Ann. Bot. Fennici 46: 280–290 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 31 August 2009

The condition and survival of *Populus tremula* and other deciduous saplings in a moose winter-foraging area in southern Finland

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Received 1 Sep. 2008, revised version received 20 Feb. 2009, accepted 23 Feb. 2009

de Chantal, M., Lindberg, H. & Kallonen, S. 2009: The condition and survival of *Populus tremula* and other deciduous saplings in a moose winter-foraging area in southern Finland. — *Ann. Bot. Fennici* 46: 280–290.

The current heavy browsing pressure by moose (*Alces alces*) affects and even prevents the regeneration of deciduous species in Fennoscandia. We studied the current establishment status of *Populus tremula* and other deciduous species in managed regeneration stands in a moose winter-foraging area in southern Finland. The regeneration of *P. tremula* was more abundant in height classes 40–100 cm. There was a lag in stem density for height class 20 cm and there were no *P. tremula* saplings taller than two meters. The majority of living *P. tremula* regeneration was healthy, despite the fact that many stems had been browsed repeatedly, particularly in stands with greater sapling densities. The majority of *Sorbus aucuparia* and *Salix* spp. stems were also healthy despite recurrent browsing in all stands, and their density decreased sharply for saplings taller than 100 cm. *Betula pendula* and *Betula pubescens* were the most abundant of the studied species. They had less bites per stem and a very high proportion of them were healthy. Due to the high moose population density in the study area, the successful recruitment of mature stems of *P. tremula*, *Salix* spp., and *S. aucuparia* in the landscape is uncertain. The situation of *Betula* spp. is less problematic, due to its greater density.

Key words: *Alces alces*, *Betula* spp., browsing, height, *Salix* spp., *Sorbus aucuparia*, stem density

Introduction

The population structure of European aspen (*Populus tremula*) and other deciduous species has significantly changed in Finland during the last century. Both *P. tremula* and other deciduous species were more common at the time when former agricultural methods produced various semi-cultural forests, e.g. old, gradually reforested slash-and-burn areas. When new silvicultural policies aiming at producing even-aged stands of pine and spruce through artificial regeneration were established in the 1950s, *P. tremula* and other broadleaved species were considered unwanted competitors of conifers and deemed of minor commercial value. *Populus tremula* was considered especially undesirable because it hosts the pine twisting rust fungus *Melampsora pinitorqua* (Reinikainen *et al*. 2001) and was previously systematically removed during forest thinnings and harvestings, or destroyed with girdling and herbicides to prevent its vegetative regeneration (Latva-Karjanmaa *et al*. 2007).

Recently, various actions, e.g. restoration acts, have been suggested to diversify future forest structures in conservation areas (Hanski 2000, Kuuluvainen 2002, Latva-Karjanmaa *et al*. 2007). In addition, current Finnish silvicultural guidelines (Forest Development Centre Tapio 2006) advise to have a moderate mixture of deciduous species in all regeneration areas and to leave old, large *P. tremula* stems as retention trees. The high value of living and dead *P. tremula* trees, and even aspen litter, in maintaining biodiversity has been shown in recent studies (Kuusinen 1994b, Koivula *et al*. 1999, Kolström & Lumatjärvi 2000, Martikainen 2001, Junninen *et al*. 2007). It has been estimated that *P. tremula* hosts hundreds of species belonging to different taxonomical and ecological groups. Out of these, about 150 can be considered aspen-dependent and 50 endangered (Siitonen 1999, Rassi *et al*. 2001, Kouki *et al*. 2004). The importance of other deciduous species, such as *Betula* spp., *Salix* spp., and *Sorbus aucuparia*, to biodiversity and red-listed species has also been demonstrated (Berg *et al*. 1994, Kuusinen 1994a, Jonsell *et al*. 1998, Gu *et al*. 2001, Pykälä *et al*. 2006, Jonsell *et al*. 2007).

Many threatened species favour large trunks (Berg *et al*. 1994, Jonsell *et al*. 1998). However, the current age structure of *P. tremula* and other deciduous species in managed forests in Finland practically lacks older cohorts with large stems (Lilja *et al*. 2006, Latva-Karjanmaa *et al*. 2007). Old, large *P. tremula* trees, for example, are mainly found in nature conservation areas, where, due to poor regeneration, young cohorts are missing (Kuusinen & Penttinen 1999, Kouki *et al*. 2004). Therefore, the quality of nature conservation areas for aspen-dependent species is gradually weakening.

Research on *P. tremula* regeneration has been active in Finland lately (Latva-Karjanmaa *et al*. 2003, de Chantal *et al*. 2005, Latva-Karjanmaa *et al*. 2005, de Chantal & Granström 2007, Latva-Karjanmaa *et al*. 2007). It appears that young managed forests are important for *P. tremula* regeneration, especially near current old-growth reserves with large *P. tremula* stems (Kouki *et al*. 2004, Latva-Karjanmaa *et al*. 2007). Although the vegetative regeneration ability of *P. tremula* and deciduous species in open areas is good (Bärring 1988, Rydberg 2000), the current heavy browsing pressure by moose (*Alces alces*) might affect and even prevent their regeneration, both in managed stands and in conservation areas (Angelstam *et al*. 2000, Kouki *et al*. 2004, de Chantal & Granström 2007). The browsing pressure is especially high in larger, remote forest areas whereas stands near arable land suffer less intense browsing pressure (Edenius & Ericsson 2007). However, contradicting results showed that the risk of an individual ramet to be browsed increases near arable land (Ericsson *et al*. 2001).

The aim of this study was to document the current establishment status and possible growth delays of *P. tremula* and other deciduous species in managed regeneration stands in a moose winter-foraging area with a relatively high, yet typical moose density. The main goal was to find out whether a general browsing impact could be observed at the landscape level.

Material and methods

Stand description

The study took place in the Evo state forest (Fig. 1) in southern Finland (61°N, 25°E), a relatively homogenous and remote area of 8000 ha that serves as winter-foraging grounds for moose. The Evo state forest also includes two important old-growth forest reserves, where old, large *P. tremula* stems are present and support threatened, aspen-dependent species known to exist in the area (Heikkinen 2005). Several stands were selected out of the forestry planning databases of the Finnish Forest and Park Service

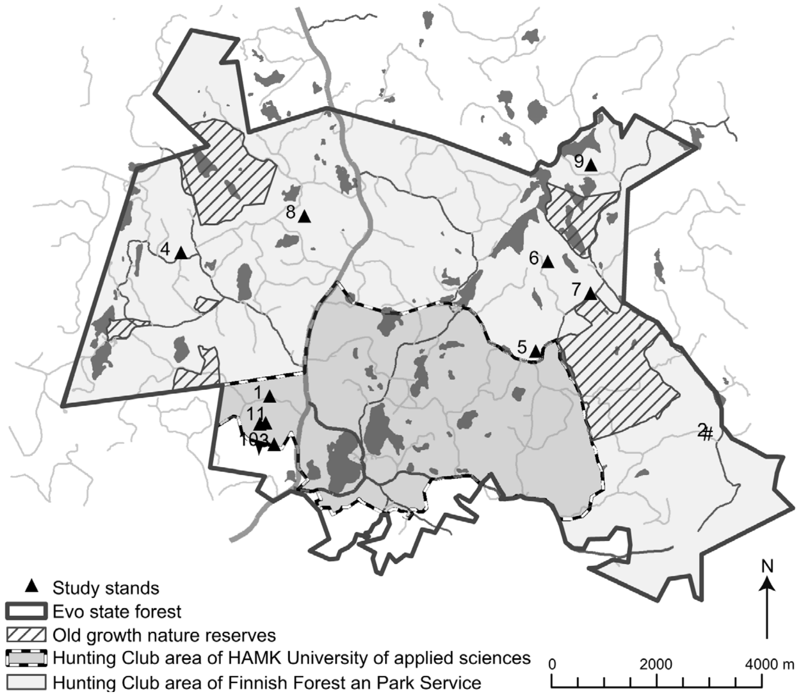

Fig. 1. Limits of the Evo state forest with the locations of the studied stands and nature reserves.

and the Evo Forestry Unit of the HAMK University of Applied Sciences. Selection criteria were topographical homogeneity, a mesic site type, i.e. *Myrtillus* type or *Oxalis–Myrtillus* type (Cajander 1926), a content of at least 500 stems per hectare of *P. tremula* and deciduous species whose average hight was 0.5–2.0 m. Following a pre-examination in the field, 11 stands that fulfilled all the selection criteria were chosen to form the sample. All stands were harvested between 1994 and 2000, followed by harrowing, prescribed burning, or both (Table 1). Stands were planted or sown with conifers, but no artificial regeneration of deciduous species took place. The main aim of the sampling was to find stands with a current potential for moose browsing of deciduous trees. Thus, variation in regeneration treatments and possible regeneration pulses was unavoidable in order to include all browsing-potential stands in the sample. The use of a larger area would have led to too high variation in moose populations.

The early-winter moose population density estimates (area-weighted) in Evo state forest since year 2000 have ranged from 3.6 to 10.9 individuals per 1000 hectare (Table 2). Throughout Finland, post-hunting season moose densities have been estimated annually by local hunting clubs on their respective hunting territories according to the national Finnish moose population census (Nygrén 1984, Nygrén & Pesonen 1993). The moose density estimates for the Evo state forest are provided by two hunting clubs (the club of HAMK University of Applied Sciences, 1784 ha, and the Club of the Finnish Forest and Park Service, 4814 ha); all studied stands were located within their territories. The estimates are considered relatively reliable in general, although high-density populations typical of winter-foraging areas may be underestimated (Nygren 1984). Therefore, the true moose densities in the Evo state forest may be higher. No other moose density inventories were available from our study area, apart from a single aerial census performed in 2001. Because the moose densities are estimates for the Evo state forest, which is larger than our study area, individual moose densities and browsing pressures could not been provided for each stand. Instead, the yearly estimated area-weighted moose densities are considered constant in all eleven stands.

The mean annual temperature in the region is +3.1 °C, the average annual precipitation is 670 mm, and the growing season is 160 days.

Table 1. Description of the stands inventoried for regeneration of *P. tremula* and other deciduous species.

Stand	Area (ha)	Pre-harvest		Harvest, year	Silvicultural	Regeneration treatments, year	Site method, year	Soil type type	Comment
		Species composition	Age (yrs)						
1	1.3	*P. sylvestris*	81	seed tree cut, 1995	harrowing, 1996	planted with *P. abies*, 1999	MT	coarse moraine	
2	1.9	90% *P. abies*, 5% *P. sylvestris,* 5% *Betula* spp.	100	clearcut, 1995	prescribed burning (uneven result), 1997	planted with *P. sylvestris*, *P. abies* and *Larix sibirica,* 1997	MT	fine moraine	Retention trees: *P. sylvestris* and *Betula* spp.
3	1.9	70% *P. abies*, 30% *P. sylvestris*	87	clearcut, 1998	harrowing, 1999	natural	MT	coarse moraine	
4	7.7	90% *P. sylvestris*, 10% *Betula* spp.	90	clearcut, 2000	prescribed burning (uneven result) and harrowing, 2001	planted with *P. sylvestris*, 2002	MT	coarse moraine	Retention trees: *Betula* spp. and *P. abies*
5	1.8	80% *P. abies*, 15% *P. sylvestris,* 5% *Betula* spp.	90	clearcut, 1997	prescribed burning, 1997	natural	MT	coarse moraine	Retention trees: *Betula* spp.
6	4.8	90% *P. abies*, 10% *Betula* spp.	120	clearcut, 1996	prescribed burning, 1996	natural	OMT	moraine	Retention trees: *Betula* spp. and *P. tremula*
7	2.4	90% *P. abies*, 10% *Betula* spp.	95	clearcut, 1995	harrowing, 1995	planted with *L. sibirica*, 1995 (removed in 2004)	MT	fine moraine	Retention trees: *Betula* spp.
8	3.5	80% *P. abies*, 15% *P. sylvestris,* 5% *Betula* spp.	90	clearcut, 1994	prescribed burning, 1995	planted with *P. sylvestris*, 1995	MT	fine moraine	Retention trees: *P. tremula*, *Betula* spp. and *P. sylvestris*
9	8.0	Undetermined	–	clearcut, 1997	Undetermined	planted with *P. abies*, end of 1990s	OMT	moraine	
10 & 11	5.2	60% *P. abies*, 10% *P. sylvestris,* 30% deciduous	97	clearcut, 1994	prescribed burning and harrowing, 1996	machine-sown with *P. sylvestris* simultaneously with harrowing, 1996	MT	coarse moraine	

The bedrock is orogenic granitoid covered by a thick morainic layer.

Inventories

Inventories were conducted in summer 2006, except for stands 1 and 10 which were inventoried in 2005. The possible effect of the inventory year was not considered. All *P. tremula* stems from 5–300 cm in height, as well as stems of other deciduous species (*B. pendula*, *B. pubescens*, *S. aucuparia* and *Salix* spp.) from 20–300 cm in height, were inventoried by systematic line-wise sampling. The data was originally collected with a focus on *P. tremula*, which explains the different lower height limits between species. In each stand, two sampling lines located 20 m apart were established. The lines were directed through the center of the stands, following the main cardinal directions, either from south to north or from west to east according to the shape of the stand. Circular plots of 20 m^2 (radius 2.52 meters) were located 20 m apart along each line. A maximum threshold value of 500 stems was set to avoid overwhelming work in dense stands, such that between 7 and 10 plots were inventoried in each stand. The plot containing the 500th stem was inventoried totally. By inadvertance, *Betula* spp. were not differentiated during inventories of stands 1 and 10. Therefore, these stands were excluded in the analyses of *Betula* spp. The sample plots were established permanently for future research.

Height was measured from the ground to the terminal bud or to the highest living part of the stem. For the analysis, saplings were grouped into various height classes spanning 20 cm each. Because *P. tremula* was inventoried from the lower height limit of 5 cm, its first height class (5–20 cm) spanned only 15 cm. The condition of each stem (health classes) was recorded as being healthy (no or little sign of browsing or growth reduction), weak (clearly visible signs of growth reduction or browsing of foliage or branches) or dead. The total number of bites per stem was also recorded.

Data analysis

The abundance of regeneration of each species per stand was calculated as the average of all plots within a stand and converted into abundance per hectare. Abundance was also calculated per health class, height class, and bite class. For each species, the difference in height between browsed and unbrowsed stems in each health class as well as the difference in proportions of browsed and unbrowsed stems between *Betula* species was also tested using a paired *t*-test. All analyses were carried out using SAS (SAS Institute Inc. 1989).

Results

The average abundances of browsed and unbrowsed stems of each species in the healthy, weak and dead categories can be found in Table 3. The variation between stands was large, though (Fig. 2 and Table 3). For *P. tremula*, regeneration

Table 2. Post-hunting season moose densities (individuals 1000 ha^{-1}) in the area of the experimental stands, as estimated by the two hunting clubs and one separate aerial census

Year	Hunting Club of Forest and Park Service	Hunting Club of HAMK University of Applied Science	Estimated area-weighted density
2000	4.2	7.8	5.2
2001	10.4	12.2	10.9
2002	6.3	10.0	7.3
2003	3.8	5.6	4.3
2004	5.2	8.9	6.2
2005	3.1	6.1	3.9
2006	2.9	5.6	3.6
Aerial census 2001	13.5	3.4	10.8

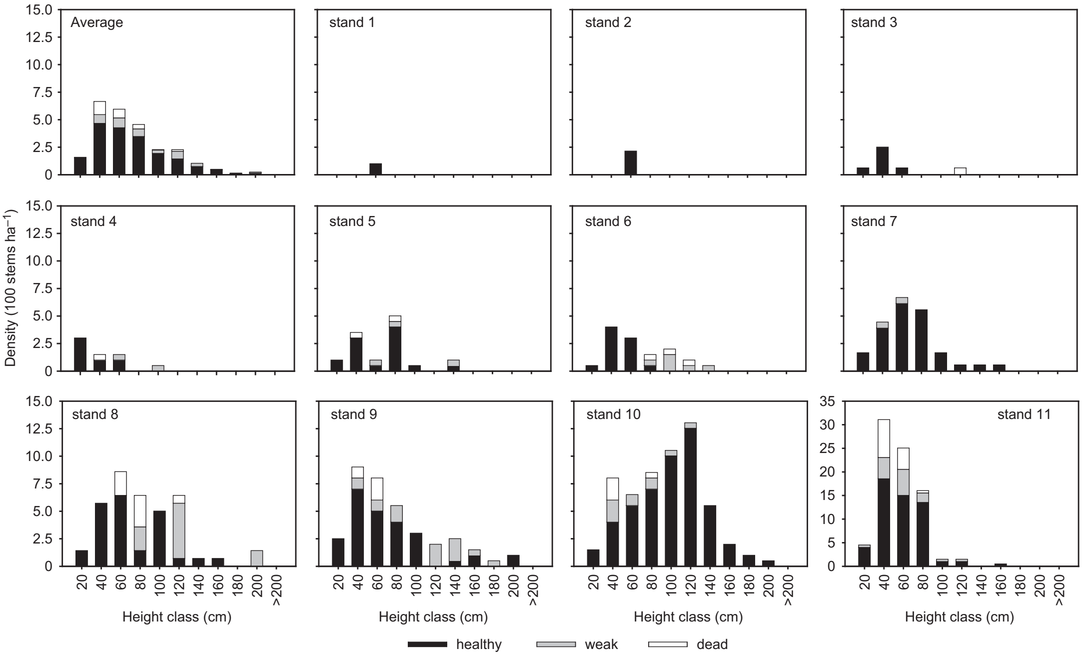

Fig. 2. Average density of healthy, weak and dead *Populus tremula* regeneration per height class. Note the difference in *y*-axis scale.

was generally more abundant in height classes shorter than 100 cm (Fig. 2). There was an apparent lag in density for height class 20 cm (which spanned from 5–20 cm, whereas the other height classes had a span of 20 cm each) and there were no *P. tremula* stems taller than two meters. In

Table 3. Average density and height of browsed and unbrowsed regeneration in the Evo state forest.

Species per health category	Browsed				Unbrowsed				p*
	Density (stems ha^{-1})	SD	ht (cm)	SD	Density (stems ha^{-1})	SD	ht (cm)	SD	
Healthy									
P. tremula	4387	1712	61	9	3116	561	42	3	0.030
B. pendula	9030	1536	154	15	4327	573	119	12	0.010
B. pubescens	10382	2149	140	15	11296	2338	107	12	0.003
S. aucuparia	5361	710	58	5	1331	341	60	11	0.970
Salix spp.	854	192	92	16	377	124	47	7	0.096
Weak									
P. tremula	1448	405	80	8	120	56	40	4	0.082
B. pendula	357	132	94	10	277	88	80	18	0.071
B. pubescens	217	80	110	13	357	140	68	8	0.004
S. aucuparia	2065	385	62	6	257	148	42	7	0.042
Salix spp.	40	28	84	16	20	20	50	0	–
Dead									
P. tremula	397	152	–	–	634	349	–	–	–
B. pendula	100	44	–	–	180	76	–	–	–
B. pubescens	20	20	–	–	417	132	–	–	–
S. aucuparia	100	44	–	–	20	20	–	–	–
Salix spp.	0	0	–	–	40	28	–	–	–

* *t*-test for ht.

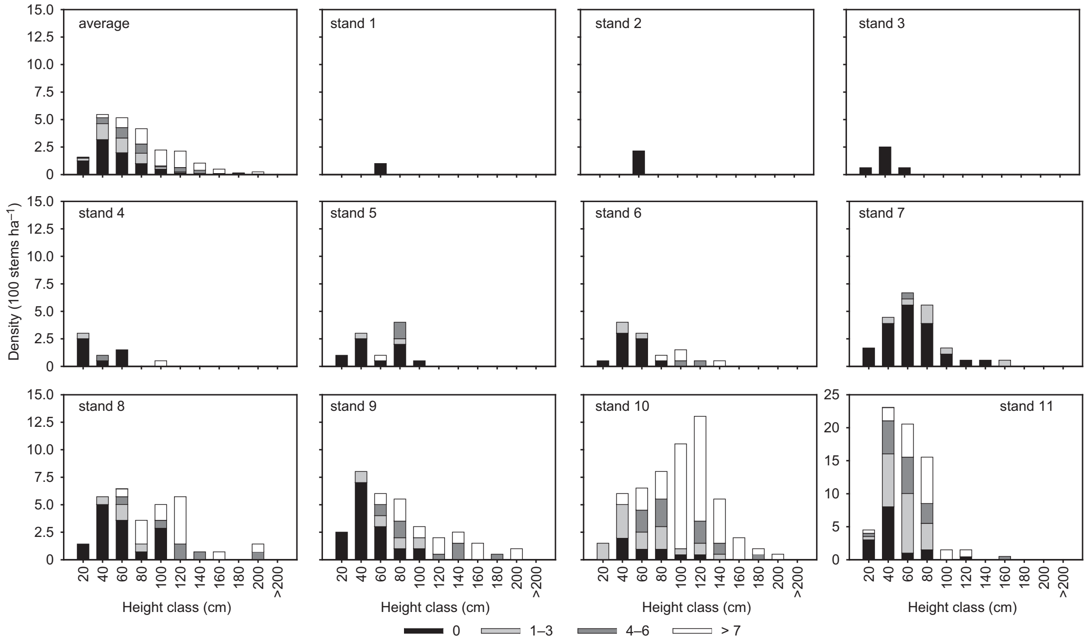

Fig. 3. Average abundance of living *Populus tremula* regeneration per height class with total number of bites per stem. Note the difference in *y*-axis scale.

each height class, the majority of living aspen stems were healthy (Fig. 2), despite the fact that many of them had been browsed repeatedly, particularly in stands with greater densities (Fig. 3). Among healthy *P. tremula*, browsed stems were taller than unbrowsed ones (Table 3) but there was no difference in height between browsed and unbrowsed weak *P. tremula* since there were few stands with unbrowsed weak stems.

Both *B. pendula* and *B. pubescens* were browsed, but the most common bite class was 1–3 bites per stem while the two highest bite classes were rare (Fig. 4a and b). A very high proportion of *Betula* stems were healthy despite being browsed (Table 3). Browsed but healthy stems of both *Betula* species were taller than the unbrowsed healthy ones (Table 3). Browsed but weak stems of *B. pubescens* were also taller than unbrowsed ones. Both *B. pendula* and *B. pubescens* were regularly distributed among height classes although *B. pubescens* had a slightly decreasing distribution above 180 cm (Fig. 4a and b). There was a higher proportion of browsed *B. pendula* than *B. pubescens* in stands 2 (t_6 = 3.161, p = 0.020) and 6 (t_9 = 2.392, p = 0.040). The majority of *S. aucuparia* stems were also healthy despite being repeatedly browsed in all stands (Table 3 and Fig. 4c). There was no difference in height between browsed and unbrowsed healthy *S. aucuparia* stems but weak browsed stems were taller than unbrowsed ones (Table 3). The density peak of *S. aucuparia* was in the 60 cm height class and density decreased sharply for saplings taller than 100 cm (Fig. 4c). Saplings of *Salix* spp. were the least abundant among the deciduous species and most of them were browsed but healthy (Table 3 and Fig. 4d). There was no significant difference in height between browsed and unbrowsed stems (Table 3).

Discussion

Judging by the number of bites per sapling, the favourite browse of moose in the Evo state forest were *P. tremula*, *S. aucuparia*, and *Salix* spp., and to a lesser extent, *B. pendula* and *B. pubescens*, which is consistent with other studies (Shipley *et al.* 1998, Hörnberg 2001, Månsson *et al.* 2007). *Betula* spp. sustained a high total number of bites, but because they were more abundant than other species, they had fewer bites

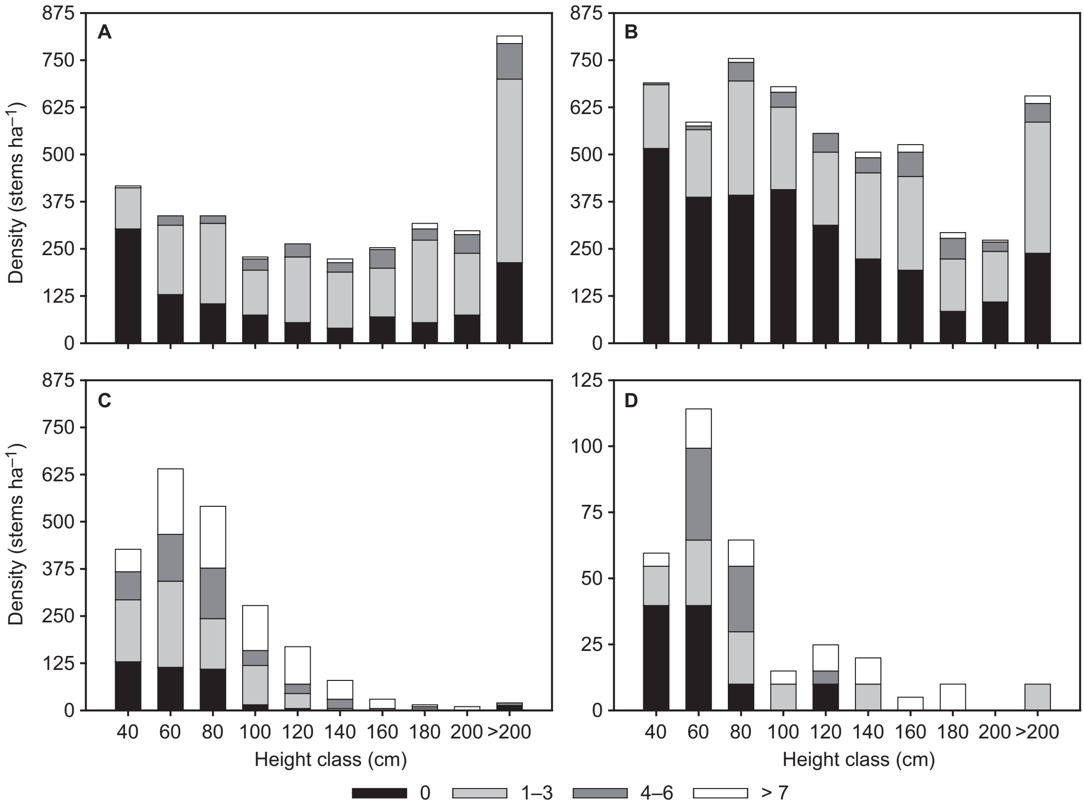

Fig. 4. Average abundance of living (**A**) *Betula pendula*, (**B**) *Betula pubescens*, (**C**) *Sorbus aucuparia*, and (**D**) *Salix* spp. regeneration in the various bite classes across height classes. Note the difference in *y*-axis scale.

per sapling. Repeated browsing may restrict the recruitment of mature stems of favourite browse species in the landscape (Angelstam *et al*. 2000, Ericsson *et al*. 2001) and intensive browsing may even change the course of forest succession and stand composition (Connor *et al*. 2000). Moose population densities larger than 3 individuals per 1000 ha will suppress the growth of favorite browse species and may even eliminate them from the landscape (Connor *et al*. 2000, Abaturov & Smirnov 2002). Because the moose population density in Evo state forest ranged from 3.6 to 10.9 moose per 1000 ha since year 2000, the prognostic for the successful recruitment of mature stems of *P. tremula*, *Salix* spp., and *S. aucuparia*, in particular, in the landscape is poor. In comparison, the average moose population density for southern Finland, including the Häme province where the Evo state forest is located, was 3.1–4.0 individuals per 1000 ha in 2005 (Ruusila *et al*. 2006).

According to Mueggler (1989), mature or overmature stands of *Populus tremuloides* with more than 1000 ramets/acre (> 2471 ramets ha^{-1}) have the potential to replace themselves successfully, while mature or overmature stands with less than 500 ramets/acre (< 1236 ramets ha^{-1}) may have regeneration problems. Similar requirements probably apply to pure *P. tremula* stands as well. Technically, many of our stands met those requirements although they were not pure *P. tremula* stands. However, due to browsing pressure, most of the stems were in the smaller height classes and no *P. tremula* stem taller than 2 m was found. The lack of stems taller than 2 m may also be due to self-thinning or to the young age of the stands. The critical height for *P. tremula* seedlings to be out of reach of moose has been reported to be 2.4–3 meters (Peterson & Peterson 1992, Ericsson *et al*. 2001). Due to recurrent browsing, saplings may linger in small height classes, which may delay the recruitment of large *P. tremula* trees in the landscape. Nevertheless, Zakrisson *et al*. (2007) found no delay in recruitment or increased mortality of *P. tremula* ramets due to browsing in an area with a moose density of 8.5 individual per 1000 ha. Instead, they observed that high initial ramet density and stand characteristics, such as genetics, disturbance, and soil fertility, were important determinants of suckering ability and high recruitment (Zakrisson *et al* 2007).

The decreased abundance and increased proportion of heavily browsed *P. tremula* saplings in height classes over 100 cm agree with the findings of Edenius and Ericsson (2007), who reported a negative relationship between the abundance of aspen ramets in the 1–1.5 m and 1.5–3 m height classes and use by moose in Sweden. In Russia, *P. tremula* rarely reached a height greater than 1 m where moose populations were at least 4 individuals per 1000 ha (Abaturov & Smirnov 2002). Most likely, taller *P. tremula* saplings in the Evo state forest were more visible or within easier reach of moose and therefore more browsed. The same could be true for *S. aucuparia*, *Salix* spp. and *B. pubescens*. Ericsson *et al*. (2001) reported that moose was more attracted to *P. tremula* ramets in young forests than in mature or interior forests, and that they were more likely to utilise stands with a high density of ramets. However, they reported that the risk of an individual ramet to be browsed increased with a decreasing density of ramets in a stand, which was not observed in the Evo state forest. In fact, browsing was more frequent and the number of bites per sapling increased in stands with greater abundances of *P. tremula*.

A few studies have reported that moose prefers *B. pendula* over *B. pubescens* (Danell *et al*. 1985, Danell & Ericson 1986, Shipley *et al*. 1998), especially stems 1.5–3.0 m tall. On the other hand, other studies have found no difference between *Betula* spp. (Löyttyniemi & Piisilä 1983). Although we observed a higher proportion of browsed *B. pendula* as compared with *B. pubescens* in two stands, the results are not conclusive.

The current study was made in a relatively small (8000 ha), forested area which functions as a moose winter-foraging area. Therefore, wider generalizations cannot be done since browsing pressure varies considerably depending on landscape structure and human influence (Edenius & Ericsson 2007). The study also focused on regeneration stands with a minimum amount of 500 deciduous saplings per hectare, so it is possible that areas with lower densities of saplings are browsed differently. However, most of the current old-growth forest reserves hosting aspen-dependent species in Finland are located in large forest areas similar to our study area. Since young managed forests near current old-growth forest reserves with large *P. tremula* stems are considered important to the success of *P. tremula* regeneration (Kouki *et al*. 2004, Latva-Karjanmaa *et al*. 2007), our results bring meaningful insights on the recruitment of *P. tremula* and other broadleaf species that are favourite moose browse.

It is unclear whether the current recruitment of *P. tremula* in the Evo state forest can ensure the future survival of aspen-dwelling species depending on the old, gradually declining large *P. tremula* trees in the old-growth forest reserves in the Evo state forest. Since the bottleneck in recruitment of *P. tremula* and other deciduous species in areas with high moose population densities is caused by browsing, silvicultural guidelines and treatments that are favourable to *P. tremula* and other deciduous species may not be sufficient to ensure the successful establishment of cohorts that are capable of growing over the browsing threshold height. Therefore, in order to ensure successful recruitment of *P. tremula* and deciduous species in the landscape, a reduction of browsing pressure should be combined with activities that promote seedling or ramet establishment (Edenius & Ericsson 2007, Zakrisson *et al*. 2007). Although it seems that the current browsing pressure may cause a growth delay, it is probable that some stems can grow beyond the browsing limit. Nevertheless it is unknown how browsed *P. tremula* and deciduous stems will develop in the future and whether currently browsed stems have the capability of growing into biodiversity-supporting large trees.

Conclusion

Due to the high moose population density in Evo state forest, the successful establishment of mature stems of *P. tremula*, *Salix* spp., and *S. aucuparia* in the landscape is affected by browsing. Mainly due to browsing pressure, most of the *P. tremula* stems were shorter than 1 m, and no stem taller than 2 m was found, which may delay the recruitment of large *P. tremula* trees in the landscape. Consequently, the quality of nature conservation areas for aspen-dependent species will gradually weaken. The abundance of *Salix* spp. and *S. aucuparia* taller than 1 m was also low. The situation of *Betula* spp. was less problematic, being more abundant than the other species studied.

Acknowledgements

Special thanks to Reetta Ahola, Riikka Fennander, Merina Lehtiö, and Asta Vaso for help with the field work, to Timo Hokka and Esa Lientola for drawing the map, to the Evo Forestry Unit of the HAMK University of Applied Sciences and the Finnish Forest and Park Service for allowing us to use their stands, and to the hunting clubs for providing data on the moose populations. The study was financed by The Finnish Ministry of Environment.

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