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Partial Substitution of Synthetic Nitrogen with Organic Nitrogen Enhances Soil Fertility, Photosynthesis, and Root Growth of Grapevine Seedlings

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Abstract

The overuse of synthetic nitrogen fertilizer in vineyards degrades soil quality and poses environmental risks. Partial substitution of synthetic nitrogen with organic alternatives may enhance grapevine performance and soil sustainability, depending on the substitution rate. This study evaluated the effects of replacing synthetic nitrogen with composted spent mushroom substrate at five different rates (0%, 25%, 50%, 75%, and 100%, denoted as NOS, OS-25, OS-50, OS-75, and OS-100, respectively) and a control with no nitrogen fertilization applied (CK), on soil fertility, root growth, and photosynthetic performance in grapevine seedlings. Compared to CK, nitrogen fertilization and organic substitution significantly increased soil electrical conductivity, organic matter, and macronutrient contents, but had no significant effect on soil pH. Organic substitution markedly improved leaf photosynthetic capacity in the summer, with the highest rates observed under OS-25, exceeding CK and NOS by 32.98–63.19% and 13.93–27.38%, respectively. Root growth was also significantly enhanced by organic substitution, with OS-25 exhibiting the best performance. Fine roots in the 0.0–0.5 mm diameter class were dominant, accounting for 56.88–63.06% of total root length and 96.22–97.31% of total root tip count. Increasing substitution rates beyond 25% yielded no further improvements in photosynthesis or root growth. Mantel test analysis indicated strong positive correlations between soil fertility parameters (e.g., alkali-hydrolyzable nitrogen, available phosphorous and potassium) and both photosynthetic efficiency and root growth. These findings suggest that an appropriate substitution rate (i.e., 25%) of organic nitrogen using spent mushroom substrate effectively improves soil fertility, simultaneously optimizing photosynthetic capacity and root growth of grapevine seedlings.

Keywords: organic substitution; nitrogen; spent mushroom substrate; soil nutrients; fine roots; leaf gas exchange; perennial crops

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1. Introduction

The orchard is an important component of the world agricultural ecosystem. The global orchard area has reached 68 million ha, of which vineyard area exceeds 6.5 million ha [1]. Grape (*Vitis vinifera* L.) is one of the most popular fruits in the world,

containing beneficial bioactive substances such as anthocyanins, flavonoids, and polyphenols [2]. The grape-growing district in China accounted for 9.2% of the global vineyard area, with 13.5 million tons of grapes produced in 2023 [3]. To pursue higher yields, however, overuse of synthetic fertilizers still exists in certain vineyards. The annual input rate of synthetic nitrogen fertilizer could be as high as 550 kg N ha^{-1} [4], and the highest synthetic N input rate has exceeded 1000 kg ha^{-1} for grape production, which is significantly higher than the recommended optimum rate [5]. Excessive use of synthetic nitrogen not only leads to resource waste and increases the economic burden on farmers, but also causes issues related to soil degradation, compaction, acidification, and secondary salinization [6]. In addition, over-fertilization results in frequent non-point source pollution problems such as eutrophication, greenhouse gas emission, and nitrogen leaching [7,8].

The combination of organic and inorganic fertilizations with organic substitution of synthetic nitrogen is considered an efficient way to solve the aforementioned issues, promoting the sustainable development of vineyards. Previous studies reported that the proper organic substitution could ameliorate soil structure, increase soil organic matter (SOM) content, efficiently provide nutrients for fruit tree growth, and enhance the circular utilization of agricultural waste [9–12]. Specifically, the combination of organic and inorganic fertilizations strengthens photosynthetic capacity and stimulates the root growth of perennial crops, which ultimately increases crop yield [13,14].

Spent mushroom substrate (SMS), the culture medium waste after the harvest of edible mushrooms, is considered an important source of organic fertilizer, which contains cellulose, hemicellulose, and nutrients for crop cultivation [15]. The global edible mushroom industry is thriving, with production reaching 18.39 million tons in 2024 and projected to grow to 32.04 million tons by 2032 [16]. On average, the production of 1 kg of fresh mushrooms generates approximately 5 kg of SMS [17]. Thus, over 60 million tons of SMS are currently produced annually, with projections indicating growth to 104 million tons by 2026 [18]. Previous studies have demonstrated the agronomic benefits of SMS in agricultural systems. Experimental evidence indicates that SMS amendment elevates soil biochemical properties, including a 12–18% increase in organic carbon fractions and enhanced nutrient bioavailability (e.g., available N by 22–35%, available P by 15–28%) while stimulating microbial metabolic activity (35–50% higher soil respiration rates) [19]. Subsequent research further confirmed its plant growth-promoting effects, with rice seedling biomass increasing by 17–24% through improved rhizosphere environment [20]. These findings position SMS as a viable organic amendment for perennial crop systems, particularly in vineyard soil management [21]. However, critical knowledge gaps remain regarding its optimized application in viticulture, mainly including: (i) the substitution efficacy of SMS for synthetic nitrogen fertilizer at varying replacement ratios (calculated as percent of N equivalence) has not been systematically evaluated; and (ii) the dose-dependent effects on grapevine root architecture and photosynthetic performance parameters require quantitative characterization.

This study aimed to systematically assess the impacts of partial synthetic nitrogen fertilizer substitution with SMS on grapevine seedling performance, with a focus on soil fertility, photosynthetic efficiency, and root growth. Specifically, we sought to (i) quantify the dose-response relationships between organic substitution ratios (0–100% N equivalence) and soil fertility indicators; (ii) identify the optimal substitution threshold for maximizing photosynthetic performance and the root growth of grapevine seedlings; and (iii) elucidate potential mechanistic linkages between soil chemical indices and grapevine growth responses. We hypothesized that graded organic substitution would enhance soil fertility through elevated organic carbon and nutrient accumulations, exhibit a nonlinear effect on photosynthetic parameters with maximal benefits at intermediate substitution levels, and stimulate root growth in a concentration-dependent manner.

2. Materials and Methods

2.1. Experimental Site and Focal Species

The pot trial was conducted at Jiangsu Academy of Agricultural Sciences (32°02′01″ N, 118°52′32″ E) in Nanjing's Xuanwu District, China, under greenhouse conditions from 1 April to 28 October 2022, spanning 210 days. During the experimental period, the greenhouse maintained an average temperature of 26.2 °C and relative humidity of 66.4%. We utilized one-year-old 'Shine Muscat' grapevine seedlings as test materials, selecting specimens with uniform growth vigor for treatment. The organic fertilizer employed was derived from *Pleurotus eryngii* residue, exhibiting the following physicochemical characteristics: pH was 6.94, electrical conductivity (EC) was 3.09 mS·cm^{-1}, organic carbon content was 49.27%, total nitrogen (TN) was 2.26%, total phosphorus (TP) was 0.53%, total potassium (TK) was 0.60%, moisture content was 15.51%, C/N ratio was 21.8, and seed germination index was 92%. Basic soil characteristics prior to experimentation are detailed in Table 1.

Table 1. Basic properties of the tested soil.

Soil Texture	pH	EC (μS cm^{-1})	SOM (g kg^{-1})	TN (g kg^{-1})	Available N (mg kg^{-1})	Available P (mg kg^{-1})	Available K (mg kg^{-1})
Loam	7.19	515.3	13.2	1.06	77.29	35.16	154

2.2. Experimental Design

The experiment comprised six fertilization treatments: no basal fertilizer (CK), 0% synthetic N substitution with organic fertilizer (NOS), 25% synthetic N substitution with organic fertilizer (OS-25), 50% synthetic N substitution with organic fertilizer (OS-50), 75% synthetic N substitution with organic fertilizer (OS-75), 100% synthetic N substitution with organic fertilizer (OS-100). The basal N input (0.36 g kg^{-1} soil) was determined according to local conventional farming practices. All treatments received this rate except CK, where no basal nitrogen was applied (Table 2). Phosphorus and potassium fertilizers were applied uniformly across all treatments. Urea was top-dressed at 0.11 g kg^{-1} soil on 29 July and 17 September 2022, respectively. The synthetic fertilizers used were urea (46% N content), potassium dihydrogen phosphate (KH_2PO_4; 52% P_2O_5; and 34% K_2O content), and potassium sulfate (K_2SO_4; 52% K_2O content). The completely randomized design included 6 replicates per treatment (1 seedling per replicate; n = 36 total). The experimental setup consisted of a plastic basin measuring 40 cm in height with top and bottom inner diameters of 40 cm and 36 cm, respectively. The test soil was air-dried, mechanically ground, and sieved through a 10-mesh standard sieve. A total of 40 kg of the processed soil was homogenously mixed with mushroom residue organic fertilizer. The soil–fertilizer mixture was then transferred into cultivation pots layered with small stones at the base for drainage. Following substrate preparation, the grape seedlings were transplanted into the pots and initially irrigated with root-establishment water. Throughout the experimental period, soil moisture was systematically maintained at 60% of field capacity (FC) through controlled irrigation. All treatments received identical agronomic management except for variations in basal fertilizer composition.

Table 2. Fertilizer regime for the organic fertilizer substitution trial (g kg^{-1} soil).

Treatment	Application Rate of SMS	Organic N Input	Inorganic N Input	Total N Input of Base Fertilizer
CK	0	0	0	0
NOS	0	0	0.36	0.36
OS-25	3.97	0.09	0.27	0.36
OS-50	7.95	0.18	0.18	0.36
OS-75	11.92	0.27	0.09	0.36
OS-100	15.90	0.36	0	0.36

2.3. Soil Property Measurements

Soil samples were collected at the conclusion of the experiment and subjected to sequential processing through natural drying, grinding, and sieving prior to nutrient analysis. Soil pH and EC were measured in aqueous suspension using a calibrated pH/conductivity meter (FE28, Mettler Toledo, Zurich, Switzerland). SOM content was quantified via the potassium dichromate oxidation method with external heating. TN was determined through sulfuric acid digestion followed by semi-micro Kjeldahl distillation (K9840, Hanon, Jinan, China). Alkali-hydrolyzable nitrogen (AN) was assessed using the alkaline hydrolysis diffusion method. Available phosphorus (AP) was extracted with 0.5 M $NaHCO_3$ ($\geq$99.0% purity) and measured spectrophotometrically (UV-1800, MAPADA, Shanghai, China), while available potassium (AK) was extracted with 1M NH_4OAc ($\geq$98.0% purity) and quantified by flame photometry (BWB-XP, BWB Technologies, Newbury, UK).

2.4. Leaf Gas Exchange

Gas exchange parameters of grapevine leaves were monitored at 30-day intervals under clear, cloud-free conditions during daytime throughout the experiment. One intact and mature leaf at the same nodal position on each grape seedling was selected for measurement. Using the LI-6800 portable photosynthesis analyzer (LI-COR, Lincoln, NE, USA), photosynthetic parameters were measured using a 3 $\times$ 3 cm red-blue LED leaf chamber with the following standardized conditions: CO_2 concentration: 400 μmol mol^{-1}, Airflow rate: 0.5 L s^{-1}, Relative humidity: 60%. We measured the net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), and intercellular CO_2 concentration (Ci) between 9:00 and 11:00 a.m. The instantaneous water use efficiency (WUE) was calculated using the Pn/Tr ratio.

2.5. Root Phenotyping

Upon experimental termination, grape root systems were harvested via destructive sampling. Following thorough deionized water rinsing, fresh root samples were subjected to morphometric analysis using the WinRHIZO root scanner (Epson Expression 12000XL, Regent Instruments, Ottawa, ON, Canada) to quantify total root length, tip count, surface area, volume, and average diameter. To determine dry biomass, samples were first heat-treated at 105 °C for 30 min to terminate enzymatic activity, and subsequently oven-dried at 80 °C until constant mass was achieved.

2.6. Statistical Analyses

In this study, data processing and analysis were performed using Excel 2023 and SPSS Statistics 25.0. One-way analysis of variance (ANOVA) was applied to analyze the data from six treatments, and significant differences among the treatments were compared using the Waller–Duncan method at the $p < 0.05$ and $p < 0.01$ levels. Pearson correlation coefficients were calculated to examine the relationships between soil properties and grape

seedling growth parameters. Graphical visualizations and Mantel tests were performed using Origin 2021 and R version 4.3.1.

3. Results

3.1. Soil Chemical Properties Under Different Organic Substitution Ratios

Comparisons of soil chemical properties under different organic substitution ratios are shown in Figure 1. Soil EC, SOM, AP, AN, and AK contents exhibited significant positive correlations with increasing organic fertilizer substitution ratios. Compared with CK, the soil EC, SOM, TN, AN, AP, and AK were increased by 7.48–26.68%, 8.60–27.09%, 24.85–39.36%, 25.51–45.60%, 90.71–118.17%, 36.25–54.03%, respectively under the organic substitution treatments. The highest values of most soil parameters were observed under the OS-100 treatment, except for TN and AN, which peaked under the OS-25 treatment. Soil pH did not differ significantly among the treatments. Notably, AN content under the OS-100 treatment showed a significant 9.90% reduction compared to the NOS treatment.

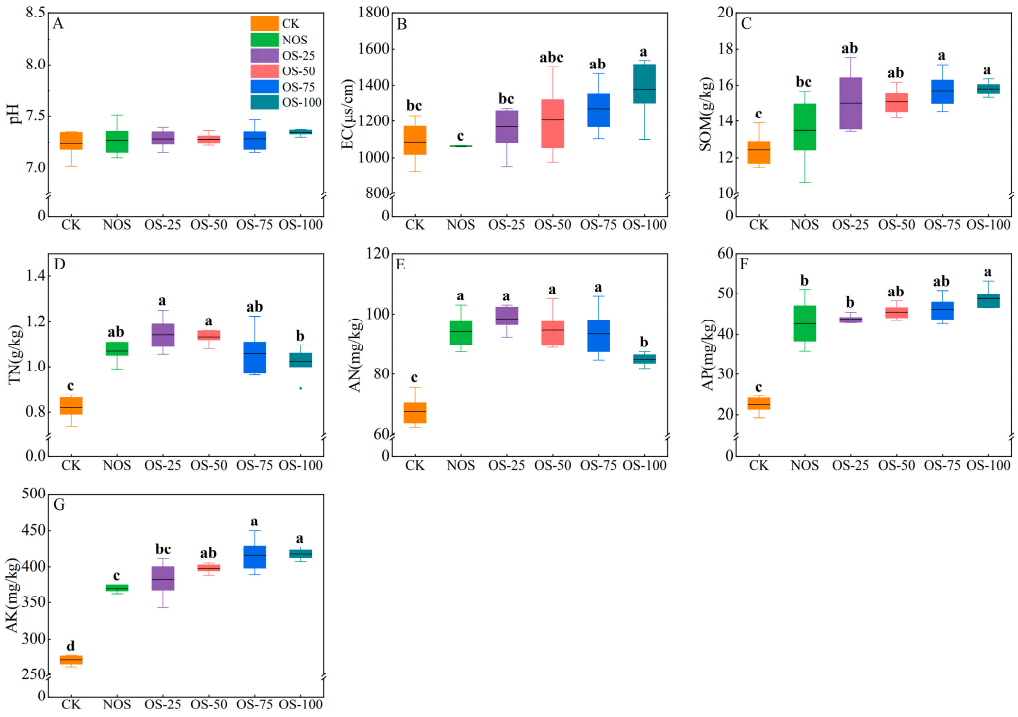

Figure 1. Soil chemical properties under different organic substitution ratios. (**A**) pH; (**B**) electrical conductivity (EC); (**C**) soil organic matter (SOM); (**D**) total nitrogen (TN); (**E**) alkali-hydrolyzable nitrogen (AN); (**F**) available phosphorous (AP); (**G**) available potassium (AK). CK: no basal fertilizer; NOS: 0% synthetic N substitution with organic fertilizer; OS-25: 25% synthetic N substitution with organic fertilizer; OS-50: 50% synthetic N substitution with organic fertilizer; OS-75: 75% synthetic N substitution with organic fertilizer; OS-100: 100% synthetic N substitution with organic fertilizer. Different lowercase letters indicate significant differences among treatments at $p < 0.05$.

3.2. Leaf Gas Exchange Under Different Organic Substitution Ratios

Variations in leaf gas exchange of grapevine under different organic nitrogen substitution treatments were shown in Figure 2 and Table S1. The Pn, Tr, and Gs of grapevine leaves showed a gradually decreasing trend over time, while the WUE showed a gradually increasing trend. During the whole growth period, the Pn of leaves was the highest under OS-25 treatment, which was 32.98–63.19% and 13.93–27.38% higher than CK and NOS treatment, respectively. The Tr and Gs were the highest in the NOS treatment in July, while the OS-25 and OS-50 treatments were higher in August. In all treatments, the Ci and WUE

of leaves fluctuated with the growth days. The Pn and Tr of leaves treated with CK and OS-100 were relatively low.

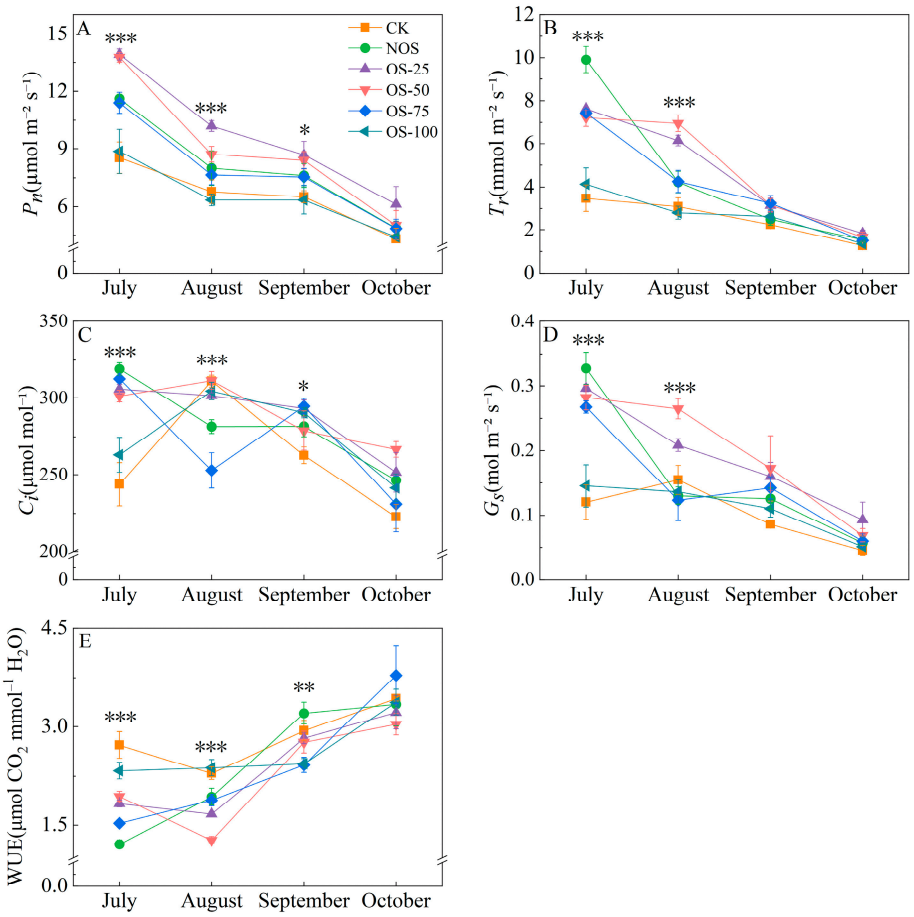

Figure 2. Leaf gas exchange under different organic substitution ratios. (**A**) Net photosynthetic rate (Pn); (**B**) transpiration rate (Tr); (**C**) intercellular CO_2 concentration (Ci); (**D**) stomatal conductance (Gs); (**E**) instantaneous water use efficiency (WUE). CK: no basal fertilizer; NOS: 0% synthetic N substitution with organic fertilizer; OS-25: 25% synthetic N substitution with organic fertilizer; OS-50: 50% synthetic N substitution with organic fertilizer; OS-75: 75% synthetic N substitution with organic fertilizer; OS-100: 100% synthetic N substitution with organic fertilizer. ***, **, * represent $p < 0.001$, 0.01, 0.05, respectively.

3.3. Root Growth Under Different Organic Substitution Ratios

The effects of organic substitution ratios on the growth of grapevine roots were significantly different, and OS-25 treatment performed the best (Figure 3). Compared with CK and OS-100 treatments, the root biomass of OS-25 treatment was significantly increased by 40.41% and 30.40%, the total root length was significantly increased by 80.15% and 56.67%, the root tip number was significantly increased by 80.41% and 54.94%, the root surface area was significantly increased by 101.55% and 33.80%, the root volume was significantly increased by 105.68% and 54.90%, and the average root diameter was significantly increased by 121.34% and 54.86%, respectively. Except for the number of root tips, other root indexes under OS-25 treatment were significantly higher than those under NOS treatment.

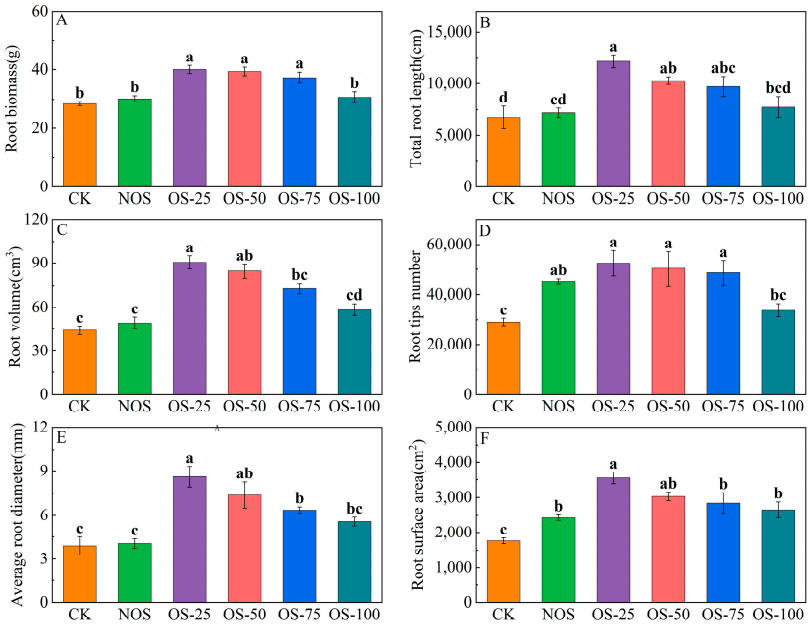

Figure 3. Root growth parameters under different organic substitution ratios. (**A**) Root biomass; (**B**) total root length; (**C**) root volume; (**D**) root tips number; (**E**) average root diameter; (**F**) root surface area. CK: no basal fertilizer; NOS: 0% synthetic N substitution with organic fertilizer; OS-25: 25% synthetic N substitution with organic fertilizer; OS-50: 50% synthetic N substitution with organic fertilizer; OS-75: 75% synthetic N substitution with organic fertilizer; OS-100: 100% synthetic N substitution with organic fertilizer. Different lowercase letters indicate significant differences among treatments at $p < 0.05$.

By analyzing the distribution ratio of fine root number of grapevines with different diameter classes, the results demonstrated that fine roots in the 0.0–0.5 mm diameter class predominated, accounting for 56.88–63.06% of the total root length and 96.22–97.31% of the total root tip count (Figure 4). Compared with CK treatment, the root length of 0.0–0.5 mm decreased by 1.56–6.18% under different organic fertilizer substitution treatments, but the root length in the range of 0.5–1.0 mm diameter increased by 1.00–2.03%, the root length in the range of 1.0–1.5 mm diameter increased by 0.28–2.31%, and the root length in the range of 1.5–2.0 mm diameter increased by 0.29–1.62%. In addition, the effect of different organic nitrogen substitution treatments on the number of fine root tips within each diameter grade was not significant.

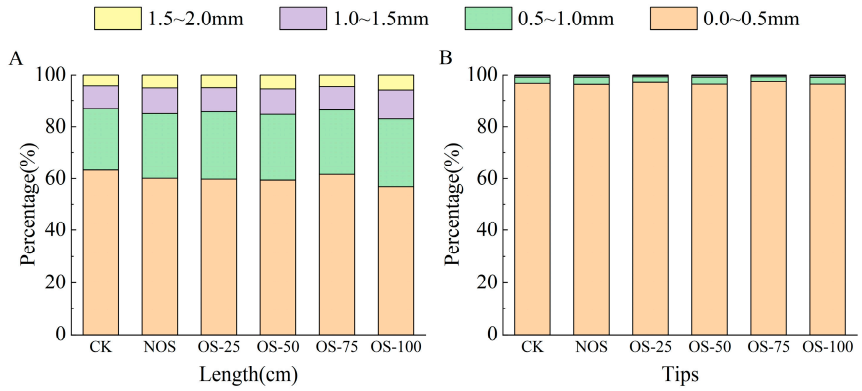

Figure 4. Distribution ratios of length and number of fine roots with different diameter grades under different organic substitution ratios. (**A**) Length of fine roots; (**B**) Number of fine roots. CK: no

basal fertilizer; NOS: 0% synthetic N substitution with organic fertilizer; OS-25: 25% synthetic N substitution with organic fertilizer; OS-50: 50% synthetic N substitution with organic fertilizer; OS-75: 75% synthetic N substitution with organic fertilizer; OS-100: 100% synthetic N substitution with organic fertilizer.

3.4. Correlations Between Soil Chemical Properties, Photosynthesis, and Root Growth of Grapevine Seedlings

A significant positive correlation was identified between the soil fertility index and the grapevine physiological index (Figure 5). The Mantel test analysis indicated that the strongest correlation was observed between root growth and AN ($p < 0.01$, $r \geq 0.4$). Root growth also showed significant correlations with TN, AP, and AK ($p < 0.01$, $0.2 < r < 0.4$), and the weakest correlation with SOM ($p < 0.05$, $r < 0.2$). Photosynthesis exhibited significant correlations with pH, SOM, and TN ($p < 0.05$, $0.2 < r < 0.4$), and highly significant correlations with AN, AP, and AK ($p < 0.01$, $0.2 < r < 0.4$). Mantel test analyses revealed intricate interactions among soil fertility parameters, root growth, and photosynthesis, which substantially influenced the nutrient utilization efficiency of grapevine.

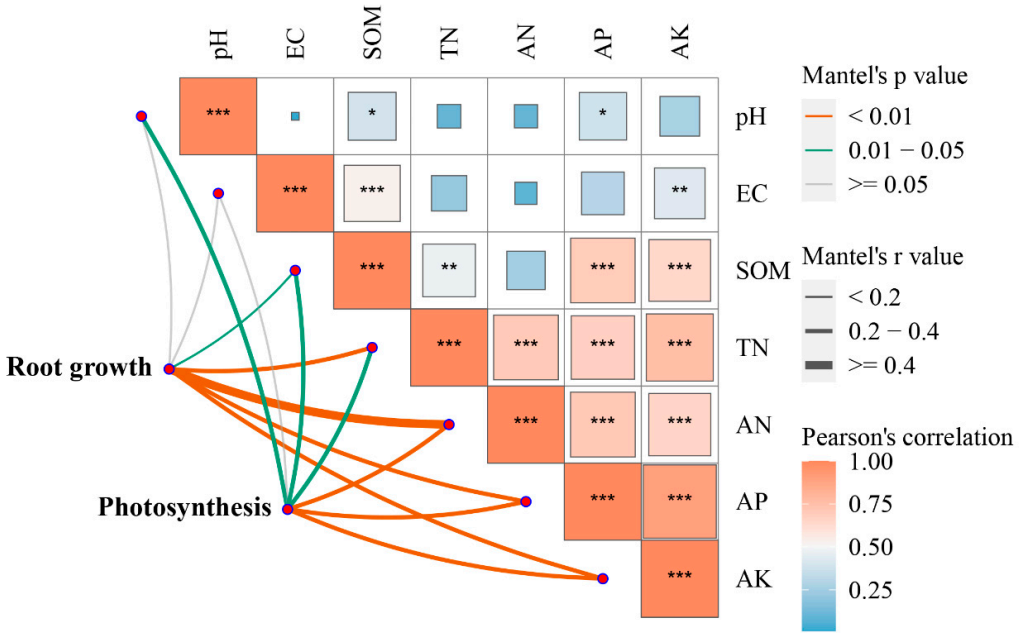

Figure 5. Mantel test for grapevine physiological indicators and soil fertility parameters. The line color corresponds to Mantel's *p* value, the line width corresponds to Mantel's r value, and the color gradient represents Pearson's r correlation coefficient. ***, **, * represent $p < 0.001$, 0.01, and 0.05, respectively.

4. Discussion

The application of organic fertilizers represents a critical strategy for improving soil nutrient retention and supply capacity. SMS contains beneficial mycelia, proteins, and essential nutrients, serving as a high-quality organic fertilizer source for horticultural soils. Previous studies have demonstrated that organic amendments enhance soil structural stability, increase carbon sequestration, stimulate microbial biomass, and improve nutrient bioavailability [22]. Our findings revealed that the partial substitution of synthetic fertilizer with organic fertilizer significantly elevated SOM content along with AP and AK levels. This improvement might be attributed to enhanced microbial activity and enzymatic processes that facilitate organic matter mineralization [23,24]. Notably, the complete replacement of synthetic nitrogen with organic fertilizer (OS-100 treatment) resulted in marginally lower TN and AN content compared to the NOS treatment. This phenomenon

may stem from the gradual mineralization patterns of organic fertilizers, which exhibit slower nutrient release kinetics relative to synthetic counterparts [25]. Interestingly, soil pH remained statistically unchanged across treatments. These collective results suggest that SMS-based nitrogen substitution constitutes an effective approach for enhancing soil carbon storage and optimizing nutrient cycling dynamics, particularly for phosphorus and potassium availability.

As the principal engine of plant biogeochemical cycling, photosynthesis serves as the foundational energy conversion mechanism sustaining crop development [26]. The findings of Chen et al. [27] demonstrated that substituting synthetic nitrogen with organic counterparts led to a significant enhancement in key photosynthetic parameters, including Tr, Gs, and Pn. This treatment resulted in 3.16–11.88% elongation of grapevine new shoots and 7.35–15.15% extension of leaf veins, which was similar to the results of this study. Our investigation revealed a dose-dependent response pattern in grapevine leaf photosynthesis to nitrogen substitution ratios. Moderate substitution levels (25–50%) optimized Pn and Tr through improved photosynthetic apparatus efficiency, whereas excessive substitution (75–100%) induced photosynthetic suppression despite concomitant increases in WUE. This paradoxical response likely originates from rhizosphere nutrient stoichiometry imbalance and depressed microbial enzymatic activity under high organic input conditions, as the photosynthetic performance of grapevine exhibited a strong correlation with soil nutrient bioavailability indices [28,29]. Organic fertilizer substitution generally enhances soil microbial activity; however, this stimulatory effect exhibits a threshold beyond which negative impacts emerge. Notably, the CK and OS-100 treatments exhibited comparable leaf photosynthetic performance despite substantial differences in nitrogen supply. As a high C/N ratio organic amendment, SMS induced progressive mineral N immobilization with increasing substitution rates. Microbial communities fixated substantial soil mineral N to meet growth demands, potentially causing short-term nutrient competition (particularly N) with grapevine seedlings and disrupting nutrient balance [30]. At the same time, the mono-application of high-proportion organic fertilizer may adversely affect the structural and functional diversity of soil microbial communities [31]. These findings delineate an optimal substitution threshold where organic amendments maximize photosynthetic efficiency without inducing soil metabolic dysregulation.

The root system serves as a vital organ for crop development and yield optimization. The substitution of synthetic nitrogen with organic nitrogen induces structural and nutritional modifications in soil, which may consequently influence root morphology and functional capacity [32]. Previous research has demonstrated that the application of organic fertilizer significantly enhances the root system architecture of rice seedlings, manifested as a 12.42–27.82% increase in root length, 18.62–24.95% augmentation in root tip number, and 2.01–26.29% improvement in root activity [33]. These morphological and biochemical improvements demonstrate notable congruence with the rhizospheric responses observed in the current investigation. In this study, partial substitution of synthetic nitrogen with organic nitrogen significantly enhanced grapevine root development metrics, including root biomass, total length, root tip density, surface area, volumetric expansion, and average diameter. These morphological improvements facilitated more efficient nutrient and water acquisition by root systems. While amino acids and humic substances in SMS may stimulate fine root development, we observed diminishing returns at higher substitution ratios. Specifically, excessive nitrogen replacement by SMS (beyond optimal levels) failed to further promote root growth. This phenomenon may be attributed to the strong positive correlation between grape root development and balanced soil fertility factors, and nutrient imbalances and altered microbial activity induced by disproportionate organic inputs [28,29]. Additionally, immature grapevine root systems under high nutrient con-

centrations may experience fine root necrosis and biomass reduction, ultimately inhibiting growth. Meanwhile, this study reveals that root growth achieved optimal performance at a 25% organic fertilizer substitution rate. While minimal differences in nitrogen supply were observed between the NOS and OS-25 treatments, grapevine seedling root systems exhibited highly significant morphological differences. This suggests that an appropriate organic substitution ratio enhances SOM, creating favorable nutrient conditions for microbial activity. It significantly alters the microbial community structure, ultimately establishing an improved soil environment conducive to both microbial processes and root development.

5. Conclusions

This study demonstrated that the partial substitution of synthetic nitrogen fertilizer with SMS enhanced soil nutrient availability while promoting root development and the photosynthetic performance of grapevine seedlings. Our findings reveal a complex soil–plant interaction, where soil fertility parameters significantly influence grapevine root morphogenesis and photosynthetic efficiency—key determinants of seedling vigor and nutrient acquisition efficiency. Notably, the substitution effects followed a distinct hormetic response: increasing SMS proportions initially enhanced but ultimately suppressed these physiological parameters when exceeding optimal levels. Specifically, higher substitution rates (i.e., >50% synthetic nitrogen replacement) failed to further improve soil nitrogen pools (TN and AN), photosynthetic indices, or root system architecture. The 25% SMS substitution treatment (OS-25) emerged as optimal, significantly elevating SOM content and demonstrating synergistic benefits for both root plasticity and photosynthetic capacity. However, future investigations should prioritize long-term field trials to evaluate (i) SMS-induced changes in vineyard soil biology; (ii) the temporal stability of the observed benefits; and (iii) potential legacy effects on grapevine productivity. These longitudinal studies will enable comprehensive assessment of SMS as a sustainable alternative to conventional fertilization in viticulture systems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/nitrogen6030049/s1, Table S1: Data on grapevine leaf gas exchange measurements.

Author Contributions: Conceptualization, Y.M. and X.M.; methodology, X.M.; software, F.H.; validation, F.H. and X.M.; formal analysis, F.H., S.W. and X.M.; investigation, F.H., B.J., W.W. and X.M.; resources, X.M.; data curation, F.H. and X.M.; writing—original draft preparation, F.H. and X.M.; writing—review and editing, F.H., S.W., J.W. and X.M.; visualization, F.H. and X.M.; supervision, X.M.; project administration, X.M.; funding acquisition, S.W., J.W. and X.M. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest.

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