Genes for Specific Resistance: Powdery Mildew of Barley

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Breeding for resistance is the most practical means of reducing losses from many cereal diseases. Effective, efficient, and reliable methods are required to develop cultivars resistant to the known strains of pathogens and to future strains. The methods should include techniques for identifying individual resistance genes and specific relationships of those genes.

Methods for identifying specific resistance genes and gene relationships, based on Flor's "gene-for-gene hypothesis" (1) that for each host gene for reaction there is a corresponding pathogen gene for pathogenicity, will be described.

Results from several studies have been published in which the methods were tested and shown to be reliable (5, 6, 7, 10, 11). Although the host barley, *Hordeum vulgare* L., and the pathogen, *Erysiphe graminis* (DC.) Merat *hordei* Em. Marchal, were used in those studies, the methods are applicable to other host-pathogen systems. Two other host-pathogen systems, in which specific host genes have been identified, will be described.

The terms used in this paper, and their relationships, are illustrated in Fig. 1, which is a modification of a figure published by Loegering & Powers (3). The disease (barley powdery mildew) is the result of the interaction between the host (barley) and the pathogen (*E. graminis hordei*). The host character is the reaction, which is phenotypically resistant or susceptible. The genotype for the resistant phenotype is *Ml/Ml* or *Ml/ml*, and for the susceptible phenotype, *ml/ml*. Specific host genes are identified by a letter or letters after the letters *Ml* or *ml*. Genes at or near the same locus are distinguished by superscript numbers following the letters designating the gene locus. The pathogen character is the pathogenicity, which is phenotypically virulent or avirulent. The genotype for the virulent phenotype is *V*, and for the avirulent phenotype, *A*. Only one letter is required to designate the genotype of the pathogen, since *E. graminis hordei* is haploid, and dominance is not a factor. Specific pathogen genes are identified by the letter or letters

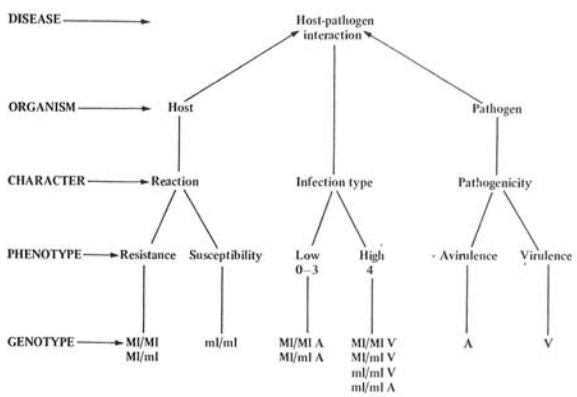

Fig. 1. Diagram of how gene interactions between host (barley) and pathogen (*Erysiphe graminis hordei*) result in the disease (barley powdery mildew).

TABLE 1. Infection types from interactions of host-pathogen combinations involving one pair of corresponding genes

Host genotype	Pathogen genotype	
	A-a	*V-a*
Ml-a/Ml-a	0-3	4
Ml-a/ml-a	0-3	4
ml-a/ml-a	4	4

for the corresponding host gene after the letters *V* or *A*. The disease character is phenotypically low (infection types "0-3") or high (infection type "4"). Low infection types "0-3" result from interactions between hosts with resistant genotypes *Ml/Ml* or *Ml/ml*, and pathogens with the corresponding avirulent genotype *A*. High infection type 4 results either from interactions between hosts with resistant genotypes *Ml/Ml* or *Ml/ml* and pathogens with the corresponding virulent genotype *V*, or from interactions between hosts with susceptible genotype *ml/ml* and pathogens with either the corresponding virulent *V* or avirulent *A* genotypes.

Host genes and gene relationships, which can be identified from the infection types resulting from the interaction of corresponding host and pathogen genes, are shown in Tables 1 to 4. The numbers of effective resistance genes and cultivars in which the genes are identified are indicated in each table. The infection types resulting from interactions involving only one pair of corresponding host and pathogen genes are shown in Table 1.

Two cultivars probably have the same gene when interactions between these cultivars and a series of cultures result in the same infection types (Table 2). The interactions of a culture with cultivars which had been resistant to all the other cultures with which they had been inoculated, but which was virulent on a cultivar which likewise had been resistant to all those cultures, would identify those varieties with the same resistance genes. All cultivars which were previously resistant and which are susceptible to the new virulent culture probably have the same resistance gene.

The infection types resulting from the inoculation of two cultivars with two cultures can indicate that those cultivars have different resistance genes, even though the genes have previously been demonstrated to be at the same locus (Table 3). When different infection types result from the inoculation of two cultivars with a new culture, the cultivars must have different resistance genes. In Table 4, the zero infection types resulting from the interaction of the first cultivar with the two cultures, indicates that either the same resistance gene in the first cultivar is effective against both cultures, or the first cultivar has two resistance genes. The infection types obtained when progeny from a cross involving the first cultivar and a susceptible cultivar are inoculated with the two cultures would show if the same or different resistance genes in the first cultivar were effective against those two cultures. If the same infection types were obtained when the progeny were inoculated with the two cultures, then the same resistance gene in the first cultivar would be shown to be effective against these two cultures. If different infection types were obtained when the progeny were inoculated with the two cultures, then the first cultivar would have two effective resistance genes. If one resistance gene in the first cultivar is effective against both cultures, then that gene, and the resistance gene in the second cultivar, although previously shown to be at the same locus, must be different, because the gene in the second cultivar was not effective against the second culture.

The infection types resulting from the inoculation of two cultivars with two cultures may indicate that those cultivars have different resistance genes, even though the genes may be at the same locus, and that one cultivar has a third resistance gene (Table 4). The infection types in Tables 3 and 4 are similar, except that the interaction of the second cultivar with the second culture resulted in a "2" rather than a "4" infection type. The infection types from the interactions of the second variety, with the two cultures, indicate that the cultivar has two resistance genes; one conditioning a "0" infection type, and the other a "2" infection type.

The genes in the cultivars and cultures in Table 5 provide examples of methods given for identifying specific resistance genes and various gene relationships. The methods, which were described, were applied in the following studies in which specific resistance genes and gene relationships were identified: cultures CR3 and 12A1 and cultivars Kwan and Goldfoil were used

TABLE 2. Infection types from interactions of host-pathogen combinations indicating two cultivars may have same resistance gene

Host genotypes	Pathogen genotypes	
	A-a	*V-a*
Ml-a/Ml-a	0	4
Ml-a/Ml-a	0	4

TABLE 3. Infection types from interactions of host-pathogen combinations indicating two cultivars can have different genes at one locus (see text)

Host genotypes	Pathogen genotypes	
	A-a, A-a^3	*A-a, V-a*^{3}
Ml-a/Ml-a, ml-a^3*/ml-a*^{3}	0	0
ml-a/ml-a, Ml-a^3*/Ml-a*^{3}	1 N	4

TABLE 4. Infection types from interactions of host-pathogen combinations indicating two cultivars can have three different resistance genes (see text)

Host genotypes	Pathogen genotypes	
	A-a, A-a^3*, V-at*	*V-a, A-a*^{3}*, A-at*
ml-a/ml-a, Ml-a^3*/Ml-a*^{3}*, ml-at/ml-at*	1 N	1 N
Ml-a/Ml-a, ml-a^3*/ml-a*^{3}*, Ml-at/Ml-at*	0	2

TABLE 5. Infection types from interactions between six barley cultivars and six powdery mildew cultures

Cultivar	C.I. no.	Host genotypes	Cultures and pathogen genotypes					
			CR3	12A1	061	59.11	59.21	D3
			A-k, A-g *A-a, A-a³* *V-at*	*V-k, V-g* *A-a, A-a³* *A-at*	*A-a* *V-a³* *A-at*	*A-a* *A-at*	*V-a* *V-at*	*V-a* *A-a³* *A-at*
Kwan	1016	*Ml-k*	2 H	4				
Goldfoil	928	*Ml-g*	0-1	4				
Algerian	1179	*Ml-a, Ml-at*	0		0	0	4	2
Rabat	4979	*Ml-a*	0		0	0	4	
Ricardo	6306	*Ml-a³*	1 N		4			1 N
Atlas	4118	*Ml-at*	4		2	2	4	2

in the first study (5), showing the one-gene-for-one-gene relationship (Table 1) between barley and *E. graminis hordei.* Cultivars Algerian and Rabat were shown to possess the same gene, *Ml-a* (Table 2), in a study (6) involving cultures 59.11 and 59.20; culture 59.20 is similar in pathogenicity to 59.21 in Table 5. The genes *Ml-a* and *Ml-a³* (Table 3) in Algerian and Ricardo, respectively, were shown to be at the same locus, but different in a study involving cultures CR3 and 061 (11). The three genes shown in Table 4 are those which have been identified in Algerian and Ricardo (10, 11), the reactions differing from those of Table 3 because different cultures were used.

Methods for distinguishing resistance genes within a locus, when in different cultivars, have been described. At least 50 barley cultivars have a resistance gene at locus *Ml-a* on chromosome 5, and eight cultivars have different genes within locus *Ml-a* (2, 7, 8, 10, 12, 14, 15). The interactions of nearly isogenic pairs of lines, developed by the following procedure, with cultures having specific pathogenic characteristics, may identify some cultivars with more than one gene at the *Ml-a* locus.

Cultivars with specific resistance genes at the *Ml-a* locus were crossed with the susceptible cultivar Manchuria (C.I. 2330), backcrossed to Manchuria 3 times, then selfed 12-15 generations. The seedlings were tested with culture CR3 of *E. graminis hordei* each generation for the presence of the resistance gene. After the last selfed generation, two lines, one homozygous for the resistance gene and another without the resistance gene, were selected, and seed from them increased.

The genes in the two lines of each pair should be identical, except for those genes at or near the *Ml-a* locus. When inoculated with a culture virulent on the susceptible line, the infection type on the resistant line should be either that produced by the resistance gene, or a type 4. An infection type on the resistant line differing from either a type 4 or that produced by the resistance gene would indicate that the original cultivar had more than one gene at or near the *Ml* locus (Table 6).

TABLE 6. Infection types from interactions of host-pathogen combinations indicating one cultivar has two genes at or near a specific locus (see text)

Host	Host genotypes	Pathogen genotypes	
		A-a, A-a^x	*V-a, A-a^x*
Original cultivar	*Ml-a/Ml-a, Ml-a^x/Ml-a^x*	0	2
Derived resistant line	*Ml-a/Ml-a, Ml-a^x/Ml-a^x*	0	2
Derived susceptible line	*ml-a/ml-a, ml-a^x/ml-a^x*	4	4

The method of identifying specific resistance genes and gene relationships in barley by the infection types produced by the interactions of that host with cultures of the pathogen, *E. graminis hordei,* is applicable to other host-pathogen systems. Examples from two other host-pathogen systems will be described. Roane & Starling (13) reported that the resistance of the three barley cultivars, Oderbrucker (C.I. 940), Speciale (C.I. 7536), and Sudan (C.I. 6489), to culture 57-19 of the pathogen, *Puccinia hordei,* was controlled by the gene *Pa* (Table 7). Since the three cultivars have the same resistance gene, a culture of *P. hordei,* virulent on one of the cultivars, should also be virulent on the other two cultivars. Several cultures of *P. hordei,* isolated from plants grown in the United States during the last 4 years, virulent on one of the cultivars, have also been virulent on the other two cultivars (8).

The barley cultivar Jet (C.I. 967) has two resistance genes, *Un3* and *Un6,* each capable of conditioning complete resistance to the pathogen, *Ustilago nuda* (4). However, only gene *Un6* is effective in conferring the resistance of Jet to culture Und 49-70 of *U. nuda* (4). The five cultivars and selections in Table 8 other than Jet were derived from crosses involving Jet by selecting plants resistant to culture Und 49-70 (9). The presence of gene *Un6,* but not *Un3,* was determined in those derivatives by testing with culture Und 49-70. Derivatives Keystone and C.I. 2211 were susceptible to inoculations with culture Und 10 of *U. nuda,* but Jet

TABLE 7. Infection types from interaction of three barley varieties with gene *Pa* with two cultures of *Puccinia hordei*

Cultivar	C.I. no.	Host genotypes	Cultures	
			57-19	64.3
Oderbrucker	940	*Pa*	0	4
Speciale	7536	*Pa*	0	4
Sudan	6489	*Pa*	0	4

TABLE 8. Per cent of plants infected from interaction of six barley cultivars with two cultures of *Ustilago nuda*

Cultivar	Host genotype	Cultures	
		Und 49-70	Und 10
Jet	*Un3, Un6*	0	0
Br. 5479-754	*Un3, Un6*	0	0
Keystone	*Un6*	0	72
Conquest	*Un3, Un6*	0	0
C.I. 2210	*Un3, Un6*	0	0
C.I. 2211	*Un6*	0	100

and the other derivatives were resistant. If gene *Un3* conferred the resistance of Jet to culture 10, then Keystone and C.I. 2211 were susceptible, because they did not have gene *Un3*, and the other derivatives were resistant because they had gene *Un3*.

To develop cultivars resistant to the known strains of pathogens, and to future strains, the plant breeder must be able to identify individual resistance genes and the relationships of those genes. The methods for identifying resistance genes and gene relationships described in this paper were efficient and reliable, and required only a few simple genetic tests. By understanding and applying these methods for identifying resistance genes and their relationships, it should be possible for plant breeders to develop varieties resistant to the known strains of pathogens and to future strains.

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