Holocene Phytolith Record at *Picea glehnii* Stands on the Dorokawa Mire in Northern Hokkaido, Japan

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Phytolith analysis was applied to clarify a vegetation history at *Picea glehnii* stands on the Dorokawa Mire, northern Hokkaido. Phytolith assemblages from surface samples and Holocene deposits from the mire are used to clarify the stand-scale vegetation history, with special focus on the dynamics of Gramineae, which includes dwarf bamboo, and the establishment of *P. glehnii* stands on the mire. The phytolith records during the early-Holocene (ca. 12,000 to 10,000 cal BP) indicate the distribution of Pooideae-dominated vegetation, which reflects the cool climate. *Phragmites* (reed) dominated vegetation from the early to mid-Holocene (ca. 10,000 to 5,000 cal BP) suggests wet conditions like low-moor. The reed was replaced by dwarf bamboo at ca. 5,000 cal BP, although the distribution of dwarf bamboo was scattered. At ca. 1,500 cal BP, dwarf bamboo increased abruptly and has been sustained to the present. Also, Pinaceae type phytoliths began to occur continuously at ca. 1,000 cal BP. Taking into account the relationship between modern vegetation and modern phytolith assemblages on the mire, the occurrence of the Pinaceae type phytoliths from the sediment samples indicates the existence of *P. glehnii* in the study sites. On the basis of these results, *P. glehnii* stands with dense undergrowth of dwarf bamboo would have been established in the study sites on the mire by ca. 1,000 cal BP at least.

Keywords : dwarf bamboo, Holocene, phytoliths, *Picea glehnii* stands, surface samples

I. Introduction

Picea glehnii dominated stands with dense undergrowth of dwarf bamboo are established on the Dorokawa Mire, which covers the drainage basin of the Dorokawa River in northern Hokkaido. On the other hand, mixed forests composed of some conifers and hardwood trees (*Abies sachalinensis*, *Quercus crispula* etc.) are

widespread on the mountain slopes of the area. In general, *P. glehnii* forests are established on specific sites. Tatewaki (1943) classified *P. glehnii* forests into six habitat types: “mire”, “volcanic ash and gravel”, “sand dunes”, “serpentinite substrate”, “conglomerate” and “remains of fire disturbance” types. According to the habitat types, the *P. glehnii* stands on the Dorokawa Mire are classified as a “mire” type.

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The main vegetation changes in Hokkaido during the Holocene have been regionally traced mainly through pollen records (*e.g.* Tsukada and Nakamura, 1988 ; Igarashi *et al.*, 1993 ; Igarashi, 1994 ; Morita, 2001). However, except some palynological studies (Igarashi and Takahashi, 1985 ; Igarashi *et al.*, 2001 ; Morita, 2001), the dynamics of *P. glehnii* forests have not yet been clarified. In addition, dwarf bamboo, which is a *Sasa* species, currently forms a dense undergrowth in *P. glehnii* stands on the Dorokawa Mire. It is well known that the dwarf bamboo undergrowth has negative effects on the growth of tree seedlings (Nakashizuka, 1988 ; Hiura *et al.*, 1996 ; Narukawa and Yamamoto, 2002). Therefore, this dwarf bamboo has great effects on the regeneration and vegetation structure of forests. Thus, to make clear the vegetation dynamics on the Dorokawa Mire, clarification of the dynamics of the dwarf bamboo is indispensable. However, there is little data about the dynamics of dwarf bamboo in palaeovegetation, because the identification of Gramineae, which includes dwarf bamboo species, by pollen is restricted to the family level. On the other hand, phytolith analysis is well known as an alternative technique available for reconstruction of the vegetation history of dwarf bamboo (Kariya *et al.*, 2004 ; Sasaki *et al.*, 2004 ; Sase *et al.*, 2004).

Phytoliths are siliceous microscopic particles found within and among the cellular tissue of many plants. The dwarf bamboo accumulates a large amount of SiO₂ in and between their cells. Therefore, phytolith analysis is a very useful tool for reconstructing the vegetation history of dwarf bamboo. In addition, some studies have shown that Pinaceae species, which include *P. glehnii*, produce distinctive leaf phytoliths (Klein and Geis, 1978 ; Kondo *et al.*, 2003). Moreover, phytoliths are resistant to decomposition in a sedimentary environment and their dispersion is shorter than that for pollen grains (Kondo and Sase, 1986). Therefore, the application of phytolith analysis for sediment samples provide a detailed basis for local vegetation reconstruction.

In this paper, we report the Holocene vegetation history with a special focus on the establishment of *P. glehnii* stands. We also report on

the dynamics of vegetation composed of Gramineae, which includes dwarf bamboo, on the Dorokawa Mire based on a phytolith analysis conducted on modern and fossil assemblages.

II. Materials and methods

1. Study area

The Dorokawa Mire is located in the Uryu Experimental Forest of Hokkaido University in Moshiri, the northern part of Hokkaido, and lies about 290 m above sea level (Fig. 1). The average annual temperature at Moshiri Station of the Uryu Experimental Forest is about 4°C, and the annual precipitation is 1,137 mm (Field Science Center for Northern Biosphere, Hokkaido University, Forest Research Station Database during 2005, unpublished data). At present, conifer stands composed of *P. glehnii* and hardwood stands composed mainly of *Fraxinus mandshurica* var. *japonica* and *Ulmus davidiana* var. *japonica* are established on the mire. In addition, *Sasa senanensis*, dwarf bamboo, forms a dense undergrowth in these stands. In this study, surface samples and core samples were collected from forest stands in the eastern part of the Dorokawa Mire.

2. Surface samples for modern analogue

Several previous studies reported that the phytolith assemblages from surface samples correspond to modern vegetation (Kondo, 1988 ; Eguchi, 1998 ; Kawano *et al.*, 2006). The relationship between modern phytolith assemblages and modern vegetation is indispensable for the reconstruction of past vegetation. In this study, in order to make clear the differences of phytolith assemblages between *P. glehnii* stands and hardwood stands, a total of ten surface samples were collected from the *P. glehnii* stands (DRS 3, 12, 17, 18, 19) and the hardwood stands (DRS 4, 13, 14, 15, 21) located on the Dorokawa Mire (Fig. 1 and Table 1). Also, to evaluate the distance of phytolith dispersion from a stand margin of *P. glehnii*, another six samples were collected by 10 m intervals along a 50 m transect from the margin of a *P. glehnii* stand (stand height about 20 m) to dwarf bamboo grassland. The first one of these six samples was collected just below the crown of one of the margin of *P. glehnii* stand. Other five were from open dwarf bamboo grassland. The top five centimeters of

the A₀ humic horizon (except litter horizon) of each soil sample were collected for analysis of the phytoliths.

3. Core samples

Two core samples (UDA1 and UDA2) were collected in *P. glehnii* stands, where the surface samples were collected (Fig. 1). The UDA1 site is located in a small open area (ca. 10 m in diam-

eter) covered by sedges and grasses, which is situated in the *P. glehnii* stand. The UDA1 site is surrounded mainly by *P. glehnii* and *Sasa senanensis*. The UDA2 site is located in *P. glehnii* stand with dense dwarf bamboo under-story, and is about 100 m from the UDA1 site. Tree density and basal area of *P. glehnii* are 541 trees/ha and 21.4 m²/ha, respectively, and the

Fig. 1 Location of study sites

Numbers beside the solid circles and squares are the sample numbers of the modern assemblages (DRS series) used in this study. Maps I and II are based on a 1 : 25,000 scale topographic map “Fukinodai” published by the Geographical Survey Institute of Japan.

Table 1 Coverage (%) of major plant species in each plot where the modern samples were obtained

Plot	Tree species					
	<i>Picea glehnii</i>	<i>Abies sachalinensis</i>	<i>Fraxinus mandshurica</i> var. <i>japonica</i>	<i>Ulmus davidiana</i> var. <i>japonica</i>	<i>Betula platyphylla</i> var. <i>japonica</i>	<i>Sasa senanensis</i>
DRS3	35	•	•	•	•	100
DRS12	30	•	•	•	+	100
DRS17	30	•	•	•	5	90
DRS18	20	+	•	•	+	100
DRS19	30	+	•	•	+	100
DRS4	•	•	30	10	•	100
DRS21	•	•	20	40	•	100
DRS13	+	•	15	•	+	80
DRS14	+	+	15	•	5	100
DRS15	•	•	20	+	10	100

+ : less than 5%

coverage of dwarf bamboo is 100% within a 30 m radius of the UDA2 site.

These two core samples were collected by a thinwall sampler (7.5 cm diameter). Twenty-six subsamples were analyzed in the 196 cm length profile of the UDA1 core. A peaty clay horizon was found in the profile from the bottom to a 182 cm depth. The profile above 182 cm is peat horizons. Thirty-one subsamples were also analyzed in the 258 cm length profile of the UDA2 core. Silt and peaty clay horizons were described in the profile from the bottom to a 250 cm depth. The profiles above 250 cm are mainly peat horizons.

4. Chronology of the cores

For the date control, AMS radiocarbon dating was carried out using macro-plant remains and organic matter. Three radiocarbon dates were obtained from the upper 200 cm depth of the UDA1 core and six radiocarbon dates from the upper 259 cm depth of the UDA2 core (Table 2). The radiocarbon dates at the 200 cm depth of the UDA1 core and at the 259 cm depth of the UDA2 core were $6,980 \pm 40$ yrs BP (7,816 cal BP of median calibrated age) and $10,160 \pm 25$ yrs BP (11,850 cal BP of median calibrated age), respectively. AMS radiocarbon datings of four samples were carried out by Beta Analytic Inc. (Beta) and other five samples by H. Kitagawa (Nagoya University) in the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory (UCIAMS). These AMS ^{14}C dates were cali-

brated with the program CALIB 5.0.1 (Stuiver *et al.*, 2005) using the IntCal04 calibration data set (Reimer *et al.*, 2004).

Two types of tephra layers were found in the profiles between the 17 and 18 cm depth of the UDA1 core and between the 14 and 15 cm depth of the UDA2 core. The volcanic ashes correspond to Ma-b (980 ± 100 yrs BP : Katsui *et al.*, 1975) or B-Tm (AD937 : Fukusawa *et al.*, 1998) and Ta-a (AD1739 : Soya, 1972) tephra, respectively (Table 3). Range of the refractive index of volcanic grasses from 14–15 cm depth of the UDA2 core indicated the three types of tephra (Ta-a, Ma-b and B-Tm). However, almost volcanic grass shards (about 83% of count number of grass shard) from this layer were corresponded to the Ta-a tephra (Table 3). Therefore, the layer was recognized as Ta-a tephra falling horizon. The petrographical data of each tephra sample were measured by Kyoto Fission-Track Co. Ltd.

In this study, the age of each horizon of both the UDA1 and UDA2 cores were estimated from the age-depth curves, which were described using the calibrated radiocarbon dates and tephrochronological dates obtained from each core (Fig. 2). The average value (5,097 cal BP) at the UDA2 core was calculated using three median calibrated ages (from 131 to 133 cm horizons) at 2σ calibrated age ranges and applied for the age-depth curve.

5. Phytolith analysis

The extraction of phytoliths from the sur-

Table 2 AMS ^{14}C dates for UDA1 and UDA2 cores

Site	Depth (cm)	Material	^{14}C age (yrs BP)	2σ calibrated age ranges (cal BP)	Median calibrated age (cal BP) ^{*1}	$\delta^{13}\text{C}$ (‰)	Lab. Code ^{*2}
UDA1	65-66	plant remain	$2,780 \pm 40$	2,778 to 2,966	2,872	-25.4	Beta-200528
	156-157	bulk	$4,580 \pm 50$	5,048 to 5,459	5,254	-29.2	Beta-200529
	200-201	bulk	$6,980 \pm 40$	7,702 to 7,929	7,816	-28.1	Beta-197967
UDA2	35-36	plant remain	$2,760 \pm 20$	2,785 to 2,922	2,854	-19.2	UCIAMS-21238
	131-132	bark	$4,605 \pm 20$	5,298 to 5,445	5,372	-25.1	UCIAMS-21243
	131-132	bark	$4,235 \pm 20$	4,712 to 4,852	4,782	-25.2	UCIAMS-21245
	132-133	bark	$4,480 \pm 20$	4,988 to 5,287	5,138	-22.6	UCIAMS-21236
	179-180	peat	$7,190 \pm 40$	7,938 to 8,154	8,046	-29.1	Beta-197966
	259	bark	$10,160 \pm 25$	11,714 to 11,986	11,850	-22.3	UCIAMS-21230

*1 Ages adapted for sediment accumulation rate *2 Beta: Beta Analytic Inc.

*2 UCIAMS: W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory (measured by H. Kitagawa, Nagoya Univ.).

Table 3 Petrographic properties of tephra samples for UDA1 and UDA2 cores

Site	Depth (cm)	Heavy mineral ^{*1}	Volcanic glass type	Refractive index of volcanic glass (mean)	Count number of glass shard	Tephra	Age (cal BP)
UDA1	17-18	Opq > Opx > GHb > Cpx	pumice	1.495-1.498 (1.497)	2	unknown	-
				1.502-1.504 (1.503)	44	Ma-b	903 ^{*2}
				1.508-1.511 (1.509)	21	B-Tm	1,013 (AD937) ^{*3}
				1.520-1.522 (1.521)	11	B-Tm	1,013 (AD937) ^{*3}
UDA2	14-15	Opx > Cpx > Opq	pumice	1.489-1.495 (1.491)	65	Ta-a	211 (AD1739) ^{*4}
				1.502-1.503 (1.503)	8	Ma-b	903 ^{*2}
				1.509-1.510 (1.509)	3	B-Tm	1,013 (AD937) ^{*3}
				1.520-1.521 (1.520)	2	B-Tm	1,013 (AD937) ^{*3}

*1 Opx, Cpx: orthopyroxene, clinopyroxene, GHb: green hornblende, Opq: opaque mineral.

*2 Median calibrated age based on 980±100 yrs BP by Katsui *et al.* (1975), *3 Fukusawa *et al.* (1998), *4 Soya (1972).

Fig. 2 Age-depth curves for UDA1 and UDA2 cores based on calibrated radiocarbon dates and ages of volcanic ashes

face samples and core samples was carried out by a procedure slightly modified from Eguchi (1996). Phytoliths were extracted from 1 cm³ samples after organic matter oxidation using 30% H₂O₂, calcium carbonate removal using 3N-HCl, and clay removal according to Stoke's law. Prior to extraction, a known amount of glass beads, which were 45 μm in diameter, were added to each sample to estimating the phytolith concentration (according to Fujiwara, 1976). Phytoliths were mounted on microscope slides in Eukitt mounting medium. Microscopic observations were performed at 400× magnification,

and more than 200 phytoliths were counted from each sample.

Identification of Gramineae phytoliths were based on Sase and Kondo (1974), Sugiyama and Fujiwara (1986), and Kondo and Ootaki (1992). Conifer trees belonging to Pinaceae produce a characteristic phytolith type. Cubic shaped phytoliths with bordered pits are produced in transfusion tracheid cells of the leaves of Pinaceae (Klein and Geis, 1978; Kondo *et al.*, 2003). Kondo *et al.* (2002) examined the classification of Pinaceae trees below genus level focusing on the size of the bordered pits on phytoliths from transfusion tracheid cell in Pinaceae leaves. However, the size of the bordered pits on the transfusion tracheid phytoliths which were extracted from the fossil assemblages used in this study could not be measured because the shape of the bordered pits was not clear. Therefore, transfusion tracheid phytoliths were classified as Pinaceae type phytolith in this study. We also referred to the reference phytoliths collection obtained from major plant species common to the region. In this study, we endeavored to follow the phytolith nomenclature described by the International Code for Phytolith Nomenclature (ICPN WORKING GROUP, 2005) and Kondo (2004) wherever possible.

III. Results

1. Modern phytolith assemblages

The modern phytolith assemblages from forest stands on the Dorokawa Mire are shown in Figure 3. Percentages for each phytolith type were calculated based on the total phytolith

counts including unidentified types.

The phytolith assemblages from the surface samples both in the *P. glehnii* stands and hardwood stands show a significant proportion of dwarf bamboo type phytoliths (sum of the *Sasa* or Bambusoideae type bulliform cells and Bam-

busoid type short cells) which were derived from dwarf bamboo (Fig. 4). The percentage values of the dwarf bamboo type phytoliths from the *P. glehnii* stands are $54.5 \pm 4\%$, and that of hardwood stands are $48.5 \pm 4\%$. The sum of each percentage value of the phytolith morphotypes

Fig. 3 Percentages of phytolith morphotypes from the surface samples in forest stands on the Dorokawa Mire

Fig. 4 Phytolith morphotypes from modern and fossil assemblages on the Dorokawa Mire
a : Pinaceae type (transfusion tracheid cell), b : *Sasa* type (bulliform cell), c : *Phragmites* type (bulliform cell), d : Bambusoid (short cell), e : Saddle (short cell), f : Rondel (short cell), g : Bilobate (short cell), h : Festucoid (short cell), i : Plate with verrucate-type, j : Elongate long cell, k : Acicular hair cell.

which are common in dwarf bamboo and other Gramineous species (Fig. 4 : saddle, rondel, elongate, and aciculate hair cells), and the percentage values of the dwarf bamboo type phytoliths mentioned above, add up to 85.2% and 83.4% in *P. glehnii* stands and hardwood stands, respectively. On the other hand, phytolith assemblages from the *P. glehnii* stands are characterized by the presence of Pinaceae type phytoliths (Fig. 4 : transfusion tracheid cell), although with low percentage values (3.3 to 0.1%). In addition, phytolith assemblages from the hardwood stands are characterized by the presence of *Phragmites* type bulliform cells and plate with verrucate-type phytoliths (Fig. 4). On the basis of the reference phytolith collection mentioned above, the plate with verrucate-type phytoliths are found only in the leaves of hardwood trees (e.g. *Ulmus davidiana* var. *japonica*).

According to the transect sampling of surface soils (Fig. 5), phytolith assemblages represent a relatively high amount of Pinaceae type phytoliths (3.5%) just below the crown of one of the margin of *P. glehnii* stand (0 m point). However, 10 and 20 m distant samples from the stand margin of *P. glehnii* show the low percent-

Fig. 5 Pinaceae type phytolith percentages of the surface samples from the margin of the *P. glehnii* stand to dwarf bamboo grassland (* just below the crown of *P. glehnii*)

Percentage values were calculated based on the total phytolith counts including unidentified types.

ages of the Pinaceae type phytoliths (0.1%), and this type of phytolith is absent from area over 30 m away.

2. Fossil phytolith assemblages

Figure 6 shows the phytoliths frequencies from the UDA1 and the UDA2 cores, respectively. Percentage values for each phytolith morphotype were calculated based on the total phytolith counts including unidentified types. These diagrams were divided into four local phytolith zones, respectively, based on significant changes in the phytoliths characteristics.

UDA1 site (Fig. 6-A)

UDA1-1 zone (ca. 8,000 to 5,000 cal BP) : The assemblages of this zone are characterized by the occurrence of *Phragmites* type bulliform cell phytoliths. Also, dwarf bamboo type phytoliths are represented in minor proportions (maximum 13%).

UDA1-2 zone (ca. 5,000 to 3,000 cal BP) : *Phragmites* type bulliform phytoliths are absent in this zone, whereas the dwarf bamboo type phytoliths increased.

UDA1-3 zone (ca. 3,000 to 1,500 cal BP) : The phytoliths are extremely poor in this zone.

UDA1-4 zone (ca. 1,500 cal BP to present) : The phytoliths from dwarf bamboo increase again. Also, the bilobate type phytoliths which belongs to the Panicoideae or Arundinoideae subfamily and the Festucoid type phytoliths which belongs to the Pooideae subfamily are relatively abundant (3.8 and 3.2%, respectively) in the beginning of this zone. The Pinaceae type phytoliths begin to occur with low percentages (<1%) at the mid part of this zone. In this zone, the percentage values of dwarf bamboo type phytoliths are high (>50%), with an abrupt increase of the phytolith accumulation rate.

UDA2 site (Fig. 6-B)

UDA2-1 zone (ca. 12,000 to 10,000 cal BP) : The assemblages are characterized by a relatively high amount of Festucoid type phytoliths (mean 4.2%) and a predominance of elongate long cell (mean 47.6%) and acicular hair cell (mean 17.7%) phytoliths. No dwarf bamboo type phytoliths were counted in the assemblages.

UDA2-2 zone (ca. 10,000 to 4,500 cal BP) : The assemblages of this zone show the continuous occurrence of *Phragmites* type bulliform phytoliths. The dwarf bamboo type phytoliths also

Fig. 6 Percentages of phytolith morphotypes and phytolith accumulation rate from the UDA1 (A) and the UDA2 (B) cores

begin to occur.

UDA2-3 zone (*ca.* 4,500 cal BP to below Ta-a tephra layer): The phytolith assemblages are characterized by the absence of *Phragmites* type bulliform phytoliths and a high percentage of dwarf bamboo type phytoliths (mean 36.6%). The percentage values of the bilobate and Festucoid type phytoliths also slightly increase in this zone.

UDA2-4 zone (below Ta-a tephra layer to present): The phytolith assemblages present the continuous occurrence of Pinaceae type phytoliths (0.4 to 2.6%). The phytolith accumulation rate and the percentage values of the dwarf bamboo type phytoliths show an abrupt increase simultaneously.

IV. Discussion

1. Interpretation of modern phytolith assemblages

Phytolith assemblages from surface samples in different vegetation sites were made clear for the interpretation of fossil phytolith assemblages in this study. As shown in Figure 5, transect modern phytolith assemblages showed the short dispersal distance (maximum 20 m) for Pinaceae type phytoliths supplied from the margin of *P. glehnii* stand. Also, as shown in Figure 3, Pinaceae type phytoliths characteristically occurred only from the surface samples collected in *P. glehnii* dominated stands, although with low percentage values (maximum 3.3%). Three pinaceous species (*P. glehnii*, *P. jezoensis* and *Abies sachalinensis*) exist on and around the Dorokawa Mire today. The conifer stands established on the mire are composed only of *P. glehnii* among them. The habitats of these three pinaceous species can be explained by their ecological features. *P. glehnii* can establish a community in a wet and oligotrophic environment (Tatewaki, 1943; Matsuda, 1989), while *A. sachalinensis* and *P. jezoensis* establish communities on fertile and mesic soil conditions (Kojima, 1983; Natsume, 1985; Nishijima *et al.*, 1997). Judging from the dispersal pattern of the Pinaceae type phytolith and ecological feature of *P. glehnii*, the Pinaceae type phytoliths from the sediment samples in the Dorokawa Mire indicate the existence of *P. glehnii* in the site.

On the other hand, through all surface samples from both conifer stands and hardwood stands with dense undergrowth of dwarf bamboo, the dwarf bamboo type phytoliths (sum of the *Sasa* or Bambusoideae type bulliform cells and Bambusoid type short cells) occurred with high percentage values (almost 50%), while the Pinaceae type phytoliths occurred only in the samples from the conifer stands with low percentage values (Fig. 3). Thus, the surface samples under the dense dwarf bamboo include considerable dwarf bamboo type phytoliths in spite of the samples from *P. glehnii* dominated stands. For this reason it seems that the abundance of Pinaceae trees is underestimated in comparison with that of dwarf bamboo in phytolith analysis.

Plate with verrucate-type phytoliths were also

found only in surface samples collected in hardwood stands. Therefore, this phytolith morphotype possibly indicates the existence of hardwood trees in the local site. However, this phytolith morphotype did not occur from fossil assemblages analyzed in this study. Thus, there is a possibility that the hardwood dominated stands which provide the plate with verrucate-type phytoliths have not been established in the core sampling sites since the early-Holocene.

With regard to pollen analysis, which is main tool for the palaeoecological study, it has following defects. There are some difficulties to define the pollen source area. Also, identification of Gramineae pollen, which includes dwarf bamboo, reed and many kinds of grasses, is restricted to the family level. On the other hand, phytolith assemblages reflect stand-scale vegetation composed of Pinaceae trees as mentioned above (Figs. 3 and 5). In addition, some types of Gramineae phytoliths can be identified at subfamily or genus level such as Pooideae, dwarf bamboo and reed. Thus, phytolith analysis can contribute to reconstruction of stand-scale vegetation composed mainly of Gramineae and Pinaceae species. The data from modern phytolith assemblages will make it possible to interpret fossil phytolith assemblages.

2. Vegetation history during the Holocene

The following vegetation history since the early-Holocene (*ca.* 12,000 cal BP to present) in the study sites on the Dorokawa Mire is reconstructed based on the results of phytolith records for the UDA1 and UDA2 cores (Fig. 6) and the modern analogue of phytoliths (Figs. 3 and 5). Summarized vegetation history is illustrated in Figure 7.

Early-Holocene (*ca.* 12,000 to 10,000 cal BP)

This period which can be correlated with the UDA2-1 zone is characterized by the occurrence of Festucoid type phytoliths derived from Pooideae grasses, and high percentages of elongate long cell and acicular hair cell phytoliths. The modern distribution pattern of Gramineae in the Japanese archipelago is characterized by two types of Gramineae subfamilies along the latitudinal gradient (Takeda *et al.*, 1985): the higher latitude with cool temperate zone is characterized by the distribution of the

Age (cal BP)	UDA1		UDA2	
	Vegetation	Phytolith zone	Vegetation	Phytolith zone
1,000	Dwarf bamboo - Pinaceae	UDA 1-4	Dwarf bamboo - Pinaceae	UDA 2-4
2,000	Dwarf bamboo			
3,000	poor phytoliths	UDA 1-3	Dwarf bamboo - Other Gramineae	UDA 2-3
4,000	Dwarf bamboo - Other Gramineae	UDA 1-2		
5,000		UDA 1-1	<i>Phragmites</i> - Dwarf bamboo	UDA 2-2
6,000	<i>Phragmites</i>			
7,000	- Dwarf bamboo			
8,000				
9,000			Pooideae	UDA 2-1
10,000				

Fig. 7 Summarized vegetation history at the *Picea glehnii* stands on the Dorokawa Mire during Holocene

Festucoideae (Pooideae) subfamily which produces the Festucoid type phytolith, and the lower latitude with warm temperate zone is characterized by the relative abundance of the Panicoideae subfamily which produces the bilobate type phytolith. In addition, Sase and Hosono (1999) reported that the Festucoid type phytolith occurred with relatively high percentages of elongate long cells and acicular hair cells among other types of phytoliths, because the Pooideae subfamily produces a large amount of both types of phytoliths. Our results from the UDA2-1 zone are in agreement with the phytoliths composition reported by the previous study mentioned above. According to the pollen records of the Kenbuchi basin, which is *ca.* 50 km from the Dorokawa Mire, a taiga forest composed of *Larix* and *Picea* which had dominated in the last glacial still remained around the site until early-Holocene (Igarashi *et al.*, 1993). Therefore, the occurrence of the Festucoid type phytolith during the UDA2-1 zone indicates the existence of Pooideae-dominated vegetation reflecting the cool climate.

The sediments of the UDA2-1 zone changed gradually from peaty clay to peat. This change and occurrence of Festucoid type phytolith imply the formation of herbaceous community dominated by Pooideae species (*e.g. Calamagrostis langsdorffii*) under wet conditions.

Early to mid-Holocene (*ca.* 10,000 to 5,000 cal BP)

In UDA2-2 zone (*ca.* 10,000 to 4,500 cal BP), phytolith morphotypes including Pooideae grasses decreased to several percentage values and the *Phragmites* type bulliform phytolith occurred. Also, in UDA1-1 zone (*ca.* 8,000 to 5,000 cal BP), the occurrence of *Phragmites* type bulliform phytolith was recognized. These results imply that the reed spread around the study sites during the early to mid-Holocene. Dwarf bamboo type phytoliths also began to occur in this period. However, low plant abundance of dwarf bamboo is estimated because of the low percentage values of dwarf bamboo type phytoliths and low accumulation rate of phytoliths (Fig. 6).

Late-Holocene (*ca.* 5,000 to 1,500 cal BP)

At both the UDA1-2 (*ca.* 5,000 to 3,000 cal BP) and UDA2-3 (*ca.* 4,500 cal BP to below Ta-a tephra layer) zones, the phytolith records are characterized by the absence of *Phragmites* type bulliform cells and the high percentages of dwarf bamboo type phytoliths. Takakuwa and Ito (1986) suggested that the dwarf bamboo invasion into the mire indicates the aridification of the mire. Therefore, the replacement of the *Phragmites* by dwarf bamboo indicates that the aridification of the mire progressed during this period. However, although there were high percentage values of the dwarf bamboo type phytoliths in these zones, the phytolith accumulation rates of these zones are actually lower than that of modern level (upper part of UDA1-4 and UDA2-4 zones), in which dwarf bamboo forms a dense community. Therefore, the distribution of dwarf bamboo during this period may be scattered.

It should be mentioned here that quite low concentrations of phytoliths from *ca.* 3,000 to 1,500 cal BP at the UDA1-3 zone. The cause of the low concentrations of phytoliths may be the development of a plant community which produced no phytoliths. At the UDA1-3 zone,

the peat with plant materials was composed mainly of fragments of *Sphagnum* sp. Therefore, *Sphagnum* covered vegetation would have been established on the UDA1 site during this period. However, at the upper part of the UDA 2-3 zone corresponding to the UDA1-3 zone, the dwarf bamboo type phytoliths occurred continuously in spite of the low phytolith accumulation rate. Thus, the differences of phytoliths composition between the UDA1 and UDA2 sites may indicate the differences of local vegetation features.

After ca. 1,500 cal BP

At the beginning of the UDA1-4 zone (ca. 1,500 cal BP) and of the UDA2-4 zone (below Ta-tephra layer : older than ca. 200 cal BP), dwarf bamboo increased abruptly and has been sustained to the present. Moreover, Pinaceae type phytoliths began to occur at both the mid part of the UDA1-4 zone (ca. 1,000 cal BP) and the beginning of the UDA2-4 zone. Taking into account the ecological features of pinaceous trees mentioned above, the Pinaceae type phytoliths extracted from the UDA1-4 and UDA2-4 zones indicate the appearance of *P. glehnii*. Therefore, *P. glehnii* trees would have existed at least ca. 1,000 cal BP in the study sites.

3. Dynamics of dwarf bamboo and establishment of *Picea glehnii* stands

As shown in Figure 6, Pinaceae type phytoliths occurred continuously from the mid part of the UDA1-4 zone (ca. 1,000 cal BP) and the beginning of the UDA2-4 zone (older than ca. 200 cal BP). It indicates that the appearance of *P. glehnii* was not temporary but successive on the study sites. Therefore, the *P. glehnii* stands would have been established in the study sites by ca. 1,000 cal BP at least.

Also, it should be pointed out here that the Pinaceae type phytoliths have been detected in the upper part of the UDA2-3 zone (ca. 2,700 cal BP). The occurrence of the Pinaceae type phytoliths at this time possibly reflects the temporary invasion of *P. glehnii* on the UDA2 site. The Pinaceae type phytoliths occurred continuously although with low frequencies from the beginning of the UDA2-4 zone. Therefore, the time of the establishment of *P. glehnii* stand in the UDA2 site may correspond to the boundary between the UDA2-3 and UDA2-4 zones.

Although dwarf bamboo began to invade into the study sites at ca. 5,000 cal BP (beginning of the UDA1-2 and UDA2-3 zones), the density of dwarf bamboo in that time was lower than that during the period between ca. 1,500 cal BP and present, because of the relative low phytolith accumulation rates in the UDA1-2 and UDA2-3 zones (right hand diagram in Fig. 6). Afterwards, however, dwarf bamboo increased abruptly at the beginning of the UDA1-4 zone and of the UDA2-4 zone. Also, the Pinaceae type phytoliths occurred continuously from the mid part of the UDA1-4 zone and the beginning of the UDA2-4 zone. Consequently, the *P. glehnii* dominated stands were established at the same time or a little bit later when the dwarf bamboo increased abruptly in the study sites. It indicates that the *P. glehnii* stands would have had dense undergrowth of dwarf bamboo since the establishment of the stands.

It can be summarized for the establishment of the *P. glehnii* stands with dense undergrowth of dwarf bamboo as follows. Dwarf bamboo began to invade into the study sites at ca. 5,000 cal BP owing to the aridification of the mire. After ca. 1,000 cal BP, *P. glehnii* invaded into the study sites where the dwarf bamboo had been dominant. Then, the *P. glehnii* stands with dense undergrowth of dwarf bamboo has been established. In this study, we made clear by the phytolith analysis that *P. glehnii* stands had not been established before the establishment of dwarf bamboo thickets. It suggests that the regeneration of *P. glehnii* occurred under the dominance of the dwarf bamboo. At present, establishment of almost seedlings and saplings of *P. glehnii* on the Dorokawa Mire are restricted on fallen logs or stump area where the coverage of dwarf bamboo is low. The dense undergrowth of dwarf bamboo has negative effects on regeneration of *P. glehnii*, because the dwarf bamboo thickets form dark conditions and thick litter accumulation (Makita, 1992 ; Maruyama *et al.*, 2004). Therefore, taking our findings into consideration with the regeneration behavior of *P. glehnii*, the fallen log regeneration by some disturbances would have been continued in these stands. The *P. glehnii* stands with dwarf bamboo understory are considered to have been maintained since ca. 1,000

cal BP on the study sites by this way of regeneration.

As noted above, this study demonstrated that the phytolith analysis is a useful method for reconstructing the stand-scale vegetation with dwarf bamboo understory. Although the phytolith records of this study reflect the local vegetation history at the *P. glehnii* stands, a combination of the phytolith data and pollen data from future studies will be able to offer both the local and regional vegetation changes in and around the Dorokawa Mire.

V. Conclusion

This study clarified the Holocene vegetation history in the *P. glehnii* stands on the Dorokawa Mire, with special focus on the dynamics of the Gramineae, which includes dwarf bamboo, and the establishment of *P. glehnii* stands based on the modern and fossil phytolith assemblages. Modern phytolith assemblages show that the short dispersal distance of the Pinaceae type phytolith (maximum 20 m). Also, the occurrence of this phytolith morphotype indicates that the existence of *P. glehnii* in the study site. Fossil phytolith assemblages show that the Pooideae-dominated vegetation, which reflects the cool climate, distributed during the early-Holocene (*ca.* 12,000 to 10,000 cal BP). The low-moor with *Phragmites* (reed) spread on the study sites from the early to mid-Holocene (*ca.* 10,000 to 5,000 cal BP). The reed was replaced by dwarf bamboo at *ca.* 5,000 cal BP. The *P. glehnii* dominated stands would have been established at the same time or a little bit later when the dwarf bamboo formed dense community in the study sites (*ca.* 1,000 cal BP). Some disturbances probably have provided suitable sites, such as fallen logs, for regeneration of *P. glehnii* under the dwarf bamboo thickets.

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北海道北部泥川湿原のアカエゾマツ林域における 完新世の植物珪酸体群集の変遷

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〔要 旨〕

北海道北部の泥川湿原上に成立するアカエゾマツ林および落葉広葉樹林内から採取した表層試料，ならびにアカエゾマツ林内で採取した完新世の堆積物試料を用いて植物珪酸体分析を行い，当湿原におけるササを中心としたイネ科植生の変遷，およびアカエゾマツ林の成立時期について検討した．堆積物の植物珪酸体分析の結果，約12,000～10,000年前には，泥川湿原上には寒冷気候下に分布するイチゴツナギ亜科が生育する植生が成立していた．その後約10,000～5,000年前には，ヨシが生育する湿潤な環境が広がっていたことが推測された．約5,000年前頃から，調査地周辺ではヨシに代わってササが進入

を開始するが，この時期のササの分布はまだ散在する程度であった．その後約1,500年前以降になるとササが急増を始め，それとほぼ同時期かやや遅れてアカエゾマツの侵入が認められた．表層試料の分析から，アカエゾマツに由来するマツ科型珪酸体はきわめて局所的なアカエゾマツの存在を反映することが明らかとなった．この結果と堆積物試料の分析結果を組み合わせると，調査地周辺におけるアカエゾマツ林の成立時期はおおよそ1,000年前頃であると推測された．また，その頃からすでにアカエゾマツ林は現在と同様なササ型林床を伴っていたと考えられた．

キーワード：アカエゾマツ林分，完新世，ササ，植物珪酸体，表層試料

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