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Soil-Driven Timberline of Spruce (*Picea abies*) in Tanaelv Belt–Lapland Granulite Transition, Finland

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Abstract

Climate-driven northern limits of cold-hardy conifers, Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), reach latitude 70°N in Fennoscandia. Spruce timberline is located at significantly lower latitudes than pine timberline, but factors contributing to this exceptional pattern have remained obscure. We assessed soil-water and soil-nutrient regimes across the spruce timberline in Finnish Lapland through the use of terrestrial electromagnetic (EM) measurements. These included soil dielectric permittivity (ϵ), which is positively correlated to soil-water content (θ_v); gamma radiation (γ), which is negatively correlated to soil-water content (θ_v); and electrical conductivity (σ_a), which is a measure of solute content of a soil. The soil EM data were acquired at 15 sites carrying mature (older than 150 yr) stands dominated by either spruce or pine; the sites fall along a 50-km-long transect that crosses the spruce timberline. The correlation and artificial neural network (ANN) analyses revealed that the soil-moisture and solute content were significantly higher in glacial tills of Norway spruce stands compared to those of stands formed by Scots pine. The stands dominated by spruce were associated with mesic-wet and nutrient-rich tills derived from mafic amphibole and hornblende gneisses of the Tanaelv Belt. Dry and nutrient-poor till derived from felsic garnet gneisses of the Lapland Granulite appeared to constitute an edaphic dispersal barrier for Norway spruce.

Introduction

East of Fennoscandia, spruce (*Picea abies* ssp. *obovata*) forms the coniferous tree limit, reaching 66°20'–69°25'N in the valleys of the Ob and Yenisei rivers in western Siberia, whereas the tree limit of Scots pine (*Pinus sylvestris* L.) reaches only latitudes 64°30'–66°N, respectively (Veijola, 1998; MacDonald et al., 2000; Payette et al., 2002). In Fennoscandia, the northern limits of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine both reach latitude 70°N, but the timberline of spruce is located at significantly lower latitudes than that of Scots pine (Kallio et al., 1971; Veijola, 1998; MacDonald et al., 2000; Fig. 1). Timberline is defined here as the species-specific northern limit at which a minimum of 30% of forest canopy closure ceases (Sihvo, 2002; see definitions in Veijola, 1998). It is known that solitary spruce trees or stands occur north to Scots pine tree limit (Kallio et al., 1971; Oksanen, 1995; Sihvo, 2002), but the reasons for the exceptional position of the spruce timberline in northern Fennoscandia have remained obscure. Even though spruce is a climax species in the (aspen)-birch-pine-spruce successional sequence (Pastor et al., 1999), it is absent over a large region in the northern boreal forests of Lapland (Fig. 1) where Scots pine is a dominant species and birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) is a principal associate.

Holocene migration of tree species, treeline fluctuations, and forest disturbances are to a great extent associated with climate-driven factors (Moe, 1970; Eronen and Hyvärinen, 1987; Agee, 1998; Richardson, 1998; Kremenetski et al., 1999; Barber et al., 2000; MacDonald et al., 2000; Kullman, 2002; Payette et al., 2002; Pitkänen et al., 2002; Kirdyanov et al., 2003). On the basis of the radiocarbon (^{14}C) dates of subfossil Scots pine logs, pine spread to northern Fennoscandia by 8000–7000 yr BP and reached its maximum distribution by 6000–4000 yr BP, followed by gradual retreat to its modern range limit (Eronen and Hyvärinen, 1987; Payette et al., 2002). As evidenced by ^{14}C -dated subfossil trunks, the expansion of spruce to

sites north of the modern treeline in Eurasian Russia occurred by 9000–8000 yr BP, and the retreat of spruce to its current treeline position occurred by 4000–3000 yr BP (Kremenetski et al., 1998; MacDonald et al., 2000). Also, spruce macrofossils well above the present alpine tree limit in the Caledonian mountain range in central Sweden indicate that spruce had been a vital part in the forest migration during the early Holocene time period (8000–11,000 yr BP; Kullman, 2002). According to the conceptual migration model, spruce reached its northernmost range limit as late as 3000–3300 yr BP in northeast Fennoscandia (Moe, 1970; Kremenetski et al., 1999; cf. MacDonald et al., 2000; Payette et al., 2002).

Climatic tolerances of the timberline tree species have been intensively studied in the circumpolar subarctic (Nikolov and Helmisaari, 1992; Stolbovoi and Nilsson, 1999; Kirdyanov et al., 2003). Spruce and pine species in high northern latitudes are able to tolerate a wide range of environmental conditions, but limited information is available on the soil-driven constraints applying to these tree species. Topographic barriers, i.e., mountain ranges, may play an important role in the migration patterns (Rupp et al., 2001), but also unfavorable soil conditions may constitute species-specific dispersal barriers in the subarctic region (Timoney et al., 1993; Sutinen et al., 2002). Soil-moisture content (θ_v) and nutrients in soil solution are two of the most important causative factors that control tree growth, species composition, and diversity (Timoney et al., 1993; van Praag et al., 1997; Reimann et al., 1998; Richardson, 1998; Vejre, 1999; Salmela et al., 2001; Alawi, 2002; Sutinen et al., 2002); hence regional variability in the soil θ_v and nutrient regimes may also be a critical driver for the species-specific timberline and treeline positions.

We targeted soil electromagnetic (EM) surveys across the Norway spruce timberline in Finnish Lapland (Fig. 1) to see whether the soil θ_v and/or nutrient regimes are different within the timberline spruce forest from those north of the timberline. The measurements of the soil ϵ , γ , and σ_a provided us with a basis to assess soil-driven factors,

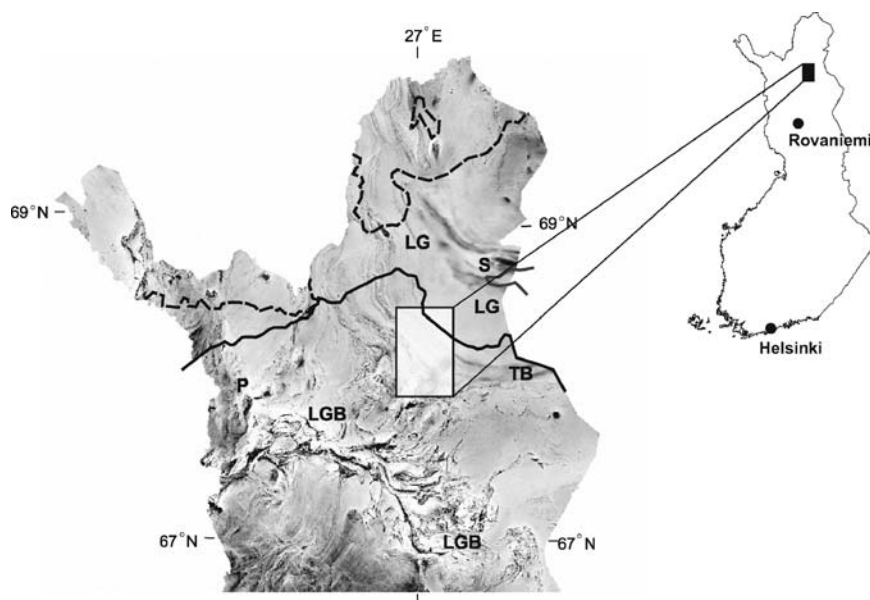


FIGURE 1. Airborne magnetic total intensity map of northern Finland. The study area is shown by a black rectangle. Norway spruce timberline (solid lines) (taken from Sihvo, 2002) is based on 30% crown coverage. Pine timberline (dashed lines) (adopted from Juntunen et al., 2002) is based on the same crown coverage. LG = Lapland Granulite Belt, TB = Tanaelv Belt (Marker, 1985), LGB = Lapland Greenstone Belt, S = Sarmittunturi, P = Pallastunturi.

soil-moisture availability, and solute content as contributors to the Norway spruce timberline in northeast Fennoscandia.

Materials and Methods

STUDY AREA

The study area in Finnish Lapland (67°56'N–68°30'N; 26°52'E–27°36'E) is characterized by gently undulating glacial terrain reaching 250–380 m (a.s.l.) elevation (Fig. 2), but with a range of treeless granulite fells (i.e., high altitude and strong relief features above timberline) that reaches 450–718 m a.s.l. The effective temperature sum ranges from 692 to 596 degree-days (Table 1) as computed according to the model presented by Ojansuu and Henttonen (1983). A degree-day is a linear temperature sum unit based on daily mean temperature minus the threshold value, $> 5^{\circ}\text{C}$. The applied model estimates temperature sums for a given location on the basis of the meteorological data by the Finnish Meteorological Institute (FMI), the digital elevation model, and the presence of water bodies (lakes). Climate is cool and humid; the long-term (1961–1990, FMI) annual average temperature ranges from -1.6°C to -2.1°C , the January mean range is -15.1°C to -15.7°C , and the July mean range is $+12.8^{\circ}\text{C}$ to $+13.4^{\circ}\text{C}$. The mean annual precipitation is 530 mm, and June–September precipitation is 250 mm (period 1961–1990; FMI). Summer precipitation exceeds evaporation by ~ 50 mm, but $> 40\%$ of precipitation falls as snow, and snowmelt is the major contributor to the runoff (Solantie, 1987).

The study area is located in the Tanaelv Belt–Lapland Granulite (TB–LG) transition (Fig. 2) that represents Archean (1.9 Ga) continental crust (Marker, 1985). Rocks of the mafic TB consist of amphibole and hornblende gneisses with a number of concordant bodies and lenses of metamorphic gabbroic, anorthositic, and ultramafic rocks (Marker, 1985). The TB is similar in lithologic composition to the Lapland Greenstone Belt, which typically is covered with forests dominated by Norway spruce and characterized by understory vegetation containing *Hylocomium*, *Polytrichum*, and *Sphagnum* mosses (Marker, 1985; Katila and Tomppo, 2001; Salmela et al., 2001; Sutinen et al., 2002; Hyvönen et al., 2003). In contrast to the TB, the LG is composed of felsic garnet gneisses. Because of the resulting dry acidic sandy till as parent soil material, forests in the LG are dominated by Scots pine with understory vegetation characterized by

Stereocaulon and *Cladonia* lichens (Salmela et al., 2001). In the transition zone the mafic granulite parts (veins, inclusions), however, are similar in geochemical composition and structural position to those of the rocks of Tanaelv Belt (Marker, 1985). A set of mafic and felsic rocks constitutes a basis for the contrasting lithogeochemical and thereby for the soil nutritional regimes (Reimann et al., 1998) across the Norway spruce timberline. The fine fraction content of parent tills may reach 50% in the Lapland Greenstone Belt and TB, but may be $< 30\%$ in the LG (Hänninen, 1997; Ruther, 1999; Salmela et al., 2001). Tills are superimposed on the bedrock only as a 1–4-m-thick veneer, but the tops of the fells frequently are frost-shattered bare rock with no or scarce vegetation. The Podzol (Spodosol) was classified as a Typic Haplocryod (see Sutinen et al., 2002).

SOIL EM PROPERTIES

Soil-moisture and nutrient regimes were assessed with the aid of terrain EM measurements coupled with airborne measurements by the Geological Survey of Finland. The soil θ_v can be measured via dielectric permittivity (ϵ) with time-domain reflectometry (TDR), electrical capacitance probing (ECP), and/or radar surface arrival detection (RSAD) (Topp et al., 1980; Hänninen, 1997; Ruther, 1999; Sutinen et al., 2002). The soil θ_v is one of the major contributors to the intensity variations of gamma-ray (γ) flux from glacial materials, and a major part (90%) of gamma radiation is emitted from the upper 30 cm of the soil (Grasty, 1997). Hence the differentiation of the root-zone soil-water regimes under pine and spruce stands can be achieved stand-wise with terrestrial methods and at landscape scale with airborne gamma-ray measurements (Grasty, 1997; Hyvönen et al., 2003). The soil-solute content, obtained with electromagnetic induction measurements of the soil electrical conductivity (σ_a), can be used to estimate soil-nutrient regimes and, along with site-specific calibrations, to estimate stand-scale soil-nutrient distributions (McBride et al., 1990; see Rhoades and Oster, 1986; Corwin and Lesch, 2003).

Fifteen sites (Table 1) were selected randomly. We applied a systematic grid of points with a spacing of 2 km covering the study area. In order to obtain soil data through the TB–LG transition in a short period of time, the point coverage was then clipped by using a 500-m buffered road network. With the aid of a GIS compartment database by the Finnish Forest and Park Service, only the sites with mature stands (older than 150 yr) and with a dominance of either

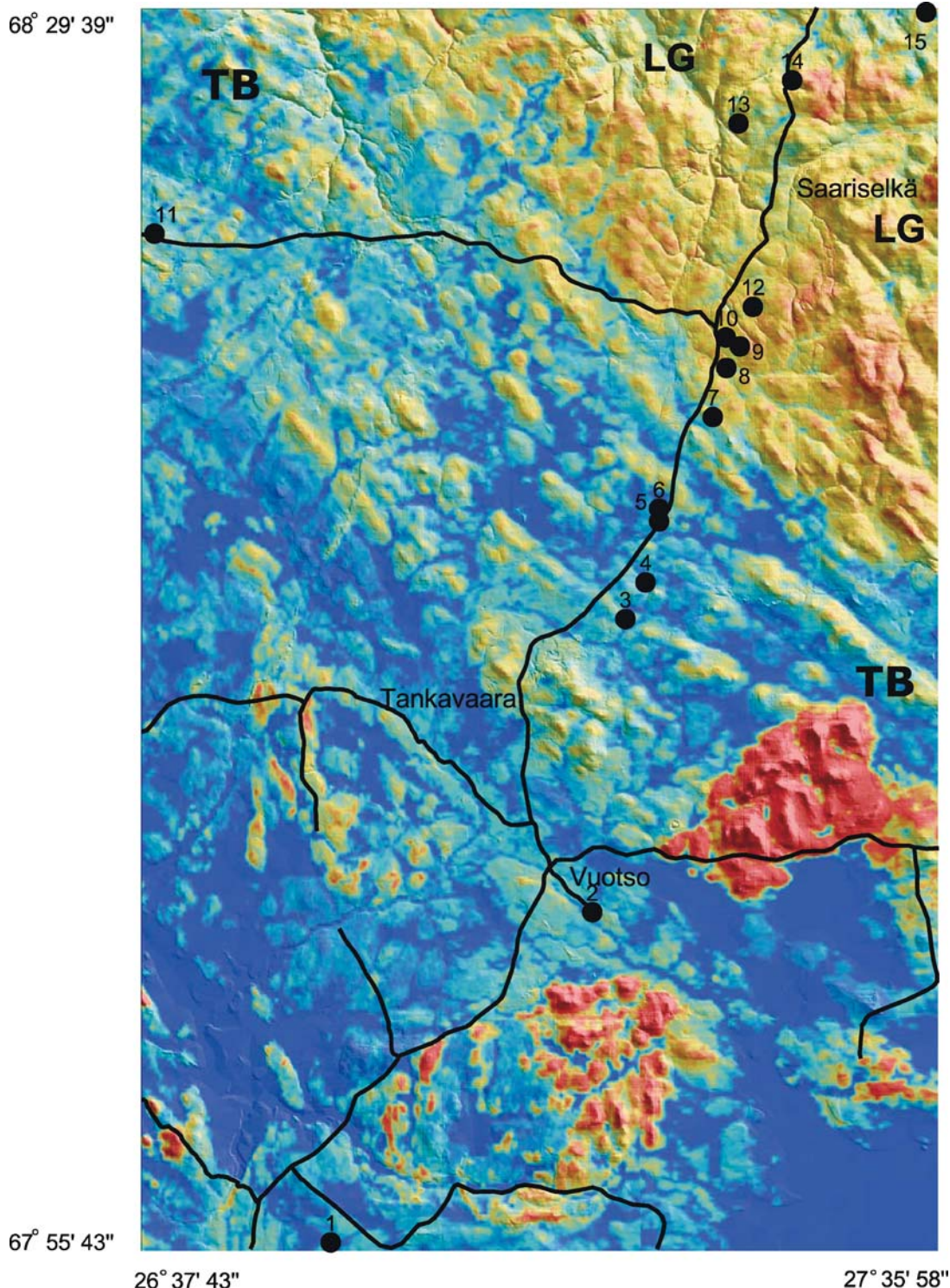


FIGURE 2. Compilation of airborne gamma-ray (potassium window) data and digital elevation model of the study area. Measured sites are at the numbered black dots (see Table 1). Main roads presented as black lines.

Norway spruce (>65%) or Scots pine (>65%) were included in the study. In the TB, spruce was dominant, and downy birch (*Betula pubescens* Ehrh.) was a principal associate. In the LG, pine was dominant, and silver birch (*B. pendula* Roth.) was a common associate of pine (see Sutinen et al., 2002); Norway spruce was absent, except on the Kuusipää site (no. 13 in Table 1). At each selected site, the soil EM properties (ϵ , σ_a , and γ) were measured along a 100-m-long line by using 1-m point spacing. Out of a total of 1500 measurement points (microsites), 16 were omitted owing to surface stoniness.

The ϵ values (i.e., soil θ_v ; see Topp et al., 1980) were determined with an electrical capacitance probe (ECP, Adek Ltd, Estonia). The measuring depth of ECP was ~ 10 cm in the mineral soil, and the obtained soil volume was 500 cm^3 (Sutinen et al., 2002). The most commonly used ϵ/θ_v calibration is the one presented by Topp et al. (1980). The gamma-ray flux from the glacial tills under stands dominated either by Scots pine or Norway spruce was measured with a portable GS-256 gamma-ray spectrometer (Geophysica Brno, Czech). The spectral windows (total counts, γ_{Tot} ; potassium, γ_K ;

TABLE 1

Site locations, lithology, tree dominance, elevation, temperature sum, mean soil dielectric values, soil gamma-ray values, and soil electrical conductivity of the study sites.

Study sites	Station	Latitude (N)	Longitude (E)	Lithological unit	Tree dominance	Temperature sum 1961–1990	Altitude (m a.s.l.)	ϵ_r mean (\pm SD)	K mean (% \pm SD)	σ mean (mS/m \pm SD)
Mäntypää	1	67°56'08"	26°51'59"	LGB	Spruce	692	245.4	12.39 \pm 1.917	1.23 \pm 0.203	1.85 \pm 0.340
Vuotso	2	68°04'59"	27°10'59"	TB	Pine	681	245.9	8.10 \pm 1.250	1.15 \pm 0.190	0.75 \pm 0.426
Ylisenvaara	3	68°12'59"	27°13'29"	TB	Spruce	632	290.9	12.83 \pm 3.196	0.87 \pm 0.124	1.01 \pm 0.246
Kotikuusikko	4	68°13'59"	27°14'59"	TB	Spruce	640	282.1	13.49 \pm 2.433	1.27 \pm 0.153	1.43 \pm 0.317
Nurmikumpu	5	68°15'39"	27°15'59"	TB	Spruce	634	278.0	16.35 \pm 4.708	1.15 \pm 0.246	2.04 \pm 0.791
Vuomaselkä	6	68°15'59"	27°15'59"	TB	Spruce	634	280.0	11.00 \pm 1.835	1.73 \pm 0.306	0.79 \pm 0.387
Pikku Vuomaselkä	7	68°18'29"	27°19'59"	TB	Spruce	612	312.5	19.52 \pm 9.495	0.80 \pm 0.259	1.76 \pm 0.221
Kakslauttanen	8	68°19'49"	27°20'59"	LG	Pine	632	267.3	7.31 \pm 1.492	1.80 \pm 0.167	1.18 \pm 0.330
Tullinpalo	9	68°20'24"	27°22'03"	LG	Pine	603	321.0	7.89 \pm 2.319	1.60 \pm 0.154	1.62 \pm 0.224
Kiilopää	10	68°20'40"	27°20'59"	LG	Pine	607	297.6	6.44 \pm 1.189	1.66 \pm 0.187	1.07 \pm 0.321
Köysivaara	11	68°23'29"	26°38'50"	TB	Spruce	600	319.0	21.26 \pm 7.705	0.89 \pm 0.445	1.40 \pm 0.284
Rönkövaara	12	68°21'29"	27°22'59"	LG	Pine	609	306.0	7.29 \pm 1.380	1.66 \pm 0.233	0.86 \pm 0.200
Kuusipää	13	68°26'29"	27°22'59"	LG	Spruce	596	295.7	16.73 \pm 7.390	1.25 \pm 0.282	1.53 \pm 0.333
Magneettimäki	14	68°27'39"	27°25'59"	LG	Pine	617	296.7	10.15 \pm 2.573	1.62 \pm 0.160	0.77 \pm 0.486
Kuutua road	15	68°29'29"	27°35'38"	LG	Pine	637	286.0	9.71 \pm 2.264	1.46 \pm 0.211	0.76 \pm 0.319

uranium, γ_U ; and thorium, γ_{Th}) of the GS-256 are equal to those applied by the airborne gamma-ray spectrometer of the Geological Survey of Finland (Hyvönen et al., 2003). At each measuring point, a 1-min counting time was applied. The soil σ_a was obtained inductively with the EM-38 conductivity meter (Geonics Ltd., Mississauga, Ont.). The EM-38 has an intercoil spacing of 1 m, which results in a penetration depth of ~ 0 –1.5 m in the vertical dipole orientation coil position (Corwin and Lesch, 2003).

STATISTICAL METHODS

A classification of the tills on sites dominated either by Scots pine or Norway spruce was performed with correlation and artificial neural network (ANN) analyses for the terrestrial soil EM data (γ_K , γ_{Th} , ϵ , and σ_a). In principle, an ANN is a massively and parallel distributed processor that is able to store the knowledge contained in the experiential data and makes it available for use (Haykin, 1994). Thereby, knowledge is acquired by the network through a training process. When training an ANN, a set of examples consisting of the input parameters (e.g., γ_K , γ_{Th} , ϵ , and σ_a) and the corresponding output parameters (e.g., desired site classification) is presented to the ANN. The rules of how to calculate the ANN output, based on given input parameters, are saved in the internal parameters of the ANN (weights between the neurons and the gains of the activation functions).

On the basis of the terrain geophysical data on 15 sites, two ANNs (ANN1 and ANN2) were trained to differentiate glacial tills typified by stands dominated either by Norway spruce or Scots pine. The classification with ANN1 was based on the measured values of γ_K , γ_{Th} , ϵ , and σ_a , but because pine is associated with low soil dielectric permittivities ($\epsilon < 15$; Sutinen et al., 2002) the classification with ANN2 was based on the measured values of γ_K , γ_{Th} , and σ_a . Of a total of 1500 microsites (i.e., measurement points), 644 for pine and 840 for spruce (owing to stoniness, 16 microsites omitted) were interpreted with the ANNs. For the training of the ANNs, only microsites in the vicinity of pine and spruce trees (i.e., no broad-leaved trees present), 877 in number, were preselected. To train ANN1 we selected 117 microsites (41 for pine and 76 for spruce) from the preselected 877 microsites by using a cluster analysis of the input values. The desired output of the ANN1 was 0.9 for pine and -0.9 for spruce microsites, respectively. In order to train the ANN2 we selected 25 microsites (10 for pine and 15 for spruce from the preselected 877 locations) by using a cluster analysis of the input values. Similar to ANN1, the desired output of ANN2 was 0.9 for pine and -0.9 for spruce microsites.

Within training, the internal parameters of the ANNs were changed by a back-propagation algorithm until the ANNs calculated the appropriate desired output for a specific input pattern. To test the generalization behavior of the trained ANNs, the whole set of the EM data (i.e., for 1484 measured microsites) was classified by the trained ANNs. In this test the mean value of the two output values, one from ANN1 and one from ANN2, was used for the final classification.

Results

The range of soil dielectric values (i.e., soil moisture) in tills of Norway spruce stands ($8 < \epsilon < 41$) was significantly ($t_\epsilon = 20.77$; $P < 0.001$) wider compared to that of Scots pine stands ($3.5 < \epsilon < 15$) (Table 1; Fig. 3A). The mean soil ϵ in the spruce sites ranged from $\epsilon = 11 \pm 1.84$ to $\epsilon = 21.26 \pm 7.71$, but northeast of the spruce timberline in the LG, the mean soil ϵ in the pine sites was in the range $6.44 \pm 1.19 < \epsilon < 10.15 \pm 2.57$. The till on the isolated spruce site at Kuusipää, presumably on a diabase vein and inside the felsic LG, showed much higher soil moisture ($\epsilon = 16.73 \pm 7.39$) than the surrounding till derived from the LG (Table 1; see Fig. 2).

A significant negative correlation (Spearman's $r_s = 0.58$, $P < 0.01$) was observed between the soil ϵ and γ_K as well as between the soil ϵ and γ_{Th} ($r_s = 0.39$, $P < 0.01$), respectively. The gamma-ray flux from the tills below Scots pine was observed to be much higher ($0.7 \leq \gamma_K \leq 2.2\%$ K) than the flux below Norway spruce ($0.2 \leq \gamma_K \leq 1.5\%$ K; Fig. 3B; see Fig. 2). A mean $\gamma_K = 1.58\%$ K ± 0.28 was found for the soil under Scots pine stands, and a mean $\gamma_K = 1.1\%$ K ± 0.33 was found for the soil under the Norway spruce stands. A major part (95%) of the observations showed soil $\gamma_K > 0.9\%$ K under Scots pine stands.

The soil-solute content, as expressed with the soil σ_a and obtained with the EM-38, was significantly higher ($t_\sigma = 38.39$; $P < 0.05$) in tills of Norway spruce stands ($0.6 < \sigma_a < 3.6$ mS/m) compared to those of Scots pine stands ($0.1 < \sigma_a < 2.2$ mS/m; Table 1; Fig. 3C). The mean σ_a values of the till in pine stands in the felsic LG ranged from $\sigma_a = 0.42 \pm 0.16$ to $\sigma_a = 0.86 \pm 0.2$ mS/m, whereas the mean σ_a values for tills in spruce stands in the TB transition ranged from $\sigma_a = 1.39 \pm 0.54$ mS/m to $\sigma_a = 2.04 \pm 0.79$ mS/m. The isolated spruce site at Kuusipää (Table 1) yielded a mean σ_a value of 1.53 ± 0.33 mS/m.

The ANN results (Fig. 4) indicated soils of spruce and pine trees to be significantly different on the basis of the terrestrial soil EM data. The ANN outputs that are >0.9 correspond to a reliability of 9.5:1 for pine. In contrast, the ANN outputs smaller than -0.9 correspond to a reliability of >80 :1 for spruce. The ANN output of 0 demonstrates

that some of the soils in the TB-LG transition could be suitable for both conifer species.

Discussion

DISTRIBUTION OF SPRUCE AND CLIMATE

Spruce timberline parallels the arc-shaped TB-LG transition for ~100 km in northeast Finnish Lapland (Fig. 1); hence the orientation of the present timberline appears inconsistent with the conceptual model of spruce migration from the southeast during the Holocene (Moe, 1970; Kremenetski et al., 1999). However, reconstruction of the postglacial history of spruce is based on pollen records and radiocarbon ages from organic deposits. No macrofossil evidence has been found to indicate distribution of spruce beyond its present timberline. The late expansion of spruce to its northern and northwestern limit by 3000–3300 ^{14}C yr BP (Moe, 1970; see Kremenetski et al., 1999; Payette et al., 2002) appears to be incoherent with simultaneous retreat of Scots pine as evidenced by pine macrofossils (Eronen and Hyvärinen, 1987). As a part of global climatic deterioration—i.e., lower solar insolation and summer temperatures—spruce retreated to its current treeline position at ca. 4000–3000 yr BP in northwest Siberia (MacDonald et al., 2000). Spruce immigrated to the Kola Peninsula between 7000 and 5000 ^{14}C yr BP, but radiocarbon dates indicate spruce to have arrived in the northwest Siberian Subarctic at ca. 9000 yr BP, i.e., much earlier than pine (which arrived by ca. 7000 yr BP; Kremenetski et al., 1998; MacDonald et al., 2000). The age of subfossil spruce stems (8000–11,000 yr BP) 400–500 m above the present alpine tree limit in the Caledonian mountain range in central Sweden suggests that spruce was not a late successor during early Holocene time (Kullman, 2002). Because of the lack of spruce macrofossils in Lapland, however, the conceptual migration model of spruce appears vague with respect to the present spruce timberline.

The Scots pine timberline roughly coincides with the temperature sum of 550 degree-days, but a major part of the spruce timberline is located at significantly lower latitudes (Veijola, 1998; Juntunen et al., 2002; Fig. 1). Climate-driven factors, crucial determinants of the treeline positions (Kallio et al., 1971; Nikolov and Helmisaari, 1992; Stolbovoi and Nilsson, 1999; MacDonald et al., 2000), seem to play a role in the northwest part of the arc-shaped TB near the Norwegian border, where the 10° to 12°C July isotherm may be associated with the northwestern spruce limit, as shown in Eurasian Subarctic (MacDonald et al., 2000). The annual average temperature range of the study area (from –1.6°C to –2.1°C) is well above the species-specific temperature (annual mean temperature) niches of –2.4°C for pine and –2.3°C for spruce observed in the northern Siberian taiga (Stolbovoi and Nilsson, 1999). It seems that spruce, rather similarly to pine, is able to thrive at high altitudes and low-temperature conditions (Kallio et al., 1971; Nikolov and Helmisaari, 1992; Stolbovoi and Nilsson, 1999; MacDonald et al., 2000). The range of the effective temperature sum (692–596 degree-days) at the study sites here (Table 1) is well above the reported temperature sum minima of 470 degree-days for Norway spruce and 450 degree-days for Scots pine (Nikolov and Helmisaari, 1992). Furthermore, the proportion of spruce has a tendency to increase along with degreasing temperature on fertile tills in Lapland (Sutinen et al., 2002), hence topoclimatic factors give no explanation for the present spruce timberline in the TB-LG transition.

Climate change in northeast Fennoscandia is evidenced by significant increase in the mean MAM (March–April–May) temperatures over the past 150 yr, particularly since the 1970s (Tuomenvirta, 2004). This change appears to be concomitant with the circumpolar reduction of snow-cover area in spring and with earlier “spring greening” (Myneni et al., 1997). On the fertile soil derived from alkaline nepheline syenite rocks of the Khibiny Mountains in the Kola

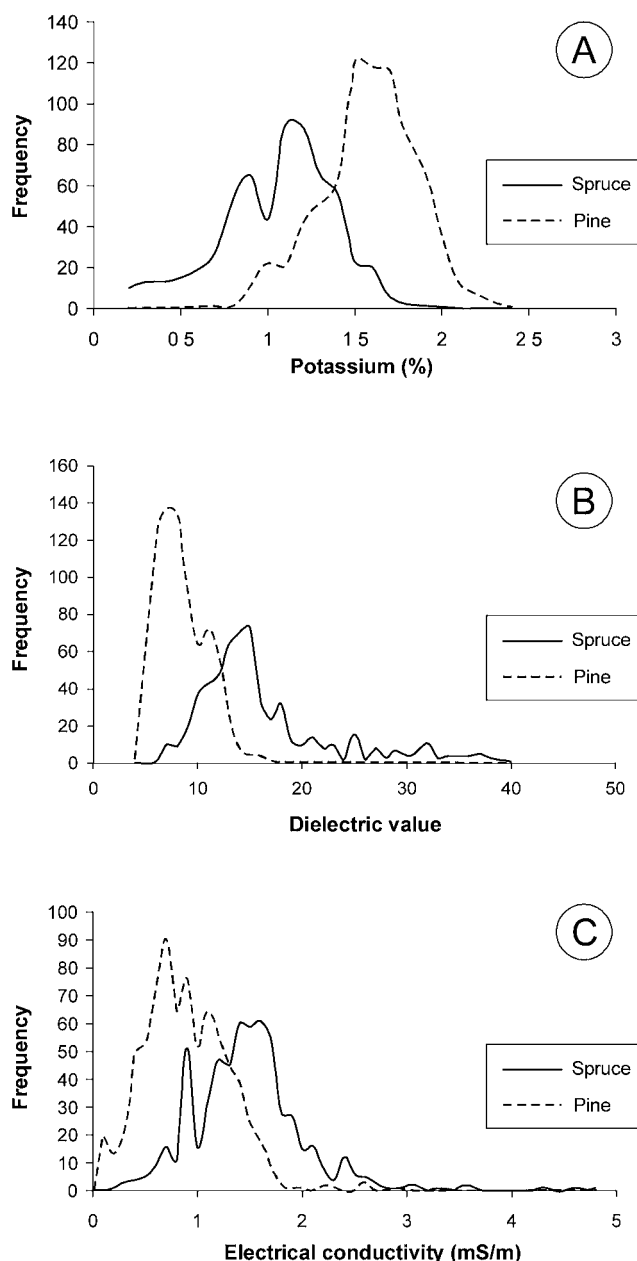


FIGURE 3. Density plot of soil gamma-ray (A), soil dielectric (B), and soil electrical conductivity values (C) for the sites dominated either by Norway spruce or Scots pine in Tanaelv Belt–Lapland Granulite transition in Finnish Lapland.

Peninsula, the twentieth-century advance of the spruce treeline suggests an increase in summer temperature by ~2°C (Kremenetski et al., 1999). Also, new regeneration and tree establishment have been observed in the “alpine” spruce treelines in Finland (Juntunen et al., 2002), but no evidence has been found to show new recruitment of spruce on the dry acidic soil of the felsic LG proper. The growth response of Norway spruce to recent climate warming has yet to be studied in the TB-LG transition, but observations elsewhere in the circumpolar region suggest that climate warming does not necessarily result in increased growth of spruce. As an example, reduced growth of Alaskan white spruce (*Picea glauca*) in the twentieth century has been linked to temperature-induced drought stress (Barber et al., 2000; Lloyd and Fastie, 2002). Inverse growth responses to temperature appear to be widespread even in the treeline conditions, but growth

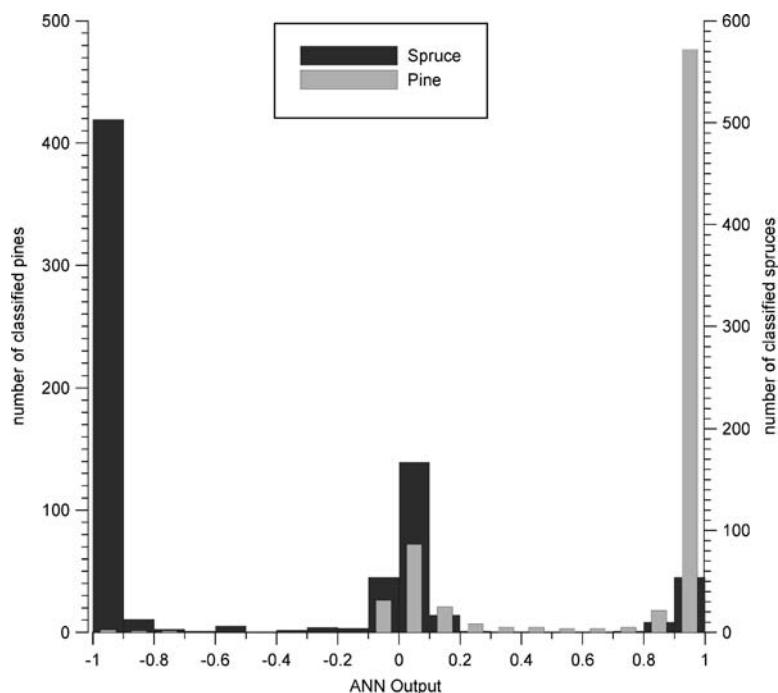


FIGURE 4. Artificial neural network classification for Norway spruce and Scots pine in Tanaelv Belt–Lapland Granulite transition in Finnish Lapland.

declines of white spruce are most common in dry soils (Lloyd and Fastie, 2002). In northeast Fennoscandia, climate warming may not result in enhanced migration of spruce to the dry, acidic, and nutrient-poor till of the felsic LG, but the Greenstone Belt–Tanaelv Belt association (Fig. 1), extending north to Norway, provides a potential “polar” pathway for spruce expansion in the future.

SPRUCE TIMBERLINE AND SOIL MOISTURE

The soil ε (i.e., soil θ_v) was significantly greater in tills below Norway spruce stands in the mafic TB transition compared to those of Scots pine stands in the felsic LG proper (Table 1), indicating soil-moisture availability to be one of the most important drivers for the timberline position of Norway spruce. As in several other studies (Salmela et al., 2001; Sutinen et al., 2002; Hyvönen et al., 2003) the present results demonstrate Norway spruce to be adapted to a much wider soil-moisture regime ($8 < \varepsilon < 41$) compared to the soil-moisture regime to which Scots pine is adapted ($3.5 < \varepsilon < 15$). Spruce seems to be able to grow even on saturated sites ($\varepsilon > 30$; $\theta_v > 0.44 \text{ cm}^3 \text{ cm}^{-3}$), according to the dielectric mixing model presented by Hänninen (1997), but is absent on sites at the dry end of the soil-moisture gradient ($\varepsilon < 8$; $\theta_v < 0.15 \text{ cm}^3 \text{ cm}^{-3}$). In accordance with our results, the sporadic spruce trees and spruce stands along the northwest tree limit have been found to be associated with edaphically moist sites (Oksanen, 1995).

Even though the soil θ_v varies seasonally owing to climatic events, the spatial pattern of the soil θ_v is primarily dependent on the soil physical properties, such that soil θ_v positively correlates, e.g., with fine fraction content in tills under forest stands (Hänninen, 1997; Sutinen et al., 2002). The clay fraction content in tills in Lapland is rather low ($< 10\%$); the fine fraction content of parent tills may reach 50% in the Lapland Greenstone Belt and TB, but may be $< 30\%$ in the LG (Hänninen, 1997; Ruther, 1999; Salmela et al., 2001). Several studies have shown that the seasonal soil-moisture content is higher in silty tills below spruce stands compared to sandy tills below Scots pine stands (Hänninen, 1997; Sutinen et al., 2002; Hyvönen et al., 2003); hence the variation in the soil θ_v values ($3.5 < \varepsilon < 41$; $0.042 < \theta_v < 0.52 \text{ cm}^3 \text{ cm}^{-3}$) through the TB-LG transition evidently was due to

spatial heterogeneity of the soil physical properties. In the humid climate of Lapland, precipitation exceeds evaporation by $\sim 50 \text{ mm}$ (Solantie, 1987), suggesting that soil texture, structure, and water-retention characteristics, rather than evaporation, are pronounced in determining the spatial distribution of soil-water regimes (Hänninen, 1997; Salmela et al., 2001). Relationships between spruce growth and soil moisture are not well known in the Fennoscandian Subarctic (cf. Kirilyanov et al., 2003), but based on the southern boreal experiments, reduced growth of Norway spruce is coincidental with soil drought (Alawi, 2002; see Barber et al., 2000; Lloyd and Fastie, 2002). In the present spruce timberline soil, drought evidently plays only a minor role in the TB (Fig. 3), but because of low retention characteristics of tills in the LG, the drought effect cannot be ruled out as one of the potential constraints for spruce.

The terrestrial gamma-ray measurements indicated a significant negative correlation between the soil ε (i.e., θ_v) and the soil γ_K and soil γ_{Th} , hence supporting the previous studies showing the attenuation of gamma-ray flux to be primarily due to the soil θ_v (Grasty, 1997; Hyvönen et al., 2003). The soil γ_K was significantly greater under Scots pine stands (mean $\gamma_K = 1.58\%$) compared Norway spruce stands (mean $\gamma_K = 1.06\%$; Figs. 2 and 3B). In accordance with several other reports (Timoney et al., 1993; Richardson, 1998; Sutinen et al., 2002; Hyvönen et al., 2003), the regional distribution of soil-moisture regimes has been shown here to be soil driven. The soil θ_v was high (indicated by low soil γ_K) within the TB transition, but significantly low (high soil γ_K) in the LG proper as shown by the by the airborne gamma-ray data (Fig. 2). Hence, the 60–80-km-wide LG (see Fig. 1) may constitute a regional drought barrier for spruce in a similar manner as dry and acidic soils present a barrier for white spruce in the Canadian Subarctic (Timoney et al., 1993).

Scots pine dominates drier habitats with sandy acidic soils, such as till in the LG (Table 1; Fig. 2). Low soil moisture seems to be a prerequisite factor for Scots pine (Figs. 3A and 3B), such that the edaphic constraint appeared to be $\varepsilon > 15$ (i.e., $\theta_v > 0.27 \text{ cm}^3 \text{ cm}^{-3}$). This finding coincides with that of several other reports from Fennoscandia and northwest Russia indicating that Scots pine stands occur only on dry sandy soils (Hänninen, 1997; Agee, 1998; Kremenetski et al., 1999; MacDonald et al., 2000; Salmela et al.,

2001; Jasinski and Angelstam, 2002; Pitkänen et al., 2002; Sutinen et al., 2002; Hyvönen et al., 2003). In contrast to the situation in Fennoscandia and the Kola Peninsula, the range limit of Scots pine is at a significantly lower position than that of spruce or Siberian larch (*Larix sibirica* (Ledeb.)) in the northwest Russian Siberia (MacDonald et al., 2000). The reverse behavior of northern limits of Eurasian spruce and pine species is not well understood, but it may be associated with differences between the soils derived from the rocks of the Baltic Shield and those derived from Cambrian sedimentary rocks in subarctic Siberia.

SPRUCE TIMBERLINE AND SOIL-SOLUTE CONTENT

The soil-solute content, as expressed by the soil σ_a (Rhoades and Oster, 1986), was significantly higher in tills below Norway spruce stands in the TB than those below stands occupied by Scots pine in the felsic LG proper (Table 1). The σ_a values of the till in the LG were low, such that a major part (95%) of the observations were $\sigma_a < 0.6$ mS/m. Even though a strong correlation has been shown between the soil σ_a and soil attributes associated with forest productivity, such as exchangeable Ca and Mg as well as cation-exchange capacity (CEC) (McBride et al., 1990), low soil σ_a values in the till of the LG may only indirectly be associated with the low concentrations of Ca and Mg. However, the concentrations of Ca and Mg are high in tills of the Greenstone Belt–Tanaelv Belt, but low within the felsic Lapland Granulite (Reimann et al., 1998). In contrast to these bases, concentration of Al in till of the TB is low compared to that in the LG (Reimann et al., 1998). Because the growth and yield of Norway spruce have been observed to be dependent on soil Ca and Mg (Vejre, 1999), an inhibitory effect of Al on the uptake of Mg (van Praag et al., 1997) may disfavor spruce on till of the LG. In a similar way, Timoney et al. (1993) found concentrations of N, Ca, and Mg to be insufficient for white spruce on Canadian Shield tills derived from acidic crystalline rocks.

Previous studies have demonstrated that lithology has pronounced impact on the initial quantity of base cations and nutrient status of the sites (Timoney et al., 1993; Reimann et al., 1998; Richardson, 1998); hence the treeline spruce occurrence at the Kuusipää site (Fig. 2; Table 1) inside the LG is puzzling. The mean $\sigma_a = 1.53 \pm 0.33$ mS/m of the till indicates a source rock type other than the felsic garnet gneisses of the LG (Table 1), possibly the diabase dikes that perpendicularly cross the LG (Pihlaja, 1987). On the Kuusipää site, spruce forms a mixed treeline with mountain birch (*Betula pubescens* ssp. *czerepanovii*) at 596 degree-days in a similar way as on fertile soil of the alkaline Khibiny Mountains in the Kola Peninsula (Kremenetski et al., 1999). The climate-driven (“alpine”) treelines of spruce in Finnish Lapland are attributed to fertile tills derived from mafic and intermediate-composition rock types, such as the ultramafic rocks and amphibolites in Pallastunturi in western Lapland (treeline at 500 m a.s.l. and 594 degree-days) and the biotite-rich diorites in Sarmitunturi in eastern Lapland (410 m a.s.l. and 607 degree-days) (see locations in Fig. 1; Juntunen et al., 2002).

The ANN classification for the terrestrial soil EM data indicated significant differences between the tills of spruce stands and those of pine (Fig. 4), suggesting good generalization behavior of the trained ANN. An advantage of this technique is that with an ANN of proper size (number of neurons), complex relationships between input and output parameters can be represented. A disadvantage of a classification using ANNs is the difficulty of suggesting causal connections to get the desired output from the internal parameters of the ANN. However, the ANN differentiation of spruce and pine coincides with contrasting lithology, lithogeochemistry, soil chemistry, and soil physical properties between the mafic TB and felsic LG (Marker, 1985; Reimann et al., 1998; Sutinen et al., 2002; Table 1; Figs. 1–3). The poor nutrient

availability (low soil σ_a) and low water content (low soil ε and high γ_K) in the till of the LG evidently are insufficient for spruce (Reimann et al., 1998; Vejre, 1999; Alawi, 2002; Sutinen et al., 2002; see also van Praag et al., 1997); hence the acidic sandy till of the LG provides low edaphic potential for spruce to migrate north-northeast.

NATURAL DISTURBANCES

In accordance with forest inventories (Kallio et al., 1971; Katila and Tomppo, 2001; Sihvo, 2002), this study indicated the absence of Norway spruce, but dominance of Scots pine, in the felsic LG (Table 1). Here, the percentage of pine may exceed 93%, and silver birch is a common associate of pine (Sutinen et al., 2002). Hence, we argue the conceptual model of a static (aspen)-birch-pine-spruce successional sequence, i.e., boreal forests repeat the same regeneration and succession stages after natural disturbances, particularly after forest fires in the boreal environment (see Pastor et al., 1999; Frelich and Reich, 1998). According to this static concept, Norway spruce, as a late-successional or climax species, should replace Scots pine, but it appears to be unable to invade nutritionally constraining glacial materials, i.e., granulitic tills with $\sigma_a < 0.6$ mS/m. In contrast, Scots pine, as an early-successional or pioneer species, is absent on fine-grained tills with constraining soil-water content ($\varepsilon > 15$; $\theta_v > 0.27$ cm³ cm⁻³; Fig. 3), i.e., tills derived from fine-grained mafic rocks of the TB and Lapland Greenstone Belt (Sutinen et al., 2002; Hyvönen et al., 2003; see also Richardson, 1998). Shade-tolerant Norway spruce is known to be adapted to the development of long-term, old-growth continuity; hence the structure of Norway spruce–dominant forests with downy birch as the principal associate of spruce in the TB may in part result from gap dynamics and self-replacement without succession of Scots pine (Drobyshev, 1999).

Successional stages after natural disturbances, such as forest fires, are associated with rotation period and severity of disturbances (Agee, 1998; Frelich and Reich, 1998). Fire-return intervals and fire severity, as attributed to soil-moisture regimes, significantly vary within boreal pine and spruce forests (Agee, 1998; Jasinski and Angelstam, 2002). Scots pine has a moderate-severity fire regime (Agee, 1998), but fire susceptibility is much higher for dry pine heaths compared to that for mesic-wet sites of Norway spruce (Jasinski and Angelstam, 2002). Through the Holocene (i.e., since 10,000 yr BP), a fire-return interval of 220–260 yr in pine forests has been recorded in eastern Finland (63°N); however, historical fire cycles are only tens of years or less (Pitkänen et al., 2002). In contrast to pine heaths, the fire-rotation period of mesic-wet and fertile spruce sites may be as long as 2600 yr (Jasinski and Angelstam, 2002). The fire regime of the study area has yet to be described, but the airborne gamma-ray data over the TB-LG transition evidently show discrete soil-moisture regimes (Fig. 2). Classification of the airborne gamma-ray data (Hyvönen et al., 2003), associated with studies on charcoal layers in peat deposits (Jasinski and Angelstam, 2002; Pitkänen et al., 2002), may bring new insight to the rotation and severity of fire disturbances within the soil-driven timberline forests of Norway spruce in Lapland.

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