—研究ノート—
Scientific Note

Growth pattern of a common feather moss, *Hylocomium splendens*, from contrasting water regimes in a high Arctic tundra

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高緯度北極において異なる水分条件下に生育するイワダレゴケの生長パターン

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要旨: イワダレゴケ *Hylocomium splendens* は，高緯度北極ツンドラの植生を構成する主要なコケ植物であり，乾燥地から湿地まで幅広い水分環境に生育する．イワダレゴケは，1 年ごとに形成される新たな植物体が連続的につながった形態をとるので，年次生長が追跡できる．我々は，生育地の水分条件がイワダレゴケの生長パターンに与える影響を明らかにするために，カナダ北極エルズミア島オーブロヤー湾奥の氷河後退域において，異なる水分条件（湿地: hydric site，中湿地: mesic site，乾燥地: xeric site）に生育するイワダレゴケの成熟期間（growth period）および年間生長量（長さと重さ）を比較した．その結果，イワダレゴケの成熟期間は湿地で 1 年，中湿地で 2 年，乾燥地で 3 年となり，乾いた環境ほど成熟期間が長くなった．年間生長量は，乾いた環境ほど値が小さくなった．これらの結果から，生育地の水分条件は高緯度北極におけるイワダレゴケの生長パターンに大きな影響を与えることが明らかとなった．

Absrtact: *Hylocomium splendens*, a widespread feather moss, is one of the major plant species found in high-Arctic tundra. It occupies a variety of habitats ranging from exposed dry ground to swampy areas. To clarify the effect of the water regime on the growth pattern of *H. splendens*, the shoot morphology of *H. splendens* growing in contrasting water regimes, *i.e.* hydric, mesic and xeric sites, was investigated using retrospective analyses of growth. The derived growth parameters for *H. splendens* differed considerably among

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the sites. The growing period at the hydric, mesic and xeric sites was 1 year, 2 years and 3 years, respectively. The annual increments in segment length and biomass were higher with increasing water availability. These results suggest that water regime has a strong influence on the growth pattern of *H. splendens* in high-Arctic tundra.

1. Introduction

The feather moss, *Hylocomium splendens* (Hedw.) Schimp., is one of the most common plant species distributed from temperate forest to high Arctic tundra in the Northern Hemisphere (Schofield, 1974; Vitt, 1990). *Hylocomium splendens* shoots produce a new, readily identifiable segment each year (Tamm, 1953; Vitt, 1990) and thus exhibit a usually annual growth pattern. Retrospective analyses of past growth of long-lived plants and their populations provide a useful tool for understanding the relationships between plant performance and environmental factors (Callaghan *et al.*, 1989; Havström *et al.*, 1995). *Hylocomium splendens* is often used as an excellent biological indicator for monitoring of environmental change, *e.g.* of weather, climate and pollutants (Pakarinen and Rinne, 1979; Potter *et al.*, 1995; Zechmeister, 1995; Callaghan *et al.*, 1997; Zechmeister, 1998; Gerdol *et al.*, 2002; Reimann *et al.*, 2006).

The growth pattern of *H. splendens* is recognized as being strongly influenced by climatic conditions according to latitude or elevation (Schofield, 1981; Vitt, 1990; Zechmeister, 1995; Callaghan *et al.*, 1997; Ross *et al.*, 1998; Ross *et al.*, 2001). Vitt (1990) determined that annual mass growth of *H. splendens* is correlated to the mean annual total precipitation. Zechmeister (1995) and Callaghan *et al.* (1997) showed that there is a strong positive correlation between annual growth rate and air temperature in *H. splendens*. Besides regional precipitation or air temperature, the growth pattern of mosses can be influenced by microtopographic variations in water availability (Watson, 1915; Birse, 1957; Ueno *et al.*, 2001). However, no information on the effects of local water regime on the growth pattern of *H. splendens* is available. Such data will enable us to assess *H. splendens* as an indicator of environmental change.

Arctic glacier foreland contains a variety of microtopographical conditions created by glaciation. The microtopographic heterogeneity creates a diversity of water regimes in Arctic tundra (Ostendorf and Reynolds, 1998). *Hylocomium splendens* occupies a wide variety of habitats ranging from exposed dry ground to swampy areas in Arctic tundra. In this paper, we present a retrospective analysis of the growth pattern of *H. splendens* in relation to water regimes at polar oasis sites on Ellesmere Island in the Canadian high-Arctic.

2. Materials and methods

2.1. Study site

The investigation was carried out from 12 to 26 July, 2002, on a glacier foreland near Oobloyah Bay in the northern part of Ellesmere Island, Nunavut, Canada (80° 51′N, 82°51′W). Microtopographic glaciation at this site has resulted in the development of a patchwork of microhabitats, each with a distinct water regime. *Hylocomium splendens* plants ranged from the margin of a mire (hydric site) to the top of the moraine (xeric site), and dominated the intermediate plain (mesic site).

2.2. Water content

Water content in the *H. splendens* colony was studied to clarify the difference in water regime among the three sites (hydric, mesic and xeric). Cylindrical cores (45 mm in diameter) of the upper, photosynthetic layers of *H. splendens* colonies were collected from each site. Each sample consisted of three cores from each site. The core samples were immediately placed in plastic bags, and the fresh weight of each sample was measured in the field. The sample dry weight was recorded after they were oven-dried (80°C, 48 h) in the laboratory. The water content of the sample was calculated as follows: (fresh weight − dry weight) / dry weight × 100. The sampling interval was every second day from 15 to 23 July, 2002.

2.3. Growth pattern

The growth form of *H. splendens* varies from erect, sympodial shoots composed of annually produced segments in temperate and boreal regions, to horizontal, monopodial shoots in the mid- and high-Arctic (Callaghan *et al.*, 1997). In the populations growing at the study site, switching between monopodial and sympodial growth, and vice versa, occurs within individual shoots (Fig. 1). Annual growth increments in sympodial shoots are identified as the axis formed from one growing point. For monopodial growth, a range of indicators of annual growth can be used, indicating the change in lateral branch size and direction of growth, and distinct changes in virescence of shoot segments (Fig. 1).

We collected shoot assemblages of *H. splendens* from the hydric, mesic and xeric sites. The shoot assemblages were air dried in the field and loosened in a water bath in the laboratory. Each segment's age was determined by counting back from the current year's growth (0 year segment; Fig. 1), assuming that shoots contained segments that were initiated in successive years without gaps. Segments more than seven years old were excluded from the analysis because almost all of these segments were brittle. After their length was measured, each segment was oven-dried (80°C, 48 h) and weighed.

3. Results

3.1. Water content

The water content of *H. splendens* colonies at the three sites is shown in Fig. 2. The colony growing at the hydric site showed significantly higher water content, ranging from about 650% to 1150%, than the other two sites throughout the study period (Fig. 2). The colony water content at the mesic and xeric sites increased only on rainy days. The colony at the mesic site tended to have a higher water content than that at the xeric site. The water content at the mesic and xeric sites reached a maximum of about 480% and 430%, respectively, under rainy conditions, but on sunny days decreased to as low as 60% and 20%, respectively.

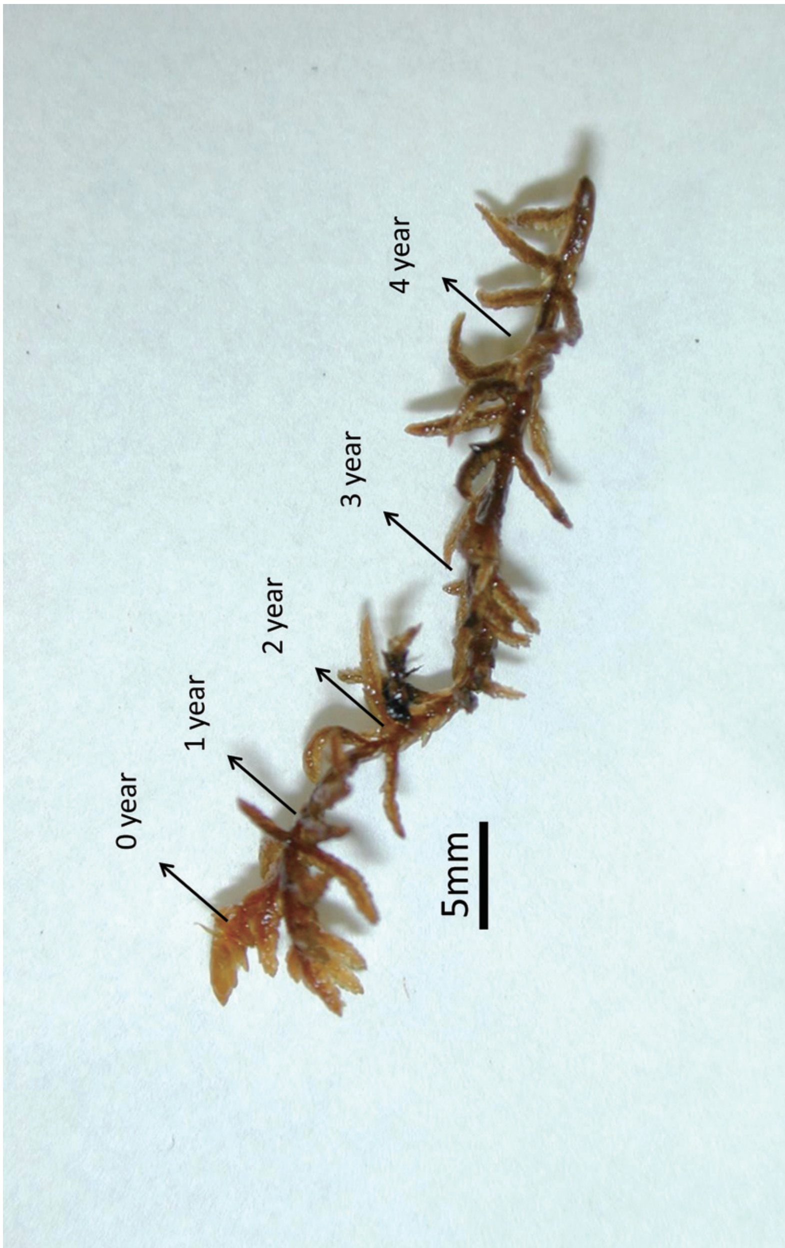

Fig. 1. A representative Hylocomium splendens *shoot. Growth between the 0 year and 1 year segments is sympodial. Growth of all other segments is monopodial.*

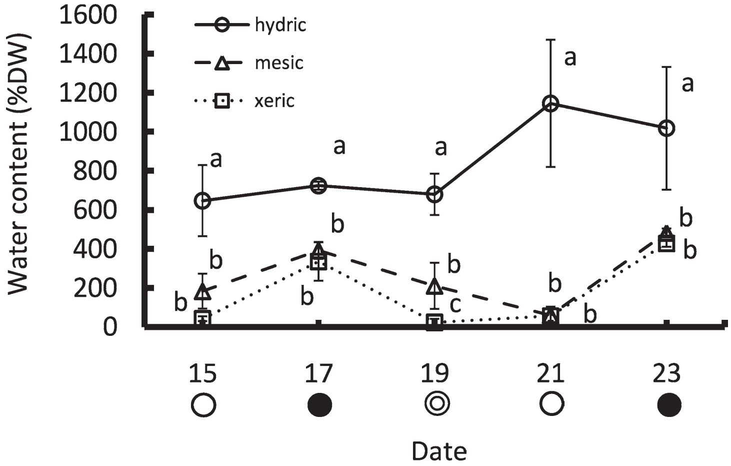

Fig. 2. Water content of Hylocomium splendens *colonies growing at the hydric, mesic and xeric sites during 15 to 23 July, 2002. Each symbol is the mean (n=3) and vertical lines indicate the standard deviation. Different letters above each symbol indicate a significant difference within the same day (P < 0.05, Fisher's PLSD test). Open circles with a solid line, open triangles with a dashed line, and open squares with a dotted line represent the hydric, mesic and xeric sites, respectively. Symbols beneath the x-axis indicate the weather on the sampling date (◎, sunny; ○, cloudy; ●, rainy).*

3.2. Growth pattern

Average annual segment length and weight for the *H. splendens* shoots from each site were plotted against segment age (Fig. 3A, B). Segment weight showed a distinct two-phase course: a steep growth phase and a more gradual senescence or degeneration phase (Fig. 3B). The critical point between the two phases was considered the growth period required for the segment to attain full size (Fig. 3B; Callaghan *et al.*, 1997). The growth rate was calculated based on the mean length and weight of full-sized segments and the growth period (Fig. 3A, B), *i.e.* segment length at critical point (mm) / growth period (year), and segment weight at critical point (mg) / growth period (year). The derived growth parameters differed considerably among sites (Table 1). The growth periods of *H. splendens* at the hydric, mesic and xeric sites were 1, 2 and 3 years, respectively. The annual segment length and biomass increments at the hydric, mesic and xeric sites were 16.7 mm and 7.1 mg a year, 7.7 mm and 1.9 mg a year, and 4.2 mm and 1.8 mg a year, respectively (Table 1).

Table 1. Summary of growth parameter.

			annual increment	
sites	*n*	growth period (year)	length (mm)	weight (mg)
hydric	32	1	16.7	7.1
mesic	30	2	7.7	1.9
xeric	32	3	4.2	1.8

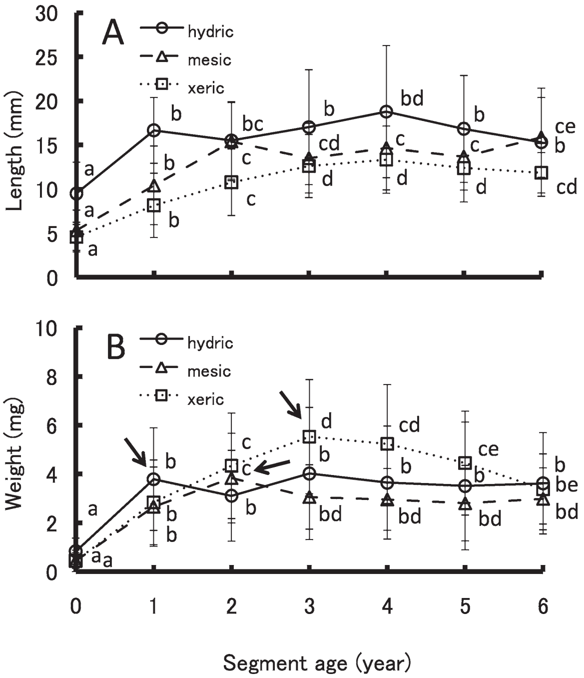

Fig. 3. *Growth of* Hylocomium splendens *samples collected from hydric, mesic and xeric sites as determined from retrospective growth analysis. A: length increment, B: weight increment. Each symbol is the mean and vertical lines indicate the standard deviation. Open circles with a solid line, open triangles with a dashed line, and open squares with a dotted line represent the hydric, mesic and xeric sites, respectively. Different letters above or below each symbol indicate a significant difference between segments within the same site ($P<0.05$, Fisher's PLSD test). Arrows at B indicate the critical point between a steep growth phase and a more gradual senescence or degeneration phase at each site. For the number of replicates see Table 1.*

4. Discussion

Growth periods for *H. splendens* shoot segments showed clear differences among the water regimes (Table 1). The growth period of *H. splendens* was shortest in the wettest habitat. The temporal variation in water content in a moss colony shows whether the moss has physiological activity or not, because mosses have a poikilohydric nature and possess the ability to suspend metabolism without dying when water is unavailable (Ueno *et al.*, 2006). At the hydric site *H. splendens* is continuously supplied with moisture regardless of weather, while at the mesic and xeric sites plants rely on precipitation as the main water supply during the peak growing season (Fig. 2). This might mean that *H. splendens* colonies at the hydric site are physiologically active throughout almost the entire growing season, while plants at the mesic and xeric sites are active on rainy days only. However, the moisture content of the colony at the mesic site tended to be prolonged compared with that at the xeric site (Fig. 2). The duration of physiological activity might lead to the differences in growth period of *H. splendens*. Økland (1995) and Uchida *et al.* (2001) showed that the growth period of *H. splendens* in temperate subalpine coniferous forest and boreal forest was from 1 to 2 years. Callaghan *et al.* (1997) reported that the growth period of *H. splendens* in Arctic tundra and alpine heath was from 3 to 4 years. Thus the growth period estimated for a high-Arctic site in the present study, which is from 1 to 3 years (Table 1), is comparable to that of temperate subalpine coniferous forest and boreal forest.

The mean annual increment in *H. splendens* shoot length increased with water availability (Fig. 3A; Table 1). The *H. splendens* colony at the hydric site also had a higher annual weight increment (annual shoot production) than that at drier sites (Fig. 3; Table 1). The observation of a higher growth rate in *H. splendens* with high water availability is in agreement with a previous finding that the annual growth rate of *H. splendens* is correlated to the mean annual total precipitation (Vitt, 1990). These findings coincide with those for many wetland mosses, such as *Meesia triquetra* (Vitt and Parkarinen, 1977) and *Sphagnum* spp. (*e.g.* Grosvernier *et al.*, 1997). The values for annual biomass growth (1.8 mg to 7.1 mg) estimated in the present study were much higher than those (0.3 mg to 1.0 mg) for other Arctic *H. splendens* populations by Callaghan *et al.* (1997). However, the present values were lower than the 10 mg calculated for *H. splendens* growing in boreal forest (Bakken, 1993).

The degeneration phase for shoots in the *H. splendens* colony from the xeric site was steeper than that for colonies from wetter sites (Fig. 3B). This might mean that *H. splendens* shoots are more readily decomposed at the xeric site. Further studies are required to fully understand this phenomenon.

Our results showed that water regime has a strong influence on the growth pattern of *H. splendens* in high-Arctic tundra. This demonstrates that the use of *H. splendens* as a bioindicator of environmental change requires consideration of the water regime of the growing site. However, alteration of the water regime influences on not only the duration of the physiological activity but also nutrient status (Ueno *et al.*, 2009) and temperature condition (Harley *et al.*, 1989). A combination of these factors strongly effects the growth pattern of *H. splendens* in high-Arctic tundra.

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