

Grazing history affects the tree-line ecotone: a case study from Hardanger, Western Norway

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Expansion of subalpine forests and upslope shift of tree-lines are expected in temperate and boreal mountain ecosystems due to global climate change. On a local scale, climatic forces are modified by a number of controlling factors. Site history is of central interest because it impacts on the importance of air and soil temperature vs. other factors. In many mountain areas, the grazing record is an important part of the site history. This study compares the tree and ground cover of two localities having different grazing histories in the tree-line ecotone of Western Norway. Data from the sampling of trees, saplings, seedlings and ground cover, tree age determinations, aerial photographs, interviews and literature research are used. The results show differences in the structure of the tree-line ecotone with regard to tree age, height, circumference and the structure of the understory. Ground cover differs in species composition, mainly with regard to light preferences. Together, the differences stress the importance of site history consideration in order to understand changes in the tree-line ecotone, because dissimilar site histories may create differing local responses to future global and regional climatic changes.

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Introduction

Among the many factors influencing the spatial and physiognomic structure of, and tree establishment at, the tree-line ecotone (see Smith et al. 2003; Dalen & Hofgaard 2005 for references; Holtmeier & Broll 2005, 2007), temperature has received special attention (see Körner & Paulsen 2004 for tree-line terminology). Based on the seasonal mean root zone temperature, the climatic altitudinal tree-line can be predicted globally with an accuracy of ± 50 m (Körner & Paulsen 2004; Körner & Hoch 2006). On a regional scale, the macroclimate (summer temperature and precipitation) controls the tree-line altitude, together with its geographical location and species composition (Kjällgren & Kullmann 2002). However, on a local scale, global and regional climatic forces are modified by controlling factors related to topography, soil, microclimate, tree species, recent biotic and human influences, and site history (Kjällgren &

Kullmann 2002; Holtmeier 2003; Hiller & Mütterthies 2005; Mellmann-Brown 2005; Holtmeier & Broll 2007). The site history is of central interest because it modifies the importance of temperature vs. the other controlling factors (Hofgaard 1997, 1999; Dalen & Hofgaard 2005; Rössler et al. 2008).

In the Norwegian mountains, as in other European mountains, grazing has been an important part of site history in numerous areas (Frödin 1940, 1941; Reinton 1955; Austrheim & Eriksson 2001; Tasser & Tappeiner 2002; Dullinger et al. 2003b; Mayer et al. 2005; Marie-Pierre et al. 2006; Potthoff 2007). Grazing influences vegetation through selective defoliation, trampling, alteration in the concentration of nutrients and propagule dispersal (Rook et al. 2004). Grazing thus affects competitive plant species interactions resulting in changes in vegetation community composition (including distribution and abundance) (Milchunas et al. 1988; Archer & Smeins 1991; Palmer et al. 2004).

The specific effect of grazing on the tree-line ecotone will presumably vary between the open and tree/shrub-covered patches of the ecotone. The influences on open patches are likely to resemble those on low-alpine vegetation where, independent of grazing intensity, the monocotyledonous vegetation seems to be less affected by grazing than shrub-dominated vegetation (Wielgolaski 1975; Spatz 1978; Cernusca 1991; Olofsson et al. 2001; Tasser & Tapeiner 2002; Olofsson 2006; Potthoff 2007). Experiments with *Nardus stricta* and *Calluna vulgaris* showed *Nardus stricta* as the stronger competitor, which may be of special relevance under intense grazing pressure or abundant nutrient input (Hartley & Amos 1999). Brancaloni and Gerdol (2006) report a conversion of subalpine dwarf shrub heath into grassland due to fertilization.

The effects of grazing on tree establishment and growth, and thus on those areas covered by trees or in the process of being covered, are complex. On the one hand, high grazing intensity reduces or prevents tree establishment; on the other hand, grazing may enhance tree establishment due to the removal of vegetation and the creation of gaps (Linhart & Whelan 1980; Mitchell & Kirby 1990; Cairns & Moen 2004; Pollock et al. 2005; Marie-Pierre et al. 2006; Camarero & Gutiérrez 2007). Competition with ground vegetation can thus be a crucial factor for tree establishment (Bolli et al. 2007). By contrast, experiments have shown that the establishment of trees influences ground vegetation, whereas the course of succession is, among other factors, altered by the presence of herbivores (Hester et al. 1991). The average current-year shoot production of saplings and above-ground biomass is reduced by grazing (Vandenberghe et al. 2007), and intense grazing decreases the height increment (Hester et al. 1996; Hester et al. 2005). The frequency of tree damage can be related to grazing intensity (Mayer et al. 2005; Mayer et al. 2006). Through its controlling effect on tree establishment and tree growth, grazing influences the structure of existing tree-covered areas; for example, by reduction of shrub cover (Perivolotsky & Haimov 1992; Kirby 2001). Moreover, grazing affects the proportion of open vs. tree-covered areas, and thereby, it also impacts upon the ratio of subalpine relative to alpine areas.

In regions with a long grazing history, as for example in many European mountains, the influences of grazing will probably have long-term effects that again may impact on the development of the

future tree-line ecotone. The latter is of special interest in the light of global climate change and potential tree-line changes. This study investigates the relevance of grazing history to tree cover and ground vegetation in the tree-line ecotone. It compares two localities in Western Norway with different grazing histories under similar climatic conditions, and aims to answer the following two questions.

How does grazing history influence:

- 1) the structure of tree cover and establishment of trees?
- 2) the composition of the ground cover?

Study area

The study area is located in Hardanger, Western Norway. The two seasonally inhabited farmsteads of Storlii (c 890 m a.s.l.) and Berastølen (914 m a.s.l.), and their respective grazing areas were investigated (Fig. 1). At present, Storlii farm is used for goat grazing and processing milk in the summer. In 2007, 131 goats were grazing at Storlii. Storlii is thus the seasonal farm at the tree-line ecotone with by far the largest number of grazing livestock in the region. At Berastølen in the same year, seven head of cattle were grazing with occasionally some sheep. However, none of these animals was observed close to the investigation site. Large herbivores grazing at both localities were moose, red deer and roe deer. According to local informants, the numbers of these visiting creatures are similar at both localities.

The annual precipitation measured at Liseth (748 m a.s.l.) gives a reference value of 1110 mm for the study area (Norwegian Meteorological Institute 2008a) (Fig. 1). The closest weather station with a longer-term temperature record is located at Bu, 117 m a.s.l. (Bu is located about 15 km north-west of Øvre Eidfjord, Fig. 1). Corrected by -0.6 °C per 100 m altitude, the mean July temperature at 900 m a.s.l. is c 9.9 °C (Aune 1993). Due to the short distance (c 10 km; cf. Fig. 1) between the two seasonal farms, the climate can be assumed to be similar on a regional scale. The bedrock at Berastølen is migmatite; at Storlii, it varies from granite to diorite, quartz diorite and monzodiorite (Sigmond 1998). All these types of bedrock are similar in their mineral content (J. Sulebak, personal communication 2008).

At each seasonal farm, a slope (west-exposed at Storlii and north-west exposed at Berastølen) was

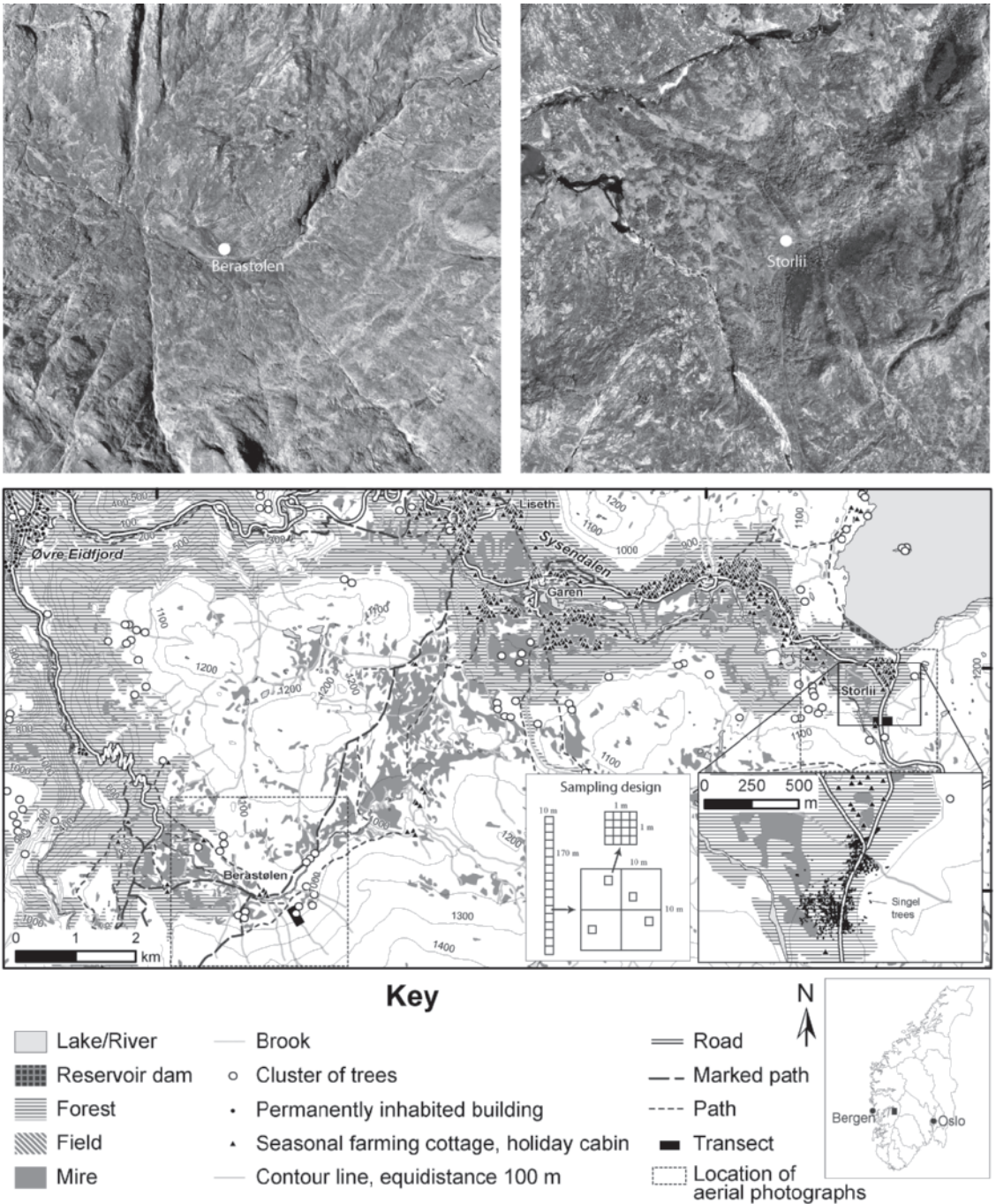


Fig. 1. Aerial photographs of Berastølen and Storlii taken in 1961 (Photos: TerraTec AS) and a map of the study area. Inserted figure: sampling design. Inserted map: tree cover as plotted from an aerial photograph; only the area between Storlii and the transect on both sides of the road was plotted. The area category for forest indicates a greater occurrence and a larger number of trees west of the seasonal farm. However, a comparison with the present situation shows that the forest is more open, as it can be depicted in map data on this scale.

chosen for closer investigation. The slope of Storlii is generally steeper than that of Berastølen, which appears to result in Storlii having a lesser proportion of moist areas. These differences have been taken into account by including moisture and inclination as environmental variables in the analysis of the ground cover (see Methods). Another difference is that a road crosses the slope at Storlii (see Fig. 1). This may affect species composition due to immigration of plants in the vicinity of the roadside and their subsequent establishment in the tree-line ecotone. To minimize the influence of plant immigration, a buffer zone along the road was excluded from the investigation (see Methods).

Methods

Trees, saplings and seedlings were sampled to document the current structure of the tree cover (including all growth stages), which reflects present and past land use. Moreover, tree age was determined based on tree-ring analysis to record the history of tree establishment. Aerial photographs taken in 1961 allowed an overview of the structure of the tree cover at that time. Ground cover was sampled to investigate the modern vegetation composition. When compared, differences in species composition can reflect different site histories. Ordination methods were used to investigate the relevance of environmental variables other than grazing history that may have created differences between the two localities. Interviews and literature research were carried out to gather historical information about land use.

Sampling of tree and ground cover

Two transects of 170 m in length and 10 m in width were selected at a distance of c 500 m from the respective seasonal farmsteads, starting at 935 (Storlii) and 957 m a.s.l. (Berastølen), and terminating just below the highest advances of trees (1016 m a.s.l. and 983 m a.s.l., respectively). When compared with the broadscale climatic map of the upper forest limit provided by Aas and Faarlund (2005), the trees grow relatively close to the climatic limit. In Storlii, the transect was discontinuous due to the road cutting the slope, and a zone of c 20 m on both sides of the road was ignored in the study. In both study areas, the transects were divided into 17 segments of 10 m in length

each, thus creating 10 × 10 m plots. Each plot was divided into four quadrants, and in each quadrant, a 1 × 1 m quadrat was placed at random (Fig. 1), but such quadrats in which stones or tree stems (living and dead) covered more than 25% were not selected.

In each 10 × 10 m plot, tree species were identified and the number of trees was counted. In order to be classified as a tree, an individual had to reach at least 2 m in height. The height and circumference of each tree were measured. Polycorm trees were treated as one individual, and the highest stem was chosen for measurement. In each 1 × 1 m square, species sub-plot frequencies (16 sub-plots) were recorded, and the selected nomenclature follows Lid and Lid (1998). *Betula pubescens* ssp. *czerepanovii* was sampled as seedlings, saplings (in different height classes) and collectively (summing up all occurrences of the species *Betula pubescens*).

Environmental variables

Specific environmental variables were considered to account for possible differences between the two localities caused by factors other than grazing (i.e. there was no intention to investigate the completeness and complexity of environmental variables controlling the composition of vegetation at the respective localities). Slope [°], aspect [°] and altitude [m a.s.l.] were documented, and the first two variables were used to calculate a heat index, modified after Parker (1988):

$$\text{heat index} = \cos(\text{aspect} - 202.5) * \sin(\text{slope}).$$

This index gives a rough estimation of the insolation and is useful for testing whether differences in inclination are controlling dissimilarities in vegetation composition between the two localities. Soil samples were taken from the root zone at about 10 cm depth. The pH (H₂O) was measured, and the actual moisture content estimated in classes from 1 = dry to 6 = strongly wet (following Arbeitsgruppe Boden 1994).

The mean height position of the lichen *Melanolia olivacea* (Holien & Tønberg 2006) was measured as an indicator of snow depth. This measurement was carried out in the 10 × 10 m plots, and average values were used for all four quadrats located within the respective plot. For those plots where trees or lichen was missing, the average value of the two adjacent plots (above and below)

was applied. Moreover, ground cover [%] (indicating bare areas, for example, due to trampling) and tree cover [%] (reflecting ground shading) were documented as environmental factors. A categorical variable (1 = Storlii, 0 = Berastølen) was used to represent seasonal-farm identity. All non-categorical variables were transformed to zero skewness to achieve homoscedasticity (Økland et al. 2001; Quian et al. 2003). Transformed data had a skewness $< 10^{-4}$, except for ground cover and tree cover, which retained a skewness of -1.23 and 1.23 respectively.

Ordination methods

Ordination methods were used to analyse the species data of the 1×1 m quadrats, including *Betula pubescens* ssp. *czerepanovii* in different height classes and the environmental variables. A preliminary Detrended Correspondence Analysis (DCA) with default settings was conducted to decide on the ordination method. The largest length of gradient of the DCA was 5.47 standard deviations (SD) (a complete species turnover occurs in 4 SD; Hill & Gauch 1980; Økland 1990). According to Lepš and Šmilauer (2003), at a value larger than 4.0 SD, unimodal methods are appropriate. Following Quian et al. (2003), both DCA and Global Non-metric Multidimensional Scaling (NMS) were applied (see also recommendations by Økland 1990; Økland 1996). The CANOCO version 4.5 program (ter Braak & Šmilauer 2002) was used to carry out DCA (default settings, down-weighting of rare species) and the PC-ORD version 4 program (McCune & Mefford 1999) was used in the NMS. The NMS was first run in the autopilot mode (slow and thorough, Sørensen distance), followed by a two-dimensional run with the best starting configuration of the autopilot results. The Kendall rank correlation coefficient τ was calculated to compare the results for the DCA and NMS. Moreover, τ was used to investigate correlations between the DCA and NMS results and the environmental variables.

Tree ring and aerial photograph analyses

Increment cores of a representative sample of trees, i.e. covering the entire range of heights and diameters, were taken along the transects as close as possible to the stem base above the root collar. Stem discs were cut from trees too thin for coring. In addition, the extraction height and stem diameter at the extraction height were measured. In

Storlii, 25 trees were sampled; in Berastølen, 26 trees. Cores and discs were sanded, and annual rings identified and counted (for standard procedures, see Schweingruber 1988). In those cases where the increment borer did not intersect the pith, the latter was estimated. Because trees could not be sampled directly at the stem base, tree ages are minimum ages.

Aerial photographs from 1961 (scale 1:15 000) were analysed to obtain an overview of the spatial patterns of the tree cover. Trees were identified following the principles for image interpretation in Jensen (2007). The trees were plotted onto a scan of the relevant photograph, and the resulting layer was inserted into a map. Due to original differences in scale between the aerial photographs and the map, the trees may slightly overlap with map elements, such as a road.

Interviews and literature on land use history

Semi-structured interviews, field conversation and a literature survey have been used to obtain an overview of land use, especially the grazing history of the two localities (cf. Lundberg 2002 for combining different sources in historical geographical research; see also Kvamme 1988, Motta et al. 2006, and Räsänen et al. 2007 for the potential of pollen analysis and dendrochronology). The first two sources provide information mainly on the recent history (since about the second half of the 20th century) while written sources were used to cover the older history. The literature survey covered material from pollen analyses (Moe 1978; Odland 2007), the history of the local authority district of Eidfjord, which includes the farms owning Storlii and Berastølen (Læg Reid & Læg Reid 1992) and other publications including information about the localities (Olafsen 1910; Opedal 1981).

Due to a lack of data, it was not possible to get a complete grazing history for the two seasonal farms. This may be one reason why Holtmeier (2003) states that it is often difficult, if not impossible, to identify and evaluate the site history influence on the present tree-line ecotone. However, the material was comprehensive enough to obtain an insight into the grazing history. The material was analysed focussing on the following aspects: estimation of the point in time when grazing/seasonal farming started; estimation of the grazing intensity (high or low); and significant changes in grazing intensity, either gradual or sudden.

Results

Structure of the tree cover

At present, the uppermost part of the tree-line ecotone at Berastølen is made up of large open areas and patches of trees with a dense understory (Fig. 2). At Storlii, the uppermost tree cover consists of tree patches that are in most cases interconnected. In flatter terrain, open areas are mainly covered by mires. The trees at Storlii are arranged more evenly than at Berastølen, and a dense understory is lacking (Fig. 3). Within a short distance, there is a shift

from an occurrence to a complete lack of trees. The aerial photographs show a similar situation prevailing for Storlii in 1961 (Fig. 1), while they reveal a complete lack of trees at Berastølen. The lack of trees at Berastølen at that time is also mentioned by informants.

Betula pubescens ssp. *czerepanovii* is the only tree species occurring in the 2007 vegetation samples other than one juvenile individual of *Sorbus aucuparia*. The transect at Berastølen includes more than three times the number of trees as at Storlii (148 vs. 41 individuals). Smaller and thinner trees dominate at Berastølen, whereas higher



Fig. 2. The tree-line ecotone at Berastølen (view southeast). The photograph depicts an area with a relatively high number of tree stands. The circle indicates the approximate location of the inserted picture. (Photo Kerstin Potthoff, 2007).

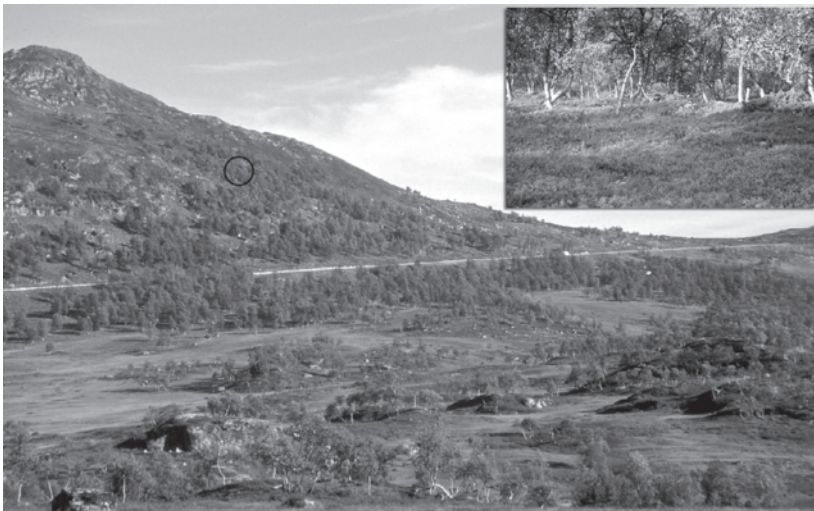


Fig. 3. The tree-line ecotone at Storlii (view east). Storlii is located just outside the left side of the photograph. The circle indicates the approximate location of the inserted picture. (Photo Kerstin Potthoff, 2007).

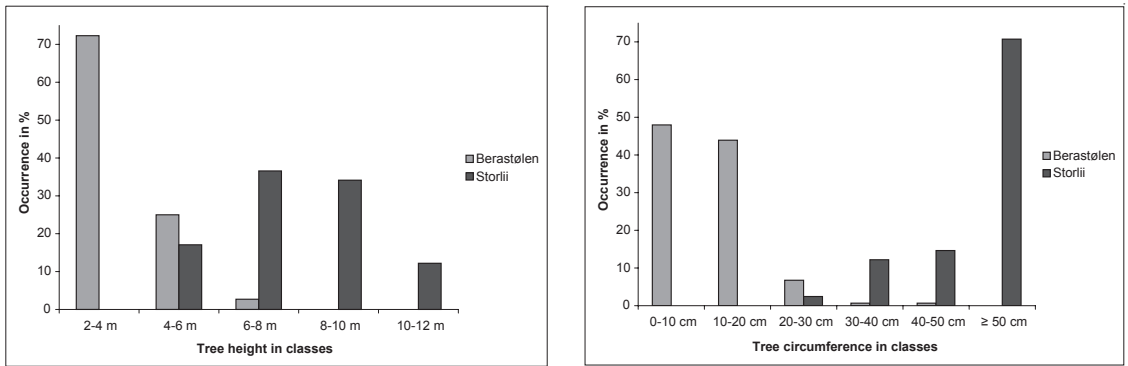


Fig. 4. Height and circumference of *Betula pubescens* at Berastølen and Storlii.

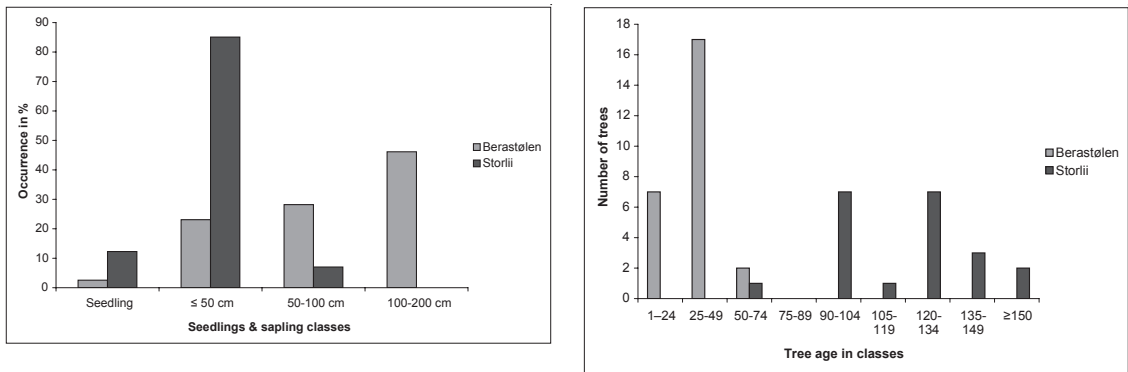


Fig. 5. Seedlings and saplings of *Betula pubescens* at Berastølen and Storlii. The occurrences at Storlii add up to slightly more than 100% because different seedling classes may occur within one plot.

Fig. 6. Age structure of *Betula pubescens* in classes. NB: Classes vary in range; the youngest tree age detected was 18 years.

and thicker trees are predominant at Storlii (Fig. 4). The number of sub-plots with seedlings and saplings is about three times the number at Storlii as at Berastølen (114 vs. 39). At Berastølen, seedlings (only one individual) and saplings from ≤ 50 cm up to 2 m occur, with the class from 1–2 m dominating, while in Storlii, the latter class is missing (Fig. 5).

Tree-age structure differs significantly between the two areas. In Berastølen, most trees are young (age classes 1–24 and 25–49 years; Fig. 6), with the youngest one being 18 years old. Only two samples are 50 years or older, the oldest aged 61 years. In contrast, the youngest sample at Storlii belongs to the age class 50–74 years, whereas all other samples are at least 93 years old, the oldest

one registering 158 years. Most of these trees belong to the age classes 90–104 and 120–134 years. Samples of four trees from Storlii were not included in the figure because the number of tree rings differed strongly between the radii. No visual cross-dating was possible, which made ring counts too unreliable. However, all trees are at least 110 years old.

Ground cover

The two localities in comparison

A comparison of the ground cover shows that the two localities are numerically quite similar in the number of species, average number of species per

Table 1. Numerical comparison of the Storlii and Berastølen vegetation.

	Storlii	Berastølen
Number of species	65	66
Number of species occurring in more than one plot	51	62
Average number of species per plot	19	18
Unique species (occurring in only one locality)	27	28
Shannon index	3.25	3.28

plot, species unique to one of the two localities, and the Shannon index (Table 1). Only the exclusion of rare species leads to a difference between the localities, with Storlii containing a higher number of rare species.

A comparison of the most frequent species (at least 10%, i.e. 109, of a maximum sub-plot frequency of 1088) shows a number of species common to both localities, but also species important for only one of the localities; some occur exclusively in one of the localities (Table 2). Comparing these species in terms of the Ellenberg ecological indicator values adjusted to Nordic conditions (Vevle 2008) and the various species occurrence in grazed habitats reveals both differences and similarities. Species favoured by grazing occur in both localities. *Agrostis capillaris* is favoured by grazing, and is especially abundant in permanent pastures (Kielland-Lund 1975; Grime et al. 2007), and *Deschampsia cespitosa* is favoured to some extent because herbivores generally avoid it because of the silica content in its leaves (Grime et al. 2007). Moreover, *Ranunculus acris* and *Rumex acetosa*, both important at Storlii, are favoured by grazing (Kielland-Lund 1975; Grime et al. 2007).

The most noticeable difference in indicator values concerns the species' light demand. Values at Berastølen mainly range from plants growing in a semi-shaded environment to species occurring in full light and "light-loving" plants (Hill et al. 1999, translation of Ellenberg indicator values). This probably reflects the large open areas of that site. The range of light demand at Storlii is extended to more shaded conditions as the occurrences of, for example, *Luzula pilosa* and *Phegopteris connectilis* show, while light-loving plants are almost absent from the table.

Temperature and moisture values do not show any distinct distribution. However, at Berastølen, *Saussurea alpina* and *Juniperus communis* are common, which are indicators of cold/cooler sites.

Both reaction and nitrogen values show clearer patterns where the range of reaction values is extended towards species growing in acid locations at Berastølen, and where a higher number of species growing in locations that are more fertile occurs at Storlii.

DCA and NMS

Only the first and second axes of the DCA are of interest for an ecological interpretation, because the results show a strong decrease of eigenvalues from axes 1–3 (0.476, 0.207, 0.009; length of gradient 3.997, 2.673, 1.587; total inertia: 2.282). However, the eigenvalue of axis 2 is already low. These results correspond with the choice of a two-dimensional NMS. Correlations between the DCA and NMS axes suggest comparable results of both types of analyses: the DCA axis 1 and NMS axis 2 are strongly correlated ($\tau = 0.881$, $p < 0.01$), and DCA axis 2 and NMS axis 1 show a relatively strong correlation ($\tau = -0.505$, $p < 0.01$).

Both NMS and DCA separate the two study areas along one of the axes (DCA along axis 1, NMS along axis 2). As visible in the diagram of the DCA results, a greater number of light-loving plants and species growing in full light (see previous section) are located more in the right part of the diagram, whereas species tolerating shade are located in the lower part of the diagram (Fig. 7).

The correlation of the DCA and NMS axes with the environmental variables shows the strongest correlation of the DCA axis 1 and NMS axis 2 with the "seasonal-farm identity" (Table 3). Neither those nor DCA axis 2 and NMS axis 1 are strongly correlated to any other environmental variable ($\tau < 0.5$). The second- and third-highest correlation values occur with pH (range: 4.2–6.4) and snow depth (range: 0.6–2.6 m), while tree cover (range: 0–100%) is not significantly correlated to any of the axes.

Table 2. The most important species in Storlii and Berastølen (at least 10% of a maximum sub-plot frequency of 1088) and their Ellenberg indicator values after Vevle (2008). The English translation of most categories follows Hill et al. (1999).

	L ^a	T ^b	M ^c	R ^d	N ^e
Berastølen & Storlii					
<i>Agrostis capillaris</i>	7	x ^f	x	4	4
<i>Cornus suecica</i>	5	4	7	2	2
<i>Deschampsia cespitosa</i>	6	x	7	x	3
<i>Deschampsia flexuosa</i>	6	x	x	2	3
<i>Geranium sylvaticum</i>	6	4	6	6	7
<i>Melampyrum sylvaticum</i>	4	4	5	2	2
<i>Solidago virgaurea</i>	5	x	5	x	4
<i>Trientalis europaea</i>	5	5	x	3	2
<i>Vaccinium myrtillus</i>	5	x	x	2	3
<i>Vaccinium vitis-idaea</i>	5	x	4	2	1
Berastølen					
<i>Bartisa alpina</i>	8	3	8	7	3
<i>Betula nana</i> *	8	3	9	1	2
<i>Carex bigelowii</i> *	8	3	5	1	3
<i>Empetrum hermaphroditum</i>	8	3	6	4	2
<i>Juniperus communis</i>	9	2	4	7	2
<i>Salix glauca</i>	– ^g	–	–	–	–
<i>Saussurea alpina</i> *	9	1	5	5	3
<i>Thalictrum alpinum</i> *	–	–	–	–	–
<i>Vaccinium uliginosum</i>	6	x	x	1	3
Storlii					
<i>Anthoxanthum odoratum</i>	7	3	6	2	2
<i>Betula pubescens</i>	–	–	–	–	–
<i>Calamagrostis epigejos</i> *	7	5	x	x	6
<i>Gymnocarpium dryopteris</i>	3	4	6	4	5
<i>Luzula pilosa</i> *	2	x	5	5	4
<i>Maianthemum bifolium</i>	3	x	5	3	3
<i>Phegopteris connectilis</i>	2	4	6	4	6
<i>Ranunculus acris</i>	7	x	6	x	x
<i>Rumex acetosa</i>	8	x	x	x	6
<i>Viola palustris</i> *	6	x	9	2	5

- a. Light. 1: plant in deep shade; 2: between 1 and 3; 3: shade plant; 4: between 3 and 5; 5: semi-shade plant, rarely in full light; 6: between 5 and 7; 7: plant generally in well-lit places, but also occurring in partial shade; 8: light-loving plant; 9: plant in full light, found mostly in full sun.
- b. Temperature. 1: indicator of extremely cold sites, only occurring in high mountain and boreal–arctic areas; 2: between 2 and 3; 3: indicator of cool sites; mainly in alpine–subalpine or temperate–boreal areas; 4: between 3 and 5 (especially montane species); 5: indicator of moderately warm sites, from lowland up to alpine areas, mainly in sub-montane-temperate areas; 6: between 5 and 7; 7: indicator of warm sites in northern Central Europe in lowlands only; 8: between 7 and 9, mainly in sub-Mediterranean areas; 9: indicator of extremely warm sites, occurring in especially warm locations only.
- c. Moisture. 1: indicator of extreme dryness, restricted to soils that often dry out for some time; 2: between 1 and 3; 3: dry-site indicator, more often found on dry ground than in moist places; 4: between 3 and 5; 5: moist-site indicator, mainly on fresh soils of average dampness; 6: between 5 and 7; 7: dampness indicator, mainly on constantly moist or damp, but not on wet soils; 8: between 7 and 9; 9: wet-site indicator, often on water-saturated, badly aerated soils; 10: indicator of shallow-water sites that may lack standing water for extensive periods; 11: plant roots under water, but for some time exposed, or plant floating on the surface; 12: submerged plant, permanently or almost constantly under water.
- d. Reaction. 1: indicator of extreme acidity, never found on weakly acid or basic soils; 2: between 1 and 3; 3: acidity indicator, mainly on acid soils, but exceptionally also on nearly neutral ones; 4: between 3 and 5; 5: indicator of moderately acid soils, only occasionally found on very acid or on neutral to basic soil; 6: between 5 and 7; 7: indicator of weakly acid to weakly basic conditions, never found on very acid soils; 8: between 7 and 9; 9: indicator of basic reaction, always found on calcareous or other high-pH soils.
- e. Nitrogen. 1: indicator of extremely infertile sites; 2: between 1 and 3; 3: indicator of more or less infertile sites; 4: between 3 and 5; 5: indicator of sites of intermediate fertility; 6: between 5 and 7; 7: plant often found in richly fertile places; 8: between 7 and 9; 9: indicator of extremely rich situations, such as cattle resting places or near polluted rivers.
- f. Indifferent.
- g. Value missing.
- * Species occurring exclusively in only one of the sampled areas.

Grazing history

The Sysendalen valley, where the Storlii seasonal farm is located, has a long history (Fig. 1). Pollen analysis indicates grazing activity since about 5000 BP, and archaeological data show the presence of humans with relationships to Neolithic agriculture; however, information about the permanency of presence or frequency of visits is lacking (Moe 1978; Indrelid & Moe 1982; Odland

2007). Moreover, bog iron ore was extracted probably between about 2000 BP and 1700 BP (Odland 2007).

Since about AD 600, use intensity increased, and anecdotal records and pollen analysis point to a permanent population, and an intensive use of the valley (including grazing) before the Black Death (AD 1349), and the following depopulation (Opedal 1981; Odland 2007). The potential traces of permanent settlement indicate the earliest pos-

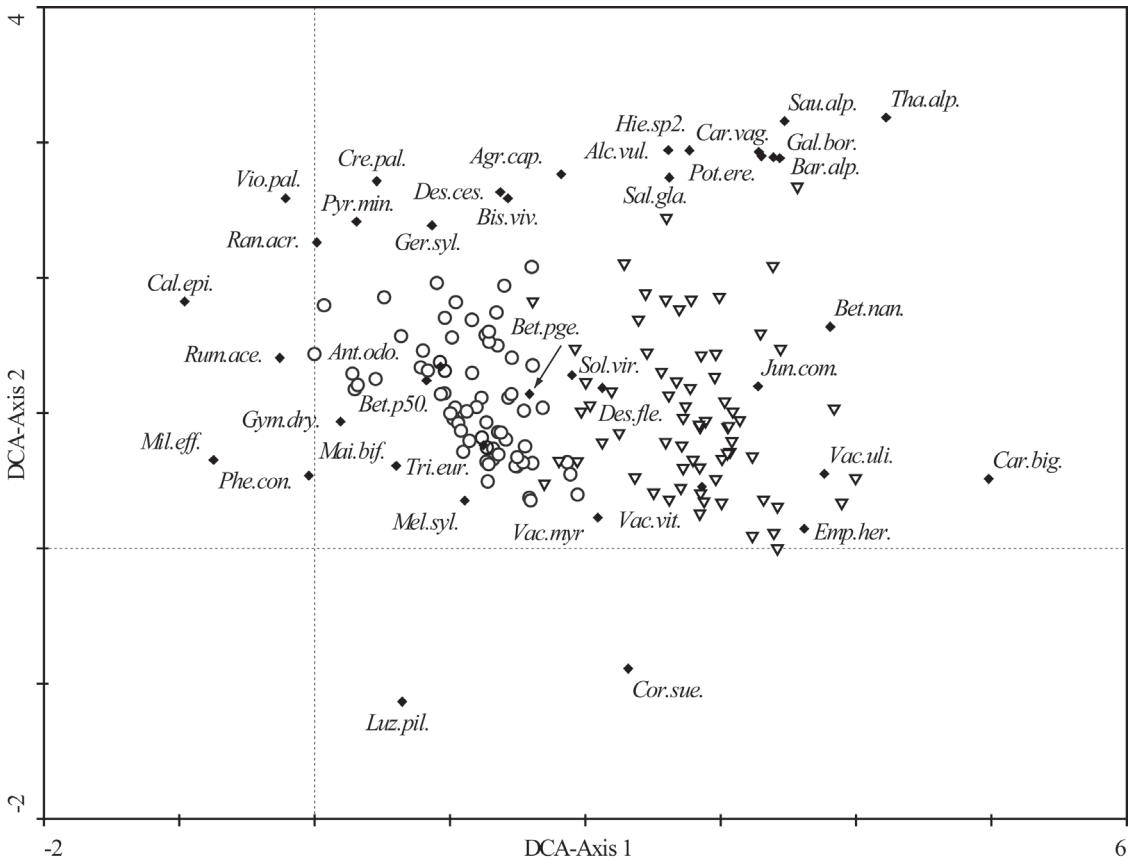


Fig. 7. Distribution of plots and species along DCA axes 1 and 2. Only species with a weight between 3% and 100% are shown. Circles: plots on Storlii; triangles: plots on Berastølen. *Bet.p50.* = individuals of *Betula pubescens* belonging to height class of 50–100 cm; *Bet.pge.* = *Betula pubescens* cumulative; *Hie.sp2.* = group probably consisting of individuals belonging to the section *Prenanθοidea*.

Table 3. Kendall rank correlation coefficient (τ) for DCA and NMS results and environmental variables.

Variable	DCA		NMS	
	Axis 1	Axis 2	Axis 1	Axis 2
Altitude	-0.024	-0.184**	0.307*	0.006
Heat index	-0.274**	-0.039	0.237*	-0.238*
pH	0.038	0.445**	0.331*	-0.025
Moisture	0.16	0.117	-0.142	0.124
Snow depth	0.422*	0.198*	0.036	-0.427*
Ground cover	0.276*	0.166	-0.33*	0.216*
Tree cover	-0.094	-0.057	0.132	-0.079
Grazing history	-0.706**	0.116	0.28*	-0.688*

* Significant $p \leq 0.001$

** Significant $p \leq 0.01$

sible use of Storlii for seasonal farming, while livestock grazing may have occurred earlier. Olafsen (1909) points out that those seasonal farms that later became spring farms (see explanation later), are the oldest seasonal farms and most likely of the same age as permanent farms. The first people to arrive after a possible depopulation are recorded in the mid-17th century (Læg Reid & Læg Reid 1992). Grazing land at a seasonal farm is explicitly mentioned for the first time in 1802 (Læg Reid & Læg Reid 1992), and it is very likely that this included Storlii. Because the number of livestock on the farm of Garen (Fig. 1), the owner of Storlii, increased from 1723 towards the mid-19th century (Læg Reid & Læg Reid 1992), it is likely that grazing intensity on the seasonal farm increased as well. Subsequently, until the 1960s, the number of cattle decreased while the number of sheep doubled. Although this development led to a general increase in grazing intensity, it has probably led to a reduction of grazing intensity on the seasonal farm because sheep use greater areas than cattle for grazing and are less attached to the seasonal farm than dairy livestock.

However, the numbers of sheep and cattle on the farm of Garen appear to influence grazing intensity at Storlii only until somewhat before 1910, because Olafsen (1910) mentions exclusive goat grazing for that year, and his phrasing (the seasonal farm is "now used as a seasonal farm for goats only" (p. 4, translated)) indicates that this practice differs from a previous one. Since the 1940s, the seasonal farm has been leased for goat grazing, and the numbers have been fairly stable with about 130 animals since the 1950s (interview data). Based on a roughly estimated grazing area of 260 ha (interview data projected onto the map), the livestock density would be 0.5 goats/ha.

Two other aspects have influenced grazing intensity on the seasonal farm. According to interview data, the farm has been used as a spring farm, i.e. used for a shorter period before proceeding to the summer farm higher up in the mountains, and commonly also in autumn before the return to the permanent farm. However, at least since the 1940s, it has been used as a summer farm. When the shift happened remains unclear, but Olafsen's phrasing already indicates summer use in 1910. Summer use means a more comprehensive use of resources due to a more extended stay than during spring and autumn. In Western Norway, this would commonly be about two weeks in each of those seasons.

The other aspect influencing grazing intensity is the use of the area in connection with livestock trading; a system that included livestock purchase, feeding it up on good mountain pastures, and long-distance movement to larger cities for sale (Læg Reid & Læg Reid 1992). Farmers of Garen were mainly involved in this kind of business in the first part of the 19th century, and kept such livestock on Storlii during summer, which again increased grazing intensity (Table 4).

Berastølen was part of a common grazing area including several seasonal farms owned by different permanently settled farms (Læg Reid & Læg Reid 1992). The earliest documentation for such permanent settlement is from AD 1398; however, undated grave mounds indicate the possibility of earlier use (Læg Reid & Læg Reid 1992). Because it is not possible to identify how many animals of the different permanent farms stayed on the respective seasonal farms belonging to the common grazing area, a relationship between the number of animals on the permanent farm and the grazing intensity on Berastølen cannot be established. However, a summing up of the animals on all the possible owner farms of Berastølen shows a pattern similar to that of Garen, as an increase in the number of livestock until about the mid-19th century, followed by a decrease in cattle and an increase in sheep until the 1960s. Goat numbers had a peak in 1939 and this decreased until the end of the 1960s when goat farming was abandoned.

According to Olafsen (1909), Berastølen is among the seasonal farms listed in the 1723 tax rolls. Berastølen was used for spring (and probably also autumn) grazing before it was turned into a summer farm when livestock density on the existing summer farm became too high (interview data). Læg Reid and Læg Reid (1992) mention 1837 as a year in which Berastølen was used as a spring farm only, which indicates that grazing intensity probably increased afterwards due to an extended stay during summer. The types of livestock grazing on the seasonal farm were cattle, goats and sheep (interview data). Most farms abandoned seasonal farming in the 1950/60s. The last farm that carried on with fully fledged summer farming had 35–36 goats and about 37–38 cows (the latter including owned and rented livestock), but it reduced its activities in the 1960s. Based on a roughly estimated grazing area of about 700 ha (equal to a grazing radius of c 1.5 km) and a cow–goat ratio of 2.6, the livestock density equals roughly 0.2 goats/ha (cow–goat ratio according to Lundberg 2005).

Thereafter, the area was used for sheep (c 10 animals) and cattle grazing (c six dairy cows early in the season), but later, cattle only until 1989. In 2007, seven head of cattle were grazing in the area and occasionally some sheep.

The somewhat restricted availability of data on the earlier grazing history of the two seasonal farms makes it challenging to compare grazing intensities. Comparing the seasonal farms, both are likely to have a grazing history of at least 200 years and probably much longer. The number of animals on their owner farms increased towards the mid-19th century, and both localities have been used for a certain time as spring, and later as summer farms, which most likely increased the grazing intensity. The change on Storlii to exclusive goat herding may have increased grazing intensity, and at least it increased pressure on the shrub vegetation. The seasonal farm of Storlii has been kept in full use until the present day, while grazing pressure on Berastølen has been reduced since the 1950/60s.

Discussion

Seasonal-farm identity vs. other environmental variables

The strong correlation between “seasonal-farm identity” and the DCA/NMS axis that separates the two localities indicates “seasonal-farm identity” to be the variable of overriding importance for the differences between the two farms. The lack of a strong correlation with any of the variables that were included to account for possible natural differences among the localities supports the “seasonal-farm identity” relevance. At the same time, the results imply that the two localities are quite similar with regard to their natural conditions. The analyses do not explain which aspect of the seasonal farm identity is the cause of the differences. Because the grazing history up to the present is an important difference between the areas, and under the assumption that no other important difference has been missed, it is likely that grazing history is

Table 4. Overview of the grazing histories of Storlii and Berastølen.

Storlii	
AD 600–1349	<ul style="list-style-type: none"> • increased use of the Sysendalen valley • permanent settlement may have occurred
1349–mid-1600s	<ul style="list-style-type: none"> • low use intensity due to depopulation of the valley
mid-1600s–mid-1800s	<ul style="list-style-type: none"> • increase in number of livestock (esp. cattle and sheep) on the farm of Garen • 1802: grazing land at a seasonal farm mentioned • livestock trading
mid-1800s–mid-1900s 1910	<ul style="list-style-type: none"> • decrease in head of cattle and increase in number of sheep on the farm of Garen • Storlii used for goats only • change from spring/autumn to summer use sometime before?
1940s–2007	<ul style="list-style-type: none"> • still used for goats; since 1950 with about 130 animals
Berastølen	
AD 1398	<ul style="list-style-type: none"> • first documentation of a permanently settled farm that was one of the owners of Berastølen
1723	<ul style="list-style-type: none"> • seasonal farm listed in tax rolls
until the mid-1800s	<ul style="list-style-type: none"> • increase in number of livestock on the owner farms
1837	<ul style="list-style-type: none"> • used as a spring/autumn farm
sometime after 1837	<ul style="list-style-type: none"> • used as a summer farm
mid-1800s–mid-1900s	<ul style="list-style-type: none"> • decrease in the head of cattle and increase in the number of sheep on owner farms
1950s/1960s	<ul style="list-style-type: none"> • significant decrease of grazing intensity due to abandonment of seasonal farming
1950s/1960s–1989	<ul style="list-style-type: none"> • first sheep (c 10 animals) and cattle (c six animals) grazing, later only cattle; milking of cattle in the beginning of the season
2007	<ul style="list-style-type: none"> • seven head of cattle grazing in the area

relevant. This will be discussed in more detail in the next section.

Higher correlation values could have been expected for the variable "tree cover" because light conditions appear to affect the composition of the vegetation. However, the tree cover density might not reflect the amount of insolation that reaches the ground due to, for example, the steepness of the slope at Storlii. Moreover, a stronger correlation could have been expected for "moisture" due to visible differences in moisture conditions in the study areas. Possible reasons for the lack of a strong correlation may be 1) a classification of the variable that is not detailed enough to capture important differences in moisture content, and 2) differences in weather conditions that impact on the actual soil moisture. However, moisture conditions are at least partly reflected by the pH values because the highest of these occur in the plots located in the wettest areas.

Grazing history and tree cover

The differences in tree cover between the two areas support the indicated relevance of grazing history. At Berastølen, high grazing intensity appears to have been a key factor for the lack of trees at the beginning of the 1960s. Several authors show that grazing may reduce not only tree growth but also the establishment of trees (Kinnaird 1974; Linhart & Whelan 1980; Hester et al. 1996; Cairns & Moen 2004; Hester et al. 2005; Pollock et al. 2005; Vandenberghe et al. 2007). Others mention a reduction of tree-covered areas due to human use such as seasonal farming in Norwegian and other mountain areas (Emanuelsson 1987; Holtmeier 1993; Aas & Faarlund 1995; Schnitzler & Muller 1998; Hofgaard 1999; Bryn & Daugstad 2001; Dullinger et al. 2003b; Hiller & Mütterthies 2005; Holtmeier & Broll 2005). The trees present at Berastølen and the old ones at Storlii show that tree growth is possible at the altitude under discussion, and the occurrence of the old trees at Storlii makes it less likely that a warmer climate is the (only) reason for present tree growth at Berastølen (for a discussion of the relevance of climate vs. land use change, see e.g. Hofgaard 1997, 1999; Gehrig-Fasel et al. 2007; Bryn 2008; Rössler et al. 2008).

A complete lack of trees in previously tree-covered areas appears to be possible, considering a long grazing history. The needed duration will depend on the maximum age of the tree species and

grazing intensity. According to Schweingruber (1993), birch has a lifespan of seldom more than 100 years. Hytteborn et al. (1987) found a *Betula pubescens* tree over 160 years old in northern Sweden, and Holtmeier et al. (2003) even found a 225-year-old specimen of *Betula pubescens* ssp. *czerepanovii* in northern Finland. However, these individuals, especially the latter, are probably rare exceptions. Assuming a maximum tree age of about 160 years (cf. results from Storlii), the duration of the Berastølen grazing history, which lasted at least 280 years, because Berastølen is listed in the tax rolls from 1723, is long enough to cause a lack of trees.

The use of firewood is very likely to have increased the rate of deforestation because the seasonal farming included milk processing that demanded an extensive amount of firewood, in addition to that needed for general heating (Kvamme 1988; Aas & Faarlund 1995; Olsson et al. 2004; Potthoff 2004). Firewood was commonly collected around the seasonal farms and supplied with wood that was cut at lower altitudes (Kvamme 1988; Potthoff 2004). The grazing animals prevented or restricted regrowth resulting in a lowering of the tree-line (Kvamme 1988; Aas & Faarlund 1995; Potthoff 2004).

The current occurrence of relatively young (age classes 1–24 and 25–49), thin and small trees (cf. Figs. 4 and 6), and saplings over the complete range of heights (cf. Fig. 5) at Berastølen coincides with a significant reduction of grazing intensity in the 1950/60s and following tree growth. Other authors (Motta et al. 2006; Bolli et al. 2007; Camarero & Gutiérrez 2007) show a similar relationship between abandonment or reduction of agricultural use, and tree establishment and regrowth is found in many Norwegian and other mountain areas where the tree-line was depressed due to human use (Holtmeier 1993; Schnitzler & Muller 1998; Olsson et al. 2000; Tasser & Tappeiner 2002; Dullinger et al. 2003b; Olsson et al. 2004; Engum 2006).

At present, the speed of establishment of new trees at Berastølen may decelerate because almost no seedlings were found in the samples, and higher saplings outnumber smaller ones. Apparently, the latter applies to the transect surroundings as well. A reason for this rarer occurrence of seedlings and small saplings may be that the most appropriate habitats for birch establishment are already colonized, while thick ground cover vegetation, moisture conditions or other environmental

factors may hamper further colonization (Miles & Kinnaird 1979; Holtmeier 1993; Dullinger et al. 2003a; Holtmeier 2003; Holtmeier et al. 2003; Broll et al. 2007). The conditions at Berastølen appear to be comparable to the patterns Broll et al. (2007) describe for subarctic Finland where low density or lack of birch seedlings is among other factors attributed to lack of soil moisture, waterlogged conditions or competition with dwarf shrub communities. However, the lack of appropriate habitats does not necessarily apply to areas at higher elevation where they may be available.

At Storlii, the present grazing intensity appears to prevent tree establishment. Although seedlings and a large number of smaller saplings occur, the sapling class of 100–200 cm height is absent in the samples, and the tree cover is dominated by higher, thicker and older trees (cf. Figs. 4, 5, and 6). However, the present grazing pressure does not appear to be strong enough to remove birch completely from the understory, although a complete removal, most likely in combination with trampling, is possible as the vegetation directly around seasonal farm buildings shows (cf. Vandvik & Birks 2004). Increased summer temperatures during the last two decades, in average about 0.6 °C higher than normal temperatures (Norwegian Meteorological Institute 2008b and data provided by the Norwegian Meteorological Institute) may have supported tree establishment. However, a similar occurrence of numerous seedlings and small saplings did not occur at Berastølen, and the short distance between the two seasonal farms of c 10 km (Fig. 1) makes differences in macroclimate unlikely. The occurrence of a larger amount of seedlings and smaller saplings may be a result of grazing causing a thinner ground cover and openings of bare ground, which support birch establishment (Kinnaird 1974; Miles & Kinnaird 1979; Helle 2001; Grime et al. 2007). Thus, the current structure of the understory and present regrowth patterns appear to be in line with the younger grazing history. However, the occurrence of larger and older trees can only be explained by the older grazing history because it appears impossible that these trees could develop under a grazing pressure comparable to that of recent times.

Nearly two-thirds of the sampled trees are at least 120 years old (Fig. 6). At the lightly grazed Berastølen farm, birch trees are 2–3 m high at an age of 15–20 years. Assuming that a birch, after about 10–15 years, has reached sufficient height to keep its top out of goat reach, the 120-year-old

trees at Storlii would have escaped destruction by goats around 1900. This time frame coincides with the data on grazing history. Goat keeping at the farm is mentioned in 1910 as a newer practice. About one-third of the sampled trees are 90–110 years old. The youngest of this group would have been above goat reach in the late 1920s; thus, at a time when goats were probably present at Storlii. Reasons that may account for the occurrence of these younger trees are a gradual increase in grazing pressure over some 20 years or an initial large number of saplings that was gradually reduced. Moreover, especially favourable climatic conditions for the establishment and growth of birch trees may have resulted in a growth of seedlings and saplings that surpassed the amount that could be grazed. Only two trees are older than 150 years; this is probably due to the maximum age of *Betula* and not to a reduction of a previously higher grazing intensity.

Grazing history and ground cover

The long history of grazing has influenced the ground cover at the seasonal farms both directly and indirectly via the tree cover. The frequent occurrence of species favoured by grazing is a direct consequence of the grazing history caused by the direct and indirect influences of grazing (Rook et al. 2004). Moreover, the grazing history exerts an indirect influence on the ground cover due to its influence on the tree cover, thereby impacting on the light conditions. At Storlii, species common in more shaded habitats occur, with Ellenberg indicator values of 2 and 3 (Vevle 2008; Table 2), which appears to be related to a long history of tree cover at that locality. In contrast, at Berastølen, a number of light-preferring species are important with Ellenberg indicator values of 8 and 9 (Vevle 2008; Table 2), which are typical for more alpine-like vegetation, pointing to an historical lack of tree cover at that locality.

Conclusions

Historical information on land use will, in many cases, be fragmented and only give time slices, which limit or even prevent the statistical hypothesis testing of causal relationships. However, data from the present study give a strong indication of the relevance of a long-lasting grazing history. The currently visible influence of grazing history on

the structure of the tree cover at Berastølen started when grazing hampered growth and the establishment of new trees at least 280 years ago. This resulted in a lack of trees. At Storlii, the presently visible influence of grazing history started most likely c 160 years ago (approximately the maximum age for trees) at a time when grazing intensity was lower than during the last c 100 years, before the farm was used for goats only. A lower grazing intensity would have allowed the establishment of the trees currently present.

Differences in the tree-line ecotone structure of Berastølen and Storlii with regard to the understory, tree age, height, circumference, and the species composition of the ground cover indicate the significance of site history as an important local factor that can modify the global and regional influences of climate on the tree-line ecotone. In areas with dissimilar site histories, the effects of future global and regional climatic changes may be modified differently, thereby creating different responses on a local scale. Assuming a continued increase in temperature and the maintenance of the management system, one can anticipate that regrowth at Berastølen will proceed; however, the speed of establishment of new growth may differ between sites depending on the accessibility of appropriate habitats. If the grazing intensity at Storlii stays high enough to prevent the regrowth of trees, the area may become treeless in a long-term perspective when considering the present age of the trees.

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