R. Van der Wal · N. Madan · S. van Lieshout
C. Dormann · R. Langvatn · S.D. Albon

Trading forage quality for quantity?
Plant phenology and patch choice by Svalbard reindeer

Abstract Plant phenology of *Luzula* heathland plots in Spitsbergen (78°N) was manipulated by adding or removing snow, which altered the time for plots (2 m×2 m; n=10) to become snow-free. A 2-week difference in snowmelt, equivalent to approximately one-sixth of the growing season, was achieved between advanced (first to be snow-free) and delayed (last to be snow-free) treatments, which influenced plant biomass and plant quality. Nitrogen content of the forage species decreased with time after snowmelt, whereas C:N ratio increased. Manipulation of snowmelt led to a shift in "phenological time", without altering these plant quality parameters as such. Early in the growing season, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) selected the advanced plots which had been snow-free for longest, presumably because of the greater biomass of both *Luzula confusa* and *Salix polaris*, major components of reindeer diet at that time of the year. Moreover, the proportion of live *Luzula* leaves was highest in advanced plots, relative to both unmanipulated control and delayed plots. In contrast, plant quality, measured as nitrogen content and C:N ratio of leaves, was lowest in the preferred plots. Phenolic content did not differ among treatments, and is therefore unlikely to play a role in reindeer selection for plots with early snowmelt. Unlike in temperate regions, where selection for plant quality seems to be of major importance, selection for plant quantity might be an outcome of generally low levels of plant biomass and high forage quality during the growing season in the high Arctic. Reindeer selection for high plant biomass is likely to lead to a more favourable nitrogen and energy return than selection for high plant quality.

Key words C:N ratio · Nitrogen content · Plant biomass · Snowmelt manipulation · Spitsbergen

R. Van der Wal (✉) · N. Madan · S. van Lieshout · C. Dormann
S.D. Albon
Centre for Ecology & Hydrology, Banchory Research Station,
Hill of Brathens,
Glassel, Banchory, AB31 4BY, Scotland
e-mail: rvdw@ceh.ac.uk
Fax: +44-1330-823303

C. Dormann
University of Aberdeen, Department of Plant and Soil Science,
Cruickshank Building, St Machar Drive,
Aberdeen AB24 3UU, Scotland

R. Langvatn[1]
University Courses in Svalbard (UNIS),
N-9170 Longyearbyen, Norway

Present address:
[1] Norwegian Institute for Nature Research (NINA), Tungasletta-2,
N-7485 Trondheim, Norway

Introduction

In temperate ecosystems, which are characterised by seasonality and high summer plant production, phenological development of the vegetation is frequently described as the driving force in habitat use by vertebrate herbivores (Klein 1990; Fryxell 1991; Albon and Langvatn 1992). Feeding patch choice and forage selection are associated with plant quality (Klein 1970; Festa-Bianchet 1988; Langvatn and Hanley 1993; Wilmshurst et al. 1995; Riddington et al. 1997), and factors like plant nitrogen content, digestible energy, fibre content and concentration of macro-minerals have proved useful to predict forage selection in herbivores (Klein 1990; Albon and Langvatn 1992; Post and Klein 1996; Van der Wal and Loonen 1998).

Rapidly growing leaves from plants in early phenological stages are generally rich in nitrogen and digestible energy, while often low in structural and defence compounds (Crawley 1983; Hartley and Jones 1997; Jones and Hartley 1999) and hence attract herbivores (White 1993). Consumption of low-quality forage not only leads to low nutrient intake, but, since low nitrogen is generally correlated with low digestibility due to high lignin and fibre content (Prop and Vulink 1992; Robbins 1993; Van Soest 1994), total intake of digestible matter will also be reduced. Furthermore, fibrous forages tend to increase retention time in the digestive tract, hence

further reducing digestible energy intake per unit time (Demment and Van Soest 1985; Van Soest 1994).

As plant quality decreases over the growing season, plant biomass increases concurrently, which places a herbivore in a trade-off situation. Plant phenology and associated quality changes over the growing season are expected to be most pronounced in strongly seasonal habitats, because of limitations set by the length of the growing season (Kudo 1991).

The high Arctic is one of the most seasonal habitats on Earth, with long cold winters and short summers. Aided by substantial below-ground storage, arctic plants progress rapidly through different phenological stages (Bliss 1971). The combination of low temperature, low rainfall and low soil nutrient status constrains plant growth (Crawford 1989), and the amount of biomass found in the high Arctic is therefore small (Brattbakk 1986). The onset of plant growth is closely linked to the disappearance of snow (Billings and Bliss 1959; Kudo 1991). Topographic variability, on both meso- and micro-scales, and associated differences in snowmelt, result in swards of different phenological stages in close proximity, causing a spatially highly heterogeneous vegetation.

In this study we tested whether the selection of arctic swards by Svalbard reindeer (*Rangifer tarandus platyrhynchus*) as related to plant quality or quantity, by manipulating the time when vegetation became snow-free. The pronounced seasonality of the environment imposes a strong pressure on reindeer to utilise vegetation in a highly efficient manner. Apart from wind-swept ridges, all forage is buried under snow and ice during most of the year and consequently reindeer depend on the 3-month summer to replenish their body reserves. Reindeer feed on a wide variety of plant species (Staaland et al. 1983, 1991). The observation that selection is related to plant quality parameters (Leader-Williams 1988; Klein 1990; Danell et al. 1994) suggests that plant quality might influence range utilisation by reindeer. On the other hand, evidence from Alaskan and Norwegian *Rangifer* supports the idea that selection for vegetation with high plant biomass explains habitat selection (Skogland 1980). Correlative data suggest that like other vertebrate grazers (red deer *Cervus elaphus*: Albon and Langvatn 1992; barnacle goose *Branta leucopsis*: Prop et al. 1984), reindeer follow the receding snow-line (Skogland 1980), thereby profiting from the first flush of nutritious growth.

By manipulating the moment vegetation became snow-free and plants started growing, we created plots of vegetation in different phenological stages. After all plots became snow-free, we simultaneously exposed them to reindeer to test whether they foraged selectively in response to induced differences in plant phenology. Nitrogen content, C:N ratio, phenolic content of the two dominant plant species were measured and standing crop linked to reindeer selection.

Methods

Study area

The study was undertaken in the valley Semmeldalen, Nordenskiöldland, Spitsbergen, Svalbard (15°20'E, 77°90'N). This valley is the central part of the Colesdalen-Reindalen system, which extends over 40 km and has a resident population of about 500 reindeer (Jordhøy et al. 1996). The density of reindeer is among the highest for the Svalbard archipelago (Øritsland and Alendal 1986). Hunting pressure is generally low, and hunting is not permitted in our study area; there are no large predators. Unlike the situation in Fennoscandia, there is no husbandry.

Semmeldalen valley is characterised by different plant communities with *Luzula* heathland being the most common. Our experimental sites were located in heathland vegetation. Over the snow-free period, about 40% of all reindeer observed were feeding in heathland vegetation both in 1997 and 1998 (R. Van der Wal, unpublished work). Heathland vascular plant communities are dominated by the rush *Luzula confusa* and the dwarf the willow *Salix polaris*, a low density of grasses (*Poa arctica*, *Alopecurus alpinus*) and also a few dicot species (*Pedicularis hirsuta*, *Polygonum viviparum*). *Luzula* and *Salix* were the test species in this experiment, since they form a significant part of the reindeer diet early in the season (Staaland 1986; R. van der Wal, personal observations). Heathlands become snow-free around early June, but due to differences in micro-topography, there is considerable variation on a scale of weeks. The end of the growing season effectively occurs early in September, when average daily temperature drops below zero.

Experimental manipulation of snowmelt

The moment vegetation became snow-free was manipulated by either removing or adding snow. Between 6 and 8 June 1998 ten sites were selected on heath vegetation, spaced 100–2000 m apart. At that time of the year, most of the valley was still covered in snow, and the selection of heathland sites was made on the basis of an aerial photograph combined with knowledge of the area. At each site, three plots of 2 m×2 m, comparable in snow depth as measured with a graduated stick, were fenced with 1-m-high fences constructed of bamboo canes and nylon rope to keep reindeer out. Within each triplet, treatments were applied at random as either advanced snowmelt, delayed snowmelt, or untreated control. To advance the process of snowmelt, snow and ice were carefully removed with a spade, without damaging the vegetation underneath. Vegetation in "advanced" plots was completely snow-free within a day of clearing. To delay snowmelt, snowdepth was increased using bucket and spade. "Delayed" plots were each supplemented with a total of approximately 1500 l of snow, applied on three occasions. Untreated "control" plots became snow-free on average 4.8±1.0 (SD) days later than advanced plots, while delayed plots were covered by snow for another 9.2±1.0 days. Therefore, we achieved a 14-day difference in the time at which the advanced and delayed plots became snow-free, which is equivalent to one-sixth of the growing season. Fences were kept up until all plots were snow-free and triplets were opened to grazing simultaneously between 21 and 28 June 1998.

The addition or removal of snow did not influence soil moisture content ($F_{2,32}$=1.32, P=0.28). Soil moisture content in the top 5 cm was measured in all plots in the periods 7–9 July and 20–21 July 1998, using a surface capacitance insertion probe (SCIP). This instrument measures the soil dielectric constant, which is closely related to soil moisture content (Robinson and Dean 1993). The mean of 20 measurements per plot was used in the analysis. Although not influenced by snowmelt treatment, soil moisture content dropped between the two measuring periods ($F_{1,32}$=17.65, P<0.001) from 19.2% (±7.4 SD, n=21) to 15.5% (±4.4, n=21).

Plant biomass

Biomass, expressed as leaf mass per shoot, was estimated in seven out of ten triplets. The fences of the three remaining triplets were

destroyed by reindeer; as a result these plots were used for plant quality determination only. In each plot, ten shoots each of *Salix* and *Luzula* were marked with a plastic coded ring and leaf length was measured for all leaves (dead and live) attached to the shoot. Measurements were made four times, once in each period: 22–28 June, 7–9 July, 20–21 July and 13–16 August 1998. For graphical presentation of the data, these time periods are indicated by the average date (24 June, 8 July, 20 July and 14 August). In the same time periods marked plants were measured: leaves were collected at random in each plot and used to establish regression lines to convert each species leaf length into leaf mass. All leaf material was dried at 70°C for 48 h and subsequently stored in a desiccator. For *Salix*, 1500 leaves were weighed and the length of each individual leaf recorded. Regression lines for each measuring period and snowmelt treatment were calculated separately using log-transformed data ($0.65 > r^2 < 0.78$, except for period 1, delayed snowmelt: 0.54). *Luzula* samples containing 25 leaves each were weighed and measured with live leaves ($n=74$) and dead leaves ($n=35$) considered separately. Conversion factors were calculated for each period and treatment combination in the case of live leaves, whereas for dead leaves the measuring periods were lumped. Flowering stems were weighed and measured and log-transformed data provided a conversion factor for both live ($n=76$) and dead ($n=13$) flowering stems. In the biomass calculations, only data from marked plants measured in all four periods were used. The few plants that were grazed or died were excluded from the analysis. The mean of all shoot measurements in a plot was used in the analysis rather than all individual shoot measurements, to avoid pseudo-replication. Means were tested using a generalised mixed model for each measuring period with snowmelt treatment as fixed effect and site as random effect.

The density of *Salix* and *Luzula* shoots was determined in all except one (20–21 July) measuring periods as the average number of shoots in 20 squares of 10 cm×10 cm per plot. Means per plot were analysed using a generalised mixed model with autoregressive order 1 covariance structure (Littell et al. 1996), with snowmelt treatment as fixed effect and site as random effect.

Plant quality

We used nitrogen, carbon and phenolic content as indicators of nutritional quality (see Hartley and Jones 1997 – N and C; Waterman and Mole 1994 – phenolics, for a critical evaluation of these measures). Nitrogen, carbon and phenolic content was determined in live leaves of both *Luzula* and *Salix* collected at random in each plot in all measuring periods. Due to low plant availability, especially early in the season, some samples had to be combined. Sample size therefore differs between measuring periods and species. Samples were milled to powder using a ball mill, and re-dried overnight at 50°C before being weighed into tin capsules for analysis. Nitrogen and carbon analyses were undertaken using a Carlo Erba NA1500 elemental analyser (Allen 1989). Phenolic content was measured as tannic acid equivalents using Folin-Ciocalteau reagent (Kerslake et al. 1998). Plant quality data were analysed using a generalised linear model with snowmelt treatment and period as fixed effects. Due to low sample size in earlier periods, tests could not be run for each period separately.

Reindeer preference

As a measure of reindeer use to a plot, signs of grazing were recorded. In each plot 20 squares of 10 cm×10 cm were laid out in a cross, and inspected for *Salix* or *Luzula* plants grazed by reindeer in the periods 7–9 July and 13–16 August 1998. The number of squares with grazed shoots was used in the analysis. Data were analysed using a generalised mixed model assuming a Poisson distribution for the count data, with snowmelt treatment as fixed effect and site as random effect.
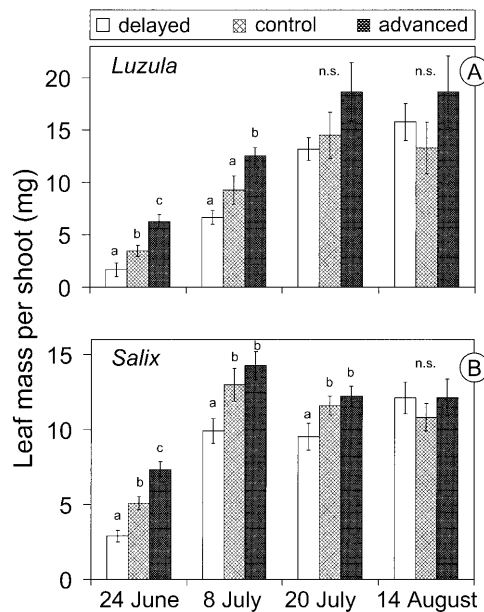
Fig. 1 Average mass of live leaves (±SE) per shoot in **A** *Luzula confusa* and **B** *Salix polaris* in plots with delayed, unmanipulated (control) and advanced snowmelt, measured at four times during the growing season. *Bars* with different *letters* are significantly different from each other
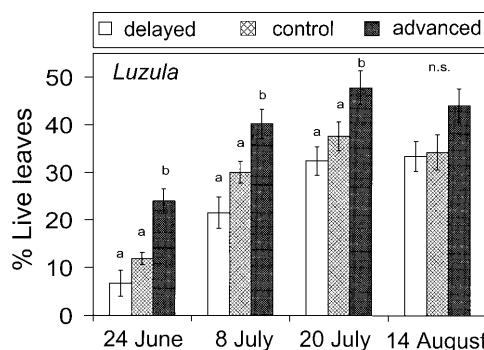
Fig. 2 Percentage live of total *Luzula* leaves in plots with delayed, unmanipulated (control) and advanced snowmelt, measured at four times during the growing season. *Bars* with different *letters* are significantly different from each other

Results

Plant biomass

Large differences in leaf mass were observed among snowmelt treatments during the first two periods of the experiment (Fig. 1A, B; $P \leq 0.01$ for both periods and species). Differences gradually became smaller over the season, with eventually no significant differences among treatments in *Luzula* in late July ($F_{2,12}=1.71$, $P=0.22$) and mid August ($F_{2,12}=1.03$, $P=0.39$) and in *Salix* in mid August ($F_{2,12}=0.54$, $P=0.60$). In the first period, leaf mass was more than twice as high in plots with advanced than in those with delayed snowmelt. In the subsequent period, *Luzula* leaf mass was significantly higher in advanced

plots, compared to both control and delayed plots. *Salix* leaf mass was significantly lower in delayed plots than in control and advanced plots, as was the case in the third period. The percentage of live leaves for *Luzula* further emphasises the differences in terms of live leaves among the snowmelt treatments. In all but the last measuring period, the percentage of live leaves was significantly higher in advanced than in both control and delayed plots (Fig. 2; $P<0.02$ for the first three periods). At the end of the season these differences were no longer significant ($F_{2,12}=2.92$, $P=0.09$). No significant differences in shoot density were found between the snowmelt treatments (Table 1).

Table 1 Average shoot density (shoots m^{-2}±SD) of *Luzula confusa* and *Salix polaris* in plots with delayed, unmanipulated (control) and advanced snowmelt, measured at three times during the growing season. No measurements were taken in the period 20–21 July. Sample size was 7 for each cell

	Snowmelt treatment		
	Delayed	Control	Advanced
Luzula confusa			
24 June	222±209	462±448	413±370
8 July	231±198	453±449	469±469
14 August	338±264	479±467	466±503
Treatment effect: $F_{2,54}=1.46$, $P=0.24$[a]			
Salix polaris			
24 June	3719±1833	5803±2251	5379±1697
8 July	7444±3506	7681±2738	6401±2062
14 August	7251±4233	6686±2614	5878±2214
Treatment effect: $F_{2,58}=0.54$, $P=0.59$[a]			

[a] Interactions between snowmelt treatment and measuring period were not significant in either *Luzula* ($P=0.98$) or *Salix* ($P=0.55$)

Plant quality

The response in leaf quality to different snowmelt treatments was largely the inverse of the leaf biomass pattern. In general, the lowest quality was associated with advanced plots and the highest quality was linked to delayed plots as measured by nitrogen concentration and carbon-to-nitrogen ratio in leaves of both *Luzula* and *Salix* (Fig. 3). Nitrogen levels decreased over the season from 2.9% to 1.4% in *Luzula* (Fig. 3A; $F_{3,63}=103.73$, $P<0.001$) and from 5.1% to 2.0% in *Salix* across treatments (Fig. 3B; $F_{3,72}=114.41$, $P<0.001$). In both species significant differences in nitrogen content among snowmelt treatments were found (*Luzula*: $F_{2,63}=4.25$, $P<0.02$; *Salix*: $F_{2,72}=7.51$, $P<0.01$) whereby delayed plots featured a higher nitrogen content than both control and advanced plots. There was no significant interaction between period and treatment (*Luzula*: $F_{6,63}=0.83$, $P=0.55$; *Salix*: $F_{6,72}=1.75$, $P=0.13$), indicating consistent differences among treatments over the whole growing season, but small sample sizes reduce our ability to detect seasonal changes.

C:N ratios increased over the season from 16.2% to 35.2% in *Luzula* (Fig. 3C; $F_{3,52}=51.55$, $P<0.001$) and from 10.0% to 26.3% in *Salix* (Fig. 3D; $F_{3,61}=42.14$, $P<0.001$), indicating a decrease in plant quality with time. *Luzula* from delayed plots had lower C:N ratios compared to plants from both control and advanced plots (effect treatment: $F_{2,52}=5.53$, $P<0.01$), whereas for *Salix* delayed plots only differed significantly from advanced plots (effect treatment: $F_{2,61}=3.87$, $P<0.05$). There was no evidence of differences among snowmelt treatments changing over the season (period×treatment interaction: *Luzula*: $F_{6,52}=1.26$, $P=0.29$; *Salix*: $F_{6,61}=0.42$, $P=0.87$).
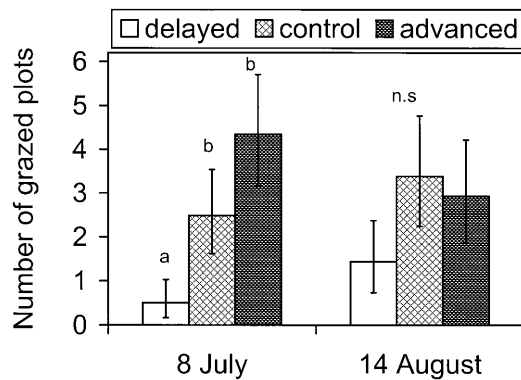
Average phenolic content of *Salix* leaves increased over the season from 11.0% to 18.9% (Table 2;

Fig. 3 Nitrogen content in leaves of **A** *Luzula confusa* and **B** *Salix polaris*, and C:N ratio in leaves of **C** *Luzula* and **D** *Salix*, in plots with delayed (white bars), unmanipulated (control; cross watched bars) and advanced (dark bars) snowmelt, measured at four times during the growing season. Sample size was 5 for each measuring period and treatment combination, except for the 1st period ($n=2$)
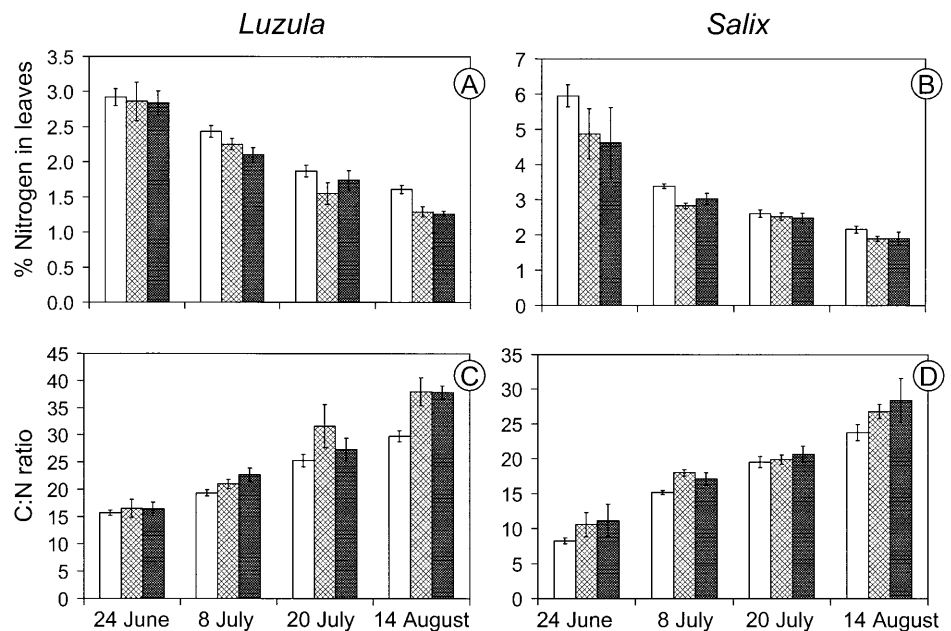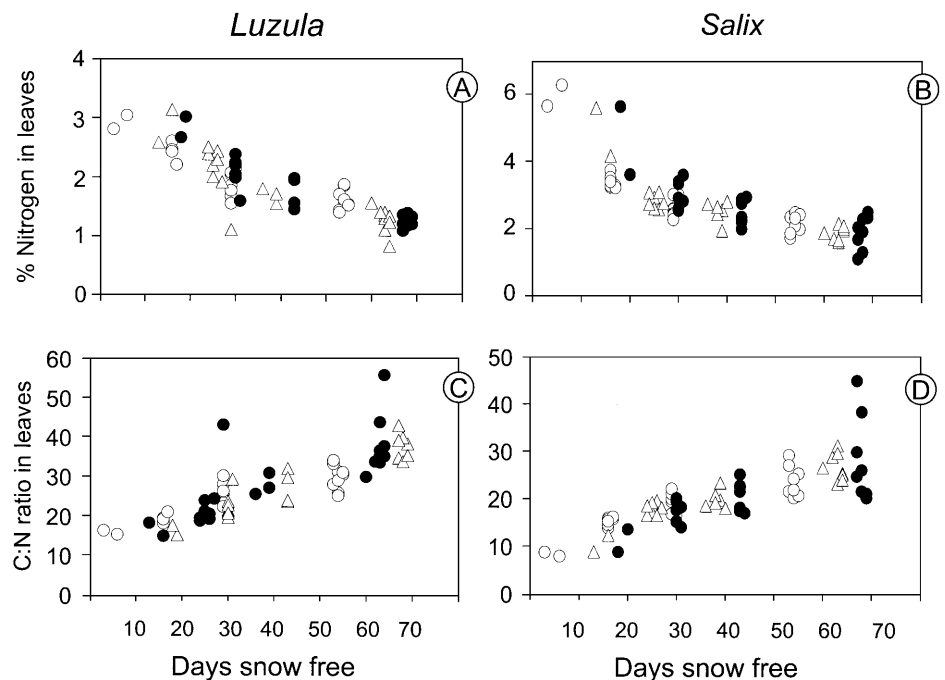
Table 2 Phenolic content in leaves of *Salix polaris*, in plots with delayed, unmanipulated (control) and advanced snowmelt, measured at four times during the growing season. Sample size was 5 for each measuring period and treatment, except for the 1st period (*n*=2), and control, advanced (*n*=3) and delayed (*n*=4) in the 3rd period

	Snowmelt treatment		
	Delayed	Control	Advanced
Salix polaris			
24 June	10.7±2.0	9.5±1.7	12.9±0.5
8 July	16.8±2.7	15.8±2.0	16.0±2.3
20 July	17.5±1.6	15.9±1.9	15.2±3.7
14 August	19.3±0.8	18.1±1.3	19.3±0.8

$F_{3,50}$=8.44, P<0.001). No significant differences in phenolic content were detected among snowmelt treatments ($F_{2,50}$=0.01, P=0.99). Phenolic content was negatively correlated with leaf nitrogen content (r=0.67, n=46, P<0.001). Only low levels of phenolics were found in *Luzula* (6.3±1.3%, *n*=12), therefore no further analyses were performed.

Reindeer selection

Early in the season reindeer strongly selected plots where snowmelt was advanced or not manipulated over plots where snowmelt was delayed (Fig. 4; $F_{2,12}$=7.17, P<0.01). Late in the season, such a selection was no longer apparent ($F_{2,12}$=0.98, P=0.40). By grazing in advanced, as opposed to in delayed plots, reindeer encounter higher biomass but lower quality.

Plant phenology

Both nitrogen content and C:N ratio strongly depended on the number of days plots were free from snow (Fig. 5) which explained a large proportion of the variance (Table 3). The lack of an independent effect of snowmelt manipulation *per se* on this relationship in both species indicates that we manipulated plant phenology. Similarly, phenolic content in *Salix* was also related to the number of days plots were snow-free, although the model fit was less good (Table 3). Here a marginally significant treatment effect was found, but this has to be largely attributed to two outliers.

Fig. 4 Reindeer grazing response in plots with delayed, unmanipulated (control) and advanced snowmelt. The average number of plots out of a total of 20 per treatment (±SE) in which signs of grazing were recorded is given for early (8 July) and late (14 August) in the season. *Bars* with different *letters* are significantly different from each other

Fig. 5 Nitrogen content in leaves of **A** *Luzula confusa* and **B** *Salix polaris*, and C:N ratio in leaves of **C** *Luzula* and **D** *Salix* in relation to the number of days plots were snow-free. The different *symbols* indicate data from plots in which snowmelt was delayed (*open circles*), unmanipulated (control *triangles*) or advanced closed *circles*. Statistical information is given in Table 3

Table 3 Summary of test results from the analyses of plant quality parameters in relation to the number of days plots were snow-free and snowmelt treatment

	Days snow-free		Snowmelt treatment		Interaction		R^2
	F	$P\leq$	F	P	F	P	
Luzula confusa							
Nitrogen content	168.66	0.001	0.82	0.45	0.45	0.64	0.75
C:N ratio	142.95	0.001	1.51	0.23	2.52	0.09	0.72
Salix polaris							
Nitrogen content	144.88	0.001	1.30	0.28	0.07	0.94	0.69
C:N ratio	122.35	0.001	0.66	0.52	0.48	0.62	0.65
Phenolic content	25.31	0.001	3.03	0.06	0.04	0.96	0.44

Discussion

Habitat selection in relation to snowmelt

Our results demonstrate that forage patch choice in reindeer is influenced by the timing of snowmelt. By selectively grazing in plots with early snowmelt, reindeer select for highest plant biomass but lower plant quality, as measured by nitrogen content and C:N ratio. Nitrogen content in both *Luzula* and *Salix* declined continuously after snowmelt, while C:N ratio increased linearly. Similarly, plant phenolic content in *Salix* increased with the length of time plots were snow-free. It appears that manipulation of snowmelt led to a shift in "phenological time", although plant quality was not altered as such. In Alaska, C:N ratio in leaves of *Eriophorum vaginatum*, *Salix planifolia* and *Betula nana* changed in a similar manner, in relation to manipulation of the timing of snowmelt (Walsh et al. 1997).

Woodland caribou (Oosenburg and Theberge 1980), red deer (Albon and Langvatn 1992), and Alaskan and Norwegian *Rangifer* (Skogland 1980) are all observed to switch during the season from grazing on south-facing slopes to grazing on slopes facing northwards, where snowmelt is generally delayed. Arctic-breeding geese concentrate on the flush of spring growth associated with snowmelt (Prop et al. 1984; Prop and Vulink 1992) and, similarly, migratory bighorn sheep *Ovis canadensis* tend to follow the retreating snowline (Festa-Bianchet 1988). In these correlative studies preference for immature swards is linked to the high quality of the emerging young shoots (Mattson 1980; McNaughton 1984; Augustine and McNaughton 1998). In contrast, our experimental study revealed that Svalbard reindeer select vegetation of highest biomass, rather than high quality.

Nitrogen or energy?

Plant quality is extremely difficult to assess, as it depends not only on the plant's morphological and chemical characteristics, but also on the needs and digestive capacity of the herbivore. In the case of reindeer, energy and protein stores have to be replenished early in the year, and in females additional protein is needed for lac-tation. Later in the year energy assimilated is deposited as body fat to survive the winter, and, in males, for the energetic demands of the rut. Therefore a switch from selection for plant quality early in the year to a preference for plant quantity later in the year might be expected. Plant quality is commonly measured as percentage of nitrogen, which is thought to reflect protein concentration. This measure, however, is confounded since nitrogen is often positively related to dry matter digestibility (Robbins 1993; Hartley and Jones 1997), and therefore might equally well represent the currency energy (Prop and Deerenberg 1991; Wilmshurst and Fryxell 1995). Moreover, as we found in *Salix* leaves, plant nitrogen content can be negatively correlated with the level of phenolics (Jones and Hartley 1999) and selection for high protein content can just as well be explained by avoidance of anti-grazing deterrents. As they are closely correlated, the controversy regarding the two currencies (energy and protein) is not easily resolved, and may not be ubiquitous. Careful experiments in both deer mice (*Peromyscus maniculatus*: Vickery et al. 1994) and white-tailed deer (*Odocoileus virginianus*: Berteaux et al. 1998) during winter reveal preference for energy- over protein-rich food, whereas studies on ruffed grouse (*Bonasa umbellus:* Beckerton and Middleton 1982) and brent geese (*Branta bernicla:* McKay et al. 1994) stress the importance of protein over energy.

Selection for plant biomass

By selecting plots of highest plant biomass, rather than of highest plant quality, both nitrogen and energy uptake by the reindeer are likely to have been maximised simultaneously. Although we did not measure intake rate, digestibility and retention time (Fryxell et al. 1994), it is unlikely that nitrogen or energy intake in the low biomass-high quality plots would exceed the intake achieved in high biomass-low quality plots. Moreover, in *Luzula* it is likely that not so much the quality of live plant tissue, but the presence of standing dead and dead leaf tips which will be of greatest importance, and this was negatively related to live biomass. Since *Luzula* leaves grow from a basal meristem, the green parts are closest to the soil surface, and the value of a bite to the herbivore will largely depend on the live-to-dead ratio.

Avoidance of areas with a high proportion of dead tissue has previously been observed in *Rangifer* (White and Trudell 1980) as well as in other vertebrate herbivores, including sheep (Arnold 1963), cattle (Wallis de Vries and Daleboudt 1994), North American bison (*Bison bison*: Coppock et al. 1983), mule deer (*Odocoileus hemionus*: Willms et al. 1981), roan antelope (*Hippotragus equinus:* Heitkönig and Owen-Smith 1998) and barnacle geese (*Branta leucopsis*: Van der Wal et al. 1998).

Latitudinal patterns in forage selection

In temperate and subarctic areas, herbivore growth rates and body size may be constrained largely by forage quality (Klein 1964; White 1983; Sæther 1985; Langvatn 1994). Several studies have demonstrated a close relationship between food quality and growth rates and body size in herbivores (Blaxter et al. 1961; McEwan and Whithead 1970; White 1983; Albon and Langvatn 1992), and variation in body size appears to be associated with the length of time animals have access to high quality forage during summer (Langvatn and Albon 1986).

Vegetation exploited by reindeer in the high Arctic is known to be of high digestibility and nutritional content (Staaland et al. 1983; Staaland 1986), but plant biomass is generally low (Brattbakk 1986). Under these conditions, biomass may play a relatively more important role in feeding behaviour and energy supply. Given a climate-induced gradient of improved forage quality with latitude (Deinum et al. 1981; Wedin et al. 1984; Van Soest 1994), it has been suggested that increased body size of cervids is associated with the nutritional quality of summer forage along this gradient (Langvatn 1994), an alternative explanation to the classical "Bergman's rule" (Langvatn and Albon 1986; see also Clutton-Brock and Harvey 1983; Geist 1987). In three genera of North American cervids, Geist (1987) reported an increase in body mass from south towards approximately the Arctic circle, followed by a decline further north. In northern Siberia, Shchelkunova (1980) reported a gradient of declining biomass from southern Taimyr towards Arctic areas at the coast of the Kara sea.

It thus seems conceivable that body size of cervids in temperate and subarctic areas is largely constrained by food quality, whereas in the high Arctic, biomass could turn out to be the limiting factor and an important predictor of foraging behaviour strategies, with the small body size of Svalbard reindeer as an outcome of generally low levels of plant biomass in the high Arctic.

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