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Analysis of the resistance of *Aegilops squarrosa* to the wheatgrass mildew fungus by using the gene-for-gene reationship

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Summary. *Pm10* and *Pm15*, resistance genes to *Erysiphe graminis* f. sp. *agropyri*, are located on the D genome of common wheat. It was determined whether or not they were carried by existing lines of the D genome donor, *Aegilops squarrosa*, using the gene-for-gene relationship. Two lines of *Ae. squarrosa* tested (one was var. *meyeri* and the other was var. *anathera*) were susceptible to culture Tk-1 of *E. graminis* f. sp. *tritici* and were highly resistant to culture Ak-1 of *E. graminis* f. sp. *agropyri*. The two lines were inoculated with an F_1 population derived from the cross Ak-1 × Tk-1. Comparative analyses of the segregation patterns revealed that *Ppm10* and *Ppm15*, avirulence genes corresponding to *Pm10* and *Pm15*, respectively, are involved in the avirulence of Ak-1 on var. *meyeri* and var. *anathera*, respectively. According to the gene-for-gene relationship, var. *meyeri* and var. *anathera* were inferred to carry *Pm10* and *Pm15*, respectively. Analysis with a synthetic hexaploid confirmed the inference.

Key words: Powdery mildew – *Erysiphe graminis* – *Aegilops squarrosa* – Wheat – Resistance

Introduction

Erysiphe graminis DC., the powdery mildew fungus of gramineous plants, comprises several formae speciales. The host range of each forma specialis is restricted to a genus of gramineous plants. This relationship has been called forma specialis-genus specificity (Tosa and Shishiyama 1984; Tosa et al. 1987).

Genetic analyses of the forma specialis-genus specificity were made possible by Hiura and his coworkers. Hiura (1962, 1964) succeeded in hybridizing different formae speciales and produced F_1 ascospores from a cross between *E. graminis* f. sp. *agropyri* (the wheatgrass mildew fungus, parasitic on *Agropyron*) and *E. graminis* f. sp. *tritici* (the wheat mildew fungus, parasitic on *Triticum*). He isolated the F_1 ascospores on wheat or wheatgrass, produced two F_1 populations, and examined their virulence on various wheat cultivars or wheatgrass accessions (Hiura 1978). Tosa (1989a) crossed culture Ak-1 of *E. graminis* f. sp. *agropyri* with culture Tk-1 of *E. graminis* f. sp. *tritici*, isolated their F_1 ascospores on a common host of the two formae speciales, and obtained an F_1 population of 240 cultures. Using these cultures, Tosa (1989b) showed that the forma specialis-genus specificity follows the gene-for-gene relationship (Flor 1956).

In analyses of host genes, we have identified four genes that condition the resistance of common wheat [*Triticum aestivum* (L.) Thell.] to the wheatgrass mildew fungus (Tosa et al. 1987, 1988; Tosa and Sakai 1990). Two of them, *Pm10* and *Pm15*, were located on the D genome. The D genome of common wheat is known to be derived from a wild species, *Aegilops squarrosa* L. [*Triticum tauschii* (Coss.) Schmal.]. It is thus interesting to determine whether or not the existing population of *Ae. squarrosa* carries *Pm10* and *Pm15*. However, direct analyses for it are difficult since *Ae. squarrosa* is a diploid and common wheat is a hexaploid.

We considered that the gene-for-gene relationship should make it possible to identify genes in *Ae. squarrosa* without crossing plants. The F_1 population from Ak-1 × Tk-1 carries *Ppm10* and *Ppm15*, avirulence genes corresponding to *Pm10* and *Pm15*, respectively. *Ae. squarrosa* may be inoculated with the F_1 cultures. If *Ppm10* or *Ppm15* condition avirulence on a line of *Ae. squarrosa*, then the line should have the corresponding resistance genes, *Pm10* or *Pm15*, respectively. In the present study,

the resistance of *Ae. squarrosa* to the wheatgrass mildew fungus was analyzed using this idea.

Materials and methods

Fungal and plant materials

Fungal materials used were the 240 F_1 cultures dervied from the cross between culture Ak-1 of *Erysiphe graminis* DC. f. sp. *agropyri* Em. Marchal and culture Tk-1 of *E. graminis* DC. f. sp. *tritici* Em. Marchal, and 45 F_2 cultures derived from a cross between two F_1 cultures, Gw-34 and Gw-180 (Tosa 1989b). These cultures were maintained on *Triticum urartu* Thum. accession 199-1 (Urr), the common host of the two formae speciales that had previously been used to isolate the F_1 and F_2 cultures (Tosa 1989a, b).

Plant materials used were three lines of the D genome donor, *Ae. squarrosa* var. *typica* accession KU20-2 (tpc), var. *meyeri* accession KU20-10 (myr), var. *anathera* accession RL5266 (anth); three cultivars of common wheat, *Triticum aestivum* (L.) Thell. cv Norin 4 (N4), cv Red Egyptian (RE), cv Canthatch (Cth); and a synthetic hexaploid accession RL5403 (TCA) produced from Tetra Canthatch (extracted AABB component of Cth) and anth (DD) (Kerber and Rowland 1974). The lines and cultivars were highly resistant (infection type 0) to Ak-1 with the exception of tpc, which allowed scant sporulation of Ak-1 (Table 1). All host material was susceptible (infection type 3) or highly susceptible (infection type 4) to Tk-1.

Determination of infection types

Seeds of test plants were sown in soil in 1.8 × 35 cm glass test tubes with paper plugs. On the same day, conidia of cultures to be tested were transferred to Urr seedlings growing in test tubes. The seedlings were grown in a controlled-environment room under fluorescent lighting (2,000–4,000 lx). The temperature in the room was 21–23 °C during the light cycle (13 h) and 19–21 °C during the dark cycle (11 h). Eight days after sowing, primary leaves of test plants were inoculated with conidia from the 8-day-old colonies using writing brushes. Eight days after inoculation, infection was rated using 13 progressive grades from 0 to 4: 0 – no mycelial growth or sporulation; 0+ – mycelial growth or conidiophore formation with no visible sporulation; 1–,1,1+ – scant sporulation; 2–,2,2+ – reduced sporulation; 3–,3,3+ – slightly reduced sporulation; and 4–,4 – heavy sporulation. Taking frequency distribution of infection types into consideration, cultures were rated as avirulent or virulent, and seedlings were rated as resistant or susceptible. In this report avirulent, virulent, resistant, and susceptible are considered only as relative.

Results

Avirulence gene analyses using F_1 cultures

The common wheat cultivar N4 carries both *Pm10* and *Pm15* (Tosa et al. 1987; Tosa and Sakai 1990). When N4 was inoculated with the F_1 cultures derived from Ak-1 × Tk-1, avirulent and virulent cultures segregated in a 3:1 ratio (Tosa 1989a), suggesting that two major genes are involved in the avirulence of Ak-1 on N4. The two avirulence genes corresponded to *Pm10* and *Pm15*, and were designated *Ppm10* and *Ppm15*, respectively (Tosa 1989b; Tosa and Sakai 1990).

When myr, an accession of *Ae. squarrosa*, was inoculated with the F_1 cultures, these cultures showed a discontinuous distribution of infection types, with one break at 1– (Table 2). Assuming that cultures showing infection types 0 to 0+ and 1– to 4 were avirulent and virulent, respectively, the segregation fitted a 1:1 ratio, indicating that the avirulence of Ak-1 on myr is conditioned by one major gene. The cultures avirulent on myr were all avirulent on N4, while the cultures virulent on myr comprised avirulent and virulent ones on N4 in a 1:1 ratio (Table 3). These results indicated that the gene conditioning avirulence on myr is the same as one of the two genes conditioning avirulence on N4, i.e., *Ppm10* and *Ppm15*. An F_1 culture, Gw-34, which carries *Ppm10* (Tosa and Sakai 1990), was avirulent on myr, whereas another F_1 culture, Gw-121, which carries *Ppm15* (Tosa

Table 1. Plant materials used, and their infection types with culture Tk-1 of *Erysiphe graminis* f. sp. *tritici*, culture Ak-1 of *E. graminis* f. sp. *agropyri*, and their F_1 hybrid, Gw-34, Gw-180, and Gw-121

Plant	Infection type[a] with				
	Tk-1	Gw-34	Gw-180	Gw-121	Ak-1
Aegilops squarrosa					
var. *typica* accession KU 20-2 (tpc)	3	2	2	3	1
var. *meyeri* accession KU 20-10 (myr)	3	0	2	2	0
var. *anathera* accession RL5266 (anth)	4	0	3	0	0
Triticum aestivum					
cv Norin 4 (N4)	4	0	4	0	0
cv Red Egyptian (RE)	4	2	3	4	0
cv Canthatch (Cth)	4	2	0	0	0
Tetra Canthatch + anth (TCA)[b]	4	2	–[c]	0	0

[a] 0 – no mycelial growth or sporulation; 1 – scant sporulation; 2 – reduced sporulation; 3 – slightly reduced sporulation; 4 – heavy sporulation
[b] Synthetic hexaploid produced from Tetra Canthatch (2n = 28 = AABB) and anth (2n = 14 = DD) (Kerber and Rowland 1974)
[c] Not examined

Table 2. Distribution of infection types on *Aegilops squarrosa* lines and a common wheat cultivar in an F_1 population derived from a cross between Ak-1 of *Erysiphe graminis* f. sp. *agropyri* and Tk-1 of *E. graminis* f. sp. *tritici*

Plant[a]	No. of F_1 cultures											χ^2 (ratio)	P
	0[b]	0+	1−	1	1+	2−	2	2+	3− to 4	Total	Avirulent:virulent		
tpc	0	0	4	15	19	45	89	43	25	240	0:240	–	–
myr	105	18	0	10	9	18	34	38	8	240	123:117	0.15 (1:1)	0.50–0.75
anth	164	23	7	11	10	6	8	5	6	240	187: 53	1.09 (3:1)	0.25–0.50
N4[c]	185	3	0	1	11	19	11	5	5	240	188: 52	1.42 (3:1)	0.10–0.25

[a] tpc – *Ae. squarrosa* var. *typica*; myr – *Ae. squarrosa* var. *meyeri*; anth – *Ae. squarrosa* var. *anathera*; N4 – *Triticum aestivum* cv Norin 4
[b] Infection type. 0 to 0+, avirulent; 1− to 4, virulent
[c] Reported by Tosa (1989a)

Table 3. The combined segregation on sets of *Aegilops squarrosa* lines or a common wheat cultivar in an F_1 population derived from a cross between Ak-1 of *Erysiphe graminis* f. sp. *agropyri* and Tk-1 of *E. graminis* f. sp. *tritici*

Plant[a]		No. of F_1 cultures					χ^2 [ratio]
p	q	A_pA_q[b]	A_pV_q	V_pA_q	V_pV_q	Total	
myr	N4	123	0	65	52	240	1.56 [2:(0:)1:1]
anth	N4	167	20	21	32	240	8.09* [5:1:1:1] 53.54** [9:3:3:1]
myr	anth	102	21	85	32	240	4.71 [3:1:3:1]

[a] myr – *Ae. squarrosa* var. *meyeri*; anth – *Ae. squarrosa* var. *anathera*; N4 – *Triticum aestivum* cv Norin 4
[b] A – Avirulent (infection type 0 to 0+); V – Virulent (infection type 1− to 4). For example, A_pV_q represents cultures that are avirulent on p and virulent on q.
* Significant at the 5% level
** Significant at the 1% level

and Sakai 1990), was virulent on it (Table 1). It was, therefore, concluded that the gene conditioning avirulence on myr is *Ppm10*.

On anth the distribution of F_1 phenotypes was not discontinuous, with a small class at infection type 1− (Table 2). If the same division was used as in N4 and myr, i.e., between 0+ and 1−, the segregation fitted a 3:1 ratio. This suggested that at least two genes are involved in the avirulence of Ak-1 on anth. As mentioned above, the avirulence of Ak-1 on N4 is also conditioned by two genes. For the relationship between the two pairs of avirulence genes, two hypotheses are possible (Hiura 1978; Tosa 1989a). One hypothesis assumes that the two pairs have one gene in common, i.e., that three genes are involved in the avirulence of Ak-1 on anth and N4: A_1, a gene conditioning avirulence on both anth and N4; A_2, a gene conditioning avirulence only on anth; and A_3, a gene conditioning avirulence only on N4. Their virulence alleles are symbolized as a_1, a_2, and a_3, respectively. The genotypes of Ak-1 and Tk-1 are then $A_1A_2A_3$ and $a_1a_2a_3$, respectively. In the F_1 generation from the cross, Ak-1 × Tk-1, eight genotypes occur. Of these genotypes, $A_1A_2A_3$, $A_1A_2a_3$, $A_1a_2A_3$, and $A_1a_2a_3$ are avirulent on both anth and N4 since they possess A_1. Another genotype, $a_1A_2A_3$, is also avirulent on both anth and N4 since it possesses both A_2 and A_3. Genotypes $a_1A_2a_3$ and $a_1a_2A_3$ are avirulent only on anth and only on N4, respectively. The eighth genotype, $a_1a_2a_3$, is virulent on both anth and N4 since it does not possess any of the three avirulence genes. Consequently, the four possible phenotypes are expected to occur in a 5:1:1:1 ratio.

The other hypothesis assumes that the two pairs of avirulence genes have no common gene, i.e., that four genes are involved in the virulence of Ak-1 on anth and N4: A_1,A_2, genes conditioning avirulence only on anth; and A_3,A_4, genes conditioning avirulence only on N4. The virulence alleles are a_1, a_2, a_3, and a_4, respectively. The genotypes of Ak-1 and Tk-1 are then $A_1A_2A_3A_4$ and $a_1a_2a_3a_4$, respectively. In the F_1 generation from the cross Ak-1 × Tk-1, 16 genotypes occur. Of these genotypes, $A_1A_2A_3A_4$, $A_1A_2A_3a_4$, $A_1A_2a_3A_4$, $A_1a_2A_3A_4$, $A_1a_2A_3a_4$, $A_1a_2a_3A_4$, $a_1A_2A_3A_4$, $a_1A_2A_3a_4$, and $a_1A_2a_3A_4$ are avirulent on both anth and N4. Three genotype – $A_1A_2a_3a_4$, $A_1a_2a_3a_4$, and $a_1A_2a_3a_4$ – are avirulent only on anth. Three genotypes – $a_1a_2A_3A_4$, $a_1a_2A_3a_4$, and $a_1a_2a_3A_4$ – are avirulent only on N4. The remaining genotype, $a_1a_2a_3a_4$, is virulent on both anth and N4. Consequently, the four possible phenotypes are expected to occur in a 9:3:3:1 ratio.

When the data on anth and on N4 were combined, the segregation of the four possible phenotypes fitted the 5:1:1:1 ratio rather than the 9:3:3:1 ratio (Table 3). This result suggested that one of the two genes conditioning avirulence on anth is the same as one of the two genes conditioning avirulence on N4, i.e., *Ppm10* and *Ppm15*. It is not clear why the actual ratio deviated from the 5:1:1:1 ratio at the 5% level. It should be noted that the deviation is characterized by lower numbers of recombi-

Table 4. Distribution of infection types on *Aegilops squarrosa* var. *meyeri* (myr) and *Triticum aestivum* cv Norin 4 (N4) in an F_2 population derived from a cross between two F_1 cultures of *Erysiphe graminis*, Gw-34 and Gw-180

Plant	No. of F_2 cultures											χ^2 (1:1)	*P*
	0[a]	0+	1−	1	1+	2−	2	2+	3− to 4	Total	Avirulent:virulent		
myr	22	0	0	0	0	0	7	8	8	45	22:23[c]	0.02	0.75–0.90
N4[b]	22	0	0	0	0	0	2	6	15	45	22:23	0.02	0.75–0.90

[a] Infection type
[b] Reported by Tosa (1989b)
[c] All of the 22 cultures avirulent on N4 were avirulent on myr, and all of the 23 cultures virulent on N4 were virulent on myr

Table 5. Distribution of infection types with an F_1 culture of *Erysiphe graminis*, Gw-121, in F_2 populations derived from crosses among *Aegilops squarrosa* lines, common wheat cultivars, and a synthetic hexaploid wheat

Cross[a]	No. of F_2 seedlings											χ^2 (3:1)	*P*
	0[b]	0+	1−	1	1+	2−	2	2+	3− to 4	Total	Resistant: susceptible		
anth × tpc	79	10	9	0	0	8	13	6	5	130	98:32	0.01	>0.90
Cth × RE	65	0	0	0	0	2	3	7	6	83	65:18	0.49	0.25–0.50
Cth × N4	251	0	0	0	0	0	0	0	0	251	251:0	–	–
TCA × Cth	255	1	0	0	0	0	0	0	0	256	256:0	–	–

[a] anth – *Ae. squarrosa* var. *anathera*; tpc – *Ae. squarrosa* var. *typica*; Cth – *Triticum aestivum* cv Canthatch; RE – *T. aestivum* cv Red Egyptian; N4 – *T. aestivum* cv Norin 4; TCA – synthetic hexaploid produced from Tetra Canthatch (2n = 28 = AABB) and anth (2n = 14 = DD)
[b] Infection type

nant cultures (A_pV_q and V_pA_q) than those expected. There may be linkage between the gene conditioning avirulence only on anth and the one conditioning avirulence only on N4.

When the data on myr and on anth were combined, the segregation of the four possible phenotypes fitted a 3:1:3:1 ratio (Table 3), indicating that the avirulence on myr and that on anth are inherited independently. Therefore, neither of the two genes conditioning avirulence on anth are *Ppm10*, which conditions avirulence on myr. It was concluded that the gene conditioning avirulence on both anth and N4 is *Ppm15*.

On tpc, which allowed scant sporulation of Ak-1, the distribution of F_1 phenotypes was continuous, with no breaks (Table 2). There were no F_1 cultures that showed infection type 0 or 0+.

Avirulence gene analyses using F_2 cultures

Gw-34 was avirulent on N4 while another F_1 culture, Gw-180, was virulent (Table 1). When N4 was inoculated with the 45 F_2 cultures derived from Gw-34 × Gw-180, avirulent and virulent cultures segregated in a 1:1 ratio (Table 4), indicating that the avirulence of Gw-34 on N4 is conditioned by a single gene (Tosa 1989b). This gene was *Ppm10* (Tosa 1989b).

Gw-34 was avirulent on myr, but Gw-180 was virulent (Table 1). When myr was inoculated with the F_2 cultures, avirulent and virulent cultures also segregated clearly in a 1:1 ratio (Table 4). The segregation pattern on myr was identical to that on N4; the 22 cultures avirulent on N4 were all avirulent on myr, while the other 23 cultures virulent on N4 were all virulent on myr. These results indicated that the avirulence of Gw-34 on myr is also conditioned by *Ppm10*.

The results of avirulence gene analyses showed that *Ppm10* and *Ppm15* condition avirulence on myr and anth, respectively. Based on the gene-for-gene relationship, it was inferred that myr and anth should carry *Pm10* and *Pm15*, respectively.

Evidence that the inference from avirulence gene analyses is correct

Anth was highly resistant to Gw-121, which had been used to identify *Pm15* (Tosa and Sakai 1990), while tpc was susceptible (Table 1). When an F_2 population from anth × tpc was inoculated with Gw-121, resistant and susceptible seedlings segregated in a 3:1 ratio (Table 5), indicating that the resistance of anth to Gw-121 is conditioned by a single gene.

N4 and Cth were highly resistant to Gw-121, while RE was highly susceptible (Table 1). The resistance of N4 to Gw-121 is conditioned by *Pm15* (Tosa and Sakai 1990). When an F_2 population from Cth × RE was inoculated with Gw-121, resistant and susceptible seedlings

segregated in a 3:1 ratio (Table 5). A cross between Cth and N4 yielded no susceptible F_2 seedlings (Table 5), indicating that these cultivars have a resistance gene in common. These results showed that the resistance of Cth to Gw-121 is also conditioned by *Pm15*.

The synthetic hexaploid produced from Tetra Canthatch and anth (TCA) was highly resistant to Gw-121 (Table 1). Tetra Canthatch should not carry genes conditioning resistance to Gw-121, since the resistance of Cth to Gw-121 is conditioned by the single gene (*Pm15*) located on the D genome. Hence, the resistance of TCA to Gw-121 is attributable to the gene carried by anth. When an F_2 population from TCA × Cth was inoculated with Gw-121, no susceptible seedlings occurred (Table 5). It was, therefore, concluded that the gene conditioning the resistance of anth to Gw-121 is *Pm15*. These results confirmed the inference that anth carries *Pm15*.

Discussion

Flor (1956) established the gene-for-gene relationship in the rust race-flax cultivar system. Moseman (1959) and Hiura et al. (1961) showed that this relationship holds true in interactions between races of *E. graminis* f. sp. *hordei* and barley cultivars. The three reports referred to the application of the gene-for-gene relationship to identify resistance genes: "If the same gene conditions the pathogenicity of a culture on two cultivars, then those cultivars should have the same gene conditioning their reaction to that culture (Moseman 1966)." In the present study, this idea was successfully applied to compare resistance genes between plant species that are different in ploidy.

Genes in tetraploid or diploid progenitors can be compared with genes in hexaploid wheat using synthetic hexaploids. However, production of a synthetic hexaploid is a laborious work. Furthermore, resistance of tetraploid or diploid species is often unexpressed when they are combined in an amphiploid (Kerber 1983). An example is found in the materials used in the present study (Table 1). Anth was resistant to Gw-34, whereas TCA was susceptible. The resistance of anth to Gw-34 was not expressed in the synthetic hexaploid. These obstacles could be overcome by the analysis using the gene-for-gene relationship.

The present study showed that the exiting population of *Ae. squarrosa* carries *Pm10* and *Pm15*. This result indicates that the two genes arose before the formation of hexaploid wheat from its tetraploid (AABB) and diploid (DD) progenitors.

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References

Flor HH (1956) The complementary genetic systems in flax and flax rust. Adv Genet 8:29–54

Hiura U (1962) Hybridization between varieties of *Erysiphe graminis*. Phytopathology 52:664–666

Hiura U (1964) Pathogenicity of the haploid progeny cultures from crosses between cultures of *Erysiphe graminis* f. sp. *tritici* and *Erysiphe graminis* f. sp. *agropyri* (preliminary note). Ber Ohara Inst Landwirtsch Biol Okayama Univ 12:131–132

Hiura U (1978) Genetic basis of formae speciales in *Erysiphe graminis* DC. In: Spencer DM (ed) The powdery mildews. Academic Press, London, pp 101–128

Hiura U, Heta H, Tsushima T (1961) Pathogenic variability attributed to hybridization in *Erysiphe graminis hordei*. Studies on variation in pathogenicity. II. Nogaku Kenkyu 48:107–115 (in Japanese)

Kerber ER (1983) Suppression of rust resistance in amphiploids of *Triticum*. In: Proc 6th Int Wheat Genet Symp, Kyoto, pp 813–817

Kerber ER, Rowland GG (1974) Origin of the free threshing character in hexaploid wheat. Can J Genet Cytol 16:145–154

Moseman JG (1959) Host-pathogen interaction of the genes for resistance in *Hordeum vulgare* and for pathogenicity in *Erysiphe graminis* f. sp. *hordei*. Phytopathology 49:469–472

Moseman JG (1966) Genetics of powdery mildews. Annu Rev Phytopathol 4:269–290

Tosa Y (1989a) Genetic analysis of the avirulence of wheatgrass powdery mildew fungus on common wheat. Genome 32:913–917

Tosa Y (1989b) Evidence on wheat for gene-for-gene relationship between formae speciales of *Erysiphe graminis* and genera of gramineous plants. Genome 32:918–924

Tosa Y, Sakai K (1990) The genetics of resistance of hexaploid wheat to the wheatgrass powdery mildew fungus. Genome 33:225–230

Tosa Y, Shishiyama J (1984) Defense reactions of barley cultivars to an inappropriate forma specialis of the powdery mildew fungus of gramineous plants. Can J Bot 62:2114–2117

Tosa Y, Tsujimoto H, Ogura H (1987) A gene involved in the resistance of wheat to wheatgrass powdery mildew fungus. Genome 29:850–852

Tosa Y, Tokunaga H, Ogura H (1988) Identification of a gene for resistance to wheatgrass powdery mildew fungus in the common wheat cultivar Chinese Spring. Genome 30:612–614