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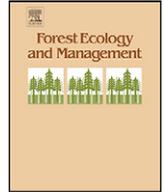
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Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline

James D.M. Speed^{a,*}, Gunnar Austrheim^a, Alison J. Hester^b, Atle Mysterud^c

^a Museum of Natural History and Archaeology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

^b The Macaulay Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK

^c Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, NO-0316 Oslo, Norway

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ABSTRACT

Treelines are advancing on a global scale and encroaching upon alpine ecosystems. Browsing by vertebrate herbivores could affect treeline dynamics and forest expansion by limiting growth of trees. However, this has not been experimentally investigated, and due to a combination of herbivore behaviour and plant responses to herbivory, is unlikely to be a simple relationship. A long term (8 years of manipulation), large scale (0.3 km²) sheep enclosure experiment, in the Scandes of Norway, was used to investigate the effect of three densities of sheep (no sheep, low and high densities with respectively 0, 25 and 80 sheep km⁻²) on tree growth within a mountain birch (*Betula pubescens tortuosa*) treeline ecotone. Birch trees were most likely to be browsed at intermediate heights of around 100–130 cm and the likelihood of an individual being browsed did not differ between low and high sheep densities. However, when browsed, the intensity of browsing increased with sheep density. High densities of sheep reduced the net annual shoot growth of young mountain birch in comparison to growth in the absence of sheep. The long-term height growth of smaller mountain birch (stem diameter < 15 mm) was also reduced at high densities of sheep, but the height growth of larger birch was resistant to browsing, even though these trees were on average still within browsing height. This study shows that susceptibility to browsing in birch decreases with size, but by restraining the height growth of trees high densities of sheep can keep trees at heights at which they remain susceptible to browsing. Reductions in livestock density over a period as short as 8 years can thus facilitate altitudinal forest expansion.

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1. Introduction

Herbivores can affect forest dynamics through impacts on recruitment and growth of trees (Horsley et al., 2003; Gill, 2006; Kuijper et al., 2010). However, at forest margins, the influence of herbivores could have a particularly dramatic effect due to other stresses such as climate also acting on trees (e.g. Gamache and Payette, 2004). The altitudinal treeline ecotone separates areas with vastly different species pools, land uses and ecosystem functions: open alpine landscapes from closed forest (Hofgaard, 1997; Hofgaard and Wilmann, 2002). Warming temperatures have driven treeline advances in many systems over the past century and further treeline advance and forest expansion is expected. However while over half of treelines have advanced with a warming climate, many have not (Harsch et al., 2009), suggesting other factors are involved. Recent landscape-scale experimental evidence has demonstrated that livestock can limit the recruitment of mountain

birch (*Betula pubescens tortuosa*) at the treeline, even at relatively low densities (Speed et al., 2010), supporting the findings from remote sensing studies (Tømmervik et al., 2009). The management of herbivores in alpine and subalpine regions may thus have implications for forest expansion.

Grazing by large herbivores has the potential to shift ecosystems between alternative vegetation states (Van de Koppel et al., 1997; Côté et al., 2004; Van der Wal, 2006). The ability of herbivores to cause such shifts in state may depend upon many factors including the ecosystem's abiotic conditions (Didham et al., 2005) and the tolerance of different plant growth forms to the impact of herbivores at different densities (Van de Koppel and Rietkerk, 2000; Van der Wal, 2006). Some growth forms are tolerant to herbivory such as graminoids, whereas others including woody species are more vulnerable, unless they can escape herbivory through size or defence (e.g. Karban et al., 1997; Hester et al., 2006). At low densities of herbivores, diet and habitat selection is likely to reflect the herbivore's preferred diet, including for instance herbs and graminoids, and utilisation of more productive habitats, while at higher densities, a broader diet including less preferred groups such as shrubs, and greater utilisation of less productive habitats is generally expected

* Corresponding author. Tel.: +47 73592251; fax: +47 73592249.

E-mail address: james.speed@vm.ntnu.no (J.D.M. Speed).

(Fretwell and Lucas, 1969; Mønbæk et al., 2009). Such selectivity of foraging herbivores, combined with the dynamics of interactions within plant communities and the interactions between abiotic factors and plant communities can lead to non-linear relationships between herbivore density and vegetation dynamics (Rietkerk and Van de Koppel, 1997; Sasaki et al., 2008). However, at range margins, where species may be close to the limits of survivability, even low levels of herbivory may be sufficient to affect the growth of plants, and hence the structure of populations and communities.

Herbivores could also hamper the development of a treeline from recruiting individuals by repeatedly browsing shoots, and preventing trees from growing above browse-height. Such an effect on tree development has been shown in other parts of the world, including African savannas (Fornara and Toit, 2007) and Mediterranean forests (Zamora et al., 2001). As the treeline delimits such contrasting ecosystem states, it is particularly important to understand how large herbivores affect tree growth within this ecotone. In contrast to the situation in North America, European agricultural practice and conservation practice are less disjunct (Warren, 1998). Crucially, livestock management has the potential to buffer the effect of climate change on treeline dynamics. Warmer temperatures are predicted to lead to increased growth of trees at the treeline and treeline advance, but, in contrast, if herbivores could reduce growth of individual trees at the treeline, treeline advance would be effectively prevented. However, densities of livestock in outlying upland areas are decreasing in many areas of Europe (MacDonald et al., 2000; Dallimer et al., 2009), which could combine with the effects of climatic warming to exacerbate treeline expansion into alpine regions.

Understanding how browsing pressure on developing trees varies with herbivore density and how the growth of treeline tree species responds to changes in browsing pressures over the tree-line ecotone is necessary to be able to predict future vegetation change. However, experimental investigations of such processes at relevant spatial and temporal scales have not been presented before now. Herbivory is likely to interact with both temperature and tree size in determining growth, so the influence of herbivores on trees at the treeline is likely to be difficult to predict. Here we test whether browsing by sheep at different densities can limit the growth of mountain birch within the treeline ecotone. Growth of birch is assessed both with a long term perspective, i.e., birch height in relation to stem diameter, and with a short term perspective, i.e., annual leading shoot growth in relation to birch height. Since the browsing of trees by sheep is not expected to be linearly related to sheep density, the likelihood and intensity of browsing on birch individuals is also assessed across sheep densities. We hypothesise both short term and long term birch growth within the treeline ecotone will be limited by high browsing pressure at high densities of sheep. We further hypothesise that birch will be more susceptible to growth limitation through browsing at higher altitudes due to additional limitations imposed by temperature, and when established for shorter periods due to the lack of structures to compensate for biomass removal.

2. Materials and methods

2.1. Study area and experimental design

A landscape-scale, replicated enclosure experiment was set up in the mountains of southern Norway. The experimental site is located on a south facing slope in the municipality of Hol (7°55' to 8°00'E, 60°40' to 60°45'N). Dwarf shrub and lichen heath communities are common with *Salix* thickets, more productive meadows, snowbeds and wetlands also present at the site (Austrheim et al., 2008) provide a detailed vegetation description). The mean annual

temperature at the site as interpolated from nearby weather stations was -0.7°C during the study period (2002–2008) and -1.6°C in the long term (1960–1991). The mean summer temperature (June to August) was 8.8°C over the study period and 7.9°C in the long term (data supplied by the Norwegian Meteorological Institute).

A single 2.7 km² enclosure was erected and split into 9 sub-enclosures of around 0.3 km² ranging from 1050 to 1320 m.a.s.l., between the forest line and tree species line (respectively the limit of closed forest and limit of distribution of individuals of any size, as defined in Körner and Paulsen, 2004). The fences were constructed using a woven-wire sheep mesh with top wire approximately 130 cm high, supported by wooden stakes. The delimitation of the sub-enclosures was perpendicular to the contours of the slope, such that the altitudinal range was common to all sub-enclosures (Fig. 1). Treatments were initiated in 2002, with no sheep, low sheep density and high sheep density at 0, 25 and 80 sheep km⁻² respectively, distributed in a randomised block design between the enclosures. These densities were based upon assessment of the vegetation and grazing value to sheep and are within the range of sheep densities typically found in Norwegian uplands (Rekdal, 2001). Norwegian white sheep (also known as the Dala breed) were grazed during the summer season, typically from late June until early September, in common with the usual grazing practice within the area. Other large herbivores, moose (*Alces alces*) and reindeer (*Rangifer tarandus*), were not excluded as they could step or jump over the fences, but they were rarely observed in the area. Smaller herbivores such as rodents and mountain hare (*Lepus timidus*) could pass through the fence meshing. The main treeline tree species at the site is the mountain birch, with occasional individuals of other species including *Populus tremula*, *Sorbus aucuparia*, *Pinus sylvestris* and *Picea abies* also found at the site. This study focused on the dominant species, mountain birch.

2.2. Birch growth data

In 2009 (8 years following the initiation of experimental herbivory), 23 belt transects were sampled along an East–West axis across the enclosures. These were regularly dispersed over the altitudinal range of the enclosures and were sampled in a stratified-random order with random direction (Fig. 1; transects were numbered from high to low altitude, odd numbers were first sampled in a random order, followed by even numbers sampled in a random order). All birch located within 5 m either side of the transect lines were recorded. Birch were more prevalent in the no sheep treatment, where a total of 960 individuals below 2 m in height were recorded, than at low sheep density and high sheep density where 99 and 106 were respectively recorded (Speed et al., 2010; the distribution of recruiting birch is also dealt with here).

When birch individuals were located along the transects, (1) the height, (2) the leading shoot growth and (3) stem diameter were measured, (4) the browsing intensity was assessed, and (5) the number of stems was counted. Birch height was measured vertically from ground level at the stem base, to the highest point on the individual without stretching the birch. The leading shoot was defined as the shoot which reached the highest point on the individual tree. Current year growth of the leading shoot was measured from the start of current years' growth to the base of the top leaf. If the leading shoot was browsed, this was noted. Stem diameter was measured at the base of the stem using a pair of callipers. In the case of polycormic individuals (those with greater than one basal stem), the height was measured to the highest point of all stems, and this shoot was defined as the leading shoot. Stem diameter was measured on the largest basal stem in polycormic individuals. Vertebrate browsing intensity was assessed as the proportion of the 30 highest shoots (counted down the stem from the leading shoot)

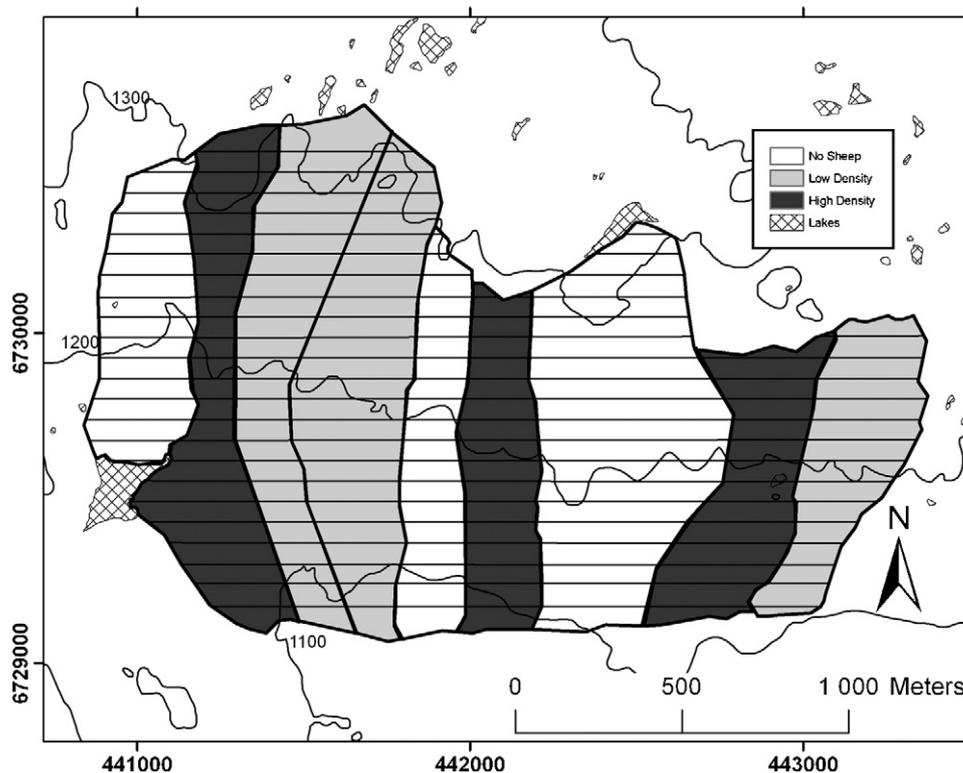


Fig. 1. Map of experimental site (UTM zone 32V) showing enclosures and approximate locations of transect lines. 100 m contour lines are also shown.

of each individual that were browsed. This measure was used to reflect that part of taller trees may escape browsing. Where the total number of shoots was less than 30, the proportion of all shoots that were browsed was used to assess browsing intensity. Browsing intensity data were presence–absence transformed in order to assess browsing likelihood, in addition to intensity.

Birch individuals were subsequently classified into three categories to assess the impact of herbivory at different growth stages. Mature birch: over 2 m in height; birch saplings: below 2 m in height with a stem diameter greater than 15 mm; birch recruits: below 2 m in height with a stem diameter less than or equal to 15 mm. Mature birch trees were not included in this study as part of these individuals were assumed to have had escaped browsing before the start of the experiment. The category of birch recruits corresponds to individuals establishing within the period of herbivory manipulation, whereas saplings and mature birch were estimated to have been present before the start of the experiment (Speed et al., 2010). The number of recorded birch recruits was 881, 65, 23 within no sheep, low sheep density and high sheep density treatments, and 79, 34, 83 saplings. The threshold of 15 mm was used as this was the maximum stem diameter reached by a birch less than or equal in age to the experimental enclosures in a destructive sampling of 100 birch from outside the enclosures (but within the same altitudinal range). Stem diameter explained 69% of the variation in age of individuals within this sample.

2.3. Statistical analyses

Data from all immature birch (recruits and saplings) were used to analyse browsing pressure and to present the distribution of different growth and size classes. However, separate models were developed for birch recruits and saplings to relate growth to sheep density and covariates. This is due to the expectation that the response in growth to the sheep density treatments will vary between individuals which have been exposed to that treatment

since established and individuals which were already developing prior to the initiation of herbivory treatments. Leading shoot growth was analysed as follows: (1) including individuals where the leading shoot was browsed in order to determine the impact of sheep density on net annual shoot growth; and (2) excluding individuals where the leading shoot was browsed to assess the full (unbrowsed) growth potential of birch shoots under the experienced browsing conditions. As the browsing of leading shoots directly affects the recorded height of the birch given the above definition of leading shoot, it was necessary to exclude individuals where the leading shoot was browsed from analyses of birch height.

Statistical analyses were carried out within the R environment (v. 2.9.2, R Development Core Team, 2009). Differences in growth and browsing intensity distributions between treatments were assessed using the Wilcoxon signed rank test on untransformed data. General linear models (GLM) were used to investigate relationships between the dependent variables of growth and browsing pressure and the independent variables of sheep density, altitude and birch size. As the response of tree growth to browsing is likely to be related to tree size (e.g. Hara et al., 1991; Coomes and Allen, 2007), birch height was included as a covariate in models of leading shoot growth, and stem diameter was included as a covariate in models of birch height (leading shoot growth was not related to stem diameter for some classes of birch). Browsing likelihood was modelled using the binomial distribution while browsing intensity, leading shoot growth and birch height were modelled using the Gaussian distribution. Browsing intensity was arcsine transformed, while a Box–Cox power transformation was applied to models of birch recruit height in relation to stem diameter in order to stabilise the variance. The selected lambda value was 0.5 within the transformation $(y^\lambda - 1)/\lambda$. The likelihood of a tree being browsed was modelled using the binomial distribution after transforming the browsing data to presence–absence format. Stepwise model selection was implemented based on analysis of deviance with F

or Chi squared tests as appropriate. The occurrence of non-linear responses of browsing likelihood to birch height was investigated using polynomial regression. The stationary points (i.e. values of birch height at which browsing likelihood peaked) were found using the polynom library within R (Venables et al., 2009).

3. Results

3.1. Browsing likelihood and intensity

The likelihood of a birch being browsed was affected by sheep density treatment and varied with the height of the birch individual (Fig. 2). The percentage of birch individuals that were browsed (within the highest 30 shoots on the plant) increased with sheep density: 13.1% ($n=960$), 63.6% ($n=99$) and 84.9% ($n=106$) were browsed at sheep densities of 0, 25 and 80 sheep per km² respectively. A quadratic term significantly improved the relationship between browsing likelihood and birch height within all sheep density treatments. The likelihood of a birch being browsed peaked when birch were of intermediate heights (Fig. 2). The height at which birch were most likely to be browsed in the no sheep treatment was 127 cm, at low sheep density 105 cm, and 110 cm at high sheep density. Browsing likelihood was significantly higher at high and low sheep density than in the absence of sheep ($P<0.001$ for both), but did not significantly differ between low and high sheep densities (Fig. 2).

Of the birch individuals that were browsed, higher browsing intensities were proportionally less common in the absence of sheep and proportionally highest at high sheep density (Fig. 3). More than half of the few (13%) individuals that were recorded as having been browsed within the no sheep enclosures had less than 10% of shoots browsed (median browsing intensity 10.0%). This was significantly lower than the median browsing intensity

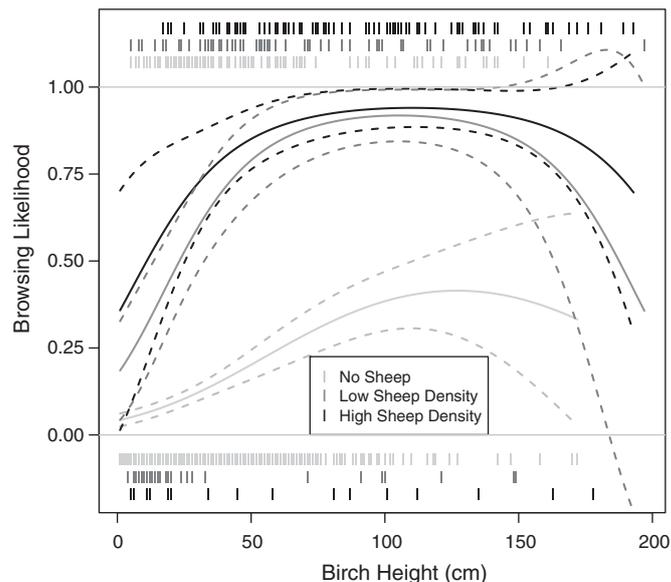


Fig. 2. Browsing likelihood (the probability that at least 1 of the top 30 shoots of an individual was browsed) of birch (*Betula pubescens tortuosa*) shown in relation to birch height and treatment for all immature birch (both recruits and saplings). Solid lines show model prediction, and broken lines give 95% confidence intervals. Dashes at the top and bottom of the figure show the heights of birch which were browsed and unbrowsed respectively.

at both low sheep density (median=17.7%, Wilcoxon rank sum test $U=2628.5$, $P<0.001$) and high sheep density (median=31.7%, $U=2544$, $P<0.001$). The browsing intensity at high sheep density was also significantly greater than at low sheep density ($U=2037.5$, $P<0.01$). Browsing likelihood was predicted based on height and sheep density, while browsing intensity was predicted by treat-

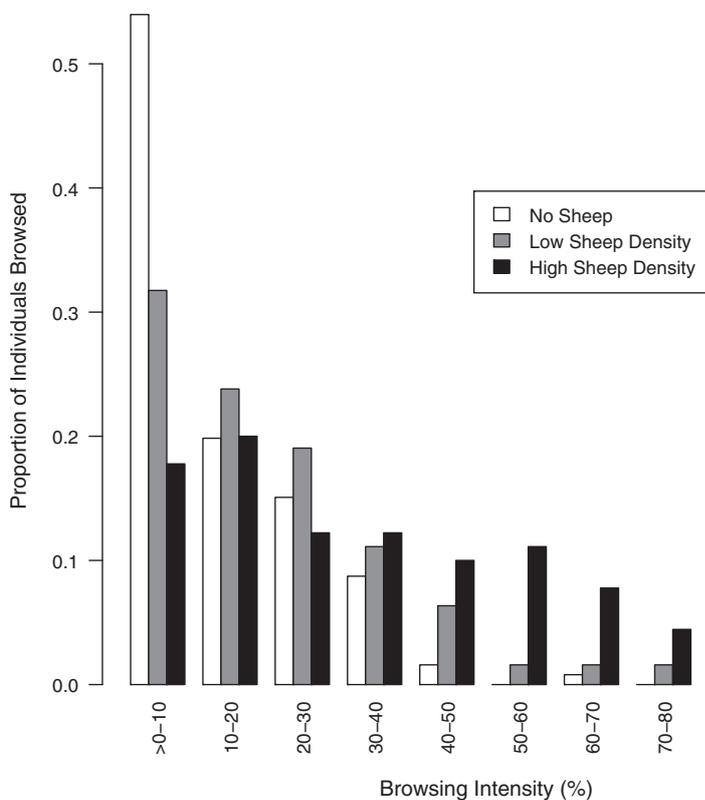


Fig. 3. The proportional distribution of browsing intensities (the percentage of the top 30 shoots browsed) of immature birch (both recruits and saplings) recorded at three experimental densities of sheep.

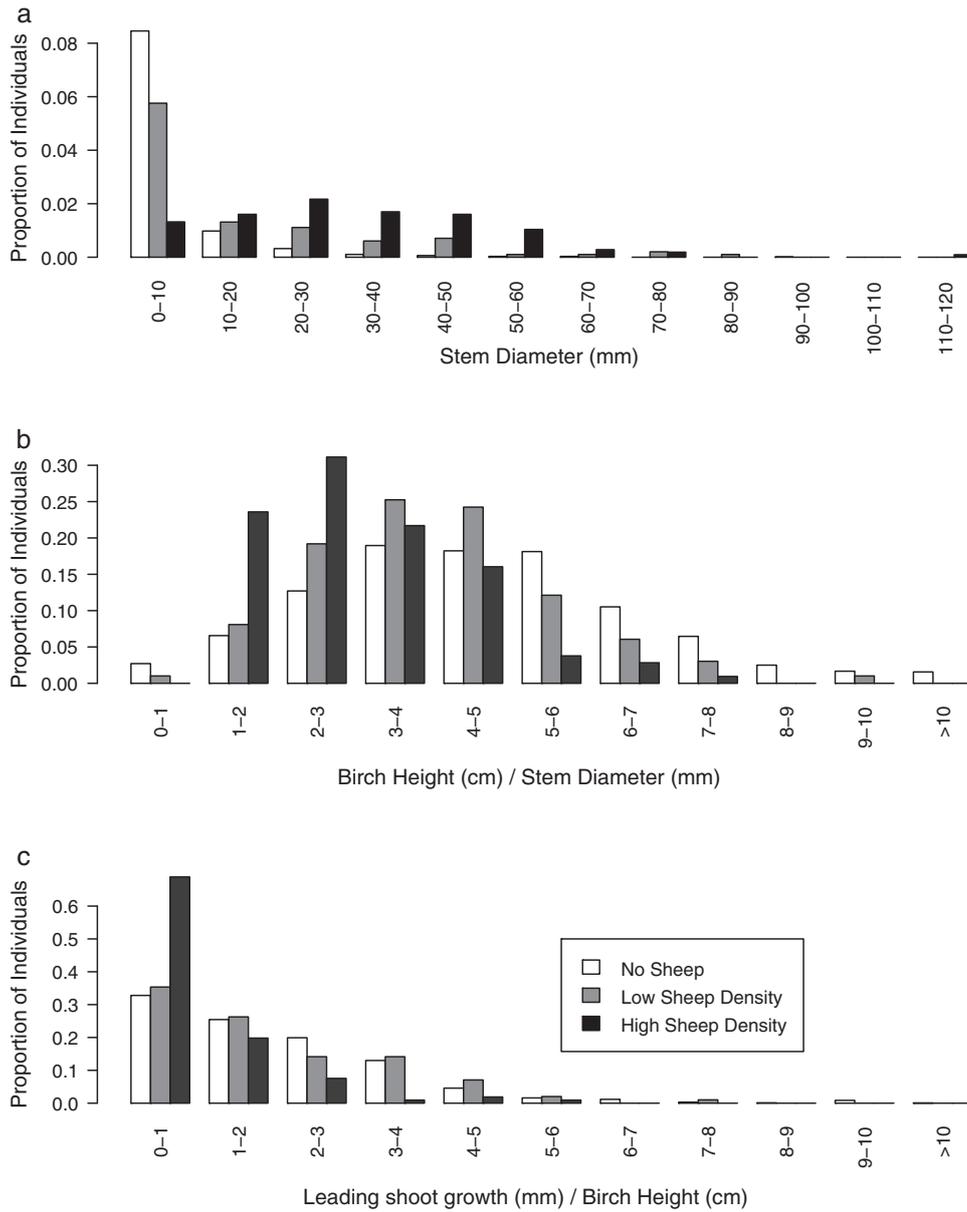


Fig. 4. The proportional distribution of (a) stem diameter, (b) height to stem diameter ratio and (c) leading shoot growth to height ratio of immature birch recorded along transects across three experimental densities of sheep.

ment alone (Table 1). Altitude was not a predictor of browsing likelihood or browsing intensity (Table 1).

3.2. Sheep density and birch growth

In the no sheep treatment, a higher proportion of birches had a small stem diameter than at either low or high sheep den-

sity (Fig. 4a), reflecting the negative effects of sheep on birch recruitment. The mean stem diameter size was 7.0 mm, significantly less than 16.5 mm at low sheep density (Wilcoxon's rank sum test $U=28379.5, P<0.001$) and 31.7 mm at high sheep density ($U=9000.5, P<0.001$). Birch height tended to be greater for a given stem diameter in the absence of sheep (Fig. 4b) with a mean ratio of 4.8 in the no sheep treatment being significantly higher than 4.0 at

Table 1
Analysis of deviance table for model selection of predictors of browsing likelihood and browsing intensity. Full model represents the model including all linear predictors. Degrees of freedom (Df) are shown for all variables in addition to model deviance and Akaike's information criterion (AIC). Browsing likelihood was assessed using a binomial distribution thus Chi squared likelihood ratio test (LRT) is shown. For browsing intensity a Gaussian distribution was used with an arcsine transformation and F test statistics are shown.

	Browsing likelihood (binomial)					Browsing intensity Gaussian (arcsine transformation)			
	Df	Deviance	AIC	LRT	P (Chi)	Deviance	AIC	F	P (F)
Full model		888.85	899			46172	2229		
Treatment	2	1061.17	1067	172.32	<0.001	57219	2285	32.78	<0.001
Birch height	1	965.29	973	76.44	<0.001	46474	2229	1.79	0.18
Altitude	1	889.25	897	0.4	0.52	46340	2228	1.0	0.32

Table 2

Estimated parameters for the selected models of net annual shoot growth (including browsed leading shoots) of birch recruits and saplings. For birch recruits $n = 881, 65, 23$ and for birch saplings $n = 79, 34, 83$ within unbrowsed, low and high sheep densities. Blank rows indicate that the variable was not retained during model selection.

Net annual shoot growth Including browsed leaders	Recruits				Saplings				
	Estimate	SE	t	P	Estimate	SE	t	P	
		$R^2 = 0.54$				$R^2 = 0.26$			
Intercept	-10.37	4.1	-2.53	0.012	39.73	28.43	1.4	0.164	
Birch height	2.19	0.07	31.94	<0.001	0.49	0.16	3.12	0.002	
Low sheep density	14.87	8.46	1.76	0.079	66.39	39.76	1.67	0.097	
High sheep density	7.99	17.29	0.46	0.644	10.58	36.31	0.29	0.771	
Altitude	0.08	0.03	2.33	0.02	0.88	0.25	3.57	<0.001	
Birch height × low sheep density	-0.47	0.24	-1.91	0.056					
Birch height × high sheep density	-1.02	0.49	-2.07	0.039					
Altitude × low sheep density					-1.29	0.53	-2.45	0.015	
Altitude × high sheep density					-1.2	0.47	-2.57	0.011	

low sheep density ($U = 57382, P < 0.001$) and 2.0 at high sheep density ($U = 76393.5, P < 0.001$). The leading shoot growth was lower for a given birch height at high sheep density than either low sheep density or in the absence of sheep (Fig. 4c, $U = 7520.5, P < 0.001$ and $U = 71574, P < 0.001$, respectively) but did not differ between low sheep density and no sheep treatments. This pattern was not sensitive to the removal of individuals where the leading shoot was browsed.

Predictors of growth were analysed separately for birch recruits and saplings. The number of basal stems was not a predictor of height or leading shoot growth for recruits or saplings and was removed by stepwise selection. The mean height (standard deviation) of birch recruits was 25.4 cm (19.8) and for saplings was 102.5 cm (38.5). Annual net leading shoot growth (i.e. including trees where the leading shoot was browsed) was positively related to the height of birch individuals for both birch recruits and birch saplings (Table 2), but was not related to stem diameter. For recruits, the annual net leading shoot growth to birch height ratio was lower at both low and high sheep densities than in the absence of sheep, although only significantly so within the high sheep density treatment (Table 2). Leading shoot net growth also increased with altitude for recruits (Table 2). For saplings there was no interaction between sheep density treatment and birch height, but leading shoot growth decreased with altitude with sheep and increased with altitude in the absence of sheep. Shoot growth potential (excluding trees with browsed leading shoots from analyses) of recruits was also positively related to both birch height and altitude, but was not affected by sheep density treatment. In contrast, sapling leading shoot growth potential was significantly reduced at high sheep density and was not related to sapling height (Table 3).

Birch height was found to increase with stem diameter and decrease with altitude, for both recruits and saplings (Table 4). There was a significant interaction between stem diameter and sheep density in determining birch recruit height. Recruit height was limited by high sheep density at larger stem diameters (Table 4). On the other hand, sheep density did not affect the height or height to stem diameter ratio of older birch saplings that were estimated to have been present before the start of the experiment

(Table 4) even though many of the birch saplings remained within browse height (mean height 102.5 cm, with sheep browsing likelihood decreasing rapidly on trees above 150 cm; Fig. 2).

4. Discussion

Browsing can affect forest dynamics (Gill, 2006), but at forest margins other factors such as climate, topography and soil properties are also important factors (Gamache and Payette, 2004; Holtmeier and Broll, 2005). Herbivory has been shown to limit tree recruitment at the alpine treeline (Speed et al., 2010). Mechanisms whereby herbivores limit treelines have been suggested, and are likely to involve the relative preference of herbivores for treeline species and field layer vegetation (Cairns and Moen, 2004; Cairns et al., 2007), as well as the tolerance of treeline species to browsing, which itself is likely to vary with size and developmental state (Danell et al., 2003). The results of this study demonstrate that browsing by sheep strongly affects growth of birch at the treeline ecotone, both within a single growing season (reduction in leading shoot growth) and over a longer time scale (lower height to stem diameter ratio), with growth most strongly reduced in smaller recruiting birch. Birch of smaller stem diameter were proportionally more common in the absence of sheep than in either of the other treatments, in the eighth year of continuous experimental herbivory. This pattern is as expected for an advancing treeline (Hofgaard et al., 2009), in this case the advance is due to the experimental cessation of sheep grazing 8 years before sampling (Speed et al., 2010). However, the long-term height growth (with stem diameter as a covariate) was lower at low and high densities of sheep than in the absence of sheep, while the annual shoot growth (with height as a covariate) was lower at high sheep density than at low sheep density and in the absence of sheep. This suggests that by constraining short and long-term growth, herbivores can limit the development of mature birch stands in the treeline ecotone. Our study thus provides insights into the mechanistic pathways by which herbivory can limit treeline advance, and thus can potentially buffer climatically driven forest expansion.

The consequences of herbivory for a population of trees at the treeline ecotone depend upon the browsing pressure on individ-

Table 3

Estimated parameters for the selected models of potential annual shoot growth (excluding browsed leading shoots) of birch recruits and saplings. For birch recruits $n = 874, 60, 18$ and for birch saplings $n = 78, 26, 61$ within unbrowsed, low and high sheep densities.

Potential shoot growth Excluding browsed leaders	Recruits				Saplings				
	Estimate	SE	t	P	Estimate	SE	t	P	
		$R^2 = 0.55$				$R^2 = 0.17$			
Intercept	-10.76	3.99	-2.7	0.007	84.84	27.56	3.08	0.002	
Birch height	2.18	0.06	33.64	<0.001	0.32	0.18	1.76	0.08	
Low sheep density					18.28	18.91	0.97	0.335	
High sheep density					-55.71	14.37	-3.88	<0.001	
Altitude	0.09	0.03	2.69	0.007	0.55	0.2	2.74	0.007	

Table 4
Estimated parameters for the selected models of height (excluding browsed leading shoots) of birch recruits and saplings. For birch recruits $n = 874$, 60, 18 and for birch saplings $n = 78$, 26, 61 within unbrowsed, low and high sheep densities. A power transformation was applied to the response variable recruit height. Lambda = 0.5.

Birch height Browsed leaders omitted	Recruits $R^2 = 0.71$				Saplings $R^2 = 0.16$			
	Estimate	SE	t	P	Estimate	SE	t	P
Intercept	3.3	0.22	14.78	<0.001	92.42	8.24	11.22	<0.001
Stem diameter	0.99	0.02	44.32	<0.001	0.86	0.17	5.17	<0.001
Low sheep density	-0.33	0.56	-0.6	0.55				
High sheep density	0.69	1.05	0.66	0.51				
Altitude	-0.01	0.002	-5.89	<0.001	-0.2	0.08	-2.53	0.012
Stem diameter \times low sheep density	-0.07	0.08	-0.85	0.4				
Stem diameter \times high sheep density	-0.34	0.12	-2.82	<0.01				

ual trees, and the response of individuals to being browsed. The browsing pressure is likely to vary with the density of herbivores and the accessibility of the trees to the herbivores. The proportion of birch individuals that were browsed increased with sheep density, as expected. The browsing pressure on individuals in the absence of sheep (13% of individuals were browsed, mostly at low intensities) represents the background herbivory from herbivores other than sheep, most likely moose, reindeer and mountain hare (the taller height of peak browsing points to either taller cervids or to hares browsing birch protruding above the snow layer in winter). Wild herbivores are known to also have a strong influence on dynamics and processes at the treeline (Cairns et al., 2007). The low level of wild-herbivore browsing here is likely to be attributable to the enclosure fences, which while they did not completely exclude wild herbivores, will have reduced the herbivore densities inside the enclosures. It was assumed that browsing by other herbivores within the sheep-browsed enclosures was less than (e.g. Osborne, 1984), or equal to (e.g. Hester et al., 1999), the browsing recorded within the no sheep treatment, thus the increase in browsing pressure on birch in the presence of sheep was attributable to the sheep density treatments. At both low and high sheep densities, browsing likelihood was greatest at intermediate birch heights of between 50 and 150 cm, in line with previous studies on sheep browse-heights (e.g. Wilson et al., 1975; Zamora et al., 2001; McEvoy and McAdam, 2008). The lower likelihood of browsing of smaller birch may be due to the lower apparency of birch within surrounding vegetation, a greater likelihood of entire removal of small birches by herbivores, or a reduced sampling detection of small and browsed birches (Speed et al., 2010). Trees of intermediate height have also been found to be more frequently browsed than smaller trees in the presence of other herbivores including cattle and cervids (e.g. Martin and Baltzinger, 2002; Vandenberghe et al., 2007).

Although net annual shoot growth of saplings decreased with altitude within the low and high sheep density treatments as expected, shoot growth in the absence of sheep increased with altitude, which is contrary to some other studies which found a decrease in shoot growth with altitude (e.g. James et al., 1994; Takahashi, 2003) and temperature (Gamache and Payette, 2004). This difference may indicate that a higher root:shoot ratio at high altitudes (e.g. Wilson, 1994) allows a greater shoot growth when browsing pressure is low or absent, while higher long-term browsing pressure suppresses both shoot and root growth. Such suppression may be more severe when herbivory interacts with harsher climatic conditions of higher altitudes (Trotter et al., 2002), as indicated by the reduced potential growth of birch saplings at high sheep density (i.e. the leading shoot growth was lower, even when only considering unbrowsed shoots). However, potential growth of recruits, as opposed to the saplings, was unaffected by sheep density treatment, even following eight years of controlled herbivore densities. This difference may be due to the likelihood that in small recruits, the leading shoot is more likely to be browsed (and hence excluded from analysis of potential growth), whereas in taller saplings, lower shoots are more likely to be browsed than

the leader shoot. In saplings leading shoot growth may then be reduced through resource depletion at the individual level due to interdependence of shoots (Henriksson et al., 1999).

As expected, due to the link between temperature and growth, birch height decreased with altitude for both recruits and saplings. Indeed, stunted and *Krummholz* trees are particularly common at altitudes above the treeline. Although altitude is known to affect the seasonal foraging behaviour of sheep (Mysterud et al., 2007), in the current study, neither browsing likelihood nor intensity was related to altitude. The reduction in height of recruits at high sheep density was consistent across the altitudinal gradient, however, annual net growth of saplings was most strongly reduced in the presence of sheep at high altitudes, possibly suggesting a lack of compensatory potential at high elevations. The growth limitation in the presence of sheep also suggests an additional increase in mortality of trees may occur, as growth limitation and mortality are often positively associated (Danell et al., 2003).

While the browsing pressure on an individual tree is likely to be related to both the density of herbivores and the apparency of the individual, the susceptibility of an individual to a given browsing pressure also relates to its size or developmental state (Danell et al., 2003; Boege and Marquis, 2005). Indeed, recruits (those estimated to be less than 9 years old at the time of sampling) were more susceptible to long-term height growth limitation through herbivory than older saplings. By constraining height growth, browsing may therefore increase the duration of susceptibility of young birch to vertebrate herbivores, by preventing them from reaching a "size refuge", a height at which individuals escape or increase resistance to browsing (Karban et al., 1997; Fornara and Toit, 2007). Previous studies have used the short-term impact of herbivores on tree growth to model the time for tree individuals to reach a size refuge (Zamora et al., 2001; Allcock and Hik, 2004). The current study shows that for a given stem diameter, the height of young birch is greater in the absence of sheep, clearly indicating faster height growth. Thus our data imply that sheep browsing birch will increase the time taken for recruiting birch to reach a size refuge within the treeline ecotone. For early successional tree species such as birch, height is more responsive to growth conditions than stem diameter (Hara et al., 1991), thus birch treeline development, and hence forest expansion, may be more sensitive to herbivory than treelines with later-successional species. Other herbivores, both domestic and wild, are likely to influence tree growth at the treeline in a similar fashion to sheep. Indeed reindeer herbivory has also been linked to forest dynamics in northern Scandinavia (Tømmervik et al., 2009).

High sheep densities (80 sheep km^{-2}) were generally required to limit the height growth of young birch at the treeline. This contrasts with the response of recruitment, which was limited even at 25 sheep km^{-2} (Speed et al., 2010). Our data therefore suggest that while low densities of sheep can limit recruitment, higher densities are required to reduce growth of birch once established. This is despite net annual shoot growth being constrained at low sheep densities. Furthermore, height growth of older birch saplings was

unaffected by browsing, even though net annual shoot growth was reduced at low and high sheep densities and potential shoot growth was reduced at high sheep density. These results support a higher tolerance of established and taller trees to browsing (Danell et al., 2003; Boege and Marquis, 2005). This suggests that the herbivore-resistance of individuals within an advancing treeline will increase with time, and vegetation state change following decreases in herbivore density will not be immediately reversible. Furthermore, relatively short periods of herbivore density decrease (<10 years) are sufficient to allow treeline advance.

The altitude of the treeline at the study site is in line with its location within Norway (Moen, 1999), suggesting that the land use history at this site is representative for at least the region. Land use histories similar to that found in Norway are reported from across Europe (Olsson et al., 2000; Tasser et al., 2007; Dallimer et al., 2009). Körner and Paulsen (2004) found that the root-zone temperature at the treeline was on global growing season mean of 6.7 °C (standard deviation 0.8), similar to observed air temperatures at treelines (Körner, 1998). At the current study's site, the growing season mean air temperature is 7.9 °C (although this is interpolated from nearby weather stations and thus cannot be regarded as the precise temperature at the treeline). While this temperature is higher than the global average, which would suggest a treeline altitude suppressed by land use, the difference is only 1.5 standard deviations (as reported by Körner and Paulsen, 2004), so in terms of land use history, the study site does not appear unusual. The results of this study may thus be relevant to a wider range of systems, within and outside Norway.

4.1. Conclusions and implications for management

Our study has important implications for understanding and managing the drivers of shifts in treelines. Increases in temperature have been linked to increases in growth of tree species at the tree-line ecotone (Gamache and Payette, 2004; Karlsson et al., 2004), and globally, treeline advance has been linked to recent global warming (see the meta-analysis of Harsch et al., 2009). However, herbivores may also play a role in treeline advances (Cairns and Moen, 2004; Speed et al., 2010). This study has shown that high densities of herbivores can limit annual shoot growth at the treeline, and can keep recruiting birch at lower heights for extended time periods, thereby increasing the length of time that recruiting trees remain susceptible to browsing and growth limitation. Short periods of reduced livestock density are sufficient to allow individuals to grow beyond herbivore susceptibility.

Traditional land uses, such as grazing of livestock, drive processes at the treeline ecotone in the opposite direction to climatic warming and could therefore constrain climatically driven treeline advance. However, densities of grazing livestock in upland pastures are currently decreasing across Europe (MacDonald et al., 2000; Dallimer et al., 2009), and this study shows that this will drive treelines in the same direction as predicted climatic warming, potentially increasing the rate of treeline advance and forest expansion into alpine regions. Correspondingly, the management of herbivore densities, in particular domestic herbivores such as sheep, could be used as a potential buffer of climate driven changes at the treeline ecotone. However, such management would require awareness of the potential long-term impacts of increased densities of herbivores on vegetation (Olofsson, 2006).

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