Inheritance of Resistance to *Orobanche cernua* Loefl. in Six Sunflower Lines

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ABSTRACT

Sunflower (*Helianthus annuus* L.) is severely affected by broomrape (*Orobanche cernua* Loefl.) in the main crop areas of the Old World. The appearance of new virulent broomrape populations has prompted the search for new sources of resistance. The objectives of this study were to elucidate the inheritance of sources of resistance from different origins and to determine allelic relationships between the resistance genes. Six resistant sunflower lines (one of them with resistance gene Or_5), two susceptible lines, the F_1 crosses between resistant and susceptible lines and resistant and resistant lines, and the F_2 and BC_1 generations were evaluated for broomrape resistance with the widespread highly virulent population SE 194. Genetic ratios from segregating generations indicated that resistance to *O. cernua* in these lines was conferred by a single dominant gene. None of the crosses between resistant lines produced susceptible F_2 or BC_1 plants. However, the reaction of the resistant lines to broomrape populations from different areas and years showed differences to new highly virulent populations. Only two lines were resistant to all populations, indicating that resistance in these lines was conferred by additional dominant alleles at the *Or* locus or by a cluster of very tightly linked non-allelic genes. The resistance found in the two cultivated lines against the new populations, which overcome the Or_5 resistance gene, is an important finding and will aid the development of new resistant cultivars since the current resistant hybrids are based on this gene. Results from this study can also be used to establish differential lines against the new broomrape populations.

Broomrape is a parasitic angiosperm infecting the roots of sunflower and causing severe crop losses in Spain and other countries of southern Europe, as well as in many of the countries of the former USSR, the Middle East and China (Parker, 1994). The seeds of *O. cernua* germinate in response to exudates from sunflower roots. The germ-tube-like or procaulome penetrates the roots of sunflower and develops haustoria that draw water and nutrients from them (Parker and Wilson, 1986). As a result of the continuous depletion of sunflower nutrients achieved by the parasite, the infected plant is stunted and crop yields can be greatly reduced. Yield losses can reach 50% in the most susceptible cultivars (Domínguez, 1996a). Broomrapes are annual plants which usually flower over a period of several weeks. Each fruiting capsule contains thousands of tiny seeds (250–400 by 120–240 μm). The production of a high number of broomrape seeds, which can be disseminated by wind, irrigation water, and sunflower achenes (Castejón et al., 1991) and the longevity of those seeds contribute to the build-up of broomrape populations in cropping systems. Though several methods of control have been proposed, herbicide control is only partially effective (García-Torres et al., 1988) and soil treatments by fumigation or solarization are effective but not economically feasible (Foy et al., 1989; Jacobsohn et al., 1980). The most economical and effective means of controlling sunflower broomrape is by growing resistant cultivars.

The development of resistance to *O. cernua* in sunflower has been an objective in Russian breeding programs with resistant varieties emerging as early as 1920 (Pustovoit, 1966). Resistance has since been reported in cultivated and wild germplasm (Vranceanu et al., 1980; Skoric, 1988; Ruso et al., 1996). A variety of genetic mechanisms has been proposed for resistance to *O. cernua*. Pustovoit (1966) reported quantitative resistance. Several authors found dominant resistance genes (Pogorletsky and Geshele, 1976; Vranceanu et al., 1980; Burlov and Artemenko, 1983; Ish-Shalom-Gordon et al., 1993; Saavedra et al., 1994b). Other studies have found two complementary genes (Krokhin, 1983), epistatic interactions and a reversal in dominance in crosses of different susceptible lines with the same resistant source (Saavedra et al., 1994b), double recessive epistatic inheritance (Kirichenko et al., 1987), and two independent dominant genes (Domínguez, 1996b).

The host-parasite system of sunflower-*O. cernua* appears to follow the gene-for-gene model. Vranceanu et al. (1980) established a set of five sunflower differentials carrying the five dominant resistance genes, Or_1 to Or_5, each one giving resistance to a new race and also to the previous race. The differentials along with a universal susceptible host permitted the identification of five physiological races designated as A through E. These differential lines were only partially valid for the Spanish racial pattern, with differentials 'Kruglik A-41' and 'Record' (carrying the resistance genes Or_1 and Or_3), being susceptible, and lines J-8281 (Or_2) and P-1380-2A (Or_5) showing resistance to most of the populations tested (Melero-Vara et al., 1989). The appearance and spread of the new and more virulent races of broomrape in different countries has intensified research aimed at developing sunflower genotypes resistant to the current and new races of the parasite. However, it has not been reported whether the resistant lines possess the same or different genes for resistance.

For breeders to efficiently use the available sources of *Orobanche* resistance, it is necessary to determine the inheritance of resistance and the genetic relationship between resistance genes. The objectives of this study were to determine (i) the inheritance of broomrape resistance in six lines that showed resistance to one virulent *O. cernua* population, (ii) the allelic relationships between resistance genes in these lines, and (iii)

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the response of different sources of resistance to different populations of *O. cernua*.

MATERIALS AND METHODS

Inheritance and Allelism Study

Six sunflower lines were selected for this study on the basis of their diverse origin and resistance to a virulent population (SE 194) of *O. cernua* widespread in southern Spain (Table 1). These lines were derived from hybrids and populations of sunflower showing resistance to several populations of the parasite. One of these lines (R-5) carried the resistance gene Or_5 (Vranceanu et al. 1980). Two types of crosses were made to determine the inheritance and allelism of *O. cernua* resistance in these lines. An estimate of the number of resistance genes present in each resistant entry was obtained by crossing with two lines, HA-89 and S-59, that are susceptible to *O. cernua*. (Table 1). To investigate allelic relationships of the resistance genes, resistant plants of the six sources were intercrossed in all possible combinations. All crosses were made in the greenhouse in the winter of 1994. The F_1 plants were used to generate F_2 and BC_1 generations by backcrossing to both parents. Since the hybrids between cytoplasmic male sterile and maintainer lines JD-6 (cms) × JM-1 and JM-1 (cms) × JD-6 were sterile, they were crossed to the susceptible line P-21, instead of producing an F_2 generation. These generations were produced in the greenhouse in 1995. To study the inheritance of resistance, both parents, F_1, F_2, and the BC_1 generations were tested in the greenhouse in artificially infested soil in the spring of 1996. F_2 populations were also evaluated in a heavily infested nursery in the field at Ecija, Sevilla, in a fine, calcareous, thermic, Typic Chromoxeret soil. The broomrape population SE 194 originated in this field. Susceptible lines HA-89 and P-21 were included as controls.

Artificial inoculations were performed by planting 2-d-old sunflower seedlings in small pots with 250 g of a soil mixture (sand: silt, 1:1, v/v) uniformly infested with 25 mg of broomrape seeds (Panchenko, 1975). After 2 wk of incubation in a growth chamber at 23 ± 2°C, 60% relative humidity, and under fluorescent light (14-h/day photoperiod of 240 μmol. m^{-2} s^{-1}), plants were transferred to pots containing 3 L (parental lines and F_1) or 2 L (F_2 and BC_1) of soil mixture (peat moss: sand: silt, 2 : 2 : 1, v/v) amended with slow-release fertilizer Osmocote plus [N, P, K: 15, 11, 13 + (2 MgO + micronutrients), The Scotts Co., Marysville, OH] at the rate of 2.5 g/kg. These plants were grown in the greenhouse at 20 to 25°C with a 16-h photoperiod. Ten pots with one plant in each were used for each parental line and F_1, 60 pots for the BC_1, and 90 pots for the F_2 generations.

Disease reactions were assessed by the degree of attack (number of emerged broomrape shoots per sunflower plant; Vranceanu et al., 1980), which was recorded twice, at 10 and 14 wk after sowing, for the plants grown in 3-L pots, and only at 10 wk (when plants initiated blooming) for those grown in 2-L pots. F_2 and BC_1 plants were carefully uprooted to recover as much of the root system as possible. The roots were cleaned and broomrape nodules attached to the roots were recorded together with the emerged broomrape plants for the final evaluation of infection. Plants were classified as resistant or susceptible according to their reaction to broomrape (Bachvarova, 1979).

In the field, disease reactions were assessed at physiological maturity by counting the number of emerged broomrape shoots around each sunflower plant. Resistant-to-susceptible plant ratios were used to determine genetic relationships. Chi-square statistic tests were used to test for goodness of fit to expected genetic ratio. A single gene model (3:1 for the F_2 and 1:1 for the BC_1 plants) was applied to evaluate the segregation ratio for inheritance of *O. cernua* resistance.

Table 1. Origin of lines selected for the genetic study and their reaction to population SE194 of *O. cernua* 14 wk after sowing sunflower in artificially infested soil.

Pedigree	Origin	Infected plants	Degree of attack†
		%	
HB	Ukraine	0.0	0.0
T2	Turkey	0.0	0.0
W-14	Yugoslavia	0.0	0.0
R-5	Romania	0.0	0.0
JM-1	Ukraine	0.0	0.0
JD-6	Ukraine	0.0	0.0
JM-1 (cms)	Ukraine	0.0	0.0
JD-6 (cms)	Ukraine	0.0	0.0
HA89	USA	100.0	8.5
S59	Yugoslavia	100.0	24.0
P21	USA	100.0	18.0

† Degree of attack: average number of emerged broomrapes per sunflower plant.

Virulence Study

All the sunflower lines used in the inheritance and allelic tests, along with hybrid S-25, the restorer line R-41, with two genes of resistance (Dominguez, 1996b), and the Romanian differentials KA-41 and J-8281, carrying genes of resistance Or_1 and Or_2 (Vranceanu et al., 1980) were evaluated under artificial conditions in 1996 for their reaction to nine virulent populations of sunflower broomrape. The populations had been collected in the main sunflower growing areas in central (Cuenca, CU) and southern Spain (Sevilla, SE) from 1993 through 1996 (Melero-Vara et al., 1996). Evaluations were performed as previously described by inoculating 15 plants of each sunflower line with each broomrape population. A randomized complete block design was used. The degree of attack was recorded twice at 11 and 13 wk after sowing. Plants were grown in 2-L pots, uprooted and their root systems cleaned as previously described, and assigned, on the basis of the number of broomrape nodules attached to the roots as well as the emerged broomrape plants, to one of four catagories of infection, i.e., Resistant (R): no infection, Moderately resistant (L): up to one third of sunflower plants with attached broomrapes averaging less than 1.5, Moderately susceptible (M): up to 50% of sunflower plants with attached broomrapes averaging less than 3, Susceptible (S): over 50% of sunflower plants with attached broomrape plants.

RESULTS AND DISCUSSION

Parental lines were different in reaction to inoculation with population SE 194 of *O. cernua* (Table 1). Degree of attack was higher in susceptible lines S59 and P21 than in HA89. All F_1 plants of reciprocal crosses between six resistant and two susceptible sunflower lines showed a resistant reaction to the virulent population SE 194 of *O. cernua*. The segregation pattern observed in the F_2 generations between resistant and susceptible lines showed a good fit to a 3:1 (resistant:susceptible) ratio (Table 2). The data of BC_1 generation also satisfactorily fit a 1:1 (resistant:susceptible) ratio, with the exception of cross S59 × JD-6, which showed too many resistant plants and was interpreted as an escape from infection. As expected, no susceptible plants were detected in the backcrosses to the resistant parent. These data indicated

Table 2. Chi-square (χ^2) tests of F_2 and BC_1 generations of crosses between resistant lines of sunflower and susceptible lines HA89 and S59 to inoculation with population SE194 of *O. cernua* under greenhouse and field conditions.

Cross	Segregating generations	Number of plants† Total	R	S	Ratio tested	χ^2	*P*
JM-1×HA89	F_2	68	52	16	3:1	0.078	0.7790
JM-1×(JM-1×HA89)	BC_1	59	59	0			
JD-6×HA89	F_2	87	67	20	3:1	0.1877	0.6641
	F_2 (F‡)	134	98	96	3:1	0.6153	0.4327
JD-6×(JD-6×HA89)	BC_1	58	58	0			
HA89×(JD-6×HA89)	BC_1	60	30	30	1:1	0	1
T2×HA89	F_2	88	65	23	3:1	0.0606	0.8055
	F_2 (F‡)	306	225	81	3:1	0.3529	0.5524
T2×(T2×HA89)	BC_1	60	60	0			
HA-89×(T2×HA89)	BC_1	60	33	27	1:1	0.6	0.4385
HA89×T2	F_2	86	64	22	3:1	0.0606	0.8055
T2×(HA89×T2)	BC_1	59	59	0			
HA89×(HA89×T2)	BC_1	59	26	23	1:1	1.8474	0.1740
HB×HA89	F_2	73	54	19	3:1	0.0454	0.8311
HB×(HB×HA89)	BC_1	57	57	0			
HA89×(HB×HA89)	BC_1	40	22	18	1:1	0.4	0.5270
R5×HA89	F_2	86	66	20	3:1	0.1395	0.7087
	F_2 (F‡)	312	228	84	3:1	0.6153	0.4327
R5×(R5×HA89)	BC_1	50	50	0			
HA89×(R5×HA89)	BC_1	60	34	26	1:1	1.06	0.3017
HA89×W-14	F_2	61	47	14	3:1	0.1366	0.7116
W-14×(HA89×W14)	BC_1	58	58	0			
S59×JM-1	F_2	85	62	23	3:1	0.1921	0.6611
JM-1×(S59×JM-1)	BC_1	59	59	0			
S59×(S59×JM-1)	BC_1	59	29	30	1:1	0.0169	0.8964
S59×JD-6	F_2	89	68	21	3:1	0.0936	0.7596
JD-6×(S59×JD-6)	BC_1	58	58	0			
S59×(S59×JD-6)	BC_1	60	47	13	1:1	19.266	<0.001
S59×T2	F_2	81	62	19	3:1	0.1028	0.7484
T2×(S59×T2)	BC_1P_1	56	56	0			
S59×(S59×T2)	BC_1P_2	60	33	27	1:1	0.6	0.4385
S59×HB	F_2	86	61	25	3:1	0.8516	0.3560
HB×(S59×HB)	BC_1P_1	60	60	0			
S59×(S59×HB)	BC_1P_2	57	30	27	1:1	0.1579	0.6912
S59×R5	F_2	90	71	19	3:1	0.7259	0.3942
R5×(S59×R5)	BC_1P_1	59	59	0			

† R: resistant, S: susceptible.
‡ F: evaluation made after natural infection in a heavily infested field.

Table 3. Reactions of F_2 and BC_1 generations from crosses between resistant lines of sunflower to inoculation with population SE 194 of *O. cernua*, under greenhouse and field conditions.

Cross	Segregating generations	Number of plants† Total	R	S
P21×(JD-6×JM-1)	BC_1	58	58	0
P21×(JM-1×JD-6)	BC_1	58	58	0
JM-1×HB	F_2	89	89	0
JM-1×(JM-1×HB)	BC_1	53	53	0
HB×(JM-1×HB)	BC_1	60	60	0
JM-1×W-14	F_2	87	87	0
JM-1×(JM-1×W-14)	BC_1	59	59	0
W-14×(JM-1×W-14)	BC_1	58	58	0
JM-1×T2	F_2	87	87	0
	F_2 (F‡)	309	309	0
JM-1×(JM-1×T2)	BC_1	56	56	0
T2×(JM-1×T2)	BC_1	57	57	0
JM-1×R5	F_2	86	86	0
	F_2 (F‡)	314	314	0
JM1×(JM-1×R5)	BC_1	59	59	0
R-5×(JM-1×R5)	BC_1	57	57	0
JD-6×HB	F_2	90	90	0
JD-6×(JD6-HB)	BC_1	59	59	0
HB×(JD-6×HB)	BC_1	59	59	0
JD-5×W-14	F_2	80	80	0
	F_2 (F‡)	306	306	0
JD-6×(JD-6×W-14)	BC_1	59	59	0
W-14×(JD-6×W-14)	BC_1	59	59	0
JD-6×T2	F_2	90	90	0
	F_2 (F‡)	302	302	0
JD-6×(JD-6-T2)	BC_1	60	60	0
T2×(JD-6×T2)	BC_1	59	59	0
JD-6×R5	F_2	90	90	0
	F_2 (F‡)	318	318	0
JD-6×(JD-6×R5)	BC_1	60	60	0
R5×(JD-6×R5)	BC_1	56	56	0
T2×HB	F_2	86	86	0
	F_2 (F‡)	311	311	0
T2×(T2×HB)	BC_1	60	60	0
HB2×(T2×HB)	BC_1	60	60	0
T2×W-14	F_2	80	80	0
T2×(T2×W-14)	BC_1	56	56	0
W-14×(T2×W-14)	BC_1	57	57	0
T2×R5	F_2	88	88	0
	F_2 (F‡)	302	302	0
T2×(T2×R5)	BC_1	60	60	0
R5×(T2×R5)	BC_1	57	57	0
HB×W-14	F_2	81	81	0
HB×(HB×W-14)	BC_1	19	19	0
W-14×(HB×W-14)	BC_1	56	56	0
HB×R5	F_2	86	86	0
HB×(HB×R5)	BC_1	58	58	0
R5×(HB×R5)	BC_1	59	59	0
R5×W-14	F_2	87	87	0
R5×(R5×W-14)	BC_1	56	56	0
W-14×(R5×W-14)	BC_1	58	58	0

† R: resistant, S: susceptible.
‡ F: evaluation made after natural infection in a heavily infested field.

that resistance to *O. cernua* in the lines studied was controlled by a single dominant gene, in agreement with previous reports (Pogorletsky and Geshele, 1976; Vranceanu et al., 1980; Burlov and Artemenko, 1983, Ish-Shalom-Gordon et al., 1993; Saavedra et al., 1994b). No cytoplasmic effect was found since the reciprocal F_1 crosses were resistant. Because the distinction between resistant and susceptible plants was very clear, quantitative inheritance was not involved.

The F_1 from crosses between resistant lines showed resistance to broomrape. F_2 and BC_1 progeny from crosses between the six sources of resistance did not segregate (Table 3). Since one would expect 1/16 of the plants to be attacked by broomrape if the parents carried different genes imparting resistance, there is strong evidence that resistance alleles in the lines JM-1, JD-6, W-14, T2, and HB are allelic with Or_5 carried by line R-5. However, it is also possible that some of the alleles are actually tandem repeats of adjacent, very tightly linked genes. Whether these six resistant lines have the identical allele (Or_5) or have either additional dominant resistance alleles at the *Or* locus or adjacent genes very tightly linked, was determined from the results of the study on virulence of broomrape populations.

Kruglik A-41 (*Or1*) was susceptible to all the broomrape populations tested (Table 4). Populations CU194 and CU794, both collected in 1994, were the least virulent of the five populations tested from central Spain. Populations CU394 and CU996 had similar levels of virulence except for the reaction of the differential line J-8281 (*Or2*). This line was susceptible to CU394 and resistant to CU996. R-5 (*Or5*) was shown to be

Table 4. Reaction of nine lines of sunflower to nine populations of *O. cernua* from different origins.

	Broomrape populations								
	Central Spain					Southern Spain			
Sunflower	CU194	CU394	CU494	CU794	CU996	SE193	SE194	SE295	SE296
KA-41	4.4† S‡	6.7 S	8.5 S	3.0 S	1.6 S	20.7 S	8.1 S	0.6 S	3.9 S
S-25	0.4 L	2.2 S	0.4 L	0.5 M	1.5 S	0.0 R	0.0 R	0.0 R	8.2 S
J-8281	0.3 L	2.1 S	0.8 M	0.3 L	0.4 L	0.0 R	0.0 R	0.4 R	8.6 S
HB	1.3 S	3.7 S	4.5 S	1.1 S	3.9 S	0.0 R	0.0 R	0.0 R	6.5 S
T2	0.3 L	1.1 S	0.8 M	0.3 L	1.2 S	0.0 R	0.0 R	0.0 R	6.8 S
R5	0.0 R	0.3 L	0.8 M	0.0 R	0.6 M	0.0 R	0.0 R	0.0 R	8.3 S
JM-1	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	3.3 S
JD-6	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R
W-14	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R
R-41	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	0.0 R	3.2 S

† Degree of attack: average number of emerged broomrape plants per sunflower plant.
‡ Broomrape on roots: R: resistant, L: moderately resistant, M: moderately susceptible, S: susceptible.

moderately resistant to CU394 but moderately susceptible to CU996. All the populations from central Spain were able to overcome the resistance of the HB line. Lines T2 and R-5, the latter carrying the Or_5 gene, were moderately susceptible to the CU494 population.

The SE193, SE194, and SE295 populations from southern Spain had the same disease reaction pattern, being nonpathogenic on all the lines tested except Kruglik A-41. In contrast, the SE296 population (collected in 1996) was highly virulent on R-5, HB, T2, S-25, and J-8281, the latter carrying Or_2 (Table 4). Lines JM-1 and R-41 were susceptible to population SE296 and resistant to the CU 996 population. JD-6 and W-14 were resistant to all the populations tested. However, the other lines were differentially susceptible to broomrape populations. It is, therefore, suggested that lines JD-6 and W-14 may have a different allele or, alternatively, an additional gene to the one imparting resistance to population SE194.

Vranceanu et al. (1980) postulated a series of independent dominant genes, Or_1 to Or_5, each conferring resistance to the last race discovered and to the previous populations. However, they did not show segregation of crosses between the differential lines to determine if they carry different genes or alleles at the same locus. In our study, the hypothesis of two independent genes would require the second gene, conferring resistance to SE296, being indistinguishable from the first when the F_2 population was inoculated with the SE194 population, to explain the 3:1 F_2 segregation when the lines JD-6 and W-14 were crossed with susceptible lines. Therefore, the results seem to suggest the presence of different dominant alleles at the Or_5 locus as the most likely explanation for the resistance in the different lines tested in this study, although the existence of additional adjacent genes very tightly linked is also possible.

Broomrape populations belonging to races A, C, and D of the parasite, respectively overcoming genes Or_1, Or_3 and Or_4, were reported in southern Spain (Melero-Vara et al., 1989; Domínguez et al., 1996). In our observations, the two populations collected in 1996, CU996 and SE296, were pathogenic on J-8281, carrying the Or_2 resistance gene, and indicated an increased pathogenicity. The previously reported (González-Torres et al., 1982; Melero-Vara et al., 1996) occurrence of a race or race complex overcoming the resistance of Or_2 gene in some areas of central Spain was confirmed by our studies. Populations CU996 and SE296 from central and southern Spain differed in pathogenicity. Lines JM-1 and R-41 reacted differently to these populations and could be used as differentials for the broomrape races.

The Or_5 gene was until recently the only effective gene against highly virulent populations of broomrape (Saavedra del Río et al., 1994a; Domínguez et al., 1996). Several populations of *O. cernua* have overcome the resistance of cultivars carrying this gene, but two sunflower lines were resistant to all of them. Because of the dissemination of the new race of the parasite, an increase in crop vulnerability in Spain is to be expected. The two resistant lines, JD-6 and W-14, identified in this study are desirable sources of resistance for sunflower breeders. The resistance genes present in JD-6 and W-14 are probably different alleles at a common locus or cluster of genes not allelic but very tightly linked. The identification of resistance to these new populations of broomrape (CU996 and SE296), against which the Or_5 gene is not effective, is an important finding since the present resistance of current cultivars is based on the Or_5 gene. The lines JD-6 and W-14 could be used as differentials for the new, more virulent populations of broomrape from southern Spain, whereas lines JM-1 and R-41 are useful for differentiating between other populations of *O. cernua*.

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