Computer-Generated Hypothetical Genotypes for Reaction and Pathogenicity of Wheat Cultivars and Cultures of Puccinia graminis tritici

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Contribution from the Missouri Agricultural Experiment Station. Journal Series Number 6902. Approved 15 January 1974.

Accepted for publication 12 April 1974.

ABSTRACT

Sixty-nine cultivars of wheat chosen at random from the Plant Introduction collection, 13 monogene lines, and three background cultivars were inoculated with 19 cultures of *Puccinia graminis tritici*. The resulting data were subjected to computer analysis to determine genotypes for high-low (H-L) reaction and pathogenicity of cultivars and cultures by means of interal and external correlation programs and a new "boxing" program. Internal correlation indicated that most of the cultivars differed in their genotypes for low reaction, and external correlation indicated that none of the cultivars had any of 13 different. *Sr* genes for low reaction represented in the monogene lines. The new "boxing" program permitted print-out of postulated H-L genotypes for reaction and pathogenicity for cultivars and cultures. It is suggested that such postulated genotypes are as valid as those obtained from F_2 data and are useful in plant breeding programs as well as in setting up hypotheses to be tested by geneticists.

Phytopathology 64:1380-1384

Additional key words: Triticum aestivum, stem rust.

The gene-for-gene concept of Flor (2) laid the foundations of interorganism genetics (4), a branch of symbiology (the study of symbiosis) (8). Application of concepts of interorganism genetics makes it possible to determine hypothetical genotypes of the two symbiotes making up an association by observing the infection type and without making crosses. The concepts and procedures were developed from those plant pathogen:host associations where data are taken as infection type (IT). That hypothetical genotypes could be developed from IT data, and that they have validity, was first demonstrated (3) for three cultivars of wheat and two cultures of *Puccinia graminis* Pers. f. sp. *tritici* Erikss. & E. Henn. The postulated genotypes of cultivars were shown to be correct by the use of conventional genetic methods. The point was made in this report that genotypes postulated in this way are as valid as genotypes postulated from F_2 data. In both methods the hypothesis must be tested before we can consider the genotypes valid. Subsequently, the H-L system of representing genotypes of host and pathogen and phenotypes of the associations was developed (5). This development made possible the utilization of a computer as an aid in organizing a mass of disease data in a format which facilitated the development of postulated genotypes for 60 cultivars of wheat with respect to genes for reaction to *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* (6). Browder (1) and H. C. Young (*personal communication*) have used the principles in their research. The present study was made to further develop the computer program so that a print-out of postulated genotypes would be possible.

MATERIALS AND METHODS.—A total of 85 lines of wheat were inoculated with 19 cultures of *P. graminis tritici* in order to generate IT data (9) for computer analysis. The wheats were from the following sources: 69 test cultivars from the USDA Plant Introduction (P.I.) Collection were selected at random and made available by J. C. Craddock; 13 lines, monogenic for low reaction, were included as standards for an external correlation program (6); Chinese Spring (C.I. 14108) and W2691 (from Australia) were added as checks as they were background for the monogene lines; and Little Club wheat was included for the high infection type standard. The 19 pathogen cultures represented an array known from previous work to differ in their genotypic makeup. The list of cultivars and cultures is available from the first author.

The data were first subjected to the external and internal correlation programs (6) with a slight modification in the print-out of the internal correlation program. This modification was such that Group 1 consisted of cultivars with the most H's in their pattern, Group 2 had the next highest number of H's, etc. When two or more groups had the same number of H's but were differentiated by their H-L pattern, the order of print-out was random. This manner of ordering the groups proved useful, though not necessary, in the computer program used for determining hypothetical genotypes of cultivars and cultures.

Following the internal correlation program a new "boxing" program was applied to the data in order to obtain a print-out of postulated L-H genotypes for cultivars and cultures. The "boxing" program, described in the next section, is based on the gene-for-gene concept which says that, for a given set of corresponding gene pairs (CGP), there are four basic combinations of the genotypes of pathogen and host which are expressed as infection types in the Category III genetic interaction (5). In the gene-for-gene system [derived from the *Melampsora lini* Pers.: *Linum usitatissimum* L. association (2)] these are Lp/Lr = Lit, Lp/Hr = Hit; Hp/Lr = Hit; and Hp/Hr = Hit where Lp and Hp represent the genotypes for low and high pathogenicity; Lr and Hr represent the genotypes for low and high reaction; and Lit and Hit are the phenotypes for low and high IT. This hypothesis can be worked backwards; ie., Lit = Lp/Lr; Hit = Lp/Hr; etc. Thus when we have Lit we know the category III genotype for at least 1 CGP, Lp for the pathogen culture and Lr for the host cultivar. When we have Hit there are three possibilities, and thus

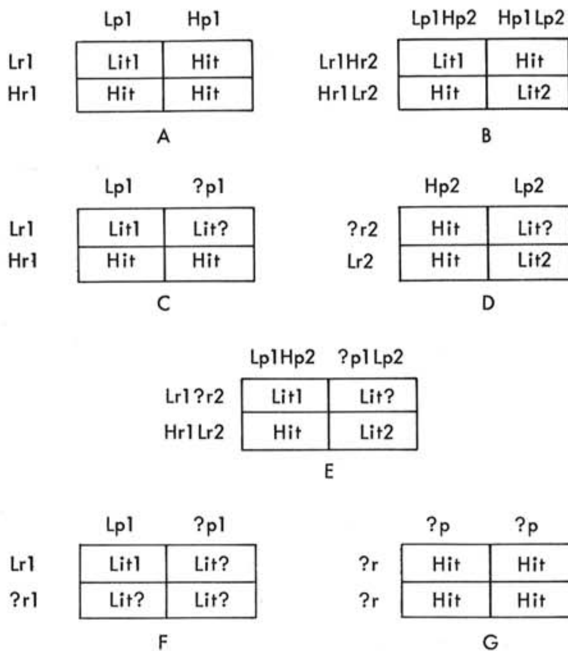

Fig. 1. The basic "box arrangements" resulting from inoculating two host varieties (sides) with two pathogen cultures (tops). Lp and Hp = genotypes for low and high pathogenicity; Lr and Hr = genotypes for low and high reaction; Hit and Lit = high and low infection type; 1 and 2 = corresponding gene pairs and their infection type; ? has two meanings—Lit? = Lit was observed but it is uncertain what the Lp/Lr genotype is, ?r1 = it is not certain whether the genotype is for Lr1 or Hr1. (See text for detailed explanation.)

knowing Hit alone only tells us that we have at least Hp or Hr. If, on the other hand, we have Hit and know either Lp or Lr for the CGP, we know that the corresponding genotype will be Hr or Hp, respectively. If then we obtain IT data from the inoculation of two host cultivars with two cultures of the pathogen which give the Lit-Hit configuration shown in Fig. 1-A, we can postulate the L-H genotypes for both cultures and both cultivars for one CGP. Fig. 1-A could be shown in four different forms with Lit in different corners of the box. This would change the L-H genotypes of cultures and cultivars, but would not represent a basic difference in analysis. The results of inoculating two random host cultivars with two random cultures may give any one of six additional basic configurations of the box arrangement (Fig. 1-B-G). Some of these may have more than one form. Each of the seven basic configurations gives varying amounts of information concerning the L-H genotype of the cultivars and cultures. In Fig. 1, each Lit has a number if its Lp/Lr genotype can be determined or a question mark (?) if its Lp or Lr genotype is uncertain. Fig. 1-A gives complete L-H genotypes for one CGP for the two cultivars and two cultures. Fig. 1-B gives complete information for two CGP's. None of the other five configurations gives complete information. Figs. 1-C and -D are very similar in that we can assign Lp/Lr genotypes to one Lit but not to the other since the second Lit could be due to the same Lp/Lr genotype as the first or could be due to a second CGP. This leaves a question as to the genotype of one culture in Fig. 1-C and one cultivar in Fig. 1-D. The configuration shown in Fig. 1-E is essentially a combination of Figs. 1-B, -C, and -D and permits identification of two CGP's for the Lit's on the diagonal; however, the Lit opposite this diagonal could result from either or both of the identified CGP's or could be due to a third CGP. This leaves a question as to the genotype in one culture for one CGP and in one cultivar for the other CGP. Fig. 1-F gives very little information. Obviously one CGP can be postulated for one Lit, but the other three Lit's could result from the same CGP or could result from one to three other CGP's. Fig. 1-G only tells us that no Lp/Lr genotypes can be identified, except that if there are any Lp or Lr genotypes known in either pathogen or host, then the corresponding genotypes are for Hr or Hp, respectively. The principles involved in these seven "box" arrangements are used in the computer as a high-low boxing correlation program to derive hypothetical genotypes.

Boxing program.—Data are arranged so that cultivars are at the side of the rows of data and cultures at the top of columns with the infection type data in the body of the table (Fig. 2). In Fig. 2 instead of printing both H and L, the actual IT is given for the L; however, the computer considers each of these as L. (If more cultures than cultivars are used, then the columns become cultivars and the rows, cultures.) The first row (cultivar) is examined. If all data are H we pass on to the next row. The first L in that row is designated Lit1. If there are more L's in the row their genotypic origin is uncertain because in making a box with them it will be like Fig. 1-C. The next row is then examined, and the first L in that row is tentatively designated Lit2. We then make a box with Lit1 by using the cultivar-culture giving Lit1 and the cultivar-culture giving tentative Lit2. If the cultures are the same, this would result in a configuration similar to Fig. 1-D or 1-F. As a result, the genotype of the tentative Lit2 would be uncertain and would not be used. If this is the case we move to the next L in the row. However, if the box is like either Fig. 1-B or 1-E, the tentative Lit2 is a valid designation. If, on the other hand, the box is like Fig. 1-F, it would not be valid, and again we would go to the next L in the row. This type of testing is continued until a valid L is found, and it is given the designation of Lit2. On occasion, none of the L's in a row will pass the tests, in which case that row is eliminated from further consideration, and we go to the next row and repeat the process.

After Lit2 is designated, we go to the next row. The first L in that row is tentatively designated Lit3. If it is in the same column as either Lit1 or Lit2 its genotype is uncertain, and the tentative Lit3 designation is not valid. If this is the case, we go to the next L in that row. When an L is found which is not in the same column as Lit1 or Lit2, we then form boxes with both Lit1 and Lit2. If both the boxes are like either Fig. 1-B or 1-E, the tentative designation is valid. If, however, either of the boxes are like Fig. 1-F, the designation is not valid, and we go on to the next L in the row.

This process continues with the following rows until as many Lit phenotypic designations as possible have been made. It is obvious that tentative Lit4 must be compared in boxes with Lit1, Lit2 and Lit3.

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HIGH - LOW BOXING CORRELATION

GROUPING  1
 HOST    1       4       7       8       9      10      13      14
 308   H       H       H       H       H       H       H       H
 324   H       H       H       H       H       H       H       H
 348   H       H       H       H       H       H       H       H
 362   H       H       H       H       H       H       H       H
IT 12 IS MARKED CULTURE 20 -HOST 308

GROUPING  2
 HOST    1       4       7       8       9      10      13      14
 331   H       H       H       H       3-      H       H       H
IT  5 IS MARKED CULTURE  9 -HOST 331

GROUPING  3
 HOST    1       4       7       8       9      10      13      14
 321   H       H       H       H       3C      H       3C      H
IT  7 IS MARKED CULTURF 13 -HOST 321

GROUPING  4
 HOST    1       4       7       8       9      10      13      14
 342   H       H       H       H       H       H       3C      3+C
IT  8 IS MARKED CULTURE 14 -HOST 342
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Fig. 2. A portion of the print-out of the actual data from which the genotypes in Fig. 3 were derived. H = high infection type. Other designations are infection type designations according to Stakman, Stewart, and Loegering (9). In the computer processing these are all considered low infection type (Lit).

In summary, there are two tests of validity for each tentatively designated Lit: (i) only one Lit can be designated in a column or row, and (ii) the new Lit must form boxes with all previously designated Lit's so that the previously designated Lit and the new Lit are on a diagonal in the box with an H in at least one of the opposite corners. These two steps are the ones actually used in the computer program.

After the total Lit designations are made, the cultivar and culture genotypes are determined. To do this, we start with Litl. We know that Litl = Lpl/Lrl, thus the culture in that column has the genotype Lpl. Any cultivar inoculated with that culture on which Hit develops must be Hrl (Hitl = Lpl/Hrl), the cultivar involved in the marked Lit1 must be Lr1, and any other cultivar with Lit will be uncertain for rl and thus is designated ?rl. Each designated Lit is considered in the same manner.

To obtain the genotype of the cultures, we reverse this process, ie. the cultivar involved in the Litl designation is Lr1, thus any culture involved in Hit on this variety must be Hp1 (Hit1 = Hpl/Lrl), the culture involved in Lit1 will be Lp1, and other cultures involved in giving Lit must be considered ?pl.

The actual computer program utilized is available from the second author.

RESULTS.—*Internal correlation.*—The internal correlation program placed the 69 test varieties into 63 groups. Only four of the groups had more than one cultivar in it. One group was comprised of four cultivars. Hit was recorded on these four cultivars with 17 cultures and Lit with only two (Table 1). Visual analysis (6) indicates that the CGP giving IT 3c (the 2++ is due to environmental variability) was common to the two cultures and four cultivars, and that a second CGP giving IT 0; is found in culture 24 and P.I. 171409 and P.I. 285783. This CGP would be epistatic in the category IV genetic interaction to the CGP giving 3c. Culture 24 is known to carry *Lpsr 18* which with *Lrsr 18* gives IT 0;. Thus it can be postulated that P.I. 171409 and P.I. 285783 are *Lrsr 18* while P.I. 124358 and P.I. 215333 are *Hrsr 18*. A second group comprised of two cultivars, P.I. 278635 and P.I. 320110, do not appear to have genes in common. Two additional groups of two cultivars (P.I. 182416 and P.I. 183856, and P.I. 230652 and P.I. 231314) each appear to have the same Lr genotype, respectively.

The other 59 groups were of one cultivar each, which indicates that their Lr genotypes are all different. This does not mean that each cultivar has a unique gene for Lr, but that each cultivar has at least a different combination of Lr genes. Thus, among the 69 cultivars at least 30 to 40 different Lrsr genes can be postulated, and the number of genes in wheat for reaction to *Puccinia graminis tritici* is indicated to be greater than previously thought.

External correlation.—Visual analysis of the external correlation print-out indicates that none of the 69 test cultivars had the Lr genotype of any of the monogene lines included in the study. These results might have been expected, since few of the test cultivars were the product of breeding programs of the past 30 yr.

Boxing analysis.—In the boxing analysis only 45 of the 69 test cultivars were used. These 45 cultivars were of spring habit and hexaploid, since it was planned to

TABLE 1. Infection type[a] data obtained by inoculating four wheat cultivars with 19 cultures of *Puccinia graminis tritici*

Wheat cultivar	Culture		17 other cultures
	20	24	
P.I. 124358	3c	3c	H
P.I. 171409	3c	0;	H
P.I. 215333	2++	3c	H
P.I. 285783	3c	0;	H

[a]According to Stakman, et al. (9).

intercross them for conventional genetic studies to test hypotheses developed by the computer program. The nature of the "boxing" program is such that no more than 19 (the number of cultures) could pass the sequential tests of the program. Actually, only 17 passed all tests, thus the "boxing" program postulated that each of 17 cultivars had a least one different gene for Lr. Likewise it was postulated that 17 of the 19 cultures differed by at least one gene for Lp. The genotypes postulated by the boxing program for the 17 cultivars and 17 cultures are given in Fig. 3. (In the computer print-out, the p and r have been capitalized to keep within the capabilities of the machine). It is evident that at least some of the cultivars and cultures were mono- or digenic for Lr or Lp. Other cultivars and cultures have largely unknown genotypes and thus need to be studied further to eliminate at least some of the ?p and ?r genotypes. In practice the H-L genotypes for the other 52 cultivars and two cultures can be printed out as well.

DISCUSSION.—The computer analysis made of IT data developed from inoculating wheat cultivars with cultures of *P. graminis tritici* permitted postulating genotypes for reaction and pathogenicity in 17 cultivars and 17 cultures for 17 CGP's. In previous studies (3) the reliability of genotypes developed from IT data has been found to be more or less equal to hypotheses developed from F_2 data. The computer analysis of IT data is much quicker and cheaper, and that is its value. Nevertheless, postulating genotypes by this method does not constitute proof that they are correct. However, the information generated in this way can be very useful to the plant breeder in development of new cultivars as well as to the research geneticist in developing hypotheses to be tested.

The degree of validity of the postulated genotypes is dependent on the accuracy of the IT data. The data used in this study were subject to several sources of error. It sometimes was difficult to distinguish the Hit as seen on Little Club and Lit on the test cultivars, since the differences were not always large. In addition, the data was obtained over a period of 6 wk between late October

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VARIETIES
 308 HR01 HR02 HR03 HR04 HR05 HR06 HR07 HR08 HR09 HR10 HR11 LR12 HR13 HR16 HR17 HR18 HR19
 331 HR01 HR02 HR03 HR04 LR05 HR06 HR07 HR08 HR09 HR10 HR11 HR12 HR13 HR16 HR17 HR18 HR19
 321 HR01 HR02 HR03 HR04 ?R05 HR06 LR07 HR08 HR09 HR10 HR11 HR12 HR13 HR16 HR17 HR18 HR19
 342 HR01 HR02 HR03 HR04 HR05 HR06 ?R07 LR08 HR09 HR10 HR11 ?R12 HR13 HR16 HR17 HR18 HR19
 349 HR01 HR02 HR03 HR04 ?R05 HR06 HR07 HR08 HR09 HR10 LR11 ?R12 HR13 HR16 HR17 HR18 HR19
 359 HR01 HR02 HR03 HR04 HR05 HR06 ?R07 HR08 HR09 HR10 HR11 ?R12 LR13 HR16 HR17 HR18 HR19
 303 HR01 HR02 HR03 HR04 HR05 HR06 HR07 HR08 HR09 LR10 ?R11 ?R12 HR13 HR16 HR17 ?R18 HR19
 310 HR01 HR02 HR03 HR04 HR05 HR06 ?R07 HR08 LR09 ?R10 HR11 HR12 HR13 HR16 HR17 HR18 HR19
 318 HR01 HR02 LR03 HR04 HR05 HR06 ?R07 HR08 HR09 HR10 HR11 HR12 HR13 HR16 ?R17 HR18 HR19
 358 HR01 HR02 HR03 HR04 HR05 HR06 ?R07 HR08 HR09 HR10 ?R11 ?R12 HR13 LR16 HR17 HR18 HR19
 315 HR01 HR02 ?R03 LR04 HR05 HR06 HR07 HR08 HR09 HR10 ?R11 ?R12 HR13 ?R16 HR17 HR18 HR19
 369 HR01 HR02 HR03 HR04 ?R05 LR06 ?R07 ?R08 HR09 ?R10 ?R11 HR12 HR13 ?R16 HR17 HR18 HR19
 304 HR01 HR02 HR03 HR04 ?R05 HR06 ?R07 HR08 HR09 ?R10 ?R11 ?R12 ?R13 HR16 LR17 HR18 ?R19
 370 HR01 HR02 ?R03 HR04 ?R05 HR06 ?R07 ?R08 HR09 ?R10 ?R11 HR12 HR13 ?R16 HR17 HR18 LR19
 302 HR01 HR02 ?R03 HR04 ?R05 ?R06 HR07 ?R08 ?R09 HR10 ?R11 ?R12 HR13 ?R16 HR17 LR18 ?R19
 313 HR01 LR02 HR03 ?R04 HR05 HR06 ?R07 ?R08 ?R09 HR10 HR11 ?R12 ?R13 HR16 ?R17 HR18 ?R19
 323 LR01 HR02 HR03 ?R04 HR05 ?R06 ?R07 ?R08 ?R09 ?R10 ?R11 ?R12 ?R13 ?R16 HR17 HR18 ?R19

CULTURES
  20 LP12 HP05 HP07 ?P08 ?P11 ?P13 ?P10 HP09 HP03 ?P16 ?P04 HP06 ?P17 HP19 ?P18 ?P02 ?P01
   9 HP12 LP05 ?P07 HP08 ?P11 HP13 HP10 HP09 HP03 HP16 HP04 ?P06 ?P17 ?P19 ?P18 HP02 HP01
  13 HP12 HP05 LP07 ?P08 HP11 ?P13 HP10 ?P09 ?P03 ?P16 HP04 ?P06 ?P17 ?P19 HP18 ?P02 ?P01
  14 HP12 HP05 HP07 LP08 HP11 HP13 HP10 HP09 HP03 HP16 HP04 ?P06 HP17 ?P19 ?P18 ?P02 ?P01
  19 HP12 HP05 HP07 HP08 LP11 HP13 ?P10 HP09 HP03 ?P16 ?P04 ?P06 ?P17 ?P19 ?P18 HP02 ?P01
  21 HP12 HP05 HP07 HP08 HP11 LP13 HP10 HP09 HP03 HP16 HP04 HP06 ?P17 HP19 HP18 ?P02 ?P01
  18 HP12 HP05 HP07 HP08 HP11 HP13 LP10 ?P09 HP03 HP16 HP04 ?P06 ?P17 ?P19 HP18 HP02 ?P01
  16 HP12 HP05 HP07 HP08 HP11 HP13 HP10 LP09 HP03 HP16 HP04 HP06 HP17 HP19 ?P18 ?P02 ?P01
   7 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 LP03 HP16 ?P04 HP06 HP17 ?P19 ?P18 HP02 HP01
  25 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 HP03 LP16 ?P04 ?P06 HP17 ?P19 ?P16 HP02 ?P01
   8 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 HP03 HP16 LP04 HP06 HP17 HP19 HP18 ?P02 ?P01
  10 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 HP03 HP16 HP04 LP06 HP17 HP19 ?P18 HP02 ?P01
  26 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 ?P03 HP16 HP04 HP06 LP17 HP19 HP18 ?P02 HP01
  28 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 HP03 HP16 HP04 HP06 ?P17 LP19 ?P18 ?P02 ?P01
  27 HP12 HP05 HP07 HP08 HP11 HP13 ?P10 HP09 HP03 HP16 HP04 HP06 HP17 HP19 LP18 HP02 HP01
   4 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 HP03 HP16 HP04 HP06 HP17 HP19 HP18 LP02 HP01
   1 HP12 HP05 HP07 HP08 HP11 HP13 HP10 HP09 HP03 HP16 HP04 HP06 HP17 HP19 HP18 HP02 LP01
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Fig. 3. Hypothetical genotypes of 17 varieties of wheat and 17 cultures of *Puccinia graminis tritici* for 17 corresponding gene pairs (CGP) developed by computer analysis of infection type data. HR01 or HP01 = genotype for high reaction (HR) or high pathogenicity (HP) for CGP 01; LR01 or LP01 = genotype for low reaction (LR) or low pathogenicity (LP) for CGP 01; ?R01 or ?P01 = genotype for reaction (R) or pathogenicity (P) for CGP 01 cannot be determined from the data available.

and early December using one culture at a time to inoculate the whole set of cultivars. The tests were made in the greenhouse, and, needless to say, there was considerable variation in the environmental conditions from time to time. Another possible source of error was the occasional mixtures in the seed used. Where this occurred the portion of the population giving the lowest IT was used unless only one or two plants out of 10 were found with this IT.

The extent to which the method can be applied to associations of other pathogens and hosts is unknown. It is axiomatic that it can only be used where specificity occurs and data are taken on IT [qualitative or topological data (10)]. A limitation on its use is the degree of discreteness between Hit and Lit. If this is not a reasonably clear distinction, difficulties may be encountered in applying the method.

The analysis reported here was handled by computer. The method can be applied manually, and where relatively small amounts of data are available, may actually be more efficient. If the work is done manually, regardless of the amount of data, it is useful to follow the program as developed for the computer.

The development of postulated genotypes for reaction and pathogenicity is of considerable value. We can assume that if a given culture has a specific array of Lp genes and produces Hit on a test cultivar, we know the cultivar has the corresponding genotype for Hr. Likewise, if we know that a culture has a specific array of Lr genes and Hit is produced by a certain culture, we know the culture has the corresponding genotype for Hp. If Lit is produced in either case we do not have the high degree of certainty that the test cultivar (or culture) has the corresponding genotype for L. Similarity of infection types may be helpful information, but not proof (7).

The large number of genes postulated in this study is striking. Many of the 17 Lp/Lr phenotypes were IT 2+ to 3c and thus differ markedly from most of the 20 or more identified *Lsr* CGP's. The internal correlation study suggests that the CGP's postulated in the test cultivars are different from the known *Lsr* CGP's, thus there are indicated 40 or more *Lrsr* genes in wheat. This large number (and undoubtedly we have hardly scratched the surface) of genes dealing with reaction to *P. graminis tritici* suggests that nonspecificity, in part, may reside in genes for specificity giving IT 3. An accumulation of such Lr genes in one cultivar would certainly appear as polygenic inheritance.

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