



Effects of nitrogen addition on root respiration of trees and understory herbs at different temperatures in *Pinus tabulaeformis* forest

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Abstract

Aims Nitrogen (N) addition had differential effects on root respiration. However, the reasons and mechanism have not yet been analyzed. We speculated that the differential effects of N addition are related to the N addition rate, root diameter, and temperature. Meanwhile, tree and understory herb in forest ecosystems

maybe another reason that root respiration has different responses.

Methods N addition was performed in a *Pinus tabulaeformis* forest for six years. *P. tabulaeformis* and *Carex lanceolata* fine roots with three size classes (< 0.5 mm; 0.5–1.0 mm; 1.0–2.0 mm) were sampled for respiration and temperature sensitivity measurement at three temperatures and chemical analysis.

Results (1) N addition increased the root respiration of *P. tabulaeformis* and had the maximum values in 3, 6, and 9 g N m⁻² y⁻¹ at 1 °C, 14 °C, and 18 °C, respectively. (2) The root respiration of *C. lanceolata* significantly decreased under N addition only at 18 °C. (3) The effect of N addition on temperature sensitivity of root respiration was also varied due to N addition rate. (4) N and carbon/nitrogen ratio were the main driving factors of root respiration of *P. tabulaeformis*, while chemical properties had a slight driving effect on root respiration of *C. lanceolata*.

Conclusions N addition rate and temperature were the reasons for the differential effect of N addition on root respiration, but not root diameter. Furthermore, root respirations of tree and understory herb have varied changing mechanism, which demonstrated an apparent species specificity.

Research highlights

- Root respiration of *P. tabulaeformis* had the maximum values in 3, 6, and 9 g of N m⁻² y⁻¹ at 1 °C, 14 °C, and 18 °C, respectively.
- Root respiration of *C. lanceolata* significantly decreased to N addition only at 18 °C.
- Temperature sensitivity of root respiration had varied responses to N addition due to the N addition rate.
- N, C/N and non-structural carbohydrate were the driving factors of root respiration of *P. tabulaeformis*, but not of *C. lanceolata*.

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Introduction

Root respiration in forest ecosystem accounts for 10%–90% (usually 40%–60%) of soil respiration, which is an important part in determining the carbon (C) cycle and global climate change (Hanson et al. 2000). Among all the environmental factors affecting root respiration, the role of nitrogen (N) deposition has received plenty of attention (Burton et al. 2012). Because the N deposition caused by industrial production has an increasingly profound effect on global ecological processes and root respiration is closely related to soil N availability (Burton et al. 2002; Galloway et al. 2004; Ryan et al. 1996).

The effect of N deposition on root respiration has been explored using simulated N addition experiments in several studies at present. The results showed different outcomes, such as stimulation, inhibition, and no effect. For example, the N fertilizer in natural forests of Northeast China significantly stimulated the root respiration of Larch (*Larix gmelinii* L.) and ash (*Fraxinus mandshurica* L.) by increasing the tissue N content (Jia et al. 2011). However, N addition inhibited root respiration in semiarid grasslands because the increased soil N availability resulted in lessened C and carbohydrate allocation to belowground biomass (Zhu et al. 2016). Phosphorus (P) and C/N are also considered to be the driving factors that directly affect root respiration (Wang et al. 2015). N addition changes root respiration by affecting these driving factors, and the reason for these different results from previous studies may be related to the following aspects.

The different rates of N addition have various effects on root respiration. Adding 5 g N m⁻² y⁻¹ of N significantly promoted root respiration in temperate forests (Zeng et al. 2018), whereas adding 10–20 g N m⁻² y⁻¹ of N had an inhibitory effect on root respiration in temperate grassland (Wei et al. 2018). Low N addition has a promoting effect, while high N addition has an inhibitory effect on root respiration, and a threshold value of N addition may be present between promotion and inhibition. By contrast, other studies have found that N addition has only an inhibitory effect on root respiration (Haynes and Gower 1995). Because the increase in soil N content alleviated the plant's nutrient requirements, reduced the allocation of C to belowground biomass, and eventually decreased root respiration. Therefore, N addition rate and tissue non-structural carbohydrate content must be considered when studying the mechanism of root respiration changes.

Root respiration with different diameters respond differently to N addition. Fine roots were characterized by absorption function, rich nutrient content, and vigorous activity, while thick root's functions are transportation and support, and they have poor nutrient content and low activity (Guo et al. 2008). Fine roots are generally more sensitive to environmental changes than thick roots (Jia et al. 2011). For example, Wang et al. (2017) found that N addition significantly increased the production and turnover rate of the fine roots of *Bothriochloa ischaemum* but had no effect on thick roots. The stoichiometry trait of the fine roots of *P. tabulaeformis* were more sensitive to N addition than that of the thick roots, and the homeostasis of thick roots was higher than that of fine roots (Jing et al. 2017). These indices and physiological functions of the root system are closely related to respiration rate. Therefore, the respiration rate of fine roots were speculated to be more responsive to N addition than that of thick roots.

The root respiration of trees and herbs have a different response to N addition. Herbs have high root nutrients and short growth cycle, while arbor roots have low nutrient content and long lifespan (Zhu et al. 2019). The physiological function of herb roots are more susceptible to environmental change than that of trees (Carson and Walter 2006). In the temperate grassland ecosystem, N fertilizer significantly improved the root length, the root tissue density, and the N content of six species herbs (Leuschner et al. 2013). However, in the larch ecosystem, N addition showed a minimal effect on root trait (Mei et al. 2010). The two types of vegetation have obvious different physiological characteristics and growth strategies, and their responses to environmental condition are also varied. However, most of the recent studies on root respiration in forest ecosystems only focused on arbor, and few attention was paid on understory herb, which may lead to underestimation of soil CO₂ emission (Mao et al. 2017). The contribution of understory vegetation to soil respiration reached 36% in two subtropical plantations (Wu et al. 2011). Thus, the combinatory effect of different plants needs to be considered when evaluating forest root respiration. Mao et al. (2017) found that N addition significantly changed the chemical composition, photosynthetic capacity, and related parameters of understory *Alchornea trewioides* in a tropical reforested ecosystem, but its effect on trees and other species was small. The root system of understory vegetation is mainly distributed in the surface soil, and it has rich nutrient content, which is easily affected

by environmental changes (Scheller and Mladenoff 2002). Therefore, in the present study, the root respiration of understory herbs was believed to be more sensitive to N addition than that of trees.

N addition has varied effects on root respiration at different temperatures. Root respiration is limited by the maximum activity of enzymes at low temperature, while it is mainly controlled by the availability of substrates at high temperature (Atkin et al. 2000). Thus, the effect of N addition on root respiration is more apparent at high temperature than that at low temperature. For example, N addition promoted root respiration by increasing tissue biomass and N content in semi-arid grasslands during summer season (Zhang et al. 2014). However, N addition had a slight effect on root respiration rate during winter season. The relationships between root respiration and chemical properties were the strongest at 18 °C and weakest at 6 °C in North American forest ecosystems (Burton et al. 2002). Considering the effect of temperature, setting multiple conditions, such as low, medium, and high temperature, when testing the effect of N addition on root respiration is necessary. As an indicator reflecting the ability of root respiration to respond to temperature change, temperature sensitivity Q_{10} was also affected by N addition (Mo et al. 2007). Previous studies have pointed out that N addition reduced root vitality and thus decreased the Q_{10} value of respiration (Zhang et al. 2014). However, other studies showed that N addition stimulated the Q_{10} value of root respiration, which is related to the increased nutrient content and faster respiration rate (Lin et al. 2016). Like root respiration, Q_{10} value is also driven by chemical properties. The effect of N addition on Q_{10} value was varied due to factors such as N addition rate, root diameter, and vegetation type (Chen et al. 2010; Jia et al. 2011). In this study, whether root respiration and Q_{10} value have a similar mechanism under N addition treatments was examined.

This study was carried out in a *P. tabulaeformis* forest on the Loess Plateau of China. Fine roots of *P. tabulaeformis* and *C. lanceolata* with different diameters were used as the research objects. Four N addition rates and three measurement temperatures were conducted to verify the following: (1) low N addition promotes root respiration and high N addition inhibits it. (2) The respiration of fine roots are more responsive to N addition than that of thick roots, while understory herbs are more sensitive to N addition than trees. (3) The effect of N addition on root respiration at high temperature is

greater than that at low temperature. Like root respiration, Q_{10} value is affected by N addition and other factors. This study aimed to explore the reason for the different results in the previous studies and evaluate the driving effect of tissue chemical properties during this process.

Materials and methods

Site description

The *P. tabulaeformis* forest was located in the Songyugou Watershed on the Loess Plateau of China (35°58'34"N, 110°05'38.1"E). It was planted in 1966 to conserve soil and water. Site description included climatic condition, plant community, and soil property, which were all described in detail by Jing et al. (2019). March, April, and May are spring season; the growing season starts in June and ends in September; and fall season starts in October and ends in December. The soil temperature of the *P. tabulaeformis* forest in recent years is shown in Fig. S1. *C. lanceolata* is the main understory vegetation with a rich biomass.

N addition experiment

Most studies added 0–12 g N m⁻² y⁻¹ in their N addition experiments; this amount was sufficient to change the soil nutrient content from limited to saturated for plant growth in most ecosystems on the Loess Plateau of China (Jing et al. 2017; Wang and Zheng 2018). On the basis of previous studies and the ambient N deposition rate in the region (currently 2.2 g N m⁻² y⁻¹), four levels of N addition treatments were designed, i.e., 0, 3, 6, and 9 g N m⁻² y⁻¹ (control, low, medium, and high N addition, respectively) in the *P. tabulaeformis* forest (Wei et al. 2010). Sixteen experimental plots of N addition were established under similar climate and terrain conditions. Each N treatment was performed in four plots, and each plot measured 10 m × 10 m. The N addition experiment started in March 2014, as described by Jing et al. (2019).

Root respiration measurements

In July 2020, fine roots of *C. lanceolata* and *P. tabulaeformis* with three diameter classes (very fine roots, < 0.5 mm; intermediate fine roots, 0.5–1.0 mm;

largest fine roots, 1.0–2.0 mm) were sampled from each plot and immediately transported to a nearby laboratory. The harvested roots were washed up with distilled water, and dead roots were removed manually on the basis of color and consistency. The root sample was divided evenly into three subsamples for respiration measurements at 1 °C, 14 °C, and 18 °C, hence a total of 12 samples in each plot ([fine roots of *C. lanceolata* and *P. tabulaeformis* with three diameter classes] × three temperatures). The three measurement temperatures were set on the basis of the average temperature of *P. tabulaeformis* forest soil in different seasons at our study plots, and experimental design of previous studies (Jia et al. 2011; Burton et al. 2002). Fine root collection, transfer and classification were completed as quickly as possible at about 4 °C according to the previous studies (Pregitzer et al. 2002; Jia et al. 2011). Root respiration was measured by changes in CO₂ concentration using an Li-6400 Portable CO₂/H₂O Analysis System (LI-COR Inc., Lincoln, NE, USA). First, petroleum jelly was applied on the root cut surface to prevent traumatic respiration. Second, the root sample with a fresh weight of approximately 3 g was placed in a closed static sample cell connected to the Li-6400 Portable CO₂/H₂O Analysis System. The sample cell was covered with tin foil to prevent interference from temperature and light changes. Equilibration at the measurement temperature for 20 min to reduce the interference from environment change and make a relatively stable respiration function for root. Then, the increase in CO₂ concentration with time was recorded for root respiration calculation. During the measurements, Flow rate to the sample cell is 500 μmol s⁻¹, The average difference of CO₂ concentration between sample cell and reference cell is 25.98 μmol CO₂ mol⁻¹. The moisture released by root was absorbed by the desiccant to keep a constant humidity in the sample cell. Approximately 10–20 min was needed to attain a constant increase in CO₂ concentration, and all laboratory processes had to be performed with 3 h of sample collection. Equilibration time and the measurement reliability were confirmed in previous studies (Wang et al. 2010; Burton et al. 2002). The temperature of root respiration was controlled by the air-conditioning system and constantly set at 1 °C, 14 °C, and 18 °C. Finally, root respiration rates were expressed on a mass basis (μmol CO₂ g⁻¹ s⁻¹), and is not corrected by transpiration rate. The root subsamples were oven-dried at 65 °C to a constant weight for chemical analysis. The distribution of root biomass in

the *P. tabulaeformis* forest was investigated using the soil coring method (Böhm 1979), as shown in Table S1.

Root chemical analysis

The organic C content (mg g⁻¹) was determined via the dichromate oxidation method (Mebius 1960). The total N content (mg g⁻¹) was determined using the Kjeldahl method (Page et al. 1982). The total P content (mg g⁻¹) was measured through persulfate oxidation, followed by colorimetric analysis (Lu 2000). The soluble sugar and starch contents (mg g⁻¹) were determined via the anthrone colorimetric method (Wise et al. 1955). 0.1 g sample was added to a 10 ml centrifuge tube, and extract three times with 2 ml of 80% ethanol. Supernatant was combined in a 25 ml volumetric flask, then make the volume constant for soluble sugar determining. Precipitation in the tube was used to analyze the content of starch. Starch in precipitation was convert into glucose using 9.2 and 4.6 mol L⁻¹ HClO₄. Supernatant was combined in a 50 ml volumetric flask, then make the volume constant for starch determining. 0.5 ml supernatant, 1.5 ml distilled water and 5 ml anthrone-H₂SO₄ reagent were added in a 10 ml tube, mixed and water bath at 100 °C for 10 min. Take out the centrifuge tube and cool it to room temperature with water, then measure the absorbance at 620 nm. Supernatant for soluble sugar determining and starch determining have a same colorimetric process. C/N is the ratio between organic C and N contents.

Statistical analysis

The temperature sensitivity coefficient of root respiration, Q_{10} , was calculated using the following equations (Boone and Nadelhoffer 1998; Chen et al. 2009):

$$F = ae^{bT} \quad (1)$$

$$Q_{10} = 10^b, \quad (2)$$

where F is the respiration rate (μmol CO₂ g⁻¹ s⁻¹), T is the incubation temperature (°C), and a and b are the fitting parameters.

Two-way ANOVA was used to analyze the effects of root diameter and N addition on chemical properties, root respiration and Q_{10} values. Statistical significance was considered at $P < 0.05$. Duncan's multiple

comparative analysis was used to compare the difference in chemical properties among the N addition treatments and root diameters. Pearson correlation analyses were used to test the relationships among root chemical properties, respiration, and temperature sensitivity coefficient. Data analyses were carried out on R software 3.5.1 (R Core Team 2018) and Origin Pro 7.5 (Origin Lab Corp., US).

Results

Root chemical properties

The N and starch contents in the root of *C. lanceolata* were higher than those in the root of *P. tabulaeformis*, whereas the C, P, and soluble sugar contents and C/N ratio were lower (Table 1). Root diameter had a significant effect on chemical properties (Table 1, Table S3, $P < 0.05$). The C, soluble sugar, and starch contents and C/N ratio increased with root diameter, whereas the N and P contents decreased. N addition had different effects on the root chemical properties among vegetation types and root diameters. The N, P, soluble sugar, and starch contents in the fine roots of *P. tabulaeformis* increased along N addition treatments, with the maximum value in the medium N or high N treatment, whereas the C/N ratio decreased with N addition and showed the minimum value in the medium N or high N treatment. The P content of *C. lanceolata* decreased with the increase in N addition treatments, with the minimum value in high N treatment. The soluble sugar content also increased with N addition and demonstrated the maximum value in high N treatment. N addition significantly increased the P content of largest fine roots but had no effect on the other diameter roots. The soluble sugar content and C/N ratio of largest fine roots were more sensitive to N addition than those of very fine and intermediate fine roots.

Root respiration

N addition significantly increased the root respiration of *P. tabulaeformis* (Fig. 1 and Table 2, $P < 0.05$). At 1 °C, the root respiration of *P. tabulaeformis* had the maximum value in low N treatment. At 14 °C and 18 °C, it exhibited the maximum value in medium N or high N treatments. With the increase in root diameter, root respiration significantly decreased. No significant

interaction effect of N addition and root diameter was found on the respiration rate. N addition significantly inhibited the root respiration of *C. lanceolata* at 18 °C but had a slight effect at 1 °C and 14 °C (Fig. 2 and Table 2, $P < 0.05$).

Temperature sensitivity

N addition significantly increased the Q_{10} value of the root respiration of *P. tabulaeformis* and had the maximum value in medium N or high N treatment (Fig. 3, $P < 0.05$). The Q_{10} value of *P. tabulaeformis* increased with root diameter. The Q_{10} value of *C. lanceolata* in the N addition treatments was smaller than that in the control treatment, although the effect of N addition on Q_{10} value did not reach a significant level.

Relationship among root respiration, temperature sensitivity, and chemical properties

The root respiration of *P. tabulaeformis* had a significant positive correlation with N and P contents and a significant negative correlation with soluble sugar content and C/N ratio at 18 °C (Table 3, $P < 0.05$). At 14 °C, the root respiration of *P. tabulaeformis* was significantly positively correlated with N content and significantly negatively correlated with C content and C/N ratio. At 1 °C, the root respiration of *P. tabulaeformis* was significantly positively correlated with N content and significantly negatively correlated with soluble sugar content and C/N ratio. The correlation coefficient between root respiration and the chemical properties of *P. tabulaeformis* was stronger at 18 °C than at 14 °C and 1 °C. The root respiration of *C. lanceolata* was negatively correlated with soluble sugar content at 18 °C (Table 3, $P < 0.05$). The Q_{10} value of the root respiration of *P. tabulaeformis* and *C. lanceolata* had no significant relationship with their chemical properties.

Discussion

The responses of root respiration to N addition varied among trees, herbs, and temperatures

The root respiration of *P. tabulaeformis* initially increased and then decreased with increasing N additions, with the maximum values in the low N, medium N, or high N treatment. This result was in line with the

Table 1 Chemical properties of different diameter classes of fine roots. (mean \pm SE)

Vegetation types	Root diameters	Treatments	C (mg g ⁻¹)	N (mg g ⁻¹)	P (mg g ⁻¹)	Soluble sugar (mg g ⁻¹)	Starch (mg g ⁻¹)	C/N
<i>P. tabulaeformis</i>	Very fine roots	Control	455.99 \pm 6.72aC	4.39 \pm 0.270bA	0.376 \pm 0.0543aA	1.497 \pm 0.5617bC	6.400 \pm 1.0662bB	104.884 \pm 5.5002aC
		Low N	456.18 \pm 7.71aB	5.25 \pm 0.296abA	0.347 \pm 0.0260aA	3.817 \pm 0.7116aB	7.721 \pm 0.7609bA	87.485 \pm 3.9336bC
		Medium N	440.85 \pm 7.58aB	6.13 \pm 0.171aA	0.444 \pm 0.0272aA	3.923 \pm 0.1077aC	11.155 \pm 0.8686aA	72.023 \pm 1.8982cB
		High N	446.40 \pm 5.63aB	5.77 \pm 0.384aA	0.369 \pm 0.0319aA	5.634 \pm 0.8625aC	6.328 \pm 0.2131bA	78.606 \pm 6.4736bcC
	Intermediate fine roots	Control	479.47 \pm 1.09aB	3.27 \pm 0.079cB	0.363 \pm 0.0158aA	4.100 \pm 0.1385bB	9.601 \pm 1.8988aAB	146.900 \pm 3.1576aB
		Low N	476.88 \pm 6.37aAB	3.87 \pm 0.174bB	0.337 \pm 0.0160aA	6.243 \pm 0.9675bAB	6.035 \pm 1.0333aA	123.998 \pm 6.3953bB
		Medium N	479.89 \pm 9.12aA	3.979 \pm 0.076bB	0.382 \pm 0.0148aAB	8.481 \pm 0.7914aB	9.692 \pm 1.9317aA	120.689 \pm 2.6847bcA
		High N	474.96 \pm 3.92aA	4.34 \pm 0.107aB	0.346 \pm 0.0104aA	10.474 \pm 0.6912aB	8.400 \pm 1.9982aA	109.663 \pm 2.6673cB
	Largest fine roots	Control	495.61 \pm 4.07aA	2.86 \pm 0.175bB	0.326 \pm 0.0121abA	7.698 \pm 0.8352bA	12.666 \pm 1.7887aA	175.346 \pm 10.8811aA
		Low N	492.23 \pm 8.23aA	3.29 \pm 0.090bB	0.295 \pm 0.0218bA	9.072 \pm 1.7064bA	7.806 \pm 1.9936bA	149.989 \pm 4.6855bA
		Medium N	477.25 \pm 6.10aA	3.92 \pm 0.225aB	0.359 \pm 0.0235aB	10.361 \pm 0.4288abA	11.040 \pm 0.8569aA	122.738 \pm 5.4388cA
		High N	488.26 \pm 3.25aA	3.83 \pm 0.085aB	0.316 \pm 0.0120abA	13.318 \pm 0.7210aA	7.931 \pm 1.8226bA	127.550 \pm 3.2417cA
<i>C. lanceolata</i>	Very fine roots	Control	455.51 \pm 11.68a	5.95 \pm 0.489a	0.373 \pm 0.0445a	1.283 \pm 0.1018b	10.542 \pm 1.9178a	78.712 \pm 8.9818a
		Low N	449.84 \pm 4.10a	6.92 \pm 0.159a	0.298 \pm 0.0127ab	4.080 \pm 0.9586a	12.973 \pm 2.7195a	65.192 \pm 2.0662a
	Medium N	High N	445.66 \pm 7.65a	6.32 \pm 0.213a	0.281 \pm 0.0164b	5.423 \pm 0.8754a	12.239 \pm 0.8915a	70.760 \pm 2.4438a
		High N	452.71 \pm 6.63a	6.16 \pm 0.195a	0.274 \pm 0.0144b	5.602 \pm 0.2040a	10.657 \pm 0.9655a	73.771 \pm 3.4024a

Values followed by different lowercase letters indicate significant difference among nitrogen addition treatments, values followed by different uppercase letters indicate significant difference among root diameter classes ($P < 0.05$). C carbon; N nitrogen; P phosphorus; C/N ratio between carbon and nitrogen. Control, low, medium, high N are 0, 3, 6, and 9 g N m⁻² y⁻¹ respectively. Very fine, intermediate fine, largest fine roots are <0.5 mm, 0.5–1.0 mm and 1.0–2.0 mm respectively

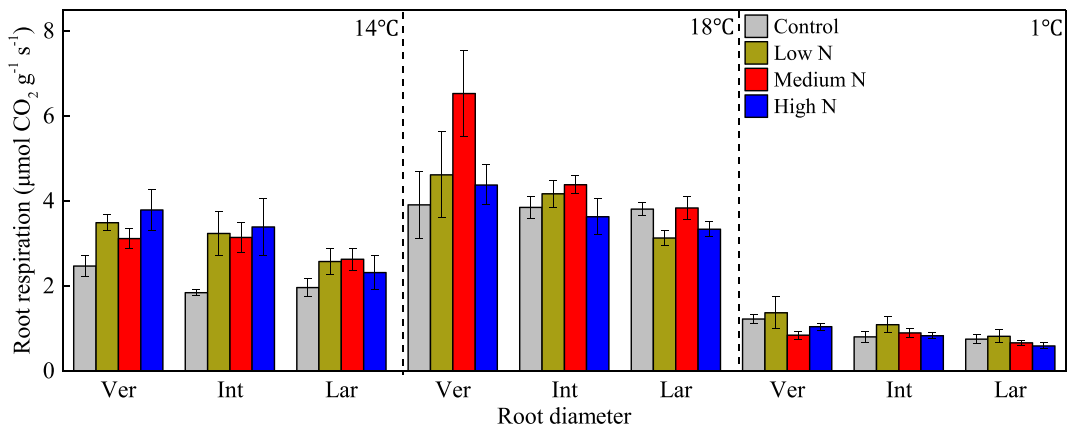


Fig. 1 Root respiration rate of *P. tabulaeformis* among nitrogen addition treatments and root diameters. Note: Vertical bars indicate the standard errors of means ($n = 4$). Ver, very fine roots (diameter

< 0.5 mm); Int, intermediate fine roots (0.5 mm $<$ diameter $<$ 1 mm); Lar, largest fine roots (1 mm $<$ diameter $<$ 2 mm). Control, low, medium, high N are 0, 3, 6, and 9 g N m⁻² y⁻¹ respectively

hypothesis of this study. The *P. tabulaeformis* forests on the Loess Plateau of China are limited by N. Low N addition improved soil microbial activity and plant growth, while high N addition inhibited these ecological factors and had a toxic effect (Wang and Zheng 2018; Zhang et al. 2017). Thus, a threshold value of N addition between promotion and inhibition may be present. Other studies in this region have confirmed that N addition has a significant effect on soil quality and litter decomposition, and the threshold value is 6–9 g N m⁻² y⁻¹ (Jing and Wang 2020; Sun et al. 2018). The results of the present study supported these claims and proved that N addition also has a threshold effect on root respiration of *P. tabulaeformis*. Chemical properties are the direct driving factors of root respiration. In this study, the chemical properties of *P. tabulaeformis* had corresponding changes, which may be the reason for the changes in root respiration with N addition at 14 °C and 18 °C. The details of the relationship between chemical properties and root respiration was discussed in the third section.

Table 2 Two-way ANOVA F values for the effects of root diameter, nitrogen addition and their interaction on root respiration

Vegetation types	Factors (df)	14 °C	18 °C	1 °C
<i>P. tabulaeformis</i>	D (2)	5.548**	6.285**	7.308**
	N (3)	5.642**	2.909*	2.299
	N×D (6)	0.671	1.247	0.545
<i>C. lanceolata</i>	N (3)	1.01	4.493*	0.821

D, root diameter include < 0.5 mm, 0.5–1.0 mm and 1.0–2.0 mm. N, nitrogen addition include 0, 3, 6, and 9 g N m⁻² y⁻¹. ** ($P < 0.01$) and * ($P < 0.05$) indicate significant differences among the treatments based on a two-way ANOVA test

N addition inhibited the root respiration of *C. lanceolata*, and this finding differed from the change in the root respiration of *P. tabulaeformis*. Arbor layer and understory vegetation have different responses to environmental change in natural ecosystems due to their different microenvironment and growth strategies (Fu et al. 2016). In a tropical ecosystem, high-light species (*Alchornea trewioides*) had a significant response to N addition, and the foliar N and photosynthetic capacity decreased (Mao et al. 2017). On the contrary, medium-light species and shade-tolerant species did not show any obvious physiological changes. N addition

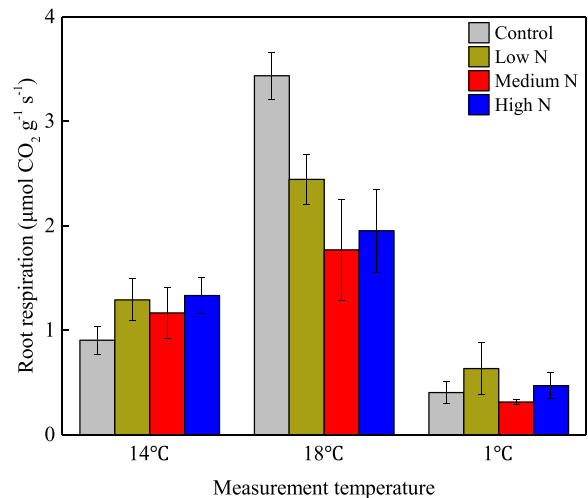


Fig. 2 Root respiration rate of *C. lanceolata* among nitrogen addition treatments. Note: Vertical bars indicate the standard errors of means ($n = 4$). Ver, very fine roots (diameter < 0.5 mm); Int, intermediate fine roots (0.5 mm $<$ diameter $<$ 1 mm); Lar, largest fine roots (1 mm $<$ diameter $<$ 2 mm). Control, low, medium, high N are 0, 3, 6, and 9 g N m⁻² y⁻¹ respectively

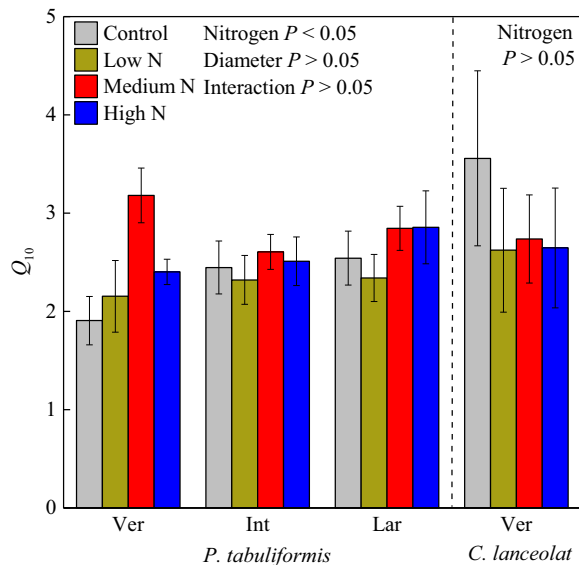


Fig. 3 Temperature sensitivity of root respiration (Q_{10}) among nitrogen addition treatments and root diameters. Note: Vertical bars indicate the standard errors of means ($n=4$). Ver, very fine roots (diameter < 0.5 mm); Int, intermediate fine roots (0.5 mm < diameter < 1 mm); Lar, largest fine roots (1 mm < diameter < 2 mm). Control, low, medium, high N are 0, 3, 6, and 9 g N m⁻² y⁻¹ respectively. * ($P < 0.01$) and * ($P < 0.05$) indicate significant differences among the treatments based on a two-way ANOVA test

improved soil N availability, alleviated the requirement of plants for N, and intensified the competition for P. *P. tabulaeformis* has a strong root system to obtain the required P. However, the competitive ability of *C. lanceolata* to soil P is relatively weak, which leads to the decrease in P content in the root system (Table 1). Therefore, the root respiration of *C. lanceolata* decreased due to the limitation of tissue P, although N addition increased the non-structural carbohydrate

content of the root system. Wang et al. (2015) confirmed that the root respiration of 50 plant species was limited by P content under different growth conditions. The root respiration of *P. tabulaeformis* and *C. lanceolata* had opposite responses to N addition. This result may complicate the effect of N addition on the release of soil CO₂ in *P. tabulaeformis* forest ecosystems. Table S1 shows that N addition reduced the root biomass of *C. lanceolata*, and its root respiration at forest region decreased. However, the negative contribution of the root respiration of *C. lanceolata* to soil CO₂ emission was little due to its small biomass. On the contrary, the root biomass of *P. tabulaeformis* was large, and N addition significantly increased its respiration rate and biomass. Therefore, N addition had a stimulation effect on root respiration in *P. tabulaeformis* forest ecosystems.

N addition had different effects on root respiration at three temperature conditions, and this finding was consistent with the hypothesis. Root was characterized by slow biochemical reaction, low enzyme activity, and less demand of substrates at low temperature (Zhang et al. 2014). Thus, the root respiration of *P. tabulaeformis* at low temperature had the maximum value in low N treatment. Increasing temperature speeds up the biochemical reaction of the root and increases the enzyme activity and substrate requirement (Atkin et al. 2000). Consequently, the root respiration of *P. tabulaeformis* had the maximum value in medium N or high N treatment. Warming up strengthened the requirement for N from *P. tabulaeformis*, thereby accelerating the root respiration rate. During the growing season, the root respiration and growth of *Populus tremuloides* improved due to the increased content of

Table 3 Pearson correlation coefficients between root respiration rate, Q_{10} , and chemical properties

Vegetation types		C	N	P	Soluble sugar	Starch	C/N
<i>P. tabulaeformis</i>	Root respiration at 14 °C	-0.347*	0.535**	0.203	-0.089	-0.283	-0.560**
	Root respiration at 18 °C	-0.270	0.612**	0.677**	-0.315*	0.172	-0.503**
	Root respiration at 1 °C	-0.218	0.356*	0.120	-0.438**	-0.227	-0.346*
	Q_{10}	0.001	0.103	0.224	0.222	0.241	-0.060
<i>C. lanceolata</i>	Root respiration at 14 °C	-0.046	0.181	-0.336	0.279	-0.073	-0.168
	Root respiration at 18 °C	0.202	0.004	0.410	-0.685**	0.110	0.100
	Root respiration at 1 °C	0.141	0.161	-0.050	-0.262	-0.365	-0.138
	Q_{10}	0.208	-0.356	-0.015	-0.191	0.244	0.430

C carbon; N nitrogen; P phosphorus; C/N ratio between carbon and nitrogen

* $P < 0.05$; ** $P < 0.01$

non-structural carbohydrates (Desrochers et al. 2002). However, during the dormant season, the driving effect of chemical properties on root respiration was weak. The different effects of N addition on root respiration in previous studies may be caused by the temperature and climate conditions in various regions. As a global environmental issue, N deposition has a long duration and a profound effect with a wide range (Galloway et al. 2004). Therefore, the influence of temperature must be considered when studying the effects of simulated N deposition on ecosystem function. In addition, the root respiration of *C. lanceolata* had a significant response to N addition only at 18 °C. Temperature had a greater effect on the root respiration of *C. lanceolata* than that of *P. tabulaeformis*. It not only affected the root respiration rate of *C. lanceolata* but also significantly changed the responses of root respiration to N addition. Understory herbs were strongly limited by temperature, followed by soil N availability. By contrast, temperature and soil quality had an equal effect for trees. Environmental limiting factors were tested on the ecosystem scale in previous studies (Chen et al. 2018; Sundareshwar et al. 2003). For example, the soil P availability in the mangrove forest ecosystem was the limiting factor for plant growth (Lovelock et al. 2006). In a high-elevation subalpine forest, temperature had an absolute control on the CO₂ flux of the ecosystems (Huxman et al. 2003). The results of the present study confirmed that within a forest ecosystem, tree and understory herb have different limiting factors, and the effect of these factors needs further evaluation.

Respiration rate decreased with root diameters, and this finding was consistent with the result of Chen et al. (2010). The nutrient content, turnover rate, and respiration of fine roots were higher than those of thick roots (Wang et al. 2017). Fine roots played a more important role in plant growth, soil quality, and microbial community than thick roots, as confirmed in previous studies (Hanson et al. 2000; Raich and Schlesinger 1992). However, thick roots had a large amount of biomass distribution (Table S1), resulting in a comparable respiration contribution with fine roots in *P. tabulaeformis* forest (Table S2). Therefore, when evaluating root respiration in ecosystems, the contribution of all diameter roots should be seriously taken into account in field study. The present study also showed that the respiration rate of different diameter roots had a similar response to N addition. This result did not support the hypothesis. In a walnut seedling experiment, N addition consistently

promoted the non-structural carbohydrate content and respiration rate of fine roots with different diameters (Li et al. 2020). These results were related to the fact that variations in chemical properties among roots of different diameters were insufficient. Experimental treatment has varied effects on root physiological characteristics only when the chemical properties among different root diameters have sufficient variations. For example, the chemical properties of *L. gmelinii* and *F. mandshurica* varied considerably among different root diameters (Jia et al. 2011). N addition significantly increased the root respiration of the first three orders, while the respiration rate of the fourth- and fifth-order roots varied with sampling time and temperature. The root diameter in the present study was less than 2 mm, thus belonging to fine roots (King et al. 2005). The variations in chemical properties among different root diameters were relatively small. This finding may be the reason that N addition had the same effect on root respiration with different diameters.

N addition increased Q_{10} value of root respiration of *P. tabulaeformis* but decreased that of *C. lanceolata*

Trees have a long growth cycle and high homeostasis ability, while herbs have a short growth cycle and a narrow suitable temperature range. The results showed that the Q_{10} value of the root respiration of *C. lanceolata* was greater than that of *P. tabulaeformis*, and this finding supported the results of previous studies (Loveys et al. 2003; Zhang et al. 2019). N addition increased the nutrient content and respiration rate of the fine root of *P. tabulaeformis*, resulting in an increase in Q_{10} value (Lin et al. 2016). On the contrary, N addition decreased the Q_{10} value of the root respiration of *C. lanceolata*. The reason was that the increase in soil available N content suppressed the root respiration rate of *C. lanceolata*, and temperature had a limited effect on low-level root respiration. Previous studies have confirmed that temperature sensitivity changes due to factors such as temperature settings and experimental treatments (Oechel and Walter 1983; Ryan 1991; Schlesler 1982). Increased Q_{10} values occur when the temperature setting is too low, while the opposite occurs when the temperature setting is too high (Burton et al. 2002). Therefore, temperature setting and respiration rate must be in line with the environmental conditions of natural ecosystem when testing the temperature sensitivity of root respiration. The response of the Q_{10} value of *P. tabulaeformis*

to N addition was the opposite of that of *C. lanceolata*. The temperature sensitivity of root respiration in forest ecosystem has species-specific trait in response to N addition. This trait is related to chemical composition, root respiration, and growth strategy.

The Q_{10} value of different diameter roots had a similar response to N addition, and this result was consistent with the changes in root respiration. Root respiration is generally more sensitive to environmental changes than Q_{10} value. For example, plant species had different root respiration rates in the North American forest ecosystem due to their specific microenvironment. *Liriodendron chinense* had the fastest respiration rate, whereas *Juniperus formosana* had the slowest (Burton et al. 2002). However, the Q_{10} value of different species did not significantly differ. This result occurred because root respiration is affected by chemical properties and Q_{10} is also related to root functions and growth strategies. In the present study, the variations in the chemical properties among different root diameters were not enough to change the response of respiration rate to N addition. Therefore, changing the Q_{10} value response to N addition was also not enough.

Root chemical properties had opposite effects on respiration and temperature sensitivity

N and C/N ratio were the main factors affecting the root respiration of *P. tabulaeformis*, and this finding supported the hypothesis. N is an essential element that forms protein and plays an important role in the physiological functions of roots (Wang et al. 2015). Some studies suggested that root N content could be used as a surrogate for root respiration (Jia et al. 2011). Plant growth and respiration require the proportional participation of C and N. However, minimal attention was paid to C/N ratio in the previous studies, resulting in an inadequate analysis of the effects of its chemical properties. The results of the present study confirmed that N and C/N ratio were the main driving factors for root respiration. Especially on the Loess Plateau of China, where soil is relatively poor, N addition alleviated the demand for N by *P. tabulaeformis*, increased the root consumption of C, and eventually accelerated the respiration rate. In addition, the root respiration of *P. tabulaeformis* was significantly negatively correlated with C and soluble sugar contents due to the opposite changes in respiration rate and C and soluble sugar contents along root

diameters. Fine roots consume a large amount of non-structural carbohydrates due to their active functions and fast respiration rate, while thick roots store non-structural carbohydrates and respire very slowly (Guo et al. 2004). These results were observed in previous studies on root respiration with different diameters (Jia et al. 2013). The soluble sugar content and root respiration had similar changes only along N addition treatments (Li et al. 2020). N and P contents had improved consistency with root respiration, and non-structural carbohydrates showed relatively less driving effect on root respiration due to root physiological functions. Different chemical properties exhibited varied effects on root respiration, and the final rate depended on the combined effect of multiple factors.

The temperature sensitivity of the root respiration of *P. tabulaeformis* had no significant relation with N content. The relationship between temperature sensitivity and N content varied among studies. For example, the temperature sensitivity of *Acacia crassicarpa* and *Eucalyptus urophylla* increased with root N content (Chen et al. 2010). By contrast, Atkinson et al. (2007) found no significant correlation between the Q_{10} value of herbal root respiration and N content because the changes in soil P availability limits the mitochondrial electron transport, adenylate production, and Q_{10} value (Atkin et al. 2002). The relationship between temperature sensitivity and chemical properties in the present study was the opposite of the relationship between respiration rate and chemical properties, possibly because of the different mechanisms of chemical properties driving the temperature sensitivity and respiration rate of fine roots. The mechanism by which root respiration was driven by nutrients, such as N and P, was discussed in the above paragraph. Temperature sensitivity was driven by chemical properties and affected by other root traits. For example, root tissue density explained 49% variation of Q_{10} value in temperate and tropical forests because warming up improved the root turnover rate and secondary root development, resulting in the changes in root absorption and transport (Jin et al. 2020). Fine roots exhibited secondary development, such as dry powdering and lignification (Antonino et al. 2015; Parts et al. 2019), which ultimately leading to an increase in root tissue density, respiration rate, and Q_{10} value (McCormack et al. 2015; Vidya et al. 2017). In addition, the mycorrhiza trait could be the factor that changed the temperature sensitivity of root respiration (Koch et al. 2007). Temperature not only affected root

respiration rate but also changed the relationship between root chemical properties and respiration rate. Warming up increased the efficiency of nutrient transportation and accelerated the rate of biochemical reaction and respiration (Gunn and Farrar 1999; Yang et al. 2004). Increasing temperature could strengthen the effect of root chemical properties on respiration rate, and this may be one of the reasons why N addition had different affecting mechanisms on root respiration in previous studies. Therefore, avoiding the interference of seasonal changes and other environmental conditions is necessary when exploring the mechanism of experimental treatments affecting root respiration in natural ecosystems.

In contrast to the hypothesis, the chemical properties of the fine root of *C. lanceolata* had a slight driving effect on respiration rate and temperature sensitivity. This finding may be due to the low-level respiration rate of *C. lanceolata* and the non-significant difference in chemical properties and Q_{10} values among N addition treatments. N addition changed the respiration rate by affecting the content of the chemical properties in the fine root of *P. tabulaeformis* but not in the fine root of *C. lanceolata*. Similarly, N addition inhibited respiration by reducing the C and non-structural carbohydrate contents in *Pinus resinosa* roots, but it did not affect the root respiration of sugar maple through this mechanism (Burton et al. 2012; Haynes and Gower 1995). Vegetation has different mechanisms in response to environmental changes, and their driving factors are also species-specific.

Conclusion

N addition had a threshold effect on the root respiration of *P. tabulaeformis* and an inhibitory effect on the root respiration of *C. lanceolata*. Tree and understory herb showed different responses to N addition due to their varied chemical properties and physiological characteristics. Warming up strengthened the effect of N addition on root respiration, and *C. lanceolata* was more deeply affected than *P. tabulaeformis*. In addition, as an indicator reflecting the tolerance of root respiration to temperature change, the responses of temperature sensitivity to N addition varied because of the N addition rate and vegetation type. N and C/N were the main driving factors of the root respiration of *P. tabulaeformis*. In particular, the role of non-structural carbohydrates had a

relatively small effect on respiration rate due to the root physiological needs. N addition changed the respiration rate by affecting the chemical properties in the fine roots of *P. tabulaeformis*, but this mechanism was not suitable for the fine roots of *C. lanceolata*. Previous studies showed that temperature sensitivity had different mechanisms with root respiration during environmental changes. In addition to being driven by chemical properties, temperature sensitivity was affected by other root traits. N addition had a similar effect on the respiration rate of fine roots with different diameters, possibly due to the small variation in root chemical property among different diameters. This study explored the mechanism of N addition affecting root respiration and revealed the possible reasons for the different results in previous studies. A notable detail that in *P. tabulaeformis* forest ecosystem, N addition only significantly promoted root respiration. Thus, its ecological effect requires further evaluation.

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