PLANT SCIENCE TODAY
Vol 13(1): 1-9
https://doi.org/10.14719/pst.11438

eISSN 2348-1900

RESEARCH ARTICLE

Allelopathic effects of silverleaf nightshade (*Solanum elaeagnifolium* Cav.) aqueous extracts on germination and early growth of wheat, broad bean and flax

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Received: 24 August 2025; Accepted: 06 November 2025; Available online: Version 1.0: 03 February 2026; Version 2.0: 28 February 2026

Cite this article: Almarie AA, Hamad HS, Almehemdi AF, Mheidi UH. Allelopathic effects of silverleaf nightshade (*Solanum elaeagnifolium* Cav.) aqueous extracts on germination and early growth of wheat, broad bean and flax. Plant Science Today. 2026; 13(1): 1-9. https://doi.org/10.14719/pst.11438

Abstract

Silverleaf nightshade (*Solanum elaeagnifolium* Cav.) is one of the most problematic invasive plants threatening agricultural lands in the northern Middle East. Its recent widespread occurrence has raised serious concern, as one of the major problems associated with lands infested by this weed is its allelopathic effect on successive crops. Therefore, the present study aimed to evaluate the allelopathic effect of different concentrations of its aqueous extracts on the germination and seedling development of three potential successive crops, wheat (*Triticum aestivum* L.), broad bean (*Vicia faba* L.) and flax (*Linum usitatissimum* L.) and to screen its chemical components. All tested concentrations of the plant extract had a negative impact, inhibiting germination and suppressing seedling growth. The highest concentration (12.5 %) inhibited germination of wheat and broad bean by 100 %, while flax seeds showed complete germination inhibition at concentration of 7.5 % and above. Furthermore, the lower concentrations exhibited an inhibitory effect on growth over time, likely due to the accumulation of active substances within seedlings, preventing normal germination and development. The results of the chemical composition analysis also indicated that the residues of this plant contain a considerable amount of bioactive secondary metabolites known to inhibit seed germination, particularly glycosides and terpenes. The study's findings demonstrate the adverse impact of this plant's spread and recommend implementing all possible measures to limit its further expansion. Conversely, the study highlights the potential use of its bioactive compounds as natural agents for biological control.

Keywords: allelochemical; antagonism; invasive plant; *Solanum*

Introduction

Silverleaf nightshade (*Solanum elaeagnifolium* Cav.) is a vivid example of the health, economic and social damage that invasive organisms, including plants, can cause, in addition to their environmental harm. This plant is a deep-rooted, broadleaf, perennial weed belonging to the Solanaceae family. It originated in tropical America and has gradually spread to environments beyond its natural range through various pathways, such as transport by trucks, feed containers, contaminated crop seeds and exported food products where biosecurity protocols are not strictly followed (1). The stem can grow up to 1 m tall and is covered with nettle-like spines less than 0.5 cm long, which vary from sparse on some plants to dense on others. Both leaves and stems are covered with downy hairs (trichomes) that lie flat against the surface, giving the plant a silvery or greyish appearance. The leaves are up to 15 cm long and 0.5 to 2.5 cm wide, with shallowly waved edges. The flowers, which appear from April to August, have five petals united to form a star shape, ranging from blue to pale lavender or occasionally white, with five yellow stamens and a pistil forming a prominent central column. The plant produces glossy yellow, orange or red berries that persist through winter and may turn brown as they dry (2).

Silverleaf nightshade is considered one of the worst alien invasive plants worldwide. Surveys have shown that the range of *S. elaeagnifolium* has increased by 175 % in the studied areas over the past decades (2). This plant today poses a serious threat to several Middle Eastern countries, particularly Palestine, Syria and Iraq. According to the National Herbarium of Iraq, this plant was identified in the latest update of the Solanaceae family as the most invasive plant in the last two decades (3). In Syria, it has invaded nearly 60 % of wheat and cotton farms, even olive fields have not been spared. In northwestern Iraq, this plant has become the sworn enemy of farmers, while in Lebanon and Jordan, it is also beginning to spread (4).

The spread of *S. elaeagnifolium* is further intensified by its rhizomatous and creeping root system, which facilitates vegetative reproduction and by its high seed production capacity. Each plant produces 60-100 fruits, with each fruit containing 16-40 seeds. These seeds do not germinate simultaneously and remain viable for a long period, even after passing through the digestive tracts of animals. Furthermore, the absence of natural enemies enables its easy dispersal to new locations. One of the distinct characteristics of silverleaf nightshade plant is that its deep roots system competes

with crops for water and nutrients, thereby depleting soil moisture and reducing the productivity of agricultural lands. In addition, it is classified among the poisonous herbs for livestock (5).

All parts of the plant contain allelochemicals, primarily alkaloids, which inhibit the germination and growth of many crop species. A study estimating the content of bioactive compounds in different plant parts found that alkaloids concentration ranged from 0.96 to 1.68 %, with the roots containing the highest levels. Among other bioactive compounds, flavonoids content ranged from 0.49 to 0.88 %, tannins from 0.13 to 0.16 % and saponins from 0.27 to 0.30 % (6). Extract prepared from leaves, stems, flowers and fruits exhibited stronger phytotoxic effects than those from roots on hard wheat (*Triticum durum)* and wild oats (*Avena fatua),* which were more sensitive than barley (*Hordeum vulgare)*. Silver nightshade caused a significant reduction in germination, tiller number total fresh and dry weights, spike number and seed yield compared with control plots (7).

Given the importance of crops grown after the ripening period of this weed in Iraq, the present study was conducted to identify the active compounds in *S. elaeagnifolium* and to examine the effects of its aqueous extracts, at different concentrations, on the germination and growth of successive crops, including wheat, broad bean and flax.

Materials and Methods

Plant collection

Plant parts of silverleaf nightshade (*S. Elaeagnifolium)* were collected from agricultural fields where this weed had widely spread along both sides of the Euphrates River, located in western Anbar Governorate, Iraq (latitude: 33° 22' 25.79" N, longitude: 43° 42' 34.19" E) during the fruiting stage. The collected plant material was washed thoroughly, oven-dried and ground into a fine powder using an electric grinder, then stored for further analysis. Fig.1 showing the maturity stage of *S. elaeagnifolium*.

Preparation of silverleaf nightshade extraction

The aqueous extract of *S. elaeagnifolium* plant parts was prepared by soaking 25, 50, 75, 100 and 125 g of the dried plant powder in 500 mL of distilled water overnight, followed by stirring on a magnetic stirrer for 1 hr. The mixtures were then filtered and the resulting filtrates were diluted with distilled water to a final volume of 1000 mL. The stock solutions were stored at 4 °C until further use.

Identification of the chemical composition of the *S. elaeagnifolium* extracts

The bioactive compounds of *S. elaeagnifolium* were analysed using gas chromatography mass spectrophotometry (GC-MS) type Shimadzu 2010 with a BPX5 non-polar fused silica capillary column (30 m x 0.25 mm, 0.25 µm film thickness). The oven temperature was programmed from 40 to 230 °C at a rate of 8 °C min^{-1} and the final

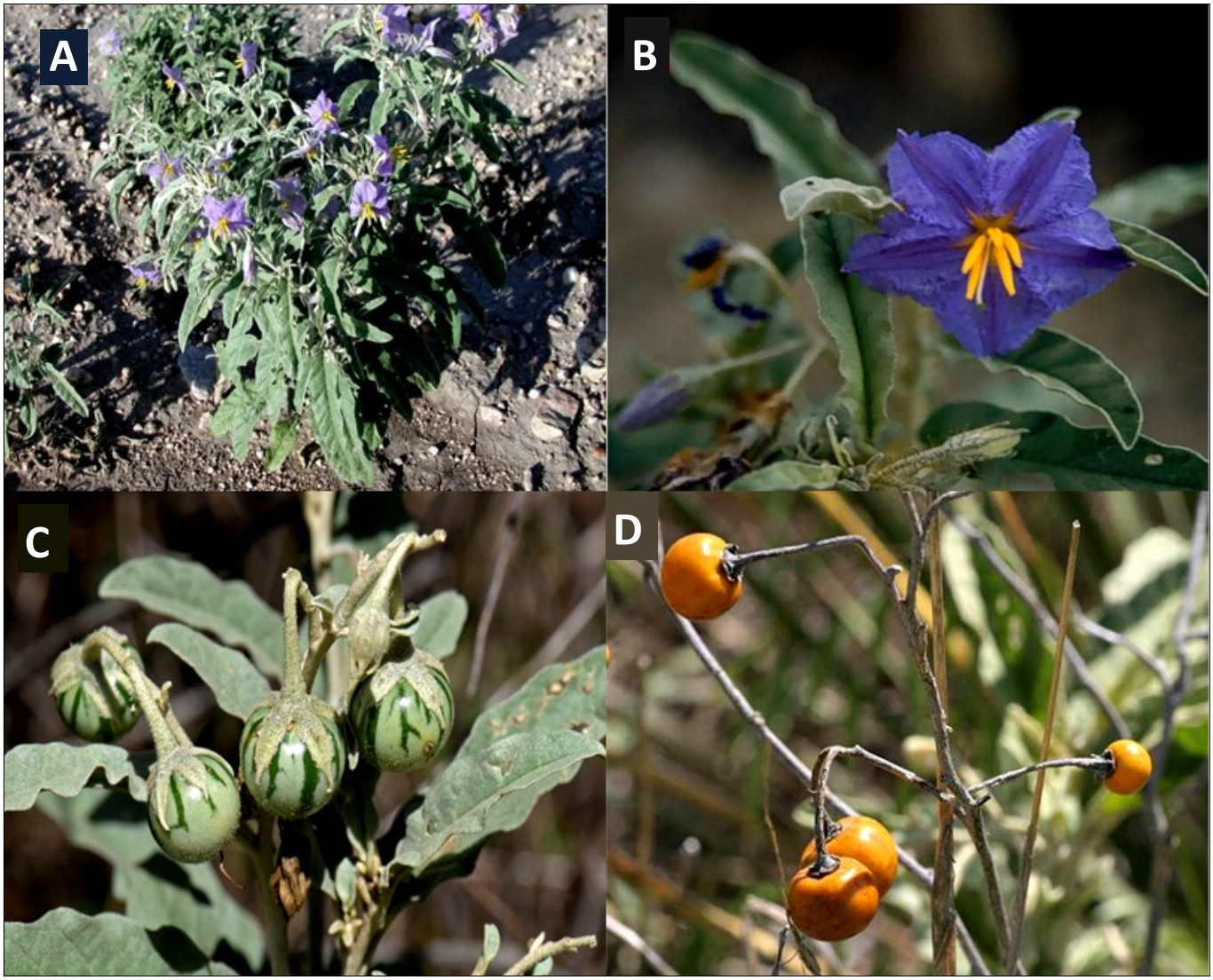

Fig. 1. Maturity stage of *S. elaeagnifolium*: (**A**) fully grown plant; (**B**) flower of the plant; (**C**) fruiting of the plant and (**D**) mature fruit.

temperature was maintained for 10 min. The injector temperature was set to 250 °C and helium (He) was used as the carrier gas at a flow rate of 1 mL min^{-1}. A 1.5 µL aliquot of the sample, diluted in 99.5 % ethanol, was injected for analysis. The chemical constituents were identified by comparing their retention indices with those reported in Adams' database and by matching their mass spectra entries in the National Institute of Standards and Technology (NIST-MS) and Wiley libraries (8).

Pot germination test

The germination test was conducted on three field crops was–wheat, broad bean and flax–which are commonly cultivated after the growing season of *S. elaeagnifolium*. Ten seeds of each crop species were sown sparsely in 15 cm-diameter plastic pots filled with sterilized fine sand. Each pot received 250 mL of the aqueous extract at the specified concentration during the first application and was subsequently moistened as needed (9, 10). The control treatment received distilled water.

Three separate experiments (one for each crop) were arranged in a complete randomized design (CRD) with five replicates. The treatment pots were maintained under laboratory room conditions for 10 days, after which the number of germinated seeds was recorded to calculate germination percentage. Radicle and plumule lengths were measured. Subsequently, the germinated crop seedlings were thinned to five per pot and washed with water to remove residual sand to before measuring the following traits.

Tolerance index (TIN %)

Tolerance index was calculated:

$$TIN = \frac{\text{Seedling dry weight in concentration treatment}}{\text{Seedling dry weight in control treatment}} \times 100$$

Relative electrolyte leakage

To assess the impact of *S. elaeagnifolium* extracts on the membrane integrity of targeted crop seedlings, we measured relative electrolyte leakage (REL %) in seedling leaves (11). A 0.5 cm-diameter disc was taken from each plumule was incubated in 5 mL of distilled water for 30 min, after which the initial conductivity (C_1) was recorded. Subsequently, the tissue was boiled for 15 min to release all electrolytes and the final conductivity (C_2) was measured.

Relative electrolyte leakage was calculated as follows:

$$REL\ \% = (C_1/C_2) \times 100$$

Cellular respiration

Cellular respiration was indirectly assessed by measuring cell viability using 2,3,5-triphenyl tetrazolium chloride (TTC) (12). 2,3,5-triphenyl tetrazolium chloride accepts electrons from the mitochondrial electron transport chain, forming a red-coloured formazan compound that indicates tissue viability. This formazan formation provides an indirect measure of cellular respiration. The red-coloured formazan was extracted with ethanol and its absorbance was measured by a spectrophotometer at 530 nm. The resulting values were compared to the control group to evaluate the effect of *S. elaeagnifolium* extracts on cellular respiration (13).

Results and Discussion

Chemical composition of *S. elaeagnifolium*

The allelochemical compounds identified in the aqueous extract of *S. elaeagnifolium* are presented in Table 1. By comparing the retention times and peak areas, GC-MS analysis revealed the presence of thirteen components, representing 55.02 % (±8.29) of the total identified compounds, as the average of four samples tested (Fig. 2). The most abundant constituents in the extracts were apigenin (20.36 ± 2.09 %), galangin (10.12 ± 1.01 %), heptadecane-9-hexyl (7.14 ± 1.27 %), tricetin (5.56 ± 0.72 %), quercetin (3.45 ± 0.65 %) and luteolin (2.11 ± 2.09 %). Most of these compounds exhibited inhibitory effects when applied as growth inhibitors against various plants and weeds, as they belong to the most potent allelopathic substances-particularly flavonoids and glycosides. These findings are consistent with previous studies reporting that such compounds have strong inhibitory potential to suppress the germination and growth of many plant species (14, 15).

Pot bioassay

Seed germination and seedling development

Table 2 shows that the *S. elaeagnifolium* aqueous extract significantly affected wheat grain germination compared to the control at all tested concentrations. Moreover, all concentrations differed significantly from each other, showing a progressive decrease in wheat germination with increasing concentration (12.5 %) completely inhibited germination, while at lower concentrations, the germination percentage decreased proportionally with increase in extract strength until it reached complete non-germination at 12.5 %. The significant negative effect of the aqueous extracts was also observed at all concentrations on the length of the plumule and radicle. The reduction in the average lengths of the plumule and radicle, along with the appearance of toxicity symptoms, was characterized by dwarfism, browning of the germinated seeds and weakness of the crown (root-stem contact area).

Table 1. Chemical composition of *S. elaeagnifolium* extracts

Peaks	[1]RT	[2]Compound	[3]Means ± S.E.	Chemical formula
1	3.91	Cinnamic acid	1.37 ± 0.14	$C_9H_8O_2$
2	7.98	Ferulic acid	0.86 ± 0.08	$C_{10}H_{10}O_4$
3	19.19	Daidazin	0.45 ± 0.07	$C_{15}H_{10}O_4$
4	20.39	Apigenin	20.36 ± 2.09	$C_{15}H_{10}O_5$
5	21.01	Galangin	10.12 ± 1.01	$C_{15}H_{10}O_5$
6	21.34	Kaempferol	1.18 ± 0.16	$C_{15}H_{10}O_6$
7	22.21	Luteolin	2.11 ± 2.09	$C_{15}H_{10}O_6$
8	23.34	Quercetin	3.45 ± 0.65	$C_{15}H_{10}O_7$
9	24.45	Tricetin	5.56 ± 0.72	$C_{15}H_{10}O_7$
10	25.11	Myricetin	1.37± 0.18	$C_{15}H_{10}O_8$
11	15.56	Naringen	0.86 ± 0.39	$C_{15}H_{12}O_5$
12	26.23	Chlorogenic acid	0.19 ± 0.07	$C_{16}H_{18}O_9$
13	34.05	Heptadecane 9-hexyl	7.14 ± 1.27	$C_{23}H_{48}$

[1]**RT**: identification based on retention time (identification based on comparison of mass spectra relative to C4-C28 n-alkanes on the Elite -5MS column); [2]**Components** are listed in order of elution from an Elite-5MS column; [3]**Values** are means of four different samples analysed individually ± standard error.

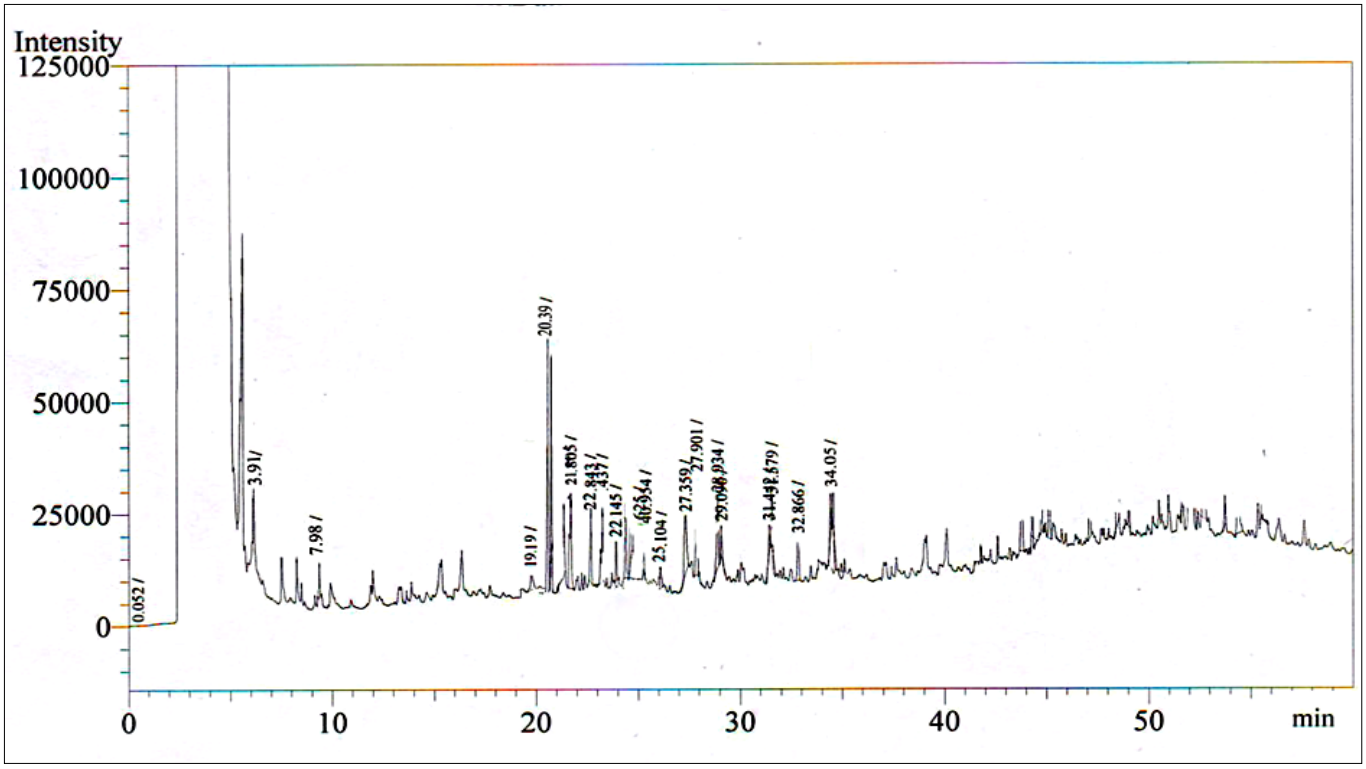

Fig. 2. GC-MS chromatogram of *S. elaeagnifolium* essential oil showing the separation of chemical components.

Table 2. Effect of *S. elaeagnifolium* aqueous extracts on germination and growth of wheat seeds

S. elaeagnifolium (concentration)	Germination (%)	Plumule length (cm)	Radicle length (cm)	Fresh weight (g)	Dry weight (g)	TIN %
0	100^{a}	15.10^{a}	11.5^{a}	1.34^{a}	0.55^{a}	100^{a}
2.5 %	66^{b}	8.17^{b}	9.21^{b}	1.10^{ab}	0.33^{b}	63^{b}
5 %	49^{c}	6.80^{c}	6.60^{c}	0.93^{bc}	0.23^{b}	55^{c}
7.5 %	36^{d}	4.33^{d}	3.18^{d}	0.77^{c}	0.18^{c}	37^{d}
10 %	22^{e}	2.10^{e}	1.17^{e}	0.38^{d}	0.13^{c}	6^{e}
12.5 %	0^{f}	0.00^{f}	0.00^{f}	0.00^{e}	0.00^{c}	0^{f}

Values in a column with different letter(s) are significantly different at $p < 0.05$ applying LSD test.

Furthermore, the radicle was more sensitive to the effect of the extracts compared to the plumule, showing a stronger negative response that increased with rising extract concentration. The results that the current study corroborate previous findings, which reported that the aqueous extracts of *S. elaeagnifolium* significantly inhibited seed germination and plant growth across a wide range of plant species (15-18). The aqueous extract of *S. elaeagnifolium* adversely affected the fresh and dry weights of wheat seedlings at all tested concentrations (Table 2). This effect was evidenced by a reduction in the average fresh weight of the seedlings with increasing extract concentration. The highest concentration (10 %) exerted the strongest inhibitory effect on the fresh weight compared to the other treatments. A significant negative effect was also observed on dry weight, which was clearly reflected in the tolerance index (TIN %). As the seeds were exposed to the stress of allelopathic compounds in the *S. elaeagnifolium* extract, both fresh and dry weights decreased; even when germination occurred, the seedling remained stunted and unable to grow or develop normally. These results are consistent with previous research, which reported that allelopathic compounds, even when not fully inhibiting germination, can suppress seedling growth and development by accumulating in plant tissues and disrupting metabolic processes.

Table 3 shows that the aqueous extract of *S. elaeagnifolium* exhibited a similar inhibitory pattern on the germination of wheat and broad beans seeds. The germination percentage ranged from 0 to 66 %, depending on the extract concentration. The highest concentration caused complete germination inhibition, indicating that an increased presence of *S. elaeagnifolium* plants or residues in crop fields may directly suppress germination and seedling development, with the allelopathic effect intensifying as residue levels increase. The allelopathic effects of *S. elaeagnifolium* were not only inhibitory but also weakened the plumule and radicle of surviving seedlings, significantly reducing their chlorophyll content compared to the control treatment (distilled water). This result is consistent with what was indicated, that although the residues did not succeed in inhibiting the seeds, the seedlings would still suffer from them and a large proportion would not reach maturity (19).

Regarding the effect of the aqueous extract on the germination and development of the flax, this crop was more sensitive among the three tested crop species as appeared from the date presented in Table 4. The three highest extract concentrations caused completely inhibited germination, while the two lower concentrations (2.5 and 5 %), although not entirely supressing germination, severely inhibited seedling growth and reduced the likelihood of flax seedlings completing their life cycle. In general, flaxseed germination is known to be highly sensitive to plant residues containing phenolic compounds. Flax plants were strongly affected by residues of sunflower previously cultivated in the same field, supporting the current findings (20, 21).

Table 3. Effect of *S. elaeagnifolium* aqueous extracts on germination and growth of broad bean seeds

S. elaeagnifolium (concentration)	Germination (%)	Plumule length (cm)	Radicle length (cm)	Fresh weight (g)	Dry weight (g)	TIN %
0	100^{a}	11.00^{a}	8.30^{a}	4.02^{a}	0.55^{a}	100.00^{a}
2.5 %	45^{b}	6.30^{b}	5.02^{b}	3.33^{ab}	0.33^{b}	44.11^{b}
5 %	44^{b}	4.73^{b}	5.00^{b}	2.79^{bc}	0.32^{b}	40.13^{bc}
7.5 %	29^{c}	3.44^{c}	2.60^{c}	2.31^{c}	0.18^{bc}	31.33^{c}
10 %	11^{d}	1.50^{d}	1.00^{d}	1.14^{d}	0.17^{bc}	9.50^{d}
12.5 %	0^{d}	0.00^{d}	0.00^{d}	0.00^{e}	0.00^{c}	0.00^{d}

Values in a column with different letter(s) are significantly different at $p < 0.05$ applying LSD test.

Table 4. Effect of *S. elaeagnifolium* aqueous extracts on germination and growth of flax seeds

S. elaeagnifolium (concentration)	Germination (%)	Plumule length (cm)	Radicle length (cm)	Fresh weight (g)	Dry weight (g)	TIN %
0	100^{a}	9.53^{a}	6.23^{a}	0.88^{a}	0.45^{a}	100.00^{a}
2.5 %	37^{b}	5.00^{b}	4.00^{a}	0.67^{a}	0.33^{b}	47.67^{b}
5 %	8^{c}	2.33^{c}	3.87^{a}	0.50^{b}	0.19^{c}	17.33^{c}
7.5 %	0^{d}	0.00^{d}	0.00^{b}	0.00^{c}	0.00^{d}	0.00^{d}
10 %	0^{d}	0.00^{d}	0.00^{b}	0.00^{c}	0.00^{d}	0.00^{d}
12.5 %	0^{d}	0.00^{d}	0.00^{b}	0.00^{c}	0.00^{d}	0.00^{d}

Values in a column with different letter(s) are significantly different at $p < 0.05$ applying LSD test.

Relative electrolyte leakage

Fig. 3 shows the changes in relative electrolyte leakage values of the three crops exposed to *S. elaeagnifolium* aqueous extracts. In general, the activity of *S. elaeagnifolium* was more pronounced at higher concentrations, causing significant electrolyte leakage in all targeted crop seedlings as the concentration increased from 2.5 (the lowest) to 12.5 % (the highest). The extract of *S. elaeagnifolium* is characterized by a high content of alkaloid compounds. Therefore, there is a possibility of plant cell membrane damage due to accumulation of these alkaloids, which can lead to membrane expansion and structural destruction. The secondary metabolites, such as phenolics and alkaloids interact with a multitude of proteins by forming hydrogen, hydrophobic and ionic bonds, thereby altering their three-dimensional structures and impairing their biological activities (22, 23).

The results of the current study are consistent with recent research, which reported that the application of *S. elaeagnifolium* inhibited plant growth through membrane disruption (7, 18). Such membrane may represent one of the primary mechanisms underlying the phytotoxic effects of plants, ultimately leading to a cell death and growth inhibition.

Cellular respiration

The effects of *S. elaeagnifolium* concentrations on the cellular respiration of the three targeted crop seedlings are presented in Fig. 4. It was observed that the application of the *S. elaeagnifolium* extracts caused significant reductions in cellular respiration rates across all four concentrations compared to the control. A progressive decrease in cellular respiration was recorded with increasing extract concentration. At the highest concentration (12.5 %), all three crop seedlings showed a marked decrease in cellular respiration, with the lowest respiration values observed at this concentration. The results obtained in the present study corroborate previous findings, which demonstrated that cellular respiration is adversely affected by increasing concentrations of allelopathic extracts. This inhibitory effect may be attributed to the presence of terpene compounds in *S. elaeagnifolium,* which likely reduce cellular respiration and disrupt the energy-carrying molecule adenosine triphosphate (ATP) production, thereby inducing physiological disorders in plants. These results are consistent with the findings, which reported that wild species belonging to the Solanaceae family possess secondary metabolites that damage the plant tissues of neighbouring species.

Phytotoxic effect of *S. elaeagnifolium* on the seedling plumule tissue

The results of light microscopy showed that the leaf structure of the three targeted surviving crop seedlings was affected by *S. elaeagnifolium*. Injury symptoms began to appear once the seedling started producing chlorophyll, as seedlings treated with *S. elaeagnifolium* extract appeared pale and yellowish. Early phytotoxicity was observed while the stomata remained open, resulting from the disabling of the guard cell mechanism responsible for stomatal regulation (Fig. 5). As a result of losing control over the stomatal mechanism, transpiration and gas (O_2 and CO_2) exchange, as well as the water regulation become uncontrolled, leading to a disruption of all vital functions within the plant. The current results may be explained by the phytotoxic substances accumulating in the cell membrane and binding with active components, especially membrane proteins, which led to membrane expansion and rupture, allowing the random movement of cellular components between them. Tissue rupture was accompanied by the inhibition of biological processes such as photosynthesis, water and nutrient translocation and respiration, as supported by the results of the studied traits, including relative electrolyte leakage and cellular respiration (Fig. 2 & 3). These results are consistent with the findings, which showed that all concentrations of turmeric extract reduced the stomatal density of *Ageratum conyzoides* leaves and impaired the regulatory function (24, 25).

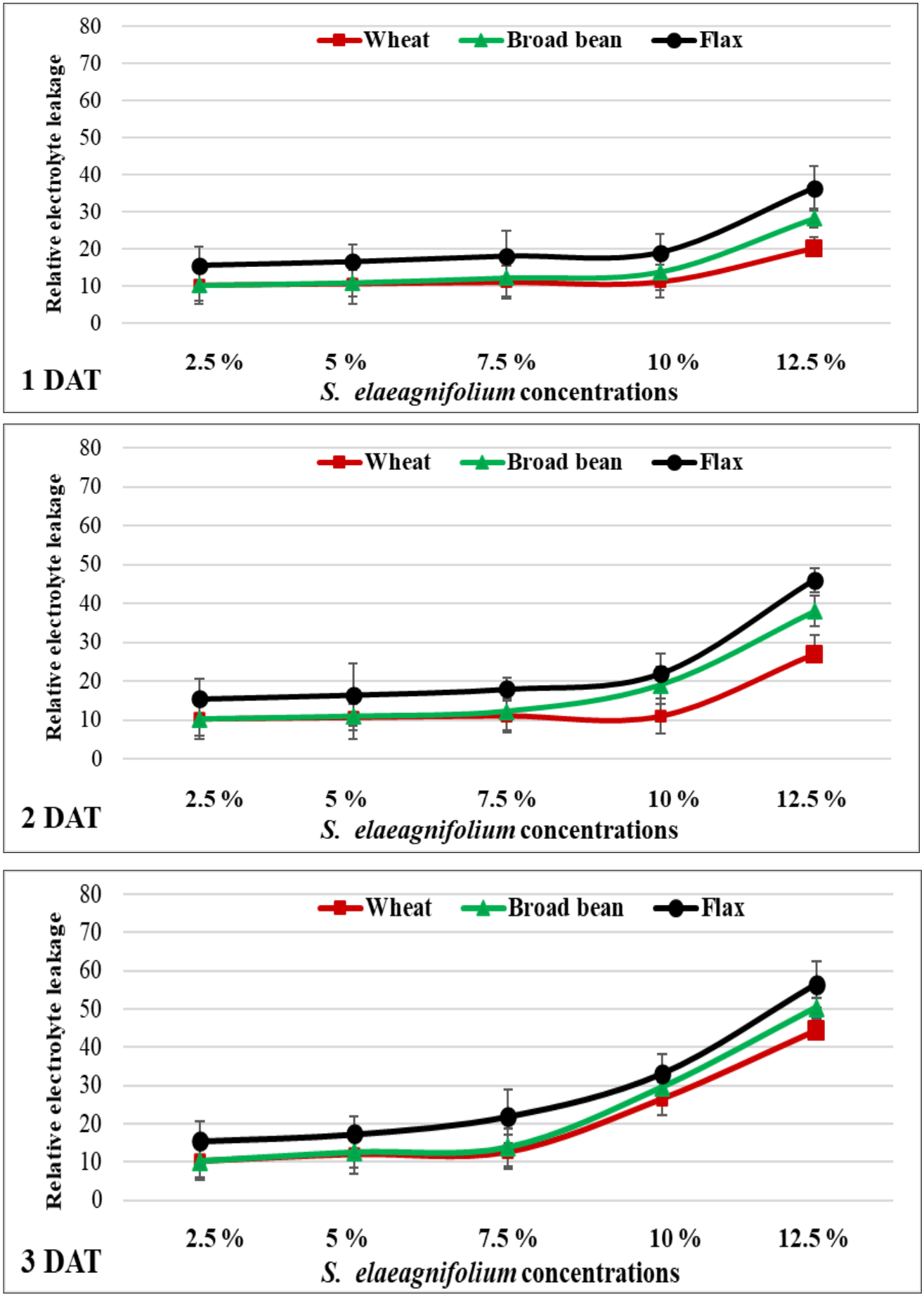

Fig. 3. Relative electrolyte leakage of wheat, broad bean and flax seedlings affected by various concentrations of *S. elaeagnifolium* aqueous extraction within 1, 2 and 3 days of the treatment (DAT).

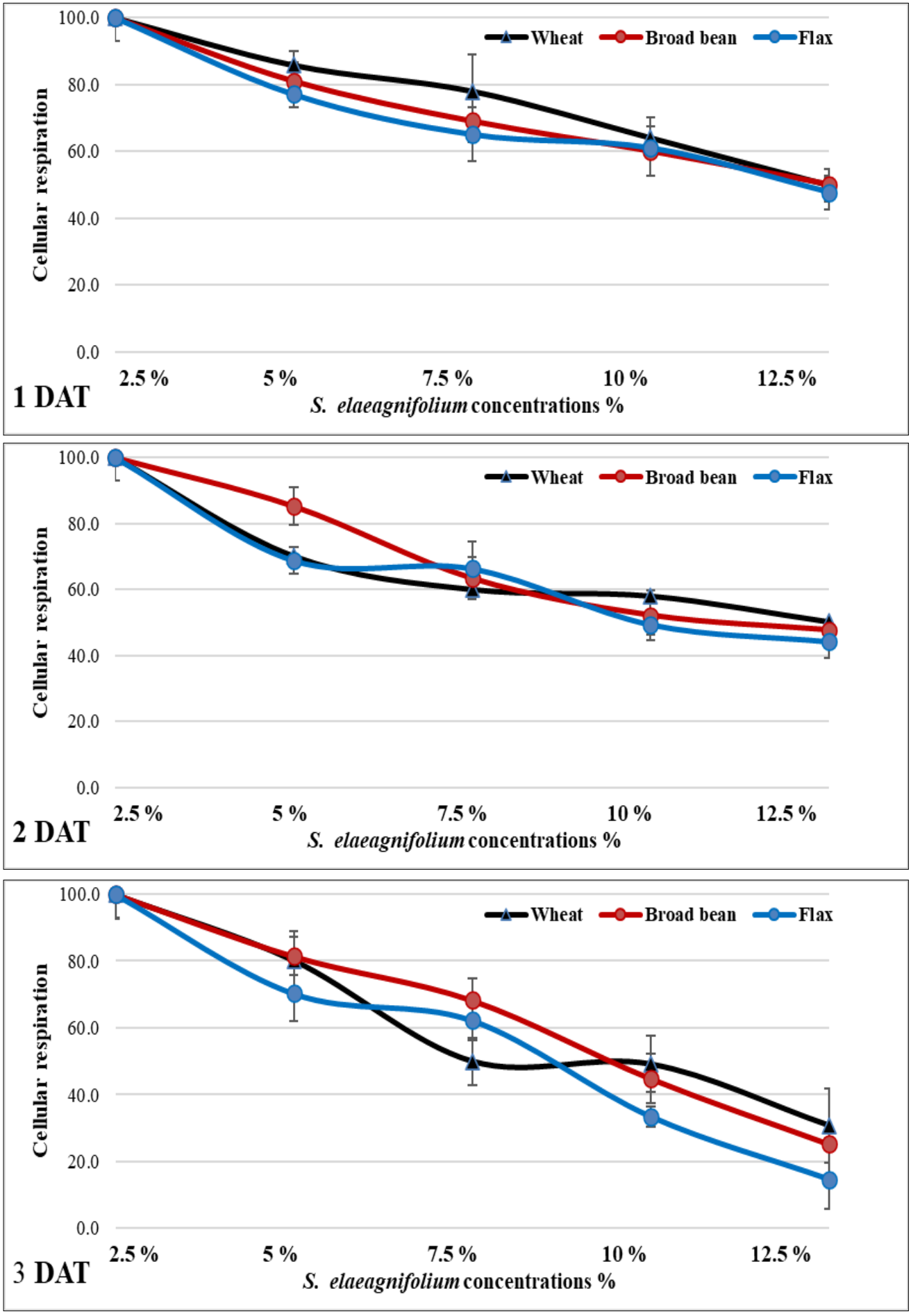

Fig. 4. Cellular respiration of wheat, broad bean and flax seedlings affected by various concentrations of *S. elaeagnifolium* aqueous extraction within 1, 2 and 3 days of the treatment (DAT).

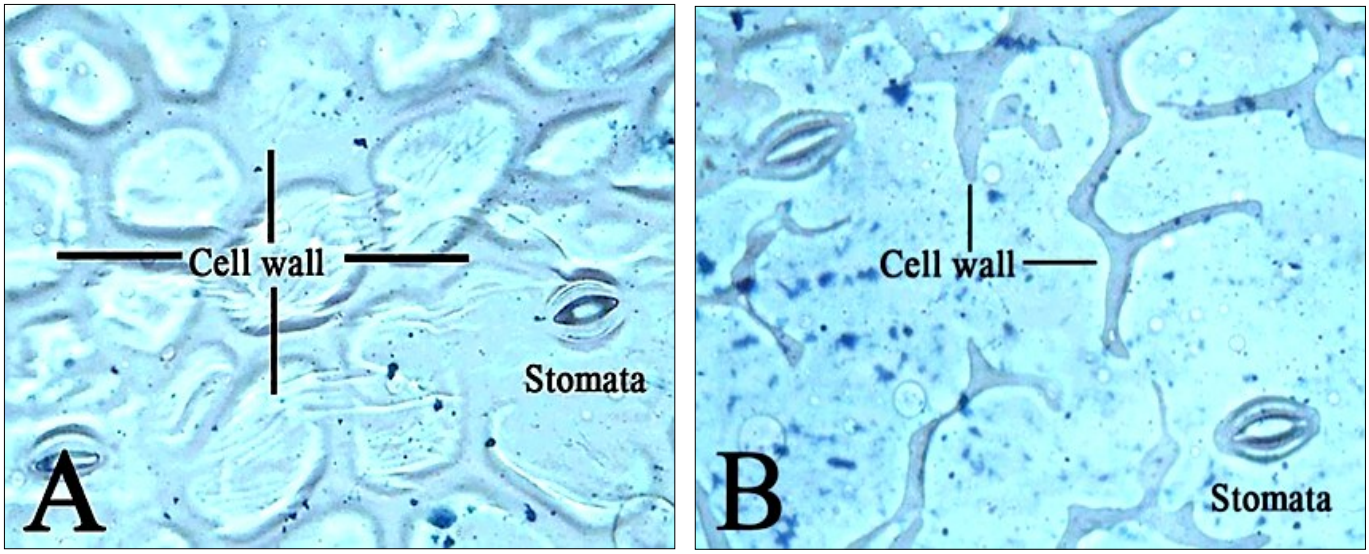

Fig. 5. Lower leaf surface of the broad bean seedling affected by 5 % of S. *elaeagnifolium*: (**A**) Control and (**B**) treated.

Conclusion

The allelopathic effects of *S. elaeagnifolium* aqueous extracts on successive crop species are multifaceted, involving biochemical and anatomical disruptions. They were manifested in the suppression of germination, reduced seedling growth and the promotion of abnormal development. Inhibitory symptoms appeared as an increase in electrolyte leakage in targeted plant tissues, inhibition of cellular respiration and structural damage to leaf tissue, suggesting that its allelochemicals target plant membranes, mitochondria and cell integrity. These findings not only highlight the competitive disadvantage imposed by this invasive plant species on cultivated crops but also reinforce the need for integrated weed management strategies to prevent its spread in agricultural systems.

Acknowledgements

The authors are thankful to the University of Anbar, Iraq and would also like to thank the working staff for their valuable help in conducting this research.

Authors' contributions

AAA contributed to the ideas, designed the experiments and performed the experiments. HHS conceived and coordinated the overall study. AAF drafted the manuscript. MUH read and approved the final manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly in small scale to refine the linguistic style and grammar of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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