Modelling the Factors Predisposing Scots Pine to Moose Damage in Artificially Regenerated Sapling Stands in Finnish Lapland

Ari Nikula, Ville Hallikainen, Risto Jalkanen, Mikko Hyppönen and Kari Mäkitalo

Nikula, A., Hallikainen, V., Jalkanen, R., Hyppönen, M. & Mäkitalo, K. 2008. Modelling the factors predisposing Scots pine to moose damage in artificially regenerated sapling stands in Finnish Lapland. Silva Fennica 42(4): 587–603.

Moose (*Alces alces*) damage in forest plantations have been at a high level in Finland in recent decades. Nowadays, moose is the most severe pest in Scots pine plantations also in Finnish Lapland. So far, despite the high level of damage and different bio-geographical conditions in Northern Finland, most of the moose-damage research has been carried out in Southern Finland. A number of research have also been performed to analyse factors affecting browsing but predictive models are rare. Data from 123 randomly selected and artificially regenerated pine plantations in Northern Finland were used in modelling the risk of moose browsing. The stands had been regenerated during 1984–1995. A total of 508 sample plots (range 2–8 plots per stand) were measured. Hierarchical logistic regression models with a random factor were constructed to predict the probability of leader-shoot browsing of pine on a plot. The number of planted pines and deciduous trees overtopping the pines were the most important predictors increasing the browsing probability. The results support earlier findings that deciduous trees overtopping or reaching the height of the pines should be cleaned from the immediate vicinity of the pines. Seedlings with a height ranging from 75 to 299 centimetres were more susceptible to browsing. Heavy soil scarification, such as ploughing or mounding, increased the browsing probability compared with lighter scarification methods. Soil type did not affect the browsing probability, but paludification decreased it. The within-stand variation in deciduous trees density and height should be taken into account in future moose browsing risk assessments. In Lapland, high moose damage risk areas are characterized by a low elevation and higher temperature sum.

**Keywords** *Alces alces*, boreal forest, damage, forestry, modelling, *Pinus sylvestris*

**Addresses** Finnish Forest Research Institute, Rovaniemi Research Unit, Eteläranta 55, FI-96300 Rovaniemi, Finland E-mail ari.nikula@metla.fi

Received 14 January 2008 Revised 28 May 2008 Accepted 22 August 2008

Available at [http://www.metla.fi/silvafennica/full/sf42/sf424587.pdf](http://www.metla.fi/silvafennica/full/sf42/sf424587.pdf)
1 Introduction

Moose (Alces alces L.) has an ambiguous position in Fennoscandian forests: on the one hand it is a valuable game animal (Mattsson 1990) and, on the other, it is a severe pest in forest plantations (Lavsund 1987). According to national forest inventories in the Fennoscandian countries, moose and other ungulates are among the most common biotic damage agents in the forests. In Finland, moose damage has been reported on 1.1% of all forest land. Regionally the area of damage varies between 7–12% of the area of forest plantations (Tomppo and Joensuu 2003). In Sweden, moose damage has been found in 16–28% of young pine forests (Hörnberg 2001b).

The increase in moose damage since the 1970’s and 1980’s paralleled the increase in the moose population in all the Fennoscandian countries (Cederlund and Bergström 1996). The moose population has grown due to controlled hunting, a low level of predators, and the commencement of so-called plantation forestry since the 1950’s (Lavsund 1987). Clear-cutting became the prevailing method in forest regeneration, and Scots pine (Pinus sylvestris L.) was favoured over other tree species. From the forestry point of view, an economically optimal age-class distribution of the forests means a high proportion of young forest. These provide continuously, and especially in winter, a practically unlimited amount of food for moose (Cederlund and Bergström 1996).

Moose cause damage to trees by browsing the apical shoots and lateral twigs, breaking the main stem or stripping the stem bark. The browsing of apical shoots has been found to be the most common type of damage in forest plantations (Bergqvist et al. 2001). Leader shoot browsing often leads to stem damage, and the technical quality of the wood is impaired (Heikkilä and Löyttyniemi 1992). Browsing also causes growth losses, and in the severest cases the whole stand has to be reforested. Scots pine is only an intermediate tree species in the preference list of moose (Cederlund et al. 1980), but it does form the bulk of the moose diet in winter (Bergström and Hjaljord 1987), and therefore most of the moose damage occurs in pine plantations.

In theory, moose select the composition and amount of food items that best fulfil their nutrient and energy requirements (Belovsky 1981). In the case of forest environments, moose should select those stands, patches of trees or individual trees which have the best amount and quality of browsable items compared with other available stands, patches or individual trees. In general, these requirements coincide with the structural stand parameters regulated by silvicultural practices in young plantations. Forestry aims at efficient timber production through controlled regeneration and the control of tree species composition, density and spatial arrangement in stands. Although coniferous trees have been favoured over the other species, monocultures are seldom achieved due to natural regeneration or the sprouting of deciduous trees. Downy birch (Betula pubescens Ehrh.), silver birch (B. pendula Roth), aspen (Populus tremula L.) and various Salix species often form an admixture of deciduous trees in plantations. In addition to tree-species mixture, there are variation in stand density and the height ratios among tree species due to differences in the growth rate of the individual tree species, soil properties and/or soil preparation.

Studies on moose damage and moose resource selection have provided information about several factors that possibly affect the risk of moose damage. These topics include the amount and regional variation of damage (Hörnberg 2001b, Tomppo and Joensuu 2003), the effect of man-made and other landscape features (Repo and Löyttyniemi 1985, Ball and Dahlgren 2002), tree-species composition (Heikkilä 1990, Danell et al. 1991, Heikkilä 1991), tree density, biomass and chemical composition of trees (Heikkilä and Mikkonen 1992, Edenius 1993), site productivity (Ball and Dahlgren 2002), and soil treatment and fertilization (Edenius 1993, Ball et al. 2000).

In addition to the effect of individual factors affecting moose browsing, at least two main conclusions can be drawn from earlier studies. First, the factors affecting the risk of moose damage operate at different scales. These levels range from regional and local differences in moose-population density and resources important for moose (Heikkilä and Härkönen 1993, Hörnberg 2001b) to the level of stands (Heikkilä 1990), patches of trees and individual trees (Danell et al. 1991, Edenius et al. 2002b) and, finally, to the individual parts of trees (Niemelä and Danell...
1988, Edenius 1993). Second, several of the factors which affect moose browsing interact, which complicates evaluation of the importance of the individual factors.

The degree and type of moose damage vary regionally (Hörnberg 2001), which implies that the factors affecting e.g. moose resource selection may vary accordingly. The northern part of Fennoscandia clearly differs from the southern part in the range of natural conditions. In northern latitudes, the snow cover is thicker and the snow-cover period longer than that in southern Fennoscandia, resulting in a longer shoot browsing period, too. Trees grow at a slower rate in the north than in the south, and this has been suggested to increase the risk of repeated browsing in plantations (Hörnberg 2001a). Also, the silvicultural practices applied in the north may differ from those in the south. For instance, a lot of Norway spruce (Picea abies (L.) H. Karst.) stands on fertile sites in northern Finland have been regenerated with Scots pine, after first ploughing the ground surface to ensure regeneration (Hyppönen et al. 2003). However, despite forestry’s interest in moose-damage problems in the north, research on this topic in Fennoscandia has mainly been carried out in the area south of latitude 64°N. Because moose damage do occur in Lapland, there is need for research about the factors affecting moose damage also in northern areas.

The aim of this study is to model the factors affecting moose damage in Scots pine sapling stands in Lapland, northern Finland. Modelling techniques that allow inclusion of variables measured at different scales and control of the interaction between variables in the same model are rather novel in ecological studies (Guisan and Zimmermann 2000), and thus rare also in moose-browsing research (Jalkanen 2001). We therefore applied logistic regression models with a random factor to find variables, measured at different scales, which explain and predict the browsing of artificially regenerated pines. Regional variables, as well as tree-species composition and other stand parameters routinely recorded in forestry, were used in the modelling.
plots were selected (197 out of 208 stands). Furthermore, in order to decrease spatial autocorrelation due to the proximity of neighbouring stands, only one of the stands locating closer than 5.7 km to each other was randomly selected for modelling purposes (59 out of 197 stands were moved to test data). The minimum accepted distance between stands is equivalent approximately to the diameter of the moose home range in winter (Cederlund and Sand 1994, Nikula et al. 2004). In addition, to increase geographical coverage of test data in the northern and eastern parts of the study area, 15 stands were randomly selected for test data. Thus, the field data in the model construction consisted of 123 stands. Of the 85 Scots pine-dominated stands not used in modelling, 74 included more than one sample plot with pine, and they were used as a test data for the models. The total number of plots was 508 in the modelling data, and 368 in the test data.

The variables used in modelling represent regional-, stand- and intensive plot-level factors (Table 1, Table 2). For modelling, however, the originally regional level variables temperature sum and moose density were interpolated for each stand and treated as stand-level variables. The temperature sums (dd<sub>≥5°C</sub>) were based on the model of Ojansuu and Henttonen (1983). Moose densities for each game management association (GMA) were based on hunters’ observations made in winter 2001 (source: Lapland Game Management District). In order to smooth abrupt changes at GMA borders, the moose densities were calculated for 5 km grid cells using pycnophylactic interpolation (Tobler 1979), which uses the variation among neighbouring GMAs. Interpolation within and among GMAs was calculated such that the average of the grid cells within each GMA was the original moose density value (mass preserving method, Tobler 1979). Stand

![Fig. 1. Research area and stands used in modelling (grey circles) and testing of models (open circles). The size of the circles denotes the proportion of browsed artificially regenerated pines in stands.](image-url)
Table 1. The variables tested during model construction. Cont. denotes a continuous variable and cat. a categori-
cal one. Interpolated denotes that the values have been calculated for a forest stand using the interpolation
models described in Materials and methods. Moose density and the number of trees have also been tested
after log-transformation.

| Variable                                                                 | Type    | Classification       | Extra information                      |
|-------------------------------------------------------------------------|---------|----------------------|----------------------------------------|
| **Forest stand level variables**                                        |         |                      |                                        |
| Moose density (moose 1000 ha\(^{-1}\))                                  | Cont.   | -                    | Interpolated                           |
| Temperature sum (d.d.)                                                  | Cont.   | -                    | Interpolated                           |
| Altitude, meters above sea level                                        | Cont.   | -                    | -                                      |
| Deciduous trees taller than pines, mean value of the sample plots, number ha\(^{-1}\) | Cont.   | -                    | -                                      |
| Potassium concentration in the soil (ppm)                               | Cont.   | -                    | Interpolated                           |
| Calcium concentration in the soil (ppm)                                 | Cont.   | -                    | Interpolated                           |
| Magnesium concentration in the soil (ppm)                               | Cont.   | -                    | Interpolated                           |
| Sodium concentration in the soil (ppm)                                  | Cont.   | -                    | Interpolated                           |
| Phosphorus concentration in the soil (ppm)                              | Cont.   | -                    | Interpolated                           |
| Site type                                                               | Cat.    | Dry and dryish, moist and more fertile |
| Soil scarification                                                      | Cat.    | Scalping or harrowing, ploughing or mounding |
| Exposition                                                             | Cat.    | East, south, north, west |
| **Sample plot level variables**                                         |         |                      |                                        |
| Artificially regenerated pines potentially available to moose, number ha\(^{-1}\) | Cont.   | -                    | -                                      |
| Pines extending above snow cover (>75 cm), number ha\(^{-1}\)            | Cont.   | -                    | -                                      |
| Pines (artificially and naturally regenerated), number ha\(^{-1}\)       | Cont.   | -                    | -                                      |
| Height index (deciduous / artificially regenerated living pines)        | Cont.   | -                    | -                                      |
| Birches, number ha\(^{-1}\)                                             | Cont.   | -                    | -                                      |
| Aspen, number ha\(^{-1}\)                                               | Cont.   | -                    | -                                      |
| Rowan, number ha\(^{-1}\)                                               | Cont.   | -                    | -                                      |
| Sallow, number ha\(^{-1}\)                                              | Cont.   | -                    | -                                      |
| Bush-like willows, number ha\(^{-1}\)                                   | Cont.   | -                    | -                                      |
| Junipers, number ha\(^{-1}\)                                           | Cont.   | -                    | -                                      |
| Deciduous trees other than bush-like willows, number ha\(^{-1}\)        | Cont.   | -                    | -                                      |
| Deciduous trees taller than pines, number ha\(^{-1}\)                   | Cont.   | -                    | -                                      |
| Deciduous trees taller than artificially regenerated pines, number ha\(^{-1}\) | Cont.   | -                    | -                                      |
| Deciduous trees shorter than artificially regenerated pines, number ha\(^{-1}\) | Cont.   | -                    | -                                      |
| Soil type                                                               | Cat.    | Peat, fine, medium, coarse (grain size) |
| Paludification                                                         | Cat.    | Non-paludified (no marshy vegetation), slightly paludified (coverage of marshy vegetation 1–25), strongly paludified (coverage of marshy vegetation > 25%) |
| Pine height (median of all pines)                                       | Cat.    | <75 cm, 75–149 cm, 150–299 cm, ≥ 300 cm (categories based on size of a moose and average snow depth) Classified because of the non-linear effect on the response |
Data on the exchangeable potassium, calcium, magnesium, sodium, and extractable phosphorus concentrations in the soil were obtained from the Geological Survey of Finland (Salminen 1995). The data originally represented a 1 × 1 km grid, but for modelling purposes they were interpolated for each stand.

### Table 2. The base statistics of continuous variables characterizing the 123 modelling stands. Bush-like willows were not included in the total number of deciduous trees.

| Variable                                      | Minimum  | Maximum  | Median  | Mean    | Standard deviation |
|-----------------------------------------------|----------|----------|---------|---------|--------------------|
| Altitude, meters above sea level              | 9        | 357      | 195.0   | 186.1   | 77.5               |
| Temperature sum, dd.                          | 634      | 1006     | 815.5   | 832.1   | 78.7               |
| Moose density, moose 1000 ha⁻¹                | 0.7      | 10       | 2.5     | 2.8     | 1.9                |
| Area of the forest stands, ha                | 0.2      | 10       | 1.6     | 2.1     | 1.9                |
| Scots pine, number ha⁻¹                       | 667      | 12200    | 2500    | 3058    | 1892               |
| Norway spruce, number ha⁻¹                    | 0        | 18667    | 600     | 1405    | 2255               |
| Pubescent birch, number ha⁻¹                  | 0        | 42000    | 8167    | 10917   | 9511               |
| Silver birch, number ha⁻¹                     | 0        | 19400    | 0       | 371     | 497                |
| Trembling aspen, number ha⁻¹                  | 0        | 9400     | 0       | 497     | 1333               |
| European alder, number ha⁻¹                   | 0        | 3600     | 0       | 53     | 359                |
| Rowan, number ha⁻¹                            | 0        | 2875     | 0       | 312     | 627                |
| Sallow, number ha⁻¹                           | 0        | 4625     | 0       | 166     | 554                |
| Willows, number ha⁻¹                          | 0        | 32000    | 1333    | 3188    | 5389               |
| Juniper, number ha⁻¹                          | 0        | 6500     | 0       | 358     | 903                |
| Total number of deciduous trees ha⁻¹          | 0        | 42833    | 9750    | 12264   | 9729               |
| Total number of deciduous trees taller than pines ha⁻¹ | 0 | 17750 | 0 | 1249 | 2864 |
| Total number of all tree stems ha⁻¹            | 3250     | 78500    | 17000   | 20326   | 14046              |
| Artificially regenerated pines, number ha⁻¹   | 500      | 3667     | 1875    | 1807    | 651                |
| Browsed pines (leader shoot damage), number ha⁻¹ | 0       | 2000     | 0       | 163     | 297                |
| Mean height of all pines, cm                  | 31       | 600      | 150     | 162     | 100                |
| Mean height of artificially regenerated pines (browsed and non-browsed), cm | 10 | 684 | 178 | 190 | 113 |
| Mean height of artificially regenerated pines (non-browsed), cm | 10 | 684 | 175 | 194 | 117 |
| Mean height of deciduous trees weighted by the number of the stems (bush-like willows excluded), cm | 0 | 266 | 66 | 75 | 49 |

### 2.3 Modelling

Preliminary analysis showed that the distribution of the browsing rate proportions on the plots was skewed and included an excessive number of non-browsed plots. Therefore, the response variable was defined as binary, browsing or non-browsing, on the basis of whether at least one of the leader shoots of the artificially regenerated pines growing on a sample plot had been browsed.

Both model and test data were hierarchically arranged, the levels being forest stand (j) and sample plot (i). A logistic regression model with a random factor was used in the modelling, expressed as follows:

\[
\log\left(\frac{p_{ij}}{1-p_{ij}}\right) = \beta_0 + \sum_{k=1}^{l} \beta_k x_{ikj} + \sum_{k=l+1}^{m} \beta_k x_{kj} + u_j
\]

where \(i=\) sample plot level index, \(j=\) stand level index, \(k=\) explanatory variable index, \(l=\) the number of variables at plot level, \(m=\) total number
of variables, \( p_{ij} \) = probability of moose browsing on sample plot \( i \) in stand \( j \), \( x_{kij} \) = the value of explanatory variable \( k \) on plot \( i \) in stand \( j \), \( \beta_k \) = fixed parameters, and \( u_j \) = the random stand effect. A binomial assumption of the distribution of the error term and logit link function were used (McCulloch and Searle 2001).

The hierarchical experiment design was taken into account via the random part of the model. The estimated likelihood function is constructed with two distributions: binomially distributed dependent variable and normally distributed random variable. Thus, the lowest level (\( i \)) error variance may differ from 1, and it was allowed to be estimated freely (Allison 1999, McCulloch and Searle 2001). The models were constructed using the MIXED procedure of the SAS statistical software, version 9.1.3 (SAS Institute Inc. 2002–2005) and GLIMMIX macro with a restricted pseudo-likelihood, REPL, (Littell et al. 1996, Allison 1999). Pearson’s \( \chi^2 \) test and Mann-Whitneys U test were used to calculate the basic statistics and cross-tabulations of the data.

The validity of the models was assessed by checking the Pearson’s residuals against the modified predicted probabilities (McCullagh and Nelder 1989). In addition, a ROC curve (Receiver Operating Characteristic) was calculated to assess the area under the curve which describes the explanatory power of a model. Specificity and sensitivity for the models were calculated using the mean values of the predicted probabilities as cut points. The ROC curve, specificity and sensitivity were also calculated in order to check the fit of the models in the test data. In addition, deciles of risk were calculated to compare the predicted and observed probabilities for the models using the modelling data (Steinberg and Colla 2004). All the predicted probabilities were calculated using the fixed part of the models.

Several alternative models were produced by testing the variables and variable combinations reported in earlier studies to affect moose browsing (moose density, tree density and density variation, tree species mixture with different tree height classes) and variables measured for this study (dd, altitude, paludification, soil scarification, geochemical variables). One model, considered as the best, was examined in more detail. The predictions given with the best model in order to visualise the function of the coefficients, and to illustrate the effect of the different levels of model variables on the probability of leader-shoot browsing.

In addition to the hierarchical logistic models, five stand-level general linear models (GLM) were also constructed to test the effects of the factors or covariates measured or calculated at the stand level. The main reason for constructing these models was to test whether the degree of browsing can be predicted with the same variables without taking into account the effect of within-stand variation in the measured variables. Thus, the average values, means (continuous variables) or medians (categorical variables) were used in modelling instead of plot-wise values.

The response in the models was the square-root and arcsin-sin transformed average proportion of browsed artificially regenerated pines on stand. Only the F-tests and significances of the independent variables and \( R^2 \) of the models are presented in the overall comparison of the models.

## 3 Results

### 3.1 Goodness of Fit of the Models

Six models were constructed to test the effect of different variable compositions on model performance at the plot level (Table 3). The fit of the models to the modelling data, assessed on the basis of the area under the ROC curve, specificity and sensitivity at the cut point of the mean value of the predicted probability, was relatively good for all the models. Similarly, the deciles of the risk curves were relatively satisfactory, although the models underestimated the browsing probability at low decile values and overestimated the probability at the highest deciles (Fig 2). Despite the small differences in fit among the models, model 3 was selected on the basis of its sensitivity and was used to illustrate in more detail the parameter estimates and predictions of the model.

### 3.2 Plot-level Variables

According to Model 1, an increase in the number
Table 3. F-tests for the fixed effects of six alternative models. The area under the ROC curve, specificity, sensitivity, deviance and scaled deviance describe the fit and classification efficiency of the models. St. denotes a variable for stand level and pl. a variable for sample plot level. Cat. denotes a categorical variable.

| Variable                                      | Model 1  | Model 2  | Model 3  | Model 4  | Model 5  | Model 6  |
|-----------------------------------------------|----------|----------|----------|----------|----------|----------|
| Log of moose density (st.)                    | 9.55     | 0.003    | 9.57     | 0.003    | 11.12    | 0.001    | 3.21     | 0.076    |
| Temperature sum*10^{-2}, d.d. (st.)           | -        | -        | -        | -        | 11.14    | 0.001    | 4.48     | 0.037    |
| Altitude, meters above sea level, (st.)       | -        | -        | -        | -        | 4.53     | 0.037    | 7.00     | 0.010    |
| Magnesium concentration in soil, 10^{-3}*ppm  | 10.92    | 0.002    | 8.37     | 0.005    | 8.45     | 0.005    | 6.78     | 0.011    |
| Soil scarification (st., cat: 1. Ploughing or mounding, 2. Scalping or disk-trenching) | 10.28    | 0.002    | 10.60    | 0.002    | 10.98    | 0.001    | 10.22    | 0.002    |
| Log of the number of artificially regenerated living pines (pl.) | -        | -        | 69.10    | 0.000    | 75.36    | 0.000    | 77.25    | 0.000    |
| Log of the number of naturally regenerated living pines (pl.) | -        | -        | 1.92     | 0.167    | -        | -        | -        | -        |
| Log of the number of all living pines (pl)    | 33.54    | 0.000    | -        | -        | -        | -        | -        | -        |
| Log of the number of deciduous trees taller than pines (pl.) | -        | -        | 16.62    | 0.000    | 17.62    | 0.000    | 16.58    | 0.000    |
| Log of the number of deciduous trees shorter than pines (pl.) | -        | -        | 2.04     | 0.153    | -        | -        | -        | -        |
| Log of the number of deciduous trees (pl.)    | 4.47     | 0.035    | -        | -        | -        | -        | -        | -        |
| Paludification (pl., cat: 1. Not paludified, 2. Slightly paludified, 3. Strongly paludified) | 6.98     | 0.001    | 8.37     | 0.005    | 8.80     | 0.002    | 9.19     | 0.000    |
| Height of living pines (pl., cat: 1. 1–74 cm, 2. 75–149 cm, 3. 150–299 cm, 4. ≥ 300 cm) | 9.34     | 0.000    | 10.49    | 0.000    | 10.33    | 0.000    | 10.18    | 0.000    |

Assessment of the models

|                        | Model 1  | Model 2  | Model 3  | Model 4  | Model 5  | Model 6  |
|------------------------|----------|----------|----------|----------|----------|----------|
| Area under ROC curve, % | 80.2     | 83.4     | 83.1     | 83.1     | 83.0     | 84.1     |
| Specificity            | 77.2     | 80.1     | 79.1     | 81.3     | 80.1     | 81.6     |
| Sensitivity            | 70.3     | 71.3     | 72.3     | 67.3     | 64.4     | 67.3     |
| Deviance               | 227.5    | 188.6    | 191.8    | 190.6    | 190.9    | 207.9    |
| Scaled deviance        | 473.1    | 472.6    | 424.9    | 424.6    | 424.3    | 477.8    |
of all living pines and deciduous trees on a plot increased the probability of browsing (Table 3). However, if the number of artificially regenerated pines and of naturally regenerated pines were added to the model as separate variables, only the number of artificially regenerated pines was significant in the same model (Table 3, Model 2). Similarly, when the number of deciduous trees was divided into two classes in relation to the mean pine height on the plot, only the number of deciduous trees taller than the pines was significant in the same model (Table 3, Model 2). In general, the number of artificially regenerated pines and the number of deciduous trees taller than pine on a plot were the most important predictors of browsing in all the models.

**Fig. 2.** Observed and expected probabilities of moose browsing by different models (Table 3) in ten classes of predicted probabilities (risk deciles).
The mean height of the living pines was a significant variable in all the models (Table 3). The 75–149 and 150–299 cm height categories were highly susceptible to browsing, the latter category being the most attractive. If the pines on a plot were on the average shorter than 75 centimetres, or taller than three metres, then the probability of moose damage was low. Soil type was not included in any of the models, but paludification was a significant variable in all the models.

### 3.3 Stand-level Variables

Of the stand-level variables, moose density, temperature sum and altitude were strongly correlated with each other. Replacing moose density with temperature sum or altitude had minimum effect on the performance of the models (Table 3, Models 4 and 5, altitude vs temperature sum Pearson’s $r = -0.860$, df = 121, $p < 0.001$). Moose density and temperature sum correlated so strongly (Pearson’s $r = 0.658$, df = 121, $p < 0.001$) that they could not be included in the same model. Although also moose density and altitude correlated significantly (Pearson’s $r = -0.443$, df = 121, $p < 0.001$), they both had explanatory power in the same model. Paludification and soil scarification were included as significant variables in all the models (Table 3). Intensive soil scarification, such as ploughing or mounding, increased the browsing probability, whereas paludification decreased it. The risk of browsing in the most susceptible height classes of pine (75–149 cm and 150–299 cm) was approximately two to six times higher in stands on ploughed ground compared to other soil-treatment methods (Fig. 3). The same also applied when the risk was calculated according to the number of living pines or the number of deciduous trees taller than pines. Of the different mineral nutrients in the soil, the exchangeable magnesium concentration was included as a significant variable in all the models (Table 3).

### 3.4 Parameter Estimates and Predictions of Model 3

The effect of moose density on the browsing probability of the plot was relatively linear, thus indicating no clear thresholds (Fig. 3a). A 50% probability was achieved only for saplings on the most heavily scarified sites with moose densities of about 4.5–6.5 1000 ha$^{-1}$. The browsing probability increased with an increasing number of artificially regenerated living pines on the plot, and the effect was again the strongest for saplings on the most heavily scarified sites. A predicted browsing probability of 50% was reached with 2100–2700 pines ha$^{-1}$ on these sites, depending on the height of the pines (Fig. 3b). If a plot was otherwise susceptible to browsing, then an increasing number of overtopping deciduous trees rapidly increased the browsing probability on the plot until the number of deciduous trees was 2500 trees ha$^{-1}$ (Fig. 3c). However, a 50% browsing probability was only reached for ploughed sites with 75–299 cm pines.

All the predictions (Fig. 3) were calculated for non-paludified plots in a forest stand. If the vegetation on the plot indicated paludification, then the predicted browsing probability decreased considerably independent of the scarification method. For example, the predicted browsing probability decreased from 55% on non-paludified plots to 19% on slightly paludified ones, and further to 3% on strongly paludified plots, when the stands had been ploughed or mounded and the continuous variables were fixed at the mean levels.

### 3.5 Stand-level Model

The stand-level models (Table 4) suggested that almost the same variables could be used to predict the proportion of browsed pines on stand as the variables predicting the risk in the sample-plot-level models. However, paludification and the total number of deciduous trees or the number of deciduous trees taller than pines were not significant variables in models.

### 3.6 Model Performance with the Test Data

Finally, the fit of the models was tested with the testing data. Based on the indicators of fit (Table 5), the fit of all six models was lower than the fit to the modelling data, although the test
Fig. 3. The probability of moose browsing risk according to Model 3 with different levels of moose density, number of artificially regenerated Scots pine and number of deciduous trees taller than pines. The probabilities were calculated for different soil treatment methods and height classes of pines. The probabilities were calculated for non-paludified sites and using mean values of additional variables included in Model 3 (Table 2).
Table 4. Type 3 F-tests of the general linear models based on variables averaged to stand level. The response variable was the arcsin and square-root transformed proportion of the browsed pines in stand. Model numbers correspond to the plot level models presented in Table 3. St. denotes a variable for stand level and pl. a variable for sample plot level. Cat. denotes a categorical variable.

| Variable                                                                 | Model 1 |          | Model 3 |          | Model 4 |          | Model 5 |          | Model 6 |          |
|-------------------------------------------------------------------------|---------|----------|---------|----------|---------|----------|---------|----------|---------|----------|
|                                                                          | F       | p        | F       | p        | F       | p        | F       | p        | F       | p        |
| Log of moose density (st.)                                               | 18.01   | 0.000    | 13.79   | 0.000    | -       | -        | -       | -        | 7.51    | 0.007    |
| Temperature sum*10^{-2}, d.d. (st.)                                     | -       | -        | -       | -        | -       | -        | 9.91    | 0.002    | -       | -        |
| Altitude, meters over sea level, (st.)                                  | -       | -        | -       | -        | 8.90    | 0.004    | -       | -        | 2.90    | 0.092    |
| Magnesium content in forest soil, 10^{-3}ppm (st.)                      | 14.79   | 0.000    | 15.20   | 0.000    | 9.60    | 0.003    | 12.79   | 0.001    | 12.44   | 0.001    |
| Soil scarification (st., cat: 1. Ploughing or mounding, 2. Scalping or disk-trenching) | 9.28    | 0.003    | 10.60   | 0.002    | 8.79    | 0.004    | 9.42    | 0.003    | 10.63   | 0.002    |
| Log of the number of artificially regenerated living pines (pl.)        | -       | -        | 4.97    | 0.028    | 4.72    | 0.032    | 4.85    | 0.030    | 2.96    | 0.088    |
| Log of the number of naturally regenerated living pines (pl.)           | -       | -        | -       | -        | -       | -        | -       | -        | -       | -        |
| Log of the number of all living pines (pl.)                             | 0.01    | 0.926    | -       | -        | -       | -        | -       | -        | -       | -        |
| Log of the number of deciduous trees taller than pines (pl.)            | -       | -        | 0.75    | 0.387    | 1.40    | 0.239    | 1.23    | 0.270    | 1.10    | 0.296    |
| Log of the number of deciduous trees shorter than pines (pl.)           | -       | -        | -       | -        | -       | -        | -       | -        | -       | -        |
| Log of the number of deciduous trees (pl.)                              | 0.76    | 0.386    | -       | -        | -       | -        | -       | -        | -       | -        |
| Paludification (pl., cat: 1. Not paludified, 2. Slightly paludified, 3. Strongly paludified) | 0.27    | 0.849    | 0.47    | 0.707    | 0.34    | 0.797    | 0.45    | 0.716    | 0.45    | 0.721    |
| Height of living pines (pl., cat: 1. 1–74 cm, 2. 75–149 cm, 3. 150–299 cm, 4. ≥ 300 cm) | 5.08    | 0.003    | 5.13    | 0.002    | 3.28    | 0.024    | 3.70    | 0.014    | 4.28    | 0.007    |
| F-test for the model                                                    | 5.37    | 0.000    | 6.02    | 0.000    | 5.39    | 0.000    | 5.25    | 0.000    | 5.86    | 0.000    |
| R²                                                                      | 0.35    |          | 0.37    |          | 0.35    |          | 0.35    |          | 0.39    |          |
data consisted of relatively similar stands to the modelling data located near the modelling stands. The area under the ROC curve and sensitivity were about 10% lower than in the modelling data (Table 5). However, the values of about 70% for the area under the ROC curve indicated that the models were moderately robust.

4 Discussion

The selectivity of moose at several levels of selection is a key issue for forest managers in understanding the moose-forest interactions (Edenius et al. 2002a). From the point of view of forest management, selection at the stand level has been perhaps the most studied. Although the stand is only one of the possible levels of selection, forest management is solely based on tree stands. Therefore, factors identified at the stand level which affect moose damage can be used in predicting the risk of damage and in formulating the necessary preventive actions.

According to our models, the probability of browsing on a plot increased when the density of artificially regenerated pines increased. In previous studies, the amount of browsed biomass of pines has been found to increase when the density of pines increases but, because the rate of browsed biomass grows slower than the density, the amount of browsed biomass per tree is lower in dense stands (Heikkilä 1991, Heikkilä and Mikkonen 1992, Ball and Dahlgren 2002). Similarly, an increasing number of pines increases browsing on leader shoots (Ball and Dahlgren 2002), but the number of saplings without stem breakage also increases along with density (Heikkilä and Mikkonen 1992, Heikkilä and Härkönen 1996). Therefore, it has been suggested that increasing the number of planted pines up to 4000–5000 trees (Lyly and Saksa 1992, Ball and Dahlgren 2002) from the present recommendation of 2000–2500 trees ha\(^{-1}\) should ensure that the number of non-browsed trees is high enough from the silvicultural point of view. Our response variable, browsing or non-browsing on a plot, does not allow direct conclusions to be drawn about the relationship between density and the number of browsed or non-browsed trees. However, if we assume that the pattern of browsing intensity in relation to density found in earlier studies also applies in our study area, then increasing the number of planted pines above the present level could be a viable strategy in areas with a high moose damage risk at least. Furthermore, increasing the number of regenerated trees is supported by the fact that other biotic, as well as abiotic, damage in plantations are more severe in northern Finland than in the south (Jalkanen 2007).

Soil scarification is commonly used on sites with a thick humus layer and fine-textured underlying mineral soil in order to increase soil temperature and to reduce the water content in the soil (Hyppönen et al. 2003). Soil scarification also suppresses the ground vegetation and thus reduces competition by other vegetation with the planted trees in their early developmental stage. The heaviest soil preparation, like ploughing, has in most cases been used in connection with pine planting on fertile soils, where the previous stand was often dominated by Norway spruce (Hyppönen et al. 2003). No earlier Fennoscandian studies have reported about the effects of soil preparation on moose damage, which implies that either no significant effects have been found or that soil scarification has not been considered to be a factor potentially affecting moose browsing. However, moose browsing has been found to occur more on fertile sites (Ball and Dahlgren 2002), and moose also prefer fertilized sites (Ball et al. 2000).

Boreal forest soils are generally characterized by low concentrations of plant-available nitrogen, which limits tree growth. Therefore, one explana-
tion for the effect of heavy soil scarification on the risk of moose browsing is that soil scarification enhances the mineralization of nitrogen and other nutrients, and thus affects the ratio between mineral nutrients in the shoots and/or the size of the shoots. Heavy site preparation like ploughing increases the height growth of pine more than lighter methods, and this difference in the height of trees has been found to continue throughout the time that the leader shoots of pine are available for moose (Mäkitalo 1999). From the silvicultural point of view, the effect of soil scarification appears to be ambiguous. On the one hand, soil scarification increases the growth of pines and, in principle, reduces the time pines are susceptible to browsing. On the other hand, an increase in growth might be counterbalanced by better palatability and a higher biomass of the trees on these sites. It is also possible that the relative increase in the palatability or biomass of the stands due to soil preparation is more pronounced at northern latitudes than in the south. However, in the absence of comparative studies from more southern latitudes, this remains to be assessed in future studies. Furthermore, as some of the heaviest soil treatment methods like ploughing are no longer used in state-owned forests, and their usage on privately owned land also has decreased, the effect of lighter soil preparation methods in the future might not be as pronounced.

Deciduous trees are a common admixture in plantations regenerated for pine. Therefore, soil scarification and the cleaning of deciduous trees are used in silviculture in order to reduce the competition between pines and other vegetation. For moose, however, the presence of deciduous trees as an admixture in coniferous plantations provides better quality browse than conifers alone and increases the total amount of browsable biomass in a stand. Studies on the effect of deciduous trees on moose browsing have, in general, shown that although deciduous tree species that are favoured by moose increase the total consumption of biomass in stands, pine browsing is only slightly affected by the presence of other tree species (Danell et al. 1991, Edenius 1991). The results from inventory-based studies have also indicated that the total cleaning of deciduous trees from pine plantations might even have a detrimental effect if the amount of alternative food is not increased (Heikkilä 1991, Härkönen 1998). Our results are thus in line with previous studies, since none of the deciduous tree species nor the total amount of deciduous trees per se affected browsing probability.

According to our models, however, the probability of browsing rapidly increased when the number of deciduous trees taller than pines within the plot \((r=2.52 \text{ m})\) increased. The effect was strongest in advanced plantations growing on the most heavily scarified sites where five deciduous trees overtopping pines on a plot gave a 50\% browsing probability. Our results are thus in line with those of Heikkilä (1990), who found that the number of damaged pines increased when birch reached or exceeded the height of the pines. Densely located, tall deciduous trees may shade pines and affect the structural characteristics of the pines by making the trunks and shoots slender, or shading may change the proportions of chemical compounds in the trees (Edenius 1993).

The result given by our models that the number of deciduous trees taller than pine predicted browsing at the plot level, but not when used as the stand mean value, may be related to the hierarchical forage selection of moose (Searle et al. 2005), i.e. that moose are selective with respect to trees, patches or larger entities of resources. There is evidence that moose increase their residence time and browse a greater number of plants in patches containing a high sapling density (Vivás and Saether 1987). However, quantitative evidence indicating that moose perceive a patch as a selection unit is lacking (Searle et al. 2005). Instead, there is more evidence that the food selection of moose occurs at the tree level rather than at the scale of stands or patches of trees (Danell et al. 1991, Edenius et al. 2002b, Stolter et al. 2005). Because we did not measure the consumption of tree species other than Scots pine, and because our response variable was binary, we cannot evaluate the question of selection level between patch and tree per se. Furthermore, the plot size used in our study is only one of numerous alternatives and it might measure scales larger or smaller than a clearly distinguishable patch of vegetation (see e.g. Searle et al. 2005). However, based on our models, we can conclude that there is variation within the stands with respect to the deciduous tree component, and that the moose browsing risk
of pines is associated with this variability.

One implication of our results is that within-stand variation with respect to the deciduous tree component should be taken into account when assessing the risk of moose browsing. Also, from the point of view of silvicultural treatment, our results suggest that the cleaning of deciduous trees should preferably be performed in the immediate vicinity of those pines to be grown to the end of the rotation further rather than applied to the whole stand (Härkönen 1998).

Large-scale studies in Sweden have suggested that, in addition to variation in forage cover, also climatic factors like snow cover and the length of the growing period contribute to the variation in the moose damage level (Hörnberg 2001a). In the north, the snow cover is deeper and the snow cover period longer than in the south. Also, the growing period is shorter in the north, which prolongs the time pines are susceptible to moose browsing due to the lower growth rate of the saplings. According to our models, temperature sum and altitude were both significant variables affecting the probability of moose browsing. There is an approximately decreasing SW–NE trend in temperature sum in our study area and, in general, altitude increases towards the north and NW. In addition, the snow depth and length of the snow cover period in the area (not used in modelling) increase towards the north and NE and also vary according to altitude. The highest moose densities and the most intensive browsing (Fig. 1) were found in the SW corner of our study area, i.e. in the area with the highest temperature sum and the lowest elevation. As the population density at the regional or landscape level reflects resource availability at these scales (Wallace et al. 1995), the size of the moose population in the area, and consequently the occurrence of moose damage might reflect the regional variation in the overall productivity of the vegetation and thus the amount of browse available for moose. However, as the effects of climatic and topographic factors are confounded in our study area, we can only conclude that climatic and topographic factors might have a more pronounced effect on the moose damage risk in northern latitudes than in the south or in areas with relatively flat terrain. From the point of view of forest management, this suggests that, although a higher temperature sum enhances the growth of the trees and subsequently reduces the time that the trees are susceptible to browsing, a relatively high temperature sum also increases the regional risk of moose browsing.

Finally, also the magnesium contents of soil, a significant variable increasing browsing probability in our models, might also reflect regional variability of soil nutrient contents due to variation of soil rockbed characteristics (Salminen 1995).

5 Conclusions

The risk of moose browsing of Scots pine increased along with the number of regenerated pines, but not with the total number of trees. Deciduous trees overtopping pines or close to the height of the pines should be cleaned from the immediate vicinity of pines to be grown to the end of the rotation. As the overall number of deciduous trees did not increase the risk of browsing, the total cleaning of stands is not necessary. When assessing the risk of moose browsing, the variation in the deciduous tree component should be assessed in relation to the pines. Probably due to more intensive nutrient mineralization, heavy soil treatment like ploughing or mounding increases the browsing risk, but paludification reduces it. At northern latitudes, the higher moose browsing risk is also related to a lower elevation and higher temperature sum of the stands.

Acknowledgements

We thank Tarmo Aalto, Martti Aikio, Pekka Närhi, Henna Penttinen, and Jouni Väisänen for measuring the field data. Tarmo Aalto also pre-processed the field data for the analysis. Kari Mikkola and Vesa Nivala are acknowledged for performing the GIS analysis. Discussions about modelling techniques with Virpi Alenius and Juha Hyvönen were enlightening. Dr. John Derome checked the English language. We thank Dr. John P. Ball and an anonymous referee for their valuable comments on the manuscript. This study was partly funded by the Ministry of Agriculture and Forestry.
References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5: 169–211.

Allison, P.D. 1999. Logistic regression using SAS system: theory and application. Series Logistic Regression Using SAS System: Theory and Application. SAS Institute Inc., Cary, NC. 288 p.

Ball, J.P. & Dahlgren, J. 2002. Browsing damage on pine (Pinus sylvestris and P. contorta) by a migrating moose (Alces alces) population in winter: Relation to habitat composition and road barriers. Scandinavian Journal of Forest Research 17: 427–435.

— , Danell, K. & Sunesson, P. 2000. Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. Journal of Applied Ecology 37: 247–255.

Belovsky, G.E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62: 1020–1030.

Bergqvist, G., Bergström, R. & Edenius, L. 2001. Patterns of stem damage by moose (Alces alces) in young Pinus sylvestris stands in Sweden. Scandinavian Journal of Forest Research 16: 363–370.

Bergström, R. & Hjeljord, O. 1987. Moose and vegetation interactions in northwestern Europe and Poland. Swedish Wildlife Research Supplements 1: 213–228.

Cederlund, G. & Bergrström, R. 1996. Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. In: DeGraaf, R.M. & Miller, R.I. (eds.). Conservation of fauna diversity in forested landscapes. Chapman & Hall. Conservation Biology Series 6: 265–281.

— & Sand, H. 1994. Home-range size in relation to age and sex in moose. Journal of Mammalogy 75: 1005–1012.

— , Ljungqvist, H., Markgren, G. & Ståhlfelt, F. 1980. Foods of moose and roe deer at Grimsö in central Sweden. Results of rumen content analyses. Swedish Wildlife Research Viltrevy 11: 169–247.

Danell, K., Edenius, L. & Lundberg, P. 1991. Herbivory and tree stand composition: moose patch use in winter. Ecology 72: 1350–1357.

Edenius, L. 1993. Browsing by moose on Scots pine in relation to plant resource availability. Ecology 74: 2261–2269.

— , Bergman, M., Ericsson, G. & Danell, K. 2002a. The role of moose as a disturbance factor in managed boreal forests. Silva Fennica 36: 57–67.

— , Ericsson, G. & Näslund, P. 2002b. Selectivity by moose vs the spatial distribution of aspen: a natural experiment. Ecography 25: 289–294.

Finnish Statistical Yearbook of Forestry 1999. Finnish Forest Research Institute. 352 p.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.

Hallikainen, V., Hyppönen, M., Jalkanen, R. & Mäkitalo, K. 2004. Metsänviljelyn onnistuminen Lapin yksityismetsissä vuosina 1984–1995. Metsätieteen aikakauskirja 1/2004: 3–20.

Härkönen, S. 1998. Effects of silvicultural cleaning in mixed pine–deciduous stands on moose damage to Scots pine (Pinus sylvestris). Scandinavian Journal of Forest Research 13: 429–436.

Heikkilä, R. 1990. Effect of plantation characteristics on moose browsing on Scots pine. Silva Fennica 24: 341–351.

— 1991. Moose browsing in a Scots pine plantation mixed with deciduous tree species. Acta Forestalia Fennica 224. 13 p.

— & Härkönen, S. 1993. Moose (Alces alces L.) browsing in young Scots pine stands in relation to the characteristics of their winter habitats. Silva Fennica 27: 127–143.

— & Härkönen, S. 1996. Moose browsing in young Scots pine stands in relation to forest management. Forest Ecology and Management 88: 179–186.

— & Löytyniemi, K. 1992. Growth response of young Scots pines to artificial shoot breaking simulating moose damage. Tiivistelmät: Hirvivioitusta jäljittelevän verson katkaisun vaikutus nuoren männyn kehitykseen. Silva Fennica 26(1): 19–26.

— & Mikkonen, T. 1992. Effects of density of young Scots pine (Pinus sylvestris) stand on moose (Alces alces) browsing. Acta Forestalia Fennica 231. 14 p.

Hörnberg, S. 2001a. Changes in population density of moose (Alces alces) and damage to forests in Sweden. Forest Ecology and Management 149: 141–151.

— 2001b. The relationship between moose (Alces alces) browsing utilisation and the occurrence of different forage species in Sweden. Forest Ecology and Management 149: 91–102.

Hyppönen, M., Hallikainen, V., Aalto, T., Jalkanen,
R., Mäkitalo, K. & Penttinen, H. 2003. Lapin lain mukainen metsänvalmistus – tilastotarkastelu. Metsätieteen aikakauskirja 1/2003: 17–32.

Jalkanen, A. 2001. The probability of moose damage at the stand level in southern Finland. Silva Fennica 35: 159–168.

Jalkanen, R. 2007. Diseases, pests and abiotic disorders of trees in the changing environment in Finnish Lapland. In Taulavuori, E. & Taulavuori, K. (eds.). Physiology of northern plants under changing environment. Research Signpost. p. 105–133.

Lavsund, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. Swedish Wildlife Research, Supplement 1: 229–244.

Lyly, O. & Saksa, T. 1992. The effect of stand density on moose damage in young Pinus sylvestris stands. Scandinavian Journal of Forest Research 7: 393–403.

Mattsson, L. 1990. Moose management and the economic value of hunting: Towards bioeconomic analysis. Scandinavian Journal of Forest Research 5: 575–581.

McCullagh, P. & Nelder, J.A. 1989. Generalized linear models. 2nd ed. Chapman & Hall, London. 387 p.

McCuolloch, C.E. & Searle, S.R. 2001. Generalized, linear and mixed models. Wiley, New York. 325 p.

Mäkitalo, K. 1999. Effect of site preparation and reforestation method on survival and height growth of Scots pine. Scandinavian Journal of Forest Research 14: 512–525.

Niemelä, P. & Danell, K. 1988. Comparison of moose browsing on Scots pine (Pinus sylvestris) and lodge pole pine (Pinus contorta). Journal of Applied Ecology 25: 761–775.

Nikula, A., Heikkinen, S. & Helle, E. 2004. Habitat selection of adult moose Alces alces at two spatial scales in central Finland. Wildlife Biology 10: 121–135.

Ojansuu, R. & Henottonen, H. 1983. Estimation of the local values of monthly mean temperature, effective temperature sum and precipitation sum from the measurements made by the Finnish Meteorological Office. Silva Fennica 17: 143–158.

Repo, S. & Löyttyniemi, K. 1985. Lähiympäristön vaikutus männyn viljelytämön hirventuloittueen. Summary: The effect of immediate environment on moose (Alces alces) damage in young Scots pine plantations. Folia Forestalia 626. 14 p.

Salminen, R. (ed.). 1995. Alueellinen geokemiallinen kartoitus Suomessa vuosina 1982–1994. Summary: Regional geochemical mapping in Finland in 1982–1994. Geologian tutkimuskeskus, Tutkimusraportti 130. 47 p. + 24 apps.

Searle, K.R., Hobbs, N.T. & Shipley, L.A. 2005. Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. Oikos 111: 417–424.

Steinberg, D. & Colla, P. 2004. Logistic regression. In: SYSTAT 11. Statistics II. SYSTAT Software Inc., Richmond. p. 207–278.

Stolter, C., Ball, J.P., Julkunen-Tiitto, R., Lieberei, R. & Ganzhorn, J.U. 2005. Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. Canadian Journal of Zoology 83: 807–819.

Tobler, W.R. 1979. Smooth pycnophylactic interpolation for geographical regions. Journal of the American Statistical Association 74: 519–536.

Tomppo, E. & Jouesuu, J. 2003. Hirvieläinten aiheutama metsätuhottomuus Etelä-Suomessa Valtakunnan met- sien 8. ja 9. inventoinnin mukaan. Metsätieteen aikakauskirja 4/2003: 507–535.

Wallace, L.L., Turner, M.G., Romme, W.H., O’Neill, R.V. & Wu, Y. 1995. Scale of heterogeneity of forage production and winter foraging by elk and bison. Landscape Ecology 10: 75–83.

Vivás, H. & Sæther, B.-E. 1987. Interactions between a generalist herbivore, the moose Alces alces, and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology 56: 509–520.

Total of 48 references