THE INFLUENCE OF SILVICULTURAL 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 were also 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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Large forest areas have been regenerated by planting Scots pine (*Pinus sylvestris*) in Finland in recent decades. 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.* 1991b), 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.* 1991a). 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?

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 the 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.

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 2 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

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

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 2 habitat types: (1) sparse (pine density <3,600/ha); and (2) dense (pine density >9,600/ha). Twenty pines from each habitat type were randomly selected for chemical analysis.

In both Viitasaari and Padasjoki/Vesijako samplings, 3 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.

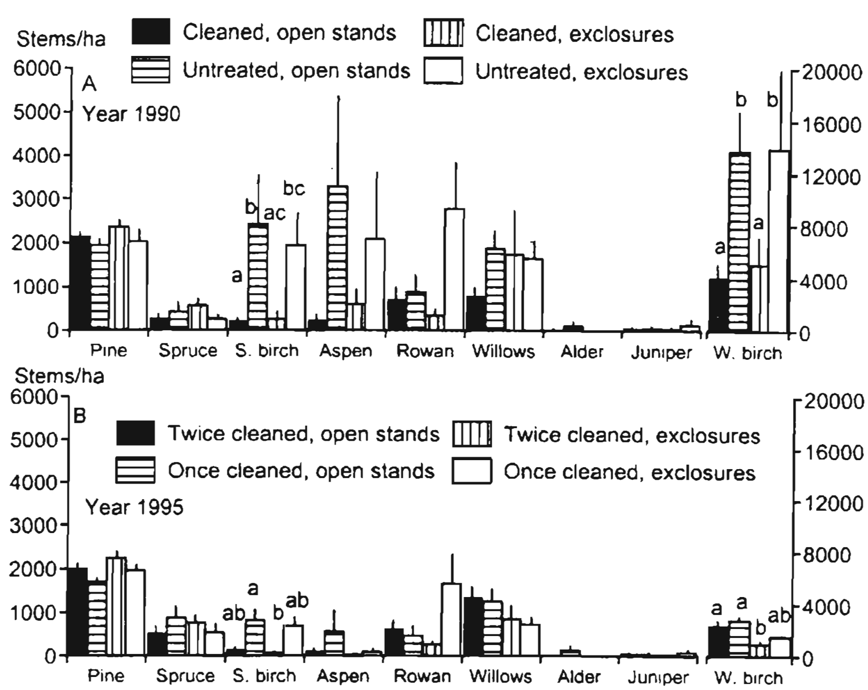

Fig. 1. Density of different tree species (+ SE) classified according to cleaning treatment at Viitasaari (A) in 1990 and (B) in 1995. Note the different scales. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

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	$24,721^{a} \pm 4,770$	$8,591^{b} \pm 1,157$	$24,840^{a} \pm 5,815$	$11,013^{b} \pm 3,408$	***
Deciduous trees and juniper	$22,346^{a} \pm 4,755$	$6,164^{b} \pm 1,149$	$22,547^{a} \pm 5,834$	$8,093^{b} \pm 3,511$	***
Total biomass availability	$910^{a} \pm 95$	$457^{b} \pm 67$	$888^{ab} \pm 291$	$644^{ab} \pm 174$	*
Proportion of pine available	$25.9^{a} \pm 5.4$	$53.2^{b} \pm 7.8$	$19.9^{a} \pm 3.6$	$53.4^{b} \pm 12.3$	**
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

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; $P = 0.28$).

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; $P < 0.001$).

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

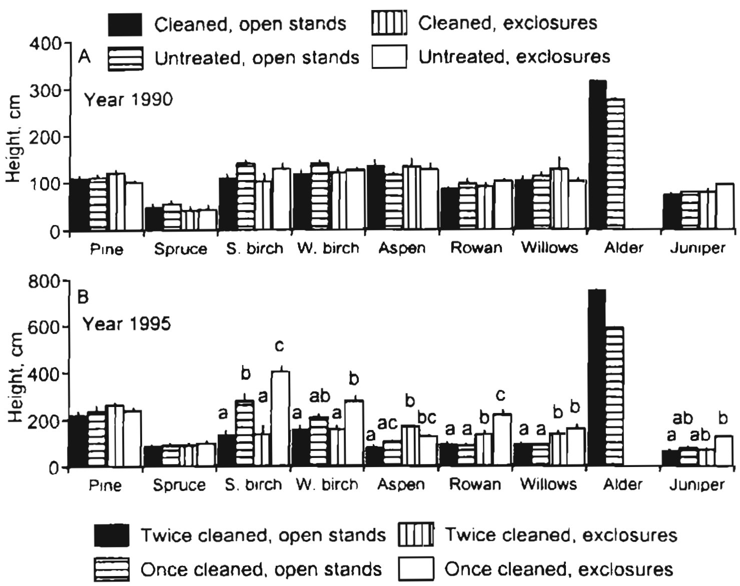

Fig. 2. Height of different tree species (+ SE) classified according to cleaning treatment at Viitasaari (A) in 1990 and (B) in 1995. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

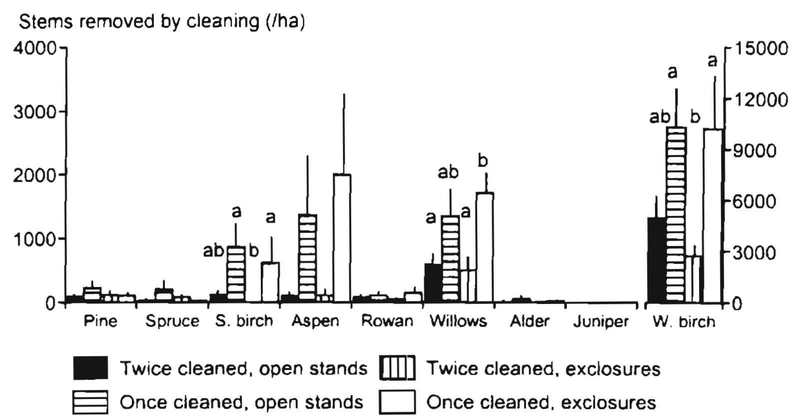

Fig. 3. Number of stems removed by cleaning (+ SE) classified according to cleaning treatment at Viitasaari in 1994. Note the different scales. Means with the same letter are not different (ANOVA with Bonferroni corrections, $P > 0.05$).

(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

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

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

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*).

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 ($r = 0.49$, $P < 0.05$, $n = 20$).

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.

In winter 1995-96, pine biomass con-

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

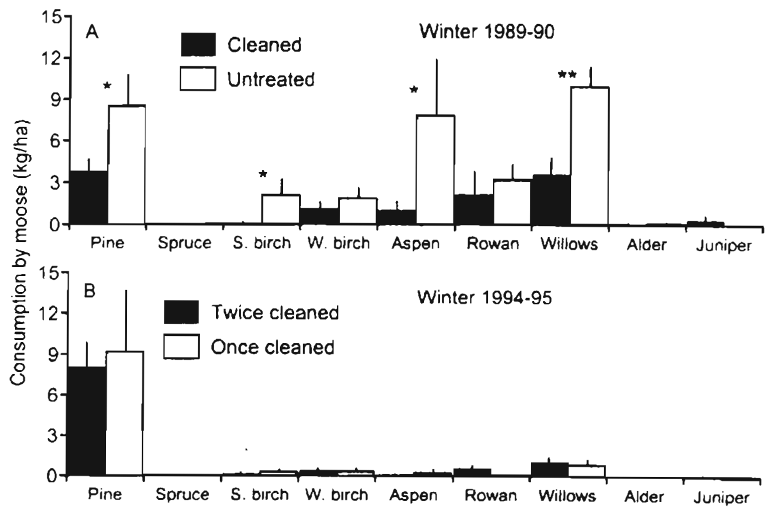

Fig. 4. Consumption of different tree species by moose (+ SE) at Viitasaari (A) in cleaned and untreated stands in winter 1989-90 and (B) in twice cleaned and once cleaned stands in winter 1994-95. Significance: * $P < 0.05$, ** $P < 0.01$ (*t*-test).

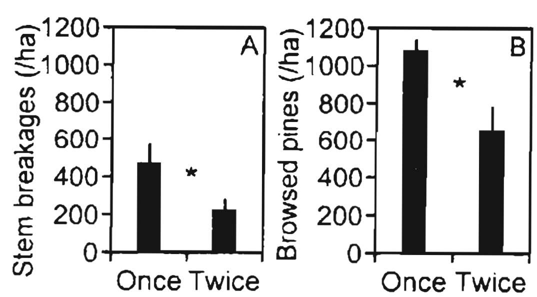

Fig. 5. (A) Total number of pine stem breakages (+ SE), and (B) total number of browsed pines (+ SE) in once cleaned and twice cleaned stands at Viitasaari during 1988-94. Significance: * $P < 0.05$ (*t*-test).

sumed 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).

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

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

(Hjeljord and Grønvold 1988, Härkönen 1998). 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 a competing species, impairing the growth conditions 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 1998).

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 later 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,

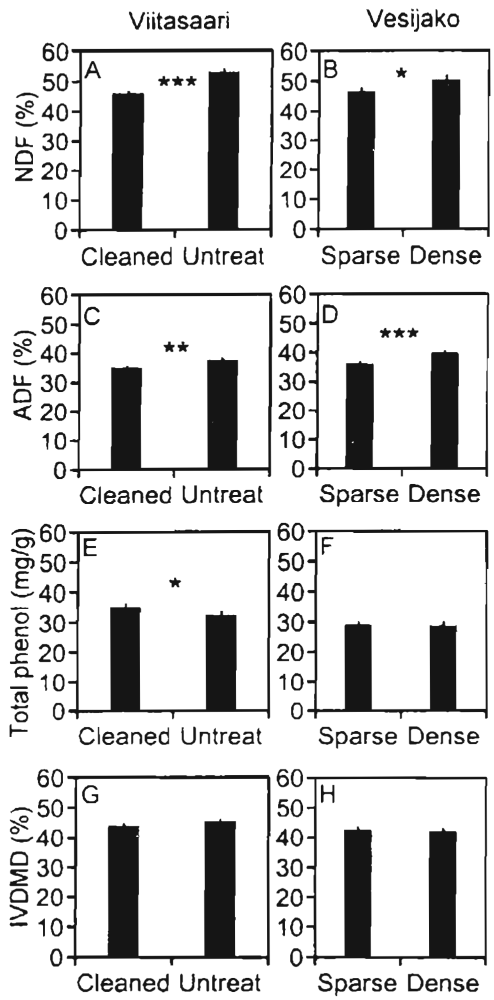

Fig. 6. Neutral detergent fiber (NDF) content (+ SE) in different habitat types (A) at Viitasaari in 1993 and (B) at Padasjoki/Vesijako in 1990. Acid detergent fiber (ADF) content (+ SE) in different habitat types (C) at Viitasaari in 1993 and (D) at Padasjoki/Vesijako in 1990. Total phenol content (+ 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).

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 the 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 occurs year after year in some stands (Löyttyniemi and Piisilä 1983). This could also explain the 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 density of 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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