Environmental Factors Influencing the Discharge of Basidiospores of *Gymnosporangium juniperi-virginianae*

R. C. Pearson, R. C. Seem, and F. W. Meyer

Assistant professors and research technician III, respectively, New York state Agricultural Experiment Station, Cornell University, Geneva, NY 14456.

Accepted for publication 24 September 1979.

ABSTRACT

PEARSON, R. C., R. C. SEEM, and F. W. MEYER. 1980. Environmental factors influencing the discharge of basidiospores of *Gymnosporangium juniperi-virginianae*. Phytopathology 70:262-266.

Discharge of basidiospores by *Gymnosporangium juniperi-virginianae* was studied under field conditions during three growing seasons. Discharge usually began within a few hours of the start of rainfall, continued throughout the rain period, and ceased when rainfall ended, leaves dried, and relative humidity (RH) dropped below 85%. The duration of the spore release period was most highly correlated with hours RH $\geq$85% ($r = 0.935$). Generally, environmental parameters had higher correlation coefficients with duration of spore discharge than with spore numbers. Delays in discharge of basidiospores following the start of rainfall were not significantly correlated with any of the environmental parameters studied. Multiple regression equations were developed to predict the amount and duration of spore discharge based on easily measured environmental parameters. On several occasions after a rain-induced spore discharge period, basidiospore release resumed 12–24 hr later in the absence of rainfall or leaf wetness. This phenomenon was highly correlated with hours RH $\geq$85% ($r = 0.869$).

Additional key words: cedar apple rust, epidemiology, *Juniperus virginiana, Malus pumila.*

There are two conflicting theories about basidiospore liberation in *Gymnosporangium juniperi-virginianae* Schw., the incitant of cedar apple rust of apple (*Malus pumila* Miller). One theory stipulates that drying of the telial horn, or at least a drop in relative humidity (RH), is required following a rain to initiate discharge of basidiospores (3–6,9,15). The second theory states that liberation of basidiospores can occur during a rain or during periods of high humidity following a rain (2,7,11,17). Much of the information on which these theories are based as well as information on basidiospore liberation by other *Gymnosporangium* spp. (11,14,17) has been derived from empirical observations rather than experimental data. Pady and Kramer (8) provided experimental data from growth chamber experiments that support the second theory. Parmelee (10), in his study of various species of *Gymnosporangium,* adopted the technique of soaking telia in water until basidia were evident by microscopic examination or basidiospore discharge turned the water yellow. This evidence indirectly supports the second theory. This paper reports on a quantitative study conducted under field conditions, the results of which also support the theory that liberation of basidiospores does not require drying of telial horns, but can occur during rain or subsequent periods of high relative humidity.

MATERIALS AND METHODS

Discharge of basidiospores by *G. juniperi-virginianae* was studied by continually monitoring aerial spore concentration in the field at Highland, New York. Branches of eastern red cedar (*Juniperus virginiana* L.) bearing abundant cedar apple rust galls were pruned from trees, placed in buckets of water, and arranged in a ring (2 m radius) around a Burkard seven-day volumetric spore trap (Burkard Manufacturing Co. Ltd., Rickmansworth, Hertfordshire, England). The trap orifice was 0.5 m above the ground at approximately the same height as the galls. Fresh, galled branches were substituted periodicially, but many of the branches remained unwilted for 3–4 wk. Basidiospores that impinged on the petrolatum-coated Melinex tapes were identified by their characteristic shape and orange color. Spore concentrations per cubic meter of air were determined hourly. Temperature and relative humidity were recorded with a 7-day recording hygrothermograph at 1.3 m above ground level in a standard weather shelter. Amount and duration of rainfall were recorded continuously by a tipping-bucket rain gauge. Leaf wetness was recorded continuously by a hemp string, leaf-wetness meter (DeWit type; Valley Stream Farms, Orono, Ontario, Canada) and by an electronic leaf-wetness detector (developed at the New York State Agricultural Experiment Station, Geneva) which was connected to the hygrothermograph and recorded on the same chart. Weather observations and airborne spore concentrations were recorded continuously from April through June in 1975, 1976, and 1977.

Weather data were manually transcribed or digitized by computer (1) into hourly values. Data were summarized for each time period in which spores were continuously released. Variables such as average temperature during the period, number of hours RH $\geq$85%, and total rainfall were compared with the dependent variables, total spores released during the period, number of hours in the period, and delay between initiation of the period and first spore catch. For statistical analysis, the primary discharge periods (PDP) were arbitrarily defined in three ways and corresponding data bases were identified as follows: the discharge period started with the hour of first spore catch and ended with the hour of last spore catch (SS); the discharge period started with the hour of first rainfall and ended when the leaf-wetness meter indicated drying or that the relative humidity was $\leq$98% whichever occurred later (RR); and the discharge period started with the hour of first rainfall and ended with the hour of last spore catch (RS). Secondary discharge periods (SDP) followed PDP by 12–24 hr, occurred in the absence of rainfall, and were defined according to the SS criteria. Correlation coefficients between the dependent and independent variables were tested for statistical significance with Student's *t*-test. Multiple regression analysis was performed on different variable sets by using variable significance and coefficients of determination ($\bar{R}^2$) as statistical tests.

RESULTS

Seasonal pattern of availability of basidiospores. Release of *G. juniperi-virginianae* basidiospores generally occurred from the last week of April through the third week of June during the 3 yr of observation. However, in 1977 release occurred from the 3rd week of April through the end of June. The 1977 release season in general was earlier, cooler, and drier than most seasons. The total rainfall

0031-949X/80/03026205/$03.00/0

during the 1977 release season was 61.5 cm compared to 142.3 and 99.2 cm for 1975 and 1976, respectively. Furthermore, the average rainfall per spore release period was 10.2, 6.2, and 3.4 cm for 1975, 1976, and 1977, respectively, although the average length of each spore release period was 22.4, 16.1, and 18.8 hr, respectively. During each of the 3 yr, the period of availability of basidiospores, determined by artificial wetting of galls in the laboratory as described previously (12), overlapped the early pink and full bloom period, the time when fruit are most susceptible to infection (5), for all susceptible apple cultivars grown in eastern New York.

Primary discharge periods. Basidiospores were liberated throughout periods of rainfall and continued to be discharged after rains ended providing the atmospheric moisture was near saturation (Fig. 1A). The $\log_e$ of the total number of spores discharged during release periods was highly correlated with the length of the discharge period (SS data base, r = 0.767). The number of hours of discharge was highly correlated with the number of hours from beginning of rainfall to leaf drying or RH $\leqslant$ 98% (RR data base, r = 0.871) and with the number of hours from beginning of rainfall to last spore catch (RS data base, r = 0.967) (Table 1). The relationship between hours of discharge and hours in the period in the RR data base strongly suggest a role for moisture.

Moisture proved to be a critical factor in determining the duration of spore release periods. The number of hours in a spore discharge period was positively correlated with total rainfall for the period as defined by data bases SS (r = 0.736), RR (r = 0.613), and RS (r = 0.647); and the relationship between length of the spore discharge period and the number of hours of leaf wetness during the spore discharge period (SS data base) gave an even higher correlation (Fig. 2). Finally, of the 48 spore discharge periods in SS, 35 had leaves wet $\geqslant$ 50% of the time and 14 of 48 had leaves wet 100% of the time.

Relative humidity was the factor that correlated best with spore discharge. Analysis of conditions during the first hour of spore discharge (SS data base) indicated that 81% of the observations had RH values in the 90–100% range. The best correlation (r = 0.935) was hours of discharge with hours of relative humidity at or above a base level of 85% (Fig. 3). As the base level increased to 100% RH, the corresponding correlation coefficients decreased to r = 0.581 (Table 1). Apparently the duration of spore discharge is highly correlated with humidity because the humidity factor includes the time when spores continue to be released after rainfall has ended.

Temperature was not a major limiting factor for most discharge periods, and average temperatures were generally in the 8–24 C range during spore release periods identified by the start of rain and the end of spore release, RS (Fig. 4). During a wetting period in 1977, precipitation changed from rain to snow after the telial horns had expanded, and no basidiospores were trapped during that period (Fig. 1B).

Darkness during rain periods appeared to have some influence on the time of major spore release. The 41 rain periods observed during the 3-yr study were separated according to the occurrence of daylight (0600 to 2000 hours) or darkness (2100 to 0500 hours) during the lst hr of rainfall and hour of peak spore discharge. Since the number of daylight hours was greater than the number of darkness hours, the data were expressed in terms of the number of events per hour. Daylight averaged 1.9 rain starts per hour and darkness averaged 1.3 rain starts per hour. Although spore discharge began within a few hours of the start of rainfall, regardless of light conditions, three times as many spore discharge peaks occurred during darkness as during daylight, 3.3 and 1.1 peaks per hour, respectively.

A delay in the release of spores following the start of a rain period was encountered frequently (Fig. 1A), but the duration of the delay was not significantly correlated with any of the variables tested (Table 1).

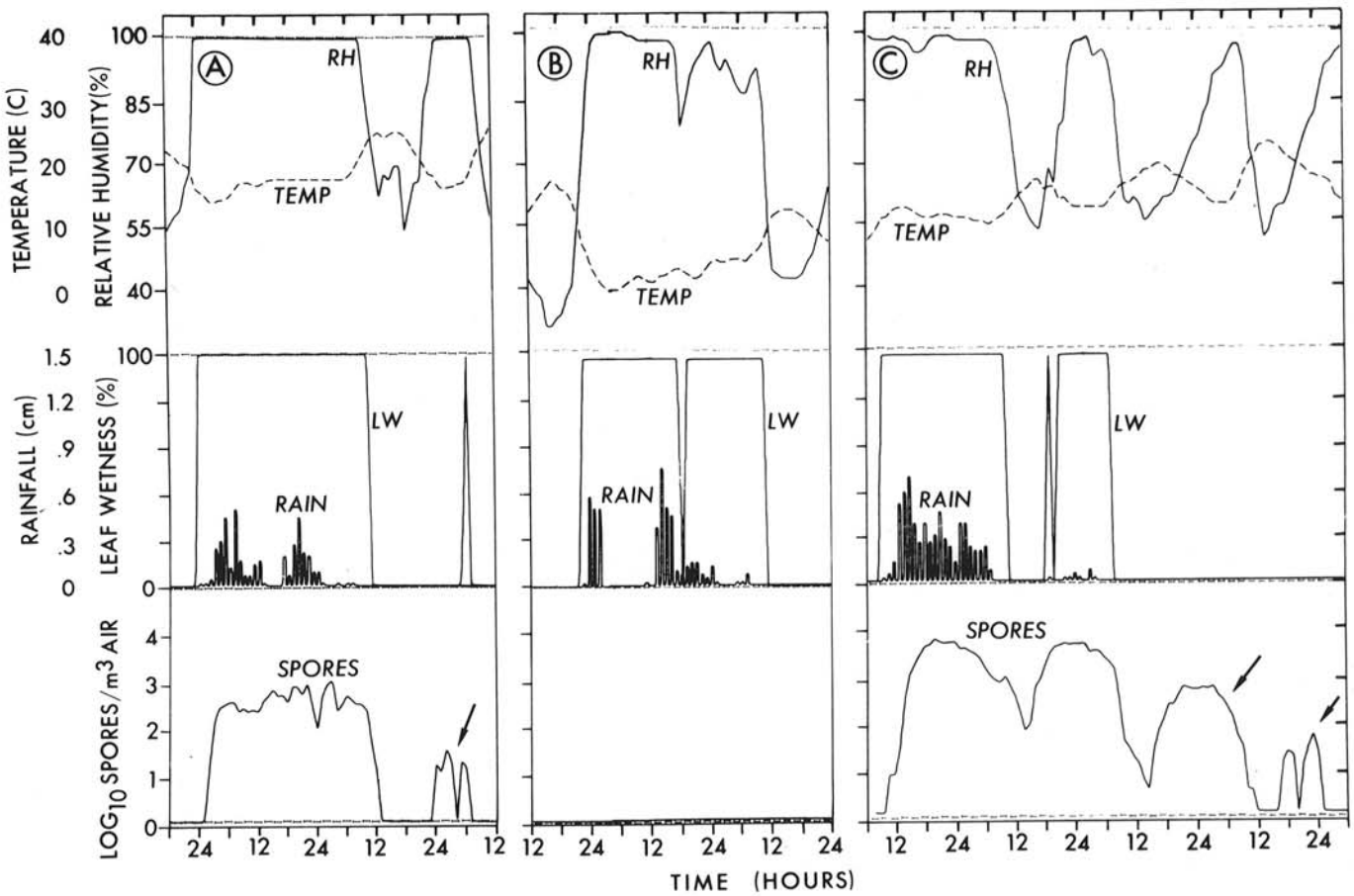

Fig. 1. A, Hourly concentration of basidiospores of *Gymnosporangium juniperi-virginianae* per cubic meter of air, with corresponding rainfall, leaf wetness, relative humidity, and temperature (12–14 June 1975). Arrow identifies secondary discharge period. **B,** Lack of spore discharge during a period of low temperature and snowfall (8–10 May 1977). **C,** Secondary spore discharge periods (arrow) (9–13 June 1977).

Multiple regression analysis on the two main dependent variables, spores discharged (SS data base) and length of discharge period (SS data base), yielded the following equations when ease of parameter estimation was considered with the statistical tests:

$$\log_e SP = -3.772 + 0.186\ RH85 + 0.184\ T_o + 0.629\ RH_o + 0.649\ R_o \quad (1)$$

$$DP = 0.7425 + 1.119\ RH85 + 0.281\ R \quad (2)$$

where SP is spores discharged per cubic meter of air per period, DP is hours per period, RH85 is hours of RH $\geq$ 85% per period, RH_0 is the percent RH at the start of the discharge period, T_0 is the temperature (C) at the start of the discharge period, R_0 is the rainfall (cm) for the first hour of the discharge period, and R is the total rainfall (cm) per period. The coefficient of determination corrected for degrees of freedom is 69.0 and 88.6% for equations 1 and 2, respectively. All terms within each equation were highly significant ($P \leq 0.01$).

Secondary discharge periods. Secondary discharge periods (SDP) (not to be confused with Crabill's [3] secondary sporidia) followed several PDP by 12–24 hr (Fig. 1A and 1C). Twenty-nine SDP were identified during the 3-yr study; all occurred in the absence of rainfall and 24 of them occurred when leaves were dry. Because of the absence of rainfall and low incidence of hours with wet leaves during the SDP, these two parameters were dropped from the analysis. The highest correlation was achieved between hours of discharge and $\log_e$ of numbers of spores per discharge ($r = 0.894$) (Table 2). The best relationship between environmental parameters and length of the SDP was the length of time RH $\geq$85% during the SDP ($r = 0.869$). Darkness did not appear to influence the initiation of SDP, but three times as many spore discharge peaks occurred during darkness as during daylight, 1.6 and 0.5 peaks per hour, respectively. Several preconditioning parameters were analyzed, but no factors seemed to have highly significant ($P \leq 0.01$) influence on SDP. The length of the SDP (hours of discharge), but not the $\log_e$ spores of SDP, was significantly ($P \leq 0.05$) correlated with the $\log_e$ number of spores caught during the PDP 24 hr before ($r = 0.419$). Both $\log_e$ total spores and hours of discharge were significantly ($P \leq 0.05$) correlated with the average temperature 2 hr prior to the SDP, and $\log_e$ spores was also correlated with the average temperature 6 hr before the SDP.

The linear combination of independent variables associated with SDP did not show an additive effect. Only hours of RH $\geq$85% was significant, alone or in combination with other variables.

The relative importance of SDP can be gauged by the percentage of total spores released during SDP for each of the three years of observation. Secondary discharge periods accounted for 3, 0.1, and 1% of the total spores released during 1975, 1976, and 1977, respectively.

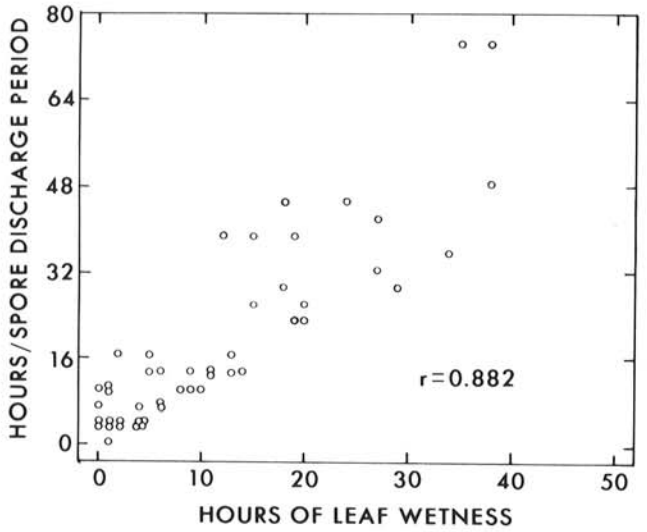

Fig. 2. Comparison of hours per primary basidiospore (*Gymnosporangium juniperi-virginianae*) discharge period and hours of wetting during the corresponding period (SS data base).

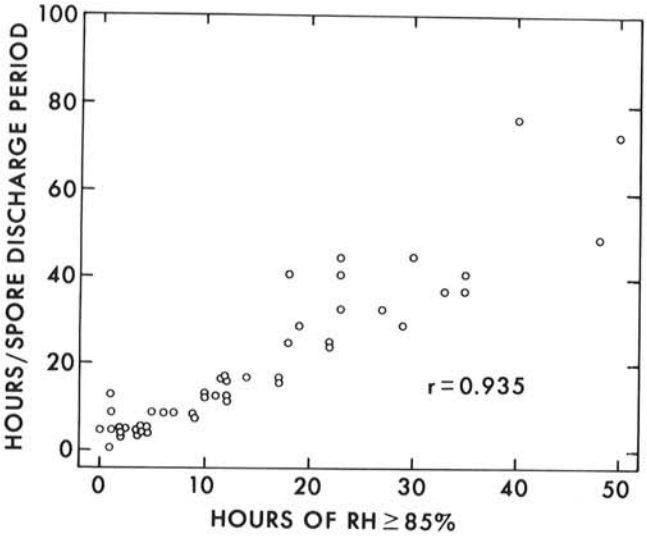

Fig. 3. Comparison of hours per primary basidiospore (*Gymnosporangium juniperi-virginianae*) discharge period and hours of relative humidity $\geq$ 85% during the corresponding period (SS data base).

DISCUSSION

At present, all commercially available fungicides for control of cedar apple rust are classified as protectants. To be effective they must be present at the infection court before an infection period begins. Recently some new experimental fungicides have shown promise as eradicants to be used after an infection period has occurred (13,16). Efficient use of these eradicant fungicides requires precise knowledge of not only whether an infection period occurred, but also its starting time and its duration. This requires knowledge of the time and duration of release of basidiospores. Reed and Crabill (15) and Hamilton (5) each suggested that the most suitable situation for a cedar apple rust infection period was an intermittent wetting period or a rain followed by drying preceding another wetting period, either rain or dew. This was

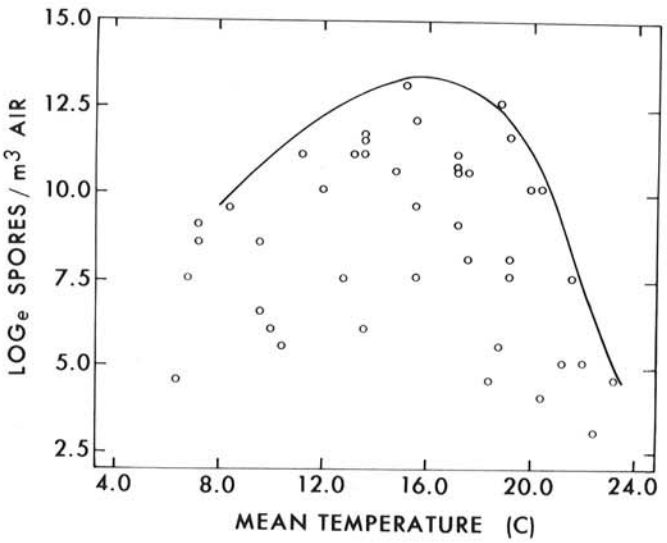

Fig. 4. Comparison of total basidiospores (*Gymnosporangium juniperi-virginianae*) caught per cubic meter of air for each primary discharge period and the average temperature (C) during the period (RS data base). The curve defines the highest spore concentrations observed during the 3-yr study.

based upon the theory that basidiospore release occurs at the end of a rain when the humidity decreases. A second wetting period would be necessary for infection by the basidiospores that had been released during the previous wetting period. Our analysis suggests that this theory is inaccurate because the assumption that basidiospore release requires drying is incorrect. Our studies support the observations of MacLachlan (7) and Pady and Kramer (8) that spore discharge begins in the rain and continues as long as moisture is available.

Coons (2) reported that relative humidity had no effect on spore discharge as long as promycelia were not desiccated. We found RH $\geq 85\%$ to be very important in determining both quantity and duration of spore discharge. Relative humidity in this range might be adequate to keep promycelia from desiccating, a hypothesis that would support Coons' qualifying statement.

The relationship between temperature during the wetting period and the highest concentration of basidiospores released under field conditions (curve, Fig. 4) closely follows reports in the literature concerning temperature requirements for formation of basidiospores under controlled laboratory conditions (5,12,15,17). Although not shown to be significant, the inverse relationship between delay of spore discharge after the beginning of a rain and temperature suggests that low temperature inhibited formation of basidiospores. This hypothesis is supported by recent laboratory studies demonstrating that low temperatures inhibit basidiospore formation (12). The period when snow followed rain also demonstrated this relationship (Fig. 1B). Although snow accumulated on the upper surface of galls, telial horns on the underside were exposed so apparently the absence of basidiospores was due to low temperature.

Pady and Kramer (8) exposed rust galls to continuous misting in growth chambers and reported continuous basidiospore discharge thoughout alternating periods of light and dark (12-hr duration). However, they observed peaks in spore discharge at fairly regular intervals, usually during periods of darkness. They theorized that light retarded spore discharge and perhaps teliospore germination. Under field conditions, we also observed release of spores throughout periods of free moisture, but major fluctuations in spore concentrations usually were associated with periods of drying. Within spore release periods, however, peaks in spore discharge could be identified and three times as many peaks occurred in the dark as in daylight. This observation under field conditions supports Pady and Kramer's observations under controlled conditions of continuous misting. Unfortunately, Pady and Kramer did not alternate wetting and drying periods, although they did state than an accidental desiccation in the chambers caused cessation of spore discharge and that discharge resumed as soon as telia had reabsorbed moisture (8).

By defining PDP in three different data bases, more critical examination of the effects of various parameters was possible. All analyses could have been accomplished with the RS data base; but by further restricting the PDP to SS or RR, more significant correlations were calculated; ie, $\log_e$ spores versus average temperature and temperature the first hour, and hours of discharge versus hours of RH = 100%. If SS only had been analyzed it would not have been possible to study factors affecting discharge delay. Generally, correlation coefficients calculated in the RS data base were lower than those in the RR or SS data bases. Analysis of the SS data base provided the major evidence for spore discharge occurring during rainfall, whereas analysis of only RS or RR would not have eliminated rainfall during hours when spores were not released. Analysis of average temperature during the discharge period provided an interesting comparison between $\log_e$ total spores and duration of discharge in the three data bases. $\log_e$ spores was positively correlated with average temperature in the SS data base, but hours of discharge were negatively correlated with average temperature in the RR and RS data bases. Both RR and RS data bases included the delay in basidiospore discharge, which also tended to be negatively correlated with average temperature and perhaps influenced the correlation with hours of discharge.

The linear combination of independent variables from the SS data base showed that 69% of the variation among $\log_e$ spores discharged per period could be accounted for using easily measured parameters (hours RH $\geq 85\%$ per period and initial values of relative humidity, temperature, and rainfall). Similarly, 88.6% of the variation among hours of discharge could be accounted for by two easily measured parameters (hours RH $\geq 85\%$ and total

TABLE 1. Correlations of various parameters with $\log_e$ of the number of spores per cubic meter of air (*Gymnosporangium juniperi-virginianae* basidiospore trap counts), hours of discharge, and hours of discharge delay during primary spore discharge periods in April, May, and June 1975, 1976, and 1977 at Highland, New York. Correlations were made for three data bases representing different definitions of the discharge period

Dependent variable	Independent variable	Data base[a]		
		SS	RR	RS
Number of spores $\log_e$	Hr of discharge	0.767***[b]	0.687***	0.684***
	Total rainfall	0.495***	0.427***	0.444**
	Hr leaves wet	0.688***	0.453***	0.466**
	Hr RH $\geq$85%	0.776***	0.501***	0.582***
	Avg temp	0.298*	−0.154	−0.145
	Temp first hr	0.332*	−0.100	−0.106
Discharge (hr)	Hr in period	...[c]	0.871***	0.967***
	Total rainfall	0.736***	0.613***	0.647***
	Hr leaves wet	0.882***	0.857***	0.819***
	Hr RH $\geq$85%	0.935***	0.883***	0.882***
	Hr RH $\geq$90%	0.925***	0.891***	0.875***
	Hr RH $\geq$95%	0.869***	0.798***	0.749***
	Hr RH = 100%	0.581***	0.558***	0.382*
	Avg temp	0.130	−0.313*	−0.377*
	Temp first hr	0.149	−0.167	0.293
Discharge delay (hr)	Avg temp	...	−0.209	−0.208
	Temp first hr	...	−0.154	−0.188
	Temp first 2 hr	...	−0.183	−0.199
	Temp first 4 hr	...	−0.094	−0.199
	Rainfall first hr	...	−0.010	0.106
	Rainfall first 2 hr	...	0.044	0.005
	Rainfall first 4 hr	...	0.032	0.060
	RH first hr	...	0.042	−0.014

[a]Discharge period definitions: SS = first spore to last spore; RR = first rain to last rain, leaf wetness or RH < 98%, RS = first rain to last spore.
[b]Student's *t*-test at $P \leq 0.05$ (*), $P \leq 0.01$ (**), and $P \leq 0.001$ (***).
[c]Three-dots mean that a correlation coefficient cannot be calculated or is not appropriate.

TABLE 2. Correlations of various parameters with $\log_e$ of the number of spores per cubic meter of air (*Gymnosporangium juniperi-virginianae* basidiospore trap counts) and hours of discharge during secondary spore discharge periods (SDP) in April, May, and June 1975, 1976, and 1977 at Highland, NY

Independent variable	Correlation with $\log_e$ spores	Correlation with hours of discharge
Average Temperature	0.342	0.335
Temp first hr	0.474**[a]	0.433*
Hr RH $\geq$85%	0.631***	0.869***
Hr of discharge	0.894***	1.000
Avg temp 2 hr prior to SDP	0.451*	0.407*
Avg temp 6 hr prior to SDP	0.394*	0.353
Avg temp 12 hr prior to SDP	0.222	0.225
Rainfall 6 hr prior to SDP	−0.006	−0.010
Rainfall 12 hr prior to SDP	−0.041	−0.048
Rainfall 24 hr prior to SDP	0.009	−0.033
$\log_e$ spores 4 hr prior to SDP	−0.091	−0.117
$\log_e$ spores 12 hr prior to SDP	0.252	0.363
$\log_e$ spores 24 hr prior to SDP	0.294	0.419*
Hr RH $\geq$85% 12 hr prior to SDP	0.198	0.227
Hr leaves wet 2 hr prior to SDP	0.061	0.038
Hr leaves wet 6 hr prior to SDP	0.145	0.099
Hr leaves wet 12 hr prior to SDP	0.266	0.257

[a]Students *t*-test at $P \leq 0.05$ (*), $P \leq 0.01$ (**), and $P \leq 0.001$ (***).

rainfall per period). While these equations account for less data variation than might be desirable, from a disease management perspective it might be possible to approximate the relative length and intensity of each discharge period. This must be verified by using independent data.

The secondary discharge periods we observed probably are not equivalent to the secondary peaks in spore discharge reported by Pady and Kramer (8), since they had exposed galls to continuous moisture and the SDP we observed occurred in the absence of free moisture. However, since RH $\geqslant$ 85% was the most highly correlated environmental parameter with SDP and because it was the only significant parameter in the multiple regression analysis of length and intensity of SDP, perhaps an explanation for their occurrence lies in the ability of the gelatinous telial horn to hold or imbibe water as noted in similar gelatinous structures of other fungi (14). The horn may retain a critical minimum amount of moisture after the PDP and then imbibe additional moisture from the air to reinitiate basidiospore formation or discharge of preformed basidiospores.

The significance of SDP is diminished when one considers the rather small contribution of spores from SDP to the total inoculum potential. Generally, large SDP followed large PDP, as indicated by the significant correlation of hours of discharge (SDP) and $\log_e$ of numbers of spores (PDP) 24 hr before (Table 2). Conditions for infection during large PDP usually were favorable and of such magnitude that infections resulting from SDP would be insignificant. Furthermore, SDP generally did not occur during periods favorable for infection; ie, no free moisture on apple foliage. Therefore, the ability of basidiospores to survive until conditions favorable for infection would be crucial. Basidiospores are capable of travelling great distances and remaining viable (5,7,11). This does not, however, imply survival for spores released during SDP which, within a matter of hours, might be exposed to conditions of low relative humidity, high temperature, or intense sunlight. In fact, Reed and Crabill (15) stated that basidiospores were killed in 2–5 hr in direct sunlight. Indeed, viable spores travelling long distances are likely to be spores from PDP that were released under conditions of high relative humidity, moderate temperatures, and cloud cover, conditions that may allow survival of basidiospores for several days (7). Before the significance of SDP can be determined, more research is needed to determine quantitatively the effect of various factors on the survival of basidiospores and the conditions required for infection in the absence of free water.

LITERATURE CITED

1. BLUME, M. C., R. C. SEEM, and J. BARNARD. 1979. Two computer programs used in the analysis of rectangular and circular charts from continuously recording weather instruments. Search 9(1) Plant Pathology Dept., No. 5, N.Y. Agric. Exp. Stn., Geneva, NY. 11 pp.
2. COONS, G. H. 1912. Some investigations of the cedar rust fungus, *Gymnosporangium juniperi-virginianae*. Nebr. Agric. Exp. Stn. Annu. Rep. 25:217-245.
3. CRABILL, C. H. 1913. Production of secondary sporidia by *Gymnosporangium*. Phytopathology 3:282-284.
4. GIDDINGS, N. J. 1918. Infection and immunity in apple rust. W. Va. Agric. Exp. Stn. Bull. 170:1-71.
5. HAMILTON, J. M. 1937. Recent investigations on the control of cedar-apple rust in the Hudson Valley. N.Y. State Agric. Exp. Stn. Bull. 678:1-34.
6. HEALD, F. D. 1909. The life history of the cedar rust fungus. Nebr. Agric. Exp. Stn. Annu. Rep. 22:104-113.
7. MacLACHLAN, J. D. 1935. The dispersal of viable basidiospores of the *Gymnosporangium* rusts. J. Arnold Arboretum 16:411-422.
8. PADY, S. M., and C. L. KRAMER. 1971. Basidiospore discharge in *Gymnosporangium*. Phytopathology 61:951-953.
9. PALMITER, D. H. 1952. Rust diseases of apples and their control in the Hudson Valley. Pages 3–26 in: N.Y. State Agric. Exp. Stn. Bull. 756.
10. PARMELEE, J. A. 1965. The genus *Gymnosporangium* in Eastern Canada. Can. J. Bot. 43:239-267.
11. PARMELEE, J. A. 1968. Effective range of basidiospores of *Gymnosporangium*. Can. Plant Dis. Surv. 48:150-151.
12. PEARSON, R. C., H. S. ALDWINCKLE, and R. C. SEEM. 1977. Teliospore germination and basidiospore formation in *Gymnosporangium juniperi-virginianae:* a regression model of temperature and time effects. Can. J. Bot. 55:2832-2837.
13. PEARSON, R. C., M. SZKOLNIK, and F. W. MEYER. 1978. Suppression of cedar apple rust pycnia on apple leaves following postinfection applications of fenarimol and triforine. Phytopathology 68:1805-1809.
14. PRINCE, A. E. 1943. Basidium formation and spore discharge in *Gymnosporangium nidus-avis*. Farlowia 1:79-93.
15. REED, H. S., and C. H. CRABILL. 1915. The cedar rust disease of apples caused by *Gymnosporangium juniperi-virginianae* Schw. Va. Agric. Exp. Stn. Bull. 9:1-106.
16. SZKOLNIK, M. 1974. Unique post-infection control of cedar-apple rust on apples with triforine. Plant Dis. Rep. 58:587-590.
17. WEIMER, J. L. 1917. Three cedar rust fungi, their life histories and the diseases they produce. Cornell Univ. Agric. Exp. Stn. Bull. 390:505-549.