

Long-term destruction of sub-arctic wetland vegetation by lesser snow geese¹

Peter M. KOTANEN², Department of Ecology and Evolution, University of Chicago, 1101 E 57th Street, Chicago, Illinois 60637, U.S.A.

Robert L. JEFFERIES³, Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada, e-mail: jefferie@botany.utoronto.ca

Abstract: During the last two decades, the mid-continent population of lesser snow geese (*Anser caerulescens caerulescens*), which breeds in the Canadian eastern Arctic, has increased dramatically to at least 3 million birds. In spring, the birds follow the retreating snowline northwards to the breeding grounds. They forage intensively on shoots of sedges just south of the snowline, eating the swollen shoot bases and discarding the remainder. Exclosures were established in 1985/86 at La Pérouse Bay, Manitoba to determine the effects of protection from foraging on the shoot densities of sedges. Between 1986 and 1995, numbers of shoots increased from 1.1 to 2.2 times in exclosed plots, while numbers in grazed plots declined to between 0.19 and 0.33 times their original values. Sedge assemblages were replaced by moss carpets or standing water rich in peat debris. The ecological significance of the results is discussed in relation to re-establishment of vegetation and the role of herbivores in changing species assemblages.

Keywords: herbivory, shoot-pulling, sedges, moss carpets, alternative vegetation states.

Résumé: Au cours des deux dernières décennies, la population de la petite oie des neiges (*Anser caerulescens caerulescens*) a augmenté fortement pour atteindre au moins trois millions d'individus. Au printemps, les oiseaux migrent vers leur aire de nidification, située dans l'est de l'Arctique canadien, en suivant la limite méridionale des neiges qui retraite alors vers le nord. Au cours de leur migration et sur les sites de nidification, les oies se nourrissent de façon intensive et broutent les tiges de cypéracées. Elles mangent plus particulièrement la base des tiges et laissent sur place les autres parties des plantes. Nous avons installé des exclos en 1985 et en 1986 à La Pérouse Bay (Manitoba) pour déterminer les conséquences de ce dispositif de protection sur la densité des tiges de cypéracées. Entre 1986 et 1995, le nombre de tiges a augmenté d'un facteur de 1,1 à 2,2 dans les exclos. Dans les sites témoins (broutés), le nombre de tiges en 1995 ne représentait plus qu'un faible pourcentage (0,19 à 0,33) de ce qu'il y avait à l'origine. Les communautés de cypéracées ont été remplacées par des tapis de mousses ou par des étangs riches en débris organiques. La signification écologique de ces résultats est discutée ici en relation avec le rétablissement de la végétation et le rôle que les herbivores peuvent jouer au niveau des communautés végétales.

Mots-clés: herbivorie, arrachement de tiges, cypéracées, tapis de mousses, type de végétation alternatifs.

Introduction

Populations of a herbivorous bird, the lesser snow goose (*Anser caerulescens caerulescens* L.) have increased dramatically in recent decades in the mid-continent region of North America. The current population size is at least 3 million birds (Abraham *et al.*, 1996), and the rate of increase in population numbers is in the order of 7% per annum (Cooke, Rockwell & Lank, 1995). The increase is thought to be related to the use of agricultural land as a source of forage on wintering grounds and along flyways (Hobaugh, Stutzenbaker & Flickinger, 1989; Alisaukas & Ankney, 1992; Robertson & Slack, 1995) which, in effect, provide an energy and nutrient subsidy to geese (Abraham *et al.*, 1996).

At one breeding colony, at La Pérouse Bay on the Hudson Bay coast, numbers of lesser snow geese have increased from just under 2000 pairs in 1968 (Cooke, Rockwell & Lank, 1995) to an estimated 23 000 pairs in 1990 (Kerbes, unpubl. photographic inventory). Such a large increase in

numbers may be expected to lead to dramatic changes in the vegetation in the area. When the birds migrate north in spring to this site and to other breeding colonies in the Hudson Bay region, they follow the retreating snowline northwards. Often, thousands of staging birds feed on vegetation immediately south of the snowline. The birds forage intensively on shoots of fresh-water sedges, particularly *Carex aquatilis* (nomenclature follows Scoggan, 1978), before growth of shoots has commenced (Jefferies, 1988a,b). A shoot is pulled from its base, the swollen basal portion, which is rich in soluble carbohydrates and total nitrogen, is eaten (Gadallah & Jefferies, 1995), and the remainder of the shoot is discarded. This type of foraging activity occurs annually in spring, but its intensity at a given site depends upon the uncertainties of weather and position of the snowline in any particular year. Over successive years the cumulative removal of vegetative and reproductive shoots of these sedges may be predicted to lead to significant changes in the species composition of the vegetation. In order to detect such changes, a series of exclosures from which geese were excluded were set up in 1985-1986 at La Pérouse Bay in fresh-water ponds and in sedge meadow habitats 0.5 km inland from the coastal salt marshes. In

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²Present address: Department of Botany, University of Toronto at Mississauga, 3359 Mississauga Road, North, Mississauga, Ontario L5L 1C6, Canada, e-mail: pkotanen@credit.erin.utoronto.ca

³Author for correspondence.

1986, 1989 and 1995, comparisons of shoot densities were made between exclosures and quadrats in which shoots were unprotected from the effects of foraging.

Material and methods

STUDY SITE

La Pérouse Bay (58° 04' N, 94° 03' W), is located on the Hudson Bay coast about 25 km east of Churchill, Manitoba. Inland from the upper limit of spring tides, the landscape consists of a mosaic of fresh-water ponds, areas of saturated moss, and graminoid communities dominated by *Carex* species. *Carex aquatilis* (50 cm - 1 m tall) frequently forms dense stands in standing water and permanently saturated ground. Smaller sedges (30 cm tall) that include *Carex atrofusca*, *C. capillaris*, *C. flavicans*, *C. microglochin*, *C. rariflora* and *C. vaginata* grow in shallow water and in saturated carpets of moss (mostly *Drepanocladus uncinatus* and *Aulacomnium* species) that surround many ponds. On frost-heave mounds between ponds, the vegetation is dominated by shrubs that include *Salix candida*, *S. lanata*, *S. planifolia*, *Betula glandulosa*, *Myrica gale* and *Empetrum nigrum*. Since the mid-1980's, the density of nests of lesser snow geese in this area has been one of the highest on the Cape Churchill peninsula, approaching 2000 nests km⁻². Geese have used the vegetation as a primary source of forage during the periods of nest initiation and incubation from late May to early June, before the aboveground growth of sedge leaves commences.

EXCLOSURES

In 1985 and 1986 a series of > 30 exclosures was established in the *Carex*-dominated fresh-water sites used by geese. Some shoot-pulling had occurred prior to the spring of 1985 (pers. observ.) at these sites. The exclosures were established for various purposes (Kotani & Jefferies, 1989a,b). They were either 0.5 m × 0.5 m (small) or 4 m × 5 m (large); all were constructed with chicken wire (2.5 cm mesh size, 50 cm high) stapled to wooden stakes anchored in the ground. The 30 exclosures were distributed along a belt transect 1 km in length and 200 m wide. Exclosures were at least 50 m apart. Two types of sedge assemblages were protected: those dominated by stands of *Carex aquatilis* and those dominated by small sedges, of which *Carex flavicans* was the most abundant. Adjacent, unexclosed plots were also set up within 5 metres of each exclosure.

In 1986, 1989 and 1995 growing shoots were counted in subplots within each exclosure and within the immediately adjacent, unexclosed plots. Observers, number of plots located, and total area sampled varied in the three years, as discussed below (Table I). All recordings of shoot densities were made in June. A consequence of having multiple observers was that different exclosures were sampled in different years. Most (> 75%) of the exclosures sampled in 1986 were small (< 1 m), while those sampled in 1989 were larger (> 1 m); a full size range was sampled in 1995.

STATISTICAL METHODS

The two types of communities sampled (*C. aquatilis* and small sedges) were analyzed separately because of their

TABLE I. Sample sizes. All plots were established in 1985 or 1986

Assemblage	Year	Treatment	Plots sampled	Subplots/plot	Area/subplot (cm ²)	Total area sampled (cm ²)
<i>C. aquatilis</i>	1986	exclosed	6	4	156	3750
		non-exclosed	6	4	156	3750
	1989	exclosed	5	3	100	1500
		non-exclosed	5	3	400	6000
	1995	exclosed	7	3	100	2100
		non-exclosed	7	3	100	2100
Small sedges	1986	exclosed	5	10	25	1250
		non-exclosed	5	10	25	1250
	1989	exclosed	4	3	100	1200
		non-exclosed	4	3	400	4800
	1995	exclosed	15	3	100	4500
		non-exclosed	15	3	100	4500

distinctly different structure and species composition. In each case, data were analyzed using mixed-model factorial ANOVAs (Kirk, 1982). Foraging, mainly shoot-pulling, was treated as a discontinuous fixed factor (exclosed plot or not), while "site" was treated as a random factor. All data were square-root transformed before analysis in order to stabilize variances (Cochran's C : $0.05 > p > 0.01$ for 1 ANOVA; $p > 0.05$ in the remainder). To help compensate for varying sample sizes, these ANOVAs were supplemented with estimates of the "strength of association" statistic, ω^2 . This statistic is analogous to r^2 in a regression, indicating the proportion of experimental variance explained by a treatment (Kirk, 1982). Unlike variance components, ω^2 is appropriate for a discontinuous fixed factor (Kirk, 1982). A time-series design was not used for two reasons. First, some plots were destroyed by polar bears, caribou and geese, so that the plots available differed on each occasion recordings were made, precluding the use of a balanced design. Second, observers, sampling areas, and the average size of the plots sampled differed on each occasion, suggesting it would be best to treat each year independently.

Results

Between 1986 and 1995, numbers of shoots in exclosed plots increased from 1.1 (small sedges) to 2.2 times (*C. aquatilis*), while numbers in non-exclosed plots declined to between 0.19 (small sedges) and 0.33 times (*C. aquatilis*) their original values (Figure 1). In 1986, densities of shoots did not differ significantly between non-exclosed and exclosed plots in either type of sedge assemblage (Table II), confirming that non-exclosed and exclosed plots initially were well matched; however, there were significant site effects, and a significant foraging × site interaction for *C. aquatilis* (Table II). Despite relatively small sample sizes, non-exclosed plots contained significantly fewer shoots than exclosures by 1989. By 1995, this difference was highly significant, in spite of foraging × site interactions (Figure 1; Table II).

In 1995, it was apparent that small (< 1 m²) exclosures had survived much more successfully than large ones which often were damaged and contained droppings, pulled shoots, and other evidence of entry by geese and other animals. When large and small exclosures were analyzed separately,

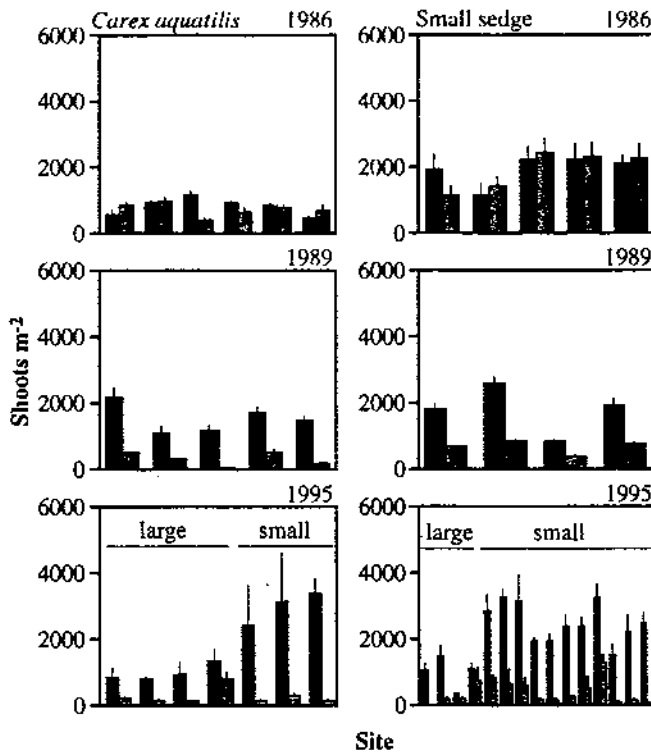


FIGURE 1. Mean densities of shoots (+SE). Results have been re-expressed as shoots m⁻². Each pair of bars represents one site: filled bars = exclosures; stippled bars = grazed areas. For 1995 data, plot size (large or small) is also shown. See Tables I and II for sample sizes and significance tests.

both analyses detected a significant and negative effect of shoot pulling in *Carex aquatilis* assemblages ($F_{1,3} = 27.28$, $p < 0.05$ and $F_{1,2} = 132.71$, $p < 0.01$, respectively). In small sedge communities, shoot pulling significantly reduced shoot numbers in small, unprotected plots compared with numbers in small exclosures ($F_{1,10} = 309.68$, $p < 0.01$), but there was no difference between large non-exclosures and large exclosures ($F_{1,3} = 9.75$, $p > 0.05$) because of damage to the latter. Damage to both plot markers and exclosures made it difficult to unambiguously identify the sizes of some of the plots that were sampled in 1986 and 1989. However, since smaller exclosures indicated a stronger effect of herbivory than larger exclosures, our pre-1995 results should be conservative both in 1986 (when mostly small exclosures were sampled and no effect of herbivory was detected) and in 1989 (when large exclosures were sampled and herbivory had a significant effect). These results strengthen the conclusion that herbivory initially had little effect, but that by 1989, strong differences had developed between exclosed and unprotected plots.

Statistical power evidently was not a problem. After the first sampling, the effects of foraging were consistently significant and strength of association (ω^2) statistics indicated that foraging explained a large fraction of the overall variance (Table II). Frequent foraging \times site interactions indicate that magnitude of foraging effects differed from one location to the next, but because $MS_{\text{foraging} \times \text{site}}$ (MS : mean square) was used as the error term, this does not alter the overall conclusion that foraging by geese produced an

TABLE II. Results of mixed-model factorial ANOVAs examining the effects of foraging by geese and location on the number of shoots cm⁻². "Foraging" (shoot-pulling) is a fixed factor, "site" is random. MS : mean square. Also shown is ω^2 , a measure of foraging treatment strength

Assemblage	Year	Factor	df	MS	ω^2
<i>Carex aquatilis</i>	1986	foraging	1	0.005	0.000
		site	5	0.005	
		foraging \times site ¹	5	0.012**	
		residual ²	36	0.002	
		residual	41	0.002	
	1989	foraging	1	0.412**	0.670
		site	4	0.024**	
		foraging \times site	4	0.006*	
	1995	foraging	1	0.785**	0.453
		site	6	0.027	
		foraging \times site	6	0.033*	
		residual	28	0.012	
Small sedges	1986	foraging	1	0.000	0.000
		site	4	0.087*	
		foraging \times site	4	0.017	
		residual	90	0.028	
	1989	foraging	1	0.163**	0.516
		site	3	0.027**	
		foraging \times site	3	0.004*	
	1995	foraging	1	1.916**	0.565
		site	14	0.048**	
		foraging \times site	14	0.015*	
		residual	60	0.007	

¹Error term for F_{foraging}

²Error term for F_{site} and $F_{\text{foraging} \times \text{site}}$

* $p < 0.05$

** $p < 0.01$

increasingly severe average reduction in densities of shoots, relative to similar values for exclosures.

Discussion

In spite of different observers, different sampling areas and destruction of exclosures over the decade, the deleterious effect of foraging and especially shoot-pulling of sedges by geese on shoot densities of these species is clearly evident. The results reflect exploitation of an annual resource pulse of nutrient-rich shoot bases by an expanding population of geese at a time of year when aboveground growth of biomass is very low or absent. Later, in the snow-free season, the nutritional value of the swollen shoot base declines as shoot growth occurs and resources are transferred to the mid- and upper sections of expanding shoots (Gadallah & Jefferies, 1995). The exploitation of nutritional pulses characterizes arctic herbivory (Jefferies, Klein & Shaver, 1994), where animals track the availability of high quality vegetation in space and time. The consequences for exploited plant populations can be severe. For example, the effects of muskox herbivory on the reproductive shoots of *Oxytropis viscida* early in the growing season may result in a decrease in the probability of flowering for a least two years following grazing (Mulder & Harmsen, 1995). The effects of these resource exploitations on plant populations are cumulative and may be expected to lead to changes in assemblages of plant species.

This has occurred in areas immediately inland from La

Pérouse Bay, where shoot-pulling has been intensive. In shallow ponds, where dense stands of *Carex aquatilis* were formerly present, the death of stands has created open ponds of standing water devoid of vegetation. Mixing of water by surface winds has resulted in increased mobility of large amounts of organic matter and peat debris. The system is dysfunctional and the depth and mobility of the debris appear to restrict germination and seedling establishment of wetland species. Muds are anoxic and some ponds have remained in this state for a decade or more. In saturated mossy areas, where small sedge assemblages formerly occurred, disappearance of sedges produces extensive moss carpets, in which only scattered shoots remain. Again, the thick moss layer appears to prevent seedling establishment. At some localities close to frost-heave mounds, *Salix reticulata* and *S. arctophila*, together with *Potentilla palustris* and *Petasites sagittatus*, have grown across the moss carpet creating a new plant assemblage. The four latter species and the mosses appear not to be eaten by the geese, except in very small quantities (Jefferies, 1988a,b). This type of species assemblage can be recognized at a number of sites on the Cape Churchill peninsula, as well as at other severely damaged goose colonies (Kerbes, Kotanen & Jefferies, 1990) and is indicative of former disturbance by populations of geese. Whether a given area of vegetation is heavily affected by foraging activities of geese depends on snow melt patterns each year, both at local and regional levels.

Herbivores may interact with physical processes so that discontinuous and irreversible transitions in several stages of plant succession may occur (Westoby, Walker & Noy-Meir, 1989). Previously, Hik, Jefferies & Sinclair (1992) described effects of grazing and grubbing by geese in modulating the direction of change in coastal salt-marsh vegetation over different time scales. This study extends earlier findings to include fresh-water plant assemblages, where foraging activities of geese have led to multiple vegetation states, at least over an ecological time scale (10-15 years). In both open standing water and where moss carpets occur, the systems fail to return to their original vegetational states, probably reflecting both continuing foraging pressure and limitations on seedling establishment. This study also provides experimental support for the contention of Kerbes, Kotanen & Jefferies (1990) that grazing by geese has destroyed the fresh-water graminoid vegetation surrounding the more northerly McConnell River snow goose colony. In both cases, community development appears to have been irreversibly altered, at least over a time scale of 15 years.

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