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Photosynthetic performance in Antarctic lichens with different growth forms reflect the diversity of lichenized algal adaptation to microhabitats

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Abstract: Lichens, as typical obligate associations between lichenized fungi and their photosynthetic partners, are dominant in Antarctica. Three Antarctic lichens, *Ochrolechia frigida*, *Umbilicaria antarctica*, and *Usnea aurantiaco-atra* with different growth forms, were sampled nearby the *Great Wall* Station, King George Island. Molecular data revealed that the photosynthetic algae in these three lichens were *Trebouxia jamesii*. The net photosynthesis (Pn) of three individuals from these species, together with environmental factors such as light and temperature, were recorded by CO_2 gas exchange measurements using a CI-340 portable photosynthetic system *in situ*. Differences between T(leaf) (the temperature of the thalli) and T(air) (the air temperature) for these lichens were not consistent, which reflected that environment and the growth form of thalli could affect T(leaf) significantly. Strong irradiation was expected to have adverse effects on Pn of *Ochrolechia frigida* and *Umbilicaria antarctica* whose thalli spread flat; but this photoinhibition had little effect on *Usnea aurantiaco-atra* with exuberant tufted thallus. These results indicated that photosynthetic activity in lichens was affected by the growth forms of thalli besides microhabitat factors. One species of lichenized alga could exhibit diversified types of photosynthetic behavior when it was associated with various lichenized fungi in different microhabitats. It will be helpful for understanding how lichens are able to adapt to and colonize in extreme environments.

Key words: Antarctic, lichens, lichenized, molecular phylogenetics, photosynthesis, *Trebouxia*.

Introduction

Lichen can be looked as a mini-ecosystem the most often composed of one fungus (lichenized fungus) and its photosynthetic partner (photobiont, which could be green algae or cyanobacterium). The photobiont provides carbohydrates for the mini-ecosystem, and obtains protection against harsh environments from mycobiont. Lichens harbor tenacious vitality to make them adapt to many extremely adverse ecological conditions.

Up to now, over 17 500 lichen species have been reported (Kirk *et al*. 2008), while only 200 photobionts species (about 100 species of cyanobacteria, and 100 species of green algae) have been known (Tschermak-Woess 1988). This means that some alga species must be shared by a wide variety of lichens. Therefore, it is rationale to hypothesize that lichenized algae could expand their distribution range by the symbiotic relationship between them and various lichenized fungi. One typical example is the green alga *Trebouxia jamesii*, which is harboured by many lichen species worldwide distributed (Li *et al*. 2013).

Lichens are the dominant vegetation of the Antarctic flora, and 427 lichen species have been recorded in the Antarctic continent (Øvstedal and Smith 2001; Engelen *et al*. 2010). Lichens play crucial roles in the terrestrial ecosystem in Antarctica, especially in the carbon cycle because of the primary production contributed by photobionts; so the CO_2 accumulation of Antarctic lichens has been a hot topic in lichenology over decades. In the King George Island where the Chinese *Great Wall* Station locate, *Ramalina terebrata* was the first lichen whose photosynthesis was measured in field using CO_2 exchange method (Kappen *et al*. 1986). Recently, the growth rate of *Usnea aurantiaco-atra* collected in this region was determined by radiocarbon (^{14}C) (Li *et al*. 2014). Up to date, the photosynthesis for many Antarctic lichens has been investigated using various ways such as chlorophyll fluorescence and CO_2 exchange (Kappen *et al*. 1990; Sancho *et al.* 2007), and numerous researches focused on the production of organic carbon in lichens based on the photosynthetic data. For lichen genera *Buellia* and *Lecidea* which were dominated in the Antarctic desert, the primary production was calculated between 0.108 and 4.41 mg C m^{-2} $year^{-1}$, and these values were regarded as the lowest ones on Earth (Vestal 1988). In another study, net photosynthetic carbon incorporation was estimated to be 84 mg C m^{-2} $year^{-1}$ for Antarctic cryptoendolithic communities, which is also an extremely low rate of net photosynthesis (Johnston and Vestal 1991). The difference between these values implies that there were numerous decomposers including filamentous fungi, bacteria and yeast under the surface rock crust consuming photosynthetic products. Besides, 606 mg C m^{-2} $year^{-1}$ of net photosynthetic gain and 3 mg C m^{-2} $year^{-1}$ of net ecosystem productivity were calculated for lichen-dominated cryptoendolithic community in Antarctica; using a computer analysis based on laboratory measurements of CO_2 exchange and field climate data during 1985–1988 the huge discrepancy between

these two values was considered to account for the leaching of organic substances to the rock (Friedmann *et al*. 1993). According to the photosynthetic determination for lichens, it is suggested that lichens contribute greatly to Antarctic ecosystem in carbon cycle.

Lichen communities of the Antarctica exhibit a psychrophilic temperature response observed at the maximal photosynthetic rate at 10°C, by contrast, the optimal temperature for cyanobacteria communities ranged between 20°C and 30°C (Johnston and Vestal 1991). Antarctic lichens have been well adapted to sub-zero temperatures. For example, *Umbilicaria antarctica* and *Xanthoria elegans*, had photosynthetic activity at -15°C (Barták *et al*. 2007), and the net photosynthesis and dark respiration could occur below zero temperature for *Umbilicaria aprina* (Schroeter and Scheidegger 1995). However, it seems that the temperature activating the photosynthesis of the Antarctic lichens is species-specific. When covered by the snow, *Xanthoria mawsonii* could be activated when temperature was below -10°C, while *Physcia dubia* just exhibited activation at temperatures around -5°C and would not be fully activated until its thallus temperature was above 0°C, but *Candelariella flava* always remained inactive even if the thallus temperature was below 0°C (Pannewitz *et al*. 2003). Though the photosynthetic activity of different lichen species was investigated and some factors affecting photosynthetic activities had been revealed (Palmer and Friedmann 1990a; Palmer and Friedmann 1990b; Liden *et al*. 2010; Munzi *et al*. 2014), the definite algal species were not identified for the photobionts in most studies. Therefore, it remains uncertain whether difference of photosynthetic performance in these lichens were mainly influenced by different photobionts. Since the photosynthetic capacity of a lichen is contributed by its photobiont, it is not surprising that lichen would display various photosynthetic response if their photosynthetic partner were different. In order to reduce photosynthetic variances caused by different photobionts, three Antarctic lichens, *Ochrolechia frigida*, *Umbilicaria antarctica*, and *Usnea aurantiaco-atra*, whose algal partners are the same green algal species *Trebouxia jamesii*, were used in the present study to investigate the algal specific response to the growth forms of lichens. The growth forms of the three lichens are crustose, foliose and fruticose respectively.

Materials and methods

Samples. — During the 27th CHINARE (from December 2010 to January 2011), a total of 11 lichen samples including one *Ochrolechia frigida* individual (crustose), five *Umbilicaria antarctica* individuals (foliose) and five *Usnea aurantiaco-atra* individuals (fruticose), were investigated (the collection information was summarized in Table 1). After a series of preliminary experiments

Table 1

Information for lichen samples investigated in this study.

No.	Species	Substrate	GenBank Accession No.		Latitude (S)	Longitude (W)
			Fungal ITS	Algal ITS		
P1	*Ochrolechia frigida**	soil	KP954318	KP954302	62°12'58.07"	58°57'45.61"
P2	*Usnea aurantiaco-atra* *	rock	KP954313	KP954305	62°12'57.71"	58°57'45.66"
P3	*Umbilicaria antarctica**	rock	KP954322	KP954311	62°12'57.31"	58°57'45.04"
P4	*Umbilicaria antarctica*	rock	KP954323	KP954312	62°12'42.14"	58°55'38.22"
P5	*Umbilicaria antarctica*	rock	KP954319	KP954310	62°13'03.57"	58°57'57.33"
P6	*Umbilicaria antarctica*	rock	KP954320	KP954303	62°13'03.58"	58°57'57.30"
P7	*Umbilicaria antarctica*	rock	KP954321	KP954304	62°13'16.35"	58°57'11.97"
P8	*Usnea aurantiaco-atra*	rock	KP954314	KP954306	62°12'42.12"	58°55'38.25"
P9	*Usnea aurantiaco-atra*	rock	KP954317	KP954307	62°12'40.68"	59°00'28.25"
P10	*Usnea aurantiaco-atra*	moss	KP954316	KP954309	62°13'34.20"	58°57'14.55"
P11	*Usnea aurantiaco-atra*	rock	KP954315	KP954308	62°13'46.50"	58°57'32.49"

* the sample was used for the measurement of photosynthetic activity formally.

that determined the optimized measurement method in field conditions, three samples (*Ochrolechia frigida* P1, *Usnea aurantiaco-atra* P2 and *Umbilicaria antarctica* P3) were selected to survey the Pn activity formally.

DNA extraction and PCR. — Total DNA of both symbionts was extracted using a modified CTAB method (Zhou *et al*. 2006). ITS sequences for mycobionts and photobionts were amplified using the fungal specific primer pairs ITS5 and ITS4 (White *et al*. 1990) and the algal specific primer pairs ITS1T and ITS4T (Kroken and Taylor 2000). The parameters for PCR reactions were as follows: initial denaturation of 95°C for 5 min, then followed by 30 cycles of 94°C for 40 s, 50–55°C for 40 s, 72°C for 2–4 min. These cycles were followed by a final extension at 72°C for 10 min. The amplification products were verified electrophoretically in 0.8% agarose gel, and were purified with Gel Extraction Mini Kit (Omega Bio-tek, Inc.).

DNA sequencing and data analysis. — Sequencing reactions were carried out with an ABI3730XL Sequencer and double-stranded PCR products were sequenced. The sequencing primers were the same as those used for PCR.

Double-directional sequences were checked and assembled using the SEQMAN (DNASTAR Inc.), and the regions of the small subunit and large subunit rDNA flanking the ITS region were trimmed. Alignments of the ITS sequences obtained from mycobionts and photobionts were performed by the ClustalW algorithm included in MEGA 5 (Tamura *et al*. 2011) respectively. The phylogenetic structure of each alignment was constructed with maximum likelihood (ML) method, and the re-

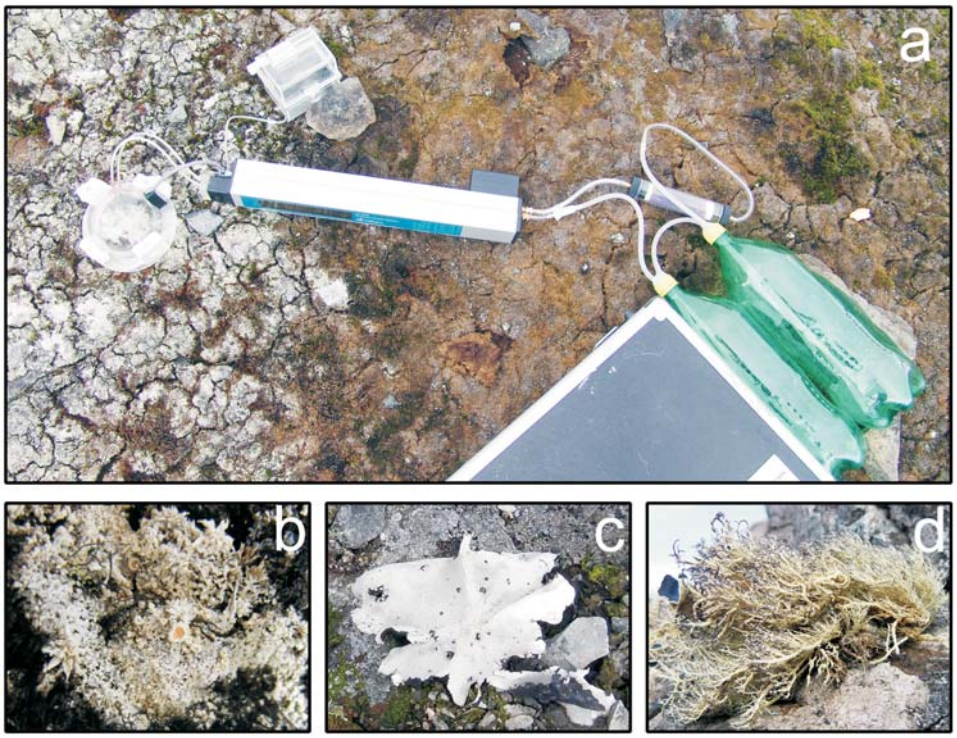

Fig. 1. Measurement of photosynthetic activity were carried out *in situ* for *Ochrolechia frigida* with a customized hemispherical leaf chambers (diameter is 10 cm) and two 2-liters buffer bottles (**a**), thallus growth forms for crustose *Ochrolechia frigida* (**b**), foliose *Umbilicaria antarctica* (**c**) and fruticose *Usnea aurantiaco-atra* (**d**).

liability of the inferred trees was tested with bootstrap searches of 1000 resamplings. The default parameters were used in all the analyses above.

Determinant of CO_2 exchanges. — The CO_2 exchanges for three Antarctic lichens, *Ochrolechia frigida* (P1), *Umbilicaria antarctica* (P3), and *Usnea aurantiaco-atra* (P2) (Fig. 1) , were determined with a Handheld Photosynthesis System CI-340 (CID Bio-Science, Inc., USA) near the Chinese *Great Wall* Station in King George Island, during the 27th Chinese National Antarctic Expedition in summer. According to the size of samples, the measurements were carried out *in situ* using different customized hemispherical leaf chambers whose diameters are 10 cm (for *O. frigida*) and 22 cm (for *Usnea aurantiaco-atra*), together with one original square chamber (5 cm × 6 cm × 1 cm) (for *Umbilicaria antarctica*) under natural conditions. The substrates for all samples were covered by the leaf chambers for all measurements when Pn was measured, and the "close system" mode was set and default parameters were used. The measurements were carried for a total of 57 hours for these three lichens in different days. The data were dealt and illustrated in EXCEL 2003 (Microsoft, Inc.), and decorated using Illustrator CS4 (Adobe, Inc.).

Results

Molecular identification of the mycobiont and photobiont of lichens. — Molecular data confirmed the morphological identification of lichen species, and identified photobiont species (Fig. 2). Individuals of lichenized fungi from *Ochrolechia frigida*, *Umbilicaria antarctica* and *Usnea aurantiaco-atra* formed well supported groups according to their species with high bootstrap values respectively; and the sequences of the same mycobiont showed few differences among distinguishable species (Fig. 2a).

All lichen individuals in the present study were found to associate with *Trebouxia jamesii* as their photobionts, and the bootstrap value for the monophyletic clade of *T. jamesii* was 96 % (Fig. 2b).The same ITS haplotypes of *T. jamesii* were found to be shared by different lichen species. For example, the algal ITS sequences from *Umbilicaria antarctica* (P7) and *Usnea aurantiaco-atra* (P2) were the same.

Photosynthetic performance for lichens. — Though our data were achieved just during the 27th Chinese National Antarctic Expedition and only 57 hours of uncontinuous measurements in the present study were carried out, typical photosynthetic performance for these three lichen species have been observed.

The photosynthetic activity of crustose lichen *O. frigida* was measured for over 16 hours in three days, and the typical results were shown in Fig. 3a. For *O. frigida*, the air temperature (T(air)) and the temperature of the thalli (T(leaf)) were almost the same all the time regardless of light intensity, and they had a strong relation to photosynthetic active radiation (PAR). When PAR was higher than about 2000 μmol m^{-2} s^{-1}, photoinhibition, namely light-induced reduction in the photosynthetic capacity, was observed, and net photosynthesis (Pn) was close to zero after PAR dropped to 500 μmol m^{-2} s^{-1}.

The photosynthetic activity of foliose lichen *Umbilicaria antarctica* was represented in Fig. 3b, which was measured for about 13 hours in five days. In these measurements, T(leaf) were nearly 2–5°C higher than T(air) if PAR was higher than about 1000 μmol m^{-2} s^{-1}, and photoinhibition could also be observed when PAR was above 2000 μmol m^{-2} s^{-1}. However, its Pn was still obviously positive even that PAR was a little lower than 500 μmol m^{-2} s^{-1}, and T(leaf) and T(air) were nearly the same at such situations.

The measurements of photosynthetic activity for fruticose lichen *Usnea aurantiaco-atra* were carried out for more than 28 hours in six days. The representative results has been illustrated in Fig. 3c. T (leaf) was over 5°C higher than T(air) even if PAR was only 500 μmol m^{-2} s^{-1}, and the difference between these two temperatures would be enlarged when the PAR increased. However, no obvious photoinhibition was observed even when Pn was higher than 2000 μmol m^{-2} s^{-1}, and T(leaf) and T(air) became identical just as PAR tended to be zero.

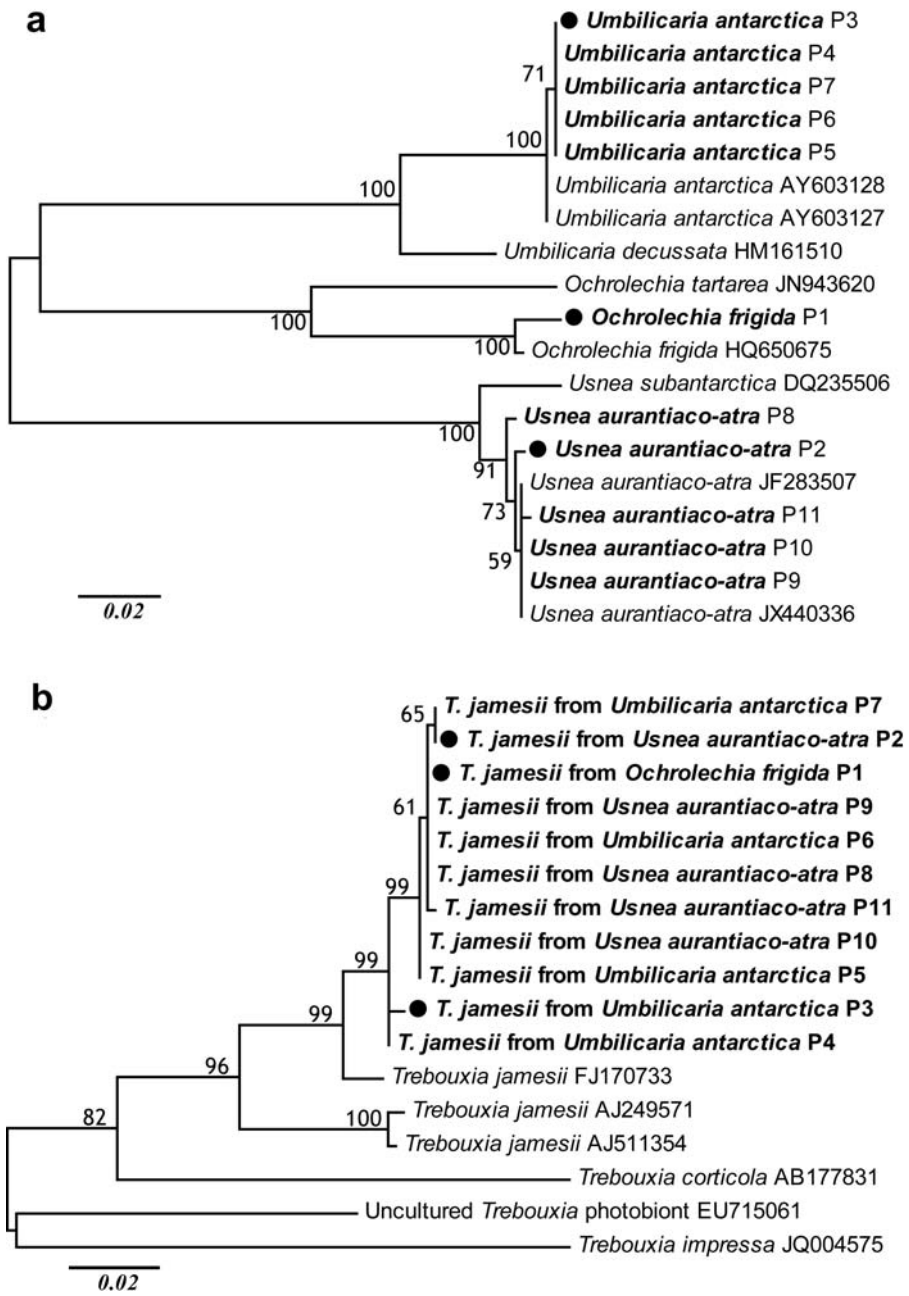

Fig. 2. The ML tree constructed with ITS rDNA sequences of the mycobionts (**a**) and photobiont (**b**). The reliability of the trees was tested by 1000 bootstrap replications, and numbers at nodes were the bootstrap support values (numbers <50 not shown). The names with bold font represent those sequences obtained in present study; names with regular font represent those sequences retrieved from GenBank; and black dots indicates that the photosynthetic activities were determined for these samples.

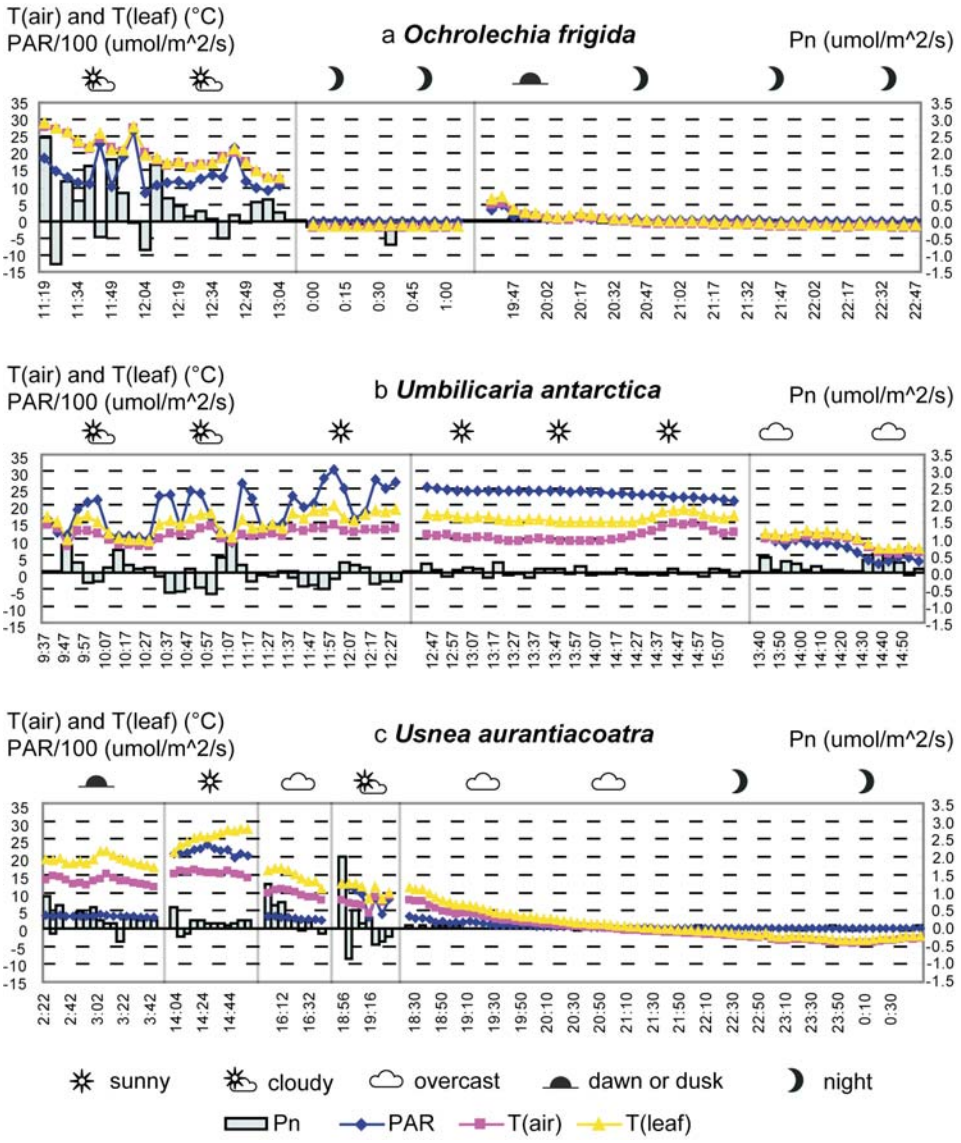

Fig. 3. Photosynthetic activity of crustose lichen *Ochrolechia frigida* (**a**), foliose lichen *Umbilicaria antarctica* (**b**) and fruticose lichen *Usnea aurantiaco-atra* (**c**). The humidity is not illustrated in the figure since it is always nearly 100% and lack of fluctuations in King George Island in summer. It also should be noticed that the measurements were not carried out on the same day even for the same individual.

Discussion

Molecular data not only confirmed the morphological identification of lichen species (Fig. 2a), but also revealed that all the photobionts in the present study

were green algae: *Trebouxia jamesii* (Fig. 2b), so the difference of photosynthetic performance among these lichens implied that photosynthesis in lichens was conferred by fungal partners besides microhabitat factors such as the types of substrate and the water content. *Usnea aurantiaco-atra* is the dominant lichen species in King George Island and *Umbilicaria antarctica* is the most popular foliose lichen in this region, so *T. jamesii,* as their algal partner, must be the most abundant photobiont in King George Island. It has been widely accepted that the association with locally adapted algae will enlarge the ecological range of lichenized fungi so that they can obtain adaptive potential for colonization (Piercey-Normore and DePriest 2001; Peksa and Škaloud 2011; Dal Grande *et al.* 2014; Werth and Sork 2014). However, our results showed that lichenized algae could exhibit various types of photosynthetic adaptation by association with different lichenized fungi. Hence, the interplay between both symbionts was critical for lichens to colonize in changing environments. In another word, the photosynthesis behavior of those three lichens, can be looked as that of the green algae *T. jamesii* located in different fungal micro habits. The same haplotypes of *T. jamesii* were shared by different lichen species, such as *Umbilicaria antarctica* (P7) and *Usnea aurantiaco-atra* (P2) (Fig. 2b), which implied that lichens in this region could obtain their photobionts from an algal pool. However, *T. jamesii* is not the only photosynthetic partner for lichens in King George Island (Romeike *et al*. 2002; De los Rios *et al*. 2005), which suggests that these lichens exhibit a high selectivity to their algal partners.

A series of preliminary experiments to explore the appropriate measure method *in situ*, not only the best optimized way was determined, but also the individuals which exhibited satisfactory performance were chosen to be used in the formal experiments. Based on the results of preliminary experiments, two 2-liters buffer bottles were linked to the vent in series in order to average CO_2 changes over time, and a column filled with silica-gel drier was appended to the system to avoid the formation of moisture or condensation inside the leaf chamber. Also, three individuals which exhibited satisfactory performance were chosen to be used in the formal experiments, to reveal the photosynthetic response to environmental factors in lichens.

There was a strong correlation between temperature and PAR in daytime revealed by Fig. 3, and our results showed that T(leaf) of lichens growing on the rock (*Umbilicaria antarctica* and *Usnea aurantiaco-atra*) was higher than T(air). Rock is easy to be heated under strong light radiation. As a result, lichens growing on rocks in the sunny side, can be warmed up easily through thermal conductivity. Though the thallus of *Umbilicaria antarctica* was close to the rock, its flat structure was also favour heat dissipation. In contrast, highly branched thallus of *Usnea aurantiaco-atra* was apt to keep heat even when light intensity was not strong. Thus, the difference between T(leaf) and T(air) for this lichen was higher than that for *U. antarctica*. For the crustose lichen *O. frigida* which grows on the land surface, its T(leaf) and T(air) were always nearly the same. In fact, photosynthetic parameters were also measured for the moss on the ground, and its T(leaf) was even

lower than T(air) (data not shown). Unlike those lichens on rock, the vegetation on the land together with their substrates (mainly soil) can maintain abundant water in this humidity environment in summer even when the PAR is high. Therefore, T(leaf) of these vegetation was not higher than T(air) because their substrates were difficult to be heated by PAR due to the high heat capacity of water. As for *O. frigida*, since the white thallus surface was against heat absorption, its T(leaf) and T(air) were always almost identical. These results indicate that T(leaf) of lichens exhibited substrate dependence. Photosynthetic efficiency of lichens could be influenced by temperature (Maphangwa *et al*. 2012; Tretiach *et al*. 2013), that means that substrate would have an impact on the photosynthesis of lichens. The maximum registered temperature is around 8°C in King George Island; however, our measurements for photosynthetic activity were executed in sealed system and heat could not dissipate to atmosphere arbitrarily, which caused that the measured air temperature were higher than that of the environment, especially when the light intensity was strong.

Generally, available water has the greatest influence on the photosynthetic activity in lichens. The lichens that occupy different ecological niches use water differently (Palmer and Friedmann 1990a), and many species absorb and utilize water vapor to adapt to terrestrial conditions. Since water vapor uptake is regarded as a physical process not affected by physiology (Palmer and Friedmann 1990b), lichens can obtain enough water as long as environmental humidity is high. The mean relative humidity (RH) in King George Island was 90.8% during 2010–2013 based on the climate data (http://www.aari.aq/default_en.html; http://polar.chinare.gov.cn/meteo/), and RH were always above 90% and often reached 100% in our measurements, which indicate that water is not a critical influential factor for the photosynthesis of lichens in this area. Hence, we suggest that temperatures including T(air) and T(leaf), and photosynthetic active radiation (PAR), instead of water, are major factors for the photosynthesis of lichens in King George Island.

Net photosynthesis (Pn) is positive if only light intensity exceeds the compensation point, but it will be decreased to zero or became negative if PAR is too high, which is a protective mechanism called photoinhibition (Bidussi *et al*. 2013). Furthermore, continuous light may also decrease the photosynthetic rate of lichens (Korhonen and Kallio 1987). It was found that Pn of *Umbilicaria antarctica* had been around zero if PAR was continuously strong (Fig. 3b), indicating that both photosynthetic and respiration activities were repressed at such occasions. These results suggest that continuous strong light decrease all the metabolism of the lichen.

The effect of growth forms of lichens on photoinhibition were not well investigated previously. Since strong light would cause photoinhibition, relative high Pn was observed when PAR was moderate. However, fruticose *Usnea aurantiaco-atra* has positive Pn while PAR is larger than 2000 μmol m^{-2} s^{-1}. Unlike flat thalli of *O. frigida* or *Umbilicaria antarctica*, the mature thallus of *Usnea aurantiaco-atra* is

generally composed of many exuberant tufted branches, and the bulky top part of thallus can block sunlight from the bottom part. As a result, the bottom part still has photosynthetic activity even when light is strong, just like shadow under canopy. When light intensity is weak, the top part also becomes photosynthetic active. Hence, *Usnea aurantiaco-atra* exhibits positive Pn in a wider range of PAR. This is just a simple effect of sunshade, so fruticose lichens may still exhibit photoinhibition if their branches are sparse; for example, high degree of photoinhibition was caused by strong irradiance (2000 μmol m^{-2} s^{-1}) in fruticose *Umbilicaria antarctica* (Barták *et al*. 2003). In contrast to those of *Usnea aurantiaco-atra* and *Umbilicaria antarctica*, Pn of *O. frigida* is about zero when PAR is just below 500 μmol m^{-2} s^{-1}. It is suggested that the white surface of its upper thallus cause a low efficiency of light utility so that its photosynthesis was weaken. It needs to be emphasized that the biomass per unit area were pronouncedly different for three lichens in the present study, which indicated that the content of *T. jamesii* per unit area were likely to vary in different lichens. Therefore, the production of CO_2 accumulation which is represented by Pn, could not be looked as a good index to judge the photosynthetic potential for lichens with different growth forms. It is also worthy of noting that the measurements were executed *in situ*, which meant that the substrates were not removed from the lichen thalli so that both lichenized and nonlichenized members in the leaf chambers were included. Hence, the Pn obtained would be less than those for separate lichen because the consumption of decomposers was not taken into account (Friedmann *et al*. 1993). Therefore, such speculation cannot be excluded, that is, the zero of Pn observed in *O. frigida* when PAR was slightly lower than 500 μmol m^{-2} s^{-1}, was just likely to be caused by more decomposers on the ground than on rock. The amount of decomposers should be in consideration if a more accurate conclusion would be drawn. Another possibility is that depression of Pn at thallus saturation was found in *O. frigida* when its thallus was water-rich at low PAR. In this scenario, Pn is decreased as internal CO_2 diffusive resistance is increased in thallus with high water content (Schipperges 1992).

Though Pn may have dramatic fluctuation in daytime because of weather conditions, it is nearly zero for lichens at night. These results indicate that light intensity is very important in determining the photosynthetic activities of organisms in King George Island. The variations of photosynthetic physiological characteristics for *T. jamesii* in different lichen species can reflect the interplay between algae and their fungal partners besides the microclimate of their habitats.

According to the monthly values of meteorological parameters from the *Bellingshausen* Station in King George Island (http://www.aari.aq/data/data.asp?lang=0&station=0), from October to March in next year, the monthly mean air temperatures generally above -5°C at which most lichens have photosynthetic activities if light and water are sufficient. Hence, the weather conditions in these months are suitable for the photosynthetic activity of lichens because the temperature is moderate and the humidity is enough high. However, a snow depth more

than 15 cm would block the light and inhibit the photosynthesis of most lichens although the photosynthetic activity was detected for a few lichens under shallow snow (Pannewitz *et al*. 2003). Hence, the months that are suitable for lichen's photosynthesis in King George Island should be December, January, February and March, and the mean sunshine duration for these four months from 2010 to 2013 was 325 hours, which was also the period that is favorable for the photosynthetic activity of lichens in a year.

Though our data were achieved just during the 27th Chinese National Antarctic Expedition and only 57 hours of discontinuous measurements in the present study were carried out, typical photosynthetic performance for these three lichen species have been observed. The present study illustrates that besides photobiont diversity and the environmental factors, growth forms of lichen thalli are also the important factor that can determine photosynthetic performance of lichens. This result provides new information for understanding how the lichens exhibit their adaptation so that they can play key role in Antarctic terrestrial ecosystem.

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