Characterization of Resistance to Leaf Rust in Pacific Northwest Wheats

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ABSTRACT

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Seven types of resistance to two local cultures of *Puccinia recondita* were identified by determining numbers of uredia per square centimeter of leaf surface, length of latent period, number of spores per uredium, and infection type (size of uredia and lesions) on seedling and adult plants of nine Pacific Northwest wheat cultivars. Two cultivars were fully susceptible to both cultures. One cultivar had hypersensitive resistance to one of the *P. recondita* cultures. The remaining six cultivars had various degrees of slow rusting in the field. As measured by the above components, two of these cultivars expressed resistance only in the adult plant stage, and four expressed resistance in both the adult and seedling stages. These four cultivars also showed culture × cultivar interactions for the above components of resistance, which indicates that slow rusting in them is culture-specific. When cultivars had fewer uredia, longer latent periods, and fewer spores per uredium they also had a range of high to low infection types (large to small uredia and lesions). The association between a range of infection types and other components of resistance may be useful for selecting breeding lines that are slow rusting.

Additional key words: specific resistance, nonspecific resistance.

Leaf rust of wheat (*Triticum aestivum* L.), caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* Eriks., has become more important in the Pacific Northwest since the early 1960s. More than 99% of the wheat acreage in the Pacific Northwest is planted with cultivars that are classified as susceptible to *P. recondita* based on the infection type (size of the uredia and lesions). However, even though the cultivars are classified as susceptible, rust increases more slowly on some cultivars than on others. No information is available about the characteristics or components of slow rusting in local wheat cultivars or its potential usefulness.

Slow rusting has been considered to be the result of nonspecific resistance (general resistance or horizontal resistance) by several investigators (4,12,19). Ohm and Shaner (12) identified three

components of slow leaf-rusting in two wheat cultivars: longer latent period, smaller uredia, and fewer uredia per square centimeter of leaf surface. Shaner et al (17) later included less sporulation per uredium as a fourth component of what they believed to be general resistance. Ohm and Shaner (11) found correlations between latent period and uredium size and hypothesized that linkage or pleiotropic effects of genes control these components. Clifford (4) reported that nonspecific resistance to leaf rust (caused by *Puccinia hordei*) in one barley cultivar was due to the slower development of fewer and smaller uredia. He concluded that nonspecific resistance could not be divided into distinct components and that fewer uredia, longer latent period, and small uredia were all expressions of the same resistance mechanism.

Parlevliet and Van Ommeren (15) reported that either the latent period of *P. hordei* is the most important component of partial resistance in 16 barley cultivars or the different components of resistance tend to be related to latent period. Parlevliet (13) reported that latent period was polygenic in inheritance, and later he (14) reported differential race-cultivar interactions for latent period and disease severity. He hypothesized that polygenic resistance genes in the host react on a gene-for-gene basis with polygenic virulence genes in the pathogen. This hypothesis conflicts with the statement of Vanderplank (19) that polygenic resistance that reduces the rate of disease increase is characterized by a lack of race-cultivar interactions.

Winter wheat cultivars Hyslop (CI 14564) and Yamhill (CI 14563) and spring wheat cultivars Borah (CI 17267), Fielder (CI 17268), Wampum (CI 17691), and Wandell (CI 15070) have been observed to have less leaf rust in the field than do highly susceptible cultivars such as Twin (CI 14588) spring wheat and Barbee (CI 17417) and Luke (CI 14586) winter wheats. The purpose of this research was to characterize the resistance to *P. recondita* in the Pacific Northwest wheat cultivars that had less leaf rust in the field but are classified as susceptible based on infection type, to determine the interrelationships of components of resistance, and to determine the interactions of the components with races of the pathogen.

MATERIALS AND METHODS

Growth and inoculation of plants. Seedling and adult plants of Barbee, Luke, Hyslop, Yamhill, Borah, Fielder, Wampum, Wandell, and Twin were grown before and after inoculation with diurnal temperature cycles programmed to change gradually from the minimum temperature at 0200 hours to the maximum temperature at 1400 hours. Before inoculation, plants were grown at a 5–15 C diurnal temperature cycle under natural light supplemented with ~4,000 lux from Sylvania Gro-Lux fluorescent lights operating on a 16-hr photoperiod. The winter wheat cultivars

TABLE 1. Latent period of *Puccinia recondita*, as measured by the percentage of infections with sporulation on primary leaves at various days after inoculation in wheat cultivar seedlings inoculated with either culture 1 or culture 2 and incubated at a 10–30 C diurnal temperature cycle

	Infections with sporulation (%)[y]					
	8 days		10 days		13 days	
Cultivar	Culture 1	Culture 2	Culture 1	Culture 2	Culture 1	Culture 2
Hyslop	0 c	89 a	0	100 a	0 d	100 a
Luke[z]	85 a	89 a	100 a	100 a	100 a	100 a
Barbee	83 a	86 a	99 a	100 a	100 a	100 a
Yamhill	81 a	87 a	99 a	95 a	100 a	100 a
Twin	82 a	89 a	100 a	100 a	100 a	100 a
Fielder	81 a	90 a	96 a	100 a	100 a	100 a
Wampum	8 c	50 b	45 c	78 b	77 b	85 b
Borah	5 c	49 b	32 d	71 b	64 c	82 b
Wandell	5 c	0 c	51 c	18 e	84 b	79 b

[y]Values are means for 10 plants. Within each day values followed by the same letter are not significantly different by Duncan's multiple range test at $P=0.05$.
[z]Values for Luke inoculated with culture 1 are only for those plants susceptible to culture 1.

TABLE 2. Latent period of *Puccinia recondita* as measured by the percentage of infections with sporulation on flag leaves at various times (days) after inoculation in adult spring and winter wheat cultivars inoculated with either culture 1 or culture 2 and incubated at a 10–30 C diurnal cycle

	Infections with sporulation (%)[x]							
	Experiment 1				Experiment 2			
	9 days		12 days		10 days		13 days	
Wheat type and cultivar	Culture 1	Culture 2	Culture 1	Culture 2	Culture 1	Culture 2	Culture 1	Culture 2
Spring[y]								
Twin	65	77	92	95	59	87	89	99
Borah	55	79	80	100	75	86	94	97
Wandell	40	12	79	83	56	24	98	70
Wampum	10	57	40	98	10	76	50	95
Fielder	0	74	0	90	0	60	0	91
LSD ($P=0.05$)	14.3		11.1		15.7		10.8	
Winter[y]								
Barbee	53	45	98	89	71	68	100	85
Luke[z]	64	47	86	91	59	64	92	90
Yamhill	28	21	86	82	47	38	95	65
Hyslop	0	64	19	89	0	79	15	80
LSD ($P=0.05$)	16.5		10.2		22.1		11.9	

[x]Values are means for eight 5-cm-long sections of flag leaves.
[y]Spring and winter cultivars were evaluated in separate experiments because they matured at different times.
[z]Values for Luke inoculated with culture 1 are only for those plants susceptible to culture 1.

used in adult plant studies were vernalized either by placing seedlings that were in the two-leaf stage in a lath house at Pullman, WA, from mid-October to mid-December, or by incubating germinated seeds for 6 wk at 0–5 C before planting.

Cultures 1 and 2 (Western *Puccinia recondita* races 1 and 2 [WPR-1 and WPR-2] respectively) were used in all experiments. The virulence of these races has been described by Milus and Line (10). Race WPR-1 has been present in the Pacific Northwest for many years. Race WPR-2, which attacks several of the local wheat cultivars that are resistant to race WPR-1, was first identified in 1976.

When the primary leaf (first seedling leaf) was fully expanded, seedlings were inoculated with urediospores of *P. recondita* mixed with talc by use of a spore settling tower similar to that described by Melching (9). Before inoculation, the leaf above the primary leaf was removed so that it would not interfere with deposition of inoculum on the primary leaf. When the adult plants were in the early heading stage, flag leaves were inoculated with urediospores mixed with talc by use of a spore settling tower similar to that described by Eyal et al (5). Flag leaves were taped to the circular table of the spore settling tower with the adaxial surface upwards. The tips of the leaves were covered with a circular piece of Plexiglas so that a 10-cm-long section near the center of each flag leaf was exposed to inoculum. In experiments designed to determine latent period, number of uredia per square centimeter of leaf surface, or infection type, the 10-cm-long length of each flag leaf was divided into two 5-cm-long sections to allow side-by-side comparisons of the two cultures. One half of the 10-cm-long section was covered with a 5-cm-wide Plexiglas ring while the other section was inoculated with one culture. The inoculated portion was then covered with another 5-cm-wide ring and the previously uninoculated section was inoculated with the second culture. Contamination was reduced and consistency improved by coating the lower surfaces of the Plexiglas with an antistatic compound (En-State MS-166, Miller-Stephenson Chemical Co. Inc., Los Angeles, CA 90012) and the upper surfaces with a light-weight lubricating oil or Vaseline. The location of each inoculated section was marked with a felt-tipped pen.

After inoculation, plants were placed in a dew chamber for 12–16 hr and then grown at either 2–18 C or 10–30 C diurnal temperature cycles, which were similar to daily spring and summer temperature ranges, respectively, in eastern Washington. Most experiments were conducted in a greenhouse under natural light supplemented with ~2,200 lux from Sylvania Gro-Lux fluorescent lights operating on a 16-hr photoperiod. A few seedling experiments at 10–30 C were conducted in a growth chamber with cool-white fluorescent lights with an intensity of ~11,600 lux for a 16-hr photoperiod. Temperature in the greenhouse during experiments at 10–30 C occasionally exceeded 30 C on hot, sunny days.

Measurements of components of resistance. The percentage of total infections with sporulation on various days after inoculation was used as a measure of latent period. Observations were made on a 7-cm-long section of the primary leaf of each inoculated seedling. Sporulating uredia within the delineated sections were counted soon after the first evidence of sporulation and again 2 and 5 days later. In adult-plant experiments, latent period was evaluated on 5-cm-long sections of flag leaves in a similar manner.

The number of uredia per square centimeter of leaf surface was calculated by dividing the number of uredia by the area of the section.

The mean number of spores per uredium was determined by counting a sample of the spores produced by a known number of uredia. Inoculated primary leaves with similar numbers of visible infections were suspended above plastic troughs as described by Heagle and Moore (6). The spores were collected when they first fell freely from the leaves and at 3-day intervals until the primary leaves began to senesce. The spores were tapped from the leaves onto the troughs and washed from the troughs with a 0.1% solution of Tween-20 surfactant (polyoxyethylene sorbitan monolaurate). A few drops of lactophenol trypan blue stain were added to each vial, and the contents were mixed with a vortex mixer for 15–20 sec. The vials were stored at 5 C until the spores could be counted with a hemocytometer. The cumulative number of spores per uredium was determined by adding the mean number of spores per uredium collected on each date to the mean of the previous collection. Sporulation on adult plants was determined similarly from uredia on 10-cm-long sections of flag leaves.

Infection types were recorded to evaluate the compatibility of the host-pathogen interaction and to estimate the size of the uredia. They were recorded when symptoms were fully expressed (14–17 days and 21–25 days after inoculation for plants at 10–30 C and 2–18 C, respectively). We used the coding system of Browder (1) with symbols for designating mixed infection types adapted from McNeal et al (8).

RESULTS

In general, Twin and Barbee were susceptible to both cultures. Hyslop was susceptible to culture 2 and resistant to culture 1. Fielder was susceptible to both cultures in the seedling stage, but it was resistant to culture 1 in the adult stage. All plants of Luke were susceptible to culture 2, and some plants were susceptible to culture 1. Data for culture 1 on Luke are only from those plants that were susceptible to culture 1.

Latent period. On primary leaves, both cultures sporulated slower on Wampum, Borah, and Wandell than on the susceptible cultivars (Table 1). However, culture 1 sporulated slower than did

TABLE 3. Percentage of infections with sporulation on primary leaves of seedling wheat cultivars inoculated with either culture 1 or culture 2 of *Puccinia recondita* and incubated at either 2–18 C or 10 –30 C diurnal temperature cycles

	Infections that sporulated (%)[y]			
	Culture 1		Culture 2	
Cultivar	2–18 C	10–30 C	2–18 C	10–30 C
Hyslop	0 c	0 e	100 a	100 a
Barbee	100 a	100 a	100 a	100 a
Luke[z]	100 a	100 a	100 a	100 a
Yamhill	100 a	100 a	100 a	100 a
Twin	100 a	100 a	100 a	100 a
Borah	100 a	64 d	100 a	82 b
Wampum	100 a	77 c	100 a	85 b
Wandell	100 a	90 b	100 a	85 b
Fielder	83 b	100 a	99 a	100 a

[y]Values are means for 10 plants. Within each column, values followed by the same letter are not significantly different by Duncan's multiple range test at $P = 0.05$.

[z]Values for Luke inoculated with culture 1 are only for those plants susceptible to culture 1.

TABLE 4. Number of uredia per square centimeter of leaf surface on primary leaves of seedling wheat cultivars inoculated with either culture 1 or culture 2 of *Puccinia recondita* and incubated at either 2–18 C or 10–30 C diurnal temperature cycles

	Uredia per square centimeter (no.)[y]			
	Culture 1		Culture 2	
Cultivar	2–18 C	10–30 C	2–18 C	10–30 C
Hyslop	0.0 e	0.0 e	12.7 a	7.4 b
Barbee	14.2 a	12.5 a	10.5 a	8.5 ab
Luke[z]	12.7 a	12.8 a	11.3 a	8.1 ab
Twin	11.0 ab	8.3 bc	9.3 ab	11.6 a
Yamhill	10.4 ab	9.4 b	7.6 ab	6.1 b
Wandell	13.7 a	6.7 bcd	10.7 a	7.0 b
Wampum	11.8 ab	5.7 cd	11.0 a	5.2 b
Borah	9.2 b	4.1 d	8.0 ab	5.2 b
Fielder	7.1 bc	7.2 bc	6.2 b	7.4 b
Mean	10.0	7.4	9.7	7.4

[y]Values are means for 10 plants. Within a culture, values followed by the same letter are not significantly different by Duncan's multiple range test at $P = 0.05$.

[z]Values for Luke inoculated with culture 1 are only for those plants susceptible to culture 1.

culture 2 on Wampum and Borah, and culture 1 sporulated slower than did culture 2 on Wandell. Latent period on Yamhill was not different from latent period on the susceptible cultivars.

On flag leaves, both cultures sporulated slower on Yamhill, Wandell, and Wampum than on the susceptible cultivars (Table 2). However, culture 1 sporulated slower than did culture 2 on Wampum, and culture 2 sporulated slower than did culture 1 on Wandell. Latent period on Borah was not different from latent period on the susceptible cultivars.

Number of uredia. Less than 100% of the macroscopically visible infections caused by cultures 1 and 2 produced uredia on primary leaves of Borah, Wampum, and Wandell at 10–30 C (Table 3). On Fielder, less than 100% of the infections by culture 1 produced uredia at 2–18 C, but all infections produced uredia at 10–30 C.

Fewer uredia developed at 10–30 C than at 2–18 C (Table 4). Primary leaves of Wandell, Wampum, and Borah had fewer uredia per square centimeter of leaf surface at 10–30 C than the susceptible cultivars. Fielder had few uredia per square centimeter of leaf surface at both temperatures. Flag leaves of Wandell, Wampum, and Borah also had fewer uredia per square centimeter of leaf surface than did Twin, but the differences were not statistically significant. The technique used to inoculate flag leaves distributed spores less uniformly than did the technique used to inoculate primary leaves. This resulted in a large variation in the number of uredia on flag leaves.

Number of spores per uredium. In general, sporulation was high on Barbee, Luke, and Twin; low to intermediate on Fielder, Yamhill, and Wampum; and low on Borah and Wandell (Figs. 1A–D). Uredia on primary leaves (Figs. 1A, B) produced more spores at 10–30 C than at 2–18 C. At both temperatures, culture 2 produced fewer spores per uredium than did culture 1 on Yamhill and Wandell. Culture 1 produced fewer spores per uredium than did culture 2 on Wampum at 10–30 C and on Borah at 2–18 C. On flag leaves (Figs. 1C, D), sporulation by culture 2 was lower than that of culture 1 on Yamhill and Wandell. Sporulation of culture 1 was lower than that of culture 2 on Wampum and Borah.

Infection type. Differences in infection type among cultivars in the seedling stage were more evident at 10–30 C than at 2–18 C (Table 5). At 10–30 C in the seedling and adult plant stages, Yamhill, Borah, Wampum, and Wandell had a range of infection types. Culture 2 produced a lower range of infection types than culture 1 on Wandell and Yamhill, and culture 1 produced a lower range of infection types than did culture 2 on Borah and Wampum.

DISCUSSION

Types of resistance. The nine cultivars in this study, which differ genetically, can be classified into seven types based on resistance or susceptibility to leaf rust as measured by the components of resistance. Type 1 cultivars (Barbee, Twin, and some plants of Luke) show little or no resistance in any of the components. Cultivars in this group also are severely infected in the field. The type 2 cultivar (some plants of Luke) is highly resistant to culture 1 and very susceptible to culture 2 in all stages of growth, at all temperatures, and by all component measurements. Other types of cultivars had various degrees of slow rusting in the field. The type 3 cultivar (Hyslop) is similar to type 2 except that infection type and number of spores produced after inoculation of adult plants with culture 2 in the adult plant stage were intermediate instead of high. The type 4 cultivar (Fielder) in the seedling stage allows both cultures to sporulate quickly, but fewer uredia are produced and spore production is intermediate. The adult plants are resistant to culture 1 and susceptible to culture 2. However, spore production by culture 2 was intermediate. The type 5 cultivar (Yamhill) allows fast sporulation in the seedling stage, but intermediate sporulation in the adult stage. Fewer uredia and fewer spores are produced after inoculation with culture 2 than with culture 1. The type 6 cultivar (Wandell) delays sporulation and has fewer uredia, fewer spores, and a lower infection type. All measurements show more resistance to culture 2 than to culture 1. Type 7 cultivars (Borah and Wampum) are similar to type 6 except that the plants are more resistant to culture 1 than to culture 2.

Hyslop and some plants of Luke appear to have gene *Lr* 1, which confers resistance to culture 1 but not to culture 2. This gene for specific resistance also appears to be present in three other Pacific Northwest wheat cultivars (Norco [CI 14482], McDermid [CI 14565], and Walladay [CI 17759]). All five cultivars have Washington Selection 101 (CI 13438) as one of their parents, and they apparently received gene *Lr* 1 from that parent.

Relationship of components of resistance. Race-cultivar combinations that produced a range of infection types at 10–30 C (Table 5) were more resistant as measured by one or more other components (Tables 1–4 and Figs. 1A–D). The range of infection types is similar to the race-specific mesothetic or "X" infection type of *Puccinia graminis* described by Stakman et al (18); but it may not consist of the complete range. The longest latent period, the fewest uredia per square centimeter of leaf surface, and the fewest spores per uredium were observed on cultivars that had infections with no sporulation and a predominance of small uredia. Cultivars with a predominance of large uredia had shorter latent periods and produced more spores per uredium. On the same leaf, the larger uredia always sporulated before the smaller uredia and produced more spores.

The association between a range of infection types and other components of resistance has not been previously reported. However, Browder (2) demonstrated that Bulgaria 88, which was reported by Caldwell et al (3) to be a slow-rusting cultivar, had a range of infection types after inoculation with 24 races of *P.*

TABLE 5. Infection types on primary leaves and flag leaves of wheat cultivars inoculated with either culture 1 or culture 2 of *Puccinia recondita* and incubated at either 2–18 C or 10–30 C diurnal temperature cycle

	Infection type[z]							
	Seedlings				Adults			
	2–18 C		10–30 C		2–18 C		10–30 C	
Cultivar	Culture 1	Culture 2	Culture 1	Culture 2	Culture 1	Culture 2	Culture 1	Culture 2
Luke	01,78	78	01,98	98	01,93	93	01,93	93
Barbee	58	68	98	98	93	93	93	93
Twin	58	58	98	98	93=42	93	93=53	93
Fielder	68+01	68	98	98	01	93=01	01	93
Hyslop	01	58	01	98	02=12	82=53	02=12	63=23
Yamhill	58	58	88=55	88=55	62	52	53=12	33=11
Borah	58	58	01=86	98=01	62=01	82=01	01=53	01=83
Wandell	58	58	66=01	02=33	83=01	32=01	11=83	12=52
Wampum	58	68	01=65	98=01	...	...	11=32	85=32

[z]The first number of the infection type code estimates the size of the sporulating area, from 0 = no sporulation to 9 = the largest sporulating area. The second number estimates the total size of the lesion, from 0 = no visible infection to 9 = the largest lesion. A comma (,) denotes a mixture of plants with different infection types, a plus sign (+) denotes two distinct types on the same leaf, and an equals sign (=) denotes a range of infection types on the same leaf. The infection type preceding the symbol is the predominant infection type. Infection types with sporulating areas estimated at 0–3, 4–6, and 7–9 are classified as low, intermediate, and high, respectively.

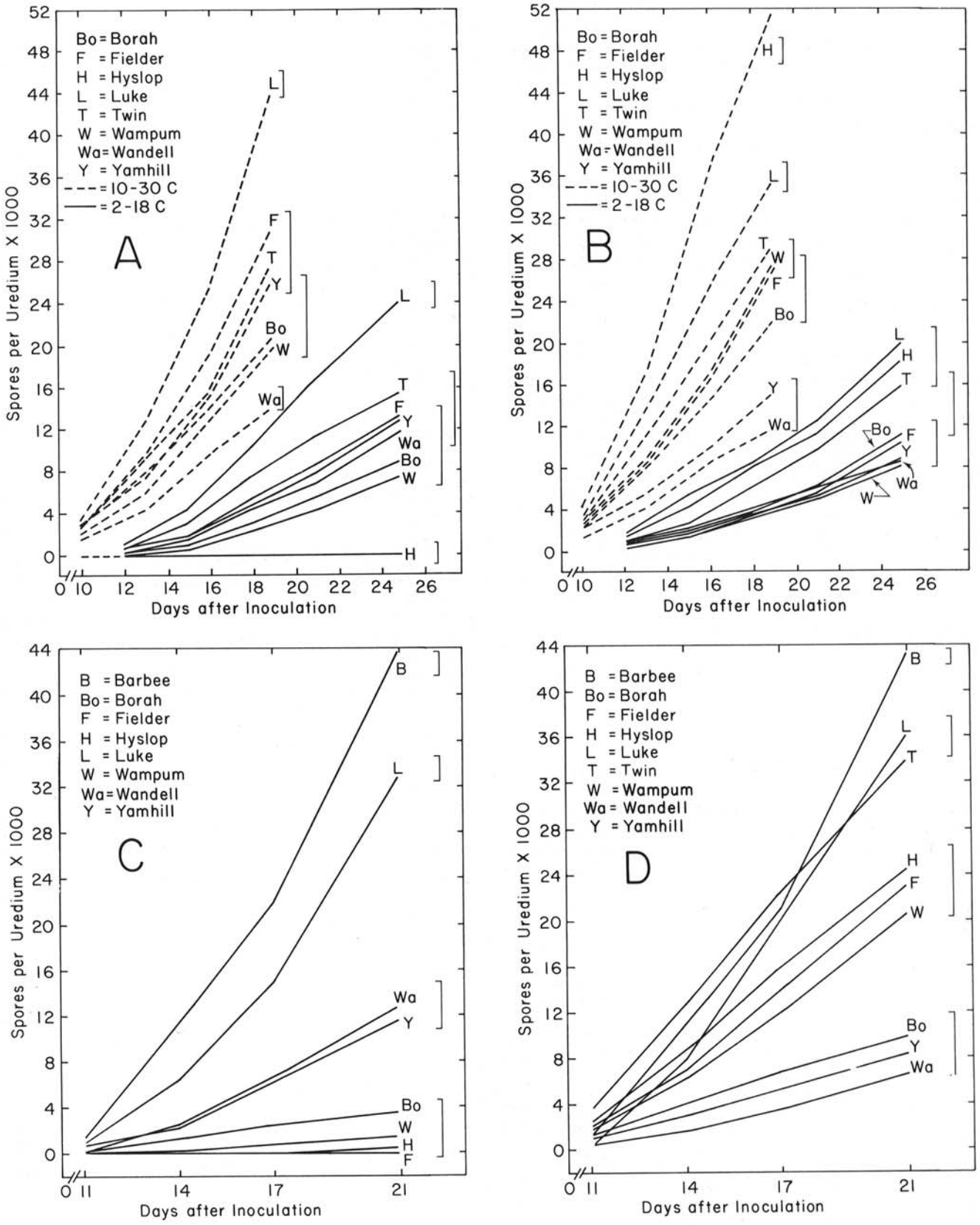

Fig. 1. Cumulative number of spores per uredium collected from leaves of wheat cultivars inoculated with urediospores of *Puccinia recondita*. The values for cultivars within a bracket are not significantly different by Duncan's multiple range test at $P = 0.05$. Data are means of four leaves. **A,** Primary leaves inoculated with culture 1 and incubated at either 2–18 C or 10–30 C. **B,** Primary leaves inoculated with culture 2 and incubated at either 2–18 C or 10–30 C. **C,** Flag leaves inoculated with culture 1 and incubated at 10–30 C. **D,** Flag leaves inoculated with culture 2 and incubated at 10–30 C.

recondita. Also, the infection type of *P. hordei* on Vada, a barley cultivar reported by Clifford (4) to be slow rusting, was observed by R. F. Line to be similar to the range of infection types reported in this study.

Race specificity of components of resistance. Components of resistance for Borah, Wampum, and Wandell consistently were culture specific. On Wampum and Borah, culture 2 had shorter latent periods (Tables 1 and 2), more infections with sporulation (Table 3), more spores per uredium (Figs. 1A–D) and higher infection types (Table 5) than did culture 1. On Wandell, culture 1 had shorter latent periods (Tables 1 and 2), more infections with sporulation (Table 3), more spores per uredium (Figs. 1A–D), and higher infection types (Table 5) than culture 2. Yamhill tended to be more susceptible to culture 1 than to culture 2, but the differences were not as great as with Wandell.

Although culture specificity for the components was evident, it was less than in the classical hypersensitive type of resistance. Therefore, the types of resistance reported here may prove to be less vulnerable to new races and, consequently, more durable. The specificity of the slow rusting resistances to *P. recondita* is in contrast to the strong evidence for nonspecificity of resistance to *Puccinia striiformis* in the cultivars grown in the Pacific Northwest (7).

The culture-cultivar interactions in this study support the integrated concept of disease resistance proposed by Parlevliet and Zadoks (16). They stated that classifying resistance into race-specific and race-nonspecific resistances is a hindrance to understanding how resistance genes operate. They contend that all resistance genes operate on a gene-for-gene basis with virulence genes in the pathogen. However, race-specific resistance is olegogenic, while race-nonspecific resistance is polygenic. According to this model, Borah, Wampum, Wandell, and Yamhill should have several genes for resistance to *P. recondita*. Borah and Wampum would have more genes effective against culture 1, while Wandell and Yamhill would have more genes effective against culture 2. Research on the genetics of these cultivars is needed to confirm this hypothesis.

Application of this work to evaluating resistance. Screening of breeding lines for a range of infection types may be a useful technique for selecting lines that produce fewer uredia, have a long latent period, and produce fewer spores per uredium. A range of infection types appears to be closely associated with these components and is easier to measure. Entries in several regional and international wheat nurseries currently are being evaluated for resistance to *P. recondita* in the seedling and adult plant stages by observation of infection types.

Evaluation of cultivars for resistance in the seedling stage does not always agree with similar evaluations in the adult stage or with evaluations in the field. In this study, cultivars that were susceptible as seedlings usually were susceptible as adults. However, Fielder was resistant to culture 1 in the adult stage but susceptible to culture 1 in the seedling stage, and Hyslop was more resistant to culture 2 in the adult stage than in the seedling stage. Resistance to both cultures in Borah, Wampum, Wandell, and Yamhill was greater in the adult stage of plant growth, but it was still possible to identify resistance in the seedling stage. Results of evaluating adult plants in the greenhouse agree with observed disease intensities in the field.

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