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Micro-relief distribution of major mosses in ice-free areas along the Sôya Coast, the Syowa Station area, East Antarctica

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Abstract: Micro-relief distribution of five major mosses, *Pottia heimii*, *Ceratodon purpureus*, *Bryum pseudotriquetrum*, *Grimmia lawiana* and *Bryum argenteum*, in the ice-free areas along the Sôya Coast, continental part of East Antarctica have been compared. Those five mosses showed three different types of micro-relief distribution, at three different types of sites: mounds, slopes and hollows. *Pottia heimii* and *Ceratodon purpureus* prevailed on mound sites mixed with cyanobacteria. In dryer mound environments cyanobacteria was supposed to play an important role in nitrogen fixation. *Bryum pseudotriquetrum* and *Grimmia lawiana* dominated on hollow sites covered with sand. A more moisture rich condition of the hollow may promote their abundance associated with their high photosynthetic ability at moist sites. *Bryum argenteum* showed a rather unclear micro-relief distribution pattern. It appeared chiefly on mounds, but on hollows also. Rich nutrient input by sea birds into its habitats may allow various site selection under environments favorable to distribution.

key words: continental Antarctica, *Grimmia lawiana*, ice-free area, micro-relief distribution, *Pottia heimii*

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 micro-relief distribution of the mosses of continental Antarctica should correspond with such an environment. According to Okitsu *et al.* (2003), the micro-relief can be classified into the following three types: hollows, slopes and mounds. Each micro-relief type shows its own environmental characteristics. A hollow suffers from sand cover. This affects moss growth negatively. However, the hollow may provide a more moisture rich condition than a mound. A mound does not suffer from sand cover. This sand-free condition provides no serious physical obstacle to the growth of mosses. However, a mound tends to be dryer than a hollow. Ohtani (1994) reveals a microclimatic difference between a hollow and a mound near Syowa Station. The mound experienced much higher temperature under sunshine exceeding

30°C, while the hollow experienced much lower temperature, exceeding 20°C. This micro-climatic difference probably relates to a difference of moisture condition. The mosses on the mound probably suffered from the dry condition as compared with the hollow. The mosses in continental Antarctica should show a micro-relief distribution corresponding to these micro-environmental differences. Taking these environmental characteristics of each micro-relief type into consideration, it is ecologically important to clarify the micro-relief distribution of the moss communities growing in ice-free areas of continental Antarctica.

Studies of the micro-relief distribution of the moss community along the Sôya Coast have been intensively carried out chiefly by researchers of the Japanese Antarctic Research Expedition (JARE) (*cf*. reviews by Kanda and Komarkova (1997), Seppelt *et al*. (1998)). Shimizu (1977) reported the relationship between distribution and micro-topography of two dominant mosses, *Ceratodon purpureus* and *Bryum pseudotriquetrum* near Syowa Station. Nakanishi (1977) comprehensively surveyed the distribution of major moss communities, *Pottia heimii*, *Ceratodon purpureus* and *Bryum pseudotriquetrum*, around Syowa Station in relation to snow cover, topography, wind direction and moisture. Okitsu *et al*. (2003) revealed the micro-relief distribution of two major mosses, *Ceratodon purpureus* and *Bryum pseudotriquetrum*, in the Yukidori Valley, Langhovde. They concluded that these species showed a clear micro-relief distribution; a *Bryum pseudotriquetrum* patch dominated on the hollow site, while a cyanobacteria-mixed *Ceratodon purpureus* patch prevailed on the mound site. Lewis Smith (1999) described the general ecology of *Ceratodon purpureus* and *Bryum pseudotriquetrum*. Despite these studies, studies of the micro-relief distribution of the major five moss species along the Sôya Coast are still insufficient.

Further, interspecific competition among mosses growing in the same colony is also an important issue in revealing the ecological characteristics of mosses growing under harsh environmental conditions. Longton and Holdgate (1979) studied replacement of moss species which appeared in vertical cross-sections of moss colonies and concluded that cyclic succession took place on Candlemas Island, the South Sandwich Islands. Nakatsubo and Ohtani (1992) examined vertical cross-sections of moss colonies composed of *Sanionia uncinata* and *Bryum pseudotriquetrum*, and concluded that the proportion of the two species in a colony has changed through colony growth, but the direction of the change varies among the colonies at each site. Okitsu *et al*. (2003) reported a similar cyclic change of *Bryum pseudotriquetrum* and *Ceratodon purpureus*. However, to understand the nature of interspecific competition among mosses in Antarctica, it is necessary to accumulate more knowledge of the micro-relief distribution of the mosses. Thus, study of the micro-relief distribution of the mosses is an important and primary theme.

According such importance of study of the micro-relief distribution of the mosses, this paper concentrates on the relationship between the micro-relief and surface cover types, and cover patterns of five major moss species along the Sôya Coast, and on comparing the characteristics of the distribution pattern among the five moss species.

Study sites

Study sites were the following five ice-free areas along the Sôya Coast, the east coast of Lützow-Holm Bay.

Langhovde (69°14′S, 39°44′E) is an extensive area (47 km^2) of bare rock hills along the Sôya Coast. The highest peak is Heito Zan (496.6 m), in the southern part of the area. In Langhovde, studies were carried out mainly in the Yukidori Valley (69°14′30″S, 39°46′00″E) in the southern part of Langhovde. The valley is well known as an area having the most prominent moss vegetation around Syowa Station (Kanda, 1987a; Kanda *et al*., 1990), being approved in 1987 as a Site of Special Scientific Interest (SSSI) (Kanda *et al*., 1990; Kanda and Inoue, 1994). Additionally three colonies of *Ceratodon purpureus-Bryum argenteum* on a stream were surveyed in Yatude Zawa, 2 km south of Yukidori Valley, where rich nutrient input from sea birds was observed.

Skarvsnes (69°28′S, 39°39′E) is the largest ice-free area (61 km^2) along the Sôya Coast. The highest peak is Skjegget (400.4 m), in the northern part of the area. Studies were carried out mainly near Suribati Ike (a pond) (69°29′15″S, 39°41′00″E) in the northern part of the area and near the Tenpyô Zan (a mountain) (69°31′00″S, 39°44′00″E) in the southern part of the area.

Skallen (69°40′S, 39°25′E) is a coastal rock hill area (14.1 km^2) projecting into eastern Lützow-Holm Bay. The highest peak is 186.2 m asl. Studies were carried out mainly around Skallen Ôike (a pond) (69°40′18″S, 39°25′00″E) in the central part of the area.

Rundvågshetta (69°54.5′S, 39°02′E) is a rock headland at the southwest margin of Rundvåg. It extends for about 3.5 km in a nearly N-S direction. Fresh glacial striae are visible on the exposed rock surface. Studies were carried out throughout the area.

Strandnibba (69°58.5′S, 38°49′E) is a bare rock hill lying at the southernmost part of the Sôya Coast. It extends in a nearly E-W direction. Owing to numerous steep cliffs facing the north, the topography of the area is characterized by many swift streams and waterfalls. Studies were carried out throughout the area.

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. Totally 65 colonies including four major community types along the Sôya Coast, the *Pottia heimii-Bryum pseudotriquetrum* community, the *Ceratodon purpureus-Bryum pseudotriquetrum* community, the *Ceratodon purpureus-Grimmia lawiana* community and the *Ceratodon purpureus-Bryum argenteum* community (Kanda, 1986), were selected in five ice-free areas (Table 1), so as to include well developed colonies. Each community was classified on the basis of the species composition. Line transects 50–280 cm in length were set on the selected colonies.

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. 2). Because the slope is situated between the mound and the hollow,

Table 1. Number of colonies surveyed in each moss community type in five ice-free areas along the Sôya Coast, East Antarctica.

Moss community	Ice-free area					
	Langhovde	Skarvsnes	Skallen	Rundvågshetta	Strandnibba	Total
Pottia heimii-Bryum pseudotriquetrum	1	16	7	3	0	27
Ceratodon purpureus-Bryum pseudotriquetrum	16	0	0	6	4	26
Ceratodon purpureus-Grimmia lawiana	0	0	0	0	9	9
Ceratodon purpureus-Bryum argenteum	3	0	0	0	0	3
Total	20	16	7	9	13	65

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 black colored mound sites, a cyanobacteria-mixed *Ceratodon purpureus* patch; on white colored hollow sites, a sand-covered patch and sand-covered *Bryum pseudotriquetrum* patch; on gray colored slope sites, a *Ceratodon purpureus* patches.

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. 2; *cf*. Table 2).

At each micro-relief site along a transect, surface cover types and the cover patterns of Bryophytes 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). Cover patterns of Bryophyte on each

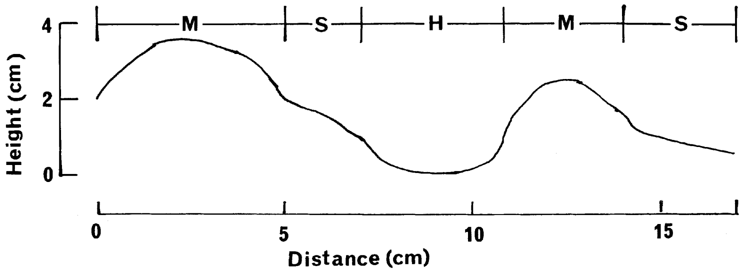

Fig. 2. Schematic representation of a cross-section of the micro-relief types. M: a mound, S: a slope, H: a hollow. The slope is situated between the mound and the hollow, and the determination of the slope is a little vague. Note that sometimes the mound borders on the hollow directly without passing through the slope.

Table 2. An example of the micro-relief distribution of patch types of *Ceratodon purpreus-Bryum pseudotriquetrum* community in the Yukidori Valley, Langhovde (after Okitsu *et al*., 2003). For abbreviation patch type, see text.

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	Mound	Cp	54	Hollow	Bp
5	Hollow	Sa-Bp	55	Hollow	Sa-Bp
10	Mound	CpBp	57	Slope	Bp
13	Slope	Bp	61	Mound	Cy-Cp
14	Hollow	Sa-Cp	63	Slope	Bp
17	Mound	Cp	64	Hollow	Sa-Bp
18	Hollow	Sa-Bp	71	Mound	Cy-Cp
19	Slope	Cy-Cp	73	Hollow	Sa-Bp
22	Mound	Cy-CpBp	76	Slope	Cp
26	Slope	Cy-Cp	84	Mound	Cy-Bp
33	Hollow	Cp	84	Mound	Cy-Bp
38	Mound	Cy-Cp	87	Hollow	Sa-Bp
39	Hollow	Sa-Bp	90	Hollow	Bp
45	Mound	CpBp	96	Mound	Cy-Bp
47	Hollow	Bp			

micro-relief type were expressed as a combination of the abbreviations of the five moss species: pure *Pottia heimii* (Ph), pure *Ceratodon purpureus* (Cp), pure *Bryum pseudotriquetrum* (Bp), pure *Grimmia lawiana* (Gl), pure *Bryum argenteum* (Ba). For example, a mixture of *Ceratodon purpureus* and *Bryum pseudotriquetrum* is expressed as CpBp, and a mixture of *Bryum pseudotriquetrum* and *Grimmia lawiana* as 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. A patch type was expressed as a combination of the abbreviations of the micro-relief and moss. For example, sand-covered mixture of *Ceratodon purpureus-Bryum pseudotriquetrum* is expressed as Sa-CpBp. Table 2 shows an example of the distribution of patch types along a line transect showing the relationship between the micro-relief and the distribution of patch types of the *Ceratodon purpureus-Bryum pseudotriquetrum* community along the Yukidori Valley, Langhovde (Okitsu *et al*., 2003). It can be seen from the table that a sand-covered patch tended to appear on a hollow site, while a cyanobacteria-mixed patch tended to appear on a mound site.

Results

Pottia heimii-Bryum pseudotriquetrum community

Table 3 presents the micro-relief distribution of the patch types of 27 transects of the *Pottia heimii-Bryum pseudotriquetrum* community. This community occurred on four ice-free areas out of five areas (except for Strandnibba), showing the widest distribution among the four communities surveyed (Table 1).

Two moss species appeared in this community: *Pottia heimii* and *Bryum pseudotriquetrum*. Eleven patch types arose including the sand only type (Sa) and the cyanobacteria only type (Cy) (Table 3). This community showed the simplest species composition and patch type among the five communities. The total occurrences of micro-relief were: hollow 229, slope 99 and mound 269.

The hollow sites were dominated by sand-covered patches (157), followed by patches of pure moss communities (19). There were only a few cyanobacteria-mixed patches (53). The slope sites were dominated by patches of pure moss communities (55), followed by sand-covered patches (31). The mound sites were, in contrast to hollow sites, dominated by cyanobacteria-mixed patches (237), followed by patches of pure

Table 3. Micro-relief distribution of *Pottia heimii-Bryum pseudotriquetrum* community.

Patch type	Micro-relief			
	Hollow	Slope	Mound	Total
Sand-covered (Sa)				
Sa	29	5	0	34
Sa-Ph	18	3	2	23
Sa-Bp	77	12	3	92
Sa-PhBp	33	11	2	46
Total	157	31	7	195
Pure moss community				
Ph	3	18	8	29
Bp	14	10	8	32
PhBp	2	27	9	38
Total	19	55	25	99
Cyanobacteria-mixed (Cy)				
Cy	22	4	94	120
Cy-Ph	23	0	65	88
Cy-Bp	4	9	51	64
Cy-PhBp	4	0	27	31
Total	53	13	237	303
Total	229	99	269	597

moss communities (25). There were only seven sand-covered patches.

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

Ceratodon purpureus-Bryum pseudotriquetrum community

Table 4 presents the micro-relief distribution of the patch types of 26 transects of the *Ceratodon purpureus-Bryum pseudotriquetrum* community. This community occurred on three ice-free areas (Langhovde, Rundvågshetta and Strandnibba) out of five areas (Table 1).

Three moss species appeared in this community: *Ceratodon purpureus*, *Bryum pseudotriquetrum* and *Grimmia lawiana.* Sixteen 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 276, slope 122 and mound 280.

The hollow sites were dominated by sand-covered patches (182), followed by patches of pure moss communities (62). There were only a few cyanobacteria-mixed patches (32). The slope sites were dominated by patches of pure moss communities (70),

Table 4. Micro-relief distribution of *Ceratodon purpureus-Bryum pseudotriquetrum* community.

Patch type	Micro-relief			
	Hollow	Slope	Mound	Total
Sand-covered (Sa)				
Sa	24	1	0	25
Sa-Cp	3	6	1	10
Sa-Bp	121	4	2	127
Sa-CpBp	4	4	2	10
Sa-BpGl	13	1	0	14
Sa-Gl	17	0	0	17
Total	182	16	5	203
Pure moss community				
Cp	17	37	21	75
Bp	28	16	3	47
CpBp	13	15	12	40
Gl	1	2	0	3
BpGl	3	0	0	3
Total	62	70	36	168
Cyanobacteria-mixed (Cy)				
Cy	5	4	124	133
Cy-Cp	11	17	83	111
Cy-Bp	11	8	22	41
Cy-CpBp	5	7	10	22
Total	32	36	239	307
Total	276	122	280	678

followed by cyanobacteria-mixed patches (36). The mound sites were, in contrast to hollow sites, dominated by cyanobacteria-mixed patches (239), followed by patches of pure moss communities (36). There were only five sand-covered patches.

The occurrence of the three moss species also clearly corresponded to the micro-relief sites. *Ceratodon purpureus* appeared chiefly on mound sites, mainly in cyanobacteria-mixed patches. *Bryum pseudotriquetrum* and *Grimmia lawiana* appeared, in contrast to *Ceratodon purpureus*, chiefly on hollow sites, mainly as sand-covered patches. They rarely occurred on mound sites.

Ceratodon purpureus-Grimmia lawiana community

Table 5 presents the micro-relief distribution of the patch types of 9 transects of the *Ceratodon purpureus-Grimmia lawiana* community. This community occurred only on Strandnibba (Table 1). Consequently the results of this community in the present study cannot illustrate the general properties of the micro-relief distribution of this community, but only the case on Strandnibba (see the discussion of the micro-relief distribution of *Grimmia lawiana*).

Three moss species appeared in this community: *Ceratodon purpureus*, *Bryum pseudotriquetrum* and *Grimmia lawiana*. 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 103, slope 44 and mound 90.

Table 5. Micro-relief distribution of *Ceratodon purpureus-Glimmia lawiana* community.

Patch type	Micro-relief			
	Hollow	Slope	Mound	Total
Sand-covered (Sa)				
Sa-Cp	2	1	0	3
Sa-Bp	2	0	0	2
Sa-CpGl	1	0	0	1
Sa-BpGl	4	0	0	4
Sa-Gl	57	2	1	60
Total	66	3	1	70
Pure moss community				
Cp	8	18	30	56
Bp	1	0	0	1
CpBp	2	0	0	2
Gl	12	0	3	15
CpGl	3	0	0	3
Total	26	18	33	77
Cyanobacteria-mixed (Cy)				
Cy	3	3	53	59
Cy-Cp	7	19	1	27
Cy-Gl	1	1	2	4
Total	11	23	56	90
Total	103	44	90	237

The hollow sites were dominated by sand-covered patches (66), followed by patches of pure moss communities (26). There were only a few cyanobacteria-mixed patches (11). The slope sites were dominated by cyanobacteria-mixed patches (23), followed by patches of pure moss communities (18). The mound sites were, in contrast to hollow sites, dominated by cyanobacteria-mixed patches (56), followed by patches of pure moss communities (33). There was only one sand-covered patch.

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

Table 6. Micro-relief distribution of *Ceratodon purpureus-Bryum argenteum* community.

Patch type	Micro-relief			
	Hollow	Slope	Mound	Total
Sand-covered (Sa)				
Sa	3	0	0	3
Sa-Bp	17	3	1	21
Sa-CpBp	0	0	1	1
Sa-BpBa	3	0	0	3
Sa-Gl	18	1	0	19
Sa-BpGl	3	1	0	4
Sa-GlBa	1	0	0	1
Sa-Ba	11	1	0	12
Sa-CpGl	3	0	0	3
Total	59	6	2	67
Pure moss community				
Cp	1	4	3	8
Bp	1	4	3	8
Ba	3	2	14	19
CpBp	0	0	1	1
BpBa	2	2	10	14
CpGl	0	1	3	4
BpGl	1	0	0	1
Gl	1	0	0	1
Total	9	13	34	56
Cyanobacteria-mixed (Cy)				
Cy	0	0	6	6
Cy-Cp	2	4	16	22
Cy-Bp	0	3	21	24
Cy-BpBa	0	0	2	2
Cy-Ba	0	2	9	11
Cy-CpBp	0	0	2	2
Total	2	9	56	67
Total	70	28	92	190

Ceratodon purpureus-Bryum argenteum community

Table 6 presents the micro-relief distribution of the patch types of three transects of the *Ceratodon purpureus-Bryum argenteum* community. This community occurred only in Yatude Zawa, Langhovde (Table 1). Consequently the results of this community in the present study can not illustrate the general properties of the micro-relief distribution of this community, but only the case of Yatude Zawa (see the discussion for the micro-relief distribution of *Bryum argenteum*).

Four moss species appeared in this community: *Ceratodon purpureus*, *Bryum pseudotriquetrum*, *Grimmia lawiana* and *Bryum argenteum*. Twenty three patch types arose including the sand only type (Sa) and the cyanobacteria only type (Cy) (Table 3). This community contained the most diverse patch types among the five communities. The total occurrences of micro-relief were: hollow 70, slope 28 and mound 92.

The hollow sites were dominated by sand-covered patches (59), followed by patches of pure moss communities (9). There were only two cyanobacteria-mixed patches. The slope sites were dominated by patches of pure moss communities (13), followed by cyanobacteria-mixed patches (9). The mound sites were, in contrast to hollow sites, dominated by cyanobacteria-mixed patches (56), followed by patches of pure moss communities (34). There were only two sand-covered patches.

The occurrence of the four moss species also clearly corresponded to the micro-relief sites. *Ceratodon purpureus* appeared chiefly on mound sites, mainly in cyanobacteria-mixed patches. *Bryum argenteum*, *Bryum pseudotriquetrum* and *Grimmia lawiana* appeared, in contrast to *Ceratodon purpureus*, chiefly on hollow sites, mainly as sand-covered patches. It rarely occurred on mound sites.

Micro-relief distribution of five species according to the cover types

Table 7 summarizes the micro-relief distribution of five species in terms of cover types. A patch consisting of a mixture of two species was counted for every two species separately. Sand only patches (Sa) and cyanobacteria only patches (Cy) were excluded from the count.

Pottia heimii prevailed on mound sites (113 of 255), but it also had a relatively high frequency on hollow sites (83 of 255). On mound sites this species was usually associated with cyanobacteria (92 of 119). On hollow sites it was basically covered by sand (51 of 83), but cyanobacteria-mixed patches also accounted for a relatively high proportion (27 of 83). Totally the cyanobacteria-mixed patches prevailed in this species (119 of 255).

Ceratodon purpureus prevailed on mound sites (186 of 398), followed by slope sites (133 of 398). It showed lower frequency on hollow sites (79 of 398). On mound sites this species was generally associated with cyanobacteria (112 of 186). On slope and hollow sites pure moss patches, occasionally being a mixture of two moss species, dominated (75 of 133 and 41 of 79, respectively). Totally pure moss patches and cyanobacteria-mixed patches co-dominated in this species (186 and 184 of 398, respectively).

Bryum pseudotriquetrum prevailed on hollow patches (355 of 682), followed by mound patches (191 of 682). On hollow patches it was typically covered with sand (264 of 355). On mound sites it was usually associated with cyanobacteria (135 of 191). Totally sand-covered patches prevailed in this species (309 of 682).

Table 7. Micro-relief distribution of five moss species according to cover type in five ice-free areas along the Sôya Coast.

Moss species/ Cover type	Micro-relief			
	Hollow	Slope	Mound	Total
Pottia heimii				
Sand-covered	51	14	4	69
Pure moss	5	45	17	67
Cyanobacteria-mixed	27	0	92	119
Total	83	59	113	255
Ceratodon purpureus				
Sand-covered	13	11	4	28
Pure moss	41	75	70	186
Cyanobacteria-mixed	25	47	112	184
Total	79	133	186	398
Bryum pseudotriquetrum				
Sand-covered	264	35	10	309
Pure moss	67	74	46	187
Cyanobacteria-mixed	24	27	135	186
Total	355	136	191	682
Grimmia lawiana				
Sand-covered	112	5	2	119
Pure moss	21	3	6	30
Cyanobacteria-mixed	1	1	2	4
Total	134	9	10	153
Bryum argenteum				
Sand-covered	15	1	0	16
Pure moss	5	4	24	33
Cyanobacteria-mixed	0	2	11	13
Total	20	7	35	62

Grimmia lawiana sharply dominated on hollow sites (134 of 153); on the other two types of sites its occurrence was rare (on slopes 9 of 153 and on mounds 10 of 153). Totally this species was usually covered with sand (119 of 153).

Bryum argenteum prevailed on mound sites (35 of 62), but it also had relatively high frequency on hollow sites (20 of 62). On mound sites pure moss patches prevailed (24 of 33). On hollow sites this species was generally covered with sand (15 of 20). Totally this species occurred mainly as pure moss patches (33 of 62).

Pure mosses (without sand or cyanobacteria) generally prevailed on slope sites. Slope sites tended to be covered neither by sand nor by cyanobacteria.

Discussion

Pottia heimii and *Ceratodon purpureus* show a similar micro-relief distribution pattern. They are concentrated basically on mound sites, usually mixed with cyanobacteria. A mound site tends to be dryer as compared with a hollow site within the same colony (Okitsu *et al*., 2003). In the extremely harsh environments in continental

Antarctica, the dry condition should be marginal for moss growth. In such environments cyanobacteria play an important role in nitrogen fixation (Henry and Svoboda, 1986). Antarctic *Nostoc commune* is capable of fixing relatively large amounts of atmospheric nitrogen during periods of high solar irradiance (Davey and Marchant, 1983; Lewis Smith, 1999). The sand-free condition of mound sites provides a suitable condition for the nitrogen fixation of cyanobacteria (Okitsu *et al*., 2003).

Ceratodon purpureus has the greatest growth at a dry site (Lewis Smith, 1999). This physiological property of *Ceratodon purpureus* should be an important factor in the success of growth on dryer mound sites (Okitsu *et al*., 2003). Unfortunately such a physiological property has not been reported for *Pottia heimii* yet. However, some studies provide evidence that support the presence of such a similar physiological properties for a dryer environment in *Ceratodon purpureus* similar to those in *Pottia heimii*. Nakanishi (1977) shows that the *Bryum antarcticum* (=*Pottia heimii*; Kanda, 1981a)-*Bryum inconnexum* (=*Bryum pseudotriquetrum*; Ochi, 1979) Sociation has a wide range of habitat distribution associated with the pattern of water supply, appearing even in a dryer habitat (medium snow drift type of Nakanishi, 1977), following the *Ceratodon purpureus* Sociation in the ice-free areas near Syowa Station. Lewis Smith (1999) shows that *Pottia heimii* appears on most dry sites along a hydrological gradient transect in Victoria Land, continental Antarctica.

Bryum pseudotriquetrum and *Grimmia lawiana* are concentrated on hollow sites, in contrast to *Pottia heimii* and *Ceratodon purpureus*. A hollow site suffers from sand cover. Sand cover generally affects moss growth negatively. However, despite this 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.

Such ecological properties as those of *Bryum pseudotriquetrum* have not been reported for *Grimmia lawiana* yet. However, a number of studies on the distribution of this species suggest that this species probably also has similar ecological properties to those of *Bryum pseudotriquetrum*. Seppelt and Ashton (1978) state that *Grimmia lawiana* is found in areas of sand and gravel in sheltered or low-lying habitats, and is best developed in areas subject to melt water drainage at Mawson Station, the Mac Robertson Land coast of continental Antarctica. Seppelt and Ashton (1978) state also that during the sequence of development of cushions of *Grimmia lawiana*, the adherence of rhizoids to the soil may help to stabilize the cushions. Kanda (1981b, 1982) reports that the *Grimmia lawiana* community along the Cape Ryûgû, Prince Olav Coast covers hollows among big boulders forming part of the moraine. Kanda (1986) points out that the *Grimmia lawiana* Sociation in Rundvågshetta occurs on wet rock covered partially with mineral-rich sandy soil on the coastal side. Kanda (1987b) describes that this species occurs occasionally along a strong stream and even in the water. Ino (1990) reports that *Grimmia lawiana* attains higher photosynthetic activity than that of the mixed community of *Ceratodon purpureus* and *Bryum pseudotriquetrum* in the Yukidori Valley, Langhovde.

However, *Grimmia lawiana* should have a wider range of ecological distribution than presented in this paper. Kanda (1981b) reports that at Cape Ryûgû on the Prince Olav Coast, this species appears on patterned ground that develops on a dry sunny lateral moraine. Kanda (1986) presumes that such differences of the habitats of *Grimmia lawiana* may be necessary to interpret the historical features of the habitats over geological time because the present habitats of *Grimmia lawiana* on the coastal side are considered to have been strongly affected by the persisting continental glacier in the past, based on the fact that the glacier in the ice-free area has retreated during relatively recent time (Moriwaki, 1976). Such a discrepancy of the ecological characteristics of this species is probably due to the limited occurrence of this species only on Strandnibba among these study areas. This limited occurrence of this species in this study reveals merely part of the ecological characteristics of this species, mentioned above.

Bryum argenteum shows a rather unclear micro-relief distribution pattern. It appears chiefly on mounds, but on hollows also. Nakanishi (1977) states that the most ornithocoplophilic moss community around Syowa Station is the *Bryum argenteum*-*Bryum inconnexum* (=*Bryum pseudotriquetrum*) Sociation. In continental Antarctica this species depends on rich nutrient input by sea birds (Nakanishi, 1977; Kanda, 1987b). Such nutrient input may allow unclear site selection under environments favorable to distribution. Under such productive environments, this species may attain the highest production (Lewis Smith, 1999), and this high production results in the highest species diversity among four moss communities. In contrast to Antarctica, this species appears mainly on nutrient poor sites such as very dry concrete walls condition (Iwatsuki, 2001). However, these ecological characteristics of this species clarified in the present study should be valid only for the case of Yatude Zawa, Langhovde, mentioned above. Further studies in various areas of Antarctica will be needed to confirm the ecological characteristics of this species.

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