

Article

Allelopathic Inhibition Associated with Ecological Stoichiometric Imbalance

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Abstract

Phenolic acids are considered important allelochemicals that can restrict nutrient uptake and inhibit plant growth. Most existing studies have focused on growth phenotypes and single nutrient changes under phenolic acid stress, while the coupled C:N:P balance responses of plant–soil systems remain poorly characterized. Ecological stoichiometry offers a holistic perspective to reveal the nutrient supply–demand mismatch underlying allelopathic inhibition by analyzing elemental ratio dynamics, thus deepening the mechanistic understanding of allelopathy beyond traditional single-indicator observations. Using lettuce (*Lactuca sativa* L.) as the test plant, this study investigated the effects of cinnamic acid (CA) and p-hydroxybenzoic acid (PHA) stress, combined with nitrogen (N), phosphorus (P), and their combined application (NP) on plant growth and plant C, N, and P stoichiometric characteristics. Soil C, N, and P contents and stoichiometric characteristics were further analyzed as supplementary indicators. The results showed that phenolic acid stress significantly reduced lettuce biomass: PHA decreased aboveground biomass by 40.11% and belowground biomass by 44.14%, with a stronger inhibitory effect than CA. Both phenolic acids induced marked stoichiometric imbalance, characterized primarily by a sharp decline in leaf nitrogen content; N content dropped by 49.80% under CA and 70.75% under PHA, corresponding to a 64.43% and 162.79% increase in leaf C:N ratio, and a 37.63% and 63.19% decrease in leaf N:P ratio, respectively. Nutrient addition alleviated these responses to varying degrees: N addition mainly promoted biomass recovery and elevated plant N status, P addition optimized elemental ratios, and combined NP application yielded the strongest overall recovery. Correlation and redundancy analyses indicated that soil C, N, and P stoichiometric characteristics were closely associated with plant growth, with soil organic carbon and total phosphorus identified as major explanatory variables associated with plant growth. Overall, phenolic acid stress altered plant stoichiometric characteristics and growth, as well as soil C, N, and P stoichiometric characteristics, while nutrient addition partially alleviated these responses. These findings provide a stoichiometric perspective for understanding allelopathic stress and may offer a theoretical basis for nutrient management under continuous cropping conditions.



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1. Introduction

Allelopathy refers to the beneficial or detrimental effects of metabolites released by plants or microorganisms on other organisms in the surrounding environment. This

process plays an important role in maintaining ecosystem and regulating interspecific interactions [1,2]. However, allelopathy is often manifested as growth inhibition. Allelochemicals released from root exudates or plant residue decomposition can accumulate in soil and negatively affect plant growth [3,4].

Among various allelochemicals, phenolic acids are widely recognized as one of the major active compounds responsible for allelopathic inhibition due to their broad sources, chemical stability, and tendency to accumulate in soils [5,6]. Previous studies have shown that phenolic acids can affect plant growth by altering cell membrane permeability and inhibiting cell division. In addition, they can interfere with the uptake, allocation, and utilization of carbon (C), nitrogen (N), and phosphorus (P) within plants, thereby disrupting ecological stoichiometric balance and its distribution patterns, ultimately leading to changes in plant biomass [7]. For example, Chen et al. [8] reported that high concentrations of coumaric acid restricted phosphorus uptake in *Dalbergia odorifera* seedlings, resulting in reduced biomass. Wu et al. [9] found that phenolic acids such as cinnamic derivatives limited nitrogen and phosphorus uptake in cucumber seedlings. However, most relevant studies have focused on growth phenotypes and single nutrient changes, while few have systematically interpreted allelopathic stress from a holistic ecological stoichiometry perspective. How phenolic acid stress reshapes plant C:N:P stoichiometric balance, with soil elemental status as an associated background factor, rather than merely altering individual nutrient concentrations, has not been fully characterized.

Ecological stoichiometry provides an important theoretical framework for understanding plant nutrient use and its responses to environmental changes. According to this framework, the concentrations and ratios of C, N, and P in plant tissues can comprehensively reflect nutrient uptake, allocation, and utilization strategies [10]. Compared with single growth indicators, stoichiometric ratios can more sensitively reveal the internal nutrient supply–demand imbalance under environmental stress and help identify the limiting elements behind growth inhibition, thus providing a deeper perspective for interpreting allelopathic mechanisms. Under favorable conditions, plants are generally able to maintain relative stability in internal elemental composition through physiological regulation, thereby sustaining a balanced nutrient status [11,12]. However, this internal balance can easily be disrupted under environmental stress, leading to shifts in elemental concentrations and ratios and consequently altering nutrient limitation patterns [13]. Therefore, ecological stoichiometry can integrate changes in nutrient uptake, allocation, and elemental balance, providing insights into plant nutrient responses that cannot be obtained from growth characteristics alone.

Exogenous nutrient addition is widely regarded as an effective approach to alleviate nutrient limitation in plants [14]. By supplementing limiting nutrients, it can not only promote plant growth but also help restore internal elemental balance through adjustments in nutrient stoichiometry. Yan et al. [15] reported that phosphorus addition under P-limited conditions significantly increased leaf P concentration and promoted the growth of *Arabidopsis thaliana*. Similarly, Wang et al. [16] found that P fertilization markedly improved the growth of *Pinus massoniana* under phosphorus limitation and restored its elevated N:P ratio to a more balanced level. However, how plant ecological stoichiometric characteristics respond to exogenous nutrient addition under phenolic acid stress remains insufficiently understood.

Taken together, existing studies have confirmed that phenolic acid stress interferes with plant nutrient uptake and induces growth inhibition and have preliminarily observed its association with changes in elemental stoichiometry. However, most relevant studies have focused on the stress effect itself, while targeted regulation research from the holistic ecological stoichiometry perspective remains scarce. It is still unclear whether exogenous

nutrient addition can restore the stoichiometric homeostasis of the plant–soil system under phenolic acid stress, and how the stoichiometric recovery patterns differ among nitrogen addition, phosphorus addition, and their combined application. This knowledge gap restricts the development of precise nutrient regulation strategies for allelopathy-induced continuous cropping obstacles.

Lactuca sativa L. (commonly known as lettuce), a typical leafy vegetable cultivated in protected systems, is characterized by a short growth cycle and high sensitivity to environmental changes [17,18]. It is also particularly susceptible to the accumulation of phenolic acids under continuous cropping, making it an ideal model for studying allelopathic effects and nutrient regulation [19,20].

Cinnamic acid (CA) and *p*-hydroxybenzoic acid (PHA) are commonly reported autotoxic components in rhizosphere soils of continuously cropped vegetables and have been widely adopted as model allelochemicals in controlled simulation studies due to their stable allelopathic activity [1]. Huang et al. [21] reported that the accumulation of cinnamic acid in the rhizosphere of cowpea can induce autotoxicity, while Živković et al. [22] identified *p*-hydroxybenzoic acid as a major active compound in extracts of *Sorghum halepense* rhizomes that significantly inhibited weed growth.

Given the ecological relevance of these two phenolic acids and the suitability of lettuce as a sensitive test organism for allelopathic studies, a controlled pot experiment was designed to explore the stoichiometric regulation patterns of nutrient addition under phenolic acid stress. On this basis, we proposed three testable hypotheses:

- (1) Phenolic acid stress disrupts lettuce's C:N:P stoichiometric balance and presents a stoichiometric pattern of relative nitrogen shortage;
- (2) Exogenous nutrient addition can alleviate phenolic acid-induced growth inhibition and partially restore the disrupted plant C:N:P stoichiometric balance;
- (3) The restoration efficacy of nutrient addition is associated with the degree of stoichiometric imbalance: targeted addition of the nutrient element with more severe relative deficiency will yield a better recovery effect on both plant growth and stoichiometric balance.

Overall, this study focuses on characterizing the C:N:P stoichiometric responses of lettuce to phenolic acid stress and exogenous nutrient addition, with soil stoichiometric indicators included for auxiliary interpretation. The findings may provide a preliminary theoretical reference for nutrient management in vegetable continuous cropping systems.

2. Materials and Methods

2.1. Study Site

The experiment was conducted from November to December 2025 in a greenhouse and laboratory at the School of Agricultural Engineering, Jiangsu University (32.2032° N, 119.5109° E), China. Natural light conditions were applied, and the temperature in the greenhouse ranged from 5 to 20 °C.

2.2. Experimental Design

2.2.1. Plant Materials and Soil

Lettuce (*Lactuca sativa* L., Italian bolting-resistant cultivar) was used as the test plant. The phenolic acids applied were cinnamic acid (CA) and *p*-hydroxybenzoic acid (PHA). The experimental soil was collected from the top layer (0–20 cm) of a local vegetable field near Jiangsu University. The soil was classified as loam, with the following initial physicochemical properties: pH 6.78, EC 0.32 mS·cm^{−1}, soil organic carbon (SOC) 16.5 g·kg^{−1}, total nitrogen (TN) 1.16 g·kg^{−1}, and total phosphorus (TP) 0.72 g·kg^{−1}. Available nutrients and microbial parameters were not determined in this study.

2.2.2. Experimental Procedure

Phenolic acid concentrations were set at $0.5 \text{ g}\cdot\text{L}^{-1}$ for CA and $5 \text{ g}\cdot\text{L}^{-1}$ for PHA, determined based on preliminary experiments and published allelopathy studies [23]. These concentrations, higher than natural field rhizosphere levels, were chosen to induce stable growth inhibition under controlled conditions for clear observation of stoichiometric responses. A total of 120 pots were established, including 20 pots for the control (CK), 50 pots for the CA treatment, and 50 pots for the PHA treatment. The experiment was conducted in two stages.

In the first stage (phenolic acid stress before nutrient addition), seeds were sown on 30 October 2025. On 20 November, uniform seedlings at the six-leaf stage were transplanted into pots containing 2 kg of soil. After a one-week acclimation period, all pots were transferred to the greenhouse. From 27 November, 200 mL of the corresponding phenolic acid solution was applied daily to the soil surface of each treatment, while the control received the same volume of distilled water. Surface application was adopted to ensure uniform and reproducible phenolic acid exposure among treatments under controlled experimental conditions. The implications of this application method are discussed in the Discussion Section. The phenolic acid treatment was terminated on 10 December when clear stress symptoms appeared. At this stage, destructive sampling was conducted, with three pots randomly selected from each treatment to determine plant growth and plant and soil C, N, and P characteristics.

In the second stage (nutrient addition), the remaining plants were continuously cultivated from 11 December. Based on the CA and PHA treatments, four nutrient treatments were established: no nutrient addition, nitrogen addition (N), phosphorus addition (P), and combined nitrogen and phosphorus addition (NP), with 10 replicates per treatment. A control group without phenolic acid or nutrient addition throughout the experiment was maintained to simulate normal growth conditions and to evaluate the recovery effect of nutrient addition after phenolic acid stress.

The total amount of fertilizer applied in each treatment is listed in Table 1. To ensure consistent potassium levels across treatments, potassium was supplemented using potassium sulfate. Fertilizers were dissolved in 1000 mL of water and applied in two equal doses at 7-day intervals over a period of two weeks. On 25 December, three pots from each treatment were randomly selected for sampling to determine plant biomass, plant and soil C, N, and P contents, and their stoichiometric characteristics.

Table 1. Total fertilizer input for each treatment ($\text{g}\cdot\text{pot}^{-1}$).

Treatment	Code	Potassium Sulfate (K_2O 50%)	Urea (N 46%)	Monopotassium Phosphate (P_2O_5 52%, K_2O 34%)
Control	CK	0.49	0	0
Cinnamic acid	T_{CA}	0.49	0	0
Cinnamic acid + N	$T_{\text{CA-N}}$	0.49	0.54	0
Cinnamic acid + P	$T_{\text{CA-P}}$	0.10	0	0.44
Cinnamic acid + NP	$T_{\text{CA-NP}}$	0.10	0.54	0.44
p-Hydroxybenzoic acid	T_{PHA}	0.49	0	0
p-Hydroxybenzoic acid + N	$T_{\text{PHA-N}}$	0.49	0.54	0
p-Hydroxybenzoic acid + P	$T_{\text{PHA-P}}$	0.10	0	0.44
p-Hydroxybenzoic acid + NP	$T_{\text{PHA-NP}}$	0.10	0.54	0.44

2.3. Sample Collection

At the end of the cultivation experiment, whole lettuce plants were carefully excavated. Rhizosphere soil was gently removed, and the roots were rinsed with deionized water. The plants were then separated into aboveground and belowground parts, heated at 105 °C for 30 min to deactivate enzymes, and subsequently oven-dried at 60 °C to a constant weight. After cooling, dry weights were measured to determine aboveground biomass (AGB) and belowground biomass (BGB).

Meanwhile, three to five fully expanded leaves were collected from each plant as samples for the determination of leaf organic carbon (LOC), leaf total nitrogen (LTN), and leaf total phosphorus (LTP). The samples were labeled and stored in a desiccator prior to analysis.

After plant sampling, soil samples were collected from the 0–5 cm layer using a soil auger. The samples were air-dried at room temperature, ground, and sieved before being stored in sealed bags. These samples were used to determine soil organic carbon (SOC), total nitrogen (STN), and total phosphorus (STP), and were stored in a desiccator until analysis.

2.4. Measurements

Plant biomass was determined using an electronic balance with a precision of 0.001 g.

Leaf organic carbon (LOC) was measured using the $K_2Cr_2O_7$ oxidation–spectrophotometric method. Leaf total nitrogen (LTN) was determined using the H_2SO_4 – H_2O_2 digestion method, and leaf total phosphorus (LTP) was measured via the molybdenum–antimony colorimetric method following H_2SO_4 – H_2O_2 digestion.

Soil organic carbon (SOC) was determined using the $K_2Cr_2O_7$ oxidation–spectrophotometric method. Soil total nitrogen (STN) was measured using the semi-micro Kjeldahl method, and soil total phosphorus (STP) was determined using the H_2SO_4 – $HClO_4$ digestion method.

2.5. Statistical Analysis

Data were initially processed using Microsoft Excel 2021. One-way and two-way analysis of variance (ANOVA), Pearson correlation analysis, and Tukey's honestly significant difference (HSD) test were performed using SPSS 27.0 (IBM, Armonk, NY, USA). Redundancy analysis (RDA) was conducted using Canoco 5.

For the first stress stage (only phenolic acid factor), one-way analysis of variance (one-way ANOVA) was used to test the differences among CK, T_{CA} , and T_{PHA} , followed by Tukey's HSD test for multiple comparisons.

For the second nutrient regulation stage, two-way ANOVA with a 2×4 factorial design was conducted to examine the main effects of phenolic acid type (two levels: CA, PHA) and nutrient treatment (four levels: no nutrient addition, N, P, NP), as well as their interaction effect on plant biomass, leaf nutrient concentrations and stoichiometric ratios. The same analytical framework was applied to soil stoichiometric indicators as supplementary analyses. The CK treatment served as a baseline reference and was not included as a factor level in the two-way ANOVA.

3. Results

3.1. Effects of Phenolic Acid Stress on Lettuce Growth and Stoichiometric Characteristics of Leaves and Soil

3.1.1. Biomass

Aboveground biomass (AGB) and belowground biomass (BGB) reflect the growth status of the shoot and root systems, respectively, and are important indicators of overall plant growth and its response to stress. As shown in Figure 1, under phenolic acid stress

in the first stage of this study, both treatments resulted in a decrease in lettuce biomass compared with CK, with a greater reduction observed under T_{PHA} . Specifically, AGB and BGB decreased by 35.06% and 37.84% under T_{CA} , and by 40.11% and 44.14% under T_{PHA} , respectively. According to Tukey's HSD multiple comparison test, these differences were statistically significant ($p < 0.05$).

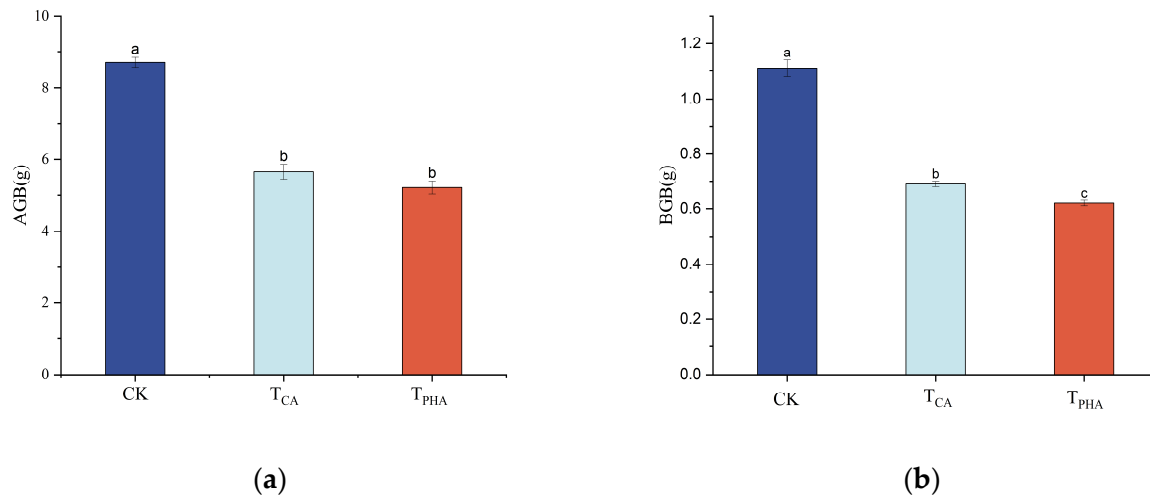


Figure 1. Aboveground biomass (AGB) and belowground biomass (BGB) of lettuce under different phenolic acid treatments before nutrient addition. (a) and (b) show AGB and BGB, respectively, under control (CK), cinnamic acid (T_{CA}), and p-hydroxybenzoic acid (T_{PHA}) treatments. Error bars represent standard deviation. Different lowercase letters indicate significant differences among treatments based on Tukey's HSD test at $p < 0.05$.

3.1.2. C, N, and P Stoichiometric Characteristics of Lettuce

Leaf C, N, and P contents and their stoichiometric ratios reflect nutrient uptake, accumulation, and allocation within plants. In the first stage of this study, phenolic acid treatments reduced leaf C, N, and P contents and altered their ratios, indicating a disruption of stoichiometric balance (Figure 2). Specifically, leaf C, N, and P contents decreased by 20.14%, 49.80%, and 20.43% under T_{CA} , and by 25.84%, 70.75%, and 22.55% under T_{PHA} , respectively. The reduction in N was the most pronounced, resulting in increases in C:N of 64.43% and 162.79% and decreases in N:P of 37.63% and 63.19% under T_{CA} and T_{PHA} , respectively. According to Tukey's HSD multiple comparison test, compared with CK, T_{CA} treatment significantly decreased leaf N content and the N:P ratio ($p < 0.05$), whereas its effects on leaf C and P contents, C:N, and C:P were not significant. T_{PHA} treatment significantly decreased leaf N and P contents and the N:P ratio and significantly increased the C:N ratio compared with CK ($p < 0.05$), whereas its effects on leaf C content and C:P were not significant.

3.1.3. Soil C, N, and P Stoichiometric Characteristics

In studies of ecological stoichiometric characteristics, soil organic C, total N, and total P contents, together with their stoichiometric ratios, are commonly used to characterize soil nutrient pool characteristics and their balance relationships [24] (Figure 3). Under phenolic acid stress in the first stage, all indicators showed varying degrees of change. Compared with CK, soil C, N, and P contents decreased under T_{CA} by 13.49%, 39.31%, and 9.52%, respectively. Under T_{PHA} , soil C content decreased by 38.63%, N content showed little change, and P content increased by 14.29%. In terms of stoichiometric ratios, soil C:N increased by 42.33% under T_{CA} , but decreased by 37.78% under T_{PHA} . The C:P ratio showed little change under T_{CA} , whereas it decreased by 46.47% under T_{PHA} . In addition, soil N:P decreased under both treatments, with reductions of 32.67% and 13.15% under T_{CA}

and T_{PHA}, respectively. According to Tukey's HSD multiple comparison test, compared with CK, T_{CA} treatment significantly decreased soil C and N contents and the N:P ratio, while significantly increasing the C:N ratio ($p < 0.05$); however, its effects on soil P content and the C:P ratio were not significant. T_{PHA} treatment significantly decreased soil C content and the C:N and C:P ratios compared with CK ($p < 0.05$), whereas its effects on soil N and P contents and the N:P ratio were not significant.

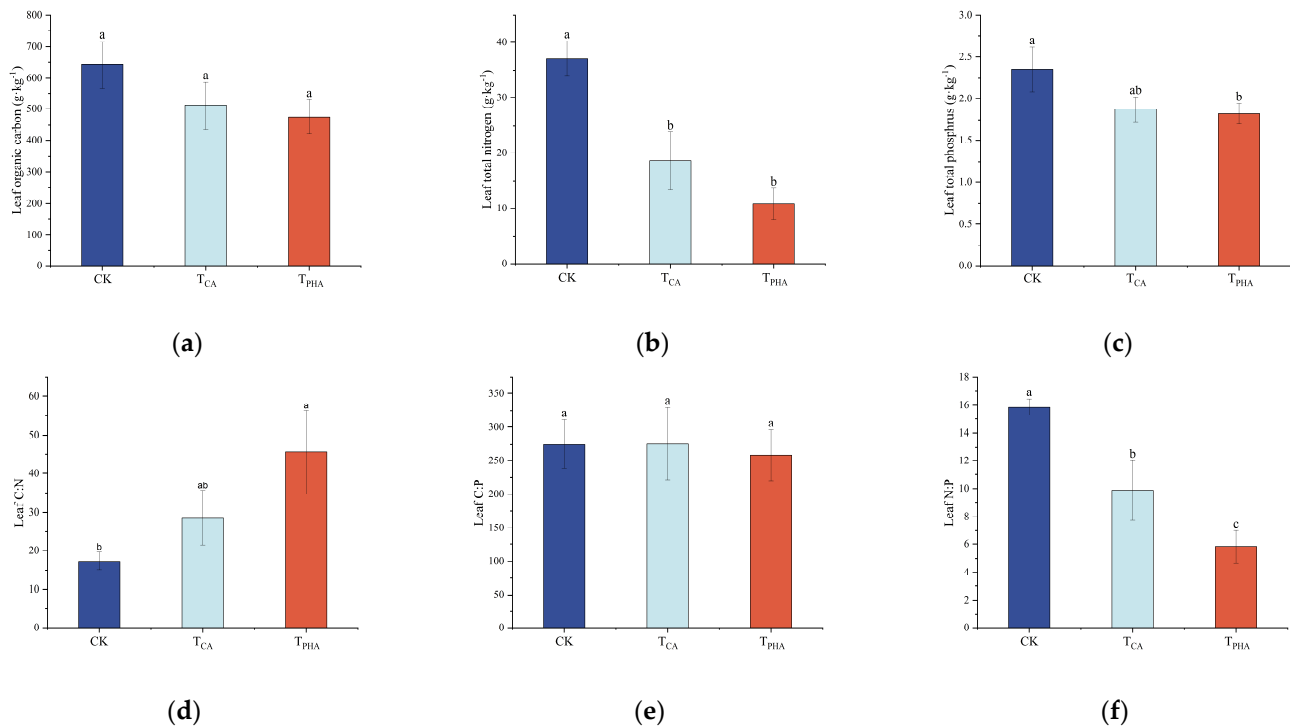


Figure 2. Leaf organic carbon (LOC), total nitrogen (LTN), and total phosphorus (LTP) contents, as well as their stoichiometric ratios in lettuce under different phenolic acid treatments before nutrient addition. (a–c) show LOC, LTN, and LTP contents, respectively; (d–f) show leaf C:N, C:P, and N:P ratios, respectively, under control (CK), cinnamic acid (T_{CA}), and p-hydroxybenzoic acid (T_{PHA}) treatments. Error bars represent standard deviation. Different lowercase letters indicate significant differences among treatments based on Tukey's HSD test at $p < 0.05$.

3.2. Effects of Nutrient Addition on Lettuce Growth and Leaf and Soil Stoichiometric Characteristics Under Phenolic Acid Stress

The results from the first stage showed that phenolic acid stress had already affected lettuce growth and the stoichiometric characteristics of both plants and soil, mainly manifested as reduced biomass and a nitrogen-associated stoichiometric imbalance. Based on this, the second stage introduced exogenous nutrient addition to regulate nutrient supply, aiming to evaluate the responses of plant stoichiometric characteristics to nutrient addition under phenolic acid stress, with soil stoichiometric characteristics included as supplementary analyses. Two-way ANOVA with a 2×4 factorial design was employed to test the main effects of phenolic acid type and nutrient treatment, as well as their interaction effect. Therefore, this section further analyzes the effects of different nutrient addition treatments on lettuce growth, as well as leaf and soil C, N, and P contents and their stoichiometric relationships under phenolic acid stress.

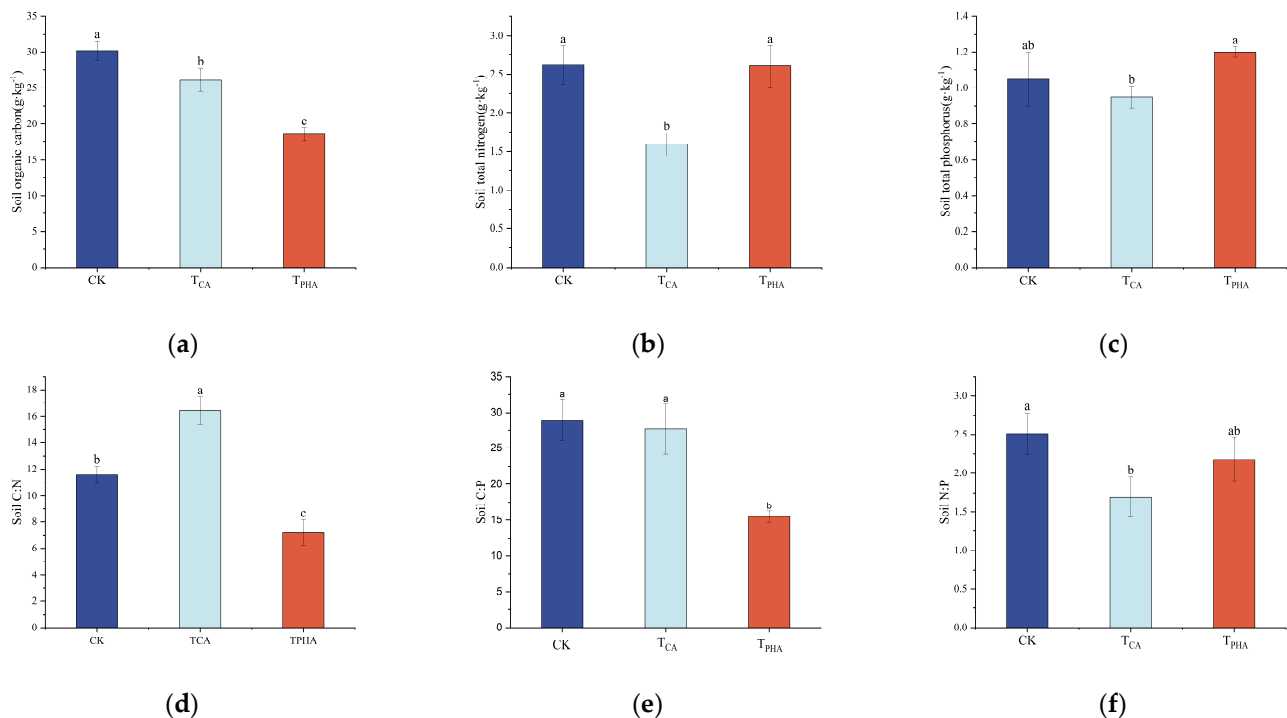


Figure 3. Soil organic carbon (SOC), total nitrogen (STN), and total phosphorus (STP) contents, as well as their stoichiometric ratios under different phenolic acid treatments before nutrient addition. (a–c) show SOC, STN, and STP contents, respectively; (d–f) show soil C:N, C:P, and N:P ratios, respectively, under control (CK), cinnamic acid (T_{CA}), and p-hydroxybenzoic acid (T_{PHA}) treatments. Error bars represent standard deviation. Different lowercase letters indicate significant differences among treatments based on Tukey’s HSD test at $p < 0.05$.

3.2.1. Biomass

As shown in Table 2, the two-way ANOVA results demonstrate that nutrient treatment exerted a highly significant main effect on both AGB and BGB ($F = 24.510$, $p < 0.01$; $F = 15.813$, $p < 0.01$), while phenolic acid type and the interaction between phenolic acid type and nutrient treatment had no significant effect on biomass ($p > 0.05$). The absence of a significant interaction suggests that the response of lettuce biomass to nutrient addition was broadly similar under CA and PHA stress.

From the variation in lettuce biomass under different nutrient addition treatments, it can be seen that under CA stress, biomass decreased markedly in the absence of nutrient addition, but showed a recovery trend following nutrient input. Both T_{CA-N} and T_{CA-P} increased AGB and BGB to some extent, with the strongest recovery observed under T_{CA-NP}. Specifically, compared with T_{CA}, AGB increased by 28.15% and 9.52% under T_{CA-N} and T_{CA-P}, respectively, while T_{CA-NP} almost restored AGB (only 1.97% lower than CK), and BGB recovered to 1.57 g. According to Tukey’s HSD multiple comparison test, compared with T_{CA}, neither T_{CA-N} nor T_{CA-P} significantly affected AGB or BGB ($p > 0.05$), whereas T_{CA-NP} significantly increased both AGB and BGB ($p < 0.05$).

Under PHA stress, lettuce biomass was also at a low level without nutrient addition and exhibited varying degrees of recovery following nutrient input. Both T_{PHA-N} and T_{PHA-P} increased AGB and BGB, with T_{PHA-NP} showing the most pronounced recovery effect. Specifically, compared with T_{PHA}, AGB increased by 24.96% and 27.30% under T_{PHA-N} and T_{PHA-P}, respectively, while T_{PHA-NP} increased AGB to 10.44 g (only 6.45% lower than CK), and BGB recovered to 1.55 g. According to Tukey’s HSD multiple comparison test, compared with T_{PHA}, T_{PHA-N} significantly increased BGB ($p < 0.05$), but its effect on AGB was not significant ($p > 0.05$); T_{PHA-P} did not significantly affect either biomass

parameter, whereas $T_{\text{PHA-NP}}$ significantly increased both AGB and BGB compared with T_{PHA} ($p < 0.05$).

Table 2. Effects of different treatments on aboveground biomass (AGB) and belowground biomass (BGB) of lettuce under phenolic acid stress.

Phenolic Acid Type	Nutrient Treatment	Code	AGB (g)	BGB (g)
Control	Control	CK	11.16 ± 0.33 a	1.65 ± 0.05 a
CA	None	T_{CA}	7.14 ± 0.64 cd	1.34 ± 0.04 cd
	N	$T_{\text{CA-N}}$	9.15 ± 1.51 abc	1.42 ± 0.07 bcd
	P	$T_{\text{CA-P}}$	7.82 ± 0.33 cd	1.36 ± 0.03 cd
	NP	$T_{\text{CA-NP}}$	10.94 ± 0.37 a	1.57 ± 0.03 ab
PHA	None	T_{PHA}	6.89 ± 0.45 d	1.29 ± 0.02 d
	N	$T_{\text{PHA-N}}$	8.61 ± 0.44 bcd	1.47 ± 0.01 bc
	P	$T_{\text{PHA-P}}$	8.77 ± 1.07 bcd	1.44 ± 0.04 bcd
	NP	$T_{\text{PHA-NP}}$	10.44 ± 0.30 ab	1.55 ± 0.14 ab
Two-way ANOVA	Phenolic acid type		NS	NS
	Nutrient treatment		**	**
	Phenolic acid $\times$ nutrient		NS	NS

Note: Data are presented as the mean $\pm$ standard deviation ($n = 3$). Different lowercase letters in the same column indicate significant differences among all treatments at $p < 0.05$ according to Tukey's HSD test. Two-way ANOVA is performed based on a 2×4 factorial design (excluding CK); ** indicates $p < 0.01$, while NS indicates no significant difference. Degrees of freedom: phenolic acid type $df = 1$; nutrient treatment $df = 3$; interaction $df = 3$.

3.2.2. C, N, and P Stoichiometric Characteristics of Lettuce

As shown in Table 3, the two-way ANOVA results indicate that nutrient treatment had a highly significant main effect on leaf total nitrogen ($F = 26.747$, $p < 0.01$), leaf C:N ratio ($F = 20.234$, $p < 0.01$) and leaf N:P ratio ($F = 22.256$, $p < 0.01$). Phenolic acid type and the interaction between the two factors showed no significant effect on all leaf C, N, P contents and their stoichiometric ratios ($p > 0.05$), indicating that the stoichiometric response of lettuce leaves to nutrient regulation was stable across different phenolic acid stresses.

Table 3. Effects of exogenous nutrient addition on leaf C, N, P contents of lettuce and their stoichiometric ratios under phenolic acid stress.

Phenolic Acid Type	Nutrient Treatment	Code	Leaf Organic Carbon ($\text{g} \cdot \text{kg}^{-1}$)	Leaf Total Nitrogen ($\text{g} \cdot \text{kg}^{-1}$)	Leaf Total Phosphorus ($\text{g} \cdot \text{kg}^{-1}$)	Leaf C:N	Leaf C:P	Leaf N:P
Control	Control	CK	839.91 ± 58.41 a	34.09 ± 3.58 a	2.65 ± 0.32 a	24.93 ± 4.19 c	320.80 ± 55.92 a	12.90 ± 1.29 a
CA	None	T_{CA}	543.19 ± 89.89 b	9.10 ± 2.16 cd	2.41 ± 0.44 a	61.30 ± 13.14 ab	228.66 ± 38.16 ab	3.76 ± 0.23 de
	N	$T_{\text{CA-N}}$	629.57 ± 30.94 b	21.48 ± 2.32 b	2.15 ± 0.15 a	29.45 ± 1.96 c	294.91 ± 34.93 ab	10.09 ± 1.78 ab
	P	$T_{\text{CA-P}}$	622.46 ± 45.87 b	16.63 ± 3.24 bc	3.08 ± 0.66 a	38.17 ± 5.76 bc	206.97 ± 36.35 b	5.41 ± 0.19 cde
	NP	$T_{\text{CA-NP}}$	578.76 ± 12.32 b	21.33 ± 2.70 b	2.70 ± 0.22 a	27.47 ± 3.90 c	215.38 ± 20.89 ab	7.91 ± 0.89 bcd
PHA	None	T_{PHA}	559.45 ± 66.45 b	7.37 ± 1.94 d	2.31 ± 0.34 a	79.07 ± 19.32 a	243.98 ± 31.00 ab	3.15 ± 0.42 e
	N	$T_{\text{PHA-N}}$	628.56 ± 61.38 b	22.73 ± 4.30 b	2.42 ± 0.29 a	28.15 ± 4.33 c	261.64 ± 37.60 ab	9.59 ± 2.91 abc
	P	$T_{\text{PHA-P}}$	626.52 ± 44.91 b	10.05 ± 2.29 cd	2.98 ± 0.29 a	64.98 ± 17.85 ab	212.18 ± 29.62 b	3.36 ± 0.51 e
	NP	$T_{\text{PHA-NP}}$	574.70 ± 57.93 b	19.31 ± 4.28 b	2.78 ± 0.29 a	30.30 ± 3.58 c	209.41 ± 43.68 b	7.10 ± 2.37 bcde
Two-way ANOVA	Phenolic acid type		NS	NS	NS	NS	NS	NS
	Nutrient treatment		NS	**	NS	**	NS	**
	Phenolic acid $\times$ nutrient		NS	NS	NS	NS	NS	NS

Note: Data are presented as the mean $\pm$ standard deviation ($n = 3$). Different lowercase letters in the same column indicate significant differences among all treatments at $p < 0.05$ according to Tukey's HSD test. Two-way ANOVA is performed based on a 2×4 factorial design (excluding CK); ** indicates $p < 0.01$, while NS indicates no significant difference. Degrees of freedom: phenolic acid type $df = 1$; nutrient treatment $df = 3$; interaction $df = 3$.

From the variation in plant C, N, and P contents and their stoichiometric ratios under CA stress with different nutrient addition treatments, it can be seen that, in the absence of nutrient addition, CA stress reduced C, N, and P contents, with the most pronounced decrease observed for N, accompanied by an increase in C:N and decreases in C:P and N:P. Specifically, compared with CK, C, N, and P contents decreased by 35.33%, 73.32%, and 9.06%, respectively, while C:N increased by 145.9%, and C:P and N:P decreased by 28.72% and 70.85%, respectively. According to Tukey's HSD multiple comparison test, compared with CK, T_{CA} had significant effects on C and N contents as well as C:N and N:P ($p < 0.05$), whereas the effect on P content and C:P was relatively weak and not significant ($p > 0.05$).

Under nutrient addition, all treatments promoted the recovery of nutrient contents and regulated stoichiometric relationships to varying degrees. Compared with T_{CA} , T_{CA-N} increased C and N contents, accompanied by a decrease in C:N and an increase in N:P; T_{CA-P} primarily increased P content and reduced C:N; T_{CA-NP} increased C, N, and P contents simultaneously, with decreases in C:N and increases in N:P. Specifically, under T_{CA-N} , N and C contents increased by 136.04% and 15.90%, respectively, with C:N decreasing by 51.96% and N:P increasing by 168.35%. Under T_{CA-P} , P content increased by 27.80%, and C:N decreased by 37.74%. Under T_{CA-NP} , N and P contents increased by 134.40% and 12.03%, respectively, while C:N decreased by 55.18% and N:P increased by 110.37%. According to Tukey's HSD multiple comparison test, compared with T_{CA} , T_{CA-N} significantly increased leaf N content and the N:P ratio, and significantly decreased the C:N ratio ($p < 0.05$), whereas its effects on leaf C, P, and C:P were not significant. T_{CA-P} did not significantly affect leaf C, N, P, C:N, C:P, or N:P compared with TCA ($p > 0.05$). T_{CA-NP} significantly increased leaf N content and significantly decreased the C:N ratio ($p < 0.05$), whereas its effects on leaf C, P, C:P, and N:P were not significant ($p > 0.05$).

From the variation in plant C, N, and P contents and their stoichiometric ratios under PHA stress with different nutrient addition treatments, it can be seen that, in the absence of nutrient addition, T_{PHA} reduced C, N, and P contents, with the most pronounced decrease observed for N, accompanied by an increase in C:N and decreases in C:P and N:P. Specifically, compared with CK, C, N, and P contents decreased by 33.39%, 78.38%, and 12.83%, respectively, while C:N increased by 217.13%, and C:P and N:P decreased by 23.95% and 75.58%, respectively. According to Tukey's HSD multiple comparison test, compared with CK, T_{PHA} had significant effects on C and N contents as well as C:N and N:P ($p < 0.05$), whereas the effects on P content and C:P were relatively weak and not significant ($p > 0.05$).

Under nutrient addition, all treatments promoted the recovery of nutrient contents and regulated stoichiometric relationships to varying degrees. Compared with T_{PHA} , T_{PHA-N} increased C and N contents, accompanied by a decrease in C:N and an increase in N:P; T_{PHA-P} primarily increased P content and slightly regulated C:N, with limited effects on N:P; T_{PHA-NP} increased C, N, and P contents simultaneously, with decreases in C:N and increases in N:P. Specifically, under T_{PHA-N} , N and C contents increased by 208.41% and 12.36%, respectively, with C:N decreasing by 64.40% and N:P increasing by 204.44%. Under T_{PHA-P} , P content increased by 29.00%, with C:N decreasing by 17.81% and N:P increasing by 6.67%. Under T_{PHA-NP} , C, N, and P contents increased by 2.73%, 162.01%, and 20.35%, respectively, while C:N decreased by 61.68% and N:P increased by 125.40%. According to Tukey's HSD multiple comparison test, compared with T_{PHA} , T_{PHA-N} significantly increased leaf N content and the N:P ratio, and significantly decreased the C:N ratio ($p < 0.05$), whereas its effects on leaf C, P, and C:P were not significant. T_{PHA-P} did not significantly affect leaf C, N, P, C:N, C:P, or N:P compared with T_{PHA} . T_{PHA-NP} significantly increased leaf N content and significantly decreased the C:N ratio ($p < 0.05$), whereas its effects on leaf C, P, C:P, and N:P were not significant.

3.2.3. Soil C, N, and P Stoichiometric Characteristics

As shown in Table 4, two-way ANOVA revealed that phenolic acid type exerted highly significant main effects on soil organic carbon ($F = 167.012$, $p < 0.01$), total nitrogen ($F = 27.934$, $p < 0.01$), total phosphorus ($F = 61.118$, $p < 0.01$), soil C:N ratio ($F = 82.132$, $p < 0.01$) and soil C:P ratio ($F = 219.731$, $p < 0.01$), whereas its effect on the soil N:P ratio was not significant ($p > 0.05$). Nutrient treatment significantly affected soil total nitrogen ($F = 21.466$, $p < 0.01$), total phosphorus ($F = 12.492$, $p < 0.01$) and soil N:P ratio ($F = 6.216$, $p < 0.05$), but had no significant effects on soil organic carbon, soil C:N ratio or soil C:P ratio (all $p > 0.05$). Notably, significant interaction effects between phenolic acid type and nutrient treatment were observed for soil total nitrogen ($F = 19.308$, $p < 0.01$), soil C:N ratio ($F = 12.170$, $p < 0.01$) and soil N:P ratio ($F = 10.986$, $p < 0.01$), indicating that the main effect of nutrient treatment alone could not fully reflect its actual regulatory effect under different allelopathic backgrounds. Therefore, combined with the research objective of clarifying nutrient regulation patterns under specific stress conditions, the responses of soil C, N, and P stoichiometric characteristics to nutrient addition are presented separately for CA and PHA systems below.

Table 4. Effects of exogenous nutrient addition on C, N, P contents and their stoichiometric ratios of soil under phenolic acid stress.

Phenolic Acid Type	Nutrient Treatment	Code	Soil Organic Carbon (g·kg ⁻¹)	Soil Total Nitrogen (g·kg ⁻¹)	Soil Total Phosphorus (g·kg ⁻¹)	Soil C:N	Soil C:P	Soil N:P
Control	Control	CK	31.55 ± 3.12 a	2.73 ± 0.37 bc	1.12 ± 0.16 bc	11.60 ± 0.49 bc	28.20 ± 1.55 a	2.43 ± 0.14 ab
CA	None	T _{CA}	27.07 ± 1.68 a	1.72 ± 0.12 d	0.97 ± 0.09 c	15.82 ± 2.03 a	28.09 ± 1.23 a	1.80 ± 0.29 bc
	N	T _{CA-N}	30.59 ± 1.57 a	2.13 ± 0.23 cd	1.16 ± 0.07 bc	14.46 ± 1.49 ab	26.56 ± 2.85 ab	1.85 ± 0.22 bc
	P	T _{CA-P}	27.86 ± 1.00 a	1.81 ± 0.21 d	1.19 ± 0.07 ab	15.52 ± 1.57 ab	23.40 ± 1.88 b	1.52 ± 0.27 c
	NP	T _{CA-NP}	29.89 ± 0.95 a	3.50 ± 0.35 a	1.18 ± 0.05 bc	8.59 ± 0.88 cd	25.35 ± 0.44 ab	2.97 ± 0.24 a
PHA	None	T _{PHA}	19.89 ± 2.43 b	2.68 ± 0.28 bc	1.23 ± 0.03 ab	7.49 ± 1.37 d	16.10 ± 1.89 c	2.18 ± 0.28 bc
	N	T _{PHA-N}	21.88 ± 0.50 b	2.88 ± 0.15 ab	1.30 ± 0.06 ab	7.61 ± 0.58 cd	16.92 ± 1.04 c	2.23 ± 0.15 abc
	P	T _{PHA-P}	21.92 ± 1.12 b	2.75 ± 0.23 bc	1.42 ± 0.05 a	7.97 ± 0.27 cd	15.51 ± 1.30 c	1.95 ± 0.23 bc
	NP	T _{PHA-NP}	22.05 ± 1.09 b	2.78 ± 0.13 bc	1.31 ± 0.05 ab	9.38 ± 2.39 cd	16.83 ± 0.22 c	1.87 ± 0.44 bc
Two-way ANOVA	Phenolic acid type		**	**	**	**	**	NS
	Nutrient treatment		NS	**	**	NS	NS	*
	Phenolic acid × nutrient		NS	**	NS	**	NS	**

Note: Data are presented as the mean ± standard deviation ($n = 3$). Different lowercase letters in the same column indicate significant differences among all treatments at $p < 0.05$ according to Tukey's HSD test. Two-way ANOVA is performed based on a 2×4 factorial design (excluding CK); * indicates $p < 0.05$, ** indicates $p < 0.01$, while NS indicates no significant difference. Degrees of freedom: phenolic acid type $df = 1$; nutrient treatment $df = 3$; interaction $df = 3$.

From the variation in soil C, N, and P contents and their stoichiometric ratios under CA stress with different nutrient addition treatments, it can be seen that, in the absence of nutrient addition, T_{CA} reduced soil C, N, and P contents, with the most pronounced decrease observed for N, accompanied by an increase in C:N, a decrease in N:P, and little change in C:P. Specifically, compared with CK, soil C, N, and P contents decreased by 14.20%, 37.00%, and 13.39%, respectively, while C:N increased by 36.38%, N:P decreased by 25.93%, and C:P decreased slightly by 0.39%. According to Tukey's HSD multiple comparison test, compared with CK, T_{CA} had significant effects on soil N contents as well as C:N ($p < 0.05$), whereas the effects on C and P content as well as C:P and N:P were relatively weak and not significant ($p > 0.05$).

Under nutrient addition, all treatments regulated soil nutrient contents and stoichiometric relationships to varying degrees. Compared with T_{CA}, T_{CA-N} increased soil N content and reduced C:N; T_{CA-P} primarily increased soil P content, with little effect on N; T_{CA-NP} increased both N and P contents, accompanied by decreases in C:N and C:P and an increase in N:P. Specifically, under T_{CA-N}, N content increased by 23.84%. Under T_{CA-P}, P content increased by 22.68%. Under T_{CA-NP}, N and P contents increased by 28.21% and

5.36%, respectively, while C:N and C:P decreased by 25.95% and 10.11%, respectively, and N:P increased by 22.22%. According to Tukey's HSD multiple comparison test, compared with T_{CA} , T_{CA-N} did not significantly affect any measured soil indicator ($p > 0.05$). T_{CA-P} significantly increased soil P content and significantly decreased the soil C:P ratio ($p < 0.05$), whereas the other indicators were not significantly affected ($p > 0.05$). T_{CA-NP} significantly increased soil N content and the soil N:P ratio, and significantly decreased the soil C:N ratio ($p < 0.05$), whereas the other indicators were not significantly affected ($p > 0.05$).

From the variation in soil C, N, and P contents and their stoichiometric ratios under PHA stress with different nutrient addition treatments, it can be seen that, in the absence of nutrient addition, T_{PHA} decreased soil C content and increased P content, while N content changed little, accompanied by decreases in C:N, C:P, and N:P. Specifically, compared with CK, soil C, N, and P contents decreased by 36.96%, 1.83%, and increased by 9.82%, respectively, while C:N, C:P, and N:P decreased by 35.43%, 42.91%, and 10.29%, respectively. According to Tukey's HSD multiple comparison test, compared with CK, T_{PHA} had significant effects on soil C content as well as C:N and C:P ($p < 0.05$), whereas the effects on N and P contents and N:P were relatively weak and not significant ($p > 0.05$).

Under nutrient addition, all treatments regulated soil nutrient contents and stoichiometric relationships to varying degrees. Compared with T_{PHA} , T_{PHA-N} increased soil N content and promoted the recovery of C and P contents; T_{PHA-P} primarily increased soil P content, with little effect on N; T_{PHA-NP} promoted the recovery of soil C, N, and P contents simultaneously. Specifically, under T_{PHA-N} , N content increased by 7.46%. Under T_{PHA-P} , P content increased by 15.45%. Under T_{PHA-NP} , C content increased by 10.86%, while relatively high levels of N and P were maintained. According to Tukey's HSD multiple comparison test, compared with T_{PHA} , T_{PHA-N} , T_{PHA-P} , and T_{PHA-NP} did not significantly affect soil C, N, P, C:N, C:P, or N:P ($p > 0.05$), although some indicators showed increasing or decreasing trends.

3.3. Relationships Between Soil Factors and Plant Traits: Correlation and Redundancy Analyses

Under CA stress, the results of correlation analysis and RDA among different nutrient addition treatments are shown in Figure 4a,b. Plant biomass (AGB and BGB) was significantly positively correlated with LOC, LTN, leaf N:P, SOC, and STP ($p < 0.05$), but showed highly significant negative correlations with Leaf C:N and soil C:N ($p < 0.01$).

The RDA results indicate that the first and second axes explained 70.36% and 4.25% of the total variation, respectively, with a cumulative explanation of 74.61%, suggesting that soil factors effectively explained the variation in plant traits under CA stress. Forward selection further identified SOC ($p = 0.008$) and STP ($p = 0.022$) as major explanatory variables, explaining 27.4% and 34.4% of the variation, respectively, indicating that soil carbon and phosphorus played important roles in regulating plant growth and stoichiometric characteristics under CA stress.

The correlation and RDA results for plants under PHA stress are presented in Figure 4c,d. Plant biomass (AGB and BGB) was significantly positively correlated with LOC, LTN, leaf N:P, STP, and soil N:P ($p < 0.05$), while showing a highly significant negative correlation with leaf C:N ($p < 0.01$).

The RDA results show that the first and second axes explained 78.21% and 3.82% of the variation, respectively, with a cumulative explanation of 82.03%, indicating a strong explanatory power of soil factors for plant trait variation under PHA stress. Forward selection further revealed that STP was the major explanatory variable ($p = 0.002$), explaining 75.3% of the variation, whereas soil N:P, SOC, STN, soil C:P, and soil C:N showed relatively low contributions and were not significant. These results suggest that soil phosphorus-

related stoichiometric characteristics were closely associated with plant trait variation under PHA stress.

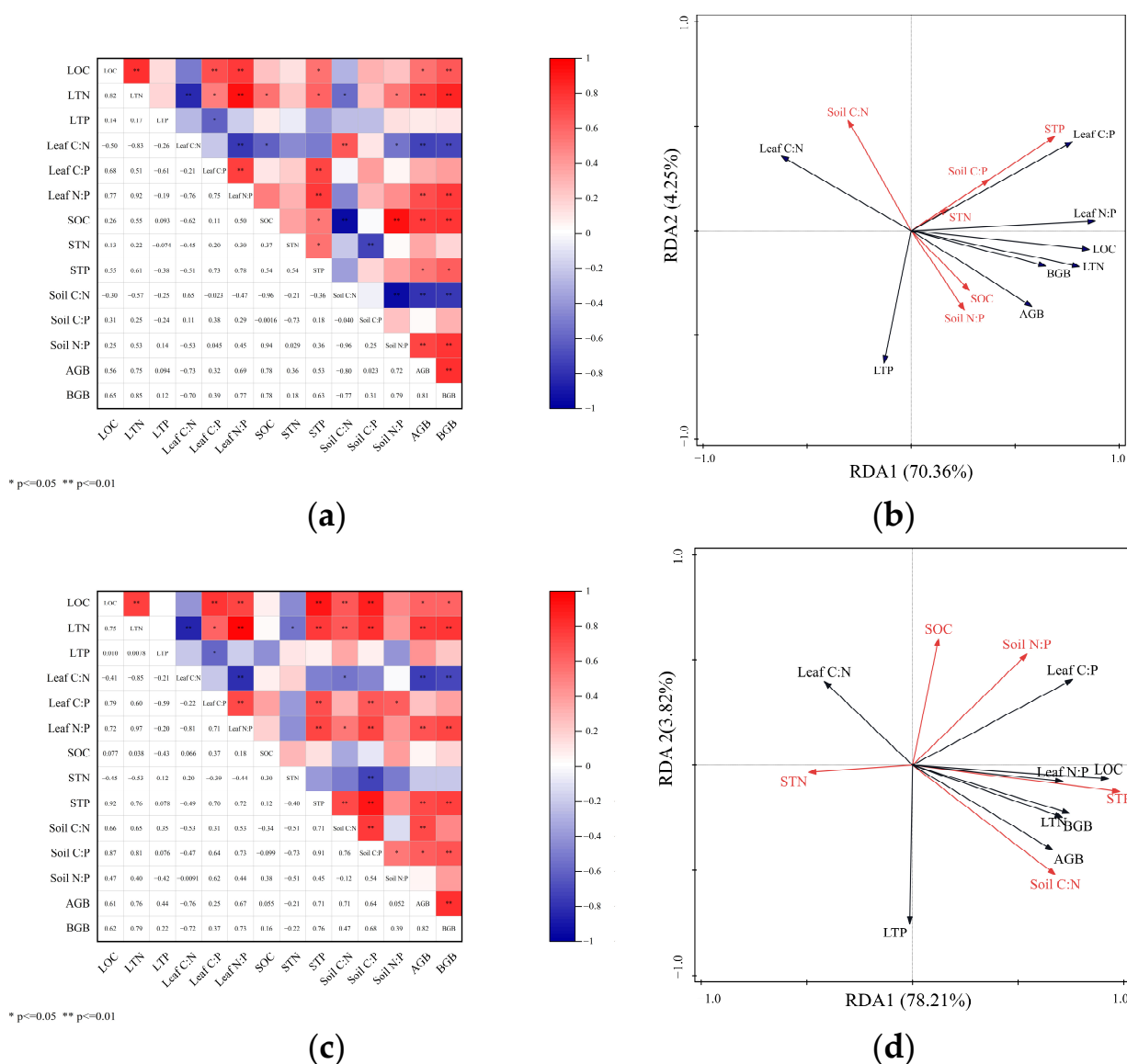


Figure 4. Correlation analysis and redundancy analysis (RDA) of plant and soil variables under phenolic acid stress. (a,b) represent the correlation heatmap and RDA results under cinnamic acid (T_{CA}) treatment, respectively, while (c,d) represent those under p-hydroxybenzoic acid (T_{PHA}) treatment. In the correlation heatmaps, colors indicate the strength and direction of correlations (red for positive and blue for negative correlations), and asterisks denote significant correlations ($p < 0.05$, $p < 0.01$). In the RDA plots, blue arrows represent plant variables and red arrows represent soil variables; arrow length indicates the strength of the relationship, and the angle between arrows reflects the correlation among variables.

4. Discussion

4.1. Effects of Phenolic Acid Stress on Lettuce Growth and Plant–Soil Stoichiometric Characteristics

This study applied phenolic acids via surface drenching at relatively high concentrations to establish pronounced allelopathic stress in a controlled pot system. This method was chosen to ensure consistent and reproducible stress intensity, facilitating the investigation of plant–soil stoichiometric responses under simplified experimental conditions. However, this approach differs substantially from natural root exudation in field soils:

phenolic acids are gradually and locally released in the rhizosphere under field conditions, resulting in lower, dynamically changing, and spatially heterogeneous concentrations. In contrast, surface application produces relatively uniform, high initial concentrations in bulk soil, which cannot fully replicate the rhizosphere microenvironment or the gradual accumulation and degradation dynamics of phenolic acids under field conditions. Thus, the observed responses should be interpreted within the context of controlled experimental settings.

In the first stage prior to nutrient addition, this study evaluated the effects of individual phenolic acid stress on lettuce growth and its stoichiometric characteristics. The results showed that both treatments significantly reduced lettuce biomass, indicating a clear inhibitory effect on plant growth, which is consistent with previous findings [25].

From a stoichiometric perspective, changes in the ratios of C, N, and P within plants reflect their strategies for nutrient acquisition and allocation [26]. When environmental stress limits the supply of a particular element, the internal elemental balance is disrupted [27], leading to shifts in stoichiometric ratios [12]. In this study, both CA and PHA reduced plant C, N, and P contents, with a greater decline observed for N than for C and P, resulting in increased C:N and decreased N:P. This pattern indicates that both phenolic acids induced a stoichiometric imbalance dominated by total nitrogen reduction. Given that only total N rather than mineral N was determined in this study, this elemental ratio pattern suggests potential nitrogen limitation at the whole-plant level, rather than direct evidence of available N deficiency.

Although the overall effects of the two phenolic acids were similar, their magnitudes differed under the present conditions. Compared with CA, PHA exerted a stronger inhibitory effect on biomass and nutrient contents, particularly in terms of N reduction and the increase in C:N. In addition, the greater decrease in N:P under PHA suggests a stronger disruption of stoichiometric balance, indicating a more pronounced effect on plant nutrient regulation.

From a soil perspective, the effects of the two phenolic acids on soil C, N, and P contents and their stoichiometric characteristics showed different patterns. In this study, CA reduced soil C and N contents, whereas PHA was mainly characterized by a decrease in soil C accompanied by an increase in P content.

This finding is consistent with previous studies [28], which reported that CA decreased soil nutrient levels, while PHA at specific concentrations increased soil P content. Such differences in soil stoichiometric responses indicate that the two phenolic acids affect soil carbon and nutrient pools through distinct pathways, resulting in different patterns of elemental imbalance. Given that soil microbial communities and extracellular enzyme activities were not determined in this study, the specific driving mechanisms behind these divergent responses remain to be further clarified. Changes in soil C, N, and P status and their stoichiometric relationships can further influence plant nutrient uptake and utilization, and are closely linked to the stoichiometric characteristics within plants [29].

Overall, in the initial stage without nutrient addition, both phenolic acids shared a common effect in reducing nitrogen content and altering C:N:P ratios, thereby disrupting the internal stoichiometric balance of plants, with nitrogen being the most sensitive element. According to ecological stoichiometric theory, a decrease in plant N:P generally indicates enhanced nitrogen limitation [30]. In combination with the observed growth inhibition, it can be inferred that phenolic acid stress may aggravate plant nitrogen limitation, as indicated by the shifted stoichiometric ratios.

Based on these results, it can be inferred that under phenolic acid-induced stoichiometric imbalance, external nutrient addition may help restore the disturbed stoichiometric balance by increasing nutrient supply and regulating C:N:P ratios, thereby alleviating the

inhibition of plant growth. To formally decouple the independent and interactive effects of phenolic acid type and nutrient addition, a 2×4 factorial design was adopted in the second stage, providing a more robust statistical basis for evaluating the universality of nutrient regulation patterns. This also provides a basis for further analysis of the effects of nutrient addition in the subsequent stage.

4.2. Effects of Nutrient Addition on Plant Growth and Stoichiometric Characteristics Under Phenolic Acid Stress

Based on the results of the first stage without nutrient addition, phenolic acid stress significantly inhibited lettuce growth and caused marked shifts in plant C, N, and P stoichiometry, particularly characterized by a decline in nitrogen content and a decrease in N:P, indicating potential nitrogen limitation as revealed by stoichiometric ratios. Under this background, whether external nutrient inputs in the second stage could restore the disturbed stoichiometric balance by regulating C, N, and P ratios became a key focus of this study.

The two-way ANOVA results showed that nutrient treatment exerted a highly significant main effect on plant growth and stoichiometric indicators, while the interaction between phenolic acid type and nutrient treatment was not significant for any plant indicator. This statistical result indicates that the regulatory pattern of nutrient addition on plant stoichiometry is stable across different phenolic acid backgrounds, despite differences in initial stress intensity.

Previous studies have shown that plant N:P can serve as an important indicator of nutrient limitation, with lower N:P generally reflecting nitrogen limitation, whereas values around 14–16 indicate relatively balanced nutrient supply [30]. It should be noted, however, that this threshold may vary depending on species and experimental conditions [31]. Moreover, since this study used total nutrient contents rather than available fractions, the N:P ratio here reflects the overall elemental allocation status of plants, and is used as an indirect indicator of nutrient limitation rather than a definitive diagnostic criterion. In the second stage, the N:P ratio of the CK treatment was 12.90; although it does not strictly fall within the typical range, it can be regarded as a relatively stable stoichiometric state in this experimental system and was therefore used as a reference for comparison.

Under the conditions of this study, nutrient addition exerted a clear regulatory effect on lettuce growth under both phenolic acid stresses. Overall, compared with treatments without nutrient addition, both nitrogen and phosphorus addition promoted biomass recovery to varying degrees, while the combined application of nitrogen and phosphorus showed the most pronounced alleviating effect. These results indicate that external nutrient inputs can effectively promote plant growth recovery and contribute to the restoration of the disturbed stoichiometric balance. Notably, the recovery amplitude differed between aboveground and belowground biomass: AGB showed a larger increase under NP addition, while BGB recovered to a lesser extent. This pattern is consistent with the plant resource allocation strategy under stress: when nutrient supply is restored, plants preferentially allocate nutrients to aboveground photosynthetic organs to maximize carbon assimilation, which is a common adaptive strategy for plants to alleviate allelopathic inhibition and restore growth rapidly [32].

From the perspective of stoichiometric balance, nitrogen addition increased plant N content and shifted N:P toward a more balanced range under both phenolic acid stresses, indicating that the alleviation of nitrogen-associated stoichiometric imbalance may be closely associated with plant growth responses in this study. This is consistent with the greater decline in nitrogen observed in the first stage, further supporting the dominant role of nitrogen-associated stoichiometric imbalance under phenolic acid stress. In contrast, phosphorus addition had a relatively weaker effect on biomass recovery but significantly

reduced plant C:P and partially increased N:P (although not significantly), suggesting that its primary role was to optimize elemental ratios rather than directly alleviate growth limitation. Notably, phosphorus addition also increased plant N content and altered N:P stoichiometric characteristics, suggesting a potential association between phosphorus availability and plant nitrogen status under phenolic acid stress. This differs from previous findings that phosphorus addition reduced N:P [33], which may be related to differences in the initial nutrient limitation status among studies. When nitrogen and phosphorus were applied together, plants not only received sufficient limiting nutrients, but also showed decreases in C:N and C:P, with N:P further approaching a relatively balanced state. This indicates that both nutrient supply and elemental coordination were improved simultaneously. Within a stoichiometric framework, this coordinated process of limitation alleviation and ratio optimization can be regarded as a comprehensive restoration mechanism of the disturbed stoichiometric balance. Previous studies have also shown that plant growth is often co-limited by multiple nutrients, and that alleviating multiple limiting factors simultaneously can produce stronger effects than single-nutrient addition [34,35], which is consistent with the findings of this study.

Further comparison of the two phenolic acid treatments revealed both similarities and differences in their responses to nutrient addition under the conditions of this study. Overall, nutrient addition promoted biomass recovery under both treatments and shifted plant N:P toward a relatively balanced range, indicating that nutrient inputs have a generally alleviating effect on phenolic acid stress. However, compared with CA, plants under PHA stress exhibited a greater degree of initial stoichiometric imbalance, characterized by a stronger decline in nitrogen content and a more pronounced decrease in N:P. As a result, the magnitude of recovery following nutrient addition was relatively greater under PHA, although a stronger stress effect still persisted overall. In contrast, plants under CA stress showed a relatively lower degree of inhibition and a more moderate response to nutrient addition. These results suggest that plant responses to nutrient addition vary under different phenolic acid treatments, and that such differences are closely related to the initial degree of stoichiometric imbalance, which is consistent with previous findings [36].

In summary, under the conditions of this study, nutrient addition alleviated phenolic acid-induced nitrogen-associated stoichiometric imbalance and promoted the recovery of plant N:P toward a more suitable range, thereby optimizing stoichiometric relationships and enhancing lettuce growth. Among the treatments, the combined application of nitrogen and phosphorus showed the most pronounced regulatory effect, indicating its superior role in restoring the stoichiometric balance disturbed by phenolic acids. From an agricultural perspective, these findings suggest that targeted nitrogen-centered nutrient regulation, especially combined N and P application, may be a potential strategy to alleviate phenolic acid-associated continuous cropping obstacles. However, given the controlled pot conditions and high phenolic acid concentrations used in this study, field verification is required before practical application.

4.3. Relationships Between Plant Growth and Soil Stoichiometric Factors Under Phenolic Acid Stress

As shown in the previous section, nutrient addition can, to some extent, alleviate the inhibitory effects of phenolic acid stress on lettuce growth and its stoichiometric characteristics, particularly reflected in the recovery of plant nutrient contents and the adjustment of N:P toward a relatively balanced state. However, the two-way ANOVA results revealed a clear discrepancy between plant and soil responses: while plant indicators showed non-significant interaction effects, soil total nitrogen, C:N ratio and N:P ratio exhibited significant phenolic acid $\times$ nutrient interaction effects, and phenolic acid type exerted a dominant main effect on most soil indicators. In studies of ecological stoichiometric

characteristics, soil organic C, total N, and total P contents, together with their stoichiometric relationships, can reflect soil nutrient pool characteristics and their balance status, and may also be associated with plant ecological stoichiometric responses [37,38]. Among these ratios, soil C:N generally indicates the potential of organic matter nitrogen release; soil C:P reflects the relative retention or release tendency of soil phosphorus; and soil N:P characterizes the relative supply pattern of soil nitrogen and phosphorus, which is closely coupled with plant elemental balance [39]. According to stoichiometric homeostasis theory, plants maintain relatively stable internal elemental composition through physiological regulation, thus buffering environmental fluctuations; in contrast, soil as an abiotic matrix is more sensitive to external perturbations, leading to stronger interactive effects of multiple factors. This difference in homeostasis may explain why soil responses are more variable while plant regulatory patterns are more consistent. Therefore, it is necessary to further analyze the changes in soil total C, total N, and total P contents and their stoichiometric relationships under nutrient addition conditions from the perspective of soil ecological stoichiometric characteristics, and to explore their relationships with plant growth and nutrient characteristics, so as to improve the understanding of plant ecological stoichiometric responses under phenolic acid stress.

Under conditions without nutrient addition, both phenolic acids exerted differential effects on soil C, N, and P status and their stoichiometric characteristics. Specifically, CA significantly reduced soil N content, accompanied by an increase in C:N and a decrease in N:P, indicating a contraction of the soil total nitrogen pool and a shift in elemental stoichiometric structure dominated by nitrogen reduction.

In contrast, PHA was mainly characterized by a significant decline in soil C content along with an increase in P content, leading to decreases in both C:N and C:P. Different from the nitrogen-lean pattern under CA, the simultaneous decrease in C:N and C:P under PHA stress indicates a relative surplus of nitrogen and phosphorus against the background of carbon pool loss, rather than absolute enrichment of a single nutrient. The reduced C:P ratio also means that phosphorus accounts for a higher proportion in the soil elemental pool, corresponding to a higher phosphorus release potential relative to carbon. This suggests that PHA primarily altered the relative balance between carbon and nutrients, influencing system stability through disruption of stoichiometric structure rather than through single-nutrient limitation. Given the inherent coupling between soil carbon and nitrogen cycles, the substantial loss of soil organic carbon may be accompanied by restricted conversion of soil organic nitrogen fractions, which could partially explain the obvious nitrogen-related elemental imbalance detected in lettuce, despite the higher total phosphorus concentration recorded in soil.

On this basis, nutrient addition exerted generally similar regulatory effects on soil C, N, and P status under both phenolic acid treatments. Nitrogen addition mainly increased soil N content and reduced C:N, whereas phosphorus addition significantly increased soil P content and regulated C:P and N:P ratios. From the perspective of stoichiometric ratio recovery, single nitrogen addition only partially corrected the elevated C:N ratio but had limited effect on C:P and N:P imbalance; single phosphorus addition mainly adjusted C:P and N:P but could not alleviate the deviation of C:N. In comparison, the combined application of nitrogen and phosphorus showed the most pronounced recovery effect, simultaneously driving C:N, C:P and N:P back toward the control level and promoting a more coordinated stoichiometric structure of the soil carbon–nitrogen–phosphorus system. Similar results have been reported by Vázquez et al. [35], who found that combined N and P addition was more effective than single-nutrient inputs in restoring soil nutrient status in grassland ecosystems.

However, the strength of these regulatory effects differed between the two phenolic acid treatments. Under CA treatment, soil C, N, and P status showed a more pronounced recovery, whereas the overall response under PHA was relatively weaker. In terms of stoichiometric ratios, nitrogen addition under CA stress directly targeted the most deviant C:N and N:P ratios, so the correction effect of elemental structure was more significant; under PHA stress, the core deviation lied in the carbon pool shrinkage, and single-nutrient addition could only adjust the relative proportion of nitrogen and phosphorus, but could not reverse the carbon-based structural imbalance, resulting in a weaker overall regulatory effect. This difference may be related to the different magnitudes of soil stoichiometric responses induced by the two phenolic acids: CA treatment showed larger changes in nitrogen-related stoichiometric characteristics and stronger responses to nitrogen addition, whereas PHA treatment was associated with larger changes in soil carbon-related stoichiometric characteristics, resulting in a more gradual and moderate recovery following nutrient addition.

Based on the above changes in soil nutrient status, correlation analysis and redundancy analysis (RDA) further revealed differences in the relationships between soil factors and plant traits under different phenolic acid treatments. Under CA treatment, correlation analysis showed that plant biomass was significantly positively correlated with soil nitrogen content, but negatively correlated with soil C:N ratio, indicating that soil nitrogen-related stoichiometric characteristics may be closely related to plant growth. This finding is consistent with the results of Batool et al. [40] on the relationship between soil nutrients and plant biomass in tropical forest soils in Hainan. Meanwhile, a higher soil C:N ratio indicates an imbalance in soil nutrient supply, which in turn suppresses biomass accumulation. This is consistent with the findings of Yang et al. [41], who reported that increased biochar application significantly raised soil organic carbon content, exacerbated the imbalance of soil C:N ratio, and consequently affected tobacco growth. From the perspective of plant stoichiometric characteristics, the plants in this study exhibited a clear nitrogen-associated stoichiometric imbalance. However, the RDA results showed that SOC and STP were the main environmental factors explaining variations in plant growth and stoichiometric characteristics. This suggests that soil nitrogen-related stoichiometric characteristics were closely related to plant growth responses, whereas soil carbon and phosphorus characteristics may also contribute to variations in plant stoichiometric characteristics under phenolic acid stress. Previous studies have shown that SOC, as an important basis for soil microbial activity and nutrient transformation, affects nitrogen mineralization and supply capacity [42,43], while STP regulates nutrient balance and availability, thereby influencing nitrogen uptake and utilization efficiency in plants [44]. Therefore, under CA stress in this study, SOC and STP may serve as important soil stoichiometric background characteristics, while soil nitrogen characteristics showed closer associations with plant growth responses.

In contrast, under PHA treatment, soil C:N ratio was positively correlated with plant biomass, opposite to the negative relationship observed under CA treatment. This difference may be attributed to the alteration in soil nutrient cycling processes by PHA, whereby the C:N ratio no longer reflects nitrogen availability alone, but instead represents the overall nutrient status of the soil [45]. In this study, PHA markedly reduced soil C content, while soil N remained relatively stable. Consequently, lower C:N ratios indicated a state of stoichiometric imbalance. As soil carbon partially recovered under certain treatments, increases in the C:N ratio were associated with improved soil nutrient conditions, which in turn promoted plant growth, leading to the observed positive relationship between C:N and biomass. The RDA results further demonstrated that SOC and STP were the dominant factors explaining variation in plant traits under PHA treatment, with more consistent relationships between soil variables and plant responses. This suggests that plant

growth became more dependent on the overall soil nutrient structure. Under these conditions, SOC and STP may be associated with changes in soil nitrogen-related stoichiometric characteristics, thereby influencing plant nutrient status and growth responses [46].

Overall, the soil–plant relationships differed markedly between CA and PHA treatments. Under CA stress, plant responses were primarily associated with nitrogen-associated stoichiometric imbalance, with soil effects mainly mediated through nitrogen supply. In contrast, under PHA stress, plant growth was more strongly influenced by stoichiometric imbalance, with soil carbon and its interactions with other nutrients playing a more prominent regulatory role.

4.4. Limitations and Future Perspectives

This study was conducted under controlled pot conditions using exogenously applied phenolic acids to establish clear allelopathic stress and to evaluate plant–soil stoichiometric responses. Therefore, the results should be interpreted mainly as stoichiometric response patterns under controlled phenolic acid stress rather than as a direct simulation of field continuous cropping conditions.

First, regarding nutrient determination, only total C, N and P contents of plants and soil were measured, while mineral nitrogen (NH_4^+ -N, NO_3^- -N), available phosphorus and other bioavailable nutrient fractions were not analyzed. Therefore, the inference of potential nitrogen limitation in this study is based on total elemental stoichiometric ratios and cannot directly reflect the actual available nutrient supply for plant uptake. This is the main limitation of the mechanistic interpretation of nutrient regulation effects.

Second, regarding the stress application method, surface drenching of high-concentration phenolic acid solutions was used to ensure reproducible stress intensity, but this method differs from natural root secretion and gradual rhizosphere diffusion in terms of concentration level, spatial distribution and temporal dynamics. In field soils, phenolic acids released from roots or plant residues may undergo accumulation, adsorption, degradation, leaching, and microbial transformation, and their actual bioavailability is much lower than the total applied concentration. Phenolic acid concentrations in soil solution or rhizosphere soil were not dynamically monitored in the present study, which limits the interpretation of actual exposure intensity and its temporal variation during the experiment.

Third, soil microbial community characteristics, extracellular enzyme activities and related biogeochemical processes were not investigated in this study. The inferred mechanisms regarding soil nutrient transformation and microbial nutrient limitation remain speculative, and the specific pathways by which phenolic acids alter soil stoichiometry cannot be directly verified.

In addition, this study focused on plant and soil total C, N, and P contents and their stoichiometric characteristics. Soil pH dynamics and salinity-related indicators were not included as major experimental variables. These omissions limit the interpretation of nutrient availability, pH or salinity-related effects, and microbial processes under phenolic acid stress and nutrient addition conditions.

Therefore, the findings should not be directly extrapolated to field rhizosphere processes without further verification. Future studies should incorporate phenolic acid concentration gradients, dynamic monitoring of rhizosphere phenolic acids, available nutrient fractions, soil pH dynamics, salinity-related indicators, and soil microbial community and enzyme activity characteristics as important experimental supplements. Field experiments under actual continuous cropping systems are also needed to verify the regulatory effects of nutrient addition. These improvements would help better clarify the ecological relevance of phenolic acid stress and nutrient addition responses in plant–soil systems.

Although this study does not directly provide field-based management recommendations, the findings provide basic information for understanding plant–soil stoichiometric responses under phenolic acid stress. These results may offer a reference for future studies on nutrient management in intensive or continuous cropping systems, particularly for improving the understanding of nutrient imbalance and avoiding blind nutrient inputs.

5. Conclusions

Using lettuce as the model plant, this study systematically investigated the stoichiometric characteristics of the plant–soil system under CA and PHA stress, as well as their responses to nutrient addition. The main conclusions are as follows:

Under phenolic acid stress in the initial stage, both CA and PHA significantly inhibited lettuce growth, reduced biomass, and altered plant C, N, and P contents and their stoichiometric relationships. Both treatments caused a greater decline in nitrogen compared with carbon and phosphorus, resulting in a nitrogen-dominated stoichiometric imbalance. Among them, PHA induced a stronger disturbance in nutrient status and stoichiometry, whereas CA was primarily associated with larger changes in nitrogen-related stoichiometric characteristics.

Exogenous nutrient addition partially alleviated phenolic acid stress. Nitrogen addition had the strongest effect on biomass recovery, while phosphorus addition mainly regulated elemental ratios and, to some extent, was associated with increased plant nitrogen content. Combined N and P application exhibited a clear synergistic effect. Despite differences between phenolic acid types, the overall response pattern was consistent, characterized by alleviation of nitrogen-associated stoichiometric imbalance.

Phenolic acid stress also altered soil C, N, and P contents and their stoichiometric characteristics. CA treatment intensified soil nitrogen-associated stoichiometric imbalance, whereas PHA mainly affected soil carbon levels and nutrient balance. Nutrient addition regulated soil nutrient status, with nitrogen increasing soil N, phosphorus increasing soil P, and combined application showing the most pronounced recovery effect. Correlation and RDA analyses further indicated that SOC and STP serve as important soil stoichiometric background characteristics, while soil nitrogen characteristics showed closer associations with plant growth responses.

In summary, phenolic acid stress induces stoichiometric imbalance in the plant–soil system by disrupting C, N, and P balance. Distinct response patterns were observed between phenolic acids: CA is mainly associated with enhanced nitrogen-associated stoichiometric imbalance, whereas PHA is more related to coordinated regulation of soil nutrient structure. Nutrient addition mitigates these effects by supplementing limiting elements and optimizing elemental balance.

Overall, this study provides evidence that phenolic acid stress alters plant–soil stoichiometric characteristics and that nutrient addition can partly modify these responses under controlled pot conditions. These findings provide basic information for understanding nutrient-related stoichiometric responses under allelochemical stress and may offer a reference for future studies on nutrient management in intensive or continuous cropping systems.

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