

The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging

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Summary

1 The North American mid-continent population of lesser snow geese now exceeds 3 million birds and the population is increasing in the order of 7% per annum. The foraging activities of the birds on Arctic breeding grounds are leading to loss of vegetation and habitat destruction, particularly in coastal areas bordering the Hudson and James Bays.

2 Multitemporal analysis of LANDSAT data has been carried out to detect vegetational change from 1973 to 1993 at La Pérouse Bay and its vicinity, the site of a breeding colony of snow geese.

3 Difference vegetation images (DVI) (difference between infra-red and red images) were prepared from images obtained in late summer in 1973, 1984 and 1993, in order to enhance vegetation density. Pair-wise differences were calculated between these DVI images, which resulted in three, secondary, classified images. Classification of the three secondary images (1973–84, 1984–93, 1973–93) yielded three well-defined classes: water, vegetation decline and no change in vegetation.

4 Histogram counts gave the following values for areas of vegetation decline: 1973–84, 1026 ha; 1984–93, 1428 ha; 1973–93, 2454 ha.

5 The loss of vegetation and the destruction of habitat are discussed in relation to the foraging activities of the expanding goose population.

Keywords: difference vegetation index, grubbing, grazing, habitat destruction, Hudson Bay coast, lesser snow geese, remote sensing

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Introduction

Herbivores strongly influence plant community dynamics (Crawley 1983). Their foraging activities interact with physical processes so that discontinuous and irreversible transitions in vegetation states may occur (Westoby *et al.* 1989). In the East African Serengeti–Maria ecosystem, fire is necessary to change the vegetation from woodland to grassland, but browsing by elephants stops regeneration of woody plants and maintains the grassland state (Dublin *et*

al. 1990), indicating an asymmetry in processes that control vegetational development (Walker *et al.* 1981; Walker & Noy-Meir 1982). Changes in the abundance of a keystone herbivore species may accentuate the asymmetry and result in abrupt and rapid changes in plant populations, species assemblages and ecosystem processes (Paine 1980; Mann 1982; Bertness 1984; Power 1990). Positive feedback processes frequently bring about these changes (DeAngelis *et al.* 1986; Power 1992; Wilson & Agnew 1992), and there is often a close synergism between allogenic and autogenic factors that operate at different spatial and temporal scales. This study examines the overall effects on coastal vegetation of intensive foraging by a keystone herbivore, the lesser snow goose *Anser caerulescens*

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caerulescens L. Changes in vegetation were detected by multitemporal analysis of LANDSAT data.

Populations of lesser snow geese 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 *et al.* 1995). The increase is thought to be related to the use of agricultural land as a source of forage on the wintering grounds and along flyways (Hobaugh *et al.* 1989; Alisaikas & Ankney 1992; Robertson & Slack 1995) which, in effect, provides 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 *et al.* 1995) to an estimated 23 000 pairs in 1990 (R. H. Kerbes, unpublished photographic inventory). Such a large increase in numbers has led to dramatic changes in vegetation as a result of the intense foraging activities of the birds (Jefferies 1988a,b; Kerbes *et al.* 1990; Iacobelli & Jefferies 1991). In particular, grubbing and shoot pulling by adults in spring and intense grazing by family groups in summer has led to the progressive destruction of salt-marsh vegetation via a positive feedback that produces hypersaline soil conditions inimical for plant growth (Srivastava & Jefferies 1995, 1996). The resultant loss of vegetation and the establishment of mudflats, and bare beach ridges in intertidal areas and exposed peat in fresh-water areas, have been interpreted in relation to the predictions of state-and-transition models, in which transitions between vegetational states are triggered by perturbations, such as foraging (Hik *et al.* 1992; Kotanen & Jefferies 1997).

As these changes are taking place at the landscape level, remote sensing imagery has been used to detect overall change in the coastal marshes of La Pérouse Bay, where the vegetational changes have been documented during the period of expansion of goose populations. Detailed descriptions of changes in coastal plant assemblages will appear elsewhere (R. L. Jefferies & D. S. Srivastava, unpublished). What is striking about this loss of vegetation is that it is not confined to La Pérouse Bay, but is occurring throughout the coastal zone of the lowlands of Hudson and James Bays, a distance of at least 2000 km, associated with increases in numbers of lesser snow geese and Canada geese *Branta canadensis* L. (Abraham & Jefferies 1996). Remote sensing provides an opportunity to detect changes over this larger geographical area in the absence of detailed ground studies.

Site description

Extensive coastal flats occur at La Pérouse Bay, Manitoba, Canada (58°45'N, 93°30'W) as a result of isostatic uplift. The vegetation of the intertidal flats,

where it still remains, is dominated by *Puccinellia phryganodes* (Trin) Scribn. & Merr. and *Carex subspatheacea* Wormsk. (Fig. 1: A) (Jefferies *et al.* 1979). At the confluence of the west and east sections of the Bay, an area of low willow tundra extends inland from the flats for approximately 2 km (Fig. 1: B). This area was formerly part of the flats before it was raised as a result of isostatic uplift. The vegetation consists of low willow bushes of *Salix brachycarpa* Nutt. and *Salix myrtifolia* Anderss. and a ground cover of two caespitose grasses, *Calamagrostis deschampsioides* Trin. and *Festuca rubra* L. The underlying marine clay and gravels are capped by a thin veneer of humified organic matter (< 8 cm deep) in which plant roots are located. The area is dissected by shallow drainage channels and ponds, most of which become dry in summer. East of Watson Point a beach ridge extends south-east for almost 3 km. Formerly, extensive stands of *Leymus mollis* (Trin) Pilger grew on the ridge and elsewhere (Fig. 1: C), and there were numerous small fringing salt marshes of *Puccinellia* and *Carex* landward of the ridge. On the east side of the Bay, inland from the tidal flats and along riverine courses, tall willows (> 3 m) fringe these habitats (Fig. 1: D). Within these willow assemblages and landward of them, extensive fresh-water sedge meadows occur dominated by *Carex aquatilis* L., but smaller sedges that include *Carex atrofusca* Schk., *C. capillaris* L., *C. flavicans* Nyl., *C. microglochin* Wahlenb. and *C. vaginata* Tausah. are also common (Fig. 1: E).

Materials and methods

REMOTE SENSING: BACKGROUND INFORMATION

Since 1972, LANDSAT satellites have provided frequent, low-resolution, multispectral digital imagery of the Earth's surface. The sun-synchronous orbit of the first three LANDSAT satellites was characterized by an altitude of 900 km and an 18-day revisit cycle. Each point on the surface was revisited at the same local sun time, which yielded repeatable illumination conditions that varied only as a result of the seasonal change of the azimuth and elevation of the sun and the prevailing atmospheric conditions. The main imaging device was a medium-resolution multispectral scanner (MSS) that produced an image of a swath 185 km wide in four spectral bands with a nominal ground resolution of 80 m. LANDSAT 4 and 5 were launched in 1982 and 1984, respectively. The orbit altitude was changed to 705 km, which resulted in a 16-day repeat coverage; other parameters remained similar. They carried, in addition to the MSS sensor, an advanced multispectral scanner, the Thematic Mapper (TM). The TM sensor records images in seven spectral bands and the nominal ground resolution is 30 m (Lillesand & Kiefer 1987).

Comparison of image pairs from the archived long-

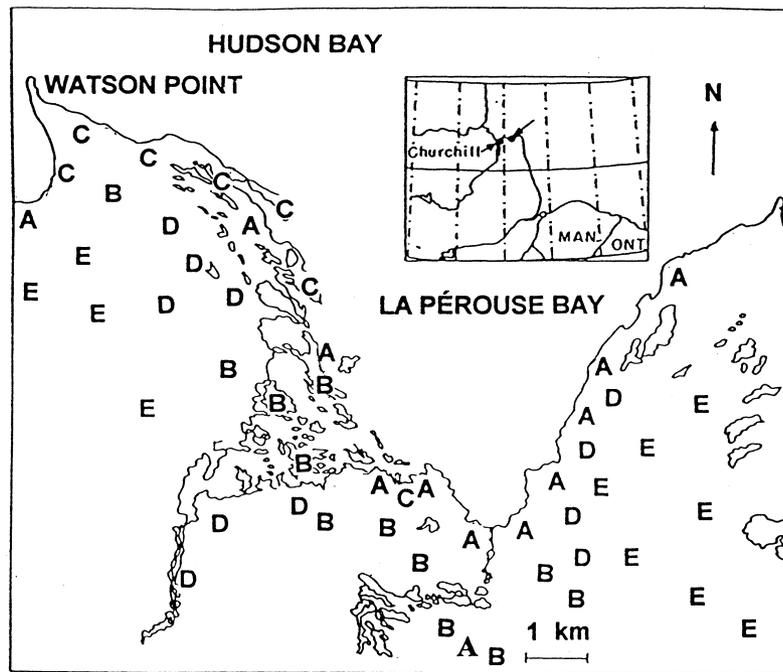


Fig. 1 Map of La Pérouse Bay and the coastal zone, the position of which on the Hudson Bay coast is indicated by an arrow on the inset map. A, Intertidal or secondary salt marshes; B, willow-grassland tundra; C, beach-ridge vegetation including *Leymus mollis*; D, high willows; E, freshwater sedge meadows.

term historical record offers the potential to detect and quantify changes occurring in land cover. Arithmetic operations such as subtraction or division applied to a pair of images yields a new image representative of the difference between the two images (Singh 1989). Although the operation is simple, the interpretation of the result is not. While such comparisons do portray the change in recorded radiance, the observed change is by no means equivalent to a change in any particular parameter of the land cover, such as the amount of vegetation present. Knowledge of the landscape and familiarity with the various agents acting upon it are required to identify correctly the nature of change.

DETECTION OF VEGETATION CHANGE

Vegetation is the most dynamic element of the landscape from a remote-sensing perspective. In order to avoid confusing seasonal changes in vegetation cover with long-term decreases or increases in cover, it is preferable to use images that are recorded at times when the development of vegetation is at an identical or very similar stage. For this reason, late-summer images are the most suitable for vegetation change studies. At this time the foliage is fully developed with little or no change in the appearance of plants. Vegetation indices derived from two or more spectral bands of multispectral imagery (usually red and infrared) are used to depict the amount of vegetation present (Tucker 1979; Lillesand & Kiefer 1987; Mather

1987). These secondary images can be used for the detection of vegetation change as described above.

IMAGES OF LA PÉROUSE BAY AND VICINITY

An analysis of multitemporal imagery was carried out in order to determine changes in coastal vegetation in the vicinity of La Pérouse Bay between 1973 and 1993. Cloud-free LANDSAT MSS images, acquired on 25 July 1973, and LANDSAT 5 TM images, from 2 August 1984 and 4 August 1993, were used in the study. The three images were registered to a common geographical base, the Universal Transverse Mercator (UTM) grid. The 1984 image was geocoded to a 25-m grid based on a 1:250 000 scale National Topographical Series (NTS) mapsheet, and the other two images were registered to the 1984 scene based on image to image registration. Visual comparison of the co-registered images indicated noticeable changes in land cover. In order to document and quantify the changes, secondary images that enhanced vegetation density and vegetation change were produced from the co-registered images.

The changing levels of the tides had to be taken into account in the analysis, as even small changes in water level can cause far-reaching changes in the area of inundated coastal salt marshes and mudflats, because of the extreme flatness of the landscape. In order to eliminate changes due to water level, water masks were created from the three images and the largest of the three masks was applied to all three

images. Limiting values of masks were determined from the histograms of the infra-red bands.

Of the numerous vegetational indices available, difference vegetation index (DVI) was selected for the study (Tucker 1979; Lillesand & Kiefer 1987; Mather 1987). DVI index images were generated from each image. The images were calculated as the difference between near infra-red and red bands; the result was scaled between 0 and 255. In the DVI images digital values were assumed to be correlated directly to the amount of green vegetation. Low DVI values corresponded to little or no vegetation.

In order to estimate the change in vegetation, pairwise differences were calculated between the DVI images by subtracting the DVI image of 1973 from the corresponding images for 1984 and 1993, and the image for 1984 from that of 1993. In the resulting secondary images, scaled again between 0 and 255, low values corresponded to a decline of the vegetation index, which indicated a loss of vegetation. Values that represented no change in the vegetation index were concentrated around the mean, and high values signified an increase in the vegetation index and in plant cover. Beyond the normalizing effect of the arithmetic operations, no attempt was made to account for differences between the original images due to differences between sensors and atmospheric conditions. For this reason and for lack of ground data, the vegetation decline class was not further subdivided into severity classes over this wide geographical area.

Histograms of the three secondary images showed two well-defined classes: vegetation decline and no change in vegetation. There were only a few instances of vegetation increase probably caused by mis-registration of images. The images were density sliced into the above two classes, and the water mask was added as a third class. The resolution of the geocoded imagery is 25 m × 25 m, or 0.0625 ha. In the case of the low-resolution MSS image for 1973, the original pixel size of 79 m × 57 m is 0.45 ha, hence reporting areas to the nearest hectare is satisfactory.

Results

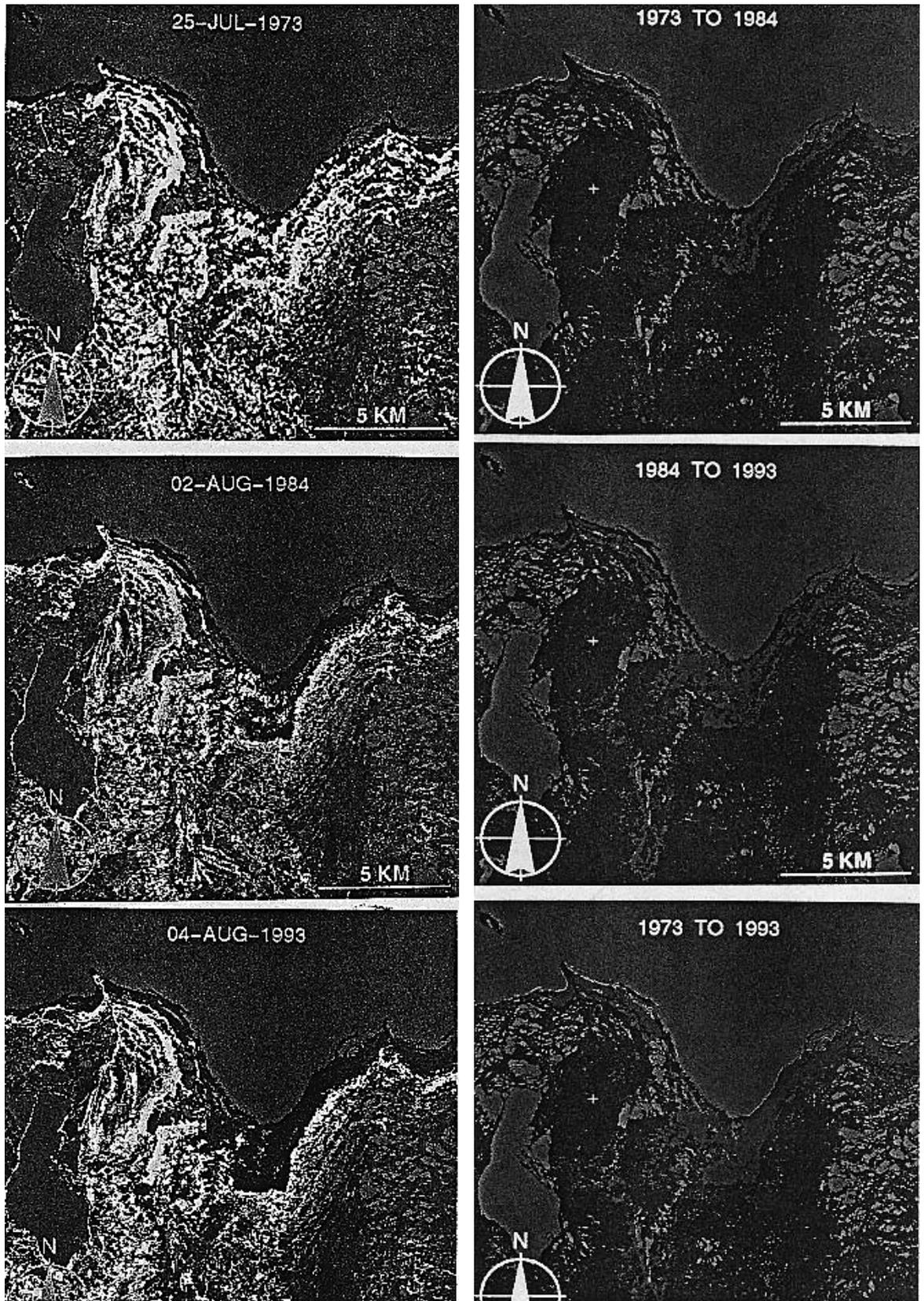
In Fig. 2 the DVI images are shown for 1973, 1984 and 1993. During this period of 20 years, substantial changes in vegetation occurred, as indicated by the increase in areas shown as black in the immediate coastal zone, where a marked decline has taken place in the vegetation index. The change is more clearly seen in Fig. 3, which shows the three classified images for intervals of 11, 9 and 20 years, respectively, where the areas representing a decline in vegetative cover are shown as red. Histogram counts of the classified images gave the following values for the areas of vegetation decline: 1973–84, 1026 ha; 1984–93, 1428 ha and 1973–93, 2454 ha. At many sites there had been a total loss of vegetation, particularly in the immediate

coastal zone, at other localities a detectable decline in vegetative cover occurred. During the most recent 9 years of the study, the total area of decline increased by 50% compared with that adversely affected during the preceding 11 years. The increase in the rate of loss of vegetation is consistent with the increase in the population of lesser snow geese on the Cape Churchill peninsula. In the period 1973–84 much of the destruction took place in the intertidal marshes on the east side of La Pérouse Bay, the intertidal marshes in the next bay to the east and in marshes to the west of Watson Point. In addition, loss of vegetation occurred on and around the beach ridge to the east of Watson Point and inland from the confluence of the west and east shores of the bay. During this period breeding colonies of lesser snow geese established at all these localities, and much of the damage at the time occurred in spring as a result of grubbing and shoot pulling by both breeding and staging birds that bred further north (R. L. Jefferies, personal observation). In addition, early snow clearance from the areas (wind-blown sites free of snow or melt water draining from the interior clearing snow) facilitated their use as nesting sites (Abraham 1980).

The second phase (1984–93) has been marked not only by a geographical expansion of the area where a decline in vegetational cover has occurred but, in addition, by an increased number of different types of vegetation adversely affected as food supplies have decreased in preferred foraging areas (i.e. in areas A, B, C; Fig. 1). In particular, sites to the south in the vicinity of lakes and drainage systems and also sedge meadows (Fig. 1: E) immediately inland from the eastern shore of La Pérouse Bay have been affected. In recent years some of these localities have had high densities of nests that have exceeded 2000 per km² in some years. Removal of sedge shoots by geese has exposed the underlying peat in sedge meadows, and each year the cumulative foraging activities of the geese have led to an expansion of these disturbed areas. During the last decade the geese have also removed the thin veneer of organic material and salt-marsh graminoids, which has exposed the underlying marine sediments close to lakes and drainage channels about 8 km south of La Pérouse Bay. In both the intertidal areas and in the willow–*Festuca*–*Calamagrostis* grassland, the destruction of the vegetation has continued unabated. The remaining patches of ground vegetation are characterized by a low standing crop (c. 10–20 g m⁻²) and foliage of poor nutritional quality, and they cover an area of only a few square metres.

Discussion

The overall conclusion from the results of this multitemporal analysis of LANDSAT data is that there has been a major loss of vegetation within the immediate coastal habitats at La Pérouse Bay, and that fur-



ther declines in vegetational cover are now occurring in fresh-water sedge meadows and wetlands inland from the coast. This conclusion is consistent with evidence of vegetational changes that have occurred within and adjacent to exclosures erected in different plant communities, and from annual records of grubbing by geese along 12 permanent transects of total length 803 m over 12 years (Bazely & Jefferies 1986; Kotanen & Jefferies 1997; R. L. Jefferies unpublished data). There is no evidence that these changes are related to isostatic uplift. Only graminoid communities are directly adversely affected by geese. Although severity classes were not established in the analysis, supporting ecological studies throughout the period have established that the loss of vegetation in the different habitats is the result of the foraging activities of the expanding breeding population of lesser snow geese and geese staging in the area (Jefferies 1988a,b; Kerbes *et al.* 1990; Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995, 1996; Ganter *et al.* 1996; Kotanen & Jefferies 1997). The cumulative foraging activities year after year in both spring and summer have stopped regeneration of vegetative cover and have led to a progressive decline in standing crop and exposure of peat and mineral sediments. This desertification of the landscape (Srivastava & Jefferies 1996) has increased dramatically in the present decade (R. L. Jefferies & D. S. Srivastava, unpublished data) as the geese have continued to exploit remaining patches of vegetation. The amount of grubbing varies from year to year depending on weather conditions in spring (R. L. Jefferies, unpublished data). Late springs have characterized many recent years compared to those of the 1970s (Skinner *et al.* 1997). When late springs occur initiation of nests is delayed and large numbers of staging birds, which breed further north, remain on the Cape Churchill peninsula (Skinner *et al.* 1997). Grubbing and shoot-pulling are often intense immediately after melt in these years. Hence the strong interaction between weather patterns, vegetation and geese may exacerbate the rate of destruction of vegetation in any given year.

Although detailed studies of the loss of coastal vegetation in recent decades are confined to the La Pérouse Bay and the Cape Churchill peninsula, surveys carried out from 1993 to 1995 indicate that destruction of vegetation and loss of habitat are widespread along the western and southern coasts of Hudson Bay and in James Bay (Kerbes *et al.* 1990; Abraham & Jefferies 1996). A similar analysis of multitemporal changes in vegetation on the north shore of Akimiski Island in James Bay has yielded comparable results (A. P. Jano, K. F. Abraham & R. L. Jefferies, unpublished results). In addition, LANDSAT imagery has been used to detect loss of habitat in Queen Maud Gulf, North-West Territories, where there are breeding colonies of lesser snow geese and Ross' geese *Anser rossii* (A. B. Didiuk, R. T. Alisaukas

& F. D. Caswell, unpublished data). It is evident that wherever there are expanding populations of lesser snow geese loss of habitat is likely to occur as a result of the foraging activities of the birds within these Arctic regions. The presence of mudflats and bare beach ridges in intertidal areas and exposed peat and ponds rich in peaty debris in fresh-water sedge meadows represent the establishment of alternative states (*sensu*, Westoby *et al.* 1989), triggered by the foraging activities of geese (Hik *et al.* 1992). The different habitats have remained in these respective states for a decade or longer. Abundant colonists of mudflats and/or beach ridges include *Salicornia borealis* and *Senecio congestus*, species that are absent or very poorly represented in intact swards of salt-marsh graminoids. In sedge meadows moss carpets, *Petasites sagittatus* and *Potentilla palustris* colonize peat surfaces where formerly stands of *Carex aquatilis* grew (Jefferies 1988a,b).

Where habitat conditions are sufficiently altered following grubbing in intertidal habitats, the cumulative effect of foraging is to severely delay the rate of vegetational development. Erosion of organic layers and sediments makes it unlikely that assemblages of plants will re-establish within 25–50 years. As the area is undergoing isostatic uplift, the species that ultimately re-establish may be different from the former assemblages (Hik *et al.* 1992). Remote-sensing imagery provides a tool for monitoring these overall changes in vegetation states triggered by herbivory.

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References

- Abraham, K.F. (1980) *Breeding site selection by lesser snow geese*. PhD thesis, Queen's University, Kingston, Ontario, Canada.
- Abraham, K.F. & Jefferies, R.L. (1996) High goose populations: causes, impacts and implications. *Arctic Goose Habitat Working Group Report* (ed. B. Batt), pp. 7–70. Arctic Goose Joint Venture Special Publication, U.S. Fish and Wildlife Service, Washington, D.C., and Canadian Wildlife Service, Ottawa, Ontario.
- Abraham, K.F., Jefferies, R.L., Rockwell, R.F. & MacInnes, C.D. (1996) Why are there so many white geese in North America? *Proceedings of the 7th International Waterfowl Symposium* (ed. J. Ratti) pp. 79–92. Ducks Unlimited, Memphis, Tennessee.
- Alisaukas, R.T. & Ankney, C.D. (1992) Winter diets and nutrition of mid-continental Lesser Snow Geese. *Journal of Wildlife Management* **56**, 43–54.

- Bazely, D.R. & Jefferies, R.L. (1986) Changes in the composition and production of salt-marsh plant communities in response to the removal of a grazer. *Journal of Ecology* **74**, 693–706.
- Bertness, M.D. (1984) Habitat and community modification by an introduced herbivorous snail. *Ecology* **65**, 370–381.
- Cooke, F., Rockwell, R.F. & Lank, D.B. (1995) *The Snow Geese of La Pérouse Bay*. Oxford University Press, Oxford.
- Crawley, M.J. (1983) *Herbivory*. University of California Press, Berkeley, California.
- DeAngelis, D.L., Post, W. & Travis, C.C. (1986) *Positive Feedback in Natural Systems*. Springer, Berlin.
- Dublin, H., Sinclair, A.R.E. & McGlade, J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* **59**, 1147–1164.
- Ganter, B., Mineau, P. & Cooke, F. (1996) Long-term vegetation changes in a Snow Goose nesting habitat. *Canadian Journal of Zoology* **74**, 965–969.
- Hik, D.S., Jefferies, R.L. & Sinclair, A.R.E. (1992) Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *Journal of Ecology* **80**, 395–406.
- Hobaugh, W.C., Stutzenbaker, C.D. & Flickinger, E.L. (1989) The rice prairies. *Habitat Management of Migrating and Wintering Waterfowl in North America* (eds L.M. Smith, R.L. Pederson & R.M. Kaminski), pp. 367–383. Texas Technical University Press, Lubbock, Texas.
- Iacobelli, A. & Jefferies, R.L. (1991) Inverse salinity gradients in coastal marshes and the death of stands of willow: the effects of grubbing by geese. *Journal of Ecology* **79**, 61–73.
- Jefferies, R.L. (1988a) Vegetational mosaics, plant–animal interactions and resources for plant growth. *Plant Evolutionary Biology* (ed. L.D. Gottlieb & S.K. Jain), pp. 340–361. Chapman and Hall, London.
- Jefferies, R.L. (1988b) Pattern and process in Arctic coastal vegetation in response to foraging by Lesser Snow Geese. *Plant Form and Vegetational Structure, Adaptation, Plasticity and Relationship to Herbivory* (eds M.J.A. Werger, P.J.M. van der Aart, H.J. During & J.T.A. Verhoeven), pp. 281–300. SPB Academic Publishing, The Hague.
- Jefferies, R.L., Jensen, A. & Abraham, K.F. (1979) Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. *Canadian Journal of Botany* **57**, 1439–1450.
- Kerbes, R.H., Kotanen, P.M. & Jefferies, R.L. (1990) Destruction of wetland habitats by Lesser Snow Geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* **27**, 242–258.
- Kotanen, P.M. & Jefferies, R.L. (1997) Long-term destruction of sub-arctic wetland vegetation by lesser snow geese. *EcoScience* **4**, 179–182.
- Lillesand, T.M. & Kiefer, R.W. (1987) *Remote Sensing and Image Interpretation*, 2nd edn. Wiley & Sons, New York.
- Mann, K.H. (1982) *Ecology of Coastal Waters: A Systems Approach*. University of California, Berkeley.
- Mather, P. (1987) *Computer Processing of Remotely Sensed Images: an Introduction*. Wiley & Sons, Chichester.
- Paine, R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**, 667–685.
- Power, M.E. (1990) Effects of fish in river foodwebs. *Science* **250**, 811–814.
- Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* **73**, 733–746.
- Robertson, R.G. & Slack, R.D. (1995) Landscape change and its effects on the wintering range of a lesser snow goose, *Chen caerulescens caerulescens* population: a review. *Biological Conservation* **71**, 179–185.
- Singh, A. (1989) Digital change detection techniques using remotely sensed data. *International Journal of Remote Sensing* **10**, 989–1003.
- Skinner, W., Jefferies, R.L., Carleton, T.J., Rockwell, R.F. & Abraham, K.F. (1997) Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology*, **4**, 3–16.
- Srivastava, D.S. & Jefferies, R.L. (1995) Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt-marsh. *Canadian Journal of Botany* **74**, 75–83.
- Srivastava, D.S. & Jefferies, R.L. (1996) A positive feedback: herbivory, plant growth, salinity and the desertification of an Arctic salt-marsh. *Journal of Ecology* **84**, 31–42.
- Tucker, C.J. (1979) Red and photographic infra-red linear combinations for monitoring vegetation. *Remote Sensing of Environment* **8**, 127–150.
- Walker, B.H. & Noy-Meir, I. (1982) Aspects of the stability and resilience of savanna ecosystems. *Ecology of Tropical Savannas* (eds B.J. Huntley & B.H. Walker), pp. 555–590. Springer, Berlin.
- Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. (1981) Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**, 473–498.
- Westoby, M., Walker, B.H. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**, 265–273.
- Wilson, J.B. & Agnew, A.D.Q. (1992) Positive-feedback switches in plant communities. *Advances in Ecological Research* **23**, 263–336.

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