# Wild Sunflower as a Potential Source of Resistance to Downy Mildew

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## Abstract

Sunflower downy mildew (SDM) (caused by *Plasmopara halstedii)* is a serious disease in the major sunflower production areas of the world. It originated in North America and has spread all over the world. The ancestor of the cultivated sunflower also originated in North America. The two have co-evolved, providing the opportunity to discover resistance genes (*Pl*) in wild sunflower that can be transferred into cultivated sunflower. The frequency of *Pl* genes in the wild species is high, especially in the annual species, and to a lesser extent in the perennial species. Many of the resistance genes identified are dominant in inheritance and control a single race. However, some annual species have resistance genes for all known races of SDM. A species can also have several genes to control the same race, as is seen in wild *H. annuus*. Considerable segregation for resistance to the dominant races of SDM has been observed in interspecific populations. Resistance genes have been successfully transferred to several inbred lines which have single and multiple race resistance. As new races of SDM evolve, new sources of genetic resistance will be needed which should be available in the diverse wild species germplasm. New sources of resistance will also be needed as the present races of SDM become resistant to the current chemicals used to control SDM.

**Key Words:** Disease, *Helianthus*, wild species, *Plasmopara halstedii*

## Introduction

Sunflower downy mildew (caused by *Plasmopara halstedii*) originated in North America and spread throughout the important sunflower growing regions of the world (Leppik, 1966). The disease reduces yield and changes the fatty acid composition of oil in sunflower production (Zimmer and Zimmerman, 1972). The susceptibility of cultivated sunflower to downy mildew may be due to the co-evolution of sunflower and the pathogen and

the sunflower's narrow genetic base. Disease control is essential for maximum production and the most effective control measure is genetic resistance. The genus *Helianthus* comprises 50 species and 19 subspecies that represents considerable genetic variability for use in the improvement of cultivated sunflower. The objective of this paper is to present an overview of the wild species that have been identified as potential sources of downy mildew resistance and to cite examples where genes have been transferred into cultivated backgrounds such as germplasm populations and inbred lines.

Resistance to sunflower downy mildew (SDM) has been observed in several wild species (Tables 1 and 2). Downy mildew resistance is conditioned by

Table 1. Wild annual species which have been identified as potential sources of resistance to downy mildew.

| | Resistance | |
|---|---|---|
| Species | Race(s) | Race(s)† |
| | WSI‡ | LDI‡ |
| *H. annuus* - various populations | 2,3,4 | -- |
| *H. argophyllus* | 2,3,4 | -- |
| *H. debilis* | NS-2 | None |
| *H. deserticola* | 2 | -- |
| *H. niveus* | NS-2 | -- |
| *H. paradoxus* | 2 | None |
| *H. petiolaris* | NS-2 | -- |
| *H. praecox* ssp. *hirtus* | 2,3,4 | -- |
| *H. praecox* ssp. *runyonii* | 2,3,4 | -- |

†Source = Seiler and Gulya (1992).
‡WSI = Whole seedling inoculation method; LDI = Leaf disk inoculation method.

Table 2. Wild perennial species which have been identified as potential sources of resistance to downy mildew.

| Species | Resistance | |
|---|---|---|
| | Race(s) | Race(s)† |
| | WSI‡ | LDI‡ |
| *H. angustifolius* | -- | 1-7 |
| *H. arizonensis* | -- | 5 |
| *H. atrorubens* | -- | 1, 3-7 |
| *H. ciliaris* | -- | 1-2, 5-7 |
| *H. decapetalus* | NS-1, NS-2 | 1-7 |
| *H. divaricatus* | NS-1, NS-2 | 1-7 |
| *H. eggertii* | -- | 1-7 |
| *H. giganteus* | -- | 1-7 |
| *H. glaucophyllus* | -- | 1-7 |
| *H. grosseserratus* | 2 | 1-7 |
| *H. hirsutus* | NS-1, NS-2 | 1-7 |
| *H. laciniatus* | -- | 1-7 |
| *H. laevigatus* | NS-1, NS-2 | 1-7 |
| *H. maximiliani* | 2 | 2-7 |
| *H. microcephalus* | -- | 2-4, 6-7 |
| *H. mollis* | -- | 2-4, 6-7 |
| *H. nuttallii* ssp. *rydbergii* | -- | 2-4, 6-7 |
| *H. occidentalis* ssp. *occidentalis* | -- | 1-7 |
| *H. occidentalis* ssp. *plantagineus* | -- | 2-7 |
| *H. pumilus* | -- | 1, 3-7 |
| *H. pauciflorus* ssp. *pauciflorus* | -- | 1-7 |
| *H. pauciflorus* ssp. *subrhomboideus* | -- | 1-7 |
| *H. salicifolius* | -- | 1-7 |
| *H. silphioides* | -- | 1-7 |
| *H. smithii* | -- | 1-7 |
| *H. xlaetiflorus* | -- | 2-4, 6-7 |
| *H. xmultiflorus* | -- | 1-2, 4-6 |

†Source = Seiler and Gulya (1992).

‡WSI = Whole-seedling inoculation; LDI = Leaf disk inoculation.

by *Pl* genes, $Pl_1$ through $Pl_9$ (Sackston et al., 1990). The continued discovery of new races of downy mildew necessitates the identification of new sources of resistance, which is often controlled by a single dominant gene. Many of the genes identified to date are dominantly inherited and control a single race.

The frequency of SDM resistance genes in the wild species is quite high. Of nine populations of *H. annuus* evaluated for resistance to Race 4 by Tan et al. (1990), only one population did not show any resistance (Table 3).

Table 3. Evaluation of wild populations of *Helianthus annuus* for resistance to Race 4 of *Plasmopara halstedii*.

| Population | Origin (Location) | % Resistance† |
|---|---|---|
| PI 413020 | Wyoming | 13 |
| PI 413035 | Nebraska | 0 |
| PI 413047 | California | 72 |
| PI 413057 | California | 18 |
| PI 413131 | California | 74 |
| PI 413146 | California | 46 |
| PI 413157 | New Mexico | 52 |
| PI 413158 | New Mexico | 66 |
| PI 413161 | Texas | 77 |

†Source = Tan et al. (1990).

In the populations that displayed resistance, the resistance varied from 13 to 77%. Variation of populations within a geographical area such as California also illustrates the variability of resistance. Because the wild populations were collected from different sites in the USA, gene differences among the populations may be the result of geographic isolation. The diversity of species (both annual and perennial) also illustrates the widespread resistance of genes for the races of SDM. Tan et al. (1992) discovered four different

single dominant genes controlling resistance to SDM Race 4 from four different populations of *H. annuus*.

Transmission of resistance genes from the wild species into cultivated sunflower was demonstrated by Pustovoit and Kroknin (1978), where resistance to SDM was controlled by a single dominant gene in interspecific hybrids between *H. annuus* ($2n = 34$) and *H. tuberosus* ($2n = 102$). Several interspecific populations based on different wild annual and perennial species have been developed and show varying degrees of resistance to single and multiple races (Tables 4 and 5). The frequency of the genes in the original populations was variable.

Table 4. Disease reaction of 12 interspecific sunflower germplasms based on perennial species to Races 2, 3, 4, and 5 of downy mildew.

| | Disease Reaction[†] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Downy Mildew Races | | | | | | | |
| | 2 | | 3 | | 4 | | 5 | |
| Germplasm | R | S | R | S | R | S | R | S |
| HIR-1734-1 | 1 | 19 | 1 | 19 | 10 | 10 | 12 | 8 |
| HIR-1734-2 | 1 | 19 | 3 | 17 | 3 | 17 | 5 | 15 |
| HIR-1734-3 | 1 | 19 | 0 | 20 | 9 | 11 | 12 | 8 |
| RES-834-1 | 3 | 17 | 9 | 11 | 6 | 14 | 3 | 17 |
| RES-834-2 | 4 | 16 | 0 | 20 | 4 | 16 | 6 | 14 |
| RES-834-3 | 2 | 18 | 10 | 10 | 9 | 11 | 11 | 9 |
| TUB-346 | 11 | 9 | 0 | 17 | 10 | 10 | 0 | 20 |
| TUB-365 | 3 | 17 | 1 | 19 | 0 | 20 | 0 | 20 |
| TUB-1709-1 | 0 | 16 | 1 | 13 | 0 | 20 | 0 | 20 |
| TUB-1709-2 | 11 | 8 | 0 | 20 | 2 | 18 | 4 | 16 |
| TUB-1709-3 | 17 | 3 | 2 | 18 | 0 | 18 | 1 | 19 |
| TUB-1789 | 0 | 20 | 0 | 20 | 0 | 20 | 2 | 18 |

[†]Source = Seiler (1990; 1991a; 1993).

Table 5. Disease reaction of 28 interspecific sunflower germplasms based on annual species to Races 2, 3, 4, and 5 of downy mildew.

| Germplasm | Disease Reaction† | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Downy Mildew Races | | | | | | | |
| | 2 | | 3 | | 4 | | 5 | |
| | R | S | R | S | R | S | R | S |
| ANO-1509-1 | 5 | 15 | 4 | 16 | 0 | 16 | 1 | 19 |
| ANO-1509-2 | 0 | 20 | 0 | 16 | 0 | 20 | 0 | 15 |
| ARG-420 | 0 | 20 | 1 | 19 | 5 | 15 | 3 | 17 |
| ARG-1575-1 | 2 | 18 | 5 | 15 | 11 | 9 | 14 | 6 |
| ARG-1575-2 | 20 | 0 | 20 | 0 | 20 | 0 | 20 | 0 |
| ARG-1575-3 | 1 | 19 | 10 | 10 | 2 | 18 | 2 | 18 |
| ARG-1575-4 | 1 | 19 | 3 | 17 | 0 | 20 | 2 | 18 |
| BOL-774 | 0 | 18 | 0 | 20 | 3 | 17 | 0 | 20 |
| DEB-SIL-367-1 | 2 | 16 | 1 | 13 | 14 | 1 | 0 | 20 |
| DEB-SIL-367-2 | 0 | 20 | 6 | 14 | 17 | 3 | 12 | 8 |
| DEB-CUC-1810 | 0 | 20 | 2 | 18 | 15 | 5 | 0 | 20 |
| DES-1474-1 | 12 | 8 | 0 | 20 | 7 | 13 | 0 | 20 |
| DES-1474-2 | 20 | 0 | 2 | 18 | 9 | 11 | 7 | 13 |
| DES-1474-3 | 0 | 20 | 2 | 18 | 2 | 18 | 0 | 20 |
| NEG-1255 | 0 | 20 | 0 | 20 | 5 | 15 | 3 | 17 |
| PAR-1084 | 2 | 18 | 0 | 20 | 3 | 16 | 0 | 20 |
| PAR-1671-1 | 1 | 19 | 0 | 20 | 15 | 5 | 5 | 15 |
| PAR-1671-2 | 3 | 17 | 3 | 17 | 17 | 3 | 5 | 15 |
| PAR-1673-1 | 20 | 0 | 1 | 19 | 4 | 16 | 0 | 20 |
| PAR-1673-2 | 0 | 20 | 5 | 15 | 12 | 8 | 5 | 15 |
| PET-PET-1741-1 | 2 | 18 | 3 | 17 | 13 | 5 | 5 | 15 |
| PET-PET-1741-2 | 0 | 20 | 3 | 17 | 8 | 12 | 6 | 14 |
| PRA-PRA-1142 | 3 | 15 | 7 | 13 | 12 | 8 | 0 | 18 |
| PRA-HIR-437 | 1 | 19 | 9 | 9 | 15 | 5 | 5 | 15 |
| PRA-RUN-417-1 | 0 | 20 | 10 | 10 | 10 | 10 | 2 | 18 |
| PRA-RUN-417-2 | 6 | 14 | 20 | 0 | 7 | 13 | 0 | 20 |
| PRA-RUN-417-3 | 20 | 0 | 4 | 16 | 1 | 19 | 2 | 18 |
| PRA-RUN-1329 | 0 | 20 | 12 | 8 | 10 | 10 | 9 | 11 |

†Source = Seiler (1990; 1991b; 1991c).

Five USDA germplasm lines, HA-335 through HA-339, and RHA 340, showed resistance to Races 1 through 3 of SDM (Miller and Gulya, 1988). When first released they were selected only for resistance to Races 1, 2, and 3, but have been immune to all subsequent races. Three different genes from the interspecific crosses have been identified for resistance to Race 4; $Pl_6$ from wild *H. annuus*, $Pl_7$ from *H. praecox,* and $Pl_8$ from *H. argophyllus* (Miller and Gulya, 1991) (Table 6). The inheritance of the resistance of the three lines to other races of SDM has not been studied. Thus, it is not known whether a single gene confers non-race-specific immunity, or a cluster of tightly linked genes is responsible (Gulya et al., 1997).

Table 6. Breeding lines based upon wild species for resistance to the various races of downy mildew.

| Line | Race(s) | Source | Gene |
|---|---|---|---|
| DM-2 | 3 | "Novinka" (*H. tuberosus*) | $Pl_5$ |
| DM-3 | 3 | "Progress" (*H. tuberosus*) | $Pl_5$ |
| HA-335 | All | *H. annuus* | $Pl_6$ |
| HA-336 | All | *H. annuus* | $Pl_6$ |
| HA-337 | All | *H. praecox* | $Pl_7$ |
| HA-338 | All | *H. praecox* | $Pl_7$ |
| HA-339 | All | *H. praecox* | $Pl_7$ |
| RHA-340 | All | *H. argophyllus* | $Pl_8$ |
| PLH-1 | 4 | *H. annuus* | Not $Pl_6$, $Pl_7$, $Pl_8$ |
| PLH-2 | 4 | *H. annuus* | Not $Pl_6$, $Pl_7$, $Pl_8$ |
| PLH-3 | 4 | *H. annuus* | Not $Pl_6$, $Pl_7$, $Pl_8$ |
| PLH-4 | 4 | *H. annuus* | Not $Pl_6$, $Pl_7$, $Pl_8$ |

Germplasm lines PLH1-PLH4 were released with resistance to Race 4 of SDM (C. C. Jan, personal communication, 1993)(Table 6). Each of the four germplasm lines has one completely dominant gene for SDM Race 4 resistance. The four SDM Race 4 resistance genes differ from each other and from the $Pl_6$ (Race 4) resistance gene in inbred line HA-336 (Tan et al., 1992). Since resistance genes $Pl_7$ and $Pl_8$ for Race 4 of SDM are derived from *H. praecox* ssp. *runyonii* and *H. argophyllus*, respectively, the resistance genes from the PLH1-PLH4 lines are presumably different. The relationship between resistance genes from these lines and $Pl_7$ and $Pl_8$ genes needs to be studied further.

## Conclusions

The frequency of resistance genes for SDM in the wild species is high, especially in the annual species, and to a lesser extent in the perennial species. Many of the *Pl* genes identified are dominantly inherited and control a single race. Some species have resistance genes for multiple (all known) races. A species can also have several genes to control the same race, as was illustrated in *H. annuus*. Resistance genes have been successfully transferred to several inbred lines that have single and multiple race resistance. The wild sunflower species will continue to be a good source of resistance genes for SDM as new races appear, and existing races become resistant to currently used fungicides.

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