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Genetic Resources of the Sunflower Crop Wild Relatives for Resistance to Sunflower Broomrape

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Abstract: One of the most threatening holoparasitic plant species is *Orobanche cumana* Wallr. (sunflower broomrape), mainly distributed in the Mediterranean region and Western Asia where it exclusively parasitizes sunflowers. Sunflower broomrape (BR) is a very destructive parasitic weed causing significant yield losses under high infestations that can easily spread and is vulnerable to mutations. Broomrape is highly variable, controlled by vertical single dominant resistance genes leading to the rapid and frequent breakdown of resistance. This subsequently leads to the continuing need for new unique genes from multiple sources for controlling new emerging virulent races. The USDA-ARS, National Plant Germplasm System crop wild relatives (CWR) collection contains 2,519 accessions of 53 species with 14 annual species (1641 accessions) and 39 perennial species (878 accessions). This CWR collection provides a vast genetic resource for new BR resistance genes, especially in Europe and the Middle East. Sunflower CWR evaluations for new resistance genes for BR races have demonstrated that they are a substantial reservoir for existing and new emerging virulent races. Resistance to sunflower broomrape, including immunity, has been reported in seven annual and 32 perennial species. These sources discovered in the sunflower CWR confer resistance to new virulent broomrape races F, G, and H, and others that have not been assigned a race designation. Since several of the resistant CWR sources are annual and have the same chromosome number as cultivated sunflower, broomrape resistance genes can be incorporated into hybrid sunflower through interspecific hybridization. The diverse sources of resistance from the CWR provide breeders with the prospect for durable broomrape control through exploiting genetic resistance for existing and newly emerging races.

Keywords: sunflower, broomrape, parasitic weed, *Helianthus* species, genetic resources

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Introduction

The global production of sunflower (*Helianthus annuus* L.) in 2015 was estimated at 23.2 million ha in 72 different countries (USDA, 2016). Oilseed sunflower accounts for up to 12 % of the worldwide production of vegetable oils, ranking fourth after palm, soybean and canola oil (Rauf *et al.*, 2017). One of the most important biotic constraints to sunflower production is *Orobanche cumana* Wallr. (sunflower broomrape), an obligatory and non-photosynthetic root parasitic plant affecting sunflower production, except in North and South America (Cantamutto *et al.*, 2014). Sunflower broomrape (BR) specifically infects sunflower in Central and Eastern Europe and Western Asia (Eizenberg *et al.*, 2003; Höniges *et al.*, 2008; Molinero-Ruiz *et al.*, 2014) and Tunisia (Amri *et al.*, 2012). Plants infected by BR are smaller with reduced head size resulting in up to 80 to100 % reduction in yield (Alcántara *et al.*, 2006; Duca, 2015). Interestingly, BR has not been found in North and South America sunflower growing areas, even though very high levels of resistance (near immunity) have been observed in over two-thirds of the perennial and several of the annual CWR in the absence of multiple BR races in the USA to explain the high level of resistance (Seiler *et al.*, 2017).

In most cases, genetic resistance to *O. cumana* in sunflower is qualitative or vertical, resulting in physiological races that periodically overcome the current sources of resistance (Fernández-Martínez *et al.*, 2015). The deployment of few sources of resistance to sunflower BR, most of them monogenic and dominant, has promoted a continuous development of increasingly virulent forms of the parasite (Velasco *et al.*, 2016). Broomrape resistance genes are denoted as *Or* genes. Eight world races of sunflower BR, A through H (Or_1–Or_7) have been reported thus far, with newer races F, G, and H being the most virulent discovered in the last ten years in Romania, Spain, Turkey, Ukraine, and Russia (Kaya, 2014). The presence of the races by country was reviewed by Molinero-Ruiz *et al.* (2015). Continually emerging new races that overcome existing resistance sources requires a need for new resistant sources.

Sunflower crop wild relatives genebank collection as a genetic resource

Preservation of important crop species cultivars, landraces, and crop wild relatives (CWR) provides the basis for a sustainable agriculture system to provide for a global food supply (Campbell *et al.*, 2010). For over 100 years, CWR have been undeniably beneficial for modern agriculture, by providing breeders with a diverse pool of potentially useful genetic resources (Hajjar and Hodgkin, 2007). Some authors (Palmgren *et al.*, 2015) have suggested that modern crops have lost properties that their CWR once possessed to tolerate emerging pests and ever-changing climate. Anderson *et al.* (2004) predicts that emerging plant diseases and agricultural pests such as BR will become more common and damaging in a warmer climate.

Breeding for resistance in sunflower appears to be the most sustainable and efficient approach to controlling BR. To do this, one needs additional sources of new resistant genes. Fortunately for the sunflower crop, there is a vast untapped germplasm pool of 53 species of sunflower CWR to search for resistance to emerging races of BR (Jan *et al.*, 2014; Marek, 2016; Seiler, 2018; Seiler and Jan, 2014; Seiler and Marek, 2011; Seiler *et al.*, 2017). Sunflower crop wild relatives have been a valuable genetic resource contributing an estimated 26 % of the annual value of the sunflower crop, with most of the value coming from disease resistance (Prescott-Allen and Prescott-Allen, 1986).

The U.S. Department of Agriculture, Agricultural Research Service, National Plant Germplasm System (USDA-ARS, NPGS) mission is to conserve genetic diversity of crop germplasm and associated information, to conduct related research, and to encourage the use of germplasm for crop development. The USDA-ARS, NPGS Germplasm Resources Information Network (GRIN) database serves as the central location of information about the accessions in the sunflower CWR collection, and also serves as the portal for requesting seed of available accessions (https://npgsweb.ars-grin.gov/gringlobal/search.aspx). The NPGS freely distributes available germplasm for research and educational purposes. However, the requester must abide by the regulations of the importing county import permit.

The USDA-ARS NPGS manages and maintains the sunflower CWR collection at the North Central Regional Plant Introduction Station, Ames, Iowa, USA. The CWR collection contains 2,519 accessions of 53 species of *Helianthus*, with 1,028 annual wild *H. annuus* (41 %), 613 accessions representing accessions of the other 13 annual species (24 %), and 878 accessions representing 39 perennial species (35 %) (Seiler *et al.*, 2017). CWR evaluations for resistance to BR have demonstrated that the wild species constitute a substantial reservoir of genes conferring resistance to new race-specific and emerging virulence races. Fernández-Martínez *et al.* (2008, 2000, 2015, 2012), Nikolova *et al.* (2000), Bervillé (2002), Škorić *et al.* (2010), Seiler (2012), Škorić and Păcureanu-Joita (2011), Jan *et al.* (2014), Seiler and Jan (2014) and Seiler *et al.* (2017) reported that sunflower germplasm evaluations for resistance to BR races have demonstrated that the *Helianthus* species are the major reservoir of resistance genes to new emerging virulence races.

Identified sources of sunflower broomrape resistance in crop wild relatives

The first variety of sunflower resistant to race A of BR, Saratovskij 169, was developed by Plachek in 1918 (Molinero-Ruiz *et al.*, 2015). The most important varieties resistant to race B were Peredovik and VNIIMK 8931 (Pustovoit, 1966). Resistance to BR from CWR began early in breeding programs of the former Soviet Union, where *H. tuberosus* L. was introgressed into cultivated sunflower (Pustovoit, 1966; Pustovoit *et al.*, 1976). Pogorietsky and Geshle (1976) described some of the first immunity to BR in lines derived from *H. tuberosus*. This source of resistance probably accounts for some of the resistance observed for the Or_1–Or_5 genes (races A–E) described by Vrânceanu *et al.* (1980). As is often the case in sunflower breeding programs, the search for resistance to the new race F often utilizes wild *Helianthus* species as a major resource (Fernández-Martínez *et al.*, 2000).

Labrousse *et al.* (2001) screened wild and interspecific sunflower for race E and suggested that there are at least two mechanisms responsible for resistance in sunflower. They concluded that resistance may be characterized by the low number of BR attachments, or by necrosis of the attachments. In their experiment with perennial CWR, *H. resinosus* Small and *H. pauciflorus* Nutt. (= *rigidus*) had only a few attachments, while interspecific annual lines LR1 (*H. debilis* subsp. *debilis* Nutt.) and 92BG1 (*H. argophyllus* T.&G.) developed attachments, but later became necrotic. Labrousse *et al.* (2004) suggested that LR1-derived RILs could have polygenic resistance.

Antonova *et al.* (2011) screened accessions of five annual and 16 perennial wild species to BR races F, G, and H from the Rostov region of the Russian Federation. Among the annual species, only *H. petiolaris* Nutt. had a high level of resistance. Most of the perennial species showed very high levels of resistance similar to Ruso *et al.* (1996). Antonova concluded that the potential immunity of the perennials to BR is not related to the absence of a stimulating effect of the host's root exudates on the seed of the parasite but is more likely related to physiological-biochemical features of the cortex of the sunflower root.

Ruso *et al.* (1996) and Fernández-Martínez *et al.* (2000) evaluated CWR for resistance to races E and F and observed high levels of resistance. They observed resistance to races E and F in 29 wild perennial species, while in annual species there were low levels of resistance to race F in only four of eight species, with annual species *H. anomalus* Blake and *H. exilis* A. Gray having the highest resistance. Germplasms BR1–BR4 resistant to race F were developed from interspecific amphiploids derived from perennial CWR of *H. grosseserratus* Martens, *H. maximiliani* Schrad., and *H. divaricatus* L. (Jan and Fernández-Martínez, 2002;

Jan *et al.*, 2002). The dominant-recessive epistasis control of race F resistance complicates the breeding process because the gene needs to be incorporated into both parents (Akhtouch *et al.*, 2002). In other studies, race F inheritance was controlled by a single dominant gene in interspecific amphiploids of *H. annuus* and two wild perennials, *H. divaricatus* L. and *H. grosseserratus* (Pérez-Vich *et al.*, 2002). Velasco *et al.* (2006) reexamined race F resistance in the J1 germplasm derived from *H. grosseserratus* by Pérez-Vich *et al.* (2002) suggesting the resistance was digenic, with the second gene being environmentaly influenced. Other perennial species, *H. giganteus* L., *H. laevigatus* T. & G., *H. pauciflorus* (= *rigidus*), and *H. resinosus* have been reported to have resistance to the Spanish race SE19. An annual interspecific cross of *H. debilis* subsp. *tardiflorus* showed resistance to race G controlled by a dominant gene, O_{rdeb} at a single locus (Velasco *et al.*, 2012).

Shindrova (2006) reported that BR races D, E, and F were found in Bulgaria, with race E widespread in all sunflower production areas, while race F was new to Bulgaria. Resistance to the local race of BR in Bulgaria was reported in perennial *H. divaricatus*, *H. eggertii* Small, *H. giganteus*, *H. grosseserratus*, *H. glaucophyllus* Smith, *H. mollis* Lam., *H. nuttallii* T. & A. Gray, *H. pauciflorus (= rigidus)*, *H. resinosus*, and *H. tuberosus* (Christov, 1996), while interspecific hybrids based on perennial *H. eggertii* and *H. smithii* Heiser were immune (Christov *et al.*, 1998). Nikolova *et al.* (2004) also reported BR resistance (race not specified) in interspecific progenies of *H. pumilus* Nutt. Perennial diploids and their interspecific hybrids of *H. divaricatus*, *H. giganteus*, *H. glaucophyllus*, *H. grosseserratus*, *H. mollis*, *H. nuttallii*, and *H. smithii* were resistant to BR (Nikolova *et al.*, 1998). Christov (2008) reported that several perennial CWR, *H. tuberosus*, *H. eggertii*, *H. smithii*, *H. pauciflorus* (= *rigidus*), and *H. strumosus* L. were completely resistant to existing BR races in Bulgaria and controlled by a single dominant gene. Christov *et al.* (2009) reported that annual species *H. debilis* and *H. argophyllus* were resistant, as well as an interspecific *H. petiolaris* selection. He also reported resistance in perennial accessions and interspecific crosses of *H. ciliaris* D.C., *H. decapetalus* L., *H. maximiliani*, *H. pumilus*, *H. mollis*, and *H. smithii*. Resistance to Bulgarian race G in five annual and 12 perennial species was reported by Christov *et al.* (2013). Entcheva *et al.* (2014) tested 88 accessions of wild annual *Helianthus* species (including *H. annuus*, *H. argophyllus*, *H. debilis*, *H. petiolaris* and *H. praecox* Engelm. & A. Gray) from the collection of the Dobroudja Agricultural Institute, General Toshevo, Bulgaria for resistance to BR race E in the greenhouse. Complete resistance to BR was observed in seven annual accessions of *H. annuus*, two accessions of *H. argophyllus*, two accessions of *H. debilis*, and one each of *H. petiolaris* and *H. praecox*.

In Serbia, resistance to races E and F in fertility restorer lines derived from annual *H. deserticola* Heiser was reported by Hladni *et al.* (2012, 2009, 2010). Terzić *et al.* (2010) reported resistance to race E in Serbia in two accessions of annual *H. debilis*, one *H. neglectus* Heiser, three *H. petiolaris*, and three *H. praecox*. They also reported high levels of resistance in F_1 hybrids with perennial species *H. tuberosus*, *H. pauciflorus* (= *rigidus*), *H. strumosus*, *H. divaricatus*, *H. hirsutus*, *H. eggertii*, *H. decapetalus*, *H. resinosus*, *H. laevigatus*, *H. mollis* and *H. grosseserratus*. Naturalized annual populations of *H. annuus* and *H. petiolaris* from Argentina were screened for resistance to race E in Serbia and found that *H. annuus* was very susceptible, while *H. petiolaris* was totally resistant (Miladinovic *et al.*, 2013). Cvejić *et al.* (2012) reported resistance to race G in fertility restoration lines based on annual *H. deserticola* in Serbia.

Anton *et al.* (2017) screened accessions of *H. praecox*, *H. debilis*, and *H. petiolaris* for resistance to race F in Romania with some having complete resistance, while interspecific hybrids with perennial *H. tuberosus* and *H. maximiliani* and annual *H. argophyllus* had good tolerance to more than race F in the Brăila region of Romania. Additionally, Anton *et al.* (2016) tested interspecific selections based on *H. tuberosus* and *H. maximiliani* to race G and found them to be resistant. Anton *et al.* (2018) field evaluated 24 populations derived from interspecific crosses of four *Helianthus* species of seven populations in the Brăila and Constanţa regions. Seven resistant populations were found with six from Constanţa and one from Brăila. All resistant populations were interspecific crosses with *H. debilis* and *H. maximiliani*. Interspecific hybrids of *H. argophyllus* were screened for resistance to Romanian races G and H with a few lines showing good resistance to BR (Petcu and Pacureanu-Joiţa, 2011, 2012).

Hristova-Cherbadzhi *et al.* (2014) evaluated resistance to the highly virulent race H of BR in five interspecific inbred lines with known resistance to the less virulent BR race F, one F_1 hybrid, and seven lines with an American parent. One F_1 hybrid, A78 × OR-7R, based on OR-7R [= *H. annuus* – 6116A × *H. nuttallii* subsp. *rydbergii* (Britt. & Long)] showed100 % resistance, while the rest of the lines were partially or completely susceptible.

Jockovic *et al.* (2018) evaluated resistance to most dominant BR race E from the Bačka region, Serbia, in the greenhouse using 13 populations of six annual wild *Helianthus* species. In total, nine populations were resistant: *H. debilis* 1134, *H. neglectus* 0457, *H. niveus* 0608, *H. argophyllus*, *H. petiolaris* 0338,1383,1910, and *H. praecox* 1151 and 1340.

Sayago *et al.* (2018) reported the identification of a new source of genetic resistance to *O. cumana* race G in annual wild species *H. praecox*. Eight plants of an *H. praecox* accession from the USDA-ARS NPGS CWR germplasm collection were evaluated with BR race G with none showing any emerged BR shoots.

Resistant interspecific hybrids were produced with the resistance trait controlled by partially dominant alleles at a single gene that was named Or_{pra1}.

Molecular aspects of resistance genes in crop wild relatives

Most BR resistance genes have been reported to be single dominant genes for races A to E and G (Velasco *et al.*, 2012; Vranceanu *et al.*, 1980). Resistance to race F can either be inherited by a single dominant gene depending on the genetic background (Pacureanu-Joita *et al.*, 1998; Pérez-Vich *et al.*, 2004) or by two recessive genes (Dimitrijevic and Horn, 2018; Rodríguez-Ojeda *et al.*, 2001). A single recessive gene in the sunflower line HA-267 was resistant to BR races higher than O_{r6} (Imerovski *et al.*, 2014). In any pyramiding strategy, minor effects genes need to be accounted for since they contribute to the durability of the resistance. This is particularly true if the mode of action occurs at the initial stages of parasitization or if it is complementary to the mode of action of major genes (Velasco *et al.*, 2016).

There have been a few reports of the molecular genetic mapping of resistance loci. Most of the early molecular analyses investigated different types of molecular markers to detect Or_5, the gene conferring resistance to race E (Lu *et al.*, 2000; Perez-Vich *et al.*, 2004; Tang *et al.*, 2003). Iuoras *et al.* (2004) tested the efficiency of RAPD and SSR primers in MAS for the Or_5 gene but concluded that none of the primers were efficient or accurate enough. More recently, a molecular characterization using RAPD-PCR for European populations of BR identified four groups with markers that might be useful as molecular tools to detect first appearances of BR in fields that had been free of virulent races (Molinero-Ruiz *et al.*, 2014). Identification of QTL for BR races F and G resistance involved 586,955 SNPs from the SUNRISE project 8 on GeneTitan® (Affymetrix) (Louarn *et al.*, 2016). Seventeen QTL from a RIL population of HA 89 × LR1 (derived from an interspecific cross with *H. debilis*) were identified that spread throughout nine LGs, among them a stable QTL on LG13 that explained 15–30 % of the phenotypic variability controlling the number of BR emergences for race F in Spain and race G in Turkey (Louarn *et al.*, 2014, 2016). This QTL was noted as one that could be the most rapidly used in marker assisted breeding. Four QTL for BR Spanish race F resistance were identified in an interspecific hybrid population derived from the LR1 line (*H. debilis* × *H. annuus*), with two related to the number of BR tubercles per plant, and two controlling necrosis (Labrousse *et al.*, 2001).

SSR markers associated with Or_2, Or_4, and Or_6 genes were identified by Imerovski *et al.* (2013) that could be used in developing resistance genotypes. Four biparental populations of BR resistant genotypes (HA-267, LIV-10, LIV-17 and AB-VL-8) were tested in Spain, Romania, Ukraine and Russia to identify the QTL resistance and determine the mode of inheritance by Imerovski *et al.* (2019). Numerous QTLs were found in all mapping populations with polygenic resistance common to all populations mapped to two major QTL on chromosome 3, designated or3.1 and or3.2. QTL or3.1 was positioned where the BR gene O_{r5} was previously mapped, while QTL or3.2 was the first to be mapped in the lower region of the same chromosome. The QTL peak for or3.2 and the CAPS markers nearest to the peak confirmed the association of these markers with BR race G resistance. The study provided molecular markers that will be useful for marker assisted selection in sunflower breeding programs.

Crosses between the resistant sunflower inbred line AB-VL-8 and the susceptible line L-OS-1 were used to evaluate the genetic analysis and mapping of a new resistance gene for BR races higher than F (Imerovski *et al.*, 2016). AB-VL-8 is a proprietary sunflower inbred line originating from the gene pool that was obtained by crossing *H. annuus* with *H. divaricatus* (Cvejić *et al.*, 2014). SSR markers revealed polymorphism only on LG3, indicating that presumably the single gene conferred resistance in this region (Imerovski *et al.*, 2013, 2014). The closest SSR marker, ORS683 to the recessive gene was tentatively designated as $O_{rab\text{-}vl\text{-}8}$ at a genetic distance of 1.5 cM. The discovery of the $O_{rab\text{-}vl\text{-}8}$ gene will provide a much-needed new gene from the CWR for races higher than F, and the associated marker will accelerate introgression of the gene into sunflower lines improving breeding efficiency and protecting sunflower from new BR pathotypes. Additional studies will be needed to include other marker techniques such as SNPs to saturate the region surrounding the resistance gene.

Sustainable sunflower broomrape resistance

The development of sustainable BR resistance will require a dedicated global research strategy. Many breeding programs have focused on the development of hybrids based on single dominant *Or* genes for BR resistance. Molinero-Ruiz *et al.* (2015) suggested that at the start of the program the breeder must determine which race or races are present in the region where the hybrids are being developed together with screening for resistance in all generations. However, to increase the durability of genetic resistance, vertical resistance should incorporate gene pyramiding achieved through interspecific hybridization of various sources of resistance. Pérez-Vich *et al.* (2004, 2006) suggest that to achieve the best use of these major genes, one needs to have a quantitative, non-race-specific resistance. One of the current major deficiencies is the lack of QTL and related molecular markers linked to major and minor resistance genes assuring introgression in the breeding process. However, for the success of any breeding strategy, detailed characterization and knowledge is required of the genetic basis of resistance, resistance mechanisms, and the diversity of parasite populations (Rubiales, 2018). The goal of conducting physiological-based breeding and pyramiding resistance genes underlying defense resistance mechanisms is hampered by the lack of information about the physiological basis of the different resistance sources (Pérez-Vich *et al.*, 2013).

Dominant genes for resistance to races A-F have been incorporated into cultivated sunflower. However, in the last fifteen years, new BR populations have been discovered for which a very limited number of hybrids have resistance. Continued discovery of novel resistance sources is imperative since BR races are constantly evolving, overcoming current race-specific genes. The vast gene pool of the 53 species of sunflower CWR needs to be continually exploited for resistance genes for current and emerging virulent races of BR. Broomrape resistance genes can be incorporated into hybrids through interspecific hybridization. Utilization of the CWR as a source of genes needs to shift to a strategy of pyramiding major genes controlling different mechanisms of resistance. Additionally, minor QTL and their associated resistance mechanisms are also important. The continued use of monogenic and dominant genes for control only promotes a continuous development of increasingly virulent races of BR (Fernández-Martínez *et al.*, 2015). Characterization of new resistance sources should include the study of the mode of inheritance, mechanism of resistance involved, and the precise marking of the genes to facilitate the development of accurate molecular markers. The availability of genomic and transcriptomic information from ongoing projects will facilitate the development of molecular tools for a wide diversity of studies on BR (Muños *et al.*, 2015). Currently, no genes have been cloned, and the molecular mechanism involved in resistance remains largely unknown.

While breeding for BR resistance is important, controlling its spread is also important. Special attention is needed to prevent human-driven BR seed dispersal in the crop seed trade, together with BR seed soil banks. A single mature BR plant can produce and disperse up to 100,000 seeds that can retain viability for up to 20 years (Chater and Webb, 1972; Parker, 2013). The minute seeds are easily dispersed by wind, water, and lax phytosanitary practices, but also are often introduced into new areas as contaminants of seed and agricultural equipment (CABI, 2018).

Over the last decade another alternate control of BR has been based on the development of imidazoline (IMI) and sulfonylurea (SU) herbicides, which have a good effective broad spectrum of weed control (Sala *et al.*, 2012). The source of the first genes for IMI and SU resistance was from a wild *H. annuus* population found in a soybean field in Kansas that had been repeatedly treated with imazethapyr herbicide for several years (Al-Khatib *et al.*, 1998). Early on, Alonso *et al.* (1998) advocated for the use of these chemicals for the control of BR. This coupled with resistance genes provides a combination of control providing protection to successfully control BR regardless of the race composition in the area where the herbicides are used. The use of weed control by IMI and SU herbicides is increasing in the areas of BR infestations. Hopefully, the combination of chemicals and genetic resistance will extend the effectiveness of both, but the herbicide traits are based on mutation sites that are not fixed and continuously evolving, similar to the new emerging virulent BR races.

Conclusions

A global set of standardized differentials is needed to clearly identify the current and emerging races A to G found in many countries, as well as studies to assess the similarities of populations from different geographic regions characterized as belonging to the same race (Molinero-Ruiz *et al.*, 2014). The use of the coded triplets system as a simple and global method to internationally determine BR races for standardized characterization and nomenclature of BR has been proposed by Molinero-Ruiz *et al.* (2015). The system is based on populations using the coded triplets system, which is based on the use of eight differential sunflower lines grouped into three sets. This system would standardize the naming of races across the distribution of the BR parasite.

In summary, there is a need for a long-term strategy to control sunflower BR involving: (1) continued discovery of new sources of genes for current and evolving races, (2) understanding the host-parasite interaction system and the integration of classical and molecular techniques, (3) establishment of a common international designation of the existing and new races of BR and genes for resistance in different countries, (4) controlling the spread of BR by anthropogenic forces, and (5) a greater level of collaboration between breeders from public institutions and private companies, which will all contribute to a more durable BR resistance.

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