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RESILIENCE OF SUNFLOWER CROP UNDER BIOTIC STRESS CONDITIONS

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Orobanche cumana Wallr., commonly known as sunflower broomrape, is a parasitic plant that severely affects sunflower (*Helianthus annuus* L.) crop, causing significant production losses worldwide. This plant attaches to sunflower roots, extracting nutrients and water, leading to stunted growth and reduced seed yield. Traditional control methods, such as crop rotation and the use of genetically resistant sunflower varieties, have proven insufficient due to the adaptability and evolution of the parasite. Advances in molecular biology and genomics, such as the use of molecular markers and next-generation sequencing, facilitate the identification of qualitative and quantitative resistance genes (marker assisted selection), as well as gene pyramiding, supporting the development of resistant hybrids. Emerging technologies such as CRISPR-Cas9 and RNA interference offer promising opportunities for creating more resistant sunflower genotypes. In addition, artificial intelligence and machine learning algorithms improve the efficiency of selection programs. This multidisciplinary approach is essential to control parasite and ensure sustainable sunflower production. Present review aims to summarise current knowledge and research gaps in methods to control broomrape and to develop resistance against parasitic plants.

Keywords: *Breeding, Broomrape, Orobanche cumana, Molecular tools, Sunflower, Races.*

REZILIENȚA CULTURII DE FLOAREA-SOARELUI ÎN CONDIȚII DE STRES BIOTIC

Orobanche cumana Wallr., cunoscută sub denumirea de lupoaie, este o plantă parazită care afectează sever cultura de floarea-soarelui (*Helianthus annuus* L.), provocând pierderi de producție semnificative la nivel mondial. Această plantă se atașează de rădăcinile florii-soarelui, extrăgând nutrienți și apă, ceea ce duce la reducerea creșterii și la o scădere a recoltei de semințe. Metodele tradiționale de control, cum ar fi rotația culturilor și utilizarea unor genotipuri de floarea-soarelui cu gene majore de rezistență, s-au dovedit a fi insuficiente din cauza adaptabilității și evoluției parazitului. Progresele în biologia moleculară și genomic*ă*, cum ar fi utilizarea markerilor moleculari (selectia asistată de markeri) și secvențierea de generație următoare facilitează identificarea genelor de rezistență calitative și cantitative, precum și combinarea acestora într-un singur genotip, asigurând bază teoretică pentru dezvoltarea hibrizilor rezistenți. Tehnologiile emergente, cum ar fi CRISPR-Cas9, oferă oportunități promițătoare pentru crearea unor genotipuri de floarea-soarelui mai rezistente. În plus, inteligența artificială și algoritmii de învățare automată îmbunătățesc eficiența programelor de selecție. Această abordare multidisciplinară este esențială pentru controlul parazitului și asigurarea unei producții durabile de floarea-soarelui. Prezenta lucrare include o analiză concisă a cunoștințelor actuale, precum și a lacunelor în metodele de control ale lupoaiei și în dezvoltarea rezistenței față de plantele parazite.

Cuvinte-cheie: *ameliorare, lupoaie, Orobanche cumana, metode moleculare, floarea-soarelui, rase.*

Introduction

Orobanche cumana Wallr., commonly known as sunflower broomrape, is a parasitic plant that affects sunflower (*Helianthus annuus* L.) crop, leading to significant production losses worldwide. This parasite attaches itself to the roots of sunflower plants, extracting nutrients and water from host tissues, which results in stunted growth, reduced seed production, and, in cases of severe infestation, total crop failure [1]. The excessive expansion of areas cultivated with sunflowers leads to the irrational use of soils, the disruption of crop rotation and, under the conditions of climate change, favors the appearance and development of pathogens, contributes to the accumulation of various parasites and their spread to new geographic areas. Ultimately, these factors can result in epiphytotic outbreaks of diseases and pests, posing serious threats to sustainable agriculture [2].

Surveys conducted among farmers and sociological studies revealed the presence of the parasitic angiosperm broomrape in sunflower agroecosystems in the Republic of Moldova. In 2014, it was reported in 63% of localities in the southern region, 47% in the central region, and 18% in the northern region [3]. By 2020, O. cumana was identified in only 10% of the analyzed lands, mainly in the central part of the country.

Traditional control methods, including crop rotation and the cultivation of sunflower hybrids with vertical genetic resistance, have offered some protection; however, these methods are increasingly proving inadequate due to the parasite's evolving resistance and adaptability. Given these challenges, modern research and control techniques for *Orobanche cumana* have become essential for ensuring sustainable sunflower production. This review aims to summarize current knowledge and research gaps in methods to control broomrape and to develop resistance against parasitic plants.

Impact of broomrape

The sunflower yield is significantly affected by various specific pathogens, parasitic plants, and pests, considerable losses being determined by the broomrape [4, 5]. Throughout its evolution, the parasite has developed a specialized multicellular structure known as haustorium, which forms tight connections with the host's vascular system retrieving water and essential nutrients from the phloem. The cells within the haustorium metabolize the host's nutrients in a manner specific to the parasite, altering osmotic potential, disrupting photosynthesis, and redirecting nutrient flow to the parasite [1, 6]. This process leads to a change in biomass allocation among the host's organs, typically resulting in decreased biomass in the following order: head > stem > leaves [7], ultimately diminishing productivity.

The impact of the parasite on sunflower crops can range from subtle, non-visible damage to complete plant death [8], especially in cases of severe infestation. The visible effects of this attack include plant wilting, yellowing of leaves, and reduced size of both underground and aerial organs, ultimately leading to decreased seed yield and lower lipid and protein content in the seeds. The damage caused by *O. cumana* can vary from 5% to 90%, depending on the aggressiveness of the parasite, the resistance of host plant, and environmental conditions [9, 10].

Parasitic plants act as a powerful sink for the host, hindering growth and development and reducing overall plant biomass. Significant decreases of stem (15,5-36%) and root systems (60-68%) growth has been observed in both sensitive and tolerant sunflower genotypes infested with broomrape collected from the Republic of Moldova [7]. *O. cumana* infestation significantly reduced the biomass accumulation in host plants (by about 20.4-57.1%), strong negative correlation (r=-0.53) between this parameter and the amount of biomass of parasitic plants per host plant being found. The parasite has a more pronounced effect on the aerial parts, with reductions of up to 58.7% compared to controls. In this case, high negative correlations (r = -0.52) between this parameter and the intensity of the attack was observed. Infection also suppressed the accumulation of root parasite biomass (by about 32-49.0%) [11].

Broomrape significantly affects the number of leaves and leaf surface area [12], leading to a reduction of 12.4% to 39.0% in leaf surface compared to non-infested genotypes [7]. Infestation can decrease head diameter by up to 20.0% compared to control [13]. The degree of *O. cumana* infestation shows a negative correlation with both head diameter and the number of full seeds per head. Hybrids with the highest levels of attack are the most severely affected, demonstrating significant reductions in all measured traits [14].

The most substantial impact of broomrape is observed in the case of total seed weight per plant [9, 15], seed production being inversely proportional to the degree of attack. Statistical analysis of the data indicated a strong negative correlation between the number of *O. cumana* attachments per host plant and sunflower yield (r=-0.62), as well as between the intensity of attack and 1000 seeds weight (r=-0.50) [16].

These results provide valuable insights into the performance of different experimental sunflower hybrids under broomrape infestation, highlighting several genotypes characterized by high and stable productivity, even under high levels of *O. cumana* attack [16].

Control of sunflower broomrape

The unique characteristics of parasitic plants, particularly their underground growth during the early stages of the life cycle, pose significant challenges for effective control strategies. Crop damage often occurs long before the parasite emerges on the surface, making diagnosis of infection difficult. Additionally, a single broomrape plant can produce over 500,000 seeds, which remain viable in the soil for decades [17].

Crop rotation has been for a long time an important agricultural practice designed to disrupt the life cycle of *O. cumana* Wallr. [18]. It is recommended to use rotation with non-host crops and sunflowers should be returned to the same field after a minimum of 6-7 years [19]. The recommended six-year rotation between successive sunflower crops was respected in only 11% and 6% of farms analyzed in 2014 and 2020 in the Republic of Moldova, respectively. In most cases, the sunflower returned to the same field after three years (observed in 35% of households) or four years (29%) [3].

In larger households, sunflowers returned to the same plot after four or more years in 67% of cases, while in small and medium-size households, this rate was 44% and 18.2%, respectively. The small size and the disaggregated nature of planting plots restrict the ability to respect the correct crop rotations [3].

Although there are various control strategies for parasitic angiosperms, due to the complexity of host-parasite interactions (biochemical, physiological and genetic), none of them are sufficiently effective and economically feasible, their management remains to be a challenge.

Advanced agronomic practices, such as precision agriculture and remote sensing technologies, can significantly enhance the monitoring and management of *O. cumana* infestations. These technologies facilitate early detection of parasite outbreaks, allowing for timely intervention and the implementation of site-specific control measures, thereby minimizing damage and optimizing crop yields. Tools such as GPS, sensors, and drones enable better monitoring of *O. cumana* infestations. Early detection allows for prompt action to mitigate damage and improve yields. Remote sensing technologies provide real-time monitoring of crop health and early identification of stress factors, including parasitic infestations. Satellite imagery and aerial drone surveys can help pinpoint areas at risk of infestation, supporting targeted management strategies.

A breeding program for sunflower resistance to broomrape integrates both traditional and modern molecular techniques and involves several key steps to develop genotypes that can provide long-term resistance to broomrape.

Breeding of sunflower for resistance to O. cumana

Mass selection was employed in the initial phases of sunflower breeding for resistance to broomrape, the sources of resistance being identified among Russian local sunflower populations. Seeds from the resistant genotypes were collected and sow the following years until desired traits are obtained. After that, the genotypes were evaluated for resistance to broomrape, as well as other important agronomic traits, under natural infested fields. This process involved multiple cycles of selection to identify and select resistant plants [20]. Consequently, several of the first resistant open-pollinated varieties were developed, including Saratovsky 169, Saratovsky 206, Kruglik A-41, Zelenka, Fuksinka, Zhdanovsky 6432, Zhdanovsky 8281, and Stepnyak [21].

Simultaneously, the classical hybridologic analyses were conducted, revealing dominance in F_1 and Mendelian segregation in F_2, which confirmed the monogenic inheritance of resistance to broomrape [21]. Subsequently, five unique dominant genes (*Or1, Or2, Or3, Or4,* and *Or5*) were identified, each associated with specific physiological races (A-E) of *O. cumana*. These genes exhibit a cumulative mechanism, providing resistance to both new and previous (less virulent) races: A; A + B; A + B + C; A + B + C + D; and A + B + C + D + E. Also, a set of differential lines carrying *Or1, Or2, Or3, Or4*, and *Or5* genes were developed, characterized and proposed for the identification of broomrape races [22].

The monogenic, dominant character of the resistance of the sunflower to the A-E races of the broomrape, controlled by the genes *Or1-Or5,* was confirmed in genetic studies involving populations of *O. cumana* from various geographical areas. These studies have a substantial contribution to the creation of resistant hybrids in Central and Western European countries.

Deviations from the classic monogenic inheritance and different mechanism of resistance have been established, in particular, for the more virulent broomrape populations representing the F, G or H race [23-25].

Researches have shown that the inheritance of resistance to race F is not only determined by a dominant gene, but can also be controlled by two recessive alleles or by a combination of a dominant allele and a recessive one, which interact epistatically [26]. In contrast to other known *Or* genes, these specific genes do not confer resistance to previous races, including race E [27]. The genes for resistance to *O. cumana* populations, which belong to the new virulent races G and H, have been identified in cultivated and wild sunflowers. Genetic studies have confirmed both dominant monogenic control [28] and recessive inheritance [29, 30], as well as polygenic determinism, with two independent dominant genes identified [31]. Also, several major quantitative trait loci (QTL) have been identified for these new virulent broomrape races [24, 25].

Using a set of genotypes with resistance to different broomrape races the racial status of *O. cumana* in eight sunflower-growing countries, in special along the Black Sea region, was determined [32] and a fast evolution of races was revealed.

Phenotypic analysis

Phenotyping for resistance to *O. cumana*, along with the evaluation of broomrape population virulence, is typically conducted under field and/or greenhouse conditions, focusing on the number of broomrape emergences on sunflower plants. An analysis of the infestation levels in differential lines with 43 broomrape populations from Moldova revealed significant changes in race composition from 2014 to 2020, highlighting the need for innovative control strategies [32]. In 2020, increased parasite virulence was observed in most localities compared to 2014 (Tab. 1), with the identified races primarily consisting of the most virulent biotypes (G, H, and possibly I), showing greater aggressiveness in southern Moldova.

Table 1. The racial status of broomrape populations in different localities of the Republic of Moldova in 2014 and 2020.

Populations	Races		Populations	Races		Populations	Races	
	2014	2020		2014	2020		2014	2020
Soroca	G	≥H	Holercani	≤ E	H	Popeasca	F	G
Balti	H	H	Chișinău	≤ E	G	Congaz	H	H
Prepelita	F	H	G. Galbenii	G	≤ E	Svetlâi	H	≥H

In addition to field and greenhouse experiments, pot experiments and mini-rhizotron systems have become increasingly popular for the evaluation of resistance in controlled conditions. Recently, alternative phenotyping methods that allow more precise assessment of parasite-host interactions at early stages, using indirect measures of broomrape attack, such as leaf chlorophyll or fluorescence have been proposed. Techniques like hyperspectral measurements (red/far-red ratios [33], blue-green fluorescence, and thermal imaging [33] have effectively distinguished between broomrape-infected and healthy plants. Additionally, various rhizotron systems, including those coupled with image acquisition systems, enable monitoring of broomrape on sunflower roots at early stages, allowing for automatic counting of tubercles [34, 35]. These systems could efficiently facilitate screening of sunflower genotypes at the tubercle stage, reducing the time required for manual counting.

Recent advances in molecular biology, genomics, and biotechnology have significantly impacted breeding practices. To facilitate the introgression of broomrape resistance genes into sunflower lines, it is essential to identify molecular markers linked to *Or* resistance genes.

The first reports in the field refer to the identification of the RAPD (Random amplification of polymorphic DNA) marker (UBC120_660) at a distance of 22.5 cM distal to the *Or5* gene and five SCAR (Sequence Characterized Amplified Region) markers – RTS05, RTS28, RTS40, RTS29, RTS41, located at the opposite end of the gene [36]. They were mapped at a distance of 5.6-39.4 cM proximal to the *Or5* locus, the closest being RTS05.

Using SSR (Simple Sequence Repeat) genotyping by fluorescent multiplex PCR as a screening tool for segregating populations, Tang et al. (2003) mapped the *Or5* gene, which confers resistance to broomrape race E in sunflower, to the telomeric region of linkage group 3. They identified the nearest SSR marker, ORS1036, located 7.5 cM downstream [37].

The studies carried out by Lu et al. [36] on resistant and susceptible lines demonstrated the presence of the 650 bp amplicon, generated by RTS05 specific primers, only in resistant genotypes. The presence of the respective amplicon is associated with the presence of the *Or5* gene, which confers resistance to race E. The RTS05 marker was applied for molecular screening of different sunflower genotypes cultivated in the Republic of Moldova to achieve a rapid and accurate selection of plants carrying resistance genes. Thus, using the RTS05 marker approximatively 70 sunflower genotypes (local hybrids and perspective lines) were analyzed and the presence of *Or5* were found [7, 14].

Employing SSR analysis Imerovski et al. has identified several potential markers associated with dominant resistance genes, revealing significant associations between *Or6* and alleles ORS1036_240 and ORS1114_265, gene *Or4* and ORS665_281, ORS1114_264 alleles, and gene *Or2* with ORS1114_260. These markers are located in linkage group 3 (LG3), confirming the hypothesis that various resistance genes are tightly linked within the same linkage group [29].

Recently, the same research group mapped a new gene, designated *Orab-vl*-8, in linkage group 3, which confers resistance to broomrape races more virulent as race F, in the inbred line ABB-VL-8. This gene was identified as recessive. The closest marker to the gene was ORS683 with the genetic distance of 1.5 centimorgan. Additionally, a major gene (*HaOr7*) conferring resistance to the F race of *O. cumana* has been mapped on chromosome 7 [38] Fernández-Aparicio et al. [39] located the *OrDeb2* gene, providing resistance to broomrape race G, within a genomic interval on chromosome 4. Furthermore, Martin-Sanz et al. [40] mapped the *OrSII* gene, which offers late post-attachment resistance to broomrape races F and G, to the same region on chromosome 4.

In addition to the major resistance genes, molecular analyses have identified several quantitative trait loci (QTLs) associated with resistance to broomrape. Pérez-Vich and colleagues identified five QTLs (or1.1, or3.1, or7.1, or13.1, and or13.2) conferring resistance to race E, with or3.1 corresponding to the dominant gene *Or5*. The QTLs located in linkage groups 1, 7, and 13 exhibit minor effects. For genotypes resistant to race F, six QTLs were identified in linkage groups 1, 4, 5, 13, and 16, all showing minor effects [24]. Recently, a total of 17 QTLs were discovered across nine different linkage groups, specific to various broomrape races (E and F) and pathogen developmental stages. One of these QTLs, located in linkage group 13, controls the number of *O. cumana* shoots and is the most stable marker for resistance to both analyzed races [25].

The polygenic nature of resistance to more virulent broomrape races was further confirmed in studies by Imerovski et al., which revealed multiple QTLs contributing to resistance. The researchers mapped two major QTLs on chromosome 3 (or3.1 and or3.2). The first corresponds to the previously mapped resistance gene Or5, while the second, identified for the first time, is located in the lower region of chromosome 3 and is associated with resistance to broomrape race G, as confirmed by genotyping with a new CAPS marker [23].

Sunflower breeding for sustainable broomrape resistance requires innovative strategies, such as gene pyramiding, which combines multiple genes to combine desirable traits, utilizing recombinant DNA technology or conventional breeding methods. Pyramiding multiple genes and quantitative trait loci (QTL) into a single genetic background enhances the plant's ability to resist parasites compared to single-gene control. However, traditional gene pyramiding faces challenges such as linkage drag, which can persist even after several backcrosses. Thus, employing marker-assisted selection (MAS) for gene pyramiding is a more effective strategy for rapid genetic improvement [41]. For example, two confection sunflower germplasm lines, HA-R20, carrying rust resistance genes R12 and R15 and DM resistance gene PlArg. and HA-R21, carrying rust resistance genes R13 and R15 and DM resistance gene Pl17, were developed using the pedigree breeding method and DNA marker-assisted selection [42].

Recent advancements in CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) gene-editing technology (gene knockouts, base editing, targeted insertions, and transcriptomic and epigenomic modifications etc.) offer promising avenues for developing resistance against the parasites. A comprehensive understanding of the genetic interactions between parasitic plants and their hosts is crucial for identifying suitable target genes for modification. Key defense mechanisms include direct repression of parasitic plant germination and indirect influences on their growth through environmental factors [43]. Recent studies demonstrate the potential of CRISPR-Cas9 to target genes involved in strigolactone biosynthesis and parasitism, enhancing crop resilience [44]. Overall, while challenges remain, CRISPR technology presents substantial opportunities to enhance crop resistance against parasitic threats.

Conclusion

In conclusion, the integration of modern techniques, including advanced agronomic practices, molecular biology, biotechnology, MAS and CRISPR technology provides a comprehensive and sustainable solution to managing *Orobanche cumana* Wallr. This multidisciplinary approach is vital for developing resistant sunflower cultivars that can withstand the evolving threats of parasitic plants. By ensuring food security and environmental resilience, these innovations contribute significantly to the sustainability of global agriculture, safeguarding future generations against the challenges posed by crop pests and diseases.

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