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Photosynthetic characteristics of dominant tree species and canopy in the broadleaved Korean pine forest of Changbai Mountains

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Abstract Based on the light-photosynthesis response measurement at leaf level, combined with over- and under-canopy eddy covariance measurements, research on photosynthetic characteristics of single trees and forest canopy was conducted. The relationship between light intensity and photosynthetic rates for leaves and canopy can be well fitted by a non-rectangular hyperbola model. Mongolian oak presented a high light compensation point, L_{cp} (28 μmol·m^{-2}·s^{-1}), a light saturation point L_{sp} (>1800 μmol·m^{-2}·s^{-1}), and a maximal net photosynthetic rate P_{max} (9.96 μmol·m^{-2}·s^{-1}), which suggest that it is a typical heliophilous plant. Mono maple presented the highest apparent quantum efficiency α (0.066) but the lowest, L_{cp} (16 μmol·m^{-2}·s^{-1}), L_{sp} (≈800 μmol·m^{-2}·s^{-1}), and P_{max} (4.51 μmol·m^{-2}·s^{-1}), which suggest that it is heliophilous plant. Korean pine showed the lowest α value but a higher P_{max}, which suggest that it is a semi-heliophilous plant. At the canopy level, the values of both α and P_{max} approached the upper limit of reported values in temperate forests, while L_{cp} was within the lower limit. Canopy photosynthetic characteristics were well consistent with those of leaves. Both showed a high ability to photosynthesize. However, environmental stresses, especially high vapor pressure deficits, could significantly reduce the photosynthetic ability of leaves and canopy.

Keywords: photosynthesis, light response curve, broadleaved Korean pine forest, eddy covariance method.

Photosynthesis is the dominant way that green plants take carbon dioxide from the air and convert it to living matter. The transformations of energy and mass in an ecosystem begin with photosynthetic activity. The major aggregate of terrestrial vegetation is forest, where photosynthetic capacity is a key factor of carbon fixation capacity[1]. Photosynthetic parameters with biological significance, derived from field data, can improve understanding of photosynthetic mechanisms. These parameters are also significant for upscaling field measurements. For example, through combining the photosynthetic parameters of leaves and canopy with light models and leaf area indices, the intensity of biome photosynthesis can be deduced, and then ecosystem carbon sink/source intensity can be obtained through modeling.

Research on forest productivity, as well as its response to climate changes based upon photosynthesis research, is always valuable in the study of tree physiology and carbon cycles[2]. In recent years, a lot of researches have been undertaken on tree photosynthetic characteristics at the leaf level, including comparisons of different functional types, tree species and leaf forms[3−5]. However, there are few studies of photosynthetic assimilation characteristics at canopy level, because it is hard to measure over- and under-canopy simultaneously. In China, most research on plant photosynthesis has focused on crops, grasses, tree seedlings and other short vegetation[6−10]. Studies of tall plants are few, especially Korean pine, Mongolian oak, Tilia tuan, and other typical northern species.

The mixed forest of broadleaf species and Korean pine on Changbai Mountain, as a typical forest ecosystem of Northeast China, has important significance for the balance of carbon budgets in the country's northern region. Past studies suggest that this forest is acting as a carbon sink[11,12]. However, the understanding of carbon exchange mechanisms, as well as process modeling, have fallen short because of the lack of some eco-physiological parameters for trees. For example, Wang *et al.* [13] and Ren *et al.* [14] simulated the exchange of carbon dioxide, water vapor and heat between forest and atmosphere by means of a process-based BEPS model and a photosynthesis-transpiration coupling model, respectively. But the accuracy of their modeling results suffered due to the lack of field-measured data, for which they compensated by using experienced values and precedents from the literature for certain photosynthetic parameters that are sensitive to model results, such as dark respiration rates and maximal stomatal conductance.

In the past decade, the eddy covariance method based on turbulence theory has emerged as an important tool for evaluating fluxes of mass and energy between forest and atmosphere. In recent years, the method has been introduced in China. Because of its high precision and high resolution, the eddy covariance method is being widely applied to the study of carbon dioxide and water vapor exchange in forests, farmlands and grassland ecosystems[15,16].

As a part of the ChinaFLUX (an independent regional network of the global FLUXNET network, established in 2003 based on the standard measurement methodology of FLUXNET), two sets of eddy covariance systems were mounted over and under the canopy of the broadleaved Korean pine forest on Changbai Mountain. These provide a valuable platform for researches of photosynthetic characteristics at canopy level. Based on field-measured flux data in the growing season, combined with measurements of photosynthetic parameters at leaf level, the objective of this paper is to analyze the relationship between photosynthesis and light intensity for leaves and canopy, respectively, and to explore the characteristics of light-response parameters, including apparent quantum efficiency, dark respiration rate, light compensation point, light saturation point, and maximal photosynthetic rate. This research can improve current understanding of the eco-physiological characteristics of tree species in northern China and provide a valuable data set for evaluating carbon sink/source, as well as productivity simulations for forests in North China.

1 Materials and methods

1.1 Site description

The experimental site is located within the mixed forest of broadleaf and Korean pine, Northeastern China (42°24′N, 128°6′E), in a temperate continental climatic zone that is monsoon influenced. Its annual average precipitation is 695 mm; annual sunshine duration is 2271−2503 h. The terrain surrounding the observation tower is flat, with the shortest fetch about 400 m. Surrounding vegetation includes a mature, natural stand of Korean pine (*Pinus koraiensis*), Tilia tuan (*Tilia amurensis*), Mongolian oak (*Quercus mongolica*), Mono maple (*Acer mono*), and other interspersed deciduous species. The soil is classified as upland dark brown forest soil. The mean canopy height is about 26 m, and its maximum Leaf Area Index (*LAI*) is 6.0 $m^2 \cdot m^{-2}$. The above-ground biomass storage is 380 $m^3 \cdot hm^{-2}$. Stand density is 560 $stems \cdot hm^{-2}$ (stem diameter >8 cm). During the period of measurement, the forest phenology was characterized by a May-September growing season.

1.2 Experimental methods

(i) Eddy covariance measurement. Two sets of open-path eddy covariance systems were installed at 40 and 2.5 m height of a 62 m meteorological tower, to measure the fluxes both over and under the canopy. Wind vector and temperature were measured using a three-dimensional sonic anemometer (CSAT3, Campbell Inc., USA). CO_2 concentration fluctuations were measured using an open-path, infrared gas analyzer (Li-7500, Li-Cor Inc., USA). The sampling frequency was 10 Hz. Flux data were stored in a CR5000 data logger (Campbell Inc., USA). Additionally, a micrometeorology observational system was installed on the tower to measure metrological factors synchronously. The sampling frequency was 0.5 Hz, and 30-min averages of wind speeds, temperature, photosynthetic active radiation, etc., were stored in a CR10X-TD datalogger (Campbell Inc., USA). Additionally, *LAI* was measured at 4—10 d intervals during the growing season with a canopy analyzer (Li2000, LI-Cor Inc., USA).

(ii) Measurements of leaf light response. During the 2004 growing season, light-photosynthesis responses were measured biweekly from 07:00 to 12:00, using a Li-Cor 6400 (Li-Cor Inc., USA) portable photosynthetic analyzer. In the experiment, the CO_2 concentration was controlled at 400±5 $\mu mol \cdot mol^{-1}$ with a plastic gas bag. Air temperature was maintained at 25℃, which is considered optimal for plants in temperate regions, and relative humidity was controlled at 70%±5%. The various light intensities (0 — 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) were provided by a Li-6400-02B red/blue LED source. Measurements were taken after 3—5 min of light exposure. The sample trees were mature Korean pine, Tilia tuan, Mongolian oak and Mono maple. Leaf gas exchange measurements were made on 3 cm-diameter branches cut from trees. Branches were selected from the top and middle levels of crowns. There were three replications for each crown level's leaves. During measurement, the branches were wrapped with water-soaked cotton to avoid water loss.

(iii) Data processing. Corrections including spike removal, detrending, planar-fit coordinate transformations and frequency response limitations were made for eddy flux data; the processes and results have been discussed in detail in another paper[17]. The net photosynthetic rates were calculated as the difference of CO_2 fluxes between over- and under-canopy. The relationships between light and photosynthetic rates for leaves and whole canopy were expressed with a non-rectangular hyperbola model[18]:

$$\theta P^2 - P(a \times PAR + P_{\max}) + a \times P_{\max} \times PAR = 0, \quad (1)$$

where P is photosynthetic rate; α is apparent quantum efficiency, i.e. the slope of light-response curve under low-light conditions; and $P_{\max}$ is the maximal net photosynthetic rate. The latter two are both significant parameters denoting light-response characteristics. PAR is the incoming photosynthetically active radiation on leaves or canopy, θ is the convexity in fitted curve ($0 \leqslant \theta \leqslant 1$). When $\theta = 0$, eq. (1) can be simplified as a rectangular hyperbola model; when $\theta \neq 0$, because

$$P_n = P - R_d, \quad (2)$$

P_n can be calculated as eq. (3), where R_d is dark respiration rate, P_n is net photosynthetic rate.

$$P_n = \frac{a \times PAR + P_{\max} - \sqrt{(a \times PAR + P_{\max})^2 - 4\theta(a \times P_{\max} \times PAR)}}{2\theta} - R_d. \quad (3)$$

The light-photosynthesis response curves were fitted using least square method. To simplify the iteration calculation, the initial value of θ was set at 0.05, and step at 0.05. The optimal value of θ was selected according to values of residuals and coefficients of determination R^2. L_{cp} is the light compensation point calculated as $P_n = 0$, and L_{sp} is the light saturation point calculated with P_n as maximum.

2 Results and analyses

2.1 Photosynthetic characteristics of leaves

The photosynthetic parameters of leaves, α, $P_{\max}$, R_d, and L_{cp}, as well as light-response curves, were obtained by fitting data sets of P_n and PAR, using a non-rectangular hyperbola model. Fig. 1 shows the measured data and fitted curves for four tree species during the peak growing season (June to August). It illustrates that the non-rectangular hyperbola model fitted the light-response curves well. When no light was available, the leaves presented CO_2 emission. With increasing light intensity, Mono maple reached L_{cp} first, then Tilia tuan and Korean pine in turn. Mongolian oak showed the highest L_{cp}. In low light conditions, leaf P_n nearly increased with *PAR* in a linear model. But when *PAR* exceeded a certain intensity (about 300 − 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$), the increase rate slowed down. When *PAR* reached 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the values of P_n for all tree species exceeded 80% of the respective maximal net photosynthetic rate P_{max}. After the P_n for Mono maple reached its maximum, at $PAR > 800$ $\mu mol \cdot m^{-2} \cdot s^{-1}$, it showed a clearly downward tend. Therefore, the L_{sp} value for Mono maple should be around 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The L_{sp} values for Tilia tuan and Korean pine are about 1000 and 1400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. But there was no obvious peak for P_n of Mongolian oak even when *PAR* reached 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which indicated that the L_{sp} value for Mongolian oak should be greater than 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

The fitted parameters derived from light-response curves show a remarkable difference for P_{max} (ranging from 4.51 to 9.96 $\mu mol \cdot m^{-2} \cdot s^{-1}$) among the studied tree species. The P_{max} values for Korean pine and Mongolian oak were generally high, and the maximum for the latter was up to 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Mono maple showed the highest apparent quantum efficiency α, but the lowest L_{cp} (no more than half of Mongolian oak). The α value for Mongolian oak was the lowest among three broadleaf tree species, but it was significantly higher than that of Korean pine. Tilia tuan and Mono maple presented similar α values. The dark respiration rates for studied tree species varied between 0.70−1.79 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Mono maple and Korean pine presented the minimum and maximum, respectively. It is worthwhile to note that the R_d values for broadleaf trees were all within 20% of P_{max}, but that Korean pine was remarkably higher.

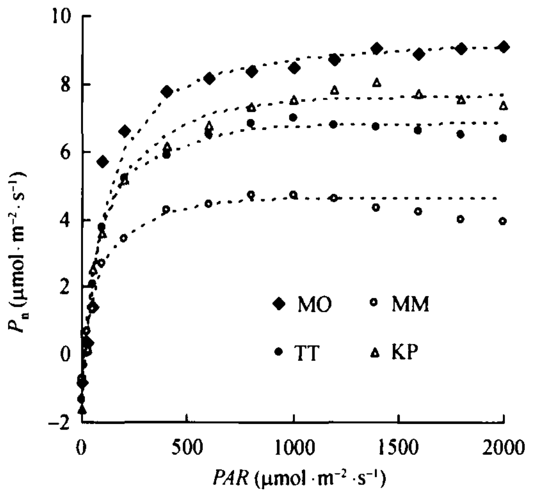

Fig. 1. Light response curves for dominant tree species in the mixed forest of broadleaved Korean pine during the peak growing season. MM, Mono maple; MO, Mongolian oak; TT, Tilia tuan; KP, Korean pine.

The seasonal variations of photosynthetic parameters are shown in Table 1. Both α and P_{max} tend to increase first and then decrease, from early to late growing seasons, but L_{cp} presents a reverse tend. The smallest variation range of photosynthetic parameters is that of Korean pine; even in early and late growing season, its leaves retained a high P_{max}. This may be because, relative to broadleaf species, indeciduous pine needles sprout early but go dormant late. Additionally, R_d showed the smallest seasonal variations relative to other parameters; no significant conclusion could be derived from these variations.

2.2 *Photosynthetic characteristics at canopy level*

Fig. 2 shows the diurnal evolutions of P_n, *PAR*, and vapor pressure deficits (*VPD*). The daily course of P_n roughly presented a single-peak pattern. When incoming *PAR* of the canopy increased to 30−50 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the values of P_n changed from negative to positive, i.e., canopy became carbon sink. The CO_2 assimilation rates increased with the increase of *PAR*. However, most of the maximal photosynthetic rates appeared at 10:00−11:00, rather than at noon with the

Table 1 Seasonal variations of photosynthetic parameters for leaves

Tree species	Early growing season (May)				Peak growing season (Jun to Aug)				Late growing season (Sept)			
	α	P_{max}	R_d	L_{cp}	α	P_{max}	R_d	L_{cp}	α	P_{max}	R_d	L_{cp}
Korean pine	0.030	4.92	1.47	27	0.038	7.64	1.79	23	0.029	4.63	1.71	30
Tilia tuan	0.039	3.55	1.05	25	0.061	6.92	1.12	19	0.030	3.67	1.18	28
Mono maple	0.037	2.86	0.61	20	0.066	4.51	0.70	16	0.039	2.37	0.69	22
Mongolian oak	0.031	4.89	1.13	32	0.051	9.96	1.55	28	0.027	4.05	1.47	39

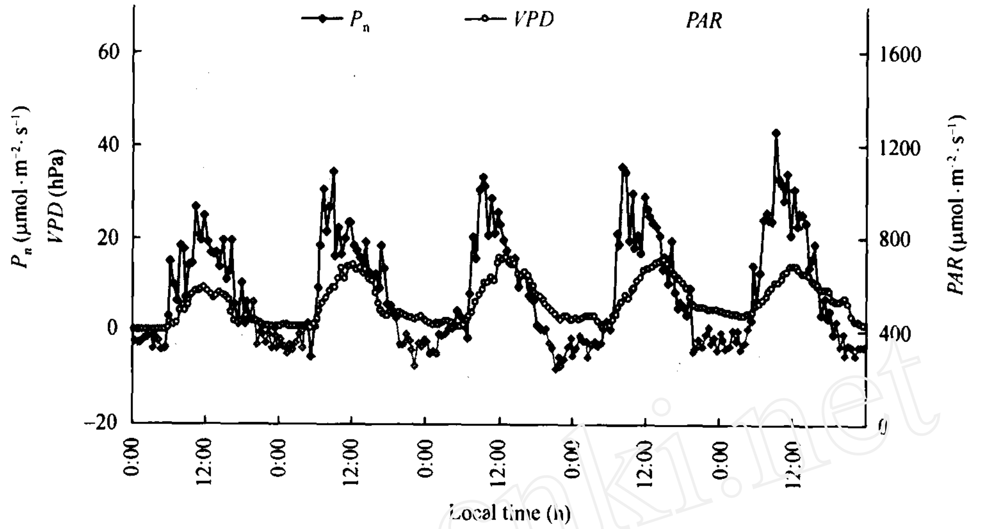

Fig. 2. Diurnal variations of P_n, *VPD* and *PAR* at canopy (13—17 July 2004).

highest light intensity. Moreover, the photosynthetic rates in the morning were obviously higher than in the afternoon, though the *PAR* values were the same. Take the observed data on 14 July as example: the maximal P_n (37 μmol·m^{-2}·s^{-1}) appeared at 10:30, when *PAR* was 1055 μmol·m^{-2}·s^{-1}. But at 1500, P_n declined to 16 μmol·m^{-2}·s^{-1}, though *PAR* was much higher for the former. The meteorological data suggested that the latter had a much higher *VPD* (13.2 hPa) relative to the former (6.3 hPa). Additionally, the evaportranspiration rates in the afternoon decreased 40% on average compared to the morning, but there was no clear decrease of soil water supply. This indicated that canopy incurred water stress with long-term exposure to strong sunshine. This key factor caused the reduction of canopy photosynthetic capacity.

Fig. 3 shows the relationships between P_n and *PAR* at different stages of the growing season (May, July and September). It can be seen that the net photosynthetic capacity was greatest in the peak growing season and smallest in the late growing season. The photosynthetic rates were low when *PAR* values were small, and the respiration rates were greater than that of photosynthesis. Then P_n increased with *PAR* increased, and the canopy accordingly became a carbon sink. The P_n reached its maximum before *PAR*, and then presented a downward trend although *PAR* continued to increase. This phenomenon was more obvious in droughty June, when the photosynthetic rates significantly deceased as *PAR* exceeded 1000 μmol·m^{-2}·s^{-1}. Fig. 3 also shows that the light saturation range was roughly 1000—1300 μmol·m^{-2}·s^{-1}, but

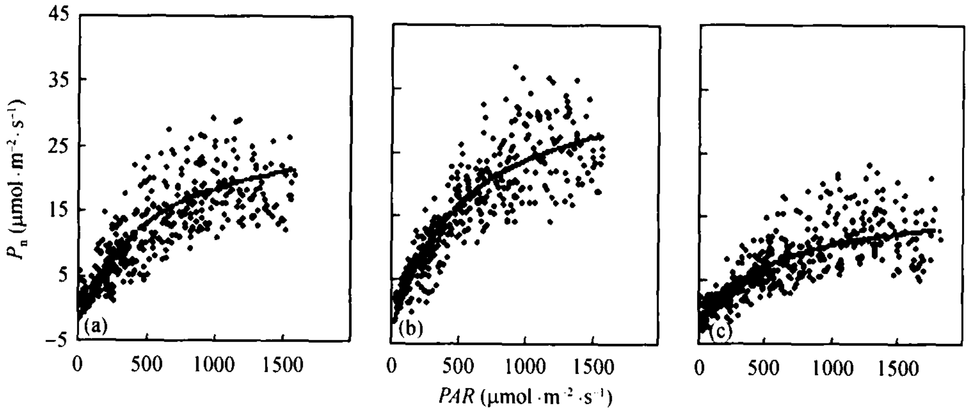

Fig. 3. Light response of canopy in different stages of the growing season. (a) Early growing season; (b) middle growing season; (c) late growing season.

there was no clear L_{sp}. This indicates that other environmental factors besides light influence canopy photosynthesis.

When VPD effects on canopy light response were analyzed using the peak growing-season data (see Fig. 4), the canopy P_n showed a rough, linear increase with the increase of PAR at low VPD levels (<8 hPa). No obvious light saturation phenomenon occurred even when PAR increased to more than 1300 μmol·m^{-2}·s^{-1} and the maximal P_n was higher than 40 μmol·m^{-2}·s^{-1}. When VPD increased to the range of 8—15 hPa, even though canopy P_n rose with the increase of PAR, there was a clear declining trend with P_n with PAR in excess of 1000 μmol·m^{-2}·s^{-1}. When VPD>15 hPa, although light conditions were similar, canopy photosynthetic rates were significantly low, with the maximal P_n no higher than 30 μmol·m^{-2}·s^{-1}.

Light-response curves were plotted to daytime (PAR > 5 μmol·m^{-2}·s^{-1}) data sets, under the hypothesis that the response of the whole canopy could be extrapolated from the response of a single leaf. The solid lines in Fig. 3 are fitted curves, indicating that the relationship in the canopy between light intensity and photosynthetic rates can be well expressed by a non-rectangular hyperbola model, although the data is dispersed because of other factors that also affect photosynthesis, such as incoming energy distribution and redistribution, canopy structure, and soil conditions. Table 2 shows the photosynthetic parameters from May to September, derived from the fitted model. Consistent with the leaf data, canopy L_{cp} decreased first and then increased, while α and P_{max} showed a reverse pattern; the maximum of both occurred in July. However, unlike that of leaves, the R_d at canopy level presented an obvious seasonal variation, first increasing and then decreasing, with the maximum occurring in August.

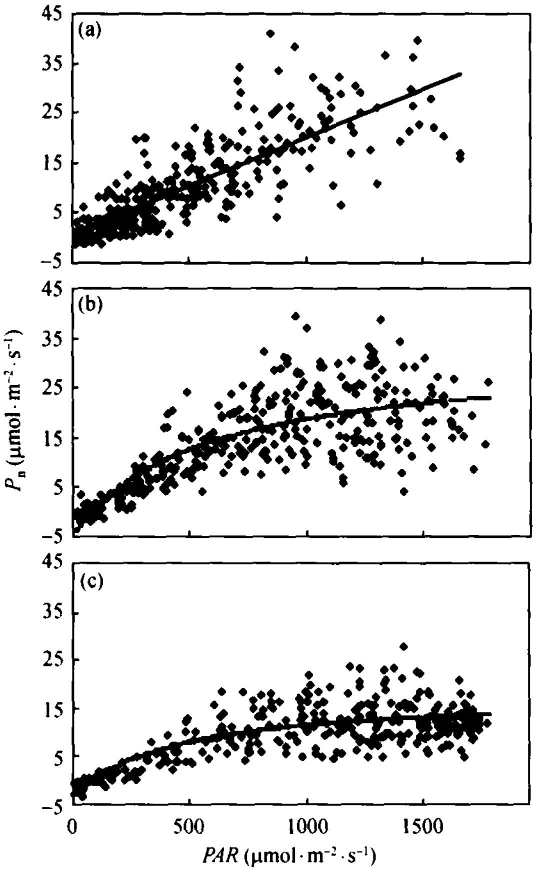

Fig. 4. Difference of canopy light response with different VPD levels in the peak growing season (June to August). (a) VPD < 8 hPa; (b) 8 hPa < VPD <15 hPa; (c) VPD > 15 hPa.

Table 2 Variations of canopy photosynthetic parameters from May to September

Month	α	P_{max}	R_d	L_{cp}	R^2
May	0.049	25.7	1.59	47	0.75
Jun	0.054	27.2	2.81	42	0.84
Jul	0.072	38.9	3.28	35	0.89
Aug	0.067	34.2	3.63	41	0.83
Sept	0.030	15.6	2.90	54	0.78

When the relationship between canopy R_d and biweekly average air temperate T_a was analyzed using the peak growing-season data, the correlation between them was significant (P < 0.05). R_d showed a linear increase with T_a (Fig. 5); notably, the value of LAI varied between 4.9—5.7 m^2·m^{-2} in the peak growing

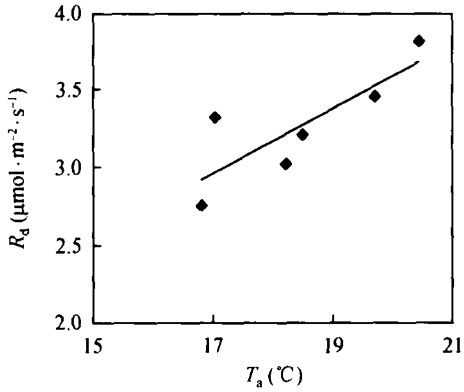

Fig. 5. Relationship between R_d and half-moth average air temperate T_a.

season. Considering the correlational effects of T_a and LAI on R_d, further studies are needed to accurately quantify the influence of T_a on R_d.

3 Discussion

3.1 Light response model

The photosynthetic parameters P_{max}, R_d, α, and L_{cp} are difficult to measure directly in the field. They are generally obtained using field data modeling. Therefore the model selection is a key process. In the recent literature, models including linear, quadratic polynomial, Mitscherlich, rectangular hyperbola, and non-rectangular hyperbola have all been used to derive these parameters[6,19−22]. But there are always variations among fitted parameters that are based on different models. For example, using the same observed data from wheat grown in North China, the parameter α derived from a rectangular hyperbola is nearly 40% higher than that of a non-rectangular hyperbola[23]. These discrepancies increase the uncertainties of inter-site comparisons.

This research does not advance the linear or the rectangular hyperbola model because neither have biological significance. Through an exponential model such as the Mitscherlich model, P_{max}, α and L_{cp} can be obtained directly, but R_d has to be calculated indirectly. Because of its simplicity, a rectangular model is generally used. But because such a model does not consider the convexity of measured data at the transition stages of low and high light, the biological indicators of its fitted parameters are not consistent with the real values. For example, the fitted values of P_{max} are always much higher than the measured values. This is one critical flaw of this model, which Lu *et al.* [23] confirmed with a light-photosynthesis response experiment involving winter wheat.

The non-rectangular hyperbola model, i.e. a corrected rectangular model, is consistent with the light-response processes of plants because the convexity θ is introduced. Additionally, its fitted parameters have biological significance. Therefore, in recent years the non-rectangular hyperbola model has been widely used. In this study, the light-response curves of leaves and canopy were well fitted by non-rectangular hyperbola model. On average, the light accounted for over 80% of the variation in photosynthetic rates. The parameters R_d, P_{max}, and α were plausible; moreover, the fitted P_{max} was close to the observed value.

3.2 Leaf photosynthesis

The parameters α and L_{cp} are the key indicators of low light utilization efficiency for plants. In this study, the values of α for the dominant tree species in a forest of broadleaved Korean pine were generally 0.038 −0.066. The parameter α for Korean pine was significantly lower than the studied broadleaf trees, but its value was within the variation range for C3 plants[24]. Subtropical studies[25] also showed that the values of α for conifers were much lower than that of broadleaf trees. This confirms that low light utilization efficiency for Korean pine is lower than that of broadleaf trees.

On the other hand, relatively high P_{max} and L_{sp} values suggest that the photosynthetic potential for Korean pine is high. Among the broadleaf trees, the α values for Mongolian oak were close to the average (0.052) for C3 plants. But the values for Tilia tuan and Mono maple were much higher than average. This study also found that the values of L_{cp} for dominant tree species on Changbai Mountain were all at or below 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$, relatively low when compared to the reported values of both coniferous and broadleaf trees in other regions. For example, Xiao *et al.* [26] found that spruce's L_{cp} was over 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The reported values for Oriental oak trees were also higher than 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ [27]. The high α and low L_{cp} values suggest that the broadleaved Korean pine forest on Changbai Mountain has a relatively high efficiency of low light utilization. This may be due to the long-term adaptation of plants to abundant rainy and cloudy days during the growing season in the Changbai Mountain region.

The parameter L_{sp} is the indicator of high light utilization characteristics for plants. In this study, photoinhibition occurred variably in Korean pine and Tilia tuan and was more obvious in Mono maple; Ma *et al.* [28] obtained a similar conclusion. These results suggest that high light is unfavorable to Mono maple. Combined with high α values, Mono maple can be characterized as heliophobous plant. No obvious light saturation occurred for Mongolian oak under artificial light, even when light intensity was increased to 2000 μmol·m^{-2}·s^{-1}. These observations suggest that this tree species is a typically heliophilous plant[29]. However, some studies found that diurnal variations of net photosynthetic rates of Mongolian oak still expressed as a double peak, even though *PAR* was no higher than 1800 μmol·m^{-2}·s^{-1} [30]. This indicates that the phenomenon of "midday depression" is induced not only by high light depression but that water stress on plants caused by long-duration, intense radiation is also a controlling factor. While it increases the L_{sp} when measure light response using artificial light. because the environmental conditions, especially air moisture condition in sampling chamber, is general better than the nature fields.

3.3 Canopy photosynthesis

Currently, research on canopy photosynthesis is mostly based on a combination of measurements obtained by eddy covariance and soil chamber methods. However, the canopy photosynthetic rates derived from these two methods have a large uncertainty, because their flux source is different. In this study, the canopy photosynthetic characteristics were well revealed using synchronous measurement of two eddy covariance system installed over- and under-canopy.

It is generally believed that no light saturation phenomenon occurs at biome scale in the field, because underlying leaves often lack light. But Fig. 3 shows that light saturation does exist at canopy. According to the analyses of Figs. 2 and 4, water stress on plants is the main cause of declining canopy photosynthetic rates[31]. Some studies also found that maximum net carbon assimilation mostly occurs on cloudy days rather than sunny days[32,33].

The apparent quantum efficiency α of broadleaved Korean pine forest averaged 0.055, close to the α value (0.057) for a temperate forest in Canada and at the upper limit of reported values (0.013−0.072) in other temperate forests[33−36]. This average is also consistent with the results of relatively high α values of the four dominant tree species in the Changbai Mountain forest and the high *LAI* there (6.0 m^{2}·m^{-2}). The high α values of leaves and canopy led to low L_{cp} canopy values; maximal L_{cp} was no higher than 60 μmol·m^{-2}·s^{-1}, whereas most other reported values were generally higher than 100 μmol·m^{-2}·s^{-1} [34, 36, 37]. Canopy P_{max} averaged 28.3 μmol·m^{-2}·s^{-1}, which was at the upper limit of reported values in other temperate forests[35], and was even higher than the P_{max} (20.5 μmol·m^{-2}·s^{-1}) of Amazonian rain forests[37].

The optimal light intensity for canopy photosynthesis in Changbai Mountain's broadleaved Korean pine forest was about 1000−1300 μmol·m^{-2}·s^{-1}. At leaf level, P_n reached 80% of P_{max} when *PAR* reached 500 μmol·m^{-2}·s^{-1}. The relatively high efficiency of low light utilization, indicated by low L_{cp} and high α values, caused normal photosynthetic assimilation among vegetation even on cloudy and rainy days. This may be one important reason that this 300-year-old forest still has a high carbon fixation ability[11] in cool-temperate region.

3.4 Photosynthetic characteristics of leaves and canopy

The α values of leaves (0.054−0.072) were close to those of canopy (0.037−0.066) during the peak growing season, when the whole canopy was treated a single big leaf and no account was made of its leaf area. But canopy P_{max} values were significantly higher than those of leaves, indicating that the increase of high light-utilization efficiency was higher than for low light, from leaves to canopy. This difference may be because active photosynthesis still occurs within the canopy with intense radiation, when there is no water stress in the morning or after rain on sunny days; at canopy level, underlying leaves in partial shade still present high photosynthetic rates even when upper leaves indicate light depression. Sands [38] found that when P_{max} of upper leaves inclined 1% with increasing radiation, the concurrent decrease of canopy P_{max} was only 0.25%. This also confirms the above conclusion.

This study also found that the canopy values of R_d and L_{cp} were both higher than leaf values, because the respiration of shaded underlying leaves and trunks increased the CO_2 efflux rates. Additionally, light-response experiments involving leaves were made in favorable temperature, air moisture and CO_2 concentration conditions. Natural environmental stress factors, especially the stress of high *VPD*, could increase the L_{cp} values of leaves[39], which could then extend to the canopy level.

4 Conclusion

This study on photosynthetic characteristics of dominant trees species and canopy in broadleaved Korean pine forest on Changbai Mountains showed that the light-response curves of leaves and canopy can be well fitted with a non-rectangular hyperbola model. Mongolian oak, Mono maple and Korean pine respectively showed characteristics of heliophilous, heliophobous and semi-heliophilous plants. Significant differences were found among the tree species in the study, especially between pine and broadleaf trees. At the canopy level, the values of both α and P_{max} were close to the upper limit of observed values in temperate forests, while L_{cp} was within the lower limit. The photosynthetic characteristics found for the canopy were well consistent with those of leaves. The biome canopy showed a high efficiency of low light utilization and photosynthetic ability, an important reason that this nearly 300-year-old cool-temperate forest still has strong carbon assimilation ability. However, environmental stresses, such as high vapor pressure deficits, can significantly reduce the photosynthetic ability of leaves and canopy. To further understand these processes, control experiments and long-term *in situ* observation are still needed.

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