DOES MOOSE BROWSING THREATEN EUROPEAN ASPEN REGENERATION IN KOLI NATIONAL PARK, FINLAND?

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ABSTRACT: Large European aspen (*Populus tremula*) trees host hundreds of species of which many are threatened species of conifer-dominated, old-growth boreal forests. Aspen is also one of the deciduous tree species most intensively used by moose (*Alces alces*) in Finland. In conservation areas aspen regeneration is facilitated by large-scale disturbances, especially fires and windstorms, and also by mortality of individual trees and small-scale disturbances that create small openings. These aggregated patches of young aspens provide high quality feeding sites for moose. In Finland, it has been hypothesized that intense browsing pressure by moose on aspen may prevent new aspen cohorts from emerging, and thus endanger the spatio-temporal continuum of aspen occurrence in the long term. The aim of this study was to analyze the influence of moose browsing on the regeneration of aspen in Koli National Park in eastern Finland at 2 different spatial scales, the landscape level and stand level. Our results indicated that moose browsing on aspen has been very intense in the area. At the landscape level, moose damaged (twig-browsing, stem breakage, or bark stripping) 96% of aspens in the southern area and 62% in the northern area of the Park. In addition, 23% of the damaged aspens (all <5 m) were dead in the southern area. According to counts of fecal pellet groups, moose activity was higher in the southern area than the northern area. At the stand level, on average, 79% of the aspens in the southern area and 73% in the northern area were damaged. The proportion of dead aspens (35%) was highest in stands in height category of 5-15 m. Aspen density declined from young to old stands in both areas. Bark stripping was relatively common in the height category of 5-15 m over the whole area. We concluded that the current browsing pressure retards the height development of young aspens because of the repeated break-off of main stems and leader shoots. Although occurrence of aspen may decline due to high browsing pressure by moose, the majority of aspens have excellent tolerance to heavy and repeated browsing. Hence, a high proportion of aspens may reach maturity, and thus maintain the spatio-temporal continuum of aspen occurrence at a level that contributes to its role in community dynamics and local and regional biodiversity.

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Browsing by cervids on tree seedlings and saplings has been regarded as a pivotal issue affecting the success of forest regeneration in managed commercial forests and in nature conservation areas across Europe (e.g., Gill 1992, Angelstam et al. 2000, Heikkilä et al. 2003, Edenius and Ericsson 2007) and in Northern America (e.g., Baker et al. 1997, Kay 1997, Rooney and Waller 2003, McLaren et al. 2004). In Finland, moose (*Alces alces*) density has increased continuously over the last few decades (Finnish Forest Research Institute 2006), which has led to intense public debate on the need to search for balance between moose and forest management, as well as nature conservation.

Large European aspen (*Populus tremula*) trees (i.e., living and decaying dead aspens) host hundreds of herbivorous and saproxylic invertebrates, polypore fungi, and epiphytic lichens of which many are threatened species of conifer-dominated, old-growth boreal forests (Kouki et al. 2004). It has been estimated that there are at least 150 specialist species that are entirely dependent on aspen in Fennoscandia (Siitonen 1999, Kouki et al. 2004). Aspen is also one of the deciduous tree species most intensively used by large herbivores, and ranks among the highly preferred woody plants in the diet of moose (Bergström and Hjeljord 1987). Due to increasing awareness about explicit ecological values of aspen on forest biodiversity, aspen is receiving more consideration in management planning of commercial forests, specifically in the restoration planning of formerly managed forests within conservation areas.

It has been estimated that only 0.3% of the forest land in Finland is covered by aspen-dominated stands (Finnish Forest Research Institute 2006). However, young mixed species stands with aspen trees are relatively common, whereas densities of large aspens are very low in older forests. According to the National Forest Inventory (NFI) of Finland, there are only 0.35 aspens/ha with diameter at breast height ≥30 cm (Finnish Forest Research Institute 2006). Aspen can regenerate sexually by seed and asexually by root suckers. However, in the Finnish landscape asexual type of reproduction is more common and in most regeneration sites practically all seedlings originate from root suckers (Tikka 1955).

Some disturbance is needed to start aspen regeneration. In natural forests, aspen regeneration is facilitated by large-scale disturbances, especially fires and windstorms, but also by the death of individual trees and small-scale disturbances that create small openings (Syrjänen et al. 1994, Cumming et al. 2000). These aggregated patches of young aspens provide high quality feeding sites for moose. In Finland, it has been hypothesized that intense browsing pressure by moose on preferred aspens may prevent new aspen cohorts from emerging (Kouki et al. 2004), thus, endangering the spatio-temporal continuum of aspen occurrence. Even in conservation areas this may result in a situation where aspen-associated species may disappear both locally and regionally.

The aim of this study was to analyze the influence of moose browsing on the regeneration of aspen in a conservation area. Specifically, we assessed past and present moose browsing pressure on aspen at the landscape and stand levels within Koli National Park in eastern Finland. The results are related to the regeneration success of aspen in forests under high browsing pressure by moose.

STUDY AREA

The study occurred in the Koli National Park in eastern Finland (Fig. 1). The central hill sites of Koli became state-owned in 1907, and from 1924-2007 the area was administered by the Finnish Forest Research Institute. Koli National Park was established by law in 1991 and covered a total area of 1,135 ha; it has since been enlarged to about 3,000 ha. As of 2008, the Finnish Forest and Park Service is responsible for administration of Koli National Park. The purpose of conserving the area by law was to ensure the preservation of Koli's heritage landscape and the old-growth forests of the Koli highlands, as well as maintain the plant communities created in the past by swidden cultivation (i.e., clearing of land for cultivation by slashing and burning the forest vegetation cover). Other aims were the promotion of environmental research, education, and nature recreation in the area.

The park area is characterized by a highly variable landscape and topography where the altitude varies from 95-347 m above sea level. The soils are fertile, especially at lower altitudes, because the crumbling substance originating from the calciferous bedrock (diabase-rich or siliceous rocks, i.e., granite-gneisses and quartzites; Piirainen *et al.* 1974)

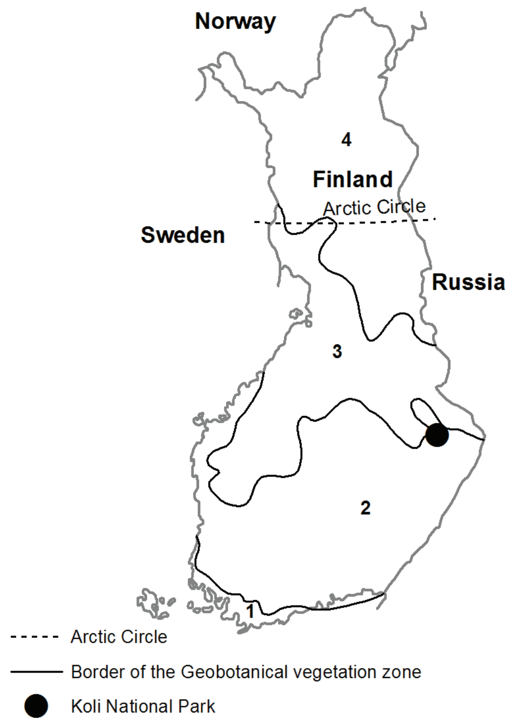

Fig. 1. Location of the Koli National Park in eastern Finland. Forest vegetation zones after Kalela (1970 in Kalliola 1973): South Finland (1= hemiboreal and 2 = southern boreal), Pohjanmaa-Kainuu (3 = middle boreal), and Peräpohjola and Metsä-Lappi (4 = northern boreal).

flow downhill with rainwater and streams of melting snow.

The study area belongs to the border area between the southern and middle boreal forest vegetation zone (see Kalliola 1973) (Fig. 1). The dominant tree species are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Other tree species such as birches (*Betula pendula* and *B. pubescens*), aspen, rowan (*Sorbus aucuparia*), and alder (*Alnus incana*) occur patchily within the area. The forests outside the Park are intensively managed and fragmented by lakes, mires, cultivated land, and small villages.

Hunting of moose is strictly prohibited in Koli National Park. The Northern Karelia Game Management District estimated the density of moose outside the Park, after the hunting season, as 0.3-0.6 moose/km^2 in 2002-2006. Local hunters estimated by snow tracking that there were about 0.75 moose/km^2 within the Park in November 2006, and that this density remained about the same in 2002-2006. Moose density increases in the Park during hunting season (starting the last Saturday of September), when they escape hunting pressure from adjacent private forestland, until spring when they disperse back to their traditional summer range.

METHODS

Moose browsing on aspen was investigated in summer 2006 at 2 spatial scales, the landscape level and the stand level. The Park was divided into northern (NO) and southern (SO) areas at both scales. This was reasonable because the NO area was characterized by representative old-growth forests close to the natural stage, whereas, in the SO area signs of forestry practices were still clearly visible both in the landscape and forest age structure. At the landscape level, data were collected from systematically located circular sample plots; 132 plots were located in the NO area and 141 plots in the SO area. The plot size was 113 m^2, and plots were placed on a systematic 300 m X 300 m grid. In addition, the stand development class was determined at each plot. Aspens were also pooled into three height categories (I: <5 m, II: 5-15 m, and III: >15 m).

At the stand level, all potential stands where aspen was dominant or was important in the mixture of tree species were identified from aerial photographs. When verified in the field, the stand was included in the sampling procedure, after which 5 young (<5 m in height), 5 middle-aged (5-15 m in height), and 5 old (>15 m in height) aspen-rich stands were randomly selected both in the NO and SO areas to ensure sufficient variation of stand structures in the data (Ericsson et al. 2001). Three circular plots of 113 m^2 were systematically located within each sampled stand, with the first plot placed in the center of the stand,

and the other 2 placed 20 m north, south, west, or east from the center plot depending on the shape of the stand.

The condition of each aspen was classified as undamaged or damaged, and alive or dead. Each measured aspen was investigated for signs of fresh and older moose browsing. Fresh browsing meant that browsing had occurred during winter 2005-2006, and was distinguished from older browsing by its white color at the browsing point. Moose browsing was divided into 3 damage categories: twig-browsing, stem breakage, and bark stripping. The total tree height was measured of all small aspens (i.e., height 0.5-4.0 m). For aspens taller than 4 m, the height was estimated to the nearest 0.5-m class. In order to estimate the moose activity in the area, the number of fecal pellet groups (1 group ≥20 pellets) was counted in each plot. Only pellet groups deposited during the winter of 2005-2006 (i.e., those on top of the previous year's leaf litter) were counted. All statistical analyses were performed with SPSS package. Nonparametric tests were employed because none of the variables had normal distributions.

RESULTS

Landscape level

The density of aspen was three-fold higher in the SO area (152 aspens/ha ± 47 SE) than in the NO area (48 aspens/ha ± 12 SE), but the difference was not significant (Mann-Whitney $U = 8759.5$, $P = 0.24$). The number of fecal pellet groups indicated that moose used the SO area (32 pellet group/ha ± 6 SE) more than the NO area (2 pellet groups/ha ± 1.5 SE) (Mann-Whitney $U = 7401.0$, $P = 0.000$). There was no difference in mean aspen height between the two areas (SO: 9.7 m ± 1.4 SE vs. NO: 10.0 m ± 2.4 SE, Mann-Whitney $U = 267.5$, $P = 0.36$).

Moose browsed aspens in the SO more often than in the NO area. In total, 96% of aspens were damaged in the SO area and 62% in the NO area; 23% of damaged aspens were dead in the SO area, all shorter than 5 m. Only 3% of the damaged aspens were dead in the NO area. Repeated stem breakage was very common. The mean number of stem breakages per aspen did not differ between the two areas (SO: 2.7 times/aspen ± 0.3 SE vs. NO: 2.2 times/aspen ± 0.5 SE, Mann-Whitney $U = 62.5$, $P = 0.12$).

In order to illustrate the effect of aspen height on moose browsing, a closer examination of moose browsing in three aspen height categories was performed (Fig. 2). There was a clear tendency that aspens in height categories I and II were damaged more often (twig-browsing and stem breakage) than aspens in height category III. Bark stripping was relatively common in height category II in both areas. In height category I, all aspens in the SO area had signs of old damage. The percentage of new damage showed

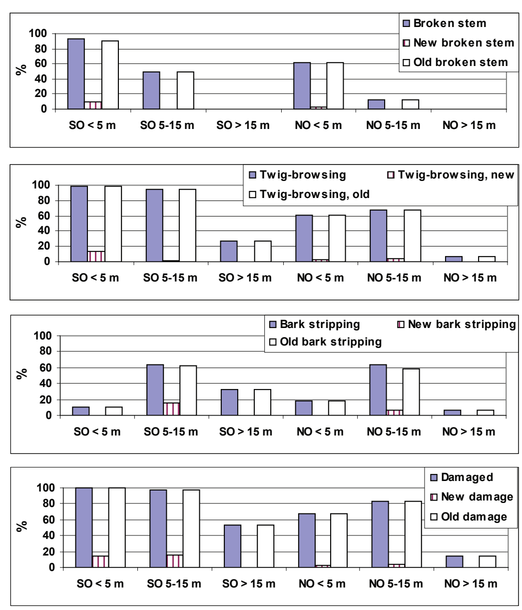

Fig. 2. Proportions of different damage types in different aspen height categories at the landscape level in Koli National Park, Finland (SO = southern area; NO = northern area). The sum of percentages of new and old damage may exceed the percentage of total damage within a height category due to repeated browsing of the same stems.

Table 1. Aspen density (trees/ha) and height (m), and number of fecal pellet groups (/ha) in young (<5 m in height), middle-aged (5-15 m in height), and old (>15 m in height) aspen-rich stands at the stand level in aspen-rich forest stands in Koli National Park, Finland. Means are given with their standard errors.

	SO <5 m	SO 5-15 m	SO >15 m	NO <5 m	NO 5-15 m	NO >15 m
Aspen density	4,458 ± 725	1,987 ± 253	383 ± 13	2,371 ± 343	2,306 ± 710	896 ± 151
Aspen height	1.4 ± 0.1	6 ± 0.6	20.1 ± 1.5	1.4 ± 0.2	4.7 ± 0.4	17.6 ± 1.8
Pellet groups	12 ± 7	-	-	-	12 ± 7	-

Note: SO = southern area of Koli National Park; NO = northern area of Koli National Park.

that re-browsing hampered young trees most. The proportion of young aspens (i.e., height category I) decreased from 45% in advanced seedling stands to 17% in mature stands indicating that regeneration of aspen, to some extent, occurs in closed older stands.

Stand level

Aspen density declined from young to old stands in both areas (Table 1). Moose seemingly used stands relatively little as the number of fecal pellet groups was very low. The mean height was similar in same aged stands in both areas (Table 1). Based on damage type, browsing pressure by moose was very similar in both areas (Fig. 3). On average, 79% of the aspens in the SO area were damaged, as compared to 73% in the NO area. The proportions of new damage showed that re-browsing occurred predominantly in young stands. The proportion of dead aspens was relatively high in middle-aged stands in the SO and NO areas (Fig. 4). The mean number of stem breakages per aspen did not differ between the two areas (SO: 2.3 times/aspen ± 0.3 SE vs. NO: 2.0 times/aspen ± 0.2 SE, Mann-Whitney $U = 48.0$, $P = 0.43$).

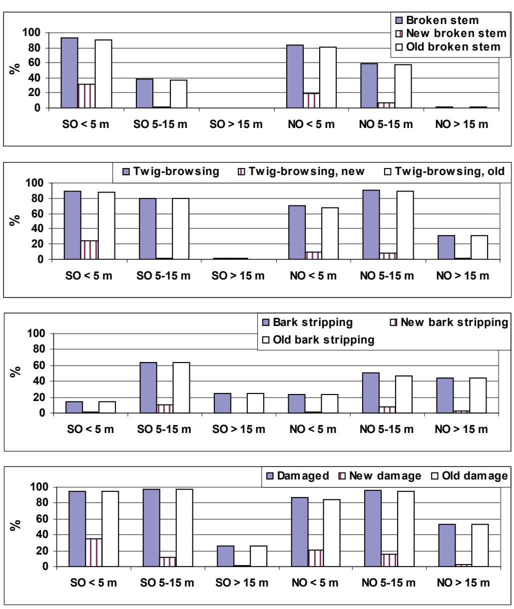

Fig. 3. Proportions of different damage types in young (<5 m in height), middle-aged (5-15 m in height), and old (>15 m in height) aspen-rich stands at the stand level in Koli National Park, Finland (SO = southern area; NO = northern area). The sum of percentages of new and old damage may exceed the percentage of total damage within a stand type due to repeated browsing of the same stems.

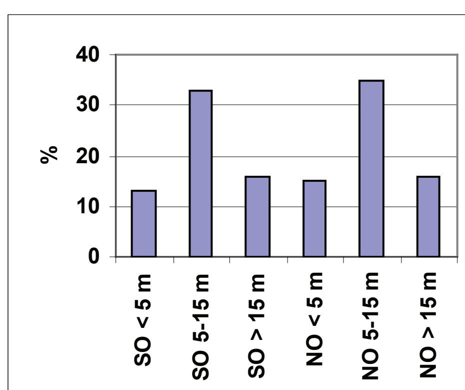

Fig. 4. Proportions of dead aspens in young (<5 m in height), middle-aged (5-15 m in height), and old (>15 m in height) aspen-rich stands at the stand level in Koli National Park, Finland (SO = southern area; NO = northern area).

DISCUSSION

Results clearly showed that the browsing pressure by moose on aspen has been very intense in Koli National Park. At the landscape level, moose had damaged (twig-browsing, stem breakage, or bark stripping) 96% of the aspens in the SO area and 62% in the NO area, and the moose damage at the stand level was 79 and 73% in the NO and SO areas, respectively. These damage levels are more than four-fold higher than frequencies observed in old-growth forests in eastern Finland. Latva-Karjanmaa et al. (2007) reported that the damage proportions at the stand level varied from 28-44% in managed forests in Finland; similarly, Härkönen (1998) found them to vary from 35-50%. The proportion of dead aspen further indicated that browsing pressure caused by moose was high. Also, at the landscape level all aspens in height category I in the SO area had signs of old browsing. Bark stripping in height category II was relatively common in the SO and NO areas indicating that relatively large aspens are also susceptible to moose damage.

At the landscape level, 23% of the damaged aspens (all in height category I) were dead in the SO area. At the stand level, the proportion (35%) of the dead aspens was highest in the middle-aged stands. These results could be explained by cumulative stem breaking and browsing which is concentrated on leader shoots and side twigs of young aspens year after year, weakening the ability of aspen to withstand sustained moose browsing.

In the case of managed forests, Edenius et al. (2002) reported that aspens growing alone are more susceptible to moose browsing than aspens aggregated within stands. Hence, a single aspen has the best chance of escaping browsing in a stand with a high aspen density (Ericsson et al. 2001). This observation corresponds to our findings because overall proportion of damaged aspens was higher at the landscape level (low aspen densities) than in the stand level (high aspen densities). Thus, moose may reinforce the spatially aggregated distribution of aspen both in managed and protected boreal forest landscapes.

That aspen density decreased from young to old stands, that low aspen density occurred in old stands at the stand level, and that low overall aspen density occurred at the landscape level were all expected results. However, the observed densities were relatively high in comparison to those found at other conservation areas in eastern Finland where aspen densities have been as low as 1 tree/hectare (Kouki et al. 2004). NFI results also indicate the relative rareness of mature aspen trees in Finnish forests (Finnish Forest Research Institute 2006). In young stands, aspen densities (2,300-4,500 trees/ha) were comparable to those in conservation areas measured by Heikkilä et al. (2003). Stand level volumes of aspen were not of primary interest in this study and they were not calculated, but it has been estimated that an average volume of 5-20 m^3/ha is typical for aspen in Norway spruce-dominated, old-growth forests in southern and middle boreal Fennoscandia (Latva-Karjanmaa et al. 2007).

Pellet group counts were used to estimate moose activity in the area. According to Neff (1968), the method can provide reliable data under most field conditions. In this study, the observed numbers of pellet groups were surprisingly low when compared to moose browsing pressure on aspens and the estimated moose density in the area, and the numbers reported from managed Scots pine-dominated forests in Finland (Heikkilä and Härkönen 1998). This may be explained by overestimation of moose density in the area or by difficulties in separating old pellet groups from new pellet groups during fieldwork (Neff 1968, Härkönen and Heikkilä 1999). However, the pellet group counts were in line with browsing intensity at the landscape level as there were more pellet groups in the SO than NO area. Also, the proportion of damaged aspens was higher in the SO area. At the stand level, the number of pellet groups was very low, whereas the browsing intensity was relatively high. This weak relationship between browsing incidence on aspen and pellet counts was also observed in Sweden (Edenius and Ericsson 2007). It is evident that Norway spruce-dominated forest sites, which are common in Koli National Park, are less favorable for moose because overall food availability is low in these closed middle-aged or older stands. In this sense, small aggregated patches of young aspens may provide so little food that moose only visit them briefly during a foraging bout.

The impact of ungulate populations on regeneration of aspen has been questioned globally, for example, in the Rocky Mountain region in western North America (Kay 1997, Suzuki et al. 1999) and in Finland (Kouki et al. 2004). However, moose or deer browsing is not the only factor behind the poor recruitment of young aspen cohorts in conservation areas. Absence of large scale disturbances (e.g., fires and windstorms) that create forest openings in conservation areas strongly hinder the possibility of successful regeneration (Latva-Karjanmaa et al. 2007) because some disturbance is needed before aspen regeneration starts from root suckers. In addition, young aspen seedlings and saplings are browsed by voles, mountain hare (*Lepus timidus*), and beavers (*Castor* spp.). The impact of these browsers on aspen mortality might have been underestimated in comparison to moose browsing.

Disease, including "black shoot blight" which is caused by a fungus (*Venturia tremulae*) and kills the leader shoot and leaves, may stunt the height development of young aspens in conservation areas (Heikkilä et al. 2003). This disease causes infected aspens to be available longer as potential forage for moose or other browsers, thereby increasing the risk that damaged aspens die due to repetitive browsing. In addition, young aspen seedlings may also die because they cannot tolerate local climate and soil conditions (Romme et al. 2005). In managed forests of Finland, aspen has been an unwanted species, especially during the 1970s and 1980s, because of its low economic value, fast early growth and high competitive ability with more valuable tree species, and its inclination to host rust disease (*Melampsora pinitorqua*) that is harmful to young Scots pine stands. For these reasons foresters have tried to control aspen with silvicultural cleanings in young stands, and by notching and girdling larger individuals in mature forests before clear-cutting. Considering these other factors in protected and managed forests, it is evident as Edenius and Ericsson (2007) have presented, that it is not possible to increase the abundance of aspen only by adjusting ungulate browsing levels. Similarly, Romme et al. (1995) concluded that low aspen regeneration cannot be explained by any single factor, but involves a complex interaction of many factors.

Aspen regeneration can be influenced by certain disturbance activities. It has been suggested that prescribed burning and man-made gaps (Latva-Karjanmaa et al. 2007) will facilitate aspen regeneration. Creating large canopy gaps in old-growth forests by killing trees around mature aspens may also promote aspen regeneration. Successful aspen regeneration can be facilitated by other human manipulations, for instance, protecting aspen recruitment physically from browsing (Angelstam et al. 2000, McLaren et al. 2004, Kaye et al. 2005, Edenius and Ericsson 2007). In managed forests, young aspens could be spared during silvicultural cleanings and thinnings, and mature aspens could be left aside as retention trees during clear-cutting.

The proportion of young aspens (<5 m in height) decreased from 45% in advanced seedling stands to 17% in mature stands. However, this clearly indicates that the regeneration of aspen is, at least to some extent, occurring in closed older stands in the study area. It can be concluded that the present browsing pressure by overabundant moose in

Koli National Park not only kills some proportion of young aspens, but also retards the height development of aspens because of the repeated break-off of main stems and leader shoots (Angelstam et al. 2000, Heikkilä et al. 2003). This is supported with the observation that where population density is >5 moose/1,000 ha, moose browsing depresses the growth of aspen (Abaturov and Smirnov 2002). At present, it seems that the major proportion of young aspens in Koli National Park can tolerate both heavy and repeated browsing without dying. However, the persistence of aspen may lead to collapse if moose density increases and stays higher than the current carrying capacity, which is an unforeseeable scenario.

The long-term existence, dynamics, and possibilities for natural regeneration of aspen in old-growth forests in Koli National Park have been determined by the compartment-wise inventory data available for the period 1910–2004 (M. Vehmas et al., University of Joensuu, unpubl. data). Their results indicated that aspen can regenerate naturally in old-growth forests and that its existence is not completely dependent on young successional stages of forests, which corresponds to the findings of this study. However, they assumed that the long-term ecological continuity may be threatened by increased population densities of large mammalian browsers such as overabundant moose. Even if their study was not focused on identifying factors related to the success of aspen regeneration, it concluded that the issue between the seemingly increasing population densities of mammalian browsers and success of aspen regeneration needs to be considered in future restoration and management measures planned for Koli National Park.

Suzuki et al. (1999) concluded that elk (*Cervus elaphus*) browsing in Rocky Mountain National Park was not causing failure of aspen regeneration at landscape scales, whereas in local areas with the highest browsing pressure from elk, little regeneration has occurred in the past 30 years. A similar observation was made by Heikkilä et al. (2003) when evaluating the effects of moose browsing on aspen in Finland, and in national parks in Newfoundland and Labrador (McLaren et al. 2004). Our study supports the conclusion that moose browsing will most likely contribute to an altered size distribution of aspen in the boreal landscape (Kay 1997, Suzuki et al. 1999, Ericsson et al. 2001). Hence, the number of aspens in Koli National Park may decrease due to the high browsing pressure by moose, but many aspens may reach maturity once having passed a risky regeneration stage. This should guarantee the spatio-temporal continuum of aspen at a level where biodiversity is maintained in the conservation area. However, aspen may not necessarily continue to exist where foresters and conservationists desire (Ericsson et al. 2001).

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