Patterns of Bean Rust Lesion Size Increase and Spore Production

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ABSTRACT

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Urediospores of *Uromyces phaseoli* var. *typica* were collected daily from first trifoliolate leaves of *Phaseolus vulgaris* grown under controlled conditions at 16, 21, 24, and 27 C. Nine lesion densities ranging from 11 to 107 lesions per leaflet, three relative humidities ranging from 51 to 87%, and two leaf ages were incorporated into the four temperature treatments. The latent period varied from 9 days at 16 C to 7 days at 24 C. Sporulation per lesion occurred in waves of decreasing amplitude over time in most treatments. Increase of total lesion area, sporulating area, and cumulative numbers of spores, however, was nearly linear with time in all treatments, except at 27 C where lesions did not develop. The average ratio of sporulating area to total lesion area was 0.27. Relative humidities between 51–87% and lesion densities ranging from 11 to 107 lesions per leaflet significantly affected cumulative spore production, but accounted for only a small part of the variation among treatments. The rates of increase of both sporulating area and total infected area could be described by quadratic temperature functions (r^2 = 0.988 and 0.956, respectively). Efficiency of both sporulating and total infected areas (sporulation per unit area) varied negatively quadratically with temperature, inversely with lesion density, and positively with leaf age. The average rate of sporulation per day appeared to be inversely proportional to lesion density over all temperature and humidity treatments. Quantitative information obtained in this study can be used to form a preliminary mathematical description of sporulation in the bean rust pathosystem.

Additional key words: epidemiology.

For polycyclic diseases such as bean rust, timing and amount of sporulation by the pathogen are among the most important factors for determining rates of disease increase. Basic understanding of epidemiology and accurate simulation of polycyclic disease epidemics requires knowledge of the effects of primary factors that determine rates and patterns of sporulation. Shrum (9) developed a flexible computer simulator of plant disease epidemics. He showed that it could be used to accurately simulate wheat stripe rust epidemics, but its adaptability to other diseases has not yet been established. Our interest in the epidemiology of bean rust caused by *Uromyces phaseoli* (Reben) Wint. var. *typica* Arth. was stimulated by the opportunities this pathosystem provides for testing the flexibility of Shrum's simulator under controlled environments as well as field conditions.

Other research workers have investigated the effects of various environmental factors on the sporulation of the bean rust fungus. Cohen and Rotem (2) found that light intensity, by affecting host photosynthesis, has a marked effect on the sporulation of many obligate parasites, including *U. phaseoli*. Rotem et al (7) found that sporulation of *U. phaseoli* in their automatic humidity chamber was inversely related to relative humidity. On the other hand, Yarwood (10) found that overnight moist chamber treatments increased sporulation 2–10 times that of pustules on plants kept overnight in standard greenhouse humidity. Yarwood's (10) study of the biotic potential of *U. phaseoli* provides daily and cumulative sporulation data. His study involved exclusive use of primary leaves, the collection of spores with daily water washings, the use of a single temperature regime, and lesion densities much higher than those typically found in field situations and, therefore, do not directly reflect typical conditions during an actual bean rust epidemic. The implied shape of Yarwood's (10) daily sporulation versus time curves is that of a gradual rise and decline, unlike those found by Melching et al (6) for soybean rust and Broyles (1) for wheat stem rust; in both of these diseases, sporulation occurred in 3- to 5-day diminishing bursts.

The purpose of this study was, therefore, to reexamine *U. phaseoli* spore production at four temperatures and at lesion densities commonly found in the field on trifoliolate leaves on whole plants to obtain quantitative data applicable for incorporation into a disease simulator.

MATERIALS AND METHODS

Experiments were conducted on plants grown in walk-in controlled environment chambers 2.44 × 3.66 × 2.13 m high at the Southeastern Plant Environment Laboratories at North Carolina State University (4). These chambers use a combination of cool-white fluorescent and incandescent lamps to provide an illuminance of 430–480 hlx at canopy level. Day length was based on a light period of 13 hr/day. Air temperatures were maintained at ± 0.25 C of the set point as measured with a type "T," 24-gauge, welded-bead thermocouple in a shielded aspirated housing. Canopy-level air temperatures were 16, 21, 24, and 27 C for appropriate experiments. Thermocouples imbedded within the leaf tissue, however, showed leaf temperatures to be 1–3 C higher than air temperature while the lights were on, depending on the amount of shading a given leaf received. Top-to-bottom airflow in the chamber was indicated by an air velocity meter (Hastings Co., Hampton, VA 23361) to average 20 m/min. Relative humidity was measured on an RO 21-10 hygrometer (Weather Measure Co., Box 41257, Sacramento, CA 95841) and maintained at 70% or more at all temperatures except in low humidity treatments. Standard

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humidity under these conditions was approximately 75% RH during the day and 83–95% RH at night. A high humidity treatment was achieved by allowing sprayers to operate within the ventilation system, raising daytime RH to 82% and nighttime to 92% (averages). A low humidity treatment was achieved by placing dehumidifiers within the chamber and keeping irrigation drainage off the floor. Daytime RH was lowered to 45%, and nighttime to 55% (averages). All RH values reported are approximately ± 5%. Carbon dioxide concentrations were measured on an IR gas analyzer (Beckman Instruments, 4177 Northeast Expressway, NE, Atlanta, GA 30340) and controlled at 300–400 ppm (0.5–0.7 $\mu g/m^3$) by injection of commercial grade CO_2.

Phaseolus vulgaris 'Bountiful' plants were grown in 15.2-cm-diameter plastic pots containing gravel: Peat-lite (2:1, v/v) substrate. Plants were irrigated twice each day with nutrient solution (4) and placed in two rows 1 m apart and containing 30 plants each on perforated metal platforms 80 cm above the chamber floor. First trifoliolates were inoculated by using Schein's quantitative inoculator (8) when they had reached at least 80% of their fully expanded leaf area (usually about 11 days after plant emergence). In one experiment, leaves were inoculated 25 days after plant emergence so that we could test the effect of leaf age. The rust culture was derived from a field collection of race 34 of *U. phaseoli* var. *typica* passed through three generations of single-pustule transfers. Race 34 (5) was chosen because it was locally available and produces a severity reaction of 5 (most severe) on a race-distinguishing scale of 1 to 5 (3) on the universal suscept cultivar Bountiful.

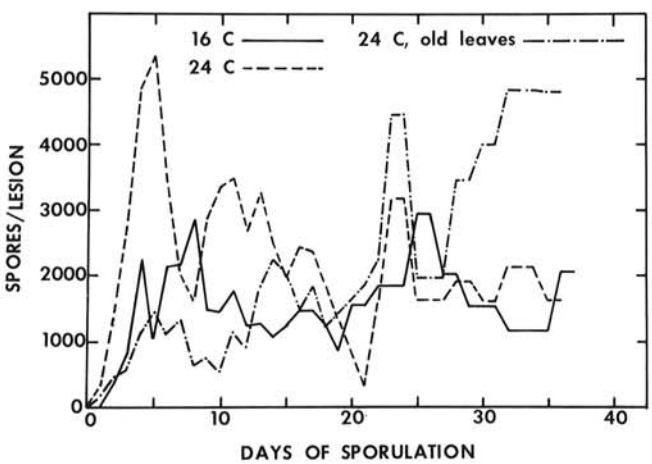

Fig. 1. Daily urediospore counts from bean leaflets infected with *Uromyces phaseoli* and incubated at 16 C (25.2 lesions per leaflet), 24 C (21.2 lesions per leaflet), and 24 C (20.4 lesions per leaflet on old leaves). Each datum is an average of five leaflets. Old leaves were from plants 25 days old at inoculation; all others were from plants 11 days old.

Distilled water was atomized onto inoculated leaflets until runoff and these plants were placed in a darkened dew chamber at 21 C for 18 hr. The latent periods were measured to be the time from inoculation to the time half the pustules had opened on the adaxial surface. Pustule opening typically occurred over a span of 1.5–2.0 days. For different temperature and relative humidity treatments, individual leaflets (five per treatment) were selected for representative lesion densities as shown in Table 1, columns 1–3. Infected leaflets were positioned over and within waxed paper-lined funnels so that the leaflets did not rest upon the waxed paper. A 4-ml plastic vial was placed at the base of each funnel.

Each day between 1600 and 1800 hr, leaflets were forcefully tapped. The spores deposited on the wax paper were tapped and then brushed down into the plastic vial. The leaflet was held vertically within the funnel for this procedure, so that spores were collected from leaf tops and bottoms simultaneously. Vials were stored 1–2 mo at about 35% RH. A Sartorius type 1801 balance (sensitivity 0.001 mg) Brinkman, Cantiague Rd., Westbury, NY 15590) was used to weigh first the plastic vial with spores, and then the vial with spores removed in order to obtain the weight of the collected spores. All weighings occurred in RH between 22–30%. Five additional collections of urediospores of known weight were counted by using a hemacytometer. The standard curve was determined as: number of spores = 13,041 + 343,846 × (mg of spores), ($r^2 = 0.982$), so that weighings of spore collections could be converted to numbers of spores.

Lesion diameters were measured on adaxial surfaces of the same leaves from which spores were collected, by using a caliper micrometer. All visibly sporulating and total lesion areas appeared and were assumed to be circular, and the areas were computed accordingly. Visibly sporulating areas of a lesion also included small satellite pustules that formed in rings around the central sporulating area. Total area of a lesion was taken to be the yellow halo around the central sporulating area plus the sporulating area. Lesion diameters were measured after each spore collection by choosing two lesions randomly (blind sampling) from each infected leaflet, giving a total of 10 lesions per sample per treatment. The coefficient of variation in all samples of size 10 and all treatments, after computation of areas, was 35–46%.

RESULTS

Latent periods were recorded to the nearest half-day as follows: 16 C, 9 days; 21 C, 7.5 days; 24 C, 7 days. At 27 C, lesions did not develop past the fleck stage, and active pustules on plants at 24 C ceased sporulation within 3 days after transfer to 27 C.

TABLE 1. Effects of temperature, lesion density, and relative humidity on rates[w] of growth and sporulation of *Uromyces phaseoli* lesions formed on bean leaves in controlled environment chambers

Temperature (C)	Density[x] (lesions per postule)	Average relative humidity, day/night	Rate of increase in: Sporulating area per day (cm^2 per day)	Rate of increase in: Total lesion area per day (cm^2 per day)	Average spores per day per lesion
16	25.2	75/83–95 (std)	0.000235 a	0.000599	1,544
21	107.2	std	0.000231 a	0.000716	2,133
21	11.8	std	0.000296	0.00101	6,383
24	21.2 c	std	0.000819 b	0.00298	2,783 a
24	30.4 a	45/55 (low)	0.000855 bc	0.00321	1,916 b
24	30.2 a	82/92 (high)	0.000914 c	0.00386	2,839 a
24	54.6 b	low	0.000855[z]	0.00321[z]	2,015 b
24	57.0 b	high	0.000914	0.00386	2,557
24[y]	20.4 c	std	0.000360	0.00131	1,248

[w] Rates derived from data in Figs. 4–6 and 8–10.
[x] Numbers in the same column followed by the same letter do not differ significantly ($P = 0.01$) according to paired t-tests. Means not followed by a letter differ significantly from every other mean as determined by paired mean comparisons.
[y] Old leaves, inoculated 25 days after plant emergence, as opposed to 11 days for all other treatments.
[z] Sporulating and total areas were averaged across the two densities at low and high humidities.

Daily spore counts varied greatly from day to day, with peaks in spore production typically occurring over 3- to 4-day spans. The pattern exhibited by these peaks in spore production varied from treatment to treatment (Figs. 1–3). In fact, sporulation per lesion at 16 C and on old leaves at 24 C was greater after 20 days than before. There were peaks in spore production in the high and low humidity treatments at 24 C at 5 and 10 days after pustule appearance, as well as in the 24 C standard humidity treatment. Old leaves at 24 C, however, did not follow this pattern.

The ratio of sporulating area to total lesion area varied among treatments with no apparent pattern, ranging from 0.33 at 16 C to 0.22 at 24 C high humidity, with an average of 0.27 ± 0.03. These ratios are the linear regression coefficients for the relationship between sporulating area and lesion area, which is: (sporulating area at time, t) = (intercept) + (total area at time, t) × (slope). For different treatments, the intercepts were very near zero and not significantly different from zero or each other in all cases.

Increase of lesion area over time was nearly linear in each treatment (Figs. 4–6). Least squares regression analysis utilizing linear and quadratic models showed that the quadratic models accounted for only 1–3% more of the variation in the data than linear models, so slopes of linear models were compared to ascertain significant treatment differences (Table 1, columns 4 and 5). All slope values of curves of sporulating area increase in Figs. 4–6 were significantly different ($P = 0.001$) from each other as determined by paired t-tests, except for those from the low- vs high-humidity treatments (Fig. 6), and the 21 C high density vs 16 C treatments (Fig. 4). Similarly, the slopes of the curves of total lesion areas differed significantly in all treatments ($P = 0.001$, paired t-tests), including those from low- and high-humidity

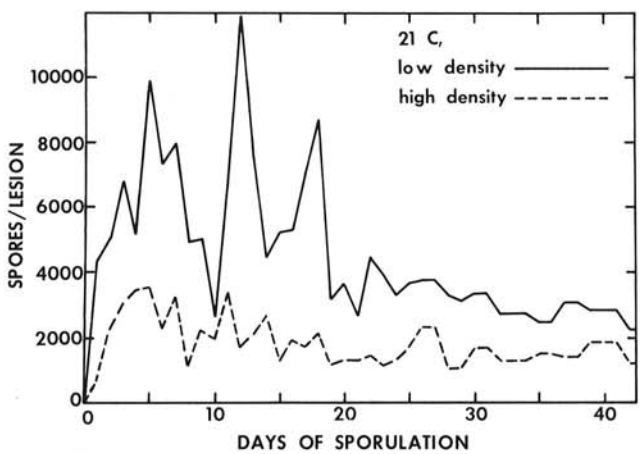

Fig. 2. Daily urediospore counts from bean leaflets infected with *Uromyces phaseoli* and incubated at 21 C, 11.8 lesions per leaflet (low density) and 21 C, 107.2 lesions per leaflet (high density). Each datum is an average of five leaflets.

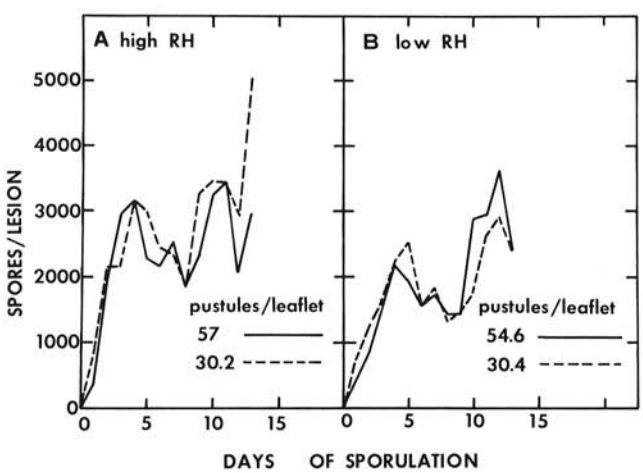

Fig. 3. Daily urediospore counts from bean leaflets infected with *Uromyces phaseoli*. **A,** High relative humidity (avg 82% day, 92% night). **B,** Low relative humidity (avg 45% day and 55% night). Each datum is an average of five leaflets.

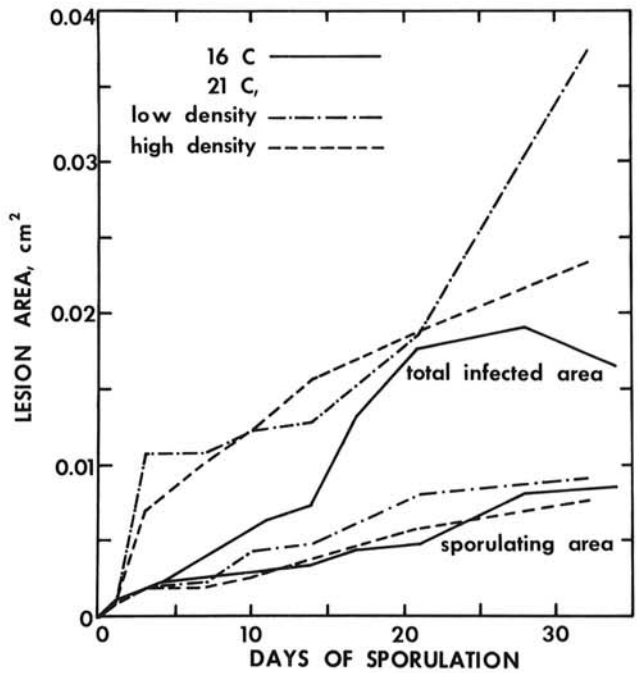

Fig. 4. Sporulating and total lesion areas vs time for *Uromyces phaseoli* on bean leaflets. 16 C, sporulating area = 0.000422 + (0.000235 × days), (r^2 = 0.951). 21 C, low density, sporulating area = 0.000678 + (0.000296 × days), (r^2 = 0.955). 21 C, high density, sporulating area = 0.000523 + (0.000231 × days), (r^2 = 0.977). 16 C, total area = 0.000792 + (0.000599 × days), (r^2 = 0.852). 21 C, low density, total area = 0.0018 + (0.00101 × days), (r^2 = 0.910). 21 C, high density, total area = 0.00319 + (0.000716 × days), (r^2 = 0.908). For all the above, probability > F = 0.01.

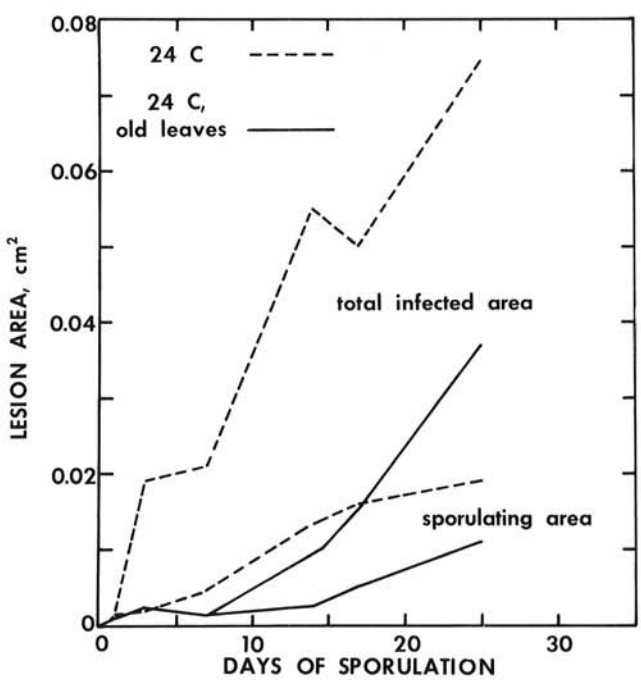

Fig. 5. Sporulating and total lesion area vs time on bean leaflets infected by *Uromyces phaseoli*. 24 C, sporulating area = 0.000215 + (0.000819 × days), r^2 = 0.970). 24 C, old leaves, sporulating area = 7.9 × 10^{-6} + (0.00036 × days). (r^2 = 0.834). 24 C, total area = 0.00305 + (0.00298) days), (r^2 = 0.956). 24 C, old leaves, total area = −0.00298 × (0.00131 × days), (r^2 = 0.869). For all the above, probability > F = 0.01.

treatments. The rates of increase in sporulating area (slopes of curves in Figs. 4–6) were plotted against temperature (Fig. 7), and least squares quadratic fits calculated (probability $>F = 0.001$). The 24 C-old leaves treatment was not included in this analysis.

Cumulative numbers of spores per lesion were plotted against time (Figs. 8–10). For all treatments except those done at 16 C and old leaves at 24 C, these plots show a distinct reduction in sporulation rate at approximately 12–20 days; with old leaves at 24 C, the sporulation rate increased at about 20 days, and at 16 C the rate did not change. The high- and low-humidity treatments at 24 C were carried out for only 13 days with no noticeable reduction in sporulation rate (Fig. 10). Daily spore production, calculated as the slope of these curves (Figs. 8–10) during the first 20 days (Table 1, column 6) and for the entire treatment time were found to differ

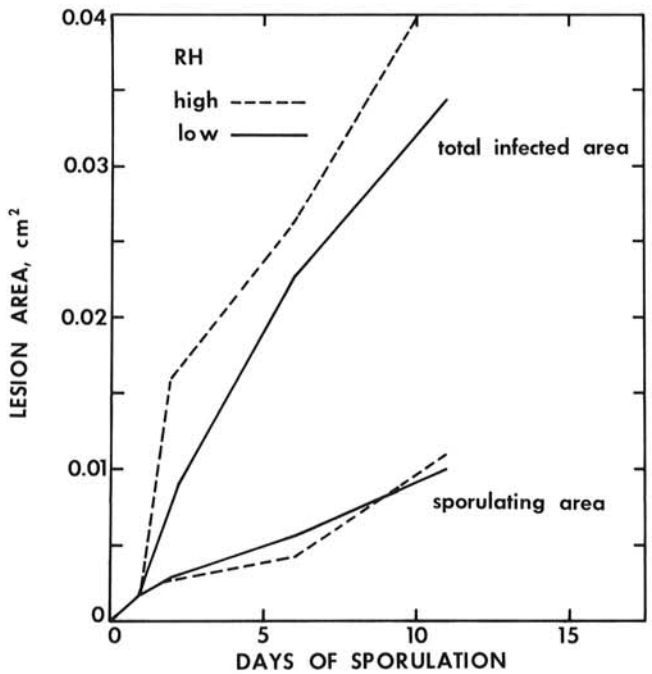

Fig. 6. Sporulating and total lesion area vs time on bean leaflets infected by *Uromyces phaseoli*. 24 C. Low humidity, sporulating area = 0.000588 + (0.000855 × days), ($r^2 = 0.988$). High humidity, sporulating area = 0.000254 + (0.000914 × days), ($r^2 = 0.951$). Low humidity, total area = 0.000713 + (0.00321 × days), ($r^2 = 0.978$). High humidity, total area = 0.001988 + (0.00386 × days), ($r^2 = 0.950$). For all the above, probability $>F = 0.01$.

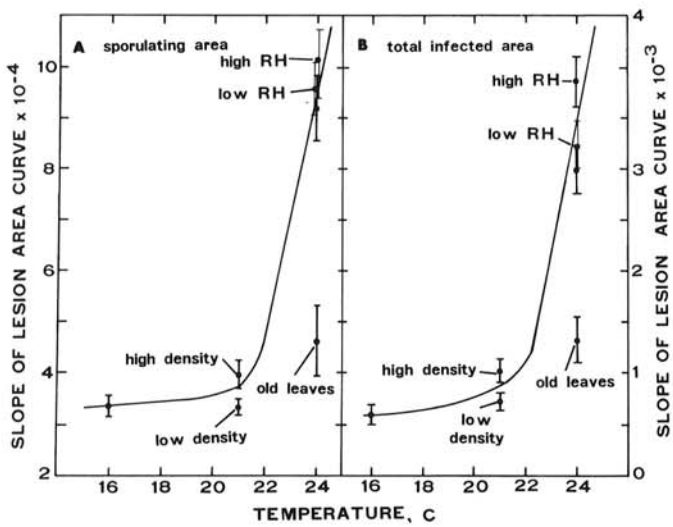

Fig. 7. Relationship of rates of increase (slope values) of sporulating area (A) and total lesion area (B) in bean rust (caused by *Uromyces phaseoli*) to the temperature at which the lesions developed (slope values are from the curves in Figs. 4–6). **A,** Slope of sporulating area increase curve = 0.00829− (0.0008916 × temp) + 2.425 × temp²), ($r^2 = 0.988$). **B,** Slope of total infected area increase curve = 0.0323 − (0.003537 × temp) + (9.7025 × temp²), ($r^2 = 0.956$). Probability $>F = 0.001$. Points not labeled correspond to standard density and humidity. Data from old leaves not used in the above analysis. Lesions did not develop at 27 C.

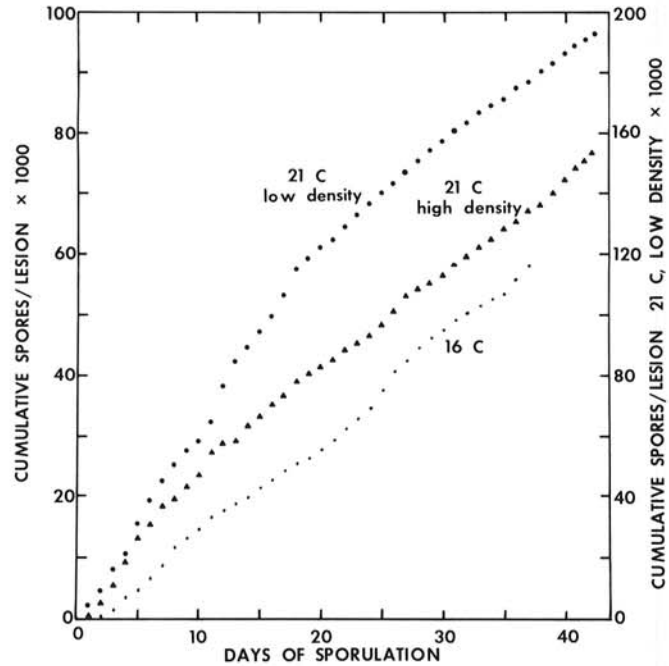

Fig. 8. Cumulative numbers of urediospores of *Uromyces phaseoli* produced per lesion on bean leaves vs time. 16 C, cumulative spores = −2,004 + (1,544 × days), ($r^2 = 0.989$). 21 C, high density, cumulative spores = 1,348 + (2,133 × days), ($r^2 = 0.983$). 21 C, low density, cumulative spores = −2,055 + (6,383 × days), ($r^2 = 0.997$). For all above, probability $>F = 0.001$. Above linear regressions for first 20 days only. Scale for 21 C low density on right vertical axis.

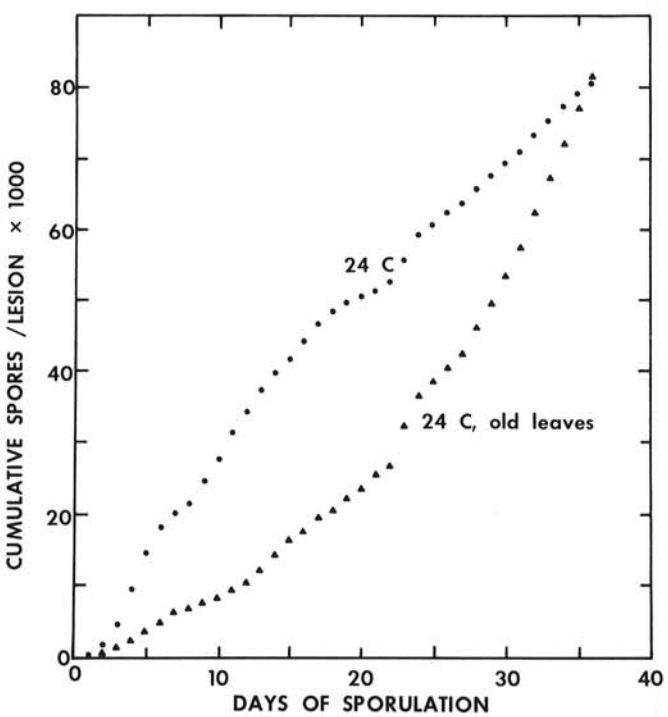

Fig. 9. Cumulative numbers of urediospores of *Uromyces phaseoli* produced per lesion on bean leaves vs time. 24 C, cumulative spores = −859 + (2,783 × days), ($r^2 = 0.986$). 24 C, old leaves, cumulative spores = −2,734 + (1,248 × days), ($r^2 = 0.979$). Probability $>F = 0.001$. Linear regressions for first 20 days only.

significantly from each other ($P = 0.01$, paired t-tests) except for those of two pairs of treatments: slopes of the two low-humidity treatments (30.4 density and 54.6 density) at 24 C did not differ significantly, nor did the slope of 24 C standard humidity differ from that of the 24 C, high humidity, 30.2 lesions per leaflet treatment. Because each value for cumulative number of spores is dependent on previous values, however, errors in each point are not independent of each other and significantly different slopes may not reflect true treatment differences.

Despite nearly equivalent sporulating areas, many more spores were produced at 21 C than 16 C (Figs. 4 and 8). Also, at 24 C, despite much greater sporulating area than at 21 C or 16 C (Figs. 5 and 7), proportionately more spores were not produced (Fig. 9). We hypothesized that the rate of spore production from a given lesion was not simply proportional to the rate of sporulating area growth, but that the efficiency with which a sporulating area produced spores was also related to temperature. The relative efficiency (spores per square centimeter) of a sporulating area at a given temperature was determined by the slopes of highly significant least squares fits to the following equation: (cumulative number of spores at time, t) = (intercept) + (sporulating area at time, t) × (slope). The intercepts did not differ significantly among treatments. These slope values, or measures of sporulating efficiency, are plotted in Fig. 11. Efficiency appears to be quadratically proportional to temperature, but the least squares fit was not highly significant (probability $> F = 0.13$). It is evident, however, that the efficiency of a sporulating area is lower at 16 C and 24 C than at 21 C.

The effect of lesion density on the average rate of sporulation per lesion, across all treatments, appears to be an inverse relationship (Fig. 12). In fact, the simple linear regression of $1/(\text{density}^2)$ on rate of sporulation alone accounts for 85% of the variability across all treatments except old leaves at 24 C ($r^2 = 0.851$, probability $> F = 0.001$).

DISCUSSION

We observed in the field that as a bean rust epidemic progresses, especially from a focus, 1–5% severity on a leaflet is a very typical disease rating for newly infected leaves. This severity range constitutes approximately 20–100 newly formed lesions per leaflet. Densities higher than these kill leaves quickly, and are rarely encountered in areas of disease onset, but instead occur almost exclusively in areas in which disease has been well established for some time. Thus, the lesion density range in this study was chosen to give data most meaningful for describing sporulation during the onset on a bean rust epidemic. Yarwood (10) studied much higher lesion densities on primary leaves only, and thus provided more information on biotic potential than epidemiology. Yarwood found up to 70,000 spores produced per lesion per day on primary leaves, whereas we found up to 11,000 spores per lesion per day on trifoliolate leaves. Yarwood trimmed his plants to a single infected leaf, which may have influenced the sporulation of the fungus.

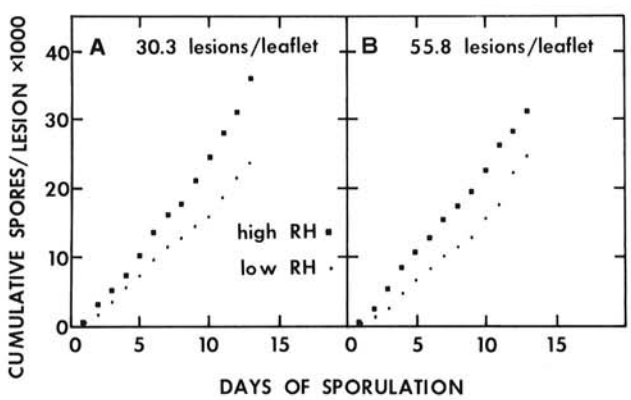

Fig. 10. Cumulative numbers of urediospores of *Uromyces phaseoli* produced per lesion on bean leaves vs time. **A,** Average 30.3 lesions per leaflet. Low humidity, cumulative spores = −2,113 + (1,916 × days), (r^2 = 0.993); high humidity, cumulative spores = −3,122 + (2,839 × days), (r^2 = 0.992). **B,** Average, 55.8 lesions per leaflet. Low humidity, cumulative spores = −3,337 + (2,015 × days), ($r^2 = 0.979$); high humidity, cumulative spores = −2,373 + (2,557 × days), ($r^2 = 0.998$). For all the above, probability $> F$ = 0.001.

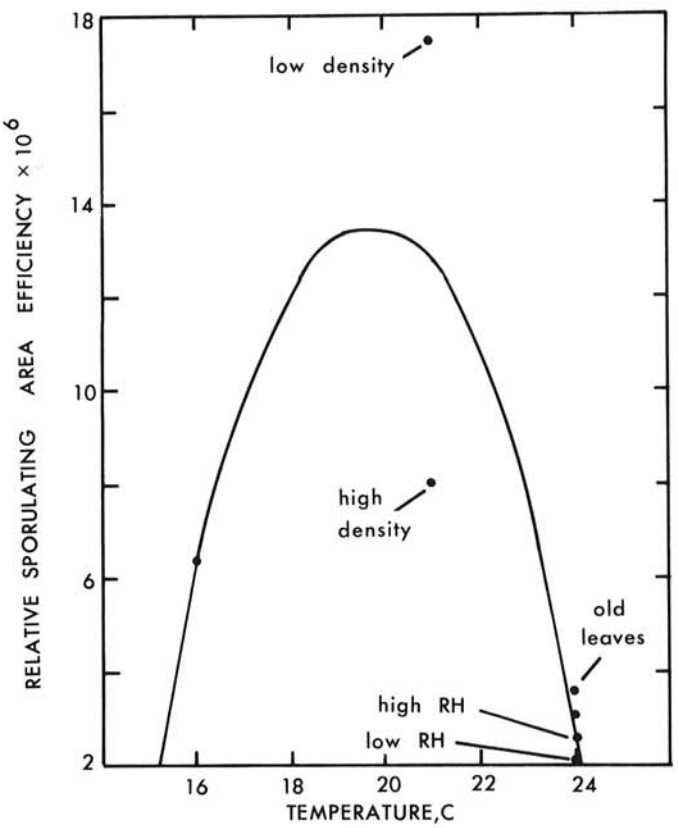

Fig. 11. Relative sporulating area efficiency (spores per square centimeter) of lesions caused by *Uromyces phaseoli* on bean leaves vs temperature. Efficiency was measured by the slope value of linear regression of sporulating area at time (t) on cumulative number of spores at time (t). Efficiency = $-2.09 \times 10^8 + (2.27 \times 10^7 \times \text{temp}) - (5.81 \times 10^5 \times \text{temp}^2)$, ($r^2$ = 0.734). Probability $> F = 0.137$.

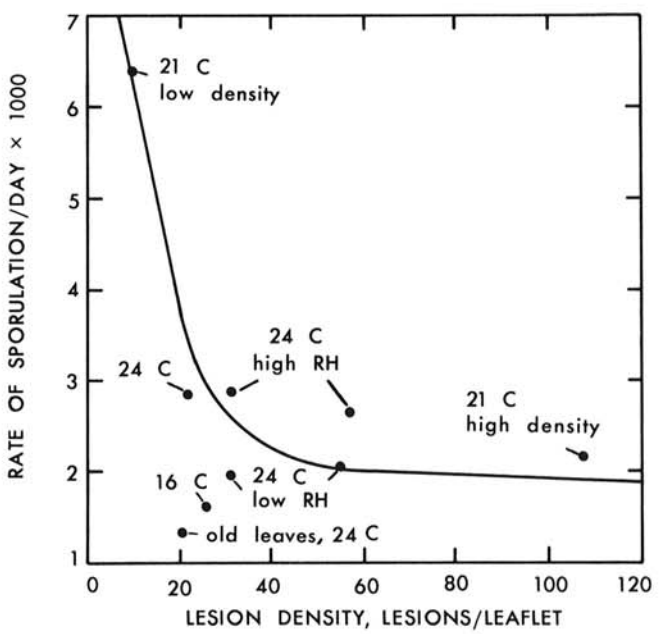

Fig. 12. Average rate of *Uromyces phaseoli* sporulation per lesion per day vs lesion density per bean leaflet. Curve is hand-drawn best fit.

Patterns of sporulation shown in Figs. 1–3 are similar to those described by Melching et al (6) and Broyles (1), and may be typical of many rust fungi. The successive peaks of sporulation found in this study were apparently determined by internal rhythms in growth of the fungus rather than by variation in light-induced phenomena as previously suggested (6), because photoperiod and intensity were constant in the growth chambers. In spite of daily variations in sporulation, the cumulative increase curves are nearly linear (Figs. 8–10), so for modeling purposes, sporulation rates could be thought of as constant, thus greatly simplifying the modeling process.

Rotem et al (7) found that increasing humidity from 40 to 92% induced *U. phaseoli* sporulation to decrease by approximately 30%, whereas Yarwood (10) found that rust-infected bean plants in nearly saturated humidity increased sporulation 2–10 times over those plants kept in the greenhouse. In our experiments, sporulation over a 13-day period was approximately 72% as great at humidities of 45–55% as that obtained at 85–92% humidity (Fig. 10). Also, because there was little difference between sporulation at 24 C standard humidity and sporulation at the two high-humidity treatments (Table 1), it appears that humidity may have relatively little effect on rate of sporulation. This discrepancy with the data of Rotem et al (7), however, is unresolved, and it may represent variation in response of different genotypes of either the host or pathogen.

We had expected that the effect of temperature on sporulation rate would be expressed as an effect on rate of lesion growth, as Fig. 7 would indicate. We had also expected that more rapidly growing lesions should have a higher rate of sporulation than less rapidly growing lesions. However, because temperature also appears to affect the efficiency of a given lesion area at producing spores (Fig. 11), there is not a simple relationship between sporulation rate and temperature.

We had further expected that lesion density should be inversely proportional to sporulation rate per lesion, as borne out by Fig. 12 and shown by Yarwood for primary bean leaves (10). But since sporulation appears to be most efficient near 21 C, the curve presented in Fig. 12, which incorporates data from three temperature treatments, may not represent the true effect of density on sporulation rate because the effect of density may be different at different temperatures.

The values for number of spores per lesion per day for low lesion densities at 21 C may be inflated by the intercept value (13,041) of the standard curve used to calculate numbers of spores from weights of spore collections. Because an average of only 11.8 lesions was used in each of the five weight determinations for this treatment, any error in the intercept value, which should ideally equal zero, was divided over few lesions, and therefore each lesion was credited with having an average of 1,100 more spores per lesion than if a much greater number of lesions had contributed to a given weight of spores. Thus, it would appear that pustule density within the range studied would have somewhat less effect than Figs. 2, 4, 11, and 12 indicate.

Information obtained in this study could be used for a preliminary mathematical description of *U. phaseoli* sporulation rates, but the best description must await, at least, incorporation of data for high and low densities at 24 and 16 C, so that any interaction with temperature, density, and sporulation area efficiency might be understood and exploited.

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