Interactions Between Chill-Hours and Degree-Days Affect Carpogenic Germination in *Monilinia vaccinii-corymbosi*

H. Scherm, A. T. Savelle, and P. L. Pusey

First and second authors: Department of Plant Pathology, University of Georgia, Athens 30602; and third author: U.S. Department of Agriculture, Agricultural Research Service, Tree Fruit Research Laboratory, Wenatchee, WA 98801.
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ABSTRACT

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The relationship of cumulative chill-hours (hours with a mean temperature $<7.2^{\circ}\text{C}$) and heating degree-days (base 7.2°C) to carpogenic germination of pseudosclerotia of *Monilinia vaccinii-corymbosi*, which causes mummy berry disease of blueberry, was investigated. In two laboratory experiments, pseudosclerotia collected from rabbiteye blueberry in Georgia were conditioned at 5 to 6°C for 26 to 1,378 h prior to placement in conditions favorable for germination and apothecium development. The number of chill-hours accumulated during the conditioning period affected the subsequent proportion of pseudosclerotia that germinated and produced apothecia, with the greatest incidence of carpogenic germination occurring after intermediate levels of chilling (≈ 700 chill-hours). The minimum chilling requirement for germination and apothecium production was considerably lower than that reported previously for pseudosclerotia from highbush blueberry in northern production regions. The rate of carpogenic germination was strongly affected by interactions

between the accumulation of chill-hours and degree-days during the conditioning and germination periods; pseudosclerotia exposed to prolonged chilling periods, once transferred to suitable conditions, germinated and produced apothecia more rapidly (after fewer degree-days had accumulated) than those exposed to shorter chilling periods. Thus, pseudosclerotia of *M. vaccinii-corymbosi* are adapted to germinate carpogenically following cold winters (high chill-hours, low degree-days) as well as warm winters (low chill-hours, high degree-days). Results were validated in a combined field-laboratory experiment in which pseudosclerotia that had received various levels of natural chilling were allowed to germinate in controlled conditions in the laboratory, and in two field experiments in which pseudosclerotia were exposed to natural chilling and germination conditions. A simple model describing the timing of apothecium emergence in relation to cumulative chill-hours and degree-days was developed based on the experiments. The model should be useful for better timing of field scouting programs for apothecia to aid in management of primary infection by *M. vaccinii-corymbosi*.

Additional keywords: thermal time, *Vaccinium ashei*.

Mummy berry disease is a key problem in the commercial production of blueberries (*Vaccinium* spp.) in North America (3,12), including Georgia (27) and other parts of the southeastern United States (6). *Monilinia vaccinii-corymbosi*, the fungus that causes the disease, survives in infected, mummified fruit (pseudosclerotia) on the orchard floor. In late winter or early spring, pseudosclerotia germinate carpogenically, forming apothecia from which ascospores are released. Ascospores, the only primary inoculum, infect and blight young, expanding leaves and shoots (3,4,15). Conidia formed on blighted tissue during spring cause secondary infections via the stigma and style of open flowers, followed by colonization of the locules of the developing fruit (19,29). During the fruit maturation phase in early summer, further growth and development of *M. vaccinii-corymbosi* within infected berries leads to the formation of fruit mummies, which drop to the ground before or at harvest and serve as overwintering and overwintering structures.

Rabbiteye blueberries (*Vaccinium ashei*), which are native to the southeastern United States, comprise $>90\%$ of the commercial acreage in Georgia. In contrast, most of the blueberry plantings in northern production regions consist of lowbush (*V. angustifolium* and *V. myrtilloides*) or northern highbush (*V. corymbosum*) cultivars. The three blueberry species differ in growth habit, phenology, and other horticultural aspects (2,30). Whereas the epidemiology of

mummy berry disease has been studied in detail on lowbush and highbush blueberries in the northern production regions of North America (3,4,11,14–16,18,19,22,23), little research has been done on this disease on rabbiteye blueberry in the Southeast (8,27).

Because apothecia formed on pseudosclerotia are the only source of primary inoculum (3,4,12), the first appearance of apothecia in late winter or early spring represents a key epidemiological event in the mummy berry disease cycle. Field scouting of sclerotia or pseudosclerotia for stipes or apothecia has been suggested as a decision aid for the timing of management tactics against primary infection by closely related discomycetes, e.g., *Sclerotinia sclerotiorum* (1). In most rabbiteye blueberry plantings in Georgia, however, pseudosclerotia are present in low densities (H. Scherm and P. L. Pusey, *unpublished data*), rendering scouting during the entire potential apothecium emergence period too time-consuming for practical use. If conditions that favor germination could be ascertained and the timing of apothecium emergence predicted, scouting could be limited to those periods when apothecium emergence is most likely, thereby rendering the approach more feasible.

Carpogenic germination of pseudosclerotia of *M. vaccinii-corymbosi* in relation to environmental conditions has been studied previously. Milholland (18,19) reported that temperature, along with soil moisture, is a critical factor in the germination of pseudosclerotia and the subsequent development of apothecia. He showed that pseudosclerotia required a cold-temperature conditioning period of at least 900 to 1,200 chill-hours (number of hours with a mean temperature $<7.2^{\circ}\text{C}$) before normal apothecium development could occur (19). This chill-hour range is very similar to that required for adequate bud break in northern highbush

Corresponding author: H. Scherm; E-mail address: scherm@uga.edu

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blueberry cultivars grown in southeastern North Carolina (where these studies were carried out), suggesting that the pathogen has adapted to resume activity in the spring concurrently with its host. The hypothesis of successful adaptation in the timing of apothecium development in *M. vaccinii-corymbosi* to the phenology of its host was supported by Bristow (5) who found that pseudosclerotia required ≈ 700 chill-hours for carpogenic germination in the maritime climate of Washington State where the chilling requirement for commonly grown blueberry cultivars is lower than in North Carolina. Lehman and Oudemans (14,16) described cultivar-specific adaptation in the phenology of *M. vaccinii-corymbosi*, whereby apothecia developed earlier on pseudosclerotia collected in plantings of early season highbush blueberry cultivars than on those collected in late season cultivars in New Jersey. It is unknown whether the apparent coevolution between the pathogen and its host can be substantiated in the commercial rabbiteye blueberry production regions of Georgia where the chill-hour requirement for commonly grown cultivars ranges from <200 to 800 h (2).

The objectives of this research were to (i) determine the chill-hour requirement for carpogenic germination of pseudosclerotia of *M. vaccinii-corymbosi* from rabbiteye blueberry in Georgia; (ii) compare development times for the production of apothecia on early and late season rabbiteye blueberry cultivars; and (iii) develop a simple model to predict timing of apothecium emergence based on thermal time accumulated during the conditioning and germination periods. Preliminary accounts of parts of this work have been given (26,28).

MATERIALS AND METHODS

Laboratory experiments. Pseudosclerotia were collected from the ground in a rabbiteye blueberry planting with a history of se-

TABLE 1. Description of five experiments in which the relationship of cumulative chill-hours and heating degree-days to subsequent germination and apothecium emergence of pseudosclerotia of *Monilinia vaccinii-corymbosi* was investigated

Exp.	Cultivar	Chilling treatment		Germination treatment	
		Location	Chill-hours ^a	Location	Degree-days ^b
1	Climax	Laboratory	26–1,344	Laboratory	202–772
2	Climax	Laboratory	34–1,378	Laboratory	229–713
3	Mixed	Field	21–429	Laboratory	652–1,022
4	Climax	Field	1,415*	Field	258
	Tifblue		1,465*		272
5	Climax	Field	1,393*	Field	373
	Tifblue		1,393*		373

^a Chill-hours represent the number of hours with a mean temperature $<7.2^{\circ}\text{C}$.

* Indicates number of chill-hours accumulated at which the proportion of pseudosclerotia with apothecia attained 25% of its maximum value.

^b Degree-days calculated with hourly measurements of air temperature with a base of 7.2°C . Accumulation of degree-days was initiated on the date when the first chill-hour was recorded. Values indicate number of degree-days accumulated at which the proportion of pseudosclerotia with apothecia attained 25% of its maximum value for each chilling treatment.

vere mummy berry disease in Murray County in northern Georgia on 8 October 1997 and 19 October 1998 (experiments 1 and 2, respectively; Table 1). At the time of their collection, the pseudosclerotia had received an estimated 26 chill-hours in 1997 and 34 chill-hours in 1998, based on air temperatures measured at a nearby agrometeorological station (13). Pseudosclerotia were rinsed by shaking in distilled water containing 0.2 ml^{-1} of Tween 80 for 20 min, enclosed in fiberglass mesh bags in groups of 32, and either buried in saturated sand (23% water content by weight) in a perforated plastic tray (treatment 1) or submerged in continuously aerated distilled water in a 4-liter beaker (treatment 2). In the latter treatment, which was included to enhance leaching of potential inhibitors of carpogenic germination, aeration was provided with an aquarium pump and bubble stone (9). The tray and beaker were placed in a refrigerated incubator (5 to 6°C) in darkness for 0, 336, 672, 1,008, or 1,344 h in 1997 and 0, 96, 336, 672, 1,008, or 1,344 h in 1998. During the conditioning period, the sand in treatment 1 was maintained at field capacity by placing the tray in a pan with distilled water; water in treatment 2 was replaced weekly.

At the conclusion of each chilling period, three bags with pseudosclerotia were recovered from each of the two treatments. Pseudosclerotia were removed from the bags and transferred onto sand maintained at field capacity in 10.2-cm-diameter plastic pots; all pseudosclerotia from a given bag were placed in the same pot. To induce carpogenic germination, pots were moved into a second incubator (referred to as the “germination chamber”) set at 16 to 17°C with $>80\%$ relative humidity and a 14-h photoperiod provided by fluorescent plant growth lights (photon flux density 160 to $180\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$). Using a stereo microscope, pseudosclerotia were assessed in situ for the presence of stipes and apothecia at 2- to 4-day intervals over a period of at least 4 months in both experiments. Data were summarized for each pot as cumulative proportion of pseudosclerotia with stipes (referred to as “germinated pseudosclerotia”) and as cumulative proportion of pseudosclerotia with apothecia. Means and standard errors of the two variables were computed and plotted against the number of chill-hours accumulated during the conditioning period (included natural chilling received prior to collection of pseudosclerotia in the field). This was done with combined data from the chilling treatments in saturated sand and aerated water after an analysis of variance showed no significant differences between these two treatments (Table 2).

For each of the chilling periods, the final cumulative proportion of pseudosclerotia with apothecia (p_{max}) was noted. Based on progress curves describing the cumulative proportion of pseudosclerotia with apothecia over time, the number of days elapsed in the germination chamber until this proportion attained 25% of p_{max} was identified for each chilling period. This percentile was used to summarize and compare the dynamics of apothecium emergence in populations of pseudosclerotia; it was considered less sensitive to extreme values than variables based on earlier events (i.e., the date that the first apothecium emerged) and more practical than indices based on later events (i.e., the date that p_{max} was reached).

TABLE 2. Results of a split-plot analysis of variance to determine the effects of chilling treatment and chilling period on the proportion of pseudosclerotia of *Monilinia vaccinii-corymbosi* that germinated or formed apothecia in the laboratory^a

Source	df	Proportion of germinated pseudosclerotia			Proportion of pseudosclerotia with apothecia		
		Mean Square	<i>F</i>	<i>P</i> > <i>F</i>	Mean Square	<i>F</i>	<i>P</i> > <i>F</i>
Experiment (block)	1	0.0024	0.15	0.7659	0.0012	0.14	0.7720
Chilling treatment (main plot)	1	0.0034	0.21	0.7281	0.0002	0.02	0.9061
Main plot error	1	0.0164	—	—	0.0083	—	—
Chilling period (subplot)	5	0.0200	10.80	0.0021	0.0110	7.64	0.0065
Chilling treatment $\times$ chilling period	5	0.0016	0.88	0.5373	0.0005	0.33	0.8804
Subplot error	8	0.0018	—	—	0.0014	—	—

^a Results from experiments 1 and 2 (Table 1). Analysis based on means of three groups of 32 pseudosclerotia per subplot. Chilling treatment represents pseudosclerotia buried in saturated sand or submerged in continuously aerated distilled water. Chilling applied for 0, 336, 672, 1,008, or 1,344 h (experiment 1) and 0, 96, 336, 672, 1,008, or 1,344 h (experiment 2).

Field-laboratory experiment. Pseudosclerotia were collected from the ground in a rabbiteye blueberry planting in Bacon County in southern Georgia on 7 November 1997, 5 December 1997, and 15 January 1998 after they had received, respectively, 21, 124, and 429 h of natural chilling (experiment 3; Table 1). The number of heating degree-days (base 7.2°C, referred to as "degree-days") received in the field prior to each collection date was determined based on air temperature measurements at a nearby agrometeorological station; accumulation of degree-days was initiated on the date when the first chill-hour was recorded (28 October). Pseudosclerotia were rinsed, placed in groups of 32 on sand kept at field capacity in pots, incubated in the germination chamber, and monitored and assessed as described above. The proportion of pseudosclerotia that germinated or formed apothecia was recorded for each pot, and means were computed based on three pots for each collection date.

Field experiments. Pseudosclerotia from early season cv. Climax and late season cv. Tifblue (chilling requirement 400 to 450 h and 600 to 800 h, respectively) were collected in Murray County in northern Georgia on 8 October 1997 and 24 October 1998 (experiments 4 and 5, respectively; Table 1). At the time of their collection, the pseudosclerotia had received 26 chill-hours in 1997 and 34 chill-hours in 1998. Pseudosclerotia were rinsed as described above, placed in groups of 37 to 42 on a layer of washed sand beneath blueberry bushes in a research planting with no history of mummy berry disease on the University of Georgia campus, and covered with wire screen cages. Beginning in late winter in both years, the planting was sprinkler-irrigated with a fine mist at 1- to 4-day intervals to provide suitable soil moisture for carpogenic germination. Environmental conditions, including accumulation of chill-hours and degree-days, were measured at a nearby agrometeorological station. Pseudosclerotia were monitored and assessed twice a week for germination and apothecium emergence as described above. The proportion of germinated pseudosclerotia and of pseudosclerotia with apothecia was calculated for each group at each assessment date, and means were computed based on four groups per cultivar (six groups for cv. Tifblue in 1997). Kolmogorov-Smirnov tests (SAS Institute Inc., Cary, NC) were applied to determine whether the progress curves describing the two variables over time were significantly different for the two cultivars.

Model for apothecium emergence. The numbers of chill-hours (c_{25}) and degree-days (d_{25}) accumulated between the onset of chilling and the time at which the cumulative proportion of pseudosclerotia with apothecia attained 25% of $p_{\max}$ were calculated for each of the chilling periods in the five experiments described above. d_{25} was plotted against c_{25} , and a hyperbola of the form $d_{25} = a \times b / (b + c_{25})$, in which a and b are parameters, was fitted (SigmaPlot version 6.0; SPSS Science, Chicago). The equation describes an isoline for the 25th percentile of apothecium emergence for a range of chill-hour and degree-day combinations.

RESULTS

Laboratory experiments. The duration of chilling strongly affected the proportion of pseudosclerotia that subsequently germinated or formed apothecia (Fig. 1, Table 2). Pseudosclerotia receiving ≤ 130 chill-hours showed very limited germination (Fig. 1A) and did not produce any apothecia (Fig. 1B) despite remaining in conditions favorable for germination for >4 months following chilling. With increasing chilling, both germination and apothecium production increased and attained a maximum at ≈ 700 chill-hours. As chill-hours increased beyond this optimum, the incidence of germination and apothecium production was reduced. The ratio of the proportion of apothecium-producing pseudosclerotia to that of germinated pseudosclerotia also peaked at intermediate levels of chilling (Fig. 1C). Germination and apothecial emergence occurred more rapidly for pseudosclerotia that had received high levels of chilling than for those that had received lower levels of chilling (Fig. 2).

Field-laboratory experiment. In pseudosclerotia that had received 21 chill-hours in the field prior to being placed in the germination chamber, the incidence of germination remained very close to zero, and only one pseudosclerotium (out of 96 total) subsequently produced an apothecium (Fig. 3). By contrast, 36.5% of the pseudosclerotia exposed to 124 chill-hours germinated, and 11.5% of the pseudosclerotia in this treatment produced apothecia. Nearly 60% of the pseudosclerotia exposed to 429 chill-hours in the field had already germinated at the time of collection, and this proportion remained relatively constant during incubation in the germination chamber; 38.5% of the pseudosclerotia in this treatment subsequently produced apothecia (Fig. 3).

Fig. 1. Proportion of pseudosclerotia (mummies) of *Monilinia vaccinii-corymbosi* that **A**, germinated or **B**, formed apothecia after exposure to various periods of chilling in the laboratory. **C**, Ratio of the proportion of apothecium-producing pseudosclerotia to that of germinated pseudosclerotia for each chilling period. Pseudosclerotia were transferred to a germination chamber at the end of their respective chilling periods. Values are means and standard errors of six groups of 32 pseudosclerotia per treatment. Results of experiments 1 (●) and 2 (○) (Table 1).

Field experiments. Germination of pseudosclerotia and apothecium production after exposure to natural chilling and germination conditions in the field was initiated earlier and continued over a longer period in the first year (Fig. 4A and C) than in the second year (Fig. 4B and D). However, apothecium emergence attained 25% of $p_{\max}$ after similar chill-hour and degree-day totals in both years (Table 1). The incidence of germination and apothecium production was considerably greater in the second year than in the first year. In both years, most of the pseudosclerotia that germinated (Fig. 4A and B) subsequently produced apothecia (Fig. 4C and D).

Pseudosclerotia from early season cv. Climax and late season cv. Tifblue germinated and produced apothecia at approximately the same time (Fig. 4). When the progress curves for germination and apothecium emergence were compared with Kolmogorov-Smirnov tests, no significant differences were detected between the two cultivars (Table 3).

Model for apothecium emergence. Thermal time (expressed as cumulative chill-hours and degree-days) accounted for a large part of the variation in the timing of apothecium emergence across the five experiments, with fewer degree-days needed to reach 25% of $p_{\max}$ as the number of chill-hours increased (Fig. 5). The relationship between d_{25} and c_{25} was described by $d_{25} = 1,032 \times 541.2 / (541.2 + c_{25})$ ($P < 0.0001$, $R^2 = 0.938$).

DISCUSSION

The number of chill-hours accumulated during the conditioning period affected the subsequent incidence of carpogenic germination of pseudosclerotia of *M. vaccinii-corymbosi*. Whereas germination and apothecium production occurred over a wide range of chill-hours, the proportion of pseudosclerotia that germinated or formed apothecia was greatest after intermediate levels of chilling (≈ 700 chill-hours). Although there was evidence for a minimum chilling requirement for carpogenic germination, its exact magnitude could not be identified as, across all experiments, a few pseudosclerotia receiving very low chill-hour totals did germinate after accumulating a high number of degree-days. However, the observation that only one apothecium was produced on pseudosclerotia that received <34 chill-hours in the field-laboratory experiment, along with the requirement of at least 130 chill-hours for the production of apothecia in the two laboratory experiments,

Fig. 2. Number of days elapsed in a germination chamber until the cumulative proportion of pseudosclerotia of *Monilinia vaccinii-corymbosi* with apothecia attained 25% of its maximum value ($p_{\max}$) after exposure to various periods of chilling in the laboratory. Pseudosclerotia were transferred to the germination chamber at the end of their respective chilling periods. Values are means of six groups of 32 pseudosclerotia per treatment. Results of experiments 1 (●) and 2 (○) (Table 1).

does provide evidence for an absolute minimum chilling requirement for apothecium production that is considerably lower than the 900 to 1,200 chill-hour minimum determined in North Carolina (19) and that of 700 chill-hours in Washington State (5) for pseudosclerotia produced on highbush blueberry. Taken together, our results on minimum and optimum chilling requirements showed that populations of *M. vaccinii-corymbosi* from rabbiteye blueberry production regions in Georgia have adapted to germinate carpogenically in the low-chill environments characteristic of these regions, where chill-hour accumulation from 1 October through 15 February ranges from 600 to 800 h in normal winters and from 400 to 500 h in warm winters (25). In a broader context, the results support the hypothesis of successful adaptation of *M. vaccinii-corymbosi* to diverse environments (ranging from Nova Scotia to Washington State to southern Georgia) and to the chill-hour requirements of the different host species grown in these environments (5,14,16,19).

In addition to chill-hour accumulation during the conditioning period, other factors apparently affected the incidence of carpogenic germination of pseudosclerotia in this study. For example, the maximum incidence of germination was 13.8 and 42.9% in experiments 4 and 5, respectively, both of which were carried out in the field in similar experimental conditions (soil type, soil moisture, and photoperiod) with similar chill-hour and degree-day totals. Differences in the levels of germination between the two experiments may have been due to differences in pseudosclerotial viability. In pseudosclerotia formed on rabbiteye blueberry, vi-

Fig. 3. Proportion of pseudosclerotia (mummies) of *Monilinia vaccinii-corymbosi* that A, germinated or B, formed apothecia after exposure to natural chilling in the field for 21 (●), 124 (○), and 429 (▲) chill-hours. Pseudosclerotia were transferred to a germination chamber in the laboratory at the end of their respective chilling periods. Values are means of three groups of 32 pseudosclerotia per treatment. Results of experiment 3 (Table 1).

ability is strongly affected by pseudosclerotial maturity (characterized by the extent of fungal colonization of the fruit and the degree of melanization of the fungal tissue) at the time when infected fruit drop to the ground in early summer and by environmental conditions during the subsequent overwintering period (8). Because the pseudosclerotia used in the two experiments were collected in different years, year-to-year variations in viability, determined in part by environmental conditions prior to collection, could explain the variations in the incidence of germination between the two experiments.

The temporal dynamics of carpogenic germination were similar in populations of pseudosclerotia from early and late season cultivars of rabbiteye blueberry. This differs from the work of Lehman and Oudemans (14,16) who described cultivar-specific adaptation in populations of *M. vaccinii-corymbosi* from highbush blueberry in New Jersey, whereby apothecia emerged earlier on pseudosclerotia from early season cultivars than on those from late season cultivars. The authors hypothesized that earlier bud break dates in the former cultivars provided sufficient selection pressure to lead to the evolution of earlier apothecium emergence in the pathogen. Highbush cultivars are generally grown in single-cultivar stands, thus infection of flowers occurs via conidia produced on blighted vegetative tissue of the same cultivar. Because of the long period that the bushes remain in production (>30 years), cultivar-specific host-pathogen coevolution is plausible in this

production system. By contrast, due to limited self-fertility, rabbiteye cultivars are always planted in mixed stands (2), where rows of two or more cultivars are alternated. These cultivars often differ in the onset of vegetative bud break, which, along with a generally more protracted period of bud development, would suggest a much reduced selection pressure for cultivar-specific adaptations in pathogen phenology. This is similar to observations by Lehman and Oudemans (16) where pseudosclerotia collected from a mixed stand of highbush blueberry cultivars were intermediate in timing of apothecium emergence compared with those collected from single-cultivar stands of early and late season cultivars.

TABLE 3. Results of Kolmogorov-Smirnov tests to determine whether the progress curves describing the proportion of pseudosclerotia of *Monilinia vaccinii-corymbosi* that germinated or formed apothecia in the field were significantly different for cvs. Climax (early season) and Tifblue (late season)^a

Variable	Year	n ^b	P
Germinated pseudosclerotia	1997–1998	17	0.1120
	1998–1999	11	0.8079
Pseudosclerotia with apothecia	1997–1998	12	0.5176
	1998–1999	6	0.8928

^a Results from experiments 4 and 5.
^b Observations at the onset of the experiments, when proportions were zero for both cultivars, were excluded from the analysis.

Fig. 4. Proportion of pseudosclerotia (mummies) of *Monilinia vaccinii-corymbosi* that **A and B**, germinated or **C and D**, formed apothecia after exposure to natural chilling and germination conditions in the field. Pseudosclerotia were from early season rabbiteye blueberry cv. Climax (●) and from late-season cv. Tifblue (○). Values are means of four to six groups of 37 to 42 pseudosclerotia per treatment. Results of experiments 4 and 5 (Table 1).

Fig. 5. Relationship between the number of chill-hours and heating degree-days accumulated until the cumulative proportion of pseudosclerotia of *Monilinia vaccinii-corymbosi* with apothecia attained 25% of its maximum value for each treatment. Treatments primarily consisted of different periods of chilling in the laboratory or in the field. Results of experiments 1 (○), 2 (●), 3 (□), 4 (Δ), and 5 (▲) (Table 1). The regression line is a two-parameter hyperbola.

The rate of carpogenic germination of pseudosclerotia of *M. vaccinii-corymbosi* was strongly affected by interactions between the number of chill-hours and degree-days accumulated during the conditioning and germination periods. Pseudosclerotia exposed to prolonged chilling periods, once transferred to suitable conditions, germinated and produced apothecia more rapidly (after fewer degree-days had accumulated) than those exposed to shorter chilling periods. This suggests that high numbers of chill-hours can compensate for low numbers of degree-days and vice versa. Thus, pseudosclerotia are adapted to germinate and form apothecia following cold winters (high chill-hours, low degree-days) as well as warm winters (low chill-hours, high degree-days). Interestingly, this relationship applied to experiments in which conditioning and germination treatments were imposed consecutively in discrete periods (i.e., chilling at a constant temperature followed by germination at a higher constant temperature; experiments 1 and 2) and to those in which the two treatments occurred concurrently in fluctuating temperatures (experiments 4 and 5).

Models incorporating both chilling and heat requirements have been used previously to describe flowering dynamics in several fruit species (7,24), including blueberries (20); however, they have not been applied to quantify the germination response to temperature in plant-pathogenic fungi. In the present study, a combined chill-hour and degree-day model adequately described apothecium emergence in data sets obtained with pseudosclerotia from different cultivars, collected at distant locations in Georgia, and exposed to different (natural vs. laboratory) conditioning and germination treatments over a wide range of chill-hours (21 to 1,465) and degree-days (202 to 1,022). The model predicts the number of chill-hours and degree-days accumulated until the proportion of pseudosclerotia with apothecia attained 25% of p_{max} . The choice of this variable to summarize the dynamics of apothecium emergence was based primarily on statistical and practical considerations as discussed above. This variable alone could be used to decide upon the optimal timing of a scouting program for the presence of apothecia. In concert with additional variables such as inoculum density (which could be determined via scouting), host phenology (10,15), and weather (11), it could serve as a key component for predicting the risk of primary infection.

It is important to note that all experiments reported in this paper were carried out in conditions of high soil moisture. It is well established that soil moisture significantly affects carpogenic germi-

nation in *M. vaccinii-corymbosi* (4,18) and closely related discomycetes (4,21). Indeed, Milholland (18) observed that pseudosclerotia from northern highbush blueberry readily germinated and produced apothecia when placed on soil held at 81% of field capacity, whereas no germination occurred at 35% of field capacity. Because apothecium development is reduced or delayed in suboptimal soil moisture conditions, many apothecia in commercial blueberry plantings, particularly those without supplemental irrigation, are likely to emerge later than suggested by the model in Figure 5. Thus, the model may be most useful in providing a worst-case scenario for irrigated fields and for low-lying, wet sites in nonirrigated fields where soil moisture is more likely to be consistently favorable for carpogenic germination (17). In a broader context, it may be useful as a tool for "negative prognosis" (31) in predicting the interval before which apothecia are unlikely to emerge. This information should be useful for better timing of field scouting programs for apothecia to aid in management decisions against primary infection by *M. vaccinii-corymbosi*.

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