastic container (40 × 24 × 12 cm) with water at the bottom to increase relative humidity. The containers were placed in a freezer at -16°C for 10 h and then transferred to a laboratory bench at 23 ± 2°C for 7 days. The proportion of fruit covered with sporulation of *M. fructicola* was recorded.

The proportion of fruit with latent infection was transformed with the arcsine transformation prior to statistical analysis (7). Analysis of variance was conducted using the ANOVA procedure of SAS with the experiment treated as replication, inoculum concentration treated as the main-plot factor and wetness duration treated as the subplot factor (7). Average temperature for each wetness duration was calculated for each experiment. In order to study the effects of inoculum concentration on latent infection, experiments were combined into one data set for each inoculum concentration. Linear regression was conducted using the REG procedure of SAS for each inoculum concentration. The proportion of fruit with latent infection was treated as the dependent variable and the wetness duration and temperature as independent variables. All combined data were also used for an overall regression analysis, with the proportion of fruit with latent infection as the dependent variable and inoculum concentration, wetness duration, and temperature as independent variables.

## RESULTS

**Effects of WC on sporulation of thinned fruit.** Water content (WC) had a significant effect on sporulation ( $P = 0.0002$ ) while the experiment (block) did not. An equation describing the amount of sporulation in relation to the WC was obtained (Fig. 2A).

A significant linear relationship between WC and duration of sporulation in days (DS) was also obtained (Fig. 2B). Duration of sporulation was prolonged with increased WC. Sporulation on fruit with 67.2% WC (fresh fruit) lasted 7 to 9 days (with an average of 8 days). The predicted difference in average duration of sporulation between fruit with 67.2% and 13.4% WC was about 3 days.

On the first day after incubation, 100% of fruit with 67.2% WC produced spores (Fig. 3), but this proportion varied on fruit

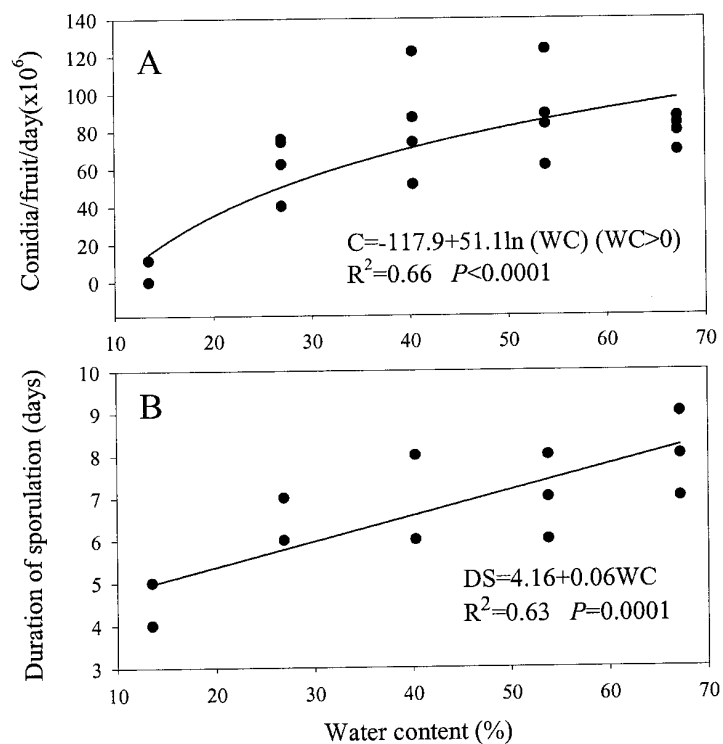
with 53.8% WC and 40.3% WC (Fig. 3), and decreased to less than 85% on fruit with 26.9% WC (Fig. 3). About 5 days after incubation, 70, 60, 60, and 50% of fruit, with 67.2, 53.8, 40.3, and 26.9% WC, respectively, were predicted to show sporulation of *M. fructicola* (Fig. 3). Generally, sporulation of fruit with higher WC was greater than that of fruit with lower WC during the first 5 to 6 days of sporulation. For example, only 20% fruit with 13.4% WC produced spores after 6 days of incubation (data not shown).

Linear relationships between days after incubation of fruit (D) and percentage of fruit with sporulation (%) (SP) were obtained for the four levels of WC (Fig. 3). Analysis of homogeneity of regression coefficients demonstrated that the absolute value of the regression coefficient (slope) for 67.2% WC (Fig. 3) was significantly greater ( $P < 0.05$ ) than those of regressions for 53.8% WC and 26.9% WC (Fig. 3). The absolute value of the regression coefficient for 26.9% WC was significantly smaller ( $P < 0.05$ ) than those of the other three regressions. Regression coefficients for 40.3% WC and 53.8% WC were not significantly different (Fig. 3).

**Effects of wetness duration, inoculum concentration, and temperature on latent infection of prune fruit.** None of the non-inoculated control fruit developed latent infection. Analysis of combined data from all experiments showed significant effects

for experiment (block) at  $P < 0.0001$ , wetness duration at  $P = 0.0196$ , and inoculum concentration at  $P < 0.0001$ . The interaction between wetness duration and inoculum concentration was not significant, and errors of wetness duration and inoculum concentration also were not significant.

Regression analysis demonstrated that when inoculum concentration of 8,000 conidia per milliliter was used, wetness duration had a significant impact on fruit with latent infections ( $P = 0.008$ ), but temperature did not ( $P = 0.86$ ). Similar results were obtained when 16,000 conidia/ml was used, that wetness duration had significant effects on latent infection ( $P = 0.0008$ ) while temperature did not ( $P = 0.23$ ). Both regressions were significant at  $P < 0.05$ . However, when inoculum concentration was increased to 24,000 conidia per milliliter, wetness duration was not significant ( $P = 0.23$ ) while temperature became significant ( $P = 0.037$ ). The overall regression from the combination of inoculum concentrations showed that wetness duration and inoculum concentration were both significant at  $P < 0.0001$  and temperature was significant at  $P = 0.043$ . The regression was significant at  $P < 0.0001$  with  $R^2 = 0.2624$ . The regression equation was  $PLI = 14.4 + 1.11IC - 0.78T + 1.13WD$ , where PLI is proportion of latent infection (%), IC is inoculum concentration ( $10^3$  conidia per milliliter),  $T$  is temperature (°C), and WD is wetness duration (h).



**Fig. 2.** Relationships between water content (WC) of thinned prune fruit and sporulation intensity in **A**, conidia ( $10^6$ )/fruit/day (C) and **B**, duration of sporulation in days (DS) of *Monilinia fructicola*. Data were from four experiments each with 5 fruit as sub-samples for testing sporulation intensity and each experiment with 30 fruit for testing duration of sporulation. Each point of **A** represents an average of five sub-samples for each experiment.

## DISCUSSION

Results of the first experiment indicated that increasing WC of thinned fruit led to a greater sporulation intensity and longer duration of sporulation. Increased inoculum production from fruit with high WC may increase potential for secondary infections of prunes. Results of the second experiment indicated that inoculum concentration, wetness duration, and temperature affect secondary infection of prune fruit. Increasing inoculum concentration, prolonging wetness duration, and decreasing temperature within the range

of 15 to 30°C all resulted in more latent infections.

The relationships between WC of thinned fruit and sporulation obtained in this study may be used to estimate how much and how long sporulation will be reduced on fruit with less than 67.2% WC. However, the results could be used only for fruit with WC greater than 13.4%. When WC decreased below 13.4%, very few thinned fruit produced spores. Hong and Michailides (9) observed that mycelial growth and sporulation of *M. fructicola* were reduced along with decreasing osmotic potential. This

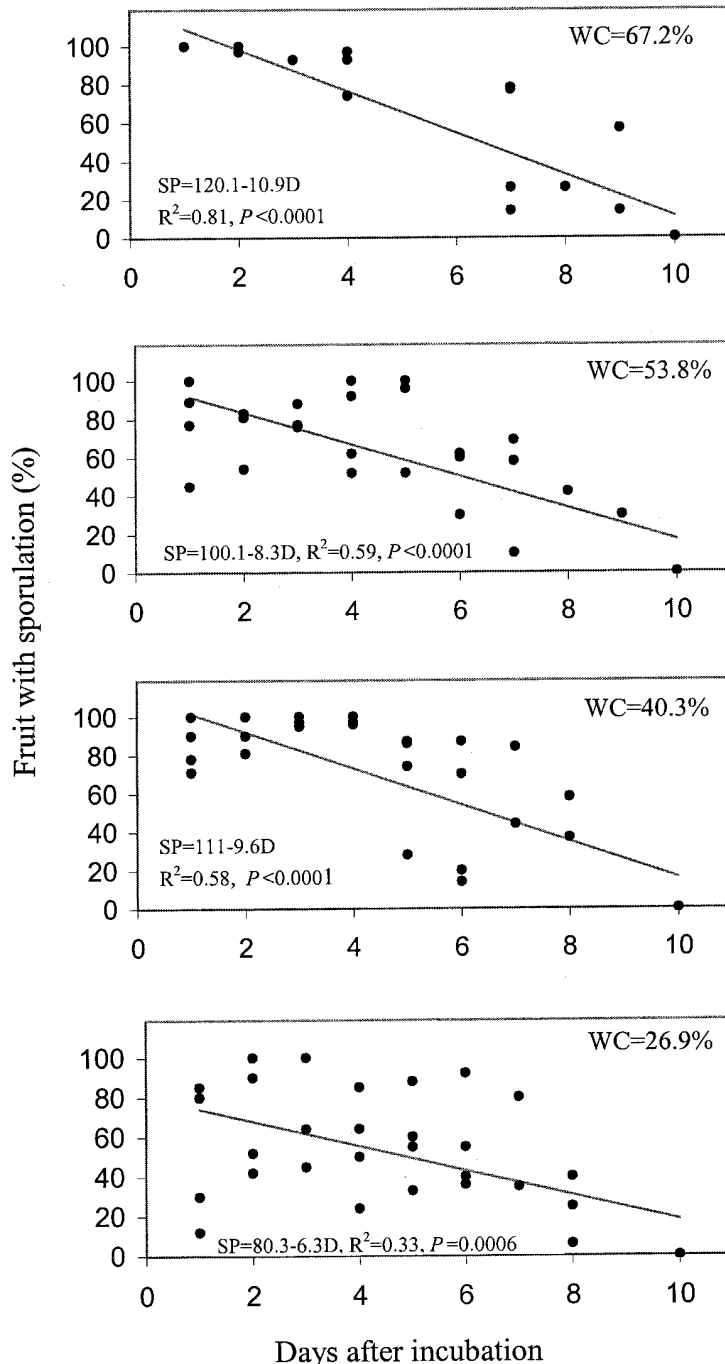
implies that sporulation is significantly related to relative humidity, which may be affected by water content of fruit.

In this study, we tested relationships between WC of thinned fruit and sporulation under simulated natural conditions. Fruit infected by *M. fructicola* were placed in an outdoor environment and sampled periodically at different times during the drying process. Undoubtedly, sporulation of thinned fruit could vary as the period of drying varies. For example, we found that the period needed to obtain different levels of WC was significantly correlated with WC ( $r = -0.89$ ), sporulation ( $r = -0.85$ ), and duration of sporulation ( $r = -0.70$ ).

Differences in WC among thinned fruit may result from many factors including time, ambient temperature, and relative humidity during the drying period. This study demonstrated that the WC of thinned fruit could be predicted based on drying period, temperature, or moisture. For example, after a rainy period or following irrigation, fruit may dry more slowly (higher WC) compared to those after a period of drought and sunlight because of changes in ambient temperature and moisture. The period needed for thinned fruit to reach a certain WC might be different under different weather conditions. The ambient temperatures varied among experiments, implying that the time required to reach each level of WC also varied. However, the interaction between sporulation of *M. fructicola* on fruit and experiment was not significant based on an analysis of individual fruit data rather than means. Therefore, the information obtained from this study is useful to predict inoculum potential in orchards based on WC of thinned fruit that relates to environment and cultural practices.

Prune fruit with higher WC produced spores over a longer period than fruit with lower WC. Therefore, infected fruit with higher WC could contribute to a higher risk of secondary infection than fruit with lower WC. Hong et al. (10) showed that thinned nectarine fruit can serve as an inoculum source for secondary infection. Controlling WC of thinned fruit could be used for disease management. Cultural practices in orchards that promote quick drying of thinned fruit may be helpful to reduce these inoculum sources for secondary infection. If WC of thinned fruit could be quickly reduced to lower than 26.9%, fruit would produce few conidia, thus reducing the risk of secondary infection. Humidity could affect the drying process of thinned fruit in the fields. Hong et al. (10) found that *M. fructicola* sporulated more frequently on thinned fruit in irrigation trenches than on fruit on the dry berms in tree rows. Thus, fruit thinning should be scheduled between irrigations, thereby providing enough time for thinned fruit to dry quickly.

Under field conditions, inoculum concentration and wetness duration were critical



**Fig. 3.** Regressions between percentages of prune fruit with sporulation (SP) of *Monilinia fructicola* and days (D) after incubation for different water contents (WC) of fruit. Each regression is from data of four combined experiments.

factors that determined the levels of secondary infections of prune fruit. High inoculum concentration combined with long wetness duration led to more fruit with latent infections than did lower inoculum concentration with shorter wetness duration. When inoculum concentration is low, wetness duration could be a critical factor in severity of infection. The relationship between spore concentration in the air and on the fruit is needed to quantitatively estimate the inoculum potential in the fields.

Temperature was shown to be an important factor at the highest inoculum concentration tested (e.g., 24,000 conidia per milliliter). Since these field experiments were conducted overnight when temperatures were within the range of those required for *M. fructicola* to cause infection (3,19), the conclusions of this study are applicable only under temperature conditions similar to those in California. Furthermore, the temperatures inside the plastic bags were probably a few degrees higher than those recorded during the incubation periods. More intensive studies on the effects of temperature on secondary infection are needed for regions where summer temperatures and levels of moisture are very different from those in California.

Differences in fruit susceptibility and temperatures between experiments may have contributed to variability. Susceptibility of fruit to infection may have changed during the field experiments. Our recent studies (data not published) showed that fruit susceptibility to infection increased with fruit growth after the pit hardening stage. The hourly temperatures among the third, fourth, and fifth inoculations were relatively consistent, but the temperatures of the first and second inoculations were higher than those of the other three inoculations (Fig. 1).

Inoculum concentration, wetness duration, and temperature in the orchard could be used to predict secondary infection. Biggs and Northover (2) found that on harvested peach fruit, the optimum temperature for infection was 22.5 to 25°C and over 70% of the fruit were infected after 12

h of wetness duration at temperatures below 27.5°C. Corbin (4) reported that on harvested peach, plum, and cherry fruits, higher inoculum dosage led to shorter incubation periods, and green fruits needed high inoculum dosages of *M. fructicola* for infection of intact fruit, and low inoculum dosages when fruits were injured. Based on the results of this study, it may be possible to predict the risk of latent infection based on estimation of sporulation on thinned fruit and microclimatic conditions, such as wetness duration and temperature.

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