

Vegetation–Permafrost Relationships in the Zone of Sporadic Permafrost Distribution in the Kamchatka Peninsula

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Abstract—Studies on vegetation and permafrost table depth in the zone of sporadic permafrost distribution in the Uksichan River valley (the central Kamchatka Peninsula) have provided evidence that these components of biogeocenosis are interrelated and develop coordinately. In open larch forests with green forest mosses dominating in the ground vegetation layer, the permafrost table lies approximately 60 cm below the soil surface. When the ground vegetation layer is dominated by sphagnum, the permafrost table rises to 40–20 cm. In areas with a dwarf shrub–lichen ground layer, the soil thaw depth increases. A hypothesis is proposed that cyclic successional replacement of plant communities may take place in open larch forests on permafrost soils, including four consecutive stages with dominance of green mosses, sphagnum, lichens, and dwarf shrubs. In areas disturbed by fires, pioneer moss or herbaceous communities develop in the ground layer.

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Most studies on the vegetation–permafrost relationship have been performed in the zone of continuous permafrost in northern Eurasia (Tyrtikov, 1995; Abaimov et al., 1997). The distribution of frozen-soil phenomena and indicator vegetation types in the zone of discontinuous and sporadic permafrost have not been studied sufficiently, since studies in these regions were aimed primarily at more accurate delimitation of the permafrost boundary (Kolesnikov, 1939). Thus, the relationship between the presence of permafrost and the successional dynamics of vegetation in the sporadic permafrost zone is poorly known. Permafrost provides for the development of a specific type of plant communities with a deep moss (sphagnum) layer, and these moist moss phytocenoses, in turn, preserve ice lenses formed in the underlying soil. These processes in biogeocenoses are either cyclic (otherwise, the whole area would gradually transform into a vast bog on permafrost soils) or are limited by certain edaphic and topographic factors. We addressed this problem in our studies performed in Kamchatka.

The Kamchatka Peninsula is located in the far northeast of Russia in the zone of cold oceanic climate (Parrurzin, 1967). Its characteristic features are mountain topography, active recent volcanism, and vegetation pattern characteristic of severe environmental conditions, with prevalence of crooked stone birch forests

and elfin-wood formations in the tundra (Khomentovskiy, 1995, 2004). According to the scheme of permafrost zoning of the Northern hemisphere, the central and northern parts of the peninsula are in the zone of discontinuous and sporadic permafrost (Ives, 1974). In mountain regions of central Kamchatka, the lower boundary of discontinuous permafrost on northern slopes lies at an elevation of about 1000 m; below, down to 450 m a.s.l., permafrost occurs sporadically (Sone et al., 2003, 2006). Kazakov (2005) studied the distribution and characteristics of frozen-soil phenomena depending on topography and soil–plant cover in the mountain forest–tundra belt of central Kamchatka. The purpose of our study was to reveal the relationships between the pattern of vegetation and the presence and depth of permafrost in the zone of its sporadic distribution in subalpine open larch forests.

OBJECTS AND METHODS

Studies were performed in the Bystrinskii Nature Park located in the central part of the Sredinnyi Ridge, in the Uksichan River valley. This region is characterized by a denudation-tectonic landscape with a sharply dissected topography, formed on Pliocene deposits (Melekestsev et al., 1974). Slopes along the right bank of the river are flat or medium steep, covered with open

larch forests with Siberian dwarf pine and dwarf shrub-moss-lichen tundras. Left-bank slopes are steeper, with larch forests and pyrogenic birch forests. Both have seasonally frozen sandy loam-loam soils on deluvial-proluvial or, in the middle parts, deluvial-colluvial deposits (N.V. Kazakov, personal communication).

Descriptions of vegetation in 2 × 2-m plots were made in the lower and middle parts of the slopes, at elevations of 600–700 m a.s.l., in areas where the active soil horizon thawed to different depth and in similar control habitats where permafrost was absent. A total of 26 descriptions at six stations were made. In each plot, species composition of plants and coverage of each species were determined.

In the course of mathematical data processing, similarity between the plots was evaluated by correlation analysis of species composition (with regard to coverage) and ecological groups of plants. To check the hypothesis of cyclic successional replacement of vegetation, we developed a special method (in collaboration with D.A. Bakalin, Petrozavodsk State University). This method is based on the concept that the role of each species in the community changes in the course of succession from pioneering (minimum coverage) to the widest possible expansion (maximum coverage) and then gradually decreases until the species disappears from the community. An analysis of these relationships, taken together and superimposed on each other, allowed us to arrange the plots into a certain series corresponding to the direction of successional changes in vegetation.

The validity of this concept was verified by studying plant remains accumulated under the sphagnum layer on frost mounds. Samples were taken from two soil pits, 60 cm deep, at 5- to 10-cm intervals. The analysis of plant remains was performed by N.V. Stoikina (Institute of Biology, Karelian Scientific Center of the Russian Academy of Sciences, Petrozavodsk).

The names of plant taxa in the text and tables are given according to the following publications: Bakalin, 2005 (for liverworts); Ignatov and Afonina, 1992 (for mosses); and Yakubov and Chernyagina, 2005 (for vascular plants).

RESULTS AND DISCUSSION

With respect to the type of ground vegetation layer and the presence or absence of permafrost, all plots were classified into six groups (for descriptions, see Table 1):

(1) Wild rosemary-sphagnum communities on frost mounds with a high permafrost table (thaw depth 20–40 cm).

(2) Dwarf shrub-green moss and dwarf shrub-sphagnum communities on permafrost soils with a thaw depth of 40–60 cm.

(3) Sedge-moss and dwarf shrub-moss communities in habitats thinned by fires, without permafrost at depths reaching 70 cm (the level of stony horizon).

(4) Dwarf shrub and dwarf shrub-lichen communities with dominance of lichens and mesoxerophytic dwarf shrubs, without permafrost.

(5) Shrub-herb communities in pyrogenic birch forests, without permafrost.

(6) Pioneer pyrogenic liverwort-moss communities in areas of lichen forests with the litter completely destroyed by fire (*Marchantia polymorpha*, *Ceratodon purpureus*, *Pohlia nutans*; of vascular plants, *Chamaerion angustifolium*).

The presence of permafrost at small depth markedly changes the temperature regime of soils, compared to that in areas without permafrost. The results of soil temperature measurements are shown in Table 2.

The division of plots into groups based on correlation analysis for similarity in the coverage and spectrum of plant species representing individual taxonomic groups (vascular plants, true mosses, liverworts, and lichens) only partially coincided with division based on general characteristics of vegetation: the spectra of liverworts proved to be different in communities growing on frost mounds (group 1) and in frozen-soil areas without mounds (group 2); the spectra of true mosses allowed differentiation between the groups of shaded and nonshaded plots; the spectra of lichens were similar in virtually all plots undisturbed by fires; and characteristic spectra of vascular plants were described in birch forest, where test plots abounded in shrubs and mixed herbs. In general, these results show that similarity in the composition of individual taxonomic groups in plant communities is not a suitable criterion for indication of frozen soils.

Hence, habitats were subsequently differentiated with respect to ecological groups of plants, instead of individual taxa. We distinguished a total of 18 such groups. Vascular plants comprised the first seven groups: (1) shrubs, (2) mesohygrophytic dwarf shrubs, (3) mesoxerophytic dwarf shrubs, (4) grasses and sedges, (5) *Chamaerion angustifolium*, (6) mixed herbs, and (7) horsetails. Then followed four groups of mosses: (8) epigeic mesophytic true (green) mosses, (9) species of the genus *Polytrichum*, (10) species of the genus *Sphagnum* (indicators of moisture regime), and (11) pioneer species characteristic of sites with a damaged ground vegetation layer (*Ceratodon purpureus*, *Pohlia nutans*, etc.). Liverworts formed four ecological groups: (12) epigeic mesophytic liverworts (all common forest species forming an individual layer or growing on mosses or foliose lichens), (13) epigeic mesohygrophytic liverworts (species of the genera *Cephalozia* and *Calypogeia* growing as epiphytes on sphagnum mosses), (14) species of the genus *Cephaloziella* growing on dying mosses and indicative of soil cover degra-

Table 1. Species composition and coverage of plants in test plots, %

Species composition	Plant communities														
	sphagnum			dwarf shrub-moss			sedg-moss		dwarf shrub-lichen			dwarf shrub-herb			
	1.1-1.3	2b.1; 2.1	4.4	3.3	3.4; 3.7; 4.3	6.3	3.1	2a.1	2.3; 2.4	3.2; 3.5	2.2	4.1; 4.2	3.6	5.1-5.3	6.1
Liverworts															
<i>Barbilophozia barbata</i>		r		r	r		2			1-2			r		
<i>B. hatcheri</i>		r	r	r	r		15								
<i>Calypogeia muelleriana</i>	0-1	r	r					r	r	0-1	1	r			
<i>Cephalozia bicuspadata</i>	1-3	r	r					r	r	r		r			
<i>Cephalozia</i> sp.															
<i>Lophozia longidens</i>			r	r											
<i>Ptilidium ciliare</i>			r	r			5								
Mosses															
<i>Aulacomnium palustre</i>	r-2							20	8-20	r-8	8	r	r		
<i>Ceratodon purpureus</i>	r-20														
<i>Dicranum bergeri</i>			r			7						6-7			
<i>D. fuscescens</i>												0-1			
<i>D. scoparium</i>															
<i>Hylocomium splendens</i>				40			r			r			r		
<i>Plagiothecium laetum</i>			r												
<i>Pleurozium schreberi</i>	r	r	25	25	40-70	9	28	r		10-15	r	1-6	8		
<i>Pohlia nutans</i>	r-5	1-2			0-1					r-3	3	r			
<i>Polytrichum commune</i>	0-10	r	r	25	0-20		35	35	r	2-4					
<i>P. juniperinum</i>	0-1	0-1				7		5	7	0-1					
<i>P. piliferum</i>								r	r-1						
<i>P. strictum</i>									3			0-2	1		
<i>Sanionia uncinata</i>			5			7									
<i>Sphagnum girgensohnii</i>	20-60	85-92	50												
Lichens															
<i>Cladonia arbuscula</i>				1	0-1		2		r	0-3	1	15-30			
<i>C. botrytes</i>					0-1					0-1					
<i>C. chlorophaea</i>					0-1					r	4				
<i>C. cornuta</i>					0-1										
<i>C. gracilis</i>	r	r			0-1		r		r			0-1	4		
<i>C. mitis</i>	0-2				0-1										
<i>C. rangiferina</i>	0-5			2			2			3-4	4	25-30	1		
<i>C. rei</i>	0-1				r										

Table 1. (Contd.)

Species composition	Plant communities														
	sphagnum		dwarf shrub-moss		sedge-moss		dwarf shrub-lichen		dwarf shrub-herb						
	1.1-1.3	2b.1; 2.1	4.4	3.3	3.4; 3.7; 4.3	6.3	3.1	2a.1	2.3; 2.4	3.2; 3.5	2.2	4.1; 4.2	3.6	5.1-5.3	6.1
<i>C. stygia</i>					r-1	r	1	r	r	r-4	r	1	25		
<i>Peltigera aphthosa</i>	0-1							r	r	r	r	1			
<i>P. didactyla</i>												1			
<i>P. malacea</i>												1			
<i>Stereocaulon paschale</i>												18-40			
Vascular plants															
<i>Betula divaricata</i>			2				r				r				1
<i>B. ermanii</i>															40
<i>Calamagrostis langsdorffii</i>								r	r	0-1	r				5
<i>Carex lasiocarpa</i>		0-15		r			r	r	40-55	r	1				3
<i>C. pallida</i>						10	r	r							
<i>Chamerion angustifolium</i>															
<i>Deschampsia cespitosa</i>															
<i>Empetrum nigrum</i>		1-3	r												
<i>Equisetum pratense</i>															
<i>Galium boreale</i>															
<i>Lathyrus pilosus</i>															
<i>Ledum decumbens</i>		13-20	20	20	0-28		10	2	r	1-20	2	6-10	5		1
<i>Lonicera caerulea</i>				r	r	5	1			r			r		2
<i>Majanthemum bifolium</i>															
<i>Pyrola incarnata</i>															
<i>Rubus arcticus</i>															
<i>Spiraea media</i>				r											
<i>S. salicifolia</i>		0-1													
<i>Thalictrum minus</i>															
<i>Vaccinium minor</i>		2-3	30	10	5-30	1	8	0	r	2-35	2	10	15		r
<i>V. uliginosum</i>		0-2	r	r	r-20		3	7	3-9	r-1			r		r

Note: Columns for more than one plot show the range of variation in coverage; "r" indicates coverage below 1%. The taxa represented by single plants and not listed in the table are as follows: *Calyptogeia intergristipula* (1.1), *Cephalozia pleniceps* (1.3), *Lophozia excisa* (3.6, 4.1), *L. ventricosa* (4.3), *Orthocaulis kanzeanus* (3.3, 4.1), *Brachythecium* sp. (1.3, 2.3), *Pohlia cruda* (1.2), *Sphagnum* sp. (4.4), *Cladonia amoro-racea* (4.1), *C. bacilliformis* (2.2), *C. coniacraea* (1.1, 1.2), *C. furcata* (3.5), *C. maxima* (4.4), *C. ochroleuca* (3.3), *Flavocetraria nivalis* (4.1), *Peltigera rufescens* (6.3), *Calamagrostis purpureus* (2.2), *Clematis fusca* (6.1), *Equisetum arvense* (4.4), *E. hiemale* (5.1-5.3, 6.3), *Filipendula palmata* (6.1), *Geranium sylvaticum* (6.1), *Moehringia lateriflora* (6.1), *Pedicularis resupinata* (6.3), *Pleurospermum uralense* (6.1, 6.3), *Salix bebbiana* (6.1), *Trisetum altaica* (5.1), and *T. sibirica* (5.2). Pioneer pyrogenic communities described in plot 6.2: *Marchantia polymorpha*, 25%; *Ceratodon purpureus*, 15%; *Pohlia nutans*, r; *Chamaerion angustifolium*, 78%.

Table 2. Soil temperatures in plots with lichen and sphagnum ground layers, °C (September 12, 2004)

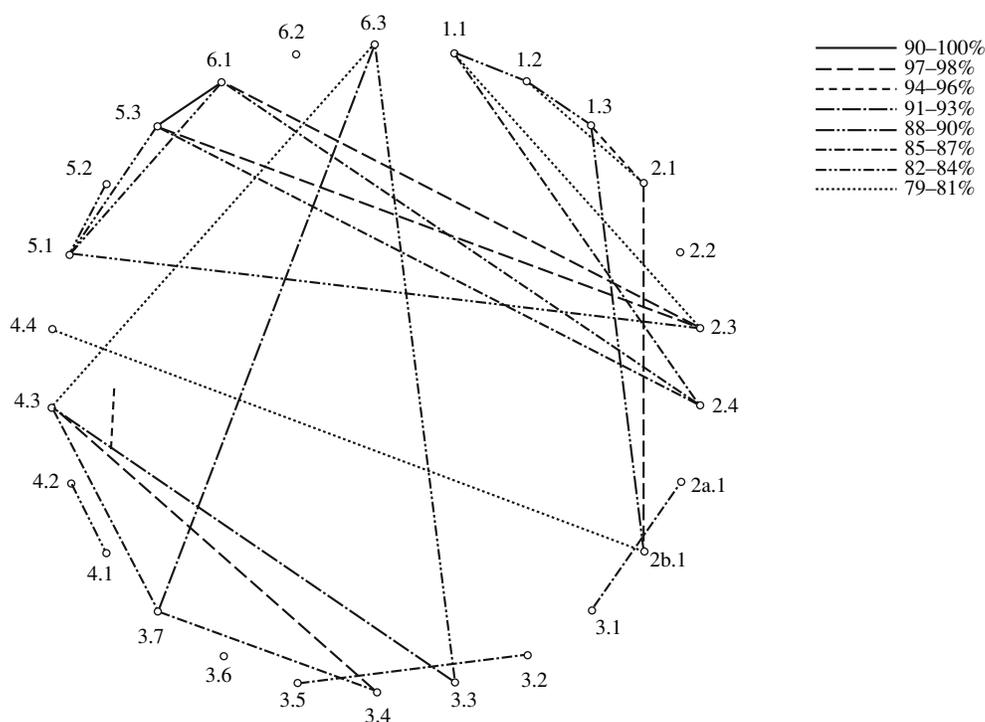
Depth, cm	Plot 4.2, lichen ground layer	Plot 4.4, sphagnum ground layer
0	7.5	8.0
10	5.2	5.2
20	4.5	2.2
30	4.3	0.5
40	4.0	0.3
45	3.9	0 (with ice below)
55	3.7	Ice

dation, and (15) *Marchantia polymorpha* (characteristic of sites with a damaged ground vegetation layer). Lichens were divided into three groups: (16) epigeic mesoxerophytic lichens, (17) xerophytic lichens (species of the genus *Stereocaulon*), and (18) species of the genus *Peltigera* (segregated into an individual group due to their specific ecological strategy: they extend their lobes and “crawl” over clusters of mosses or other lichens, eventually killing them).

The results of correlation analysis for similarity between the plots with respect to the total coverage of

ecological plant groups agreed well with the aforementioned division of habitats by the type of ground vegetation depending on the presence and depth of permafrost. At a similarity level of 97%, three groups of plots were identified (Fig. 1): plots with a well-developed herbaceous layer (5.3, 6.1, and 2.3), plots with a sphagnum layer almost undamaged by fires on frozen soils (2.1 and 2b.1), and dwarf shrub–*Pleurozium synusiae* on frozen soils in shaded areas (4.3 and 3.4). At a similarity level of 91–94%, additional group connections were revealed between plots with a sphagnum layer on permafrost (1.1–1.3, 2.1, and 2b.1), communities on permafrost in shaded areas (4.3, 3.4, 3.7, and 6.3), and plots with a herbaceous layer (5.1–5.3, 6.1, and 2.3).

The results of statistical analysis show that the total spectrum of plant species divided into ecological groups is a good indicator of habitat conditions. Plots with a relatively high permafrost table (20–40 cm) are characterized by the presence of sphagnum layer and formation of sphagnum cushions and mounds with a complex of hygrophytic liverworts (species of the genera *Calypogeia* and *Cephalozia*). These species are the main indicators of permafrost location close to the surface. The permafrost–sphagnum relationship is bilateral: due to the low heat conductivity of peaty layer, the active horizon of frozen soils thaws to a smaller depth and, therefore, the permafrost table rises. Siberian dwarf pine and forest mosses (*Pleurozium*, *Hyloco-*

**Fig. 1.** Similarity of vegetation in test plots according to the results of correlation analysis.

mium, etc.) growing under its canopy form another heat-insulating complex. Siberian dwarf pine thickets with sphagnum are regarded as reliable indicators of permafrost throughout the geographic range of the Siberian dwarf pine (Kolesnikov, 1939; Molozhnikov, 1975; Kazakov, 2005). Permafrost under Siberian dwarf pine thickets of wild rosemary and moss-lichen types occurs less frequently (Molozhnikov, 1975).

Fires destroy dwarf pine thickets and damage the moss layer, which leads to the replacement of vegetation, changes in the soil thermal regime, and recession or degradation of the permafrost table. In larch forests on well-warmed steep slope of southern exposure, post-fire regeneration involves the replacement of primary communities by pyrogenic birch forests with a shrub-herb ground layer. Under such conditions, permafrost occurs only in the lower parts of the slopes, in areas slightly disturbed by fire (with the moss layer being preserved) and shaded by larch and Siberian dwarf pine crowns.

An analysis of relationships between the structure of ground vegetation layer and the depth of permafrost thawing in open areas within dwarf shrub-lichen-moss open larch forests and open larch forests with Siberian dwarf pine undergrowth suggested that the pattern of cyclic replacements of vegetation in these habitats may be as follows:

(1) *Forest moss stage*. The ground layer consists of common forest mosses such as *Pleurozium schreberi*, *Hylocomium splendens*, or, less frequently, *Polytrichum commune*. The permafrost table is at a depth of about 60 cm. Increased moisture content promotes invasion of sphagnum mosses.

(2) *Sphagnum stage*. Sphagnums displace forest mosses and produce a peaty layer of nondecomposed remains accumulating under the cover of live sphagnum plant. The soil thaw depth decreases, and the permafrost table rises to 20–40 cm from the surface. As the cover of sphagnum mounds grows thicker, the hydrologic connection between the permafrost lens, soil, and mound surface become disturbed. Sphagnums begins to die off and provide a substrate for invading ruderal moss species (*Ceratodon purpureus*, *Pohlia nutans*, etc.) and forest lichens (*Cladonia*, *Cladina*, or, less frequently, *Peltigera*). Lichens subsequently displace mosses almost completely.

(3) *Lichen stage*. The soil thaw depth under the lichen ground layer increases, and the permafrost table recedes significantly. Later, dwarf shrubs appear amid lichens, and a lichen-dwarf shrub layer is formed.

(4) *Dwarf shrub stage*. A developed dwarf shrub layer is composed mainly of *Ledum palustre* subsp. *decumbens* and *Vaccinium uliginosum*. Under their canopy, green forest mosses begin to settle. The permafrost table rises, and soil moisture increases. Mosses

gradually displace dwarf shrubs, and the ground vegetation layer returns to the forest moss stage.

An analysis of plant remains from under the sphagnum layer on frost mounds showed that sphagnum mosses were a permanent component of samples from both soil pits, but their species composition and amount varied considerably (Table 3). The distribution of plant remains provided evidence for periodic change to more xerophytic vegetation of a dwarf shrub type with the involvement of sedges and shrub birch (probably *Betula exilis*). Distinct layers containing the remains of forest mosses (*Dicranum*, *Polytrichum*, *Pleurozium schreberi*) were identified. Most layers contained the remains of *Pinus pumila*, which were often charred.

Probable vegetation changes reconstructed on the basis of samples from pit 1 is as follows:

(1) Sedges and horsetails settle on alluvial deposits. This layer is gradually invaded by dwarf shrubs of the heath family (Ericaceae) and shrub birch (supposedly *Betula exilis*).

(2) Sedges and birch remain in the community, and a small proportion of sphagnum appears. Later, the vegetation undergoes eutrophication.

(3) The eutrophic period gives place to a mesotrophic period; alder, Siberian dwarf pine, and crowberry appear.

(4) The stage of forest mosses begins (*Pleurozium schreberi*, *Polytrichum* spp., *Dicranum* spp.). The proportion of sphagnums is small but gradually increases.

(5) Forest mosses are mostly displaced by increasingly abundant sphagnums. Species diversity is reduced. The surface is covered with a continuous sphagnum layer with sporadic sedges and dwarf shrubs.

(6) Oligotrophic mosses and liverworts appear.

(7) The sphagnum layer on top of the mound begins to die off; lichen and dwarf shrubs appear. Later, a lichen-dwarf shrub stage will probably begin.

This reconstruction confirms the probability of a successional cycle with the change of plant communities from the herbaceous stage, through the green moss stage, to the sphagnum stage. The results of reconstruction based on samples from pit 2 are generally similar. The only difference is that dwarf birch-moss-dwarf shrub tundra vegetation was found to prevail at the initial stage, with the herbaceous layer being less developed. Similar successional transformation of the ground vegetation layer on permafrost—from the herbaceous stage, through the green moss stage, to the sphagnum and dwarf shrub-lichen stages—was revealed in open larch forests growing on alluvial deposits in river valleys of northeastern Yakutia and western Siberia (Tyrtikov, 1995). In these lowland regions, however, open larch forests are replaced by tundras.

A mathematical analysis of interrelated changes in the proportions of individual ecological groups of plants confirmed the validity of the above scheme of

Table 3. Composition of plant remains (% , relative to their total volume) in the peaty layer on frost mounds

Plant species composition	Depth, cm								
	0–10	10–20	20–30	30–35	35–40	40–45	45–50	50–55	55–60
Pit 1									
<i>Betula exilis</i>	+	+		20	20	5	10	10	
<i>Betula</i> sp.				5					10
<i>Larix cajanderi</i>				5					+
<i>Salix</i> sp.					5		5		
<i>Alnus</i> sp.					5	+			
<i>Pinus pumila</i>	+	5	5	10		+			
<i>Ericaceae</i>					5	5	+	5	5
<i>Ledum</i> sp.			5						
<i>Empetrum nigrum</i>	10	10	10	5	+	5			
<i>Vaccinium</i> sp.		5	+	5	+				
<i>Oxycoccus</i> sp.	5								
<i>Equisetum</i> sp.									5
<i>Carex</i> spp.	+	5	5	5	20	80	70	65	65
<i>Eriophorum</i> sp.				+	5		5	5	5
<i>Calamagrostis</i> sp.	10	+		5	15		+	5	
Unidentified herbaceous remains	5	5	5				5	5	
<i>Sphagnum girgensohnii</i>	70	70	70	35	20	5			
<i>Sp. sect. Acutifolia</i>								5	10
<i>Scorpidium scorpidioides</i>							+		
<i>Pleurozium schreberi</i>				5	+				
<i>Polytrichum</i> sp.				+	5			+	
<i>Aulacomnium palustre</i>	+								
<i>Dicranum</i> sp.					+				
Liverworts	+								
Pit 2									
<i>Betula exilis</i>		10	15	20	55	25	75	65	45
<i>Betula</i> sp.	5				5				
<i>Larix cajanderi</i>			5	15		+			
<i>Salix</i> sp.									+
<i>Alnus</i> sp.							+		
<i>Pinus pumila</i>	+	5	10	50	10	5	5	+	5
Unidentified (charred) woody remains						20			20
<i>Ericaceae</i>				5	5	5	+	5	
<i>Empetrum nigrum</i>	10	5	5					+	
<i>Vaccinium</i> sp.	+		5						
<i>Oxycoccus</i> sp.	5	+	+						
<i>Equisetum</i> sp.						10	5	5	5
<i>Carex</i> spp.	5	15	5	5	15	20	15	15	15
<i>Eriophorum</i> sp.			5	+		5			
<i>Calamagrostis</i> sp.	+				5	5		+	
Unidentified herbaceous remains						5		5	5
<i>Sphagnum girgensohnii</i>	75	65	40	5	5				
<i>Sp. squarrosum</i>			+						
<i>Sp. sect. Acutifolia</i>						+	+	5	5
<i>Pleurozium schreberi</i>			10						

Note: Samples from the layer 35–40 cm and deeper consisted mainly of ash and sand, with the proportion of plant remains being about 15%. The plus sign indicates an insignificant content of plant remains.

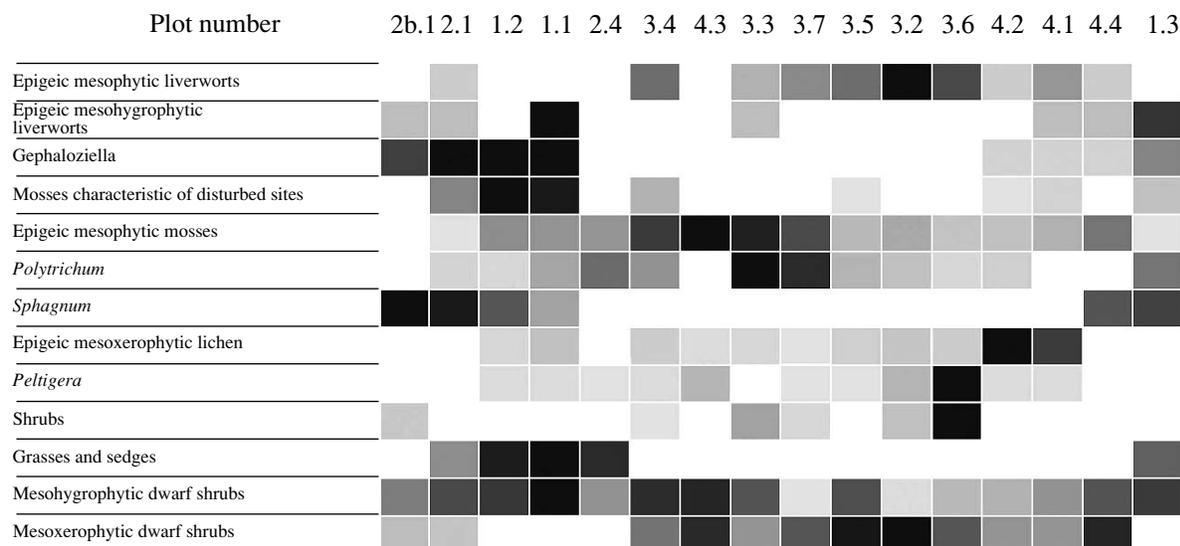


Fig. 2. Sequence of plots calculated from changes in the total coverage of species belonging to different ecological groups.

changes in the ground vegetation layer on permafrost. To eliminate the influence of random factors related to fire damage of plant communities, corresponding plots were excluded from analysis. After computer data processing, we obtained the following sequence of stages (Fig. 2): sphagnum stage (plots 2.b1, 2.1, 1.2, 1.1) ↔ moss–herb (plot 2.4) or moss–dwarf shrub stage (plot 3.4) ↔ forest moss stage (plots 4.3, 3.3, 3.7) ↔ lichen–xerophytic dwarf shrub stage (plots 3.5, 3.2, 3.6, 4.2, 4.1) ↔ sphagnum–mesohygrophytic dwarf shrub stage (plots 4.4, 1.3).

Thus, the results of field observations and analytical data provide evidence that the development of ground vegetation in the study region has a bilateral connection with the permafrost table depth. Successional changes of the ground vegetation layer show a sequence of stages during which the permafrost table recedes and rises again. Fires lead to the replacement of vegetation and increasing depth of permafrost thawing. Upon restoration of the moss layer and rise of the permafrost table, the replacement of pyrogenic communities by primary communities is probable.

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