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Contents

Abstract

Intensive forestry and small-scale forest fragmentation have favoured moose (*Alces alces* L.) populations in Finland. Each year moose browsing causes considerable damage in high-density, winter range areas in young Scots pine (*Pinus sylvestris* L.) stands with an admixture of deciduous trees. As a generalist herbivore, the moose feeds selectively on several tree species to a varying extent, and all browsing does not cause damage. When attempting to keep moose damage at a sustainable level, information is needed about the effects of food resources and their occurrence in relation to browsing damage. In this thesis, I studied methods of reducing moose damage with respect to the possibility of combining modern forestry and moose management.

The studies were conducted by examining both the quantitative and qualitative factors affecting moose browsing behaviour in southern and central Finland during 1988-96. The early development of young pine stands was studied in relation to the effects of silvicultural cleaning and moose browsing. The effects of stand composition and the chemical composition of pines on moose browsing were also investigated. The use of salt stones to direct moose browsing to advanced young pine stands was studied in order to determine whether the residence time of moose in habitats with no risk of moose damage could be increased.

The exclosure studies showed that moose browsing reduces the height of preferred tree species within a short period of time. However, silvicultural cleaning usually has a greater effect than browsing. Early cleaning is certainly needed to avoid the harmful competition of dense and overtopping deciduous, mainly birch (*Betula* spp.), vegetation even in high-density moose areas. However, the cleaning operation could, in many cases, obviously be carried out more selectively in order to preserve moderate densities of seedlings valuable as moose forage. A considerable reduction in the amount of food taken from preferred trees after cleaning could increase the residence time of moose in pine monocultures and the risk of damage. I concluded that, if cleaning is widely applied to remove the trees preferred by moose, it is not a reasonable method for preventing damage. This is because

such species usually do not compete with pine, but are considered to be an alternative food source. The dynamics of stand development should, however, be taken into account to keep abreast of the situation during risky years.

There is variation in the distribution and quantity of tree species selected by moose. For instance, young aspens (*Populus tremula* L.) occur patchily as root suckers. In situations where the densely growing preferred tree species is highly attractive and browsed by moose, the young pine seedlings are also easily damaged resulting in openings in the pine stands.

Individual differences between browsing on young pines may be related to plant chemistry. Pines strongly competing with birches were highly browsed, probably reflecting the effects of shading. Differences in phenolic and fiber concentrations compared to *in vitro* digestibility supported the conclusion that moose is a relatively tolerant herbivore towards the defensive compounds produced by plants. The concentration of terpenes such as sesquiterpenes and resin acids was relatively high in only lightly browsed young pines on sites of the dryish forest type. However, in more fertile site types this effect was not significant, probably due to the possibility available to moose of reducing the negative effects of resins by using a mixed diet.

Salt stones are most useful in advanced young pine stands during winter, because they can increase the residence time of moose in feeding habitats where there is no risk of moose damage. The risk of moose damage is apparently reduced in pine seedling stands due to increased feeding on the lateral twigs of pine close to salt stones.

The results indicate that forestry and moose management can be combined in high-density moose areas. The suitable timing of silvicultural cleaning and the use of salt stones to direct moose browsing to alternative feeding habitats could be used to minimise moose damage in mixed pine-deciduous stands.

List of publications

This thesis is based on the following articles, which in the text will be referred to by their Roman numerals.

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

II Heikkilä, R. & Härkönen, S. 1998. The effects of salt stones on moose browsing in managed forests in Finland. Alces. In press.

III 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: 000-000. In press.

IV Härkönen, S., Heikkilä, R. & Kitunen, V. 1997. Moose (*Alces alces* L.) browsing on young Scots pines (*Pinus sylvestris* L.) in relation to terpene compounds. Zeitschrift für Säugetierkunde 62, Suppl. 2: 88-92.

V Härkönen, S., Heikkilä, R., Faber, W. E. & Pehrson, Å. 1998. The influence of cleaning on moose browsing in young Scots pine stands in Finland. Alces. In press.

The published papers I and IV are reproduced by permission of the journals concerned.

Sauli Härkönen has participated in planning the studies, gathered the field data, done the statistical analyses, and written the manuscripts (I, II, IV, V).

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1. Introduction

Intensive forestry and small-scale forest fragmentation resulted in an increase of the moose (*Alces alces* L.) population during the 1970's (Strandgaard 1982, Nygrén & Pesonen 1993). In Finland, large forest areas have been regenerated with Scots pine (*Pinus sylvestris* L.). Moose are especially attracted to young pine-deciduous stands because of their high supply of food (Cederlund & Okarma 1988). In Europe, Scots pine is the winter food most commonly used by moose (Bergström & Hjeljord 1987). Moose browsing can lead to damage on pine especially in high-density winter range areas (Lavsund 1987). The economical losses to forestry caused by moose damage can amount to tens of millions of Finnmarks per year (Lääperi & Löyttyniemi 1988). These losses are also of considerable importance for wildlife management owing to the need to reduce moose population densities to a sustainable level (Nygrén & Pesonen 1993).

In Finnish forestry, attention has been paid to obtaining information about the possible reasons for moose damage (Löyttyniemi & Piisilä 1983, Lääperi & Löyttyniemi 1988, Heikkilä 1990, Heikkilä & Härkönen 1993). Recommendations based on earlier studies have been given about ways of preventing moose damage in forestry. For example, Löyttyniemi & Lääperi (1988) recommended that rowan (*Sorbus aucuparia* L.) and aspen (*Populus tremula* L.) should be removed by silvicultural cleaning because these species increase the risk of moose damage to pine. In addition, the presence of birches (*Betula* spp.) as an overgrowth above pine increases the likelihood of stem breakage by moose (Heikkilä 1993, Heikkilä & Härkönen 1993). The results obtained so far have been based on randomly inspected pine stands in southern Finland. In Sweden, moose browsing has been studied in relation to theories on herbivory and optimal foraging using cafeteria tests under controlled conditions (Lundberg & Danell 1990, Åström et al. 1990, Danell et al. 1991a). The results have also been used in predicting the occurrence of moose damage. For example, Edenius (1991) reported that the tree species composition did not affect moose browsing. There is clearly a lack of studies on moose browsing in mixed pine-deciduous stands with experimentally controlled variation in food availability.

Moose feeding has been studied at the habitat scale (Bobek et al. 1975, Heikkilä & Härkönen 1993) and stands (Löyttyniemi & Piisilä 1983, Lääperi & Löyttyniemi 1988, Danell et al. 1991a, Heikkilä 1993). In addition, tree-level selection by moose has been studied in relation to the biomass availability (Lundberg et al. 1990, Danell et al. 1991a) and secondary compounds such as terpenes (Löyttyniemi 1985, Danell et al. 1990) and phenols (Sunnerheim-Sjöberg & Hämäläinen 1992). Secondary compounds in food plants affect moose winter browsing (Bryant & Kuropat 1980). The origin of pines (Niemelä et al. 1989), pine phenotypes (Danell et al. 1991b), the density of pine stands (Heikkilä & Mikkonen 1992), and a high density of deciduous saplings (Heikkilä et al. 1993a) can all affect the quality of pine and hence moose browsing. In addition, resource availability can affect the content of secondary compounds in food plants (Bryant et al. 1983, Coley et al. 1985). Studies have also been carried out in relation to the twig size and digestibility (Hjeljord et al. 1982, Palo et al. 1992).

Artificially regenerated pine stands usually contain an admixture of naturally regenerated deciduous tree species which compete strongly with the pines. Silvicultural measures such as cleaning have been performed in these stands to reduce competition and to promote the growth of pine. In managed forests both cleaning and moose browsing have implications for the early development of young stands. In the short term, cleaning affects the tree species composition and reduces food availability for moose (Hjeljord & Grønvold 1988). There is also a threat of long-term consequences because moose browsing can alter the expected development of forest stands (Lavsund 1987, Thompson et al. 1992). Furthermore, repeated heavy browsing can reduce the height growth of the trees (Risenhoover & Maass 1987, Heikkilä & Härkönen 1993), increase the mortality of deciduous shrubs (Thompson et al. 1992), and affect forest productivity in the long term (McInnes et al. 1992) by depressing nitrogen mineralization (Pastor et al. 1993).

Attention has been paid to combining forestry and moose management (Löyttyniemi & Lääperi 1988). Lääperi (1990) suggested that moose damage could be reduced by providing cutting residues in artificial winter feeding stations. In addition, Lääperi (1990) showed that moose regularly visit feeding stations equipped with salt stones. However, the method is difficult to apply and it has not been widely used in wildlife management. Because alternative food sources could be useful, attempts should be made to improve these methods.

The winter diet of moose consists of woody plants that contain relatively small amounts of sodium (Jordan et al. 1973, Jordan 1987). Sodium is important for moose (Jordan 1987, Faber 1993) and it may also be an important factor in dictating the home ranges of moose (Fraser & Reardon 1980, Miller & Litvaitis 1992). Placing salt stones to keep moose in hunting areas is a common method in moose management in Finland. Salt stones contain sodium in the form of NaCl. Thus, there might be possibilities of using salt stones to direct moose to habitats where there is no risk of browsing damage.

2. Aims

The general aims of these papers were to study moose winter browsing in relation to the effects of forest management, and to determine the possibilities of preventing moose damage in young Scots pine stands.

The specific aims were to answer the following questions:

What are the effects of silvicultural cleaning on the food availability of moose (I, III, V)?

Is there selectivity in moose browsing in relation to the composition and density of young Scots pine stands (I, III, V)?

Are there any differences in moose damage to Scots pine in relation to early applied (III, V) and delayed (I, V) silvicultural cleanings?

Is the use of silvicultural cleaning (III, V) and salt stones (II) to prevent moose damage a reasonable practice?

Can the chemical composition of Scots pine twigs affect moose browsing (IV, V)?

What are the effects of moose browsing and cleaning on the early development of young managed stands (I, III, IV)?

What are the effects of salt stones on moose browsing in advanced young Scots pine stands (II)?

3. Material and methods

3.1. Study areas and sampling procedures

The effects of moose browsing on the early development of pines (I) were investigated at Lapinjärvi (60°30'-60°40'N, 26°00'-26°30'E) in southern Finland in 1994. The experimental area was divided into 39 blocks (40 x 40 m) with nine sample plots per block. The pines planted in the study area were in three density classes (<1300/ha (n = 12), 1300-2100/ha (n = 14), and >2100/ha (n = 13)).

The effects of silvicultural cleaning in relation to moose browsing were studied at Viitasaari (63°14'N, 25°28'E) in central Finland (I, V), and at Tohmajärvi (62°19'N, 30°39'E), Mynämäki (60°46'N, 22°15'E), and Hyvinkää (60°37'N, 24°39'E) in southern Finland (III). Exclosures (25 x 50 m) were also used for comparisons in order to obtain information about the combined effect of cleaning and moose browsing (I, V).

Nineteen Scots pine stands (1-2 ha) established by planting were selected for the cleaning experiment in southern Finland (III). In late summer 1991, the stands were divided into two treatments: 1) cleaned; silviculturally cleaned area, i.e. the deciduous tree stems competing with pine were removed mechanically, and 2) untreated; control area containing the original deciduous tree species. The stands were inspected in spring 1992. By examining the plots immediately after a browsing period of one winter it was assumed that no chemical changes would have occurred in the trees in the cleaned area, and thus differences in moose browsing should reflect only changes in stand density and biomass availability.

Experimental Scots pine stands were established in central Finland (V) by planting in 1984. The early applied cleaning was performed in 1988-89. There were 13 cleaned and 7 untreated stands. The first inspection was made in 1990. In those stands left untreated the deciduous trees were competing strongly with pine. In 1993-94 cleaning was completed to promote the pine growth. This treatment can be considered to be delayed cleaning. The treatment was also repeated in the stands cleaned in 1988-89. The experimental stands were re-inspected in 1995 and 1996.

The effects of salt stones in relation to moose browsing (II) were studied in central Finland (62°54'N, 25°38'E). Salt stones weighing 10 kg each and containing more than 99% NaCl were placed in 17 advanced young Scots pine stands in autumn 1994. The average height of the pines was more than 4 m, and there was therefore no longer any risk of stem breakage by moose (Heikkilä & Mikkonen 1992). The stones were placed in the middle of the stands on posts at a height of ca. 2 m, the distance between adjacent stones being at least 300 m. Salt stones had not previously been used in the area. The stands were divided into two groups according to the accessibility of pine twigs for moose. The shorter pine stands (n = 9) had more lateral branches within the reach of moose than the taller stands (n = 8). New stones were placed in the stands prior to winter 1995/96. The sample plots were inspected in spring 1995 and 1996. Ten control stands without salt stones were inspected in 1996. In addition, the moose browsing intensity in 30 young pine seedling stands was inspected in order to estimate the amount of damage occurring at different distances from the salt stone stands. The seedling stands were located less than 1 km (n = 11), 1-2 km (n = 12), and over 2 km (n = 7) from the salt stone stands.

3.2. Moose browsing and biomass estimations

Moose browsing was measured on circular plots. The plot size was 20 m^2 (III), 30 m^2 (I) and 50 m^2 (I, II, V). A systematic line-plot method (Lääperi & Löyttyniemi 1988) was used in the inspections (II, III), and systematically located permanent plots were used for monitoring purposes (I, II, V). The density and height of the tree stems (I, II, III, V) were determined by species. The number of saplings removed in cleaning (V) was counted in 1995.

Pine stem breakages caused by moose browsing were counted. The scent marking of trees by moose was not noted (cf. Bowyer et al.

1994). The number of moose fecal pellet groups accumulated during winter were counted on every plot (I, II, III, V).

Browsing was measured by counting all the bites made by moose (I, II, III, V). Bite diameter was measured on all tree species to the nearest millimeter. The bites were converted to consumed dry-weight biomass (I, II, III, V) according to Telfer (1969). The relationships were calculated by weighing twigs (dried at 70 °C to constant weight) from the diameter categories most browsed by moose (V). Biomass availability (I, II, III, V) was determined using the equations presented by Heikkilä & Härkönen (1993).

3.3. Plant material for chemical analysis

The pine needle material for terpene analysis (IV) was collected from Viitasaari and Hattula (61°02'N, 24°33'E) in March 1995. The former pine stand was growing on a dryish forest site (*Vaccinium vitis-idaea* type, VT type) and the latter one on a relatively fertile forest site (*V. myrtillus* type, MT type) (Cajander 1909). The pine stands had been established by planting in 1984. The height of the pines was ca. 2 m.

In both the Viitasaari and Hattula samplings, the needle samples from current annual shoots were randomly collected from 12 lightly browsed and 12 intensively browsed pines. The nonbrowsed pine samples were collected at Viitasaari from 24 trees and at Hattula from 12 trees close to each browsed tree. The lightly browsed pines had less than 10 moose bites, indicating that moose had tasted the trees but not continued browsing. In the case of the intensively browsed pines, on the other hand, only a few twigs were still available after moose feeding. There were no signs of browsing in the nonbrowsed pines. In both study areas the sampled pines were growing in different parts of a 4-5 ha stand. According to the tracks, 2-4 moose had been browsing just before sampling.

In December 1993 (V), 40 unbrowsed pines were randomly selected in the Viitasaari study area for the analysis of *in vitro* dry matter digestibility (IVDMD), total phenol content, neutral detergent fiber (NDF), and acid detergent fiber (ADF). Twenty pines were chosen in each of the following two habitat types: 1) cleaned; mechanically cleaned pine stand without competition from an overstory of deciduous trees, and 2) untreated; pine stand with competition from an overstory of deciduous trees, mainly white birch (*B. pubescens* Ehrh.). The pines were growing on a dryish forest site.

Another sampling was carried out in order to analyse the response of browsing to the quality of pine twigs at Padasjoki/Vesijako (61°30'N, 25°10'E), in southern Finland, in March 1990. The pine stand growing on a dryish forest site type had been naturally regenerated in 1970-71. The stand was a monoculture and there was therefore no competition from deciduous tree species. Pine twigs for the analysis of IVDMD, total phenol, NDF, and ADF were collected from two habitat types: 1) sparse stand (pine density <3,600/ha), and 2) dense stand (pine density >9,600/ha). Twenty pines of each habitat type were randomly selected for chemical analysis. In both the Viitasaari and Padasjoki/Vesijako samplings, three shoots of the current annual growth were taken randomly from every tree. The sampled twigs were cut at a height of ca. 1.5 m, which is the typical feeding height of moose.

3.4. Chemical analysis

The needle samples (IV) were stored at -70 °C. The pine twigs (V) and needles (IV) were dried at 70 °C for 24 hours and milled to pass through a 1.0 mm screen. Concentrations of terpene compounds were determined (IV) by gas chromatography mass spectrometry (GC-MS analysis). Identification of the terpene compounds was done using retention and mass spectral data presented by Pohjola (1993). The terpenes determined were: a) monoterpene hydrocarbons (α-pinene, β-pinene, 3-carene, camphene, limonene, tricyclene, α-phellandrene, α-terpinene, γ-terpinene, and sabinene), b) oxygen-containing monoterpenes (bornylacetate, α-terpineol), c) diterpenes (manoyloxide, manool), d) sesquiterpene hydrocarbons (β-caryophyllene, γ-muurolene, germacrene D, δ-cadinene, α-humulene, and bicyclogermacrene), and e) oxygen-containing sesquiterpenes (germacra-1-E, 5E-dien-4-ol, cubenol). Cyclic diterpenes referred as the resin acids were determined on the basis of their retention time and mass spectral data published by Holmbom (1977), Gref & Tenow (1987), and Morales et al. (1992). The resin acids identified were: isopimaradienoic acid, pimaradienoic acid, pimaric acid, sandaracopimaric acid, isopimaric acid, palustric acid, dehydroabietic acid, abietic acid, neoabietic acid, 4-epiimbricatolic acid, pinifolic acid, and an unidentified (UI) group of resin acids eluting after pinifolic acid.

In vitro dry matter digestibility (IVDMD) was measured (V) using moose ruminal inoculum from moose harvested at Grimsö Wildlife Research Station, southcentral Sweden, in winter 1993-94. The analysis is described in detail by Pehrson & Faber (1994). The analysis was repeated 2-3 times depending on the sample size. Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were analysed (V) according to Van Soest (1963) and Van Soest & Wine (1967). Total phenols were determined (V) by the Folin-Ciocalteau method (Singleton & Rossi 1965). Analysis of total phenols was repeated 2 times.

3.5. Statistical analysis

Statistical analysis was performed using the Mann-Whitney *U*-test (I), Student *t*-test (II,V), paired *t*-test (III), one-way analysis of variance (ANOVA) with Bonferroni corrections (I, II, IV, V), Pearson correlation analysis (I, II, III, V), linear regression analysis (V), and stepwise regression analysis (III, V). Because short-term food selection by moose occurs in small patches, even at the individual tree level within a stand (Vivås & Saether 1987, Danell et al. 1991a), the experimental blocks (III) and browsing categories (IV) were treated as independent units in the comparisons. Proportional data (III, V) were arcsine square-root transformed before the statistical analyses. Densities of the tree species were $\log_{10} + 1$ transformed (V). Multicollinearity between variables was taken into account in the stepwise regression analyses (III, V).

4. Results and discussion

4.1. Effects of silvicultural cleaning on food availability

The presence of fast-growing deciduous trees means that young Scots pine plantations have to be silviculturally cleaned. In this thesis, for example, the number of stems removed by both early applied and delayed cleaning was >14,000 stems/ha in once-cleaned areas (V). In general, cleaning is used to promote the growth of pine in Finnish forestry (Jakkila & Pohtila 1978). However, if we take into account not only silvicultural but also wildlife management aspects, it is evident that cleaning also has disadvantageous effects.

Silvicultural cleaning reduces the amount of browse available for moose (Hjeljord & Grønvold 1988). In this thesis, total stand density was 65% and total biomass availability 50% lower in cleaned areas than in untreated areas after the early applied cleaning in the Viitasaari study area (V). The respective proportions in another study (III) were 52% and 18%. In both experiments, the density of deciduous trees and juniper in the cleaned areas (III, V) was together reduced by 72% compared to the untreated areas. The total available biomass of deciduous trees and juniper was 83% lower in the cleaned than in the untreated areas (III). Early applied cleaning mainly reduced the densities of silver birch (*B. pendula* Roth.) (III, V), white birch (III, V), and rowan (III). Delayed cleaning also reduced the densities of white birch, silver birch, aspen, and willows (*Salix* spp.) in once-cleaned areas (V), and significantly reduced the height of deciduous tree species.

In general, the diet of moose is very broad (Morow 1976). The nutritional needs of moose are well satisfied if the winter browse consists of several browse species (Oldemeyer et al. 1977). In this thesis, the tree species most removed by silvicultural cleaning were birches (I, III, V), resulting in food availability dominated by pine (I, III, V). After delayed cleaning, for example, the proportion of pine out of the total available biomass was 80% in once-cleaned areas and 90%

in twice-cleaned areas (V). After early cleaning, pine also accounted for a significantly higher proportion of the total available biomass in the cleaned areas than in the untreated areas (III, V). However, I suggest that a high proportion of birch saplings can most likely be cleaned without any negative effects on moose foraging, because birches are of medium preference as browse species (Bergström & Hjeljord 1987). The opposite is true when cleaning is directed at deciduous species preferred by moose. Preferred tree species such as aspen, rowan, and willows (Bergström & Hjeljord 1987) are considered to be important for moose in winter owing to their high digestibility and diversifying effect in the diet (Hjeljord et al. 1982, Salonen 1982, Sæther & Andersen 1990). In the present studies, cleaning clearly reduced the availability of deciduous tree species preferred by moose (III, V).

In Alaska, the diet of moose consists mostly of willows (Van Ballenberghe et al. 1989). Pine is, however, the main winter food of the moose in Scandinavia (Cederlund et al. 1980), although it is ranked medium in preference (Bergström & Hjeljord 1987). The results of this thesis also show that pine was the tree species that was consumed the most in quantitative terms (II, III, V). On the other hand, cleaning affected the browsing alternatives of moose. The availability and consumption of preferred forage was high in the untreated areas compared to that in the cleaned areas (III). In addition, the amount of deciduous tree and juniper biomass consumed was ten times higher in the untreated areas than in the cleaned areas (III). This means that moose have the possibility to select for browse of better quality (expressed as preferred tree species) in the untreated areas. This is consistent with the results of Andersen & Sæther (1992) who showed that moose selected more digestible forage when the availability of browse increased. This can consequently lead to increased survival and reproduction of moose (Moen et al. 1997). A high resource availability also allows moose to move over longer distances and to be selective (Sæther & Andersen 1990). In such conditions, concentrated browsing in small areas is not likely to be expected and moose damage to pine might be reduced.

A late cleaning in advanced young stands can also have positive effects on food availability for browsers (Newton et al. 1989). In this thesis, the regrowth of deciduous trees after early cleaning was considerable, and a lot of stems were also removed in later treatment (V). In this respect, mechanical cleaning is advantageous for moose compared to chemical cleaning (cf. Connor & McMillan 1988, Hjeljord & Grønvold 1988). At present, mechanical cleaning is practically the only method used in controlling excess deciduous trees in Finland. In conclusion, cleaning removes a high proportion of the food resources of moose. However, the regrowth of browse can be expected in the new sprouts formed after cleaning treatment.

4.2. Effects of tree species composition and biomass availability on moose damage to pine

Preferred tree species can have an attractive influence on the habitat use of moose (Goulet 1985). This can also affect moose browsing behaviour. For example, the presence of preferred tree species such as rowan and aspen may increase the risk of moose damage to pine in certain conditions (Löyttyniemi & Piisilä 1983, Lääperi & Löyttyniemi 1988, Heikkilä 1990). In this respect, Löyttyniemi & Lääperi (1988) recommended the removal of tree species preferred by moose as a means of preventing damage to pine. In this thesis, the browsing of small pine seedlings by moose was common in patches with a higher density of the preferred and highly utilized deciduous trees, aspen and rowan (I). In older pine stands, the density or amount of biomass available in the form of different deciduous tree species did not, however, explain the variation in moose browsing on pine (III). These results (III) are consistent with those of Edenius (1991), who found that moose browsing on pine was only slightly affected by the species composition of the tree mixtures. In another study (V), the density of white birch best explained the variation in the number of broken pine stems and pine biomass consumption, whereas the densities of other deciduous tree species did not explain moose damage to pine. This also demonstrates how tree species dynamics in natural conditions makes the situation different from that in artificial browsing trials (cf. Edenius 1991).

In natural stands the presence of birches as an overgrowth above pine can increase the risk of stem breakages by moose (Heikkilä 1993, Heikkilä & Härkönen 1993). In my study (III), there were no differences between the treatments as regards the amount of pine consumed and in the amount of moose damage to pine. The lack of significant differences can be explained by the fact that the pines were not overtopped by birch (cf. Heikkilä et al. 1993a). In another study (V), there were more broken pine stems in untreated areas in winter 1989/90. When the cumulatively damage to pines was compared, there were significantly more browsed pines and stem breakages in once-cleaned areas. This shows, indirectly, that a high density and overgrowth of birches in the untreated areas during 1988-94 increased the risk of moose damage to pine.

However, is it in fact the birch density itself which is the driving mechanism for moose damage to pine? I believe that this question cannot be explained only by quantitative factors. The mechanism may be even more complicated, because the qualitative composition of pine can affect moose browsing in certain conditions (Niemelä et al. 1989, Danell et al. 1990, Danell et al. 1991b). In my study (III), there were evidently no chemical differences between the pines in the cleaned and untreated areas (i.e. at the stand level) caused by excess deciduous vegetation. Furthermore, no growth occurred between cleaning and winter browsing. However, there may have been differences at the tree level in relation to terpene compounds (IV). If there were no chemical differences in the pines between the areas (III), moose probably made the decision to start browsing on the basis of biomass availability or stand composition.

Moose damage to small pine seedlings occurred in patches with a high density of aspen root suckers (I). The associational plant refuge hypothesis (APRH) predicts that a plant species gains protection from herbivory due to association with unpalatable neighbours (cf. Pfister & Hay 1988). Thus, plant species occurring alone or in association with species of higher quality should increase the risk of herbivory. According to Pfister & Hay (1988), APRH might explain herbivory in mixed stands. The validity of the hypothesis was, however, put in question on the basis of a moose experiment (Danell et al. 1991a). APRH was also rejected in a willow-sawfly system (Hjälten & Price 1997). In contrast, Hjälten et al. (1993) found that when hares and voles had knowledge of stand quality and were able to move between stands, birch gained protection through its association with unpalatable alder. In this thesis, moose damage to pine was higher in high density birch areas (V). Birches can be considered as species of lower quality compared to pine (Andersson & Markkula 1974, Salonen 1982). Thus, pine did not gain protection from herbivory due to its association with less-palatable birch, which is a result in conflict with the APRH. On the other hand, the experiments were carried out from autumn to spring and the results are therefore not directly comparable with short-term experiments with APRH (cf. Danell et al. 1991a).

The results (I) are consistent with the nutrient mixture hypothesis. The nutrient mixture hypothesis predicts negative frequency-dependent food selection (Westoby 1974, Pulliam 1975, Crawley 1983, Lundberg et al. 1990). This means that moose should over-utilize rare plant types. Small pines represented such a marginal food resource, and there were more browsed pines when there was a higher density of aspen and rowan saplings (I).

In monocultures, moose browsing follows a functional response (Vivås & Saether 1987, Heikkilä & Mikkonen 1992). This means that the total consumption increases along with increasing total biomass availability. An increase can be considered continuously decelerating not only in a stand of equal sized trees, but also in a stand of unequal tree size (Lundberg & Åström 1990). On the other hand, proportional consumption simultaneously decreases. If moose damage to pine is taken into account, this means, for example, that the proportion of browsed pines should decrease with increasing pine density. This was also the result obtained in this thesis (I).

Biomass availability at the tree level affects moose browsing even more than that at the stand level (Danell et al. 1991a). This allows us to consider an individual pine as a patch, and consumption by moose can be viewed with respect to optimal patch use models (Lundberg & Danell 1990, Lundberg & Åström 1990, Åström et al. 1990, Danell et al. 1991a). According to the marginal value theorem (MVT) (Charnov 1976), the general prediction is that a herbivore should leave a patch when the intake rate in that patch drops below the average intake in the whole habitat. In a moose-pine system, pine is a patch where the consumption should be optimized by moose. The handling time of a pine by moose is comparable to the patch residence time, and biomass extraction from trees decelerates with increasing handling time (Åström et al. 1990). The moose-pine system can, however, be even more complicated. When moose is browsing it also has to take optimal twig-size selection into account (Vivås et al. 1991). If moose selects a large diameter twig, a longer time will be needed to extract the available energy because of its high fibre content. On the other hand, the selection of small twigs will decrease the intake rate and a longer time will be needed to fill its stomach. Furthermore, in mixed pine-deciduous stands moose have several tree species on which to optimize their consumption. Thus, it is difficult to find an optimal solution using theories of optimal foraging (Hanley 1997).

Moose can even prefer birch over rowan both in terms of selection and the use of trees in winter when quantitative requirements probably rule out slight differences in quality (Lundberg et al. 1990). This means that moose have to make a decision to browse with respect to biomass availability. The diet selection problem of moose is, however, very complex because of interactions between constraints and objectives and the high heterogeneity of food resources in managed pine stands (cf. Hanley 1997). However, moose can gain benefit by using nonrandom foraging strategies compared to random foraging strategies (Moen et al. 1997). On the other hand, it is easy to predict that moose use pine as browse in winter. Pine is easily available (II, III, V) and individual pines contain a lot of relatively palatable browse. Furthermore, this means that moose damage to pine is difficult to prevent by regulating the tree species composition (cf. Danell et al. 1991a, Edenius 1991).

If cleaning is used, total cleaning should be avoided. In this thesis, the proportion of consumed pine biomass out of total consumption was significantly higher in cleaned stands (74%) than in untreated stands (51%) (III). Thus, moose browsing is likely to be directed at pine if pine is the only tree species available as winter forage for moose. In addition, an admixture of birch in pine stands may improve the timber production and the technical quality of the wood (Ikäheimo & Norokorpi 1986).

4.3. Effects of the chemical composition of pine on moose browsing

Food quality in terms of secondary compounds affects moose winter browsing (Bryant & Kuropat 1980). Terpenes are one group of secondary compounds in pine needles that may help trees to defend against herbivores (Larsson et al. 1986, Elliott & Loudon 1987). It has been shown that diterpenes in pine needles may have a negative effect on moose browsing (Danell et al. 1990), whereas monoterpenes have no marked effect (Löyttyniemi & Hiltunen 1978, Löyttyniemi 1985, Danell et al. 1990). In addition, sesquiterpenes inhibit the digestion of mule deer (*Odocoileus hemionus*) (Schwartz et al. 1980). The phenol composition of pine needles may also affect the food choice of moose (Sunnerheim-Sjöberg & Hämäläinen 1992).

According to the resource-availability hypothesis (RAH), plant species should invest more in defence against herbivores under conditions of slow growth than under conditions with rapid growth (Coley et al. 1985). The carbon/nutrient balance (CNB) theory also predicts that growth on infertile sites should be limited more by nitrogen than by light (Bryant et al. 1983). In such conditions, carbon could be used for the synthesis of carbon-based defences. Under light limitation or on fertile sites, chemical defence should be nitrogen-based. In this thesis, the dryish forest site (VT type) can be considered as a slow growth, infertile site, whereas the fertile site (MT type) had rapid growth (IV).

There were less resin acids, oxygen-containing sesquiterpenes, and total terpenes in intensively browsed pines than in lightly browsed pines on a dryish forest site. After analysing individual terpene compounds, I found that the pines growing on the dryish forest site had higher concentrations of one monoterpene (α-phellandrene), three sesquiterpene (bicyclogermacrene, δ-cadinene, and germacra-1-E, 5E-dien-4-ol), and six resin acid (sandaracopimaric acic, dehydroabietic acid, abietic acid, neoabietic acid, 4-epiimbricatolic acid, and pinifolic acid) compounds in lightly browsed trees than in intensively browsed trees. Pinifolic acid, for example, has also previously been shown to affect moose feeding (Danell et al. 1990). To my knowledge, there is no earlier report of sesquiterpenes affecting moose food selection. On the relatively fertile forest site, differences between individual terpene compounds were mainly insignificant or even opposite to those on the dryish site. However, these results indicate that moose may be able to detect differences between trees when browsing. The possible deterring effects of terpenes in individual pines seem to be related to the sesquiterpenes and resin acids. Between-tree selection by moose may be more pronounced on dryish forest sites than on fertile sites. Also moose damage to pines is more common on fertile sites than on dryish sites, as presented by Heikkilä (1990) and Heikkilä & Härkönen (1993).

Shaded pines are more vulnerable to moose browsing (Edenius 1993). Moose browsing in dense pine monoculture can be intensive, which may be related to the positive effect of shading on twig quality through the role of nitrogen compounds (Heikkilä & Mikkonen 1992). In addition, both individual and total resin concentrations are higher in sun than in shade needles of pine (Gref & Tenow 1987). Furthermore, shaded willows are more palatable for moose than those growing in the sun (Molvar et al. 1993). In this thesis, high density and an overgrowth of birches (V) could have produced a shading effect. In this sense, a high density of birches would more likely be important as a competing species impairing the growth conditions of pine and affecting the chemical properties of pine, as presented by Heikkilä et al. (1993a). Shading also increases the palatability of silver birches to hares, whereas the palatability to voles tends to decrease (Rousi et al. 1993). This may, however, indicate vertical differences in the defence of birch seedlings to herbivore feeding.

In this thesis, the total phenol content of the pine twigs was slightly higher in the cleaned areas than in the untreated areas (V). On the other hand, the neutral detergent fiber and acid detergent fiber contents of the pine twigs were higher in the untreated areas with a high density and overstory of deciduous trees than in the cleaned areas (V). NDF and ADF were also higher in the dense pine monoculture than in the sparse pine monoculture. However, the *in vitro* dry matter digestibility did not differ between the pine phenotypes. In conclusion, it is difficult to explain, on the basis of the examined plant chemicals, the relatively high cumulative number of browsed pines and stem breakages in the untreated stands during 1988-94. This emphasizes that there must be variables other than the examined chemical parameters, that have an effect on moose browsing. In this sense, terpenes could be such compounds (IV). However, I found that on the relatively fertile forest site with highly preferred tree species such as aspen, rowan, and willows, terpene compounds in the pine needles did not affect moose browsing (IV). In good feeding habitats moose can use a mixed diet (cf. Oldemeyer et al. 1977, Westoby 1978, Miquelle & Jordan 1979), which helps moose to minimise the negative effects of secondary compounds in one food plant by consuming several food plants (cf. Freeland & Janzen 1974).

Digestibility has been shown to decrease with increasing twig diameter (Hjeljord et al. 1982, Vivås & Saether 1987, Palo et al. 1992). On the other hand, increasing twig diameter can reduce the proportion of phenols (Palo et al. 1992). In this thesis, current annual shoots were used for the chemical analyses (V), but the diameter of the sampled shoots was not measured. Thus, I cannot exclude any differences between twig diameters in the cleaned and untreated areas. However, there should be a close relationship between the diameter at the browsing point and the basal diameter of current annual shoots (Bergström & Danell 1986). In contrast, Niemelä & Danell (1988) reported that moose usually consume more than the average current year's growth. On the other hand, high biomass availability in dense stands can encourage moose to browse despite the low quality (Heikkilä & Mikkonen 1992). In addition, determination of total phenolics might be of a limited value only and should not be used as a single estimate of plant palatability (Hjälten et al. 1996) since phenolics are a complex group of compounds with different effects on herbivores. It also appears that chemical defence is less effective against moose, which adjust their foraging decisions at a variety of temporal and spatial scales (Danell et al. 1991a, Edenius 1993).

Moose damage occurs year after year in the same stands (Löyttyniemi & Piisilä 1983). In this sense, I have to take into account the effect of previous browsing. The carbon/nutrient balance (CNB) theory predicts that repeated browsing on juvenile woody plants reduces the carbon reserves and the plants can no longer maintain their resistance against browsers (Bryant et al. 1983). In this thesis, I cannot explain moose browsing on the basis of the examined chemical variables (V). However, this does not mean that repeated browsing did not affect the chemical composition of pines. Simulated winter browsing by moose in a birch experiment has resulted in lower amounts of ether-extractable compounds in comparison with untreated trees (Danell & Bergström 1989). The number of secondary compounds is so large that it is not possible to determine all the compounds affecting moose browsing. It has to be noted that repeated browsing especially affects quantitative factors, increasing e.g. the size of pine needles (Löyttyniemi 1985), the size of birch shoots (Danell et al. 1985), and the growth of willows (Molvar et al. 1993, Bowyer & Bowyer 1997). I cannot exclude whether an increased size of pine needles or shoots was a potential factor affecting moose browsing on pine during 1988-94 (V) because these variables were not determined. However, I believe that the effects of repeated browsing should be smaller than the competitive impact of deciduous trees on the growth of pine.

The density and availability of preferred tree species such as aspen, rowan, and willows are normally low compared with birches in artificially planted pine stands (III, V). The preferred trees are usually not competing with pine and they have no significant effect on moose damage to pine. Thus, silvicultural cleaning to prevent moose damage is not a reasonable practice when it is directed especially at the preferred tree species. I suggest that the birch vegetation has a stronger effect on moose damage to pine than that of the preferred tree species. Birches occurring as overgrowth above pine can have an effect on the chemical composition of pine through shading. Shaded pines may also have small twigs, and thus may suffer more than vigorous pines after moose browsing. I suggest moose damage could be reduced by cleaning. Cleaning should be primarily directed at reducing the overdensity of all deciduous trees, as well as to prevent the competitive effect of overtopping birches.

4.4. Effects of moose browsing on the early development of pine stands

Moose can alter the expected development of young pine stands in Scandinavia and Finland (Lavsund 1987). In general, moose damage has been reported to occur in 5- to 15-year-old pine stands (Löyttyniemi & Piisilä 1983). Moose damage can, however, occur relatively early (I). Early browsing by moose can be the reason for a low density or uneven distribution of pine saplings. After a few years, however, it is no longer possible to determine the real reason for reduced density. Furthermore, early browsing can decrease the capacity to withstand the effect of stem breakage (cf. Heikkilä & Mikkonen 1992). Especially stem breakages lowers the technical quality of the wood (Heikkilä & Löyttyniemi 1992, Heikkilä et al. 1993b).

The moose density affects the moose browsing pressure. In southern Finland, the proportion of browsed trees at a moose density of 0.6-0.7/km^2 (Löyttyniemi & Piisilä 1983) was higher than that in the same area at a moose density of 0.4/km^2 (Heikkilä 1993). Moose browsing can deplete the growth of deciduous trees (I, II) and reduce the competition with pine seedlings (I). Especially highly preferred tree species such as aspen, rowan, and willows (Bergström & Hjeljord 1987) are sensitive to moose browsing (V). The effects become clearly evident in high-density moose areas where the height growth is inhibited due to continuous browsing (Heikkilä & Härkönen 1993). Repeated heavy browsing on palatable species may even affect the ability of these species to regenerate (Risenhoover & Maass 1987). On Isle Royale, USA, balsam fir (*Abies balsamea* (L.) Mill.) was unable to become dominant at a moose density of 2.5-5.0/km^2 (Brandner et al. 1990). In Newfoundland, paper birch (*B. papyrifera* Marsh.) was eliminated at a moose density of 3/km^2 (Thompson & Curran 1993). Moose browsing can also cause mortality and elimination of some deciduous shrubs (Thompson et al. 1992). In general, a high proportion of the browsed trees in high-density moose areas are capable of recovery (Heikkilä & Härkönen 1993). In addition, according to simulated moose browsing pine has a good ability for compensatory growth (Edenius et al. 1993). However, moose can reduce the densities of certain tree species, and this should be taken into account with reference to biodiversity. Deciduous trees are also considered to be beneficial for the succession of conifer stands (Mikola 1955, Berg & Staaf 1987).

In Newfoundland, Canada, moose have altered the expected forest successional patterns on black spruce (*Picea mariana* Mill.) sites (Thompson et al. 1992). In uncontrolled natural stands, moose browsing has long-term consequences by reducing forest productivity (McInnes et al. 1992, Pastor et al. 1993). On the other hand, moose can also slow the rate of succession (Risenhoover & Maass 1987). The expected long-term consequences are difficult to demonstrate in managed pine stands in Finland. Silvicultural practices such as cleaning and thinning can also have a relatively great effect, which should be noted when estimating the effects of moose.

In Norway, Hjeljord & Grønvold (1988) reported that intensive moose browsing on rowan could be advantageous for the growth of spruce (*P. abies* (L.) Karsten). In addition, moose can have a positive effect on forest growth by reducing stem densities to the level of precommercially thinned stands (Thompson & Curran 1993). Thus, I can hypothesize that intensive moose browsing on deciduous trees might also reduce the need for silvicultural cleaning in mixed pine-deciduous stands. This may be true under certain conditions (I), but the hypothesis is not supported by all the results (III, V). In Finland, birches are the main competitors of pine, and moose browsing did not reduce the stem density or height of less-preferred birches at a moose density of 0.5-1.0/km^2 (III, V). Birches also have a good capacity for compensatory growth without suffering from mortality (Bergström & Danell 1987). In addition, overtopping birches can increase the risk of moose damage to pine. As far as the silvicultural aspects are concerned, I conclude that cleaning is needed in high-density moose areas even to regulate the competition between pine and birch (III, V). On the other hand, the densities of rowan, aspen, and willows are likely to be reduced by heavy moose browsing during autumn and winter, supporting the idea that these species should not be removed.

4.5. Effect of salt stones on moose browsing in managed forests

Moose gather together in specific winter range areas (Sweanor & Sandegren 1989, Andersen 1991). In such areas young pine plantations are a risk from heavy moose browsing (Lavsund 1987). Forest habitats with peatland compartments in particular are widely used by moose (Heikkilä & Härkönen 1993). In addition, the residence time of moose in winter may be longer in freshly cut areas (Heikkilä et al. 1996) and at forest edges with dense palatable browse (Histøl & Hjeljord 1993).

In this thesis, I have examined moose browsing in relation to the salt stones provided in advanced young pine stands (II). In the stands there was no risk of stem breakages because the top parts of the young pines had grown out of the reach of moose. On the other hand, there were plenty of lateral pine twigs, the browsing of which can be considered as an alternative to young seedling and sapling stands. During the first winter, moose browsed more in stands with a high twig accessibility than in stands with a low twig accessibility. During the second winter, moose browsed more in salt stone stands with a high twig accessibility than in control stands with a high twig accessibility. The availability of preferred tree species did not attract the moose to browse in the experimental stands. In addition, according to the moose fecal-pellet groups the residence time of moose was greater in the salt stone stands with a high twig accessibility in both winters. The results show that moose can intensively utilize twig biomass in advanced pine stands. The total amount of biomass consumed by moose was even greater than that in young mixed pine-deciduous stands (I, III, V), and close to the average values for high-density moose areas (Heikkilä & Härkönen 1993). One might ask whether moose can browse more pine twig biomass after licking salt stones. According to the present results, however, it is impossible to answer this question, but it is evident that moose browse intensively around salt stones.

Moose show a seasonal pattern in salt stone use. The use of salt stones by moose is rather low during winter, rising sharply in spring, and then showing another peak in autumn before declining again (Jordan et al. 1991). In this thesis, salt stones were available during winter time. Salt stones can also be used by other wildlife (Faber et al. 1993). For comparison, in the Isle Royale National Park moose use mineral licks all year-round (Risenhoover & Peterson 1986). Thus, salt stones can be provided all the time for moose, and this may even increase the possibilities of directing the habitat use of moose to specific forest areas.

The results indicate that using salt stones to direct moose browsing in winter could be used to increase the residence time in habitats with no risk of moose damage. The risk of moose damage in young pine stands might be simultaneously reduced. I suggest that using salt stones in advanced pine stands could be a reasonable wildlife management method. This method is also easier to apply than e.g. artificial winter feeding.

5. Conclusions

Moose browse selectively, and may alter the expected development of young pine-deciduous stands. In stands where the densely growing preferred tree species is highly attractive and browsed by moose, the young pine seedlings are easily damaged. The densities of rowan, aspen, and willows are likely to be reduced by heavy moose browsing. On the other hand, birches can effectively withstand moose browsing. Thus, silvicultural cleaning is needed even in high-density moose areas in order to regulate the competition between birch and pine.

Silvicultural cleaning has a negative effect on moose browsing alternatives in mixed pine-deciduous stands by reducing the available browse. The tree species composition and biomass availability in young pine stands, as well as the qualitative composition of pine in terms of terpene compounds, have an effect on moose browsing. In uncleaned stands, overtopping deciduous trees increase the risk of moose damage obviously by affecting the qualitative composition of pine through shading. Silvicultural cleaning is needed not only to reduce the competition between deciduous trees and pine, but also to reduce the risk of moose damage to pine in stands with overtopping deciduous trees. However, complete cleaning is not a reasonable practice because of its negative effects in reducing alternative food sources. Thus, cleaning should be carried out more selectively in order to maintain moderate densities of seedlings valuable as moose forage.

Advanced young pine stands contain food resources, the browsing of which could be an alternative to young pine seedling and sapling stands. The results indicate that moose browsing can be directed to habitats with no risk of moose damage. The residence time of moose in the habitats could be increased by providing salt stones.

It is not easy to affect moose browsing, since moose adjust their foraging decisions at different levels. The results, however, indicate that moose damage can be prevented in mixed pine-deciduous stands. Modern forestry and moose management could be combined in a way that increases the carrying capacity even in high-density moose areas. The suitable timing of silvicultural cleaning and the use of salt stones are promising methods. These methods are also easy to use in forestry and wildlife management. Consequently, moose damage could be prevented and the conflicts between forestry and moose management reduced.

In the future, additional research is needed on alternative food sources and salt stones. Special attempts should be made to increase the use by moose of cutting residues and browse in advanced young Scots pine stands. This should be implemented by taking into account such possibilities through forest and wildlife management planning.

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Moose browsing in young Scots pine stands in relation to forest management

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Abstract

The effects of moose browsing in young Scots pine stands were studied in southern Finland during 1993–94. The influence of moose on tree species composition starts during the early development of young plantations. A considerable proportion of small pine seedlings was damaged, and hence the future development of the stand was retarded. The average biomass consumption of pine was relatively low increasing slightly with the density of pine seedlings. Browsing of pine was common in the patches with high density of preferred and highly utilized deciduous tree species, aspen and rowan. As elucidated by means of exclosure studies, the availability of tree species preferred and highly utilized by moose, e.g. rowan, is likely to be reduced also by early silvicultural cleaning. Removing excess birches by cleaning appears to be needed even in high-density moose areas to regulate the competition between tree species, especially the birch/pine height ratio. At the present average moose density of 0.4–0.6 km^{-2} forest land, considerable depletion of highly palatable tree species occurs locally in high-density moose ranges. When optimizing the development of young stands, silvicultural treatment timing and browsing by moose should be taken into account. It is considered important when combining forest and wildlife management to identify the conditions under which damage, overconsumption and possible long-term effects on forest ecosystems take place.

Keywords: Alces alces; Scots pine; Plantations; Browsing; Carrying capacity; Biodiversity

1. Introduction

Large mammals have gained considerable benefit from small-scale forest fragmentation and the intensive forestry typical of Scandinavian countries (Strandgaard, 1982). General upwards trends in the size of moose populations during recent decades (Markgren, 1974; Nygrén and Pesonen, 1993) have demonstrated that the conditions favour this animal species.

In Europe Scots pine (*Pinus sylvestris* L.) is generally the most commonly used winter food in quantity by moose (Bergström and Hjeljord, 1987). Moose can considerably alter the expected development of young pine stands (Löyttyniemi and Piisilä, 1983; Lavsund, 1987). The relationships between the effects of consumption by large mammals and the development of young stands are considered important for both forestry and successful wildlife management (Gill, 1992).

Food availability and use by browsers have been studied in relation to the characteristics of forest habitats (Bobek et al., 1975; Peek et al., 1976). Attention has been paid to estimating the moose

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carrying capacity of young forest stands (Morow, 1976; Kuznetsov, 1987; Crête, 1989). As a result of the tendency of moose to use the same areas in winter (Sweanor and Sandegren, 1989), high consumption is likely to occur in young stands in certain forest areas. The influence of deciduous tree species on the future development of the stands has to be taken into account in silvicultural treatments (Jakkila and Pohtila, 1978). Attempts have been made in forest and wildlife management to identify the seasonally used forest areas and the permanently occurring highly utilized areas.

There is often a considerable proportion of naturally regenerated deciduous tree species in young Scots pine stands. The response of different tree species to moose browsing varies considerably, depending on their quality (Hjeljord et al., 1982) and their morphological ability to resist browsing (Saether, 1990). The size and relative abundance of food plants greatly predict moose feeding behaviour (Belovsky, 1981). The quality and mixture of forage species are important in food selection and in the impact of herbivores on plant communities (Westoby, 1974, Westoby, 1978).

In this study the relationships between moose browsing and food availability are examined with respect to the tree species composition of young Scots pine stands. The browsing of pine seedlings is studied in young plantations with a new growth of deciduous sprouts preferred by moose. The influence of browsing on stand development is also studied in relation to the forest management and the areal variation in moose population densities.

2. Materials and methods

The effects of browsing on the early development of pines were examined 2 years after planting in 1994 at Lapinjärvi, southern Finland (60°30′–60°40′N, 26°00′–26°30′E). The experimental area had been divided into 39 blocks (40 × 40 m) with nine sample plots (30 m^2) per block. The blocks were divided into three density classes of planted pines (< 1300 ha^{-1}, 1300–2100 ha^{-1}, > 2100 ha^{-1}). Deciduous tree vegetation, mainly aspen (*Populus tremula* L.) and rowan (*Sorbus aucuparia* L.) and to a lesser extent silver birch (*Betula pendula* Roth.), pubescent birch (*B. pubescens* Ehrh.) and willows (*Salix* spp.), covered the area unevenly. The amount of browsing on different tree species as well as their densities were counted.

The effect of moose browsing on stand development, taking into account the silvicultural cleaning, was examined using two exclosures for comparison. The study was conducted at Viitasaari in central Finland (63°14′N, 25°28′E) in a forest area with a moose density of 0.5–0.7 km^{-2}. The size of the block in the exclosures was 25 × 50 m and the measurements were performed on five systematically located sample plots (50 m^2). The size of the block outside the exclosures was 50 × 50 m, with nine sample plots per block, respectively. The first silvicultural cleaning was made in 1988 using glyphosat and the second in 1993 mechanically. The inspections were carried out in 1993 before the treatment and in 1994.

The estimations for consumed biomass were made using the twig diameter/weight method (Telfer, 1969). Available biomass was estimated using regression equations presented earlier (Heikkilä and Härkönen, 1993). The calculations were performed according to the average height of the stands and the observed maximum bite diameter on different tree species in the area. Infrequently occurring species such as spruce (*Picea abies* L.) and grey alder (*Alnus incana* L.) were excluded from the calculations.

Statistical analyses were done using the Mann–Whitney *U*-test, ANOVA and the Pearson correlation analysis (BMDP-programs).

3. Results

3.1. Effect of browsing during the early development of pine plantation

Moose frequented the area planted in 1992 from the first fall onwards, feeding on the fast-growing aspen sprouts especially. The following year the planted small pines were also utilized, until the snow covered the seedlings less than 30 cm tall. Leader shoot damage occurred on 22%, 26% and 19% of the pines at different densities, with no significant difference between the densities (ANOVA, $F = 1.22$, $P >$

0.05). Thus the number of unbrowsed pines increased significantly with the pine density (Fig. 1). The proportion of damaged pines increased slightly with increasing biomass consumption of aspen and rowan ($r = 0.364$, $P < 0.05$).

The biomass utilized of pines correlated positively with the density of pine ($r = 0.40$, $P < 0.05$) as well as with the biomass consumption of rowan ($r = 0.33$, $P < 0.05$). The amount of biomass consumed of deciduous saplings was relatively high (Fig. 2) and was highly correlated with the sapling density ($r = 0.82$, $P < 0.001$). The average amount of biomass used of small pines was negligible (0.9 kg ha^{-1}) compared with that of deciduous saplings (15.8 kg ha^{-1}, of which 94% was aspen).

The density of aspen and rowan saplings was higher on those sample plots with damage on pine than on those without (4748 ha^{-1} ± 566 SE, $n = 135$, vs. 3336 ha^{-1} ± 595 SE, $n = 216$, Mann–Whitney U-test, $P < 0.001$). Also the consumption of deciduous saplings was correspondingly relatively high on the sample plots with the incidence of pine damage (18.6 kg ha^{-1} ± 2.6 SE, vs. 11.5 kg ha^{-1} ± 2.2 SE, Mann–Whitney U-test, $P < 0.05$). Over 90% of the deciduous saplings (maximum height 55–80 cm) were browsed to the extent that their height development was retarded and competition with pine seedlings reduced.

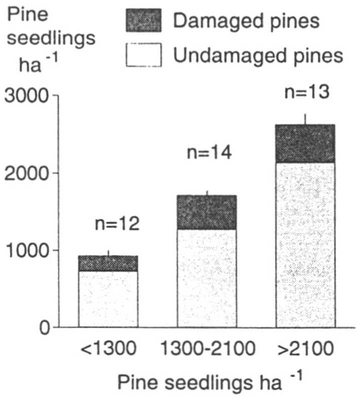

Fig. 1. Density of pine seedlings (mean and SE). The increase in undamaged seedlings is significant (ANOVA, $F = 64.78$, $P < 0.001$).

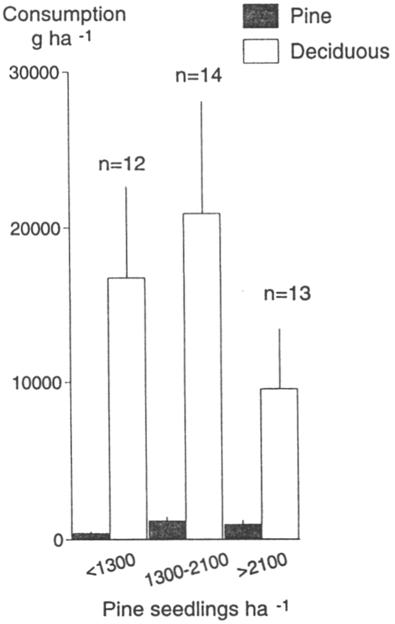

Fig. 2. The biomass consumed by moose of pine seedlings (ANOVA, $F = 3.2$, $P = 0.053$) and deciduous saplings (ANOVA, $F = 0.97$, $P > 0.05$).

3.2. Relationships between the effect of browsing and silvicultural treatment in young pine stands

The total stand density inside the exclosures 10 years after planting in 1994 was 27660 stems ha^{-1} and the twig biomass availability 4105 kg ha^{-1} (Fig. 3). The relatively low availability of deciduous trees in the open stands outside the exclosures was due to the first cleaning in 1988 and the influence of browsing thereafter. In the second cleaning in 1993 excess pubescent birches were mainly removed. The density of deciduous tree stems outside the exclosures subsequently fell from 7566 ha^{-1} to 3823 ha^{-1} and the biomass from 411 kg ha^{-1} to 201 kg ha^{-1}. The average height of deciduous saplings was relatively low after the treatment.

The biomass removed by moose in the open areas outside the exclosures was high in winter 1992–93 compared with 1993–94 owing to the fact that the sapling density had been decreased by cleaning (Fig. 4). The proportion of the reduced available biomass

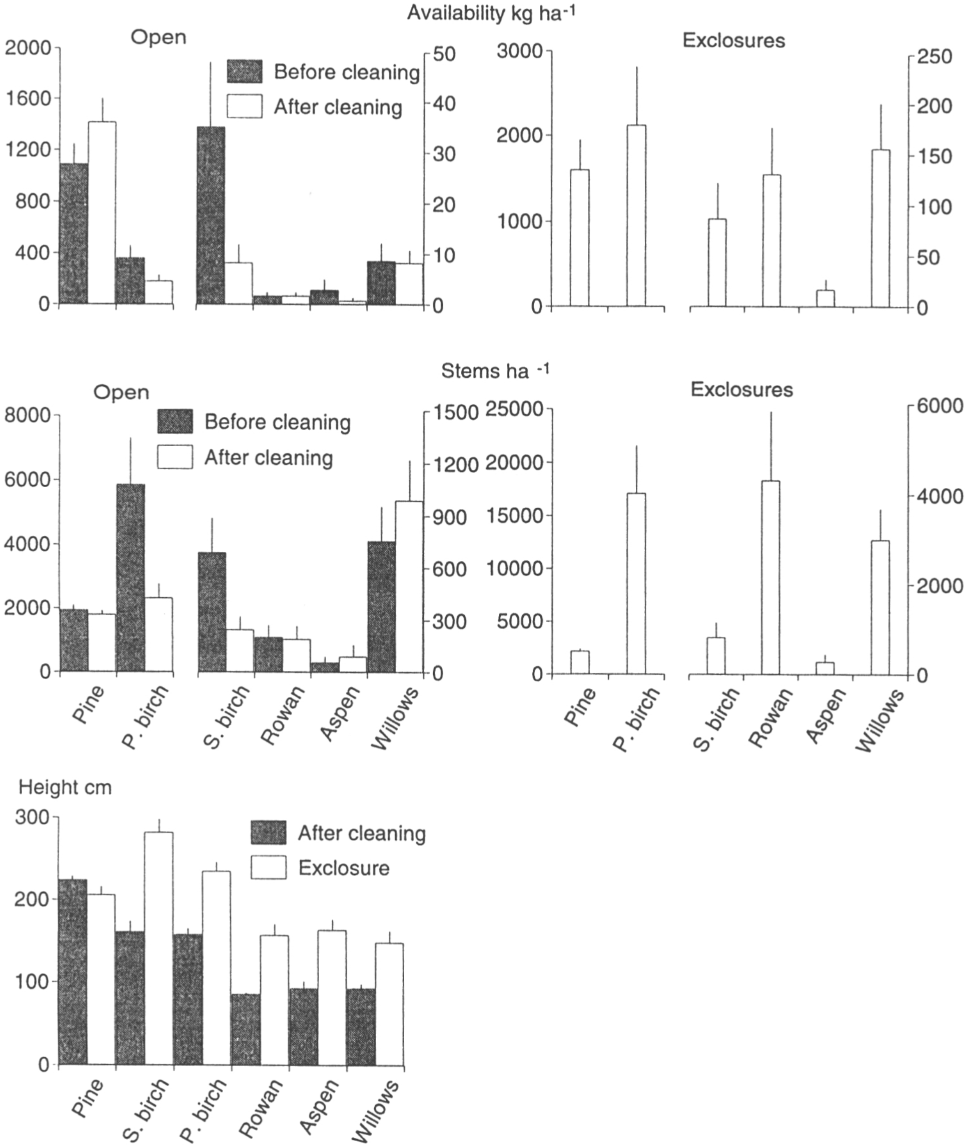

Fig. 3. Food availability and sapling height (mean and SE) in two exclosures and open areas in relation to silvicultural cleaning in 1993. Notice different scales.

consumed was also consistently lower for all tree species.

The availability of rowan was high in the exclosures compared with the open areas, where the stem density of this species was 5% of that in the exclosures. The proportion of this species consumed was over 50% during the winter 1992–93 indicating a high browsing pressure, which was, however, rela-

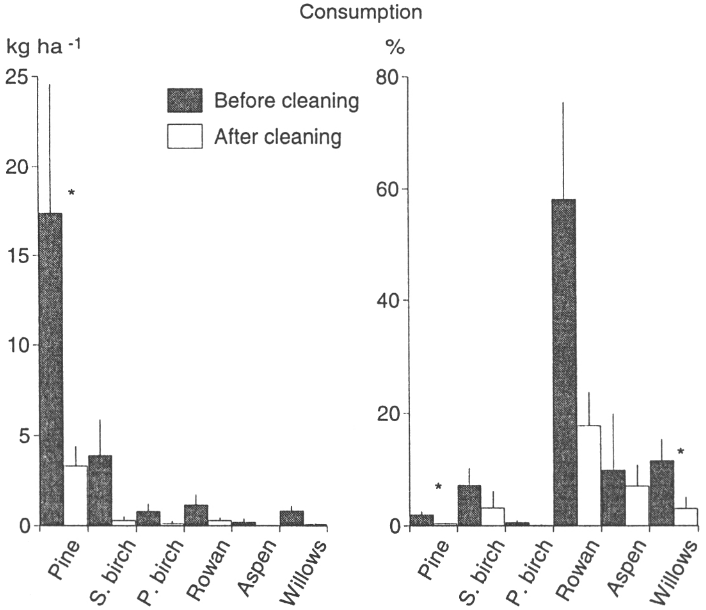

Fig. 4. Consumed biomass (mean and SE) of new browsings before and after cleaning (* = $P < 0.05$, Mann–Whitney *U*-test). Significance respectively ($P < 0.05$) for birch species as well as for deciduous species altogether (kg ha^{-1} consumed) and for birch species as well as for other deciduous species altogether (% consumed).

tively low during the subsequent year. The proportion of yearly browsed biomass was considerably lower for other tree species (Fig. 4). Although the effect of moose could not be accurately distinguished from that of the first silvicultural cleaning, also the availability of aspen and willows was apparently reduced due to browsing. In spite of the treatments and the effect of moose there was still an excess of birch stems indicating a birch dominance in future.

4. Discussion

The results presented here indicate that browsing can considerably reduce the pine seedling density during the first few years after planting. In previous studies damage has been found in 5- to 10-year-old stands characterized by a low density or uneven distribution of saplings (Löyttyniemi and Piisilä, 1983; Heikkilä, 1993). Reasons for an early retarded stand condition have not always been possible to determine. An early browsing by moose obviously increases the future risk of damage by reducing the stand density and the capacity to withstand the effect of stem breakages (Heikkilä and Mikkonen, 1992).

At Lapinjärvi the biomass consumed of small pines was negligible compared with that of aspen and rowan. It is questionable whether the availability of such a marginal food resource alone has any great importance in habitat selection. Thus the deciduous trees obviously were important for the choice of feeding habitat and promoted also moose browsing on small pines. Habitat usage in young stands has been found to correlate with a composition of preferred tree species (Goulet, 1985). In experiments with a relatively high availability of Scots pine biomass, the tree species mixture had only a slight effect on the moose browsing on pine (Edenius, 1991) and the moose fed at the tree level (Danell et al., 1991). The functional response of an optimally foraging herbivore suggests an increase of browsing with stand density (Vivås and Saether, 1987; Lundberg and Danell, 1990). The browsing pattern in our area appeared to follow the functional response, taking into account the importance of preferred tree species (Andersen and Saether, 1992). A preference for mixed diet (Westoby, 1978; Miquelle and Jordan, 1979) could not be proved. The present results, however, indicate an increasing browsing pressure on small pines growing with an abundance of preferred deciduous species.

Browsers are known to remove a high proportion of the available biomass of new growth deciduous vegetation compared with taller seedling stands (Telfer, 1972). A high utilization of untreated versus cleaned plantations (Connor and McMillan, 1988; Lautenschlager, 1992) is advantageous for the development of conifers such as spruce, which is avoided by the moose (Hjeljord and Groenvold, 1988).

The combined effect of silvicultural cleaning and moose appears to result in a depletion of rowan. When destroyed by chemicals, this species returns only rather slowly (Hjeljord, 1994). The effect of moose can be subsequently intensive owing to the high digestibility and unresistant morphology of this species against browsing (Saether, 1990). In order to retain a more uniform mixture of tree species, cleaning should take into account the influence of moose. As regards the timing of the treatment, a late cleaning has been found to be advantageous owing to the increase in food availability in the regrowth of deciduous saplings in advanced young stands (Newton et al., 1989).

Height and density ratios in the exclosures indicated that birch is the main species competing strongly with pine. Because the relatively palatable pines overtopped by an excess birch vegetation are highly utilized by moose (Heikkilä et al., 1993), cleaning of birch is often necessary to avoid such damage.

The consumption by moose greatly alters the tree species composition in young stands in forest areas with a moose density of over 1 km^{-2} forest land (Heikkilä and Härkönen, 1993). During the first 10–15 years most of the rowan, aspen and willows will obviously disappear much faster than could be attributed to competition with pine and birch. In the present study a yearly increase of ca. 53% of the available biomass could be calculated for rowan in the exclosures. Approximately 18–58% was respectively consumed in conditions with less than 1 moose km^{-2}

The possible variation in estimating areal moose population densities should be taken into account when comparing the browsing effects, as well as the differences in forest productivity. In Russia, average moose densities exceeding 0.3–0.5 km^{-2} are reported to considerably reduce aspen and pine and increase the dominance of spruce, rowan and oak (Abaturov and Smirnov, 1992). A study conducted in Newfoundland (Thompson and Curran, 1993) showed that white birch (*Betula papyrifera*) had been eliminated at an average density of about 3 moose km^{-2}. Our results indicate that naturally regenerated birches in young pine stands will sustain the present browsing pressure in Finland. Although a reduction in the density of birch is expected, birch species are likely to retain their position as mixed trees in conifer stands.

According to the inspections in 1976 (Löytyniemi and Piisilä, 1983) and 1988 (Heikkilä, 1993), the reduced proportion of browsed saplings in randomly selected areas in southern Finland correlates well with the estimated decrease in average moose density from 0.9 to 0.5 km^{-2} forest land (Finnish Game and Fisheries Research Institute, unpublished data, 1989). The average proportion of saplings browsed to some extent did not exceed 50% for any tree species (Heikkilä, 1993), indicating that at present there is no general risk of overbrowsing.

At moose densities of 2.5–5.0 km^{-2} balsam fir (*Abies balsamea*) on Isle Royale, USA, was unable to dominate and the effects of browsing on stand development were strongly dependent on fir density (Brandner et al., 1990). At a constant browsing pressure an increase in pine stand density (Heikkilä and Mikkonen, 1992) or a moderate increase of birch density in mixed stand (Heikkilä, 1991) may essentially reduce the effect of damage to pine. Relationships between moose density and the availability of food in young stands of forest areas (Morow, 1976), along adjacent forest edges (Histoel and Hjeljord, 1993) and other alternative food resources (Lääperi, 1990), are important in relation to browsing pressure in young stands.

In order to determine the carrying capacity in young stands, attention should be paid to relationships between the average and local moose densities as well as food resources in relation to forest management. An admixture of rapidly decomposing deciduous trees is considered to be beneficial for the long-term development of conifer stands (Mikola, 1955; Berg and Staaf, 1987). In uncontrolled natural conditions a high-density moose population may greatly alter the tree species composition, resulting in long-term consequences for forest productivity and moose populations (McInnes et al., 1992). The influence of moose in reducing certain tree species is an aspect to be examined with reference to biodiversity in different forest areas. Because the tree species availability depends on the activity in renewing forests, the relationships between forest stand dynamics and moose populations should be included in management planning.

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II

THE EFFECTS OF SALT STONES ON MOOSE BROWSING IN MANAGED FORESTS IN FINLAND

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ABSTRACT: Forest trees mainly used by moose are known to contain relatively small amounts of sodium. Young Scots pine stands are an important food source for moose in winter, and are often used for several years after the risk of stem damage is over. The lateral twigs of advanced pine saplings represent considerable browse reserves. The availability of sodium can gradually decrease in areas that are permanently subjected to high-density moose browsing. Sodium losses can be compensated by providing salt stones. The provision of salt stones was studied in relation to winter browsing during 1995-96 in central Finland. In autumn 1994 and 1995, a 10 kg stone was placed in each of 17 advanced young Scots pine stands. Experimental stands were selected according to the accessibility of food on the pines estimated on the basis of the height of the lowest living twigs. Each stand was inspected after winter in 1995 and 1996 using 17 plots (50 m^2) centered around the stones. In 1996 ten control stands without stones were also included. During the first winter on average 8.3 kg/ha of pine twigs were consumed by moose in stands with low twig accessibility and 72 kg/ha in those with high twig accessibility. The total consumption from saplings of different tree species was respectively 10.9 kg/ha and 79.3 kg/ha ($P < 0.05$) and the number of pellet groups 113 and 429 per ha ($P < 0.05$). During the second winter the amount of pine consumed was 7.1 kg/ha and 45.3 kg/ha ($P < 0.05$), respectively. In the control stands twig accessibility was also relatively high and the consumption (14.1 kg/ha) was significantly less than in salt stone stands with high twig accessibility ($P < 0.01$). The total consumption per ha was 11.7 kg, 53.3 kg and 17.2 kg ($P < 0.01$), respectively, and the corresponding number of pellet groups per ha was 71, 205 and 106 ($P < 0.01$). The average weight of the salt stones by the end of the winter was 4.8 kg in the low-consumption stands and 2.3 kg

($P < 0.01$) in the high-consumption stands. Twig biomass consumption correlated negatively with the weight of the salt stones ($r = -0.67$, $P < 0.01$). The amount of pine consumed by moose decreased with increasing distance from the salt stones. There was relatively little damage in seedling stands near the salt stone stands. Using salt to direct moose browsing in winter could be used to increase the residence time in habitats with a high food availability and thus reduce the risk of damage in young stands.

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Key words: *Alces alces*, browsing, *Pinus sylvestris*, salt stones, Scots pine, sodium

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The importance of sodium (Na) for moose (*Alces alces*) has been reported in several studies (see review by Jordan 1987). In inland, boreal regions of North America, this mineral nutrient is known to be present in only small amounts in woody plants, which are the main constituents of the moose diet (Jordan *et al.* 1973, Jordan 1987). Owing to a lack of dietary sodium during winter, moose search for mineral-rich sources such as aquatic vegetation and licks in spring and summer (Fraser and Reardon 1980, Fraser *et al.* 1982, Risenhoover and Peterson 1986). In Scandinavia the moose populations tend to inhabit traditional winter range areas for long periods (Sweanor and Sandegren 1989, Andersen 1991). Gathering in specific forest areas leads to above average population densities and increased browsing pressure. This can subsequently reduce access to natural sources of less available minerals. Changes caused by forest management in Finland, such as the extensive drainage of mires, have reduced the availability of several emergent plants. As a result, we suggest that sodium is becoming a limiting factor among the mineral nutrients and affects habitat use by moose.

In addition to natural mineral sources, sodium can be ingested by moose as NaCl, which is commonly used to meet the nutritional needs of mammalian herbivores (see review by Faber 1993). Placing salt stones in forest areas is a well known method in moose management in Fennoscandia, and attention has been paid to combining their use with feeding habitats and practical forestry (Lääperi 1990). In Finland salt is often used in moose management to ascertain the availability of sodium and to keep moose in hunting areas.

Managed forests are divided into compartments representing different age classes, causing high food availability for moose on deciduous and coniferous saplings of young stands. Young plantations risk heavy browsing in moose areas (Lavsund 1987, Heikkilä and Härkönen 1993). Stem breakage on commercially valuable trees, as well as long-term impacts of browsing on vegetation, have to be taken into account when assessing moose carrying capacity.

Landscape characteristics are related to habitat use by moose in managed forest areas. The small-scale fragmentation of different-aged stands typical of forests in Nordic countries is generally beneficial for moose throughout the year (Cederlund and Okarma 1988, Heikkilä *et al.* 1996). Owing to the importance of Scots pine (*Pinus sylvestris*) in the moose winter diet in Europe, large amounts of food are consumed in young sapling stands (Morow 1976, Cederlund *et al.* 1980, Bergström and Hjeljord 1987). In managed forests the feeding habitats also include large areas of advanced young pine stands with a high availability of pine shoots, as well as considerable amounts of deciduous browse in the form of undergrowth.

The lateral twigs of taller young pines can be extensively used by moose (Heikkilä and Mikkonen 1992). After the top parts of young pines have grown out of the reach of moose, the lateral twigs are still accessible for several years. This source of winter food is considered an alternative to young seedling and sapling stands, the browsing of which may considerably reduce the potential to maintain a high moose population. The aim of the present study is to determine the effect of salt stones on moose feeding intensity in advanced young Scots pine stands and to estimate the effects of moose damage in seedling stands.

STUDY AREA

The study area was part of a large managed forest area in central Finland (62°54'N, 25°38'E), where the average moose density was about 0.4 per km^2 in summer and increased to ca. 0.8 per km^2 in winter due to migration from summer ranges. The experiment was conducted in a ca. 3000 ha subarea, which according to fixed-wing aircraft surveys, had a moose density of ca. 2 per km^2 in winter 1996. The forests were intensively managed with regular logging each year. The forest sites were mainly dryish and dominated by Scots pine, whereas on fertile sites Norway spruce (*Picea abies*) was the main climax tree species. Most stands had an admixture of deciduous trees, mainly white birch (*Betula pubescens*) and silver birch (*B. pendula*). Aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and willows (*Salix* spp.) were common food plants. Grey alder (*Alnus incana*) and juniper (*Juniperus communis*) also grew in the area. The average size of the forest compartments was relatively small, less than 5 ha, and there were also some lakes and brooks in the area making it relatively suitable for moose in all seasons. Snow depth during the study period was ca. 30-60 cm. Precipitation was in December 1994 - April 1995 on average 44.0 mm and in winter 1995-96 22.4 mm, respectively (Monthly report...).

METHODS

This study began in autumn 1994 when salt stones weighing 10 kg each and containing more than 99% NaCl were placed in 17 advanced young Scots pine stands in different parts of the area. The stands were randomly selected on forestry map. There was no longer any risk of stem breakage in the experimental pine stands because the average height of the trees was more than 4 m (Heikkilä and Mikkonen 1992). The stones were placed in the middle of the stands on posts (unbarked pines ca. 15-cm diameter) at a height of ca. 2 m with the distance between adjacent stones being at least 300 m. Stones had not previously been used in the area and moose had therefore not become conditioned to visiting certain habitats for salt. Stands were divided into two groups according to the accessibility of pine twigs for moose. The shorter pine stands (*n* = 9) had, on average, more lateral branches within reach of moose than the taller stands (*n* = 8), which could not be browsed as easily during winter.

A network of 17 experimental plots (50 m^2 in size) was marked out around the stones. Stones were located at the midpoint of the first plot. The nearest 4 plots were placed 20 m from the stones to the north, south, east and west, and the other 12 plots at an additional 50, 80 and 110 m along the same lines, respectively.

New stones were placed in the stands prior to winter 1995-96. They were weighed again (50-g precision) after the experimental period in order to estimate the amounts of salt removed, and to compare salt removal with browsing. We assumed that moose accounted for essentially all mass loss in the stones (cf., Faber *et al.* 1993). The sample plots were inspected in spring 1995 and 1996. Ten additional advanced young pine stands without stones were inspected as controls in 1996. Their height class was comparable to the shorter stone stands where lateral branches were well within reach of moose. The control plots were marked and measured in the same way as the salt stone stands.

The twig biomass consumption and availability were measured using twig/diameter calculations for different tree species according to Heikkilä and Härkönen (1993). Only new browsing was included in the calculations. The number of fecal pellet groups was also counted.

Moose browsing intensity in 30 young pine seedling stands in the study area was inspected in order to estimate the amount of damage at different distances from the salt stone stands. The seedling stands were located less than 1 km (*n* = 11), 1-2 km (*n* = 12) and over 2 km (*n* = 7) from the salt stone stands.

The one-way analysis of variance with Bonferroni corrections, Student *t*-test and Pearson correlation analysis were used in statistical analyses.

RESULTS

In winter 1994-95 moose had browsed 40% of the pines in the salt stone stands with good lateral branch accessibility, and 15% of the pines in stands with branches located higher up the stem (i.e., low accessibility; Fig. 1). The twig biomass utilized from pine was significantly higher in the former stands; over 70 kg/ha compared to less than 10 kg/ha in the latter stands (Fig. 2). There was no significant difference between stands in pine density (2098 stems/ha + 253 SE vs. 2454 stems/ha + 297 SE, *P* = 0.37, respectively). The number of fecal pellet groups (Fig. 2) indicated a significantly longer residence time for moose in stands with a higher accessibility and consumption of pine twigs.

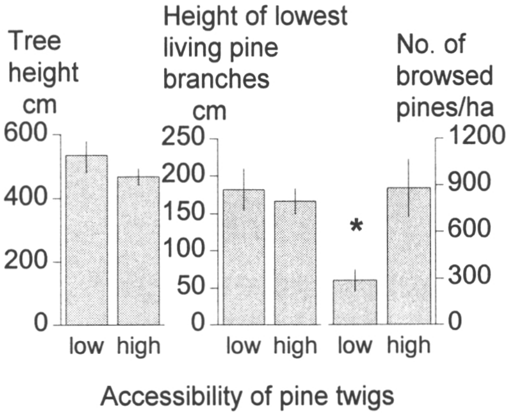

Fig. 1. Tree height, pine twig accessibility determined as the height of the lowest living branches, and the number of pines browsed by moose in advanced young stands containing salt stones in 1995. *=*P*<0.05.

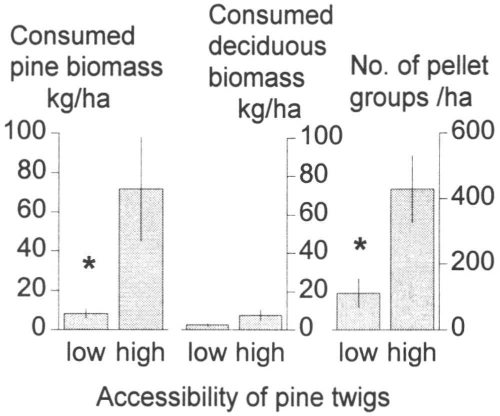

Fig. 2. Twig biomass consumed by moose and number of fecal pellet groups in salt stone stands with low and high pine twig accessibility in 1995. *=*P*<0.05.

The amount of biomass removed from deciduous saplings was considerably less, 11% and 32%, respectively, than that consumed from pines (Fig. 2). White birch was freely available, constituting on the average 59% of all deciduous tree species and 26% of the deciduous browse consumed. The respective proportions for availability and biomass consumption of silver birch were 18% and 23%. Aspen, rowan and willows together constituted 23% of the availability and 51% of the consumption of deciduous trees. The stands had been used by moose during previous years and, as a result, 18-56% of the deciduous saplings of different species had lost their apical growth.

In winter 1995-96 the number of browsed pines was greatest in the salt stone stands with a high accessibility of pine twigs, although the difference compared to the control stands was not significant (Fig. 3). The average height of the pines was 5.29 m (+ 0.38 SE) in the salt stone stands, and 4.40 m (+ 0.39 SE) in the control stands. Moose consumed on average 22 kg/ha (+ 6.6 SE) pine in the salt stone stands, which was somewhat greater than in the control stands, 14.1 kg/ha (+ 3.8 SE). However, the difference was not significant (*P* = 0.26). Considerably less pine was used in 1995-96 compared to the previous winter. Consumption of deciduous trees was, however, at the same level as earlier (*P* = 0.72). The consumed deciduous tree biomass in the salt stone stands was on average 6.0 kg/ha (+ 1.2 SE), and in the control stands 3.1 kg/ha (+ 0.8 SE) (*P* < 0.05).

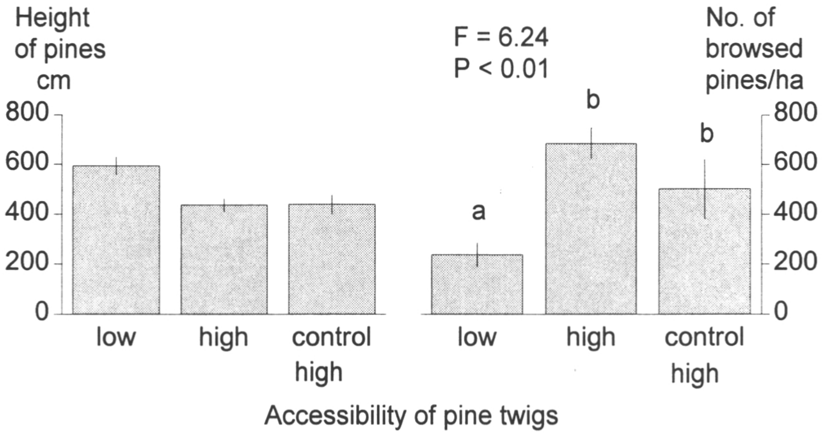

Fig. 3. Tree height, pine twig accessibility and number of pines browsed by moose in salt stone stands and control stands in 1996. Means with the same letter are not different (*P* > 0.05).

In 1995-96, moose consumed more pine in the salt stone stands with a high accessibility of twigs compared to the other stand types (Fig. 4). This was the case despite good pine twig accessibility in the control stands, where the average height of pine did not differ significantly of that in salt stone stands with good twig accessibility (Fig. 3). In addition, there was no significant difference in pine density between control stands (2659 stems/ha + 235 SE) and salt stone stands with high accessibility of twigs (2460 stems/ha + 260 SE, $P = 0.53$).

Deciduous trees were more heavily browsed in salt stone stands with high pine twig accessibility compared to control stands (Fig. 4). There was no significant difference in the density of preferred deciduous browse (aspen, rowan and willows) in control stands (1996 stems/ha + 626 SE) and in salt stone stands with high accessibility of pine twigs (1686 stems/ha + 633 SE) ($P = 0.74$). The number of fecal pellet groups was relatively high in the salt stone stands where lateral pine twigs were readily available. This result was in agreement with biomass consumption.

The twig biomass consumed by moose on pines during winter increased with increasing removal of salt (Fig. 5). The original weight of stones was 10 kg and the average weight of stones in spring was 2.3 kg (+ 0.8 SE) in the stands with a high pine accessibility and 4.8 kg (+ 0.2 SE) in the other stands ($P < 0.01$).

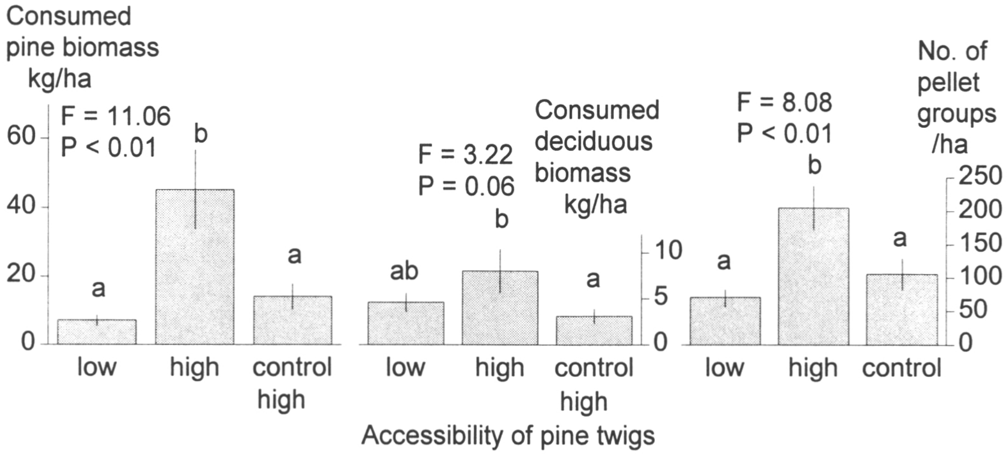

Fig. 4. Twig biomass consumed by moose and number of fecal pellet groups in salt stone stands with low and high pine twig accessibility and in control stands in 1996. Means with the same letter are not different ($P > 0.05$).

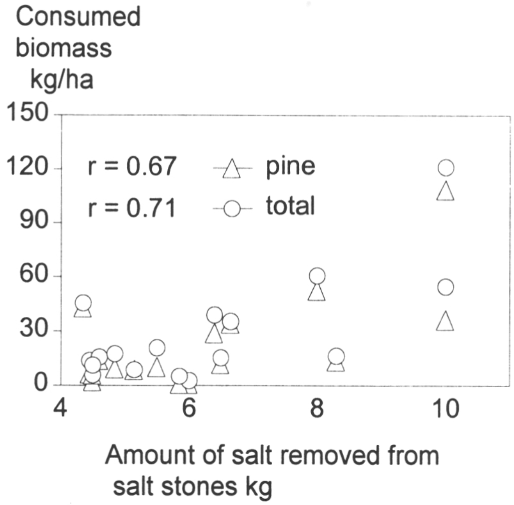

Fig. 5. Biomass consumed by moose in salt stone stands in relation to amounts of salt removed in 1996.

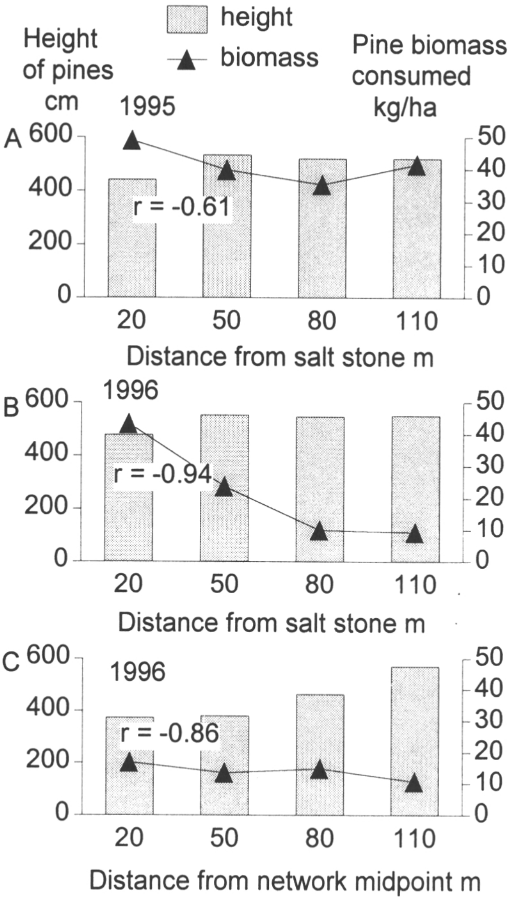

Fig. 6. Tree height and correlation between the amount of pine consumed and distance (m) to salt stones in the stands. 6 A,B = salt stone stands, 6 C = control stands.

The twig biomass consumed by moose in salt stone stands decreased with increasing distance from the salt stones (Fig. 6 A,B). The decrease for the winter 1994-95 was not as clear as that for the following winter, probably due to a lighter browsing pressure in 1995-96. Also in control stands the consumed pine biomass correlated negatively with the distance from the network midpoint (Fig. 6 C). In turn, in control stands twig accessibility tended to be relatively high on the plots located farther away.

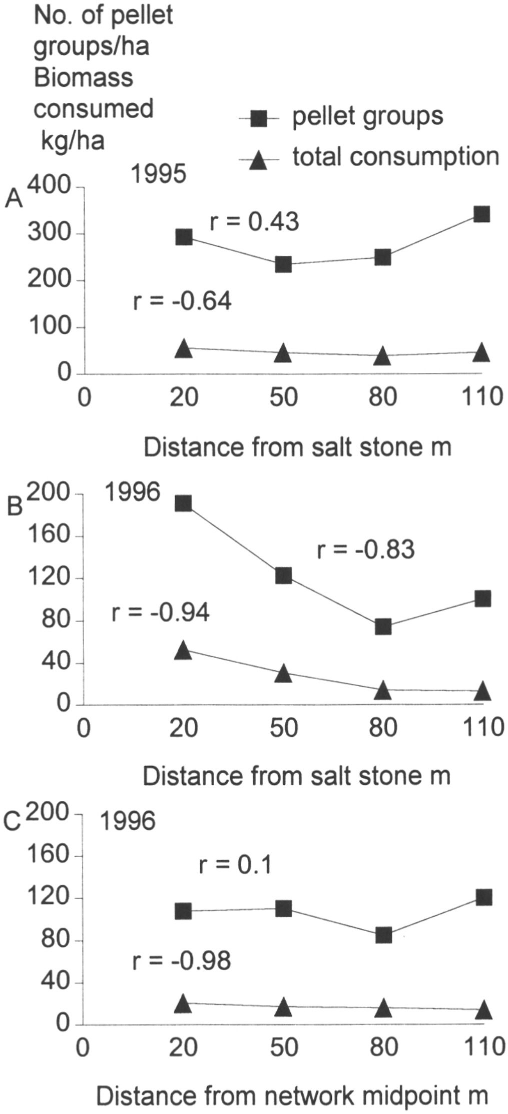

Fig. 7. Number of fecal pellet groups and total consumption by moose in relation to the distance to the salt stones in the stands. 7 A,B = salt stone stands, 7 C = control stands.

The total consumption of pine and deciduous twigs correlated in a similar fashion to that between pine consumption and the distance from the stones (Fig. 7 A,B). The number of pellet groups generally appeared to follow the amount of feeding on pine except in the control stands (Fig. 7 C). Moose browsing intensity tended to be higher in pine seedling stands located relatively distant from salt stone stands than in those located near stones (Fig. 8).

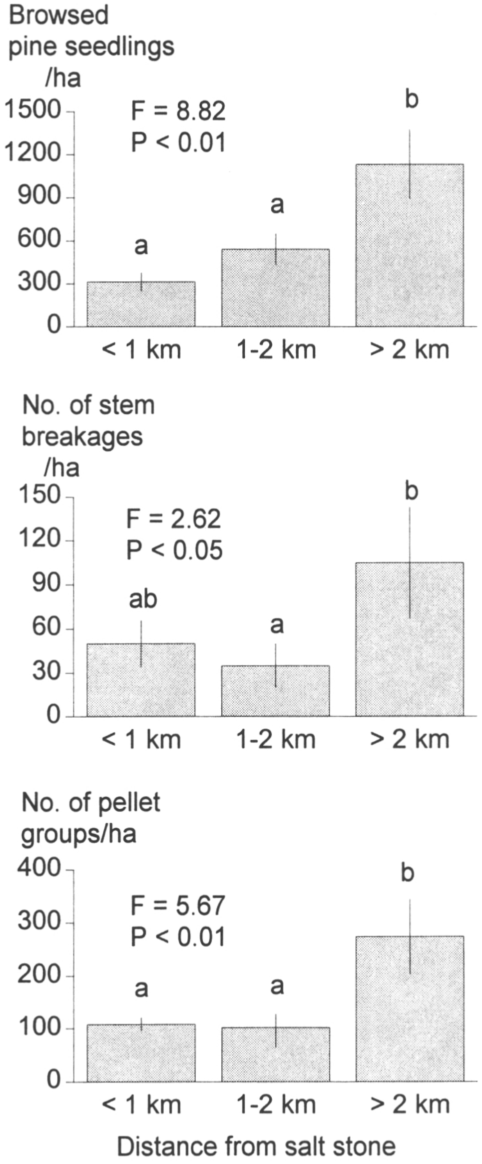

Fig. 8. Moose browsing intensity in seedling stands at different distances from salt stone stands in 1996. Means with the same letter are not different ($P > 0.05$).

DISCUSSION

Salt (NaCl) stones are a widely used wildlife management practice to benefit game, particularly deer, in the Nordic countries. The results of the present study indicate that it is important to take into account the effects on moose browsing of pine when using salt. Earlier attempts have been made to increase moose feeding on alternative food sources away from the youngest Scots pine stands. Lääperi (1990) reports that the establishment of special feeding stations equipped with salt stones encourages regular moose visits. Artificially provided sodium may be an important factor in dictating home ranges. Miller and Litvaitis (1992) found that moose regularly visited salted roadsides and included them in their home ranges.

We tested salt stones to find out if they can be placed in forest stands with a high food supply in winter. Advanced young pine stands are widely available in managed forests and the lateral twigs of pine are often intensively used by moose. However, nutritional status of the twigs depends also on stand density (Heikkilä and Mikkonen 1992), and intensive browsing in dense stands can be explained by availability and by the effects of shading on food quality.

Our results indicate that providing an additional source of sodium in the form of salt stones can increase moose winter feeding in advanced young pine stands. Differences in use between stands were largely attributed to variation in lateral twig accessibility. Although a height of about 1.5 m is preferred (Löyttyniemi and Piisilä 1983), browsing frequently occurs at heights over two meters depending on snow conditions. Higher consumption in salt stone stands compared to control stands, where pine twigs were highly accessible, lends support to the importance of salt stones in relation to feeding intensity. As regards average stand densities and heights, the availability of neither pine nor preferred deciduous browse could be concluded to attract moose to browse more in salt stone stands.

The characteristics of neighboring forest stands may also be important for habitat selection. Residence time of moose in winter may for example be greater at forest edges with dense undergrowth and in freshly cut areas (Histøl and Hjeljord 1993, Heikkilä *et al.* 1996).

The habitat choice of deer species depends on several qualitative factors related to the characteristics of forests (Telfer 1970). The amount of browsing in the salt stone stands indicate that feeding intensity correlates negatively with distance from the stones. According to Lääperi (1990), moose use feeding stations containing both cut tree tops and salt stones relatively frequently compared to nearby sapling stands. In addition to the effect of cutting residues, the ongoing studies on habitat affinity in our study area have shown that some forest habitats such as peatland compartments are commonly used by moose (cf., Heikkilä and Härkönen 1993).

The amount of salt and minerals ingested by moose may be related to a number of physiological effects. According to the review by Jordan (1987), seasonal requirements for sodium intake have been suggested to be related to potassium:sodium (K:Na) imbalance in early summer and the demands of growth and reproduction processes of animals. It has also been assumed that sodium losses in mammals can result from feeding on plants with higher contents of certain secondary compounds (Palo *et al.* 1983, Pehrson 1983). In this study it was not possible to elucidate the driving mechanism in moose consuming salt and pine browse. According to preliminary results of ongoing study (R. Heikkilä and S. Härkönen, *unpubl. data*), however, it appears that browsing of pine increases after providing salt stones. Moose are able to avoid the harmful effects of excess sodium, if sufficient water is available. However, when attempting to balance sodium availability by means of supplementary salt, the natural conditions in forest areas with regards to mineral supply and related aspects should be known. In managed forest habitats these questions obviously should be understood in relation to browsing effects.

Although feeding on pine increased along with increasing removal of salt stones, it cannot be directly concluded that moose used more pine than without any salt stones in the area. In winter moving activity is low and feeding bouts short (Cederlund 1989), and the importance of salt stones would more likely be in directing browsing to certain subareas. The study area has been subjected to relatively high browsing pressure and the preferred deciduous tree species have been highly utilized. The moose is known to prefer deciduous tree habitats in the summer and autumn in order to improve their physical condition for winter. Moose are adapted to ingest a lot of food in a short time with rapid passage (Renecker and Hudson 1990) and a high intake of pine shoots is typical during the winter. Pine-dominated feeding habitats can be found in seedling and sapling stands, as well as in advanced young stands. Stem damage in seedling stands distant from salt stones may indicate an uneven dispersion of moose population in relation to salt stones. Information of characteristics and situations of habitats used by moose in winter in other stand types could be important for comparisons. By improving habitat affinity in winter ranges the effects of moose browsing may be distributed in a way that increases the sustainability of the forests.

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III

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Effects of Silvicultural Cleaning in Mixed Pine-Deciduous Stands on Moose Damage to Scots Pine (*Pinus sylvestris*)

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Silvicultural cleaning is commonly carried out in young stands to control competition between conifers and deciduous tree species. However, it has been questioned whether this practice affects moose (*Alces alces* L.) browsing on Scots pine (*Pinus sylvestris* L.) with respect to damage at the stand level. In this study, moose winter browsing was examined in relation to food availability in 19 Scots pine stands divided into silviculturally cleaned and non-cleaned blocks. Cleaning had a negative effect on moose foraging in terms of reduced density, biomass availability, and height of the deciduous tree species. The total biomass consumed by moose was significantly lower on the cleaned blocks than on the non-cleaned ones. There were no differences between the treatments in the amounts of pine consumed and in moose damage to pines. The density or biomass available of different deciduous tree species did not explain the variation in moose browsing on pine. In conclusion, timing of silvicultural cleaning with reference to moose browsing should be taken into account. If pines are not overtopped by deciduous trees, as in the present study, silvicultural cleaning is not necessary to prevent moose damage. *Key words: Alces alces, cleaning, food availability, moose, moose damage, Pinus sylvestris, Scots pine.*

INTRODUCTION

In Fennoscandia Scots pine (*Pinus sylvestris* L.) is the main winter food of the moose (Cederlund et al. 1980, Bergström & Hjeljord 1987). In winter, it is energetically profitable for moose to browse on pine because of its high availability at both the tree and stand levels in managed forests. Browsing can lead to damage to pine, especially in high-density winter range areas, and it has been concluded that the moose is the main animal pest in young pine stands in Scandinavia (Lavsund 1987). In Finland, Löyttyniemi & Lääperi (1988) have reported that in forestry the economic losses caused by moose damage can be as high as 40–50 million FIM year^{-1}.

High food availability and diversity are considered important for generalist herbivores (Westoby 1974, Oldemeyer et al. 1977). Artificially regenerated Scots pine stands usually contain an admixture of naturally regenerated deciduous tree species; this increases the biomass availability and density of alternative forage for moose. Attention has been paid to means of regulating the tree species composition in young stands (e.g., Ikäheimo & Norokorpi 1986). In forest management, silvicultural cleaning is used to reduce competition between pine and other tree species but as a short-term consequence of this, however, is that the availability of deciduous tree species as moose browse is reduced (Hjeljord & Grønvold 1988).

Tree species diversity may have multiple effects on moose browsing on pine, depending on the tree species composition. For example, it has been concluded that the presence of trees preferred by moose, such as rowan (*Sorbus aucuparia* L.) and aspen (*Populus tremula* L.), increases damage to pine (Löyttyniemi & Piisilä 1983, Lääperi & Löyttyniemi 1988, Heikkilä 1990), probably due to their attractive influence on habitat use. On the other hand, the effect of deciduous browse on damage to pines is generally considered to be insignificant (Löyttyniemi & Piisilä 1983), or to occur only at very high densities of deciduous trees or if they overtop pine (Heikkilä 1993, Heikkilä & Härkönen 1993). However, the removal of tree species preferred by moose in silvicultural cleaning has been recommended as a means of preventing damage to pine (Löyttyniemi & Lääperi 1988).

Moose feeding has also been studied under controlled conditions. Lundberg et al. (1990) concluded in experiments with white birch (*Betula pubescens* Ehrh.) and rowan that moose have an energy-maximizing feeding strategy in winter. In monocultures the proportional consumption by moose has been reported to decrease with increasing density of birch

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(Vivås & Sæther 1987) and pine (Heikkilä & Mikkonen 1992). Cafeteria tests with pine and deciduous saplings indicate that moose employ a tree-level choice (Danell et al. 1991). However, there has been a lack of work on moose browsing in natural conditions with an experimentally controlled variation in food availability in young pine stands containing several deciduous tree species.

In general, a high availability of resources allows moose to cover longer distances and to be selective, whereas in an area of poor food quality, moose remove a relatively higher proportion of the available biomass (Sæther & Andersen 1990). As a result, it can be hypothesized that moose damage to pines would be lower in a high-quality area because of increased selectivity. In this study I examined moose winter browsing in relation to a variation in food availability after silvicultural cleaning. I asked the following questions: (1) what are the effects of cleaning on the food availability for moose, (2) what are the responses of moose winter browsing to cleaning, and (3) is the use of silvicultural cleaning to reduce forest damage by moose a reasonable practice?

MATERIALS AND METHODS

The study areas were located in southern Finland: Tohmajärvi (62°19′ N, 30°39′ E), Mynämäki (60°46′ N, 22°15′ E), and Hyvinkää (60°37′ N, 24°39′E). Nineteen artificially regenerated Scots pine stands situated in moose winter range areas were selected for the experiment. The average moose winter densities at each site were 0.5–1.0 km^{-2} (Uusimaa, Pohjois-Karjala, and Varsinais-Suomi Game Management Districts, unpubl. data).

In late summer 1991, each of the experimental stands was divided into two treatments: (1) cleaned block: silviculturally cleaned area, i.e., deciduous tree stems competing with pine were removed mechanically, and (2) non-cleaned block: control area containing the original deciduous tree species. The stands had not been cleaned before the experiments, and there were at least five different deciduous tree species in each stand. The stands had been established 7–10 yrs earlier by planting. The size of the stands was 1–2 ha, and the forest site types were *Vaccinium myrtillus* type (MT) or *V. vitis-idaea* type (VT) (Cajander 1909).

In spring 1992, the stands were inspected using a systematic line-plot method (Lääperi & Löyttyniemi 1988). The circular sample plots were 20 m^2 in size, and the distance between the lines and plots was 20–40 m depending on the area of the stand. In all, 768 cleaned and 762 non-cleaned plots were examined. By examining the plots immediately after a browsing period of one winter it was assumed that no chemical changes had occurred in the trees in the cleaned areas. Thus, any differences in moose feeding behaviour would reflect only changes in stand density and biomass availability.

Moose browsing during winter 1991–1992 was recorded on each plot. If there were signs of moose browsing on a tree, it was classified as browsed. All moose bites (i.e., browsed twigs) were counted and the diameter of bites on all tree species was measured to the nearest millimetre. Breakages of pine stems were counted. The density and height of tree stems over 0.5 m were measured. The number of moose fecal pellet groups accumulated during winter 1991–1992 was counted.

Bites were converted into dry weight of biomass consumed using the twig diameter/~~winter~~ weig method of Telfer (1969). Biomass availabilities of pine, silver birch (*Betula pendula* Roth.), white birch, rowan, aspen, willows (*Salix* spp.), alder (*Alnus incana* (L.) Moench) and juniper (*Juniperus communis* L.) were determined according to Heikkilä & Härkönen (1993). Norway spruce (*Picea abies* (L.) Karsten) was excluded from the calculations because it was not used by moose.

Because food selection by moose occurs in small patches, even at the individual tree level within a stand (Vivås & Saether 1987, Danell et al. 1991), the experimental blocks were treated as independent units in the comparisons. The statistical methods used were paired *t*-test, the Pearson correlation analysis, and stepwise regression analysis. Stepwise regression analyses were used in studying the relationships between moose browsing and stand characteristics. Proportional data were arcsine square-root transformed before statistical analyses. Means are given with their standard errors.

RESULTS

Browse availability

The total density and the density of deciduous tree species and juniper together were higher on the non-cleaned blocks than on the cleaned blocks (Table 1). Cleaning greatly reduced the densities of silver birch, white birch and rowan. Pine accounted for the highest proportion (44% ± 4; mean ± SE) of total

Table 1. *Average density and height (±SE) of tree species classified according to cleaning treatment*

	Sapling (ha^{-1})		Height (cm)	
Tree species	Cleaned	Non-cleaned	Cleaned	Non-cleaned
Pine	2471 ± 330	2212 ± 276 (NS)	139 ± 11	134 ± 9 (NS)
Spruce	710 ± 190	607 ± 184 (NS)	98 ± 6	117 ± 15 (NS)
Silver birch	634 ± 152	3675 ± 1125 (*)	120 ± 21	146 ± 11 (NS)
White birch	1149 ± 269	3586 ± 716 (**)	109 ± 11	137 ± 9 (*)
Rowan	412 ± 71	1174 ± 213 (**)	79 ± 3	98 ± 5 (***)
Aspen	117 ± 55	366 ± 158 (*)	93 ± 8	103 ± 9 (NS)
Willows	137 ± 37	259 ± 50 (*)	85 ± 5	114 ± 11 (**)
Alder	24 ± 14	101 ± 56 (NS)	96 ± 8	214 ± 27 (*)
Juniper	86 ± 43	54 ± 21 (NS)	86 ± 11	75 ± 2 (NS)
Combined	2558 ± 427	9216 ± 1482 (***)		
Total density	5739 ± 475	12035 ± 1482 (***)		

Combined: density of deciduous tree species and juniper.
Significance levels: * $= p < 0.05$, ** $= p < 0.01$, *** $= p < 0.001$ (paired t-test).

stem density on the cleaned blocks. On the non-cleaned blocks the proportional density of pine (22% ± 3) was significantly lower than on cleaned blocks ($p < 0.001$). In contrast, silver birch had the highest proportion (24% ± 4) of the total density on the non-cleaned blocks, and silver birch and white birch accounted for 53% (±5) of the stems. Rowan, willows, white birch, and alder were significantly lower on the cleaned blocks, whereas the heights of silver birch and aspen were only slightly reduced compared to the non-cleaned blocks (Table 1). Pines were not overtopped by birch vegetation, although the birch/pine height ratio was significantly lower on the cleaned blocks than on the non-cleaned ones (0.89 ± 0.07 vs. 1.14 ± 0.06, $p < 0.05$).

The total biomass available was 587 kg ha^{-1} (±149) on the cleaned blocks and 715 kg ha^{-1} (±185) on the non-cleaned blocks ($p = 0.08$). The total biomass available of deciduous tree species and juniper was significantly higher on the non-cleaned blocks than on the cleaned blocks (207 kg ha^{-1} ± 29 vs. 35 kg ha^{-1} ± 7, $p < 0.001$). Cleaning mainly reduced the available biomass of silver birch, white birch, rowan, and aspen (Fig. 1). The combined biomass availability of aspen, rowan, and willows was significantly lower on the cleaned blocks than on the non-cleaned blocks (4.6 kg ha^{-1} ± 1.2 vs. 20.0 kg ha^{-1} ± 3.5, $p < 0.001$). The proportion of Scots pine biomass of total available biomass was higher on cleaned than on non-cleaned blocks (87% ± 4 vs. 58% ± 6, $p < 0.001$).

Moose browsing

The numbers of stems of silver birch, white birch, rowan and willows browsed by moose were significantly higher on the non-cleaned blocks than on the cleaned blocks (Fig. 2A). The number of browsed pines did not differ between the treatments ($p = 0.67$). Although the proportional browsing of some tree species was considerably higher on the non-cleaned blocks, the differences compared with the cleaned blocks were not significant (Fig. 2B). The numbers of bites (i.e., browsed twigs) on white birch, rowan, and willows were greater on the non-cleaned blocks than on the cleaned blocks (Fig. 2C), but for pine no difference was observed ($p = 0.57$).

There was no difference ($p = 0.24$) in pine stem breakages by moose between the non-cleaned (103 ha^{-1} ± 31) and cleaned blocks (78 ha^{-1} ± 21). The proportion of pine stems broken by moose was 3.9% (±0.9) on the non-cleaned blocks and 3.0% (±0.6) on the cleaned blocks ($p = 0.34$). The number of moose fecal pellet groups was 110 ha^{-1} (±35) and 102 ha^{-1} (±47) ($p = 0{\cdot}71$), respectively.

The total biomass consumed by moose was significantly lower on the cleaned blocks than on the non-cleaned ones (33.8 kg ha^{-1} ± 13.4 vs. 53.0 kg ha^{-1} ± 14.1, $p < 0.01$). Moose had consumed 6.8% (±2.3) of the total available biomass on the cleaned blocks and 11.1% (±3.9) on the non-cleaned blocks ($p = 0.10$). There was a 10-fold difference in the amount of biomass of deciduous tree species and juniper browsed between the cleaned and non-cleaned blocks (2.0 kg ha^{-1} ± 0.5 vs. 21.1 kg ha^{-1} ± 5.5,

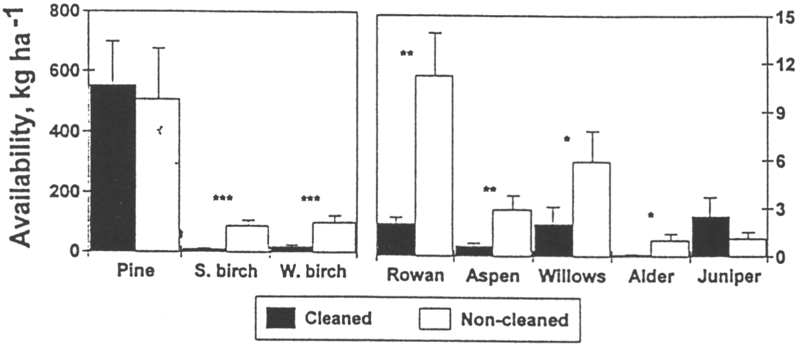

Fig. 1. The biomass availability of different tree species (kg ha^{-1} + SE) on the cleaned and non-cleaned blocks. Significance levels: *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$ (paired t-test). Note the different scales. ■ = Cleaned, □ = noncleaned.

$p < 0.01$). Moose had consumed 13.3% (±4.2) of the biomass available as deciduous tree species on the cleaned blocks and 16.8% (±6.0) on the non-cleaned blocks ($p = 0.30$).

More Scots pine was consumed than any other tree species in either treatment (Fig. 3A). More deciduous tree species had been used on the non-cleaned blocks than on the cleaned blocks. Proportional consumption indicated that the tree species preferred by moose, such as rowan, aspen, and willows, had been heavily browsed in both treatments (Fig. 3B). Moose had consumed 26.2% (±6.3) of the biomass available as rowan, aspen, and willows on the cleaned blocks, and 40.3% (±8.9) on the non-cleaned blocks ($p = 0.08$). There was no difference in consumed pine biomass ($p = 0.99$) or in proportional pine consumption ($p = 0.23$) between the treatments. The proportion of pine in the total biomass consumed was 73.8% (±7.1) on the cleaned blocks and 51.3% (±5.6) on the non-cleaned ones ($p < 0.001$).

Browsing of pine in relation to browse availability

There were more than 10 000 deciduous saplings ha^{-1} in 6 non-cleaned blocks out of 19 blocks. However, on only one of these blocks was the proportion of stem breakages and the proportion of browsed pines higher than the average.

The pine biomass consumed, number of browsed pines, and number of pine stem breakages increased with total biomass available, biomass available of pine, biomass available of white birch, and density of pine (Table 2). In addition, the number of pine stem breakages caused by moose was positively correlated with the biomass available of deciduous trees. In stepwise regression analyses the biomass availability of pine alone explained 48% of the variation in the pine biomass consumed, and 45% of the variation in the number of browsed pines (Table 2). The total biomass available alone explained 33% of the variation in the number of pine stem breakages. The density or biomass available of different deciduous tree species, deciduous tree species combined, and preferred deciduous tree species (aspen, rowan, and willows together) did not explain the variation in moose browsing on Scots pine.

Total consumption was positively correlated with total available biomass ($r = 0.65$, $p < 0.001$, $n = 38$). The consumed pine biomass ($r = 0.95$, $p < 0.001$, $n = 38$), number of browsed pine stems ($r = 0.95$, $p < 0.001$, $n = 38$), and pine stem breakages by moose ($r = 0.87$, $p < 0.001$, $n = 38$) were positively correlated with total consumption.

DISCUSSION

Quantitative factors such as stand density can affect the quality of twigs browsed by moose (Thompson et al. ~~1990~~, Heikkilä & Mikkonen 1992). It has been shown that qualitative aspects of forage can have an effect on moose winter browsing (Bryant & Kuropat 1980, Danell et al. 1990, Sunnerheim-Sjöberg & Hämäläinen 1992). In this study, I assumed that there were no chemical differences between the trees in the two treatments, because no growth occurred between cleaning and winter browsing. 198

Mechanical cleaning is a practical way of controlling deciduous trees in young coniferous stands in Finland. Mechanical treatment is advantageous for moose compared with treatment by chemical means because of the regrowth of deciduous vegetation from stump sprouts (Hjeljord & Grønvold 1988). Removing deciduous tree species is, however, disadvantageous for moose in the short-term. In this study, deciduous browse availability declined by about 80%.

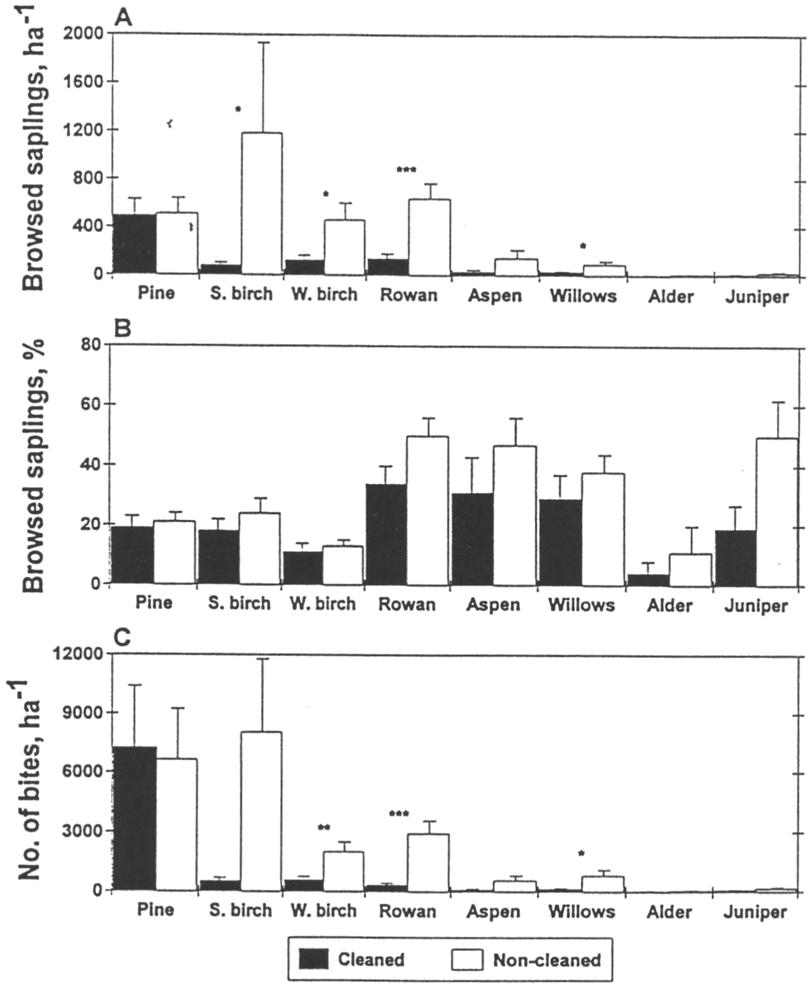

Fig. 2. A: The number of browsed saplings (ha^{-1} + SE), B: the proportion of browsed saplings (% + SE), and C: the number of bites (ha^{-1} + SE) on the cleaned and non-cleaned blocks. Significance levels: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$ (paired *t*-test). ■ = Cleaned, □ = non-cleaned.

In addition, cleaning considerably reduced the mean densities and heights of the deciduous tree species.

The availability of birch species was greatly reduced by cleaning. This had a considerable effect on moose feeding alternatives, because over 50% of the total density in the non-cleaned stands was birch. Birches are of medium preference as browse species for moose (Bergström & Hjeljord 1987). Therefore, a high proportion of birch saplings can likely be cleaned without any detrimental effects on moose forage. However, from a forest management perspective, total cleaning should be avoided because an admixture of birch in pine stands has been recommended as a way of improving timber production and the technical quality of the wood (Ikäheimo & Norokorpi 1986).

The nutritional needs of moose are better fulfilled if the winter forage consists of several browse species (Oldemeyer et al. 1977). The most preferred deciduous tree species such as aspen, rowan, and willows are considered to be important in moose winter nutrition owing to their high digestibility and diversifying effect in the diet (Salonen 1982). According to the proportional consumption, these tree species were most preferred. Scots pine, which ranks medium in preference for moose (Bergström & Hjeljord 1987), was, however, the tree species most consumed in quantity in both treatments. In my study, cleaning greatly reduced the availability of deciduous tree species preferred by moose, resulting in food

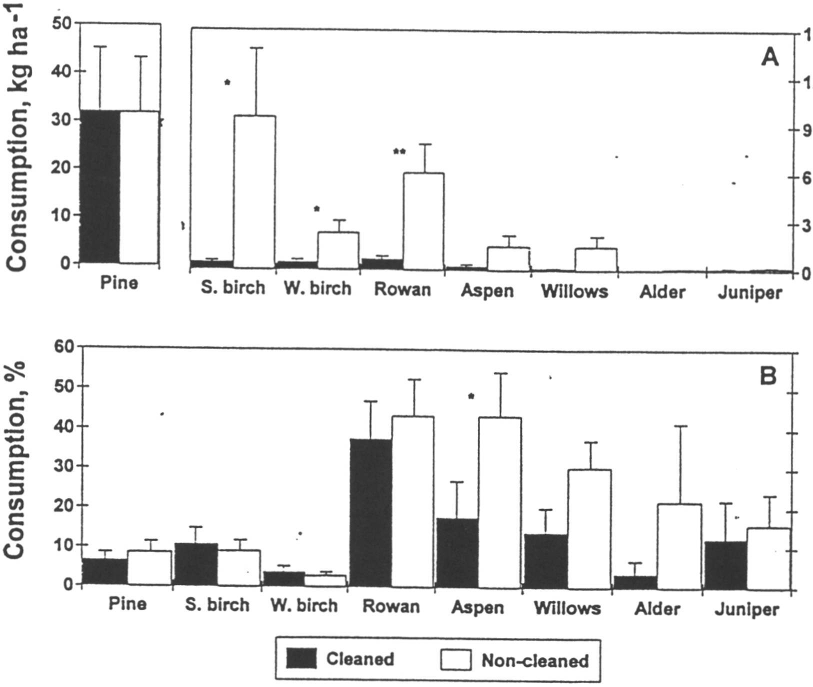

Fig. 3. A: The consumed biomass (kg ha^{-1} + SE), and B: proportional consumption (% + SE) on the cleaned and non-cleaned blocks. Significance levels: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$ (paired *t*-test). Note the different scales. ■ = Cleaned, □ = non-cleaned.

availability dominated by pine on the cleaned blocks. In addition, the availability and consumption of preferred deciduous forage was high in the non-cleaned stands compared with that in the cleaned stands. The proportional consumption of deciduous species was also considerably higher in the non-cleaned stands, whereas the proportion of consumed pine biomass of total consumption was higher in the cleaned stands. Thus, the moose could select for browse of better quality in the non-cleaned stands, illustrating the negative effect of cleaning on moose feeding. This is consistent with Andersen & Sæther (1992), who found that moose selected browse of better quality (expressed as digestibility) when the availability of browse increased.

The browsing pattern of moose follows a functional response, (i.e., total consumption increases with total biomass availability) (Vivås & Sæther 1987, Lundberg & Åström 1990). In my study, moose consumed an increased amount of food with a higher availability of biomass. However, the number of moose fecal pellet groups was the same between the treatments. If we assume, according to the pellet groups, that the time spent by moose in the stands was constant, then the proportion of available browse consumed should have decreased with increased food availability. Furthermore, the proportion of trees browsed and damaged should have decreased with increasing stand density, because in high-quality habitats search time for high-quality food is lower than that in poorer habitats. According to the proportion of available browse consumed, however, the residence time of moose in a good habitat is obviously relatively long, indicating an optimal feeding strategy in winter conditions.

Heavy browsing on deciduous trees could be advantageous for conifers such as spruce that are not browsed by moose (Hjeljord & Grønvold 1988). In young pine stands, high browsing pressure can result in the depletion of preferred deciduous tree species, and a risk of moose damage to pines (Heikkilä & Härkönen 1993). If large amounts of deciduous but not coniferous tree species are consumed by moose, the competition for pine from deciduous tree species may be reduced. In my study, moose used ten times more biomass from deciduous tree species and juniper per hectare on the non-cleaned than on the cleaned blocks. However, the proportion of the

Table 2. *Pearson correlation coefficients (r) between moose browsing on Scots pines and average values of biomass availability ($g\ ha^{-1}$) and tree density (ha^{-1}) ($n = 38$). Results of stepwise regression analyses are also shown*

Factor	Consumed pine biomass $g\ ha^{-1}$	Browsed pines ha^{-1}	Pine stem breakages ha^{-1}
Total biomass available	0.69***	0.67***	0.58***
Pine biomass available	0.69***	0.67***	0.55***
White birch biomass available	0.37*	0.36*	0.42**
Deciduous trees available	0.25	0.26	0.38*
Pine density	0.61***	0.62***	0.57***

Dependent variable	Equation	r^2	F	p
Consumed pine biomass	$Y = 2773 + 0.05\ X_2$	0.48	33.6	***
Browsed pines	$Y = 190 + 0.58 \times 10^{-3}\ X_2$	0.45	29.0	***
Pine stem breakages	$Y = 32 + 0.9 \times 10^{-4}\ X_1$	0.33	17.9	***

Factors with non-significant differences are not included.
Significant levels: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$; X_1 = Total biomass available; X_2 = Pine biomass available.

biomass available consumed as deciduous trees was less than 20% on the non-cleaned blocks. Thus, moose cannot reduce the density of deciduous trees sufficiently by browsing, and silvicultural cleaning is needed even in high-density moose areas in order to regulate, in particular, the competition between pine and birch as presented by Heikkilä & Härkönen (1996).

Danell et al. (1991) and Edenius (1991) showed in browsing experiments that the effects of tree species composition on moose damage to pines is insignificant. However, Heikkilä & Härkönen (1996) reported that the high density of aspen sprouts can increase damage to young pine seedlings. In my study, the available biomass of white birch was significantly positively correlated with the number of browsed pines and the number of pine stem breakages. However, the biomass availability of pine and the total available biomass alone explained the highest proportion of the variation in moose damage to pine. The densities or biomass availabilities of saplings of other deciduous tree species, deciduous tree species combined, and preferred deciduous saplings (aspen, rowan and willows together) did not explain moose browsing on pines.

Heikkilä & Mikkonen (1992) showed that the number of undamaged pine saplings in pine monocultures increased with stand density. This has also been suggested to be true in pine stands with deciduous tree species where there was no strong competition between tree species (Heikkilä 1991). Heikkilä (1993) and Heikkilä & Härkönen (1993) reported that the presence of birch as an overstorey above pine resulted in an increase in pine stem breakage by moose. According to the present results, there were no differences in the moose damage to pine between the treatments. This could be explained by the fact that the pines were not overtopped by deciduous trees.

Löyttyniemi & Lääperi (1988) recommended that rowan and aspen should be cleaned as a means of preventing moose damage in pine. I suggest that early silvicultural cleaning is not necessary to prevent moose damage in conditions where there is not strong competition between tree species. When combining forestry and wildlife management, the timing of silvicultural cleaning with reference to moose browsing should be taken into account, because intensive cleaning activity reduces the availability of deciduous forage for moose. Thus, in cleaned stands a high proportion of available forage consists of pine, and moose have no possibility of consuming highly digestible browse to the same extent as in the non-cleaned stands. In this sense a more selective treatment is recommended, i.e., deciduous saplings should be removed only when they are competing strongly with young pines that are suppressed by an overgrowth or high density of deciduous trees. Tree species preferred by moose such as rowan, aspen and willows should be left non-cleaned. This is also in accordance with maintaining biodiversity in managed forests.

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IV

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Moose (*Alces alces* L.) browsing on young Scots pines (*Pinus sylvestris* L.) in relation to terpene compounds

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Abstract

Moose browsing in relation to the contents of terpene compounds of intensively and lightly browsed as well as nonbrowsed Scots pines was studied on two forest sites in Finland. On dryish forest site there were more resin acids, oxygen-containing sesquiterpenes and total terpenes in lightly browsed trees than in intensively browsed ones. The concentrations of one monoterpene, three sesquiterpene and six resin acid compounds were higher in lightly browsed trees compared to intensively browsed ones. On fertile forest site the concentration of monoterpene hydrocarbons was relatively high. Other differences were insignificant or opposite to the dryish forest site, possibly reflecting variation also in browsing pressure and habitat quality. The terpene concentrations between browsed and not tasted trees did not differ significantly in the pooled data. It is suggested that sesquiterpenes and resin acids can have an effect on the selective browsing by moose on Scots pines especially on dryish, natural pine forest sites.

Introduction

In Europe Scots pine is the main winter food used by moose in quantity (Bergström and Hjeljord 1987). It has been presented that food quality in terms of secondary compounds has an effect on moose winter browsing (Bryant and Kuropat 1980). Terpenes such as mono-, sesqui-, di-, and triterpenes are secondary compounds of pine needles. These compounds may help trees to defend against herbivores (e.g. Larsson et al. 1986; Elliott and Loudon 1987). According to previous studies (Löyttyniemi and Hiltunen 1978; Löyttyniemi 1985; Danell et al. 1990) the concentration of monoterpenes in pine needles has no marked effect on moose browsing, in contrast to diterpenes (Danell et al. 1990). Because an increase of resin compounds retards digestion (Schwartz et al. 1980), the moose derives benefit from selective feeding. The effect of sesquiterpenes on moose browsing has not previously been investigated. The aim of this study is to find out if moose browsing intensity between Scots pine saplings can be explained by terpene compounds and if there are differences in forest site factors in respect to choice between pine individuals.

Material and methods

Field sampling

The pine twig material for chemical analysis was collected from two different localities in southern Finland at Viitasaari (63°14′N, 25°28′E) and Hattula (61°02′N, 24°33′E) in March 1995. The former was on dryish forest site (Vaccinium vitis-idaea type, VT-type) and the latter was on fertile forest site (V. myrtillus type, MT-type) (Cajander 1909). The pine stands were established by planting in 1984. The height of pines was ca. 2 m.

In both study areas the needle samples of current annual shoots were randomly collected from 12 lightly browsed and 12 intensively browsed trees. The samples of nonbrowsed trees were collected at Viitasaari from 24 trees close to each browsed tree. At Hattula the sampled trees were growing on feeding sites close to each other and 12 nonbrowsed ones were respectively included. In the lightly browsed trees there were less than 10 moose bites indicating moose had tasted the trees but not continued feeding. In the intensively browsed trees only few twigs were available after moose browsing. All moose bitings were fresh, i. e. the trees had been browsed shortly before sampling. There were no signs of older browsing in the sampled trees. The nonbrowsed trees had not been tasted by the moose. On both sites the browsed saplings were growing in different parts of the study areas of 4–5 ha and according to the tracks 2–4 moose had recently been present.

Chemical analysis

The needle samples were stored at –70 °C. They were dried at 70 °C for 24 hours and milled to pass through a 1.0 mm screen. The concentrations of terpene compounds were determined by gas chromatography masspectrometry (GC-MS analysis). Identification of terpenes was based on retention and mass spectral data published by Pohjola (1993). The determined terpenes were: a) monoterpene hydrocarbons (α-pinene, β-pinene, 3-carene, camphene, limonene, tricyclene, α-phellandrene, α-terpinene, γ-terpinene, sabinene), b) oxygen-containing monoterpenes (bornylacetate, α-terpineol), c) diterpenes (manoyloxide, manool), d) sesquiterpene hydrocarbons (β-caryophyllene, ~~δ~~-muurolene, germacrene D, ~~γ~~-cadinene, γ δ α-humulene, bicyclogermacrene), and e) oxygen-containing sesquiterpenes (germacra-1-E, 5E-dien-4-ol, cubenol). The cyclic diterpenes referred as the resin acids were identified by their mass spectral data and retention time data published by Holmbom (1977), Gref and Tenow (1987) and Morales et al. (1992). The determined resin acids were: isopimaradienoic acid, pimaradienoic acid, pimaric acid, sandaracopimaric acid, isopimaric acid, palustric acid, dehydroabietic acid, abietic acid, neoabietic acid, 4-epiimbricatolic acid, pinifolic acid, and unidentified (UI) group of resin acids eluding after pinifolic acid.

Statistical analysis

Because the short-term food selection by moose can be concluded to occur at the tree level (Danell et al. 1991), browsing categories in the present study are independent. Thus the Student t-test, ANOVA and the pairwise t-test with Bonferroni significance level (BMDP-programs) were used when comparing the mean values.

Results

In the pooled data the concentrations of monoterpene hydrocarbons (F = 5.65, P < 0.01), and total terpenes (F = 3.14, P < 0.05) differed significantly between all the browsing categories (Tab. 1). The total terpene concentration was considerably high in lightly browsed pines. The terpene concentrations between browsed pines and those not tasted by moose did not differ significantly in the pooled data (38.4 µg/mg ± 2.7 S. E., n = 48 vs. 32.0 µg/mg ± 2.2 S. E., n = 36, P = 0.09).

The total terpene concentration of browsed trees was higher on fertile forest site than on dryish forest site (46.0 µg/mg ± 4.3 S. E., n = 24 vs. 30.9 µg/mg ± 2.7 S. E., n = 24, P < 0.01). This was due to the relatively great difference between monoterpene hydrocarbons (26.5 µg/mg ± 4.2 S. E. vs. 6.3 µg/mg ± 0.8 S. E., p < 0.001, respectively). The main terpene compounds were/-pinene and pinifolic acid in every browsing category. Because of α considerable variation in terpene compounds between the forest sites, results of dryish and fertile site are presented separately.

On dryish forest site there were significantly less resin acids (9.1 µg/mg ± 1.1 S. E., n = 12 vs. 18.5 µg/mg ± 2.4 S. E., n = 12, P < 0.01), oxygen-containing sesquiterpenes

Table 1. The terpene compounds of needles (mean S. E.) in different browsing categories (pooled data). Means with the same letter do not differ statistically (ANOVA, the pairwise t-test and Bonferroni significance level of 5%).

	Concentration µg/mg		
	Intensively n = 24	Lightly n = 24	Nonbrowsed n = 36
Monoterpene hydrocarbons	13.3 ± 3.3^{ab}	19.5 ± 3.9^{a}	7.4 ± 0.6^{b}
Oxygen-containing monoterpenes	0.13 ± 0.02^{a}	0.14 ± 0.02^{a}	0.10 ± 0.01^{a}
Diterpenes	6.3 ± 1.7^{a}	4.5 ± 1.4^{a}	7.7 ± 1.4^{a}
Resin acids (cyclic diterpenes)	10.4 ± 1.0^{a}	13.1 ± 1.7^{a}	11.0 ± 1.0^{a}
Sesquiterpene hydrocarbons	0.54 ± 0.06^{a}	0.72 ± 0.07^{a}	0.60 ± 0.05^{a}
Oxygen-containing sesquiterpenes	3.5 ± 0.5^{a}	4.7 ± 0.4^{a}	5.2 ± 0.6^{a}
Total	34.2 ± 3.9^{ab}	42.7 ± 3.7^{a}	32.0 ± 2.2^{b}

(2.4 µg/mg ± 0.3 S. E., n = 12 vs. 4.2 µg/mg ± 0.6 S. E., n = 12, $P < 0.05$), and total terpenes (24.7 µg/mg ± 3.1 S. E., n = 12 vs. 37.0 µg/mg ± 3.8 S. E., n = 12, $P < 0.05$) in intensively browsed trees than in lightly browsed ones. The concentrations of following compounds were higher in lightly browsed trees than in intensively browsed trees: α-phellandrene ($P < 0.05$), bicyclogermacrene ($P < 0.01$), δ-cadinene ($P < 0.05$), germacra-1-E, 5E-dien-4-ol ($P < 0.05$), sandaracopimaric acid ($P < 0.05$), dehydroabietic acid ($P < 0.05$), abietic acid ($P < 0.01$), neoabietic acid ($P < 0.05$), 4-epiimbricatolic acid ($P < 0.01$), pinifolic acid ($P < 0.01$), and UI resin acids ($P < 0.01$). No significant differences were found between other terpene compounds. There was no significant difference in total terpene concentration between browsed and nonbrowsed trees (30.9 µg/mg ± 2.7 S. E., n = 24 vs. 34.6 µg/mg ± 3.0 S. E., n = 24, $P = 0.36$).

On fertile forest site there were more resin acids in intensively browsed trees than in lightly browsed ones (11.7 µg/mg ± 1.6 S. E., n = 12 vs. 7.8 µg/mg ± 0.6 S. E., n = 12, $P < 0.05$).

There were less sandaracopimaric acid ($P < 0.05$), palustric acid ($P < 0.05$), neoabietic acid ($P < 0.05$), 4-epiimbricatolic acid ($P < 0.05$), and UI resin acids ($P < 0.05$) in lightly browsed trees than in intensively browsed ones. No significant differences were found in other terpene compounds. The browsed pines on fertile site contained more total terpenes than the nonbrowsed ones (46.0 µg/mg ± 4.3 S. E., n = 24 vs. 26.9 µg/mg ± 2.1 S. E., n = 12, $P < 0.01$).

Discussion

According to the pooled data, the insignificant difference in total terpenes between browsed and nonbrowsed pines could be expected because the moose had not tasted the latter ones. This implies that biting some shoots would be the way moose make decision on whether to continue browsing or not. Because of considerable variation between the forest sites it is reasonable to respectively compare the intensively and lightly browsed trees.

Selective feeding by moose appears to be connected with the fertility of forest sites. On dryish forest site there were more resin acids, oxygen-containing sesquiterpenes, and total terpenes in lightly browsed trees than in intensively browsed ones. Furthermore, the concentrations of one monoterpene, three sesquiterpene and six resin acid compounds were lower in intensively browsed trees than in lightly browsed trees. On fertile forest site differences between individual terpene compounds were mainly insignificant or even opposite to those at dryish site. For instance, the resin acid concentration was relatively high in intensively browsed trees. It has been presented that site productivity affects plant chemistry, i. e. carbon-based chemical defence is more advanced on sites with low nutrient availability (Bryant et al. 1983). In the present study, the total terpene concentration was relatively high on fertile forest site due to the high monoterpene fraction which, however, has been reported to be insignificant in relation to moose browsing (Löyttyniemi and Hiltunen 1978).

These results indicate that terpene compounds can have an effect on moose food selection at the tree level. Pinifolic acid, which made up 52 % of resin acids, has also previously found to correlate negatively with moose browsing on pines (Danell et al. 1990). To our knowledge the present results are the first example of sesquiterpenes correlating negatively with moose winter browsing. Sesquiterpenes have been reported to inhibit the digestion of mule deer (*Odocoileus hemionus*) (Schwartz et al. 1980).

Not only food quality, but also quantity such as biomass availability can affect moose browsing on pines (Heikkilä and Mikkonen 1992). The moose is more selective and consume more of highly digestible twigs when availability of forage is high (Andersen and Sæther 1992). There were more highly preferred deciduous tree species such as aspen (*Populus tremulus*), rowan (*Sorbus aucuparia*) and willows (*Salix* spp.) on fertile forest site than on dryish forest site. The residence time of moose in winter is obviously longer in a good feeding habitat owing to the benefits of using mixed diet (Oldemeyer et al. 1977; Westoby 1978; Miquelle and Jordan 1979). When consuming several food plants the negative effects of secondary compounds can be reduced due to dilution in digestive process. It has also been shown that moose damage on pines is higher on fertile forest site than on dryish forest site (Heikkilä 1990; Heikkilä and Härkönen 1993).

In the present study, the browsing pressure was higher on fertile site, which also can explain the browsing intensity together with habitat quality and food availability. However, the importance of browsing pressure can not be emphasized because of the high relative availability of young pines in both areas. The characteristics of dryish, natural Scots pine site obviously allowed relatively selective moose feeding among pine saplings. In such condidions it is reasonable to conclude that concentrated browsing on certain plant individuals indicate qualitative between-tree differences perceived by moose when tasting the shoots.

In conclusion, we suggest that the possible deterring effects of terpenes in needles of individual Scots pines are related to the sesquiterpenes and resin acids. Between-tree selection by moose is likely to appear on dryish forest sites typical of naturally growing pines. Relationships between food availability, habitat quality and browsing pressure may also explain the variation in feeding behaviour.

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V

THE INFLUENCE OF CLEANING ON MOOSE BROWSING IN YOUNG SCOTS PINE STANDS IN FINLAND

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ABSTRACT: Assessing the intensity of silvicultural cleaning in young stands of Scots pine (*Pinus sylvestris*), which are an important food source for moose (*Alces alces*), was studied in relation to the effects of feeding. Field data were collected in central Finland from 1990-96. The study area was divided into 13 silviculturally cleaned (1988-89) and 7 untreated control stands. A second cleaning was done in all of the cleaned and untreated control stands in 1993-94. Six exclosures established in 1989 also were included in the study. White birch (*Betula pubescens*) was the main tree species removed by cleaning both in open areas and in exclosures. Total biomass consumed by moose in winter 1989-90, 1 year after the first cleaning, was significantly higher in untreated stands than in cleaned stands (33.3 kg/ha ± 3.7 SE vs. 12.0 kg/ha ± 3.7 SE, $P < 0.01$). Moose browsing on pine in silviculturally cleaned stands of pine was less intensive than in untreated ones. The total biomass consumed by moose in winter 1994-95, 1 year after the second cleaning, did not differ between cleaning treatments (10.4 kg/ha ± 2.2 SE vs. 11.0 kg/ha ± 5.1 SE, $P = 0.90$), nor did consumed pine biomass in winter 1995-96, 2 years after the second cleaning (4.6 kg/ha ± 1.3 SE vs. 9.0 kg/ha ± 3.8 SE, $P = 0.20$). Several factors were correlated with moose browsing on pine in winter 1994-95. Stepwise regression analysis revealed that total stem density and white birch density best explained moose browsing on pine. Significantly higher cumulative numbers of pine stem breakages and browsed pines occurred in sites cleaned once versus those cleaned twice during 1988-94. The neutral detergent fiber (NDF) and acid detergent fiber (ADF) contents of pine twigs prior to the second cleaning in 1993-94 was higher in the untreated stands than in the cleaned ones. However, *in vitro* dry matter digestibility did not explain the difference in browsing between cleaning treatments. Total phenol content of pine twigs was slightly higher in the cleaned stands than in the untreated stands. The preferred species of trees, aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), and willows (*Salix* spp.), were taller in exclosures than in open areas in 1995. The differences were evidently caused by browsing. Results indicated that moose browsing was not high enough to reduce the stem density of less-preferred white birch, which was strongly competing with pine especially in the single-cleaning treatment. Thus, relatively early cleaning is needed in conditions with excess birches because they can increase the risk of moose damage to pine. The importance of a mixture of tree species as well as the timing of silvicultural cleaning in relation to moose browsing has to be taken into account when combining moose management and forest practices.

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Key words: *Alces alces*, browsing, cleaning, damage, deciduous trees, moose, *Pinus sylvestris*, Scots pine.

In recent decades large forest areas have been regenerated by planting Scots pine (*Pinus sylvestris*) in Finland. In these stands silvicultural practices to promote the growth of pine have been done, whereby fast-growing deciduous tree species strongly competing with economically valuable Scots pine have been removed by silvicultural cleaning. At present, mechanical cleaning is practically the only method used in controlling excess deciduous trees.

In Nordic countries a high proportion of winter food of moose (*Alces alces*) consists of Scots pine (Bergström and Hjeljord 1987), leading to moose damage especially in high-density wintering areas (Lavsund 1987). Browsing of pine twigs by moose is not generally harmful, whereas breakage of stems can considerably impair the technical quality of the wood (Heikkilä and Löyttyniemi 1992). Attention has been given to ways of combining forestry and moose management without conflicts (Löyttyniemi and Lääperi 1988).

The origin of pines (Niemelä *et al.* 1989), phenotypes of pines (Danell *et al.* 1991), density of pine stands (Heikkilä and Mikkonen 1992), and high density of deciduous saplings (Heikkilä and Härkönen 1993) can each affect the quality of pine and browsing intensity by moose. If composition of tree species could affect moose feeding and damage on pine, it has been recommended to remove deciduous trees such as rowan (*Sorbus aucuparia*) and aspen (*Populus tremula*), preferred by moose, through cleaning in pine stands (Löyttyniemi and Piisilä 1983, Lääperi and Löyttyniemi 1988). Moreover, excess birches (*Betula* spp.) occurring as overgrowth above pine can increase the risk of stem breakages by moose (Heikkilä 1993, Heikkilä and Härkönen 1993). Contradictory results indicate that there is no need for modifying the composition of tree species (Edenius 1991).

Moose browsing is known to be selective, i.e., certain tree species are preferred over others (Bergström and Hjeljord 1987). In addition, moose utilize food resources patchily (Danell *et al.* 1991). Moose browsing can greatly alter the tree species composition at high densities of moose (Brandner *et al.* 1990, McInnes *et al.* 1992, Thompson and Curran 1993). At lower moose densities the high browsing pressure can also retard the growth of preferred deciduous species of trees, whereas less preferred birches are not harmfully affected (Heikkilä and Härkönen 1993). On the other hand, moose can also have a positive influence on their food supply where habitats are not undergoing succession (Molvar *et al.* 1993). The combined effects of moose and silvicultural practices in managed stands should be taken into account in relation to changes in forest ecosystem.

The aim of the present study was to examine moose browsing in young managed Scots pine stands in relation to silvicultural cleanings during winter. We were especially interested in the following questions: 1) is there selectivity in moose browsing in relation to the composition and density of young Scots pine stands, 2) are there any differences in moose damage to Scots pine in relation to the early and lately applied silvicultural cleanings, and 3) what is the combined effect of moose and cleaning on the development of young Scots pine stands?

MATERIAL AND METHODS

Field sampling

The study site, in an area of moose winter range (moose density 0.5-0.7/km^2) in Viitasaari (63° 14'N, 25°28'E) in central Finland, was divided into 13 silviculturally treated and 7 untreated stands of Scots pine in 1988. The experimental stands were established by planting in 1984. The treatments were silvicultural cleanings, in which the deciduous saplings were partly removed. The first treatment was applied in 1988-89.

In 1993, deciduous trees were competing strongly with pine in those stands left untreated in 1988; to improve the growth of pine, silvicultural cleaning was completed in 1993-94. This treatment also was repeated in those stands cleaned in 1988-89. According to this procedure, 13 stands were treated twice and 7 stands treated once.

There were 6 exclosures (25 by 50 m in size) in the study area. Each exclosure was divided into treated (i.e., cleaned) and untreated blocks. The first treatment in these exclosures was done in 1989. The second treatment was in 1994, and all blocks were treated. Thus, there were 6 blocks treated once and 6 blocks treated twice.

Each stand had 9 permanent plots established in 1988 surrounding the exclosures. There were 5 permanent plots per block in each exclosure. The size of each circular plot was 50 m^2. Every plot was inspected in 1990, 1995, and 1996. The density and height of tree stems >0.5 m were determined by species. The number of saplings removed of each tree species was counted in 1995.

Moose browsing was measured and the number of moose fecal-pellet groups was counted on every plot outside exclosures. All bites by moose were counted and diameter of bites from every tree species was measured. Bites were converted to consumed dry-weight biomass according to Telfer (1969)(Table 1). The relationships in Table 1 were calculated by weighing twigs (dried at 70°C to constant weight) from diameter categories most browsed by moose in study area. Ten twigs were weighed in each category. Biomass availability was determined using equations presented by Heikkilä and Härkönen (1993). Pine stem breakages with moose browsing were counted. Thus, scent marking of trees by moose was excluded (cf., Bowyer *et al.* 1994). In 1996 only moose browsing on pine was measured.

Table 1. Relationships between twig diameter (mm) and dry biomass (g) for different tree species in most browsed diameter categories at Viitasaari. Regressions have the form:

$$\log_{10} (\text{dry biomass}) = b (\log_{10}(\text{twig diameter})) + a.$$

Tree species	a	b	r^2	Diameter category
Scots pine	-1.0914	2.8879	0.97	2 - 10
Silver birch	-1.3937	3.1982	0.99	1 - 6
White birch	-1.0459	2.7204	0.95	1 - 6
Aspen	-1.3718	2.7614	0.99	1 - 8
Rowan	-1.6799	3.1631	0.99	2 - 9
Willows	-1.7679	3.3010	0.99	1 - 8
Alder	-1.4593	3.2729	0.98	1 - 5
Juniper	-1.0185	2.7134	0.99	1 - 6

Chemical analysis

In December 1993, 40 unbrowsed pines were randomly selected in Viitasaari study area for analysis of *in vitro* dry matter digestibility (IVDMD), total phenol content, neutral detergent fiber (NDF), and acid detergent fiber (ADF). Twenty pines were chosen in each of the following two habitat types: 1) cleaned: mechanically cleaned pine stand without competition from an overstory of deciduous tree species; and 2) untreated: pine stand with competition from an overstory of deciduous tree species, mainly white birch (*B. pubescens*). The pines were growing on a dryish forest site (*Vaccinium vitis-idaea* type)(Cajander 1909).

Another sampling was undertaken to analyse the response of browsing to the quality of pine twigs in an area in southern Finland, at Padasjoki/Vesijako (61°30'N, 25°10'E) in March 1990. The pine stand growing on a dryish forest site type had been naturally regenerated in 1970-71 and was a monoculture; there was no competition from deciduous tree species. Pine twigs analysed for

IVDMD, total phenol, NDF, and ADF were collected from two habitat types: 1) sparse (pine density <3,600/ha), and 2) dense (pine density >9,600/ha). Twenty pines of each habitat type were randomly selected for chemical analysis.

In both Viitasaari and Padasjoki/Vesijako samplings, three shoots of current annual growth were taken randomly from every tree. The sampled twigs were cut at a height of ca. 1.5 m, the typical feeding height of moose. The twigs were dried at 70°C for 24 hr and milled to pass through a 1.0 mm screen.

Analysis for IVDMD was done using moose ruminal inoculum from moose harvested at Grimsö Wildlife Research Station in southcentral Sweden in winter 1993-94. The method is described completely by Pehrson and Faber (1994). Analysis was replicated 2-3 times depending on sample size. The concentration of total phenols was determined by the Folin-Ciocalteau method (Singleton and Rossi 1965). Total phenol analysis was replicated 2 times. Neutral detergent fiber and acid detergent fiber were determined according to Van Soest (1963) and Van Soest and Wine (1967).

Statistical analysis

The data were statistically analysed using Student *t*-test, one-way analysis of variance (ANOVA) with Bonferroni corrections, Pearson correlation analysis, linear regression analysis, and stepwise regression analysis. Densities of tree species were $\log_{10} + 1$ transformed and proportional data were arcsine square-root transformed before statistical analyses. Multicollinearity between variables was taken into account in stepwise regression analysis. Data for 1990, 1995, and 1996 were analysed separately.

RESULTS

Effect of treatments on food availability

In 1990, the total stem density was significantly higher in untreated areas than in cleaned areas (ANOVA; $F = 9.75$; 3, 28 df; $P < 0.001$)(Table 2). Cleaning reduced the density of deciduous trees and juniper (*Juniper communis*)($F = 8.75$; 3, 28 df; $P < 0.001$), whereas Scots pine density did not differ between treatments (Fig. 1a). The densities of white birch ($F = 5.68$; 3, 28 df; $P < 0.01$) and silver birch (*B. pendula*)($F = 6.98$; 3, 28 df; $P < 0.01$) were significantly lower in cleaned areas (Fig. 1a). Cleaning did not reduce significantly the heights of different tree species (Fig. 2a). Total biomass availability was lowest in cleaned open stands and highest in untreated open stands ($F = 3.39$; 3, 28 df; $P < 0.05$)(Table 2). Pine constituted highest proportion from total available biomass in cleaned areas ($F = 5.12$; 3, 28 df; $P < 0.01$). Birch:pine height ratio did not differ between treatments ($F = 1.33$; 3, 28 df; $P = 0.28$).

Table 2. Total stem density (stems/ha), density of deciduous trees and juniper (stems/ha), total biomass availability (kg/ha), proportion of pine from total available biomass (%), and birch:pine height ratio classified according to cleaning treatment in open stands and exclosures at Viitasaari in 1990. Means are given with their standard errors. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

	Open stands		Exclosures		
Variable	Untreated	Cleaned	Untreated	Cleaned	*P*
Total stem density	24,721^{a} ± 4,770	8,591^{b} ± 1,157	24,840^{a} ± 5,815	11,013^{b} ± 3,408	***
Deciduous trees and juniper	22,346^{a} ± 4,755	6,164^{b} ± 1,149	22,547^{a} ± 5,834	8,093^{b} ± 3,511	***
Total biomass availability	910^{a} ± 95	457^{b} ± 67	888^{ab} ± 291	644^{ab} ± 174	*
Proportion of pine available	25.9^{a} ± 5.4	53.2^{b} ± 7.8	19.9^{a} ± 3.6	53.4^{b} ± 12.3	**
Birch:pine height ratio	1.2 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.0 ± 0.1	NS

NS=Not significant, *$P<0.05$, **$P<0.01$, ***$P<0.001$

In 1995, the total stem density was highest in once cleaned open areas and lowest in twice cleaned exclosure areas ($F = 3.79$; 3, 28; $P < 0.05$)(Table 3). The densities of white birch ($F = 8.22$; 3, 28 df; $P < 0.001$) and silver birch ($F = 3.61$; 3, 28 df; $P < 0.05$) differed significantly between treatments (Fig. 1b). Total number of stems removed by cleaning was significantly higher in once cleaned areas than in twice cleaned areas ($F = 7.45$; 3, 28 df; $P < 0.001$)(Table 3). Stems of white birch, silver birch, and willows removed by cleaning differed significantly between treatments (Fig. 3). Cleaning treatments affected significantly the heights of deciduous tree species (Fig. 2b). Aspen, rowan, and willows were taller in exclosures than in open stands. Total biomass availability ($F = 1.87$; 3, 28 df; $P = 0.16$) did not differ between treatments (Table 3). Proportion of pine from total available biomass ($F = 6.33$; 3, 28 df; $P < 0.01$) was highest in twice cleaned areas in exclosures. Birch:pine height ratio was lowest in twice cleaned areas ($F = 7.30$; 3, 28 df; $P < 0.001$).

Table 3. Total stem density (stems/ha), number of stems removed by cleaning (stems/ha), total biomass availability (kg/ha), proportion of pine from total available biomass (%), and birch:pine height ratio classified according to cleaning treatment in open stands and exclosures at Viitasaari in 1995. Means are given with their standard errors. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

	Open stands		Exclosures		
Variable	Once cleaned	Twice cleaned	Once cleaned	Twice cleaned	*P*
Total stem density	8,565^{a} ± 589	7,202^{ab} ± 707	7,247^{ab} ± 450	5,173^{b} ± 524	*
Number of stems removed	14,454^{a} ± 2,846	6,067^{b} ± 1,261	14,813^{a} ± 3,403	3,553^{b} ± 714	***
Total biomass availability	1,949 ± 301	1,820 ± 229	2,268 ± 239	2,604 ± 141	NS
Proportion of pine available	80.2^{a} ± 4.5	89.9^{ab} ± 2.6	81.1^{a} ± 4.0	96.6^{b} ± 1.2	**
Birch:pine height ratio	1.1^{ab} ± 0.2	0.7^{a} ± 0.1	1.3^{b} ± 0.1	0.6^{a} ± 0.1	***

NS=Not significant, *$P<0.05$, **$P<0.01$, ***$P<0.001$

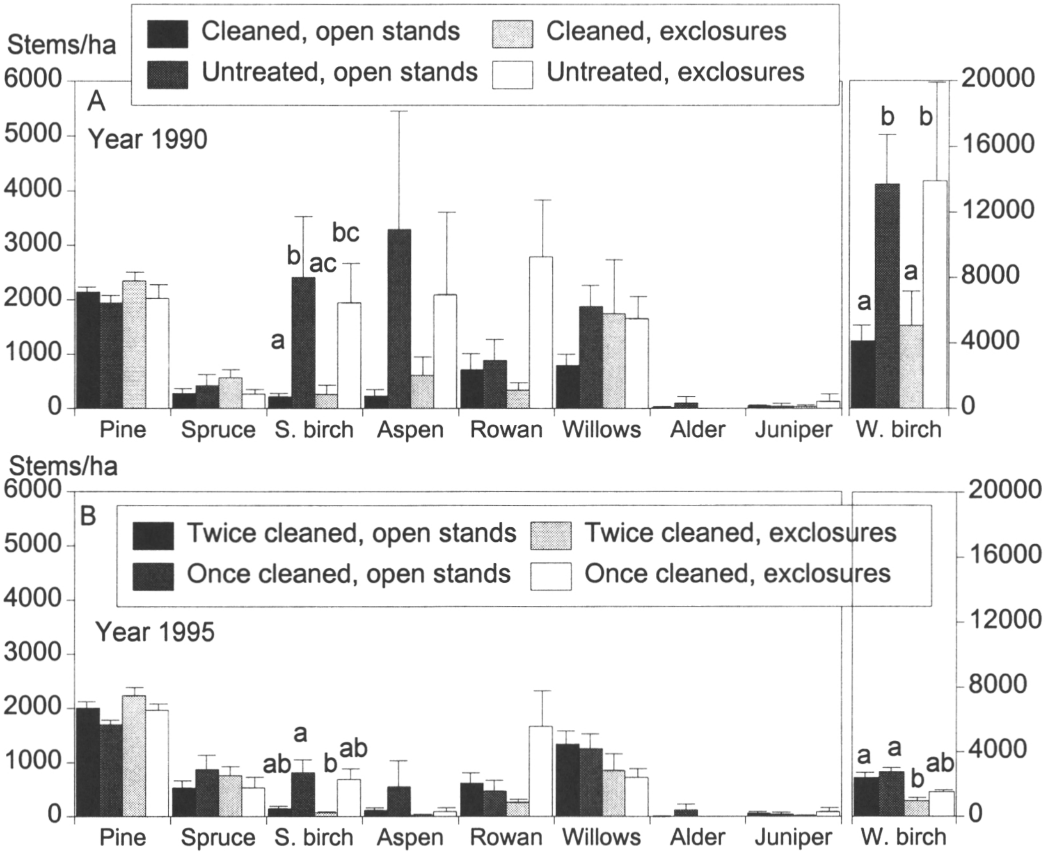

Fig. 1. Density of different tree species (+ SE) classified according to cleaning treatment at Viitasaari a) in 1990 and b) in 1995. Note the different scales. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

Response of moose browsing to treatments

In winter 1989-90, the total biomass consumed by moose was significantly higher ($t = 3.70$, 18 df, $P < 0.01$) in untreated stands (33.3 kg/ha ± 3.7 SE) than in cleaned stands (12.0 kg/ha ± 3.7 SE). Total biomass used from total available was 3.0% (± 1.0 SE) in cleaned stands and 3.8% (± 0.4 SE) in untreated stands ($t = 1.05$, 18 df, $P = 0.31$), and the proportion of consumed deciduous tree species biomass was 4.3% (± 1.3 SE) and 3.8% (± 0.5 SE), respectively ($t = 0.19$, 18 df, $P = 0.85$). Of the biomass available in preferred deciduous trees (aspen, rowan, and willows), 21.0% (± 3.5 SE) had been consumed in cleaned and 28.0% (± 6.9 SE) in untreated stands ($t = 1.05$, 18 df, $P = 0.31$). The biomass removed by moose from pine, silver birch, aspen, and willows was higher in untreated than in cleaned stands (Fig. 4a), and the proportion of consumed pine biomass of total consumption was

26.0% (± 6.9 SE) and 40.0% (± 9.2 SE)(t = -0.60, 18 df, P = 0.56), respectively. Moose had not consumed spruce (*Picea abies*).

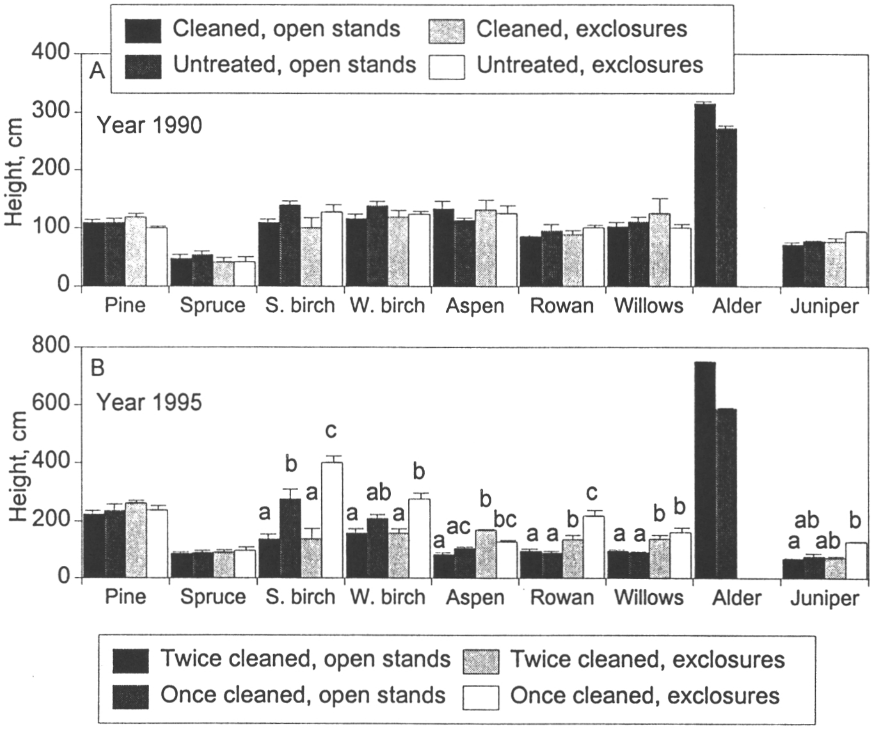

Fig. 2. Height of different tree species (+ SE) classified according to cleaning treatment at Viitasaari a) in 1990 and b) in 1995. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

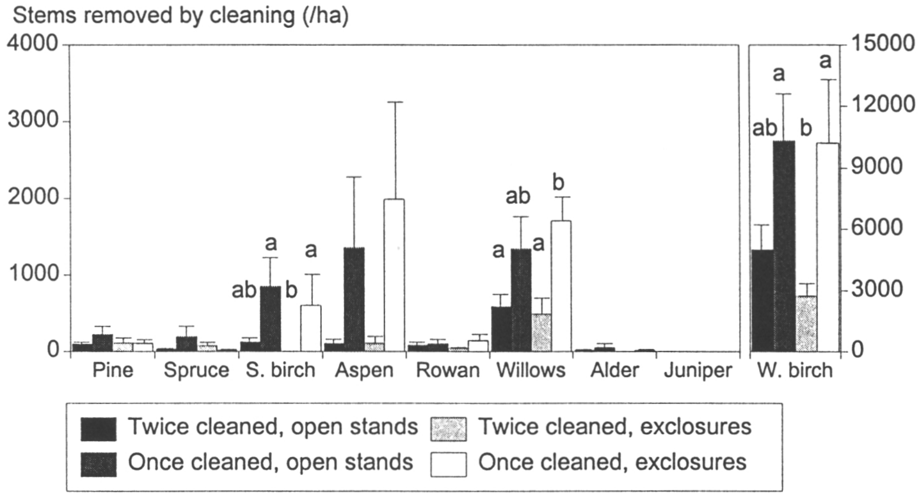

Fig. 3. Number of stems removed by cleaning (+ SE) classified according to cleaning treatment at Viitasaari in 1994. Note the different scales. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

In winter 1989-90, the number of broken pine stems was significantly lower in cleaned stands than in untreated stands (Table 4). The number of browsed pines and fecal-pellet groups did not differ between treatments. The total biomass consumed by moose was positively correlated with total stand density ($r = 0.69$, $P < 0.01$, $n = 20$) and with total biomass availability ($r = 0.49$, $P < 0.05$, $n = 20$).

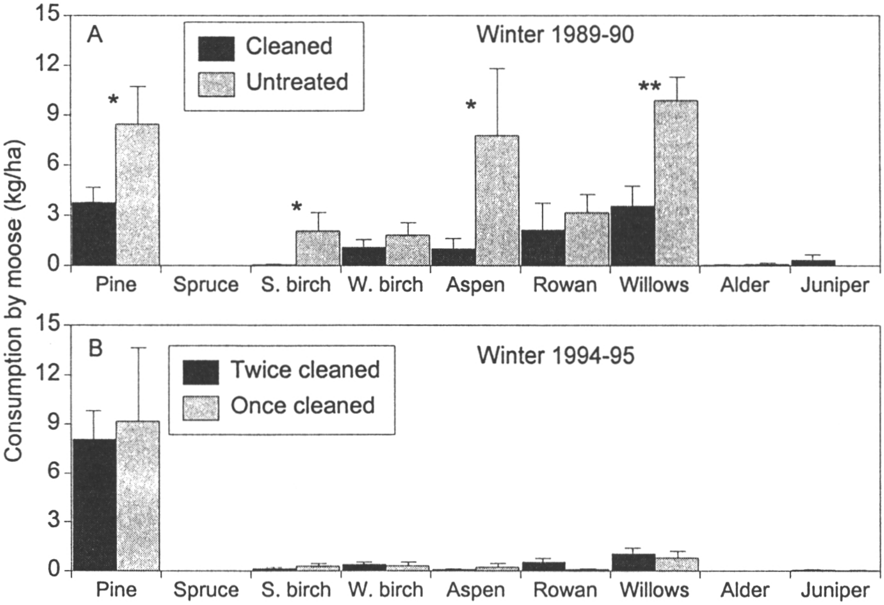

Fig. 4. Consumption of different tree species by moose (+ SE) at Viitasaari a) in cleaned and untreated stands in winter 1989-90 and b) in twice cleaned and once cleaned stands in winter 1994-95. Significance: * : $P < 0.05$, ** : $P < 0.01$ (*t*-test).

In winter 1994-95, total biomass removed by moose was 10.4 kg/ha (± 2.2 SE) in twice cleaned and 11.0 kg/ha (± 5.1 SE) in once cleaned stands ($t = 0.12$, 18 df, $P = 0.90$). Consumed pine biomass averaged 8.5 kg/ha (± 1.9 SE) with no statistical difference between experiments ($t = 0.28$, 18 df, $P = 0.78$, Fig. 4b). Consumed pine biomass composed 80.1% (± 3.8 SE) of total consumption ($t = 0.54$, 18 df, $P = 0.60$). The most consumed deciduous tree species by moose were willows (Fig. 4b). Spruce and alder (*Alnus incana*) were not used. The total biomass utilized was 0.7% (± 0.2 SE) of the total available biomass in twice cleaned and 0.6% (± 0.2 SE) in once cleaned stands ($t = 0.34$, 18 df, $P = 0.74$). The proportional biomass consumed from deciduous tree species was 2.3% (± 0.5 SE) in twice cleaned and 0.8% (± 0.4 SE) in once cleaned stands ($t = 1.80$, 18 df, $P = 0.09$), and from preferred tree species (aspen, rowan, and willows) was 8.0% (±1.6 SE) and 5.4% (± 2.1 SE)($t = 0.79$, 18 df, $P = 0.44$), respectively.

In winter 1994-95, number of browsed pines, stem breakages, and fecal-pellet groups did not differ between treatments (Table 4). There were significantly higher cumulative numbers of stem breakages (Fig. 5a) and browsed pines (Fig. 5b) in once cleaned versus twice cleaned stands. The cumulative proportion of stem breakages was 31.2% (± 8.0 SE) in once cleaned and 12.2% (± 2.9 SE) in twice cleaned stands ($t = 2.91$, 18 df, $P < 0.01$), and of browsed pines was 68.4% (± 6.8 SE) and 34.6% (± 5.7 SE)($t = 3.62$, 18 df, $P < 0.01$), respectively.

Table 4. Number of pines browsed by moose (stems/ha), pine stem breakages (stems/ha), and fecal-pellet groups of moose (/ha) classified according to cleaning treatment at Viitasaari in winter 1989-90 and 1994-95 (*t*-test). Means are given with their standard errors.

	Winter 1989-90			Winter 1994-95		
Variable	Untreated	Cleaned	*P*	Once cleaned	Twice cleaned	*P*
Browsed pines	200 ± 24	116 ± 31	NS	308 ± 90	277 ± 72	NS
Stem breakages	83 ± 18	39 ± 12	*	54 ± 21	56 ± 15	NS
Pellet groups	95 ± 22	53 ± 14	NS	35 ± 13	55 ± 17	NS

NS=Not significant, **P*<0.05

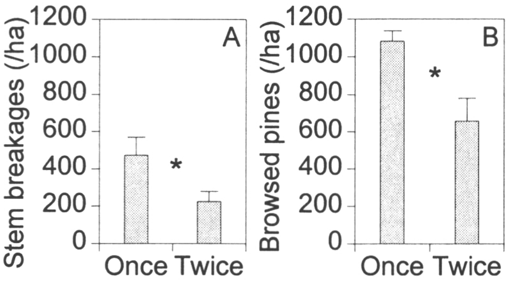

Fig. 5. a) Total number of pine stem breakages (+ SE), and b) total number of browsed pines (+ SE) in once cleaned and twice cleaned stands at Viitasaari during 1988-94. Significance: * : $P < 0.05$ (*t*-test).

In winter 1995-96, pine biomass consumed was 4.6 kg/ha (± 1.3 SE) in twice cleaned and 9.0 kg/ha (± 3.8 SE) in once cleaned stands (t = -1.32, 18 df, P = 0.20). Number of browsed pines was lower in twice cleaned than in once cleaned stands (106 stems/ha ± 28 SE vs. 273 stems/ha ± 79 SE)(t = -2.44, 18 df, $P < 0.05$). Respective numbers of broken pine stems (26 stems/ha ± 9 SE vs. 32 stems/ha ± 14 SE)(t = -0.38, 18 df, P = 0.71) and fecal-pellet groups (38 groups/ha ± 10 SE vs. 51 groups/ha ± 15 SE)(t = -0.76, 18 df, P = 0.46) did not differ between treatments.

Moose browsing and stand characteristics in winter 1994-95

Tree species density and composition.-- In winter 1994-95, moose consumed more total biomass with increasing stem density ($r^2 = 0.25$, $P < 0.05$, $n = 20$). The total biomass consumed by moose was not correlated with total biomass availability ($r = -0.08$, $P = 0.73$, $n = 20$).

Several tree densities were significantly correlated with moose browsing on pine (Table 5), whereas biomass availabilities of different tree species had no effect on the consumed pine biomass, the number of browsed pines, and the number of pine stem breakages.

The biomass removed by moose from pines increased as the density of white birch increased (Table 6). A stepwise regression analysis revealed that densities of deciduous tree species other than white birch did not explain consumption of pine by moose.

The number of browsed pines by moose was dependent on the total stem density, which alone explained 39% of the variation (Table 6). The number of broken pine stems by moose increased with the density of white birch (Table 6). The degree of explanation was, however, low (25%). The densities of other deciduous tree species did not explain the number of pine stem breakages.

Chemistry of Scots pine.-- The fiber content of pine twigs was relatively high in the stand where pines had been growing with a high density of deciduous trees (Fig. 6a,c). Fiber content also was high in pine twigs in the dense pine monoculture stand (Fig. 6b,d). The total content of phenolic compounds was slightly higher in pine stands with low density of deciduous trees (Fig. 6e), but did not differ between dense and sparse pine stands (Fig. 6f). The digestibility of pines (IVDMD) growing in these different types of feeding habitats did not differ (Fig. 6g,h).

Table 5. Pearson correlation coefficients (r) between moose browsing on pines and average values of tree density (stems/ha) at Viitasaari in winter 1994-95. Factors with nonsignificant difference are not included. All correlations are positive ($n = 20$).

Factor	Consumed pine biomass (g/ha)	Pine stem breakages (stems/ha)	Browsed pines (stems/ha)
Density of white birch	0.53*	0.50*	0.54*
Density of willows	0.52*	0.33	0.60**
Total stem density	0.44	0.48*	0.62**
Density of deciduous trees and juniper	0.43	0.45*	0.61**
Density of aspen, rowan, and willows	0.37	0.49*	0.61**

*$P<0.05$, **$P<0.01$, ***$P<0.001$

Table 6. Results of stepwise regression analyses at Viitasaari in winter 1994-95 ($n = 20$). Independent variables: X_1 = Density of white birch (stems/ha), X_2 = Total stem density (stems/ha).

Dependent variable	Equation	r^2	F	P
Consumed pine biomass (g/ha)	$Y = - 2{,}547 + 4.4\ X_1$	0.28	7.07	<0.05
Browsed pines (stems/ha)	$Y = - 222 + 0.27\ X_2$	0.39	11.40	<0.01
Pine stem breakages (stems/ha)	$Y = - 10.1 + 0.03\ X_1$	0.25	5.95	<0.05

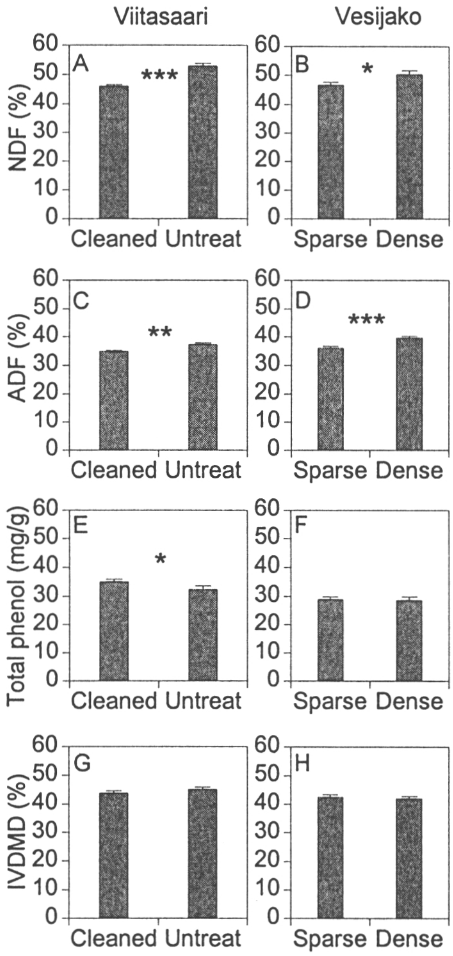

Fig. 6. Neutral detergent fiber (NDF) content (+ SE) in different habitat types a) at Viitasaari in 1993 and b) at Padasjoki/Vesijako in 1990. Acid detergent fiber (ADF) content (+ SE) in different habitat types c) at Viitasaari in 1993 and d) at Padasjoki/Vesijako in 1990. Total phenol content (+ SE) in different habitat types e) at Viitasaari in 1993 and f) at Padasjoki/Vesijako in 1990. *In vitro* dry matter digestibility (IVDMD) (+ SE) in different habitat types g) at Viitasaari in 1993 and h) at Padasjoki/Vesijako in 1990. Significance: * : $P < 0.05$, ** : $P < 0.01$, *** : $P < 0.001$ (*t*-test).

DISCUSSION

Moose browsing after the first treatment in seedling stands

Fast growing deciduous trees, especially stump and root suckers cause a need for silvicultural cleaning treatment even relatively early in young plantations. In our study, food availability for moose was two times lower after early cleaning compared with untreated stands, because densities of birches were considerably reduced. The short-term reduction of food availability by early cleaning can be even more effective (Hjeljord and Grønvold 1988, Härkönen, *in press*). On the contrary, the proportion of pine available as food was double in cleaned stands compared with untreated stands.

Moose consumed more biomass in untreated than in cleaned stands; however, the proportional consumption was rather low in both treatments. Only the consumed proportion of preferred tree species biomass was >20%, which indicates a low browsing pressure (cf., Heikkilä and Härkönen 1993). Scots pine, the main winter food of moose in Scandinavia (Cederlund *et al.* 1980), constituted 40% of total consumption in cleaned stands and 26% in untreated stands. In untreated stands moose could consume significantly more aspen and willows, which are highly preferred species (Bergström and Hjeljord 1987), obviously owing to their high digestibility (Hjeljord *et al.* 1982, Sæther and Andersen 1990).

Moose damage on pine seedlings was more common in untreated stands than in cleaned stands in terms of biomass consumed and the number of stems broken. Owing to the high density of deciduous trees in untreated stands the choice by moose would be expected to reduce browsing pressure on pine. The main tree species in untreated stands was, however, white birch at a density of ca. 14,000 stems/ha. Because this species is not preferred (Bergström and Hjeljord 1987), it is probably not a good alternative for browsing pine. An excess density of white birch would more likely be important as competing species impairing the growth conditions of pine and affecting chemical properties of pine (Heikkilä *et al.* 1993). In addition, the risk of moose damage to pine is higher when birches occur in high densities as overstory (Heikkilä 1993, Heikkilä and Härkönen 1993), whereas a birch:pine height ratio close to 1.0 does not result in such damage (Härkönen, *in press*).

Moose browsing after the second treatment in sapling stands

In 1994, the high competition between pine and deciduous trees in untreated stands was eliminated by an additional cleaning. This treatment was done more lately than normally applied cleaning in Finnish forestry. White birch was the tree species mostly removed both in open stands and in exclosures. Also densities of aspen and willows were considerably reduced in the previously uncleaned stands. Pine constituted the highest proportion of total biomass available, and no difference occurred in total biomass between treatments.

The total biomass removed by moose in open stands in winter 1994-95 was rather low with no difference between treatments. The proportional consumptions were considerably lower than those in winter 1989-90. Biomass consumed of different deciduous trees by moose were especially low, whereas pine constituted 80% of total consumption. Moose are known to respond selectively to the increase of browse availability (Andersen and Sæther 1992). Present results clearly indicate that intensive silvicultural cleaning reduces moose browsing alternatives. This can negatively affect winter nutrition of moose, because it would be preferable to have several food plant species available (Oldemeyer *et al.* 1977). However, moose can survive fine on a diet of mostly willows (Van Ballenberghe *et al.* 1989).

No differences occurred in the number of browsed pines, stem breakages, and consumed pine biomass between treatments in winter 1994-95. The lack of significant differences in moose damage could be explained by stands being similar after treatments, with no high density and overgrowth of deciduous trees above pines (cf., Heikkilä and Härkönen 1993). When comparing cumulatively damage in pines, there were significantly more browsed pines and stem breakages in once cleaned stands. This shows indirectly, that a high density and overgrowth of deciduous trees in untreated stands during 1988-94 increased the risk of moose damage on pine. If cleaning is done late as in the once cleaned stands, the risk of moose damage appears to be higher than in the normally managed stands. We concluded that if silvicultural cleaning is used in preventing moose damage on pine, it should be done before the deciduous trees are competing too strongly with pine. However, moose damage obviously is not totally prevented by cleaning. If pine is only tree species available as forage by moose, browsing is likely directed to pine. Thus, total cleaning should be avoided.

Increasing stand density in conifer monocultures diminishes the quality of twigs browsed by moose (Thompson *et al.* 1989, Heikkilä and Mikkonen 1992). In our study, fiber content was higher in pine twigs in dense pine monoculture stand. In mixed pine-deciduous stands, young pines suppressed by birch overgrowth contained less fiber and lignin than did the freely growing pines

(Heikkilä *et al.* 1993). In our study, total phenol contents of pine twigs tended to be higher in cleaned stands, whereas NDF and ADF contents were higher in untreated stands. Because there was no difference in IVDMD-values between freely growing pines and pines growing with a dense deciduous tree mixture, it is difficult to explain the relatively high cumulative number of browsed pines and stem breakages in untreated stands during 1988-94. This emphasizes that there are also variables other than examined plant chemicals which have an effect on moose browsing. In this sense, previous browsing should also be taken into account (Molvar *et al.* 1993, Bowyer and Bowyer 1997), because moose damage occur year after year in same stands (Löyttyniemi and Piisilä 1983). This could also explain relatively high amount of browsed pines in once cleaned stands in winter 1995-96.

After cleaning treatments several factors related to stand density were correlated with moose damage on pine. Stepwise regression indicated the density of white birch accounted for 28% of the observed variation in the consumed pine biomass, whereas total stem density accounted for 39% of the observed variation in the number of browsed pines. The density of white birch best explained the number of pine stem breakages, but the degree of explanation remained low (25%). The individual tree species other than white birch did not explain moose damage on pine. Our results indicate that white birch can affect moose damage on pine (cf., Heikkilä 1993, Heikkilä and Härkönen 1993).

Effects of browsing on young Scots pine stands

Moose browsing can deplete the growth of preferred deciduous trees in high-density moose areas (Risenhoover and Maass 1987, Heikkilä and Härkönen 1993). In our study, despite low browsing pressure, highly preferred tree species such as aspen, rowan, and willows (Bergström and Hjeljord 1987) were taller in exclosures than in open stands both in once cleaned and twice cleaned areas. The combined effect of moose and silvicultural cleaning is not easy to recognise, but the differences in heights of preferred deciduous trees were evidently caused by browsing.

Our results indicate clearly that silvicultural cleaning is needed in removing excess birch vegetation in pine stands, because moose browsing does not adequately reduce the stem density of less-preferred birches at a moose density of 0.5-0.7/km^2. Thompson and Curran (1993) have shown that paper birch (*B. papyrifera*) was eliminated at a density of 3 moose/km^2, which is far denser than in our area in Finland.

The long-term consequences of moose browsing such as reduced tree biomass and production, reduced amount of litter, and opening of the tree canopy (McInnes *et al.* 1992) are obviously not commonly expected in managed forests in Finland, because the effect of silvicultural cleaning is much more intensive than the effect of moose browsing. A high supply of food resources of moose in terms of preferred browse species is destroyed by cleaning; however, a regrowth of browse can be expected, because in mechanically cleaned stands new sprouting is a common occurrence.

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