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Silva Fennica, joka vuosina 1926–66 ilmestyi sarjajulkaisuna (niteet 1–120), on vuoden 1967 alusta lähtien neljännesvuosittain ilmestyvä aikakauskirja. Suomen Metsätieteellinen Seura julkaisee myös *Acta Forestalia Fennica*-sarjaa vuodesta 1913 (nide 1) lähtien.

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SUSCEPTIBILITY OF PINE TO MAMMALIAN HERBIVORES IN NORTHERN FINLAND

MATTI ROUSI

Seloste

MÄNNYN ALTTIUS NISÄKÄSTUHOILLE POHJOIS-SUOMESSA

Saapunut toimitukselle 26. 10. 1983

An inventory of pine graft collection in Kolari (67°15′ N, 23°45′ E) showed that severe damage by the arctic hare, root and bank vole and moose was done to grafts small in size and in rather poor condition. Furthermore, the damage by the arctic hare was dependent on the dry matter content of the needles. Another inventory in a fertilization experiment in a pine pole-stage forest showed that nitrogen fertilization increased the damage by the arctic hare.

On the base of the present results an assumption was made that the formation of repellent substances against herbivorous mammals is connected with the wintering process of northern pines.

1. INTRODUCTION

The arctic hare (*Lepus timidus* L.) and the moose (*Alces alces* L.) had browsed several of the grafts in a collection of *Pinus sylvestris* L. at the Kolari Research Station Teuravuoma experimental area (67°15′ N, 23°45′ E) in the winter of 1982. In the spring, after the thaw, traces of the vole were also seen in the same collection. The damage drew special attention as the grafts were in the middle of a vast region full of the deciduous species usually preferred by rodents in winter.

Birch and willow are regarded the most important winter food of the hare (Kangas 1935, Brander 1954, Seiskari 1954, 1956). The importance of these deciduous species is further enhanced, particularly in northern Finland (Lindelöf et al. 1974, Nyholm 1968, Pulliainen 1971, 1972). In southern Finland the hare browses on pine only occasionally as emergency food (Brander 1954). Similarly, the browsing of pine by the hare had no serious consequences in Kuusamo (Nyholm 1968) or northeastern Lapland (Pulliainen 1971 and 1972), although it is known to have occasionally caused extensive damage to pine in northern Finland (Granit 1900). Pulliainen (1972) points out, however, that the hare does not seriously affect pine or spruce (*Picea abies* (L.) Karst) in northeastern Lapland.

Information on vole damage has been collected in Kolari since 1934, when the field vole (*Microtus agrestis* L.) and the bank vole (*Clethrionomys glareolus* Schreb.) were recorded to "have damaged rathed badly" a spruce plantation set up on a drained area (Kangas 1935). Some vole species (the root vole and field vole) have benefitted from human activity since the turn of the century; e.g. clearing natural habitats for hay-fields and modern forestry has created a lot of suitable habitats for these herbivorous vole species. Thus, the damage to forestry during microtine peaks has probably increased (Christiansen 1975, Korhonen 1982, Teivainen 1982).

Today the moose is the greatest cause of damage in mature plantations of pine and deciduous species in Finland (Löyttyniemi 1981); pine is the most important winter food of the moose because of its high nutritive value and easy availability (Löyttyniemi

1981, Salonen 1982). Although the density of the moose population in northern Finland is relatively low, the moose may cause local damage to pine plantations in Lapland, too.

The damage to the pine grafts in Teuravuoma provided an opportunity for investigating the susceptibility of various pine clones to mammal damage. Attempts were also made to find out why mammals preferred certain pine individuals. Is a "choice" actually made or do they browse any trees they come across? If mammals choose between tree individuals, do the various rodent species choose the same trees? To acquire further material the inventories also included other research plantations in the area and a pine fertilazation experiment. The inventory results are presented in this publication.

Dr Erkki Annila, Prof. Max Hagman, Mr Asko Kaikusalo, Mr Heikki Henttonen, Dr Veikko Koski, Dr Kari Löyttyniemi, Dr Pekka Niemelä, Mr Erkki Numminen, Dr C. J. Westman and Prof. Arne Rousi read the manuscript, giving valuable suggestions. Mr Teuvo Eskola, Rovaniemi, chief gamekeeper in Lapland, provided the information on the density of the moose population in Lapland. Mrs Leena Kaunisto translated the text into English and Mr Nigel Billany checked the translation. The measurements of the material were carried out by Mr Reijo Rauniomaa. Mr Juha Numminen was in charge of the calculations. The figures were drawn by Mr Mikko Rousi and Mrs Sisko Salminen. Miss Eija Virtanen typed the final manuscript. I wish to thank all who have participated in the completion of the work.

2. MATERIAL

In 1968 a graft collection of plus trees originating from an area with a temperature sum of 700–850 d.d. (see e.g. Solantie 1976) was set up on a peatland plantation at Teuravuoma (800 d.d.). In 1975 12 pine grafts originating from Alta in Norway were added to the collection. Originally, six grafts of each of the 475 clones were planted. In 1978 56 grafts were planted to replace the dead ones. The grafting point was at about 10–30 cm, above which scaly bark begins. At the spring inventory in 1982, 891 grafts were alive, of which 90 had been protected against the vole by wire nets. The protected saplings were omitted from the inventory.

The study area is c. 500 ha, and is dotted with small conifer and hardwood stands and protective forest zones. Various experiments occupy part of the area, and part of the area has been left to regenerate naturally. The graft collection is surrounded by willows, which cover c. 50 % of the area. In the graft collection itself the willows covered c. 30 % of the area in the winter of 1981/82. About 90 % of the willows are *Salix phylicifolia* L., and less than 10 % are *Salix lapponum* L. and some *Salix caprea* L. A naturally regenerated stand of weeping birch (*Betula pubescens* Ehrh.) covered 2–3 % of the area. The height of the willow bushes and weeping birch varied, reaching three metres. Apart from the Scots pine and Norway spruce the field is also stocked with black spruce (*Picea mariana* (Mill) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss) provenances originating from Canada and Alaska and with black larch (*Larix laricina* (Dur) K. Koch). The black and white spruces come from the vicinity of Fairbanks in Alaska, from the river valleys of the upper reaches of the River Yukon and the outlet of the river Mackenzie in western Canada. All the black larches come from the vicinity of Fairbanks. The plantations were also surveyed in the spring of 1982.

No estimates of the density of the hare population at Teuravuoma can be given , but on the basis of tracks in the snow, pellets and visual observations the population was very dense in 1981/82. The density of neither the vole or the hare population at Mustivinsa (see page 303) was recorded. When the vole had gnawed the graft above the snow, at needles, buds or branches, the bank vole was considered the culprit. If the parts below the snow had been damaged, the root vole (*Microtus oeconomus* Pallas) was to blame.

The graft collection was surveyed throughout the winter of 1981–82. However, the browsing by the hare was not discovered until early March. All the trees were measured for height, breast-height diameter and average browsing level. As the trees were still dormant, their prebrowsing condition could also be estimated.

The major vole species in both the areas of reclaimed bog and the areas with willows and grassy vegetation in Teuravuoma is the root vole. The bank vole is common in the small shelterwoods. The field vole and grey-sided vole (*Clethrionymus rufocanus* Sund.) were also found in more shady biotopes, although they were very rare. As a matter of fact only root and bank voles were responsible for the damage in the experimental area. In autumn 1981 both species had reached their cyclic population peak and in the spring of 1982 the voles were still numerous.

The density of the moose population is 0.3–3 moose per 1000 hectare in Lapland and about one moose/1000 ha in Kolari.

Damage by the root vole and hare was divided into five classes: 0 = intact, 1 = nibbled, 2 = slightly eaten, 3 = over half the tree girth eaten and 4 = the whole stem at the lower branches eaten. The damage classes for the bank vole and moose corresponded to these classes so that class 4 consisted of trees that were not expected to recover from the damage.

A needle sample (previous-year needles) was taken from the uppermost, southern branch whorls of nine grafts severely damaged by the hare in April 1982. Control samples were taken from nine grafts which were not eaten by the hare but resembled as much as possible the eaten grafts. The needle samples were analyzed using conventional methods for the contents of dry matter, ash, N, P. K, Ca, Mg, Fe, Mn, Cu and B by Mr Pietiläinen at the Muhos Research Station. The samples were dried before determination. Student's t-test was used to compare the affected and unaffected trees.

The same measuring method was used for the fertilization experiment at Mustivinsa, Muonio, close to the border of Kolari, in spring 1981. The experiment was set up in a pole-stage pine stand of Empetrum-Vaccinium site-type which originated after a forest fire. The experimental area has 4802 pines whose average height is 7.5 m and average breast-height diameter 8.5 cm. The experiment consists of seven treatments with four replications in early spring 1981. A nine-are plot for each treatment was fertilized according to the following scheme:

Treatment	Calcium ammonium nitrate kg/ha	(= pure) N kg/ha	Rock phosphate 300 kg/ha Potassium chloride 167 kg/ha Micronutrient mixture 200 kg/ha
1	–	–	–
2	400	100	–
3	800	200	–
4	1600	400	–
5	400	100	+
6	800	200	+
7	1600	400	+

Mammal damage was observed not only in pine plantations but also in other plantations of pine, spruce, black spruce, white spruce and black larch at Teuravuoma.

3. RESULTS

The moose had browsed on over 50 % of the pine grafts in the Teuravuoma clone collection. The root vole and hare had damaged almost 50 % of the grafts and the bank vole about 15 %. The number of severely damaged saplings (classes 3 and 4) only reflects the magnitude of mammal damage. The moose had severely damaged 13 % of the grafts, the root vole 22 %, the hare 14 % and the bank vole 1 % (Fig. 1, Table 1).

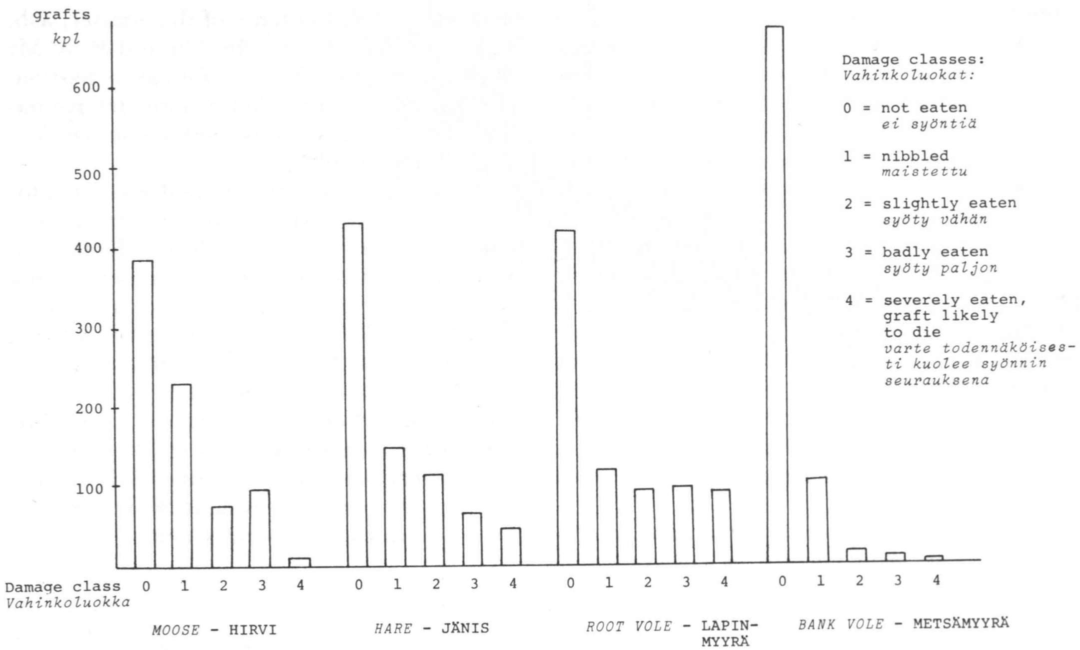


Fig. 1. Number of pine grafts damaged and unaffected by mammals. Teuravuoma in Kolari.
Kuva 1. Eri nisäkkäiden vahingoittamien ja koskemattomien mäntyvartteiden kappalemäärät. Kolari, Teuravuoma.

The mean height of the trees in the Teuravuoma graft collection was about 3 m and the average breast-height diameter about 4 cm. The prebrowsing condition of the 801 live trees in the graft collection was estimated very good in 7 %, good in 51 % and poor in 42 % of the cases. Mammals primarily badly damaged the poor grafts and usually caused less damage to those in slightly better condition than average (Tables 1 and 2). If all the grafts browsed by mammals are combined, it can be seen that their condition class distribution does not deviate from that of the whole material ($\varkappa^2$ = 2.23). The severely damaged grafts were usually smaller in size than those of the whole material and the "only slightly damaged" grafts (Fig. 2). This can be particularly clearly seen in gafts eaten by the moose and bank vole. It should be pointed out that the poor condition of grafts usually resulted from abiotic factors. In some cases the cause was previous moose or vole damage. Thus the condition of grafts was not considered to have been affected by being eaten during the inventory winter.

The root vole had eaten 47 % of the pines in the graft collection. The hare had eaten 46 % of grafts, 43 % of which had also been eaten by the root vole. As the percentages are almost the same, the vole and hare clearly started eating the grafts independently of each other. Trees with severe hare damage (classes 3 and 4) numbered 110. Severe vole damage was observed in 163 grafts. Both the vole and hare had badly damaged 52 grafts. In comparison to the entire material, the hare had often more damaged the trees that had also been badly affected by the vole; the difference was highly statistically significant ($Z = 5.7$; $P < 0.001$). The other mammals did not show a similar correspondence.

The results from Mustivinsa fertilization experiment showed that nitrogen fertilization increases the palatability of pines to hares to a statistically significant degree ($P = 0.004$). Mineral nutritients did not show any effect (Figure 3). The needle analysis shows that the dry matter content of grafts severely damaged by the hare at Teuramuoma was lower than in the needles of grafts untouched by the hare (Table 3).

In the plantation of black and white spruce or black larch were no sign of damage by mammals.

Table 1. Teuravuoma in Kolari: The effect of the condition of grafts on mammal damage.
Taulukko 1. Kolarin Teuravuoma: Vartteiden kunnon vaikutus nisäkästuhoihin.

Damage class *Syöntiluokka*	Condition Class *Kuntoluokka*	Moose *Hirvi* grafts *kpl*	Moose %	Hare *Jänis* grafts *kpl*	Hare %	Root vole *Lapinmyyrä* grafts *kpl*	Root vole %	Bank vole *Metsämyyrä* grafts *kpl*	Bank vole %
0	1	34	9	32	7	28	7	43	6
	2	203	52	232	54	215	51	351	52
	3	150	39	167	39	177	42	280	42
		387		431		420		674	
1	1	20	9	12	8	11	9	11	9
	2	162	71	70	47	71	60	57	55
	3	51	22	66	45	36	31	36	35
		233		148		118		104	
2	1	0	0	9	8	7	8	0	0
	2	30	40	67	60	48	53	3	21
	3	45	60	36	32	35	39	11	79
		75		112		90		14	
3	1	0	0	1	2	4	4	0	0
	2	16	17	28	43	49	52	0	0
	3	80	83	36	55	41	44	8	100
		96		65		94		8	
4	1	0	0	0	0	4	5	0	0
	2	0	0	14	31	28	35	0	0
	3	10	100	31	69	47	60	1	100
		10		45		79		1	

Damage class – *Syöntiluokka*
0 = intact – *koskematon*
1 = nibbled –*maistettu*
2 = slightly eaten – *syöty vähän*
3 = badly eaten – *syöty paljon*
4 = will die – *kuolee syönnin seurauksena*

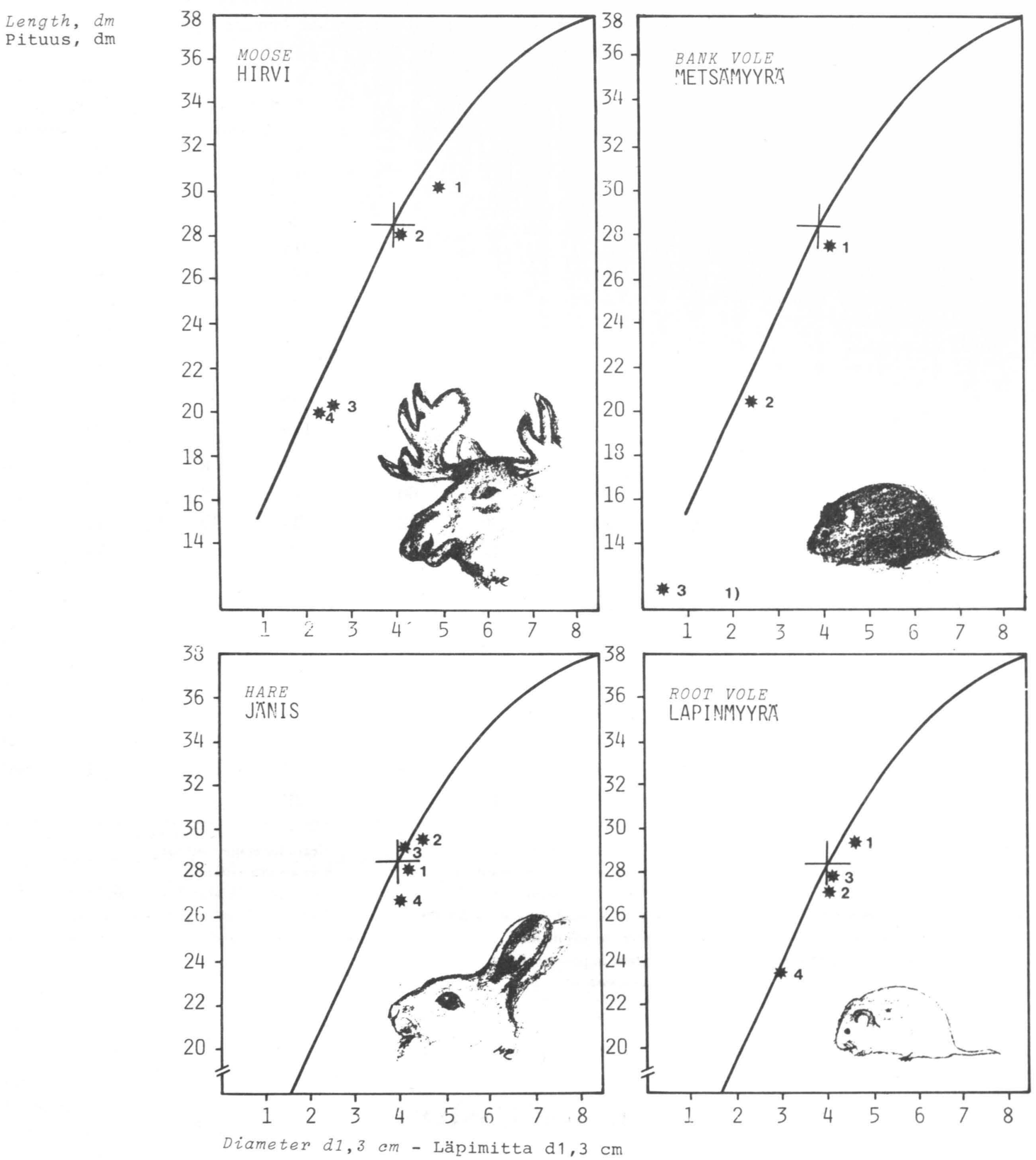
Condition class – *Kuntoluokka*
1 = grafts in very good condition *erittäin hyväkuntoiset vartteet*
2 = grafts in good, normal condition *hyvät, normaalit vartteet*
3 = grafts in poor condition *huonokuntoiset vartteet*

Means for entire material
Koko aineiston keskiarvo
1st class – 1. *luokka* 7 % 54 grafts-*kpl*
2nd class – 2. *luokka* 51 % 411 grafts-*kpl*
3rd class – 3. *luokka* 42 % 336 grafts-*kpl*

4. DISCUSSION

Several reports have been published about the food selection in winter by the arctic hare. In Finland the hare prefers the weeping birch and shuns the silver birch (Sulkinoja 1983). According to Hewson (1977) the hare does not care for the weeping birch in Scotland. The proportion of willow in the winter food of the hare is particularly accentuated in northern Finland (Nyholm 1968, Pulliainen 1971, 1972).

Although the area in Kolari where the grafts grew abounded in willow and weeping birch, the pines had been damaged to a considerable extent. If log pines are felled during winter hares seem to eat quite often phloem and kambium from the crown parts. Main reason to this may be scaly bark or/and the chemical composition, lack of phenolic compounds, of crowns (see also Rhoades and Cates 1976). When grafted from old trees the crown parts maintain their characteristics (topofysis and cyclofysis) and because of that may be attractive to hare. In ordinate pine plantations near the graft collection pine bark



CLASSES – *LUOKAT*

+ = mean height and diameter of trees – *keskiarvo puiden pituudesta ja läpimitasta*

1 = nibbled – *maistettu*
2 = slightly eaten – *syöty vähän*
3 = badly eaten – *syöty paljon*
4 = severely eaten, graft likely to die – *kuolee syönnin seurauksena*

1) Only one graft belonged to Class 4 in the case of the bank vole. Not included in the figure.
Metsämyyrällä luokkaan 4 kuului vain yksi varte. Sitä ei ole merkitty kuvioon.

Fig. 2. Severity of mammal damage in relation to the height curve of grafts.
Kuva 2. Nisäkkäiden syönnin ankaruuden suhde vartteiden pituuskäyrään. Kolari, Teuravuoma.

Table 2. Condition class distribution of grafts badly and slightly eaten by different mammal species as compared to the condition class distribution of the entire material, according to Table 1.
Taulukko 2. Eri nisäkäslajien pahoin ja lievästi syömien vartteiden kuntoluokkajakauma verrattuna koko aineiston kuntoluokkajakautumaan (ks. taulukko 1).

Mammal *Nisäkäs*	Badly eaten – *Paljon syöty* (damage classes 3 and 4) *(syöntiluokat 3 ja 4)* χ^2	P-value *P-arvo*	Slightly eaten – *Vähän syöty* (damage classes 1 and 2) *(syöntiluokat 1 ja 2)* χ^2	P-value *P-arvo*
Moose *Hirvi*	80.82	P<0.001	15.88	P<0.001
Hare *Jänis*	18.69	P<0.001	2.29	P<0.10
Root vole *Lapinmyyrä*	6.0	0.05>P> 0.01	5.60	0.10>P> 0.05
Bank vole *Metsämyyrä*			1.6	P>0.1
Mammals combined *Nisäkkäät yhdist.*	80.6	P<0.001	18.0	P<0.01

Table 3. Results from the needle analyses of badly eaten (hare) and intact grafts. Significances * = 0.05 > P > 0.01; ° = 0.1 > P > 0.05.
*Taulukko 3. Jäniksen pahoin syömien ja syömättömien vartteiden neulasanalyysin tulodset. Merkitsevyydet * = 0.05 > P > 0.01; ° = 0.1 > P > 0.05.*

	Eaten – *Syöty* X̄ ± S.D.	t-value *t-arvo*	Not eaten – *Syömätön* X̄ ± S.D.
Dry matter % *Kuiva-aine, %*	94.80±017	2.38*	95.04±0.26
Ash % *Tuhka %*	1.84±0.22	1.59	1.69±0.16
N %	1.28±0.36	0.64	1.37±0.24
P mg/g	1.80±0.14	0.13°	1.78±0.27
K mg/g	4.63±1.03	1.62	3.87±0.95
Ca mg/g	1.62±0.36	0.79	1.51±0.16
Mg mg/g	1.07±0.20	0.71	1.15±0.24
Fe PPM	40.96±7.37	1.98°	35.53±3.63
Mn PPM	498.89±164.39	0.10	505.22±99.10
Zn PPM	34.70±7.33	0.80	32.07±6.65
Cu PPM	4.39±0.58	0.90	4.76±1.08
B PPM	27.09±10.04	1.07	21.25±11.70

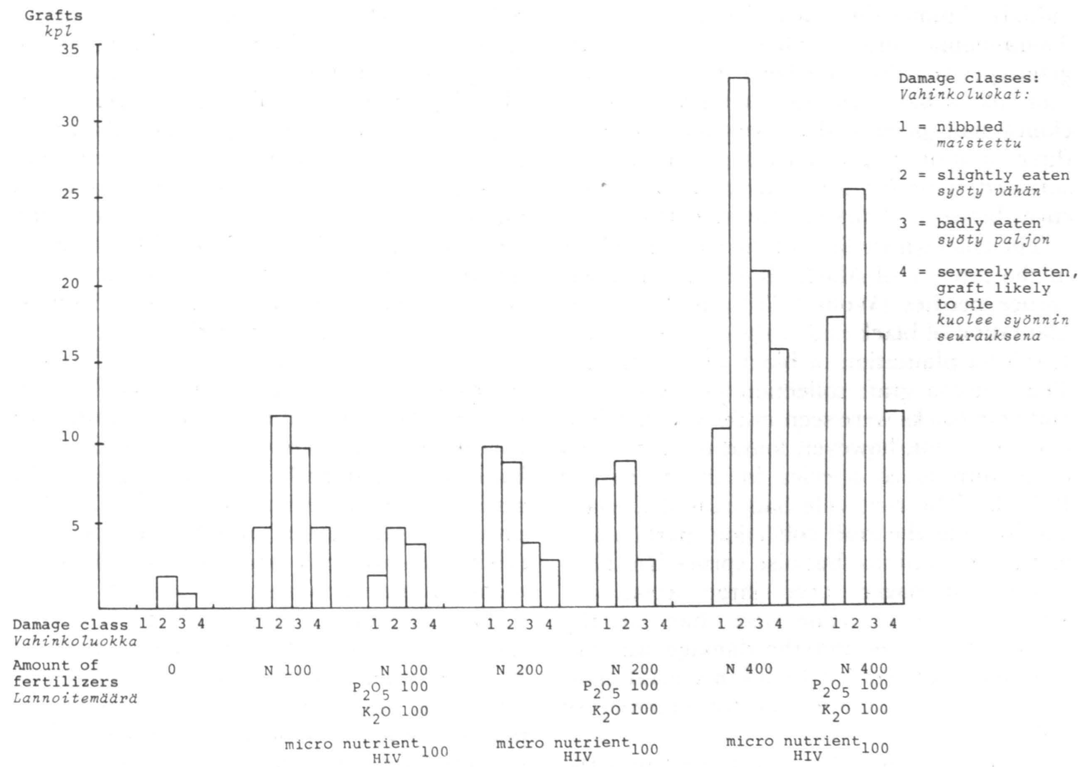


Fig. 3. Effect of nitrogen fertilization on browsing by the hare. Mustivinsa in Muonio. (Damage classes see Fig. 1).
Kuva 3. Typpilannoituksen vaikutus jäniksen syöntiin. Muonio, Mustivinsa. (ks. vahinkoluokkien selitys kuvasta 1).

was left completely untouched by the hare. Here and there, however, the hare had broken leaders in small pines (see also Bryant and Kuropat 1980). The size of grafts eaten by the hare did not deviate much from the mean of the whole material. Most of the severely damaged saplings had been in poor condition.

Both the snowshoe hare (*Lepus americanus* Erx.) and the mule deer (*Odocoileus hemionus columbianus* Richardson) select certain genotypes of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Dimock et al. (1976) showed that the relative palatability of needles in the genotypes of Douglas fir was a strongly heritable, additive characteristic. It was also possible to predict the most preferred genotypes of Douglas fir by a mathematical model based on the availability and digestibility of needles (Dimock and Silen 1978. cf. Rawdan 1972). Investigations have shown that voles reattack the same lodgepole pine they had earlier damaged (Rousi 1983 a), which might be at least partly attributable to the genetic difference between lodgepole individuals. Among the nearly 500 clones in the Teuravuoma graft collection there are genotypes that had not been touched by the root vole or hare, whereas each graft in some clones had been badly damaged. As only three or four grafts of each genotype have survived, more specific analyses on the differences between clones cannot be carried out.

The chief winter food of the snowshoe hare in the interior of Alaska is black and white spruce needles (Wolff 1978). In the 4.5 ha plantation of black and white spruce and the c. 0.5 ha plantation of black larch near the Teuravuoma graft collection plenty of hare and vole tracks were seen in the snow. Mammals were not, however, found to have eaten these introduced species in the winter of 1981/82. The root vole had caused damage not far from the graft collection, particularly in pine plantations, but also spruce had been severely damaged over large areas (cf. Teivainen 1982). The vole had usually gnawed the roots and the damage was not seen until trees started to fall in several plantations in Teuravuoma in the summer of 1982.

It has previously been suggested that the bank and root vole select their food according to some external factors between tree species. Thus the vole does not taste the sapling before selecting a particular tree species. The amount eaten depends on the palatability of different individuals of the same species (Rousi 1983 a and b). The present results also indicate that the hare and root vole at least partially select their food on the same basis. Furthermore the palatability of the tree chosen by the hare and root vole seems to depend on the same chemical factors. The condition class distribution of the damaged trees in the Teuravuoma graft collection does not, according to this investigation, deviate from the entire material. However, the grafts severely damaged by mammals were usually in poor condition (Tables 1 and 2). This would suggest that mammals start eating trees randomly. The most palatable trees those in poor condition are then further eaten a great deal, while those in good condition are only slightly damaged.

Attempts have been made to find reasons for the choice of winter food by the moose in the nutrient contents of plants (e.g. Kubota et al. 1970, Andersson and Markkula 1974, Salonen 1982). The results have been somewhat varied (e.g. Laine and Mannerkoski 1980, Löyttyniemi 1981, cf. Salonen 1982, Haukioja et al. 1983). The moose prefers pine saplings that have become weakened for various reasons (Sainio 1956, Yli-Vakkuri 1956, Westman 1958), although contradictory views also exist (Kangas 1949, Etelälahti 1950, Laine and Mannerkoski 1980, Löyttyniemi 1982). Every other tree in this graft collection had been browsed by the moose (Fig. 1). This limited material suggests that the moose selects the pines on the basis of their condition (Table 1). Over 80 % of the severely damaged saplings had been in poor condition before browsing (Table 2). The badly damaged grafts were also among the smallest trees in the material (Fig. 2). The present result agrees with Sainio's findings (1956) dealing with saplings browsed by the moose in the far north.

The phosphorus and crude protein contents, in particular, have proved to affect the food selection of the hare (Lindelöf et al. 1974). In Scotland the nitrogen and phosphorus contents in heather (*Calluna vulgaris* L.) were not found to have any effect on the eating habits of the hare (Hewson 1974). It has been argued (Bryant and Kuropat 1980) that the food selection of neither the hare nor moose correlates with the nutrient content. Instead, there is a negative correlation between the food selection and gross energy content of the food. The hare and moose seem to prefer the same easily digestible species (e.g. willow and aspen). Those with a higher energy content but which are less digestible (birch, alder and conifers) are less palatable (e.g. Seiskari 1954, 1956, Sainio 1956, Yli-Vakkuri 1956, Dodds 1960, Nyholm 1968, Pulliainen 1971, 1972, Telfer 1974, Bryant and Kuropat 1980, Salonen 1982). It appears that the content of the secondary substances in plant tissue affect the food selection of the hare and moose (Bryant and Kuropat 1980, Haukioja et al. 1983, see also Löyttyniemi and Hiltunen 1978). The secondary metabolites of these plants or their compounds do not affect the feeding habits of the moose and hare in the same way; the moose prefers silver birch and pine, which usually remain untouched by the hare. Similarly, the palatability of Douglas fir to the snowshoe hare and deer are probably caused by slightly different combinations of factors (Dimock et al. 1976). The quantitative variation of different resin types seems to explain the food selection of the hare as far as the same tree species is concerned, while the qualitative variation explains the difference between different three species (Bryant and Kuropat 1980). According to earlier studies, the field vole prefers the more southern provenances of spruce (Kangas 1935 and Heikinheimo 1958 p. 23, Hagman 1973, Christiansen 1975). Investigations in northern Finland have also shown that the root vole damages the southern lodgepole pine (*Pinus contorta* var. *latifolia* S. Watts.) provenances significantly more than the northern ones (Rousi 1983 a). The pine grafts in this investigation come from such a small area (150 d.d.) that it is unlikely that there are any differences in the susceptibility due to the transfer of different provenances. In this respect the nitrogen fertilization experiment with pine contributes some interesting information. Nitrogen fertilization increased the browsing of pine by the hare. The same kind of results have been obtained also in the case of moose in southern Finland (Laine and Mannerkoski 1980, Löyttyniemi 1981). The nitrogen fertilization and the transfer of provenances from the south to the north are known to affect the growth rhythm of trees by delaying the physiological processes related to wintering in the autumn (see e.g. Gusta et al. 1982). Thus experiments in northern Finland, including the present one, have revealed frost damage to the tops of nitrogen fertilized trees (Numminen 1982).

In a pine graft collection in central Finland the moose browsed pine whose needles had a (to a highly significant degree) lower dry matter content than the pine needles shunned by the moose (Haukioja et al. 1983). In the present experiment the hare browsed the bark of those grafts whose needles had a lower dry matter content than the pine untouched by the hare. The dry matter content in pine needles is reportedly a reliable sign of wintering. The foliar dry matter content is used to estimate, among other things, the susceptibility of pine to snow blight (*Phacidium infestans* Karst.) (Langlet 1934, 1936). It might be that the palatability of conifers to mammals depends on the success of wintering.

There is now more evidence for the fact that the secondary metabolites have an ecological significance in the adaptation process of plants. Plenty of evidence has lately been produced about the antagonistic effect of particularly phenolic substances such as tannins and lignins on herbivores (e.g. Swain 1979, see also Rhoades 1979). The content of repellent substances in different plant species is determined by their availability to herbivores, and it has been assumed that the different concentrations of repellent substances found within a species are due to the importance of that particular plant part to the survival of the species (Rhoades and Cates 1976). The contents of repellent substances have proved to explain the food selection of the moose and some other northern herbivores better than the positive factors in food (Bryant and Kuropat 1980, Haukioja et al. 1983.).

Conifers are among the easily available sources of winter food for mammals. As the function of the phloem and cambium is vitally important for trees, the conifers have had to develop protection agains the vole and hare in the course of their evolution. The hare does not usually browse pine, whereas e.g. the root vole gnaws the base of pine during its peak years. As the vole damage usually occurs before or during the decline of the population, pine bark .may be unsuitable for it. The vole, hare and moose use conifers only for winter food. The lignin and tannin contents in plants correlate with winter endurance, and the tannin content has, in fact, been found to increase during the winter (Levitt 1956, 1972). Secondary metabolites that prevent the breakdown of proteins in the intestines of herbivores and other substances that disturb the digestion of herbivores are also known to disturb the metabolism of the plant cell. Hence the plants have to use a lot of energy to isolate these antagonistic substances from the function of the cell (Rhoades and Cates 1976). The present results indicate that, in particular, the small and weak saplings which do not have sufficient energy to form repellent agents are very susceptible to severe mammal damage (see also Rhoades 1979, cf. Hansson and Larsson 1980). Conifers need the repellent agents that disturb the digestion or physiology of mammals only in the winter when the tree tissue is dormant, the isolation of repellent agents from the metabolism of the cell then probably being far simpler than when the cells are active.

There is reason to believe that mammals use poorly wintering conifers foor food. The assumption is based on the earlier observations on the low foliar dry matter content in pine preferred by the moose (Haukioja et al. 1983), the present similar results in the case of the hare, the present observation on the hare focusing on nitrogen fertilized pines and the earlier findings that the root vole prefers the southern provenances of spruce and lodgepole pine. This assumption which links the wintering of conifers and the formation of repellent substances, would make it possible for the conifers to protect themselves against mammals at the right time without needing much energy.

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SELOSTE

MÄNNYN ALTTIUS NISÄKÄSTUHOILLE POHJOIS-SUOMESSA

Miksi nisäkkäät valitsevat tietyt mänty-yksilöt ravinnokseen? Onko yleensä kysymys "valitsemisesta", vai syövätkö ne vain sattumalta eteen osuvia puita? Jos nisäkkäät valitsevat eri puuyksilöiden kesken, valitsevatko eri nisäkäslajit samoja puita. Näiden seikkojen selvittämiseksi inventoitiin jänisten, myyrien ja hirvien vahingoittama 801 vartteen mäntykloonikokoelma Kolarin Teuravuomalla. Lisäaineiston hankkimiseksi inventoitiin vahinkojen esiintymistä eräissä muissa alueen tutkimustaimikoissa ja männyn lannoituskokeessa. Inventointien tulokset esitetään tässä julkaisussa. Lisäksi Teuravuoman kloonikokeen yhdeksästä jäniksen pahoin syömästä ja yhdeksästä jäniksen koskemattomasta vartteesta otettiin neulasnäyte.

Jänis, lapinmyyrä ja hirvi olivat talvella 1981/82 kukin vahingoittaneet miltei joka toista kloonikokoelman vartteista. Jänikset olivat aiheuttaneet pahoja vikuutuksia 14 %:lle, lapinmyyrät 22 %:lle ja hirvet 13 %:lle alueen vartteista. Jänisten ja lapinmyyrien aiheuttama tuho löytyi erittäin todennäköisesti samasta vartteesta.

Nisäkkäiden pahoin vahingoittamat taimet olivat pienikokoisia ja huonokuntoisia jo ennen syöntiä. Jäniksen syömien vartteiden neulasten kuiva-ainepitoisuus oli pienempi kuin jäniksen syömättömissä vartteissa. Lannoituskokeen perusteella typpilannoitus lisää männyn alttiutta jäniksen syönnille.

Vartekokoelman läheisyydessä kasvavia musta- ja valkokuusi- sekä kanadanlehtikuusiviljelyksiä nisäkkäät eivät olleet vahingoittaneet. Sen sijaan mänty- ja kuusiistutuksissa havaittiin runsaasi myyrien vioituksia.

Nyt ja aiemmin saatujen tulosten perusteella voidaan olettaa, että erityisesti huonosti talveentuneet taimet ovat alttiita nisäkästuhoille. Jos puut muodostaisivat nisäkäskasvinsyöjiä torjuvia aineita talveentumisen yhteydessä, niin puiden oikea-aikainen ja energiataloudellisesti edullinen puolustautuminen varmistuisi. Epäonnistuneen talveentumisen seurauksena puiden kemiallinen puolustautuminen ei mahdollisesti ole riittävä. Tämä selittäisi huonosti talveentuneiden puiden alttiuden jänis-, myyrä- ja hirvituhoille talvella.