Influence of Interrupted Dew Periods, Relative Humidity, and Light on Disease Severity and Latent Infections Caused by *Cercospora kikuchii* on Soybean

W. Schuh

Assistant professor, Department of Plant Pathology, The Pennsylvania State University, University Park 16802.
Contribution 1880, Department of Plant Pathology.
Accepted for publication 16 September 1992.

ABSTRACT

Schuh, W. 1993. Influence of interrupted dew periods, relative humidity, and light on disease severity and latent infections caused by *Cercospora kikuchii* on soybean. Phytopathology 83:109-113.

Germination of *Cercospora kikuchii* conidia, at 25 C, with relative humidities of 100% wet, 100% dry, and 99%, was influenced by light-period regime. Germination was significantly lower at 24 h of light (35.6%) compared to 24 h of dark, to, sequentially, 12 h of light/12 h of dark, and to, sequentially, 12 h of dark/12 h of light. Identical light treatments (25 C and 24 h of leaf wetness) had a similar, significant effect ($P = 0.05$) on disease severity, based on pairwise comparisons. When ranked, 12 h of dark/12 h of light was most conducive to infection, followed in descending order by 24 h of dark, 12 h of light/12 h of dark, and 24 h of light. Interruption of 24-h leaf-wetness periods for 4, 8, 12, and 16 h after an initial wetness period of 12 h had a significant influence on disease severity and on the number of latent infections. The effect depended on the relative humidity during the interruption. High-relative humidity (>95%) resulted in higher disease severity and number of latent lesions with increases in interruption periods, whereas low-relative humidity (~55%) resulted in lower values. The relationship between duration of leaf-wetness interruption and disease severity versus number of latent infections was statistically significant ($P = 0.01$) under both relative humidities. Additionally, there was evidence that the posttreatment relative-humidity conditions influenced the number of latent infections.

Leaf-wetness duration is a major component in the infection success of a variety of fungal pathogens, such as *Botryosphaeria obtusa, Mycosphoraella fijiensis* var. *difformis, Coccomyces hiemalis, Septoria glycines,* and *Colletotrichum acutatum* (2,4,7, 15,23). The minimum dew-period lengths necessary for infection by these pathogens ranged from 1–2 to 40 h. *Cercospora kikuchii* (Matsumoto & Tomoyasu) M. W. Gardner (13) is an important pathogen, causing leaf blight, latent infections, and purple seed stain on soybean (*Glycine max* (L.) Merr.). A minimum dew period of 18 h is reportedly necessary for leaf and pod infection by *C. kikuchii* (18). Dew periods of this length, however, are too infrequent under growing conditions in central Pennsylvania to explain the level of leaf and pod infection observed at the end of the growing season, as well as the level of inoculum caught in spore traps during the growing season. In addition to temperature, leaf-wetness duration, and relative humidity, researchers have shown light period and intensity to be influential in important stages of the disease cycle, such as infection by and sporulation (9,10,21) of fungal pathogens. The influence of light on infection has not been investigated for *C. kikuchii.*

The purpose of this study was to investigate the influence of interrupted dew periods, relative humidity during dry periods, and light regimes on the infection of soybean by *C. kikuchii.* The results of this study should be useful in understanding the infection process under field conditions, help explain epidemic development during the growing season, and lead to improved techniques for inoculations under controlled conditions.

MATERIALS AND METHODS

Plant production and maintenance. Two seeds of the susceptible, soybean cultivar Amsoy were planted, each pair in a 473-ml plastic container, in a mixture of steam-disinfested sand: peat:loam, 1:2:2 (v/v/v). Plants were placed on greenhouse benches, where temperatures, monitored by a hygrothermograph, ranged from 20 to 27 C, with the relative humidity at 30–80%. Plants were watered with deionized water and fertilized biweekly with Peter's 20:20:20 (N-P-K) fertilizer. After approximately 3 wk, plants were thinned to one plant per pot to achieve uniformity of plant material. Plants were maintained in the greenhouse until the second trifoliate developed fully.

Inoculum maintenance and production. An isolate of *C. kikuchii*, obtained from infected soybean seed collected at the Russell E. Larson Agricultural Research Center at Rock Springs, of The Pennsylvania State University, was maintained on clarified V-8 agar, pH 6.0, at 25 C. Five days before inoculation, 10-day-old fungal colonies and attached agar substrate were macerated in a Waring blender. The resulting slurry was spread on petri plates containing clarified V-8 agar. The plates were incubated at 25 C with 24 h of light (two 20-W cool-white fluorescent lights set 15 cm above the plate) per day for 4 days. This resulted in the production of numerous conidiophores, but conidial production was absent. After this treatment, plates were exposed to 12 h of darkness followed by 12 h of light, for 1 day, which induced the production of mature conidia of uniform age and size. This procedure was repeated for each inoculation. After four consecutive transfers, new fungal material from the original cultures was obtained from liquid-nitrogen storage; retrieval of original cultures prevented loss of pathogenicity due to prolonged culture on artificial media.

Inoculation. Cultures with mature conidia were flooded with 15 ml of distilled water (0.5% Tween 20). The surface of the colonies was gently rubbed with a camel-hair brush to dislodge conidia. The water/spore mixture was strained through a single layer of cheesecloth to remove mycelium fragments and was adjusted to 120,000 conidia per milliliter using a hemacytometer. Soybean plants were inoculated at the second-trifoliate stage, using a Badger airbrush (Franklin Park, IL) at 103.5×10^3 Pa of pressure. The fully-developed second-trifoliate leaf of each plant was sprayed for 2 s from a distance of 15 cm. Leaves were allowed to dry before the treatment began.

Disease assessment. After 4 wk, disease severity on the second trifoliate was assessed; standard-area diagrams (key 24, reference 8) were used to assess disease severity for each leaflet (reported values were the average for each leaf). Latent infections were assessed on the same leaf. Leaf area was measured using a LI-COR model LI-3000 leaf-area meter (Lincoln, NE). Leaves were then surface-sterilized for 30 s in 10% bleach and dessicated in petri dishes for 3 days, after which the leaves were placed in a moist chamber for 48 h. The number of latent infections per leaf was determined and standardized as the number of latent infections per square centimeter.

Influence of light period on germination in vitro. The influence of light on conidial germination was investigated in three incubators (model CEC-23 LPT-A, Rheem Environmental, Asheville, NC) under 2.5 W m^{-2} of cool-white, fluorescent light at 25 C. Light treatments consisting of 24 h of light, 24 h of dark, 12 h of light/12 h of dark, and 12 h of dark/12 h of light were carried out. Within each light treatment, germination of conidia deposited on coverslips was investigated at relative humidities of 100% wet, 100% dry, and 99%. A droplet containing conidia was allowed to evaporate before insertion into the humidity chamber for the 100% dry treatment; in the 100% wet treatment, it was not allowed to evaporate. Techniques used in this experiment were identical to those described by Jacome et al (7). Relative humidities were obtained using the agar dish, isopiestic-equilibration method developed by Harris et al (6) and modified as described by Arauz and Sutton (1). After each 24-h period, 100 randomly selected conidia per coverslip were assessed for germination. The whole experiment was repeated three times. Incubators were randomly assigned to a specific light treatment.

Influence of light period on infection. The influence of the light period on infection was investigated in two Percival dew chambers (Percival, Boone, IA) with approximately 1.46 W m^{-2} of cool-white, fluorescent and incandescent light, measured at a distance of 48 cm from the light source. Treatments consisted of 24 h of light, 24 h of dark, sequentially, 12 h of light/12 h of dark, and, sequentially, 12 h of dark/12 h of light. Temperature in the dew chambers was 25 C, with a leaf-wetness period of 24 h. Plants were allowed to dry in the lab after inoculation. A misting system was engaged for 15 min at the beginning of each treatment to ensure rapid, and uniform, dew formation. After the end of the treatment, plant surfaces were allowed to dry (15–30 min) before transport to the greenhouse. The plants were maintained in the greenhouse under the conditions described for plant maintenance. Due to variable temperature conditions in the greenhouse (22–30 C), treatments were compared in a pairwise fashion, in all possible combinations. Sixteen plants were inoculated for each treatment/replication. Dew chambers were randomly assigned to a specific treatment. The experiment was repeated four times.

Influence of interrupted leaf-wetness periods on infection. The influence of interrupted leaf-wetness periods on infection was investigated in Percival dew chambers set at 25 C, with plants in the dark. After an initial leaf-wetness period of 12 h, plants were removed from the dew chambers. Foliage was dried for 10 min using a fan. Afterwards, plants were subjected to 0, 4, 8, 12, and 16 h of dry leaves, at 25 C, with relative humidities of either >90% or approximately 55%, using growth chambers. After the appropriate dry period, plants again were subjected to 12 h of leaf wetness. At the end of the treatment, plants were moved to greenhouse benches. Disease severity and the number of latent infections were determined. There were five plants per treatment. The entire experiment was repeated two times. Temperatures in the greenhouse were 22–26 C. Relative humidity in the greenhouse during the first replication was 40–60%; relative humidity was >80% during the second replication. Differences in relative humidity were caused by an evaporative-cooling system in use during the second replication.

Statistical analysis. The influence of light periods on germination in vitro and on infection was analyzed using SAS Proc Anova (SAS Institute, Cary, NC [17]). The statistical significance of differences between means was determined using the Waller-Duncan K-ratio test and the t test for pairwise comparisons (13).

The influence of interrupted dew periods on infection was analyzed using SAS Proc GLM (SAS Institute, [17]). Data from the two experimental runs were combined for the analysis of the disease-severity variable, based on a full- and reduced-model (13) F-test.

RESULTS

Influence of light period on germination in vitro. The amount of light in a light period had a statistically significant ($P = 0.01$) influence on germination in vitro. When data values were averaged over the three relative humidities used, the 24 h of light treatment had a significantly lower germination rate (35.6%) than the other treatments had. For 12 h of dark/12 h of light, the average germination rate was 89.5%; for 12 h of light/12 h of dark, the average rate was 88.8%; and for 24 h of light/24 h of dark, the average rate was 87.7%. These values were not statistically different from each other. Similar results were observed when the relative-humidity treatments were analyzed separately (Fig. 1). The 24 h of light treatment had the lowest germination rate for each of the relative humidities. Rankings among the other treatments varied.

Influence of light period on infection. Germination in vivo was similar (>90.0%) for the 12 h of dark/12 h of light, the 12 h of light/12 h of dark, and the 24 h of dark treatments. Germination during the 24 of light treatment (63.5%) was significantly lower. When comparing disease severity of the treatments in a pairwise fashion, in all possible combinations, the 12 h of dark/12 h of light and the 24 h of dark treatments were not significantly different ($P = 0.05$) (Table 1). Both treatments had significantly higher disease severity than had the 12 h of light/12 h of dark and the 24 h of light treatments. The 12 h of light/12 h of dark treatment had significantly higher disease severity than the 24 h of light treatment had. Overall, disease severity ranged from 7.3 to 2.1%.

Influence of interrupted dew periods on infection. The length of the dry periods had a significant influence ($P = 0.01$) on disease severity. The influence, however, depended on the relative-humidity regime followed during the dry periods. When plants were subjected to high humidity during a dry period, disease severity increased with increases in dry periods (Fig. 2). Disease severity increased from an average of 5.3% with no leaf-wetness interruption to 9.5% with 16 h of interruption. A regression model ($y = 5.097 + 0.016DP^2$), in which y is the disease severity in percent and DP is the dry period in hours, described the relationship with an R^2-value of 0.87. Both parameters were significant at $P = 0.01$. When the relative humidity during the leaf-wetness interruption was low (~55%), however, disease severity declined with increases in dry periods. Maximum-disease severity, averaged at 5.3%, was observed after continuous leaf wetness; minimum-disease severity, averaged at 1.8%, was observed after the 16-h dry period (Fig. 3). A regression model ($y = 5.423 - 0.015DP^2$), in which the parameters were defined as before, described the relationship with an R^2-value of 0.84.

The effect of leaf-wetness interruption on the number of latent infections mirrored the results observed for disease severity. Results from the two replications could not be combined. The trend was similar between the two replications; the magnitude

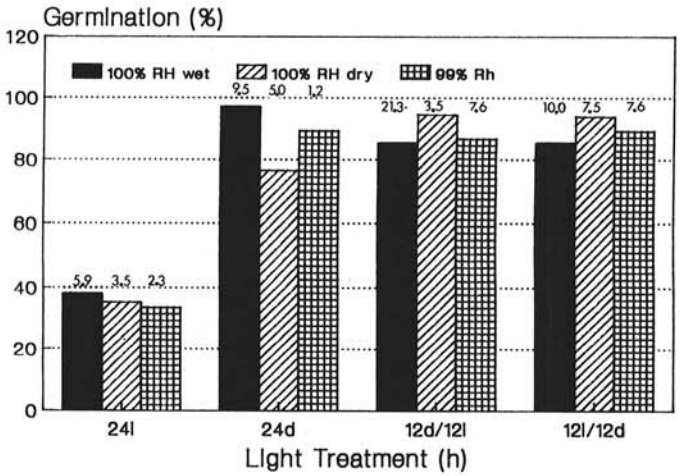

Fig. 1. Influence of four light treatments on the germination in vitro of *Cercospora kikuchii* conidia at three relative humidities (RH), at 25 C. 24l = 24 h of light; 24d = 24 h of dark; 12d/12l = 12 h of dark/12 h of light; and 12l/12d = 12 h of light/12 h of dark. Values are the averages of three runs. Numbers above bars are standard deviations.

of change and minimum and maximum values were different, however. During the high-humidity treatment, the number of latent infections increased with the length of the dew-period interruption. For replication 1, the observed values increased from 0.12 latent infections per square centimeter, with no leaf-wetness interruption, to 0.31, with 16 h of interruption. In replication 2, the values were 0.69 and 1.84 latent infections per square centimeter, respectively (Fig. 2). A regression model ($NL = 0.110 + 0.0007DP^2$ [$R^2 = 0.93$] and $NL = 0.680 + 0.075DP^2$ [$R^2 = 0.94$]), in which NL is the number of latent infections per square centimeter, described the relationship for replications 1 and 2, respectively.

When the humidity was low during dew interruption, the number of latent infections decreased with increases in dry periods. In replication 1, the observed values decreased from 0.12 with no dry period to 0.03 with the 16-h dry period. The values for replication 2 were 0.69 and 0.31, respectively (Fig. 3). A regression model ($NL = 0.119 - 0.005DP^2$ [$R^2 = 0.91$] and $NL = 0.695 - 0.001DP^2$ [$R^2 = 0.90$]) described the relationships for replications 1 and 2, respectively. The parameters were defined as before.

DISCUSSION

Experiments attempting to elucidate the influence of environmental factors on infection and/or disease development under controlled conditions generally have been conducted using continuous dew periods and continuous light or dark periods. Such an approach, although satisfactory for the development of resistance-screening methods, may not adequately reflect environmental conditions observed in the field and their effect on the infection process. In the case of dew periods, a minimum of 18 h was necessary for infection of soybean leaves under controlled conditions (18). Under field conditions in Pennsylvania, *C. kikuchii* generally sporulates between 0400 and 0800 and 1800 and 2100 (C. Orth and W. Schuh, *unpublished data*). In the absence of rain, the length of dew periods in central Pennsylvania rarely exceeds 9 h in the period from 0000 to 1200 and 5 h from 1200 to 2400 during the soybean-growing season (Table 2) (22). Shorter dew periods are observed frequently. Therefore, conidia deposited on soybean leaves after each of the diurnal sporulation events undergo periods of wetting, drying, and rewetting, with each of the individual dew periods shorter than the minimum, continuous dew periods established under controlled conditions. Similarly, conidia deposited on leaves are subjected to discontinuous light/dark events.

Results obtained in this study point to a potential mechanism enabling *C. kikuchii* to infect soybean leaves in the field, utilizing subminimal dew periods. When the relative humidity during the intervening dry period was low increasing the length of the dry period resulted in decreased disease severity and decreased latent infections. Even though the observed disease values during extended dry periods were low and probably negligible in economic terms, they were sufficient to ensure the survival of the fungus until soybean plants reached the growth stages in which they are susceptible to pod and seed infection. A similar situation was observed by Eisensmith et al (4). They found that interrupted dew periods led to reduced infection by cherry leaf spot when compared to continuous dew periods and constituted an important component of the disease-forecasting system. Relative humidities during the dry periods were uncontrolled (40–90%) in their study. When observing the shape of the curve for disease severity (Fig. 3), we saw a strong decrease in disease severity when the dew-period interruption extended for more than 8 h. The shape of the curve for latent infections showed similar behavior. In the apple scab pathosystem, Moore (12) determined that a dry period of 48 h was required to significantly reduce infection levels. Schwabe (19), using the same host-pathosystem, found that dry intervals of 16 h were necessary for ascospores and dry intervals of 32 h were necessary for conidia before wet periods could be treated differently. Relative humidity during the dry periods was uncontrolled. However, in experiments concerning the infection of apples by *Botyosphaeria obtusa* (3), infection of apple foliage stopped irreversibly with dew-period interruptions of 1 h or more.

If the humidity was high (>90%) during intervening dry periods, however, disease severity and latent infections increased with increases in dry periods. The high-relative humidity during the dry period enabled *C. kikuchii* to continue germ-tube development. This agrees with Schuh's (18) findings that conidia of *C. kikuchii* were able to germinate at relative humidities as low as 92.5%. Shaw (20) reported similar results when investigating the influence of interrupted dew periods on infection of wheat by *Mycosphaerella graminicola*. When periods of 100% relative humidity were interrupted by dry periods with 75% relative humidity, infection was only slightly reduced, whereas relative humidities of 50% during dry periods led to a drastic reduction in infection.

TABLE 1. Comparison of disease severities (percent leaf area diseased) of *Cercospora kikuchii* on soybeans (cv. Amsoy 71) under different light-period treatments

Light Treatments[a]	Disease Severities (%)
12 d/12 l vs. 24 d	4.3 vs. 3.6 ns[b]
24 d vs. 24 l	5.6 vs. 2.1 *
12 d/12 l vs. 24 l	4.4 vs. 2.8 *
24 d vs. 12 l/12 d	5.3 vs. 3.0 *
12 d/12 l vs. 12 l/12 d	5.6 vs. 3.2 *
12 d/12 l vs. 24 l	7.3 vs. 4.7 *

[a] 12 d/12 l = 12 h of dark/12 h of light; 12 l/12 d = 12 h of light/12 h of dark; 24 d = 24 h of dark; and 24 l = 24 h of light.
[b] ns = not significant, * = significant at $P = 0.05$ (t test).

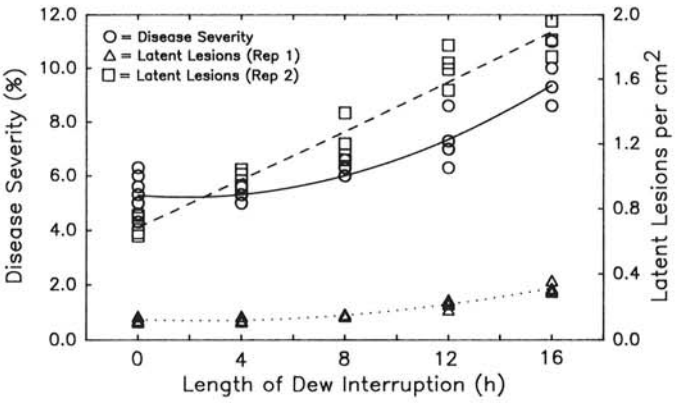

Fig. 2. Influence of dew-period interruption on disease severity (percent) and latent infections (square centimeter) of *Cercospora kikuchii* on soybean, under high humidity (>90%).

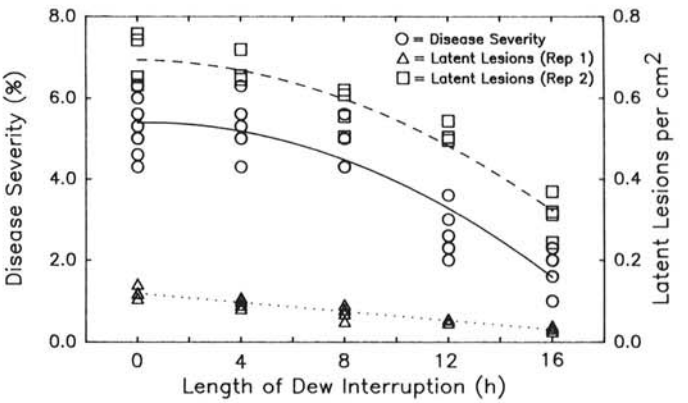

Fig. 3. Influence of dew-period interruption on disease severity (percent) and latent infections (square centimeter) of *Cercospora kikuchii* on soybean, under low humidity (~55%).

There was a significant difference between the number of latent infections observed for replications 1 and 2, but not for disease severity, independent of the relative-humidity regime, during the dry periods. The main difference between replications 1 and 2 was the relative humidity prevalent in the greenhouse after the treatments. This was caused by the use of an evaporative-cooling system during the second replication. Typical *C. kikuchii* lesions are the result of stomatal penetration by the germ tube and subsequent intercellular growth in the parenchyma (5,11,14). As long as conditions are sufficient for germ-tube elongation, increases in disease severity are likely. Even though the relative humidity in the greenhouse during the second replication was approximately 80%, this was not sufficient for continued germ-tube growth. Therefore, the posttreatment difference in relative humidity did not result in different disease severities. Latent infections, however, are caused by the formation of appressoria, resulting in penetration of epidermal cells without visible symptoms (14). Once the fungal development has reached a certain stage in the infection process (e.g., appressoria have been formed), high-relative humidities (80%), insufficient for germ-tube elongation, are sufficient to complete the infection process, whereas low-relative humidities (40–60%) are not. Alternately, high-relative humidity following leaf wetness induces the formation of appressoria. Both mechanisms could explain the differences in the number of latent infections between replications 1 and 2. The effect of relative humidity on infection during the incubation period is currently being investigated in greater detail.

Light periods had a significant impact on the germination and infection of soybean plants. Differences among the treatments, although statistically significant, were small. Light intensity under controlled conditions was abnormally low compared to field conditions. The light intensity was 2.5 W m^{-2} in the incubators and 1.46 W m^{-2} in the dew chambers, compared to an average 545 W m^{-2} in the field, during June and July (16). To ascertain the relevance of the results to infection processes under field conditions, higher light intensities are needed. Studies by Stevenson and Pennypacker (21) showed that inhibition of germination of *Alternaria solani* increased from 7.6% at 62 W m^{-2} to 44.8% at 545 W m^{-2}. The influence of light on germination and infection of corn by *Exserohilum turcicum* was observed by Levy and Cohen (10). The lowest amounts of infection and germination were observed under continuous-light conditions. Germination in Levy and Cohen's treatments increased from continuous light, to light/dark, to dark/light, to continuous dark.

The ability of *C. kikuchii* to infect the leaves of soybeans utilizing noncontinuous wet periods of relatively short duration helps explain the disease symptoms and sporulation events observed in Pennsylvania throughout the growing season. The results point to potential mechanisms by which pathogens that require extended dew periods for infection under controlled conditions infect host plants in the field. The determination of which light periods are most conducive to infection is useful for optimizing environmental parameters for resistance screening under controlled conditions. This study also points to the importance of relative humidities during the leaf wetness-interruption period and during the incubation period. The vast number of possible factor combinations (leaf-wetness duration, leaf wetness-interruption duration, and relative humidity during and after the treatments) precludes the utilization of mathematical models to predict disease severities per number of latent infections under field conditions.

LITERATURE CITED

1. Auraz, L. F., and Sutton, T. B. 1989. Influence of temperature and moisture on germination of ascospores and conidia of *Botryosphaeria obtusa*. Phytopathology 79:667-674.
2. Auraz, L. F., and Sutton, T. B. 1989. Temperature and wetness duration requirements for apple infection by *Botryosphaeria obtusa*. Phytopathology 79:440-444.
3. Auraz, L. F., and Sutton, T. B. 1990. Effect of interrupted wetness periods on spore germination and apple infection by *Botryosphaeria obtusa*. Phytopathology 80:1218-1220.
4. Eisensmith, S. P., Jones, A. L., and Cress, C. E. 1982. Effects of

TABLE 2. Average leaf-wetness duration per day (1982–1991) in central Pennsylvania for July and August, measured using a gold-plated electronic grid placed at the Russell E. Larson Agricultural Research Center at Rock Springs, of The Pennsylvania State University

Month	Day	Leaf Wetness (h)		Month	Day	Leaf Wetness (h)	
		000–1200	1200–2400			000–1200	1200–2400
July	1	6	3	August	1	8	2
	2	6	3		2	6	3
	3	8	4		3	5	2
	4	6	4		4	5	3
	5	6	5		5	7	3
	6	7	3		6	6	2
	7	7	1		7	5	4
	8	6	3		8	9	4
	9	6	3		9	8	4
	10	7	3		10	7	3
	11	6	4		11	6	4
	12	7	4		12	7	1
	13	7	3		13	6	3
	14	6	4		14	7	2
	15	6	2		15	7	2
	16	7	4		16	7	2
	17	5	2		17	6	3
	18	6	2		18	7	3
	19	6	3		19	8	3
	20	9	5		20	8	3
	21	9	4		21	8	4
	22	7	3		22	7	2
	23	7	4		23	6	4
	24	7	2		24	5	3
	25	6	3		25	7	1
	26	7	5		26	5	4
	27	8	2		27	7	3
	28	8	2		28	5	4
	29	6	2		29	7	3
	30	7	3		30	8	2
	31	7	3		31	5	2

interrupted wet periods on infection of sour cherry by *Coccomyces hiemalis*. Phytopathology 72:680-682.
5. Fujita, V. 1990. Ecology and control of purple seed stain of soybean caused by *Cercospora kikuchii*. Bull. Tohoku Natl. Agric. Exp. Stn. (Morioka) 81:51-109.
6. Harris, R. F., Gardner, W. R., Adebayo, A. A., and Sommers, L. E. 1970. Agar dish isopiestic equilibration method for controlling the water potential of solid substrates. Appl. Microbiol. 19:536-537.
7. Jacome, L. H., Schuh, W., and Stevenson, R. E. 1991. Effect of temperature and relative humidity on germination and germ tube development of *Mycosphaerella fijiensis* var. *difformis*. Phytopathology 81:1480-1485.
8. James, W. C. 1971. An illustrated series of assessment keys of plant diseases, their preparation and usage. Can. Plant Dis. Surv. 51:39-65.
9. Kaneko, S. 1989. Effect of light intensity on the development of pine wilt disease. Can. J. Bot. 67:1861-1864.
10. Levy, Y., and Cohen, Y. 1983. Differential effect of light on spore germination of *Exserohilum turcicum* on corn leaves and corn leaf impressions. Phytopathology 73:249-252.
11. Matsumoto, T., and Tomoyasu, R. 1925. Studies on purple speck of soybean seed. Ann. Phytopathol. Soc. Jpn. 1:1-14.
12. Moore, M. H. 1964. Glasshouse experiments on apple scab. 1. Foliage infection in relation to wet and dry periods. Ann. Appl. Biol. 54:423-435.
13. Neter, T., and Wasserman, W. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, IL. 842 pp.
14. Orth, C. E., and Schuh, W. 1992. Histological comparison of latent and active infections of soybean foliage by *Cercospora kikuchii* (Abstr.) Phytopathology 82:1159.
15. Peterson, D. J., and Edwards, H. H. 1982. Effects of temperature and leaf wetness period on brown spot disease of soybeans. Plant Dis. 66:995-998.
16. Reifsnyder, W. E., and Hull, H. W. 1965. Radiant energy in relation to forest. U.S. Dep. Agric. For. Serv. Tech. Bull. 1344. 111 pp.
17. SAS Institute. 1985. SAS User's Guide: Statistics Version 5 ed. SAS Institute, Cary, NC. 956 pp.
18. Schuh, W. 1991. Influence of temperature and leaf wetness period on conidial germination in vitro and infection of *Cercospora kikuchii* on soybean. Phytopathology 81:1315-1318.
19. Schwabe, W. F. 1980. Wetting and temperature requirements for apple leaf infection by *Venturia inequalis* in South Africa. Phytophylactica 12:69-80.
20. Shaw, M. W. 1991. Interacting effects of interrupted humid periods and light on infection of wheat leaves by *Mycosphaerella graminicola* (*Septoria tritici*). Plant Pathol. 40:595-607.
21. Stevenson, R. E., and Pennypacker, S. P. 1988. Effect of radiation, temperature, and moisture on conidial germination of *Alternaria solani*. Phytopathology 78:926-930.
22. Stevenson, R. E., and Pennypacker, S. P. 1990. Metereological Summary for the Russell E. Larson Agricultural Research Center at Rock Springs. The Pennsylvania State University College of Agriculture, Metereological Report, University Park. 58 pp.
23. Wilson, L. L., Madden, L. V., and Ellis, M. A. 1990. Influence of temperature and wetness duration on infection of immature and mature strawberry fruit by *Colletotrichum acutatum*. Phytopathology 80:111-116.