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Research Article

Influence of Drought Stress and Rehydration on Moisture and Photosynthetic Physiological Changes in Three Epilithic Moss Species in Areas of Karst Rocky Desertification

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The drought resistance mechanism of typical mosses in the karst area was studied, and the water and photosynthetic physiological adaptation of mosses to karst environmental change was analyzed in this paper, which provided the basis for the restoration and control of karst rocky desertification ecological environment. Three superior plants in the rocky desertification area of Guizhou province were selected; they are, respectively, *Erythrodontium julaceum* (Schwaegr.) Par., *Barbula unguiculata* Hedw., and *Bryum argenteum* Hedw. Results show that the three kinds of plant rock mosses of leaf water potential (Ψs), free water content (V_a), total water content, and relative water content (RWC) decreased; bound water (V_s), water saturation deficit (*WSD*), and V_s/V_a ratio increased; transpiration rate (Tr) fell slightly, under drought stress. The physiological indexes of water have different degrees of recovery after rehydration. The total chlorophyll content shows a trend of first increasing followed by falling and then rising. RWC was negatively related to *qN* and positively related to F_v/F_m, yield, ETR, and *qP*. After rewetting, the fluorescence parameters are returned to average level under mild-to-moderate stress. At the same time, it is hard to get back to the control level under severe pressure. The water use efficiency (WUE) decreased with stress and recovered to different degrees after rehydration.

1. Introduction

Biological crusts are complex complexes formed by cementation of cryptogam plants (such as algae, lichens, and bryophytes), soil microorganisms, and surface soil particles. The crust is an essential component of the ecological system in arid and semiarid regions. The karst plateau area in south China is located in the subtropical monsoon humid climate zone. In this area, the soil layer is shallow, the bedrock is exposed, the infiltration coefficient of atmospheric precipitation is large, and the leakage is serious. This area is prone to the formation of karst seasonal arid habitat characteristics, such as rain logging and sunny drought [1]. This drought is not caused by dry air but by the growth of lichen on the limestone surface, caused by a sharp seepage of precipitation. The water required for long-term maintenance inevitably causes different physiological responses of bryophytes to drought and rehydration, such as the physiological regulation of bound water together with free water. Changes in leaf transpiration and photosynthetic rates may be a physiological adaptation mechanism of bryophytes to harsh karst conditions, but there is little literature in the area.

Bryophytes are highly drought-resistant. Previous studies primarily focused on the characteristics and mechanism of drought tolerance, such as the morphological variation in mosses in the process of drought resistance [2, 3], physiological and biochemical mechanisms [4, 5], and modes of reproduction [6, 7]. Mosses can tolerate physiological water loss and physiological tissues with long-term tolerance to drought and can quickly resume various physiological activities when water conditions improve [8, 9]. In contrast to corresponding vascular plant, water potential of drought-tolerant moss is much lower. The obvious water potential gradient established between plants

and the environment can accelerate the movement of water [10]. Some researchers have studied the water relationship and drought resistance of bryophytes using thermocouple hygrometers and hygrometers from the $p - v$ curve, moisture relationship index, water potential, and hydraulic retention [11–14]. Some other researchers studied changes in the chlorophyll fluorescence of mosses [15, 16] and liverworts [17, 18] during dehydration and rehydration by using the chlorophyll fluorescence technique. Csintalan analyzed chlorophyll fluorescence of three moss species under drying-wetting actions; the chlorophyll fluorescence parameters of moss plants would remain relatively constant as relative water content within a certain range. Similarly, chlorophyll fluorescence parameters, that is, F_v/F_m, F_m, ΦPS II, and qN, reduced with the loss of water; ΦPS II and F_v/F_m after rehydration could gradually return to normal levels at short notice [19]. Domestic researchers (Chinese) found that Grimmia pilifera P. Beauv.'s chlorophyll fluorescence parameters have relatively low water content threshold value in dehydration and rehydration. At extremely low temperatures in winter and high-temperature dry environment in summer, Mitt. in northwestern deserts will enter a dormant state through water loss. Furthermore, when the snow melts in the early winter and spring, *Syntrichia caninervis* Mitt. can rapidly recover fluorescence activity [20]. Zhang studied *Barbula fallax* Hedw., *Stereodon taxirameus* Mitt., and *Bryum argenteum* in a drought environment in karst areas of Guizhou and believed karst bryophytes could cope with arid karst environment in the process of metabolism and photosynthesis [21, 22].

Moss plays an essential role in forest ecosystems, because it is an irreplaceable component in moisture, soil, and water conservation and improvement in the ecological microenvironment [23]. Existing research studies on the relationship between drought resistance and water content in *Syntrichia caninervis* have focused on extreme arid desert areas without rainfall. However, there are few studies on the changes of water physiology and photosynthetic characteristics of bryophytes in drought and rehydration. Therefore, the typical epilithic mosses, namely, *Barbula unguiculata* Hedw., *Erythrodontium julaceum* (Schwaegr.) Par., and *Bryum argenteum* Hedw., were selected and used to study the changes of the physiological and photosynthetic characteristics after drought stress and rehydration. This provides the scientific basis for in-depth understanding of the adaptive characteristics of epilithic mosses to the environmental changes in karst and the restoration and control of ecological environments undergoing rocky karst desertification.

2. Materials and Methods

2.1. Study Materials. The crusted mosses for testing included *Erythrodontium julaceum* (Schwaegr.) Par., *Barbula unguiculata* Hedw. and *Bryum argenteum* Hedw. *Erythrodontium julaceum* (Schwaegr.) Par. is an interwoven type, which grows on the surface of stones; *Barbula unguiculata* Hedw. and *Bryum argenteum* Hedw. are cluster types, growing on rock surfaces. The study materials were collected from Chenqi Severe Rocky Desertification Area, Observation, and Research Station of Puding Karst Ecological System, Chinese Academy of Sciences. When the mean temperature is $25 \pm 1^{\circ}$C, the samples could be gathered on sunny days.

2.2. Culture and Treatment with Material. According to the methods described by Zhang [24], drought stress treatment will not be repeated here. After 0, 12, 24, 48, and 72 h treatment, the determination of each index was repeated after 24 h.

2.3. Methods

2.3.1. Water Physiological Index. Water content was measured by drying and weighing method. Relative water content and natural saturation deficiency were measured using expansion drying method. Leaf water potential was detected by drop flowing method. The above indexes were measured according to Edition 4 raised by Zhang [25]. Bound water and free water were detected by Weighing Method raised by Liu. [26].

$$\begin{aligned}
\text{Natural water content}\,(\%) &= \frac{W_f - W_d}{W_d} \times 100,\\
\text{Relative water content}\,(\%) &= \frac{W_f - W_d}{W_t - W_d} \times 100,\\
\text{Natural saturation deficiency}\,(\%) &= \frac{W_t - W_f}{W_t - W_d} \times 100,\\
\text{Free water}\,(\%) &= \frac{\text{Natural fresh weight of tissue} - \text{Weight of tissue after immerse}}{\text{Natural fresh weight of tissue}} \times 100,\\
\text{Bound water}\ (\%) &= \text{Natural water content}\ (\%) - \text{Free water}\ (\%),\\
\text{Leaf water potential } P &= \text{RTIC},
\end{aligned} \tag{1}$$

where P refers to atmospheric pressure (1 atmospheric pressure = 1.0133 bar, 1 MPa = 10 bar). R refers to gas constant (0.0821). T refers to absolute temperature ($T = 273 + t$°C). I refers to isotonic coefficient. Isotonic coefficient of sucrose is 1. C refers to concentration of isotonic solution.

2.3.2. Determination of Chlorophyll Fluorescence Activity. According to the method described by Bao [27], chlorophyll content is determined. Moss gametophytes with different treatments were maintained in the sample chamber for half an hour of dark adaptation. A portable pulse modulated chlorophyll fluorometer, PAM-2100 (Walz, Germany), is employed for detecting the maximum photochemical quantum yield (F_v/F_m), initial fluorescence (F_0), photochemical quenching (qP), nonphotochemical quenching (qN), yield (actual photosynthetic efficiency), rETR (electron transport rate), and other fluorescence parameters for all the labeled gametophytes, among which ΦPSII = $(F_m' - F)/F_m'$, $qP = (F_m' - F_t)/(F_m' - F_o')$, $qN = (F_m - F_m')/F_m - F_o'$, $F_v/F_m = (F_m - F_0)/F_m$, and ETR = ΦPS II (photosystem II) × PAR (photosynthetically active radiation intensity) × 0.84 × 0.5 [28]. This is repeated for six times to acquire average value. The physical meanings of parameters contained are as follows: real-time fluorescence yield (F_t), maximum fluorescence (F_m), variable fluorescence (F_v), initial fluorescence yield under light (F_0'), and maximum fluorescence yield (F_m').

2.4. Statistical Analysis. All of the experiments were implemented 5 times. SPSS 13.0 software was applied to process the data expressed as the mean ± standard deviation of three independent experiments. Mapping was performed using Origin 8.0 and Microsoft Excel 2017 software.

3. Results and Analysis

3.1. Water Content, Free Water Content (V_a), and Bound Water Content (V_s) of Leaf Tissue. The water content of the epilithic mosses shows a gradually declining trend as stress increases. For *Bryum argenteum* Hedw., water content is down from 65.7% at the beginning to 48.2% after stress for 72 h, falling by 26.6%. *Barbula unguiculata* Hedw. decreased from 77.4% to 43.2% after stress for 72 h, falling by 44.2%. For *Erythrodontium julaceum* (Schwaegr.) Par., it is down from 84.2% to 48.6% after stress for 72 h, falling by 42.3%. Among the three, the declining range of *Barbula unguiculata* Hedw. is the highest. After 24 h of rehydration, each of the three moss species exhibits different degrees of recovery in water content, but they cannot restore to the control level in a short time. If the stress is higher, the degree of recovery is lower (Table 1).

It can be found from Table 1 that V_a, V_s, and V_s/V_a of the three mosses are significantly changed with the aggravation of water stress, among which, V_s and V_s/V_a are increased and V_a is decreased. After rehydration, all indexes restore to a certain degree. However, variance analysis shows that the difference is not significant. In this paper, after 72 h of stress, the indices for *Bryum argenteum* Hedw. are 1.31 and 1.41 for *Barbula unguiculata* Hedw. and 1.41 for *Erythrodontium julaceum* (Schwaegr.) Par. After rehydration, the ratios slightly decrease.

3.2. Changes in Relative Water Content (RWC), Water Saturation Deficiency (WSD), and Leaf Water Potential (Øs) of Leaves. It can be seen from Table 1 that as stress increases, the RWC of each treatment shows a declining trend. For *Bryum argenteum* Hedw., RWC is down from 61.3% at the beginning to 33.1% after stress for 72 h, falling by 46.0%. For *Barbula unguiculata* Hedw., it is down from 67.4% to 39.7% after stress for 72 h, falling by 41.1%. For *Erythrodontium julaceum* (Schwaegr.) Par., it is down from 83.2% to 47.3% after stress for 72 h, falling by 43.2%. By comparison, the declining range of *Bryum argenteum* Hedw. is the highest, followed by *Erythrodontium julaceum* (Schwaegr.) Par., and that of *Barbula unguiculata* Hedw. is the lowest. WSD is up as stress increases. After 72 h of stress, WSD increases from 38.7% to 67.9% for *Bryum argenteum* Hedw., from 32.6% to 60.3% for *Barbula unguiculata* Hedw., and from 16.8% to 52.7% for *Erythrodontium julaceum* (Schwaegr.) Par. This indicates that the responsiveness of epilithic mosses in karst to environmental change is different in long-term drought stress. After rehydration, RWC increases and WSD declines in varying degrees. This shows that epilithic mosses have a certain hysteresis effect against water stress in a short time. RWC and WSD of the three mosses have specific adaptability to the arid environment. In this paper, *Erythrodontium julaceum* (Schwaegr.) Par. has the smallest WSD at 16.8% and *Bryum argenteum* Hedw. has the largest at 38.7%. For *WSD*, the trend is *Bryum argenteum* Hedw. > *Barbula unguiculata* Hedw. > *Erythrodontium julaceum* (Schwaegr.) Par.

It can be found from Table 1 that, upon aggravation of water stress, water potential will be down in different degrees. For *Bryum argenteum* Hedw., it is down from −1.65 MPa at the beginning to −8.16 MPa after stress for 72 h, falling by −6.51 MPa; for *Barbula unguiculata* Hedw., water potential is down from −0.05 MPa at the beginning to 8.79 MPa after stress for 72 h, falling by −8.74 MPa; for *Erythrodontium julaceum* (Schwaegr.) Par., it is down from −0.03 MPa to −9.27 MPa after stress for 72 h, falling by −9.23 MPa. *Erythrodontium julaceum* (Schwaegr.) Par. has the highest declining range followed by *Barbula unguiculata* Hedw. and *Bryum argenteum* Hedw. has the lowest declining range (Figure 1). After rehydration, each moss plant has a different degree of recovery in water potential. It indicates that karst moss plants have stronger drought resistance and dewatering ability. Further exploration of the relationship between RWC and water potential (Figure 2) among the three mosses shows a slight difference. Water potential is decreased with decreasing RWC. A significant correlation exists between both of them ($P < 0.05$).

3.3. Drought Stress and Rehydration Influence on the Photosynthetic Physiology and Ecology of 3 Epilithic Mosses

3.3.1. Drought Stress and Rehydration Influence on Changes in Photosynthetic Pigments of 3 Epilithic Mosses. Table 2

Table 1: The effect of drought stress together with replenishment on water physiological indexes of three epilithic mosses. *Erythrodontium julaceum* (Schwaegr.) Par. with permission from [29].

Species	Treatment	Water content (%)		Free water (%)		Bound water (%)		B/F		Water potential (MPa)		Water saturation deficiency (%)		Relative water content (%)	
		Stress	Rewatering	Stress	Rewatering	Stress	Rewatering	Stress	Rewatering	Stress	Rewatering	Stress	Rewatering	Stress	Rewatering
Bryum argenteum Hedw.	CK	65.7 ± 1.74	—	43.3 ± 1.25	—	32.4 ± 1.22	—	0.52 ± 0.08	—	−1.65 ± 0.16	—	38.7 ± 1.06	—	61.3 ± 2.09	—
	6	63.3 ± 0.89	65.6 ± 1.77	40.6 ± 1.08	38.4 ± 1.11	26.7 ± 1.27	27.2 ± 1.27	0.56 ± 0.11	0.78 ± 0.15	−2.01 ± 0.21	−1.98 ± 0.21	41.5 ± 1.25	39.2 ± 1.08	58.5 ± 2.16	60.8 ± 2.01
	12	61.0 ± 2.12	62.5 ± 1.85	39.4 ± 1.21	35.6 ± 1.21	25.6 ± 1.31	26.9 ± 1.44	0.65 ± 0.13	0.76 ± 0.14	−2.32 ± 0.13	−2.12 ± 0.34	48.4 ± 1.27	44.2 ± 1.13	51.6 ± 2.11	55.8 ± 1.88
	24	56.7 ± 1.88	58.7 ± 2.01	36.6 ± 1.09	32.9 ± 1.30	23.1 ± 1.08	25.8 ± 1.38	0.63 ± 0.06	0.78 ± 0.16	−3.53 ± 0.25	−2.49 ± 0.38	54.3 ± 1.33	46.7 ± 1.32	45.7 ± 1.88	53.3 ± 1.68
	48	48.5 ± 1.32	54.6 ± 1.56	24.4 ± 1.82	27.8 ± 1.73	24.1 ± 1.16	26.8 ± 1.09	0.99 ± 0.15	0.96 ± 0.21	−8.11 ± 0.31	−4.55 ± 0.42	64.8 ± 1.42	55.4 ± 1.42	35.2 ± 1.24	44.6 ± 1.57
	72	48.2 ± 1.27	49.0 ± 1.23	20.9 ± 1.31	21.6 ± 1.22	27.3 ± 1.28	27.4 ± 1.21	1.31 ± 0.12	1.27 ± 0.32	−8.16 ± 0.27	−4.98 ± 0.46	66.9 ± 1.36	56.8 ± 1.57	33.1 ± 1.06	43.2 ± 1.45
Barbula unguiculata Hedw.	CK	77.4 ± 2.31	—	63.5 ± 2.08	—	23.9 ± 1.24	—	0.22 ± 0.04	—	−0.05 ± 0.01	—	32.6 ± 1.06	—	67.4 ± 2.05	—
	6	68.4 ± 2.02	73.7 ± 2.03	49.8 ± 1.76	49.1 ± 2.03	18.6 ± 1.36	24.6 ± 1.63	0.37 ± 0.10	0.50 ± 0.08	−0.35 ± 0.04	−0.23 ± 0.05	38.8 ± 1.21	36.9 ± 1.31	61.2 ± 2.12	63.1 ± 1.27
	12	62.6 ± 1.98	62.2 ± 1.99	41.4 ± 1.59	39.6 ± 1.92	21.2 ± 1.28	22.6 ± 1.52	0.51 ± 0.09	0.57 ± 0.10	−2.65 ± 0.21	−1.76 ± 0.14	43.2 ± 1.35	40.4 ± 1.29	56.8 ± 2.01	59.6 ± 1.54
	24	53.8 ± 1.74	55.3 ± 1.79	30.3 ± 1.06	31.0 ± 1.28	23.5 ± 1.24	24.3 ± 1.43	0.78 ± 0.13	0.78 ± 0.09	−4.65 ± 0.33	−2.47 ± 0.31	48.8 ± 1.41	45.3 ± 1.21	51.2 ± 1.25	54.7 ± 1.31
	48	46.1 ± 1.23	49.7 ± 1.47	22.4 ± 1.53	25.2 ± 1.65	23.7 ± 1.04	24.5 ± 1.61	1.06 ± 0.21	0.97 ± 0.14	−5.47 ± 0.29	−2.97 ± 0.28	55.4 ± 1.63	52.7 ± 1.52	44.6 ± 1.33	47.3 ± 1.25
	72	43.7 ± 2.01	48.2 ± 1.55	18.1 ± 1.24	23.3 ± 1.32	25.6 ± 1.20	24.9 ± 1.43	1.41 ± 0.32	1.07 ± 0.21	−8.79 ± 0.34	−5.86 ± 0.51	60.3 ± 1.58	56.6 ± 1.31	39.7 ± 1.02	43.4 ± 1.22
Erythrodontium julaceum (Schwaegr.) Par.	CK	84.2 ± 2.33	—	65.6 ± 1.78	—	28.6 ± 1.65	—	0.28 ± 0.07	—	−0.03 ± 0.01	—	16.8 ± 1.01	—	83.2 ± 2.84	—
	6	75.3 ± 2.41	79.7 ± 2.01	49.7 ± 2.21	51.9 ± 2.13	25.6 ± 1.82	27.8 ± 1.78	0.52 ± 0.09	0.54 ± 0.08	−0.06 ± 0.02	−0.04 ± 0.01	29.3 ± 1.23	20.7 ± 1.06	70.7 ± 1.76	79.3 ± 1.99
	12	70.6 ± 1.84	71.7 ± 1.84	41.2 ± 1.43	42.9 ± 1.96	27.4 ± 1.27	28.8 ± 1.57	0.71 ± 0.12	0.67 ± 0.09	−0.1 ± 0.01	−0.07 ± 0.02	32.2 ± 1.21	28.4 ± 1.21	67.8 ± 1.31	71.6 ± 1.84
	24	64.5 ± 1.67	65.6 ± 1.99	34.7 ± 2.01	47.3 ± 1.74	27.8 ± 1.42	28.3 ± 1.91	0.86 ± 0.21	0.60 ± 0.10	−2.89 ± 0.21	−1.29 ± 0.13	38.8 ± 1.34	35.6 ± 1.13	61.2 ± 1.28	64.4 ± 1.67
	48	51.8 ± 1.55	58.3 ± 1.76	25.7 ± 1.09	28.9 ± 1.54	26.1 ± 1.34	29.4 ± 1.12	1.02 ± 0.34	1.03 ± 0.16	−7.65 ± 0.32	−4.38 ± 0.25	49.9 ± 1.51	41.9 ± 1.52	50.1 ± 1.06	58.1 ± 1.53
	72	48.6 ± 1.09	52.8 ± 1.62	20.2 ± 1.17	23.6 ± 1.25	28.4 ± 1.09	29.2 ± 1.26	1.41 ± 0.29	1.24 ± 0.19	−9.27 ± 0.41	−5.22 ± 0.27	52.7 ± 1.62	45.5 ± 1.61	47.3 ± 1.64	54.5 ± 1.24

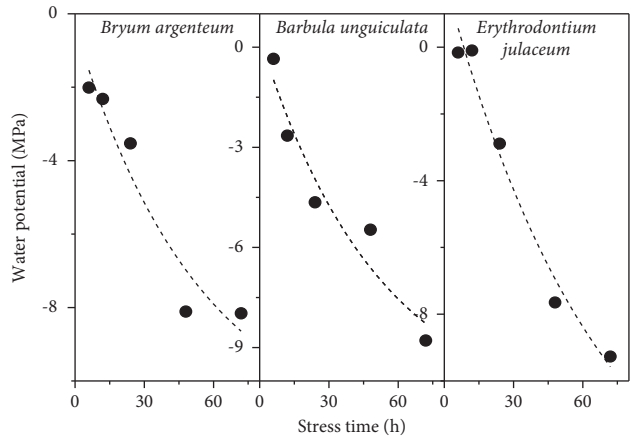


Figure 1: Effect of drought stress on water potential in three epilithic mosses.

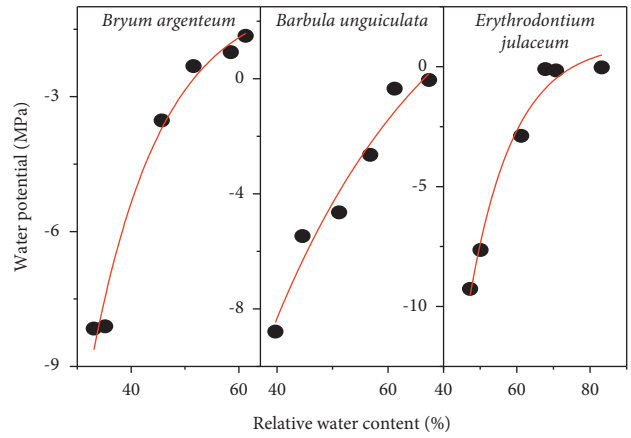


Figure 2: Relationship between water potential and RWC in three epilithic mosses during dehydration.

Table 2: The effect of drought stress and the replenishment on photosynthetic physiology indexes in three epilithic mosses. *Erythrodontium julaceum* (Schwaegr.) Par. with permission from [24]. Copyright 2016 open-access from Bangladesh botanical society.

Species	Treatment	Chlorophyll a		Chlorophyll b		Transpiration (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$)		Net photosynthetic rate (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	
		Stress	Rewatering	Stress	Rewatering	Stress	Rewatering	Stress	Rewatering
Bryum argenteum Hedw.	CK	0.61 ± 0.12	—	0.28 ± 0.04	—	1.07 ± 0.21	—	15.19 ± 1.02	—
	6	0.59 ± 0.09	0.57 ± 0.08	0.19 ± 0.02	0.24 ± 0.05	0.98 ± 0.09	0.65 ± 0.12	12.44 ± 0.84	8.76 ± 1.33
	12	0.58 ± 0.11	0.67 ± 0.10	0.21 ± 0.03	0.24 ± 0.05	0.97 ± 0.12	0.69 ± 0.10	10.65 ± 0.69	8.78 ± 1.24
	24	0.43± 0.06	0.69 ± 0.14	0.20 ± 0.02	0.28 ± 0.07	0.99 ± 0.20	0.58 ± 0.08	7.51 ± 0.77	8.09 ± 1.08
	48	0.72 ± 0.12	0.58 ± 0.07	0.34 ± 0.05	0.53 ± 0.14	0.88 ± 0.16	0.58 ± 0.10	6.26 ± 0.95	8.74 ± 1.21
	72	0.64 ± 0.18	0.68 ± 0.08	0.27 ± 0.04	0.32 ± 0.12	0.75 ± 0.14	0.62 ± 0.13	3.12 ± 0.86	8.10 ± 1.11
Barbula unguiculata Hedw.	CK	0.65 ± 0.22	—	0.33 ± 0.12	—	1.01 ± 0.12	—	30.93 ± 1.78	—
	6	0.52 ± 0.19	0.65 ± 0.26	0.25 ± 0.09	0.29 ± 0.05	0.76 ± 0.10	0.92 ± 0.14	18.04 ± 1.86	11.22 ± 1.74
	12	0.52 ± 0.17	0.69 ± 0.27	0.26 ± 0.07	0.26 ± 0.04	0.72 ± 0.11	0.74 ± 0.10	15.01 ± 1.75	10.03 ± 1.63
	24	0.54 ± 0.15	0.71 ± 0.25	0.22 ± 0.06	0.24 ± 0.06	0.72 ± 0.14	0.78 ± 0.09	14.35 ± 1.38	9.96 ± 1.02
	48	0.89 ± 0.24	0.67 ± 0.20	0.33 ± 0.11	0.38 ± 0.21	0.67 ± 0.09	0.77 ± 0.08	10.01 ± 1.21	9.99 ± 1.13
	72	0.92 ± 0.36	0.68 ± 0.21	0.35 ± 0.10	0.35 ± 0.19	0.64 ± 0.08	0.70 ± 0.10	8.73 ± 1.08	9.97 ± 1.11
Erythrodontium julaceum (Schwaegr.) Par.	CK	0.48 ± 015	—	0.31 ± 0.19	—	1.03 ± 0.10	—	27.74 ± 1.48	—
	6	0.51 ± 0.22	0.61 ± 0.22	0.24 ± 0.12	0.42 ± 0.21	1.43 ± 0.21	0.99 ± 0.13	16.17 ± 1.55	18.06 ± 2.05
	12	0.39 ± 0.18	0.53 ± 0.19	0.19 ± 0.09	0.17 ± 0.08	1.03 ± 0.18	0.74 ± 0.15	12.48 ± 1.19	16.28 ± 1.56
	24	0.79 ± 0.31	0.87 ± 0.26	0.35 ± 0.21	0.47 ± 0.24	0.77 ± 1.12	0.79 ± 0.12	8.73 ± 1.21	11.82 ± 1.43
	48	0.65 ± 0.24	0.73 ± 0.25	0.37 ± 0.16	0.47 ± 0.26	0.69 ± 0.13	0.80 ± 0.17	2.5 ± 0.43	14.35 ± 1.11
	72	0.85 ± 0.34	0.90 ± 0.29	0.38 ± 0.14	0.41 ± 0.18	0.67 ± 0.11	0.74 ± 0.14	0.62 ± 0.18	9.35 ± 1.13

shows that chlorophyll shows a trend of an initial decline and a later increase as stress aggravates. Our previous article published the influences of drought stress and replenishment on chlorophyll content in *Erythrodontium julaceum* (Schwaegr.) Par. [24]. Chlorophyll a in *Bryum argenteum* Hedw. reaches its lowest levels under stress for 24 h, whereas *Erythrodontium julaceum* (Schwaegr.) Par. [24] and *Barbula unguiculata* Hedw. reach the lowest chlorophyll a levels under stress for 12 h. The change in chlorophyll b levels shows a similar trend. Chlorophyll a in *Bryum argenteum* Hedw. is at 0.614 mg g^{-1} FW at the beginning, down to 0.429 mg g^{-1} FW under stress for 24 h, and goes up to 0.644 mg g^{-1} FW under stress for 72 h. Chlorophyll a in *Barbula unguiculata* Hedw. decreases from 0.653 mg.g^{-1}FW at the beginning to 0.515 mg g^{-1} FW under stress for 12 h and increases to 0.917 mg·g^{-1}·FW after stress for 72 h, whereas that of *Erythrodontium julaceum* (Schwaegr.) Par. [24] changes insignificantly, with an inevitable fluctuation. Externally, plants do not show yellowing. The decrease in chlorophyll content is possibly related to the temporary decline in photosynthetic capacity. Moreover, due to significant dehydration, the moss plants curled firmly into hibernation. The decline of chlorophyll content is related to the unit increase of chlorophyll caused by the significantly reduced water content. After rehydration, chlorophyll content is restored to a certain extent under moderate-to-mild water stress.

3.3.2. Drought Stress and Rehydration Influence on Changes in Chlorophyll Fluorescence in Three Epilithic Mosses

(1) Drought Stress and Rehydration Influence on Changes in F_v/F_m. During the early stages of stress, F_v/F_m of the three mosses is slowly reduced. As stress aggravates, for *Bryum argenteum* Hedw. and *Barbula unguiculata* Hedw., F_v/F_m decreases significantly in comparison with control group, from 0.763 to 0.240 and from 0.796 to 0.266, respectively, at the early stage of stress compared to being under stress for 72 h. F_v/F_m of *Erythrodontium julaceum* (Schwaegr.) Par. [24] does not decrease significantly, from 0.753 to 0.552. After rehydration, F_v/F_m of the mosses is restored. *Barbula unguiculata* Hedw. is restored to the highest degree, from 0.266 under stress for 72h to 0.607, followed by *Bryum argenteum* Hedw., and *Erythrodontium julaceum* (Schwaegr.) Par. [24] is restored to the lowest degree. The three mosses show a compensation phenomenon in the process of rehydration, wherein F_v/F_m is higher than those in the corresponding treatment groups. This is mainly because plants will avoid drought through temporary reduction of photosynthesis in adverse conditions. Although plants incur specific damage, they can recover quickly after drought relief. Although the physiological activities of the photosynthetic apparatus are influenced through the relative water content of plant, the relationship between the two is not a simple linear one. From the change in F_v/F_m among the mosses with relative water content, it can be found (Figure 3) that *Barbula unguiculata* Hedw. has a strong desiccation tolerance. Before relative water content of plants is reduced to 45%, F_v/F_m is almost unchanged as relative water content declines. As such, when the relative content of water is in the range of 45–100%, F_v/F_m is relatively constant. Only when the relative water content of plants is lower than 45% does F_v/F_m sharply decrease. For *Bryum argenteum* Hedw. and *Erythrodontium julaceum* (Schwaegr.) Par., F_v/F_m is sharply down with relative water content. Relative water content causing F_v/F_m to suddenly reduce called the threshold value of relative water content causing F_v/F_m to change. The relative water content threshold of *Barbula unguiculata* Hedw. is 45%. However, there is no threshold value for *Bryum argenteum* Hedw. and *Erythrodontium julaceum* (Schwaegr.) Par. [24] in this paper. This indicates that when relative water content inside *Barbula unguiculata* Hedw. is more than 45%, the maximal photochemical efficiency will not be affected and photosynthetic organs will be not damaged. But if the water content is beyond this threshold, it will cause damage to plants.

(2) Drought Stress and Rehydration Influence on PS II Quantum Efficiency (Yield) and Electron Transport Rate (ETR). In the early period of stress (in twelve hours), the *yields* of *Erythrodontium julaceum* (Schwaegr.) Par. [24] and *Barbula unguiculata* Hedw. slightly increase and later decrease. It indicates that the adaptation process can be produced in early stages of drought stress and that the photosynthetic system can be restored by itself (*yield* of *Bryum argenteum* Hedw. is gradually reduced). *Yields* of the three mosses at the late stage of stress are significantly reduced ($P < 0.05$). In the early periods of the rehydration, *yields* of *Erythrodontium julaceum* (Schwaegr.) Par. [24] and *Barbula unguiculata* Hedw. increase slightly but are slightly lower compared to the control group. Within 0–48 hours, there is no evident difference compared with control group ($P < 0.05$), but 48 h later, the difference is significant ($P < 0.05$). After rehydration, the *yield* of *Bryum argenteum* Hedw. is slightly restored, but it is lower compared to the control group. As stress aggravates, *ETR* of the three mosses show the same trend as *yield*, namely, significant declining. After rehydration, the *ETR* of 3 mosses are slightly up. For *Erythrodontium julaceum* (Schwaegr.) Par. [24] and *Barbula unguiculata* Hedw., the difference with the control group within 48 h is not significant. 48 h later, it is slightly restored but not to the control level. During drought stress, the change in PSII actual photochemical efficiency in the mosses is similar to that of F_v/F_m. Dehydration first influences the maximum light-harvesting efficiency of the moss photosynthetic mechanism, which affects the actual photochemical efficiency and then influences its electron transfer chain. When the relative water content of plants is lower than the threshold value, the decline of the actual photochemical efficiency of mosses is caused by the decline in light energy capture and electron transfer rate.

(3) Drought Stress and Rehydration Influence on qP and qN. As drought intensifies, *qP* of the three mosses gradually decline. *Erythrodontium julaceum* (Schwaegr.) Par. [24] declines in a small range, from 0.958 to 0.950, with an insignificant difference ($P > 0.05$). *Bryum argenteum* Hedw. decreased from 0.908 to 0.717, falling by 21.04%, with a

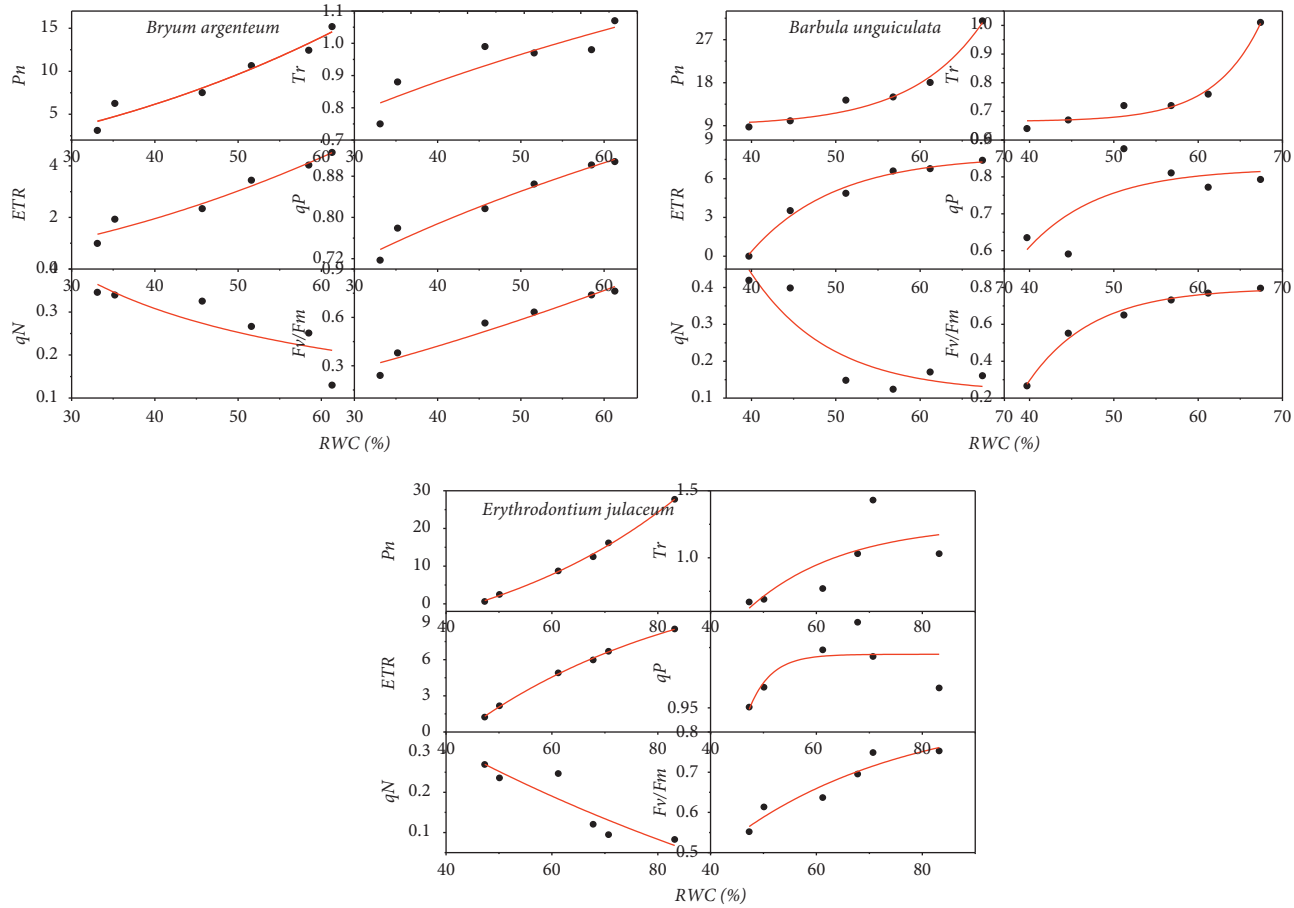
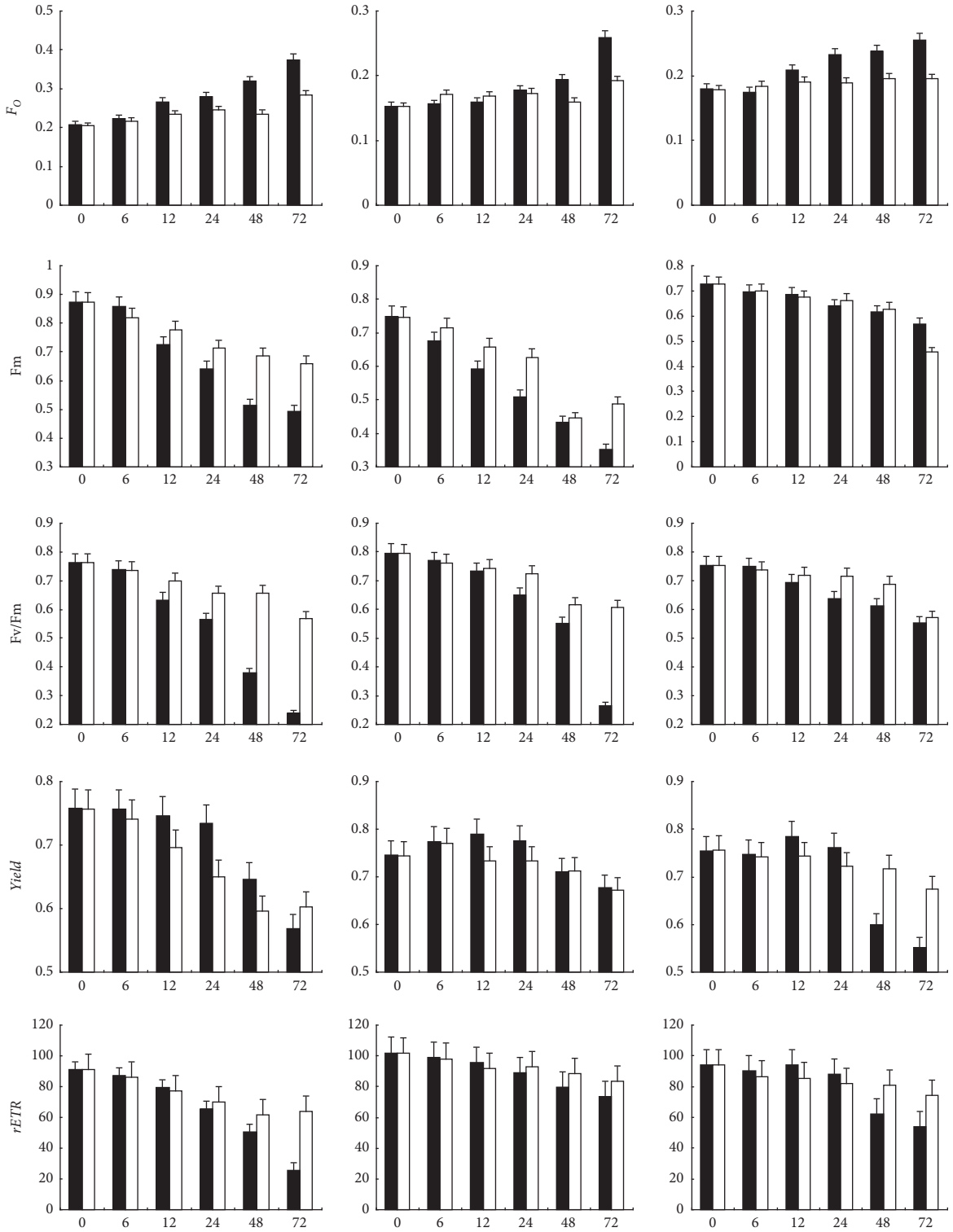


FIGURE 3: Relationship between photosynthesis indexes and RWC in three epilithic mosses during dehydration. *Erythrodontium julaceum* (Schwaegr.) Par. with permission from [29].

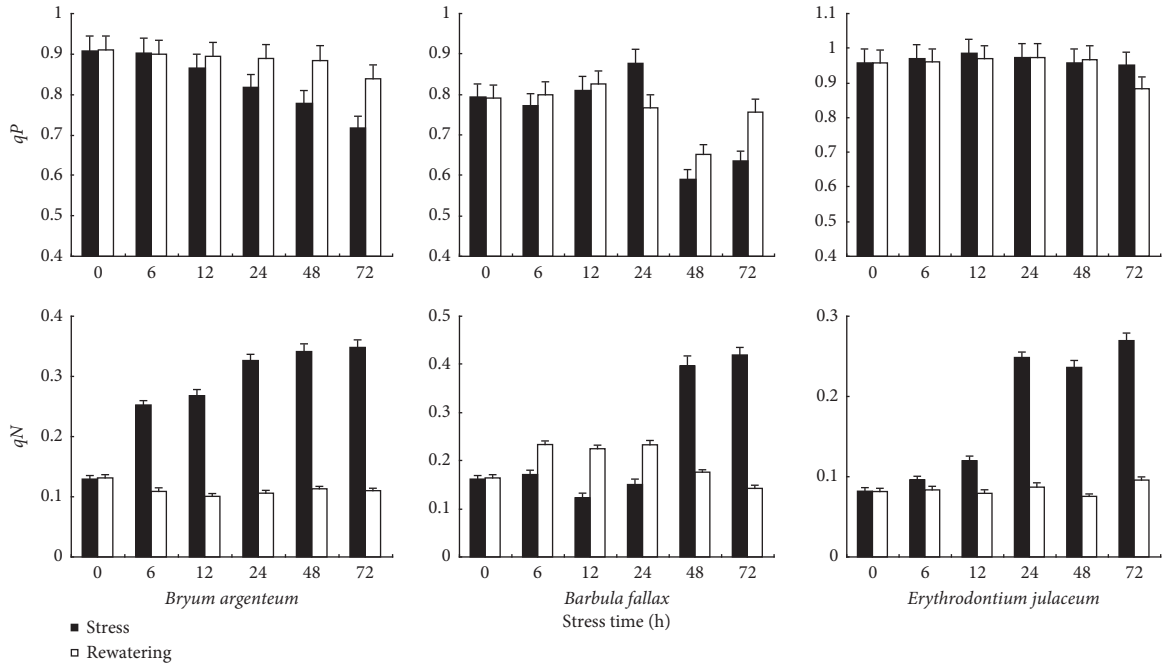
significant difference ($P < 0.05$). For *Barbula unguiculata* Hedw., it slightly increased at the beginning. This finding represents a drought stress response. It gradually decreased in 12–48 h and slightly increased 48 h later, showing a generally increasing trend with three phases. The first and last phases are characterized by an increase interspaced by a second decreasing phase. After rehydration, *qP* can get a specific increase. *Bryum argenteum* Hedw. restored more slightly but not to the control level, whereas, for *Barbula unguiculata* Hedw., it is higher than the control level in 6–12 h, generating a super compensation effect, and then goes lower than the control level. Before 48 h, *Erythrodontium julaceum* (Schwaegr.) Par. [24] is slightly more than the control level, generating a super compensation effect, and then goes lower than control level, but the change is minimal. The decline in *qP* shows that the number of open PSII reaction centers is reduced under drought stress, causing a significant reduction in photosynthetic electron transport. *qN* shows an increasing trend with the duration of water stress. *Bryum argenteum* Hedw. and *Erythrodontium julaceum* (Schwaegr.) Par. [24] show a similar trend characterized by an initial slight increase that balances later. But the increase in *Bryum argenteum* Hedw. is greater than that of *Erythrodontium julaceum* (Schwaegr.) Par. [24] *Barbula unguiculata* Hedw., initially increases slightly, followed by a decrease, and concludes with a final sharp increase that is three times higher under severe stress for 72 h, with very significant difference ($P < 0.01$). The increase in *qN* shows that a large amount of absorbed light energy dissipates by nonphotochemical ways under the condition of water stress-induced photoinhibition. After rehydration, *qN* can be restored to the normal level. All three mosses varied with relative water content. *qP* will increase, while *qN* will decrease with the increase in relative water content (Figures 3 and 4).

3.3.3. Drought Stress and Rehydration Influence on Photosynthesis and Transpiration Rate. The too high or too low water content will decrease net photosynthetic rate [30]. Dilks & Proctor's research has shown that water membranes with extremely high surface tension would increase the gas exchange resistance and has an inhibitory effect on the photosynthesis of mosses [31]. As a whole, net photosynthetic rates (*Pn*) of the mosses are positively correlated to relative water content. It can be found from Table 2 and Figure 3 that, after a period of drought and dehydration, net photosynthetic rates (*Pn*) in the mosses decline gradually. In normal conditions, the net photosynthetic rate (*Pn*) of *Barbula unguiculata* Hedw. is the largest at 30.93 μmol



(a)

Figure 4: Continued.



(b)

Figure 4: The effect of replenishment and drought stress on chlorophyll fluorescence parameters in three epilithic mosses. *Erythrodontium julaceum* with permission from [24]. Copyright 2016 open-access from Bangladesh botanical society.

$CO_2 \cdot m^{-2} \cdot s^{-1}$ and that of *Bryum argenteum* Hedw. is the smallest at 15.19 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$. After 3 days' stress, the net photosynthetic rates (*Pn*) of the three mosses are sharply declined. For *Bryum argenteum* Hedw., *Barbula unguiculata* Hedw., and *Erythrodontium julaceum* (Schwaegr.) Par., it is 3.12 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, 8.73 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, and 0.62 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$, respectively, falling by 4.87, 3.54, and 44.74 times. *Erythrodontium julaceum* (Schwaegr.) Par. is the largest in the declining range, and photosynthesis was seriously affected. After rehydration, the net photosynthetic rate (*Pn*) of *Erythrodontium julaceum* (Schwaegr.) Par. is restored most greatly, and those of *Bryum argenteum* Hedw. and *Barbula unguiculata* Hedw. are restored just slightly. This indicates that dehydration does not cause damage to PS II of plants.

The changes in the transpiration rates of the mosses in the process of dehydration and rehydration are shown in Table 2 and Figure 3. In the beginning, transpiration rates of *Bryum argenteum* Hedw., *Barbula unguiculata* Hedw., and *Erythrodontium julaceum* (Schwaegr.) Par. are, respectively, 1.07 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$, 1.01 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$, and 1.03 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$. The difference between the species is not obvious ($P > 0.05$). After stressing for 72 h, transpiration rates among the mosses decrease to different extents, but the decrease is not very large. This is related to the characteristic of the moss plants belonging to poikilohydric plants. After rehydration, all mosses are restored to different degrees, but the differences between species and between treatments do not reach a significant level.

3.4. Water Stress on Water Use Efficiency. According to Figure 5, between the mosses, there exists an evident difference in WUE, generally showing a gradual declining trend as stress aggravates. For *Bryum argenteum* Hedw., WUE is 14.20 $\mu molCO_2/mmo1H_2O$ in the expected condition and goes down to 4.16 $\mu molCO_2/mmo1H_2O$ after stress for 72 h, falling by 3.14 times. *Barbula unguiculata* Hedw. decreased from 30.62 $\mu molCO_2/mmo1H_2O$ at the beginning to 11.84 $\mu molCO_2/mmo1H_2O$ after stress for 72 h, falling by 2.59 times. For *Erythrodontium julaceum* (Schwaegr.) Par., it decreased from 26.93 $\mu molCO_2/mmo1H_2O$ to 5.32 $\mu molCO_2/mmo1H_2O$, falling by 5.06 times. The drought resistance as WUE reflects

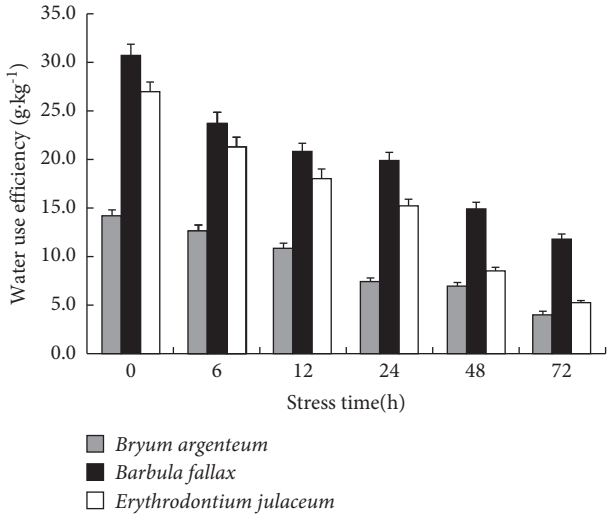


Figure 5: Effects of the drought stress on water use efficiency in three types of epiphytic mosses.

is *Barbula unguiculata* Hedw.>*Erythrodontium julaceum* (Schwaegr.) Par.>*Bryum argenteum* Hedw. *Barbula unguiculata* Hedw. with higher WUE can more effectively transport energy and water use. In the case of a low water supply level, it can maintain lower transpiration and higher photosynthesis rates.

4. Discussion

Berger-Langefeldt divide plants into two ecological types, namely, constant water and variable water, according to the characteristics of the plant water balance. Constant water plants reduce the rate of water loss using stomatal closure to maintain leaves' relatively stable water content. In contrast, variable water plants reduce the rate of water loss using tissue moisture content reduction. Variable water plants are at the cost of tissue water content declining [32]. Generally, bound water content and V_s/V_a are closely related to drought resistance in plants [32]. When V_s/V_a is low, plant metabolism is active with fast growth, but the resistance is weak. When V_s/V_a is high, plant metabolism is inactive with slow growth and with strong resistance. V_a, V_s, and V_s/V_a of the three mosses changed significantly with the aggravation of water stress, in which V_s and V_s/V_a increased, while V_a content decreased. After rehydration, free water increases rapidly and V_s/V_a ratio decreases. This phenomenon indicates that plants maintain the water balance in the body by adjusting the content of free water and bound water. The lack of water saturation and relative water content of leaves are important indexes to reflect the hydration tension of plants. With the increase of the stress process, RWC showed a trend of decrease in this study. After rehydration, RWC increased to different degrees and WSD dropped to different extents, but the variation was not significant, indicating that rock moss had a certain hysteresis effect on water stress within a relatively short time. The water potential gradient is the driving force to maintain the normal operation of water and water in plants flows from high to low. *Erythrodontium julaceum* (Schwaegr.) Par. declines most, followed by *Barbula unguiculata* Hedw., and *Bryum argenteum* Hedw. declines the least. After rehydration, the water potential of the three species of bryophytes recovered to different extents, indicating that bryophytes in karst areas have intense drought and dehydration tolerance. RWC and water potential of the three mosses are very different, which is consistent with similar studies abroad [33]. The unique geology and geomorphology in the karst area cause the uneven distribution of water; some places are dry perennially, and some are prone to waterlogging. After raining, surface karst water quickly seeps underground, and the ground cannot store rainwater. Therefore, even in areas with abundant rainfall, a special karst seasonal arid environment will be formed, different from the arid environment caused by lack of rainfall in the desert and other environments.

In this paper, chlorophyll contents of three types of crusted mosses generally show a trend of declining first and increasing later with increased stress. This is related to the influence on the plant photosynthetic capacity. This is also related to the increase in chlorophyll content per unit mass, which is due to a large amount of dehydration in the moss sphaerophyta which causes the plant to curl into dormancy, resulting in a substantial decrease in water content. RWC of the mosses is negatively correlated to *qN* and positively correlated to F_v/F_m, *yield, ETR*, and *qP*. After rehydration, the fluorescence parameters could be recovered to normal levels under mild-to-moderate stress but could not be recovered under severe stress. Chlorophyll fluorescence characteristics under drought stress of photosynthetic quantum conversion efficiency are low, photosynthetic system II reaction center closed, and once the environment quickly absorbs moisture, it gradually returned to normal metabolism [44]. For example, F_v/Fm and non-photochemical quenching (*qP*) of *Rhytidiadelphus loreus* can be restored in a short period. It indicates that its photosynthetic system can still work after rehydration [15]. The whole rehydration for *Syntrichia caninervis* Mitt. can be completed within 3 m. More than 50 percent of the PS II revives, containing oxygen metabolism, excitation energy transfer, electron transfer, charge dislocation, and so on, which can be restored to normal upon rehydration for 0.5 m. If the rehydration is longer, the energy transferring to PS II reaction center tends to balance; at the same time, NPQ is down [34]. *RWC* is negatively correlated to *qN* and positively correlated to F_v/F_m, *yield*, *ETR*, and *qP*. After rehydration, the fluorescence parameters could be recovered to normal levels under mild-to-moderate stress and could not be recovered under severe stress. It is the same as the changing trends of *Syntrichia caninervis* Mitt. and *Grimmia pilifera* P. Beauv. Therefore, after drought stress, rehydrated chlorophyll fluorescence characteristics reflect the adaptability of plants to stress and the corresponding protective mechanism. The studies show that as the water content of *Rhytidium rugosum* and *Rhytidiadelphus* triquetrus declines, the dark respiration rate would increase. There is a sudden leaped peak before closing to natural drying, and then it goes down. *Myuroclada maximowiczii*, *Mnium cuspidatum* Hedw., and *Ptilium crista-castrensis* do not have apparent peaks. During rehydration, the respiration rate of moss plants is similar to the photosynthetic rate, with a declining trend. Dry plants do not have significant gas exchange. For these five moss plants, photosynthetic activity can be restored to the original level after water absorption for 24 h. It indicates that the photosynthesis of most of the mosses can be rapidly restored after rehydration [35]. This paper has proved that water use efficiency (WUE) will be constantly down as stress aggravates. At the early stages of stress, the recovery potential of WUE after rehydration is higher than that in the late stage. It is consistent with the result that the respiration rate after rehydration is quicker than the net photosynthetic rate [36].

Epilithic mosses in karst areas are mostly exposed on rock surfaces under drought stress during their growth and even need to endure rapid dehydration stress. A series of the characteristics adaptive to the dry environment are formed in a long-term evolution process. Plants are usually densely pulvinate, clump, or blanket-like moss clump. The water holding ability of capillary system is improved, and the movement of air on the blade's surface is decreased with the

aim of reducing the water evaporation. During dehydration, the photosynthetic mechanisms of three crusted mosses have strong dehydration-resistant capacity. In a drought environment, the water content in the body can be lowered to survive in a dormant state. Cell integrity and structure are maintained as far as possible to minimize cell injury and metabolites destruction. Once rehydration occurs, physiological metabolic activity can be quickly recovered. During rehydration, the repair mechanism is quickly triggered for the repair of photosynthetic mechanism resulting from dehydration [37].

Data Availability

The data used to support the results of this work can be obtained from the associated authors upon request.

Conflicts of Interest

The authors declare no conflicts of interest.

Acknowledgments

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