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Undaria pinnatifida Extracts Promote Tomato Growth and Enhance Protection against *Phytophthora infestans*

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Main Conclusion

Undaria pinnatifida extracts differentially modulate tomato growth, pigment accumulation, and peroxidase activity. It also provides novel evidence for heat-treated extract-mediated protection against *Phytophthora infestans* in tomato.

Abstract

Seaweed-derived biostimulants are increasingly recognized as sustainable alternatives to synthetic agrochemicals because they can promote plant growth and improve crop yields. Among marine macroalgae, the invasive brown seaweed *Undaria pinnatifida* is an abundant, underexploited source of bioactive compounds with considerable agricultural

potential. This study evaluated the biostimulant activity of aqueous and ethanolic extracts of *U. pinnatifida* in tomato (*Solanum lycopersicum L.*), an economically important horticultural crop. It also assessed whether a heat-treated aqueous extract could improve resistance to *Phytophthora infestans*, the causal agent of late blight. Both the aqueous and ethanolic extracts increased the tomato germination percentage. Aqueous extracts showed the strongest growth-promoting effects, increasing root elongation and chlorophyll content, while the total aqueous extract also enhanced seedling biomass. Ethanolic extracts did not significantly affect seedling growth but increased carotenoid accumulation and markedly reduced peroxidase activity.

In contrast, the heat-treated aqueous extract markedly reduced disease severity and enhanced peroxidase activity in infected plants. Zymographic analysis showed the induction of a peroxidase isoform of approximately 37 kDa, suggesting the activation of specific oxidative defense mechanisms associated with increased resistance. Overall, the results show that *U. pinnatifida* exhibits both growth-promoting and bioprotective effects through extraction procedures optimized for different biological responses. These findings support the potential utilization of this invasive macroalga as a renewable source of environmentally friendly agricultural inputs.

Keywords: *Solanum lycopersicum*; seaweed extract; biostimulant; bioprotection; sustainable agriculture.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the world's most economically important crops and essential for human nutrition (Dorais et al. 2008; Raiola et al. 2014). However, abiotic and biotic stresses increasingly limit tomato productivity by reducing plant growth, fruit quality, and yield, making them a major challenge for sustainable horticultural production (Bergougnoux 2014; Egea et al. 2022). Therefore, strategies that support early plant development and strengthen protection against major pathogens are especially important for improving the resilience of tomato production systems.

Traditionally, crop production has relied on synthetic fertilizers and pesticides. Although these compounds have significantly increased agricultural productivity, their intensive, long-term use has raised growing environmental concerns (Carvalho 2017). In this context, modern agriculture is increasingly shifting toward sustainable, bio-based products that improve crop performance while reducing reliance on conventional agrochemicals. Among these alternatives, marine macroalgae have emerged as one of the most promising sources of agricultural bioinputs. A wide range of evidence demonstrates that applications of macroalgal extracts have consistently improved seed germination, root architecture, shoot growth, biomass accumulation, chlorophyll content, photosynthetic efficiency, and crop productivity across numerous horticultural species (Khan et al. 2009; Craigie 2011; Shukla et al. 2019; Ali et al. 2021; Baroud et al. 2021). These responses are associated with coordinated regulation of phytohormone signaling, carbon and nitrogen metabolism, nutrient transport, antioxidant metabolism, and cellular energy balance, ultimately increasing plant vigor and resource-use efficiency under both optimal and stressful environmental conditions (Goñi et al. 2018; Kergosien et al. 2023; Kumar et al. 2024). Beyond affecting plant growth, macroalgae can also activate plant immune responses. Seaweed-derived compounds modulate defense-associated hormonal signaling pathways involving salicylic acid, jasmonic acid, and ethylene, while stimulating antioxidant metabolism and defense enzymes

(Shukla et al. 2019; Agarwal et al. 2021; Raja et al. 2023; Kumar et al. 2024). Rather than triggering a constitutive defense, these responses often prime a physiological state, allowing plants to respond more rapidly and effectively after pathogen attack. Thus, seaweed extracts represent a unique agricultural bioinput that integrates plant growth promotion with enhanced resistance to environmental and biological stresses. This multifunctionality is particularly relevant for managing late blight caused by Phytophthora infestans, one of the most destructive diseases affecting tomato production worldwide (Jehani et al. 2025). Environmental conditions strongly influence disease development and are expected to become increasingly favorable under current climate change scenarios. Under this scenario, aggressive, fungicide-resistant *P. infestans* populations will emerge, compromising chemical control and reinforcing the need for complementary disease-management strategies (Cooke et al. 2012).

Brown macroalgae (Phaeophyceae) contain diverse bioactive compounds, including alginates, fucoidans, laminarin, polyphenols, amino acids, vitamins, minerals, and phytohormone-like substances (Craigie 2011; Shukla et al. 2019). Among brown seaweeds, *Undaria pinnatifida* (Harvey) Suringar is a particularly attractive source of bioactive compounds. This edible macroalga, commonly known as wakame, has been extensively studied for its nutritional and pharmaceutical properties because of its high content of polysaccharides, polyphenols, and antioxidant molecules (Holdt & Kraan 2011; Wang et al. 2018; Lee et al. 2022). The biochemical composition of *U. pinnatifida* varies by thallus structure and extraction method (Yu et al. 2021; Lee et al. 2022; Park et al. 2024). In Argentina, *U. pinnatifida* has become an invasive species distributed along the Patagonian coast (Dellatorre et al. 2014), causing ecological impacts while also representing a large, renewable biomass resource (Raffo et al. 2022). Therefore, developing agricultural products from this invasive macroalgae is an attractive strategy that supports both biomass valorization and sustainable crop production. Despite extensive research on commercial seaweed biostimulants, little is known about the agricultural potential of *U. pinnatifida*

(Kergosien et al. 2023). In addition, the influence of extraction procedures on its biological activity remains poorly understood, and relatively few studies have simultaneously evaluated its effects on plant growth, physiological performance, and disease resistance. This knowledge gap is particularly relevant because different extraction methods may selectively recover distinct groups of bioactive compounds, yielding extracts with complementary biological properties. Recent work from our research group demonstrated that aqueous extracts of *U. pinnatifida* activate defense responses and reduce disease severity caused by *P. infestans* in potato (Lobato et al. 2023), providing the first evidence that this invasive macroalga can function as a natural defense elicitor. However, it is not yet known whether tomatoes show similar responses, whether aqueous and ethanolic extracts affect plant growth and physiological performance differently, or whether aqueous extracts also improve resistance to *P. infestans*. Therefore, this study aimed to evaluate the effects of aqueous and ethanolic extracts of *U. pinnatifida* on tomato plant growth, physiological performance, and resistance to *P. infestans*.

2. Materials and Methods

2.1 Plant material

Seeds of *Solanum lycopersicum* L. cv. Platense were kindly provided by the Plant Stress Physiology Research Group at the Instituto de Investigaciones Biológicas (IIB), Universidad Nacional de Mar del Plata (UNMdP)–CONICET, Mar del Plata, Argentina.

2.2 *Undaria pinnatifida* aqueous and ethanolic extracts

Algal biomass of *Undaria pinnatifida* (Undaria) was collected from the harbor of Mar del Plata (Buenos Aires Province, Argentina). For the biostimulant assays, seaweed was washed with tap

116 water to remove shells, debris, and sand; air-dried at 26°C for 2–3 days; then hand-crushed and
117 powdered using a high-speed universal grinder. For the ethanolic extract, 1 g of dried algal
118 powder (total, EE-T, or sporophyll-enriched, EE-S) was suspended in 15 mL of 75% (v/v)
119 ethanol. The suspension was stirred at room temperature for 1 h, then centrifuged at 10,000 rpm
120 for 10 min. The supernatant was carefully collected and used for subsequent analyses. For the
121 aqueous extracts, 1 g of dried algal powder (total, AE-T, or sporophyll-enriched, AE-S) was
122 suspended in 15 mL of distilled H_2O. The suspension was stirred for 1 h at room temperature and
123 then centrifuged at 7,000 rpm for 20 min. The supernatant was collected and used for subsequent
124 analyses.

125 For the bioprotection assays, the aqueous extract (AE) was prepared from a mixture of Undaria
126 lamina and sporophyll according to Lobato et al. (2023). The extraction procedure included a
127 heating step followed by dilution in water before application. This procedure was previously
128 optimized to protect potato plants from *Phytophthora infestans*.

129

130 **2.3 Bioassay for germination analysis**

131 Tomato seeds were placed in Petri dishes containing filter paper soaked with 3 mL of the
132 corresponding *Undaria pinnatifida* extract or with distilled water (control, C). Treatments
133 included 0.1% (v/v) aqueous extracts and 0.0001% (v/v) ethanolic extracts prepared from either
134 whole algal biomass or sporophyll-enriched biomass. We selected these concentrations based on
135 preliminary assays to identify levels suitable for evaluating the extracts' effects on tomato seed
136 germination. Thus, four extract treatments were evaluated: AE-T, AE-S, EE-T, and EE-S. Three
137 Petri dishes containing 20 seeds each were prepared for each treatment, and the experiment was
138 independently repeated three times. Plates were incubated in a growth chamber at 25°C. Seed
139 germination was assessed 6 days after treatment, and the germination percentage was calculated

for each Petri dish. A seed was considered germinated when the radicle had emerged through the seed coat.

2.4 Plant Growth Conditions

Tomato seeds were incubated overnight in 50-mL Falcon tubes containing 0.1% AE-T, 0.1% AE-S, 0.0001% EE-T, 0.0001% EE-S, or distilled water (C). Subsequently, the seeds were sown in polystyrene seedling trays filled with a soil-perlite mixture (2:1 v/v) and grown at 25°C under a 16:8 h light:dark cycle. Fourteen days after sowing, seedlings were harvested to determine total fresh weight, shoot fresh weight, root fresh weight, and primary root length. All plants per treatment were scanned, and root length was measured using ImageJ v.1.52a (National Institutes of Health, USA).

2.5 Bioassay for bioprotection analysis

Tomato plants 5 weeks old were treated with a foliar spray (3 ml/plant) of different dilutions (10 and 30% v/v in water) of an aqueous extract (AE) prepared from a mixture of *U. pinnatifida* blades and sporophylls, with ten plants per treatment, and the experiment was independently repeated three times. Water spray was used as a control (Lobato et al. 2023). Three days after AE foliar treatments, detached leaves were infected with drops of a *P. infestans* sporangia suspension (4×10^4 sporangia mL^{-1}) in separate Petri dishes and incubated at 18°C. Protection was assessed 5 days after inoculation, and the lesion area was quantified using ImageJ software. Leaves from each treatment were stored at −80°C for further analysis.

2.6 Chlorophyll a, b, and Total Carotenoid Content

Fresh leaves were collected from tomato seedlings grown in germination trays for 14 days. Leaf samples (100 mg) were ground with liquid N_2 in a mortar, and chlorophylls were extracted with 80% acetone for 60 min at 4°C in the dark, followed by centrifugation at 10,000 *g* for 15 min. The absorbance of the supernatant was measured at 663, 645, and 470 nm using a spectrophotometer (GeneQuant 1300, GE Healthcare, USA). Chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoid contents were calculated according to the equations described by Lichtenthaler (1987). Pigment contents were expressed as μg g^{-1} fresh weight (FW).

2.7 Protein extraction

To quantify POD activity, we ground 0.1 g of leaf tissue with liquid N_2 in a mortar and extracted it with 2 volumes of buffer (50 mM Tris-HCl, pH 7.5, 3 mM $MgCl_2$, and 150 mM NaCl). The homogenate was then centrifuged at 10,000 rpm for 20 min, and the supernatant was used to measure antioxidant activities.

2.8 POD activity

Peroxidase activity was measured in tomato seedlings treated with aqueous and ethanolic extracts of *U. pinnatifida* and in five-week-old tomato plants subjected to bioprotection assays against *P. infestans*. Enzyme activity was determined according to Chance and Maehly (1955), with minor modifications. The reaction mixture (final volume 1 mL) contained 400 μL of 100 mM sodium phosphate buffer (pH 7.0), 100 μL of enzyme extract, guaiacol (final concentration 8.6 mM), and H_2O_2 (final concentration 3.6 mM). The increase in absorbance due to tetraguaiacol formation was monitored at 470 nm for 1 min. We defined one unit of POD activity as the amount of enzyme that increases absorbance by 0.01 units per minute under the assay conditions. Peroxidase activity was expressed as units per gram of fresh weight (U g^{-1} FW).

2.9 POD activity gels

Soluble protein extracts from leaves of five-week-old tomato plants subjected to bioprotection assays against *P. infestans* were precipitated with 5 volumes of cold acetone and resolubilized in 50 mM phosphate buffer (pH 7.4). Electrophoresis was performed under semi-denaturing conditions: samples were treated with SDS but not boiled. Equal fresh-weight amounts (2 mg) were loaded onto a 10% SDS-PAGE gel. Peroxidase (POD) activity isoforms were visualized according to Chen et al. (2000) using guaiacol as a substrate.

2.10 Statistical analysis

All statistical analyses were performed using R software (version 3.5.1 (2018-07-02); R Foundation for Statistical Computing).

Germination percentage was evaluated using a generalized linear mixed-effects model (GLMM) with a binomial distribution and logit link function. Treatment was included as a fixed effect and experiment as a random effect to account for variability among the three independent experiments (n = 9). Pairwise comparisons between treatments were performed with Holm-Bonferroni correction for multiple comparisons.

For seedling growth assays, 18 plants per treatment were evaluated across three independent experiments (n = 3). Data were analyzed by one-way analysis of variance (ANOVA), followed by Tukey's HSD test.

For bioprotection assays against *Phytophthora infestans*, relative lesion areas were analyzed using a linear mixed-effects model (LMM), with treatment as a fixed effect and experiment as a random

effect (n=3). Model residuals were assessed for normality using the Shapiro–Wilk test. Pairwise comparisons among treatments were performed using Tukey-adjusted tests.

For all analyses, differences were considered statistically significant at $P < 0.05$.

3. Results

3.1 Effect of Undaria extracts on tomato seed germination

Because seed germination and early seedling growth are reliable indicators of biostimulant activity, tomato seeds were treated with aqueous or ethanolic extracts of *Undaria pinnatifida* from the lamina and sporophylls (T) or from the sporophylls alone (S). Fig. 1 shows that T and S extracts increased seedling germination by about 25% in both ethanolic and aqueous extracts. No significant differences were observed among the four treatments, indicating a similar germination-promoting effect regardless of extract type.

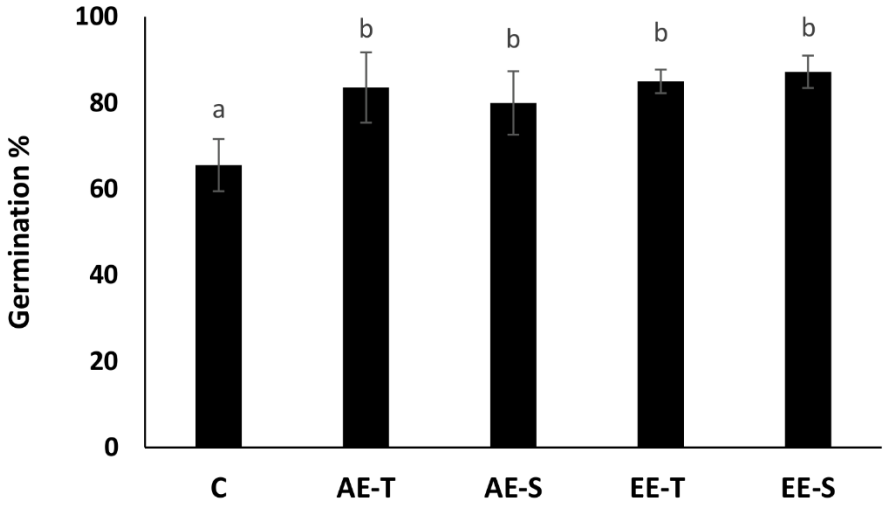

Fig. 1. Tomato seed germination assay. Seed germination percentage was calculated 6 days after the initial treatments. C: H_2O, AE-T: total aqueous extract, AE-S: sporophyll aqueous extract,

EE-T: total ethanolic extract. EE-S: sporophyll ethanolic extract. Values are presented as mean ± SD of three biological replicates (n=9). Different letters indicate significant differences among treatments at $P < 0.05$

3.2 Effect of Undaria extract treatments on root length

Measuring root length in tomato seedlings is a standard method for assessing biostimulant efficacy. Assay results showed that AE-T induced the greatest root elongation compared with the control (C). Similarly, the sporophyll aqueous extract (AE-S) significantly increased root length compared with the control, but to a lesser extent than AE-T. In contrast, the ethanolic extracts (EE-T and EE-S) showed no significant differences compared with the control (Fig. 2).

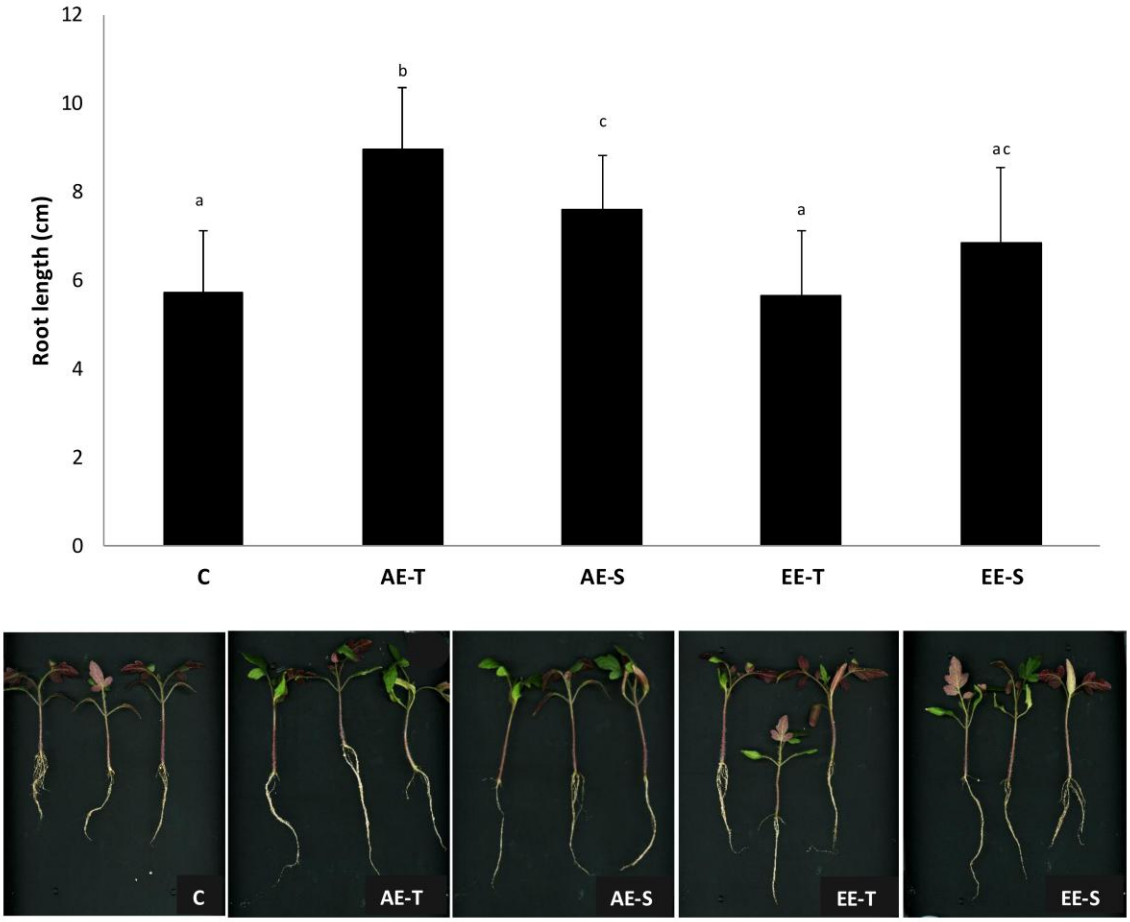

Fig. 2. Effect of Undaria extract treatments on root length. C: H_2O, AE-T: total aqueous extract, AE-S: sporophyll aqueous extract, EE-T: total ethanolic extract. EE-S: sporophyll ethanolic extract. Values are presented as mean ± SD (n = 3). Different letters indicate significant differences according to Tukey's post hoc test ($P < 0.05$)

3.3 Effect of Undaria extracts on tomato seedlings fresh biomass

To further assess the growth-promoting effects of *Undaria pinnatifida* extracts, the fresh biomass of tomato seedlings was measured after seed treatment with the different aqueous and ethanolic extracts. Table 1 shows changes in tomato seedling fresh weight. Only AE-T significantly affected biomass, increasing root fresh weight by 131%. For the aerial parts, it increased by 33%.

Total fresh weight increased by 38%. Other seaweed extract treatments did not significantly affect overall fresh weight.

Table 1. Effect of Undaria total aqueous extract (AE-T), sporophyll aqueous extract (AE-S), total ethanolic extract (EE-T), and sporophyll ethanolic extract (EE-S) on growth parameters of tomato plants. The control consists of plants with seeds primed in distilled water. Values are presented as mean ± SD (n = 3). Values marked with an asterisk differ significantly at $P < 0.05$

Undaria extracts	Total plant fresh weight (g)	Root fresh weight (g)	Aerial part fresh weight (g)
C	0.285±0.10	0.016±0.008	0.264±0.06
AE-T	**0.393±0.09***	**0.037±0.011***	**0.351±0.09***
AE-S	0.311±0.07	0.024±0.011	0.261±0.06
EE-T	0.296±0.12	0.022±0.009	0.264±0.07
EE-S	0.260±0.09	0.019±0.007	0.243±0.06

3.4 Changes in Chlorophyll and Carotenoid content of tomato seedlings treated with Undaria extracts

Undaria pinnatifida extracts differentially affected chlorophyll and carotenoid contents in tomato seedlings (Table 2). Plants treated with AE-T, AE-S, and EE-S showed significantly higher chlorophyll *a* content than the control, with increases of 28%, 23%, and 18.6%, respectively. In contrast, EE-T plants showed chlorophyll *a* levels similar to the control. Total chlorophyll content showed a similar tendency. AE-T, AE-S, and EE-S treatments showed significant increases, with the highest value in AE-T-treated seedlings (364.83 µg g^{-1} FW), followed by AE-S (337.36 µg g^{-1} FW) and EE-S (328.74 µg g^{-1} FW). Chlorophyll *b* content did not differ significantly among

267 treatments, although EE-T plants tended to show lower values. Moreover, carotenoid
268 accumulation was significantly higher in EE-T and EE-S treatments (28% and 16%, respectively)
269 than in the control.

270

271 **Table 2.** Effect of Undaria extract treatments on chlorophyll and carotenoid content. C: H_2O; AE-
272 T: total aqueous extract; AE-S: sporophyll aqueous extract; EE-T: total ethanolic extract; EE-S:
273 sporophyll ethanolic extract. Values are presented as mean ± SD (n = 9). Values marked with an
274 asterisk differ significantly at $P < 0.05$

Undaria extracts	Chlorophyll *a* µg/ g FW	Chlorophyll *b* µg/ g FW	Total Chlorophyll µg/ g FW	Carotenoids µg/ g FW
C	198.34± 14.2	97.95± 28.3	296.30± 4.12	38.84± 2.65
AE-T	**254.64± 1.9***	110.18± 12.8	**364.83± 10.87***	43.38± 3.68
AE-S	**244.54± 8.67***	92.81± 13.7	**337.36± 12.39***	41.95± 6.78
EE-T	200.93± 16.5	71.97± 22.3	272.90± 18.9	**49.94± 5.5***
EE-S	**235.30± 5.4***	93.43± 14.7	**328.74± 8.8***	**44.96± 3.67***

275

276

277 **3.5 Effect of Undaria unheated aqueous and ethanolic extracts on peroxidase (POD) activity**

278 Because aqueous seaweed extracts have been reported to modulate antioxidant activity,
279 peroxidase (POD) activity was evaluated in tomato leaf tissue 12 days after treatment with
280 Undaria extracts. POD activity was significantly lower than in the control in plants treated with
281 both EE-T and EE-S. Among the aqueous extracts, POD activity decreased significantly relative
282 to the control only in plants treated with AE-T (Fig. 3).

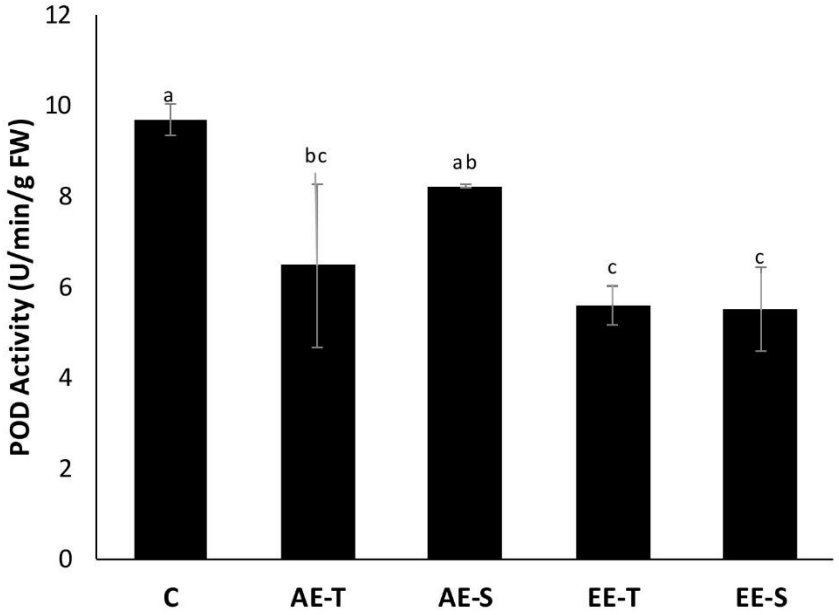

Fig. 3. Effect of Undaria extracts on peroxidase (POD) activity. POD activity was measured in tomato leaf tissue after 12 days of growth. C: H_2O; AE-T: total aqueous extract; AE-S: sporophyll aqueous extract; EE-T: total ethanolic extract; EE-S: sporophyll ethanolic extract. Values are presented as mean ± SD (n = 3). Different letters above the bars indicate statistically significant differences among treatments ($P < 0.05$)

3.6 Undaria heated aqueous extract protects tomato plants against *P. infestans.*

To test whether *Undaria pinnatifida* aqueous extracts protect tomato plants against *Phytophthora infestans*, disease severity was assessed by measuring lesion expansion on inoculated leaves following treatment with different extract concentrations.

As shown in Fig. 4, *Undaria pinnatifida* aqueous extracts (AE) protected tomato leaves from *P. infestans*. AE30 significantly reduced disease severity by approximately 72% relative to the control, whereas AE10 reduced *P. infestans* lesions by 30%.

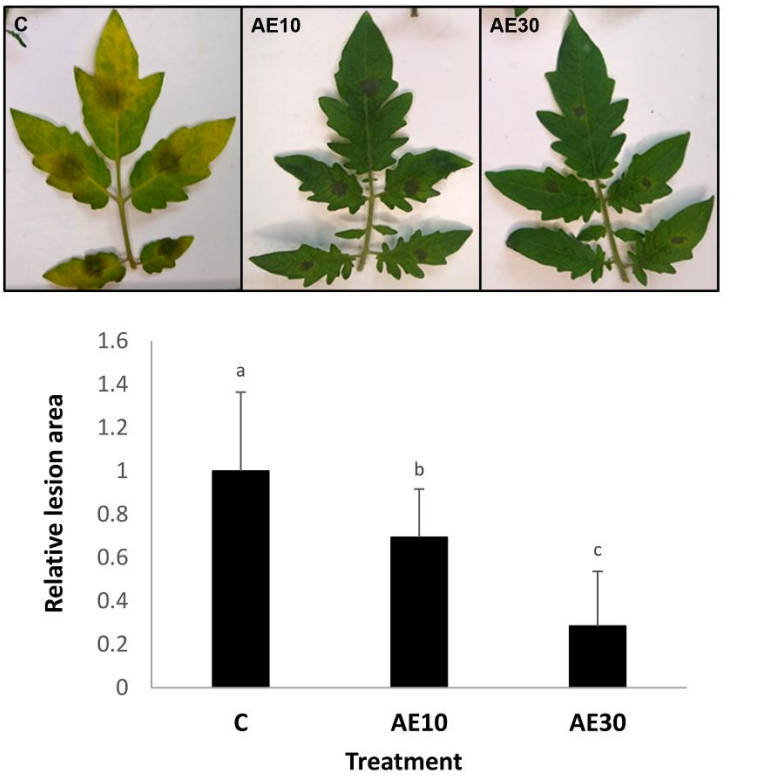

Fig. 4. Protective effect of *Undaria pinnatifida* aqueous extract on tomato leaves challenged with *P. infestans.* Algal extracts at 10% (AE10) and 30% (AE30) dilutions, or water (C), were applied via foliar spray to tomato plants. Three days later, leaves were detached and inoculated with *P. infestans*. Disease severity was evaluated 5 days after inoculation, and leaf lesion area was measured using ImageJ. Bars indicate mean ± SD (n=3). Different letters above the bars indicate significant differences among treatments at $P < 0.05$

3.7 Peroxidase activity in tomato plants treated with heated aqueous extracts and infected with *P. infestans*

Because plant peroxidases are multifunctional enzymes essential for plant defense, structural strengthening, and redox regulation, we measured their total activity in tomato plants treated with AE extracts and infected with *P. infestans*. Peroxidase (POD) activity was significantly affected by both pathogen infection and treatment with *Undaria pinnatifida* aqueous extracts (Fig. 5). Compared with control plants (C), peroxidase activity increased by approximately 45% in infected plants (CI). Treatment with *U. pinnatifida* extract further increased enzyme activity, reaching approximately 57% (AEI10) and 69% (AEI30) relative to the control. AEI30 showed the highest activity and differed significantly from all other treatments.

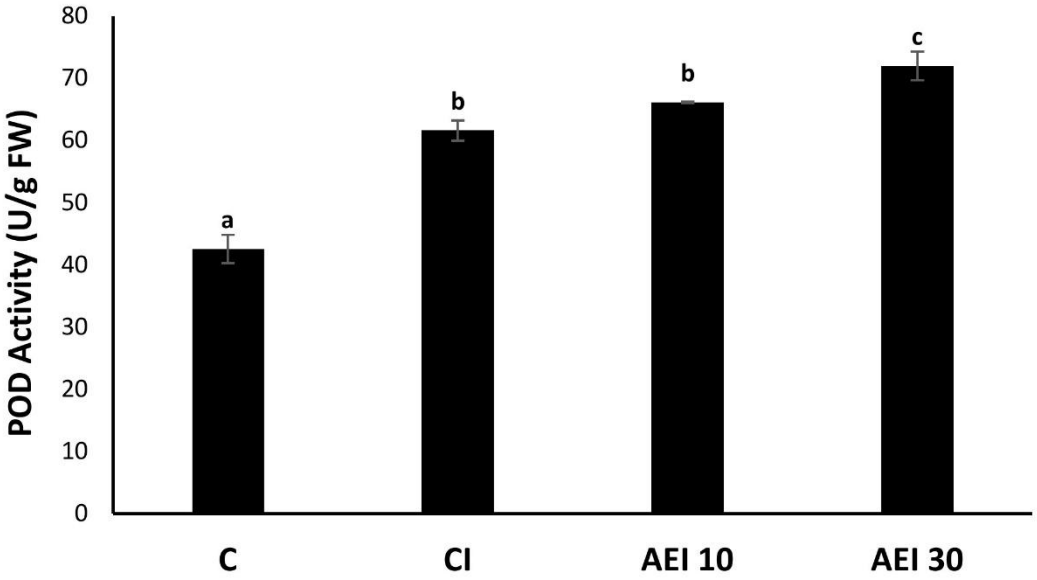

Fig. 5. Effect of Undaria heat extracts on peroxidase (POD) activity in tomato leaf extracts. Peroxidase activity was measured in leaf tissue from tomato plants treated for 5 days after inoculation with *P. infestans*. C: H_2O-treated, non-inoculated plants; CI: H_2O-treated, inoculated

plants; AEI 10: AE 10%-treated, inoculated plants; AEI 30: AE 30%-treated, inoculated plants. Values are presented as the mean ± SD (n = 3). Different letters above the bars indicate statistically significant differences among treatments, determined by Tukey's post hoc test following one-way ANOVA ($P < 0.05$)

To determine whether changes in total peroxidase activity were linked to specific peroxidase isoforms, we performed zymography, which revealed a peroxidase isoform with an apparent molecular mass of approximately 37 kDa (Fig. 6). This isoform was weakly detected in infected plants (CI). In contrast, the uninfected control (C) showed little or no activity. Treatment with aqueous extracts of *Undaria pinnatifida* increased this isoform's activity, with the strongest signal observed in plants treated with AEI10. A visible band, though less intense, was also observed in plants treated with AEI30 (Fig. 6).

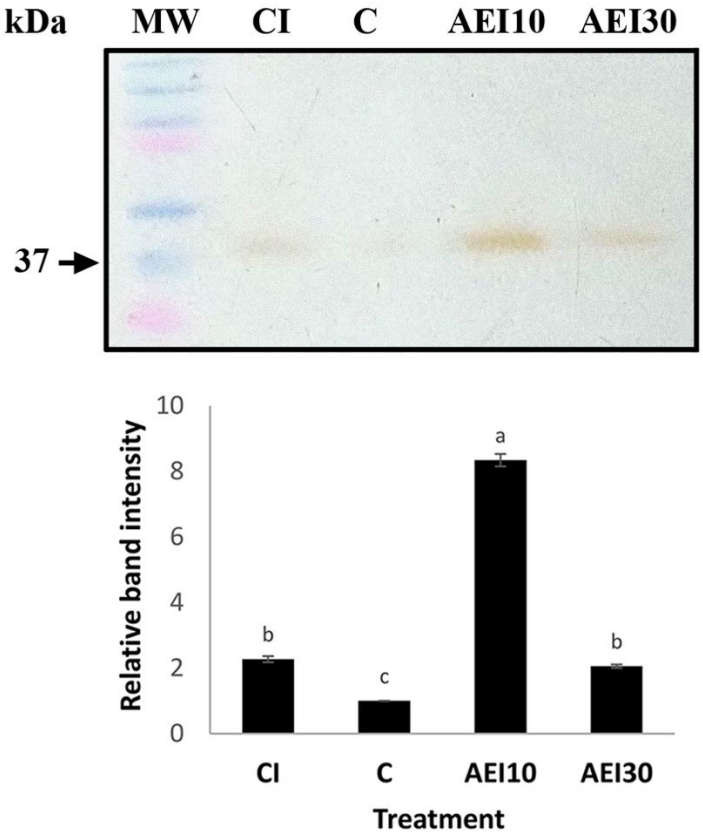

Fig. 6. Effect of heat-treated *Undaria pinnatifida* aqueous extract on peroxidase (POD) activity in tomato plants challenged with *Phytophthora infestans*. Leaf protein extracts were prepared from: C: H_2O-treated, non-inoculated plants; CI: H_2O-treated, inoculated plants; AEI 10: AE 10%-treated, inoculated plants; AEI 30: AE 30%-treated, inoculated plants. Peroxidase (POD) activity was measured in leaf extracts by semi-denaturing 10% SDS-PAGE using guaiacol as the substrate. Equal fresh weights were loaded in each lane. Values are presented as the mean ± SD (n = 3). Different letters above the bars indicate statistically significant differences among treatments by Tukey's post hoc test following one-way ANOVA ($P < 0.05$)

4. Discussion

Replacing synthetic agrochemicals with biologically derived compounds is a central goal of sustainable agriculture worldwide. The intensive, long-term use of synthetic fertilizers and pesticides has been linked to soil degradation, loss of microbial diversity, groundwater contamination, and outbreaks of pathogen populations resistant to conventional treatments (Savci 2012; Pahalvi et al. 2021). In this context, natural products from plants, microorganisms, and macroalgae are increasingly viewed as promising bioinputs to reduce the environmental impact of crop production while maintaining or even improving plant yield and stress tolerance (du Jardin 2015; Rouphael & Colla 2020).

Undaria pinnatifida is a brown macroalga traditionally consumed as a food (wakame) in several Asian countries. It is also cultivated on a large scale for the food and nutraceutical industries (Holdt & Kraan 2011; Wang et al. 2018). Beyond its nutritional value, this species has recently attracted interest as a potential source of agricultural bioinputs because it contains polysaccharides, phenolic compounds, and phytohormone-like substances similar to those found in other commercially exploited brown algae, such as *Ascophyllum nodosum* and *Sargassum muticum* (Craigie 2011; Shukla et al. 2019). Recent chemical characterizations show that different parts of the alga (blade, sporophyll, and root) are rich in phenolics, sulfated polysaccharides, and other bioactive compounds (Lee et al. 2022; Park et al. 2024). To date, research has focused mainly on aqueous extracts used as biostimulants in tomato (Salcedo et al. 2020) and as plant defense elicitors, with promising results in potatoes against *P. infestans* (Lobato et al. 2023). However, unlike other seaweed species widely used in commercial production, the application of *U. pinnatifida* as a biostimulant and bioprotectant in horticultural crops remains relatively unexplored.

The results indicate that aqueous and ethanolic extracts of *Undaria pinnatifida* exert biostimulant and bioprotectant effects on tomato plants, influencing seed germination, seedling growth, photosynthetic pigment accumulation, and resistance to *Phytophthora infestans*. These findings

375 align with previous reports identifying brown macroalgae as a rich source of bioactive
376 compounds—including polysaccharides, phytohormone-like substances, and antioxidant
377 molecules—that can modulate plant physiology and defense responses (Esserti et al. 2017; Pohl
378 et al. 2019; Baroud et al. 2021; Shukla et al. 2021; Mughunth et al. 2024).

379 The increase in seed germination observed with both total extracts (T) and sporophyll extracts
380 (S), regardless of the extraction solvent, suggests that the bioactive molecules responsible for this
381 effect are present in multiple tissues and can be extracted under both aqueous and ethanolic
382 conditions. These findings are consistent with previous reports showing that seaweed extracts can
383 promote seed germination and early plant growth, potentially through phytohormone-like
384 compounds (Crouch & van Staden 1993; Sharma et al. 2014). The germination response was
385 relatively uniform across extract types, unlike the more selective effects observed at later
386 developmental stages (e.g., root length and biomass). Among all treatments, the total aqueous
387 extract (AE-T) was the most effective, significantly increasing root length, root and aerial fresh
388 weight, and chlorophyll a content. This pattern may be associated with water-soluble bioactive
389 compounds, such as alginates, fucoidans, and laminarin, in the total aqueous fraction. These
390 polysaccharides can improve nutrient and water uptake and promote root architecture
391 development (Crouch et al. 1990; Khan et al. 2009), which may explain the marked stimulation of
392 root growth and the consequent increase in total seedling biomass. Seaweed-derived
393 polysaccharides, particularly alginates and laminarins, can act as signaling molecules that
394 stimulate meristem activity and root branching, thereby improving nutrient and water acquisition
395 (Tariq et al. 2025). The lower activity of ethanolic extracts suggests that the most relevant
396 biostimulant compounds in *U. pinnatifida* are predominantly polar and are therefore recovered
397 more efficiently through aqueous extraction. This interpretation aligns with previous studies
398 showing that extraction methods influence the chemical composition and biological activity of
399 seaweed-derived biostimulants (Battacharyya et al. 2015; Godlewska et al. 2016). The ability of

both aqueous and ethanolic extracts to enhance seed germination suggests that this response may involve a broader range of bioactive compounds. In contrast, subsequent seedling growth appears to be more dependent on the specific composition and concentration of the extracted constituents.

The increases in chlorophyll content induced by AE-T, AE-S, and EE-S extracts, along with the enhanced carotenoid accumulation observed with ethanolic extracts (EE-T and EE-S), highlight the differential effects of *U. pinnatifida* extracts on photosynthetic pigment metabolism in tomato seedlings. Pigment accumulation is commonly associated with improved photosynthetic performance and is considered a physiological indicator of biostimulant efficacy in horticultural species (Rouphael & Colla 2020; Ali et al. 2021). The differential responses of chlorophyll a and chlorophyll b suggest that *U. pinnatifida* extracts may affect specific aspects of pigment metabolism. Similar effects on chlorophyll content and antioxidant metabolism have been reported in tomato plants treated with seaweed extracts under abiotic stress (Goñi et al. 2018; Krid et al. 2023).

Interestingly, ethanolic extracts (EE-T and EE-S) promoted carotenoid accumulation without significantly affecting seedling biomass or root growth, suggesting specific modulation of pigment metabolism rather than a general stimulation of plant growth. Given carotenoids' photoprotective and antioxidant functions (Ramel et al. 2013; Sun et al. 2022), this response may reflect an adjustment in tomato seedlings' photoprotective capacity in response to bioactive compounds in the ethanolic extracts. Similarly, Borella et al. (2023) reported changes in carotenoid accumulation in tomato plants treated with a brown seaweed extract under cold stress, supporting the ability of seaweed-derived biostimulants to influence pigment metabolism. The concomitant reduction in peroxidase (POD) activity suggests that ethanolic extracts may also influence antioxidant metabolism. This response could reflect reduced demand for enzymatic antioxidant defenses or changes in their regulation, but further studies are needed to clarify the mechanisms.

Different aqueous extraction procedures were used depending on the biological response under investigation. We prepared the aqueous extract for the biostimulation trials without heat treatment to preserve water-soluble compounds that might promote growth. In contrast, the extract used for the bioprotection assays followed the protocol previously optimized by Lobato et al. (2023), which includes a heating step and dilution before application. Unlike the unheated aqueous extract used for growth promotion, heat-treated aqueous extracts of *U. pinnatifida* conferred a dose-dependent protective effect against *P. infestans,* with the 30% dilution reducing lesion area by approximately 72%. This protective capacity aligns with the well-documented elicitor activity of brown algal polysaccharides, particularly laminarin and sulfated polysaccharides, which can activate plant defense responses against pathogens (Aziz et al. 2003; Shukla et al. 2021; Kumar et al. 2026). These results also align with previous findings that aqueous extracts of *U. pinnatifida* induce protective responses against *P. infestans* in potato, a closely related Solanaceous host (Lobato et al. 2023), reinforcing the hypothesis that this seaweed species contains conserved elicitor molecules active across different crop–pathogen systems.

Activated peroxidase activity further supports the protective effect of the extracts. The increase in total POD activity observed in infected plants, and its further enhancement by extract treatment (particularly at AEI30), is consistent with the well-established roles of peroxidases in detoxifying reactive oxygen species, lignin biosynthesis, and cell-wall reinforcement during plant–pathogen interactions (Freitas et al. 2024; Li et al. 2024). This finding aligns with recent tomato studies showing that other macroalgal- and yeast-based biostimulants enhance resistance to bacterial pathogens, in part by boosting apoplastic class III peroxidase activity (Fiorillo et al. 2025). Zymographic analysis revealed enhanced activity of a peroxidase isoform of approximately 37 kDa in extract-treated and infected plants, suggesting that specific peroxidase isoenzymes may participate in the defense responses induced by *U. pinnatifida*. This interpretation aligns with

449 previous evidence that seaweed-derived β-1,3-glucans can elicit plant defense responses
450 (Klarzynski et al. 2000).

451 Interestingly, the dose that induced the strongest isoform (AEI10) did not coincide with the dose
452 that reduced lesion area the most (AEI30), which instead showed the highest total POD activity.
453 This discrepancy suggests that the protective effect of *U. pinnatifida* extracts is unlikely to rely on
454 a single defense mechanism but rather on the combined action of multiple, dose-dependent
455 processes, including direct antimicrobial activity of algal compounds, priming of basal defenses,
456 and modulation of specific antioxidant enzymes that together determine the overall outcome of
457 the plant pathogen interaction. Further biochemical and molecular analyses are needed to
458 determine the contributions of these mechanisms to the observed resistance to *P. infestans*.

459 Taken together, these results indicate that aqueous extracts of *U. pinnatifida*, particularly those
460 prepared from both the lamina-and-sporophyll, exhibit biostimulant and bioprotective activities
461 depending on their preparation, promoting tomato seedling growth, photosynthetic performance,
462 or enhancing protection against a major oomycete pathogen. This dual functionality supports the
463 view that marine macroalgal extracts are multifunctional agricultural bioactives that they
464 potentially integrate nutritional, growth-promoting, and protective properties in a single
465 formulation (du Jardin 2015). Given the increasing incidence of *P. infestans* under climate change
466 scenarios (Wu et al. 2022) and the environmental concerns associated with conventional
467 fungicide use, *U. pinnatifida*-derived formulations emerge as a promising, sustainable component
468 of integrated crop management strategies for tomato. However, further field studies and chemical
469 characterization of both aqueous extracts will help identify the bioactive compounds associated
470 with growth promotion and disease resistance, confirm practical applicability, and optimize
471 dosage for commercial use.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declaration of AI-assisted manuscript preparation

During manuscript preparation, the authors used ChatGPT (OpenAI) to assist with English language editing and improving clarity, all scientific content, interpretations, and references were reviewed and verified by the authors, who take full responsibility for the final manuscript.

Author contributions

Mariana Laura Feldman: Conceptualization, Funding acquisition, Investigation, Methodology,Writing – original draft, Writing – review and editing.

Mariana Agustina Gómez: Investigation.

María Candela Lobato: Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – review and editing.

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Andrea Yamila Mansilla: Funding acquisition, Methodology, Writing – review and editing.

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