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

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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*
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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 Hjeljord 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.

2 Materials and Methods

2.1 Study Area

The study area covers the southern and central parts of Finnish Lapland (Fig. 1). Most of the area belongs to the northern boreal vegetation zone, but parts of the south-western area are located in the mid-boreal vegetation zone (Ahti et al. 1968). The main tree species are Scots pine, Norway spruce, birches (*B. pendula*, *B. pubescens*), aspen, rowan (*Sorbus aucuparia* L.) and alder (*Alnus incana* L.). The shrub layer comprises different willows (*Salix* spp.) and juniper (*Juniperus communis* L.). About 36% of forestry land is privately owned, and most of the forests are commercially managed in the area. Scots pine is the dominant tree species in 72% of the forests, Norway spruce in about one fifth, and mainly downy birch in the rest of the forests. Regeneration areas and sapling stands cover about 26%, thinning stands about 43% and older forests about one fifth of the forest area (Finnish Statistical Yearbook… 1999). The period with a permanent snow cover is 190–215 days and lasts from October to May, and the maximum depth of the snow cover is 50–70 cm (Jalkanen 2007).

2.2 Modelling Data

A total of 208 randomly selected Scots pine stands, regenerated artificially in private-owned forests between 1985–1995 in Finnish Lapland, were surveyed for regeneration success in 2001 (Hallikainen et al. 2004). Each stand was inventoried using systematic cruising by lines and sample plots of 20 m^2 ($r = 2.52$ m) (referred to as intensive sample plots in this study). On each plot, the number of tree stems (height ≥ 10 cm) and their median height were measured by tree species. Moose browsing directed at a leader shoot of an artificially regenerated Scots pine was recorded as moose damage. The time of browsing was not defined by year, but the browsing had to be clearly identifiable on the basis of the remains of the browsed leader stem. In practise, most of the browsing had occurred during the last five years.

For the modelling, only stands with Scots pine as the dominant tree species and with at least one artificially regenerated living pine on the sample

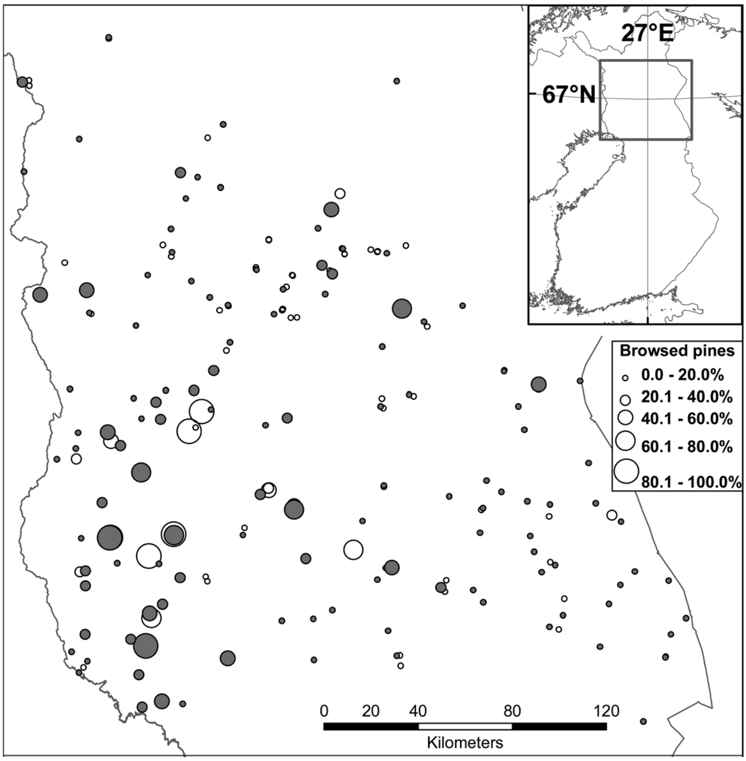

Fig. 1. Research area and stands used in modelling (grey circles) and testing of models (open circles). The size of the circles denotes the proportion of browsed artificially regenerated pines in stands.

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 ($dd_{+5°C}$) 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 pychnophylactic 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

Table 1. The variables tested during model construction. Cont. denotes a continuous variable and cat. a categorical 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

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

elevation was obtained from a digital elevation model (source: National Land Survey).

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.

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:

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

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}, x_{kj} = the value of explanatory variable k on plot i in stand j, β_0, β_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 χ^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 by the most powerful variables were calculated 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 arcos-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	
	F	p	F	p	F	p	F	p	F	p	F	p
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.)	-	-	-	-	-	-	-	-	10.92	0.001	-	-
Altitude, meters above sea level, (st.)	-	-	-	-	-	-	11.14	0.001	-	-	4.48	0.037
Magnesium concentration in soil, 10^{-3}*ppm (st.)	10.92	0.002	8.37	0.005	8.45	0.005	4.53	0.037	7.00	0.010	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	10.23	0.002	10.22	0.002	12.22	0.001
Log of the number of artificially regenerated living pines (pl.)	-	-	69.10	0.000	75.36	0.000	76.57	0.000	77.25	0.000	45.11	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	16.35	0.000	16.58	0.000	21.98	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	9.32	0.000	9.19	0.000	8.99	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	10.40	0.000	10.18	0.000	14.11	0.000
							Assessment of the models					
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	

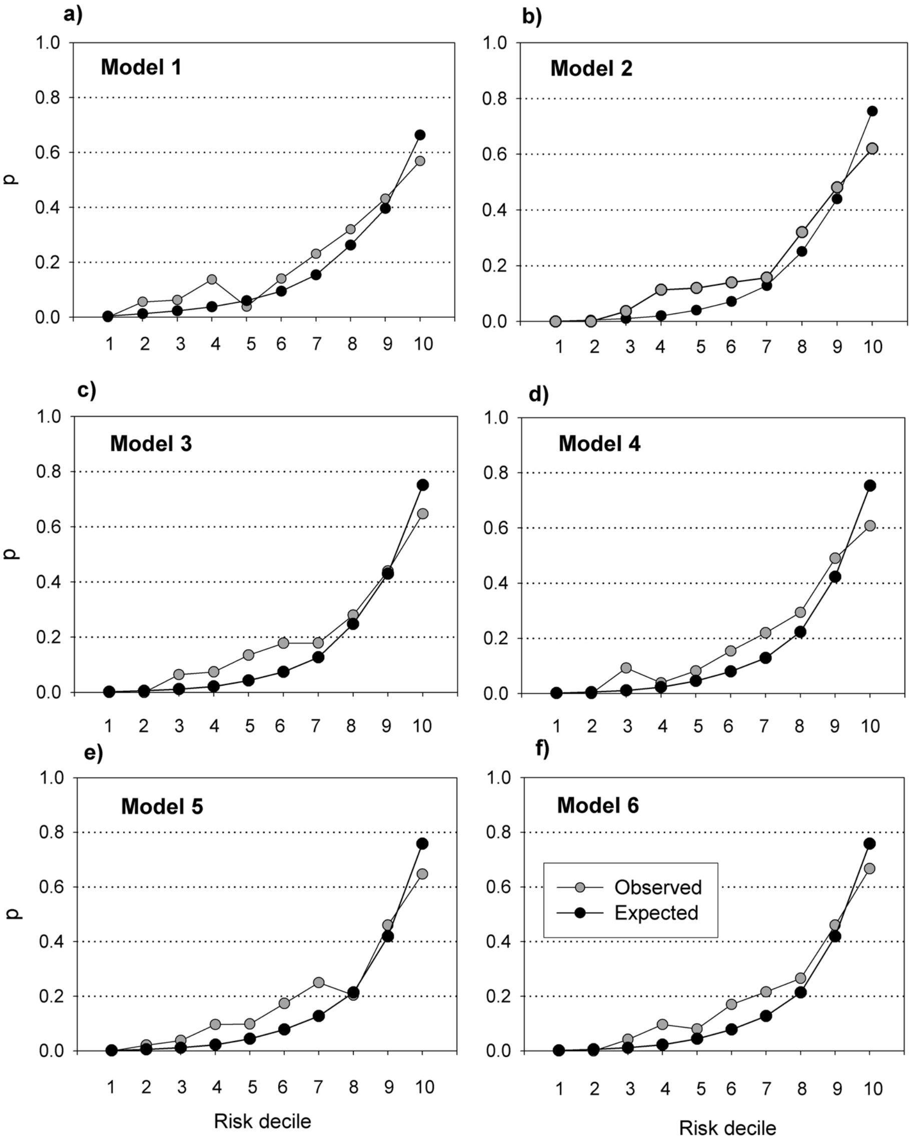

Fig. 2. Observed and expected probabilities of moose browsing by different models (Table 3) in ten classes of predicted probabilities (risk deciles).

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.

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 (Table 3, Model 6).

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

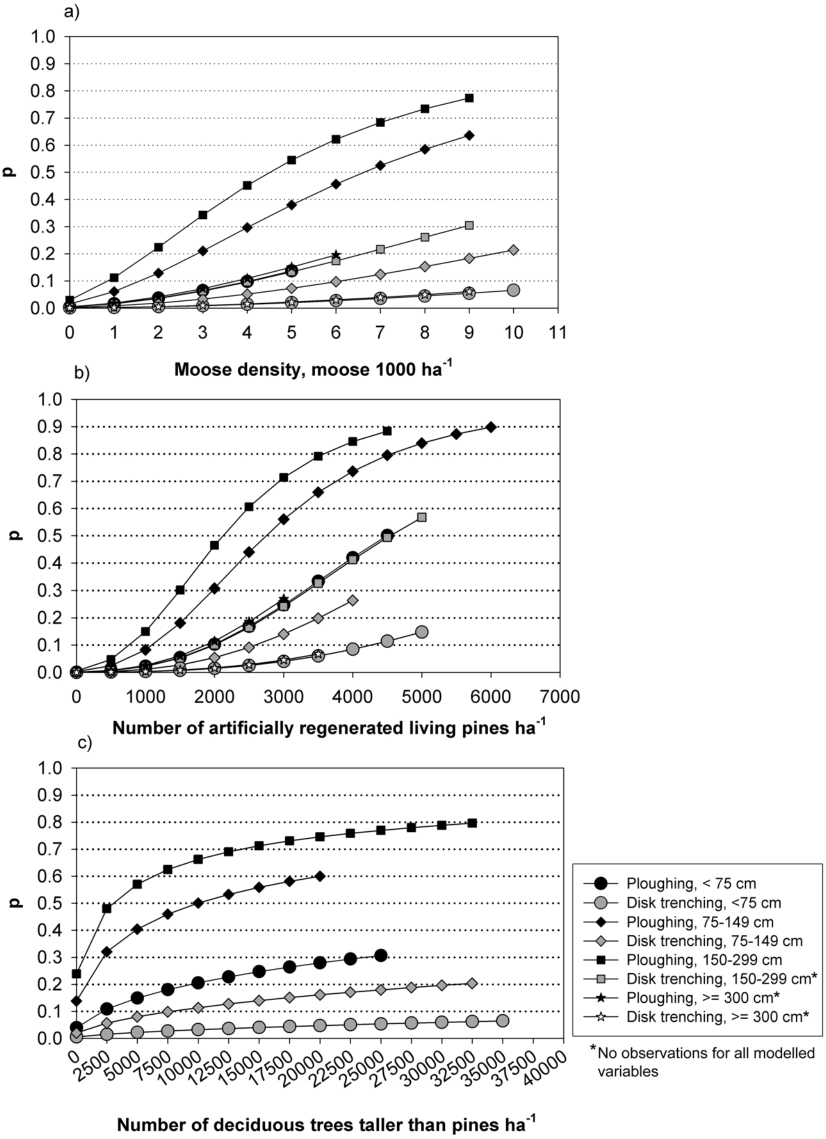

Fig. 3. The probability of moose browsing risk according to Model 3 with different levels of moose density, number of artificially regenerated Scots pine and number of deciduous trees taller than pines. The probabilities were calculated for different soil treatment methods and height classes of pines. 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
R^2	0.35		0.37		0.35		0.35		0.39	

Table 5. Fit of the models in the test data. Specificity and sensitivity were calculated at the mean values of predicted probabilities. The model numbers correspond to those in Table 3.

Model number	Specificity	Sensitivity	Area under ROC-curve
1	0.74	0.59	0.74
2	0.76	0.58	0.74
3	0.77	0.58	0.74
4	0.74	0.58	0.71
5	0.76	0.61	0.73
6	0.79	0.62	0.74

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 explanation 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 ($r = 2.52$ 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 (Vivås 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.

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