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SUNFLOWER BREEDING FOR RESISTANCE TO BROOMRAPE (*OROBANCHE CUMANA* WALLR.)

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ABSTRACT

The parasitic angiosperm broomrape (*Orobanche cumana* Wallr) causes economic damage in sunflower production in a number of countries around the world, but especially in Central and Eastern Europe, Spain, Turkey, Israel, Iran, Kazakhstan, and China. For almost a century, there has been a constant tug-of-war between sunflower breeders and *Orobanche cumana*, with frequent changes in which side has the upper hand. Almost as soon as the breeders find a source of resistance to the latest race of the pathogen, broomrape responds by evolving another virulent race. Sunflower selection for broomrape resistance makes use of different methods for testing breeding materials (in the field, greenhouse, or at the molecular level), looks for resistance sources in certain wild species of the genus *Helianthus*, and has so far produced significant results. Dominant genes for resistance to races A, B, C, D, E, and F have been found and incorporated into cultivated sunflower genotypes.

In the last two to three years, however, new broomrape populations have been discovered in several different countries (two each in Romania, Russia and Turkey, one in Spain, and most likely another one in Ukraine). None of the existing commercial hybrids resistant to races A, B, C, D, E, and F have proven resistant to these new populations of the pathogen. Fortunately, greenhouse testing conducted by the Fundulea Institute in Romania in 2009 has managed to identify two restorer lines that are resistant to all the new populations and can be used directly in developing hybrids.

Sunflower breeders and geneticists have achieved significant results in the use of molecular markers for identifying new broomrape races (A-F). Marker-assisted selection should be used even more in the future search for *Orobanche* resistance.

Broomrape can also be managed by the development of IMI-resistant hybrids or by using biological control measures. In parallel with the search for broomrape resistance genes, efforts should be made to alter the anatomy of plant organs as well as biochemical parameters (mechanical barriers, germination inhibitors, phytoalexins etc).

To speed up the progress of sunflower breeding for resistance to Orobanche, there should be a greater level of collaboration between the breeders from public institutions and private companies.

Key words: breeding, broomrape, molecular markers, races, resistance , sunflower.

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INTRODUCTION

Broomrape (*Orobanche cumana* Wallr. = *Orobanche cernua* Loelf.) is a parasitic angiosperm that has been causing a great deal of damage to sunflower production for more than a century. According to Morozov (1947), the first reports of broomrape in sunflower came from Saratov Oblast in Russia and date back to the 1890s. The same author mentions that the first sunflower varieties resistant to race A of *Orobanche* were developed by Plachek (1918) at the Saratov breeding station. Morozov (1947) and Pustovoit (1966) both note that Ždanov (1926) identified a new broomrape race (B) in Rostov Oblast and soon after the discovery developed a number of sunflower varieties resistant to it. In the period that followed, according to Pustovoit (1966), a number of high-oil varieties resistant to race B were developed at the VNIIMK institute in Krasnodar, Russia that thereafter played an important role in the spread of sunflower around the world. Later on, a new race that could not be controlled by the genes for resistance to races A and B was discovered in Moldova by Sharova (1968) and in Bulgaria by Petrov (1970). Through genetic research, Vrânceanu et al. (1980) established that there were five broomrape races in Romania and identified dominant genes controlling resistance to them. Alonso et al. (1996) found a new, virulent race (F) of the pathogen in 1996 in Spain. Papers by Alonso et al. (1996), Škorić and Jocić (2005) and Fernandez-Martinez et al. (2007) each provide a detailed overview of the achievements of sunflower breeding for resistance to *Orobanche*.

Extensive research on broomrape resistance has been conducted in countries of the former USSR as well as in Romania, Bulgaria, Turkey, and Spain. In all these countries, broomrape causes great damage to sunflower production and new races of the pathogen appear frequently. In addition to Russia, Ukraine, Romania, Bulgaria, Turkey, and Spain, broomrape is also present in Serbia, Hungary, Moldova, Greece, Israel, Iran, Kazakhstan, China, Mongolia, and Australia, and possibly in a few other countries as well. Sunflower breeders and geneticists have been trying to develop genotypes resistant to all known races of the parasite.

The objective of this paper was to make an overview of what has been achieved in sunflower breeding for *Orobanche* resistance so far and to describe the sources and genetics of this resistance as well as the breeding methods and directions employed in the field.

SOURCES OF BROOMRAPE RESISTANCE

Genes for resistance to broomrape races A, B, C, and D are present in varietal populations of sunflower developed in breeding programs from Krasnodar, Armavir, Odessa, Fundulea and several other places. Genes that confer resistance to races E, F, G and the latest ones, on the other hand, have been identified in certain wild species of the genus *Helianthus* and have been incorpora-

ted into cultivated sunflower genotypes by interspecific hybridization. A species of wild sunflower (*Helianthus tuberosus*) was first used as a source of *Orobanche* resistance by Ždanov in the 1930s (Morozov, 1947). Later on, Galina Pustovoit (1975) and her team made a great contribution in this area by developing sunflower varieties through interspecific hybridization in which *H. tuberosus* was used as the donor of *Or* genes. These varieties were used in the identification of Or_5 and Or_6 genes. Confirmation of this can be found in a study by Venkov and Shindrova (2000), who over a 10-year period tested six of Galina Pustovoit's sunflower cultivars for resistance to broomrape races present in different parts of Bulgaria. The study's findings showed that the Russian varieties Progress and Oktobar, the Bulgarian variety Vega, and the Romanian hybrid Sorem 80 all had stable resistance to the latest races of *Orobanche* (D + E) found in Bulgaria at the time.

In more recent times, a number of authors have used wild *Helianthus* species in their search for resistance to broomrape. Thus, Ruso et al. (1996) tested wild sunflower species for resistance to three virulent races of *Orobanche* and determined that most of the perennial species examined were immune to the three races. Furthermore, some of the annual wild species and lines obtained by interspecific hybridization were resistant as well. Sukno et al. (1998) crossed several wild species (*H. resinosus*, *H. pauciflorus*, *H. laevigatus*, *H. nuttallii* ssp. *nuttallii*, *H. giganteus* etc.) of sunflower with cultivated sunflower genotypes and obtained plants of the F_1 and BC_1F_1 generation as well as some BC_2F_1s. The wild species and interspecific hybrids all proved resistant to broomrape infestation except for the species *H. nuttallii*, in which segregation occurred, indicating that the resistance was dominant.

Jan et al. (2000) describes the procedure for and the results of transferring genes for resistance to broomrape from perennial wild sunflower species into cultivated sunflower genotypes. Three Spanish populations of *Orobanche cumana* Wallr. were involved. The results of the study showed that two of them could be controlled by the Or_5 gene, while the third was the virulent race F.

Fernandez-Martinez et al. (2000) tested 54 wild sunflower accessions (representing 27 perennial and four annual species) and 55 cultivated sunflower accessions, which they raised in a growth chamber and then transplanted to a greenhouse. The material was inoculated with the virulent race F (population SE 296). Most of the perennial species proved fully resistant to race F. The only exceptions were some populations of four of the wild perennials, which had a certain percentage of susceptible plants. Among the wild annual species, *H. anomalus* and *H. agrestis* were completely resistant, while *H. debilis* ssp. *cucumerifolius* and *H. exilis* segregated with regard to *Orobanche* resistance.

Jan and Fernandez-Martinez (2002) employed interspecific hybridization to incorporate genes for resistance to race F from several wild species into cultivated sunflower. Where necessary, they used embryo culture and chromosomal doubling by colchicine in order to bypass the barriers and enable the

transfer of desirable genes. The newly developed genotypes had resistance to race F, which was controlled by a single dominant gene.

An overview of how races of broomrape progressed from race A to F in Spain over time can be found in Melero-Vara et al. (2000). Cultivated sunflower genotypes were found to have a low frequency of genes controlling races E and F, while of the 18 annual species studied, only *H. agrestis* and *H. anomalus* exhibited full resistance. Among the wild perennials involved in the study, 74% of the species were fully resistant to races E and F, while 11% showed segregation concerning resistance to race F. Genetic analysis showed that resistance to races A through E is by and large controlled by a single dominant gene. In some cases, two dominant genes, epistatic interaction, and reversal in the dominance were observed.

Jan et al. (2002) crossed the wild sunflower species *H. maximilianii* Schrad, *H. grosseserratus* Mart., and *H. divaricatus* L. with cultivated sunflower and developed four populations (BR1-BR4) resistant to race F in Spain.

According to Fernandez-Martinez et al. (2007), research on the resistance of sunflower germplasm to different broomrape races has shown that wild *Helianthus* species are the main source of resistance to the new, virulent races of the pathogen. Still, cultivated sunflower genotypes, especially those developed by interspecific hybridization, cannot be completely disregarded as a source of genes for broomrape resistance. The use of molecular markers should also provide further clarification of the genetic control of broomrape resistance in sunflower.

Christov et al. (1992, 1998, 2009) have achieved outstanding results in identifying genes for broomrape resistance in the wild species of the genus *Helianthus* and incorporating them into cultivated sunflower genotypes. Especially important are the findings reported in Christov et al. (2009), which concern the detection of *Or* genes in 11 perennial wild sunflower species and their incorporation into elite cultivated sunflower lines by means of interspecific hybridization.

Sources of *Orobanche* resistance can also be found by the use of induced mutations. Venkov and Shindrova (1998) reported that they obtained a mutant with partial resistance to *Orobanche cumana* Wallr. using a 0.4% solution of the mutagen nitrosomethylurea.

METHODS USED FOR EVALUATING BROOMRAPE RESISTANCE IN BREEDING PROGRAMS

In order to attain their breeding goals and identify sources of broomrape resistance, sunflower breeders must develop a breeding strategy, decide on a breeding method, secure the necessary germplasm and differential lines for broomrape race identification, and choose the appropriate inoculation method and molecular marker technique (MAS). To ensure the success of the program, the best way to go is to pick out an elite line and cross it with a source of *Or*

genes, which should then be incorporated into the breeding material using certain techniques in order to create new genetic variability. At the start of the program, the breeder must determine which race or races are present in the region for which the hybrids are being developed. A set of differential lines for races A, B, C, D, and E has been provided by Vrânceanu et al. (1980), while Păcureanu-Joița et al. (1998) have identified such a line for race F. As of yet, there are no differential lines for the new, virulent races of this pathogen that have appeared in the last few years. Developing a set of such lines would be desirable.

In the years in which races A through E were discovered, sunflower breeders tested their breeding materials in the field, usually on plots that had been severely infested by broomrape the year before. This method is still employed by some breeders. However, this approach does not always produce reliable results due to the influence of environmental factors and an inadequate amount of broomrape seeds in the soil. In an effort to avoid this, breeders resorted to collecting broomrape seeds and incorporating them into the hills in which sunflower seeds were placed at planting. This method too, however, is prone to producing experimental errors, caused primarily by the effects of environmental factors. Much more accurate results can be obtained by putting broomrape seeds into containers filled with a pre-prepared medium (soil + some other substances), which are then placed in the controlled environment of a growth chamber or greenhouse. Panchenko (1975) developed a screening method for assessing resistance to broomrape in greenhouse conditions during autumn and winter. This method was further honed by Grezes-Besset (Rustica Prograin Genetique), who made testing using plastic test tubes part of the procedure. The advantage of this technique is that it provides a higher level of reliability and makes it possible to test a large number of genotypes in a short period of time. Labrousse et al. (2004) has recently developed a new method based on hydroponic co-culture, which has been producing outstanding results. However, the most reliable and most easily applicable method of screening breeding materials for broomrape resistance is the use of molecular markers QTL, RFLP, RAPD, TRAOP, and SSR markers have so far been used for this purpose.

GENETICS OF SUNFLOWER RESISTANCE TO *OROBANCHE CUMANA* WALLR.

In parallel with the appearance of new broomrape races and sources of broomrape resistance, the genetics of resistance to this pathogen has been studied as well. As sources of resistance to races A and B were identified by Plachek (1918) and Ždanov (1930), respectively, it was also determined that resistance to the pathogen was controlled by dominant genes. Burlov and Kotyuk (1976) and Pogorletsky and Geshele (1976) studied the genetic basis of *Orobanche* resistance and discovered that it was controlled by a single dominant gene, which they labeled *Or*.

Vrânceanu et al. (1980) conducted extensive genetic research as part of his study of broomrape in Romania from 1976 to 1980. They established that there were five pathogenic races of this parasite and labeled them A, B, C, D, and E. They also identified a set of differential lines that had cumulative resistance to the five successive races, conferred by the dominant genes *Or1, Or2, Or3, Or4*, and *Or5*, respectively. When race F subsequently appeared in Romania and resistance to it was discovered in the line LC-1093 (*Or6*) by Păcureanu-Joiţa et al. (1998), this cycle of genetic research was completed.

The appearance of new broomrape races in Spain triggered a new cycle of large-scale genetic analyses. Dominquez et al. (1996) noted that there is a low frequency of genes for resistance to race E in cultivated sunflower and that this resistance is controlled by two dominant genes.

Sukno et al. (1999) reported that resistance to race E is controlled by a single dominant gene. They tested sunflower lines for resistance to broomrape populations from different regions and found that only two were fully resistant to the pathogen. They assumed that the resistance was conferred by additional dominant alleles at the *Or* locus or by a cluster of very tightly linked non-allelic genes. The two lines were shown to be resistant to the new *Orobanche* populations that are able to overcome the *Or5* resistance gene. Alonso (1998) noted that, the known dominant genes notwithstanding, resistance to *Orobanche* may be more complex than previously thought and that genes other than single dominant ones may also be involved. In some cases involving cultivated sunflower germplasm, resistance to race F is controlled by recessive genes. Thus, *Orobanche* resistance found in the lines P-96 and KI-534 is controlled by recessive alleles at two loci (Rodrigez-Ojeda et al., 2001; Akhtouch et al., 2002). The same recessive genes control resistance to race E in the line KI-534 (Rodrigez-Ojeda et al., 2001). Akhtouch et al. (2002) crossed lines resistant to race F with those that are susceptible to it and found segregation ratios of 1:15 and 1:3 in the F_2, F_3, and BC_1 generations, which in most cases indicates double dominant epistasis. Cases of segregation ratios of 3:13 and 1:1 were also recorded in the F_2s and BC_1s, which is indicative of dominant-recessive epistasis. Perez-Vich et al. (2002) tested some interspecific hybrids (cultivated sunflower x *H. divaricatus* and *grosserratus*) in combination with a susceptible genotype and found that the resultant lines had a single dominant gene for resistance to race F in the segregating generations (F_2 and BC_1F_1).

Velasco et al. (2007) crossed a line resistant to race F (JI) with three susceptible lines and obtained segregation ratios of 3:1, 13:3, and 15:1 (R + MR + S) in the F_2, F_3, and BC_1 generations, indicating incomplete dominance of the *Or6* alleles and the presence of a second gene, *Or7*, whose expression was influenced by the environment.

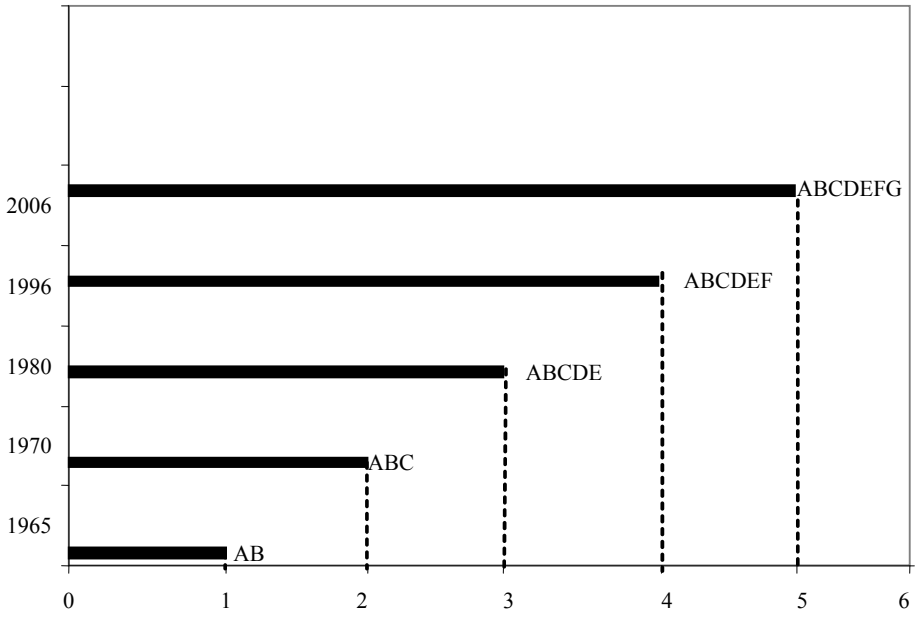

Fig. 1 – The evolution of the broomrape races in sunflower crop in Romania

P ă c u r e a n u - J o i ț a et al. (2008) tested the latest, virulent race of broomrape from Romania through a cross between the resistant line AO-548 and the susceptible line AD-66 and their F_2 and BC_1F_1 generations, in which segregation ratios of 15:1 and 3:1 were observed, indicating that the resistance of AO-548 to the latest race of this pathogen is controlled by two independent dominant genes.

The latest research conducted in Romania under field and greenhouse conditions has shown that sources of resistance to the newest populations of *Orobanche* found in Romania, Turkey, and Spain are present in the lines LC-009 and AO-548 (Tables 1 and 2). The genetics of this resistance and the race composition of the new populations remain to be studied.

In the Trakya region in Turkey, the race composition of the broomrape populations changes frequently. According to B u l b u l et al. (1991), race E was dominant from 1983 to 1990, after which race F appeared. Recently, as reported by K a y a et al. (2004), at least one new race of broomrape has appeared in the country that cannot be controlled by the Or_6. K a y a et al. (2009) have reported that genes for resistance to the newest, virulent race of *Orobanche* have been found in several lines and hybrids.

Table 1

Infestation with four populations of broomrape (*Orobanche cumana* Wallr.) for four sunflower genotypes (Fundulea, 2008-2009)

Orobanche population / Sunflower genotypes	Romania			
	Tulcea	**Brăila**	**Călăraşi**	**Constanța**
LC-1093	5/9	0/10	0/9	3/10
	4/10	0/8	0/10	4/9
	7/10	0/9	0/7	4/10
	5/10	0/10	0/10	3/10
	5/9	0/10	0/9	3/9
LC-009	0	0	0	0
	0	0	0	0
	0	0	0	0
	0	0	0	0
	0	0	0	0
PR 64 A 71	1/10	0	0	0
	0/10	0	0	2/10
	2/10	0	0	0
	0/9	0	0	1/9
	2/10	0	0	0
LC-058	0	0	0	0
	0	0	0	0
	0	0	0	0
	0	0	0	0
	0	0	0	0

Table 2

Infestation with six populations of broomrape (*Orobanche cumana* Wallr.) for four sunflower genotypes (Fundulea, 2008-2009)

Orobanche population / Sunflower genotypes	Russia				Turkey	Spain
	Krasnodar	**Stavropol**	**Rostov 1**	**Rostov 2**		
LC-1093	0/7	2/10	6/10	7/10	4/10	3/9
	0/9	0/10	5/10	4/8	5/10	5/10
	0/8	1/9	5/9	6/10	3/9	4/10
	0/10	1/7	7/9	7/10	4/8	3/8
	0/6	2/10	6/10	6/10	5/10	4/8
LC-009	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
PR 64 A 71	0	0	1/9	1/10	2/10	1/9
	0	0	0/9	0/10	6/9	0/8
	0	0	0/10	1/10	1/10	1/10
	0	0	2/10	0/9	0/10	2/10
	0	0	0/10	0/10	1/8	0/9
LC-058	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0

Races A and B were dominant in Bulgaria until 1968. Then, P e t r o v (1970) reported that a new race of the pathogen had appeared that could not be controlled by the Or_1 and Or_2 genes. S h i n d r o v a (2006) made an overview of the broomrape races found in Bulgaria. According to her findings, races D, E, and F are present in the country. Race E is the most widely distributed one, race F is spreading, while race D is disappearing.

Studies by A n t o n o v a et al. (2009) and G o n c h a r o v (2009) both discuss the dynamic change of broomrape races in Russia. It is known that *Orobanche* races change frequently in Ukraine and Moldova too, and that, although no public reports have been made yet, there are at least seven races of the pathogen in the two countries. According to Š k o r i ć and J o c i ć (2005), race E is the dominant form of broomrape in Serbia. *Orobanche* has been present in China for a long time too, and identification has been made of race A by B a i c h u n et al. (1996). New races have appeared in the country since, but the race composition has not been determined yet.

Molecular research for the purposes of race characterization and mapping is developing rapidly. M e l e r o - V e r a et al. (1996) used RFLP for the characterization of broomrape races. L u et al. (1999) determined that there is a linkage group that contains the Or_5 gene conferring resistance to *Orobanche cumana* Wallr race E. These findings confirm that the Or_5 linkage group could be integrated with the linkage group 17 of the GIE Cartisol RFLP map. According to T a n g et al. (2003), the Or_5 has been mapped to the end of LG3 distal to the marker loci. P e r e z - V i c h et al. (2004) analyzed resistance of the line P-96 to races E and F at the molecular level. Based on a linked map comprising 103 marker loci distributed on 17 linkage groups, it was determined that only five QTLs (*or1.1, or3.1, or7.1, or13.1,* and *or13.2*) were responsible for resistance to race E, while only 6 QTLS (*or1.1, or4.1, or5.1, or13.1, or13.2,* and *or16.1*) controlled resistance to race F and were found on seven of the 17 linkage groups.

These results suggest that sunflower resistance to broomrape is controlled by a combination of qualitative, race-specific resistance effecting the presence or absence of broomrape and quantitative, non-race-specific resistance affecting the number of broomrape stalks per plant.

I u o r a ş et al. (2004) used RAPD and SSR markers in the detection of broomrape resistance and determined that the RAPD markers USC 73, UBC 318, UBC 264, UBC 685, and OP-A 17 and the SSR markers ORS 1:14 and ORS 1036 can be successfully used for such detection.

M a r q u e z - L e m a et al. (2008) used TRAP and SSR markers responsible for the Or_5 gene and were able to map efl-alfa (elongation factor 1-alfa) chit. (chitinase, PR 3 protein) and HaACl (aldo-keto reductase) loci to LGs 7, 9, and 17, respectively, none of which were co-located to Or_5. These results were partially expected, since the chit. and HaACl genes play a role in defense responses and efl-a is a housekeeping gene, and dominant race-specific genes such as Or_5 are hypothesized as essentially playing a role in an early stage of the plant-pathogen interaction.

A study by J o e l et al. (2004) confirmed the importance of molecular markers for the study of sunflower resistance to *Orobanche*. They found that RAPD patterns of DNA extracted from soil-borne *Orobanche* seeds is identical to that of DNA from vegetative plant material, provided that the seeds had not deteriorated. They also note that DNA of reasonable diagnostic quality could be extracted not only from tetrazolium-positive soil-borne *Orobanche* seeds but also from tetrazolium-negative seeds. This makes it possible to perform quick genetic analysis without having to wait for broomrape seeds to germinate or develop into plants.

It is very important to know all the mechanisms of broomrape resistance (physiological, biochemical, mechanical, etc.) in order to be able to understand all aspects of this phenomenon. These resistance mechanisms have been studied for a long time. Thus, M o r o z o v (1947) cites the results of R i c h t e r (1924) that indicate that broomrape-susceptible sunflowers have root systems with a low pH. The same author also found that broomrape from Saratov Oblast in Russia (race A) had two physiological thresholds – one in acidic soils, up to which broomrape seeds germinate easily, and one in alkaline soils, beyond which susceptible cultivars become "resistant" and no broomrape infestation occurs.

M o r o z o v (1947) also cited the results of S u h o r u k o v (1930) concerning the link between peroxidase values and sunflower susceptibility to broomrape, according to which increased soil acidity increased peroxidase activity and the susceptibility of sunflower plants to *Orobanche*. Much later, A n t o n o v a (1978) showed that the action of peroxidases excreted by the parasite was involved in the lignification of host cells.

A n t o n o v a and T e r B o r g (1996) reported that differences in peroxidase production can be used for interpreting the different virulence of races A and B as well as to explain the gene-for-gene interaction between sunflower and broomrape.

According to M o r o z o v (1947), B a r c i n s k i y (1932, 1935) reported that sunflower root cells contain substances that stimulate the germination and development of broomrape seeds and seedlings. Long after that, W e g m a n n (1998), A l o n s o (1998), M a t u s o v a et al. (2004), and H o n i g e s et al. (2009) also pointed out the importance of broomrape germination stimulants. The most widely known such stimulants are strigol, electrol, orobanchol, and the synthetic stimulant GP 24.

M a t u s o v a et al. (2004) studied germination stimulants as well. Their results indicate that parasitic weed seeds are highly sensitive to the germination stimulant GR 24 for a short period of time and then enter into secondary dormancy relatively quickly.

H o n i g e s et al. (2008) notes that there are sunflower genotypes that can be characterized as low-stimulant or germination-inhibiting towards broomrape. W e g m a n n (1986, 2004) and W e g m a n n et al. (1991) stressed the importance of phytoalexins as factors of resistance to *Orobanche*, while S a u e r b o r n et al. (2002) did the same with benzothiadiazole (BTH).

Panchenko and Antonova (1975) concluded that the protective response of sunflower plants from different cultivars they investigated came down to the accumulation of lignin and its precompounds in injured host cells, resulting in the haustoria losing the ability to supply themselves with water and nutrients from the host cells.

Pustovoit (1966) and Honiges et al. (2008) talk of mechanical barriers as being essential to the phenomenon of broomrape resistance. Several studies by Labrousse et al. (2000, 2002, 2004) discuss different criteria for assessing *Orobanche* resistance and the different mechanisms by which such resistance operates. The authors were able to distinguish between three types of broomrape resistance in their work: 1. resistance acting at an early stage in broomrape development (*H. debilis* ssp. *debilis*), when broomrape seedlings were present on the sunflower root, but an impassable encapsulation layer blocked the intruding parasite, which then died; 2. resistance found in the resistant line LR1, which involves two types of action: i) decreased stimulation of broomrape germination (a three-fold reduction compared to susceptible line 2603); and ii) rapid necrosis that appeared as early as stage 2 of parasite development; 3. resistance observed at a later stage of broomrape development in the line 92B6 (necrosis developing prior to broomrape flowering).

Genetic control of broomrape resistance can also be achieved by incorporating into the cultivated sunflower genes for resistance to imidazolinone-based herbicides, which are effective in controlling this parasitic weed.

CONTROLLING BROOMRAPE BY DEVELOPING IMI-RESISTANT SUNFLOWER HYBRIDS

The rapid changes in broomrape race composition have forced sunflower breeders and geneticists to not only search for genes for resistance to the new races of *Orobanche* but to also look for alternative solutions to the problem of broomrape control. In the past 10 years, the development of sunflower hybrids resistant to the imidazolinone herbicides has made it possible to successfully control broomrape regardless of its race composition.

Wild *Helianthus annuus* L. resistant to imidazolinones (imazethapyr, pursuit) was first identified in Kansas (USA) in 1996 in a soybean field treated for seven consecutive years with a herbicide from this group (Al-Khatib et al., 1998). The use of imidazolinone resistance in sunflower breeding through the introduction of IMI-resistance genes into cultivated sunflower genotypes provides a broad spectrum of weed control (covering over 40 broadleaf species and over 20 grass weed species) and is especially effective in controlling *Orobanche* in sunflower, as discovered by Alonso et al. (1998). The USDA-ARS (NDSU) research group quickly transferred this genetic resistance into cultivated sunflowers and released the public populations IMISUN-1 and IMISUN-2. Similar programs were developed in parallel by Alonso et al. (1998) in Spain, by Malidža et al. (2000) and Jocić et al. (2001) in Serbia, and by several pri-

vate companies in Argentina. Bruniard and Miller (2001) reported that IMI-resistance is controlled by two genes (semi-dominant type of gene action). *Imr*$_1$ is the gene responsible for imidazolinone resistance, while *Imr*$_2$ has the modifier effect when the major gene is present. Malidža et al. (2000) and Jocić et al. (2001) showed that resistance to imidazolinones is controlled by a single, partially dominant gene. These differences in the mode of inheritance could perhaps be attributed to the presence of mutations on several different loci in the original population of wild *Helianthus annuus* L.

Imidazolinones inhibit acetolactate synthase (ALS), also called acetohydroxyacid synthase (AHAS), which is responsible for synthesizing the amino acids valine, leucine and isoleucine. Imidazolinone-tolerant plants with altered AHAS genes and enzymes have been discovered in many species (Sala et al., 2008).

Sala et al. (2008) obtained another gene for resistance to imidazolinones through ethyl methane-sulfonate mutagenesis of seeds and selection with the imazapyr herbicide. They labeled the gene CLHA-PLUS. Based on genetic analysis (F_1, F_2 and BC_1F_1), the authors determined that the IMI-resistance gene CLHA-PLUS is controlled by a partially dominant nuclear gene. Using the SSR marker for the AHASL1 gene, they concluded that the mutation present in CLHA-PLUS is different from *Imr*$_1$, but that both these genes are allelic variants of the locus $AHASL_1$.

CONCLUSIONS AND FUTURE PROSPECTS

Sunflower breeders and geneticists have been successful in responding to the rapid changes in the race composition of broomrape (*Orobanche cumana* Wallr). They found genes for resistance to this pathogen and incorporated them into elite lines of cultivated sunflower, making it possible to develop *Orobanche*-resistant hybrids. Research so far has shown that the genes for broomrape resistance are present in some wild species of the genus *Helianthus*. For this reason, it would be desirable to set up an international project that would investigate all wild sunflower species and all populations within each species for resistance to the existing populations and races of broomrape using screening on infested plots, in greenhouses, and at the molecular level. This would produce a map of genes for broomrape resistance within the genus *Helianthus*. Another international project could be set up to establish an international collection of broomrape populations (races) that would be kept within the confines of a single institution and accessible to all users. The variability of all the populations would be studied at the molecular level and a map would be developed, making it possible to develop resistant hybrids more rapidly and with a greater rate of success. It is also very important to make an effort to establish a new set of differential lines for the new races that have appeared in Russia, Romania, Ukraine, Turkey, Bulgaria, and some other countries. It is desirable that universal protocols (methods) be established for screening for resistance to bro-

omrape in field and greenhouse conditions and at the molecular level, so that the findings of teams from different parts of the world can be compared to each other.

In parallel with the development of IMI-resistant sunflower hybrids, it is necessary to also develop new kinds of herbicides capable of controlling broomrape in addition to other weeds.

To speed up the progress of sunflower breeding for resistance to Orobanche, there should be a greater level of collaboration between the breeders from public institutions and private companies.

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