Géographie physique et Quaternaire

Holocene Development and Permafrost History of the Usinsk Mire, Northeast European Russia
Évolution à l'Holocène et histoire du pergélisol de la tourbière d'Usinsk, au nord-est de la Russie d'Europe
Развитие в голоцене и история вечной мерзлоты Усинского болота на Северо-Востоке европейской России

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Résumé de l'article

Cette étude discute de la succession de la végétation, de la dynamique du pergélisol et de l'accumulation de la tourbe à l'Holocène dans la tourbière d'Usinsk, située dans les basses terres de Pechora, au nord-est de la Russie d'Europe. La région se trouve dans l'extrême nord de la taïga actuelle, près de la limite méridionale du pergélisol. Les reconstitutions sont fondées sur l'analyse macrofossile des plantes, l'analyse physico-chimique et les dates au radiocarbone déterminées par spectrométrie de masse à l'aide d'un accélérateur de particules (SMA) de deux profils de tourbe étudiés en détail. De l'information additionnelle provient de sept autres sites. L'accumulation de matière organique a commencé vers 11 350 BP (années ^{14}C). L'accumulation de tourbe dans les étangs était alors le point de départ le plus habituel des tourbières. Pendant une grande partie de leur formation, ces sites ont été des marais dominés par les Cyperaceae. La transition vers des écosystèmes dominés par les *Sphagnum* est enregistrée entre 3700 et 3000 BP. Le pergélisol s'est établi vers 2300 BP, bien que des signes de formation embryonnaire de palses soient déjà observables vers 2900 BP. Les palses ont connu plusieurs épisodes de gel et de dégel complet ou partiel. Les couches de pergélisol actuellement observables sont d'origine récente. Le taux d'accumulation du carbone à long terme dans les sites étudiés est de 19 g/m^2/an. Le taux moyen d'accumulation du pergélisol en phase active est de 23 g/m^2/an.

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HOLOCENE DEVELOPMENT AND PERMAFROST HISTORY OF THE USINSK MIRE, NORTHEAST EUROPEAN RUSSIA

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ABSTRACT This study discusses Holocene vegetation succession, permafrost dynamics and peat accumulation in the Usinsk mire, located in the Pechora lowlands of Northeast European Russia. At present, the area is situated in the extreme northern taiga subzone near the southern limit of permafrost. Reconstructions are based on plant macrofossil analysis, physico-chemical analysis and AMS (accelerator mass spectrometry) radiocarbon dating of two peat profiles investigated in detail. Additional information is available from seven other sites. Organic accumulation started at *ca.* 11 350 BP (^{14}C yrs). Terrestrialization of ponds was the most common pathway for mire initiation. During a large part of their history, the sites have been Cyperaceae-dominated fens. A change into *Sphagnum*-dominated ecosystems is recorded at 3700-3000 BP. Permafrost became established around 2300 BP, although first signs of embryonic palsa formation can be tentatively traced back to about 2900 BP. Palsas and peat plateaus have experienced several periods of freezing and entire or partial thawing. The extant permafrost stages are young. The long-term carbon accumulation rate in the investigated sites is 19 g/m^2/yr. The average rate of carbon accumulation in the dynamic permafrost stage is 23 g/m^2/yr.

RÉSUMÉ *Évolution à l'Holocène et histoire du pergélisol de la tourbière d'Usinsk, au nord-est de la Russie d'Europe.* Cette étude discute de la succession de la végétation, de la dynamique du pergélisol et de l'accumulation de la tourbe à l'Holocène dans la tourbière d'Usinsk, située dans les basses terres de Pechora, au nord-est de la Russie d'Europe. La région se trouve dans l'extrême nord de la taïga actuelle, près de la limite méridionale du pergélisol. Les reconstitutions sont fondées sur l'analyse macrofossile des plantes, l'analyse physico-chimique et les dates au radiocarbone déterminées par spectrométrie de masse à l'aide d'un accélérateur de particules (SMA) de deux profils de tourbe étudiés en détail. De l'information additionnelle provient de sept autres sites. L'accumulation de matière organique a commencé vers 11 350 BP (années ^{14}C). L'accumulation de tourbe dans les étangs était alors le point de départ le plus habituel des tourbières. Pendant une grande partie de leur formation, ces sites ont été des marais dominés par les Cyperaceae. La transition vers des écosystèmes dominés par les *Sphagnum* est enregistrée entre 3700 et 3000 BP. Le pergélisol s'est établi vers 2300 BP, bien que des signes de formation embryonnaire de palses soient déjà observables vers 2900 BP. Les palses ont connu plusieurs épisodes de gel et de dégel complet ou partiel. Les couches de pergélisol actuellement observables sont d'origine récente. Le taux d'accumulation du carbone à long terme dans les sites étudiés est de 19 g/m^2/an. Le taux moyen d'accumulation du pergélisol en phase active est de 23 g/m^2/an.

РЕФЕРАТ *Развитие в голоцене и история вечной мерзлоты Усинского болота на Северо-Востоке европейской России.* Изучены развитие растительности в голоцене, динамика вечной мерзлоты и аккумуляция торфа на Усинском болоте, которое находится на Печорской равнине Северо-Востока европейской Россий. В настоящее время район расположен в крайнесеверной тайге вближи южной границы вечной мерзлоты. Реконструкция основана на анализе растительных остатков, физико-химического анализа и радиоуглеродной датировки (AMS) двух подробно изученных профилей торфа. Также получена информация из семи других точек. Органическая аккумуляция началась примерно в 11 350 BP (^{14}C годы). Заболачивание как правило пройсходило путем зарастания озер. На протяжении большей части их развития в растительности изученных болотных участков преобладало семейство Cyperaceae. Изменение в преобладании *Sphagnum* отмечено в 3700-3000 BP. Вечная мерзлота сформировалась в 2300 BP, хотя первые признаки формации эмбрионального мерзлотного бугра можно проследить в 2900 BP. Мерзлотные бугры проходили многие периоды замерзания и полного или частичного таяния. Существующие в настоящее время мерзлотные фазы молодые. Долгосрочная скорость аккумуляции угля на изученных участках 19 гр/м^2/г. Средняя скорость аккумуляции в динамичной фазе вечной мерзлоты 23 гр/м^2/г.

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INTRODUCTION

In the southernmost regions of its distribution, like in the northern taiga of European Russia, permafrost occurrence is restricted to mires. Typical permafrost landforms are palsas and peat plateaus (Andreev, 1935; P'yavchenko, 1955; Oksanen, 2002). These landforms consist of frozen peat/mineral soil and segregated ice. Palsas are usually 1-7 m high and a few metres to 100 m in diameter. Peat plateaus are larger, flat-topped elevated expanses of peat (van Everdingen, 1998). *Aapa* ridges can in some cases be considered permafrost landforms as well, maintaining frost over several years and longer (string palsas). Permafrost degradation in mires is most noticeably observed as collapse scars and thermokarst ponds.

Through its effect on topography and hydrology, permafrost is significant for the ecology and carbon balance of mires. An estimated 22 % of the carbon pool in mires of the former Soviet Union is located in permafrost mires (Botch *et al.,* 1995). A warming climate resulting in permafrost thawing and enlarged wet surface areas would probably cause increased organic accumulation but also increased methane production in northern taiga and tundra (Martikainen, 1996).

The Usinsk mire is situated at the southern limit of discontinuous permafrost distribution. It is likely that the predicted climate warming will cause permafrost thawing in this area. This paleoecological study contributes to the understanding of the significance of permafrost for the ecology and carbon balance of mires and the sensitivity of permafrost to climate changes. Research on the mire history before and after permafrost aggradation gives information on the base of which the development of this type of mires under conditions of climate warming may be predicted.

As the largest peatland area of the Komi Republic and Europe, the Usinsk mire has long attracted scientific and other interests (particularly conservation efforts). Yet, very few publications about this mire are accessible to the international scientific community. In addition to being an enormous peat store, the mire covers oil reserves in its northeastern part. It is an important nesting place for several rare bird species and was protected in 1978, but oil drilling is still possible.

The Usinsk mire is first mentioned in Katz (1928) and Tsinzerling (1929). A large-scale peat study, with profiles across the mire, was made by Getmanov (1950), but was not published. Nikonov (1958) studied vegetation and peat deposits. His results are published as part of a report on 'Peat Resources of the Komi Republic', which is considered as classified literature. Preliminary results of permafrost dates in the mire are given by Oksanen (2002).

In the northern and extreme northern taiga subzones of Northeast European Russia, mire vegetation studies have been conducted by Katz (1928, 1930), Tsinzerling (1929) and Alekseeva (1972, 1977). Vegetation studies are presented in a generalized form only, *e.g.*, they do not include relevés giving information on small-scale habitats within permafrost mires. Peat-stratigraphic descriptions for Northeast European Russia are reported in Nikonov (1953), P'yavchenko (1955) and Alekseeva (1971, 1974a, b, 1978, 1988). Absolute permafrost aggradation dates are not available in these studies but P'yavchenko (1955) used pollen stratigraphy for indirect dating of permafrost occurrence.

Plant macrofossil studies with radiocarbon dates from mires are reported in Oksanen *et al.* (1998, 2001) from the forest-tundra zone and in Väliranta *et al.* (2003) from the tundra zone. The same methods used in these previous studies are applied to the Usinsk mire, in the northern taiga, in order to compare the age and dynamics of permafrost in different eco-climatic zones. The main purpose of the present study is to date permafrost aggradation and study its effect on ecology, hydrology and carbon balance of the mire ecosystem. The research is conducted in the central part of the Usinsk mire, where permafrost landforms occur. Modern vegetation is studied as a reference for the interpretation of plant macrofossil assemblages. The Holocene vegetation succession and peat accumulation rates are discussed.

STUDY AREA

The Usinsk mire occupies an area of about 1 400 km^2 near the confluence of the rivers Pechora and Usa, Komi Republic, Russia (Fig. 1). Our investigations are limited to an area of about 12 km^2 in the central part of the mire (Fig. 2). The coordinates for the investigated area are approximately 65° 45' N and 57° 30' E; the elevation is about 50 m asl.

The study area belongs to the Timan-Pechora region, which is a post-Baikalian (Lower Paleozoic) platform (Khain, 1985). At Usinsk, Jurassic and Cretaceous clays, sands and sandstones are found under Quaternary glaciofluvial and glaciolacustrine sediments (Anonymous, 1964). The glacial history of Northeast European Russia is a much debated subject (*e.g.*, Guslitser and Isaichev, 1983; Faustova, 1984; Velichko *et al.,* 1984; Tveranger, 1995; Astakhov *et al.,* 1998; Grosswald, 1998). According to most interpretations, the area was glaciated during the Quaternary, possibly the Moscowian glaciation or earlier. The southern limit of the last glaciation, Valdai, was located at least 100 km north of our study area. At some time during Valdai, the area was covered by proglacial Lake Komi, the shorelines of which are found at *ca.* 100 m asl (Faustova, 1984; Lavrov *et al.*, 1986; Astakhov *et al.,* 1999; Mangerud *et al.*, 1999; Svendsen *et al.*, 1999).

The Usinsk mire is located in the extreme northern taiga subzone. Forests are mainly composed of *Picea abies* ssp. *obovata*, *Pinus sylvestris* and *Betula pubescens* (Tolmachev, 1974). The southern limit of discontinuous permafrost in the Pechora lowlands follows approximately the 65° 30' N latitude. Permafrost occurs as isolated patches in the form of small peat plateaus, palsas and strings in *aapa* mires. The mean annual temperature in the nearest town, Ust'-Usa (Fig. 1), for the period 1961-1990, is -3.3 °C, and the mean temperature of the warmest month, July, is 14.8 °C. The mean total annual precipitation is 487 mm (average for 19 years during 1961-1990). Snow cover lasts 210 days in average, and the average maximum depth of snow in March is 60 cm (Anonymous, 1989). In the town of Pechora (Fig. 1), outside the permafrost region, the mean annual temperature for the period 1961-1990 is -2.4 °C, and the mean July temperature 16.1 °C. The mean total annual precipitation is 579 mm (Anonymous, 1996). Snow cover lasts 205 days, and

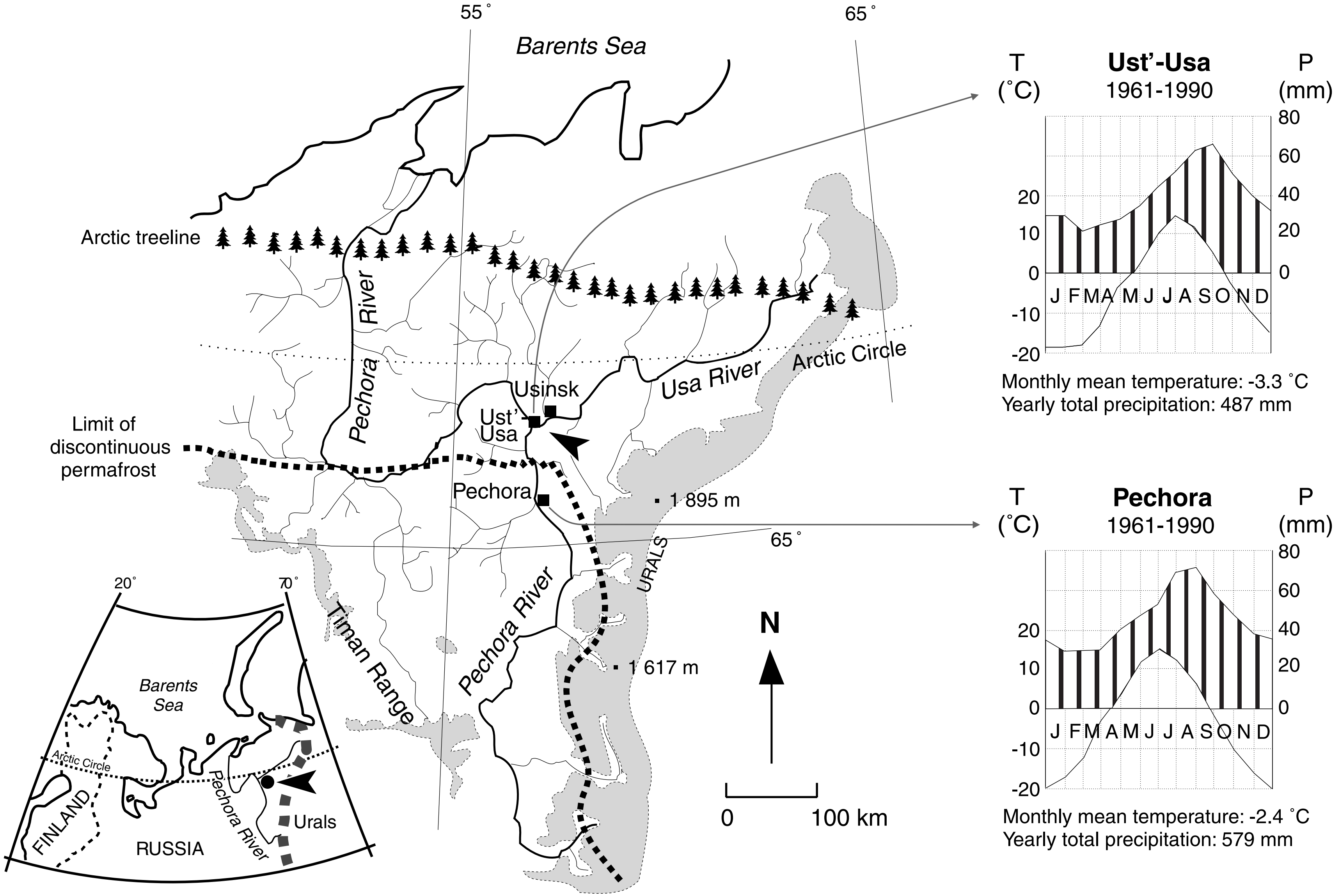

FIGURE 1. The Pechora Region with the location of the Usinsk mire indicated by the black arrow. Monthly mean temperatures and total precipitation for 1961-1990 are from the nearest stations. Climate diagrams are drawn after Walter (1973).

Région de Pechora et localisation de la tourbière d'Usinsk indiquée par la flèche noire. Les températures mensuelles moyennes et les précipitations totales pour 1961-1990 proviennent des stations les plus proches. Les diagrammes climatiques sont établis d'après Walter (1973).

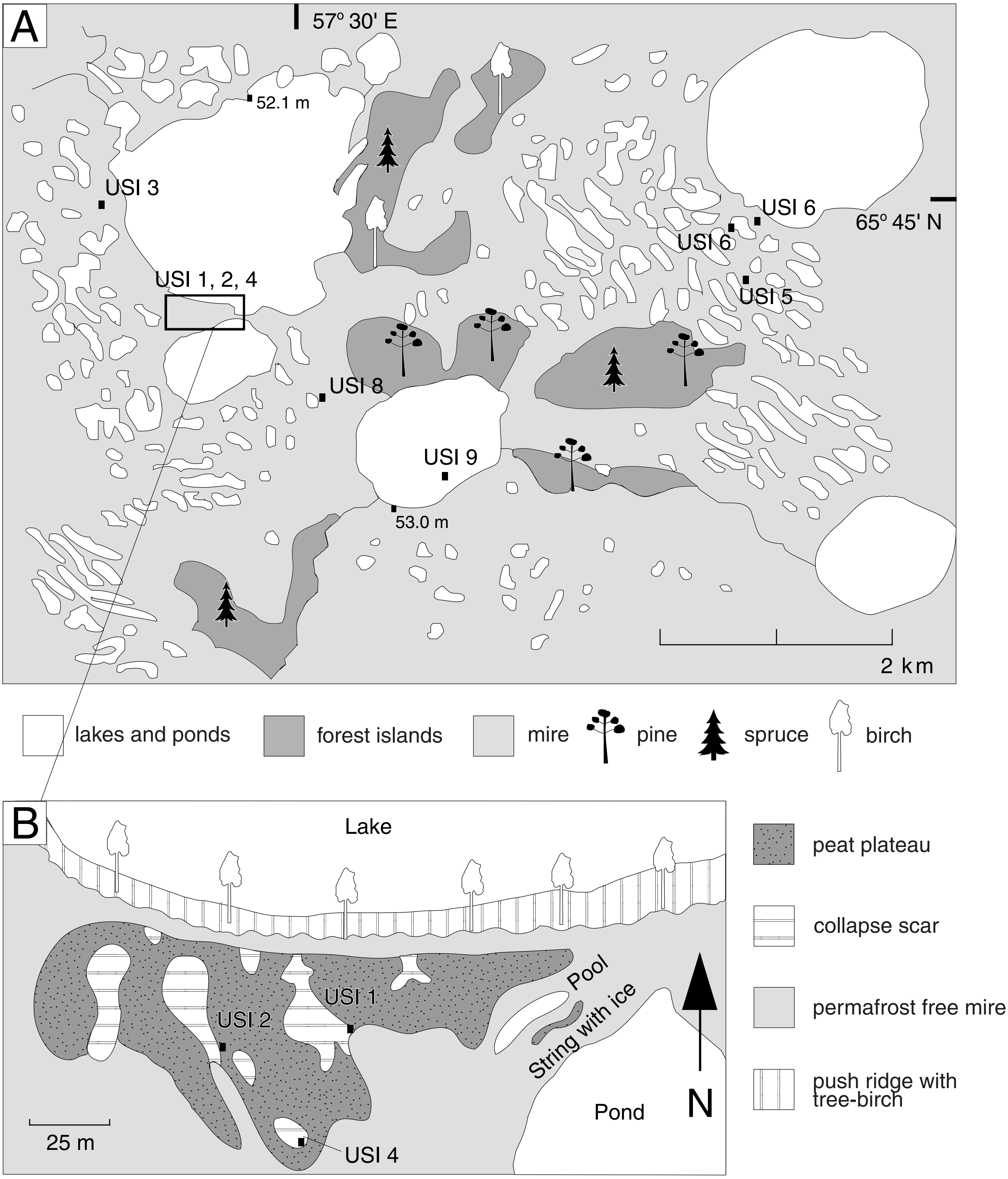

FIGURE 2. Study area in the central part of the Usinsk mire (A), with a more detailed sketch from a peat plateau area (B).

Zone d'étude (A), dans la partie centrale de la tourbière d'Usinsk, et croquis plus détaillé d'un secteur de plateau palsique (B).

the average maximum depth of snow in March is 90 cm in forests and 50 cm in open fields (Anonymous, 1989). The temperature of the permafrost at its southern limit of distribution is about 0 to -1 °C (Brown *et al.,* 1997).

METHODS

In the field, vegetation descriptions were made from 1 m^2 quadrats that were randomly picked within selected habitats. Plant cover in percentage values was estimated for the field and ground layers. Depth of the water level and/or permafrost table was measured. The pH was determined with test paper (Merck), from free water or from interstitial water of mosses. Water samples were taken for electrical conductivity analysis.

Material for peat analyses was collected from natural exposures in palsas and peat plateaus that were cleaned and further excavated. In the unfrozen mire sections, a Russian peat corer (Jowsey, 1966) was used. In profile USI 1, immediately below the lower boundary of permafrost at 170 cm, the unfrozen material was very loose and difficult to collect with the corer. The material between 170-270 cm was collected by hand and a certain compaction cannot be excluded; therefore, bulk density and peat accumulation values obtained for this layer are possibly too high. The stratigraphy of peat profiles was described. Samples were collected continuously at 10 cm intervals and packed in plastic bags until further processing.

In the laboratory, electric conductivity was measured from the water samples at 20 °C and corrected for hydrogen ions (Sjörs, 1950). For macrofossil analysis, subsamples of 5 cm^3 were heated in 5 % potassium hydroxyde (KOH) for deflocculation, washed through a 150 µm sieve, and stored in water. Subsamples of known volume (usually 8 cm^3) were dried 18 h at 95 °C to measure bulk density (as g of dry weight/cm^3), then ignited 2 h at 550 °C to determine loss on ignition (as % of dry weight). The carbon and nitrogen contents were measured with an Elemental Analyser, Model EA 1110 (CE Instruments). Identified plant macrofossils were used for radiocarbon dating by accelerator mass spectrometry (AMS) at the R.J. van de Graaff Laboratory, Utrecht University. Years BP in the text refer to radiocarbon years before present (1950 AD).

The amount of macrofossils was estimated as volume percentages (mosses, epidermia, roots, etc.) or as numbers per sample of 5 cm^3 (seeds, leaves of higher plants, etc.). In addition to plant macrofossils, charcoal particles and some easily distinguishable groups of animal remains were counted. Degree of decomposition is given as reciprocal values of moss preservation classes, where 0 indicates intact mosses and 5, fragmented leaf remains (Janssens, 1983). Macrofossil abundance as cover value on a petri dish was counted for each sample taking the top sample as a standard (Kuhry *et al.,* 1992).

For the interpretation of permafrost dynamics in the investigated peat profiles, a review of observations on vegetation-permafrost relationships in continental European permafrost mires (Oksanen, 2002) and local vegetation data presented in this study are used. Based on peat macrofossil analysis, the probable occurrence of permafrost can be indicated or ruled out. There are no obvious indicator species exclusively occurring on permafrost, but certain plant communities and vegetation successions are characteristic for a permafrost environment. For example, *Dicranum elongatum* and *Polytrichum strictum* with lichens are usually the first invader species on palsa embryos succeeding wet flark species. Large and flat palsa/peat plateau surfaces, however, can support *Sphagnum fuscum* and *S. capillifolium*. The limitations and advantages of the method are more extensively discussed in Oksanen *et al.* (2001).

The zonation of peat profiles is based on paleobotanical, physical and chemical properties. Nomenclature follows Eurola *et al.* (1992) for mosses and Hämet-Ahti *et al.* (1998) for vascular plants.

RESULTS

MODERN VEGETATION AND PERMAFROST CONDITIONS

The Usinsk mire is predominantly an *aapa* complex, with a well developed structure of low strings and wet flarks (often open water pools). Numerous sandy uplands protrude from the mire surface as forest islands, with pine (*Pinus sylvestris)* forest in dry habitats and mixed forest with spruce (*Picea abies)* and birch (*Betula pubescens)* in more mesic locations (Fig. 2A). Palsas or small peat plateaus are found near the margins of the largest lakes. Based on field reconnaissance, the total area of permafrost is estimated to represent less than 1 % of the total mire surface.

The most typical vegetation of strings is *Sphagnum fuscum, Ledum palustre* and *Chamaedaphne calyculata. S. lindbergii, S. balticum* and *Carex limosa* are common in flarks. On the shores of pools *S. majus, S. riparium, S. fimbriatum, Eriophorum vaginatum* and *Menyanthes trifoliata* are typically found. The central parts of the mire surface are treeless. At the margins, *Pinus sylvestris* and *Betula pubescens* are found on strings. In August-September 1996, parts of the strings contained frost in the form of about 30 cm thick ice lenses found between 40-100 cm depth below the surface. pH in low hummocks, lawns and flarks was 4.3-5.2 and in lakes, 5.3-5.7. All measured electric conductivity values were very low, below 10 mS/m.

All peat plateaus and palsas observed in the field were degrading. No embryonic palsas were observed. Two peat plateau areas were studied in detail. In a relatively large peat plateau (Fig. 2B; sites USI 1, 2 and 4), the plateau was 1.5-2 m higher than the adjacent unfrozen mire surface; the upper permafrost table was found at 30-100 cm depth. In the USI 1 profile, which was described for its entire depth to the mineral subsoil (430 cm), permafrost was restricted to the upper part of the peat deposit (between 45-170 cm). In a smaller peat plateau (Fig. 2A; USI 6), the plateau was at maximum 1 m high. The upper permafrost table was found at 45-65 cm.

A vegetation survey with six relevés was conducted on the larger peat plateau (Table I). A drier and a moister type of peat plateau vegetation can be distinguished (two relevés). The ground layer of the drier peat plateau site consists mainly of lichens and bare peat. The moister peat plateau site supports

TABLE I

Vegetation survey in the Usinsk mire

Relevé	Peat plateau						String-pool complex			
	Dry surface	Moist surface	Collapse scar, -180 cm, hummock	Collapse scar, -115 cm, hollow	Collapse scar, -200 cm, hollow	Collapse scar, -220 cm, pool	Hummock 1	Hummock 2	Lawn 1	Lawn 2
pH	4.7	4.7	4.7	4.7	5.0	5.2	4.7	4.4	4.7	5.2
Depth of water (cm)	–	–	35	7	0	0	35	35	11	3
Depth of permafrost (cm)	45	35	–	–	–	–	–	–	–	–
Depth of mineral ground (cm)	~430	~430	>100	>100	>100	>100	>100	>100	>100	>100
Corrected electric conductivity (mS/m)	–	–	7.3	5.4	1.9	4.1	–	–	5.4	3.9
% of ground layer										
Sphagnum capillifolium		1		50						
S. fuscum	2	93	30				45	2	100	
Dicranum elongatum	5									
Pleurozium schreberi		4	70				3			
Lichens	50	2					15	80		
Mylia anomala							15	1	+	
Cladopodiella fluitans					50					
Sphagnum annulatum				40						
S. balticum					5					
S. lindbergii										80
S. russowii				10						
Pohlia nutans							22			
Bare	43							17		
Water					45	100				20
% of field layer										
Betula nana	2	2	5				15	5	+	
Ledum palustre	30	20	5				20	20	15	
Andromeda polifolia	1	1	5	2					5	
Vaccinium microcarpum		2	+				10	2	3	
V. vitis-idaea	1	3								
V. uliginosum	5	4	15					20		
Empetrum nigrum	15		3				20	10		
Rubus chamaemorus	3	10	10				15	15	15	3
Pinus sylvestris									+	
Betula pubescens			+							
Chamaedaphne calyculata				3			5			5
Vaccinium oxycoccos										25
Drosera rotundifolia									1	
D. anglica			+							
Eriophorum vaginatum				60	30					4
E. russeolum						10				
Carex rostrata						30				
C. limosa										40

+ : less than 1 %

Sphagnum fuscum, *S. capillifolium* and *Pleurozium schreberi*. The pH of both types is rather high, 4.7. Additional vegetation observations from peat plateau surfaces include *Polytrichum strictum* and *Dicranum fuscescens*. Occasional stunted *Pinus sylvestris* trees grow on the plateau and stunted *Betula pubescens* trees near to the edges of the plateau. *Chamaedaphne calyculata* was found in small depressions and in the peat plateau margins. Four relevés from the vegetation of collapse scars, located at 115-220 cm below the larger peat plateau surface, are presented in Table I. In a smaller collapse scar, at 50 cm below the peat plateau surface, *Carex*, *Eriophorum, Scheuchzeria* and *Sphagnum annulatum* were encountered.

Hummock and lawn vegetation from a string-pool complex near site USI 8 (see Fig. 2A) is described in four relevés (Table I). The low hummocks were free from permafrost. Their vegetation does not significantly differ from that of the peat plateaus, although *Pohlia nutans* and *Mylia anomala* are not encountered on peat plateaus within this study.

ABSOLUTE DATING AND PEAT STRATIGRAPHY

A total of 10 radiocarbon dates are available for this study. Uncalibrated and calibrated ages are shown in Table II. We have opted for uncalibrated ages to discuss the periods of Late Quaternary-Holocene vegetation succession to make comparison with previous studies easier. Ages have been interpolated linearly between available radiocarbon dates and rounded to the nearest hundred years. Accumulation rates are given in Table III. Vertical peat increment and carbon accumulation rates are discussed based on median calibrated ages (van der Plicht, 1998).

The stratigraphy of profiles is presented in Figure 3. The average depth of the organic deposit (which includes peat and, where present, basal dy or gyttja) in the central part of the Usinsk mire is 2.4 m based on 12 probings to the mineral subsoil; the measured range is 0.5-4.3 m. In lakes (4 probings), the average depth of organic sediment is 60 cm (range 20-100 cm). The water depth in these lakes is only up to about 1 m. The mineral subsoil is usually sand; in one case the underlying proglacial clays were reached (Lake Komi deposit). Charcoal particles are absent or rare in all studied peat profiles.

Results of the physico-chemical analyses performed on profiles USI 1 and USI 8 are presented in Figure 4. The average dry bulk density of the entire organic deposit, weighed for depth, is 0.20 g/cm^3, and that of the peat deposit, 0.14 g/cm^3. Organic content of the entire organic deposit, weighed for depth, is 73.9 %, and that of the peat, 98.5 %. Carbon content in dry organic matter is 52.6 %.

PLANT MACROFOSSIL ANALYSES

Paleoecological studies are based on plant macrofossil analysis, physico-chemical analysis and AMS radiocarbon dating of two peat profiles investigated in detail (USI 1 and USI 8). Additional information is available from seven other sites.

PROFILE USI 1: PEAT PLATEAU

A macrofossil diagram of profile USI 1 is presented in Figure 5. The USI 1 site is located in a small, 2 m high peat plateau covered by lichen-dominated vegetation (for location see Fig. 2B). The deposit is not frozen to the mineral bottom: permafrost reaches only down to 170 cm. The following profile zones were recognized:

Zone USI 1 0, 470-430 cm, >11 350 BP

Average dry bulk density (BD) is 1.69 g/cm^3, organic content (LOI), 1.85 %, and the carbon/nitrogen ratio (C/N), 14. The material is sand with some macrofossils, which are moderately decomposed. The main taxon is *Equisetum* (up to 50 % epidermia and roots). Brown mosses are represented by *Scorpidium scorpioides*, *Limprichtia* and *Hypnum*. Some *Sphagnum* Sect. *Acutifolia* and *S.* Sect. *Cuspidata* are present; a few leaves are recognized as *S. rubellum*. A *Betula* leaf is found, but it is too decayed to decide if it originates from tree- or dwarf-birch.

Zone USI 1 A, 430-400 cm, 11 350-ca. 10 300 BP

BD decreases from 1.60 to 0.30 g/cm^3; average LOI is 29.9 % but shows an increasing trend; average C/N is 20. The deposit is sandy dy with quite low macrofossil abundance, moderately to well decomposed. The main components are detritus (up to 40 %) and *Equisetum* remains (10-20 % epidermia and 40 % roots). Mosses (*Scorpidium scorpioides, Limprichtia, Tomentypnum nitens* and *Sphagnum teres*) are regularly present in small numbers. Both triangular and biconvex *Carex* seeds are registered. *Betula* remains are frequent, but poorly preserved. One seed of *Potamogeton* and a Cladocera ephippium are found.

Zone USI 1 B, 400-350 cm, ca. 10 300-8520 BP

BD is 0.16 g/cm^3, LOI, 95.7 %, and C/N, 22. The material is moderately decomposed peat. At the beginning of the zone, the remains of *Equisetum* (epidermia) and Cyperaceae (epidermia and seeds) are abundant. Among mosses *Limprichtia, Paludella squarrosa, Scorpidium scorpioides, Sphagnum teres* and *S. squarrosum* are found. *Betula* is well represented. In the latter half, *Equisetum* is less important and *Limprichtia* (10-50 %) becomes dominant. Other mosses (*Paludella squarrosa, S.* Sect. *Acutifolia* and *S.* Sect. *Cuspidata*) are found in minor amounts. Wood, *Betula* bark, leaves, samaras, bud- and catkin scales, Cyperaceae epidermia and *Carex* seeds are frequently present. Some *Betula* leaves are recognized as belonging to the dwarf-shrub type. Single seeds of *Menyanthes* are encountered.

Zone USI 1 C, 350-160 cm, 8520-3580 BP

BD is 0.19 g/cm^3, which should be considered a maximum value since part of the material was possibly compacted during sampling (see Methods). LOI is 99.1 % and C/N, 23. This peat layer is moderately to well decomposed. Cyperaceae remains are present (30 % epidermia and seeds) almost throughout the zone, but at times, those of *Scheuchzeria* (up to 35 % epidermia and seeds) are abundant instead. *Carex* seeds are mainly represented by the biconvex type in the

TABLE II

Radiocarbon dates from peat profiles

Lab. No.	Profile/depth	δ13C	14C age BP[1]	Calibrated age BP[2] Median probability	1-σ min	1-σ max	Dated material
UtC-7402	USI 1 / 40-50 cm	-27.8	315 ± 45	387	307	435	*Sphagnum fuscum*
UtC-8675	USI 1 / 120-130 cm	-31.6	2775 ± 40	2862	2789	2923	*Betula* bark and *Sphagnum* leaves
UtC-7403	USI 1 / 160-170 cm	-28.7	3580 ± 50	3875	3737	3965	*Betula, Ledum, Carex* leaves and *Menyanthes* seed
UtC-7404	USI 1 / 270-280 cm	-29.2	5110 ± 50	5826	5753	5915	*Carex* epidermia, seeds, *Betula* seed and twig
UtC-8551	USI 1 / 350-360 cm	-27.1	8520 ± 90	9511	9331	9599	*Sphagnum* peat
UtC-7405	USI 1 / 420-430 cm	-30.0	11 350 ± 70	13 301	13 189	13 393	*Betula* seeds, wood and leaves
UtC-7406	USI 2 / 84-87 cm	-28.8	3490 ± 45	3757	3695	3829	*Ledum* leaves
UtC-8676	USI 3 / 65-67 cm	-27.1	3745 ± 40	4101	3991	4215	*Carex* epidermia, seed and *Betula* leaf
UtC-7407	USI 8 / 70-80 cm	-31.1	3150 ± 40	3375	3273	3441	*Betula* bark
UtC-7408	USI 8 / 200-210 cm	-16.7	9550 ± 60	10 901	10 706	11 071	*Potamogeton*, *Najas* seeds and *Sphagnum*

1. dated at the R.J. van de Graaff Laboratory, Utrecht University

2. calibrated with the Groningen programme (Van der Plicht, 1998)

lower part and by the triangular type in the upper part of the zone. *Equisetum* is not present after the beginning of the zone. Some *Menyanthes* seeds are found. Mosses are present in small quantities. Through the zone, their composition shifts from *Limprichtia* and *Sphagnum subsecundum* to *Warnstorfia* and *S. warnstorfii* and, finally, to *S. annulatum*. Dwarf-shrub remains (*Ledum, Andromeda, Vaccinium, Chamaedaphne*) are also few but regularly present. Wood and *Betula* remains are abundant. Some leaves are of the dwarf-birch type. Cf. *Alnus* bark is encountered in the middle part of the zone. The zone is rich in different types of animal remains. A layer at ~195 cm is characterized by unidentified organic matter and a sharp rise in the amount of Acari.

Zone USI 1 D, 160-110 cm, 3580-ca. 2300 BP

BD is 0.14 g/cm^3, LOI, 99.5 %, and C/N, 56. The material is moderately humified *Sphagnum* peat. Some dark bands could be observed in the profile from the middle part of the zone upwards. The *Sphagnum* species composition changes gradually from *S. balticum* to *S. magellanicum* and, finally, to *S. fuscum*. Cyperaceae remains are at first common, represented largely by *Eriophorum*. Some wood and *Betula* bark is present; Ericaceae remains are rare; animal remains are less abundant than in the previous zone.

Zone USI 1 E, 110-0 cm, <*ca*. 2300 BP

BD is 0.11 g/cm^3, organic content, 99.8 %, and C/N, 67. The deposit is weakly decomposed *Sphagnum* peat, interlayered by numerous thin dark bands. In some of the dark layers, Cyperaceae remains are abundant, while in others, shrub remains (mainly roots) are important. One of the dark bands is found at ~70 cm. This thin layer is characterized by remains of Cyperaceae, smaller amounts of *S. fuscum*, the presence of unidentified organic matter and maxima in the occurrence of Acari and other animals. The dominant species in the zone up to about the 30 cm level is *S. fuscum* (95 %). Wood and *Betula* bark are present. The *S. fuscum* layer is followed by a Cyperaceae-dominated layer and, later on, by *Pleurozium schreberi*. From the 20 cm level upwards, the main species is *S. capillifolium* (80 %), accompanied by some *P. schreberi* and *Dicranum* cf. *elongatum*. Dwarf-shrubs (*Ledum, Andromeda, Vaccinium)* and *Betula* are frequent. One *Betula* leaf is identified as dwarf-birch. Animal remains are rather rare. At the very top, *Pohlia* and lichen remains are found.

OTHER PEAT PLATEAU/PALSA PROFILES

In addition to the detailed studies of peat plateau profile USI 1, gross-stratigraphic descriptions, some macrofossil analyses and two radiocarbon dates are available from the upper part of another three peat plateau sites (USI 2, 3 and 7) and one palsa site (USI 6) (see Fig. 3). All these sequences are characterized by the presence of *Sphagnum* peat with numerous dark interlayers. The contact with the underlying sedge peat (remains of *Carex* and *Menyanthes,* detritus) is dated to 3490 BP in profile USI 2 and to 3745 BP in profile USI 3. In profile USI 2, *S.* cf. *fallax* is recorded directly above the contact. For profile USI 3, the *Sphagnum* species is not known.

The 40 cm surface sequence at profile USI 4 was collected from a small internal collapse scar, 50 cm below the adjacent peat plateau of profiles USI 1 and USI 2 (see Fig. 2B). Dry bulk density of the studied layer is 0.09 g/cm^3 and the organic content, 99.1 %. Decomposition is low. In the lowermost sample (30-40 cm), *Sphagnum fuscum*, *S. capillifolium* and *S. magellanicum* are prevalent, with *Warnstorfia fluitans*. Dwarf-shrubs are present in minor quantities. Between 10-30 cm remains of dwarf-shrubs, especially *Betula nana* and *Ledum* are abundant. *Warnstorfia fluitans* is the dominant

TABLE III

Accumulation rates in peat profiles

Profile number	Age interval (BP)	Age interval (cal. BP)[1]	Depth interval (cm)	Profile zone	Material type	Accumulation rate				Site characteristics
						Vertical (mm/yr)[2]	Dry matter (g/m^2/yr)[2]	Organic (g/m^2/yr)[2]	Carbon (g/m^2/yr)[2]	
USI 1	0-315	0-387	0-45	E	peat	1.43 (1.16)	133.5 (107.3)	133.0 (106.9)	60.3 (48.5)	peat plateau
USI 1	315-2775	387-2862	45-125	E, D	peat	0.33 (0.32)	41.8 (41.5)	41.6 (41.3)	18.8 (18.7)	peat plateau
USI 1	2775-3580	2862-3875	125-165	D	peat	0.50 (0.39)	74.7 (59.5)	74.4 (59.2)	35.6 (28.3)	bog
USI 1	3580-5110	3875-5826	165-275	C	peat	0.72 (0.56)	118.6 (93.0)[3]	117.9 (92.5)[3]	62.7 (49.2)[3]	wet fen
USI 1	5110-8520	5826-9511	275-355	C	peat	0.23 (0.22)	49.5 (44.8)	48.9 (44.2)	26.5 (24.0)	wet fen
USI 1	8520-11 350	9511-13 301	355-425	B, A	peat + dy	0.25 (0.18)	90.2 (69.0)	40.9 (31.3)	21.5 (16.5)	mire initiation
USI 1	0-11 350	0-13 301	0-425	A-E	organic	0.37 (0.32)	71.4 (60.9)	58.8 (50.1)	30.1 (25.6)	long term
USI 2	0-3490	0-3757	0-85.5	X	peat	0.25 (0.23)				peat plateau
USI 3	0-3745	0-4101	0-66	X	peat	0.18 (0.16)				peat plateau
USI 8	0-3150	0-3375	0-75	E, D, C	peat	0.24 (0.22)	27.7 (25.9)	27.3 (25.4)	13.5 (12.6)	fen + bog
USI 8	3150-9550	3375-10 901	75-205	C, B, A	peat + dy	0.20 (0.17)	47.4 (40.3)	32.6 (27.8)	18.3 (15.6)	pond + wet fen
USI 8	0-9550	0-10 901	0-205	A-E	organic	0.21 (0.19)	40.9 (35.9)	30.9 (27.0)	16.7 (14.6)	long term

1. calibrated with the Groningen programme (Van der Plicht, 1998); median values used
2. values between brackets are based on calibrated years
3. could be overestimated due to possible compaction during field sampling (see 'Methods')

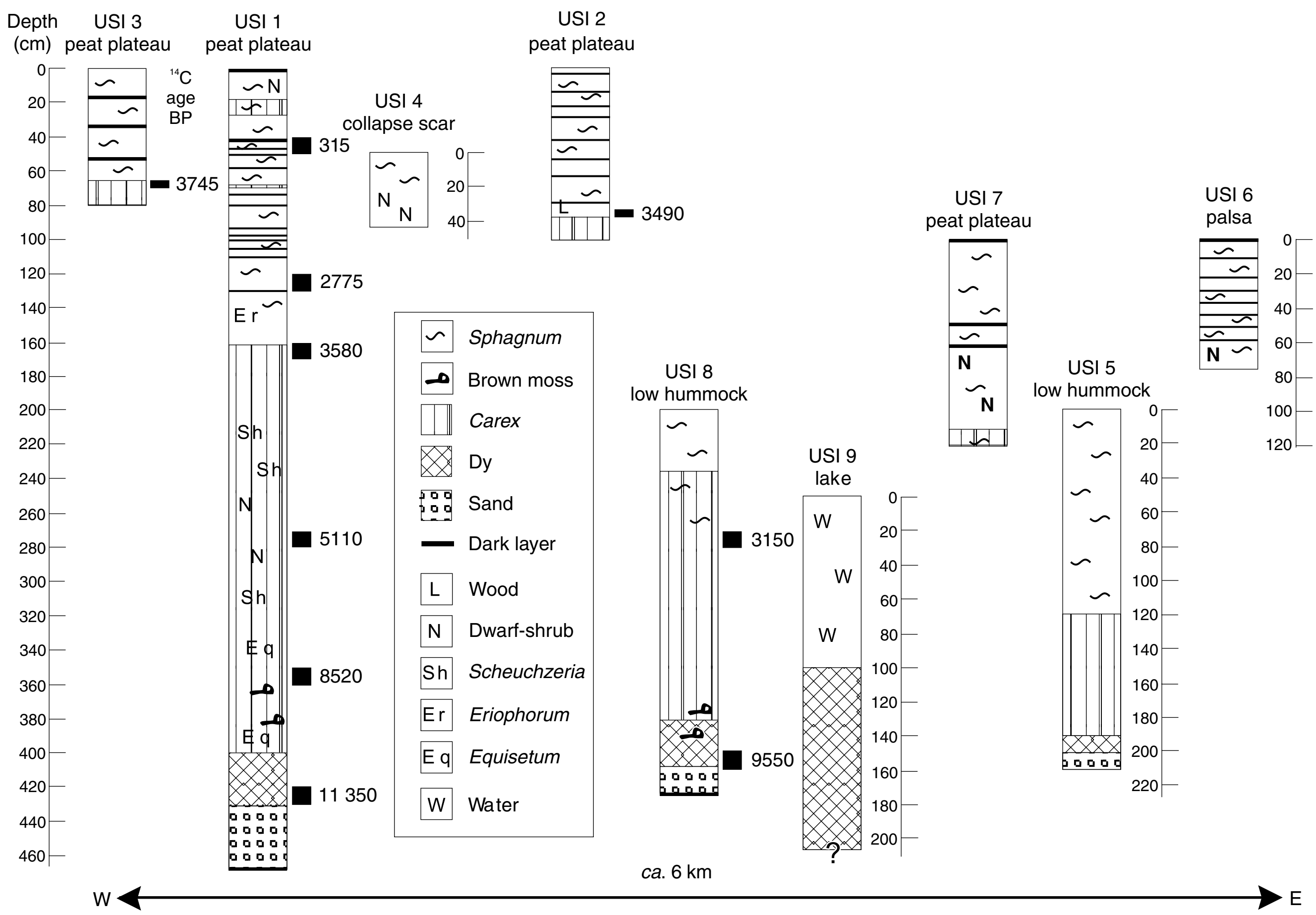

FIGURE 3. Stratigraphy of the deposits (profiles USI 1-9).

Stratigraphie des dépôts (profils USI 1 à 9).

moss species (40-60 %). At the surface (0-10 cm), *S. annulatum* and *S. balticum* account for 97 % of the remains.

PROFILE USI 8: NON-PERMAFROST HUMMOCK

A macrofossil diagram of profile USI 8 is given in Figure 6. The profile is from a string-pool complex in a permafrost-free zone of the study area (see Fig. 2A). The coring site is a hummock, located 28 cm above the adjacent flark surface. Local vegetation is dominated by *Sphagnum fuscum*, with *Chamaedaphne calyculata, Andromeda polifolia, Vaccinium oxycoccos* and *Rubus chamaemorus*. The following zones are described:

Zone USI 8 0, 225-210 cm, >9550 BP

The average dry bulk density (BD) is 1.69 g/cm^3, organic content (LOI) 2.32 % and the carbon/nitrogen ratio (C/N) is 13. The deposit is sand, with few moderately decomposed macrofossils, mostly roots of *Equisetum* and unrecognized herbs (55 %). *Equisetum* epidermia and remains of *Scorpidium vernicosum* are frequent as well. *Tomentypnum nitens* and *Sphagnum* are found in minor quantities. Some remains of *Betula* are present, but the type (tree- or dwarf-birch) cannot be distinguished. Water plants and animals are strongly represented: seeds of *Najas* cf. *flexilis* and *Zannichellia,* seeds and a leaf of *Potamogeton* cf. *gramineus,* and a Bryozoa statoblast.

Zone USI 8 A, 210-190 cm, 9550-ca. 8800 BP

BD is 0.67 g/cm^3, LOI, 15.2 %, and C/N, 15. The material is sandy dy. The macrofossil abundance is moderate and the remains are weakly decomposed. Dominant taxa are *Equisetum* (mainly roots), *Warnstorfia* cf. *tundrae*, *Limprichtia* and *Scorpidium vernicosum.* Up to 10 % of the material is detritus. Some leaves of *Sphagnum annulatum* are found. Aquatics (*Najas, Potamogeton, Myriophyllum,* Cladocera and Bryozoa) are abundant.

Zone USI 8 B, 190-170 cm, *ca*. 8800-*ca*. 7800 BP

BD is 0.21 g/cm^3, LOI, 72.0 %, and C/N, 23. The lower part of the zone is still dyic material. The upper part is weakly decomposed peat. In the whole zone the macrofossil abundance is very high. The dominant species is *Warnstorfia* cf. *tundrae* (35-75 %). Other mosses are *Drepanocladus aduncus, Hypnum* and *Sphagnum* Sect. *Cuspidata*. *Equisetum* and Cyperaceae are frequently represented. The majority of *Carex*

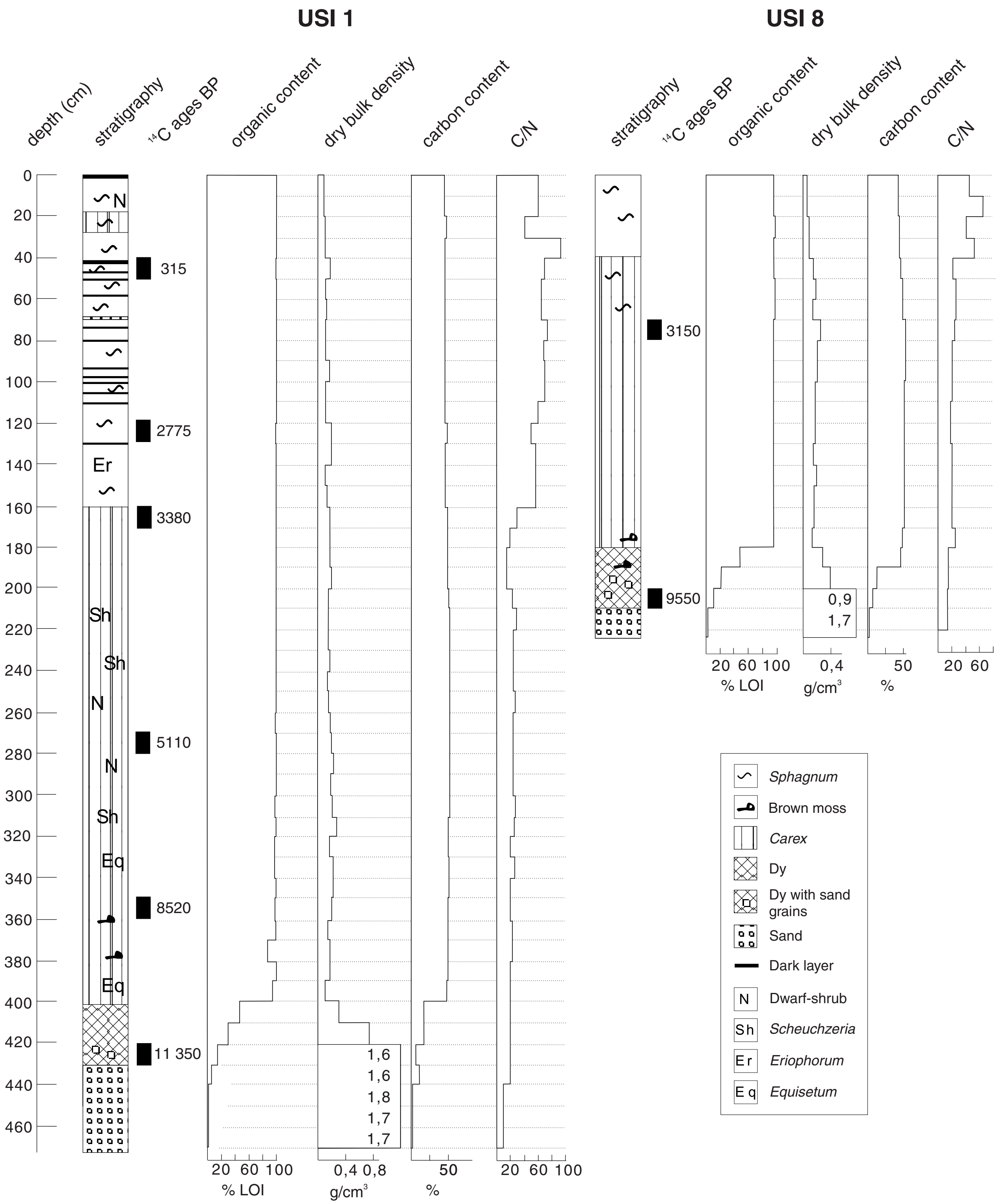

FIGURE 4. Results of the physico-chemical analysis of profiles USI 1 and USI 8.

Résultats de l'analyse physico-chimique des profils USI 1 et USI 8.

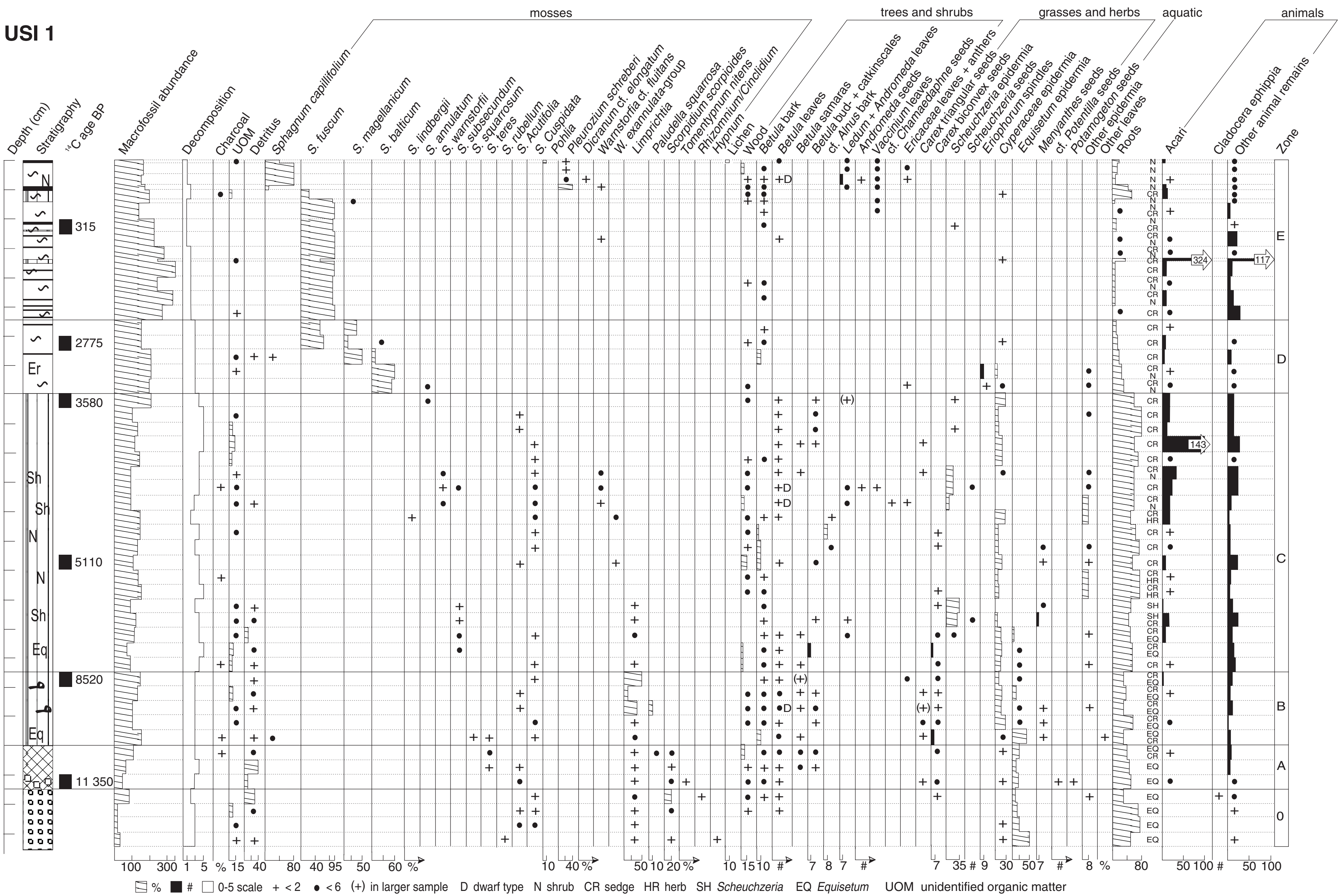

FIGURE 5. Plant macrofossil diagram of profile USI 1. Legend of the stratigraphic units as in Figures 3 and 4.

Diagramme des macrofossiles de plantes du profil USI 1 (voir les figures 3 et 4 pour la légende des unités stratigraphiques).

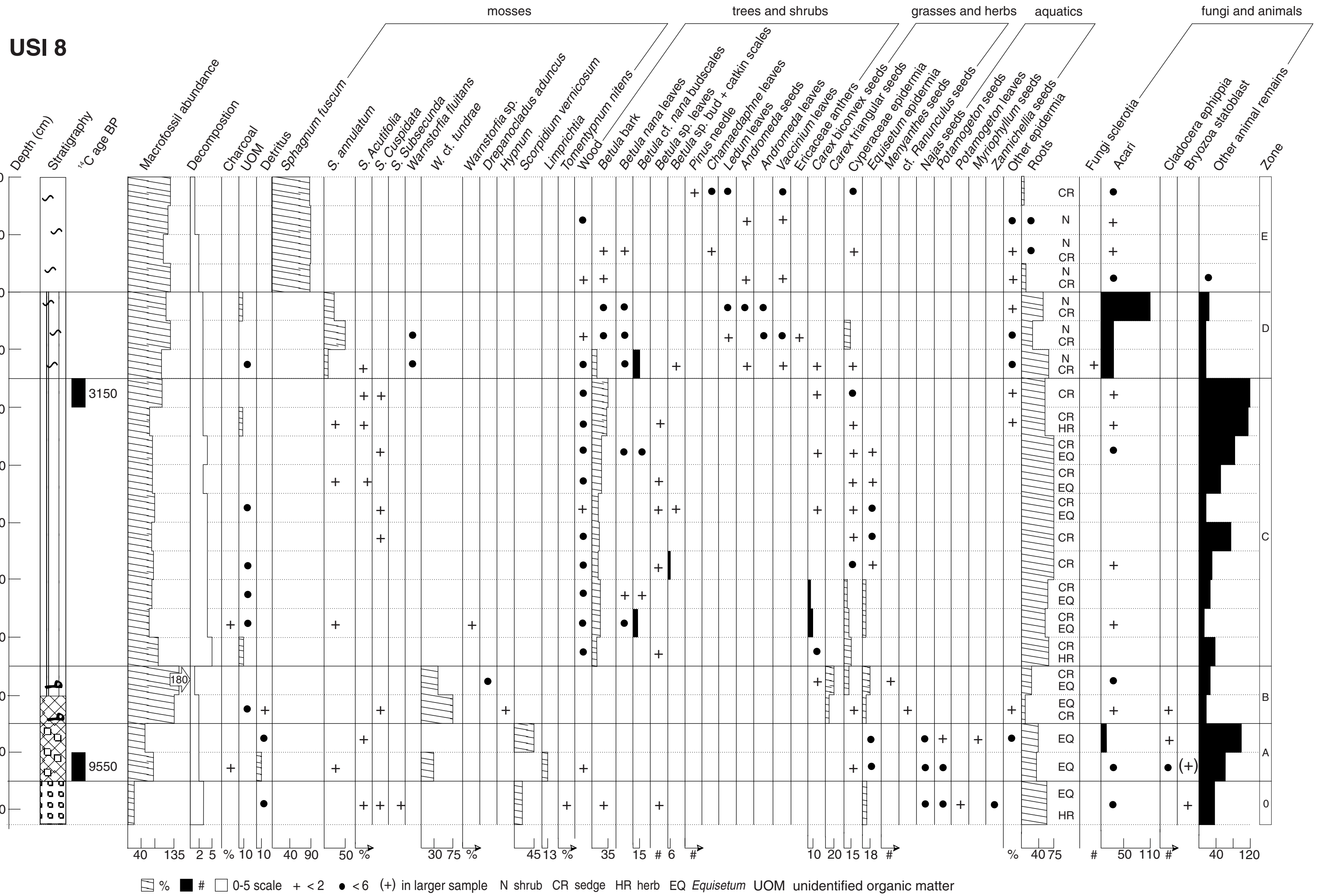

FIGURE 6. Plant macrofossil diagram of profile USI 8. Legend of the stratigraphic units as in Figures 3 and 4.

Diagramme des macrofossiles de plantes du profil USI 8 (voir les figures 3 et 4 pour la légende des unités stratigraphiques).

seeds are of the triangular type. There are single findings of seeds of *Menyanthes* and cf. *Ranunculus,* and an ephippium of Cladocera.

Zone USI 8 C, 170-70 cm, *ca*. 7800-*ca*. 3000 BP

BD is 0.18 g/cm^3, LOI, 97.5 %, and C/N, 21. The material is moderately to well-humified peat, mainly composed by roots of Cyperaceae, *Equisetum* and herbs (50-75 %). Bark of *Betula* (10-30 %) is an important component as well. All the recognized *Betula* remains are of the dwarf-shrub type. *Equisetum* and Cyperaceae *epidermia* are frequently present. All *Carex* seeds are of the biconvex type. A few leaves of *Sphagnum annulatum* and other *Sphagna* are found.

Zone USI 8 D, 70-40 cm, *ca*. 3000-*ca*. 1700 BP

BD is 0.17 g/cm^3, LOI, 98.5 %, and C/N, 23. Peat is moderately decomposed. *Sphagnum annulatum* (10-50 %) has a prevalent role together with roots of Cyperaceae and shrubs. Cyperaceae epidermia and other dwarf-shrub remains (*Betula nana, Ledum, Andromeda, Vaccinium*) are also well represented. *Warnstorfia fluitans* is present. The amount of Acari is noticeable.

Zone USI 8 E, 40-0 cm, <*ca*. 1700 BP

BD is 0.06 g/cm^3, LOI, 98.5 %, and C/N, 51. The deposit is weakly humified peat, mostly composed by *Sphagnum fuscum* (85-90 %). Also present are *Betula nana, Chamaedaphne, Ledum, Andromeda* and *Vaccinium*. A *Pinus* needle is found in the uppermost sample.

OTHER NON-PERMAFROST SITES

A gross stratigraphic description is available for another site from the string-pool complex in a permafrost-free zone of the study area (for location see Fig. 2A). Profile USI 5 was collected from a *Sphagnum fuscum* hummock located 35 cm above the adjacent flark level. No ice was encountered. The uppermost 120 cm of the profile is *Sphagnum* peat without any dark layers.

Probing was conducted in a small lake (profile USI 9 in Fig. 2A). Water depth was measured to a maximum of 1.2 m. One sample was taken at 100 cm from the basal dy deposit. Dry bulk density of the sample is 0.15 g/cm^3, organic content, 59.0 %, and C/N, 14. The deposit consists mostly of red-coloured detritus (90 %). The few other remains are moderately decomposed and include epidermal tissues of sedges and herbs, leaves of *Betula* (tree birch), *Drepanocladus* (*sensu lato*) and ephippia of Cladocera.

INTERPRETATION

MIRE DEVELOPMENT BEFORE PERMAFROST AGGRADATION

In all described Usinsk profiles, the mineral bottom is sand, pointing to the activity of glacial melt water rivers after a channel had broken in the ice front that blocked the waters of Lake Komi (Mangerud *et al.,* 1999). The former lake and river activity left behind a wet landscape with numerous small lakes and ponds. In this study, the oldest dated organic material is dy (profile USI 1), providing an age of 11 350 BP. Characteristic taxa found in this deposit are *Equisetum*, *Betula* and *Scorpidium scorpioides.* The basal date falls into the Allerød (12 000-11 000 BP), which was a warmer episode of the Late Glacial. Climate was severely continental (Khotinskyi, 1984a). According to Neustadt (1984) the oldest modern mires in the former Soviet Union date from about 12 000 ^{14}C BP. Permafrost was most likely present in the region (Zelikson, 1997), but local development at site USI 1 started under wet, permafrost-free conditions. The site was first a pond, as shown by detritus and the presence of *Potamogeton* and Cladocera. A fair amount of *Equisetum, Carex* and mosses indicates shallow water, with *Equisetum* probably growing *in situ*. The pool subsequently terrestrialized into a wet eutrophic fen.

The other available basal date, 9550 BP, has been obtained from the dy deposit of profile USI 8. At that time, the site was probably a small body of open water with nearby shores, as indicated by the presence of remains of some terrestrial taxa. In the pond grew plants like *Najas* cf. *flexilis* and *Zannichellia*, which are not found in the area today. Their nearest modern growing sites in Russia are the Onega Lake, Russian Karelia, for *Najas flexilis* and the White Sea shores for *Zannichellia palustris* (*sensu lato*). The main present distribution of *Zannichellia* and of all *Najas* species in Russian freshwater habitats is more than 800 km to the south or southwest, although in Finland they are also found at the latitude of the study area. However, in the north, *Zannichellia* and most *Najas* species are restricted to brackish water and/or a maritime environment. Furthermore, *N. flexilis*, *Potamogeton gramineus* and *Scorpidium vernicosum,* remains of which are also found in the pond deposit, are more common in freshwater ecosystems (Tolmachev, 1974; Hultén and Fries, 1986; Eurola *et al.,* 1992; Hämet-Ahti *et al.,* 1998). Thus, we conclude that the former presence of *Najas* cf. *flexilis* and *Zannichellia* supports the interpretation that climate was warmer during the early Holocene than at present (MacDonald *et al.,* 2000). The site USI 8 developed from a pond into a wet, meso- or eutrophic brown-moss fen. The moss composition indicates the effect of moving surface waters.

The early Holocene seems to have been a favourable time for mire initiation; oldest reported basal dates from the modern forest-tundra (Oksanen *et al.,* 2001) and tundra (Kaakinen and Eronen, 2000) fall into the period 9400-9200 BP. In Usinsk, wet eutrophic fens prevailed. The main peat formers were Cyperaceae, *Equisetum, Limprichtia* and *Warnstorfia* cf. *tundrae*. After about 8000 BP, mosses became less important; fens were Cyperaceae or *Scheuchzeria*-dominated. All studied sites were wet, with rather open ground layers. Shrub *Betula* was common. These local conditions persisted almost unchanged until about 3700-3000 BP.

The macrofossil assemblages (wet Cyperaceae communities) in the peat deposits indicate a permafrost-free environment in the Usinsk mire during the early and middle Holocene. Especially *Scheuchzeria* is very rare in palsa mires (Botch and Solonevich, 1965; Alekseeva, 1974a; Tolmachev *et al.*, 1995; Oksanen, 2002). The lack of permafrost is in accordance with climate reconstructions, according to which mean annual temperatures were generally 2-4 °C higher between 9000-4600 BP than at present (Bolikhovskaya *et al.*, 1988; Kremenetski *et al.*, 1998; Andreev and Klimanov, 2000; MacDonald *et al.,* 2000). Soil temperatures during the Holocene climatic optimum have been estimated at 2-3 °C higher than today (Baulin *et al.,* 1984). An important cooling episode took place between about 4600-4100 BP (P'yavchenko, 1955; Khotinskyi, 1984b; Klimenko *et al.*, 1996; Andreev and Klimanov, 2000). Mean temperatures are estimated to have been lower than at present (Bolikhovskaya *et al.*, 1988). At this time, however, the studied Usinsk sites remained Cyperaceae-dominated fens without permafrost.

LATE HOLOCENE PERMAFROST AGGRADATION AND DYNAMICS

Significant changes in the local environment took place in the Usinsk mire between 3700 and 3000 BP, with the replacement of Cyperaceae or *Scheuchzeria*-dominated fens by *Sphagnum*-dominated communities. In three peat plateau sites, this succession is dated to 3745-3490 BP. The site USI 1 developed into a wet *S. balticum* bog. In nearby site USI 2, the lowermost *Sphagnum* peat sample is dominated by *S.* cf. *fallax*. In both cases, *in situ* permafrost was most probably absent at this stage. Both these species can occur near permafrost bodies (Oksanen, 2002), but without any other evidence, we assume that permafrost was not the cause for their appearance. Local autogenic succession (peat accumulation) seems a more probable reason. For profile USI 3, the *Sphagnum* species is not observed. Based on gross stratigraphy, Oksanen (2002) tentatively dated permafrost formation at sites USI 2 and USI 3 to 3750-3500 BP. In light of the more detailed information presented in this study it seems likely that permafrost aggraded, at least in USI 2, at a later stage. A *Carex* to *Sphagnum* peat transition was also observed at the peat plateau site USI 7 (not dated).

In profile USI 1, *Sphagnum balticum* was replaced by *S. magellanicum* between about 3000-2800 BP. Later on, *S. fuscum* became dominant. A cooler climate and the *Sphagnum* cover at the sites made permafrost aggradation possible (see also Zoltai and Pollett, 1983), frost heave causing further local surface drying. The *Sphagnum* peat deposit is characterized by the presence of numerous dark layers, which are also found in the *Sphagnum* peat of the other peat plateau and palsa profiles described in this study (see Fig. 3). The first dark layer in profile USI 1 is found in *S. magellanicum* peat (at about 2900 BP). The thin dark band (not analysed) could represent the first unstable embryonic palsa at the site, but *in situ* permafrost is absent for most of the time: *S. magellanicum,* which is not found on recent palsas/peat plateaus (Oksanen, 2002), remains present until about 2300 BP. After 2300 BP, permafrost became more established. In USI 1, permafrost remained highly dynamic. Some of the thin dark layers in the *S. fuscum* deposit represent wet phases (Cyperaceae), others correspond to dry phases (dwarf shrubs). At the *ca.* 70 cm level in USI 1 is found a layer (unidentified organic matter and abundance of animal remains), which points to the temporary development of a small pool. This indicates several stages of permafrost aggradation and (partial) degradation at the site. A similar development was revealed in the Rogovaya River peat plateau, where the first dark bands appear in *S. warnstorfii* peat (Oksanen *et al.*, 2001). Apparently, under very unstable permafrost conditions (freeze-thaw cycles in the scale of a few years or longer) low hummock species like *S. warnstorfii* and *S. magellanicum* are able to reappear after permafrost degradation, but are gradually replaced by *S. fuscum* that better tolerates drier conditions. Also the later, moist *S. fuscum/S. capillifolium* bog stage, is interrupted with a number of drier and wetter phases. It most likely represents a peat plateau stage, where shallow depressions developed and dried up several times. Just below the recent peat plateau deposit in USI 1 is a thick (5 cm) wet phase deposit (Cyperaceae), which probably indicates a more significant collapse of permafrost. The youngest absolute date, 315 ± 35 BP, is from below the wet phase, indicating that the extant peat plateau is recent. The collapse scar developed through a dry *Pleurozium* stage back into a moist peat plateau stage. The botanical composition of the uppermost deposits is somewhat unusual (*S. capillifolium, Pohlia*), but still compatible with a peat plateau habitat (Oksanen, 2002). The modern peat plateau is covered by dry lichen stage vegetation.

The development at USI 2 and USI 3 seems to be similar to USI 1. The sites developed through a wet *Sphagnum* stage to a stage with unstable permafrost conditions as suggested by the presence of dark layers in the *Sphagnum* peat. Based on gross stratigraphy, the development at palsa site USI 6 and peat plateau site USI 7 apparently displays the same characteristics. The lower macrofossil assemblage in the USI 4 profile indicates noticeably drier conditions than higher up. Although no peat deposit was reached within this short profile suggesting former permafrost conditions, the development from relatively dry to wet conditions supports field observations that the formation is a collapse scar.

The transition to *Sphagnum* in the string-pool complex at site USI 8 took place at around 3000 BP, when the *Carex* fen changed to a poor *S. annulatum* fen, with Cyperaceae and shrubs in the field layer. The *S. fuscum* peat starts from about 1700 BP. This stratum is without dark layers characteristic for upper peat plateau and palsa deposits. It also contains remains of *Pinus, Chamaedaphne* and Cyperaceae, which are rare in peat deposits formed under permafrost conditions (Oksanen, 2002). Dark interlayers are also absent in the USI 5 profile from a hummock in another string-pool complex (see Fig. 3). Both the USI 5 and USI 8 sites most likely developed under permafrost-free conditions for their entire history.

PEAT ACCUMULATION RATES

The peat and carbon accumulation rates calculated for this study are based on calibrated radiocarbon years (see Table III). The long-term average carbon accumulation rate (weighed for depth) calculated for profiles USI 1 and USI 8 is 19 gC/m^2/yr. That is within the normal range for the (extreme) northern taiga subzone. The value is slightly less than the average values obtained for northern boreal Canada, 23 gC/m^2/yr (Tarnocai, 1988), or for Finland, 26 gC/m^2/yr (Tolonen and Turunen, 1996), and higher compared to subarctic Russia, 13 gC/m^2/yr (Oksanen *et al.*, 2001), or subarctic Canada, 9 gC/m^2/yr (Tarnocai, 1988). The mean long-term vertical peat increment rate is 0.27 mm/yr, which is somewhat lower than values reported for peat deposits (0.34-0.70 mm/yr) in boreal Russia (Botch *et al.,* 1995).

The difference between carbon accumulation rates in the two dated intervals of the hummock profile USI 8 is small (Table III). The combined value calculated for the dy and *Carex* peat stages is 16 gC/m^2/yr; the value for the late Holocene *Sphagnum* peat stage is 13 gC/m^2/yr. The overall average is 15 gC/m^2/yr.

In the peat plateau site USI 1, the average carbon accumulation rate for the entire profile is 26 gC/m^2/yr. Particularly high accumulation rates are reported for two periods. The mean value obtained for the interval 5110-3580 BP is 49 gC/m^2/yr. This value is possibly too high due to compaction during sample collection (as discussed in Methods). Vigorous peat accumulation accompanies the latest collapse scar-peat plateau succession since 315 BP (49 gC/m^2/yr). Similarly high values are reported from ombrotrophic (apparently) palsa peat deposits from northern Sweden (36-45 gC/m^2/yr) corresponding to about the last 800 years (Malmer and Wallén, 1996). Oksanen *et al.* (2001) give an even higher value for a short interval of incipient permafrost in a peat plateau at Rogovaya River (93 gC/m^2/yr). During the mature peat plateau stages at Rogovaya, accumulation was low (7 gC/m^2/yr), mainly because of ceased accumulation after *ca.* 1500 BP (P.O. Oksanen, unpublished). This kind of mature permafrost stage is missing from the profiles of the Usinsk mire where accumulation seems to have continued until present. A lower vertical peat increment rate and fewer dark interlayers in peat plateau profile USI 3 suggest more stable permafrost conditions at this site. Apparently, incipient and highly dynamic permafrost conditions can be conducive to high peat accumulation rates compared to low or even negative rates observed in more mature permafrost. The dynamic permafrost stages can have even higher peat accumulation values than sites under permafrost-free conditions.

DISCUSSION

The detailed paleoecological results presented in this study and similar recently published data provide a first basis to discuss the timing of permafrost aggradation and subsequent dynamics in palsa and peat plateau mires of Northeast European Russia.

The oldest permafrost aggradation in mires of Northeast European Russia is radiocarbon-dated to *ca.* 4800 BP (Väliranta *et al.,* 2003). It is reported from the Ortino II peat plateau in the modern tundra zone, located about 280 km to the northwest of the Usinsk study area. First permafrost aggradation in the Rogovaya River peat plateau occurred at *ca.* 3100 BP (Oksanen *et al.*, 2001). This peat plateau is located in the modern forest-tundra zone, about 280 km to the northeast of the Usinsk mire. Also, the Ortino I peat plateau (Väliranta *et al.,* 2003) probably formed around this time. Conditions at the site of profile USI 1 in Usinsk remained permafrost-free through these time intervals, although an unstable embryonic palsa might have developed briefly around *ca.* 2900 BP. An important period of (renewed) permafrost aggradation at Rogovaya occurred at *ca.* 2200-1900 BP (Oksanen *et al.*, 2001). At profile USI 1, permafrost became well established after *ca.* 2300 BP although its condition remained highly dynamic. More permafrost aggradation took place also at Rogovaya since 600 BP (Oksanen *et al.*, 2001). The periods of permafrost aggradation seem largely to correspond with known periods of climatic cooling between 4600-4100 BP (early Subboreal), 3200-1900 BP (late Subboreal-early Subatlantic) and 600-100 BP (Little Ice Age) (see also Oksanen, 2002).

The upper layers of the peat plateau and palsa profiles in the Usinsk mire are characterized by *Sphagnum* deposits with many dark interlayers. Other processes than permafrost dynamics can cause this type of peat stratigraphy. For example, Tolonen (1987) interpreted humified lichen bands in *Sphagnum* peat of a southern Finnish bog to be a result of internal life cycles of *Sphagna*. Nevertheless, in a permafrost environment, the freeze-thaw cycles seem to be the main reason for relatively sudden changes observed in the local environment. In the Usinsk mire, this dynamic system is found in all five described palsa/peat plateau profiles. For comparison, in Rogovaya from six peat plateau profiles, only one points to similar conditions. The other sites include *Sphagnum* deposits without dark interlayers (permafrost flark at peat plateau level) and rapid *Carex* fen-*Sphagnum* bog-lichen peat plateau successions (Oksanen *et al.*, 2001).

The Usinsk type of palsa/peat plateau stratigraphy is not that common elsewhere either. In Scandinavia, the most usual palsa stratigraphy is an uppermost xerophilous peat layer directly covering flark peat (Vorren and Vorren, 1976; Oksanen, 2002). Alternating dry, moist and wet peat plateau phases have been earlier described from northern Québec (Couillard and Payette, 1985), and palsa deposits from the Scandinavian pine limit (Vorren, 1972) can be interpreted in the same way. A similar stratigraphy is reported from strings in some *aapa* mires, but at least some of these formations contain permafrost and more likely should be called string palsas (Vorren, 1972; Oksanen, 2002). Under colder climates like at the Rogovaya River peat plateau (Oksanen *et al.*, 2001) permafrost is probably more stable, whereas under warmer conditions like those prevailing at the southern limit of permafrost distribution in Northeast European Russia (the Usinsk mire) and Fennoscandia (Oksanen, 2002) repeated periods of aggradation and degradation seem to be more common. These highly dynamic permafrost conditions can be conducive to high peat accumulation rates in contrast to the low or even negative rates observed in more mature peat plateau stages (Oksanen *et al.*, 2001).

The rapid changes described in the permafrost stages of all Usinsk palsa/peat plateau sites and in one of the peat plateau profiles at Rogovaya (Oksanen *et al.*, 2001) are not exactly the same phenomenon as the full cycles of palsa growth and decay defined by Seppälä (1988). In both Usinsk and Rogovaya, dynamic permafrost conditions during the *Sphagnum fuscum* phase are probably related to changes in the depth of the active layer and surface moisture of the site, frequently without complete thawing of the permafrost. According to the theory of internal cyclicity of palsa development (Seppälä, 1988), a palsa matures and collapses into a flark from which a new palsa may arise. Remains of the earlier palsa stage may be preserved. The corresponding stratigraphy, as reported by P'yavchenko (1955), Sonesson (1970), Oksanen *et al.* (2001) and Oksanen (2002), is a thin xerophilous peat layer (*Dicranum,* etc.) followed by flark peat (*e.g.*, *S. lindbergii* and *S. riparium*). In west central Canada, peat fires play a major role in cyclic development of palsas (Zoltai, 1993). The absence of any significant amounts of charcoal in the peat deposits of palsas and peat plateaus in Northeast European Russia (this study; Oksanen *et al.*, 2001; Väliranta *et al.*, 2003) indicates that fire did not play a significant role in the permafrost dynamics of mire ecosystems in this region.

CONCLUSIONS

The studied part of the Usinsk mire started to develop at 11 350-9000 BP through the terrestrialization of ponds. The presence of *Zannichellia* and *Najas* cf. *flexilis* in the plant macrofossil record supports the interpretations that climate in the onset of the Holocene was already warmer than at present. Plant macrofossil assemblages with Cyperaceae and/or brown-mosses indicate that permafrost was absent during the early and middle Holocene. *Sphagna* became dominant peat-formers at 3700-3000 BP, mainly because of autogenic succession. *Sphagna* (and a colder climate) provided suitable conditions for permafrost aggradation. The first tentative sign of permafrost is dated to 2900 BP. More established permafrost is found after 2300 BP, but permafrost conditions remained highly dynamic. Repeated (partial) thawing and renewed permafrost aggradation resulted in the characteristic peat stratigraphy with numerous dark interlayers. Organic accumulation is high in this kind of dynamic permafrost environment.

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