

Browsing interacts with climate to determine tree-ring increment

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Summary

1. A warming climate has been linked to shifts in plant distribution and growth. The relationship between climate and growth is used to infer past climate conditions within dendrochronological studies. However, browsing may interact with climate to determine growth, yet the impact of large herbivores on tree-ring growth series is largely unknown.

2. Here, we disentangle the interactions between climate and herbivory in determining plant growth at the upper distribution limit of mountain birch (*Betula pubescens* ssp. *czerepanovii*).

3. Stem discs of 206 birch were sampled within an altitudinal tree line ecotone in southern Norway, after 9 years of experimental browsing at three sheep densities (unbrowsed, low and high with 0, 25 and 80 sheep km⁻²). Annual radial growth was measured using digital microscopy and related to summer temperatures, altitude and sheep density.

4. Radial growth was negatively related to altitude and related to summer temperature in a nonlinear fashion, increasing from low temperatures and saturating and decreasing at high temperatures. However, the variation between browsing treatments overrode the influence of interannual temperature in determining growth. Increasing sheep densities limited radial growth and interacted with both temperature and altitude. The temperature of peak radial growth increased at higher densities of sheep, and growth was less limited by altitude at low sheep density.

5. This demonstrates that browsing interacts with temperature to determine the growth of mountain birch at the upper distribution limit and that the variation in growth linked to sheep density was greater than that linked to the 50-year range of interannual temperatures. The ability of browsing to affect radial growth has important implications for the use of dendrochronology to infer past climatic conditions, where samples are taken from regions that have undergone past land-use change.

Key-words: birch, dendrochronology, herbivory, land use, sheep, treeline

Introduction

A warming climate has been linked to shifts in plant distribution (Grabherr, Gottfried & Pauli 1994; Lenoir *et al.* 2008) and tree line advance in alpine regions (Harsch *et al.* 2009). The signal of a warming climate can also be seen in recent expansion of tree-ring widths at the tree line (Salzer *et al.* 2009). However, there is an increasing evidence that the response of vegetation to climate warming varies with large-herbivore densities (Post & Pedersen 2008; Olofsson *et al.* 2009) and that tree line advance may be constrained by vertebrate herbivores (Cairns & Moen 2004; Speed *et al.* 2010).

One use of dendrochronological analysis is to reconstruct past climates and to investigate changes in climate over time. However, other factors can also influence dendrochronological series (Briffa *et al.* 1998). Defoliation caused by the outbreaks of herbivorous moths influences tree-ring growth (Hoogesteger & Karlsson 1992; Karlsson *et al.* 2004; Van Bogaert *et al.* 2009). Land above the forest line, particularly in Europe, has historically been used for the grazing of domestic livestock (Austrheim, Olsson & Grontvedt 1999; MacDonald *et al.* 2000; Gehrig-Fasel, Guisan & Zimmermann 2007). In contrast to insects, densities of domestic herbivores are not irruptive, and they normally vary over longer time-scales largely driven by socioeconomic drivers. To date, separating the role of climatic and browsing effects on tree lines has proven difficult

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because of lack of adequate data. Indeed, the impact of large herbivores on tree-ring series is largely unknown, despite the importance of such knowledge given that tree-ring data are frequently used to reconstruct past climate conditions.

Here, we combine a long-term herbivore enclosure study with dendrochronological analysis to disentangle the interactions between climate and herbivory in determining plant growth at a distribution limit: birch radial growth at the tree line. We demonstrate that the radial growth of mountain birch at the tree line is influenced by the interaction between climate and browsing and that the dendrochronological record is thus sensitive to browsing by vertebrate herbivores.

Materials and methods

STUDY AREA

This study was based in the southern Scandes of Norway in the municipality of Hol (7°55′–8°00′ E, 60°40′–60°45′ N, altitudinal range 1050–1320 m a.s.l.). Sheep management in this region is similar to management in many other European mountain areas, with sheep being released into summer outfields (unenclosed and unimproved land) in mountain regions during summer and brought to lower-lying farms in winter.

Nine enclosures were erected above the forest line on a south-facing slope with a mean area of 0.3 km². Enclosures were built using sheep mesh and top wire supported by wooden stakes and delimited parallel to the contours, so that the altitudinal range was approximately common to all enclosures. Experimental grazing of sheep (Norwegian white breed) started in the summer of 2002 with three sheep densities, no sheep, low density (25 km⁻²) and high density (80 km⁻²) distributed in a randomized block design between the enclosures. Densities were selected on the basis of commonly found densities within the subalpine habitats of the region. Sheep were released into the enclosures in late June and removed in late August or early September, in accordance with traditional management practice. Prior to the initiation of experimental grazing in 2002, the sheep density at the study site was estimated to have been low (ca. 10–20 km⁻²). The tree line at this site is formed by mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti) and is advancing in the unbrowsed treatment but is constrained (by both reduced growth and recruitment) by browsing at both low and high sheep densities (Speed *et al.* 2010, 2011). No moth irruptions occurred at the site between 2001 and 2010. Sheep density at the site was estimated to be comparable with the low-density treatment prior to the initiation of the browsing enclosures.

Monthly mean temperature data for the site were interpolated by the Norwegian Meteorological Institute from nearby weather stations (to an altitude of 1150 m). Data were available from 1957 to 2010. Mean summer temperature was calculated because summer temperatures relate best to birch radial growth (Karlsson *et al.* 2004; Young *et al.* 2011). Mean summer temperature was averaged over June–August, because the growing season is longer at our site than at the northern Swedish site in these studies. Radial growth of mountain birch is generally not affected by precipitation (Young *et al.* 2011), so this was not considered.

SAMPLING AND RING MEASUREMENTS

During the late summer of 2010 (10th–15th August), 207 birch trees were sampled using a line transect method. Transects were walked on an east-west axis (approximately parallel to the contours) with random direction and order. Birch trees falling on or within 5 m of the transect

line were sampled. To avoid autocorrelation, no two individuals were sampled unless separated by at least 10 m where multiple individuals were present within 10 m of transect length, the individual closest to the start of the transect was sampled. Birch trees over 2 m in height or with a stem diameter >50 mm in 2010 were not sampled, as taller trees were assumed to be unaffected by the experimental browsing and meteorological data were only available from 1957. The likelihood of sheep browsing the top shoots of birch at the site decreased at around 1.5 m (Speed *et al.* 2011). The threshold of 2 m was thus selected as trees between 1.5 and 2 m may have been affected by browsing at the start of the experimental period.

A total of 206 trees were sampled ($n = 119, 52$ and 35 within no sheep, low-density and high-density treatments respectively). The coordinates of selected individuals were recorded using a handheld GPS (global positioning system) unit before destructively sampling a basal stem disc using a fine handsaw. Owing to hybridization between *B. pubescens* and *B. nana*, mountain birch may vary greatly in growth form. However, only birch trees with an upright growth form (i.e. not prostrate growth form) were sampled, and the majority were monocormic. As radial growth response to drivers can be spread over multiple stems, where polycormic individuals were found, the largest (main) stem was sampled because this is most responsive to climate (Karlsson *et al.* 2004). Because variation in the growth form of birch may affect the likelihood of browsing and the tree's response and may itself vary with altitude, height and stem diameter of all trees was also recorded before destructive sampling. The height and stem diameter of the 206 sampled birch trees are shown in Fig. 1a. All birch were of an upright growth form, although there is some variation in height for a given stem diameter. However, the ratio of height to stem diameter did not vary with altitude (Fig. 1b), and the number of basal stems did not affect the relationship between height and stem diameter nor affect the relationship between height-to-stem diameter ratio and altitude. Thus, we assume the sampled birch trees are of consistent growth form.

Stem discs were air-dried. A scalpel was used to smooth the upper surface of the disc, and zinc cream was used to increase the contrast between early and late wood (Hofgaard, Dalen & Hytteborn 2009). Ring width was then measured from the pith and outward to the nearest 0.001 mm using a Leica MZ16 A microscope, Leica DFC420 digital camera and Leica Application Suite 3.2 imaging and analysis software (Leica Microsystems, Wetzlar, Germany). Four radii at 90° were sampled, unless damage to the disc prevented this, in which as many radii separated by 90° as possible were sampled.

DATA PROCESSING AND ANALYSIS

A mean chronology across the four radii was made prior to data quality control and analysis. Data analysis was undertaken within the R environment (v.2.11.1. R Development Core Team 2010). Dendrochronological analyses were carried out using the dplR library (Bunn 2008, 2010). Tree-ring width data were converted to basal area increment (BAI), because area represents tree growth better than a linear measure (Phipps 2005; Biondi & Qeadan 2008), assuming a circular cross-section. Chronology series were quality assessed, and the mean correlation between all possible pairs (i.e. mean of r in a correlation matrix) was calculated, both overall and for all trees within each treatment.

The biological age trend was standardized by $\log_e(\text{BAI}) = a + b \times \log_e(\text{Age})$ (see Fig. 2). The residuals from this standardization were modelled against the independent variables using linear mixed models with a Gaussian error distribution within the nlme R package (Pinheiro *et al.* 2009). Ring BAI was used as the sample unit, so the tree individual was taken as a random factor. Fixed effects were sheep

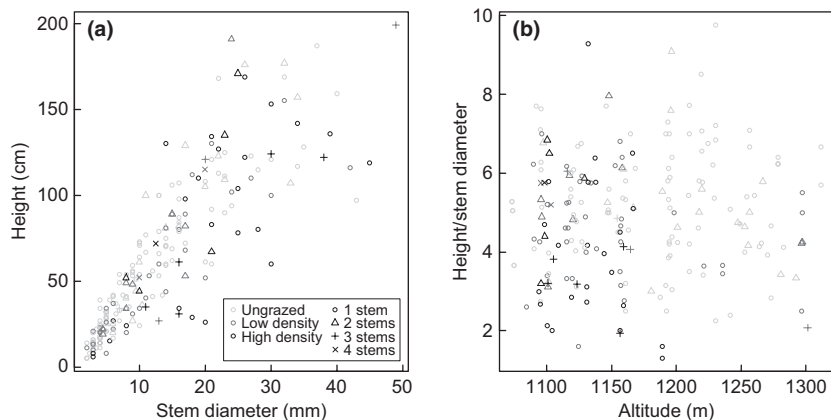


Fig. 1. (a) The stem diameter and height of sampled birch and (b) the height-to-stem diameter ratio of sampled birch in relation to altitude. Symbol shape represents the number of stems on the tree, and colour, the treatment.

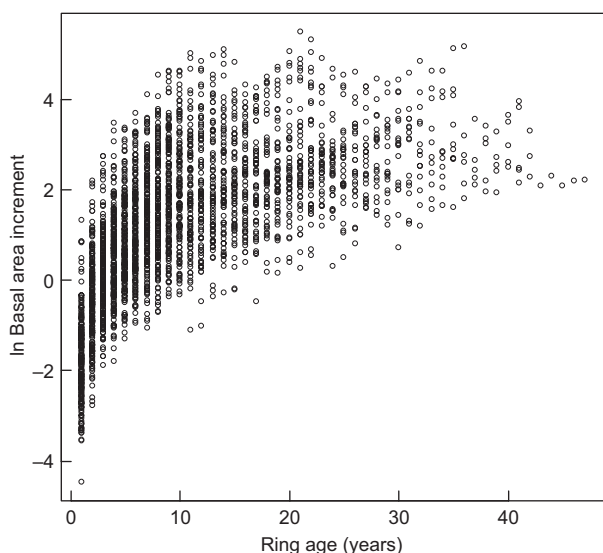


Fig. 2. The age trend in basal area increment across trees at the site. Series of BAI were age-standardized using parameters estimated from a linear regression. $\ln(\text{BAI}) = -1.33 + 1.31 \times \ln(\text{Age})$. $R^2 = 0.57$, $P < 0.001$.

density (factor, assuming a low sheep density across treatments prior to 2002), altitude, habitat (factor) and mean summer temperature. Non-linearities in tree radial growth response to temperature may occur in sub-alpine systems (Graumlich 1991). These were tested for using polynomial terms in the linear mixed models. Selection of the model fixed effects was top-down from the full model, on the basis of Akaike's Information Criterion and nested model comparisons using the maximum-likelihood framework.

Results

Trends in radial growth over time are shown in Fig. 3. Differences in radial growth between treatments become apparent following a lag time of around 3 years after the start of the herbivore manipulations (Fig. 3). The difference between treatments increases with time, with a lag during the first 3–5 years of experimental grazing. By 2010, in the absence of sheep,

radial growth was double that at low sheep density and three times higher than at high sheep density (Fig. 3).

The mean correlation of annual radial growth between all pairs of series was 0.61. Within only the unbrowsed treatment, the mean correlation was 0.79. However, within both browsed treatments, the mean correlation was lower, 0.59 at low sheep density and 0.39 at high sheep density (Table 1).

The selected mixed model predicting radial growth included sheep density, altitude, summer temperature and interactions between sheep density and altitude and sheep density and summer temperature (Table 2). Age-standardized radial growth was positively related to temperature, with a negative quadratic term, indicating a decline at higher temperatures. The interaction between the quadratic temperature term and sheep density was not retained during model selection. Unsurprisingly, radial growth was also negatively related to altitude. The relationship between each of altitude and summer temperature and radial growth, in interaction with sheep density, is visualized in Fig. 4 by plotting predicted radial growth derived from the model presented in Table 2, across the independent variables. Radial growth peaked at the lowest altitude across all treatments, at a mean summer temperature of around 8 °C in the absence of sheep, 8.5 °C at low sheep density and 9.5 °C at high sheep density. The rate of decrease in growth with altitude was greater at high sheep density and in the absence of sheep than that at low sheep density (Fig. 4, Table 2). Radial growth of birch was predicted to be more limited by low summer temperatures at high sheep density than that in the absence of sheep or at low sheep density (Fig. 4, Table 2). Growth declined at a greater rate with altitude in the absence of sheep than at low sheep density, whilst growth varied more with summer temperature at low sheep density than in the absence of sheep (Fig. 4). Habitat was not a predictor of radial growth and was not retained in the final mixed model.

Discussion

Previous studies have attempted to disentangle the impacts of climatic and land-use change on vegetation change in the tree

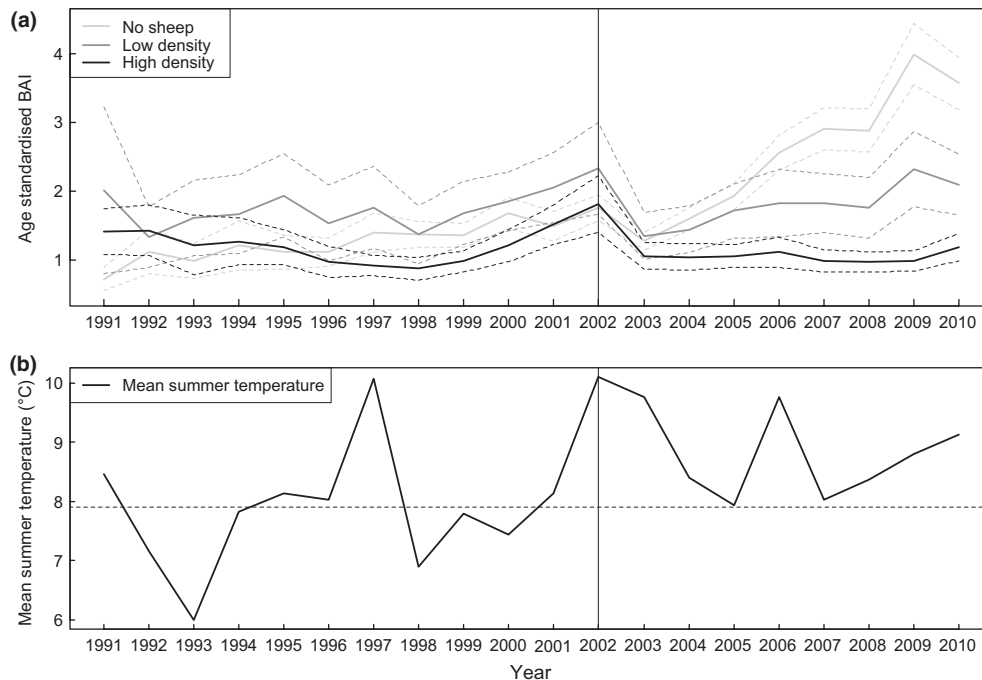


Fig. 3. (a) Trend in age-standardized basal area increment (BAI \pm SE) and (b) mean summer temperature over time. Data are shown for the period with at least 10 individuals in each treatment (1991–2010). The vertical line shows the start of experimental grazing in 2002; the horizontal dashed line in b. shows the long-term (1957–2010) mean summer temperature at the site of 7.9 °C. Solid lines in a. shows the mean, and dotted lines show the SE.

Table 1. Summary of tree-ring series across and between treatments

Treatment	<i>n</i> trees	Time span	Mean (SD) age in 2010	Mean <i>r</i>
All trees	206	1963–2010	14.4 (9.9)	0.61
Ungrazed	119	1974–2010	10.8 (5.6)	0.79
Low sheep density	52	1975–2010	13.8 (7.8)	0.59
High sheep density	35	1963–2010	26.9 (13.3)	0.39

Table 2. Fixed-effect parameters from mixed model. Tree was a random effect in the model, which has 2902 observations and 206 groups

	Value	SE	<i>t</i> -value	<i>P</i> -value
Intercept	3.543	1.528	2.319	0.021
High sheep density	-2.393	1.897	-1.261	0.207
Low sheep density	-5.913	0.81	-7.304	<0.001
Altitude	-0.005	0.001	-5.08	<0.001
Mean summer temperature	0.828	0.196	4.23	<0.001
Mean summer temperature ²	-0.053	0.011	-4.868	<0.001
High sheep density \times Altitude	-0.0002	0.002	-0.127	0.899
Low sheep density \times Altitude	0.004	0.001	6.231	<0.001
High sheep density \times Mean summer temperature	0.18	0.05	3.592	<0.001
Low sheep density \times Mean summer temperature	0.062	0.033	1.846	0.065

line ecotone (Hofgaard 1997; Gehrig-Fasel, Guisan & Zimmermann 2007; Tasser *et al.* 2007). Here, we used an experimental manipulation of herbivore densities over a 9-year period and climate data over a 50-year period to study their interactive influence on the radial growth of birch at the tree line, finding that

summer temperature, herbivore density and their interaction are important predictors.

The data presented here show that browsing by sheep and climate interact to determine the radial growth of birch at the tree line, and highlight that the effects of browsing by livestock can be observed within tree-ring series. The importance of browsing in limiting radial growth in the tree line ecotone is demonstrated by the differences between treatments after 9 years of experimental browsing treatments. However, the divergence in growth trend did not emerge immediately following treatment initiation, indicating a lag time which may reflect a recovery period or initial allocation of resources to other aspects of growth. The mean annual growth correlation between all pairs of series was relatively high, as expected, coming from a single species growing at a single site. The reductions in intertree correlation in annual radial growth with increasing sheep density suggest that variation in yearly growth is increased by the activity of livestock, although there was also a smaller sample size, of older trees, at high sheep density.

Birch trees growing at the tree line are particularly sensitive to temperature (Kullman 1993; Karlsson *et al.* 2004). There was a nonlinear response of radial growth to mean summer temperature, with the temperature optimum for radial growth being higher at high sheep density than at low density or in the absence of sheep. This implies that growth is more likely to compensate for browsing at higher temperatures. Growth limitation at higher temperatures may be related to a negative relationship between summer temperature and soil moisture (Graumlich 1991); higher root/shoot ratios in browsed trees (Bergstrom & Danell 1987; Haukioja *et al.* 1990; Hester *et al.* 2004) may make them less susceptible to reductions in soil moisture, which

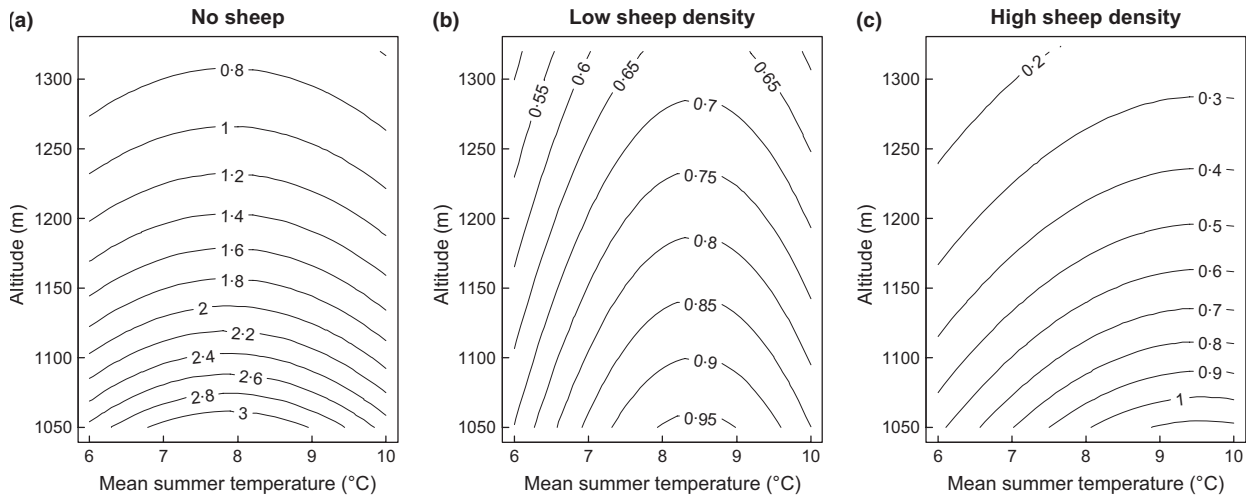


Fig. 4. Contour plot showing age-standardized basal area increment of birch predicted for each of the three sheep density treatments. Predictions of BAI are made over the experiment's altitude range and 50-year range of mean summer temperature from the linear mixed model (Table 2). Contours indicate the predicted age-standardized BAI for summer temperature x and altitude y . Note the differing intervals of contours between treatments.

could also limit birch growth. However, such moisture limitations are likely to be local because of the lack of consistent relationship between birch growth and precipitation (Young *et al.* 2011).

A linear reduction in growth with increasing altitude was observed, not a threshold response, in contrast to other studies (Paulsen, Weber & Körner 2000; Salzer *et al.* 2009), and may be attributed to the importance of interannual temperature in determining performance at the tree line (Paulsen, Weber & Körner 2000). The least steep altitudinal decline in ring growth was at low sheep density, implying that low sheep density was less limiting of radial growth at higher altitudes than at lower altitudes. Conversely, shoot growth has been observed to be more reduced at high altitudes than at lower altitudes in the presence of sheep, although neither browsing likelihood nor intensity was predicted by altitude (Speed *et al.* 2011). Thus, at high altitudes, browsed trees may prioritize stem radial growth over height growth, possibly due to the combination of browsing damage and exposure-related damage and thermal limitation at high altitudes (Grace, Berninger & Nagy 2002; Smith *et al.* 2003).

The contrast between no sheep and low or high densities of sheep is greater than the variation in growth seen within the range of summer temperature over the past 50 years, whilst the contrast between low and high sheep densities becomes important at higher altitudes and lower temperatures. The greater importance of herbivore density over climate in determining tree radial growth contrasts with the dominant role of climate over herbivore density in determining the population dynamics of herb species (Evju *et al.* 2010, in press). This may be related to the differing growth forms and life cycle lengths found in birch and herb species. The dominance of herbivory over climate in determining birch growth is consistent with the importance of herbivory in determining tree line shifts (Speed *et al.* 2010; Van Bogaert *et al.* 2011).

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