

UPDATE ON BREEDING FOR RESISTANCE TO SUNFLOWER BROOMRAPE

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SUMMARY

Sunflower broomrape (*Orobanche cumana* Wallr.) is currently regarded as one of the most important constraints in sunflower (*Helianthus annuus* L.) production. In the last fifteen years, efforts to introduce genetic sources of resistance to this parasite in sunflower hybrids were followed by the occurrence of new virulent races that promptly overcame all known resistance genes. Due to this situation, most of the research efforts have focused on the development and characterization of new sources of genetic resistance to the most virulent races and also on the genetic structure and variability of *O. cumana* populations and their evolution, in order to develop long-term strategies for sunflower broomrape management. Results of evaluation of sunflower germplasm for resistance to different broomrape races have demonstrated that wild *Helianthus* species constitute the major reservoir of genes conferring resistance to new virulent races. Cultivated germplasms are also valuable sources of resistance genes. Most of the resistant sources have been found to be controlled by major genes, although quantitative resistance and epistatic effects have also been reported. Different dominance reactions, depending on the race of broomrape, the source of resistance and the susceptible parental line used for crossing have been observed. Molecular studies have shown that phenotypic variance for race E resistance was mainly explained by a major QTL associated to the resistance or susceptibility character, while race F resistance was explained by several QTL with a small to moderate effect, mainly associated with the number of broomrapes per plant, suggesting the existence of a quantitative component in the resistance to race F. The relevance of these findings for sunflower breeding for resistance to broomrape is discussed.

Key words: *Orobanche cumana*, broomrape races, genetic resistance, inheritance

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INTRODUCTION

Sunflower broomrape (*Orobanche cumana* Wallr.) is an obligate, holoparasitic angiosperm that lives attached to the roots of sunflower (*Helianthus annuus* L.), depleting them of nutrients and water. This parasitic plant is currently regarded as one of the most important constraints for sunflower production in Southern Europe, the Black Sea region, Ukraine and China (Parker, 1994). Broomrape attacks are frequently severe and yield losses can reach up to 50% (Domínguez, 1996a). Control of this parasite remains extremely difficult, as thousands of tiny seeds produced by a single broomrape plant can be easily dispersed by wind, water, animals, humans, machinery or attached to sunflower seeds. Broomrape seeds may remain viable for 15-20 years and will only germinate in the presence of the host plant (Škorić, 1988). Although use of herbicides is being considered as a promising control measure, at present genetic resistance offers the most effective and feasible control against *O. cumana*. However, the introduction of new resistance sources has been frequently followed by the occurrence of new pathogenic races overcoming the resistance, which determines the need for additional sources of resistance.

In a classic study, Vrânceanu *et al.* (1980) identified five pathogenic races, named A through E, with a set of sunflower differentials carrying the dominant resistance genes *Or1* through *Or5*, that provide an accumulative resistance to the five successive races. In 1995, a new race F, overcoming all the known resistance genes, *Or1* through *Or5*, was identified in Spain and it spread rapidly (Alonso *et al.*, 1996; Domínguez, 1999). Resistance to this new race was found in germplasm of both cultivated and wild sunflower (Sukno *et al.*, 1999; Fernández-Martínez *et al.*, 2000; Rodríguez-Ojeda *et al.*, 2001). However, a more virulent race (designated race G), attacking the cultivars resistant to race F, has been recently identified (Molinero-Ruiz and Melero-Vara, 2005). Virulent races overcoming the resistance gene *Or5* were also identified in Romania in 1996 (Pacureanu *et al.*, 2004) and in Turkey, where the new races seem to be more virulent than the races present in other countries (Kaya *et al.*, 2004).

SOURCES OF RESISTANCE

The sources of resistance to *Orobanche* races found in the early sunflower breeding work in the former USSR originated from land races of cultivated sunflowers, but genetic resistance was also introduced into susceptible sunflower from wild species, mainly *H. tuberosus* (Pustovoit, 1966). Cultivated material tracing back to early USSR cultivars and *H. tuberosus* were also important sources of resistance for the *O. cernua/cumana* complex of races in Romania (Vrânceanu *et al.*, 1980). Sources of resistance to recent virulent races have been scant in cultivated germplasm. Gulya *et al.* (1994) found only 22 resistant entries in a field evaluation of 903 accessions in Turkey. Domínguez *et al.* (1996) found only 8 resistant and 33

Table 1: Disease reaction of annual and perennial species to broomrape race F

Species	Num. of entries	Incidence ¹	DS ²
Annual species			
<i>H. agrestis</i>	1	0	0
<i>H. annuus</i>	1	100	12.5
<i>H. anomalus</i>	1	0	0
<i>H. argophylus</i>	1	100	2.1
<i>H. debilis</i> (several subsp.)	3	0-35	0-1.6
<i>H. deserticola</i>	1	100	5.0
<i>H. exilis</i>	1	0-42	0-3.2
<i>H. petiolaris</i>	1	100	4.5
<i>H. praecox</i>	1	100	2.3
Diploid perennials (2n=34)			
<i>H. atrorubens</i>	2	0	0
<i>H. decapetalus</i>	2	0	0
<i>H. divaricatus</i>	3	0-10	0-1
<i>H. giganteus</i>	1	0	0
<i>H. glaucophylus</i>	1	0	0
<i>H. gracilentus</i>	1	0	0
<i>H. grosseserratus</i>	5	0	0
<i>H. maximiliani</i>	5	0-80	0-3
<i>H. microcephalus</i>	1	0	0
<i>H. nuttallii</i> (4 subsp.)	6	0	0
<i>H. salicifolius</i>	1	0	0
<i>H. smithii</i>	1	0	0
Tetraploid perennials (2n= 68)			
<i>H. hirsutus</i>	1	0	0
<i>H. laevigatus</i>	1	0	0
<i>H. pumilus</i>	1	0	0
<i>H. strumosus</i>	3	0	0
Hexaploid perennials (2n=102)			
<i>H. californicus</i>	1	0	0
<i>H. ciliaris</i>	1	0	0
<i>H. xlaetiflorus</i>	1	0	0
<i>H. pauciflorus</i>			
subsp. <i>pauciflorus</i>	2	0-10	0-1
subsp. <i>subrhomboideus</i>	2	0	0
<i>H. tuberosus</i>	3	0	0
Cultivated checks			
P-1380 (Or5)	-	100	5.6
P-21	-	100	18.2

¹Incidence= (Numb.of infected plants/total numb. of sunflower plants) x100

²DS= disease severity: average numb. of broomrape plants per infected sunflower plant

segregating entries in the evaluation of 429 accessions of different origins for resistance to race E, carried out in Spain under controlled conditions. In a more recent evaluation, only 4 entries out of 55 cultivated accessions, previously reported as resistant in Turkey (Gulya *et al.*, 1994), were found resistant against the race F pathotypes predominant in Spain (Fernández-Martínez *et al.*, 2000). In contrast, a high level of resistance to races E and F has been found in the evaluation of wild *Helianthus* species. In Spain, Ruso *et al.* (1996) and Fernández-Martínez *et al.* (2000) found resistance to several virulent races, including race F, in 29 perennial wild species. The annual species showed a much lower level of resistance, with only four out of 18 evaluated entries showing resistance to race F (Fernández-Martínez *et al.*, 2000). Resistance to *O. cumana* has also been identified in wild *Helianthus* species in other countries (Pogorletsky and Geshele, 1976; Christov *et al.*, 1996; Škorić, 1988). All these evaluations demonstrated that wild *Helianthus* species constitute the major reservoir of genes controlling resistance to the new virulent races. Results of evaluation of wild species for resistance to the virulent race F are summarized in Table 1.

In general, transferring broomrape resistance genes from wild annual species into cultivated lines can be accomplished rather easily with a conventional crossing and backcrossing scheme. Conversely, crossing perennial *Helianthus* species with the cultivated sunflower is generally difficult due to early hybrid embryo abortion as well as high levels of sterility in the F₁ or BC F₁ generations. These problems can be overcome with the utilization of the embryo culture technique, chromosome doubling of the F₁ and the creation of amphiploids (Jan and Fernández-Martínez, 2002). Using these techniques, amphiploids of the perennial wild species *H. grosseserratus*, *H. maximiliani* and *H. divaricatus*, resistant to race F, were produced and used as a bridge to transfer the resistance to cultivated sunflower (Jan and Fernández-Martínez, 2002). As a result, four germplasm populations named BR1 through BR4, resistant to race F, were developed and released (Jan *et al.*, 2002).

Table 2: Released lines resistant to broomrape race F

Resistant line	PI number	Origin	Pedigree ¹
BR1	PI 617026	Wild species (<i>H. grosseserratus</i>)	P-21// <i>H. gro.</i> -001/P21 (PD)/3/ HA89
BR2	PI 617027	Wild species (<i>H. maximiliani</i>)	<i>H. max.</i> -004/P-21(D)// P21/3/ HA89
BR3	PI 617028	Wild species (<i>H. divaricatus</i>)	<i>H. div.</i> -830/P-21(D)// P21/3/ HA89
BR4	PI 617026	Wild species (<i>H. grosseserratus</i> and <i>H. divaricatus</i>)	<i>H. div.</i> -830/P-21(D) // <i>H. gro.</i> -001/P21(D)/3/ P-21/4/HA89
P96	PI 633612	Cultivated sunflower	KREM-94-8 (Yugoslavia)
K-96	PI 633613	Cultivated sunflower	PER-94-5 (Yugoslavia)
R-96	PI 633614	Cultivated sunflower	ROD-94-15 (Yugoslavia)
L-86	PI 633615	Cultivated sunflower	Ames 3377 (VIR-115)
AM-1	PI 641057	Cultivated sunflower	VNIIMK 6540 (Russia)
AM-2	PI 641058	Cultivated sunflower	Romsun V-1352 (Romania)
AM-3	PI 641059	Cultivated sunflower	VIR 101 (Russia)

¹Jan *et al.* (2002); Fernández-Martínez *et al.* (2004); Pérez-Vich *et al.* (2005).

Although a higher frequency of resistance has been observed in wild sunflower species, some resistance to the new virulent races has also been found in cultivated germplasm, especially in material tracing back to old Russian cultivars. From this material, four lines uniformly resistant to races B, E and F and susceptible or showing segregation for race G (Fernández-Martínez *et al.*, 2004) and three lines showing quantitative resistance to race F (Pérez-Vich *et al.*, 2005) were developed. Resistance to broomrape races F and G has also been reported by several seed companies. A list of released lines resistant to race F from wild and cultivated origin is given in Table 2.

GENETICS OF SUNFLOWER RESISTANCE TO *Orobanche* AND STRATEGIES OF BREEDING FOR RESISTANCE

The host-parasite system of sunflower-*O. cumana* described for races A through E appears to follow the gene-for-gene model. Vrânceanu *et al.* (1980) established a set of five sunflower differentials carrying five dominant resistant genes, *Or1* through *Or5*, each providing resistance to a new race and also to the previous ones. Genetic studies carried out by other authors agreed with monogenic and dominant inheritance of resistance to sunflower broomrape (Pogorletsky and Geshele, 1976; Ish-Shalom-Gordon *et al.*, 1993; Sukno *et al.*, 1999), although two dominant genes (Dominguez, 1996b) and one recessive gene (Ramaiah, 1987) have also been reported. Genetic resistance to race F in the germplasm sources P-96 and KI-534, derived from cultivated sunflower, was found to be controlled by recessive alleles at two loci (Rodríguez-Ojeda *et al.*, 2001; Akhtouch *et al.*, 2002). These recessive genes also controlled resistance to race E in the case of KI-534 (Rodríguez-Ojeda *et al.*, 2001), while resistance to race E in P-96 was conferred by the dominant gene *Or5* (Pérez-Vich *et al.*, 2004b).

In contrast to the resistance derived from cultivated sources, the race F resistant population BR4, derived from wild species, was found to be under the control of a single dominant gene designated *Or6* (Pérez-Vich *et al.*, 2002). Pacureanu *et al.* (2004) reported also a single dominant gene controlling the resistance to race F in Romania. However, the results of the evaluation of crosses between different race F resistant lines and different susceptible parental lines have shown that dominance relationships and genetic control of broomrape resistance in sunflower is highly dependent on the race of broomrape, the source of resistance, and also the susceptible parental line used for the cross (Pérez-Vich *et al.*, 2004a). For example, F₁ hybrids segregating for resistance and deviations from the monogenic inheritance previously reported by Pérez-Vich *et al.* (2002) were observed in some crosses between the race F resistant line J1 and susceptible lines (Velasco *et al.*, 2006). This indicated incomplete dominance of the *Or6* alleles and the presence of a second gene, *Or7*, whose expression appeared to be environmentally dependent. Even though gene nomenclature *Or6* and *Or7* has been utilized in several different stud-

ies to designate genes that confer resistance to broomrape races superior to race E, no comparative research has been conducted and probably different loci/alleles are being reported by different authors under the same designation. A summary of different inheritance studies on broomrape resistance is given in Table 3.

Table 3: Inheritance of broomrape resistance in sunflower

Resistance source	Race tested	Gene	Gene action	References
Kruglik-A-41	A-E	<i>Or1</i>	Single, dominant	Vrânceanu <i>et al.</i> (1980)
Jdanov 8281	A-E	<i>Or2</i>	Single, dominant	Vrânceanu <i>et al.</i> (1980)
Record	A-E	<i>Or3</i>	Single, dominant	Vrânceanu <i>et al.</i> (1980)
S-1358	A-E	<i>Or4</i>	Single, dominant	Vrânceanu <i>et al.</i> (1980)
P-1380	A-E	<i>Or5</i>	Single, dominant	Vrânceanu <i>et al.</i> (1980)
SW501	Unknown	Unknown	Single, dominant	Ish-Shalom-Gordon <i>et al.</i> (1993)
NR-5	E	<i>Or5</i>	Single, dominant	Sukno <i>et al.</i> (1999)
R-41	E	Unknown	Two dominant genes	Dominguez (1996b)
P-96	F (Mencia) (Spain)	<i>or6, or7</i>	Two recessive genes	Akhtouch <i>et al.</i> (2002)
P-96	E	<i>Or5</i>	Single, dominant	Pérez-Vich <i>et al.</i> (2004b)
KI-534	E	<i>or6, or7</i> ¹	Two recessive genes	Rodríguez-Ojeda <i>et al.</i> (2001)
KI-534	F (EK23) (Spain)	<i>or6, or7</i>	Two recessive genes	Rodríguez-Ojeda <i>et al.</i> (2001)
J1 (BR-4)	F (Mencia) (Spain)	<i>Or6</i>	Single, dominant	Pérez-Vich <i>et al.</i> (2002)
LC-1093	F (Romania)	<i>Or6</i>	Single, dominant	Pacureanu <i>et al.</i> (2004)
J1 (BR-4)	F (Mencia) (Spain)	<i>Or6, Or7</i>	Two partially dominant genes	Velasco <i>et al.</i> (2006)

¹The nomenclature *Or6* and *Or7* has been utilized by several authors, although no comparative studies have been conducted to test whether they correspond to the same loci/alleles.

The development of broomrape resistant inbred lines is not an easy task, mainly because of the large difficulties to assess resistance in experimental conditions, where the existence of escapes, genetic background effects, and genotype x environment interactions lead to a sometimes inefficient selection. Molecular studies aimed to map genes conferring resistance to races E and F have been carried out. The *Or5* gene conferring resistance to race E has been mapped to a telomeric region of linkage group (LG) 3 of the sunflower genetic map (Lu *et al.*, 2000; Tang *et al.*, 2003; Pérez-Vich *et al.*, 2004b) (Figure 1). Quantitative trait loci (QTL) analyses showed that phenotypic variance for race E resistance was mainly explained by a major QTL, corresponding to the *Or5* gene, associated to the resistance or susceptibility character, whereas race F resistance was explained by several QTL with small to moderate effects, mainly associated with the number of broomrape stalks per plant (Pérez-Vich *et al.*, 2004b). These results suggested that resistance to broomrape in sunflower is controlled by a combination of a qualitative, race-specific resistance component affecting the presence or absence of broomrape, and a

quantitative, non-race specific resistance component affecting the number of broomrape stalks per plant.

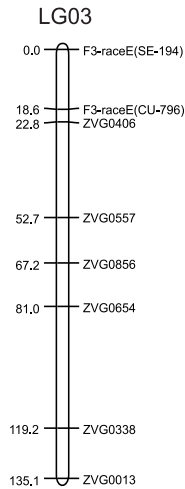


Figure 1: Molecular map of linkage group three of sunflower containing the scores for race E (populations SE-194 and CU-796) of broomrape in phenotypic evaluations of F_3 populations from the cross P-21 \times P-96 (Pérez-Vich et al., 2004b).

One important aspect in breeding for resistance to *Orobanche* is the study of the mechanisms involved in the resistance. As mentioned above, the use of resistant cultivars, usually monogenic in nature, has been followed by the occurrence of new, more virulent races of the parasite that overcome the existing sources of resistance. Therefore an effective breeding strategy to achieve a more effective and durable resistance seems to include a combination of several resistance mechanisms in one genotype. Several groups of mechanisms of resistance to *Orobanche* have been described (reviewed by Alonso, 1998):

- Deficient production of germination stimulants released by the roots of the host plant;
- Mechanical or chemical barriers preventing haustorium penetration of the host root (lignification or hypersensitive-like reaction);
- Accumulation of toxic compounds that slow down the growth of tubercles and the connection to the host vascular system.

Resistance mechanisms were proposed in early studies on resistance to sunflower broomrape. Resistance based on mechanical barriers was reported by Pustovoit (1966), who proposed that resistance was produced by the formation of a callus through swelling of the roots. The action of peroxidases excreted by the parasite was suggested to be involved in the lignification of host cells (Antonova, 1978). Differences in peroxidase production were suggested as an explanation of the different virulence of races A and B as well as an explanation of the gene-for-gene interaction in the sunflower *O. cernua/cumana* system (Antonova and Ter Borg, 1996). Different resistance mechanisms have been described for differential lines resistant to several races. For example, the mechanism of resistance of the cultivar Jdanov 8281, carrying the *Or2* gene, was reported to include a hypersensitive-like reaction

(Antonova and Ter Borg, 1996), while the accumulation of phenolic compounds in damaged cells and lignin formation in sunflower vessels were reported to be involved in the resistance controlled by the gene *Or3* (Tolmachev, 1991). More recently, Labrousse *et al.* (2001) and Echevarría-Zomeño *et al.* (2006) compared resistant and susceptible sunflower genotypes and identified several resistance mechanisms such as reduced stimulation of broomrape seed germination, suberization and protein cross-linking in the cell wall in contact with the parasite, and secretion of phenolic compounds that poisoned the parasite.

CONCLUSIONS AND FUTURE PROSPECTS

The rapid evolution of *O. cumana* populations leading to the occurrence of new virulent races requires a continuous search for new resistance sources. Results of evaluation of sunflower germplasm for resistance to different races have demonstrated that wild *Helianthus* species constitute the major source of resistance genes conferring resistance to new virulent races, but cultivated germplasms are also valuable sources of resistance. Most of the resistant sources have been found to be controlled by major genes (vertical resistance), although quantitative (horizontal) resistance has also been reported. Race-specific dominant genes are considered an ideal source of resistance for single-cross hybrid breeding by seed companies, because they only need to be incorporated into one of the parents. However, the combination of vertical and horizontal resistance mechanisms on the same genotype could contribute to the development of a more durable resistance. Molecular marker studies to identify QTL associated with broomrape resistance genes are increasingly contributing to clarification of the genetic control of broomrape resistance in sunflower, facilitating the pyramiding of different resistance genes, and speeding up the development of resistant inbred lines through marker-assisted selection.

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ACTUALIZACIÓN DE LA SITUACIÓN DE LA MEJORA GENÉTICA DE GIRASOL PARA RESISTENCIA AL JOPO

RESUMEN

El jopo de girasol (*Orobanche cumana* Wallr.) está considerado en la actualidad como uno de los problemas más importantes del cultivo de girasol (*Helianthus annuus* L.). En los últimos quince años, los esfuerzos realizados para incorporar fuentes de resistencia genética a este parásito en híbridos de girasol han estado acompañados por la rápida aparición de nuevas razas virulentas que superaban todos los genes de resistencia conocidos. Debido a esta situación, la mayoría de los esfuerzos de investigación se han centrado en el desarrollo y caracterización de nuevas fuentes de resistencia genética a las razas más virulentas del parásito, así como en la investigación de la estructura

genética y variabilidad de las poblaciones de *Orobanche cumana* y de su evolución, con el objetivo de desarrollar estrategias duraderas a largo plazo para el control del jopo de girasol. Los resultados de evaluación de germoplasma de girasol para resistencia a diferentes razas han demostrado que las especies silvestres de *Helianthus* constituyen la mayor fuente de genes de resistencia a las nuevas razas virulentas. El germoplasma cultivado es también una valiosa fuente de genes de resistencia. La mayoría de las fuentes de resistencia están controladas por genes mayores, pero tanto resistencia cuantitativa como efectos epistáticos han sido también identificados. Se han observado diferentes reacciones de dominancia dependiendo de la raza de jopo, la fuente de resistencia y la línea utilizada como parental susceptible. Estudios moleculares han mostrado que la varianza fenotípica para la raza E se explica principalmente por un QTL mayor asociado con la resistencia o susceptibilidad del carácter, mientras que la resistencia a la raza F estuvo controlada por varios QTL de efecto pequeño o moderado asociados principalmente con el número de jopos por planta, lo que sugiere la existencia de un componente cuantitativo en la resistencia a la raza F. Se discute la relevancia de estos resultados en la mejora para resistencia al jopo de girasol.

MISE À JOUR DES ACTIONS DE SÉLECTION POUR LA RÉSISTANCE À L'OROBANCHE DU TOURNESOL

RÉSUMÉ

L'orobanche du tournesol est couramment vue comme l'une des plus importantes contraintes de la production de tournesols. Ces 15 dernières années, des efforts pour introduire des sources génétiquement résistantes à ce parasite dans les hybrides de tournesol ont rapidement été suivis de l'apparition de nouvelles races virulentes qui sont venues à bout de tous les gènes de résistance connus. Au regard de cette situation, la majorité des efforts de recherche se sont concentrés sur le développement et la caractérisation de nouvelles sources de résistance génétique aux plus virulentes des races et aussi pour examiner la structure génétique et la variabilité des populations d'orobanches et leur évolution, afin de développer des stratégies à long terme, pour la gestion de l'orobanche du tournesol. Les résultats de l'évaluation de "germplasm" du tournesol pour la résistance aux diverses races a démontré que l'espèce sauvage d'*helianthus* constitue un le plus grand réservoir de gènes conférant une résistance aux nouvelles races virulentes. Les germplasms cultivés sont aussi une source valable de gènes résistants. La plupart des sources résistantes ont révélé être contrôlées par des gènes majeurs, bien que la résistance quantitative et les effets épistatiques aient été aussi reportés. Divers réactions de dominance, dépendant de la race d'*orobanche*, de la source de résistance, et de la susceptibilité de la lignée parentale utilisée pour le croisement ont été observées. Des études moléculaires ont montré que la variation du phénotype pour la résistance de la race E était principalement expliquée par une majeur QTL associée à la résistance ou au caractère susceptible, alors que la résistance de la race F était expliquée par divers QTL avec un effet de petit à modéré, principalement associé avec le nombre d'orobanche par plant, suggérant l'existence d'un composant en quantité dans la résistance à la race F. La pertinence de ces constatations pour les cultures de tournesol résistantes à l'orobanche est discutée.

