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JPLPH-52306; No. of Pages 10
ARTICLE IN PRESS

Journal of Plant Physiology xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Physiology

Physiological regulation of *Syntrichia caninervis* Mitt. in different microhabitats during periods of snow in the Gurbantünggüt Desert, northwestern China

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ARTICLE INFO

Article history:
Received 7 October 2015
Received in revised form 21 December 2015
Accepted 22 January 2016
Available online xxx

Keywords:
Biological soil crusts
Bryophyte
moss
Antioxidant enzymes
Chlorophyll fluorescence
Snow

ABSTRACT

Moss crusts, the most advanced stage of biological soil crust (BSC) development, play important roles in BSC biomass and soil surface stabilization. They usually survive freeze–thaw cycles and remain active during periods of extremely low temperatures. We selected *Syntrichia caninervis* Mitt., the dominant moss crust species, to study physiological characteristics in winter in three different microhabitats (under the canopy of living shrubs, under dead shrubs, and in exposed areas) in the Gurbantünggüt Desert of northwestern China. The results show that soluble sugar content and antioxidant enzyme activity were significantly higher when heavy snow covered the ground in midwinter, than in early winter and late winter. Soluble protein content was highest in mosses in BSCs under shrub canopies. In contrast, antioxidant enzyme activity was at its maximum in BSCs of exposed areas. Our results indicate that moss crusts have the potential to effectively survive rapid environmental change during winter by an increase in osmoregulatory substances and by increased antioxidant enzymes activity. Mosses in BSCs in exposed areas showed the highest antioxidant enzyme activity, in direct contrast to that of mosses in BSCs growing under canopies of both dead and living shrubs. This may indicate that plants of *S. caninervis* growing in exposed conditions are better adapted to harsh environmental conditions than plants growing in more sheltered habitats.

1. Introduction

Biological soil crusts composed of various combinations of cyanobacteria, bacteria, algae, fungi, lichens, and bryophytes (mosses and liverworts) are widespread in polar, arid, and semi-arid lands worldwide (Belnap et al., 1994; Zhang et al., 2007). The presence of crusts can roughen the soil surface, impacting on nutrient cycling, soil stability, and hydrological processes. Soil crusts can also influence the germination and establishment of vascular plants and provide habitats for numerous arthropods and microorganisms (Kidron et al., 2009; Li et al., 2010). Moss-based crusts are recognized as the most highly developed stage in ecological succession of BSCs where they play a major role in these micro-ecosystems and contribute most of the biomass (Brotherson and Rushforth, 1983; Xu et al., 2003; Cornelissen et al., 2007). However, mosses are poikilohydric and thus extremely sensitive to environmental change, especially changes related to water.

Water is the major limiting factor for plant growth in arid and semiarid regions worldwide. In order to survive extreme environments, mosses have evolved a variety of stress-resistant morphological (Tao and Zhang, 2012; Wu et al., 2014), physiological and biochemical attributes (Martin and Churchill, 1982; Khandelwal et al., 2010), and reproductive strategies (Herrnstadt and Kidron, 2005; Benassi et al., 2011). Unlike most vascular plants, desiccation tolerant bryophytes have highly variable water-related features and can change both morphologically and physiologically as ambient water conditions change (Proctor, 2000; Oliver et al., 2005). However, in summer, high light intensity and temperatures lead to their rapid dehydration. They become dormant as growth slows and may stop almost completely (Benassi et al., 2011). Bryophytes growing under ice in early winter and spring have shown high levels of robustness. Bryophytes, already adapted to the cold, can rapidly become active when minimum thresholds for

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http://dx.doi.org/10.1016/j.jplph.2016.01.015

Please cite this article in press as: Yin, B.-f., Zhang, Y.-m., Physiological regulation of *Syntrichia caninervis* Mitt. in different microhabitats during periods of snow in the Gurbantünggüt Desert, northwestern China. J Plant Physiol (2016), http://dx.doi.org/10.1016/j.jplph.2016.01.015

Table 1
Comparison of soil physicochemical properties in different microhabitats.

	Under living shrubs	Under dead shrubs	Exposed areas
Organic matter (g kg^{-1})	3.721 ± 0.318a	3.898 ± 0.737a	2.300 ± 0.574b
Total N (g kg^{-1})	0.475 ± 0.073a	0.495 ± 0.048a	0.301 ± 0.047b
Total P (g kg^{-1})	0.400 ± 0.014ab	0.445 ± 0.013a	0.394 ± 0.059b
Total K (g kg^{-1})	13.119 ± 0.249a	12.977 ± 0.127a	12.194 ± 0.136b
Total NaCl (g kg^{-1})	0.576 ± 0.018a	0.567 ± 0.079a	0.514 ± 0.045a
pH	7.936 ± 0.031a	7.672 ± 0.036b	7.652 ± 0.262b
Electrical conductivity (μS cm^{-1})	0.131 ± 0.009a	0.129 ± 0.008a	0.125 ± 0.016a

Different letters indicate significant difference ($P < 0.05$) among three microhabitats.

temperature, light and humidity are reached (Lange, 2003; Kappen and Valladares, 2007; Bjerke, 2011; Su et al., 2013). Growth and reproduction of desert mosses have previously been reported as being limited to cold and wet winter months, and sexual reproduction has been more evident in shaded conditions (Herrnstadt and Kidron, 2005; Benassi et al., 2011). In early winter and spring, moisture from snowmelt and warmer temperatures can prolong the photosynthetic activity of mosses in soil crusts by increasing their capacity to intercept light energy and absorb CO_2 (Su et al., 2013; Yin and Zhang, 2014). However, little is known about how mosses adapt to extreme winter conditions, particularly with respect to their physiological regulation.

Microhabitat differences can also result in varied survival strategies for bryophytes. Most studies report that bryophyte coverage is more extensive, and individual plants are taller, in shaded sites than in exposed ones (Pintado et al., 2005; Zhang et al., 2007). Shaded sites experience lower temperatures, lower light intensities, and higher moisture levels than exposed ones and there is potential for these differences in microenvironments to result in morphological changes in bryophytes. Although moss morphology does not undergo obvious change during short-term changes (some weeks) in microhabitat, photosynthetic rates are maintained at the same level as those of the current living environment of measuring. Lenne et al. (2010) discovered that dehydration, together with the associated accumulation of soluble sugars in the moss *Ceratodon. purpureus* Hedw., protected plants from frost damage at low temperatures. During the process of dehydration, mosses accumulate free proline, soluble sugars, and other materials (e.g., amino acid and glycinebetaine), and cell osmotic pressure increases, protecting membranes from damage and stabilizing the structure and activities of proteins and enzymes, and allowing the plants to maintain normal functions (Oliver et al., 1997; Crowe et al., 1998; Wu et al., 2009). Moreover, the synthesis of antioxidant enzymes, such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), protects plant membranes and plant cell activity from damage as a result of excessive oxidation and the activities of other oxyradicals (Sgherri et al., 1994; Herrnstadt and Kidron, 2005; Pintado et al., 2005; Shen et al., 2011). Shrubs and biological soil crusts form mosaics in deserts so the morphological structures and physiological characteristics of bryophytes may differ in diverse micro-environmental conditions. Bryophyte photosynthetic physiology may be affected by both snow cover and winter thawing. Temperate desert ecosystems have varied microhabitats but the way in which those microhabitats affect the physiological and biochemical characteristics of mosses in winter remains poorly understood (Bjerke et al., 2011).

The Gurbantünggüt Desert receives abundant snow in winter, forming a natural cover on the ground up to 20–30 cm thick and maintained for 100–150 days (Zhou et al., 2010). Snow is a very good insulator for mosses, having both a wetting and warming effect. Snow also allows for better water permeability than plastic covering (Bjerke, 2009) and thus may create a favorable environment for bryophyte growth during winter. There has been a strong focus on the effects of drought, high levels of radiation, and high

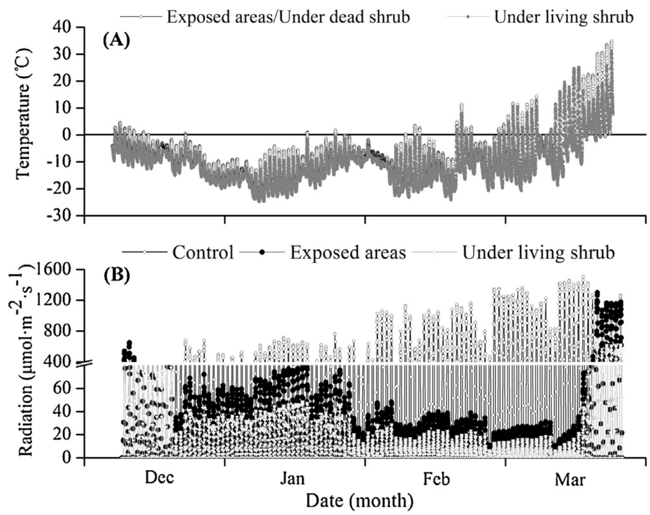

Fig. 1. Variations in temperature and light intensity in different microhabitats.

temperature on bryophytes (Stark et al., 2005; Belnap et al., 2008) and most bryophyte research related to snow cover, snowmelt, and extremely low temperatures has been confined to the arctic, subarctic, and alpine areas. Studies on the physiological adaptation of desert mosses to different microenvironments in winter is limited (Bjerke et al., 2011). The Gurbantünggüt Desert is thus an ideal location to study characteristics of physiological responses of mosses in winter.

The objectives of this study were to explore the adaptive strategies of desert mosses based on the physiological characteristics of *Syntrichia caninervis* under different microhabitat conditions in winter. Based on previous studies, we hypothesized that: 1) the stress-related substances in *S. caninervis* under deep snow would be higher than elsewhere because of the extremely low temperatures; and 2) microhabitats would affect the performance of *S. caninervis* through their effects on temperature and snow conditions.

2. Materials and methods

2.1. Site description

The study was conducted in the Gurbantünggüt Desert (44°11′–46°20′N, 84°31′–90°00′E) located in the center of the Junggar Basin, in Xinjiang Uygur Autonomous Region of China. This desert contains the largest area of fixed and semi-fixed desert dunes in China, covering 4.88×10^4 km^2. Moist air currents from the Indian Ocean are blocked by the Himalayan range and fail to reach this area, resulting in a vast expanse of arid terrain. Annual precipitation ranges from 70 to 160 mm, while mean annual evaporation is estimated at 2606.6 mm. Mean annual temperature is 7.26 °C (Zhang et al., 2007; Zhou et al., 2010). Unlike many other desert ecosystems, the Gurbantünggüt Desert experiences predictable and abundant snow cover in winter. The average snow