Rust Resistance of Wild Helianthus Species of the North Central United States

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ABSTRACT

Plants free of rust, *Puccinia helianthi*, were observed in 190 of 200 populations of wild annual and perennial *Helianthus* spp. in the North Central United States. Seed were collected from 100 randomly selected plants of each population, and *P. helianthi* was obtained from 27 populations. Rust from *H. annuus* belonged to races 1, 2, and 3, whereas only race 1 was recovered from *H. petiolaris*. Rust of the perennial species *H. grosseserratus, H. maximiliani, H. nuttallii, H. rigidus,* and *H. tuberosus,* with the exception of one collection from *H. tuberosus,* were avirulent on *H. annuus* 'S-37-388', the "universal suscept." Cross-inoculation studies revealed that *P. helianthi* comprised many pathogenic races with considerable, but not restrictive, specificity to the annual or perennial group, and to the species from which it was collected. Collectively, all rust collections had one of more common hosts that allowed exchange of virulence genes, which made it difficult to postulate the existence of biologic forms. Wild *Helianthus* spp. contained a multiplicity of rust resistances. Plants resistant to all races were identified. Resistance to rust was more prevalent in wild annual sunflower populations collected from Nebraska and Kansas, than from northern states. Wild sunflowers of the North Central United States offer unexplored sources of rust resistance, as well as a breeding sanctuary for *P. helianthi* in the absence of susceptible domestic cultivars.

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Sunflowers are native to the North American continent and occur throughout the United States (6). Heiser et al. (6) recognized over 50 species. Seven of these species, two annual (*Helianthus annuus* L. and *H. petiolaris* Nutt.) and five perennial [*H. grosseserratus* Martens, *H. maximiliani* Schrader, *H. nuttallii* T. & G., *H. rigidus* (Cass.) Desf., and *H. tuberosus* L.] occur in the Red River Valley region of Minnesota, North Dakota, and northeastern South Dakota. Domestic sunflower production in the U.S. is centered in this region. The cultivation of sunflowers in a region where wild ancestral forms exist could expose cultivated cultivars to serious attack by one or more diseases of the native wild types. One such disease is rust, incited by the autoecious macrocyclic species *Puccinia helianthi* Schw. Besides being a serious pathogen of domestic sunflowers in North America (10, 15), *P. helianthi* has been reported (2) or observed by the authors on all seven species of wild sunflowers in the major sunflower production area of the USA. The pathogenic relationship, if any, between the rust on the wild species and domestic sunflower in this region is not well understood. Earlier workers (1, 3, 4, 8, 13) found evidence of specialization among rust collected from some wild species. Hennessy and Sackston (7) concluded that most species of wild annual sunflowers in Texas were heterogeneous for rust resistance; thus, cross-inoculation tests were inconclusive.

Rust resistance originated in wild annual sunflowers (11). Both the R_1 and R_2 resistance genes widely used by sunflower breeders originated from outcrosses with wild sunflowers in Texas (12).

We studied wild *Helianthus* spp. as sources of rust resistance, to establish their relationships with rust in the main sunflower producing area of the U.S. and to assess their role in rust epidemiology.

MATERIALS AND METHODS.—Over 200 populations of seven wild sunflower species, *H. annuus, H. grosseseratus, H. maximiliani, H. nuttallii, H. petiolaris, H. rigidus,* and *H. tuberosus,* were observed for rust along a 4,800 km route in the North Central region of the U.S. during September 1970 and 1972 (Fig. 1). Seed were collected from 100 randomly selected plants in each population. Urediospore collections of *P. helianthi* were obtained from seven populations of *H. annuus,* two of *H. grosseserratus,* three of *H. maximiliani,* two of *H. nuttallii,* six of *H. petiolaris,* four of *H. rigidus,* and three of *H. tuberosus* within the major area of domestic sunflower production.

Field trials.—About 200 seeds from each population were planted in individual rows at Fargo, ND, on 14 October 1972. Overwintering in the field broke the dormancy and provided excellent stands the next spring. Stands were thinned to about 20 plants per 5-m row.

Race 1 of *P. helianthi* was obtained from W. E. Sackston, McGill University, Ste. Anne de Bellevue, Quebec, Canada. It was introduced on 1 June by inoculation of spring-planted spreader rows of the cultivar Commander with a 10:1 mixture of talc and urediospores.

Greenhouse trials.—Field rust collections were isolated and increased on the host from which collected. Resulting urediospores were used to inoculate the Canadian differential cultivars (CM 90RR, Cr 29, and S-37-388). Cross-inoculation studies were conducted by inoculating five plants of two-to-five populations of each *Helianthus* sp. with each of the 27 rust collections. To further delineate pathogenic specialization, three to 20 plants of 290 populations were individually inoculated with race 2 and 3 and two cultures, 70-30 and 70-41. One leaf on each plant was inoculated with urediospores of each race and culture, respectively. Cultures 70-30 and 70-41 belong to race group 1 and were obtained from *H. petiolaris* and *H. annuus*, respectively. The inoculated plants were 6-weeks-old, and had been grown at 20-25 C under a 14-hour day. Data were obtained 12 days after inoculation.

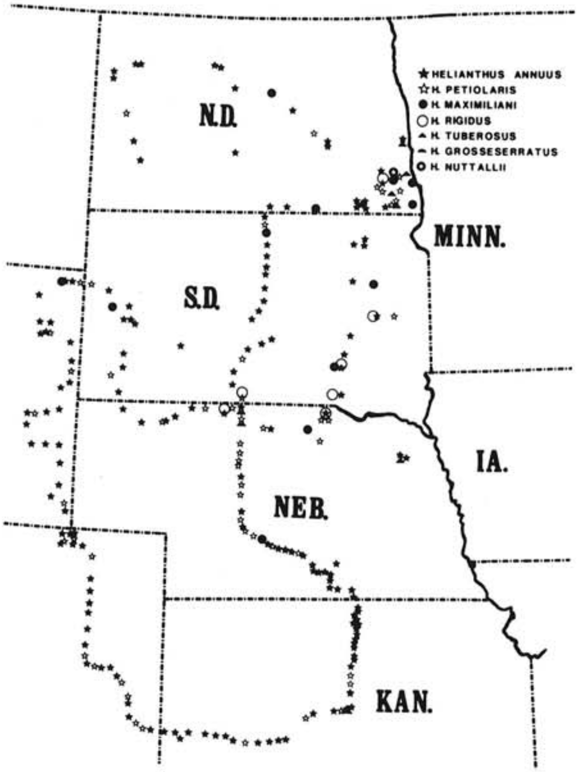

Fig. 1. Collection sites for populations of wild annual and perennial *Helianthus* spp. in a survey.

RESULTS.—*Resistance of wild field populations.*—Most field populations of the seven wild *Helianthus* spp. contained both rusted and nonrusted plants (Table 1). The frequency of rusted plants in 200 field populations ranged from 1 to 100%, with only 12 populations containing all nonrusted plants and 10 populations containing all rusted plants. Rust infection was sufficiently intense in most wild populations to make it unlikely that any plants could escape infection. That some plants have inherent rust resistance is more likely.

The frequency of plants resistant to race 1 in a disease nursery was different than the frequency of resistant plants observed in the original wild populations. This difference is assumed to reflect differences in virulence between race 1 and the naturally occurring races at the collection sites (Table 1). Race 1 originated from domesticated *H. annuus* (13). Thus, greater specificity to the wild populations of *H. annuus* than to *H. petiolaris* or the perennial species could have been anticipated. Of 142 collections of *H. annuus*, 55 were fully susceptible to race 1, whereas only 3 of 56 collections of *H. petiolaris* were completely susceptible.

A multiplicity of resistances within the wild populations was suggested from reactions expressed when individual plants of collections of *H. annuus* and *H. petiolaris* were inoculated with different races and cultures of rust (Table 2). Within a single collection, it was not unusual to observe individual plants with all possible

TABLE 1. Frequency of rust-resistant plants in about 200 populations of wild *Helianthus* spp. at the collection site (A) and of race 1-resistant plants in a field nursery (B)

Species	Location	Populations (no.) with indicated frequency (%) of rust-resistant individuals							
		0	1-10	11-30	31-50	51-70	71-90	91-99	100
H. annuus	A	1	6	33	32	23	12	11	9
	B	55	20	51	14	1	1	0	0
H. grosseserratus	A	0	0	0	2	0	0	0	1
	B	0	0	0	0	0	0	0	2
H. maximiliani	A	0	0	0	4	1	2	1	0
	B	0	1	1	0	0	0	0	10
H. nuttallii	A	0	0	0	1	1	0	0	1
	B	0	0	0	0	0	0	0	1
H. petiolaris	A	4	8	16	9	5	1	2	0
	B	3	1	2	1	1	5	4	40
H. rigidus	A	5	1	0	0	0	0	0	1
	B	0	0	1	0	0	0	0	3
H. tuberosus	A	0	0	0	1	1	2	0	0
	B	0	0	0	0	0	0	0	4

combinations of resistance and susceptibility to the four test races and cultures. Collectively, *H. annuus* populations contained a higher percentage of plants susceptible to race 2, race 3, and culture 70-41, than to culture 70-30. Collectively, *H. petiolaris* populations contained a higher percentage of plants susceptible to culture 70-30 than to the other races and culture. Races 2 and 3 and culture 70-41 were collected from wild or domesticated *H. annuus*. Culture 70-30 was collected from wild *H. petiolaris*, and was identical in virulence to 70-41 when tested on the Canadian rust differential cultivars.

Cross-inoculation studies.—Plants from 25 populations of seven wild *Helianthus* spp. reacted differently to 27 collections of rust from the wild species which occur in the main sunflower producing area of the North Central U.S. (Table 3). Collections from annual sunflowers were generally specific to the annuals, with greater specificity to the species from which they had been collected. Although the numbers of rust and host collections were small, the virulence reciprocity of rust collections from *H. annuus-H. petiolaris, H. rigidus-H. tuberosus*, and *H. maximiliani-H. grosseserratus-H. nuttallii* suggests strong phylogenetic relationships within these groups.

Race identification.—Collections of *P. helianthi* from the seven wild *Helianthus* spp. differed in virulence on the three Canadian rust differential lines. All seven collections from wild *H. annuus* were virulent on S-37-388, the "universal suscept". Two of the seven were virulent only on S-37-388 and belong to race group 1. Three were virulent on Cr 29 and belong to race group 2. None of those from *H. annuus* were virulent on both CM 90RR and Cr 29. All six collections from *H. petiolaris* were virulent only on S-37-388 and belong to race group 1. Only one of 12 collections from perennial sunflowers

TABLE 2. Distribution of rust resistance among collections of *Helianthus annuus* and *H. petiolaris* from six states to four races and cultures of *Puccinia helianthi* in greenhouse trials

State	Species	Percentage of plants classed resistant[a] to			
		70-30[b]	70-41[b]	Race 2	Race 3
North Dakota	*H. annuus*	20.0	3.5	5.7	17.6
	H. petiolaris	14.7	48.6	45.7	58.8
South Dakota	*H. annuus*	39.4	11.6	17.1	17.1
	H. petiolaris	53.5	65.6	84.4	64.1
Nebraska	*H. annuus*	56.6	31.5	34.4	34.3
	H. petiolaris	31.9	82.6	85.9	76.4
Kansas	*H. annuus*	67.0	21.1	26.2	26.1
	H. petiolaris	–[c]	–	–	–
Colorado	*H. annuus*	44.4	6.9	19.1	12.1
	H. petiolaris	47.3	79.0	89.5	85.1
Wyoming	*H. annuus*	18.9	1.0	3.1	4.3
	H. petiolaris	48.3	87.4	81.3	90.6
All locations	*H. annuus*	44.0	13.1	19.5	19.4
	H. petiolaris	36.5	76.7	80.0	75.3

[a]Rust reaction classes 0 and 2 were considered resistant.
[b]Cultures 70-30 and 70-41 belong to race group 1, but were originally isolated from *H. petiolaris* and *H. annuus*, respectively.
[c]No samples tested.

TABLE 3. Cross infectivity of collections of *Puccinia helianthi* on annual and perennial species of *Helianthus* indigenous to the North Central United States

Helianthus species	No. of rust collections	Host species and number of collections[a] represented						
		H. annuus (5)	*H. grosseserratus* (2)	*H. maximiliani* (6)	*H. nuttallii* (2)	*H. petiolaris* (4)	*H. rigidus* (2)	*H. tuberosus* (4)
H. annuus	7	±[b]	±	–	–	±	–	–
H. grosseserratus	2	–	–	–	–	±	±	±
H. maximiliani	3	±	–	–	–	±	±	±
H. nuttallii	2	–	–	–	–	±	±	±
H. petiolaris	6	±	±	–	–	±	–	–
H. rigidus	4	±	–	–	–	±	±	±
H. tuberosus	3	±	–	±	±	–	–	–

[a]Each collection represented three to five plants.
[b]Rating system: + = all cultures were virulent on the indicated host;
± = some cultures were virulent and some avirulent on the indicated host; and
– = all cultures were avirulent on the indicated host.

was virulent on S-37-388.

DISCUSSION.—Field observations substantiated those of Hennessy and Sackston (7) that resistance occurs widely in wild sunflowers, not only in Texas as they report, but throughout the central region of the USA. On the basis of coevolution of host and parasite, the geographic center of origin of the host species would be the center of diversity of rust-resistant genotypes. Texas appears to be at least a secondary center of origin of cultivated sunflower (6). Although resistance was present in most collections of *H.annuus* and *H. petiolaris,* the frequency of resistance was higher in collections from Kansas and Nebraska. The collection sites in Kansas and Nebraska more closely coincide climatologically and geographically with the assumed center of origin of cultivated sunflower. The higher frequency of resistant plants in *H. petiolaris* from more southern locations suggests that *H. petiolaris* may have a center of origin similar to *H. annuus*. Regardless of their center of origin, the wild species of *Helianthus,* especially *H. annuus* and *H. petiolaris,* must be considered a vast source of rust resistance that can be exploited by plant breeders to broaden the rust protection of domestic cultivars. Both *H. annuus* and *H. petiolaris* cross readily with domesticated cultivars (6). Thus, the transfer of rust resistance genes into domestic types should not be difficult.

The host specificity within the rust of wild sunflowers is probably not enough to restrict the exchange of genes for virulence. Collectively, the rust collections shared one or more common hosts. This allows gene exchange needed to perpetuate *P. helianthi* when new combinations of resistance genes develop from hybridization among wild *Helianthus* spp. *Helianthus annuus* and *H. petiolaris* cross readily in nature, as do *H. tuberosus* and *H. rigidus*, and *H. grosseserratus* and *H. maximiliani* (4). Artificial hybrids have been produced among *H. nuttallii, H. grosseserratus,* and *H. maximiliani,* and between *H. annuus* and *H. tuberosus* (4). *Puccinia helianthi* completes the sexual cycle each spring, and mixed populations of two or more *Helianthus* spp., each with rust, often grow in the same area. Thus, opportunities exist for the exchange of virulence genes.

Through interspecific hybridization between *H. tuberosus* and domestic *H. annuus* (9), Soviet scientists have developed sunflower lines with rust immunity that are phenotypically indistinguishable from domestic types. If cultivars derived from such hybrids were grown commercially in the North Central USA, the immediate threat of new virulent races of *P. helianthi* would probably be reduced. However, our observations suggest that where rust occurs on both *H. annuus* and *H. tuberosus*, races with combined virulences on both species could be produced by hybridization.

The variable frequency of resistant plants within populations of the same *Helianthus* species could well account for the conflicting reports of previous workers regarding the existence or absence of biologic forms (1, 3, 4, 7).

Race group 1 predominates on domestic sunflower cultivars in the North Central USA. Attempts to discover race groups 2 or 3 on domestic cultivars have failed. Sackston (13), however, reported these races to be rather common in the prairie provinces of Canada in 1954-58. Since we have collected both race groups 2 and 3 from wild *H. annuus* in the area of domestic sunflower production, it is difficult to explain their absence on domestic cultivars, unless some unknown biological factor restricts their occurrence to wild annual sunflowers.

Wild sunflowers may be important in epidemics of rust on domestic sunflowers where heavily rusted wild sunflowers occur when domestic cultivars are planted. During the moderately severe rust years of 1972 and 1973 in Minnesota and North Dakota, volunteer seedlings of rust-susceptible cultivars were heavily rusted before rust was observed on seedlings of wild sunflowers. Wild sunflowers apparently were unimportant in these epidemics. Rust-susceptible cultivars, however, are being replaced by resistant cultivars and hybrids (5, 14). In the absence of rust-susceptible cultivars, wild *Helianthus* spp. will furnish a breeding sanctuary from which new virulent races of *P. helianthi* can arise. The occurrence of such sanctuaries in the area of commercial sunflower production, makes it unlikely that vertical resistance will impart long-term protection against rust.

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