

## VIRULENCE AND AGGRESSIVENESS OF SOME SUNFLOWER BROOMRAPE POPULATIONS BELONGING TO DIFFERENT COUNTRIES

Steliana CLAPCO

Moldova State University, Center of Functional Genetics, 3/2 Academiei Street, Chisinau,  
Republic of Moldova

Corresponding author email: clapcostela@gmail.com

### Abstract

*Broomrape (Orobanche cumana Wallr.) is a non-photosynthetic, obligatory, root parasitic plant, that specifically infects sunflower crop, causing significant yield losses. The parasite is widely spread in the majority of sunflower growing countries from Europe, Middle East and Asia. In the last years broomrape rapidly evolves, developing more aggressive races, which spread to new areas. In order to understand dynamics of pathogen populations and their adaptation to environment the knowledge related the virulence and aggressiveness of plant pathogens are required. Contrary to virulence which reveal the qualitative component of pathogenicity that is expressed vertically, aggressiveness refers to the quantitative variation of pathogenicity on susceptible hosts, without any restriction related to specificity. Present study was focused on the evaluation of aggressiveness of different broomrape populations belonging to different countries, such as Republic of Moldova, Bulgaria, Serbia, Romania, Ukraine, Spain, Turkey and China. Experience was carried out in green house using different sunflower genotypes (without qualitative resistance or genes or caring some or genes). The numbers of aerial and underground broomrape shoots, as well as of tubercles were counted and the frequency, intensity and degree of attack were calculated. The significant differences between broomrape populations for all analysed parameters were found. Thus, the most aggressive populations were those belonging to Soroca, Republic of Moldova and Ismail, Ukraine, followed by some populations from Turkey and Romania.*

**Key words:** sunflower, broomrape, aggressiveness, virulence.

### INTRODUCTION

Virulence and aggressiveness are key characteristics of pathogens. Virulence, defined as the ability of a particular genotype of parasite to infect a susceptible host, is the qualitative component of pathogenicity and determines the specialization of parasites within host families. Contrary to virulence, aggressiveness is a quantitative component, representing the degree of pathogenicity of the virulent strain. These two traits are interdependent. Thus, if the parasite is avirulent to a particular species or variety of plants, it is not aggressive towards these hosts, while a virulent strain of parasite could manifest different level of aggressivity (high, moderate or low), causing disease to a strong or weak degree (Shaner et al., 1992; Dyakov et al., 2007).

Host plant-pathogen association coevolves, so that, resistance and pathogenicity depend on specific interactions between single or multiple genes, determining qualitative or quantitative resistance in hosts, with the specific genes in parasites. Hosts and parasites may modulate the dynamics and genetic structure of each other, so

in response to disease emergence, hosts evolve resistance, which reduces pathogen invasion, while the pathogens evolve greater virulence and aggressiveness as response to the selection imposed by qualitative and quantitative resistance of host (Woolhouse et al., 2002).

In many pathosystems interaction between host and parasite follows gene-for-gene model, with complete resistance in the host and avirulence in parasite, determined by *R* and, respectively, *Avr* dominant genes (Flor, 1971). According to Van der Plank, virulence is expressed vertically and it is linked to the presence or absence of *R* genes, whereas aggressiveness, mostly determined polygenic, is expressed horizontally, without specificity to host genotypes (Van der Plank, 1968). The products of *Avr* genes may act as effectors of pathogen virulence (Mundt, 2014; Jones and Dangl, 2006). Recent reports suggest that aggressiveness is also conditioned by minor gene-for-gene interactions (Niks et al., 2015).

The evolution of virulence ensures the emergence of pathogens, extension of hosts range, overcoming of specific host resistance genes and development of new pathotypes/

physiological races able to successful invasion and may compromise the effectiveness of control strategies. The phenotypic variation in aggressiveness is a key factor for pathogen adaptation to host and environment (Sacristan et al., 2008). It has to be mentioned that parasites present significant differences in aggressiveness, even they belong to the same pathotype, which are apparently homogenous (Pariaud et al., 2009; Geffroy et al., 2000). Large variation in aggressiveness has been detected within and between populations of different agriculturally important fungal pathogens, such as *Puccinia striiformis* f. sp. *tritici* (Milus et al., 2006), *P. triticina* (Pariaud et al., 2007), *Phytophthora infestans* (Andrison et al., 2007), as well as parasitic angiosperm (Molinero-Ruiz and Melero-Vara, 2004).

In order to understand dynamics of pathogen populations and their adaptation the knowledge related the aggressiveness and virulence of plant pathogens are required (Leach et al., 2001).

Parasitic angiosperm *Orobanche cumana* Wallr. is one of the most critical constraints for sunflower production in the majority of European countries, as well as in the Middle East and Asia. In the last two decades, the aggressiveness and virulence of sunflower broomrape, naturally distributed from central Asia to south-eastern Europe, increased significantly and highly virulent races have appeared and spread very quickly to new areas outside the natural distribution area, such as France, Northern Spain, United Kingdom, Tunisia, Morocco and Portugal (Parker, 2014; Jestin et al., 2014; González-Cantón et al., 2019; Pineda-Martos et al., 2014).

The continuous introduction of new sunflower hybrids with monogenic race-specific resistance exert a selection pressure on broomrape populations evolution and contribute to the development of new more virulent races that overcome sunflower genetic resistance of cultivated genotypes (Rubiales, 2018). Thus, until now, eight races of *O. cumana*, A through H, have been identified.

Present study was focused on the evaluation of virulence and aggressiveness of different broomrape populations belonging to different countries, such as China, Turkey, Bulgaria, Serbia, Spain, Ukraine, Romania and Republic of Moldova.

## MATERIALS AND METHODS

The virulence and aggressiveness of 27 populations of *O. cumana* was assessed and compared after infection of five sunflower inbred lines and hybrids. Particularly, as biological materials were used broomrape populations belonging to China (Inner Mongolia – nr. 1 and 6; He Bei); Turkey (Edirne, Merkez; Edirne, Kesan; Kirklareli, Luleburgaz; Adana); Bulgaria (Debovo); Serbia (conventionally noted as – ORSR 04; ORSR 07; ORSR 11; ORSR 14; ORSR 24; ORSR 25; ORSR 43); Spain (Seville); Ukraine (Ismail); România (Braila; Tulcea); Republic of Moldova (Cazanesti; Singera; Carabetovca; Rassvet; Chisinau; Popeasca; Sarata-Mereseni; Soroca).

The virulence of *O. cumana* populations was evaluated on a set of differential lines and sunflower commercial hybrids carrying different genes of resistance, including one susceptible (Performer from National Agricultural Research and Development Institute Fundulea – NARDI) and four resistant genotypes, as follow: LC1003A (from NARDI) – resistant to race E; LC1093A (NARDI) – resistant to race F; H<sub>1</sub>E – resistant to race G (NARDI) and H<sub>2</sub>Lg (Limagrain) – resistant to race H. Thirty plants for each sunflower line, separated into two replications of fifteen plants each, have been planted in boxes, which contained a mix of sand and peat in ratio 1:1, v/v, uniformly infected with broomrape seeds (30 mg seeds at 200 g of mix) from each population. The sunflower lines were grown in the greenhouse for 80 days at 18/24°C (night/day) temperatures with a 14h/10h photoperiod.

After the cultivation period, the plant root system was removed from the substrate and washed. To establish the aggressiveness of broomrape populations the total number of infested plants, as well as the number of broomrape attachments (tubercles, aerial and underground shoots) per host was quantified. The incidence of broomrape (attack frequency) and the average number of broomrape attachments per plant (attack intensity) have been established using the following formulas:

$F (\%) = (N / Nt) \times 100$ , where

*N* – number of infested plants,

*Nt* – total number of observed plants;

$I = a / N$ , where  
*a* – total number of broomrape attachments,  
*N* – number of infected plants.

## RESULTS AND DISCUSSIONS

Resistance to *O. cumana* in sunflower is controlled by a combination of qualitative, race-specific resistance, associated with *Or*, dominant genes, and quantitative, non-race specific resistance, determined by multiple genes. The first type of resistance affects the presence or absence of infection with broomrape, while the second one affects the number of *O. cumana* attachments per host plant (Pérez-Vich et al., 2004).

Broomrape populations analysed in present study shown different pattern of virulence. All populations have infected susceptible hybrid Performer and were avirulent against the genotype H<sub>2</sub>Lg carrying genes of resistance to race H (Table). The most virulent were the populations from Turkey, Romania, Ukraine, one population collected from China (Inner Mongolia region) and two from the Republic of Moldova (Soroca and Sarata Mereseni), which affected all sunflower genotypes, excepting the hybrid H<sub>2</sub>Lg. Such results are not surprising, as it is known that more virulent broomrape races were found especially in the countries around the Black Sea (Molinero-Ruiz et al., 2015). Also, according to recent studies highly virulent race G was identified in China, being mainly limited to the western part of Inner Mongolia (Shi et al., 2015).

Six of analysed populations (Inner Mongolia nr. 1, He Bei, China; Debovo, Bulgaria; Seville, Spain; Popeasca and Chisinau, Moldova) parasitized only the deferential lines LC1003 and LC1093 carrying *Or5* and *Or6* genes conferring resistance to race E and F, and two populations belonging from Moldova (Carabetovca and Rassvet) affected only the line LC1003. The results are supported by previously reported data. Thus, the presence of new virulent populations of broomrape able to parasitize most of the race F resistant hybrids has been revealed in sunflower fields from Bulgaria and Spain (Shindrova and Penchev, 2012; Martin-Sanz et al., 2016).

Moldovan broomrape populations from Chisinau and Stefan-Voda (Popeasca) have

affected inclusively LC1093 line resistant to race F, contrary to previously reported data, when they showed virulence only on the susceptible genotype and LC1003 line (Duca et al., 2017). These results suggest the existence of pathotypes with different virulence in the same or nearly situated fields. A high heterogeneity in virulence of broomrape and presence in the same field of an admixture of biotypes (races), where one or other type is dominant, was reported by Antonova et al. (Antonova et al., 2020).

Table. Virulence of *O. cumana* belonging to different countries on sunflower differential lines

Broomrape populations	Performer (sensible)	LC1003A (resistant to race E)	LC1093A (resistant to race F)	H <sub>1</sub> E (resistant to race G)	H <sub>2</sub> Lg (resistant to race H)
<b>China</b>					
Inner Mongolia nr. 1	+	+	+	-	-
Inner Mongolia nr. 6	+	+	+	+	-
He Bei	+	+	+	-	-
<b>Turkey</b>					
Edirne, Merkez	+	+	+	+	-
Edirne, Keşan	+	+	+	+	-
Kirklareli, Luleburgaz	+	+	+	+	-
Adana	+	+	+	+	-
<b>Bulgaria</b>					
Debovo	+	+	+	-	-
<b>Serbia</b>					
ORSR 04	+	-	-	-	-
ORSR 07	+	-	-	-	-
ORSR 11	+	-	-	-	-
ORSR 14	+	-	-	-	-
ORSR 24	+	-	-	-	-
ORSR 25	+	-	-	-	-
ORSR 43	+	-	-	-	-
<b>Spain</b>					
Seville	+	+	+	-	-
<b>Ukraine</b>					
Ismail	+	+	+	+	-
<b>Romania</b>					
Braila	+	+	+	+	-
Tulcea	+	+	+	+	-
<b>Republic of Moldova</b>					
Cazanesti	+	-	-	-	-
Singera	+	-	-	-	-
Carabetovca	+	+	-	-	-
Rassvet	+	+	-	-	-
Chisinau	+	+	+	-	-
Popeasca	+	+	+	-	-
Sarata Mereseni	+	+	+	+	-
Soroca	+	+	+	+	-

“+” indicates compatible interaction (presence of infection) and “-” indicates incompatible interaction (absence of infection).

The less virulent were the *O. cumana* belonging from Serbia, which infested only the susceptible hybrid, being highly aggressive against it (number of broomrape shoots per plant ranged from 7.3 to 14.0, with the incidence of attack

50.0-93.8%). In contrast to frequent changes in race composition and rapid appearance of new more virulent pathotypes of broomrape reported in Russia, Ukraine, Moldova, Romania, Turkey and Spain, data regarding racial status of this parasite in Serbia supported the opinion of slow evolution of *O. cumana*. Even the first report on broomrape in Serbian sunflower growing areas dates from 1951, until now only two races have been identified, the most virulent being race E (Miladinovic et al., 2014). Recently the presence of race F on small infestation spots has been established (Dedic et al., 2018).

Unlike virulence, aggressivity as a quantitative trait can be discussed in terms of a higher or lower level (Dyakov et al., 2007). In many

cases, plant parasites manifest different levels of aggressiveness even within the same race. Thus, significant differences in aggressiveness were found among *P. halstedii* pathotypes (Sakr, 2013) and *O. cumana* race F (Molinero-Ruiz et al., 2009).

The analysed broomrape populations showed different aggressiveness on the susceptible sunflower hybrid and genotypes resistant to different *O. cumana* races. The incidence of parasite ranged between 40.0-100.0%; 26.7-100.0%; 11.0-100.0% and 5.0-100.0%, with average numbers of attachments per plant between 1.4-22.9; 1.0-9.4; 1.0-5.0 and 1.0-5.9, on susceptible hybrid Performer, LC 1003, LC1093 and H<sub>1</sub>E, respectively (Figure 1-4).

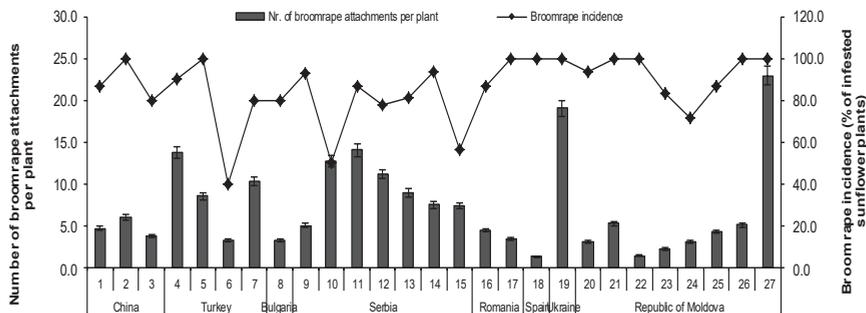


Figure 1. The broomrape incidence and average number of *Orobanche cumana* attachments per plant on the sunflower susceptible hybrid Performer

1 – Inner Mongolia, nr. 1; 2 – Inner Mongolia nr. 6; 3 – He Bei; 4 – Edirne, Merkez; 5 – Edirne, Kesan; 6 – Adana; 7 – Kirkareli, Luleburgaz; 8 – Debovo; 9 – ORSR 04; 10 – ORSR 07; 11 – ORSR 11; 12 – ORSR 14; 13 – ORSR 25; 14 – ORSR 26; 15 – ORSR 43; 16 – Braila; 17 – Tulcea; 18 – Seville; 19 – I-smail; 20 – Cazanesti; 21 – Sangera; 22 – Carabetovca; 23 – Rassvet; 24 – Chisinau; 25 – Popeasca; 26 – SarataMereseni; 27 – Soroca.

Hybrid Performer was most severely affected, with high level of incidence (80 to 100%) and a high number of attachments per plant (10.3 to 22.9), by two broomrape populations from Turkey (Edirne, Merkez and Kirkareli, Luleburgaz), one populations from Serbia (ORSR11), one collected from Soroca, Moldova and Ukrainian broomrape. The highest level of aggressivity was observed in the case of broomrape from Soroca (Figure 1).

A moderate incidence of attack (40.0 and 50.0%), with moderate and high number of broomrape shoots was revealed in the Adana (Turkey) and ORSR07 populations. A low number of attachments per plant (1.3 to 2.2) and high level of incidence (83.3 to 100.0%) was showed by two populations from Moldova

(Carabetovca and Rassvet) and Spanish *O. cumana*.

About a half of populations virulent against the sunflower line LC1003 with resistance to race E manifested a high level of attack (75.0 to 100.0%) and moderate number of attachments per host (3.8 to 9.4) (Figure 2).

The maximal values were observed in the case of Ukrainian population, followed by the populations from Chisinau and Soroca (Moldova), Tulcea (Romania) and broomrape belonging from Edirne, Kesan and Kirkareli, Luleburgaz (Turkey). The less aggressive populations were those collected from Inner Mongolia, China (conventionally noted as nr. 6) and Popeasca, Moldova, with 1-2 attachment per plant and moderate level of incidence (31.3 and 26.7%, respectively).

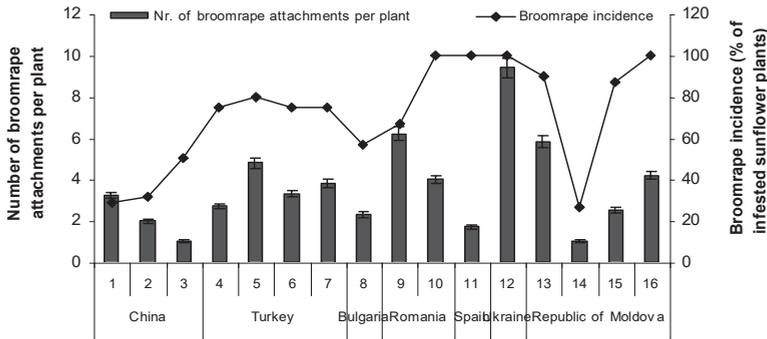


Figure 2. The broomrape incidence and average number of *Orobancha cumana* attachments per plant on the sunflower line LC1003A resistant to race E

1 – Inner Mongolia, nr. 1; 2 – Inner Mongolia nr. 6; 3 – He Bei; 4 – Edirne, Merkez; 5 – Edirne, Kesan; 6 – Adana; 7 - Kirklareli, Luleburgaz; 8 – Debovo; 9 – Braila; 10 – Tulcea; 11 – Seville; 12 – Ismail; 13 – Chisinau; 14 – Popeasca; 15 – Sarata Mereseni; 16 – Soroca.

*O. cumana* belonging from Turkey, Romania (Braila), Ukraine and Moldova (Soroca) were the most aggressive inclusive against line LC1093 resistant to broomrape race F (Figure 3). The number of detected broomrape shoots ranged from 3.3 to 5.0, with high number of parasitized plants (80.0 to 100.0%).

Sunflower genotype was least affected, with an average of 1.2 to 2.0 broomrape attachments per host and incidence of attack 11.0-35.7%, by populations from Adana (Turkey), Popeasca (Moldova) and Inner Mongolia nr. 1 (China).

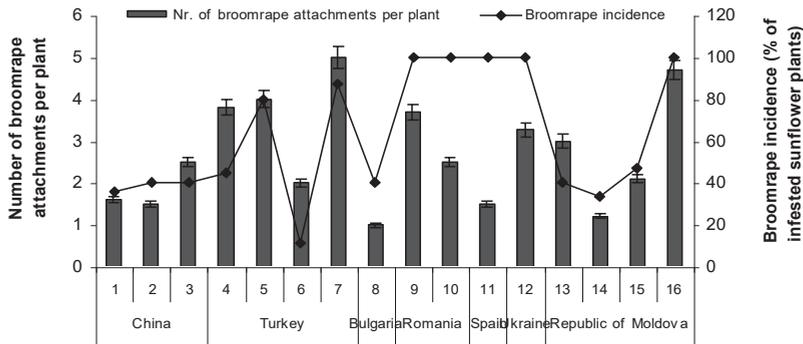


Figure 3. The broomrape incidence and average number of *Orobancha cumana* attachments per plant on the sunflower line LC1093A resistant to race F

1 – Inner Mongolia, nr. 1; 2 – Inner Mongolia nr. 6; 3 – He Bei; 4 – Edirne, Merkez; 5 – Edirne, Kesan; 6 – Adana; 7 - Kirklareli, Luleburgaz; 8 – Debovo; 9 – Braila; 10 – Tulcea; 11 – Seville; 12 – Ismail; 13 – Chisinau; 14 – Popeasca; 15 – Sarata Mereseni; 16 – Soroca.

Only 10 from 27 *O. cumana* populations presented virulence on the H<sub>1</sub>E hybrid with resistance to race G (Figure 4). Broomrape belonging from Luleburgaz, Edirne Merkez and Kesan (Turkey), Ismail (Ukraine) and Tulcea (Romania) manifested a similar pattern of aggressivity – 80.0-100.0% of parasitized host plants and a moderate number of shoots per plant (3.6 to 5.9).

There were significant differences in aggressivity between populations of *O. cumana* with similar virulence (that infect the same host genotypes). Thus, a part of populations, which attacked all sunflower genotypes (excepting H<sub>2</sub>Lg) and supposed to belong to race H, are characterized by low or moderate level of aggressivity (ex. Inner Mongolia nr. 6, Adana, Sarata Mereseni), while other were highly aggressive

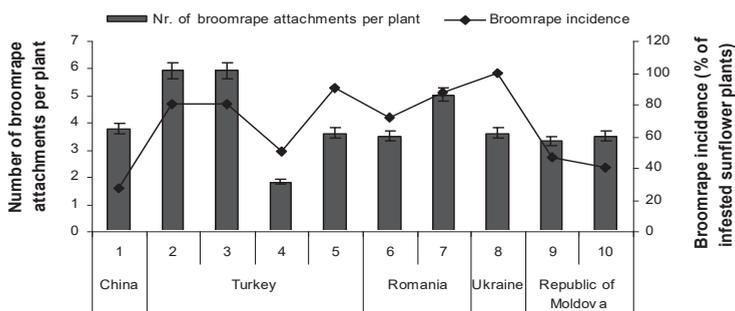


Figure 4. The broomrape incidence and average number of *Orobancha cumana* attachments per plant on the sunflower hybrid H1E resistant to race G

1 – Inner Mongolia, nr. 6; 2 – Edirne, Merkez; 3 – Edirne, Kesan; 4 – Adana; 5 - Kirklareli, Luleburgaz; 6 – Braila; 7 – Tulcea; 8 – Ismail; 9 – Sarata Mereseni; 10 – Soroca.

The highest level of aggressivity against all host genotypes was observed in populations from Turkey (Kesan and Luleburgaz), Romania, Ukraine and Moldova (Soroca), the data being in accordance with those reported by other researchers (Pacureanu et al., 2012; Molinero-Ruiz et al., 2013; Rîșnoveanu et al., 2016). According to obtained data the populations from China are less aggressive as European and Turkish broomrape.

## CONCLUSIONS

The results of the study of twenty-seven populations of broomrape belonging to different sunflower growing countries (China, Turkey, Bulgaria, Serbia, Spain, Ukraine, Romania and Republic of Moldova) showed their heterogeneity in virulence and aggressiveness. The most aggressive populations with a wide virulence were those from Turkey, Ukraine, Romania and Republic of Moldova. Knowledge related sunflower parasite *O. cumana* and periodic monitoring of pathogenicity of broomrape from different fields are important to design feasible and long-term control strategies.

## ACKNOWLEDGEMENTS

We thank prof. Maria Pacureanu-Joita (National Agricultural Research and Development Institute, Romania), dr. Luxita Risnoveanu (Agricultural Research and Development Station of Braila, Romania), prof. Yalcin Kaya (Trakya University, Turkey), prof. Valentina Encheva (Dobrudja Agricultural Institute, Bulgaria), prof.

Dragana Miladinovic (Institute of Field and Vegetable Crops, Serbia) and prof. Jun Zhao (Inner Mongolia Agricultural University, China) for providing broomrape seeds samples for the research.

This study was supported by the national research project 20.80009.5107.01 „Genetico-molecular and biotechnological studies of the sunflower in the context of sustainable management of agricultural ecosystems”.

## REFERENCES

- Andrison, D., Pilet, F., Montarry, J. (2007). Adaptation of *Phytophthora infestans* to partial resistance in potato: evidence from French and Moroccan populations. *Phytopathology*, 97. 338–343.
- Antonova, T.S., Araslanova, N.M., Pitinova, J.V. (2020). Racial belonging of broomrape (*Orobancha cumana* Wallr.) seeds, collected on the fields of different regions of the Russian Federation in 2019. *Agrarian Science*, 339(6), 62–65.
- Dedić, B., Miladinović, D., Jocić, S., Cvejić, S., Jocković, M., Miklić, V. (2018). Increase in virulence of sunflower broomrape in Serbia. *Proceedings of the 4th International Symposium on Broomrape in Sunflower, Bucharest, Romania, 2–4 July 2018*, 27–35.
- Duca, M., Acciu, A., Clapco, S. (2017). Distribuția geografică și caracteristica unor populații de *O. cumana* din Republica Moldova. *Buletinul Academiei de Științe a Moldovei. Științele vieții*, 332(2), 65–76.
- Dyakov, Yu. T., Dzhavakhiya, V.G., Korpela, T. (2007). *Comprehensive and Molecular Phytopathology*, Elsevier.
- Flor, H. H. (1971). Current status of the gene-for-gene concept. *Annual Review of Phytopathology*, 9. 275–279.
- Geffroy, V., Sévignac, M., De Oliveira, J. C., Fouilloux, G., Skroch, P., Thoquet, P. et al. (2000). Inheritance of partial resistance against *Colletotrichum lindemuthianum* in *Phaseolus vulgaris* and co-localization of quantitative trait loci with genes

- involved in specific resistance. *Molecular Plant-Microbe Interactions*, 13, 287–296.
- González-Cantón, E., Velasco, A., Velasco, L., Pérez-Vich, B., Martín-Sanz, A. (2019). First Report of Sunflower Broomrape (*Orobanche cumana*) in Portugal. *Plant Disease*, 103(8).
- Jestin, C., Lecomte, V., Duroueix, F. (2014). Current situation of sunflower broomrape in France. *Proc. 3rd Int. Symp. on Broomrape (Orobanche spp.) in Sunflower, Córdoba, Spain. Int. Sunflower Assoc., Paris, France*, 28–31.
- Jones, J.D., Dangl, J.L. (2006). The plant immune system. *Nature*, 444(7117), 323–332.
- Leach, J.E., Cruz, C.M.V., Bai, J., Leung, H. (2001). Pathogen fitness penalty as a predictor of durability of disease resistance genes. *Annu Rev Phytopathol*, 39, 187–224.
- Martín-Sanz, A., Malek, J., Fernández-Martínez, J., Pérez-Vich, B., Velasco, L. (2016). Increased Virulence in Sunflower Broomrape (*Orobanche cumana* Wallr.) Populations from Southern Spain Is Associated with Greater Genetic Diversity. *Frontiers in Plant Science*.
- Miladinović, D., Jocić, S., Dedić, B., Cvejić, S., Dimitrijević, A., Imerovski, I., Malidža, G. (2014). Current situation of sunflower broomrape in Serbia. *Proc. 3rd Int. Symp. on Broomrape (Orobanche spp.) in Sunflower, Córdoba, Spain. Int. Sunflower Assoc., Paris, France*, 33–38.
- Milus, E.A., Seyran, E., McNew, R. (2006). Aggressiveness of *Puccinia striiformis* f. sp. *tritici* isolates in the south-central States. *Plant Disease*, 90, 847–852.
- Molinero-Ruiz, L., Delavault, Ph., Pérez-Vich, B., Pacureanu-Joita, M., Bulos, M., Altieri, E., Domínguez, J. (2015). History of the race structure of *Orobanche cumana* and the breeding of sunflower for resistance to this parasitic weed: A review. *Spanish Journal of Agricultural Research*, 13(4), 1–19.
- Molinero-Ruiz, L., García-Carmeros, A., Collado-Romero, M., Raranciuc, S., Domínguez, J., Melero-Vara, J. (2013). Pathogenic and molecular diversity in highly virulent populations of the parasitic weed *Orobanche cumana* (sunflower broomrape) from Europe. *European Weed Research Society*, 54, 87–96.
- Molinero-Ruiz, M. L., Melero-Vara, J. M. (2004). Virulence and aggressiveness of sunflower broomrape (*Orobanche cumana* Wallr.) populations overcoming the *Or5* gene. *Proc. 16th International Sunflower Conf., Fargo, USA, Int. Sunfl. Assoc., Paris, France*, 165–169.
- Molinero-Ruiz, M., Garcia-Ruiz, R., Melero-Vara, J. M., Domínguez, J. (2009). *Orobanche cumana* race F: performance of resistant sunflower hybrids and aggressiveness of populations of the parasitic weed. *Weed Research*, 49, 469–478.
- Mundt, C.C. (2014). Durable resistance: A key to sustainable management of pathogens and pests. *Infect Genet Evol.*, 446–455.
- Niks, R. E., Qi, X., Marcel, T. C. (2015). Quantitative resistance to biotrophic filamentous plant pathogens: Concepts, misconceptions, and mechanisms. *Annual Review of Phytopathology*, 53, 445–470.
- Pacureanu-Joita, M., Ciuca, M., Sava, E. (2012). Broomrape (*Orobanche cumana* Wallr.), the most important parasite in sunflower: virulence, race distribution, host resistance. *Proc. 18th International Sunflower Conf., Mar del Plata, Argentina. Int. Sunflower Assoc., Paris, France*, 1–6.
- Pariaud, B., Ravigné, V., Halkett, F., Goyeau, H., Carlier, J., Lannou, C. (2009). Aggressiveness and its role in the adaptation of plant pathogens. *Plant Pathology*, 58, 409–424.
- Pariaud, B., Robert, C., Goyeau, H., Lannou, C. (2007). Quantitative adaptation of wheat leaf rust populations (*Puccinia triticina*) to a host cultivar and correlations between components of aggressiveness. *Phytopathology*, 97, S89.
- Parker, C. (2014). *Orobanche crenata* in UK- an update. *Haustorium*, 65, 5–6.
- Pérez-Vich, B., Akhtouch, B., Mateos, A., Velasco, L., Jan, C., Fernández, J., Domínguez, J., Fernández-Martínez, J.M. (2004). Dominance relationships for genes conferring resistance to broomrape (*Orobanche cumana* Wallr.) in sunflower. *Helia*, 27, 183–192.
- Pineda-Martos, R., Pujadas-Salvà, A., Fernández-Martínez, J., Stoyanov, K., Velasco, L., Pérez-Vich, B. (2014). The Genetic Structure of Wild *Orobanche cumana* Wallr. (*Orobanchaceae*) Populations in Eastern Bulgaria Reflects Introgressions from Weedy Populations. *The Scientific World Journal*, 150432.
- Rîşnoveanu, L., Joita-Păcureanu, M., Anton, F. G. (2016). The virulence of broomrape (*Orobanche cumana* Wallr.) in sunflower crop in Braila Area, in Romania. *Helia*, 39(65), 189–196.
- Rubiales, D. (2018). Can we breed for durable resistance to broomraps? *Phytopathologia Mediterranea*, 57 (1), 170–185.
- Sacristán, S., García-Arenal, F. (2008). The evolution of virulence and pathogenicity in plant pathogen populations. *Mol Plant Pathol.*, 9(3), 369–384.
- Sakr, N. (2013). Pathogenic, morphological and genetic diversity in *Plasmopara halstedii*, the causal agent of sunflower downy mildew. *Acta Sci., Agron.*, 35(1), 9–19.
- Shaner, G., Stromberg, E.L., Lacy, G.H., Barker, K.R., Pirone, T.P. (1992). Nomenclature and concepts of aggressiveness and virulence. *Annu Rev Phytopathol.*, 30, 47–66.
- Shi, B. X., Chen, G. H., Zhang, Z. J., Hao, J. J., Jing, L., Zhou, H.Y., Zhao, J. (2015). First report of race composition and distribution of sunflower broomrape, *Orobanche cumana*, in China. *Plant Dis.*, 2, 291.
- Shindrova, P., Penchev, E. (2012). Race composition and distribution of broomrape (*Orobanche cumana* Wallr.) in Bulgaria during 2007–2011. *Helia*, 35(57), 87–94.
- Van der Plank, J.E. (1968). *Disease Resistance in Plants*. New York, Academic Press.
- Woolhouse, M. E. J., Webster, J. P., Domingo, E., Charlesworth, B., Levin, B. R. (2002). Biological and biomedical implications of the co-evolution of pathogens and their hosts. *Nat. Genet.*, 32, 569–577.