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Effect of light intensities on the photosynthetic characteristics of *Abies holophylla* seedlings from different provenances

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Abstract. The photosynthetic characteristics of *Abies holophylla* seedlings from six provenances under four artificial light intensities in a greenhouse (full light, 75.08%, 55.42%, and 30.38% of full light) were studied to explore the underlying genetic differences in foliar photosynthesis. Varying light intensities significantly affected the foliar photosynthetic parameters of *A. holophylla* seedlings from six provenances. As the light intensity dropped, the foliar CO_2 assimilation capacity of *A. holophylla* seedlings sharply decreased, and the foliar light utilization capacity significantly increased. Analysis of genetic variation showed highly significant differences in terms of CO_2 assimilation capacity, light utilization capacity, and respiration depletion of *A. holophylla* seedlings among different provenances under different light intensities. The variations were mainly controlled by the genetic factors of the provenance itself. The obtained results revealed that different sensitivities of *A. holophylla* seedlings from different provenances in response to changed light intensities elicited significant differences in foliar photosynthesis among different provenances. The relationships between sensitivities and annual temperature difference, mean temperature in January, and mean annual evaporation of provenance were found to be the most closely related, which indicated that temperature range and effective precipitation of provenance were the main factors that affected photosynthetic plasticity of *A. holophylla* seedlings.
Keywords *Abies holophylla* seedling, provenance, light intensity, genetic difference, photosynthetic characteristics.

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Introduction

Light is one of the foremost environmental factors that affect survival, growth, and regeneration of trees. The need for light and the characteristics of the response and adaptation to different light environments vary among different tree species and different developmental stages for a given tree species (Wyka et al. 2012). The seedling stage is the period when trees are the most vulnerable and the most sensitive to environmental stress throughout the whole life cycle (Pérez-Ramos et al. 2010, Castanha et al. 2013). Light is a crucial factor that influences early survival and growth of tree seedlings growing under forest canopies (Wang et al. 2006). As a result, tree seedlings have evolved to adapt to a certain light environment by modifying their morphological and physiological plasticity (Carne 2013), which are important countermeasures for the survival, growth, and reproduction of trees in a changing environment.

Through natural selection and adaptation, the kindred tree seedlings, which grow under a certain environmental condition, will mutate to share the same or similar morphological and physiological characteristics, eventually resulting in a specific geographic population (Chong et al. 2013, Babaei et al. 2014). Light availability is an important factor controlling phenotypic plasticity (Rodríguez-García & Bravo 2013). Photosynthetic ability in a seedling is affected by the combination of both endogenous genetic characteristics and exogenous environment and climate influences (Reinhardt et al. 2011) and inevitably mutate among different provenances (Goldblum et al. 2012, Nasr et al. 2013). Therefore, variation in photosynthetic characteristics is a major trait that depends on the different provenances (Okuto & Ouma 2010, Sunil et al. 2013). Variation in foliar photosynthesis among different genotypes is related to the presence of different degrees of genetic variation reflecting gas exchange capabilities (Aspinwall et al. 2011). Inherent genetic physiological difference is one of the main causes that results in differences in the variation modes of photosynthetic characteristics (Andrews et al. 2012, Soustani et al. 2014). Photosynthetic plasticity greatly improves the resistance and the ability to obtain resources of an individual tree seedling (e Silva et al. 2012) and also improves the competitive ability in the environment (Paquette et al. 2012), thereby laying a solid foundation for the survival and reproduction. Therefore, studying the photosynthetic characteristics of different trees is an effective way to understand the survival mechanisms of adaptation to the light environment (Klein et al. 2013, Flexas et al. 2014). However, the extent of environmental influence and genetic influence of photosynthesis in different genotypes of plants should be studied. The changes in photosynthetic characteristics in response to light gradients among different genotype groups are also an important aspect to be studied. At present, only a few studies focused on the above mentioned questions.

Abies holophylla, a typical species of the genus *Abies*, is one of the main timber species that exists in temperate coniferous and broadleaved mixed forest during late succession in Northeast China. *A. holophylla* generationally coexists with other species to form multi-tier and uneven aged stand in natural forests. Most natural communities of *A. holophylla* have a scattered distribution with little clumps in the forest. The regeneration of *A. holophylla* mainly occurs in the understory in natural forests. The regenerated seedlings grow poorly in a full light environment (Jin et al. 2008) and grow slowly in the environment with a canopy density greater than 0.8 (Yao et al. 2012). However, regenerated seedlings grow well in moderate light environment (e.g. canopy gap) (Liu 2012) mainly because *A. holophylla* seedlings can better absorb nutrients from soil when subjected to moderate light environment (Liu 2012), and their photosynthetic rates are relatively high (Jin et al. 2008). However, systematic studies on the differences in the photosynthetic characteristics of *A. holophylla* seedlings among different provenances under different light intensities have not been conducted. Therefore, the present work aimed to study systematically the changes in photosynthetic characteristics of *A. holophylla* seedlings from different provenances in weak light intensities, compare the differences in light adaptability of seedlings from different provenances, and explore the light acclimation mechanisms of seedlings by using setups with different light intensities in the greenhouse.

Materials and methods

Acquisition, processing of seeds, and cultivation of seedlings

Seeds were collected from six provenances with a natural distribution area of *A. holophylla* and included the following areas: Xiuyan Manchu Autonomous County, Fengcheng City, Huanren Manchu Autonomous County, Xinbin Manchu Autonomous County, Qingyuan Manchu Autonomous County in Liaoning Province and Ningan City in Heilongjiang Province in Northeast China. The climatic conditions varied among different provenances (Table 1).

Seeds from each provenance were collected from late September to early October 2011. Seed trees were selected from individual *A. holophylla* plants that are superior in local coniferous and broad-leaved mixed forest. The heights of the seed trees were greater than 30 m, and the tree ages exceeded 40 a. The cones were picked, desiccated, and threshed to obtain seeds. The wings of the seeds were removed in the modulation process in local forest farms and sent to the laboratory afterward. The seeds were cleared from debris and sealed in Ziploc plastic bags in the laboratory before being stored in the refrigerator at 4 °C.

In the laboratory, seeds were soaked in warm

Table 1 Geographical location and climatic conditions of six *Abies holophylla* provenances in Northeast China

Factors	Provenances					
	Xiuyan	Fengcheng	Huanren	Xinbin	Qingyuan	Ningan
North latitude	40°16′49″	40°27′08″	41°16′02″	41°44′03″	42°06′02″	44°10′06″
East longitude	123°17′14″	124°04′01″	125°21′40″	125°02′34″	124°55′27″	129°24′46″
Mean annual temperature (°C)	7.20	6.90	6.30	5.80	5.90	3.50
Mean temperature in January (°C)	-9.90	-17.10	-12.40	-13.90	-14.60	-18.70
Mean temperature in July (°C)	23.20	28.20	23.00	23.70	23.10	21.90
Annual temperature difference (°C)	33.10	45.30	35.40	37.60	37.70	40.60
Accumulated temperature (°C)	3151	3300	3184	3000	2853	2575
Mean annual precipitation (mm)	855	1040	815	780	770	500
Mean annual evaporation (mm)	1214	1237	1213	1225	1275	1320
Aridity index	0.70	0.84	0.67	0.64	0.60	0.38
Temperature-humidity index	0.10	0.12	0.11	0.11	0.10	0.11
Sunshine duration (h)	2373	2390	2370	2386	2419	2650
Frost-free period (d)	151	156	140	130	130	130

water at 45 °C (initial temperature) in mid-August 2012. The soaked time continued for 48 h, and the water was renewed every 12 h. After that, seeds were soaked in 0.5% $KMnO_4$ solution to disinfect for 3 h, and sterilized seeds were thoroughly rinsed with purified water. The pure seeds were then mixed with the appropriate amount of sand before the mixture was placed in the artificial climate chamber to accelerate germination at the variable temperatures (Pan 2011). Most seeds germinated about 15 d later. The gemmiparous seeds were sown into containers (cylinder-shaped container, 10 cm in height and 5 cm in diameter) when the length of the radicle was equal to the length of seed. The culture medium for seedlings is the mixture of peat and vermiculite (1:1 by volume). Entire container seedlings were planted during the end of August.

Experimental design

Four light gradients were set up with different layers of black shade nets within the glasshouse of Silviculture discipline in Experimental Forest Farm of Beijing Forestry University. The average light intensity was 650 $\mu mol \cdot m^{-2} \cdot s^{-1}$ within the glasshouse. The setup with 100% of full light (L0) served as a control. Three weak light intensity treatments were 75.08%, 55.42%, and 30.38% of full light, which were set up with one layer (L1), two layers (L1), and three layers (L3) of nets, respectively. A total of 300 robust seedlings selected from each provenance were moved into the shade nets in early September, including five repetitions from each plot. Each plot had 15 seedlings and 120 plots in total. The seedlings were fertilized weekly under exponential fertilization regimes (Duan et al. 2013) and were irrigated weekly. All seedlings were harvested 60 d later in early November.

Measurement of light response curve and CO_2 response curve

Before the end of the experiment, five robust seedlings were selected from each plot. The light response curve and CO_2 response curve of each seedling were measured using a portable photosynthetic measurement system (LI-6400, Li-Cor Inc., USA) according to the method of Xu et al. (2012). During measurement of light response curve, the CO_2 concentration was maintained at 400 $\mu mol\ mol^{-1}$ by using a CO_2 injection system in the leaf chamber. Air velocity, temperature, and air relative humidity were maintained at 500 $mL\ min^{-1}$, (25 ± 0.5) °C, and (40 ± 5)%, respectively. Photosynthetic photon flux density was changed through a red-blue light source, which is attached to the leaf chamber when the measurements were taken. During measurement of CO_2 response curve, photosynthetic photon flux density was maintained at 450 $\mu mol\ m^{-2}\ s^{-1}$ by using a red-blue light source in the leaf chamber. The maintained air velocity, temperature, and air relative humidity parameters were the same as in the measurements of the light response curve. CO_2 concentration was changed using a CO_2 injection system when measurements were taken.

Statistical analysis

All experimental data were collated and mapped by Microsoft Office Excel 2007. Multiple comparisons and analysis of variance were conducted by SPSS 16.0. The calculation of aridity index of each provenance was equal to the local mean annual precipitation divided by the local mean annual evaporation, and the temperature-humidity index was equal to the local aridity index divided by the mean annual temperature.

The non-rectangular hyperbolic photosynthetic model (Farquhar et al. 1980) was adopted in the fitting analysis of nonlinear regression of the light response curve and CO_2 response curve. Photosynthetic parameters, such as max net photosynthetic rate (P_{max}), photosynthetic capacity (P_{cap}), carboxylation efficiency (CE), CO_2 compensation point (CCP), CO_2 saturation point (CSP), apparent quantum yield (AQY), light compensation point (LCP), light saturation point (LSP), dark respiration rate (R_d), and photo respiration rate (R_p), were calculated using the method of Xu et al. (2012). Percentage of respiration (PR) was the ratio of R_d-plus-R_p to P_{max}. Genetic parameters, such as phenotypic coefficient of variation (PCV), genetic coefficient of variation (GCV), repeatability (R), and broad-sense heritability (H^2), were calculated according to the method of Zhao et al. (2011).

The sensitivity of each provenance to different light intensities was analyzed using grade scoring method of fuzzy mathematics (Jiang et al. 2008). The rate of change of each parameter of six provenances under the strongest (L0) and the weakest light intensity was scored. The rate of change was represented by the percentage of difference value between the values of L0 and L3, and the absolute values of the rate of change were graded as the score of sensitivity. The score of sensitivity of each parameter of each provenance was added to obtain the total score of sensitivity of each provenance. The larger the total score, the higher the sensitivity.

Results

Effect of light intensities on the foliar CO_2 assimilation capacity of *A. holophylla* seedlings from different provenances

The changed light intensity and provenance had a highly significant effect ($P < 0.01$) on the parameters of foliar CO_2 assimilation capacity of *A. holophylla* seedlings. The interactions between light intensity and provenance also had a highly significant effect ($P < 0.01$) on the parameters of foliar CO_2 assimilation capacity, except for CE (Table 2). The differences that caused by provenances of P_{max}, P_{cap}, CE, CCP and CSP accounted for 19.73%, 9.16%, 29.90%, 35.92%, and 25.76% of total differences, respectively.

P_{max} and P_{cap} of *A. holophylla* seedlings from all six provenances decreased by 50.33% to 16.96% and 63.84% to 48.15%, respectively, accompanied by a drop in light intensity (Figure 1a, b) and showed a highly significant

Table 2 Results of analysis of variance (ANOVA) on the foliar photosynthetic parameters of *Abies holophylla* seedlings from different provenances under different light intensities

Variant Sources	LC		P		LC × P	
	F	*Sig.*	*F*	*Sig.*	*F*	*Sig.*
P_{max}	231.636	0.000	59.605	0.000	10.786	0.000
P_{cap}	224.051	0.000	22.979	0.000	3.958	0.000
CE	9.089	0.000	4.203	0.003	0.763	0.709
CCP	170.772	0.000	100.050	0.000	7.685	0.000
CSP	3868.000	0.000	1422.000	0.000	229.892	0.000
AQY	9.397	0.000	4.945	0.001	0.345	0.986
LCP	413.853	0.000	269.537	0.000	20.540	0.000
LSP	145.774	0.000	47.130	0.000	8.534	0.000
R_d	119.064	0.000	26.435	0.000	5.219	0.000
R_p	202.275	0.000	43.580	0.000	10.128	0.000
PR	117.174	0.000	58.475	0.000	12.356	0.000

Note. Abbreviations: LC - light intensity, P - provenance, Pmax - net photosynthetic rate, Pcap - photosynthetic capacity, CE - carboxylation efficiency, CCP - CO2 compensation point, CSP - CO2 saturation point, AQY - apparent quantum yield, LCP - light compensation point, LSP - light saturation point, Rd - dark respiration rate, Rp - photo respiration rate, PR - percentage of respiration, *F* - F value, *Sig.* - significance level.

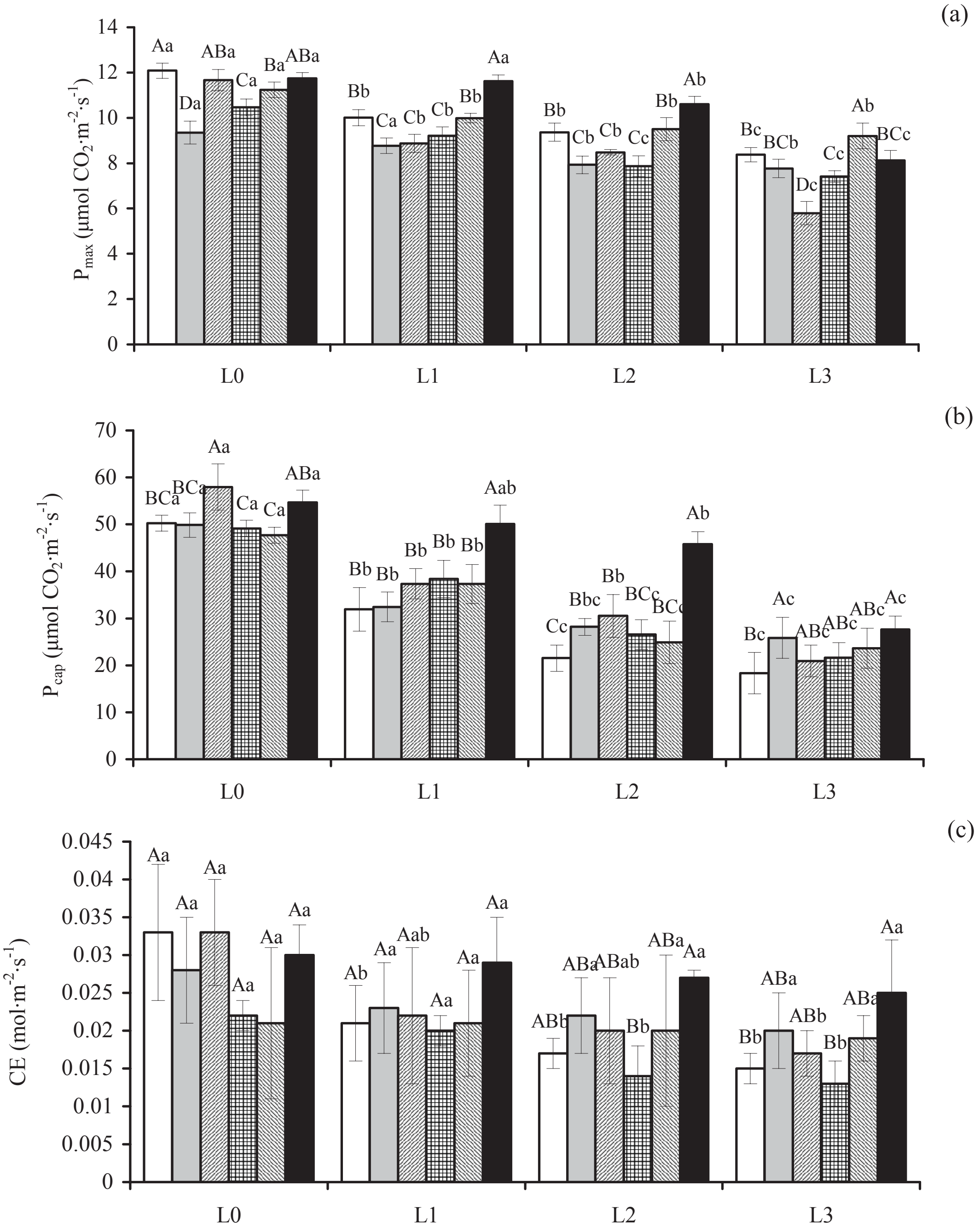

Figure 1 Effect of light intensities on the foliar CO_2 assimilation capacity of *Abies holophylla* seedlings from different provenances. (a) P_{max}, (b) P_{cap}, (c) CE, (d) CCP, and (e) CSP. Error bars are SDs. Different capital letters above the error bars represent significant differences among different provenances under the same light intensity at the 0.05 level, and different small letters above the error bars represent significant differences among different light intensities of the same provenance at the 0.05 level

difference ($P < 0.01$) among different light intensities. CE decreased with decreased light intensity (Figure 1c). Xinbin and Xiuyan provenances showed highly significant differences ($P < 0.01$) and significant differences ($P < 0.05$) among different light intensities. CCP and CSP decreased by 33.03% to 10.85% and 43.44% to 19.67%, respectively, with decreased

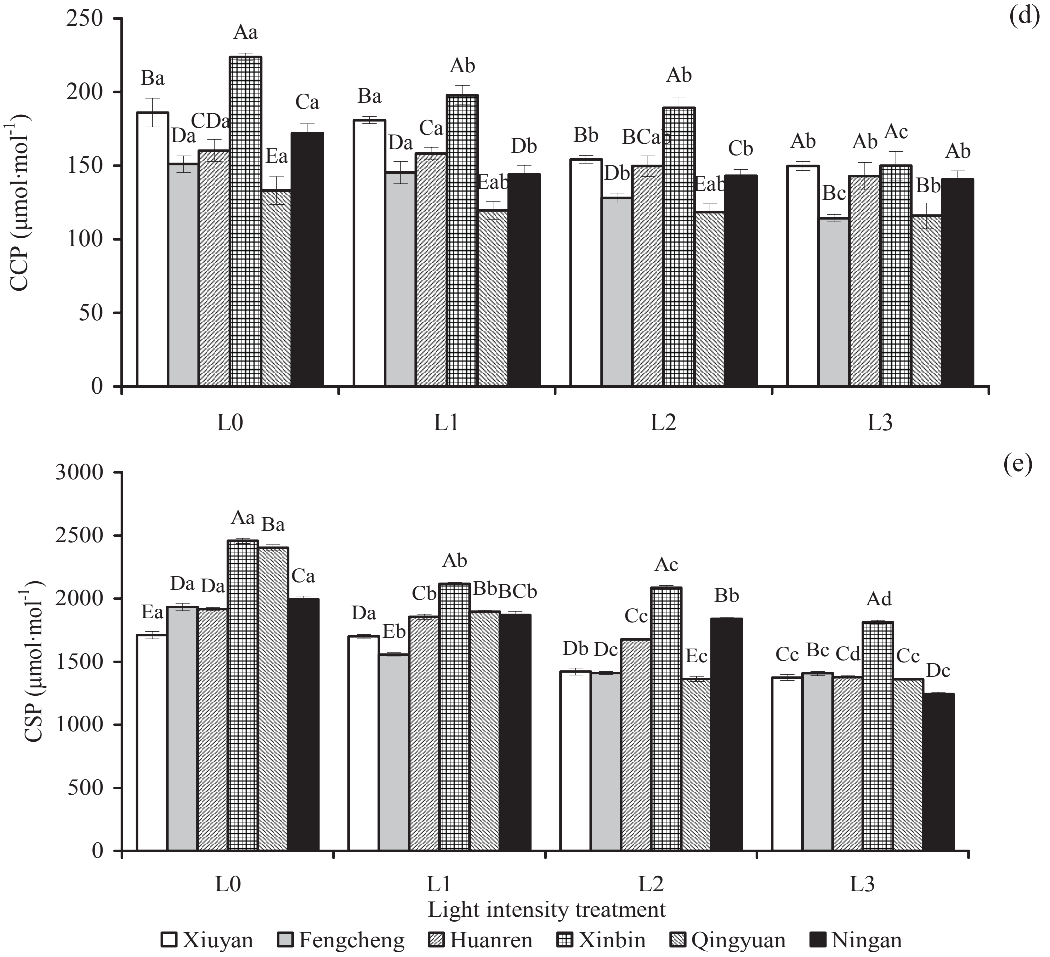

Figure 1 (continuation)

light intensity (Figure 1d, e), except for Huanren and Qingyuan provenances, which had the smallest decrease in CCP with no significant difference between different light intensities. CCP and CSP of all other provenances showed highly significant differences ($P < 0.01$) among different light intensities.

Effect of light intensities on the foliar light utilization capacity of *A. holophylla* seedlings from different provenances

The changed light intensity and provenance had a highly significant effect ($P < 0.01$) on the foliar light utilization capacity of *A. holophylla* seedlings. Interaction between light intensity and provenance also showed a highly significant effect ($P < 0.01$) on foliar light utilization capacity, except for AQY (Table 2). The differences in AQY, LCP, and LSP among different provenances accounted for 33.67%, 38.29%, and 23.40% of the total differences, respectively.

As the light intensity dropped, the AQY of *A. holophylla* seedlings from all six provenances sharply increased by 29.17% to 100.00% (Figure 2a), but no significant difference in AQY was observed at different light intensities. LCP and LSP decreased by 92.41% to 59.65% and 38.93% to 14.37%, respectively, with the drop in light intensity (Figure 2b, c), except for the LSP of Huanren provenance, which showed significant differences ($P < 0.05$) at different light intensities. The LCP and LSP of all other provenances showed highly significant differences ($P < 0.01$) at different light intensities.

Effect of light intensities on the foliar respiration depletion of *A. holophylla* seedlings from different provenances

The changed light intensity and provenance had a highly significant effect ($P < 0.01$) on the parameters of foliar respiration depletion of *A. holophylla* seedlings. Interactions between light intensity and provenance also had a highly significant effect ($P < 0.01$) on the parameters of foliar respiration depletion (Table 2). The differences in R_d, R_p and PR due to provenance accounted for 17.54%, 17.02%, and 31.10% of the total differences, respectively.

As the light intensity dropped, the R_d, R_p, and PR of *A. holophylla* seedlings from six provenances decreased by 68.52% to 45.35%, 63.41% to 21.22%, and 46.88% to 11.96%, respectively (Figure 3a-c). Except for the R_p and PR of Qingyuan provenance, which showed no significant difference between different light intensities, the R_d, R_p, and PR of all other provenances showed highly significant differences ($P < 0.01$) at different light intensities.

Genetic variation analysis of foliar photosynthetic parameters of *A. holophylla* seedlings from different provenances under different light intensities

Except for CE, the differences in terms of P_{max}, P_{cap}, CCP and CSP of *A. holophylla* seedlings from six provenances were highly significant ($P < 0.01$) under each light intensity treatment (Table 3). Under different light intensities, the PCV and GCV of the parameters of foliar CO_2 assimilation capacity ranged from 8.43% to 32.23% and 4.87% to 19.76%, respectively. Except for the R of CE, which was about 0.5, the R of the parameters of foliar CO_2 assimilation capacity was above 0.8, which indicates a higher genetic stability of foliar CO_2 assimilation capacity in the *A. holophylla* population. The H^2 of P_{max}, CCP, and CSP was higher than 0.7, which suggests that the foliar CO_2 assimilation capacity of *A. holophylla* seedlings from six provenances was strongly controlled by genetic factors.

The differences in AQY of *A. holophylla* seedlings from six provenances were not significant difference ($P < 0.05$) under each light intensity treatment, but the differences in LCP and LSP showed a highly significant difference ($P < 0.01$) under each light intensity treatment (Table 3). Under different light intensities, the values of PCV of LCP reached the maximum, and the value range was the broadest among the parameters of foliar light utilization capacity. However, the value and the value range of PCV of LSP showed opposing trends; the GCV showed a similar trend. The R of LCP and LSP was above 0.8, which indicates a high genetic stability of foliar light utilization capacity in the *A. holophylla* population. The H^2 values of LCP and LSP were above 0.4, implying moderate and over heritability, respectively. This finding shows that the foliar light utilization capacity of *A. holophylla* seedlings from six provenances is also strongly controlled by genetic factors.

All of the differences in R_d, R_p, and PR of *A. holophylla* seedlings from six provenances were all highly significant ($P < 0.01$) under each light intensity treatment (Table 3). Under different light intensities, the PCV of R_d, R_p, and PR ranged from 12.18% to 39.11% and were slightly higher than 8.14% to 23.48% of GCV. The R of R_d, R_p, and PR ranged from 0.84 to 0.98. The H^2 values ranged from 0.46 to 0.90, which indicates that the foliar respiration depletion of *A. holophylla* seedlings from six provenances had high genetic stability and was also strongly controlled by genetic factors.

On the basis of the above genetic variation analysis, the change in trend of PCV of foliar photosynthetic parameters of *A. holophylla* seedlings from different provenances was found to be similar to the change in the trend of GCV in response to changed light intensity. The change in the R was also similar to the change in the trend of H^2.

Table 3 Genetic parameters of foliar photosynthetic parameters of *Abies holophylla* seedlings from different provenances under different light intensities

Parameters	Treatments	*F*	*Sig.*	Mean	SD	PCV (%)	GCV (%)	R	H^2
P_{max}	L0	20.680	0.000	11.09	1.01	9.12	6.34	0.95	0.77
	L1	30.009	0.000	9.74	1.04	10.65	7.59	0.97	0.83
	L2	22.028	0.000	8.96	1.05	11.71	8.18	0.95	0.78
	L3	21.381	0.000	7.78	1.14	14.60	10.17	0.95	0.77
P_{cap}	L0	5.880	0.006	51.60	4.35	8.43	4.87	0.83	0.45
	L1	8.484	0.001	37.92	6.98	18.40	11.49	0.88	0.56
	L2	18.748	0.000	29.58	8.48	28.66	19.76	0.95	0.75
	L3	7.954	0.008	23.00	4.51	19.59	9.76	0.87	0.54
CE	L0	1.679	0.214	0.03	0.01	27.72	-	0.40	-
	L1	1.849	0.541	0.02	0.01	26.48	-	0.46	-
	L2	1.711	0.206	0.02	0.01	32.23	-	0.42	-
	L3	2.895	0.061	0.02	0.01	29.48	-	0.65	-
CCP	L0	55.696	0.000	171.03	30.25	17.69	12.92	0.98	0.90
	L1	73.508	0.000	157.71	26.79	16.99	12.50	0.99	0.92
	L2	66.122	0.000	147.16	23.59	16.03	11.76	0.98	0.92
	L3	15.568	0.000	135.57	16.43	12.12	8.22	0.94	0.71
CSP	L0	481.245	0.000	2068.88	279.08	13.49	10.12	0.99	0.99
	L1	361.590	0.000	1833.14	179.55	9.79	7.34	0.99	0.98
	L2	818.059	0.000	1632.27	271.73	16.65	12.51	0.99	0.99
	L3	474.548	0.000	1428.89	184.57	12.92	9.69	0.99	0.99
AQY	L0	2.239	0.117	0.02	0.01	34.74	-	0.55	-
	L1	1.703	0.632	0.02	0.01	32.95	-	0.41	-
	L2	1.351	0.309	0.03	0.01	23.19	-	0.26	-
	L3	2.638	0.078	0.03	0.01	21.02	-	0.62	-
LCP	L0	129.141	0.000	21.59	9.86	45.66	33.93	0.99	0.96
	L1	86.463	0.000	15.81	9.23	58.39	43.11	0.99	0.93
	L2	66.675	0.000	7.70	6.56	85.17	62.52	0.99	0.92
	L3	35.385	0.000	5.17	4.70	90.99	65.34	0.97	0.85
LSP	L0	41.641	0.000	468.02	83.66	17.88	12.93	0.98	0.87
	L1	6.127	0.005	387.07	35.67	9.22	5.38	0.84	0.46
	L2	5.286	0.009	354.96	35.70	10.06	5.65	0.81	0.42
	L3	21.472	0.000	327.52	38.97	11.90	8.29	0.95	0.77
R_d	L0	14.838	0.000	0.84	0.17	20.69	13.92	0.93	0.69
	L1	16.282	0.000	0.57	0.17	30.46	20.83	0.94	0.74
	L2	6.247	0.004	0.49	0.14	28.73	16.87	0.84	0.46
	L3	6.945	0.003	0.34	0.13	39.11	23.48	0.86	0.48
R_p	L0	36.439	0.000	4.76	1.11	23.26	16.73	0.97	0.86
	L1	12.922	0.000	3.55	0.61	17.08	11.34	0.92	0.67

Table 3 (continuation)

Parameters	Treatments	*F*	*Sig.*	Mean	SD	PCV (%)	GCV (%)	R	H^2
	L2	9.591	0.000	2.89	0.55	19.02	12.13	0.90	0.59
	L3	10.399	0.000	2.44	0.57	23.56	15.19	0.90	0.61
PR	L0	54.877	0.000	50.51	8.48	16.78	12.25	0.98	0.90
	L1	13.710	0.000	42.42	5.17	12.18	8.14	0.93	0.68
	L2	10.316	0.000	37.75	5.18	13.71	8.83	0.90	0.61
	L3	26.651	0.000	36.32	8.31	22.89	16.19	0.96	0.81

Note. Abbreviations: *F* - F value, *Sig.* - significance level, Mean - mean value, SD - standard deviation, PCV - phenotypic coefficient of variation, GCV - genetic coefficient of variation, R - repeatability, and H2 - broad-sense heritability.

Comprehensive assessment of the sensitivities of *A. holophylla* seedlings from different provenances to changed light intensities

The sequence of the reaction sensitivities of *A. holophylla* seedlings from six provenances to changed light intensities was Xinbin> Xiuyan> Huanren> Ningan> Fengcheng > Qingyuan (Table 4). The above results indicate that the adaptability of the seedlings from Xinbin provenance was the strongest when subjected to weak light intensity, and the rangeability of foliar photosynthetic parameters was the widest; thus, its sensitivity was the highest. The adaptability of the seedlings from Qingyuan provenance was the weakest, and the effect of changed light intensities on foliar photosynthetic parameters was the smallest; thus, its sensitivity was the lowest.

Correlation was found between the sensitivities of *A. holophylla* seedlings to changed light intensities and the geological and climatic conditions of *A. holophylla* provenances (Table 5). The correlation between sensitivity scores and annual temperature difference was the strongest ($r = -0.717$), followed by mean tempera-

Table 4 Sensitivity analysis of *Abies holophylla* seedlings from different provenances to changed light intensities

Parameters	Provenances					
	Xiuyan	Fengcheng	Huanren	Xinbin	Qingyuan	Ningan
P_{max}	2	1	3	2	1	2
P_{cap}	4	3	4	3	3	3
CE	3	2	3	3	1	1
CCP	1	2	1	3	1	1
CSP	1	2	2	2	3	2
AQY	4	2	4	3	2	3
LCP	4	3	4	4	4	4
LSP	2	2	1	2	2	2
R_d	3	3	4	4	3	4
R_p	4	3	3	4	2	2
PR	3	1	1	3	1	1
Total score	31	24	30	33	23	25
Sensitivity order	2	5	3	1	6	4

ture in January (r = 0.654) and mean annual evaporation ($r = -0.584$). However, all the correlations were not statistically significant ($P <$ 0.05). The correlation coefficients between sensitivity scores and other geological and climatic factors of *A. holophylla* provenances were smaller than the three above mentioned values.

The results showed that temperature range and effective precipitation of provenance probably were the main factors that affected the sensitivities of *A. holophylla* seedlings to changed light intensities on some level. The *A. holophylla* seedlings from the large annual temperature difference and high effective precipitation area were less sensitive to changed light intensities compared with the seedlings from the small annual temperature difference and low effective precipitation area, which had lower photosynthetic plasticity in changed light environments. Therefore, the adaptability to light intensities of the latter was worse than that of the former.

Discussion

The light response curve and the CO_2 response curve of plant photosynthesis are significant in understanding the photochemical efficiency in photochemical processes of plants (Wientjes et al. 2013). P_{max} is an important indicator that directly reflects the photosynthetic capacity of plants. All P_{max} of *A. holophylla* seedlings from six provenances were significantly lower than the control (L0) under weak light intensity treatments in varying degrees (Figure 1a). However, the range of declines was broad, which indicates that variations existed among *A. holophylla* seedlings from different provenances to adapt with changed light intensities. The increase in atmospheric CO_2 concentration can promote plant photosynthesis at a certain range. The P_{cap} that could be achieved by *A. holophylla* seedlings from different provenances varied under different light environments (Figure 1b), which suggests that differences in the foliar CO_2 assimilation capacity exist among different provenances under changed light intensities. CE of *A. holophylla* seedlings from different provenances decreased with decreased light intensity (Figure 1c). The results suggest that the activity and content of ribulose bisphosphate carboxylase/oxygenase (Rubisco) were restrained under weak light environments, and different levels of restrictions led to differences among different provenances under same light intensities. The general characteristics of low CCP crops were high P_n and yield. The CCP of C_3 plants was about 30 μmol·mol^{-1} to 70 μmol·mol^{-1} (Mao et al. 2012), but the CCP of *A. holophylla* seedlings remained above 110 μmol·mol^{-1} under the weakest light intensity (Figure 1d), implying a higher demand for CO_2 by *A. holophylla* seedlings. High CSP reflects strong adaptability of plants to the environment (Shi et al. 2010). Obvious CO_2 saturation was not

Table 5 Correlation coefficients of sensitivity scores and geological and climatic factors of *Abies holophylla* provenances

Factors	Sensitivity scores	Factors	Sensitivity scores
North latitude	−0.168	Mean annual precipitation (mm)	−0.106
East longitude	−0.153	Mean annual evaporation (mm)	−0.584
Mean annual temperature (°C)	0.143	Aridity index	−0.026
Mean temperature in January (°C)	0.654	Temperature-humidity index	−0.401
Mean temperature in July (°C)	−0.441	Sunshine duration (h)	−0.353
Annual temperature difference (°C)	−0.717	Frost-free period (d)	−0.206
Accumulated temperature (°C)	0.169		

observed in *A. holophylla* seedlings from all six provenances under different light intensities, consistent with the theory that the CSP of C_3 plants was not obvious, and the P_n of C_3 plants will rise with the increase with an increase in atmospheric CO_2 concentration even if the CO_2 concentration was relatively high (Larcher 2003).

The AQY of plants ranged from 0.03 to 0.05 in general (Galmés et al. 2013), but AQY of *A. holophylla* seedlings from different provenances ranged only from 0.01 to 0.04 (Figure 2a), which is slightly lower than the normal range. This result suggests that the foliar weak light utilization capacity of *A. holophylla* seedlings is not very strong under normal circumstances. The range of values in terms of LCP and LSP reflects the utilization range of light energy of plants. Lower LCP and LSP values were conducive to sufficient utilization of low photon density for plant photosynthesis under weak light environments, thereby increasing the accumulation of organic matter to maintain the carbon balance (Sun et al. 2007).

The decrease in R_d resulted in dry matter accumulation, which allowed the plants to maintain a relatively stable state even though P_n decreased under weak light intensities. The relative stability is of great significance to the plants that survive in a frequently changing environment (Song et al. 2009). The process of R_p leads to the loss of carbon, which has been assimilated with CO_2 (Zhu et al. 2010). Therefore, the reduction in R_p has a similar function with the reduction in R_d under weak light environments, and also decreased the respiration depletion of photosynthetic products. In this study, the reduction in R_d and R_p under weak light environments (Figure 3a, b) could serve as a strategy of *A. holophylla* seedlings to maintain the accumulation of assimilation products. Notably, the PR decreased as the light intensity dropped (Figure 3c) but was still maintained at a high level. This finding demonstrates that photosynthetic products of *A. holophylla* seedlings were largely consumed by respiration and the amount of net accumulations of assimilation products was less, which is likely the main reason for the slow growth of *A. holophylla* seedlings during the seedling stage.

Generally, plants need a protection mechanism, a damage repair mechanism, or a combination of both to survive in stressful environments (Dinakar et al. 2012). Being a species which situating later succession stage in communities, the regenerated seedlings of *A. holophylla* were shaded for a long time in natural stand. The foliar weak light utilization capacity is critical to the survival and development of the species. In this study, the foliar photosynthesis of *A. holophylla* seedlings enhanced CO_2 assimilation capacity through the reduction of CCP and CSP, improved weak light utilization capacity, and reduced light energy demand, thereby resulting in enhanced light utilization capacity through the increase in AQY and the reduction in LCP and LSP. Those changes also reduced respiration depletion though the decrease in R_d and R_p. The above mentioned series of photosynthetic physiological changes in *A. holophylla* seedlings effectively improved the utilization efficiency of weak light, and made the plant fully adapted to the understory shaded environment to secure the energy required for survival and growth so that regeneration can be carried out.

Phenotypic variation is the result of genetic factors and environmental factors working together. The differences in terms of CO_2 assimilation capacity, light utilization capacity, and respiration depletion of *A. holophylla* seedlings from six provenances were all highly significant ($P < 0.01$). PCV and GCV were highly varied, which indicates the large differences in photosynthetic parameters of *A. holophylla* seedlings among different provenances, implying abundant genetic variation basis and the enormous selection potentials. *R* and H^2 were proven to be reasons for the existence of differences in photosynthetic parameters among different provenances. The *R* and H^2 of each

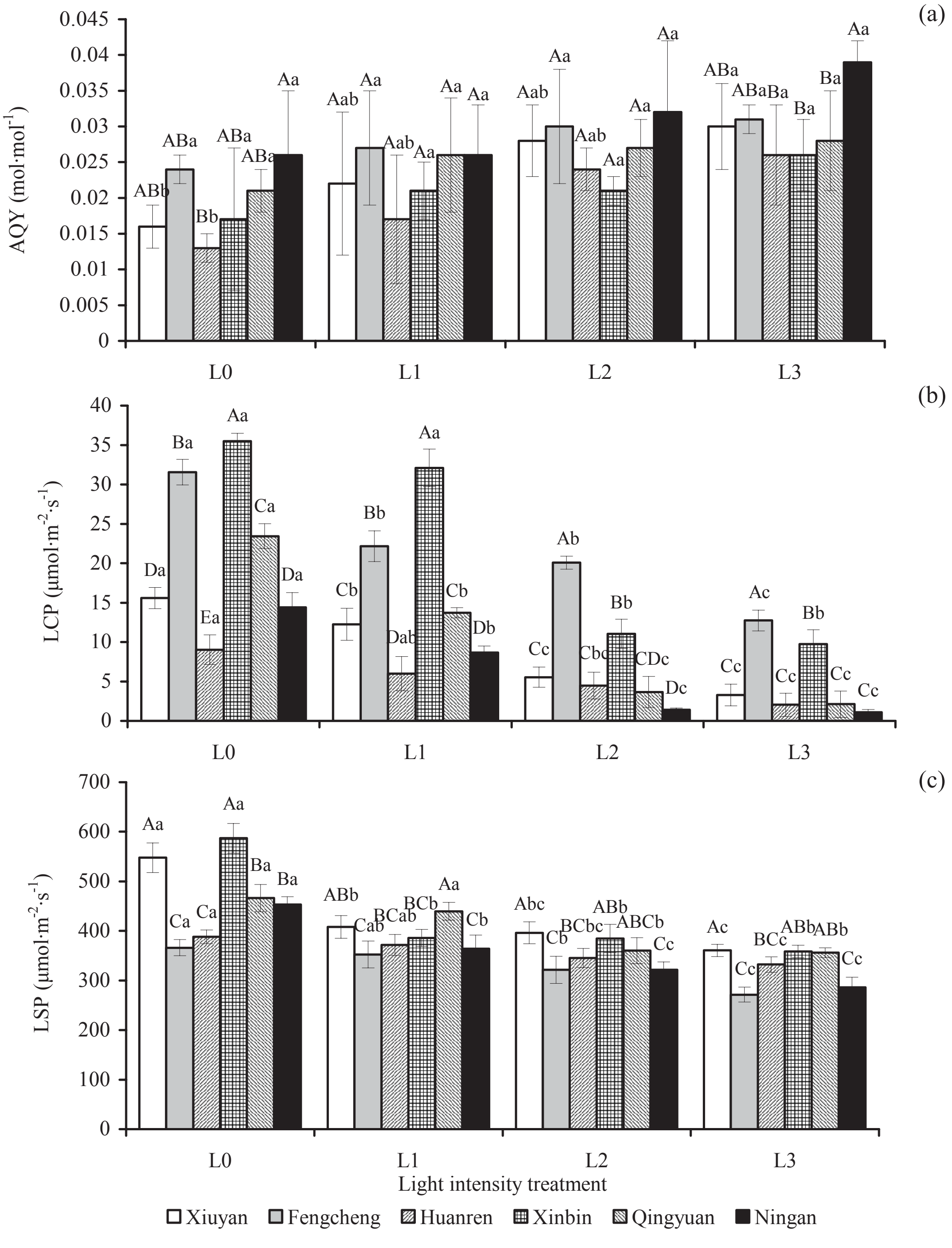

Figure 2 Effect of light intensities on the foliar light utilization capacity of Abies holophylla seedlings from different provenances. (a) AQY, (b) LCP, and (c) LSP. Same notes as Figure 1

photosynthetic parameter were higher than other factors, thus indicating that the variations in the parameters were strongly controlled by genetic factors instead of environmental factors. The genetic stability of populations was also relatively high.

The foliar photosynthetic characteristics of *A. holophylla* seedlings were mainly controlled by genetic factors, which led to different sensitivities and different adaptabilities of seedlings from different provenances to changed light intensities (Table 4), which resulted in signifi-

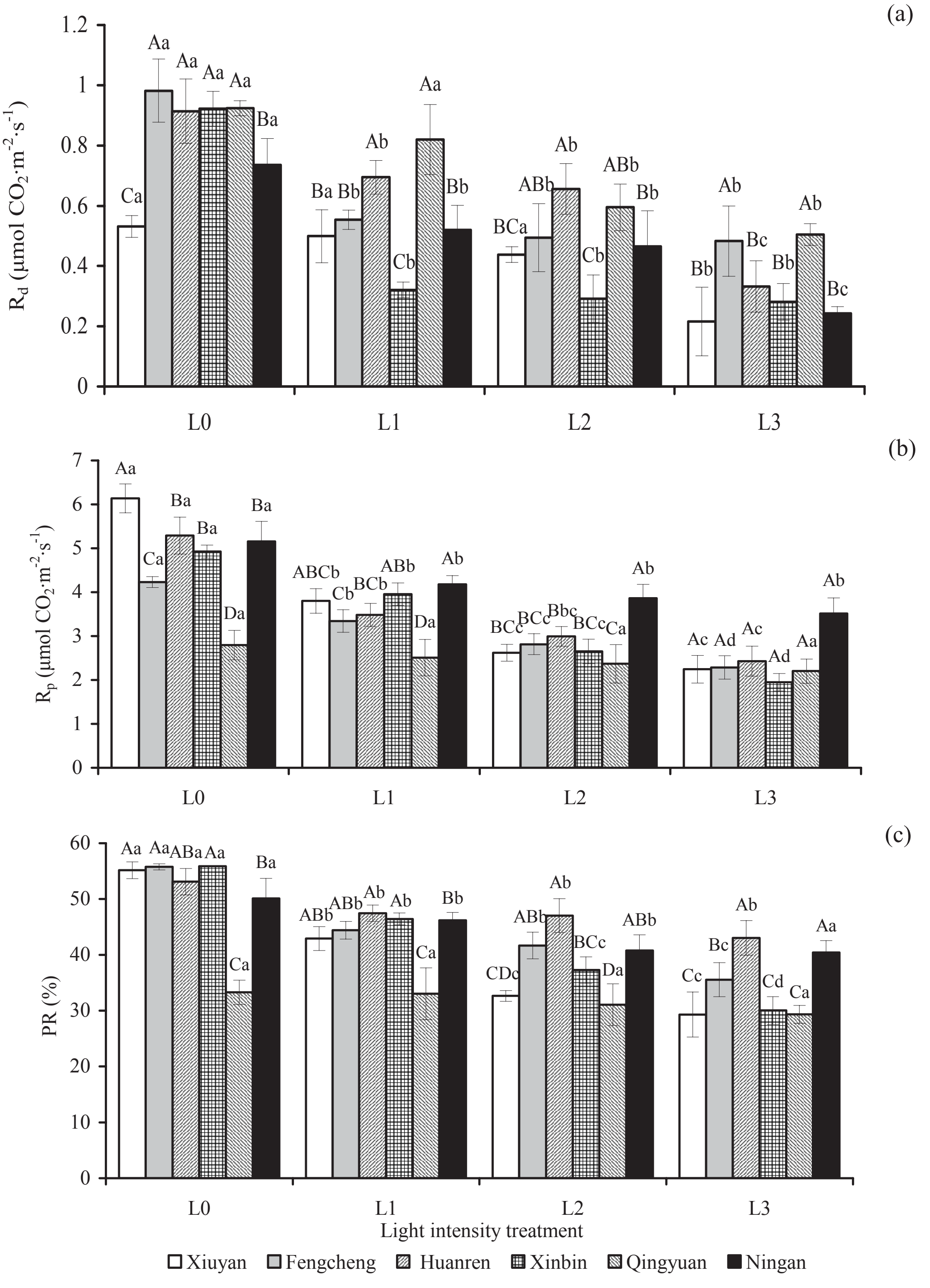

Figure 3 Effect of light intensities on the foliar respiration depletion of Abies holophylla seedlings from different provenances. (a) Rd, (b) Rp, and (c) PR. Same notes as Figure 1

cant differences among different provenances. There were no significant correlation ($P < 0.05$) between the sensitivities of *A.holophylla* seedlings to changed light intensities and the geological and climatic conditions of *A. holophylla* provenances (Table 5), but the relationships of sensitivities and annual temperature difference, mean temperature in January and mean annual evaporation of provenance were most closely related. The results showed that though the sensitivities of *A. holophylla* seedlings to changed light intensities were not controlled by a single environmental factor. Instead, temperature range and effective precipitation of provenance probably were the main factors which affected phenotypic plasticity of *A. holophylla* seedlings.

Conclusions

Light intensities have significant effects on the foliar photosynthetic parameters of *A. holophylla* seedlings from six provenances. As the light intensity dropped, the foliar CO_2 assimilation capacity of *A. holophylla* seedlings sharply decreased, and the foliar light utilization capacity significantly increased. The observed photosynthetic physiological changes are crucial to the survival and growth of regenerated seedlings of *A. holophylla* in natural stand. Highly significant differences in the CO_2 assimilation capacity, the light utilization capacity, and the respiration depletion of *A. holophylla* seedlings were observed among six provenances under different light intensities. The variations in foliar photosynthetic parameters of *A. holophylla* seedlings were abundant among different provenances and were mainly controlled by the genetic factors of the provenance itself. The observed significant differences in foliar photosynthesis of *A. holophylla* seedlings among different provenances were caused by the different sensitivities to changed light intensities. Correlation analysis showed that temperature range and effective precipitation of provenance were probably the main factors that affected phenotypic plasticity of *A. holophylla* seedlings.

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