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# Potential of four mosses as aquarium plants-deduced from their photosynthetic parameters in water

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**Abstract:** Aquatic mosses could be used as aquarium plants, many semi-aquatic mosses are also able to grow in aquaria. In eastern China, there are few aquatic mosses. Is it possible to use some terrestrial mosses in aquaria? In order to answer the question, we elucidated the adaptability of focal terrestrial mosses to water environment. In the present work, we measured the photosynthetic parameters of four terrestrial mosses including *Brachythecium procumbens*, *Hypnum hamulosum*, *Leucobryum glaucum*, and *Hedwigia ciliata* under conditions similar to their natural habitats and those after their submersion in water. We also made their photosynthetic light-response curves by using rectangular hyperbolic model. We found significant differences among their maximum net photosynthesis rate ( $P_n$ ), light saturation point ( $LSP$ ), and light compensation point ( $LCP$ ). The variation ranges of their maximal  $P_n$ ,  $LSP$  and  $LCP$  were from 122.575 to 19.099  $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , from 1 166.00 to 670.030  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , and from 85.000 to 5.3  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively. After *Brachythecium procumbens*, *Hedwigia hamulosum* and *Leucobryum glaucum* had been submerged in water for 30 d, their maximal  $P_n$  were 110.78%, 80.84% and 109.63% of the control, respectively, indicating that these three mosses are able to survive in water during the experimental period. While submerged in water for 20 d, *Hedwigia ciliata* had only 5.25% net photosynthetic rate of the control, revealing that *H. ciliate* is not able to grow in aquatic environment. We also discussed the relationships of their photosynthesis with their morphological structure and habitat conditions. Our analyses showed that *Brachythecium procumbens*, *H. hamulosum* and *Leucobryum glaucum*, though distribute in terrestrial habitats in the field, were three potential aquarium plants.

**Key words:** terrestrial mosses; photosynthesis; submersion; aquarium plants

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## 基于光合参数探讨四种藓类作水族箱植物的应用潜力

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**摘要:** 水生藓类植物适宜作为水族箱植物,许多半水生藓类植物同样能够生长于水体环境中。中国东部地区的水生藓类植物种类不多,陆生藓类植物能否应用于水族箱中?为了回答这一问题,需要阐明陆生藓类植物对水体环境的适应能力。该研究测定了匍枝青藓(*Brachythecium procumbens*),弯叶灰藓(*Hypnum hamulosum*)、白发藓(*Leucobryum glaucum*)和虎尾藓(*Hedwigia ciliata*)在与它们的自然生境相似条件下以及沉水环境下的光合参数,并应用直角双曲线模型拟合了它们的光—光合响应曲线。结果表明:这四种藓类植物在最大净光合

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速率( $P_n$ )、光饱和点(LSP)和光补偿点(LCP)上存在很大差异。它们的最大净光合速率、光饱和点和光补偿点的变异范围分别为  $122.575\sim 19.099 \mu\text{mol CO}_2 \cdot \text{kg}^{-1}\text{DW} \cdot \text{s}^{-1}$ 、 $1\ 166.00\sim 670.030 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  和  $85.000\sim 5.3 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 。在沉水环境中生长 30 d 后,匍枝青藓、弯叶灰藓和白发藓的最大净光合速率分别是对照的 110.78%、80.84% 和 109.63%,说明在实验周期里这三种藓类植物能够在水体环境中生存,而虎尾藓在水体中浸泡 20 d 后,其最大净光合速率仅为对照的 5.25%,反映出该种植物并不适应水体环境。综上可知,四种藓类植物的光合速率与其形态结构和原生境条件有很大的关系,虽然匍枝青藓、弯叶灰藓和白发藓主要分布于陆生环境,但作为水族箱植物也具有一定的应用潜力。

**关键词:** 陆生藓类; 光合作用; 沉水环境; 水族箱植物

Aquatic mosses have been applied as decorative plants in aquaria. They also provide oxygen, hiding places, and egg-laying substrates for fishes (Benl, 1958; Takaki *et al.*, 1982). In markets, the representative aquarium bryophytes are *Fissidens fontanus*, *Bryum pseudotriquetrum*, *Fontinalis antipyretica*, *Lep- todictyum riparium*, *Platyhypnidium riparioi- des*, *Riccia fluitans*, *Ricciocarpos natans*, *Taxiphyl- lum barbieri*, and *Vesicularia dubyana* (Benl, 1958; Takaki *et al.*, 1982; Gradstein *et al.*, 2003; Tan *et al.*, 2004).

Mosses are fundamentally similar to other plants in their basic nutrition requirements. However, they have specific way to obtain nutrients. Even if mosses are able to use their rhizoids to gather some nutrients, their rhizoids can not penetrate into soils. Mosses mainly rely on nutrients from dust on their surfaces or dissolved in rainfall, which is a quite different strategy from vascular plants. Typically, mosses have leaves of only one cell layer in thickness and without cuticle and special protection structures, exposing every leaf cell directly to their surroundings to get nutrients. The gametophytes of many mosses are of shape of sheets, filaments, twigs, etc., with relatively large leaf surface area. Therefore, compared with mesic or xeric tracheophytes, mosses are morphologically similar to aquatic tracheophytes. From evolutionary views and recapitulation law, bryophytes belong to a clad evolved from aquatic to terrestrial taxa. Therefore, terrestrial or semi-aquatic mosses may be easier introduced into and adapted to aquatic environments. For example, *Bryum pseudotriquetrum*, a species growing on thin soils of rocks, has been found in the Antarctic deep-water area (Wanger *et al.*, 2006). *Fissidens fontanus*, a moss species originating from North America, usually grows on rocks, tree trunks, and is also able to grow in shallow

water (Crum *et al.*, 1981), now it is cultured as a aquarium plant in Singapore (Tan *et al.*, 2004).

In eastern China along the Pacific ocean, there is few aquatic bryophytes (Xu, 1989; Liu *et al.*, 2005). Is it possible to find some terrestrial bryophytes as aquarium plants? In order to answer the question, we conducted experiments to test the adaptability of some terrestrial bryophyte species to water environment.

*Brachythecium procumbens*, *Hypnum hamulosum*, *Leucobryum glaucum* and *Hedwigia ciliata* are four abundant and widely distributed terrestrial moss species in eastern China. In some stands, *Brachytheci- um procumbens* and *Hedwiagia hamulosum* often cover wide areas, appear as "green carpet", and *H. cil- iata* appears as "grey patch" on stones and boulders, while *Leucobryum glaucum* as "white greenish patch" on forest floor or trunk base of *Pinus massoniana* Association. These four moss species are valuable as ornamental plants. However, their adaptability in aquatic environment is not clear.

Photosynthetic parameters are important reference values indicating their ability to adapt to environments. There have been considerable reports about bryophyte photosynthesis (Liu *et al.*, 2001; Van Gaalen *et al.*, 2007; Goffinet *et al.*, 2008). Water availability is one of the most important factors that limit distribution and productivity of bryophytes. Dilks *et al.* (1975) found that there was a specific range of water content for xeric mosses to keep normal photosynthetic activity. Generally speaking, moss photosynthesis rate is positively correlated with moisture content of ambient environment. However, if above or below a certain range of water content, the net photosynthetic rate of most mosses would be inhibited. Liu *et al.* (2001) found that the optimum moisture content of *Thuidium cym-*

*bifolium* and *Chrysocladium retrorsum* was 200% to 400% of their dry weight for their photosynthesis. For the bryophytes mainly growing in humid environments, the moisture content has no significantly effects on net photosynthetic rate, such as *Hylocomium splendens* in B.S.G. and *Pleurozium schreberi* (Busby *et al.*, 1978). Though there are many reports about the tolerance of mosses to drought based on their physiological responses including photosynthetic and chlorophyll fluorescence parameters (Kalapos *et al.*, 2001, Zhang *et al.*, 2011), little work about the tolerance of terrestrial mosses to submerged environment has been conducted.

The purpose of this work is to compare the adaptability of the above four moss species to water via measuring their photosynthetic capacity in water, to elucidate the possibility to apply water-tolerant terrestrial mosses as aquarium plants.

## 1 Materials and Methods

Experimental samples of four moss species were collected from eastern China on March 12–13, 2009. Among them, *Leucobryum glaucum* was collected from Nanming Mountain in the suburb of Lishui city in Zhejiang (28°26'05" N, 119°54'10" E, elevation ca. 82 m), *Hedwigia hamulosum* from northern suburb of Jinhua city, Zhejiang (29°13'19" N, 119°37'56" E, elevation ca. 1 180 m), *H. ciliata* from the suburb of Jinhua city, Zhejiang (29°12'55" N, 119°38'26" E, elevation ca. 1 090 m), and *Brachythecium procumbens* from the Botanical Garden, Xuhui Campus of Shanghai Normal University (31°09'51" N, 121°24'50" E, elevation 3 m). Plant materials were confirmed under a microscope, sporophytes and impurities were removed from the samples. The materials (green gametophytes) were washed three times with distilled water, then were dried by natural ventilation for experiment.

A week after the collection, 3 g dry material were put into a nylon bag (12 cm × 6 cm, with mesh of 5 mm in diameter) to make a moss bag, a total of five moss bags were made for each moss species, the moss bags were immersed in a plastic bucket (height 18 cm

× diameter 20 cm) with tap water (10 cm in depth). During the experiment, the samples were kept at the temperature of 12–22 °C and not pumped oxygen into the water. After being submerged in water for 5, 10, 15, 20, 30 d, the moss bags were removed from water, respectively. Five samples (each with ca. 0.2 g fresh weight) were took for each species as five duplicates. The material (as control) was soaked into tap water for one minute before the determination of its photosynthesis rate. After the measurement, the materials were dried at 80 °C for 8 h and then weighed.

The net photosynthetic rate ( $P_n$ ) of four moss species was measured with a portable photosynthesis system (GFS-3000, Walz company, Germany) from 9:30 am to 11:00 am, with the leave cuvette condition being set with relative humidity of (60 ± 10)%, temperature of 20 °C and CO<sub>2</sub> concentration of 340 μmol · mol<sup>-1</sup>. PAR was given by LED Light Source 3040-L of the GFS-3000 at different intensities. Data were recorded three times for every PAR intensity.

The photosynthetic light-response curves were modeled using rectangular hyperbolic model as  $P_n = a \cdot b \cdot PAR / (a \cdot PAR + b) - c$ , here  $P_n$  is net photosynthetic rate,  $PAR$  is photosynthetic active radiation measured in the upper part of the cuvette of the standard measuring head 3010-S,  $a$ ,  $b$  and  $c$  are parameters. Based on photosynthesis-light response curve equation,  $LSP$  corresponding to 95% of measured maximal  $P_n$  and  $LCP$  were calculated.

All the treatments were replicated five times. The data presented are the means ± SE. One-way ANOVA was employed to test the differences of the data from the experiments with the procedure of SPSS 11.0 statistical package (SPSS Corp).

## 2 Results and Analysis

The photosynthetic light-response curves, maximal  $P_n$ ,  $LSP$  and  $LCP$  of four moss species under natural condition are listed in Table 1.

According to their maximal  $P_n$  from high to low, four moss species are ranked as *B. procumbens*, *Hedwigia hamulosum*, *Leucobryum glaucum* and *Hedwigia*

*ciliata*, their maximal  $P_n$  ( $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ ) being 122.58, 87.24, 41.10 and 19.10, respectively; *Hedwigia ciliata* has the highest  $LSP$ , being  $1\ 166.00 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , then *B. procumbens* and *H. hamulosum*, being  $1\ 018.60$  and  $941.80 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively, and *Leucobryum glaucum* has the lowest  $LSP$  at  $670.00 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ; As for  $LCP$  ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) from high to low, four species are ranked as *Hedwigia ciliata* (85.00), *Brachythecium procumbens* (56.80), *Hedwigia hamulosum* (20.50) and *Leucobryum glaucum* (5.3).

$P_n$  of *Brachythecium procumbens* after immersion in water: After being submerged in water for 5 d, the  $P_n$  of *B. procumbens* at  $1\ 600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  is

$127.10 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , being 98.74% of the control, which is not significantly different from the control. After being submerged in water for 10, 15 and 20 d, its net photosynthetic rates at  $1\ 600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  decrease to some extent, being 78.21%, 87.77% and 94.87% of the control, respectively (Table 2). Interestingly, even after being submerged in water for 30 d, its net photosynthetic rate at  $1\ 600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  is  $142.61 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , being 110.87% of the control significantly higher than the control. Overall, the net photosynthetic rate of *B. procumbens* in water decreases firstly and then increases gradually with the extension of submersion time (Table 2).

$P_n$  of *Hedwigia hamulosum* after immersion in

Table 1 Photosynthetic light-response curve equations and photosynthetic parameters of four moss species

Moss species	Photosynthetic light-response curve equations	Maximal $P_n$ ( $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ )	$LSP$ ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )	$LCP$ ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )
<i>Brachythecium procumbens</i>	$P_n = 96.19 \cdot PAR / (0.49 \cdot PAR + 195) - 24.48, r = 1.00 *$	$122.58 \pm 1.73$	1018.60	56.75
<i>Hedwigia hamulosum</i>	$P_n = 38.24 \cdot PAR / (0.31 \cdot PAR + 115) - 1.32, r = 0.99 *$	$87.24 \pm 0.71$	941.76	5.30
<i>Leucobryum glaucum</i>	$P_n = 9.91 \cdot PAR / (0.11 \cdot PAR + 91) - 1.60, r = 0.98 *$	$41.10 \pm 1.45$	670.03	20.50
<i>Hedwigia ciliata</i>	$P_n = 340.28 \cdot PAR / (3.74 \cdot PAR + 91) - 70.94, r = 0.97 *$	$19.10 \pm 0.25$	1166.00	85.00

\* : at the 0.01 level of significance.

Table 2 Net photosynthetic rates of *Brachythecium procumbens* after submersion in water for different days ( $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ )

Immersed days	Photosynthetic active radiation ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )							
	120	200	400	600	800	1 200	1 400	1 600
0	$18.37 \pm 0.67\text{a}$	$41.06 \pm 1.42\text{a}$	$72.56 \pm 0.90\text{a}$	$92.38 \pm 0.71\text{a}$	$106.44 \pm 0.46\text{a}$	$126.70 \pm 0.99\text{a}$	$129.56 \pm 0.35\text{a}$	$128.74 \pm 1.73\text{a}$
5	$17.04 \pm 0.54\text{ac}$	$34.31 \pm 1.12\text{b}$	$65.24 \pm 0.94\text{b}$	$83.11 \pm 0.91\text{b}$	$98.03 \pm 1.14\text{b}$	$123.04 \pm 1.18\text{a}$	$123.47 \pm 1.79\text{b}$	$127.12 \pm 0.71\text{a}$
10	$11.58 \pm 1.21\text{b}$	$27.55 \pm 0.87\text{c}$	$45.89 \pm 0.78\text{c}$	$63.85 \pm 0.99\text{c}$	$74.94 \pm 1.05\text{c}$	$97.16 \pm 0.60\text{b}$	$100.39 \pm 0.54\text{c}$	$100.68 \pm 0.59\text{b}$
15	$19.46 \pm 2.95\text{a}$	$27.57 \pm 0.55\text{c}$	$47.97 \pm 1.27\text{c}$	$63.91 \pm 0.96\text{c}$	$79.83 \pm 1.93\text{d}$	$110.15 \pm 2.80\text{c}$	$108.98 \pm 2.90\text{e}$	$113.00 \pm 1.56\text{c}$
20	$13.99 \pm 1.16\text{bc}$	$30.58 \pm 1.57\text{c}$	$62.11 \pm 1.16\text{b}$	$80.17 \pm 1.11\text{b}$	$91.81 \pm 0.86\text{e}$	$117.24 \pm 0.79\text{d}$	$119.33 \pm 1.52\text{b}$	$122.13 \pm 1.05\text{d}$
30	$17.52 \pm 0.28\text{ac}$	$47.43 \pm 2.27\text{d}$	$71.49 \pm 2.50\text{a}$	$97.81 \pm 1.72\text{d}$	$119.31 \pm 2.13\text{f}$	$133.78 \pm 0.61\text{e}$	$138.92 \pm 0.80\text{e}$	$142.61 \pm 1.38\text{e}$
Significant test	df=29 MSE=10.248 F=4.292 P=0.006	df=29 MSE=9.925 F=32.397 P=0.000	df=29 MSE=9.604 F=68.800 P=0.000	df=29 MSE=6.189 F=161.463 P=0.000	df=29 MSE=9.654 F=142.328 P=0.000	df=29 MSE=9.644 F=87.785 P=0.000	df=29 MSE=12.463 F=77.660 P=0.000	df=29 MSE=7.762 F=132.837 P=0.000

Note: Data were average of five replications  $\pm$  SEMs and the same superscript letter within a row means no difference at the 0.01 level of significance by the LSD test. The same below.

water: *Hypnum hamulosum*, if submerged in water for 20 and 30 d, its net photosynthetic rates at  $50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  are  $7.80$  and  $7.34 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , respectively, significantly lower than the control ( $10.60 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ ), while those submerged for 5, 10, 15 d at the same light intensity are significantly higher than that of the control. Overall, the net photosynthetic rate of *H. hamulosum* in-

creases firstly and then decreases gradually with the extension of submersion time, but the net photosynthetic rates of *H. hamulosum* at 200, 350, 550, 750, 1 000, 1 100  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , even submerged in water for 30 d, are 96.63%, 104.82%, 106.10%, 95.55%, 104.05% and 96.96% of the control, respectively. Therefore, *H. hamulosum* is able to survive in water after 30-day submersion (Table 3).

Table 3 Net photosynthetic rates of *Hedwigia hamulosum* after submersion in water for different days ( $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ )

Immersed days	Photosynthetic active radiation ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )							
	50	100	200	350	550	750	1 000	1 100
0	10.60±0.96a	24.43±1.39a	39.30±1.37ab	54.10±2.04a	67.00±1.22a	82.89±0.95a	84.11±1.87ab	89.05±0.71a
5	11.51±0.55a	27.09±0.98ab	43.97±1.01ac	63.53±0.66b	83.45±0.43b	99.20±1.40b	106.62±0.92c	106.87±2.92b
10	13.21±0.83b	22.74±1.20ac	40.17±1.80ab	54.55±0.52a	70.37±0.57cd	99.34±1.34b	102.60±1.97cd	103.46±0.77b
15	12.53±2.93b	28.94±2.66bde	46.80±2.97cd	63.45±2.42b	75.66±1.97e	86.50±0.99c	91.72±0.46e	94.29±0.26c
20	7.80±0.54c	25.36±1.00ae	41.01±0.44ae	53.93±0.48a	69.72±0.44adf	77.13±1.59d	82.42±1.55a	83.06±0.63d
30	7.37±0.59c	19.75±1.38cf	37.97±0.90be	56.71±0.52a	71.09±1.08cf	79.20±0.74d	87.51±1.07b	86.34±1.09ad
Significant test	df=29	df=29	df=29	df=29	df=29	df=29	df=29	df=29
	MSE=9.281	MSE=11.901	MSE=13.295	MSE=9.338	MSE=6.041	MSE=7.265	MSE=9.959	MSE=9.398
	F=3.188	F=4.414	F=4.019	F=11.264	F=28.710	F=65.493	F=50.095	F=48.733
	P=0.024	P=0.005	P=0.009	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000

Table 4 Net photosynthetic rates of *Leucobryum glaucum* after submersion in water for different days ( $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ )

Immersed days	Photosynthetic active radiation ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )							
	50	150	250	350	500	650	800	900
0	5.13±0.44ab	10.42±0.16a	17.60±1.04a	25.09±0.33a	32.80±0.86a	41.49±1.12a	44.15±1.46a	42.70±1.35a
5	13.87±0.45c	24.73±1.45b	35.27±0.33b	42.28±0.78b	48.78±0.87b	51.03±0.92b	51.83±0.57b	50.45±0.76b
10	6.83±1.72a	19.71±1.42c	32.42±0.98c	37.36±0.61c	47.19±0.60b	47.39±0.67c	47.47±0.57c	47.44±0.97c
15	6.83±0.64a	19.48±0.84c	26.69±0.43d	31.48±0.50d	39.19±0.37c	44.69±1.06d	46.07±0.69ac	46.27±1.23c
20	6.14±0.75a	18.61±0.66c	32.53±0.46c	40.42±0.49e	47.15±0.53b	52.41±0.51b	57.18±0.46d	57.66±0.21d
30	3.37±0.87b	17.69±0.50c	27.55±0.31d	33.30±0.26f	38.62±0.36c	42.49±0.22ad	45.99±0.47ac	46.75±0.22c
Significant test	df=29	df=29	df=29	df=29	df=29	df=29	df=29	df=29
	MSE=4.208	MSE=4.609	MSE=2.193	MSE=1.361	MSE=1.991	MSE=3.314	MSE=3.068	MSE=4.106
	F=15.382	F=23.248	F=91.320	F=148.159	F=101.956	F=30.390	F=38.503	F=31.760
	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000

Table 5 Net photosynthetic rates of *Hedwigia ciliata* after submersion in water for different days ( $\mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ )

Immersed days	Photosynthetic active radiation ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )							
	100	160	300	500	700	900	1 000	1 100
0	3.38±0.42a	7.64±0.39a	11.02±0.47a	14.30±0.13a	16.56±0.17a	19.01±0.09a	18.82±0.28a	19.10±0.25a
5	2.91±0.10a	6.08±0.17b	10.17±0.15a	13.40±0.12b	16.61±0.11a	17.93±0.17b	18.31±0.18a	18.70±0.21a
10	0.84±0.43b	3.35±0.29c	6.70±0.16b	8.32±0.26c	11.63±0.18b	13.31±0.11c	13.79±0.12b	14.61±0.16b
15	ND	2.89±0.34c	7.10±0.48b	11.91±0.18d	14.16±0.11c	16.13±0.10d	16.96±0.07c	17.82±0.07c
20	ND	ND	0.17±0.04c	0.48±0.04e	0.63±0.01d	0.86±0.02e	0.82±0.21d	0.99±0.02d
30	ND	ND	ND	ND	ND	ND	ND	ND
Significant test	df=14	df=19	df=24	df=24	df=24	df=24	df=24	df=24
	MSE=0.622	MSE=0.474	MSE=0.498	MSE=0.132	MSE=0.086	MSE=0.062	MSE=0.172	MSE=0.134
	F=14.697	F=53.717	F=182.860	F=1199.068	F=2565.208	F=4401.172	F=1625.677	F=2163.061
	P=0.001	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000	P=0.000

$P_n$  of *Leucobryum glaucum* after immersion in water; The net photosynthetic rates of *L. glaucum*, except that submerged in water at  $50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  for 30 d, are significantly higher than the control (Table 4). After submerged in water for 5, 10, 15, 20 and 30 d, the net photosynthetic rates of *L. glaucum* at  $900 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  are 50.45, 47.44, 46.27, 57.66, and  $46.75 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , respectively, being

118.16%, 111.11%, 108.37%, 135.03% and 109.49% of the control, respectively, indicating that *L. glaucum* is also able to survive in water, at least for 30 d (Table 4).

$P_n$  of *Hedwigia ciliata* after immersion in water; After being submerged in water for 10–20 d, the net photosynthetic rate of *H. ciliata* slightly increased firstly, then decreased sharply, no net photosynthetic rate of *H. ciliata* was detected after submerged in wa-

ter for 30 days (Table 5), indicating that *Hedwigia ciliata* is not adapted to water environment over 10 d.

### 3 Discussion

The *LCP* of shade herbs are lower than  $20 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , and their *LSP* are from 500 to 1 000  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  or lower (Niu *et al.*, 2004). The *LCP* of *H. hamulosum* and *Leucobryum glaucum* are 5.30 and  $20.50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively, and their *LSP* are 941.80 and  $670.00 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively, indicating that both are typical shade plants. Compared with *L. glaucum*, *Hedwigia hamulosum* has wider light adaptation range under natural condition; *Brachythecium procumbens* and *Hedwigia ciliata* belong to sunny plants, which is revealed by their higher *LCP* from 56.75 to  $85.00 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , and also higher light saturation points from 1 018.60 to  $1 166.00 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . Compared with *Brachythecium procumbens*, *Hedwigia ciliata* is a typical heliophyte, similar to other terrestrial sunny herbs in its adaptation to light.

The *LCP* and *LSP* of the four moss species are related to their natural habitats. The samples of *Hedwigia ciliata* were taken from rock surface in open field. *H. ciliata*, an extremely drought-tolerant moss species, often distributes on surface of open rocks with strong light; *Brachythecium procumbens* occasionally grows on grasslands, hills in sunny and open habitats, but also on floor and boulders under forest (Hu *et al.*, 2005). The samples of *B. procumbens* were taken from roadside of a sparse forest in Xuhui Campus of Shanghai Normal University. Its higher *LCP* and lower light saturation point indicating that *B. procumbens* is neither a typical shade plant, nor a typical sunny plant. The samples of *Hedwigia hamulosum* were taken from a patch of shrub by roadside (elevation ca. 1 180 m) of Jinhua Mountain, the habitat is shady and often misty, the photosynthetic parameters of *H. hamulosum* reflects the habitat conditions to some extent.

Four moss species vary much in their *Pn*. Among them, *Brachythecium procumbens* has the highest value, being  $122.575 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , while *H.*

*ciliata* the lowest, being  $19.10 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , the former has 6.42 times higher *Pn* of that of the latter. Their photosynthetic parameters are related to their morphological traits. The reason for *H. ciliata* has lower *Pn* could be explained as follows: (1) *Hedwigia ciliata* are grey greenish with lower chlorophyll content compared with *Brachythecium procumbens*, its leaf hyaline tips are not a photosynthetic tissue, accounting for a large part of leaf; (2) its leaves densely covered with many sharp transparent papillae on both sides, which may affect the absorption of light; (3) *Hedwigia ciliata* has procumbent and stout stems, the photosynthetic capacity of this part will certainly be weaker than the leaves.

The *Pn* of *Leucobryum glaucum* is  $41.10 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , higher than that of *Hedwigia ciliata*, but significantly lower than those of *Brachythecium procumbens* and *Hedwigia hamulosum*, which is related to its gametophyte features. The leaves of *Leucobryum glaucum* have smooth surface without papillae and hyaline tips like *Hedwigia ciliata*, but they have flat and wide costae, and only one layer of green cells with photosynthetic function, and the larger cells on both sides of the green cell layer are colorless, without photosynthetic pigments.

Most previous reports about bryophyte photosynthesis took leaf area as unit, so we can not compare our photosynthetic data with those of previous work. Del-toro *et al.* (1999) reported that the *Pn* of *Leucodon sciuroides* in Mediterranean was  $8-10 \text{ mg CO}_2 \cdot \text{g}^{-1} \text{DW} \cdot \text{h}^{-1}$  at  $15^\circ\text{C}$ , which is equal to  $50-60 \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{DW} \cdot \text{s}^{-1}$ , and close to that of *Leucobryum glaucum* in the present work. Convey (1994) reported that the *Pn* of *Bartramia patens* and other twelve moss species in the Antarctic varied from 0.879 to  $0.134 \text{ mg C} \cdot \text{g}^{-1} \text{DW} \cdot \text{h}^{-1}$ . if converted into the same unit, the *Pn* of *Brachythecium procumbens* is  $0.82-4.50 \text{ mg C} \cdot \text{g}^{-1} \text{DW} \cdot \text{h}^{-1}$ . Considering the harsh Antarctic environment, the *Pn* of the bryophytes measured by Convey are naturally lower than those of the present work. Therefore, the photosynthetic data of the four moss species fall into the reasonable scope. Ueno *et al.* (2006) reported the net photosynthetic rate of

*Calliergon giganteum* (a semi-aquatic moss species) as  $1.2-1.6 \text{ mg CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , about  $113-150 \text{ } \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{ DW} \cdot \text{s}^{-1}$ , which is similar to that of *Brachythecium procumbens*. Liu *et al.* (2001) found that the  $P_n$  of *Plagiomium acutum* and *P. maximoviczii* in summer is  $125.67$  and  $94.63 \text{ } \mu\text{mol CO}_2 \cdot \text{kg}^{-1} \text{ DW} \cdot \text{s}^{-1}$ , which shows that *Plagiomium acutum* and *Brachythecium procumbens*, *Plagiomium maximoviczii* and *Hedwigia hamulosum* have similar photosynthetic capacity, respectively.

After submerged for different times, the  $P_n$  of *Brachythecium procumbens* increases firstly and then decreases gradually with the extension of submersion in water at all PAR intensities except for  $120 \text{ } \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . The photosynthesis of *Brachythecium procumbens*, if submerged for a short time, was inhibited because of water stress in relation to deficiency of oxygen and  $\text{CO}_2$ . With the extension of submerged time, *B. procumbens* is gradually adapted to water environment and its photosynthetic capacity recovered, and even exceeded the control. During the submersion, the gametophytes of *B. procumbens* kept green all the time, indicating that *B. procumbens* is able to survive well in aquatic environment. In the field, *B. procumbens* often distributes on stones on edge of some streams, sometimes submerges in water during rainy season.

The net photosynthetic rate of *Leucobryum glaucum* increased firstly and then decreased gradually with the extension of submersion, its  $P_n$  reached a peak after being submerged for 20 d, indicating that *Leucobryum glaucum* is able to live well in water for a short time. The gametophyte of *L. glaucum* is somewhat similar to that of *Sphagnum* sp., say *Sphagnum palustre*, the latter is able to live well in swamps and wet environments. Therefore, *L. glaucum* has morphological and structural ground to adapt to aquatic environment to a certain degree. When submerged in water, *Hedwigia hamulosum* and *Leucobryum glaucum* share a similar change pattern in their  $P_n$ . Their  $P_n$  increased firstly and then decreased gradually with the extension of submerged time, but higher or not significantly lower than their control, respectively, even after

30-day submersion in water, showing their good adaptability to water environment.

*Hedwigia ciliata* is a drought-tolerant saxicolous moss species. The  $P_n$  of *H. ciliata* decreased sharply with the extension of submerged time, indicating that *H. ciliata* is not adapted to aquatic environment.

## 4 Conclusions

Overall, *Brachythecium procumbens*, *Leucobryum glaucum* and *Hedwigia hamulosum* are adapted to aquatic environments to some extent, and they seems to be potential aquarium plants. It should be noted that this study has measured the  $P_n$  of only four mosses after their being submerged, if we extend our present work with more other terrestrials and wet moss species, we maybe find more species adapted to water environments, and thus provide more new potential aquarium plants.

## References:

- Benl G. 1958. Java moss for decoration and as a spawning medium—a useful aquatic plant which has yet to be seen in Britain[J]. *Fish Keep*, **11**: 655
- Busby JR, Whitfield DWA. 1978. Water potential, water content and net assimilation of some boreal forest mosses[J]. *Can J Bot*, **56**: 151–158.
- Convey P. 1994. Photosynthesis and dark respiration in Antarctic mosses: an initial comparative study[J]. *Pol Biol*, **14**: 65–69
- Crum HA, Anderson LE. 1981. Mosses of Eastern North America [M]. New York: Columbia University Press
- Deltoro VI, Calatayud, Morales F, *et al.* 1999. Changes in net photosynthesis, chlorophyll fluorescence and xanthophyll cycle inter conversions during freeze-thaw cycles in the Mediterranean moss *Leucodon sciurooides*[J]. *Oecologia*, **120**: 499–505
- Dilks TJK, Proctor MCF. 1975. Comparative experiments on temperature response of bryophytes: assimilation, respiration and freezing damage[J]. *J Bryol*, **8**: 317–336
- Goffinet B, Shaw AJ. 2008. Bryophyte Biology[M]. New York: Cambridge University Press
- Gradstein SR, Reiner-drehwald ME, Muth H. 2003. Über die Identität der neuen Aquarienflechte “*Pellia endiviifolia*” [J]. *Aqua Plant*, **3**: 88–95
- Hu RL, Wang YF. 2005. *Flora Bryophytorum Sinicorum* (Vol. 7) [M]. Beijing: Science press
- Kalapos T, Mázsa K. 2001. Juniper shade enables terricolous lichens and mosses to maintain high photochemical efficiency in a semiarid temperate sand grassland [J]. *Photosynthetica*, **39**: 263–268
- Larcher W. 1982. Physiological Plant Ecology [M]. Beijing: Science Press
- Liu YD, Chen J, Cao T. 2001. Photosynthetic characteristics of two (下转第 672 页 Continue on page 672 )