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3 种藓类植物水分含量与光合作用、呼吸作用和水势的关系

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摘 要: **对湿地匍灯藓**〔*Plagiomnium acutum* (Lindb.) T. Kop.〕、**大羽藓**〔*Thuidium cymbifolium* (Dozy & Molk.) Dozy & Molk.〕**和垂藓**〔*Chrysocladiun retrorsum* (Mitt.) Fleisch.〕**的水分含量与光合作用、呼吸作用和水势的关系进行了初步研究**(1999 **年** 5 **月** 20 **日到** 6 **月** 10 **日**)。**在这** 3 **种藓类植物中, 其水分含量与光合作用速率**(Pn)**的关系可以分为** 2 **种类型: 一种类型如大羽藓和垂藓, 在藓体水分含量** 20%～70% **时**, Pn **随着水分含量增加而增加, 但是在** 80%～95% **时**, Pn **随水分含量增加而下降, 光合最适水分含量约** 70%～80%; **另一种出现在湿地匍灯藓, 水分含量** 20%～80% **时**, Pn **随着水分含量增加而增加, 在** 80%～95% **时**, Pn **维持一个较高的水平, 光合最适水分含量为** 80%～90%。**在一个大的水分含量范围内**(60%～95%), **暗呼吸**(Rd)**保持相对稳定, 但是在水分含量较低时**(20%～70%), Rd **随着水分含量的下降而下降。在藓体水分含量与水势之间的关系方面**, 3 **种藓类植物相似, 水分含量与水势对数之间的回归曲线为** S **形曲线。**

关键词: **藓类; 光合作用; 呼吸作用; 水分含量; 水势**

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Relationships of Water Content to Photosynthesis, Respiration and Water Potential in Three Species of Mosses

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Abstract: The relationships of water content to photosynthesis, respiration and water potential in three species of mosses, *Plagiomnium acutum* (Lindb.) T. Kop., *Thuidium cymbifolium* (Dozy & Molk.) Dozy & Molk., and *Chryso-*

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cladiun retrorsum (Mitt.) Fleisch. were studied during May 20 to June 10, 1999. Among these three mosses, there are two types of water response models for net photosynthetic rate (Pn). One appeared in *Thuidium cymbifolium* and *Chrysocladium retrorsum*, in which Pn increased with the water content from 20% to 70%, but decreased from 80% to 95%. The optimum water content was 70%～80%. Another was presented in *Plgiomnium acutum*, in which net Pn increased with water content increasing from 20% to 80%, and a high level of Pn maintained from 80% to 95% of water content. The optimum water content was 80%～90%. In a wide range of water content from 60(70)% to 95%, the Rd remained relatively stable. But in the range of lower water contents from 20% to 70%, the Rd decreased with decreasing water contents. Changes in between water contents and water potentials within these three mosses are similar to each other. The whole curve of water contents to logarithm of water potentials appears to be S-formed.

Key words: Mosses; Photosynthesis; Respiration; Water content; Water potential

1 Introduction

Bryohpytes face the same basic problems of life on the land as flowering plants. Water is essential for metabolism, but is limited and erratic supply in the aboveground environment where the leaves must be exposed in order to photosynthesize[1]. Bryophytes and vascular plants exemplify two alternative patterns of adaptation to these conditions. Vascular plants have evolved roots and an efficient conducting system, bringing water from the soil where it is relatively plentiful and constant supply. Bryophytes have evolved to utilize water where and when it is available above ground; some are confined to moist habitats, but many can tolerate drying out, and some are extremely desiccation-tolerate and highly adapted to a poikilohydric existence. The studies of water relations of some bryophytes were well documented in resent publications in the world[2-8], but were neglected in China.

It is necessary to cultivate the winter host mosses for the gallnut production in China[9-17], which requires us to understand the physiology of mosses. So our attention has also been paid to the physiological studies including light and temperature response in photosynthesis, diurnal course of photosynthesis and dark respiration of mosses[18-21]. This paper reports some experimental results on the relationships of water content of winter host mosses with photosynthesis, dark respiration and water potential.

2 Materials and Methods

2.1 Materials

The three mosses used in the experiments were collected from Dehang scenic spot in Jishou, western Hunan, China, 28°15′N, 109°40′E, at an elevation of 300～350 m. The mosses include three abundant and common species. One is *Plagiomnium acutum* (Lindb.) T. Kop. it usually grows on a thin layer of soil over rochs near streams or on the hillsides of wooded mountains. Its habitat is shaded, wet, or sometimes unshaded. Another common species is *Thuidium cymbifolium* (Dozy & Molk.) Dozy & Molk.. This moss often grows on exposed rocks beside roads or near streams in wooded mountains. The third, *Chrysocladiun retrorsum* (Mitt.) Fleisch. It is a distinctive moss that grows only in the humid habitats of wooded mountains, commonly hanging on cliffs or rocks faces. The voucher specimens are housed in the Herbarium of Jishou University.

2.2 Measurement of the water content and net photosynthesis

The CI-301PS (CID Ins., USA) was used to measure the moss net photosynthesis (Pn). The open system was used in the experiment. The Pn in the output of this system was based on the amount of CO_2 per leaf area unit ($\mu mol \cdot m^{-2} \cdot s^{-1}$), which must be converted. In this paper, the Pn is expressed based on the amount of CO_2 per dry weight unit of materials ($\mu mol \cdot kg^{-1} DW \cdot s^{-1}$).

When measuring the water relation of Pn, the Photosynthetic active radiation (PAR) on the assimilation chamber was controlled within 800～900 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and the temperature of the samples, within 24～26℃. The dark respiration (Rd) was measured in darkness. The materials were selected and cleaned before measuring. At first, the samples were wetted and weighed. They were then placed in the chamber and measured rapidly (in 3～5 min.). Then the samples were removed from the chamber and placed in sunlight or under electric lamp for evaporation of the water in the samples. About 10 minutes later, the samples were again placed in the chamber and measured, and so on. Interval time between the two measurements depended on the evaporation rate of water in the samples. Usually 5～7 measurements were needed for a single sample from the saturated to about 15%～25% water content. The results reported in this paper include measuring values of five parallel samples for one species of mosses, and a single measuring value is an average of five readings in the experiment. After the measurement, the materials were dried at 80℃ for 8 hours and then weighed.

2.3 Measurement of relation of water content to water potential

The method for measuring relationship between water content and water potential was approximately the same as Busby & Whitfield[4] and Dilks & Proctor[3]. Saturated salt solutions in closed containers (at certain temperature) provide precise relative humidity that can be transformed into water potential values. A range of relative humidity percent of values (15, 32.3, 44, 54, 75.5, 81, 86, 90, 93, 95, 98) was chosen and salt solutions that provide these humidity were selected according to Wylie[22], Weast[23] and Dilks & Proctor[3].

Moss samples were suspended over the saturated salt solutions in closed flasks. The temperature in the flasks were maintained at 20℃±0.5℃. The samples were weighed at an interval of two days until a constant weight was reached. The water contents were determined from the equilibrium weight and dry weight (80℃ for 8 h). Measurements were made on both wet and dry materials. Water potential near zero (0.1 mPa) was obtained by suspending the materials over distilled water in the flasks.

3 Results

Optimal temperatures and PAR levels have been established for these three mosses in our previous studies[21, 24]. According to these results, measurements of influence of water content on net photosynthetic rate were made at PAR level of 800~900 μmol·m^{-2}·s^{-1} and a sample temperature of 24~26°C. The results obtained under the same condition but with the chamber covered with dark fabric represent dark respiration rate. The experiments were carried out in the laboratory from May 20 to June 10, 1999. The results are shown in Figs 1 and 2.

3.1 Water content and net photosynthesis (Pn)

Among these three mosses, there are two types of water response models for net photosynthesis rate (Pn). One appeared in *Thuidium cymbifolium* and *Chrysocladium retrorsum*, in which Pn increased with the water content from 20% to 70(80)%, but decreased from 80% to 95%. The optimum water content was 70%~80% (Fig. 1: B, C). Another was presented in *Plgiamnium acutum*, in which Pn increased with water content increasing from 20% to 80%, and a high level of Pn maintained from 80% to 95% of water content. The optimum water content was 80%~90% (Fig. 1: A).

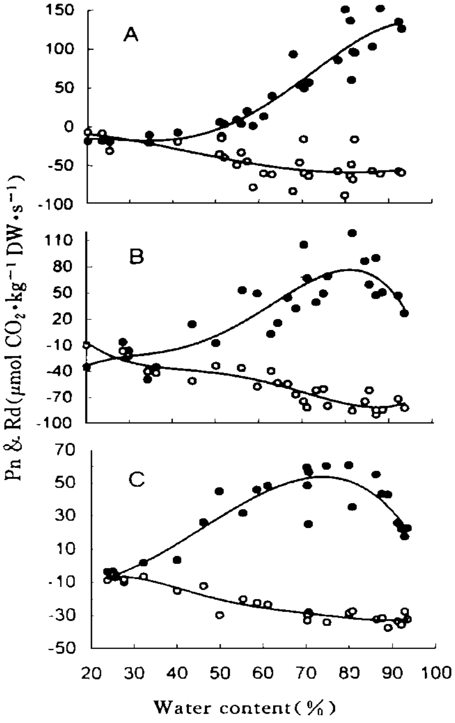


Fig. 1 Relationships of net photosynthesis (Pn, solid circles) and dark respiration (Rd, open circles) to water content of the mosses *Plagiamnium acutum* (Lindb.) T. Kop. (A), *Thuidium cymbifolium* (Dozy &Milk.) Dozy &Milk. (B), and *Chrysocladium retrorsum* (Mitt.) Fleish. (C)

The relationship between water content and Pn has been well documented in various mosses[3~6, 25, 26]. According to Stålfelt[25] and Dilks & Proctor[3], water response curves for Pn of many mosses growing in dry habitat exhibited an optimum, with the rate declining again at high water content. Only in species growing in wet habitat such as *Hookeria lucens*, did the rate of Pn increase continually at the high level of water content. In our experiment, the water response model for Pn shown by *Thuidium cymbifolium* and *Chrysocladium retrorsum* is approximately the same as that which appeared in mosses growing in dry habitats described by Stålfelt[25] and Dilks & Proctor[3]. But in *Plagiomnium acutum*, the model is similar to that of mosses growing in wet habitats.

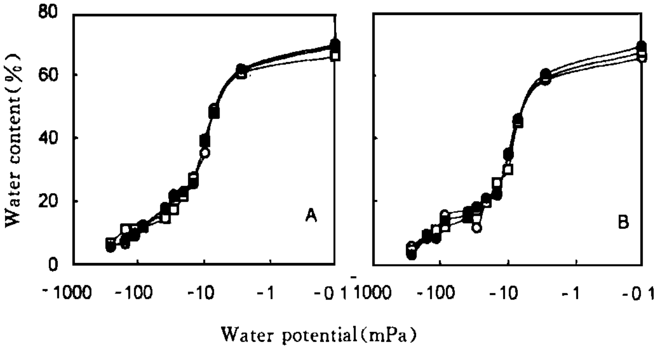
3.2 Water content and dark respiration (Rd)

Although there were different models of water response for Pn, the water response model for dark respiration rate (Rd) in the three mosses was similar. In a wide range of water content from 70% to 95% the Rd maintained relatively stable. But in the range of lower water content from 20% to 60(70)%, the Rd decreased with the water content decreasing.

Among these three mosses, the water response of Rd in the range of lower water content is roughly synchronous with that of Pn for *Thuidium cymbifolium* (Fig. 1:B) and *Chrysocladium retrorsum* (Fig. 1:C) but behind for that of *Plagiomnium acutum* (Fig. 1:A). This shows that photosynthesis is more sensitive to desiccation than respiration for mosses growing in wet habitats, such as *Plagiomnium acutum*. In mosses growing dry habitats, such as *Thuidium cymbifolium* and *Chrysocladium retrorsum*, however, the response to desiccation for Pn and Rd is roughly the same.

3.3 Water content and water potential

Relationships between water content and water potential for these three mosses are presented in Fig. 2. The differences among species are minor, and there are no significant differences between desorption curves (obtained from wet samples) (Fig. 2:A) and absorption curves (from dry samples) (Fig. 2:B) except for the data measured from near 0 to -2.7 mPa of water potential. The equilibrium water contents over distilled water were difficult to determine[4]. Because the water potential gradient between mosses and the saturated atmosphere was minute, the rate of water vapor movement was minute as well. Although the samples were maintained for two weeks on distilled water and a saturated solution of $CuSO_4$ (-2.7 mPa of water potential) in our experiment, it did not eliminate the hysteresis effect on wetting and drying curves from near 0 to -2.7 mPa of water potential as shown in Fig. 2. From -14.3 to -257 mPa of water potential, irregardless of wetting or drying curves, the equilibrium water content of these three mosses is quite similar, and a linear relation between the water contents and the logarithm of water potential was presented. The entire



A. Desorption (wetting) curves; B. Absorption (drying) curves
● *Plagiomnium acutum*; ○ *Thuidium cymbifolium*;
□ *Chrysocladium retrorsum* (Mitt.) Fleish. (C)

Fig. 2　Relationships of water content (%) to water potential curve of water content to logarithm of water potential appears to be S-formed (Fig. 2).

The differences for relation of water content to water potential among species of mosses have been proven to be minute by many workers[3, 4]. Dilks & Proctor put forward a schematic relation of water content to water potential for a poikilohydric moss[1, 3]. We averaged the values measured from our three mosses, both wet and dry samples, and also plotted out a schematic relation of water content to water potential (Fig. 3). Compared with Dilks & Proctor, our schematic relation demonstrated a similar general water content response model to water potential, but included a little description of external capillary water associated with shoots of mosses.

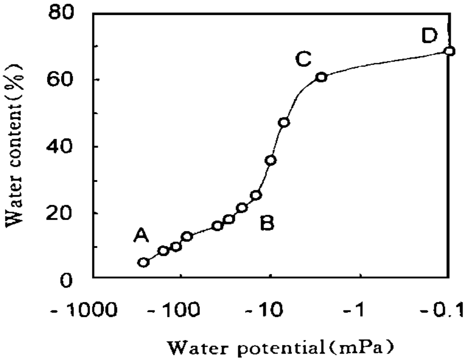


Fig. 3 Relationships of water content to water potential for the mosses *Plagiomnium acutum*, *Thuidium cymbifolium* and *Chrysocladium retrorsum*. The curve was fitted according to averages of data from both wet and dry samples of the three mosses. From A to B, most water is closely associated with surfaces and is relatively immobile. From B to C, increase of water content is mainly within the cells. C is the point of incipient plasmolysis; from C to D the water content increases with the built-up of wall pressure and the first appearnce of external capillary water

4 Discussion

Stålfelt (1937) pointed out that the water response curve of photosynthesis for *Hylocomium splendens* exhibited an optimum, with the rate declining again at high water content, in contrast to the behavior of respiration[25]. This is probably a consequence of the much slower diffusion of gases through water than through air; and excess water would be expected to restrict gas exchange at the low concentration gradients available for CO_2 uptake but should have negligible effect on respiration. But Dilks & Proctor[3] presented data that the Pn rate declining at high water contents only appeared in mosses growing in dry habitats. This means that the Pn rate declining at high water contents probably showed the physiological characteristics of the mosses growing in dry habitats, and was not, or was not completely, a consequence of the slower diffusion of gases through water than through air. Our results also support this idea. *Thuidium cymbifolium* and *Chrysocladium retrorsum* are both mosses that grow on rock, and they are not only the desiccation-resistant mosses, but are also sensitive to excess water in their habitats. *Plagiomnium acutum*, however, growing on soil and in a wet habitat, is a desiccation-sensitive moss, and can tolerate excess water in its habitat.

Respiration, on other hand, shows little change over a wide range of water content for these three mosses in our experiment. According to the experiment described by Dilks & Proctor, portions of the curves over which Pn and Rd are steeply related to water content are not conspicuously separated for mosses growing in dry habitat (Fig. 2), but are separated for mosses growing in wet habitats (Fig. 1)[3]. This is a consequence of a slower increase with water content increasing more for Pn than for Rd for the mosses growing in wet habitats. In our experiment, Pn and Rd of *Thuidium cymbifolium* and *Chrysocladium retrorsum* increased rapidly with increasing water content, both reached their maximum at 70% of water content. These two mosses behaved the same as mosses growing in dry habitats described by Dilks & Proctor[3]. For another species, *Plagiomnium acutum*, the Pn increased with water content slower than did Rd, behaving the same as mosses growing in wet habitats as described by Dilks & Proctor[3].

For the relationship between water content and water potential, Busby & Whitfeld pointed out that differences among species are minor[4]. This was confirmed in our experiment. But some problems existed with this measurement especially at a water potential near zero. In the experiment described by Busby & Whitfeld[4], water potential near zero was obtained by suspending dried material (- 29.3 to - 281 mPa) over distilled water. Equilibrium water contents, however, could not be accurately determined because the samples were overgrown by fungi before their weights stabilized. The data obtained in the measurement described by Busby & Whitfeld[4] were presumably lower than the real values. We used wet and dry samples to measure the equilibrium water content for water potential near zero by suspending the samples over distilled water (near zero) and a saturated solution of $CuSO_4$ (- 2.7 mPa) for two weeks. The average of values obtained from wet and dry samples may be close to the real value.

The differences between mosses and flowering plants is put in perspective by the fact that Pn in the latter decreases as soon as water potential drops below - 0.1 to - 0.3 mPa. Indeed, in most flowering plants Pn may reach zero or even become negative (i.e., respiration is exceeding photosynthesis) when water potential drops below - 1.2 to - 1.5 mPa. Thus, to survive, flowering plants and ferns must control their water contents so that they remain within the limits set by their water potential values[4]. But in mosses, especially in mosses growing in dry habitats, Pn decreases more slowly with a decreasing water potential (See Fig. 1 and Fig. 2). When water potential dropped to - 1.0～- 1.5 mPa, the Pn decreased only a little. When water potential continued to drop below - 2.7 to - 9.8 mPa, Pn decreased quickly. When water potential dropped below - 9.8 to - 14.3 mPa, Pn approached zero or became negative. This result shows that the mosses cannot control their water contents or water potentials within a relatively stable range, but they can viably response to the fluctuation of water potential in their habitat.

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