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Response of Photosynthetic Capacity to Climate Warming and Its Variation among 11 Provenances of Dahurian Larch (*Larix gmelinii*)

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Response of Photosynthetic Capacity to Climate Warming and Its Variation among 11 Provenances of Dahurian Larch (*Larix gmelinii*)

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Abstract: We investigated the response of leaf photosynthetic capacity to climate warming and its variation among provenances of *Larix gmelinii* (Dahurian larch). Seedlings of 11 *L. gmelinii* provenances were transplanted into two common gardens with different climate conditions (control and warming climate). We measured the leaf photosynthetic capacity and explored its influencing factors. The warming treatment significantly increased the maximum net photosynthetic rate (Pmax-a), photosynthetic nitrogen use efficiency (PNUE), maximum carboxylation rate (Vcmax), maximum electron transport rate (Jmax), triose phosphate utilization rate (TPU), mesophyll conductance (gm), leaf nitrogen content (Narea), and chlorophyll content (Chlm). The Pmax-a was significantly positively associated with Vcmax, Jmax, TPU, gm, and Narea, and the slope of the correlations between Pmax-a and Vcmax, Jmax, and TPU was steeper in the warming treatment. The responses of Pmax-a, PNUE, Vcmax, Jmax, TPU, Narea, and Chlm to warming differed among provenances. The effects of warming on Pmax-a, Vcmax, Jmax, and TPU increased and then decreased as the aridity index of the original site increased. Overall, the warming treatment improved the photosynthetic capacity of L. gmelinii, but the extent of the improvement varied among provenances. These findings provide insights into the mechanisms underlying the responses of L. gmelinii to climate warming.

Keywords: boreal forest; climate change; photosynthetic capacity; adaptation

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1. Introduction

Climate warming will change the structure and function of forest ecosystems, especially the growth of boreal forests [1]. Because of experimental limitations, it is still challenging to research the effects of climate warming on tree growth in boreal forests, and to explore the mechanisms of such effects [2,3]. Photosynthesis is the physiological basis of tree growth. The response of photosynthesis to climate warming not only affects tree growth, but also reflects the ability of trees to adapt to climate warming [4,5]. Many studies have examined the effect of climate warming on the photosynthetic capacity of trees, but these have obtained diverse results, ranging from a promoting effect [3] to an inhibiting effect [6] or no effect [7]. To understand the mechanisms underpinning the response of photosynthetic capacity to climate warming, previous studies have explored the factors that affect photosynthesis, such as leaf nitrogen content, chlorophyll content, and stomatal limitation [8–11]. Some other studies have shown that photosynthesis can acclimatize to a warming climate, and the photosynthetic capacity can change during the warming process [12,13]. If photosynthetic capacity can acclimate to new climatic conditions, then climate warming can have a positive or negative effect [3,14]. To date, most studies on this topic have focused on the response of photosynthetic capacity to a short-term warming treatment. It is still unknown how the photosynthetic capacity changes in response to warming over a long period of time. Therefore, the response of photosynthetic capacity to a long-term warming treatment should be determined.

Some previous studies have analyzed interspecific differences in the responses of trees' photosynthetic capacity to climate warming, and found that the species in temperate forests near their cold range limit responded positively to a warming treatment [2,3,15]. Because they grow in different habitats, trees from the same species can be grouped into different provenances, i.e., populations containing local genetic variations. Provenances show intraspecific differences in a range of physiological characteristics [16]. However, it is still unknown whether the response of photosynthetic capacity to climate warming shows intraspecific differences, and if so, whether it follows the same pattern as interspecific differences, that is, whether trees near their cold range limit respond positively to climate warming. The mechanism underlying intraspecific differences in photosynthetic capacity is also unclear. Some studies have shown that photosynthetic capacity is mainly affected by the environment, and that differences in photosynthetic capacity among provenances are attributable to phenotypic plasticity [17,18]. Other studies have found that differences in photosynthetic capacity among provenances may be attributed to ecotypic adaptation, where the differences are driven by genetic differentiation [19–22]. It is important, therefore, to determine whether the response of photosynthetic capacity to climate warming differs among provenances, and to clarify whether this difference is controlled by phenotypic plasticity or by genetic adaptation.

Dahurian larch (*Larix gmelinii*) is a dominant tree species in boreal forests. This tree species is distributed over a wide geographical range and grows in diverse environments. Whether larch shows phenotypic plasticity to adapt to climate warming has important implications for carbon sequestration in forests. In 1983, we established a warming experiment by transplanting seedlings from 11 provenances into two common gardens that were located near the cold and warm range limits of larch. Forty years later, we examined the responses of photosynthetic capacity to this long-term climate warming treatment, and explored the variations in responses among the 11 provenances. We tested the following hypotheses: 1) Warming will enhance leaf photosynthetic capacity by increasing leaf nitrogen content and mesophyll conductance [23,24]; 2) The effects of warming on photosynthetic capacity will vary significantly among provenances, and those near their cold range limit will respond positively to warming [21,22].

2. Materials and Methods

2.1. Site Description and Experimental Design

The two common gardens were located at the Maoershan Forest Ecosystem Research Station (MES) (45.40 N, 127.50 E) and the Jiagedaqi Forest Silvicultural Station (JGDQ) (50.42 N, 124.07 E) (Table 1). At MES and JGDQ, the annual mean precipitation was 629.0 and 525.4 mm, respectively, and the annual mean air temperature was 2.8 and −1.2℃, respectively. In the autumn of 1980, the seeds were collected from the original sites of the 11 provenances in the natural distribution area of *L. gmelinii* in China. The seeds were sown in the nursery early in the spring of 1981. In the spring of 1983, the 2-year-old seedlings of the 11 provenances were transplanted into the two common gardens. In each common garden, the experiment was established with a randomized complete block design, consisting of five blocks with a 10-m buffer in between. Each block contained 11 plots with a 4-m buffer in between. In each plot, 80 trees from one provenance were planted in double rows with 1.5 m × 2.0 m spacing. Trees in one row were cut down in 1997. In 2001, two out of three trees in the remaining row were cut down, so that the final spacing was 4.5 m × 4.0 m.

Table 1. Geographic and climatic conditions of the two common garden sites*.

Common garden	Latitude (°N)	Longitude (°E)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Soil nitrogen concentration (g·kg^{-1})	Soil phosphorus concentration (g·kg^{-1})
Maoershan (MES)	45.40	127.50	3.1	629.0	10.94a	2.31a

Jiagedaqi (JGDQ)	50.42	124.07	−1.2	525.4	6.37b	1.98b

*Lowercase letters in the same column indicate significant differences between two common gardens ($P < 0.05$).

Table 2. Geographic and climatic conditions of the origins of 11 provenances of Dahurian larch.

Provenance	Code	Latitude (°N)	Longitude (°E)	Mean annual temperature (℃)	Mean annual precipitation (mm)	Mean annual evaporation (mm)	Average temperature in January (°C)	Average temperature in January July (°C)
Hebei (HB)	1	47°33′	130°25′	1.6	575	1235	-22.0	20.3
Wuyiling (WYL)	2	48°40′	129°25′	-0.96	650.54	1038	-24.28	19.06
Sanzhan (SZ)	3	49°37′	126°48′	-1.3	527.2	1076	-18.0	25.0
Zhongyangzhan (ZYZ)	4	50.7	126.72	-2.20	484.4	1387	−26.80	17.6
Tahe (TH)	5	52°19′	124°43′	-2.74	487.9	1028	-25.48	16.69
Xinlin (XL)	6	51°42′	124°20′	-3.35	507.3	912	-26.32	17.61
Chuoer (CE)	7	48°10′	121°15′	-3.4	462.3	1122	-24.95	16.19
Kuduer (KDE)	8	49°47′	121°53′	-4.0	500.0	1280	-27.5	16.2
Moerdaoga (MEDG)	9	51°15′	120°35′	-4.5	471.0	999	-30.0	17.0
Genhe (GH)	10	50°41′	121°57′	-5.0	436.3	991	-25.7	17.8
Mangui (MG)	11	52°03′	122°11′	-5.83	466.0	1100	-31.3	16.13

2.2. Measurements of Leaf Gas Exchange

The leaf gas exchange measurements were conducted in late July 2022. First, the diameter at breast height (DBH) of all trees in each common garden was measured, and the average DBH was calculated for each block and overall. The block with average DBH closest to the overall average DBH was selected for further measurements. In the selected blocks, five standard trees were selected from each provenance. Three standard branches were cut from the middle canopy of each standard tree, and the needles from the 2–3 cm portion at the end of three short shoots of each standard branch were used for gas exchange measurements. The light and CO_2 response curves were measured with a portable infrared gas analyzer (LI-6400, Li-Cor Inc., Lincoln, NE, USA) equipped with a red-blue LED light source (Li-6400-02B), a temperature controller (Li-6400-88), and a CO_2 mixer/injector system (Li-6400-01). Before measurements were conducted, the leaves were allowed to equilibrate under the following environment-controlled conditions: chamber CO_2 concentration, 400 $\mu mol \cdot mol^{-1}$; block temperature of the chamber, 25 °C; relative humidity in the chamber, 45% – 65%; flow rate of air, 500 $\mu mol \cdot s^{-1}$. The light response curve of photosynthesis was measured over a range of photosynthetic photon flux density (2000, 1500, 1200, 800, 400, 200, 150, 100, 50, and 0 μmol photons$\cdot m^{-2} \cdot s^{-1}$). The CO_2 response curve of photosynthesis was measured with a CO_2 concentration gradient of 400, 200, 150, 100, 50, 600, 800, 1200, and 1500 $\mu mol\ CO_2 \cdot mol^{-1}$.

2.3. Measurements of Leaf and Soil Traits

All needles sampled for gas exchange measurements were harvested and placed in a cooler at 4°C. In the laboratory, the needles were scanned, dried to constant mass at 65°C, and then weighed to calculate the specific leaf area (SLA = leaf area/leaf dry mass).

Needles (approximately 100 g) on the short shoot of each branch were sampled, randomly divided into two portions, and placed in a cooler at 4°C. One portion was ground, extracted with a 1:1 mixture of acetone and ethanol, and then the absorbance of the solvent was determined at 645 nm and 663 nm using a spectrophotometer (Evolution300, Thermofisher Scientific Inc, Waltham, MA, USA). The other portion was heated in a 600-W microwave oven for 90 s, crushed, and then oven-dried at 65°C to constant weight. The nitrogen concentration in the dried crushed needles was determined using an automatic nitrogen analyzer (Kjeltec 8400, Foss Tecator AB, Hillerød, Denmark).

In the selected blocks in each common garden, 30 soil sampling points were arbitrarily selected, and three replicate soil cores of 0–10 cm depth were taken at each point. The three soil cores were mixed and about 500 g soil was collected by the four-fraction method. All soil samples were stored in a cooler at 4°C and returned to the laboratory to determine the nitrogen concentration using the same method as that used for leaves.

2.4. Data Analyses

The measured values of photosynthetic characteristics of trees in the JGDQ were used as the control, and the measured values of photosynthetic characteristics of trees in MES were used as the warming treatment. The effect size of the warming treatment on photosynthetic characteristics for each provenance was calculated as follows:

$$\Delta X_{\mathrm{i}} = X_{\mathrm{i\text{-}warming}} - X_{\mathrm{i\text{-}control}}$$

where X_{warming} and X_{control} represent each variable (e.g., $P_{\max}$, V_{cmax}, $J_{\max}$, TPU) measured in MES and JGDQ, respectively, and $_{\mathrm{i}}$ indicates each provenance.

The genetic differentiation and phenotypic plasticity were estimated with the variance component feature using the restricted maximum likelihood method. The variances of the random effects (provenance σ^2_{P}, treatment σ^2_{T}, interaction between provenance and treatment σ^2_{i}, residual σ^2_{ε}) were calculated. The overall genetic differentiation (D_{G}) among the provenances was estimated as $\sigma^2_{\mathrm{P}} / (\sigma^2_{\mathrm{P}} + \sigma^2_{\mathrm{i}} + \sigma^2_{\varepsilon})$. The phenotypic plasticity (P_{P}) among treatments was estimated as $\sigma^2_{\mathrm{T}} / (\sigma^2_{\mathrm{T}} + \sigma^2_{\mathrm{i}} + \sigma^2_{\varepsilon})$.

All statistical analyses were conducted using R software (version 4.1.3, The R Foundation for Statistical Computing, Vienna, Austria). Data were subjected to analysis of variance (ANOVA) to test the main effects (warming treatment, provenance) on photosynthetic characteristics and related needle traits with the “agricolae” package. The data were tested for normal distribution and homogeneity of variance before ANOVA. Multiple comparisons of photosynthetic characteristics and related needle traits were conducted with the “multcomp” package. The regression model was applied to explore potential relationships between photosynthetic characteristics and needle traits or the climatic features of original sites with the “car” package. The CO_2 response curves were fitted and the relevant parameters were calculated using the analysis software described in the article by Sharkey et al. [25].

3. Results

3.1. Comparison of Photosynthetic Characteristics

The warming treatment significantly ($P < 0.05$) affected the maximum net photosynthetic rate ($P_{\mathrm{max\text{-}a}}$), photosynthetic nitrogen use efficiency (PNUE), maximum carboxylation rate (V_{cmax}), maximum electron transport rate ($J_{\max}$), and triose phosphate utilization rate (TPU) (Table 3), and the interaction between the warming treatment and provenance was significant for all of these indexes. The effect of the warming treatment was significant ($P < 0.01$) for mesophyll conductance (g_{m}) (Table 3). The overall average values of $P_{\mathrm{max\text{-}a}}$, PNUE, V_{cmax}, $J_{\max}$, TPU, and g_{m} in the control were 6.23±0.61 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, 4.06±0.41 $\mu\mathrm{mol\ g^{-1}\ s^{-1}}$, 101.54±7.10 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, 120.95±5.87 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, 9.43±0.52

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μmol·m^{-2}·s^{-1}, and 1.18±0.12 μmol·m^{-2}·s^{-1}, respectively, and were increased by 22.13%, 26.17%, 28.25%, 28.47%, 19.54%, and 55.93%, respectively, in the warming treatment (Figure 1).

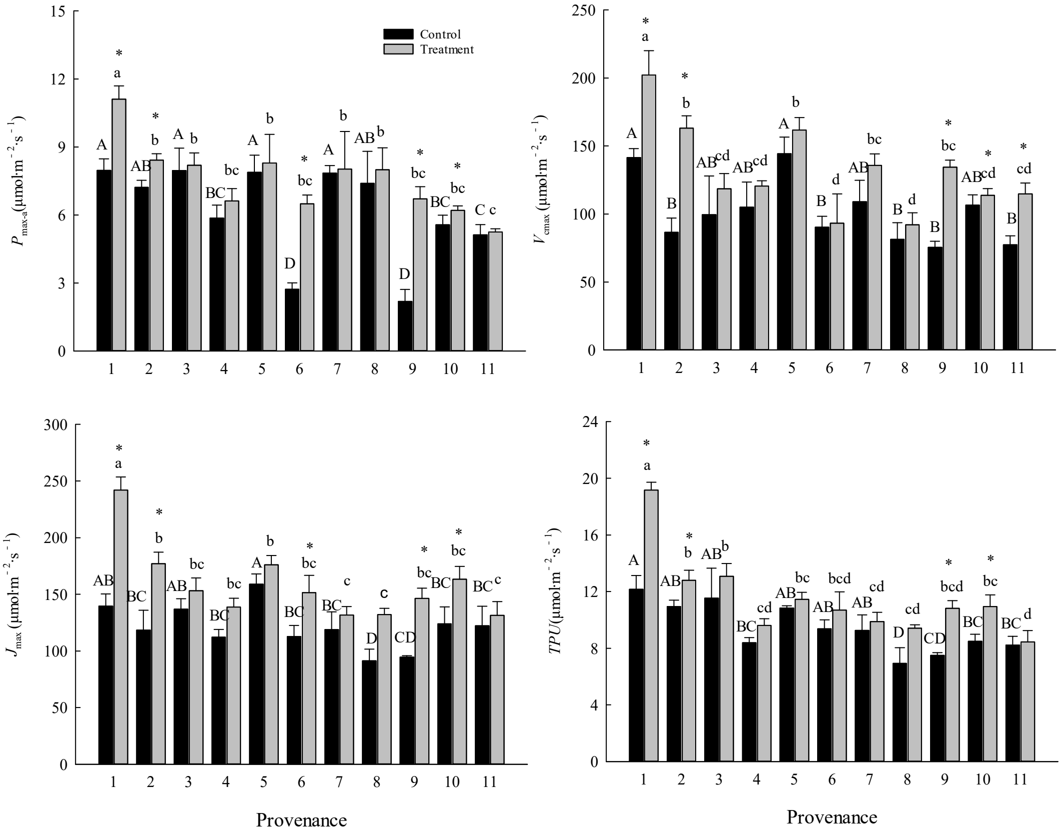

Figure 1. Comparisons of $P_{\text{max-a}}$, V_{cmax}, J_{max}, and TPU between treatments and among provenances (mean ± SE). Different capital letters indicate significant differences among provenances in the control ($P < 0.05$), and different lowercase letters indicate significant differences among provenances in the warming treatment ($P < 0.05$). * indicates a significant difference in that provenance between the control and warming treatment ($P < 0.05$). Refer to Table 2 for provenance codes, and Table 3 for abbreviations of photosynthetic characteristics.

The warming treatment significantly ($P < 0.05$) increased the $P_{\text{max-a}}$ and J_{max} of trees from Hebei, Wuyiling, Xinlin, Mordaoga and Genhe, increased the V_{cmax} of trees from Hebei, Wuyiling, Mordaoga, Genhe and Mangui, and increased the TPU of trees from Hebei, Wuyiling, Mordaoga, Genhe. Pooling the data for the 11 provenances in each common garden, $P_{\text{max-a}}$ was consistently ($P < 0.05$) and positively correlated with V_{cmax}, J_{max} and TPU, but the slope of the correlations was steeper in the warming treatment than in the control (Figure 2).

Table 3. Two factor analysis of variance to determine the effects of provenance, treatment, and their interaction on the photosynthetic capacity and related needle traits of Dahurian larch*.

Variable	Unit	Provenance		Treatment		Provenance × Treatment	
		F	P	F	P	F	P
$P_{\text{max-a}}$	μmol m^{-2} s^{-1}	11.76	< 0.01	21.83	< 0.01	2.81	< 0.01
PNUE	μmol g^{-1} s^{-1}	12.86	< 0.01	26.78	< 0.01	5.00	< 0.01
V_{cmax}	μmol m^{-2} s^{-1}	9.38	< 0.01	35.67	< 0.01	2.07	< 0.05
J_{max}	μmol m^{-2} s^{-1}	6.34	< 0.01	46.15	< 0.01	2.20	< 0.05

TPU	μmol m^{-2} s^{-1}	11.36	< 0.01	25.80	< 0.01	2.17	< 0.05
SLA	cm^2 g^{-1}	7.15	< 0.01	16.37	< 0.01	4.59	< 0.01
N_{area}	g m^{-2}	5.31	< 0.01	71.24	< 0.01	2.93	< 0.01
g_m	μmol m^{-2} s^{-1} Pa^{-1}	1.01	0.45	8.73	< 0.01	1.61	0.13
Chl_m	mg g^{-1}	4.95	< 0.01	6.47	< 0.05	3.51	< 0.01

*$P_{max\text{-}a}$: maximum net photosynthetic rate; PNUE: photosynthetic nitrogen use efficiency; V_{cmax}: maximum carboxylation rate; J_{max}: maximum electron transfer rate; *TPU*: triose phosphate utilization rate; SLA: specific leaf area; N_{area}: area-based nitrogen content; g_m: mesophyll conductance; Chl_m: chlorophyll content. The same below.

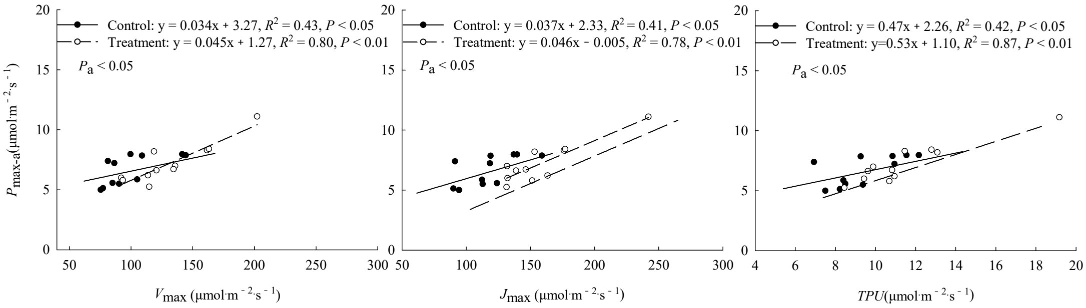

Figure 2. Relationships between $P_{max\text{-}a}$ and V_{cmax}, J_{max}, and *TPU*. P_a represents the significance of the difference in slope between regression equations. Refer to Table 3 for abbreviations of photosynthetic characteristics.

In the control and warming treatment, $P_{max\text{-}a}$, V_{cmax}, J_{max}, and *TPU* were significantly ($P < 0.01$) positively linearly correlated with the average annual temperature of the original site of the provenances (Figure 3). The magnitude of the warming treatment's effect on photosynthetic capacity varied among provenances, and was related to the climate of the original site of the provenances. The $\Delta P_{max\text{-}a}$, ΔV_{cmax}, ΔJ_{max}, and ΔTPU were significantly ($P < 0.01$) correlated with the aridity index of the original site. As the aridity index of the original site increased, the magnitude of the warming effect on each index first increased and then decreased (Figure 4).

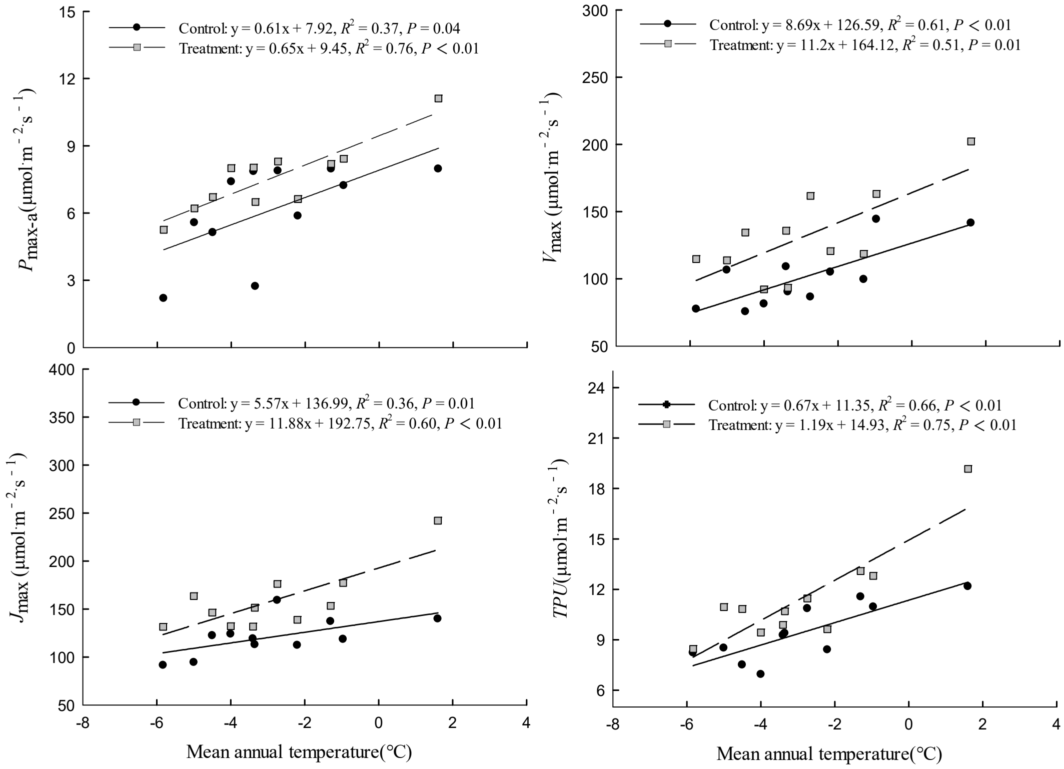

Figure 3. Relationships between $P_{\text{max-a}}$, V_{cmax}, J_{max}, *TPU* and the mean annual temperature of original sites. Refer to Table 3 for abbreviations of photosynthetic characteristics.

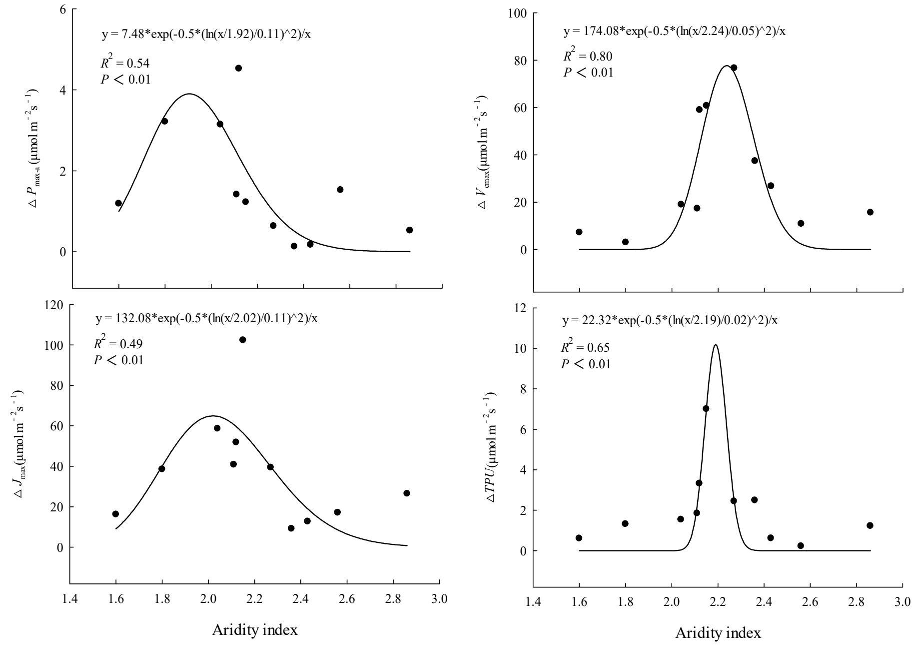

Figure 4. Relationships between effect of warming on maximum net photosynthetic rate ($\Delta P_{\text{max-a}}$), maximum carboxylation rate (ΔV_{cmax}), maximum electron transport rate (ΔJ_{max}), triose phosphate utilization rate (Δ*TPU*) and aridity index of the original sites. Aridity index = mean annual evaporation/mean annual precipitation.

The provenance effect accounted for 43.22%, 35.54%, 48.08%, 32.63%, and 51.51% of the total variance in $P_{\text{max-a}}$, PNUE, V_{cmax}, J_{max}, and *TPU*, respectively (Table 4). The environment effect accounted for 25.41%, 27.71%, 42.46%, 48.17%, and 34.73% of the total variance in $P_{\text{max-a}}$, PNUE, V_{cmax}, J_{max}, and *TPU*, respectively (Table 4).

Table 4. Genetic differentiation and phenotypic plasticity of photosynthetic characteristics among 11 Dahurian larch provenances*.

Leaf traits	D_{G}	P_{P}
$P_{\text{max-a}}$	43.22	25.41
PNUE	35.54	27.71
V_{cmax}	48.08	42.46
J_{max}	32.63	48.17
TPU	51.51	34.73

*D_{G} is overall genetic differentiation among the provenances, P_{P} is phenotypic plasticity among the treatments.

3.2. Comparison of Factors Related to Photosynthetic Capacity

The warming treatment, the provenance, and their interaction significantly ($P < 0.05$) affected SLA, Chl_{m}, and N_{area} (Table 3). The warming treatment decreased the overall average SLA by 27.00%, and increased the overall average Chl_{m} and N_{area} by 10.16% and 14.09%, respectively. There were significant differences ($P < 0.05$) among provenances in the responses of SLA, Chl_{m}, and N_{area} to the warming treatment (Figure 5). The warming treatment significantly ($P < 0.05$) decreased the SLA of trees from Hebei, Wuyiling, Xinlin, Mordaoga, and Genhe, increased the Chl_{m} of trees from Hebei, Wuyiling, Sanzhan, Zhongyangzhan, Xinlin, Chaoer, and Genhe, and increased the N_{area} of trees from Hebei, Wuyiling, Zhongyangzhan, Xinlin, Mordaoga, Genhe, and Mangui. The N_{area} was significantly

($P < 0.01$) positively associated with $P_{\text{max-a}}$, V_{cmax}, and J_{max}, (Figure 6a), and $P_{\text{max-a}}$ was significantly ($P < 0.01$) positively associated with g_{m} (Figure 6b).

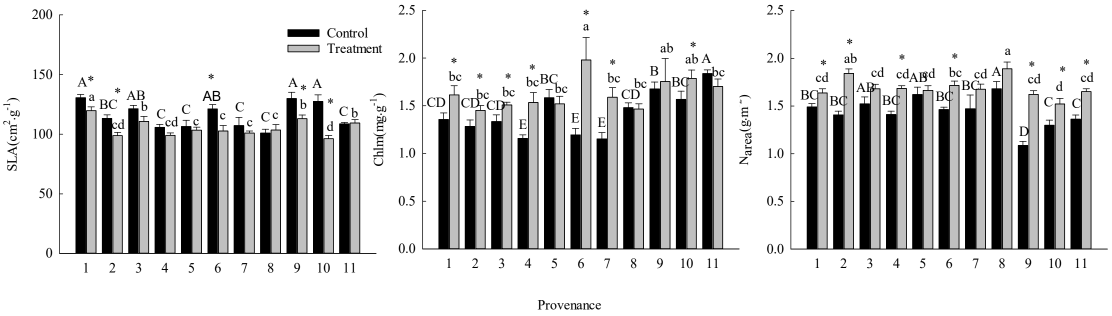

Figure 5. Comparisons of SLA, Chl_{m} and N_{area} between treatments and among provenances (mean ± SE). Different capital letters indicate significant differences among provenances in the control ($P < 0.05$), different lowercase letters indicate significant differences among provenances in the warming treatment ($P < 0.05$), * indicates significant difference between the treatment and control in that provenance ($P < 0.05$). Refer to Table 2 for provenance codes, refer to Table 3 for abbreviations of photosynthetic characteristics.

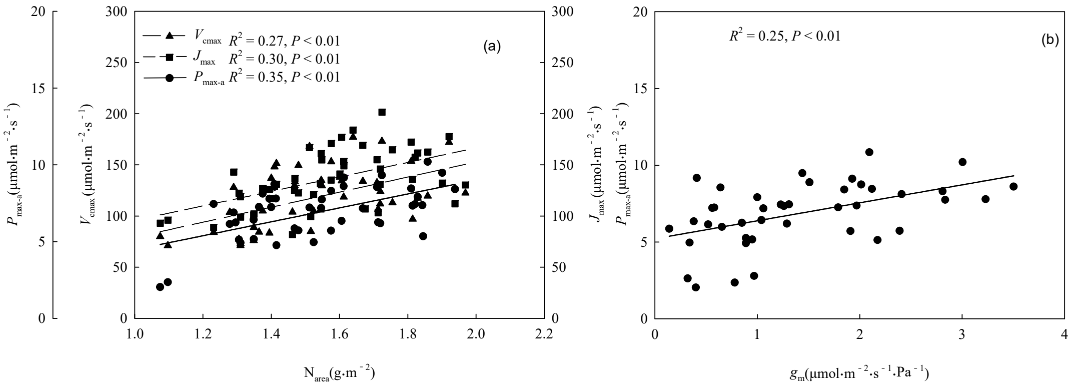

Figure 6. Relationships (a) between $P_{\text{max-a}}$, V_{cmax}, J_{max} and N_{area}; and (b) between $P_{\text{max-a}}$ and g_{m}. Refer to Table 3 for abbreviations of photosynthetic characteristics.

4. Discussion

4.1. Effect of Warming on Photosynthetic Capacity

Consistent with our hypothesis, the warming treatment significantly increased the $P_{\text{max-a}}$, V_{cmax}, J_{max}, and *TPU* of *L. gmelinii* by 19.54%–28.47%, and increased the slope of the linear correlation between $P_{\text{max-a}}$ and V_{cmax}, J_{max}, and *TPU*. These results indicate that warming increased the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the regeneration rate of 1,5-ribulose diphosphate, and the CO_2 utilization capacity, and consequently improved $P_{\text{max-a}}$. Meanwhile, N_{area} also increased under the warming treatment and was positively associated with $P_{\text{max-a}}$, V_{cmax}, and J_{max}, indicating that the increased nitrogen content in the leaves was one reason for the increased photosynthetic capacity. This is because Rubisco is the largest nitrogen sink in the leaves [26]. The increased nitrogen content in the leaves would increase the carboxylation rate by affecting the Rubisco protease content, which affects the photosynthetic capacity [27]. In addition, the PNUE increased significantly under the warming treatment. Trees allocate more nitrogen to the photosynthetic apparatus under a warming treatment [21,28], and increases in leaf nitrogen content and nitrogen-use efficiency can promote the photosynthetic capacity [24].

The increase in leaf nitrogen content might be related to changes in leaf structure. One of the most important leaf functional traits is SLA, which represents the resource utilization strategy of plants. A smaller SLA usually corresponds to higher N_{area} [29]. In this study, the SLA decreased significantly in the warming treatment, indicating that larch leaves became thicker in response to long-term warming. Further analyses of leaf anatomy indicated that the increase in leaf thickness was mainly caused by thickening of the mesophyll layer, and an increase in the proportion of the mesophyll in the leaf (unpublished data). The increase in mesophyll thickness and proportion would lead to increased numbers of chloroplasts and increased nitrogen content, which was supported by the significant increase in Chl_m and N_{area}. The leaf nitrogen content may also be related to soil nitrogen content, as reported in other studies [30,31]. The higher soil nitrogen content in the Maoershan common garden than in the Jiagedaqi common garden may have caused trees to absorb more nitrogen to meet their photosynthetic requirements.

Previous studies identified mesophyll conductance as one of the limiting factors of the photosynthetic rate [32], and found that mesophyll conductance limited photosynthesis to a similar extent as stomatal conductance, and was affected by temperature [33]. Some other studies reported that mesophyll conductance increased with increasing temperature [34,35]. Our results show that long-term warming significantly increased leaf g_m, and there was a significant positive linear correlation between P_{max-a} and g_m. These findings indicate that warming promoted CO_2 diffusion and conductance in the leaf of *L. gmelinii*, which was beneficial for photosynthetic carbon assimilation. In summary, our results show that the photosynthetic capacity of *L. gmelinii* significantly increased during a 40-year warming treatment. This indicates that the promoting effect of warming on the photosynthetic capacity can be sustained, and that the photosynthetic capacity of *L. gmelinii* can actively adapt to climate warming.

4.2. Differences among Provenances in the Response of Photosynthetic Capacity to Warming

Many studies have explored whether there are differences in photosynthetic capacity among provenances of various tree species, and have tried to determine the regulatory mechanism underlying such differences [19–22]. Our results show that there were significant differences in P_{max-a}, V_{cmax}, J_{max}, and *TPU* among the 11 provenances in the control and the warming treatment, and the values of all these indexes increased with increasing annual mean temperature of the original sites of the provenances. Genetic differentiation among the provenances accounted for 32.63%–51.51% of the total phenotypic variation in the photosynthetic capacity. These findings confirm the existence of variation in photosynthetic capacity among the provenances; and indicate that this variation is driven by genetic adaptation to the original habitats of the provenances. In our study, the trees had grown in the common garden for 40 years and had suitable row spacing to attenuate competition among individuals. Therefore, our results are credible and support the viewpoint that differences among provenances are mainly under genetic control [19–22].

Consistent with our hypothesis, the responses of photosynthetic capacity to warming differed significantly among the 11 provenances. However, we found that warming only significantly increased the P_{max-a}, V_{cmax}, J_{max} of five provenances and the *TPU* of four provenances. This indicated that the photosynthetic capacity of at least 50% of the provenances acclimated to warming, and suggested that the effect of warming on photosynthetic capacity weakened with prolonged duration of the warming treatment. To explore the mechanism by which warming affected the photosynthetic capacity, we calculated the differences in photosynthetic characteristics between the control and the warming treatment for each provenance, and defined it as the warming effect. Although this definition has some limitations, it has certain indicative significance. The results show that the effects of warming on P_{max-a}, V_{cmax}, J_{max} and *TPU* had significant nonlinear relationships with the aridity index of the original sites. As the aridity index of the original sites increased, the ΔP_{max-a}, ΔV_{cmax}, ΔJ_{max} and ΔTPU increased first and then decreased, and the peak values appeared when the aridity index was between 2.1 and 2.2. As an appropriate indicator of climatic conditions, aridity index is affected by both temperature and precipitation. Therefore, we believe that the responses of photosynthetic capacity to warming were jointly affected by both the temperature and precipitation of the original sites. This slightly differs from the hypothesis that trees growing near their cold range limit will respond positively to warming. Because of the minimal changes in temperature and precipitation conditions, the effect of climate warming on the photosynthetic capacity of trees from less arid sites was not significant. For the trees from more arid sites, the warming temperature might have exceeded the optimal photosynthetic temperature, so it did not significantly increase the photosynthetic capacity. Therefore, we should consider differences among provenances when studying the effects of climate warming on photosynthetic capacity.

5. Conclusions

A long-term (40-year) climate warming treatment increased the leaf chlorophyll content, leaf nitrogen content, and photosynthetic nitrogen use efficiency of *L. gmelinii*, which enhanced its photosynthetic capacity. The photosynthetic capacity varied significantly among the provenances, and this was explained by the climatic conditions at the provenances' sites of origin. About half of the 11 provenances showed a significant increase in photosynthetic capacity under the warming treatment. The response of photosynthetic capacity to warming showed a single-peak curve as the aridity index of the site of origin increased. These results contribute to our understanding of how photosynthetic capacity will respond to climate warming, and its regulatory mechanisms. Notably, the warming treatment in this study represented the combined effect of temperature and precipitation, without considering the effect of soil on photosynthetic capacity. Therefore, further research is required to determine whether soil nutrients also affect the photosynthetic response to climate warming.

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