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RESPONSES OF TWIG FUNCTIONAL TRAITS AND LEAF STOICHIOMETRIC CHARACTERISTICS OF TWO PLANTATIONS TO SIMULATED NITROGEN DEPOSITION IN THE HILLY AREA OF CENTRAL SICHUAN

PENG Xiu-Tao[1], REN Liang[2] and XIAO Juan*[1]

[1]College of Environmental Science and Engineering, China West Normal University, Nanchong Sichuan 637002, China
[2]Langzhong Ecological Environment Monitoring Station of Nanchong City, Nanchong Sichuan 637400, China

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Corresponding author: XIAO Juan

ABSTRACT

The effects of nitrogen deposition on the nutrient limitation pattern and growth strategy of forest trees have already become the research frontiers of forest ecological ecology. In order to clarify the influence of N deposition on the nutrient limitation characteristics and growth strategies of plantations in the hilly area of central Sichuan, this study took *Pinus massoniana* plantation and *Cupressus funebris* plantation as the research objects in this area, and analyzed the responses of the functional traits of the current twigs and foliar N and P stoichiometry to N addition in the two plantations. The results showed that: 1) Under nitrogen addition, the TM and MLI of the current twigs of *Pinus massoniana* plantation and *Cupressus funebris* plantation were significantly decreased. 2) Under nitrogen addition, the foliar P concentration of the two plantations was significantly decreased, and the foliar N:P was significantly increased. 3) Under nitrogen addition, the LDMC of the two plantations increased significantly, while the SLA decreased significantly. Therefore, N addition enhanced the P-limiting degree of *Pinus massoniana* plantation and *Cupressus funebris* plantation in the hilly area of central Sichuan, resulting in the inhibition of tree growth, and in this case, the two plantations tended to adopt a conservative "slow investment-return" growth strategy. And this result can provide a scientific basis for the adaptive management and ecological function restoration of plantations in this area.

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INTRODUCTION

As one of the key limiting nutrients for forest productivity and plant growth, N element can change the aboveground-belowground ecological processes of plants [1]. Therefore, exogenous N addition is bound to affect the soil N nutrient supply in forest ecosystem, leading to changes in structural tissue characteristics and chemical properties of plants [1, 2]. Studies have shown that appropriate exogenous N input can promote plant growth [1-3], increase plant photosynthetic rate, and result in the increase of forest productivity[1, 4]; And long-term exogenous N addition will enrich the forest ecosystem with N[5], which resulted in the difference in the input of N and P elements into the ecosystem, destroyed the balance between the soil N and P supply and plant N and P absorption, and led to the P limitation of plant growth in forest [6-8]. Therefore, N deposition has a profound impact on the stability of forest structure and function. Understanding the stoichiometry changes of foliar N:P in plants under different N deposition concentrations is of great significance to reveal the changes of nutrient limitation pattern in ecosystem. Forest tree growth is affected by a variety of environmental factors, such as slope, soil water content, interspecific resource competition and soil nutrient limitation [9-11]. Among them, soil nutrient limitation is one of the key factors affecting forest tree growth, productivity and survival [12]. Trees will adjust or change their functional traits timely according to the nutrient limitation status in the environment, and optimize the allocation of resources to adapt to the changing living environment [13]. As one of the most active tissues in the branching system of trees, the current twigs can reflect the changes of the external environment better than the whole tree [14, 15]. The twigsare composed of two parts: stemand leaves. The leaf is an important place for photosynthesis, and the stem plays a role in water and nutrient transport and mechanical support [12]. Previous studies have shown that plants can adapt to the changing environment through the combination and trade-off of stem and leaf functional traits, which determines the growth strategy of plants [15, 16]. For example, in the environment of resource scarcity, plants tend to adopt conservative growth strategies, which have longer leaf life and higher leaf dry matter concentration, lower specific leaf area and photosynthetic rate[17, 18]. Conversely, in the environment of resource abundance, plants tend to adopt open growth strategies, which usually have higher specific leaf area, lower leaf dry matter concentration and higher photosynthesis capacity [17, 18]. Therefore, understanding the dynamic response of the current twig's functional traits under N addition is crucial for evaluating the growth strategies of plants in response to global changes, such as atmospheric N deposition. Plantations in the hilly area of central Sichuanare a part of the middle and upper reaches of the Yangtze River shelterbelt project, which plays an important role inthe sustainable development of ecological environment and economy [19, 20]. As a mid-latitude subtropical forest, the productivity and tree growth of the plantations in this area may be affected by P nutrient stress.In addition, the hilly area of central Sichuan is located in the southwest of China and belongs to the N deposition area[21]. The continuous N deposition input will cause the N enrichment in the plantations of this area, which will have a profound impact on the structural and functional stability of the plantations[22].Although some scientific issues such as soil physical and chemical properties and plant nutrient stoichiometry have been studied in this area, there are still few studies on the changes in tree growth and nutrient limitation pattern of plantations in this area under N deposition[23, 24].Based on this, this study selected *Pinus massoniana* plantation and *Cupressus funebris* plantation in this area to conduct N addition experiments, and studied the responses of the functional traits of the current twigs and the foliar N and P stoichiometry of the two plantations on different N addition concentrations, aiming to reveal the change of nutrient limitation pattern and the variation of growth strategies in the plantationsof the hilly area of central Sichuan under N deposition.

MATERIALS AND METHODS

Study area: The test plot is located in Jincheng Mountain Forest Park, Nanchong City, China. The soil of this mountain is mainly calcareous purple sandstone and shale, with light yellow sandstone distributed on the top, and the altitude is generally 800 ~ 900m[21]. The climate is mild and rainless in winter, hot and rainy in summer, which is a typical subtropical monsoon humid climate[20]. The frost-free period of the whole year is more than 300 d, which is suitable for plant growth, and the forest coverage rate is more than 98%. The existing vegetation of the mountain is mainly composed of coniferous species, often accompanied by broad-leaved species. The arbor layer is composed of *Pinus massoniana*, *Cupressus funebris*, *Symplocos setchuenensis*, and *Fraxinus* chinensis, etc.; the shrub layer is mainly composed of *Anaphalis lactea*, *Rubus coreanus*, and *Rhododendron simsii*, etc.; the herb layer is mainly composed of *Arachniodes chinensis*, *Dryopteris labordei*, *Capilipedium prviflorum*, and *Causonis japonica*, etc.[21, 23].As common afforestation restoration species in southern China, *Pinus massoniana* and *Cupressus funebris* have strong adaptability and drought and barren resistance, which occupy an important position in forest resources of Sichuan and play an important role in forest carbon sinks[25, 26].

Experimental design: We took two plantations of *Pinus massoniana* and *Cupressus funebris* as study objects, and the plot setting adopted random block design. According to the estimated value of atmospheric N deposition in the early stage of the critical value of atmospheric N deposition in southwest China (50 kg N/(hm^2·a))[1, 27], a total of one control and two N addition gradients were set up, which separately were low N addition (25 kg N/(hm^2·a)) and high N addition (50 kg N/(hm^2·a)). Each treatment has three repetitions, with a total of 18 test plots. And each plot was 10 m×10 m in size, and adjacent plot were provided with ≥10m buffer zone[28]. The N addition test started in March 2018. At the beginning of each month, we dissolved the corresponding mass of NH_4NO_3 in 12L water according to the requirements of different gradients, and used the knapsack sprayer to spray evenly in each test plot. And also, the control was sprayed with equal volume of water to prevent the water effect caused by the addition of solution.

Sample collection: The current twigs and leaves were collected in August, 2023 (middle of the growing season). We randomly selected three healthy trees with basically the same growth in each test plot. After climbing the target tree with the foot clasp,the primary branches on all sides and the same height of the target trees were cut with tall branch scissor. And then the end of each primary branchwas cut and mixed as one sample of the current twigs, and the current twig samples were stored in a numbered plastic bag and refrigerated. After the samples were brought back to the laboratory, the current twigs with fullystretchedandhealthilymaturedleaves were selected, and the green leaves on the current twigs were cut as leaf samples.

Sample measurement

The acquisition of blade projection area: Firstly, a certain amount of current twigs with healthy and intact leaveswere randomly selected from the current twig samples. Secondly, the impurities on the surface of the current twigs were washed with tap water, and the water on the surface of the twigs was quickly dried. And thirdly, all the leaves on the twigs were cut with scissors, and the number of leaves on each twig was recorded. Fourthly, all the leaves of each current twig were laid on the root tray of the root scanner, and all the leaves were scanned into a 400dpi grayscale image with scanner. And fifthly, winRhizo software was used to analyze the leaf image of each current twig to obtain the total leaf projected area.

The measurement of leaf saturated fresh mass, leaf dry mass and foliar dry foliar Nand Pconcentration: Firstly, After the scanning leaves were soaked in water for 24hours, drying the surface water of the leaves of each current twig and weighing them to obtain the leaf saturated fresh mass. And secondly, after weighing, the leaves were killed green at 105℃, and then the dry weight of leaves and stems of current twigs was obtained by drying them in the oven at 65℃ until the mass was constant. Thirdly, the leaf samples after killing green and drying were ground and passed through a 60-mesh sieve, and were determined by using an element analyzer for total nitrogen concentration. Fourthly, the sieved leaf samples were extracted with concentrated sulfuric acid and hydrogen peroxide, and the extraction was determined by the Mo-Sb anti spectrophotometric method for foliar total phosphorus concentration.

Statistical analyses

$$LMA = LDM / LPA$$
$$TM = LDM + SDM$$
$$MLI = LN / TM$$
$$LDMC = LDM / LSFM$$

Here, LMA represents leaf mass per area; LDM represents leaf dry mass; LPA represents leaf projected area; TM represents twig mass; SDM represents stem dry mass;MLI represents mass-based leafing intensity; LN represents leaf numbers; LDMC represents leaf dry matter concentration; LSFM represents leaf saturated fresh mass. Microsoft Excel 2021 was used for data processing, and IBM SPSS 26.0 was used for normality test, variance homogeneity test, and one-way analysis of variance in the subsequent analysis stage. The differences in current twig functional traits and leaf physiological characteristics between different N addition treatment plots and control plots in two plantations of *Pinus massoniana*and *Cupressus funebris*were compared. And all graphs in this article were drawn by using Origin 2021.

RESULTS

Effects of nitrogen addition on the MLI and TM of the current twig: Under different nitrogen addition treatments, the mass-based leafing intensity (MLI) of *Pinus massoniana* and *Cupressusfunebris* plantations showed the same trend.Specifically, under LN treatment, the MLI of *Pinus massoniana* and *Cupressusfunebris* plantations was also significantly lower than that of CK(P< 0.05), which respectively decreased from 73.86 leaves/g and 56.91 leaves/g of CK to 63.03 leaves/g and 42.23 leaves/g, with an average decrease of 14.49% and 25.82%. And furthermore, under HN treatment, the MLI of the two plantations was also significantly lower than that of CK(P< 0.05), which respectively decreased from 73.86 leaves/g and 56.91 leaves/g of CK to 54.17 leaves/g and 37.59 leaves/g, respectively, with an average decrease of 26.43% and 33.89% (Figure 1). Similarly, under different nitrogen addition treatments, the twig mass (TM) of the two plantations showed a downward trend. Specifically, under LN treatment, TM of *Pinus massoniana* plantation was lower than CK, but not significantly ($P>$ 0.05), while TM of *Cupressus funebris* plantation was significantly lower than CK ($P<$ 0.05), decreasing from 0.49 g to 0.32 g, with an average decrease of 34.39%.Similarly, under HN treatment, TM of *Pinus massoniana* and *Cupressusfunebris* plantations wereboth significantly lower than CK($P<$ 0.05), respectively decreasing from2.72 g and 0.49 g of CK to 1.93 g and 0.24 g, an average decrease of 28.94% and 52.45% (Figure 1). The variation range of each indicator is detailed in Table 1.

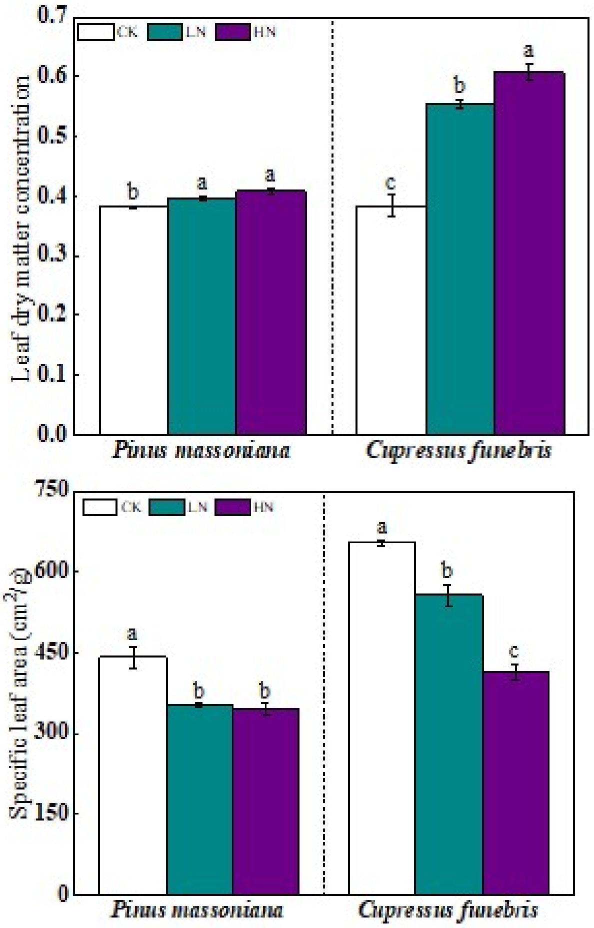

Figure 1 Effects of nitrogen addition on the MLI and TM of the current twig. "MLI" represents "mass-based leafing intensity"; "TM" represents "twig mass"; "a, b" and "a, c" indicates "significant difference"; "a, a" and "b, b" indicates "no significant difference"

Effects of nitrogen addition on foliar LDMC and SLA: Under different nitrogen addition treatments, the leaf dry matter concentration (LDMC) of the two plantations showed a consistent response trend.Concretely speaking, under low nitrogen addition (LN), the LDMC of *P. massoniana* and *Cupressusfunebris*plantations were significantly higher than that of the control (CK) ($P <$ 0.05), respectivelyincreasing from CK's 0.382 and 0.383 to 0.396 and 0.555, an average increase of 3.89% and 45.65%.Similarly, under high nitrogen addition (HN), the LDMC of the two plantations were significantly higher than that of CK($P <$ 0.05), respectivelyincreasing from 0.382 and 0.383 of CK to 0.409 and 0.608, with an average increase of 7.11% and 59.08% (Figure 3). Similarly, under different nitrogen addition treatments, the specific leaf area (SLA) of the two plantations also showed a consistent response trend.To be more specific, under LN treatment, the SLA of *Pinus massoniana* and *Cupressusfunebris* plantations were significantly lower than that of CK($P<$ 0.05), respectivelydecreasing from 441.05 cm^2/g and 654.35 cm^2/g of CK to 352.67 cm^2/g and 556.45 cm^2/g, with an average decrease of 19.59% and 15.01%. Similarly, under HN treatment, the SLA of *Pinus massoniana* and *Cupressusfunebris* plantations were also significantly lower than that of CK($P<$ 0.05), respectively decreasing from 441.05 cm^2/g and 654.35 cm^2/g of CK to 344.74 cm^2/g and 415.33 cm^2/g, with an average decrease of 21.20% and 36.56% (Figure 3).The variation range of each indicator is detailed in Table 1.

Table 1. Variation range of functional traits of current twigs in two plantations under nitrogen addition treatment

Functional traits	Treatments	Species	
		Pinus massoniana	*Cupressus funebris*
LDMC	LN	3.89%	45.65%
	HN	7.11%	59.08%
SLA	LN	-19.59%	-15.01%
	HN	-21.20%	-36.56%
TM	LN	-10.54%	-34.39%
	HN	-28.94%	-52.45%
MLI	LN	-14.49%	-25.82%
	HN	-26.43%	-33.89%

Note: "LN" indicates "low nitrogen addition"; "HN" indicates "High nitrogen addition".

Effects of nitrogen addition on the foliar N and P stoichiometry: In this study, under different nitrogen addition treatments, the foliarphosphorus (P) concentration of the two plantations showed a consistent response trend. Concretely speaking, under LN treatment, the foliar P concentrationof *Pinus massoniana* plantation and *Cupressusfunebris* plantations were significantly lower than that of CK ($P<$ 0.05), respectivelydecreasing from CK's 0.95 g/kg and 0.95 g/kg to 0.82 g/kg and 0.86 g/kg, with an average decrease of 13.23% and 8.89%.

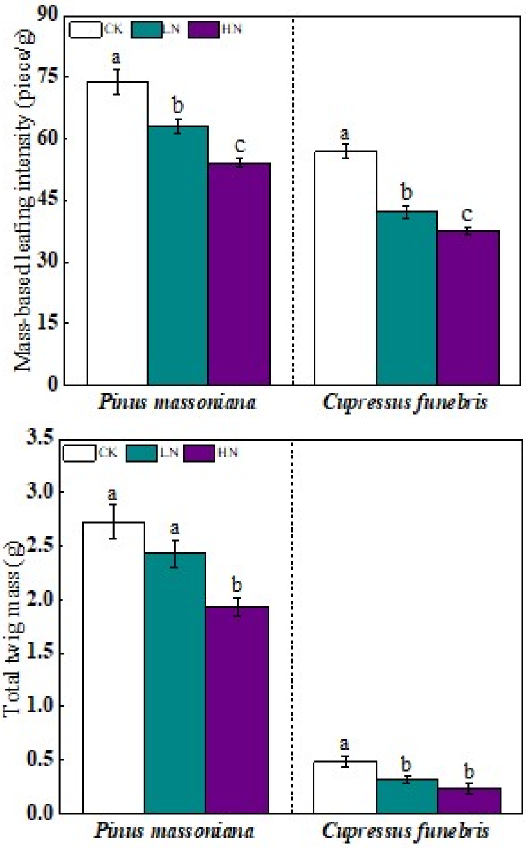

Figure 3. Effects of nitrogen addition on foliar LDMC and SLA. "LDMC" represents "leaf dry matter concentration"; "SLA" represents "specific leaf area"; "a, b" and "a, c" indicates "significant difference"; "a, a" and "b, b" indicates "no significant difference".

Meanwhile, under HN treatment, the foliar P concentration of the two plantations was also significantly lower than that of CK ($P<$ 0.05), respectively decreasing from CK's 0.95 g/kg and 0.95 g/kg to 0.84 g/kg and 0.81 g/kg, with an average decrease of 10.82% and 14.91%.

Similarly, under HN treatment, the foliar N concentration of the two plantations also showed a consistent response trend. Specifically, under HN treatment, the foliar N concentration of *Pinus massoniana* plantation and *Cupressus funebris* plantations were significantly higher than that of CK ($P< 0.05$), respectivelyincreasing from 15.63 g/kg and 15.33 g/kg of CK to 16.96 g/kg and 16.97 g/kg, with an average increase of 8.49% and 10.67% (Figure 2).

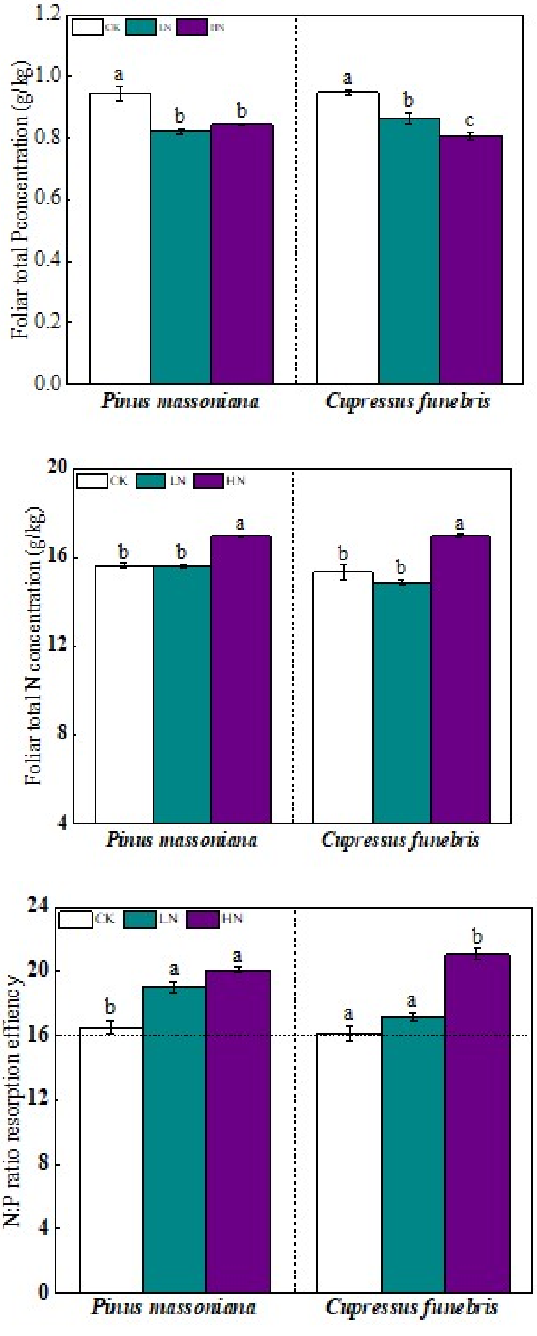

Figure 2. Effects of nitrogen addition on the foliar N and P stoichiometry. "a, b" and "a, c" indicates "significant difference"; "a, a" and "b, b" indicates "no significant difference"

Similarly, under different nitrogen addition treatments, the foliar N:P ratio of the two plantations also showed a consistent response trend.To be more specific, under LN treatment, the foliar N:P of *Pinus massoniana* plantation was significantly higher than that of CK ($P < 0.05$), increasing from 16.53 of CK to 19.00, with an average increase of 14.94%, while the foliar N:P ratio of *Cupressus funebris* plantation was also higher than that of CK, but not significantly ($P > 0.05$).And under HN treatment, the foliar N:P ratio of the two plantations was significantly higher than that of CK ($P< 0.05$), respectivelyincreasing from 16.53 and 16.17 of CK to 20.08 and 21.03, with an average increase of 21.50% and 30.06% (Figure 2). The variation range of each indicator is detailed in Table 2.

Table 2. Variation range of functional traits of foliar N and P stoichiometry in two plantations under nitrogen addition treatment

Foliar N and P stoichiometry	Treatments	Species	
		Pinus massoniana	Cupressus funebris
Foliar N concentration	LN	-0.19%	-3.07%
	HN	8.49%	10.67%
Foliar P concentration	LN	-13.23%	-8.89%
	HN	-10.82%	-14.91%
Foliar N:P ratio	LN	14.94%	6.40%
	HN	21.50%	30.06%

Note: "LN" indicates "low nitrogen addition"; "HN" indicates "High nitrogen addition".

DISCUSSION

Compared with perennial branchlets, the current twigs are easily changed with the external environment, and the transport of nutrients and carbohydrates in thecurrent twigs are more flexible[29]. As one of the most active tissues in thebranching system of trees, the growth trend of current twigs can better reflect the response of trees to the changes in the external environment, especially the changes in soil nutrient status[12].The effects of nutrient addition on plant growth and productivity depends on the dynamic balance between soil nutrient supplies and plant nutrient demands[12].In general, exogenous N addition would increase soil phosphorus activity, thereby improving soil phosphorus availability to promote plant absorption of restricted nutrients[30].In this study, MLI and TM of the two plantations decreased with the N addition gradient, indicating that low N addition and high N addition had inhibitory effects on the tree growth of the two plantations.Previous studies have shown that in the subtropical forests of low and middle latitudes in China, the P limitation of forest tree growth is becoming more and more obvious with the progress of forest succession[31, 32]. The plantations in the hilly area of central Sichuan belongs to the mid-latitude subtropical forest, and is also an area with a relatively low availability of P. And, exogenous N input may enhance the imbalance between N and P nutrient supply of soil and N and P nutrient absorption of plants, further aggravating the P-limiting degree of plantations in this area, resulting in the decrease of the current twig's TM and MLI in two plantations with the N addition gradient.Seftigen et al. found that N addition inhibited the radial growth of Scots pine, which may be due to the shortage of soil P, K, Ca and other nutrients in the research site of Scots pine with the input of N addition, which is basically consistent with our study[33].

Nutrient concentration and stoichiometry in plant leaves are important indicators to reflect soil nutrient status and judge plant growth nutrient limitation[34-37]. Therefore, N:P in plant leaves can be used to characterize the relative strength of N and P elements in limiting plant growth[38].Koerselman and Meuleman proposed the principle of the effect of N:P stoichiometry on plant growth based on long-term fertilization experiments[38, 39]: when foliar N:P is higher than 16, compared with N, the P limitation of plant growth is stronger; when foliar N:P is between 14 and 16, the plant growth is limited by both N and P; when foliar N:P is lower than 14, compared withP, the N limitation ofplant growth is stronger. Our results showed that the foliar N:P ratios of the two plantations under the control treatment and N addition were both higher than 16, and the foliar N:P ratios increased with N addition, indicating that the growth of *Pinus massoniana* plantation and *Cupressusfunebris*plantation in the hilly area of central Sichuan was limited by P nutrients, and the degree of P limitation would increase with N addition.Generally speaking, under the condition of increased exogenous N input, plants will absorb lots of N elements and transport them to leaves to promote photosynthesis and carbohydrate accumulation[40]. Meanwhile, in order to maintain their own N and P balance, plants will invest lots of N to promote soil acid phosphatase activity[40], increasing the concentration of plant-available P in soil, and stimulating the plants' P absorption toincrease the foliar P concentration[41]. However, continuous exogenous N input will increase the growth rate of plant biomass and exceed the absorption rate of P nutrients in plants. In order to maintain the balance of N and P nutrients in the body, the demand for P nutrients in plants will also increase accordingly, resulting in "biomass dilution effect" and a decrease of foliar P concentration[41].Deng Haojun et al. conducted N addition experiments on *Pinus massoniana* plantation and found that the foliar P concentration of plants in *Pinus massoniana* plantation showed a decreasing trend with the increase of nitrogen application time and nitrogen concentration, and believed that the decrease of foliar P concentration is caused by the decline of soil available P content[42].In conclusion, continuous N input stimulated the growth of *Pinus massoniana*and *Cupressus funebris* plantations in the hilly area of central Sichuan, and induced higher P nutrient demands in the two plantations.However, the soil available P in the two plantations in this area is insufficient to meet the P nutrient demand of plant growth, which intensifies the P-limiting degree of the two plantations, resulting in a significant decrease in foliar P concentration and an increase in foliar N:P ratio of the two plantations.Casson et al.believed that N deposition would reduce the soil P availability, leading to the decline of foliar P concentration, which is consistent with our study[43].

As an important portal for material exchange and energy flow between plants and the outside world, leaf functional traits can not only reflect the strategies of plant resource acquisition, resource preservation and resource utilization, but also reflect plant growth strategies[44].In our study, low N addition and high N addition both led to significantly lower foliar SLA and significantly higher LDMC in the two plantations. And it has been reported that in an environment with relatively sufficient nutrient resources, foliar SLA of plants is usually higher, and the nutrient utilization efficiency and growth rate of individual plants are correspondingly stronger; conversely, in an environment with relatively poor nutrient resources, individual plants tend to have lower foliar SLA and stronger nutrient stress adaptation ability[45, 46]. Taking foliar SLA and LDMC into comprehensive consideration can more accurately reflect the growth strategy of plants. It is generally believed that the decrease of SLA and the increase of LDMC in plant leaves indicate the deterioration of plant growth environment, specifically, the available nutrients required for plant growth are reduced, and in order to adapt to the deteriorating growth environment, individual plants tend to adopt conservative growth strategies[45, 46]. Studies have shown that species with higher LDMC and lower SLA tend to have stronger resource acquisition ability and are better able to adapt to the harsh living environment[46].It can be seen, N addition led to the change of soil N availability in the *Pinus massoniana* plantation and *Cupressus funebris* plantation in the hilly area of central Sichuan, making the two plantations have relatively high resource acquisition capacity and gradually adopt relatively conservative growth strategies in the growth process of trees.

According to the leaf economic spectrum theory, LDMC, SLA, foliar P concentration, foliar N concentration and foliar N:P ratio are important indicators for evaluating environmental resource acquisition strategies in plants[17]. Studies have shown that plants with lower SLA, higher LDMC, lower foliar N concentration and foliar P concentration tend to have higher environmental adaptability (or have higher resource acquisition ability), and such plants usually tend to adopt "slow investment-return" strategy, while plants with higher SLA, higher LDMC, lower foliar N concentration and foliar P concentration tend to adopt "fast investment-return" strategy[47].In this study, under the nitrogen addition treatments, the LDMC of the two plantations increased significantly, while the SLA and foliar P concentration in the two plantations decreased significantly, indicating that the two plantations tended to adopt a"slow investment-return"strategy.It has been reported that when the external environment changes, plants will adjust their functional traits in time to change resource acquisition and optimize resource allocation, so as to quickly adapt to the new environment[13].Therefore, under the condition of nitrogen addition, the plantations of *Pinusmassoniana* and *Cupressus funebris* in the hilly area of central Sichuan tend to adopt a "slow investment-return" strategy in the process of adapting to the external environment. In summary, the results of TM, MLI and foliar N and P stoichiometry showed that nitrogen addition enhanced the P-limiting degree of *Pinusmassoniana*plantation and *Cupressus funebris* plantation in the hilly area of central Sichuan to some extent, and significantly inhibited the tree growth of the two plantations.In addition, the results of LDMC, SLA and foliar N and P stoichiometry showed that the two plantations tended to a conservative growth strategy of "slow investment-return" when tree growth was limited by P nutrients.

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