HELIA, **31**, Nr. 49, p.p. 1-12, (2008) UDC 633.854.78:631.524.86
DOI: 10.2298/HEL0849001H

Orobanche RESISTANCE IN SUNFLOWER

Höniges, A., Wegmann, K.* and Ardelean, A.

Universitatea de Vest „Vasile Goldiş“, Arad, Romania

Received: October 20, 2008
Accepted: December 10, 2008

SUMMARY

This report presents the current knowledge of *Orobanche* resistance in sunflower from the breeder's standpoint and from the biochemists' standpoint.

The parasitic relations in *Helianthus annuus* / *Orobanche cumana* associations differ in many respect from relations of other *Orobanche* spp. and their hosts.

A major difficulty for the breeder is the fast development of new pathotypes of *Orobanche cumana*, which overcome the resistance of newly developed sunflower lines. The basis of increasing aggressiveness of *Orobanche cumana* pathotypes is discussed. Nevertheless, there is still large potential for resistance breeding in the genus *Helianthus*, since very different resistance factors are already known or shall be elucidated.

A survey is presented of known resistance factors, such as low stimulants, mechanical barriers and how they develop, phytoalexins, *Orobanche* seed germination inhibitors, inhibition of exoenzymes of the *Orobanche* radicles, in particular of polygalacturonase, which enables the penetration of *Orobanche* tissue into the host root along the middle lamellae. In this context an interesting new approach may be found in the polygalacturonase-inhibiting proteins occurring in cell walls, which inhibit the invasion of pathogenic fungi.

The need for molecular biological studies will be stressed. Interdisciplinary collaboration of breeders with biochemists and molecular biologists may lead to more advanced breeding strategies.

Key words: sunflower, *Orobanche cumana* resistance, resistance factors, phytoalexins, polygalacturonase inhibitors, phytoalexins

INTRODUCTION

The root parasitic angiosperm *Orobanche cumana* is a major problem in sunflower in all south European countries and Turkey. While biological control has so far been unsuccessful, and the application of herbicides is limited for health and economic reasons, only resistance breeding provides a long-term solution. Compared with other *Orobanche*/crop systems *Helianthus annuus*/*Orobanche cumana* systems differ in two important details. Germination stimulants from sunflower

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* Corresponding author: e-mail: Wegmann@uvvg.ro

(parthenolide and related compounds) are specific for *O. cumana* (Pérez-de-Luque *et al.*, 2000, Pérez-de-Luque *et al.*, 2001, Chaudhuri *et al.*, 2006), while other *Orobanche* species are stimulated by strigolactones, and the parasite *O. cumana* rapidly evolves new, increasingly dangerous pathotypes.

RESULT AND DISCUSSION

***Orobanche* resistance from the breeder's standpoint**

The fast evolution of new pathotypes is characteristic for *Orobanche cumana.* They were called race A, B, C, D, E, and for each of them a resistance gene was identified, *Or1*, *Or2*, *Or3*, *Or4* and *Or5*, respectively. These resistance genes are monogenically and dominantly inherited. However, in some cases, the influence of a still unidentified gene has been discussed (cytoplasmic; Russell, 1981), which might make the resistance a quantitative factor, depending for example on temperature.

Generally a root-specific promoter can be expected, which controls the expression of resistance gene(s) upon infection.

While the chemical nature of resistance factors has been studied, neither of these factors has been assigned to one of the *Or* genes until now.

Turbo, Favorit, Alcazar, Florina and Justin were Romanian sunflower lines resistant to *O. cumana* which carried *Or1-Or5* genes.

The situation became complicated for sunflower breeders around 1980, when a new *O. cumana* race F occurred in south-east Romania. Pacureanu-Ioita identified a resistance gene *Or6*. At the COST 849 Meeting held in Reading in 2005, she reported about trials with resistant sunflower lines organized in Braila and in Spain. Odessa 507-1 proved resistant to F race in Braila but not in Spain while KR-3-2b proved resistant in Spain but not in Braila. This meant that the F lines from Braila and Spain were not identical.

Mold-1-2 line, Kiz 321-3-3b line, VYP-70-4 population and Alinka-1 population were resistant to F races from Romania and Spain, but were sensitive to broomape from Turkey. Did that mean that a new race G existed in Turkey?

O. cumana race F in Russia is called biotype D. Such discrepancies in nomenclature should strictly be avoided.

Better knowledge of *Orobanche cumana* races (pathotypes) is useful for breeders. Identification of races has become possible by molecular biological analysis (Román *et al.*, 2007).

The sunflower inbred line KI-374 is resistant to race F. Crosses were carried out between the *Orobanche*-susceptible line HA300 and the KI-6 line, which carries the *Or5* gene of resistance. The evaluation of F_1, F_2, BC_1P_1 and BC_1P_2 progenies of both crosses indicated that the inheritance of resistance to broomrape in KI374 is due to two independent recessive genes: *Or6* and *Or7* (Rodriguez-Ojeda *et al.*, 2001).

The occurrence of a new pathotype overcoming sunflower resistance may indicate a gene-for-gene relation. The new pathotype has either a higher aggressiveness or a new specificity; this is not necessarily the same. The breeder should combine at least two independent resistance factors in order to interrupt the gene-for-gene development. The parasite cannot overcome two different resistances at the same time. This strategy has recently been applied by Pacureanu-Ioita *et al.* (2008). The line AO-548 carries two independent dominant resistance genes and is fully resistant to all *O. cumana* pathotypes.

Sources of resistance genes

There is common agreement among sunflower breeders that some wild annual and almost all perennial *Helianthus* species (Fernandez-Martinez *et al.*, 2000, Nikolova *et al.*, 2000, Fernandez-Martinez *et al.*, 2004, Bervillé 2004) are potential sources of resistance genes against *Orobanche cumana*.

Pérez-Vich *et al.* (2002) studied the inheritance of resistance to race F derived from interspecific amphiploids of *H. annuus* and two wild perennials, *H. divaricatus* and *H. grosseserratus*. They suggested that the resistance is controlled by a single dominant gene. In a re-examination by the same working group (Velasco *et al.*, 2007), however, the resistance of the sunflower variety J1, derived from *H. grosseserratus*, proved to be digenic, the second gene being influenced by environmental factors.

During the COST 849 Meeting in Athens in 2003, Pacureanu-Ioita has reported about sources of resistance in *Helianthus divaricatus*, *H. mutelii*, *H. grosseserratus* and *H. tuberosus* (Marinescu and Pacureanu-Ioita, 2002).

At the COST 849 Meeting in Naples in 2004, Wegmann mentioned microscopic studies conducted by Teryokhin in Wegmann's laboratory (1997). Several perennial *Helianthus* species stimulated *Orobanche* germination but the radicle could not penetrate the host root.

Batchvarova *et al.* (2001) worked with mutant lines after ^{60}Co irradiation of cultivar VNIIMK and others and found promising results concerning resistance to highly aggressive *O. cumana* races in northern Bulgaria.

There are several reports about *O. cumana* resistance in cultivated sunflower lines. Lines VB 3090, VB 24 and VB 368 are considered totally resistant to *O. cumana*, including the new races (Tikhomirov and Chiryaev, 2005). Four sunflower populations have been released as resistant to *O. cumana* race F: BR1, BR2, BR3, BR4 (Martinez *et al.*, 2002). Resistant hybrids have also been released in Russia (Gontcharov *et al.*, 2004) and in Turkey (Kaya *et al.*, 2004).

***Orobanche* resistance from the biochemist's standpoint**

The breeder ascribes resistance to genes and studies their inheritance, while the biochemist searches for biochemical resistance factors and resistance mechanisms, the causal relation between chemical compounds and resistance.

During the 1st *Orobanche* Workshop in Wageningen, Wegmann (1986) has proposed a number of tentative resistance factors against *Orobanche*. In the meantime, much effort has been invested into investigations of resistance factors, the list of tentative resistance factors was extended, and there is considerable progress in understanding *Orobanche* resistance.

"Low stimulant", the exudation of insufficient amount of germination stimulant is a weak resistance factor. To our knowledge, "low stimulant" is not known in any *Helianthus* line or wild species. Moreover, "low stimulant" could also be mimicked by the presence of germination inhibitors.

Mechanical barriers, like lignification of the cell wall by peroxidase-catalyzed reactions could probably play a role. In his PhD work, Labrousse (2002) has compared several *Helianthus* genotypes concerning their defence mechanisms against *Orobanche cumana*. The resistant genotype LR1 deposits callose inside the xylem in close contact with the parasite, due to an overexpression of the callose synthase cDNA gene *HaGSLI* (Delavault *et al.*, 2006). In some cases vessels were completely closed, so that water and nutrients could not flow to the parasite. A defensin gene has been identified in LR1 genotype, which is correlated with *Orobanche* resistance (Letousey *et al.*, 2007). In the wild relative *Helianthus debilis debilis*, an encapsulation layer stopps the intrusion of the parasite. Pérez-de-Luque *et al.* (2006) have shown by cytochemical studies, however, using peas resistant to *O. crenata*, that protein crosslinking, peroxidase and ß-1,3-endoglucanase are involved in *Orobanche* resistance. These findings have also been reported for sunflower resistance to *O. cumana* by Echevarría-Zomeño *et al.* (2006).

Phytoalexins as resistance factors against *Orobanche* have been hypothesized for the first time by Wegmann (1986). Phytoalexins are valuable resistance factors. They are low molecular weight secondary metabolites, which serve the plant in self-defence: they are only synthesized after the attack by a pathogen. Examples for phytoalexin-caused resistance have been identified by Wegmann *et al.* (1991) for sunflower *cv.* 81-14 and chickpea cv. ILC 280. The toxicity of phytoalexins to *Orobanche* was shown in submersed *Orobanche* cell cultures. Since then the phytoalexin concept has developed considerably.

When the attacked root responds by a hypersensitive reaction, necrosis and the subsequent death of the parasite, the search for phytoalexins should be carried out. Phytoalexins are generally simply inherited.

The phytoalexin concept has been adopted by Jorrín, who, during the COST 849 Meeting in Bari in 2001, confirmed the synthesis of 7-hydroxylated coumarins, scopoletin and ayapin, in the defence system of sunflower against *Orobanche.* See also Serghini *et al.* (2001).

Phytoalexins are active defence compounds only if they are produced fast enough and in sufficient local concentration. This was supported by studies of susceptible and resistant sunflower lines (Letousey *et al.*, 2004). A phytotoxic root extract from the resistant sunflower variety Amber (Eizenberg *et al.*, 2001) may, according to its effect on established invaders and due to its chemical behaviour, be considered a chemically yet unidentified phytoalexin. The resistance of Amber, which is observed only at high temperature (Eizenberg *et al.*, 2003), may indicate that a temperature-controlled gene is involved in the synthesis of the toxic compound.

"Plant fortifiers" BTH (Bion) (Buschmann *et al.*, 2001, Sauerborn *et al.*, 2002) or prohexadione-calcium (Fan *et al.*, 2007) induce dystemic scquired resistance (SAR), fortify phytoalexin formation and therefore contribute to resistance against *Orobanche cumana* without affecting the parasite itself.

Germination inhibitors. If the (non)host plant would exude germination inhibitors for *Orobanche* seed, this could be an efficient resistance factor. The sunflower phytoalexins scopoletin and ayapin showed germination inhibiting activity, when germination was induced by the synthetic stimulant GR24 (Pérez-de-Luque *et al.*, 2001). The search for germination inhibitors shall be continued.

Inhibition of the germ tube (*Orobanche* radicle) exoenzymes. Wegmann (2004) proposed the search for inhibitors of the germ tube exoenzymes and germination inhibitors as resistance factors at the COST 849 Meeting in Naples in 2004. Pectinases have always been found the most active enzymes in the exudates of *Orobanche* radicles. This fits well to microscopic studies by Ben-Hod *et al.* (1993) according to which the radicle invades the host root tissue along the middle lamellae. Inhibition of polygalacturonase (EC 3.2.1.15) and pectinmethylesterase (EC 3.2.1.11) by root exudates could be a perfect resistance factor, because the penetration of the *Orobanche* radicle into the root is inhibited. There are a number of metabolites, particularly from the phenylpropanoid pathway, which are known inhibitors for enzymes. Their inheritance is not yet investigated, however, simple inheritance is expected. An indication for the existence of such resistance factors is the microscopic observation (Teryokhin, Wegmann) that germ tubes in certain cases touch the host root and even bend around it, but do not penetrate it.

Little attention has so far been given to polygalacturonase-inhibiting proteins (PGIPs), well known in fungal resistance of higher plants, discovered by Albersheim *et al.* (1971). These are widespread, leucin-rich cell wall proteins, which bind tightly to polygalacturonases and inhibit them (De Lorenzo *et al.*, 2001). The PGIPs family exhibits specificity for polygalacturonases. This could distinguish resistant from susceptible hosts, and possibly could contribute to understanding host specificity.

Evidence for unfavorable phytohormone supply from the host root to the haustorium, which does not allow normal development of the parasite, has been observed in the *Linum usitatissimum/Orobanche ramosa* system (Chen, 1991). The tubercle remains small and differentiates too early with the formation of tiny leaflets on the tubercle surface. However, for breeding programs these findings are difficult to handle, as the inheritance of phytohormone concentration ratios is polygenic, and it may also vary with host development, environmental conditions and host nutrition.

Aggressiveness

Antonova (1994) and Antonova and ter Borg (1996) have presented data on peroxidases in *Orobanche cumana* races. The races differ insofar as they exude the peroxidase or keep it inside their cells. The exudation of peroxidase causes defence action of the attacked root cells (brown staining is observed; oxidation of polyphenols?). The more virulent form (race D) does not exude peroxidase, thus avoiding the host's reaction. Also differences in pectinases in differently virulent *Orobanche cumana* races could be a reason for different aggressive performance of parasite pathotypes (Simier *et al.*, 2004). More active exoenzymes for germ tube penetration into the host root could partly overcome defence reactions of the host. The metabolic decomposition of phytoalexins by *Orobanche* tissue (shown for the decomposition of scopoletin, Wegmann *et al.*, 1991) would be another example for increased aggressiveness.

Molecular biological studies on *Orobanche* resistance

Unlike very complex and polygenic traits such as drought resistance, *Orobanche* resistance similar to disease resistances is accessible for gene analytical studies. In sunflower, marker assisted selection for resistance to downy mildew (Brahm *et al.*, 2000) and male sterility (Pérez-Vich *et al.*, 2005) has been carried out.

All authors working with *Orobanche cumana* resistance to sunflower have so far concentrated to the *Or5* gene, probably because this is a dominant gene with simple resistance to race E of *Orobanche cumana*. Genetic mapping of the *Or5* gene was carried out by Tang *et al.* (2003), where all the problems of the genetic analysis of a "simple gene" are found. These studies do not reflect "genomic analysis of *Orobanche* resistance" but just the presence of the *Or5* gene.

Quantitative traits loci (QTLs) need to be identified to correlate genomic analysis with various phenomena of resistance. Bervillé *et al.* (2001) presented strategies for QTL mapping in interspecific progenies between the cultivated and wild *Helianthus* forms and discussed the problems arising during selection for *Orobanche* resistance.

Pérez-Vich *et al.* (2004) suggested that resistance to *Orobanche cumana* in sunflower is controlled by a combination of qualitative, race-specific resistance genes affecting the presence or absence of broomrape and a quantitative non-race specific resistance affecting the number of infections. The biochemist's task is to identify the two different resistance factors.

Pérez-Vich *et al.* (2004) have reported about QTL mapping of resistance to broomrape races E and F (*Orobanche cumana* Wallr.) in sunflower. Sunflower line P-96 shows dominant resistance to race E and recessive resistance to race F. Crossing P-96 with the susceptible line P-21 was phenotyped for broomrape resistance in four experiments, two for E and two for F, and was genotyped with microsatellite and RFLP markers. A linkage map comprising 103 marker loci distributed on 17 linkage groups was developed, and composite interval mapping analyses were performed. Five QTLs (*or1.1*, *or3.1*, *or7.1*, *or13.1*, and *or13.2*) for resistance to race E, and 6 QTLs (*or1.1*, *or4.1*, *or5.1*, *or13.1*, *or13.2* and *or16.1*) for resistance to race F were detected on 7 of the 17 linkage groups. Iuoras *et al.* (2004a) and Iuoras *et al.* (2004b) studied the use of marker-assisted selection for resistance to *Orobanche cumana* Wallr. in sunflower. Sunflower line LC1093 as carrier of resistance to race E has been used for hybridization. For marker-assisted selection the RAPD markers UBC73, UBC318, UBC264, UBC685 and OP-A17, and the SSR markers ORS1114 and ORS1036 proved useful for the analysis of F_2 and BC_1 generations. The crucial point of the correlations of QTLs with genomic analysis is the dependence of *Orobanche* resistance (different pathotypes) on environmental factors. Here is the greatest opportunity for cooperation of breeders/geneticists and biochemists.

CONCLUSIONS

There is still a great potential of *Orobanche* resistance factors, which has not yet been exploited for *Orobanche* resistance breeding in sunflower.

In order to avoid overcoming resistance by the evolution of new pathotypes (races) of *Orobanche cumana*, the combination of at least two independently acting resistance factors in sunflower breeding is recommended.

Interdisciplinary cooperation between breeders/geneticists and biochemists could lead to faster progress in sunflower breeding.

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RESISTENCIA A *Orobanche* EN GIRASOL

RESUMEN

Este informe presenta el conocimiento actual acerca de la resistencia a *Orobanche* en girasol desde el punto de vista de los mejoradores y los bioquímicos.

Las relaciones de parasitismo en las asociaciones *Helianthus annuus*/ *Orobanche cumana* difieren de muchas maneras de otras relaciones entre *Orobanche* spp. con sus hospedantes.

Una dificultad severa para el mejorador es el rápido desarrollo de nuevos patotipos de *Orobanche cumana* que vencen la resistencia de las líneas de girasol desarrolladas recientemente. Se discuten las bases del incremento de la agresividad de los patotipos de *Orobanche cumana*. Sin embargo, hay todavía un gran potencial para la obtención de resistencia a través del mejoramiento en el género *Helianthus*, ya que muchos factores de resistencia son conocidos o deben ser dilucidados todavía.

Se presenta una revisión sobre factores de resistencia conocidos, como baja estimulación, barreras mecánicas y cómo éstas se desarrollan, fitoalexinas, inhibidores de la germinación de la semilla de *Orobanche*, inhibidores de las exoenzimas de las radículas de *Orobanche*, en particular poligalacturonasa, la que permite la penetración de los tejidos de *Orobanche* en la raíz del hospedante. En este contexto se puede encontrar una nueva aproximación interesante en las proteínas inhibidoras de la poligalacturonasa que se observan en las paredes celulares y que inhiben la invasión de hongos patogénicos.

Se discute la necesidad de estudios de biología molecular.

La colaboración interdisciplinaria de mejoradores con bioquímicos y biólogos moleculares puede generar estrategias de mejoramiento más avanzadas.

RÉSISTANCE À L'*Orobanche* CHEZ LE TOURNESOL

RÉSUMÉ

Ce document se propose de faire le point des connaissances actuelles sur la résistance du tournesol à *Orobanche* chez le tournesol du point de vue du sélectionneur et du point de vue biochimique.

La relation parasitique *Helianthus annuus/Orobanche cumana* diffère par beaucoup d'aspects de celles des autres espèces *Orobanche* spp. avec leurs hôtes.

La difficulté majeur pour le sélectionneur est le développement rapide de nouveaux pathotypes de *Orobanche cumana*, qui contourne la résistance des lignées de tournesol nouvellement développées. La base d'une augmentation de l'agressivité des pathotypes de *Orobanche cumana* est discutée.

Néanmoins, il y a un potentiel encore important d'amélioration de la résistance au sein du genre *Helianthus*, du fait que les facteurs de résistance très différents sont déjà connus ou seront élucidés

Une revue est présentée sur les facteurs connus de résistance, tels que la faible stimulation, les barrières mécaniques et la façon dont elles se mettent en place, les phytoalexines, les inhibiteurs de la germination des graines d'Orobanche, l'inhibition des exoenzymes des radicules d' *Orobanche* et en particulier de la polygalacturonase, qui rend possible la pénétration des tissus d' *Orobanche* à l'intérieur de la racine de l' hôte. Dans ce contexte une nouvelle approche intéressante peut être trouvée dans les protéines inhibitrices de la polygalacturonase qui se trouvent dans les parois cellulaires, et qui inhibent l'invasion du pathogène.

Le besoin d' études de biologie moléculaire est souligné.

Une collaboration interdisciplinaire des sélectionneurs avec les biochimistes et les biologistes moléculaires peut conduire à des stratégies de sélection plus avancées.