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Sunflower Resistance to Race G of Broomrape (*Orobanche Cumana* Wallr.) In the Russian Federation: the Development of the Lines and the Study of Inheritance

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Abstract: The objective of this work is the development of sunflower lines that are not affected by race G of broomrape, as well as the determination of genetic control of resistance. The testing of the resistance of VNIIMK's collection accessions of a cultivated sunflower of various origins was carried out on an artificial background made from the seeds of race G of broomrape. 6 lines resistant to race G were developed by the method of inbreeding on the basis of the obtained unaffected forms. The genetic control of resistance of one of them was studied. The resistance was inherited monogeneuosly, with incomplete dominance. There was established the presence of a reciprocal effect and the dependence of the resistance characteristic on the genotype of a susceptible parent under crossbreeding with certain lines. The other 5 sunflower lines are in the process of a hybridological analysis in order to determine the genetic control of their resistance. The combination of different genes of resistance to the same race of broomrape in one sunflower genotype could contribute to the long-term resistance of the crop to the parasite. The results of the presented study are of high importance for breeders, since the gene that we studied provides a new source of resistance to race G, thereby ensuring the protection of sunflower from the spread of new *Orobanche* pathotypes.

Keywords: sunflower, broomrape, race G, resistance, inheritance

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Introduction

Sunflower (*Helianthus annuus* L.) is the most important oil crop all over the world. The persistent weed broomrape (*Orobanche cumana* Wallr.) is an obligate parasite from higher flowering herbaceous plants, belonging to the family *Orobanchaceae* of the order *Scrophulariales* and is the main biotic deterrent for growing sunflower in all countries where it grows, with the exception of North and South America. On average, crop losses caused by weed infestation of fields by broomrape reach from 50 % to 100 %. The history of parasitism of broomrape on sunflower in Russia dates back to about 200 years. Here the sunflower was first affected by a broomrape, which usually parasitized on wormwood. The sunflower turned out to be a more suitable host for the parasite. By the end of the XIX century and the beginning of the XX century, the zone of habitation of *O. cumana* in the former USSR had spread to such an extent that this parasite became a serious threat to sunflower. Then the races A and B, the first races of broomrape, were identified, and a breeding material resistant to them was developed.

The intensification of sunflower cultivation as a high-yielding crop resulted in the emergence and rapid spread of new highly virulent races of the parasite that overcame the immunity of sunflower varieties and hybrids that were previously resistant to it. In the early 70s of the XX century a new biotype of broomrape, race C, began to affect previously resistant genotypes and quickly spread in all regions of sunflower cultivation, especially in the North Caucasus. Varieties and hybrids resistant to this race were developed, which allowed to effectively control broomrape infestation of sunflower in the former USSR for several decades. However, nowadays, sunflower crops are often largely infested with broomrape in the Rostov, Volgograd, Stavropol and Krasnodar regions. Identification of the racial structure of the parasite from these areas showed the presence of the following generation of races – E, F and G (Antonova *et al.*, 2014).

At present, the nine races of *O. cumana* are known, they are denoted by the letters of the Latin alphabet from A to G. Of these, the races F and G are the most virulent. Scientists and breeders from different countries are studying both the racial structure of broomrape populations and the genetic control of sunflower resistance to different races of this parasitic plant. Five physiological races of sunflower broomrape A, B, C, D and E have been described by A.V. Vrânceanu *et al.* (Vrânceanu *et al.*, 1980). As the authors have shown, the sunflower resistance to these races is ensured by the cumulative action of the genes from Or_1 to Or_5, with the dominant and monogenic nature of inheritance. Other studies have shown that the genes from Or_1 to Or_5 are allelic or strongly linked (Fernández-Martínez *et al.*, 2008). For example, there were found two dominant genes in the resistant line R-41 (Domínguez, 1996), and in some lines – one recessive gene (Ramaiah, 1987) and even a double recessive epistasis (Kirichenko *et al.*, 1987). Molecular studies have revealed that resistance to race E is controlled by the dominant gene Or_5, which is mapped in the top of the LG3 chromosome of the genetic map of SSR loci (Guchetl *et al.*, 2012; Tang *et al.*, 2003).

Resistance to race F in a resistant sunflower genotype is controlled either by the recessive alleles of two independent loci Or_6 and Or_7, or by the dominant-recessive epistasis of two loci (Akhtouch *et al.*, 2016), or by the dominant allele of one gene designated by Or_6 (Pérez-Vich *et al.*, 2002). Dominance also depends on the source of resistance, the reaction of a susceptible parental line used in cross-breeding. In some cases, F_1 hybrids showed resistance cleavage or were susceptible, and this was due to the presence of a minor or modifying gene in some susceptible lines (Velasco *et al.*, 2007).

In recent years, the biotypes of broomrape that overcome resistance to race F have been identified in several countries, and they are called race G. A continuous search for sources of resistance to this new race is under way. In the line AO-548, two independent dominant genes control genetic resistance to the population of race G of broomrape from Romania (Pacureuanu-Joita *et al.*, 2008). In Bulgaria, as a result of hybridization of a cultivated sunflower with several wild species of *Helianthus*, several donors of resistance to race G were identified (Christov *et al.*, 2009). The line developed in Serbia as a result of interspecies cross-breeding of cultivated sunflower with wild sunflower (*H. divarticatus*) is resistant to races higher than F and its resistance is controlled by one recessive gene $or_{ab\text{-}vl\text{-}8}$. Molecular studies have revealed that recessive gene $or_{ab\text{-}vl\text{-}8}$ is mapped in the lower region of LG3 chromosome of the genetic map of SSR loci (Imerovski *et al.*, 2015). In Spain, L. Velasco *et al* (Velasco *et al.*, 2012) found that resistance to race G of broomrape in *H. debilis* subsp. *tardiflorus* in cross-breeding with cultivated sunflower is controlled by the dominant allele of one gene.

The monitoring of the racial composition of broomrape, carried out by us every year, showed that race G prevails in most populations of broomrape in the southern regions of the Russian Federation (Antonova *et al.*, 2013). Therefore, the search for sources of immunity to this race in order to deve lope a resistant source material of sunflower and to study the genetic control of this trait is of high priority. It is known that the nature of the inheritance of resistance to different races of broomrape is often individual for each genotype, and the resistance of the hybrid generation can be influenced by the genotype of the susceptible parental line. In this connection, the aim of this work was to search for possible sources of resistance, the development on their basis sunflower lines that are not affected by race G of broomrape, and the determination of genetic control of this trait.

Materials and methods

Seeds of broomrape were collected on the fields of the Bokovskiy district of the Rostov region in 2014. The identification of their race with the help of the known differentiation lines: Record 1–3 (C), S-1358 (D), P-1380 (E), LC1093 and P96 (F) showed that the seeds belong to the race G. The material for research were over 1000 accessions of cultivated and wild sunflower from the collection of the Kuban Experimental Station VIR, the collection accessions of VNIIMK of cultivated sunflower of various origin, as well as the breeding lines VK 551, VK 678 B, VK 678 A, VK 1 IMI B, VK 1 IMI A, VK 301, VK 580, PRO2, VK 680 B susceptible to broomrape.

Forced self-pollination and hybridization of sunflower plants were carried out using the method, which is customary for VNIIMK (Gundaev, 1971).

Collected broomrape seeds were stored in the frozen condition. To create an infectious background in the greenhouse, the broomrape seeds were added to the boxes with soil-sand mixture at the rate of 200 mg per 1 kg of mixture, distributing them evenly. Sunflower plants were grown for 30 days at a temperature of 25–27 °C and a 16-hour photoperiod. The plants were digged out in 25 days after the sprouts emergence and the broomrape specimens on their roots were counted. The variety VNIIMK 8883 was used as a control, which is susceptible to the modern races *O. cumana*.

Analysis of variance of the received data was carried out according to the method laid down by B. A. Dospekhov (Dospekhov, 1985). Chi squared analyses were carried out to detect the deviations from the expected Mendelian ratios 1:2:1 or 1:1 (Gershenzon, 1979).

Results and discussion

Over the last century of the joint evolution of sunflower and *O. cumana* plants there has been a constant rapid adaptation of the parasite to the mechanisms of host immunity. Consequently, the detection of resistance genes in cultivated sunflower has become problematic. Thus, from the accessions of the cultivated sunflower of the VIR collection, evaluated for resistance to the race G, none was found having 100 % resistance. Most of the accessions were affected to a high degree, some at the control level. Some of them, originating from France, Spain, Mexico, Hungary, are listed in Table 1. Only some accessions of the cultivated collection were divided into weakly affected and non-affected genotypes, further work with which can make it possible to develop lines immune to race G. Table 1

Table 1: The degree of infestation by race G of broomrape (*O. cumana*) of some accessions of cultivated sunflower of VIR collection in greenhouse conditions.

Catalog No.	Origin	Number of evaluated plants, pcs.	Plants infested, %	Degree* of infestation
667	Kabardino-Balkaria	30	23.3	2
769	Armenian SSR	30	23.3	1
1010	England	30	80.0	5
3300	The Krasnodar region, line VIR-221	30	33.3	4
3475	The Krasnodar region, line VIR-665	30	10.0	2
2005	The Primorsk region	26	26.9	2
3109	Bulgaria	23	17.4	2
3301	The Krasnodar region, line VIR-222	30	50.0	3
1434	Bulgaria	28	60.7	6
3046	Argentina	22	9.0	2
2954	Argentina	30	80.0	12
2925	France	30	100	110
2978	Spain	29	100	62
2982	Spain	30	100	121
3080	Mexico	30	100	115
3015	Hungary	30	100	65
VNIIMK 8883 susceptible control	Russia	30	100	115

* – number of broomrape specimens per one affected plant.

shows selection of such accessions of sunflower of domestic and foreign origin. Among the presented material, accessions of local breeding from the Krasnodar Region attract attention: Kabardino-Balkarian (No. 667 catalog), Armenian (No. 769 catalog), lines VIR-665, VIR-221, VIR-222, The Primorsk region (No. 2005 catalog), Bulgaria (No. 3109 catalog), Argentine (No. 3046 catalog).

On the basis of the obtained unaffected forms from all the studied collections, 6 lines resistant to race G were developed using inbreeding method. Genetic control of the resistance of one of them, line RG, has been studied. Line RG was developed from accession VIR-665 (No. 3475 catalog) after 7 of inbreeding generations. In order to study the inheritance of resistance there were carried out the cross-breedings of RG with susceptible lines of sunflower of VNIIMK breeding: VK 551, VK 678 B, VK 678 A, VK 1 IMI B, VK 1 IMI A,

Table 2: The degree of infestation by broomrape of families of hybrid combinations of sunflower in F_1.

Hybrid combination	Number of evaluated families	Plants infected, %	The average number of broomrape tubercles per one plant, pcs.	
			affected	acccountable*
RG × VK 580	3	43.0	2	1.2
RG × VK 551	8	56.5	5.1	4.7
VK 551 × RG	6	97.5	11.5	11.4
RG × VK 301	5	26.0	1	0.2
VK 301 × RG	6	67.0	4.8	3.2
RG × VK1-imi B	7	51.0	2.3	1.4
VK1-imi B × RG	5	62.0	2.6	1.6
VK1-imi A × RG	6	74.0	3	2.2
RG × VK 678 B	8	89.0	3	2.8
VK 678 B × RG	6	88.0	3.8	3.3
VK 678 A × RG	8	83.6	4.4	3.6
PRO2 × RG	3	55.2	2.4	1.6

*accountable plant – total number of analyzed plants from the family: affected and not affected by broomrape.

VK 301, VK 580 and PRO2. 12 combinations of cross-breeding were obtained, 3–8 families of each hybrid. Fifty plants of each family were evaluated for resistance to broomrape. The degree of plant infestation from the F_1 families of the studied hybrid combinations is shown in Table 2.

All hybrid combinations F_1 were affected by broomrape. On the basis of their damage to the plants of each family they have showed a segregation to the unaffected and affected to a small extent in comparison with the severe lesion of the control susceptible genotype. The minimum percentage of affected F_1 plants (RG × VK 301) averaged 26. The average number of broomrape tubercles per the affected plant was 1 piece, per the accountable plant it was 0.2 pieces. The maximum percentage of affected plants of F_1 hybrid (VK 551 × RG) averaged 97.5. The average number of broomrape tubercles per the affected plant was 11.5 pieces, per the accountable plant it was 11.4 pieces. But it should be noted that this combination of cross-breeding is uncharacteristic in the general number of hybrids in terms of the number of affected plants and the number of broomrape tubercles. In general, the average number of broomrape tubercles per the affected plant did not exceed 5.1 pieces, and per the accountable plant was 4.7 pieces. The obtained data indicate an incomplete dominance of the resistance trait to race G of broomrape of the line RG in F_1.

Table 3: The degree of infestation by broomrape of families of reciprocal hybrid combinations.

Hybrid combination	Number of evaluated families	Plants infected, %	The average number of broomrape tubercles per one accountable plant, pcs.
RG × VK 1IMI B	7	51	1.4
VK 1 IMI B × RG	5	62	2.3
SSD_{05}		11.14	1.09
RG × VK 678 B	8	89	2.80
VK 678 Б × RG	6	88	3.30
SSD_{05}		3.72	0.89
RG × VK 551	8	56.5	4.7
VK 551 × RG	6	97.5	11.4
SSD_{05}		11.91	7.5
RG × VK 301	5	26	0.2
VK 301 × RG	6	67	3.2
SSD_{05}		16.01	3.3

To study the influence of the reciprocal effect and the dependence of the resistance on the genetic plasma of the susceptible parent line, reciprocal cross-breeding of the line RG with sunflower lines VK 551, VK 678 B, VK 1 IMI B, and VK 301 (Table 3) were analyzed. 8 combinations of cross-breeding were received, 5–8 families of each hybrid. Fifty plants of each family were evaluated for resistance to broomrape.

In terms of the "the percentage of infected plants" and "the average number of broomrape tubercles per accountable plant" statistically significant difference SSD_{05} was calculated for all reciprocal cross-breeding. Differences in these characteristics were unreliable at the 5 % significance level for the susceptible parental lines of VK 1 IMI B and VK 678 B. Consequently, the presence of the reciprocal effect and the dependence of resistance on the genetic plasma of susceptible parent lines participating in hybrid combinations were not proved. For the other two lines VK 551 and VK 301, differences in "the percentage of infected plants" are valid at a 5 % significance level. This indicates the presence of a reciprocal effect in these genotypes.

To confirm the type of inheritance and to establish the number of genes that control resistance to race G the plant of F_1 were self-pollinated or crossed with susceptible or RG lines. The progeny F_2 and BC_1 were developed in the field conditions and were evaluated in the greenhouse for resistance and susceptibility to race G of broomrape with artificial infection. Depending on the degree of infestation, sunflower plants were divided into 3 groups. The plants were considered susceptible when more than 5 tubercles or formed broomrape sprouts were found on their roots. The plants were considered resistant when no healthy tubercles or sprouts were found on their roots, but there were numerous necroses of cells in the area of broomrape penetration and dead tubercles. Sunflower plants affected to a small extent and having five and less broomrape tubercles on the roots have been identified as genotypes with incomplete resistance (intermediate group). This classification of broomrape was previously defined by Velasco (Velasco *et al.*, 2007). For several plants from each group, F_2 individuals were self-pollinated and F_3 seeds were harvested. F_3 families were tested for resistance and in generally confirmed the validity of our classification. For example, the intermediate group showed segregating progenies (data not shown). In F_2 populations, the segregation into 3 phenotypic classes for 2 crosses: RG with VK 678 B and RG with VK 1 IMI B were observed: resistant, slightly affected (intermediate group), and susceptible in a ratio of 1:2:1. Chi squared for first cross was 1.40 with probability 0.50–0.30, and second cross 4.57 with probability 0.20–0.10 (Table 4).

Table 4: The inheritance of resistance of sunflower to the race G of broomrape in F_2 in cross-breeding of resistant line RG with susceptible lines.

Hybrid combination	The average number of broomrape tubercles per one accountable plant in F_1, pcs.	Number of plants, pcs			Expected segregation ratio	χ^2	df	P
		resistant	intermediate	susceptible				
RG × VK 678 B	2.4	26	65	35	1:2:1	1.40	2	0.50–0.30
RG × VK 1 IMI B	1.9	25	81	38	1:2:1	4.57	2	0.20–0.10

In BC_1, the segregation into 2 phenotypic classes was observed: susceptible and affected to a small extent (intermediate group) for the first two cross-breeding (VK 678 B × RG) × VK 678 B and (VK 1 B × RG) × VK 1 B and resistant and affected to a small extent for the second two cross-breeding (VK 680 B × RG) × RGI and (PRO2 × RG) × RG in a ratio of 1:1 (χ^2 = from 0.03- to 0.24, P = 0.70–0.90) (Table 5).

The actual segregations of F_2 and BC_1 corresponded to the monohybrid inheritance model with incomplete dominance of the trait. The other 5 sunflower lines that we have developed and which are not affected by race G are in the process of a hybridological analysis to determine the genetic control of their resistance.

Table 5: The inheritance of resistance of sunflower to the race G of broomrape in BC_1 in cross-breeding of resistant line RG with susceptible lines.

Hybrid combination	The average number of broomrape tubercles per one accountable plant in F_1, pcs	Number of plants, pcs			Expected segregation ratio	χ^2	df	P
		resistant	intermediate	susceptible				
(VK 678 B × RG) × VK 678 B	3.1	0	16	17	1:1	0.03	1	0.90–0.80
(VK1-imi B × RG) × VK1-imi B	1.4	0	12	11	1:1	0.04	1	0.90–0.80
(VK 680 B × RG) × RG	2.1	55	59	0	1:1	0.14	1	0.70
(PRO2 × RG) × RG	1.8	36	32	0	1:1	0.24	1	0.70

Inheritance of resistance to race G in the line of sunflower RG differs from the type of inheritance in sunflower accessions studied by other researchers. In the line AO-548, two independent dominant genes provide control of genetic resistance to the population of race G of broomrape (Pacureuanu-Joita *et al.*, 2008). The line developed as a result of interspecies cross-breeding of cultivated sunflower with wild sunflower (*H. divarticatus*) is resistant to race G and its resistance is controlled by one recessive gene $or_{ab\text{-}vl\text{-}8}$ (Imerovski *et al.*, 2015). It found that resistance to race G of broomrape in *H. debilis* subsp. *tardiflorus* in cross-breeding with cultivated sunflower is controlled by the dominant allele of one gene (Velasco *et al.*, 2012). The study is an evidence that different genes control different sources of resistance. Thus, the combination of different genes of resistance to the same race of broomrape in one sunflower genotype and the cultivation of hybrids carrying genes that control different mechanisms of resistance could contribute to the long-term resistance of the crop to the parasite. Since breeding for resistance seems to be the most efficient and sustainable approach to controlling broomrape, to do this, one needs additional sources of new resistance genes. The results of the presented study are of high importance for breeders, since the gene that we studied provides a new source of resistance to race G, thereby ensuring the protection of sunflower from the spread of new *Orobanche* pathotypes. From the breeding perspective, incomplete dominance nature of resistance to broomrape in the line RG suggests the necessity to introduce resistance genes into both parental lines in order to obtain resistant hybrid.

Conclusions

Thus, 6 sunflower lines of RG line resistant to race G were developed. It is established that the resistance of one of them (RG line) is inherited monogeneuosly with incomplete dominance of a trait. In cross-breeding, the presence of the reciprocal effect and the dependence of resistance on the genotype of some susceptible parental line are established. There is no evidence of a reciprocal effect for the VK 1 IMI B and VK 678 B lines. The other 5 sunflower lines that we have developed and which are not affected by race G are in the process of a hybridological analysis to determine the genetic control of their resistance.

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