A Proposed International System for Designating Races of *Plasmopara halstedii*

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Downy mildew caused by *Plasmopara halstedii* (Farl.) Berl. & de Toni is one of the major diseases of sunflower (*Helianthus annuus* L.) (25). It is known to occur almost everywhere in the world where sunflower is grown extensively except in Australia, South Africa, and possibly parts of North Africa (16). Detailed reviews of the disease have been published (12,16). The number of known or postulated genes for resistance to downy mildew has increased from two to nine since 1980, and others are certain to be discovered (11). In order to make the naming of races that can be distinguished in a gene-for-gene system useful to plant breeders, epidemiologists, and others anywhere in the world, we propose that the designations be based on the genes for resistance that the respective races can overcome, and we present information on the genes and races already described.

Resistant varieties have given control of downy mildew in Europe since the widespread adoption of hybrid sunflower carrying the Pl_1 and/or Pl_2 genes for resistance, and in north-central North America until the occurrence of new races of *P. halstedii* there in 1980 and subsequent years (2,6,7). The number of races that can be distinguished depends on the number of distinct genes for resistance. When the gene-for-gene relationship applies, as it has been shown to do for many obligate parasites, the maximum number of races is 2^n, where n is the number of resistance genes (4,13). The known genes for resistance of sunflower to *P. halstedii* are listed in Table 1.

Only two races of *P. halstedii* had been identified prior to 1980. Race 1, the "European race," was prevalent in Europe and in a small area in the province of Quebec, Canada. It appears able to affect only those sunflower genotypes with no known genes for resistance. Race 2, the "Red River race," was prevalent in the Red River Valley of north-central United States and adjacent areas in Canada. Race 2 was also known or suspected to occur in small areas in several countries of Europe, in most cases confined to experiment stations (16). It induces typical systemic infection in sunflowers carrying the Pl_1 gene for resistance, but not in those with gene Pl_2.

Race 3, the "new race," was first recognized in the north-central United States in 1980, affecting sunflowers resistant to race 2, and was considered the dominant race in the Red River Valley of the United States and Canada (2,7). Since the development of sunflower lines carrying both genes Pl_2 and Pl_5, conferring resistance to races 2 and 3, races 4 and 5 have been identified in the Red River Valley (6,9). Races 2 and 3, and possibly others, have appeared recently in farm fields in the Indres region of France (18; Gulya and Sackston, *unpublished*).

Plant breeders attempting to discover and incorporate genes for downy mildew resistance into sunflower lines for production of hybrids must know what races are present in the areas where those hybrid varieties are likely to be grown. Identification of the races by names or numbers may be adequate when only a few resistance genes and races are known. With the recent increase in number of identified and postulated

Table 1. Genes for resistance to downy mildew of sunflower

Gene	Source	Description and history
Pl_1	Encountered in lines at Morden, Canada, from crosses of sunflower with wild annual species in Texas and California (15).	Conferred resistance to downy mildew in field tests in eastern Canada (14) and in seedling tests (5). Shown in Romania to be single dominant gene linked with gene R_1 for rust resistance; named Pl_1 (21). Ineffective against downy mildew in Red River Valley of north-central United States and adjacent Canada (23,24).
Pl_2	Encountered in line HA 61 developed in Texas from Canadian line 953-88-3 carrying gene R_2 for rust resistance (27).	Conferred resistance to downy mildew in Red River Valley area of United States and Canada; named Pl_2; synonymous with one of H_1 or H_2 reported to be present in HA 61 in France (20,26,27).
Pl_3	Encountered in line HA 61 in France (20).	One of the two genes in HA 61 reported to confer resistance to downy mildew in France (20), distinct from Pl_2 (27).
Pl_4	Encountered in line HIR 34 derived in France from cross of cultivated sunflower with *H. tuberosus* (19).	Conferred resistance to downy mildew in France: apparently different from genes in HA 61 (19); conferred resistance to downy mildew in the Red River Valley of United States but was not distinguishable from Pl_2 (24).
Pl_5	Encountered in the line RF-S 11-5566-74 derived in Romania by Vranceanu and Stoenescu (22). Also encountered together with gene Pl_2 in lines DM 2 and DM 3 derived in North Dakota from cultivars Novinka and Progress produced in USSR from crosses of cultivated sunflower with *H. tuberosus* (10).	Named Pl_5 by Vranceanu and Stoenescu (22). Confers resistance only to downy mildew race 3. Distinct from gene Pl_2 (10).

(*continued on next page*)

Table 1. (*continued from preceding page*)

Gene	Source	Description and history
Pl_6 + ?	Encountered in lines HA 335 and 336 derived in North Dakota from backcrosses to cultivated sunflower with crosses of wild *H. annuus* 423 and 432, respectively (11).	Conferred homozygous resistance to downy mildew races 1, 2, 3, 4, 5, and 6 in tests in North Dakota. Resistance to race 4 is controlled by a single gene (11).
Pl_7 + ?	Encountered in lines HA 337, 338, and 339 derived in North Dakota from backcrosses to cultivated sunflower of crosses with *H. praecox* 417, 419, and 424, respectively (11).	Conferred homozygous resistance to downy mildew races 1, 2, 3, 4, 5, and 6 in tests in North Dakota. Resistance to race 4 is controlled by a single gene (11).
Pl_8 + ?	Encountered in line RHA 340 derived in North Dakota from backcrosses to cultivated sunflower of crosses with *H. argophyllus* (11).	Conferred homozygous resistance to downy mildew races 1, 2, 3, 4, 5, and 6 in tests in North Dakota. Resistance to race 4 is controlled by a single gene (11).
Pl_9	Encountered in line RHA 274 developed in North Dakota from line HA 61 (3).	Different from Pl_2, also present in RHA 274, which confers resistance to race 6 (J. F. Miller and T. J. Gulya, *unpublished*).

Table 2. Races of the downy mildew pathogen of sunflower

North American race designation	Apparently effective resistance genes	Apparently ineffective resistance genes	Proposed international race designation
1	Pl_1, Pl_2, Pl_3, Pl_4, Pl_5, Pl_6 + ?,[a] Pl_7 + ?, Pl_8 + ?	None	0
2	Pl_2 (Pl_4), Pl_2 + Pl_5,[b] Pl_6 + ?, Pl_7 + ?, Pl_8 + ?	Pl_1 (Pl_3)	1
3	Pl_2 + Pl_5, Pl_6 + ?, Pl_7 + ?, Pl_8 + ?	Pl_1 (Pl_3), Pl_2 (Pl_4)	1,2
4	Pl_6 + ?, Pl_7 + ?, Pl_8 + ?	Pl_1 (Pl_3), Pl_2 (Pl_4), Pl_2 + Pl_5 (CL)[c]	1,2,5 (CL)
5	Pl_6 + ?, Pl_7 + ?, Pl_8 + ?	Pl_1 (Pl_3), Pl_2 (Pl_4), Pl_2 + Pl_5	1,2,5
6	Pl_2, Pl_6 + ?, Pl_7 + ?, Pl_8 + ?	Pl_1 (Pl_3), Pl_9	1,9

[a] + ? = More than one unidentified gene may be involved.
[b] Pl_2 and Pl_5 present in genotype, Pl_5 not yet isolated.
[c] CL = Cotyledon-limited infection.

resistance genes to nine (11), and the consequent increase in the number of races theoretically distinguishable to 512, a more informative and useful system of designating races is required.

A comparable situation with sunflower rust (*Puccinia helianthi* Schw.) led to the adoption of an international system of naming races on the basis of the genes for resistance that they could overcome (1,8,17). We propose that a similar international system be adopted for naming races of *P. halstedii*. Pathologists and plant breeders in any country could continue to use any convenient or familiar designation for the isolates or cultures important in their areas or encountered in a given season. All such isolates, however, should also be identified by listing the genes for resistance that each isolate can overcome in an internationally agreed standard series of differential hosts. Such identification should include also any resistance genes that have been shown to be effective against the particular isolate or culture. The system is flexible. For example, if genes Pl_3 and Pl_4 are confirmed as being distinct from Pl_1 and Pl_2, respectively, designation of the races that attack them would be changed by the addition of the appropriate numbers.

Table 3. Resistance genes and sources for differentiating "internationally designated" races of *Plasmopara halstedii*

Resistance genes	Possible differential lines
0	Peredovik, Krasnodarets, IS 003,[a] HA 89, HA 300
Pl_1	CM 5RR, CM 90RR, HA 60, R 18, RHA 265, RHA 266
Pl_2	RHA 274, IS 7000
Pl_3 (=Pl_1 ?)	HA 61? with Pl_2
Pl_4 (= Pl_2 ?)	HIR 34
Pl_5	With Pl_2 in DM 2, DM 3, IS 2000, IS 3003
Pl_6 + ?[b]	HA 335, HA 336
Pl_7 + ?	HA 337, HA 338
Pl_8 + ?	HA 340

[a] IS genotypes are proprietary lines or hybrids of Interstate Seed Co., Fargo, ND, used by the second author but not available for distribution.
[b] + ? = More than one unidentified gene may be involved.

The races we already know, with their current and recommended designations, are listed in Table 2. Some lines currently available and suggested as differentials, and their respective resistance genes, are listed in Table 3. Addition or substitution of differential lines on a continuing basis could be arranged by an ad hoc committee meeting during the International Sunflower Conferences, held every 3 or 4 years. The next is scheduled for Pisa, Italy, in 1992.

The Red River Valley of North Dakota, Minnesota, and Manitoba at present appears to be a center of rapid changes in the population of *P. halstedii*. All but race 1 of the known races have been identified there. The Oilseeds Research Unit of the U.S. Department of Agriculture currently develops and releases germ plasm lines to sunflower breeders throughout the world and identifies and stores new races of the pathogen as they are discovered. It may therefore be a suitable clearinghouse for information on race identification and for distributing seed of differential lines for identifying races of *P. halstedii* elsewhere.

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