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Structure and dynamics of the *Ceratodon purpureus*–*Bryum pseudotriquetrum* community in the Yukidori Valley, Langhovde, continental Antarctica

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Abstract: The structure and dynamics of the *Ceratodon purpureus–Bryum pseudotriquetrum* community along the Yukidori Valley, Langhovde near Syowa Station, continental Antarctica have been documented. This moss community showed a clear vegetation structure with a micro-relief distribution, consisting of three different sites; a mound, a slope and a hollow. On the hollow site a sand-covered *Bryum pseudotriquetrum* patch dominated. On the slope site a pure *Ceratodon purpureus* patch, a *Bryum pseudotriquetrum* patch, and a *Ceratodon purpureus–Bryum pseudotriquetrum* mixed patch abundantly occurred. On the mound site a cyanobacteria-mixed *Ceratodon purpureus* patch prevailed. The dynamics of this community was basically unclear. However, some change patterns were infered from the results. The sand-covered *Bryum pseudotriquetrum* patch and the cyanobacteria-mixed *Ceratodon purpureus* patch generally showed no clear change. It is also speculated that some of the patches of this community undergo cyclic changes. A suggested cyclic pattern is as follows; some of the sand-covered *Bryum pseudotriquetrum* patches turned on *Ceratodon purpureus–Bryum pseudotriquetrum* mixed patches, and finally those patches became a cyanobacteria-mixed *Ceratodon purpureus* patch. Some of them, on the other hand, degraded into sand-covered *Bryum pseudotriquetrum* patches, probably because of strong wind or water flow. However, more detailed studies will be needed to confirm these inferences.

key words: *Bryum pseudotriquetrum*, *Ceratodon purpureus*, micro-relief, vegetation dynamics, vertical structure

Introduction

The continental Antarctic region is characterized by extremely harsh environmental conditions for mosses, with low temperature, short growing season, dry soil and strong wind. In ice-free areas the vegetation cover is generally very scarce, including mainly mosses and lichens. The structure and dynamics of the moss communities of continental Antarctica should correspond with such a environment. It is ecologically important to clarify the structure and dynamics of the moss communities growing in ice-free areas of continental Antarctica. Syowa Station is situated in the eastern part of continental Antarctica. The area around Syowa Station offers a suitable

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field to study the ecology of moss communities under a harsh environment because ice-free areas with easy access occur near the station.

Ecological studies of the moss community around Syowa Station have been led chiefly by researchers of the Japanese Antarctic Research Expedition (JARE), and have focused primarily on the floristic, plant sociological and environmental aspects (*cf.* reviews of Kanda, 1983; Kanda and Komarkova, 1997; Seppelt *et al.*, 1998). Matsuda (1968) first reviewed the ecology of the moss community near Syowa Station, clarifying the topographic distribution of the moss communities, and analyzed the microclimate in moss communities on East Ongul Island. As for the plant sociological aspects, Kobayashi (1974) preliminarily described the species composition of the moss community near Syowa Station. Kanda (1981, 1986, 1987a) comprehensively reviewed the distribution of major mosses and moss communities of the Sôya Coast and Prince Olav Coast, East Antarctica. Shimizu (1977) reported the relationship between moss distribution and micro-topography. Yamanaka and Sato (1977) analyzed the soil condition for the moss community near Syowa Station. Nakanishi (1977) comprehensively surveyed the distribution of major moss communities around Syowa Station in relation to snow cover, topography, wind direction and moisture.

Studies on the dynamic aspects of moss communities including the micro-relief distribution around Syowa Station are, however, not enough yet. Matsuda (1968) first reported the development of the *Bryum pseudotriquetrum* turf based on cross sections of tufts or turfs, clarifying innovation of stems. Imura *et al*. (1994) investigated the morphological structure of moss colonies in Antarctica, and discussed the process of colony development. Despite those pilot studies, studies on the dynamic aspects of the moss community around Syowa Station still remain unclear.

Yukidori Valley, Langhovde, 25 km south of Syowa Station is appropriate to investigate the dynamic aspect of the moss community. This valley contains exceptionally prominent moss communities. Ecological surveys of the moss community in this valley have concentrated on the flora and distribution of major moss communities (Kanda, 1987a, b; Kanda *et al.*, 1990; Kanda and Inoue, 1994), and also on the relationship between the distribution of moss communities and soil properties (Ayukawa *et al.*, 1998). However, no dynamic study of the moss community in the valley has appeared yet.

Aims of this paper are 1) to clarify the relationship between the micro-relief and surface cover types, and cover patterns of Bryophyte of the *Ceratodon purpureus–Bryum pseudotriquetrum* community, the dominant moss community in the Yukidori Valley; 2) to show the relation between the below-surface patch type and that of the surface patch types of the *Ceratodon purpureus–Bryum pseudotriquetrum* community, and 3) to discuss the vegetation dynamics of the *Ceratodon purpureus–Bryum pseudotriquetrum* community.

Study sites

The Yukidori Valley (69°14′30″S, 39°46′00″E) is located in the southern part of Langhovde, Sôya Coast, East Antarctica. It runs 2.5 km east to west from the edge of the continental ice sheet at altitude 200 m to Lützow-Holm Bay. In the middle of the valley is Lake Yukidori, 200 m in diameter. The Yukidori Valley area was selected as a site for ecological monitoring with special emphasis on mosses and lichens, being approved in 1987 as a Site of Special Scientific Interest (SSSI) (Kanda *et al.*, 1990; Kanda and Inoue, 1994).

The valley is well known as an ice-free area having the most prominent moss vegetation in the Syowa Station area (Kanda, 1987b; Kanda *et al.*, 1990). The dominant mosses of the valley are *Bryum argenteum*, *Bryum pseudotriquetrum*, *Ceratodon purpureus*, *Grimmia lawiana* and *Pottia heimii* (Kanda, 1987b). The moss vegetation is composed of three main communities, the *Ceratodon purpureus* Sociation, the *Bryum pseudotriquetrum* Sociation and the *Ceratodon purpureus–Bryum pseudotriquetrum* Sociation (Kanda, 1987b). These moss communities are the most typical of those developing along streams and around lakes in the Syowa Station area (Kanda, 1987b). *Ceratodon purpureus* Sociation is distributed throughout the valley, but it is most abundant at drier sites in the middle part of the valley. *Bryum pseudotriquetrum* Sociation is abundant in the mouth of the valley and around shores of Lake Yukidori. *Ceratodon purpureus–Bryum pseudotriquetrum* Sociation has similar distribution pattern to that of *Bryum pseudotriquetrum* Sociation (Kanda, 1987b). This Sociation seems to be the dominant moss community in the valley.

Methods

A line transect method was taken to follow the changes of micro-relief distribution of mosses in a colony. In this paper a colony is defined as a whole assemblage of mosses that spread like a mat without reference to the size of the mat. Nine colonies of the *Ceratodon purpureus–Bryum pseudotriquetrum* community were selected along the Yukidori Valley so as to include well developed colonies. Line transects 100–280 cm in length were set on the selected colonies (Table 1). The vitality of the colony was fairly high (from 3 to 5 on the scale of Nakanishi, 1977), although the altitude, colony size and water supply pattern differ among the transects (Table 1). This suggests that the colonies selected represent well developed ones.

Table 1. General description of nine line transects.

Transect No.	1	2	3	4	5	6	7	8	9
Altitude (m)	145	135	120	100	65	55	60	55	27
Colony size (m^2)	1.7×0.8	2.1×1.8	2.5×0.8	4.5×3.5	5.5×4.0	6.5×2.8	4.5×1.2	7.0×1.8	3.5×0.8
Pattern of water supply*	V	II	II	V	II	V	V	V	II
Vitality**	5	5	4	3	3	5	4	5	4
Length of transect (cm)	100	150	190	160	200	200	190	200	280
Number of micro-lelief sites	29	34	33	27	34	33	35	29	43

* : After Nakanishi (1977). II: medium snow drift type, V: seepage type.

** : After Nakanishi (1977). 3: a quarter to a half is green, 4: half to three quarters is green, 5: three quarters to the whole community is green.

Fig. 1. An example of a colony of the *Ceratodon purpureus–Bryum pseudotriquetrum* community. The scale indicates a line transect on the community. Four types of patches can be distinguished at three different micro-relief sites here: on the black colored mound site, a cyanobacteria-mixed *Ceratodon purpureus* patch; on the white colored hollow site, a sand-covered patch and sand-covered *Bryum pseudotriquetrum* patch; on the gray colored slope site, a *Ceratodon purpureus* patch.

The micro-relief sites in the colony were surveyed along the line transects (Fig. 1). Micro-relief sites were classified into the following three types: a hollow, a slope, and a mound site (Fig. 1). Because the slope is situated between the mound and the hollow, the determination of the slope is a little vague. However, this does not seriously bias the results or the discussion in this paper, which will focus mainly on the mound and hollow. Each micro-relief site generally has a horizontal length of *ca.* 30 mm to 60 mm, and vertical height of *ca.* 10 mm to 40 mm (Fig. 1; *cf.* Table 2).

In each micro-relief site along the transects, surface cover types and the cover patterns of Bryophyte were determined. Three surface cover types were distinguished as follows: sand-covered (Sa), pure moss, and cyanobacteria (mainly *Nostoc* sp. and *Phormidium* sp. (Kanda and Inoue, 1994))-mixed (Cy). Five cover patterns of Bryophyte on each micro-relief type were distinguished: pure *Ceratodon purpureus* (Cp), pure *Bryum pseudotriquetrum* (Bp), pure *Grimmia lawiana* (Gl), mixture of *Ceratodon purpureus* and *Bryum pseudotriquetrum* (CpBp), and mixture of *Bryum pseudotriquetrum* and *Grimmia lawiana* (BpGl).

In this paper a micro-relief site was taken as the basic unit of moss distribution analysis. This unit will be called a patch. A patch is characterized by its micro-relief and patch type. A patch type in turn is characterized by its surface cover type and Bryophyte cover pattern.

To clarify the dynamics of the *Ceratodon purpureus–Bryum pseudotriquetrum*

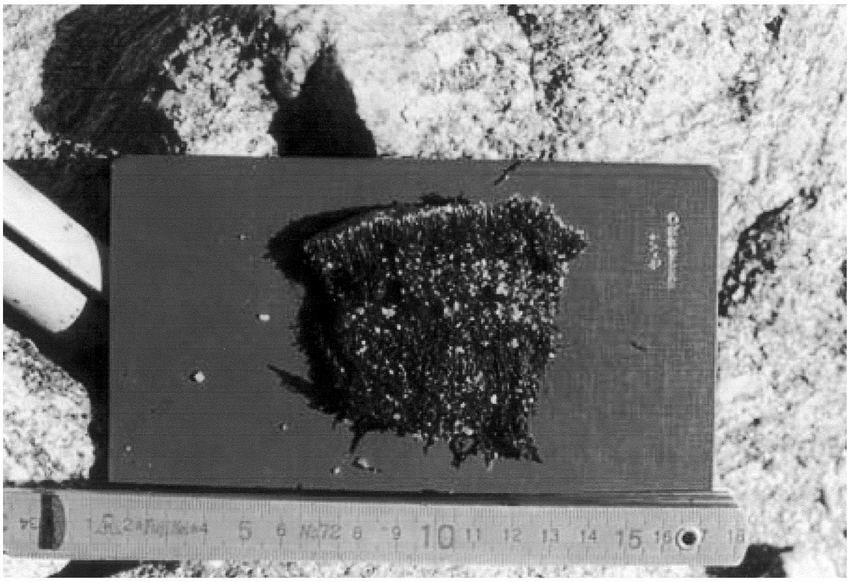

Fig. 2. A cross section of a *Bryum pseudotriquetrum* patch in the *Ceratodon purpureus–Bryum pseudotriquetrum* community. An alternation of patch pattern from the bottom to the surface can be observed. A sand patch occurred just below the surface layer of the *Bryum pseudotriquetrum* patch.

community, patch types just below the surface patch (below-surface patch type) were also recorded, cutting each patch vertically using a small spatula. The moss colonies in continental Antarctica sometimes show a vertically layered structure (Fig. 2, *cf.* Nakatsubo and Ohtani, 1992; Imura *et al.*, 1994). The thickness of each layer is generally very thin, usually several millimeters (Fig. 2; Okitsu, unpublished). Such a layered structure is considered to show successional stages of the moss colonies (Longton and Holdgate, 1979; Nakatsubo and Ohtani, 1992; Imura *et al.*, 1994). The changes from the below-surface patch type to the surface patch type suggest the current dynamics of the *Ceratodon purpureus–Bryum pseudotriquetrum* community. If the below-surface patch type was the same as the surface one, or no clear layered structure existed, the below-surface patch type is the same as the surface patch type. This paper focuses only on the below-surface patch, although the layered structure of moss colonies provides ecological interactions of the colony mosses as well as the dynamic aspect of the colony (Nakatsubo and Ohtani, 1992; Imura *et al.*, 1994), because of the difficulty of determination of patch types in deeper layers; the identification of decayed mosses in deeper layers is generally not simple.

Results

Micro-relief distribution of patch types

Table 2 shows the distribution of patch types along line transect 1 as an example of the relationship between the micro-relief and the distribution of patch types. It can be

Table 2. The micro-relief distribution of patch types along line transect 1.

Distance from the start point of the transect (cm)	Micro-relief*	Patch type**	Distance from the start point of the transect (cm)	Micro-relief*	Patch type**
4	m	cp	54	h	bp
5	h	sa-bp	55	h	sa-bp
10	m	cpbp	57	s	bp
13	s	bp	61	m	cy-cp
14	h	sa-cp	63	s	bp
17	m	cp	64	h	sa-bp
18	h	sa-bp	71	m	cy-cp
19	s	cy-cp	73	h	sa-bp
22	m	cy-cpbp	76	s	cp
26	s	cy-cp	79	s	bp
33	h	cp	84	m	cy-bp
38	m	cy-cp	87	h	sa-bp
39	h	sa-bp	90	h	bp
45	m	cpbp	96	m	cy-bp
47	h	bp			

*: m–mound, h–hollow, s–slope.
**: See text for abbreviations.

seen from the table that a sand-covered patch tended to appear on the hollow site, while a cyanobacteria-mixed patch tended to appear on a mound site.

Table 3 presents the micro-relief distribution of the patch types of a total of nine transects of the *Ceratodon purpureus–Bryum pseudotriquetrum* community to clarify the relationship between micro-relief and the distribution of patch types. Thirteen patch types arose including the sand only type (Sa) and the cyanobacteria only type (Cy) (Table 3). The total occurrences of micro-relief were: hollow 124, slope 50 and mound 123.

The hollow sites were dominated by sand-covered patches (83), followed by patches of pure moss communities (34). It contained only a few cyanobacteria-mixed patches (seven). The slope sites were dominated by patches of pure moss communities (31), followed by cyanobacteria-mixed patches (11). The mound sites were, in contrast to hollow sites, dominated by cyanobacteria-mixed patches (95), followed by patches of pure moss communities (27). It contained only one sand-covered patch.

The occurrence of the two Bryophyte species also clearly corresponded to the micro-relief sites. *Ceratodon purpureus* appeared chiefly on mound sites, mainly in cyanobacteria-mixed patches. *Bryum pseudotriquetrum* appeared, in contrast to *Ceratodon purpureus*, chiefly on hollow sites, mainly as sand-covered patches. It rarely occurs on mound sites.

Major change patterns of patch types of the *Ceratodon purpureus–Bryum pseudotriquetrum* community

Table 4 gives the major change patterns from below-surface patch types to surface patches. The table lists only dominant surface patch types arising with more than 27

Table 3. Relation between micro-relief and patch types of the *Ceratodon purpureus–Bryum pseudotriquetrum* community in the Yukidori Valley, East Antarctica.

Patch type	Micro-relief			
	Hollow	Slope	Mound	Total
Sand-covered (Sa)				
Sa	6	0	0	6
Sa-Bp	68	2	1	71
Sa-Cp	3	3	0	6
Sa-CpBp	1	3	0	4
Sa-BpGl	5	0	0	5
Total	83	8	1	92
Pure moss community				
Bp	14	10	3	27
Cp	12	10	12	34
CpBp	6	10	12	28
Gl	2	1	0	3
Total	34	31	27	92
Cyanobacteria-mixed (Cy)				
Cy	1	2	41	44
Cy-Bp	0	0	4	4
Cy-Cp	2	7	45	54
Cy-CpBp	4	2	5	11
Total	7	11	95	113
Total	124	50	123	297

Bp: *Bryum pseudotriquetrum,* Cp: *Ceratodon purpureus,*
Gl: *Grimmia lawiana.*

Table 4. Major change patterns of patch types of the *Ceratodon purpureus–Bryum pseudotriquetrum* community. Abbreviations are the same as those of Table 3.

	Surface layer						
	Sa-Bp	Bp	Cp	CpBp	Cy	Cy-Cp	Total
Below the surface							
Sa	12	4	4	6	0	0	26
Sa-Bp	50	20	0	14	0	0	84
Sa-Cp	0	0	26	0	19	34	79
Sa-CpBp	0	0	0	2	0	0	2
Bp	8	3	0	3	0	0	14
Cp	0	0	3	0	21	20	44
CpBp	0	0	1	3	0	0	4
Cy-Bp	1	0	0	0	4	0	5
Total	71	27	34	28	44	54	258

counts (Bp) (*cf.* Table 3). In total eight patch types arose below the surface. The proportion of these below-surface patch types did not necessarily coincide with that of the surface patch type. For example only four *Ceratodon purpureus–Bryum pseudotriquetrum* mixed patches (CpBp) arose below the surface, while it arose 28 counts on the surface. Twenty six sand only patches (Sa) arose below the surface, while it never arose on the surface in Table 4, although it appeared on the surface with 6 counts (Table 3). Likewise the sand-covered *Ceratodon purpureus* patch (Sa-Cp) arose below the surface with 79 counts, while it never arose on the surface in Table 4, although it appeared on the surface with 6 counts (Table 3). Such inconsistency of the proportion of patches between the below-surface patch type and the surface patches may result partly from the difficulty of the identification of the below-surface patch type, as mentioned above. Another possible reason for the inconsistency may be that sand can easily penetrate into the lower part of the moss colony so that patches just below the surface tend to contain more sand than surface patches. This inconsistency would give, however, no serious bias for the general results of Table 4.

Most of the sand-covered *Bryum pseudotriquetrum* patches (Sa-Bp) below the surface showed no change (50 of 84 patches). Some of them changed into sand free *Ceratodon purpureus–Bryum pseudotriquetrum* mixed patches (CpBp) on the surface, although the number was relatively small (14 of 84 patches). Sand-covered *Ceratodon purpureus* patches (Sa-Cp) below the surface changed generally into sand free patch types on the surface: twenty-six into pure *Ceratodon purpureus* patches (Cp), nineteen into cyanobacteria only patches (Cy), and thirty-four into cyanobacteria-mixed *Ceratodon purpureus* patches (Cy-Cp). Pure *Ceratodon purpureus* patch (Cp) changed into cyanobacteria only patches (Cy) (twenty-one of 44 patches) or into cyanobacteria-mixed *Ceratodon purpureus* patches (Cy-Cp) (twenty of 44 patches). Sand only patches (Sa) diversified into several types: sand-covered *Bryum pseudotriquetrum* patches (Sa-Bp), *Ceratodon purpureus–Bryum pseudotriquetrum* patches (Cp-Bp), *Bryum pseudotriquetrum* patches (Bp) and *Ceratodon purpureus* patches (Cp). *Bryum pseudotriquetrum* patches (Bp) changed mainly into sand-covered *Bryum pseudotriquetrum* patches (Sa-Bp) (eight of fourteen patches).

Discussion

Ecological characteristics of the two species

Ceratodon purpureus was concentrated basically on mound sites usually mixed with cyanobacteria. A mound site does not suffer from sand cover; only rare sand-covered patches appeared here. This sand-free condition provides no serious physical obstacle to the growth of mosses. It can be assumed that a mound site tends to be dryer as compared with a hollow site within the same colony, although papers on the precise comparative measurement of water contents between mound sites and hollow sites have not appeared yet. A comparative temperature measurement between a mound site and a hollow site in a moss community near Syowa Station (Ohtani, 1994) reveals a microclimatic difference between the two sites; the mound site experienced much higher temperature under sunshine, exceeding 30℃, while the hollow site experienced much lower temperature, exceeding 20℃. This micro-climatic difference probably relates to a difference of moisture condition. The mosses on the mound site probably suffered from the dry condition as compared with the hollow site within the same colony. *Ceratodon purpureus* has the greatest growth at a dry site (Lewis Smith, 1999). This physiological property of *Ceratodon purpureus* should be a most important factor in the success of growth on mound sites. Additionally, the mixing with cyanobacteria could also contribute to the success of *Ceratodon purpureus* on a mound site. Cyanobacteria probably play an important role in the nitrogen fixation. For example, Antarctic *Nostoc commune* is capable of fixing relatively large amounts of atmospheric nitrogen during periods of high solar irradiance when the surface temperatures exceed 8℃ (Davey and Marchant, 1983; Lewis Smith, 1999). Nakatsubo and Ino (1987) also suggested that nitrogen fixation by cyanobacteria in the moss community is important as a nitrogen source for the community growth on East Ongul Island. The sand-free condition of the mound site provides a suitable condition for the nitrogen fixation of cyanobacteria. Lewis Smith (1999) reported that *Ceratodon purpureus* and cyanobacteria synchronously increase in dryer soil along a transect of moisture gradient. Broady (1982) and Ohtani (1994) reported that algae tend to grow on mound sites in moss communities. Those reports agree with the micro-relief distribution of *Ceratodon purpureus* and cyanobacteria described in this paper.

However, cyanobacteria also have negative effects on the distribution of *Ceratodon purpureus*. For example, Broady (1982) stated that mound sites in a moss community become exposed to the scouring effects of ice and rock particles and this could cause damage and death to moss tissues, whereas blue-green algae, growing within coalesced, firm, mucilaginous sheaths may be more resistant to damage. This would lead to development of algal crusts on the exposed mounds. Ohtani (1986, 1994) noted a similar observation near Syowa Station. Thus the co-existence of cyanobacteria with *Ceratodon purpureus* is complicated, and further studies are needed.

Bryum pseudotriquetrum is concentrated at hollow sites, in contrast to *Ceratodon purpureus*. A hollow site suffers from sand cover. Sand cover generally affects moss growth negatively. However, despite such a negative effect, the hollow site may provide a more moisture rich condition than a mound site. *Bryum pseudotriquetrum* usually shows higher photosynthetic activity than *Ceratodon purpureus*, especially in a moist condition (Lewis Smith, 1999). This moss maintains vigorous growth under the moist condition (Lewis Smith, 1999).

The rhizoid system of *Bryum pseudotriquetrum* is extensive, with individual rhizoids attaining 20 mm in length (Lewis Smith, 1999). This plays an important role in stabilizing the soil in which *Bryum pseudotriquetrum* is established, and also in retaining moisture. Matsuda (1968) reports that in vertical cross sections of tufts or turfs, *Bryum pseudotriquetrum* exhibits horizontal bands formed by aggregations of rhizoids or innovation of stems. These morphological characteristics of this species help it to become established on a sand-covered site.

The ecological characteristics of the two mosses discussed above, *Ceratodon purpureus* on dryer sites and *Bryum pseudotriquetrum* on moisture sites, are in close agreement with studies in Wilkes Land (Lewis Smith, 1988, 1990); at Edmonson Point, Wood Bay (Lewis Smith, 1999); and around Syowa Station (Nakanishi, 1977; Kanda, 1986, 1987a; Kanda and Inoue, 1994; Imura *et al.*, 1994).

The dynamics of the *Ceratodon purpureus–Bryum pseudotriquetrum* community

From Table 4, a major part of the sand-covered *Bryum pseudotriquetrum* patch and the cyanobacteria-mixed *Ceratodon purpureus* patch basically showed no clear change of the patch.

In case of changes of patches take place, the manner may vary among the patches. Nakatsubo and Ohtani (1992) documented a similar variety of changes of moss colony growth of the two species, *Bryum pseudotriquetrum* and *Sanionia uncinata*, on King George Island, South Shetland Islands. Seppelt and Ashton (1978) suggested a sequence of development of cushions of *Bryum algens* and *Grimmia lawiana* near Mawson Station, continental Antarctica. Longton and Holdgate (1979) considered that sectional profiles of moss colonies could reveal a succession among stages.

Some of the sand-covered *Bryum pseudotriquetrum* patch, however, changed into the *Ceratodon purpureus–Bryum pseudotriquetrum* mixed patch, and finally this patch shifted to the cyanobacteria-mixed *Ceratodon purpureus* patch. A part of them, again, degraded into a sand-covered *Bryum pseudotriquetrum* patch probably because of strong wind or water flow. Thus, it is possibly, although the evidence is still not adequate, that the changing pattern of this community includes in part a cyclic process, from the sand-covered *Bryum pseudotriquetrum* patch through the *Ceratodon purpureus–Bryum pseudotriquetrum* mixed patch via the cyanobacteria-mixed *Ceratodon purpureus* patch, and finally again to the sand-covered *Bryum pseudotriquetrum* patch. In other words, if such a cyclic process never occurs, the *Ceratodon purpureus–Bryum pseudotriquetrum* community as a whole should change into a cyanobacteria-mixed *Ceratodon purpureus* community, but this may not actually occur. The proportion of cyanobacteria-mixed *Ceratodon purpureus* is not high (54 of 297 patches), and it is hardly expected that the rest of the patches (243 patches) all change into cyanobacteria-mixed *Ceratodon purpureus* patches.

Longton and Holdgate (1979) and Nakatsubo and Ohtani (1992) also reported examples of a cyclic succession of moss colonies.

Strong wind and other harsh environmental conditions in continental Antarctica probably promote such cyclic change, though different from the cyclic succession that commences as a consequence of biological changes such as degradation and recolonization (Watt, 1947). A mound site in a moss community becomes exposed to the scouring effects of ice and rock particles caused by strong wind, as already mentioned, and this could cause damage and death to the moss tissues. The damaged moss tissues are easily blown off by the strong wind. There a sand-exposed new depression may appear, if cyanobacteria do not succeed in entering the surface of dead mosses.

However, more detailed studies will be needed to confirm these speculations.

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