Egyptian Journal of Biological Pest Control

RESEARCH

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Systemic resistance induction of tomato plants against tomato mosaic virus by microalgae

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Abstract

Background: Tomato mosaic virus (ToMV) is a dangerous disease of tomato (*Lycopersicon esculentum*) that reduces dramatically the yield. To reduce ToMV infection, microalgal isolates were utilized. Microalgal species (*Chlorella vulgaris, Anabaena oryzae, Spirulina platensis, Nostoc linckia* and *Dunaliella salina*) were shown to be responsible for the stimulation of tomato resistance against ToMV.

Results: Initial signs of discoloration and mosaic in ToMV-inoculated plants were detected and identified on inoculated leaves at 6 and 12 dpi in control and treated plants, respectively, suggesting that microalgae may inhibit ToMV growth. Treatment with microalgae resulted in a significant decrease in symptoms (up to 63% reduction in disease severity) and negative ELISA readings, indicating that the microalgae induced resistance in tomato against ToMV infection. The isolates also enhanced the activity of pathogenesis-related enzymes (PPO and POX reaching to 0.033 and 0.054 in *D. salina,* respectively), as well as tomato growth characters in comparison with the control. Microalgal treatments demonstrated that the salicylic acid (SA) and jasmonic acid (JA) pathways were involved in tomato plant defense responses. The relative gene expressions of *PR1* and *phenylalanine ammonia lyase* (*PAL*), which are involved in the SA and JA pathways, respectively, were improved in treated plants compared to the control.

Conclusion: The findings indicated that algal-induced ToMV resistance was mediated via several defense pathways in tomato. The antiviral mechanism was described, which provides a light on the potential of algae in plant viral disease management.

Keywords: Algae, Tomato mosaic virus, Tomato, Jasmonic acid, Salicylic acid, Defense response

Background

Plant diseases are widely regarded as one of agriculture's most damaging factors. Several viral diseases have seriously affected tomato production, resulting in significant financial losses (Balogun 2008). Tomato mosaic virus (ToMV) is one of the tobacco mosaic virus (TMV) strains (Fernandes et al. 2006). ToMV triggers prevalent plant viral infections, causing significant crop losses all over the world. ToMV has been found to infect different plant species, including crops, flowers, and weeds. The growing leaves may be deformed, usually twisted with the leaflets becoming considerably narrower. The fruits are typically tiny and misshaped, develop irregularly and exhibit yellow discoloration, often in rings, as well as interior localized brown necrotic regions (Cerkauskas 2004). ToMV is difficult to control, because it is easily spread anywhere as it is mechanically transferred, and symptoms appear 6–14 days after infection (dpi) in susceptible plants (Ara et al. 2012). Additionally, the traditional chemical treatments are ineffective in protecting plants against ToMV

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infection due to the virus's great genetic variability. Furthermore, the application of non-biodegradable chemicals pollutes the environment severely. Physical barriers and reflecting mulches have traditionally been used to control viral diseases (Hilje et al. 2001). As a result, it is critical to search for new biocontrol agents against plant viral disease. Plants that have been treated with beneficial endophytes have improved their induced systemic resistance (ISR) against a variety of diseases. The molecular mechanism of their antiviral action, on the other hand, is still unclear.

Biological control agents that are effective, dependable and environmentally friendly have received a lot of attention in recent decades (Elsharkawy et al. 2012). Viral plant diseases were mostly controlled with the use of bacterial biocontrol agents such as *Bacillus* spp. and fungal biocontrol agents such as *Trichoderma* spp. (Kumar et al. 2016). Algae are old photosynthetic microorganisms that is between prokaryotic cyanobacteria and eukaryotic microalgae (Parker et al. 2008). Algae are often categorized based on morphology and life cycle (Blaby-Haas and Merchant 2019). There are about 800,000 species of algae in the world, but only 5,000 of them have been identified until now. Only a limited number of algal species have been chosen to test their practical applicability in plant development under controlled conditions. Prokaryotic *Anabaena variabilis* application as a root-drench treatment decreased damping-off symptoms in tomato (Chaudhary et al. 2012).

Disease-resistant proteins constitute the majority of the resistance pathways. In the ISR signaling pathways, salicylic acid (SA) plays a critical role. SA levels in the phloem were improved after infection (Elsharkawy et al. 2012). Transgenic plants carrying the bacterial *nahG* gene, which encodes naphthalene hydroxylase G, are unable to accumulate SA, and their ISR response was blocked (Delaney et al. 1994). The PAL enzyme is critical for plant defense and is one of the most extensively researched enzymes in all secondary metabolisms. It is involved in defense mechanisms and operates upstream of SA biosynthesis (Buchanan et al. 2000). PAL begins biochemical processes that lead to the production of SA. Plant proteins that are activated in pathogenic conditions are known as pathogenesis-related proteins (PRs). A variety of PRs are effective anti-pathogenic compounds (Van Loon et al. 1994). Infection with bacteria, viruses, fungi or viroids may induce the production of PRs in plants (Elsharkawy et al. 2012). Additionally, biotic inducers stimulate the production of many PR proteins, including isozymes of peroxidase and chitinase (Singh et al. 2008). The basic pathogenesis-related protein (PAL), which is grouped in JA dependent marker genes, is essential for the JA pathway. Tomato plants infected with tomato spotted wilt virus (TSWV) have been demonstrated to produce defense-related proteins after treatment with *P. fluorescens* (Kandan et al. 2005).

The study aimed to evaluate the antiviral activity of algal species; *Chlorella vulgaris, Anabaena oryzae, Spirulina platensis, Nostoc linckia* and *Dunaliella salina* against ToMV infection in tomato, as well as the potential mechanisms involved.

Methods

Leaf samples, demonstrating dark green mosaic or mottling, were collected. The tomato mosaic virus (ToMV) was detected in tomato plants by enzyme-linked immune sorbent assay (ELISA), using antiserum specific for ToMV (Elsharkawy et al. 2012). The virus was biologically purified using a modified single local lesion method on *Nicotiana glutinosa* (El-Kammar et al. 2016). Symptomatology and methods of transmission were considered for virus identification.

Plant materials and growth conditions

Algal treatments of the species (*C. vulgaris, A. oryzae, S. platensis, N. linckia* and *D. salina*) were prepared before soil drench applications. In 50 ml conical tubes, 10 g of dried algae and 20 ml of solvent, such as ethanol, were mixed. The tubes were placed in a reciprocating shaker for 24 h to ensure constant agitation at 150 revolutions per minute for mixing and full clarification of bioactive components to dissolve in the appropriate solvent. The tubes were then centrifuged at 4 °C for 15 min at 4000 rpm to collect the supernatants, which were then filtered using Whatman no. 1 filter paper. The solvent was extracted by vacuum evaporation at 50 °C in a water bath. The residues were then obtained and utilized in the experiments. Specific media were used for *A. oryzae* (watanabe medium), *S. platensis* (Zarrouk medium) and *D. salina* (modified Johnson medium).

Under greenhouse conditions (Kafr Elsheikh University), 120 tomato (*Lycopersicon esculentum*) seedlings were carefully transplanted into plastic pots (25 cm in diameter) containing sterilized sand and clay soil mixtures (3:1, v/v). Seedlings were cultivated in a growth chamber with a 16/8 h photoperiod and fertilized as recommended once a week. Twenty infected seedlings were utilized for viral replication. Twenty seedlings (3-week-old seedlings) were utilized for each algal treatment (6.0×10^6 cells/ml and 10 ml per seedling), and the remaining 20 seedlings were used as a control treatment.

Assessment of disease severity

The severity of symptoms and the concentration of ToMV were used to determine the level of ToMV resistance. The disease severity was calculated at

2 weeks post-virus inoculation (WPI) and represented as a percentage of plants exhibiting ToMV symptoms. The severity of the disease was determined by visual observation of viral symptoms using an arbitrary scale devised by Wang et al. (2009), with 0 indicating no symptoms, 1 indicating light mottling and a few thin yellow veins, 2 indicating mottling and vein clearing unequally distributed on the leaf, 3 indicating mottling, leaf distortion and stunting and 4 indicating severe mottling, leaf curling and stunting. The severity index was calculated for each group of plants using the method given by Raupach et al. (1996).

$$\text{Disease severity index (\%)} = \sum \left(\frac{\text{Disease grade} * \text{number of plants in that grade}}{\text{Total number of plants} * \text{the highest disease grade}} \right) * 100$$

ToMV concentration was determined by enzyme-linked immunosorbent assay (ELISA) as described by Elsharkawy et al. (2012). Plant height, shoot fresh and dry weights and fruits weight per plant were measured by the end of the experiment.

Enzyme activity assays

Polyphenol oxidase (PPO) activity was assessed according to Zhu (1990). Homogenized leaf tissue (1 g) was centrifuged at 8000*g* in 250 µl of 50 mM of sodium phosphate buffer (0.1 M, pH 6.5) for 30 min at 4 °C. As an enzyme extract, 0.1 mL of the supernatant was mixed with 25 mM phosphate buffer (pH 6.8) and 0.1 mM pyrogallol. There was no pyrogallol in the control mixture. Each sample's absorbance was measured as the rate of increase in absorbency at 525 nm.

Peroxidase (POD) activity was determined by Moerschbacher et al. (1998). Homogenized leaf tissue (1 g) was centrifuged at 12,000 rpm in 5 ml of buffer (pH 7.0) with 0.1% EDTA (SIGMA) and 10% polyvinylpyrrolidone (SIGMA) for 20 min at 4 °C. The supernatant (0.1 ml) as an enzyme extract was mixed with 100 µl guaiacol 20 mM and 40 µl of 0.1% H_2O_2. Each sample's absorbance was monitored at 470 nm. The activities were measured as absorbance min^{-1} g^{-1} fresh weight.

Real-time (RT)-qPCR analysis of defense-related genes expression

After 2 days of virus inoculation, samples were taken from both treated and control tomato plants in triplicate. RNA-later kit (Applied Biosystems, Courtaboeuf, France) was utilized for RNA extraction. Revert Aid First Strand cDNA Synthesis Kit (K1621, Fermentas) was used for reverse transcription. For PCR analysis, the reverse transcription products were utilized as templates. In a final volume of 25 µl, 1X SYBR green Fluorescein Mix, 250 nM of each primer and 1 µl of cDNA were added to conduct real-time PCR. The relative expression of *PR1* and *PAL* genes was calculated against the *UBI3* (Table 1). The threshold cycles were determined using a melt curve temperature after amplification (Livak and Schmittgen 2001).

Data analysis

Analysis of variance was performed on experimental data. The experiments were carried out 3 times. Using WASP—Pro Software, Duncan's multiple range test (DMRT, $P \leq 0.05$) was used to split the mean values into two groups.

Results

Effect of algae treatments on disease severity

Discoloration and mosaic symptoms were initially observed on the leaves of ToMV-infected plants at 7 dpi (days post-inoculation) in non-treated pots, whereas non-inoculated plants did not exhibit any ToMV symptoms. For the plants treated with algae, the symptoms began to appear on the leaves at 11 dpi. ToMV-inoculated plants were smaller in the absence of algae, having smaller and narrower leaves. Plants treated with algae, especially *D. salina*, had less severe ToMV symptoms (Fig. 1). Infected plants were typically healthier, taller, and more robust in algal treatment than those growing in non-treated pots. When compared to non-treated plants, treatments with *D. salina* and *C. vulgaris* decreased the severity of ToMV-inoculated plants by 63 and 56%,

Table 1 Forward and reverse primers sequence for pathogenesis-related genes

Gene	Forward primer	Reverse primer	Size	Accession number
PR1	GCCAAGCTATAACTACGCTACCAAC	GCAAGAAATGAACCACCATCC	139	DQ159948
PAL	CTGGGGAAGCTTTTCAGAATC	TGCTGCAAGTTACAAATCCAGAG	150	AW035278
UBI3	TCCATCTCGTGCTCCGTCT	GAACCTTTCCAGTGTCATCAACC	144	X58253

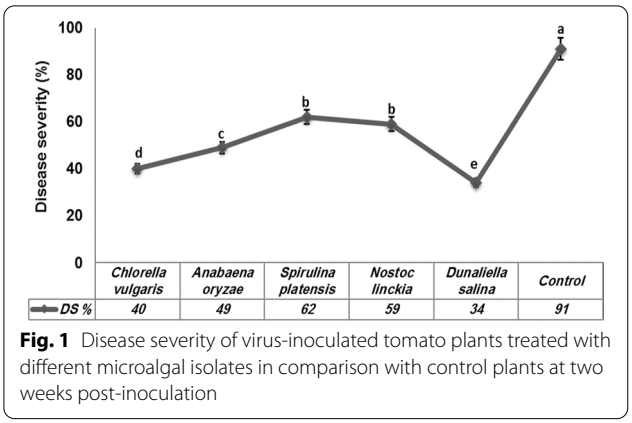

Fig. 1 Disease severity of virus-inoculated tomato plants treated with different microalgal isolates in comparison with control plants at two weeks post-inoculation

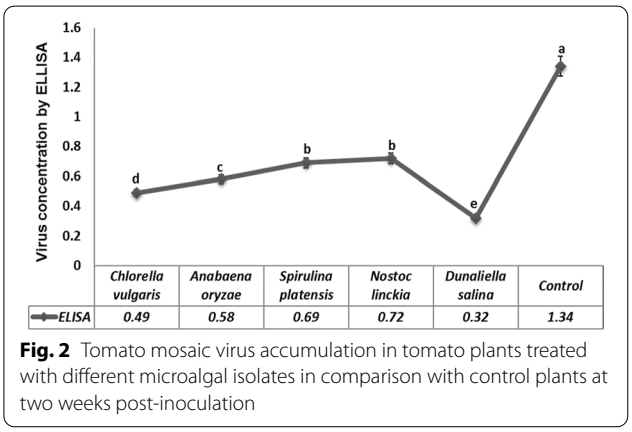

Fig. 2 Tomato mosaic virus accumulation in tomato plants treated with different microalgal isolates in comparison with control plants at two weeks post-inoculation

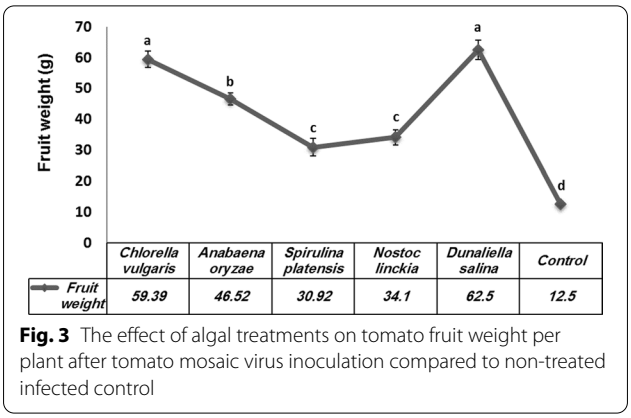

Fig. 3 The effect of algal treatments on tomato fruit weight per plant after tomato mosaic virus inoculation compared to non-treated infected control

respectively (Fig. 1). Similarly, when diseased plants were treated with *A. oryzae, N. linckia* and *S. platensis*, the virus severity was decreased by 46, 35 and 32%, respectively (Fig. 1).

Effect of algae treatments on ToMV concentration

Two weeks after being inoculated with ToMV-infected sap, seedlings of inoculated tomato plants began to exhibit symptoms and provided a positive ELISA response. Infected plants (control) displayed the ideal severe symptoms with a fully positive ELISA reactions, whereas the plants treated algae displayed no symptoms with negative ELISA reactions. In *D. salina* treatment, there was a significant decrease in symptoms with complete negative ELISA readings. Infected plants treated with other algal species exhibited the same impact of significant symptom reduction with full negative ELISA readings, indicating algae's antiviral activity (Fig. 2).

Plant growth, and morphological parameters

When compared to the control, the treated plants exhibited significant increases in height, fresh and dry weights and fruits weight per plant (Fig. 3). The leaves, especially the freshly emerging ones, were distorted to varying degrees. Algae had typically accelerated the development of non-infected and ToMV-inoculated plants, with the greatest impact at *D. salina*. In the presence of pathogen, *D. salina* treatment enhanced plant height to 44.7 cm than corresponding controls (29.7 cm) (Table 2). Plant fresh and dry weights increased to 44.8 and 5.1 g, respectively, in response to *D. salina* treatment, when compared to the corresponding controls (Table 2).

Table 2 Plant height (cm), shoot fresh weight (g) and dry weight (g) of tomato plants treated with algae isolates and infected with tomato mosaic virus

Treatments	Plant height (cm)	Fresh weight (g)	Dry weight (g)
Chlorella vulgaris	43.3^{a}	39.9^{b}	4.6^{b}
Anabaena oryzae	40.9^{ab}	35.9^{c}	4.0^{c}
Spirulina platensis	35.8^{c}	33.1^{d}	3.2^{d}
Nostoc linckia	38.7^{bc}	35.7^{c}	3.9^{c}
Dunaliella salina	44.7^{a}	44.8^{a}	5.1^{a}
Control	29.7^{d}	24.7^{e}	2.4^{e}

Different letters denote significant differences

Defense-related enzymes activity

When compared to the control, the activity of POX in the plants treated with algae was elevated in response to ToMV infection (10 dpi) (Table 3). In comparison with their respective controls, infected plants treated with *D. salina* and *C. vulgaris* exhibited the highest increase in POX activity (Table 3). Furthermore, when treated with at *A. oryzae, N. linckia* and *S. platensis*, ToMV-infected plants showed slight increases in POX activity than corresponding controls (Table 3).

Tomato plants treated with *D. salina* and infected with ToMV had a greater impact on PPO enzyme activity than other treatments, including treatment with *C. vulgaris*. The PPO activities reached 0.033 and 0.028 in *D. salina*

Table 3 Activities of peroxidase (POX) and polyphenol oxidase (PPO) enzymes in tomato plants treated with microalgal isolates and infected with Tomato mosaic virus

Treatments	Peroxidase μM tetraguaiacol g^{-1} FWmin^{-1}	Polyphenol oxidase Arbitrary units
Chlorella vulgaris	0.043[b]	0.028[b]
Anabaena oryzae	0.033[c]	0.021[c]
Spirulina platensis	0.023[d]	0.016[d]
Nostoc linckia	0.022[d]	0.018[d]
Dunaliella salina	0.054[a]	0.033[a]
Control	0.017[e]	0.009[e]

Different letters denote significant differences

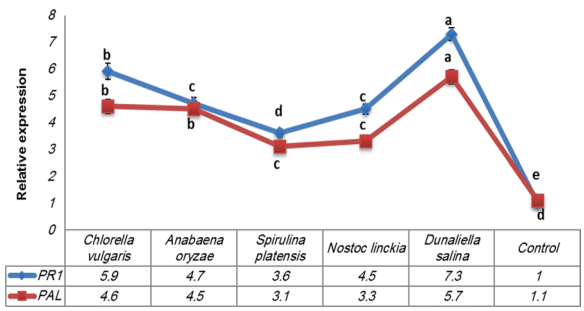

Fig. 4 The transcription levels of *PAL* and *PR1* genes in tomato plants in control and treated plants using real-time quantitative PCR analysis at 2 days post-inoculation

and *C. vulgaris*, respectively. Treatment by *N. linckia* achieved the lowest activity of PPO, reaching 0.022 (Table 3).

Effect of algae on defense-related gene expression

PAL and *PR1* transcription levels significantly increased in the treated plants than in the non-treatment plants at 2 dpi (Fig. 4). *D. salina*- and *C. vulgaris*-treated plants showed 5.7- and 4.6-fold increases in the relative expression of *PAL*, respectively, as compared to the control plants. *PR1*, like the PAL expression, was considerably elevated, with relative transcription levels in the *D. salina*- and *C. vulgaris*-treated tomato plants being 7.3- and 5.9-fold higher than the control, respectively (Fig. 4).

Discussion

Viral plant disease management using useful microorganisms has gained a lot of attention, since it is a safe and environmentally friendly method of managing viruses (Elsharkawy et al. 2013). Bacteria and fungi constitute the majority of the biocontrol agents employed to control viral plant diseases (Elsharkawy et al. 2012). The use of algae for biocontrol of viral plant diseases is still limited, and their potential actions against viral diseases are not understandable. High activities of certain important enzymes, such as peroxidase (POX) and polyphenol oxidase (PPO), the first enzymes to react and provide rapid defense against plant diseases, are usually linked with increased lignification (Sulman et al. 2001). POX activity was substantially increased in algae-treated and ToMV-inoculated plants with the impact being much more pronounced in ToMV-inoculated plants treated with *D. salina*. Induction of POXs in response to pathogen inoculation has been observed in many pathosystems, with resistant plants showing a greater rise than susceptible plants (Houterman et al. 2007). POX activity was also enhanced in plant–virus interactions in beans—white clover mosaic potexvirus (Clarke et al. 2002), and pumpkin—cucumber mosaic virus and zucchini yellow mosaic virus (Clarke et al. 2002). During the defensive response, POXs are known to engage in a variety of processes including polysaccharide bonding, phenol oxidation, suberization and lignification of cell walls (Carvalho et al. 2006). As a result, the increased activity of POX in algae-treated plants reported in this research may contribute to the lignification process, which is thought to be a pathogen resistance mechanism.

Algae have just recently been used as biocontrol agents for plant diseases. The antiviral activity of algae against ToMV on tomato plants was investigated in this research. Furthermore, the POX and PPO activities in leaves of treated plants at 10 dpi have been identified. The effects of algae on ToMV-CP accumulation and expression of two defense-related genes (*PAL* and *PR1*) at 2 dpi, on the other hand, were analyzed. The transcription levels were sharply raised in tomato plants infected with ToMV in the research model. Algal treatments improved plant growth parameters, reduced disease symptoms and lowered viral accumulation levels in greenhouse studies as compared to infected control tomato plants. ToMV-infected tomato plants cultivated with algae grew faster and better than virus-infected tomato control plants. The shoot fresh and dry weights were greatly increased in tomato plants treated with algae and inoculated with ToMV, but decreased dramatically in tomato plants infected with ToMV only. Increased plant development may be a result of algae's potential to promote the production of a variety of phytohormones and their ability to generate a variety of substances.

Obtained findings were consistent with those of the previous research on the utilization of plant secondary metabolites to control plant viral diseases such as ToMV. Actinomycetes, fungi and bacteria are among the microorganisms employed in the treatment against plant disease (Elsharkawy et al. 2013). Plant pathogens such as

ToMV and cucumber mosaic virus treated with elicitors produced from microorganisms, improved plant's resistance to these pathogens (Elsharkawy et al. 2013).

Antiviral action of algae against ToMV was demonstrated in this research. This research is the first to look into how algae work against plant viruses. The suppressive impact of algae may be due to induced systemic resistance (indicated by higher POX and PPO activities and transcription levels of *PAL* and *PR1* in the leaves of tomato plants treated with algae). In this study, algae's antiviral and stimulant abilities were shown by reducing ToMV virus symptoms and activating the expression of 2 genes, *PR1* and *PAL*, which are involved in the SA and JA pathways, respectively. The expression levels of both treated and control tomato plants were assessed, 2 days following ToMV inoculation. *PR1* and *PAL* expression levels were greater in algae-treated tomato seedlings than in untreated seedlings. Treated tomato plants and challenged with ToMV showed increasing *PAL* and *PR1* levels, with relative expression levels representing sixfold and eightfold changes, respectively, which were higher than control samples. Interestingly, both treatments, i.e., *D. salina* and *C. vulgaris* + virus-treated plants, exhibited an induction and overexpression of *PAL* and *PR1*. The *D. salina* + virus-treated plants showed the highest expression levels of *PR1* and *PAL*, with a relative expression level representing a 7.3- and 5.7-fold change higher than the control plants. Consequently, it is suggested that *D. salina* may work as an elicitor molecule that induced the immune defense system, which may result in ISR activation. In this context, tomato plants pre-treated with *Streptomyces pactum* Act12 exhibited an induction of *PR1* and enhanced POX and PAL activities in tomato leaves, resulting in the development of SAR against TYLCV (Li et al. 2019). Plant resistance was regulated by *PR2* gene, which is a common marker gene involved in the SA biosynthesis pathway, and their expressions were observed after infection in tomato (El-Shafeey et al. 2019).

Conclusions

In addition to all their other activities in the environment and agriculture, algae should be examined more in the areas of plant resistance induction and biocontrol. The findings revealed that algae promoted tomato resistance to ToMV infection by activating various plant defense systems. When compared to the untreated control, the treated plants showed much higher levels of defensive enzyme activities. Finally, this research may represent a step forward in the use of useful algae as a potential environmentally friendly disease control strategy. However, further research is required to determine the specific pathways behind algae-induced systemic resistance in other phytopathosystems.

Abbreviations

ToMV: Tomato mosaic virus; SA: Salicylic acid; JA: Jasmonic acid; PAL: Phenylalanine ammonia lyase; ELISA: Enzyme-linked immunosorbent assay; PPO: Polyphenol oxidase; POD: Peroxidase.

Acknowledgements

The authors extend their appreciation to Taif University for funding current work by Taif University Researchers Supporting Project number (TURSP—2020/142), Taif University, Taif, Saudi Arabia.

Author contributions

EMM and HA carried out the experiments and wrote the manuscript. EMK, GKE, SIB, AA, SH and AMKM revised the manuscript. All authors read and approved the final manuscript.

Funding

The authors were appreciated Taif University Researchers Supporting Project number (TURSP—2020/142), Taif University, Taif, Saudi Arabia.

Availability of data and materials

All data and materials are available.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 16 January 2022 Accepted: 9 April 2022
Published online: 16 April 2022

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