Sorting of *Puccinia recondita:Triticum* Infection-Type Data Sets Toward the Gene-for-Gene Model

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ABSTRACT

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Infection-type data, derived from inoculating 14 randomly arranged lines of *Triticum aestivum* with seven randomly arranged cultures of *Puccinia recondita,* were machine sorted sequentially by first rearranging culture order (data columns) according to ascending values of infection-type codes to each host line (data rows). Host-line order (data rows) was then sequentially rearranged according to descending values of infection-type codes to each culture (data columns). This sorting resulted in a table in which lines and cultures were arranged with a generally increasing number of low infection types from top to bottom and a generally increasing number of high infection types from left to right, as in the theoretical gene-for-gene model. Lines were sorted so that a given line could not have all the genes for low reaction carried by any line listed below it in the table. This procedure has direct application in comparing host lines with unknown reaction genotypes and host lines with known reaction genotypes. Lines with similar reaction genotypes occur together and cultures with similar pathogenicity genotypes occur together within the sorted table. The data were retained in the original form so that visual analysis of the data set could easily be made. The data were arranged so that low infection types produced by different corresponding gene pairs occurred diagonally left to right and top to bottom within the table.

Additional key words: leaf rust, genetics, wheat, disease resistance, host:parasite relationships.

The development of a theoretical model of a gene-for-gene system involving five corresponding gene pairs (CGPs) by Person (13) in 1959 placed new emphasis on Flor's (8) hypothesis and gave new direction to analysis of infection-type (IT) data. Simons (15) used similarity of reaction to different cultures of *Puccinia coronata* to group lines of oats and to postulate that each group differed genetically as a source of resistance to crown rust. Bartos et al (1) used the same method to relate wheat cultivars of unknown genotypes to lines with known genes for low reaction.

Loegering (10) outlined a method whereby genetic differences in host lines could be shown through the use of IT data. Browder (3,4) used essentially the same method to demonstrate differences in host-reaction genotypes and to relate lines with unknown reaction genotypes to those with known genotypes. Loegering et al (12) and Loegering and Burton (11) have shown that machine-processing methods can be used to analyze IT data to indicate genotype similarities and differences. We (5) previously reported a recording and processing system for analysis of *Puccinia recondita:Triticum* IT data. Robinson (14) has shown that order of genotype within the theoretical model influences the symmetry of the model.

In this paper, we show an extension of our processing system that sorts IT data toward the model shown by Robinson (14) and facilitates comparing the ITs produced on wheat lines by cultures of *P. recondita* having differential pathogenicity.

MATERIALS AND METHODS

We used IT data from 14 lines of wheat, *Triticum aestivum* L. emend. Thell., inoculated with seven cultures of *Puccinia recondita* Rob. ex. Desm. The materials used, along with appropriate accession numbers for the wheat lines and American Type Culture Collection Plant Rust (PR) accession numbers for the cultures are listed in Tables 1 and 2. The tests were made with previously described techniques (2); the ITs were produced under growth chamber conditions at 20 ± 2 C and a 12-hr day at 21,520 lux. Infection types were coded according to the system proposed by Browder and Young (7). In that coding system, estimates of the relative amount of sporulation and the relative lesion size are coded as separate characters on a 0 to 9 scale; an alphabetically coded descriptor, such as C for chlorosis around the lesion or N for necrosis around the lesion, completes the code for a given IT. The alphabetic descriptor codes in the infection-type data were not included in the sorting procedure. They are, however, carried forth in the program because such information is useful in visual analysis of sorted data sets.

The symbolization of Loegering and Burton (11) for host and parasite genotypes and for IT phenotypes is used in this section: L = low, H = high, r = reaction of the host, p = pathogenicity of the parasite, and IT = infection type of the parasite:host association. A '?' is used where the L or H condition of a reaction or pathogenicity locus cannot be determined. In the Results and Conclusions and the Discussion sections, however, *Lr* refers to specific known wheat genes for low reaction to *P. recondita,* while *Lp* and *Hp* refer to the hypothetical genotypes for pathogenicity corresponding to the known *Lr* genes. LRn (recurrent parent abbreviation) is used to designate a near-isogenic line having the respective *Lrn* gene.

A computer program was written in PL/1 language to sort the IT data set. The program is available from the senior author. Data columns, including the culture-name headings, were sorted (rearranged) according to ascending order (left to right) of the sporulation- and lesion size-code values of the IT from each wheat line (data rows). Sorting proceeded sequentially downwards from row to row. The data rows, including the host-line name information, were then sorted according to descending order (top to bottom) of the sporulation- and lesion size-code values of the IT produced by each culture (data columns). Sorting proceeded sequentially through the columns from right to left within the table. In sorting any row or column, the order left in the previous sort was used as a beginning point. During a particular sort, the order of items having equal value was not altered.

The program was tested, using data from a five CGP theoretical model. The order of host lines and cultures was left unchanged when the original order followed Robinson's (14) model. Host line and culture order was sorted to the theoretical order identically when the original order was random.

As an example, the sorting of a hypothetical 3 × 3 table of:

	IT produced by culture		
Line	1	2	3
A	99P	01C	01C
B	99P	99P	99P
C	23X	23X	99P

would be done by:

(i) rearranging culture order three times according to ascending order of IT codes in each row. The order after sorting row A would be 2, 3, 1; the order after sorting row B would be 2, 3, 1; and the order after sorting row C would be 2, 1, 3.

(ii) rearranging line order according to descending order of IT codes in each column, beginning with the last column and progressing toward the first. The line order after the first sort (culture 3) would be B, C, A; the order after sorting the middle column (culture 1) would be B, A, C; and the final order (after sorting culture 2) would be B, C, A.

The resulting sorted table would be:

	IT produced by culture		
Line	2	1	3
B	99P	99P	99P
C	23X	23X	99P
A	01C	99P	01C

In this example, all lines and all cultures are different. Line B is of no value in determining differences in low IT. Lines C and A differentiate pathogenicity genotypes of all the cultures and conversely, culture 2 differentiates A, B, and C, while culture 1 differentiates C from A and B, and culture 3 differentiates A from B and C.

Loegering and Burton (11) showed that when two low ITs occur on a diagonal within a two-line × two-culture matrix of IT data, as a set or subset, and either or both of the other ITs are high, the two low ITs were effected by two different CGPs. This relationship can be proven as the general case, accepting a tenet of the gene-for-gene relationship that low IT is effected only by *Lr*/*Lp* and all other interactions of one CGP result in a high IT. In the hypothetical data set:

		Cultures:	
		4	5
Lines	D	low IT	high IT
	E	...	low IT

the low IT from D/4 must be caused by an *Lp* gene in culture 4 interacting with an *Lr* gene in D. We can designate these, for purposes of this illustration, as *Lp1* and *Lr1*. Then, because culture 5 caused a high IT on D, having *Lr1*, culture 5 must be *Hp1*. Because E has a low IT caused by culture 5, with *Hp1*, E must have another gene for low reaction, *Lr2*, and culture 5 must have its corresponding gene for low pathogenicity, *Lp2*. Because D has high IT caused by culture 5, D must have *Hr2*. The genotypes at locus 2 in either E or 4 cannot be determined from these data. A high IT at E/4 would indicate *Hp2* in 4 and *Hr1* in E, but a low IT would *not* necessarily indicate *Lp2* and 4 and *Lr1* in E, because either or both CGPs or a third CGP could effect the low IT.

Thus, in the sorted example data presented above, we find that C/1, C/3, and A/3 form a diagonal check and indicate that the low IT at C/1 and the low IT at A/3 are caused by different CGPs. A diagonal check is also formed by C/1, A/2, and A/1. However, these two diagonal checks both include the low IT at C/1 and differentiate C/1 from either A/2 or A/3, but not from both A/2 and A/3. The net result is that A/2 and A/3 cannot be differentiated, nor can C/2 and C/1. Thus, only the effect of two CGPs can be ascertained. We will consider the low ITs at C/1 and A/3, because the high IT demonstrating them occurs at the upper right, the general direction to which high ITs are sorted with the sorting program.

The hypothetical genotypes (11) that can be determined from the sorted example data then are: host-line B is *Hr1Hr2*, C is *Lr1Hr2*, and A is *Hr1Lr2*; culture 2 is *?p1?p2*, 1 is *Lp1Hp2*, and 3 is *Hp1Lp2*.

The theoretical model of the gene-for-gene relationship has no "universally resistant" (UR) cultivar nor "universally avirulent" (UA) culture. In real, partially complete, data sets; such cultivars and cultures do occur. It was found that when either occurred as the last member of a set, that the sorting procedure was adversely

TABLE 1. Infection-type data obtained by inoculating 14 lines of *Triticum aestivum* with seven cultures of *Puccinia recondita*

Entry no.	Line name	Line no.[a]	Infection type produced by *P. recondita* culture:						
			UN01-68B	UN01-68A	UN17-68A	UN09-66A	0967-1	6B-NA65-9	65359-01
			PR51	PR67[b]	PR62	PR66	...	PR76	...
1	LR1(TC)	RL 6003	01C[c]	01C	01C	99P	99P	99P	99P
2	LR2A(TC)	RL 6000	01C	01C	99P	99P	99P	14C	01C
3	LR3(TC)	RL 6002	03C	03C	99P	03C	03C	99P	99P
4	LR9(TC)	RL 6010	01C	01C	01C	03C	01C	01C	01C
5	LR2D(PL)	RL 6001	03C	24C	99P	99P	99P	99P	03C
6	LR19(TC)	RL 6040	01C	01C	01C	02C	01C	01C	01C
7	LR24(Agent)	CI 13523	03C	03C	03C	03C	03C	03C	03C
8	LR10(TC)	RL 6004	03C	99P	99P	03C	99P	99P	99P
9	LR17(TC)	RL 6008	03C	14C	24C	99P	99P	99P	23C
10	LR16(TC)	RL 6005	24N	24N	34N	34N	34N	34N	99P
11	Waldron	CI 13958	01C	01C	99P	03C	13C	03C	01C
12	Era	CI 13986	02C	99P	99P	02C	99P	99P	99P
13	Chiccoro "S"	...	01C	01C	01C	03C	03C	23X	23X
14	Marquis	CI 03641	99P	99P	99P	99P	99P	99P	99P

[a] RL number refers to wheat collection accession series of the Canada Department of Agriculture. The lines used resulted from studies of inheritance of reaction by P. L. Dyck, D. J. Samborski, R. G. Anderson, and D. R. Knott. CI numbers refer to a wheat collection accession series of the U.S. Department of Agriculture.

[b] PR numbers refer to the Plant Rust accession series of the American Type Culture Collection, 12301 Parklawn Dr., Rockville, MD 20852.

[c] The coding system used includes a 0–9 estimate of sporulation, a 0–9 estimate of lesion size, and an alphabetic descriptor code as: C = chlorotic areas associated with lesions, N = necrotic areas associated with lesions, P = pale areas associated with lesions, and X = mosaic pattern of different sized lesions.

influenced. It was further found that if data sets with UR cultivars or UA cultures were sorted twice by culture that this difficulty was overcome. A culture sort was made once before and once after the host-line sort.

Because two CGPs can be shown to be operating in a 2 × 2 IT data set, more than two CGPs can be shown by using sequential 2×2 subsets within larger data sets. We used this method to make visual analysis of probable genotypes for reaction and probable genotypes for pathogenicity after machine sorting of IT data tables.

We used similarity of IT spectra produced on paired host lines by a group of cultures to indicate possible genetic relationships between the lines. We have used this method to formulate some hypotheses concerning three wheat cultivars.

RESULTS AND CONCLUSIONS

The IT data obtained with the lines and cultures in original order are shown in Table 1. The data were sorted with the sorting program described in this paper. The sorted data set, shown in Table 2, can be analyzed in two ways:

(i) A minimum number of CGPs that will explain the variation in the IT data can be determined. Ten genes for low reaction to *Puccinia recondita*, determined by conventional genetics in other studies, were known to be represented; only some of them can be demonstrated by the diagonal check method and the IT data obtained in this study.

(ii) The IT spectra of cultivars of unknown genotypes can be compared with those of lines having known reaction genotypes and hypotheses can be made concerning the reaction genotype of each unknown.

Both of these analytic approaches were used with the data in Table 2.

Five CGPs were readily demonstrated with the available data. The genes for low reaction in LR10(TC), LR2D(PL), LR17(TC), LR3(TC), and LR24(Agent) were demonstrated. The low ITs involved are underlined with a broken line. The high ITs which occur in the critical diagonal checks are boldly underlined. LR10(TC) and LR2D(PL) were demonstrated to have different genes for low reaction; cultures UN01-68B and UN01-68A have their corresponding genes for low pathogenicity. This was shown by the low ITs occurring on a diagonal flanked by the high IT produced by UN01-68A on LR10(TC). A third CGP was demonstrated on LR17(TC) by the low IT produced by culture UN17-68A, which produced a high IT on both LR10(TC) and LR2D(PL). The high IT produced by UN17-68A on LR10(TC) shows LR17(TC) to be different from LR10(TC); the high IT on LR2D(PL) shows LR17(TC) to be different from LR2D(PL). Thus, LR17(TC) was demonstrated to have a third gene for low reaction. By the same logic, the high ITs produced by culture 0967-1 on LR10(TC), LR2D(PL), and LR17(TC) and the low IT produced by the same culture on LR3(TC) showed LR3(TC) to have a fourth gene for low reaction and culture 0967-1 the corresponding gene for low pathogenicity.

Culture 65359-01 was of no use in demonstrating further CGPs. The next culture in the sorted data set, 6B-NA65-9, however, produced a low IT on Agent and high ITs on LR10(TC), LR2D(PL), LR17(TC), and LR3(TC) and it therefore demonstrated a fifth CGP. Cultures needed to conclusively demonstrate further CGPs were not included in the experiment. Several other lines had genes for low reaction that were shown to be different from some of the five conclusively demonstrated genes; however, these additional genes for low reaction could not be shown to differ from all the first five and, therefore, they could not be added as a sixth. Culture UN09-66A added no information to the data set for this kind of analysis.

Three of the four cultivars of unknown genotype had IT data spectra similar to those of lines with known *Lr* genotype. The IT spectra of LR2A(TC) and Waldron matched for the cultures that produce a low IT on LR2A(TC). This also has been true in several other tests (Browder and Eversmeyer, *unpublished*). Among cultures that produced a high IT on LR2A(TC), one, UN17-68A, produced a high IT on Waldron, but others produced a low IT, phenotypically different from the 01C characteristic of *Lr2a*/*Lp2a*, on Waldron. These matches of low ITs–low on LR2A(TC), low on Waldron–and additional low ITs on Waldron indicate that Waldron has *Lr2a* and an additional gene for low reaction. The diagonal check method also can be used in this case. Here, Waldron and LR2A(TC) can be conclusively shown to have different genes for low reaction by the low ITs produced on them by cultures UN01-68A and 0967-1 and the high IT on LR2A(TC) produced by 0967-1. This pattern conclusively shows the additional gene,

TABLE 2. Infection-type data obtained by inoculating 14 lines of *Triticum aestivum* with seven cultures of *Puccinia recondita* (from Table 1) sorted toward the gene-for-gene model

Entry no.	Line name	Line no.[a]	Infection type produced by *P. recondita* culture:						
			UN01-68B	UN01-68A	UN17-68A	0967-1	65359-01	6B-NA65-9	UN09-66A
			PR51	PR67[b]	PR62	...	...	PR76	PR66
14	Marquis	CI 03641	99P[c]	99P	99P	99P	99P	99P	99P
10	LR16(TC)	RL 6005	24N	24N	34N	34N	99P	34N	34N
8	LR10(TC)	RL 6004	03C[d]	99P	99P	99P	99P	99P	03C
5	LR2D(PL)	RL 6001	03C	24C	99P	99P	03C	99P	99P
9	LR17(TC)	RL 6008	03C	14C	23C	99P	23C	99P	99P
3	LR3(TC)	RL 6002	03C	03C	99P	03C	99P	99P	03C
7	LR24(Agent)	CI 13523	03C	03C	03C	03C	03C	03C	03C
12	Era	CI 13986	02C	99P	99P	99P	99P	99P	02C
2	LR2A(TC)	RL 6000	01C	01C	99P	99P	01C	14C	99P
11	Waldron	CI 13958	01C	01C	99P	13C	01C	03C	03C
1	LR1(TC)	RL 6003	01C	01C	01C	99P	99P	99P	99P
13	Chicorro "S"	...	01C	01C	01C	03C	23X	23X	03C
4	LR9(TC)	RL 6010	01C	01C	01C	01C	01C	01C	03C
6	LR19(TC)	RL 6040	01C	01C	01C	01C	01C	01C	02C

[a] RL numbers refer to wheat collection accession series of the Canada Department of Agriculture. The lines used resulted from studies of inheritance of reaction by P. L. Dyck, D. J. Samborski, R. G. Anderson, and D. R. Knott. CI numbers refer to a wheat collection accession series of the U.S. Department of Agriculture.

[b] PR numbers refer to the Plant Rust accession series of the American Type Culture Collection, 12301 Parklawn Dr., Rockville, MD 20852.

[c] The coding system used includes a 0–9 estimate of sporulation, a 0–9 estimate of lesion size, and an alphabetic descriptor code as: C = chlorotic areas associated with lesions, N = necrotic areas associated with lesions, P = pale areas associated with lesions, and X = mosaic pattern of different sized lesions.

[d] Infection-type codes underscored with a broken line indicate low infection types effected by five conclusively demonstrated corresponding gene pairs. Codes underscored with bold lines are the high infection types critical to demonstrating the five corresponding gene pairs. Vertical lines connect low infection types where infection-type spectra were similar on lines with known genotype and unknown genotype.

assuming that Waldron has *Lr2a*. The hypothesis that Waldron has *Lr2a* is based on probability and can be proven only by testing LR2A(TC) × Waldron segregates with a culture such as UN01-68B. Statler (16) showed that Waldron has two genes for low reaction, but did not relate them to any named *Lr* genes.

The IT spectra of LR1(TC) and Chiccoro "S" also were similar. Where low ITs occurred on both, the lows were phenotypically similar, coded 01C. Each culture that produced a high IT on LR1(TC) produced a low IT on Chiccoro "S". However, these low ITs were phenotypically different from the 01C typically produced by *Lr1*/*Lp1*. Two additional low ITs, one coded 03C and another coded 23X, were observed on Chiccoro "S". Each of these, the 03C and 23X, were different, as shown by the diagonal check method, from the 01C on LR1(TC). No conclusive data were available to show that the 03C and 23X were caused by different CGPs. They were, however, consistently different phenotypically and thus due either to different CGPs or to homozygosity-heterozygosity differences in pathogenicity genotypes in the cultures used in this experiment. From this analysis, we hypothesize that Chiccoro "S" has *Lr1* and one or more other genes for low reaction.

The low IT phenotypes on LR1(TC) and LR2A(TC) and the parallel low ITs on Waldron and Chiccoro "S" were very similar, usually indistinguishable, suggesting that all may have a gene in common. The diagonal check method, applied sequentially to these host lines and cultures UN01-68A, UN17-68A, and 0967-1 showed that LR1(TC) and LR2A(TC) differ genotypically, even beyond their use as knowns within the experiment, although the cultures used did not show LR1(TC) and LR2A(TC) to have CGPs different from the five demonstrated above. The same logic showed that the 01C IT on Waldron was caused by a different CGP from that on LR1(TC) and that the 01C IT on Chiccoro "S" was caused by a different CGP from that on LR2A(TC).

The IT spectra of LR10(TC) and Era were similar. The two cultures that produced a low IT on LR10(TC) also produced a low IT on Era. The two low ITs were, however, coded slightly differently, 03C on LR10(TC) and 02C on Era. Although slight, this difference in coding separated LR10(TC) and Era in the sorted data set. Five cultures that produced a high IT on LR10(TC) also produced a high IT on Era. Based on these data, we hypothesize that Era has *Lr10*. Virulence to LR10(TC) in the North American population of *P. recondita* is very high (6); thus, if *Lr10* resides in Era, it is of relatively little value in effecting the resistance of Era. Era must have at least one additional gene for low reaction not demonstrated in these data. It is probably a gene for adult-plant reaction, because Heiner and McVey (9) indicate that Era is resistant to leaf rust in field tests. Frontana, the cultivar origin of *Lr13*, is included in the Era pedigree (9); *Lr13* can be detected only in the adult plant stage.

DISCUSSION

The results presented confirm that the diagonal check method can be used to show differences in genotypes of host lines and parasite cultures, assuming a gene-for-gene relationship. The results also show that the sorting of IT data sets toward the theoretical gene-for-gene model (14) can facilitate visual analysis (12). Sorting of IT data also facilitates analyzing similarity of IT spectra and formulating hypotheses about cultivars of unknown reaction genotype in relation to lines with known reaction genotype.

Accepting the tenet of epistasis of a high infection type by a low infection type and assuming accurate coding of IT data, a line of unknown genotype cannot have all the genes for low reaction of any line occurring below it in the sorted data set, unless the reaction genotypes are identical. For example, it was demonstrated that Era does not have *Lr2a, Lr1, Lr9,* and *Lr19* and that Chiccoro "S" does not have *Lr9* nor *Lr19*. Such negative conclusions can be used as positive information.

The demonstration of only five CGPs in a data set where 10 genes for low reaction were known to be represented may seem to be, but is not, incongruous. The number and genotype of the cultures used limited the number of CGPs that could be demonstrated. The number of CGPs demonstrated by this method cannot exceed the lesser of the number of lines or the number of cultures used (11)—in this case, seven. The same number of CGPs could have been demonstrated if the lines used had been the same, but of unknown genotype.

Infection type in the parasite:host associations of the cereal rusts is influenced greatly by environment, particularly by temperature during the latent period (3). Environment must be considered in any genetic study of IT, especially in IT sorting and comparison of IT spectra as we suggest in this paper. A constant environment must be assured for all ITs that are critically compared in such studies.

The validity of results obtained by using the analytic methods we suggest in this paper depends on accurate coding of ITs. Visual estimates are usually less accurate for ITs in the midrange of the scale. Thus, the sorting method described here is less useful for midrange ITs. A complete range of ITs occur in the *P. recondita:Triticum* system. Only a small portion of the ITs that occur are included in the limited data set used in this paper. The characteristic low IT effected by known CGPs at 20 C range from the 01C-02C for LR19(TC) shown in these data to a 56X-78X on lines with *Lr18* (Browder and Eversmeyer, *unpublished*).

We believe it is important to compare IT on lines of unknown genotype to IT on lines of known genotype when such materials are available. Only in this way can we extend knowledge of the systems being studied. It is also important to include a high IT standard, such as cultivar Marquis in the present study, as a base for comparison of other ITs. The validity of the sorting method, per se, however, is not dependent on such comparisons.

Loegering and Burton (11) propose a method for deriving hypothetical genotypes for host reaction and parasite pathogenicity in which IT data are sorted by only two categories, low or high, and then processed by a "boxing" program. The "boxing" program uses the principle referred to as the "diagonal check" in this paper. Their "boxing" program outputs hypothetical genotypes of the host lines and parasite cultures that are critical in determining the minimum number of CGPs operative in the materials represented by the data set. We use a method in which the IT codes for sporulation amount and lesion size are sorted numerically. This results in an output of the original IT data, listed in different culture and line order. This method facilitates further visual analysis by arraying ITs in sorted order. Loegering and Burton's (11) method of outputting hypothetical genotypes after using our sort method may be a useful approach.

This analytic method can be applied in at least three ways. First, this method can be used to ascertain that new sources of resistance have a different gene(or genes) for low reaction than previously used sources of resistance. These new materials can be included in breeding programs before detailed genetic analysis is done. Second, the method can be used to easily and conclusively demonstrate that a given host line does not have certain genes for low reaction, eliminating the need for making laborious host crosses and reaction tests of their progeny. Third, the method also can be used to formulate hypotheses that certain host line(s) have certain gene(s). These hypotheses should be tested by conventional host crosses and tests of progeny with appropriate cultures. Infection-type data analysis is not an adequate substitute for classic methods of host reaction genotype study, but we believe it to be a useful adjunct to those methods.

The sorting procedure described in this paper also facilitates the choice of parasite cultures that will be useful in making reaction tests in conventional genetic studies and in plant breeding work. An option is included in the computer program which lists culture pairs which differentiate specified host-line pairs. For example, the data in Table 2 show that UN01-68B and UN01-68A differentiate LR10(TC) and LR2D(PL). We project that this option can be used to build a data bank of all such combinations and that such a data bank will thoroughly describe the *P. recondita:Triticum* specificity system.

LITERATURE CITED

1. BARTOS, P., D. J. SAMBORSKI, and P. L. DYCK. 1969. Leaf rust resistance of some European varieties of wheat. Can. J. Bot.

47:543-546.
2. BROWDER, L. E. 1971. Pathogenic specialization in cereal rust fungi, especially *Puccinia recondita* f. sp. *tritici*. Concepts, methods of study, and application. U. S. Dep. Agric. Tech. Bull. 1432. 51 pp.
3. BROWDER, L. E. 1973. Specificity of the *Puccinia recondita* f. sp. *tritici:Triticum aestivum* 'Bulgaria 88' relationship. Phytopathology 63:524-528.
4. BROWDER, L. E. 1973. Probable genotype of some *Triticum aestivum* 'Agent' derivatives for reaction to *Puccinia recondita* f. sp. *tritici*. Crop Sci. 13:203-206.
5. BROWDER, L. E., and M. G. EVERSMEYER. 1976. Recording and machine processing of cereal rust infection-type data. Plant Dis. Rep. 60:143-147.
6. BROWDER, L. E., and M. G. EVERSMEYER. 1977. Pathogenicity associations in *Puccinia recondita tritici*. Phytopathology 67:766-771.
7. BROWDER, L. E., and H. C. YOUNG, Jr. 1975. Further development of an infection-type coding system for the cereal rusts. Plant Dis. Rep. 59:964-965.
8. FLOR, H. H. 1956. The complementary genetic systems in flax and flax rust. Adv. Genet. 8:29-54.
9. HEINER, R. E., and D. V. McVEY. 1971. Registration of Era wheat. Crop Sci. 11:604.
10. LOEGERING, W. Q. 1968. A second gene for resistance to *Puccinia graminis* f. sp. *tritici* in the Red Egyptian 2D wheat substitution line. Phytopathology 58:584-586.
11. LOEGERING, W. Q., and C. H. BURTON. 1974. Computer-generated hypothetical genotypes for reaction and pathogenicity of wheat cultivars and cultures of *Puccinia graminis tritici*. Phytopathology 64:1380-1384.
12. LOEGERING, W. Q., R. A. McINTOSH, and C. H. BURTON. 1971. Computer analysis of disease data to derive hypothetical genotypes for reaction of host varieties to pathogens. Can. J. Genet. Cytol. 13:742-748.
13. PERSON, C. 1959. Gene-for-gene relationships in host:parasite systems. Can. J. Bot. 37:1101-1130.
14. ROBINSON, R. A. 1976. Plant Pathosystems. Springer-Verlag, Berlin, Heidelberg, and New York. 184 pp.
15. SIMONS, M. D. 1955. The use of pathological techniques to distinguish genetically different sources of resistance to crown rust of oats. Phytopathology 45:410-413.
16. STATLER, G. D. 1973. Inheritance of resistance to leaf rust in Waldron wheat. Phytopathology 63:346-348.