

Intensive grazing by Barnacle geese depletes High Arctic seed bank

D.P.J. Kuijper, J.P. Bakker, E.J. Cooper, R. Ubels, I.S. Jónsdóttir, and M.J.J.E. Loonen

Abstract: Studies in the Canadian Arctic show dramatic effects of increased goose grazing on vegetation structure and soil conditions, but little is known of the role of goose grazing in the European Arctic. We focused on how geese might affect plant recruitment via effects on seed production and soil seed bank in High Arctic Svalbard. Experimental grazing by captive Barnacle geese (*Branta leucopsis* (Bechstein, 1803)) decreased flower densities both at normal and at high grazing pressure. Geese showed a clear preference for reproductive rather than vegetative shoots. Soil samples collected inside and outside 7-year-old exclosures in an intensively goose-grazed area revealed significant effects on the germinable soil seed bank. The density of viable seeds in the top soil layer inside exclosures was six times higher than in grazed plots. Lower densities of viable seeds occurred in the basal than in the top layer but there was no difference in basal layer seed density between exclosed and grazed plots. This study shows that geese have strong effects on floral abundance and consequently on the seed bank. We argue that goose grazing in these systems influences the potential for recovery after a disturbance event and thus the long-term plant species diversity and dynamics.

Key words: vegetation, *Branta leucopsis*, increasing goose numbers, exclosure, Svalbard.

Résumé : Les études conduites dans l'Arctique Canadien révèlent des effets considérables suite à l'augmentation du broutage par les oies sur la structure de la végétation et les conditions du sol, mais on sait peu de choses sur le rôle du broutage par les oies dans l'Arctique Européen. Les auteurs ont cherché à savoir comment les oies peuvent affecter le recrutement des plantes via leurs effets sur la production des graines et la banque de graines du sol, dans le Svalbard en Haut Arctique. Le broutage expérimental par des bernaches captives diminue la densité des fleurs, aussi bien par le broutage normal qu'à haute intensité. Les oies montrent une nette préférence pour les tiges reproductives plutôt que les tiges végétatives. Des échantillons de sols récoltés à l'intérieur et à l'extérieur d'exclos âgés de 7 ans, dans une région intensivement broutée par les oies, révèlent des effets significatifs sur la banque des graines du sol, aptes à germer. Dans les exclos, la densité des graines viables des couches superficielles du sol est six fois plus élevée que dans les parcelles broutées. On retrouve des densités plus faibles de graines viables dans la couche basale que dans la couche supérieure, mais à ce niveau il n'y a pas de différence entre la densité des graines des parcelles excloses et broutées. Cette étude montre que les oies exercent un effet considérable sur l'abondance des fleurs et conséquemment sur la banque de graines dans le sol. Les auteurs suggèrent que dans ces systèmes, le broutage par les oies influence le potentiel de recouvrement après un événement perturbant et ainsi la diversité des espèces à long terme et leur dynamique.

Mots clés : végétation, *Branta leucopsis*, augmentation du nombre des oies, exclos, Svalbard.

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Introduction

Geese can play an important role in structuring arctic vegetation assemblages (Mulder and Ruess 1998; Hik et al. 1992; Zacheis et al. 2001). Grazing by geese can directly affect the vegetation by reducing the plant standing crop and plant species composition by selective grazing of high-quality plant species (Zacheis et al. 2001). Geese can also indirectly influence the vegetation by altering competitive interactions between plants. Selective grazing of one plant species may release other species from competition (Mulder and Ruess 1998; Van der Wal et al. 2000a), or changed abiotic conditions may differentially affect competing plant species (Bazely and Jefferies 1985; Van der Wal et al. 2000b; Van der Wal and Brooker 2004).

The population size of several goose species has been increasing during the past decades (Madsen et al. 1999; Owen and Black 1999; Jefferies and Rockwell 2002). This has re-

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D.P.J. Kuijper.¹ Arctic Centre, University of Groningen, P.O. Box 716, 9700 AS Groningen, Netherlands, and Animal Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, Netherlands.

J.P. Bakker. Community and Conservation Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, Netherlands.

E.J. Cooper and I.S. Jónsdóttir. Department of Biology, The University Centre in Svalbard, P.O. Box 156, N-9171 Longyearbyen, Norway.

R. Ubels. Animal Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, Netherlands.

M.J.J.E. Loonen. Arctic Centre, University of Groningen, P.O. Box 716, 9700 AS Groningen, Netherlands.

¹Corresponding author (e-mail: d.p.j.kuijper@rug.nl).

sulted in an increased grazing pressure in their arctic breeding areas and has caused several changes in biotic and abiotic conditions in some areas. The best documented example is the dramatic effects of increased grazing pressure by Lesser Snow geese on vegetation and soil characteristics in La Pérouse Bay in the Canadian Low Arctic. The overexploitation of the vegetation (Jefferies and Rockwell 2002) in combination with changed abiotic conditions (Iacobelli and Jefferies 1991; Jefferies and Rockwell 2002) has resulted in near irreversible changes in the vegetation (Srivastava and Jefferies 1996; Handa et al. 2002). The limitation on recovery to the original situation is reinforced by the absence of a soil seed bank (Chang et al. 2001). Although populations of European arctic breeding goose species have also been increasing rapidly (e.g., Pinkfooted goose (Madsen et al. 1999); Barnacle goose (*Branta leucopsis* Bechstein, 1803 (Owen and Black 1999))), their role in structuring arctic vegetation assemblages in their breeding range is unclear. Most studies on plant-animal interactions in European High Arctic areas have focused on reindeer as the dominant grazer (Wegener and Odasz-Albrigtsen 1998; Van der Wal et al. 2001; Cooper and Wookey 2003; Van der Wal and Brooker 2004). Previous studies suggest that geese do not have large effects on species composition of plant communities in these systems (Drent et al. 1998; Loonen and Solheim 1998). However, they potentially play a role in the ability of the vegetation to recover from heavy grazing or other major disturbances via effects on seed production and soil seed bank.

Geese are selective grazers and preferentially feed on high-quality plant species (Prop and de Vries 1993; Gadalal and Jefferies 1995) and plant parts (Therkildsen and Madsen 1999). The metabolizable energy content of seeds and flowers for geese is high compared with other plant parts (Prop and de Vries 1993). By selectively grazing on these high-quality plant parts, geese may directly affect the seed set by consuming the reproductive organs of plants. Grazing can also indirectly affect seed production.

Continuous grazing can change plant species composition and can deplete the resources of a plant, thereby reducing the resources that can be allocated to reproductive organs such as flowers (Hickman and Hartnett 2002; Gustafsson 2004). Both these direct and indirect effects of goose grazing on seed production are expected to lead to a depleted soil seed bank in long-term goose-grazed areas.

In the present study on goose grazing in High Arctic habitats of the European Arctic, we focused on the role that geese can play in affecting plant species composition via effects on production of seeds and other propagules and the seed bank. We studied the direct effects of grazing on flowering and thus seed and other propagule production and consequent formation of a viable seed bank in the long term as a combination of direct and indirect effects of grazing on seed production. We asked two questions. First, do geese reduce vascular plant fertile shoot abundance, thus significantly affecting the potential for seed or other propagule production? Second, does continuous goose grazing affect the soil seed bank in the long term? To answer these questions, we carried out grazing trials with captive geese to determine the number of fertile shoots removed at different levels of grazing pressure and sampled the soil for germination trials inside and outside 7-year-old exclosures in an in-

tensively goose-grazed area to establish the density of viable seeds present in the soil seed bank.

Materials and methods

Experimental grazing by captive geese

Four wild geese, caught in the beginning of the breeding season on Spitsbergen, Svalbard, were used for experimental grazing. Each pair of geese was kept in a cage of 2 m × 2 m. Grazing trials were carried out in the first week of July 2003 in Adventdalen, Svalbard (78.2°N, 15.7°E). This area is only visited by wild geese during spring and autumn migration. However, reindeer are major flower consumers (Cooper and Wookey 2003) and graze year-round in the area. All experiments therefore took place in fenced areas effectively excluding reindeer from the plots. Fences (approximately 10 m × 10 m) were erected in autumn 2002 around each block of plots to exclude grazing in the year in which the experiments were carried out. The area is characterized by wet moss-dominated tundra with vascular plant species such as *Dupontia fisheri*, *Equisetum arvense*, *Eriophorum scheuchzeri*, *Ranunculus hyperboreus*, *Saxifraga cernua*, and *Saxifraga foliolosa* and mesic tundra dominated by *Salix polaris*, *Alopecurus borealis*, and *Bistorta vivipara*; nomenclature followed Elven and Elvebakk (1996).

Two grazing experiments were started in 2003 as part of a larger experiment studying the effects of grazing and increased surface temperature (FRAGILE (fragility of arctic goose habitat: impact of land use, conservation, and elevated temperature), EU project No. EVK2-2002-00235)). Data are presented from 2003, the first season of the experiment. The first grazing experiment had a randomized block design in which the effects of grazing and increased surface temperature are studied. In this experiment, two levels of grazing were applied to simulate normal and high grazing intensity. A pair of geese was put for either 1 or 5 h on a plot (2 m × 2 m) that had been subjected to ambient conditions or open-top chambers used for enhancement of surface temperature (for further details, see Cooper et al. 2004b, Cooper et al. 2006). Each treatment was replicated five times in each of the dominant habitat types in the area, the wet-moss tundra and the mesic tundra. Although the experiment considers both temperature and grazing, in this paper, we focus on the effect of goose grazing on the abundance of fertile shoots in different plant species.

The second experiment consisted of eight plots subjected to increasing goose grazing pressure, carried out in both the wet and mesic tundra. A pair of geese was put for a different amount of time on each plot (0, 0.5, 1, 2, 3, 4, 5, and 7 h) to create a gradient in grazing pressure. This experiment was used to study the relationship between goose grazing pressure and reduction in total floral abundance.

Before each grazing trial, geese were starved for 2 h, resulting in immediate grazing when the experimental grazing started in the 2 m × 2 m caged plots. Every second minute during a grazing trial, the time spent grazing was monitored during 30 s for each individual goose. This number was used to calculate the total grazing time per plot.

This resulted in a value of actual grazing pressure, defined as the minutes of grazing per square metre per day, that ranged between 0.8 and 1.2 min·m⁻²·d⁻¹ on the 1 h plots

Table 1. Actual grazing pressure achieved with two captive geese on experimentally grazed plots that were either ambient temperature or temperature enhanced by means of an open-top chamber for a wet and a mesic tundra in Adventdalen.

Habitat	No. of hours geese were on plot		Grazing pressure (min·m ⁻² ·d ⁻¹)
	Ambient or open-top chamber		
Wet	1	Ambient	1.0 (0.1)a
		Open-top chamber	1.2 (0.1)a
	5	Ambient	4.4 (0.8)b
		Open-top chamber	4.8 (0.7)b
Mesic	1	Ambient	0.8 (0.1)a
		Open-top chamber	1.0 (0.2)b
	5	Ambient	2.9 (0.3)b
		Open-top chamber	1.8 (0.3)b

Note: Data are means with SE in parentheses, $n = 5$. Grazing times are based on behavioural observations made during the grazing trial on experimental plots. Different letters indicate significant differences ($P < 0.05$).

in the mesic and wet habitats (Table 1). Grazing in the wet habitat was generally more intense (Table 1) owing to a higher abundance of preferred food plants such as *Dupontia fisheri* and *Equisetum arvense*. These numbers are within the range of values found for natural grazing pressure of wild Barnacle geese on Svalbard. Natural grazing pressure is found to range between 0.2–0.3 min·m⁻²·d⁻¹ on low-productive dry tundra (Prop et al. 1984) to 0.5–1.3 min·m⁻²·d⁻¹ on highly productive wet tundra (Loonen et al. 2000); no values exist for mesic tundra. The 1 h treatment was regarded as a simulation of normal grazing pressure. The 5 h grazing treatment led to a grazing intensity at a maximum 2.2 and 3.7 times greater than the maximum levels found for natural grazing pressure on the mesic and wet tundra, respectively.

Before and after each grazing trial, the total number of shoots and the number of fertile shoots of all plant species were counted on each plot in nine fixed squares of 7.5 cm × 7.5 cm, giving a measure of plant and floral abundance. The maximum time between shoot density counts (before and after grazing) on any plot was 24 h. The flowering frequency was calculated as the number of flowering shoots divided by the total number of shoots (flowering and nonflowering) and expressed as a percentage. The reduction in flowering frequency resulting from goose grazing and the absolute number and percentage of flowers grazed were determined.

Samples to determine soil seed bank

Soil samples for seed bank analyses were collected in July 1999 in Ny-Ålesund, Svalbard (78.9°N, 11.9°E). We define the seed bank here as a bank of vascular plant propagules including seeds, spores, and asexual bulbils (often produced on flowering stems or inflorescences). A Barnacle goose population established in this area in the early 1980s (Loonen et al. 2000) and has increased to a present number of 250–300 pairs (Loonen, unpublished data). Between 1991 and 1993, four exclosures were erected in the village, all in a moist moss-dominated tundra area close to a small lake (Solvatnet). This is the most intensively grazed area inside the village of Ny-Ålesund. In spring, this area is grazed by families of Barnacle geese, and later in the season, it is an

important moulting area for both families and nonbreeders (Loonen et al. 2000). Owing to the wet conditions and the nearly constant presence of people, reindeer grazing intensity is lower on these intensively goose-grazed areas than elsewhere in the surrounding area (M.J.J.E. Loonen, unpublished data). The vegetation in this area consisted mainly of moist moss-dominated tundra with plant species such as *Poa arctica*, *Ranunculus hyperboreus*, and *Saxifraga cernua* and on the drier parts species such as *Cerastium arcticum*, *Bistorta vivipara*, *Saxifraga cespitosa*, and *Cardamine pratensis* subsp. *polemonioides*. The vegetation is comparable with the Adventdalen wet habitat in the experimental grazing trials with captive geese. The minimum distance between exclosures was approximately 50 m. Each exclosure (2 m × 1 m) consisted of a mesh wire fence 50 cm high effectively preventing goose grazing.

Five randomly selected soil cores of 2 cm diameter were taken inside each exclosure and in grazed plots within 10 m from each exclosure within the same wet tundra habitat. Soil samples were separated into an upper layer consisting primarily of moss and dead organic material and a bottom layer consisting of mineral material. The thickness of each layer was measured to the nearest 0.05 cm. The top soil layer ranged between 1 and 7 cm. The underlying bottom soil layer was sampled to a depth ranging between 1 and 7 cm depending on the thaw depth. The five soil samples collected in each exclosure and grazed plot were later pooled, resulting in two samples (one for the top layer and one for the bottom layer), each between 100 and 400 mL of soil. Soil samples were pooled to increase the amount of seeds per sample, as low seed density was expected. Soil samples were kept for 4 months at 4 °C, as many seeds need a cold treatment before they can germinate. The seed contents of samples were quantified using a modified seedling emergence technique (Ter Heerd et al. 1996). The seeds were concentrated by forcing the samples through two sieves (2 and 0.212 mm) using a strong jet of water. The remaining soil material and seed concentrate were transferred to a greenhouse (25 °C day temperature, 15 °C night temperature, 15 h light period, automatic watering for 1 min twice a day). Although these temperatures were higher than normally experienced by plants in the High Arctic, previous work based on pilot studies of appropriate temperatures for maximizing germination (Cooper et al. 2004a) showed that 70% of the vascular flora of the regions sampled on Svalbard germinated in greenhouse trials at 18–22 °C. Our samples were spread in a thin layer (<5 mm) in pots (12 cm × 12 cm) filled with sterile potting soil and a fine layer (around 4 mm) of sterile sand. Emerging seedlings were counted and removed as soon as identification was possible. After 10 weeks, no new seedlings emerged. All data were expressed as number of germinating seedlings per cubic decimetre of the top or bottom soil sample.

Vegetation composition was determined inside each exclosure and grazed plot in July 1999. A frame of 10 cm × 25 cm, subdivided in 10 adjacent cells (each of 10 cm × 2.5 cm), was placed 10 times randomly inside each plot. Within each cell of the frame, the occurrence (present or absent) and the flowering status (flowering individuals or no flowering individuals) of all vascular plant species were recorded, resulting in a total of 100 points per plot. The result-

ing number showed the frequency of occurrence and frequency of flowering within each plot.

Statistical analyses

Differences in actual grazing pressure (minutes per square metre per day) experienced by ambient and open-top chamber plots and between plots that received a normal and high grazing pressure were analysed with two-way ANOVA followed by a Tukey test ($P < 0.05$). Differences in floral density for all species combined and per species before experimental grazing (experiment 1) were tested using MANOVA for the wet and mesic tundra separately. Grazing level (normal and high intensity grazing) and temperature (ambient and open-top chambers) were entered as fixed factors and blocks as random factors. As there were no significant effects of grazing, temperature, and blocks ($P < 0.1$) on initial floral density, data for the ambient and open-top chamber plots were combined in the rest of the analysis and plots within a block were treated as independent samples.

The effects of grazing treatment on flowering frequency and the absolute number and percentage of flowers grazed (experiment 1) were determined using ANOVA followed by a Tukey test ($P < 0.05$). Data for reduction in flowering frequency and percentage of flowers grazed were arcsine transformed before analysis. ANOVAs were carried out on data for all species combined and per species from the wet and mesic habitat separately for all plots with flowers present before grazing.

The relationship between grazing pressure and percentage flowers removed (experiment 2) was tested for significance by fitting different regression models (linear, logarithmic, inverse, S curve, quadratic, power, exponential) through the data points (SPSS statistical package). The significant model that explained the largest part of the variation (based on R^2 values) was chosen (Zar 1984).

The effects of grazing on plant species composition inside and outside exclosures in Ny-Ålesund were tested using MANOVA, entering grazing treatment as the fixed factor and exclosure number as the covariate. Paired sample t tests were applied to test for differences in the frequency of occurrence of plant species and percentage of flowering plants inside exclosures and in grazed plots. Frequencies of occurrence and percentage of flowering plants inside and outside exclosures were arcsine transformed prior to analyses. Differences in seed density between exclosed and grazed plots were tested with paired samples t tests for each species separately and for all species combined. Seed density was log transformed prior to analyses to improve homogeneity of variances (Zar 1984). Untransformed data are presented in the figures and tables.

Results

Experimental grazing

Experiment 1

Flowering frequencies in both the mesic and the wet sites at the time of the grazing trials were low (Table 2) but not unusual for the study area. In the wet site, this may partly be attributed to the late snowmelt in 2003 and the relatively early date of the grazing experiments. Despite the fact that

there were very few flowers present originally, grazing by Barnacle geese significantly reduced the number and proportion of flowers on the plot in both habitats and lowered the flowering frequencies still further (Table 2). At the individual species level, all species had a significant proportion of flowers grazed, and in the wet site, all had a significant reduction in number of flowers grazed. A reduction in flowering frequency shows that a greater proportion of flowers than vegetative shoots were grazed. Grazing reduced flowering frequency (i.e., reduction in flowering frequency >0) in most species, showing that the geese preferentially grazed inflorescences. In the field, selective grazing was very clear to see for some species as the seeds of *Alopecurus* and the flowers and bulbils of *Bistorta* were stripped off, leaving the peduncles in place. Interspecific differences were not tested statistically owing to too many missing values (i.e., plots without flowers before grazing). Inflorescences of species with large and colourful flowers were almost completely grazed even in the 1 h grazing treatment. Some species had almost all of the inflorescences removed ($>94\%$) by geese on the plots for 1 h (*Alopecurus*, *Pedicularis*, *Bistorta*, *Stellaria*, *Saxifraga cernua*, *Saxifraga foliolosa*), whereas others experienced a tendency towards increasing proportion grazed with increasing time on the plot (*Salix*, *Dupontia*, *Eriophorum*). Interpretation of these interspecific differences has to be undertaken with care. The density of *Salix* shoots and flowers on the plots was much higher than that of any of the other species. Many fluffy seedheads of *Eriophorum* were bitten off and discarded rather than consumed during the 5 h grazing treatment. True interspecific differences cannot be shown here but could be determined by a "cafeteria" experiment.

Experiment 2

The proportion of the total number of flowers removed increased with the grazing pressure on the plot (Fig. 1). Even at a low grazing pressure, a high proportion of the total number of flowers on the mesic tundra were removed. At an actual grazing pressure of 20 min grazing·m⁻², a reduction of $>50\%$ in total floral abundance was observed. On the more intensively grazed plots, few or no flowers remained after grazing.

Species composition and flowering inside long-term excluded plots

The vegetation inside and outside the 7-year-old exclosures was dominated by *Poa arctica* and dicots such as *Saxifraga cernua* and *Cardamine pratensis* (Table 3). Of the nine species that had a frequency of occurrence $>3.0\%$ in the exclosed plots, seven had a higher frequency inside exclosures than outside. These were *Saxifraga cernua*, *Cardamine pratensis*, *Cerastium arcticum*, *Bistorta vivipara*, *Cochlearia groenlandica*, and *Equisetum arvense*. The frequency of occurrence of *Deschampsia alpina*, *Ranunculus hyperboreus*, and *Poa abbreviata* was higher in the grazed plots than in the exclosures, but not significantly. Three species exclusively occurred inside the exclosures and two were exclusively found in grazed plots. No overall significant effects of grazing on species composition ($F_{[1,4]} = 0.60$, $P = 0.7$) or on individual species could be detected ($P > 0.05$, note the small sample size and large variation between

Table 2. Reduction of flower abundance by grazing on wet and mesic tundra.

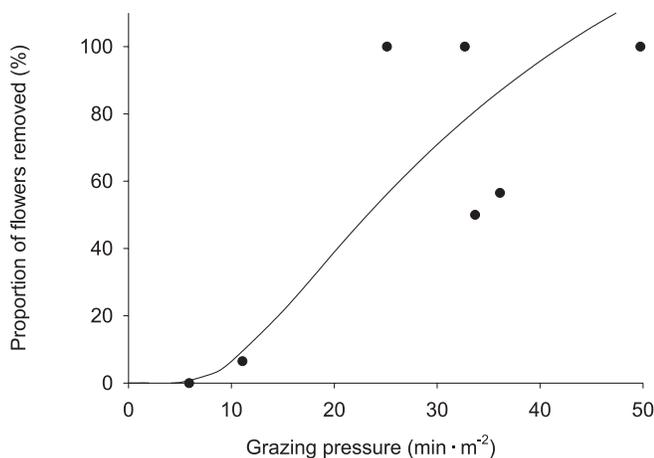
Species	No. of hours geese were on plot	Initial flowering frequency (%)	Reduction in flowering frequency	No. of flowers grazed-m ⁻²	% flowers grazed
Wet plots					
Flowering species data combined	0	1.08±0.22	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	0.98±0.19	0.3±0.2ab	7.5±2.9ab	42.1±13.3b
	5	1.15±0.33	1.0±0.3b	15.8±5.7b	89.9±5.3c
df			2,24	2,24	2,24
F			6.71	4.64	20.92
P			0.005	0.020	<0.001
<i>Dupontia fisheri</i>	0	0.9±0.2	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	0.7±0.3	0.3±0.2a	5.6±1.1ab	51.4±19.3b
	5	1.1±0.4	0.9±0.3a	17.8±8.4b	88.1±8.0b
df			2,16	2,16	2,16
F			2.41	3.83	8.43
P			0.122	0.044	0.003
<i>Eriophorum scheuchzeri</i>	0	7.0±1.5	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	32.7±17.7	-0.1±0.1a	0.3±0.3a	14.3±14.5a
	5	39.3±18.2	2.8±1.3a	7.4±2.3b	87.5±8.0b
df			2,15	2,15	2,15
F			3.96	10.51	12.96
P			0.042	0.001	<0.001
<i>Saxifraga cernua</i>	0	100.0±0.0	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	54.1±46.3	4.1±4.2a	6.2±0.9b	100.0±0.0b
	5	3.6±2.1	3.6±2.1a	2.7±0.9ab	100.0±0.0b
df			2,3	2,3	2,3
F			0.64	17.895	3.6×10 ³¹
P			0.587	0.022	<0.001
<i>Saxifraga foliolosa</i>	0	69.4±31.2	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	68.1±32.5	1.4±1.5a	3.6±0.0b	100.0±0.0b
	5	5.7±0.0	5.7±0.0a	3.6±0.0b	100.0±0.0b
df			2,4	2,4	2,4
F			3.95	8.77×10 ³³	7.0×10 ³²
P			0.113	<0.001	<0.001
Mesic plots					
Flowering species data combined	0	1.9±0.4	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	2.9±0.5	0.7±0.2a	56.3±20.9b	32.6±11.1ab
	5	2.7±0.7	0.6±0.2a	49.6±9.6b	54.3±10.2b
df			2,27	2,27	2,27
F			3.60	5.40	6.55
P			0.041	0.011	0.005
<i>Alopecurus borealis</i>	0	0.9±0.5	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	1.5±0.5	1.4±0.5a	7.5±2.1a	96.4±3.6b
	5	0.9±0.4	0.2±0.8a	4.6±3.0a	60.0±24.6ab
df			2,11	2,11	2,11
F			1.24	2.50	7.97
P			0.326	0.127	0.007
<i>Salix polaris</i>	0	2.2±0.5	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	3.4±0.7	0.7±0.3a	47.4±21.7a	28.7±11.8a
	5	2.9±0.9	0.7±0.3a	43.9±11.8a	39.0±11.2a
df			2,25	2,25	2,25
F			2.54	3.07	3.04
P			0.099	0.064	0.066
<i>Pedicularis lanata</i> subsp. <i>dasyantha</i>	0	8.8±0.5	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	41.6±30.2	41.6±30.2a	7.1±2.8a	100.0±0.0b
	5	7.1±3.6	7.1±3.6a	7.1±0.0a	100.0±0.0b
df			2,5	2,5	2,5
F			1.12	5.37	1.4×10 ³²
P			0.395	0.057	<0.001

Table 2 (concluded).

Species	No. of hours geese were on plot	Initial flowering frequency (%)	Reduction in flowering frequency	No. of flowers grazed·m ⁻²	% flowers grazed
<i>Bistorta vivipara</i>	0	4.3±0.8	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	2.5±0.8	2.4±0.9a	6.7±0.4a	95.0±5.0b
	5	4.7±2.9	4.7±2.9a	11.4±4.0a	100.0±0.0b
df			2,9	2,9	2,9
<i>F</i>			0.91	3.45	74.88
<i>P</i>			0.436	0.077	<0.001
<i>Stellaria longipes</i>	0	54.8±45.4	0.0±0.0a	0.0±0.0a	0.0±0.0a
	1	5.7±0.0	5.7±0.0b	3.6±0.0a	100.0±0.0b
	5	1.0±0.3	1.0±0.3b	2.4±0.6a	100.0±0.0b
df			2,3	2,3	2,3
<i>F</i>			55.5	7.5	1.4×10 ³²
<i>P</i>			0.004	0.068	<0.001

Note: Mean ± SE is given. Different letters indicate significant differences between grazing treatments.

Fig. 1. Proportion of flowers (of all species) removed by grazing geese in relation to the grazing pressure in the mesic habitat on experimentally grazed plots in Adventdalen. Data from the wet habitat are not shown, as the total floral abundance was low in this habitat. The line shows the best fit through data ($y = e^{(5.46 - 35.96/x)}$; $r^2 = 0.85$, $F_{[5,7]} = 27.48$, $P = 0.003$).



plots). The average number of species inside (6.3) and outside (5.3) the enclosures did not differ significantly ($P > 0.05$). However, the average number of plant species that flowered was more than four times higher in enclosed than in the grazed plots ($t_{[3,4]} = 4.33$, $P = 0.002$). Most plant species showed a low proportion of flowering or did not flower at all in the grazed plots, whereas a high proportion were flowering inside the enclosures.

Soil seed bank

The top soil layer ranged between 1 and 7 cm and was on average thicker inside enclosures than outside enclosures (3.60 versus 2.98 cm; $t_{[3,4]} = 4.91$, $P = 0.016$). In the top layer (organic layer, mostly moss) inside the enclosures, the density of total viable seeds and other propagules was six-fold higher than that of grazed plots ($t_{[3,4]} = 3.77$, $P = 0.033$) (Fig. 2a). However, for individual species, we detected no significant differences between enclosures and grazed plots in the density of germinable seeds in the top layer. Five plant species from enclosure samples and three

species from grazed plot samples germinated seed. Of the five species from the enclosure samples, three were found only inside the enclosures and were absent in the seed bank of the grazed plots, i.e., *Ranunculus hyperboreus*, *Equisetum arvense* (although *Equisetum* does not produce seeds and sexually reproduces via spores, for simplicity, it is included in the seed bank) and *Sagina nivalis*. The species accounting for most of the germinable seeds or other propagules inside the enclosures were *Saxifraga cernua* (from bulbils), *Ranunculus hyperboreus*, and *Cardamine pratensis*. No difference was found in the density of viable seeds in the bottom soil layer between enclosed and grazed plots ($t_{[3,4]} = -0.002$, $P = 0.998$) (Fig. 2b). *Ranunculus hyperboreus* was the most recorded plant species inside and outside the enclosures. In total in the bottom layer, four species were found inside enclosures compared with three in grazed plots. *Cardamine pratensis* and *Juncus* spp. were found only inside enclosures, whereas *Phippsia algida* was only encountered in the grazed plots. The composition of species found in the seed bank in the top layer resembled the plant species composition of the established vegetation more than that of the seed bank found in the bottom layers. In the bottom layer, a large proportion of the seeds consisted of *Phippsia algida* and *Juncus* spp., which did not occur in the established vegetation. The common species *Saxifraga cernua* was absent in the bottom soil seed bank, reflecting its representation by relatively short-lived bulbils rather than seed. The density of viable seeds in the bottom layer was low compared with that in the top layer inside the enclosures. Some species were found only in the top layers (*Saxifraga cernua*, *Equisetum arvense*, *Sagina nivalis*), whereas others were found only in the bottom layers (*Phippsia algida*, *Juncus* spp.).

Discussion

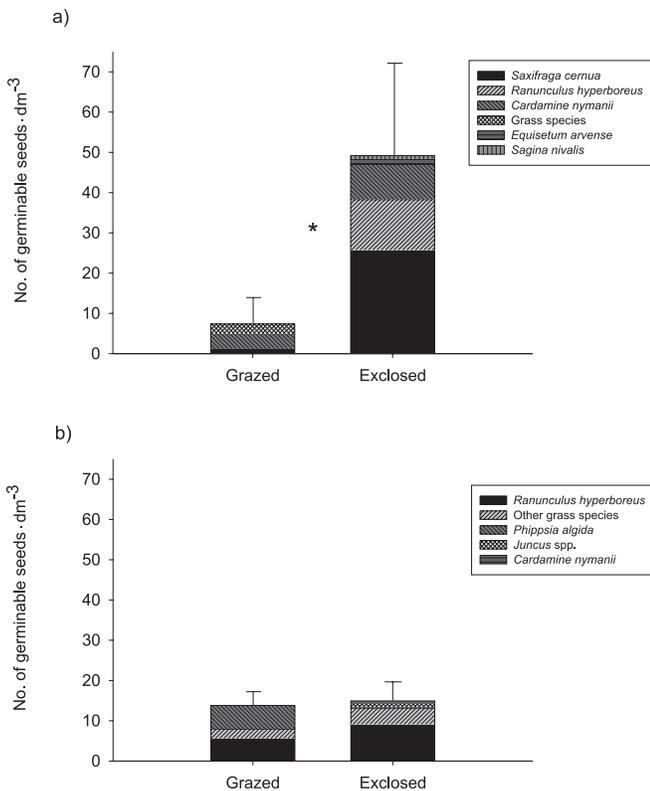
The main conclusion of this study is that preferential floral grazing by Barnacle geese on arctic vegetation decreases the floral abundance of a variety of species with consequences for seed production. Long-term intensively grazed vegetation had lower floral abundance than plots excluded from grazing for 7 years, mainly owing to a lower frequency of flowering of grazed plants and possibly also owing to a shift in vegetation composition. This resulted in a depletion of the

Table 3. Mean frequency of occurrence (SE) and the mean number of plant species inside exclosures ($n = 4$) excluding wild geese for 7 years and on grazed plots in Ny-Ålesund.

Species	Frequency of occurrence		Frequency of flowering	
	Exclosure	Grazed	Exclosure	Grazed
<i>Poa arctica</i>	99.5 (0.5)	98.3 (1.0)	29.8 (18.8)	0 (0)
<i>Saxifraga cernua</i>	45.8 (20.9)	12.0 (5.8)	50.1 (14.6)a	0 (0)b
<i>Cardamine pratensis</i> subsp. <i>polemonioides</i>	32.3 (19.4)	11.8 (7.8)	0 (0)	0 (0)
<i>Cerastium arcticum</i>	14.5 (13.5)	0 (0)	70.6 (2.8)	0 (0)
<i>Bistorta vivipara</i>	7.0 (7.0)	1.0 (1.0)	35.7	0 (0)
<i>Cochlearia groenlandica</i>	6.5 (3.2)	1.8 (1.0)	35.7 (16.0)	33.3 (23.6)
<i>Equisetum arvense</i>	3.5 (3.5)	0 (0)	—	—
<i>Deschampsia alpina</i>	3.0 (2.1)	5.0 (2.9)	11.1 (7.9)	0 (0)
<i>Ranunculus hyperboreus</i>	2.5 (1.7)	11.5 (11.5)	38.1 (3.4)	6.5
<i>Saxifraga cespitosa</i>	1.0 (1.0)	5.3 (4.3)	75.0	37.0 (16.3)
<i>Poa pratensis</i> subsp. <i>alpigena</i>	0.3 (0.3)	0 (0)	100.0	—
<i>Poa abbreviata</i>	0 (0)	3.8 (3.8)	—	0 (0)
<i>Carex</i> spp.	0 (0)	0.3 (0.3)	—	0 (0)
No. of species	6.3 (0.6)	5.3 (1.1)	4.3 (0.9)a	1.0 (0.4)b

Note: The frequency of flowering for each species (as a percentage of plants present of that species) and the mean number of plant species that flowered are indicated (SE is given in parentheses when the species was flowering on more than one plot). Different letters indicate significant differences ($P < 0.05$).

Fig. 2. Density of germinable seeds and other propagules found in the (a) top soil layer and (b) bottom soil layer inside and outside exclosures ($n = 4$ with SE of total number of seeds) that excluded wild geese for 7 years in Ny-Ålesund. The asterisk indicates a significant difference in total seed density ($P < 0.005$).



seed bank in the upper soil layers in long-term goose-grazed areas. A number of arctic plant species were found to produce a long-lived seed bank buried in deeper soil layers.

This could serve as a long-term reservoir for recovery when grazing pressure is relaxed.

Impact of geese on flower density, vegetation, and seed banks

The experiments with captive Barnacle geese showed unequivocally that geese have a strong preference for flowers and fertile shoots compared with vegetative shoots, and despite the low floral frequency (proportion of flowers to total shoots) and the low floral density (number of flowers per square metre) of most plant species, a high proportion of flowers were removed by the geese even at relatively low grazing pressure. Other studies report that flowers are intensively grazed upon by geese (Alsos et al. 1998; Prop and de Vries 1993). In addition to flowers, seed heads (fruits) can be an important food source and can make up to 7% of the diet in wild geese (Prop and Vulink 1992). Compared with other food items, flowers and seed heads contain high amounts of metabolizable energy, which makes them an attractive food source.

Long-term (7 years) exclusion of goose grazing also had large effects on flowering frequency. On average, a fourfold higher number of plant species flowered inside the exclosures compared with the grazed plots. All plant species present inside the exclosures produced fertile shoots, except for *Cardamine pratensis* and *Equisetum arvense*. *Cardamine pratensis* is a plant species normally flowering after the end of July (D.P.J. Kuijper, personal observation) and was therefore not flowering at the time of vegetation observations (early July). *Equisetum arvense* does not flower but reproduces via spores. In contrast, of the 10 species found as mature plants on the grazed plots, only three were found flowering. The low density of flowers on these long-term grazed plots can be the result of the direct selective grazing by geese on flowers, as was also observed in the grazing experiment in Adventdalen. However, the low floral density may also be

explained by indirect effects of grazing. Firstly, goose grazing may lead to a reduction in flower frequency by changing the overall species composition. Although no significant effects of grazing on plant species could be detected, the results of the enclosure study suggested that species composition could be changing. Long-term exclusion of goose grazing led to a higher (nonsignificant) frequency of occurrence of *Saxifraga cernua*, *Cardamine pratensis*, *Cerastium arcticum*, *Bistorta vivipara*, and *Cochlearia groenlandica*: all are species known to be florally grazed by herbivores on Svalbard (Prop and de Vries 1993; Alsos et al. 1998; Cooper and Wookey 2003; E.J. Cooper, personal observation). A change in species composition was further indicated by the exclusive occurrence of a number of species inside excluded or grazed plots. This means that the total seed production on these plots may be partially affected by this shift in species composition. *Equisetum arvense* was found only inside enclosures; the vegetative shoots of this species are very much favoured by Barnacle geese (E.J. Cooper and I.S. Jónsdóttir, unpublished data). Secondly, continuous grazing can deplete the resources of a plant, which can be allocated to reproductive organs such as flowers (e.g., see Hickman and Hartnett 2002; Gustafsson 2004). In the long term, this may lead to selection of individuals that are adapted to a high grazing pressure and mainly reproduce clonally. *Deschampsia alpina*, *Ranunculus hyperboreus*, and *Poa abbreviata* were slightly (but not significantly) more frequent in the grazed than in the excluded plots. Graminoids are generally grazing tolerant and *Ranunculus hyperboreus* can often be found in disturbed wet tundra areas (E.J. Cooper, personal observation). Since the establishment of the Barnacle goose population in Ny-Ålesund in the 1980s (Loonen et al. 2000), the study area has been intensively grazed (with grazing pressure of up to 22 min·m⁻²; Loonen et al. 2000) throughout the season. This history of continuous grazing may have indirectly led to an overall reduction of flowering plant species throughout the season and thus the selection of species more dependent on clonal growth.

Both direct and indirect effects of grazing reduce floral abundance and hence seed production on grazed plots. As a result, the supply of seeds to the seed bank decreases. Long-term grazing by Barnacle geese is thus expected to result in a depleted seed bank. We found that exclusion of Barnacle geese for 7 years resulted in sixfold higher densities of viable seeds and other propagules in the top soil layers compared with those in grazed plots. Moreover, the number of species found in the seed bank inside the enclosures was higher than in grazed plots. In salt marshes in La Pérouse Bay in the Canadian Low Arctic, loss of vegetation as a result of intensive grazing and grubbing by Lesser Snow geese also led to a decline in the density of the soil seed bank (Chang et al. 2001). The seed density was only affected on sites with large-scale and long-term degradation as a result of grazing by Lesser Snow geese. In contrast, the present study shows that goose grazing in the High Arctic can have significant effects on the density of seeds in the soil seed bank long before loss of the established vegetation occurs as a result of goose grazing and grubbing. Selective grazing of these herbivores on flowering shoots and seed heads, possibly in combination with a reduction in floral frequency in-

directly caused by grazing, results in a depleted soil seed bank. In this way, avian herbivores can have an important influence on the soil seed bank in addition to more generalist large herbivores (O'Connor and Pickett 1992; Erkkilä 1998; Sternberg et al. 2003).

Germinable seed densities were converted to seedlings per square metre for comparison with published densities for other places on Svalbard (see Cooper et al. 2004a). In the top layer, grazed plots had a total germinable density of 8–559 seedlings·m⁻², whereas the density of excluded plots was 500–3496 seedlings·m⁻² and the bottom layers germinated 140–979 seedlings·m⁻². The seed densities of the basal layers are similar to those of published values for polar heath in the north west coast of Svalbard (Brøggerhalvøya and Sarsøyra) and grazed plots are at the lower end of this range. Excluded plots had higher seed bank densities, ranging between that of the north west coast and of thermophilic heath in Colesdalen. The data are therefore within the range of values that may be expected from previous studies on Svalbard.

Persistence of seed bank

Seeds can persist in the soil and remain viable for a long time. McGraw et al. (1991) suggested that buried seeds can persist in the soil for several centuries in arctic environments; low soil temperatures associated with slow decomposition rates are likely to increase the seed longevity. Soil temperatures are lower under a thick insulating moss layer (Van der Wal et al. 2000b; Van der Wal and Brooker 2004) inside compared with outside the enclosures in Ny-Ålesund. Viable seeds were found in the present study under a top layer (mostly moss) ranging between 1 and 7 cm. Considering an increase of moss layer of 2.7 mm·year⁻¹ inside the enclosures (Van der Wal et al. 2000b), we calculate that the seeds have a minimum age of 3.7–25.9 years. As the enclosures in Ny-Ålesund were erected 7 years before sampling took place, this means that germinating seeds could have been deposited well before the enclosures were erected, explaining why no effects of herbivore exclusion were found in the bottom soil layer. Additionally, the population of Barnacle geese in Ny-Ålesund has increased during the past decades (Loonen et al. 2000), which may have reduced the seed rain proportionately.

Role of geese in European arctic tundra vegetation

Reindeer are known to reduce floral abundance on Svalbard (Cooper and Wookey 2003). In areas where reindeer densities are relatively low and goose densities are high, we predict that geese are the primary flower consumers. The populations of the Barnacle geese and Pink-footed geese breeding on Svalbard have shown a large increase during the past decades (Madsen et al. 1999; Owen and Black 1999). Previous studies of goose grazing on Svalbard do not report a major impact on the vegetation species composition (Drent et al. 1998; Loonen and Solheim 1998), although the data presented here from the 7-year enclosures indicate grazing-induced changes. The ability of many arctic plants species to reproduce clonally (Jónsdóttir et al. 1996) rather than depending entirely on sexual reproduction may explain the slow rate of response of vegetation composition and the resilience of the vegetation in this area to grazing. In our

study area, we found a long-term persistent seed bank in the deep soil layers. The germinable density of these seeds was higher than the upper layer of the grazed plots but not as high as the upper layer in the excluded plots. A reserve of seeds in such areas with deep moss and soil layers could be used for recolonization if grazing pressure reduced the plant cover dramatically.

Seed banks can play an important role in vegetation dynamics in the Arctic. Most arctic plant species have viable seed banks (McGraw and Vavrek 1989). More than 60% of the total vascular plant species found on Svalbard are estimated to frequently reproduce sexually (Eurola 1972; Brochmann and Steen 1999). The production of seeds and the emergence of plants via seedlings thus seem to be important processes for a large part of the Svalbard flora (Cooper et al. 2004a). Habitat disturbances (e.g., overgrazing, freeze–thaw dynamics, glacial processes, and anthropogenic disturbance) are a common phenomenon in the Arctic (Forbes et al. 2001; Walker and Walker 1991) and stimulate germination of seed from the seed bank and thus enhance recolonization. In addition, many areas of Svalbard have a very thin soil of <2 cm depth and the density of germinable seeds is low (Cooper et al. 2004a). In these cases, a lower, persistent seed bank is not present, since there is little, if any, soil. Any reduction in the seed bank owing to grazing is thus likely to have a very important effect on the reestablishment of vegetation following disturbance. This study indicates that increased goose grazing pressures may in the long term reduce resilience to such disturbances in low-productive tundra ecosystems through soil seed bank depletion and thus potentially change species composition of the tundra vegetation.

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