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Effects of volcanic activity on mire development: case studies from Hokkaido, northern Japan

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Abstract: Field stratigraphy and macrofossil composition of four mires in Hokkaido, northern Japan, were investigated to test whether tephra deposition induces long-term vegetation shifts. Macroscopic tephras of known origin ranging from 0.5 to > 25 cm in thickness were found in two or more of the study sites, allowing correlation of the stratigraphic development of the mires. Major peat types and position of macroscopic mineral layers were determined in the field, and selected cores were analysed by quantitative macrofossil analysis. Some macrofossil groups and the content of unidentifiable organic matter showed changes in the vicinity of tephra layers, but they did not indicate a clear response pattern of the vegetation or the decomposition dynamics of plant material. Mosses were expected to be most strongly affected by tephra deposition, but even in cases where tephra fell on *Sphagnum*-dominated vegetation, no fundamental shifts to new plant communities were found. This suggests that disturbance by widespread tephras less than 10 cm thick did not alter site conditions sufficiently to induce shifts in the peat-forming plant communities, or short-term changes did not become manifest in the macrofossil record. A correlation between tephra deposition and vegetation change from nutrient- and mineral-poor bog communities to richer fen communities that had been postulated by some authors was not found at our study sites.

Key words: Tephra, macrofossils, peat stratigraphy, mire development, vegetation shifts, resilience, Hokkaido, Japan, late Holocene.

Introduction

Volcanic influence on structure and species composition of vegetation in the vicinity of eruptive vents is well documented. Areas affected by lateral blasts, flow deposits or thick tephra (aerially transported volcanic ejecta) layers will either go through a process of primary succession, or secondary succession leads to plant communities that often differ considerably from those that were found prior to the event (eg, Bilderback, 1987; Tsuyuzaki, 1997; Zobel and Antos 1997; Titus *et al.*, 1999). The effects of thinner, distal tephra fallout are less obvious, but a number of studies have associated volcanic ash deposition with vegetation change, in particular in mires or lake basins (eg, Tokito, 1915; Yamada, 1942; Blinman *et al.*, 1979; Blackford *et al.*, 1992; Dwyer and Mitchell, 1997; Wells *et al.*, 1997; Edwards and Craigie, 1998). Shifts of plant communities or changes in abundance of plant species or groups with certain ecological traits have been linked to tephra impact, and physical as well as chemical effects have been suggested as underlying mechanisms. Physical effects are limited to areas where tephra is sufficiently thick to bury plants or form surface crusts (Mack, 1987; Grishin *et al.*, 1996; Zobel and Antos, 1997; Hotes *et al.*, 2004), but chemical effects of volcanic gases, aerosols, compounds adhering to tephra or dissolved in precipitation have the potential to affect much larger regions (Thorarinsson, 1979; Grattan and Charman, 1994; Hall, 2003; Grattan, 2005; Payne and Blackford, 2005). More or less severe damage to living organisms and decline of biodiversity has often been reported in the wake of volcanic eruptions, but it has also been pointed out that certain taxa may benefit from the disturbance in the medium or long term. The abundance of 'fen species' in Japanese ombrotrophic mires was attributed to leaching of minerals from tephra by Wolejko and Ito (1986) and Damman (1988). Successional patterns leading from nutrient- and mineral-poor to richer communities following tephra deposition and subsequent recovery of oligotrophic conditions were deduced from field observations of peat profiles in Hokkaido (Tokito, 1915; Shoji *et al.*, 1966),

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and in some cases they were repeated at several tephras within the same profile (Yamada, 1942; Tachibana and Sato, 1983).

In contrast to these findings that suggest deterministic vegetation change induced by tephra deposition, much of the fossil record concerning tephra effects hitherto has been equivocal, and processes unrelated to volcanic disturbance (or only indirectly linked to it) may have generated the vegetation changes that were deduced from pollen or macrofossil analyses (Birks, 1994; Hall *et al.*, 1994; Charman *et al.*, 1995; Hotes *et al.*, 2001; Bogaard *et al.*, 2002; Edwards *et al.*, 2004).

The aim of this study was to clarify whether tephra deposition during the late Holocene induced long-lasting vegetation changes in mires in Hokkaido. This would have interesting theoretical implications as such shifts might indicate the existence of alternative stable states in mire vegetation that have been described for a number of aquatic and terrestrial ecosystems (Adema *et al.*, 2002; Folke *et al.*, 2004). Field stratigraphical investigations and macrofossil analyses were carried out for this purpose.

Methods

Study sites

Four lowland mires in Hokkaido, northern Japan, were selected as study sites: Utonai, Kimonto, Bekanbeushi and Sarobetsu (Figure 1A). Their characteristics are summarized in Table 1. The criteria used in the selection were the location relative to active volcanic centres, the resulting frequency and intensity of volcanic impact and the degree of anthropogenic influence on the vegetation. The mires are located in different climatic regions: the three sites along the Pacific coast have relatively little snow cover in winter, summer temperatures decline from west to east. Sarobetsu, on the other hand, receives high snowfall and has relatively high summer temperatures (Sapporo Kanku Kishodai, 1993; Yabe and Uemura, 2001). All sites were affected by the Jomon transgression that peaked *c.* 5000 BP (Sakaguchi *et al.*, 1985; Ohira *et al.*, 1994); peat formation started after the sea retreated from the coastal plains. Thirteen marker tephras have been deposited mostly in the south and east of Hokkaido during the Late Holocene (Table 2). They were produced by the volcanoes Koma, Usu, Tarumae, Meakan and Mashu in Hokkaido and Baegdusan in the Korean peninsula (Figure 1A,B; Table 2). Land reclamation for agriculture in Hokkaido started in the late 1800s, and the hydrology at Utonai, Kimonto and Sarobetsu may have been influenced by drainage at the mire margins. However, water levels were close to the ground surface at the coring sites; Bekanbeushi is considered to be in a pristine state.

Field and laboratory methods

Samples were collected between 1999 and 2002 using two types of corers: a 1-m monolith corer (cross-section 8 cm × 8 cm) and a Russian-type peat sampler (chamber length 50 cm, diameter 5 cm). In each mire, sites with the lowest level of human disturbance (no significant drainage, no grazing of livestock, no peat cutting) and vegetation indicative of oligotrophic conditions were chosen for coring. Main macrofossil types and positions of macroscopic mineral layers were determined in the field. Tephras visible to the naked eye are referred to as ‘macrotephras’. Samples in which no tephra was visible, but in which more than 3% tephra were found during macrofossil analysis (see below), were tentatively called ‘microtephras’. Eight cores were taken at Utonai, three at Kimonto, eight at Bekanbeushi and four at Sarobetsu. An open profile exposed in a drainage ditch near Kimonto was also investigated.

Eight cores were chosen for quantitative macrofossil analysis. They represent the most oligotrophic sites with the lowest vegetation in each mire where the greatest potential impact of tephra deposition was expected. At Bekanbeushi, further cores from the mire margin were also investigated to test whether different vegetation types show different responses to volcanic disturbance. Contiguous 1-cm slices of the core from Utonai and of the tephra-bearing layers from Kimonto were investigated. Core sections without macroscopic tephras from Kimonto were subsampled at 5-cm intervals. At Bekanbeushi, 2-cm intervals were chosen in the tephra-bearing layers and 5-cm intervals in sections without macroscopic tephras. At Sarobetsu, all subsamples were taken at 5-cm intervals. A simplified method based on the techniques of Janssens (1983) and Barber *et al.* (1994) was used: 1 cm^3 of material was wet-sieved through a 125 μm mesh. Fine particles that passed the sieve were collected and checked for volcanic glass shards. The material retained was transferred to a petri dish and dispersed evenly to form a thin, homogeneous layer. The petri dish was placed on a 1 cm × 1 cm square grid under an incident light microscope, main macrofossil types were identified, and their cover was estimated in 15 randomly chosen grid cells. The following cover classes were used: < 1%, 1–5%, 5–10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80%, 80–90%, 90–100%. The cover of unidentifiable organic material (UOM), charcoal fragments and mineral particles was estimated in the same way. If necessary, macrofossils were removed and mineral particles were redispersed to achieve a thin, homogeneous layer. Because of the cover classes used, changes in abundance of a macrofossil type between samples had to be greater than 10% (or greater than 5% if the total abundance was less than 10%) in order to be detected. The relative proportions of the sample components were calculated based on the cover sum of all constituents. Almost all samples contained some tephra particles; therefore, a tephra content of 3% was arbitrarily chosen to separate tentative microtephras from ‘background noise’ tephra that could have been relocated after primary deposition or might have been incorporated while handling the samples. At least 50 moss fragments were determined to the lowest taxonomic level possible in each sample. Nomenclature follows Kankyocho (1987) for vascular plants, Daniels and Eddy (1985) for *Sphagnum* and Noguchi (1987–1994) for Bryopsida.

In order to provide a quantitative measure of the rate of change in overall macrofossil composition between samples, the quantitative Sorensen dissimilarity coefficient (software package PC-Ord; McCune and Mefford, 1995) was used. Mineral components and unidentifiable organic matter were not included in the calculation. The relation between tephra thickness and changes in abundance of monocots, *Sphagnum* and unidentifiable organic matter (UOM) was also investigated in separate regression analyses. Monocots and *Sphagnum* represent dominant macrofossil types that were expected to show opposite responses to tephra deposition (*Sphagnum* decrease, relative monocot increase), and UOM should increase in the vicinity of tephras based on the hypothesis that tephra deposition accelerates decomposition of plant material below and /or above the layer.

Macroscopic tephra layers were identified according to their stratigraphical position, grain size and colour using published profiles from the literature as references. The identity of macrotephras from Bekanbeushi was verified by Y. Nakamura,

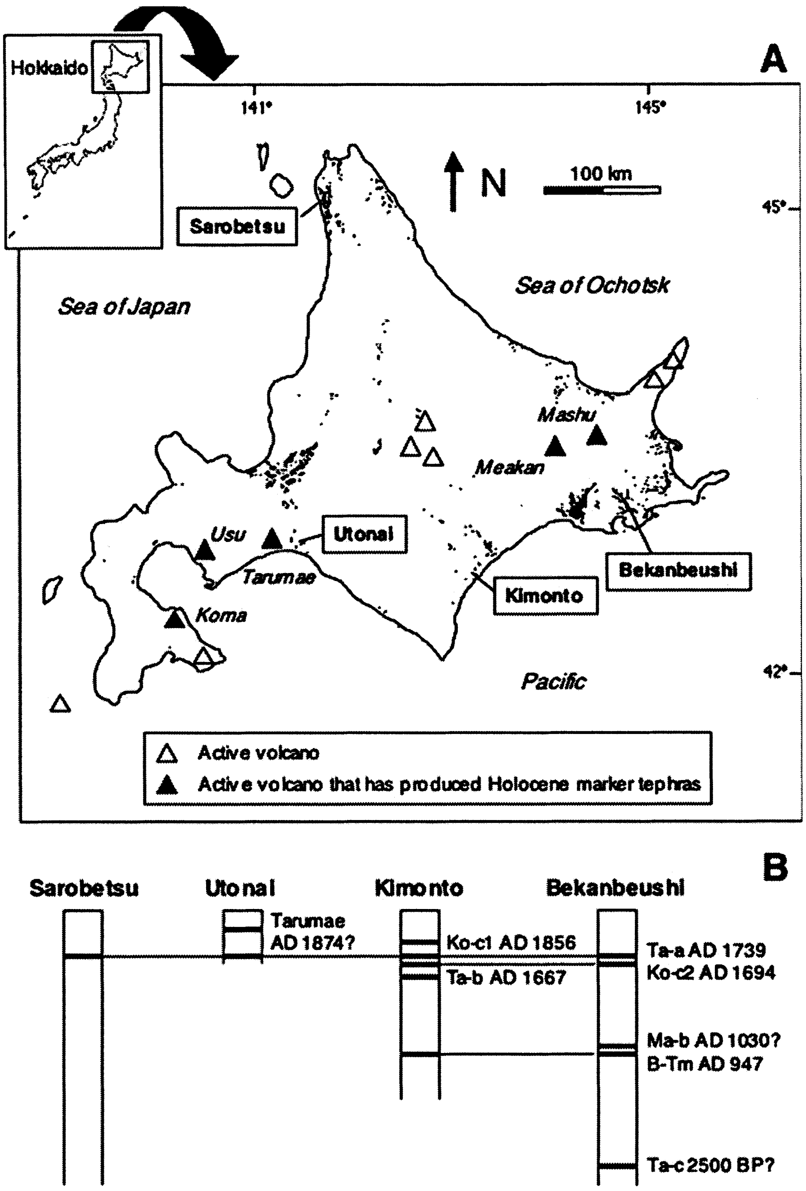

Figure 1 (A) Distribution of main active volcanoes in Hokkaido and location of study sites. Names of volcanoes that produced widespread marker tephras during the Holocene are given in italics. Names of mires in which cores were taken are indicated in boxes. Shaded areas represent the original distribution of mires after Sakaguchi (1979). (B) Diagrammatic summary of the macroscopic tephras in the peat profiles of each mire. Further details on tephras are given in Table 2

Graduate School of Environmental Earth Science, Hokkaido University, Sapporo, based on the refractive indices of volcanic glass shards.

Results

Field survey

A total of 38 macroscopic tephras were found in the 21 stratigraphic sequences investigated at Utonai, Kimonto and Bekanbeushi. None were detected at Sarobetsu. The number, thickness and grain size of the tephra layers differed among the study sites, and there was also considerable variation between different cores taken at the same mire. Two macrotephras were found at Utonai and five each at Kimonto and Bekanbeushi (Figure 1B). A tephra that probably originated from the AD 1874 eruption of Tarumae volcano occurred at Utonai, and Ko-c1 from Koma volcano (AD 1856) formed the uppermost tephra at Kimonto. The tephra Ta-a (Tarumae volcano, AD 1739) was found at Utonai, Kimonto and Bekanbeushi, and glass shards from this eruption have recently been identified at Sarobetsu (Sato *et al.*, 2004). Ko-c2 of Koma volcano (AD 1694) occurred directly below Ta-a at Kimonto and Bekanbeushi; B-Tm of Baegdusan volcano (AD 947) was also found at these two sites. At Bekanbeushi, a tephra that was tentatively correlated with Ma-b (Mashu volcano, AD 1030) was located above B-Tm. The thickness of macroscopic tephras ranged from 0.5 to more than 25 cm. The mean tephra thickness at Utonai was 8.5 cm (standard deviation (SD) ±8.58 cm, $n = 4$), at Kimonto it was 4.4 cm (SD±4.2 cm, $n = 9$), and at Bekanbeushi it was 3.0 cm (SD ±2.2 cm, $n = 18$). Ta-a at Utonai consisted of very fine gravel-sized particles, whereas all other tephras consisted of sand- or silt-sized particles.

Average peat accumulation rates calculated from the thickness of peat layers between tephras were highest at Bekanbeushi (1.6 mm/yr), lower at Utonai (1.2 mm/yr) and lowest at Kimonto (0.5 mm/yr). No estimate can be given for Sarobetsu as no macrotephra was found, but if a layer containing tephra

Table 1 Characteristics of the study sites

	Utonai	Kimonto	Bekanbeushi	Sarobetsu
Location	42°42′ N 141°44′ E	42°36′ N 143°29′ E	43°10′ N 144°50′ E	45° 5′ N 141° 42′ E
Altitude (m)	4	8	5	8
Area (ha)	1129	232	8320	6658
Annual mean temperature (°C)	7.5	5.3	5.4	5.9
Annual precipitation (mm)	1227	1177	1153	1087
Vegetation types	*Phragmites australis* – *Calamagrostis langsdorffii* community, *Alnus japonica* community, *Sphagnum* spp. – *Myrica gale* community	*Carex lasiocarpa* var. *occultans* community, *Phragmites australis* community, *Alnus japonica* community	*Ledum palustre* var. *diversipilosum* – *Sphagnum fuscum* community, *Scheuchzeria palustris* – *Rhynchospora alba* community, *Alnus japonica* community	*Sphagnum papillosum* – *Carex middendorffii* community
Maximal hummock height (cm)	30	0	40	5
Mean water level (SD) (cm)	−0.6–1.3 (3.3–3.8)	No data	−30–5	−17.9– −8.6 (3.6–6.6)
Mean pH	6.1–7.0	No data	4.3–6.3	4.7
Mean EC (μS/cm)	95–138	No data	15–85	55
Trophic status	Minerotrophic	Minerotrophic	Ombrotrophic	Ombrotrophic
Number of cores/profiles[a]	R: 5; B: 3; P: 1	R: 1; B: 2; P: 1	R: 1; B: 7	R: 3; B: 1
Maximum peat depth (cm)	50	140	398	588
Number of macroscopic tephras	2	5	5	0

[a] R, Russian type peat sampler core; B, monolith sampler core; P, open profile.

Mire areas were taken from Fujita *et al.* (1997), climate data from Sapporo Kanku Kishodai (1993); main vegetation types, water levels, pH and electric conductivity are based on own observations and Tachibana (2002), Yabe (1989; Utonai) and Asada (2002; Bekanbeushi).

particles found during macrofossil analysis (see below) represents the tephra Ta-a, the peat accumulation rate in the uppermost layer was 0.9 mm/yr.

Mineral layers other than tephra occurred in the peat deposits of Bekanbeushi and Sarobetsu mires. A layer at about 20 cm depth near the margin of Bekanbeushi mire consisted of whitish pumice that probably originated from the adjacent slope, and a silt layer between 3.5 and 4.0 m depth in Sarobetsu mire was most likely formed by overbank flood sediments of a river.

The peat deposits at Utonai and Kimonto were dominated by monocot remains except for hummocks at Utonai that

Table 2 Holocene marker tephras in Hokkaido, northern Japan, based on Arai *et al.* (1986), Machida and Arai (1992), Takahashi and Kobayashi (1998), Hayakawa (1999) and Nakamura *et al.* (2002)

Age	Scale	Source volcano	Code	Direction	Distance[a]	Area[b]
1929	AD	Komagatake	Ko-a	ESE	>25	?
1874[c]	AD	Tarumae	–			
1856	AD	Komagatake	Ko-c1	ENE	>10	?
1739	AD	Tarumae	Ta-a	EEN	>270	4
1694	AD	Komagatake	Ko-c2	ENE	350	4
1667	AD	Tarumae	Ta-b	E (N)	>170	4
1663	AD	Usu	Us-b	E (S)	200	3–4
1640	AD	Komagatake	Ko-d	NW	120	4
1000?	AD	Meakan?	Me-a	?	?	?
900–1000 (1030)	AD	Mashu	Ma-b	N	>80	3–4
900–1000 (947)	AD	Baegdusan	B-Tm	E	>1500	
300	AD	Komagatake	Ko-e	SE–SW	>55	3
2500–3000[d]	BP	Tarumae	Ta-c	E (N)	>80	4
3000–4000	BP	Komagatake	Ko-f	E	>30	3
5000–6000	BP	Komagatake	Ko-g	E	>30	3
7000[e]	BP	Mashu	Ma-f	ESE	100	4
8000–9000	BP	Tarumae	Ta-d	E	>200	3–4
9000–10000	BP	Mashu	Ma-1	NE–SE	80	4

[a] Distance is given in km.

[b] Area is given as logarithm to the base 10.

[c] This eruption did not produce a widespread marker tephra, but it is likely that its deposits reached Utonai.

[d] Dating of some peat samples from Bekanbeushi mire below a tephra that is probably Ta-c yielded lower ages of 2300–2960 BP (Kanda *et al.*, 2001; Igarashi, 2002).

[e] Between 6500 and 7200 four further tephras were issued from the Mashu caldera (Ma-g to Ma-j).

contained layers rich in Pteridophyta and had a top layer made up by *Sphagnum* spp. In the centre of the raised part of Bekanbeushi mire, 2.6 m of *Sphagnum* peat overlay 1.4 m of monocot peat. The top 0.5 m at the study site in Sarobetsu mire also consisted of *Sphagnum* peat, and deeper layers were dominated by monocots.

Except for a transition from monocot peat to *Sphagnum* peat that occurred at an indistinct mineral layer (it could not be clarified whether it was an airfall tephra or a fluvial deposit) near the base of a hummock at Utonai, no shifts in peat type were found at tephra layers during the field survey.

Macrofossil analysis

Changes in macrofossil composition during the development of the four mires are shown in Figures 2–5. At Utonai (Figure 2), monocots including up to 50% *Phragmites* dominated following the deposition of the Ta-a tephra (AD 1739). A thin tephra at 28 cm depth that probably originated from the AD 1874 eruption of Tarumae volcano did not induce major vegetation change, but an isolated branch with leaves of *Sphagnum* section Acutifolia was found directly above the layer. More than 3% tephra > 125 µm were found in most samples in the monocot peat layer. After a sudden shift to pteridophyte dominance the amount of tephra decreased below the 3% threshold, although all samples contained tephra particles > 125 µm as well as fine mineral particles. The change to *Sphagnum* vegetation, represented by *S. subfulvum* at the surface, was not related to a peak in tephra content.

The monolith from Kimonto was dominated by monocot remains throughout; however, considerable amounts of *Sphagnum palustre* and a pleurocarpous bryophyte occurred during a phase before and shortly after the deposition of the B-Tm (AD 947) tephra (Figure 3). Ericaceae appeared before B-Tm was deposited; they increased sharply after this tephra fell and were an important peat component from 84 to 54 cm depth. Branch leaves of *Sphagnum* cf. *cuspidatum* occurred in and above the tephra Ta-b (AD 1667). Above another tephra – possibly Ta-a (AD 1739) – *S.* cf. *cuspidatum* showed a peak but disappeared before the youngest tephra (probably Ko-c1, AD 1856) was deposited.

Only three discrete tephras could be distinguished between 35 and 10 cm depth, although four (Ta-b, Ko-c2, Ta-a and Ko-c1) were expected (Figure 1). It is likely that Ko-c2 was too thin or too close to either Ta-b or Ta-a to be recognized as a separate layer. Above Ta-b, all samples contained tephra particles > 125 µm (0–21 cm depth), and grains of this size class were also found at 44 cm, 60 cm, 82–86 cm (B-Tm tephra), 95 cm and 100 cm. They formed less than 3% of the sample volume (except for 83–84 cm) and therefore were not classified as tentative microtephras. Fine mineral particles < 125 µm were present in all samples except between 64 and 80 cm and at 94 cm depth.

Five macrotephras were identified at Bekanbeushi (Figures 1B and 4); tephra particles at the boundary between the basal mineral layer and the peat deposit may be relocated secondary sediments. The first unambiguous tephra (371–378 cm) fell

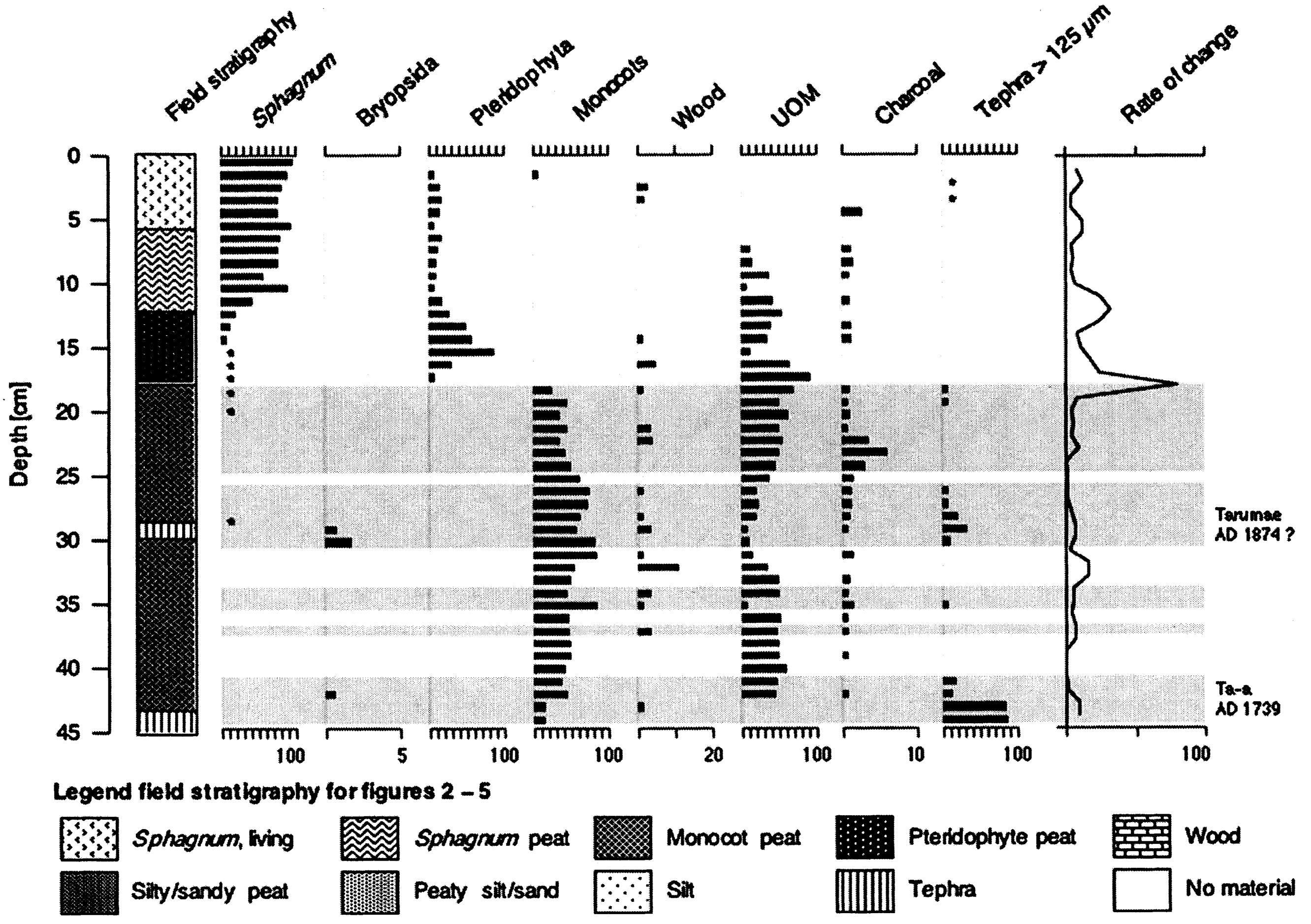

Figure 2 Field stratigraphy and macrofossil diagram of monolith B1 from Utonai. Contiguous 1-cm samples were investigated. Relative abundance of sample components is given in percent. The rate of change is given as Soerensen dissimilarity coefficient in percent. Samples with a shaded background contained more than 3% tephra > 125 µm. Asterisks indicate occurrence of a sample component that was too scarce to be displayed as a bar

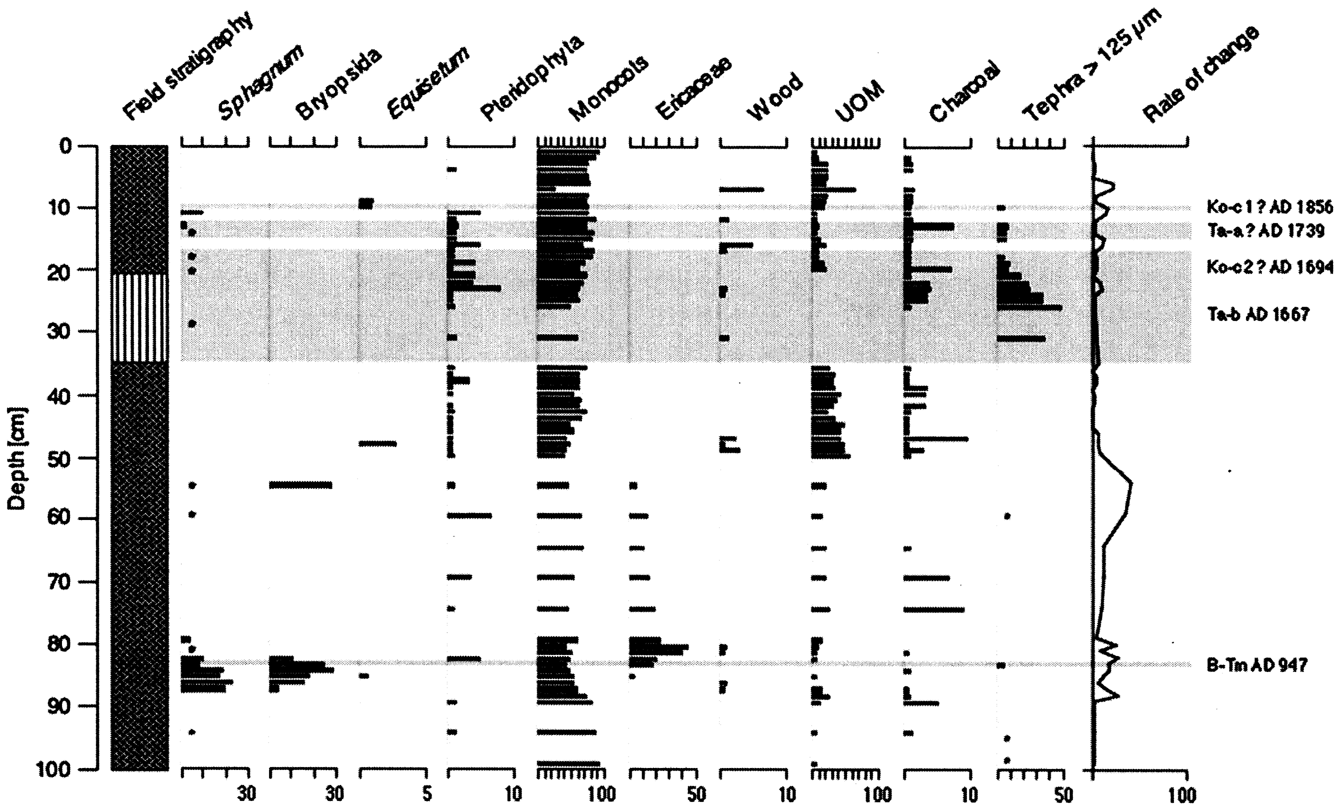

Figure 3 Field stratigraphy and macrofossil diagram of monolith B2 from Kimonto. Samples were taken at 5-cm intervals, but in the sections 0–26 cm, 35–50 cm and 79–90 cm, contiguous 1-cm samples were analysed. Relative abundance of sample components is given in percent. The rate of change is given as Soerensen dissimilarity coefficient in percent. Samples with a shaded background contained more than 3% tephra > 125 µm. Asterisks indicate occurrence of a sample component that was too scarce to be displayed as a bar

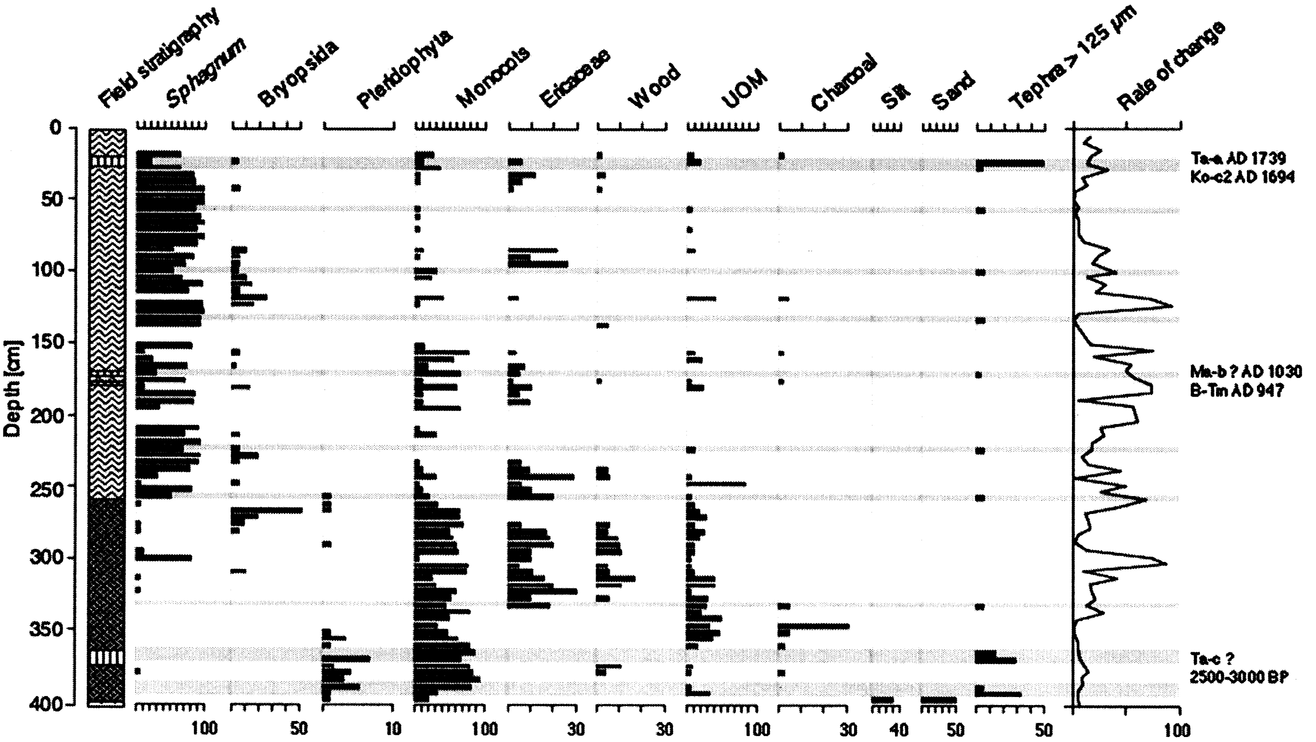

Figure 4 Field stratigraphy and macrofossil diagram of core R1 from Bekanbeushi. Samples taken at 5-cm intervals are shown (sections containing macrotephras were subsampled at 2-cm intervals, see text). Relative abundance of sample components is given in percent. The rate of change is given as Soerensen dissimilarity coefficient in percent. Samples with a shaded background contained more than 3% tephra > 125 µm

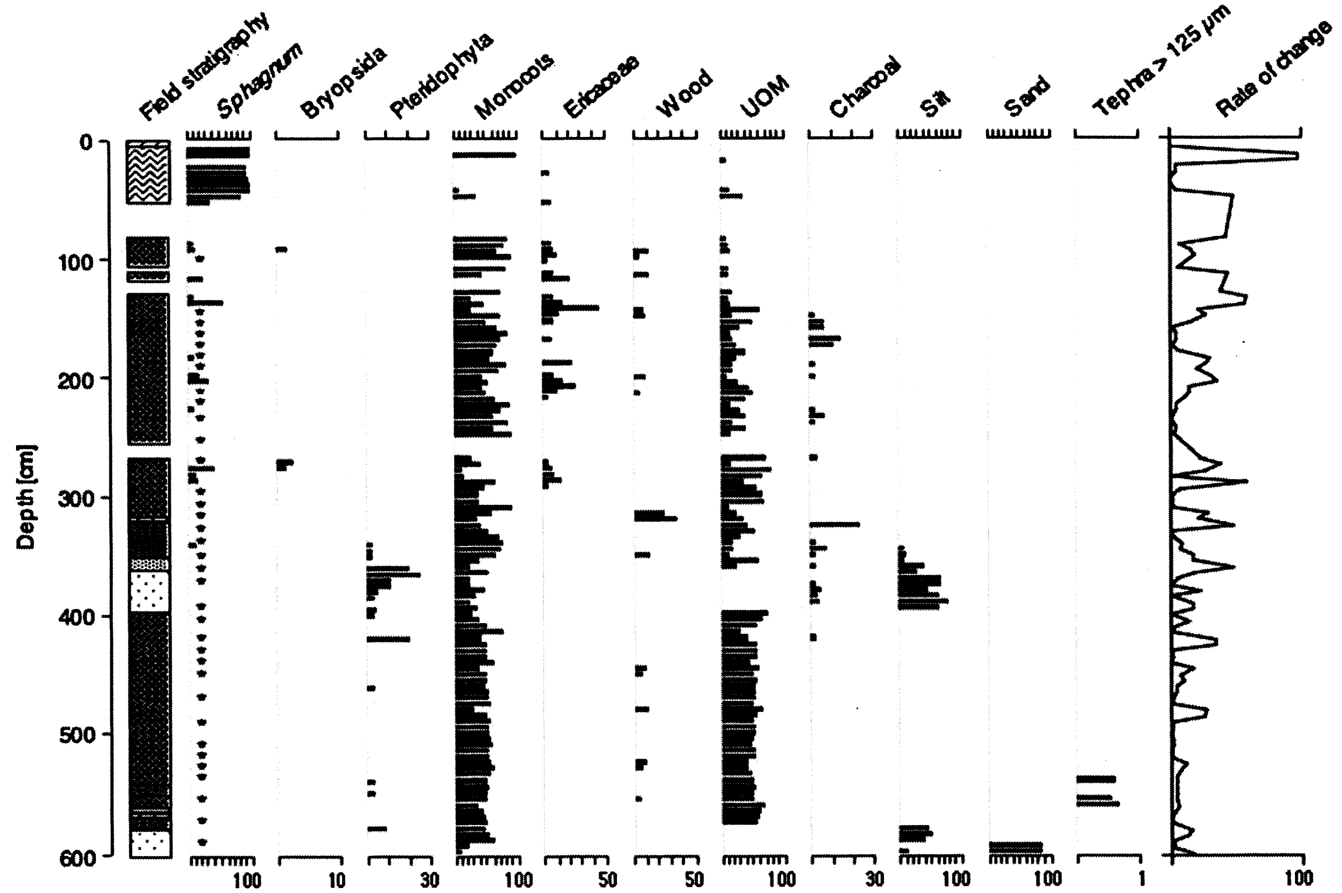

Figure 5 Field stratigraphy and macrofossil diagram of core R1 from Sarobetsu. Samples were taken at 5-cm intervals. Relative abundance of sample components is given in percent. The rate of change is given as Soerensen dissimilarity coefficient in percent. Asterisks indicate occurrence of a sample component that was too scarce to be displayed as a bar

early during mire development when the vegetation was dominated by monocots including *Phragmites*. It was tentatively correlated with the tephra Ta-c (2500–3000 BP). No distinct changes of bulk macrofossils occurred at this tephra, but *Phragmites* disappeared above it, whereas fern sporangia (cf. *Thelypteris*, not shown in Figure 4) counts increased from three directly below it to 199 at its upper boundary. The number fell to 151 at 2 cm above the tephra, and 44–61 sporangia were counted in the samples between 367 and 361 cm depth. The other four macrotephras were deposited on vegetation dominated by *Sphagnum* section Acutifolia, most likely *S. fuscum*. B-Tm (173–174 cm; AD 947) consisted of particles < 125 µm and therefore was not retained during sieving. It was separated from the overlying tephra which was tentatively correlated with Ma-b (AD 1030) by 1 cm of peat. *Sphagnum* section Acutifolia decreased directly above B-Tm, but increased through the 4-cm Ma-b layer (not visible in Figure 4 because of the 5-cm sampling interval). Monocots, Ericaceae and unidentifiable organic matter showed the opposite trend, although strong oscillations make it difficult to state clear changes. The tephras Ko-c2 (AD 1694) and Ta-a (AD 1739) formed a contiguous layer between 26 and 19 cm depth. *Sphagnum* cf. *fuscum* was reduced in the actual tephra layer, but recovered directly above it. Six samples with relatively high contents of glass shards were found that may represent microtephras. In three cases Ericaceae increased at such layers (at 355 cm, 260 cm (this one also coincided with the main shift from monocot to *Sphagnum* dominance) and 100 cm depth). A slight increase of unidentifiable organic matter occurred at tentative microtephras at 220 and 60 cm depth.

Sarobetsu mire was dominated by monocots during most of its development, but *Sphagnum* was present from the beginning of peat accumulation, and in the top 0.5 m it was the most abundant peat component (Figure 5). A few tephra grains > 125 µm were found at 30 cm, 35 cm, 45 cm and 100 cm, 540 cm, 555 cm and 560 cm. No changes in macrofossil composition coincided with these layers. All samples contained fine mineral particles < 125 µm, but the amounts were much lower than at the three sites in southern and eastern Hokkaido. It could not be clarified whether these represent material from airfall tephras, or whether they are of non-volcanic origin. Table 3 summarizes the changes found at tephra layers in the cores that were subjected to macrofossil analysis.

Tephra thickness did not influence the similarity of macrofossil composition of samples below and above tephras as expressed by the Sorensen dissimilarity coefficient (linear regression, $R^2 = 0.0003$, $p = 0.93$; $n = 28$), and there was no significant difference between tephras that fell on *Sphagnum*-dominated vegetation and those that fell on monocot-dominated sites (unpaired *t*-test, $t = -0.3$ $p = 0.73$; $n = 12$ (*Sphagnum*), $n = 16$ (monocots)). No significant differences were found either when comparing Sorensen dissimilarity coefficients of samples bracketing tephra layers with those of adjacent samples not separated by macroscopic tephra (unpaired t-test, $t = -1.7$ $p = 0.09$; $n = 28$ (bracketing tephra), $n = 280$ (no tephra)). The change rate of the abundance of the two main macrofossil types at tephra layers also showed no relation with tephra thickness (linear regression for *Sphagnum* spp., $R^2 = 0.004$, $p = 0.86$, $n = 11$; linear regression for monocots, $R^2 = 0.014$, $p = 0.73$, $n = 11$).

Table 3 Changes of macrofossil composition and unidentifiable organic matter (UOM) content at tephra layers in peat cores analysed for macrofossils

Location	Core no.	Depth (cm)	Thickness (cm)	Macro-/ microtephra	Macrofossil change	%	UOM change	%
Utonai	B1	18–24	6	Micro	Monocots −	50–1	+	44–92
					Pteridophyta +	0.6–5.1		
		26–31	5	Macro	Monocots −	84–61	+	12–37
Kimonto	B2	9–10	1	Micro	*Sphagnum cuspidatum* −	9.8–1.1	+	4.9–21
		12–15	3	Micro	*Sphagnum cuspidatum* +	0–1.1	−	20–5.6
		17–35[a]	18	Micro Macro	Monocots +	74–87	−	25–9.6
		83–84	1	Micro	*Sphagnum palustre* −	19–9.9	+	1–5
					Pleurocarpous moss −	29–9.9		
					Ericaceae +	1–20		
Bekanbeushi	R1	19–26[b]	7	Macro	*Sphagnum* sect. Acutifolia −	83–71	=	
					Monocots +	0.9–27		
					Ericaceae −	12–0.5		
		31–32	1	Micro	*Sphagnum* section Acutifolia – in tephra layer	82–36 – [80][c]	=	
		167–171	4	Macro	*Sphagnum* section Acutifolia +	9.3–72	=	
					Polytrichum sp. −	24–0.1		
					Monocots −	53–16		
		173–174	1	Macro	*Sphagnum* section Acutifolia −	69–1.5	=	
					Monocots +	11–78		
		254–255	1	Micro	*Sphagnum* section Acutifolia +	5.1–77	−	10–1
					Polytrichum sp. −	51–1		
					Ericaceae +	1–9.6		
					Monocots −	31–9.6		
		334–335	1	Micro	Monocots −	77–51	+	19–30
					Ericaceae +	0–10		
					Wood +	0–5.1		
		371–378	7	Macro	Monocots +	42–67	−	55–25
					Thelypteris +	2–7.2		
					Fern sporangia +	3–151[d]		
	B1	30–34	4	Macro	*Sphagnum* section Acutifolia – in tephra layer	83–0 – [80][c]	+	0.9–12
		[25–36][e]	[11]		Monocots+in tephra layer	7.3–62 – [3.3][f]		
	B4	62–65	3	Macro	*Sphagnum* section Acutifolia +	8.4–71	−	14–1
					Polytrichum sp. +	0.1–12		
		80–82	2	Macro	*Sphagnum* section Acutifolia −	51–8.4	+	3.4–14
		[75–81][e]	[6]		*Polytrichum* sp. −	20–0.1		
	B6	60–61	1	Micro	Monocots −	42–24	+	45–71
					Wood −	10–3.8		
		83–84	1	Macro	Monocots +	23–33	−	77–54
		[80–81][e]			Wood +	0.7–12		

[a] Probably two tephras: Ko-c2 (17–20 cm) and Ta-b (20–35 cm).

[b] Two tephras: Ta-a (19–23 cm) and Ko-c2 (23–26 cm).

[c] *Sphagnum* section Acutifolia cover increased to 80% in the next higher sample.

[d] Numbers represent counts, not cover.

[e] The numbers without brackets represent the boundaries of the tephra layer that were recorded during the field survey; those in brackets represent the boundaries that were found during macrofossil analysis in the laboratory.

[f] Monocot cover decreased to 3.3% in the next higher sample.

+ indicates increase, − decrease and = no change. Because of the cover classes used only changes > 10% (or > 5% if the total cover was < 10%) are included. Percentage cover data are given for the samples directly below and above the boundaries of tephra layers at Utonai and Kimonto. For Bekanbeushi, data of the closest samples that were taken at 2- or 5-cm intervals are shown. 'Macrotephras' are those that were recognized in the field, 'microtephras' are samples in which no tephra was discernible in the field, but > 3% tephra particles were found during macrofossil analysis.

Discussion

The changes in macrofossil composition and content of unidentifiable organic matter found in the vicinity of tephra layers did not show a clear response pattern to the disturbance (Table 3). Increases as well as decreases of macrofossil types occurred following tephra deposition, and neither the direction nor the magnitude of change were related to tephra thickness. Based on observations by Tokito (1915), Yoshii and Hayashi (1931), Suzuki (1961), Shoji *et al.* (1966), Dierssen (1982), and Yabe (1993) it was expected that *Sphagnum* would be reduced and vascular plants would increase after tephra fall. Re-establishment of oligotrophic, mineral-poor conditions was expected to take decades to centuries, leading to a phase of monocot peat accumulation that would eventually be followed again by *Sphagnum* peat deposition. The lack of such a simple pattern could be caused by the variable characteristics of disturbance by tephra as well as by other factors that are known to influence vegetation dynamics in mires.

Effects of tephra deposition

In order to assess the relative importance of tephra deposition in plant succession and mire development, the mechanisms by which tephra can influence plants on different spatial and temporal scales have to be clarified. Physical and chemical characteristics of the tephra as well as attributes of the ecosystems on which it falls (physiognomy and species composition of the vegetation, phenology, nutrient status, acid neutralization capacity, etc.) will determine whether any changes occur that can be traced in the fossil record.

Physical effects of tephra on plants depend both on tephra thickness and grain size (Mack, 1987; Zobel and Antos, 1997; Hotes *et al.*, 2004). Damage to plants increases with increasing thickness of the tephra layer and with decreasing grain size. Tephra thickness and grain size normally decrease exponentially with increasing distance from the vent, although deviations from this pattern are often observed because of differential settling velocities of tephra particles in the plume (Sparks *et al.*, 1997). Fine tephra particles that can be transported over great distances can penetrate small cavities and form coatings on horizontal as well as vertical surfaces (Martin, 1913), and they can damage plants more strongly than coarse particles (Mack, 1987; Hotes *et al.*, 2004). Such coatings impede photosynthesis and gas exchange and, depending on the phenology, reproductive success can be disrupted, which may affect annual plants in particular (Blinman *et al.*, 1979; Mack, 1987). However, these mechanisms are effective only for relatively short periods of time (days to months) until ash is removed from plant surfaces by wind and rain, and they are not likely to leave a detectable signal in the macrofossil record of mires where perennial plants are dominant.

Where tephra forms thicker layers it can cause immediate vegetation change by reducing the cover of small plants through burial (Zobel and Antos, 1997). The minimum tephra depth for such effects was 1 cm in steppe communities, and severe damage of the moss layer was also reported from forests that received similar amounts (Mack, 1987). Whether burial under tephra induces lasting vegetation change depends on the ability of plants to grow through the mineral layer or to establish themselves on the new surface from propagules. In primary successional substrates, stochastic processes of propagule dispersal and seedling establishment are important in plant community development, whereas in secondary successional substrates site conditions are of greater importance (Titus *et al.*, 1999). Erosion of tephra layers plays an important role in this context as it can reduce tephra thickness and facilitate recovery of plants from seeds or belowground organs (Tsuyuzaki, 1987; Tsuyuzaki and Goto, 2001). In the case of a *Sphagnum* lawn community, recovery of the original vegetation by growth through the tephra took less than a year where 1 cm of coarse sand tephra was applied in a field experiment, and although damage to the moss layer increased dramatically with application of 3 cm and 6 cm of tephra, eventual recovery of the vegetation type before the disturbance was predicted (Hotes *et al.*, 2004). New results from a repeated survey of the plots in 2005 suggested, however, that vegetation structure may be different with a higher cover of the dwarf shrub *Myrica gale* (S. Hotes, unpublished data, 2005). Aquatic biota and vegetation of depressions in the landscape tend to be more strongly affected by tephra than communities in surrrounding uplands (Blinman *et al.*, 1979; Lotter and Birks, 1993; Edwards and Craigie, 1998), probably because of secondary accumulation of tephra particles. Relocation of tephra may also cause small-scale variation in mires with a hummock-and-hollow microtopography (Lees and Neall, 1993). In even areas, lateral relocation of tephra particles is less likely, but downward transport of silt-sized particles has been observed in a *Sphagnum* lawn community (Hotes, 2004). Silt-sized tephra can form hard surface crusts in dry habitats, and germination occurs only in cracks with favourable conditions (Mack, 1987). Silt-sized glass on a *Sphagnum* lawn community, however, formed a soft, moist layer that was colonized by ubiquitous bryophytes (Hotes *et al.*, 2004). Wetness of mire surfaces has been suggested to increase as a result of sealing of surface pores in combination with enhanced peat decomposition (Tsuji and Kosugi, 1991; Crowley *et al.*, 1994), but other authors expected it to decrease as tephra forms a dry 'cap' over the moist mire surface (Lees and Neall, 1993; Giles *et al.*, 1999). Oxygen saturation and redox potentials in the acrotelm were not altered significantly by sand-sized tephra and decreased (although not statistically significant) under silt-sized tephra (Hotes *et al.*, 2004), contradicting the hypothesis that tephra deposition increases the aeration and decomposition of the surface peat (Sakaguchi, 1974; Yamagata, 1982). Dependence of tephra effects on the season has also been found. The differences were mediated by snow cover during the 1980 eruptions of Mount St Helens (Antos and Zobel, 1982), but seasonal differences occurred also without the influence of snow (Hotes *et al.*, 2004).

In addition to physical effects of tephra, chemical damage caused by volcanic gases (sulphur dioxide, fluorine) has been found even in areas far from the eruptive vent (Thorarinsson, 1979; Brayshay and Grattan, 1999). However, this occurs only under special meteorological conditions (Grattan and Sadler, 1999), and there is no indication of long-term vegetation change that can be ascribed to direct effects of volcanic volatiles (Martin, 1913; Thorarinsson, 1979; Le Guern *et al.*, 1988). Acid deposition caused by sulphur, chlorine and nitrogen compounds emitted during volcanic eruptions has been discussed as a potentially powerful driver of environmental change especially in Britain and Ireland (Blackford *et al.*, 1992; Grattan and Gilbertson, 1994; Charman *et al.*, 1995; Hall, 2003), and Grattan (2005) stressed that continental flood basalt volcanism may have affected ecosystems on a continental scale through acid deposition. Payne and Blackford (2005) simulated the effect of acid deposition thought to have occurred in Scotland during the Hekla-4 eruption and found that vegetation was severely damaged where 700 ml of 1 M sulfuric acid were applied to a *Calluna*-dominated mire. The effect of H_2SO_4 in lower concentrations was less pronounced, as was application of HCl mixed with H_2SO_4 or given alone. The lethal effect of the high concentration treatment was persistent during the study period, and recovery had hardly started after two years. Although this experiment shows the detrimental consequences of a strong acid pulse on vegetation, it is necessary to assess how closely it resembles a natural volcanic acid deposition event before extrapolating the results. In natural volcanic events, tephra and associated acid deposition occurs over hours, days or even months, and it is often accompanied by rain. Therefore, the acid input is more gradual, reaction with minerals in tephra particles can neutralize part of the acid ions (Dethier *et al.*, 1981), and the chemical composition can change further when precipitation is intercepted by plants (Tomizawa *et al.*, 1997). It would be interesting to test whether spacing out the acid application changes the effect on mire vegetation. Increased sulphate concentrations and lower pH of precipitation have been observed during recent volcanic eruptions in Japan

(Okuda *et al.*, 2005), but pronounced effects on ecosystems have not been reported. We have not found any estimates of the amount of acids associated with the tephras at our study sites, but sulphur emission data for other Japanese volcanoes are near the lower end of the scale of published values (Le Guern *et al.*, 1988; Halmer *et al.*, 2002). Searching for acidification signals in peat (Coulson *et al.*, 2005) or tree-rings (Pearson *et al.*, 2005) would help assess the extent of acid deposition in the context of Holocene volcanic eruptions in Hokkaido. Whether volcanogenic acids can induce vegetation change over large areas similar to that documented for anthropogenic acidification (Ferguson *et al.*, 1984; Gorham, 1998) needs to be tested further. Large-scale volcanic events typically last less than a year, and the most active phases during which high plumes are generated are usually not longer than a few hours or days (Sparks *et al.*, 1997), generating a pulse of limited duration rather than continuous input such as is caused by anthropogenic sources. Sulphate added to ecosystems can within certain limits be sequestered by microorganisms and plants (Gorham, 1998), and recovery from sulphate-related acidification is observed when the input is reduced. Where recovery is slow, high levels of anthropogenic nitrogen input are often observed (Brouwer *et al.*, 1997; Monteith *et al.*, 2005). Experimental acidification of mire vegetation with sulfuric and nitric acid initially stimulated *Sphagnum* growth, but this effect disappeared after four years of continuous treatment (Rochefort *et al.*, 1990). Excess sulphate is reduced to sulfide under anaerobic conditions in waterlogged soils, and if toxic levels of sulfide are reached, vegetation change can occur (Hotes *et al.*, 2005). This process may also have played a role in the experiment of Payne and Blackford (2005) who reported a smell of rotten eggs in their plots treated with high concentrations of sulfuric acid. Indication of pH increases rather than decreases after tephra deposition were found in aquatic environments by Tsuji and Kosugi (1991) and Lotter and Birks (1993), and Hodder *et al.* (1991) detected elevated levels of magnesium and calcium in peat pore water below a tephra. Rainwater containing dissolved volcanic volatiles is acidic (often pH < 2) and tephra leachates are either acidic or close to the pH of unpolluted rainwater (Oskarsson, 1980; Fruchter *et al.*, 1980; Witham *et al.*, 2004), but not alkaline. As base elements are usually only a minor component of tephras (Kittleman, 1979; Fruchter *et al.*, 1980), the pH increase inferred from lake sediments was probably not due to leaching from tephra. Moderate tephra deposition had no lasting effects on pH or ion composition of ground- and surface water after the 1980 eruption of Mount St Helens (Lee, 1996). Enrichment of mire water and peat with minerals and nutrients leached from tephra is ecologically significant according to Wolejko and Ito (1986) and Damman (1988) who coined the term 'tephratrophic mire'. Yamada (1942) and Sakaguchi (1974) postulated that eutrophication occurs because of tephra fall, and the former linked vegetation shifts to these events. Later authors have published contradicting views on the content of potentially limiting nutrients in tephra: Shoji *et al.* (1993) stated that tephra initially contains high amounts of phosphorus which enhances revegetation, whereas Zobel and Antos (1997) emphasized that low nutrient content in tephra causes slow recovery of plants. Changes in mire pore water chemistry were found after experimental tephra application, most of which could be explained by leaching from the tephra (Hotes *et al.*, 2004). Only ammonium increased more than proportional under a 6-cm tephra layer, suggesting that secondary processes can influence the chemical composition of mire water after tephra deposition.

Mire vegetation dynamics at different spatio-temporal scales

An inverse relationship between the abundance of vascular plants and mosses, in particular *Sphagnum* species, is commonly observed in mire vegetation. It can be found in horizontal patterns of modern vegetation (eg, Wheeler and Proctor, 2000; Asada, 2002) as well as in stratigraphical sequences (eg, Frenzel, 1983; Barber *et al.*, 1994, 1998). Hydrological conditions and water chemistry have been shown to be important determinants of patterns in modern vegetation, although considerable overlap in environmental variables exists between different mire vegetation types (Yabe and Onimaru, 1997; Hotes *et al.*, 2001), and it has been pointed out that vegetation forms a continuum along environmental gradients with gradual transitions rather than sharp boundaries (Wheeler and Proctor, 2000). Nevertheless, different types of mire vegetation can be clearly distinguished, and shifts from one type to another can take place during relatively short periods of time (Hogg *et al.*, 1995). The threshold values of variables beyond which fundamental shifts from one type to another occur have rarely been determined under field conditions, and the existing data show high variability (Bobbink *et al.*, 1998; Wamelink and van Dobben, 2003), which may partly be due to differences in site history. It is possible that the theory of alternative stable states can be applied in the case of mire vegetation, which would help to explain the overlap of environmental conditions between different vegetation types and hysteresis in changes from one type to another. Alternative stable states have been described in a number of aquatic and terrestrial ecosystems (Adema and Grootjans, 2003; Scheffer and Carpenter, 2003; Folke *et al.*, 2004), and mires also show characteristics necessary for the development of such states. Positive feedback mechanisms involving acidification and oligotrophication due to selective uptake and release of ions by *Sphagnum* species exert great influence on the transition from fen to bog (Frenzel, 1983; Zobel, 1988; Hughes, 2000), and nutrient enrichment or hydrological change can cause the system to shift towards fen conditions, which may be stabilized by shading, litter accumulation and enhanced nutrient cycling (Hogg *et al.*, 1995). However, our results did not show the expected shifts between *Sphagnum* and monocot dominance under the influence of tephra deposition, and we cannot support the hypothesis that volcanic disturbance triggers transitions from one stable state to another. A potential problem that needs to be considered when interpreting patterns that were derived from the analysis of cores is the spatial scale at which vegetation change occurs: the surface area of the core is many orders of magnitude smaller than that of the system about which information is sought, and the effect of tephra deposition may be obscured by unrelated changes that take place on a centimetre scale, eg, resulting from clonal growth or stochastic processes such as propagule dispersal (Poschlod, 1995; Sundberg, 2000). Potential bias caused by the scale at which observations are made can be minimized when replicate cores from the same site are investigated. In the present study, detailed macrofossil analyses were carried out only on single cores because of limited resources, so that a scale-dependent bias in these data cannot be ruled out.

Conclusions

We found only minor changes in macrofossil composition at tephra layers in late Holocene peat sequences in Hokkaido, which suggests that mire vegetation is resilient to disturbance by moderate tephra deposition. Direct observations of tephra impact have shown distinct vegetation responses that are primarily caused by the physical effects of burial under a mineral layer. Damage to plants caused by acid deposition during eruptions has also been reported, but evidence supporting the hypothesis of persistent vegetation change due to volcanogenic acidification is scarce. The great variability of vegetation responses to volcanic events is due to the variable physical and chemical characteristics of eruptions and to traits of the vegetation, eg, life forms, microtopography and the phenological stage. This variability makes it difficult to detect patterns in a limited number of cores, and further investigations are needed before more detailed conclusions can be drawn.

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