

Landscape mosaic in the treeline ecotone on Mt Rodjanoaivi, Subarctic Finland

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The objective of this paper is to differentiate the landscape in the treeline ecotone in Subarctic Finland with an examination of its mosaic structure and functional role in treeline dynamics. Highly varying topography is a key factor controlling drainage conditions, vegetation, local climates and soils. Natural drainage classes, soil data (pH, C_{org} , N_t , C/N ratio, moisture) and dominant vegetation were used to characterize site conditions and to show the grouping of six representative sites along a synthetic topographical transect (model). The abrupt increase in soil moisture and pH values at the distal end of the lowest zones indicates a relatively sharp and ecologically important limit between well drained sites (ridge tops, upper valley side, interfluves) and valleys with both poorly and very poorly drained sites. Remains of birch wood in wind-scarps, hummocks and peaty layers give evidence of former open birch forest in present treeless sites. Forest decline has enforced the contrasts in site conditions between wind-swept and snow accumulating topography. The landscape mosaic and resultant site conditions are strongly influencing treeline dynamics and consequently, the landscape mosaic needs to be carefully considered when discussing the possible effects of the changing climate in the treeline ecotone.

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Introduction

In the Subarctic Finland, treeline usually occurs as altitudinal ecotones reaching from the closed mountain birch forests (*Betula pubescens* ssp. *czerepanovii*) to the scattered and usually stunted individuals of this tree species. Due to the effect of high latitude the treeline is located at relatively low elevation at about 300 to 380 m a.s.l. (Holtmeier 1974; Seppälä & Rastas 1980). The width of the treeline ecotone depends for its most part on the mountain slope gradients and is usually wider on gently sloping terrain than on steep slopes. The treeline is characterized by considerable patchi-

ness mainly caused by the effects of topography on site conditions – such as drainage, wind and translocation of snow, and the resulting effects on soil moisture, and temperature, etc. The distribution pattern of the vegetation units clearly reflects these conditions (Holtmeier 2003, 2005a).

The objective of this paper is to differentiate the landscape mosaic in the treeline ecotone using topography-dependent landscape spatial-ecological units (site types) identified by vegetation, soils and natural drainage classes and to assess the influence of the landscape mosaic on natural regeneration of the mountain birch. This is demonstrated with examples from one of our study areas, which

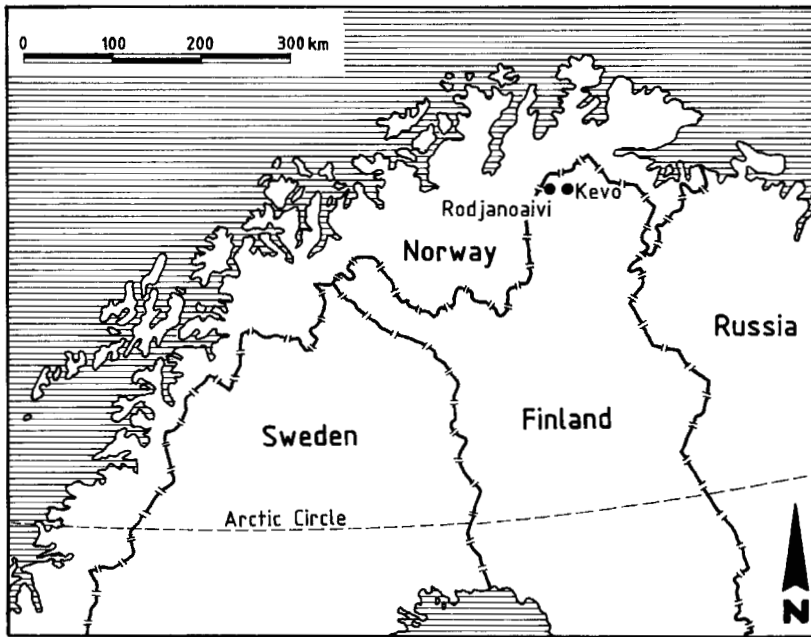


Fig. 1. Location of Rodjanoaivi, northern Utsjoki.

we consider to be representative of the treeline ecotone in northern Finnish Lapland. The intention of the present paper is to draw attention to the spatial structures and their functional role (e.g., Forman 1995) in treeline dynamics at the landscape scale, particularly in view of the on-going discussion on the possible response of the altitudinal and northern treeline to a changing climate (Holtmeier & Broll 2005).

Study area

The studies were carried out on the northwest-exposed slope of Rodjanoaivi (509 m a.s.l.), a gently rounded fell top (Figs. 1 and 2). While the upper and lower parts of the mountain slope are relatively steep, the slope gradient at the level of the treeline ecotone is comparatively gentle. The study area is located within the zone of discontinuous permafrost where periglacial processes are active and diverse (Seppälä 1997; Hjort 2006). The area belongs to the granulite complex of northern Finnish Lapland (Korsman et al. 1997). Sandy-skeletal basal melt-out till mixed with preglacial saprolite covers the bedrock in most parts of the treeline ecotone. A thick till (up to three metres) has become dissected by melt waters and the small tribu-

aries of the Teno River. As a result, the land surface is characterized by a locally varying topography. Small ridges rounded and widened on top with gently sloping interfluves slightly rise for a few metres up to about 20 metres above the Tsierrromjohka and its diminutive headwaters. Locally, small bedrock outcrops project through the till. Due to the influence of the varying surface in the treeline ecotone on blowing snow (Holtmeier et al. 2004; Holtmeier 2005a), snow depth varies widely and abruptly. In wind-swept places, the snow cover does usually not exceed a few centimetres depth whereas it may reach a metre or more at accumulation sites (Holtmeier 1974).

In northern Finland, the winter is the windiest season (Autio & Heikkinen 2002). On Rodjanoaivi, wind comes mainly from the west and northwest. The nearest meteorological station is located at the field station of Kevo Subarctic Research Institute (Fig. 1). The climate at Kevo meteorological station (107 m a.s.l.) is subcontinental with a mean annual air temperature of -1.7°C and a mean annual precipitation of 414 mm (Haapasaari 1988; Oksanen & Virtanen 1995). However, the climate can be compared with only caution to the windier climate at Rodjanoaivi as Kevo is located within pine forest in a relatively protected valley, whereas Rodjanoaivi lies within the subcontinental zone of

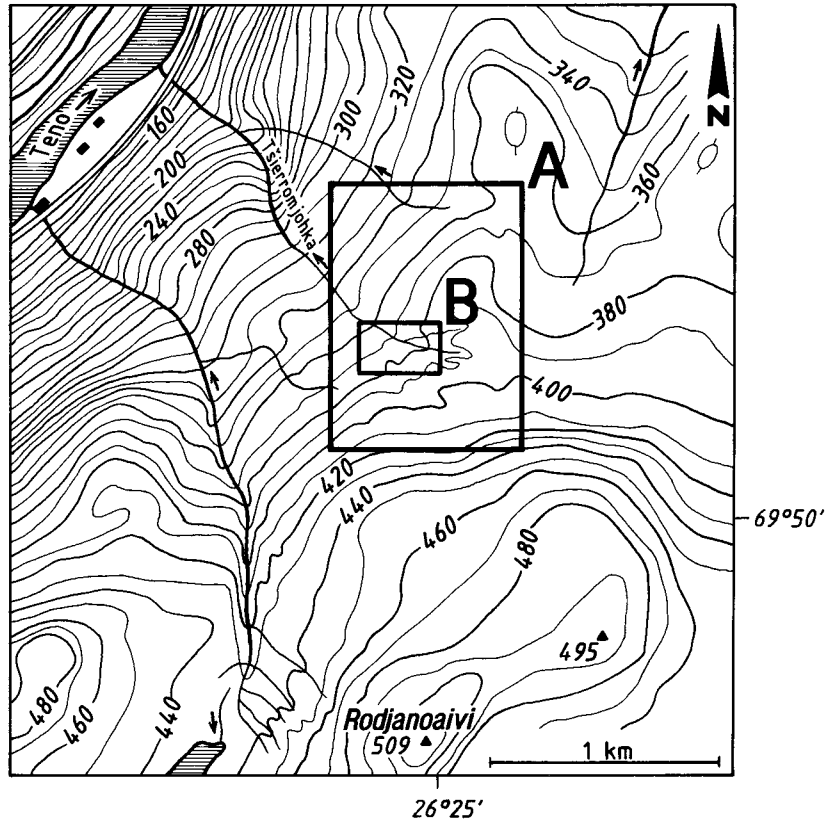


Fig. 2. Rodjanoaivi study area. A = area covered by the aerial photo (Fig. 3), B = mapped area (see Fig. 4).

northernmost Fennoscandia. In the treeline ecotone, winter temperatures are likely to be higher than at Kevo or in the valley of the Teno River where inversions are very common. Summer temperatures are likely to be lower because of greater elevation and mostly windy conditions.

On the wind-swept topography, the mountain birch forest becomes increasingly scattered at an altitude of about 240 m a.s.l. to 300 m a.s.l. Solitary trees (3 m to 5 m high, diameter 8 cm to 20 cm) and tree groves occur up to about 370 m a.s.l. mainly within the valleys and on wind-sheltered slopes (Figs. 4 and 5). In the present treeline ecotone, oligotrophic dwarf shrub-lichen-heath prevails locally alternating with exposed mineral soil.

Different kinds of Podzols and hydromorphic soils form a very locally varying mosaic, which largely corresponds to the vegetation spatial distribution pattern (Drees 2004; Wald 2004). Bare soil and bedrock debris (saprolite) are typical above the historical treeline. Soil acidity is generally high (ultra acid to very strongly acid, Schoeneberger et

al. 2002). The seasonally frozen soils show a cryic temperature regime with the long-term mean annual temperature at 50 cm depth above 0 °C (Broll 1994, 2000; Yli-Halla & Mokma 1998; Holtmeier 2003; Holtmeier et al. 2004).

Methods

The landscape mosaic was mapped using an enlarged oblique black-and-white-air photo (Topographical Survey of Finland) together with coloured photos taken by ourselves from an airplane cruising about 300 m above ground (Fig. 3). The map (Fig. 4) is based on the Topographical Map of Finland 1:20 000 (sheet no. 3914 06, Rodjanoaivi, 1977) and on aerial images. Detailed mapping was carried out in the field from 1998 onwards focusing on the distribution of soils and vegetation along characteristic topographical gradients from wind-swept and dry convex topography to better wind-protected moist to wet sites (leeward slopes, concavities). The results were used to develop a synthetic transect (model).



Fig. 3. North-west-facing slope of Rodjanoaivi. Photo taken from a low-flying aircraft (250–300 m above ground). View to the southeast. Extremely wind-eroded sites (ridge tops, upper rim of valley sides) occur as nearly-white patches. Wind-swept, gently sloping or almost level interfluvies show light-grey colour, whereas valleys and other depressions occur in dark-grey. (Photo F.-K. Holtmeier, 5 August 1998).

Vegetation was mapped using the Braun-Blanquet-method (Braun-Blanquet 1964; Westhoff & van der Maarel 1973). Coverage was estimated using a modified scale of Hult-Sernander-Du Rietz (after Daniëls 1987; for further information see Drees 2004; Anschlag 2006). The size of the plots varied from 4 m² in heath vegetation and hummocks to 9 m² on deflation sites, in willow shrub and grass bogs. Ten plots per site were mapped. The distribution pattern of the vegetation (identified by the dominant species) was used to demarcate different sites. Some dwarf shrub species, in particular *Betula nana* and *Empetrum hermaphroditum* are ubiquitous in the study area and show comparatively tall growth in wind-sheltered, snow-rich and moist sites. By contrast on wind-swept and dry topography they display espalier-like or mat-like growth. The differing physiognomy can therefore be used as an indicator of site properties.

Humus profiles were described and sampled at representative sites (= spatial-ecological units). Soil samples were taken from the litter layer, from the O horizon and from the A horizon. All soil chemical analyses refer to fine soil (≤ 2 mm). The samples were analyzed using standard methods for soil acidity, carbon and nitrogen. Organic carbon and total nitrogen content were measured by an elemental analyzer (Euro EA, EUROVECTOR) and soil acidity in 0.01 M CaCl₂ by using a glass electrode (Sparks et al. 1996). To describe soil acidity we use the descriptive terms (Schoeneberger

et al. 2002) based on pH classes: ultra acid (< 3.5), extremely acid (3.5 to 4.4) and very strongly acid (4.5 to 5.0). Higher pH does not occur in the study area.

Soil moisture was measured in the topmost 5 cm by TDR (Time domain reflectometry, Delta-T Devices Ltd., Cambridge) on one representative plot per site. Each plot measurement consisted of 10 randomly selected local measurements ($n = 700$). Soil moisture was measured weekly from 25.06.2003 to 27.08.2003. To characterize soil moisture conditions the following “natural drainage classes” (i. e. prevailing wetness condition of a soil; Schoeneberger et al. 2002) were used: excessively, well, moderately, somewhat poorly, poorly and very poorly drained.

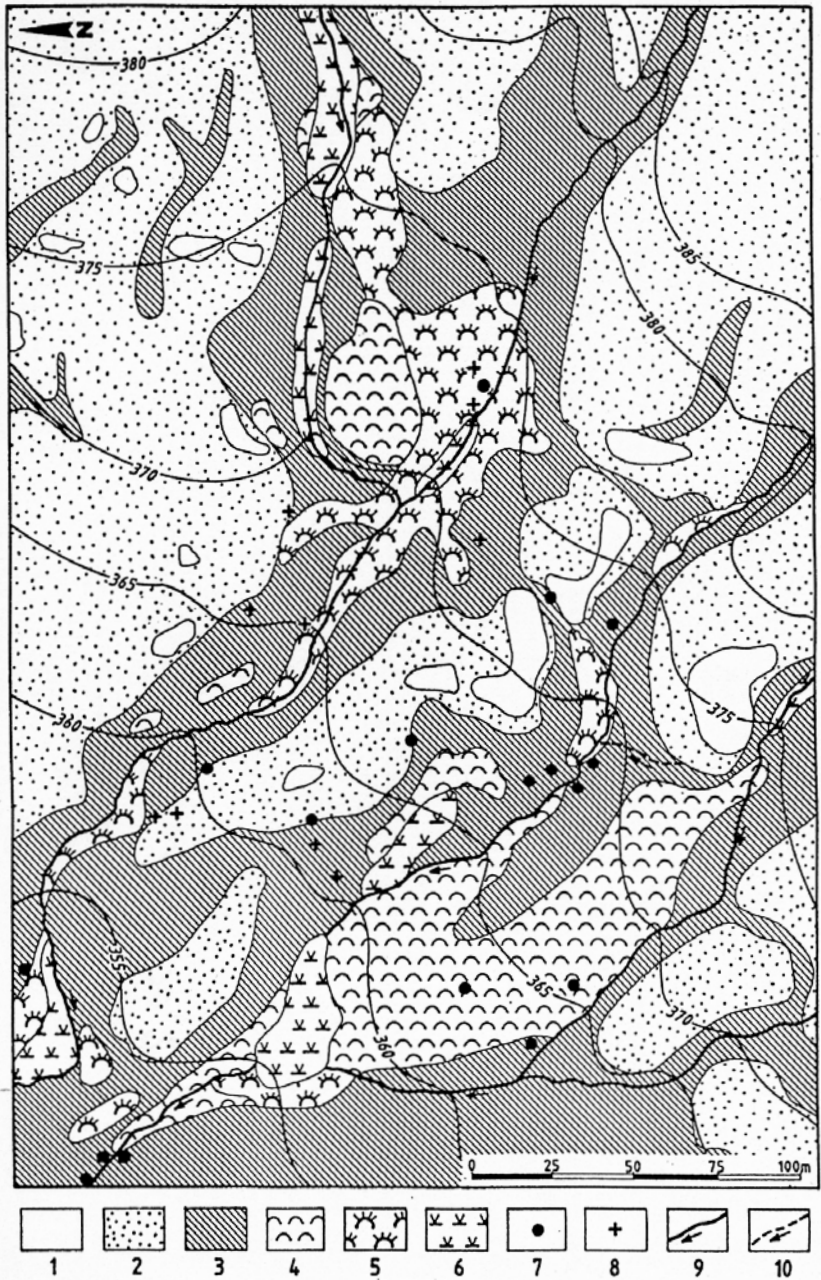
A few wooden remains (mainly from buried rootstocks) and peat were collected for radiocarbon-dating to provide a better insight into treeline history. The dating was done by the Leibniz Institute for Applied Geosciences (Hannover, Germany) (Holtmeier & Broll 2006).

Results

The air photo, showing the northeast-facing slope of Rodjanoaivi (Fig. 3), provides a first impression of the spatial pattern of the landscape (Fig. 4) in the upper drainage area of Tsierromjohka. Convex, relatively gently sculptured, wind-exposed dry terrain (light-grey colour) alternate with shallow val-

Fig. 4. Mosaic of topography-dependent vegetation types, soils, and drainage classes on the northwest-facing slope of Rodjanoaivi.

- 1 Extremely wind-eroded sites with exposed mineral soil. Small dwarf shrub and lichen patches. Excessively to somewhat excessively drained.
- 2 Wind-swept interfluves. Somewhat excessively or excessively drained. Mosaic of low-growing dwarf shrub-lichen heath only locally interspersed with exposed mineral soil.
- 3 Slopes of interfluves and valley sides. Well to moderately drained. Closed dwarf shrub-lichen cover.
- 4 Foot zone (slope bottom) of interfluves and shallow depressions. Well drained. "Dry/Mineral hummocks". Dwarf shrub vegetation and willow shrub.
- 5 Valleys and depressions. Valley floor poorly drained. "Wet/Organic hummocks". Luxuriant dwarf shrub vegetation and willow shrub.
- 6 Grass bogs. Poorly or very poorly drained.
- 7 Solitary living old mountain birches (tree height 3–5 m, diameter up to 20 cm).
- 8 Dead old mountain birches. Stems still in upright or leaning position (diameter up to 20 cm).
- 9 Stream.
- 10 Intermittent run-off channel.



leys, former drainage channels, swales and other depressions (dark-grey colour) exhibiting moist to wet conditions. The most heavily wind-eroded, dry places (mainly on top of small ridges and at the upper rim of valley sides) almost lacking vegetation, emerge as nearly-white patches in the air

photo (see also Fig. 5). The mapped area (Fig. 4) is considered to be representative of the landscape mosaic on Rodjanoaivi. Soil data (soil moisture, C_{org} , N_t , C/N and pH) from the identified spatial-ecological units are presented in the Figs. 6, 7 and 8).



Fig. 5. Tsierrromjohka drainage area. View northwest. Norwegian high fells in the background. Wind-eroded soils and patchy low-growing dwarf shrub-lichen heath on wind-exposed topography. Comparatively tall dwarf shrub vegetation and willow shrub (grey colour) in more wind-protected, snow-rich and moister places. (Photo F.-K. Holtmeier, 2 September 2000).

Convex topography

Ridge tops, slightly convex gently sloping interflues and the upper rim of valley sides are usually characterized by dry conditions due to strong winds and permeable substrate (Fig. 6, type E, L). These sites can be attributed to the drainage classes “excessively drained” to “somewhat excessively drained”. Because of the sandy-skeletal substrate soil moisture varies rapidly in dependence from precipitation (Anschlag 2002).

Ridge tops, interflues, upper valley sides

Wind-exposed sites are covered by a locally varying mosaic of low, scattered dwarf shrub-lichen

heath (*Empetrum hermaphroditum*, mat-like *Betula nana*, *Arctostaphylos alpina*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*), espaliers of *Loiseleuria procumbens*, scattered cushions of *Diapensia lapponica*, and – admixed – grasses (*Juncus trifidus*, *Carex bigelowii*, *Luzula spicata*, *Luzula arcuata*, *Deschampsia lapponica*) and mosses (e.g., *Polytrichum piliferum*, *Polytrichum juniperinum* and *Gymnomitrium corallioides*). The coverage of lichens and mosses is low. The prevailing lichens including *Cetraria nivalis* and *Ochrolechia frigida* are interspersed with *Thamnomlia vermicularis*, *Alectoria ochroleuca*, *Alectoria nigricans*, *Stereocaulon paschale* and different *Cladonia* species. The latter are usually represented by their thallus fragments which remain after reindeer grazing.

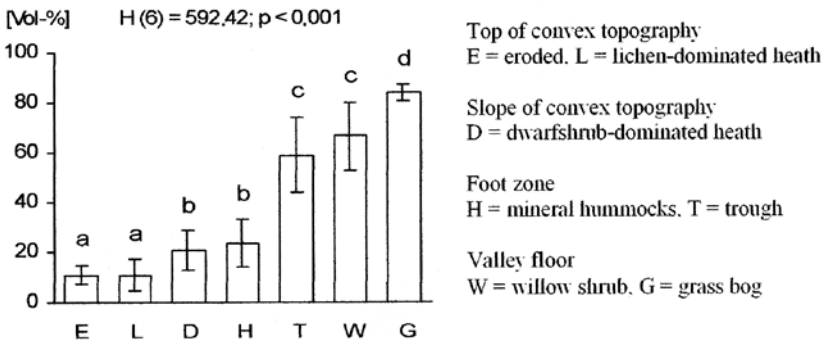


Fig. 6. Mean values and standard deviation of soil moisture of topmost 5 cm at different sites, based on weekly TDR measurements from 25 June to 27 August 2003 (n = 700). For multiple comparison, the Nemenyi-test was used ($\alpha = 0.05$) (Lozán & Kausch 1998). Differences in soil moisture between sites E and L (a), D and H (b) and T and W (c) are not significant, whereas these groups differ significantly from each other and from site G (d).

The lichen-dominated patches correspond to the Arctic *Empetrum-Cetraria* type of Haapasaari (1988).

Shallow but well developed Podzols occur, with a maximum depth of about 15 cm under lichen-dominated patches and about 20 cm under dwarf shrub cover (mainly *Empetrum*, *Betula nana* and *Vaccinium* species) with *Pleurozium schreberi*. Under lichen cover, the thickness of the organic layer varies from 2 cm to 4 cm, while litter is almost missing. Under dwarf shrub vegetation, an almost 10 cm thick organic layer has built up.

In the litter layer (lichens and dwarf shrubs), C/N ratios are comparatively wide due to an elevated soil organic carbon content and low total nitrogen. Carbon and nitrogen sharply decline in the top-

soil. Soil acidity of the topsoil is extremely high (ultra acid to extremely acid, Schoeneberger et al. 1998, Fig. 7a).

The dwarf shrub-heath is interspersed with comparatively large patches of open mineral soil exposed by wind erosion. Towards extremely wind-swept places the plant cover becomes increasingly lower and dispersed. The species number (about 15) is low compared to better wind-protected sites. Vegetation coverage is at a minimum (< 5%). Low mats of *Empetrum hermaphroditum* with *Cetraria nivalis* and *Cetraria nigricans* admixed show the highest coverage. Other hardy species such as *Loiseleuria procumbens*, *Diapensia lapponica*, *Carex bigelowii* and *Juncus trifidus* also occur at very low coverage.

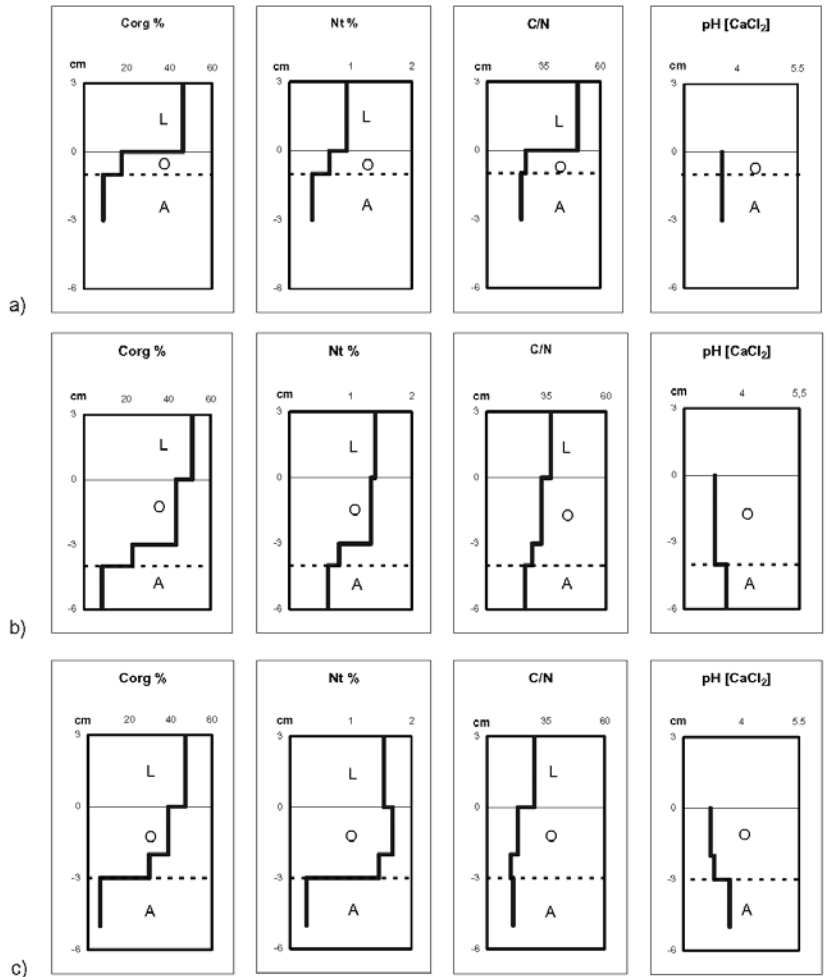


Fig. 7. Soil data from convex topography and its foot zone. a – Top, lichens and dwarf shrubs, b – slope of convex topography, c – footzone, dwarf shrubs, mineral hummocks (podzolised). L – litter, O – organic horizon, A – A horizon.

The few individuals of *Betula nana* display espalier-like growth (1 cm to 2 cm high). This vegetation type corresponds to the "deflation sites" of Haapasaari (1988). Mountain birch seedlings are exceptional on extremely wind-eroded topography (Holtmeier 2003; Holtmeier et al. 2003) although open mineral soil is favourable to birch seedling establishment in general.

Extremely wind-eroded sites

Wind erosion is particularly strong on prominent convex topography and along the upper rim of the wind-facing valley sides (Figs. 3 and 5). The sandy-skeletal mineral soil has become widely exposed and about 60–90% of the soil profile has eroded. Enrichment of coarse material on the surface is mainly due to deflation of the finer fractions (Holtmeier et al. 2004). Organic carbon and total nitrogen content are low, whereas pH (very strongly acid, Schoeneberger et al. 1998) is higher than under dwarf shrub-lichen patches (cf. Holtmeier et al. 2004). Soil moisture conditions on the extremely wind-eroded sites with mineral soil exposed (Fig. 6 type E) are not significantly different from the sites covered by low lichen-dominated vegetation (Fig. 6 type L).

On the wind-eroded sites, there still exist isolated patches of shallow undisturbed Podzol covered with dwarf shrub-lichen heath. Wind erosion is also active. The wind-driven mineral particles cause abrasive damage similar to ice-particle abrasion to exposed dwarf shrubs and mountain birches. These vegetation patches may become completely destroyed in the not too distant future. Wind-scarps (10 cm to 20 cm high) mark the gradually downwind receding front of remaining closed dwarf shrub vegetation (see also Broll & Holtmeier 1994). Downwind migration of this front will come to an end on the upper leeward side of convex topography where wind velocity decreases and a snow drift builds up (Holtmeier et al. 2003; Holtmeier et al. 2004; Holtmeier 2005a).

Locally, in wind-exposed sites remains are found of an up to 20 cm thick organic layer usually covered with a thin fragmentary lichen crust and a few low-growing dwarf shrubs and grasses. The weakly decomposed organic matter (reddish colour) accumulated about 700 to 1300 years ago, most probably under more humid climatic conditions, when the plant cover was more luxuriant than at present. Largely rotten stems and other wooden residues found in the peat provide evidence of

former birch stands (cf. Holtmeier & Broll 2005, 2006).

On the well drained gently sloping interfluves, closed dwarf shrub-lichen vegetation is restricted to relatively snow-rich and moist sites such as small former drainage channels and shallow hollows (dark-grey colour), where they form dense mats. *Betula nana* may reach 20 cm to 30 cm in height. This vegetation type is equivalent to the *Betula nana*-Lichenes-subtype of Haapasaari (1988). Also low growing willows (*Salix glauca*, *Salix lapponum*) occur.

Soil moisture (Fig. 6 type L) is significantly higher than in the more wind-exposed sites. Mountain birch stands became established only on more wind-sheltered, snow-rich sites, such as leeward (south, southeast exposures) slopes of convex topography and a few metres deep depressions. At such sites, melt water and seepage provide more favourable moisture conditions than on excessively drained convex topography. Young birches become increasingly affected by the strong winds when growing beyond the relatively wind-protected zone close to the surface.

Hummock terrains

On gently sloping terrain of the interfluves, there are large areas of small, usually closely spaced low hummocks (height 10 cm to 30 cm, diameter 30 cm to 50 cm). Low lichens (*Ochrolechia frigida*, *Cladonia* species, mostly thallus fragments) with sporadic dwarf shrub (*Empetrum*, *Vaccinium uliginosum*, *Vaccinium vitis idaea*, *Arctostaphylos alpina*) and grass specimen associated cover the relatively dry tops of the hummocks, while taller-growing dwarf shrubs (mainly *Empetrum* and low *Betula nana*), with lichen and mosses admixed, grow in the moist grooves between the hummocks.

Most of these hummocks have a silt content of 40% to 50%. Mineral hummocks are usually podzolised and became cryoturbated after the Podzol had developed. The tops of the hummocks show cracks caused by desiccation. Many of them are wind-eroded. Some organic hummocks consist almost completely of weakly decomposed (reddish colour) organic matter. Probably, the hummocks developed under a plant cover that was more luxuriant than at present. The peaty hummocks often contain wooden residues that probably indicate a former open birch forest similar to the present uppermost forest stands at lower elevation (cf. Holtmeier & Broll 2006).

Slopes

The more wind-protected and relatively snow-rich slopes of the ridges, interfluves and the valley sides (cf. Fig. 4) are well drained (upper slope) to moderately drained (lower slope, footzone). Closed dwarf shrub vegetation, mainly *Empetrum*, *Betula nana* and different *Vaccinium* species (*Vaccinium uliginosum*, *Vaccinium myrtillus*) are typical of the well drained section. Coverage increases from the relatively dry upper slopes towards the foot zone. The organic layer is deeper than in lichen-dominated heath. The relatively high nitrogen content results in a comparatively narrow C/N ratio. As on top of convex topography soil acidity is very high (Fig. 7b).

Foot zone of ridges, interfluves and valley sides

In the foot zone, deep and long-lying winter snow cover and lateral seepage cause comparatively moist conditions to prevail (Fig. 6 type D). With some reservation (see below) this zone can be considered a transition zone between the dry and wind-swept convex terrain to the more wind-protected, snow-rich and moist valleys of Tsierrromjohka and its headwaters.

Empetrum hermaphroditum again has the highest coverage. *Vaccinium myrtillus*, which needs protection by snow in the winter and usually does not occur on wind-swept topography, is well represented in the dwarf-shrub-lichen heath. In contrast to the more wind-exposed topography *Cladonia*-species (*C. gracilis*, *C. rangiferina*, *C. stellaris*, *C. uncialis*, etc.) are common. In addition *Barbilophozia hatcheri* and *Stereocaulon paschale* occur with greater frequency. *Phyllodoce coerulea* and *Salix herbacea*, both chionophilous species, are well represented at these sites. Moreover, *Pedicularis lapponica*, *Solidago virgaurea* and *Cornus suecica* that are typical forest plant species are very common. This vegetation type corresponds to the Arctic *Myrtillus*-Lichenes-Type of Haapasaari (1988). Willows (*Salix glauca*, *Salix lapponum*) are common in the footzone.

In the moister sites of the foot zone, particularly on somewhat poorly drained or poorly drained terrain gently sloping towards the little streams, mineral and organic hummocks (up to 50 cm high) occur, separated by deep troughs. The sides of the hummocks are usually steep or even vertical, in

contrast to the low dome-shaped hummocks on the comparatively dry interfluves. The tops of most hummocks, from which the strong winds usually blow the snow off in the winter, are covered with snow-intolerant (chionophobic) lichens or/and with dwarf shrub vegetation (*Betula nana*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Vaccinium vitis idaea*). Also, *Rubus chamaemorus* (generally more typical of bog areas) regularly occur within the dwarf shrub-vegetation though at low coverage. Moss cover (*Sphagnum fuscum*), on the other hand, may reach 20% to 40%, locally even up to 90%. After longer-lasting dry weather conditions the lichen cover usually shows cracks although these hummocks have higher moisture content than those on the wind-swept and dry convex areas.

The lower parts of the hummocks are covered by relatively tall-growing dwarf shrubs, willow shrub, herbs (e.g., *Potentilla palustris*, *Cornus suecica*), different mosses and lichens. Locally solitary mountain birches (3 m to 4 m high) are growing in the hummocky area. The average age of the living trees ranges between 80 and 90 years. The oldest living birch tree we found growing at about 360 m a.s.l. was 225 years old (tree ring analysis, Holtmeier et al. 2003). As is evidenced by wood remains, the foot zone as well as in the not-too-wet valley sites (cf. Fig. 4) were once covered with open birch forests up to at least 380 m a.s.l. (Holtmeier et al. 2003; Holtmeier & Broll 2006).

We may distinguish between "dry" (well drained) and "wet" (poorly drained) hummocks. "Dry" hummocks are more common in the well drained parts of the foot zone than in poorly drained depressions. "Wet" hummocks are located in the poorly drained places, often bordering bogs (see also Van Vliet-Lanoë & Seppälä 2002).

The hummock terrain in the foot zone is considered to be a spatial subunit characterized by a vertical rather than a horizontal moisture gradient. On top of the well-drained hummocks (Fig. 6 type H, see also Fig. 7c), soil moisture is similar to soil moisture in the places covered by dwarf shrub-dominated heath (Fig. 6 type D) but significantly higher than on wind-eroded sites. Soil moisture usually increases towards the hummock basis. The troughs of the "dry hummocks" are partly covered by shallow peat layers where intermittent runoff has not prevented the accumulation of plant residues. The litter layer, consisting mainly of dwarf shrub leaves, is usually less deep than on the "wet"

hummocks and ranges from 11 cm to 15 cm. In “dry” hummocks in most cases not affected by cryoturbation, organic carbon content and C/N-ratio usually decrease from the L horizon to the basis of the humus profile, while pH increases. High total nitrogen content results in a narrow C/N ratio when compared to the Podzols on flat topography and gentle slopes. As in the other places characterized by Podzols, pH in the topsoil is extremely low (ultra acid to extremely acid, Schöneberger et al. 2002, Fig. 7c) However, pH increases slightly in the mineral soil. Occasionally, thin peaty layers embedded in the more decomposed organic matter indicate the influence of temporary higher moisture (anaerobic conditions) due to more humid climatic conditions or change of the drainage system.

Most hummocks have become podsolized. In hummocks with a high content of fine mineral, soil horizons have become cryoturbated. As reported by Seppälä (1998; see also Luoto & Seppälä 2002; Van Vliet-Lanoë & Seppälä 2002) permafrost may exist in high hummocks (> 1 m; 0.7 m, Luoto & Seppälä 2002). In August 2001 and in the following three summers we did not find any with a frozen core, but may be soil temperature was below 0°C over more than two years indicating permafrost in this area. Even in organic hummocks, the organic matter may be interspersed with clay and sand layers pushed upward from the mineral substrate (till) by frost action even though the contents of silt and clay (about 40 %) and fine sand (25–35%) are not unusually high. Also, aeolian material has been deposited in these places. At poorly drained sites, gleyzation occurs locally resulting in Podzols with hydromorphic features.

The troughs between the hummocks are comparatively wet (wet to permanently wet) (Fig. 6 type T), showing moisture conditions similar to poorly drained willow shrub (Fig. 6 type W). During the winter, snow accumulates within the troughs and around the basal part of the hummocks. The troughs are partly covered with grasses (e.g., *Carex vaginata*, *Deschampsia flexuosa*, *Calamagrostis lapponica*), *Dicranum* species and other mosses (mainly *Sphagnum* spp.). *Phyllodoce coerulea* is well represented. *Salix* species and *Betula nana* are also common, while the coverage by the other dwarf shrub species and by lichens is low. Locally moss coverage exceeds 70% with *Dicranum* species prevailing. In some troughs between the “dry” hummocks a few centimetres thick peaty layer has accumulated. In other troughs, acting as drainage

channels for intermittent run-off after rain or snow melt, the stony (very stony or boulder-rich loam) substrate is exposed or covered with only little organic matter. The troughs between the “wet” hummocks show hydromorphic features similar to the grass bogs and willow shrub sites.

Valley floor

Topographical gradients vary in Tsierrromjohka and its headwaters and around the older drainage channels (only intermittent run-off). In the low-gradient sections, mineral and organic sediments have accumulated on block-rich material with the development of wide floodplains several metres in extent. In the steeper sections, the streams have made two to three metres deep cuts into the sediments and locally exposed the bedrock. Although moisture in the valleys is generally higher in comparison to the windy convex terrain, variegated microtopography causes conspicuous differences between sites. The valley floors are poorly drained and covered by closed, almost luxuriant dwarf shrub vegetation (dark-grey colour). Coverage decreases from the moist valley bottom to the relatively dry upper edge of the valley sides.

Some valley sections are characterized by a dense net of narrow, intermittently flooded block-rich drainage channels. In these channels and also in places where lateral seepage and run-off from higher terrain cause wet conditions, grow up to one metre high willow shrubs (mainly *Salix lapponum*, *Salix glauca* and hybrids (Fig. 6 type W). The willows are usually mixed with *Betula nana* (same height as the willows but lower coverage), other common dwarf shrub species, mosses, lichens, grasses (*Carex bigelowii*, *Carex aquatilis*, *Carex brunescens*, *Carex magellanica*, *Deschampsia flexuosa*, *Juncus filiformis*, *Vahlodea atropurpurea*, *Agrostis mertensii*) and *Equisetum* species (*Equisetum sylvaticum*, *Equisetum palustre*). Moss species such as *Warnstorfia exannulata* and *Polytrichum commune* respectively *alpinum* typically occur. The coverage of the mosses varies widely.

Typically, this kind of willow shrub covers 50 cm to 80 cm high hummocks. Most of them are “wet” hummocks (see also Van Vliet-Lanoë & Seppälä 2002). These consist of fine mineral and/or organic (peaty) material. The mineral content is usually low. Dark, highly decomposed matter, alternating with less decomposed material, indicates climatic fluctuations and/or temporary water table rise. The “wet” hummocks are characterized by a

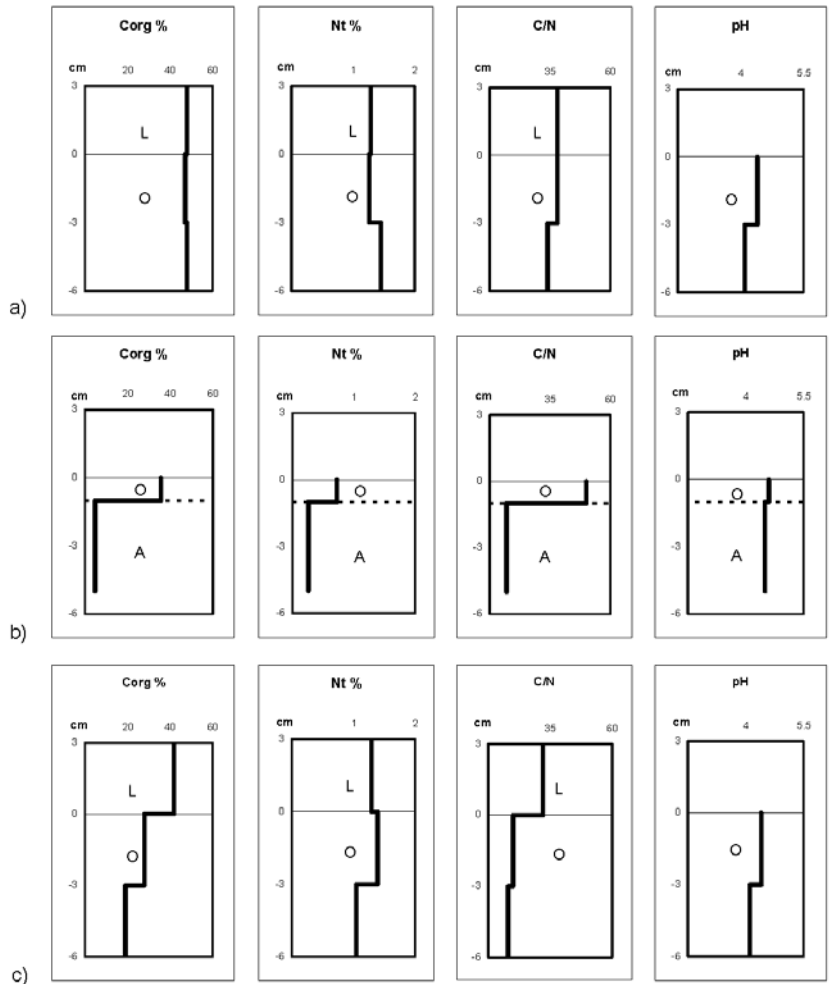


Fig. 8. Soil data from the valley floor. a – Willows and dwarf shrubs, organic hummocks, b – willows, humus-rich skeletal soils, c – grass bogs. L – litter, O – organic horizon, A – A horizon.

comparatively thick organic layer varying from 15 cm up to 30 cm in the moister places. The L horizon, which usually consists of mosses and dwarf-shrub litter, is characterized by a wide C/N ratio (> 35). Neither organic carbon, nor total nitrogen and C/N change much by depth. Soil acidity, however, is lower compared to the podzolised sites (> 4, extremely acid, Schoeneberger et al. 2002) in the upper topsoil and changes little with depth (Fig. 8a). Soil moisture conditions in the “wet” hummocky sites are not significantly different from willow shrub sites (Fig. 6 type H and W). Due to poorly drained conditions podzolisation does usually not occur in these hummocks. Where minimal amounts of fine material accumulate, willows can also be found on the humus-rich coarse skeletal soils.

The comparatively narrow floodplains are usually covered with willow shrub and grass vegetation growing on fine to coarse sediments or on stones and boulders. On stream banks, skeletal soils occur with a thick (≥ 10 cm) organic layer on stones and boulders. Also, in gullies (steep gradient sections), skeletal humus-rich soils develop locally where rock fragments (pebbles, cobbles, stones and boulders) accumulate.

Intermittent flooding prevents almost any accumulation of litter at the stream sides and here the organic carbon content of the organic layer is lowest in comparison with other sites. As total nitrogen is very low as well, resulting C/N ratio is comparatively wide. Soil acidity is even lower than in the Podzol sites and increases little with depth (Fig. 8 b).

Next to the streams (e.g. alongside Tsierronjohka) and in very poorly-drained or waterlogged depressions, small grass bogs (with percolating water) developed (cf. Figs. 3 and 4). The largest is about 500 m². Small sedge stands dominated by *Carex rostrata* occur with *Eriophorum angustifolium*, *Carex brunescens* and *Calamagrostis stricta* admixed. Also represented are scattered plants of *Equisetum palustre*, *Andromeda polyfolia* and *Potentilla palustris*. In addition, bryophytes such as *Sphagnum teres*, *Mnium pseudopunctatum*, *Warnstorffia exannulata* and *Paludella squarrosa* are characteristic of such sites. The mosses cover up to 100%. *Betula nana*, *Salix* species and also *Betula czerepanovii* are found at very low densities at the rim of the bogs, the latter usually on slightly convex sites.

As in the other poorly and very poorly drained places, pH is not extremely low (very strongly acid) compared to the Podzol sites (ultra to extremely acid, Fig. 7 c). Soil moisture is significantly higher than in troughs between the hummocks and in willow shrub (Fig. 6, type G). The organic layer is up to 30 cm, locally even up to 60 cm deep. In many cases it has built up above a continuous stony layer. The degree of decomposition and the amount of un-decomposed plants vary in the different layers and do not show a regular decrease or increase with depth. The same holds true for organic carbon content, total nitrogen, C/N ratio, and pH (Fig. 8c). At the bog edges and also in other wet places within the valleys, mountain birch seedlings may be numerous, if not suppressed by dense dwarf shrub vegetation (cf. Holtmeier et al. 2003). Nevertheless, many birch seedlings were found also in some dense willow stands (Anschlag 2002, 2006). Birch seedlings occur at high densities also in periodically flooded sites. However, survival rate is very low as can be concluded from the absence of older young growth.

Discussion

The choice “natural drainage classes” combined with soil types, soil moisture and vegetation proved to be an appropriate tool for characterizing site conditions (site types). In the treeline ecotone on the northwest-facing slope of Rodjanoaivi, six significantly different spatial-ecological units, characterized by a combination of natural drainage classes (Schoeneberger et al. 2002), soils and vegetation, can be grouped along the topographic

gradient from excessively-drained convex topography to very poorly drained concave topography. Fig. 9 provides a visualized synthesis. Extremely wind-eroded sites and lichen-dominated dwarf shrub-heath are at the dry end of the transect, while grass bogs are at the wet end. Soil moisture data (cf. Fig. 6) closely correspond to the natural drainage classes.

However, instead of following a steady gradient, soil moisture increases abruptly from the distal end of the foot zone towards the valley floor thus demarcating the two main spatial ecological units (cf. Figs. 7, 8 and 9). That limit is also reflected in an abrupt change in soil acidity from about pH 3 on the Podzol sites to about pH 4 and above on the valley floor sites (see below). This great difference in pH between the “dry” sites and the poorly drained sites (stream sides, bogs, and “wet hummocks”) indicates different ecological properties, for example a higher base saturation in the valley floor sites compared to the surrounding areas. Higher base saturation might be explained in terms of translocation of Ca and Mg by seepage from excessively and somewhat excessively drained convex to poorly and very poorly drained valley sites.

By contrast, the vegetational aspect changes little from the foot zone towards the hummock areas on the valley floor (cf. Fig. 9), and does not reflect the abrupt change in soil moisture conditions and soil acidity. More distinct vegetation limits, reflecting different soil moisture conditions, occur between organic-hummock areas on the valley floors and the stream sides and between valley floors and grass bogs, the latter restricted to the wettest, poorly drained or waterlogged depressions. They are characterized by plant communities of the *Scheuchzerio-Caricetea nigrae* (Drees 2004) and they can be classified as low-moor bogs (Schoeneberger et al. 1998). The most conspicuous vegetation limits occur where contrasts in wind velocity, snow depth and soil temperature are strongest: i.e. between wind-swept and wind-eroded convex topography (tops) and the more wind-sheltered snow-rich areas including the leeward slopes of convex topography (low ridges, interfluvies) and upper valley sides (cf. Fig. 9). Soil temperatures vary most on wind-eroded convex terrains and in summer due to low heat conductivity of excessively drained sandy-skeletal substrate and lacking litter layer and/ or humus-rich topsoil (cf. Broll 2000; Holtmeier 2003; Holtmeier et al. 2003; Holtmeier et al. 2004) whereas the other more wind-protected and moister sites with a closed

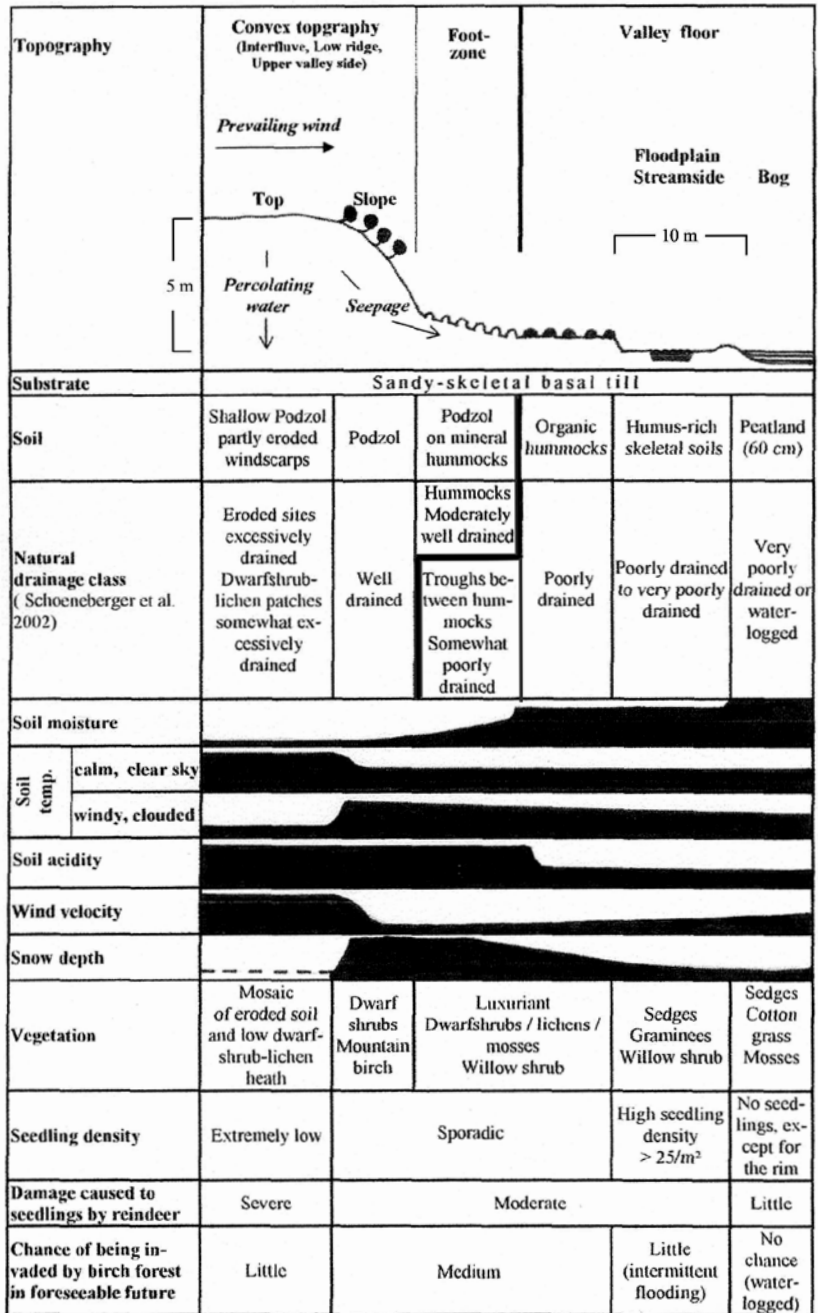


Fig. 9. Visualized synthesis of topography-dependent spatial-ecological units (site conditions, vegetation types, soils, and drainage classes) in the treeline ecotone.

vegetation cover show relatively smooth temperature amplitudes.

The contrasts between microclimates and soil moisture conditions of wind-swept convex topography and wind-sheltered leeward slopes, valleys and other depressions probably became more pro-

nounced after the decline of the upper mountain birch forest and resulting downslope advance of the alpine zone in most parts of the study area (Holtmeier 2005a; Holtmeier & Broll 2006). Consequently, the intensity of wind erosion and the extent of deflation areas have considerably in-

creased. On wind-eroded topography, soil moisture became more dependent on actual precipitation and thus varies rapidly often causing moisture stress to the plants.

The differences in birch-seedling densities correspond to these changes in the vegetational aspect. This holds also true for the chance of being invaded by birch in foreseeable future. Extremely low birch-seedling densities or even lack of birch seedlings can be primarily attributed either to lack of soil moisture, nutrients and reindeer damage or to waterlogged conditions, while in the well drained to poorly drained sections of the transect (landscape units) competition with closed dwarf shrub communities occurs to be the main factor responsible for only sporadic seedling establishment. On the streamsides (poorly drained conditions), chance of being invaded by birch is low because of intermittent flooding despite high seedling densities.

The many deflation sites and great intensity of wind erosion are due mainly to the high susceptibility of the sandy substrate to wind erosion. In subarctic Finland, wind erosion (aeolian activity) is quite common in sandy areas (e.g., Seppälä 1995, 2004; Tikkanen & Heikkinen 1995; Käyhkö et al. 1999a, b). Wind erosion had probably begun about 4800 years BP (Seppälä 1995). In the Rodjanoaivi study area, however, the onset of wind erosion below the present altitudinal tree limit seems to be younger as is evidenced by the eroded Podzols and also by the peat layers that were still accumulating at these sites about 700–1300 years ago and the wood residues indicating (open) birch stands that still existed in many present treeless wind-eroded places 350–150 years BP or even longer (Holtmeier & Broll 2006). Thus, wind erosion on Rodjanoaivi occurred rather late during the “latest episode of aeolian activity” (onset at AD 1100–1650) as suggested by Käyhkö et al. (1999a) for inland dunes in northern Fennoscandia. Wind-erosion is still active in the present treeline ecotone and in the former forested zone above. Consequently, the area of exposed mineral substrate is expanding as has also been observed on mountains about 30 km northeast of Rodjanoaivi (cf. Holtmeier et al. 2003; Holtmeier et al. 2004). In Finnmark (northern Norway), Evans (1995) has estimated a lowering of the surface by one to three millimetres per year due to deflation. Käyhkö (2007) found the deflation rate in some dune blow-out basins in northern Finland to be even 9 mm per year on a decadal basis. These dune blow-outs

are the most active deflation areas in Lapland. In modern times, excessive overgrazing (Holtmeier 1974, 2005b; Kumpula & Nieminen 1992; Oksanen et al. 1995; Burgess 1999; Helle 2001) trampling and also reindeer wallowing (in peat remains) have enhanced wind erosion (cf. Holtmeier 2003, 2005a; Holtmeier et al. 2004). Similar observations were made in the southern Swedish Scandes (Kullman 2005).

Podzols are the most common soils in the treeline ecotone except for grass bogs and organic hummocks. Jauhiainen (1969) considers “sub-alpine” Podzols as a relic of a warmer period (5000–3000 BP), when the treeline was about 150–200 m higher than at present (Aas & Faarlund 2001). Indeed, the rotten root stocks and other wooden residuals found in many present treeless sites provide evidence of former forests, particularly when taking into account that many trees have decayed without leaving any visible remains (cf. Holtmeier & Broll 2006). The very shallow Podzols on well-drained and wind-exposed convex topography, at present covered with mat-like growing dwarf shrub-lichen heath, are common also to other areas in northern Fennoscandia where permeable glacial till covers acidic bedrock (e.g., Meier et al. 2005). However, the current vegetation (see above) is very probably different from the vegetation that existed when the Podzols developed. More humid climatic conditions might have favoured podzolisation at excessively to somewhat excessively drained sites. It may be speculated that in the treeline ecotone on Rodjanoaivi, podzolisation on wind-swept topography is likely to have been more intensive before the open birch stands declined. These stands would have trapped blowing snow (cf. also for Holmgren & Tjus 1996) thus increasing soil moisture (Holtmeier 2005a). Very likely, soil moisture was not only higher but also less variable than at present. On the other hand, however, lower transpiration might have compensated for the reduced melt water supply. However, podzolisation is going on also at present where dwarf shrub-lichen heath on a permeable substrate ensure low pH values (Broll 2000).

At all sites, organic carbon ranges between 40% and 50% in the litter layer, except for the grass-covered stream sides, where it is below 40% (top-soil) because almost no litter accumulates. Total nitrogen is mostly above 1%. Lower nitrogen (< 1%) content was measured on windswept convex topography and at the streamsides sites (top-soil). Soil acidity is generally higher in the Podzol

sites (excessively, well to moderately drained and somewhat poorly drained sites) than in the wetter sites (grass-covered stream sides, grass bogs, “wet hummocks”) below.

In the hummock areas within the valleys, shallow depressions and in the footzone of convex topography, long-lying winter snow, lateral seepage and near-surface water tables will ensure a permanent moisture supply. Moreover, the vegetation here is generally more productive than on dry (excessively drained and well-drained) convex topography. These conditions have favoured podsolization of minerogenic hummocks, except for poorly drained sites. Podzolization of “dry” hummock soils must have been completed before the hummocks became cryoturbated, maybe during the Little Ice Age (Van Vliet-Lanoë & Seppälä 2002) or earlier. The troughs of the “dry” hummocks are partly covered by shallow peat layers where intermittent run-off has not prevented accumulation of plant residues.

The usually deep organic horizon on “wet” (mineral and organic) hummocks in the poorly drained places is likely to have accumulated at higher soil moisture than at present. Besides climatic change or change of the drainage system (pattern) increased accumulation of blowing snow from the previously forested low ridges and interflues in valley and other depressions may have enhanced soil moisture increase (Holtmeier 2005a; Holtmeier & Broll 2006).

Conclusions

In general, heat deficiency is the main factor controlling plant growth and many other biological processes in the Subarctic. In the present study area, i. e. at the local scale, however, the highly varying local topography is the key factor controlling drainage (run-off, seepage), vegetation, soils, local climates (microclimates), and also reindeer grazing in the treeline ecotone resulting in marked landscape patchiness. Site quality (e.g., soil moisture conditions, soil acidity, soil types, snow cover, relative wind velocities, etc.) can almost be deduced from the topographic position.

The present situation (e.g., wind-erosion, topographically-controlled relocation of snow and its effects on soil moisture distribution), however, can be explained only by including the past (historical) combined effects of climate, occasional mass outbreaks of the autumnal moth (*Epirrita autumnata*)

and over-grazing by reindeer (in modern times) on the mountain birch forest.

The landscape mosaic may have a lasting effect on treeline dynamics. Topographically-controlled distribution of soil moisture, wind velocity and relocation of snow and resultant effects override the influence of the regional thermal conditions (see also Kullman 2005). Local topography will not radically change in the near future. The effects of local topography on site mosaic and ecological conditions will override the influence of rising temperature. Under warmer and drier conditions local topography is likely to influence site conditions in a way different from its effects in a warmer and more humid climate (Holtmeier & Broll 2005).

The results of the present local study may be applied to other subarctic treeline areas characterized by similar geomorphology and substrates (sandy-skeletal basal till) and thus allow – *cum grano salis* – upscaling of the relationships between topography, drainage classes and resulting ecological conditions identified on Rodjanoaivi, for example by interpretation of topographic maps, air photos or satellite imagery.

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