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ORIGINAL PAPER

Effect of nitrogen levels on photosynthetic parameters, morphological and chemical characters of saplings and trees in a temperate forest

Jinwei Sun[1] · **Fuqi Yao**[1] · **Jiabing Wu**[2] · **Pingcang Zhang**[1] · **Wensheng Xu**[1]

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Abstract Exploring the response differences of leaf physiology parameters to enhanced nitrogen deposition between saplings and trees is vital for predicting the variations of terrestrial ecosystem structure and function under future global climate change. In this study, the ecophysiological parameters of saplings and trees of *Fraxinus mandshurica* Rupr. were measured at different levels of nitrogen addition in a temperate forest. The results show that ecophysiological parameters maximum net photosynthetic rate (P_{max}), apparent quantum efficiency (α), dark respiration (R_d), light saturation point (L_{sp}), photosynthetic nitrogen use efficiency (PNUE), specific leaf area (SLA) and stomatal conductance under saturated light intensity (G_{smax}) were higher in saplings than in trees. These physiological parameters and not N_{leaf} (leaf nitrogen content) led to relatively lower P_{max} and R_d in trees. For both saplings and trees, low and median nitrogen addition (23 and 46 kg ha^{-1}a^{-1}) resulted in significant increases in P_{max}, R_d, L_{sp}, Chl, PNUE, SLA and G_{smax}. These parameters tended to decline under high additions of nitrogen (69 kg ha^{-1}a^{-1}), whereas N_{leaf} was always enhanced with increasing nitrogen. Variations in P_{max} and R_d with increasing nitrogen were attributed to variations in the strongly related parameters of, L_{sp}, Chl, PNUE, SLA and G_{smax}. Overall, the response sensitivity of physiological parameters to enhanced nitrogen levels was lower in trees compared with saplings.

Keywords Physiology parameters · Added nitrogen · Saplings · Trees · Deciduous broadleaved species

Introduction

Experimental results from saplings are often used to extrapolate the possible responses of trees (Ehleringer and Field 1993). This extrapolation has been applied to global climate change research (Körner 2000; Norby et al. 1999) because of limitations to experiment on tall trees. For example, many process-based models of carbon exchange in terrestrial ecosystems are applied on parameters measured from saplings (Amichev et al. 2010; Fournier and Andrieu 1998; Morin and Thuiller 2009). However, the accuracy of this extrapolation is unclear. Many biological processes will change with increasing age of the tree, however, the age relationship to physiological traits has received much less attention (Thomas and Winner 2002). Several studies have shown that photosynthetic capacities and growth of mature trees were lower than that of saplings (Kolb et al. 1997; Waring 1987; Yoder et al. 1994). Ryan

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Corresponding editor: Zhu Hong.

✉ Fuqi Yao
fuqiyao163@163.com

Jinwei Sun
sunjinwei615@126.com

[1] Changjiang River Scientific Research Institute, Wuhan 430010, People's Republic of China

[2] State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, People's Republic of China

et al. (1997) indicated that a significant decrease in net primary productivity with increasing stand age was due to variable leaf traits. These differences were caused by the decrease of stomatal conductance and leaf nitrogen with increasing leaf age (Gower et al. 1996; Kolb et al. 1997). In addition, LMA (leaf mass per unit area) of saplings was lower than that of mature trees (Thomas and Winner 2002; Yoder et al. 1994). Thomas and Ickes (1995) showed that leaf traits develop in continuous and nonlinear patterns during tree ontogeny. Tree heights increase with increasing age and distances of photosynthate and hormone molecules transport increase as well. Responses to the environment shift with plant life-stages (Sandquist et al. 1993). Exploring the response differences of leaf physiology parameters to changing environmental factors between saplings and trees is important for predicting variations of terrestrial ecosystem structure and function under future climate change scenarios.

Nitrogen availability has long been recognized as a key constraint to plant growth (Chapin et al. 1986; Schulze et al. 1994) especially in many temperate forests (Ågren 1985). The creation of reactive nitrogen species has increased tenfold since the late nineteenth century, nearly doubling the total N input into terrestrial ecosystems (Galloway 1998; Galloway et al. 2004). The examination of the response of leaf traits to nitrogen has become vital to evaluating terrestrial ecosystem response to global changes. Previous studies have shown that photosynthesis increased with rising nitrogen supply (Chen et al. 2005; Makino and Osmond 1991; Wang et al. 2012) and enhanced photosynthesis with nitrogen may result from increased stomatal conductance (Chen et al. 2005) or from increased carboxylation capacity (Brown et al. 1996). Fleischer et al. (2013) showed that photosynthesis of boreal and temperate evergreen forests rises with increased nitrogen deposition but levels out at a threshold value of available nitrogen in soils. Other studies have reported that photosynthesis decreased under high nitrogen loads (Nakaji et al. 2001, 2002). Compared with photosynthesis, information on the variation of other leaf characteristics with nitrogen addition is scare and conflicting. Theoretical and experimental research suggests that species must differ in resource requirements in order to coexist in a community (Bazzaz 1987; May 1974). Therefore, responses of physiological traits to the environment may be different between saplings and trees. Some studies reported differences in responses to drought and ozone between saplings and trees (He et al. 2005; Samuelson and Kelly 1996), whereas as yet there is no study to explore response differences between saplings and trees under enhanced nitrogen deposition.

In this study, we explored the effect of nitrogen addition on photosynthetic parameters, morphological and chemical characters of saplings and trees in a temperate forest. The results will contribute to understanding the differences in the response sensitivity between saplings and trees to nitrogen deposition and to estimating carbon budgets accurately in the future.

Materials and methods

We selected saplings and trees of *Fraxinus mandshurica* Rupr. in a temperate mixed forest in Changbai Mountain, northeastern China (42°24′09″N,128°05′45″E) in the monsoon-influenced temperate continental climatic zone (Guan et al. 2006). Mean annual air temperature is 3.6 °C and mean annual precipitation 695.3 mm according to meteorological records from 1982 to 2003. The soil is dark brown forest soil. Natural nitrogen deposition level is 23 kg ha^{-1} a^{-1}.

The treatment of potted saplings was in an opening within the mixed forest. Pot diameter was 45 cm and filled with a homogenized mixture of local forest soil (same soil as for the trees). Forty vigorous saplings were selected following transplanting to the pots for 3 years, and were 7 years old. The saplings had a mean height of 1.6 m and average basal diameter of 2 cm. The trees of *F. mandshurica* were randomly selected in the mixed forest.

Nitrogen addition treatment

Three treatments of nitrogen at 23 (LN), 46 (MN), and 69 kg ha^{-1} a^{-1} (HN) were added to the potted saplings. Control plants (CK) were untreated. Four potted saplings of each nitrogen treatment were designed for *F. mandshurica*, respectively. Four 15 m × 15 m quadrats of trees were treated at the nitrogen levels above. Ammonium nitrate was added twice, on the first of May and at the end of June each year.

Measurement of gas exchange rate and data analysis

Measurements under each nitrogen level were taken once a month from June to September. The leaves distributed in different positions in the sapling were measured. Small branches located in different positions in the tree canopy were cut by pruning shears and then immediately re-cut under water, and remained in water throughout all measurements. Various study results have shown that measurements on branches re-cut under water are accurate and reliable and did not significantly differ from those carried out on uncut branches (Dang et al. 1997; Richardson and Berlyn 2002). Net photosynthetic rate (P_n), leaf conductance (g_s) and intercellular CO_2 concentration (c_i) were measured in a series of photosynthetic photon flux density (I) values with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA). During measurement, leaf temperatures and relative humidity were controlled at 25 °C and 60%, respectively. Measurements were taken from 08:00 to 12:00 am on clear days. Photosynthetic parameters, i.e., maximum net photosynthetic rate ($P_{\max}$), apparent quantum efficiency (α), dark respiration (R_{d}) and light saturation point (L_{sp}) were calculated with each sample's light response curve according to Long et al. (1993). All these parameters were determined by fitting the following non-rectangular hyperbolic function:

$$P_n = \frac{\alpha \times I + P_{\max} - \sqrt{(\alpha \times I + P_{\max})^2 - 4 \times k \times \alpha \times I \times P_{\max}}}{2 \times k} - R_d \quad (1)$$

where k is the convexity of the curves. P_{n} is Net photosynthetic rate; $P_{\max}$ is cmaximum net photosynthetic rate; R_{d} is dark respiration; α is apparent quantum efficiency.

Data analysis was performed using SPSS version 17.0 (SPSS, Chicago, IL, USA) software. Multiple comparisons were used to separate means of photosynthetic parameters, morphological and chemical characters at each nitrogen level. The differences were tested with a one-way ANOVA (Duncan test). Student's t test was used to determine the differences of these leaf traits between saplings and trees. Relationships were fitted with linear or polynomial functions. All tests were based on a significance level of 0.05.

Results

Changes of photosynthetic parameters

Changes in $P_{\max}$, α, R_{d} and L_{sp} with different nitrogen levels for saplings and trees are shown in Figs. 1, 2, 3and 4. $P_{\max}$, α, R_{d} and L_{sp} of the saplings were all higher than those of the trees. This suggests that there are original differences in photosynthetic performances between saplings and trees. Variation in $P_{\max}$, α, R_{d} and L_{sp} with increasing nitrogen showed that the parameters increased gradually from CK to MN, whereas these values began to decline at the HN level. The photosynthetic parameters demonstrated different increased degree under the same nitrogen level. The increased degree of photosynthetic parameters ($P_{\max}$, α, R_{d}, and L_{sp}) for LN and MN levels compared with CK level in saplings was significantly higher than in trees (Table 1). The highest level of nitrogen addition (HN) caused significant decline in these values of photosynthetic parameters compared to the MN treatment which suggests that photosynthetic parameters could be inhibited when the deposited nitrogen is increased to certain high levels.

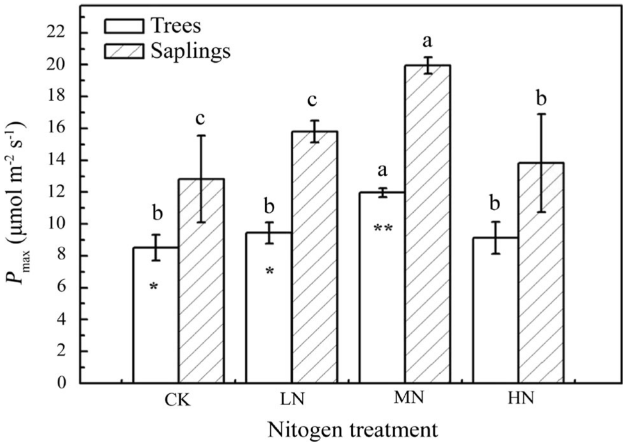

Fig. 1 Response of the maximum net photosynthetic rate ($P_{\max}$) to increasing nitrogen (i.e., CK, LN, MN and HN) as mean ± SE. Letters represent significant differences in $P_{\max}$ among different nitrogen addition levels. Asterisks represent significant differences of $P_{\max}$ between saplings and trees ($^{*}P < 0.05$, $^{**}P < 0.01$)

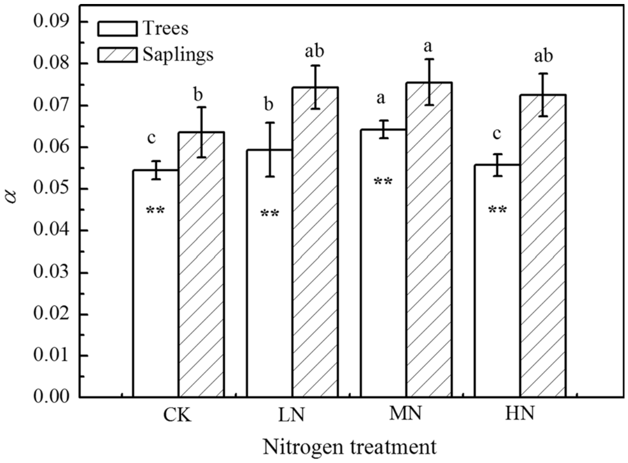

Fig. 2 Variations in apparent quantum efficiencies (α) at different nitrogen levels (i.e., CK, LN, MN and HN) presented as mean ± SE. Letters represent significant differences in α among different nitrogen addition rates. Asterisks represent significant differences between saplings and trees ($^{*}P < 0.05$, $^{**}P < 0.01$)

Changes of leaf chemical characters with nitrogen levels

Changes in chlorophyll (Chl) and nitrogen contents (N_{leaf}) are shown in Fig. 5 and Fig. 6. The N_{leaf} of trees was higher than that of saplings for each nitrogen level (Fig. 6). The photosynthetic nitrogen use efficiency (PNUE) was significantly higher in saplings than in trees (Table 2). Chl and PNUE increased with increasing nitrogen from LN to MN, and declined at the HN level. High nitrogen additions caused significant declines in Chl and PNUE compared to those of MN treatments, indicating that Chl and PNUE could be inhibited when nitrogen is further increased to a threshold level. N_{leaf} was continually promoted with

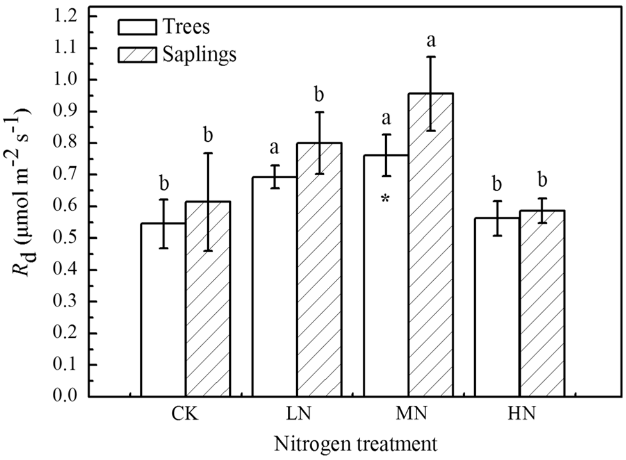

Fig. 3 Response of dark respiration (R_d) to increasing nitrogen levels (i.e., CK, LN, MN and HN) presented as mean ± SE. Letters represent significant differences in R_d among different nitrogen rates. Asterisks represent significant differences between saplings and trees ($^*P < 0.05$, $^{**}P < 0.01$)

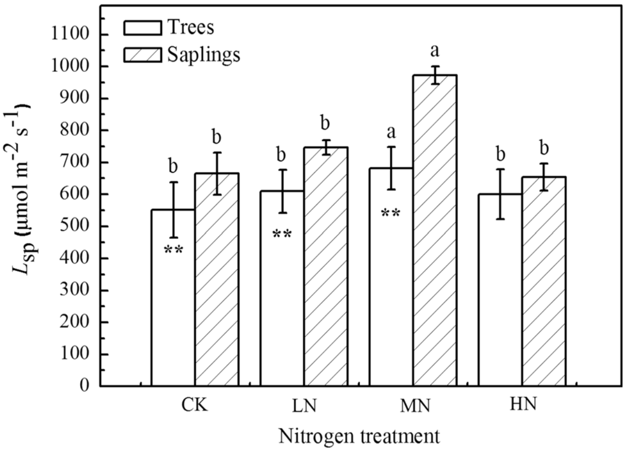

Fig. 4 Variations in light saturation point (L_{sp}) at different nitrogen levels (i.e., CK, LN, MN and HN) presented as mean ± SE. Letters represent significant differences in L_{sp} among different nitrogen levels. Asterisks represent significant differences between saplings and trees ($^*P < 0.05$, $^{**}P < 0.01$)

increasing nitrogen from LN to HN (Fig. 6). The increased degree of N_{leaf} for LN and MN levels compared with CK level was always higher in saplings than in trees (Table 1).

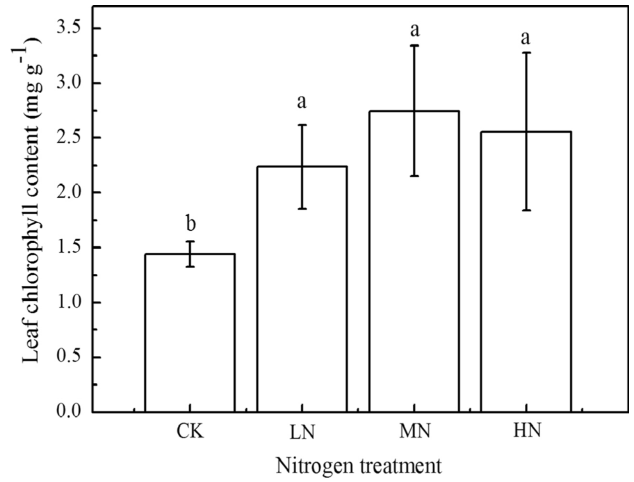

Fig. 5 Variations in chlorophyll content at different nitrogen levels (i.e., CK, LN, MN and HN). Vertical bars indicate standard errors of the mean. Letters represent significant differences in chlorophyll content at different nitrogen levels

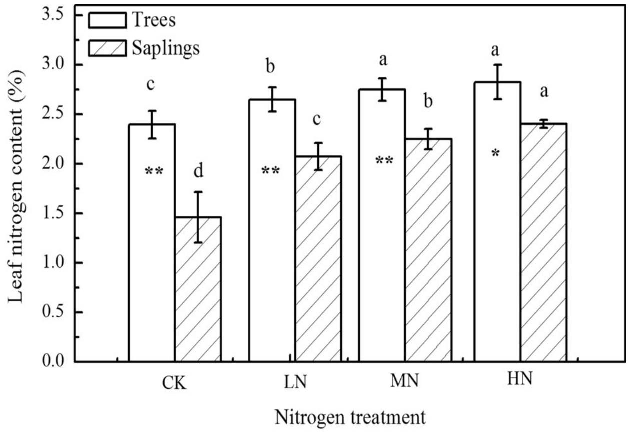

Fig. 6 Variations in leaf nitrogen content (%) with increasing nitrogen input (i.e., CK, LN, MN and HN) presented as mean ± SE. Letters represent significant differences in nitrogen content among different nitrogen levels. Asterisks represent significant differences between saplings and trees ($^*P < 0.05$, $^{**}P < 0.01$)

Changes in leaf morphological characters

Leaf morphological characters (SLA and G_{smax}) were affected by increasing nitrogen levels (Figs. 7, 8). The SLA and G_{smax} values of trees were lower than that of the

Table 1 Increased degree (%) in maximum net photosynthetic rates P_{max} (μmol m^{-2} s^{-1}), apparent quantum efficiency (α), leaf dark respiration R_d (μmol m^{-2} s^{-1}), light saturation point L_{sp} (μmol m^{-2} s^{-1}), leaf nitrogen content N_{leaf} (%), specific leaf area SLA (cm^2 g^{-1}), and stomatal conductance under saturated light intensity G_{smax} (mol m^{-2} s^{-1}) at different nitrogen levels of saplings and trees

Parameters	P_{max}				R_d		L_{sp}		N_{leaf}			SLA		G_{smax}	
Treatments	LN	MN	LN	MN	LN	MN	LN	MN	LN	MN	HN	LN	MN	LN	MN
Saplings	11.0	40.7	9.1	18.0	27.0	39.6	10.5	23.4	10.6	14.8	18.0	5.8	14.5	19.1	48.0
Trees	23.2	55.4	16.9	18.9	30.1	55.4	12.1	46.2	42.1	54.1	64.5	7.0	14.7	24.8	60.0

Table 2 Photosynthetic nitrogen use efficiency (PNUE, μmol mol^{-1} s^{-1}) of saplings and trees at different nitrogen levels (i.e., CK, LN, MN and HN) presented as mean ± SE

Nitrogen levels	CK	LN	MN	HN
Trees	68.6 ± 8.2c	75.8 ± 11.7b	100.3 ± 13.7a	70.3 ± 6.4bc
Seedlings	179.5 ± 17.8c	193.4 ± 14.9b	223.8 ± 11.7a	142.6 ± 6.2d

Letters represent significant differences in PNUE between nitrogen levels (ANOVA Duncan test, $P < 0.05$)

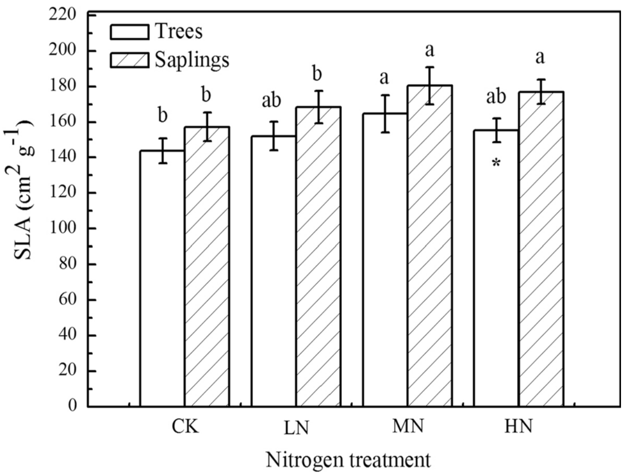

Fig. 7 Response of specific leaf area (SLA) to increasing nitrogen levels (i.e., CK, LN, MN and HN) presented as mean ± SE. Letters represent significant differences in SLA among nitrogen levels. Asterisks represent significant differences between saplings and trees (*$P < 0.05$, **$P < 0.01$)

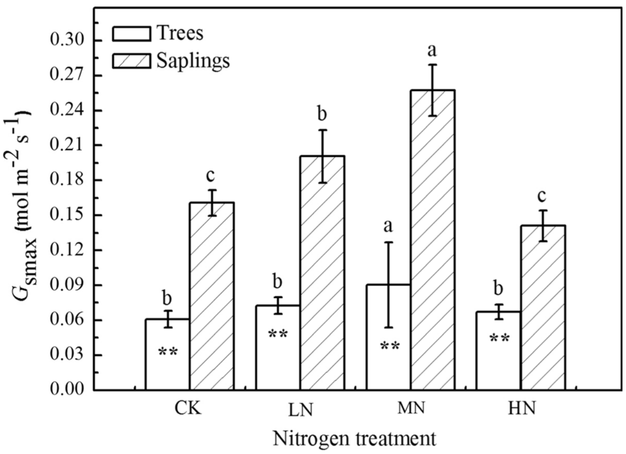

Fig. 8 Changes in stomatal conductance for H_2O at saturating photosynthetic photon flux density and ambient CO_2 (G_{smax}) at different nitrogen levels (i.e., CK, LN, MN and HN) presented as mean ± SE. Letters represent significant differences in G_{smax} among different nitrogen levels. Asterisks represent significant differences between saplings and trees (*$P < 0.05$, **$P < 0.01$)

saplings for all nitrogen treatments. With increasing nitrogen, SLA and G_{smax} were enhanced for the LN and MN treatments, and then declined at the HN level. This resulted in significant decrease of the SLA and G_{smax} compared to the values of MN. This suggests that SLA and G_{smax} could be inhibited if nitrogen is increased to higher levels. The increased degree of SLA and G_{smax} values for LN and MN treatments compared with the values of CK were higher in saplings than in trees (Table 1).

Discussion

Effects of nitrogen levels on physiological characteristics

P_{max} reflects photosynthetic capacity and was enhanced with nitrogen from the LN to MN levels. This may be attributed to the following reasons. Firstly, higher nitrogen levels resulted in higher N_{leaf} and Chl, consistent with studies by Chandler and Dale (1995), Ripullone et al. (2003), and Wang et al. (2012). Secondly, chlorophyll content is a good indicator of photosynthetic rate, and rubisco (ribulose-1, 5-bisphosphate carboxylase/oxgenase) is a key enzyme and a limiting factor in photosynthesis (Evans 1986), and protein synthesis was influenced by leaf nitrogen content (Stitt 1996). Evans (1989) also suggested that electron transport capacity is strongly correlated with leaf nitrogen when irradiance was a constant. Increasing PNUE also demonstrates a higher proportion of leaf nitrogen distributed to the photosynthetic process in this study. With increasing G_{smax}, however, c_i had no obvious changes among the nitrogen treatments which suggests that increased P_{max} might be a consequence of greater carboxylation capacity. This is consistent with Brown et al. (1996). Wang et al. (2012) suggested that added nitrogen likely accelerated the transport of photosynthetic CO_2 due to increased stomatal conductance and led to enhanced P_{max}. Therefore, increases in photosynthesis rates with nitrogen also may result from increased G_{smax}. Knops and Reinhart (2000) suggested that SLA influenced competitive ability for species in ecosystems, and SLA substantially increased aboveground competition for light along rising nitrogen levels, and therefore, P_{max} increased from the LN to MN. The value of α reflects the utilization ability of low light, and L_{sp} represents the light requirement when photosynthesis reaches P_{max}. Variation in α and L_{sp} with increasing nitrogen indicated that utilization of low and high light increased with increasing nitrogen from LN to MN, and indicated that *F. mandshurica* had high competition for light and had high P_{max}.

R_d increased with increasing nitrogen from LN to MN, which may result from enhanced P_{max} and N_{leaf}. Photosynthesis can limit the substrate supply in the respiration process, which is consistent with Ayub et al. (2011) and Reich et al. (1998). R_d increased with increasing N_{leaf} from CK to MN which may be because leaves with higher N_{leaf} have large complements of N-rich enzymes and other metabolites which are used in respiration costs and re-synthesis requirements (Reich et al. 1998; Sugiura and Tateno 2011). Bouma et al. (1994) reported that 90% of the nitrogen in plant cells is in proteins which require energy from respiration for replacement and repair. Leaf chlorophyll is one of the main nitrogen storage sites, so higher chlorophyll content also requires larger R_d used to repair and replace. PNUE, SLA and G_{smax} enhanced P_{max} which was closely related with R_d. Therefore, leaf chlorophyll content, SLA and G_{smax} strongly affected R_d by direct or indirect processes. P_{max} and R_d both declined at the HN level compared with that at the MN level. The decreased P_{max} result from the decreased utilization of low and high I at the HN. Leaf chlorophyll content as a good indicator of photosynthesis decreased at the HN level. PNUE, G_{smax} and SLA which were strongly correlated with P_{max} also were reduced under HN. R_d showed similar response processes compared to P_{max}, which may be attributed to the closely related P_{max}, leaf chlorophyll content, SLA and G_{smax} at the HN level. The P_{max} and R_d declined under HN which may be because the high nitrogen- treated samples had not used the surplus nitrogen to synthesize more rubisco, instead accumulating as putrescine, a plant stress indicator (Minocha et al. 2001). This was verified by Nakaji et al. (2001, 2002) who found that the N/P and Mn/Mg ratios were significantly enhanced under high nitrogen loads because of disturbances in the mineral nutrient balance in the plants.

Comparison of physiological characteristics of saplings and trees

There was higher P_{max} in saplings than in trees which may be attributed to higher α and L_{sp} which mirrored the utilization ability of low and high I. In addition, G_{smax} of saplings was higher than that of trees, and many studies have also indicated that stomatal conductance is reduced with the increasing age (Ryan and Yoder 1997; Kolb et al. 1997; Niinemets 2002). Ryan and Yoder (1997) proposed that total resistance of the hydraulic pathway increased with age, reducing the supply of water transpiration and limiting stomatal conductance and P_{max}. In this study, SLA, which may enhance P_{max}, was higher in saplings than in trees. The study of Thomas and Winner (2002) also confirmed this and Gunn et al. (1999) found that SLA decreased with age. Some studies suggested that decreased photosynthesis results from declining N_{leaf} (Gower et al. 1996; Niinemets 1997). However, N_{leaf} of saplings was lower than that of trees in this study, thus N_{leaf} was not the reason for the difference in photosynthetic capacity between saplings and trees. R_d of saplings was higher than in trees because less respiratory substrate originating from photosynthesis was produced in the trees and also results from the variation of other related leaf traits.

Variations of physiological parameters to increasing nitrogen were more obvious in saplings than in trees which indicated higher response sensitivity for the saplings. This may be owing to the difference in nitrogen requirements between saplings and trees. Previous studies showed that there is stronger nitrogen limitation at the sapling stage because of lower leaf nitrogen concentrations and greater photosynthetic nitrogen use efficiency (Ishida et al. 2005; Mediavilla and Escudero 2003; Palow et al. 2012). Nitrogen distribution patterns in trees tend to immobilize more nitrogen because there is more accumulated live biomass and woody debris, and nitrogen is less available for growth (Bond 2000; Gower et al. 1996). Additionally, nutrient transport generally declined for trees with longer distances between shoot apices and roots (Maggs 1964). The growth of trees also might be limited by the transport of water and nutrients because the xylem may be blocked when not adequately replaced by refilling or by the production of new xylem (Zimmerman 1983). Furthermore, more substances (chlorophyll, proteins and hormones) which are important to pant growth were produced in saplings because of the associated genes expressed (Greenwood 1995). Finally, a “go for broke” strategy of higher photosynthesis and transpiration rates was demonstrated to provide higher growth potential in saplings, in contrast, the growth strategy was more conservative in trees (Amrita and Soyza 1996; Donovan and Ehleringer 1991, 1992; Miller et al. 1995). Collectively these arguments may cover the reasons that lead to the differences of the inner mechanisms between saplings and trees.

Conclusions

There were higher leaf physiological parameters, except for leaf nitrogen content, in saplings than in trees of *F. mandshurica* in this study. Therefore, the other physiological parameters rather than leaf nitrogen content led to lower P_{max} and R_d in trees. Increasing nitrogen levels enhanced the value of most physiology parameters (P_{max}, α, R_d, L_{sp}, Chl, PNUE, SLA and G_{smax}). However, the parameters tended to become inhibited when nitrogen was increased over a threshold level. There was similar variation among leaf characteristics with increasing nitrogen levels due to strong dependent relationships existing among physiology parameters. In addition, leaf nitrogen content continually enhanced with increasing nitrogen. Response sensitivity was higher for saplings than for trees. The comparisons of these physiology parameters will help to better understand terrestrial ecosystems response to global climate change, and will contribute to accurate model estimations and carbon evaluations under climate change scenarios.

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