

青海高原矮嵩草和珠芽蓼的光合适应性比较

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摘要: 对生长在两个海拔地带(3 200 m, 3 980 m)的矮嵩草(*Kobresia humilis* Serg.) 和珠芽蓼(*Polygonum viviparum* L.) 叶片的叶绿素荧光特性及其叶绿体超微结构进行了比较研究。海拔升高, 矮嵩草和珠芽蓼叶片的 F_v/F_o 、 F_v/F_m 和 Rfd 值均增大, 且矮嵩草的 F_v/F_o 、 F_v/F_m 和 Rfd 值均大于珠芽蓼。叶绿体超微结构的结果显示, 海拔升高, 珠芽蓼和矮嵩草的叶绿体都表现出一定程度的变形, 但珠芽蓼的叶绿体变形和类囊体膜肿胀现象更为显著。研究表明, 矮嵩草和珠芽蓼光合作用对高山胁迫环境具有很强的适应性, 且矮嵩草的适应能力比珠芽蓼强。

关键词: 高山植物; 矮嵩草; 珠芽蓼; 叶绿素荧光; 叶绿体超微结构

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Comparison of Photosynthetic Adaptability Between *Kobresia humilis* and *Polygonum viviparum* on Qinghai Plateau

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Abstract: The chlorophyll fluorescence parameters of *Kobresia humilis* Serg. and *Polygonum viviparum* L. grown at two different altitudes (3 200 m, 3 980 m) were measured and the ultrastructure of chloroplasts were observed for studying the photosynthetic adaptability of plants to the influences of stress conditions in alpine environment. Rfd -values, the vitality index, in leaves of *K. humilis* and *P. viviparum* grown at 3 980 m were higher than those at 3 200 m. The higher ratio of F_v/F_o and F_v/F_m in leaves of *K. humilis* and *P. viviparum* indicated that the rate of photosynthetic conversion of light energy increased at higher altitude. Ratios of F_v/F_o and F_v/F_m and Rfd -values in *K. humilis* were higher than that in *P. viviparum* grown at the same altitude. There were more irregular chloroplasts in leaves of both species grown at higher altitude. Many irregular chloroplasts such as swollen thylakoid, deformed chloroplast envelope, were observed in *P. viviparum* grown at 3 980 m, but few in *K. humilis*. These results were discussed in relation to the photosynthetic adaptability of alpine plants and the different adaptive competence between *K. humilis* and *P. viviparum*.

Key words: alpine plants; *Kobresia humilis*; *Polygonum viviparum*; chlorophyll fluorescence; ultrastructure of chloroplast

The influences of stress factors on photosynthesis have been studied by some authors^[1,2], but none was interested in the photosynthetic adaptability of plants grown in adverse environments. Studies of the alpine plants that adapted to low temperature, strong radiation, and low atmospheric pressure would benefit the understanding of the mode of resistance of plants on stress. Investigations on photosynthetic characteristics of alpine plants, including gas exchange, pigment content and optimal growing temperature, have been described^[3], but those on the

efficiency of the conversion light energy and the ultrastructure of chloroplast are still absent. This paper describes characteristics of chlorophyll fluorescence and ultrastructure of chloroplast in typical alpine plant *Kobresia humilis* and *Polygonum viviparum*, species widely distributed in the area of high altitude. Adaptability to stress of these two species was compared.

1 Materials and Methods

1.1 Experimental materials

Leaves of the two species were collected in sunny

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days after the flowering stage of the plants at 3 200 m and 3 980 m altitude respectively in the area near the Haibei Alpine and Frigid Meadow Ecosystem Station of The Chinese Academy of Sciences in Qinghai Plateau. At the altitude of 3 200 m, *Kobresia humilis* Serg. was collected from the river-flood-land meadow and *Polygonum viviparum* L. from the *P. viviparum* meadow, while at the altitude of 3 980 m, both of the species were collected from the ridge meadow of Daban Mountain. Part of the collected leaves was fixed immediately for ultrastructural study (see below for the detailed description) and part was sealed in plastic bags kept at 0–5 °C for physiological measurement in the laboratory. The experiments were repeated for two years.

1.2 Methods

For the estimation of the fluorescence dynamic parameters, Pulse-amplitude-modulation (PAM) fluorometer was used, with 480 nm as the exciting light, the light intensity was lower than $10 \text{ ergs} \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$. The saturation light with far-red light filtered intensity was higher than $2 \times 10 \text{ ergs} \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$. The actinic light gate was controlled by an electronic shutter with a half-time $t_{1/2} < 2.5 \text{ ms}$. Thirty min dark pretreatment of the leaves was conducted at room temperature before the measurement.

For ultrastructure investigation, the leaves were cut into $0.5 \text{ mm} \times 0.5 \text{ mm}$ pieces and immediately fixed in 5% glutaldehyde (in sodium-cacodylate buffer, pH 7.2) for 3 h and then washed in the same buffer 3 times, each for 30 min. The specimens were refixed in 1% osmic acid (in the same buffer) overnight in the refrigerator, and then washed three times with the buffer, three times with distilled water, (30 min each time), and then dehydrated in the alcohol series, kept overnight in acetone, and embedded in the resin Epson 812. The specimen were sectioned and stained with uranium acetate-lead citrate, and finally observed and photographed under the JEM-100 CX transmission electron microscope.

2 Results

2.1 Dynamic induction of chlorophyll fluorescence

Table 1 presents the ratios of variable fluorescence to constant fluorescence (F_v/F_o) that reflects PS II activity, and the ratios of variable fluorescence to maximum fluorescence (F_v/F_m) that show the efficiency of the primary conversion of light energy in PS II [4]. These two ratios in both species were stronger in the samples from the higher altitude, which might indicate that the activities and the efficiency of light energy conversion in PS II were much higher at higher altitude than at the lower altitude.

The ratios (Rfd) of fluorescence decay (F_d) to stable fluorescence (F_s) is shown in Table 2, Rfd is an index of plant vigor [5] in terms of potential photosynthetic quantum conversion. Similar to the results of Table 1, the values of Rfd were also higher in the samples of both species from higher altitude, indicating higher potential photosynthetic activity.

Table 1 Comparison of F_v/F_o , F_v/F_m in the leaves of *Kobresia humilis* and *Polygonum viviparum* grown at two altitudes

Altitude (m)	<i>K. humilis</i>		<i>P. viviparum</i>	
	F_v/F_o	F_v/F_m	F_v/F_o	F_v/F_m
3 200 m	3.272 ± 0.022	0.781 ± 0.007	3.217 ± 0.020	0.763 ± 0.005
3 980 m	3.604 ± 0.032	0.815 ± 0.009	3.460 ± 0.025	0.784 ± 0.010

Table 2 Comparison of Rfd in leaves of *Kobresia humilis* and *Polygonum viviparum* grown at two altitudes

Altitude (m)	3 200 m	3 980 m
<i>K. humilis</i>	6.2 ± 0.2	7.9 ± 0.5
<i>P. viviparum</i>	2.9 ± 0.3	3.5 ± 0.3

It is interesting to notice that the values of all the above parameters in *K. humilis* (F_v/F_o , F_v/F_m , Rfd) were more or less higher as compared to *P. viviparum* at the same altitude.

2.2 Ultrastructures of chloroplast

The structure of chloroplast from *K. humilis* grown at 3 200 m was orderly arranged with elliptic shapes and regular thylakoid membranes (Fig. 1, A), only few chloroplasts were deformed. But some irregularities, including shrunk chloroplast envelopes, particularly narrow protoplasmic spaces, etc., obviously increased in the specimens collected at 3 980 m (Fig. 1, B).

The chloroplasts of *P. viviparum* is the specimens collected at different altitudes were much more different. In specimen at 3 200 m altitude, chloroplasts had the regular and elongated-elliptic appearance, but at 3 980 m altitude, chloroplasts were irregularly deformed with loosely arranged thylakoids and more starch grains (Fig. 1, C and D).

3 Discussion

The alpine plants are always well adapted to stress environmental conditions such as low temperature, strong radiation and low atmospheric pressure, but it has been described that photosynthetic activity and the efficiency of quantum conversion decreased under some stress conditions [6]. The two species used in this work were collected from the typical alpine environs. At the location of 3 200 m altitude, the average temperature of a year, is 0.6 °C and the temperatures in January and July are -13.0 °C,



Fig. 1. Electron micrographs of mesophyll cells of *Kobresia humilis* and *Polygonum viviparum* grown at two altitudes. A. *K. humilis* (EI. 3 200 m). Chloroplasts are regular elliptic in shape, $\times 5\ 000$. B. *K. humilis* (EI. 3 980 m). Some chloroplasts are irregular oval in shape, $\times 3\ 300$. C. *P. viviparum* (EI. 3 200 m). Chloroplasts are regular long elliptic in shape. Thylakoids are arranged in order, $\times 5\ 000$. D. *P. viviparum* (EI. 3 980 m). Chloroplasts are swollen and controlled, thylakoids are loosen, with more starch grain, $\times 5\ 000$.

Abbreviations: Chl, chloroplast; S, starch grain.

12.3 °C respectively, and the minimum and maximum of the temperature throughout a year are - 31.5 °C and 27.5 °C, respectively, while at the location of 3 980 m altitude, the environment is especially cold, along with occasional strong atmospheric current and sleet and hail. The values of Rfd increased with increasing altitude, indicating that the potential photosynthetic activity did not reduce with chlorophyll concentration at higher altitude, this means the photosynthetic adaptability of these two plant species. The values of F_v/F_o and F_v/F_m were also higher at the higher altitude, indicating their higher efficiency of quantum conversion in PS II. Our former investigation has already shown the higher photosynthetic rate of these two plant species at higher altitude^[7]. In this work, we have found again the reduced chlorophyll contents and elevated ratio of chlorophyll a to b of these two plant species at the higher altitude^[7,8].

Observations on the ultrastructures of chloroplasts of these two species demonstrated that *P. viviparum* suffered more impacts of alpine stress than *K. humilis* (such as the chloroplast deformation and the irregular appearance of the thylakoids, etc.), but the increased values of F_v/F_o , as well as F_v/F_m were not in correlation with these structural changes, therefore more work are needed to reveal the relation between the structure of chloroplasts and their photosynthetic activities.

In other papers we have also reported the higher light saturation and compensation points, the lower optimal growing temperature, the higher efficiency of primary light energy conversion in PS II and the lower contents of light-harvesting antenna pigment-protein complexes^[7-9] in these two alpine plants, that might reflect the adaptive and regulative ways for plants to fit to the influences of environmental stress. All the above characteristics of the two plant species might be a sort of adaptive strategy, more work is needed to study the mechanism of such strategy at molecular level.

Both characteristics of the chlorophyll fluorescence and the ultrastructure of chloroplasts showed the higher adaptability of *K. humilis* to the alpine conditions comparing with *P. viviparum*, that coincided with their

natural distributions in the Qinghai Plateau, where both are growing well at 3 200 m, but only few of *P. viviparum* at the 3 980 m.

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