Variation in quality of mountain birch and tea-leaved willow for mammal and insect herbivores: differences among trees, among sites and between tree species

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We evaluated palatability of winter dormant tree twigs to the mountain hare *Lepus timidus* and the grey-sided vole *Clethrionomys rufocanus* with captive animals We tested differences among trees within sites, among sites, and between two tree species (the mountain birch *Betula pubescens* ssp *czerepanovii* and the tea-leaved willow *Salix phylicifolia*) In one of the sites, we also measured growth rates of autumnal moth *Epirrita autumnata* larvae on the same trees that were used in preference trials with the hares and voles The differences in palatability to hares and voles were greatest at the level of tree species, both hares and voles preferred birches over willows, but with the hare there was some overlap in palatability between the tree species There were also large and significant differences among sites and among trees within sites Within sites, variation in tree palatability seemed to be larger among willows than among birches Hares and voles may select willows at least partly on the same basis, but there was no correlation between palatability of the trees to the mammals and the growth rate of the larvae of the autumnal moth on the same trees Variation in twig palatability to the hares and voles was so large at all levels (among trees within sites, among sites and between tree species) that we suggest it also has implications for food selection of these mammalian herbivores under natural conditions

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The emphasis in studies of woody plants and small mammalian herbivores during the last two decades has been on the nutritional and chemical factors that determine food plant selection by herbivores Comparisons have been conducted among tree species (Lindlöf et al 1974a, Tahvanainen et al 1985, Rousi et al 1991), among trees of different geographical origins (Niemelä et al 1989, Rousi et al 1989, 1991) and among different parts of trees (Bryant and Kuropat 1980, Bryant 1981, Tahvanainen et al 1985, Danell et al. 1987, Reichardt et al 1990, Bryant et al. 1991, Palo et al. 1992) Effects of resource availability on tree resistance

has also been intensively studied, particularly at the within-species level (Bryant et al. 1983, Bryant 1987, Bryant et al 1987, Rousi et al 1991, 1993, Hartley et al 1995).

It is generally known among game-biologists and foresters that vertebrate herbivores prefer some tree individuals over others However, surprisingly few studies have quantified the natural variation in palatability among con-specific individuals growing in the same location, e g. within the home range of a mammalian herbivore (but see Dimock et al 1976, Snyder 1992, Molvar et al. 1993) Since homogeneous forests with

one or two dominant tree species are typical for the boreal and subarctic regions, differences in quality among con-specific trees growing in a same location may thus be important in diet selection of mammalian herbivores, especially during winter

In this study, we measured palatability of mountain birch *Betula pubescens* ssp *czerepanovii* (Orlova) Hämet-Ahti, *B tortuosa* auct and tea-leaved willow *Salix phylicifolia* (L) for different herbivore species The aim was to compare tree palatability at different scales both between and within species We used different herbivore species, since it is probable that a plant is not as resistant to all herbivore species, particularly if the herbivores belong to different taxa or use different plant parts (Linhart 1991)

We examined 1) palatability of winter-dormant twigs to the mountain hare *Lepus timidus* (L), and the grey-sided vole *Clethrionomys rufocanus* (Sund) among con-specific trees within and among sites, and between the two tree species We were particularly interested in identifying the level that differences are the largest We also 2) bioassayed leaf quality of trees for larvae of the autumnal moth *Epirrita autumnata* (Bkh) on one of the sites, and 3) tested if hares and voles showed similar preferences and if there was any relationship between twig palatability to the mammals and growth rate of *E autumnata* larvae on leaves from the same trees

Materials and methods

Study sites and trees

The study was conducted at the Kevo Subarctic Research Station (69°45′N, 27°E) in northern Finland In January 1992 we selected three study sites close to the station 1) at the base of the fell Jesnalvaara (80 m a s.l), 2) at the middle slope of the fell Skallovaara (180 m a s.l) and 3) at the high slope of Skallovaara (280 m a.s l), which are henceforth referred to as low, middle and high elevation sites, respectively The distance between the two farthest sites was ca 10 km

The mountain birch is the dominant tree species in the study area, where it forms large monospecific forests The tea-leaved willow occurs regularly in bogs, banks and other moist sites

At each of the three sites, we marked 15 mountain birches (4–7 m tall), and 15 tea-leaved willows (1–3 m tall) in an area of ca 1 ha For both species, we randomly sampled six individual trees All the trees were mature, and we used only mature twigs in the experiments, since in woody species twigs of juvenile developmental stage are generally of lower palatability for mammalian herbivores than mature twigs (Bryant and Kuropat 1980, Bryant 1981, Tahvanainen et al. 1985).

Males of several willow species are usually preferred to females, both by voles (Danell et al 1985, 1991b) and hares (Hjältén 1991) We had planned to sample only male willows for the experiments to evaluate how much variation there is within a sex We could not identify sexes of all willows, however, since they did not all produce catkins At the high elevation site, all six willows were males, but at both the low and middle elevation sites, three trees were males, the sex of two willows could not be determined, and one later appeared to be female

Study animals

Mountain hare is the only lagomorph in northern Fennoscandia and is common in the study area Its winter food consists mainly of woody species (e g *Betula* spp , *Salix* spp , *Juniperus communis, Populus tremula, Pinus sylvestris*), but it prefers grasses and dwarf shrubs when snow cover is not too thick to prevent access to these small-sized plants (Lindlöf et al 1974b, Pulliainen and Tunkkari 1987)

The grey-sided vole is a common microtine rodent at the Kevo area Bilberry shoots and other green plant parts comprise an important food source during winter (Kalela 1957, Hansson 1985), but *C rufocanus* also gnaws the bark of woody species (Kalela 1957, Hansson 1985, Suomela unpubl) However, bark probably only plays a minor role in vole nutrition

Thus, we evaluated twig palatability to two types of mammals hares, which are specialized to use twigs of trees during winter, and grey-sided voles, which are not specialists on woody plants

The hares and voles used in the experiments were trapped around the Kevo Station The voles were caught during the previous summer and the hares at least 2 wk prior the start of trials

The autumnal moth is a univoltine geometrid, whose larvae feed on the mountain birch as well as on other deciduous trees (Neuvonen et al 1987, Haukioja et al. 1988) At Kevo, the larval period lasts usually from June to the beginning of July

Preference trials with hares and voles

We conducted multiple-choice preference trials in which twigs of different trees were simultaneously offered to caged animals We only sampled living branches from 0 to 2 m height over snow cover (depth of the snow cover varied from 0 5 m to 1 5 m), i e. low and middle branches of birches and middle and upper branches of willows Before use, the branches were preserved 1–6 wk in sealed plastic bags under outdoor conditions (−5°−−30°C) Preserving winter dormant twigs in the cold for several months has not been found to affect their palatability (Uotila pers comm.)

The trials were conducted separately for hares and voles We first tested for differences among the six trees (separately for birch and willow) of each site (low, middle and high) After the within-site trials, we chose the most and the least palatable tree of each site, and compared their palatability (again separately for birch and willow). After the among-site trials, we chose, from both tree species, the most, least and intermediately preferred tree, and compared their palatability in the same trial Thus, in all trials, the animals were offered twigs of six different trees

The hare trials were conducted under outdoor conditions and replicated with four hares The hares were kept individually in cages (2 × 1 5 × 1 m) made of metallic net (mesh size 1 5 cm) In each trial, the hares were simultaneously offered small bundles (ca 20 g and 25 cm) of twigs from experimental trees Each bundle consisted of twigs from one tree The basal diameter of twigs used in the bundles was measured

There is a lot of variation in birch growth rate among and within trees For example, palatability of twigs with new long shoots, i e twigs which have grown in the previous summer, may differ from ungrown branches (Suomela unpubl) Consequently, we used, within a trial, only birch twigs which had not grown during the previous summer or if this was not possible, tried to keep the amount of long shoots on different bundles as equal as possible

The bundles were fastened to modified electronic balances, which were side by side with 20 cm intervals in a wooden box The mass of bundles on each balance was registered by a microcomputer at 2–3 min intervals Position of the bundles was randomized within each trial The trials usually lasted overnight (11–14 h)

Due to practical reasons, the amount of twigs offered to the hares during the trials was small compared to the hare food requirement Consequently, the hares had usually consumed most or all of the bundles during a given feeding trial For this reason, we used as a measure of twig palatability, an index that took into account the amount of twig mass eaten and the point of time of feeding

We first calculated, for each bundle, the area under the cumulative consumption curve (time in x-axis and cumulative consumption in y-axis) The bundles were then standardized to the most preferred bundle by dividing the area of each bundle by the area of the most preferred bundle of the trial The index for the most preferred tree was thus 1.0 The calculation was otherwise similar to the "Rodger's index" (Krebs 1989, pp. 399–404), but we used in the calculations the absolute twig mass eaten instead of cumulative proportions

Prior to and between experiments, hares got ad libitum birch and willow (tea-leaved willow and other willow species) twigs from the Kevo area, commercial pellets for guinea pigs and ice for water requirements

The vole trials were conducted in aluminium boxes (45 × 23 × 13 cm, with a wire net as a roof) kept indoors and replicated with 10 voles One twig segment (150 mm long and 7–10 mm thick, twigs given to an individual vole were as similar as possible) of each study tree were simultaneously offered to the voles These were more basal parts of the same branches whose tip parts were used in the hare trials The twigs were marked with a thin metal wire and placed in random order at the bottom of the trial box with one vole

The length of the trials varied from two to five days, depending on the vole individual and the tree species (willows were debarked more slowly than birches) The trials were terminated when a vole had debarked at least half of the bark of two or three twigs As a measure of twig palatability to the voles, we used the amount of debarked area (cm²), standardized to the most preferred tree, whose index will thus be 1 0

Prior to and between trials, the voles had birch and willow twigs, commercial pellets and water ad libitum During the trials they also had ca 20 g of pellets and water available Temperature in the vole room was kept at 0°–+5°C Light conditions corresponded to the natural light rhythm at Kevo

Growth trial with *E. autumnata*

We measured growth of the fourth instar *E autumnata* larvae on leaves of the low elevation site trees The growth trial was conducted in the laboratory at the end of June 1993, i e the second summer after the preference trials with hares and voles Birch leaf quality may have been ameliorated by previous cutting of apical parts of twigs (Danell and Huss-Danell 1985, Haukioja et al 1990) for the preference trials We suppose, however, that the possible increase would have been similar in all trees

On leaves of each tree, we reared 13 larvae individually in 48 ml plastic vials in the laboratory For birch, we used only short shoot leaves (see Suomela and Nilson 1994), willow leaves were of the distal part of the branches We sampled leaves by cutting whole shoots without damaging the leaf lamina. The shoots were sampled haphazardly from 1–2 m height and from all sides of the canopy just prior to the start of the growth trial

On birch, each larva was reared on the two largest leaves of one short shoot, and on willow, on three or four leaves of one individual shoot A 1 cm moistened plaster of paris substrate maintained leaf turgor in the vials

The experiment was started by weighing the just-moulted fourth instar larvae (which had already, however, started to feed), and by placing them into vials with experimental leaves The larvae were allowed to

feed for ca 24 h, after which they were reweighed The starting order and sequence of the larvae on rearing trays was randomized with respect to the trees The temperature in the trial room was 19°C and lights were on constantly, corresponding to the natural light conditions at Kevo during summer

As a measure of leaf quality, we used the relative growth rate of larvae, which was calculated with the equation $\ln(m_e) - \ln(m_b)/time$, in which m_b and m_e are the dry masses of the larvae at the beginning and at the end of the trial, respectively Dry masses were obtained from fresh masses with the equation of Neuvonen and Haukioja (1984)

Statistical analyses

In multiple-choice preference trials, in which different foods are simultaneously offered to an animal, foods for the same animal are not statistically independent from each other (Peterson and Renaud 1989, Roa 1992) Consequently, we analyzed the data with the analysis of variance with repeated measures, which allows for different samples to be dependent (Winer 1971)

The analyses were conducted by using Proc GLM of the SAS statistical software (SAS 1990) In the within-site trials, trees were used as a within-subject factor in the model Site and rank of the trees in the within-site trials, and species and rank of the tree in the among-site trials were used as within-subject factors in the analysis among sites and between tree species, respectively The model included no between-subject factors (Winer 1971)

Mauchly's criterion test (see Potvin et al 1990, von Ende 1993) was performed to test the sphericity assumption of the variance-covariance matrix (in the within-site trials with the hares the test could not be done due to insufficient degrees of freedom) In some trials Mauchly's test indicated that the sphericity condition was not met In those cases we scrutinized also Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) corrected probabilities, which are not as sensitive to violation of the sphericity assumption as probability based on F-test (Potvin et al 1990, von Ende 1993) There were generally no crucial differences between actual p-values and G-G and H-F probabilities Consequently, we in the results present G-G and H-F probabilites only, if they differ essentially from actual p-values

In the E autumnata growth trial, difference between the tree species was analyzed by Kruskal-Wallis test (Proc Nparlway, SAS 1990) and differences among trees and E autumnata broods with a two-way ANOVA (Proc Glm, SAS 1990)

Spearman rank correlation coefficients between twig diameter and palatability to the hares, and between palatabilities to the hares and voles and growth of E

autumnata larvae were obtained by Proc Corr (SAS 1990)

Assumption of normality was verified by evaluating the residuals by Shapiro-Wilk's Test (Proc Univariate, SAS 1990) Homogeneity of variances was tested by Cochran's test (Winer 1971)

Results

Preference trials with hares and voles

Variation among trees within sites
Both hares and voles preferred some trees over others in the within-site trials (Figs 1 and 2) To hares, differences in palatability among birch trees were significant at the high ($F_{5\,15} = 5\,2$, $p = 0\,006$) and low elevation ($F_{5\,15} = 3\,7$, $p = 0\,022$) sites, but non-significant at the middle elevation site ($F_{5\,15} = 0\,76$, ns) To voles, differences in palatability among birches were non-significant ($F_{5\,45} < 2\,1$, $p > 0\,083$ at all sites)

Hares clearly discriminated among willows of the high elevation site ($F_{5\,15} = 11\,75$, $p < 0\,001$), but at the low ($F_{5\,15} = 1\,67$, ns) and middle ($F_{5\,15} = 2\,21$, $p = 0\,107$) elevation sites there were no significant differences in palatability among trees (Fig 2) For voles, on
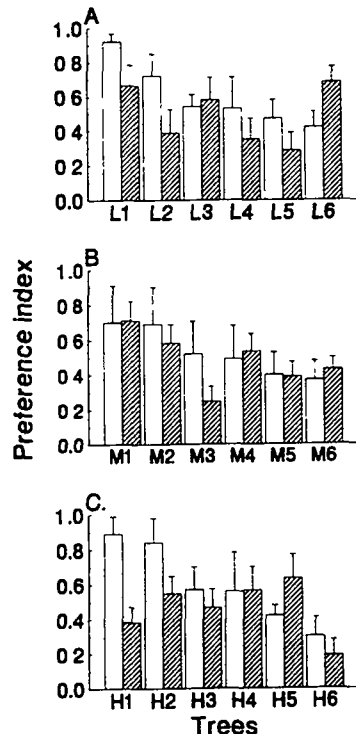

Fig 1 Palatability of birch trees (mean + 1 SE) to hares (open bars) and voles (hatched bars) at the low (A), middle (B) and high elevation (C) sites Trees are ordered and numbered on the basis of their palatability to hares
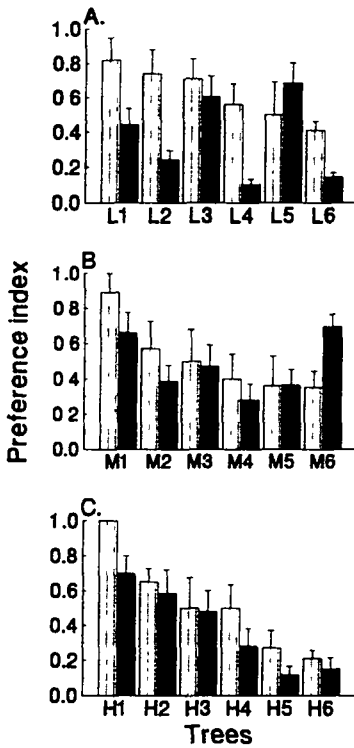
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Fig 2 Palatability of willows (mean +1 SE) to hares (pointed bars) and voles (cross-hatched bars) at the low (A), middle (B) and high elevation (C) sites Trees are ordered and numbered on the basis of their palatability to hares

the other hand, differences in palatability among willows were significant at all sites ($F_{5\,45} = 7\,75$, $p < 0.001$, $F_{5\,45} = 3.10$, $p = 0\,017$; $F_{5\,45} = 5.87$, $p < 0.001$ for low, middle and high sites, respectively)

Willows were generally more variable than birches in their palatability for hares and voles Only for hares in the low site, variation in tree palatability was slightly larger among birches than among willows (Table 1)

Variation among sites
In the among-site trials, we compared the most and the least palatable trees of each of the three sites (based on within-site trials) and used this rank type (two levels) as another factor in the analysis Since the hares and voles partly preferred different trees in the within-site trials, most of the tree individuals tested in the among-site

Table 1 Coefficients of variation (CV) in palatability among birches and willows for hares and voles at the different sites

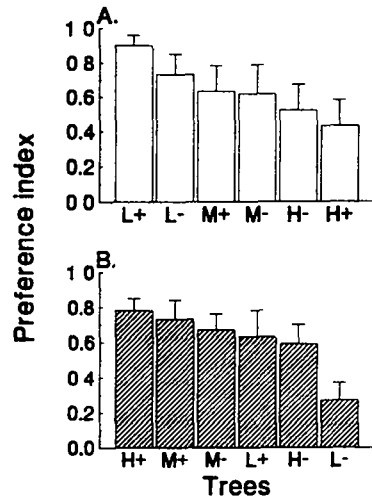| Sites	Birch		Willow	
	Hares	Voles	Hares	Voles
Low site	31 1	34.9	25 3	65 9
Middle site	26 6	33 7	39 9	35 2
High site	38 7	34.7	54 7	61 8

Fig 3 Palatability of birches of different sites (mean +1 SE) to hares (A) and voles (B) L = low, M = middle, H = high elevation sites, + and − are the most and the least palatable trees of the within-site trials (see Fig 1) Trees are ordered on the basis of their palatability

trials (and also in the trials between tree species) were not the same for the hares and the voles

In the birch trial, the hares preferred birches of the low elevation site and consumed the least of the high site trees (Fig 3A), but the difference among sites was not quite significant ($F_{2\,6} = 3\,86$, $p = 0.084$) Voles, on the other hand, preferred birches of the high and middle elevation sites over the low elevation site (Fig 3B, $F_{2,18} = 4\,10$, $p = 0\,034$, Greenhouse-Geisser (G-G) adjusted probability = 0 061, Huynh-Feldt (H-F) adjusted probability = 0 057) The most and least palatable trees of within-site trials mainly preserved their rankings in the among-site trials (Fig 3)

In the willow trial with the hares, there were no significant differences in tree palatability among sites (Fig 4A, $F_{2,6} = 2\,57$, ns) The rankings between the most and the least preferred trees remained constant in the low and middle elevation sites, but the order was reversed between the high site trees (Fig 4A), as indicated by the significant S × R interaction ($F_{2,6} = 12\,37$, $p = 0\,007$)

Voles preferred the most palatable willows of each of the within-site trials over the least preferred trees, the low elevation site trees being the most palatable in both rank types (Fig 4B). Consequently, both the site ($F_{2,18} = 7\,17$, $p = 0\,005$, G-G adjusted probability = 0 014, H-F adjusted probability = 0 011) and the rank type ($F_{1,9} = 67\,4$, $p < 0.001$) had significant effects on palatability of the willows to voles.

Differences between tree species
Of each tree species, we compared the most, intermediate and the least palatable trees of the among-site trials, and used this rank type (three levels) as a factor in the
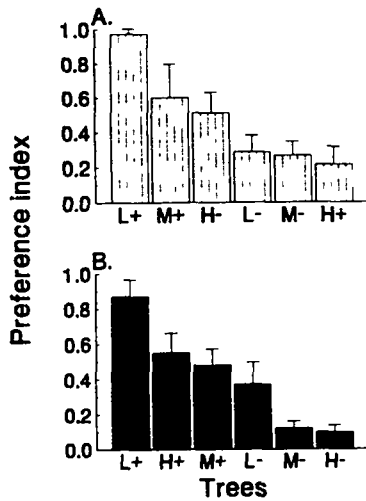
Fig 4 Palatability of willows of different sites (mean + 1 SE) to hares (A) and voles (B) L = low, M = middle, H = high elevation sites, + and − are the most and the least palatable trees of the within-site trials (see Fig 2) Trees are ordered on the basis of their palatability

Fig 6 Relative growth rate of *E autumnata* larvae (mean + 1 SE) on birches (A) and willows (B) of the low elevation site Trees are ordered on the basis of the preference ranking by the hares (see Figs 1A and 2A)

analysis Both hares and voles preferred birches over willows (Fig 5), but with voles, the difference was larger and significant ($F_{1,3} = 2.83$, ns and $F_{1,9} = 169.3$, $p < 0.001$ for hares and voles, respectively) With the hares there was some overlap in palatability between the tree species, since the most preferred willow was slightly more palatable than the least preferred birch (Fig 5A) Trees with different rank types differed in their palatability both to hares ($F_{2,6} = 13.25$, $p = 0.006$) and voles ($F_{2,18} = 14.90$, $p < 0.001$) The interaction between site and rank type was significant in the vole trial ($F_{2,18} = 7.16$, $p = 0.005$), probably since the differ-
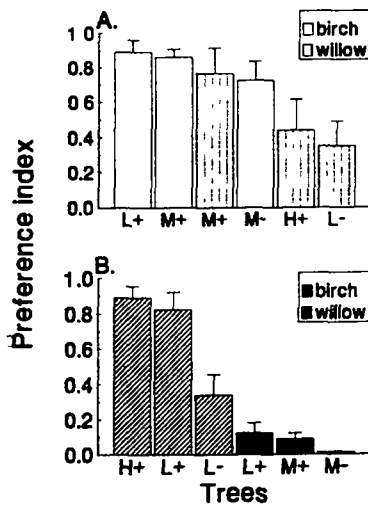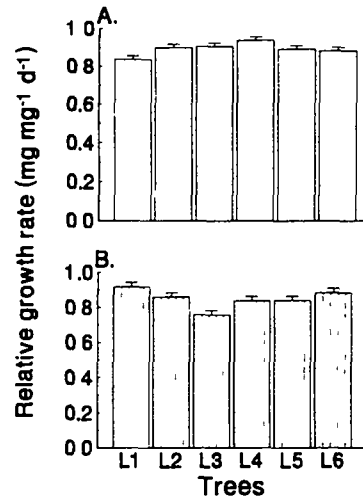
ences between the ranks were unequal between the tree species

Correlations between twig diameter and palatability to hares

Correlation between the basal diameter of twigs and palatability to hares varied depending on the trial There was one significant correlation, namely in the high elevation site birches ($r_s = 0.57$, $p = 0.004$, $n = 24$) In other cases there was no relationship between twig diameter and preference

Growth trial with *E. autumnata*

Growth rates of larvae were slightly higher on birches than on willows (relative growth rates were 0.90 and 0.86 on birch and willow, respectively), although difference between the species was not quite statistically significant (Kruskal-Wallis test $\chi^2 = 3.41$, $DF = 1$, $p = 0.065$) In the species-specific analysis (Fig 6), birch trees did not differ significantly from each other ($F_{5,25} = 2.04$, ns), but willows did ($F_{5,25} = 5.68$, $p < 0.01$)

Tree-specific correlations between herbivore species

Relationships in palatability between hares and voles were first analyzed separately for each site Only in willows of the high elevation site was there a significant positive correlation between hare and vole preferences ($r_s = 0.93$, $p < 0.01$, $n = 6$) In other tests were there no significant relationship between hare and vole preferences, r_s's ranging from −0.09 to 0.60, $n = 6$ in all cases. Since tree number was low in site-specific analyses, we

Fig. 5 Palatability of birch and willow twigs to hares (A) and voles (B) (mean + 1 SE) For tree codes, see Figs 3 and 4 Trees are ordered on the basis of their palatability

also conducted correlation analyses with standardized values of the whole data (Sokal and Rohlf 1981, p 110) There was a significant positive correlation in palatability between hares and voles for willow ($r_s = 0.50$, $p < 0.05$, n = 18) but not for birch ($r_s = 0.28$, $p = 0.27$, n = 18)

Correlations between palatability to hares and growth of *E autumnata* larvae (n = 6 in all cases) were non-significant both for birch ($r_s = -0.03$) and willow ($r_s = 0.20$) Correlations between palatability to voles and larval growth were also non-significant for birch ($r_s = -0.43$) and willow ($r_s = -0.14$)

Discussion

There were large and significant differences in twig palatability to hares and voles between tree species and among conspecific trees within and among sites, but the results varied depending on the tree and animal species Assuming that palatability reflects twig quality (Batzli and Lesieutre 1991), the results imply that there is considerable variation in birch and willow quality for small mammalian herbivores

Differences in twig palatability were largest between tree species Voles clearly preferred birches over willows, but in palatability to hares there was some overlap among birches and willows (Fig 5) The overlap in palatability to hares is not surprising, since birches and willows belong to the most important winter food of the mountain hare (e.g. Lindlof et al 1974b, Aarnio 1983, Pulliainen and Tunkkari 1987) and detoxification of a diet of mixed species is probably easier than that consisting of a single plant species (Pehrson 1981)

According to the within-site trials, variation in tree palatability seemed to be larger among willows than among birches Large variation among willows at the high elevation site (Table 1) shows that there are considerable differences in palatability of tea-leaved willows even within a sex, since willows of the high elevation site were all males (see Materials and methods) Among-tree variation was higher in the willow than in the birch also for growth rates of *E autumnata* larvae

In the among-site trials, voles preferred willows from the low elevation site but the trend was less clear and non-significant, for hares. Birches from the different sites, however, seemed to differ in their palatability to the animal species the hares preferred birches from the low elevation site, whereas to the voles the low-site-birches were among the least palatable Differences in site preferences between hares and voles are difficult to interpret, however, since the trees in the among-site trials were partly different for the animal species

The ranking of different trees by herbivores was quite consistent in successive experiments Trees that were the most or least palatable in the within-site trials maintained their rankings in the among-site trials Only in the among-site trials with hares, was the order of the most and the least palatable trees of the high elevation site reversed (Figs 3A and 4A) In the willow trial, this may partly be due to the fact that we had to use the second-most palatable tree of the high elevation site instead of the most palatable one, since suitable branches of the most preferred tree were exhausted during the within-site trials

Results on palatability of individual trees to hares and voles were equivocal In the correlation analysis with standardized values over all sites, the relationship between palatability to the hares and voles was positive both in willow and birch, but significantly so only in willow In site-specific tests (which suffer from low sample size), however, there was only one significant positive correlation and in the five other tests the correlation coefficient was small ($|r_s| < 0.14$) Thus, the results give some indication that hares and voles may select willows at least partly on the same basis, but for the birch there was no such evidence It is important to note, however, that we offered different parts of branches for the hares and voles, which may also have caused extra variation in the results

In studies with other species, different mammalian herbivores have shown more or less similar preferences on con-specific plant individuals (Dimock et al 1976, Rousi 1983, Hjaltén 1991, Rousi et al 1996) There are almost no studies on tree quality for different types of herbivores (e g mammals vs insects) Rousi et al (1996) found that the same *B pendula* clones were good for both mountain hares and *Polydrosus*–weevils, but noted that the relationship might be significant by chance alone In the present study, there was no correlation between growth of *E autumnata* larvae on birch leaves and palatability of the same trees either to hares or voles Consequently, our results do not suggest that individual birches or willows have general mechanisms of resistance against different herbivores feeding on different plant parts.

Secondary compounds (Bryant and Kuropat 1980, Tahvanainen et al 1985, Marquis and Batzli 1989, Reichardt et al 1990) and nutrients (Angerbjorn and Pehrson 1987, Marquis and Batzli 1989, Hansson 1991) probably affected palatability in our trials, but some morphological factors of the twigs may also have been involved This is especially true for the hare trials Although we tried to use twigs of equal size, there were small differences in the basal diameter of twigs of different trees In one birch trial (high elevation site) there was a significant positive correlation between twig preference and diameter, but in the other birch trials in which the diameter was measured, relationships were negative and non-significant It is thus difficult to estimate whether the correlation at the high elevation site was real or accidental, or whether it was an indication of some other character, e.g. tree growth rate, age or chemical constituents (Palo et al 1992).

The effects of variation in food plant quality on an herbivore depend on the size and moving ability of the animal Food selection of browsing herbivores can be regarded as a patch-use process (Åstrom et al 1990, Danell et al 1991a) Assuming that food plant palatability and quality is also important for food selection in nature, hares should consider trees or plant parts, e g individual branches, as patches, whose quality is compared by the herbivore to other plants Due to high mobility, hares may also profit from differences among sites, and feed mainly on the best sites of their home range We do not know, in general, how large variation is among closely growing trees within sites compared with variation among sites The closer the sites, the less probable it is that genetic or climatic (e g altitude in our study) factors are sources of variation On the other hand, soil properties must surely differ within the home range of an individual hare (e g Robertson et al 1988), which may cause variation in tree quality

Voles have small home ranges (Viitala 1977) compared with hares Thus, for voles, patch selection probably occurs at the level of individual plants or plant parts but site-differences may be important for habitat selection Patch-selection during winter also differs depending upon whether or not the vole forages under the snow cover or above it, since moving is easier on the snow than below it

In conclusion, our results suggest that food plant palatability plays an important role in food selection by mammalian herbivores both between and within tree species Within-species variation in food plant quality may be especially relevant in areas where only one or two food plant species dominate However, food selection by mammalian herbivores in nature is also based on other plant characters besides chemical or nutritive ones (Vivås et al 1991, Edenius 1993), on effects of neighbouring plant species (Atsatt and O'Dowd 1976, McNaughton 1977, Hjaltén et al 1993) and on constraints set by the behaviour and physiology of the herbivore (Belovsky 1984, Belovsky and Schmitz 1991) The results further suggest that the number of replicates, i.e trees, must be large in preference trials This also holds for experiments testing effects of experimental manipulations as for experiments testing differences between trees of different species or geographic origins

References

Aarnio, M 1983 Selection and quality of winter food of the mountain hare in southern Finland – Finn Game Res 41 57–65

Angerbjörn, A and Pehrson, Å 1987 Factors influencing winter food choice by mountain hares (*Lepus timidus* L) on Swedish coastal islands – Can J Zool 65 2163–2167

Åstrom, M, Lundberg, P and Danell, K 1990 Partial prey consumption by browsers trees as patches – J Anim Ecol 59 287- 300

Atsatt, P R and O'Dowd, D J 1976 Plant defence guilds – Science 193 24–29

Batzli, G O and Lesieutre, C 1991 The influence of high quality food on habitat use by arctic microtine rodents – Oikos 60 299–306

Belovsky, G E 1984 Snowshoe hare optimal foraging and its implications for population dynamics - Theor Popul Biol 25 235–264

– and Schmitz, O J 1991 Mammalian herbivore optimal foraging and the role of plant defenses – In Palo, R T and Robbins, C T (eds), Plant defenses against mammalian herbivory CRC Press, pp 1–28

Bryant, J P 1981 Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees – Science 213 889–890

- 1987 Feltleaf willow-snowshoe hare interactions plant carbon/nutrient balance and floodplain succession – Ecology 68 1319–1327

– and Kuropat, P J 1980 Selection of winter forage by subarctic browsing vertebrates The role of plant chemistry – Annu Rev Ecol Syst 11 261–285

– , Chapin, F S III and Klein, D R 1983 Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory – Oikos 40 357–368

– , Chapin, F S III, Reichardt, P B and Clausen, T P 1987 Response of winter chemical defence in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance – Oecologia 72 510–514

– , Kuropat, P J, Reichardt, P B and Clausen, T P 1991 Controls over the allocation of resources by woody plants to chemical antiherbivore defense - In Palo, R T and Robbins, C T (eds), Plant defenses against mammalian herbivory CRC Press, pp 83–102

Danell, K and Huss-Danell, K 1985 Feeding by insects and hares on birches earlier affected by moose browsing – Oikos 44 75–81

– , Elmqvist, T, Ericson, L and Salomonson, A 1985 Sexuality in willows and preference by bark-eating voles defence or not? – Oikos 44 82–90

– , Elmqvist, T, Ericson, L and Salomonson, A 1987 Are there general patterns in bark-eating by voles on different shoot types from woody plants? – Oikos 50 396–402

– , Edenius, L and Lundberg, P 1991a Herbivory and tree stand composition moose patch use in winter – Ecology 72 1350–1357

– , Hjaltén, J, Ericson, L and Elmqvist, T 1991b Vole feeding on male and female willow shoots along a gradient of plant productivity – Oikos 62 145–152

Dimock, E J II, Silen, R R and Allen, V E 1976 Genetic resistance in douglas-fir to damage by snowshoe hare and black-tailed deer – For Sci 22 106–121

Edenius, L 1993 Browsing by moose on Scots pine in relation to plant resource availability – Ecology 74 2261–2269

Hansson, L 1985 *Clethrionomys* food generic, specific and regional characteristics – Ann Zool Fennici 22 315–318

- 1991 Bark consumption by voles in relation to mineral contents – J Chem Ecol 17 735–743

Hartley, S E, Nelson, K and Gorman, M 1995 The effect of fertiliser and shading on plant chemical composition and palatability to Orkney voles, *Microtus arvalis orcadensis* – Oikos 72 79–87

Haukioja, E , Neuvonen, S , Hanhimäki, S and Niemelä, P
1988 The autumnal moth *Epirrita autumnata* in
Fennoscandia – In Berryman, A A (ed), Dynamics of
forest insect populations patterns, causes, and manage-
ment strategies Plenum, pp 163–178

– , Ruohomäki, K , Senn, J , Suomela, J and Walls, M
1990 Consequences of herbivory in the mountain birch
(*Betula pubescens* ssp *tortuosa*) importance of the func-
tional organization of the tree – Oecologia 82 238–247

Hjalten, J 1991 Food selection by small mammalian herbi-
vores and its impact on plant populations – Ph D -thesis,
Swedish Univ Agricult Sci , Sweden

– , Danell, K and Lundberg, P 1993 Herbivore avoidance
by association vole and hare utilization of woody plants
– Oikos 68 125–131

Kalela, O 1957 Regulation of the reproduction rate in sub-
arctic populations of the vole *Clethrionomys rufocanus*
(Sund) – Ann Acad Sci Fenn (A IV) 34 1–60

Krebs, C J 1989 Ecological methodology – Harper and
Row

Lindlöf, B , Lindström, E and Pehrson, Å 1974a Nutrient
content in relation to food preferred by mountain hare –
J Wildl Manage 38 875–879

– , Lindström, E and Pehrson, Å 1974b On activity, habi-
tat selection and diet of the mountain hare (*Lepus timidus*
L) in winter – Viltrevy 9 27–43

Linhart, Y B 1991 Disease, parasitism and herbivory multi-
dimensional challenges in plant evolution – Trends Ecol
Evol 6 392–396

Marquis, R J and Batzli, G O 1989 Influence of chemical
factors on palatability of forage to voles – J Mamm 70
503–511

McNaughton, S J 1977 Serengeti ungulates feeding selectiv-
ity influences the effectiveness of plant defense guilds –
Science 199 806–807

Molvar, E M , Bowyer, R T and Van Ballenberghe, V 1993
Moose herbivory, browse quality, and nutrient cycling in
an Alaskan treeline community – Oecologia 94 472–479

Neuvonen, S and Haukioja, E 1984 Low nutritive quality as
defence against herbivores induced responses in birch –
Oecologia 63 71–74

– , Haukioja, E and Molarius, A 1987 Delayed inducible
resistance against a leaf-chewing insect in four deciduous
tree species – Oecologia 74 363–369

Niemelä, P , Hagman, M and Lehtilä, K 1989 Relationship
between *Pinus sylvestris* L origin and browsing preference
by moose in Finland – Scand J For Res 4 239–246

Palo, R T , Bergström, R and Danell, K 1992 Digestibility,
distribution of phenols, and fiber at different twig diame-
ters of birch in winter Implication for browsers – Oikos
65 450–454

Pehrson, Å 1981 Winter food consumption and digestibility
in caged mountain hares – In Myers, K and MacInnes,
C D (eds), Proc world lagomorph conf , Guelph, On-
tario, pp 732–742

Peterson, C H and Renaud, P E 1989 Analysis of feeding
preference experiments – Oecologia 80 82–86

Potvin, C , Lechowicz, M. and Tardif, S 1990 The statistical
analysis of ecophysiological response curves obtained from

experiments involving repeated measures – Ecology 71
1389–1400

Pulliainen, E and Tunkkari, P S 1987 Winter diet, habitat
selection and fluctuation of a mountain hare *Lepus timidus*
population in Finnish Forest Lapland – Holarct Ecol 10
261–267

Reichardt, P B , Bryant, J P , Mattes, B R , Clausen, T P ,
Chapin, F S III and Meyer, M 1990 Winter chemical
defense of Alaskan balsam poplar against snowshoe hares
– J Chem Ecol 16 1941–1959

Roa, R 1992 Design and analysis of multiple-choice feeding-
preference experiments – Oecologia 89 509–515

Robertson, G P , Huston, M A , Evans, F C and Tiedje, J
M 1988 Spatial variability in a successional plant commu-
nity patterns of nitrogen availability – Ecology 69 1517–
1524

Rousi, M 1983 Susceptibility of pine to mammalian herbi-
vores in northern Finland – Silva Fenn 17 301–312

– , Tahvanainen, J and Uotila, I 1989 Inter- and intraspe-
cific variation in the resistance of winter-dormant birch
(*Betula* spp) against browsing by the mountain hare –
Holarct Ecol 12 187–192

– , Tahvanainen, J and Uotila, I 1991 A mechanism of
resistance to hare browsing in winter-dormant European
white birch (*Betula pendula*). – Am Nat 137 64–82

– , Tahvanainen, J , Henttonen, H and Uotila, I 1993
Effects of shading and fertilization on resistance of winter-
dormant birch (*Betula pendula*) to voles and hares –
Ecology 74 30–38

– , Tahvanainen, J , Henttonen, H , Herms, D A and
Uotila, I 1996 Clonal variation in susceptibility of white
birches (*Betula* ssp) to mammalian and insect herbivores
– For Sci in press

SAS 1990 SAS user's guide statistics, Ver 5 – SAS Inst ,
Cary, North Carolina

Snyder, M A 1992 Selective herbivory by Abert's squirrel
mediated by chemical variability in Ponderosa pine –
Ecology 73 1730–1741

Sokal, R R and Rohlf, F J 1981 Biometry – Freeman

Suomela, J and Nilson, A 1994 Within-tree and among-tree
variation in growth of *Epirrita autumnata* on mountain
birch leaves – Ecol Entomol 19 45–56

Tahvanainen, J , Helle, E , Julkunen-Tiitto, R and Lavola, A
1985 Phenolic compounds of willow bark as deterrents
against feeding by mountain hare – Oecologia 65 319–
323

Viitala, J 1977 Social organization in cyclic subarctic popula-
tions of the voles *Clethrionomys rufocanus* (Sund) and
Microtus agrestis (L) – Ann Zool Fennici 14 53–93

Vivås, H J , Saether, B E and Andersen, R 1991 Optimal
twig-size selection of a generalist herbivore – the moose
Alces alces implications for plant – herbivore interactions
– J Anim Ecol 60 395–408

von Ende, C N 1993 Repeated-measures analysis growth
and other time-dependent measures – In Scheiner, S M.
and Gurevitch, J (eds), Design and analysis of ecological
experiments Chapman and Hall, pp 113–137

Winer, B J 1971 Statistical principles in experimental design
– McGraw-Hill