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The condition of Scots pine stands in Lahemaa National Park, Estonia 25 years after browsing by moose (*Alces alces*)

Marek Metslaid[1)]*, Timo Palli[2)], Tiit Randveer[1)], Allan Sims[1)], Kalev Jõgiste[1)] and John A. Stanturf[3]

[1)] *Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, EE-51014 Tartu, Estonia (*corresponding author's e-mail: marek.metslaid@emu.ee)*
[2)] *VMF Estonia OÜ, Ruuksu küla, Rõuge vald, EE-66280 Võrumaa, Estonia*
[3)] *Center for Forest Disturbance Science, USDA Forest Service, 320 Green Street, Athens, GA 30602, USA*

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The effects after 25 years of moose browsing on Scots pine stands in Lahemaa National Park were evaluated, emphasizing economic damage. A re-evaluation in 2001 examined stands that had been evaluated in 1975–1976. Moose damage significantly affected the tree species composition which changed over time as pine dominance increased and the number of mixed stands declined. The smaller proportion of severely damaged pine trees in more pine-dominated stands and on poor sites in the first evaluation in 1975–1976 may indicate that moose preferentially browsed the available broadleaved tree species. In 2001 there was a lower proportion of severely damaged trees overall and stands with higher density had smaller percentages of moderately and severely damaged trees. Stands on poor sites had more damaged pines than in 1975–1976, but also a greater proportion of undamaged and lightly damaged trees.

Introduction

Moose (*Alces alces*) are large ungulates distributed throughout the circumboreal forest region. In Eurasia, pine is one of the main tree species browsed by moose. Heavy browsing on young Scots pine (*Pinus sylvestris*) stands leads to production and quality losses (Vahter and Kaimre 2009). A high moose population between 1960 and 1980 in Estonia resulted in damage to commercial forest plantations by heavy browsing (Tõnisson and Randveer 2003). Similar problems with moose browsing in young Scots pine stands can be found in other European countries including Finland (Nikula *et al*. 2008), Sweden (Lavsund and Sandegren 1989, Hörnberg 2001, Ezebilo *et al*. 2012), Norway (Danielsen 2001) and Russia (Angelstam *et al*. 2000).

Even though moose can be found year-round in plantations and young stands (Heikkilä 1994), as a selective ruminant moose prefer rapidly digestible food to meet their energy needs. Summer food is particularly rich in terms of nutrients. At the end of the vegetation period (growing season) moose switch to winter food (Heikkilä 1994). Given the choice, the winter diet preferentially contains willows (*Salix* spp.), followed by aspen (*Populus tremula*) and pine (Lil-

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lenberg 1986). Rowan (*Sorbus aucuparia*) and aspen are often overbrowsed so that their height growth is inhibited, which rarely occurs for birch (*Betula* spp.; Heikkilä and Härkönen 1993).

Browsing on pine starts in October and continues during the winter; needles and branches form the bulk of the diet (Heikkilä 1999). Eating pine bark by stripping or peeling it from the stem of larger pines is connected with the season and peaks in April and May; bark damage is small during the rest of the year. Moose prefer more productive phenotypes over less productive ones (Danell *et al*. 1991). Although this selectivity is more frequently observed in drier areas than in moist habitats, moose damage on pine is more common in nutrient-rich forest-site types than in drier and less fertile site types (Heikkilä and Härkönen 1993, Härkönen 1998).

Several studies have examined how moose browsing of young Scots pine trees correlates with tree and stand characteristics (Bergqvist *et al*. 2001). Some studies have shown that variation in browsing intensity on pine does not depend on tree size or distance to forest edge, but mainly is related to differences among forest stands (Andren and Angelstam 1993). A significant correlation has been found between the proportion of young pine stands in the landscape and damaged hectares of young pine stands per moose (Hörnberg 2001). At the stand level moose exploit existing gaps and create spatial heterogeneity by browsing patchily. Variation in damage depends on the proportion of young Scots pine in stands, with damage decreasing (Lyly and Saksa 1992, Heikkilä and Härkönen 1996, Faber and Edenius 1998, Ball and Dahlgren 2002, Nikula *et al*. 2008) or increasing (Andren and Angelstam 1993) with increasing pine density. The number of planted pines and broadleaved trees overtopping the pines, and high broadleaved tree densities help to predict the probability of browsing and stem breakage by moose (Heikkilä and Härkönen 1993, Härkönen *et al*. 2008, Nikula *et al*. 2008). A high proportion of broadleaved trees, especially aspen (Heikkilä 1990) and birch (*Betula pendula* Roth.) (Heikkilä and Härkönen 1993, Jalkanen 2001) increase the risk of damage to pine trees. The distance between trees within a stand affects the foraging behaviour of moose (Edenius *et al*. 2002). At high tree densities, moose eat less from each tree and select twigs of better quality, however the browse biomass consumed per area can be higher than at low tree densities (Vivås and Sæther 1987).

Recent stem damage has been found to be positively correlated with the extent of previous stem damage (Bergqvist *et al*. 2001). The amount of damage may be higher in plantations with openings (Heikkilä 1990). Unlike spruce, which are more susceptible to stem damage, pines are more resistant to stem rot and able to recover from injuries (Vasiliauskas 2001). Pine trees usually can heal a wound if bark is removed from one-third or less of the stem circumference. The wood layer that grows over the wound remains decoupled from the wood underneath. Such a stem is seemingly healthy but has reduced commercial quality. If more than half of the stem circumference is stripped, the wound does not heal and the stem cross section becomes irregular at the damage location. Therefore, it is not possible to get high quality timber from the damaged portion of the bole (Seemen *et al*. 1994).

The aim of this study was to evaluate long-term effects of moose-damaged Scots pine stands in Lahemaa National Park using inventory data 25 years apart. A re-evaluation in 2001 examined the current situation of the stands that had been previously evaluated in 1975–1976. During the two evaluations only the characteristics that are specific for moose damage, browsed lateral branches, browsed top shoots, striped bark and stem breakage, were taken into account. We hypothesized that (1) higher stand density reduces the proportion of damaged pine trees in the stand; (2) low site quality increases the proportion of undamaged and lightly damaged pine trees and reduces the proportion of severely damaged pine trees in the stand; and (3) higher proportion of pine trees in the stand increases the proportion of undamaged and lightly damaged trees and reduces the proportion of severely damaged trees in the stand.

Material and methods

Original stand data

Moose damage was originally evaluated in an inventory in 1975–1976 conducted in eight forest districts and other forests with young Scots pine stands in the Lahemaa National Park. The Lahemaa National Park was established in 1971 with a special management regime; in certain areas forest management activities were permitted. Sanitary clear-cuts and gap or shelterwood cuttings were permitted, but almost no planting or cleaning of young stands was allowed. The original data were collected in 1085 stands with a total area of 1408.3 ha. At the time of the initial inventory, the average age of the stands was about 16 years. Because of changes in ownership and other factors, it was necessary to reduce the number of stands that were re-evaluated for this study. Stands were removed from our sample in several steps; the first step was to remove stands that were located within former collective and state farms as these are now in private ownership and are no longer accessible. In this step, we removed 218 stands with a total area of 219 ha.

The next step was to rationalize the numbering of compartments and stands that have been altered since the 1975–1976 inventory, and match them with corresponding designations used in the 2001 forest management planning system. This was accomplished by comparing the original sketches and data on the stands with current maps. Some of the original stands no longer have their original shape and size; some were divided into smaller stands or smaller stands were merged into a larger stand. If an old stand was divided into several stands, in the present study they were assessed as separate units. Alternatively, where the old stands were merged into a larger stand, we assessed the portion of the current stand that matched the old stands and noted whether the new stand covered a part or the whole of an old stand.

The first step (removing stands that were located within former collective and state farms) reduced the number to 867 stands. From these, in the second step it was possible to identify the location of 492 stands with the total area of 664 ha. From the 492 stands, 180 were located outside the current forest district boundaries or we were unable to determine the exact locations of the stands. As a result, we were left with 313 stands with a total area of 440.2 ha, and those were used in the current study.

In addition to ensuring that stands inventoried in 1975–1976 could be matched with the stands in the 2001 inventory of the Loobu forest district, which was one of the forest districts within the Lahemaa National Park territory, it was necessary to make sure that the current stands were those evaluated for moose damage in 1975–1976 and had not been harvested or otherwise altered. We obtained stand-level data for 313 stands. Stands currently younger than 28 years were considered unsuitable for field assessment because they were most probably not established during 1975–1976 (the youngest stands in the older inventory were 3 years old). Also excluded were the data from stands older than 65 years (because the oldest stands in the original inventory were 38 years old). In addition, stands where the current proportion of pine was less than 30% were removed. The remaining 280 stands were divided into groups according to the level of moose damage in the 1975–1976 inventory; in order to ensure randomness, every third stand was chosen for evaluation of the current condition. Altogether 108 stands with a total area of 96.1 ha were evaluated and the distributions of their mean diameter, height and age in 2001 were calculated (Table 1).

Fieldwork

In 1975–1976 strip sample plots with a width of 2.5–3 meters were used. In sample plots, which covered 5%–12% of the surface area of the stands, all pine trees were counted and the damage was classified as follows: (1) undamaged and light damage: tree top and bark intact, lateral branches browsed less than 25%; (2) moderate damage: tree top intact or browsed once on

Table 1. Distribution of mean diameter, mean height and age in 2001.

Quantiles (%)	Diameter	Height	Age
0	7.0	7.4	30
25	12.9	12.6	40
50	16.1	15.4	44
70	18.3	17.7	47
100	23.3	24.8	65

trees younger than 10 years, lateral branches browsed 25%–75%, stem bark stripped (peeled) up to 1/2 of the tree circumference; (3) severe damage: tree top broken or browsed repeatedly, lateral branches browsed 75%–100%, stem bark stripped (peeled) more than 1/2 of the tree circumference. The damage to other tree species was assessed using the following scale: undamaged, lightly damaged (lateral branches browsed on less than 50% of natural regeneration), and severely damaged (in addition to side branches top branches were browsed on more than 50% of natural regeneration).

Average height, tree species composition and stand density of young pine stands was evaluated based on undamaged, lightly damaged and moderately damaged trees. Severely damaged trees were not taken into account.

In 2001 the selected stands were plotted on current maps taken from the forest management plans of the Loobu forest district. In each, strip sample plots with a width of 4 or 6 meters, depending on the width of the stand, were laid out systematically in the field. A minimum of two strip sample plots were placed in each stand to sample all the variation within the stand (e.g., edges and interior). Size and shape of the stand was the main criteria for the number of sample plots and distance between sample plots; larger stands required more plots with greater distance between strips. These strip sample plots covered from 2.7% to 24% (mean = 13.4%) of the stand surface area.

In each sample plot, diameters of all pine trees were measured using a Haglöf caliper and the height of every seventh tree measured with a Suunto height meter PM-5. In addition, the condition of all pine trees was assessed. Tree species composition and the stand site index class were taken from the forest management plans of the Loobu forest district.

Damage classes

Pine tree condition was evaluated from the ground up to 3 meters on the stem, which is the range where moose damage is likely to occur. During the evaluation only the characteristics that are specific for moose damage, browsed lateral branches, browsed top shoots, stripped bark and stem breakage, were taken into account. Other signs of damage and damage that occured higher than 3 meters were not considered; these trees were considered as undamaged and lightly damaged trees. Standing dead trees or trees with severe damage from other causes than moose, such that the tree most likely will die and be removed during the next entry into the stand, were not considered.

Damage classes were compiled according to currently valid roundwood quality requirements. Since the trees growing on less productive sites can usually provide small dimension logs, all the trees were considered suitable for sawn timber production. Damages were classified as follows:

1. Undamaged and lightly damaged trees (class BC): stems are allowed to have a closed wound with a length that does not exceed twice the diameter of the top of the bole; simple crookedness up to 1 cm per 1 m. Dead second top with a diameter up to 60 mm, creating a wound scar that slopes to the wood at less than 90 degrees.
2. Moderately damaged (class D): stems are allowed to have an open wound, steep and simple crookedness of the stem. Simple crookedness up to 2 cm per 1 m. Dead second top with a diameter up to 100 mm reaching undamaged wood at an acute angle.
3. Severely damaged (class Paper): all stems that do not fit into the previous classes, but have moose damage characteristics. A crooked log must fit through a cylinder with a diameter of 70 cm.

Data analysis

Dependent variables were the proportion of undamaged and lightly damaged, severely damaged and moderately damaged trees in 1975–1976 and 2001. Independent variables were proportion of pine, stand density in 2001, site index class, stand mean diameter and height; the proportions of undamaged and lightly damaged, severely damaged and moderately damaged trees in 1975–1976 were treated as independent variables in analyzing the damage in 2001. Site index

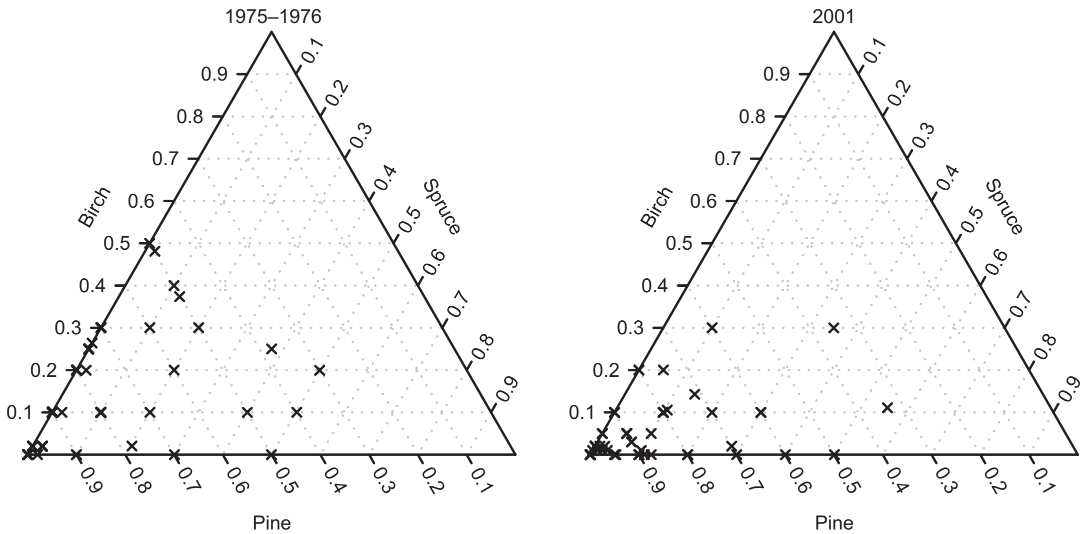

Fig. 1. Tree species composition in the stands in 1975–1976 and in 2001. The scale on each axis shows the proportion of each species.

is the expected stand mean height of Scots pine at age of 100 years. In 1975–1976 it was common to use site index class instead of site index; therefore, for comparability we converted the 2001 site index to classes (Table 2). The higher the site index class number, the lower the site quality.

Data were analysed using both non-parametric and parametric approaches using the statistical software R (2.15.2) with functions *lm* and *gam* [in packages *mgcv* (ver. 1.7-24)]. Lm is a function for linear regression and gam is a function for a generalized additive model. For analysis of variance we used the R function *anova.lm*. Normality of the distribution of each dependent variable was verified with Shapiro-Wilk's test and the appropriate analytical procedure chosen. If the distribution was not normal, a non-parametric approach was used. In all analyses differences at the $p < 0.05$ were considered statistically significant.

Results

Tree species composition in the stands in 1975–1976 and in 2001 was determined (Fig. 1) in terms of the proportion of Scots pine, Norway spruce, and birch. Initially (1975–1976) there were more mixed stands than in 2001 and the number of pine-dominated stands increased. The proportion of stands with more than 90% pine increased from 56% in 1975–1976 to 66% in 2001. There were more birch and spruce in stands in the initial inventory (1975–1976) and some stands retained spruce in 2001.

The proportion of pine in the studied stands increased over time (Fig. 2).

The relationship among site index class, proportion of pine trees within a stand, and proportion of severely damaged trees in 1975–1976 was identified (Fig. 3) by *F*-test in ANOVA with linear regression. Both site index class and proportion of pine trees within stand were significant ($F = 4.02$, $p = 0.0096$ and $F = 13.95$, $p = 0.0003$, respectively). The amount of severely damaged trees was smaller when the proportion of pine trees in a stand was high, and stands on poor sites (site index classes 4 and 5) had fewer

Table 2. Correspondence between site index classes and site index ranges.

Site index class	Site index range
1A	> 31.49
1	27.50–31.49
2	23.50–27.49
3	19.50–23.49
4	15.50–19.49
5	11.50–15.49
5A	< 11.49

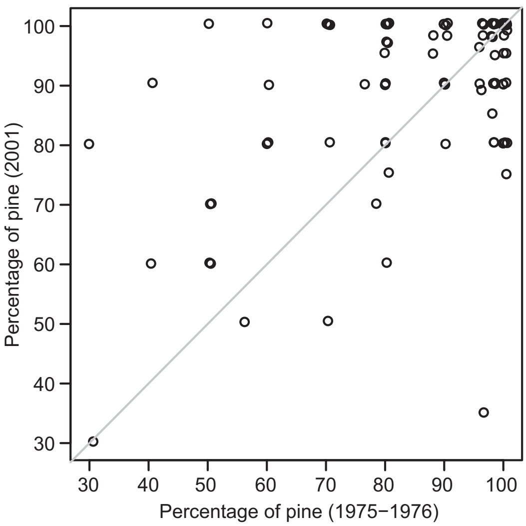

Fig. 2. Proportion of pine in stands in 1975–1976 *vs.* 2001. Each circle in the figure represents a stand. The diagonal line indicates no change in the pine dominance between the two periods. Stands where the dominance of pine increased and decreased are above and below the diagonal the diagonal, respectively.

severely damaged trees. Similarly the amount of undamaged and lightly damaged trees was greater when there was a greater proportion of pine trees in the stands and in stands on poor sites (Fig. 3; both site index class and proportion of pine trees within a stand were significant; $F = 2.75$, $p = 0.046$ and $F = 13.48$, $p = 0.0004$, respectively).

The relationship among site index class, proportion of pine trees within a stand and proportion of severely damaged trees in 2001 was different than in the previous measurement (Fig. 4). There appeared to be more severely damaged trees when the proportion of pine trees in the stand was high, and stands with lower site index class had more severely damaged trees. Although these trends appear to be the opposite to the results from the 1975–1976 inventory, the trends are not significant. The relationships among site index class, proportion of pine trees within stand and proportion of undamaged and lightly damaged trees in 2001 are also somewhat different when compared with those from the first evaluation in 1975–1976 (Fig. 4); however, the trends are not significant. At lower proportions of pine in a stand, there were fewer undamaged and lightly damaged trees. Stands on poor sites had fewer undamaged and lightly damaged trees.

In spite of large variability, there was a positive and significant (F-test in ANOVA: $F = 3.96$,

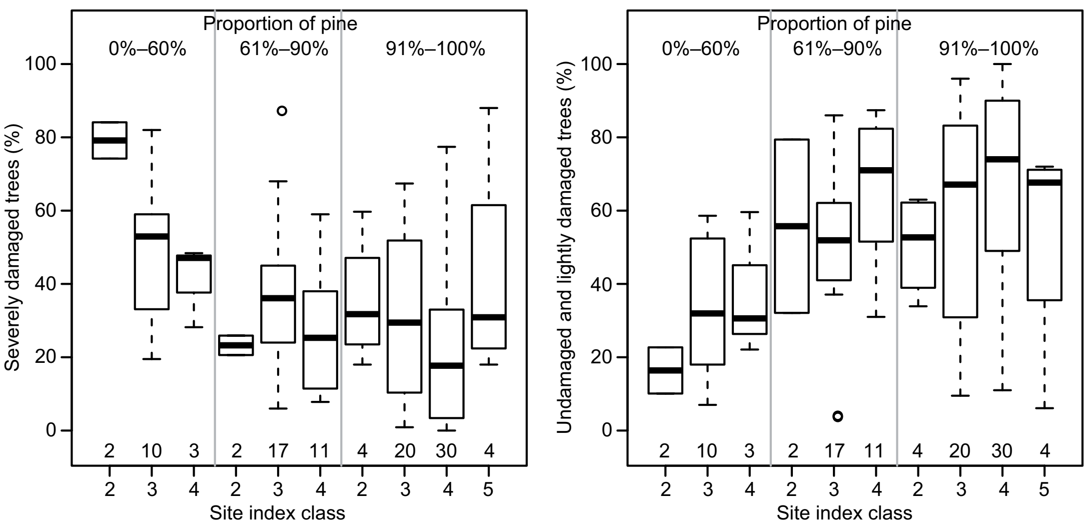

Fig. 3. Proportion of severely damaged, and undamaged and lightly damaged trees in 1975–1976 depending on site index class and proportion of pine trees within a stand. Below the figure is the number of stands in each site index class (the higher the site index-class number the poorer the site conditions). The box shows the first and third quartiles and the line inside the box indicates the median value. Whiskers show minimum and maximum values without outliers, circles are outliers. Outliers are observations which are away from the box more than 1.5 times of the box size.

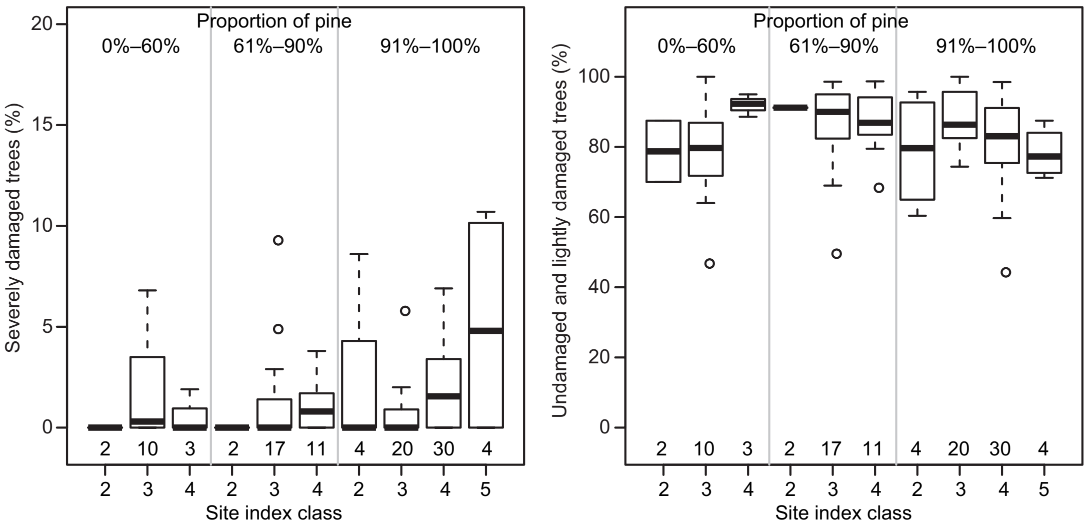

Fig. 4. Proportion of severely damaged, and undamaged and lightly damaged trees in 2001 depending on site index class and proportion of pine trees in the stand. The box shows the first and third quartiles and the line inside the box indicates the median value. Whiskers show minimum and maximum values without outliers, circles are outliers. Outliers are observations which are away from the box more than 1.5 times of the box size.

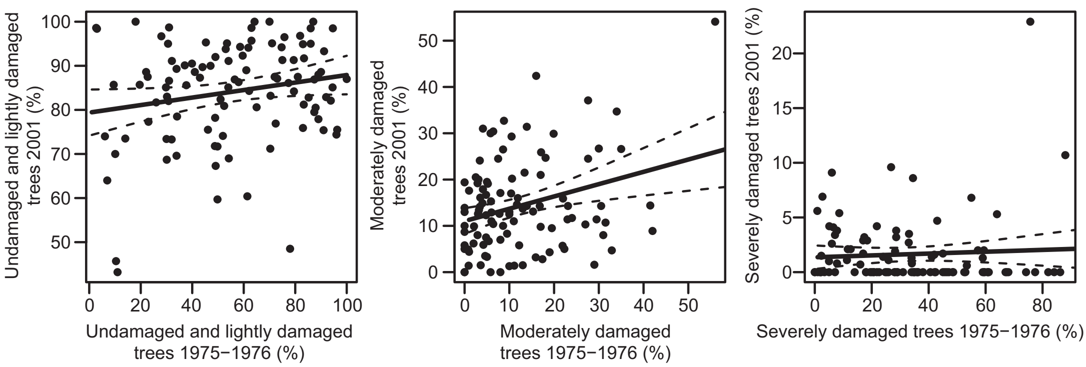

Fig. 5. The relationship between the proportion of damage classes in 1975–1976 and in 2001. The relationships were significant for the undamaged and lightly damaged and the moderately damaged classes. The solid lines are the regressions while the dashed lines are 95% confidence limits.

$p = 0.049$) relationship between the proportion of undamaged and lightly damaged trees both in 1975–1976 and in 2001 (Fig. 5). The relationship between the proportion of moderately damaged trees was also positive and significant in both periods (F-test in ANOVA: $F = 9.51$, $p = 0.003$; Fig. 5). However, the relationship between the proportion of severely damaged trees was neither significant in 1975–1976 nor in 2001 (F-test in ANOVA: $F = 0.37$, $p = 0.543$; Fig. 5). In this analysis, stand density in 2001 also was included as a variable and the results showed that the higher the stand density the smaller the percentage of moderately damaged trees in 2001.

The relationship between stand density in 2001 and the proportion of severely and moderately damaged pine trees in 2001 indicates that stands with higher density had smaller percentages of moderately damaged trees (F-test in ANOVA: $F = 6.39$, $p = 0.013$; Fig. 6).

Discussion

The results of our study showed that there was a shift between the studied periods from somewhat mixed stands towards more pine-dominated stands. The smaller proportion of severely dam-

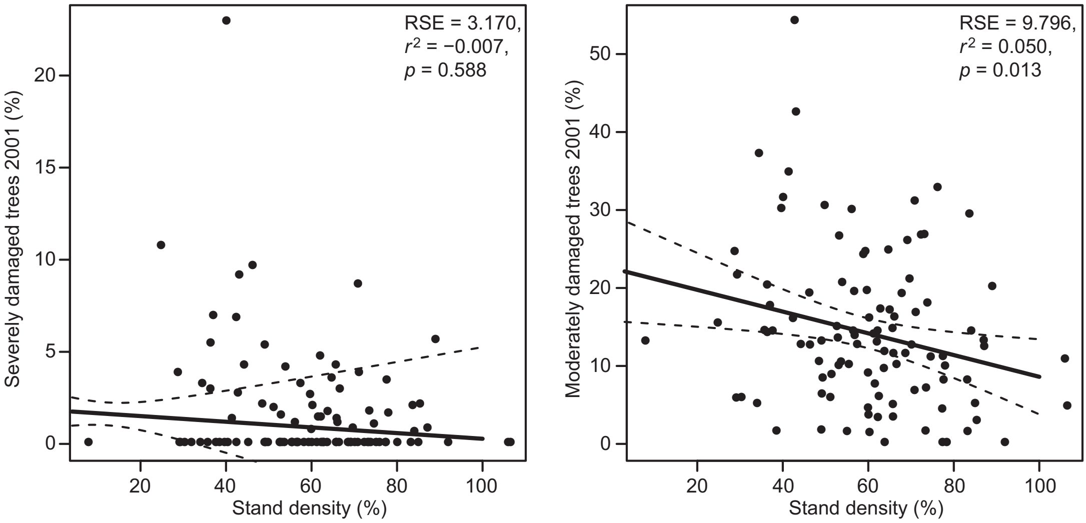

Fig. 6. The relationship between stand density in 2001 and the proportion of severely damaged and moderately damaged trees in 2001. The solid lines are regressions while the dashed lines are 95% confidence limits. RSE is the relative standard error.

aged pine trees in pine-dominated stands and on poor sites in the first evaluation in 1975–1976 may indicate that moose preferentially browsed the available broadleaved tree species. This finding is in agreement with the results reported in several studies (e.g. Andren and Angelstam 1993, Heikkilä and Härkönen 1993, Faber and Edenius 1998, Bergqvist *et al*. 2001). On poor site types, the damage to pine was generally lower and probably the available broadleaved trees more heavily browsed. The higher proportion of undamaged and lightly damaged trees in pine-dominated stands and on poor sites tends to confirm this finding.

The results from the re-evaluation in 2001 were somewhat different and stands on poor site types had more severely damaged pines, but at the same time in stands with a low proportion of pine (< 61%) on poor sites, there were more undamaged and lightly damaged trees. Otherwise the trends for undamaged and lightly damaged trees were similar to those from the first evaluation where a higher proportion of least damaged trees was found in pine-dominated stands and on medium-fertility site types. This pattern may indicate that the damage to pine increased as the availability of broadleaved trees decreased. Heikkilä and Härkönen (1993) found that on fertile sites moose consumed more deciduous trees because of their higher availability. Pines growing on poor sites suffer more from moose damage, partly because pines are better able to compete with spruce on poor sites and consequently there are more pines to browse. Additionally, pines on poor sites are probably less able to recover from damage than pines on fertile sites (Danell *et al*. 1991), which may explain the trend in 2001. Moose prefer fertile sites for browsing and pines on those sites are better able to survive heavy browsing than pines on poor sites (Ball and Dahlgren 2002).

The amount of planted pines (regeneration density) and broadleaved trees overtopping the pines are usually the main factors increasing the damage probability by moose (Nikula *et al*. 2008). There is a significant correlation between the proportions of young pine stands (availability of pine) and amount of damaged young pine stands (Hörnberg 2001, Månsson 2009). Positive correlation has been found between the damage to pine trees and the proportion of deciduous trees (Heikkilä 1990, Andren and Angelstam 1993, Heikkilä and Härkönen 1993, Härkönen *et al*. 2008, Nikula *et al*. 2008). In contrast, in some other studies no significant relationship between the density of different deciduous tree species and moose damage on pine was found (Härkönen 1998, Ball and Dahlgren 2002, Bergqvist *et al*. 2012). A high proportion of aspen increases the risk of damage (Heikkilä 1990, Jalkanen 2001).

Heikkilä and Härkönen (1993) reported that pine stem breakages were most numerous at high birch densities where birch occurred as overgrowth above pines. Similarly, Härkönen *et al.* (2008) found that the amount of damage on pines increased in the areas with a higher number and taller broadleaved trees. In forest management, height and density of deciduous trees around pines should be considered when planning cleaning activities (Härkönen 1998, Nikula *et al.* 2008, Bergqvist *et al.* 2012).

In the present study, the proportion of low quality saw logs and pulpwood decreased with higher stand density in 2001. Andren and Angelstam (1993) reported a decrease in damage with increased pine density. In several other studies, the proportion of damaged trees increased when the stand density increased (Lyly and Saksa 1992, Heikkilä and Härkönen 1996, Faber and Edenius 1998, Ball and Dahlgren 2002, Nikula *et al.* 2008), but at the same time also the number of saplings that escape damage may increase (Lyly and Saksa 1992). Furthermore, the amount of damage per tree is lower in dense stands (Ball and Dahlgren 2002, Nikula *et al.* 2008). It has been suggested that the regeneration density of pines should be increased up to 4000–5000 trees ha^{-1} (Lyly and Saksa 1992, Ball and Dahlgren 2002) from the present recommendation of 2000–2500 trees ha^{-1} to ensure that the proportion of undamaged and lightly damaged trees is sufficient from the silvicultural point of view (Nikula *et al.* 2008).

In conclusion, moose damage had a significant effect on tree species composition in the stands as the proportion of birch and spruce in many stands declined over time, and there were overall fewer mixed stands in 2001 than in 1975–1976. Initially the proportion of pine trees within a stand and site index class had a significant effect on the proportion of undamaged and lightly damaged as well as severely damaged trees. In young stands there was a smaller proportion of severely damaged pine trees and a higher proportion of undamaged and lightly damaged trees in more pine dominated stands and on poor site types. Subsequently in the re-evaluation (middle-aged stands) there was a lower proportion of severely damaged trees overall; there did appear to be a higher proportion of severely damaged trees and a higher proportion of undamaged and lightly damaged trees in pine-dominated stands and on poor site types but these trends were not significant. Stands with higher density had smaller percentages of moderately and severely damaged trees.

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