



# Nitrogen supplying capability of wool pellets as an alternative fertilizer depending on soil biological activity

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## Abstract

Pellets made from waste wool, typically sourced from sheep shearing residues generated by the textile or wool industry, have recently emerged as a promising alternative for plant nutrition. However, limited information is available on the impact of wool pellets (WP), applied at a dosage of 4 g per pot, on soil functioning, biological activity, plant physiology, and nutrient supply. A pot experiment was set up in a randomized block design with four replicates on sweet peppers (*Capsicum annuum* L.). The effect of WP on permanganate-oxidizable carbon, fluorescein diacetate, and  $\beta$ -glucosidase enzyme activities were investigated in two soils differing in their soil organic matter (SOM) contents (low and high) and compared to the control and a reference N fertilizer solution. The nitrate and total nitrogen content of plants, the photosynthetic pigments, gas exchange intensity, shoot and root biomass, pepper fruit, and photosynthetic rate per total N-uptake were also examined. WP treatments (4 g per pot) increased soil biological activity in both soil types (with 0.58% and 1.84% soil organic matter, respectively) and significantly improved plant physiological parameters and N-use efficiency compared to the control and reference N fertilizer addition. Although the total N content in wool pellets was higher than in the mineral reference N-solution, this reference treatment served as a baseline dose allowing comparison with the N-supply intensity of the WP. WP significantly increased shoot biomass in both soil types, with a more pronounced effect in the low SOM soil due to faster mineralization and higher air capacity. In contrast, higher fruit was achieved in the high SOM soil. WP treatment increased N-uptake to 2.18 and 2.34 mg/week in low and high SOM, respectively. The research findings highlight wool pellets as a powerful alternative to inorganic fertilizers, offering a sustainable nutrient supply. Moreover, utilizing wool a by-product often considered waste as an organic fertilizer contributes to solving both economic and environmental challenges associated with wool disposal.

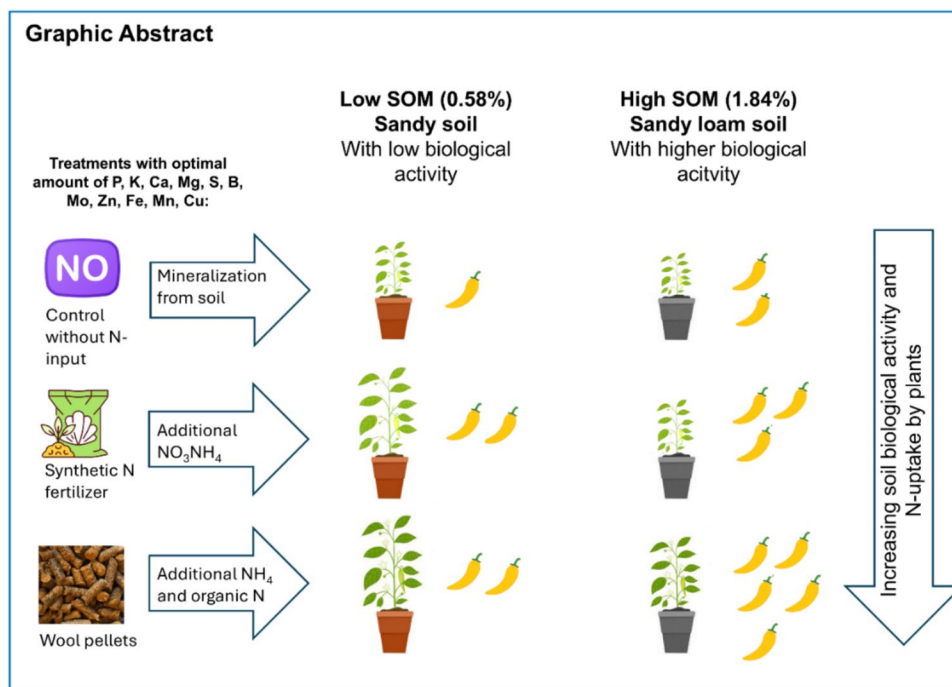
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## Graphic abstract



**Keywords** Wool pellet · Soil organic matter · Alternative nitrogen source · Enzyme activity · Photosynthesis · Pepper

## Introduction

Maintaining healthy soil quality and ensuring the long-term viability of agricultural production depend on optimal management practices (Luo et al. 2018). Several previous studies have demonstrated that organic nutrient sources can provide greater benefits over mineral fertilization by improving soil fertility parameters (Zheljazkov 2005), maintaining soil health in the long term, and in some cases, even yielding higher crop outputs (Luo et al. 2018). These benefits are primarily related to changes in soil biological and biochemical properties (Ling et al. 2016).

Wool pellet biodegradable nitrogenous organic amendment is derived as a secondary product from wool manufacturing processes (Abdallah et al. 2019; Sharma et al. 2019). Due to its role as a primary nutrient reservoir in the soil, the beneficial nutrient composition of wool pellets enhances both the productivity and yield of various plant species (Zheljazkov 2005). Organic amendments, regardless of its origin, are increasingly preferred over synthetic fertilizers for better soil quality and sustainability (Luo et al. 2018).

In the EU, there are around 85 million sheep in various production systems (Theodoridis et al. 2021), although Hungary is not one of the main sheep-producing countries. However, this sector has recently been in decline in the EU

for economic reasons (Gambelli et al. 2021; Rossi 2017). Sheep are primarily kept for meat production and, to a lesser extent, for milk and wool. Nevertheless, the annual EU wool production exceeds 200 thousand tons, classified into several groups (Petek and Marinšek Logar 2021). Low-priced, low-quality wool is mainly considered a by-product (Chereji and Munteanu 2022). The production of raw wool poses an economic burden for sheep breeders in many EU countries. According to European Commission Regulations 1069/2009 and 142/2011, shorn greasy wool not used in the textile industry is classified as an animal by-product (category 3) and must be sent to landfill as special waste. This regulation creates economic problems for farmers, as the cost of shearing often exceeds the selling price of the wool (Camilli et al. 2015), leading to unsustainable practices like burning or landfilling the wool (Zoccola et al. 2015). However, the new EU Regulation on organic fertilizers (2019/1009) provides opportunities to use wool as fertilizer in open fields and greenhouses. Although unprocessed wool may carry pathogens and requires risk mitigation (European Commission Regulation No 1069/2009), it has been tested as a fertilizer with positive results on crop production. The application of sheep wool into the soil to aid plant growth and development has been studied extensively, with several studies

reporting the beneficial effects of various wool wastes or wool residues on soil properties and fertility (Abdallah et al. 2019; Nustorova et al. 2006; Sharma et al. 2019; Zheljzakov 2005). Wool waste significantly affects the biological properties of soil (Lal et al. 2020).  $\beta$ -glucosidase activity, which plays a crucial role in the decomposition of cellulose and the cycling of carbon within the soil, has been shown to increase with sheep wool treatments (Çetin Karaca et al. 2023). The close relationship between  $\beta$ -glucosidase activity and soil organic matter makes  $\beta$ -glucosidase and labile carbon content reliable indicators of soil health and a predictor of changes in organic carbon (Adetunji et al. 2017).

The utilization of organic by-products as potential fertilizers has been shown to enhance nutrient uptake by plants (Ordiales et al. 2016). Consequently, the application of by-products from the wool industry as organic fertilizers in horticulture has recently gained popularity (Abdallah et al. 2019; Górecki and Górecki 2010; Russell and Ireland 2016). One of the main properties of wool material is its biodegradability, providing a potential continuous nutrient supply in soils (Lal et al. 2020). When introduced into the soil, the keratin biopolymer of wool pellets is broken down by microorganisms, releasing essential nutrients for plant growth. Since wool material degrades slowly in soils, it can serve as effective slow-release fertilizer, providing NPK nutrients and other essential elements (i.e. sulfur) for a longer period compared to conventional inorganic fertilizers (Broda et al. 2023; Sharma et al. 2019). In an experiment with hydrolyzed wool, Nustorova et al. (2006) found that the C:N ratio in wool-treated soil increased with higher doses of wool. Additionally, some authors have reported that the addition of wool waste to soil increased  $\text{NO}_3^-$  and  $\text{NH}_4^+$  levels. This phenomenon might be attributed to the high keratin content of wool and the subsequent increase in microbial biomass (Böhme et al. 2012; Broda et al. 2023; Suruchi et al. 2014; Zheljzakov 2005; Zheljzakov et al. 2008).

Wool also contains essential nutrients necessary for plant growth (McNeil et al. 2007), and known to be rich in nutrients typically applied in form of inorganic synthetic N sources (Abdallah et al. 2019; Broda et al. 2023; Sharma et al. 2019). Wool shows a prolonged N release due to gradual decomposition processes (Michel et al. 2008; Nustorova et al. 2006). This characteristic facilitates sustained N-uptake by plants (Broda et al. 2023) and reduces the propensity for N to leach from the soil, ensuring its retention and availability (Bradshaw and Hagen 2022; Broda et al. 2023). Due to its high N content, wool positively affects plant biomass (Abdallah et al. 2019; Böhme et al. 2012). Zheljzakov (2005) reported that the application of wool waste to soil increased the total nitrogen and protein

content of plant tissues. Similarly, Nustorova et al. (2006) demonstrated that treatments with wool increased the biomass and macroelement content of rye. Górecki and Górecki (2010) observed that the  $\text{NO}_3^-$  content of tomato leaves decreased after treatment with wool hydrolysate, while P, Mg, Ca content increased. Research by Zheljzakov et al. (2009) demonstrated that wool facilitated the growth and development of calendula and basil, providing plants with significantly higher amounts of nitrogen, phosphorus, and potassium. However, the uptake of micronutrients and other soil properties, such as soil organic carbon and pH, were not affected by the application of wool (Smk 2014). In addition to providing a significant source of nutrients for plants, wool pellets also affect yield. Górecki and Górecki (2010), in a study with tomato, eggplant, and pepper observed that substrate amendment with wool significantly increased the yield, leading to higher plant height, increased fresh weight and greener leaves. It was also reported that adding clay soil to the basic peat substrate reduced the yield of tomato plants, but enriching this substrate with sheep wool increased the yield by 29% compared to the control substrate. Peppers showed a 30% increase in yield when wool was incorporated into the substrate. Given these considerations, we hypothesized that in sandy soils, known for their rapid nitrification and nitrate-leaching processes, the N-uptake efficiency of horticultural crops might be enhanced by employing wool pellets as an organic alternative. Since N can have a substantial impact on the physiological parameters of plants, a thorough analysis of these observations was deemed necessary to better understand the dynamics of plant N-uptake. However, the literature still lacks comprehensive references on the N-supply capacity of wool and its impact on soil biological activity, particularly in relation to key soil organic matter contents.

The objectives of this study were:

1. To investigate the mineralization intensity of wool pellets in two soils differing in biological activity and organic matter content (low and high SOM), and
2. To examine the effect of wool pellets on nitrogen uptake, photosynthetic pigment levels, gas exchange, and growth parameters of pepper plants in both soils

We hypothesized that the nutrient release from wool pellets and their effects on plant physiological responses would be strongly influenced by soil type, with enhanced effects under high SOM due to greater biological activity and water retention capacity. These findings are expected to contribute to the development of sustainable horticultural practices by utilizing an organic waste product to partially replace synthetic fertilizers.

## Materials and methods

### Experimental design and treatments

The pot experiment on sweet peppers (*Capsicum annuum* L.) ‘Amy F1’ variety was set up in a randomized block design with four replicate treatments (4 pots/treatment) on 24 plants. This pilot setup ensured statistical validity while allowing precise control over environmental conditions based on previous studies (Ferreira et al. 2018; Gong et al. 2005; Kovács et al. 2024). Seedlings were pre-grown in a light chamber for 8 weeks and were subsequently

**Table 1** Physical and chemical parameters of the two different sandy soils in the pot experiment

Soil characteristics	Soil organic matter (0.58%)	Soil organic matter (1.84%)
Soil texture	Sandy	Sandy loam
pH (KCl)	7.91	7.4
Total water-soluble salts (m/m%)	<0.02	<0.02
CaCO <sub>3</sub> (m/m%)	1.3	1.2
Soil organic matter (m/m%)	0.58	1.84
Nitrit + Nitrate–N (KCl, mg/kg)	<2.0	9.7
Available P <sub>2</sub> O <sub>5</sub> (mg/kg)	240.9	157.0
Available K <sub>2</sub> O (mg/kg)	74.0	98.4

transplanted into the greenhouse (0 DAT). One seedling was placed in each pot (1 l). Each pot was filled with 0.6 kg of dry soil, ensuring a uniform initial soil condition. The amount of dry soil per pot was determined based on the bulk density of the soil and the volume of the pot, using the equation: Dry soil mass (kg) = Pot volume (l) × Soil bulk density (kg/l). In this experiment, the bulk density of the soil was approximately 0.6 kg/l, resulting in 0.6 kg of dry soil per 1 l pot.

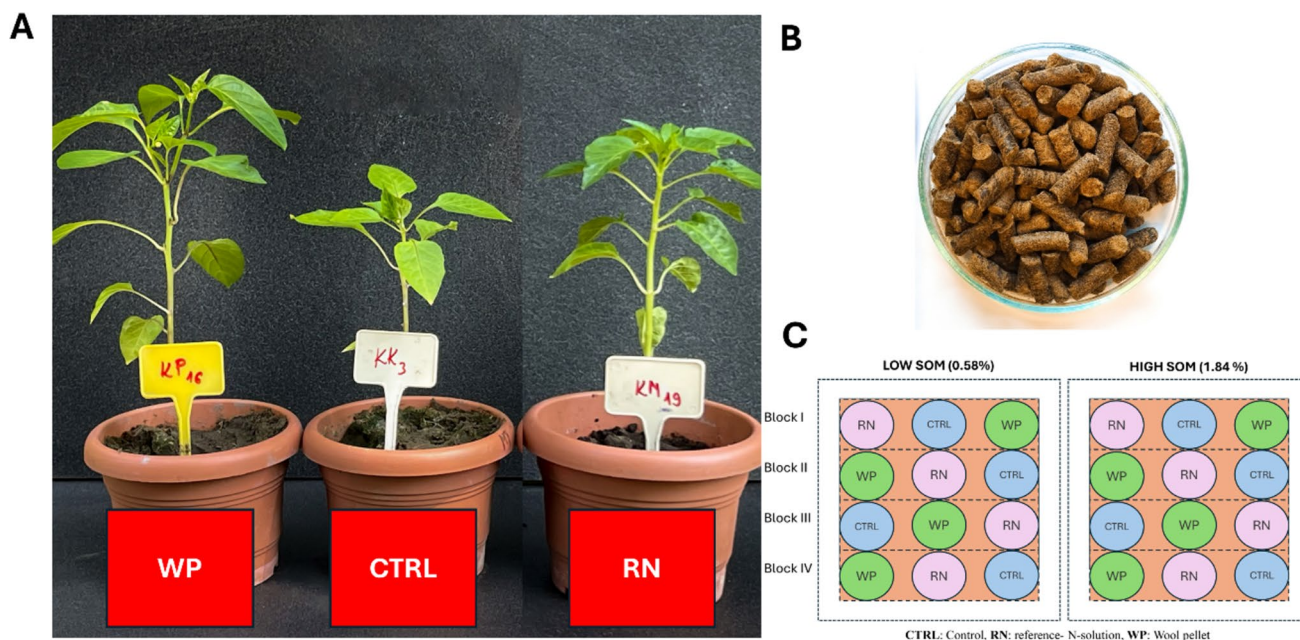
The pot experiment was carried out in two soil types, both characterized by a sandy texture: one with low (SOM 0.58%) and one with high (SOM 1.84%) soil organic matter content. The main differences in soil parameters are presented in Table 1. The nutrient requirements of this pepper variety are as follows: it removes 2.5 kg of N, 0.9 kg of P<sub>2</sub>O<sub>5</sub>, and 3.4 kg of K<sub>2</sub>O per hectare from the soil (Szuvandzsiev 2017).

Three treatments were used in the experiment, which were: 1) no amendment (control, CTRL); 2) reference N-solution (RN): synthetic N fertilizer solution without wool pellets; 3) wool pellets (WP) mixed into the soil.

Figure 1A shows the growth of pepper plants under three treatments—WP (wool Pellet), CTRL (control), and RN (reference N-solution)—on low SOM soil.

Figure 1B illustrates the wool pellets used in the experiment, which were mixed into the soil as a treatment for the pepper plants.

Figure 1C illustrates the experimental layout, showing the arrangement of treatments (WP, CTRL, RN) across two



**Fig. 1** Demonstration of a greenhouse experiment using pepper as a model plant. **A** Experimental pots and test plants in case of low SOM, **B** wool pellets, **C** experimental design on two soils with differ-

ent organic matter contents CTRL: control, RN: reference inorganic N-solution, WP: wool pellets

soil types with different organic matter content (low SOM and high SOM).

Wool pellets were applied according to the method described by Böhme et al. (2012). A total of 4 g of wool pellet were added per liter of soil, amounting to 407 mg of N per pot. Wool pellets (Agrologica Ltd., Hungary) rich in ammonium and organic N (keratin N: 11.2 m/m%; ammonium N: 592 mg kg<sup>-1</sup>; nitrate N: 25 mg kg<sup>-1</sup>). Wool pellets are produced from unwashed sheep wool, which is dried using sunlight until its moisture content reaches 15%, then chopped into 4–6 mm pieces, and pelletized at a temperature of 110 °C under high pressure. This process ensures that pathogenic microorganisms remain below acceptable threshold. The resulting pellets are brown, have a distinctive odor, and range in length from 10 to 20 mm and are 5 mm in diameter. These pellets are highly hygroscopic, capable of absorbing water up to three times their weight. Their physicochemical characteristics include 82% dry matter content, 75% organic matter content, a minimum of 0.1% total phosphorus (P) content, and at least 4.1% total potassium (K) content. To prevent other nutrient deficiencies, all plants were treated weekly with 20 ml per pot of a special nutrient solution similar to the Hoagland solution (see Supplementary Table S1), with all nutrients except N being available in equal amounts. K<sub>2</sub>SO<sub>4</sub> was added to the solution instead of KNO<sub>3</sub>, allowing us to monitor the rate of N mineralization of the wool pellets while avoiding other nutrient deficiencies. The untreated control plants were not provided with N but received the nutrient solution weekly. A reference N-solution treatment was set up alongside the wool pellets to monitor N-uptake. These plants received weekly 20 ml per pot nutrient solution containing N in addition to other elements. In total, 9.8 mg N were applied per plant (1.4 mg N/week/plant) with the reference N nutrient solution during the growing season. For all three treatments, the nutrient solution was started 2 days after transplanting (2 DAT). The pots were placed in a controlled environment greenhouse at 22 ± 3 °C in ambient sunlight. Irrigation and nutrient application were managed by a micro-irrigation system from a tank in the greenhouse using an electric pump. After planting, watering occurred on average 1–2 times a day during the initial root growth period and later twice a week. From the development of the first fruits, irrigation occurred on average 2–3 times a day, using an average of 150–200 ml of water per plant. Watering was carefully controlled to prevent any water loss, ensuring that no drainage occurred from the pots according to Kovács et al. (2024).

### Soil sampling and analysis

After conclusion of the experiment (70 DAT), soil samples were collected from the pots to assess soil biological activity. Freshly obtained soil samples were preserved at +4 °C

(Cao et al. 2021) and subsequently utilized for enzyme activity assays.

The fluorescein diacetate enzyme (FDA) assay was used to estimate overall microbial activity in the soil. The total catabolic enzyme activity of soil microorganisms was measured using (FDA) assay (Biró et al. 2012) in four replicates per pot. The FDA assay was conducted according to the specific laboratory conditions described by Villányi et al. (2006). 0.5 g of sieved soil was incubated with the buffered substrate in reaction flasks for 1 h at 37 °C, under continuous stirring. The enzymatic reaction was halted by adding acetone, and the concentration of fluorescein was measured by absorbance at 490 nm to determine the total catabolic enzyme activity of soil microorganisms.

β-glucosidase activity was measured to assess the microbial capacity to decompose cellulose. The β-glucosidase activity was determined using the method presented by Sinsabaugh et al. (1999). The measurements were carried out following the protocol described by Kotroczó et al. (2014).

Soil permanganate-oxidizable carbon (POXC) was measured as an indicator of labile carbon available to soil microbes. POXC was measured according to the method described by Weil et al. (2003). The method was carried out by shaking 1 g of air-dried soil in 10 ml 0.02 M KMnO<sub>4</sub> + 0.1 M CaCl<sub>2</sub> solution for 2 min. 0.2 ml of the supernatant was carefully poured into a 15-ml tube and mixed with 10 ml distilled water. The absorbance of the sample was measured at 565 nm wavelength. To determine the sample KMnO<sub>4</sub> concentration, the sample absorbance was compared with a standard curve that ranged from 0.005 to 0.02 mol l<sup>-1</sup> KMnO<sub>4</sub>. Sample POXC was calculated as follows:

$$\text{POXC (mg kg}^{-1}\text{)} = (0.02 - \text{KMnO}_4 \text{ mol L}^{-1}) \times 9000 \text{ mg C mol}^{-1} \times 10$$

To determine mineral nitrogen concentration in soil, a 1:5 of soil and 0.1 M CaCl<sub>2</sub> suspension was prepared and shaken for 60 min. For determining the NO<sub>3</sub><sup>-</sup> concentration, 5 ml of the filtered soil extract was mixed with 1 ml of C<sub>7</sub>H<sub>5</sub>NaO<sub>3</sub> and evaporated. The precipitate was dissolved in 1 ml of cc H<sub>2</sub>SO<sub>4</sub>. Then, 25 ml of distilled water was poured into a beaker, and 5 ml of 10 M NaOH was added, followed by the addition of the dissolved substrate. The volume was then made up to 50 ml with distilled water. NO<sub>3</sub><sup>-</sup> concentration was measured from the substrate using a spectrophotometer at 410 nm according to Monteiro et al. (2003). For determining NH<sub>4</sub><sup>+</sup> concentration, 10 ml of soil extract was mixed with 1 ml of oxidizing reagent (NaOH + dichlorocyanuric acid sodium salt) and 1 ml of salicylate reagent (Na-salicylate + trisodium citrate + sodium nitroprusside). The concentration was measured from the substrate using a spectrophotometer at 655 nm wavelength.

## Determination of plant growth characteristics, photosynthetic parameters, and nitrogen content

To assess plant growth and development, shoot and root biomass were also measured at the end of the growing season. Fresh biomass was measured immediately after harvesting, while dry biomass was obtained after drying the samples at 70 °C for 48 h. At the end of the growing season, the harvested part was measured.

Leaf  $\text{NO}_3^-$  and total N content were measured at the end of vegetation (70 DAT). Leaf  $\text{NO}_3^-$  content was determined using the salicylic acid–sulphuric acid method according to Hesari et al. (2023). The total N content of pepper leaves was measured according to the Kjeldahl method (Nelson and Sommers 1980). The total biomass N content was determined by multiplying the total N content of the pepper leaves by the amount of dry biomass. The photosynthetic N-use efficiency (PNUE) was calculated as the photosynthetic rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) per total N-uptake by the plants (mg) according to Li et al. (2024)

The chlorophyll content index (CCI) of leaves was monitored using an Apogee MC-100 (Apogee Instruments, Inc., Logan, UT, USA). The MC-100 provides an estimate of the actual chlorophyll concentration in units of  $\mu\text{mol per cm}^2$  of leaf area (Padilla et al. 2018). Chlorophyll content is closely associated with photosynthetic capacity and N status in leaves and thus serves as a non-destructive physiological indicator of plant health, N-use efficiency, and overall vigor. Therefore, monitoring CCI allows for the evaluation of how different treatments influence photosynthetic potential over time. Measurements with the chlorophyll meter began at 22 DAT. The chlorophyll content of leaves was measured weekly, for a total of 7 times until the end of the experiment (from 22 to 62 DAT). Measurements were performed in the morning hours, between 9:00 and 11:00 AM, in four replicates, on two soil types.

Laboratory chlorophyll measurements were taken at the end of the experiment (70 DAT) on the same pepper leaves where MC-100 measurements were monitored. Leaf tissue (0.1 g fresh weight) was ground in 3 ml of 80% acetone with the addition of 0.15 g of sodium carbonate using a pre-cooled mortar and pestle. The homogenized samples were transferred into polyethylene conical tubes, and the final volume was adjusted to 10 ml with 80% acetone. The slurry was centrifuged at 97 g for 5 min at 4 °C. The purified solution was poured into cuvettes, and the optical density was measured at wavelengths of 663 nm, 644 nm, and 480 nm against a blank (80% acetone) using a spectrophotometer. Chlorophyll “a” and “b” levels and carotenoid content were calculated according to the method of Arnon, (1949) (mg pigment/g fresh weight):

$$\text{Chla } 12.7 \times A_{663} - 2.69 \times A_{644},$$

$$\text{Chlb } 22.9 \times A_{644} - 4.68 \times A_{663},$$

$$\text{Cc } 5.01 \times A_{480},$$

where Chla and Chlb are chlorophyll a and b, Cc is the carotenoid content and A is the absorbance value.

All chlorophyll measurements (CCI and laboratory-based) were performed on fully developed, mature leaves located on the third or fourth node from the top of each pepper plant.

Photosynthesis, transpiration rate, and stomatal conductance were evaluated using a TARGAS-1 Portable Photosynthesis System (PP Systems, Amesbury, MA, USA) equipped with an infrared gas analyser and a PLC5 Leaf Cuvette (4.5  $\text{cm}^2$ ). Measurements were performed according to the method of González et al. (2023) Measurements were taken at the end of the experiment (70 DAT) on four plants per treatment, on the second youngest leaf between 11:00 and 12:00 (Li et al. 2013a).

Chlorophyll fluorescence was measured with a FluorPen FP 110-LM/D measuring system (Photon Systems Instruments). Pepper plants were dark-adapted for 30 min to record the minimal (Fo) and maximal (Fm) fluorescence. The maximum quantum yield of PSII (Fv/Fm) and thylakoid membrane damage (Fo/Fm) were calculated as follows:  $Fv/Fm = (Fm - Fo) / Fm$ , and  $Fo/Fm$ , respectively, according to Li et al. (2024).

## Statistical methods

The statistical evaluation of the research results was conducted using R version 4.2 (RStudio 2011). The effects of three treatments (control, reference N-solution, wool pellets), two soil types (SOM 0.58% and SOM 1.84%), and their interaction on soil and plant parameters were assessed using the general linear model (GLM, MANOVA). The efficacy of treatments was evaluated based on Wilks'  $\lambda$ . The homogeneity (homoskedasticity) of the covariance matrix was examined using Box's test. The normality of the GLM model's residuals was confirmed by the Shapiro–Wilk test for all dependent variables. The post hoc test was selected based on Levene's test for homogeneity of variances. Statistical analyses were conducted at a 95% significance level. Statistical analyses were performed using the packages 'lm' (Elzhov et al. 2016), 'ggcorrplot' (Kassambara and Kassambara 2019), 'stats', and 'lattice'. Additionally, visual representations were generated with the 'ggplot2' package. The values presented above the graphs denote the average mean + standard deviation (SD). As an indicator of the GLM effect size, the partial eta squared ( $\eta^2$ ) value is also shown. The relationship between plant physiological parameters on both soil types was tested using Pearson's correlation.

## Results

### The effects of wool pellets on soil biological activity, soil nitrogen, and carbon content

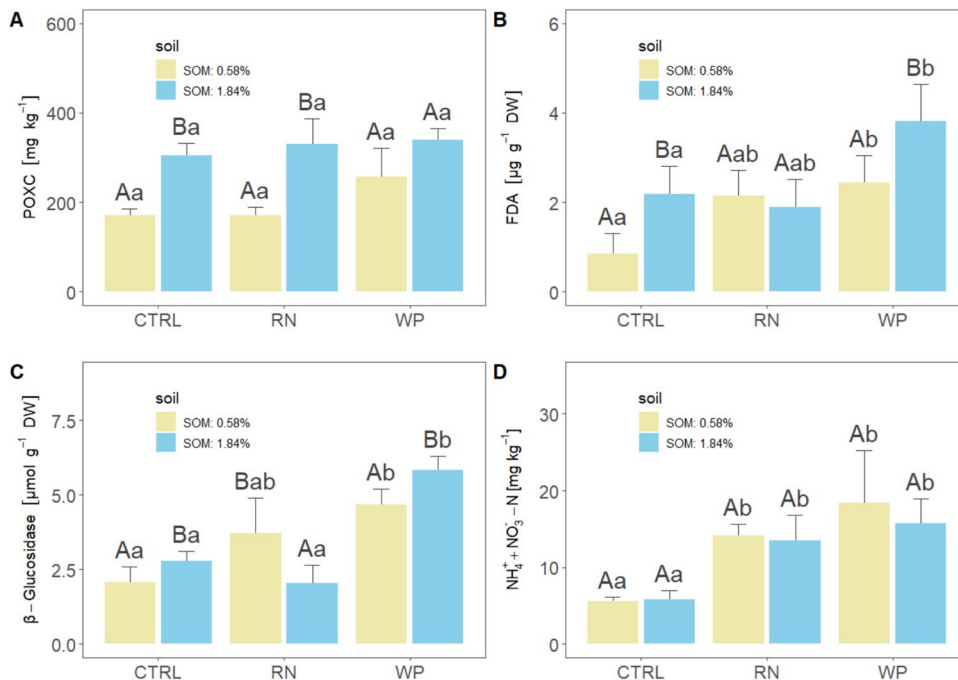
There was no significant effect of treatments on POXC levels, neither for low ( $F_{(2,12)} = 1.40$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.26$ ) nor for high SOM ( $F_{(2,12)} = 0.27$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.04$ ). In the GLM model, the effect of soil, treatment, and soil interaction was included as a factor. Soil alone had a significant effect on POXC ( $F_{(1,18)} = 10.78$ ;  $p < 0.01$ ; partial  $\eta^2 = 0.37$ ), while soil and treatment interaction had no significant effect ( $F_{(2,18)} = 0.49$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.05$ ). Both the CTRL and RN treatments showed higher values in the higher SOM and were significantly different from the low SOM ( $p < 0.05$ ). For wool pellet, no significant difference was detected between the two soils ( $p > 0.05$ ). Tukey's post hoc test showed no significant difference between the treatments ( $p > 0.05$ ). In the case of low SOM, WP treatment had the highest POXC level, followed by the RN and the untreated CTRL. For this soil type, the WP treatment increased POXC levels by 50% compared to CTRL. In case of high SOM, the lowest POXC level was observed for the untreated CTRL, followed by the RN and WP treatments (Fig. 2A).

FDA hydrolysis showed statistically significant differences between treatments for both low ( $F_{(2,27)} = 4.15$ ;  $p < 0.05$ ; partial  $\eta^2 = 0.23$ ) and high SOM ( $F_{(2,27)} = 6.27$ ;  $p < 0.05$ ; partial  $\eta^2 = 0.30$ ) (Fig. 2B). A higher partial  $\eta^2$  was observed for the higher SOM, indicating that

treatments had a stronger effect on FDA activity in this soil type. The untreated CTRL showed the lowest FDA activity in the condition of low SOM, followed by the RN and WP treatments. Higher SOM also had significantly higher FDA on average than low SOM. For this soil type, no significant difference was detected between the CTRL and the RN ( $p > 0.05$ ). However, the WP treatment alone also showed higher FDA values compared to the other treatments and was also significantly different from the untreated CTRL ( $p < 0.05$ ). Furthermore, the effect of two factors, soil, treatments and their interaction on FDA enzyme activity was also investigated using a GLM model. The main effect of soil was not statistically significant ( $F_{(1,56)} = 2.27$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.03$ ). However, there was a significant soil and treatment interaction ( $F_{(2,56)} = 2.51$ ;  $p < 0.05$ ; partial  $\eta^2 = 0.08$ ), indicating that the effect of soil on FDA activity depended on the type of treatment. As shown in Fig. 2B, significant differences between the two soil types were observed within the CTRL and WP treatments ( $p < 0.05$ ), supporting the interaction effect.

Treatments significantly affected  $\beta$ -glucosidase activity both at low SOM ( $F_{(2,36)} = 8.10$ ;  $p < 0.01$ ; partial  $\eta^2 = 0.31$ ) and high SOM ( $F_{(2,36)} = 0.042$ ;  $p < 0.001$ ; partial  $\eta^2 = 0.54$ ) (Fig. 2C). A higher partial  $\eta^2$  was obtained for higher SOM, suggesting that treatments had a stronger effect on the enzyme in this soil type. The CTRL treatment exhibited the lowest  $\beta$ -glucosidase activity at low SOM, with the RN and WP treatments following suit. The WP had the highest  $\beta$ -glucosidase activity at the higher SOM, with the CTRL and RN following closely behind. The WP treatment showed the maximum enzyme activity for both types of soil. In the

**Fig. 2** Effect of treatments on **A** permanganate-oxidizable organic carbon content (POXC), **B** fluorescein diacetate (FDA) activity, **C**  $\beta$ -glucosidase activity, and the **D** mineral nitrogen content ( $\text{NH}_4^+ + \text{NO}_3^- - \text{N}$ ) in the soils. CTRL: control, RN: reference N-solution, WP: wool pellets. Different letters indicate significantly different groups. Capital letters indicate significant differences between soils (SOM: 0.58%; SOM: 1.84%) under the same treatment. Lowercase letters indicate comparisons of treatments with fixed soil organic matter content (Games–Howell post hoc test,  $p < 0.05$ )



GLM model, soil had no significant effect on  $\beta$ -glucosidase activity ( $F_{(1,66)} = 0.042$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.001$ ). However, interaction between soil and treatment had a significant effect on  $\beta$ -glucosidase activity ( $F_{(2,66)} = 6.39$ ;  $p < 0.01$ ; partial  $\eta^2 = 0.162$ ). Significant differences are shown in Fig. 2C.

In the case of low SOM, the lowest  $\text{NH}_4^+ + \text{NO}_3^- - \text{N}$  content was detected in the CTRL, followed by the RN and the WP treatments (Fig. 2D). A similar trend was observed for higher SOM. The highest  $\text{NH}_4^+ + \text{NO}_3^- - \text{N}$  content was found in the WP, followed by the RN treatments with the lowest detected in the CTRL. In addition to soil N content, the soil mineralization was also determined as the total N-uptake by plants minus the initial mineral  $\text{NO}_3^-$  content of the soils. The N mineralization in the low SOM soil was 22.41 mg/pot, while in the high SOM soil it was 13.95 mg/pot. This indicates a higher mineralization rate in the low SOM soil compared to the high SOM soil.

The research analysis also focused on how the treatments affected the five soil variables, based on partial  $\eta^2$  values in two different SOM soils. For the low SOM soil, treatments affected the soil  $\text{NH}_4^+ + \text{NO}_3^- - \text{N}$  content the most while the lowest partial  $\eta^2$  value was observed for POXC (Fig. 2A). In the case of the higher SOM soil,  $\text{NH}_4^+ + \text{NO}_3^- - \text{N}$   $\eta^2$  was the highest, and POXC had the lowest value. Overall, among the soil characteristics, the highest  $\eta^2$  for both soil types of the treatments was detected for  $\text{NH}_4^+ + \text{NO}_3^- - \text{N}$  content (see supplementary Fig S1).

### The effects of wool pellets on plant growth and physiological parameters

The effect of treatments on plant growth parameters was investigated in both soil types. Treatments had a significant effect on plant growth parameters ( $F_{(12,26)} = 4.60$ ;  $p < 0.001$ ; Wilk's  $\lambda = 0.10$ ; partial  $\eta^2 = 0.68$ ). Furthermore, soil ( $F_{(6,13)} = 4.76$ ;  $p < 0.001$ ; Wilk's  $\lambda = 0.10$ ; partial  $\eta^2 = 0.68$ )

and the interaction between soil and treatment were also significant ( $F_{(12,26)} = 3.68$ ;  $p < 0.001$ ; Wilk's  $\lambda = 0.14$ ; partial  $\eta^2 = 0.62$ ). The partial  $\eta^2$  does not clearly indicate which factor has the strongest effect on plant growth parameters. Significant differences in plant growth intensity are illustrated in Table 2.

The smallest root dry biomass weight was found in untreated control plants, significantly differing from the WP treatment ( $p < 0.05$ ) in the low SOM soil. However, less root growth was detected in the higher SOM across treatments. Mean root weight was also lower for this soil type in the RN and WP treatments, whereas no significant difference was observed in the CTRL. Shoot dry biomass, the WP treatment was significantly different from CTRL plants and the RN treatment for low SOM ( $p < 0.05$ ). Similarly, in the high SOM soil, the shoot biomass dry weight in the WP treatment was the highest, significantly differing from both the RN and the CTRL plants ( $p < 0.05$ ). Comparing the two soils, the biomass weight was higher for the low SOM, but the WP treatment showed the highest biomass for both soil types. At the same time, the biomass weight of wool pellets-treated plants was 1.78 times greater for low SOM than for high SOM. Differences in fruit production were also observed: soils with high SOM content resulted in higher average fruit numbers compared to soils with low SOM. Regardless of soil type, plants treated with wool pellets exhibited the highest fruit yields. For both soil types, plants treated with wool pellets showed the highest yields. In the high SOM soil, the fruit production of WP-treated plants was approximately twice as high as in the low SOM soil.

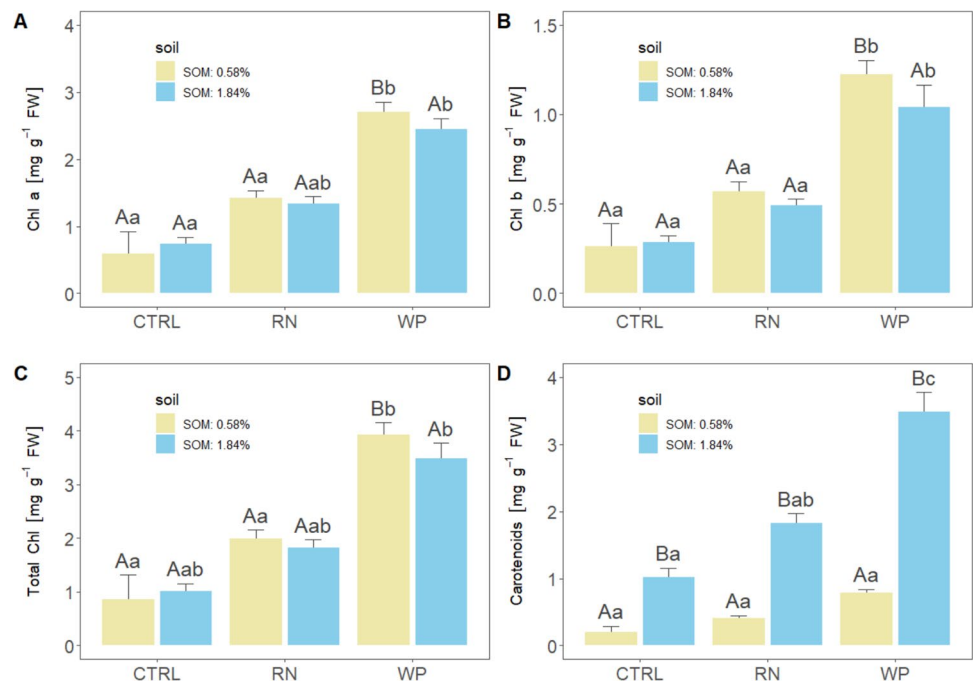
The treatments had a significant effect on the pigment content of pepper plants in both soils (Fig. 3). In the low SOM soil, treatments showed a smaller multivariate effect on photosynthetic pigments ( $F_{(10,10)} = 3.20$ ;  $p < 0.05$ ; Wilk's  $\lambda = 0.05$ ; partial  $\eta^2 = 0.76$ ) compared to the high SOM soil ( $F_{(10,10)} = 3.20$ ;  $p < 0.01$ ; Wilk's  $\lambda = 0.02$ ; partial  $\eta^2 = 0.85$ ).

**Table 2** Effect of treatments on plant growth parameters depending on different soil characteristics: Soil with low organic matter content (SOM: 0.58%) and soil with higher organic matter content (SOM: 1.84%)

Parameters	Treatment	Mean $\pm$ SD	
		SOM: 0.58%	SOM: 1.84%
Root dry biomass (g)	Control	0.77 $\pm$ 0.10 A <sup>a</sup>	0.94 $\pm$ 0.14 A <sup>ab</sup>
	Reference N-solution	1.53 $\pm$ 0.25 A <sup>ab</sup>	0.90 $\pm$ 0.15 B <sup>ab</sup>
	Wool pellets	2.44 $\pm$ 0.91 A <sup>b</sup>	1.81 $\pm$ 0.12 A <sup>b</sup>
Shoot dry biomass (g)	Control	1.21 $\pm$ 0.37 A <sup>a</sup>	0.83 $\pm$ 0.13 B <sup>a</sup>
	Reference N-solution	3.42 $\pm$ 1.41 A <sup>a</sup>	1.15 $\pm$ 0.11 B <sup>a</sup>
	Wool pellets	3.76 $\pm$ 1.40 A <sup>b</sup>	1.98 $\pm$ 0.18 A <sup>b</sup>
Pepper fruit (g)	Control	6.68 $\pm$ 1.03 A <sup>a</sup>	7.86 $\pm$ 1.81 B <sup>a</sup>
	Reference N-solution	9.22 $\pm$ 1.77 A <sup>b</sup>	12.03 $\pm$ 2.40 B <sup>ab</sup>
	Wool pellets	9.99 $\pm$ 2.19 A <sup>c</sup>	2091 $\pm$ 3.92 A <sup>b</sup>

Different letters indicate significantly different groups. Capital letters indicate significant differences between soils (SOM: 0.58%; SOM: 1.84%) under the same treatment. Lowercase letters indicate comparisons of treatments with fixed soil organic matter content (Games–Howell post hoc test,  $p < 0.05$ ,  $p < 0.05$ )

**Fig. 3** Effect of treatments on pigment contents: A) chlorophyll *a* (Chl*a*); B), chlorophyll-*b* (Chl*b*); C) total chlorophyll, D) carotenoids. CTRL: control, RN: reference N-solution, WP: wool pellets. Different letters indicate significantly different groups. Capital letters indicate significant differences between soils (SOM: 0.58%; SOM: 1.84%) under the same treatment. Lowercase letters indicate fixed soil organic matter content (Games–Howell post hoc test,  $p < 0.05$ )



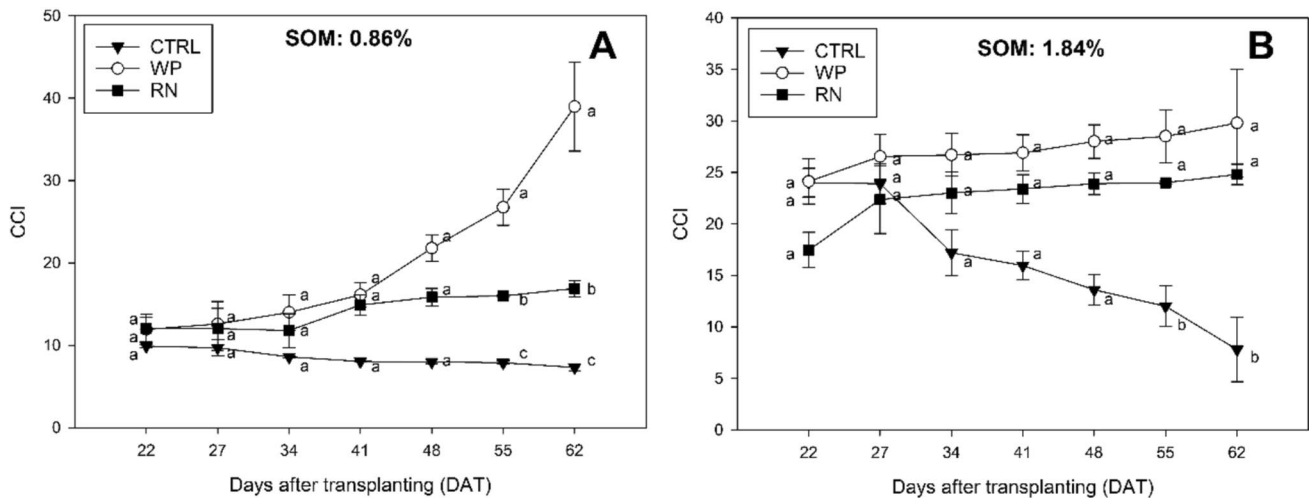
Partial  $\eta^2$  was smaller at low SOM than at high SOM. Overall, the three treatments affected photosynthetic pigment concentration more strongly for high SOM. While the overall MANOVA statistics suggest a stronger effect in the high SOM soil, this was mainly due to carotenoids, which increased significantly only in that soil. In contrast, chlorophyll *a*, *b*, and total chlorophyll contents showed greater relative increases in the low SOM soil, where CTRL values were lower and the WP treatment had a more pronounced impact.

Furthermore, we investigated the effect of soil and the interaction between soil and treatment on photosynthetic pigment concentration. Soil type alone did not significantly affect photosynthetic pigment content of pepper plants ( $F_{(5,14)} = 3.20$ ;  $p > 0.05$ ; Wilk's  $\lambda = 0.65$ ; partial  $\eta^2 = 0.34$ ) and the interaction between soil and treatment was not significant either ( $F_{(10,28)} = 0.10$ ;  $p > 0.05$ ; Wilk's  $\lambda = 0.73$ ; partial  $\eta^2 = 0.11$ ). It is clear that the three treatments had the highest partial  $\eta^2$  values and the most significant effect on the degree of pigment concentration. The detailed significant differences between treatments are illustrated in Fig. 3.

The lowest levels of chl*a* and chl*b* and total chlorophyll content were found in the CTRL plants in both soil types, while the highest chlorophyll content was found in the WP treatment, followed by the RN. The only significant difference between the two soils was for the wool pellet ( $p < 0.05$ ). For carotenoid content at low SOM, no significant difference was detected between treatments ( $p > 0.05$ ). However, at high SOM, the highest carotenoid concentration was detected in the WP, which was significantly different from the other treatments ( $p < 0.05$ ). In all three treatments, higher carotenoid content was detected in the high SOM soil.

During the vegetation period, the CCI dynamics of all three treatments were evaluated at a total of seven times, from which the relative chlorophyll content of the plants was inferred. A different trend was observed for the two soil types, especially for the WP treatment (Fig. 4). Comparing the WP treatments, similar increasing CCI values were observed in the growth dynamics of the two soil types, but the growth rates were different. In the case of low SOM, the CCI of the plants was much higher and showed an increasing trend over time.

In the case of low SOM, the CCI of untreated CTRL plants decreased progressively over time (Fig. 4A). The CCI of CTRL plants had the highest value ( $9.9 \pm 2.14$  CCI) at the first measurement time (22 DAT) and the lowest value ( $7.32 \pm 4.39$  CCI) at the last measurement time (62 DAT). The CCI value of CTRL plants was significantly different ( $p < 0.01$ ) compared to the RN and WP treatments at 55 DAT and 62 DAT measurement time. The lowest CCI value ( $12.02 \pm 1.72$ ) of the RN plants was at 22 DAT, which was not significantly different from the CTRL and WP-treated plants ( $p > 0.01$ ), and the highest value ( $16.9 \pm 0.98$ ) was at 62 DAT. The initial CCI value of WP pepper plants ( $11.92 \pm 1.47$ ) was not significantly different from CTRL and RN plants ( $p > 0.05$ ). However, CCI value of WP plants showed a pronounced increasing trend after transplanting. The CCI of WP plants at 55 DAT and 62 DAT was significantly ( $p < 0.01$ ) different from both RN and CTRL plants. The highest value ( $38.97 \pm 5.38$ ) was detected for low SOM at the last measurement time. Overall, the highest CCI value for low SOM was found in the WP plants, showing a continuous increasing trend over time.



**Fig. 4** Temporal trends of chlorophyll content index (CCI) measurements under the three treatments. A) soil with low organic matter content (SOM: 0.58%), B) soil with higher organic matter content

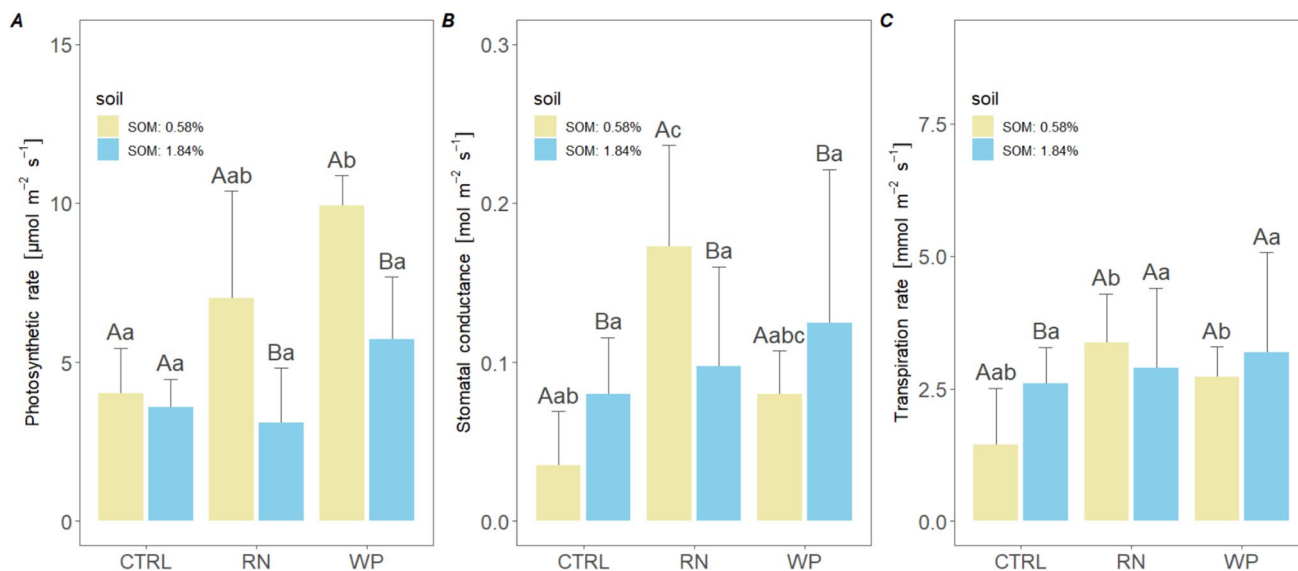
(SOM: 1.84%). Values are shown as means  $\pm$  SD. Statistical significance was determined using Games–Howell post hoc test ( $p < 0.05$ )

In the case of high SOM, the CCI value of untreated control plants decreased sharply with time compared to the WP treatment (Fig. 4B). The CCI value of CTRL plants had the highest value ( $24.00 \pm 1.38$ ) at the first measurement time (22 DAT), while the lowest value ( $7.8 \pm 3.13$ ) was at the last measurement time (62 DAT). The CCI value of CTRL plants at 55 DAT and the last 62 DAT measurement time was significantly different ( $p < 0.01$ ) from the RN and WP treatments, similar to the previous soil variety. The CCI of plants treated with the reference N-solution showed a similar trend as the previous soil: no significant difference ( $p < 0.01$ ) was detected in the initial values between treatments, then over time, continuous N-solution increased the CCI value, while no significant difference was detected from the WP at any time ( $p > 0.01$ ).

When comparing the WP treatments, both soils showed a similar increasing trend in CCI values, but the plant growth dynamics differed depending on soil type. CCI growth of WP-treated peppers was fourfold higher for low SOM than for high SOM conditions. At low SOM, the CCI of the plants was much higher and showed an increasing trend over time. Similarly, an increasing trend was observed in the case of higher SOM, but the trend was less steep than that for low SOM. Statistically significant differences were observed between the two soil types across all measured time intervals. The growth rate in low SOM soil significantly increased after 41–48 days, while in high SOM soil, the growth rate remains relatively low and stable throughout the period.

The effects of different treatments on the gas exchange intensity of pepper plants under different soil organic matter conditions were examined. The gas exchange intensity of pepper plants was significantly influenced by treatments

in both low and high SOM conditions (Fig. 5). In the case of low SOM, treatments had a considerable impact on gas exchange intensity ( $F_{(6,14)} = 3.20$ ;  $p < 0.001$ ; Wilk's  $\lambda = 0.02$ ; partial  $\eta^2 = 0.83$ ). Similarly, treatments also significantly affected gas exchange intensity at higher SOM ( $F_{(6,14)} = 3.20$ ;  $p < 0.05$ ; Wilk's  $\lambda = 0.2$ ; partial  $\eta^2 = 0.50$ ). The partial  $\eta^2$  value suggests that gas exchange intensity was more strongly affected by treatments at low SOM. In the case of low SOM, the effect of the three treatments on gas exchange intensity was 66% greater than in the case of high SOM. Moreover, soil type as a factor alone significantly affected gas exchange intensity parameters ( $F_{(3,16)} = 3.20$ ;  $p < 0.001$ ; Wilk's  $\lambda = 0.45$ ; partial  $\eta^2 = 0.54$ ), and the soil and treatment interaction effect was also found to be significant ( $F_{(6,32)} = 3.20$ ;  $p < 0.001$ ; Wilk's  $\lambda = 0.20$ ; partial  $\eta^2 = 0.54$ ). The effects of the treatments on the parameters of gas exchange intensity are shown in Fig. 5. At low SOM, CTRL plants had the lowest photosynthetic rate, which was significantly different from the WP treatment ( $p < 0.05$ ). No significant difference was detected between the WP and the RN treatments ( $p > 0.05$ ). The increase in photosynthetic rate achieved by the WP treatment was 2.46 times that of the CTRL plants. At the higher SOM, neither treatment had a significant effect on photosynthetic rate ( $p > 0.05$ ). However, the highest photosynthetic rate was again found for the wool pellets. In both the RN and WP treatments, the low SOM soil showed significantly higher net photosynthetic activity compared to the higher SOM soil ( $p < 0.05$ ). Here, the increase in photosynthetic intensity achieved by the WP treatment is 1.58 times the value of the CTRL plants (Fig. 5A). Similarly, for low SOM, the untreated control plants had the lowest stomatal conductance, followed by the WP and the RN treatments. For the higher SOM, the highest stomatal conductance was



**Fig. 5** Effect of treatments on gas exchange parameters in two types of soil: A) photosynthetic rate, B) stomatal conductance, C) transpiration rate. CTRL: control, RN: reference N-solution, WP: wool pellets. Different letters indicate significantly different groups. Capital letters

indicate significant differences between soils (SOM: 0.58%; SOM: 1.84%) under the same treatment. Lowercase letters indicate comparisons of treatments with fixed soil organic matter content (Games–Howell post hoc test,  $p < 0.05$ )

observed for the WP plants, while the lowest was observed for the untreated CTRL plants (Fig. 5B). The highest transpiration rate was detected for the RN and WP treatments, while the lowest was detected for the CTRL pepper plants. The transpiration rate of the reference N-solution and the WP treatment was nearly identical for both soil types. The difference between the RN and WP treatments in terms of transpiration rate was 23.88% in the low SOM soil. In contrast, in the higher SOM soil, the effect of the WP treatment was 10.30% greater than that of the RN treatment (Fig. 5C). The  $F_v/F_m$  ratio was lower in the CTRL treatment in the low SOM soil, but higher in the high SOM soil. WP and RN treatments did not show significant differences between the two soil types ( $p < 0.05$ ). The  $F_o/F_m$  ratio was higher in the low SOM soil in the CTRL treatment, while WP and RN treatments significantly ( $p < 0.05$ ) reduced the damage in both soil types (see supplementary Fig S2).

The plant physiological parameters responded differently to the treatments. In the case of low SOM soil, transpiration rate, stomatal conductance, photosynthetic rate, shoot and root biomass exhibited higher  $\eta^2$  values compared to the high SOM soil, indicating the strongest effect of treatments on these parameters (see supplementary Fig S3).

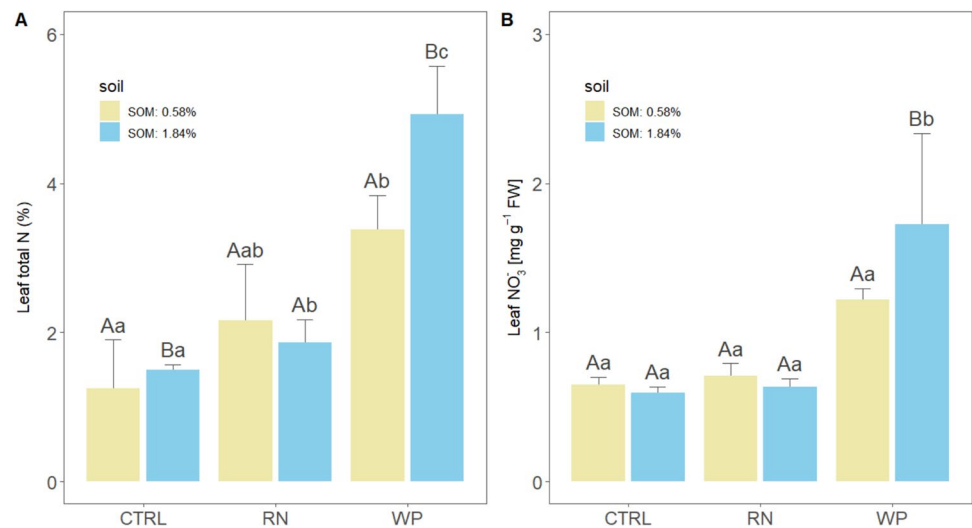
### The effects of wool pellets on nitrogen use efficiency of pepper plants

At the end of the growth experiment (70 DAT), the total-N and  $\text{NO}_3^-$  concentrations of pepper leaves were examined. The treatments had a significant effect on the total-N

content of the leaves, both for low ( $F_{(2,12)} = 4.44$ ;  $p < 0.05$ ; partial  $\eta^2 = 0.49$ ) and high SOM ( $F_{(2,12)} = 20.58$ ;  $p < 0.001$ ; partial  $\eta^2 = 0.82$ ) (Fig. 6A). Higher partial  $\eta^2$  values were observed in the case of higher SOM, indicating that treatments had a stronger effect on the total N content of pepper leaves in this soil type. In the GLM model, the effect of two factors, soil and the interaction between treatments and soil on total N content was also investigated. Soil as a single factor had no significant effect on the total N content of pepper plants ( $F_{(1,18)} = 1.73$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.08$ ), and the interaction between soil and treatment was not significant ( $F_{(2,18)} = 19.78$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.18$ ). Thus, treatments within soil types resulted in significant differences in total N content of leaves. The higher SOM also had significantly higher N values on average than the low SOM. The lowest total N content was observed in CTRL plants ( $1.25 \pm 0.01$ ), followed by the RN treatment ( $2.15 \pm 1.49$ ) and WP ( $3.38 \pm 0.92$ ). A similar trend was also observed for low SOM. The lowest N content in pepper leaves was observed for the CTRL ( $1.49 \pm 0.13$ ), followed by the RN ( $1.86 \pm 0.62$ ) and the highest N content was observed for the WP treatments ( $4.93 \pm 1.29$ ).

Treatments had different effects on  $\text{NO}_3^-$  concentrations in pepper leaves in the case of low SOM ( $F_{(2,12)} = 1.89$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.29$ ) than for high SOM ( $F_{(2,12)} = 5.91$ ;  $p < 0.05$ ; partial  $\eta^2 = 0.56$ ) (Fig. 6B). No significant difference between treatments was detected for low SOM. At the low SOM, the lowest  $\text{NO}_3^-$  concentration was found in the CTRL plants, followed by the RF and the WP treatments. At the high SOM, the lowest  $\text{NO}_3^-$  concentration was also

**Fig. 6** Effect of treatments on plant nitrogen status. A) Total nitrogen content of leaves, B) nitrate ( $\text{NO}_3^-$ ) concentration of leaves. CTRL: control, RN: reference N-solution, WP: wool pellets. Different letters indicate significantly different groups. Capital letters indicate significant differences between soils (SOM: 0.58%; SOM: 1.84%) under the same treatment. Lowercase letters indicate comparisons of treatments with fixed soil organic matter content (Games–Howell post hoc test,  $p < 0.05$ )



found in the untreated CTRL plants, followed by the RN and the WP. The effect of soil type as a factor and the interaction between soil and treatment on  $\text{NO}_3^-$  concentrations in pepper leaves were investigated in a GLM model. The two soil types significantly influenced the leaf  $\text{NO}_3^-$  concentration ( $F_{(1,18)} = 5.47$ ;  $p < 0.05$ ; partial  $\eta^2 = 0.23$ ), but the interaction between soil and treatment was not significant ( $F_{(2,18)} = 1.74$ ;  $p > 0.05$ ; partial  $\eta^2 = 0.16$ ). Thus, the leaf  $\text{NO}_3^-$  concentration was mainly influenced by the treatments to the greatest extent, especially for higher SOM as evidenced by the partial  $\eta^2$  (Supplementary material Fig S3).

Total N-uptake per plant was also determined (Table 3). In the case of low SOM, the highest total N-uptake per plant was observed in the WP treatment, followed by the RN and the lowest was for the untreated CTRL plants. On average, in the case of low SOM, the wool pellet provided approximately 120 mg more N per plant than the untreated control. For the higher SOM, the WP treatment had the highest total N-uptake per plant; however, it was 29.55% less than the value observed for low SOM. After the WP treatment, the

highest biomass N content was observed for the RN treatment and the lowest was observed for the CTRL plants. Overall, for both soils, the highest N-uptake was observed in the WP treatment. N-use efficiencies were higher in CTRL plants. The N-use efficiency values for the CTRL treatment were  $0.17 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the low SOM soil and  $0.13 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the high SOM soil, which were higher than the values observed for the WP and RN treatments.

### Discussion

Wool pellet treatments exerted significant effects on soil biological properties in both soil types. The noticeable increases in FDA and  $\beta$ -glucosidase activity suggest that wool pellet treatments may enhance soil microbial and enzymatic activities in organic matter-rich soils compared to the reference inorganic N-solution and untreated control. This enhancement is particularly evident in soils with higher organic matter content, where the availability of degradable substrates

**Table 3** The average of nitrogen uptake, biomass production, and nitrogen use efficiency of pepper plants under different soil organic matter conditions and treatment at end of the experiment

Treatment	Soil type	N-uptake by shoot mg/plant	N-uptake by pepper fruit mg/plant	Total N-uptake/ plant mg	N-uptake/ week/plant mg	PNUE* $\mu\text{mol CO}_2$ $\text{mg}^{-1} \text{N s}^{-1}$
CTRL	low SOM 0.58%	15.2	7.25	22.41	0.36	0.17
RN		73.8	13.99	87.77	1.42	0.07
WP		127.2	17.98	145.16	2.34	0.06
CTRL	high SOM 1.84%	12.4	14.15	26.56	0.43	0.13
RN		21.4	21.65	43.07	0.69	0.07
WP		97.7	37.64	135.30	2.18	0.04

CTRL: control, RN: reference N-solution, WP: wool pellets. \* PNUE=photosynthetic rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) per total N-uptake by the plants (mg)

supports microbial proliferation. From the results, it can be assumed that the decomposition of the wool pellets was not completed by the end of the experiment.

The increase in soil biological activity can be attributed to the gradual decomposition of wool pellets, leading to an increase in degradable soil organic matter content (Abdallah et al. 2019). This gradual release of nutrients over time supports the maintenance and growth of soil microbial communities (Górecki and Górecki 2010; Zheljzakov et al. 2009). The increased organic matter content serves as a food source for microbes, consequently boosting their activity and reproductive capacity (Abdallah et al. 2019). Moreover, the slow-release nature of wool pellets ensures a sustained supply of nutrients, promoting long-term microbial activity.

The research findings align with those of Lal et al. (2020) who demonstrated that FDA and  $\beta$ -glucosidase activities were significantly higher for waste wool treatments compared to controls. Additionally, the research findings are also supported by the research of Karaca et al. (2023), who investigated the effect of sheep wool fertilizer on  $\beta$ -glucosidase enzyme activity. Compared to the untreated control, the wool treatment significantly promoted the increase of  $\beta$ -glucosidase enzyme activity; however, it decreased the enzyme activity rate in the higher SOM containing soil. Karaca et al. (2023) also emphasized the importance of considering application rates of wool fertilizer, as excessive amounts (e.g., exceeding one ton of sheep wool per acre) may lead to higher soil salt concentrations. Soil microbiological activity is also influenced by various soil properties, particularly soil texture and the levels of organic matter content (Nugroho et al. 2023; Shahid et al. 2016). The research experiment revealed that the wool pellet treatment had a more pronounced effect on soil microbiological activity in high SOM soils. This suggests that in soils with low organic matter content, there may be limited organic substrates available to support microbial life and survival capacity. Consequently, the nutrients provided by the wool pellet treatment may be rapidly utilized by microbes in both soils. Additionally, the sandy soil with low SOM is known to have higher porosity and greater aerobic microbial activities (Ferraz De Almeida et al. 2015), potentially leading to accelerated organic matter decomposition. Overall, the slow decomposition of wool pellets led to a gradual increase in soil organic matter content, thereby sustaining nutrient availability over the long term. This is particularly beneficial for soil microbes, which efficiently utilize the increased organic matter content. The soils with higher SOM content can provide greater organic matter substrates, a longer-term nutrient for microbial activity. In the sandy soils with low SOM, nutrients are utilized more rapidly by microbes, facilitated by the soil's higher porosity and aerobic conditions.

The application of sheep wool to soil introduces nitrogen primarily in the form of amino acids, di- and tripeptides,

which stimulate microbial feeding and organic matter decomposition (Abdallah et al. 2019; Broda et al. 2023; Jan et al. 2009). This not only enhances microbial activity but also contributes to the nitrogen pool accessible to plants. When mixed into the soil, wool also increases the  $\text{NH}_4^+$  and  $\text{NO}_3^-$  content of the soil solution, as well as its microbial activity (Vončina and Mihelič 2013).

As wool degrades slowly in soil, it serves as a slow-release fertilizer, providing NPK nutrients and S over an extended period compared to conventional fertilizers (Broda et al. 2023; Sharma et al. 2019). This slow-release property is advantageous for maintaining soil fertility without causing the rapid nutrient leaching associated with some inorganic fertilizers. The research findings are supported by studies that highlighted the role of wool in augmenting soil  $\text{NO}_3^-$  and  $\text{NH}_4^+$  content due to its high keratin-rich composition and its promotion of microbial biomass (Böhme et al. 2012; Broda et al. 2023; Gupta and Sharma 2014; Zheljzakov 2005; Zheljzakov et al. 2008).

In both soil types, the wool pellet treatment led to significantly higher total N content in pepper leaves compared to the untreated control. However, only the higher SOM content in the soils produced a significant difference in the  $\text{NO}_3^-$  content of the leaves. This discrepancy suggests that most of the N from the wool pellet was available to the plants in the form of  $\text{NH}_4^+$  ions, and that this cation was the preferred cation by the plants. Increased metabolism of N to amino acids and other organic compounds can lead to a relative decrease in the  $\text{NO}_3^-$  content of the leaf. When the concentration of organic nitrogen forms in the leaf is elevated, nitrate uptake may be inhibited due to feedback repression mechanisms (Li et al. 2022). This is supported by lower partial  $\eta^2$  values of  $\text{NO}_3^-$  relative to total N, suggesting a shift toward organic forms of N in plant tissues. The increased total N content is due to the fact that  $\text{NH}_4^+$  ions are rapidly incorporated into organic compounds such as amino acids, while  $\text{NO}_3^-$  ions are first reduced to  $\text{NH}_4^+$  and then incorporated into organic forms (Li et al. 2013b). Overall, research measurements suggest that the  $\text{NH}_4^+$  ions delivered to the soil by the wool pellet treatment can be rapidly taken up and integrated into the plant metabolism by the GS-GOGAT enzyme system. This enzymatic pathway efficiently converts  $\text{NH}_4^+$  to glutamate and other amino acids, supporting plant growth and N assimilation (Lea and Mifflin 2010). Research findings align with previous studies demonstrating higher biomass in sheep wool-treated plant species (Abdallah et al. 2019; Górecki and Górecki 2010; Gupta and Sharma 2014; Lal et al. 2020; Mubarak et al. 2009; Ordiales et al. 2016), which is mainly related to the higher N content in wool materials used as fertilizer (Abdallah et al. 2019; Broda et al. 2023; Sharma et al. 2019). The higher total N and  $\text{NO}_3^-$  content and higher biomass of pepper leaves can be explained by the fact that wool provides a prolonged

N replenishment due to its gradual decomposition process (Michel et al. 2008; Nustorova et al. 2006), which facilitates sustained N-uptake by plants (Broda et al. 2023) and reduces the tendency of N to leach from the soil, thus ensuring its retention and availability (Bradshaw and Hagen 2022; Broda et al. 2023). The continuous uptake of relative chlorophyll content by wool pellet was also investigated by monitoring the CCI value of the plants. The wool pellet treatment resulted in a continuous increase in CCI value of the plants, which was significantly different from that of untreated control plants. However, the CCI value of wool pellet-treated plants showed a sharper increase for low SOM compared to high SOM. In a similar finding, Abdallah et al. (2019) also observed that plants treated with wool and without fertilization showed higher pigment concentrations, which could be largely attributed to increased N content in the plants. Contrary to this, in the present study,  $\text{NO}_3^-$  content of pepper leaves did not increase significantly in the low SOM conditions. Górecki and Górecki, (2010) similarly found that wool application led to a decrease in leaf  $\text{NO}_3^-$  content in tomato, which may indicate effective N-uptake and incorporation into organic compounds. The lower  $\text{NO}_3^-$  content may also be related to the rapid nitrification rate of sandy soils (Zhu and Wen 1992).

Photosynthetic rate was highest in the WP and RN treatments under low SOM conditions, while lower values were observed in the high SOM soil. Similar trends were observed for photosynthetic rate and stomatal conductance, with both parameters showing higher values in the low SOM soil, particularly under WP and RN treatments. A strong positive correlation between N-uptake by shoot and net photosynthetic rate ( $r = 0.92$ ) was observed suggesting that increased nitrogen uptake directly enhances photosynthetic activity. The increased photosynthetic rate can be attributed to the higher carotenoid content, which plays a central role in enhancing the photosynthetic efficiency of pepper plants. Carotenoids are known to contribute to plant defense by neutralizing reactive oxygen species (ROS) and reducing oxidative stress (Razmjooei et al. 2022). The reduced stomatal conductance and photosynthetic rate observed in untreated control pepper plants compared to other treatments is largely due to lower N levels. In conditions of nitrate deficiency, stomatal function is impaired, which can increase water loss through transpiration. Nitrogen deficiency also promotes the biosynthesis of abscisic acid (ABA), and higher ABA levels cause chloride channels to open, leading to a decrease in turgor pressure in stomatal cells. When plants take up more nitrogen, their growth and photosynthesis typically improve, which can increase the transpiration rate. Furthermore, the openness of stomata influences the extent of transpiration; if increased nitrogen uptake enhances stomatal conductance, the transpiration rate will also rise (De Angeli et al.

2006). In conclusion, the increase in photosynthetic rate in pepper plants is attributed to the beneficial effects of wool pellet and reference N-solution. These treatments enhance the  $\text{CO}_2$  fixation capacity of the plant. N deficiency impairs the structure and function of the thylakoid membrane, which reduces photosynthetic pigment content, thus hindering photosynthetic electron transfer and photochemical reactions (Li et al. 2024). In low SOM soils, wool pellet-treated pepper plants were able to maintain thylakoid membrane integrity, thus contributing to efficient photosynthesis, while control plants showed membrane damage. The enhanced thylakoid membrane integrity and PSII efficiency observed in WP-treated plants are likely to support improved growth and fruit production, as these factors are critical for sustainable photosynthetic productivity (Supplementary Fig S3). This finding highlights the dual role of wool pellet treatment in nitrogen supply and in maintaining the functional stability of photosynthetic structures, which is particularly beneficial in soils with low SOM content.

Nevertheless, it is important to note that the total N supplied in the wool pellets was higher than that in the reference solution. The mineral N dose was deliberately kept lower to reflect typical horticultural practice and to avoid salt stress in small pots. Future research could include additional treatments with multiple mineral N rates to match or exceed the total N provided by wool pellets or measure the exact N mineralization of wool pellets in soil without plants.

Significant differences in plant growth parameters were observed between treatments in the two soil types. In the soil with a lower air capacity but a higher SOM content, the total N-uptake of the pepper plants from the wool pellet was much more efficient than from the synthetic N fertilizer. The difference between the two treatments was smaller in the sandy soil with low SOM content. Wool pellets decomposed faster in the low SOM soil due to its higher soil air capacity and porosity, which also promoted faster nitrification rates and increased plant biomass. The total biomass N content per plant was 29.55% higher for the low SOM than for the high SOM. Nevertheless, pepper fruits were significantly lower in the low SOM. Conversely, in the high SOM, higher water retention and organic matter content led to slower rates of decomposition and nitrification of wool pellets, resulting in lower observed biomass levels. However, significantly higher pepper fruits were measured in this soil, which can be attributed to the higher organic matter content and more gradual decomposition of wool pellets. Since nitrification is continuous, wool pellets are less prone to leaching from the soil solution compared to mineral N fertilizers, thus feeding plants and ensuring their growth and optimal development (Huang et al. 2017), demonstrating that wool acts as a slow-release N fertilizer. The enhanced plant growth effect of wool pellets has been demonstrated in several

studies (Abdallah et al. 2019; Böhme et al. 2008; Górecki and Górecki 2010; Lal et al. 2020; Mubarak et al. 2009; Ordiales et al. 2016; Suruchi et al. 2014; Zheljazkov 2005).

These findings highlight the potential of wool pellets as an effective and sustainable alternative to mineral N fertilization, especially in soils with different SOM levels. Importantly, the use of wool pellets may also contribute to reducing fertilizer input costs and environmental impacts associated with synthetic N application, such as  $\text{NO}_3^-$  leaching and soil degradation, thereby supporting more sustainable and circular horticultural systems.

## Conclusions for future biology

The research findings on the use of wool pellets, a relatively understudied alternative to nutrient supplementation, provides significant insights into their impact on soil quality, with great relevance to the soil biological activity and plant nutrition. The results show that wool pellets increased microbiological activity in both studied soils with different soil organic matter contents. The application of wool pellets, even without additional nitrogen fertilizer, led to a significant increase in soil and plant N content, along with improvements in physiological parameters and biomass of pepper plants. This effect is more pronounced in low organic matter soils due to a greater dependence of faster mineralization rates in such low-quality soils. However, in less-aerated soils with higher organic matter content, the N content of wool pellets is utilized more efficiently by plants than that of synthetic N fertilizers. This results in a higher fruit production compared to the control and yields that are comparable to those obtained with synthetic N fertilizers. Overall, these results suggest that wool pellets are not only a valuable source of nitrogen and other nutrients for pepper plants, but also help to maintain the stability of the photosynthetic apparatus in low organic matter soils. Together with their biological effects, they play a crucial role in enhancing soil biological activity. However, the intensity of these benefits is closely related to soil mineralization and decomposition dynamics, highlighting the need for context-specific application in sustainable agricultural practices. In future research, we recommend applying multiple mineral N levels (both lower and higher than the wool pellet-derived N) and measuring N release dynamics from wool in the absence of plants, thereby quantifying mineralization more precisely.

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

## Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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