



Green microalga (*Coelastrella* sp.) cultivated in wastewater is an effective phosphorus biofertilizer

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Abstract

Phosphorus (P) is an essential macronutrient for plants, yet its reserves are finite and non-renewable. Microalgae present a promising solution for recovering P from wastewater, providing a sustainable source of biofertilizer. This study assessed the potential of the green microalga *Coelastrella* sp. cultivated in nutrient-rich synthetic centrate, as a source of slow-release P biofertilizer for crops. A P starvation–repletion approach was applied to enhance P assimilation during outdoor cultivation in photobioreactors, and the resulting biomass was analyzed for nutrient composition and P-release dynamics in calcareous soil in comparison with triple superphosphate (TSP). The algal cells rapidly accumulated more than 2% P (dry weight) within six hours of repletion and showed sustained P release over 84 days, maintaining higher levels of Olsen-extractable P than TSP after four weeks. In pot trials with tomato (*Solanum lycopersicum*), *Coelastrella*-based fertilization at both 30 and 60 mg P kg^{−1} achieved biomass and fruit yields comparable to TSP, while significantly increasing fruit P uptake and micronutrient (Fe, Zn, Ni) concentrations. Moreover, algal fertilization enhanced arbuscular mycorrhizal colonization compared with mineral P. These results demonstrate that *Coelastrella* sp. can efficiently recover P from wastewater and provide a slow-release biofertilizer that sustains P availability, promotes symbiotic root interactions, and improves plant nutrient acquisition. The use of this algal biomass thus represents a sustainable strategy for recycling wastewater-derived nutrients and reducing dependence on conventional P fertilizers.

Keywords Phosphorus recovery · *Coelastrella* · Chlorophyceae · Mycorrhiza fungi · Slow release biofertilizer

Introduction

In many agricultural and ecological ecosystems, phosphorus (P) ranks as the second most limiting nutrient for plant growth after nitrogen (N) (Cordell and White 2011). P is the least mobile nutrient in the soil due to its pronounced reactivity with clay minerals and metal oxides, which prevail in most agricultural soils. Adsorption, fixation, or precipitation reactions results in insoluble P complexes, leading to low P

solubility and mobility and the accumulation of legacy P in the topsoil (Hedley and McLaughlin 2005). These processes result in low P-availability for plant uptake (Hernández and Munné-Bosch 2015). To maintain high crop productivity, the conventional approach is generous application of P-fertilizers (Powers et al. 2016). The remaining P tends to accumulate in the upper soil layers (Li and Erel 2020), and is particularly vulnerable to surface runoff and leaching, causing eutrophication and other environmental challenges (Zheng et al. 2023).

A major concern for P fertilization is the finite nature of the primary source for synthetic P fertilizer: rock phosphate (Obersteiner et al. 2013). Rock phosphate is a sedimentary, nonrenewable resource that is expected to be gradually depleted (Cordell et al. 2009). An additional concern is the uneven distribution of P reserves which is dominated by a handful of countries (Zou et al. 2022). The overall increasing P demand is expected to raise the prices of the resource in the coming decades (Brunelle et al. 2015), thus making it less affordable to farmers (Cordell and White 2014).

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Therefore, there is an urgent need to enhance P management strategies.

A large unexploited source of P is found in domestic and industrial wastewater. The estimated P discharge in wastewater is 1.8 g per capita per day (Cornel and Schaum 2009), leading to typical P concentrations in the range of 12 to 30 mg L⁻¹, while the target P concentration in the treated wastewater should be lower than 1 mg L⁻¹ to minimize environmental degradation (De-Bashan and Bashan 2004). Globally, approximately 1.3 Mt P year⁻¹ is treated in wastewater treatment plants (WWTPs), and rates are expected to increase, especially in developing countries (Van Drecht et al. 2009). Phosphorus in wastewater can substitute up to 15–20% of the demand for agriculture (Zoboli et al. 2016). Among the various waste streams generated in WWTPs, the centrate produced during sludge dewatering is typically the most nutrient-rich. This stream often contains extremely high concentrations of N and P, commonly around 1,000 mg L⁻¹ N and 100 mg L⁻¹ P (Ferrari et al. 2022). Despite representing only a small fraction of the total treated volume, the centrate can account for roughly one third of the total P discharged from the facility (Min et al. 2011). Its treatment poses a significant challenge as conventional biological processes are largely ineffective due to the combination of high nutrient load and elevated salinity (Min et al. 2011). To recover P from the centrate, several efforts are being made such as precipitation to create struvite (Sena et al. 2021). Recently, increasing interest has been directed towards utilization of microalgae grown on wastewater to recover P and as a potential biofertilizers for sustainable agriculture (Di Capua et al. 2022).

Microalgae are photosynthetic eukaryotes capable of growing in a variety of conditions and on different substrates, including marginal water and nutrient-rich streams (Shrestha et al. 2022). Photosynthetic microalgae can utilize CO₂ and inorganic nutrients for biomass production. Microalgae can thrive under conditions of both P and N limitations as well as abundance. Microalgae maintain biomass production while adjusting cellular metabolism and growth under P limitation (Solovchenko et al. 2019). Microalgae has been proven to be efficient in the accumulation of P from a wide variety of wastewaters (Slocombe et al. 2020) and storing it in intracellular P depots as polyphosphates (Solovchenko et al. 2019). This ability positions them as highly promising candidates for P recycling and pollution mitigation from wastewater (Osorio-Reyes et al. 2023). The resulting nutrient-rich valuable biomass can serve as a renewable biofertilizer.

Previous studies have demonstrated the feasibility of utilizing microalgae as a biofertilizer. For example, *Scenedemus* sp. matched conventional fertilizers in lettuce yield (Álvarez-González et al. 2023). Similarly, fertilization with *Chlorella vulgaris* achieved yields comparable to mineral fertilizers and improved soil microbial activity; however,

heavy metal accumulation following wastewater-based cultivation raises concerns for its agricultural application (Schreiber et al. 2018; Akca et al. 2025). The beneficial effects of microalgae fertilization have been attributed to slow P release, driven by polyP-rich biomass and elevated microbial activities that enhances P cycling (Yu et al. 2025). There was a significant reduction in N oxide emissions following fertilization with *Coelastrella* sp., further expanding the environmental advantages of microalgae-based fertilization (Stamenov et al. 2025). Together, these findings highlight the potential of microalgae as biofertilizers (Coppens et al. 2016), while emphasizing the need for species-specific studies to better understand phosphorus accumulation, release behavior, and agronomic efficacy.

Despite the recognized potential of microalgae, there is a gap in research concerning the efficacy of *Coelastrella* sp. in P-release profiles in soil and supplying P for plants. Different strains of microalgae vary in assimilating and releasing P, thus understanding the effect of this unique strain is crucial for optimizing its use as biofertilizer. The interaction between its algal biomass and soil microbiota, including beneficial microorganisms such as arbuscular mycorrhizal fungi (AMF), should be explored to understand the benefits and mechanisms of microalgal biofertilizers. This study aimed to address this gap by investigating the potential of the novel and resilient microalga *Coelastrella* sp. cultivated outdoors in synthetic centrate to (i) optimize cultivation conditions to enhance P accumulation in the algal biomass, and (ii) assess its efficiency as a P biofertilizer relative to conventional fertilizer, using tomato as model crops.

Materials & methods

Biomass production phase

This study utilized the green microalga *Coelastrella* sp. (Chlorophyta), a local isolate from the Microalgal Biotechnology Laboratory of Ben-Gurion University, Sde Boker campus, Israel. The growth medium consisted of a synthetic centrate solution formulated to mimic the mineral composition of real wastewater centrate. The seed cultures were first inoculated into a modified BG11 medium (mBG11) in 50-mL Erlenmeyer flasks placed in an incubator shaker with 2% CO₂ in the air and illuminated with 70 μmol PAR photons m⁻² s⁻¹ and agitation 150 rpm (Boussiba and Vonshak 1991). The cultures were grown for five days, before transferring to 100 mL fresh mBG11 medium, under the same conditions. After a week, the cultures were inoculated into 500 mL mBG11 medium into 1-L glass columns (6 mm wall thickness) and placed in a water bath with temperature controlled at 25 °C. Columns were bubbled with a mixture of 2% CO₂ in air and

illuminated from one side with cool white, fluorescent lamps at $100 \mu\text{mol PAR photons m}^{-2} \text{ s}^{-1}$. 100 mL of fresh mBG11 was added to the growing culture every two days to exponential growth and P supply, resulting in 900 mL growth medium after one week in the column. This is aimed at obtaining an ample biomass quantity to initiate biomass production in outdoor conditions.

Growing cultures were transferred to 2.5-L columns and moved to outdoor conditions to scale up the cultivation. Outdoor cultivation was conducted at the pilot facilities of the Microalgal Biotechnology Laboratory in an arid environment at Sde Boker campus of the Ben-Gurion University of the Negev ($30^{\circ}52'27.3'' \text{ N}$; $34^{\circ}47'33'' \text{ E}$; 475 m elevation) during the winter (February) of 2023. Daily average temperatures during cultivation were between 8° C and 21° C and global radiation ranged from 0 to 700 W m^{-2} during the night and day, respectively. Growth conditions were in semi-transparent flat panel photobioreactors (PBR, thickness 0.5 mm) placed in metal stands. Each panel was 115 cm long while the width was 30 and 180 cm for 15-L and 100-L panels, respectively (Fig. S1). Culture sparged with 2% CO_2 in the air during the daytime. Panels were exposed to natural solar illumination without temperature control and shading.

After a week of acclimatizing to outdoor conditions, in order to enhance P uptake in the biomass, a strategy of P starvation and repletion, previously described by Solovchenko et al. (2019), was adopted. Briefly, cultures growing in mBG11 were centrifuged and inoculated into mBG11 without P in 15-L flat panel PBR with initial biomass density of 0.5 g L^{-1} . After 9 days, P starved cultures were centrifuged and inoculated in 100 L P-rich synthetic centrate with the following composition in stock solution: Peptone 16 g L^{-1} , meat extract 11 g L^{-1} , urea 3 g L^{-1} , sodium chloride (NaCl) 0.7 g L^{-1} , calcium chloride dihydrate ($\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$) 0.4 g L^{-1} , magnesium sulfate heptahydrate ($\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$) 0.2 g L^{-1} , anhydrous potassium mono hydrogen phosphate (K_2HPO_4) 2.8 g L^{-1} . Biomass density was set at 1 g L^{-1} , based on a previous study by Lau et al. (1995) who stated that denser cultures can remove high nutrient loads while enhancing high biomass productivity. This P starvation and repletion strategy was repeated for three consecutive cycles (pseudo replicates), with the overall experimental period lasting one month.

For biomass growth measurements in the P repletion phase, biomass was monitored after 3, 6, 24, and 48 h. Briefly, 5 mL of the growing cultures were collected and filtered through pre-weighted $47 \mu\text{m}$ glass fiber filters (Whatman GF/C). The filters with loaded biomass samples were dried in a microwave at 30% power for 9 min. Dried filters were weighed on an analytical scale and biomass density (g L^{-1}) was calculated. At each sampling time point, three analytical replicates were collected.

Phosphate uptake analysis

To determine P uptake during the P repletion stage, biomass was harvested at 0, 3, 6, 24, and 48 h following a modified protocol derived from Solovchenko et al. (2019). The cell pellet and supernatant were collected separately for P analysis remaining in the medium and P concentration in the biomass. At each harvesting point, 150 mL of culture was withdrawn from the columns and centrifuged (5000 rpm, 10 min, 25° C). After 48 h, the whole biomass was harvested from the panel. This was repeated for three consecutive batches of P starvation and P repletion.

The biomass was frozen at -80° C for 24 h and then lyophilized for 48 h before analyzing for total P (TP) after digestion in sulfuric acid. Briefly, 0.1 g biomass was weighed into Pyrex tubes and 2 mL of 98% concentrated sulfuric acid was added and kept in a fume hood overnight. The following day, the tubes were heated at 180° C for 20 min and cooled between intervals (typically 3–4 times), with 1 mL 30% hydrogen peroxide added until a clear solution was obtained. After digestion, the contents were transferred to volumetric flasks, and the final volume was brought to 100 mL. P concentration in the digested biomass and supernatant was analyzed using the ammonium molybdate method (Murphy and Riley 1962) in an automated photometric analyzer (Gallery Plus, Thermo Scientific) and referred as algae-P with and P-removal in the growth solution, respectively.

P form in the biomass was determined in the samples collected only after 48 h. Organic and inorganic P forms were characterized following a modified Hedley P fractionation protocol (Hedley et al. 1982). To determine P storage form in the microalgae, cells were harvested after 0, 3, and 6 h of growth, centrifuged, and washed to remove residual growth medium. The washed cells were then stained with 4',6-diamidino-2-phenylindole (DAPI) and examined using a fluorescence microscope equipped with Filter Set 38 HE (excitation 470/40 nm, emission 525/50 nm), as described by Aschar-Sobbi et al. (2008).

Mineral composition of the algae

Mineral composition of the *Coelastrella* biomass harvested after 48 h from the 100-L PBR panels were determined. N, C, and H were analyzed by elemental analyzer (FlashSmart #11,206,125, Thermo Fisher Scientific, UK). Mineral concentrations of K, Ca, Mg, S, Na, Fe, Mn, and Zn were analyzed following nitric acid digestion in microwave system (MARS-6, CEM Corporation, US) and quantified through ICP-OES analysis (Spectro, Green', Spectro Analytical Instruments).

Agronomic test

Soil incubation

The extractable P dynamic of *Coelastrella* was compared to the conventional triple superphosphate (TSP) fertilizer over 84 days in a soil incubation experiment in a calcareous P-fixing loam soil (Table S1). All fertilizers were homogeneously mixed with the soil at a dosage of 100 mg P kg⁻¹. Subsequently, 80 g fertilized soil was weighed into Petri dishes (90 × 15 mm) in 14 replicates and moistened to 60% of saturation with distilled water. The plates were covered with aluminum foil and incubated at a temperature of 25 °C until the analysis. Additional 14 replicates of untreated soil were included as negative control.

Soil extractable P was measured after 1, 3, 7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77, and 84 days after fertilizer application. For each sampling time, two Petri dishes from each treatment were destructively sampled and extracted for Olsen P (Olsen and Watanabe 1957). Briefly, 2 g of soil was sampled from each Petri dish in 3 replicates (n = 6) and agitated in 40 mL 0.5 M NaHCO₃ at a pH 8.5 for 30 min, then centrifuged (4000 rpm, 3 min, 25 °C) and filtered. The pH of the extracts was adjusted to 6.5 using 2.5 M H₂SO₄ with p-nitrophenol indicator before analyzing P by Gallery Plus Aqua Master discrete analyzer (Thermo Scientific).

Pot experiment

To assess the agronomic efficiency of the biofertilizer versus TSP, pot experiment was performed using tomato (*Solanum lycopersicum* var. Ikram, Syngenta) in a controlled greenhouse facility located in Gilat research center, Western Negev, Israel. Three weeks old seedlings were planted on 16 July and harvested on 19 November 2023 (116 days). The pots were filled with ground calcareous loam soil with low extractable P level (Table S1). Seven kg soil was supplied with either 30 or 60 mg kg⁻¹ P as biofertilizer *Coelastrella* sp. collected at the end of P starvation and repletion growth strategy, TSP, or no P control (-P). Supplementary N- Urea 133 mg kg⁻¹ and K- KCl 70 mg kg⁻¹ were homogeneously mixed in the soil with an electric Magnum concrete mixer. A week before planting, the pots were manually irrigated to 60% saturation to restore microbial and chemical activity. Irrigation was performed daily via automated irrigation systems aimed to maintain soil moisture content at 60%, with irrigation water supplemented with 10 mg L⁻¹ Mg and micronutrients (Kortin, ICL) at identical concentrations across all treatments. The pots were arranged in a completely randomized design, each treatment had 6 replicates.

Regular pruning and plant protection techniques were implemented to ensure optimal plant growth and

development. Temperature was controlled at 25/18 °C day/night, while relative humidity maintained around 60% over the entire growing season.

To assess extractable P level, soil samples were collected three times during the experiment: Three days after planting, after two months, and before harvest (106 days after planting). At each sampling, soil extractable P was assessed as described above.

Plants were harvested when the first three nodes had reached maturity. At harvest, root, shoot, and fruits biomass were separated, oven-dried at 70 °C for 72 h and weighed. The number of fruits were recorded, and fruits were divided into ripe and unripe fruits. The total soluble sugars (TSS) were recorded by a refractometer in ripe fruits only. Root length and surface area were analyzed using WinRhizo software (Winrhizo 2016a, Regent Instruments Inc., Canada), and the specific root length was calculated by dividing the root's length by its dry biomass.

For chemical analysis, dried biomass was ground to fine powder by ball grinder and 0.25 g was digested in 5 mL concentrated nitric acid and 1 mL hydrogen peroxide in a microwave-accelerated digestion system (MARS-6, CEM) at a temperature of 180 °C. The digested solution was brought to 50 mL with distilled water and analyzed for P concentration using the ammonium molybdate method in an automated photometric analyzer (Gallery Plus, Thermo Scientific). P uptake was determined by multiplying the P concentration by the tissue dry weight. Additionally, mineral concentrations in the fruits were analyzed using ICP-OES.

Arbuscular mycorrhiza fungi (AMF) colonization was assessed by Trypan blue staining, proposed by Ho-Plágaro et al. (2020). Briefly, the roots were washed from the soil and soften in 10% KOH at 70 °C water bath for 45 min, then washed and stained with Trypan blue (0.01% w/v). Thirty root fragments per plant were examined under a light microscope for AMF morphological parameters (i.e., mycorrhizal frequency, mycorrhizal intensity, arbuscular development, and arbuscule abundance). The colonization percentage was calculated using open-source R-script code as described by Chiapello & Gutjahr (2019).

Data analysis

Statistical analysis was completed using the JMP version (17). For all experiments, statistical significance was set at p-value < 0.05, differences between treatments were determined using the Tukey-post hoc test. Algal growth and P uptake rate were analyzed as three pseudo replicates, each measured in duplicates (technical replicates) at every sampling time point. For the pot experiments, two-way ANOVA was used to test the effects of P fertilizer type

(Alga or TSP) and P level (30 or 60 mg P kg⁻¹ soil) on plant growth and yield. Control treatment was excluded from the statistical analysis considering P fertilization is essential for plant growth.

Results

Microalgal growth and P uptake kinetics

Algal growth in P repletion medium increased rapidly from 1 g L⁻¹ to approximately 2.5 g L⁻¹ within 48 h (Fig. 1a). The P concentration in the synthetic centrate medium decreased from 31.5 to 1.2 mg L⁻¹ after 48 h (Fig. 1b). The algae-P concentration (DW basis) increased from 0.2% to a peak of ~2% after 6 h, followed by a gradual decrease to 1.67% after 48 h (Fig. 1c). The total P assimilated into biomass (expressed as mg of P measured after biomass digestion per L of culture) increased from 2 to 35 mg L⁻¹ after 48 h (Fig. 1d), thus exceeding 31.5 mg L⁻¹ P initially provided

in solution. P uptake rate was highest at the initial 3 h after resuspension in P replete medium (Fig. 1e), with 5 mg L⁻¹ h⁻¹. Subsequently, the uptake rate gradually declined to 2 mg L⁻¹ h⁻¹ between 3–6 h and decreased significantly 6–48 h after exposure. DAPI staining revealed distinct intracellular poly P granules in *Coelastrella* sp. (Fig. S2), consistent with P accumulation patterns previously reported for a wide range of microalgae (Su 2021).

Characterization of the algal biomass

The harvested biomass, collected after 48 h, was analyzed for various P fractions using modified Hedley sequential fractionation (Hedley et al. 1982). The total P content was 1.69%, comprising both inorganic and organic P fractions. The labile inorganic P pool, extracted by water and bicarbonate solutions, were 0.44 and 0.46%, respectively. The organic P pool, calculated by subtracting the inorganic P from the total, was 1.25%. P as poly P form was

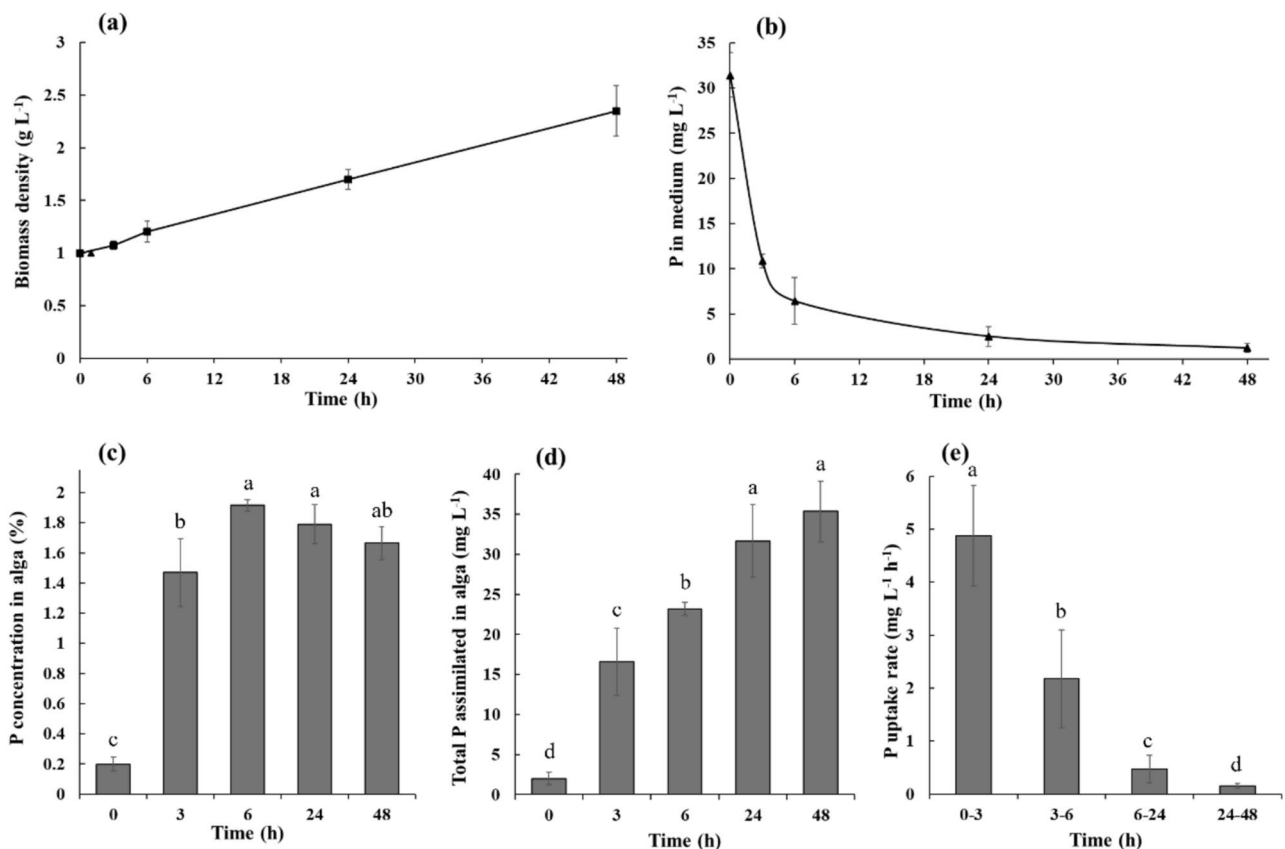


Fig. 1 Alga (*Coelastrella* sp.) biomass production in three consecutive outdoor batches experiments using the P starvation and repletion strategy (a) biomass growth under P repletion, (b) kinetics of P removal in P repletion, (c) Algae-P concentration in biomass (d) total algae-P assimilated in alga and (e) the P uptake rate under P-replete

conditions. Error bars represent the standard deviation of three pseudo replicates (Mean $\pm$ SD, n=3), derived from two analytical replicates collected across three consecutive growth cycles. Statistical differences were evaluated using Tukey's HSD test.

Table 1 Mineral composition and P fractionation of the *Coelastrella* sp. used in soil incubation and pot experiments

Mineral	Unit	Concentration
Total P	%	1.64 ± 0.06
Water extractable P	%	0.44 ± 0.04
HCO ₃ extractable P	%	0.46 ± 0.01
HCl extractable P	%	0.70 ± 0.09
C	%	43.71 ± 0.41
H	%	7.12 ± 0.16
N	%	7.17 ± 0.07
K	%	0.61 ± 0.023
Ca	%	1.23 ± 0.045
Mg	%	0.53 ± 0.009
S	%	0.41 ± 0.02
Na	%	0.13 ± 0.001
Fe	mg kg ⁻¹	2430.37 ± 36.52
Mn	mg kg ⁻¹	149.23 ± 1.7
Zn	mg kg ⁻¹	57.94 ± 1.12

approximately 0.1% of the biomass DW. Table 1 summarized the biomass macro- and micronutrient content.

Soil incubation of Algae-based fertilizers

On day one, the TSP treatment exhibited the highest Olsen-extractable P of 37 mg kg⁻¹, while soil amended

with *Coelastrella* sp. recorded 26 mg P kg⁻¹ (Fig. 2a). During the first seven days, extractable P decline rapidly, followed by a more gradual decrease until the end of the incubation, reaching 18.3 mg kg⁻¹ P, a pattern consistent with the rapid sorption and fixation of soluble P in soil, also reported in previous studies (Erel et al. 2022). In contrast, soil amended with *Coelastrella* sp. showed a modest decline from 26 to 23 mg kg⁻¹ during the first week. From day 7 to day 84, Olsen-extractable P in algae-amended treatment remained stable. At the conclusion of the incubation period, *Coelastrella* sp. maintained a slightly higher extractable P (average of 20.3 mg kg⁻¹) than TSP treatment (18.3 mg kg⁻¹).

The average net Olsen-extractable P was analyzed across three incubation stages: Early (0–21 days), Middle (28–56 days), and Late (56–84 days) stages as illustrated in Fig. 2b. During the early-incubation stage, TSP showed net Olsen-extractable P comparable to *Coelastrella* sp., with a slightly lower net Olsen-extractable P value, however, data analysis revealed no significant differences. During the middle incubation stage, the net Olsen-extractable P in TSP decreased, while *Coelastrella* sp. remained stable at 21 mg kg⁻¹. Transitioning to the late incubation stages, TSP further decreased to 18 mg kg⁻¹, while *Coelastrella* sp. maintained the net Olsen-extractable P values observed during the middle stages. Statistical analyses revealed significant differences between the two treatments, with *Coelastrella* sp. having

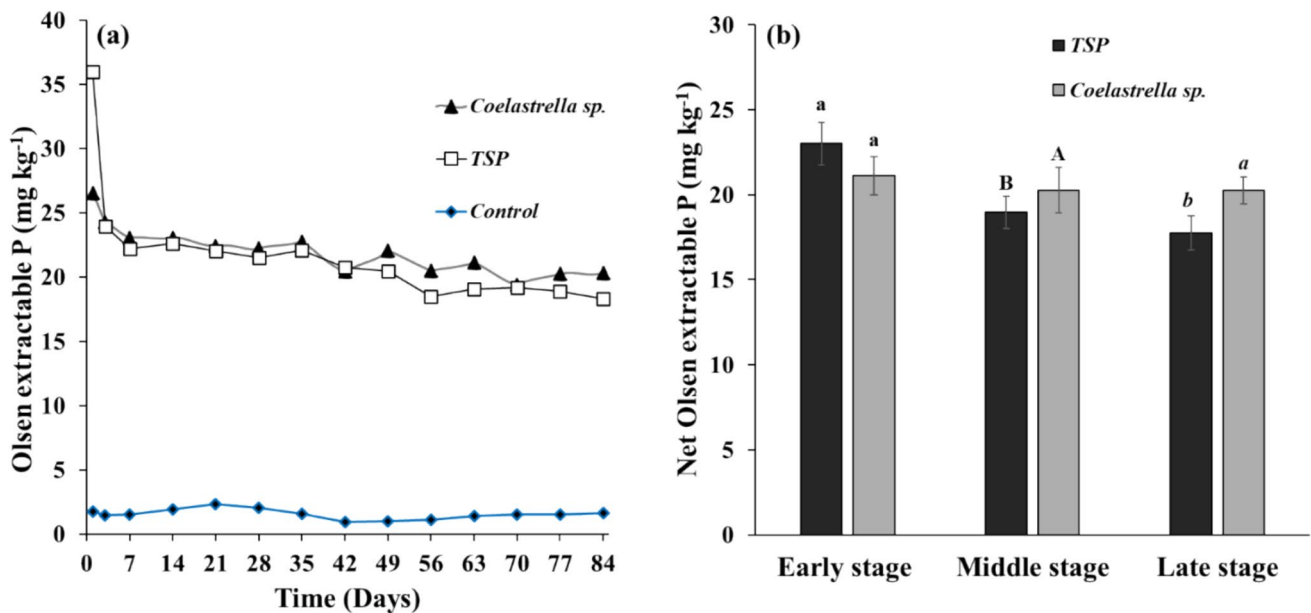


Fig. 2 Olsen-extractable P dynamic following application of 100 mg P kg⁻¹ to calcareous loam soil **(a)** Effect of P fertilizer type throughout the 84 days of incubation **(b)** Comparison between Algae-based fertilizer and TSP in extractable P at three stages: 0–21 days (early stage), 28–56 days (middle stage) 56–84 days (late stage). Control

treatments are not included in data analysis. In panel (a), each data point represents an average of six replicates. In panel (b) letters indicate significant differences between P types for each incubation stage according to the Tukey HSD test ($P < 0.05$). Error bars represent the standard deviation for six replicates (Mean ± SD, $n = 6$)

higher net Olsen-extractable P, compared to TSP throughout the middle and late incubation stages.

Pot experiment

Effect of P-fertilizer type and level on extractable P

Soil samples were collected from pots at three time points: three days, two months, and before harvest (four months). The negative control consistently exhibited low Olsen P levels, reflecting severe P deficiency. At three days, soils treated with Alga at a P dose of 30 mg kg⁻¹ had significantly lower extractable Olsen P compared to TSP-treated soils (Fig. 3a). At the higher P dose of 60 mg kg⁻¹, extractable Olsen P in Alga-treated soils was higher, compared to TSP, though the difference was not statistically significant.

After two months, residual P levels decreased across all treatments (Fig. 3b). At 30 mg kg⁻¹, Olsen P levels were similar for Alga and TSP. At 60 mg kg⁻¹, TSP-treated soils had slightly higher Olsen P levels than algae-treated soils, though this difference was not statistically significant.

By harvest (four months), residual Olsen P levels further decreased in all treatments (Fig. 3c) with both algae and TSP showing insignificant differences at 30 mg kg⁻¹. Similar trend was also observed between Alga and TSP at 60 mg kg⁻¹.

Across all sampling points, increasing the P dose from 30 to 60 mg kg⁻¹ consistently elevated extractable P levels.

Shoot biomass and P uptake

Shoot dry biomass (excluding fruits) was measured by the end of the experiment (116 days after planting). At the lower P level of 30 mg kg⁻¹, plants fertilized with Alga produced a higher shoot biomass compared to TSP, representing a 14.6% increase (Fig. 4a). Similarly, at the higher P level of 60 mg kg⁻¹, plants treated with Alga yielded higher shoot biomass per plant compared to TSP, corresponding to an 18.9% increase. Despite these trends, the differences in shoot biomass between fertilizer types or P levels were not statistically significant.

At a P level of 30 mg kg⁻¹, Alga fertilization significantly enhanced shoot P uptake compared to TSP, representing a significant 40.2% increase in P uptake and allocation to the shoot. In contrast, at the 60 mg kg⁻¹ P level, P uptake showed similar trends between Alga and TSP.

Root growth, morphology, and P uptake

At a P level of 30 mg kg⁻¹, root dry weight was slightly lower in Alga-treated plants compared to TSP-treated plants. Similarly, at 60 mg kg⁻¹, roots weighed slightly lower in

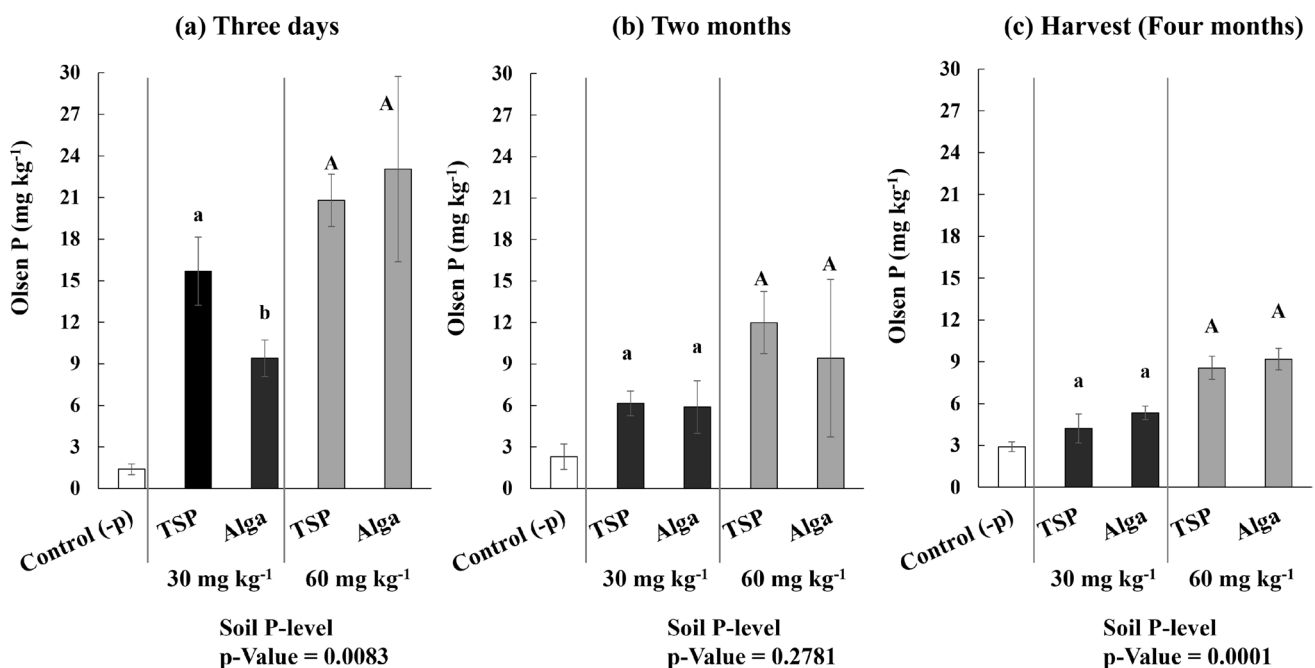


Fig. 3 The effect of P fertilizer type (Alga or TSP) and application dose (30 or 60 mg kg⁻¹) on Olsen extractable P over the growing period of tomatoes in a calcareous loam soil. P was assessed after (a) Three days (b), Two months, and (c) Four months. Control treatments are not included in data analysis. Error bars represent the standard

deviation for six replicates (Mean ± SD, n=6). Data was analyzed by two-way ANOVA; different letters indicate significant differences within each P-type at given P level. The p-value of P-level, regardless of P-type, is presented below the Y-axis title

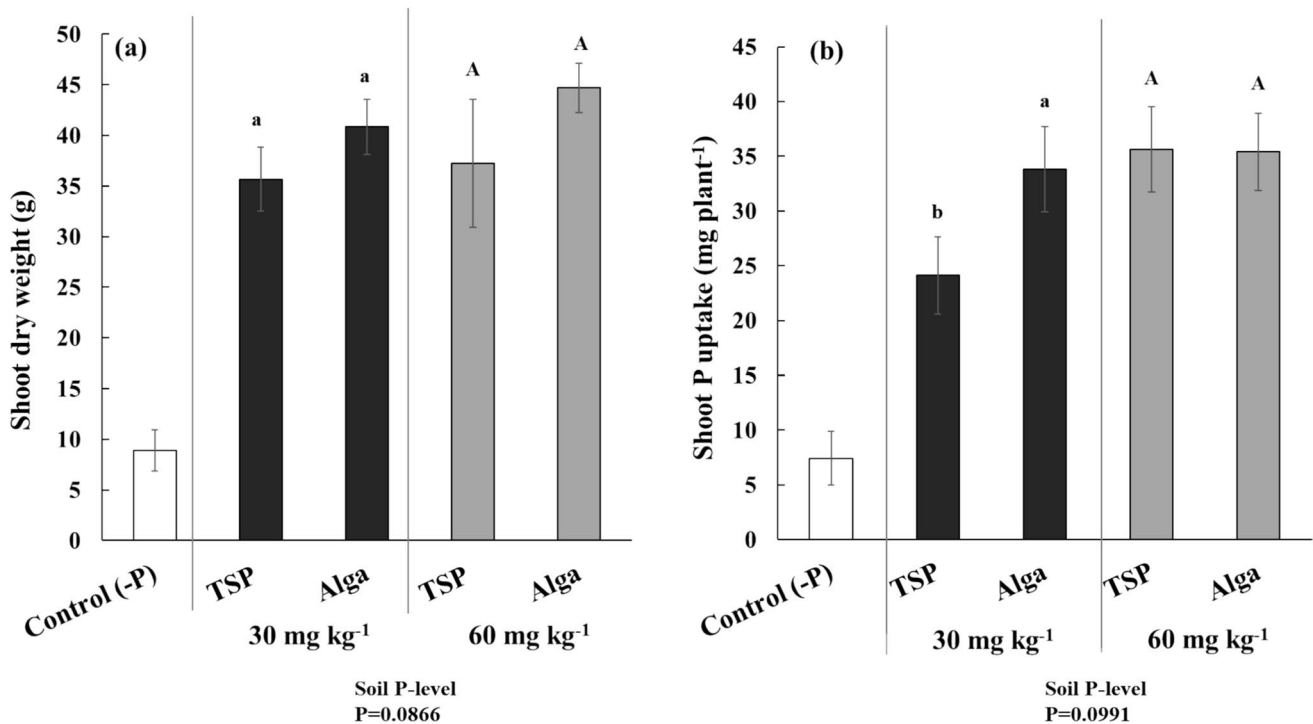


Fig. 4 The effect of P fertilizer type (Alga or TSP) and application dose (30 or 60 mg kg⁻¹) on (a) Shoot dry weight and, (b) shoot P uptake. Control treatments are not included in data analysis. Error bars represent the standard deviation for six replicates (Mean ± SD,

n=6). Data was analyzed by two-way ANOVA; different letters indicate significant differences within each P-type at given P-level. The p-value of P-level, regardless of P-type, is presented below the Y-axis title

Alga compared to TSP (Fig. 5a). Differences in root dry weight between fertilizer types and soil P levels were not statistically significant.

The average root length at 30 mg kg⁻¹ was higher for Alga compared to TSP, with a 20.3% increase. Surprisingly at the 60 mg kg⁻¹ P level, root length was reduced in Alga compared to TSP (Fig. 5b), although the differences were not statistically significant. Specific root length (SRL) did not differ significantly between treatments (Fig. 5c). At 30 mg kg⁻¹, Alga showed a SRL slightly higher compared to TSP, while at 60 mg kg⁻¹, TSP recorded slightly higher results. Additionally, measurements of root diameter and root surface area revealed no statistically significant differences between fertilizer types or soil P levels (Fig. S4).

P allocation to roots was not significantly influenced by P type or soil P level (Fig. 5d). At 30 mg kg⁻¹, pots amended with Alga allocated slightly lower P to the roots compared to TSP, though the difference was not statistically significant. At 60 mg kg⁻¹, this trend was also observed with no significant differences detected.

Root AMF colonization

The effect of P type and P level on arbuscular mycorrhizal fungi (AMF) colonization was evaluated based on four

morphological parameters: mycorrhizal frequency, mycorrhizal intensity, arbuscular development, and arbuscule abundance, according to the method proposed by Ho-Plágaro et al. (2020). At both P levels, Alga-treated plants consistently exhibited higher colonization compared with those supplied with TSP. Mycorrhizal frequency reached significantly higher colonization percent compared to TSP (Fig. 6a). Mycorrhizal intensity followed a similar trend, with higher mean values for Alga of 47.1% and 41.9%, than for TSP with 31.9% and 27.7%, although the differences were not statistically significant (Fig. 6b). Similarly, arbuscular development and abundance were significantly higher in the Alga treatments compared with TSP. P levels did not significantly influence any of the AMF colonization parameters, although a general decrease in colonization was observed when P levels increased from 30 to 60 mg kg⁻¹.

Fruit yield and P uptake

At P level of 30 mg kg⁻¹, Alga and TSP treatments produced comparable fruit numbers, averaging 12.2 fruits per pot, while at 60 mg kg⁻¹, alga yielded slightly more fruits per pot compared to TSP (not significant, Fig. 7a). However, increasing P levels from 30 mg kg⁻¹ to 60 mg kg⁻¹ resulted in a significant 33% overall increase in fruit yield across both treatments. At

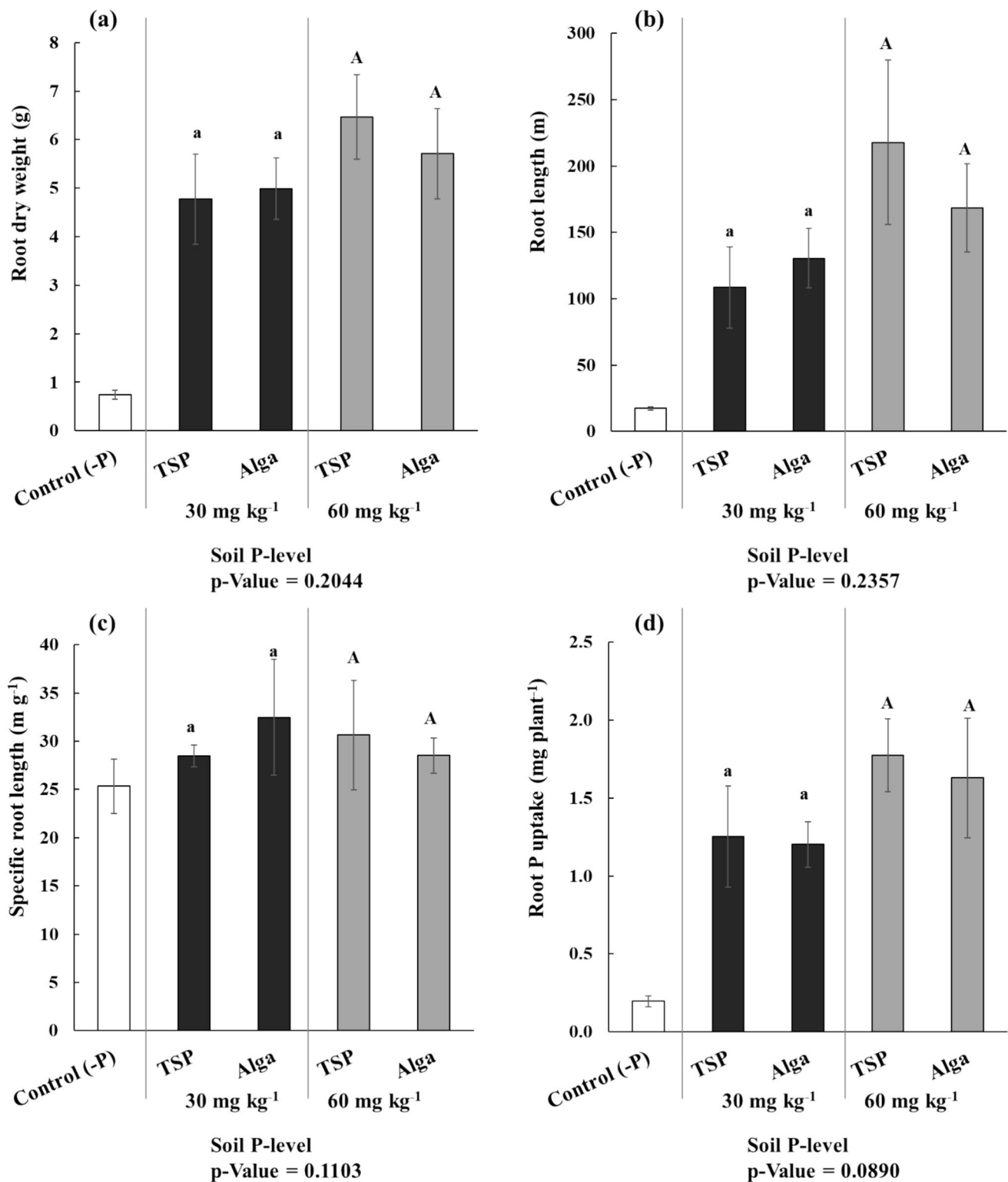


Fig. 5 The effect of P fertilizer type (Alga or TSP) and application dose (30 or 60 mg kg⁻¹) on root morphological properties and P uptake. (a) Root dry weight, (b) Average root length, (c) Specific root length, and (d) Root P uptake of tomato roots. Control treatments are not included in data analysis. Error bars represent the standard deviation for six replicates (Mean ± SD, n=6). Data was analyzed by two-way ANOVA; different letters indicate significant differences within each P-type at given P level. The p-value of P-level, regardless of P-type, is presented below the Y-axis title

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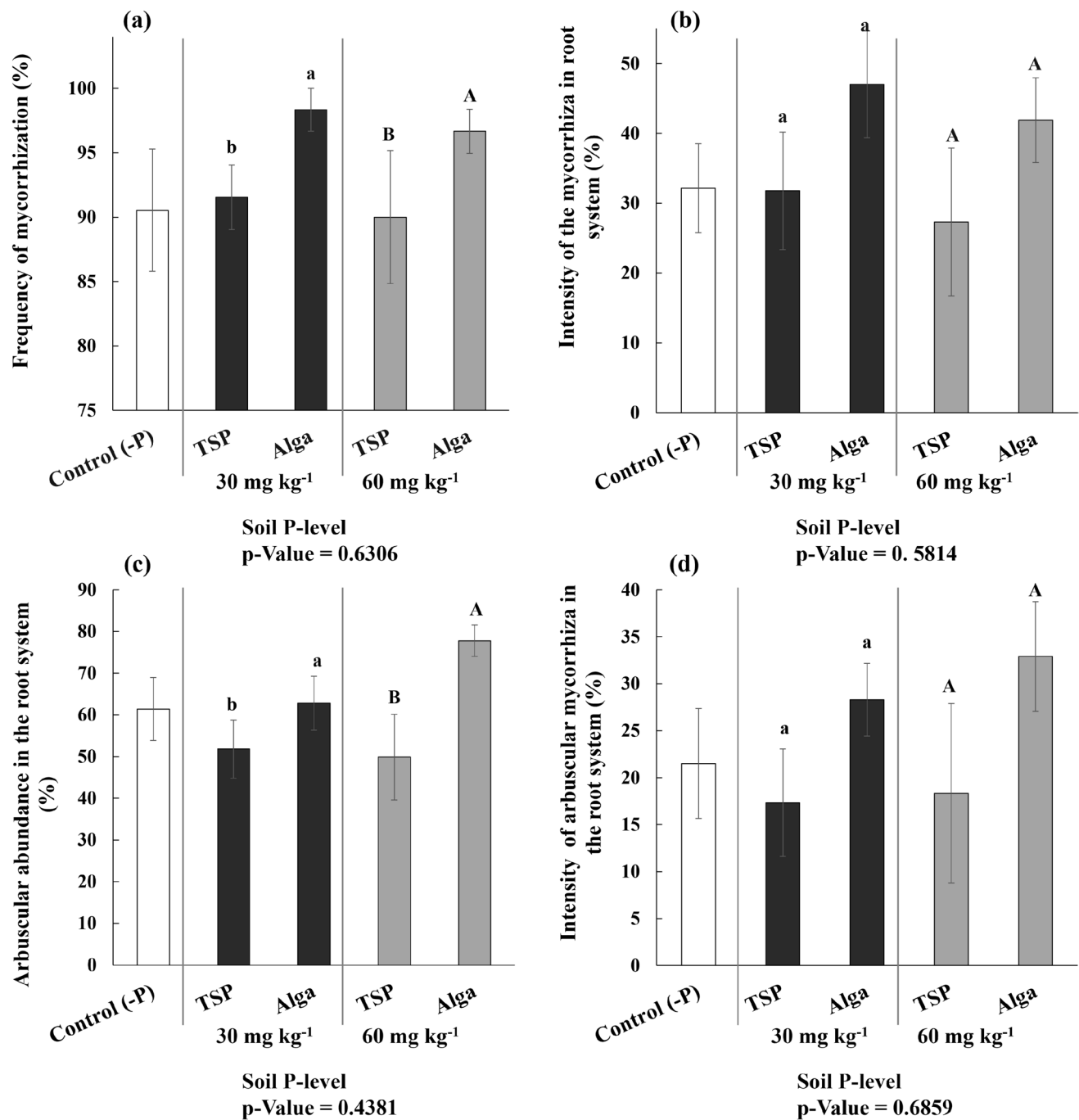


Fig. 6 The effect of P fertilizer type (Alga or TSP) and application dose (30 or 60 mg kg⁻¹) on AMF morphological parameters in tomato roots at harvest. **(a)** Frequency of mycorrhiza colonization in the root system, **(b)** Intensity of the mycorrhizal colonization in the root system, **(c)** Arbuscular abundance in the root system, and **(d)** Intensity of arbuscular mycorrhiza in the root system. Control

treatments are not included in data analysis. Error bars represent the standard deviation for six replicates (Mean $\pm$ SD, $n=6$). Data was analyzed by two-way ANOVA; different letters indicate significant differences within each P-type at given P level. The p-value of P-level, regardless of P-type, is presented below the Y-axis title

30 mg kg⁻¹, both treatments yielded similar average fruits weight per pot, while at 60 mg kg⁻¹, Alga-treated fruits weight were higher compared to TSP, although differences were insignificant. While fruit weight was consistently higher in

Alga-treated pots, statistical analysis indicated no significant differences between the two fertilizers. Increasing P levels from 30 to 60 mg kg⁻¹ significantly enhanced the total fruit weight from 355 to 453 g per pot (Fig. 7b).

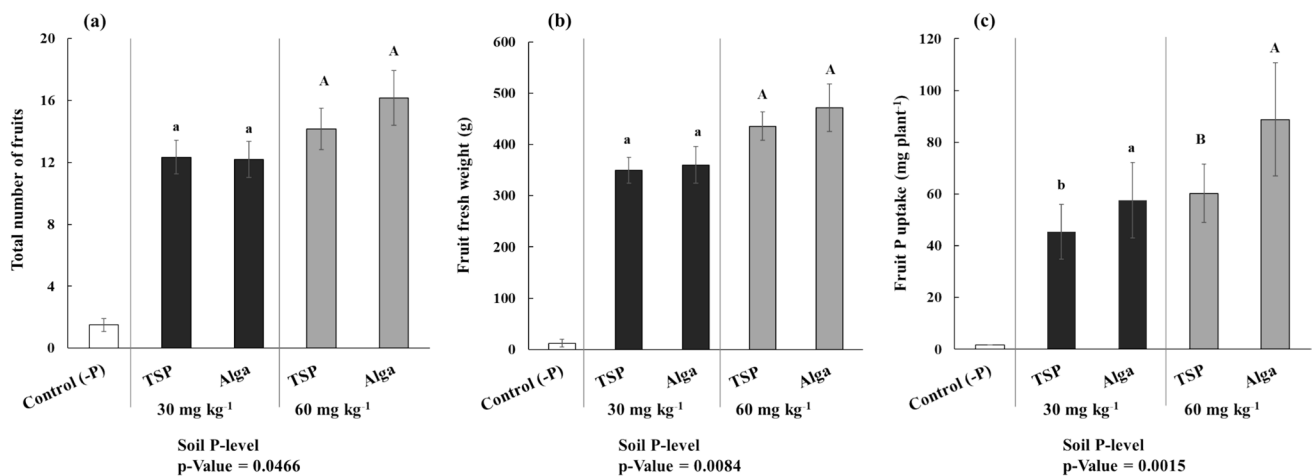


Fig. 7 The effect of P fertilizer type (Alga or TSP) and application dose (30 or 60 mg kg⁻¹) on (a) Number of fruits per pot, (b) Fresh fruit weight, and (c) Fruit P uptake. Control treatments are not included in data analysis. Error bars represent the standard deviation

The P uptake and allocation was also evaluated. At 30 mg kg⁻¹, plants treated with Alga showed statistically significant higher P uptake compared to TSP. Similarly, at 60 mg kg⁻¹ P uptake in Alga treated plants was significantly higher than in TSP. When P levels were raised from 30 to 60 mg kg⁻¹, fruit P uptake was significantly increased (Fig. 7c). Overall, across all P-amended treatments, the highest P uptake in tomato organs was observed in fruits with 63 mg plant⁻¹, followed by shoots with 31 mg plant⁻¹ and 2 mg plant⁻¹ in the roots.

TSS was analyzed as a quality parameter with no effect of P type or P level on Brix level, which were between 6 to 7 °Brix for all treatments except the control (Fig. S5).

Mineral composition of fruits

The mineral composition of harvested fruits is summarized in Table 2. In general, fruits from Alga-treated plants exhibited higher concentrations of all 11 minerals assessed compared to TSP, though the differences were statistically significant only for P. Increasing the P level from 30 to 60 mg kg⁻¹ significantly enhanced the concentrations of P, copper (Cu), and zinc (Zn) in the fruits.

Discussion

Kinetics of P uptake from wastewater and biomass accumulation

Microalgae-based technology provides a sustainable alternative to traditional wastewater treatment methods for nutrient recovery (Maity et al. 2014; Arora et al. 2020). This study

adopted the P starvation and repletion strategy outlined by Solovchenko et al. (2019), to enhance P accumulation in the algae biomass. Despite seven days of P deprivation, *Coelastrella* sp. continued to accumulate biomass, likely through cellular adaptations that optimize survival in P-limited conditions (Tan et al. 2014; Lavrinovičs et al. 2020). Upon P repletion, biomass accelerated rapidly, consistent with responses reported for other microalgae like *Desmodesmus communis* and *Tetradismus obliquus* (Lavrinovičs et al. 2020). P accumulation in biomass and the rapid P depletion from the synthetic centrate medium shows the ability of *Coelastrella* sp. to uptake P effectively, aligning with similar reports in *Chlamydomonas reinhardtii* (Plouviez et al. 2021, 2022). This result highlights *Coelastrella* sp. as a promising candidate for wastewater P recovery, given its ability to maintain growth under P starvation and efficiently accumulate P upon repletion.

Algal growth was carried out in a synthetic medium designed to mimic concentrated wastewater (centrate) with exceptionally high nutrient concentrations. The use of synthetic medium allowed the P deprivation and repletion growth method. However, the findings specifically reflect the capacity of *Coelastrella* sp. to take up and store P under those controlled conditions only. Previous studies have demonstrated that *Coelastrella* sp. can grow in real municipal and agricultural wastewater while effectively removing nutrients (Luo et al. 2016; Qader & Shekha 2023), highlighting the broader applicability of this microalga in wastewater-based cultivation systems. Centrate serves as a concentrated reservoir of phosphorus, nitrogen and potassium (Johansson et al. 2019; Munasinghe-arachchige et al. 2020), which would otherwise exacerbate environmental contamination. However, centrate also contains various

for 6 replicates (Mean ± SD, n=6). Data was analyzed by two-way ANOVA; different letters indicate significant differences within each P-type at given P level. The p-value of P-level, regardless of P-type, is presented below the Y-axis title

Table 2 The effect of P fertilizer type (Alga or TSP) and application dose (30 or 60 mg kg⁻¹) on mineral concentration in the fruits at harvest. Control treatments are not included in data analysis. Data are means ± SD (n=6). P type and P level were tested in two-way ANOVA, interaction was not significant and thus, was removed from the model. Significant p-values are in bold (p < 0.05).

Macronutrients (%)			Micronutrients (mg kg ⁻¹)									
P type	P level	P	K	Ca	Mg	S	B	Cu	Fe	Mn	Ni	Zn
TSP	30	0.17 ± 0.0	2.37 ± 0.3	0.09 ± 0.0	0.12 ± 0.0	0.15 ± 0.0	16.5 ± 4.3	8.97 ± 1.3	70.8 ± 9.1	13.23 ± 1.1	0.51 ± 0.0	28.08 ± 2.2
Alga	30	0.19 ± 0.0	2.73 ± 0.5	0.11 ± 0.0	0.13 ± 0.0	0.16 ± 0.0	20.4 ± 3.5	10.91 ± 2.7	86.6 ± 7.2	14.95 ± 2.9	1.46 ± 0.3	33.51 ± 8.2
TSP	60	0.20 ± 0.0	2.34 ± 0.2	0.08 ± 0.0	0.12 ± 0.0	0.14 ± 0.0	19.4 ± 3.2	11.18 ± 1.5	75.3 ± 6.8	13.89 ± 1.5	0.36 ± 0.2	33.29 ± 1.4
Alga	60	0.23 ± 0.0	2.58 ± 0.4	0.09 ± 0.0	0.13 ± 0.0	0.15 ± 0.0	23.0 ± 2.2	12.56 ± 1.7	81.3 ± 10	14.94 ± 4.4	0.73 ± 1.3	38.11 ± 6.1
<i>p</i> -Value												
P-type		0.05	0.11	0.09	0.15	0.07	0.18	0.12	0.32	0.26	0.07	0.07
P-level		<0.001	0.59	0.09	0.79	0.34	0.14	0.03	0.98	0.87	0.21	0.05

contaminants, such as antibiotics and heavy metals. These substances can influence algal growth rates and nutrient uptake. Consequently, the accumulation of such contaminants in algal biomass could limit its suitability for use as a biological fertilizer, given concerns about plant uptake and transmission via the food chain. These restrictions do not diminish the significance of exploring wastewater-cultivated algae as a fertilizer option. Numerous related risks may be mitigated by downstream processing, biomass mixing, and regulated application rates. In addition, the gradual nitrogen release from algal biomass may confer agronomic benefits relative to traditional fertilizers (Zou et al. 2021). Within a circular nutrient management framework, algae cultivated from wastewater provide a potential, although carefully controlled, alternative for sustainable fertilizer generation.

Extractable P release dynamics

Chemical P fertilizers are integral to modern agriculture, yet their environmental impact is considerable (Mahapatra et al. 2022; Zhang et al. 2024). To assess P release patterns, this study compared *Coelastrella* sp. with traditional available TSP fertilizer in soil incubation trial. The rapid decline in available P from TSP indicate strong immobilization in soil resulting from sorption and precipitation, a phenomenon repeatedly observed (Erel et al. 2022; Zhou et al. 2023). Conversely, alga-based amendments exhibited a more gradual P release, exceeding TSP-derived available P from day 42 onward. This behavior may be attributed to two concurrent mechanisms. First, mineralization of organic P within algal cells progressively generates plant-available P forms. Second, the gradual hydrolysis of intracellular polyphosphate (PolyP), as indicated by DAPI staining, contributes to sustained P release. PolyP hydrolysis in soil can persist for several weeks and is strongly influenced by microbial activity. In this context, the addition of algal organic matter likely stimulates soil microbial growth, thereby enhancing phosphatase activity and promoting continued P release (Lori et al. 2017). Soil P fractionation was not conducted in this study; therefore, the redistribution of Olsen-extractable P into organic or insoluble inorganic pools, which are not captured by the Olsen extraction, could not be directly resolved.

The stable extractable P level observed over 84 days highlights the beneficial of *Coelastrella* sp. potential as a biofertilizer, acting as slow-release fertilizer (Mulbry et al. 2005; Coppens et al. 2016), matching the plants' P demand at early growth stage when high P level is not immediately required (Rupawalla et al. 2021). The algal fertilizer supplied both intracellular and surface-associated P, supporting immediate and sustained P availability to plants. This finding underscores the comparative advantage of *Coelastrella* as a biofertilizer candidate and highlights its potential for further

development. Future research should focus on enhancing P uptake efficiency in *Coelastrella*, which would strengthen its applicability as an independent and sustainable P source for agricultural production.

Plant response to alga biofertilizer

The alga *Coelastrella* sp. was evaluated as a P source in a tomato pot experiment. Algae biofertilization was comparable to TSP in plant biomass and yield, while P uptake was greater in the Alga-treated plants. This is likely associated with growth-promoting substances produced by microalgae, including phytohormones precursors for auxin, which promote fruit development and lateral root formation, and salicylic acid, which contributes to plant tolerance under abiotic stress conditions, thereby collectively supporting plant growth (Oancea & Velea 2013; Chiaiese et al. 2018). The alga-based fertilizer enhanced P allocation within the plant, particularly to fruits, suggesting improved nutrient partitioning and potential gains in crop productivity. This effect is likely related to the slow-release characteristics of the biofertilizer. Micro and macronutrients were also all elevated under alga-fertilization, although not all had significant differences. Similar trends have been reported in previous studies evaluating algal-based fertilizers (Dasgan et al. 2022; Ferreira et al. 2023). This effect can be explained by polyP in the algae biomass. Several studies reported enhance uptake of Mg, Zn, Mn, and Fe under synthetic polyP fertilization, attributed to favorable chemical transformations in the soil (Gao et al. 2020; Erel et al. 2022).

It is important to note that nutrient concentrations other than P were not strictly balanced among treatments. Alga-fertilized plants received greater amount of organic matter, nitrogen, and micronutrients than those fertilized with TSP. These differences suggest that microalgae may offer a nutritional advantage, supplying a wider range of elements. Although this imbalance should be carefully considered when comparing nutrient availability across treatments, nutrient supply (except for organic matter) in both treatments was sufficient to avoid growth limitations. Consequently, the enhanced nutrient uptake observed in alga-fertilized plants cannot be attributed solely to the higher micronutrient inputs. Rather, the results indicate that micronutrient availability was influenced by the chemical form and soil dynamics of phosphorus, rather than by differences in micronutrient supply per se.

P strongly influences root development morphology (Péret et al. 2014). In this study, root development under algae fertilization was comparable to TSP. Similar findings were reported for arugula (*Eruca sativa*) and pak choi (*Brassica rapa* ssp. *chinensis*), where microalgal biofertilization did not result in significant improvements relative to synthetic fertilizers (Wuang et al. 2016). In contrast, other

species such as pea (*Pisum sativum*) and garlic (*Allium sativum*) have exhibited enhanced root elongation under organic fertilization regimes (Joshi et al. 2015). Therefore, while *Coelastrella* sp. can be an alternative to synthetic P fertilizers, its benefits for root development and morphology appear limited.

Arbuscular mycorrhizal colonization

Arbuscular mycorrhizal fungi (AMF) enhance plant P uptake, however colonization diminished by high soil P levels (Liu et al. 2014). In this study, *Coelastrella* treatments promoted AMF colonization, likely due to P within the algae occurs in less readily available polyP and organic P forms (Lynch 2011). Application of the algae biofertilizer also increases soil organic material compared to synthetic fertilizers. This promotes microbial activity and diversity, which was found to positively correlate with AMF colonization (Ferreira et al. 2021; Toren et al. 2025). TSP treatments resulted in lower AMF colonization, possibly due to the abundance of readily available P at the first days of growth (Liu et al. 2014; Riaz et al. 2022). Increasing P levels from 30 to 60 mg kg⁻¹ reduced AMF colonization in both treatments, consistent with previous findings (Wang et al. 2017). Thus, *Coelastrella* fertilization appears to promote AMF colonization, improving P accusation and potentially enhancing plant growth.

Conclusion

This study demonstrates the potential of the alga *Coelastrella* sp. for enhanced P uptake from wastewater and its application as a sustainable P fertilizer, reducing reliance on non-renewable rock phosphate. Agronomic assays revealed that *Coelastrella* can match or surpass conventional P fertilizer in extractable P in calcareous soils, with more prolonged P availability. *Coelastrella* proved as effective as TSP in supporting tomato growth and development while significantly enhancing P uptake and AMF colonization. Alga-based fertilizer promoted the uptake of several micronutrients, thereby indirectly supporting plant growth. Appropriate fertilizer management should consider the N contribution from the alga, together with its associated organic matter and micronutrient inputs. Future work should address engineering design, logistical integration, and economic feasibility to enable implementation of algae-based nutrient recovery within wastewater treatment plants.

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Data availability Data will be made available upon request.

Declarations

Competing interests The authors declare no competing interests.

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