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Seasonal Responses of Soil–Plant Nutrient Relationships and Nutrient Resorption to Nitrogen Addition in Chinese Pine (*Pinus tabuliformis*) Plantations

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Abstract

Aim: Nitrogen (N) deposition is an important driver of forest nutrient dynamics, yet its effects on soil–plant nutrient relationships across growing seasons and stand ages remain incompletely understood. Methods: This study examined the effects of nitrogen addition [N0 (0 g m^{-2}), N1 (5 g m^{-2}), N2 (10 g m^{-2}), N3 (15 g m^{-2}), and N4 (20 g m^{-2})] and stand age (29-, 37-, and 48-year-old stands) on soil nutrient concentrations and stoichiometry, leaf nutrient concentrations and stoichiometry, and nitrogen (N) and phosphorus (P) resorption efficiencies in Chinese pine (*Pinus tabuliformis*) plantations. Seasonal variations and relationships among soil properties, leaf nutrient traits, and nutrient resorption were further evaluated. Results and conclusions: Nitrogen addition induced nonlinear and season-dependent changes in soil nutrient concentrations. Intermediate N addition (particularly N1–N2) was generally associated with higher soil organic carbon, total nitrogen, and available N concentrations during the middle and late growing seasons, whereas higher N inputs did not consistently increase soil nutrient levels. Soil C, C, and N ratios also exhibited contrasting responses across sampling periods. Leaf carbon concentrations generally increased under intermediate N addition during the middle and late growing seasons, whereas leaf N and P concentrations showed more variable responses. Leaf C tended to decrease with N addition, while leaf C and N exhibited contrasting seasonal patterns. N resorption efficiency (NRE) generally decreased under intermediate nitrogen addition (N1–N2) and increased under higher N inputs (N3–N4), particularly during the early and middle growing seasons. In contrast, phosphorus resorption efficiency (PRE) showed more variable responses, with relatively high values often occurring under N2 but no consistent increase at higher N levels. Mixed-effects models indicated that accounting for plot-level variation improved model performance, particularly for PRE. Redundancy analysis further revealed that the relationships between soil properties, leaf nutrient traits, and nutrient resorption varied among growing-season stages. Although responses varied among stand ages, no consistent age-related patterns were observed across the measured variables. Overall, nitrogen addition altered soil–plant nutrient relationships in a nonlinear and season-dependent manner, highlighting the importance of considering seasonal dynamics, nitrogen input levels, and plot-level heterogeneity when assessing nitrogen effects on nutrient cycling in Chinese pine plantations.

Keywords: nitrogen addition; Chinese pine; soil nutrients; leaf nutrients; nutrient stoichiometry; stand age; growing season

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1. Introduction

In recent decades, atmospheric nitrogen (N) deposition has increased substantially and has become an important driver of forest ecosystem structure and functioning [1,2]. Nitrogen inputs can modify soil nutrient availability and plant nutrient status, thereby influencing nutrient cycling and ecosystem processes. Numerous studies have reported that N addition increases soil mineral N availability, particularly ammonium (NH_4^+-N) and nitrate (NO_3^--N), although the magnitude and direction of these responses depend on N input intensity, ecosystem characteristics, and environmental conditions [3–5]. Nitrogen enrichment can also alter soil carbon (C), N, and phosphorus (P) pools and their stoichiometric relationships. For example, changes in soil C:N, C:P, and N:P ratios have been reported under elevated N inputs, potentially reflecting shifts in soil nutrient balance and plant–microbe nutrient interactions [6,7]. However, these responses are not necessarily linear, and excessive N inputs do not always result in further increases in soil nutrient availability. Understanding how different levels of N addition affect soil nutrient concentrations and stoichiometry is therefore essential for assessing the consequences of atmospheric N deposition in forest ecosystems.

Soil nutrient dynamics are also subject to pronounced seasonal variation. Changes in temperature, soil moisture, and plant nutrient demand throughout the growing season can influence microbial activity, N mineralization, nitrification, and nutrient uptake, resulting in temporal fluctuations in soil nutrient availability [8–10]. Consequently, the effects of N addition on soil nutrient pools may differ among early, middle, and late growing-season stages. Soil C and N may respond relatively rapidly to changes in nutrient inputs, whereas soil P dynamics can be regulated by additional processes, including biological uptake, mineralization, and soil chemical transformations. Thus, the responses of soil C, N, and P, as well as their stoichiometric ratios, may vary in both magnitude and direction across sampling periods. Evaluating seasonal changes is important for identifying temporal differences in soil nutrient responses to N enrichment rather than relying on measurements from a single sampling period.

Changes in soil nutrient availability can further influence leaf nutrient concentrations and stoichiometric balance. Nitrogen addition is frequently associated with increased foliar N concentrations, whereas leaf C and P responses vary among species, ecosystems, and experimental conditions [11,12]. Leaf nutrient concentrations also change during the growing season as a result of leaf development, nutrient accumulation, metabolic activity, and nutrient remobilization. In particular, seasonal changes in leaf N and P can modify leaf CN, CP, and NP ratios, reflecting temporal variation in plant nutrient status and the relative balance between nutrient supply and demand [13,14]. These stoichiometric characteristics provide useful indicators of plant nutrient status, although they should not be interpreted as direct evidence of ecosystem-level nutrient limitation without additional physiological or experimental assessments. Despite increasing attention to foliar nutrient responses under N enrichment, the extent to which leaf nutrient concentrations and stoichiometric ratios respond consistently across N addition levels and growing-season stages remains unclear.

In addition to nutrient accumulation, plants regulate nutrient demand through internal nutrient resorption before leaf senescence. Nitrogen and P resorption efficiencies (NRE and PRE) are important components of plant nutrient conservation, allowing nutrients to be recovered from senescing leaves and reused in subsequent growth. These processes are influenced by soil nutrient availability, leaf nutrient status, plant developmental stage, and environmental conditions. Nitrogen enrichment may reduce N resorption when external N availability increases, whereas its effects on P resorption can be more variable because changes in N availability may modify plant P demand and nutrient balance. Seasonal variation in leaf development and senescence may further affect NRE and PRE. Therefore,

examining both NRE and PRE is necessary to understand how N addition influences internal nutrient recycling, particularly when their responses may differ across nutrient elements and sampling periods.

Stand age is another potential factor influencing forest nutrient dynamics under N enrichment. Forests at different developmental stages differ in stand structure, biomass accumulation, nutrient demand, and internal nutrient cycling. These differences may influence soil nutrient availability, leaf nutrient composition, and nutrient resorption responses to external N inputs [7,15]. However, the direction and magnitude of age-related differences may depend on ecosystem conditions and the nutrient variables considered. Ecological stoichiometry provides a useful framework for examining C, N, and P balance in soil–plant systems and for evaluating changes in nutrient status under varying environmental conditions [16,17]. Soil and leaf C, C, and N ratios, together with NRE and PRE, can therefore provide complementary information on nutrient availability, plant nutrient balance, and internal nutrient recycling. Nevertheless, how stand age modifies the seasonal responses of these soil and leaf nutrient characteristics to different levels of N addition remains insufficiently understood.

Chinese pine (*Pinus tabuliformis*) is an important plantation tree species in northern China and plays an important role in regional forest restoration and ecosystem functioning. Although previous studies have investigated the effects of N addition or stand development on forest nutrient dynamics, their combined influences across the growing season remain inadequately characterized. In particular, the seasonal responses of soil C, N, and P concentrations and stoichiometry, leaf nutrient concentrations and stoichiometry, and N and P resorption efficiencies have rarely been evaluated together across multiple N addition levels and stand ages. Moreover, the relationships between soil nutrient properties, leaf nutrient characteristics, and nutrient resorption may change during the growing season, but these temporal relationships remain poorly understood. Addressing these knowledge gaps requires an integrated assessment of soil and leaf nutrient characteristics, nutrient resorption, and their relationships across different N addition levels, sampling periods, and stand ages.

To address these knowledge gaps, this study investigated the effects of five N addition levels (N0–N4) on soil nutrient concentrations and stoichiometry, leaf nutrient concentrations and stoichiometry, and N and P resorption efficiencies in 29-, 37-, and 48-year-old Chinese pine plantations. Measurements were conducted during the early, middle, and late growing seasons to examine temporal variation in soil–plant nutrient responses. Mixed-effects models were used to examine the relationships of NRE and PRE with soil and leaf nutrient characteristics while accounting for plot-level variation. Redundancy analysis (RDA) was further applied to investigate seasonal associations among soil properties, leaf nutrient traits, and nutrient resorption.

We hypothesized that: (1) soil nutrient concentrations and stoichiometric ratios would respond nonlinearly to increasing N addition, with response patterns differing among growing-season stages; (2) leaf nutrient concentrations, stoichiometric ratios, and N and P resorption efficiencies would exhibit distinct responses to N addition, with the magnitude and direction of these responses varying seasonally; and (3) the responses of soil and leaf nutrient characteristics and nutrient resorption to N addition would vary among stand age groups, although the magnitude and direction of these differences may depend on the nutrient variables and sampling periods considered. By testing these hypotheses, this study provides an integrated assessment of seasonal soil–plant nutrient dynamics under N enrichment and improves understanding of how N input intensity, stand age, and plot-level heterogeneity are associated with nutrient cycling in Chinese pine plantations.

2. Result

2.1. Seasonal Responses of Soil Nutrients to Nitrogen Addition

Nitrogen addition induced distinct and generally non-linear responses in soil nutrient properties across the three sampling periods, with variation in response patterns among stand age groups (Figure 1). During the early growing season (May), SOC generally decreased under N1–N3, whereas SAN and SNO showed increases under certain nitrogen treatments, particularly N4. STN fluctuated across treatments, while STP remained relatively stable. During the mid-growing season (July), SOC, STN, SAN, and SNO generally showed higher values under intermediate nitrogen addition (N1–N2), followed by decreases under N3–N4, whereas STP exhibited relatively little variation. At the end of the growing season (September), SOC and STN generally peaked under N2 and declined at higher nitrogen levels. SAN and SNO also tended to show higher values under intermediate nitrogen addition, while STP generally decreased with increasing nitrogen addition.

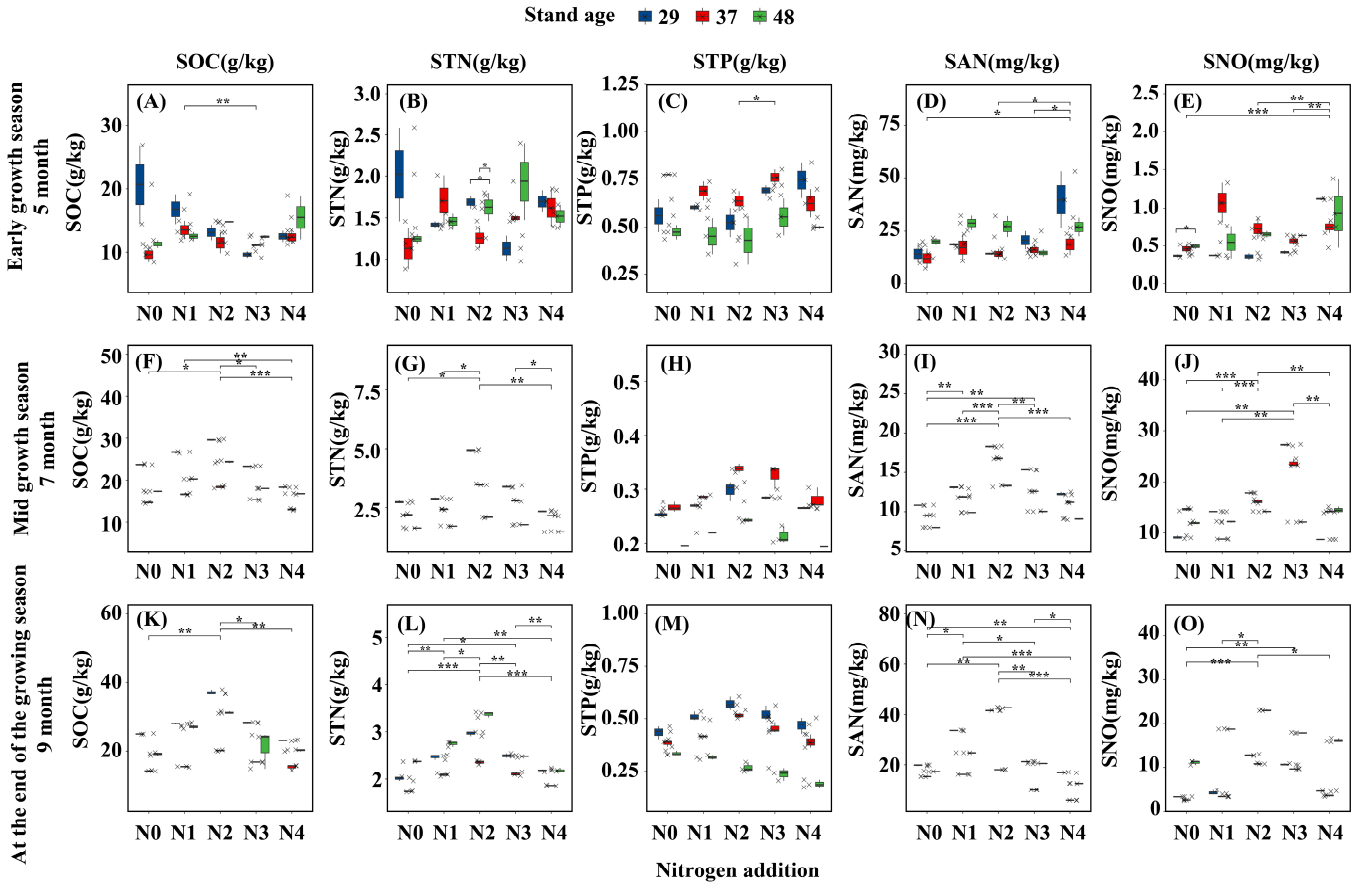

Figure 1. (**A**–**O**) Seasonal responses of soil nutrients in Chinese pine to nitrogen addition. Notes: SAN, soil ammonium nitrogen; SNO, soil nitrate nitrogen; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. This indicates statistically significant differences at the 0.05, 0.01, and 0.001 levels, respectively.

Across the three sampling periods, the soil nutrient profiles showed varying trends among the 29-, 37-, and 48-year-old stands. The direction and magnitude of these age-related patterns differed among soil properties and nitrogen treatments, with no consistent trend across all variables. Overall, intermediate nitrogen addition (particularly N1–N2) was generally associated with higher SOC, STN, and available nitrogen concentrations, whereas higher nitrogen levels did not consistently increase soil nutrient concentrations.

2.2. Seasonal Responses of Soil Nutrient Stoichiometry to Nitrogen Addition

Nitrogen addition altered soil C:N, C:P, and N:P ratios, with responses varying among sampling periods (Figure 2). In the early growth season (5 month), soil C:N generally decreased under N2 and N3 but increased under N1 and N4 in some cases (Figure 2A). Soil C:P showed an overall increasing tendency under N2 and N4, particularly at higher nitrogen addition levels (Figure 2B). Soil N:P also tended to increase under N2 and N3, with relatively high values under N2 (Figure 2C). In the mid-growth season (7 month), soil C:N and C:P ratios showed relatively small variations across nitrogen treatments (Figure 2D,E), whereas soil N:P exhibited a pronounced peak under N2, followed by a decline under N3 and N4 (Figure 2F). At the end of the growing season (9 month), soil C:N generally decreased with increasing nitrogen addition, while soil C:P and N:P showed higher values under N2–N4 than under the control in some cases (Figure 2G–I).

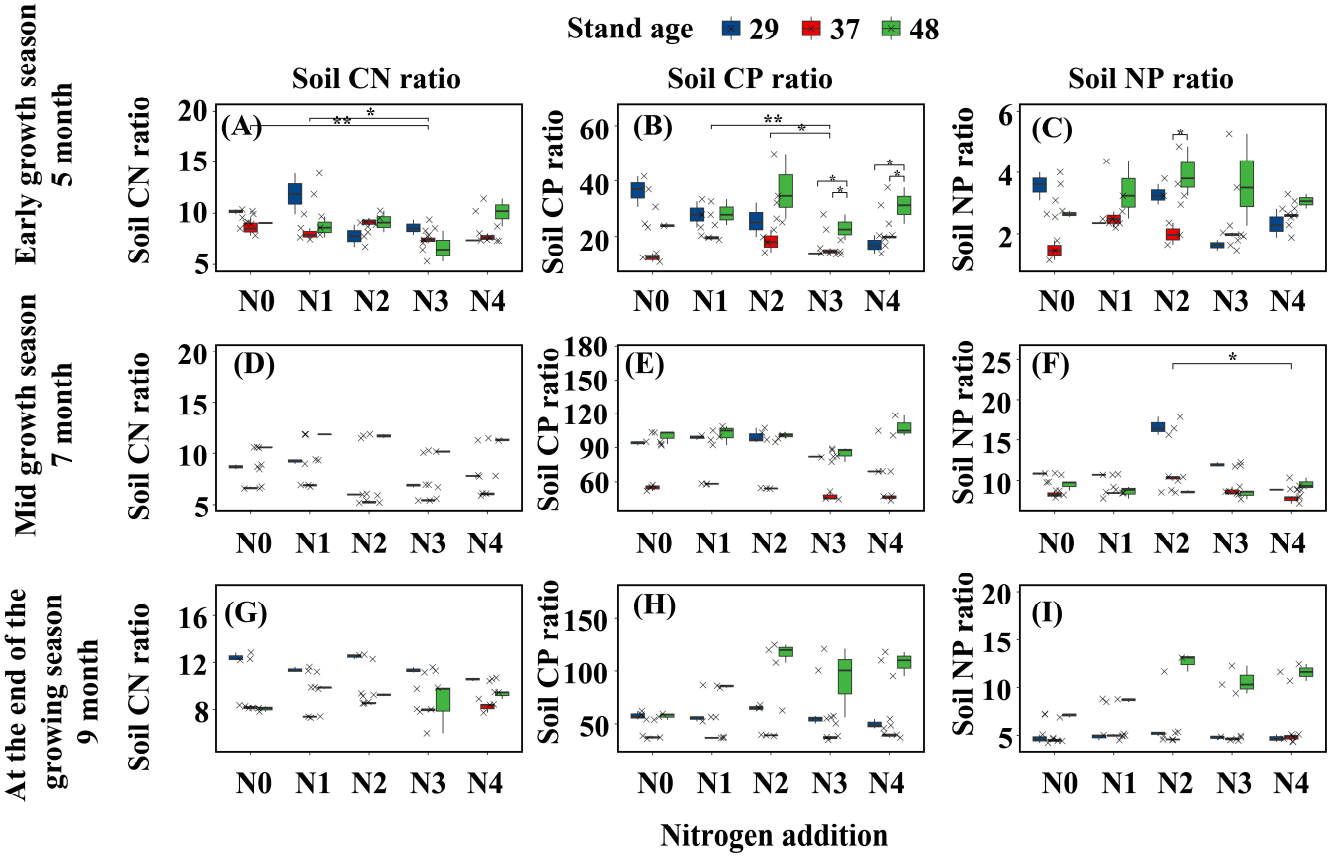

Figure 2. (**A**–**I**) Seasonal responses of soil nutrient stoichiometry in Chinese pine to nitrogen addition. Notes: * $p < 0.05$; ** $p < 0.01$. This indicates statistically significant differences at the 0.05, 0.01, and 0.001 levels, respectively.

Overall, nitrogen addition affected soil stoichiometric ratios in a non-linear and sampling-period-dependent manner. Intermediate nitrogen addition (particularly N2) generally resulted in higher soil N:P ratios, while soil C:N and C:P exhibited more variable responses across treatments.

2.3. Seasonal Responses of Chinese Pine Leaf Traits to Nitrogen Addition

Nitrogen addition induced contrasting responses in leaf C, N, and P concentrations across the three sampling periods, with some variation in response patterns among stand age groups (Figure 3). During the early growing season (May), leaf C showed relatively small fluctuations across nitrogen treatments, with no consistent dose-dependent trend

(Figure 3A). Leaf N generally increased slightly under higher nitrogen addition, with relatively high concentrations under N3 and N4 (Figure 3B). Leaf P remained relatively stable across treatments, although some fluctuations were observed (Figure 3C). Among stand age groups, the differences in leaf nutrient concentrations varied across treatments, without a consistent age-related pattern.

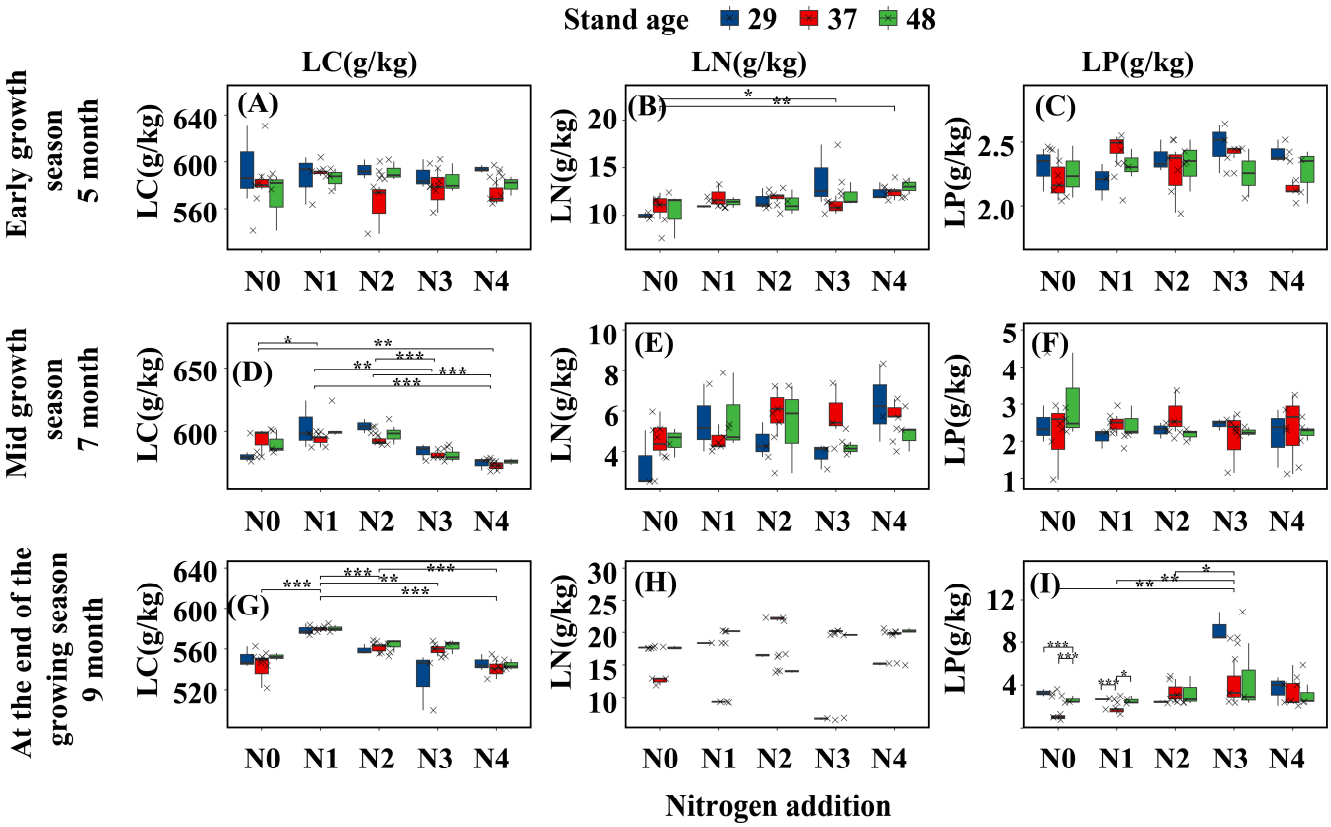

Figure 3. (**A**–**I**) Seasonal responses of leaf nutrient concentrations in Chinese pine to nitrogen addition. Notes: LC, leaf carbon; LN, leaf nitrogen; LP, leaf phosphorus. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. This indicates statistically significant differences at the 0.05, 0.01, and 0.001 levels, respectively.

During the mid-growing season (July), leaf C increased under N1 and N2 but declined under N3 and N4, with relatively low concentrations under N4 (Figure 3D). Leaf N varied across nitrogen treatments, with relatively high values under N2 and N4 (Figure 3E), whereas leaf P showed no consistent response to increasing nitrogen addition (Figure 3F). The three age groups showed overlapping and variable patterns in leaf C, N, and P concentrations across nitrogen treatments.

At the end of the growing season (September), leaf C generally reached higher concentrations under N1, followed by a decline under N2–N4 (Figure 3G). Leaf N varied among nitrogen treatments without a consistent increasing or decreasing trend (Figure 3H). In contrast, leaf P generally showed higher concentrations under N2 and N3, particularly N3, before declining under N4 (Figure 3I). Differences among stand age groups also varied across nitrogen treatments, with no consistent age-related trend across the three leaf nutrient variables.

Overall, leaf C showed a relatively consistent response in the mid- and late-growing seasons, with higher concentrations under intermediate nitrogen addition (N1–N2) and lower concentrations under higher nitrogen levels (N3–N4). In contrast, leaf N and P exhibited more variable responses across sampling periods. Although leaf nutrient concentrations

varied among the 29-, 37-, and 48-year-old stands, these patterns were not consistent across nitrogen treatments or sampling periods.

2.4. Seasonal Responses of Leaf Nutrient Stoichiometry in Chinese Pine to Nitrogen Addition

Nitrogen addition induced contrasting changes in leaf stoichiometric ratios (Figure 4). Leaf C:N generally decreased with increasing nitrogen addition, particularly in the mid-growth season (7 month), whereas changes were relatively small in the early growth season (5 month) and the end of the growing season (9 month). Leaf C:P showed variable responses, with a pronounced decline under N2–N4 in the 9-month group. Leaf N:P exhibited contrasting responses, remaining relatively stable at 5 and 7 months but decreasing markedly following nitrogen addition at the end of the growing season (9 month).

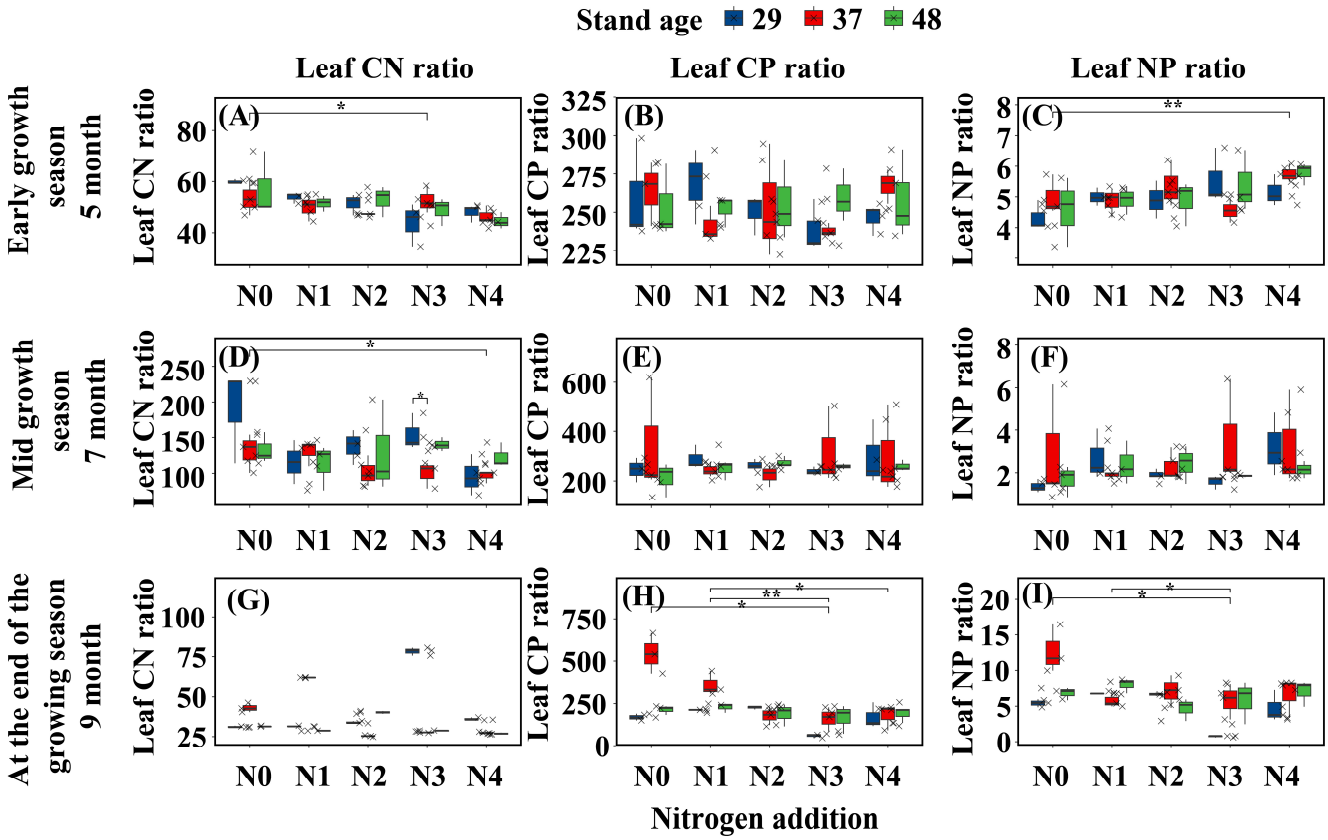

Figure 4. (**A**–**I**) Effects of nitrogen addition on leaf nutrient stoichiometry across growing seasons in Chinese pine. Notes: * $p < 0.05$; ** $p < 0.01$. This indicates statistically significant differences at the 0.05, 0.01, and 0.001 levels, respectively.

Overall, nitrogen addition altered leaf stoichiometric balance, with leaf C:N and C:P generally declining under certain nitrogen treatments, while leaf N:P responses were strongly dependent on the sampling period.

2.5. Seasonal Variation in Leaf C, N, and P Concentrations in Chinese Pine

Leaf carbon (LC), nitrogen (LN), and phosphorus (LP) in *Chinese pine* displayed distinct seasonal patterns under different nitrogen addition levels (N0–N4) (Figures 5–7). LC peaked in July and declined by September; mid- to low-N treatments (N1–N2) slightly increased LC compared with the control, whereas high-N treatments (N3–N4) showed a stronger late-season decline, suggesting potential suppression of carbon accumulation under excessive nitrogen. LP gradually increased over the growing season, with N_3 showing

significantly higher values in September, indicating that moderate to high nitrogen may enhance phosphorus uptake and reflect N–P synergistic effects. LN exhibited a "V-shaped" pattern, lowest in July and higher in May and September, increasing with nitrogen addition; N_2 and N_4 reached maximum LN in September, showing that external nitrogen substantially elevated leaf N, while the mid-season dip likely reflected growth-related N translocation and metabolic use. Overall, leaf C peaked mid-season, N showed a mid-season minimum followed by recovery, and P increased gradually, with late-season sensitivity to high N, highlighting seasonal nutrient dynamics and leaf responses to nitrogen addition in Chinese Pine.

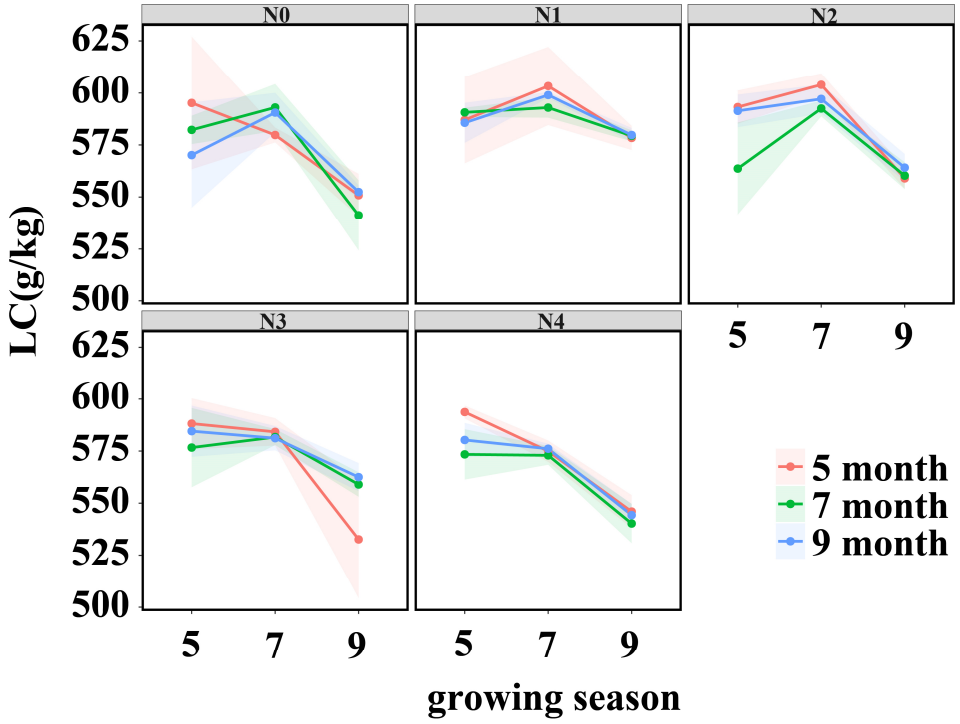

Figure 5. Seasonal dynamics of leaf carbon content in Chinese pine. Notes: The early growth season (5 month), the mid-growth season (7 month) and the end of the growing season (9 month).

2.6. Seasonal Responses of Leaf Nutrient Use Efficiency to Nitrogen Addition in Chinese Pine

Nitrogen addition had pronounced effects on both nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE), although the responses varied across nitrogen addition levels. Overall, NRE showed a relatively consistent response to nitrogen addition, whereas PRE exhibited greater variation among nitrogen treatments.

For NRE, the values generally decreased from N0 to N2, followed by an increase under higher nitrogen addition levels (N3 and N4). This pattern was particularly evident in the early growth season (5 month) and mid-growth season (7 month), where NRE tended to be lower under intermediate nitrogen addition (N1–N2) but increased under higher nitrogen addition (N3–N4). In contrast, the end of the growing season (9 month) showed relatively little variation in NRE across nitrogen treatments, although slightly higher values were generally observed under N4. These patterns suggest that the effects of nitrogen addition on NRE were dependent on nitrogen addition level, with intermediate nitrogen inputs tending to reduce NRE and higher inputs potentially alleviating this reduction.

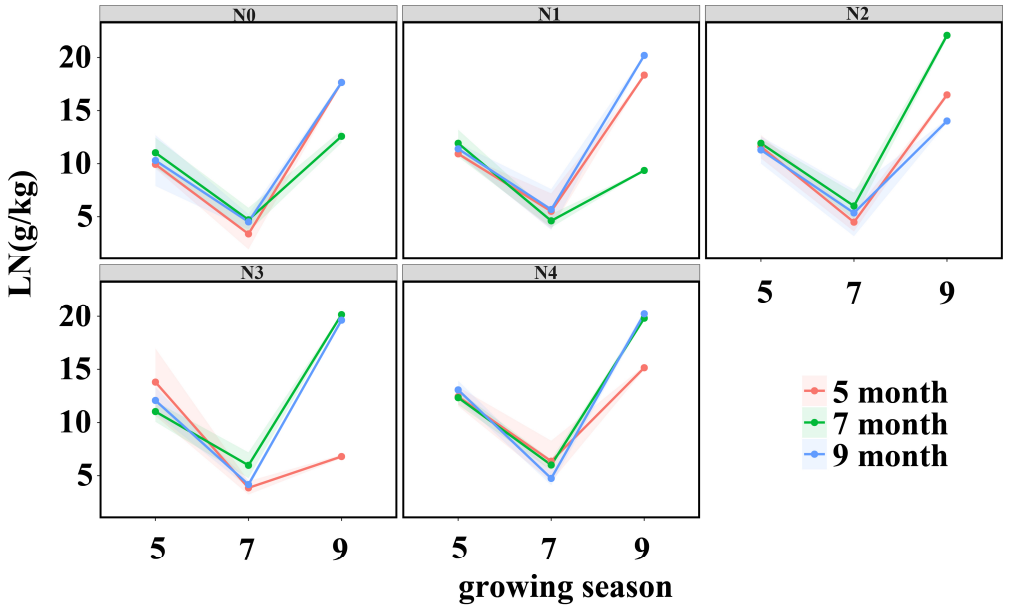

Figure 6. Seasonal dynamics of leaf N content in Chinese pine. Notes: The early growth season (5 month), the mid-growth season (7 month) and the end of the growing season (9 month).

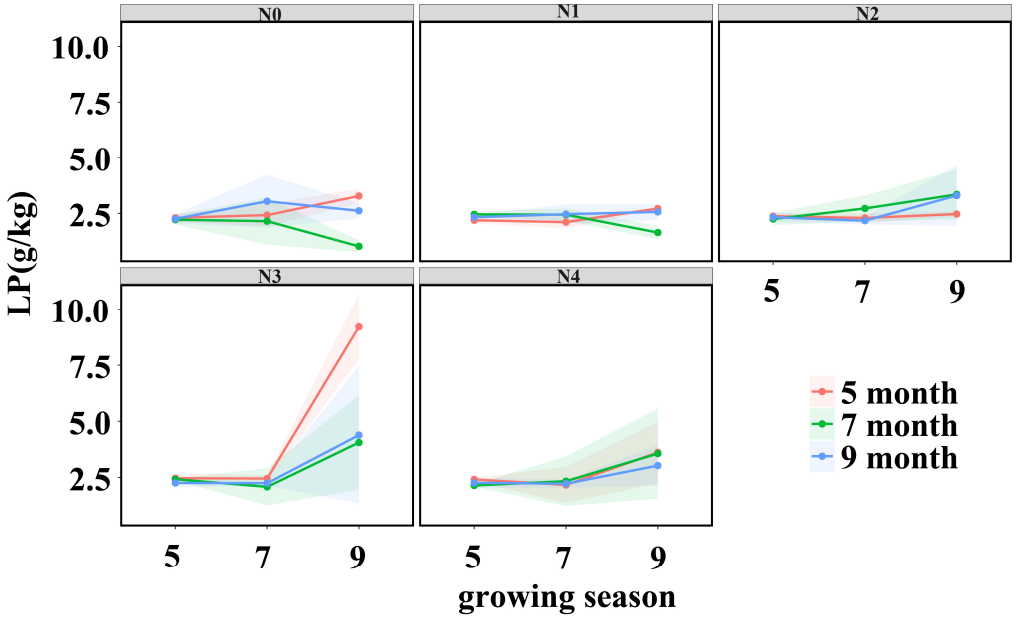

Figure 7. Seasonal dynamics of leaf P content in Chinese pine. Notes: The early growth season (5 month), the mid-growth season (7 month) and the end of the growing season (9 month).

For PRE, the response to nitrogen addition was more variable. PRE generally declined under N1 compared with N0, while relatively high values were frequently observed under N2. However, further increases in nitrogen addition (N3 and N4) did not consistently enhance PRE, with values generally remaining low to moderate. This pattern was particularly apparent in the early growth season (5 month). In the mid-growth season (7 month) and end of the growing season (9 month), PRE also tended to decrease under N1, whereas the responses to higher nitrogen addition levels were more variable, with no consistent increasing or decreasing trend across treatments.

Overall, these results indicate that nitrogen addition altered NRE and PRE differently. NRE generally exhibited a decrease under intermediate nitrogen addition followed by a

recovery under higher nitrogen inputs, whereas PRE showed a more variable response, characterized by an initial decline and a transient increase under N2. Although the magnitude and direction of these responses varied among age groups, the overall patterns highlight the differential sensitivity of NRE and PRE to nitrogen addition (Figure 8).

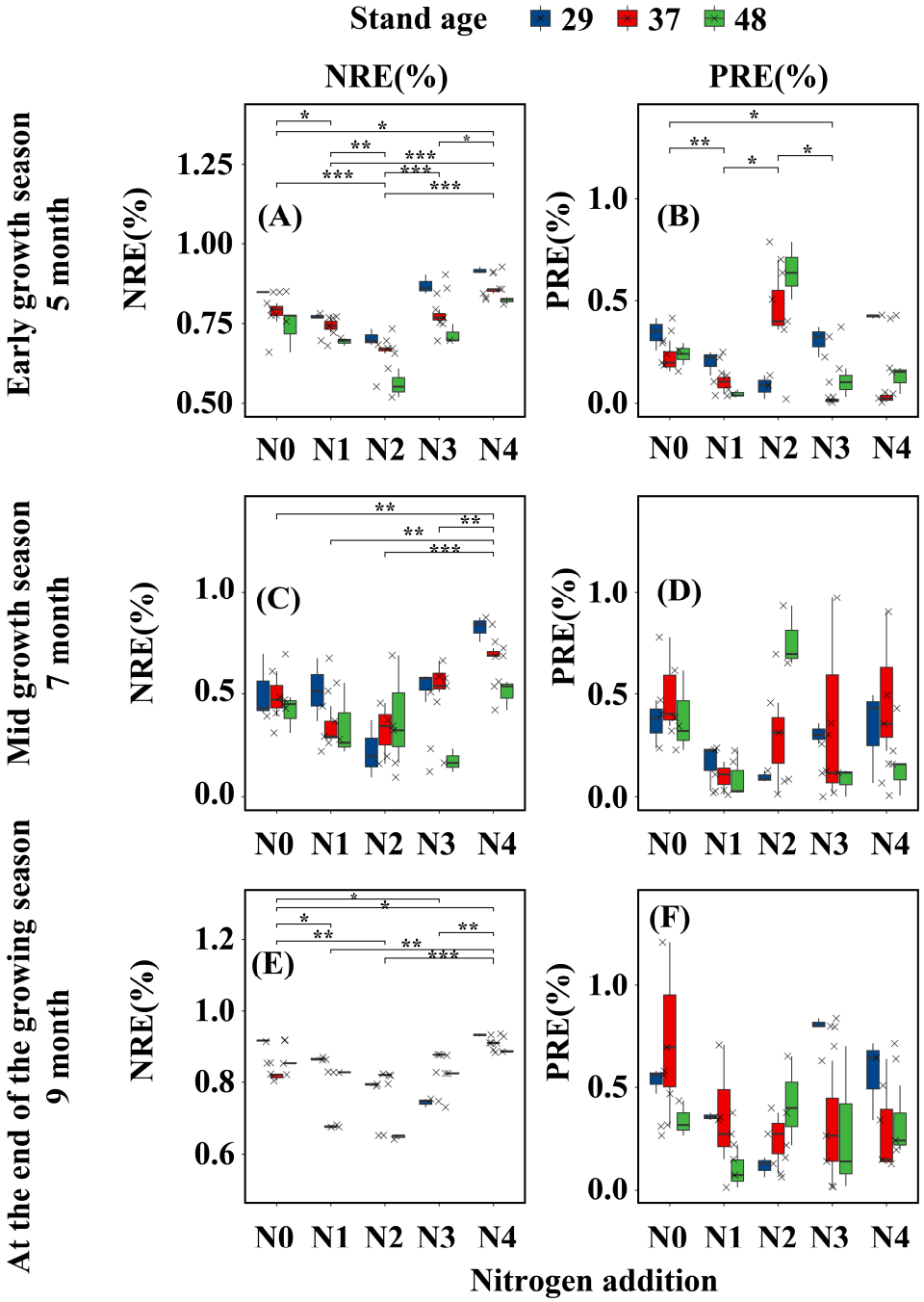

Figure 8. (**A**–**F**) Seasonal variation in leaf nitrogen and phosphorus use efficiency under different nitrogen addition levels in Chinese pine. Notes: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. This indicates statistically significant differences at the 0.05, 0.01, and 0.001 levels, respectively.

2.7. Linear Mixed-Effects Model

The fixed-effect estimates were generally consistent across the three model specifications for both NRE and PRE, although some coefficients changed slightly after accounting for plot-level variation and temporal autocorrelation. For NRE, LN was positively associated with NRE ($\beta = 0.022$), whereas DN showed a negative association ($\beta = -0.084$) in

the LMM with an AR(1) correlation structure. The coefficients for July and September were −0.143 and −0.045, respectively, relative to May. Similarly, the coefficients for the 37- and 48-year-old stands were −0.010 and −0.025, respectively, relative to the 29-year-old stands. Incorporating the plot-level random intercept increased R^2 slightly from 0.837 to 0.840, whereas the additional AR(1) structure reduced it to 0.821. The estimated plot-level random-effect variance was 0.0008, and the estimated AR(1) correlation parameter (φ) was 0.343.

For PRE, LP showed a positive association (β = 0.044), whereas LC and SC had negative coefficients (β = −0.002 and −0.008, respectively) in the LMM with an AR(1) correlation structure. The coefficients for July and September were positive (β = 0.065 and 0.101, respectively), indicating higher PRE than in May. In contrast, the coefficients for the 37- and 48-year-old stands were negative (β = −0.077 and −0.108, respectively), relative to the 29-year-old stands. Incorporating the plot-level random intercept substantially increased R^2 from 0.166 to 0.459. After further accounting for temporal autocorrelation, R^2 decreased slightly to 0.455. The estimated plot-level random-effect variance was 0.147, and the AR(1) correlation parameter was 0.021. Overall, accounting for plot-level heterogeneity substantially improved the explanatory performance for PRE, whereas the inclusion of the AR(1) structure resulted in only minor changes in model fit for both NRE and PRE (Table 1).

Table 1. Fixed-effect estimates, plot-level random-effect variances, and coefficients of determination (R^2) for the basic and mixed-effects models of nitrogen and phosphorus resorption efficiencies (NRE and PRE).

Parameter	NRE			Parameter	PRE		
	Base Model	**LMM**	**LMM + AR(1)**		**Base Model**	**LMM**	**LMM + AR(1)**
intercept	0.801	0.795	0.779	intercept	1.763	1.565	1.557
LN	0.020	0.020	0.022	LP	0.041	0.044	0.044
DN	−0.088	−0.088	−0.084	LC	−0.002	−0.002	−0.002
STN	−0.014	−0.012	−0.017	STC	−0.005	−0.008	−0.008
7 month	−0.162	−0.163	−0.143	STP	−0.215	−0.199	−0.194
9 month	−0.026	−0.028	−0.045	7 month	0.040	0.064	0.065
37	−0.005	−0.003	−0.010	9 month	0.061	0.102	0.101
48	−0.019	−0.018	−0.025	Stand age-37a	−0.056	−0.078	−0.077
-	-	-	-	Stand age-48a	−0.102	−0.110	−0.108
μ_j	-	0.0006	0.0008	μ_j	-	0.022	0.147
Phi	-	-	0.343	Phi	-		0.021
R^2	0.837	0.840	0.821	R^2	0.166	0.459	0.455

Notes: The mid-growth season (7 month) and the end of the growing season (9 month); LC, leaf carbon; LN, leaf nitrogen; LP, leaf phosphorus; DN, litter nitrogen; STN, soil total nitrogen; STP, soil total phosphorus. R^2, coefficient of determination.

2.8. RDA

The RDA results showed that the relationships between leaf nutrient characteristics, nutrient resorption efficiencies, and soil properties varied across the three growing-season stages (Figure 9). In the early growth season (5 month), the first and second RDA axes explained 58.75% and 24.25% of the variation, respectively, accounting for 83.00% cumulatively. NRE was oriented toward the positive directions of both axes, whereas LN was oriented toward positive RDA1 and negative RDA2. LC showed an opposite orientation to LN. Among the soil variables, STP was oriented toward the positive directions of both axes, while SOC pointed toward negative RDA1 and positive RDA2.

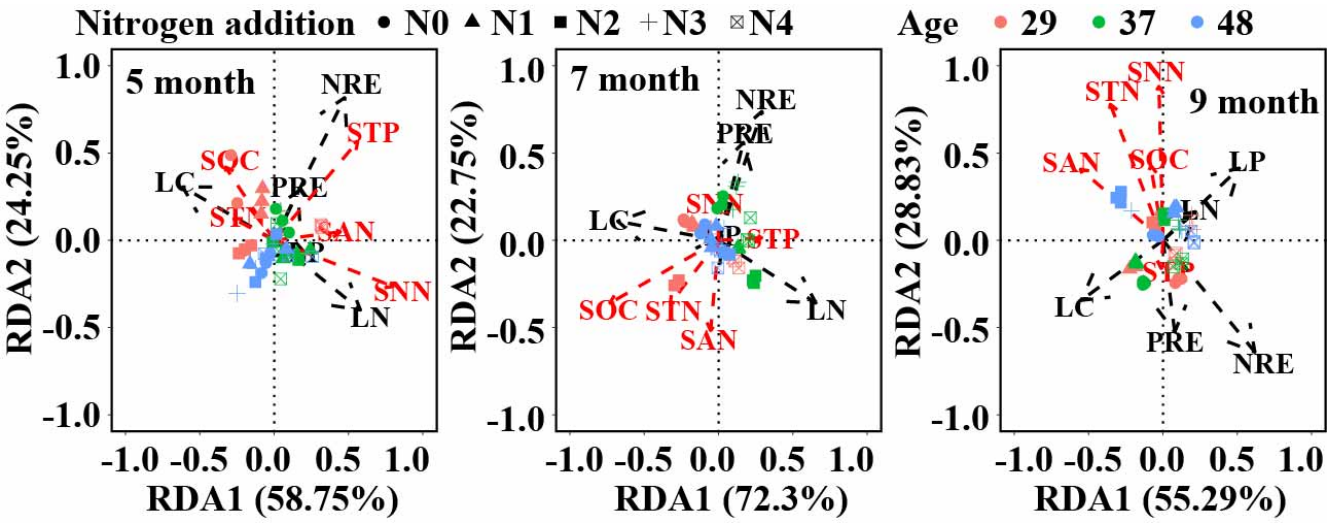

Figure 9. Regression analysis of soil nutrients and leaf nutrient contents of Chinese pine across different growth seasons. Notes: The early growth season (5 month), the mid-growth season (7 month) and the end of the growing season (9 month); LC, leaf carbon; LN, leaf nitrogen; LP, leaf phosphorus; NRE, nitrogen resorption efficiency; PRE, phosphorus resorption efficiency; SAN, soil ammonium nitrogen; SNN, soil nitrate nitrogen; SOC, soil organic carbon; STN; soil total nitrogen; STP, soil total phosphorus.

In the mid-growth season (7 month), RDA1 and RDA2 explained 72.30% and 22.75% of the variation, respectively, with a cumulative explanation of 95.05%. NRE and PRE were both oriented mainly toward positive RDA2, whereas LN pointed toward positive RDA1 and negative RDA2. SOC and STN were oriented toward the negative directions of both axes, while SAN mainly pointed toward negative RDA2.

At the end of the growing season (9 month), the first two axes explained 55.29% and 28.83% of the variation, respectively, accounting for 84.12% cumulatively. NRE and PRE were oriented toward negative RDA2, whereas LN and LP were mainly oriented toward positive RDA1. Among the soil variables, STN and SNO pointed mainly toward positive RDA2, while SAN was oriented toward negative RDA1 and positive RDA2.

Across the three sampling stages, sample scores for different nitrogen addition treatments and stand age groups were generally concentrated around the origin, with considerable overlap among groups.

3. Discussion

3.1. Effects of Nitrogen Addition on Soil

The responses of SOC, STN, STP, and mineral nitrogen (SAN and SNN) to nitrogen addition varied across the three sampling periods, indicating that soil nutrient dynamics in Chinese pine plantations were seasonally dependent (Figure 1). During the early growing season, SOC generally decreased under N1–N3, whereas SAN and SNN showed increases under certain nitrogen treatments, particularly N4. STN fluctuated across treatments, while STP remained relatively stable. These contrasting responses suggest that different soil nutrient pools may respond differently to nitrogen inputs, depending on their forms and availability. The relatively variable responses of mineral nitrogen may reflect its direct involvement in soil nitrogen transformations and its sensitivity to external nitrogen inputs [18,19].

During the mid-growing season, SOC, STN, SAN, and SNN generally showed higher concentrations under intermediate nitrogen addition (N1–N2), followed by decreases under higher nitrogen levels (N3–N4). In contrast, STP exhibited relatively little variation among

nitrogen treatments. The increases in SOC and STN under intermediate nitrogen addition may be associated with changes in plant-derived carbon inputs and soil organic matter turnover. Previous studies have suggested that nitrogen availability can influence microbial decomposition and soil nutrient cycling, although these processes were not directly examined in the present study [20,21]. The relatively stable STP concentrations during this period indicate that soil phosphorus did not exhibit a response pattern comparable to those of soil carbon and nitrogen.

At the end of the growing season, SOC and STN generally peaked under N2 and declined at higher nitrogen addition levels. SAN and SNN also tended to show relatively high concentrations under intermediate nitrogen treatments, whereas STP generally decreased with increasing nitrogen addition. These patterns indicate that the effects of nitrogen addition on soil nutrient concentrations were not consistently proportional to the amount of nitrogen applied. In particular, the relatively high mineral nitrogen concentrations under intermediate nitrogen addition suggest that moderate nitrogen inputs may be associated with greater soil mineral nitrogen accumulation during this period. However, the observed patterns alone do not establish whether nitrogen retention capacity was exceeded or whether nitrate leaching increased.

Variation among the 29-, 37-, and 48-year-old stands was also observed in the patterns of soil nutrient responses across nitrogen treatments and sampling periods. However, these age-related patterns varied among soil properties and sampling periods and did not show a consistent direction across all variables. Therefore, the results provide a descriptive indication of variation among stand age groups but do not support conclusions regarding significant age-related differences in soil nutrient dynamics or differences in nutrient retention capacity.

Overall, intermediate nitrogen addition, particularly N1–N2, was generally associated with higher SOC, STN, and mineral nitrogen concentrations during the mid- and late-growing seasons, whereas higher nitrogen levels did not consistently increase soil nutrient concentrations. The responses of STP differed from those of the carbon and nitrogen variables, particularly toward the end of the growing season. These findings highlight the importance of considering seasonal variation when evaluating soil nutrient responses to nitrogen addition in Chinese pine plantations.

3.2. Effects of Nitrogen Addition on Leaf

Nitrogen addition induced contrasting responses in leaf carbon (LC), nitrogen (LN), and phosphorus (LP) concentrations across the three sampling periods in Chinese pine plantations (Figure 4). In contrast to a consistent increase in LN, its response varied across sampling periods and nitrogen addition levels. During the early growing season, LN showed a slight overall increase under higher nitrogen addition, with relatively high concentrations under N3 and N4. During the mid-growing season, LN varied among treatments, with relatively high values under N2 and N4. By the end of the growing season, LN showed no consistent increasing or decreasing trend across nitrogen treatments. These results indicate that the effects of nitrogen addition on leaf N concentration varied seasonally rather than producing a uniform increase throughout the growing season. Such variation may be related to seasonal changes in plant nutrient demand, leaf development, and nutrient allocation [22,23].

Leaf C showed relatively small fluctuations among nitrogen treatments during the early growing season. However, during the mid- and late-growing seasons, LC generally exhibited higher concentrations under intermediate nitrogen addition (N1–N2) and lower concentrations under higher nitrogen levels (N3–N4). This pattern suggests that leaf C concentration responded differently to nitrogen addition across growth stages. Leaf P also

showed season-dependent responses. LP remained relatively stable during the early and mid-growing seasons, whereas it generally increased under N2 and N3, particularly N3, before declining under N4 at the end of the growing season. Thus, the response of LP did not follow a consistent decreasing trend with increasing nitrogen addition. Previous studies have suggested that nitrogen enrichment can influence plant phosphorus acquisition and allocation through changes in soil nutrient availability and plant nutrient demand [7,18]. However, the mechanisms underlying the seasonal variation in LP observed in this study require further investigation.

Differences in LC, LN, and LP patterns were also observed among the 29-, 37-, and 48-year-old stands across nitrogen treatments and sampling periods. However, these patterns varied among nutrient variables and growth stages, without a consistent age-related direction. Therefore, the observed variation provides a descriptive indication of differences among stand age groups but does not establish that younger or older stands were more sensitive to nitrogen addition. Previous studies have reported that stand development can influence plant nutrient allocation and stoichiometric characteristics, although the magnitude and direction of these effects may depend on species, environmental conditions, and nutrient availability [24].

Nitrogen addition altered leaf nutrient stoichiometry in Chinese pine plantations (Figure 4). Leaf CN and CP ratios generally decreased with increasing nitrogen addition during the early and mid-growing seasons but remained relatively stable at the end of the growing season. In contrast, CN and CP ratios showed variable responses during the first two sampling periods but declined markedly following nitrogen addition in September, particularly under N2–N4. Leaf NP ratios increased slightly during the early growing season, showed no consistent trend in July, and decreased following nitrogen addition in September. These contrasting patterns indicate that nitrogen addition altered the relative balance of leaf C, N, and P in a season-dependent manner. Such changes may reflect seasonal variation in plant nutrient demand and nutrient allocation [7,23,24]. These observations align with previous research in coniferous species, where nitrogen addition has been shown to reduce leaf C:P ratios while increasing N:P ratios, reflecting enhanced nitrogen accumulation coupled with relatively constrained phosphorus availability [24,25]. Furthermore, variations in soil nitrogen availability can influence leaf C, N, and P contents, with subsequent impacts on litterfall and nutrient return; nitrogen enrichment has been found to increase litter production and nutrient return, although it may simultaneously reduce leaf N and P concentrations [19,26].

Differences in leaf nutrient stoichiometry were also observed among the 29-, 37-, and 48-year-old stands. However, age-related patterns varied among indices and sampling periods, without a consistent trend. Overall, the effects of nitrogen addition on leaf stoichiometry depended on both the ratio considered and the sampling period, highlighting the importance of seasonal variation when assessing nutrient responses in Chinese pine plantations.

3.3. Effects of Nitrogen Addition on Nutrient Reabsorption

Nitrogen addition affected nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) differently, with distinct response patterns across the three sampling periods (Figure 9). NRE generally decreased from N0 to N2 and subsequently increased under N3 and N4, particularly during the early and mid-growing seasons. By contrast, NRE showed relatively little variation among nitrogen treatments at the end of the growing season. This pattern indicates that the response of NRE to nitrogen addition depended on both nitrogen input level and sampling period. The initial decline under intermediate nitrogen addition may be related to changes in plant nitrogen demand and nutrient allocation following nitrogen enrichment. However, the subsequent increase under

higher nitrogen treatments suggests that the response was not simply proportional to nitrogen availability.

PRE exhibited more variable responses than NRE. It generally decreased under N1 relative to N0, while relatively high values were observed under N2, particularly during the early growing season. Further increases in nitrogen addition did not consistently enhance PRE, and its responses during the mid- and late-growing seasons showed no clear dose-dependent pattern. These results suggest that PRE was less consistent in its response to nitrogen addition than NRE. Previous studies have indicated that nitrogen availability can influence plant phosphorus demand and resorption processes through changes in nutrient balance and allocation [27]. Nevertheless, the observed PRE responses do not provide sufficient evidence to conclude that nitrogen addition enhanced phosphorus uptake or utilization.

Variation in NRE and PRE was also observed among the 29-, 37-, and 48-year-old stands. However, the age-related patterns varied across nitrogen treatments and sampling periods, without a consistent direction. Therefore, the results do not establish that particular stand ages were more sensitive to nitrogen addition or had greater nutrient resorption capacity. Stand development may influence nutrient demand and allocation, but its contribution to the observed variation requires further investigation [28,29].

Overall, NRE showed a relatively consistent decrease under intermediate nitrogen addition followed by an increase under higher nitrogen inputs, whereas PRE exhibited more variable responses, including an initial decline and a transient increase under N2.

An important limitation of this study is the lack of independent stand-level replication within each age class. Only one stand represented each age class, with five plots established within that stand. Consequently, the observed differences in stand density and baseline soil properties among age classes may reflect not only differences associated with stand development but also stand-specific structural and edaphic conditions. Because stand age was confounded with stand identity, the effects of stand age could not be separated from those of other site-specific factors. Therefore, differences among the 29-, 37-, and 48-year-old stands should be interpreted as differences among the three sampled stands rather than as general age-related patterns. Future studies should include multiple independent stands within each age class to distinguish stand-age effects from variation in stand structure and site conditions.

An important methodological limitation is that nutrient resorption efficiency was estimated from nutrient concentrations without correcting for dry-mass loss during leaf senescence. Because senescence-related mass loss can affect nutrient concentrations, the resulting estimates may overstate the amount of nutrients resorbed before leaf abscission. Therefore, the estimated values should be interpreted as concentration-based resorption efficiencies rather than direct measurements of the proportion of the initial nutrient pool recovered by the tree.

3.4. Model Development

The mixed-effects models indicated that both growing-season period and stand age were associated with variation in nutrient resorption, although the direction and magnitude of these relationships differed between NRE and PRE. Relative to the reference period, the negative coefficients for July and September in the NRE model suggest lower N resorption efficiency, whereas the positive coefficients in the PRE model indicate higher P resorption efficiency. The contrasting seasonal patterns may reflect differences in the regulation and remobilization of N and P during leaf senescence. Previous studies have also reported that N and P resorption can respond differently to nutrient availability and seasonal changes [30,31].

Adding a plot-level random intercept slightly improved the NRE model (R^2 from 0.837 to 0.840), but substantially improved the PRE model (R^2 from 0.166 to 0.459). This suggests that plot-level heterogeneity contributed more to explaining variation in PRE than in NRE. Such heterogeneity may partly reflect differences in nutrient resorption responses under N addition, as well as variation in local soil conditions and other unmeasured environmental factors. Accounting for plot-level variation therefore helps capture differences among plots that may influence the observed responses to N addition. Overall, incorporating plot-level random effects improved model performance, particularly for PRE.

3.5. Future Research Directions

Future research should focus on elucidating the long-term ecological impacts of nitrogen enrichment in Chinese pine plantations, with particular attention to stand age and seasonal variability. Long-term experiments integrating continuous nitrogen deposition with monitoring of soil microbial communities, available phosphorus, and leaf nutrient dynamics would help clarify how nitrogen inputs interact with other limiting nutrients across multiple growing seasons. In addition, investigating the effects of nitrogen enrichment on litter decomposition, nutrient return, and potential nitrogen leaching could improve predictions of nutrient cycling and ecosystem stability under future deposition scenarios. Finally, evaluating management strategies, such as targeted phosphorus supplementation or mixed-age stand configurations, may provide practical solutions to mitigate nutrient imbalances and enhance the resilience and productivity of coniferous plantations under elevated nitrogen inputs.

4. Conclusions

This study demonstrated that nitrogen addition altered soil nutrient dynamics, leaf nutrient status, and nutrient resorption in Chinese pine plantations, with responses varying across growing-season stages and nitrogen addition levels. Soil nutrient concentrations generally exhibited nonlinear and season-dependent responses. Intermediate nitrogen addition (particularly N1–N2) was generally associated with higher soil organic carbon, total nitrogen, and available nitrogen concentrations during the middle and late growing seasons, whereas higher nitrogen inputs did not consistently increase soil nutrient levels. Soil C, C, and N ratios also showed contrasting seasonal responses, indicating changes in soil nutrient stoichiometry under nitrogen addition.

Leaf nutrient responses were similarly dependent on sampling period and nitrogen addition level. Leaf carbon concentrations generally showed higher values under intermediate nitrogen addition during the middle and late growing seasons, whereas leaf nitrogen and phosphorus concentrations exhibited more variable responses. Nitrogen addition also altered leaf stoichiometry, with C generally tending to decrease, while C and N showed contrasting patterns among sampling periods. These findings indicate that nitrogen addition modified the relative balance of leaf C, N, and P, but did not produce a uniform shift in foliar nutrient status.

Nitrogen resorption responded differently to nitrogen addition, with NRE generally decreasing under intermediate nitrogen inputs (N1–N2) and increasing under higher inputs (N3–N4), particularly during the early and middle growing seasons. In contrast, PRE showed greater variation, with an initial decline under N1 and relatively high values often occurring under N2, but no consistent increase at higher nitrogen levels. The mixed-effects models further showed that accounting for plot-level variation improved model performance, particularly for PRE, highlighting the contribution of spatial heterogeneity to variation in nutrient resorption. RDA results also revealed that the relationships between

leaf nutrient characteristics, nutrient resorption, and soil properties differed among growing-season stages.

Overall, nitrogen addition affected soil–plant nutrient relationships in a nonlinear and season-dependent manner. Although responses varied among the 29-, 37-, and 48-year-old stands, no consistent age-related pattern was observed across the measured variables. These findings highlight the importance of considering seasonal dynamics, nitrogen input levels, and plot-level heterogeneity when evaluating nitrogen effects on nutrient cycling in Chinese pine plantations. They also provide a basis for understanding soil–plant nutrient responses to atmospheric nitrogen deposition and for informing the sustainable management of Chinese pine plantations.

5. Materials and Methods

5.1. Study Area

The study area is located in Jinshatan Forest Farm, Huairen City, Shuozhou, Shanxi Province, northern China (Figure 10). The region is situated in the northern part of the Loess Plateau and is characterized by a temperate continental monsoon climate, with four distinct seasons, cold and dry winters, and warm summers with most precipitation concentrated during the growing season. The mean annual temperature of Huairen City is approximately 7.3–7.9 °C, and mean annual precipitation is approximately 367–380 mm. The regional vegetation reflects a transition between forest and grassland ecosystems. The main tree species include Chinese pine, while other woody species include *Quercus liaotungensis*, *Betula platyphylla*, and *Populus* spp. Shrub and herbaceous communities are also present in the forest understory. The study site represents a typical forest ecosystem in the semi-arid region of northern Shanxi Province.

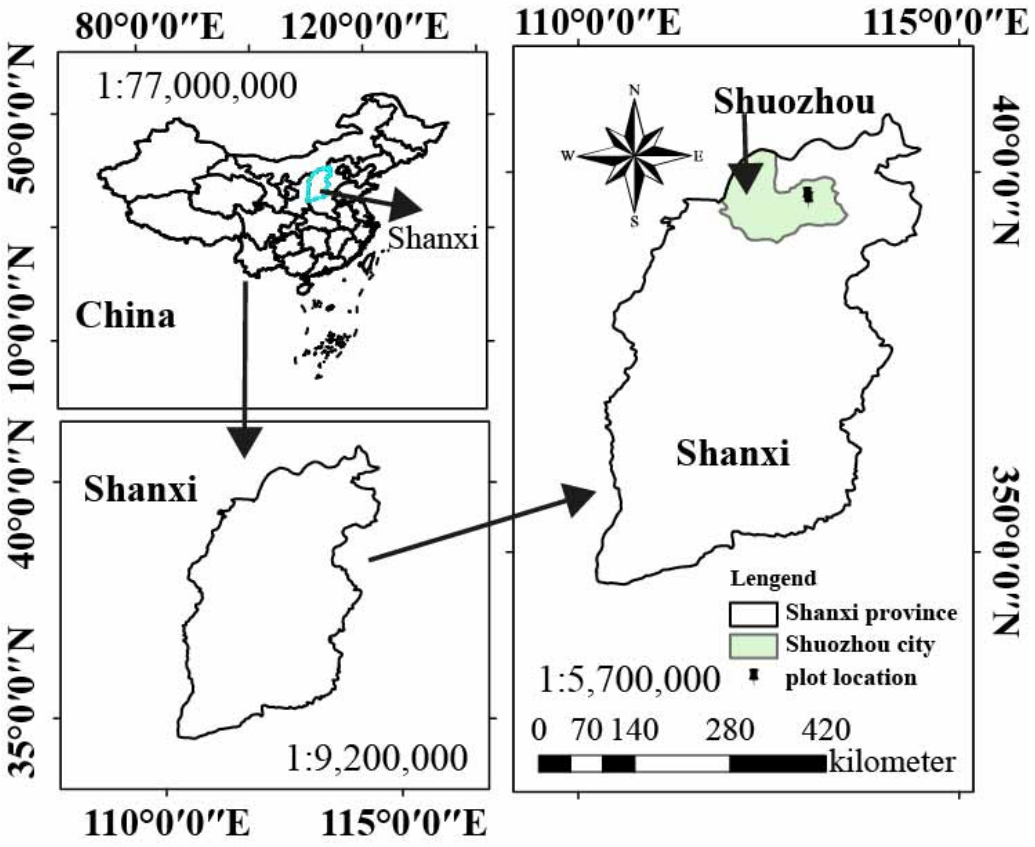

Figure 10. Location map of sampling plots.

5.2. Plot Setting and Sampling

In October 2020, homogeneous Chinese pine plantations representing three age classes (29-, 37-, and 48-year-old stands) were selected in the Jinshatan Forest Farm based on preliminary field surveys (Figure 10). The plantations were selected to ensure comparable site conditions, well-developed stand structure, and a Chinese pine proportion exceeding 90%. For each age class, five 20 m × 20 m plots were established, with a minimum distance of 20 m between plots, resulting in 15 plots in total (Table 2). All plots were surveyed, oriented using a compass, and permanently marked with stakes. Stand characteristics and understory vegetation were recorded, and all trees within each plot were measured. Before nitrogen addition, baseline soil samples were collected using the five-point sampling method to determine soil carbon (C), nitrogen (N), and phosphorus (P) concentrations. Nevertheless, differences in stand structure and baseline soil properties among the sampled stands were retained and documented.

Table 2. Initial stand characteristics and soil physical and chemical properties of sample plots.

Plot	Age	Altitude (m)	Slope (°)	Stand Density (Stem ha^{-1})	MD (cm)	pH	SOC (g kg^{-1})	STN (g kg^{-1})	STP (g kg^{-1})
plot1	29	1044.1	5	625	15.1	7.62	11.42	0.47	0.25
plot2	29	1044.4	3	625	14.1	7.72	11.84	0.49	0.25
plot3	29	1041.2	2	675	15.4	7.60	12.04	0.42	0.21
plot4	29	1040.8	4	650	15.2	7.49	11.48	0.42	0.25
plot5	29	1042.1	6	700	14.4	7.53	10.97	0.46	0.25
plot6	37	1079.2	7	750	15.7	7.65	17.64	0.47	0.37
plot7	37	1078.1	4	750	14.7	7.48	14.45	0.45	0.30
plot8	37	1078.7	6	725	14.1	7.52	14.02	0.45	0.30
plot9	37	1077.5	2	700	15.0	7.49	14.27	0.43	0.31
plot10	37	1080.1	7	775	14.0	7.62	16.74	0.42	0.28
plot11	48	1043.3	5	1525	14.7	7.52	9.87	0.35	0.36
plot12	48	1043.7	6	1625	14.6	7.37	9.58	0.27	0.32
plot13	48	1042.8	4	1650	14.2	7.34	9.92	0.36	0.29
plot14	48	1044.1	6	1625	15.3	7.51	10.89	0.35	0.28
plot15	48	1043.2	3	1475	13.5	7.63	9.71	0.32	0.31

Notes: MD, mean diameter at breast height; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus.

The nitrogen addition experiment comprised five treatments based on single-application urea rates: N0 (0 g m^{-2}), N1 (5 g m^{-2}), N2 (10 g m^{-2}), N3 (15 g m^{-2}), and N4 (20 g m^{-2}). These rates refer to the mass of urea applied per unit area, rather than the mass of elemental nitrogen. Urea was applied once during the experiment. For each treatment, the designated amount of urea was dissolved in 20 L of water and uniformly sprayed across the corresponding plot. N0 plots received the same volume of water without urea to ensure consistent application procedures across treatments. The treatments were designed to simulate increased nitrogen inputs to the forest ecosystem, although aqueous urea application does not fully reproduce the chemical composition, deposition pathways, or temporal patterns of atmospheric nitrogen deposition.

Based on the tree inventory, five dominant trees were selected from each plot for subsequent measurements and sampling. The selected trees had straight stems, intact terminal shoots, no forks or visible damage, and no obvious signs of suppression. The distance between any two selected trees exceeded 5 m. Plant and soil samples were collected from beneath each selected tree, resulting in 75 sampled trees across the 15 plots (Figure 11).

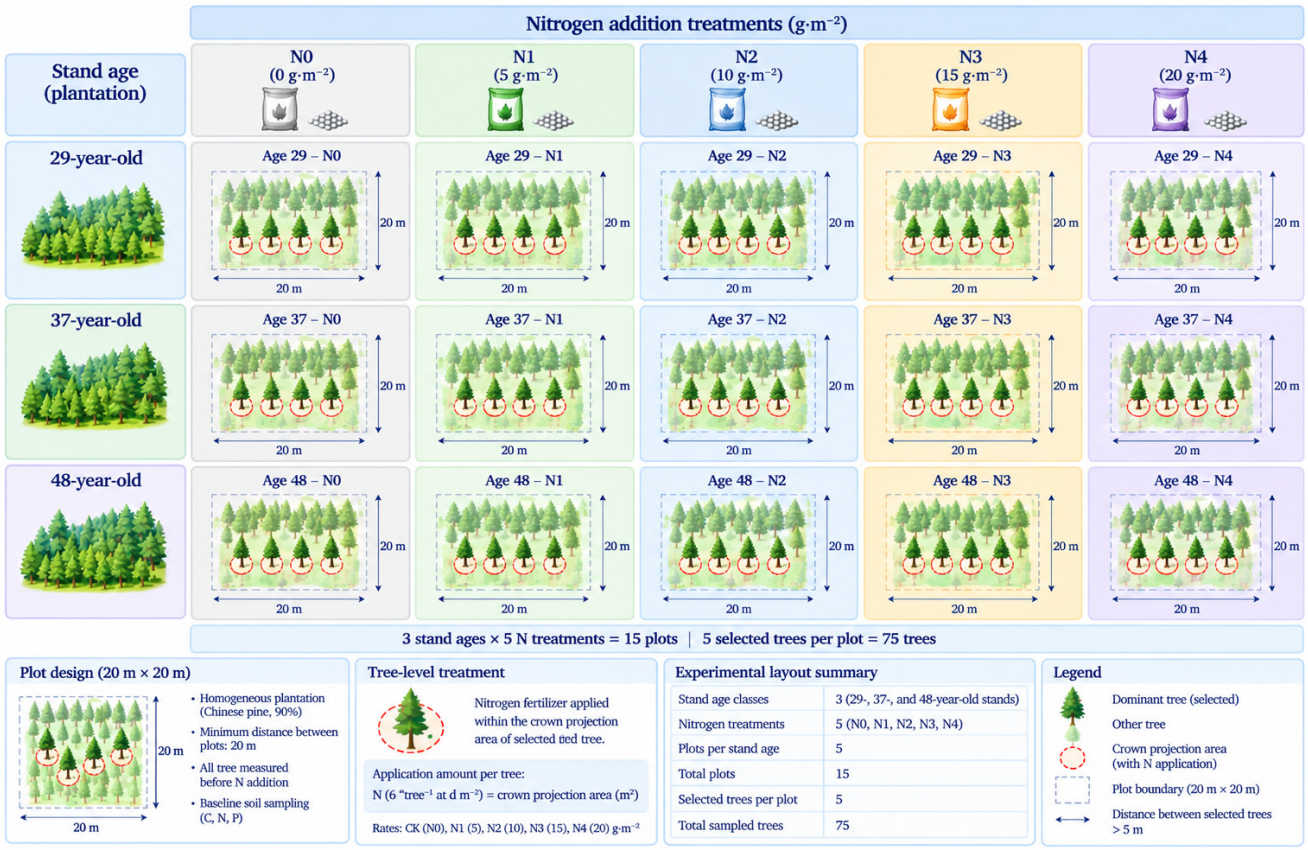

Figure 11. Schematic of the experimental design, showing the factorial arrangement of stand age and nitrogen addition treatments and distinguishing plots as experimental units from individual trees as subsamples.

Five 20 m × 20 m plots were established within each of the three stand age classes, yielding 15 plots in total. The five plots within each age class were located in the same stand and therefore represented within-stand sampling units rather than independent stand-level replicates. Consequently, stand age was associated with the characteristics of the sampled stands, and potential effects of stand age could not be completely separated from differences in stand structure and site conditions.

Plant sampling: Plant sampling was conducted three times during the 2021 growing season, in May (early growth stage), July (peak growth stage), and September (late growth stage). In each plot, one dominant tree and one average tree were selected based on stem form, terminal-shoot integrity, and the absence of branching or visible damage. For each selected tree, one lateral branch was collected from the third or fourth crown whorl in each of the four cardinal directions (southeast, southwest, northwest, and northeast). Three current-year shoots were collected from each branch, yielding 12 shoots per tree. Green and senesced leaves were matched by tree identity and leaf-age cohort to ensure comparability in subsequent nutrient analyses. Leaves collected from the 12 shoots of each tree were pooled and thoroughly mixed to obtain a composite sample for each tree, sampling occasion, and leaf category. A representative subsample was then obtained using the quartering method, placed in a labeled plastic bag, and transported to the laboratory for further analysis.

Soil sampling: Soil samples were collected around each selected tree at a distance equal to the crown radius. Three sampling points were established at 120° intervals around the tree. Soil samples were collected from three randomly selected sampling points around each of the five selected trees in each plot. At each sampling point, the surface litter layer, including undecomposed and partially decomposed litter, was removed to expose the

humus layer. Soil was then collected from a depth of 0–30 cm using a soil auger. For each selected tree, the soil collected from the three sampling points was thoroughly mixed to form a single composite sample. The quartering method was then used to obtain approximately 500 g of soil from each composite sample. The samples were placed in resealable plastic bags and stored for subsequent laboratory analyses.

To calculate nutrient resorption efficiency, senesced leaves were considered as litter, which was obtained by gently shaking and collecting recently fallen leaves from living plants [32]. Since it is challenging to extract senescing leaves directly from living plants, leaves were sampled from freshly fallen litter beneath the trees. The collected leaves showed no obvious oxidation or decomposition during the interval between litterfall and collection, were not significantly affected by precipitation leaching [33], and exhibited minimal photodegradation [34]. Therefore, nutrient losses due to other factors were considered negligible. All samples were placed in plastic bags and stored at 4 °C until laboratory analysis.

5.3. Laboratory Analyses

Plant and litter samples were oven-dried at 65 °C after preheating at 105 °C for 15 min to inactivate enzymes. The dried samples were then ground and passed through a 100-mesh sieve. For soil analysis, samples intended for the determination of ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were kept fresh or refrigerated prior to extraction, whereas samples for the determination of total carbon (C), total nitrogen (N), and total phosphorus (P) were air-dried, ground, and passed through a 100-mesh sieve. Plant leaf and litter samples were analyzed for total C, total N, and total P. Detailed analytical procedures are provided in Table 3.

Table 3. Methods of soil and plant nutrient measurement and instruments used.

Measured Index	Method	Instruments	References
TC/SOC (leaf and soil)	Potassium permanganate external heating method, dry burning method	Multi N/C 2100	[35]
TN (leaf and soil)	H_2SO_4 digestion method, Kjeldahl nitrogen determination method	FoodALYT D5000	[35]
TP (leaf and soil)	H_2SO_4–$HCLO_4$ digestion method, molybdenum antimony colorimetric method	Rayleigh UV-2601	[35]
SAN (soil)	Spectrophotometry	Rayleigh UV-2601	[35]
SNN (soil)	Spectrophotometry	Rayleigh UV-2601	[35]

Notes: SAN, soil ammonium nitrogen; SNN, soil nitrate nitrogen; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

5.4. Data Analysis

Before statistical analysis, all variables were examined for normality and homogeneity of variance. To account for repeated measurements collected during the three sampling periods (May, July, and September), linear mixed-effects models (LMMs) were used to evaluate the effects of nitrogen addition on leaf and soil nutrient properties. Nitrogen addition treatment, stand age, sampling period, and their relevant interactions were specified as fixed effects, while plot identity was included as a random intercept to account for between-plot heterogeneity. Furthermore, a first-order autoregressive correlation structure [AR(1)] was incorporated to account for temporal autocorrelation among repeated residuals within the same plot. This structure assumes that residual correlations decrease with increasing temporal separation between sampling periods. The suitability of the AR(1) structure was evaluated using model fit criteria. This modeling framework accounted for both between-plot variability and temporal dependence among repeated observations.

Redundancy analysis (RDA) was performed to examine the relationships between leaf nutrient characteristics, nutrient resorption efficiencies, and soil properties at three stages of the growing season: the early growing season (May), the middle growing season (July), and the end of the growing season (September). The response variables included leaf carbon (LC), leaf nitrogen (LN), leaf phosphorus (LP), nitrogen resorption efficiency (NRE), and phosphorus resorption efficiency (PRE). Soil properties were used as explanatory variables and included soil ammonium nitrogen (SAN), soil nitrate nitrogen (SNN), soil organic carbon (SOC), soil total nitrogen (STN), and soil total phosphorus (STP).

To explore stage-specific relationships, RDA was conducted separately for each sampling period. Before analysis, all variables were standardized using Z-score transformation by subtracting their respective means and dividing by their standard deviations. The significance of the overall RDA model and individual canonical axes was assessed using permutation tests with 999 permutations. Statistical significance was evaluated at $p < 0.05$. Because the RDA analyses were conducted separately for each sampling period, they were used to characterize stage-specific associations rather than to test statistically significant differences in these associations among sampling periods.

Nutrient resorption efficiency (NuRE) was calculated from the nutrient concentrations of green and senesced leaves using Equation (1). Green and senesced leaves were matched by tree identity and leaf-age cohort. The calculation was based on differences in nutrient concentrations and did not include a correction for dry-mass loss during senescence. Accordingly, the resulting values represent concentration-based estimates of nutrient resorption efficiency rather than mass-loss-corrected estimates. This limitation should be considered when interpreting the estimated efficiencies.

$$NuRE = \frac{N_m - N_l}{N_m} \times 100\% \quad (1)$$

where N_m is the nutrient concentration of mature leaves and N_l is the nutrient concentration of litter for leaves that were beginning to senesce [36]. The NuRE capacity of the litter is correlated with the nutrient concentration.

5.5. Model Development and Advancementt

To investigate the relationships between nutrient resorption efficiency and leaf and soil nutrient characteristics, separate statistical models were developed for nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE). Leaf nutrient concentrations, soil nutrient concentrations, and nutrient loss-related variables were considered as potential explanatory variables. Based on preliminary correlation analyses, LN, DN, and SN were selected as explanatory variables for the NRE model, whereas LP, LC, and SC were selected for the PRE model.

To account for temporal and age-related variation, sampling month and stand age were incorporated into the models as categorical fixed effects. Nitrogen addition treatment was also included as a categorical fixed effect to account for differences among experimental treatments. Sampling month (May, July, and September), stand age (29, 37, and 48 years), and nitrogen addition treatment (N0, N1, N2, N3, and N4) were represented by dummy variables. May, 29-year-old stands, and N0 were used as the respective reference categories. The interaction between nitrogen addition treatment and sampling month was additionally considered to evaluate whether the effects of nitrogen addition on nutrient resorption efficiencies varied across sampling periods.

To account for repeated observations within sampling plots, linear mixed-effects models were fitted with plot identity included as a random intercept. In addition, a first-order autoregressive correlation structure [AR(1)] was incorporated to account for temporal autocorrelation among residuals from repeated measurements within the same plot. This

structure assumes that residual correlations decrease with increasing temporal separation between sampling periods. The combination of a plot-level random intercept and an AR(1) residual correlation structure allowed us to account for both between-plot heterogeneity and within-plot temporal dependence. The general model structure was expressed as follows:

$$NuRE = \beta_0 + \sum_{k=1}^{p} \beta_k X_{kij} + \sum_{m=1}^{2} \gamma_m month_{mij} + \sum_{a=1}^{2} \delta_a age_{aij} + \mu_j + \xi_{ij} \quad (2)$$

where NuRE represents NRE or PRE for observation i in plot j; β_0 is the fixed intercept; X_{kij} represents the selected nutrient-related explanatory variables; β_k denotes their corresponding regression coefficients; $month_{mij}$ and age_{aij} are dummy variables representing sampling month and stand age, respectively; and γ_m and δ_a are their corresponding coefficients. The plot-level random intercept μ_j was assumed to follow a normal distribution with mean zero and variance, while the residual error ξ_{ij} was assumed to follow a normal distribution with mean zero and variance.

The basic models containing only fixed effects were compared with the mixed-effects models to evaluate the contribution of plot-level variation to model performance. Model fit was assessed using the coefficient of determination (R^2). All statistical analyses were conducted in R, and linear mixed-effects models were fitted using the nlme package.

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Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding authors.

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