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UPDATE ON SUNFLOWER BROOMRAPE SITUATION IN SPAIN: RACIAL STATUS AND SUNFLOWER BREEDING FOR RESISTANCE

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SUMMARY

A review of the racial situation of *Orobanche cumana* in Spain and of several studies on sunflower resistance to broomrape is presented. In the nineties, populations of *O.cumana* attacking sunflower crops in Spain have evolved first towards the increase in frequency of race B simultaneous to the decrease of race A. Later, race E has appeared with increasing frequency. However, the subsequent change to resistant hybrids carrying the *Or5* gene has prompted the recent appearance of a new race (race F) that overcomes this resistance gene, and is expanding mainly in southern Spain. Collections of cultivated P.I. accessions tested for resistance to races E or F indicated a low frequency of entries resistant or segregating for resistance. A low frequency of resistance was also observed in accessions of wild annual species. Among 18 species, only *H.agrestis* and *H.anomalus* showed full resistance to both races, whereas *H.debilis* ssp. *cucumerifolius* and *H.exilis* segregated. Lines breeding true for resistance, derived from *H.anomalus, H.exilis* and *H.debilis* have been produced. In contrast, inoculation of races E and F to wild perennials resulted in complete resistance in 74% of the species, and segregation for resistance to race F in 11%. The transference of resistance from wild perennial species into cultivated sunflower is, however, much more difficult than that of annuals. Embryo rescue and chromosome doubling techniques were often required. Although inheritance studies indicated dominance and one single gene involved in the resistance to races A and E in most crosses, two dominant genes, epistatic interactions and reversal in the dominance were observed in some cases.

Key words: ***Orobanche cumana*, wild sunflower, broomrape races, resistance**

INTRODUCTION

Orobanche cumana Wallr. is the most important parasitic angiosperm attacking sunflower *(Helianthus annuus* L.) crop in countries surrounding the Black Sea

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as well as in Central Europe, Spain and Israel (Alonso *et al.*, 1996; Bülbül *et al.*, 1991; Domínguez *et al.*, 1996a; Shindrova, 1994). Severe attacks are not uncommon and yield losses frequently reach 50% (Domínguez, 1996a). *O.cumana* is closely related to *O.cernua* Loefl. (Katzir *et al.*, 1996), in which *O.cumana* was included as a subspecies specific to *Compositae,* whereas *O.cernua* ssp. *cernua* is parasitic to solanaceous crops (Parker and Riches, 1993).

The attacks of *O.cumana* to sunflower crops in Spain seemed to be restricted to confectionery type cultivars until the late seventies, when oilseed cultivars begun to be slightly attacked in the areas where confectionery sunflower had been traditional (González-Torres *et al.*, 1982). A rapid spread of the pathogen, concomitant with increasing attacks to oilseed cultivars, was noticed during the last two decades of the 20th Century in Spain (Dominguez *et al.*, 1996a; Melero-Vara *et al.*, 1989; 1996).

Simultaneous to sunflower breeding in Russia to increase oil content, resistance to broomrape was introduced in oilseed cultivars mainly from the wild species *H.tuberosus* (Pustovoit, 1966). However, broomrape populations able to overcome resistance in these cultivars appeared soon, leading to the report of races A and B of the parasite in the thirties. After resistance to these races was discovered, it was incorporated into new sunflower cultivars, but races of higher virulence, that attacked these resistant cultivars, were determined in Eastern Europe (Škoriæ, 1988). Thus, race C appeared in the former USSR (Antonova, 1994) and also in Romania, where the resistant variety Record was developed, and races A-E were described (Vranceanu *et al.*, 1980). Sunflower differentials to these broomrape races were established (Kruglik A-41, Jdanov-8281, Record, S-1358, and P-1380-2) with one single dominant gene each *(Or1* to *Or5*, respectively), providing resistance to all the previous races of *O.cumana* (Vrânceanu *et al.*, 1986). These differentials have been widely used for racial determination of broomrape populations in several countries but, when used in Spain, some variation from the previous scheme was observed. Thus, broomrape populations that attacked cv. Record (resistant to races A-C) were not able to attack Jdanov-8281, considered resistant only to races A and B (Melero-Vara *et al.*, 1989).

Although some reports point to a complex inheritance of the resistance to *O.cumana* in sunflower (*e.g.*, Domínguez, 1996; Krokhin, 1983; Kirichenko *et al.*, 1987; Pustovoit, 1966; Saavedra del Río *et al.*, 1994b), monogenic dominant inheritance was found in most cases (Ish-Shalom-Gordon *et al.*, 1993; Pogorletsky and Geshele, 1976; Pustovoit, 1966; Sukno *et al.*, 1999; Vrânceanu *et al.*, 1986).

Racial status of *O.cumana* in Spain

The evaluation of 47 populations of sunflower broomrape collected in different areas in Spain from 1989 to 1996 was conducted by carrying out several experiments of inoculation of sunflower differentials. Inoculation method followed was a modification of that of Panchenko (1975). Pregerminated (incubated in humid chamber kept at 26-28°C for 2 days) seeds of the sunflower differentials used in Romania were placed in pots containing 250 g of a sand:silt (1:1, vol) mixture artificially infested with 25-50 mg of the broomrape seed. Ten pots with one plant each were used for every sunflower differential-broomrape population combination. These were incubated in a growth chamber at 20-26°C during 2 weeks, then transplanted to larger pots filled with uninfested soil mixture (peat:sand:silt, 2:1:1, vol) which were placed in a greenhouse for 2 additional months. Emerged broomrapes were recorded at 15-day intervals, and averages were calculated for the last record to determine whether the reaction was of susceptibility or resistance (less than 1 broomrape stalk per plant of sunflower).

Whereas most populations collected in 1989 were of very low virulence (only two out of eight were virulent to one or three of the differentials carrying resistance genes *Or1-Or3*), 77% of the 13 populations from 1990-91 attacked Kruglik A-41 (gene *Or1)* and Record (gene O*r3),* although Jdanov-8281 (gene *Or2)* and P-1380-2 (gene *Or5)* were fully resistant (Saavedra *et al.,* 1994a). In contrast, these two latter differentials were moderately infected, by one of the 14 broomrape populations tested in 1992-1993, whereas all of them overcame resistance genes *Or1* and *Or3*. The differentials carrying these genes were susceptible to the nine populations of *O.cumana* collected in 1994, whereas 7, 5 and 4 of them were able to attack differentials with resistance genes *Or4, Or5,* and *Or2,* respectively (Melero-Vara *et al.*, 1996). Six of the most virulent populations of broomrape collected in 1993-1996 were shown to attack Kruglik A-41, and two of them (CU494 and SE296) also overcame resistance genes *Or2* and *Or5* (Table 1) and were designated as race F. Only two out of the nine sunflower lines used in this experiment, *i.e*., JD-6 and W-14, showed full resistance to the six broomrape populations tested, and two other lines (JM-1 and R-41) were resistant to all the nine populations of *O.cumana* except to SE296 (Table 1; Sukno *et al.,* 1999).

Table 1: Reaction of nine lines of sunflower to six populations of *O.cumana* from different origins

Sunflower line	Broomrape population											
	Central Spain						Southern Spain					
	CU194		CU494		CU996		SE194		SE295		SE296	
KA-41	4.4	S	8.5	S	1.6	S	8.1	S	0.6	S	3.9	S
J-8281	0.3	L	0.8	M	0.4	L	0.0	R	0.4	R	8.6	S
P-1380-2	0.0	R	0.8	M	0.6	M	0.0	R	0.0	R	8.3	S
S-25	0.4	L	0.4	L	1.5	S	0.0	R	0.0	R	8.2	S
HB	1.3	S	4.5	S	3.9	S	0.0	R	0.0	R	6.5	S
JM-1	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
W-14	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	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

Sukno *et al.* (1999)

Race E and, more recently, race F have been detected both in southern and central Spain. Broomrape populations belonging to race B seem to have substituted those of race A in southern Spain during the first half of this decade. This increase in virulence has been recently followed by a moderate decrease in the frequency of race B, which was simultaneous to an increase in the frequency of the populations belonging to races E and F. During the last ten years, *O.cumana* races B and F seem to have increased their frequencies in central Spain while race A decreased (Melero-Vara, 1997).

The application of PCR techniques to the characterization of *Orobanche* was successful in obtaining reproducible and unique RAPD profiles that allow the discrimination among different *Orobanche* species (Katzir *et al.*, 1996). However, one attempt to characterize races of *O.cumana* using RAPD analysis failed, since it was not possible to find molecular markers that discriminate DNA from populations of sunflower broomrape. Polymorphic bands were obtained with some random primers, but these were unrelated to the virulence of the parasite (Melero-Vara *et al.*, 1996). Recent molecular studies conducted with eight populations of *O.cumana* from several European countries showed a reduced intrapopulation genetic variability in a Spanish broomrape population of race E, as compared with the other populations tested (Gagne *et al.*, 1998).

Table 2: Origin and resistance of USDA breeding lines artificially inoculated with *Orobanche cumana* (race E)

Number of lines	Origin	Host reaction
3	RHA 274 x Exp. hybrids	Segregating
2	RHA 801 x Odessa hybrids	Resistant
3	RHA 801 x Odessa hybrids	Segregating
2	RHA 274 x Turbo hybrids	Resistant
5	RHA 274 x Turbo hybrids	Segregating
2	RHA 801 x RO-12-27 (Romanian hybrid)	Segregating
4	RHA 274 x Edirne 87 (Turkish hybrid)	Resistant
10	RHA 274 x Edirne 87 (Turkish hybrid)	Segregating

Adapted from Domínguez *et al*. (1996), Plant Breeding **115**: 201-202

Screening for resistance to broomrape

Sources of resistance to race E of *O.cumana* within cultivated material are not frequent. Only eight resistant and 33 segregating entries were found among a total of 160 USDA breeding lines of different origins which were artificially inoculated with one population (CU 192) of race E (Table 2; Domínguez *et al.*, 1996b). Only ten out of 240 P.I. accessions similarly evaluated, segregated for resistance, the rest being susceptible to race E (Table 3; Domínguez *et al.*, 1996b). No resistance was found in a set of 29 lines from Morden, Canada. The resistant entries traced back to Russian, Romanian and Turkish origins. Besides, four out of 55 cultivated accessions inoculated with one population (SE296) race F, were resistant and 11 segregated for resistance (Fernández-Martínez *et al.*, in press).

Table 3: Identification of USDA P.I. accessions segregating for resistance to *Orobanche cumana* (race E)

P.I. number	Origin	USDA germplasm description
265102	USSR	Armavirsky; No. 9345
287182	Chile	Peredovik
297481	France	V8931 MN 48% Oil; V8931
307935	USSR	Donsky; Col. No. 944
340784	USSR	USSR Mayak 66; A-1132
372255	USSR	Luch
430538	USSR	Novinka
431514	Romania	
431538	Romania	
497249	USSR	VIR 130

Adapted from Domínguez *et al.* (1996), Plant Breeding **115**: 201-202

Gulya *et al.* (1994) also reported a reduced frequency of entries resistant to a highly virulent population of *O.cumana* in an infested field in Turkey. Only 22 entries were found resistant out of the 903 accessions tested. Under broomrape natural infection, the evaluation of sunflower hybrids in Romania showed five Romanian hybrids, including Turbo and Favorit, to be resistant. In addition, five other hybrids from France, The Netherlands, Turkey and Ukraine were resistant in an artificial infestation test (Vrânceanu and Pacureanu, 1995).

In contrast, resistance to broomrape has been much more frequent in collections of wild *Helianthus* ssp. Different sources of resistance have been reported in several countries (Pogorletsky & Geshele, 1976; Korell *et al.*, 1996; Christov *et al.*, 1996; Škoriæ, 1992).

Studies of artificial inoculation with three Spanish populations of race E showed that three out of 18 wild annual species of *Helianthus* (*i.e.*, *H.agrestis*, *H.anomalus* and *H.exilis*), were resistant (Ruso *et al.*, 1996). In addition, the evaluation of these three species as well as *H.debilis* ssp. *cucumerifolius*, against one broomrape population of race F resulted in complete resistance in *H.agrestis* and *H.anomalus*, whereas the two other species segregated for resistance (Fernández-Martínez *et al.*, in press). Also, 27 wild perennials were inoculated with race E (Ruso *et al.*, 1996), and 50 accessions of 27 wild perennials (23 in common with the previous test) were artificially inoculated with one broomrape population (SE296) of race F. Resistance to both races was shown in 23 of these species (*i.e.*, *H.californicus, H.ciliaris, H.decapetalus, H.divaricatus, H.glaucophyllus, H.gracilentus, H.grosseserratus, H.hirsutus, H.x laetiflorus, H.laevigatus, H.maximiliani, H.mollis, H.nuttallii* ssp. *nuttallii, H.occidentalis* ssp. *occidentalis* and *plantagineus, H.pauciflorus* ssp. *pauciflorus,* and *subrhomboideus, H.pumilus, H.resinosus, H.salicifolius, H.smithii, H.strumosus* and *H.tuberosus),* although most of the entries of *H.maximiliani,* two of *H.divaricatus* and one of *H.pauciflorus* ssp. *pauciflorus* segregated for resistance to race F (Ruso *et al.,* 1996; Fernandez-Martinez *et al.,* in press). In addition, four species (*i.e.*, *H.cusickii, H.eggertii, H.nuttallii* ssp. *parishii,* and *H.simulans*) not tested for race F, were resistant to race E (Ruso *et al.,* 1996). Likewise, four other species not tested for race E (*i.e.*, *H.atrorubens, H.giganteus, H.microcephalus,* and *H.nuttallii* ssp. *rydbergii),* showed resistant to race E (Fernández-Martínez *et al.,* in press). These results indicate the very high frequency of resistance in perennial wild species of *Helianthus,* which contrasts with the scarcity of resistance in wild annuals and in cultivated material.

Transfer of resistance from wild to the cultivated material

Although the resistance found in annual wild sunflower species may be easily transferred to cultivated material, the transference is much more complex in the case of perennials due to interspecific incompatibility, postzygotic abortion of the hybrids and to their sterility, thus rendering this resistance unexploited.

However, cultivated germplasm with resistance to *O.cumana* transferred from wild species has been obtained in the former USSR using *H.maximiliani, H.mollis, H.pauciflorus* and *H.divaricatus* (Pogorletsky and Geshele, 1976), and more recently in Yugoslavia, using *H.glaucophyllus, H.resinosus* and *H.debilis* (Škorić, 1992), and in Bulgaria using *H.pauciflorus, H.decapetalus, H.tuberosus* and *H.argophyllus* (Christov *et al.,* 1996).

A breeding program to transfer *O.cumana* resistance from wild resistant species to cultivated sunflower has been carried out since 1994 at the Institute of Sustainable Agriculture, Cordoba, Spain, in collaboration with USDA-ARS, Fargo, North Dakota, USA, where the most difficult interspecific hybrids with perennial species were produced. Three annual and six perennial species, with three ploidy levels: diploids (2n=34), tetraploids (2n=68) and hexaploids (2n=102), showing resistance to race E, were used (Sukno *et al.*, 1998). Special techniques such as embryo rescue to overcome abortion of F_1 hybrids, and chromosome doubling to improve the fertility of interspecific hybrids (Jan, 1997) were applied.

For the annual species (2n=34), no special techniques were required. BC_1F_1 resistant plants (cultivated x wild) x cultivated were selected and selfed during several generations to obtain BC_1F_4 lines, derived from *H.anomalus* and *H.exilis,* breeding true for resistance to races E and F, and BC_1F_1 resistant plants of the cross (cultivated x *H.debilis)* x cultivated.

For wild perennial species, interspecific hybrids and backcross generations of *H.giganteus* (2n=34), *H.laevigatus* (2n=102), *H.nuttallii* ssp. *nuttallii* (2n=34), *H.pauciflorus (*syn. *H.rigidus)* (2n=102) and *H.resinosus* (2n=102) were obtained and tested for broomrape resistance (Sukno *et al.,* 1998). Plants of the BC_1F_1 of all the species used and the BC_2F_1 of *H.nuttallii* showed segregation for resistant plants, indicating that the transfer of resistance to *Orobanche* is feasible. In the case of *H.giganteus* and *H.nuttallii* resistant plants with 34 chromosomes were obtained. For the hexaploid perennial resistant BC_1F_1, plants with 51 chromosomes were recovered, which are being backcrossed to cultivated lines to recover resistant plants with 34 chromosomes.

Inheritance studies

Early breeding of sunflower for broomrape resistance consisted of the selection of open pollinated varieties. Thus, Russian varieties such as Kruglik A-41, Saratowski 169 and Fuxinka-3 were released with resistance to race A in 1930. The appearance of race B a few years later prompted the development of new varieties resistant to these two races of broomrape (Jdanov 8281, Jdanov 8885). Later, after World War II, VNIIMK and Armavirski groups of varieties, as well as Peredovik and Smena, were also released in the USSR. When a new race of broomrape, race C, appeared on VNIIMK8931 and other varieties, the Romanian variety Record was developed.

The discovery in sunflower of cytoplasmic male sterility and fertility restoration in the early seventies allowed the development of hybrid cultivars. Consequently, breeding for resistance to broomrape was carried out by the selection of inbred lines of sunflower resistant to the new races of *O.cumana*. Thus, resistant lines S-1358 and O-7586 were selected to control race D of the parasite and lines P-1380-2 and LC-1093 were selected for resistance to race E in Romania (Vranceanu *et al.*, 1980). The resistant reactions to races A-E paralleled the simple major genes *Or1-Or5*, which are dominantly inherited and are effective against not only the corresponding race but also to the older ones. However, allelic relationships between these genes were not determined and, therefore, it remained to establish whether genes *Or1-Or5* were in the same locus or independently inherited (Vranceanu *et al.*, 1986).

Studying resistance to race B of *O.cumana* in the USSR, Krokhin (1983) concluded that two complementary genes were involved in this resistance. Using different races of broomrape, a study on the inheritance of resistance showed dominance in most cases, but in one cross resistant x susceptible (X502 x X1005) the segregations in the generations obtained suggested double recessive epistatic inheritance (Kirichenko *et al.*, 1987). Furthermore, epistatic interactions and a reversal in the dominance was the best explanation for the segregations observed in the F_2 and BC_1F_1 generations of several crosses of different susceptible lines (AD-66, S-59) with the same resistant source (J-8281) inoculated with race A of *O.cumana*. However, in many other crosses, monogenic dominance inheritance was shown (Saavedra *et al.*, 1994b). In a study of inheritance of broomrape resistance in Israel, Ish-Shalom-Gordon *et al.* (1993) concluded that one single dominant gene was responsible for the resistance carried in oil type lines SW-50l and RW-637 when they were crossed to the respectively ornamental and confectionery type susceptible cultivars Aya and DI-1. Another study on the inheritance of resistance to race E of *O.cumana*, conducted in Spain, indicated that two dominant independent genes occurred in the restorer oil type line R-41 when the cross with susceptible HA89 was studied (Domínguez, 1996b).

Recently, also using a population belonging to race E from Spain (Sukno *et al.*, 1999), the resistance in six sunflower inbred lines (*i.e.*, JM-l, JD-6, T-2, HB, R-5, and W-14) was determined as monogenic dominant, since F_2 and BC_1F_1 generations of crosses of these with a susceptible line (HA89 or S59) segregated 3:1 and 1:1, respectively. The allelism tests indicated that the same gene was present in all these resistant lines since the F_2 and BC_1F_1 generations of crosses between them did not segregate for resistance. However, they observed that lines JD-6 and W-14 were also resistant to race F, suggesting that resistance to this race could be conferred by additional alleles at the *Or* locus or by a cluster of very tightly linked non-allelic genes.

Molecular markers could facilitate the transfer of resistance genes between sunflower inbred lines by means of marker-assisted selection techniques. In this context, a recent work on bulked segregant analysis of two F_2 populations of crosses susceptible x resistant sunflower lines was conducted to generate five SCAR markers. These, along with one RAPD marker identified, were significantly linked to the *Or5* gene, and allowed to define a consensus molecular linkage map of 61.9 cM that contains that gene of resistance to race E of *O.cumana*. This map would possibly test the hypothesis of clustering of genes for broomrape resistance in sunflower (Lu *et al.*, in press).

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ACTUALIZACIÓN DE LA SITUACION DEL JOPO DE GIRASOL EN ESPAÑA: STATUS RACIAL Y MEJORA DEL GIRASOL PARA RESISTENCIA

RESUMEN

Se presenta una revisión de la situación racial de *Orobanche cumana* en España y de estudios de resistencia de girasol a jopo. Durante los 90, las poblaciones de *O.cumana* que atacan girasol han evolucionado primero a incrementar la frecuencia de la raza B, mientras que disminuye la de la raza A, y más tarde a la aparición e incremento de frecuencia de la raza E. El consiguiente cambio varietal a híbridos con el gen de resistencia *Or5* ha facilitado la aparición de una nueva raza (designada raza F) que supera este gen, y se está expandiendo principalmente en Andalucía (sur de España). Las evaluaciones de colecciones de accesiones (P.I.) cultivadas para resistencia a las razas E y F de jopo han indicado una baja proporción de entradas resistentes o que segregan por resistencia. También se observó una baja frecuencia de resistencia en las especies anuales silvestres. De 18 especies evaluadas, sólo *H.agrestis* y *H.anomalus* mostraron completa resistencia a las razas E y F de jopo, mientras que hubo segregación para resistencia en *H.debilis* ssp. c*ucumerifolius* y *H.exilis*. Por el contrario, las inoculaciones de especies silvestres perennes con dichas razas de *O.cumana* mostraron resistencia completa en el 74% de las especies, en tanto que 11% segregaron por resistencia a raza F. Se han producido líneas de mejora derivadas de *H.anomalus, H.exilis* y *H.debilis*. La transferencia al girasol cultivado de la resistencia proveniente de especies perennes es, sin embargo, mucho más difícil, requiriéndose con frecuencia técnicas de rescate de embriones y duplicación cromosómica. Aunque en la mayoría de los cruces se observó herencia monogénica dominante para la resistencia a las razas A y E, se observaron dos genes dominantes, interacciones epistáticas y reversión de dominancia en algunos casos.

SITUATION DE L'OROBANCHE ET DU TOURNESOL EN ESPAGNE: RACES ET SÉLECTION POUR LA RÉSISTANCE

RÉSUMÉ

Cet article propose un examen de la situation des races d'*Orobanche cumana* en Espagne ainsi qu'une revue des études qui ont été faites sur la résistance à l'orobanche. Au cours des années quatre-vingt-dix du siècle dernier, les populations *O.cumana* qui ont attaqué le tournesol en Espagne ont d'abord montré une tendance à l'augmentation de la fréquence de la race B et à la diminution de la race A. Plus tard, on a pu constater une augmentation de la fréquence d'apparition de la race E. Cependant, le passage à des hybrides résistants contenant le gène Or_5 a provoqué l'apparition d'une nouvelle race (race F) que ce gène de résistance ne contrôle pas. La nouvelle race s'étend surtout dans les régions méridionales de l'Espagne. Des examens de collections de tournesol de culture pour leur tolérance aux races E ou F ont démontré qu'il existe une fréquence peu élevée de sortes résistantes ou qui se divisent pour la résistance. Une fréquence peu élevée de matériel résistant a aussi été remarquée dans les collections d'espèces sauvages annuelles. Parmi 18 espèces, seules les espèces *H.agrestis* et *H.anomalus* ont montré une résistance totale aux deux races de parasites, alors que les espèces *H. debilis* ssp. *cucumerifolius* et *H.exilis* se divisaient pour la résistance. Les lignes avec résistance véritable étaient dérivées des espèces *H.anomalus, H.exilis* et *H.debilis*. Au contraire, l'infection artificielle des espèces sauvages vivaces par les races E et F ont démontré que 74% des espèces possédaient une résistance totale alors que pour 11% des espèces, on arrivait à une division pour la résistance à la race F. Il est beaucoup plus difficile d'implanter la résistance des espèces sauvages vivaces dans le tournesol de culture que dans les espèces annuelles. Il est souvent nécessaire d'avoir recours aux techniques de préservation des embryons et de duplication des chromosomes. Bien que les études sur l'hérédité aient démontré que la domination et un gène déterminaient la résistance aux races A et E dans la plupart des croisements, dans certains cas, on a pu remarquer deux gènes dominants, des interactions épistasies et reversal in the dominance.