CARBOHYDRATE OXIDASE GENE EXPRESSION IN SUNFLOWER DURING *OROBANCHE CUMANA* INFECTION

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Abstract

Carbohydrate oxidases (SCO) represent a class of enzymes involved in carbohydrate metabolism and in the generation of hydrogen peroxide (H_2O_2), a key molecule in redox signaling and in the activation of plant defense responses. In this study, the transcriptional responses of the *SCO* gene were analyzed in three sunflower genotypes exhibiting contrasting reactions to *O. cumana* infestation, using a controlled artificial infestation system. The resulting expression profiles were correlated with the resistance or susceptibility phenotypes of the analyzed genotypes. The results revealed significant transcriptional differences among genotypes. Resistant genotypes showed an early and tightly regulated induction of *SCO* expression during the pre-attachment phase, followed by moderate and sustained activation associated with effective restriction of parasite establishment. In contrast, the susceptible genotype Performer exhibited a delayed and unbalanced response, insufficient to prevent successful infestation.

Keywords: carbohydrate oxidase (*SCO*), *Helianthus annuus* L.*, Orobanche cumana* Wallr., post-attachment, pre-attachment, pathogen resistance, biotic stress.

Introduction

Early defense responses in plant-pathogen and plant-parasite interactions are critically dependent on tightly regulated redox signaling (Lamb et al., 1997; Torres et al., 2006; Mittler et al., 2011). These responses are characterized by a rapid and transient accumulation of reactive oxygen species (ROS), particularly hydrogen peroxide (H_2O_2), which functions both as a direct antipathogen agent and as a central signaling molecule coordinating local and systemic immunity (Apel et al., 2004; O'Brien et al., 2012; Waszczak et al., 2018). While excessive ROS accumulation leads to oxidative damage and cellular dysfunction, controlled ROS production is essential for the activation of defense-related transcriptional networks, cell wall reinforcement, and the establishment of effective resistance (Bolwell et al., 2002; Suzuki et al., 2011). Moreover, maintaining ROS homeostasis is increasingly recognized as crucial not only for defense responses but also for regulating plant growth and development under both biotic and abiotic stresses (Lopez, 2024; Xu, 2024).

Carbohydrate oxidases (SCO) establish a direct mechanistic link between carbon metabolism and redox-mediated defense signaling (Bolouri-Moghaddam, 2010). At the molecular level, H_2O_2 produced by these enzymes has been shown to activate pathogenesis-related (PR) genes, stimulate phytoalexin biosynthesis, and promote cell wall fortification via lignification and cross-linking of structural polymers (Hückelhoven, 2007; Passardi et al., 2004; Wojtaszek, 1997).

Evidence from model plant systems indicates that carbohydrate oxidase-encoding genes are rapidly induced following fungal or bacterial infection, as well as upon treatment with defense-

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associated phytohormones, including salicylic acid (SA), jasmonic acid (JA), and ethylene (Custers et al., 2004). In *Nicotiana tabacum*, carbohydrate oxidase activity has been directly implicated in the hypersensitive response (HR), where localized ROS accumulation contributes to programmed cell death and restriction of pathogen spread (Custers et al., 2004; Heath, 2000). These findings support the concept that carbohydrate oxidases function as regulators of oxidative burst amplitude and timing rather than merely as metabolic enzymes (Mittler et al., 2004; Baxter et al., 2014).

SCO shares high sequence homology with a carbohydrate oxidase that exhibits antifungal activity and confers resistance to fungal pathogens when expressed in transgenic *Arabidopsis*.*SCO* (Hu et al., 2003). SCO shares high homology with the berberine bridge enzyme (BBE) (Lu, G., 2003). These oxidases can transfer a hydride to the FAD cofactor, facilitating complex substrate transformations such as cyclizations, C–C bond formation, and nucleophilic additions (Tjallinks G, 2024). For example, BBE-like enzymes in *Arabidopsis* contribute to plant defense by oxidizing cell wall-derived oligosaccharides, such as oligogalacturonides and cellodextrins, thereby reducing their activity as damage-associated molecular patterns, limiting *Botrytis cinerea* growth, and helping maintain immune homeostasis (Locci, F., 2019). Similar carbohydrate oxidases have been described as antifungal proteins in sunflower (*Helianthus annuus*) and lettuce (*Lactuca sativa*) (Custers, 2004). However, most studies to date have focused on plant-fungi interactions, whereas the role of these enzymes in plant-plant parasitic interactions, as well as in the timing and regulation of plant defense responses and associated gene expression, remains poorly understood.

This knowledge gap is particularly relevant in the context of the *Helianthus annuus* L. and *Orobanche cumana* Wallr. interaction. *O. cumana* is a holoparasitic plant that establishes a haustorial connection with sunflower roots, enabling the extraction of water, carbohydrates, and other metabolites (Fernández-Melero et al., 2024; Auriac MC, 2024). Successful parasitism requires extensive remodeling of host cell walls and manipulation of host carbon fluxes, processes that are strongly influenced by host redox status and ROS signaling (Hegenauer et al., 2017). Transcriptomic analyses of resistant sunflower genotypes have consistently reported early activation of redox-associated genes, enhanced ROS signaling, and reinforcement of host cell walls, whereas susceptible genotypes exhibit delayed, excessive, or poorly coordinated oxidative responses (Letousey et al., 2007; Louarn et al., 2016).

Despite these findings, the transcriptional dynamics of *SCO* during the different stages of *O. cumana* infection, and its association with host resistance or susceptibility, remain insufficiently studied.

Therefore, investigating *SCO* expression dynamics in sunflower genotypes with contrasting resistance phenotypes provides an opportunity to clarify the role of redox-regulated carbohydrate oxidation in host-parasite interactions. Such insights may not only advance the mechanistic understanding of sunflower resistance to *O. cumana* but also support the identification of redox-related molecular markers for breeding durable resistance.

The present study investigates the temporal and genotype-dependent regulation of a sunflower carbohydrate oxidase gene (*SCO*) during two critical phases of host-parasite interaction: (i) the pre-attachment stage, corresponding to early perception and signaling events, and (ii) the post-attachment stage, associated with haustorial penetration and sustained defense responses.

Materials and Methods

In this study, three sunflower genotypes (Favorit, PR64LE20, and Performer) provided by the National Agricultural Research and Development Institute (NARDI) Fundulea, Romania, were evaluated. According to NARDI data and the specialized literature, the Favorit genotype carries the Or6 gene, which confers specific resistance against race F of the parasitic plant *Orobanche*

cumana. The PR64LE20 genotype is characterized by a high level of differential resistance, showing resistance to races A-G of the pathogen. The Performer genotype does not contain *Or* genes associated with resistance and exhibits high susceptibility to *O. cumana* infestation.
For the establishment of the artificial infestation background, broomrape seeds collected in 2014 from Singera, Republic of Moldova, characterized by a high aggressiveness toward sunflower genotypes, were used (Duca, 2017, Tabara, 2020). Only broomrape seeds with a germination rate ≥ 80%, verified in preliminary tests for viability - Figure 1 A-D and germination capacity - Figure 1 E-G, were used in the experiment.

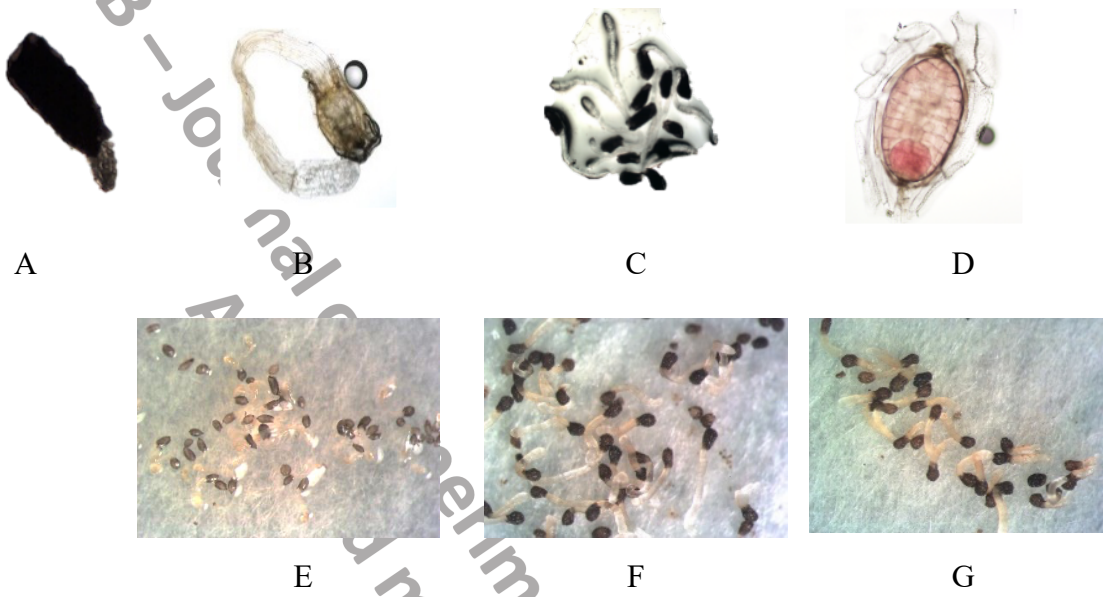

Figure 1. Germination of *Orobanche cumana* seeds tested in water (A), sunflower root exudate (B), GR24 (C), tetrazolium chloride (D), and at germination levels of 25% (E), 50% (F), and 75% (G)

To characterize the transcriptional profile of the *SCO* gene within defense mechanisms, two experimental systems were used, designed to both immediate responses, illustrated in Figure 2A and medium- to long-term molecular changes, presented Figure 2B.

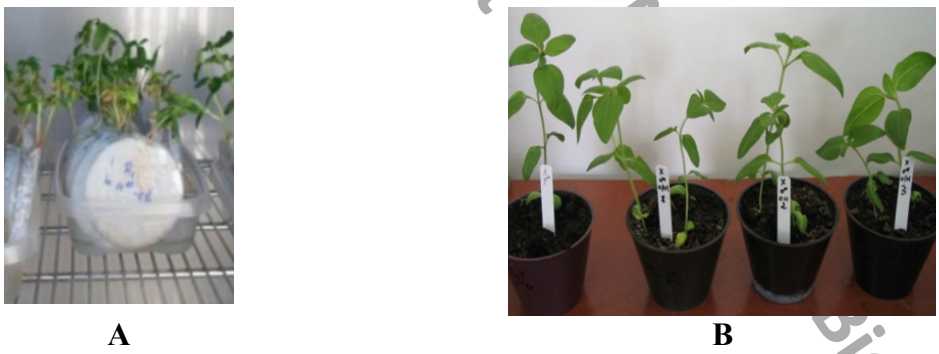

Figure 2. Cultivation of sunflower against an infection background in Petri dishes (A) and in pots (B).

The first experimental system involved cultivating sunflower plants in Petri dishes on a perlite substrate (rhizotron model) in a germination chamber at 20-25 °C under a 16 h light / 8 h dark photoperiod Figure 2.A, allowing for the evaluation of early root responses associated with pre-attachment mechanisms. Pre-germinated (on exudate) broomrape seeds were applied to sunflower root grown *a priory* until two-leaf stage. To monitor the dynamics of gene

expression, samples were collected after 2, 6, 12 and 24 h (post-infestation: *hpi*) of host-parasite co-cultivation.

The second experimental system was designed to analyze the host-parasite response under conditions closer to the natural environment and involved the cultivation of genotypes in pots (Figure 2.B). Substrate infestation was performed at a rate of 37 mg of *O. cumana* seeds per 200 g of soil mixture. Sunflower roots samples were collected at the critical developmental phases of the pathosystem, namely the formation of the first attachments (18–21 days), tubercle development (35 days), underground shoot formation (53 days), and emergence of aerial shoots (67 days).

Uninfested substrate-grown genotypes were used as controls. Biological material was collected from three biological replicates, frozen in liquid nitrogen, and subsequently stored at −80 °C.

RNA isolation and cDNA synthesis

Total RNA was extracted from root tissues of each of the three plants using the TRI-zol method (Applied Biosystems). RNA quality and quantity were assessed via spectrophotometry (260/280 nm) and 1% agarose gel electrophoresis. RNA was treated with DNase (Thermo Scientific) prior to cDNA synthesis, which was carried out using Revertaid.

RT with Oligo-dT18 and random hexamer primers

Analysis of relative *SCO* gene expression. *SCO* gene expression levels were determined by real-time PCR using a DT-96 amplifier (DNA Technology, Russia). Specific primers were designed based on EST sequences available in the NCBI database using the Primer3Web v.3.0.0 and OligoAnalyzer 3.1 bioinformatics tools. Actin (AF282624.1) was used as the reference gene (Table 1).

Fluorescence detection was performed with Maxima SYBR Green/ROX PCR Master Mix using 0.4 µM primers and 2 µL of cDNA per reaction. The amplification program included an initial denaturation at 95 °C for 10 min, followed by 5 cycles of 95 °C for 15 s and 64 °C for 20 s, then 40 cycles of 95 °C for 15 s and 60 °C for 40 s. The absence of nonspecific amplicons and primer dimers was verified by 1.4% agarose gel electrophoresis and melting curve analysis.

Table 1. Nucleotide sequences of the primers.

Nr.	Gene	Acces ID	F Primer	R Primer	Amp.
1.	carbohydrate oxidase	AF364866.1	gggtggacttcgtggatcag	ctcgggttactcgtcacgta	112 pb
2.	actin (reference gene)	AF282624.1	gctaacagggaaaagatgactc	actggcataaagagaaagcacg	96 pb

qPCR reactions were performed in three technical replicates for each of the three biological replicates. The obtained results were statistically processed by calculating the following parameters: arithmetic mean ($\bar{x}$), variance (s^2), standard deviation (s), coefficient of variation (CV), and standard error of the mean (SEM). All data are presented as mean ± SEM. Differences were evaluated using the t-test. All these indices were calculated to assess data variability, the precision of estimates, and significant differences between experimental variants.

Normalized expression levels were calculated using the $2^{-\Delta Ct}$ method, where ΔCt = (Ct_target gene − Ct_reference gene). To compare gene expression between plants grown in the presence of broomrape seeds and control plants, fold changes were determined using the $2^{-\Delta\Delta Ct}$ method. When $2^{-\Delta\Delta Ct} < 1$, downregulation of gene expression was expressed as the negative reciprocal value ($-1/2^{-\Delta\Delta Ct}$), representing the fold reduction in gene expression (Schmittgen and Livak, 2008). Fold changes with values ≤ -1.5 or ≥ 1.5 were considered biologically relevant for evaluating the defensive response of the genotypes to *O. cumana* infestation. Statistical significance of differences in gene expression was assessed using Student's t-test, and differences were considered statistically significant at $p \leq 0.05$.

Results and discussions

***SCO* expression in non-infested plants.**

In the absence of *Orobanche cumana*, *SCO* transcript levels during the pre-attachment phase followed a comparable temporal pattern across all three sunflower genotypes, as illustrated in Figure 3A, characterized by a transient decrease at 6 and 12 hpi and recovery at 24 hpi. This behavior is consistent with the dynamic regulation of ROS-related genes under basal growth conditions, reflecting their involvement in developmental redox signaling rather than in stress-induced responses (Apel, 2004; Mittler et al., 2004; Waszczak et al., 2018). Despite this shared trend, clear genotype-dependent differences in expression magnitude were evident. The resistant genotypes Favorit and PR64LE20 maintained relatively stable and moderate *SCO* transcript levels, whereas the susceptible genotype Performer displayed significantly higher expression at early time points.

In the post-attachment experimental system (18–67 days), non-infested plants again displayed genotype-specific *SCO* expression dynamics as displayed in Figure 3B.

Oscillatory expression patterns observed in Favorit and PR64LE20 suggest a tightly regulated redox network, in agreement with reports describing coordinated ROS production and scavenging during plant development (Bolouri-Moghaddam et al., 2010; Waszczak et al., 2018).

In contrast, the early high *SCO* expression followed by attenuation in Performer supports the notion of inefficient redox control, which may predispose this genotype to ineffective stress responses.

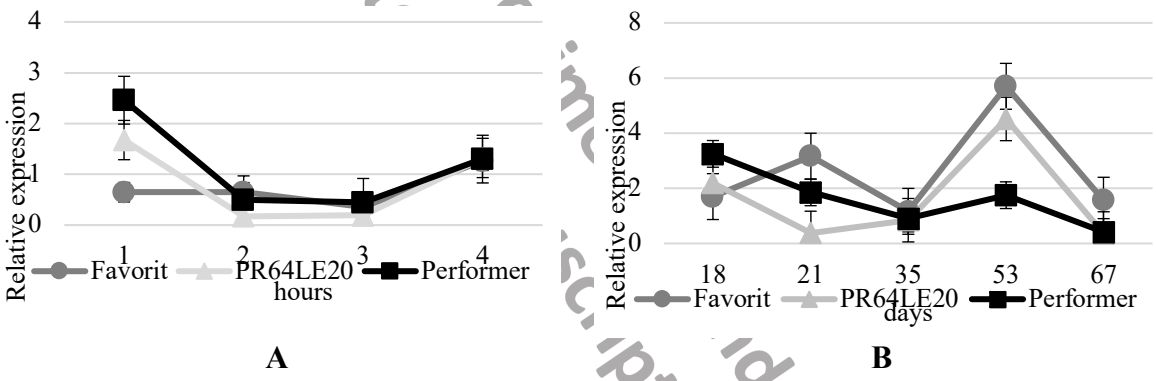

Figure 3. Relative expression of the *SCO* gene in sunflower hybrids grown under standard conditions (without *Orobanche* seeds) in Petri dishes (A) and in pots (B).

This common regulatory trend suggests that *SCO* expression is dynamically regulated even in the absence of parasite-derived signals.

***SCO* expression in infested plants during pre-attachment (*first experimental system*).**

During the pre-attachment phase of *O. cumana* infection, *SCO* expression exhibited clear genotype-dependent modulation, is shown in Figure 4 and Figure 5.

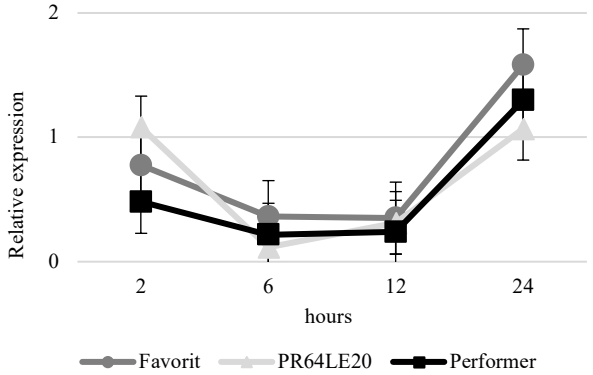

Figure 4. Relative expression of the *SCO* gene in sunflower hybrids under artificial infestation in first experimental system.

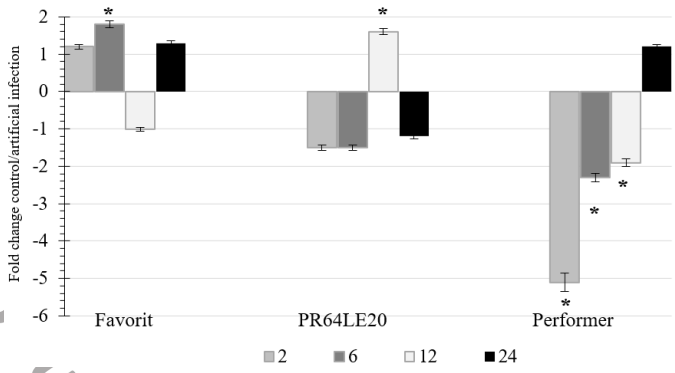

Figure 5. *SCO* gene expression levels (fold change) in different sunflower genotypes under artificial *O. cumana* infestation. *An asterisk (*) indicates a statistically significant difference at $p \leq 0.05$ (t-test).*

The reduced levels of SCO transcripts at 2 and 6 hpi in the majority of genotypes compared with control samples indicate a transient modulation of ROS signaling following parasite recognition, resembling the early oxidative burst adjustments reported in other host-pathogen systems (Wojtaszek, 1997; Lamb, 1997). The subsequent induction at 24 hpi was observed in all genotypes.

Contrary to the findings of Letousey et al. (2007), who reported similar expression patterns in both resistant and susceptible sunflower genotypes during the early induction phase, our study revealed distinct transcriptional responses between resistant and susceptible genotypes. Thus, in resistant hybrids, *SCO* expression changes remained moderate and statistically insignificant relative to controls, indicating a restrained response maintained within a functional reaction norm.

In contrast, the susceptible genotype Performer showed significant early repression followed by late overexpression of *SCO*, a pattern indicative of delayed and poorly coordinated defense activation.

Thus, the resistant hybrids Favorit and PR64LE20 exhibit a distinct response to artificial infection, with no statistically significant changes in fold change compared with the control, while the susceptible hybrid Performer displays a time-dependent response, characterized especially by the subexpression of analyzed gene.

Overall, the figure highlights clear genotype-dependent differences in *SCO* gene expression under *O. cumana* infestation, with Favorit showing a transient response, PR64LE20 and Performer exhibiting a moderate, respectively, strong downregulation.

***SCO* expression in infested plants during post-attachment (*second experimental system*).** During post-attachment stages, *SCO* transcriptional dynamics further emphasized genotype-dependent defense strategies, is presented in Figure 6 and Figure 7.

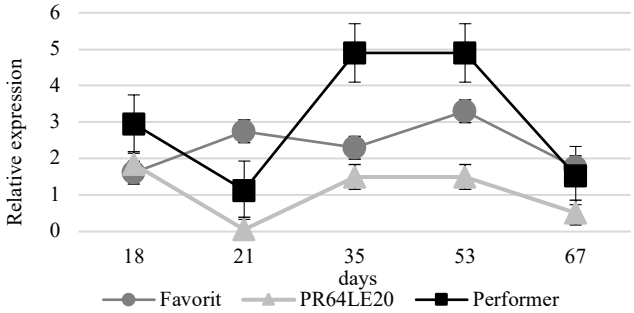

Figure 6. Relative expression of the *SCO* gene in sunflower hybrids under artificial infestation in second experimental system.

Resistant genotypes exhibited coordinated phases of *SCO* induction and repression corresponding to key developmental stages of the parasite. The observed repression of *SCO* in PR64LE20 during haustorial attachment and underground shoot formation suggests an active regulation (Bolwell et al., 2002; Bindschedler et al., 2006; O'Brien et al., 2012).
In contrast, the susceptible genotype showed delayed but strong *SCO* overexpression at later stages, likely reflecting stress-induced ROS accumulation rather than an effective defense response. Late ROS bursts have been shown to coincide with irreversible tissue damage and unsuccessful defense outcomes (Heath, 2000; Hückelhoven, 2003).

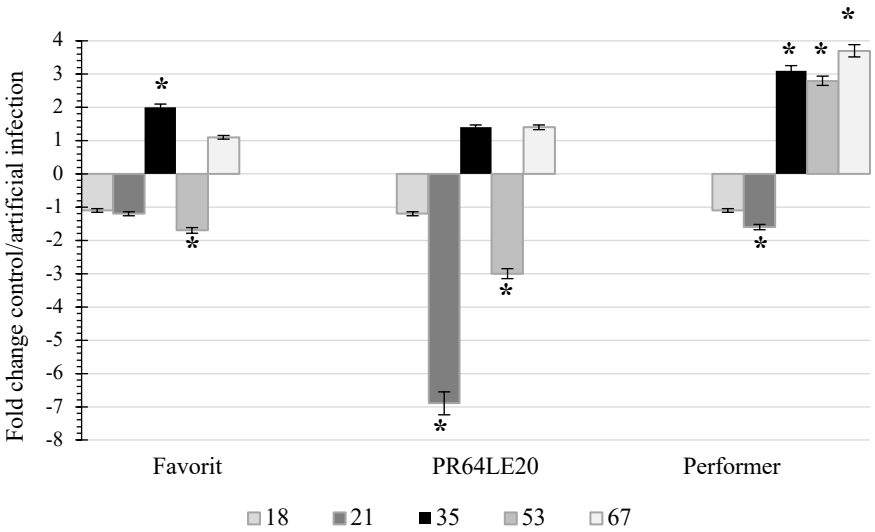

Figure 7. Fold-change expression of the *SCO* gene in different sunflower genotypes under artificial *Orobanche cumana* infestation. *An asterisk (*) indicates a statistically significant difference at p ≤ 0.05 (t-test).*

These findings align with previous studies on sunflower – *Orobanche* interactions, which demonstrated that resistance is associated with early, localized responses, whereas susceptibility correlates with delayed systemic reactions (Letousey et al., 2007; Louarn et al., 2016).
Overall, the results obtained in the second experimental system corroborate those observed in the first system, confirming that *SCO* transcriptional regulation is strongly influenced by genotype.
The resistant sunflower genotypes Favorit and PR64LE20 employ distinct redox-based strategies to limit *Orobanche cumana* infection. Favorit displays moderate, well-timed *SCO* activation at critical developmental stages, supporting ROS-mediated signaling and structural defenses, whereas PR64LE20 maintains predominantly repressed *SCO* expression, restricting excessive apoplastic ROS while preserving effective defense (Apel, 2004; Mittler et al., 2011; Bolwell et al., 2002; Passardi et al., 2004). In contrast, the susceptible genotype Performer exhibits constitutively high basal *SCO*, followed by early repression and delayed, excessive late induction upon infestation, reflecting poorly coordinated defense signaling and stress-induced ROS accumulation after parasite establishment (Heath, 2000; Hückelhoven, 2003; Waszczak et al., 2018).
These observations indicate that resistance depends on precise temporal regulation of ROS-related genes, rather than on maximal ROS production, highlighting the importance of coordinated redox homeostasis in sunflower defense (Torres et al., 2006; Suzuki et al., 2011;

Letousey et al., 2007). This concept aligns with current models of plant immunity, where finely tuned ROS signaling networks, rather than excessive oxidative bursts, underpin durable resistance (Suzuki et al., 2011; Mittler et al., 2011; Waszczak et al., 2018). The deregulated and energetically inefficient *SCO* expression observed in the susceptible genotype likely contributes to its failure to restrict *O. cumana* development. Similar defense mechanisms have been documented in sunflower lines overexpressing ROS-generating enzymes, which show enhanced resistance responses (Hu et al., 2003).

Conclusions

The results indicate that the transcriptional dynamics of *SCO*, rather than its absolute expression levels, may be associated with sunflower responses to *Orobanche cumana*. The balance between ROS production and antioxidant control appears to contribute to resistance mechanisms. Overall, *SCO* may represent a candidate gene for further investigation as a potential molecular marker in resistance breeding programs

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