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# DOMINANCE RELATIONSHIPS FOR GENES CONFERRING RESISTANCE TO BROOMRAPE (*Orobanche cumana* Wallr.) IN SUNFLOWER

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SUMMARY

The holoparasitic angiosperm sunflower broomrape (*Orobanche cumana* Wallr.) is currently regarded as one of the most important constraints of sunflower production in many areas in Southern Europe and the Black Sea region. Breeding for resistance is considered to be the most effective and feasible method of controlling sunflower broomrape. Commercial hybrids cultivated in Spain carry the *Or1* to *Or5* genes that confer resistance to races A to E. However, a new race, designated F, has been identified. Germplasm with race F resistant genes derived from wild and cultivated sunflowers has been developed. Dominance reaction of these genes is an essential feature that determine the breeding method to produce race F resistant sunflower hybrids. Crosses between different sources of race F resistant lines, including those derived from wild and cultivated sunflower, and different susceptible parental lines were made. Allelic crosses between race F resistant lines, as well as crosses between race F resistant lines and race E resistant lines were also carried out. $F_1$ plants, $F_2$ plants, and their parental lines were evaluated for their disease reaction to race F or race E of broomrape. Different dominance reactions and inheritance mechanisms for broomrape resistance were observed. These depended on the race of broomrape, the source of race F resistance, and also the susceptible parental line used for the cross. The relevance of the results obtained for sunflower breeding for resistance to sunflower broomrape is discussed.

**Key words:** **sunflower, broomrape resistance, susceptible lines, resistance lines, genetic control of broomrape resistance**

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## INTRODUCTION

Sunflower broomrape (*Orobanche cumana* Wallr.) is a parasitic angiosperm, totally devoid of chlorophyll, that infects the roots of sunflower (*Helianthus annuus* L.) plants. This parasitic plant is regarded as one of the most important constraints on sunflower production in areas of eastern and southern Europe, the Middle East, Russia, Ukraine and China (Parker, 1994). Broomrape attacks are frequently severe and yield losses reach up to 50% (Domínguez, 1996a). Though several methods of control have been proposed, the most economical and effective means of controlling sunflower broomrape is the use of resistant cultivars.

Genetic resistance to broomrape has been introduced into sunflower cultivars from early sunflower breeding programs in the former USSR (Pustovoit, 1966). However, the widespread use of resistant cultivars has led to the appearance of new races of the parasite that overcome the resistance genes (Škorić, 1988), and a continuous need for new resistance sources. Races A to E of broomrape have been described (Alonso, 1998) and these can be identified using a set of sunflower differentials, each carrying a single dominant gene (*Or1* through *Or5*, respectively) (Vrânceanu et al., 1980). Although this monogenic and dominant inheritance of resistance to races A to E was found in most genetic studies (Pogorletsky and Geshele, 1976; Vrânceanu *et al.*, 1980; Ish-Shalom-Gordon, 1993; Sukno *et al.*, 1999), some reports pointed to a more complex inheritance of the trait, including two dominant genes (Domínguez, 1996b), one recessive gene (Ramaiah, 1987), or even double recessive epistasis (Kirichenko *et al.*, 1987).

In Spain, broomrape has been traditionally restricted to limited areas planted to the confectionary sunflower. From the early 1970's onwards, the parasite quickly spread to central and southern Spain, causing serious infections in oilseed cultivars. Racial studies in this country identified races overcoming *Or1*, *Or3*, and *Or4*, but not *Or2* and *Or5* (reviewed in Melero-Vara et al., 2000); subsequently, however, a rapid racial evolution took place, mainly in the south of Spain. Further racial studies have shown the presence of a new race, named race F, which overcomes all of the known resistance genes, including *Or2* and *Or5* (Alonso et al., 1996; Domínguez 1999). Resistance to this new race of broomrape has been found in both cultivated and wild sunflowers (Sukno et al., 1999; Fernández-Martínez et *al.* 2000; Jan *et al.* 2002; Fernández-Martínez *et al.*, 2003). For breeders to efficiently use the available sources of broomrape resistance to race F, it is necessary to determine the genetic control of resistance to this race and the relationship between this control and that for race E resistance. In this paper we describe the genetic studies carried out on different race F resistant lines to determine the dominance relationships for genes conferring resistance to race F of broomrape (*Orobanche cumana* Wallr.) and their relationship to those controlling race E resistance.

## MATERIALS AND METHODS

### Plant materials

The following plant materials used were:

1. **Lines resistant to race F of broomrape developed from cultivated germplasm**: P-96, R-96, and L-86 (Fernández-Martínez *et al.*, 2003), and ADV37017, which is a race F resistant line from the seed company ADVANTA.
2. **Lines resistant to race F of broomrape developed from wild germplasm**: J1 (Jan *et al.*, 2002; Pérez-Vich *et al.*, 2002).
3. **Susceptible lines**: P21, a genetic male sterile (GMS) line of sunflower highly susceptible to broomrape races E and F, R-5, which carries the resistance gene *Or5* (Sukno et al., 1999), and a set of 27 susceptible CMS lines from the seed company ADVANTA.

### Genetic studies

Crosses between the different lines used for the genetic studies were carried out. P-21 was used as female for crosses with P-96, R-96, and L-86. A set of 27 CMS susceptible lines from ADVANTA was also used as female for crosses with ADV37017. The $F_1$ together with both parents were planted and evaluated for broomrape resistance, and $F_2$ seeds were produced by self-pollinating the $F_1$ plants, as described by Akhtouch et al. (2002), and Pérez-Vich et al. (2002). $F_2$ plants were also evaluated for broomrape resistance and self-pollinated to produce $F_3$ seeds. The $F_3$ generation was evaluated when necessary. The same procedure was used for the allelic crosses and for crosses between P-96 and R-5, with the exception that crosses were achieved through the emasculation of florets of the female parent followed by pollination of their stigmas with pollen from the male parent.

### Broomrape populations

Race-E broomrape population used was SE-194, collected in southern Spain in 1994 (Sukno *et al.*, 1999), which was classified as race E by artificial inoculation on sunflower differentials carrying the resistance genes *Or1*, *Or4* and *Or5*. Race-F broomrape population was SE-296, collected in southern Spain in 1999 from broomrapes attacking cultivars which incorporated genes of resistance to race E. SE-296 was confirmed as resistant to race F by artificial inoculation on sunflower differentials carrying the resistance genes *Or1* and *Or5* (Akhtouch et al., 2002).

### Phenotypic evaluation for broomrape resistance

In all experiments, artificial inoculation was carried out by planting 2-day-old sunflower seedlings in small pots (7×7×8 cm) containing a mixture of sand and peat (1:1, v:v). Each pot (approximately 180 g of the mixture) was carefully mixed with 50 mg of broomrape seeds to obtain a homogeneously infested substrate. The plants were kept in a growth chamber for 15-20 days for incubation at 25şC/18şC (day/night) using a 14 h photoperiod. For growth chamber experiments, the plants were kept in the chamber until evaluation (40-45 days). For experiments in the greenhouse and mesh-cage, the plants were then transplanted to larger pots containing 3 l of fertilized and uninfected sand-silt-peat (2:1:1, v:v:v) soil mixture. For field experiments, the plants were transplanted into the field. Evaluation for broomrape resistance was made on mature plants, with the exception of the growth chamber experiments. Plants were uprooted and their root system carefully washed to observe any established broomrape nodules or stalks. These were indicative of susceptibility to broomrape, whereas those lacking these structures were considered resistant.

## RESULTS AND DISCUSSION

### Genetic studies and dominance relationships for broomrape resistance to race F

*Resistant lines derived from cultivated germplasm*

Selection and selfing within cultivated germplasm have produced sunflower lines that bred true for resistance to race F of broomrape. Some of these lines, P-96, R-96 and L-86, have been released (Fernández-Martínez et al., 2003). $F_1$ evaluation from crosses between these lines and the susceptible line P21 indicated that resistance to race F of broomrape was recessive, since all $F_1$ plants evaluated from these crosses were susceptible to this race of broomrape (Table 1) (Akhtouch et al., 2002). The $F_2$ generations from the crosses between the three resistant lines and P21 segregated mainly in a 1:15 (resistant : susceptible) ratio (Akhtouch *et al.*, 2002), which indicated that resistance to race F of broomrape is conditioned by two recessive genes. This hypothesis was confirmed by the 1:3 (resistant : susceptible) segregation in the backcrosses to the resistant parents (Akhtouch et al., 2002), and is in accordance with other studies carried out in other lines (Rodríguez-Ojeda et al., 2001). However, one third of the $F_2$ populations evaluated (four out of twelve) segregated for broomrape resistance following a 3: 13 ratio (resistant : susceptible), suggesting that dominant and recessive epistasis may also be involved in the genetic control of resistance to race F of broomrape.

All previous genetic studies were carried out using the same susceptible line (P21) for crossing. To determine if susceptible parental lines could carry some genes affecting resistance to race F of broomrape, as it occurs for other characters, crosses were made between the race F resistant line (ADV37017) and a set of 27 female susceptible lines. The $F_1$ from the 27 crosses was evaluated for resistance to race F under a controlled environment (growth chamber) (Table 1). The majority of the $F_1$ evaluated were susceptible (9 out of 27) or segregated with a greater proportion of susceptible plants (11 out of 27) (Table 1). The rest of the $F_1$ were completely resistant (3 out of 27) or segregated with a greater proportion of resistant plants (4 out of 27). Despite the $F_1$ reaction was in general susceptible, indicating a recessive nature of the resistance in the line ADV37017, the existence of segregation in some of the $F_1$ and completely resistant $F_1$ indicated that the susceptible line used for the crosses may also carry some genes contributing to broomrape resistance to race F, which in some of the susceptible lines may still be in the heterozygous state.

Table 1: Dominance relationships for the genes controlling broomrape resistance in sunflower through the evaluation of $F_1$ plants from crosses between resistant lines an a set of selected lines (lines for crossing).

| Resistant parental line | Line for crossing | Broomrape race | No of $F_1$ plants | |
|---|---|---|---|---|
| | | | Resistant | Susceptible |
| P-96 | P21 | F | 0 | 15 |
| R-96 | P21 | F | 0 | 20 |
| L-86 | P21 | F | 0 | 15 |
| ADV37017 | ADVCMS1 | F | 2 | 18 |
| ADV37017 | ADVCMS2 | F | 17 | 3 |
| ADV37017 | ADVCMS3 | F | 1 | 19 |
| ADV37017 | ADVCMS4 | F | 8 | 12 |
| ADV37017 | ADVCMS5 | F | 0 | 20 |
| ADV37017 | ADVCMS6 | F | 0 | 18 |
| ADV37017 | ADVCMS7 | F | 1 | 18 |
| ADV37017 | ADVCMS8 | F | 19 | 0 |
| ADV37017 | ADVCMS9 | F | 19 | 0 |
| ADV37017 | ADVCMS10 | F | 15 | 4 |
| ADV37017 | ADVCMS11 | F | 14 | 6 |
| ADV37017 | ADVCMS12 | F | 0 | 19 |
| ADV37017 | ADVCMS13 | F | 1 | 19 |
| ADV37017 | ADVCMS14 | F | 7 | 13 |
| ADV37017 | ADVCMS15 | F | 7 | 13 |
| ADV37017 | ADVCMS16 | F | 0 | 20 |
| ADV37017 | ADVCMS17 | F | 7 | 11 |
| ADV37017 | ADVCMS18 | F | 4 | 15 |
| ADV37017 | ADVCMS19 | F | 6 | 12 |
| ADV37017 | ADVCMS20 | F | 0 | 19 |
| ADV37017 | ADVCMS21 | F | 20 | 0 |
| ADV37017 | ADVCMS22 | F | 11 | 9 |
| ADV37017 | ADVCMS23 | F | 0 | 17 |
| ADV37017 | ADVCMS24 | F | 9 | 11 |
| ADV37017 | LC1093B | F | 0 | 20 |
| ADV37017 | ADV37015 | F | 0 | 20 |
| ADV37017 | ADV37014 | F | 0 | 20 |
| P-96 | R-96 | F | 15 | 0 |
| P-96 | L-86 | F | 9 | 0 |
| J1 (Spring-2001) | P21 | F | 15 | 0 |
| J1 (Summer-2001) | P21 | F | 10 | 0 |
| P-96 | P21 | E | 10 | 0 |
| P-96 | R-5 | F | 0 | 5 |
| P-96 | R-5 | E | 5 | 0 |

The fact that susceptible lines may carry genes that affect broomrape resistance was supported by differences in the degree of attack among susceptible lines observed in field evaluations for resistance to broomrape race F. The inbred line HA-89 showed an average number of broomrapes per plant of 4.5 in 17 susceptible plants which were evaluated in a field trial in the spring 2002. In the same field trial, the average number of broomrapes per plant was 20.0 for 29 susceptible plants from the inbred line HA-821, 25.5 for 14 plants from the R-5 line, and 29.3 for 20 plants from P21. Divergent selection for the number of broomrapes is currently being carried out in order to confirm these data.

Allelic crosses have been made between different sources of resistance derived from cultivated germplasm. Evaluation for race F resistance to broomrape in $F_1$ plants from crosses between the resistant lines P-96, R-96, and L-86 showed an $F_1$ resistant reaction (Table 1). A total of 600 $F_2$ plants from the P-96 × L-86 cross were evaluated in a 2003field trial, and all them gave also a resistant reaction to race F. These data indicated that the genetic control of broomrape resistance to race F in the P-96 and L-86 lines is similar. Whether these lines have identical alleles at the loci controlling resistance to race F or have additional recessive resistance alleles at these loci or at adjacent, very tightly linked loci should be determined in further studies, such as those carried out by Sukno et al. (1999), to distinguish different alleles conferring resistance to race E in different race E resistant lines.

*Resistant lines derived from wild germplasm*

Results of evaluation of sunflower germplasm for resistance to broomrape race F have shown that wild *Helianthus* species constitute a major source of resistance genes (Fernández-Martínez et al., 2000; Jan et al., 2000). Four germplam populations, BR1 to BR4, resistant to race F have been developed through interspecific hybridization of cultivated susceptible material with resistant perennial wild *Helianthus* species *H. divaricatus*, *H. maximiliani*, and *H. grossesserratus* (Jan et al., 2002). Genetic studies have been carried out in a resistant line derived from the population BR4 (J1) which was developed from a mixed-amphiploid resulting from the intercross between chromosomally doubled heads of *H. divaricatus* × P21, and *H. grossesserratus* × P21. For the genetic study, J1 was crossed with the susceptible line P21 (Pérez-Vich *et al.*, 2002). The $F_1$ plants from the P21 × J1 cross, evaluated in two different environments (spring 2001, and summer 2001), were always resistant (Table 1) (Pérez-Vich *et al.*, 2002). These results indicated a dominant gene action for resistance to race F of broomrape in J1. In addition, the segregation pattern of resistance to this race of broomrape observed in the $F_2$ generation from the P21 × J1 cross which fit a 3:1 (resistant: susceptible) ratio (Pérez-Vich *et al.*, 2002) indicated that resistance to race F broomrape in J1 is controlled by a single dominant gene. This was confirmed by the evaluation of the backcrosses to both parents (Pérez-Vich et al., 2002). In contrast to these results, recent field evaluations for race F resistance in the $F_1$ generation from crosses between resistant sources derived from the wild species *H. divaricatus* and *H. maximiliani* and the susceptible line P21 indicated that resistance to race F in these sources was recessive, since the evaluated $F_1$ plants exhibites a susceptible reaction.

**Comparative studies for resistance to broomrape races F and E**

Broomrape resistance to race E in the line P-96 was studied in the cross P21 × P-96. $F_1$ plants from this cross were resistant to race E of broomrape (Table 1), indicating that resistance to this race in P-96 is dominant. In addition, segregation for resistance to race E in the $F_3$ generation from the cross P21 × P-96 followed a 1:2:1 [resistant $F_3$ families (R) : segregating $F_3$ families (H) : susceptible $F_3$ families (S)] ratio (18R:32H:10S; $\chi^2$=2.4; $P$=0.30), which indicated that race E resistance was controlled by a single gene. Therefore, clear differences have been detected in the dominance relationships and the inheritance mechanisms of the genes controlling race E and race F resistance in the line P-96. While resistance to race E is dominant and controlled by a single gene, resistance to race F in the same line is recessive and determined by two genes. These results are in contrast to those of Rodríguez-Ojeda et al. (2001). These authors evaluated resistance to race E and to race F in the resistant line KI-374 from Koipesol Semillas in crosses between this line and HA300 (very susceptible to all races of broomrape) and found that resistance to both races was recessive and controlled by two genes.

In addition, crosses were also made between P-96 and the race E resistant line R-5, which carries the *Or5* gene conferring resistance to race E but not to race F, and evaluated for both race E and race F resistance. The $F_1$ from the P-96 × R-5 cross was susceptible to race F of broomrape (Table 1), while the $F_2$ generation from the same cross evaluated for the same race segregated following a 1:15 ratio (6 resistant $F_2$ plants: 83 susceptible $F_2$ plants; $\chi^2$=0.04; $P$=0.85). The P-96 × R-5 cross evaluated for race E showed no segregation. All $F_1$ plants (Table 1) and all $F_2$ plants (180 $F_2$ plants) from this cross were resistant to broomrape race E. These results suggest that genetic control of resistance to race E broomrape in the line P-96 is dominant, monogenic and determined by the *Or5* gene, and that the R-5 line does not carry any allele conferring resistance to race F. If *Or5* in the line P-96 is allelic to one of the genes conferring resistance to race F should be determined in further experiments.

These results are in contrast to the genetic studies carried out by Vrânceanu et al. (1980). These authors established a set of five sunflower differentials carrying five dominant resistance genes, *Or1* to *Or5*, each one giving resistance to a new race of broomrape but also to the previous race. We have shown that resistance to race F and the previous race (race E) does not follow this model in the line P-96. This line shows a dominant resistance to race E, conferred by the *Or5* gene, but resistance to race F is neither dominant nor monogenic. These results suggest that race E and race F resistance in the line P-96 might be controlled by different mechanisms.

## CONCLUSION

In conclusion, dominance relationships and genetic control of broomrape resistance in sunflower is highly dependent on the race of broomrape, source of resistance and also the susceptible parental line used for the cross. Therefore, breeding for broomrape resistance and hybrid production should take into consideration all these factors. Molecular marker studies that are currently being carried out for race F resistance and those already done for race E resistance (Lu et al., 1999; Lu et al., 2000; Tang et al., 2003) should clarify the mechanism of genetic control of broomrape resistance in sunflower and should constitute a powerful tool for the breeding of this trait. Research is also needed on testing methodology such as incubation procedures (amount of inoculum, temperature, moisture, etc.), correlation between artificial tests and evaluations under field conditions and determination of the resistance parameters (resistance or susceptibility versus number of broomrapes per plant).

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## RELACIONES DE DOMINACIÓN EN LOS GENES DE RESISTENCIA A JOPO DE GIRASOL (*Orobanche cumana* Wallr.) EN GIRASOL

RESUMEN

El jopo de girasol (*Orobanche cumana* Wallr.) es una planta angiosperma haloparásita considerada actualmente como uno de los mas importantes factores limitantes de la producción de girasol en muchas áreas del Sur de Europa y en la región del Mar Negro. La mejora genética para resistencia está considerada como el método más efectivo y factible de control del jopo. Los híbridos comerciales de girasol cultivados en España incorporan los genes *Or1* a *Or5* que confieren resistencia a las razas A a E. Sin embargo, una nueva raza, denominada raza F, ha sido identificada. Se ha desarrollado germoplasma que incorpora genes de resistencia a la raza F derivados de girasol cultivado y silvestre. La reacción de dominancia de estos genes es una característica esencial que determina el método de mejora para producir híbridos resistentes a la raza F. Se realizaron cruces entre líneas con distintas fuentes de resistencia a la raza F, incluyendo las derivadas de girasol cultivado y silvestre. Cruces alélicos entre líneas resistentes a la raza F, así como cruces entre líneas resistentes a la raza F y líneas resistentes a la raza E se llevaron también a cabo. Las plantas $F_1$ y $F_2$, y sus líneas parentales, fueron evaluadas para resistencia a las razas F y E de jopo. Se observaron diferentes reacciones de dominancia y mecanismos de herencia para resistencia a jopo, que dependieron de la raza de jopo, la fuente de resistencia a la raza F, y también de la línea parental susceptible utilizada en el cruce. Se discute la relevancia de los resultados obtenidos para la mejora de girasol para resistencia a jopo.

## RELATIONS DE DOMINANCE DES GENES CONCERNANT LA RÉSISTANCE DU TOURNESOL A L'OROBANCHE (*Orobanche cumana* Wallr.)

RESUME

Le parasite angiosperme orobanche (Orobanche cumana Wallr.) est considéré l'un des facteur le plus limité de la production de tournesol dans beaucoup de domaines de l'Europe du Sud et de la région de la Mer Noire. Le développement de résistance est considéré le moyen le plus efficace et faisable afin de réprimer l'orobanche chez le tournesol. Les hybrides commercialisés qui se cultivent en Espagne, porteurs du gène *Or1-Or5*, transmettent la résistance des races A-E de l'orobanche. Récemment une nouvelle race de ce pathogène est identifiée, désignée comme race F. Utilisant le tournesol cultivé et sauvage, un germe plasmique des gènes résistants à la race F est créé. La réaction de dominance chez ces gènes est l'une des caractéristiques essentielles qui détermine la méthode de développement des hybrides résistants à la race F. Les croisements entre les différentes sources de lignes résistantes à la race F. incluant les sources dérivées de tournesol cultivé et sauvage et de sensibles lignes différentes parentales, sont réalisés. Les croisements allélomorphes entre les lignes résistantes à la race F. et celles résistantes à la race E., sont effectués. La réaction vers la race F. ou race E. de l'orobanche chez les plantes des générations de $F_1$ et $F_2$ aussi bien chez leurs lignes parentales, est évaluée. Les différentes réactions dominantes et les mécanismes d'hérédité pour la résistance de l'orobanche sont examinées, dépendant de la race de l'orobanche, source résistante à la race F. et sensibilité de plantes parentales utilisées dans le croisement. Les résultats obtenus dans le développement de résistance du tournesol à l'orobanche sont considérablement discutés dans cette recherche.