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Soils at the Altitudinal and Northern Treeline: European Alps, Northern Europe, Rocky Mountains - A Review

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Abstract

No treeline-specific soil types exist. The treeline ecotone is usually characterized by a mosaic of soil types closely related to the locally varying conditions. Microtopography and the patchiness of the plant cover play an important role in this respect. Most soils in the treeline are shallow, and rich in skeletal material. Freeze-thaw processes are important agents for pedogenesis. Natural disturbances such as landslides, avalanches and fire affect soil development in the treeline ecotone. Human impact has also been an important factor historically. Fossorial mammals and wild-living and domestic ungulates have been equally-involved in soil development. In the long-term, forest expansion into currently treeless terrain within the treeline ecotone and beyond the existing tree limit will be closely associated with changes in soil conditions irrespective of whether it is driven by climate warming and/or cease of pastoral use.

Keywords

Mountains, Pedogenesis, Soil mosaic, Soil types

Introduction

Treeline position, spatial pattern and dynamics depend on a multitude of interacting factors [1-4]. Among them soil is undoubtedly one of the most complex factors (Figure 1). However, the influence of soil on the treeline ecotone is usually less conspicuous than the effects of other factors such as heat deficiency, wind, and snow-pack on tree growth and treeline spatial patterns. Thus, in most treeline studies, soils have been considered rather cursorily.

In the European Alps, research on soils in the treeline ecotone and in the alpine zone has been stimulated already almost 50 years ago by the challenge of restoring high elevation forests and afforestation above the present forest limits [5-9]. Broad information is also available on alpine soils in the Rocky Mountains [10-19]. Recently high-elevation soils in a worldwide view are considered in a FAO report and with focus on Asia by Müller, et al. [20,21]. In addition, Egli, et al. presents a review on soils of mountainous landscapes [22].

The possible influence of global warming on soil ecological conditions, especially in cold regions, has increasingly attracted researchers' interest [19,20,23-29]. In

high-mountains, soils, in particular, play an important role in maintaining ecosystem services [20,30], such as buffering surface runoff, flood control, preventing slope erosion, and reduction of slumps and landslides.

The objective of this paper is to highlight the multiple interactions of soil conditions and tree stands and their possible effects on treeline spatial pattern and dynamics in the European Alps, in northernmost Europe, and in the Rocky Mountains, where the authors studied treeline ecological conditions during many field campaigns (see reference list). In the Alps, most studies were carried out in the Engadine and its neighboring valleys (Switzerland). In the north, the authors focused on treeline patterns and dynamics in northernmost Finnish Lapland. In addition, the authors studied the treeline ecotone from

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the southern to the northern Rocky Mountains and in some other mountain ranges in the American west. We apply the term 'treeline' to the transition zone (ecotone) between closed subalpine or northern forests to the elevational or northern limit of tree species. Depending on the local conditions, the transition zone varies in width [31,32].

General Characteristics of Soils at Treeline

The relative young age of soils is a common characteristic of formerly glaciated mountain landscapes. Most

soils in the treeline ecotone are shallow und rich in skeletal material. Block-rich saprolite is usually lacking a continuous soil cover. On mountain ridges that were not covered by Pleistocene glaciers, such as some broad, rolling high interfluvies in the Colorado Rocky Mountains and in Glacier National Park (Montana), for example, deep soils that developed over longer temporal scales can be found on gentle terrain [14,33-35]. In the Alps, buried relict soils that developed during the last interglacial period [28], can be found in the treeline ecotone and in the alpine zone.

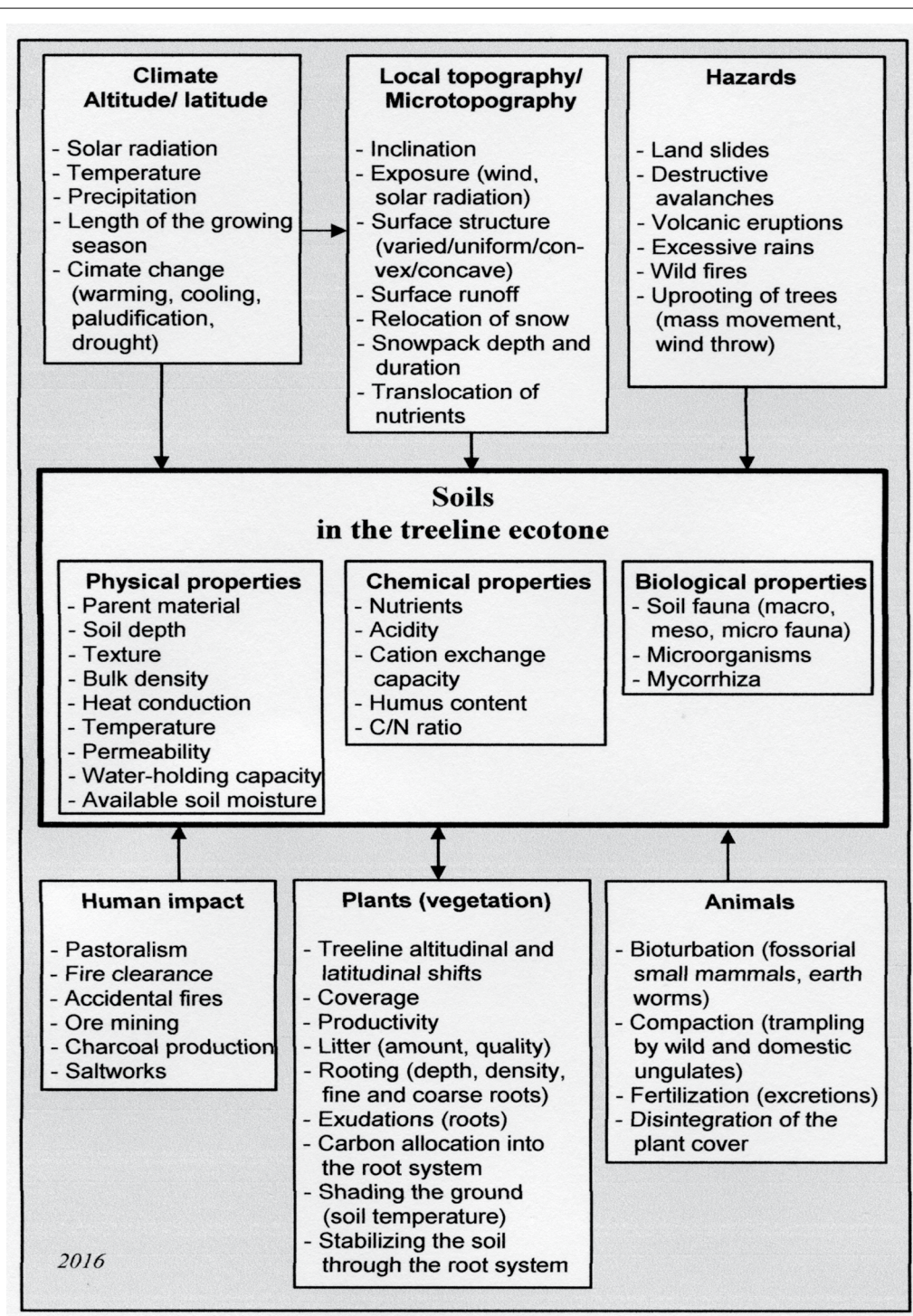


Figure 1: Factors and processes influencing soils in the treeline ecotone.

Influence of elevation

Soils in the treeline ecotone are influenced by the altitudinal gradients of temperature and precipitation (Figure 1). Heat deficiency is of overall importance. Changes in plant nutrients, for example, driven by decrease of temperature with elevation are associated with changes in soil organic matter and quality (C/N-ratio) [29]. As most soils in the treeline ecotone are shallow and rich in skeletal material, their water-holding capacity may be relatively low [35,36]. Soil moisture conditions may however vary considerably under the influence of local topography. Freeze-thaw processes (e.g., cryoturbation, frost heave, needle ice formation) are important factors for soil development [37-41].

Very often, the soils in the treeline ecotone and in the lower alpine zone are relatively rich in humus due to slow decomposition [42]. In many cases, in addition to low soil temperatures and insufficient or excessive soil moisture, the wide C/N ratio of dwarf shrub and conifer litter and low pH values reduce microbial activity and decomposition [8]. In the treeline ecotone in the Upper Engadine (Switzerland), for example, C/N varies from 40-50 in dwarf shrub litter, whereas it is 25 in the litter of grass vegetation on pastures [43,44]. At treelines in northern Finland the authors found C/N varying from 50 in the litter layer (0-3 cm depth) on convex topography, covered with lichens and low dwarf shrubs, to 35 on the slopes, and 30 in the foot zone (dwarf shrubs, podzolised mineral hummocks). In the organic layer and A horizons C/N was ≤ 20 on top and in the foot zone, while ranging between 20 and 32 on the slopes of convexities (Figure 2) [45]. Podzolisation in and above the

treeline ecotone is reduced due to low plant productivity and high evaporation [43,44]. High evaporation loss is a result of patchy plant cover, permanent wind and - at high elevation - intense solar radiation and relatively low air pressure. Low nitrogen availability and phosphorus deficiency are also characteristic of the altitudinal and northern treelines [16,18,46-48]. Moreover, the decrease of ectomycorrhizal fungal taxa is at least partly an elevational effect [48-51].

Despite the general elevational effects on soil formation, there are no treeline-specific soil types in the temperate mountains. Instead, a mosaic of soil types prevails, closely related to the locally varying conditions, among which local topography is the dominant factor. The overlapping influences of parent material together with soil properties and plant cover may be more important than elevational effects [5].

Disturbances

Disturbances by landslides, soil creep, and avalanches not only destroy trees but also affect soils in the treeline ecotone (Figure 1). Uprooting of trees, for example, by avalanches may locally initiate soil erosion. On steep slopes, soil development was often interrupted through downslope redistribution of soil material. Thus, truncated or buried soils are very common. Large block fields often cause a low elevation of the actual treeline on steep terrain. On unstable slope debris, soil formation usually remains at an initial stage for a long time. However, if coarse block-rich debris in backslope and footslope positions becomes covered with finer enhanced water-holding material from the upper slope soil formation will accelerate. In northern Norway, for example, Holtmeier

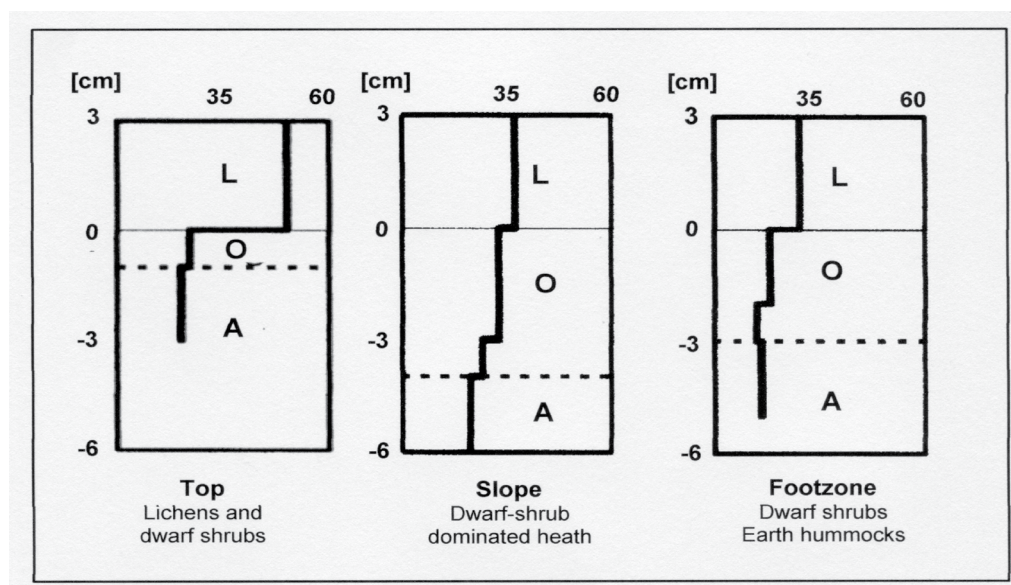


Figure 2: C/N on convex topography at the birch treeline on Mt. Rodjanoaivi (Northern Finnish Lapland). L: Litter; O: Organic horizon; A: A horizon. Data from Broll, et al. 2007 [45].

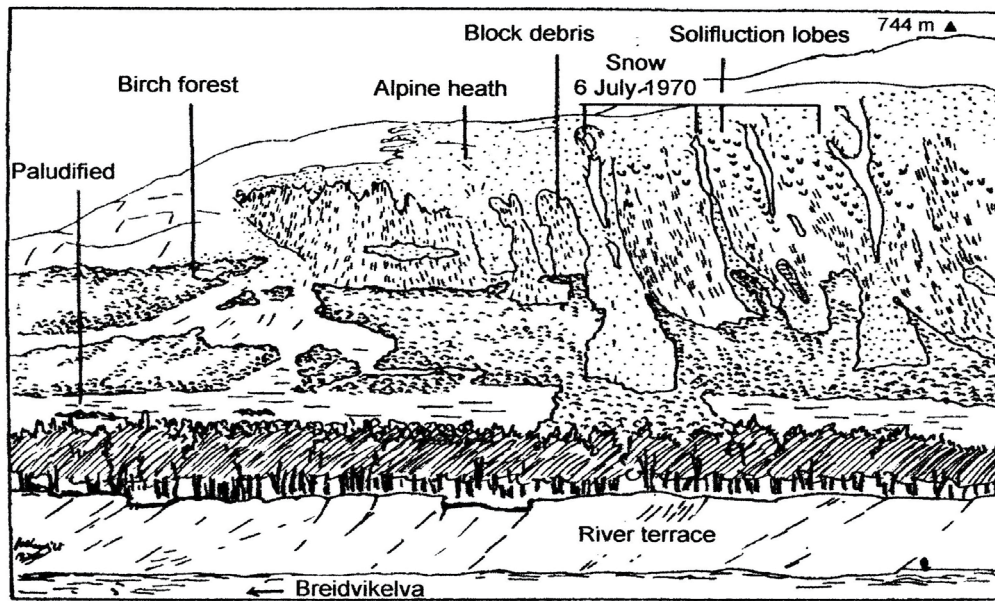


Figure 3: The steep blockfield on the north-west-exposed slope of Nakkefjell (Breidvikeidet, Tromsø; Norway) is partly covered with fine material resulting from collapsed solifluction lobes on the upper slope. Alpine heath (from above) and mountain birch forest (from below) are colonizing these sites. Field sketch by F-K Holtmeier (modified after Holtmeier 1974 [52]).



Figure 4: Turf exfoliation triggered by ibex (*Capra ibex*), sheep and cattle and enforced by needle ice formation on the south-west-exposed side of Languard Valley above Pontresina (Upper Engadine, Switzerland) at about 2500 m a.s.l. Photo by F-K Holtmeier.

[52] observed steep block debris areas partially covered with relatively fine material from solifluction lobes that had collapsed when entering the steep trough wall from above (Figure 3). The accumulated lobe material increases the water holding capacity on the otherwise extremely dry block debris and thus facilitates the establishment of birches, and willow shrub and other vegetation. Their root system stabilize the soil on steep terrain. Similar observations have been reported from steep mountain terrain in the Yukon Territory [53].

On steep alpine pastures, turf exfoliation [54,55] may truncate the soil profile and expose the mineral soil. Turf exfoliation is often triggered by cattle or wild ungulates that destroy the plant cover by trampling (Figure 4). Once the mineral soil is exposed, needle ice formation may enforce erosion by wind and surface runoff. On many subalpine and alpine pastures that have been grazed for hundreds of years, a dense network of cattle tracks has developed, which often enforces linear erosion through surface runoff.



Figure 5: Conifer krummholz (*Pinus albicaulis*) was destroyed by a big forest fire ('Red Eagle Burn') at treeline near to Divide Peak (Glacier National Park, Montana) in July 2006. No remains of the organic layer were left. Grasses and herbs invading the burn can be seen at the right-hand side. Photo by F-K Holtmeier.

During the Holocene, climatically-driven and anthropogenically influenced treeline fluctuations have influenced soils at regionally and locally varying intensities [31]. Pastoral use, forest fires, ore mining, charcoal production, and salt works played a major role in many treeline areas. In the Alps, for example, human impact has lowered treeline by 150 m to 300 m compared to its uppermost position during the postglacial optimum. In many areas, human impact dates back several thousand years [31,56-60]. The practice of fire clearance of high-elevation forests has been used for the past 4,500 years to create alpine pastures. In some areas, fire clearing started even earlier, probably during the Neolithic [61,62]. In the Himalayas, for example, a depression of more than 500 m is likely, mainly due to pastoral use [63]. In the Rocky Mountains, the oldest artifacts found in the treeline ecotone are over 8,000-years-old [64]. Thus, it is possible the first local human impact on the treeline occurred long before the Europeans arrived and caused severe disturbances, often combined with the use of fire. Fires often destroy the organic layers for the most part and locally expose the ground to splash, sheet, rill and gully erosion and/or strong winds in the burn areas (Figure 5). The loss of the organic layer resulted in nutrient impoverishment and reduced water holding capacity. Hence, soil susceptibility to erosion increased.

On heavily grazed pastures in the subalpine and alpine zone, mycorrhiza declined locally due to soil compaction and resultant stagnant water conditions. Moreover, the abundance of mycorrhizae also decreased in

sites where permeable substrate, high soil temperatures or wind cause dry conditions [49]. In northern Norway and Finland, overgrazing by semi-domestic reindeer had similar effects on soil erosion in the treeline ecotone and above [45,52,65-67], Ectomycorrhiza make organically bound soil nutrients available to the plants and contribute to rapid turnover of soil organic carbon stock in the organic horizons [68].

Wildfires have locally affected soils in the treeline ecotone. At the northern treeline, destruction of the forest by fire-initiated paludification has led to a thicker moss cover, and accumulation of dead organic matter (Histsols) [69]. In areas of thawing permafrost and increased paludification, the forest has been regionally retreating to a more southern position [70].

Not least, fossorial animals (e.g., ground squirrels, pocket gophers, marmots) as well as wild-living ungulates locally influenced soil development (bioturbation, nutrient fluxes, erosion) (Figure 1). Animals' influence on soils in the treeline ecotone has widely been disregarded, with a few exceptions [31,52,71-73].

Variety of Soils in the Treeline Ecotone

A great variety of soils can be found in the treeline ecotone: Shallow and deep soils, truncated and buried soil profiles, soils rich or poor in nutrients, water-logged and well-drained soils [74]. In the treeline ecotone and alpine zone, both well-watered or adequately drained sites are usually less common compared to sites with in-

sufficient or excessive moisture. Depending on substrate chemistry, substrate permeability and age of soil formation, Leptosols or Regosols developed. Plant cover varies with pH. On silicate substrate, the spectrum of soils in the treeline ecotone and lower alpine zone ranges from initial soils to fully developed Podzols and Cambisols, usually covered with zone typical acidic dwarf shrub vegetation and *Carex curvula* swards.

Locally varying soil moisture, as result of the direct influence of local topography (e.g., runoff) and wind-mediated relocation of winter snow (Figure 1), decomposition, nutrient content, nutrient availability, soil temperature (particularly near the soil surface), bulk density, heat conductance, and heat capacity are important for soil development, seedling establishment and performance of young growth in and above the treeline ecotone. Long-lasting low soil temperatures reduce min-

eralization and nutrient availability while simultaneously affecting photosynthesis, carbon investment, and thus root growth and nutrient uptake [18,75,76]. Available soil moisture plays a major role in this respect. However, under well insulating deep snowpack, microbial activity and decomposition continue significantly even outside the growing season [77-81].

While soils, particularly their organic layers, are the main nutrient source for plants, the latter influence pedogenesis by carbon allocation, nutrient uptake, exudations from the roots, amount and quality of the litter (e.g., nitrogen content, retention time of nutrients, acidity) all of which serve to modify the microsites [7,82,83]. In the treeline ecotone in Lapland, for example, the nitrogen cycle in microsites covered by dwarf shrubs was found to be different from that of lichen-covered sites (Figure 6) [46].

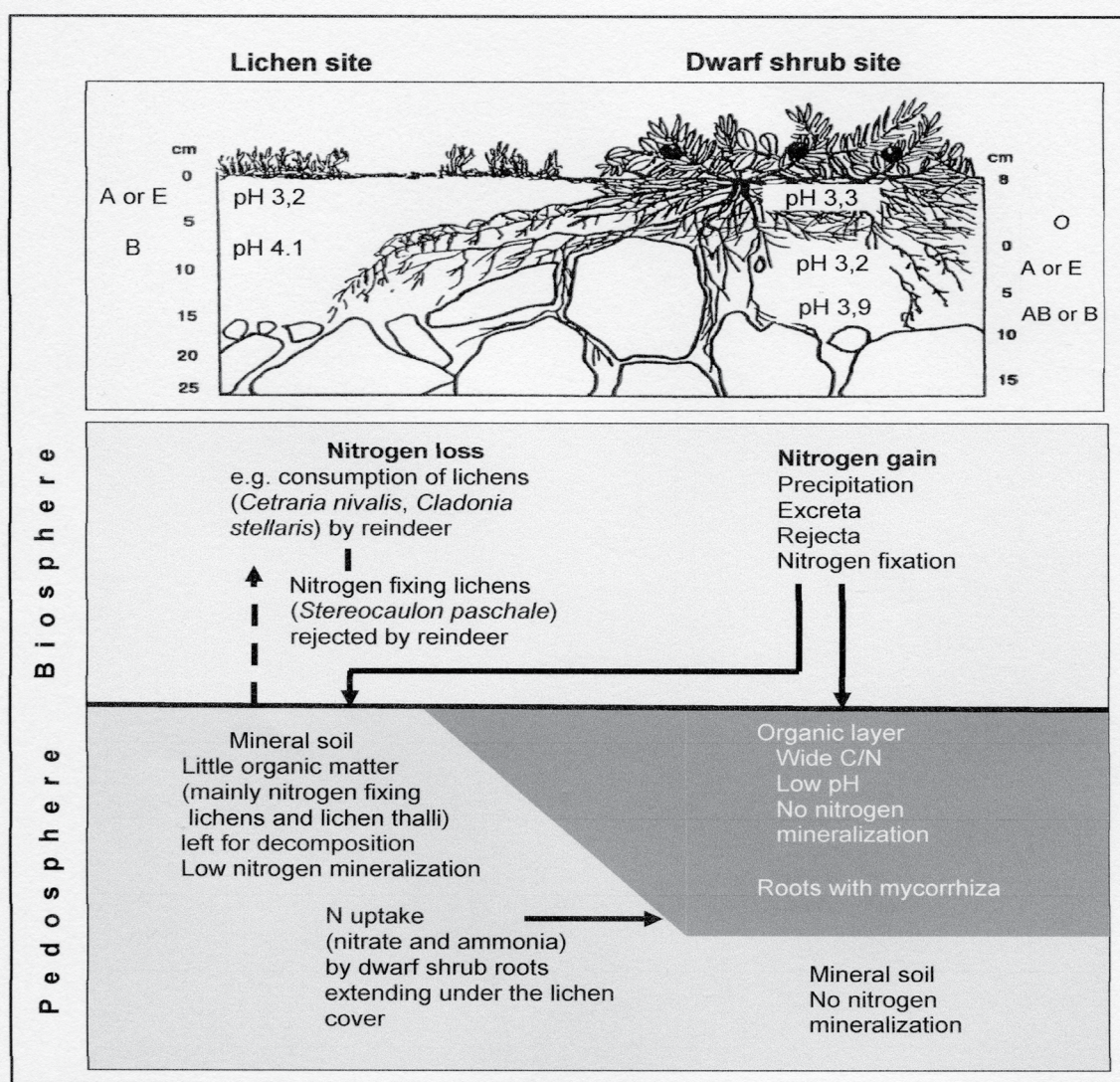


Figure 6: Selected processes of the nitrogen cycle at a treeline site characterized by a mosaic of dwarf shrubs and lichens near Kevo Subarctic Research Station, northernmost Finland. Modified from Broll [46]. On the lichen-covered patches, nitrogen fluxes mainly occur between the atmosphere, the living vegetation, and reindeer, whereas in the shrub-covered sites the organic layer and humus-rich mineral horizons also play a role.

In the treeline ecotone, present vegetation patterns reflect, to a certain extent, the multiple interactions of above-ground and below-ground processes. On crystalline parent material in the Central Alps for example, deep Podzols are associated with dwarf shrub-conifer forests. Thus, occurrences of well-developed Podzols above the present forest have been considered indicators of former forests [5,6,84,85] that were previously destroyed by humans. The Podzols probably developed during the last interglacial period [28]. Although well differentiated Podzol profiles were not always found, podzolisation could be evidenced analytically [86]. Podzolisation, however, may also occur under dwarf-shrub cover above the current treeline [44,86]. In the Alpine zone, percolating melt water may have a greater effect on podzolisation than vegetation [29]. On carefully managed alpine pastures, Cambisols have frequently developed. Soon after abandonment, however, dwarf shrubs recolonized these pastures and initiated podzolisation [87] when sufficient percolating water was present.

On well-drained terrain in the treeline ecotones of northern Europe, only shallow Podzols developed due to low productivity of the oligotrophic dwarf-shrub-lichen heath [88] and reduced litter supply. In addition, seasonally frozen ground prevents effective leaching. Under clusters of trees, more organic matter usually accumulates. In addition, open birch stands trap blowing snow which may increase the amount of melt water that would translocate minerals and dissolved substances into the soil. On the rolling land surfaces and low fells (< 1,000 m), annual precipitation at the treeline is less in comparison to the subalpine/alpine zone in the Alps.

Like relict Podzols in the Alps, 'subalpine Podzols' [89] have been considered as a relic of a warmer period (5,000-3,000 BP), when the treeline was 150-200 m higher than its present elevation [90]. In the Central Swedish Scandes, relict Podzols [91] together with mega fossils indicate the presence of conifers (forest?) at about 300-400 m above the current treeline [92]. On wind-swept and well-drained convex topography, the authors [93] found Podzol remains under partly eroded peat layers that probably accumulated during a wet and cool climate (since about 1,000 yr BP and 'Little Ice Age'), and under the influence of good drainage conditions, most likely under mountain birch stands with dwarf shrub under-growth. However, in sites, where dwarf shrub-lichen heath on permeable substrate ensures low pH values, podzolization can also be evidenced at present [45,94]. Very shallow Podzols (formerly called 'Nanopodzols') on well-drained and wind-swept terrain, currently covered with low mats of dwarf shrub-lichen heath, are also common in other areas of northern Fennoscandia where permeable glacial till covers acidic bedrock [95].

On well-drained subalpine and alpine grassland in the Rocky Mountain treeline ecotone (Colorado Front Range) Cambisols prevail, whereas Podzols developed under coniferous forest [12,14]. In the upper part of the treeline ecotone (3,350-3,500 m), remnants of Podzols that had developed under downwind 'migrating' clonal conifer groups were observed [33,34]. In general, there is only a short period after snowmelt with above freezing temperatures and sufficient percolation to ensure the essential pre-conditions for leaching.

Soil formation does not just depend on local factors but may also be influenced by allochthonous impacts such as deposition of eolian dust carried great distances by prevailing winds, exhibited for example by the 'alpine loess' in the Colorado Front Range [13,15,33,34,96], or Saharan dust in the Alps [97-100] and dust from inland deserts (Taklimakan; Gobi) in the Tien Shan and Altai ranges [101]. In the Rocky Mountains, dust deposition increased considerably after the intensification of grazing and agriculture had caused widespread disturbance of soils on the Colorado Plateau and other desert regions of the western United States during the 1880s. In addition, recurrent periods of severe drought regularly increase emission of dust from the desert areas and deposition in the Rocky Mountains [102,103]. In the windy treeline ecotone on the Front Range, the authors found enriched silty eolian material in the soil under and downwind of tree islands, i.e. at sites accumulating blowing snow in winter [33,34]. The eolian dust is rich in calcium, which buffers soil acidity and increases cation exchange capacity. Thus, decomposition may accelerate and nutrient availability increase. Highest Ca contents and corresponding high pH values and CEC were measured at the leeward sites, while under the tree islands pH values were relatively low and initial podzolisation occurred [33]. The relatively high amounts of fine material that were found in the topsoil of very shallow Podzols in the treeline ecotone in northern Norway have also been ascribed to deposition of eolian dust [104]. Thin, fine-sandy and silty layers that were found in organic hummocks in the treeline ecotone in northern Finland are also of eolian origin [45].

Topographic Control of Soil Distribution Pattern

While the distribution pattern of soil types in the treeline ecotone is only partly related to the altitudinal gradient of temperature and precipitation, pronounced differences can develop in response to local topography [7,8,14,31,43,45,86,104-110]. The direct and indirect effects of topographical factors on soil forming processes and vegetation development are key factors in the treeline ecotone and the adjacent alpine zone. Local topography influences microclimates, snow relocation, depth and

duration of the winter snowpack, distribution of soil temperatures, freeze-thaw cycles, soil moisture, and translocation of solid and dissolved substances by runoff, seepage and leaching (Figure 1) [31,108,111,112]. Pronounced differences exist between convex and concave sites and between northern and southern exposures. The same holds true for microbial biomass and humus forms [105,113].

Convexities

Soils on convexities are usually of coarse texture and rich in skeletal material due to surface runoff and/or prevailing

strong winds. Frequently the organic layers and the upper mineral horizon on the top and upwind side of convex terrain are eroded. Needle ice formation was also frequently noted in such situations, sufficient fine sandy-silty material provided. Freeze-thaw of the topsoil and frost heaving may cause mechanical damage of fine roots of tree seedlings. Frost heave largely depends on the presence of fine soil texture. On the other hand, tree islands that became established on convex topography may accumulate snow that prevents the soil from freezing to great depth [33,112].

In many places, trampling effects by wild ungulates



Figure 7: View along the north-facing slope of Koahppeloaiivi. As depicted, the soil has eroded completely from convex, wind-swept terrains after reindeer disintegrated the plant cover and birch stands declined due to recurrent periodic or episodic defoliation by the autumnal moth (*Epirrita autumnata*). Aerial photo taken by F-K Holtmeier from about 300 m above ground.



Figure 8: Downwind-migrating wind scarp on the northeast-facing slope of Koahppeloaiivi at 327 m a.s.l. Prevailing winds from the left (W). Photo by F-K Holtmeier.

triggered or enforced soil erosion. In the mountain-birch treeline ecotone in northern Finnish Lapland, for example, the original acidic dwarf shrub-lichen heath on wind-swept convex terrain became fragmented or destroyed completely by excessive numbers of semi-domestic reindeer (Figure 7). Under such conditions up to 60-90% of the soil profile can be eroded. Occasionally only down-wind 'migrating' wind scarps (Figure 8) were left [34,114]. Skeletal material relatively increased on the surface, as wind removed the fine material. Organic carbon and total nitrogen content are low in such places, whereas pH (very strongly acid) is a little higher on the eroded sites than under dwarf shrub-lichen patches. Deep freezing in winter due to missing or episodic winter-snow cover, frequent dry conditions (soil moisture often < 20% volume) and lack of nutrients can impede establishment of mountain birch seedlings in such places [115]. Warming climate may exacerbate drought stress that would affect not only the above-ground tissues of the seedlings and young trees but also adversely affect their fine roots in the organic layer and topsoil.

In high mountains, such as the American Rockies and the central European Alps, overheating may locally occur at sun-exposed but wind-protected sides of ribs and other convexities in the treeline ecotone, under dry and calm weather conditions on and immediately below dark and dry soil surfaces that are either sparsely vegetated or not vegetated at all. Maximum absolute temperatures may range between 40-60 °C for several hours and for short time even higher [116,117]. Such conditions may be critical to fine roots near the soil surface, that are vulnerable to both deep freezing and occasional extremely high temperatures [115,118-121]. Such temperatures may also cause serious damage to tree seedlings through heat girdling [122]. Drought damage, however, is usually more common in such sites, particularly on rapidly draining soils. At greater depth, excessive low or high temperatures and damage to the roots do not usually occur.

In water-saturated substrates on sloping terrain, soilfluctuation may affect tree seedlings. At similar elevations, freeze-thaw events are more frequent in the upper soil layers on sunny exposures than on shaded rib sides. By contrast, late-lying deep snowpack on the shaded side of convex micro-topography usually prevents soil freezing at greater depths [31,123-125], provided snow comes early in winter when the soil is still unfrozen. In spring, however, warming of the soil on the shaded and often snow-rich side of convexities is delayed due infiltration of cold melt water and evaporation from the wet surface. As a result, soil usually remains relatively cool until snow has disappeared [126-128] as was also observed at the downwind edge of compact conifer groups where large

snowdrifts had built up [33,34,112,129]. At late thaw sites, soil temperatures may rise rapidly after the snowpack melted and soil dried [130]. Winter snowpack and its influence of soil temperature vary by slope, aspect, and climatic regions (maritime, continental).

The critical root zone temperature for root growth has been found to be about 6 °C, which is near the world-wide mean soil temperature at climatic treeline [131]. Anyway, root growth in young conifers (*Pinus cembra*, *Picea abies*, *Pinus mugo*) at treeline (2,000 m-2,300 m) on Stillberg (near Davos, Switzerland) started shortly after snow melt at soil temperatures between 2°C and 3°C and ceased at the same temperatures in mid-October [132]. At late thaw sites soil temperatures rose rapidly. Shoot elongation began earlier than root growth [130]. Significant growth of young trees may however be delayed. Conditions will be different if significant amounts of blowing snow accumulate on the sun-exposed side, i.e. prevailing winds from directions opposite to direct solar radiation. In continental climates (e.g., central Rocky Mountains), melt water supply from late-lying snowdrifts on southern exposures may reduce drought stress and prevent overheating of the topsoil at the beginning of the growing season, thus facilitating potential tree seedlings [32].

In general, relatively dry conditions prevail on convex topography due to run-off, seepage, low water holding capacity (coarse texture, thin or lacking organic layer) and wind (Figure 9). Direct wind impact, soil freezing to great depth, and drought stress may impair seedling establishment. Moreover, wind (turbulent flow and evaporation) lowers soil temperature during the growing season and prevents overheating. In addition, wind relocates loose fine mineral material and organic matter from the top of convexities to their leeward slopes and adjacent depressions, where it partly accumulates. Moreover, seepage relocates dissolved and fine solid substances from the surface to greater depth and from convex terrain to the adjacent gullies and other concavities. Therefore, convexities are usually relatively poor in nutrients [45].

Bedrock outcrops, roche moutonnées and rock bars (Lithic Leptosols; Stöhr 2007) [74] are partly covered with rapidly draining skeletal soil and/or fragmented lichen mats associated with moss layers and dwarf shrubs. Drought, low winter temperatures and limited nutrient availability are hostile to tree establishment in such places. Bedrock clefts, however, occasionally provide suitable conditions for seedlings on such terrain.

Concavities

Due to surface runoff, lateral seepage and snow accumulation, soil moisture and amounts of nutrients in-

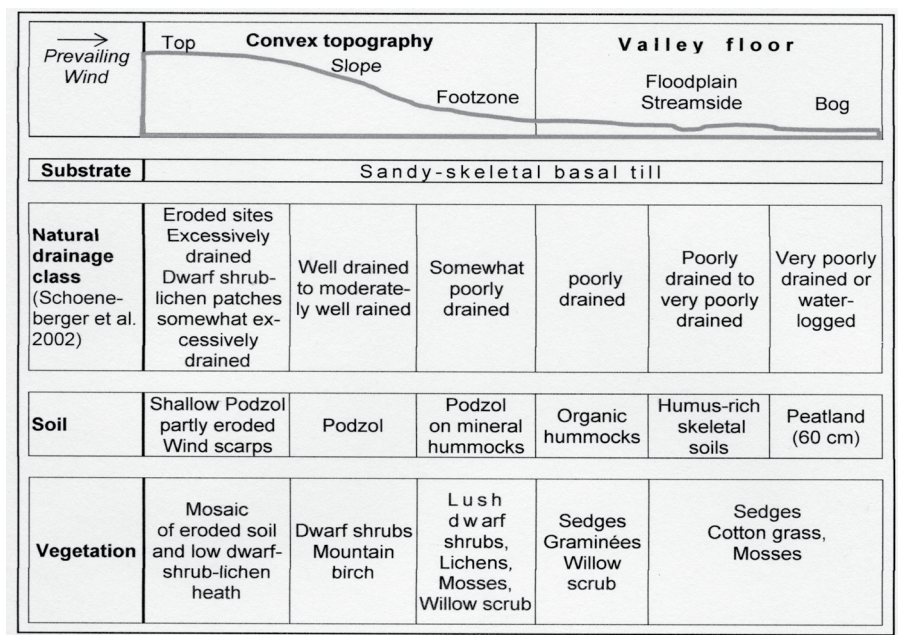


Figure 9: Transect (schematic) showing the distribution of soil types, natural drainage classes, vegetation, and microclimate as related to microtopography (modified after Broll, et al., 2007 [45]).



Figure 10: Roche-moutonnées separated by small alluvial flats that accumulated in former glacial drainage channels on Muottas da Celerina (Upper Engadine) at about 2,200 m a.s.l. On convex topography covered with dwarf shrubs (*Vaccinium uliginosum*, *Calluna vulgaris*, *Arctostaphylos uva ursi*, and others) and Swiss stone pine (*Pinus cembra*) Podzols are found, while peaty Gleysols developed in the alluvial flats that are covered with sedges and bulrush. Photo by F-K Holtmeier.

crease at the foot of convex slopes and in adjacent gullies and other concavities [45]. Due to the insulation from deep (2-3 m) winter snowpack, soil temperatures do not drop far below the freezing point and rise to zero (0°C) even before the snow melts. Freeze-thaw events are considerably reduced. In snow-rich gullies, decomposition during wintertime may account for 40% of the total annual decomposition [133]. In steep gullies, avalanches and late-lying snow, rather than soil conditions, prevent the long-term establishment of trees. In contrast to

steep gullies, that are normally ‘well-drained’ or ‘excessively-drained’ [45,105], stagnant water conditions may occur in closed concavities (e.g., kettle holes), on small alluvial flats on gently sloping or level terrain. In both the alpine and the northern treeline ecotone, Gleysols, Stagnosols, and Histosols (peat-land) are found in such very poorly-drained places.

Gradient conditions may be reflected in the distribution pattern of plant communities [8,32,45,123,134]. On gentle trough shoulders (Figure 10) or gently slop-



Figure 11: Glacial cirque in the head of fourth of July Valley (Colorado Front Range) at about 3,420 m a.s.l. The mosaic of convex topography (roche moutonnées), former drainage channels and alluvial flats cause a distinct mosaic of soil types. These comprise organic soils in poorly-drained or waterlogged depressions and Dystric Cambisols, as well as Podzols occurring on convexities covered with tree and krummholz stands. Photo by F-K Holtmeier.



Figure 12: Rib-and-groove topography on the west-facing side of the south-north-oriented Roseg Valley (Upper Engadine, Switzerland at 2,000-2,200 m). On the north-facing rib sides, Podzols developed under coniferous forests (*Larix decidua*, *Pinus cembra*) and dwarf shrub vegetation (mainly *Rhododendron ferrugineum*). On the south-facing rib sides, shallow skeletal-rich Leptosols and initial soils prevail. In the gully outlet, frequent avalanches and instable coarse debris impeded soil formation. Photo by F-K Holtmeier.

ing northern fells and in glacial cirques (Figure 11), for example, roche moutonnées associated with former glacial drainage channels, spillways, and small alluvial flats cause a distinctive distribution of vegetation and soil types. At the Rocky Mountain treeline, for example, Dystric Cambisols and also Podzols are found on bedrock outcrops covered with conifers, whereas organic soils developed in the depressions because of poor drainage or even water saturation, deep late-lying winter snowpack, and resultant poor decomposition. Willow thickets, bog and spring communities typically occur in these wet

places [31,135,136]. However, the situation in the Alps differs as the anthropogenic upper limit of the treeline ecotone is usually located at lower elevations than the cirque-floors and back-slopes.

The effects of microtopography on microclimates and consequently on soils vary depending on regional climate. They are most remarkable in continental climates with relatively low precipitation, long exposure to sunlight and intense direct solar radiation. Similar effects may occur in climates with a dry summer season. The influence of slope orientation on microclimates and soil



Figure 13: In the west-east oriented Val Muragl (Upper Engadine), sharp contrasts occur between the north-facing (right) and south-facing (left) valley sides due the different sun angles as is clearly reflected in the snow pattern several days after a snowfall in the end of September. No influence of microtopography on solar radiation loads can be seen on both valley sides. Photo by F-K Holtmeier.

pattern is of major importance in this respect (Figure 12 and Figure 13).

Soils in the Treeline Ecotone and Climate Change

Potential effects of changing thermal and humid regimes on soils in the treeline ecotone can be roughly assessed. Recurrent periods of drought, particularly in continental climates, are likely to reduce decomposition and impede root development, and thus nutrient supply. In addition, increasing wild fires would not only destroy trees, but also the organic layer and thereby the main nutrient source.

As soil physical and chemical properties are usually more closely related to the effects of the varying microtopography and geological substrates than to elevational gradients, potential changes need to be assessed at local and regional scales. Thus, in the mountain treeline ecotone on heavily dissected and rugged mountains, stagnant water conditions are restricted to relatively small depressions, and the peat is relatively shallow compared to the vast paludified areas on gently rolling land surfaces in the north. Under warmer and drier conditions, mineralization of these peaty soils (Histosols) will accelerate. Better nutrient availability may facilitate colonization of such sites by trees and shrubs, whereas the convexities soils will be affected by more frequent droughts [3,137,138]. Under the influence of warmer and more humid conditions, on the other hand, decomposition and leaching of soils are likely to increase on convex terrain. Better nutrient availability, however, might be overcompensated by increased leaching.

By contrast, in waterlogged depressions an increase of

anaerobic decomposition and release of methane to the atmosphere are likely. Deposition of drifting snow and a greater amount of melt water may play an important role. In addition, wet conditions are adverse for mycorrhizae and thus impede nutrient uptake. In the treeline ecotone on gently rolling land surfaces in the north, such changes would influence much larger areas than in steep-sided mountains.

As may be concluded from snow fence experiments in Alaska tree islands and tree clusters becoming established in the present tundra may locally destabilize permafrost and thermokarst [127]. Thus, a long-term cycle controlled by the interaction of *Pinus pumila* patches and the permafrost level as described by Kryuchkov [31,139] from the northern treeline in Siberia is not unlikely.

While historical removal of high-elevation forests has had lasting effects on the soils in the treeline ecotone, treeline upward shift - irrespective of whether driven by climate warming and/or cease of pastoral use - brings about changes in soil conditions in areas currently devoid of tree growth. Infilling these gaps and forest in growth [140-146] will probably have a greater effect than establishment of new trees above the existing tree limit. In the Ural Mountains, for example, climatically-driven forest expansion into the mountain tundra is likely to increase ectomycorrhizal biomass [147].

The influence of altered vegetation on litter input and microclimate on soil organic matter may result in a faster cycling of organic matter and increase available nitrogen in the area being invaded by trees [26,68]. In the long-term, however, nitrogen turnover would decrease due to fixation in long-lived trees [148]. Moreover, increasing

tree density may buffer warming of the soil and reduce decomposition of the litter. Thus, organic layers would increase and podzolisation may become revived, provided that percolation is sufficient. However, direct (primary) and indirect (secondary) effects of climate warming overlap. Their effects are often difficult to distinguish [26].

Conclusions

No treeline-specific soil types exist. The direct and indirect effects of topographical factors on soil forming processes and vegetation development are key factors in the treeline ecotone and the adjacent alpine zone. Thus, the spatial distribution pattern of soils and the multiple interactions of soil formation processes and vegetation development in the mountain treeline environment can only be assessed at local and regional scales.

In the European Alps, the anthropogenically induced after-effects have a lasting influence on soils in the current treeline ecotone for many hundreds or thousands of years at different intensities. In northern Europe and in the Rocky Mountains, humans have influenced soils more locally. The after-effects of anthropogenic impact may overrule the influence of climate on soil development.

Forest expansion to higher elevations than at present will be associated with changes in soil conditions. Potential variations, however, are difficult to predict, as at small scales (local, micro), climatic (thermal) differences may occur that are as great in magnitude as those that occur over thousands of kilometers in lowland sites. Soil responses to changing climate are a long-term process lagging far behind forest advance. Increasing tree cover, litter supply and reduced decomposition will cause changes in the medium term (decades). Such changes will be more important in the present ecotone than above the existing tree limit. Abrupt changes caused by severe fires, landslides, wind throw and other natural factors may also have lasting effects on soil development in both the medium- and long-term.

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