Journal of Agricultural Sciences
(Tarim Bilimleri Dergisi)

J Agr Sci-Tarim Bili
e-ISSN: 2148-9297
jas.ankara.edu.tr

Physiological Effects of Arbuscular Mycorrhizal Fungi (AMF), Plant Growth-Promoting Rhizobacteria (PGPRs), and *Trichoderma harzianum* on Tomato (*Solanum lycopersicum* L.) Infected with Branched Broomrape [*Phelipanche ramosa* (L.) Pomel]

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ARTICLE INFO
Research Article
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Received: 21 January 2025 / Revised: 11 April 2025 / Accepted: 06 May 2025 / Online: 30 September 2025

Cite this article
Fidan E, Tepe I (2025). Physiological Effects of Arbuscular Mycorrhizal Fungi (AMF), Plant Growth-Promoting Rhizobacteria (PGPRs), and Trichoderma harzianum on Tomato (Solanum lycopersicum L.) Infected with Branched Broomrape [Phelipanche ramosa (L.) Pomel. Journal of Agricultural Sciences (Tarim Bilimleri Dergisi), 31(4):917-930. DOI: 10.15832/ankutbd.1624187

ABSTRACT
Tomato (*Solanum lycopersicum* L.), one of the most produced and consumed vegetables in the world, belongs to Family Solanaceae. Branched broomrape [*Phelipanche ramosa* (L.) Pomel; Syn: *Orobanche ramosa* L.] parasitizes many cultivated plants, especially tomatoes. The parasitic weeds, for which there is no effective control method, cause serious yield and quality losses in their host crops. In this study, two different mycorrhizal (AMF) species, *Funneliformis mosseae*, and a commercial product, Endo Roots Soluble (ERS), along with *Trichoderma harzianum* T22, two different plant growth-promoting rhizobacteria (PGPR) isolates (*Pseudomonas caspiana* V30G2 and *Bacillus velezensis* V40K2), were applied to tomatoes. Additionally, a commercial product, Plant Success Great White Premium Mycorrhiza, and their combinations were used to determine the changes occurring in both the plants and the broomrape. This study investigated the number of tubercles, the levels of several oxidative stress enzymes (catalase, CAT; superoxide dismutase, SOD; and ascorbate peroxidase, APX), the level of lipid peroxidation (malondialdehyde, MDA), and the total phenolic and antioxidant contents of tomato plants infected and not infected with broomrape. Compared to the control group, the treatments were found to prevent tubercle formation at rates ranging from 60 to 72.7%. Broomrape infection caused oxidative stress in the tomatoes; the CAT and MDA contents in the broomrape-contaminated plants were higher than those in the noncontaminated plants. The results revealed that the bioproducts including some microorganisms and biological preparations applied to tomatoes responded differently to broomrape stress through enzymatic and nonenzymatic antioxidant activities.

Keywords: Bioproducts, Branched broomrape, Oxidative stress, Plant physiology, Tomato

1. Introduction

Tomato (*Solanum lycopersicum* L.), a member of the Family Solanaceae, is cultivated in numerous countries across diverse ecologies. In recent years, there has been a significant expansion in tomato production areas globally (Lops et al. 2022). However, this increasing production presents various challenges. Tomatoes are particularly vulnerable to weed competition, especially during the early stages following the seedling period (Mennan et al. 2020). Approximately 34% of the yield losses in agricultural fields are attributed to weeds (Junaid & Gokce 2024). Notably, among these weeds, branched broomrape [*Phelipanche ramosa* (L.) Pomel; Syn: *Orobanche ramosa* L.] stands out as one of the most significant threats. Yield losses caused by root parasitic weeds in cultivated plants can reach 100%, depending on factors such as environmental conditions, host sensitivity, attachment time, and intensity (Fernández-Aparicio et al. 2016).

Broomrape species, belonging to the *Orobanche* and *Phelipanche* genera of the family Orobanchaceae, are predominantly holoparasitic plants (Parker 2009; McNeal et al. 2013; Fidan et al. 2024). Obligate parasites are completely dependent on the physiological functioning of their hosts to complete their life cycle (Cochavi 2025). Broomrape relies on stimulant chemicals released from the roots of their host plants to initiate germination. The primary germination stimulants include sorgoleone, isoflavanone, sesquiterpene lactones, and strigolactones (Demirkan 1992; Joel 2007; Parker 2009; Jain et al. 2025). Germinating broomrape seeds parasitize the roots of the host, forming a small, grass-like structure called a haustorium, with a circumference typically measuring only 2-3 mm (Kadıoğlu 2009). Once attached, broomrape extracts carbohydrates from the phloem and water along with mineral substances from the xylem of the host, thereby negatively impacting the host plant's development (Joel 2007; Krupp et al. 2019). The proliferation of the broomrape can be attributed to its high seed production, extensive spread, and rapid expansion of cultivation areas for its host crops in recent years (Demirkan 1992). Exudates released by host plant roots,

particularly during early growth stages such as germination and tubercle formation, play crucial roles in the development of this parasitic plant (Vurro et al. 2006; Lops et al. 2017).

Considering the negative effects of pesticides, there is a growing need for sustainable and environmentally friendly methods. Biological preparations, which have recently demonstrated effectiveness in agricultural production and are less harmful to the environment, are promising alternatives to chemicals (Daniel et al. 2022). For this purpose, microorganisms such as fungi and bacteria, which are found in soil microflora and constitute an essential part of the soil, are used as control agents in the biological control of various diseases, pests, and weeds (Glick 2012; Sharma et al. 2020). Plant growth-promoting rhizobacteria and fungi, including arbuscular mycorrhizal fungi and *Trichoderma* species, are the most important biocontrol agents against different pathogens (Dames 2014; Kumari et al. 2020).

Arbuscular mycorrhizal fungi (AMF) are vital components of natural ecosystems and can form symbioses with plant roots (Prasad et al. 2017). AMF symbiosis is known to protect plants against biotic and abiotic stresses by increasing water and nutrient absorption (Gianinazzi et al. 1996). Many rhizosphere microorganisms, such as AMF, play an essential role in biological control by reducing the germination of parasitic weeds (Lendzemo et al. 2007). Some *Trichoderma* species used for biological control are highly effective at suppressing plant diseases through biological control mechanisms such as hyperparasitism, antibiosis and competition, thereby stimulating plant systemic acquired resistance (SAR) and induced systemic resistance (ISR) (El-Maraghy et al. 2021; Sood et al. 2020). Furthermore, all bacteria that live in plant roots and positively affect plant growth are called plant growth-promoting rhizobacteria (PGPRs) (Arshad & Frankenberger 1997). Although the initial applications of PGPRs in crop production were for plant growth promotion, it has been reported that they increase the ISR in plants and can be used as biological control agents, especially against soil-borne pathogens (Altın & Tayyar 2005; İmriz et al. 2014). The relationships with tomato plants, broomrape plants, and plants treated with bioproducts are shown in Figure 1.

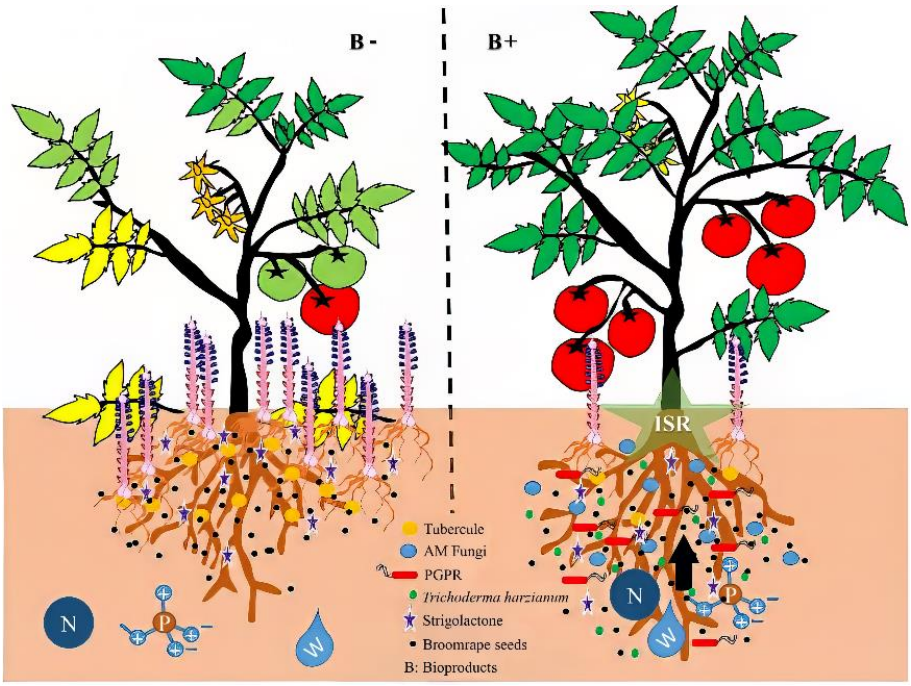

Figure 1- Relationship with tomato, broomrape, and bioproducts

Some plants can respond to high levels of reactive oxygen species (ROS) by activating enzymatic antioxidant defense systems to protect themselves against stressors (Kwon et al. 2002; Cho & Seo 2005). These responses may involve various induced defense mechanisms such as flavonoids, phenolic compounds, and antioxidant enzymes (Borges et al. 2022; Kaur et al. 2022). Enzymatic and non-enzymatic antioxidative defense systems exist to prevent the toxic effects of ROS. The enzymatic ROS scavenging mechanisms in plants include superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), and glutathione peroxidase (GPX) (Apel & Hirt 2004).

The positive effects of beneficial soil-borne microorganisms on cultivated plants raise the possibility that these microorganisms can also be used in weed control through the enzymatic antioxidant defense system. In recent years, *P. ramosa* (L.) Pomel, a holoparasitic plant, has caused significant yield losses in several crops, including tomato, eggplant, tobacco, and lentil. Unfortunately, no effective control method has been developed for this parasitic plant. This study aimed to determine the physiological changes occurring in tomatoes during broomrape infestation and the effects of some of the most emphasized biological preparations on broomrape parasitism.

2. Material and Methods

2.1. Plant and biological materials

The Rio Grande tomato variety (*Solanum lycopersicum* L.) was selected as the plant material for this study. Branched broomrape [*Phelipanche ramosa* (L.) Pomel] seeds used in the study were collected from tomato-growing fields in the Van province of Türkiye in 2019. The studies were repeatedly carried out in the climate rooms of the Department of Plant Protection, Faculty of Agriculture, Van Yüzüncü Yıl University, both in 2021 and 2022.

In this study, the ERS (Endo Roots Soluble) commercial AMF strain, *Trichoderma harzianum* preparation (T-22 Planter Box, Bioglobal Ltd.), and MIX preparation (obtained from Plant Revolution, Great White Premium Mycorrhizae, Plant Success) were utilized. Mycorrhizal and plant growth-promoting rhizobacteria (*Pseudomonas caspiana* V30G2 and *Bacillus velezensis* V40K2) isolates of *Funneliformis mosseae* (Syn: *Glomus mosseae*) cultured in culture were obtained from the laboratory stocks of Van Yüzüncü Yıl University, Faculty of Agriculture, Department of Plant Protection.

2.2. Experimental design

Broomrape seeds were homogeneously distributed to a depth of 8 cm, approximately 0.05 g per pot, before planting the tomato seeds [modified from (Aksoy 2003)]. Tomato seeds were planted in prepared 4-liter pots containing a sterile peat-perlite mixture at a ratio of 2:1. The study followed a randomized plot experimental design with four replications, and two tomato plants were placed in each pot. Hoagland nutrient solution was applied to the seedlings when the first true leaves appeared. Plants were regularly supplied with water and Hoagland nutrient solution as needed (Song et al. 2013).

In this study, tomato and broomrape seeds were sterilized with 70% ethanol, washed with sterile water, and dried on blotting paper (Xu et al. 2014). The procedures performed in the following stages are explained below and given in Table 1.

Before sowing, 2.5 g (150 spores/g) of *F. mosseae* and ERS AMF (250 g/decare) were added to the seed bed in each pot before sowing the tomato seeds in the media prepared for mycorrhiza applications that were not contaminated with broomrape. *T. harzianum* T22 was applied after sowing (106 spores/mL), and *P. caspiana* (V30G2) and *B. velezensis* (V40K2) were applied after the first true leaves of the tomatoes emerged (1x108 cfu/mL). In the group infected with broomrape, approximately 0.05 g of broomrape seeds were mixed homogeneously to a depth of 8 cm in each pot before planting the tomato seeds, and the treatments were carried out as described above. Great White Premium Mycorrhizae (MIX, Plant Success) was applied to the seed beds according to the label. At a rate of 100 millilitres in each pot, 1.25 grams of MIX was added to 7.57 liters of water. This application was repeated for 2 time periods (Rişvanli 2022).

Table 1- Treatments in the experiment

Treatments	***Uninfected tomatoes with branched broomrape***	***Infected tomatoes with branched broomrape***
C	Untreated (uninfected control)	Untreated (infected control)
M1	AMF (*Funneliformis mosseae*) inoculation	AMF (*Funneliformis mosseae*) inoculation
M2	AMF (ERS) inoculation	AMF (ERS) inoculation
P1	*Pseudomonas caspiana* (V30G2) inoculation	*Pseudomonas caspiana* (V30G2) inoculation
P2	*Bacillus velezensis* (V40K2) inoculation	*Bacillus velezensis* (V40K2) inoculation
TH	*Trichoderma harzianum* (T22) inoculation	*Trichoderma harzianum* (T22) inoculation
MIX	Great White Premium Mycorrhiza inoculation	Great White Premium Micorrhiza inoculation
M1P1	*F. mosseae* + *P. caspiana* (V30G2) inoculation	*F. mosseae* + *P. caspiana* (V30G2) inoculation
M1P2	*F. mosseae* + *B. velezensis* (V40K2) inoculation	*F. mosseae* + *B. velezensis* (V40K2) inoculation
M2P1	ERS + *P. caspiana* (V30G2) inoculation	ERS + *P. caspiana* (V30G2) inoculation
M2P2	ERS + *B. velezensis* (V40K2) tomato plants inoculation	ERS + *B. velezensis* (V40K2) inoculation
THM1	*T. harzianum* T22 + *F. mosseae* inoculation	*T. harzianum* T22 + *F. mosseae* inoculation
THM2	*T. harzianum* T22 + ERS tomato plants inoculation	*T. harzianum* T22 + ERS inoculation
THP1	*T. harzianum* T22 + *P. caspiana* (V30G2) inoculation	*T. harzianum* T22 + *P. caspiana* (V30G2) inoculation
THP2	*T. harzianum* T22 + *B. velezensis* (V40K2) inoculation	*T. harzianum* T22 + *B. velezensis* (V40K2) inoculation

2.3. Number of tubercles

Tubercles were counted by enumerating the formations generated as a result of broomrape seeds attaching to the roots of the tomato plant.

2.4. Enzymatic assays

One day before harvest, fresh plant samples were collected and stored at -80 °C until analysis. Frozen leaf samples were first homogenized with 5 mL cold 50 mM potassium phosphate and 0.1 mM NaEDTA (pH: 7.6) and then centrifuged at 15000 rpm for 30 minutes at 4 °C. Superoxide dismutase (SOD) activity was detected spectrophotometrically by inhibiting nitroblue tetrazolium (NBT) at a wavelength of 560 nm (Jebara et al. 2005). A reduction of 50% of the NBT in units was considered to indicate SOD activity. Catalase activity was determined by monitoring the disappearance of H_2O_2 at a wavelength of 240 nm based on the method outlined by (Çakmak et al. 1993). Ascorbate peroxidase (APX) activity was measured by H_2O_2 reduction due to ascorbic acid (Nakano & Asada 1981). The supernatant was obtained by homogenizing 1 g of plant sample with the prepared extraction solution at a pH of 7.6. For the reaction solution, 50 mM KH_2PO_4, 10 mM H_2O_2, 0.5 mM ascorbic acid, and 0.1 mM Na-EDTA were used. The pH of this mixture was adjusted to 7. After adding 0.1 mL of supernatant and 3 mL of the reaction solution, the absorbance change at a wavelength of 290 nm was recorded in the 1st minute.

2.5. Lipid peroxidation (MDA) assays

Plant samples taken one day before harvest were homogenized with 0.1% trichloroacetic acid (TCA) solution and then centrifuged at 15000 rpm for 15 minutes. After centrifugation, 1 mL of the supernatant was removed, and 4 mL of 20% TCA and 0.5% thiobarbituric acid (TBA) were added. This mixture underwent a 30-minute incubation in a 95 °C water bath and was then subjected to a second centrifugation at 10000 rpm. The absorbance was determined at 532 and 600 nm in a spectrophotometer, and the MDA content was calculated using a molar absorption coefficient of 155 mM/cm (Heath & Packer 1968).

2.6. Total phenolic content and antioxidant activity assays

The total phenol content in leaves was analyzed according to (Swain & Hillis 1959), and the total antioxidant content was analyzed according to FRAP (Benzie and Strain 1996). At the analysis stage, 5 mL of methanol was added to each sample, which was subsequently crushed in a homogenizer and centrifuged at 12000 rpm for 10 min. The resulting supernatant was transferred to 2 mL Eppendorf tubes for analysis. To determine the phenolic content, 150 µl of the extract was removed, and 2400 µl of pure water and 150 µl of Folin-Ciocalteu solution (1:10 solution) were added. Then, this mixture was vortexed for 3-4 seconds, 300 µl of 20% saturated sodium carbonate was added, the mixture was kept at room temperature in the dark for 30 minutes, and the absorbance at 760 nm was read with a spectrophotometer. To determine the total antioxidant activity, a FRAP solution consisting of 150 µl of acetate buffer, TPTZ, and ferric chloride was prepared from the extract. A total of 2850 µl of the prepared FRAPs was transferred to 10 mL glass tubes. Then, the samples were kept in the dark for 30 minutes under room conditions, and readings were taken with a 593 nm wavelength spectrophotometer.

2.7. Statistical analyses

The data obtained from the experiment were evaluated using the SPSS statistical software at a significance level of $P<0.05$, according to the random plots experimental design. Differences between treatments were determined using Duncan's multiple comparison test (SPSS 2021).

3. Results and Discussion

Since the studies were conducted in a climate room, the differences between years were not statistically significant. Therefore, analyses were performed by combining the data from both years.

3.1. Tubercule density in tomato roots caused by branched broomrape

The differences in the number of broomrape tubercles in the roots of tomatoes treated with or without the bioproducts were statistically significant ($P<0.05$, Figure 2, Table 2). The data analysis revealed that MIX had at least one tubercle overall (3.75 pots/piece), followed by M1 (5.25 pots/piece), M2P2 (5.37 pots/piece), and TH (5.50 pots/piece). All treatments, except for the THP1 and P1 treatments, decreased broomrape attachment compared to that in the control group; the most effective treatments were MIX, M1, TH, and M2P2. Compared to the control group, MIX, M1, M2P2, and TH prevented tubercle formation by 72.72%, 61.82%, 60.95% and 60.0%, respectively.

Table 2- Effect of bioproducts - on the number of branched broomrape tubercles in tomato roots (average over two years, number of tubercles per pot)

Treatments	*Number of tubercules (Mean ± SE)*	*Rate of change compared to control (%)*
C	13.75 ± 0.65^{ab}	
M1	5.25 ± 0.65^{e}	-61.82
M2	9.37 ± 0.84^{cd}	-31.85
P1	13.75 ± 1.19^{ab}	0.00
P2	9.12 ± 0.48^{cd}	-33.67
TH	5.50 ± 0.71^{e}	-60.00
MIX	3.75 ± 0.41^{e}	-72.73
M1P1	9.87 ± 0.72^{bcd}	-28.22
M1P2	11.37 ± 1.21^{abc}	-17.31
M2P1	10.00 ± 0.63^{bcd}	-27.27
M2P2	5.37 ± 0.71^{e}	-60.95
THM1	6.87 ± 0.79^{de}	-50.04
THM2	9.12 ± 0.77^{cd}	-33.67
THP1	15.25 ± 0.70^{a}	10.91
THP2	11.62 ± 0.94^{abc}	-15.49
Mean	9.33 ± 0.76	

a, b, c, d, e: The difference between the means shown with different letters in the same column is statistically significant (P<0.05).

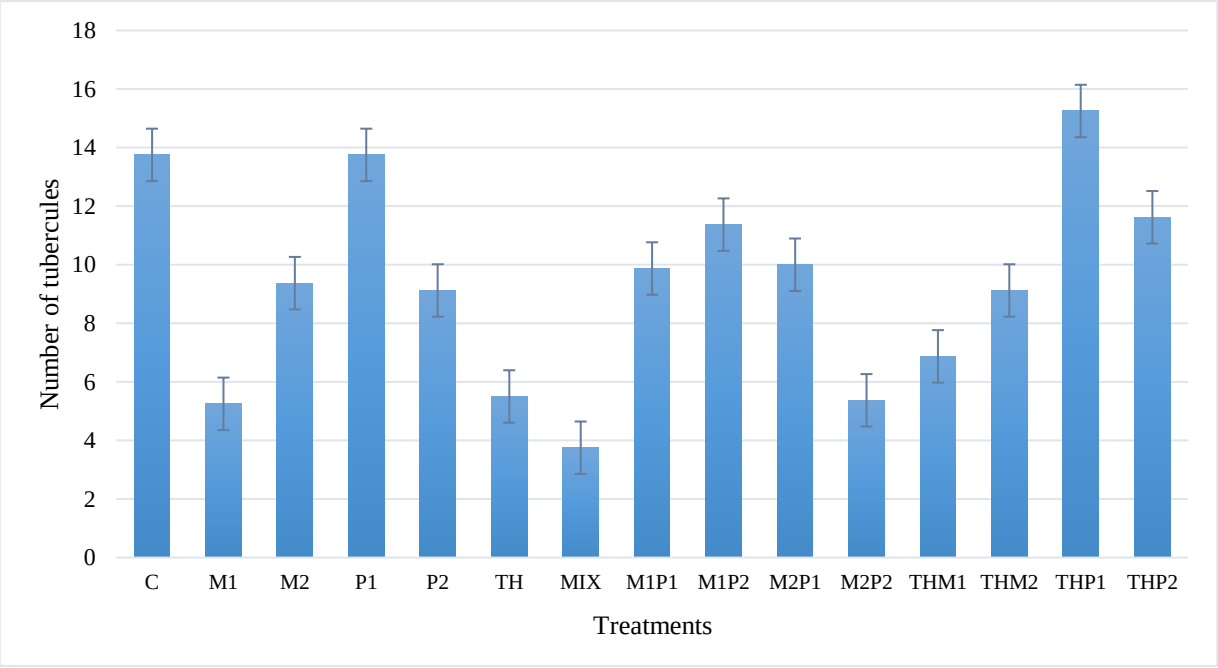

Figure 2- Effect of bioproducts on the number of branched broomrape tubercles in tomato roots

Studies have shown that AMF have the potential to reduce *P. ramosa* infection and partially mitigate its negative effects on tomato plant growth (Gworgwor & Weber 2003; Lendzemo et al. 2007; Fernández-Aparicio et al. 2010). In studies conducted in faba beans, it was reported that the use of AMF, *T. harzanium*, and some bacterial isolates reduced *O. crenata* germination (Hassan & Abakeer 2013). The application of *G. intraradices*, *G. mosseae*, and Glomus Sprint® to tomato plants reduced the percentage of *P. ramosa* tubercles by 22.2%, 42% and 56.8%, respectively (Musa 2012). The results of this study were in parallel with those of several previous studies, and it was observed that all the microorganisms and biological preparations used, except P1 and THP1, prevented the formation of broomrape tubercles. It is thought that the fact that P1 and THP1 application did not prevent the decrease in tubercle number may be due to an antagonistic effect.

Several potential mechanisms are thought to explain the negative effects of biological control agents on weeds. One of them can be considered a direct effect, such as the reaction of the plant's defense system depending on the fungus used and the production of toxic compounds that can inhibit seed germination (Boari & Vurro 2004; Campos-Soriano et al. 2012). Studies have reported that the attachment of the parasite to the host plant leads to the activation of the host plant's immune system (Bouraoui et al. 2024; Leman et al. 2024). Other researchers (Yoneyama et al. 2007; Fernández-Aparicio et al. 2010; Mishev et al. 2021) have reported that AMF increase plant nutrient uptake, especially phosphorus, which may be due to a decrease in the amount of germination stimulants such as strigolactone present in root secretions. Therefore, it has been reported that nutrients as well as organic matter applied from the soil may cause serious physiological disorders in the germination of *P. ramosa* seeds with a decrease in weed infestation (Lops et al. 2017). It is also thought that some microorganisms thicken the cell wall of the host plant through enzymes and consequently affect the penetration between the host and the parasite by affecting the vascular connection, making it difficult for the broomrape to attach to the roots of the host plant (Pérez-de-Luque et al. 2005; Brahmi et al. 2016). Thickening of the cell wall is achieved through the accumulation of callus, suberin and lignin in the attachment zone. This process suggests that penetration and haustorium formation can be prevented by the resistance mechanism formed in the plant (Sisou et al. 2021; Albanova et al. 2023).

3.2. Effects of branched broomrape infection and bioproducts on some antioxidative enzymes and MDA activity in tomato

3.2.1. Effect on catalase (CAT) enzyme activity

For the antioxidant activity of CAT, as shown in Table 3, the differences between the means of the treatments infected and not infected with broomrape were statistically significant. Compared with that in the noninfected treatment group, the CAT content in the broomrape-infected treatment group increased. Specifically, the CAT activity was 80.95% greater in the plants infected with the branched broomrape than in the control plants.

Table 3- The effect of branched broomrape infestation and bioproducts on the CAT enzyme activity (mmol g^{-1} FW)

Treatments	*Uninfected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*	*Infected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*
C	0.0021 ± 0.0002^{abcB}		0.0038 ± 0.0004^{bcA}	
M1	0.0024 ± 0.0004^{abc}	14.77	0.0032 ± 0.0004^{bc}	-13.89
M2	$0.0018 \pm 0.0003^{abcdB}$	-13.92	0.0035 ± 0.0002^{bcA}	-5.56
P1	0.0022 ± 0.0002^{abcB}	7.23	0.0053 ± 0.0006^{aA}	41.67
P2	0.0021 ± 0.0003^{abcB}	-0.20	0.0056 ± 0.0005^{aA}	50.00
TH	0.0010 ± 0.0001^{dB}	-50.10	0.0026 ± 0.0003^{cA}	-30.56
MIX	0.0015 ± 0.0003^{cdB}	-30.14	0.0025 ± 0.0002^{cA}	-33.33
M1P1	0.0021 ± 0.0002^{abc}	1.05	0.0029 ± 0.0003^{c}	-22.92
M1P2	0.0015 ± 0.0003^{cdB}	-30.14	0.0035 ± 0.0003^{bcA}	-5.56
M2P1	0.0026 ± 0.0005^{a}	22.26	0.0030 ± 0.0007^{c}	-19.44
M2P2	0.0024 ± 0.0003^{ab}	17.27	0.0035 ± 0.0006^{bc}	-6.94
THM1	0.0025 ± 0.0002^{aB}	19.76	0.0047 ± 0.0005^{abA}	25.00
THM2	0.0021 ± 0.0003^{abcB}	-0.20	0.0040 ± 0.0005^{bcA}	5.56
THP1	0.0027 ± 0.0003^{a}	29.12	0.0029 ± 0.0004^{c}	-23.71
THP2	0.0015 ± 0.0001^{bcdB}	-27.64	0.0027 ± 0.0005^{cA}	-27.78
Mean	0.0020^{B}		0.0036^{A}	

a, b, c: The difference between the means shown with different letters in the same column is statistically significant (P<0.05).
A, B: The difference between the treatments with and without weed is significant at P<0.05. SE: Standard error.

3.2.2. Effect on superoxide dismutase (SOD) enzyme activity

For the antioxidative stress enzyme SOD, as shown in Table 4, the differences between the means of the treatments infected and not infected with broomrape were statistically significant. When comparing the treatments with and without broomrape infection, statistically significant differences were observed only for the C, M2, P1, M1P1, M2P1, and THP2 treatments. The highest SOD activity was detected in the P1 and M2P1 treatments, while the lowest SOD activity was detected in the M2 and THP2 treatments. Among the broomrape treatment groups, the highest SOD activity was detected in the M2 and M2P2 treatment groups, while the lowest SOD activity was detected in the M1P1 and THP2 treatment groups.

Table 4- The effect of branched broomrape infestation and bioproducts on the SOD enzyme activity (U mg^{-1} FW)

Treatment	*Uninfected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*	*Infected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*
C	137.99 ± 13.27^{abcA}		93.17 ± 6.51^{bcdB}	
M1	93.89 ± 11.48^{de}	-31.96	105.40 ± 12.98^{bc}	13.13
M2	64.93 ± 8.31^{eB}	-52.94	168.91 ± 13.33^{aA}	81.29
P1	157.66 ± 9.33^{aA}	14.25	103.86 ± 8.75^{bcB}	11.47
P2	109.01 ± 16.09^{bcd}	-21.00	97.17 ± 4.81^{bc}d	4.29
TH	88.32 ± 13.28^{de}	-36.00	63.48 ± 9.19^{de}	-31.87
MIX	112.42 ± 14.57^{bcd}	-18.53	86.47 ± 7.56^{bcd}	-7.19
M1P1	83.50 ± 9.31^{deA}	-39.49	46.97 ± 4.00^{eB}	-49.59
M1P2	98.55 ± 9.53^{de}	-28.58	88.88 ± 12.02^{bcd}	-4.60
M2P1	142.59 ± 11.48^{abA}	3.34	77.96 ± 15.23^{cdeB}	-16.33
M2P2	95.14 ± 14.66^{de}	-31.05	121.51 ± 9.64^{b}	30.42
THM1	104.04 ± 14.12^{cde}	-24.61	75.28 ± 16.81^{cde}	-19.20
THM2	109.98 ± 12.71^{bcd}	-20.30	102.77 ± 19.31^{bc}	10.30
THP1	99.36 ± 11.37^{de}	-28.00	118.49 ± 6.27^{b}	27.17
THP2	73.09 ± 3.99^{deB}	-47.04	111.48 ± 14.26bc^{A}	19.65
Mean	104.7 ± 3.66		97.45 ± 3.77	

a, b, c: The difference between the means shown with different letters in the same column is statistically significant (P<0.05).
A, B: The difference between the treatments with and without weed is significant at P<0.05. SE: Standard error.

3.2.3. Effect on ascorbate peroxidase (APX) enzyme activity

According to the APX activity data in Table 5, the differences between the treatments with and without broomrape infection were found to be statistically significant. Comparing the branched broomrape infected and uninfected treatments, the differences between the means were significant only for the C, P2, M1P2, THM1, and THP2 treatments. The highest APX content was detected in C and M1 in the treatments not infected with broomrape, while the highest APX content was detected in P2 and THM1 in the infection treatments. The lowest APX content was detected in P2, M1P2, M2P2, and THM1 in the noninfected treatments, and the lowest APX content was detected in P1, M2P2 and THP2 in the infected treatments.

Table 5- The effect of branched broomrape infestation and bioproducts on the APX enzyme activity (mmol g^{-1} FW) in tomato

Treatment	*Uninfected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*	*Infected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*
C	0.045 ± 0.005^{aA}		0.027 ± 0.004^{cdeB}	
M1	0.031 ± 0.006^{b}	-30.00	0.038 ± 0.005^{abc}	41.67
M2	0.029 ± 0.003^{bc}	-35.00	0.025 ± 0.003^{cde}	-5.55
P1	0.022 ± 0.003^{bcd}	-50.00	0.018 ± 0.001^{e}	-33.33
P2	0.018 ± 0.001^{dB}	-60.00	0.043 ± 0.006^{aA}	61.11
TH	0.022 ± 0.003^{bcd}	-50.00	0.033 ± 0.005^{abcd}	22.22
MIX	0.024 ± 0.003^{bcd}	-46.67	0.025 ± 0.003^{cde}	-5.55
M1P1	0.021 ± 0.002^{bcd}	-53.33	0.029 ± 0.006^{bcde}	8.33
M1P2	0.020 ± 0.002^{cdB}	-55.00	0.033 ± 0.005^{abcdA}	25.00
M2P1	0.022 ± 0.003^{bcd}	-50.00	0.028 ± 0.006^{bcde}	5.56
M2P2	0.020 ± 0.002^{cd}	-55.00	0.018 ± 0.001^{e}	-33.33
THM1	0.020 ± 0.002^{cdB}	-55.00	0.040 ± 0.004^{abA}	50.00
THM2	0.025 ± 0.003^{bcd}	-43.33	0.024 ± 0.003^{de}	-11.09
THP1	0.030 ± 0.004^{bc}	-33.33	0.020 ± 0.002^{de}	-25.00
THP2	0.028 ± 0.003^{bcdA}	-38.33	0.018 ± 0.001^{eB}	-33.33
Mean	0.025		0.028	

a, b, c, d: The difference between the means shown with different letters in the same column is statistically significant (P<0.05).
A, B: The difference between the treatments with and without weed is significant at P<0.05. SE: Standard error.

All plants are exposed to biotic and abiotic stresses throughout their life (Davis & Swanson 2001; Jamshidi et al. 2020). Plant enzymes, such as CAT, SOD and APX, play a critical role in the growth and development of plants. These enzymes constitute

the antioxidant defense system of plants, protecting them against oxidative stress induced by reactive oxygen species (ROS) (Rajput et al. 2021; Bhat et al. 2022). An increase in the SOD enzyme under biotic and abiotic stress conditions is crucial for plant survival under such stress (Büyük et al. 2012). When the SOD enzyme converts O_2 formed under stress conditions into H_2O_2 and O_2, the CAT enzyme directly converts H_2O_2 into H_2O and O_2, thereby shielding the plant against stress factors (Van Camp et al. 1997). Antioxidant enzymes such as ascorbate peroxidase (APX), glutathione reductase, catalase (CAT), and superoxide dismutase (SOD) reduce ROS production, preventing the harmful accumulation of H_2O_2 (Gill & Tuteja 2010; Kang et al. 2014). In addition, Abbes et al. (2020) suggested that this system has an effect that enhances the lignification process through H_2O_2 and peroxidase. This effect limits parasite penetration by strengthening the plant cell wall and protects plant tissues against infection-induced oxidative damage by consuming the overproduction of H_2O_2.

Researchers have reported that plants respond differently to oxidative stress conditions in weeds (Davis & Swanson 2001; Caverzan et al. 2019). The complex structure of beneficial microorganisms is the main reason that different microorganism treatments affect enzyme activity in plants in various ways. Plants tend to determine the optimal strategy to minimize damage caused by pest organisms, resulting in diverse responses of microorganisms to pests (Van der Putten et al. 2001; Caccavo et al. 2022). For instance, Madany et al. (2020) reported that CAT activity was significantly greater in tomato plants infected with broomrape than in uninfected control plants. Chen et al. (1993) reported that, along with the increase in CAT activity, plant cell wall resistance also increased, serving as a signal for the stimulation of defense genes. In three sunflower cultivars contaminated with broomrape, it was observed that broomrape caused variations in total SOD activity depending on the attachment time (Demirbaş & Acar 2008). Alam et al. (2023) reported that the APX content in three different tomato cultivars grown under drought stress differed according to the AMF species. In a study investigating the effects of *F. oxysporum* on *Orobanche* spp., it was determined that compared with the control treatment, *F. oxysporum* treatment increased the SOD content and decreased the CAT content (Aybeke 2017). This is thought to be related to the penetration of the parasite into the tissue and the development of resistance against ROS in cells (Demirbaş & Acar 2008).

In this study, the CAT content was significantly greater in the branched broomrape-infected plants than in the uninfected plants. The SOD content varied in both the broomrape-infected and uninfected treatments, showing an increase in some treatments and a decrease in others. Compared with that in the control group, the APX content decreased in the plants not infected with broomrape; however, compared with that in the control group, the APX content increased in some treatments and decreased in others in the plants infected with broomrape. Similarly, in a previous study conducted in various parts of the world, under stress conditions caused by broomrape infection, both the increase and decrease in the oxidative enzyme content increased and decreased, respectively.

3.3. Effect on lipid peroxidation [Malondialdehyde (MDA)] activity

For the MDA content shown in Table 6, the differences between the means of the treatments not infected with broomrape were found to be statistically insignificant, while the differences between the means of the infected treatments were significant. The MDA content increased in all the treatments except for the C and M1P1 treatments compared with that in the uninfected treatment. The MDA content increased in all treatments in the presence of broomrape infection compared to that in the control group.

Table 6- The effect of branched broomrape infestation and bioproducts on the MDA content (µmol g^{-1} FW)

Treatment	*Uninfected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*	*Infected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*
C	3.00 ± 0.23^{A}		2.12 ± 0.20^{dB}	
M1	3.10 ± 0.44	3.32	4.52 ± 0.88^{ab}	112.93
M2	2.77 ± 0.26^{B}	-7.44	5.00 ± 0.88^{aA}	135.74
P1	2.32 ± 0.32	-22.69	2.53 ± 0.51^{cd}	19.39
P2	2.08 ± 0.26^{B}	-30.76	3.24 ± 0.37^{bcdA}	52.60
TH	2.87 ± 0.36	-4.22	3.90 ± 0.65^{abc}	84.03
MIX	3.11 ± 0.33	3.68	3.68 ± 0.42^{abcd}	73.38
M1P1	2.71 ± 0.43	-9.60	2.55 ± 0.30^{cd}	20.15
M1P2	2.79 ± 0.33^{B}	-6.91	4.49 ± 0.26^{abA}	111.91
M2P1	2.53 ± 0.29^{B}	-15.70	3.58 ± 0.23^{abcdA}	68.82
M2P2	2.60 ± 0.27^{B}	-13.18	4.08 ± 0.45^{abcA}	92.52
THM1	2.91 ± 0.41	-2.78	3.46 ± 0.53^{abcd}	63.24
THM2	3.48 ± 0.31	16.14	4.10 ± 0.36^{abc}	93.54
THP1	2.98 ± 0.50	-0.63	3.78 ± 0.22^{abc}	78.45
THP2	1.77 ± 0.20^{B}	-41.08	3.81 ± 0.55^{abcA}	79.47
Mean	2.73 ± 0.9^{B}		3.66 ± 0.14^{A}	

a, b, c, d: The difference between the means shown with different letters in the same column is statistically significant (P<0.05).
A, B: The difference between the treatments with and without weed is significant at P<0.05. SE: Standard error.

ROS cause increased lipid peroxidation in plants, and ROS production is inevitable in response to stress (Abogadallah 2010; Jamshidi et al. 2020). Lipid peroxidation leads to cell membrane damage, loss of cell fluid, and cell death, resulting in the plant producing MDA. In other words, the greater the degree of damage to the cell membrane structure, the greater the MDA content (Dhindsa & Matowe 1981; Yonghua et al. 2005). Therefore, MDA, a product of lipid peroxidation, is considered a biochemical indicator of oxidative damage (Apel & Hirt 2004). Madany et al. (2020) reported that IAA (indole acetic acid) and SA (salicylic acid) application to seeds had no significant effect on the MDA content in tomatoes compared to the control group, but the MDA content increased by 34% in tomatoes infected with broomrape. In cucumber studies, the MDA content increased in all cucumber genotypes as a result of *P. aegyptiaca* infection compared to that in the control (Faradonbeh et al. 2020; Faradonbeh et al. 2021). This study revealed that the MDA content generally increased in the broomrape-infected plants compared to that in the uninfected plants. In addition, in parallel with the studies mentioned above and in previous years, it was determined that the MDA content increased in the treatments infected with broomrape compared to the control.

3.4. Effects of branched broomrape contamination and bioproducts on total phenolic and antioxidant substances in tomato

The differences between the means of both the infected and noninfected treatments were found to be statistically significant for the number of phenolic substances given in Table 7. The greatest amount of phenolic matter was found in the M2 and M2P1 treatment groups in the noninfected treatment group, and the greatest amount was found in the THP2 and THP1 treatment groups in the infected treatment group. The lowest phenolic content was found in P1 and C in the uninfected treatments, and the lowest phenolic content was found in THM1 and P1 in the infected treatments. Compared with those in the control treatments, there was no significant increase in the amount of total phenolic substances in either the infected or noninfected plants, but there were differences between the treatments.

Table 7- The effect of branched broomrape infestation and bioproducts on total phenolic matter content (mg GAE/100 g)

Treatment	*Uninfected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*	*Infected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*
C	22.01 ± 1.70^{c}		25.82 ± 0.53^{cdef}	
M1	25.22 ± 0.65^{abc}	14.59	23.67 ± 0.71^{ef}	-8.30
M2	27.82 ± 1.76^{a}	26.44	25.73 ± 1.31^{cdef}	-0.35
P1	21.23 ± 1.07^{c}	-3.53	22.70 ± 1.43^{f}	-12.08
P2	24.80 ± 0.62^{abc}	12.70	27.32 ± 1.23^{bcde}	5.83
TH	23.28 ± 0.61^{bc}	5.77	24.68 ± 1.92^{def}	-4.41
MIX	22.48 ± 1.13^{cB}	2.15	27.88 ± 1.21^{bcdA}	7.97
M1P1	22.57 ± 1.37^{cB}	2.56	28.71 ± 0.85^{abcdB}	11.20
M1P2	27.27 ± 0.90^{ab}	23.92	29.05 ± 0.77^{abc}	12.52
M2P1	27.77 ± 1.11^{a}	26.20	25.93 ± 0.54^{cdef}	0.44
M2P2	27.57 ± 1.37^{a}	25.30	27.81 ± 1.56^{bcd}	7.74
THM1	23.99 ± 1.79^{abc}	9.01	22.66 ± 1.52^{f}	-12.22
THM2	25.47 ± 1.73^{abc}	15.72	27.98 ± 1.62^{bcd}	8.38
THP1	24.55 ± 1.54^{abcB}	11.57	30.90 ± 1.65^{abA}	19.71
THP2	23.22 ± 0.78^{bcB}	5.51	32.41 ± 1.03^{aA}	25.56
Mean	24.62 ± 0.36^{B}		26.88 ± 0.39^{A}	

a, b, c, d, e, f: The difference between the means shown with different letters in the same column is statistically significant ($P<0.05$).
A, B: The difference between the treatments with and without weed is significant at $P<0.05$. SE: Standard error.

The total antioxidant content shown in Table 8 revealed statistically significant differences between the means of both the infected and noninfected treatments. In the noninfected treatments, the highest total antioxidant amounts were observed in the M1 and M2P1 treatments, whereas in the infected treatments, the highest total antioxidant amounts were found in the M1 and M1P1 treatments. Conversely, the lowest levels of total antioxidants were found in M2P2 and P1 in the noninfected treatments and in THP1 and M2P1 in the infected treatments. Upon comparing the plants infected and not infected with broomrape to the control plants, an increase in the total antioxidant amount was observed in some treatments, while a decrease was observed in others.

Table 8- The effect of branched broomrape infestation and bioproducts on the total antioxidant content (Trolox µmol (Trolox equivalent) TE/100g)

Treatment	*Uninfected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*	*Infected with broomrape (Mean ± SE)*	*Rate of change compared to control (%)*
C	238.12 ± 13.34^{bc}		189.64 ± 21.65^{abcd}	
M1	326.76 ± 30.04^{a}	37.22	259.33 ± 25.98^{a}	36.75
M2	232.68 ± 11.29^{cd}	-2.29	214.79 ± 29.39^{abc}	13.26
P1	166.15 ± 14.99^{ef}	-30.22	220.70 ± 54.29^{ab}	16.38
P2	213.73 ± 15.37^{cdeA}	-10.24	134.33 ± 13.60^{defB}	-29.16
TH	192.67 ± 11.00^{cde}	-19.09	214.64 ± 17.15^{abc}	13.18
MIX	239.03 ± 34.62^{bc}	0.38	187.74 ± 11.35^{abcd}	-1.00
M1P1	169.18 ± 13.85^{efB}	-28.95	258.58 ± 24.91^{aA}	36.35
M1P2	210.09 ± 16.75^{cde}	-11.77	226.00 ± 11.08^{ab}	19.18
M2P1	291.15 ± 28.98^{abA}	22.27	105.17 ± 11.48^{efB}	-44.54
M2P2	127.89 ± 10.19^{f}	-46.29	105.58 ± 9.42^{ef}	-44.32
THM1	174.48 ± 23.41^{def}	-26.72	164.26 ± 24.92^{bcde}	-13.38
THM2	168.48 ± 12.55^{ef}	-29.25	145.64 ± 6.46^{cde}	-23.20
THP1	222.59 ± 11.04^{cdeA}	-6.52	69.62 ± 3.28^{eB}	-63.29
THP2	182.78 ± 16.19^{cdef}	-23.24	172.02 ± 12.72^{bcde}	-9.29
Mean	210.39 ± 6.5^{A}		177.87 ± 7.37^{B}	

a, b, c, d, e, f: The difference between the means shown with different letters in the same column is statistically significant (P<0.05).
A, B: The difference between the treatments with and without weed is significant at P<0.05. SE: Standard error.

Phenolic compounds, which are found in many plant organs, are nonenzymatic secondary metabolism products. These compounds play a role in ecological and physiological events and have antioxidant activity (Kıpçak et al. 2019). The total phenolic content of host plants can be affected by the use of biological control agents (Doley & Jite 2014). In addition, the total phenolic content also changes due to infection of host plants by pathogens (Singh et al. 2013). Singh et al. (2013) reported that differences in the host plant's total antioxidant activity occurred due to pathogen infection, while Doley & Jite (2014) reported that the total antioxidant content was affected by the use of biological control agents. Faradonbeh et al. (2020) reported that increased phenol compounds in sunflower due to broomrape contamination can be considered a protective response against *O. cumuna*. It is believed that the accumulation of phenolic compounds, lignin, and peroxidases can be triggered to inhibit the penetration of haustoria into the host's vascular system (Echevarria et al. 2006; Mutuku et al. 2019). In a study, examined the impacts of several mycorrhiza species on organic carrot farming and revealed that antioxidant activity was positively impacted (Kiracı et al. 2014). In a study by Boyno et al. (2022), it was found that the biological control agents used against *Alternaria solani* in tomatoes did not significantly affect the total phenolic content or antioxidant activity, although changes were observed depending on the type of application. According to the data obtained in the present study, compared with those in the control group, the total phenolic matter and antioxidant content in plants not infected with broomrape increased in some treatment groups but decreased in other treatment groups.

4. Conclusions

As a result of the study, the number of broomrape tubercles decreased in all treatments except for the P1 and THP1 treatments compared to that in the control group. MIX, M1, TH, M2P2, THM1, and THM1 were the most effective treatments for preventing the attachment of the weed by 50-72%. It was also observed that oxidative stress occurred in the plants infected with broomrape, and the plants responded differently to this stress. According to the total phenolic matter and antioxidant activity data, there was no statistically significant increase or decrease in phenolic matter content in the plants infected with broomrape compared to the control plants. These results support the theory that bioproducts used in tomato cultivation negatively affect broomrape attachment in the controlled conditions; however, more significant conclusions can be drown when the trials are conducted under field conditions. Nevertheless, there is a paucity of precise information elucidating the mechanisms through which these

microorganisms curtail broomrape germination. Findings indicates a plausible association with soil-dwelling microorganisms during the dormancy phase of broomrape seeds. It is proposed that enzymatic mechanisms, which enhance cell wall thickness, arise from soil microorganisms that facilitate plant nutrient uptake. In addition, a decrease in stimulants secreted by the host and an increase in systemic resistance in the plant are the other suggested causative causes. This research investigated the significance of introducing a novel paradigm for broomrape control by leveraging the use of bioproducts that preserve the natural ecosystem and mitigate physiological perturbations during broomrape infection.

Declaration of conflicting Interest

The authors declared no conflicts of interest with respect to the research, authorship and publication of this article.

This study was funded by Van Yüzüncü Yıl University, Scientific Research Projects Department (FDK-2020-8850).

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