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Photosynthesis, leaf morphology and chemistry of *Pinus koraiensis* and *Quercus mongolica* in broadleaved Korean pine mixed forest

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Abstract

Leaf traits and physiology are species-specific and various with canopy position and leaf age. Leaf photosynthesis, morphology and chemistry in the upper and lower canopy positions of *Pinus koraiensis* Sieb. *et* Zucc and *Quercus mongolica* Fisch. ex Turoz in broadleaved Korean pine forest were determined in September 2009. Canopy position did not significantly affect light-saturated photosynthetic rate based on unit area (P_{area}) and unit dry mass (P_{mass}), apparent quantum yield (α), light compensation point (LCP), light saturation point (LSP); total nitrogen (N_m), phosphorus (P_m), carbon (C_m), and chlorophyll content (Chl_m) per unit dry mass; leaf dry mass per unit area (LMA) and photosynthetic nitrogen-use efficiency (PNUE) for *P. koraiensis* current-year needles and *Q. mongolica* leaves. While in *P. koraiensis* one-year-old needles, P_{area}, P_{mass}, α and LCP in the upper canopy were lower than those in the lower canopy. The needles of *P. koraiensis* had higher C_m and LMA than leaves of *Q. mongolica*, but P_{mass}, Chl_m and PNUE showed opposite trend. There were no differences in P_{area}, LSP, N_m, and P_m between the two species. Needle age significantly influenced photosynthetic parameters, chemistry and LMA of *P. koraiensis* needles except LCP, LSP and C_m. In contrast to LMA, P_{area}, P_{mass}, N_m, P_m, Chl_m, and PNUE of one-year-old needles were significantly lower than those of current-year needles for *P. koraiensis*. The negative correlations between LMA and P_{mass}, N_m, P_m, Chl_m, and positive correlations between P_{mass} and N_m, P_m, Chl_m were found for *P. koraiensis* current-year needles and *Q. mongolica* leaves. Our results indicate that leaf nitrogen and phosphorus contents and nutrient absorption from soil are similar for mature *P. koraiensis* and *Q. mongolica* growing in the same environment, while difference in carbon content between *P. koraiensis* and *Q. mongolica* may be attributed to inherent growth characteristics.

Additional key words: canopy position; leaf chemistry; leaf dry mass per unit area; needle age; photosynthetic parameters.

Introduction

Leaf traits, such as photosynthesis, specific leaf area, and the relationship between photosynthetic rate and leaf nitrogen (N), have been widely used in evaluating ecosystem productivity and carbon (C) cycling (Poorter and Evans 1998, Green and Kruger 2001, Hikosaka 2004, Wright *et al.* 2005, Atkin *et al.* 2008). Photosynthetic capacity of leaves is the first highlighted because photosynthesis is the original responses between plant leaves and atmosphere. In forest ecosystem, canopy photosynthetic capacity is a complex function of solar

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Abbreviations: C_m – total carbon content per unit dry mass; Chl – chlorophyll; Chl_m – chlorophyll content per unit dry mass; DM – dry mass; LCP – light compensation point; LMA – leaf dry mass per unit area; LSP – light saturation point; N_m – total nitrogen content per unit dry mass; P_{area} – light saturated photosynthetic rate per unit area; P_m – total phosphorus content per unit dry mass; P_{mass} – light saturated photosynthetic rate per unit dry mass; P_N – net photosynthetic rate; PNUE – photosynthetic nitrogen-use efficiency; PPFD – photosynthetic photon flux density; R_D – dark respiration rate per unit area; α – apparent quantum yield; θ – the convexity of the light response curve.

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radiation, canopy architecture, leaf chemistry, soil nutrient availability, *etc.* (Baldocchi *et al.* 2001, Proietti and Famiani 2002). Photosynthesis is maximized in the conditions when resources are optimally distributed. Generally, top canopy has higher photosynthetic rate due to acceptance of higher light irradiance (Fu *et al.* 2010), but higher leaf water stress and excessive accumulation of carbohydrates in leaves on the top of canopy may lower canopy photosynthetic rate (Horton and Hart 1998, Koike *et al.* 2001). Moreover, canopy environments affect leaf size, toughness, chlorophyll (Chl) content and N content (Koike *et al.* 2001). According to econometric and evolutionary arguments, N allocation patterns within a plant canopy should change according to the light extinction properties of a canopy so as to maximize the rate of photosynthetic C assimilation per unit N allocated to a leaf (Field 1983). The optimal distribution of leaf traits within canopy will make plants capture more C in order to enhance survival and competitive ability of plant individuals in forest ecosystem (Meir *et al.* 2002). In contrast to deciduous trees, evergreen species had relatively lower photosynthetic capacity but higher leaf toughness, while longer lifespan of utilizing nutrients can compensate their growth construction cost (Wright and Westoby 2002).

LMA is widely used to predict plant photosynthetic capacity (Medhurst and Beadle 2005, Han *et al.* 2008) and to determine interspecific variation of relative growth rate (Niinemets 2001, Davi *et al.* 2008, Han *et al.* 2008). Plants growing under high irradiance have thicker leaves, consequently having higher LMA (Björkman 1981). Since LMA is sensitive to irradiance (Terashima *et al.* 2001, Oguchi *et al.* 2003), it is expected to vary with canopy positions. As is shown in Hollinger (1989) and Lewandowska and Jarvis (1977), LMA generally increases from the bottom to the top of the canopy in evergreen species. The higher LMA is mainly resulted from the increase of palisade mesophyll layers or the extension of palisade cells (Hanson 1917). Leaf toughness and density affect leaf pigments content and distribution, so LMA is closely related to photosynthesis (Reich *et al.* 1991, 1992, 1997, 1999). In addition, plants with high LMA have higher total C_m but lower N_m (Davi *et al.* 2008).

N is an essential component of chlorophyll (Chl) and photosynthetic proteins (Gulmon and Chu 1981). About 75% of leaf N is in the chloroplasts, most of which is invested in photosynthetic machinery (Evans 1989, Takashima *et al.* 2004). Therefore, leaf N content strongly correlates with photosynthetic capacity. For example, a positive correlation between P_{mass} and leaf N_m has been observed (Field and Mooney 1986, Evans 1989, Green and Kruger 2001).

PNUE has been a good indicator of photosynthetic capacity (Pons and Pearcy 1994, Hikosaka 2005). PNUE is often used to distinguish interspecific growth potential (Field and Mooney 1986, Pons and Pearcy 1994). Reich *et al.* (1991) found that PNUE was low in species having relatively longer leaf life-span, high LMA and tough leaves. Kazda *et al.* (2000) reported that plants with higher PNUE could compensate the effects of low light irradiance although leaf nitrogen content was lower under this condition.

The information of leaf traits (photosynthesis, leaf chemistry and morphology LMA) is essential to illuminate leaf economics and plant life history strategies (Reich *et al.* 1992, Wright *et al.* 2004, Westoby 2006). Especially for mature leaves, C and nutrient contents can reflect growth and soil conditions *per se*. *P. koraiensis* and *Q. mongolica* are the dominant tree species in broad-leaved Korean pine forest within Changbai Mountain area, evergreen coniferous *vs*. deciduous broadleaved. In order to elucidate the leaf morphology, leaf chemistry and photosynthetic capacity of the two dominant mature tree species in temperate forest, photosynthetic parameters (P_{area}, P_{mass}, α, LCP, and LSP), LMA, and leaf chemistry (N_m, P_m, C_m, Chl_m, and PNUE) at two canopy positions (upper and lower) for *P. koraiensis* and *Q. mongolica* were determined. We hypothesize: (*1*) canopy position (upper and lower) affects photosynthetic parameters, LMA and leaf chemistry; (*2*) photosynthetic parameters, nutrient contents and LMA are species dependent; (*3*) needle age (one-year-old and current-year) influences photosynthetic parameters, LMA and leaf chemistry of *P. koraiensis* needles; (*4*) there are significant relationships among photosynthesis, LMA and leaf chemistry for both tree species. Heterogeneity within canopy profile may result in dynamic CO_2 exchange between atmosphere and forests. The estimation of photosynthetic capacity and leaf chemistry along forest canopy can provide essential information in evaluating the role of forest in global carbon cycle, while the comparison of leaf traits between different species can also reflect species adaptation strategies in the same environments.

Materials and methods

Study site and plant materials: The study was conducted in the National Natural Conservation Park of Changbai Mountain, Jilin province, northeastern China (42˚01′N, 128°06′E). The climate of the study area belongs to temperate continental monsoon climate with distinct seasons. The average annual temperature and precipitation are 3.6ºC and 695 mm, respectively. The study site is relatively flat and herbaceous cover is 40%. The study areas are within a broadleaved Korean pine forest dominated by *P. koraiensis*, *Q. mongolica* and other broadleaved trees, such as *Tilia amurensis* Rupr, *Fraxinus mondshurica* Rupr, *Acer mono* Maxim, with leaf area index of 5.3 $m^2 m^{-2}$ (Zhang *et al.* 2009). Three plots, each 50 by 50 m, were established in the experiment area in 2009. In each plot, we selected one *P. koraiensis* and *Q. mongolica* of similar canopy height (26 m) and tree age (180 years old). Measurements of photosynthesis and leaf sampling were conducted during September 2 to 11 when soil water contents based on mass were about 80% and air temperature averaged 18ºC. *P. koraiensis* and *Q. mongolica* canopy were divided into two parts, the upper one and the lower one. Sun leaves in the upper part were sampled within 5 m from the top of the canopy and the leaves in the lower canopy were sampled 7 m below the tree top for each tree species. The branches on the canopy surface from each species were cut at the same height. In addition, one-year-old and current-year needles of *P. koraiensis* were separately measured and sampled.

Photosynthesis measurement: Photosynthesis of *P. koraiensis* and *Q. mongolica* was measured with a portable photosynthesis system (*LI-6400*, *LI-COR*, *Inc.*, Lincoln, Nebraska, USA). The measurements were made between 08:00 and 11:00 h during September 2 to 11, 2009. Sun branches in the upper- and lower canopy of *P. koraiensis* and *Q. mongolica* were cut and put into water within 5 min to avoid embolism caused by water loss. And then fully expanded and mature *Q. mongolica* leaves, one-year-old and current-year *P. koraiensis* needles from three different whorls were used to measure photosynthesis, each three times. The response curves of net photosynthetic rate (P_N) to photosynthetic photon flux density (PPFD) (P_N/PPFD) were generated by increasing irradiance at 14 levels from 0 to 1,450 µmol m^{-2} s^{-1} (25; 50; 75; 100; 150; 250; 400; 550; 700; 850; 1,000; 1,150; 1,300; 1,450 µmol m^{-2} s^{-1}) provided by a LED light source at ambient CO_2 concentration of 375 µmol mol^{-1}. Leaf temperature, relative humidity and leaf-to-air vapour pressure deficit in the leaf chamber were maintained at approximately 20ºC, 50% and 0.8 kPa, respectively. Leaves were allowed to acclimate each PPFD for 1–3 min until values of photosynthetic rate and stomatal conductance were stable. Each light-response curve was typically completed within 30 min. Stomatal conductance during measurement period ranged from 0.15 to 0.30 mol m^{-2} s^{-1}.

According to the relationship between P_N and PPFD, light-response curves of *P. koraiensis* and *Q. mongolica* at different canopy positions were fitted by non-rectangular hyperbolic model:

$$P_N = \frac{\alpha\,\mathrm{PPFD} + P_{area} - \sqrt{(\alpha\,\mathrm{PPFD} + P_{area})^2 - 4\theta\,\alpha\,\mathrm{PPFD}\,P_{area}}}{2\theta} - R_D$$

where α is calculated from the initial slopes by linear regression using PPFD values below 200 µmol m^{-2} s^{-1}, θ is the convexity of the light response curve, and R_D is the dark respiration rate per unit area. LCP is calculated as the PPFD at which P_N equaled zero for each curve. The PPFD required for saturation of photosynthesis is estimated by calculating the PPFD at which $P_N = 0.9\ P_{area}$.

In our study, we compared light-saturated photosynthetic rate based on unit area (P_{area}) and unit dry mass ($P_{mass} = P_{area}$/LMA), while leaf chemistry determination was expressed by per unit dry mass to compare with other studies.

Leaf morphology: After photosynthetic measurement, *P. koraiensis* needles and *Q. mongolica* leaves were collected. Leaf area of *Q. mongolica* can be directly measured by leaf area meter (*LI-3100A*, *LI-COR Inc.*, Lincoln, NE, USA), while *P. koraiensis* needles were cut and closely put on the tape, and then measured by *LI-3100A*. The leaves were dried at 70ºC for at least 48 h and weighed. Leaf structural parameter LMA was expressed as the ratio of leaf dry mass (DM) to leaf area.

Leaf chemistry determination: The collected leaves after photosynthesis measurement were killed at 100ºC for 10 min in the oven in order to fix chemical components of leaves and maintain constant chemistry of leaves, and then dried at 70ºC for at least 48 h. C_m was measured with potassium dichromate and sulphuric acid (K_2CrO_7-H_2SO_4) oxidation in oil bath. Samples were digested with H_2SO_4 and H_2O_2, and then the supernatant was used to analyze N_m and P_m (Bao 2000). Chl_m was determined colorimetrically using the acetone and ethanol method with a spectrophotometer at 645 and 663 nm (Arnon 1949). PNUE was calculated by the following equation (Poorter and Evans 1998):

$$\mathrm{PNUE} = P_{area}/(1/14\ \mathrm{N} \times \mathrm{LMA}).$$

Statistical analysis: The normal distribution tests were carried out with K-S test. Effects of plant species (*P. koraiensis vs. Q. mongolica*) and canopy positions (upper and lower) on photosynthetic parameters, LMA, and leaf chemistry of *P. koraiensis* current-year needles and *Q. mongolica* leaves were tested using two-way *ANOVA*. We used independent-samples *t*-test to test the differences in photosynthetic parameters, LMA and leaf chemistry between upper and lower canopy positions for *Q. mongolica* and *P. koraiensis*, and between current-year and one-year-old needles for *P. koraiensis*. The correlation between photosynthetic parameters and leaf chemistry for both tree species were analyzed with the *Pearson* correlation. The statistical analysis was conducted with *SPSS 13.0* for Windows (*SPSS*, Chicago, USA).

Results

P_N/PPFD response curves: P_N of *P. koraiensis* and *Q. mongolica* increased linearly when PPFD was below 150 µmol m^{-2} s^{-1} (Fig. 1), and the increase rate of P_N in *Q. mongolica* leaves was relatively higher than *P. koraiensis* needles. P_N of both *P. koraiensis* needles and *Q. mongolica* leaves increased slowly when PPFD was over 500 and 400 µmol m^{-2} s^{-1}, respectively (Fig. 1).

Photosynthetic parameters at different canopy positions: In our study, P_N was expressed by two different ways for both tree species, based on leaf area (P_{area}) and leaf mass (P_{mass}). No statistically significant differences in P_{area}, P_{mass}, α, LCP, and LSP of *P. koraiensis* current-year needles and *Q. mongolica* leaves were found between upper canopy and lower canopy (Table 1). P_{area} and P_{mass} of current-year needles for *P. koraiensis* in the upper canopy was 11.4% [16.6 *vs*. 14.9 µmol(CO_2) m^{-2} s^{-1}] and 16.7% [0.07 *vs*. 0.06 µmol(CO_2) g^{-1} s^{-1}] higher than those in the lower canopy (Table 2). However, P_{area} and P_{mass} of one-year-old needles for *P. koraiensis* in the upper canopy were 32.5% [7.9 *vs*. 11.7 µmol(CO_2) m^{-2} s^{-1}] and 60% [0.02 *vs*. 0.05 µmol(CO_2) g^{-1} s^{-1}] lower than those in the lower canopy ($P<0.05$), respectively. α and LCP of one-year-old needles in the upper canopy were

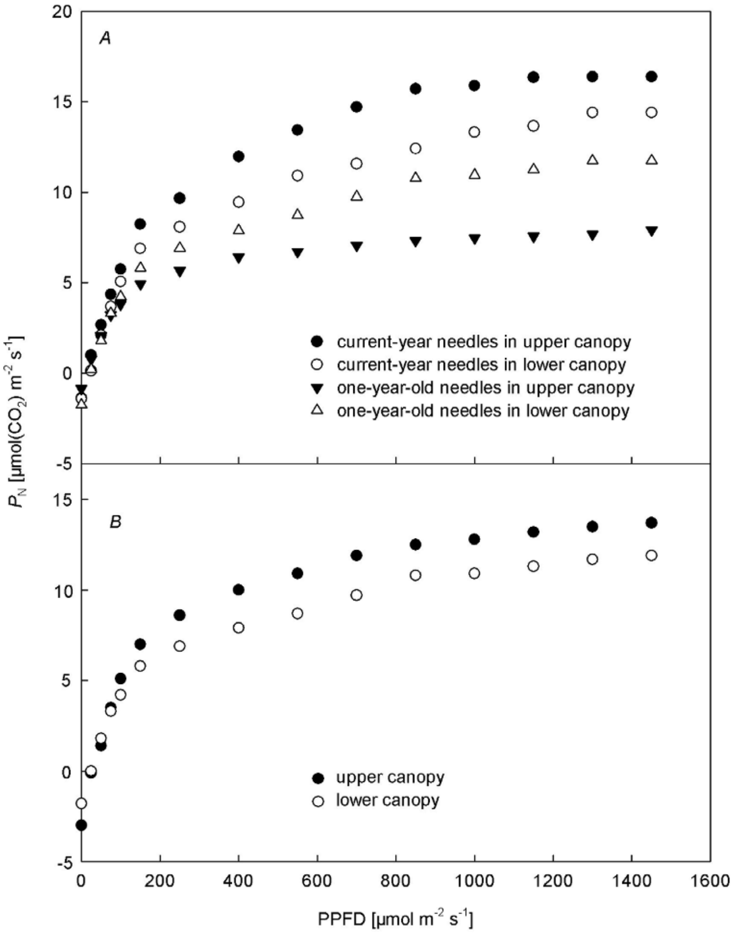

Fig. 1. Response curves of net photosynthetic rate (P_N) to photosynthetic photon flux density (PPFD) of *Pinus koraiensis* needles (*A*) and *Quercus mongolica* leaves (*B*) within different canopy positions.

Table 1. Effects of species (*Pinus koraiensis* and *Quercus mongolica*) and canopy position (upper and lower) on photosynthetic parameters of *Pinus koraiensis* current-year needles and *Quercus mongolica* leaves. Light-saturated photosynthetic rate per unit area (P_{area}), light-saturated photosynthetic rate per unit dry mass (P_{mass}), apparent quantum yield (α), light compensation point (LCP) and light saturation point (LSP). *F*- and *P*-values are given. $^*P<0.05$, $^{**}P<0.01$.

	P_{area}		P_{mass}		α		LCP		LSP	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species (S)	3.952	0.082	26.241	0.001^{**}	6.046	0.039^{*}	4.804	0.060	0.945	0.359
Position (P)	4.900	0.058	0.757	0.410	1.295	0.288	0.039	0.848	2.076	0.189
S × P	0.001	0.981	0.264	0.621	0.373	0.558	1.606	0.241	0.891	0.373

Table 2. Photosynthetic parameters estimated from response curves of net photosynthetic rate to photosynthetic photon flux density of *Pinus koraiensis* and *Quercus mongolica* leaves within different canopy positions. Light-saturated photosynthetic rate per unit area (P_{area}) and per unit dry mass (P_{mass}), apparent quantum yield (α), light compensation point (LCP) and light saturation point (LSP). Data are means ± SE, $n = 3$.

	Position	*P. koraiensis* Current-year needle	One-year-old needle	*Q. mongolica*
P_{area} [μmol(CO$_2$) m^{-2} s^{-1}]	Upper	16.6 ± 0.5	7.9 ± 0.1	14.1 ± 0.9
	Lower	14.9 ± 0.6	11.7 ± 0.4	12.4 ± 0.8
P_{mass} [μmol(CO$_2$) g^{-1} s^{-1}]	Upper	0.07 ± 0.01	0.02 ± 0.01	0.25 ± 0.04
	Lower	0.06 ± 0.01	0.05 ± 0.01	0.21 ± 0.04
α [mol mol^{-1}]	Upper	0.068 ± 0.001	0.045 ± 0.002	0.090 ± 0.007
	Lower	0.064 ± 0.003	0.056 ± 0.003	0.077 ± 0.012
LCP [μmol m^{-2} s^{-1}]	Upper	18.3 ± 2.7	12.1 ± 1.7	8.3 ± 0.9
	Lower	15.2 ± 4.0	27.5 ± 3.1	12.5 ± 3.0
LSP [μmol m^{-2} s^{-1}]	Upper	1,065.1 ± 49.0	1,144.4 ± 82.3	1,062.1 ± 122.7
	Lower	1,311.1 ± 104.0	1,354.8 ± 57.0	1,113.4 ± 119.5

Table 3. Effects of species (*Pinus koraiensis* and *Quercus mongolica*) and canopy position (upper and lower) on total nitrogen content per unit dry mass (N_m), total phosphorus content per unit dry mass (P_m), total carbon content per unit dry mass (C_m), chlorophyll content per unit dry mass (Chl_m), leaf dry mass per unit area (LMA) and photosynthetic nitrogen use efficiency (PNUE) of *Pinus koraiensis* current-year needles and *Quercus mongolica* leaves. *F*- and *P*-values are given. $^{**}P<0.01$, $^{***}P<0.001$.

	N_m		P_m		C_m		Chl_m		LMA		PNUE	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species (S)	0.165	0.695	0.089	0.773	22.980	0.001**	38.428	<0.001***	205.287	<0.001***	185.994	<0.001***
Position (P)	0.343	0.574	0.249	0.631	0.047	0.833	0.216	0.655	0.516	0.493	0.278	0.612
S × P	0.143	0.715	0.694	0.429	0.227	0.647	0.108	0.750	0.029	0.868	0.044	0.840

19.6% and 56.0% lower, respectively, than those in the lower canopy ($P<0.05$) (Table 2). Consistent with LSP of *P. koraiensis* current-year needles, LSP of one-year-old needles in the upper canopy was slightly lower than that in the lower canopy (1,144.4 *vs*. 1,354.8 μmol m^{-2} s^{-1}) (Tables 1, 2).

In contrast to LCP and LSP, P_{area}, P_{mass} and α of *Q. mongolica* leaves in the upper canopy were slightly higher compared with the lower canopy (Tables 1, 2).

Photosynthetic parameters: Significant differences in P_{mass} between *P. koraiensis* current-year needles and *Q. mongolica* leaves were observed (Table 1). P_{mass} of *P. koraiensis* were 72.0% in the upper canopy and 71.4% in the lower canopy lower than that of *Q. mongolica* ($P<0.01$) (Tables 1, 2). In the upper canopy, α and LCP of *Q. mongolica* leaves were 32.4% higher and 54.6% lower than those of *P. koraiensis* current-year needles ($P<0.05$), respectively; while in the lower canopy, no significant differences in α and LCP were found between *P. koraiensis* and *Q. mongolica*. There were no significant differences in P_{area} and LSP between *P. koraiensis* and *Q. mongolica* leaves for upper and lower canopy positions (Tables 1, 2).

Leaf chemistry and LMA at different canopy positions: No significant differences in N_m, P_m, C_m, Chl_m, LMA, and PNUE were observed between upper- and lower canopy for both tree species (Tables 3, 4). N_m, Chl_m, and PNUE of *P. koraiensis* current-year needles in the upper canopy were 4.2%, 12.5%, and 12.0% higher than those in the lower canopy, respectively; on the contrary, P_m, C_m, and LMA in the upper canopy were slightly lower than those in the lower canopy. N_m, C_m, Chl_m, and PNUE of one-year-old needles in the lower canopy were 28.4%, 3.5%, 11.1%, and 23.9% higher than those in the upper canopy, respectively. Almost no changes in P_m of *P. koraiensis* needles were found between canopy positions (Tables 3, 4).

Variation in N_m, Chl_m, and PNUE of *Q. mongolica* leaves within the crown profile showed the same trend as *P. koraiensis* needles. N_m, P_m, C_m, and Chl_m in the upper canopy were 19.2%, 37.5%, 2.4%, and 11.2% higher than those in the lower canopy, respectively, while LMA in the lower was 40% higher (Table 4).

Leaf chemistry and LMA: There were no differences in N_m and P_m between *P. koraiensis* and *Q. mongolica* ($P>0.05$, Table 3). *P. koraiensis* had higher C_m and LMA, but lower Chl_m and PNUE than *Q. mongolica* (Tables 3, 4). In the upper canopy, C_m and LMA of *P. koraiensis* current-year needles were 14.5% (497.7 *vs*. 434.6 mg g^{-1})

Table 4. Leaf chemistry and leaf dry mass per unit area (LMA) of *Pinus koraiensis* current-year needles and *Quercus mongolica* leaves within different canopy positions. Total nitrogen content per unit dry mass (N$_m$), total phosphorus content per unit dry mass (P$_m$), total carbon content per unit dry mass (C$_m$), chlorophyll content per unit dry mass (Chl$_m$), and photosynthetic nitrogen-use efficiency (PNUE). Data are means ± SE, *n* = 3.

	Position	*P. koraiensis*		*Q. mongolica*
		Current-year needle	One-year-old needle	
N$_m$ [mg g^{-1}]	Upper	12.4 ± 0.9	8.1 ± 1.5	14.3 ± 3.2
	Lower	11.9 ± 1.0	10.4 ± 1.2	12.0 ± 3.2
P$_m$ [mg g^{-1}]	Upper	1.6 ± 0.1	1.2 ± 0.2	2.2 ± 0.5
	Lower	1.7 ± 0.1	1.2 ± 0.1	1.6 ± 0.3
C$_m$ [mg g^{-1}]	Upper	497.7 ± 16.1	465.2 ± 10.4	434.6 ± 16.1
	Lower	501.5 ± 8.5	481.3 ± 12.8	424.4 ± 16.3
Chl$_m$ [mg g^{-1}]	Upper	0.45 ± 0.07	0.27 ± 0.04	2.59 ± 0.47
	Lower	0.40 ± 0.04	0.30 ± 0.02	2.33 ± 0.46
LMA [g cm^{-2}]	Upper	0.022 ± 0.002	0.029 ± 0.003	0.005 ± 0.001
	Lower	0.023 ± 0.001	0.025 ± 0.001	0.007 ± 0.001
PNUE [μmol(CO$_2$) mol¯1(N) s^{-1}]	Upper	86.0 ± 3.4	50.2 ± 4.3	255.2 ± 18.1
	Lower	76.8 ± 1.6	62.2 ± 4.0	251.1 ± 17.1

Table 5. Effects of needle age on photosynthetic parameters, leaf chemistry, and leaf dry mass per unit area (LMA) of *Pinus koraiensis* needles. Light-saturated photosynthetic rate per unit area (P_{area}), and per unit dry mass (P_{mass}), apparent quantum yield (α), light compensation point (LCP), light saturation point (LSP), total nitrogen content per unit dry mass (N$_m$), total phosphorus content per unit dry mass (P$_m$), total carbon content per unit dry mass (C$_m$), chlorophyll content per unit dry mass (Chl$_m$), and photosynthetic nitrogen-use efficiency (PNUE). The mean values within the same row sharing the *different small letters* are significantly different ($P<0.05$). Data are means ± SE, *n* = 3.

	Current-year needles	One-year-old needles
P_{area} [μmol(CO$_2$) m^{-2} s^{-1}]	15.8 ± 0.5^a	9.8 ± 0.9^b
P_{mass}[μmol(CO$_2$) g^{-1} s^{-1}]	0.07 ± 0.01^a	0.04 ± 0.01^b
α [mol mol^{-1}]	0.066 ± 0.002^a	0.051 ± 0.003^b
LCP [μmol m^{-2} s^{-1}]	16.7 ± 2.3^a	19.8 ± 3.8^a
LSP [μmol m^{-2} s^{-1}]	1,188.1 ± 75.3^a	1,249.6 ± 64.9^a
N$_m$ [mg g^{-1}]	12.2 ± 0.6^a	9.3 ± 1.0^b
P$_m$ [mg g^{-1}]	1.7 ± 0.1^a	1.2 ± 0.1^b
C$_m$ [mg g^{-1}]	499.6 ± 8.2^a	473.3 ± 8.2^a
Chl$_m$ [mg g^{-1}]	0.42 ± 0.04^a	0.29 ± 0.02^b
LMA [g cm^{-2}]	0.022 ± 0.001^a	0.027 ± 0.002^b
PNUE [μmol(CO$_2$) mol¯1(N) s^{-1}]	81.4 ± 2.7^a	56.2 ± 3.7^b

Table 6. *Pearson*'s correlation coefficients P_{mass}, N$_m$, P$_m$, LMA, Chl$_m$, and PNUE of *P. koraiensis* needles with different age classes. Light-saturated photosynthetic rate per unit dry mass (P_{mass}), total nitrogen content per unit dry mass (N$_m$), total phosphorus content per unit dry mass (P$_m$), leaf dry mass per unit area (LMA), chlorophyll content per unit dry mass (Chl$_m$), photosynthetic nitrogen-use efficiency (PNUE). * $P<0.05$, ** $P<0.01$.

Needle age		P_{mass}	N$_m$	P$_m$	LMA	Chl$_m$	PNUE
Current-year	P_{mass}	1	0.883*	0.668*	–0.966**	0.954**	0.739
	N$_m$		1	0.793	–0.928**	0.879*	0.339
	P$_m$			1	–0.837*	0.845*	0.175
	LMA				1	–0.992**	–0.596
	Chl$_m$					1	0.639
One-year-old	P_{mass}	1	0.823*	0.486	–0.740	0.594	0.384
	N$_m$		1	0.744	–0.892*	0.817*	–0.207
	P$_m$			1	–0.842*	0.970**	–0.363
	LMA				1	–0.827*	0.189
	Chl$_m$					1	–0.284

Table 7. *Pearson*'s correlation coefficients among P_{mass}, N_m, P_m, LMA, Chl_m, and PNUE of *Quercus mongolica* leaves. Light-saturated photosynthetic rate per unit dry mass (P_{mass}), total nitrogen content per unit dry mass (N_m), total phosphorus content per unit dry mass (P_m), leaf dry mass per unit area (LMA), chlorophyll content per unit dry mass (Chl_m), photosynthetic nitrogen-use efficiency (PNUE). * $P<0.05$, ** $P<0.01$.

	P_{mass}	N_m	P_m	LMA	Chl_m	PNUE
P_{mass}	1	0.979^{**}	0.984^{**}	-0.948^{*}	0.968^{**}	-0.673
N_m		1	0.990^{**}	-0.904^{**}	0.998^{**}	-0.805
P_m			1	-0.922^{*}	0.987^{**}	-0.771
LMA				1	-0.899^{**}	0.565
Chl_m					1	-0.836^{*}

and 340% (0.022 *vs*. 0.005 g cm^{-2}) higher than those of *Q. mongolica* leaves; in the lower canopy, C_m (501.5 *vs*. 424.4 mg g^{-1}) and LMA (0.023 *vs*. 0.007 g cm^{-2}) of *P. koraiensis* were 18.2% and 228.6% higher than those of *Q. mongolica*, respectively. Chl_m and PNUE of *Q. mongolica* leaves were 475.6% (2.59 *vs*. 0.45 mg g^{-1}) and 196.7% [251.1 *vs*. 86.0 μmol(CO_2) mol^{-1}(N) s^{-1}] in the upper canopy, 482.5% (2.33 *vs*. 0.40 mg g^{-1}) and 218.8% [251.1 *vs*. 76.8 μmol(CO_2) mol^{-1}(N) s^{-1}] in the lower canopy higher than *P. koraiensis* ($P<0.001$) (Tables 3, 4).

Effects of needle age on photosynthetic parameters, leaf chemistry, and LMA of *P. koraiensis*: There were significant effects of needle age on P_{area}, P_{mass}, α, N_m, P_m, LMA, Chl_m, and PNUE, but no differences in LCP, LSP and C_m between one-year-old and current-year needles were observed (Table 5). P_{area}, P_{mass}, α, N_m, P_m, Chl_m, and PNUE of current-year needles were 61.2%, 75.0%, 29.4%, 31.2%, 41.7%, 44.8%, and 44.8% higher than those of one-year-old needles ($P<0.05$), while LMA was 18.5% lower than that of one-year-old needles ($P<0.05$) (Table 5).

Relationship among photosynthetic parameters, leaf chemistry, and LMA: P_{mass} was positively correlated with N_m, P_m, and Chl_m, and LMA was negative to P_{mass}, N_m, P_m, and Chl_m for both *P. koraiensis* current-year needles and *Q. mongolica* leaves (Tables 6, 7). The correlation coefficients between P_{mass} and N_m, P_m, Chl_m, and LMA of current-year needles were higher than those of one-year-old needles of *P. koraiensis*. The correlation coefficients of P_{mass}–N_m, P_{mass}–P_m, P_{mass}–Chl_m of *Q. mongolica* were relatively higher than those of *P. koraiensis* needles, but correlation coefficients of P_{mass}–LMA showed opposite trend.

Discussion

Effects of canopy position on photosynthesis, leaf chemistry, and LMA: A forest has vertical microenvironmental gradients (Koike *et al.* 2001). The variations in temperature and light radiation within canopy influence leaf photosynthesis and other physiological characteristics, such as leaf area and biomass accumulation (Koike *et al.* 2001, Liao *et al.* 2005). Light utilization is a primary factor determining ecosystem productivity, which is a function of light interception by the plant canopy and the response of photosynthesis to irradiance (Lewis *et al.* 2000). Some studies based on leaf level showed that P_{area} (P_{mass}) within the crowns of individual coniferous and broad-leaved trees increased with tree height, ranging from 10% to 290% (averaging 50%) (Ellsworth and Reich 1993, Bond *et al.* 1999). Inconsistent with our hypothesis 1, no significant differences in P_{area} and P_{mass} between upper- and lower canopy for *P. koraiensis* current-year needles and *Q. mongolica* leaves were found (Table 2). Similar results were also found in previous studies. For example, P_{area} of *Liquidambar styraciflua* L. (Herrick and Thomas 1999), *Dacrydium cupressinum* Lamb., *Meterosideros umbellate* Cav. and *Weinmannia racemosa* L.f. (Tissue *et al.* 2005), P_{mass} of *Acer saccharum* Marsh. (Ellsworth and Reich 1993), *Pinus ponderosa* (Laws.), *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg (Bond *et al.* 1999) were similar between upper- and lower canopy. In addition, α and LCP of *P. koraiensis* current-year needles and *Q. mongolica* leaves showed little response to light gradients, consistent with previous studies in *Quercus coccinea* Muenchh and *Quercus prinus* L. (Sullivan *et al.* 1996), *Pinus contorta* Dougl. ssp. *latifolia* Engelm. (Schoettle and Smith 1998), *Pinus sylvestris* Linn. (Palmroth and Hari 2001), *Pinus elliottii* var. *elliottii* Engelm. and *Pinus Taeda* L. (McGarvey *et al.* 2004).

At the leaf level, LMA is one of the important parameters to predict photosynthetic capacity for a wide range of species (Reich *et al.* 1997). In our study, LMA of *P. koraiensis* and *Q. mongolica* was not affected by canopy position (Table 4). Similar results were observed in *L. styraciflua* (Herrick and Thomas 1999). Low N and P contents are known to reduce photosynthesis by limiting carboxylation activity (Loustau *et al.* 1999). Whether the distribution of leaf N and P contents is influenced by canopy position is still uncertain. Our results that the distribution of N and P contents in the upper canopy did not differ from that in the lower canopy position for *P. koraiensis* and *Q. mongolica* were consistent with many previous studies based on *Fagus sylvatica* L. (Jayasekera and Schleser 1988), *A. saccharum* (Ellsworth and Reich, 1993), *Quercus petraea* (Matt.) Liebl and *Picea sitchensis* (Bong.) Carr (Meir *et al.* 2002), *Betula nana* L., *B. pubescens* Ehrh and *B. pendula* Roth (Niinemets *et al.* 2002), *D.cupressinum*, *M. umbellata*, *W.racemosa* and *Quintinia acutifolia* Kirk (Tissue *et al.* 2005) and *Hesse Fagus sylvatica* L. (Davi *et al.* 2008).

The allocation of leaf chemistry, LMA and photosynthetic capacity within canopies is a function of metabolic requirements (Kull and Niinemets 1998) and ecological factors (Hollinger 1996). The even distribution of leaf chemistry, LMA, and photosynthetic capacity within canopy positions for *P. koraiensis* current-year needles and *Q. mongolica* leaves may be related to the limitations of photosynthesis in the upper canopy of old stands due to the ontogenetic aging effects (Fredericksen *et al.* 1996) or hydraulic limitations (Yoder *et al.* 1994). In addition, acclimation strategies to lower light should also be taken into account. For example, decrease of leaf size and increase of leaf inclination angle can permit deeper penetration of light within the canopy and increase light-use ability with available resources (Leuning *et al.* 1991, Lewis *et al.* 2000), which indicated that leaves in the lower canopy could increase light-capturing capabilities through physiological or morphological changes (Björkman 1981), just like *A. saccharum* enhanced light capture in lower light with higher N_m (Niinemets and Tenhunen 1997). Thus, Tissue *et al.* (2005) found lower light intensity in lower canopy did not generally affect the biochemical or photosynthetic capacity of the trees.

Species-dependent and -independent responses of photosynthesis, LMA, and leaf chemistry: Partly consistent with our hypothesis 2, P_{mass}, α, C_m, Chl_m, LMA and PNUE were highly species-specific. α is closely related with light response characteristics of species (Meng *et al.* 2007). The higher α may be beneficial for *Q. mongolica* to use relatively weak light in the forest. Similar N and P contents between *P. koraiensis* current-year needles and *Q. mongolica* leaves indicated that native dominant mature species had developed similar survival strategies to some extent, which was consistent with studies based on the same environments as the present study (Sun and Chen 2001). Species with long-lived leaves generally have low P_{mass} but dense and thick leaves (high LMA) (Reich *et al.* 1998). The observed difference in P_{mass} between *Q. mongolica* and *P. koraiensis* was a direct consequence of variation in LMA rather than N_m (Field *et al.* 1983, Reich *et al.* 1995). In addition, *P. koraiensis* had higher C_m compared with *Q. mongolica*. Thus, expression on photosynthesis based on mass is related to leaf construction and reflecting morphology characteristics (Givnish 1988).

PNUE is related to photosynthetic capacity, leaf morphology, LMA, and N content. N partitioning between photosynthetic and nonphotosynthetic structures might explain the difference in PNUE between species (Field and Mooney 1986, Hikosaka and Hirose 2000, Hikosaka 2004). Generally, fast-growing species with thicker and denser leaves (higher LMA) may have lower PNUE (Field and Mooney 1986, Reich *et al.* 1992), such as *Cecropia*, *Quercus* and *Piper* species (Reich *et al.* 1998). Leaf thickness, palisade and parenchyma cell sizes, and the proportion of cell wall to cell volume may influence N partitioning (Loomis 1997). In our study, PNUE of *P. koraiensis* was lower than that of *Q. mongolica*, consistent with the study based on other tree species (Reich *et al.* 1995).

Effects of needle age on photosynthesis, LMA, and leaf chemistry for *P. koraiensis*: Leaf age directly affects physiological characteristics (Reich *et al.* 1992). For instance, species with longer lifespan usually have relatively lower P_{area}, P_{mass}, and N content. However, longer life span can compensate their growth cost under the conditions of lower photosynthesis and N content (Reich *et al.* 1997, 1999, Wright *et al.* 2004, Hikosaka 2005). Our third hypothesis was supported that needle age significantly affected photosynthetic parameters, LMA and chemistry, except LCP, LSP and C_m. Similarly to *P. koraiensis* in the present study, net photosynthetic rate of *P. contorta, P. sylvestris*, *Pinus pinaster* Aiton and *Pinus densiflora* Sieb. *et* Zucc., decreased with needle age (Mediavilla and Escudero 2003, Niinemets *et al.* 2006, Han *et al.* 2008). Tissue *et al.* (2001) also found an increased demand of photosynthate for supporting rapid growth and development of current-year needles may result in higher P_{area} in current-year needles.

Similarly to P_{area}, N_m, P_m, Chl_m, and PNUE of current-year needles were also significantly higher than one-year-old needles (Table 5). The previous studies showed leaf N content decreased with leaf age (Reich *et al.* 1991, Luo *et al.* 2005, Han *et al.* 2008). Further, the decrease in N_m may lead to a significant reduction in P_{area} (Jach and Ceulemans 2000). Differently from leaf chemistry and photosynthesis, LMA of *P. koraiensis* increased with needle age (Table 5), which was consistent with Tissue *et al.* (2001) and Wright and Westoby (2002). Thus, the interaction of photosynthetic rate, LMA, and N_m resulted in a lower PNUE in *P. koraiensis* one-year-old needles.

Relationships among photosynthesis, leaf chemistry, and LMA: N_m and LMA are important parameters in evaluating photosynthesis (Field and Mooney 1986, Evans 1989, Niinemets *et al.* 2002, Hikosaka 2005). Positive correlation between P_N and N content, and negative correlation between P_N and LMA have been found in many species (Field and Mooney 1986, Evans 1989, Reich *et al.* 1997, Niinemets 2001, Wright *et al.* 2004), such as *Eucalyptus globulus* (Sheriff and Nambiar 1991) and E*ucalyptus grandis* W. Hill ex Maiden (Leuning *et al.* 1991). Consistently with hypothesis 4, *P. koraiensis* and *Q. mongolica* also showed similar results mentioned above between P_{mass} and N_m and between P_{mass} and LMA (Tables 6, 7).

Conclusions: *P. koraiensis* and *Q. mongolica* are typically dominant species in broadleaved Korean pine forest in Changbai Mountain area. P_{area}, P_{mass}, α, LCP, and LSP of *P. koraiensis* current-year-needles and *Q. mongolica* leaves showed little responses to light gradients between canopy positions; while in *P. koraiensis* one-year-old needles, significant differences in P_{area}, P_{mass}, α, and LCP between canopy positions were observed. Leaf chemistry of both two species didn't vary greatly between canopy positions. Both tree species grown under the same soil nutrition conditions have similar leaf N and P contents although *P. koraiensis* has significantly higher LMA than *Q. mongolica*. C_m of *P. koraiensis* differed greatly from that of *Q. mongolica* mainly due to inherent growth characteristics and production distribution of photosynthesis, such as higher proportion of carbon conserved as structural substances (*i.e*., lignin and tannin) (Coste *et al*. 2005). For conifers, it is necessary to separate needle age effects due to different physiological activities between different age classes.

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