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Hitoshi Shirasaki[1] and Masaji Sato[2] : Relationships among distribution, climatic conditions and phenology of the moss *Pogonatum urnigerum* in Niigata Prefecture and adjacent regions

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Abstract

The relationships among climatic conditions, phenology and distribution were investigated for the moss *Pogonatum urnigerum* in Niigata Prefecture and adjacent regions. The moss is frequent in the interior mountainous areas, but very rare in the coastal lowlands including the midwestern area of the prefecture. Although fertilization occurs in early spring in areas where snowfall is fairly light, it is delayed until May or June in the deep snow-covered district. Its sporophyte develops in warmer seasons and matures before snowfall, and spore dispersal occurs in May of the following year. Although it takes only 6 months for sporophyte maturation during snow-free seasons, the moss usually needs a value for Kira's warmth index of 35.1 or more for sexual reproduction. Therefore, the sporophyte distribution may be inhibited by the lower air temperature during its growing seasons in the alpine zone. Growth appears to be restricted to the areas, in which potential evapotranspiration of 130–190 mm in August. The moss may be more sensitive to a drier climate than higher air temperature, because its vegetative growth is well adapted to a wide range of air temperatures. As the moss requires higher air humidity and strong sunlight at open sites, it may be excluded from the coastal lowlands and the midwestern area of the prefecture, which show higher evapotranspiration in summer than at higher elevations.

Key words : distribution, evapotranspiration, phenology, *Pogonatum urnigerum*, snow.

Introduction

In the deep snow-covered district of Niigata Prefecture, the distribution of many bryophytes associated with sporophyte production is reduced by the local climatic conditions, such as the hotter and drier summer in the lower coastal area and deep winter snow in the interior mountainous area (Shirasaki 1999). Although the two species of epiphytic mosses, *Neckera humilis* and *N. yezoana*, have been reported to grow near each other in the coastal lowlands, they are segregated by their different air temperature requirements for sporophyte maturation in the interior mountain area of the prefecture (Shirasaki 2000 a). One of the terrestrial mosses, *Pogonatum urnigerum* (Hedw.) P. Beauv., is frequent in the interior mountain area, but is rarely found in the coastal lowlands and in the midwestern area of the prefecture. The distribution of the species is similar to that of *Polytrichum formosum*, which belongs to the same family, Polytrichaceae (Shirasaki 1990 a). Furthermore, both species sometimes grow near together at the cool location known as the "wind hole area", where the air temperature is lower and humidity is higher for a long period (Shirasaki 1990 b). As the sporophyte-bearing *Pog. urnigerum* is widely distributed vertically, vegetative growth, fertilization and sporophyte development seem to be well adapted to the various climatic conditions in the district.

Lackner (1939) observed the phenology of many mosses including *Pog. urnigerum* in western Russia, but there was no information on the climate. Hughes (1990) investigated the seasonal development of the apical meristem of the sporophyte in seven species of *Polytrichum* and *Pogonatum*, including *Pog. urnigerum*. *Polytrichum* is more widely distributed and adaptable than *Pogonatum* in higher latitudes, probably because sporophyte formation by the former is delayed until the following summer, whereas the sporophyte of the latter matures completely before snowfall. There is no detailed explanation, however, for the relationship between the distributions of these two genera and climate in northern Europe. The polar, sub-Arctic and sub-Antarctic moss, *Pol. alpestre*, is well adapted to a wide air temperature range during snow-free periods, because vegetative growth and sporophyte production are not affected by the differing periods of snow cover at different latitudes (Longton 1979). However, the relationship between the factors limiting its distribution and its phenological features has received little comment.

The aim of this study was to clarify the relationship among the distribution pattern, phenology and local climatic factors for this moss. This was done by a field investigation of their growth conditions at sites in and adjacent to Niigata Prefecture, central Japan.

Distribution of *Pogonatum urnigerum* in Japan

Pogonatum urnigerum is widely distributed in Japan, China, Korea, Mongolia, India, Himalayas, the Russian Far East, Europe and North America, but also occurs in scattered high mountain localities in Africa, south-east Asia, Philippines and Papua New Guinea (Osada 1965; Lawton 1971; Hyvönen 1989; Redfearn et al. 1996). The southernmost distribution in south-east Asia is Papua New Guinea, at about 8° S (Hyvönen 1989). It is common in mountain and subalpine regions of central Japan, whereas it is rare in those regions of southwestern Japan in the warm temperate zone, such as Shikoku and the Kyushu Islands (Osada 1966). Vertically, it is distributed from lower elevations of 10 m to above 3,100 m a.s.l. on Mt. Fuji (Takaki and Watanabe 1987) and Mt. Kitadake (Takaki et al. 1970), central Japan, while at lower latitudes in South West Japan its lowermost elevation tends to increase (Horikawa 1955).

Methods

Study sites and materials

The study area is in Niigata Prefecture and adjacent areas, located at ca 36°40′ N, 137°40′ E to 38°40′ N, 140°0′ E in the northern part of central Japan (Fig. 1). The prefecture is severely affected by the winter monsoon, and is well known to be one of the regions with the deepest snowfall in Japan (for climatic details, see Shirasaki 1996). Field surveys were carried out between 1972 and 2001 throughout the study area. Observations on habitat conditions were made at the time of specimen collection.

With respect to microclimate measurements, one of the locations for *Pog. urnigerum*, the ski ground on Mt. Naeba, Niigata Prefecture (36° 51′52.5″ N, 138°43′7.5″ E, 1,350 m a.s.l.), was selected for this study. This is one of the deepest snowfall areas in the prefecture, where the mean maximum snow depth is 3.26 m in February. The moss grows at this site with a dense coverage of about 80% or more in a quadrat of 1 m×1 m and produces many sporophytes every year. It is therefore well adapted to the microclimatic conditions there. The moss also grows at lower elevations with deep snowfall. However, the higher elevation was selected for investigation, because the strong influence of snow cover on its growth is shown rather than that of earlier exposure from snow in spring. The site is convenient for microclimate measurements in winter, because there is an approachable path, avoiding dangerous snow avalanches in early spring. It seemed likely that microclimate measurements would be the key to explaining largely its mountain distribution in the prefecture.

The ski ground is surrounded by the sparse foliage of beech trees remaining after deforestation for skiing. *Pogonatum urnigerum* grows on open ground, which is intermingled with a sparse meadow of short grasses and herbs such as *Carex nubigera* and *Trifolium pratense*, and small colonies of other mosses such as *Pol. commune*, *Pol. juniperinum* and *Racomitrium japonicum*, usually being exposed to direct sunlight.

Voucher specimens are deposited in the herbaria of the Biological Laboratory, Niigata College of Pharmacy, and of Y. Ikegami in Niigata City. The occurrence of the sporophyte in these specimens was also investigated.

Climatic factors

Using the grid method (Watanabe and Shirasaki 1991), the occurrence of the species in the grid was analysed along with various climatic factors. Factors such as Kira's warmth index (Kira 1976), maximum snow depth, summer (total for July and August) and winter (total from December to March) precipitation, and potential evapotranspiration in August were used for the analysis (for details, see Shirasaki and Watanabe 1995; Shirasaki 1996). Kira's warmth index is important for the growth on ground surfaces exposed to the air in warmer seasons, because plants usually grow in the accumulative condition of mean monthly air temperature above 5℃. Deep snow delays its gametangial fertilization and causes a short period of its growing seasons. Although epiphytic plants on well-drained trees may be controlled by air humidity, terrestrial plants at open ground are exposed to rain alternated with strong sunlight and use soil water in warmer seasons. As evapotranspiration shows as moisture condition on ground surface, it may be also important for the terrestrial moss growth. The value in August which is the maximum of mean monthly potential evapotranspiration is calculated by Thornthwaite's (1948) method, for it requires only the two variables: mean monthly air temperature and net solar radiation. Climatological data were supplied by the Japan Meteorological Agency (1996).

Microclimate measurement

Air temperature and relative humidity at the site of the ski ground on Mt. Naeba were measured with two thermo-hygrographs (SS–206 C, Log Electronics, Inc., Tokyo, Japan). Two sensors were placed on a beech tree at 0.5 m and 3.6 m above the ground. The former was covered by deep snow in winter, but the latter was exposed to the air all year round. Each sensor was connected to the logger, and the data were recorded at 30–min intervals from 29 December 2000 to 14 January 2002.

Vegetative growth

The moss stem shows annual growth segments similar to tree rings in wood (Lackner 1939). Male or female gametangia of the moss are annually produced on the upper part of each segment of the shoot. The segment length of each shoot is considered to suggest historical events within a region (Watson 1975). As the moss shows a wide distribution, its annual growth rates at different Kira's warmth indices may indicate the influence of air temperature during its growing seasons on vegetative growth. Ten dry shoots were selected from each package of all specimens. Leafy shoot length with number of segments except for the naked foot portion of first year shoot was measured on graph paper ruled into one-millimeter squares by microscopy, and its annual growth rate per shoot was calculated (Fig. 3).

Sporophyte maturation

Although 2–5 archegonia occur in the gynoecium of this moss, only one is fertilized and matures. As the moss also has a two-year gynoecium with archegonia or sporophytes on a gametophyte, the second-year sporophyte maturation stage and the juvenile stage in first year were distinguished by microscopy. Observations on sporophyte maturation were also made at the time of monthly sampling at the Mt. Naeba ski ground. Each stage is distinguished as follows (for details, see Greene 1960; Deguchi and Yananose 1989; Shirasaki 2000 a); Maturation stage: SV (swollen venter), ET (embryotheca), SC (seta with calyptra), CE (capsule expanding), OI (operculum intact), OF (operculum fallen), EF (empty and fresh).

Although male shoots with antheridia were frequent on the specimens, almost all their antheridia were dehisced and shriveled, except for the materials collected in November at the ski ground on Mt. Naeba. No mature antheridium was found on specimens collected in autumn or winter. This can mature rapidly and disperse sperm just after snow clearance in early spring.

Results

1. Distribution

In Niigata Prefecture and adjacent regions, *Pog. urnigerum* is frequent in the interior mountainous areas, which are near the eastern and southern margins of the prefecture and the

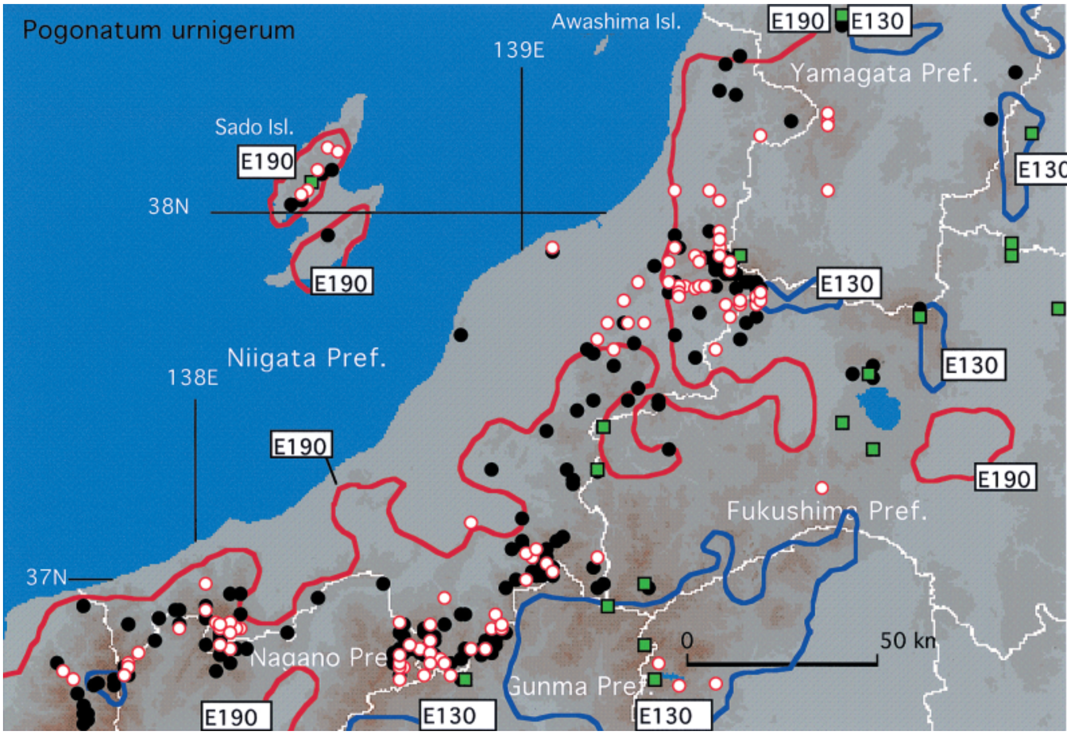

Fig. 1. Horizontal distribution of *Pogonatum urnigerum* with the isograms of potential evapotranspiration of 130 mm (blue line) and 190 mm (red line) in August, ●=specimens without sporophytes, ○=with sporophytes, □=localities from the literature.

Fig. 3. Male and female shoots of *Pogonatum urnigerum*. Each arrow shows antheridium and annual growth segments on the shoot. (Mt. Naeba, 1,350 m a.s.l., 17. Jun. 2001. no.18083).

mountainous area of Sado Island (Fig. 1). Its distribution falls largely within the area of deep winter snow cover (for isograph of maximum snow depth in the prefecture, see Ishizawa 1986). However, it is rarely found in the area from Joetsu-shi to the Shinanogawa River, the midwestern area of the prefecture. This is also a mountainous area above 500 m a.s.l. with deep snow above 3.0 m in winter, but summer precipitation is less than 440 mm (for isograph of total precipitation for July and August, see Shirasaki 1989). Vertically, the species occurs from elevations of 10 m a.s.l. to the alpine zone at 2,930 m a.s.l. (Shirouma Mountains, Nagano Prefecture) (Fig. 2). However, its lowermost distribution forty years ago has now disappeared due to urbanization (10 m a.s.l. Niigata-shi, Niigata Prefecture).

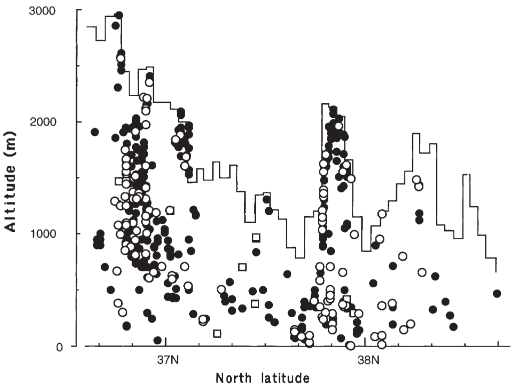

Fig. 2. Vertical distribution of *Pogonatum urnigerum*, ●=specimens without sporophytes, ○=with sporophytes, □=localities from the literature.

2. Relationship between frequency of occurrence and climatic factors

Table 1 shows the frequencies of occurrence of *Pog. urnigerum* in relation to several climatic factors, such as Kira's warmth index, maximum snow depth, summer and winter precipitation, and potential evapotranspiration in August.

In Niigata Prefecture, the moss occurs more frequently at cool sites with values for Kira's warmth index of 80 or less, and precipitation of 440–620 mm in summer. Figure 1 also shows the isograms of potential evapotranspiration of 130 mm and 190 mm in August; 83.6% of its distribution falls within the areas where are 130–190 mm in August. With respect to winter conditions, it occurs more frequently at sites with precipitation of 600–1,400 mm and a snow depth greater than 1.5 m. Table 2 shows the results of correlation analysis among the five climatic factors. Among these climatic factors in warmer seasons, the frequency of the value for Kira's warmth index is correlated the most closely with that of potential evapotranspiration in August. The higher correlation between the both factors results from the same variables of mean monthly air temperature in August is used in the both formulas estimated. The frequency of the value for maximum snow depth shows a negative correlation with that of Kira's warmth index and of potential evapotranspiration in August. Deep snow for a long period until summer decreases both the value for Kira's warmth index and the potential evapotranspiration in August at the habitats. Although the frequency of the value for maximum snow depth shows a low correlation with that of summer precipitation, that of snow depth shows a significant correlation with that of winter precipitation. With respect to summer and winter precipitation, the frequency of the value for summer precipitation shows a significant correlation with that of winter precipitation. Therefore, the three climatic factors such as potential evapotranspiration in August, and summer and winter precipitation are important independent variables for the value for Kira's warmth index.

3. Vegetative growth

Table 3 shows the vegetative growth of *Pog. urnigerum* such as shoot length with number of segments in a shoot and annual growth rate at different Kira's warmth indices. The age of the moss is estimated by the number of segments in a shoot. The lower the value for Kira's warmth index, the shoot length and annual growth rate tend to decrease, while the number of segments per shoot increases. The most aged shoot shows 9 segments at 2,550 m a.s.l. (Korenge-san, Shirouma Mountains) and the next aged one has 7 segments at 1,780 m a.s.l. (Tanemaki-yama, Iide Mountains). The value for Kira's warmth index is correlated closely with vertical distribution of

Table 1. Frequencies of occurrence of *Pogonatum urnigerum* in relation to climatic factors as Kira's warmth index, maximum snow depth (m), summer and winter precipitation (mm), and evapotranspiration in August (mm)

Warmth Index	<50	<65	<80	<95	>=95		
%	23.7	29.3	28.6	14.3	4.1		
Snow depth (m)	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	>=3.0
%	2.1	2.1	8.4	19.2	22.6	16.0	29.6
Summer precipitation (mm)	<320	<380	<440	<500	<560	<620	>=620
%	1.7	5.6	13.6	21.3	30.8	16.8	10.1
Winter precipitation (mm)	<400	<600	<800	<1000	<1200	<1400	>=1400
%	3.5	5.2	13.9	17.1	32.4	19.2	8.7
Evapotranspiration (mm)	<110	<130	<150	<170	<190	<210	>=210
%	0.7	1.4	17.8	38.0	27.9	7.7	6.6

n=288. For the result of the correlation analysis among the five factors, see Table 2.

Table 2. Correlation analysis among the five climatic factors such as Kira's warmth index, maximum snow depth, summer and winter precipitation, and evapotranspiration in August on the distributional grids of *Pogonatum urnigerum*

	Warmth Index	Snow depth	Summer precipitation	Winter precipitation	Evapotranspiration
Warmth Index	1.000				
Snow depth	−0.626*	1.000			
Summer precipitation	−0.043^{ns}	0.218*	1.000		
Winter precipitation	0.028^{ns}	0.499*	0.538*	1.000	
Evapotranspiration	0.834*	−0.512*	−0.062^{ns}	0.066^{ns}	1.000

n=288. *, $P<0.0001$; ^{ns}, non-significant. (adjusted the probabilities of error to $\alpha=0.05$).

Table 3. Mean shoot length, number of segments, and annual growth rate of *Pogonatum urnigerum* at different Kira's warmth indices

Number of specimens	Kira's warmth index	Shoot length Average (s.d.), mm	Number of segments Average (s.d.)	Annual growth rate Average (s.d.), mm
14	>=95	22.1 (5.9)	2.1 (0.9)	7.2 (1.6)
54	<95	20.7 (5.6)	1.9 (1.0)	7.4 (1.6)
109	<80	20.8 (6.4)	2.2 (1.0)	6.8 (1.8)
182	<65	20.1 (7.1)	2.2 (1.1)	6.7 (1.8)
127	<50	18.0 (6.1)	2.3 (1.5)	6.1 (2.1)

the moss along elevation (correlation coefficient : −0.925). Although the vegetative growth is inhibited by the lower air temperature during the growing seasons, the moss persists for a long period in the severe climate of the interior mountainous area.

4. Relative humidity

At 3.6 m above the ground, where the sensor is usually exposed to the air, atmospheric humidity fluctuated widely throughout winter. However, at 0.5 m above the ground with its snow cover, a value of 100% was maintained during November and May near the ski ground on Mt. Naeba. After the snow melted on 20 May 2001, the values at 0.5 m above the ground fluctuated similar to those at the higher one. Spore dispersal occurs during May and June, when humidity fluctuates markedly, ranging from 100 to 50% or less. Although the higher site sometimes tended to be drier, the lower site at 0.5 m above the ground maintained a high value for relative humidity (88% or more) during July and September. After snowfall in 14 November 2001, the lower site beneath snow again had 100% relative humidity.

5. Air temperature

Figure 4 shows the mean daily air temperature and the sporophyte maturation cycles of *Pog. urnigerum* at the same location as mentioned above. At the site exposed to the air throughout winter, the minimum mean monthly air temperature was −7.5℃ in January and the mean daily air temperature fell to the extreme minimum of −12.2℃ on 15 January 2001. However, the temperature beneath snow was usually −1.4℃ during January and May, except for the beginning of snowfall. After the snow had melted on 20 May 2001, the air temperature rapidly increased from freezing point to 11.3℃. Gametangia maturation and fertilization occur at almost the same time as the rapid increase in air temperature in May. During June and August 2001, the mean monthly air temperature at 0.5 m above the ground ranged from 13 to 18℃ and was usually 0.1 to 0.5℃ lower than that at 3.6 m above the ground. The temperature at the lower one was about 0.2 to 0.3℃ warmer during September and November until snowfall on 14 No-

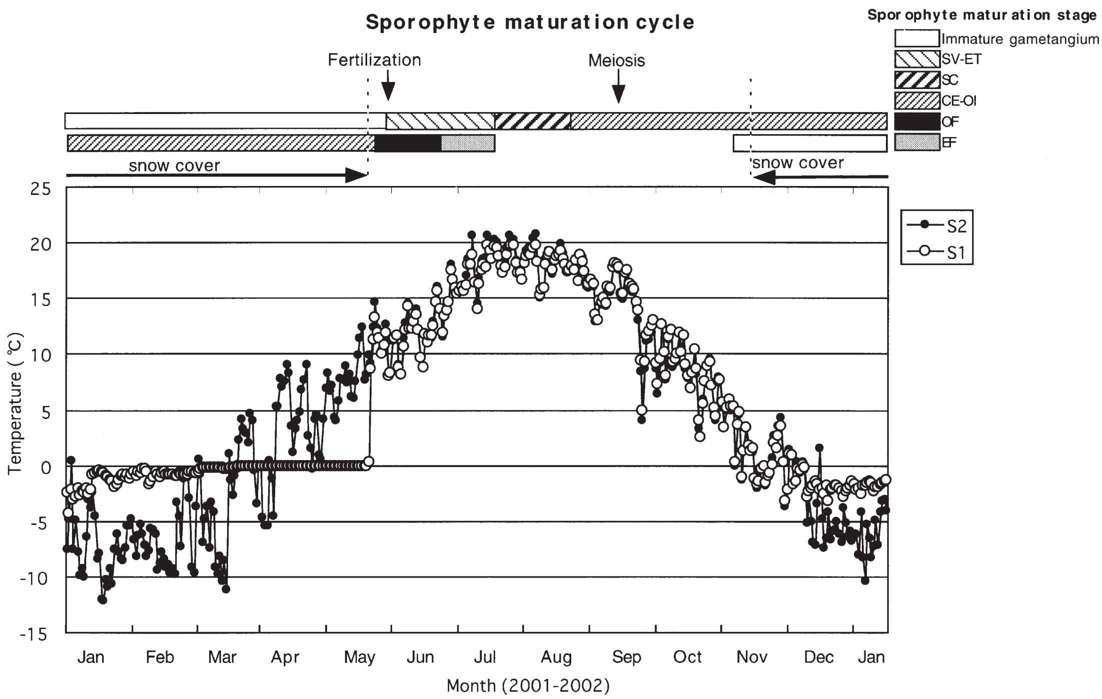

Fig. 4. Mean daily air temperature with sporophyte maturation cycle of *Pogonatum urnigerum* at the ski ground on Mt. Naeba, Niigata Prefecture. (for sporophyte maturation stages, see author's methods).

vember 2001. After snowfall it was about 0℃.

6. Production and maturation of sporophyte

Figures 1–2 show the distribution of specimens of *Pog. urnigerum* bearing the sporophyte. Although it shows dioecious sexuality (Osada 1965), it frequently produces sporophytes. The occurrence of sporophytes was observed in 165 of 495

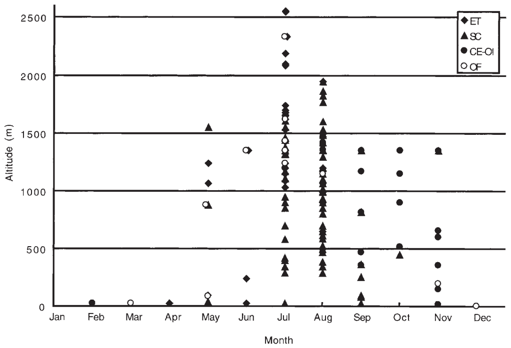

Fig. 5. Seasonal distribution of sporophyte maturation stage of *Pogonatum urnigerum* at different elevations.

specimens (33.3%). Figure 5 shows seasonal distribution of sporophyte maturation stage of the moss with its elevation in the district. The first embryo after fertilization (stage ET) was observed on 29 April 2000 at 30 m a.s.l. (Mikawa-mura, Niigata Prefecture). Archegonial fertilization and sporophyte development usually rest until April or May after snow clearance. The juvenile sporophyte develops to stage ET-SC with its elevation rising up from 40 to 2,560 m between May and July. Relationship between the sporophyte development and vertical distribution in stage ET-SC is unclear during summer. Rapid sporophyte maturation from stage SC to stage OI occurs at elevation ranged from 350 to 1,470 m a.s.l. during August to November. Despite at the higher elevations, the moss produces mature sporophytes before snowfall. In the mountain regions of the prefecture the sporophyte opercula are never released until the following spring, due to the completely developed sporophyte (stage SC-OI) being covered by deep snow in November or December. In following spring after snow clearance, stage OF with spore dispersal occurs more frequently during June to August at higher elevations.

In rare cases at Uchinokura Valley (200 m a.s.l., Shibata-shi) and Niigata-shi (20 m a.s.l.), it had already dispersed spores on 12 November 1949 and 30 December 1958, respectively. Although at Mikawa-mura (30 m a.s.l.), one of the lowermost distribution in elevation, where is estimated to have a minimum monthly snow depth of 93 cm in February, the moss was exposed to the air on 26 February 1999. It produced a completely developed sporophyte (stage OI). The sporophyte opercula are released and the capsules dispersed spores in early March.

At the site (1,350 m a.s.l.) near the ski ground on Mt. Naeba, fertilization occurs at a mean daily air temperature of 10℃ in late May after snow clearance (Fig. 4). The sporophyte develops during the four months from May to August, and matures in the middle of September with an air temperature decreasing to 15℃ or less and sporocyte meiosis occurring in the same season. The sporophyte matured completely by November at a mean daily air temperature ranging from 7.1 to 14.0℃, but its capsules had not dispersed spores before snowfall on 14 November 2001 (Fig. 4). Its capsules rest in the stage OI during winter, and spore dispersal occurs in May and June of the following year after snow clearance. Thus, the moss requires only 7 months from fertilization to sporophyte maturation at the higher elevation. Spore dispersal, however, is controlled by the local climatic conditions, such as earlier snowfall in winter and exposure to the air in spring.

The uppermost record for gametangial fertilization was at 2,560 m a.s.l. (Korenge-san, Shirouma Mountains), where the mean monthly air temperature ranges from 5.3 to 14.0℃ during May and September, and the value for Kira's warmth index is 27.7. The moss at this site, however, had not produced sporophytes in the previous year. The next uppermost record for fertilization was at 2,340 m a.s.l. (Hiuchi-yama, Myoko Mountains), where the mean monthly air temperature ranges from 6.5 to 15.6℃ during May and September, and the value for Kira's warmth index is 35.1. The moss produced juvenile sporophytes with previous year sporophyte setae. Thus, it is suggested that the moss usually needs a value for Kira's warmth index of 35.1 or more for sexual reproduction.

Discussion

1. Climatic factors

The midwestern area of Niigata Prefecture is one of the regions with the deepest snowfall in Japan. Deep snow means as much precipitation in winter and supplies much water with rapid rise in air temperature. Although, at the lower site beneath snow, a value of 100% in relative humidity is maintained, ground surface is the same as submerged condition in usual. The extremely wet conditions beneath snow for a long period, which is considered to occur when winter precipitation is 1,400 mm or more, causes damage to many vascular plants and some bryophytes, and eventually excludes them from such areas (Ishizawa 1986 ; Shirasaki and Watanabe 1995). The distribution of *Pog. urnigerum* is also restricted by a higher winter precipitation. However, it is evident that the moss is not affected by a long period of snow cover and a depth snow. Deep snow on the moss shut out against severe cold and desiccation rather than injures it.

The higher frequency within the areas for Kira's warmth index below 80 shows its well adaptations to a lower air temperature during its growing seasons on vegetative growth. It is also correlated closely with the frequencies in potential evapotranspiration. The maximum value for potential evapotranspiration, which is estimated in August, appears to restrict the moss growth, because its distribution is included largely within the area with a potential evapotranspiration of 130–190 mm in August (Fig. 1). A higher value for potential evapotranspiration decreases available water for the moss growth and desiccates the moss. Therefore, the lower evapotranspiration may supply good conditions for the moss growth in the interior mountainous area. The wide range of variation in air humidity within short time intervals shows that rain frequently alternated with strong sunlight on Mt. Naeba in summer. The moss shows normal vegetative growth and develops many gametangia and sporophytes, despite exposure to strong sunlight at the open ground. It is considered to be more sensitive to drier climate, because sporophyte elongation is 50% less in a dry site than in a moist one during June and September (Hughes 1990). Thus, gametophyte of the moss also may be excluded from the coastal lowlands including the midwestern area of the prefecture where is the higher value for the evapotranspiration above 190 mm in August.

The annual growth rate of the moss tends to decrease at lower value for Kira's warmth indices (Table 3). Differences in growth segments of *Pol. alpestre* have been observed at different latitudes in both Circum-Polar Regions, Sub-Arctic and Sub-Antarctic Zones (Longton 1979). Farther north or south, the mean air temperature in the warmest month falls down. With the cooler trend at higher latitudes, the moss decreases its segment length and number of leaves per segment. The growth variation in the both Circum-Polar materials is considered to be of adaptive value in cool, relatively dry, Circum-Polar climates. Similar growth inhibitions in *Pog. urnigerum* at lower value for Kira's warmth indices suggest that its features are also adapted to a wide range of variation in air temperature.

2. Phenology

Lackner (1939) observed that sporophyte production of *Pog. urnigerum* takes 8 months from fertilization to maturation, and spore dispersal begins in March of the following year in W. Russia. Many *Pogonatum* species in N. Europe completely develop sporophytes within the succeeding snow-free season (Hughes 1990). Also at the two sites of lower elevations in the prefecture (30 m a.s.l., Mikawa-mura, and 200 m a.s.l., Uchinokura River, Shibata-shi), it takes 8 months from April to November. However, in the interior mountainous areas such as Mt. Naeba, it takes only 6 months for sporophyte maturation during snow-free seasons. Therefore, the moss may be well adapted to the local variation in snow depth. There is no evidence, however, for the sporophytes developing completely at its uppermost locations with elevations above 2,340 m a.s.l. The lower air temperature, reflected in a value for Kira's warmth index less than 35.1, may be not enough for sporophyte maturation at higher elevations.

The farther north, the earlier archegonia of

Pol. alpestre are fertilized after snow clearance (Longton 1979). The exact time of fertilization in *Pog. urnigerum* is unclear, but it may occur in middle March in Mikawa-mura (30 m a.s.l.) and in early June on Mt. Naeba (1,350 m a.s.l.) for 3 weeks or less after snow clearance. Sporocyte meiosis of *Pol. formosum*, *Pol. commune* and other *Polytrichum* species occurred in June (Longton 1979; Hughes 1990), and that of *Pog. urnigerum* in July (Hughes 1990). Therefore, these species are considered to be well adapted to the short growing seasons of higher latitudes by the common phenological features (Hughes 1990). On Mt. Naeba, however, sporocyte meiosis of *Pog. urnigerum* occurs in September. This phenological feature is clearly different from that of *Pol. commune* and N. European materials. The different distributions of *Pol. formosum* and *Pol. commune* are considered to reflect their differences in requirements for moisture and sunlight (Shirasaki 1990 a). Although the uppermost elevation of *Pog. urnigerum* in the prefecture is higher than that of *Pol. formosum*, the horizontal distribution of both mosses is quite similar. Both frequently grow near together in the same habitats, the so-called "wind hole area", where lower air temperature and higher air humidity are maintained throughout the year (Shirasaki 1990 b). Therefore, the similar distributional pattern rather than phenological differences may show the similar requirement in air humidity between both species.

Pogonatum urnigerum, which occurs at higher elevations than *Pol. formosum*, frequently has caducous leaves in Arctic populations (Long 1988), and fragments have been obtained from the surface of the snow in northern New York (McDaniel and Miller 2000). Caducous leaves and fragments of the moss may also serve as vegetative diaspores in the alpine zone of the prefecture.

3. Geological factor

Pogonatum urnigerum is rarely found within the midwestern area of the prefecture despite the elevation being about 500–800 m a.s.l. Landslides sometimes occur here, giving a distinctive geological feature known as "Fossa Magna" (Yamashita 1995). Some bryophytes such as *Rhizogonium dozyanum*, *Leucobryum scabrum*, *Trichocolea tomentella* and *Trichocoleopsis sacculata*, are excluded from the area with the unstable ground, because of their asexual reproduction (Shirasaki 1989, 1991, 2000 b). *Pogonatum urnigerum*, however, may be strongly affected by the higher evapotranspiration in August rather than the landslides, because it can be established by spore dispersal every year.

In conclusion, the lower drought resistance for its vegetative growth may cause the distributional gap in the coastal lowlands including the midwestern area of the prefecture, despite of its growth well on open ground with strong sunlight. The moss is well adapted to the cool temperatures and deep snow of the interior mountainous area, while its sporophyte production may be reduced by lower air temperature with too short a snow-free season in the alpine zone of the prefecture.

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References

Deguchi, H. and Yananose, N. 1989. Development of sporophyte, calyptra and vaginula in *Pogonatum neesii* (C. Müll.) Dozy. Proc. Bryol. Soc. Japan **5**: 1–6. (in Japanese with English summary)

Greene, S. W. 1960. The maturation cycle, or stages of development of gametangia and capsules in mosses. Trans. Brit. Bryol. Soc. **3**: 736–745.

Horikawa, Y. 1955. Distributional studies in Japan and the adjacent regions. 152 pp. Hiroshima Univ., Hiroshima.

Hughes, J. G. 1990. Seasonal growth and development of sporophytes in wild populations of *Pogonatum* and *Polytrichum*. J. Bryol. **16**: 97–108.

Hyvönen, J. 1989. A synopsis of genus *Pogonatum* (Polytrichaceae, Musci). Acta Bot. Fenn. **138**: 1–87.

Ishizawa, S. 1986. The plants distributed around the range of snow-camellia, *Camellia rusiti-*

cana Honda, in Niigata Prefecture and its adjacent area 2. Bull. Nagaoka Mun. Sci. Mus. **21**: 1–18. (in Japanese)

Japan Meteorological Agency (ed.). 1996. The monthly normals for AMEDAS Stations in Japan (1979–1990). CD-ROM. Japan Meteorological Agency, Tokyo.

Kira, T. 1976. Rikujo seitaikei. 166 pp. Kyoritsu Shuppan, Tokyo. (in Japanese)

Lackner, J. 1939. Über die Jahresperiodizität in der Entwicklung der Laubmoose. Planta **29**: 534–616.

Lawton, E. 1971. Moss flora of the Pacific Northwest. 537 pp. Hattori Bot. Lab., Nichinan.

Long, D. G. 1988. *Pogonatum urnigerum* with caducous leaves in Scotland. J. Bryol. **15**: 495–496.

Longton, R. E. 1979. Studies on growth, reproduction and population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre*. Bryologist **82**: 325–367.

McDaniel, S. F. and Miller, N. G. 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. Bryologist **103**: 592–600.

Osada, T. 1965. Japanese Polytrichaceae. I. Introduction and the genus *Pogonatum*. J. Hattori Bot. Lab. **28**: 171–201.

Osada, T. 1966. Japanese Polytrichaceae. II. The genera *Polytrichum*, *Oligotrichum*, *Bartramiopsis*, and *Atrichum*, and phytogeography. J. Hattori Bot. Lab. **29**: 1–52.

Redfearn, P. L. Jr., Tan, B. C. and He, S. 1996. A newly updated and annotated checklist of Chinese mosses. J. Hattori Bot. Lab. **79**: 163–357.

Shirasaki, H. 1989. Ecological distribution of *Leucobryum scabrum* Lac. and *Rhizogonium dozyanum* Lac. (Musci). J. Phytogeogr. Taxon. **37**: 15–25. (in Japanese with English summary)

Shirasaki, H. 1990 a. Ecological distribution of bryophyte. 1. *Polytrichum commune* Hedw. and *P. formosum* Hedw. (Musci). J. Phytogeogr. Taxon. **38**: 27–41. (in Japanese with English summary)

Shirasaki, H. 1990 b. Ecological distribution of bryophyte. 2. Distribution types in the wind hole areas of Mt. Naeba, Niigata and Nagano Prefecture. J. Phytogeogr. Taxon. **38**: 137–147. (in Japanese with English summary)

Shirasaki, H. 1991. Method to process the distribution maps of the plants and analysis of distribution pattern of bryophytes. Bull. Niigata Coll. Pharm. **11**: 1–12. (in Japanese with English summary)

Shirasaki, H. 1996. Distribution and ecology of *Ricciocarpos natans* in Niigata Prefecture and its adjacent regions, central Japan. Proc. Bryol. Soc. Japan **6**: 209–215.

Shirasaki, H. 1999. Relationship between distribution types of bryophyte sporophyte and climatic conditions in Niigata Prefecture and its adjacent regions, central Japan. Natur. Environ. Sci. Res. **12**: 75–83.

Shirasaki, H. 2000 a. Relationships among distribution, environmental factors, and phenology of the epiphytic mosses, *Neckera humilis* and *N. yezoana* in Niigata Prefecture and its adjacent regions, central Japan. J. Phytogeogr. Taxon. **48**: 149–161.

Shirasaki, H. 2000 b. *Trichocoleopsis sacculata* (Mitt.) Okam. Ishizawa, S. (ed.). Distribution maps of plants in Niigata Prefecture, Japan. 20, pp. 89–92. Jinenjo-kai, Niigata. (in Japanese)

Shirasaki, H. and Watanabe, S. 1995. Analysis of distribution pattern of bryophytes in relation to climate of the Sea of Japan region. Bull. Niigata Coll. Pharm. **15**: 9–19. (in Japanese with English summary)

Takaki, N., Amakawa, T., Osada, T. and Sakuma, E. 1970. Bryophyte flora of Mt. Kaikoma, Mt. Senjo and Mt. Kitadake (southern Japan Alps). J. Hattori Bot. Lab. **33**: 171–202.

Takaki, N. and Watanabe, R. 1987. A checklist of the mosses of Mt. Fuji, central Japan. pp. 529–537. Kobe Geobotanical Society, Kobe. (in Japanese)

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geogr. Rev. **38**: 55–94.

Watanabe, S. and Shirasaki, H. 1991. A new method to process the distribution maps by using the fine mesh and analysis of distribution pattern of bryophytes. J. Phytogeogr. Taxon. **39**: 131–135. (in Japanese with English summary)

Watson, M. A. 1975. Annual periodicity of incremental growth in the moss *Polytrichum commune*. Bryologist **78**: 414–422.
Yamashita, N. 1995. Fossa magna. 310 pp. Tokai University Press, Tokyo.（in Japanese）
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白崎　仁[1]・佐藤政二[2]：新潟県とその隣接地域における蘚類ヤマコスギゴケの分布，環境要因，および生活史の関連性

ヤマコスギゴケは，新潟県とその周辺では，主に佐渡ケ島北部と内陸部の県境付近の山岳地域に多く，新潟県の中西部と，日本海沿岸沿いの低地には比較的少ない。垂直分布は海抜10 mほどの低地から2,930 m（白馬岳）の高山の山頂まで広く分布する。本種は，日当たりの良い開けた土上に生育することが多い。生殖器官の成熟と受精は雪消え直後に行われ，胞子体はその年の11月までに成熟するので，受精と胞子体の発達は多雪と積雪下の長期の多湿には影響されない。少雪地では降雪前の12月に胞子を散布することもあるが，多雪地では主に，5月の雪解け後，気温が10℃に急上昇する頃に胞子を散布する。雪解けがより遅い所では，胞子の散布時期が遅れて，高海抜では7〜8月になる。受精個体の最高海抜は2,550 mだが，胞子体が毎年成熟するのは海抜2,340 mが限界である。高海抜では胞子体の成熟期間が短縮されるため，生活史を完結できるのは，温かさの指数が35.1以上の所と推定される。シュート（配偶体）の年間生長率は温かさの指数が下がるにつれて低下するので，配偶体の生育は温かさの指数の高い所ほど良いが，高山で低温が長く続く環境でも強い耐性をもっている。本種は，8月の可能蒸発散量が190 mm以下の範囲に主に分布しており，山岳地域では夏にしばしば雨が降る。海岸沿いや県中西部では8月の可能蒸発散量がより高く，植物体は強い乾燥を受けることになるが，山岳地域の蒸発散量は比較的低いため，内陸の山岳地域に分布が偏っていると考えられる。
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