

Availability and quality of herbivore winter browse in relation to tree height and snow depth

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The vertical distribution of biomass, nutrients, and concentrations of secondary defence compounds in the current annual growth of the main winter forage trees (birch and willows) of herbivores was studied in the mountain range of northern Scandinavia. In addition, forage availability in relation to snow accumulation was studied throughout winter. The quantity and quality of forage improved with the height of the trees, i.e. biomass and nitrogen concentrations increased, and fibre decreased. The concentration of defensive compounds increased with height for willow, but decreased for birch. Shoots of willow were of better quality than of birch. The negative effect of the higher levels of total defensive compounds in birch may to some extent be balanced by their higher nutrient content and total forage biomass as compared with that of willow, however willow had more available biomass within the heights browsed by herbivores. Although snow accumulation had significant effects on forage availability, the effects within the entire height range browsed by herbivores were small.

Introduction

For herbivores in boreal areas, winter is the period when food resources are at their lowest availability. The reduction in available forage caused by snow accumulation and the subsequent decrease in food intake is potentially one of the most important mechanisms affecting these animals during the winter season (Hovey & Harestad 1992, Klein 1995, Larter & Gates 1995, Loison *et al.* 1999, Ball *et al.* 2001). The availability and quality of forage are considered as the main factors governing herbivore feeding

patterns within landscapes, as well as in selection among individual plants and individual plant parts (Bergström & Danell, 1987, Palo *et al.* 1992, Suomela *et al.* 1995, Hóðar & Palo 1997, Ball *et al.* 2000). One of the critical aspects of snow accumulation is how it reduces accessibility of forage at the lower levels of the trees, but if the snow supports the weight of the herbivores, it also allows them to reach browse previously out of reach. Variations in forage quantity and quality with height within a tree may thus be particularly important during the winter season, due to the changes in forage availability caused by snow.

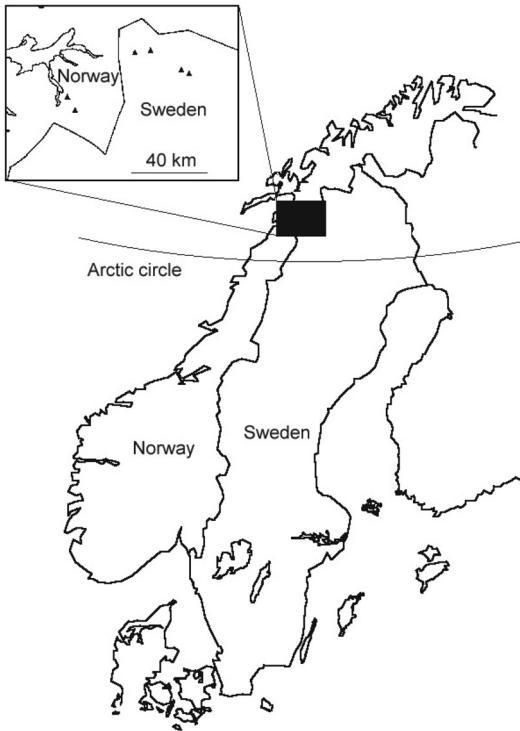


Fig. 1. Study area where food availability, quality and quantity was assessed during late winter 1999. Points depict the sampling localities.

Many previous studies have considered forage quality within a tree and among trees with respect to invertebrates (Suomela & Ayres 1994, Sumeola *et al.* 1995, Laitinen *et al.* 2000, Tenow & Bylund 2000, Kaitaniemi & Ruohomäki 2001). However, although Wollnough *et al.* (2001) provides an African example, scientific studies considering the vertical aspect of forage quality with respect to the mammalian herbivore community are rare, especially regarding the quality of the forage eaten by herbivores that are active throughout the winter season (Bergström & Danell 1987).

In the mountainous areas of northern Scandinavia, the community of winter browsing herbivores consists of moose (*Alces alces* L.), mountain hare (*Lepus timidus* L.), willow grouse (*Lagopus lagopus* L.), and small rodents (*Microtus* spp., *Clethrionomys* spp. and *Lemmus lemmus*). Despite differences among these herbivore species in their physiology and feeding behaviour, they respond to the same plant quality factors

(Hóðar & Palo 1997). However, the effects of food burial by snow and any vertical patterns in quality or availability may affect the members of the winter browsing community differentially, as the herbivores have to choose among the foods within their reach: voles feed close to the ground (Johannessen & Mauritzen 1999), mountain hare and willow grouse on the twigs below one metre (Iar & Andersen 2001), and moose up to three metres above ground (Borkowska & Konopko 1994). The dominant winter forage for these browsers is the annual shoots ("shoots" hereafter) of deciduous trees (Bryant & Kuropat 1980, Lundberg *et al.* 1990, Tahvanainen *et al.* 1991, Shipley *et al.* 1998), mainly birch *Betula pubescens* Ehrh. and willow *Salix* spp., predominantly *S. myrsinifolia* and *S. phyllifolia* L.

Following up the suggestions of Bergström and Danell (1987), we examine vertical trends in browse for vertebrate herbivores in winter. First, we consider vertical trends in the quantity and quality of browse within trees. Second, we consider if burial by snow significantly reduces availability at the lower levels of a tree by covering browse. Finally, we briefly consider how browse availability might differ if climate changes lead to the accumulation of more snow hard enough to support herbivores and thus enable them to reach browse formerly unavailable.

Material and methods

Study area

The study was performed in northwestern Scandinavia, and three locations were used: Abisko (68°21'N, 18°49'E), Vassijaure (68°26'N, 18°17'E), and Skjomedal (68°14'N, 17°25'E) (Fig. 1). The area is characterised by a steep climatic gradient with large differences in temperature and precipitation (Alexandersson *et al.* 1991, Aune 1993, Bjørnbæk 1993, Forland 1993; Table 1). The most continental eastern location at Abisko is situated in a local precipitation shadow with low annual precipitation, while the precipitation at the western Vassijaure and Skjomedal locations is about twice as high (Table 1). In all locations, the ground is generally covered by snow from October to May.

The mountainous study area is intersected by a number of forested valleys. The treeline is at 700–800 m a.s.l. in the east and at 550–600 m a.s.l. in the west. The surrounding mountain summits reach 1000 to 1700 m a.s.l. The valleys around Abisko and Vassijaure are dominated by birch in dry to mesic areas, and willow in moist areas. Additionally, aspen *Populus tremula* L., rowan *Sorbus aucuparia* L., and pine *Pinus sylvestris* L. occurs as scattered individuals or stands. In the Skjomedal study area, the forest is dominated by pine, mixed with birch, aspen, and rowan in mesic areas, and by willows in moist areas. During the growing season, the Abisko and Vassijaure locations are used as grazing grounds for reindeer *Rangifer tarandus*, whereas the Skjomedal location is occasionally used for livestock grazing.

Study design and sampling

Three study locations were used to reflect the climatic gradient ranging from the mountains in the east to the valleys close to the Atlantic coast in the west. The distance between the two farthest locations was 66 km (Fig. 1). Within each of the three locations, two triangular study sites (with one km sides) were selected within the forested parts of the valleys for sample collection.

The vertical distribution of shoot biomass and quality (assessed as the concentrations of nitrogen, total non-tannin phenols, tannins, and fibre) within trees were determined for the Abisko and Vassijaure locations. Six trees of birch and willow were randomly selected in order to reflect the trees available within the areas. The trees were cut at ground level within each of the four sampling triangles between November 1997 and February 1998, and brought to the laboratory. In total, 24 birch and 23 willow trees were used (one willow was lost). Each tree was stratified into 25-cm height zones from ground level up to maximum tree height. Within each height zone all annual shoots were harvested and held separately for each zone and individual tree. In order to avoid confounding the current annual growth with previous years, we report only the current annual growth here, up to the limit in bite diameter of the largest herbivore, the moose (3.2 mm

Table 1. Site characteristics and type of data collected at each site. Mean annual temperature (°C) and precipitation data (mm) for Abisko and Vassijaure refer to the period 1971–2000. Precipitation data for Skjomedal refer to the period 1987–2000, and temperature data to 1971–1994. Distance to used meteorological station (cf. study area) is given in km. Mean snow depth (cm) is given by the mean height position of *Parmelia olivacea* on birch stems (Sonesson *et al.* 1994). B = forage biomass. Q = forage quality. S = forage availability in relation to snow depth. Climate data given in Table 1 are from the Abisko meteorological station, Katterjåkk meteorological station (for Vassijaure), and from the Skjomen-Stiberg (precipitation), and Skjomen-Slettdal (temperature) stations for Skjomedal.

Study site	Coordinates	Elevation (m a.s.l.)	Distance to met. station (km)	Snow depth (cm)	Annual temp. (°C)	Annual precip. (mm)	Dominating tree species	Type of data		
								B	Q	S
Abisko 1	68°21'N 18°53'E	460	3.5	66	−0.5	320	<i>B. pubescens</i>	x	x	x
Abisko 2	68°19'N 18°59'E	640	8.5	140	−0.5	320	<i>B. pubescens</i>	x	x	x
Vassijaure 1	68°24'N 18°29'E	420	13.0	140	−1.4	859	<i>B. pubescens</i>	x	x	x
Vassijaure 2	68°24'N 18°18'E	520	5.5	180	−1.4	859	<i>B. pubescens</i>	x	x	x
Skjomedal 1	68°14'N 17°26'E	40	2 & 5	53	4.3	751	<i>P. sylvestris</i>			x
Skjomedal 2	68°11'N 17°34'E	120	8.5 & 15.5	55	4.3	751	<i>P. sylvestris</i>			x

for birch and 3.1 mm for willow, estimated by a pilot study in which we measured 400 browsed twigs of each species). This size thus also covers the diameters at browsing point of the smaller herbivores (Hóðar & Palo 1997). The height of sampled trees ranged from 391 to 727 cm for birch, and 152 to 442 cm for willows. The sampled shoots were oven dried at 70 °C, weighed to the nearest 0.01 g, and ground to pass through a 0.5 mm sieve.

The effect of snow accumulation on forage availability was studied at all three locations. At each of the triangular study sites, six birch and six willow trees were selected to monitor the effect of snow accumulation on forage availability. The sample trees were selected by restricted randomization along the sides of the triangles such that trees were never closer to each other than 110 m. In total, 36 birch and 36 willow trees were used, ranging in height from 175 to 804 cm for birch, and 110 to 604 cm for willow. The trees were stratified into 25 cm height zones from the ground up to 300 cm. In each of the height zones, six shoots were marked with colour-coded tags, so that every tagged shoot could be related to a specific height zone. In total 1373 birch shoots and 598 willow shoots were tagged. The position of all tagged shoots was re-determined after every snowfall of more than five cm during the winter 1997–1998. During each visit, snow depth, number of visible strips, and the vertical displacement of shoots due to snow load was recorded. Shoots lost due to removal by browsing or loss of tags were excluded from further analysis, but this was rare.

Chemical analyses and their relevance

One of the most important nutrients for herbivores is nitrogen (N) (Albon & Langvatn 1992, Hanley *et al.* 1992, Cook *et al.* 1996), and a continuous supply of dietary nitrogen must be available to maintain a large number of body functions, such as growth, reproduction and lactation (White 1993). Nitrogen is generally positively correlated with energy and digestibility (Church & Fontenot 1979, Palo *et al.* 1985, Palo *et al.* 1992, Staaland *et al.* 1992), and may also affect the level of secondary compounds in

woody browse by affecting the carbon nutrient balance (Hakulinen 1998). Both nitrogen and phenols accumulate in apical parts of winter dormant twigs (Rousi *et al.* 1991), where they may defend against browsing. Nitrogen content was analysed using the Kjeldahl digestion method (Persson 1995) followed by flow injection analysis (EnviroFlow 5012 System, Foss Tecator AB, Höganäs, Sweden).

The concentrations of fibre and secondary defence compounds (phenols and tannins) can sometimes be crucial to forage quality through their digestibility-reducing properties (Palo & Robbins 1991, Hjältén & Palo 1992, Danell *et al.* 1994, Harborne 1994, Allen 1996, Palo *et al.* 1997, McSweeney *et al.* 2001). Total non-tannin phenols were analysed using the Folin-Ciocalteu reagent method, which is superior in many aspects to other common methods (Waterman & Mole 1994, Shofield *et al.* 2001). The protein precipitation capacity of tannins were analysed using a protein precipitating (BSA) procedure, to mimic the protein binding processes occurring *in vivo* (Asquith & Butler 1985, Waterman & Mole 1994, Shofield *et al.* 2001). Although some previous studies have utilised analyses which include tannins in the total phenols, we used a modified procedure to allow us to differentiate them to a large extent. Because tannins bind strongly to proteins at low pH (*see* Barry & Blaney 1987), the pH during the tannin analyses was kept at 5, whereas an alkaline solution was used during the analysis of non-tannin phenols (Waterman & Mole 1994).

The composition of phenols is known to vary between the two studied willow species, but in our study area, *S. myrsinifolia* and *S. phylicifolia* hybridise frequently and the hybrids are very difficult to differentiate from the parental species in the field. We therefore took the conservative approach of analysing total non-tannin phenols only, rather than risk mis-identifying the parent species and the hybrids.

Fibre content was analysed on a subset of the shoot samples using acid detergent fibre (ADF) extraction according to the methods described by Mould and Robbins (1981), modified to suit glass filter tubes. A near infrared spectrophotometer (NIR System Process Analytics 6500) was then used to interpolate the results of fibre analy-

sis to the total sample set (Foley *et al.* 1998). In this study, we did not consider the concentration of terpenes, minerals, or carbohydrates, as many previous studies indicate that information about nitrogen, fibre and defence compounds are often sufficient to capture the most important information regarding forage quality (Palo & Robbins 1991, Albon & Langvatn 1992, Hanley *et al.* 1992, Hjältén & Palo 1992, Danell *et al.* 1994, Harborne 1994, Allen 1996, Cook *et al.* 1996, Palo *et al.* 1997, González-Hernández *et al.* 2000).

Statistical analyses

Residual analyses (Tabachnick & Fidell 2001) were used to test that the assumptions of parametric tests were met. The disappearance rate of shoots in relation to snow depth, as well as the variation in quantity and quality with height within trees, was analysed by Pearson correlation analysis. Differences among locations and species was analysed by a general linear model in using the software packages SAS (SAS Institute Inc. 1998), and JMP (SAS Institute Inc. 2000).

Results

Quantity and quality of forage

The quantity and quality of forage varied with height within the trees. For both birch and willow, shoot biomass increased with increasing height ($r_{504} = 0.57$ and $r_{266} = 0.49$ for birch and willow respectively, $p < 0.01$, Fig. 2). 27% and 87% of the total shoot biomass of birch and willow, respectively, was found within currently-available browse height (i.e. from ground level up to three metres) of the largest winter active herbivore, the moose (Fig. 2). When extending our analysis to four m from ground level (the height to which moose would potentially be able to reach when standing on top of additional compacted snow), 56% and 98% of the birch and willow browse, respectively, would be found within this height.

For both forage species, the concentration of nitrogen increased with height ($r_{304} = 0.35$ and

$r_{125} = 0.30$ for birch and willow, respectively, $p < 0.01$, Fig. 2), and fibre decreased ($r_{246} = -0.30$ and $r_{107} = -0.52$, $p < 0.01$, Fig. 2). The concentration of non-tannin phenols increased with height in willow ($r_{125} = 0.29$, $p < 0.01$, Fig. 2) but showed no significant association with height in birch (Fig. 2). For tannins, the only shown change was a slight decrease for birch ($r_{315} = -0.16$, $p < 0.01$, Fig. 2). When comparing overall forage quality between the two species, birch had more biomass, and higher concentrations of nitrogen, non-tannin phenols, and tannins than willow, but less fibre ($p = 0.04$ for non-tannin phenols, and $p < 0.01$ for all other variables, Fig. 2 and Table 2). However, willow contained more biomass than birch within the browse height of herbivores.

Snow and forage availability

Within individual trees, forage availability (measured by the disappearance rate of twigs) was negatively correlated with snow depth for both birch and willow ($r_{666} = -0.51$, $p < 0.01$ for birch, $r_{326} = 0.52$, $p < 0.01$ for willow, Fig. 3, Table 3). However, when calculating forage availability as biomass for entire trees, rather than as percentage of available tagged twigs only, the relationship with snow depth was not significant ($r_{656} = -0.06$ and $r_{336} = -0.02$, $p > 0.31$, Fig. 3). Analyses of the vertical displacement of shoots showed that only 3.9% of the birch shoots, and 0.04% of the willow shoots changed in height from the ground due to sagging from snow (range 25 to 175 cm from their original level). Of the 72 tagged trees, 13 willow and 2 birch trees were completely buried by snow on at least one occasion during the winter.

The accumulated snow depth differed greatly among the study sites. The maximum snow depth ranged from 46 to 240 cm (Table 3), with the deepest snow cover at the Vassijaure locations, followed by Abisko and Skjomedal ($p < 0.01$). Consequently, forage availability differed among locations according to snow depth. Most forage was available at the Skjomedal locations (with the least snow), as compared with the Abisko and Vassijaure locations ($p < 0.01$, Table 3).

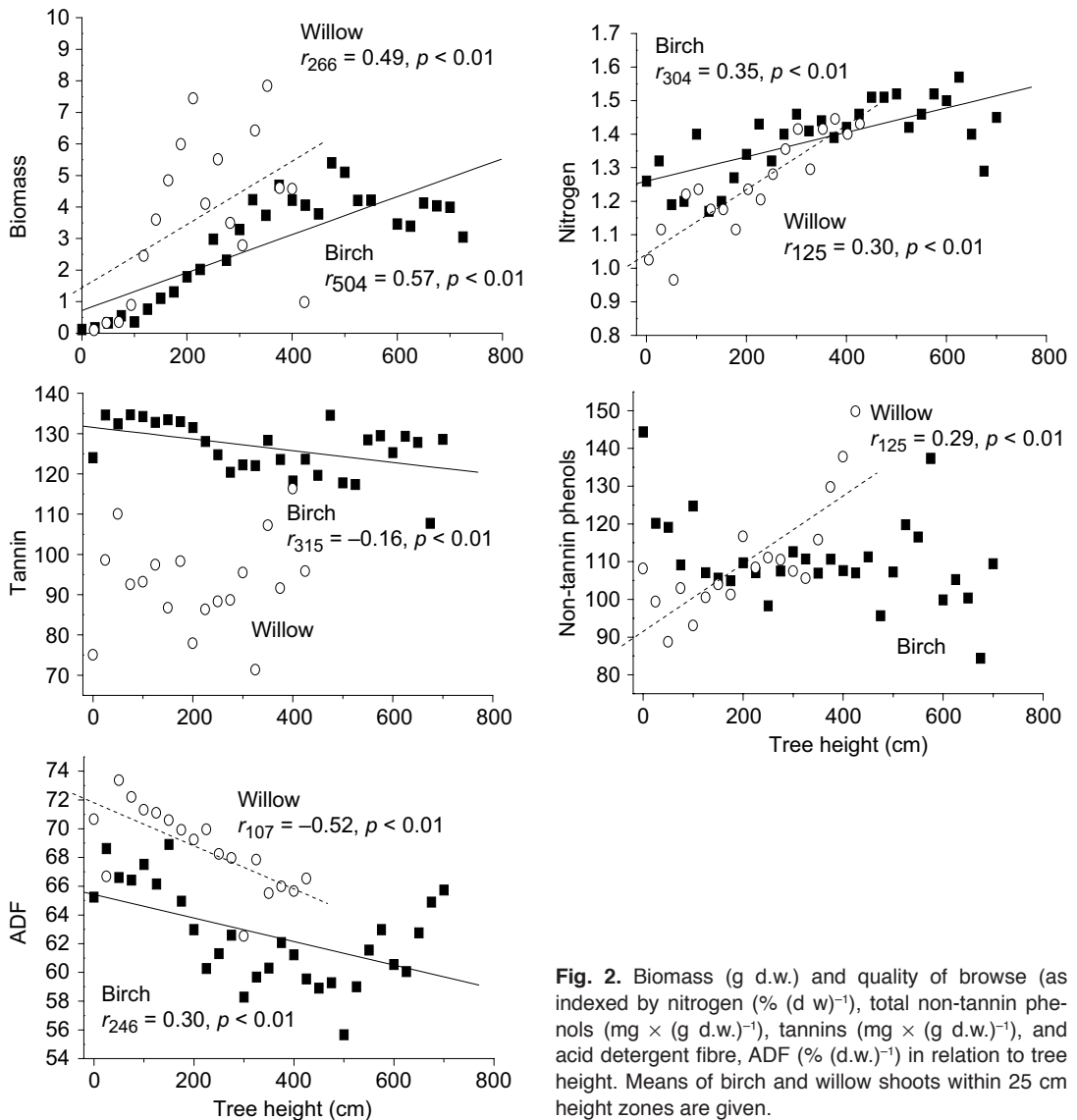


Fig. 2. Biomass (g d.w.) and quality of browse (as indexed by nitrogen (% d.w.⁻¹), total non-tannin phenols (mg × (g d.w.)⁻¹), tannins (mg × (g d.w.)⁻¹), and acid detergent fibre, ADF (% d.w.)⁻¹) in relation to tree height. Means of birch and willow shoots within 25 cm height zones are given.

Discussion

Although snow accumulation did affect forage availability, the total effect was small as most of the forage was found above the mean snow depths, and still within the reach of herbivores. There was a clear difference in forage availability between locations, as the sites with the least snow also had most available forage throughout winter.

Shoots of birch and willow species showed the same pattern in forage quality, although non-

tannin phenols increased with height in willow. Variation with height may thus differentially affect herbivore species, depending on how high they can browse. Generally, digestibility is positively correlated with the amount of nitrogen and negatively correlated with fibre and defence compounds (Palo & Robbins 1991, Tahvanainen *et al.* 1991, Hjältén & Palo 1992, Danell *et al.* 1994, Harborne 1994, Allen 1996, Palo *et al.* 1997). Note however, that phenols and tannins have multiple functions and defence against vertebrate herbivores is only one function. We

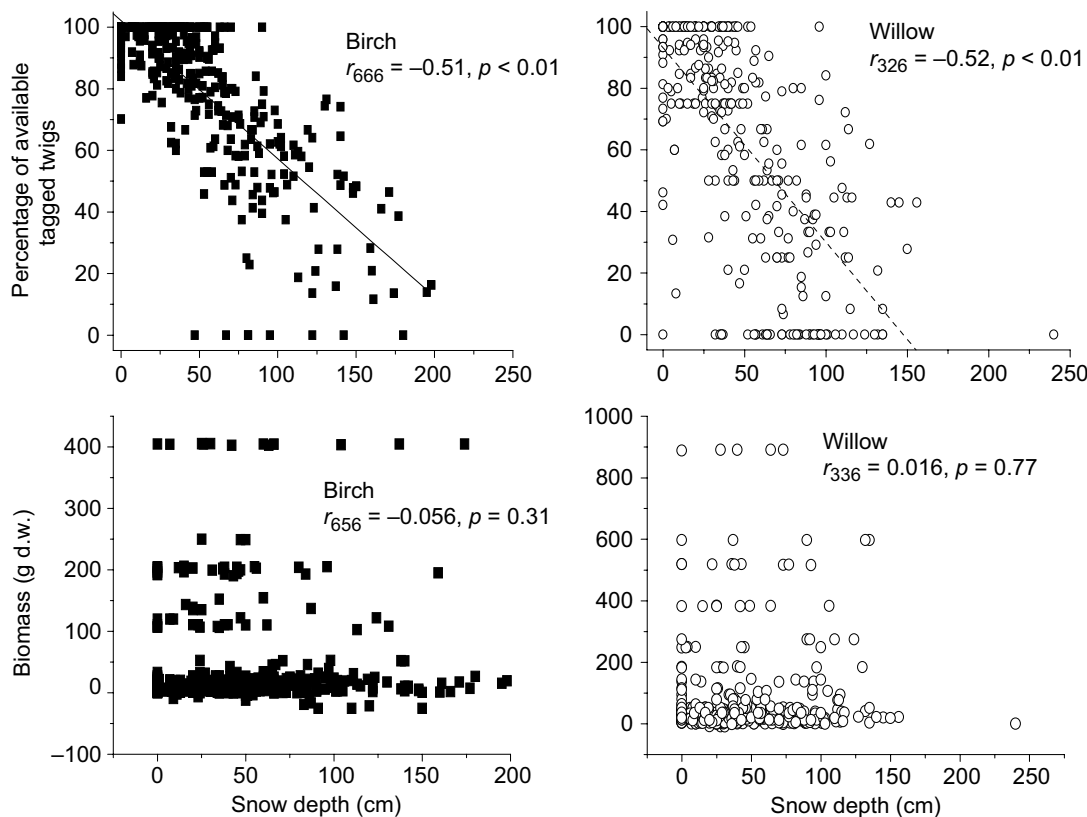


Fig. 3. Availability of birch and willow forage in relation to snow depth. Forage availability is given as percentage of tagged twigs per tree, and as biomass of entire trees, for all observation occasions during winter.

do not suggest that the pattern of non-tannin phenols and tannins we observed with tree height are necessarily the result of vertebrate herbivory: our perspective is that, given these patterns, we consider how they may affect feeding conditions for mammalian herbivores. Furthermore, phenols may not always be correlated with digestibility in twigs because of the ratio of bark to wood, and

Table 2. Biomass and quality of birch and willow shoots. Number of trees used in the analyses, $n = 6$ for all, except for willow where $n = 5$ for Abisko 1). All values are given as means for each location calculated from the means of individual trees within that location (gdw = grams dry weight).

	Biomass (g)	N (mmol \times (g d.w.) ⁻¹)	Non-tannin phenols (mg \times (g d.w.) ⁻¹)	Tannins (mg \times (g d.w.) ⁻¹)	ADF (% (d.w.) ⁻¹)
Birch					
Abisko 1	54.42	0.93	110.96	135.72	63.85
Abisko 2	84.09	0.97	98.26	121.16	65.34
Vassijaure 1	33.39	1.02	118.66	124.86	56.29
Vassijaure 2	38.44	1.08	110.34	123.33	62.14
Willow					
Abisko 1	22.49	0.74	84.31	98.92	71.36
Abisko 2	73.49	0.78	105.16	79.06	69.74
Vassijaure 1	22.08	0.75	114.14	105.61	69.63
Vassijaure 2	35.31	0.83	107.06	85.74	68.25

the different concentrations of many components in these two fractions (Palo *et al.* 1992).

We found a 28% increase in nitrogen with height within trees (Fig. 2), which is probably substantial from a herbivore's perspective. Ball *et al.* (2000), reported a change in the choice of feeding sites made by moose and other browsers in a field experiment in which the nitrogen content of pine browse was changed only from 1% to 1.5%, suggesting that nitrogen (or a correlated factor) may be important in the choice of forage. Because our analysis also revealed that fibre content decreased with height, our analysis thus suggests that the best forage is found at the top of birch trees, and (depending on the effects of the specific phenols on digestion) at the middle to top levels of willow (Fig. 3).

Comparing the two browse species, our analysis suggests that willow was in general of higher quality than birch. As willow are the preferred species of most northern herbivores (Lundberg *et al.* 1990, Shipley *et al.* 1998), our results regarding the inter-specific differences in quality are in accordance with the hypothesis that herbivores prefer the species with lower concentrations of secondary defence compounds and fibre (Chapin *et al.* 1985, Rousi *et al.* 1991),

and that nitrogen may be of lesser importance in the choice of browse species during winter (Hjältén & Palo 1992, Palo *et al.* 1997, Shipley *et al.* 1998). However, when choosing among trees within the same species, herbivores have been noted to select the trees with the higher nitrogen content (Ball *et al.* 2000).

Herbivores in general, and moose in particular, are negatively affected by the concentrations of secondary defence compounds and fibre in their forage (Palo *et al.* 1992, White 1993), but this does not entirely explain diet selection (Tahvanainen *et al.* 1985). The herbivores inhabiting our study area are subject to the same plant defences and nutrients, but they may be unequally important for different herbivore species. The variations in forage quality and quantity with tree height may thus affect herbivore species differently, both due to differences in their tolerances to the different compounds, and their consumption of forage at different heights of the trees.

When considering the vertical variations in food quality, the smaller herbivores (willow grouse and rodents) feed to a large extent on small buds and thin twigs at the lower levels of the trees, where the quality of the forage is lower as compared with the shoots consumed by the larger herbivores feeding higher up in the trees. Willow grouse and rodents may thus be more positively affected than the other herbivores by increases in snow depth during winter which allows them to reach higher quality foods by standing on the snow, if it supports them. Furthermore, during late winter and early spring, willow grouse also forage on birch buds at the top of the trees. As small mammals may be able to deal more effectively with specific secondary metabolites than larger mammals (Freeland 1991), voles might be able to better tolerate several types of plant metabolites as compared with mountain hare and moose (Hjältén & Palo 1992). For willow grouse, little is known about their metabolic processes (Foley & Cork 1992), but other game birds are known to tolerate a low quality diet with high concentrations of chemical defence compounds (Pendergast & Boag 1971, Moss 1973, Spidsø & Korsmo 1994). The two larger herbivores, mountain hare and moose, are perhaps most affected by forage quality as

Table 3. Maximum snow depth (cm), and shoot availability at the study sites. Number of trees used in the analyses ($n = 6$ for all) are given along with number of observations during the winter 1997–1998. Available forage is given as the minimum % of the tagged shoots that was available during winter.

	No. of observ.	Max snow depth (mm)	Forage availability
Birch			
Abisko 1	12	110	65
Abisko 2	9	160	46
Vassijaure 1	13	198	33
Vassijaure 2	14	180	37
Skjomedal 1	5	45	94
Skjomedal 2	5	59	87
Willow			
Abisko 1	12	103	18
Abisko 2	9	240	14
Vassijaure 1	13	135	9
Vassijaure 2	14	156	10
Skjomedal 1	5	46	83
Skjomedal 2	5	64	83

compared with the other herbivores considered in this study (Pehrson 1981, Tahvanainen *et al.* 1985, White 1993, Palo *et al.* 1997). However, both mountain hare and moose are able to choose forage from a wider height range than the smaller herbivores, so hares, and moose in particular, may be less sensitive to changes in forage quality with height within trees as compared with the smaller herbivore species. Overall, our analyses support Bergström and Danell (1987) regarding the variation in browse quality with tree height for vertebrate herbivores, and we suggest that future studies (particularly regarding winter ecology) should not overlook this aspect.

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