

EFFECT OF NITROGEN AND SOIL WATER ON LEAF RESPIRATION OF *PINUS KORAIENSIS* AND *TILIA AMURENSIS* SAPLINGS IN A TEMPERATE FOREST

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Abstract. Leaf respiration drives plant energy use and greatly influences global carbon balance. It is inhibited by light. The climate-driven effects of changes in nitrogen deposition and soil moisture on leaf respiration in light (R_L) are not well understood. To better understand the response of R_L and its inhibition by light, we experimentally determined R_L and light inhibition degree, an index of the inhibitory effect of light on leaf respiration with respect to dark leaf respiration, for potted specimens of an evergreen conifer species (*Pinus koraiensis*) and a deciduous broadleaved species (*Tilia amurensis*) in Changbai Mountains forests that were subjected to soil nitrogen and moisture treatments. R_L increased as nitrogen deposition increased to a particular level (46 kg/ha/y N), when enzymes and mineral nutrients became imbalanced. R_L decreased as soil moisture decreased to a drought level. Light inhibition degree behaved inversely to R_L , and the average range for both species combined was 42.0%–78.4% for nitrogen treatments and 58.3%–87.0% for soil moisture treatments. The results are fundamental to accurate modeling of terrestrial carbon budgets and assessment of the carbon economy in forest ecosystems in a rapidly changing climate.
Keywords: leaf respiration, light inhibition, nitrogen addition, soil water content, climate change

Introduction

Leaf respiration is an important factor in determining whether a forest is a net carbon source or a sink and its behavior in response to climate change is therefore of particular interest (Valentini et al., 2000; Duman and Schafer, 2018). Respiration significantly influences the daily carbon assimilation of a tree; leaf respiration in forest canopies consumes 9%–22% of gross primary production and accounts for 50%–70% of autotrophic respiration (Linder, 1985; Malhi et al., 2002). Gonzalez-Meler et al. (2004) showed that CO₂ production by leaf respiration represents approximately 25% of total plant carbon consumption and that 3 Gt of CO₂ is released annually from the terrestrial ecosystem through leaves. Understanding leaf respiration is clearly a fundamental prerequisite for modeling carbon budgets in an ecosystem. CO₂ efflux from leaf respiration accounts for a large proportion of the gross atmospheric CO₂ uptake and occurs in light and in darkness as well (Tombesi et al., 2022). Balancing leaf respiration with photosynthesis is required when estimating carbon use by individual plants, net ecosystem CO₂ exchange, and global carbon balance (Gifford, 2003). Many studies have analysed photosynthesis over a wide range of environments and have incorporated past and future climate scenarios (Kirschbaum, 2008; Wang et al., 2012); however, leaf respiration has received little attention. Leaf respiration in light (R_L), unlike leaf respiration in darkness (R_D), is difficult to measure directly. Researchers often use leaf respiration in darkness as a proxy for leaf respiration in light (Chi et al., 2020; Scafaro et al., 2021). However, this practice can result in an overestimation of leaf respiration and gross primary production since it is generally accepted that respiration is

significantly inhibited by daylight (Tcherkez and Atkin, 2021; Souza et al., 2021). Accurate prediction of R_L is critical to accurate prediction of ecosystem respiration and gross primary production in a global vegetation model, so models of R_L must incorporate the inhibited response of leaf respiration to light and to various other environmental factors (Keenan et al., 2019).

Many studies have investigated the response of leaf respiration to temperature and ambient CO₂ concentrations (Atkin and Tjoelker, 2003; Gonzalez-Meler et al., 2004; Lai Fern et al., 2010), but there has been little research into the response of leaf respiration in light to changes in nitrogen deposition and water availability. Many studies have demonstrated that leaf constituents (e.g., chlorophyll and soluble protein) related to leaf respiration vary with different nitrogen depositions and under drought conditions (Nakaji et al., 2001; Crous et al., 2011; Wang et al., 2012), but more knowledge of leaf respiration and its inhibition by light in different nitrogen and soil water conditions is required to accurately model R_L .

In this study, we analysed R_L and light inhibition of leaf respiration for various levels of soil water content and nitrogen deposition to gain a better understanding of the drivers of R_L . Maximum photochemical fluorescence rate (F_v/F_m) and soil and plant analysis development (SPAD) measurements were obtained and analyzed for different soil nitrogen additions and soil water levels. We quantified R_L for specimens of a deciduous broadleaf species and an evergreen conifer tree species in a typical temperate forest and subjected the experimental subjects to treatments that represent two major global climate change factors, increased nitrogen deposition and drought. The specific aims of the present study were: (1) to accurately model how R_L responds to increased nitrogen deposition and drought conditions; (2) to determine how nitrogen deposition and drought influence light inhibition; and (3) to identify proxies for R_L by analyzing relationships between R_L and leaf constituents. The research object is a typical natural temperate forest that is a crucial component of the global carbon budget; it is therefore critical to accurately predict R_L for the forest by accurately modeling the action of light inhibition on R_L in different climate scenarios.

Materials and methods

Study site

The experimental site was at Changbai Mountain Station, Chinese Academy of Science in eastern Jilin province in northeastern China (42°24'09"N, 128°05'45"E) at an elevation of 738 m. The site is situated in the monsoon-influenced temperate continental climate zone. Mean annual temperature is 3.5 °C, and mean annual precipitation is 695 mm, according to meteorological records for 1982–2003. The soil is dark brown forest soil. Natural nitrogen deposition is 23 kg/ha/y N, and mean soil field capacity is 27.4%. The main species comprising the homogeneous broad-leaved deciduous and coniferous forest are *Pinus koraiensis*, *Fraxinus mandshurica*, *Tilia amurensis* and *Quercus mongolica*.

Experimental design

The experimental potted sapling specimens were situated in an opening within the mixed forest. Pot diameter was 45 cm and each pot was filled with a homogenized mixture of local forest soil (i.e., the same soil as for the forest trees). Vigorous seven-

year-old saplings were selected 3 y after being transplanted to the pots. The mean height of the saplings was 1.6 m, and their average basal diameter was 2 cm. Treatments were one of four nitrogen additions and maintenance of one of three different controlled soil water levels in seven-year-old specimens of one evergreen conifer species (*P. koraiensis*) and one deciduous broadleaved species (*T. amurensis*). The four nitrogen treatments were 0, 23, 46 and 69 kg/ha/y N (identified respectively as N₀, N₂₃, N₄₆ and N₆₉) that were 0×, 1×, 2× and 3× multiples, respectively of the nitrogen deposition level of the study location (23 kg/ha/y N); other environmental factors were not controlled. Ammonium nitrate was applied twice each year on the first day of May and the last day of June. Three soil water regimes were designed for the saplings of the two tree species and were maintained by sheltering the potted plants. Soil volumetric water content θ was measured periodically in the 0–30 cm depth range with a portable time-domain reflectometer (TDR 100, Campbell Scientific, USA). The three soil water content regimes were 85%–100%, 65%–85% and 45%–65% of field capacity and were identified respectively as CK, MW and LW, respectively.

Gas-exchange measurements

The following parameter measurements were made to estimate dark respiration of the two tree species. Net photosynthesis rate (A_n) was measured from June to September under different photosynthetic photon flux densities (PPFDs) of 150, 120, 90, 60, 50, 40, 30, 20, 10, 7, 4, 2 and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at normal ambient CO₂ concentrations (approximately 380 $\mu\text{mol mol}^{-1}$) using a portable photosynthesis measurement system (LI-6400, LI-COR, Lincoln, NE, USA). Each measurement was conducted in equivalent conditions; leaf temperature was 25 °C, relative humidity was approximately 60% and, flow rate was 500 $\mu\text{mol s}^{-1}$. All measurements were taken between 08:00 h and 11:30 h on a sunny day. Measurements for different nitrogen and soil water treatments were taken once a month from June to September. For each measurement, four leaves of three individuals per replicate were randomly selected for sampling. Leaf respiration in darkness was measured after 20 min dark acclimation for the specimens.

Other measurements

Maximum photochemical fluorescence rate (F_v/F_m) was measured after 20 min darkness acclimation using a portable chlorophyll fluorescence meter (OS-30p, Opti-Sciences, USA). The soil and plant analysis development (SPAD) was measured by the chlorophyll meter (SPAD-502, Konica Minolta, JPN). SPAD measurement of the relative amount of chlorophyll in each leaf was made fifteen times at regular intervals, and the average value was taken to be the SPAD value for the leaf. SPAD was measured only for the broadleaved specimens (*T. amurensis*).

Estimation of leaf respiration in light and degree of light inhibition by the Kok method

In this study, Kok method was chosen to estimate light leaf respiration in light (Kok, 1948). The method analyzes the empirically determined response of the net photosynthesis rate A_n to light at low intensities, where the response is assumed to be linear and A_n increases as light intensity increases from 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The point at which the linear regression curve meets the vertical (A_n) axis indicates the level of dark respiration R_D . However, there is a discontinuity in the slope of the linear regression

curve as it moves away from zero light intensity, close to the light compensation point, at which the slope decreases markedly as light intensity continues to increase. The A_n response remains linear, and if the line of lower slope is extended back to the vertical axis, the point of intersection (i.e., light intensity = 0) indicates R_L . However, there is a drawback to the Kok method of extrapolation that cannot be ignored. During the construction of the empirically determined light curves, it is assumed that intercellular CO_2 concentration (C_i) increases gradually due to decreased stomatal conductance as $PPFD$ decreases, and that related A_n increases correspondingly. This has the effect of decreasing the slope of the regression line that is extended to extrapolate R_L , and the true R_L value is therefore underestimated. Kirschbaum and Farquhar (1987) showed that the Kok method underestimates R_L because the method assumes that C_i is constant as $PPFD$ changes. To reduce the underestimation inherent in the Kok method, we estimated R_L after correcting C_i , following the approach of Kirschbaum and Farquhar (1987). The quantum yield of RuP₂ regression (J) was calculated as:

$$J = \frac{[(A_n + R_d) \times (c_i + 2 \times \Gamma_*)]}{c_i - \Gamma_*} \quad (\text{Eq.1})$$

$$\Gamma_* = \frac{[O_2]}{21} \times \frac{pr}{1000} \times g_s \times \exp\left[\frac{9.46 \times (T - 25)}{T + 273.2}\right] \quad (\text{Eq.2})$$

where Γ_* is the CO_2 compensation point at which photosynthetic CO_2 uptake equals photorespiration CO_2 evolution, $[O_2]$ is the partial pressure of oxygen in ambient air, pr is atmospheric pressure, g_s is stomatal conductance and T is leaf temperature. R_L was finally calculated using an iterative correction procedure.

Another correction, that of considering the respired CO_2 under the leaf chamber gaskets, was also taken into account. Respired CO_2 diffused from the leaf area under the gaskets may travel into the cuvette of the Li-Cor 6400. R_L and R_D were recalculated after taking into account this effect as described by Pons and Welschen (2002) and Shapiro et al. (2004). R_L was recalculated according to Equation 3:

$$\text{recalculated } R_L = [(\text{extrapolated value of } R_L \times 6 \text{ cm}^2) - (\text{recalculated value of } R_D \times S)] / 6 \text{ cm}^2 \quad (\text{Eq.3})$$

where 6 cm^2 is the window area of the Li-Cor 6400 and S represents the area of the inward side of the gasket.

The light inhibition degree of R_L (i.e., the extent that R_L differed from R_D due to the inhibitory effect of light as a proportion of R_L) was then recalculated by the following formula:

$$\text{Light inhibition degree} = \frac{(R_D - R_L)}{R_L} \times 100\% \quad (\text{Eq.4})$$

Data analysis was performed using SPSS version 17.0 (SPSS, Chicago, IL, USA) software. The differences were tested with Student's t test to determine the differences of these leaf traits between each nitrogen addition or soil water levels. All tests were based on a significance level of 0.05.

Results

Effect of different nitrogen additions on day respiration and the light inhibition

We first analyzed the response of R_L and the effects of light inhibition on R_L to variation in nitrogen addition. R_L values for the evergreen conifer species *P. koraiensis* and the deciduous broadleaved species *T. amurensis* were calculated using the Kok method for the four nitrogen treatments, N₀, N₂₃, N₄₆ and N₆₉ (Fig. 1). R_L increased gradually as nitrogen addition increased from N₀ to N₄₆. However, R_L for N₆₉ decreased from R_L for N₄₆ for both species. R_L for N₂₃ and R_L for N₄₆ were significantly greater than R_L for N₀. For *P. koraiensis*, the average difference in R_L between N₂₃ and N₀ over four months was 15.2% and between N₄₆ and N₀ was 23.7% ($P < 0.05$, Student's *t*-test). Corresponding differences for *T. amurensis* were 16.7% and 37.6% ($P < 0.05$, Student's *t*-test). In contrast, R_L for N₆₉ was significantly less than for R_L for N₄₆ for both species; the difference for *P. koraiensis* was -27.1% and for *T. amurensis* was -24.2% ($P < 0.05$, Student's *t*-test).

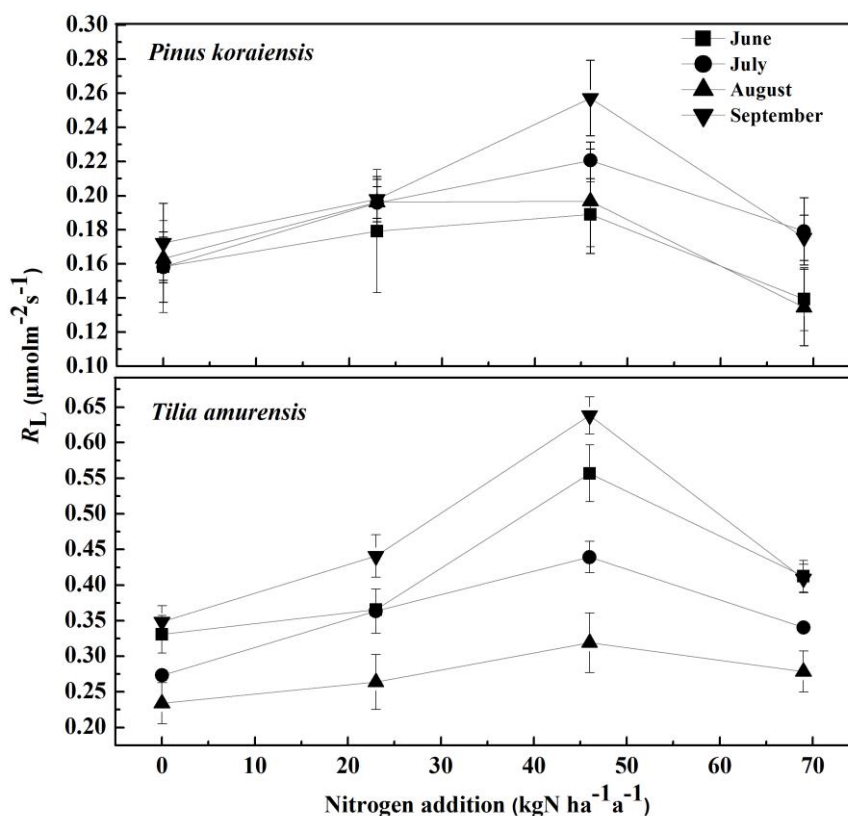


Figure 1. R_L for four nitrogen addition treatments (0, 23, 46 and 69 kg/ha/y N) for the two main tree species of Changbai Mountain (*P. koraiensis* and *T. amurensis*) from June to September. The data are presented as mean \pm SE, $n=4$

The values of R_L and R_D for *P. koraiensis* were significantly less than the values for *T. amurensis* for each nitrogen treatment over the four months. The average differences in R_L and R_D between the two species for the four treatments over the four months were in the range 43.8%–55.6%.

The light inhibition degree for four nitrogen treatments of one conifer tree species (*P. koraiensis*) and one deciduous tree species (*T. amurensis*) is shown in Fig. 2. The light inhibition degree gradually decreased as the nitrogen level increased from treatment N₀ to N₄₆. However, the light inhibition degree increased for N₆₉ over N₄₆ for both species. The light inhibition degree for N₂₃ and N₄₆ was significantly less than that for N₀. The average difference in light inhibition degree for the four months between N₂₃ and N₀ was -4.7% and between N₄₆ and N₀ was -7.7% for *P. koraiensis* ($P < 0.05$, Student's *t*-test); corresponding differences for *T. amurensis* were -5.6% and -16.6% ($P < 0.05$, Student's *t*-test). In contrast, the light inhibition degree for N₆₉ was significantly greater for N₄₆; the difference was 9.9% for *P. koraiensis* and 22.0% for *T. amurensis* ($P < 0.05$, Student's *t*-test). There was no significant difference in light inhibition degree between *P. koraiensis* and *T. amurensis*. The average light inhibition degree of the two tree species for different nitrogen treatments was in the range of 42.0%-78.4%.

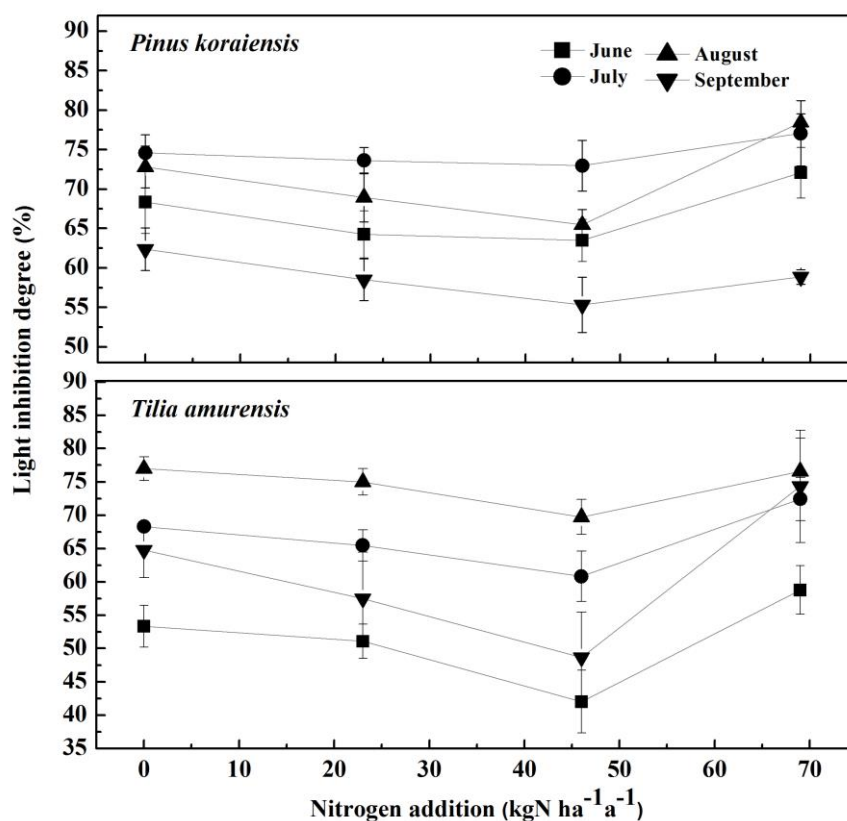


Figure 2. Effects of nitrogen addition (0, 23, 46 and 69 kg/ha/y N) on light inhibition degree for the two main tree species of Changbai Mountain (*P. koraiensis* and *T. amurensis*) from June to September. The data are presented as mean \pm SE, $n=4$

Change of the maximum photochemical fluorescence rate and SPAD value to nitrogen addition

F_v/F_m is the maximum photochemical efficiency of PSII in the dark and it indicates whether the plant is stressed in terms of growth. F_v/F_m decreases if the plant is stressed. F_v/F_m and SPAD were measured for the different nitrogen treatments to determine how

nitrogen addition affected physiological activity, as shown in *Fig. 3* and *Fig. 4*. F_v/F_m for *P. koraiensis* for treatments N_{23} was 3.2% greater and for N_{46} was 4.0% greater than for N_0 ; corresponding values for *T. amurensis* were 7.4% and 12.2%. F_v/F_m decreased for N_{69} from N_{46} by 2.8% for *P. koraiensis* and by 5.2% *T. amurensis*. All differences were significant ($P < 0.05$, Student's *t*-test).

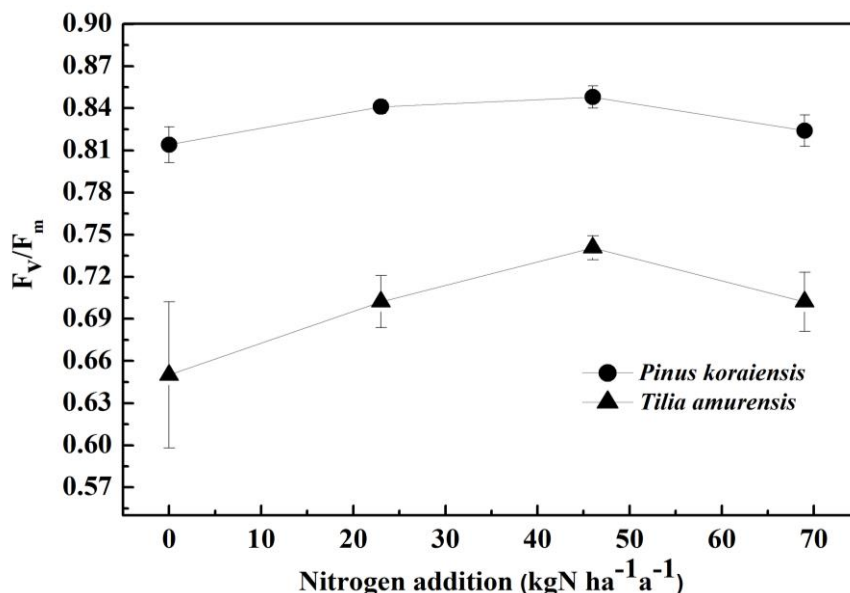


Figure 3. Maximum photochemical fluorescence rate (F_v/F_m) for different nitrogen treatments (0, 23, 46 and 69 kg/ha/y N) for the two main tree species (*P. koraiensis* and *T. amurensis*) of Changbai Mountain. The data are presented as mean \pm SE, $n=4$

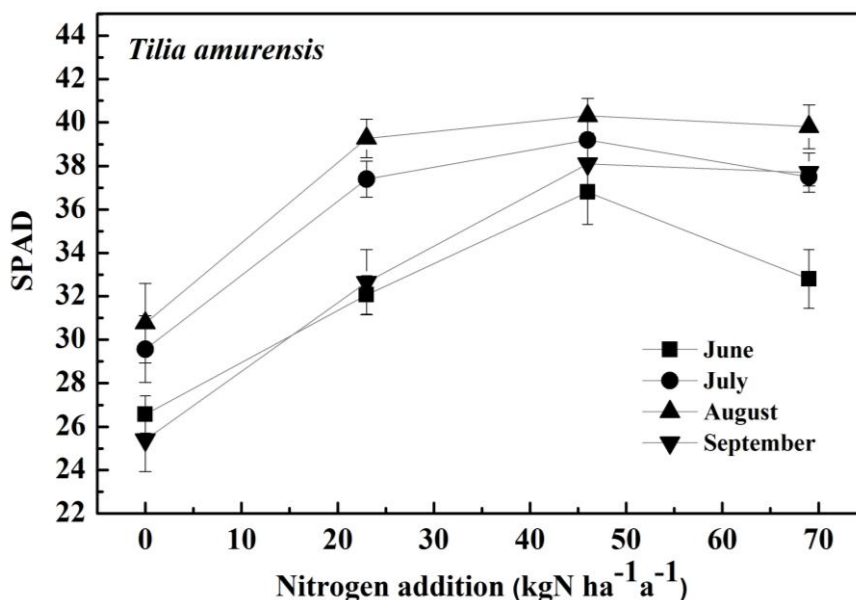


Figure 4. SPAD for four nitrogen treatments (0, 23, 46 and 69 kg/ha/y N) for the broadleaf tree species of Changbai Mountain (*T. amurensis*) from June to September. The data are presented as mean \pm SE, $n=4$

SPAD represents leaf chlorophyll content. Variation in SPAD was similar to that in F_v/F_m , for nitrogen treatments N_{23} and N_{46} , being respectively 20.5% and 27.3% greater than for N_0 for *T. amurensis* in the four months ($P < 0.05$, Student's *t*-test). SPAD decreased by 4.4% in N_{69} from N_{46} ($P < 0.05$, Student's *t*-test).

Effect of water regime on day respiration

R_L for different soil water content values in three different water regimes (CK, MW and LW) is shown in Fig. 5 for *P. koraiensis* and *T. amurensis* from June to August. All R_L values for the two species were the greatest in treatment CK (sufficient watering) and gradually decreased as soil water content decreased. The average R_L value for *P. koraiensis* for MW was 17.0% less and for LW was 37.7% less than for CK ($P < 0.05$, Student's *t*-test). Corresponding values for *T. amurensis* were 22.2% and 44.3% ($P < 0.05$, Student's *t*-test). There was no significant difference in R_L between *P. koraiensis* and *T. amurensis*.

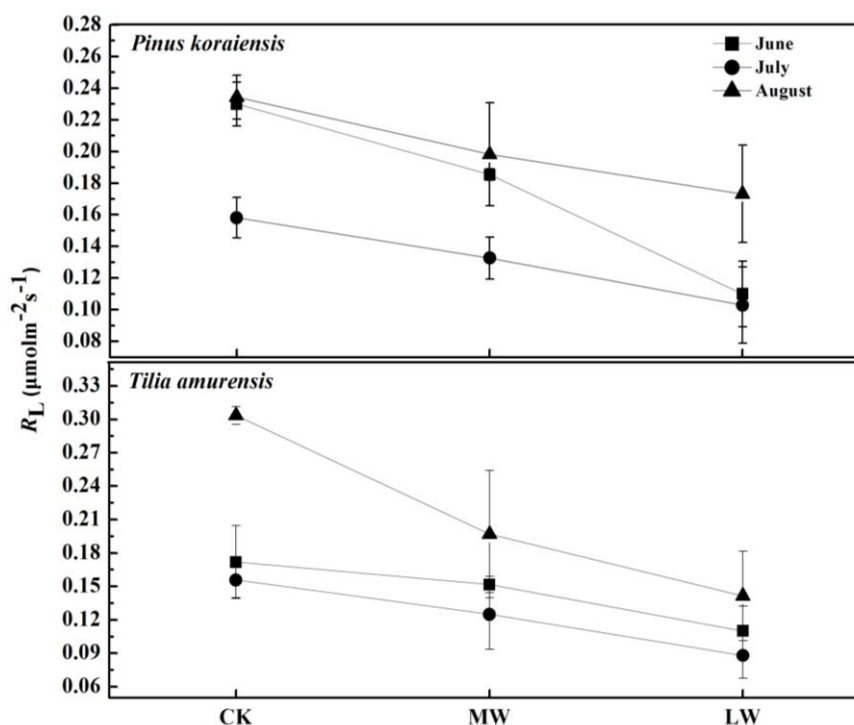


Figure 5. Response of R_L to different water regimes for the two main tree species of Changbai Mountain (*P. koraiensis* and *T. amurensis*) from June to August. The data are presented as mean \pm SE, $n=4$

Effect of different water regimes on light inhibition degree

We also calculated light inhibition degree for the three different water regimes (CK, MW and LW) for *P. koraiensis* and *T. amurensis* in June and July, as shown in Fig. 6. In all cases, the lowest values of light inhibition degree were for CK and the value increased each month as soil water content decreased. The average light inhibition degree of *P. koraiensis* was 14.2% greater for MW and 17.0% greater for LW than for CK ($P < 0.05$, Student's *t*-test). Corresponding values for *T. amurensis* were 6.2% and

11.1% ($P < 0.05$, Student's *t*-test). Average light inhibition degree for the two species was in the range of 58.3%–87.0%. There was no significant difference in light inhibition degree between *P. koraiensis* and *T. amurensis*.

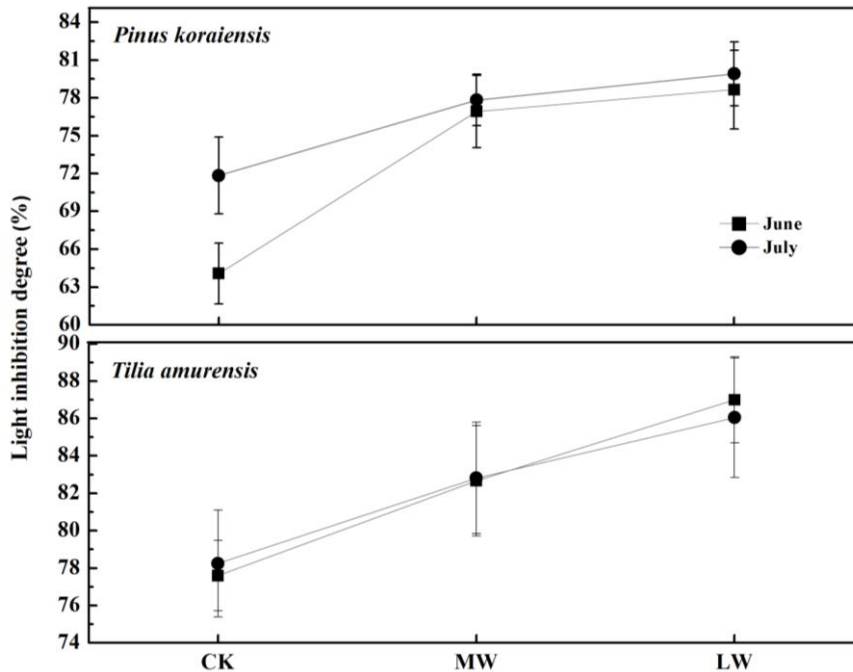


Figure 6. Light inhibition degree for different soil water levels for the two main tree species of Changbai Mountain (*P. koraiensis* and *T. amurensis*) in June and July. The data are presented as mean \pm SE, $n=4$

F_v/F_m for *T. amurensis* was measured during the water control period in September (Fig. 7). F_v/F_m decreased gradually; for MW it was 17.2% less than for CK and for LW it was 47.4% less than for CK ($P < 0.05$, Student's *t*-test).

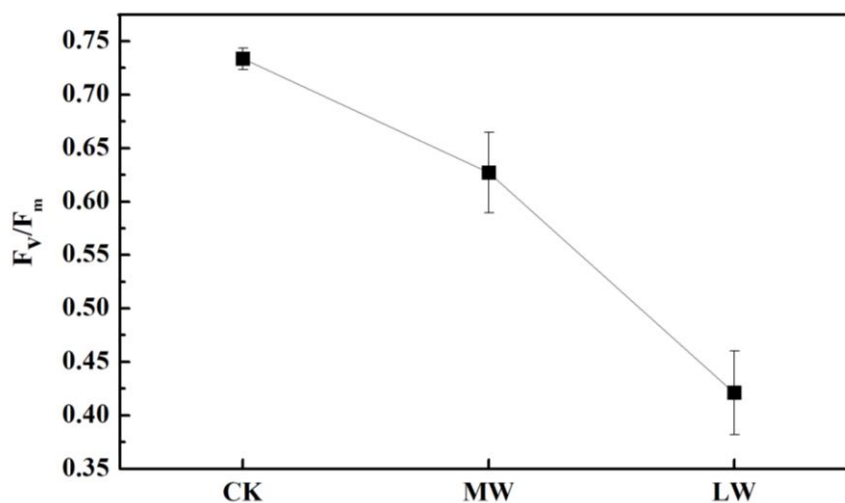


Figure 7. Maximum photochemical fluorescence rate (F_v/F_m) for different soil water levels for *T. amurensis* in September. The data are presented as mean \pm SE, $n=4$

Discussion

Response of day respiration and light inhibition degree to different nitrogen levels

Our findings suggested that R_L increased as soil nitrogen increased in treatments N_0 through N_{46} , and decreased with further nitrogen addition. In contrast, light inhibition degree decreased as soil nitrogen increased in treatments N_0 through N_{46} . R_L had a maximum value and light inhibition degree had a minimum value for treatment N_{46} .

The increase in R_L is explained as follows. The increase in nitrogen deposition induced an increase in plant tissue nitrogen content (Manter et al., 2005; Jia et al., 2011). Many studies have found a positive correlation between leaf nitrogen content and leaf respiration (Ryan et al., 1996; Reich et al., 1998; Sugiura and Tateno, 2011). Jia et al. (2011) showed that nitrogen fertilization increased both tissue nitrogen content and root respiration, and root respiration has been found to closely mirror leaf respiration (Reich et al., 2002). Manter et al. (2005) found that leaf net photosynthesis rate of saplings increased as soil nitrogen content increased through fertilizer application and that there were similar trends in variation of photosynthesis rate and leaf respiration. Finally, total sapling biomass was found to increase as nitrogen fertilizer concentration increased (Manter et al., 2005). Greater R_L and lower light inhibition degree were necessary for the production of more carbon skeletons, higher energy, and more reductant-producing organelles that originate during the respiration process.

The four reasons outlined in the preceding paragraph account for increased nitrogen contributing to the increase in R_L ; we also found that light inhibition degree decreased from treatment N_0 to N_{46} . However, Minocha et al. (2001) found that surplus nitrogen due to a high soil nitrogen addition was not used to increase Rubisco synthesis and was instead accumulated as putrescine, which is a stress indicator. It has been found that the ratios of N/P and Mn/Mg in sapling leaves significantly increased under a high nitrogen load and led to an imbalance of mineral nutrients (Nakaji et al., 2001, 2002). Therefore, both R_L decreased and light inhibition degree increased because of the additional nitrogen in treatment N_{69} .

We found that the value of R_L was significantly less for the evergreen conifer species than that for the deciduous broadleaved species in each nitrogen treatment. Reich et al. (1998) and Stockfors and Linder (1998) showed that R_L and stem respiration varied similarly, and other studies have found that stem respiration was positively correlated with plant growth rate (Stockfors and Linder, 1998). We found greater R_L values in the higher growth rate species (*T. amurensis*) than in the lower growth rate species (*P. koraiensis*). This finding is consistent with the findings of Poorter et al. (1990), who investigated respiration for two species with different growth rates and found a higher tissue nitrogen fraction and greater leaf respiration for the faster growing species than for the slower growing species.

Effect of different water regimes on day respiration and light inhibition degree

R_L decreased and light inhibition degree increased as soil water content decreased for both species in this study. Previous studies have suggested that decreased leaf respiration in drought was most likely due to decreased substrate availability (Lawlor and Fock, 1977) or greater restriction of adenylate because of decreased ATP demand (Atkin and Macherel, 2009). However, Crous et al. (2011) found that soluble sugar content was not significantly affected by drought conditions, so the decreased supply of respiration substrate induced by drought was not responsible for the decrease in R_L and

greater value of light inhibition degree that we found, and the decreased demand for respiration products (e.g., ATP, NADPH or TCA cycle intermediates) was most likely responsible. In addition, Crous et al. (2012) found that the starch concentrations increased in drought conditions, which suggests that the transport of organic matter by phloem decreased, so ATP demand decreased. Leaf nitrogen content decreased in sustained drought, which decreased the demand for respiratory ATP used in protein turnover (Crous et al., 2012). It has been found that phosphorus concentrations decreased in drought-affected leaves and intensified the adenylate restriction of leaf respiration (Plaxton and Podestá, 2006). Our findings that R_L decreased and light inhibition degree increased in the water stress treatment are similar to the findings of the majority of studies that estimated R_L using the Kok method (Ayub et al., 2011; Crous et al., 2012).

Variation in SPAD and maximum photochemical efficiency with increasing nitrogen addition and decreasing soil water content

We found that variations in SPAD and F_v/F_m were similar in the different nitrogen and soil water treatments. Both SPAD and F_v/F_m increased as soil nitrogen increased from N_0 to N_{46} and then decreased for treatment N_{69} and both decreased as soil water content decreased. Chlorophyll content is key to photosynthesis, and it is indicated by SPAD. Variation in chlorophyll content as indicated by SPAD was consistent with the results of Warren et al. (2003), who found that chlorophyll content increased as soil nitrogen content increased. Yan et al. (2012) found a positive correlation between A_n and F_v/F_m , so variation in SPAD and F_v/F_m also indicates variation in the rate of photosynthesis. Other studies have found tight coupling between photosynthesis rate and R_L (Ayub et al., 2011). Increase in R_L may therefore be because of increased photosynthesis, as indicated by SPAD and F_v/F_m , due to nitrogen addition in treatments N_0 through N_{46} . However, Nakaji et al. (2001, 2002) found that the chlorophyll content of *P. densiflora* saplings decreased under high nitrogen load due to loss of mineral nutrition balance in the plants, which is consistent with the variation in chlorophyll content for different nitrogen treatments that we found. Ayub et al. (2011) found that the photosynthesis rate decreased due to a decrease in F_v/F_m and that R_L was tightly coupled with the rate of photosynthesis, so R_L decreased as soil water content decreased. Buckley and Adams (2011) found that light inhibition degree ranged from 24% to 90%, which suggests that R_L and R_D respond differently to environmental signals. Light inhibition degree varied from 42.0% to 78.4% (*T. amurensis*) and 58.3% to 87.0% (*P. koraiensis*) for the two species in this study. The values of light inhibition degree we obtained were within the higher part of the range for leaves under stress. Light inhibition degree values for different water regimes in this study were similar to those found by Crous et al. (2012), which were approximately 50%–80%.

Conclusion

Clear relationships between environmental factors and plant functional traits are vital for accurate prediction in modeling plant behavior. In this study, we intended to gain a better understanding of the leaf respiration response to two different climate change scenarios. Leaf respiration of two prominent tree species (one evergreen conifer species and one deciduous broadleaved species) was quantified for different nitrogen deposition and soil moisture treatments in a typical temperate forest. Drawing on some previous

studies, we analyzed changes in R_L and light inhibition degree as they affected leaf respiration for different soil nitrogen and moisture levels to produce an explanation of how these parameters influenced leaf respiration.

Our findings suggested that in all cases R_L was inhibited by light and gradually increased when nitrogen deposition increased within a certain range (treatments N_0 – N_{46}) and decreased when nitrogen deposition was over-saturated (treatment N_{69}). In contrast, light inhibition degree decreased as nitrogen deposition increased from N_0 to N_{46} and increased for treatment N_{69} . R_L decreased as soil water content decreased, but light inhibition degree increased stepwise. SPAD and F_v/F_m varied in line with R_L for different nitrogen and soil water treatments.

The marked variation in respiration for different nitrogen and soil water treatments has important implications for understanding the balance between photosynthetic carbon uptake and respiratory carbon loss. However, analysis of the relationship between leaf respiration and photosynthesis and understanding the physiological mechanisms more deeply demands research that recognizes the influence of different factors of climate change.

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