



Original article

Reindeer grazing has contrasting effect on species traits in *Vaccinium vitis-idaea* L. and *Bistorta vivipara* (L.) GrayFrida Lindwall^a, Tage Vowles^a, Alf Ekblad^b, Robert G. Björk^{c,*}^a Department of Biological and Environmental Sciences, University of Gothenburg, P.O. Box 461, SE-405 30 Gothenburg, Sweden^b School of Science and Technology, Örebro University, SE-701 82 Örebro, Sweden^c Department of Earth Sciences, University of Gothenburg, P.O. Box 460, SE-405 30 Gothenburg, Sweden

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ABSTRACT

That reindeer grazing can have large effects on plant communities is well known, but how reindeer grazing affects plant traits and plant carbon (C) and nitrogen (N) allocation has not been studied to the same extent. This study was conducted in a sub-arctic dry heath in northern Sweden. 17-year-old reindeer enclosures were used to test whether reindeer grazing affects the C:N ratio (a plant quality index), and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (indicators of changes in C and N dynamics) as well as the C and N content of above- and below ground parts of the evergreen dwarf shrub *Vaccinium vitis-idaea* L. and the perennial forb *Bistorta vivipara* (L.) Gray. A lower C:N ratio was found in *B. vivipara* compared to *V. vitis-idaea* suggesting a higher grazing pressure on that species. We found that grazing reduced the total C content, by 26%, and increased the $\delta^{15}\text{N}$, by 1‰, in the leaves of *B. vivipara*, while no changes were observed in *V. vitis-idaea*. Fine roots of *B. vivipara* had higher $\delta^{13}\text{C}$ (1‰) and $\delta^{15}\text{N}$ (2.5‰) than the leaves, while such differences were not found in *V. vitis-idaea*. The results also highlight the importance of analysing both above- and belowground plant parts when interpreting natural variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

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1. Introduction

It is well known that the native grazers on the tundra play a central role in structuring the vegetation (Oksanen, 1990) by shaping the tree line (Van Bogaert et al., 2011) and influencing the density of plants, species composition and species richness (Eskelinen and Oksanen, 2006; Manseau et al., 1996; Ravolainen et al., 2011; Suominen and Olofsson, 2000; van der Wal et al., 2001; Virtanen, 2000). However, the impact of herbivores on internal carbon (C) and nitrogen (N) pools and allocation in arctic and subarctic plant species is far from clear (Cargill and Jefferies, 1984; Gauthier et al., 1995; Johnson and Matchett, 2001; McNaughton, 1979; Mulder, 1999; Olofsson et al., 2004; Pastor et al., 1993; Ritchie et al., 1998; Stark and Grellman, 2002; Zhu et al., 2008). Rapid climate change may also cause dramatic changes in the distribution of plants and ecosystems (Callaghan et al., 2007; Elmendorf et al., 2012; Gottfried et al., 2012), especially since

tundra species are adapted to exceptionally cold and harsh conditions. In order to gain a deeper insight into the processes that may shape our future landscapes it is therefore important to understand how individual species respond to changes in different environmental drivers.

There are three mechanisms by which plants are affected by grazing – defoliation, fertilization and trampling (Sørensen et al., 2009) – and there is ample evidence to suggest that these mechanisms, on their own or in combination, can have a profound impact on vegetation (van der Wal, 2006). Reindeer (*Rangifer tarandus* L.) feed on different plant species depending on season. Grasses, forbs and leaves of deciduous shrubs and trees dominate their diet during the summer while during winter they mostly eat lichens (*Cetraria* spp., *Sterocaulon* spp., and *Cladonia* sp.) but also tissue from evergreen dwarf shrubs such as *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher and *Vaccinium* spp. (Eriksson et al., 2007). Many tundra ecosystems are N limited due to suppressed N mineralization in the cold environment. The direct impact on vegetation caused by trampling and browsing by herbivores may have immediate effects on the ecosystem N pools and availability (Cargill and Jefferies, 1984; Gauthier et al., 1995; Johnson and Matchett, 2001; McNaughton, 1979; Mulder, 1999; Olofsson et al., 2004; Pastor et al., 1993; Ritchie et al., 1998; Stark and Grellman, 2002; Zhu et al., 2008). To determine plants'

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internal allocation patterns of N and C, stable isotopes analyses have frequently been used (Brooks et al., 1997; Brüggemann et al., 2011). Isotopes can give indications on the origin of nutrients (Michelsen et al., 1996), the availability of N in soil (Craine et al., 2009) and how nutrients and C are transported and allocated in plants (Brüggemann et al., 2011). The C to N (C:N) ratio of the plant tissue determines the palatability of the plants (White, 1978). It has been found that the C:N ratio in plant tissue tends to be lower when herbivores are present, suggesting that herbivores improve plant tissue quality (Sjögersten et al., 2011). Furthermore, Evju et al. (2009) have shown that plants with a high R:S ratio increase in abundance when the grazing pressure increased, suggesting that high R:S ratio is a tolerance strategy against herbivores. However, no study exists on how reindeer grazing affects individual plant species' internal allocation of C and N in the arctic and sub-arctic region, which is N limited.

Therefore, the aim of this study was to investigate how traits of two plant species in a sub-arctic dry heath were affected by the exclusion of reindeer. Utilizing seventeen-year old reindeer exclosures, the perennial forb *Bistorta vivipara* (L.) Gray, a preferred forage species, and the perennial evergreen dwarf shrub *Vaccinium vitis-idaea* L., a less preferred forage species, were examined for responses to grazing. The traits investigated were biomass allocation (above- and below ground), C and N content of fine roots and leaves and their isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$).

2. Materials and methods

2.1. Study site

The study site is a dry heath located at 840 m above sea level in northern Sweden (N67°46.5' E17°32.1'). The site is situated in an area grazed by reindeer from April to December, and the area has an annual mean air temperature of $-1.0\text{ }^{\circ}\text{C}$ and a precipitation of 460 mm per year. There is no information available on the exact number of reindeer visiting the site each year. However, reindeer droppings were counted at the site in 1997 and again in 2011. The number of droppings found in 1997 (\pm standard deviation) was 2076 ± 1415 per hectare (Eriksson et al., 2007), and in 2011 it was 1667 ± 1414 (T. Vowles, unpublished data). During this time the number of reindeer owned by the Sami village, Unna Tjerusj, has fluctuated between about 4000 and 6000 (around 6000 at the time of sampling) and was even higher prior to 1997. Thus, the grazing pressure has been fairly constant over the past 15 years. Dominating plant species in the field layer are the dwarf shrubs *E. nigrum* ssp. *hermaphroditum*, *Vaccinium myrtillus* L. and *V. vitis-idaea*, the graminoids *Deschampsia flexuosa* L., *Calamagrostis lapponica* Wahlb. and *Carex bigelowii* Torr. ex Schwein. Dominating forbs were *B. vivipara*, *Solidago virgaurea* L. and *Hieracium alpina* L. The bottom layer consisted of several moss species of the genera *Dicranum* and *Polytrichum* and lichens of the genera *Cladonia*, *Cetraria* and *Stereocaulon*.

2.2. Sampling and processing

Six plots, 25×25 m, were established in 1996 (Eriksson et al., 2007). Three plots were surrounded by fences (1.7 m high) to exclude reindeer (hereafter called exclosures) and three were left unprotected (ambient plots). The sampling was done in mid-August 2011, where three *B. vivipara* and three *V. vitis-idaea* were randomly collected from each plot. The two species were chosen to represent one preferred and one less preferred forage species. To standardize the sample volume, a 125 cm^3 soil cube ($5 \times 5 \times 5$ cm) was cut out from the soil. Each plant was then placed in a plastic bag along with its soil cube and was frozen within a few hours of collection before

further processing. After thawing, the root system was cleaned from soil (see Björk et al., 2007) after which the above- and belowground parts of the plant were separated. The dry mass was determined after drying for 24 h at $70\text{ }^{\circ}\text{C}$. After weighing the above- and belowground biomass, the leaves and the fine roots (diameter <2 mm) were collected and weighed separately. To get a sufficient amount of sample, the fine roots from the three samples from each plot were put together, and ground for C and N analyses. The C and N concentrations and isotopic composition ($\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ((R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}) \times 1000$ (‰), where R is the molar ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$), were determined from the milled materials as described by Boström et al. (2007).

2.3. Statistic analyses

To investigate grazing effects on R:S ratios, aboveground-, belowground- and total biomass, each species was analysed separately using a nested ANOVA. In this analysis, treatment was a fixed factor and plot and replications were random factors within a hierarchical design. Because of the limited amount of fine root and leaf biomass, the three replicates were pooled together to plot samples to ensure a large enough sample for C and N analysis. Thus, to investigate treatment effects on C and N traits in fine root and leaf biomass, C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, a MANOVA was used with treatment as fix factor and plot as random factor. Furthermore, the differences in C:N ratio, C and N content, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ between species and fine roots and leaves were determined using a nested ANOVA with species and treatment as fixed factors and plot as random factor. However, the limited amount of fine roots of *V. vitis-idaea* made it impossible to test for differences between species and grazing. All data were, after addition of a constant, log-transformed and concomitantly scaled to unit variance to achieve a normal distribution and to eliminate skewness and ensure homogeneity of variances according to Økland et al. (2001). To increase the statistical power and to reduce the risk of making Type II errors, an $\alpha = 0.10$ was used to test for significant differences.

3. Results and discussion

The exclusion of reindeer made the leaves of *B. vivipara* more depleted in $\delta^{15}\text{N}$ ($P = 0.044$), whereas the leaves of *V. vitis-idaea* were unaffected (Fig. 1). It seems possible that the fine roots of *V. vitis-idaea* were more depleted in $\delta^{15}\text{N}$ when excluding reindeer. However, the fine roots of *V. vitis-idaea* was not statistically tested since we just got one pooled sample from each treatment, but the effect size of the treatment is in the same range as for *B. vivipara* leaves, 1‰. There are three possible explanations for the overall pattern of ^{15}N enrichment in the grazed plots. Firstly, reindeer faeces, which are only deposited in grazed plots, are likely to be enriched in ^{15}N (Finstad and Kielland, 2011). Enrichment of faeces has also been found in other organisms: 1–4‰ in goose faeces (Sjögersten et al., 2010), about 6‰ in faeces from small mammals (Hwang et al., 2007), about 3‰ in goat faeces (Codron et al., 2011) and 3‰ in sheep faeces (Wittmer et al., 2010). But while faeces are enriched in ^{15}N , urine is depleted compared to the diet. Therefore, if urine and faeces are circulated back to the soil–plant system, our data suggest that faeces would be a central N source and also much more important than urine for the plants targeted in this study. However, this N source is allocated differently in the two species, since when reindeer were excluded the greatest depletion of ^{15}N in *B. vivipara* was in the leaves whereas in *V. vitis-idaea* it was in the roots. A second possibility may be differences in mycorrhiza association. Hobbie and Hobbie (2006) found that plants were more ^{15}N depleted in symbiosis with fungi, i.e. mycorrhiza, than if not. The transport of N through hyphae towards the plant discriminates

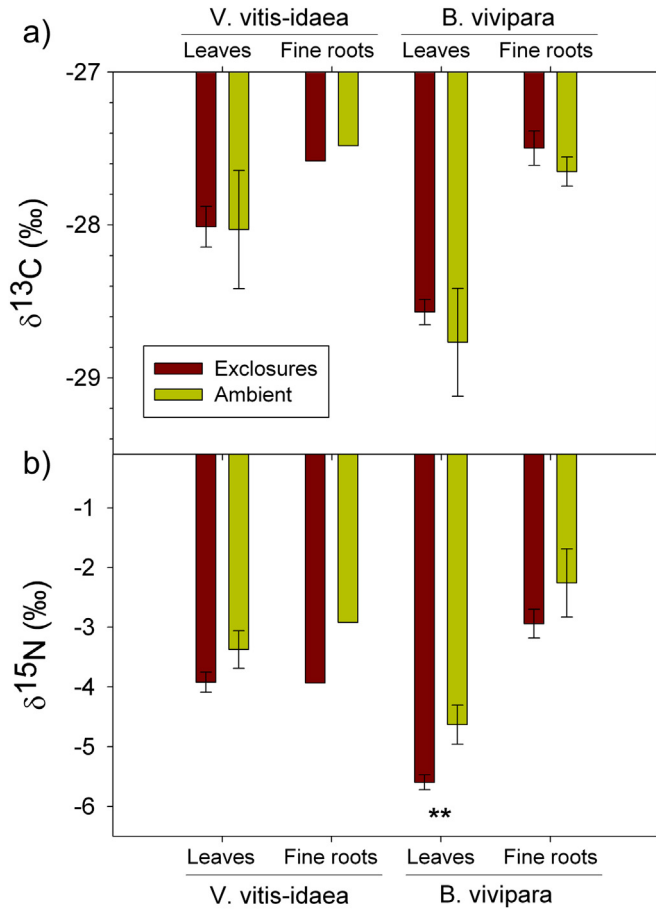


Fig. 1. $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) in leaves and fine roots in *Vaccinium vitis-idaea* and *Bistorta vivipara* ($n = 3$) exposed (Ambient) or not exposed (Exclosures) to grazing by reindeer. The error bars represent standard error. ** $P < 0.05$ indicates significant difference between treatments.

against ^{15}N . As a consequence, the N remaining in the fungus is enriched in ^{15}N , while the N transferred to the plant is ^{15}N depleted. Due to the lower grazing pressure on plants in exclosures it is feasible to believe that more C is available to fungi inside the exclosures. With more C available, mycorrhiza colonization may increase (Gehring and Whitham, 1991) and, consequently, more ^{15}N depleted N would be transported to the plants in exclosures compared to plants in the ambient plots. However, when comparing extramatrical mycelia production at other sites in Fennoscandia this trend could not be detected (F. Lindwall, unpublished data) and the effect of aboveground herbivores on mycorrhizal colonization and mycelia production is still unclear (Gehring and Whitham, 2002). Thirdly, Schulze et al. (1994) found that the $\delta^{15}\text{N}$ increases with the soil depth, and since the whole root system was not examined in this study, it is possible that plants in the ambient plots had deeper root systems than in the exclosures. However, the $\delta^{15}\text{N}$ signature follows the same pattern between treatments for both species but the belowground biomass does not. Furthermore, earlier studies (Björk et al., 2007; Michelsen et al., 1996) have found that the majority of the root system of arctic plants is in the organic layer, usually only a few centimetres thick in dry tundra heaths, making the third explanation unlikely. Thus, we conclude that the most likely explanation for the ^{15}N enriched plants in grazed plots is the addition of ^{15}N enriched droppings into the system, but changes in ectomycorrhizal mycelia production or community change cannot be ruled out.

Furthermore, we found a higher ($P = 0.099$) amount of C in the leaves of *B. vivipara* in exclosures than in ambient plots (Table 2), suggesting that the plants protected from grazers are able to allocate more C to the leaves. There is a weak trend ($P = 0.16$) that the R:S ratio in *B. vivipara* was higher in ambient plots (Table 1). As Evju et al. (2009) argue, an increase of C to the roots is a tolerance strategy against herbivory. If plants are protected against herbivory, C may instead be allocated to the leaves. If there also is a sufficient amount of N, the productivity inside the exclosures will increase (Larcher, 2003). However in contrast with earlier studies that showed an increased abundance and height of forbs in exclosures (Bråthen and Oksanen, 2001; Oksanen and Moen, 1994; Pajunen et al., 2008), we found no effect on total, above ground or below ground biomass or on total abundance (T. Vowles, unpublished result) in either of the species (Table 1), and also, no significant grazing effect on total C and N content in *V. vitis-idaea* leaves (Table 2). The effect of reindeer on primary production and soil nutrient availability is not clear and contrasting results from earlier studies show both negative (Stark and Grellman, 2002) and positive effects (Johnson and Matchett, 2001) of grazing on the available N. The lemming population peak in 2011 was one of the largest for decades and had a large impact on the alpine areas in Sweden. This may explain the lack of treatment effect on biomass, and even though we found treatment effects in C and N traits in *B. vivipara*, the differences may have been larger if lemmings also were excluded (Olofsson et al., 2012). Despite potential interfering lemming effects, our results show that the examined plant species respond differently to reindeer grazing, which also will have implications on how species will respond to environmental change in sub-arctic ecosystems.

Moreover, there was a clear difference in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, C:N ratio, and C, N and biomass allocation patterns between the species, under ambient conditions (see Table 2 and Fig. 1). The C:N ratio, which is about twice as high in *V. vitis-idaea* than in *B. vivipara* ($P < 0.001$), indicates that *B. vivipara* is, as hypothesized, of higher quality as forage. The C:N ratio is in general higher in evergreens than deciduous plants because evergreens have higher concentrations of lignin and other secondary C substances (often used as defense substance against grazing) than plants with shorter leaf lifespan (Aerts, 1995). The $\delta^{15}\text{N}$ was significantly lower ($P < 0.001$) for *B. vivipara* than for *V. vitis-idaea*, especially in the leaves. The $\delta^{15}\text{N}$ in leaves of both plants were more depleted than the fine roots, which was also found by Emmerton et al. (2001), and may be explained by an internal discrimination of ^{15}N that occurs between roots and shoots (Brüggemann et al., 2011). Thus, above- and belowground plant parts should both be taken into account when considering plant isotope composition. There is also a difference in $\delta^{13}\text{C}$ in the leaves between the two species, where *B. vivipara* is more depleted ($P = 0.057$), which is consistent with results shown by Brooks et al. (1997). They explained the differences between

Table 1

Total biomass, above- and belowground biomass and root: shoot (R:S) ratio for the species *Bistorta vivipara* and *Vaccinium vitis-idaea* in ambient plots (exposed to grazing by reindeer) and exclosures (not exposed reindeer). Values show mean and standard error (\pm SE) for $n = 3$ plots.

| | <i>Bistorta vivipara</i> | | <i>Vaccinium vitis-idaea</i> | |
|--------------------------|--------------------------|--------------|------------------------------|--------------|
| | Ambient | Exclosure | Ambient | Exclosure |
| Total biomass (mg) | 160.8 (22.8) | 207.7 (31.3) | 104.0 (20.7) | 138.2 (41.2) |
| Aboveground biomass (mg) | 39.5 (5.5) | 51.2 (8.1) | 80.3 (16.6) | 118.5 (40.3) |
| Belowground biomass (mg) | 121.3 (18.8) | 156.5 (26.7) | 23.7 (5.2) | 19.7 (4.1) |
| R:S | 4.29 (1.2) | 2.86 (0.3) | 0.39 (0.1) | 0.27 (0.1) |

Table 2
The C and N content and the C:N ratio for leaves and fine roots of the two species *Bistorta vivipara* and *Vaccinium vitis-idaea* in ambient plots (exposed to grazing by reindeer) and in enclosures (not exposed to reindeer). Values show mean and standard error (\pm SE) for $n = 3$ plots. Significant treatment effects are shown with * ($P < 0.1$).

| | <i>Bistorta vivipara</i> | | | | <i>Vaccinium vitis-idaea</i> | | | |
|------------------------------|--------------------------|-------------|------------|------------|------------------------------|-------------|------------------------|-----------|
| | Leaf | | Fine root | | Leaf | | Fine root ^a | |
| | Ambient | Enclosure | Ambient | Enclosure | Ambient | Enclosure | Ambient | Enclosure |
| C (g C plant ⁻¹) | 8.8 (0.9) | 11.9 (1.2)* | 7.9 (0.9) | 9.3 (1.2) | 38.1 (7.5) | 47.2 (12.4) | 0.8 | 0.5 |
| N (g N plant ⁻¹) | 0.4 (0.03) | 0.5 (0.04) | 0.2 (0.03) | 0.3 (0.06) | 0.9 (0.14) | 1.1 (0.3) | 0.01 | 0.01 |
| C/N | 24.2 (0.8) | 21.8 (1.2) | 33.1 (1.5) | 35.0 (0.8) | 42.5 (1.7) | 42.4 (1.6) | 54.5 | 63.8 |

^a The fine root samples of *V. vitis-idaea* were, because of the limited amount of sample, merged into one pooled sample, making it impossible to test for differences between species and grazing.

plant functional types as an effect of different photosynthetic rates and different degrees of discrimination against ¹³C in the assimilation of carbon dioxide (CO₂). Differences in boundary layer and stomatal- and internal conductance (Brüggemann et al., 2011; Warren, 2007) may occur between the two species and there are also different responses between plant functional groups due to environmental factors (Brooks et al., 1997; Warren, 2007). Research including more species from the same plant functional type is necessary to separate species specific responses from differences between functional groups.

4. Concluding remarks

The herbivore population has important effects on plant carbon and nitrogen dynamics. The higher $\delta^{15}\text{N}$ signatures in the ambient plots are probably an indication that faeces, which are ¹⁵N enriched, are an important N source for plants in tundra ecosystems. Reindeer affect plant traits either directly, by removing and destroying biomass, or indirectly, by addition of nitrogen via faeces. The difference in response between the species was visible in differences in the isotope signature between roots and shoots, where *B. vivipara* showed a larger internal isotope fractionation between roots and shoots than *V. vitis-idaea*. If these differences in isotopic fractionation and/or photosynthetic rate are species-specific or plant functional type specific requires further research. For deeper insights into how reindeer affect nutrient dynamics in tundra ecosystems, more mechanistic studies (e.g. isotopic labelling studies) are needed to separate the processes behind the specific differences in allocation patterns found in this study.

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