



Exploring the Fertilizing Potential of the Lichen *Pseudevernia furfuracea* (L.) Zopf. on the Growth of *Capsicum annuum* L

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Abstract

The nutritional richness of lichens in mineral nutrients and organic metabolites makes them innovative candidates for the development of biofertilisers, contributing to the biostimulation of plant growth. In this context, this work aims to evaluate the effect of the lichen *Pseudevernia furfuracea* on the growth of *Capsicum annuum* L. Inductively coupled plasma atomic emission spectroscopy (ICP-AES) and high-performance liquid chromatography (HPLC) analysis were used for the biochemical characterisation of *P. furfuracea*. The crushed lichen biomass was applied as a soil amendment at doses of 5, 20 and 30 g·kg⁻¹. The morphophysiological and biochemical parameters of *C. annuum* were evaluated by comparison with a negative and positive control (NPK). The results obtained by ICP showed that *P. furfuracea* biomass is rich in macro and micro elements essential for plant growth. Thus, HPLC analysis revealed an abundance of indole-3-butyric acid (IBA) (2.49 mg·g⁻¹). The application of 20 g·kg⁻¹ of this lichen resulted in a significant increase in shoot dry weight (+21.39%), number of leaves (+200%) and internodes (+128.8%) compared to untreated plants. In addition, the fruits weighed 167.6% more than those obtained by NPK treatment. This improvement was accompanied by an amelioration of the physiological and biochemical characteristics of *C. annuum*, resulting in an increase accumulation of pigments and minerals (N, P, Ca, Cl and Fe). This study supports the hypothesis that the application of *P. furfuracea* lichen improves the productivity of *C. annuum* plants. However, further research in the field is essential for sustainable agronomic validation.

Keywords *Pseudevernia furfuracea* · Biofertilization · *Capsicum annuum* L. · Growth · Photosynthetic pigments · Nutritive elements

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1 Introduction

Agricultural production based on the use of synthetic fertilizers is the main approach adopted by several farmers to respond to the nutritional needs and to provide economic growth (Akanni et al. 2011). However, the irrational and excessive use of this agricultural practice poses various environmental problems, which can negatively impact the ecosystem and lead to a loss of biodiversity (Kumar et al. 2023; Paharvi et al. 2021). In this regard, the evolution of scientific research towards the development of advanced technologies that are ecologically sustainable and economically viable for sustainable agriculture, is a worldwide trend aimed to maximize agricultural yields and meet the food needs of a growing global population (Kalfas et al. 2024; Rusdiyana et al. 2024). This global scientific momentum aligns closely with international policy frameworks, notably the second goal of the United Nations Agenda 2030 for Sustainable Development “Eradicate hunger, achieve food security and improved nutrition, and promote sustainable agriculture.” (Gil et al. 2019) to minimize the negative environmental impacts generated by chemical fertilizers while preserving and enhancing the quantitative and qualitative gains of the green revolution. In line with these global objectives, various scientific studies have focused on promoting and developing sustainable organic farming practices through the use of organic fertilizers, generating a wide variety of beneficial substances that offer promising advantages for healthy plant development. Among the biological resources often explored for biofertilization are marine seaweeds particularly *Sargassum muticum* (Ouala et al. 2025), *Ascophyllum nodosum* (Abidi et al. 2017), *Sargassum vulgare*, *Codium tomentosum* (El-Din 2015), and *Ulva lactuca* (Ramarajan et al. 2012). In addition, bacteria such as *Azospirillum brasilense* and *Rhodotorula glutinis* (El-Kholy et al. 2005), fungi, such as mycorrhizal fungi and *Trichoderma harzianum* (Samolski et al. 2012), as well as cyanobacteria such as *Chroococcidiopsis* sp. and *Anabaena* sp. species, have also been studied for their potential as biofertilizers (Hussain and Hasnain 2011). Furthermore, certain biological resources remain largely unexplored, despite their proven agronomic potential.

In fact, the hypothesis that the nutritional value of lichens could make them an innovative and sustainable option for biofertilization is based on their ability to be an effective natural source of essential macro- and micronutrients (N, P, K, Ca, Mg, Mn,...), amino acids (proline, methionine, cysteine, asparagine, and alanine), organic acids (oxalic acid, lactic acid, tartaric acid, and malic acid), as well as plant growth regulators (gibberellic acid, indole acetic acid, and abscisic acid) (Aslan et al. 2004; Bano et al. 2022; Gunes et al. 2016; Swamy et al. 2016). In the same way, lichens

produce substances such as norstic acid, psoromic acid, usnic acid, and iso-usnic acid (Jannah et al. 2022), which interact with minerals like K, Cu, and Fe, forming complexes that contribute to the bioaccumulation of trace elements in lichens (Huneck 1999).

In Morocco, a catalogue updated in 2013 stated the presence of 1169 lichen species, distributed in 21 orders, 75 families, and 241 genera (Ajaj et al. 2013). A more recent revision was provided based on the changes in nomenclature and indicated that Moroccan national biodiversity includes 1237 lichen species (Seaward and Amrani 2023). Amidst this broad national diversity, *Pseudevernia furfuracea* (L.) Zopf, a lichen of the Parmeliaceae family, is found in large populations in Morocco's Middle and High Atlas regions (Egea 1996), and in North Africa in general (Hale and Mason 1968). This lichen species was widely used in the fragrance industry under the appellation ‘cedarmoss’ when growing on *Cedrus atlantica*, or ‘treemoss’ when growing on other trees (Joulain and Tabacchi 2009). In 1997, 1900 tons of this lichen, harvested globally, including in Morocco, were processed in France (Joulain and Tabacchi 2009). However, to date, few studies have been conducted to examine the effects of lichens from an agronomic perspective, despite their nutritional importance. Nevertheless, certain species, such as *Lobaria pulmonaria*, *Dermatocarpon miniatum*, and *Parmelia saxatilis*, have already been identified as effective natural organic fertilizers, highlighting a biofertilizer potential that remains largely unexplored (Aslan et al. 2024; Gunes et al. 2016). This gap justifies the need for further research to evaluate the beneficial properties of lichens as biofertilizers and to understand their effects on plant development.

In this context, the main objective of this study is to evaluate the nutritional richness of the lichen species *Pseudevernia furfuracea* and its impact on biofertilization and the improvement of the physiological and biochemical properties of *Capsicum annuum* plants.

2 Materials and Methods

2.1 Harvesting and Preparing of *P. furfuracea*

Pseudevernia furfuracea (L.) Zopf. was collected in the Middle Atlas region (33°25'2"N, 5°11'10"W) in June 2022 approximately 1776 m altitude, on low branches of *Cedrus atlantica*. Its identification was carried morphologically and biochemically by E.Y (Essadki et al. 2024). The biomass was then dried in the shade at room temperature (± 25 °C), the contaminants (bark, branches, debris, other lichens, plants) were removed by hand, the biomass was then ground to a fine powder with a particle size of less than 2 mm using

an electric grinder and stored in a clean, airtight container away from moisture and light until use to preserve their biological activity.

2.2 Characterization of *P. furfuracea*

2.2.1 Physico-Chemical Characterization

The studied lichen powder was characterized through pH measurement, protein quantification using the Bradford method (Bradford 1976), and determination of pigment contents according to the method described by Upadhyaya et al. (2014). The Kjeldhal method was used to determine its nitrogen content (Lahrouni et al. 2012). Detailed descriptions of the analytical methods will be provided in a subsequent section. Phosphorus, potassium, and micronutrient contents were analyzed by inductively coupled plasma atomic emission spectroscopy (ICP-AES, PerkinElmer Version 5.5) following acid digestion of the organic matter. Briefly, 0.5 g of dried sample was digested with 5 mL of concentrated nitric acid (HNO_3). Subsequently, 5 mL of hydrogen peroxide (H_2O_2) was added to ensure complete digestion. After cooling, the digested solution was filtered and appropriately diluted prior to ICP-AES analysis (Farias et al. 2002). All analyses were conducted in six replicates.

2.2.2 Extraction, Identification, and Quantification of Phytohormones by HPLC Analysis

The phytohormone content of *P. furfuracea* was determined by HPLC-UV following the method of Yang et al. (2014). Briefly, 0.5 g of lichen biomass was homogenized with 5 ml of cold methanol (80%) with traces of silver diethyldithiocarbamate, after incubation at 4 °C for 24 h, centrifugation at 2×10^4 g for 20 min at 4 °C was performed, and the resulting supernatant underwent rotary evaporation at 40 °C, then 0.3 g polyvinylpyrrolidone (PVPP) was added, and a second centrifugation was performed at 2×10^4 g at 4 °C for 20 min, the supernatant was maintained at pH 2.5 and extracted with an equal volume of ethyl acetate. Identification and quantification of phytohormone were based on retention times and UV spectral characteristics matched between 200 and 600 nm. Solution of indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), and gibberellic acid (GA) were prepared as external standards. HPLC analysis was carried out using a gradient elution system at a flow rate of 1 mL min⁻¹ with a sample injection volume of 100 µL. The mobile phase consisted of methanol (solvent A) and 0.1 M acetic acid (solvent B), and the gradient program was applied over a 40 min run at 30 °C. Six replicates were performed for each sample.

2.2.3 Seedling Preparation and Experimental Design

The uniformly sized seeds of *C. annuum* were surface sterilized with sodium hypochlorite solution and then rinsed thoroughly with sterile distilled water. After 7 days, germinated seeds from sterile Petri dishes incubated in the dark at 25 °C were selected and sown in trays filled with peat at 26 ± 2 °C for 14 days. The young plants of *C. annuum* were then transplanted into 1.5 L plastic pots containing 1 kg of sand per pot mixed with different concentrations (5, 20, and 30 g·kg⁻¹) of *P. furfuracea* powder. The experiment was conducted following a completely randomized design with 10 replicates per treatment. Parallely, two controls were carried out, one negative (untreated plants) and the other positive (plants grown with chemical fertilizer treatment NPK (15-15-15)). This experiment took place over a 5-month period in a controlled growth chamber under the following conditions: temperature of 26 ± 2 °C, light intensity of 200 µmol. m⁻². s⁻¹, light/dark cycle of 13 h/11 h, and a humidity of 70–80%. During the experiment, each pot was treated with Hoagland's nutrient solution (Hoagland and Arnon 1950) once a week, and irrigated with tap water.

2.2.4 Evaluation of the Morphological Characteristics of *C. annuum* Plant Growth

The fresh plant samples from each treatment were harvested and carefully washed with tap water. The root system was separated from the shoot. The following biometrical data were assessed: Shoot and root length (cm), number of leaves and internodes per plant. Then, the different vegetative parts of the plants (shoots, roots, and fruits) were dried at 75 °C for 48 h to record their dry weight (mg/plant). Six replicates were performed for each measurement.

2.3 Evaluation of the Physiological and Biochemical Characteristics of *C. annuum* Plant Growth

2.3.1 Pigment Contents

Photosynthetic pigment contents (chlorophyll *a*, *b*, *a*+*b*, and carotenoids) were determined in fresh leaves sampled according to the method described by Upadhyaya et al. (2014). Fresh leaf (50 mg) was extracted with 5 ml of 95.5% acetone and incubated at 4 °C for 48 h in the dark. Thereafter, centrifugation for 5 min at 5000 rpm was performed to remove the pellet. The optical density (OD) of the supernatant was read at different absorption wavelength (470, 644, and 662 nm). Chlorophylls and carotenoids contents were determined in six independent aliquots. and expressed on a dry weight basis (mg·g⁻¹ FW) using the following formulas:

$$\text{Chlorophyll } a = (9.784 \times \text{OD at } 662\text{nm}) - (0.99 \times \text{OD at } 644\text{nm})$$

$$\text{Chlorophyll } b = (21.42 \times \text{OD at } 644\text{nm}) - (4.65 \times \text{OD at } 662\text{nm})$$

$$\text{Total Chlorophyll} = \text{Chl } a + \text{Chl } b$$

$$\text{Carotenoids} = (1000 \times \text{OD at } 470\text{nm}) - (1.9 \times \text{Chl } a) - (63.14 \times \text{Chl } b) / 214$$

2.3.2 Protein Contents

The total protein content was assessed using the Bradford method (Bradford 1976). Briefly, 250 mg of leaves, roots, and fruit were homogenized with 2 ml of phosphate buffer (0.05 M, pH 6), followed by centrifugation at 4000 rpm for 20 min. Thereafter, 2 mL of Bradford's reagent and 100 μL of distilled water were added to 100 μL of each supernatant. The reaction mixture absorbance was read at 595 nm using a spectrophotometer. Bovine Serum Albumin (BSA) was used as the standard reference, and the protein content was expressed as $\text{mg} \cdot \text{g}^{-1}$ FW. Six replicates were effectuated.

2.3.3 Mineral Contents

The powder of the different samples studied (leaves, roots, and fruits) of *C. annuum* was prepared to determine their mineral element contents (P, K, Cl, Ca, Si, S and Fe), using an using XRF fluorescence X spectrometer (Handheld X-ray Fluorescence).

Total nitrogen was determined by the Kjeldahl method, as described by Lahrouni et al. (2012). Digestion of 0.5 g of plant material on a dry weight basis was digested with 10 mL of sulfuric acid (98%) and 1 g of a mixture of Kjeldahl catalysts until boiling at 420 $^{\circ}\text{C}$ for 90 min. The samples were recovered in 100 ml of distilled water, 40 ml of these solutions were distilled into Kjeldahl flasks containing a few drops of 1% phenolphthalein and NaOH (8 N). The

resulting distillate was collected with boric acid and titrated with 0.05 N sulfuric acid. Six replicates were performed.

2.4 Statistical Analysis

The data treatment was done using SPSS 20 software. The data were expressed as mean of replicates $\pm$ standard deviation. The normality of the data was tested using the Kolmogorov-Smirnov test. All analyses were performed in six replicates, and mean values were subjected to the statistical analysis using a one-way analysis of variance (ANOVA). Separation of means was performed by the Tukey test. Significant differences were considered at $p < 0.05$ and were indicated by different letters.

3 Results

3.1 Physic-chemical and biochemical characteristics of *P. furfuracea*

The results of *P. furfuracea* content characterization is presented in Table 1; Fig. 1. The pH determined in the lichen biomass is nearly at the neutrality of value 6.02 ± 0.06 . Thus, the results showed the presence of photosynthetic pigments (chlorophyll *a* and *b*) and proteins at high levels in the thallus of *P. furfuracea*. The mineral analysis of this lichen revealed the abundance of various compounds such as nitrogen, potassium, calcium, iron, chlorine, magnesium, and sulfur (Table 1). The results of the HPLC analysis of the crude extract of *P. furfuracea* are shown in Fig. 1, highlights the peak and retention time detected at an absorption intensity of 280.0 nm. In comparison with the chromatograms of the indole acetic acid (IAA), indole butyric acid (IBA), and gibberellic acid (GA) standards used, it can be deduced that IBA is the most abundant in the *P. furfuracea* biomass at a content of $2.49 \text{ mg} \cdot \text{g}^{-1}$.

3.2 Influence of *P. furfuracea* on the Morphological Growth of *C. annuum* Plants

The results of several biological parameters on the *C. annuum* plant growth treated with *P. furfuracea* at different treatments (5, 20, and 30 $\text{g} \cdot \text{kg}^{-1}$) are presented in the Figs. 2 and 3; Table 2. A one-way ANOVA revealed that there was a statistically significant difference between the effects of *P. furfuracea* concentrations on shoot ($F(4, 45) = 269.835$, $P < 0.0001$) and root length ($F(4, 45) = 320.475$, $P < 0.0001$) (Fig. 2). The *C. annuum* plant treated with 20 and 30 $\text{g} \cdot \text{kg}^{-1}$ of *P. furfuracea* showed significantly higher shoot lengths (38.5 and 34.8 cm respectively) was more identical to the positive control (45.5 cm) (Fig. 2A) ($P < 0.0001$). While the

Table 1 Physical and chemical properties of *P. furfuracea*

Component	Value
pH	6.02 ± 0.06
Protein content ($10^{-1} \text{ mg} \cdot \text{g}^{-1}$ FW)	5.50 ± 0.1
Chl <i>a</i> ($\text{mg} \cdot \text{g}^{-1}$ FW)	8.56 ± 0.37
Chl <i>b</i> ($\text{mg} \cdot \text{g}^{-1}$ FW)	5.75 ± 0.20
Total Nitrogen NTK ($\text{mg} \cdot \text{g}^{-1}$)	13.8 ± 0.8
P_2O_5 ($\text{mg} \cdot \text{g}^{-1}$)	1.02 ± 0.41
K_2O ($\text{mg} \cdot \text{g}^{-1}$)	18.8 ± 0.56
CaO ($\text{mg} \cdot \text{g}^{-1}$)	85.8 ± 0.14
Fe_2O_3 ($\text{mg} \cdot \text{g}^{-1}$)	3.20 ± 0.14
Cl ($\text{mg} \cdot \text{g}^{-1}$)	80.3 ± 0.51
MgO ($\text{mg} \cdot \text{g}^{-1}$)	16.65 ± 0.49
SO_3 ($\text{mg} \cdot \text{g}^{-1}$)	16.60 ± 0.14
Mn ($\text{mg} \cdot \text{g}^{-1}$)	0.45 ± 0.007
Zn ($\text{mg} \cdot \text{g}^{-1}$)	0.33 ± 0.07
Cu ($\text{mg} \cdot \text{g}^{-1}$)	0.05 ± 0.002

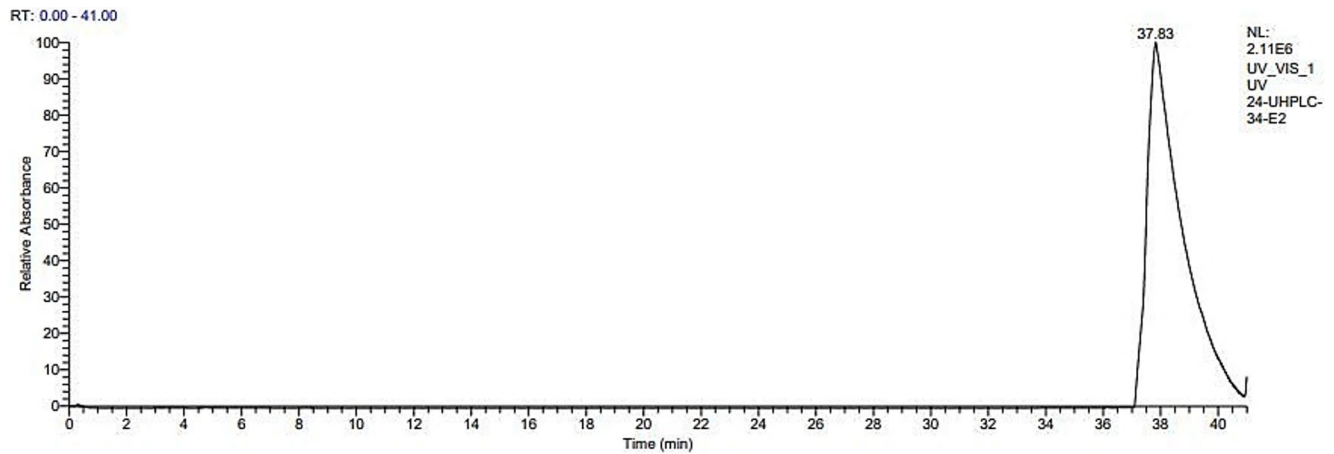


Fig. 1 HPLC chromatogram for the main phytohormone compound identified in *P. furfuracea*

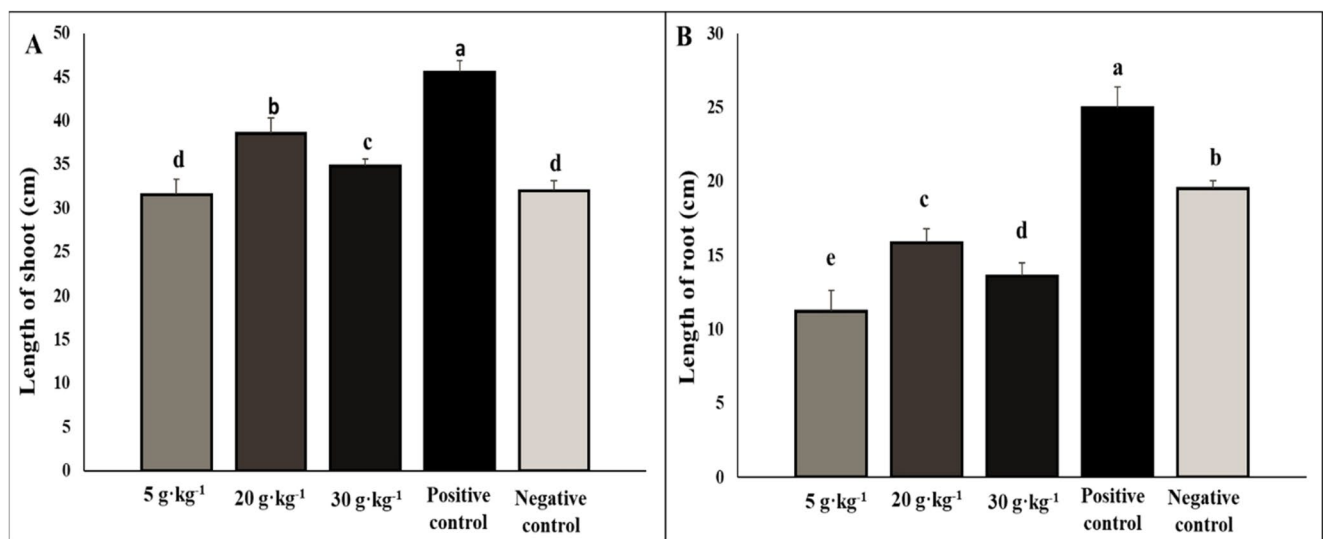


Fig. 2 Length of the shoot (A) and root (B) of the *C. annuum* plant exposed to the *P. furfuracea* treatments. Results are replicate means $\pm$ SE (standard error). Different letters indicate significant differences at $P < 0.05$ based on Tukey test

rooting response of plants under the effect of lichen tested at different concentrations was statistically lower in comparison with the positive and negative controls (Fig. 2B) ($P < 0.0001$).

The one-way ANOVA analysis showed that there was a highly significant effect of the different concentrations of *P. furfuracea* studied ($F(4, 45) = 389.507$, $P < 0.0001$) for the number of leaves and internodes ($F(4, 45) = 69.414$, $P < 0.0001$) in comparison with the positive and negative controls (Fig. 3). The treatment of the *C. annuum* plant with *P. furfuracea* at $20 \text{ g} \cdot \text{kg}^{-1}$ produced a maximum number of leaves (15.9 per plant), significantly higher in comparison with the negative control (5.3 per plant), moreover, this effect was statistically greater compared to the positive control (14 leaves per plant) ($P < 0.0001$) (Fig. 3A). The $20 \text{ g} \cdot \text{kg}^{-1}$ treatment showed no significant difference in the number of internodes (16.7 per plant) compared to the

positive control (15.5 per plant) ($P = 0.320$), and higher compared to the negative control (7.3 per plant) ($P < 0.001$) (Fig. 3B). However, the treatment of plants with $5 \text{ g} \cdot \text{kg}^{-1}$ of *P. furfuracea* showed significant positive effects on the number of leaves (9.6 per plant), and internodes (12 per plant) compared to the negative control, but remained significantly low compared to the positive control ($P < 0.0001$) (Fig. 3). Regarding the treatment of plants with a high concentration of *P. furfuracea* ($30 \text{ g} \cdot \text{kg}^{-1}$), the number of leaves (13.8 per plant) and internodes (11.9 per plant) was significantly higher compared to the negative control ($P < 0.0001$), no significant difference in the number of leaves was observed to the plants treated with the chemical fertilizer NPK ($P = 0.965$) (Fig. 3), additionally, the number of internodes produced by $30 \text{ g} \cdot \text{kg}^{-1}$ treatment (11.9 per plant) was the same as that observed in the $5 \text{ g} \cdot \text{kg}^{-1}$ treatment (12 per plant) ($P = 1$) (Fig. 3B).

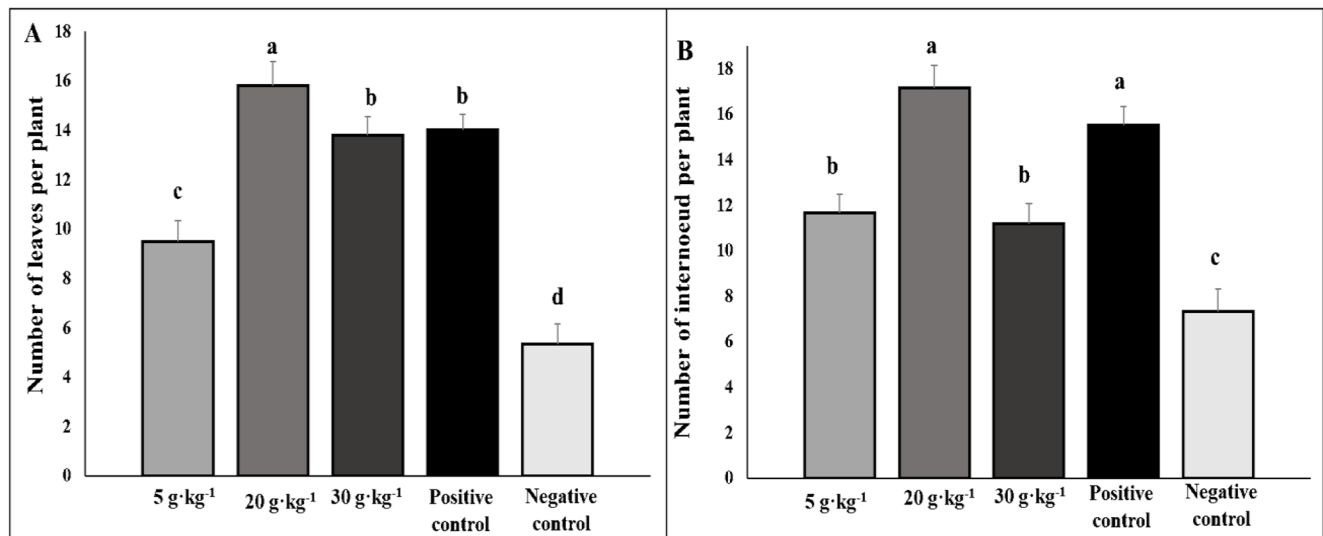


Fig. 3 Effect of *P. furfuracea* on the number of leaves (A), and internode (B) of *C. annuum* plant. Results are replicate means $\pm$ SE (standard error). Different letters indicate significant differences at $P < 0.05$ based on Tukey test

Table 2 Effect of *P. furfuracea* on *C. annuum* plant dry weight (mg) Results are replicate means $\pm$ SE (standard error). Different letters indicate significant differences at $P < 0.05$ based on Tukey test

	5 g·kg ⁻¹	20 g·kg ⁻¹	30 g·kg ⁻¹	Positive control	Negative control
Shoot	613.77 $\pm$ 14.51 ^c	893.28 $\pm$ 18.03 ^a	596.66 $\pm$ 15.27 ^c	924.60 $\pm$ 5.04 ^a	735.87 $\pm$ 5.53 ^b
Root	288.81 $\pm$ 13.80 ^e	562.07 $\pm$ 16.43 ^b	350.82 $\pm$ 8.58 ^d	622.13 $\pm$ 13.32 ^a	411.25 $\pm$ 15.89 ^c
Fruit	-	367.23 $\pm$ 38.11 ^a	-	137.24 $\pm$ 10.83 ^b	-

The obtained plants showed significant difference of dry weights (DW) depending on the concentration applied (F (4, 45) = 835.344, $P < 0.0001$) (Table 2). Generally, 20 g·kg⁻¹ of *P. furfuracea* resulted in a significant improvement in shoot DW of *C. annuum* plants in comparison with untreated plants with a P value < 0.001 , and no significant difference in comparison with the positive control ($P = 1$). The DW root of plants treated by 20 g·kg⁻¹ is higher compared to the negative control, but lower than the positive control ($P < 0.0001$). Thus, this concentration (20 g·kg⁻¹) enables plants to reach the fruiting stage and form fruits with a significant higher DW than those formed under the NPK chemical fertilizer treatment ($P < 0.0001$).

3.3 Effect of *P. furfuracea* on the Biochemical and Nutritional Constituents of the *C. annuum* Plant

3.3.1 Leaf Pigment Contents

Photosynthetic pigment content (Chlorophyll *a*, Chlorophyll *b*, Total Chlorophyll, and Carotenoids) synthesized by the *C. annuum* plant treated with various concentration studies of *P. furfuracea* is presented in Fig. 4. ANOVA analysis showed that the different treatments used significantly influenced the Chlorophyll *a* content (F (4, 45) = 207.921, $P < 0.0001$). The highest yields of Chl *a* are obtained in the

20 g·kg⁻¹ (22.42 mg·g⁻¹ FW) and 30 g·kg⁻¹ (18.10 mg·g⁻¹ FW) treatments compared to the negative control (15.09 mg·g⁻¹ FW) (Fig. 4a) ($P < 0.0001$), and no difference statistic between 20 g·kg⁻¹ treatments and NPK fertilizer treatments (22.73 mg·g⁻¹ FW) ($P = 0.315$) (Fig. 4A). The chlorophyll *b* and total chlorophyll content also showed significant differences depending on the different treatments studied (F (4, 45) = 66.732, $P < 0.0001$ for Chl *b* and F (4, 45) = 69.386, $P < 0.0001$ for total Chl). The 20 g·kg⁻¹ treatment also generates high levels of chlorophyll *b* (18.57 mg·g⁻¹ FW) and total chlorophyll (40.07 mg·g⁻¹ FW) compared to the negative control (10.71 mg·g⁻¹ FW for chlorophyll *b* and 25.35 mg·g⁻¹ FW for total chlorophyll) ($P < 0.0001$), and no significant difference in comparison with plants treated with NPK fertilizer (17.59 mg·g⁻¹ FW for chlorophyll *b* and 40.63 mg·g⁻¹ FW for total chlorophyll) ($P = 0.742$ for Chl *b* and $P = 0.991$ for total Chl) (Fig. 4B and C). The statistical difference, evaluating the positive effect of the lichen treatment is also reflected in the carotenoid content (F (4, 45) = 202.287, $P < 0.0001$), which is more significant in the treatments of 20 and 30 g·kg⁻¹ (10.69 mg·g⁻¹ FW and 8.27 mg·g⁻¹ FW respectively) compared to the positive and negative controls (6.79 and 3.83 mg·g⁻¹ FW respectively) (Fig. 4d) ($P < 0.0001$) (Fig. 4D). No significant difference was observed for the 5 g·kg⁻¹ treatment compared to the negative control ($P = 0.795$) (Fig. 4).

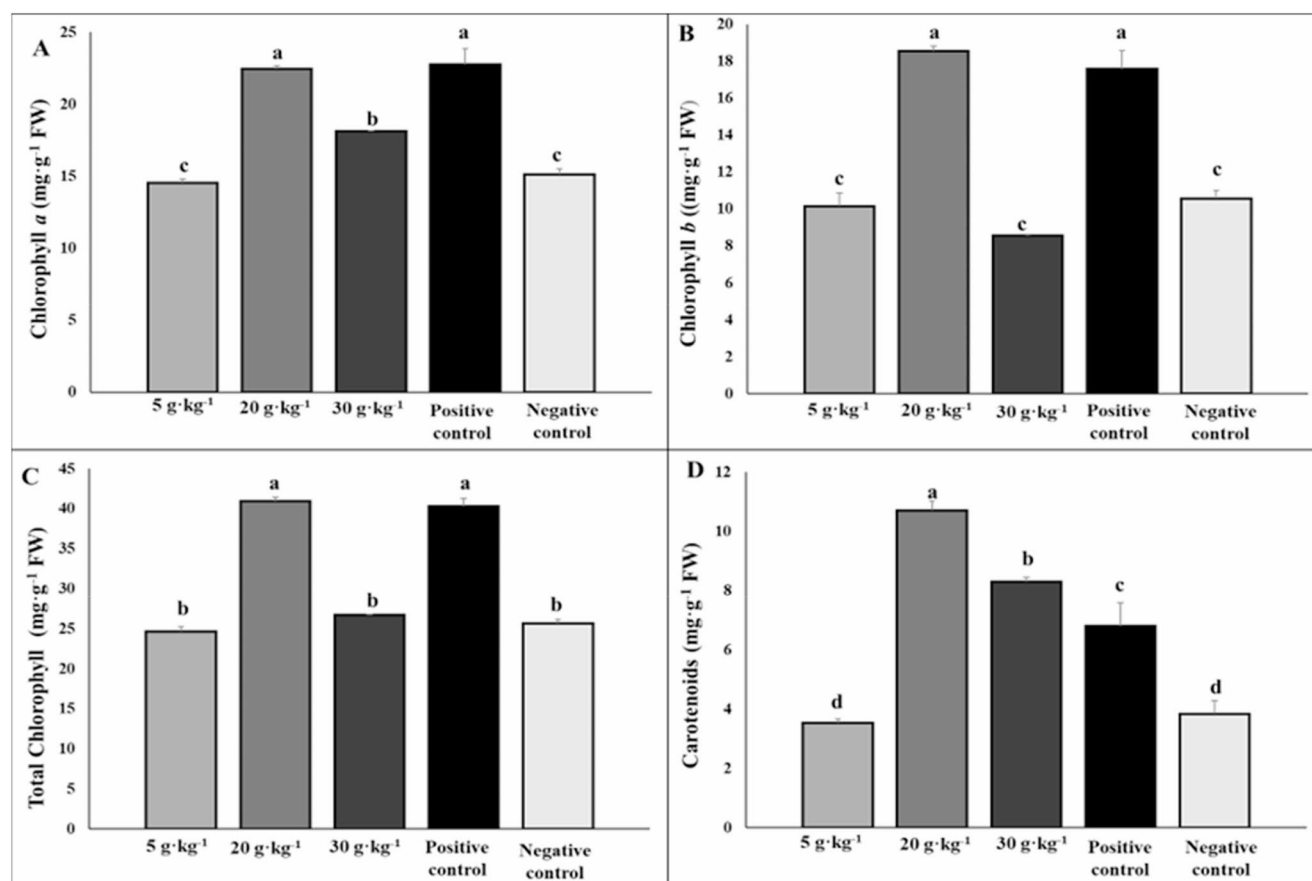


Fig. 4 Effect of *P. furfuracea* on Chlorophyll *a* (A), Chlorophyll *b* (B), Total chlorophyll content (C) and on Carotenoids content (D) of *C. annuum* plant. Results are replicate means $\pm$ SE (standard error). Different letters indicate significant differences at *P* < 0.05 based on Tukey test

Table 3 Effect of *P. furfuracea* on protein content (10^{-1} mg·g⁻¹ FW) of the *C. annuum* plant

	5 g·kg ⁻¹	20 g·kg ⁻¹	30 g·kg ⁻¹	Positive Control	Negative control
Shoot	6.75 $\pm$ 0.04 ^c	7.81 $\pm$ 0.01 ^b	5.08 $\pm$ 0.02 ^d	8.87 $\pm$ 0.04 ^a	7.75 $\pm$ 0.03 ^b
Root	1.10 $\pm$ 0.04 ^{bc}	1.34 $\pm$ 0.04 ^b	1.25 $\pm$ 0.03 ^b	1.74 $\pm$ 0.04 ^a	0.97 $\pm$ 0.05 ^c
Fruit	-	0.97 $\pm$ 0.05 ^b	-	1.41 $\pm$ 0.07 ^a	-

Results are replicate means $\pm$ SE (standard error). Different letters indicate significant differences at *P* < 0.05 based on Tukey test

3.3.2 Protein Content

Protein content values for shoots, roots, and fruits of *C. annuum* plants formed under *P. furfuracea* treatment are presented in Table 3. ANOVA revealed that different concentrations of *P. furfuracea* differentially influenced the protein content in *C. annuum* shoots (*F* (4, 45) = 245.872, *P* < 0.0001). The shoots treated with 20 g·kg⁻¹ of *P. furfuracea* showed no significant difference in protein content compared with the negative control (*P* = 0.987). However, a significant reduction in protein content was observed with the application of 5 and 30 g·kg⁻¹ of lichen compared to the negative control (*P* < 0.0001). Compared with shoots from

plants treated with NPK fertilizer, their protein content is significant (*P* < 0.001) and close to that observed with the 20 g·kg⁻¹ treatment. The statistical analysis of protein content in root plants treated under different treatments showed *F* (4, 45) = 18.121, *P* < 0.0001. 20 and 30 g·kg⁻¹ lichen-treated plant roots showed a slight increase in protein content compared to the negative control with *P* = 0.003 for 20 g·kg⁻¹ and *P* = 0.033 for 30 g·kg⁻¹. Compared with the positive control, treatments at 20 and 30 g·kg⁻¹ showed lower values (*P* = 0.002 for 20 g·kg⁻¹ and *P* < 0.001 for 30 g·kg⁻¹). On the other hand, treatment with 20 g·kg⁻¹ of *P. furfuracea* resulted in a significant reduction of protein content in the fruits compared with those treated with NPK (*P* < 0.0001).

Table 4 Contents of mineral content in aerial part (A), root part (B) and fruit part (C) of *C. annuum* plant under different treatments

Minerals element	5 g·kg ⁻¹	20 g·kg ⁻¹	30 g·kg ⁻¹	Positive control	Negative control
A: Shoot					
N (mg·g ⁻¹)	34.7±4.4 ^d	43±2.6 ^b	38.2±2.5 ^c	63.6±4 ^a	25.3±0.2 ^c
P (mg·g ⁻¹)	0.98±0.03 ^e	1.34±0.04 ^b	1.05±0.03 ^d	1.40±0.05 ^a	1.25±0.04 ^c
K (mg·g ⁻¹)	5.19±0.04 ^e	7.45±0.05 ^d	8.62±0.06 ^c	15±0.08 ^a	13±0.08 ^b
Ca (mg·g ⁻¹)	7.83±0.05 ^b	7.41±0.05 ^c	8.84±0.06 ^a	1.43±0.08 ^d	1.37±0.07 ^e
Fe (mg·g ⁻¹)	0.19±0.01 ^d	0.25±0.01 ^b	0.22±0.01 ^c	0.30±0.03 ^a	0.21±0.01 ^c
Cl (mg·g ⁻¹)	89.60±0.53 ^b	92.50±0.60 ^a	90.50±0.55 ^c	35.90±0.45 ^d	33.20±0.45 ^e
Mg (mg·g ⁻¹)	23.8±0.18 ^b	25.7±0.22 ^a	14.3±0.08 ^d	15.9±0.04 ^c	12.1±0.29 ^e
S (mg·g ⁻¹)	3.46±0.21 ^c	3.25±0.22 ^d	2.52±0.21 ^e	5.02±0.26 ^a	4.77±0.25 ^b
Si (mg·g ⁻¹)	0.32±0.01 ^e	0.34±0.01 ^c	0.33±0.01 ^d	0.44±0.001 ^a	0.43±0.001 ^b
B: Root					
N (mg·g ⁻¹)	30.20±0.5 ^c	75.30±4.7 ^a	62.66±4.5 ^b	75.20±2.4 ^a	31.50±2.6 ^c
P (mg·g ⁻¹)	0.96±0.04 ^e	1.02±0.04 ^c	0.90±0.04 ^d	1.41±0.07 ^a	1.22±0.03 ^b
K (mg·g ⁻¹)	5.66±0.05 ^d	5.77±0.05 ^c	4.25±0.04 ^e	18.26±0.1 ^a	14.58±0.08 ^b
Ca (mg·g ⁻¹)	8.43±0.53 ^b	9.03±0.57 ^a	8.70±0.56 ^a	1.21±0.30 ^c	1.16±0.79 ^c
Fe (mg·g ⁻¹)	1.11±0.24 ^{bc}	1.39±0.16 ^b	1.37±0.27 ^b	2.60±0.46 ^a	1.04±0.24 ^c
Cl (mg·g ⁻¹)	89.90±0.56 ^c	101.9±0.57 ^a	91.50±0.55 ^b	36.50±0.50 ^d	31.40±0.47 ^e
Mg (mg·g ⁻¹)	19.9±0.11 ^a	16.7±0.02 ^b	9.8±0.56 ^c	9.2±0.02 ^d	7.2±0.05 ^e
S (mg·g ⁻¹)	0.32±0.02 ^c	0.32±0.04 ^c	0.24±0.02 ^d	0.58±0.03 ^a	0.55±0.02 ^b
Si (mg·g ⁻¹)	3.52±0.99 ^b	3.73±1.03 ^b	3.29±0.93 ^b	4.37±0.12 ^a	4.32±0.13 ^a
C: Fruit					
N (mg·g ⁻¹)	-	734.4±4.5 ^a	-	709±4.2 ^b	-
P (mg·g ⁻¹)	-	1.03±0.04 ^a	-	0.98±0.03 ^b	-
K (mg·g ⁻¹)	-	4.66±0.05 ^b	-	5.71±0.04 ^a	-
Ca (mg·g ⁻¹)	-	4.05±0.03 ^a	-	3.62±0.03 ^b	-
Fe (mg·g ⁻¹)	-	0.13±0.01 ^a	-	0.15±0.01 ^b	-
Cl (mg·g ⁻¹)	-	86.30±0.52 ^a	-	86.40±0.50 ^a	-
Mg (mg·g ⁻¹)	-	0.25±0.01 ^b	-	0.7±0.04 ^a	-
S (mg·g ⁻¹)	-	0.25±0.02 ^b	-	0.29±0.02 ^a	-
Si (mg·g ⁻¹)	-	3.30±0.09 ^a	-	3.35±0.09 ^a	-

Results are replicate means±SE (standard error). Different letters indicate significant differences at $p<0.05$ based on Tukey test

3.3.3 Mineral Contents

The mineral element contents accumulated in the *C. annuum* plants amended by the *P. furfurace*, with the chemical fertilizer NPK or without fertilizer, are presented in Table 4. The results of ANOVA analysis indicate that the use of *P. furfurace*, particularly at 20 g·kg⁻¹, enables shoots to reach maximum levels of N, P, Ca, Cl, Mg, and Fe ($P<0.0001$) compared with the negative control, noting that Cl and Mg level in the plants tested exceeded those observed in NPK-amended shoots (Table 4A). However, K, S, and Si levels in shoots showed no significant effect following the application of *P. furfurace* as a fertilizing amendment at different concentrations compared with negative and positive controls ($P<0.0001$) (Table 4A). Similarly, ANOVA showed that the application of lichen powder induced a significant increase in mineral uptake by the roots of *C. annuum* plants, particularly at the 20 g·kg⁻¹ treatments. Notably, nitrogen content was comparable to that of the positive control ($P=0.997$) and significantly higher than the negative control

($P<0.0001$). Ca, Fe, Cl, and Mg levels were significantly higher than those in both the positive and negative controls ($P<0.0001$) (Table 4B). On the other hand, a reduction in P, K, S, and Si ($P<0.0001$) content was observed in the roots of plants subjected to the various treatments studied compared the positive and negative controls (Table 4C). However, we deduce that the treatment of 20 g·kg⁻¹ allows the shoot and root parts of *C. annuum* plants to accumulate high contents of certain mineral elements such as N, Ca, Cl, Mg, and Fe. In this effect, this concentration seems to be beneficial to the growth of the vegetative parts of *C. annuum*. Thus, it gives the plants the capacity to reach the fruiting stage and to form fruits whose contents in mineral elements are illustrated in Table 4C. The ANOVA results show that the fruits obtained with the 20 g·kg⁻¹ treatment have higher contents of the elemental constituents N, P, Ca and Fe ($P<0.0001$) than the positive controls, while the contents of the other elements Cl and Si are significantly similar to those obtained with the NPK treatment (Table 4C) with P value 0.978 and 0.057 respectively.

4 Discussion

Exploiting an innovative, ecological and sustainable strategy for agricultural applications is the primordial goal of this study. In this regard, the lichen *P. furfuracea* used in this research as a potential biofertilizer produced significant results, offering beneficial advantages for the growing of *C. annuum* plants. These positive effects can be explained by its biochemical composition, as the biochemical characterization of *P. furfuracea* revealed its richness in various nutrient compounds, notably their accumulation of a high levels of mineral elements (N, P, Ca, Cl, Mg, and S). These findings are consistent with previous studies reporting the strong capacity of *P. furfuracea* to efficiently accumulate a wide range of mineral elements, including N, Cr, Fe, K, Mg, Mn, Na, and Zn (Adamo et al. 2007; Malaspina et al. 2014; Sorbo et al. 2008). Furthermore, the ability of lichens to accumulate minerals is amplified under humid conditions, as demonstrated by Adamo et al. (2003). The total nitrogen content determined in the *P. furfuracea* biomass used in this study (13.8 mg·g⁻¹) is comparable to that reported by Maninen (2018), who estimated that the nitrogen content of the same species can vary between 1.32% and 1.55%. Indeed, the nitrogen present in the thallus of *P. furfuracea* originates mainly from atmospheric nitrogen and is directly absorbed by the lichen in bioavailable forms (Vingiani et al. 2004). In addition, a significant accumulation of other mineral compounds has been observed in various lichen species, notably those of the *Cetraria* genus, known for their high sodium and potassium content (Storeheier et al. 2002). This elemental composition has been mainly affected by natural factors, including the interception of airborne particles and soil dust on their surface, as well as the anthropogenic input of pollutants (Johansson et al. 2012; Nash 2008; Pirintsos et al. 2006; Sorbo et al. 2008). However, once absorbed, these minerals can be transferred to plant communities through litter deposition, leaching, or microbial incorporation, thereby contributing to soil nutrient enrichment and improved soil fertility (Pike 1978). Furthermore, the biochemical characterization of *P. furfuracea* have also revealed its richness in biochemical components, demonstrating its high nitrogen content, particularly through the presence of chlorophyll *a* and *b*, derived from its symbiotic photobiont partners (green algae) (Kranner et al. 2005), as well as proteins involved in regulating plant growth and development, such as kinases, phosphatases and DNA-binding proteins, and in protecting against environmental stress (Calchera et al. 2019; Singh et al. 2021). In line with the present study, similar observations have been reported in previous work, demonstrating the abundance of photosynthetic pigments and proteins in various other lichen species such as *Usnea antarctica*, *Hydropunctaria maura*, *Wahlenbergiella mucosa*, and *Sticta* sp

(Balarinová et al. 2014; da Silva et al. 1993; Badridze et al. 2019; Higgins et al. 2015).

It is undeniable that many phytohormones are synthesized by bacteria, algae, fungi, and bryophytes, acting as plant growth regulators and playing a crucial role in plant growth and development, as well as in the regulation of various physiological processes (Chanclud and Morel 2016; Decker et al. 2006; Swamy et al. 2016; Tarakhovskaya et al. 2007). HPLC analysis conducted in this study revealed the abundance of IBA in the tissue of *P. furfuracea*. However, several studies have demonstrated that lichens are a significant source of phytohormones, including auxin (Indole-3-acetic acid, IAA), gibberellic acid (GA₃), abscisic acid (ABA), and cytokinin (zeatin). The production of these hormones largely depends on the specific species of photobionts and microbiota. Like as IAA is known to be synthesized by both mycobionts and photobionts, whereas the production and release of ABA, GA₃, and IBA are primarily influenced by the photobiont species (Ergün et al. 2002; Pichler et al. 2020). These compounds are released in large quantities into the extracellular space, where they can be perceived by other microorganisms, potentially affecting their genetic expression, metabolism, and physiology (Pichler et al. 2020).

In fact, the high nutritional and mineral potential of lichens, compared to certain sources of organic fertilizer, appears to be a promising lever for sustainable agriculture, as demonstrated by the results of this study (Gunes et al. 2016). That the nutritional assessment of *P. furfuracea* points the way to a better understanding of its biofertilizer potential for the growth and development of *C. annuum* plants, namely at a dose of 20 g·kg⁻¹. In fact, statistical analysis of the various growth parameters recorded in this study, highlighted the promotion of shoot maturation, an increase in the number of leaves and internodes, and a significant improvement in the dry weight of the various parts of the plant. In addition, *P. furfuracea* enables *C. annuum* plants to reach the fruiting stage and form fruits of good nutritional quality. This morphological improvement results from the enrichment of the biochemical profile of *C. annuum*, mainly through an increase in photosynthetic pigment content due to the action of the symbiotic photobiont *P. furfuracea*, whose high nitrogen content promotes chlorophyll synthesis (Goga et al. 2018; Badridze et al. 2019; Pfeifhofer et al. 2002; Thakur et al. 2024), and by enriching plants with essential mineral elements, particularly calcium (Ca), chlorine (Cl) and iron (Fe). This mineral evolution results from the action of the fungal component of the lichen *P. furfuracea*, which is capable of mineralizing nutrients and facilitating their transfer to plants (Barrow et al. 2008). Furthermore, the high contents of manganese (Mn), copper (Cu), and zinc (Zn) associated with lichens may act as

enzymatic cofactors, thereby strengthening plant defense mechanisms. Manganese plays a protective role by reducing reactive oxygen species without inducing toxicity, while copper and zinc, at low concentrations, activate secondary defense systems in plants (Zhao et al. 2012).

The biofertilizing effect exercised by lichens can vary significantly depending on the species, dose applied, and the crop plant. Comparable to the present study, the research of Aslan et al. (2024) showed that the application of *Lobaria pulmonaria* lichen at a dose of 5 g·kg⁻¹ led to the highest growth values in *Zea mays*, compared to other lichen species, including *P. furfuracea*. Furthermore, in this study, sandy soil was used as an inert substrate for the cultivation of *C. annuum* plants, suggesting that the applied dose of 5 g·kg⁻¹ is insufficient to ensure optimal plant growth. On the other hand, the dose of 30 g·kg⁻¹ did not induce any toxic effects, but probably led to a nutritional imbalance, which explains the dose-dependent effect observed.

In general, research on lichens as potential biofertilizers remains limited. Nevertheless, the role and functioning of their symbiotic partners may explain the beneficial effects that have been demonstrated. In fact, the study conducted by Swamy et al. (2016) evaluated lichen bacterial strains for plant growth due to their high ethylene production, which is closely linked to nitrogenase activity, nitrogen fixation, and the capacity to produce ammonia and IAA in plants (Patten and Glick 1996). Similarly, the study carried out by Medison et al. (2023), evaluated the potential of *Bacillus licheniformis*, derived from the lichen *Collema undulatum*, to promote maize growth and biocontrol of plant pathogens. Their beneficial effect is due to their ability to produce IAA, siderophores and biofilms, solubilize phosphate and potassium, and present extracellular enzymes (cellulases, proteases, amylases and β -1,3-glucanase). This improves maize germination, increases shoot and root length, and increases chlorophyll content. In addition, inoculation of plants with *Bacillus licheniformis* can be used as a bioinoculant to protect crops from salt stress (Singh and Jha 2016). In a similar line, Santiago et al. (2018) showed that growing *Genipa americana* seedlings alongside *Cladonia salzmännii* Nyl. lichen associated with arbuscular mycorrhizae significantly improved their growth. This improvement is mainly attributed to the secretion of barbaric acid by the lichen, which strengthens the symbiotic interaction between plant roots and arbuscular mycorrhizae.

In addition, the application of lichens to agricultural soils can contribute to improving their physico-chemical and nutritional properties, increasing water retention, regulating the soil surface microclimate, reducing soil pH through the secretion of organic matter (Ghiloufi et al. 2023; Ji et al. 2014; Santiago et al. 2018; Tunç and Doğan 2022).

Indeed, this improvement in soil quality by lichen secretion is accompanied by an improvement in microbial activity beneficial to plant growth (Ghiloufi et al. 2023; Sedia and Ehrenfeld 2005).

In the light of the results of the present study, the use of *P. furfuracea* lichen as naturally fertilizer rich of nutritional agents is extremely beneficial for *C. annuum* growth, offering a sustainable and ecologically responsible alternative for improving plant growth and health.

5 Conclusions

This study demonstrates that the use of *Pseudevernia furfuracea* lichen as a biofertilizer at a dose-dependent rate improves the growth of *Capsicum annuum* plants. This improvement is mainly due to increased availability and transfer of essential mineral nutrients, particularly nitrogen, which promote improved photosynthetic activity through chlorophyll synthesis, thereby stimulating the physiological vegetative and biochemical development of the fruit. These results confirm the hypothesis that lichens have potential as unconventional and sustainable biofertilizer resources, offering a new approach to improving plant nutrition. This work provides a mechanistic basis for the use of lichen-based amendments in sustainable agriculture and opens up new perspectives for the valorization of the different partners of *Pseudevernia furfuracea* in order to evaluate the underlying mechanisms of the interaction between lichens and plants. In addition, for large-scale agronomic validation, while taking into account the availability of lichen biomass and its low growth rate, it is essential to optimize application methods by favouring use of aqueous extracts or fractions enriched with bioactive compounds.

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Data Availability The data generated and/or analyzed during the current study are contained in this manuscript and presented in tables and figures.

Declarations

Conflict of interest the authors declare that they have no conflict of interests.

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