

1Comparison of C:N:P stoichiometry in the plant–litter–soil system between poplar
2and elm plantations in the Horqin Sandy Land, China

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Abstract: Afforestation is among the most effective means of preventing and controlling desertification. Silver poplar (*Populus alba*) is commonly planted tree species for afforestation of the Horqin Sandy Land of China. However, this species has exhibited some drawbacks such as top shoot dieback, premature senescence and mortality, and soil and ecosystems degradation. In contrast, Siberian elm (*Ulmus pumila*) rarely experiences these problems in the same regions. Ecological stoichiometry plays a vital role in exploring ecological processes and nutrient cycle relationships in plant–litter–soil systems. We measured C, N, and P concentrations in leaves, branches, roots, litter, and soils and analyzed N and P resorption efficiencies, and stoichiometric homeostasis in elm and poplar plantations in the Horqin Sandy Land. The results showed that soil C and N concentrations, C:P, and N:P were greater in the elm plantation than in the poplar plantation. The plant N concentrations, C:P, and N:P and litter N and P concentrations were greater, whereas N and P resorption efficiencies were lower, in the elm plantation than in the poplar plantation. Generally, elm exhibited greater homeostasis than poplar. These findings indicate that poplar exhibited more developed internal nutrient conservation and allocation strategies but poor nutrient accumulation in soil, which may contribute to degradation of poplar plantation. In contrast, elm tended to return more nutrients to the soil. Therefore, compared with poplar, elm may be a more suitable afforestation tree species for the Horqin Sandy Land, where it may promote the accumulation of soil nutrients and enhance ecosystem stability.

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43Keywords: desertified region, forest decline, plant–litter–soil system, stoichiometric
44homeostasis, tree species selection for afforestation

451 | INTRODUCTION

46Desertification is a serious global environmental problem, with substantial effects on
 47the survival and development of some plant and animal species, human wellbeing and
 48society, and ecosystem stability maintenance (Sterk et al., 2016; Capozzi et al., 2018).
 49The Horqin Sandy Land (42°41'–45°15' N, 118°35'–123°30' E) is among the most
 50seriously desertified and ecologically fragile regions in China's agro-pastoral ecotone;
 51originally a prairie, this sandy land developed due to climate change and human
 52disturbances such as overgrazing, non-manure cropping, and arbitrary land use and
 53management (Zeng & Jiang, 2006). During the desertification process, an estimated
 5490% of carbon (C) and 86% of nitrogen (N) were lost from the ecosystem (Li et al.,
 552006). To combat and control desertification, afforestation programs have been
 56launched since the 1970s, including the Three-North Shelterbelt Program, the Grain
 57for Green Project and the Conversion of Cropland to Forest and Grassland Program
 58(Wang, 2014b; Bai et al., 2018; Chu et al., 2019).

59 These afforestation programs selected tree species with drought tolerance, rapid
 60growth, and high timber production traits (Song et al., 2020). Silver poplar (*Populus*
 61*alba*) is among the most common afforestation tree species due to its relatively high
 62initial growth and seedling survival rates (Lindroth & Clair, 2013), and it has been
 63planted as a monoculture in large areas for wind speed reduction, sand fixation, and
 64soil and water conservation (Zhao et al., 2008; Ahmed et al., 2020). However, these
 65large-scale poplar plantations have many drawbacks including top shoot dieback, tree
 66premature senescence and mortality, and soil and ecosystem degradation (Wang et al.,

672017; Zhou et al., 2020). In contrast, Siberian elm (*Ulmus pumila*) rarely exhibits
 68these problems in either natural or plantation forests in the same regions (Zhao et al.,
 692010). Nevertheless, elm is seldom planted for afforestation in the sandy land due to
 70its slow growth rate and production of crooked trunks, which limit its economic value
 71(Wang et al., 2017). Vegetation conversions after afforestation often involve
 72tremendous changes in plant and soil nutrient concentrations, biomass production, soil
 73quality, and nutrient cycling processes, which profoundly influence the stability and
 74sustainable development of ecosystems (Zhao et al., 2008; Liu et al., 2018; Luo et al.,
 752020). Therefore, it is necessary to explore the differences in plant and soil nutrients
 76and their interactions between poplar and elm plantations to determine which is more
 77suitable for afforestation.

78 C, N and phosphorus (P) are major macroelements necessary for life; their cycling
 79in plant–litter–soil systems has substantial effects on the function and stability of
 80ecosystems (Mulder & Elser, 2009). Soil C, N, and P greatly affect plant growth and
 81development and are simultaneously affected by organic matter, litter, and microbes
 82(Sinsabaugh et al., 2008). Litter stores nutrients and returns them to soil; these
 83processes are restricted by nutrient resorption, which contributes to optimal nutrient
 84use efficiency by plants (Deng et al., 2019). Plants adjust their growth rates by
 85coordinating the ratios of C, N, and P and allocating nutrients among different organs
 86to adapt to soil nutrient conditions (Daufresne & Loreau, 2001). Thus, the balances
 87and interactions of C, N, and P are highly complex in plant–litter–soil systems
 88(Manzoni et al., 2018; Yang et al., 2019).

89 Ecological stoichiometry, which is used to evaluate the balances of energy and
90chemical elements in ecosystems, is a powerful tool for understanding ecological
91processes and relationships among element cycles in plant–litter–soil systems (Elser
92et al., 2010). Plant C:N:P stoichiometry reflects the efficiency of plants nutrient use
93(Niklas & Cobb, 2005) and can be used to determine nutrient limitations for growth
94(Koerselman & Meuleman, 1996). Soil C:N:P stoichiometry reflects soil fertility and
95nutrient availability and regulates plant growth and the nutrient state (Bui &
96Henderson, 2013). Stoichiometric homeostasis, a central concept of ecological
97stoichiometry, is defined as the ability of plants to maintain a relatively stable nutrient
98composition, regardless of soil nutrients changes (Sternner & Elser, 2002). Higher
99stoichiometric homeostasis in plants contributes to sustaining the functions and
100stability of the ecosystem (Yu et al., 2010). When soil nutrients limit plant growth,
101plants can respond via multiple physiological mechanisms to improve the internal
102availability and use efficiency of the limiting nutrient, thereby maintaining stability
103and its associated functions in the body at the limited nutrient level (Hessen et al.,
1042004). These mechanisms of nutrient conservation in plants include excreting
105hydrogen ions or enzymes into the soil (Yuan et al., 2019), altering the allocation of
106photosynthetic products and nutrients among different organs (Peng et al., 2016), and
107remobilizing nutrients from senescent to other organs before senescence (i.e., nutrient
108resorption) (Kobe et al., 2005). Therefore, evaluating C:N:P stoichiometry and
109stoichiometric homeostasis in a plant–litter–soil system could improve our
110understanding of plant adaptive mechanisms, nutrient cycles and ecosystem stability.

111 In this study, we examined seasonal variations in C, N, and P concentrations and
 112 their ratios in the leaves, branches, roots, and soils of poplar and elm trees in
 113 plantations in the Horqin Sandy Land, China, throughout the growing season. We
 114 quantified C, N, and P stoichiometry in leaf litter and analyzed the nutrient resorption
 115 efficiency (NuRE) and stoichiometric homeostasis of both tree species. One objective
 116 of this study was to determine whether the soil C, N, and P concentrations are lower
 117 in the poplar plantation than in the elm plantation, since poplar has a higher growth
 118 rate and greater biomass ([Zhao et al., 2010](#)) and therefore is expected to consume
 119 more nutrients than elm. We also aimed to determine whether poplar has lower plant
 120 N and P concentrations than those of elm, due to N and P dilution in response to
 121 higher poplar growth rates ([Zhao et al., 2010](#)), and whether elm, a native tree species,
 122 exhibits greater stoichiometric homeostasis than does poplar, an exotic tree species,
 123 since native tree species tend to adapt better than exotic species in local environments
 124 ([Song et al., 2020](#)).

125

1262 | MATERIALS AND METHODS

1272.1 | Study site

128 This study was conducted at the Zhanggutai Experimental Base of Liaoning Institute
 129 of Sandy Land Control and Utilization, Liaoning Province, China (42°32'–42°51' N,
 130 121°53'–122°35' E; average elevation, 226 m), which is located in the southeastern
 131 region of the Horqin Sandy Land, China. This region has a semiarid climate, with a

mean annual precipitation of 474 mm, largely during June–August, and mean annual potential evaporation of approximately 1580 mm (Song et al., 2020). The mean annual temperature is approximately 6.8°C, with minimum and maximum mean temperatures of −29.5 in January and 37.2°C in July, respectively. The zonal soil in this region is classified in the Semiaripsamment taxonomic group, which develops from sandy parent material through wind; the distributions of soil salinity, texture, and structures were homogeneous (Zhu et al., 2008). The main vegetation type is psammophytes, which are typical Inner Mongolia flora. The Zhanggutai Experimental Base was established in 1978; it covers an area of 2620 hm² and is characterized by flat, stable sand dunes and large *Pinus sylvestris* var. *mongolica* and *P. alba* plantations, interspersed with small patches of degraded grassland and *U. pumila* and *Pinus tabulaeformis* plantations.

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1452.2 | Experimental design

In 2017, three plots were selected among pure elm and poplar plantations on the Zhanggutai Experimental Base (Table 1). These plots had similar site conditions (elevation, slope, and soil type) and history and land management prior to afforestation. All plots were separated by at least 1 km. The selected trees were approximately 20 years old and therefore suitably represented the effects of plant and soil interactions on nutrients following afforestation (Zhao et al., 2010). No management techniques such as fertilization, pruning, or thinning were conducted in any of the plots. Three replicate subplots (20 m × 20 m) were established within each

154plot.

155 Within each subplot, three healthy individuals with average diameter at breast
 156height were randomly selected for plant sample collection. Leaf, branch, root, and soil
 157samples were collected in mid-May, July, and September. From each selected tree, we
 158collected three branches from the upper, middle, and lower parts of the crown; we
 159selected mature leaves without diseases and/or insect pests and their corresponding
 160branches. The fine roots (< 2 mm) of each selected tree were excavated from several
 161locations below the canopy by carefully removing the surrounding soil. Soil samples
 162were simultaneously collected using a soil auger (diameter, 5 cm) at depths of 0–20,
 16320–40, and 40–60 cm. After removing the understory plants and surface litter, we
 164randomly collected four soil samples within 1 m of the base of each selected tree;
 165these were pooled into a single composite soil sample per tree. In mid-October, we
 166collected newly fallen and undecomposed leaf litter from the litter layer under the
 167canopy of each selected tree. Three replicate samples of leaves, branches, roots, litter,
 168and soil were collected in each subplot. All plant samples were ground using a
 169mechanical grinder after oven drying for 72 h at 60°C, and soil samples were air-dried
 170after the removal roots and stones. All plant and soil samples were passed through a
 1710.25-mm sieve and then used to measure C, N, and P concentrations.

172

1732.3 | Chemical measurements

174C concentrations in plant and soil samples were measured using the oil bath $K_2Cr_2O_7$
 175titration method. To measure N and P concentrations, plant and soil samples were

initially digested with H₂SO₄-H₂O₂ and H₂SO₄-HClO₄, respectively, and then the total N and P concentrations were determined following the semi-micro Kjeldahl method using a Kjeldahl auto-analyzer (JY-SPD60, Beijing, China) and the colorimetric method using a spectrophotometer (T6, Beijing, China) (Bao, 2000). Plant and soil C, N, and P concentrations were expressed as in dry mass (g kg⁻¹), and C:N, C:P, and N:P ratios were calculated as mass ratios.

2.4 | Calculations

NuRE was calculated as follows:

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

where N_m and N_l are the nutrient concentrations in mature leaves (July) and litter leaves (October), respectively (Yan et al., 2016), and the MLCF is mass loss correction factor, which we set at 0.784 for broadleaf trees (Vergutz et al., 2012).

Using the nutrient stoichiometry of plant organs and soils, the homeostatic regulation coefficient (*H*) was derived from the following model (Sterner & Elser, 2002):

$$y = c + \frac{1}{H} \times \log x \quad (2)$$

where *y* is the N or P concentration or N:P for leaves, branches, and roots; *x* is the corresponding value in the soil layer; and *c* is a constant. If the regression relationship is not significant (*P* > 0.05), then 1/*H* is set at zero, and the organism is considered strictly homeostatic. If the regression relationship is significant (*P* < 0.05),

then species with $|1/H| \geq 1$ are considered not to be homeostatic, where those with $0 < |1/H| < 1$ are classified as follows: $0 < |1/H| < 0.25$, homeostatic; $0.25 < |1/H| < 0.5$, weakly homeostatic; $0.5 < |1/H| < 0.75$, weakly plastic; or $|1/H| > 0.75$, plastic (Persson et al., 2010; Bai et al., 2019).

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2022.5 | Statistical analyses

For all datasets, Kolmogorov–Smirnov and Levene’s tests were conducted to test the normality and homogeneity of variances before statistical analysis. Repeated measures analysis of variance was used to assess the effects of sampling time, soil layer, tree species, and their interactions, as well as sampling time, organ, tree species, and their interactions on nutrient concentrations and their ratios. Nutrient stoichiometry of soil, plant, and leaf litter, as well as the NuRE, were compared between elm and poplar using the two-sample *t*-tests. All figures were prepared using SigmaPlot 10.0 software, and all data were analyzed using SPSS 16.0 software for Windows (SPSS Inc., Chicago, IL, USA). Significance was evaluated at a level of 0.05.

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2143 | RESULTS

2153.1 | Soil C, N, and P stoichiometry

The soil C concentrations showed an upward trend during the growing season and decreased significantly with soil depth in both plantations; soil C concentrations were

218 higher in the elm plantation than in the poplar plantation (Table 2; Figure 1a). Soil N
 219 concentrations tended to increase in the elm plantation but remained unchanged in the
 220 0–20 and 20–40 cm soil layers in the poplar plantation over time; the soil N
 221 concentrations were higher in the elm plantation than in the poplar plantation and
 222 decreased significantly with soil depth (Table 2; Figure 1b). There were no seasonal
 223 changes in soil P concentrations except in the 40–60 cm soil layer in the elm
 224 plantation, and no significant differences were found among soil layers or between
 225 plantations (Table 2; Figure 1c).

226 The soil C:N ratio in the 0–20 cm soil layer showed a downward trend in the elm
 227 plantation but an upward trend in the poplar plantation over time. Tree species had no
 228 significant effect on soil C:N (Table 2; Figure 1d). Generally, soil C:P showed an
 229 upward trend over time and was greater in the elm plantation than in the poplar
 230 plantation (Table 2; Figure 1e). Soil N:P tended to increase in the elm plantation but
 231 remained stable in the 0–20 and 20–40 cm soil layers in the poplar plantation during
 232 the growing season; soil N:P was higher in the elm plantation than in the poplar
 233 plantation (Table 2; Figure 1f).

234

235 3.2 | Plant C, N, and P stoichiometry and nutrient resorption

236 Neither tree species nor organ had a significant effect on C concentrations, although
 237 sampling time had a significant effect, with an initial decreasing and subsequent
 238 increasing trend (Table 3; Figure 2a). N concentrations decreased in leaves but
 239 increased and then decreased in branches and roots among elm samples during the

growing season, whereas they increased and then decreased in poplar leaves and branches but showed the opposite trend in poplar roots. Overall, N concentrations were higher in elm than in poplar (Table 3; Figure 2b). P concentrations tended to decrease in the leaves, branches, and roots of elm and in the leaves and branches of poplar, whereas they increased in poplar roots during the growing season. The difference in the P concentrations of leaves and branches between tree species was not significant, but concentrations were higher in poplar roots than in elm roots (Table 3; Figure 2c).

In elm samples, the C:N ratio increased in leaves, whereas in branches and roots, it initially decreased and then increased during the growing season; in poplar samples, the C:N ratio initially decreased and then increased in leaves and branches but showed the opposite trend in roots. Overall, the C:N ratio was lower in elm than poplar (Table 23; Figure 2d). C:P showed an upward trend in all three organs of both elm and poplar samples over time, with the exception of poplar roots, in which it decreased and then increased. Overall, C:P was higher in elm than poplar (Table 3; Figure 2e). Leaf N:P decreased in elm but initially increased and then decreased in poplar during the growing season, and it was higher in elm than poplar (Table 3; Figure 2f).

Leaf litter N and P concentrations were significantly higher, but C:N and C:P were lower, in the elm plantation than in the poplar plantation, and no significant differences were found in C concentrations or N:P between the two plantations (Table 4). N and P resorption efficiencies were significantly greater in the poplar plantation than in the elm plantation (Figure 3).

262

2633.3 | Stoichiometric homeostasis

264 We detected differences in the stoichiometric homeostasis of N, P, and N:P in leaves,
 265 branches, and roots between elm and poplar plantations (Figure 4). We found strict N
 266 concentration homeostasis in elm branches and roots ($P > 0.05$) and weak plasticity in
 267 elm leaves (Figure 4a). However, N concentrations were not homeostatic in poplar
 268 leaves or roots and were strictly homeostatic in poplar branches (Figure 4b). P
 269 concentrations were strictly homeostatic in the leaves, branches, and roots of both tree
 270 species (Figure 4c, d). N:P was weakly homeostatic, weakly plastic, and strictly
 271 homeostatic in elm leaves, branches, and roots, respectively (Figure 4e), whereas N:P
 272 was not homeostatic in poplar leaves, branches, or roots, decreasing in leaves and
 273 branches and increasing in roots as soil N:P increased (Figure 4f).

274

2754 | DISCUSSION

2764.1 | Comparison of soil C, N, and P stoichiometry between elm and poplar 277 plantations

278 Afforestation can improve plant and soil nutrient concentrations and stocks, soil
 279 quality, and vegetation structure via more efficient use of resources for primary
 280 production (Nosetto et al., 2006). Afforestation increases water-holding capacity and
 281 nutrient retention (Evrendilek et al., 2004), increasing the efficacy of C sequestration
 282 and enhancing ecosystem biodiversity and resilience in semiarid regions (Hernandez-

Ramirez et al., 2011). In this study, compared with wild grassland without afforestation in the Horqin Sandy Land (the C, N and P concentrations were 4.50, 2.35 and 1.54 g kg⁻¹ at 0–20 cm; 0.31, 0.12 and 0.10 g kg⁻¹ at 20–40 cm; and 0.11, 0.10 and 0.10 g kg⁻¹ at 40–60 cm, respectively), both elm and poplar plantations increased the concentrations of soil C and N, especially in deeper soil layers, whereas there was no significant influence on P concentrations (Figure 1). Similar results were reported for *P. sylvestris* var. *mongolica* afforestation in the Horqin Sandy Land (Li et al., 2012); however, Zhao et al. (2008) reported that afforestation significantly reduced soil P concentrations but had no significant effect on soil C or N concentrations, perhaps due to differences in tree species or stand density. Thus, the choice of afforestation species and plantation management technique may be key factors for successful afforestation (Zhao et al., 2008; Bai et al., 2019; Ahmed et al., 2020).

As predicted, the soil C and N concentrations were greater in the elm plantation than in the poplar plantation (Figure 1a, b), perhaps due to possible nutrient consumption for plant growth and nutrient return in the form of leaf litter. Poplar is a fast-growing, high-yield tree species (Ahmed et al., 2020), which implies that it requires more soil nutrients than does elm (Zhao et al., 2010). Additionally, our elm plantation samples had higher N and P concentrations and lower C:N and C:P in leaf litter (Table 4) and lower N and P resorption efficiencies in leaves (Figure 3) compared with poplar samples, indicating the return of high-quality litter to soil, which accelerated litter decomposition and nutrient mineralization in the elm

305plantation. Improved soil C and N contents in the elm plantation may have created
 306opportunities for the settlement or development of other plant species, which in turn
 307enhanced nutrient and water conservation. These conditions created a positive
 308feedback between soil and plants for nutrient accumulation and stock in the elm
 309plantation. However, there was no significant difference in soil P concentrations
 310between the poplar and elm plantations (Figure 1c), which was inconsistent with
 311predictions, perhaps due to the differences in soil P sources and transformation
 312processes compared with soil C and N content. The accumulation of soil C and N is
 313driven mainly by the decomposition of plant litter and dead roots, whereas soil P
 314transformation is driven primarily by phosphate decomposition which requires long
 315periods of time (Deng et al., 2019). The N and P cycles can become decoupled under
 316drought stress (Delgado-Baquerizo et al., 2013), and soil P diffusivity is more
 317sensitive to soil water than that of N (Lambers et al., 2008); therefore, cation
 318exchange and P sorption capacity are very low in sandy soil (Leinweber et al., 1999).
 319Thus, the total P in the soil remained at levels too low for adequate absorption and use
 320by plants (Ma et al., 2009). A similar result was reported for *Pinus radiata* in a
 321temperate Andisol soil, in which the P concentrations remained unchanged following
 322afforestation (Farley & Kelly, 2004).

323 Generally, the soil C concentrations showed an upward trend in both plantations
 324over time, and the increase was greater in the elm plantation than in the poplar
 325plantation (Figure 1a). Hu et al. (2016) reported that soil C sequestration was driven
 326mainly by root input rather than leaf litter input after afforestation. Higher fine root

327biomass was found in the elm plantation than in the poplar plantation (Wang et al.,
 3282014a), which produced more root litter and exudates to facilitate soil C
 329transformation processes. Soil N concentrations increased in the elm plantation, but
 330no significant changes were observed in the 0–20 or 20–40 cm soil layers in the
 331poplar plantation during the growing season (Figure 1b), perhaps due to the leaf litter
 332decomposition rate (Wojciech et al., 2019). Elm leaves are small and soft, whereas
 333those of poplar are larger and tougher with a thicker wax layer; lignin and cellulose
 334contents are higher in poplar leaf litter (87.21 and 114.42 mg g⁻¹, respectively) than in
 335elm leaf litter (48.14 and 86.61 mg g⁻¹, respectively) (unpublished data). These
 336findings indicate higher litter decomposition rates in the elm plantation than in the
 337poplar plantation. Soil P concentrations remained stable during the growing season in
 338both plantations (Figure 1c), which is consistent with a previous study of *P. sylvestris*
 339var. *mongolica*, *P. tabulaeformis* and *Populus simonii* plantations in the Horqin Sandy
 340Land (Zhao et al., 2009). P cycling is driven mainly by plant P demand and sustained
 341by forest leaf litter inputs (Chen et al., 2008). The relatively constant total P may be
 342caused by limited direct organic input from leaf litter (Zhao et al., 2009).

343 Soil C:N:P stoichiometry is an important indicator of nutrient cycling and
 344elemental limitations in plants (Luo et al., 2020). In our study, the average surface soil
 345C:N, C:P, and N:P of the two plantations were 10.7, 55.6 and 5.1, respectively (Fig
 3461d, e, f), which were lower than average values in China (14.4, 136.0 and 9.3) and
 347worldwide (14.3, 186.0 and 13.0) (McGroddy et al., 2004; Tian et al., 2010).
 348Compared with sandy grassland (Liu et al., 2013) and shrubland (Yang & Liu, 2019),

we found lower C:N and higher C:P and N:P in the plantations, implying that soil P content is lower in forest plantations in the Horqin Sandy Land. This result may have been caused by greater sensitivity of P than N ion movement to soil moisture conditions (Walbridge, 2000; Smith, 2002; He & Dijkstra, 2014), leading to a greater dependence of soil P availability on soil water availability under the drought conditions at the study site (Yang & Liu, 2019). Furthermore, most of the P absorbed and assimilated by trees is sequestered within biomass (Kuznetsova et al., 2011; Yan et al., 2017). Soil C:N and C:P have negative effects on soil N and P availability, respectively (Li et al., 2016). In our study, soil C:P and N:P were generally greater in the elm plantation than in the poplar plantation (Figure 1d, e), whereas there was no significant difference in soil C:N between the plantations (Table 2; Figure 1c), indicating lower soil P availability but similar soil N availability in the elm plantation relative to the poplar plantation. Meanwhile, increased soil N availability and decreased soil P availability in the elm plantation and decreased soil N and P availability in the poplar plantation were also found during the growing season (Figure 1d, e).

365

4.2 | Comparison of plant C, N, and P stoichiometry between elm and poplar plantations

C, N, and P concentrations and stoichiometric ratios in different plant organs can reflect adaptive strategies to various regimes in terms of nutrient uptake, allocation, and utilization during plant growth (Niklas & Cobb, 2005). C concentrations did not

371 differ significantly among plantation species or organs, whereas they decreased and
 372 then increased over time (Table 3; Figure 2a). Lower C concentrations often lead to
 373 higher specific leaf area and photosynthetic and growth rates (Niklas & Cobb, 2005),
 374 implying faster growth for both tree species during July than during May and
 375 September. Consistent with our second prediction, plant N concentrations were
 376 generally lower in poplar than in elm (Figure 2b), perhaps due to growth dilution
 377 effects caused by the greater biomass and growth rate of poplar compared with those
 378 of elm in nutrient-poor sandy soil (Zhao et al., 2010). However, P concentrations were
 379 similar in poplar leaf and branch and higher in poplar roots compared with elm
 380 (Figure 2c). Drought stress can induce a decrease in available soil P (He & Dijkstra,
 381 2014), thus limited P absorption from soil leads to low P concentrations in plants to
 382 maintain C assimilation in arid and nutrient-poor environments (He & Dijkstra, 2014),
 383 which may explain the similar P concentrations observed in the leaves and branches
 384 between poplar and elm. Drought often induces xylem embolism in taller tree species
 385 (McDowell et al., 2008), and water transport failure can affect nutrient translocation
 386 and allocation (He & Dijkstra, 2014). Poplar is taller and more susceptible to
 387 hydraulic failure in sandy regions (Song et al., 2021), which may lead to nutrient
 388 accumulation in roots. This process may also explain the higher NuRE of poplar than
 389 elm (Figure 3).

390 In poplar, N and P concentrations were higher in roots than leaves and branches
 391 during September (Figure 2b, c), whereas N and P resorption efficiencies were higher
 392 than that of elm (Figure 3). These findings indicate that most N and P were

393reabsorbed and transferred to roots for storage, implying a more conservative nutrient
 394use strategy that benefits sprouting and new leaf growth during the following spring.
 395C:N was generally higher in poplar than in elm ([Figure 2d](#)), indicating greater N use
 396efficiency in poplar under nutrient deficient conditions (Sternner and Elser, 2002). N
 397concentrations were higher in leaves and branches but lower in roots during July than
 398those during May and September ([Figure 2b](#)), implying that more resources are
 399allocated to leaves and branches during the rapid growth season to promote the
 400growth of aerial plant part.

401 Elm organ N and P concentrations decreased in September ([Figure 2b, c](#)),
 402whereas N and P resorption efficiencies were lower in elm than in poplar ([Figure 3](#)).
 403This finding indicates the return of high-quality leaf litter to the soil, leading to
 404greater N and P acquisition by elm via root uptake and implying more efficient
 405nutrient cycles in the plant–litter–soil system. C:P was generally higher in elm than in
 406poplar ([Figure 2e](#)), indicating higher P use efficiency in elm in the Horqin Sandy Land
 407([Zhao et al., 2008](#)). The N concentrations in branches and roots were higher during
 408July than during May and September, with no significant differences between these
 409organs ([Figure 2b](#)). This implies that resource allocation between aerial and
 410underground plant parts may be more balanced in elm than in poplar, promoting root
 411growth during the rapid growing season for greater absorption of nutrient and water.

412 The leaf N:P can be used to determine potential N or P limitations for plant
 413growth, and a ratio < 14 indicates N limitation, whereas a ratio >16 indicates P
 414limitation ([Koerselman & Meuleman, 1996](#)). In this study, the leaf N:P of elm was

generally > 16 during the entire growing season (Figure 2f), indicating P limitation for elm growth. However, the leaf N:P of poplar was > 16 in July but < 14 in May and September (Figure 2f), which indicates that poplar experienced more P limitation during the fast-growing season and more N limitation during the early and late growing seasons.

420

421 4.3 | Comparison of stoichiometric homeostasis between elm and poplar plantations

Stoichiometric homeostasis reflects the balance between resource consumption and storage in plants during growth period (Blouin et al., 2012), and it is positively correlated with vegetation stability (Yu et al., 2010). In this study, both elm and poplar exhibited N and P concentration and N:P ratio homeostasis to some extent across the growing season (Figure 4), indicating relatively conservative nutrient use in both species, which improves their adaptation to this arid and nutrient-deficient environment. The maintenance of stable elemental composition in the plant body in a changeable environment is beneficial for growth, development and survival (Blouin et al., 2012). Consistent with our third hypothesis, elm generally showed greater stoichiometric homeostasis than did poplar (Figure 4), indicating that elm may have more developed nutrient modulation systems than poplar, or that elm contains more functional materials, leading to a faster response to nutrient regime changes (Bai et al., 2019). Native species such as elm have a longer life history in a given local environment, which could allow it to adapt better to adverse environmental

conditions, thereby improving ecosystem stability in the elm plantation compared with the poplar plantation.

Limiting elements in plants with homeostasis generally have low variability and environmental sensitivity (Han et al., 2011); thus, they are the main regulators of homeostasis (Sternner & Elser, 2002). Leaves, branches, and roots in both elm and poplar trees were found to have strict P homeostasis (Figure 4c, d), indicating that P may be the main nutrient limiting factor for the growth of mature elm and poplar plantations. Similar results were found in *P. sylvestris* var. *mongolica* plantations (Zhao et al., 2009) and *Caragana* shrubs (Yang & Liu, 2019) in the same region.

The degree of stoichiometric homeostasis appears to vary among organs (Bai et al., 2019), reflecting a fundamental trade-off in nutrient investment and allocation among organs (Gu et al., 2017). In this study, elm branch and root N concentrations and root N:P showed strict homeostasis, whereas the leaf N concentrations and N:P were weakly plastic and weakly homeostatic, respectively (Figure 4a, e). These results are inconsistent with those of previous studies demonstrating that leaf homeostasis is often greater than that of other organs such as branches, roots, and fruits (Bai et al., 2019; Wang et al., 2019), perhaps because leaf nutrient contents are constrained within a certain range to provide optimal physiological traits for the maintenance of survival and growth (Aerts & Chapin, 2000). Elm can survive after disastrous weather, insect or disease events, even if all leaves are lost. Therefore, maintaining the nutrient balance in elm roots may be an adaptive strategy in arid and barren environments. In poplar, the N concentrations and N:P among the three organs

were not homeostatic, except for the N concentrations in branches; the N concentrations and N:P decreased in leaves and branches but increased in roots as soil N concentrations and N:P increased (Figure 4b, f). These findings indicate that poplar coordinates nutrient allocation among organs and nutrient translocation between aerial (leaf and branch) and underground (root) part, which showed opposite trends. When poplar experienced nutrient limitation, it decreased nutrient supply to the aerial parts and increased nutrient storage in underground parts. Poplar produces many root shoots and can sprout from roots in the spring following nutrient limitation, even if the aerial parts have died.

468

4695 | CONCLUSIONS

In this study, nutrient conservation, use mechanisms, and stoichiometric homeostasis traits differed between elm and poplar plantations in the Horqin Sandy Land of China. The elm plantation had greater plant N, litter N and P, and soil C and N concentrations, which enhanced nutrient cycling in the plant–litter–soil system. Elm showed higher P use efficiency and evenly allocated N and P contents between aerial and underground parts. In contrast, poplar had higher root N and P concentrations in September and higher N and P resorption efficiencies but lower soil C and N concentrations, implying a more conservative nutrient use strategy and more developed internal nutrient cycles. Poplar had more efficient plant N use and allocated more N and P to leaves and branches in the rapid growth season. These traits are beneficial for early poplar growth, although stand degradation is expected to occur once soil nutrients can no longer sustain the nutritive requirements for growth.

Generally, elm exhibited greater homeostasis than poplar. Elm showed greater homeostasis in roots than in leaves and branches, whereas poplar coordinated nutrient allocation among organs. P was the main nutrient limiting factor in both elm and poplar plantations. Overall, elm was more adaptable to the arid, nutrient-deficient environment in terms of fostering soil nutrient accumulation and improving ecosystem stability and nutrient cycles in plant–litter–soil systems of the Horqin Sandy Land.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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TABLE 1 The basic information of Siberian elm and Silver poplar plantations

Forest species	Plot number	Longitude	Latitude	Elevation (m)	Stand (year)	age	Density (trees ha ⁻¹)	Mean height (m)	Mean diameter at breast height (cm)
Siberian elm	1	122°33'15" E	42°40'47" N	218	22		780	5.4±0.3	10.1±0.4
	2	122°32'19" E	42°43'31" N	238	23		800	5.6±0.3	9.5±0.9
	3	122°33'34" E	42°41'2" N	214	25		910	6.5±0.4	10.3±0.4
Silver poplar	1	122°34'17" E	42°41'12" N	217	21		833	11.8±0.6	14.2±0.4
	2	122°33'13" E	42°41'1" N	212.	23		825	13.2±0.4	15.2±0.8
	3	122°34'46" E	42°40'13" N	206	24		920	12.0±0.4	15.3±0.7

TABLE 2 Results (*P* values) of repeated measures analysis of variance on the effects of sampling time (T), soil layer (L), tree species (S), and their interactions on nutrient concentrations and their ratios

	C	N	P	C:N	C:P	N:P
T	<0.001	<0.001	0.002	<0.001	<0.001	<0.001
L	<0.001	<0.001	0.447	<0.001	<0.001	<0.001
S	<0.001	<0.001	0.603	0.339	<0.001	<0.001
T×L	<0.001	<0.001	<0.001	<0.001	0.004	0.005
T×S	<0.001	<0.001	0.954	<0.001	<0.001	<0.001
L×S	0.002	0.001	0.277	0.001	<0.001	<0.001
T×L×S	<0.001	<0.001	0.032	<0.001	<0.001	0.017

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TABLE 3 Results (*P* values) of repeated measures analysis of variance on the effects of sampling time (T), organ (O), tree species (S), and their interactions on nutrient concentrations and their ratios

	C	N	P	C:N	C:P	N:P
T	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
O	0.259	<0.001	0.002	<0.001	<0.001	<0.001
S	0.961	<0.001	<0.001	<0.001	<0.001	<0.001
T×O	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
T×S	0.299	<0.001	<0.001	<0.001	<0.001	<0.001
O×S	0.492	<0.001	<0.001	<0.001	<0.001	<0.001
T×O×S	0.003	<0.001	<0.001	<0.001	<0.001	<0.001

TABLE 4 The C, N, and P concentrations and their ratios in leaf litter of elm and poplar plantations

Tree species	C (g kg ⁻¹)	N (g kg ⁻¹)	P (g kg ⁻¹)	C:N	C:P	N:P
Siberian elm	449.54±10.48a	4.79±0.20a	0.51±0.02a	93.94±1.83b	883.35±14.56b	9.40±0.03a
Silver poplar	419.39±13.56a	3.84±0.16b	0.41±0.01b	109.30±1.23a	1034.27±8.93a	9.47±0.16a

Different letters indicate significant differences between the tree species at $P < 0.05$

Figure Legends

FIGURE 1 Seasonal variations in soil C (a), N (b), and P (c) concentrations and C:N

(d), C:P (e), and N:P (f) in Siberian elm and Silver poplar plantations ($n = 3$).

Different lowercases indicate significant differences among soil layers within the

same sampling time at $P < 0.05$. Different capital letters indicate significant

differences among sampling time within the same soil layer at $P < 0.05$.

FIGURE 2 Seasonal variations in plant C (a), N (b), and P (c) concentrations and C:N

(d), C:P (e), and N:P (f) in Siberian elm and Silver poplar plantations ($n = 3$).

Different lowercases indicate significant differences among organs within the same

sampling time at $P < 0.05$. Different capital letters indicate significant differences

among sampling time within the same organ at $P < 0.05$.

FIGURE 3 N and P resorption efficiencies of Siberian elm and Silver poplar ($n = 3$).

Different lowercases indicate significant differences between the tree species within

the same element at $P < 0.05$.

FIGURE 4 Relationships between plant and soil N concentration in Siberian elm (a)

and Silver poplar (b) plantations, P concentration in Siberian elm (c) and Silver poplar

(d) plantations, and N:P in Siberian elm (e) and Silver poplar (f) plantations. Solid and

dash lines indicate the regression relationship is not significant ($P > 0.05$) and

significant ($P < 0.05$), respectively. If the regression relationship is not significant (P

> 0.05), then $1/H$ is set at zero, and the organism is considered strictly homeostatic. If

the regression relationship is significant ($P < 0.05$), then species with $|1/H| \geq 1$ are

considered not to be homeostatic, where those with $0 < |1/H| < 1$ are classified as

follows: $0 < |1/H| < 0.25$, homeostatic; $0.25 < |1/H| < 0.5$, weakly homeostatic; $0.5 < |$

$7381/H| < 0.75$, weakly plastic; or $|1/H| > 0.75$, plastic.

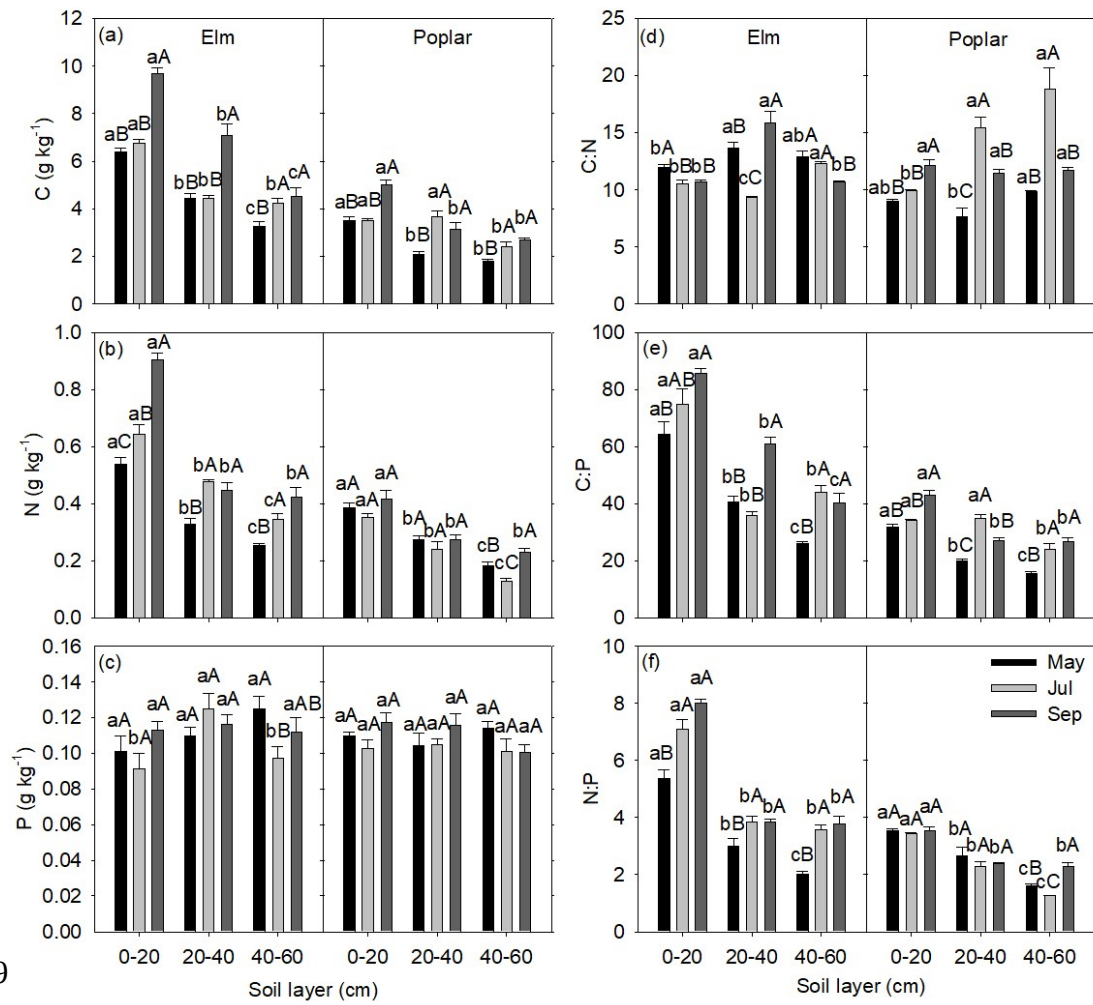


FIGURE 1

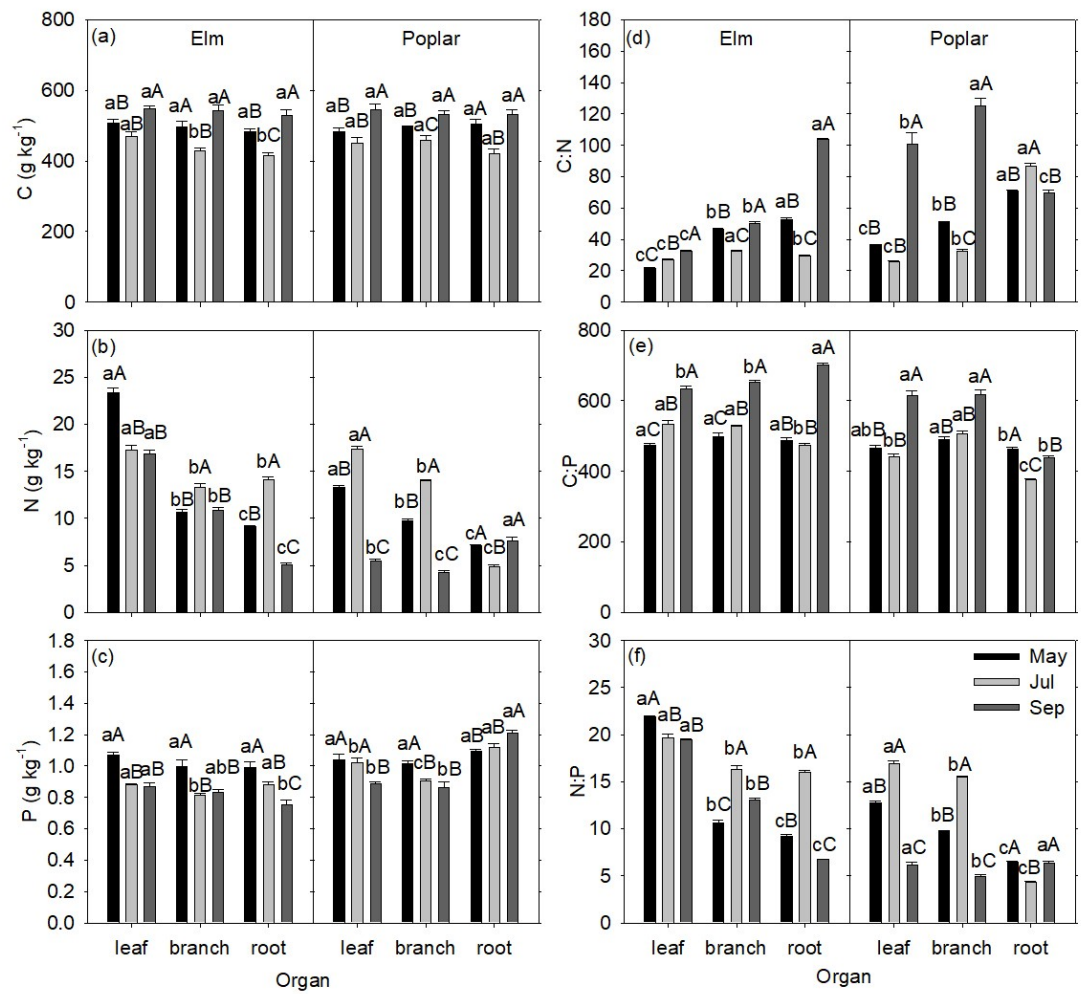
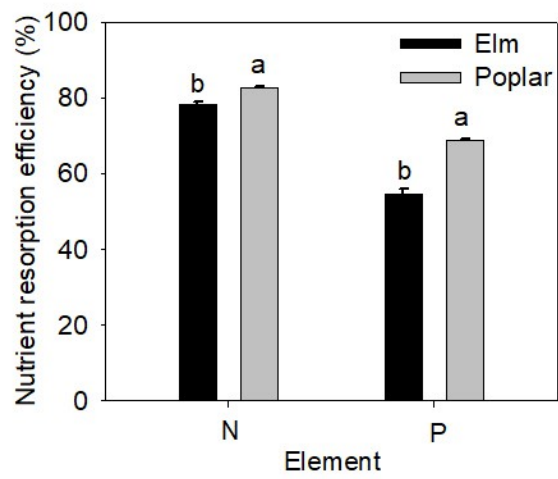


FIGURE 2



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744

FIGURE 3

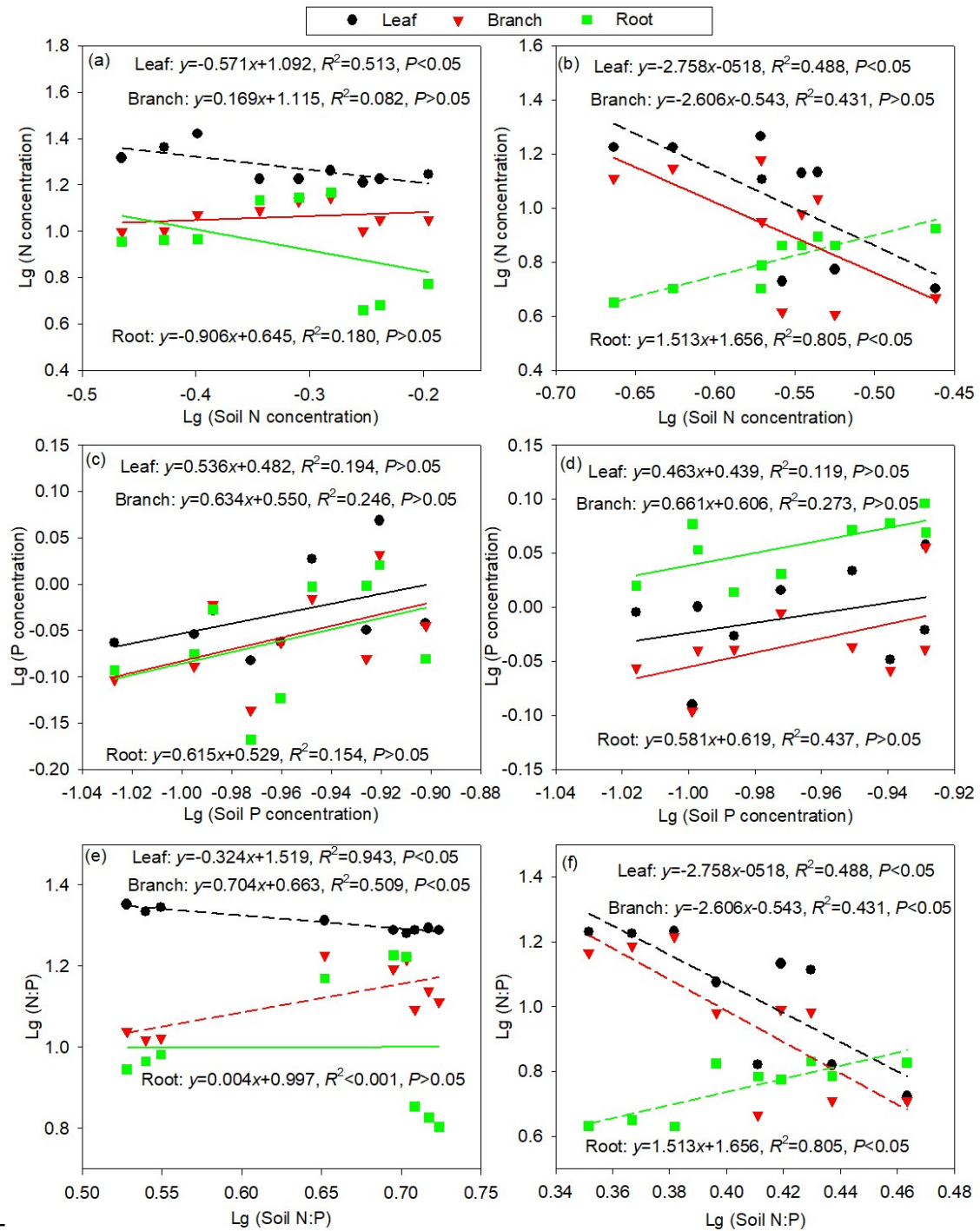


FIGURE 4