Examensarbete
i ämnet biologi

Variation of moose (*Alces alces*) damage to Scots pine (*Pinus sylvestris*) in young forest stands

Markus Olsson

Handledare: Roger Bergström **30 Poäng, D-nivå**

Vilt, Fisk och Miljö
SLU
901 83 Umeå, Sweden

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Supervisor: Roger Bergström **30 Point, D-Level**

Wildlife, Fish, and Environmental Studies
Swedish University of Agricultural Sciences
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Abstract

Forest damage by moose is an important issue in Swedish forest and wildlife management. This study aimed at understanding the variation of moose (*Alces alces*) damage to Scots pine (*Pinus sylvestris*). By plots in twenty-five young forest stands damage level, damage variation and stand characteristics were investigated through a survey in April 2005.

On average 2.4% of the main stems showed recent damage (i.e. from the preceding winter) and 29.4% of the main stems had previous damage (from before preceding winter).

The variation of damage within stands was negatively correlated with damage level. Compared to damage level, damage variation showed inversely correlations to several stand characteristics. These relationships were interpreted as an interaction mainly between the unique characteristics of a stand and moose browsing pattern. Such interactions determine the damage level, which in turn determines the predominant level of damage variation.

The risk of a pine to be browsed, if its neighbour is browsed, is significantly higher than what expected from random browsing. That risk decreased linearly with increasing distance to the browsed pine.

The patterns revealed are discussed in terms of how to decrease the share of damaged main stems in future stands and how to improve surveys and predictions of damage levels in young pine stands.

Sammanfattning

I studien undersöktes variationen av stamskador på tall *(Pinus sylvestris)* vilka orsakats av älgens (*Alces alces*) vinterbete i 0,5-3 m höga ungskogsbestånd. Genom provytor studerades beståndsegenskaper, skadenivåer och skadors variation inom 25 ungskogsbestånd. Dessutom undersöktes skaderiskerna på slumpmässigt valda tallar och deras närmsta tallgranne.

I genomsnitt hade 2,4 % av huvudstammarna skador som uppkommit under den senaste vintern (färska skador) och 29,4 % av huvudstammarna hade skador som uppkommit vid tidigare tillfälle (äldre skador). Studien visar också att det beräkningssätt som används för att bestämma skadenivå har stor betydelse för utfallet.

Skadornas variation inom bestånden var signifikant negativt korrelerade med skadenivån, d.v.s. ju mera skador desto jämnare var skadorna fördelade över bestånden. Enligt teorier om växt - växtätarsamspel är det en interaktion mellan älgens beteende och miljöns egenskaper som bestämmer älgens betesmönster. I den här studien kartlades beståndens egenskaper för att få en uppfattning om denna interaktion. De speciella egenskaper som varje bestånd har antas påverka skadenivån, vilken i sin tur i hög grad tycks styra variationen på skadorna. De beståndsegenskaper som gav tydligast uttryck för detta var trädhöjd och täthet av begärligare lövträd än björk, vilka båda hade en signifikant positiv korrelation med variationen på de äldre skadornas fördelning inom bestånden.

När en tall är granne till en betad tall ökas risken signifikant att den också skall vara betad, om man jämför med risken hos en slumpmässigt vald tall. Enligt den här studien ökar denna risken linjärt med närheten till den betade tallgrannen, sett över en säsong av vinterbete.

Skadenivån var den faktor som till största delen påverkade skadornas variation. Kunskapen om det sambandet kan användas i framtida arbete för att angripa problem med älgskador på tall. Uppsatsens resultat diskuteras med avseende på, dels utvecklingen av inventeringsmetoder och prognoser för skador, dels om man med skötselmetoder kan minska andelen skadade huvudstammar i bestånd.

1. Introduction

The effect of herbivore browsing on plants depends on the interactions between the behaviour of the animal, plant characteristics and the habitat. These interactions can be studied on different spatial and temporal scales (Roguet et al. 1998).

In Sweden the moose (*Alces alces*) obtains its major food from young Scots pines (*Pinus sylvestris*) during winter (Bergström & Hjeljord 1987). The silvicultural method, clear-cutting, used in Sweden creates young forest stands, which provide plenty of and well distributed winter food (Cederlund & Bergström 1996). The browsing in the young forests results in considerable economical losses for the forest industry (Lavsund 1987).

The moose usually browse from trees at an height of 0.5-4 m and the browsing takes place either at the stem (i.e. leader browsing, stem breaking or bark stripping) or at the lateral shoots. The browsing at the stem affects the future quality of the butt log and is therefore categorised as damage. On the other hand, browsing of lateral shoots may affect the tree growth, but not the quality of the butt log. Recent stem damage (e.g. originating from browsing during the last winter) and several years of previous accumulated browsing are separated in recently developed survey methods. The surveys produce a valid picture of the annual damage level and an indication of the moose population density that have caused the damage. Only the main stems, which are expected to make up the stand after pre-commercial thinning and therefore are interesting from a forestry point of view, are considered during damage surveys. The occurrence of stem damage varies a lot between different stands and regions. Generally in Sweden, 5-10% of all Scots pine main stems have recent stem damage and the corresponding figure of previous stem damage is usually in the order of 20-50% (Bergqvist et al. 2001; Hörnberg 1995).

For a moose to gain high fitness it is necessary to get sufficient amount of high quality food (Moen et al. 1997). This is the reason for a strong evolutionary selection for food selection strategies at different spatial scales (Manley et al. 1993). One can discern four spatial scales: (1) Habitat (migration, dispersal), where for example forage abundance, water availability and competition can influence selection. (2) Feeding site (i.e. animal reorientation to a new location, long travels), where for example forage abundance and quality, plant species and predator risks are important. (3) Feeding station (i.e. an area accessible without moving the forefeet), where for example forage abundance and quality and plant species can influence selection. (4) Bite (i.e. jaw, tongue and neck movements), where for example nutrients, toxins and height and structure of the plant can influence the selection (Roguet et al. 1998).

There are three superior factors determining food selection: energy intake, essential nutrients and toxic and digestibility-reducing substances (Bergquist & Kalén 2002). To optimise these factors, both proportions and availability of different food items seem important. Moose can, for example, strive to maintain a balanced diet, therefore aspen (*Populus tremula*) in young forests can be over-utilised when rare (negative frequency-dependent food selection) and young pine forests can function as attractants because availability of food is high (Edenius et al. 2002).

Pre-commercial cleaning both reduces availability and moose browsing, especially by reducing deciduous tree species. It is shown that the consumption of deciduous trees can be reduced ten times after pre-commercial cleaning (Härkönen 1998). Nevertheless, cleaning is needed, from forestry point of view, to regulate the competition between pine and deciduous trees, even in high-density moose areas (Heikkilä & Härkönen 1996).

The effect of pre-commercial cleaning on the outcome of moose browsing on pine in young forests is complex with many affecting factors, such as stand densities, composition of tree species, management practises, site productivity and moose population density (Bergström & Hjeljord 1987; Härkönen et al. 1998; Lyly 1992; Lyly & Saksa 1992).

An experiment of winter browsing behaviour of moose in relation to birch, reported a non-linear relationship between food intake and food availability. Further, the experiment showed that exploitation of the browse supply was strongly determined by the spatial distribution of the birches (i.e. distances between trees; Vivås & Saether 1987).

Red deer (*Cervus elaphus*) prefer to browse at the level of their shoulder height, despite it do not improve the intake rate in comparison to browsing of other heights (Renaud 2003). Moose damage to pine is, as mentioned above, of tree kinds and they tend to occur at different heights. The most common damage in pine, browsing of apical leader, standing for approximately 78% of all damage, occurs at low tree heights (around 1 m). The other two kinds of damage occur at a higher level (around 2-3 meters). This may be explained by moose and tree size relationships, and by impact from the current quality of a specific plant part (Bergqvist et al. 2001).

Plant morphology and chemistry affect moose selection of browse. In average three twigs per stem used to be browsed by moose (population density of 5-10 per 1000 ha) in a winter (Siipilehto & Heikkilä 2005), and the number of browsed twigs is higher on slow-growing trees. But, even if the number of browsed twigs is fewer on rapidly growing trees the total biomass removed is greater due to larger bites (Danell et al. 1991; Thompson et al. 1989). A previously browsed pine tends to be browsed again coming seasons. The rebrowsing pattern is stronger in stands with low levels of previous browsing and with increasing stand age (e.g. number of years a site is in reach of moose browsing; Bergqvist et al. 2003).

The knowledge of the spatial distribution of moose damage in young forests stands is poor. According to previous studies the distribution seems to be uneven due to spatial variation in food quantity and quality (Heikkilä & Härkönen 1996; Pastor et al. 1998). The question arises whether rational forestry, which strives at even forest stands in terms of age and stem distribution, gives an even distribution of forest damage.

To know how to handle extensive moose damage in pine forests, there is a need to know the spatial distribution of the damage. It is important to minimise negative effects to butt logs, that will show up in commercial thinning and final felling. This study is one step in understanding if and how already damaged stands can be managed to reduce the share of damaged stems before commercial cutting takes place.

2. Objectives

Browsing and damage of free-ranging moose were investigated in managed young pine stands. The study aimed at:

1) Investigating variation of moose damage to pine in young forest stands. This was done at three scales relevant both for moose and forestry. First, at stand level, which can be seen as moose feeding site and the scale for stand management planning. Second, in plots containing a few main stems, seen as a moose feeding site and also the scale at which practical pre-commercial cleaning operates. Third, at the level of neighbouring trees that can be seen as the whole or a part of moose feeding station and the level where some decision takes place in pre-commercial cleaning.
2) Analysing if stand characteristics or damage level affect variation of damage.
3) Suggesting forestry management methods to decrease the economical losses caused by moose browsing.

3. Methods

3.1 Study area

The fieldwork was performed in central Sweden in the western part of Västmanland and eastern part of Örebro counties (66°25' N, 14°85' E), located within the southern part of the boreal forest zone. The Sveaskog Company is the landowner of the used area, which has a maximal east-west extension of 22 km, and a north-south extension of 28 km. The winter population density of moose in parts of the area was estimated by pellet group counts to 6-11 animals/ km^2 (Person & Manson 2005).

3.2 Forest stands and plot layout

The data were collected in young forest stands between 13^{th} of April and 4^{th} of May 2005 by two persons who were experienced field workers and had attended a one-day course before the survey.

A total of 25 separate stands were investigated. The stands were chosen according to several criteria. The amount of Scots pine (*Pinus sylvestris*) should be 40% or more and the mean tree height should be between 0.5 and 3 m. The pre-commercial thinning varied over the stands in accordance to the current management of the landowner. The stand size had to be between 3 and 8 hectares and this range is typical for stand sizes in Sweden. To enhance the fieldwork, stands far from forest roads were not included. In addition, stands divided by a major road or railway were excluded.

Fifty plots were laid out in a regular 30 m grid over the entire stand. To avoid a subjective selection of the grid, the position of the first plot in every stand was chosen by moving 10 m in north/south direction and 10 m in west/east direction from where the field worker spontaneously entered the stand. If a single stand could hold more than 50 plots the data collection stopped at 50 plots. The specific position of each plot was reached either by compass and step-counting or by a GPS-apparatus set at RT90. In a single stand the two methods were not mixed. If a part of a plot fell outside the stand it was moved along the (north/south) grid line until it was totally inside the stand. All plots were given a GPS position (RT90), although these positions were not further used in this thesis.

Two separate surveys of the moose browsing were done in the plots (hereafter referred to as the plot survey and survey of paired-pines). First, a total inventory of the plot was done, including number of different tree species and moose damage on Scots pine. Second, two young Scots pine was selected for a specific recording. Damage and browsing were only noted when there was no doubt it was done by moose. Browsing impact on a stem (i.e. browsing of apical leader, breaking of the stem or bark stripping) was categorised as damage. Browsing is here used in a more general sense to describe all signs of browsing on a tree, i.e. browsing of lateral shoots as well as stem breaking, top shoot browsing and bark stripping.

Older and dominant trees left in the young forest stand, like seed trees or shelter trees, were neglected. Plots on impediment within the target stand was done if there were trees that fulfilled the criteria. Otherwise the plot fell out.

3.2.1 Plot survey

Circular plots was delineated by using a 3.5 m long stick (area 38,5 m^2) and all trees with more than half of the stem inside the plot border and a height of 0.5 m or more was included in the survey. Height of browsed trees was recorded as estimated pre-browsing height.

A total of 9-15 main stems, which were expected to make up the stand after pre-commercial thinning, were sorted out. This corresponded roughly to 2500-4000 main stems/ha, and was governed by the site productivity of the specific stand. Site-index (Hägglund & Lundmark 1981) for the pine stands were taken from the landowner’s list of stand characteristics. In the selection of main stem, conifers (i.e. Scots pine and Norway spruce) were preferred to deciduous trees and two main stems were not allowed to stand closer than 0.6 m. The choice of main stem were not allowed to be affected by any type of browsing from moose. Various types of stem damage on each main stem of Scots pine were categorised, according to the method called ÄBIN [http://www.svo.se/ (in Swedish)], where "recent" refers to damage from the preceding winter and "previous" to those from before previous winter:

1. with recent and previous moose damage;
2. with recent, but not previous, moose damage;
3. with previous, but not recent, moose damage;
4. without moose damage.

Previous damage was not taken into count if it was located lower than 0.3 m above ground. Finally, we counted (or estimated when there were many) stems other than main stems of Scots pine and placed them in one of the following four categories:

1. Scots pine, other than main stem;
2. Norway spruce;
3. Birch (i.e. *Betula pendula* and *B. pubescens*);
4. Other deciduous tree species (mostly aspen [Populus tremula], willows [Salix spp] and mountain ash [Sorbus aucuparia]).

3.2.2 Survey of paired pines

The pine closest to the centre of the plot and its closest neighbour were chosen. If there was no living pine within 15 m from centre no pines were chosen and this was also the case if there was no living pine within 15 m from the one closest to the plot centre. Only pines with a height 0.5 meter or more were included in the survey and no consideration was taken to the stem being a main stem or not.

For the two pines in each pair we measured height (only estimated on pines that had become lower because of browsing from moose), and distance between pines. We also recorded each tree as being a main stem or secondary stem. Further, presence of damage and browsing from moose were registered on the two pines in each pair and the following types were recorded:

1. recent stem damage (i.e. from the preceding winter)
    - browsing of the apical leader
    - breaking of the stem
    - bark stripping
2. recent browsing of lateral shoots
3. previous stem damage (i.e. before preceding winter)

3.3 Data analyses

Four response variables were used in the analyses:

1. Browsing: all browsing signs on a pine (browsing of lateral shoots and damage as below) from preceding winter;
2. Browsing on lateral shoots: only browsing on lateral shoots from the preceding winter;
3. Recent damage: stem damage (browsing of apical leader, breaking of the main stem or bark stripping) from preceding winter;
4. Previous damage: stem damage (browsing of apical leader, breaking of the main stem or bark stripping) from before preceding winter and now showing up as morphological deformations.

3.3.1 Plot values

The data from the plot survey were used in two ways to estimate stem density and damage levels. First, to get a total view of the damage level, the proportion damaged main stems out of all main stems were calculated. Second, the mean proportion of damaged main stems out of all main stems, in every plot, was calculated and used for an overall mean for the survey. These plot means were used in all analyses of the plot survey. Plots without main stems were not included in these calculations.

To analyse the variation of damage between plots in each stand, the coefficient of variation, CV, (standard deviation in percent of the mean) was used. Scatter plots of different constellations between damage level, damage variation and stand characteristics were established and correlation coefficient (r) was used to determine the relationships between stand values. Twenty-five stands were used in these correlation analyses, except for analyses of recent damage variation, where twenty-one stands were included (four stands fell out because no damage was observed). Most of the stand characteristics used in these analyses were taken from the plot survey. But, estimation of stand height (mean stand height of the stand-forming tree layer) and site productivity was obtained from the landowner.

3.3.2 Paired pines

All stands were analysed together in the paired pine inventory. Different stem categories (i.e. these with browsing, recent stem damages, previous stem damage, only main stems and tree height differences) of paired pines were analysed separately.

To detect if the risk of a pine being browsed (or damaged) or not depends on whether its neighbour being browsed (or damaged) or not, a Chi-2 test was used. The observed browsing or damage frequency was tested against expected values based on an assumption of random browsing.

The effect of distance between paired pines on frequency of browsing was analysed.

The proportion of damaged stems out of all paired pines stems was calculated. Comparisons of damage levels in all stems versus only main stems were done. The proportion of recent damaged stems out of those with browsing of lateral shoots was also calculated, and so were the proportion recent damaged stems out of those with browsing.

All analyses were done in Microsoft Exel and significance level was set at $p<0.05$.

4. Results

4.1 Stand characteristics and levels of browsing and damage

The mean plot number per stand was 45.5 (range 21-50), but in analyses where plots without main stems were excluded, the mean plot number per stand decreased to 44. In total, the plot inventory encompassed 52 403 stems in 1135 plots. Of these stems, 18 282 (34.9%), were pines and 9 817 (18.7% of all stems and 53.7% of all pines) were main stems of pine. The most common species was birch (the two species were treated as one), with 26 248 stems (50.1% of all stems).

In the entire survey area, the average total stand density was estimated to 11 997 stems/ha. On average 2 247 pine main stems/ha was identified and on 2.7% of the plots there were no main stems. Among the pine main stems, 2.4% was recently damaged and 29.4% was previously damaged. If the mean proportion recently damaged stems in each plot (n=1104 plots) was used for the damage level estimation of the whole area, the corresponding figures were 3,5% and 30,1%, respectively. In these analyses, average number of stems and main stems per ha also increased slightly to 12 022 and 2 305, respectively. A third way to calculate damage is to base the overall mean on stand means, giving a mean damage of 4.1% (SD=10.5).

Based on the paired pines, the survey of which included damage recording on both main and secondary stems, it was obvious that recent damage was higher on main pine stems than on all pine stems (recent damage to main stems (n=1373): 5.0%; all stems (n=2264): 3.9%, previous damage to main stems: 32.3%; all stems 26.7%). Of the paired pines, 10.0% had browsed lateral shoots and 32.3% of those pines also had recent damage. The proportion of damaged stems of all browsed paired pines was 36.8%.

Stand height and age of stand were correlated (r=0.62; p<0.01; df=23).

Table 1. Proportion (%) of damaged main stems from all 25 stands and calculated in four different ways.

Type of damage	% of all stems	Mean % of all plots (n=1104)	% of paired pines	Mean % in all stands
Recent	2.4	3.5	5.0	4.1
Previous	29.4	30.1	32.3	30.8

Table 2. Number of plots and stems, separated into all and main stems, and recent and previous damage presented for each stand. Plots without main stems were not included.

Stand nr.	No. of plots	All stem No./ha	Main stem No./ha	Recent damage No./ha	Recent damage Mean %	Previous damage No./ha	Previous damage Mean %
4	34	15988	1307	688	52.4	1078	83.0
11	47	10770	2156	6	0.7	691	28.8
33	47	11549	2040	44	2.6	1261	62.8
34	50	12665	2656	10	0.3	1367	47.8
40	50	14416	2541	16	0.8	1091	42.6
43	21	16345	2425	25	1.2	1274	51.8
47	46	5435	1497	6	0.3	119	9.5
48	30	14906	2746	26	0.8	450	16.3
49	45	5920	1305	17	3.2	203	7.9
63	48	7498	2490	11	0.3	623	26.3
67	46	18941	2106	17	0.6	155	6.9
69	49	9152	2614	0	0,0	175	7.9
71	48	14346	1976	0	0,0	119	5.5
72	50	13756	2796	21	1.2	156	8.1
85	37	13077	2296	0	0,0	28	1.3
87	35	14952	3237	0	0,0	82	2.9
109	50	14614	2219	5	0.3	166	8.5
125	50	7733	2422	83	4.3	1211	54.6
261	48	10221	2663	27	0.8	785	26.4
289	49	12982	2545	27	1.1	483	17.6
324	30	5543	1542	208	14.6	901	60.0
333	50	14754	3264	68	1.9	1091	33.4
334	50	10378	2578	146	5.4	1502	59.0
351	45	12761	2258	63	5.6	797	32.3
354	45	7339	1721	35	3.7	1184	69.7
Mean	44	11842	2296	62	4.1	680	30.8

A correlation analysis based on stand means indicates that the level of recent damage is associated with the level of previous damage (r=0.57; p<0.01; df=23; Fig. 1).

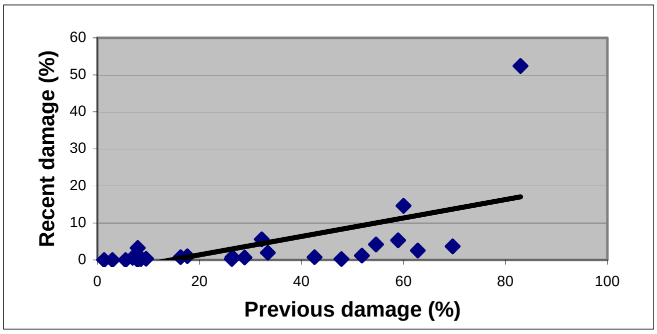

Figure 1. Recent damage in relation to previous damage in 25 stands.

Both recent and previous damage levels showed a negative relationship, although not significant, to stand height (r=-0.18; p>0.05, df=23, Fig. 2; r=-0.38, p>0.05, df=23, Fig. 3).

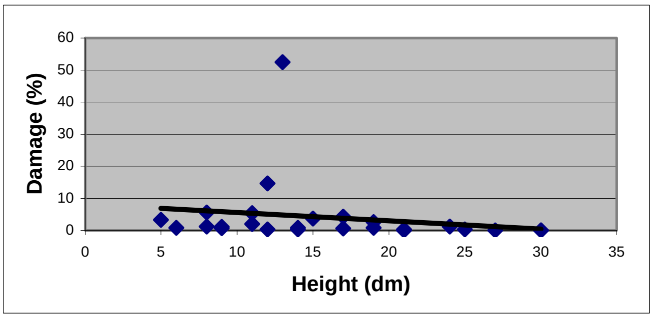

Figure 2. Recent damage level in relation to stand height in 25 stands.

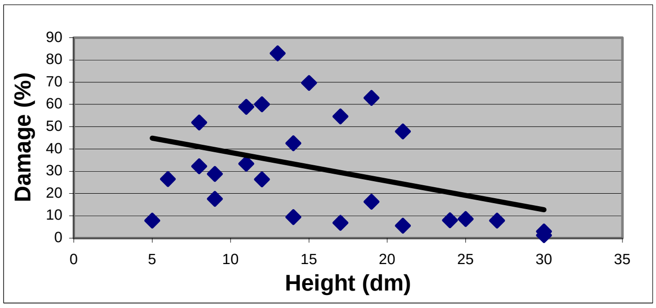

Figure 3. Previous damage in relation to stand height in 25 stands.

Recent and previous damage were negatively correlated to number of other deciduous stems (i.e. without birch), but significantly so only for previous damage (r=-0.16, p>0.05, df=23, Fig. 4; r=-0.41, p<0.05, df=23, Fig. 5).

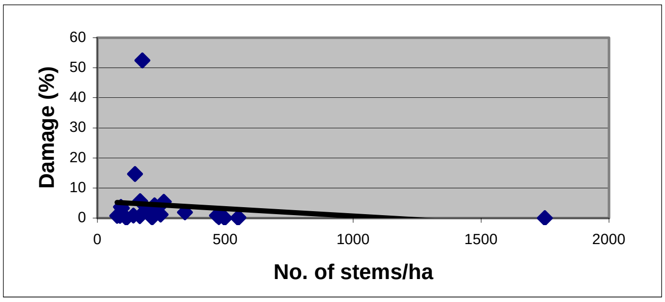

Figure 4. Recent damage in relation to number of other deciduous tree species.

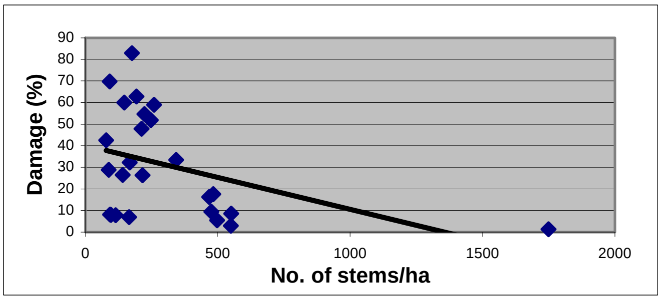

Figure 5. Previous damage in relation to number of other deciduous tree species.

Proportion of damaged pine main stems was negatively correlated (close to significance) to number of pine main stems in plot (r=0.70; p>0.05; df=6, Fig. 6). Nevertheless, number of damaged stems increased with density.

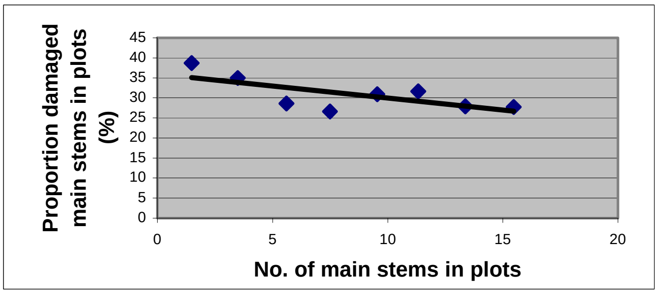

Figure 6. Main stem density (number of main stems separated in eight classes) influence to proportion damaged main stem in plots.

At stand leve, proportion of recent or previous damaged main stems of pine showed no significant correlation to density of all stems, pine stems, pine main stems, birch stems, Norway spruce stems or stand age or site productivity, p>0.05, df=23 for all analyses).

4.2 Variation of damage and browsing distribution

Damage variation (expressed as CV) within stands was negatively correlated with levels of recent (r=-0.86; p<0.001, df=19, Fig. 7) and previous damage (r=-0.95; p<0.001, df=23; Fig. 8).

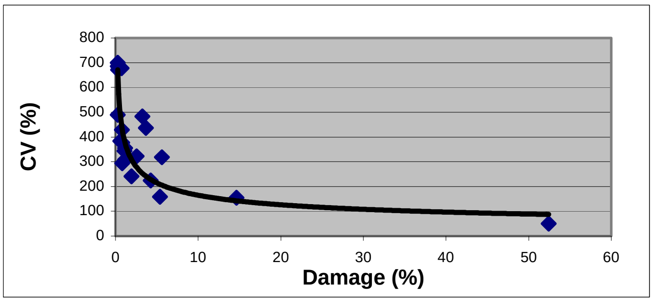

Figure 7. Recent damage variation expressed as coefficient of variation in relation to damage level in 21 stands (only stands with recent damage included).

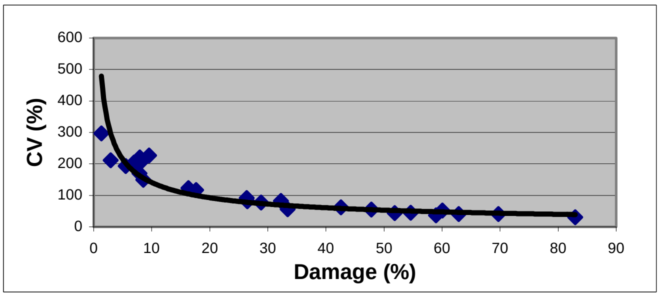

Figure 8. Previous damage variation expressed as coefficient of variation in relation to damage level in 25 stands.

Variation of previous damage and stand height and density of other deciduous tree species, respectively, were positively correlated between stands ($r=0.51$, $p<0.01$, $df=23$, Fig. 10; $r=0.57$, $p<0.01$, $df=23$, Fig. 12). Variation of recent damage in relation to these characteristics only showed a trend in the same direction ($r=0.38$, $p>0.05$, $df=19$ Fig. 9; $r=0.22$, $p>0.05$, Fig. 11.)

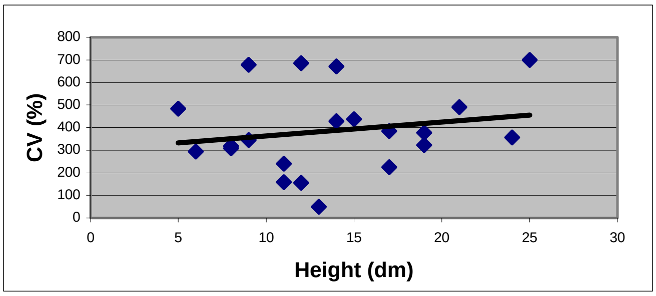

Figure 9. Recent damage variation expressed as coefficient of variation in relation to stand height in 21 stands.

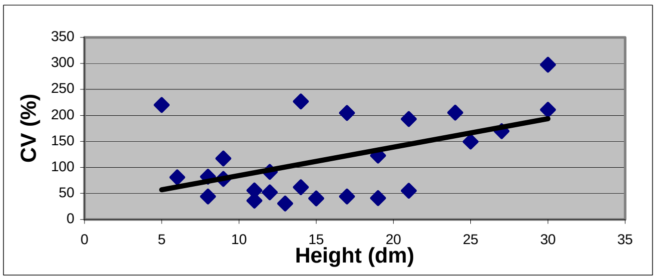

Figure 10. Previous damage variation expressed as coefficient of variation in relation to stand height in 25 stands.

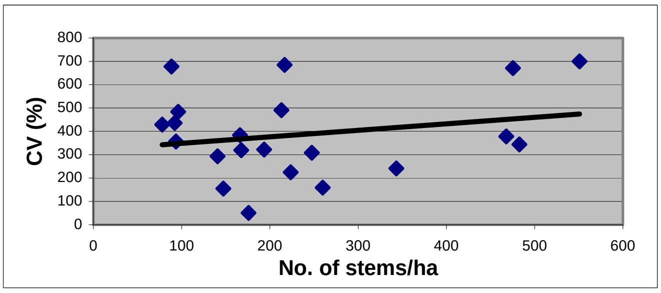

Figure 11. Recent damage variation expressed as coefficient of variation in relation to number of other deciduous tree species in 21 stands

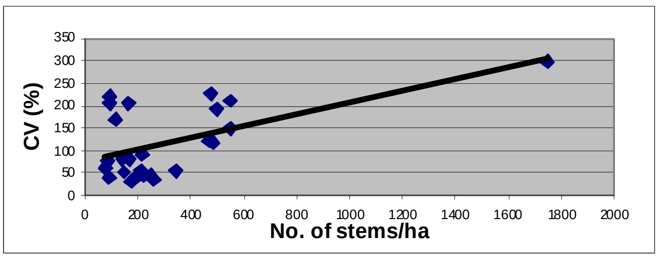

Figure 12. Previous damage variation expressed as coefficient of variation in relation to number of other deciduous tree species in 25 stands

At stand level, variation of recent and previous damage was not significantly correlated with total stem density, pine stem density, pine main stem density, birch stem density, spruce stem density, stand age or site productivity (p>0.05 for all analyses).

4.3 Paired pines

There were more browsing and damage on a neighbour of a browsed or damaged pine than expected from a random browsing among pines. Browsing (p<0.001), recent damage (p<0.001; just indicative because too few expected damaged pines) and previous damage (p<0.001) showed strong connection between paired pines, respectively (Table 4, 5 and 6).

A significant positive correlation between proportion browsed pine 1 and distance to pine 2 was observed (r=0.92, p<0.05, df=3). The decreased proportion browsed, from largest to smallest distance class, was 73.4% (Table 4.)

The closer the neighbour stood to the first pine, the more deviated the observed probability from expected probability in terms of the neighbour being browsed (r=-0.98, p<0.001, df=3; Fig. 13).

Table 4. Browsing (i.e. recent damages and browsing of lateral shoots) of paired pines.

Distance class/	Category	Pine 1		No. of browsed pine 2 on pine 1					
Average distance (dm)		No. of pines	% of total	Obs browsed pine 2	Obs (%)	Exp browsed stems	Exp (%)	Obs/ Exp	Chi-test p<
All/	Unbrowsed	997	88.1	51	48.1	93.4	88.1		
10.2	Browsed	135	11.9	55	51.9	12.6	11.9	4.4	0.001
	Sum	1132	100.0	106	100.0	106.0	100.0		
0-5/	Unbrowsed	334	93.0	11	52.4	19.5	93.0		
3.3	Browsed	25	7.0	10	47.6	1.5	7.0	6.8	0.01
	Sum	359	100.0	21	100.0	21.0	100.0		
6-10/	Unbrowsed	428	90.1	13	39.4	29.7	90.1		
7.8	Browsed	47	9.9	20	60.6	3.3	9.9	6.1	0.001
	Sum	475	100.0	33	100.0	33.0	100.0		
11-15/	Unbrowsed	185	88.5	11	50.0	19.5	88.5		
12.8	Browsed	24	11.5	11	50.0	2.5	11.5	4.4	0.001
	Sum	209	100.0	22	100.0	22.0	100.0		
16-20/	Unbrowsed	72	84.7	8	61.5	11.0	84.7		
18.0	Browsed	13	15.3	5	38.5	2.0	15.3	2.5	0.1
	Sum	85	100.0	13	100.0	13.0	100.0		
21+/	Unbrowsed	73	73.7	8	47.1	12.5	73.7		
32.2	Browsed	26	26.3	9	52.9	4.5	26.3	2.0	0.05
	Sum	99	100.0	17	100.0	17.0	100.0		

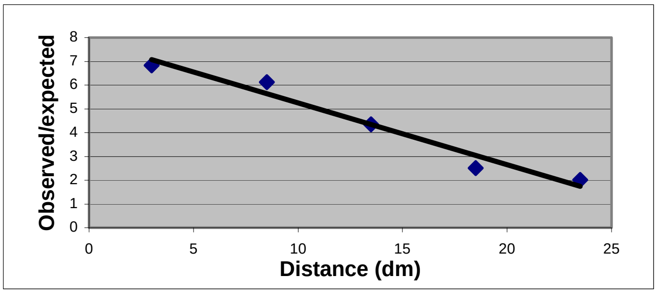

Figure 13. Observed/expected (from random) risk of being browsed in relation to distance between paired pines.

Table 5. Recent damage on paired pines (the Chi-2-test is just indicative cause of the low number of expected damaged pines).

Distance between pines (dm)	Category	Pine 1		No. of browsed pine 2 on pine 1					
		No. of pines	% of total	Obs damaged pine 2	Obs (%)	Exp damaged pines	Exp. (%)	Obs/ Exp	Chi-test p<
All	Undamaged	1083	95.9	29	69.0	40.2	95.9		
(Average	Damages	46	4.1	13	30.1	1.7	4.1	7.6	0.001
10.2)	Sum	1129	100	42	100	42.0	100		

Table 6. Previous damage to paired pines.

Distance class/ Average distance (dm)	Category	Pine 1		No. of browsed pine 2 on pine 1					
		No. of pines	% of total	Obs damaged pine 2	Obs (%)	Exp damaged pines	Exp. (%)	Obs/ Exp.	Chi-test p<
All/	Undamaged	828	73	127	42	221.2	73.3		
10.2	Damages	303	27	175	58	80.8	26.7	2.2	0.001
	Sum	1131	100	302	100	302	100		
0-5/	Undamaged	261	73	34	40	62.7	72.9		
3.3	Damages	97	27	52	60	23.3	27.1	2.2	0.001
	Sum	358	100	86	100	86	100		
6-10/	Undamaged	292	78	46	51	70.0	77.9	2.2	0.001
7.8	Damages	83	22	45	50	21.0	22.1		
	Sum	375	100	91	100	91	100		
11-15/	Undamaged	148	71	20	34	41.1	70.8		
12.8	Damages	61	29	38	66	16.9	29.2	2.2	0.001
	Sum	209	100	58	100	58	100		
16-20/	Undamaged	57	67	14	41	22.8	67.0		
18.0	Damages	28	33	20	59	11.2	32.9	1.8	0.01
	Sum	85	100	34	100	34	100		
21+/	Undamaged	65	66	13	39	21.9	66		
32.2	Damages	33	34	20	61	11.1	34	1.8	0.01
	Sum	98	100	33	100	33	100		

The same pattern, as for all stems, was observed for browsing (p<0.001) and previous damages (p<0.001) when only main stems of paired pines were included (Table 7)

Table 7. Browsing and damage to main stems of paired pines.

Type of Browsing	Category	Pine 1		No. of browsed pine 2 on pine 1					
		No. of pines	% of total	Obs browsed pine 2	Obs (%)	Exp browsed pines	Exp. (%)	Obs/ Exp	Chi-test p<
Recent browsing	Unbrowsed	336	82,4	27	43	51.9	82,4		
	Browsed	72	17,6	36	57	11.1	17,6	3.2	0.001
	Sum	408	100	63	100	63	100		
Previous damage	Undamaged	276	67,6	54	39	94	67,6		
	Damages	132	32,4	85	61	45	32,4	1.9	0.001
	Sum	408	100	139	100	139	100		

Increasing height differences between the paired pines seems (indicative) to decrease the probability of a pine to be browsed if the neighbour is browsed (Table 8.)

Table 8. Effects of tree height differences (all, five and ten decimetres or more, respectively) on probability of one or two pines being browsed.

Height differences between pines (dm)	No. browsed of 1132 pairs		
	single of a pair	both in a pair	% both/ single
All	241	55	23
5+	84	13	15
10+	36	4	11

5. Discussion

5.1 Stem density and levels of browsing and damage

The damage levels found were within the range of damage levels recorded during the last decades in Sweden (Hörnberg, 1995; [http://www.svo.se/ (in Swedish)]. The differences between the four estimations of average recent damage to main stems (2.4, 3.5, 4.1 and 5.0%) were considerable. The first three values (from the plot survey) are created from different calculating methods that make the discrepancy understandable. Considering the uneven distribution of pines, both in plots and stands, the first value, 2.4% is best representing the recent damage of the area. It is harder to explain the large difference (about 100%) between the first value (2.4%; all main stems lumped from plot survey) and the fourth value (5.0%; all main stems from paired pine survey), as they are calculated by the same method. A possible reason for the difference is that categorisation of main stems have differed between the plot inventory and the paired pine inventory. When trying to achieve the suitable number of main stems per area, in plot inventory, categorisation of main stems could have been more generous in comparison to the case in paired pine inventory. This may possibly decrease the estimation of damage in plot inventory in comparison to paired pine inventory. No effect from pairing of the paired pine was observed, as damage level was similar if calculated from one of the two sets of pines.

With an average recent damage level of 52.4 and 14.6%, two stands, no. 4 and no. 324, stand for 77% of all recorded recent damage (Table 2). Similar large variation between stands is commonly found in inventory of moose browsing (e.g. Bergqvist et al. 2001).

The corresponding differences between different estimations for previous damages (29.4, 30.1, 30.8 and 32.3%) are reasonable and in line with the discussion about recent damages above.

When damage level of all paired pines, secondary stems included, was calculated, the damage level was less (recent: 3.9%; previous: 26.7%), in comparison to when only main stems were included. That was expected because secondary stems probably have a smaller average size (and age) and therefore have less recent and accumulated damages (due to height and a lower quality of food) than main stems (cf. Danell et al. 1991; Nordengren 2003).

The strong positive correlation between recent and previous damage, at stand level, found in this survey is comparable with earlier reports (e.g. Lyly & Saksa 1992; Bergqvist et al. 2001). These authors found similar relation between these variables at tree level. The suggested explanations for such relationships, at stand level, are that moose population density is an important factor and that there is a tendency for moose to return to the same stands winter after winter. That means that there is not only a rebrowsing at the tree level, as has been shown in many studies (e.g. Lyly & Saksa 1992; Bergqvist et al. 2001), but also a rebrowsing pattern on the stand level.

In spite of one criterion for the selection of stands being that at least 40% of the stems were pine, the proportion pine stems among all stems in this survey was estimated to 34.9%. This is probably explained by the landowner’s way of classifying the share of pines. The density of deciduous tree species did not decrease with increasing stand height (pers. obs. unpublished), indicating that the landowner cleans young forests higher than three meter or does not clean at all. Both the average stand height and stem density when pre-commercial cleaning is carried out have increased during the last 10-20 years and were in the beginning of this century about 4.2 m, and 10 000/ha, respectively (Nilsson, pers. com. in Ligné 2004).

However, Lyly & Saksa (1992) reported that the stem density had no essential effect on the number of damaged saplings when the density was below 11 000 stems/ha. But, above that level, there was a considerable increase in damage frequency. In my survey 15 of the 25 stands were estimated to have more than 11 000 stems/ha and the average number of stems/ha in the survey was approximately 12 000.

Lyly & Saksa (1992) and Heikkilä & Härkönen, (1996) found that the proportion of damaged stems decreased with pine density. Using stand mean values and recording only main stems, Bergqvist et al. (2001) did not find this relationship. But, in my survey the relationship is apparent at the plot level and is similar to that found by Vivås & Saether (1987) in an experimental study on artificially arranged birch saplings. In my study the decrease of damage was about 20% when considering the whole density range. But, when comparing corresponding densities of 2500/ha with 4000/ha, which is the density range used for main stems in my study, the decrease in proportion of browsed stems was about 10%.

5.2 Variation of damage in relation to damage level

As far as I know, there is no previous survey aiming to quantify moose damage variation within stands. Hence, to define what is high or low damage variation by comparing to earlier reports is impossible.

Damage levels explain the damage variation between plots, both for recent and previous damages. The effect of rebrowsing (i.e. repeated browsing to plant individuals between years) may likely explain part of the observed relation. According to Bergqvist et al. (2003), the intensity of rebrowsing decreases the number of damaged stems, compared to random browsing. Moreover, since rebrowsing was found to be stronger in stands with low levels of previous damage, damage variation of such stands may be more affected from rebrowsing. But Bergqvist et al. (2003) also observed that at 30% previous damage level, which roughly is the average level in this survey, the rebrowsing was approximately two times higher than would be expected from random. Hence, damage level will be kept at a lower level because of rebrowsing and thereby damage variation may get higher. In addition, rebrowsing may prevent damage to be as evenly distributed as if it originated from random browsing.

When interpreting the damage level-damage variation pattern, another possible factor may be that certain trees or patches differ from the rest of the stand. Such differences in attraction may depend on tree species composition (Heikkilä & Härkönen 1996), initial differences of trees or differences in positions of trees (Danell et al. 1990). In addition differences created by selective feeding (Edenius et al. 2002) or rebrowsing may play a role (Bergqvist et al. 2003).

By using two contrasting examples the idea of differences within stands impact to damage level-damage variation can be illustrated. First, stands with low average quality of browse, but with a few attractive patches, give low damage level and high variation. Second, stands with high average quality of browse, but with a few less attractive patches may give high damage level and less variation. Both these cases will create a pattern in line with the observations in this study. The patterns observed and the mechanisms involved are most certainly related to forestry practices, such as regeneration and cleaning.

Both recent and previous damage showed a dramatic decrease in damage variation from the lowest observed damage levels to about 10% damage level where the variation levels out. The overall observation of previous damage showing less variation in comparison with recent damage is reasonable for two reasons. First, the mix of different browsing seasons involved in previous damage hides parts of the damage pattern coming out of one season's browsing. Second, as reported by Bergqvist et al. (2003), the strength of rebrowsing declines with increasing previous damage levels (the stand may get higher damage level and less damage variation). When previous damage level was more than 50%, which was the case in seven of the twenty-five stands, the effect from rebrowsing had disappeared. According to this study, stands with 50% damage levels will have relatively evenly distributed damage (CV about 50%). Moreover, this can be the case for lots of young pine forest stands regenerated under conditions similar to those in this study. Because none of the stand in my study had grown out of reach of moose browsing (cf. Bergqvist et al. 2001; the stands with highest average height are 3 m), the damage level is likely to increase further.

5.3 Variation of damage in relation to stand characteristics

It appears that the observed positive correlation between damage variation and some stand characteristics (e.g. stand height, density of deciduous tree species other than birch) is a result of damage level having a negative correlation to these characteristics. The inversely and proportionally similar levels of the correlation coefficient between a specific stand character and type of damage level and damage variation, respectively, can be seen as a support for damage level explaining the majority of damage variation. Relations between stand characteristics and levels of browsing (and damage) are reported to consist of complex interactions between stand characteristics and moose browsing (Bergström & Hjeljord 1987; Härkönen et al. 1998; Lyly 1992; Lyly & Saksa 1992). As long as surveys or experiments that separate these factors are missing, the discussion must be one of assumptions and guesses (Fig. 14).

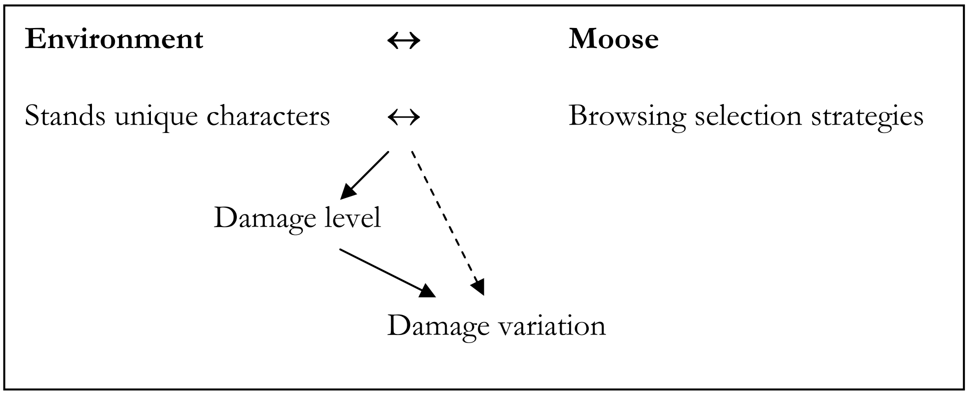

Figure 14. The interaction (↔) between environment and moose determines damage level, which in turn, to a high extent, determines damage variation.

5.3.1 Stand height

This study found that high damage level followed low stand height. An explanation is that browsing of apical leader, first, is the most common type of stem damage (around 78% of all damage), and second, is most common at moderate tree height (around 1 meter; Berqvist et al. 2001). This in turn, depends on the fact that quantity and quality of browse improve with higher position of a shoot within a tree (Nordengren et al. 2003). At moderate tree heights, moose easily reach the preferred apical parts. But, Lyly & Saksa (1992) findings are a bit contradicting, as they state that recent stem damage occurs on pines with average height of 1-2 m. But they also reported that trees with moderate height sometimes could have been protected from winter browsing by snow. Moreover, initial browsing to woody species changes tree height in a positive way for moose. Given continuous browsing, height is kept within reach of moose browsing for a longer period. Thus, about 90% of the browsing, which appears as damage (i.e. browsing of apical leader or breaking of main stem), temporary decreases tree height. Browsed trees often produce shoots, which are preferred by moose (Bergström 1984; Danell et al. 1985).

Thereby, initially browsed trees tend to be browsed again. (Bergqvist et al. 2001; Ericsson et al. 2001). Consequently, stands of moderate height are more browsed than taller stands.

Although, absence of stands with both high average height and high previous damage level is strange, as damage at low tree heights should accumulate until the stand reaches a high average height. There can be several reasons for this pattern: (1) Random effect due to absence of tall stands with lots of previous damage among the sampled stands, (2) Some of the stands in the sample were initially browsed and more or less got caught in a “browsing pit” (Ericsson et al. 2001); thereby, these stands have a lower average height for a longer period and also get high damage levels in comparison to stands less initially browsed, and (3) Pre-commercial cleaning can decrease the amount stems with accumulated (previous) damage.

Another reason, also linked to damage level, for variation of previous damage showing positive correlation to stand heights could be an effect of rebrowsing (which may prevent decrease of damage variation, see discussion of rebrowsing above). Thus, stand height follows stand age according to this study. So the fact that increase of previous damage variation follows stand height is therefore conclusive with an earlier report (Berqvist et al. 2003) saying that rebrowsing pattern is stronger with increasing age.

5.3.2 Density of other deciduous tree species than birch

Damage variation was positively correlated to stem density of other (and preferred; Bergström & Hjeljord 1987) deciduous tree species than birch. Browsing of pine is common in patches with high density of preferred deciduous tree species (Heikkilä & Härkönen 1996). So, if one assumes these preferred stems to be unevenly distributed in the stands, the relationship seems reasonable. Aspen, willows and mountain ash, i.e. "other deciduous species", have sporadic and irregular abundance in the surveyed stands (pers. obs.). But, the relationship between damage level and level of damage variation most likely explains this stand property too. Thus, density of deciduous trees has a negative correlation to damage level. This is in line with Hörnberg (1995), who reported that intake of pine decreases when broad-leaved species are present.

There is probably a multi-factorial explanation for recent damage (compared to previous damage) showing less correlation to density of deciduous stems. But the historical events of a stand (i.e. pre-commercial cleaning, moose population density etc.) may affect the differences in recent and previous damage. Recent damage is mainly affected by the status of the stand during the last winter, whereas, previous damage is affected by the situation during some or several years.

5.3.4 Other stand characteristics

The stand characteristics, which did not show any significant correlation to damage variation, did not correlate significantly to damage level either. But these characteristics showed equivalent low correlation to damage variation and damage level, but inversely so. For example some stand characteristics (e.g. total stem density, birch stems/ha and site-index) showed weak positive correlation to recent damage level and equivalent negative correlation against recent damage variation. Perhaps this can be seen as an effect of the reported positive correlation between total available browse of tree biomass and moose damage to pine (Härkönen et al. 1998). Further, several investigations (e.g. Lyly & Saksa 1992) have shown a negative correlation between proportion browsed pines and stem density. In this survey this correlation is not very obvious. Absence of such correlation are reported earlier by Bergqvist et al. (2001) who, apart from other studies and in accordance with this survey, only paid attention to main stems of pine. Therefore it is reasonable to find a lack of positive correlation between damage variation and stem density or site productivity.

My study made no discrimination between birch species, but approximately half of all the stems in the survey were birch. Under conditions where white birch (*Betula pubescens*) is the main tree species, the risk of moose damage to pine increases. Thus, white birch is a strong competitor of pine and exact (e.g. repeated) cleaning is especially important (Härkönen et al 1998), due to white birch being less preferred (Bergström & Hjeljord 1987). This relation between pine and birch has some support from a positive correlation between damage level and birch stem density in my study (recent damage: r=0.30, pers. obs., unpublished), as well as by Härkönen et al. (1998). Likely that is the reason for the negative correlation between damage variation and birch stem density.

Effects of stand history may explain the almost total absence of correlations between some stand characteristics and previous damages. For example, the degree of available browse (via total stem density or number of birch stem/ha) is not expected to have been constant during the last years. The fact that site-index did not show a similar correlation to recent damages is unexpected because site productivity would have been the same during the years when the previous damages have accumulated. An explanation may be that the range of site productivity in this survey was too narrow to reveal possible relationships.

5.4 Paired pine

The paired pines represent a fine scale (mean distance between neighbouring pines was 1.2 m) of moose browsing in terms of making damage. Bergqvist et al. (2001) and Härkönen (1998) assumed that stem damage develops randomly as a result of browsing. In my study, a pine had four and seven times higher risk (compared to random browsing) of being browsed or recent damaged, respectively, if it was neighbour of a browsed or recently damaged pine. The observed pattern is in line with the theory on herbivore behaviour to maximise the net rate of energy gain. Herbivore tends to limit movement between feeding stations. In addition, an herbivore carefully selects among parts of close-standing plants (Roguet et al. 1998) in order to obtain a balanced diet with essential nutrients and low contents of secondary compounds (Wieren 1996). My study also indicated that the observed dependence in browsing of neighbouring pines, is evened out when it comes to previous damage, although not totally so.

When only main stems were included from the paired pines, the risk decreased of a pine to be browsed if its neighbour is browsed (i.e. browsing: three times increased risk; previous damages: less than two times increased risk) in comparison with when all stems were included. An explanation could be that it depends on a difference in distance between the two sets of pines. The average distance between the main stem set is not calculated, but from number of pine main stems per ha (2 247), the average distance should be about 2.1 m. Thus, the mean distance between main stems is longer than the mean distance between all pine stems. This will decrease the dependence between the pines in terms of browsing (see further below).

5.4.1 Effect of distance on use of paired pines

The risk that a pine will be browsed or damaged if its neighbour is browsed or damaged decreases with distance to its attacked neighbour. The decrease is steeper for browsing in general than for previous damage. And, again (see above), the explanation could be that moose browsing behaviour aims at limiting energy losses and at the same time obtain high quality food. But, in previous damage, the pattern obtained from browsing is evened out and less dependence between stems is observed. Still, within the distance interval of 0-1.5 m there was an increased risk (2.2 times), compared to the risk expected from a random pattern, of a pine having a previous damage. At longer distances the risk decreased to about 1.8 times (Table 6).

Vivås & Sather (1987) reported that moose spent more time in plots where sapling density was high. This indicated an aggregative response and a non-random search strategy. As sapling density increased, the moose used a lower proportion of the saplings - but still browsed on more saplings per area. This is in line with this study where proportion of browsed stems increased with longer distance between stems despite the probability of a pine being browsed increases the closer it were to its neighbour (see % browsed pine 1, Table 4).

5.4.2 Height differences between paired pines

Increasing height differences between paired pines also seem to decrease the probability of a pine to be browsed, if the neighbour is browsed (indicative results). There is at least two explanations for this. First, if a tree for example is 5 dm lower than its neighbour it could be of less quality as food, due to it being underdeveloped (Danell et al. 1991). Second, lots of vertical body movements, due to browsing at different heights, imply unnecessary energy costs (Renaud et al. 2003). Thus, browsing on paired main stems, compared to browsing on paired all stems, may be a result of main stems both being more equal in height and being farther away from each other.

6. Management implications

Moose browsing of economically important trees, as well as on other trees, is shown to be complex. Regional differences in landscape and stand characteristics, management practices and varying moose population densities make it hard to link results together. However, I believe the observed patterns in my study can be used in discussions for improving forest management practices and the economical outcome of forestry.

According to my findings and earlier studies (e.g. Lyly & Saksa 1992; Vivås & Saether 1987) the proportion of damaged stems is less when stems stand fairly dense and are of same species and similar type (e.g. in terms of height). Thus, it seems to be favourable to have as many main stems per area as stand productivity allows. In addition, the options during pre-commercial cleaning may increase with high main stem density.

If one selectively cleans damaged main stems in patches where pines are heavily damaged, the result may be a stand with less than optimal spatial distribution. Either, the undamaged main stems get too unevenly distributed (i.e. gap formation) or, if one compensates damaged main stems with underdeveloped stems, there may be too large height variation. In patches where stems do not stand densely enough, the option to compensate a damaged stem with an undamaged neighbour does not exist. On the other hand, in denser patches there is a fairly high probability that a damaged stem also has a damaged neighbour, which in turn will decrease the success of selective cutting of damaged stems. Suppose the risk of a pine to be previously damaged is 30% and that risk get doubled when the pine is the neighbour of an already damaged pine. Then, the chance to compensate for a damaged pine is 100% - (30% * 2)=40%, provided that there is a neighbour close enough. This indicates that the option to compensate already damaged stems with undamaged neighbours seems limited, during pre-commercial cleaning.

A potential, but unexplored way to deal with more or less discrete patches with much damage is to plan strip-cleaning at pre-commercial cleaning or haulage roads at commercial thinning to reduce the occurrence of the damaged patches. Further investigations are needed to understand the spatial positions of such patches. When having knowledge if such methods are appropriate to certain conditions my study will likely be more valuable. Thus, the strong connection between damage level and damage variation indicates a possibility to understand damage variation by just knowing the damage level. Eventually, that is enough information to predict which methods being most appropriate to use.

This study can potentially facilitate surveys with the aim to estimate damage level. The knowledge of damage variation could be used to optimise surveying effort, by adjusting sample size to a current stands estimated damage level and thereby estimated damage variation.

My results can also help in predicting final outcome of forest damage caused by moose. Consider constant browsing pressure to main stems via stable moose population and stable supply of available browse. Under these circumstances it should be possible to make models including rebrowsing patterns and damage variation patterns to predict the damage impact to forest stands.

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