

Effects of nitrogen on the hydraulic characteristics and biomass allocation in *Notopterygium franchetii* in the Qinghai-Tibet Plateau

SHENGRONG XU^{1,3}, LILI PEI¹, HONGHONG ZHOU¹, YIJIN HU¹, LI TONG³, RUILI MA^{2,3*}

¹School of Pharmacy, Qinghai University, Xining, Qinghai, P.R. China

²Department of Traditional Chinese Medicine, Medical College, Qinghai University, Xining, Qinghai, P.R. China

³Qinghai Provincial Key Laboratory of Traditional Chinese Medicine Research for Glucolipid Metabolic Diseases, Qinghai University, Xining, Qinghai, P.R. China

*Corresponding author: 2020990036@qhu.edu.cn

Citation: Xu S.R., Pei L.L., Zhou H.H., Hu Y.J., Tong L., Ma R.L. (2026): Effects of nitrogen on the hydraulic characteristics and biomass allocation in *Notopterygium franchetii* in the Qinghai-Tibet Plateau. Hort. Sci. (Prague), 53: 193–203.

Abstract: Nitrogen fertiliser changes the soil environment, regulates the water balance of plants, and directly affects nitrogen and water use efficiency. In order to identify the adaptation mechanism and water regulation strategy of *Notopterygium franchetii* to the soil nitrogen environment, this study was conducted. Two-year-old *Notopterygium franchetii* plants grown in farmland were used as the test material. The hydraulic characteristics, natural dehydration, water capacitance and biomass allocation were investigated at three nitrogen application levels (0, 40, 80 kg/ha) and four growth periods (seedling, jointing, flowering and harvesting period). Nitrogen content in roots, stems and leaves increased with different levels of nitrogen treatments at each growth stage, and the change of nitrogen content in stems was the most significant. The overall water capacitance of all tissues was root > stem > leaf. After medium nitrogen treatment and high nitrogen treatments, the average water capacitance of leaves was 122.00% and 129.26% of low nitrogen treatment, and the average water capacitance of stems was 125.78% and 134.59% of low nitrogen treatment, the average water capacitance of leaves was 112.28% and 116.37% of low nitrogen treatment. Nitrogen treatment can improve the water use efficiency of plant roots, stems and leaves, and the relative content of stable carbon isotope ($\delta^{13}\text{C}$) in the whole growing season increased by 0.77%, 1.96% and 5.27% of the control group after medium nitrogen treatment, and 1.60%, 2.18% and 1.61% of the control group after high nitrogen treatment. The ratio of root to canopy decreased significantly in each growth stage after nitrogen treatment, and the change was most significant at seedling period (from 1.25 to 0.66), and the change was the most least at jointing period (from 0.77 to 0.63). Our study thus indicates that nitrogen addition could regulate water balance in plants, which is beneficial to water storage and utilisation, but excessive nitrogen fertiliser supply will also affect the distribution of plant biomass.

Keywords: water capacitance; natural dehydration; stable carbon isotope; biomass distribution

Blind fertilisation not only seriously pollutes the soil environment of farmland but also leads to a decline in the quality of medicinal herbs,

directly impacting the national quality assurance system of medicinal herbs. Nitrogen fertiliser is the most common fertiliser in agricultural production;

Supported by the Natural Science Foundation of Qinghai Province (2025-ZJ-715).

© The authors. This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International (CC BY-NC 4.0).

the different supply levels can affect the physiological and metabolic characteristics of crops. Rational application of nitrogen fertiliser plays an important role in crop high yield. Plants have different physiological responses in different nitrogen environment and growth stage. Nitrogen fertiliser utilisation efficiency (NUE) of the plant depends on absorption efficiency in a high nitrogen environment and on metabolic operation efficiency in a low nitrogen environment, and the plants mainly utilise the nitrogen stored in their tissues during the reproductive growth stage. (Liu et al. 2021). After the nitrogen is absorbed by the roots, a part of the nitrogen will enter the xylem ducts, transported to the stem and leaf tissues above ground under the action of transpiration pull and root pressure, and stored in the cellular vacuoles of plant organs or be metabolised, and a part of the nitrogen was stored directly in the root system or used directly by the root system. The water state in plants directly affects the nitrogen distribution ratio between roots and stems and leaves, and thus affects biomass accumulation and distribution. With plant growth and insufficient nitrogen supply, nitrogen in old leaves will be transferred to new tissues for supply and utilisation, which will also affect the redistribution of biomass. The sensitivity of different plants to changes in nitrogen availability was significantly different, and herbaceous plants showed higher leaf nitrogen content and water use efficiency than woody plants after nitrogen application (Liang et al. 2020), thus increasing biomass (Feng et al. 2023). Nitrogen utilisation in plants is significantly related to water conditions. A dry environment will limit nitrogen uptake by roots (Sun et al. 2023), and excessive nitrogen uptake will hinder plant growth (Ma et al. 2020). Leaf assimilation could also produce different responses to nitrogen addition under different water conditions (He et al. 2024).

Water is the main medium for nitrogen absorption and transport in plants, and the higher the free water content, the higher the sensitivity to nitrogen change (Kebbas et al. 2015). Nitrogen is involved in the synthesis of plant aquaporins and alters the morphology and structure of xylem vessels (Borghetti et al. 2017), thereby influencing the hydraulic properties of plant tissues. High nitrogen environment increases the vulnerability of the root to drought, leading to the imbalance of water supply and demand, and the regulation of water transport rate (Ying et al. 2022). Plant tissue water capacitance can

be used to reflect the relationship between water potential and water content change in various tissues of plants, which plays a very important role in regulating water dynamic balance in plants (Sack et al. 2005). The water capacitance of each plant tissue can be used to reflect the relative balance between water supply and transpiration dissipation of each tissue, which will decrease with the decrease of water content in the tissue, resulting in the increase of the water potential gradient in the water transport system and the acceleration of the absorption efficiency of soil water (Jin, Wang 2015). Plant hydraulic conductivity reflects physiological indicators of a plant's ability to absorb and transport water. The feedback regulation of water conduction mainly depends on the water status of the whole plant and the continuity of the hydraulic structure of the xylem ducts in the soil-plant-atmosphere system (SPAC), so as to achieve water supply balance among various tissues in the plant, and to achieve efficient water use (Huang et al. 2017).

Notopterygium franchetii H. de Boiss is an important resource of medicinal plants, has a short annual growth period and a long growth cycle of wild plants on the Qinghai-Tibet Plateau, and the wild population cannot be renewed and restored in time, thus vigorously promoting the construction of standardised cultivation bases. As a common fertiliser used in agricultural production, nitrogen fertiliser directly changes the soil environment, transmits soil environment change signals to various organs through roots, regulates plant water balance, and changes nitrogen and water use efficiency. In recent years, there have been many researches on the coupling effect of water and nitrogen in plant cultivation, but the balance relationship of water and nitrogen in plant remains unclear. In this study, water status in plants and its effects on biomass accumulation were studied through the treatments of different nitrogen application amounts, and the adaptation mechanism and water regulation strategy of *Notopterygium franchetii* to nitrogen in the soil environment were revealed, in order to provide a theoretical basis for scientific cultivation and high-quality yield research of *Notopterygium franchetii*.

MATERIAL AND METHODS

Site description. A two-year field study was conducted beginning in April 2023 at the Huzhu

<https://doi.org/10.17221/53/2025-HORTSCI>

Notopterygium franchetii model garden (36.8°N, 102.16°E, 2 809 m altitude), located on the Qinghai-Tibetan Plateau of Northwest China. The field site has a continental cold-temperate climate, with a mean annual air temperature of 5.8 °C. Mean annual rainfall is 477 mm, with a frost-free period of 105 to 128 days from June to October. The study area was chestnut soil, and the soil layer of 10–30 cm containing 145.8 mg/g organic matter (potassium dichromate oxidation – heating method), rapidly-available P (molybdenum antimony anticolorimetric method) 28.5 mg/kg, rapidly-available K (flame photometry) 196.9 mg/kg, 39.44 mg/kg inorganic N (Auto Analyzer 3 SEAL, Bran and Luebbe, Norderstedt, Germany), pH is 7.8 and the bulk density is 1.36 g/cm³.

Experimental conditions of the treatments.

Two-year-old *Notopterygium franchetii* plants transplants to the farmland in March 2023 were used as the test material. The row spacing used was 0.3 × 0.5 m, and plants with uniform growth potential were selected for analysis. The field experiment consisted of three nitrogen application levels [0 kg N/ha (TL, low nitrogen treatment), 40 kg N/ha (TM, medium nitrogen treatment), 80 kg N/ha (TH, high nitrogen treatment)] and four growth periods [SP (seedling period), JP (jointing period), FP (flowering period), HP (harvesting period)]. The experimental treatments were arranged using a completely randomised design with three replicates. All experimental areas, tillage methods and pest control were the same among experimental plots, with no fertilisation applied prior to the study. In April 2023, nitrogen fertiliser (NH₄NO₃) was applied to the seedlings according to schedule. After 7 days of nitrogen fertiliser application, the complete plants were randomly selected to determine the relevant indices. All treatment plots were sampled three times each, and each sampling was repeated three times. After sampling, several indices were determined according to the test needs.

Nitrogen content and biomass determination.

The plants were classified according to the roots, stems and leaves, cleaned with distilled water and put into the oven at 110 °C for 30 min, and then dried at 80 °C until the quality was constant. The quality of the dried samples was weighed with a balance with an accuracy of 0.0001 g. Nitrogen content was determined with the alkaline solution diffusion method (Wang et al. 2022).

After absorbing nitrogen, boric acid is titrated with standard hydrochloric acid, and the content of alkali-hydrolysed nitrogen is calculated according to the consumption of standard acid.

$$N \text{ (mg/kg)} = \frac{C \times (V - V_0) \times 14 \times 1\,000}{W}$$

where: N – the alkalolytic nitrogen concentration; C – the hydrochloric acid standard solution concentration; V – the sample consumption of hydrochloric acid standard liquid volume; V_0 – the standard liquid volume of consumed hydrochloric acid determined in blank; 14 – the molar mass of nitrogen; 1 000 – the conversion coefficient; W – the soil sample weight.

Tissue water capacitance. Stems 0.5–1.0 cm in diameter and 10 cm in length, roots 0.3–0.5 cm in diameter and 10 cm in length, and mature leaves free of pests and diseases were selected to determine water capacitance. The fresh weight (FW), corresponding water potential (Ψ_f), diameter and length of the samples were measured by an electronic balance with an accuracy of 0.0001 g. The labelled samples were immersed in distilled water overnight, and saturated fresh weight (SW) and corresponding water potential (Ψ_s) were measured the next morning, respectively. Plant tissue water capacitance (C) refers to the change of water content in plant tissue caused by a change in unit water potential (kg/cm³/MPa).

$$C = \frac{dW}{d\Psi \times V} = \frac{SW - FW}{(\Psi_s - \Psi_f) \times V} \times 100\%$$

where: C – the plant tissue water capacitance; $d\Psi$ – the tissue water potential difference; dW – change in water content; V – the plant sample volume.

Natural dehydration rate. Mature leaves free of pests and diseases, stems and roots of 0.4–0.6 cm in diameter and 10 cm in length were selected to determine the natural dehydration rate. The samples were dehydrated for 48 h under shade, dry and ventilated conditions. The natural dehydration process of tissue was divided into three stages: the first stage was from the beginning of the dehydration experiment to 12 h, the second stage was from 12 h to 24 h, and the third stage was from 24 h to 48 h. The sample weight was measured every 3 h in the first and second stages, and every 6 h

in the third stage. After 48 h, the sample was dried at 80 °C for 48 h to a constant weight of the sample, the dry weight of the sample was determined, and the relative water content of the sample was calculated. According to the relationship between the natural dehydration of samples and time, the natural dehydration rate in different time periods was analysed by fitting the trend index equation (Pan et al. 2019).

$$y = a \times e^{b \times x}$$

where: y – the plant tissue relative water content; x – the natural dehydration treatment time; a , b – exponential equation coefficients.

Stable carbon isotope ($\delta^{13}\text{C}$). Three mature leaves without pests and diseases were randomly selected, dried, crushed and mixed, and then put into an 8 mL polyethylene sample bottle for sealed storage. After the sample is burned at high temperature in the elemental analyser (Elementarac, CS-r, ELTRA, Germany) and CO_2 was generated. The mass spectrometer calculates the $\delta^{13}\text{C}$ ratio of the sample by detecting the ratio of ^{13}C to ^{12}C of CO_2 and comparing it with the international standard substance (Vienna Pee Dee Belemnite, V-PDB).

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where: R_{sample} – the ratio of heavy and light isotope abundance of C element in the sample; R_{standard} is the

ratio of heavy and light isotope abundance of C element in the international standard sample.

Statistical analyses. Statistical analyses were performed using the SPSS version 27.0 (SPSS Inc., Chicago, IL, USA). The nitrogen content, water capacitance and natural dehydration rate were compared among treatments using an analysis of variance followed by Tukey's honestly significant difference (HSD) test to determine the significantly different individual means. Means and corresponding standard deviations (SD) are presented. All statistically significant differences were tested at the 0.05 significance level.

RESULTS

Nitrogen content. Nitrogen is the main regulatory factor of plant metabolism, directly affecting water balance and assimilation synthesis in the plant (Figure 1). Nitrogen content in roots, stems and leaves increased with different levels of nitrogen treatments at each growth stage, but the difference was not significant in stems and roots. The average nitrogen content in the entire growth period, roots, stems, and leaves of TM was increased by 7.92%, 18.86% and 12.51% compared with the control, respectively; the average nitrogen content in TH was increased by 17.39%, 27.02% and 15.69%, respectively. The change of nitrogen content in stems was the most significant. The average nitrogen content of leaves was significantly higher than that of stems and roots at JP

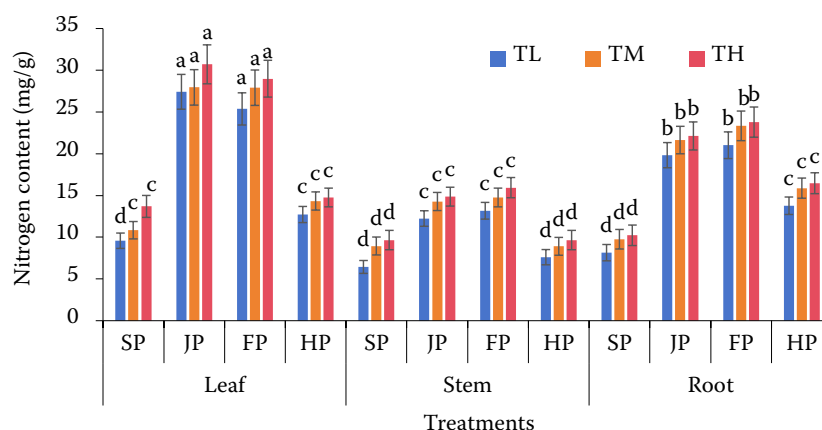


Figure 1. The effect of nitrogen treatments on nitrogen content in stems, leaves, and roots at different growth stages SP – seedling period; JP – jointing period; FP – flowering period; HP – harvesting period; TL – low nitrogen treatment; TM – medium nitrogen treatment; TH – high nitrogen treatment; the histograms are given as means and the bars are given as standard deviation; different lowercase letters indicate significant differences at the $P < 0.05$ level

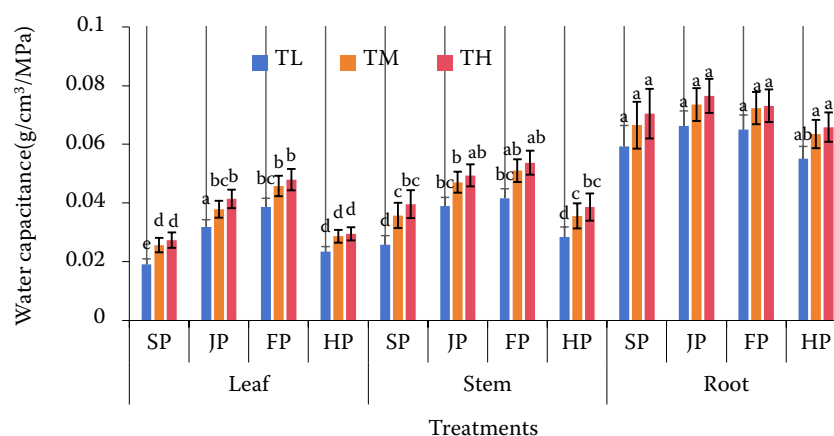


Figure 2. The effect of nitrogen treatments on water capacitance in stems, leaves, and roots at different growth stages SP – seedling period; JP – jointing period; FP – flowering period; HP – harvesting period; TL – low nitrogen treatment; TM – medium nitrogen treatment; TH – high nitrogen treatment; the histograms are given as means and the bars are given as standard deviation; different lowercase letters indicate significant differences at the $P < 0.05$ level

and FP, which was significantly decreased at HP, and the difference between leaves and roots was not significant. Nitrogen content in stems was significantly lower than that in leaves and roots at each growth stage.

Water capacitance. Water capacitance can adjust and control water storage and release in the plant in real time, which reflects the ability of the system to regulate water itself. The overall water capacitance of all tissues of *Notopterygium franchetii* was root > stem > leaf (Figure 2). After TM and TH treatments, the average water capacitance of leaves was 122.00% and 129.26% of TL, and the average water capacitance of stems was 125.78% and 134.59% of TL, the average water capacitance of leaves was 112.28% and 116.37% of TL, respectively. The tissue water capacitance increased gradually at SP, JP and FP, and the roots, stems and leaves water capacitance of FP increased to 103.83~109.75%, 135.62~161.80% and 175.24~202.19% of SP, respectively. Tissue water capacitance decreased to different degrees in the HP, and significantly in leaves and stems, which decreased to 60.51~62.59% and 68.23~71.88% of FP, respectively.

Natural dehydration rate. The lower the natural dehydration rate of plant tissue, and the stronger the water retention of the plant body, the better the resistance to stress. Based on the statistics of the relative water content of leaves, stems, and roots under natural conditions within 48 h, exponential equation ($y = a \times e^{b \times x}$) was used to fit the natural

dehydration curve, and the average natural dehydration of leaves, stems, and roots in three time periods was analysed (Figure 3, Table 1). After treatments with different nitrogen concentrations, the natural dehydration rate of leaves at each stage increased, but the difference was not significant (Figure 3A, B, C). Stems natural dehydration rate in the first stage of TH was significantly higher than that in the TL (130.39%), the second stage of TH was significantly lower than that in the TL (79.33%), and the third stage of TL and TH were significantly higher than that in the TL, but there were no significant difference between TM and TH, which were 137.94% and 114.79% of TL, respectively (Figure 3D, E, F). Roots natural dehydration rate of TM in the first and second stage were decreased to 83.80% and 87.46% of the TL, and in the third stage was increased to 152.26% of the TL. Roots natural dehydration rate was no significant difference between TH and TL at each stage (Figure 3G, H, I).

Stable carbon isotope ($\delta^{13}\text{C}$). Water use efficiency can be directly reflected by the difference of stable carbon isotope content in plants. By measuring stable carbon isotope of plants (Figure 4), it can be found that nitrogen treatment can improve water use efficiency of plant roots, stems and leaves, and the relative content of stable carbon isotope in the whole growing season increased by 0.77%, 1.96% and 5.27% of the control group after TM, and 1.60%, 2.18% and 1.61% of the control group after TH, respectively. The $\delta^{13}\text{C}$ of leaves and

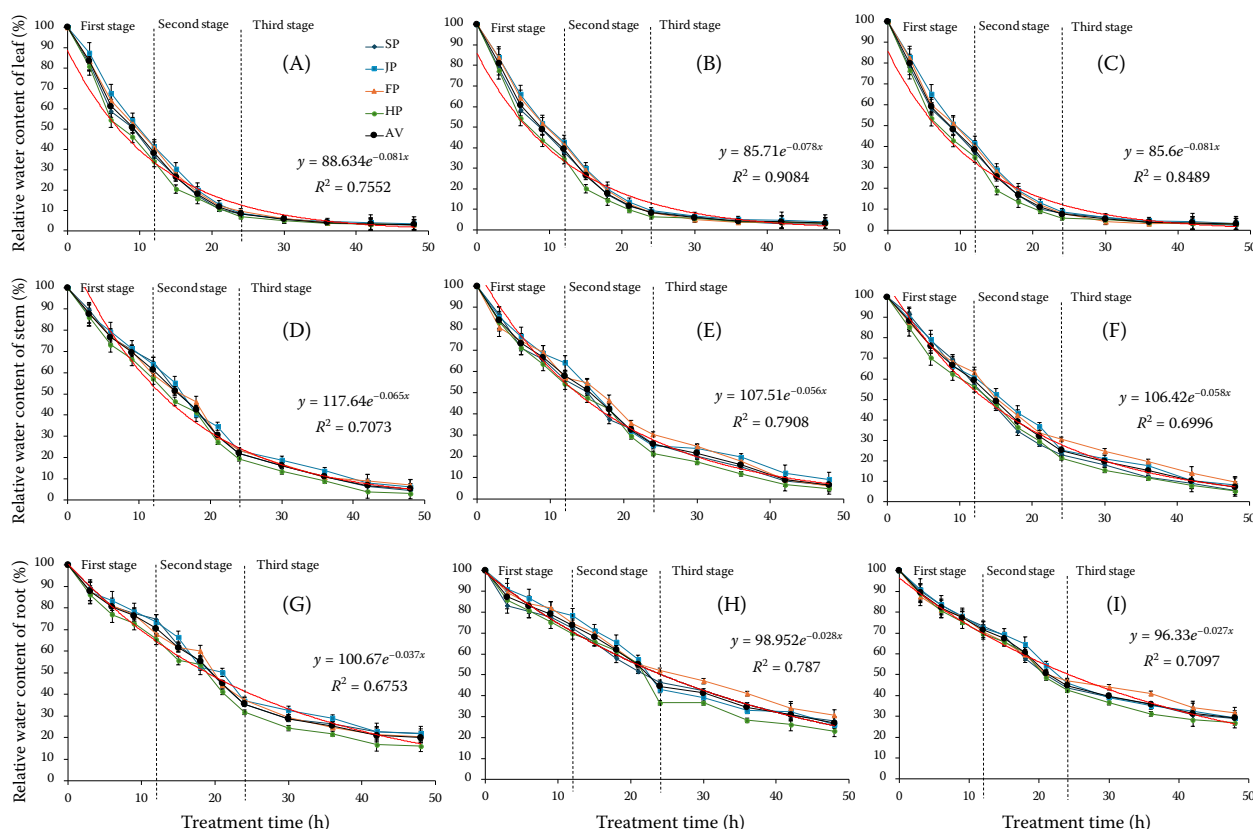


Figure 3. The effect of nitrogen treatments on natural dehydration in stems, leaves, and roots at different growth stages: (A, D, G) low nitrogen treatments, (B, E, H) medium nitrogen treatment, (C, F, I) high nitrogen treatment SP – seedling period; JP – jointing period; FP – flowering period; HP – harvesting period; AV – average value; the histograms are given as means and the bars are given as standard deviation

stems were the highest in JP, and the $\delta^{13}\text{C}$ in leaves and stems at the HP decreased by 8.74%, 8.87%, 8.55% and 7.65%, 7.01% and 7.21% compared with

JP in TL, TM and TH. The $\delta^{13}\text{C}$ of roots was the highest in FP, and that was increased by 4.37%, 4.40% and 4.48% compared with SP in TL, TM and

Table 1. The effect of nitrogen treatments on natural dehydration rate in stems, leaves, and roots at different growth stages (average values of different growth stages)

Treatments	Natural dehydration trend			Average natural dehydration rate (g/g/h)		
	equation of the trend line	R^2		first stage	second stage	third stage
Leaf	TL	$y = 88.634e^{-0.081x}$	0.7522*	4.809 ± 0.212^a	1.981 ± 0.141^d	0.123 ± 0.031^h
	TM	$y = 85.710e^{-0.078x}$	0.9084*	4.822 ± 0.127^a	2.018 ± 0.106^d	0.136 ± 0.012^h
	TH	$y = 88.600e^{-0.081x}$	0.8489*	5.006 ± 0.318^a	2.024 ± 0.114^d	0.140 ± 0.015^h
Stem	TL	$y = 117.640e^{-0.065x}$	0.7073*	2.553 ± 0.182^c	3.343 ± 0.341^b	0.622 ± 0.042^g
	TM	$y = 107.510e^{-0.056x}$	0.7908*	3.089 ± 0.134^{bc}	2.885 ± 0.326^{bc}	0.858 ± 0.107^f
	TH	$y = 106.420e^{-0.058x}$	0.6996*	3.329 ± 0.142^b	2.652 ± 0.191^c	0.714 ± 0.059^f
Root	TL	$y = 100.670e^{-0.037x}$	0.6753*	2.074 ± 0.221^d	2.959 ± 0.118^{bc}	0.509 ± 0.046^g
	TM	$y = 98.952e^{-0.028x}$	0.7870*	1.738 ± 0.162^e	2.588 ± 0.243^c	0.775 ± 0.101^f
	TH	$y = 96.330e^{-0.027x}$	0.7097*	2.113 ± 0.343^d	2.759 ± 0.130^{bc}	0.601 ± 0.044^g

TL – low nitrogen treatment; TM – medium nitrogen treatment; TH – high nitrogen treatment; the dates are given as means $\pm$ SD;

* and different small letters mean the significance at the 0.05 level

<https://doi.org/10.17221/53/2025-HORTSCI>

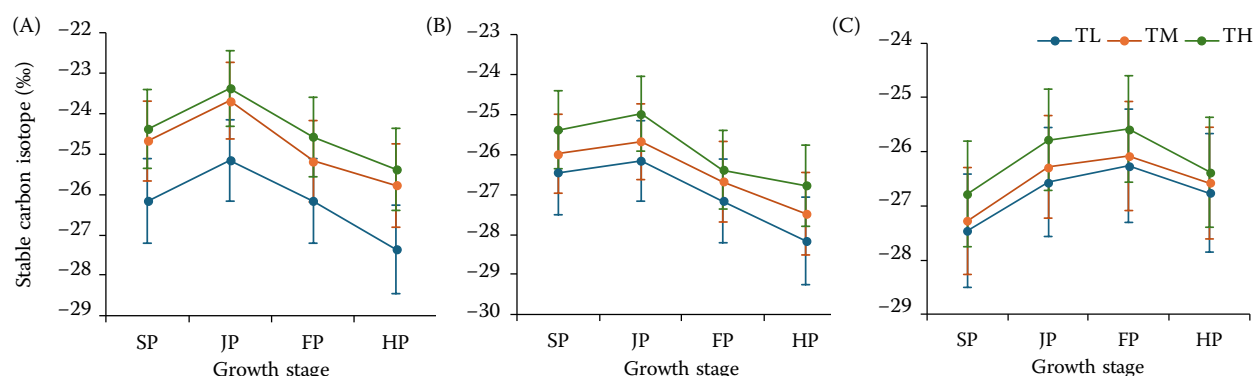


Figure 4. The effect of nitrogen treatments on stable carbon isotope in: (A) leaves, (B) stems, (C) roots at different growth stages

SP – seedling period; JP – jointing period; FP – flowering period; HP – harvesting period; TL – low nitrogen treatment; TM – medium nitrogen treatment; TH – high nitrogen treatment; the bars are given as standard deviation

TH, and that was decreased by 1.90%, 1.92% and 3.13% in HP compared with FP in TL, TM and TH.

Allocation of root and canopy biomass. Root and canopy biomass can reflect the influence of water and nitrogen status on assimilation and biomass allocation (Figure 5). The total biomass increased with the increase of nitrogen application at each growth stage. Under TM, the increase of SP was the largest (137.04%), the increase of FP was the smallest (129.10%), and under TH, the increase of SP was the largest (162.96%), and the increase of JP was the smallest (145.50%). The ratio of root to canopy decreased significantly in each growth stage after nitrogen treatment, and the change was most significant at SP (from

1.25 to 0.66), and the change was the most least at JP (from 0.77 to 0.63).

Heatmap of correlation. The clustering analysis of relevant indices of water and biomass in different growth stages of plants treated with different nitrogen applications was found that 12 treatment groups could be mainly divided into 4 categories (Figure 6). The first category was plants treated with TM and TH at JP and FP, which had higher nitrogen content, water capacitance, water use efficiency and biomass, but smaller ratio of root to canopy. The second category was plants treated at JP, FP and HP with TL, and HP with TM and TH, which had lower nitrogen content and water use efficiency. The third category was plants treated

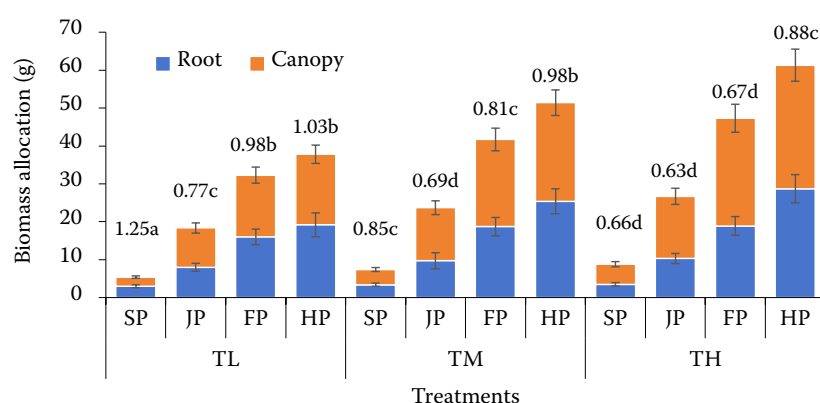


Figure 5. The effect of nitrogen treatments on biomass allocation in the canopy and roots at different growth stages SP – seedling period; JP – jointing period; FP – flowering period; HP – harvesting period; TL – low nitrogen treatment; TM – medium nitrogen treatment; TH – high nitrogen treatment; the histograms are given as means and the bars are given as standard deviation; the number represents the root to canopy ratio; different lowercase letters indicate significant differences at the $P < 0.05$ level

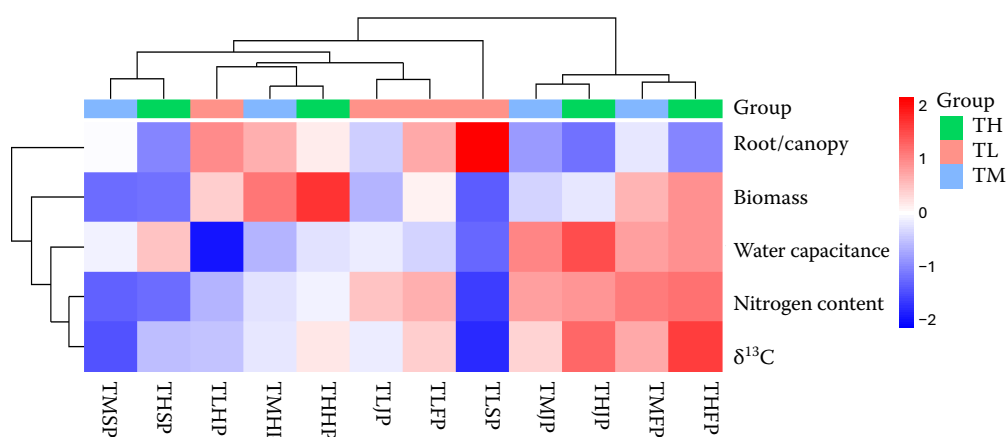


Figure 6. Heatmap of correlation between plant water factors and biomass accumulation indicators

TH – high nitrogen treatment; TM – medium nitrogen treatment; TL – low nitrogen treatment; SP – seedling period; JP – jointing period; FP – flowering period; HP – harvesting period; the bars are given as standard deviation

with TM and TH at SP, which had lower nitrogen content, water use efficiency, biomass, and ratio of root to canopy. The fourth category was plants treated with TL at SP, which had higher ratio of root to canopy, and the other indexes were smaller.

DISCUSSION

As an important element in plant growth and development, nitrogen directly affects plant growth and development and biomass accumulation through key physiological processes such as enzyme system activation and nitrogen assimilation (Liu et al. 2025). Nitrogen application increased the nitrogen content in all organs of *Notopterygium franchetii*, and the nitrogen content of leaves was significantly higher than that of stems and roots. The ascending range of nitrogen content in stems was significantly higher than that in leaves and roots, but the nitrogen content was still significantly lower than that in leaves and roots. Nitrogen is also the main component of many enzymes and chlorophyll, and participates in protein and hormone synthesis (Ma et al. 2017). The xylem in the stem is the main channel for water and nitrogen to be transported from roots to leaves, and nitrogen must be dissolved in water after being absorbed by roots to be transported. Adequate nitrogen fertiliser supply promotes plant metabolic activity and leaf assimilation, accelerates the rate of nitrogen transport by xylem in the stem, and increases the nitrogen content in plant leaf and stem tissues (Liu et al. 2025). Plants use nitrogen in soil in a variety

of ways, and under different environmental pressures, they will also change their own nitrogen use ways, in order to be more favourable to nitrogen absorption and metabolism (Li et al. 2023).

Water capacitance can adjust and control water storage and release in the plant in real time, which reflects the ability of the system to adjust water (Liu et al. 2023). The water capacitance of each tissue of *Notopterygium franchetii* plant was generally root > stem > leaf. The water capacity of leaf and stem tissues was significantly higher than that of root tissues. The water consumption process of plants is also a down-top transfer process of water transport in plants, and the water capacity in plants is generally larger at the lower than the upper, which is transferred successively. When a water potential gradient is generated between roots and soil, the roots begin to absorb water from the soil (Christophe, Philippe 2020). The water capacity of each tissue increased gradually between SP, JP and FP, and decreased to different degrees in the HP. The variation of water capacity in plant tissues is related to structure, function and differentiation degree. At FP and the growth stage before it, the plants mainly vegetative growth, have vigorous metabolic activities, and have strong water regulation ability of various substances in the plant, thus showing increased water capacitance (Xiong, Nadal et al. 2020). In the HP, the plant is ageing, the vegetative growth slows down, and the water regulation effect is reduced, resulting in the water capacitance of each tissue of the plant gradually decreasing, so that the water capacitance of each

<https://doi.org/10.17221/53/2025-HORTSCI>

tissue increases gradually with the growth season, and then decreases slightly (Huang et al. 2024).

The lower the natural dehydration rate per unit time, the stronger the water retention capacity of the plant, which can be used to judge the drought resistance of the plant (Li et al. 2023c). The natural dehydration process experienced a rapid decline from the initial stage of water loss to a slower transition stage and finally entered a gentle stage with minimal changes. Nitrogen treatments significantly increased the natural dehydration rate of stems in the first and third stages. The root natural dehydration rate decreased significantly in the first and second stages but increased significantly in the third stage. With the increase of nitrogen application, the tissue water capacitance and free water content increased, the water potential gradient increased, and the natural dehydration rate increased. With natural dehydration, tissue water capacitance and water content decreased in the second stage, water potential gradient decreased, and natural dehydration rate decreased. Excessive water loss can damage tissue structure and the loss of osmotic pressure regulation function, resulting in increased natural dehydration rate in the third stage. In order to adapt to the long-term dry soil environment, the roots differentiate into water-retaining structures of the cork layer, so they also show high water retention capacity when the tissue water capacitance and water content increase, and the natural dehydration rate decreases (Li et al. 2018).

The long-term water use efficiency (WUE) of plants can be expressed by the difference in tissue stable carbon isotope content. Studies have shown that increased nitrogen fertiliser application affects water consumption and WUE of winter wheat (Li et al. 2023a), and there is no significant difference in water consumption of winter wheat under high nitrogen conditions (Ye et al. 2022). With the increase of nitrogen application rate, plant WUE increased continuously, but after a certain nitrogen application level, WUE showed a stable or declining trend (Shen et al. 2023), which depended on climate and soil conditions (Si et al. 2020; Yang et al. 2025). In this study, it was found that nitrogen treatments could improve the water use efficiency of *Notopterygium francheti* plants, and the change in water use efficiency of leaves after TM was the most significant. Water use efficiency of all organs increased after nitrogen fertiliser application, but it changed little under TH. This

is mainly due to the imbalance of soil reservoirs caused by excessive nitrogen fertiliser, which was consistent with previous research results (Cheng et al. 2021). It can be seen that the high nitrogen content in plant tissues will affect the assimilation, water transport, and utilisation, leading to an increase in ineffective dissipation.

The biomass of the root and canopy can reflect the influence of water and nitrogen status on assimilation and biomass allocation. The effect of nitrogen treatments on canopy biomass was more significant than that of the root system, and the root-canopy ratio was significantly reduced after nitrogen treatments, especially at SP. Nitrogen fertiliser increased the drought threshold of above-ground biomass (Li et al. 2023b), induce plants to prioritise the allocation of limited resources to the above-ground parts and enhance their photosynthesis capacity, promoted rice plant growth, and regulated plant dry matter weight and above-ground nitrogen accumulation (Shi 2022). Nitrogen fertiliser significantly increased plant biomass, especially on aboveground biomass, resulting in a decrease in root-canopy ratio.

As an essential nutrient for plant growth and development, nitrogen is involved in key metabolic processes such as plant protein synthesis (Cabeza et al. 2024), cell division, water storage and utilisation (Navarro-Morillo et al. 2024), assimilation, etc., improving crop yield and quality (Cheng et al. 2021). Nitrogen treatments increased the nitrogen content and water use efficiency of plants at JP and FP, promoted the accumulation of assimilative substances, especially in the aboveground part, and reduced the root-canopy ratio. The plants began to senescence at HP, nitrogen began to return and redistribute, resulting in lower nitrogen content and decreased water utilisation. At SP, the above-ground part of the plant cannot produce energy through its own assimilation, so long as it relies on the root system to provide nutrients, and the nitrogen in its stems and leaves mainly comes from the redistribution of the root system, so the nitrogen content, water use efficiency and biomass are small.

CONCLUSION

Nitrogen, as an important nutrient for crop growth and development, is involved in water storage and utilisation, accumulation and distribution

of assimilating substances. Nitrogen application increased the nitrogen content in all organs and tissues of *Notopterygium francheti*. The nitrogen content of leaves was significantly higher than that of stems and roots, and the increase range of stem nitrogen content was significantly higher than that of leaves and roots, but the content of stem nitrogen was still significantly lower than that of leaves and roots. The water capacitance of each tissue of *Notopterygium francheti* plant was root > stem > leaf. The water capacitance of leaf and stem tissue was significantly higher than that of root tissue after nitrogen treatments. The water capacitance of each tissue increased gradually between SP, JP and FP, and decreased to different degrees in the HP. Nitrogen treatments significantly increased stem natural dehydration rate in the 0 to 12 h and 24 h to 48 h stages, significantly decreased root natural dehydration rate in the 0 to 12 h and 12 h to 24 h stages, and significantly increased in the 24 h to 48 h stage. The water use efficiency of various organs of *Notopterygium francheti* increased after nitrogen treatments, but the change of water use efficiency was not significant under high nitrogen treatment. The content of nitrogen fertiliser in soil directly affects the water state and assimilation efficiency of plants. Further research will be required to comprehensively test the mechanism of nitrogen fertiliser affecting the water state of plants and regulating assimilation, providing strong theoretical guidance to further improve the quality of medicinal materials obtained in plants grown in farmland.

REFERENCES

- Borghetti M., Gentilesca T., Leonardi S., van Noije T., Rita A. (2017): Long-term temporal relationships between environmental conditions and xylem functional traits: A meta-analysis across a range of woody species along climatic and nitrogen deposition gradients. *Tree Physiology*, 37: 4–17.
- Cabeza R.A., Schulze J., Salinas-Roco S., Morales-González A., Amigo R., Pérez-Díaz R., Carrasco B., Contreras-Soto R., Maldonado C., Pedreschi R., Espinoza S., del Pozo A. (2024): The inhibition of N₂ fixation by nitrogen is attenuated by the P supply, altering the plant metabolism. *Environmental and Experimental Botany*, 222: 105762.
- Cheng M., Wang H., Fan J., Xiang Y., Tang Z., Pei S., Zeng H., Zhang C., Dai Y., Li Z., Zou Y., Zhang F. (2021): Effects of nitrogen supply on tomato yield, water use efficiency and fruit quality: A global meta-analysis. *Scientia Horticulturae*, 290: 110553.
- Christophe M., Philippe N. (2020): Root architecture and hydraulics converge for acclimation to changing water availability. *Nature Plants*, 6: 744–749.
- Feng H., Guo J., Peng C., Kneeshaw D., Roberge G., Pan C., Ma X., Zhou D., Wang W. (2023): Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: A global meta-analysis. *Global Change Biology*, 29: 3970–3989.
- He Y., Geng Y., Han B., Shi L., Shao X., Liu K. (2024): Water controls the divergent responses of terrestrial plant photosynthesis under nitrogen enrichment. *Journal of Ecology*, 112: 2638–2651.
- Huang C.W., Domec J.C., Ward E.J., Duman T., Manoli G., Parolari A.J., Katul G.G. (2017): The effect of plant water storage on water fluxes within the coupled soil–plant system. *New Phytologist*, 213: 1093–1106.
- Huang X., Hou Z., Ma B., Zhao H., Jiang Z., Cai J. (2024): Seasonality in embolism resistance and hydraulic capacitance jointly mediate hydraulic safety in branches and leaves of oriental cork oak (*Quercus variabilis* Bl.). *Tree Physiology*, 44: 109.
- Jin Y., Wang C. (2015): Trade-offs between plant leaf hydraulic and economic traits. *Chinese Journal of Plant Ecology*, 39: 1021–1032.
- Kebbas S., Lutts S., Aid F. (2015): Effect of drought stress on the photosynthesis of *Acacia tortilis* subsp. *rad-diana* at the young seedling stage. *Photonythetica*, 53: 288–298.
- Li H., Li X., Mei X., Vinay N., Rui G., Hao W., Wang J. (2023a): An alternative water-fertilizer-saving management practice for wheat-maize cropping system in the North China Plain: Based on a 4-year field study. *Agricultural Water Management*, 276: 108053.
- Li H., César T., Miguel B., Fernando T.M., Zhu Z., Josep P., Yu K., Luo L., Gong J., Ye J. (2023b): Nitrogen enrichment delays the emergence of an aridity-induced threshold for plant biomass. *National Science Review*, 242: 10.
- Li J., Liu W., Yang Y., Dong X., Gu X., Jing J. (2023c): Comparative analysis and comprehensive evaluation of the natural dehydration rate of pods of 35 peanut cultivars. *Molecular Plant Breeding*, 21: 6232–6243.
- Li S., Zhang C., Li W., Wang H., Yang D., Li X. (2018): Measurement of kernel natural dehydration rate in maize single-cross hybrids and its application. *Molecular Plant Breeding*, 9: 80–86.
- Liang X., Zhang T., Lu X., Ellsworth David S., BassiriRad H., You C., Wang D., He P., Deng Q., Liu H., Mo J., Ye Q. (2020): Global response patterns of plant photosynthesis

<https://doi.org/10.17221/53/2025-HORTSCI>

- to nitrogen addition: A meta-analysis. *Global Change Biology*, 26: 3585–3600.
- Liu C., Dong X., Yan Y., Chen R., Ben H., Huang C., Xu W. (2025): Effects of foliar spraying with selenium on nitrogen metabolism and yield of rice grown under different nitrogen levels in cold regions. *Journal of Agro-Environment Science*, 44: 2253–2263.
- Liu H., Luo Z., Dong H. (2021): Research progress on the regulation of NO_3^- uptake and transport in plant. *Bio-technology Bulletin*, 37: 192–201.
- Liu J., Uri H., Asaf A., Shabtai C. (2023): Trade-offs between residual conductance, hydraulic capacitance and water access in Mediterranean species. *Tree Physiology*, 45: tpa023.
- Ma F., Song B., Quan Q., Zhang F., Wang J., Zhou Q., Niu S. (2020): Light competition and biodiversity loss cause saturation response of aboveground net primary productivity to nitrogen enrichment. *Journal of Geophysical Research: Biogeosciences*, 125: e2019JG005556.
- Ma Y., Qian C., Deng L. (2017): Effects of combining Chinese milk vetch with nitrogen fertilizer on grain and dry matter yield, nitrogen absorption and utilization of double-cropping rice. *Journal of Nuclear Agricultural Sciences*, 31: 2399–2407.
- Navarro-Morillo J., Blasco B., Cámara-Zapata J., Muñoz-Acero J., Simón-Grao S., Alfosea-Simón M., Plasencia F., García-Sánchez F. (2024): Corn steep liquor application on pepper plants (*Capsicum annum* L.) stimulates growth under nitrogen-deficient growing conditions. *Scientia Horticulturae*, 328: 112955.
- Pan Q., Zhang J., Meng P., Wang G., Yang H. (2019): Hyperspectral estimation of water content in walnut leaves in hilly areas of North China. *Journal of Northeast Forestry University*, 47: 68–74.
- Sack L., Tyree M., Holbrook N. (2005): Leaf hydraulic architecture correlates with regeneration irradiance in tropical rainforest trees. *New Phytologist*, 167: 403–413.
- Shen H., Gao Y., Sun K., Gu Y., Ma X. (2023): Effects of differential irrigation and nitrogen reduction replacement on winter wheat yield and water productivity and nitrogen-use efficiency. *Agricultural Water Management*, 282: 108289.
- Shi A. (2022): Effects of Nitrogen Density Interaction on Physiological Characteristics, Yield and Nitrogen Use Efficiency of Double Cropping Hybrid Rice. Hunan Agricultural University, Changsha, Hunan.
- Si Z., Muhammad Z., Faisal M., Wang G., Gao Y., Duan A. (2020): Effects of nitrogen application rate and irrigation regime on growth, yield, and water-nitrogen use efficiency of drip-irrigated winter wheat in the North China Plain. *Agricultural Water Management*, 231: 106002.
- Sun J., Zhang B., Pan Q., Liu W., Wang X., Huang J., Chen D., Wang C., Han X. (2023): Non-linear response of productivity to precipitation extremes in the Inner Mongolia grassland. *Functional Ecology*, 37: 1663–1673.
- Wang Z., Sun J., Du Y.D., Sun D., Gan H.C., Niu W.Q. (2022): Effects of mulching practices on soil carbon, nitrogen contents, and grain yield, water and nitrogen use efficiencies of summer maize. *Chinese Journal of Eco-Agriculture*, 30: 913–923.
- Xiong D., Nadal M. (2020): Linking water relations and hydraulics with photosynthesis. *The Plant Journal*, 101: 800–815.
- Yang Y., Zou J., Feng B., Hu S., Qiao B., Huang W., Zhang L., Zheng H., Matthew T., Liu K., Wen X., Chen F., Yin X. (2025): Long-term N fertilization increases water use and use-efficiency of winter wheat. *Field Crops Research*, 325: 109808.
- Ye T., Ma J., Zhang P., Shan S., Liu L., Tang L., Cao W., Liu B., Zhu Y. (2022): Interaction effects of irrigation and nitrogen on the coordination between crop water productivity and nitrogen use efficiency in wheat production on the North China Plain. *Agricultural Water Management*, 271: 107787.
- Ying J., Wang C.K., Zhou Z.H., Gu J.C. (2022): Leaf hydraulic traits of larch and ash trees in response to long-term nitrogen addition in northeastern China. *Journal of Plant Ecology*, 14: 1105–1114.

Received: April 16, 2025

Accepted: January 6, 2026

Published online: July 31, 2026