

Flowering, growth and defence in the two sexes: consequences of herbivore exclusion for *Salix polaris*

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Summary

1. For a long time, dioecious plants have been a model system for understanding the interactions between plants and herbivores. Differences in growth rate and, consequently, investment in defence between sexes may lead to skewed sex ratios due to differential herbivory.
2. In this study we evaluated the applicability of this idea to polar willow (*Salix polaris*), which in the study site, Svalbard, displays a female-biased sex ratio.
3. Excluding reindeer for 3 years increased the abundance of male flowers in one of two vegetation types investigated. Growth rates differed only slightly between the sexes, with females investing more in inflorescences.
4. The concentration of chemical defence compounds (phenolics and condensed tannins) did not differ between the sexes.
5. On the basis of these findings, the idea that growth rate-dependent herbivory caused the unbalanced sex ratio in *S. polaris* has to be rejected. Possibly an interaction of niche differentiation between male and female willows, in combination with reindeer grazing, produced the observed female-biased sex ratio, but the mechanism remains unclear.

Key-words: Antiherbivore defence, herbivory, retrospective growth analysis, *Salix polaris*, sex ratio

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Introduction

A biased sex ratio in dioecious plants has been reported for a number of species in various environments (Crawford & Balfour 1990; Dupont & Kato 1999; Freeman *et al.* 1976; Hjältén 1992; Lloyd & Webb 1977; Nichols-Orians *et al.* 1993). Commonly, sex ratios are male-biased, but female bias occurs too often to be regarded as an exception (Dupont & Kato 1999; Lloyd & Webb 1977; Opler & Bawa 1978; Williams 1995). Even within a genus, sex ratios can shift from extreme female bias to male bias (Dupont & Kato 1999).

In willows (*Salix* spp.), female-biased sex ratios have been described from a wide range of habitats and geographical regions (Åhman 1997; for review of northern willows see Crawford & Balfour 1990). Differential herbivory has often been invoked to explain this phenomenon (Boecklen *et al.* 1990; Danell *et al.* 1985; Danell *et al.* 1991; Elmqvist *et al.* 1988; Elmqvist *et al.*

1991; Hjältén 1992; Hjältén & Palo 1992). This theory is attractive as it can be deduced from a set of defence theory concepts: female plants have higher reproductive costs *per gamete* (as eggs are bigger than pollen), and have to bear the costs of seed set (Silvertown & Lovett Doust 1994). They are therefore likely to have higher total reproductive costs. These costs lead to retarded growth, which in turn favours investment in antiherbivore defence (Coley *et al.* 1985; De Jong 1995). Thus male plants are less well defended than females, and hence are preferred by herbivores (Hjältén & Palo 1992).

Support for the idea that differential herbivory causes a female-biased sex ratio in *Salix* spp. is so far purely descriptive (Boecklen *et al.* 1990; Danell *et al.* 1991; Elmqvist *et al.* 1988). Here we provide a test of the hypothesis that exclusion of reindeer (*Rangifer tarandus platyrhynchus* Vrolik 1829) will cause a change in the sex ratio of *Salix polaris* Wahlenb. (polar willow, Salicaceae). Moreover, we test whether (i) female *S. polaris* allocated more biomass than males to reproductive tissue; (ii) female *S. polaris* grow more quickly than males; and (iii) female plants are better defended than males against herbivores.

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Methods

STUDY AREA

The study was carried out in Semmeldalen (77°90' N, 15°20' E), a valley *c.* 20 km south of Longyearbyen, Svalbard. This and the neighbouring valleys host a population of *c.* 500 Svalbard Reindeer (*Rangifer tarandus platyrhynchus*) which has been closely monitored since 1994 (Irvine *et al.* 1999). Grazing pressure is among the highest in all of Svalbard (Van der Wal *et al.* 2001). Apart from a few Ptarmigan (*Lagopus mutus*) and Pink-footed Geese (*Anser brachyrhynchus*), reindeer are the only vertebrate herbivores in the system.

Two vegetation types are used most intensively by foraging reindeer during the summer: dry heath (dominated by *Luzula confusa*, *S. polaris* and the bryophytes *Aulacomnium turgidum*, *Drepanocladus uncinatus* and *Ptilidium ciliare*); and the wetter, graminoid-dominated communities (*Festuca cryophila*, *Poa* spp., *S. polaris*, and various bryophytes – for data on soil moisture see Van der Wal *et al.* 2000). The heath has a thick layer of peat causing a soft, dry upper soil horizon; the graminoid sites have shallow soil, with waterlogged clay on layers of undrained schist. The vegetation cover is $54 \pm 12\%$ in the graminoid sites, compared to $95 \pm 3\%$ in the heath.

EXCLOSURES AND SAMPLING

In July 1997, half-way through the growing season, three permanent exclosures (20 × 30 m with 1.5 m high fences) were erected in each of the two vegetation types (heath and graminoid) to prevent grazing by reindeer. The exclosure treatment was randomly assigned to one plot of a matched pair, the other serving as control. *Salix polaris* is the dominant plant species, with cover values between 30 and 65% in all sites.

From 24–27 July 2000, the sex ratio of *S. polaris* was assessed in all exclosures and controls. As *S. polaris* spreads vegetatively (as well as by seed) and its cover is relatively high, a dense system of rhizomes and stems is formed, and it is impossible to distinguish individuals. Therefore 200–300 10 × 10 cm quadrats were placed randomly in each exclosure and control. In each quadrat, the presence of male and female inflorescences was scored. Quadrats without any *S. polaris* were ignored. As many quadrats contained no flowers at all, enough quadrats were assessed to yield at least 40 sexed quadrats per treatment. Male and female inflorescences were in their prime at the time of recording. The size of the flowers (*c.* 0.8 cm diameter) and their scarcity made them very visible, and a recorded sex bias due to different detection rates can therefore be excluded. This way of assessing the sex ratio will not represent the true sex ratio of the population. It can, nevertheless, serve as an indicator of differential response of the sexes to the treatments.

To estimate annual growth of *S. polaris*, *c.* 20 above-ground branches of *S. polaris* of each sex were randomly sampled in every treatment. Leaves were separated from the rest of the plant. Stems and flowers were bagged and frozen, and later used for retrospective growth analysis. Leaf area for both sexes was assessed using a portable leaf-area meter (CI-202; CID Inc., Vancouver, WA, USA): 30 leaves were placed together on the measuring surface and scanned five times to yield a stable area estimate.

All leaves were subsequently dried at *c.* 45 °C for 7 days and stored for further analysis. Plants were re-dried at 65 °C for 24 h and weighed to the nearest 0.01 mg. Samples were then ground in a ball mill and analysed colorimetrically for phenolic compounds and tannins, following the recommendations of Hagerman (1998): phenolics were determined using the modified Prussian blue assay and are expressed as percentage dry weight on the basis of tannic acid equivalents. Tannins were analysed by employing the acid butanol method, expressing the content as percentage dry weight on the basis of Quebracho equivalents (Hagerman & Butler 1989).

RETROSPECTIVE ANALYSIS OF *SALIX POLARIS* GROWTH

In *S. polaris* each year's growth ends in a terminal bud and usually one or two side buds. As the stem grows out of one of the side buds in the following year (all *Salix* species grow sympodially; Raven 1992), annual segments can be recognized by those bud scars, which encircle the stem. This was used to measure the length (and width) of annual stem growth increments for the current year (= *C*) and previous years (*C*–1 ... *C*–6). Stems that showed signs of having been grazed in any of the previous 6 years were excluded from retrospective analysis. Thus, only five of the *c.* 20 stems harvested per replicate could actually be used as subsamples.

The current year's production is not only utilized for the growth of this year's segment, but also thickens the segments of previous years. For this reason, the total length of stem growth increments per year, rather than the volume or weight of the annual growth increments, was used in the statistical analysis. The weight of older segments would be confounded by the growth of the plant after their initiation. Using the total length of all growth increments per branch also takes account of differences in branching pattern (which might be different between sexes; Sakai & Burris 1985).

STATISTICS

Analysis of the percentage of quadrats with female plants (per number of plots containing either sex) was performed using the generalized linear mixed model (GLIMMIX) macro in SAS (SAS Institute Inc. 1989). The module allows the analysis of binomial data from

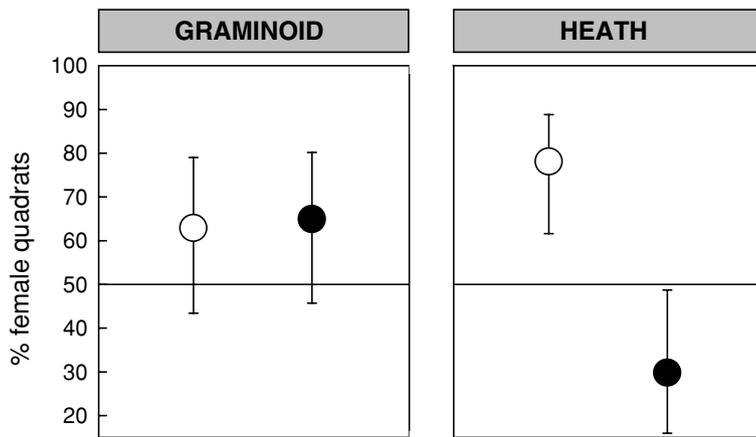


Fig. 1. Sex ratio as percentage of female *Salix polaris* in the two vegetation types in controls (○) and exclusions (●). Data are corrected for difference in allocation to number of flowers per plant. Error bars, ± 1 SE.

experiments with fixed (vegetation type and exclusion) and random (block, quadrat) effects, and nesting (block was nested in vegetation type and quadrat in exclusion). To correct for different numbers of flowers per plant between sexes, the analysis was weighted by 1 for female quadrats, and the ratio (number of flowers per female plant/number of flowers per male plant) for male quadrats. This ratio was calculated for each treatment combination separately. The model used a logit link: $\text{logit}(p) = \ln[p/(1-p)]$, where p = proportion of females. Denominator degrees of freedom were computed using the Satterthwaite option.

Measurements of cumulative weight since the erection of the exclusion (stems of C-2, C-1 and C, as well as leaves and inflorescences); leaf and flower weights; leaf characters; and levels of secondary defence compounds were analysed using the MIXED procedure of SAS, with the same nesting structure as described above (subsampling branches instead of quadrats, and using stem weight in C-4 as covariate). For this pur-

Table 1. Statistical results of the effects of vegetation type and exclusion on the sex ratio of *Salix polaris* (generalized linear mixed model). NDF and DDF are numerator and denominator degrees of freedom, respectively

Effect	NDF	DDF	F	P
Vegetation type	1	5	0.12	0.7483
Exclusion	1	5	7.42	0.0364
Interaction	1	5	11.18	0.0358

pose, length and width measurements of all shoot increments were transformed into weights, using a separate calibration curve for each year and treatment. All measurements were \log_{10} -transformed to comply with the assumptions of ANOVA (Sokal & Rohlf 1995).

The length of annual stem growth increments was also analysed using the MIXED procedure, but as a repeated measurement (unspecified covariance matrix) for the years 1994–2000, with exclusion effects introduced into the model for the data from 1998 onwards. Errors indicated throughout the paper refer to standard error of the mean.

Results

SEX RATIO

The sex ratio in *S. polaris* was female-biased only in the heath (78% female in controls), and closer to even in the graminoid vegetation. Exclusion of reindeer caused a slightly male dominated sex ratio of flowers in the heath, but had no effect in the graminoid community (Fig. 1; Table 1).

REPRODUCTIVE ALLOCATION

Female plants invested more than males in reproductive tissue ($F_{1,12} = 66.55$, $P < 0.001$; Fig. 2). In controls,

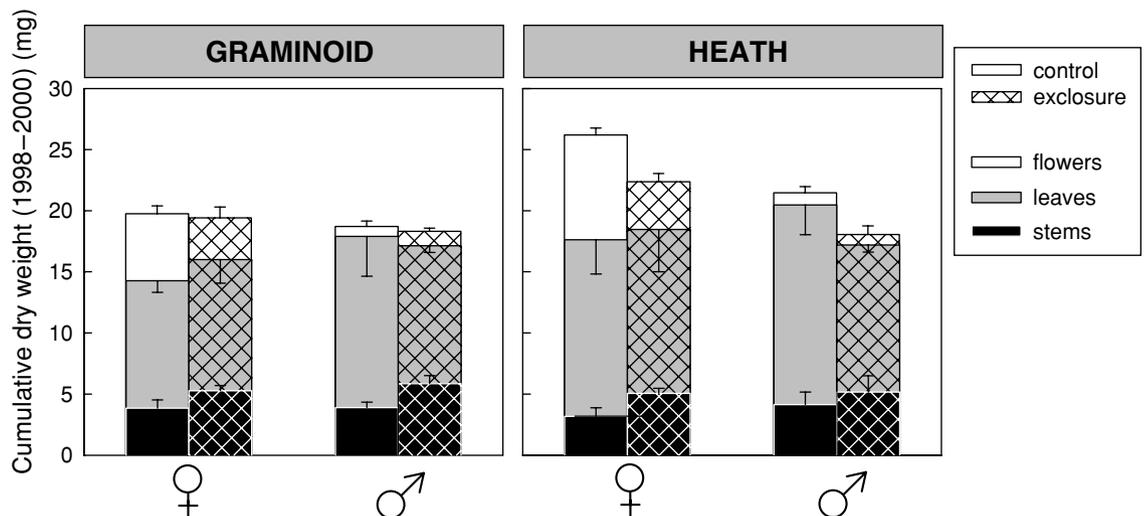


Fig. 2. Cumulative biomass since the erection of exclusions in 1998 for male and female *Salix polaris* in the two vegetation types. Stems (1998–2000), black; leaves (2000 only), grey; flowers (2000 only), white.

Table 2. Leaf and flower characteristics of male and female *Salix polaris* in the two vegetation types inside and outside exclosures (\pm SE)

Characteristic	Vegetation type	Control		Exclosure		Statistic
		Female	Male	Female	Male	
Leaf mass (mg leaf ⁻¹)	Graminoids	3.06 \pm 0.085	3.84 \pm 0.770	3.49 \pm 0.229	2.79 \pm 0.300	
	Heath	4.04 \pm 0.766	3.99 \pm 0.413	3.74 \pm 0.085	2.75 \pm 0.137	sex \times exclosure: $F_{1,10} = 6.34^*$
Leaf area (cm ²)	Graminoids	0.38 \pm 0.039	0.41 \pm 0.065	0.47 \pm 0.041	0.37 \pm 0.046	sex: $F_{1,10} = 5.00^*$
	Heath	0.47 \pm 0.080	0.49 \pm 0.065	0.52 \pm 0.042	0.34 \pm 0.030	sex \times exclosure: $F_{1,10} = 9.71^{**}$
Number of flowers per current year's growth	Graminoids	0.42 \pm 0.024	0.32 \pm 0.108	0.54 \pm 0.142	0.31 \pm 0.059	
	Heath	0.51 \pm 0.059	0.33 \pm 0.139	0.50 \pm 0.072	0.24 \pm 0.124	sex: $F_{1,11} = 13.84^{**}$
Flower dry weight (mg)	Graminoids	0.91 \pm 0.249	1.54 \pm 0.026	0.54 \pm 0.089	1.32 \pm 0.203	
	Heath	2.08 \pm 0.584	0.84 \pm 0.255	0.84 \pm 0.255	1.90 \pm 0.146	sex: $F_{1,11} = 7.85^*$

Differences due to vegetation type were never significant; the statistics given refer to pooled data for graminoid and heath (generalized linear mixed model). Where main effects or interactions are not indicated they were not significant.

*, $P < 0.05$; **, $P < 0.01$.

flower biomass per branch was eight times that of males, while in exclosures it was four times as much (sex \times exclosure: $F_{1,14} = 6.78$, $P < 0.05$).

The average number of flowers per current year's growth and the weight of the individual flower were higher for females (Table 2). Flower weight was unrelated to the total weight of stem, this year's stem growth, or the weight of leaves ($P > 0.5$).

GROWTH

Cumulative biomass and leaf characteristics

Cumulative biomass of 1998–2000 differed significantly between sexes (Fig. 2; Table 3), the total weight of females being slightly higher than that of males. Exclosures reduced total biomass in both sexes, but this effect was only marginally significant (Table 3; Fig. 2).

No difference between sexes with respect to total leaf biomass could be detected (Fig. 2). Reindeer exclusion reduced leaf biomass marginally ($F_{1,6} = 4.87$, $P = 0.0724$). The number of leaves per branch did not differ between sexes, treatments or vegetation types (1.62 ± 0.031 ; $N = 24$). The average weight of an individual leaf was significantly affected by the interaction of sex and exclosure. This is because leaves of male *S. polaris* inside the exclosures were lighter than those outside (Table 2). No main effect of vegetation

type, sex or exclosure was detectable ($P > 0.15$ for all factors).

Area per leaf differed between sexes, with female leaves being larger than male leaves. The sexes responded differently to the exclosures: the exclusion of reindeer increased the leaf area of female plants, but had the opposite effect in male plants (Table 2). There were no detectable differences between vegetation types. Specific leaf area was similar for both sexes, irrespective of vegetation type and exclosure (0.126 ± 0.004 cm² mg⁻¹, $N = 24$, $P > 0.16$ for all factors).

Retrospective growth analysis

Annual stem growth (length of annual growth increment) did not differ consistently between sexes (Table 4). There were pronounced interannual variations which were common to both sexes in both vegetation types (Fig. 3). Reindeer exclusion led to significantly longer annual growth increments (Table 4; Fig. 3). The marginally significant three-way interaction of vegetation type, sex and exclosure (Table 4) indicates the tendency of females to profit from herbivore exclusion in the heath, and that of males to profit in the graminoid community.

Variations in annual stem growth showed no significant correlation with summer temperature or summer precipitation pattern (data not shown).

ANTI-HERBIVORE DEFENCE

The phenolic content of *S. polaris* leaves did not differ between sexes ($P > 0.42$). Leaves of plants in exclosures contained more phenolics than in controls (exclosure: $11.3 \pm 0.39\%$ dry weight; control: $10.3 \pm 0.25\%$; $F_{1,6} = 6.33$, $P < 0.05$; Fig. 4). No difference related to vegetation type could be detected ($P > 0.35$).

Condensed tannin and phenolic contents were significantly positively correlated ($r = 0.598$, $P < 0.05$). However, concentrations of condensed tannins did not differ significantly between sexes, exclosure/control or

Table 3. Statistical results for cumulative biomass since reindeer exclusion (1998–2000) using the weight of the annual growth increment in 1996 as covariate (generalized linear mixed model)

Effect	NDF	DDF	<i>F</i>	<i>P</i>
Weight 1996	1	101	27.92	0.0001
Vegetation type	1	4	1.30	0.3145
Exclosure	1	6	4.78	0.0719
Sex	1	117	6.80	0.0103

Table 4. Statistical results from analysis of length of annual growth increments; data were log₁₀-transformed prior to analysis (generalized linear mixed model)

Source	NDF	DDF	F	P
Vegetation type	1	1	1.12	0.5744
Exclosure	1	169	10.72	0.0013
Sex	1	10	1.37	0.2692
Year	6	225	4.89	0.0001
Vegetation type × sex	1	9	0.27	0.6160
Vegetation type × exclosure	1	262	0.28	0.5974
Sex × exclosure	1	275	0.19	0.6657
Vegetation type × sex × exclosure	1	262	2.98	0.0855

vegetation types ($13.0 \pm 0.33\%$ dry weight; $P > 0.26$; Fig. 4). Following the computation of Cohen (1969) and the tables in Zar (1996), the minimal detectable difference at $P = 0.05$ for condensed tannins would have been 1.2% dry weight, about twice the maximal difference measured (Fig. 4). It is therefore safe to assume that sexes did not differ in the defence types assessed.

Discussion

Our results are only partly consistent with the hypothesis that the female-biased sex ratio in willows is caused by herbivory. In one vegetation type (heath), the sex ratio as assessed by the incidence of flowers

of a given sex changed in favour of the male sex, while in the other (graminoid) it did not. Female plants of *S. polaris* allocated more biomass to reproduction, consistent with expectations. Nevertheless, female plants were significantly larger than males. Considering only vegetative growth, no difference between the sexes could be detected. Also, the last point of the chain of explanations had to be rejected in our study: no difference in phenolic or tannin content of leaves could be found. Thus while the sex ratio in reindeer exclosures changed according to the prediction of the hypothesis, the mechanism behind this remains obscure.

GROWTH, DEFENCE AND HERBIVORY IN *SALIX*

Growth and defence or herbivory have been assessed for seven *Salix* species in relation to gender (*Salix myrsinifolia-phylicifolia*, Danell *et al.* 1985; Danell *et al.* 1991; Elmquist *et al.* 1988; *Salix cinerea*, Allende 1989; *Salix lasiolepis*, Boecklen *et al.* 1990; Price *et al.* 1989; *Salix rigida*, Elmquist *et al.* 1991; *Salix sericea*, Nichols-Orians *et al.* 1993; *Salix viminalis*, Åhman 1997; *S. polaris*, this study); none of these seven species showed a consistent gender-related pattern (Ågren *et al.* 1999; Åhman 1997). In two species (*S. rigida* and *S. lasiolepis*), females grew more slowly than males and were better defended. In three species (*S. cinerea*, *S. myrsinifolia-phylicifolia* and *S. sericea*),

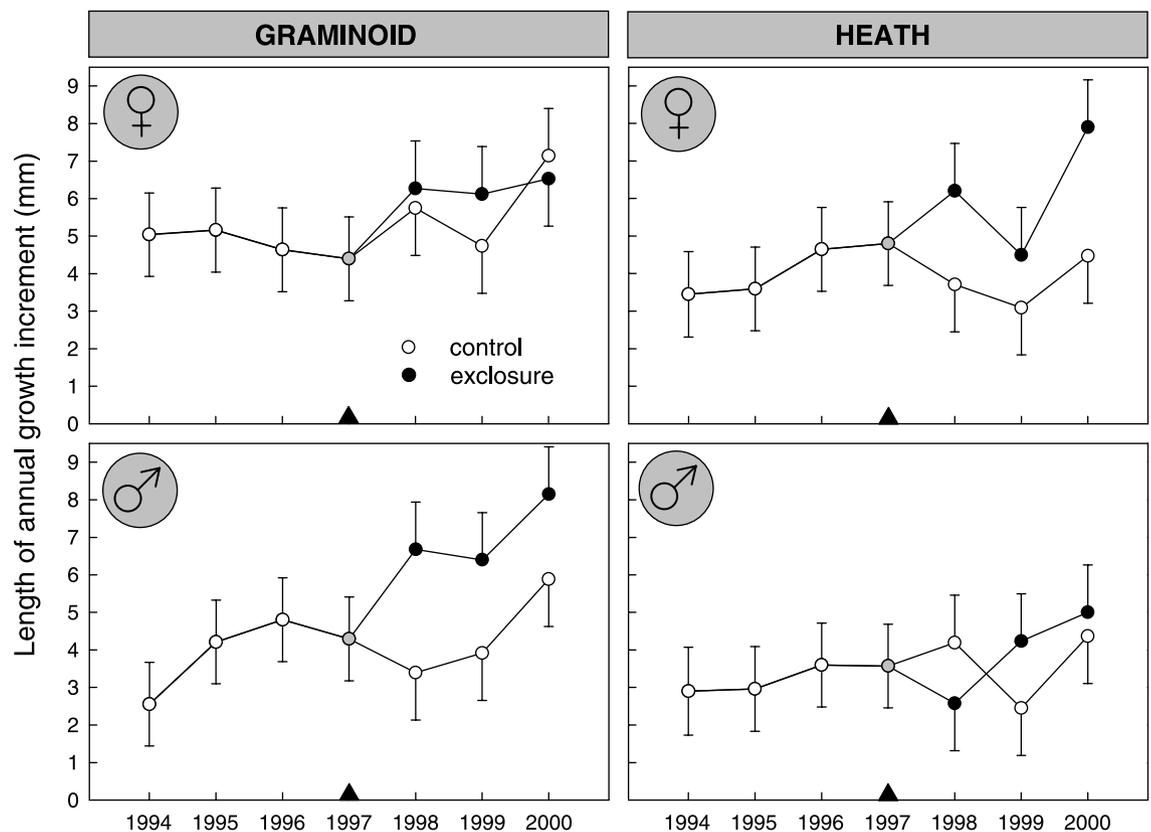


Fig. 3. Length of annual growth increments (1994–2000) for the two vegetation types and sexes. Exclosures were erected in 1997 (triangle).

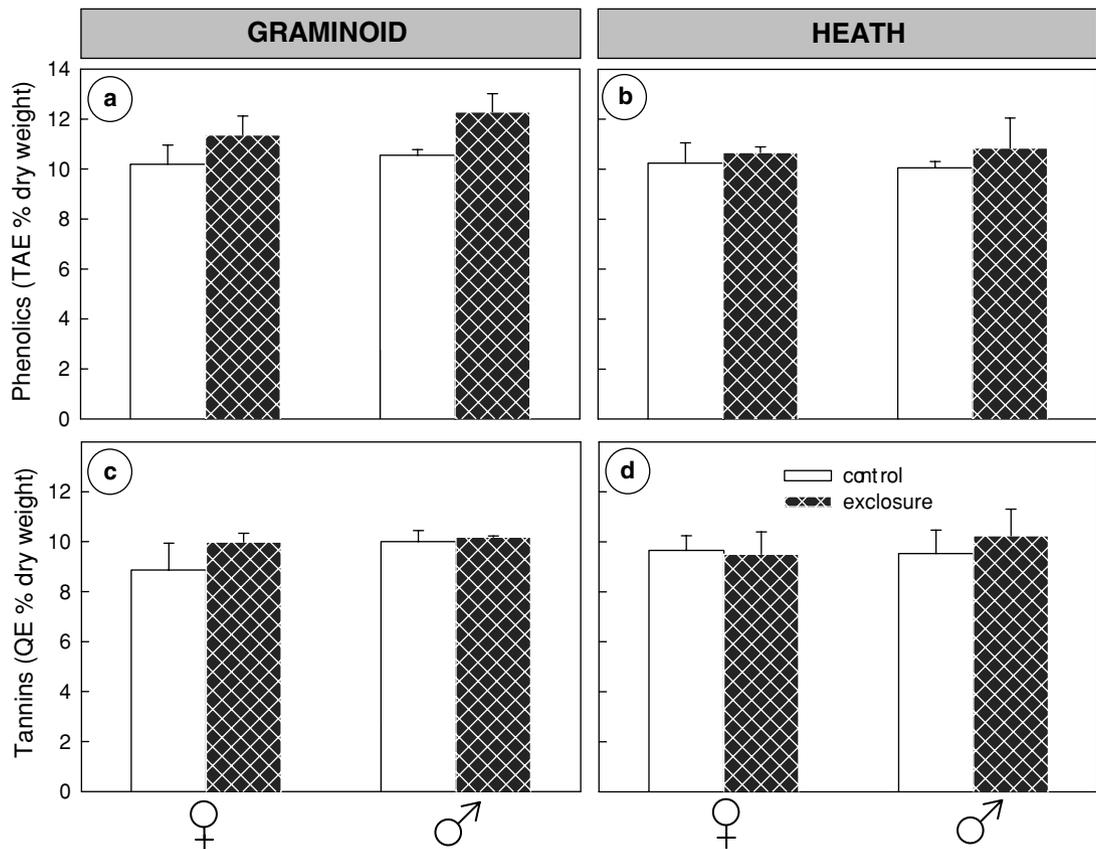


Fig. 4. Defence characteristics of *Salix polaris* leaves: total phenolics in tannic acid equivalents (TAE, a,b) and condensed tannins in Quebracho equivalents (QE, c,d) for the two sexes and vegetation types.

no growth difference was detected but, nonetheless, females were better defended. In *S. viminalis*, neither growth nor herbivory intensity was different between sexes, and in our study females grew better but were as well defended as males. Overall, there appears to be a tendency for female *Salix* to be better defended than males (five out of seven species; Ågren *et al.* 1999; Palo 1984), but not to grow more slowly (two out of seven).

The idea that slower-growing plants should be defended better than faster-growing ones was derived from a comparison of tropical tree species (Coley 1987; Coley *et al.* 1985), but on theoretical grounds the idea has also been extended to within-species comparisons (De Jong 1995). Growth differences between male and female plants are generally much smaller than between species (Ågren *et al.* 1999), and it is not surprising that it has proved difficult to show that gender-related differences in defence reduce herbivory on the slower-growing sex (for a successful example see Jing & Coley 1990).

Another problem is that a difference in defence investment might not necessarily lead to differences in herbivory. Boecklen *et al.* (1994) showed that different herbivores had different patterns in plant usage: total consumption did not relate to plant sex, while defence investment did (Boecklen *et al.* 1990). However, this would not apply to the system investigated here, as there is only one herbivore present.

ECOPHYSIOLOGICAL DIFFERENCES BETWEEN SEXES

Biased sex ratios may be caused by differential drought or salinity tolerance (Freeman *et al.* 1976), photosynthesis or water-use efficiency (Crawford & Balfour 1983; Dawson & Bliss 1989; Jones *et al.* 1999), soil pH or phosphate availability preferences (Cox 1981). Along a spatial ecological gradient, female plants were often found at the more benign end (Cox 1981; Freeman *et al.* 1976). Dawson & Bliss (1989) describe male *Salix arctica* to be more flexible in their water use and seemingly adapted to drier microsites than female plants, which have an inferior water-use efficiency. However, Crawford & Balfour (1983) report for *S. polaris* a higher range of leaf stomatal resistance to H₂O exchange for female plants, concluding that females reduce water losses more than males (Retuerto *et al.* 2000). At the same time, female plants have higher growth rates at low temperatures (Dawson & Geber 1999). However, quite often no ecological cause for a bias in sex ratio can be found (Dupont & Kato 1999; Williams 1995).

In this study, male and female *S. polaris* co-occurred at the same sites, at least at the scale of the enclosure (20 × 30 m). At the scale of the sampling quadrat (0.1 × 0.1 m), however, the sexes were separated: only 27 out of 498 quadrats (5.4%) in which the sex of *S.*

polaris was assessed contained flowers of both sexes. There was no detectable pattern of spatial segregation with respect to exclosures and vegetation type.

CAUSES OF FEMALE-BIASED SEX RATIO IN *S. POLARIS*

In contrast to most other *Salix* species, the female bias in sex ratio of *S. polaris* seen in this study could have been caused by the greater above-ground biomass of females, which itself might be caused by a microsite separation between the sexes. The higher biomass productivity is entirely used for reproduction (Fig. 2), supporting the idea that females have to occupy more benign sites to compensate for their additional costs of reproduction ('Jack Sprat effect': Cox 1981).

Nevertheless, herbivory is apparently important for creating or maintaining the female-biased sex ratio, otherwise there would not be any exclosure effect. However, this effect is confined to the dry heath sites, and some sort of indirect herbivore control appears to influence the abundance of male and female flowers in the heath (Väre *et al.* 1996). On the other hand, grazing pressure in the graminoid community is also less than in the heath (C.S., personal observation), and an effect of herbivore exclusion might become apparent in the longer term.

Surprisingly, the exclosures in the heath (and to a lesser extent in the graminoid community as well) reduced inflorescence biomass compared to controls. This was probably caused by the increase in stem length, which diverted assimilates from the flowers. The increase in stem length, then, might be interpreted as a response to taller-growing surrounding vegetation (mosses in particular), over which *S. polaris* has to position its leaves. A reduced inflorescence biomass might be a result of competition for light in a denser and taller ungrazed and untrampled vegetation.

The role of defence compounds in this context remains unclear. While phenolics also serve as UV-B absorbents and protectors against fungal infections, tannins appear to function primarily as grazing deterrents (Harborne 1991; Zucker 1983). The significant increase in phenolic content in the exclosures suggests that defence is a constitutive character of *S. polaris*. According to Bryant & Reichardt (1992), lower phenolic content under grazing compared to exclosures can be explained by the following reasoning. Herbivory on slow-growing species can lead to a carbon limitation of growth. Roots still take up nutrients, but as leaf area is consumed by grazers, carbon is in relatively short supply. As phenolics and proteins compete for the same precursor, phenylalanine (Jones & Hartley 1999), phenolic production is reduced in favour of proteins and hence leaf growth. Inside exclosures, nitrogen will be limiting because of higher leaf area and thus higher carbon provisioning, leading to the production of secondary compounds in an overflow reaction (Hartley & Jones 1997).

An alternative explanation for the observed pattern is a differential response of male and female plants to the cessation of grazing, leading to an increase in flowering in males, but not in females. But this would not explain the skewed sex ratio in the controls, nor the difference in response in the two vegetation types. Moreover, Houli (1999) found no evidence for differential response of sexes to defoliation treatments in *Salix*.

Conclusions

The hypothesis that the female-biased sex ratio of *S. polaris* is caused by herbivory was supported in one vegetation type but refuted for the other. Moreover, the mechanism of growth rate-dependent defence was not applicable, and therefore the link between *S. polaris* sex and reindeer preference remains obscure (Ågren *et al.* 1999).

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