Modeling Infection of Spring Onion by *Puccinia allii* in Response to Temperature and Leaf Wetness

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ABSTRACT

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The influence of temperature and leaf wetness duration on infection of spring onion (Japanese bunching onion) leaves by *Puccinia allii* was examined in controlled-environment experiments. Leaves of potted spring onion plants (*Allium fistulosum* cv. Yoshikura) were inoculated with urediniospores and exposed to 6.5, 10, 15, 22, or 27 h of wetness at 5, 10, 15, 20, or 25°C. The lesion that developed increased in density with increasing wetness duration. Relative infection was modeled as a function

of both temperature and wetness duration using the modified version of Weibull's cumulative distribution function ($R^2 = 0.9369$). Infection occurred between 6.5 and 27 h of leaf wetness duration at 10, 15, 20, and 25°C and between 10 and 27 h at 5°C, and increased rapidly between 6.5 and 15 h of wetness at 10, 15, and 20°C. At 25°C, few uredinia developed regardless of the wetness duration. Parameter H , one of eight parameters used in the equation and which controls the asymmetry in the response curve, varied markedly according to the temperature, so that the model could be improved by representing H as a function of wetness duration ($R^2 = 0.9501$).

Puccinia allii (DC.) F. Rudolphi causes rust diseases in onion (*Allium cepa* L.), scallion (*A. chinense* G. Don: rakkyo), spring onion or Japanese bunching onion (*A. fistulosum* L., porrum group: naganegi), garlic (*A. sativum* L.: nin-niku), and Chinese chive (*A. tuberosum*: nira) in Japan. Among these crops, spring onion is the most widely planted, with $\approx 24,000$ ha sown every year. The rust causes serious damage as a cosmetic disease in the absence of fungicide application, reducing the commercial value of the crop by almost one-third (regional agronomist of Plant Protection Office, Akita Prefecture, *personal communication*).

P. allii is an autoecious rust, producing pycnia, aecia, uredinia, telia, and basidia on a single host (2). However, pycnia and aecia have not been found in Japan (13) and some other countries (2,25). Urediniospores are the main inocula for secondary infections throughout the year in onion and spring onion fields in Japan. Teliospores are sometimes found on spring onion plants in late autumn to winter. Although their role as inocula in fields has been poorly investigated, it is considered that teliospores might be unimportant as secondary inocula during early summer to late fall.

Spring onion favors cooler temperatures, growing best at 15 to 20°C, and is grown from April to December in Akita Prefecture, which is located in the northern part of Honshu island, Japan. Severe disease outbreaks usually occur in spring and late autumn in the region, suggesting that disease is favored by a cooler climate. Morinaka (18) reported that urediniospores germinated in water at 5 to 25°C. Infection of spring onion by urediniospores is significantly affected by temperature and wetness duration (21, 22,27). Experiments conducted under artificial conditions in different studies showed that infection can occur at 10 to 20°C (9) or 16 to 25°C (7), but the optimum temperature for infection is

ambiguous. Morinaka (18) suggested that urediniospores needed at least 6 h to infect spring onion leaves. Yamakage et al. (27) studied the climatic conditions under which infection of spring onion might increase significantly based primarily on observation of disease development in fields and found that infection might significantly develop under the conditions of at least 7.5 h of wetness, an air temperature of 6 to 20°C, wind velocity of up to 1 m s^{-1} , and rainfall ≤ 8 mm during the wetness duration.

The objectives of this study were to collect data on the effects of temperature and wetness duration on infection of spring onion by the rust fungus *P. allii* and develop a response model based on the measured relative infection rate of spring onion grown in a controlled environment.

MATERIALS AND METHODS

Inoculum production. Urediniospores of *P. allii* were obtained from a single uredinium produced on a spring onion collected from a commercial field located in Noshiro city, Akita, and were painted onto the surface of spring onion (*A. fistulosum* cv. Yoshikura) leaves. The inoculated plant was kept in a moisture chamber at 20°C for 24 h, and then grown mostly at 15 to 22°C in a glasshouse for 2 weeks. This single-uredinium inoculation was repeated three times, and a single uredinium isolate (AP0402) was obtained. The isolate was maintained on onion leaves by inoculation every 3 to 6 weeks and used for inoculation throughout the study.

To obtain a sufficient quantity of urediniospores, leaves of 10 to 12 spring onion seedlings grown in a plastic case filled with potting medium (Nitten Negi-baido; Nippon Beet Sugar Manufacturing Co. Ltd.) were inoculated by rubbing with leaves carrying urediniospores of the AP0402 isolate. The inoculated plants were grown for another 15 to 21 days in the glasshouse. Urediniospores produced on the inoculated leaves were collected and suspended in distilled water at a density of 4×10^4 urediniospores ml^{-1} for a conidial germination test, and in water containing 0.01% Tween

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20 at a density of 7.2 to 21.2×10^4 urediniospores ml^{-1} for the inoculation experiments.

Conidial germination. Conidial germination on 2% agar (WA) plates was investigated in relation to temperature. The aqueous urediniospore suspension (1 ml) was spread on each WA plate, which was incubated at 5, 10, 15, 20, or 25°C. Five replicate plates were prepared for each temperature treatment. After 1, 2, 3, 4, and 5 h, square discs (20 by 20 mm) were cut from the WA plates and stained with lactophenol trypan blue (Wako Pure Chemical Industries, Ltd., Japan). Fifty conidia, randomly selected from each disc, were observed with a compound microscope. Conidia were considered germinated when the germ tube was at least half the length of the conidia.

Inoculation of plants and treatments. Seedlings of spring onion cv. Yoshikura were transplanted into plastic tubes (28 mm in diameter, 11.5 cm high) containing Nitten Negi-baido potting medium and were grown in the glasshouse for 6.5 to 7.5 weeks, until the second leaf of the plants was fully developed and the third leaf was developing. In all, 150 plants were placed on a circular table (73 cm in diameter), which rotated automatically at 8.2 rpm. Three replicate experiments were performed. In each experiment 50 ml of 7.2×10^4 , 40 ml of 7.3×10^4 , and 30 ml of 21.2×10^4 urediniospore suspensions were sprayed onto the leaves with an air brush (Toricon set YT-02 NS, Holbein Art Materials, Inc.) to form a uniform layer of fine droplets on the leaf surface.

Inoculated plants, except those exposed to 0 h of wetness, were placed immediately in five different growth chambers (Model Biotron LPH200, KPH300 and LH300, Nippon Medical & Chemical Instruments Co. Ltd.; and MDF-350HT, Sanyo Electric Co. Ltd., Japan) in which the atmosphere was kept saturated with an ultrasonic humidifier (Model TUH-6, Toyotomi Co. Ltd.) and the temperature was maintained at 5, 10, 15, 20, or $25 \pm 0.5^\circ\text{C}$. Twenty-five plants were held in the leaf-wet condition at each temperature. Immediately following the postinoculation wetness treatment for 6.5, 10, 15, 22, or 27 h, five plants per wetness duration were dried with an electric fan for 15 min, and then transferred to a growth chamber (Koitoiron, Koito Industries Ltd.) in which the atmosphere was dehumidified throughout the day with a dehumidifier (MJ-63LGX, Mitsubishi Electric Co.) and the temperature was maintained at 22°C during the day (06:00 to 18:00) and 18°C during the night. To minimize variation, the order in which plants were inoculated and allocated to temperature and wetness duration treatments was randomized. The experimental design was a split plot with main units represented by temperature and subunits by leaf wetness duration.

A preliminary experiment was conducted to define the minimum duration of postinoculation wetness at 5, 10, 15, 20, and 25°C required for infection to occur. No uredinia were produced on inoculated leaves exposed to 4 or 5.25 h of wetness in all of the temperatures. In further preliminary experiments conducted twice, no uredinia developed at 20°C with 4 h of wetness, but a few uredinia developed with 5.25 h of wetness.

Two replicate preliminary experiments were performed to determine the incubation period at 20°C. Uredinia first developed 8 to 9 days after inoculation in the experimental conditions. Significant differences were not detected between mean numbers of uredinia produced on leaves 13 and 24 days after inoculation with 24 h of wetness at 20°C ($P = 0.9069$), indicating that the uredinia number scarcely increased during the incubation period. Thus, in the following experiments, the number of uredinia produced on a 10-cm-long central portion of the second and third leaves of each seedling was scored after incubation for 15 days. The number of uredinia per 10-cm leaf segment in each treatment was transformed to give a relative infection (*RI*) by dividing the number of uredinia by the maximum number obtained for the same leaf age from any of the temperature–leaf wetness duration combinations in the same experiment.

Data analysis. To test the effects of temperature and leaf wetness duration on uredinia production on the leaves, the mean uredinia number per 10-cm leaf segment for each treatment was calculated. Differences in uredinia production among the three replicate experiments were insignificant as determined by the Kruskal-Wallis (KW) test. Consequently, the effects of temperature and leaf wetness duration on *RI* were compared by analysis of variance (ANOVA), in which the three replicate experiments were treated as blocks.

Model development. A response model (equations 1 and 2) was fitted to the data according to Carisse et al. (5), in order to describe the effects of temperature on *RI* for each different wetness duration. Another response model (equation 3) was fitted to the data in order to describe the effects of wetness duration on *RI* at each temperature (7). Equation 3 is the modified version of Weibull's cumulative distribution function, which is defined when $w > C$.

$$y_t = f(t) = E' \frac{\exp \left[\frac{(t - F)G}{H + 1} \right]}{1 + \exp [(t - F)G]} \quad (1)$$

$$E' = E \left[\frac{(H + 1)}{H} \right] H \frac{1}{H + 1} \quad (2)$$

$$y_w = f(w) = A \{1 - \exp \{-[B(w - C)]^D\}\} \quad (3)$$

where t is temperature and w is wetness duration. The meaning of the parameters in equations 1 to 3 are described by Duthie (7). Briefly, according to Duthie (7), parameter A is the upper limit of the response, B is the intrinsic rate of increase in the response with respect to wetness duration, C is the length of delay before the start of the response, D is the portion of the period of wetness, E is the maximum response, F is directly proportional to the optimum temperature, G is the intrinsic rate of decline from the maximum as temperature deviates from the optimum, and H is the difference in the rate of acceleration in the decline from the maximum as temperature increases or decreases from the optimum. The above equations represent the influence of temperature and wetness duration, respectively. By substituting equation 1 for parameter A in equation 3, we can obtain an integrated model. Infection by *P. allii* responds with different maximum values depending on temperature and wetness duration; therefore, we decided that the integrated model is the appropriate form with which to describe the response of this disease.

We evaluated the estimated parameters by the following coefficient of determination:

$$R^2 = \frac{\left(\sum (x_i - \bar{x})(y_i - \bar{y}) \right)^2}{\sum (x_i - \bar{x})^2 \sum (y_i - \bar{y})^2}$$

where x_i is measured each *RI* and y_i is estimated *RI* which corresponds to i of x_i . $\bar{x}$ and $\bar{y}$ are mean value of measured and estimated *RI*, respectively.

The modeling procedure was as follows. First, a response model that describes the effects of temperature (equations 1 and 2) was estimated at each wetness duration; then, a similar model of wetness duration (equation 3) was estimated. The value of parameters E , F , G , and H in equations 1 and 2 and parameters A , B , and D in equation 3 was estimated by a nonlinear least squares (NLS) method implemented in MATLAB (6). The parameter C was fixed to 0 assuming that *RI* responded immediately to the increase in leaf wetness duration after a minimum of 5.25 h. In order to obtain an integrated model affected by temperature and wetness duration, we substituted equation 1 for A in equation 3. The set of parameters that describe the maximum relative infec-

tion rate were selected. In other words, we selected the set of parameters *A*, *B*, *C*, and *D* for which the output of equation 3 reaches the maximum relative infection rate after a long wetness duration. In addition, the set of parameters *E*, *F*, *G*, and *H* in equations 1 and 2 for which the maximum response was obtained around the optimum temperature were selected. The three-dimensional response model was obtained using the integrated model with the parameters described above.

Several criteria were used to evaluate the models: (i) randomness and normality of residuals, (ii) goodness of fit between estimated and observed values (*R*²), and (iii) standard deviation around the regression lines. All nonlinear regressions were evaluated by performing a simple regression analysis between the estimated values and the actual observations as paired observations. These regressions were analyzed by testing the significance of the difference in the intercept from 0 and the slope from 1, and the significance of the appropriate *F* value.

RESULTS

Effect of temperature and wetness duration on urediniospore germination and infection. The response of urediniospore germination to incubation time was similar at temperatures of 5 to 20°C; percent germination increased rapidly from 1 to 2 h of incubation and reached a plateau at ≈95% spore germination. At 25°C, percent germination remained low regardless of the incubation time (Fig. 1).

Small white spots (1 to 2 mm in diameter) first appeared on each leaf 7 to 8 days after inoculation and developed into orange-colored uredinia within 1 to 2 days. The mean number of uredinia produced in the central 10-cm portion of the leaf within 15 days after inoculation was similar (i.e., there was no significant block effect) for the three replicate experiments (*P* = 0.3980, one-factor

Fig. 1. Effect of temperature on germination of *Puccinia allii* urediniospores on 2% agar medium. Points represent the means of three replicate experiments and error bars represent the standard deviation.

TABLE 1. Analysis of variance for the effects of temperature and leaf wetness duration on infection of spring onion leaves by *Puccinia allii*

Source ^a	df	Sum of squares	<i>F</i>	<i>P</i>
Temp	4	3.945	52.107	<0.0001
WD	4	2.875	37.973	<0.0001
Temp–WD	16	1.221	4.032	<0.0001
Error	50	0.852	...	...

^a Temp = temperature and WD = wetness duration.

ANOVA). However, temperature, leaf wetness duration, and the interaction between temperature and leaf wetness duration significantly affected the number of uredinia produced per leaf segment (Table 1).

Infection of spring onion leaves by *P. allii* at 6.5 to 27 h of postinoculation wetness at 10, 15, and 20°C, and the number of uredinia increased rapidly between 6.5 and 15 h of wetness (Fig. 2). Infection occurred between 10 and 27 h at 5°C, increasing gradually with wetness duration. At 25°C, few uredinia developed regardless of the duration of postinoculation wetness. The highest number of uredinia in each replicate experiment was observed at 20°C for 27 h of wetness, 15°C for 15 h, and 15°C for 22 h with 98.8, 142.0, and 75.0 uredinia produced per 10-cm leaf segment, respectively. Uredinia developed following 6.5 h of wetness at 10, 15, 20, and 25°C.

Parameter estimates for which the response of *RI* to temperature for each different wetness duration was best described in equation 1 and those for which the response to wetness duration at each temperature was best described in equation 3 are presented in Tables 2 and 3, respectively. The initial values for the parameter estimation procedure were set by trial and error: (*A*₀, *B*₀, *D*₀) = (0, 0.1, 1) and (*E*₀, *F*₀, *G*₀, *H*₀) = (0.5, 10, 0.5, 3). An

Fig. 2. Effect of temperature and leaf wetness duration on relative infection of spring onion by *Puccinia allii*. Points represent the means of three replicate experiments and error bars represent the standard deviation.

TABLE 2. Estimation of parameters in equations 1 and 3 (*A*₀, *B*₀, *D*₀) = (0, 0.1, 1) at different temperatures

Temperature (°C)	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>
5	0.6073	0.0500	0	5.0490
10	0.7909	0.0798	0	5.8711
15	0.8773	0.0877	0	2.8087
20	0.7457	0.1022	0	3.6391
25	...	...	...	...

TABLE 3. Estimated parameters in equations 1 and 3 (*E*₀, *F*₀, *G*₀, *H*₀) = (0.5, 10, 0.5, 3) at different wetness durations (WD)

WD (h)	<i>E</i>	<i>F</i>	<i>G</i>	<i>H</i>
6.5	0.2809	18.8688	0.9373	2.1228
10	0.7698	19.2550	1.0125	3.5956
15	0.9178	20.1629	0.7214	6.3993
22	1.0077	20.2380	0.8902	14.5168
27	0.9602	21.0547	1.0814	29.4431

estimated parameter set of the model was selected in which the parameters A and E were maximum (i.e., the parameters at 15°C [Table 2] and those at 27 h of wetness duration [Table 3] for a three-dimensional model). Although the maximum value of E was 1.0077 (Table 3), we selected the parameters at 27 h of wetness duration because the actual maximum RI value never exceeded 1. The two-dimensional representation is given in Figure 2, and the three-dimensional representation is presented in Figure 3 ($R^2 = 0.9369$).

Combination of two parameter groups (i.e., parameters A , B , and D , and parameters E , F , G , and H , in which A and E indicate maximum values) was chosen (Tables 2 and 3). The derived equations were as follows:

$$f(w, t) = f(t) \left(1 - \exp \left\{ -[0.0877(w - 0)]^{2.8087} \right\} \right) \quad (4)$$

$$f(t) = E' \frac{\exp \left[\frac{(t - 21.0547)1.0814}{29.4431 + 1} \right]}{1 + \exp [(t - 21.0547)1.0814]} \quad (5)$$

Fig. 3. Three-dimensional response of relative infection of spring onion by *Puccinia allii* to the combined effects of temperature and leaf wetness duration depicted by integrated model (equations 4 to 6).

Fig. 4. Asymptotic values of parameter A in equation 3. Points are the maximum value of A in the estimated model at each leaf wetness duration. Solid line shows the output of the integrated model at 27 h of wetness duration. Points reflect the observed mean of three replicate experiments and the line reflects the estimated value.

$$E' = 0.9602 \left[\frac{(29.4431 + 1)}{29.4431} \right] \frac{1}{29.4431 + 1} \quad (6)$$

The surface response was reasonably well fitted to the experimental data.

Asymptotic values for the estimated parameter A are shown in Figure 4. The solid line in the figure was drawn using equations 5 and 6. Each point indicates the maximum output of the model of wetness duration for each temperature. As a result, this figure indicates the high activity of the rust fungus at lower temperatures. On the other hand, the RI of the rust fungus was drastically reduced $>20^\circ\text{C}$.

The optimum temperature for infection in each different wetness duration, calculated based on the estimated parameters in Table 3 (equation 7), was 18.07, 17.99, 17.59, 17.23, and 17.93°C for 6.5, 10, 15, 22, and 27 h of wetness, respectively.

$$t_{\text{opt}} = F - \frac{1}{G} \ln(H) \quad (7)$$

The mean optimum temperature was 17.76°C.

Effect of time-varying parameters. The predictive model considerably differs from the experimental results at lower temperatures. This is because the asymmetry of measured RI to temperature is strong (Fig. 5). The symmetry affects the shape of the RI response curve of the temperature (Fig. 5). We see that the estimated parameter H increases according to the increase in wetness duration from Table 3. Because the values for H differed markedly for each different wetness duration, the parameter was expressed as a function of wetness duration to improve the model fit at lower temperatures and was integrated into equations 1 and 2. The variation in parameter H with wetness duration can be represented by equation 8:

$$H(w) = 1.0196e^{0.1231w} \quad (8)$$

Three-dimensional representation of the response model represented by equations 4, 5, and 6 with time-varying parameter H is given in Figure 6 ($R^2 = 0.9501$). It appeared that this model fitted the experimental data better than the model expressed by equations 4, 5, and 6 at lower temperatures (5 to 10°C) but fitted the data less well at higher temperatures (15 to 20°C).

Fig. 5. Relative infection of spring onion by *Puccinia allii* in response to temperature at each leaf wetness duration. The dashed line represents the measured relative infection and the solid line represents the estimated relative infection. The response becomes increasingly asymmetric with increasing wetness duration.

The correlation between the estimated *RI* and the observed value is illustrated in Figure 7. The correlation with the constant parameter *H* is shown in Figure 7A and correlation with the time-varying parameter *H* is shown in Figure 7B. Although both models approximate the observed *RI*, the model with time-varying parameters exhibited a slightly better correlation than the model with constant parameters.

DISCUSSION

Severe infection of spring onion leaves by *P. allii* was observed at 10 to 20°C with ≥6.5 h of wetness duration, and significant infection occurred at 5°C with ≥15 h of wetness. Infection increased with increasing wetness duration of 6.5 to 15 or –22 h at 10, 15, and 20°C. The results are consistent with the preliminary reports by Morinaka et al. (18) and Takeuchi (21), clearly demonstrating that temperature and wetness duration profoundly influence infection of spring onion by *P. allii*.

As mentioned earlier, rust disease occurs in May and the first half of June as well as the second half of September to the first half of December, but seldom becomes severe in May and June and often become more severe in October to December in that region. Mean daily temperatures of July and August are >20°C,

whereas those of May, June, and September to December are 14.2, 18.8, 19.9, 13.6, 7.6, and 2.8°C, respectively (data were obtained from home pages of Japan Meteorological Agency, <http://www.jma.go.jp/jma/indexe.html>). It is apparent that absence of the disease during summer is because the temperature is too high for infection, suggesting that infection-free periods could be defined based on mean daily temperatures and wetness duration.

Disease response curves for most plant diseases caused by fungi to temperature are more or less asymmetric, being negatively skewed ($H > 1$) (1,3,9,11,14,15,17,19,20,24) or positively skewed ($H < 1$) (4,8,10,12,23,26). Degree of asymmetry in the curves of many diseases varies with leaf wetness duration. Such diseases include those caused by *Botrytis cinerea* (4), *Colletotrichum acutatum* (26), *Mycosphaerella fijiensis* var. *difformis* (15), *Phytophthora* spp. (12,19), *Uromyces phaseoli* (14), *Monilinia laxa* (23), and others (8,9). Because so many such response curves are reported, the change in degree of asymmetry is possibly a rule for these curves. The nonlinear model for evaluating the combined effects of temperature and wetness duration described using a modified version of Weibull's equation is capable of much wider application and more accurate representation by making parameter *H* time varying. The methodology presented here can be extended to the other parameters. The model could be improved effectively by this method because every parameter is of biological significance and appears to vary with wetness duration or temperature.

Parameter *B* means intrinsic rate of increase in the response, similar to *H* (7). However, in our experimental result, it is important to model the variation of asymptotic (parameter *A*) of the model in Figure 2. On the other hand, asymmetry of the response to temperature is so strong in our measurements that we have constructed the model mainly to include the effect of parameters *A* and *H*. As a result, the variation of parameter *B* was included in the model with time-varying parameter *H*.

The effect of temperature on urediniospore germination was similar to that on infection of leaves (Figs. 1 and 2). The response was also adequately described by the same model (*unpublished data*) and the optimum temperature range estimated by the model was 16.8 to 18.1°C, depending on wetness duration, which highlights the similarity in response to temperature to that for leaf infection. Leaf spot of strawberry caused by *Mycosphaerella fragariae* is another example in which temperature effects on spore germination and infection are similar (2,5). The temperature might affect fungal behavior more strongly than fungus–host plant interactions during the infection process in these diseases.

Favorable weather conditions for infection of spring onion by *P. allii* that result in rapid increases of lesion number have been empirically elucidated by Yamakage et al. (27). The conditions

Fig. 6. Three-dimensional response of relative infection of spring onion by *Puccinia allii* to the combined effects of temperature and leaf wetness duration depicted by integrated model (equations 4 to 6) with time-varying parameter *H*.

A Constant *H*

B Time varying *H*

Fig. 7. Regression of estimated values to the observed relative infection of spring onion leaves by *Puccinia allii*. Correlations of the model are shown with **A**, constant parameter *H* and **B**, time-varying parameter *H*.

can be detected based on observation of leaf wetness duration and temperature, wind speed, and precipitation during wetness. Forecast of whether and when the disease severity would increase rapidly, made possible by detecting the conditions (i.e., infection periods), were carried out for two crop seasons and a rapid increase of disease severity actually occurred after an incubation period from 25 of 33 infection periods detected (27). The weather conditions favorable for the infection of rice leaves by *Pyricularia grisea*, blast fungus, are well elucidated (16); therefore, the rapid increase of the disease actually occurred after an incubation period from >90% of the infection periods detected every year for the last two decades in Akita Prefecture (plant pathologist of Agricultural Experiment Station of Akita Prefecture, *personal communication*). Because favorable weather conditions play a major role in the early stages of the disease epidemic (16), the forecast works very effectively to manage the disease and is an important component of the disease management strategy in the region. Forecast of rapid increases may be highly effective for the diseases in which generations do not overlap and stepwise increase of disease severity occurs. For nonoverlapping generations, a latent period should be sufficiently long and, preferably, spores are produced by lesions over a limited period. The latent period for spring onion rust is 8 days or more under environmental conditions favorable for an epidemic. This latent period is longer than that for blast disease of rice leaves, suggesting that forecast of rapid increases in disease incidence by detecting infection periods in the early stages of an epidemic may be useful to delay or prevent subsequent development of the disease.

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Erratum

Corrections were made to page 954 in the third paragraph of the right column to read as follows. "The optimum temperature for infection in each different wetness duration, calculated based on the estimated parameters in Table 3 (equation 7), was 18.07, 17.99, 17.59, 17.23, and 17.93°C for 6.5, 10, 15, 22, and 27 h of wetness, respectively.

$$t_{\text{opt}} = F - \frac{1}{G} \ln(H) \quad (7)$$

The mean optimum temperature was 17.76°C." Changes to this article were made on December 22, 2009.