

## Temperature and Host Effects on Latent and Infectious Periods and on Urediniospore Production of *Puccinia recondita* f. sp. *tritici*

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### ABSTRACT

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Effects of temperature and host growth stage on development of *Puccinia recondita* f. sp. *tritici* culture UN02-64A on the wheat cultivar Thatcher (TC) and near-isogenic lines LR16(TC) and LR18(TC) were determined. Latent and infectious periods were lower on seedlings and flag leaves at higher than at lower temperatures. Generally, latent and infectious periods were shorter on seedlings than on adult plants. Cumulative urediniospore production per uredinium 14 days postinoculation (PI) on seedlings of TC and LR18(TC) was lower at lower temperatures in the 21.1–29.4 C range. No marked effect of temperature occurred over this range on LR16(TC) seedlings. Cumulative urediniospore production per uredinium 14 days PI was depressed at temperatures below 21.1 C, particularly on LR18(TC). Total sporulation on LR16(TC) seedlings was slightly depressed at

temperatures above 21.1 C, whereas total sporulation on TC seedlings was slightly stimulated at 23.9 and 26.7 C. Total sporulation on LR18(TC) seedlings was lower at 21.1 than at 29.4 C and much lower at 15.6 and 18.3 C. Total sporulation on TC inoculated at either heading or anthesis was lower at higher temperatures in the 21.1–29.4 C temperature range. This response was not as marked on LR16(TC) or LR18(TC). Cumulative sporulation 14 days PI was greater on seedlings than on adult plants, but infectious period was longer on flag leaves, so total sporulation on adult plants was generally greater than on seedlings. Higher temperatures resulted in shorter latent and infectious periods, indicating that at higher temperatures, a leaf rust epidemic could proceed quickly, but that each generation would be shorter lived than at lower temperatures.

Latent period, infectious period, and spore production greatly influence development of foliar diseases of cereals. These in turn are affected by temperature, host age, and genotype of host and pathogen (8–10, 12–15, 17–21). The possibility of epidemic disease development increases as the latent period decreases, as the infectious period lengthens, or as spore production per lesion increases.

Genetic variation in the host and pathogen interact in different environments and result in variable expression of wheat leaf rust. Browder (5) tabulated 38 genes for low reaction to *Puccinia recondita* f. sp. *tritici* Rob. ex Desm. that demonstrate characteristic low-infection types ranging between 01P and 78X (3).

In our study, three cultivars of wheat (*Triticum aestivum* L. em Thell) and a single culture of *P. recondita* were used to determine the effects of temperature and host age on latent period, infectious period, and urediniospore production in host-parasite combinations producing high-, intermediate-, and low-infection types.

### MATERIALS AND METHODS

The spring wheat cultivar Thatcher (TC) (CI 10003) and near isogenic lines LR16(TC) (Thatcher 6\*/Exchange, RL 6005) (1,7) and LR18(TC) (Africa 43/7\* Thatcher, RL 6009) (2,7) were tested with *P. recondita* culture UN02-64A (ATCC PR3). Culture UN02-

64A produces a high-infection type of 88P on Thatcher and is avirulent on LR16(TC) and LR18(TC). It typically produces a low-infection type of 23N on LR16(TC) and an intermediate-infection type of 56X on LR18(TC) (3).

Plants were grown in plastic pots in a greenhouse with day/night temperatures of 18–24/12–21 C until inoculated. Each pot was fertilized at 3, 6, and 9 wk with approximately 5 g of a 20-20-10 granular fertilizer. Plants with apparently equal vigor, as judged by leaf size, plant height, and color, were used.

Urediniospores of the pathogen were increased on Trison wheat (CI 17278) and stored in liquid nitrogen at –195 C (6). After retrieval from liquid nitrogen, urediniospores were placed in a water bath at 40 C for 5 min. Test plants were inoculated with a suspension of urediniospores in Soltrol 170 (4). After inoculation, plants were misted and placed in a moist chamber at 18 C for 12–16 hr.

Studies were conducted in controlled environment chambers at 15.6, 18.3, 21.1, 23.9, 26.7, and 29.4 C with seedlings in the 3–4 leaf stage (Feekes scale 2) (16) and at the four higher temperatures with plants inoculated at anthesis (Feekes scale 10.5.3–10.5.4). The chambers were programmed for a 16-hr, 11,926-lx photoperiod. In another experiment with seedlings and plants inoculated at heading (Feekes scale 10.0–10.1), seedlings were placed on stands to bring infected leaves to the same level in the environmental chambers as infected flag leaves of adult plants. All light and temperature measurements were taken at that level. Experiments were also conducted at 32.2 C, but sporulation did not occur at this temperature.

Five days after inoculation, the third seedling leaf or the flag leaf of adult plants was examined for chlorotic flecking. The middle halves of infected leaves were delimited with a nonphytotoxic nursery marker. Leaves having between 15 and 30 flecks within the designated area were then monitored for subsequent uredinium

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development and sporulation.

Urediniospores from the adaxial surface of designated leaves were collected daily with a liquid-impingement spore collector. The suction tube was connected to a vacuum pump, and airflow through the collector was maintained at 10 L/min. The tip of the intake tube was passed over uredinia, and urediniospores were impinged into approximately 4 ml of 2% LiCl (w/v) in methanol (LCM). Samples were counted every two or three days with a model B Coulter® Counter (Coulter Electronics, Hialeah, FL 33010).

Urediniospores adhering to the inside of intake tubes were flushed into collection tubes with LCM. Volume in the collection tubes was brought up to 20 ml with LCM. To verify that the LCM solution was effectively dispersing the urediniospores and that single urediniospores rather than clumps were being counted, we counted spot samples with a model F Coulter Counter equipped with a multichannel electronic analyzer. After correcting for background counts from uredinium-free leaves, urediniospore counts were divided by the number of uredinia per sample area to obtain the average number of urediniospores produced per uredinium.

Latent period (LP) data included the number of days between inoculation and appearance of the first uredinium, the number of days between inoculation and appearance of at least 50% of the uredinia (LP<sub>50</sub>), and the number of days between inoculation and the appearance of the last uredinium. Preliminary analyses indicated that, within each growth stage, cultivar-temperature treatments were ranked the same, regardless of which LP data were used. Consequently, we used LP<sub>50</sub> to describe the latent period of *P. recondita*. The infectious period was calculated by subtracting LP<sub>50</sub> from the number of days between inoculation and cessation of sporulation. Sporulation was judged to have ceased when uredinia appeared dead and urediniospore counts were indistinguishable from background counts.

Data from experiments using seedlings or plants inoculated at anthesis were analyzed in a split-plot design having the following model:

$$Y_{ijk} = \mu + R_i + T_j + \delta_{ij} + C_k + TC_{jk} + \epsilon_{ijk}$$

where  $i = 1, 2, \dots, 4$  or 6 replications (R);  $j = 1, 2, \dots, 4$  or 6 temperature treatments (T); and  $k = 1, 2, 3$  cultivars (C) (15). Each replicate consisted of four leaves per temperature-cultivar combination. Data from the experiment with seedlings and plants inoculated at heading were analyzed in a split-split-plot design having the following model:

$$Y_{ijkl} = \mu + R_i + T_j + \delta_{ij} + S_k + TS_{jk} + \theta_{ijk} + C_l + TC_{jl} + SC_{kl} + TSC_{jkl} + \epsilon_{ijkl}$$

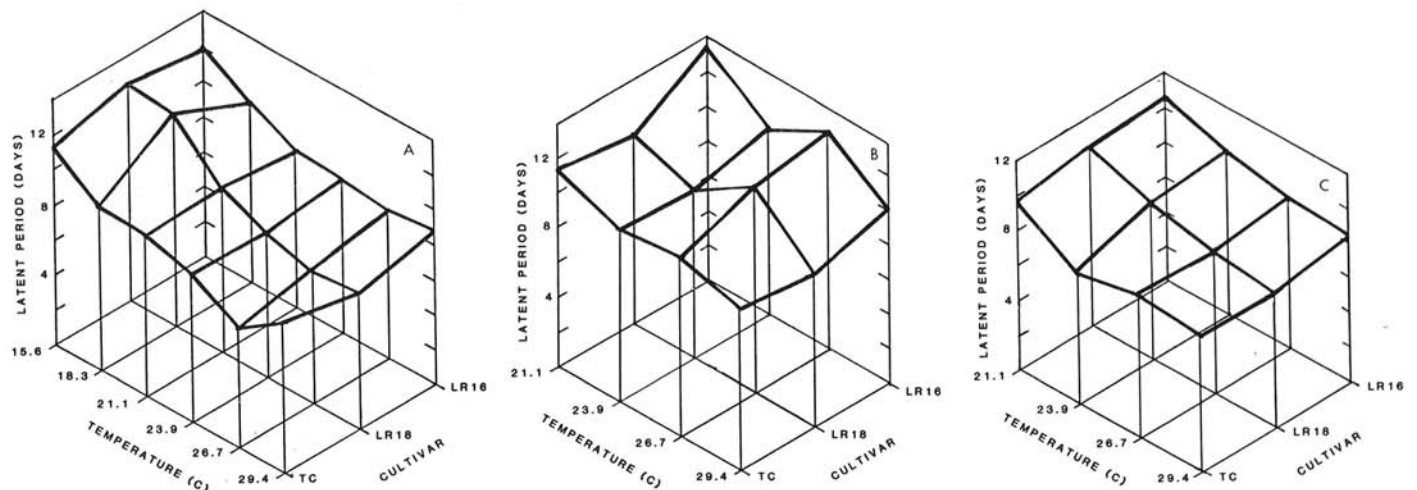


Fig. 1. Latent period of *Puccinia recondita* at several combinations of temperature and host cultivar inoculated at the A, seedling; B, heading; and C, anthesis growth stages. Seeding data are from seedling-only experiments.

where  $i = 1, 2, 3, 4$  replications (R);  $j = 1, 2, 3, 4$  temperature treatments (T);  $k = 1, 2$  growth stages (S); and  $l = 1, 2, 3$  cultivars (C) (15). Each replicate was comprised of three leaves per temperature-growth stage-cultivar combination. Each experiment was repeated as many times as there were temperature treatments. Chamber temperatures were rotated between experiments to allow for possible chamber effects. Preliminary analyses indicated that chamber effects were not significant, so chamber effects were not included in the above models.

## RESULTS

Results from the experiment with seedlings only were similar to those obtained in the experiment with seedlings and plants inoculated at heading.

**Latent period.** Latent period on seedlings generally was shorter at higher temperatures (Fig. 1A). Regression analysis using orthogonal polynomials (26) demonstrated that linear and quadratic trends were significant for all three cultivars ( $P < 0.01$ ). The effect of cultivar was not significant on seedlings, but the interaction of temperature and cultivar was.

On plants inoculated at heading, the linear trend was significant ( $P < 0.05$ ) for LR16(TC), and the cubic trend was significant ( $P < 0.05$ ) for LR16(TC) and LR18(TC) (Fig. 1B). On plants inoculated at anthesis, the linear trend of temperature was significant ( $P < 0.05$ ) for TC and LR16(TC) and ( $P < 0.01$ ) for LR18(TC) (Fig. 1C). At both adult growth stages, latent period was longer on LR16(TC) than on TC or LR18(TC) (Table 1).

The effect of growth stage was highly significant ( $P < 0.01$ ). Mean

TABLE 1. Latent and infectious periods of *Puccinia recondita* on three wheat cultivars at three growth stages<sup>a</sup>

| Cultivar | Latent period (days)<br>on plants inoculated at |        |       | Infectious period (days)<br>on plants inoculated at |        |        |
|----------|---|--------|-------|---|--------|--------|
|          | Seed <sup>y</sup>                               | Head   | Anth  | Seed  | Head   | Anth   |
| Thatcher | 8.3 e <sup>z</sup>                              | 10.1 f | 8.3 m | 17.8 e  | 33.9 g | 19.3 m |
| LR18(TC) | 8.3 e   | 10.3 f | 8.7 m | 17.5 e  | 37.3 h | 21.4 n |
| LR16(TC) | 8.8 e   | 11.6 g | 9.1 n | 14.2 f  | 33.9 g | 18.3 m |

<sup>a</sup>Seedling data are from an experiment with seedlings and plants inoculated at heading. Cultivar means are averaged over the temperatures 21.1, 23.9, 26.7, and 29.4 C.

<sup>y</sup>Seed = seedling stage, Head = heading, Anth = anthesis.

<sup>z</sup>Values in a column followed by different letters differ significantly according to Duncan's multiple range test,  $P = 0.05$ . Seedling and heading values in a row followed by different letters differ significantly according to Student's *t* test,  $P = 0.01$ .

latent periods averaged over the 21.1–29.4 C range and were significantly shorter on seedlings than on plants inoculated at heading (Table 1).

**Infectious period.** Infectious period exhibited a curvilinear response to temperature on seedlings, particularly on TC and LR18(TC) (Fig. 2A). Infectious period on TC was generally lower at higher temperatures, whereas infectious period on LR18(TC) was generally higher. Regression analysis using orthogonal polynomials showed significant linear trends for TC ( $P < 0.05$ ) and LR16(TC) ( $P < 0.01$ ) and significant quadratic trends for TC ( $P < 0.01$ ) and LR18(TC) ( $P < 0.05$ ). Infectious period was shorter on LR16(TC) seedlings than on TC or LR18(TC) (Table 1).

The infectious period on plants inoculated at heading was considerably shorter at 26.7 C than at 21.1 C (Fig. 2B). Linear and quadratic trends were significant at  $P < 0.01$  and cubic trends were significant at  $P < 0.05$  for all three cultivars.

On plants inoculated at anthesis, the infectious period was shorter at higher temperatures (Fig. 2C). Linear trends were significant on TC at  $P < 0.01$  and on LR16(TC) and LR18(TC) at  $P$

$< 0.05$ . The cubic trend was significant ( $P < 0.05$ ) on LR16(TC). At both adult growth stages, infectious period was longer on LR18(TC) than on TC or LR16(TC) (Table 1). The interaction of temperature and cultivar was significant only at the anthesis growth stage.

In the experiment with seedlings and plants inoculated at heading, infectious period on all three cultivars averaged over 21.1–29.4 C was longer on adult plants than on seedlings (Table 1).

**Sporulation.** All measures of sporulation were lower on LR16(TC) than on TC or LR18(TC) (Tables 2 and 3). On seedlings, cumulative sporulation 14 days postinoculation (PI) was low at 15.6 and 18.3 C on TC and LR18(TC) and considerably higher above 18.3 C (Fig. 3A). Linear trends were significant ( $P < 0.01$ ) on TC and LR18(TC), and quadratic trends were significant on TC ( $P < 0.05$ ). Total sporulation during the infectious period on seedlings was depressed at 15.6 and 18.3 C on LR18(TC), but not on TC (Fig. 4A). Linear trends of total sporulation were significant ( $P < 0.01$ ) for all three cultivars, and quadratic trends were significant for LR18(TC) ( $P < 0.01$ ). The interaction of temperature and cultivar for cumulative sporulation 14 days PI and for final sporulation

TABLE 2. Cumulative urediniospore production per uredinium of *Puccinia recondita* on three wheat cultivars at three growth stages<sup>w</sup>

| Cultivar | At 14 days PI <sup>x</sup><br>on plants inoculated at |         |         | For entire infectious period<br>on plants inoculated at |          |                   |
|----------|---|---------|---------|---|----------|-------------------|
|          | Seed <sup>y</sup>                                     | Head    | Anth    | Seed  | Head     | Anth <sup>z</sup> |
| Thatcher | 5,422 a <sup>z</sup>                                  | 2,837 c | 3,103 m | 10,684 a  | 20,604 d | 12,974 m          |
| LR18(TC) | 5,857 a   | 1,505 d | 2,644 m | 12,346 b  | 10,149 e | 10,361 n          |
| LR16(TC) | 1,762 b   | 675 e   | 894 n   | 3,046 c   | 5,067 f  | 2,630 o           |

<sup>w</sup>Seedling data are from an experiment with seedlings and plants inoculated at heading. Cultivar means are averaged over the temperatures 21.1, 23.9, 26.7, and 29.4 C.

<sup>x</sup>PI = postinoculation.

<sup>y</sup>Seed = seedling stage, Head = heading, Anth = anthesis.

<sup>z</sup>Values in a column followed by different letters differ significantly according to Duncan's multiple range test,  $P = 0.05$ . Seedling and heading values in a row followed by different letters differ significantly according to Student's *t* test,  $P = 0.01$ .

TABLE 3. Rate of urediniospore production per uredinium per day of *Puccinia recondita* during different phases of the infectious period<sup>a</sup>

| Cultivar | Stage of infectious period and time of inoculation |      |          |      |              |      |           |      |
|----------|--|------|----------|------|--------------|------|-----------|------|
|          | BOS <sup>b</sup> to 14 PI                          |      | 15–21 PI |      | 22 PI to EOS |      | Entire IP |      |
|          | Seed <sup>c</sup>                                  | Head | Seed     | Head | Seed         | Head | Seed      | Head |
| Thatcher | 951  | 727  | 628      | 661  | 170          | 571  | 600       | 608  |
| LR18(TC) | 1,028  | 407  | 772      | 326  | 226          | 239  | 705       | 272  |
| LR16(TC) | 339  | 281  | 158      | 178  | 88           | 128  | 214       | 149  |

<sup>a</sup>Rate of urediniospore production is calculated as total production during the period/length of the period. Seedling data are from an experiment with seedlings and plants inoculated at heading. Cultivar means are averaged over the temperatures 21.1, 23.9, 26.7, and 29.4 C.

<sup>b</sup>BOS = Beginning of sporulation, PI = days postinoculation, EOS = end of sporulation, and IP = infectious period.

<sup>c</sup>Seed = seedling stage, and Head = heading.

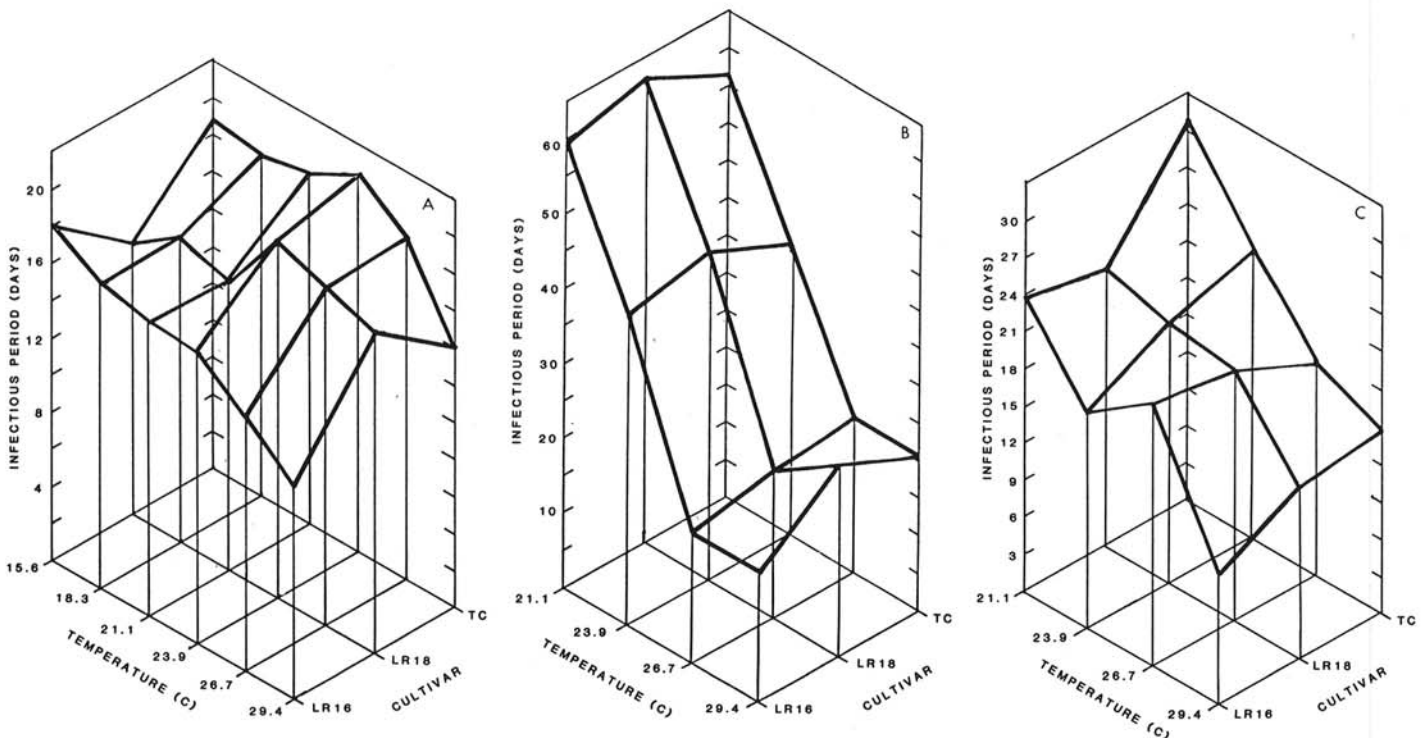


Fig. 2. Infectious period of *Puccinia recondita* at several combinations of temperature and host cultivar inoculated at the A, seedling; B, heading; and C, anthesis growth stages. Seedling data are from seedling-only experiments.

were significant on seedlings.

At 29.4 C, cumulative sporulation 14 days PI was slightly greater on LR16(TC) and LR18(TC) than at 21.1 C. However, on TC, cumulative sporulation 14 days PI was much greater at 29.4 C than at 21.1 C (Fig. 3B). Linear trends were significant on TC and LR18(TC) ( $P < 0.05$ ), and quadratic trends were significant on TC ( $P < 0.05$ ).

Total sporulation on all three cultivars inoculated at heading was less at higher temperatures than at lower temperatures (Fig. 4B). Linear trends were significant on TC and LR18(TC) ( $P < 0.01$ ) and LR16(TC) ( $P < 0.05$ ), and quadratic trends were significant on LR18(TC) ( $P < 0.05$ ).

On plants inoculated at anthesis, cumulative sporulation 14 days PI was not significantly affected by temperature on LR16(TC), was highest at 29.4 and 21.1 C on LR18(TC), and was variable on TC (Fig. 3C). Quadratic and cubic trends were significant ( $P < 0.05$ ) on LR18(TC) and TC, respectively. Total sporulation on plants inoculated at anthesis was not affected by temperature on LR16(TC), was lower at higher temperatures on LR18(TC), and was highest at 29.4 C on TC (Fig. 4C). Linear and quadratic trends were significant on TC and LR18(TC) ( $P < 0.05$ ). The interactions of

temperature and cultivar were significant for cumulative sporulation 14 days PI and for total sporulation on plants inoculated at anthesis.

In the 21.1–29.4 C temperature range, cumulative sporulation 14 days PI and final sporulation on seedlings were approximately the same on LR18(TC) as on TC (Figs. 3 and 4). However, at both adult growth stages, sporulation on LR18(TC) was less than on TC, although the infection type on LR18(TC) seedlings was not noticeably different than on plants inoculated at heading or anthesis.

In the experiment conducted with seedlings and plants inoculated at heading, cumulative sporulation 14 days PI was greater on seedlings than on adult plants (Table 2). However, because of the longer infectious periods on plants inoculated at heading, total sporulation was greater on plants inoculated at heading than on seedlings (Table 2).

We estimated average sporulation rates for several phases of sporulation by dividing the number of urediniospores produced per uredinium during the given phase by the number of days in the phase (Table 3). For the first phase, the number of days available for sporulation was assumed to be 14 minus  $LP_{50}$ . On seedlings of

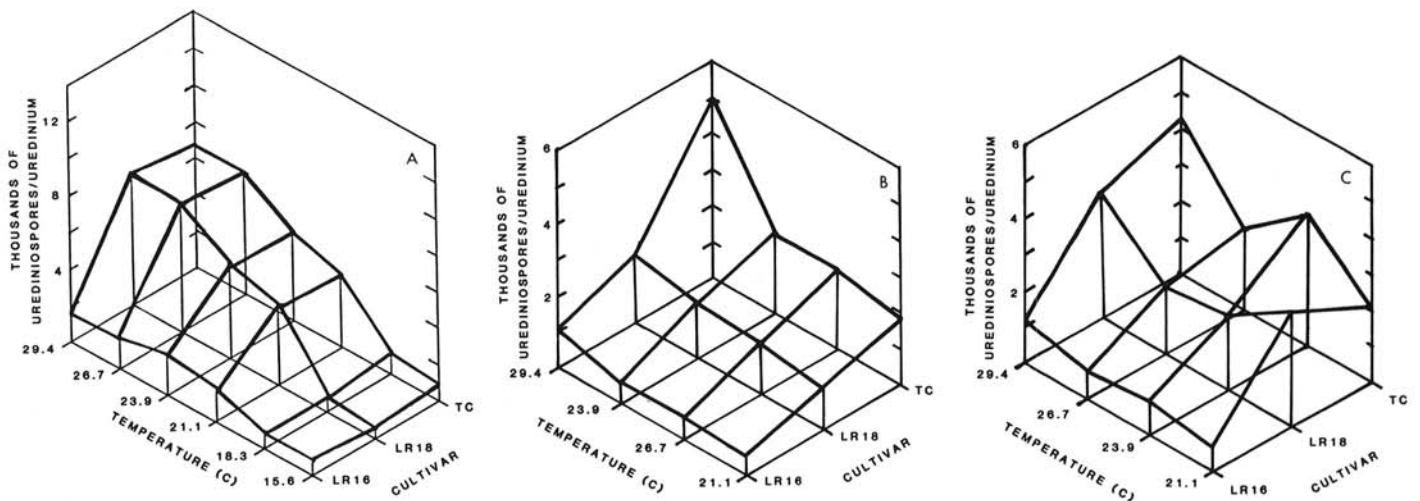


Fig. 3. Cumulative urediniospore production during the first 14 days after inoculation by *Puccinia recondita* at several combinations of temperature and host cultivar inoculated at the A, seedling; B, heading; and C, anthesis growth stages. Seedling data are from seedling-only experiments.

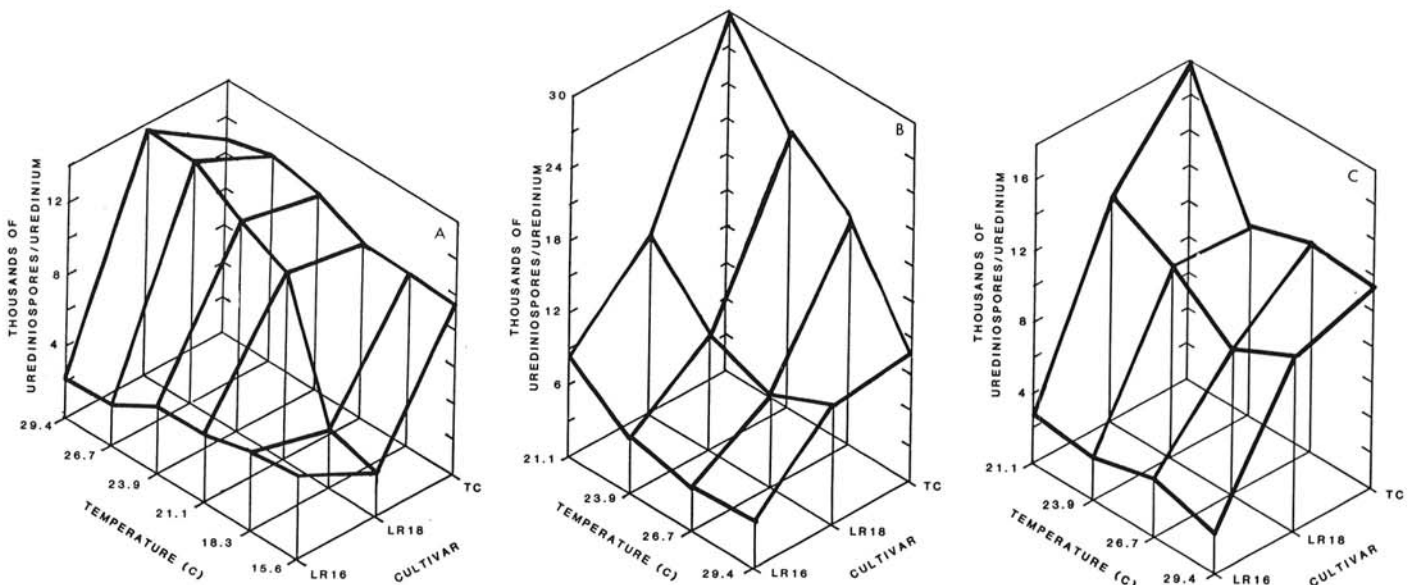


Fig. 4. Total urediniospore production during the entire infectious period by *Puccinia recondita* at several combinations of temperature and host cultivar inoculated at the A, seedling; B, heading; and C, anthesis growth stages. Seedling data are from seedling-only experiments.

all three cultivars, the sporulation rate was maximal during the first 14 days PI and minimal from 22 days PI to the end of the infectious period. A similar, but much less pronounced, trend was evident on plants inoculated at heading (Table 3).

The sporulation rate during the first 14 days PI was greater on seedlings than on plants inoculated at heading for all three cultivars (Table 3). Between 15 and 21 days PI, the sporulation rate on LR18(TC) seedlings was greater than that on plants inoculated at heading. The sporulation rate on TC over the entire infectious period was the same on seedlings as on plants inoculated at heading. On LR16(TC) and LR18(TC), the sporulation rate over the entire infectious period was greater on seedlings than on plants inoculated at heading (Table 3).

## DISCUSSION

Development of plant disease is a process composed of many interwoven components, each of which may be influenced by environmental factors such as temperature. Latent period has been reported to be shorter at higher temperatures for *Puccinia hordei* (28), *P. graminis* f. sp. *tritici* (13), and *P. recondita* (8). Latent period of *P. graminis* f. sp. *avenae* was shorter at 30–35 C than at 20–25 C, although in parallel experiments, latent period of *P. coronata* was shorter at 20–25 C than at 30–35 C (14). In our experiments, latent period of *P. recondita* was shorter at higher temperature on all three wheat cultivars at the three growth stages investigated (Fig. 1). The effect of temperature on latent period was particularly noticeable on LR18(TC) seedlings (Fig. 1A). We observed, as have others (24,28), that uredinia became erumpent over a period of several days.

Infectious period of *P. hordei* was not significantly affected by temperature in the 10–20 C range, although infectious period was significantly shortened at 25 C (28). We observed a similar phenomenon for *P. recondita* on seedlings of TC and LR16(TC), although infectious period on LR18(TC) tended to be higher at higher temperatures (Fig. 2A). The maximum infectious period we observed (62 days) is comparable to that reported by Metha and Zadoks (18). Infectious period may influence the rate of an epidemic as well as being a factor in overwintering (29), although it is difficult to measure accurately (18).

Spore production is generally greater at higher temperatures in the 10–25 C range for *P. hordei* (28), *P. graminis* f. sp. *tritici* (13), and *P. recondita* (9). Temperatures of 30 C and above are often detrimental, a finding corroborated by the lack of urediniospore production at 32.2 C in our experiments.

Spore production on each cultivar at each growth stage in our study was generally greater at higher than at lower temperatures (Figs. 3A and 4A). The interaction of temperature and cultivar is best illustrated in Fig. 4A, in which total sporulation at lower temperatures is greater on LR16(TC) but less on TC and LR18(TC). A reduced rate of sporulation on TC at 15.6 and 18.3 C was apparently compensated for by longer infectious periods. Even though warm temperatures may result in decreased infectious periods and perhaps lower total spore production, more infection cycles could occur, and more urediniospores would be produced and released early in the infection cycle.

The growth stage of the host may also influence disease development. Six days after inoculation, lower percentages of *Erysiphe graminis* colonies were sporulating on flag leaves than on seedling leaves (22). The latent period of *P. graminis* f. sp. *avenae* was slightly less on seedlings than on flag leaves of plants inoculated at anthesis (27). Latent period is less on seedlings than on flag leaves of plants inoculated at heading (Table 1, Figs. 1A and 1B). The latent period of *P. graminis* f. sp. *avenae* was slightly shorter on seedlings than on flag leaves inoculated at anthesis (27). In general, longer infectious periods occurred on plants inoculated at heading (Table 1, Figs. 2A and 2B).

Cumulative urediniospore production by *P. graminis* f. sp. *avenae* was greater on flag leaves than on seedlings (27). For *P. recondita*, some cultures produced more urediniospores on seedlings and others produced more on flag leaves (19). In our experiments, cumulative sporulation 14 days PI was greater on

seedlings than on plants inoculated at heading, but this is somewhat confounded by the shorter latent periods occurring on seedlings. In general, total sporulation was greater on plants inoculated at heading, apparently because of extended infectious periods on flag leaves. However, assuming constant urediniospore production from day to day (24), the rate of urediniospore production through the first 14 days PI on all three cultivars was greater on seedlings than on plants inoculated at heading.

Development of *P. recondita* culture UN02-64A was consistently poorest on LR16(TC). Pathogen development on all three cultivars was influenced by temperature and growth stage of the host, with the effect of *Lr18* most dependent on these two factors. Cumulative sporulation 14 days PI, total sporulation, and rate of sporulation on LR18(TC) seedlings equaled or exceeded those on TC seedlings. These three measures of urediniospore production were generally less on LR18(TC) adult plants than on TC adult plants, suggesting that *Lr18* may function differently in adult plants than in seedlings.

Cultivar differences have been reported for latent period and spore production of several of the cereal rusts (11,15,21,23,25,27). However, in each of these cases, slow rusting was being investigated. In our study, host lines having known *Lr* genes, when inoculated with an avirulent culture, appeared to inhibit disease development in a manner similar to that of slow rusting.

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