RESPONSES OF SALT-MARSH VEGETATION TO GRAZING BY LESSER SNOW GEESE (*Anser caerulescens caerulescens*)

by

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A thesis submitted in conformity with
the requirements for the degree of
Master of Science
in the University of Toronto

For my parents.

ACKNOWLEDGEMENTS

There are many people to whom I am indebted for their help and support given so freely during the course of this study. First, I would like to thank Prof. Bob Jefferies, my supervisor, for his guidance in connection with the science, and his boundless energy and optimistic outlook under field conditions that were often adverse. Under his supervision, I have come to truly understand what it means to work to a tight deadline!

I extend especially warm thanks to Jo-Anne Rzadki, who was an invaluable field worker during both field seasons, combining high proportions of expertise, patience, and friendship. Dan Kozlovic, Thor Thorleifson, Robin Labatt and Dave Bolster also helped out greatly with the field work, enduring conditions which included polar bears and a lot of mud, rain and snow.

Logistic support and encouragement were also provided by Peter Dueck, director of the Churchill Northern Studies Centre: 1982-83, Isabel Dueck, Steve Miller and the many workers at Camp Finney, the Queen's Tundra Biology Station.

Logistic support in Toronto was provided by my parents, Sue Cargill, Sue Jefferies, Valerie Anderson, Sharon Wolff and François Roberge who helped me to meet numerous deadlines by acting as chauffeurs, typists, editors, couriers, and fast food restaurant chefs when necessary. I dedicate these lines to them:

"As 'research students' always discover, however long they are allowed, and careful their work and notes, there is always a rush at the end, when the last date suddenly approaches on which their thesis must be presented." J.R.R. Tolkien, 1956. Thank you all for helping me at various points in the "rush".

Dr. T. Sawa, Dr. T. Carleton and Dr. J. Hellebust advised me on questions relating to this research. I would also like to thank Annette Henry (née Branton) who typed this manuscript and Mrs. N. Nolan who prepared the figures. Also I must again thank Sue Jefferies who kindly stepped in to continue typing, when Annette went on her honeymoon!

The Fellows of Massey College in the University of Toronto provided a stimulating environment in which to live. It was at Massey that I met Tim Swartz and Martin Bilodeau, two Junior Fellows, who helped greatly with various statistical problems.

I also thank the Natural Sciences and Engineering Research Council, the Canadian Wildlife Service and the Department of Indian and Northern Affairs for financial support.

SUMMARY

1. The mechanisms by which grazing by lesser snow geese bring about an increase in cumulative net above-ground primary production (NAPP) of salt marsh vegetation at La Pérouse Bay, Manitoba were investigated.
2. In the absence of grazing, cumulative NAPP was approximately 80 g m^{-2} in swards dominated by *Puccinellia phryganodes* in 1982 and 1983. Grazing by snow geese resulted in increases in cumulative NAPP of 46% in 1982 and 106% in 1983. These increases were significant ($p < 0.05$).
3. There was a significant correlation between values of leaf area index and live standing crop in grazed and ungrazed sites ($p < 0.05$).
4. Grazing stimulated tillering in *P. phryganodes*. This increase in axillary shoot production accounted for the increase in cumulative NAPP of grazed sites compared with ungrazed sites in 1982 and 1983.
5. The rate of appearance of leaves and the rate of death of leaves was similar on main shoots of *P. phryganodes* in both grazed and ungrazed sites. However, the total number of leaves produced on axillary shoots of grazed plants was substantially higher than that of ungrazed plants. The average age of a leaf when grazed was 14 days, whereas the mean age of ungrazed leaves was 39 days.

6. Significant increases in live standing crop were observed in exclosed plots fertilised with fresh snow goose droppings compared with that in control plots which received no droppings ($p < 0.05$).

7. Rates of nitrogenase activity, measured by acetylene reduction, were consistently greater in grazed than in ungrazed sites in 1983.

8. Grazing maintained the total nitrogen content of P. phryganodes at a level of 2.4% on a dry weight basis, while that of ungrazed shoots of P. phryganodes declined by 30% two weeks after hatch.

9. In the absence of snow geese, over a period of four years plant species diversity increased in exclosures while live standing crop declined and litter accumulated. The soil environment of ungrazed sites was cooler than that of grazed sites.

10. It was concluded that the intensive grazing activities and colonial feeding behaviour of snow geese result in higher nitrogen availability for plant growth in grazed sites, and the maintenance of better quality forage as a result of the higher nitrogen content. Nitrogen is supplied from goose droppings and increased rates of nitrogen fixation in grazed sites. P. phryganodes, a grass, is able to withstand heavy grazing, and plants respond by producing tillers so that the amount of forage is increased significantly.

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CHAPTER 1

GENERAL INTRODUCTION

The coasts of Hudson and James Bay are dominated by extensive salt marshes (Sims, Riley and Jeglum,1979), which provide breeding grounds for large numbers of waterfowl, including snow geese, Canada geese, pintail and common eider (Godfrey, 1966; Owen, 1980; Cooke et al., 1982). Inspite of the biological importance of these areas, few ecological studies have been carried out on them, mainly because of their inaccessibility. However, at La Pérouse Bay, the site of the Queen's Tundra Biology Station, there is a breeding colony of lesser snow geese (Anser caerulescens caerulescens) which has been studied for over 15 years by a team of researchers led by Dr. F.C. Cooke of Queen's University.

In recent years, there has been some concern amongst wildlife management personnel that various breeding populations of snow geese may be overgrazing the marshes on which they feed (Cargill, 1981; A. Dzubin; pers. comm.). Overgrazing during the period following hatch was thought to be partly responsible for the decline in numbers of the McConnell River breeding colony of lesser snow geese from 1976 onwards, which consisted of more than 163,000 pairs of nesting birds in 1973 and up to 250,000 nesting pairs in 1974 and 1975 (Kerbes, 1975; A. Dzubin, pers. comm.). Cargill (1981) investigated the effects of grazing by geese at La Perouse Bay. Her main objective was to study "the interaction between snow geese and marsh vegetation at a single location and to examine the functional relationship between grazing and plant growth" (Cargill, 1981. p.4).

In summary, Cargill's (1981) findings were the following: that in the absence of grazing, the cumulative net above-ground primary production (NAPP) of the marsh at La Perouse Bay was between 55 and 100 g dwt. m^{-2} in 1979 and 1980 in swards dominated by Puccinellia phryganodes and Carex subspathacea; that in the presence of grazing by lesser snow geese NAPP increased by 30% in 1979 and by 80% in 1980. She also determined that NAPP at La Pérouse Bay was limited by the availability of nitrogen (Cargill, 1981). This limitation has also been observed in temperate salt marshes (Ranwell, 1972). Lesser snow geese consumed approximately 80% of the NAPP before the migration south, and the weight of both adults and goslings increased appreciably following the hatch period (Cargill, 1981). The geese were major exporters of nitrogen from the marsh, but inspite of this, the average total nitrogen content of grazed shoots increased over that of ungrazed shoots (Cargill, 1981). Thus, export of nitrogen by the geese, is apparently compensated for by inputs of this element to the grazed areas of the marsh.

At the conclusion of Cargill's study, it was apparent that the investigation could be continued along two lines: the first experimental and the second theoretical. The former encompassed studies with the general objective of elucidating the underlying mechanisms which accounted for the enhanced NAPP and the higher nitrogen content of the tissue under the influence of grazing. Puccinellia was emphasized in these studies because of time constraints. This species contributed to about 90% of NAPP in grazed swards which it dominated, and other grazed swards were dominated by Carex or by both species to the same extent.

Specific objectives were as follows:

(1) To determine morphological and demographic changes of shoots of Puccinellia phryganodes in response to grazing, particularly those changes associated with the increases in NAPP. Puccinellia is one of two codominant species on the salt marsh flats, and is heavily grazed by the geese.

A number of researchers have determined that grazing and mowing cause changes in rates of leaf turnover in grass swards (Grant, Bartham and Torvell, 1981; Jones, Collett and Brown, 1982). Rabbit grazing in Breckland significantly changed the age structure of a Hieracium pilosella population (Bishop and Davy, 1984). The size and possibly the age structure of tillers from different genets has also been found to change when they are clipped, because there may be selection for genets which produce small tillers (Westoby, 1980).

(2) Because of enhanced NAPP and the higher nitrogen content of grazed plants, the cumulative demand for nitrogen for above-ground growth is higher in grazed areas compared with ungrazed areas. The second objective, therefore, was to determine the mechanisms whereby additional nitrogen is made available for plant growth.

Since Cargill (1981) found that the availability of nitrogen limited the growth of exclosed swards of Puccinellia, part of the second objective involved determining whether nitrogen fixation is greater in grazed than in ungrazed swards; whether snow goose faeces provide a source of nitrogen for plant growth; whether mineralization rates of organic nitrogen are greater in grazed than in ungrazed areas.

(3) In the absence of grazing, above-ground biomass, plant litter and standing dead plants accumulate. The lower NAPP at ungrazed sites may be caused by the attenuation of irradiance through the canopy, thereby causing reduced rates of photosynthesis. The objective was to assess whether reduced irradiance was likely to affect photosynthesis and growth.

Leaf area indices were measured in 1983 in grazed and ungrazed sites in order to give an indication whether attenuation of irradiance in the canopy may have limited photosynthesis and growth in the ungrazed sites, as peak live standing crop was significantly higher than that in the grazed sites. For example, Brougham (1956) found that at a leaf area index of above 3.0, the photosynthetic efficiency of a grass sward diminished.

(4) If geese are excluded from areas of the marsh rapid changes in the vegetation occur. The objective was to determine changes in live standing crop, in amounts of litter and in amounts of standing dead plants. In addition, changes in the species composition were recorded in order to assess the extent to which the frequency of different species was dependent on grazing.

The fourth objective is related to the long term effects of the limitation of nitrogen, and the low amounts of litter and standing dead observed by Cargill (1981) in both grazed and ungrazed sites. The latter were low compared with values that have been recorded in other arctic and sub-arctic locations, in which nitrogen has also been found to limit growth. For example, in a wet sedge meadow community at Barrow, Alaska, the litter and standing-dead fluctuated around levels of 128 g m^{-2} during the summer of 1970 (Dennis, Tieszen and Vetter, 1978). The importance of the role of grazing animals in the prevention of the accumulation of senescent vegetation has been noted by a number of investigators (Kelly and Walker, 1976; McNaughton, 1976, 1979; Parsons, Leafe, Collett, Penning and Lewis, 1983). Therefore, it was predicted that long-term exclusion of snow geese from grazed sites would result in the accumulation of litter, and lower levels of biomass production, as increasing amounts of nitrogen became immobilised in this litter. Also, a casual inspection in 1981 of sites exclosed in 1979 and 1980, indicated that changes in the frequency of species were occurring in the absence of grazing. The frequency of plant species in the exclosures was recorded from 1982 onwards in an attempt to assess the extent to which the frequency was dependent on grazing.

Although the objectives set out above were practical and involved a study of the interactions between the geese and the vegetation from a mechanistic point of view, it became apparent that the data might be used to address objectives more theoretical in their intent. There were two general objectives based on theoretical considerations.

(1) To assess whether there may be mutualistic or co-evolutionary relationships between the graminoid plants and the grazers in this system: namely, _Puccinellia phryganodes_ and _Carex subspathacea_ (both graminoid species) and lesser snow geese (the grazers).

(2) To determine the stability of this plant-herbivore interaction.

Interest in the first objective was raised by the large number of papers and comments that have recently appeared in the literature addressing the question of whether grasses and grazers are co-evolved (Owen and Wiegert, 1976, 1981, 1982a, 1982b, 1983; Stenseth, 1978, 1983, 1984; Owen, 1980; Petelle, 1982; Silvertown, 1982; Herrera, 1982; Thompson and Uttley, 1982; Bleken and Ugland, 1984). Co-evolution is the process in which "the fitness of each genotype depends on the population densities and genetic composition of the species itself and the species with which it interacts" (Futuyma, 1979). The "fitness" of the genotype is its ability to survive and reproduce (Futuyma, 1979). Owen and Wiegert (1981) suggest "that grasses and their grazers are co-evolved to the extent that one would not be possible without the other". They further suggest that there are a variety of ways in which grazers can maximize the fitness or contribution of a particular genotype relative to the contributions of others (Owen and Wiegert, 1976, 1981).

Given Cargill's (1981) results in which production of the preferred forage species is higher in grazed sites, and that the preferred species are co-dominant on the marsh, such a theoretical objective was of particular relevance. Advantages of "fitness" appear to accrue to both the geese that benefit from the increased forage supply and Puccinellia and Carex, which dominate the grazed plant community. According to Owen and Wiegert's (1981) hypothesis, and the underlying assumptions of co-evolutionary theory, neither of the two graminoid species should be able to survive in the absence of snow geese. Therefore, the practical objective (3) seeking to determine whether any changes in plant species composition occur in the absence of grazing, was expected to provide data pertaining to this point.

Another theory that deals with the attempt of an organism to maximise its fitness, is that of optimal foraging (Charnov, 1976; Krebs and McCleery, 1984). The theory of optimal foraging states that animals will forage in such a way that their fitness is maximised (Charnov, 1976). Experiments involve assessing whether a predator selects the most profitable prey (Krebs and McCleery, 1984). This profitability may for example, be measured in calories (Krebs and McCleery, 1984). Neither the nitrogen and caloric content of the various plant species, nor the choices and preferences of snow geese presented with them were tested at La Pérouse Bay. However, the overall results of the study were evaluated with reference to whether the geese appear to be optimising their foraging behaviour, in order to eat what is apparently the most profitable food. Cargill and Jefferies (1984b) have suggested that the demand for nitrogen by the geese is the most important factor determining forage quality. Following hatch, the goslings increase in weight from 70 g to 1600 g before migration, and the adults regain up to one third of weight lost during incubation (Cargill and Jefferies, 1984b). The experiments of Cargill and Jefferies (1984b) to determine cumulative net above ground primary production in grazed and ungrazed areas, and to measure the nitrogen content of grazed and ungrazed shoots of Puccinellia were repeated in 1982 and 1983. The purpose was to determine whether there were any interseasonal trends in the increased availability of forage and in the nutritional quality of the forage for snow geese.

The second theoretical objective arises from Cargill's (1981) observation that the La Pérouse Bay ecosystem is relatively simple, in that it is dominated by the herbivore-plant interaction of the geese and Puccinellia and Carex. Up to the early 1970's many researchers believed that large, complex, diverse ecosystems are the most stable (MacArthur, 1955; Paine, 1966; May, 1974). However, May (1972, 1974) suggested that simple systems, involving few trophic levels and links between food web components are more stable. In a mathematical sense, stability is the tendency of perturbations in populations to damp out, returning the system to some persistent configuration (May, 1974). In a biological sense, stability may be defined in terms of resilience to the effects of perturbations, resistance to the effects of perturbations or else persistence, or low variability in species abundance or population numbers, (Orians, 1975; Pimm, 1984). A stable system should respond to a perturbation by returning to its original state in time (resilience) (Pimm, 1984). Given the low species richness and diversity in grazed areas of La Pérouse Bay, this ecosystem would originally have been characterized as relatively unstable, but in the light of May's (1974) work, it may well be regarded as very stable. The long term exclusion of snow geese from exclosures was a perturbation in which one of the interacting species was removed. In this sense, the grazing action of the geese was not considered to be a distrubance or perturbation, but rather, the grass-grazer interaction was considered to be at some sort of equilibrium. Thus, the removal of the grazer from the system may be considered to be a perturbation to its interaction with its food source. The subsequent response of the system in the absence of the grazer was expected to give an indication of the stability of the plant community.

In subsequent chapters each of these objectives is examined further in relation to published studies and specific hypotheses.

CHAPTER 2

SPECIES STUDIED AND SITE DESCRIPTION

2-1 BIOLOGY OF THE LESSER SNOW GOOSE

2-1-1 Description and Distribution

Snow geese are members of the tribe Anserini, in the family Anatidae, the ducks, geese and swans (Johnsgard, 1978). Two races of snow geese are recognized: the greater and the lesser (Owen, 1980). There is a breeding colony of Lesser snow geese (*Anser caerulescens caerulescens*) at La Pérouse Bay. They weigh 2,300 - 3,100 g on average, compared with Greater snow geese (*A. c. atlanticus*) which weigh 2,700 - 3,500 g on average (Owen, 1980). Males tend to be larger and heavier than the females, and the plumage is similar in both sexes (Owen, 1980). Lesser snow geese are dimorphic, and there are two colour phases: white and blue. There is a great variation in the amount of blue on blue phase birds. Both colour morphs have black primary wing feathers.

Lesser snow geese breed at arctic and sub-arctic sites between the latitudes of 55°N and 72°N (Owen, 1980). The eastern and western limits of the breeding range are Baffin Island and Wrangel Island respectively (Owen, 1980). The more eastern colonies contain a higher proportion of blue phase birds than those in the west (Owen, 1980). La Pérouse Bay, which is one of the southernmost breeding colonies, contains a high proportion of blue phase geese.

In the winter the eastern Canadian and Siberian populations of birds migrate south to areas on the Gulf of Mexico and Pacific coasts respectively (Johnsgard, 1981). The location of the wintering grounds is determined by the breeding colony, and the birds from La Pérouse Bay winter at sites on the coasts of Texas and Louisiana. They follow the "central flyway" route through southern Manitoba, the Dakotas and Iowa (Cooke *et al*., 1982).

2-1-2 Breeding Biology and the Phenology of the Breeding Season at La Pérouse Bay

Snow geese migrate to their breeding ground and arrive between May and June (Owen, 1980). The females are generally ready to initiate nests and start laying eggs immediately upon arrival (Owen, 1980). However, at La Pérouse Bay, the majority of the birds initiate nests 11 to 12 days after arrival (Cooke *et al*., 1982).

Snow geese are colonial nesters, and their nests may be as close as one metre to each other. At La Pérouse Bay, the size of the colony was estimated at 3,500 pairs in 1980, and it increased to 9,500 pairs of snow geese, present at hatch, in 1983 (R. Rockwell, pers. comm.).

The clutch size varies from one to seven eggs, but the average clutch size is three to five eggs (Cooke *et al*., 1982). Following initiation, there is an incubation period of 22 to 23 days (Johnsgard, 1978). During this period, the weight of the incubating female drops to less than 60% of that on arrival (Owen, 1980). The

The male, which feeds more often while he is guarding the female, experiences a weight loss of approximately 20% (Owen, 1980).

The hatch period is highly synchronized within the colony, and takes place within approximately eight days. Goslings are precocial. They are covered with down and their eyes are open immediately after they hatch. They leave the nest within 6 to 24 hours following hatch, and at this time they weigh approximately 70 g (Owen, 1980). The snow goose families stay together as they move out onto the salt marsh, where they feed for up to 18 hours per day on Carex subspathacea and Puccinellia phryganodes. Following hatch, the adults moult their primary wing feathers, so that all of the family members are flightless during much of the ensuing six week period (Owen, 1980). The adults regain their lost weight at this time, and the weight of the goslings increases to 1,500 - 1,800 g.

Table 2-1 gives a summary of the phenology of the breeding seasons at La Pérouse Bay in 1982 and 1983. 1982 was an early year in that the mean initiation date was May 19. The earliest initiation date of the fifteen years up to 1983 was May 17 in both 1977 and 1980, when there was an early thaw (Cooke et al., 1982). 1983 was the latest season ever on record, with the first nest initiated on June 7. Previously, the latest season on record out of the fifteen years was that of 1978, when the mean initiation date was June 4 (Cooke et al., 1982). One reason for this late initiation date, was that in 1983, thaw did not occur until mid-June. Up to this point there was complete snow cover, and no nest sites were available.

Table 2-1. Phenology of the breeding season at the La Pérouse Bay, Manitoba, lesser snow goose colony in 1982 and 1983.

EVENT	1982	1983
Peak arrival of snow geese	May 11-12	June 4-5
Date first egg found	May 14	June 7
Mean nest initiation date	May 19	June 11
Mean hatch date	June 18	July 7
Hatch period	June 14-21	July 2-12
Approximate time at which first fledged goslings were seen	end of July	mid-August
Date of departure of bulk of colony	August 22-30	August 26-30

2-3-3 Social Behaviour

Adult snow geese generally form pair bonds for life or until the death of one of the pair (Owen, 1980). They are long lived birds, and there are individuals in the La Pérouse Bay population which are greater than 14 years of age. Female birds do not breed until they are two years old, but some individuals do not breed until the age of three or four years (Cooke *et al.*, 1982). The females return to their natal colony to breed, bringing their males with them (Rockwell and Cooke, 1977). The male defends the nest territory from neighbouring males, guarding it during incubation against predation by gulls and jaegers. Following hatch, the male spends much time in an alert posture during feeding periods (Harwood, 1974). At La Pérouse Bay, the families form flocks of 30 to 100 birds on the salt-marsh flats while they feed. Data indicate that many families stay together during the migration to and on the wintering grounds, and that unpaired birds choose their mates here (Owen, 1980).

2-3-4 Feeding Behaviour

Lesser snow geese are herbivores, and the plant species that they eat vary according to season. During the summer they are grazers. At La Pérouse Bay they feed on *C. subspathacea* and *P. phryganodes*. At other breeding colonies they have been observed feeding on other species of sedge and grass (Harwood, 1974). In the spring and fall when they stage for migration, they tend to "root" or "grub" (Owen, 1980). During fall migration, they feed selectively on the underground perennating bulbs of Triglochin palustris in the James Bay coastal zone (Thomas and Prevett, 1980). In addition, various species of Carex, Puccinellia langeana and Equisetum variegatum are consumed in large amounts by fall staging geese in this area (Prevett, Marshall and Thomas, 1979). Snow geese, which winter in the Fraser River Estuary in British Columbia, root almost exclusively for bulrush rhizomes (Burton, Hudson and Bragg, 1979). Further south, they also eat bulrush rhizomes during the winter (Owen, 1980).

The digestive system of geese is relatively simple (Harwood, 1974; Owen, 1980). They appear unable to breakdown cellulose (Mattocks, 1971), and most food passes through the gut in under four hours (Harwood, 1977). The mean retention time of food in wintering birds was found to be two hours (Burton, Hudson and Bragg, 1979).

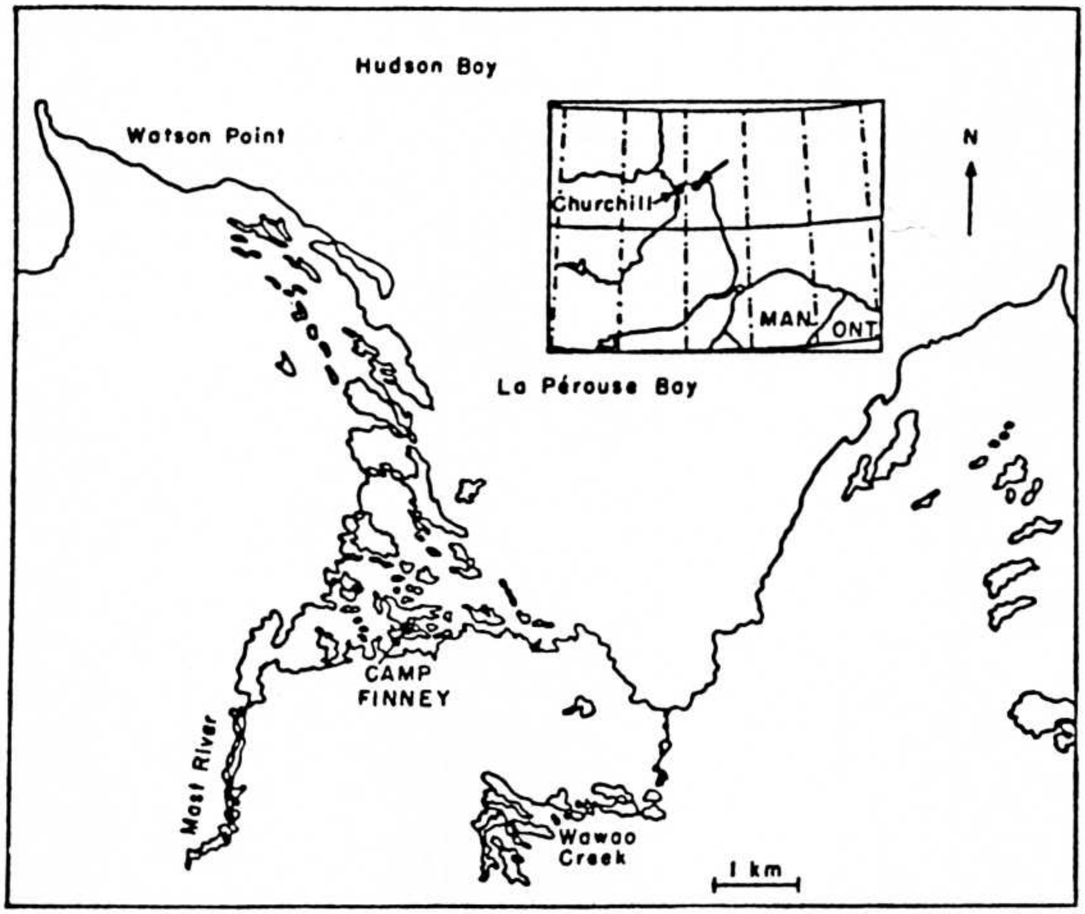
2-2 GENERAL SITE DESCRIPTON

2-2-1 Topography and vegetation

La Pérouse Bay is located approximately 40 km east of Churchill, Manitoba (58°N, 94.3°W), on the west coast of Hudson Bay (Fig. 2-1). La Pérouse Bay lies in the Hudson Bay Lowland (HBL) physiographic region. The HBL is a low, flat coastal plain varying from 161 to 418 km in width, and it is approximately 1360 km long, extending from the Nottaway River in Quebec to the North Knife

Figure 2-1. Map of La Pérouse Bay, Manitoba.

Inset: Map showing the location of Churchill (58°N, 94.3°W) and La Perouse Bay, indicated by an arrow, on the coast of Manitoba.


Hudson Bay
Watson Point
Churchill
MAN
ONT
N
La Pérouse Bay
CAMP
FINNEY
Mast River
Wawao
Creek
1 km

River in Manitoba (Sandford, Norris and Bostock, 1968).

In La Pérouse Bay, a delta has formed where the Mast River enters Hudson Bay. The predominant vegetation is tidal and estuarine salt marsh. The levels of salinity are < 18 parts per thousand in the waters of these and other salt marshes in Hudson and James Bay (Jefferies, Jensen & Abraham, 1979). Therefore, the water is actually brackish rather than highly saline, as the salinity of sea water is in the region of 32 ppt.

The impeded drainage at La Pérouse Bay is the cause of the marshy conditions. Most of the HBL has a gradient of 0.5 to 1 m km^{-1} sloping towards Hudson Bay (Jefferies, Jensen and Abraham, 1979). This region is still being affected by isostatic rebound. Since depression by the Laurentide ice sheet 10,000 years BP, the land has been rising out of Hudson Bay at a rate of 1.5 m 100 yr^{-1} (Sims, Riley and Jeglum, 1979). The only high point of land at La Pérouse Bay is Knight's Hill, an esker approximately five km west of the Mast River. Running parallel to the coast are a series of beach ridges which where were formed as a result of isostatic rebound. The intertidal salt marshes, and those further inland have formed between these ridges. Many large limestone boulders and stones are scattered on the intertidal flats, which are dissected by numerous small, often intermittent, streams. The river delta consists of many small (2 to < 30 m in diameter) islands, some of which have been formed by frost heave (Jefferies, Jensen and Abraham, 1979). Also, occurring along the salt marsh flats, away from the Mast River and its associated pools, are smaller ponds (c.1m in diameter) which are formed by the trampling activities of the lesser snow geese that nest there (Jefferies, Jensen and Abraham, 1979).

In northern Manitoba and throughout the salt marshes of the HBL, relatively little research has been carried out on the vegetation (Sims, Riley and Jeglum, 1979). This is largely due to the inaccessibility of the area. Researchers have tended to divide the vegetation into large scale units running parallel to the Hudson and James Bay coastlines (Ritchie, 1957; Ritchie, 1962; Sims, Riley and Jeglum, 1979). Ritchie (1962) placed La Pérouse Bay in the "Lower Coastal" category, which is characterized by salt marshes and scrub communities. Both Ritchie (1956) and Scoggan (1959) have carried out descriptive research on the vegetation of the Churchill area. In the Flora of Churchill, Scoggan (1959) lists species found in the salt marshes and coastal flats in the Churchill area, many of which also occur at La Perouse Bay.

Jefferies, Jensen and Abraham (1979) carried out vegetation studies in order to establish the species composition of the vegetation occurring at different stages in the colonization process of the mounds and islands in the delta region and on the intertidal flats. Seawards,away from the flats, there are beds of Zostera marina in the "sub-tidal" region (Jefferies, Jensen and Abrahams, 1979). A grass, Puccinellia phryganodes, and a sedge, Carex subspathacea, are the initial colonizers of the tidal flats, the former being the dominant species. In the delta, C. subspathacea is codominant with this grass. The snow geese graze on the latter two species. Hippuris tetraphylla and H. vulgaris colonize wet, silt areas on the edges of the islands in the delta. Other species that occur in low frequencies in the swards of Puccinellia and Carex, and on slightly higher areas of the islands, include: Potentilla egedii, Chrysanthemum articum, Calamagrostis deschampsiodes, Stellaria humifusa, Salix brachycarpa, and occasionally Elymus arenarius (Jefferies, Jensen and Abrahams, 1979).

Within the more heavily vegetated areas in the delta, and south of the salt marsh flats, willow bushes grow among pools and small streams. Carex glareosa, C. aquatilis and Triglochin maritima grow along the edges. Halophytic species such as Salicornia europaea, Plantago maritima var. juncoides, and T. maritima grow where salinity is high along some of the small channels and pool edges (Jefferies, Jensen and Abrahams, 1979). Many of these species are on the northern limits of their distribution (Jefferies, Jensen and Abraham, 1979; Jefferies, Jensen and Bazely, 1983). Other shrubs that grow in the low willow areas include dwarf birch, Betula glandulosa and Myrica gale. Only Salix spp. occur in the high willow areas which are slightly further inland. There are no clear cut divisions between the salt marsh, low and high willow areas. Salt marsh vegetation stretches inland to a distance of up to two miles along the banks of the streams and ponds, while on the islands in the Mast River delta, willow bushes grow to heights of up to 1 m. Hultén's (1968) Flora of Alaska was the reference used for plant species identification.

2-2-2 Environmental Data

The climate of La Pérouse Bay is greatly influenced by the coastal location of the bay. The area is classified in the categories B_1 humid (moisture region) and C_1 cool microthermal (thermal climates), in the Thornthwaite Climatic Classification System (Muller and Oberlander, 1974). Compared with true arctic sites, the climate of Churchill and the surrounding region is much less severe during the summer-growing season (Ritchie, 1956). However, pack ice forms on Hudson Bay in November of each year, and it persists until well into May of the next year.

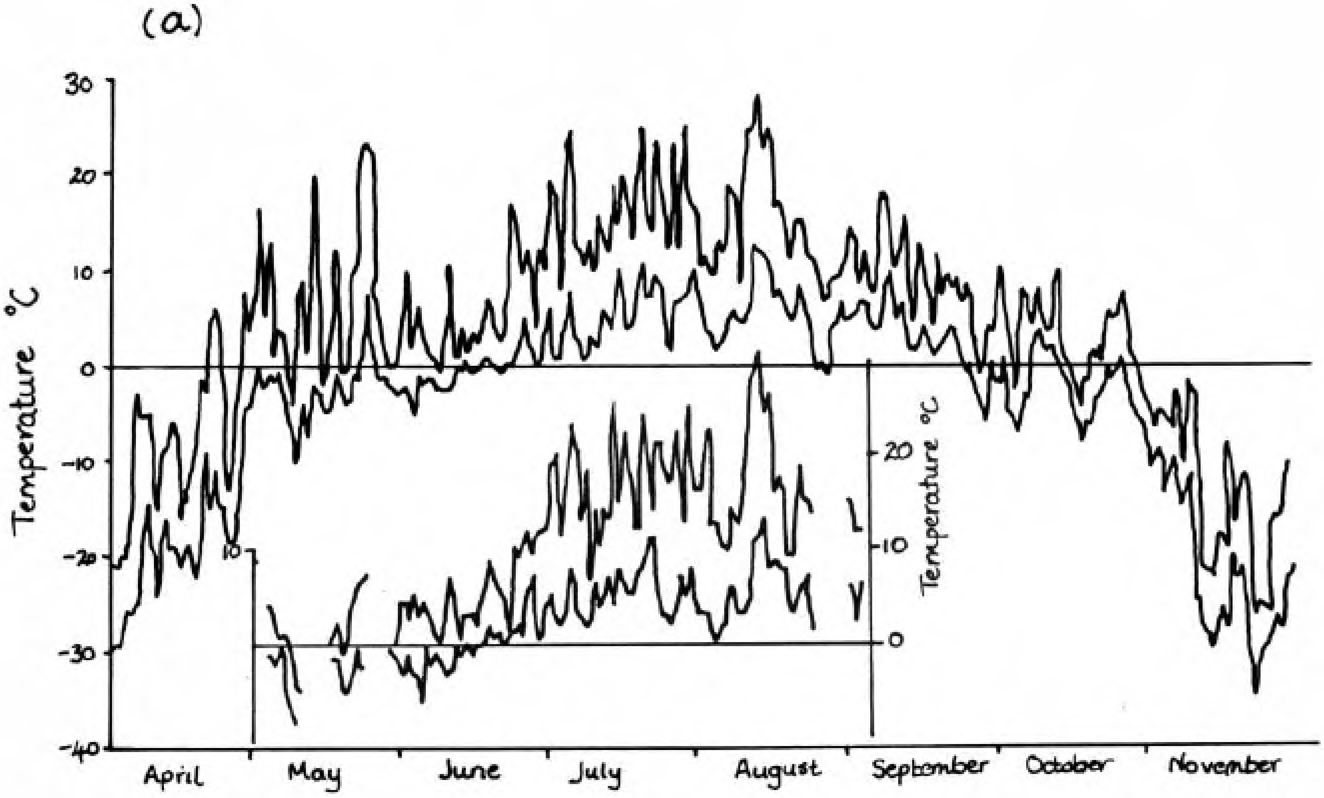
Figure 2-2 shows daily maximum and minimum temperatures for April to November 1982 and 1983 in Churchill, Manitoba, and inset in brown are those for the summer field seasons at La Pérouse Bay in the same years. Table 2-2 and 2-3 show total monthly precipitation data and total hours of sunshine respectively for April to November for both years. The normal temperatures etc. referred to in the following discussion were established from the ten-year running average. The data for Churchill were provided courtesy of the Churchill Weather Office, Environment Canada.

Compared with previous years, the 1982 maximum temperatures were in general lower, and the May to September period was very wet (Figure 2-1a, Table 2-2). Temperatures in April 1982 were well below normal, and at 1.4 mm, precipitation was greatly below the norm of 24.1 mm. In May 1982, there were above normal temperatures, and there was a very warm spell from the 22nd to 24th, and more than double normal precipitation. Both April and May were exceptionally sunny months (Table 2-3). In June 1982, the temperatures were again well below normal, and the monthly mean was 3.0°C (normal = 6.3°C). Precipitation was almost triple the normal amount during June, and

Figure 2-2. Daily maximum and minimum temperatures (°C) at Churchill, Manitoba. Inset in brown: maximum and minimum temperatures at La Pérouse Bay during the field season.

a. Temperatures from April to November 1982.

b. Temperatures from April to November 1983.


(a)
Temperature °C
30
20
10
0
-10
-20
-30
-40
10
0
20
10
0
Temperature °C
April
May
June
July
August
September
October
November

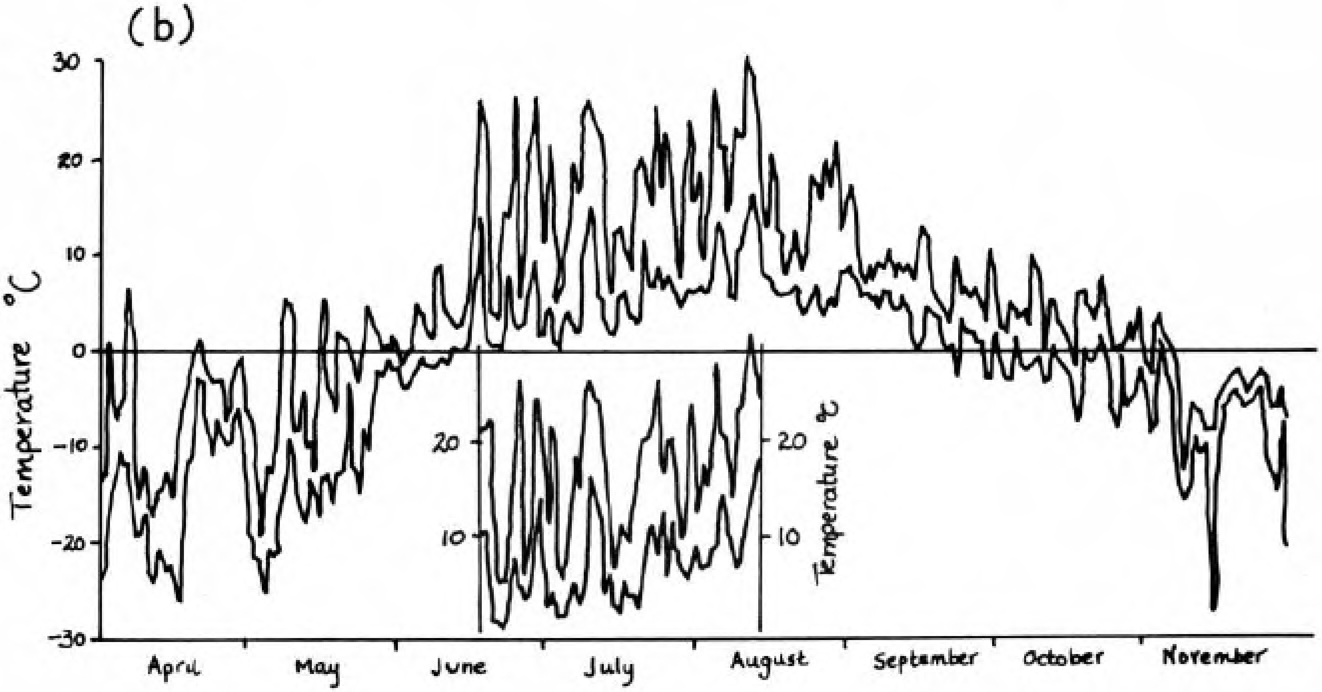

(b)
Temperature °C
30
20
10
0
-10
-20
-30
20
10
20
10
Temperature °C
April
May
June
July
August
September
October
November

Table 2-2. Total hours of sunshine per month at Churchill, Manitoba, and normals, based on a ten-year running average.

Month	1982	NORM	1983	NORM
April	239.8	196	154.5	203.7
May	195.5	182	208.6	195.3
June	149.4	234	205.1	233.7
July	305.7	285	244.2	232.1
August	231.9	234	186.9	232.1
September	94.2	110.8	95.1	NA
October	60.4	61.7	68.1	61.7
November	56.3	49.5	25.4	49.5

Table 2-3. Total monthly precipitation (mm) at Churchill, Manitoba and normals, based on a ten-year running average.

Month	1982	NORM	1983	NORM
April	1.4	24.1	60.9	22.9
May	77.8	31.9	13.2	31.9
June	120.6	43.5	58.1	43.5
July	69.7	58.3	64.1	58.3
August	53.7	58.3	100.5	58.3
September	87.6	50.9	119.1	NA
October	33.8	44.2	39.5	43.0
November	49.9	37.8	55.0	38.8

NA - not available

and there were 149.4 hours of sunshine (normal = 234 hours). In July 1982, the temperatures were around the average values, but precipitation was still higher than normal, and there were more than the expected hours of sunshine. Again, temperatures were lower than expected in August 1982, while precipitation was slightly lower than the norm. September 1982 was a very wet month with near normal temperatures and low sunshine, while October 1982 was a relatively dry month, also with near normal temperatures. However, November was a very cold month with high snowfall.

April to November of 1983 was overall a normal to warm period, and was, in general, much warmer than the same period in 1982. Both 1982 and 1983 were relatively wet years (Table 2-2). In April 1983, temperatures were near normal (Fig. 2-1b), while the total hours of sunshine were very low, at 154.5 hours (normal = 204 hours). The amount of precipitation, 60.9 mm which fell mainly as snow, was greatly above the norm of 22.9 mm. May 1983 was a very cool, dry month compared with 1982, and the mean temperature was more than 6°C below the norm. There was no warm spell as in May 1982. During June and July 1983, there were near normal temperatures. As in 1982, June 1983 was also a wet month with below normal hours of sunshine. August 1983 was a warm, wet month compared with the previous year and the normal values. September 1983, was again very wet, and temperatures were near normal. During October 1983, there were well above average temperatues, and in November 1983, the mean monthly temperature of -6.3°C was greatly above the norm of -12.1°C.; there was also above average snowfall. Thus, 1983 had a much later thaw than 1982, probably because of the cooler temperatures in May. Also, freeze-up was much later in 1983 due to the above normal temperatures in October and November. This comparison of the environmental data for 1982 and 1983 gives some indication of the enormous between-year and within-year variation in the climate at Churchill.

Inset in Figure 2-2 in brown are the daily maximum and minimum temperatures at La Pérouse Bay. Because of the rapid shifts in weather in this area, with temperatures dropping as much as 10°C in 20 minutes, when a fog rolls in from Hudson Bay, La Pérouse Bay weather patterns do not always accurately reflect those found in Churchill. In general though, the temperatures in 1982 and 1983 corresponded very closely with those found at Churchill. On occasions the maximum and minimum temperatures were lower at La Pérouse Bay, probably because of its more exposed location.

2-3 BIOLOGY OF PUCCINELLIA PHRYGANODES

2-3-1 Biology of Grasses

A sward of grass comprises of a population of tillers or plants (Langer, 1979). A series of foliar organs, each consisting of a lamina or leaf blade, and a sheath arising from a node, forms each tiller. Each leaf has a corresponding node, and the latter are highly contracted, so that the stem of the vegetative tiller is short. The apical meristem is situated immediately above the highest node. Thus, during the vegetative phase, many grasses are well adapted to being grazed or cut (Langer, 1979). This is because, at this stage of growth, the apical meristem is very close to the ground, so that although the leaves may be clipped off, the region of active growth is not greatly affected (Langer, 1979).

The meristem or shoot apex, is a highly active region of growth which produces leaf primordia, which eventually form nodes, on opposite sides, just beneath the apex (Langer, 1979). At the beginning of its development, each primordium is entirely meristematic, but as it grows, cell division ceases to occur in the tip of the growing lamina or leaf blade, and is restricted to an intercalary meristem at its base (Langer, 1979). This meristem becomes divided into two regions of activity: in the upper region, the lamina is formed and in the lower region, the sheath is formed. Therefore, it is apparent that the tip of a lamina contains the oldest cells of a grass leaf, and is the first part to senesce as the leaf starts to die.

Axillary buds form at approximately the same time at which leaf primordia are produced (Langer, 1979), and they eventually grow into tillers. After a leaf primordium has developed to the stage at which it encircles the stem axis, a deeper layer of cells starts to divide on the opposite side from which the primordium initially developed. These cells form a bud which is located in the axil of the next lower leaf. Each axillary bud is an exact "replica of the parent structure, complete with apical meristem, leaf primordia and axillary buds" (Langer, 1979).

Axillary buds may develop into tillers in two ways. An "intravaginal" tiller forms from the axillary bud grows from the base of the main tiller within the sheath before emerging (Fig. 2-3a) (Bews, 1929; Langer, 1979; Hubbard, 1984). These tillers tend to develop in grass species characterized by a densely tufted growth habit (Hubbard, 1984). "Extravaginal" shoots, which result in the growth of loosely tufted plants, are formed when axillary buds "burst" through the base of the leaf sheath (Fig. 2-3b) (Bews, 1929; Langer, 1979; Hubbard, 1984). These shoots form stolons, which are overground creeping stems, having the capability of rooting at their nodes (Langer, 1979; Hubbard, 1984). In general, intravaginal shoots are much more common than extravaginal shoots (Gould and Shaw, 1983).

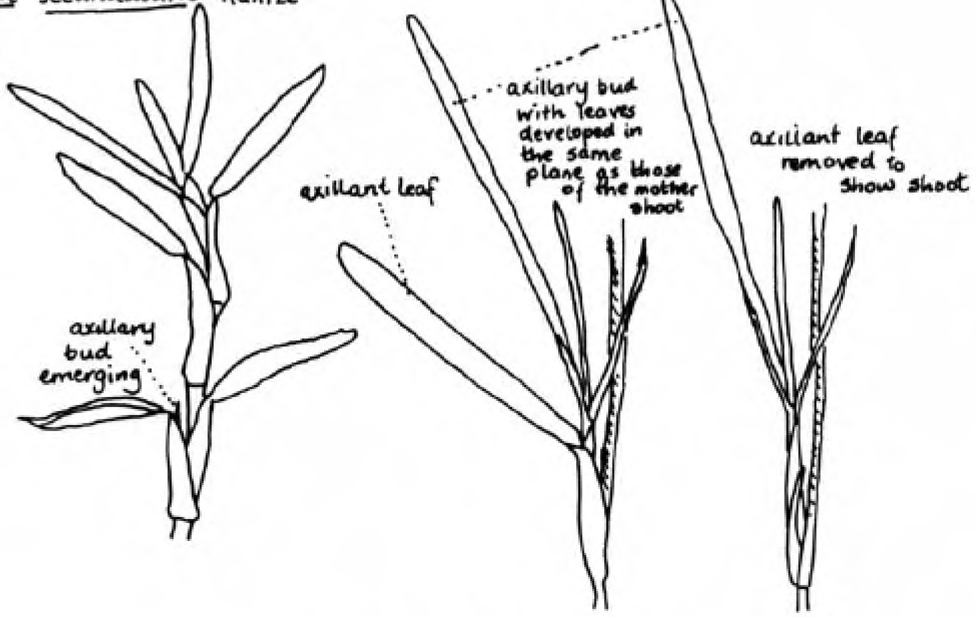
The vascular system, consisting of xylem and phloem, of a tiller is most directly related to the leaf at the next higher node (Fletcher and Dale, 1974). This a logical relationship, given that the axillary bud, formed subsequent to the development of a leaf primordium, develops in the axil of the next lower leaf. The vascular system trace of a lamina runs down into the sheath, but rather than joining with vascular traces running down from higher points in the stem, it passes the node and fuses with the main vascular system at the next node (Fletcher and Dale, 1974). However, the vascular traces of axillary buds join with the main system at their node of insertion (Fletcher and Dale, 1974).

Figure 2-3 a. Diagram of an intravaginal grass tiller.
Adapted from A. Arber, 1934 p. 264.

Figure 2-3 b. Diagram of an extravaginal grass tiller.
Adapted from A. Arber, 1934. pp. 265-6.

Stenotaphrum secundatum Kunize

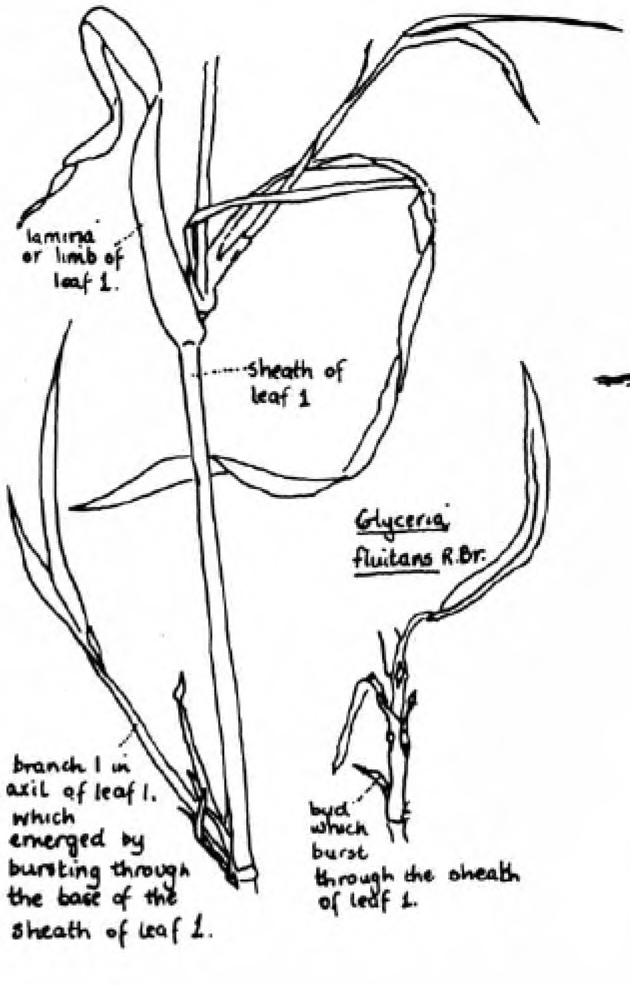
(a)



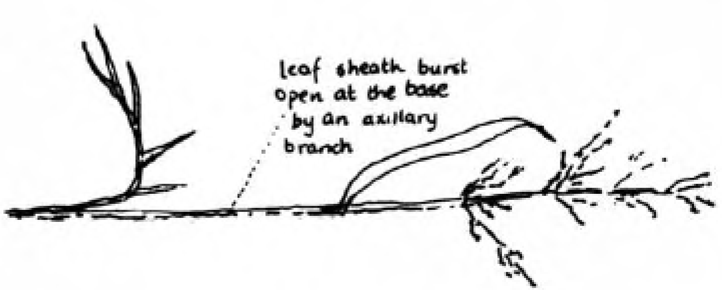
INTRA-VAGINAL BRANCHING

(b)

Phalaris arundinacea L.



Agrostis palustris Huds.



Prostrate axes with extra-vaginal branching in a dead tiller of Agrostis palustris.

EXTRA-VAGINAL BRANCHING

Tillers that form stolons, usually have elongated internodal regions (Langer, 1979). During the early stages of tiller growth, the leaf primordia are very close together. However, as cell division occurs in the region between each primordium and its neighbour, an internodal region is formed. Meristematic activity becomes restricted to the base of this internode, where a basal intercalary meristem forms. Internodes form immediately prior to the initiation of flowering, as well as during the growth of a stoloniferous tiller.

2-3-2 Ecology, Taxonomy and Distribution of Puccinellia phryganodes

Puccinellia phryganodes (Trin.) Scribn. and Merr., is one of the two codominant species on the salt-marsh flats at La Perouse Bay, and is a member of the Gramineae (Fig. 2-4) (Porsild and Cody, 1980). The Puccinellia or "Goose Grass" genus contains generally caespitose or stoloniferous, yellowish-green, smooth grasses of alkaline or saline environments (Porsild and Cody, 1980). P. phryganodes is a halophyte that dominates coastal shores in the arctic and sub-arctic (Polunin, 1940). It is the only member of its genus with a circumpolar distribution (Polunin, 1940; Hulten, 1968; Porsild and Cody, 1980).

P. phryganodes is a stoloniferous species that forms caespitose,or densely tufted mats (Hulten, 1968; Porsild and Cody, 1980). It often occurs in pure swards, and does not reach heights

Figure 2-4. Diagram of Puccinellia phryganodes (Trin.) Scribn. and Merr.

Adapted from Porslid and Cody, 1980., p. 161.

Figure 2-5. Diagram of Carex subspathacea Wormsk.

Adapted from Porslid and Cody, 1980, p.

greater than 15 cm (Polunin, 1940). However, in the grazed areas of La Perouse Bay, it does not exceed 2 cm in height.

The culm or stem of each P. phryganodes tiller or shoot is procumbent, or sharply bent at the base of the plant, and thus is trailing (Porsild and Cody, 1980). However, observations made at La Pérouse Bay suggest that this is not always the case. The leaves of the stolons are flat and bright green, and short, rooting shootlets are often found in their axils (Porsild and Cody, 1980). Hultén (1968) stated that P. phryganodes forms extra-axillary shoots, which are referred to as "infranodal" shoots by Dore and McNeil (1980). However, neither source provided a definition of these terms, which presumably refer to the extravaginal mode of tillering and shoot formation, which has been observed at La Pérouse Bay. Dore and McNeil (1980) indicate that P. phryganodes is unusual in producing "infranodal" shoots.

P. phryganodes flowers consist of a narrow, thin panicle or inflorescence comprised of a few comparatively large spikelets (Porsild and Cody, 1980). The spikelets contain three to six flowers that are pale purple or whitish in colour (Porsild and Cody, 1980). The anthers, which are 1.5 - 2.0 mm long, commonly lack pollen (Porsild and Cody, 1980). Pollen that has been examined was found to be sterile (Jefferies and Gottlieb, 1983). This species flowers rarely, and does not set seed (Polunin, 1940). Plants collected from the Hudson Bay region are thought to be sterile triploids ($2n = 21$) (Jefferies and Gottlieb, 1983). The chromosome numbers of material collected from La Pérouse Bay was also $2n = 21$ (Jefferies and Gottlieb, 1983).

P. phryganodes reproduces vegetatively, and the ice rafting of pieces of turf is thought to be an important means of dispersal (Jefferies and Gottlieb, 1983). However, electrophoretic data indicate that there is a much larger degree of genetic variation within and between populations of *P. phryganodes* from various sites in the Arctic, than would be expected if the only mode of reproduction was vegetative (Jefferies and Gottlieb, 1983). Jefferies and Gottlieb (1983) suggested that sexual reproduction has occurred on rare occasions in this species, thus accounting for the high degree of genetic variation based on electrophoretic enzyme markers that has been found. At La Pérouse Bay, a few flowers have been found in areas from which snow geese were excluded. They did not set seed (Jefferies and Gottlieb, 1983).

2-4 BIOLOGY OF CAREX SUBSPATHACEA

2-4-1 Biology of Sedges

Carex subspathacea Wormskj. is a member of the Cyperaceae or Sedge Family (Fig. 2-5) (Porsild and Cody, 1980). Sedges are similar to grasses in their appearance, having long narrow leaves. Their leaves have basal intercalary meristems similar to grasses, and this characteristic enables them to be grazed without great damage being inflicted (Christiansen, 1979). Sedges may form both stolons and rhizomes. The latter are similar to stolons, except that they occur below-ground.

2-4-2 Biology of Carex subspathacea

C. subspathacea Wormskj. is a turf forming dwarf species, with a creeping rhizome system (Porsild and Cody, 1980). Hultén (1968) describes this species as loosely caespitose, or loosely tufted, but at La Pérouse Bay, it also occurs in densely tufted swards. The culms are erect ascending, and very short (Porsild and Cody, 1980).

C. subspathacea has a circumpolar distribution in the High Arctic and its range extends south to the Low Arctic and Sub-Arctic (Porsild and Cody, 1980). It is confined to coastal marshes, and brackish environments, and it grows in sites flooded by high tides (Porsild and Cody, 1980).

CHAPTER 3

STANDING CROP AND PRIMARY PRODUCTION IN GRAZED AND UNGRAZED AREAS

3-1 INTRODUCTION

An objective of this study was to monitor leaf-area indices and amounts of standing crop during the growing season in grazed areas and in exclosed, ungrazed areas in 1982 and 1983. The cumulative net above-ground primary production (NAPP) in both areas was calculated from the differences in standing crop between consecutive harvests. These estimates of NAPP and standing crop represented a continuation of experiments initiated by Cargill (1981); the techniques that she used continued to be employed in this study.

There were two main reasons for continuing these experiments. First, measurements of standing crop enabled comparisons to be made between the hatch date of goslings and the stage of growth of plants for different years. Cargill's (1981) data indicated that differences in plant growth in grazed and ungrazed sites became apparent 1 1/2-2 months after the peak-hatch date. The peak-hatch date has varied from June 14 to July 4 and has been correlated with weather conditions (Cooke _et al_, 1982). Differences in plant growth between grazed and ungrazed sites occurred at different times in the summer of 1979 and 1980. Although these differences may have been caused by inter-seasonal environmental variation, they may also have been influenced by the time of hatch and onset of grazing. Utilization of the same techniques in 1982 and 1983 enabled comparisons to be made of the NAPP over four years as well as a comparison of the pattern of plant growth and hatch dates. Secondly, these data provided a necessary background for the interpretation of data from other experiments on the growth of *Puccinellia phryganodes*. These included a detailed demographic study of individual shoots of *Puccinellia* in grazed and ungrazed areas.

In the following section a number of terms are used to describe the parameters of plant growth that were measured. Since this is a grazing study, the terminology and definitions used will correspond as closely as possible with those used by Hodgson (1979) and Thomas (1980). The term "sward" refers to an area of grassland "with a short continuous foliage cover, including both above and below-ground parts" (Thomas, 1980). In this study, sward refers only to above-ground parts. Standing crop as used here refers to the mass of above-ground parts of the vegetation per unit area at a particular instant of time (Chapman, 1976). It may be divided into live or dead standing crop, depending on whether the vegetation was sorted following harvest. A harvest is the defoliation of a sward with a cutting machine (Thomas, 1980). Net above-ground primary production (NAPP) is the amount of organic matter incorporated by the above-ground parts of an area of vegetation over a given period of time. In this study, NAPP was measured between June and September 1982 and June and October 1983.

3-2 METHODS

3-2-1 Standing Crop and Net Primary Production of Ungrazed Vegetation

Large chicken-wire exclosures were erected as soon as possible after snow melt in grazed swards of *Puccinellia phryganodes* and *Carex subspathacea*, so as to prevent grazing at selected sites. Each exclosure was 4 m x 4 m in area and consisted of approximately 0.5 m high chicken wite stapled to wooden posts positioned along the perimeter. A length of twine was strung across each diagonal of the exclosure, and flagging tape was tied at intervals along the twine. This discouraged geese from flying into the exclosure.

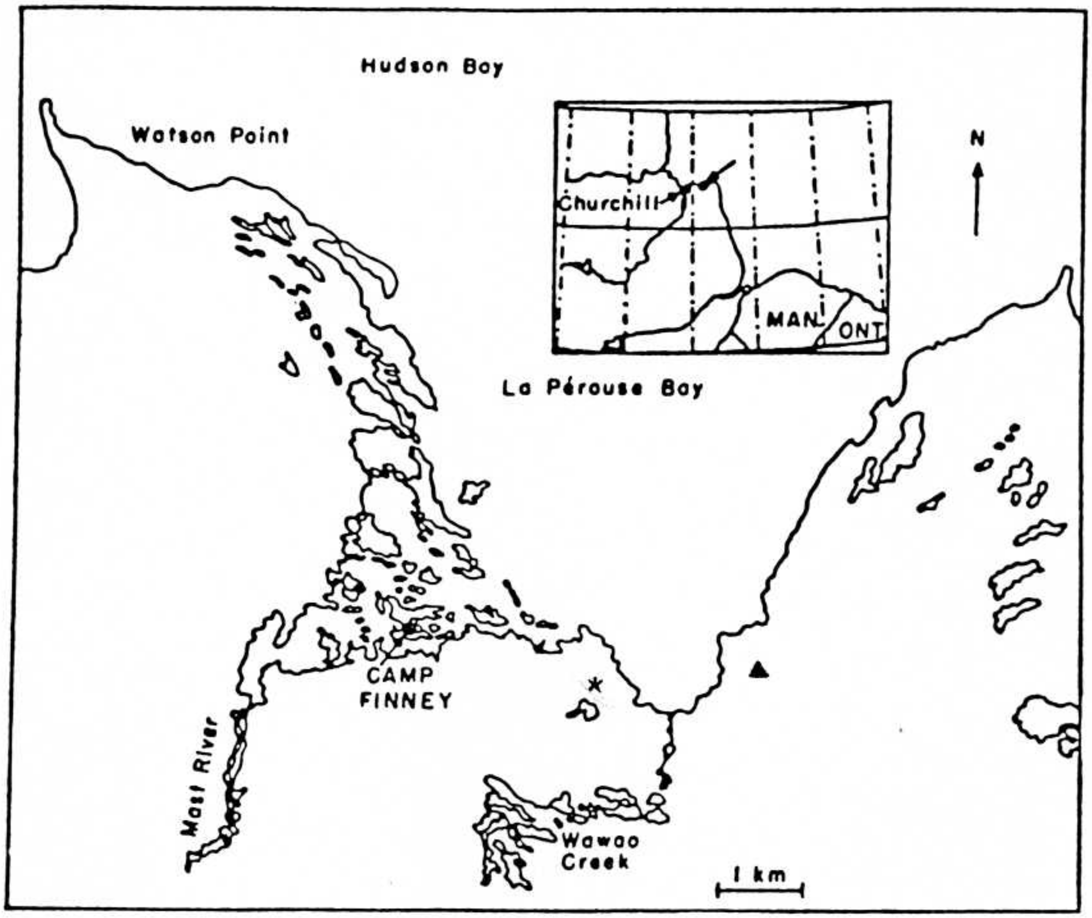
On May 29, 1982, three exclosures were erected in grazed swards dominated by *Puccinellia phryganodes* (Fig. 3-1). The main criterion for the choice of site was the apparent uniformity in the appearance of the sward. The standing crop in the exclosures was measured every 10 days from June 8 to August 17; the last turfs were collected 16 days later on September 2. On each of the nine harvest dates, two 16 cm x 16 cm turfs were cut at random from each exclosure using random number tables to locate the coordinates. As the below-ground biomass was not sampled, the turfs were cut only 1 cm deep. They were placed in plastic bags and on the same day, all of the above-ground biomass and litter were clipped from each turf. Each sample of vegetation was washed in a coarse sieve (1 mm mesh: Tyler no. 18), in order to remove soil from the plant material. Samples were refrigerated and sorted within three days of collection. They were floated in shallow trays of water and the live material of each species was separated; all dead material, standing dead and litter were combined. The samples were blotted with paper towels, placed in envelopes and dried above a propane heating stove. At the end of the summer they were dried again in an oven at 80°C for 48 hours in Churchill and weighed to the nearest 0.01 g on a Mettler PK 500 Analytical Balance.

In 1983, the area chosen for exclosures was approximately 1 km east of the previous year's site (Fig. 3-1). In 1982, I noticed that the area had been heavily grazed by snow geese. A site dominated by Puccinellia phryganodes was again chosen and a 4 m x 4m exclosure was built on June 18. Compared with previous years, this was a late date for erection of exclosures. However, 1983 was an exceptionally late season and snow melt occurred as late as mid-June, so that sites could not be chosen earlier than this time.

On June 23, the first turfs were cut at random from inside the exclosure. Additional turfs were collected in August and October. On each occasion, three turfs, each 16 cm x 16 cm, were cut at random from inside the exclosure. The reason for decreasing the number of sample dates and number of sites which were sampled was based on evidence from previous years which suggested that three sample dates and three replicates from within a site would result in sufficient data to enable an estimate to be made of net above-ground primary production in ungrazed swards.

On each sample date, the turfs were transported to the field station, clipped, sorted into species, dried and weighed as described previously.

Figure 3-1. Map of La Pérouse Bay showing the locations of exclosures built in 1982 and 1983. (* 1982 sites; ▲ 1983 sites).


Hudson Bay
Watson Point
Churchill
MAN.
ONT.
N
La Pérouse Bay
CAMP
FINNEY
Mast River
Wawao
Creek
1 km

3-2-2 Net Primary Production of Grazed Vegetation

Estimates of net above-ground primary production in grazed areas were obtained as follows. Six small (1 m x 1 m x 0.5 m high) moveable chicken wire exclosures were placed for a period of approximately ten days in areas that had been grazed the previous day. After this time they were moved to another site which had just been grazed for a further ten days. This procedure continued throughout the summer.

The standing crop in an exclosure was measured at the beginning and end of each ten day period and the increments in the growth of the *Puccinellia* - dominated vegetation were calculated. By summing these regrowth increments for the different exclosures for the duration of the summer, the cumulative NAPP was estimated for grazed areas.

At intervals of every ten days from June to August in 1982 in grazed sites in the vicinity of the three permanent exclosures, six 16 cm x 16 cm turfs were cut. The vegetation was clipped, washed, sorted and weighed as described earlier. The total dry weight of the live above-ground vegetation was a measure of the live standing crop of grazed swards on each sample date, and also served as a measure of the initial standing crop in each exclosure erected for ten days. The six moveable exclosures were placed on sites immediately adjacent to those from which the grazed turfs had been cut. After approximately ten days, a turf 10 cm x 10 cm was cut from the centre of each small exclosure, and the vegetation was clipped, washed, sorted and weighed as previously described. There were eight consecutive regrowth periods, all of which were 9 to 12 days, except for the last, which was 16 days in length.

In 1983, the same technique was used to estimate NAPP, the only difference being that the size of six turfs collected at the beginning of each regrowth period was 10 cm x 10 cm. This decrease in size was necessary due to less time being available for washing and sorting. Those turfs collected from within the moveable exclosures at the end of the period were 10 cm x 10 cm, as in 1982. The periods of regrowth were not as uniform in length, varying from 8-16 days between June and September. The final regrowth period was 43 days in length, from September 3 to October 15. This was because we returned to Toronto in September and subsequently made the decision to return to La Pérouse Bay in October. There were seven consecutive periods of regrowth between June 23 and October 15.

These methods for estimation of standing crop and NAPP of grazed vegetation, were essentially the same as those used by Cargill (1981).

3-2-3 Leaf Area Indices of Grazed and Ungrazed Vegetation

The leaf area index (LAI) is the leaf area (one surface only) per unit area of land. It is a ratio and is consequently dimensionless. In 1983, leaf area indices of vegetation in newly built permanent exclosures were estimated on three occasions, while those of grazed vegetation were estimated six times, between June and September. In addition, the LAI's were measured on turfs collected from the small (1 m x 1 m) moveable exclosures at the end of four of the periods of regrowth of vegetation. The LAI gives a useful broad index of the productive capacity of a stand of vegetation (Hunt, 1982), and thus a comparison could be made between LAI values for La Pérouse Bay vegetation and the actual standing crop values and estimates of production.

Three replicate turfs, 5 cm x 5 cm, were collected at random from within the permanent exclosure. In the case of the moveable exclosures, three were chosen at random, and one 5 cm x 5 cm turf was removed from each at the start and at the conclusion of each ten day period. At all times, the sample dates corresponded with those for standing crop measurement, enabling direct comparisons to be made between standing crop values and LAI values for specific dates.

Each small turf was carefully trimmed to 2 cm x 2cm. Vegetation and litter were clipped from each turf at the soil surface, using nail scissors. The material was washed over a 1 mm sieve and sorted into live and dead material. Because the turfs were small, it was possible to separate live and dead material to the extent of removing all dead leaves attached to live shoots. After drying with paper towels, the leaf area of live material and the area of dead material were determined using a Li-Cor Portable Leaf-Area Meter, Li-3000. By dividing the leaf area and area of dead material by the surface area of the turf, the LAI was determined for each sample.

Thomas (1980) observed that in grasses, the leaf consists of the lamina, ligule and sheath, and is ot synonymous with lamina. In this study, the live material consisted of the leaf as defined by Thomas (1980).

3-3 RESULTS

3-3-1 Live Above-Ground Standing Crop in Grazed and Ungrazed Sites

All of the standing crop measurements and estimates of production are expressed in grammes dry weight of vegetation per metre squared, and the abbreviation "g m^{-2}", used in the following sections refers to this, unless otherwise stated.

The initial measurement of standing crop was 12.8 g m^{-2} on June 8, 1982, in both grazed and ungrazed sites (Fig. 3-2a). After June 15 there was a rapid increase in the amount of live standing crop in the exclosures. The standing crop peaked in mid-August at a value of 91.3 m^{-2}, before dropping to 63.3 g m^{-2} by September 2.

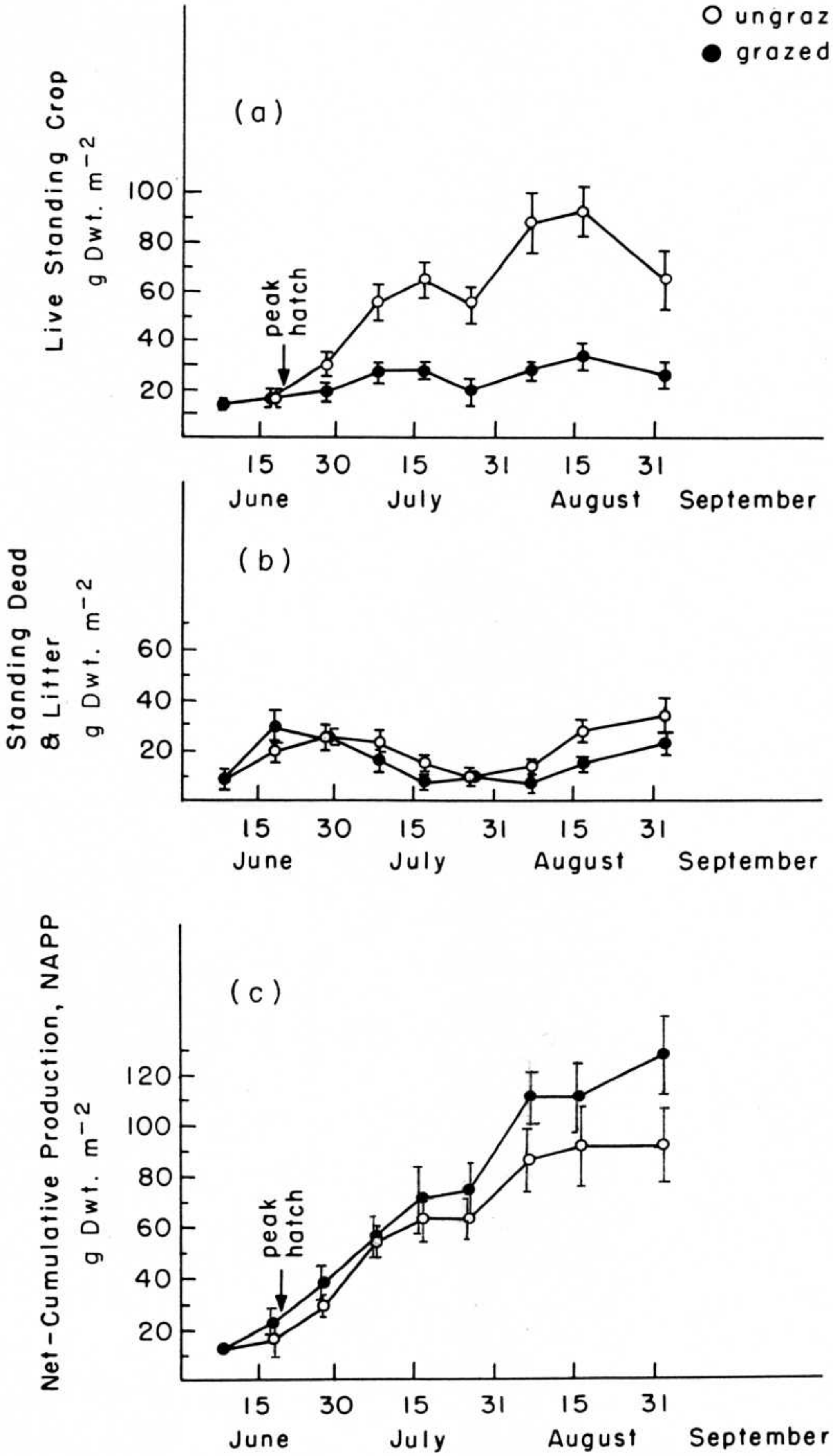
In the adjacent grazed area, standing crop increased from 12.8 g m^{-2} at the start of the season to 32.5 g m^{-2} on August 17. After this date, it dropped to 24.8 g m^{-2} on September 2. The difference in the amount of above-ground live biomass between grazed and ungrazed areas became discernible after June 18, which corresponded with the beginning of the snow goose hatch period in 1982. Once the goslings hatched, the geese moved out to the marsh where they fed for up to 18 hours per day. Consequently, the standing crop was always much lower than that in ungrazed areas.

Figure 3-2 a. Seasonal trends in live above-ground standing crop (g dry weight m^{-2}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1982. (mean +/- S.E., n=6).

Figure 3-2 b. Seasonal trends in litter and standing dead (g dry weight m^{-2}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1982. (mean +/- S.E., n=6).

Figure 3-2 c. Estimated cumulative net above-ground primary production (g dry weight m^{-2}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1982. (Bars are +/- 95% Confidence Intervals).

1982 : *Puccinellia phryganodes* – dominated sward.



In 1983, similar trends were observed. Following hatch the standing crop in the ungrazed exclosure attained a much higher value than that in the adjacent grazed area (Fig. 3-3a). The season was much later in 1983 than in 1982; snow melt did not occur until mid-June. Nesting of snow geese was three weeks later than the norm (Cooke _et al_, 1982). Hatch dates are shown in Table 2-1.

The initial standing crop in both grazed and ungrazed areas was 27.1 g m^{-2} on June 23. The standing crop rose rapidly to 95.2 g m^{-2} on July 30, and peaked at 104 g m^{-2} on August 25 in ungrazed exclosures. Dashed lines connect the live standing crop value for August 25 with that of October 15, because the value of 104 g m^{-2} for the latter date is for both dead and live material combined. Samples collected in October contained large amounts of senescent vegetation which was difficult to separate, so both the live and dead plant material were combined.

In the adjacent grazed areas, standing crop increased rapidly to 41.5 g m^{-2} on July 4, after which date it was approximately 40 g m^{-2}, except for a drop to 22.8 g m^{-2} on August 25. On October 15 the combined live and dead material weighed 91.3 g m^{-2}. On September 2 the combined live and dead vegetation weighed 51.3 g m^{-2}, indicating that there was considerable growth in grazed areas from September 2 to October 15, after the geese had migrated from La Pérouse Bay.

3-3-2 Standing Dead and Litter in Grazed and Ungrazed Areas

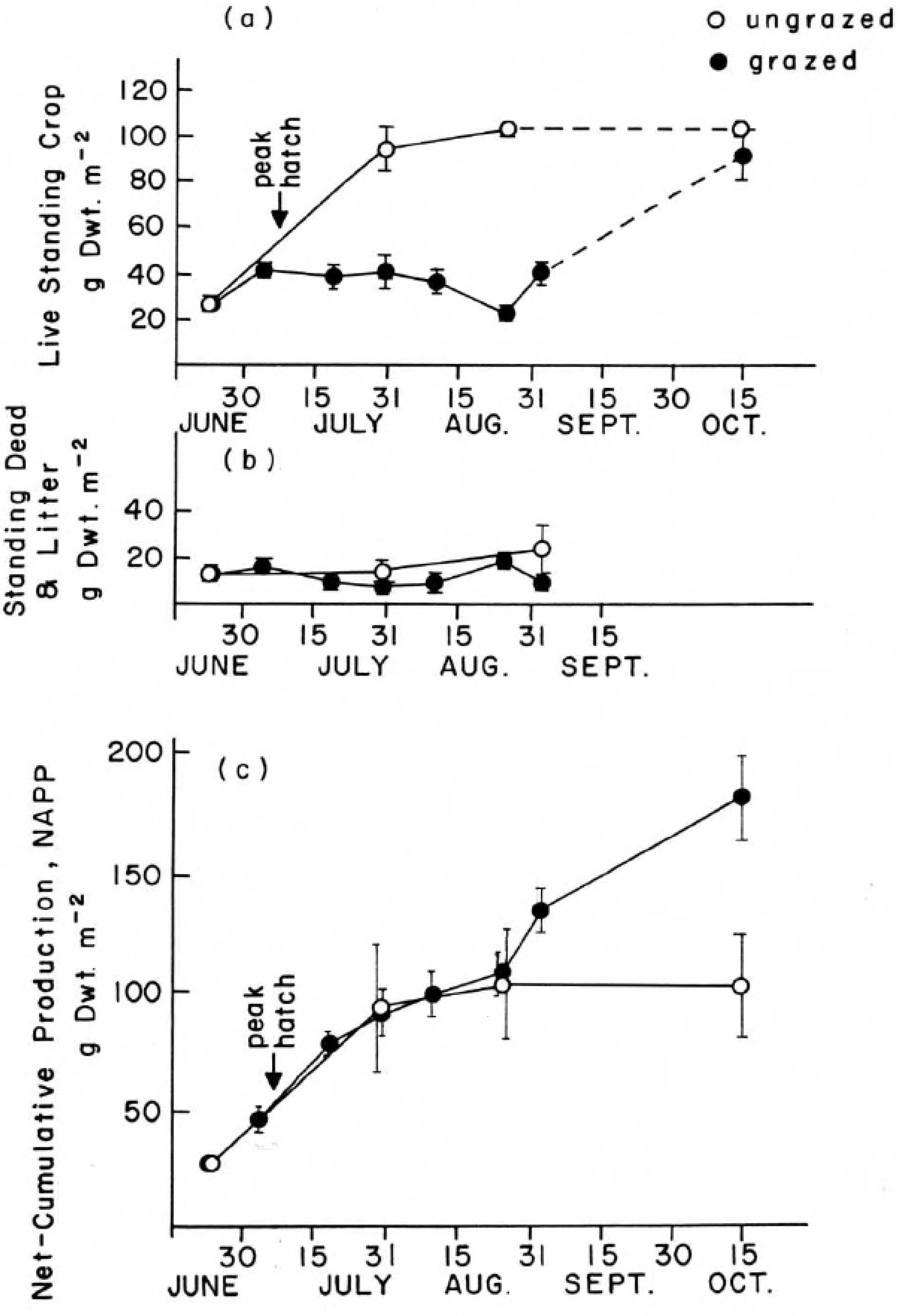
Figure 3-2b shows seasonal trends in above-ground litter and standing dead for 1982. "Standing dead" refers to dead leaves

Figure 3-3 a. Seasonal trends in live, above-ground standing crop (g dry weight m^{-2}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1983. (mean +/- S.E., n=3).

Figure 3-3 b. Seasonal trends in litter and standing dead (g dry weight m^{-2}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1983. (mean +/- S.E., n=3).

Figure 3-3 c. Estimated cumulative net above-ground primary production (g dry weight m^{-2}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1983. (Bars are 95% Confidence Intervals.

1983: *Puccinellia phryganodes*-dominated sward.



attached to live shoots. During the sorting process, these leaves were not separated from the shoots on an individual basis, because of the amount of time involved. However, the bulk of the attached dead leaves became detached when the vegetation was clipped from the turfs.

Amounts of standing dead and litter were similar for both grazed and ungrazed areas. Values rose from 9.5 g m^{-2} on June 8 to 30 g m^{-2} by June 18 in the grazed site. The initial measurement was probably an underestimate, as separation of live and dead material was difficult at this date. This was because even live *Puccinellia* shoots had a green-brown appearance, as the weather was not yet warm enough for active plant growth. In late July, the amount of dead material dropped to about 10 g m^{-2} in both exclosures and grazed areas. It increased again later in the summer, particularly in the exclosures where it reached 34.0 g m^{-2} in late August.

In 1983, the initial amount of litter was 13.1 g m^{-2} on June 23 (Fig. 3-3b). The litter levels in both the exclosure and the grazed site were similar throughout the season, although in the exclosure 25 g m^{-2} of litter was recorded on September 2. The amounts of litter and standing dead were similar in 1982 and 1983. However, a marked end-of-season increase of dead material was not observed in grazed or ungrazed areas in 1983. This may have been caused by 1983 being a later season, and, had a harvest in mid-to late-September been possible, this increase may have been observed.

3-3-3 Cumulative Production in Grazed and Ungrazed Areas

The cumulative production in ungrazed areas was estimated by summing positive increments in standing crop between each sample date. Any negative increments were noted but not subtracted from the running total which was held the same until the addition of the next positive increment. In grazed areas, the positive increments in growth for consecutive periods of regrowth were summed to give an estimate of NAPP.

Figure 3-2c shows cumulative NAPP for grazed and ungrazed areas in 1982. It is apparent that in grazed areas, which had a much lower live standing crop than that in the exclosures, there was a greater cumulative production. The total NAPP of ungrazed vegetation was estimated as the difference between the peak standing crop minus the initial standing crop. This gave the same result as summing all positive increments, and total NAPP was 78.5 g m^{-2}. Live biomass present at the onset of sampling, shortly after snow melt, was assumed to represent the previous season's growth.

The estimated NAPP in grazed sites in 1982 was 114 g m^{-2} (Fig. 3-2c), which represents a 46% increase in over the NAPP of ungrazed swards. The difference in cumulative NAPP between grazed sites and exclosures became apparent towards the end of July, approximately six weeks after peak hatch. Cumulative growth occurred in the exclosures until the beginning of August, but after this time, unlike in the grazed sites, no further increases in live standing crop occurred.

In 1983, a season in which the spring thaw was particularly late, cumulative NAPP was similar in both grazed and ungrazed sites until August 25, approximately seven weeks after peak hatch (Fig. 3-3c). The increase in production observed at the end of August in grazed swards of Puccinellia phryganodes was maintained until mid-October when the cumulative NAPP peaked at 159 g m^{-2}. This value is lower than that given in Figure 5-3c for this date, as it was obtained by subtracting the initial standing crop on June 23 from the value for October 15 given in the Figure. The cumulative NAPP of ungrazed sites on the same date was 77 g m^{-2}, following the adjustment involving subtraction of the June 23 standing crop value on June 23 at the start of the season from the NAPP value on October 15 for ungrazed sites. Therefore, grazing increased NAPP by 106%, which was the largest increase observed for data collected over four years. The increase was 30% in 1979 and 80% in 1980 (Cargill and Jefferies, 1984b). The 1983 result reflected the late sampling date in October; in previous years the final sampling date was in late August or early September. The NAPP of ungrazed vegetation was similar in 1982 and 1983, at a value of approximately 80 g m^{-2} in both summers.

The cumulative production in grazed sites was significantly higher than that in ungrazed sites in 1982 and 1983 ($p<0.05$, df=10). The statistical test used to compare the cumulative NAPP values is given in Appendix 3-1 along with calculations for the 95% confidence intervals.

3-3-4 Leaf Area Indices

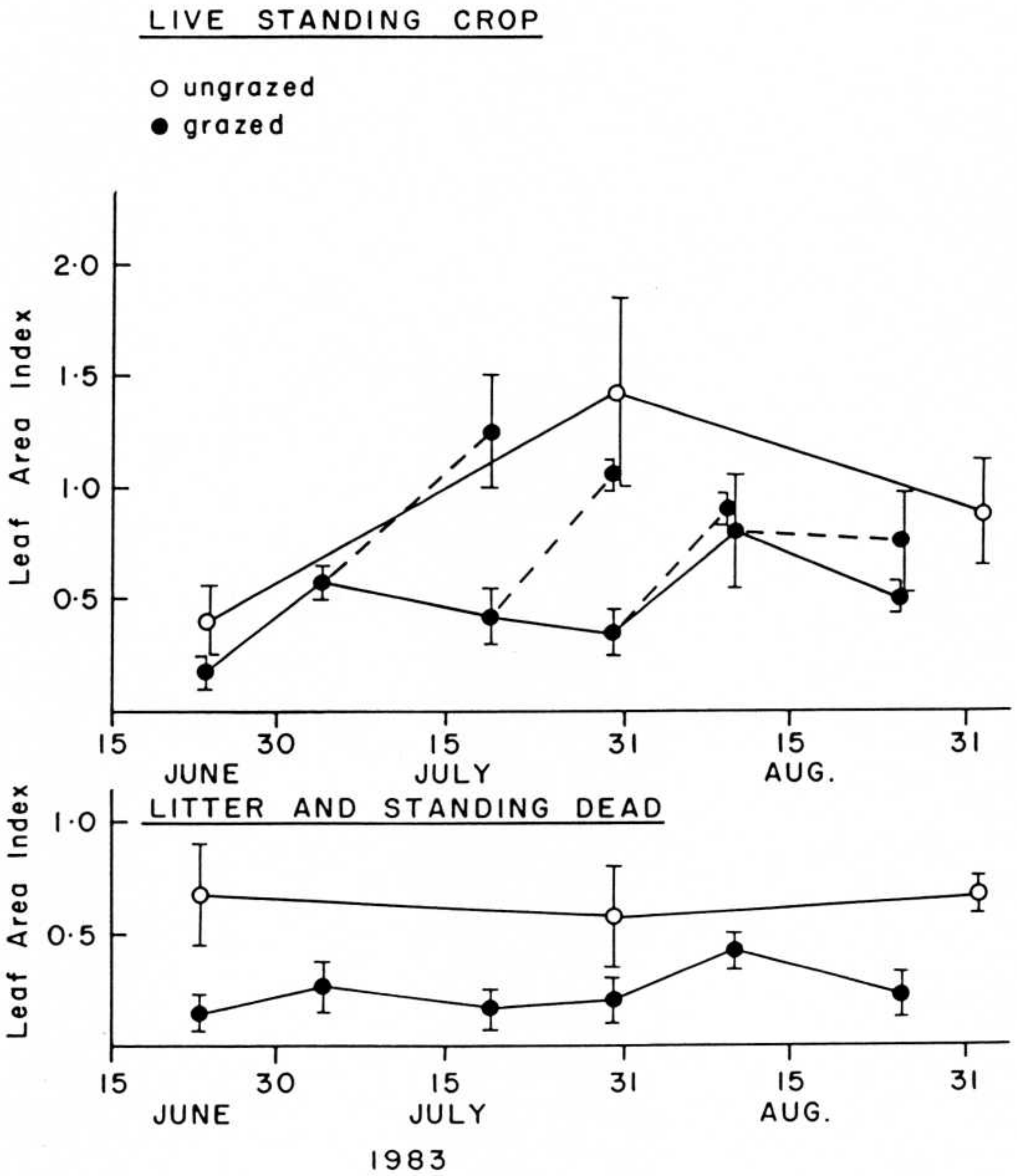
In 1983, the initial value for leaf area index (LAI) of the live vegetation in the exclosure was 0.4 on June 23 (Fig. 3-4a). The LAI rose to 1.4 by July 30 and dropped to 0.9 in early September. LAI in the grazed areas was lowest early on in the growing season and failed to rise above 0.8 throughout the summer. It fluctuated around 0.5 before rising to its highest value of 0.8 on August 10. This increase in LAI was not associated with an increase in the amount of live standing crop in grazed areas on the same date (Fig. 3-3a). LAI in ungrazed areas was consistently higher than that in grazed areas, reflecting the differences between the sites in standing crop.

The dashed lines in Fig. 3-4a connect points showing LAI in grazed areas at the beginning and end of a period of regrowth of the Puccinellia sward. During the first three periods, LAI increased by more than 100% over the initial value. Measurements of the LAI of regrowth swards on August 10 and August 25 failed to show an increase. However, NAPP increased from 36.6 g m^{-2} to 46.6 g m^{-2} over the same period (Fig. 3-3c). Sampling variability most likely accounted for the absence of an increase in LAI.

The LAI of litter and standing dead in the exclosure showed little change throughout the summer; it fluctuated between 0.57 and 0.67 (Fig. 3-4b). Corresponding values for grazed areas also showed little change, and the LAI ranged between 0.15 and 0.43 (Fig.

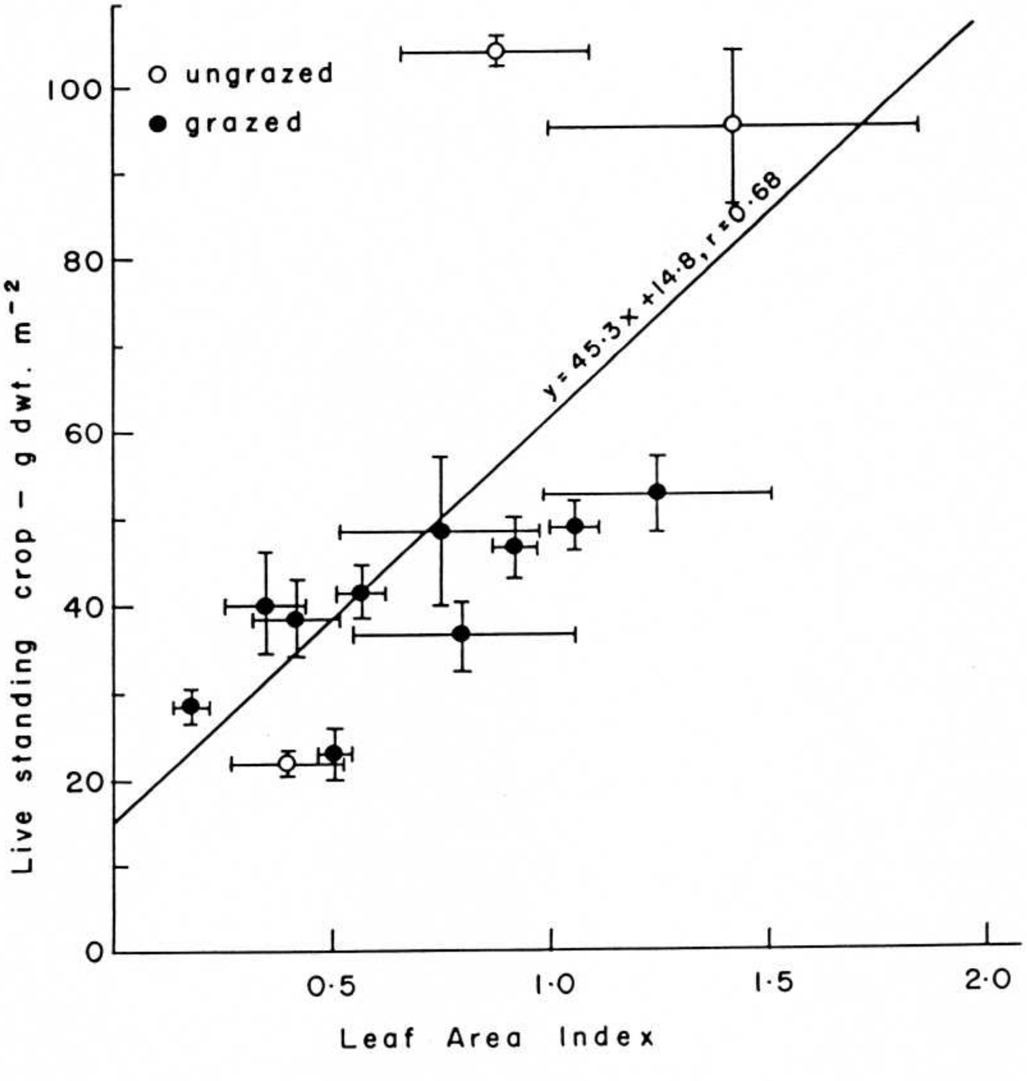
Figure 3-4 a. Leaf area indices of live above-ground biomass in grazed (●) and ungrazed (O) sites at La Pérouse Bay, June to September, 1983. The dashed lines connect LAI's of the live above-ground biomass in grazed sites with LAI's following 9-14 day periods of exclusion of geese from these sites. (Mean +/- S.E., n=3)

Figure 3-4 b. Leaf area indices of litter and standing dead in grazed (●) and ungrazed (O) sites at La Pérouse Bay, June to September, 1983. (Mean +/-S.E., n=3).



LIVE STANDING CROP
○ ungrazed
● grazed
Leaf Area Index
2·0
1·5
1·0
0·5
15
30
15
31
15
31
JUNE
JULY
AUG.
LITTER AND STANDING DEAD
Leaf Area Index
1·0
0·5
15
30
15
31
15
31
JUNE
JULY
AUG.
1983

Figure 3-5. Live above-ground standing crop (g dry weight m^{-2}) versus leaf area index in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay (Mean of leaf area index +/- S.E., n=3; Mean of live standing crop +/- S.E., n=3. Linear regression equation: $y = 45.3x + 14.8$, $r = 0.68$*).



○ ungrazed
● grazed
y = 45·3 x + 14·8 , r = 0·68
Live standing crop – g dwt. m^{-2}
0
20
40
60
80
100
0·5
1·0
1·5
2·0
Leaf Area Index

3-4b). Values for LAI through the summer at both grazed and ungrazed sites are consistent with those for standing dead and litter in 1983 (Fig. 3-3b).

Figure 3-5 shows values of live above-ground standing crop plotted against their respective leaf area indices. The low value of live standing crop in an ungrazed sward was measured at the beginning of the summer in 1983. There was significant correlation ($p < 0.05$, df=11) between live standing crop and LAI, indicating that the latter gives a good indication of the live biomass present at grazed and ungrazed sites.

3-4 DISCUSSION

The results for live standing crop and NAPP in ungrazed exclosures are similar to those of Cargill and Jefferies (1984b). In 1979 the NAPP was estimated as 100 g m^{-2} in a mixed Puccinellia/ Carex sward, and in 1980 the corresponding value was 56 g m^{-2} in Puccinellia-dominated swards. In both 1982 and 1983, NAPP for ungrazed sites was estimated as 80 g m^{-2} (Table 3-1). In all four years, rapid growth occurred during June and July, and thereafter, the accumulation of live above-ground biomass slowed considerably in the exclosures.

As Cargill and Jefferies (1984a,1984b) point out, the results for NAPP were similar to those found for other tundra graminoid communities, which were in the order of 100 g m^{-2}. For example, in Dupontia meadow vegetation at Barrow, Alaska, the NAPP of vascular plants, was 57g m^{-2} and in a Carex-Poa meadow it was 108 g m^{-2} (Miller, Webber, Oechel and Tieszen, 1980). In the Truelove Lowland, Devon Island, NAPP of wet sedge-moss vegetation was estimated at 46 g m^{-2} (Muc, 1977).

Table 3-1. Cumulative net above-ground production in ungrazed and grazed swards dominated by _Puccinellia phryganodes_ at La Pérouse Bay, 1979, 1980, 1982 and 1983.

YEAR	CUMULATIVE PRODUCTION IN GRAZED SITES g Dwt m^{-2}	CUMULATIVE PRODUCTION IN GRAZED SITES g Dwt m^{-2}
1979*	100	135
1980*	56	99
1982	78.5	114
1983	77	159

* Data from Cargill and Jefferies, 1984b. (In Press).

In wet meadow Arctic sites, the bulk of the biomass is located below ground (Miller, Webber, Oechel and Tieszen, 1980; Wielgolaski, Bliss, Svoboda and Doyle, 1981). Cargill and Jefferies (1984b) also found that over 90% of the total standing crop consisting of above and below-ground biomass, was below-ground at La Pérouse Bay.

The Barrow and Truelove Lowland sites are at latitudes higher than 70°N. Although La Pérouse Bay is at 58°N, the prevailing winds are from the north-west, and coastal summer temperatures tend to be lower than those further inland (R. Bello pers. comm.). This may explain why values of NAPP are more similar to those found in Arctic sites and lower than those observed in more southern salt marshes on James Bay (51°N). The latter are dominated by Puccinellia phryganodes and by P. lucida, and NAPP of these marshes has been estimated at 230 g m^{-2} yr^{-1} (Glooschenko and Harper, 1982). However, in other years, NAPP of these sites was estimated at 500 g m^{-2} yr^{-1} (Glooschenko and Martini, 1978). These figures are in the range of NAPP values observed in salt marshes at much more southerly latitudes. For example, NAPP estimates for an English salt marsh at Colne Point in Essex were in the range of 250 g m^{-2} yr^{-1} (Hussey and Long, 1982). In a New England Spartina alterniflora salt marsh, NAPP in the low marsh was estimated at 510 ± 110 g m^{-2} (Valiela, Teal and Sass, 1975). Therefore, it appears that the La Pérouse Bay salt marsh which is in a sub-arctic zone, is more arctic in its production characteristics than marshes at a latitude of 8° further south.

The values of NAPP for La Pérouse Bay were not given as annual production figures because they did not cover the entire growing season. They were for the June to September period, and, as the October, 1983 sample date revealed, considerable growth may occur after early September. Further growth may have occurred between October 1983 and the time of freeze-up and snow cover. Also, it is not known whether any growth occurs in early and late winter, under the snow when the ground may not be frozen.

The standing dead and litter estimates for 1982 and 1983 in both grazed and ungrazed areas were similar to those of Cargill and Jefferies (1984b) for 1979, which fluctuated around 15 g m^{-2} (Table 3-2). They are lower than those found in 1980, which were approximately 40 g m^{-2} during the summer (Cargill and Jefferies, 1984b). Cargill and Jefferies (1984b) suggest that litter levels are dependent upon the previous year's production. Since 1982 was not as productive a year as 1979, in which NAPP was estimated at 135 g m^{-2} (Cargill and Jefferies, 1984b), one would expect to find lower litter levels in 1983 than in 1981, as was the case. Cargill and Jefferies (1984b) also found no observable differences between the litter and standing dead in exclosures and grazed areas, which was also the case in 1982 and 1983.

In general these amounts of litter and standing dead are much lower than those that have been found in both tundra graminoid communities and in more temperate salt marshes. In the <u>Dupontia</u> meadow at Barrow, amounts were 125 g m^{-2} at their maximum (Miller, Webber, Oechel and Tieszen, 1980). Litter accumulation occurs in

Table 3-2. Levels of litter and standing dead in grazed and ungrazed swards dominated by Puccinellia phryganodes at La Perouse Bay, 1979, 1980, 1982 and 1983.

YEAR	MINIMUM/MAXIMUM LITTER AND STANDING DEAD LEVELS IN UNGRAZED SITES g Dwt m^{-2}	MINIMUM/MAXIMUM LITTER AND STANDING DEAD LEVELS IN GRAZED SITES g Dwt m^{-2}
1979*	15/20	9/28
1980*	33/47	32/50
1982	10/34	10/30
1983	13/25	8/1

* Data from Cargill (1981).

many arctic tundra communities because lower temperatures are thought to cause a reduction in decomposition rates (cf. Chapter 5; Haag, 1974); Webber, 1978; Miller, Webber, Oechel and Tieszen, 1980). However, Glooschenko and Harper (1982) found peak litter levels of 25 g m^{-2} at James Bay, which are similar to the results from La Pérouse Bay. Even so, they state that tidal-flushing may have reduced the amounts of litter present (Glooschenko and Harper, 1982). The results from La Pérouse Bay are much lower than those from salt marshes at more southerly latitudes. For example, in Delaware salt marshes, mean litter values of 462 g m^{-2} have been observed (Linthurst and Reimold, 1978), while in England, at Colne Point, standing dead and litter values were found to be 1000 g m^{-2} in September, 1977 (Hussey and Long, 1982). Cargill (1981) suggested that litter levels were lower at La Pérouse Bay as a result of grazing, which prevents accumulation. Data presented later, in Chapter 6 will show this to be the case.

A major concern of ecologists in estimating standing crop and production, is that they use the "best", most accurate method (Chapman, 1976; Wielgolaski, 1981). NAPP determinations necessitate accounting for the mortality of plant parts that occurs between sample points of live standing crop. Suggested methods for estimating litter accumulation and loss, and their subsequent inclusion in NAPP estimates are outlined in Smalley (1960), Wiegert and Evans (1964), Lomnicki, Bandola and Jankowska (1968), Chapman (1976), and Linthurst and Reimold (1978), the latter two being syntheses of the different methods.

Cargill (1981) gave practical reasons for not using these methods, which were found to be still valid during this study. In basing NAPP values on increments in live standing crop, she made the following assumptions: (1) tidal removal of litter is minor; (2) little mortality of plant parts occurs prior to the attainment of peak standing crop, and (3) the substantial amount of live material present at the beginning of the growing season represents either green tissue that survived over winter, or is the result of translocation of carbohydrates from root-rhizome reserves to above-ground plant parts. The assumptions can be tested with a demographic study of individual *Puccinellia* shoots.

Tidal action affects the marsh in late July and August, so, if any litter is lost via tidal flushing, it would occur at this time. The drop in the LAI of live standing crop in September is not reflected by a rise in the LAI of litter (Fig. 3-4 a,b), suggesting that some loss of litter does occur in August. In 1982 the drop of approximately 20 g m^{-2} in live standing crop observed in September, was not mirrored by a rise of the same proportion in litter levels, again suggesting some loss of litter as a result of tides. However, this latter observation could also be the result of the translocation of above-ground material to below-ground biomass, so that the resultant amount of dead material would not be equal to that of the live material. Even so, in 1983, one would expect to observe more of a rise in the amount of litter present in early September. It is apparent that no firm conclusion about the assumption regarding loss of litter from the marsh as a result of tidal action can be made based on the results discussed thus far.

The values of LAI for the live ungrazed vegetation are similar to those of other tundra communities in the Truelove Lowland, Devon Island and at Barrow, Alaska, which were between 0.1 and 1.72 (Muc, 1977; Dennis, Tieszen; and Vetter, 1978). These communities were composed of either wet sedge-moss or dwarf shrub heath vegetation. In comparison with plant species growing at more temperate latitudes, the LAI values for live vegetation in the exclosures are very low. For example, in a crop of winter wheat in in England LAI was low (<1.0) from January to April, but increased to above 1.0 in May, and peaked at a value of 3.0 (Evans, 1972). Watson (1947) observed peak LAI values of 4.5 for wheat and sugar beet in some years, while in other years, peak LAI values were less than 2.0.

Most LAI values include only the lamina or blade of the leaf, particularly if a graminoid species is measured. However, if other plant parts, such as stem, sheath and flowers, which may be photosynthetic, are included, then LAI may reach values as high as 9.0. At La Pérouse Bay, stems and sheaths of Puccinellia were included in LAI determinations, but the values were still very low.

It appears that live standing crop and LAI corresponded well (Fig. 3-5), with a correlation coefficient (r) of 0.68, which was significant at $p \leq 0.05$ (df = 11). Data from Freyman (1980) indicate that up to 48 days after planting, both LAI and dry-matter yield of barley increased, with $r = 0.998$. By day 48, the maximum LAI value was 9.2, and the maximum dry matter yield was 632 g m^{-2} (Freyman, 1980). However, from day 48 to day 80, the LAI dropped to 2.2 while the dry matter yield increased slightly to 700 g m^{-2} (Freyman, 1980). Presumably these results were obtained because the plants were senescent or dead but still intact and all parts were used to calculate yield. Freyman (1980) did not separate yield into live and dead material, and if he had, then the fit betwen LAI and "live" dry matter yield would have been better.

Given the high LAI values observed in more temperate crops, it appears unlikely that the growth of ungrazed plants at La Pérouse Bay is irradiance-limited. Brougham (1956) suggested that irradiance becomes limiting for photosynthesis of a plant at an LAI between 3 and 5.

Limitation of growth of Puccinellia arising from low nutrient availability is a more likely explanation. Fertilization experiments carried out in exclosures at La Pérouse Bay have shown the marsh to be nitrogen-limited, but not phosphorus-limited (Cargill and Jefferies, 1984a). Cargill and Jefferies (1984a) have suggested that in late July and August the availability of mineral nitrogen declines, as earlier in the summer unfertilized control plots had the same relative growth rates as fertilized plots (Cargill and Jefferies, 1984a). Nitrogen-limitation has been observed in a number of tundra communities and salt marshes (Haag, 1974; Valiela, Teal and Sass, 1975; Gallagher, 1975; Shaver and Chapin, 1980). Reasons for nutrient limitation in the tundra include low temperatures, which slow down decomposition and release of inorganic ions into the soil (Haag, 1974).

From the results presented here, and those of Cargill and Jefferies (1984b) it is evident that grazing significantly increased

NAPP. Also, from the comparisons of live standing crop in grazed areas with NAPP curves for the same sites, it is apparent that snow geese consume a large proportion of NAPP. Cargill and Jefferies (1984b) estimated this consumption to be up to 80% of NAPP. They used two independent methods of calculation, which yielded similar results (Cargill and Jefferies, 1984b). By calculating herbage consumption according to the second method, which involves the use of NAPP and live standing crop values, it was found to be 87% in 1982 and 84% in 1983. The calculation for 1983 is based on the NAPP and live standing crop values for early September. The consumption figures were calculated for the June to September periods for 1979, 1980, 1982 and 1983. They represent percent consumption of the herbage available for the snow geese while they are on the marsh. If results for October, 1983 are included in estimates of NAPP for 1983, forage consumption was 60% of NAPP in that year.

1983 was the first year that an attempt was made to collect standing crop samples immediately before freeze-up in October. There was an increase of 50 g m^{-2} in the cumulative NAPP in the grazed area but none in the ungrazed area compared with the previous harvest. This suggests that the month of September may be important for the regrowth of vegetation in grazed areas, after the geese have migrated. Had it been possible to make measurements in October in 1979, 1980 and 1982, the NAPP of grazed areas would have been even greater. Consequently, the percentage of the NAPP consumed by snow geese on an annual basis would have been less, perhaps between 50% and 60%.

The levels of consumption are very high for terrestrial systems and have generally only been observed in grassland areas grazed by large mammals (Campbell, 1966; Frame, 1966; Wiegert and Evans, 1967). However, Schultz (1969) reported that lemmings may graze from 20% to 90% of tundra graminoid production. The high consumption figures usually refer to localized areas of very intensive grazing (Schultz, 1969). In most cases, terrestrial herbivores consume about 10% of net primary production (Crawley, 1983).

Some workers have noted stimulatory effects of grazing by herbivores on plant growth (Dyer and Bokhari, 1976; McNaughton, 1979) but in general, grazing and defoliation are viewed as destructive activities that slow growth (McNaughton, 1979). As mentioned in the Introduction, one of the objectives of this study is to determine why "grazing" stimulates NAPP in this system. Cargill and Jefferies (1984b) suggested that the continued NAPP in grazed areas in August is the result of increased nitrogen availability in these areas. This may be brought about by the enhanced availability of nitrogen from goose droppings which contain 66% of their total nitrogen as soluble nitrogen, largely in the form of ammonium ions (Cargill and Jefferies, 1984b). In Chapter 5, the nitrogen budget of the marsh in relation to the increased availability of nitrogen is discussed.

The effect of grazing on plant growth has long been of interest to agricultural workers interested in maintaining the presence of certain desirable forage species, or maximizing NAPP, mainly for the benefit of livestock production (Robertson, 1933; Baker, 1961). Many studies have attempted to simulate grazing by clipping or cutting the herbage. However, Hodgson (1979) points out that in the general sense "grazing may also carry implications of the associated effects of treading and the deposition of dung and urine (while) in a specific sense it refers only to the defoliation process." Apart from the fact that cutting does not account for the associated effects, the clipping or mowing procedure does not defoliate plants in the same manner as a herbivore, which may selectively remove one or two leaves from one plant, and not touch its neighbour. Nevertheless, grazing management decisions have been based on the results of cutting studies. Many of the latter suggest that frequent, intense cutting (or grazing) decreases growth and production (Robertson, 1933; Baker, 1961; Alexander and Thompson, 1982; Archer and Tieszen, 1983).

Agricultural studies of the grazing process itself, rather than of its simulation by cutting, have tended to concentrate on experiments where grazing is not as continuous as it is at La Pérouse Bay (Baker, 1961; Akiyama, Takahashi, Shiyomi and Okubo, 1984). However, in one detailed study of grass production under continuous grazing, animal intake of herbage was found to be greater in the hard grazed sward than in the lightly grazed sward, because less vegetation was lost to litter (Parsons, Leafe, Collett, Penning and Lewis, 1983). This was inspite of canopy gross photosynthesis being lower in the hard grazed sward. In other words, high gross photosynthetic uptake is not equivelant to high harvested yield, which is contrary to the findings of Brougham (1956). In this experiment, maintenance of the grazed sward at an LAI of 1.0 was considered a "hard-grazing" treatment, while an LAI of 3.0 constituted the light or "lenient" grazing treatment (Parsons, Leafe, Collett, Penning and Lewis, 1983).

Unfortunately, in the Parsons, Leafe, Collett, Penning and Lewis (1983) study, there was no ungrazed control, so it is not known whether grazing increased NAPP over that of an ungrazed system. Rather, Parsons and his co-workers (1983) showed that in a heavily, continuously grazed system, the animals eat a greater amount and the grass survives, which is contrary to the view that low levels of grazing are better (McNaughton, 1983). Therefore, it may be to the advantage of the snow geese to maintain their sward at an LAI of less than 3.0.

More workers are realizing that an understanding of the effects of grazing and cutting on plant production involves carrying out demographic studies of the swards under consideration (King, Lamb and McGregor, 1979; Westoby, 1980; Grant, Barthram and Torvell, 1981; Parsons, Leafe, Collett, Penning and Lewis, 1983). Jones, Collett and Brown (1982) pointed out that characteristics of the structure of a continuously grazed ryegrass sward were very different from those of an infrequently cut sward. This is one possible reason why cutting does not simulate grazing well.

The extent to which the act of defoliation is responsible for increases in NAPP is difficult to distinguish from the importance of the effect of availability of nitrogen in grazed areas at La Perouse Bay. In June and early July of 1982 and 1983 the relative growth rates of both grazed and ungrazed Puccinellia swards were similar, even though intensive defoliation occurred during this period. There may well be a delayed effect of defoliation. This point will be raised in Chapter 7 following presentation of the demography data.

A trend that emerged during the four years of data collection was that the difference between cumulative NAPP in grazed and ungrazed areas consistently became apparent approximately six weeks after the hatch period. It is difficult to determine the degree to which this difference depends on the geese stimulating growth. This is because the nest initiation period is highly correlated with Churchill weather conditions, which in turn determine the time at which thaw takes place, and vegetation starts to grow (Cooke et al, 1982). Thus, growth in exclosures may slow after some set period of time when nitrogen availability declines. Nevertheless, the constancy of the point after hatch at which grazed NAPP becomes greater than ungrazed NAPP is worth noting because geese on the colony are present to take advantage of this extra forage.

CHAPTER 4

DEMOGRAPHY OF GRAZED AND UNGRAZED PUCCINELLIA PHRYGANODES

4-1 INTRODUCTION

A number of investigators have employed demographic techniques to determine life history parameters of plant populations (Kays and Harper, 1974; Bishop, Davy and Jefferies, 1978; Solbrig, 1980; Bierzychudek, 1982; Vine, 1983). By examining birth and death rates of plants or individual plant organs (eg. tillers), changes in plant populations and communities may be recorded. Bishop and Davy (1984) examined the role of rabbits in the population regulation of Hieracium pilosella, and found that in the presence of rabbits, which graze on this species, the turnover rate of rosettes was much higher than that in exclosed areas.

Increases in cumulative NAPP in grazed areas compared with ungrazed areas were recorded by Cargill (1981) in 1979 and 1980 and by the author in 1982 and 1983. A demographic study of the growth of individual Puccinellia shoots was carried out during the latter two years in order to determine whether there were differences in the growth and turnover of shoots and leaves in grazed and ungrazed swards which could account for the differences in cumulative NAPP. As discussed in Chapter 2, Puccinellia phryganodes is stoloniferous and produces axillary shoots; a possible response to grazing could be increased production of shoots.

As discussed in Chapter 3, the results of a demographic study would also indicate whether there is much leaf and shoot mortality before peak live standing crop is attained, and whether vegetation present following snowmelt represents the previous year's growth.

4-2 METHODS

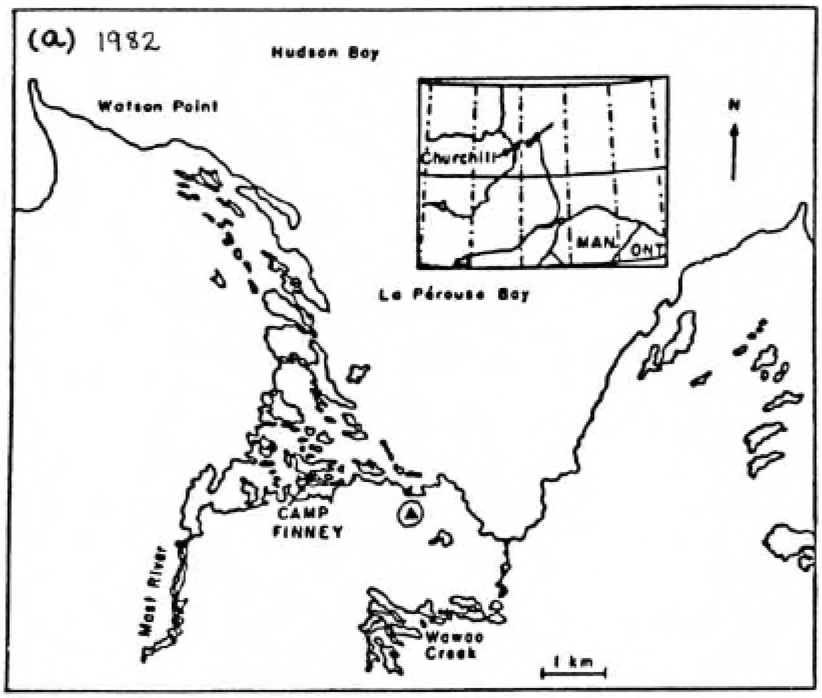
In 1982, 648 shoots of *Puccinellia phryganodes* were monitored between mid-June and September. Four sites were chosen; observations indicated that the geese were frequently grazing at these sites. At each site, two permanent quadrats were established in early June - one which was enclosed with chicken wire (0.5 x 0.5 x 0.5 m) and one which was unprotected. Of the eight permanent quadrats, the vegetation in four of the quadrats was grazed, and in the remainder the vegetation was ungrazed. All these sites were 100-250 m from the exclosures built in 1982 (Figure 4-1a).

Shoots were located in each quadrat with the aid of a 0.5 m x 0.5 m metal quadrat, strung at 5 cm intervals with thin wire or monofilament pulled taut, to form a grid. The metal quadrat was placed over four permanent wooden corner pegs. The grid of the quadrat had 81 wire intersections, and the *Puccinellia* shoot nearest to each intersection was identified.

Figure 4-1. Locations of grazed and ungrazed plots dominated by *Puccinellia phryganodes* used for the demography study at La Pérouse Bay.

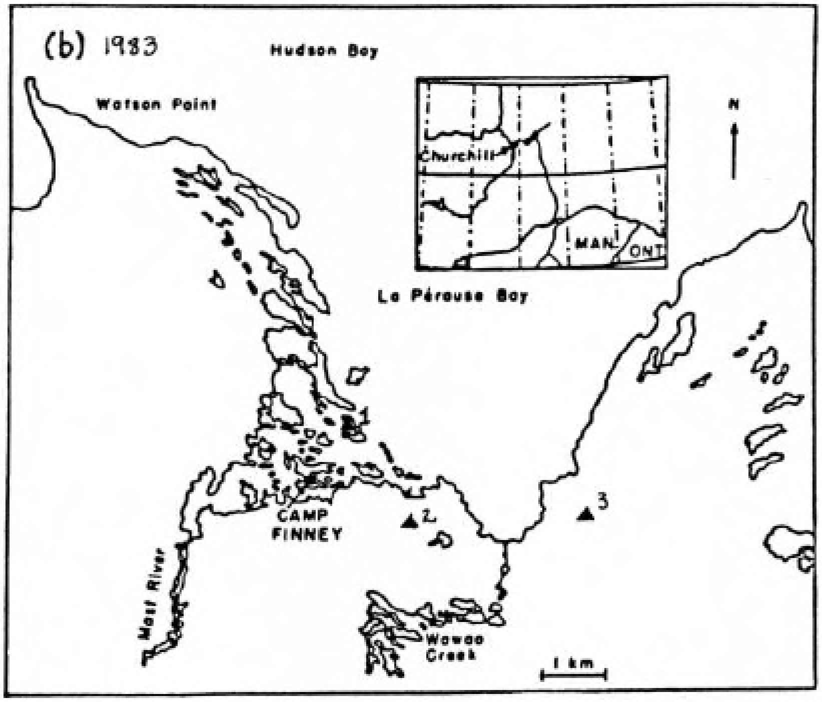
a. Eight plots were located in the area indicated by the triangle (◬), four grazed and four ungrazed, in 1982.

b. Three plots were located at site 1 (▲) (1 grazed and 1 ungrazed), six plots were located at site 2 (▲) (3 grazed and 3 ungrazed) and three plots were located at site 3 (▲) (2 grazed and 1 ungrazed) in 1983.



(a) 1982

Hudson Bay
Watson Point
Churchill
MAN.
ONT.
N
La Pérouse Bay
CAMP FINNEY
Mast River
Wawao Creek
1 km



(b) 1983

Hudson Bay
Watson Point
Churchill
MAN.
ONT.
N
La Pérouse Bay
1
CAMP FINNEY
2
3
Mast River
Wawao Creek
1 km

Thus, the growth of 648 shoots (8 quadrats x 81 intersections) was tracked during the season: 324 shoots from both grazed and ungrazed sites. Demographic changes for each shoot were recorded five times between June 23 and September 2. Information was collected on the number of leaves per shoot, and their condition, whether alive, grazed, missing, senescent, dead or emergent (<2 mm length). In scoring the condition of each leaf, the definitions of Thomas (1980) were followed. Therefore, a live leaf had a completely green lamina, while a senescent or dying leaf was one in which the lamina was only partly green, and a dead leaf had an entirely yellow or brown lamina (Thomas, 1980). The presence of axillary shoots and their location was also recorded, together with information on the number and condition of leaves on the axillary shoot.

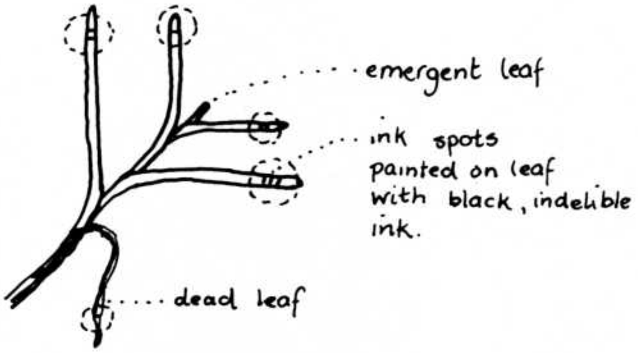
A modified technique was used in 1983, as it was not always possible to identify the shoot nearest to a grid intersection. Insulated telephone wire, 1 mm in diameter and approximately 4 cm in length, was bent into a loop and pushed into the ground around the <u>Puccinellia</u> shoot closest to each grid intersection. This ensured that the same shoot would be monitored from one sample date to the next. The small wire loops did not interfere with goose grazing as they sat flush with the ground.

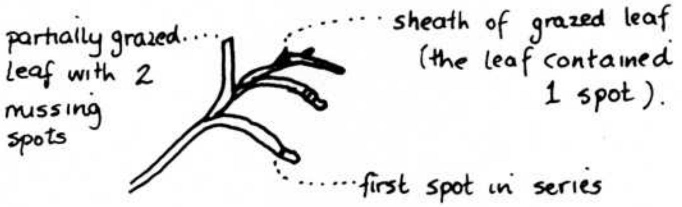
A larger number of permanent quadrats was set up in 1983 than in 1982: six in small exclosures and six in grazed areas. Each contained 81 marked shoots. However, three of the sites were about 1 km apart (Fig. 4-1b). One site was located on an island in the Mast River delta, to the north of the field station. Two ungrazed quadrats and one grazed quadrat were set up here (243 shoots in total). The second site was in the vicinity of the heavily grazed area which was used for the similar study in 1982. Three grazed and three ungrazed quadrats were set up here (486 shoots in total). The third site was 50 m from the exclosures set up in 1983 on the east side of La Pérouse Bay, and two grazed and one ungrazed quadrats were established here. The sites were established at distances of 1 km from each other so as to minimize the disturbance to the geese at the two other sites when the Puccinellia shoots at the third site were being measured. Since it took one day to score three quadrats (243 shoots), the sites containing three quadrats could be measured in one day and not be disturbed for another ten days. The shoots in each quadrat were measured on at least five occasions between June 25 and September 1983, every 11 to 25 days.

As in 1982, information on the condition of leaves on both main and axillary shoots was collected. However, since there had been uncertainty about whether the same leaves were observed from week to week in 1982, the leaves were marked on an individual basis in 1983. Black waterproof drawing ink was painted on leaves with a fine sable brush. As Puccinellia phryganodes leaves are approximately 1 cm in length and <1 mm in width, a series of tiny ink dots was used to identify individual leaves. The series consisted of one, two or three dots painted in sequence on the

Figure 4-2. Diagrams of shoots of *Puccinellia phryganodes* painted with repeating series of one, two or three ink spots on their leaves, in order of their appearance.

Shoots of *Puccinellia phryganodes* marked with indelible ink spots





undersides of a group of three consecutive leaves from the oldest to the youngest leaf (Fig. 4-2). This series was repeated as new leaves developed on a shoot. On each sample date, the dots were located on existing leaves, and the appropriate number of dots was painted on all new leaves. If the dots on existing leaves had faded, they were repainted. In this manner, leaves could be identified on consecutive sample dates. Leaves which developed on axillary shoots were not marked with ink.

In addition to examining leaf and shoot demography within a season, we have also observed survival of leaves and shoots from one season to the next. One of Cargill's (1981) assumptions was that any live vegetation present immediately after snow melt represented the previous year's growth. Therefore, in June 1984, we located marked shoots from 1983 in order to examine shoot and leaf survival over the winter.

4-3 RESULTS

Figure 4-3 shows results from the demographic investigation carried out in 1982. Figure 4-3a indicates that by the end of August on average, nearly every grazed *Puccinellia phryganodes* shoot had at least one axillary shoot, whereas the corresponding value for ungrazed shoots was 0.5. The increase in the number of axillary shoots in grazed plants was particularly evident after mid-July. The axillary shoots usually grew in the axils of the bottom two or three leaves of the main shoot. Some of the main shoots which

Figure 4-3. Seasonal trends in a variety of parameters measured in populations of grazed (0) and ungrazed (△) shoots of _Puccinellia_ _phryganodes_, La Pérouse Bay, 1982. (n>/ = 320).

a. Mean number of axillary shoots per main shoot.

b. Percentage of main shoots with grazed leaves.

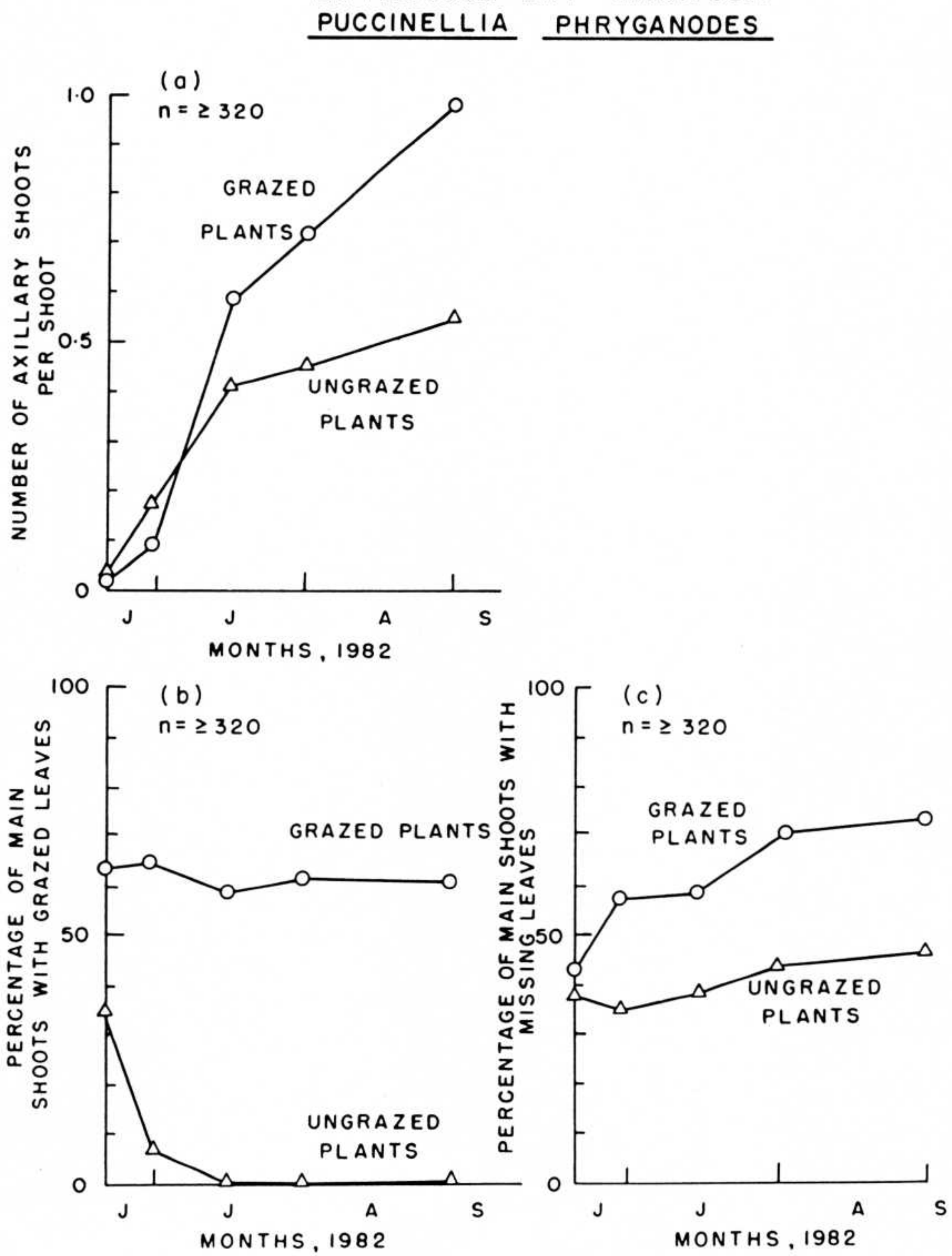
c. Percentage of main shoots with missing leaves.

d. Mean number of dead leaves per main shoot.

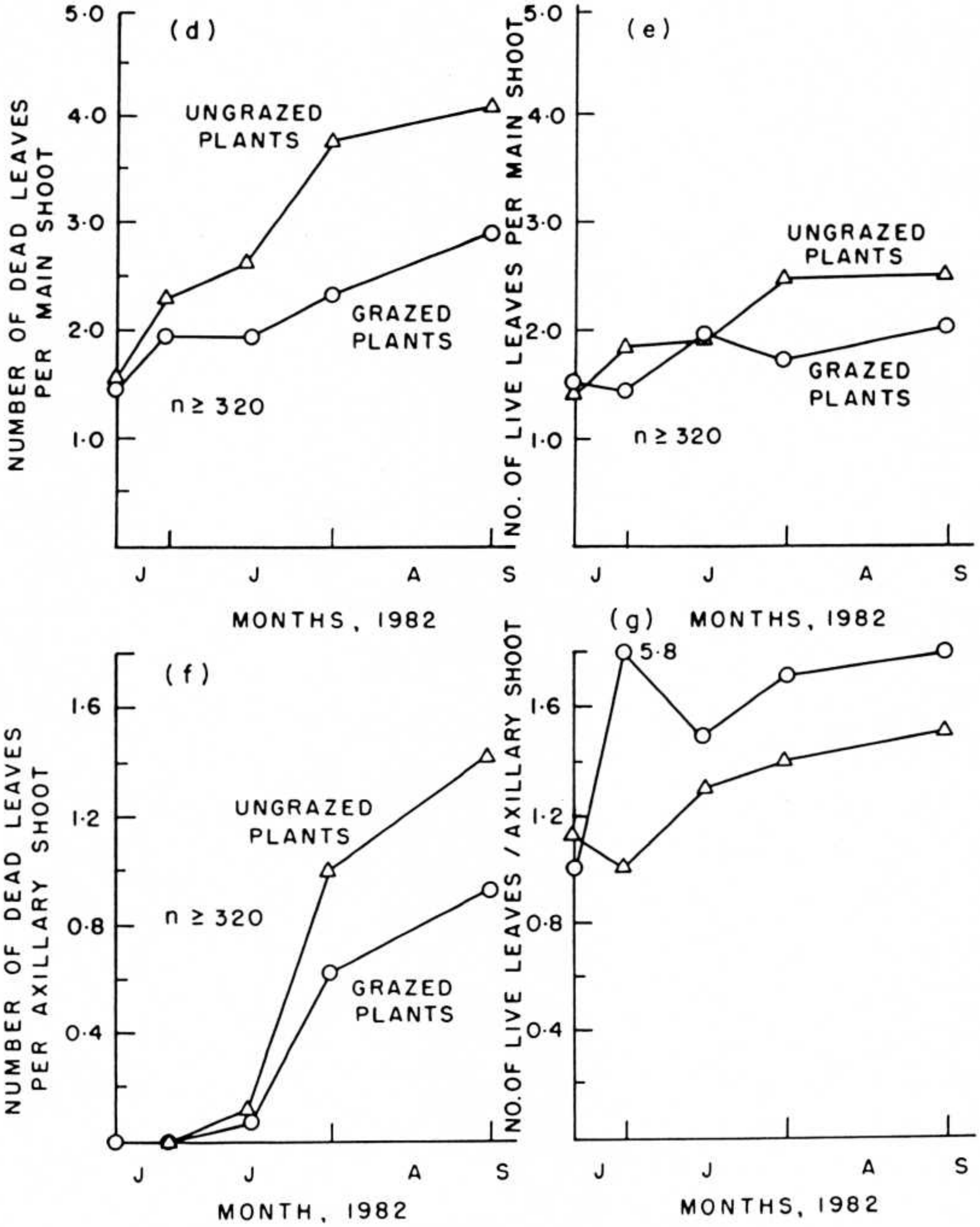
e. Mean number of live leaves per main shoot.

f. Mean number of dead leaves per axillary shoot growing on main shoots of _Puccinellia_.

g. Mean number of live leaves per axillary shoot growing on main shoots of _Puccinellia_.


LA PÉROUSE BAY - MANITOBA
PUCCINELLIA PHRYGANODES
(a)
n = ≥ 320
NUMBER OF AXILLARY SHOOTS PER SHOOT
1·0
0·5
0
GRAZED PLANTS
UNGRAZED PLANTS
J
J
A
S
MONTHS, 1982
(b)
n = ≥ 320
PERCENTAGE OF MAIN SHOOTS WITH GRAZED LEAVES
100
50
0
GRAZED PLANTS
UNGRAZED PLANTS
J
J
A
S
MONTHS, 1982
(c)
n = ≥ 320
PERCENTAGE OF MAIN SHOOTS WITH MISSING LEAVES
100
50
0
GRAZED PLANTS
UNGRAZED PLANTS
J
J
A
S
MONTHS, 1982

LA PÉROUSE BAY, MANITOBA *PUCCINELLIA PHRYGANODES*



grew to about 25 mm in length had up to eight axillary shoots growing in as many axils. In some cases extra-axillary shoots were observed, which grew from the parts of the stem between the nodes.

Figure 4-3b shows that approximately 65% of main shoots had one or more grazed leaves. A grazed leaf was defined as a leaf which was only partly missing (i.e. at least 2 mm of the original leaf remained on the shoot after it had been grazed). Not all of the shoots were grazed at any one time. The ungrazed sites contained some grazed shoots on the first sample date because they were enclosed shortly after the geese commenced grazing. However, after these leaves died, no grazed leaves were observed on the shoots. By August 31, 70% of grazed shoots had missing leaves compared with 45% of ungrazed shoots (Fig. 4-3c). There was an increase in the number of missing leaves on grazed shoots during the season, from 43% to 70%, indicating that either grazing pressure had increased with time, or that a greater number of dead leaves were removed from the shoot by a mechanical action, such as trampling by geese. On the ungrazed shoots, leaves classified as missing were only those that abscissed. The number per shoot remained steady over the season, indicating that many of the dead leaves on ungrazed shoots were not removed and were left as standing dead. A missing leaf lamina was revealed by the presence of the sheath, which remained attached to the stem. Consistent with this observation is that by August 31, each ungrazed shoot had an average of four dead leaves per shoot, compared with 2.8 on grazed shoots (Fig. 4-3d). This represented a substantial increase from the mean of 1.5 dead leaves per main shoot observed on June 23 on both grazed and ungrazed shoots.

Since there was a greater number of dead leaves on ungrazed shoots by the end of the season, it was postulated that either grazing caused a reduction in leaf mortality, or that because some leaves were eaten, not as much standing dead built up in grazed areas. The average number of live leaves per main shoot was not substantially different between grazed and ungrazed shoots (Fig. 4-3e).

Figures 4-3f and 4-3g suggest that the increased NAPP in grazed Puccinellia swards was the result of the enhanced production of axillary shoots later in the summer. In addition to the increased number of axillary shoots per main shoot for grazed plants, these shoots also had approximately 20% more live leaves than axillary shoots of ungrazed Puccinellia from mid-June onwards. There was a sharp increase to 5.8 in the mean number of live leaves per axillary shoot in grazed Puccinellia sites at the end of June, compared with the previous value. However, there was a small sample size for this date.

The data presented in Figure 4-3 of the responses of individual shoots of Puccinellia to grazing, follow the trends shown in Figures 3-2 and 3-3, for standing crop and NAPP. The increased productivity in grazed areas observed in late July and early August was associated with the development of axillary shoots of Puccinellia. These data did not provide enough information for turnover rates of individual leaves to be calculated.

Because of time constraints, results from only two of each of the six demographic plots in grazed and ungrazed sites monitored in 1983 have been analysed so far. In some cases only data from one grazed and ungrazed plot was analysed for inclusion in these results. Thus, some sample sizes of main shoots of Puccinellia phryganodes were 162 and others were 81.

Figure 4-4 shows the production of axillary shoots in a grazed and ungrazed plots on an island in the Mast River delta. As in 1982, the number of axillary shoots produced during each interval between sample dates was consistently higher in the grazed site (Fig. 4-4a). The production of shoots peaked in early to mid-July, 1983, which was immediately after hatch (Fig. 4-4a). At this time, eleven more axillary shoots were produced in the grazed population. Production subsequently dropped, but increased again at the beginning of September. Thus, in Figure 4-4b, the accumulative production of axillary shoots was higher by 15 in the grazed population of main shoots. An inspection of the raw data from other plots indicated that this trend predominated in all grazed sites.

Similar data for leaf production are given in Figure 4-5, for larger populations of main shoots (n = 162). The accumulative births of leaves in both grazed and ungrazed populations of main shoots were similar (Figs. 4-5a and b). The net number of live leaves present on any given sample date fluctuated between 460 and 600 leaves on 162 main shoots in the ungrazed plots, but dropped from approximately 570 to 290 during the summer in the grazed plots. However, leaves were born continuously on both grazed

Figure 4-4a. Total number of axillary shoots produced during consecutive intervals of approximately twelve days by populations of grazed (●) and ungrazed (O) shoots of *Puccinellia phryganodes*, June 27 to August 30, 1983. (n = 81 shoots in each population).

Figure 4-4b. Accumulative production of axillary shoots by grazed (●) and ungrazed (O) populations of shoots of *Puccinellia phryganodes*, June 27 to August 30, 1983. (n = 81 shoots in each population).

PRODUCTION OF AXILLARY SHOOTS IN GRAZED AND UNGRAZED PLANTS OF PUCCINELLIA PHRYGANODES

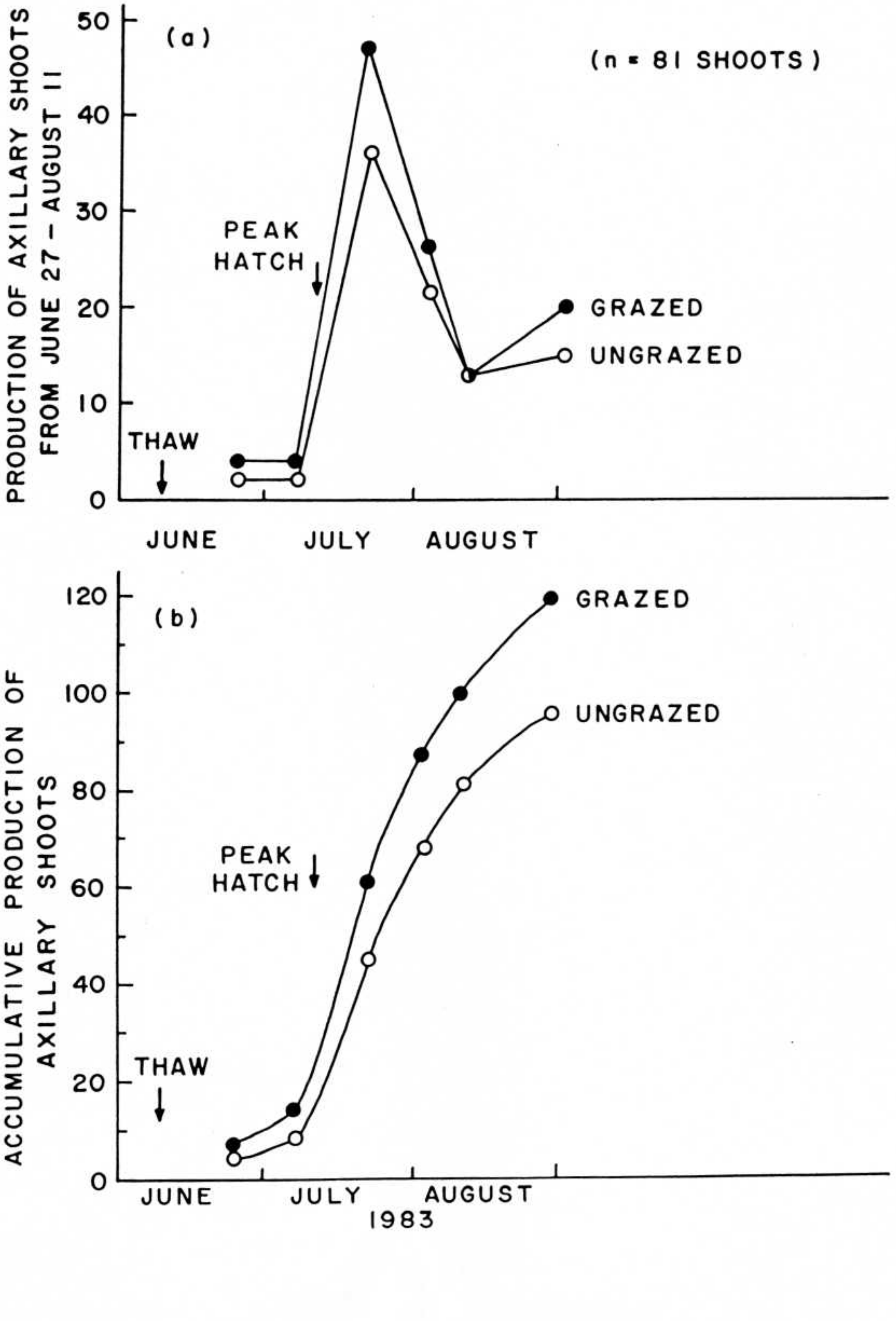


Figure 4-5. Demographic parameters measured in grazed and ungrazed populations of shoots of Puccinellia phryganodes at La Pérouse Bay, 1983. (n = 162 shoots in each population).

a. Total number of accumulative births of leaves (O) and the net number of live leaves (●) present in a population of ungrazed Puccinellia shoots.

b. Total number of accumulative birth of leaves (O) and the net number of both grazed and ungrazed live leaves (●) present in a population of grazed Puccinellia shoots.

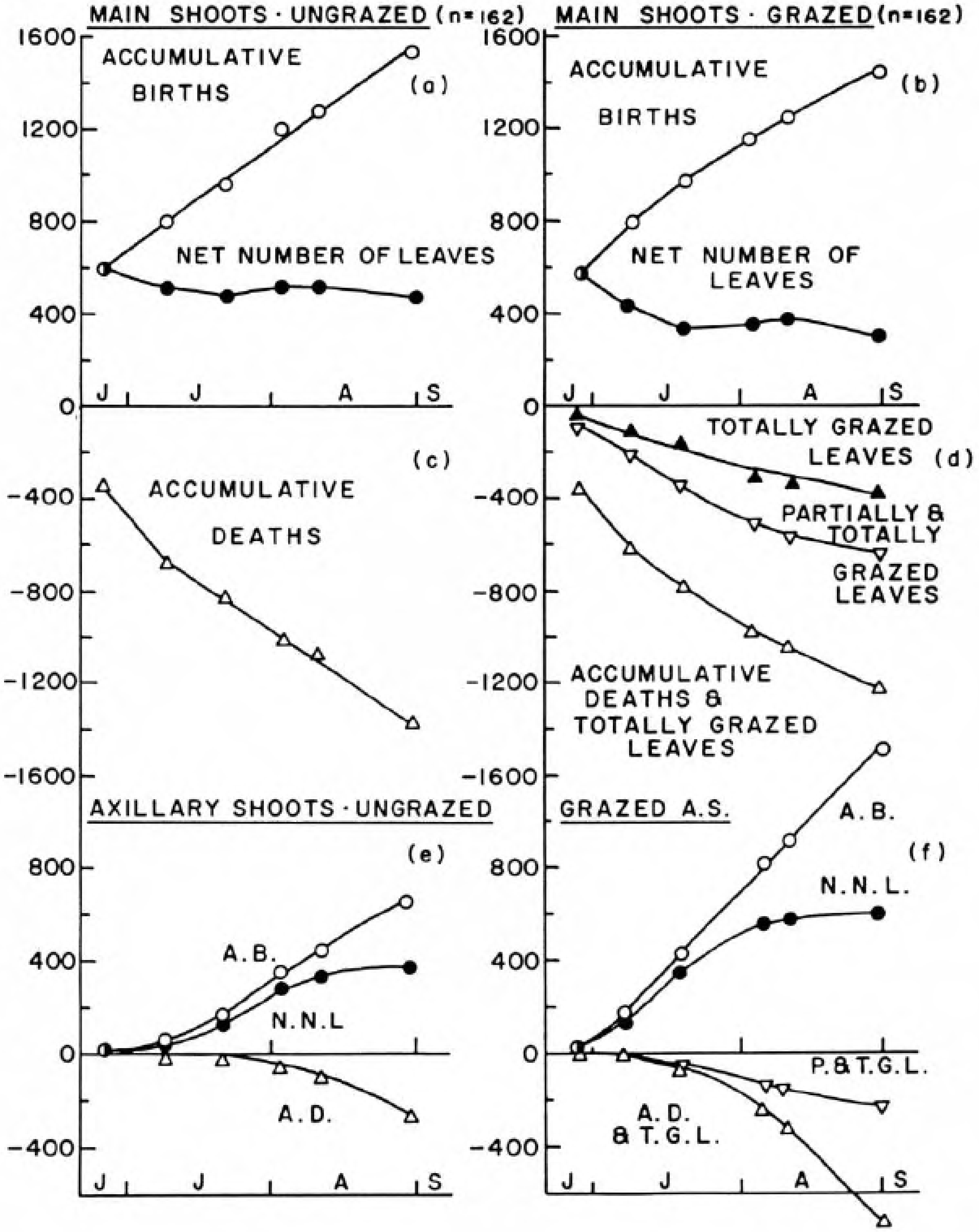
c. Total number of accumulative leaf deaths (△) in a population of ungrazed Puccinellia shoots.

d. Total number of accumulative leaf deaths and totally grazed leaves (△) in a population of grazed Puccinellia shoots. The proportion of this accumulative total made up by totally grazed leaves (▲) is shown, as is the proportion made up by combining the numbers of totally grazed leaves and partially grazed leaves which died (▽).

e. Total number of accumulative leaf births (A.B.,O), net number of live leaves (N.N.L.,●) and accumulative leaf deaths (A.D.,△) in axillary shoots in a population of ungrazed Puccinellia shoots.

f. Total number of accumulative leaf births (A.B.,O), net number of live leaves (N.N.L.,●), total number of (A.D. & T.G.L.,△), and the proportion of partially and totally grazed leaves (P & T.G.L.,▽)contributing to A.D. & T.G.L. in axillary shoots in a population of grazed Puccinellia shoots.

LEAF DEMOGRAPHY OF PUCCINELLIA PHRYGANODES (LPB., 1983)



and ungrazed main shoots throughout the period of observation.

The accumulative numbers of leaf deaths tended to balance the accumulative births (Figs. 4-5c and d). This was why the net number of live leaves or ungrazed main shoots remained steady. The slope of the accumulative birth line is the rate of appearance of leaves, while that of the accumulative death line is the rate of death. The rate of appearance of live leaves was one leaf per ungrazed shoot ever 11.5 days. Therefore, there was a fairly rapid turnover of leaves throughout the summer in both grazed and ungrazed populations of shoots.

Figure 4-5d shows the accumulative total of totally grazed leaves. A totally grazed leaf was one missing completely, and noted only by virtue of its sheath. Also shown is the accumulative number of totally grazed leaves plus partially grazed leaves which had died. The evidence indicates that there is not an overall increase in the rate of leaf death in grazed main shoots of Puccinellia in response to grazing. If there was, then the total number of accumulative leaf deaths from all sources would be higher. By the end of August 1983, partially and totally grazed leaves accounted for more than 50% of the deaths.

There was a large difference between the accumulative production of leaves on axillary shoots in grazed and ungrazed plots (A.B., Figs. 4-5e and f). By the beginning of September, 1983, approximately 660 leaves had accumulated on ungrazed axillary shoots, compared with approximately 1300 on grazed axillary shoots. The net number of live leaves (N.N.L.) present on the latter was much greater than on the former from early July onwards. A similar trend in the net number of live leaves present on axillary shoots was observed in 1982 (Fig. 4-3g). The increase observed in 1983 was directly related to the increased number of axillary shoots in grazed sites.

The slopes of the accumulative birth (A.B.) lines in Figures 4-5e and f are the rates of appearance of leaves on axillary shoots. By adjusting for 162 main shoots, the rate of appearance of axillary shoot leaves was one axillary leaf per main shoot every 14.3 days for ungrazed plots and one axillary leaf per main shoot every 7.7 days for grazed plots. Although there was a higher number of accumulative deaths of leaves on axillary shoots in grazed areas than on those in ungrazed areas, it was not as high as the accumulative births on grazed shoots. Also, a lower proportion of leaves dying were being entirely or partially grazed compared with leaves on main shoots.

Together, Figure 46 and Table 4-1 give information on the mean life span of each cohort of leaves born during consecutive sample intervals in both grazed and ungrazed populations of shoots of Puccinellia. The mean age of ungrazed leaves born on main grazed shoots did not fluctuate greatly during the summer; they usually lived for approximately 35 days. The life span of an ungrazed leaf was greater than that of a partially grazed leaf (PGD) which lived for between 15 and 30 days, but the life span appeared to decline during the course of the summer (Fig. 4-6). However, the sample sizes of the August 3 and August 11, 1983 cohorts were low compared with others (n=12 and n=3 respectively for partially grazed leaves these times). The ages at which leaves were entirely (GR) or partially (PG) grazed by snow geese ranged between three and 18 days. It is clear that geese preferentially selected younger leaves. The small sizes of the August 3 and August 11 cohorts again contributed to the appearance that the age at death of partially grazed leaves declined.

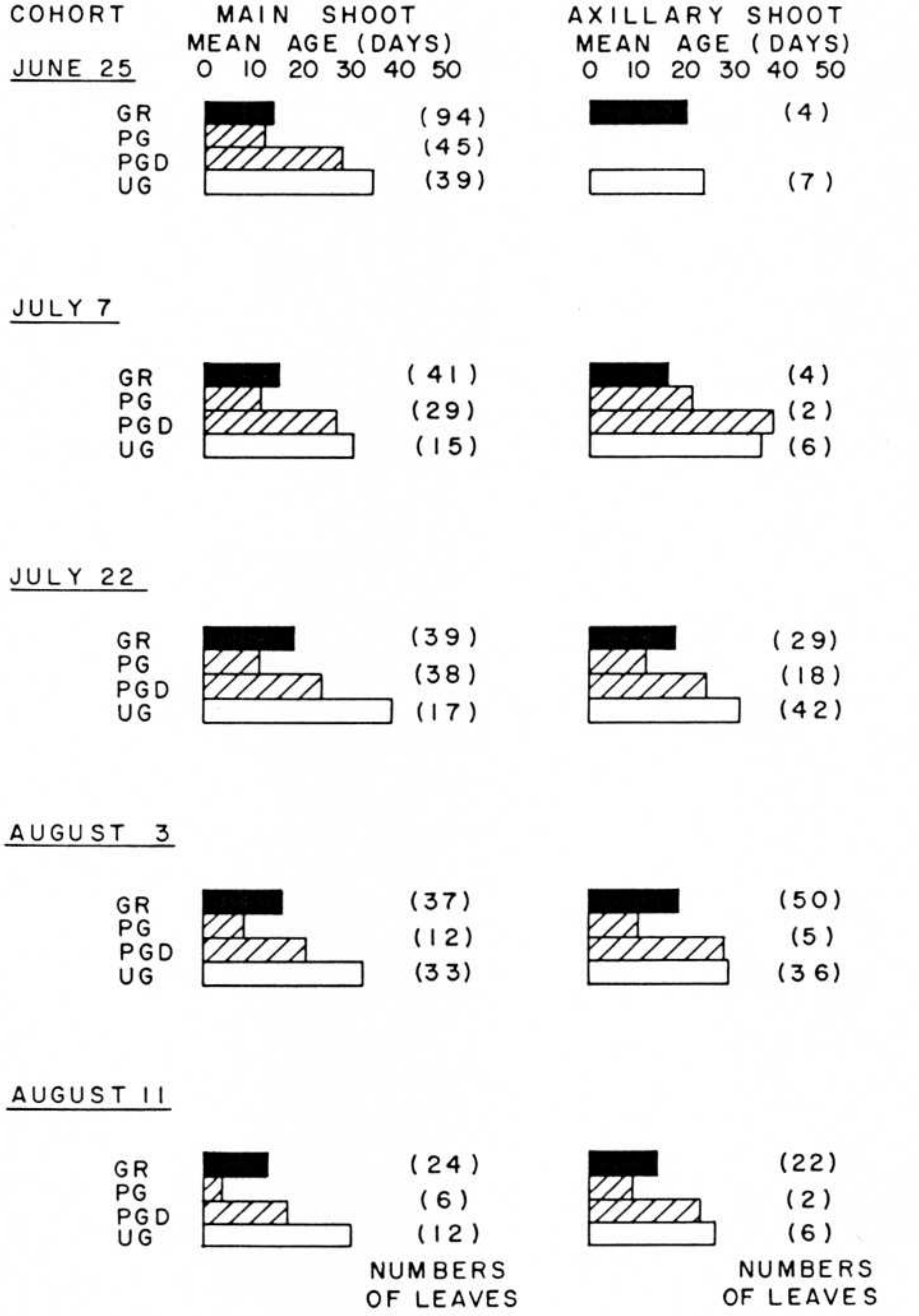
The main lifespan of leaves on axillary shoots ranged between 20 and 38 days (Fig. 4-6). The most realistic estimates were those for the July 22 and August 3 cohorts, which had a mean life span of 30-31 days. Other cohorts had small sample sizes. This mean age was less than that of live leaves on main shoots in the same cohorts. The ages of partially grazed leaves were often nearly equal to those of ungrazed leaves on axillary shoots. The ages at which totally grazed leaves on axillary shoots were eaten was always less than twenty days, and often greater than the ages at which leaves were partially grazed. However, as with the leaves on main shoots, the sample sizes of the latter were two or five in some cases.

A comparison may be made between the mean life spans of leaves on ungrazed and grazed shoots (Figure 4-6 and Table 4-1). Leaves tended to live longer on ungrazed shoots, but even for sample sizes of up to 188 or 308, the standard deviations were high. Apart from the July 8 and August 3, 1983 cohorts, mean ages were very close. The largest numbers of leaves on axillary shoots were produced in the July 20 and July 22 cohorts respectively for ungrazed and grazed shoots. This coincided with the increased production of axillary shoots.

Figure 4-6. Demography of leaves on main and axillary shoots in a grazed population of shoots of <u>Puccinellia phryganodes</u>. (n = 81 main shoots in the population). The leaves are placed in cohorts according to the two week period in which they were born. The mean age at which a live leaf was entirely grazed (GR,■), or partially grazed (P.G.,▨), and the mean age at which partially grazed (P.G.D.,⧄) and ungrazed leaves (U.G.,□) died is shown. The sample size of leaves is shown in parentheses after each bar.

LA PEROUSE BAY – MANITOBA (1983)

DEMOGRAPHY OF LEAVES OF GRAZED PUCCINELLIA SHOOTS



GR = GRAZED LEAVES

PG = PARTIALLY GRAZED LEAVES

PGD = MEAN AGE AT DEATH OF P. GRAZED LEAVES

UG = UNGRAZED LEAVES

Table 4-1. Life span (days ± S.D.) of leaves of main shoots and axillary shoots of ungrazed swards of _Puccinellia phryganodes_. (The date refers to the date on which the presence of a leaf was first detected).

	Main Shoot		Axillary Shoot	
1983	Number of leaves	Age span* ± S.D.	Number of leaves	Age span* ± S.D.
June 26	308	34.56 ± 5.59	13	21.75 ± 8.79
July 08	188	38.68 ± 8.44	37	33.02 ± 10.95
July 20	160	40.73 ± 7.22	120	31.47 ± 11.41
August 03	56	39.66 ± 5.02	62	33.90 ± 10
August 08	161	32.20 ± 4.21	111	31.85 ± 5.75
August 11	20	34.45 ± 4.86	20	30.05 ± 5.78

* It was necessary to interpolate between dates in order to estimate the age span. Death of leaves was recorded in addition to the appearance of a leaf on a shoot.

S.D. = Standard Deviation.

In 1984, the demography plots established during the previous year were examined immediately after thaw in early June. Many of them had been covered by a large amount of silt deposited either in October 1983 or during the thaw in 1984. Of 972 main shoots of Puccinellia marked in 1983, 244 (108 grazed and 136 ungrazed) were relocated (Table 4-2). Only 32 shoots, nearly all of which were in ungrazed plots had recognizable ink spots which were put on in August 1983. Thaw took place at different times in different areas on the marsh, and the plots were examined five to twelve days after melt. Thus, 22, or 4%, of the grazed shoots contained up to four live leaves. Most shoots had one or two live leaves, and 18% of shoots had died in the ungrazaed population since September, 1983. There were some new leaves produced in 1984 which were eaten by snow buntings. The latter migrate further north soon after melt.

The fact that only two grazed shoots contained recognizable spots is indicative of the continuation of leaf production by grazed shoots well into October, while the ungrazed shoots produced few new leaves after September 1983. This was consistent with the increase observed in live standing crop in grazed areas in October 1983. The marked ungrazed shoots had produced an additional three to six leaves beyond the marked leaves.

Most shoots contained one live leaf immediately after snowmelt. These leaves were a light green colour with yellow patches, and appeared to be the previous season's growth. However, a second leaf was produced within six to seven days after melt.

Table 4-2. Status of shoots of Puccinellia phryganodes immediately following thaw at La Pérouse Bay, June 7-10, 1984.
These shoots had been tracked in the demographic study in 1983, and were in grazed or ungrazed sites both in 1983 and immediately following thaw.

CATEGORIES OF STATUS OF SHOOTS	GRAZED SHOOTS (n = 108) (% in category)	UNGRAZED SHOOTS (n = 136) (% in category)
1 live leaf	23	42
2 live leaves	38	34
3 live leaves	22	.01
4 live leaves	4	-
all dead leaves (shoot dead)	6	18
missing leaves	7	6

4-4 DISCUSSION

The data from the demographic study of shoots of Puccinellia phryganodes in grazed and ungrazed swards were not presented in their entirety. Nevertheless, they were more than sufficient to indicate the nature of the main differences in growth between the two populations.

The increase in NAPP in grazed versus ungrazed swards of Puccinellia was accounted for by an increased production of axillary shoots or tillers in grazed sites in 1982 and 1983. Also, during both years, the axillary shoots in grazed sites bore a greater number of live leaves. There was no major difference between the overall turnover rates of ungrazed leaves in grazed and ungrazed swards, although leaves which were totally grazed and those which were partially grazed died earlier than ungrazed leaves.

Production of leaves was observed in ungrazed sites throughout the summer of 1983, indicating continued growth of main shoots, and this coincided with an increase in live standing crop which continued until late in the summer compared with previous years' cumulative growth pattern. There was a relatively rapid turnover of leaves on both grazed and ungrazed shoots, and this along with the continuous production of leaves suggests that the varying environmental parameters did not affect the birth or death rates of leaves between June and early September 1983. The slopes of the curves of accumulative births and deaths of leaves approach linearity.

The effects of grazing and mowing on tillering have been observed by several workers. Jones, Collett and Brown (1982) found that the number of tillers in a field of Lolium perenne that was continuously stocked with sheep, increased greatly, while in a sward that was cut approximately once every two to six weeks for three months, tiller density was much less. There were two regimes of grazing, one "hard" and one "lenient", and the former brought about an even higher increase in tiller numbers (Parsons, Leafe, Collett and Stiles, 1983). However, there was no evidence of increased production in grazed sites versus mown sites, and no suggestions as to what caused the increased tillering or axillary shoot production were given (Jones, Collett and Brown, 1982; Parsons, Leafe, Collett and Stiles, 1983).

Grant, Barthram and Torvell (1981) also found that under heavy compared with light grazing regimes, rates of tillering increased in swards of L. perenne. They suggested that since the rate of appearance of leaves was also higher in the harder grazed swards, the number of positions for tiller-bud formation was higher, and that this brought about the increased tillering. However, at La Pérouse Bay, rates of leaf appearance were similar in both grazed and ungrazed sites on main shoots.

Reuss, McNaughton and Coughenour (1983) observed that increased availability of nitrogen resulted in increased rates of tillering in the east African sedge, Kyllinga nervosa. Clipping stimulated rates of uptake of both ammonium and nitrate ions (Reuss, McNaughton and Coughenour, 1983). At La Pérouse Bay, the combined effects of defoliation and increased nitrogen availability from droppings are likely to be responsible for the increased tillering or axillary shoot production in grazed sites. This combination of events, with nitrogen supplied from sheep faeces may also explain increases in tillering observed in agricultural studies.

The ages of leaves, and their rates of turnover are similar to results from other studies. Vine (1983) observed that a new leaf appeared on a tiller of Lolium perenne every 15 days on average between April and the beginning of September, 1975. This is slightly slower than the rate of appearance of approximately 12 days for Puccinellia leaves on main shoots. Between September and February, the rate of appearance of leaves of Lolium perenne dropped to once every 52 days (Vine, 1983) while at La Perouse Bay, no leaves were produced during the winter. Jones, Collett and Brown (1982) found that in a sward of L. perenne which was grazed to LAI levels of 0.8 to 3.0 by sheep, the rate of leaf appearance was 12 to 15 days between May and October in Scotland.

Cutting and fertilising affected the rate of leaf appearance in swards of L. perenne (Vine, 1983). In late May 1975, cutting shortened the rate of leaf appearance, and nitrogen fertilizer application also resulted in a decrease in leaf appearance interval (Vine, 1983). This was not observed at La Pérouse Bay. The higher rate of accumulation of leaves on grazed axillary shoots of Puccinellia was caused by the increased presence of tillers. The rate of appearance of leaves on each axillary tiller did not itself increase. It is probable that if demographic observations had continued into September and October, a decrease in the rate of appearance of leaves would have been observed in ungrazed shoot populations.

It has been suggested that defoliation stimulates photosynthesis (Nowak and Caldwell, 1984), and that this in turn stimulates growth. Thus, at La Pérouse Bay, grazing may stimulate photosynthesis enough to bring about extra growth that the root reserves cannot support. However, in field tests on two Agropyron species, negligible amounts of "compensatory" photosynthesis were observed following defoliation (Nowak and Caldwell, 1984). In any event, at La Pérouse Bay, nitrogen is the most obvious limit to production (Cargill and Jefferies, 1984a) and the geese provide a readily available source of it in their faeces.

As discussed in Chapter 3, the demographic data can answer some uncertainties regarding the estimates of production. The data for 1984 indicate the final leaf produced the previous year survived over the winter, and immediately following melt it started to photosynthesize. Therefore, standing crop estimates taken immediately after melt represent the previous year's growth. However, within 12 days of melt, the Puccinellia shoots started to produce new foliage. The utilization of this new growth by snow buntings (Plectrophenax nivalis) has not been observed before at La Pérouse Bay. However, as these birds migrate to nesting grounds further north (Godfrey, 1966), they are only present on the marsh for approximately two weeks following thaw.

Another aspect of interest in this study was the phenotypic plasticity of Puccinellia phryganodes. In grazed plots, the shoots tended to be prostrate with short, wide leaves, while in ungrazed plots, the shoots were upright, with long, thin leaves. The work of Jefferies and Gottlieb (1983) indicates that there is a large amount of genetic variability between and within populations of Puccinellia phryganodes. Thus, it is of interest to determine whether there are different genotypes of Puccinellia which respond differently to grazing, or whether all genotypes exhibit the same phenotypic response (Jefferies, 1984).

Demographic studies such as this are useful in that they allow ecologists to take an evolutionary approach to their work (Jefferies, 1984). The reproductive success of grazed and ungrazed tillers of different genotypes would have to be examined during a period longer than one summer in order to determine whether the geese have some selective effect. However, the fact that in the presence of grazing, some main shoots produce many axillary shoots, both inter- and extravaginally, while other produce hardly any, suggests that the geese are agents of selection. During the summer of 1983, there was no mortality of main and axillary shoots, except when entire shoots were grazed. In nearly all cases other axillary shoots survived.

There is scope for more extensive studies at La Pérouse Bay regarding individual tiller survival, and genotypic variation, similar to those described by White (1980) and Sarukhan, Martinez-Ramos and Pinero (1984). Preliminary results from such a study indicate that there are morphological differences in the growth habit of Puccinellia tillers from different areas of the marsh, which are maintained when they are grown in a "neutral" environment (Jefferies, 1984; H. Sadul and R.L. Jefferies, unpubl.).

CHAPTER 5

AVAILABILITY OF NITROGEN FOR PLANT GROWTH

5-1 INTRODUCTION

The most frequent limitation on the growth of herbivores and the plants on which they graze, is the availability of nitrogen (Henzell and Norris, 1962). The latter is also a limiting factor in the growth of ungrazed, exclosed Puccinellia phryganodes swards (Cargill and Jefferies, 1984a). Therefore, it is likely that grazed swards must be able to maintain growth in late summer each year while growth in ungrazed swards ceases, at least in part as a result of increased availability of nitrogen.

Plants take up inorganic nitrogen in the form of ammonium or nitrate ions (Haynes and Goh, 1978). There are a number of microbial transformations that take place in the soil, known as mineralization processes, in which complex organic molecules are broken down, and nitrogen made available for uptake by roots (Alexander, 1979; Atlas and Bartha, 1981). In addition to the constant, internal cycling of nitrogen within the soil, there are inputs from, and losses to, the atmospheric nitrogen pool. Nitrogen-fixation by micro-organisms, such as Rhizobium bacteria and blue-green algae, results in the incorporation of atmospheric nitrogen or dinitrogen into nitrogen containing molecules. The subsequent death and breakdown of these organisms, or exudation of nitrogen-containing molecules, results in the release of this element into the soil (Sprent, 1979, Atlas and Bartha, 1981; Stewart, 1982).

Denitrification is the process by which certain micro-organisms reduce nitrate ions to gaseous nitrogen and nitrous oxide (Atlas and Bartha, 1981). By this mechanism, nitrogen is lost to the atmosphere.

An examination of the contribution of some components of the nitrogen cycle to the availability of nitrogen in the marsh for plants was made. Three hypotheses were proposed, based on the findings of Cargill and Jefferies (1984a, 1984b).

Since snow geese are net exporters of nitrogen from the marsh (Cargill, 1981; Cargill and Jefferies, 1984b), then one could conjecture that there is a compensatory input of nitrogen, both in order to prevent the system from running down over a series of years, and to provide nitrogen for enhanced plant growth observed in grazed areas. There are groups of micro-organisms which fix atmospheric nitrogen (N_2) by reducing it to ammonia (Postgate, 1982). There is little litter accumulation in grazed areas compared with that which accumulates in ungrazed areas over a number of years. In the former sites extensive colonization of bare surface sediments by blue-green algae occurs. Certain species of cyanobacteria are known to fix atmospheric nitrogen. Therefore, the first hypothesis was that rates of nitrogen-fixation are higher in grazed than in ungrazed areas. In order to test this hypothesis, nitrogenase activity, an indicator of nitrogen fixation, was examined in grazed areas and in exclosures, with the use of the acetylene-reduction technique (Stewart, Fitzgerald and Burris, 1967).

Snow goose droppings contain a high proportion of soluble nitrogen (Cargill, 1981). The diversion of plant material into droppings instead of standing dead and litter may result in the more rapid recycling or turnover of nitrogen in the marsh. The absence of droppings in the exclosures may account for the slow growth recorded in them in August in 1982 and 1983. Thus, the second hypothesis was that the addition of fresh droppings to exclosed plots at rates similar to those observed in the marsh, would result in an increase in above-ground biomass, because they provide additional sources of nitrogen for growth. In addition to testing this hypothesis, levels of soluble and total nitrogen in snow goose droppings were measured, as were the rates of loss of soluble and insoluble nitrogen from the droppings. The objective was to determine whether significant amounts of nitrogen are lost from droppings during the summer. There are two possible sinks for this nitrogen: the atmosphere and the marsh sediments.

The third hypothesis was that the increased standing crop and the accumulation of standing dead and litter in the exclosures compared with grazed swards would bring about a change in the soil environment by causing increased insulation of the soil from the aerial environment. Based on these changes, and the knowledge that rates of mineralization of nitrogen are affected by the prevailing environmental conditions in the soil (Atlas and Bartha, 1981) it was predicted that insulation of the sediments in the exclosures has a cooling effect. The lower temperature of the sediments causes rates of mineralization to slow and a decreased availability of inorganic nitrogen for plant growth. Therefore, water content, redox potential, temperature and salinity of the sediments were monitored in grazed and ungrazed areas. Also, KCl^- exchangeable levels of ammonium (NH_4^+) and nitrate (NO_3^-) ions in the soil were monitored, and incubation tubes were placed in situ in grazed and ungrazed areas, to determine rates of mineralization of nitrogen.

5-2 METHODS

5-2-1 Activity of The Enzyme Nitrogenase in Soil Micro-organisms

In 1983, nitrogenase activity was measured in grazed and ungrazed sites using the acetylene-reduction technique. The dinitrogen (N_2) fixing enzymic complex, nitrogenase, is a versatile reducing catalyst (Hardy, Holsten, Jackson and Burns, 1968). In the presence of acetylene (C_2H_2) at a level of 10% volume in air, the acetylene is preferentially (compared with nitrogen) reduced to ethylene (C_2H_4) by nitrogenase (Stewart, Fitzgerald and Burris, 1967; Hardy, Holsten, Jackson and Burns, 1968). The presence of ethylene in gas samples is easily detected with the use of a gas chromatograph (Stewart, Fitzgerald and Burris, 1967).

The acetylene incubations were carried out in clear, cylindrical, plexiglass chambers, 14 cm in diameter and 10 cm in height with a volume of 1.55 litres. Attached to the open edge of the cylinder was a 10 cm wide tin strip which formed a flange. This enabled the chamber to be pushed into the ground until the plexiglass part of the cylinder was level with the sediment surface. The enclosure thus formed was airtight (volume = 1.55 l). A small, perspex tube, 1.5 cm in diameter was fitted to the top of the chamber, and over it was placed a rubber septum.

The ungrazed site was a three year-old exclosure, erected in 1980. On each sample date, three plexiglass chambers were pushed firmly into the ground at random points within the exclosure, and a further three chambers were inserted into the ground at random, in the adjacent grazed area. Acetylene gas was generated by mixing approximately 20 g of technical grade calcium carbide with approximately 2 litres of river water in a plexiglass cylinder, which was then inverted in a larger cylinder. The acetylene gas that was generated was trapped in the top of the inverted cylinder, and the displaced water collected in the large cylinder. The smaller, inverted cylinder had a small plexiglass tube attached to its base, covered with a rubber septum, through which a syringe needle was inserted, and the acetylene gas withdrawn.

At time zero, the start of each incubation, 50 ml of the acetylene was injected into each of the incubation chambers through the rubber septum, using a 25 ml syringe. This represented a level of acetylene of 3% which was found to yield the same rates of reduction as acetylene present at 10% volume in air. Immediately before these injections, a vacutainer holder needle was placed in the chamber septum in order to allow equalization of the air pressure within the chamber, upon addition of the acetylene. Immediately following this addition, a sample of the chamber gas was taken in a 5 ml vacutainer (Becton-Dickinson Red Stopper, no additive tubes #6434). This was done in order to determine the background level of ethylene in the chamber at the start of the incubation. Following removal of the vacutainer from the holder needle, the latter was removed from the chamber septum. Further samples of gas were taken after ten minutes and twenty minutes from each chamber, using a 5 ml vacutainer for each sample. At these times, no allowance was made for equalizing the chamber air pressure. Thus, after twenty minutes, each chamber was missing 15 ml or one per cent of its gas volume at ambient pressure and temperature. The syringe needles used were Yale Luer Lok 25 gauge, 1 1/2" disposable needles. The vacutainer needles were single use 22 gauge Becton-Dickinson brand needles. Besides, the collection of the samples described above additional samples were taken from a chamber in which previously acetylene was not injected. The procedures where were used were as described. The amount of ethylene present in the samples was subtracted from that present in samples withdrawn from chambers which received acetylene.

The vacutainers were returned to the field station. A 1.0 ml sample of gas was withdrawn from each and injected into a portable gas chromatograph (L & D Instruments Portable GLC), with a 1.0 ml Hamilton gas tight syringe (1000 series), with a teflon luer-lok tip.

Gas-liquid chromatography is one of a diverse group of methods that "permit the scientist to separate...and identify closely related components of complex mixtures" (Skoog and West, 1980). The sample to be analyzed is introduced as vapor at the head of the chromatographic column. It is pushed or "eluted" through the column by means of an inert carrier gas (Skoog and West, 1980). As the gas moves through the column, which contains a stationary liquid phase, the different components of the mobile gaseous phase separate out as they move at different rates, depending upon their tendancy to dissolve in the stationary liquid phase (Skoog and West, 1980). A sensor unit situated at the end of the column detects the peak of each component gas of the sample as it passes through. The peaks are permanently recorded if the chromatograph is connected up to a recorder. Heights of peaks, or areas under them, correspond to the amounts of the component gases present in the sample.

As mentioned, the chromatograph used was an L & D Instruments Portable GLC (Gas Liquid Chromatograph). It operates off a 12 V car battery, and it uses air as the carrier gas. The column is 0.15 cm I.D. x 60 cm teflon stainless steel, and is packed with Poropak T. The gas detector is a TGS gas-sensitive semiconductor sensor, consisting of two elements: a heater and a temperature-sensitive resistor. As gases of different thermal conductivity flow through the sensor, they have a varying cooling effect on the resistor. The magnitude of this resistance is proportional to gas concentration, and is translated into peaks on the attached recorder.

The ethylene peak was easily detected on the recorder and was observed approximately 45 seconds after the gas sample was injected into the chromatograph. Since the amount of background ethylene, present at time zero was known, any increases in the heights of the ethylene peaks that followed were assumed to be the result of nitrogenase activity in the soil enclosed by the chamber. These heights were calibrated against the peak heights of known concentrations of ethylene obtained from canisters of standard gas of 100 ppm C_2H_4 concentration (Alltech Associates Calibration Gases). The calculations used to determine ethylene concentration from peak heights are given in Appendix 5-1.

Acetylene incubations were run on six occasions between July and September 1983. On each sample date, except for July 5, when only a grazed site was tested, three chambers were placed in the exclosure and three outside. All incubations were carried out between 15:00 and 19:00 hours. During July, a Yellow Springs Instrument Telethermometer, Model 4250 and YSI thermistor probes, Model 418, were used to measure air temperature within the chambers 20 minutes after their insertion into the ground, as well as the ambient air temperature. The gas samples collected in the vacutainers were analyzed in the gas chromatograph as soon as possible after collection.

Samples collected on July 25 and September 2 were analyzed in Toronto, within six weeks of collection.

Soil samples collected from grazed areas in September and October 1983 were returned to Toronto, where the algae on the surface of the sediments were examined, in order to determine whether genera of blue-green algae were present.

5-2-2 The Role of Snow Goose Faeces in the Nitrogen Budget of the Marsh

5-2-2a Effects of the Addition of Snow Goose Faeces to Experimental Plots

In late May 1982, a 4 m x 4 m exclosure was built in a Puccinellia-dominated area of the marsh according to the method described in Section 3-1. Strong twine was strung between opposite sides at 50 cm intervals, to form a grid consisting of 64 squares, 50 cm x 50 cm in dimension (8 rows x 8 columns). Every alternate row and column was used as a walkway. The remaining 16 squares (4 rows x 4 columns) were treated with different amounts of fresh snow goose droppings. A Latin-Square experimental design was used so that each of the four treatments was applied once in each row and column (Ott, 1977). The four treatments consisted of the addition of high, medium and low amounts of droppings, and a control treatment in which no droppings were applied to plots. Droppings were applied eleven times between June 8 and August 17, every six to ten days. They were collected in small plastic bags by 10:00 hours of the day on which they were applied, because up to 60% of the nitrogen content of droppings was in water-soluble form and might be released rapidly into the soil and air following defaecation (Cargill, 1981). It was easy to distinguish droppings less than two hours old by their green, moist appearance. A quantitative attempt to choose fresh droppings of uniform weight and size was not made.

However, very large (> 8 g fresh weight) droppings were rejected, as were very small ones (< 3 g fresh weight).

The application levels were determined for each date from the densities of droppings observed in six 4 m x 4 m quadrats established in heavily grazed areas of the marsh. The snow geese were able to move freely through these quadrats, which were marked only by four corner posts. Every ten days, the number of droppings deposited during the period in each quadrat was counted, and the mean number of droppings calculated for all quadrats. Each dropping was flattened, in order to prevent it from being counted a second time on the following observation date.

The mean number of droppings per 0.5 m^2 was calculated for each sample date, which gave the medium treatment application level for that period. This number was doubled to yield the high treatment application level and halved to obtain the low level application. Since the plots in the exclosure were 50 cm x 50 cm, it should be noted that the medium treatment was double the dropping rate observed on the marsh. The mean numbers of droppings per 0.5 m^2 frequently contained fractions. Consequently, the numbers applied to the plots were rounded up or down to the nearest whole number. The applications varied from 0-4 droppings m^{-2} for the low treatment, 4-8 droppings m^{-2} for the medium treatment and 8-16 droppings m^{-2} for the high treatment. Droppings were applied at random within each plot.

The standing crop in each plot was measured on five occasions between June 8 and September 2, 1982. A 10 cm x 10 cm x 1 cm deep turf was cut from each of the 16 plots. They were transported to the field station where they were processed according to the methods described in Section 3-2.

In 1983, the same method was used for a similar experiment, except that a larger exclosure (5 m x 5 m) was built at a grazed site approximately 1.5 km east of the 1982 exclosure. The exclosure was again divided at 50 cm intervals to form a grid of 100 squares. Every alternate row and column was a walkway, and there were 25 experimental plots, 50 cm x 50 cm in size (5 rows x 5 columns). As in 1982, there were four treatments: high, low and medium rates of applications of droppings, and control plots which received no droppings. The number of plots which received the medium rate of application was doubled in the latin square design. Thus, all treatments had sample sizes of five plots except for the medium treatment, which had an overall sample size of ten plots. Dropping rates were estimated by monitoring eight 4 m x 4 m quadrats through which the geese could move freely, and the application rates were calculated in the same way as 1982. Fresh droppings were applied to the exclosure on eight occasions from June 23 to August 25, 1983. The low treatment varied from 0-4 droppings m^{-2}, medium treatment from 4-8 droppings m^{-2} and the high treatment from 8-16 droppings m^{-2}. The *Puccinellia* site chosen in 1983 was heavily influenced by tidal movement in late July and August, and applied droppings were held in place with 10 cm lengths of thin telephone wire formed into loops and pushed into the ground, thereby preventing them from being washed from the plots.

The standing crop in this exclosure was sampled on four occasions between June 23 and October 15. On each occasion, a turf 10 cm x 10 cm x 1 cm deep was cut from each plot. In all cases, except on October 15, the turfs were transported to the field station and processed in the established manner (Section 3-2). In October, the turfs were clipped following removal, and the vegetation was frozen and transported to Toronto, where it was washed and sorted.

5-2-2b Loss of Nitrogen from Faeces

In 1982, an experiment to determine the extent of the loss of nitrogen during the summer from snow goose droppings deposited on grazed areas of the marsh was initiated on June 14. In the first experiment, 70 bags (5 cm x 5 cm) were constructed from 1 mm mesh mosquito netting. Each bag was sewn closed on three sides and the fourth side was left open. On June 14, 70 fresh goose droppings were collected and their fresh weights taken. A dropping was placed in each bag, which was numbered with a small tag, and the bags were placed at random in a 30 m x 30 m grazed area of the marsh. Each was held in place by a toothpick pushed through the mesh into the ground. Every ten days, between June 23 and August 12, ten bags were collected at random. The last ten droppings were collected on September 2. At each harvest, a second fresh weight was taken. Following this, the droppings were placed in manila envelopes and dried on a rack above a propane heater for several days. They were stored in wooden boxes and transported to Churchill in September,where they were dried in a drying oven at 80°C for 48 hours and their dry weights were taken. They were transported to Toronto for Kjeldahl analyses of total nitrogen present in the material.

On July 15, a second experiment involving 60 droppings was set up according to the same procedure. However, the mesh bags were made from a fine netting material with a 2 mm mesh. They were collected at ten day intervals and dried. Between June 12 and August 17, six fresh snow goose droppings were collected every ten days. Their fresh weights and dry weights were taken as described, and they were transported to Toronto.

In 1983, total amounts of nitrogen in fresh droppings and in live Puccinellia and Carex leaves were monitored between June 8 and August 26. Five fresh droppings were collected every 5-16 days, and were weighed before being dried in manila envelopes for 48 hours at 80°C. Dry weights of the faeces were taken subsequently. The samples were sent to Toronto, where the nitrogen content of the material was determined, as described in Appendix 5-2. In addition, between July 4 and August 10, approximately 1 g fresh weight samples of live Puccinellia and Carex leaves were taken from grazed and ungrazed sites and treated according to the procedures described above, to determine total nitrogen content. These data were compared with the results of the concentrations of soluble nitrogen in the tissues.

5-2-2c Loss of Nitrogen from Snow Goose Faeces During a 48 Hour Period

Cargill (1981) found that snow goose droppings contain high levels of soluble nitrogen. In 1983, levels of soluble nitrogen in fresh goose droppings were again tested, and the rate of loss of soluble nitrogen from droppings determined.

Between June 17 and August 26, five fresh droppings were collected from the marsh every five to fifteen days, and placed in small plastic bags. The fresh weight of each dropping was recorded, and it was placed in a 60% w/v ethanol solution for 24 hours in order to extract the soluble fraction of nitrogen in the dropping (see Appendix 5-2 for details of the procedure). The filtered extracts were frozen and transported to Toronto, where following acid digestion, levels of soluble nitrogen, as ammonium ions, were determiend. In July and August, ethanol extractions of live Puccinellia and Carex tissue were also prepared according to the procedure described in Appendix 5-2. Plant samples were collected from both grazed and ungrazed areas.

On July 31, an experiment to determine the rate of loss of soluble nitrogen over a short time period was conducted. It was essential that the goose droppings were as fresh as possible. At about 05:30 hours on July 31, approximately 50 snow goose families were grazing in the immediate vicinity of an observation tower on the marsh. At 09:30 hrs, we collected approximately 90 fresh snow goose droppings. They were transported to the field station and their fresh weights were measured between 12:40 hr and 13:40 hr.

Grazed turfs were laid out in an area south of the field station, to form a flat, unshaded surface. A grid of 5 rows x 10 columns was marked with toothpicks. Each dropping was placed next to a toothpick, at a distance of 6-7 cm from its neighbours. At this time, (13:40 hrs), ten droppings were placed in 60% w/v ethanol for 24 hours, and another five were dried at 80°C in manila envelopes. Also, a grid of 5 rows x 5 columns was marked out next to the 5 x 10 grid, and 25 fresh droppings were placed on the grid at random at 13:40 hrs. At 2, 6, 19, 30 and 48 hours following time 0 (13:40 hrs), ten droppings were selected at random from the 5 x 10 grid, and five from the 5 x 5 grid. The former were dropped in 60% w/v ethanol and the latter were placed in envelopes and dried. Fresh weights were taken immediately after harvest at each sample time. Thus, the water content of the droppings placed in ethanol at the various harvest times could be calculated from the fresh weight - dry weight measurements taken on the groups of five droppings harvested at the same times. The ethanol extracts were analyzed for soluble nitrogen in Toronto, according to the procedure given in Appendix 5-2.

5-2-3 Environmental Measurements and Concentrations of Exchangeable Ammonium Ions in the Sediments in Grazed and Ungrazed Sites

5-2-3a Soil Temperatures

In 1982, soil temperatures were measured in a number of exclosures built between 1979 and 1982, and in adjacent grazed areas. A Yellow Springs Instrument Telethermometer, Model 4250 and YSI thermistor probes, Model 418 were used. Temperatures were measured in at least one grazed and one ungrazed site on most days between June 13 and September 2, between 13:00 hrs and 16:00 hrs. It was during this time that soil temperatures were found to be highest on a diurnal basis. Temperatures were taken by inserting the probe in the top 1 cm of mineral soil beneath any accumulated litter. Five measurements were taken at random at each depth at a site. They were also taken at depths of 5 cm and 10 cm on various days throughout the summer. Cargill (1981) found that the majority of the roots of *Puccinellia* were confined to the top 10 cm of sediment, and the decision to measure temperatures at the specified depths was based on this.

In 1983, soil temperature measurements were taken on several occasions between June 14 and July 15 in a three-year old exclosure and in an adjacent grazed area. This site was used for other environmental measurements in 1983. As in 1982, the soil temperature at 1 cm was taken and also measurements were made at 5 cm and 10 cm depths on several occasions. Five random measurements were made at each depth in the grazed and ungrazed areas. After July 15, time constraints prevented further measurements from being taken.

5-2-3 b Soil Water Content, Salinity and Conductivity

Soil water content was measured in 1982 in a one-year old exclosure and in a grazed area adjacent to the exclosure, on 13 occasions between May 31 and September 2. The sample intervals varied from 5-20 days, because the sample schedules of other studies overlapped.

Four soil samples, approximately 4 cm x 4 cm x 10 cam deep were cut from inside the exclosure and a further four were cut from outside the fence. They were place in plastic bags and carried to the field station where they were trimmed to 2 cm x 2 cm x 7 cm, and their fresh weights taken. They were then wrapped in Saran plastic wrap and in aluminium foil, and frozen. In September, they were transported to Toronto where, after thawing, second fresh weights were taken. The soil samples were dried for 48 hours at 100°C and dry weights were taken. The water content was calculated from data obtained from the difference between fresh and dry weights.

In 1983, soil water content was measured on nine occasions between June 18 and October 15 in a three-year old exclosure built in 1980, and in a grazed area approximately 50 m away. Other measurements were made in grazed and ungrazed sites at a variety of locations in June 1983. The soil samples were collected in the same manner as in 1982. However, they were dried at the field station immediately following the recording of their fresh weight. After drying the samples for 48 hours at 80°C, dry weights were taken.

Soil-water salinity and conductivity were measured on nine occasions during the summer of 1982 with a Yellow Springs Instrument S-C-T Meter, Model 33. Water from the top 7 cm of soil blocks cut from inside and outside of the exclosure used for the measurement of soil-water content was squeezed into beakers at the field station. The water was filtered through Whatman Glass Microfibre Filter Paper (GF/A) and measured with the appropriate YSI probe attached to the meter.

5-2-3c Soil Redox Potential in Grazed and Ungrazed Areas

In 1983, Soil Eh measurements were made using a Corning pH meter, model 610 A, in conjuction with a Fisher platinum electrode, model 13-639-82. The electrode was calibrated with Zo Bell's solution (Howes, Howarth, Teal and Valiela, 1981). Because the cell component in addition to platinum was a saturated calomel half cell, a potential of + 250 mV was added to each meter reading.

The Eh or redox potential of a system "is a measure of its tendency to receive or supply electrons and is governed by the nature and properties of the oxidizing and reducing substances which it contains" (Etherington, 1982). Soil Eh is a useful measurement for characterizing the level of aeration in soils, as a low Eh is reflective of a waterlogged environment (Etherington, 1982).

Eh measurements were taken on eight occasions between June 14 and September 2. A soil block, 10 cm x 10 cm x 10 cm, was cut from a three-year old exclosure and from a grazed area approximately 50 m away. The blocks were wrapped in plastic bags and transported to the field station, where five measurements were taken within a few hours of collection at a depth of 2 cm, and five at a depth of 5 cm.

Immediately prior to the taking of the measurement, the outside layers of the soil block were cut away to reveal a clean face, previously unexposed to the air. For each measurement, the electrode was firmly inserted into a 1 cm deep and 1 cm wide hole cut into the face of the soil block at the appropriate depth. On June 20, the measurements were made in the field, and the sediment blocks were subsequently carried back to the field station. A second set of measurements was made after six hours, in order to determine whether Eh changed significantly within this period. This served as a check on whether the Eh measurements taken a few hours after soil blocks were harvested were similar to those taken in the field, immediately after a soil block was cut.

In early June, the Eh of soil from a range of locations at La Pérouse Bay was measured, in order to determine the range of variation across the marsh. As mentioned earlier in this section, a reference potential of +250 mV was added to each measurement (Howes, Howarth, Teal and Valiela, 1981). Although Eh values are quoted for a standard pH of 7, no correction was made in these studies as the pH of the sediments was between 7.2 to 7.6.

5-2-3 d Rates of Mineralization of Nitrate and Ammonium and Background Levels of Ammonium and Nitrate in Sediments of Grazed and Ungrazed Areas

In 1982, the rates of mineralization of organic nitrogen in sediments in a one-year old exclosure (built in 1981) and in adjacent, grazed areas were measured, using an *in situ* soil incubation method (Aziz and Nedwell, 1979). Twenty-five ml plastic syringe barrels, with the plungers removed and needle holders sawn off were inserted in the sediment at random, and ammonium and nitrate accumulation based on exchangeable KCl-extracts determined at 10, 20, 30 and 40 days from the start of the incubation.

Four incubation series were started on four occasions between June and September. At the start of the first series, 48 tubes were inserted into the soil, 24 inside and 24 outside the exclosure. Care was taken to ensure that the soil column was not compressed. At the begining of the second, third and fourth series, 18 tubes were inserted in the grazed area and 18 in the exclosure on each occasion. Six tubes were removed from each site every ten days. Each tube was numbered, and those removed were selected from random number tables. A soil block containing a tube was cut from the sediment, wrapped in Saran wrap and frozen.

On each occasion that the incubation tubes were sampled, sediment was also collected to determine in situ levels of ammonium and nitrate ions in the soil. Six soil block, 6 cm x 6 cm x 7 cm deep, were cut from grazed and ungrazed sites. Their fresh weights were measured and they were wrapped in Saran wrap and aluminium foil, and frozen. A duplicate set of samples, 2 cm x 2 cm x 7 cm deep was cut at the same time. After their fresh weights were taken, each sample was incubated in 50 ml of 1 M potassium chloride (KCl) solution, for approximately three hours. This allowed the exchange of ammonium ions, bound to negative sites in the soil matrix, for potassium ions. The nitrate ions, which are negative, occur in the soil water solution, and tend not to be bound to sites in the soil matrix (Atlas and Bartha, 1981). The extraction procedure is fully described in Appendix 5-2.

Frozen KCl extracts and soil samples were transported to Toronto in September 1982. The soil cores were thawed, removed from the incubation tubes, and incubated in a solution of 1 M potassium chloride in Toronto, as were the soil blocks collected for determination of background *in situ* levels of ammonium and nitrate. The latter were first trimmed to 2 cm x 2 cm x 7 cm deep. The volume of KCl used was 15 ml to 1 g fresh weight of sediment. The levels of ammonium and nitrate ions in the extractions were analyzed using colorimetric methods described in Appendix 5-2 (Solorzano, 1969).

On each sample date, soil-water samples were collected according to the same procedure described in Section 5-2-3b, filtered, frozen and transported to Toronto for analyses of the concentrations of nitrate and ammonium ions. Table 6-1 gives a summary of the exclosures which were used for environmental measurements and measurements of inorganic nitrogen.

In 1983, background concentrations of ammonium ions were measured in an ungrazed three-year old exclosure, built in 1980, and in a grazed area approximately 50 m away. Between June 20 and October 15, on ten occasions, soil blocks, 5 cm x 5 cm x 7 cm deep, were cut from the grazed and ungrazed areas. At the field station, they were cut into blocks of size 2 cm x 2 cm x 7 cm, and a KCl-extraction was carried on each block. The volume of 1 M potassium chloride solution used in the incubation was determined by the fresh weight of the soil block. A ratio of 5 ml KCl solution to 1 g fresh weight of soil was used. This was determined as being a suitable extraction ratio after a series of tests were carried out in 1982, on different ratios of volumes of KCl solution to 1 g fresh weight of soil. The extracts from different solutions:soil ratios were analyzed for their ammonium content, and the minimum ratio at which the total amount of KCl-exchangeable ammonium ions were brought into solution was established.

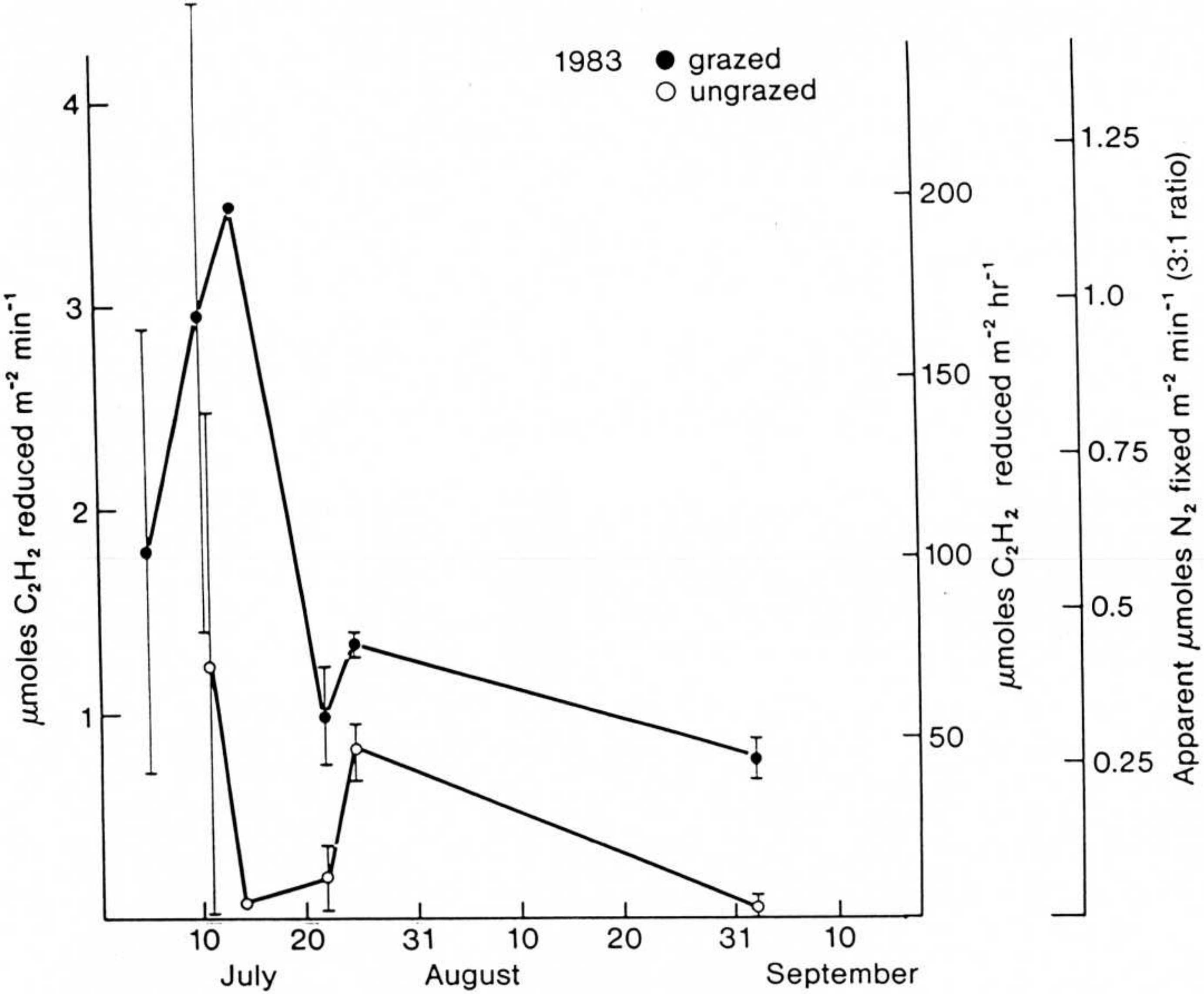
The colorimetric analysis of ammonium ions (see Appendix 5-2) followed immediately with the use of a hand-held Bausch and Lomb Spectronic Mini 20 spectrophotometer. Samples of filtered soil water squeezed from soil blocks cut to the same depth as those incubated in solutions of potassium chloride, were also analyzed for their ammonium content.

5-3 RESULTS

5-3-1 Activity of the Enzyme Nitrogenase in Soil Micro-organisms in Grazed and Ungrazed Sites

Nitrogenase activity, as reflected by the rate of acetylene reduction, was higher in grazed than in ungrazed areas on all occasions during which measurements were made (Fig. 5-1). the highest activity was detected during the first two weeks of July 1983; it peaked at 3.5 μmoles C_2H_2 reduced m^{-2} min^{-1} in the grazed

Figure 5-1. Nitrogenase activity measured by rates of acetylene reduction (µmoles C_2H_2 reduced m^{-2} min^{-1} and µmoles C_2H_2 reduced m^{-1} hr^{-1}) and apparent rates of nitrogen fixation (µmoles N_2 fixed m^{-2} min^{-1}) in grazed (●) and ungrazed (O) swards dominated by Puccinellia phryganodes at La Pérouse Bay, 1983. (Mean +/- S.E., n=3; n=2 on July 14).


1983
● grazed
○ ungrazed
μmoles C_2H_2 reduced m^{-2} min^{-1}
4
3
2
1
μmoles C_2H_2 reduced m^{-2} hr^{-1}
200
150
100
50
Apparent μmoles N_2 fixed m^{-2} min^{-1} (3:1 ratio)
1.25
1.0
0.75
0.5
0.25
10
20
31
10
20
31
10
July
August
September

site on July 14. Thereafter, nitrogenase activity in the grazed site dropped to approximately 1 μmole C_2H_2 reduced m^{-2} min^{-1} for the remainder of the summer.

The trend in nitrogenase activity in the three-year old exclosure tracked that in the grazed area, and peaked at 1.24 μmoles C_2H_2 reduced m^{-2} min^{-1} on July 11. Thereafter, activity dropped to about 0.5 μmoles C_2H_2 reduced m^{-2} min^{-1}. These rates of reduction were 37% to 97% less than the rates in the grazed sites.

Ambient temperatures were found to be 2 to 3°C lower than those in the perspex incubation chambers after one hour of insertion of the chambers into the ground.

The turfs collected from the grazed site in September and October bore colonies of blue-green algae visible to the naked eye on the surfaces of the sediments. The two most common genera observed were Oscillatoria and Lyngbya. These filamentous blue-green algae do not form heterocysts (Desikachary, 1959), which are the sites of nitrogen fixation in some filamentous blue-green algae (Postgate, 1982). However, non-heterocystous forming, filamentous species have also been found to fix nitrogen (Stewart and Lex, 1970). The filaments of Lyngbya formed large bundles, up to 1 mm thick; Oscillatoria grew with the Lyngbya, although it was not as abundant.

When the surface sediments of turfs from the three-year old exclosure were examined in early September, no blue-green algae were observed.

5-3-2 The Role of Snow Goose Faeces in the Nitrogen Budget of the Marsh

5-3-2a Effects of the Addition of Snow Goose Faeces to Experimental Plots

Figure 5-2 shows that the addition of fresh snow goose droppings to *Puccinellia* stands caused significant increases in the above-ground live biomass. In 1982, the live standing crop increased from an initial mean value of 8 g m^{-2} (Fig. 5-2a) in all plots subject to the different treatments. By July 20 it was 46 g m^{-2} in the plots which received the lowest amount of faeces. This treatment corresponded to the dropping rates recorded on the marsh. By August 8, the mean above-ground live biomass reached 67 g m^{-2} for this treatment, whereas the corresponding value for untreated plots was 42 g m^{-2}. However, there were no significant differences in standing crop among the different plot treatments on this date. On September 2, the standing crop was highest in the plots which received twice the amount of droppings that were observed in the field (103 g m^{-2}), and it was lowest in the control plots, (67 g m^{-2}).

An analysis of variance, based on a Latin-square experimental design, performed on data obtained for September 2, showed that the final mean standing crop for the treated and untreated were significantly different ($p < 0.10$, $df_1 = 3$,$df_2 = 6$). However, rows in the exclosure showed a greater significant difference ($p < 0.05$, $df_1 = 3$, $df_2 = 6$).

Figure 5-2 a. Seasonal trends in live, above-ground standing crop (g dry weight m^{-2}) in an exclosure fertilised with different levels of fresh snow goose droppings at La Pérouse Bay, 1982. (Mean +/- S.E. Treatments: high level of application (●); medium level of application (O); low level of application (▲); control, no droppings (▽); n = 4 for each treatment and control).

Figure 5-2 b. Seasonal trends in litter and standing dead (g dry weight m^{-2}) in an exclosure fertilised with different levels of fresh snow goose droppings at La Perouse Bay, 1982. (Mean +/- S.E.
Treatments: high level of application (●); medium level of application (O); low level of application (▲); control, no droppings (▽); n = 4 for each treatment and control).

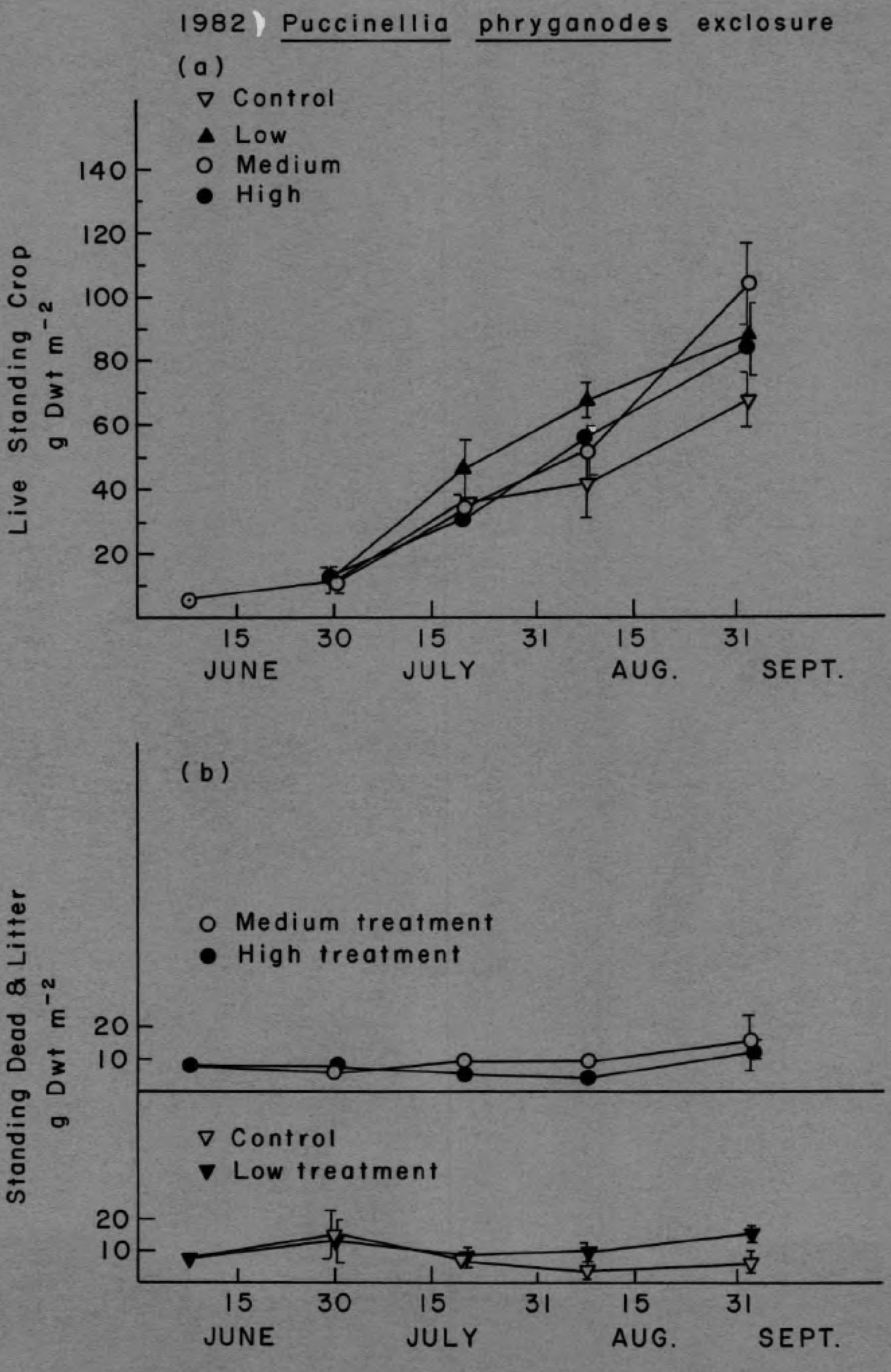
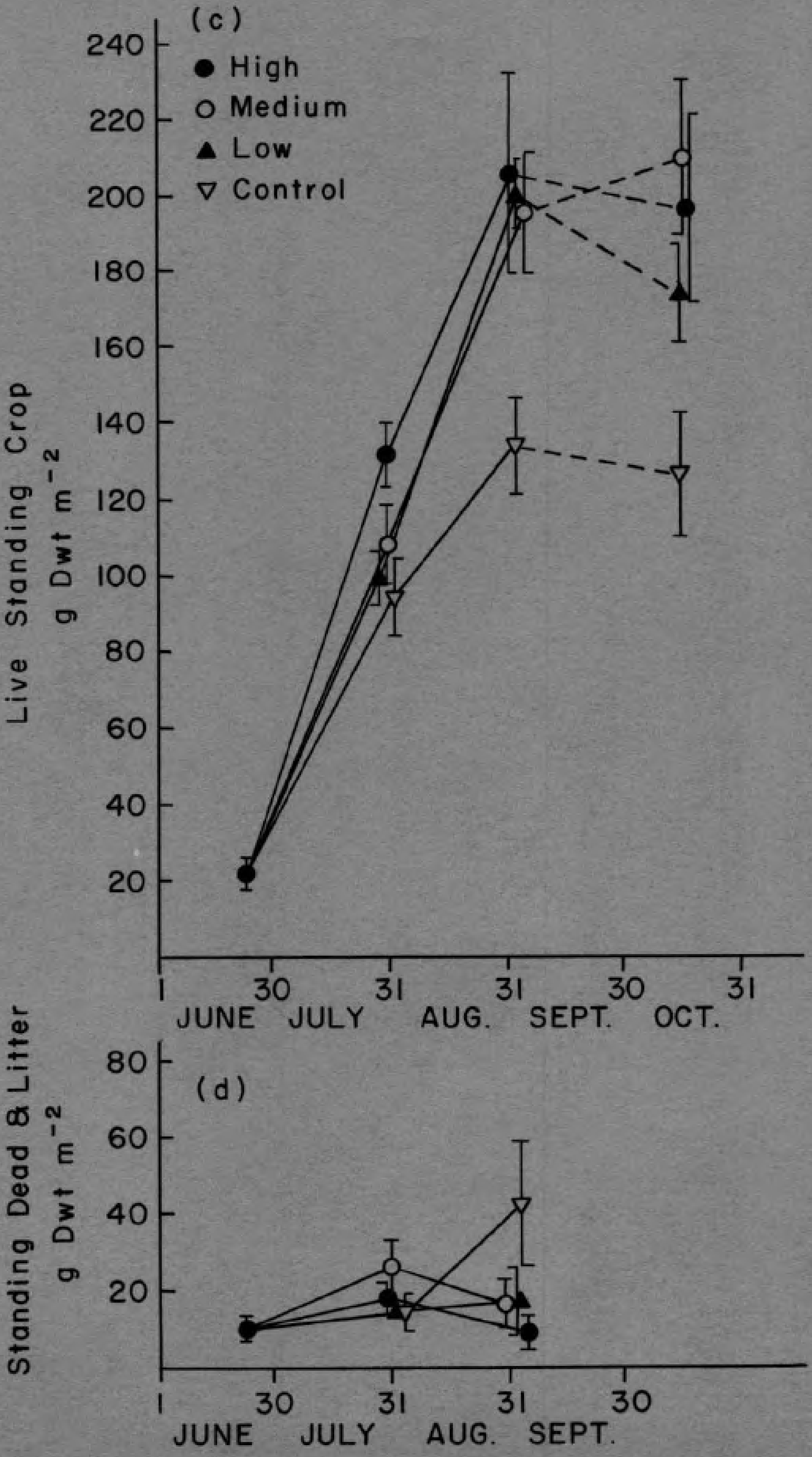

1982 Puccinellia phryganodes exclosure
(a)
Control
Low
Medium
High
Live Standing Crop g Dwt m^{-2}
140
120
100
80
60
40
20
15
30
15
31
15
31
JUNE
JULY
AUG.
SEPT.
(b)
Medium treatment
High treatment
Control
Low treatment
Standing Dead & Litter g Dwt m^{-2}
20
10
20
10
15
30
15
31
15
31
JUNE
JULY
AUG.
SEPT.

Figure 5-2 c. Seasonal trends in live, above-ground standing crop (g dry weight m^{-2}) in an exclosure fertilised with different levels of fresh snow goose droppings at La Pérouse Bay, 1983. (Mean +/- S.E. Treatments: high level of application (●); low level of application (▲); control, not droppings (▽); n = 5 for each treatment and control; medium level of application (O); n = 10).

Figure 5-2 d. Seasonal trends in litter and standing dead (g dry weight m^{-2}) in an exclosure fertilised with different levels of fresh snow goose droppings at La Pérouse Bay, 1983.(Mean +/- S.E. Treatments: high level of application (●); low level of application (▲); control, no droppings (▽); n = 5 for each treatment and control; medium level of application (O); n = 10).

1983 *Puccinellia phryganodes* exclosure



Amounts of litter were not significantly different among the experimental plots (Fig. 5-2b). Values fluctuated around 10 g m^{-2} during the summer in 1982.

In 1983 there was a much greater effect on live standing crop brought about by the addition of fresh snow geese droppings (Fig. 5-2c). The initial mean standing crop on June 23 was 22 g m^{-2} for all plots. This value increased rapidly in July and reached 86 g m^{-2} by July 30 in the untreated plots. The values for standing crop in treated plots were higher, and the mean value for plots which received the high application of droppings was 135 g m^{-2}. This value was found to be significantly higher ($p \leq 0.05$, $df_1 = 4$, $df_2 = 12$) than other mean values, based on an ANOVA for a Latin Square design and Fisher's Least Significant Difference Tests. By September 2, the mean standing crop in the untreated control plots was 122 g m^{-2}, which was much lower than those for the treated plots, which ranged from 195 g m^{-2} in the plots receiving the medium application level of droppings, to 204 g m^{-2} in the plots receiving the high application level of droppings. An ANOVA, and Fisher's Least Significant Difference Test indicated that the standing crop in all treatment plots to which fresh goose droppings had been added, was significantly different at $p \leq 0.01$ ($df_1 = 4$, $df_2 = 12$) from that in the untreated (control) plots. The ANOVA showed that there were no significant effects on the live standing crop associated with rows and columns.

Dashed lines were used to connect data of standing crop for September 2 to those for October 15, because the latter represent total rather than live standing crop. When the October samples were collected, much of the vegetation was senescent, and it was difficult to distinguish between live and dead material. All of the vegetation clipped from the turfs was combined to produce these values. The mean value for the control plots was 124 g m^{-2}, while the values for the treated plots ranged from 173 g m^{-2} to 210 g m^{-2}. The plots to which the medium level of fresh droppings had been added, had the highest mean value.

In 1983, litter and standing dead values fluctuated around 18 g m^{-2} from June 23 to September 2 (Fig. 5-2d). An ANOVA, based on a Latin Square design, showed no significant differences between the values for September 2, in spite of an increase in the litter levels in the untreated plots. This increase was caused by the standing crop in one sample reaching 95 g m^{-2}. Exclusion of this sample yielded a mean of 30 g m^{-2} from the remaining four control values, which was in the range of values observed for the treated plots.

The standing crop values in the control plots were much higher throughout the summer in 1983 than in 1982. The exclosure used for this experiment in 1982 was located in a sparse Puccinellia sward, compared with the site chosen for the similar experiment in 1983. Large differences in standing crop between treated and untreated plots were recorded in early August, 1982 and in late August, 1983. The later date in 1983 may have been a reflection of the very late thaw. The differences in cumulative net primary production between grazed and ungrazed areas (Figs. 3-1c and 3-2c) also occurred in early and late August in 1982 and 1983 respectively.

In 1982, the medium application level of snow goose droppings was the most effective in bringing about an increase in live standing crop in late August. The final values for the live standing crop in the treated plots were not as distinctively different from those in the untreated plots in 1982, as they were in 1983. As in 1982, the medium application level of droppings appeared to bring about the highest standing crop at the end of the summer in 1983.

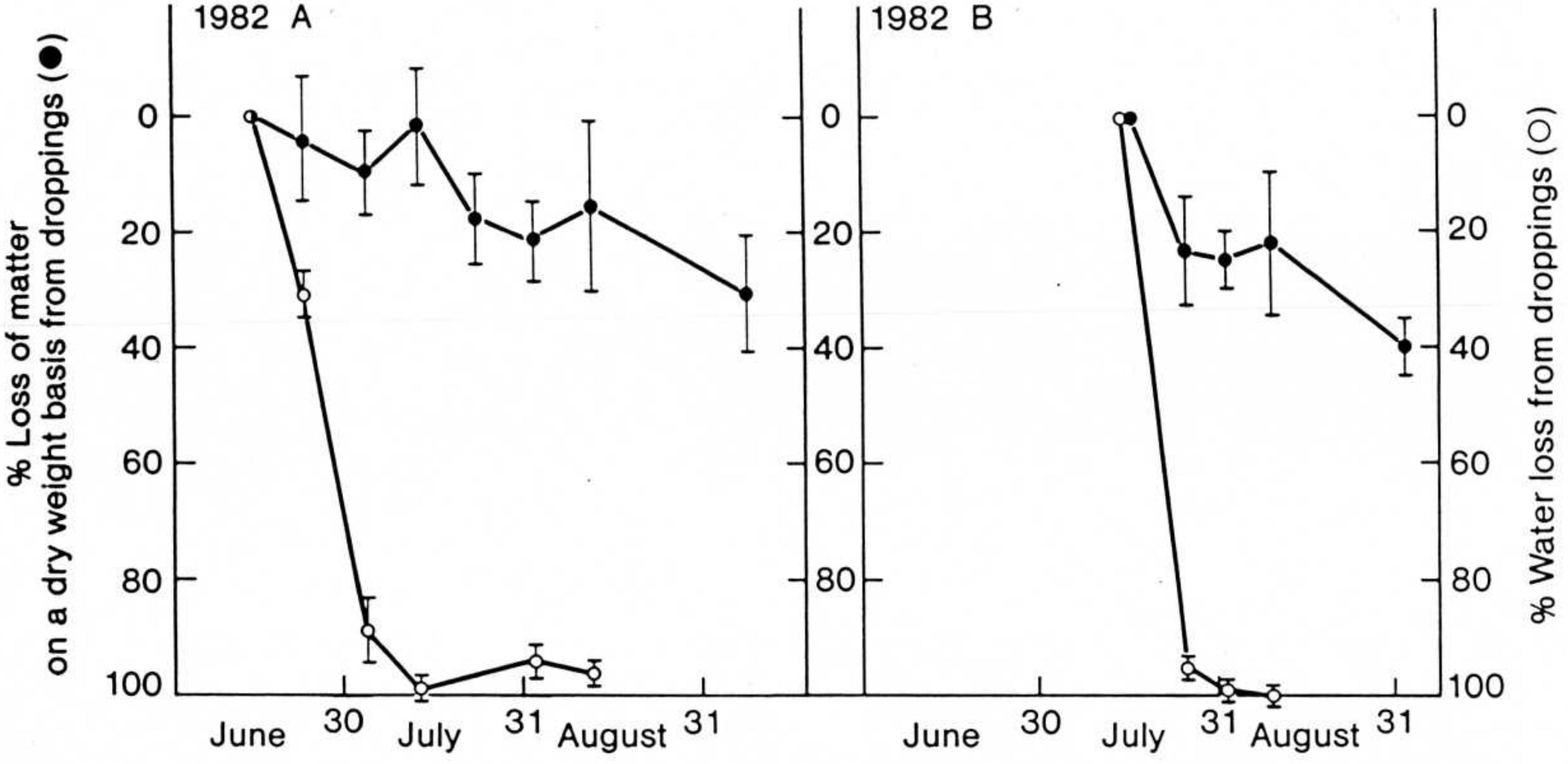
5-3-2b Loss of Water and Nitrogen from Snow Goose Faeces

Figure 5-3 shows that droppings were subjected to breakdown and/or decomposition following their deposition on the marsh in small mesh bags in 1982. Droppings placed on the marsh in mid-June lost 30% of the initial dry weight after two and a half months. The pieces of dropped vegetation would have to have been less than 1 mm in size in order for them to pass through the mesh. The droppings placed on the marsh on July 15, 1982, lost 40% of their dry matter after one and a half months, probably because the size of the mesh used was larger (2 mm). The fate of the pieces of droppings which were lost was not known.

The percentage of water lost was similar in both groups (Fig. 5-3), in that 90-96% of the water content of the droppings

13

Figure 5-3. Water loss (% total water content, O) and dry matter loss (% dry weight, ●) from fresh snow goose droppings placed on marsh at La Pérouse Bay (A) June 15, 1982 (n = 70) (B) July 15, 1982 (n = 60). (Mean +/- S.E. n>/ = 10 for each sample date).


1982 A
1982 B
% Loss of matter on a dry weight basis from droppings (●)
% Water loss from droppings (○)
0
20
40
60
80
100
June
30
July
31
August
31

evaporated after two weeks. This drying-out occurred in spite of showers during early July, 1982.

Figure 5-4 shows that between June 15 and September 2, there was a drop in the net nitrogen content of the droppings placed on the marsh on June 14. Their initial nitrogen content was 16.6 mg N g dwt^{-1} of droppings, which dropped to 11.6 mg N g dwt^{-1} of droppings after nine days. By July 4, the total nitrogen content was 8.2 mg N of dwt^{-1}, which was significantly lower ($p \leq 0.05$, df = 13) than that in fresh droppings on June 14. This represented a 30% drop in the nitrogen content after 20 days. Thereafter, the nitrogen content of the droppings remaining on the marsh fluctuated around 10 mg N g dwt^{-1} of droppings. All of the mean total nitrogen values observed after July 4 were significantly different at $p \leq 0.05$ from the initial total nitrogen value, except for the July 23 value of 11.4 mg N g dwt^{-1}, which was significantly different at $p \leq 0.10$. T-tests were used to compare the means for each date to the initial total nitrogen value.

The total nitrogen content of fresh goose droppings did not vary greatly during the summer in 1983 (Table 5-1). Values ranged from 11.6 to 22.6 mg N g dwt^{-1} of droppings. In the Puccinellia shoots from heavily grazed areas, the total nitrogen content was slightly higher, ranging from 23.0 to 24.3 mg N g dwt^{-1} of Puccinellia. Puccinellia shoots from exclosures sampled early in the summer had a total nitrogen content of 22.1 mg N g dwt^{-1} Puccinellia, which was in the same range as that of the grazed shoots. This declined during the summer to approximately 13 mg N g dwt^{-1} live Puccinellia shoots on August 10.

Figure 5-4. Total nitrogen content (mg $N\text{-}NH_4$ per g dry weight of droppings) of snow goose droppings placed on the marsh at La Pérouse Bay on June 15, 1982 (n = 70) during the ensuing two and a half month period. (Mean +/- S.E. n>/ = 8 for each sample date).

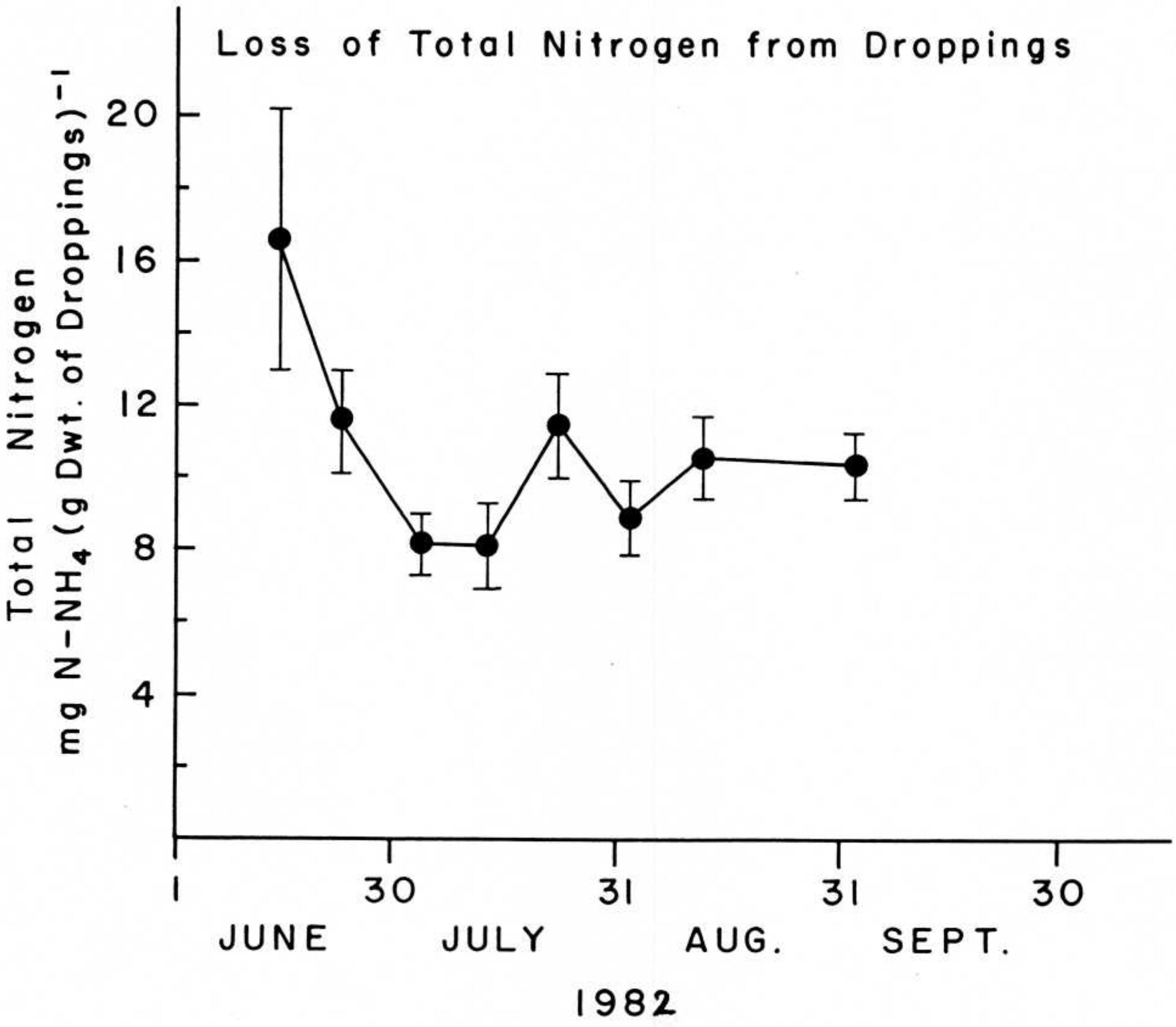

Loss of Total Nitrogen from Droppings
Total Nitrogen
mg N-NH$_4$ (g Dwt. of Droppings)$^{-1}$
20
16
12
8
4
1
30
31
31
30
JUNE
JULY
AUG.
SEPT.
1982

Table 5-1. Total and soluble nitrogen content of snow goose faeces, and grazed and ungrazed live <u>Puccinellia</u> shoots in 1983. (All values in mg $N\text{-}NH_4$ g dwt^{-1}).

FAECES

1983	Total Nitrogen	Standard Error	Sample Size (n)	Soluble Nitrogen	Standard Error	Sample Size (n)
18-20 June	17.7	4.1	8	6.8	0.9	10
27 June	19.0	0.4	3	8.2	1.4	5
4 July	16.6	3.4	5	16.4	1.5	4
12 July	22.6	2.0	5	10.1	3.7	4
17 July	11.6	1.2	5	4.9	0.8	5
31 July	-	-	-	11.3	1.6	10
10 August	17.3	2.1	5	9.3	2.1	5
26 August	11.6	0.7	8	10.7	0.7	7

SHOOTS OF <u>PUCCINELLA</u> (n = 2)

	Total Nitrogen		Soluble Nitrogen	
1983	Grazed Shoots	Ungrazed Shoots	Grazed shoots	Ungrazed shoots
4 July	24.3	22.1	3.0	2.8
17 July	23.0	17.4	3.8	3.5
26 July	-	17.4	-	1.5
10 August	23.3	13.3	6.3	2.0
10 August	-	13.1	-	1.7

5-3-2 c Loss of Nitrogen from Snow Goose Faeces During a 48 Hour Period

Data pertaining to fresh snow goose droppings are given in Figure 5-5 for 1982 and 1983. The water content of fresh droppings ranged between 80% and 90% on a fresh weight basis throughout the summer, in both years. There was a large variability in the fresh weights of droppings between June and August. The changes in fresh weights followed no detectable trends. In 1982, fresh weights ranged between 5.5 and 8 g, except for a mean value of 11 g fresh weight observed on June 28. In 1983, mean values ranged between 5.5 and 8.5 g fresh weight, and no higher values were observed.

The levels of soluble nitrogen in the droppings ranged from 49 to 16.4 ng N g dwt^{-1} of droppings between June 18 and August 26, 1983 (Table 5-1). Between 42% and 99% of the total nitrogen content of droppings was composed of soluble nitrogen compounds (Table 5-1). The soluble nitrogen content of live Puccinellia shoots was lower than that in the droppings. During July 1983, values were about 3 mg N g dwt^{-1} for Puccinellia shoots from both grazed and ungrazed areas. In August, the soluble nitrogen content dropped in ungrazed shoots. The soluble nitrogen fraction of Puccinellia accounted for 19% or less of the total nitrogen in the grazed and ungrazed shoots.

Figure 5-6 indicates that significant amounts of the soluble nitrogen fraction of fresh droppings monitored on July 31, 1983 were lost two hours after the start of the experiment ($p \leq 0.05$ df = 18).

Figure 5-5. Water content (●) as percent of fresh weight (O) in grammes of fresh snow goose droppings at La Pérouse Bay. (a) in 1982, (b) in 1983. (Mean +/- S.E. n>/ = 5).

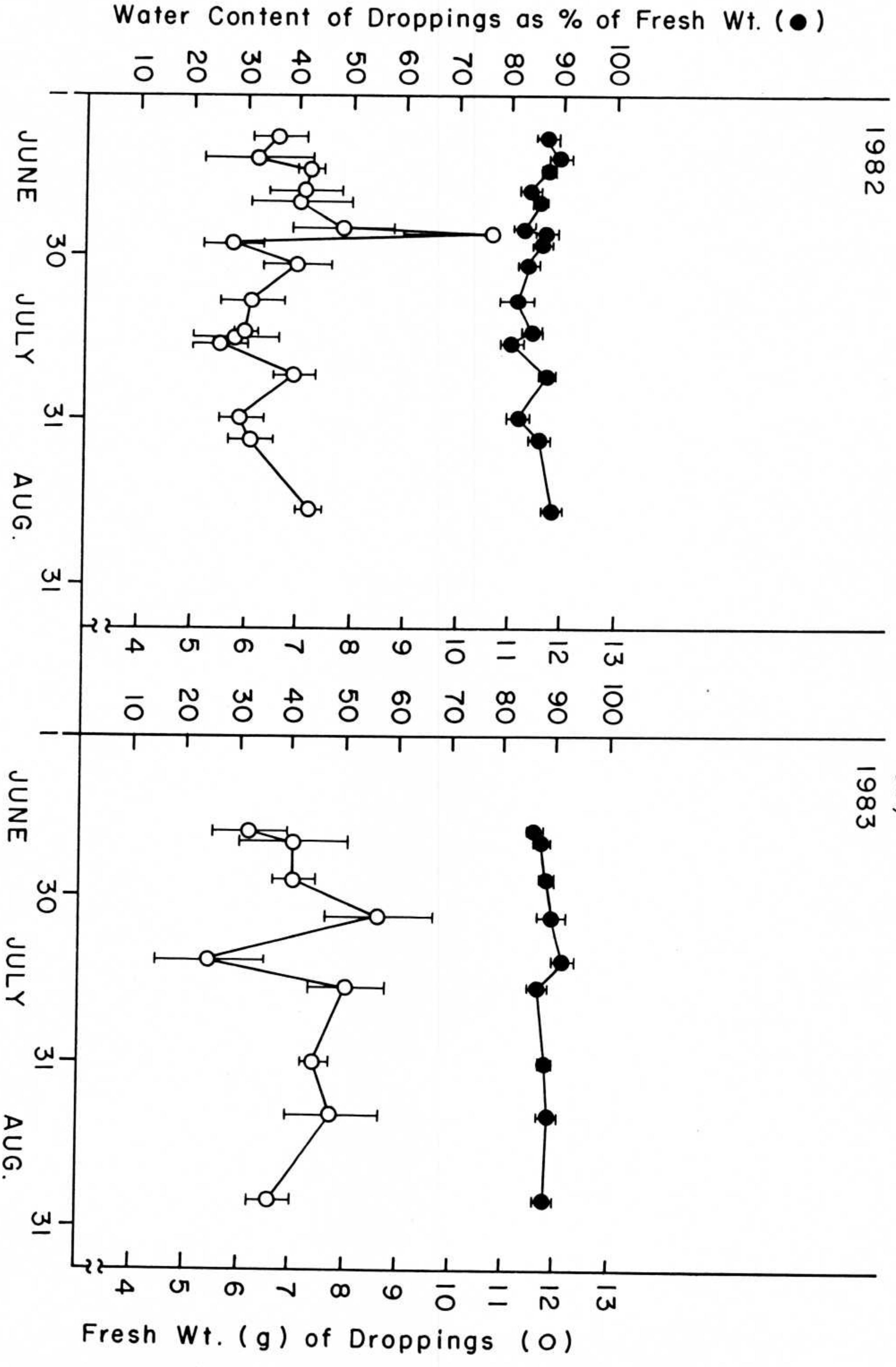
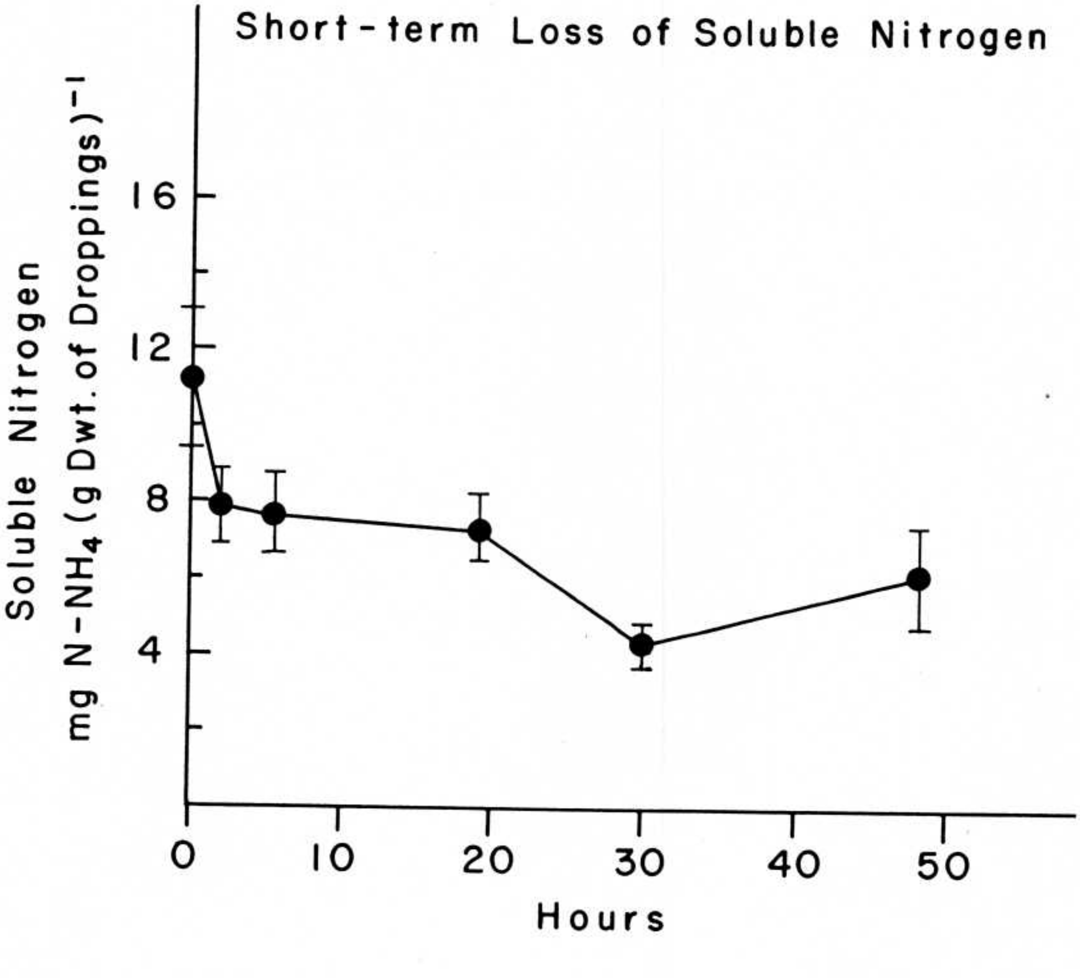

Water Content of Droppings as % of Fresh Wt. (●)
Fresh Wt. (g) of Droppings (○)
(a)
1982
(b)
1983
10
20
30
40
50
60
70
80
90
100
4
5
6
7
8
9
10
11
12
13
JUNE
30
JULY
31
AUG.
31

Figure 5-6. Decline in soluble nitrogen content (mg $N-NH_4$ per g dry weight of droppings) of fresh snow goose droppings during a 48 hour period at La Pérouse Bay, July 31, 1983. (Mean +/- S.E. n>/ = 8 for each sample point).


Short-term Loss of Soluble Nitrogen
Soluble Nitrogen
mg N-NH$_4$ (g Dwt. of Droppings)$^{-1}$
16
12
8
4
0
10
20
30
40
50
Hours

This loss amounted to 31% of the soluble nitrogen fraction. After 30 hours, 62% of the soluble nitrogen content had been lost from the droppings. After 48 hours, the soluble nitrogen content of the droppings was 6.1 mg N g dwt^{-1}, which was not a significant increase from 4.3 mg N g dwt^{-1} at 30 hours.

The rapid loss of water from fresh droppings is shown in Figure 5-7. After six hours, 22% of the water content of the droppings had been lost. There was a slight increase following showers, but by 30 hours, more than 50% of the water content had evaporated. However, following another period of showers, the water content of the droppings increased, so that only 18% of the initial water content appeared to have been lost. The mean fresh weight of the droppings collected at various times followed these trends. It dropped from 7.5 g to 4.0 g after 30 hours, as the percentage of water loss increased, and rose again to 7.0 g following the showers.

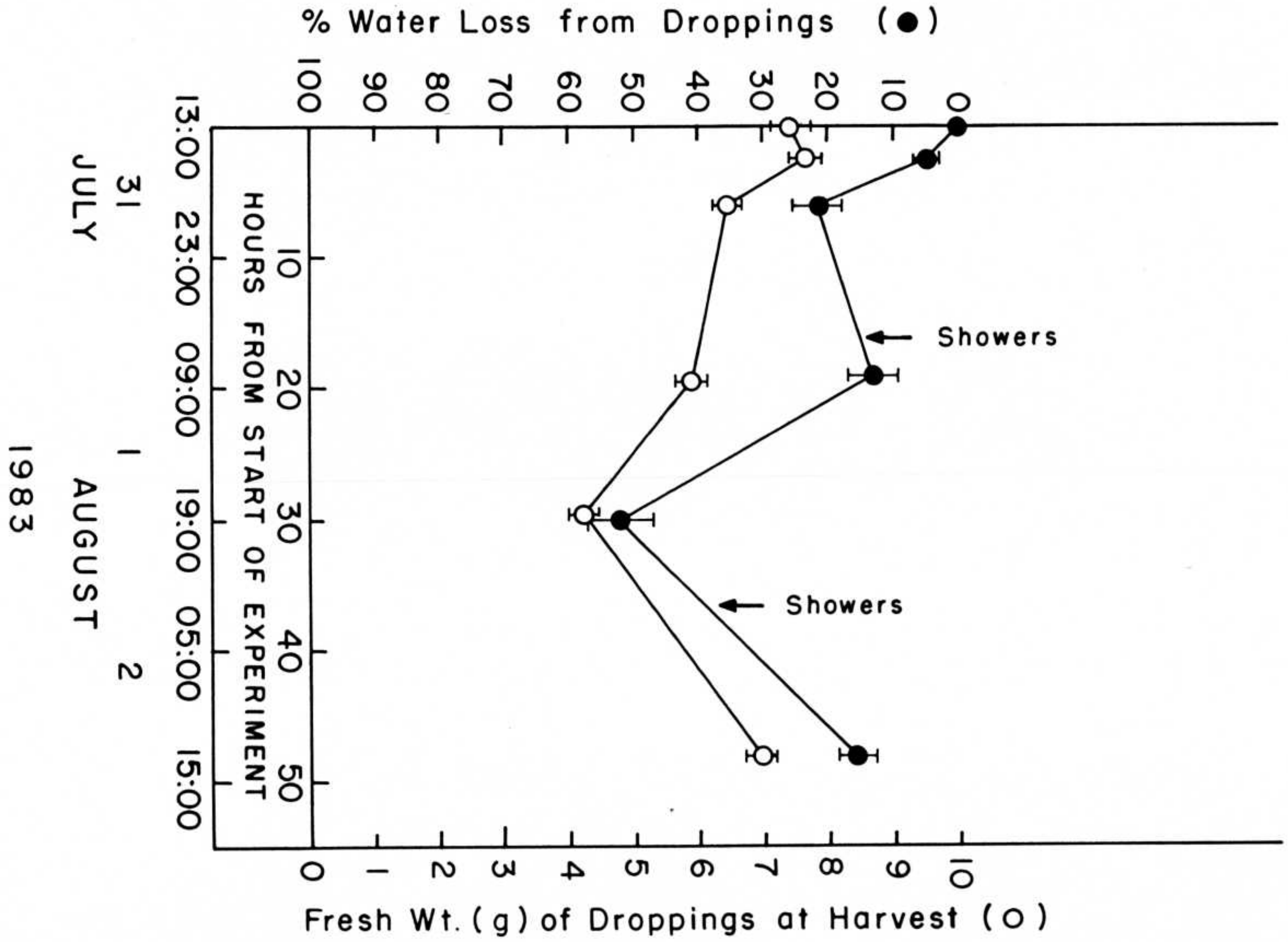
Observations made on the appearance of the droppings during this time indicated that although fresh weights were high after 48 hours, the colour of the droppings had changed from green to a dull brown-green.

5-3-3 Environmental Measurements and Concentrations of Exchangeable Ammonium Ions in the Sediments in Grazed and Ungrazed Areas

5-3-3a Soil Temperatures

Since a large amount of data was collected from exclosures ranging in age from zero to three years in 1982, only those from the one year-old exclosure have been plotted in Figure 5-8. On all sample dates, mean soil temperatures in grazed areas, at a depth of

Figure 5-7. Loss of water (●) as a percentage of the initial water content of fresh snow goose droppings, and fresh weight (o) in grammes of droppings harvested following their initial placement on the marsh, during a 48 hour period at La Pérouse Bay, July 31, 1983. (Mean +/- S.E. n = 10 for each sample point).


% Water Loss from Droppings (●)
0
10
20
30
40
50
60
70
80
90
100
Showers
Showers
13:00
23:00
09:00
19:00
05:00
15:00
10
20
30
40
50
HOURS FROM START OF EXPERIMENT
31
JULY
1
AUGUST
2
1983
0
1
2
3
4
5
6
7
8
9
10
Fresh Wt. (g) of Droppings at Harvest (O)

0.5 cm, were either equal to or higher than those in the exclosure. The difference ranged from 0 to 4°C. Soil temperatures were between 5 and 10°C in June at the beginning of the growing season and increased to 20-25°C on warm days in July and August. The trends in the soil temperatures followed those in air temperature in the summer of 1982. The differences in soil temperature between the grazed site and the one-year old exclosure were greatest on sunny days. On cloudy, cooler days, when the soil temperatures dropped, they were often equal at both sites.

Soil temperatures in both the one-year old exclosure and the adjacent grazed site, dropped at increasing soil depths (Table 5-2). Trends in soil temperature at depths of 5 cm tended to follow the trends observed in the top soil layer of a depth of 0.5 cm, and rose at the end of June and early July (Table 5-2). Temperatures were 0 to 2.7°C higher in the grazed area. At depths of 10 cm, no significant differences were observed between the grazed and ungrazed sites, and on some occasions temperatures were slightly higher in the exclosure.

Table 5-3 gives a summary of the temperatures observed at a depth of 0.5 cm in exclosures of different ages and in the adjacent grazed sites in 1982. The mean temperatures in the grazed and ungrazed areas were compared on each date on which they were measured, with t-tests, to determine whether they were significantly different. Temperatures were measured on only two occasions (in mid-June) in the three-year old exclosure. As in the one-year old exclosure, (Fig. 5-8), there was no significant difference between

Table 5-2. Soil temperatures in grazed and ungrazed sites at 0.5 cm, 5 cm and 10 cm soil depths at La Pérouse Bay, Manitoba, 1982. (n = 5).

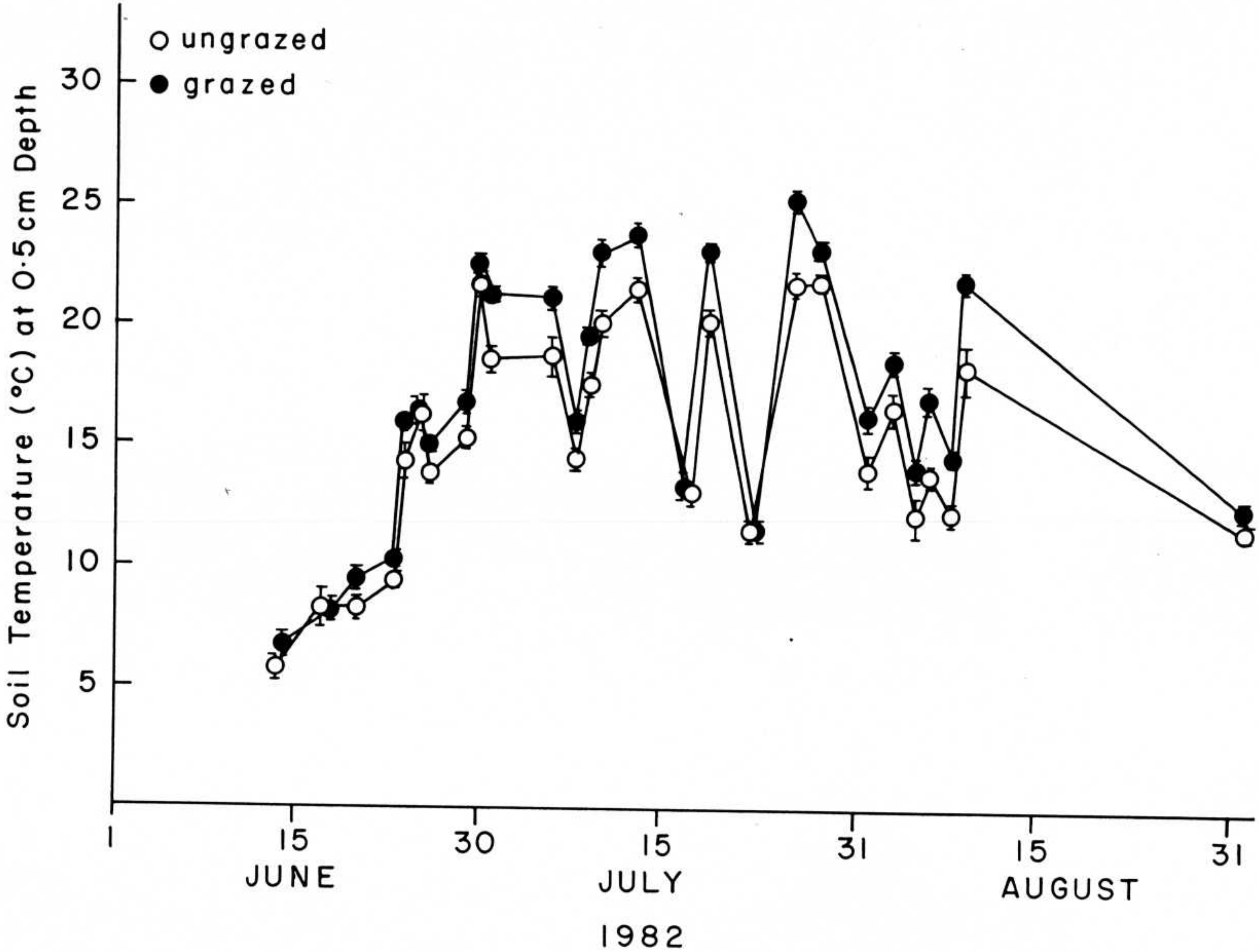
Date of Measurement	Mean temperature at 0.5 cm soil depth - °C			Mean temperature at 5 cm soil depth - °C			Mean temperature at 10 cm soil depth - °C		
	Exclosure	Grazed Site	Difference	Exclosure	Grazed Site	Difference	Exclosure	Grazed Site	Difference
June 24	14.4	15.9	1.5	12.2	13.0	0.8	9.2	9.0	0.2
June 25	16.1	16.4	0.4	14.0	14.1	0.1	11.2	10.7	0.5
June 30	21.8	22.4	0.6	18.2	18.3	0.1	14.2	13.5	0.7
July 09	17.6	19.5	1.9**	15.3	16.3	1.0**	12.5	13.0	0.5
July 19	20.2	23.3	3.1**	16.9	19.6	2.7**	14.7	15.6	0.9
August 01	14.0	16.3	2.3**	12.6	13.9	1.3**	11.5	11.6	0.1

** difference in means significant at $p \leq 0.05$, df = 8

Table 5-3. Maximum and minimum soil temperatures at a depth of 0.5 cm in exclosures of different ages and in adjacent grazed sites, and the number of days on which the temperatures were significantly higher in the grazed sites between 13 June and 2 September, 1982.

	Age of Exclosure - Years			
	0-1	1	2	3
maximum temperature observed in exclosure -°C	24.1	21.6	7.5	9.4
maximum temperature in grazed area - °C	25.5	23.7	9.5	9.6
Difference in temperatures and date of observation	1.4 12 Aug.	2.3 13 July	2.0 24 June	0.2 24 June
minimum temperature observed in exclosure - °C	4.9	4.8	2.1	3.0
minimum temperature in grazed area - °C	5.0	5.2	2.8	3.5
Difference in temperatures and date of observation	0.1 13 June	0.4 13 June	0.7 13 June	0.5 13 June
No. of days on which soil temperatures were measured	31	31	4	2
No of days on which the temperature was significantly greater in the grazed area (t - test $P < 0.05$)	10	18	3	0

Figure 5-8. Soil temperatures (°C) at 0.5 cm depth in a sward dominated by *Puccinellia phryganodes* left ungrazed for one year (O) and in the adjacent grazed (●) site at La Pérouse Bay, 1982. (Mean +/- S.E. n = 5).



○ ungrazed
● grazed
Soil Temperature (°C) at 0·5 cm Depth
30
25
20
15
10
5
1
15
30
15
31
15
31
JUNE
JULY
AUGUST
1982

the grazed and exclosure sites at this time. However, in the two-year old exclosure, which was measured on only four occasions, the soil temperature was significantly higher ($p \leq 0.05$, df = 8) on three occasions in mid-to-late June. In the one-year old exclosure, the temperature at a depth of 0.5 cm in the sediments was significantly higher in the grazed site ($p \leq 0.05$, df = 4 or 8), on 18 out of 34 days. These values are plotted in Figure 5-8. Measurements from seven of the 34 days were omitted from this diagram, in order to prevent points in late July and early August from becoming indistinguishable from each other. By comparison with the one-year old exclosure, there were fewer days on which the temperature at 0.5 cm was significantly greater in the grazed site than in the exclosure built in 1982, which was not yet one season old. On no occasions were the temperatures at a depth of 10 cm, significantly greater in the grazed sites compared with those in the ungrazed sites at the same depth.

In 1983, similar trends were recorded in June and July, in that the mean temperatures of the sediments at 0.5 cm and 5 cm depths were significantly higher in grazed sites than in the adjacent three-year old exclosure (Table 5-4). A t-test was used to compare the means from the grazed and ungrazed sites. Unlike the 1982 result there was a highly significant difference of 2°C ($p \leq 0.01$ df = 8), between the temperatures at 10 cm depths in the grazed site and in the three-year old exclosure on July 6. However, in 1982, the exclosure measured was only one year in age, while in 1983 a three-year old exclosure was measured.

Table 5-4. Mean soil temperatures at depths of 0.5, 5 and 10 cm in a three year old exclosure and in the adjacent grazed area, at La Pérouse Bay, Manitoba, 1983. (n = 5).

	Soil Temperature - °C					
Soil Depth	Exclosure (Ungrazed site)			Grazed Site		
Date	0.5 cm	5 cm	10 cm	0.5 cm	5 cm	10 cm
June 20	2.0	-*	-*	7.5	4.5	-*
June 29	14.3	11.1	-	17.8	16.2	-
July 06	13.7	-	8.0	16.8	-	10.0
July 13	10.0	-	-	11.3	-	-
July 15	13.7	7.8	-	14.8	11.1	-
July 25	16.4	-	-	18.4	-	-

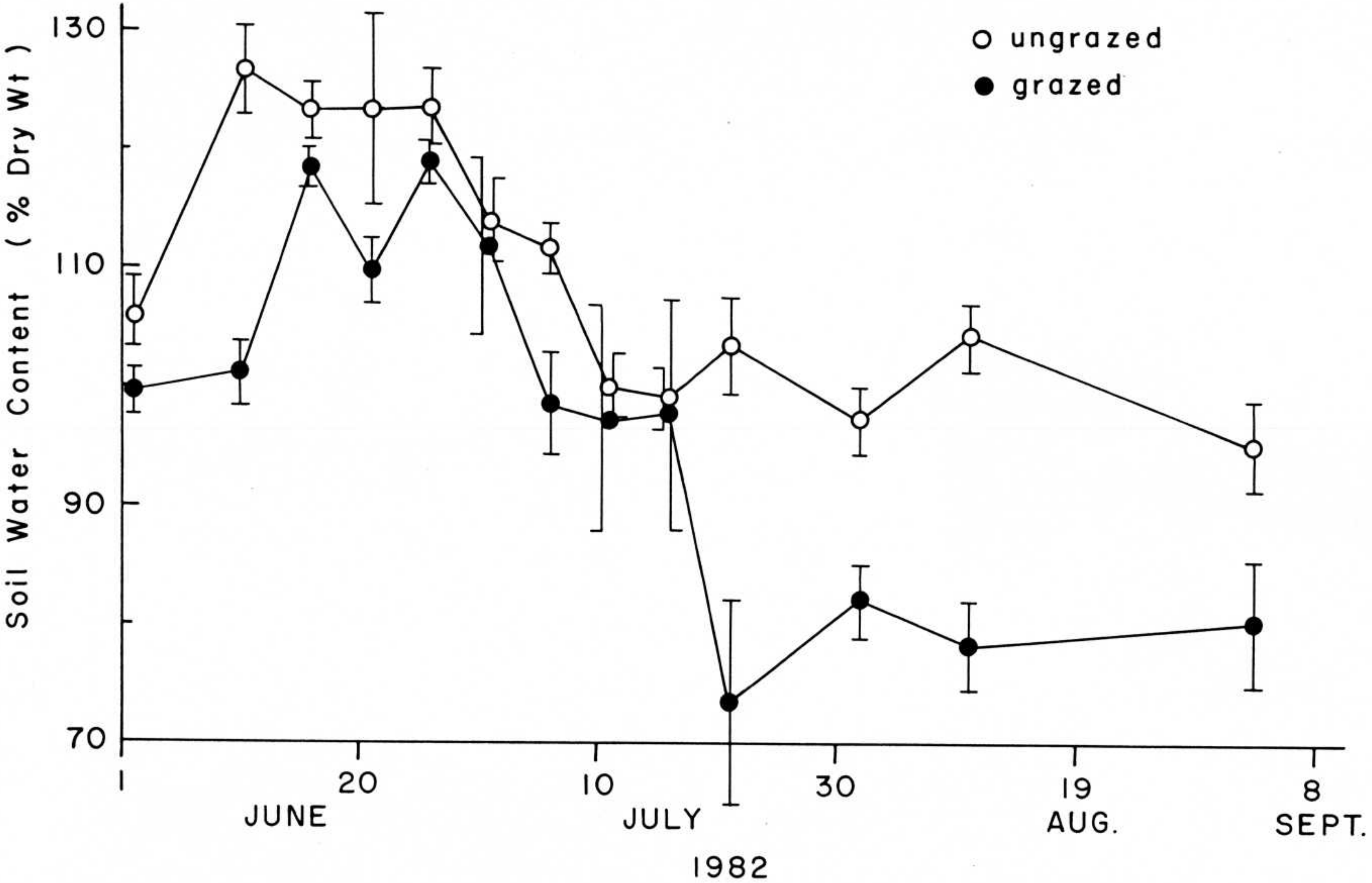
* Frozen Sediments

5-3-3 b Soil Water Content, Salinity and Conductivity

Figure 5-9 shows the soil water content as a percentage of sediment dry weight in a one-year old exclosure, and in the adjacent grazed area, during the summer of 1982. The soil water content was consistently higher in the ungrazed area, fluctuating around 125% g dwt^{-1} from June 10 to June 26, after rising from 105% g dwt^{-1} on May 31. In the grazed site, the water content ranged between 100% g dwt^{-1} and 120% g dwt^{-1} during this period. During late June and early July, there was a spell of warm weather, with daily maximum temperatures reaching 18 to 24°C. At this time, soil water content dropped to 100% g dwt^{-1} in both grazed and ungrazed sites. It stayed at this level in the exclosure for the remainder of the summer, but dropped to about 80% g dwt^{-1} in the grazed site.

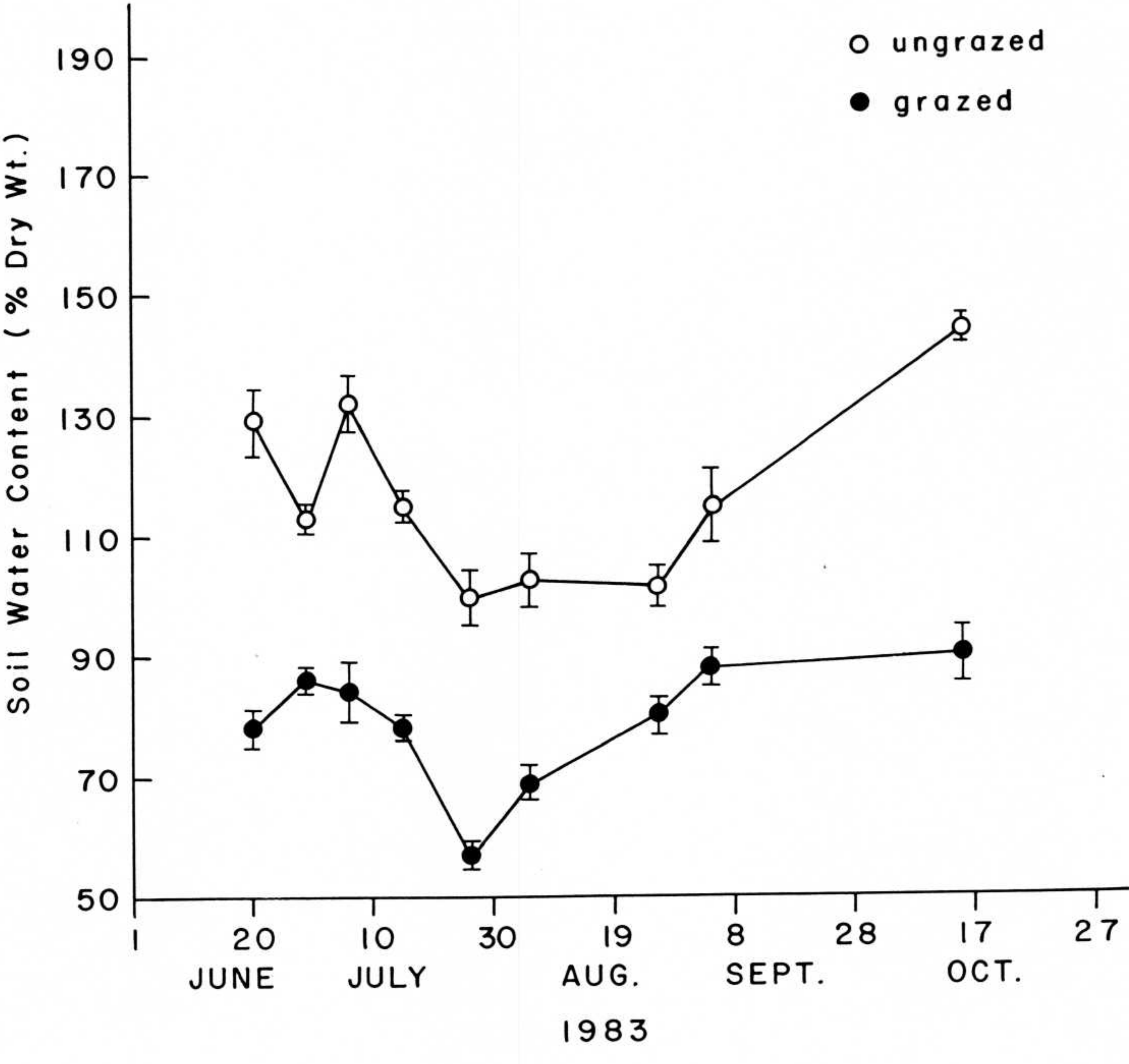
In 1983, the soil water content was consistently higher in a three year-old exclosure than in a grazed site approximately 50 m away (Fig. 5-10). In the exclosure, it was initially 129% g dwt^{-1} on June 20, and by the end of July, it dropped to approximately 100% g dwt^{-1}. At the end of August, the soil water content rose in the ungrazed area, and reached a level of 144% g dwt^{-1} by October 15. The drop in soil water content in early July, coincided with a spell of hot weather, when daily maxima were as high as 25°C. The months of September and October were exceptionally wet in 1983. For example, in early September 1983, there were flood warnings in Churchill, following two days of heavy rain.

Figure 5-9. Soil water content (% of dry weight) in sediments beneath a sward dominated by *Puccinellia phryganodes* left ungrazed for one year (O) and in the adjacent grazed (●) site at La Pérouse Bay, 1982. (Mean +/- S.E. n = 4).



Soil Water Content (% Dry Wt)
130
110
90
70
○ ungrazed
● grazed
1
20
10
30
19
8
JUNE
JULY
AUG.
SEPT.
1982

Figure 5-10. Soil water content (% of dry weight) in sediments beneath a sward dominated by Puccinellia phryganodes left ungrazed for three years (O) and in the adjacent grazed (●) site at La Pérouse Bay, 1983. (Mean +/- S.E. n = 4).



○ ungrazed
● grazed
Soil Water Content (% Dry Wt.)
190
170
150
130
110
90
70
50
1
20
10
30
19
8
28
17
27
JUNE
JULY
AUG.
SEPT.
OCT.
1983

In the grazed site, soil water content fluctuated around 80% g dwt^{-1} in late June and early July and dropped to 57% g dwt^{-1} in late July, during the warm weather. It started to rise in August, and reached 90% g dwt^{-1} in September and October.

The trends in soil water content in the three year old exclosure during the summer of 1983 were similar to those in the one year old exclosure in 1982. However, the levels of soil water content were much lower in the grazed site in 1983 than in 1982.

Table 5-5 shows soil water content values obtained from various locations in La Pérouse Bay during the thaw in June 1983 and the period which immediately followed. Values were as high as 488% g dwt^{-1}, indicating the high degree of saturation at this time, particularly in the top 2 cm of the sediment. In many of these sites there was up to 5 cm of standing water for two to three days following the initial thaw. The early summer values for the soil water content of grazed Puccinellia areas were higher than those observed on June 20 (Fig. 5-10). Observations made on soil profiles, indicated that there was more organic matter in the exclosures and in the Puccinellia sites further inland, compared with the grazed sites. Therefore the water in the sediments of grazed areas may have drained faster following thaw, due to the lower retention capacity, while the organic matter in the other sites may have caused higher amounts of water to be retained.

Table 5-5. Soil water content as a percentage of dry weight from various sites at La Pérouse Bay, Manitoba, at thaw, 1983. (n = minimum of 3).

DATE	SITE	DEPTH OF SOIL (cm)	SOIL WATER CONTENT (% g Dwt Soil)
June 07	*Puccinellia* sward in high willow area	0-2 0-5	488 269
June 11	*Puccinellia* sward in low willow area	0-5	233
June 11	Grazed *Puccinellia* area on salt marsh flats near Mast River	0-5 0-5	131 138
June 12	*Puccinellia* sward in low willow area	0-2 2-5 5-8	336 149 161
June 17	Grazed *Puccinellia* swards on salt marsh flats on east side of La Pérouse Bay	0-5	131

Table 5-6 shows the salinity and conductivity of the soil water of a one year old exclosure and of the adjacent grazed area in 1982. Salinity, measured in parts per thousand (ppt), was initially low in both the grazed and ungrazed sites. As temperatures increased in late June and early July, the salinity increased from one to three ppt at both sites. Values in grazed areas were consistantly higher than corresponding salinity levels in the exclosure.

The trends in conductivity of soil water followed a similar pattern, with the lowest values being recorded in June and the highest values of 18.9 and 10.9 mS occurring in mid-July and August in grazed sites. Conductivity was consistently higher in the grazed site, except for July 10, when a value of 5.2 mS was recorded in both sites. This followed a day of extremely wet weather on July 7, 1982.

Table 5-6. Salinity (parts per thousand) and conductivity ($\mu S \times 10^3$) of soil water in a one year old exclosure and in the adjacent grazed site at La Pérouse Bay, 1982.

DATE	SALINITY - (ppt)		CONDUCTIVITY-($\mu S \times 10^3$)	
	Grazed Site	Ungrazed Site	Grazed Site	Ungrazed Site
June 09	-	-	4.1	2.4
June 30	<1.0	1.1	7.0	1.95
July 02	2.5	0.9	4.2	1.25
July 05	4.5	3.0	6.9	4.7
July 10	3.5	3.2	5.2	5.2
July 15	14.5	4.5	18.9	6.5
July 20	7.2	2.1	10.9	3.5
August 02	6.0	2.9	8.0	4.25
August 11	8.6	2.1	11.8	3.35

5-3-3 c Soil Redox Potential in Grazed and Ungrazed Areas

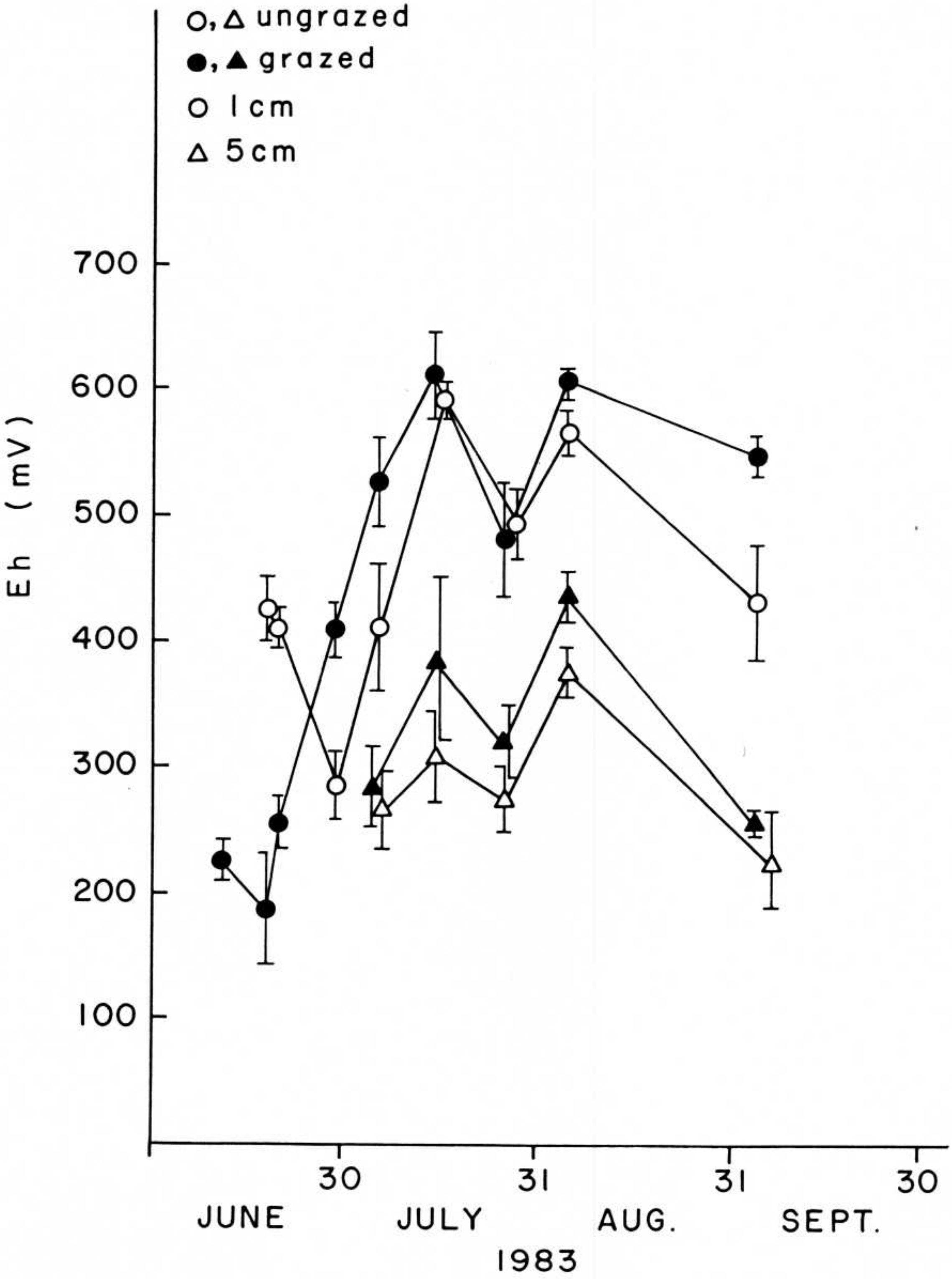
Figure 5-11 shows the redox potential (Eh) in the same sites in which soil water content was measured in 1983. At a 1 cm depth, Eh was initially lower in the grazed site; it fluctuated around 200 mV in early to mid-June. In the three-year old exclosure it was 412 mV on June 20. However, by the end of June 1983, the level of Eh in the ungrazed site had dropped to 290 mV, while in the grazed site, Eh rose to 400 mV. Thereafter, levels of Eh increased in both sites, and reached a peak of 600 mV on July 15. After this date, they fluctuated around 550 mV in both grazed and ungrazed sites. Levels of Eh tended to be lower in the exclosure, or equal to those in grazed sites indicating that the former was in general, a more reduced site. In September, the Eh in the exclosure, dropped to 430 mV, compared with an Eh of 550 mV in the grazed site.

Levels of Eh at a depth of 5 cm in the sediments, were consistently higher in the grazed site than in the exclosure. They fluctuated between 200 mV and 450 mV. The trends followed those observed at the 1 cm depth.

The rapid rise in Eh in the grazed site in late June and early July, coincided with the drop in soil water content at this time (Fig. 5-10), while the drop in Eh in August in the exclosure occurred at the same time as the soil water content increased at this site.

The Eh measurements made in the field and in the field station

Figure 5-11. Soil Eh (mV) at 1 cm (O,●) and 5 cm (△,▲) depths, in a sward dominated by *Puccinellia phryganodes* left ungrazed for three years (O,△), and in the adjacent grazed site (●,▲), at La Pérouse Bay, 1983. (Mean +/- S.E. n = 5).


○, △ ungrazed
●, ▲ grazed
○ 1cm
△ 5cm
Eh (mV)
700
600
500
400
300
200
100
30
31
31
30
JUNE
JULY
AUG.
SEPT.
1983

on June 20 were similar. This indicates redox potential did not change in sediment blocks cut in the field and transported to the field station for measurement.

Table 5-7 shows a range of Eh measurements taken in the marsh in 1982, just after thaw. Eh of the sediments varied, depending upon the site and the degree of water-logging. The most oxidized site, with an Eh of 610 mV was a grazed Puccinellia sward on a hummock at a higher level than the adjacent flooded flats. The most reduced site was a Puccinellia area in the low willows to the west of the Mast River on which algal mats from the small ponds and streams had been deposited. The Eh of this site was only 24 mV. Eh was lower at the wetter sites, and the grazed site from which the measurements plotted in Figure 5-11 were taken, was in this category.

5-3-3 d Rates of Mineralization of Nitrate and Ammonium and Background Levels of Ammonium and Nitrate in Sediments of Grazed and Ungrazed Areas

There were no detectable levels of nitrate (NO_3^-) in the frozen soil water samples and the potassium chloride extracts which were analysed at both La Pérouse Bay and Toronto. Since nitrate tends to

Table 5-7. Eh measurements taken at various locations in La Perouse Bay, 1983. (n = 3 or 5; calomel electrode: Eh = E + 250 mV).

DATE	SITE	DEPTH OF SOIL MEASURED (cm)	Eh (mV)
June 07	*Puccinellia* sward in high willow area	1	200
		3	218
June 10	Grazed *Puccinellia* sward on hummock that was above melt water	1	610
		3	583
June 11	Grazed *Puccinellia* sward on flats under 4 cm of melt water	0.5	190
		2	188
June 12	*Carex* sward in low willows - unflooded	0.5	473
		2	402
June 12	Algal mat on sediment in low willow area	1	24

be present in the soil solution, rather than being held on exchange sites of the soil matrix (Brady, 1974; Atlas and Bartha, 1981), any detectable nitrate present should have been found in the soil water.

The predicted accumulation of exchangeable ammonium ions in the sawn-off syringe tubes was not observed in 1982 (Figure 5-12). In incubation series one, for example, KCl- exchangeable ammonium in ungrazed sites increased during the first ten days; and then dropped during the next ten days, from 127 μg N-NH4 (g dwt soil)$^{-1}$ to 48 μg N-NH_4 (g dwt soil)$^{-1}$. Similar fluctuations were observed for all of the incubations. It is possible that ammonium ions produced by ammonification were either taken up by plant roots and micro-organisms within the soil core, or were lost to the atmosphere by volatilization and denitrification. In any event, these data were insufficient to calculate rates of ammonification. Rates of nitrification could not be calculated because of the lack of accumulation of nitrate ions within these soil areas.

The background levels of KCl-exchangeable ammonium ions in frozen soil blocks which were transported to Toronto were in the order of 20 to 120 μg N-NH_4 (g dwt soil)$^{-1}$. The levels of ammonium ions in the duplicate potassium chloride extractions carried out at La Pérouse Bay in 1982, immediately following their collection, were in the range of 3 to 20 μg N-NH4 (g dwt soil)$^{-1}$. Thus, it was apparent that changes had occurred in either the frozen KCl extracts or the frozen soil samples causing a difference of almost an order of magnitude in the two sets of results. There may have been loss of nitrogen from the KCl extracts, or there may have been microbial

Figure 5-12. Levels of KCl - exchangeable ammonium ions (μg N-NH_4 per g dry weight of soil) in sediments beneath a sward dominated by Puccinellia phryganodes left ungrazed for one year (O) and in the adjacent grazed (●) site, during the course of four, thirty day incubation periods at La Pérouse Bay, 1982.

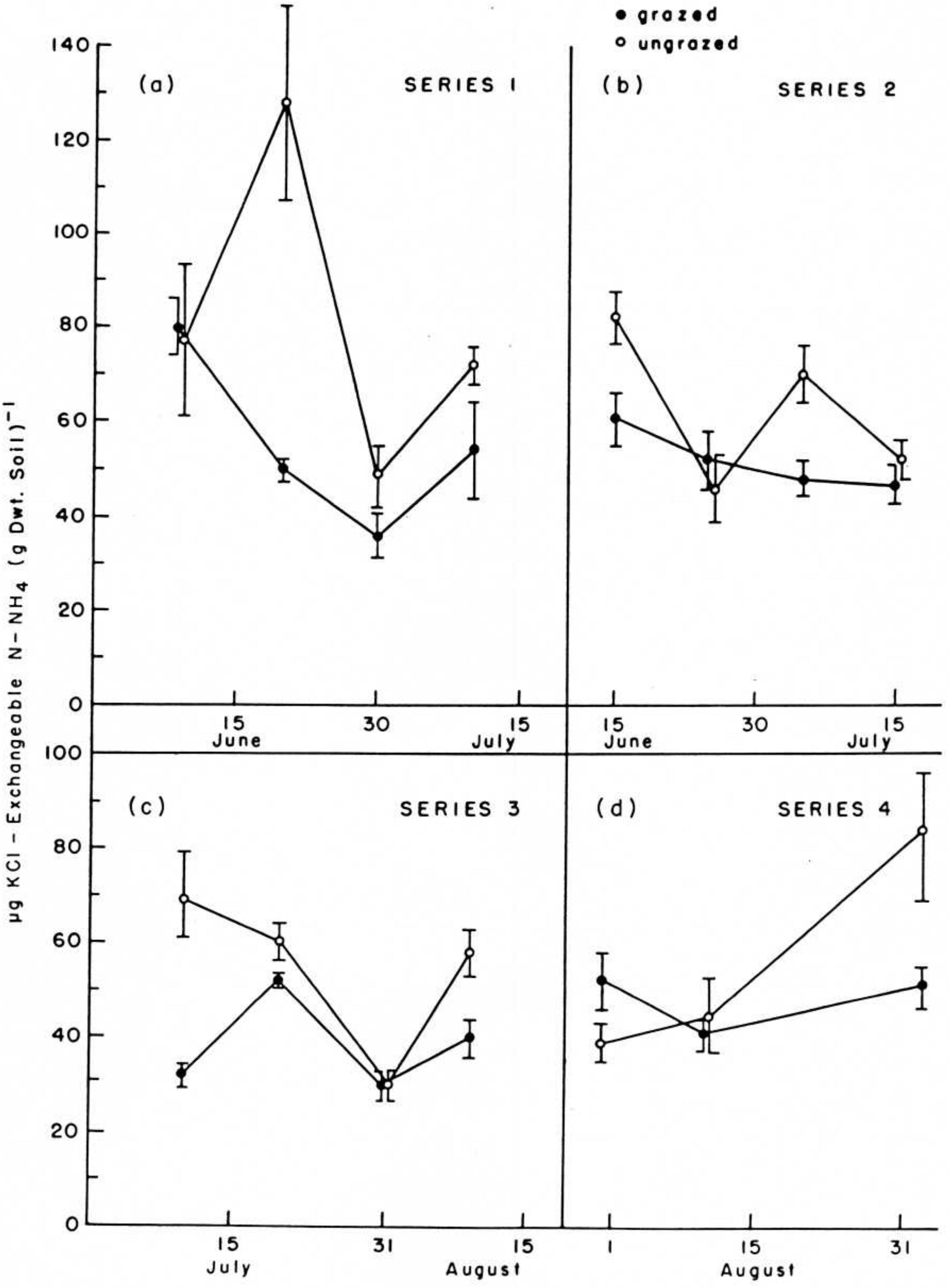
(a) Incubation series one, commenced June 10, 1982.

(b) Incubation series two, commenced June 15, 1982.

(c) Incubation series three, commenced July 10, 1982.

(d) Incubation series four, commenced July

(Mean +/- S.E. n = 6).


● grazed
○ ungrazed
μg KCl - Exchangeable N-NH_4 (g Dwt. Soil)$^{-1}$
(a)
SERIES 1
(b)
SERIES 2
(c)
SERIES 3
(d)
SERIES 4
140
120
100
80
60
40
20
0
15
June
30
15
July
15
June
30
15
July
100
80
60
40
20
0
15
July
31
15
August
1
15
31
August

activity in the soil samples, resulting in the mineralization of organic matter, particularly as they were not always frozen solid, due to inadequate freezing facilities at the field station.

Results from 1983, in which extracts were immediately analysed for their KCl-exchangeable ammonium content, indicated that the results obtained in 1982 from the frozen KCl extracts transported to Toronto for analysis were of a similar magnitude. Therefore, the latter are presented in Figure 5-13a. In mid-June, 1982, more than two weeks after the final snow melt, KCl-exchangeable ammonium levels were 10 μg N-NH_4 (g dwt soil)$^{-1}$, (abbreviated to 10 μg NH_4 g dwt^{-1}). Levels in both sites fluctuated around 5 μg NH_4 g dwt^{-1} until July 10, after which time they increased, reaching 14.2 μg NH_4 g dwt^{-1} in the grazed site, and 19.3 μg NH_4 g dwt^{-1} in the exclosure, on August 9. In June and early July, KCl-exchangeable ammonium levels were similar in the sediments of both grazed and ungrazed sites. However, on August 9, they were significantly different ($p \leq 0.01$, df = 7); the concentrations of ammonium ions were higher in the exclosure.

In 1983, initial values of KCl-exchangeable amonium ions were significantly higher in the grazed site, at 13 μg NH_4 g dwt^{-1}, compared with 1.3 μg NH_4 g dwt^{-1} in the sediments of the three year old exclosure (Fig. 5-13b). By late June, ammonium levels fell in the grazed site, and until the middle of October, they fluctuated between 1 and 6 μg NH_4 dwt^{-1} in both grazed and ungrazed sites. As in 1982, the concentration of ammonium ions was consistently higher in the ungrazed site, and in 1983, on July 26 and September 9, these

Figure 5-13 a. Seasonal trends in background levels of KCl - exchangeable ammonium ions (μg N-NH_4 per g weight of soil) in sediments beneath swards dominated by Puccinellia phryganodes left ungrazed for one year (O) and in the adjacent grazed (●) site at La Pérouse Bay, 1982. (Mean +/- S.E. n = 5).

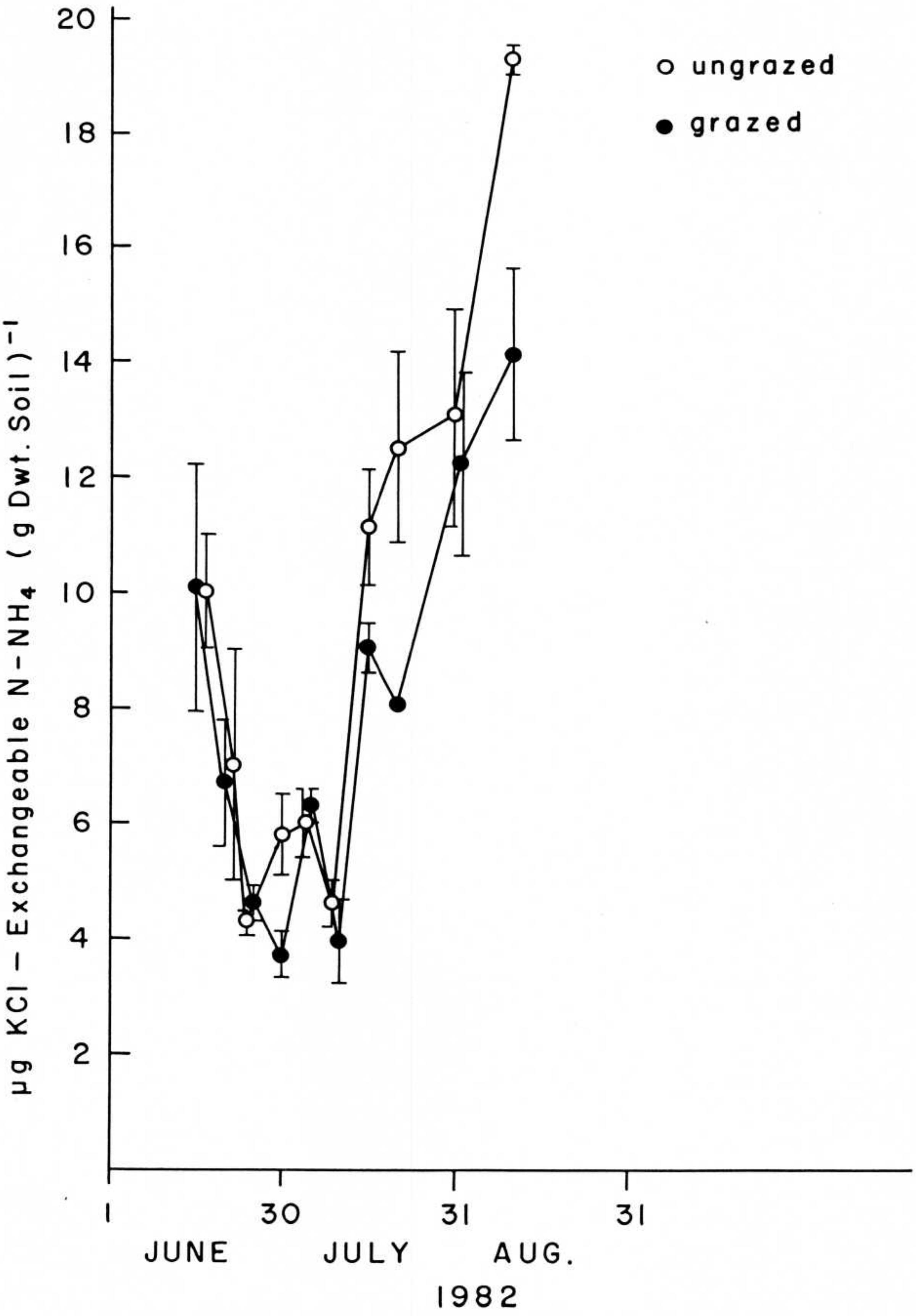
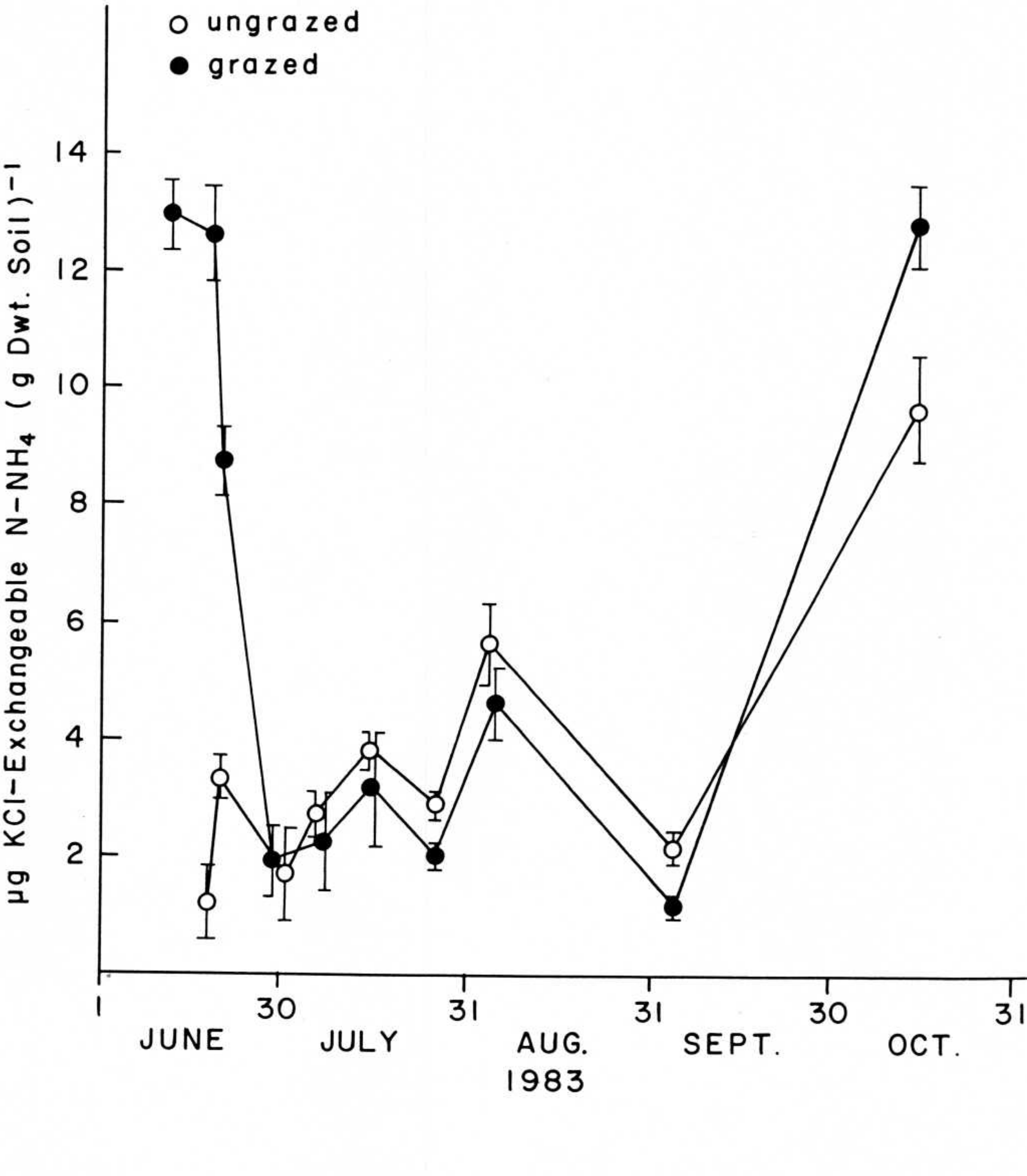

µg KCl – Exchangeable N-NH₄ (g Dwt. Soil)⁻¹
20
18
16
14
12
10
8
6
4
2
1
30
31
31
JUNE
JULY
AUG.
1982
o ungrazed
● grazed

Figure 5-13 b. Seasonal trends in background levels of KCl - exchangeable ammonium ions (µg N-NH_4 per g dry weight of soil) in sediments beneath swards dominated by <u>Puccinellia phryganodes</u> left ungrazed for three years (O) and in the adjacent grazed site (●) at La Pérouse Bay, 1983. (Mean +/- S.E. n = 5).



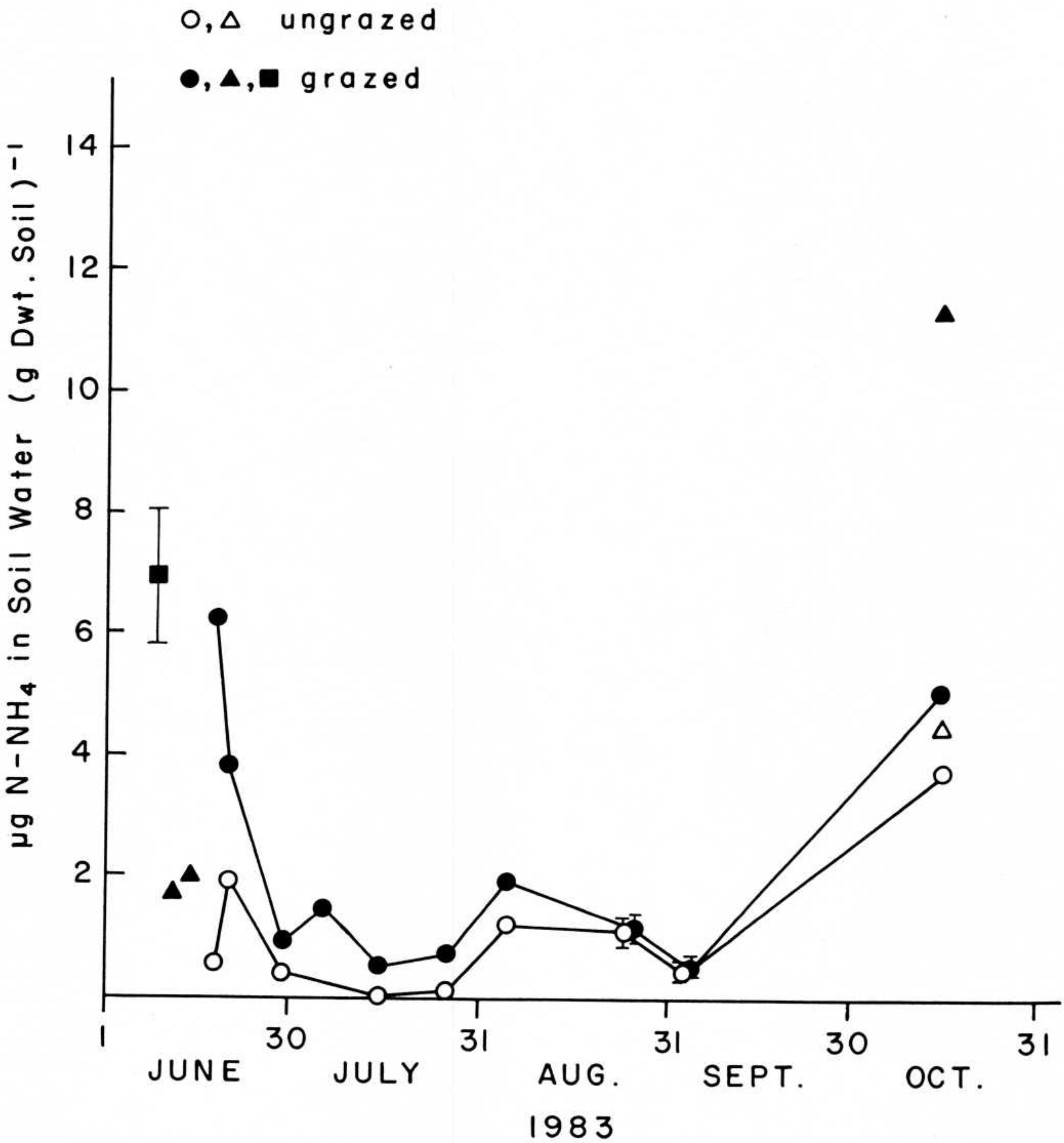
○ ungrazed
● grazed
μg KCl-Exchangeable N-NH$_4$ (g Dwt. Soil)$^{-1}$
14
12
10
8
6
4
2
1
30
31
31
30
31
JUNE
JULY
AUG.
SEPT.
OCT.
1983

differences were significant ($p \leq 0.01$ df = 8). By October 15, the ammonium levels had increased to 12.8 μg NH_4 g dwt^{-1} in the grazed site and 9.6 μg NH_4 g dwt^{-1} in the exclosure ($p \leq 0.10$, df = 8). Thus, concentrations of KCl-exchangeable ammonium ions were significantly higher in the grazed site immediately after snowmelt and just before freeze-up, which occurred in November, 1983.

Concentrations of ammonium ions were not measured throughout the summer of 1982, so the early and late season rises recorded in 1983 were not detected. However, soon after thaw, during both summers, ammonium levels were similar; they ranged between 2 and 6 μg NH_4 g dwt^{-1} immediately after melt. The amounts increased in the exclosures in late July and early August. However the increase was much greater in 1982.

Figure 5-14 shows the concentrations of ammonium ions in the soil water in grazed and ungrazed sites in 1983. The results from 1982 were not presented, because, like the soil blocks, they were not continually frozen before analysis in Toronto. In the three-year old exclosure, ammonium levels in soil water fluctuated between 0 and 2 μg N-NH_4 (g dwt $soil)^{-1}$ between June and September. In the soil water of the nearby grazed areas, initial concentrations of ammonium ions were 4 to 6 μg NH_4 g dwt^{-1}. They dropped in late June and subsequently fluctuated in the same range as those in the ungrazed exclosure, from 0.5 to 2 μg N-NH_4 g dwt^{-1}. The levels of ammonium ions in soil water were consistently higher in the grazed area. In October, these levels increased again, and reach 5 μg NH_4 g dwt^{-1} in the grazed site, compared with 3.75 μg NH_4 dwt^{-1} in the

Figure 5-14. Seasonal trends in the background levels of ammonium ions in the soil water of sediments (μg N-NH_4 per g dry weight of soil) beneath swards dominated by <u>Puccinellia phryganodes</u> left ungrazed for three years (O) or one year (Δ) and in the adjacent (●,▲) and other (■) grazed sites at La Pérouse Bay, 1983. (Where mean is +/- S.E., n = 3, otherwise n = 2).


○, △ ungrazed
●, ▲, ■ grazed
μg N-NH₄ in Soil Water (g Dwt. Soil)⁻¹
14
12
10
8
6
4
2
1
30
31
31
30
31
JUNE
JULY
AUG.
SEPT.
OCT.
1983

exclosure. The point values in Figure 5-14 without standard error bars were based on sample sizes of $n = 1$ in late June and early July, and on sample sizes of $n = 2$ on all other dates. Thus, in most cases, statistical comparisons could not be made.

In other grazed sites in the marsh, levels of ammonium ions in soil water varied from 1.5 to 7 $\mu g\ NH_4\ g\ dwt^{-1}$ in early June. Measurements made in a grazed site and in a one year old exclosure on October 15, 1983, indicated that the ammonium levels were much higher in the grazed site, reaching 11.2 $\mu g\ NH_4\ g\ dwt^{-1}$, compared with 4.4 $\mu g\ NH_4\ g\ dwt^{-1}$ in the ungrazed site.

The trends in the concentrations of ammonium ions in soil water followed the trends of the concentrationof KCl-exchangeable ammonium ions (Fig. 5-13b). Levels of ammonium ions were higher in grazed sites just after thaw, and they subsequently dropped, until October, when their concentrations increased in both grazed and ungrazed sites.

5-4 DISCUSSION

The results indicate that the first two hypotheses stated in the introduction (5-1) should be accepted. Nitrogen fixation and nitrogenase activity, reflected by rates of acetylene reduction were greater at grazed sites on all occasions. Also, the addition of fresh snow goose droppings to exclosed plots brought about an increase in live biomass. The third hypothesis, which consisted of three parts was ultimately not tested in its entirety, and cannot be fully accepted. The soil environment in ungrazed sites was cooler, but, since mineralization rates were not determined, no conclusion may be drawn as to the effects of temperature on rates of mineralization. However, the environmental data collected were useful in assessing the potential limitations on nitrogen fixation and rates of mineralization in grazed and ungrazed sites.

The acetylene reducting activity (ARA) data may be converted into apparent rates of nitrogen fixation. The ARA rate, expressed as moles, is divided by three to yield moles of dinitrogen fixed. This conversion is based on the assumption that for every three moles of acetylene reduced, one mole of dinitrogen is fixed (Stewart, Fitzgerald and Burris, 1967). The reduction of one molecule of dinitrogen (N_2) which results in the production of two molecules of ammonia (NH_3) requires the transfer of six electrons, while that of one acetylene molecule (C_2H_2) requires two electrons, to produce one molecule of ethylene (C_2H_4) (Stewart, Fitzgerald and

Burris, 1967). Acetylene is a structural analogue of dinitrogen (Postgate, 1982). Each molecule possesses a pair of triple bonded atoms, and this similarity is believed to be the reason why nitrogenase acts on both molecules (Postgate, 1982).

Although the conversion described above was calculated, and has been included in Figure 5-1 in the results, the apparent rates of nitrogen fixation cannot be accepted without question. Researchers, comparing rates of nitrogen fixation obtained with acetylene reduction techniques with those rates obtained from the use of N^{15}, have found ratios varying from 1.5 to 15 moles of acetylene reduced per mole of dinitrogen fixed (Stewart, Fitzgerald and Burris, 1967; Bergersen, 1970; Postgate, 1982). Since tests with N^{15} were not carried out at La Pérouse Bay, the 3:1 ratio was used, in order to make comparisions with results from other studies if necessary.

The ARA and apparent rates of nitrogen fixation in grazed sites observed at La Pérouse Bay were considerably higher than those found in high arctic sites (Stutz, 1977; Alexander, Billington and Schell, 1978; Jordan, McNicol and Marshall, 1978). They appeared to be in the same range as those observed in algal mats in a sub-arctic mire in Sweden (Granhall and Selander, 1973) and in the mid to lower end of the range of values found in more temperate salt marshes in Nova Scotia and Massachusetts (Carpenter, Van Raalte and Valiela, 1978; Patriquin and Keddy, 1978; Patriquin and McClung, 1978; Smith, McLachland and Patriquin, 1979).

Rates of acetylene reduction fluctuated between 0.46 and 2.41 μmoles of C_2H_2 reduced m^{-1} hr^{-1} at a wet meadow site at Barrow, Alaska, between June 25 and August 14, 1971 (Alexander, Billington and Schell, 1978). In 1972, the highest ARA was found in wet ice polygon troughs and marshy areas, and the rates of reduction reached 10.5 µmoles C_2H_2 reduced $m^{-2}hr^{-1}$ in August (Alexander, Billington and Schell, 1978). The lowest ARA was in dry areas of high-centred ice polygons. ARA appeared to be influenced by temperature and moisture, and in 1973, the highest rates of reduction were observed on days when clear skies and warmer temperatures, up to 12°C prevailed (Alexander, Billington and Schell, 1978). The highest ARA value observed in three years was 21 µmoles C_2H_2 reduced m^{-2} hr^{-1} on June 30, 1973 at a site of intermediate moisture.

At Truelove Lowland in the high Arctic, maximum ARA values were lower than those found at Barrow. The highest rate of reduction observed by Stutz (1977) was 7.53 µmoles C_2H_2 reduced m^{-2} hr^{-1} on July 10, 1971, in wet meadow soil. In mesic meadow soil, mean rates of 11.4 µmoles C_2H_2 reduced m^{-2} hr^{-1} were observed in 1976 (Jordan, McNicol and Marshall, 1978). Both these values and those found at Barrow are much lower than the minimum ARA values observed in grazed sites at La Pérouse Bay, which were above 40 µmoles C_2H_2 reduced m^{-2} hr^{-1} (Fig. 5-1). However, the lower values observed in exclosures were in the range of 3.2 to 12.1 µmoles C_2H_2 reduced m^{-2} hr^{-1}. During the three-day period preceeding July 11, 1983, when ARA reached 74 and 177 µmoles C_2H_2 reduced m^{-2} hr^{-1} in exclosures and grazed sites respectively, daily maximum temperatures were above 24°C, and on July 11, the high was 21°C. The increase in ARA at La Pérouse Bay between July 21 and July 24, 1983 also coincided with a warm spell of above 20°C temperatures beginning on July 21. Thus, at La Pérouse Bay, as at Barrow, warmer temperatures appear to influence rates of nitrogenase activity.

At the sub-artic, ombrotorphic mire at Stordalen, Sweden (68°N), the greatest ARA was found in moss samples from wet depressions (Granhall and Selander, 1973). ARA reached 2.7 µmoles C_2H_2 reduced g^{-1} dwt of moss hr^{-1}. Unfortunately, these rates cannot be compared with those from La Pérouse Bay as they are expressed in different units. However, Granhall and Selander (1973) also measured ARA in algal mats, dominated by Nostoc species, and found values of up to 120 µmoles C_2H_2 reduced m^{-2} of algal mat hr^{-1}, which was greater than the lower end of the range of values observed in grazed sites.

It should be noted that the rates of reduction given above are representative of the soil surface rather than the below-ground sediments. Patriquin and McClung (1978) found large differences between ARA of surface soil samples cut to a depth of 0.3 cm and soil cores cut to depths of 20 to 30 cm. Reasons for these differences will be discussed later, and all ARA values refer to surface activity unless specified.

ARA in more temperate salt marshes in Nova Scotia was higher than at La Pérouse Bay, and peaked in July at a mean value of 380 µmoles C_2H_2 reduced m^{-2} hr^{-1} (Patriquin and McClung, 1978). During July, values ranged from 200 to 700 µmoles C2H2 reduced m^{-2} hr^{-1} (Patriquin and McClung, 1978). In May, June, September and

and October, ARA was approximately 10 µmole C_2H_2 reduced m^{-2} hr^{-1} (Patriquin and McClung, 1978). Elsewhere in Nova Scotia, at Minas Basin, Smith, McLachlan and Patriquin (1979) reported apparent surface fixation rates of 0.1 to 2 mg N_2 fixed m^{-2} hr^{-1} between April and July (see Fig. 1 in their paper). These figures were based on a conversion ratio of 3:1 moles of acetylene to dinitrogen reduced. Therefore, they were derived from ARA rates ranging from 10.7 to 214 µmoles C_2H_2 reduced m^{-2} hr^{-1}, which is in the range for both grazed and ungrazed sites at La Pérouse Bay. Patriquin and Keddy (1978) examined a variety of vegetation zones at Lawrencetown Lake salt marsh, Nova Scotia, and found that at heavily vegetated sites, the soil surface did not contribute at all to ARA. At sites where the soil surface did contribute to ARA, rates were as high as 72.6 µmoles C_2H_2 reduced m^{-2} hr^{-1} (Patriquin and Keddy, 1978).

In salt marshes at Colne Point in Essex, maximum rates of acetylene reduction were found to be 40 µmoles C_2H_2 reduced m^{-2} hr^{-1} in April 1976, in "black" salt marsh pans dominated by Oscillatoria limosa (Aziz and Nedwell, 1979). Peak rates of acetylene reduction varied between 27 and 300 µmoles C_2H_2 reduced m^{-2} hr^{-1} in various vegetation zones in the great Sippewissett Marsh in Massachusetts, during the June to August period (Carpenter, Van Raalte and Valiela, 1978). However, these were mean values based on a number of measurements made during day long periods, and individual peak values of up to 375 µmoles C_2H_2 reduced m^2 hr^{-1} were also observed (Carpenter, Van Raalte and Valiela, 1978).

The main difference between the sites tested for ARA by Patriquin and Keddy (1978) in Nova Scotia, and those at La Pérouse Bay, was the high degree of activity observed at heavily vegetated stands of Carex mackenziei in Nova Scotia. Values of ARA reached 110 µmoles C_2H_2 reduced m^{-2} hr^{-1}, and at other fairly densely vegetated sites, they ranged from 14.4 to 45.8 µmoles C_2H_2 reduced m^{-2} hr^{-1} at the end of July (Patriquin and Keddy, 1978). These are generally higher than the range of values observed at the more densely vegetated ungrazed sites at La Pérouse Bay. Patriquin and Keddy (1978) suggested that the vegetation was contributing towards ARA, because as at La Pérouse Bay they observed few blue-green algae on the sediment surfaces. Below-ground ARA is usually caused by diazotrophic bacteria in root nodules or in the rhizosphere (Patriquin and Keddy, 1978; Patriquin and McClung, 1978).

To put the La Pérouse Bay ARA results into a wider context, they may be compared with those from native Australian legumes, in which Rhizobium- bacteria in root nodules are responsible for dinitrogen fixation (Lawrie, 1981). Mean ARA values in nodules of Acacia mearnsii were 1.8 µmoles C_2H_2 reduced m^{-2} hr^{-1}, for 100% vegetation cover of this species (Lawrie, 1981). This is much lower than the La Pérouse Bay ARA rates. However, in Australia, fixation is year round, and there may be other sources of diazotrophic activity in addition to legumes. Carpenter, Van Raalte and Valiela (1978) quote other sources from warmer environments which indicate that on an annual basis, the levels of nitrogen input that they observed for the Sippewisset Marsh were relatively low. This is probably also the case at La Pérouse Bay, but as will be discussed shortly, the data do not permit calculations of annual input to be made.

In the arctic sites, Nostoc commune, a heterocystous blue-green alga was probably responsible for the ARA (Alexander, Billington and Schell, 1978; Jordan, McNicol and Marshall, 1978). Species of Oscillatoria and Lyngbya were not found at the sites at Barrow (Cameron, Knox and Morelli, 1978). However, Stutz (1977) and Jordan, McNicol and Marshall (1978) did find members of the Oscillatoriaceae at Truelove Lowlands, including species of Oscillatoria. At Stordalen, the blue-green algae associated with Sphagnum were species of Anabaena and Nostoc, and the algal mats consisted of colonies of Nostoc (Granhall and Selander, 1973). In more temperate marshes in Nova Scotia and England, non-heterocystous blue-green algae were implicated as the main nitrogen fixers, particularly species of Oscillatoria and Lyngbya (Jones, 1974; Patriquin and McClung, 1978; Smith, McLachlan and Patriquin, 1979). Aziz and Nedwell (1979) also found that Oscillatoria was responsible for nitrogen fixation. In addition, Patriquin and McClung (1978) observed purple photosynthetic bacteria on the sediment surfaces. It appears that the blue-green algae responsible for surface nitrogen fixation at La Pérouse Bay were also species of Lyngbya and Oscillatoria, at least in September. Thus, fixation rates in grazed sites were in the same range as those observed in more temperate salt marshes. It is possible that the ARA observed in the exclosure was caused by the vegetation, in a manner similar to that observed by Patriquin and Keddy (1978). Patriquin and Keddy (1978) also tested excised roots of plant species present in the vegetation zones of interest, for nitrogenase activity, and they found some agreement between in situ and in vitro ARA although direct comparisons were not possible. Nevertheless, given these results, there may have been some nitrogenase activity associated with the roots of plants growing at La Pérouse Bay. Jones (1974) detected rhizosphere stimulation of nitrogen fixation in the roots of Puccinellia maritima, and Patriquin and Keddy(1978) recorded nitrogenase activity associated with excised roots of species of Carex, Potentilla and Triglochin, other than those occurring at La Perouse Bay. It would be of interest to test below-ground soil samples and excised roots of various species growing in exclosures, for nitrogenase activity.

Many researchers extrapolate annual rates of nitrogen input for ecosystems from acetylene reduction data (Postgate, 1982). However, the data from La Pérouse Bay are insufficient at the present time to carry out such calculations. This is because rates of fixation vary on both a diurnal and an annual basis (Azis and Nedwell, 1979; Alexander, Billington and Schell, 1978; Carpenter, Van Raalte and Valiela, 1978; Smith, McLachlan and Patriquin, 1979; Sprent, 1979; Fay, 1983). In general, fixation occurs at higher rates at warmer temperatures, in the summer months, and between 10:00 and 12:00 a.m. (Carpenter, Van Raalte and Valiela, 1978). The reasons for this are related to the physiology and chemistry of the nitrogen-fixing process in organisms.

The enzyme nitrogenase is comprised of two protein sub-units: an Mo-Fe protein incorporating labile sulphur known as dinitrogenase, and a smaller Fe-labile sulphur containing protein, known as dinitrogenase reductase (Stewart, 1980; Postgate, 1982). In addition, a low potential reductant, such as ferrodoxin or flavodoxin is required, along with magnesium (Mg^{2+}) ions (Postgate, 1982). Cellular energy, in the form of 12 to 15 molecules of ATP is required for the reduction of each molecule of dinitrogen (Fay, 1983). The reduction of dinitrogen begins with that of dinitrogenase reductase by the reductant. The presence of Mg-ATP stimulates the transfer of the electrons to the dinitrogenase sub unit. The latter binds the dinitrogen molecule and reduces it to ammonia (NH_3) (Postgate, 1982). During the process, at least one ATP molecule is hydrolysed to ADP. The activity of nitrogenase is irreversibly inhibited by the presence of oxygen, for which it has a high affinity (Sprent, 1979; Postgate, 1982; Fay, 1983). Hydrogen gas is also a by-product of nitrogen fixation, and at high enough concentrations, it inhibits nitrogenase activity (Postgate, 1982). In addition, the presence of ammonium or nitrate suppresses the activity of nitgrogenase, probably because the organism preferentially uses a nitrogen source that is less costly in terms of energy (Knowles and Denike, 1974; Carpenter, Van Raalte and Valiela, 1978; Postgate, 1982).

Various researchers have tested the response of ARA of various organisms to fluctuations in such environmental variables as external nitrogen levels, salinity, and moisture. Some have noted the importance of moisture in stimulating ARA responses (Alexander, Billington and Schell, 1978; Patriquin and Keddy, 1978). This is probably the case because, besides the necessity for water, at high levels of moisture oxygen concentrations tend to be lower. Although the sediments at La Pérouse Bay did have a high soil water content, the water content fell as the summer progressed. The drop in ARA rates in both grazed and ungrazed sites did coincide with a drop in soil water content. Unfortunately, changes in water content of the surface sediments (0-3 mm depth) were not measured, but it is likely that drying- out of the surface may have accounted in part for a fall in ARA rates. Patriquin and Keddy (1978) found that ARA in excised roots was not affected by a salinity range of 0 to 21%. In 1982, the highest value of salinity observed at La Pérouse Bay was 14.5°/oo on July 15, but most values were between 1 and 8.6 %.

Data from Patriquin and Keddy (1978) indicate that ARA in stands of salt marsh angiosperms is inhibited at ammonium levels of above 33 µmolar in the groundwater. At La Perouse Bay, ammonium concentrations in soil water ranged between 47 and 439 µM in early June, 1983. From July to September, the concentrations fluctuated between 2 to 64 µM in ungrazed sites and 34 to 154 µM in grazed sites. The higher concentrations were observed in August, and they may well have had a depressant effect on ARA. At all times, the ammonium concentration in the soil water of grazed sites was above 33 µM, and thus was greater than the threshold at which ARA appears to be depressed. However, the colonies of blue-green algae on the sediment surfaces may not be as affected by these ammonium levels to the same extent as diazotrophic bacteria associated with roots.

Another explanation for the drop in ARA towards the end of July, 1983, is that the species of blue-green algae were different, and greater numbers of heterocystous species may have been present before this. Unfortunately, samples of algae were not collected at this time. Smith, McLachlan and Patriquin (1979) observed an increase in ARA in August, when the blue-green algal population became dominated by species of Anabaena, rather than by Oscillatoria. Anabaena is heterocystous, and is a more efficient diazotroph than the micro-aeophilic, non-heterocystous blue-green algae.

Among diazotrophs, blue-green algae are more sensitive to high oxygen concentrations, and high light intensities, at which photosynthesis may be stimulated, thus producing more oxygen (Postgate, 1982). This may be why Carpenter, Van Raalte and Valiela (1978) observed maximum rates of ARA before noon, and maximum insolation in the afternoon at approximately 15:00 hours. However, shading of algal mats was found to reduce ARA (Carpenter, Van Raalte and Valiela, 1978). Therefore, there is an optimum point for ARA at some level of photosynthetic activity. Even with the depressant effect of shading, Carpenter, Van Raalte and Valiela (1978) observed some ARA at all hours of the day and night. In the Arctic and Sub-Arctic, rates of photosynthesis may not be high enough to inhibit ARA, and this may have been why the highest rates were observed on the sunniest days both at La Pérouse Bay and in the Truelove Lowlands (Alexander, Billington and Schell, 1978).

Because of the need for low oxygen concentrations by diazotrophs, researchers tended to concentrate their attention on heterocystous blue-green algae. The thick-walled heterocysts were an obvious site of reducing activity that could be supplied with ATP from photosynthesis in neighbouring cells (Postgate, 1982). However, evidence of nitrogenase activity under anaerobic conditions has been observed in many non-heterocystous blue-green algae in laboratory tests (Stewart and Lex, 1970; Kenyon, Rippka and Stanier, 1972; Stewart, 1980, 1983). Out of nine species of Oscillatoria tested, five were found to contain nitrogenase, while 16 out of 24 species of the Lyngbya, Plectonema, Phormidium, group have been observed to exhibit ARA (Stewart, 1980). Some of the species tested were able to fix dinitrogen under micro-aerophilic or low oxygen conditions, as well as in anaerobic conditions. They may do this by separating diazotrophy and photosynthesis on a temporal basis (Postgate, 1982). The bundles of Lyngbya and Oscillatoria found at La Pérouse Bay may well be able to satisfy the low oxygen requirements for diazotrophy.

Although nitrogen fixation rates were higher in grazed areas in 1983, it is not known whether the nitrogen fixed was made available for plant growth during the summer of 1983. Patriquin and McClung (1978) point out that the assumption, that nitrogen fixed by colonies of blue-green algae on sediment surfaces becomes rapidly available for plant growth, is not valid unless accompanied by N^{15} tracer studies that demonstrate this effect. Thus, at the most, one is only able to surmise that this was the case at La Pérouse Bay.

There is some evidence that this does occur from Jones (1974), who found that plant roots of various halophytes, including Puccinellia maritima took up N^{15} which had been fixed by blue-green algae.

It is more probable that on a short term basis much of the nitrogen for plant growth at grazed sites was derived from the soluble fraction of snow goose droppings. The increases in standing crop brought about by the fertilization experiments involving droppings may be compared with increases observed in the nutrient perturbation experiment carried out at La Pérouse Bay by Cargill and Jefferies (1984a). In mid-August 1979, the mean live-standing crop in the control plots was 140 g m^{-2} compared with 250 g m^{-2} in plots treated with ammonium salts (Cargill and Jefferies, 1984a). In 1980, by mid-August, the standing crop of controls was 100 g m^{-2} compared with 212 g m^{-2} in plots treated with ammonium salts (Cargill and Jefferies, 1984a) Cargill and Jefferies (1984a) fertilised the plots approximately twice a month for two months, whereas droppings were added every ten days for approximately two and a half months. Increases in live standing crop were in the range of 20 g m^{-2} to 70 g m^{-2} with fertilisation with droppings, which is less than those achieved with ammonium salts.

Lotero, Woodhouse and Petersen (1966) found that urine from beef cows increased dry matter production of vegetation by 300%, and the total nitrogen content of the vegetation by 30% within a 14" (35.8 cm) radius around the point of urination. However, because of the limited number of areas affected in this way, they concluded that the fertilisation effect of urine voided by cattle is of limited benefit to the fertility of pastures as a whole. Weeda (1976) found low levels of increased growth of vegetation around dung patches. Thus, although the limited fertilization effects of the urine and faeces from herbivores have been noted by some researchers, La Pérouse Bay appears to differ from other sites, in that the scale of the effect is much wider. This undoubtedly stems, in part, from the very high rate of defaecation of the geese - once every six minutes on average (Cargill, 1981). Also, snow goose droppings are relatively small and are distributed fairly evenly in grazed areas of the marsh. Large faecal droppings may not be as effective in fertilising plants because they represent a "disaster for the plants in and around" them (Harper, 1977).

As proposed by Cargill (1981), the soluble nitrogen fraction of the droppings is the most likely component providing nitrogen for plant growth. Up to 60% of this fraction was lost during a 48 hour period from droppings. The percentage of nitrogen lost from droppings placed on the marsh for two months corresponded with the levels of solublew nitrogen found in droppings. However, the total input of nitrogen to the grazed areas of the marsh from the droppings cannot be calculated from these results, because an unknown portion of the ammonium ions may have been volatilized and lost as ammonia. Denmead, Simpson and Freney (1974) found that up to 50% of the nitrogen fixed in pasture which was grazed by sheep was lost as a result of volatilization, particularly that in urine. These high rates of loss are probably not applicable to La Perouse Bay, since temperatures are cooler than those in the Australian fields studied by Denmead, Simpson and Freney (1974). Also, the urinary products of snow geese are in the form of a white paste on droppings, and are not liquid (Cargill, 1981). Snow goose droppings apparently contain a higher level of soluble nitrogen than faeces of other herbivores,such as cows, which according to Simpson and Stobbs (1981) have a large insoluble faecal nitrogen content.

Although one of the suggestions made by Cargill (1981) was that snow goose droppings may be more prone to decomposition than litter, Floate (1970a) found that plant material decomposed more rapidly than did sheep faeces containing the same vegetation. However, nitrogen was mineralized at a similar rate as that found in the plant material (1970a). Other experiments conducted by Floate (1970b) indicated that mineralization of nitrogen from sheep faeces was slowed down considerably under low moisture conditions. Thus, it would seem likely that very little nitrogen is derived from old droppings which have dried out after two weeks on the marsh.

Cargill and Jefferies (1984b) demonstrated that grazing maintained higher levels of total and soluble nitrogen in grazed shoots, and this trend was also observed in 1983. The Puccinellia phryganodes shoots at La Pérouse Bay contained "average" levels of soluble nitrogen in the range of 10-20% of the total nitrogen content. These percentages have been recorded in other grazed plants (Simpson and Stobbs, 1981). The mean total nitrogen content of above-ground parts of Spartina alterniflora in Georgia salt marshes was 1.05%, which is about 50% of the levels observed in grazed plants at La Pérouse Bay in 1983 (Hopkinson and Schubauer, 1984). The highest value was observed in December and was 1.82% (Hopkinson and Schubauer, 1984). Patriquin and McClung (1978) observed higher, although declining levels (from 3% to 1.5%) of nitrogen in tissues of Spartina alternifora between June and early September. End of summer nitrogen levels in Spartina alterniflora in marshes further south than those in Nova Scotia, were similar to those observed by Hopkinson and Schubauer (1984), Valiela and Teal (1974), Gallagher (1975). Total nitrogen levels in July and August in Juncus gerardii and Spartina patens were 1.38% and 0.60% respectively (Smith, McLachland and Patriquin, 1979). Thus, compared with other salt marshes, some of which are grazed, total nitrogen levels in grazed Puccinellia phryganodes were relatively high.

A point worth noting is that the total nitrogen content of ungrazed vegetation starts to decline within as little as two weeks following the hatch period. Cargill and Jefferies (1984b) found that total nitrogen in grazed shoots of Puccinellia was significantly higher than in ungrazed shoots on July 16, 1979, and peak hatch was around June 27, 1979 (Cargill, 1981). Thus, although, as discussed in Chapter 3, the differences in NAPP between grazed and ungrazed sites are usually observed approximately six weeks after peak hatch, the nitrogen content of the ungrazed shoots declines well before this. The demography data indicated that live leaves from grazed and ungrazed populations of shoots were all of similar age, since turnover rates of leaves were similar. This has implications for the snow geese, which have a high demand for nitrogen at this time.

Although differences in the rates of mineralization between grazed and ungrazed areas were not detected, the circumstantial evidence of the large environmental differences between the two areas suggests that they may well be higher in grazed sites.

The activities of decomposers have been found to decrease with decreasing temperatures (Whidden, 1977; Swift, Heal and Anderson, 1979; Flanagan and Bunnell, 1980; Heal, Flanagan, French and MacLean, 1981). This is a major reason why such large amounts of litter have been observed in arctic and sub-arctic ecosystem. Thus, in the exclosures, the cooler temperatures were assumed to have a similar effect. Mineralization was significantly lower in soil cores incubated at 5°C than in those incubated at 20°C, in an experiment carried out on sediments from Colne Point (Aziz and Nedwell, 1979).

Redox levels have also been found to affect rates of mineralization, because oxygen is required by heterotrophic decomposers. The highest rates of decomposer activity have been observed in areobic environments (Swift, Heal and Anderson, 1979). However, the redox potential was generally quite high at La Perouse Bay, and it is doubtful whether it was low enough to inhibit nitrifying bacteria. Redox values were higher than those in a tall stand of <u>Spartina</u> <u>alterniflora</u> in a Massachusetts salt marsh (Howes, Howarth, Teal and Valiela, 1981). In this stand, the mean Eh was 340 mV at a depth of 2cm, and 275 mV at 5cm, between June and September, 1978 and 1979 (Howes, Howarth, Teal and Valiela, 1981), while in ungrazed sites at La Pérouse Bay, Eh ranged from 280 to 590 mV at a depth of 1 cm, and from 220 to 380 mV at 5cm, between June and September, 1983. The well established root systems of

Puccinellia swards in both grazed and ungrazed sites are probably responsible for these higher Eh values, as they form a pathway for oxygen to enter the sediments (Howes, Howarth, Teal and Valiela, 1981). Redox potentials fluctuated greatly according to the sediment depth, and tidal condition, in a Puccinellia maritima site in Humber Bay, England (Etherington, 1982). At a depth of 2.5 cm, it fluctuated between -120 mV and 600 mV (Etherington, 1982).

The higher moisture content of the sediments in the exclosures was responsible for the lower Eh, as a waterlogging sediment has a low Eh (Etherington, 1982). However, as mentioned earlier, Eh was not low enough to inhibit nitrification (Hansen, Henriksen and Blackburn, 1981), yet there was no nitrate detectable in the sediments at La Perouse Bay. However, potential nitrification rates have been found to be high in the sediments (A. Jensen and R.L. Jefferies, unpubl.). It is possible that any nitrate ions produced are immediately absorbed by plant roots or bacteria. In an English salt marsh at Colne Point, there was no evidence of nitrification processes occurring, due to the reduced nature of the sediments (Aziz and Nedwell, 1979).

There may have been a number of reasons why no build-up of ammonium-nitrogen was observed in incubation tubes in the soil. Any ammonium produced may have been mineralized to nitrate, and subsequently denitrified and lost to the atmosphere. Indeed, Aziz and Nedwell (1979) found that denitrification was rapid in the salt marsh at Colne Point. However, it is more likely that the reason why ammonium did not build-up in the soil cores was that many of them contained live Puccinellia or Carex roots, which absorbed any mineralized nitrogen.

It is likely that the higher concentrations of water soluble and KCl-exchangeable ammonium ions observed in October, 1983, represented the release of nitrogen from dying algae. Both spring and fall peaks in levels of ammonium ions in soils have been observed in soils in Britain (Davy and Taylor, 1974). The higher levels of ammonium observed in grazed sites indicate that more nitrogen is available for plant growth in these sites than in ungrazed sites, immediately after and before freeze-up.

CHAPTER 6

CHANGES IN THE SPECIES COMPOSITION OF VEGETATION AND CHANGES IN STANDING CROP IN EXCLOSURES FROM 1 TO 4 YEARS IN AGE

6-1 INTRODUCTION

Although, as stated in the introduction, this study was initially an experimental study, I realized that the data being collected were such they they would allow more theoretical questions to be addressed. One of the experimental objectives stated in Chapter 1 was to determine the effects of long-term exclusion of the snow geese from grazed sites. It was predicted that litter would accumulate, as it would not be converted into droppings, and that NAPP would continue to be lower than in adjacent grazed sites, as a result of lower availability of nitrogen. Also, it was predicted that the relative abundances, and possibly the total number of plant species would change in the absence of grazing.

Live biomass, as it may reflect numbers of species and species diversity are closely related to theories of stability, and so an application of ideas stemming from stability-diversity theory was a logical step in this study. The stability of plant-herbivore interactions is of interest to theoretical ecologists, for whom they form a subset of a larger group of interactions (May, 1972, 1974; Caughley and Lawton, 1981). The term stability may be defined in a number of ways, but it generally refers to the tendency of a system to return its initial state after being perturbed (May, 1974; Orians, 1975; Pimm, 1984). Some predator-prey interactions may have a cyclic-stability in that the populations may continually fluctuate up and down around a certain point (May, 1974). It is also conceivable that a predator, be it a carnivore or herbivore, may drive its prey to extinction, so that the original state is not regained. The stability of the grazed plant community may be dependant upon the snow geese, which may in turn have their numbers stabilized by resource limitation i.e. available forage. Thus, the removal of the snow geese, the herbivore in this particular plant-herbivore interaction, constitutes a perturbation to the system, and the response of the plant species to this change may give some indication of the stability of the goose-grass interaction. It is possible that in the absence of the snow geese which have been found to cause the increase the biomass production, by accelerating the rate at which nitrogen cycles through the system, the plant community might move towards a new equilibrium point in which nitrogen is less available for growth.

Researchers have long realised that herbivores greatly affect the species composition of the plant communities on which they graze (Harper, 1969, 1977; Caughley and Lawton, 1981; Crawley, 1983). In some studies, herbivore activity increased plant species richness, while in other studies it brought about a decrease in species richness (Harper, 1969; 1977; Caughley and Laughton, 1981; Watts, 1981a, Crawley, 1983). In general, there is a prevailing view that grazing should increase diversity. In addition to affecting species diversity, herbivores have also been observed to prevent successional processes from proceeding (Watt, 1981a, 1981b; Crawley, 1983). This has been observed in fields and chalk grasslands invaded by shrubs and trees following the removal of sheep or cattle (Harper, 1977; Watt, 1981a, 1981b; Crawley, 1983).

Herbivores may potentially affect plant species competition in four ways (Crawley, 1983). They may selectively graze on the most competitive species; they may selectively graze on the least competitive species; they may switch their feeding preference to whichever species is most abundant; they may be neutral in their feeding habits, taking amounts of the different species in proportion to their abundance (Crawley, 1983). The dynamics of plant community interactions will differ according to the mode of grazing. One category of experiment (Harper, 1969, 1977) advocates the withdrawl of the herbivore from the grazed vegetation in order to determine the effects of grazing on plant species richness.Not only is it predicted that changes in species composition will occur, but also the changes should give some indication of the competitive nature of the interactions and whether the herbivore is retarding succession. The exclusion of snow geese from exclosures erected between 1979 and 1983 enabled such an experiment to be carried out.

6-2 METHODS

In 1982 the standing crop was monitored in the four exclosures built in previous years. The ages, and codes assigned to these exclosures are given in Table 6-1. A one year-old *Puccinellia* dominated exclosure was sampled five times between June and September. The other three exclosures were sampled on four occasions during this period. At each sampling five turfs 10 cm x 10 cm in size were cut at random from each of the latter three exclosures and three turfs were cut from each adjacent grazed area. Four 10 cm x 10 cm replicates were cut from the one-year old exclosure and four were also cut from the adjacent grazed area. All turfs were transported to the field station and processed according to methods described in Section 3-2.

In 1983 the same procedure was followed and four previously built exclosures were monitored (Table 6-1). The standing crop was sampled on three occasions between June and September. On each sample date, three turfs, 10 cm x 10 cm, were cut from each exclosure and three were cut from the adjacent grazed areas. The standing crop was determined in the same manner as in 1982. Leaf area indices were also measured for each grazed and ungrazed area according to methods described in Section 3-2.

Table 6-1. Code numbers of exclosures of different ages erected between 1979 and 1983 at La Pérouse Bay, Manitoba, and the years in which various parameters were measured in them.

Number of Exclosure	1	2	3	4	5	6	7	8
Year of Erection	1982	1981	1980	1980	1979	1983	1982	1981
Age in 1982 - years	-	1	2	2	3	-	-	1
Age in 1983 - years	1	2	3	3	4	-	1	2
Parameter Measured								
Standing Crop	*	*	*	82	*	83	-	-
Plant Species Present	-	-	*	-	*	83	*	*
Soil Water Content	-	82	83	-	-	-	-	-
Soil Temperature	-	82	*	-	*	-	-	-
Salinity	-	82	*	-	*	-	-	-
Eh	-	-	83	-	-	-	-	-
NH_4^+ background levels	-	82	83	-	-	-	-	-
Nitrogenase activity	-	-	83	-	-	-	-	-

* Parameter measured in 1982 and 1983

82 " " in 1982 only

83 " " in 1983 only

\- " not measured in exclosure

In 1982, shoot frequency data for different plant species were collected from four ungrazed exclosures and their adjacent grazed areas (Table 6-1). The exclosures ranged in age from 0 to 3 years. A 5 cm x 5 cm quadrat was used. This was thrown at random 200 times in each exclosure and each species present in a quadrat was recorded. A further 200 quadrats were thrown at random in the adjacent grazed areas. Each exclosure was surveyed in August, and they were inspected in September for the presence of any late developing species, such as Sagina nodosa. In 1983 these data were collected in the same way from five exclosures (see Table 6-1).

Following their collection, two different calculations were carried out on the data. First, the relative frequency of each species present in each grazed or ungrazed site was calculated. The calculation is shown in Section 6-3-4, and it expresses the frequency of occurrence of other species. The results were also expressed as the percentage of occurrence of each species in 200 quadrats. Thus, although Puccinellia may have been present in nearly every one of 200 quadrats in both grazed and ungrazed sites, the calculation of relative frequency indicates whether it alone of all species is present at a high frequency, or whether other plant species are also prsent at high rates.

6-3 RESULTS

6-3-1 Live-Standing Crop in Exclosures of Different Ages and in Grazed Sites

Figure 6-1 shows the live standing crop in exclosures ranging in age from one to four years old and in adjacent grazed areas. Table 6-1 gives a list of the numbers assigned to the exclosures and their ages in 1982 and 1983. As discussed in Chapter 3, leaf area index is indicative of standing crop, so LAI's were measured in exclosures in 1983 and the results are shown in Figure 6-1.

During 1982 and 1983, the standing crop in the older exclosures followed similar trends to those observed in new exclosures erected following snowmelt. Peak live biomass was attained in mid-July to early August (Figs. 3-2a and 3-3a). Initial values of live standing crop were low, at approximately 50 g m^{-2} in most of the exclosures. The values attained their peak in July or August (Fig. 6-1). In the grazed sites the amounts of standing crop were substantially lower than those in the exclosures during both summers. At the onset of the growing season, they were often less than 50% of the standing crop in the exclosures. They reached maximum values of approximately 50 g m^{-2} at some grazed sites.

Figure 6-1. Seasonal trends in live, above ground standing crop (g dry weight m^{-2}) in grazed (●) swards dominated by Puccinellia phryganodes and in ungrazed (O) swards of different ages, originally dominated by P. Phryganodes at La Pérouse Bay, 1982 and 1983. Leaf area indices were measured at the grazed (▲) and ungrazed (△) sites in 1983.

a. Exclosure 1, 1983, one-year old (Mean +/-S.E., n=3).

b. Exclosure 2, 1982, one-year old. (Mean +/-S.E., n=4).

c. Exclosure 2, 1983, two-year old. (Mean +/-S.E., n=3).

d. Exclosure 3, 1982, two-year old. (Mean +/-S.E., n=3).

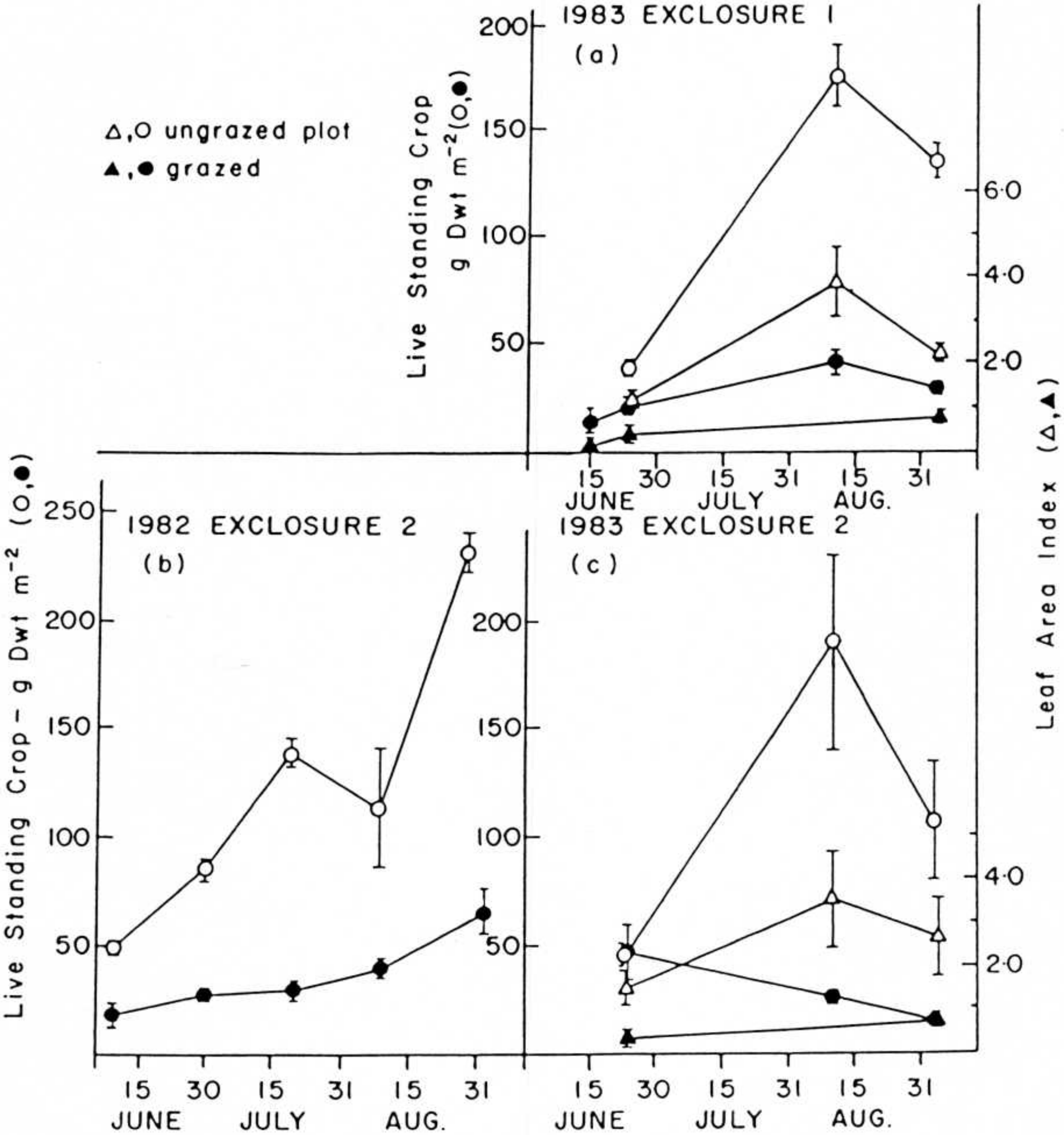
e. Exclosure 3, 1983, three-year old. (Mean +/-S.E., n=3).

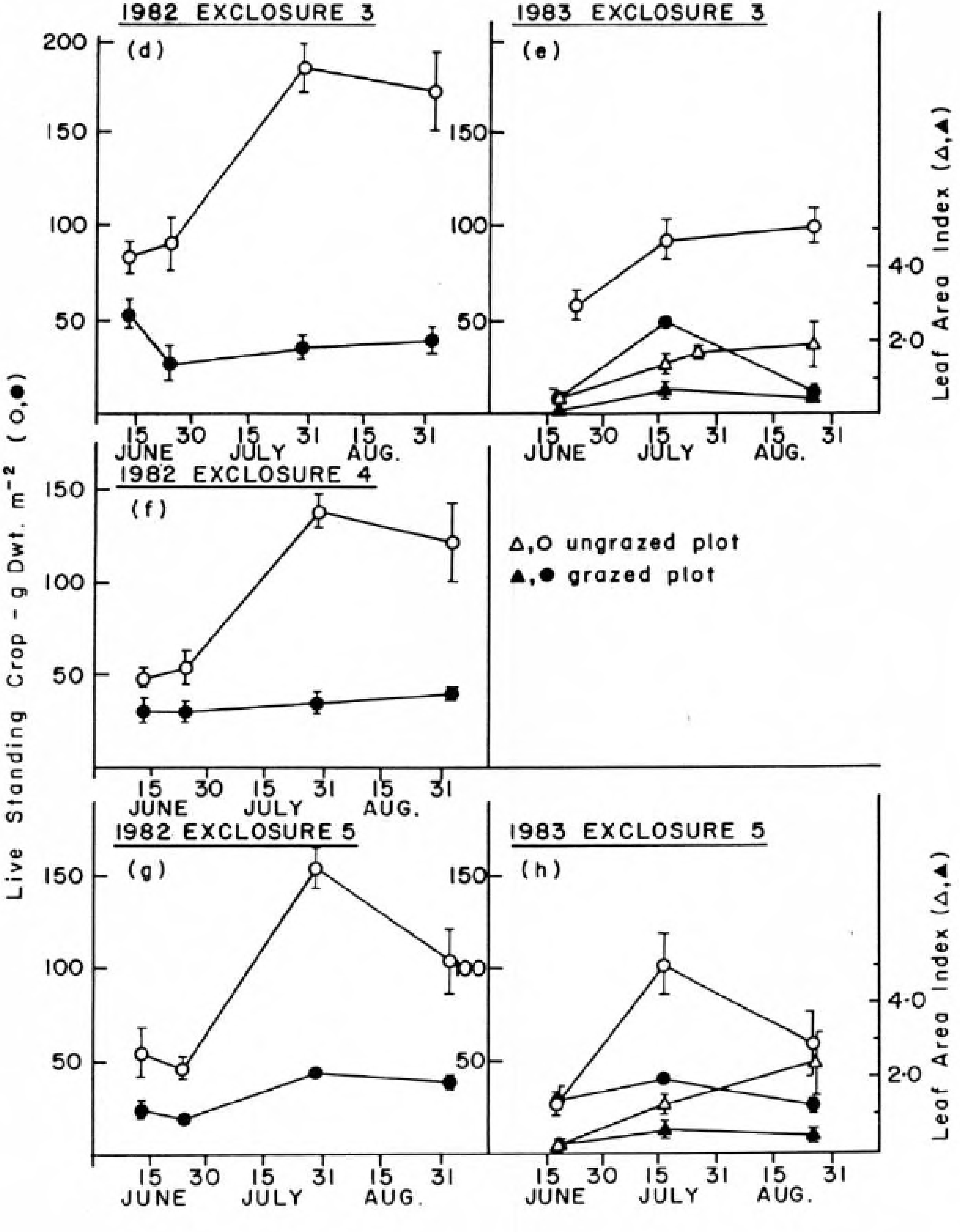
f. Exclosure 4, 1982, two-year old. (Mean +/-S.E., n=3).

g. Exclosure 5, 1982, three-year old. (Mean +/S.E., n=3).

h. Exclosure 5, 1983, four-year old. (Mean +/-S.E., n=3).

CHANGES IN STANDING CROP OF EXCLOSURES AT LA PEROUSE BAY, MANITOBA




1982 EXCLOSURE 3
(d)
1983 EXCLOSURE 3
(e)
1982 EXCLOSURE 4
(f)
1982 EXCLOSURE 5
(g)
1983 EXCLOSURE 5
(h)
Live Standing Crop - g Dwt. m⁻² (O,●)
Leaf Area Index (Δ,▲)
200
150
100
50
4·0
2·0
15 30 15 31 15 31
JUNE JULY AUG.
Δ,O ungrazed plot
▲,● grazed plot

In 1983, Exclosure 1 was a year old. The initial standing crop in it was 38 g m^{-2} on June 23 (Fig. 6-1a). It increased to 175 g m^{-2} on August 10, and dropped to 138 g m^{-2} in early September. These values may be compared with those obtained from this exclosure and two others in the previous year (Fig. 3-2a). In 1983, the peak standing crop was higher than that of 1982 which was 104 g m^{-2}. In the adjacent grazed area in 1983, standing crop values were initially much lower, and they increased from 12 g m^{-2} on June 23 to 40 g m^{-2} in mid-August, and then dropped to 29 g m^{-2} by September 3. In 1982, the standing crop at this grazed site fluctuated between 12 and 35 g m^{-2} during the summer (Fig. 3-2a).

In 1982, the initial standing crop in the one-year old Exclosure 2 was 49 g m^{-2} on June 9, and this increased steadily to 138 g m^{-2} on July 20 (Fig. 6-1b), and to 230 g m^{-2} on September 2. This was the highest live standing crop value recorded in any exclosure in either 1982 or 1983. The rise in standing crop in late August was the opposite of the trends observed in the other exclosures. In 1981, some standing crop measurements were made in this exclosure when it was one summer old, and the maximum value was 141 g m^{-2}.

In 1983 when this exclosure was again measured, the initial mean standing crop was slightly lower than in the previous year, and was similar to that in the adjacent grazed site, at 45 g m^{-2} on June 23 (Fig. 6-1c). The standing crop peaked in the exclosure on August 10, at 190 g m^{-2}, and dropped to 106 g m^{-2} in early September. There were large standard errors associated with both of these mean values.

The trends in the values of the standing crop in the grazed site near Exclosure 2, were dissimilar in 1982 and 1983 (Figs. 6-1b and 6-1c). In 1982, the initial live standing crop was 18 g m^{-2},and it increased gradually during the summer, reaching a value of 63 g m^{-2} on September 2. In 1983, the initial standing crop on June 23, following thaw, was 46 g m^{-2}, and this dropped to 13 g m^{-2} on September 3, rather than increasing or remaining at the same level. However, both sets of data were within the range of values observed at other sites.

Exclosures 3 and 4, were both two years old in 1982 (Figs. 6-1d and 6-1f), and the values for live standing crop followed the same pattern as that observed in Exclosure 2, when it was two-years old in 1983. However, the mean values observed in Exclosure 3, were consistently 40 to 50 g m^{-2} higher than those measured in Exclosure 4, and they attained their peak at the end of July in both exclosures at 184 g m^{-2} and 137 g m^{-2} respectively. The former exclosure was located in a sheltered site, south of a ridge of willows on an island in the Mast River delta, which may explain the higher standing crop values.

In 1983, the standing crop in Exclosure 3, which was three years old by this time, was much less than in 1982 (Fig. 6-1e). It rose from 59 g m^{-2} on June 23 to 94 g m^{-2} on July 17, which was 90 g m^{-2} less than the previous year's maximum value, recorded on July 29, 1982. Following July 17, 1983, the mean standing crop value increased slightly to 101 g m^{-2}.

The possible effect of the sheltered location of Exclosure 3 on standing crop, was evident in that the highest initial value among the grazed sites was observed here (53 g m^{-2} on June 9, 1982) (Fig. 6-1d). Following snow goose hatch, it dropped to 26 g m^{-2}, and it fluctuated between 30 and 40 g m^{-2} for the remainder of the summer in 1982. The live standing crop in the grazed site adjacent to Exclosure 4 fluctuated between 30 and 40 g m^{-2} during the entire summer in 1982 (Fig. 6-1f). In 1983, the standing crop in the grazed site next to Exclosure 3 was 11 g m^{-2} on June 18 and it increased to 50 g m^{-2} by mid-July (Fig. 6-1e).

In 1982, the oldest exclosure monitored, was three years old (Exclosure 5). In mid-June, the initial standing crop was 54 g m^{-2}. The peak standing crop was 153 g m^{-2} on July 30, which subsequently dropped to 104 g m^{-2} in early September (Fig. 6-1g). Except for the July 30 value, these values were much the same as those observed in Exclosure 3 in 1983, which was also three years-old.

In 1983, the initial standing crop following melt was 27 g m^{-2} in Exclosure 5, and was similar to that in the adjacent grazed site (Fig. 6-1h). The peak value was recorded on July 17, at 101 g m^{-2}, which was considerably lower than that measured in the previous year, when the exclosure was three-years old. In late August, the standing crop dropped to 64 g m^{-2}. During both 1982 and 1983, the live standing crop in the grazed site was similar, fluctuating between 20 and 45 g m^{-2} (Figs 6-1g and 6-1h).

The trend that emerged in the standing crop of ungrazed sites, was that standing crop decreased in relation to the number of summers the sites had not been grazed. However, this trend was obscured by site to site variability in the location of exclosures so that the best means of observing it, was to sample the same exclosure over a number of years. Thus, the value of the maximum live standing crop decreased in Exclosures 3 and 5 from 1982 to 1983. These values were much lower than the peak standing crops observed in the one-and two-year old exclosures also measured in 1983. However, there is also evidence, that this decline in standing crop is delayed. In Exclosures 1 and 2, there appeared to be an increase in peak standing crop after one year of exclusion of geese from the sites.

6-3-2 Litter Levels and Standing Dead in Exclosures of Different Ages and in Grazed Sites

Figure 6-2 indicates that litter levels and amounts of standing dead increased as an exclosure increased in age. Therefore, the exclusion of geese from areas normally grazed, caused a build-up of litter. The youngest ungrazed site was a year old in 1983, and contained more than twice the amount of litter at the beginning of the summer than did the adjacent grazed site (Fig. 6-2 a). This value rose to 70 g m^{-2} in the ungrazed site. The increase was associated with a drop in standing crop in the exclosure (Fig. 6-1a).

Figure 6-2. Seasonal trends in litter and standing dead (g dry weight m^{-2}) in grazed (O) swards dominated by <u>Puccinellia</u> <u>phryganodes</u> and in ungrazed (O) swards of different ages, originally dominated by <u>P. phryganodes</u> at La Pérouse Bay, 1982 and 1983. Leaf area indices of litter and standing dead were measured at the grazed (▲) and ungrazed (△) sites in 1983.

a. Exclosure 1, 1983, one-year old. (Mean +/-S.E., n=3).

b. Exclosure 2, 1982, one-year old. (Mean +/-S.E., n=4).

c. Exclosure 2, 1983, two-year old. (Mean +/-S.E., n=3).

d. Exclosure 3, 1982, two-year old. (Mean +/-S.E., n=3).

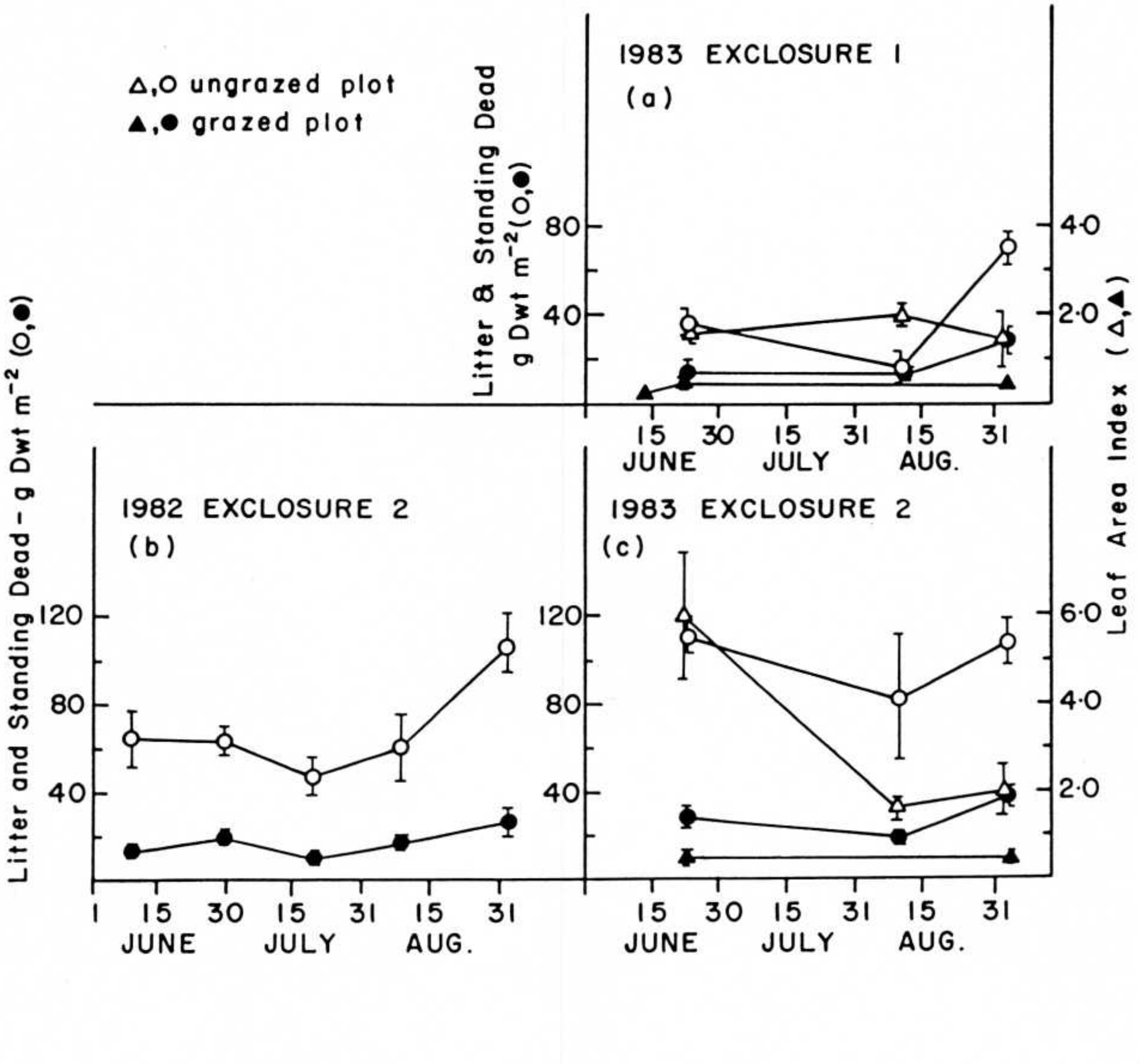
e. Exclosure 3, 1983, three-year old. (Mean +/-S.E., n=3).

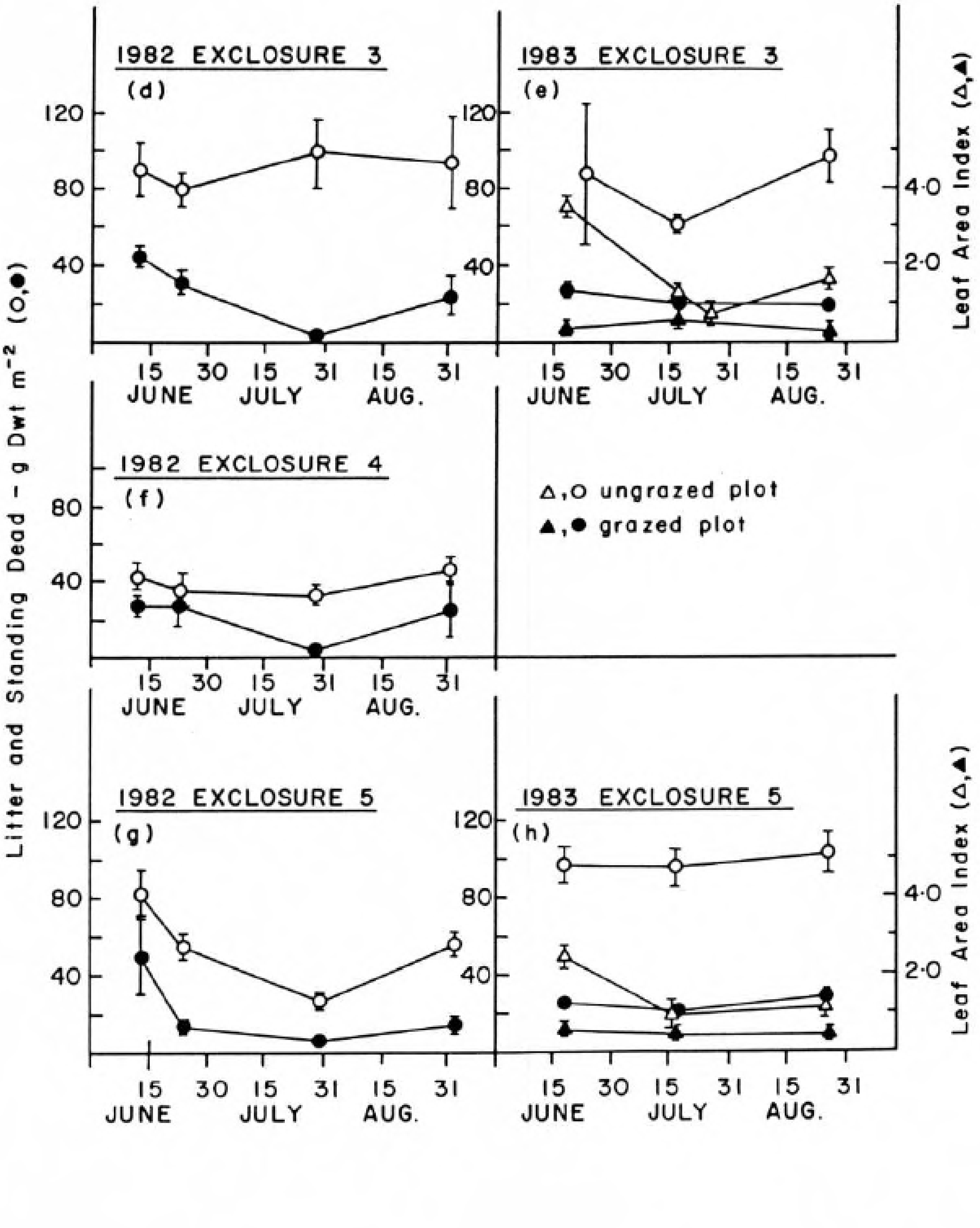
f. Exclosure 4, 1982, two-year old. (Mean +/-S.E., n=3).

g. Exclosure 5, 1982, three-year old. (Mean +/-S.E., n=3).

h. Exclosure 5, 1983, four-year old. (Mean +/-S.E., n=3).

CHANGES IN LITTER LEVELS AND STANDING DEAD OF EXCLOSURES AT LA PEROUSE BAY, MANITOBA



1982 EXCLOSURE 3
(d)
1983 EXCLOSURE 3
(e)
1982 EXCLOSURE 4
(f)
1982 EXCLOSURE 5
(g)
1983 EXCLOSURE 5
(h)
Δ,○ ungrazed plot
▲,● grazed plot
Litter and Standing Dead - g Dwt m^{-2} (○,●)
Leaf Area Index (Δ,▲)
120
80
40
4·0
2·0
15 30 15 31 15 31
JUNE JULY AUG.

The build-up of litter and standing dead was much greater in the year-old exclosure sampled during the previous year (Exclosure 2) than that in Exclosure 1. The initial value of 65 g m^{-2} in Exclosure 2 rose to 110 g m^{-2} on September 2 (Fig. 6-2b). The variation in the accumulation of litter after one year is a reflection of the higher standing crop of the previous year in Exclosure 2.

In 1983, litter levels increased in Exclosure 2 and they fluctuated between 80 and 110 g m^{-2} (Fig. 6-2c). The values were in the same range as those observed in Exclosure 3 in 1982, which was also two years old (Fig. 6-2d). The other two-year old exclosure, no. 4, had much lower levels of litter in 1982; they fluctuated around 40 g m^{-2} (Fig. 6-2f). In 1983 the litter levels did not rise noticeably in Exclosure 3, and by mid-July, they had dropped to 60 g m^{-2} (Fig. 6-2e). In 1982, Exclosure 5, which was three-years old, did not contain the highest amounts of litter among the exclosures, and the initial value of 85 g m^{-2} dropped to 30 g m^{-2} on July 29, before increasing again to 55 g m^{-2} on September 2 (Fig. 6-2g). The following year, the litter levels increased greatly, fluctuating around 100 g m^{-2} (Fig. 6-2h).

The litter levels in all of the grazed sites were in the range of 5 to 30 g m^{-2}, except for initial values of 40 to 45 g m^{-2} in Exclosures 3 and 5 in 1982 (Fig. 6-2). In the one-year old exclosures, the litter levels were much less than the live standing crop, but in Exclosures 3 and 5, the amounts of litter were similar to the amounts of live standing crop.

6-3-3 Leaf Area Indices in Exclosures of Different Ages and in Grazed Sites

In 1983, leaf area indices were measured in the exclosures and their adjacent grazed areas (Figs. 6-1 and 6-2). The LAI values for live material at all of the grazed sites, remained below 1.0 during the summer. In the ungrazed sites, the highest LAI values were observed in Exclosure 1, where LAI increased from 1.1 to 3.9 on August 10, and dropped to 2.2 on September 4 (Fig. 6-1a). In Exclosure 2, the peak LAI was 3.5 (Fig. 6-1c), while in Exclosure 3, it was 1.9 (Fig. 6-1e). Thus, it appeared that the maximum amount of live material in an exclosure decreased with the length of time that the site had not been grazed. However, the maximum LAI in Exclosure 5, the oldest ungrazed site in 1983 was 2.4 (Fig. 6-1h), which was slightly higher than the value from Exclosure 3.

Not all of the patterns in the LAI values corresponded with the trends in amounts of live standing crop. For example, in Exclosure 2, the initial LAI value in the adjacent grazed area, was not greater than the value at the end of the summer, as was the case with the standing crop measurements (Fig. 9-1c). In the grazed site next to Exclosure 3, the LAI did not increase as much as the standing crop value, in mid-July (Fig. 6-1e). Finally, in Exclosure 5, unlike the standing crop, the LAI value continued to increase in August 1983, rather than declining (Fig. 6-1h).

In general, the trends in LAI values for litter and standing dead corresponded with similar trends in the amounts of live above-ground biomass (Fig. 6-2). In the exclosures, LAI values were consistently higher than those from the adjacent grazed sites. LAI values for litter in the latter sites ranged between 0.1 and 0.5, while the values from the exclosures were between 0.5 and 6.0. In Exclosures 2,3 and 5, the initial LAI values, which were obtained in June 1983, were the highest for the summer; they dropped in mid-July onwards in all three exclosures. Such large decreases were not observed in measurements of standing crop.

6-3-4 Changes in the Composition of Plant Species in Exclosures of Different Ages

In addition to changes in the litter levels and live standing crop values in exclosures left ungrazed for various lengths of time, there were considerable changes in the species composition of the

Figure 6-3 shows the relative frequency of different species in 1982 and 1983 in Exclosure 5, which was established in 1979, and in the adjacent grazed area. Relative frequency was calculated according to the following method:

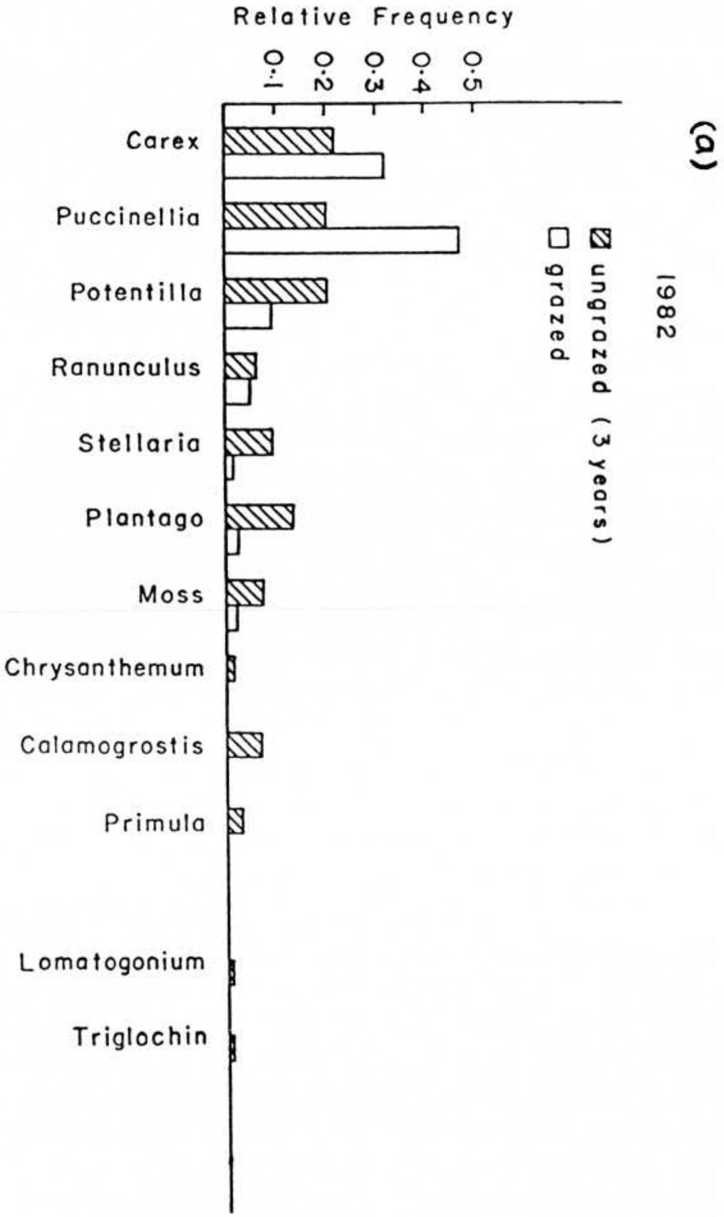
$$\text{Relative frequency of Species a} = \frac{x_a}{x_a + x_b + \ldots x_n}$$

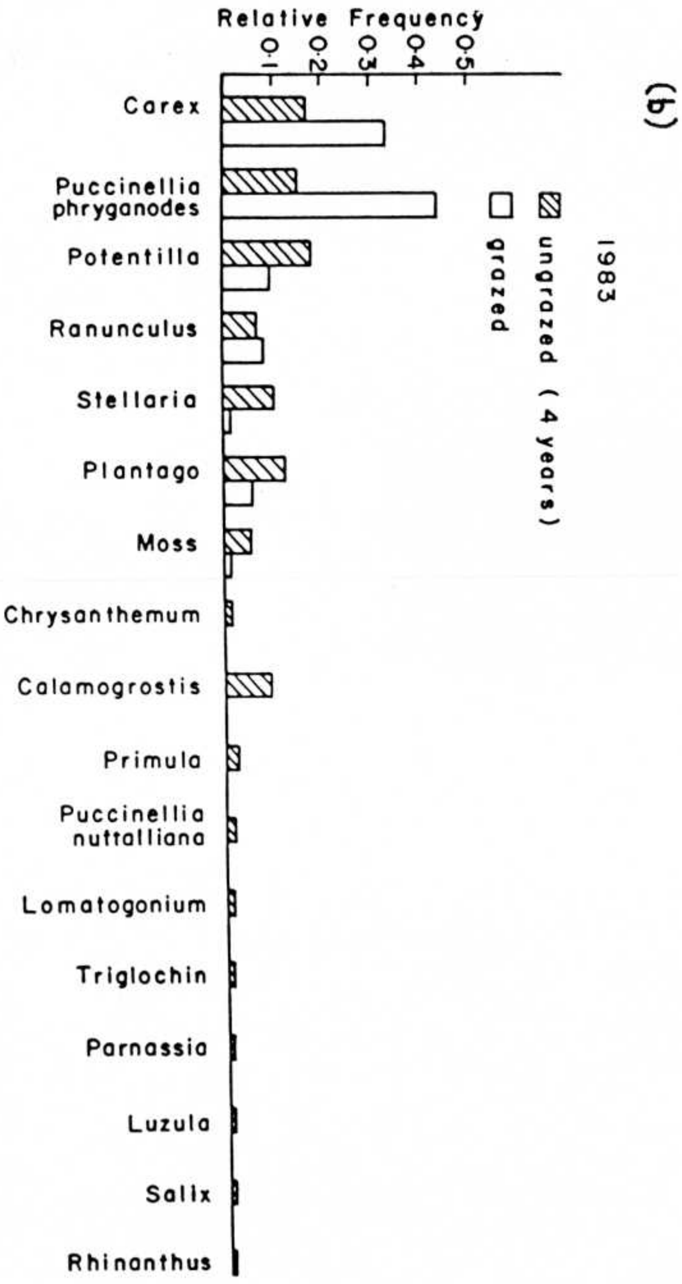
where Xn = number of 5 cm x 5 cm quadrats out of a total of 200, in which species "n" was present .

Figure 6-3. Relative frequency of plant species present in grazed (□) swards dominated by *Puccinellia phryganodes*, and in an ungrazed exclosure (▨) erected in 1979 in a sward originally dominated by *P. phryganodes* at La Pérouse Bay. (Relative frequency based on presence-absence of species in 200, 5cm x 5cm quadrats thrown inside the exclosure and 200 quadrats thrown in the adjacent grazed site.)

a. Relative frequency in 1982. Exclosure aged three years.

b. Relative frequency in 1983. Exclosure aged four years.


(a)
1982
▨ ungrazed (3 years)
☐ grazed
Relative Frequency
0·1
0·2
0·3
0·4
0·5
Carex
Puccinellia
Potentilla
Ranunculus
Stellaria
Plantago
Moss
Chrysanthemum
Calamogrostis
Primula
Lomatogonium
Triglochin


(b)
1983
▨ ungrazed (4 years)
☐ grazed
Relative Frequency
0·1
0·2
0·3
0·4
0·5
Carex
Puccinellia phryganodes
Potentilla
Ranunculus
Stellaria
Plantago
Moss
Chrysanthemum
Calamogrostis
Primula
Puccinellia nuttalliana
Lomatogonium
Triglochin
Parnassia
Luzula
Salix
Rhinanthus

This calculation gives a measure of the occurrence of a particular species relative to the occurrence of other species. Figure 6-4 shows the absolute frequency of the occurrence of these species as a percentage of the number of the 200 quadrats in which they were present.

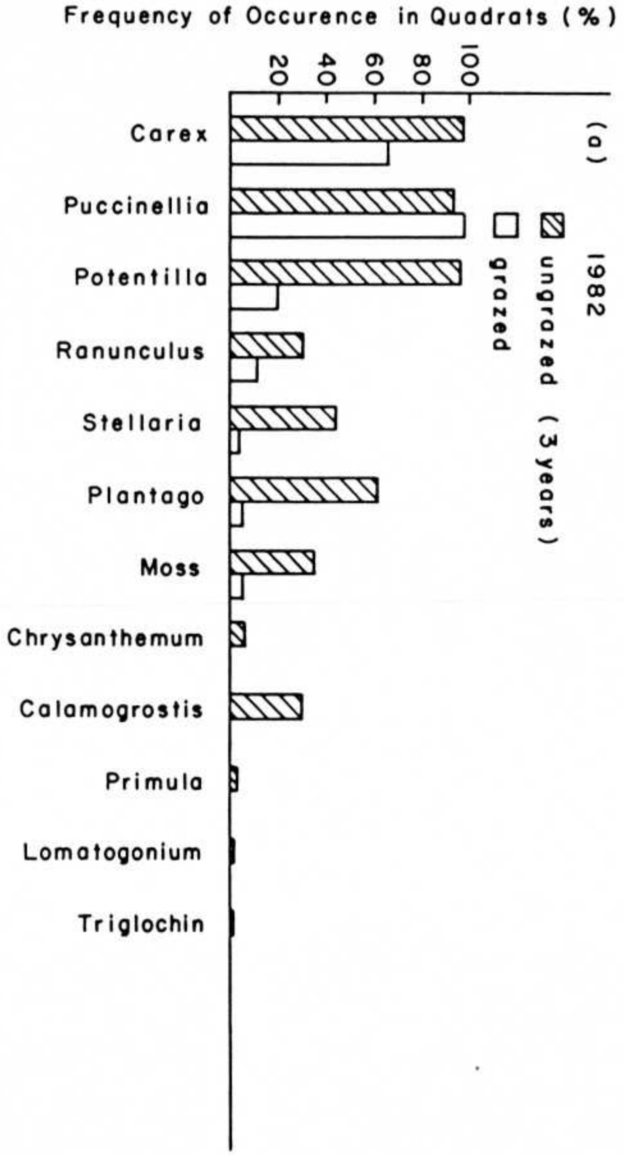
In both 1982 and 1983, the grazed area adjacent to the exclosure, was dominated by Carex subspathacea and Puccinellia phryganodes, both of which were present in nearly all of the quadrats (Figs. 6-3 and 6-4). Puccinellia was observed more frequently than Carex. Five other species occurred in the grazed site at much lower frequencies. Potentilla egedii was observed at frequencies of 0.095 and 0.09 in 1982 and 1983 respectively (Fig. 6-3). Ranunculus cymbalaria was the next most frequently occurring species. Stellaria humifusa, Plantago maritima, and a species of moss were also present at very low frequencies. In 1983, there was an increase in the relative frequency of Ranunculus and Plantago; a trend which has continued in 1984. The value for Ranunculus was 0.08 in 1983, and 0.05 in 1982. That for Plantago was 0.05 in 1983 and 0.025 in 1982 (Fig. 6-3).

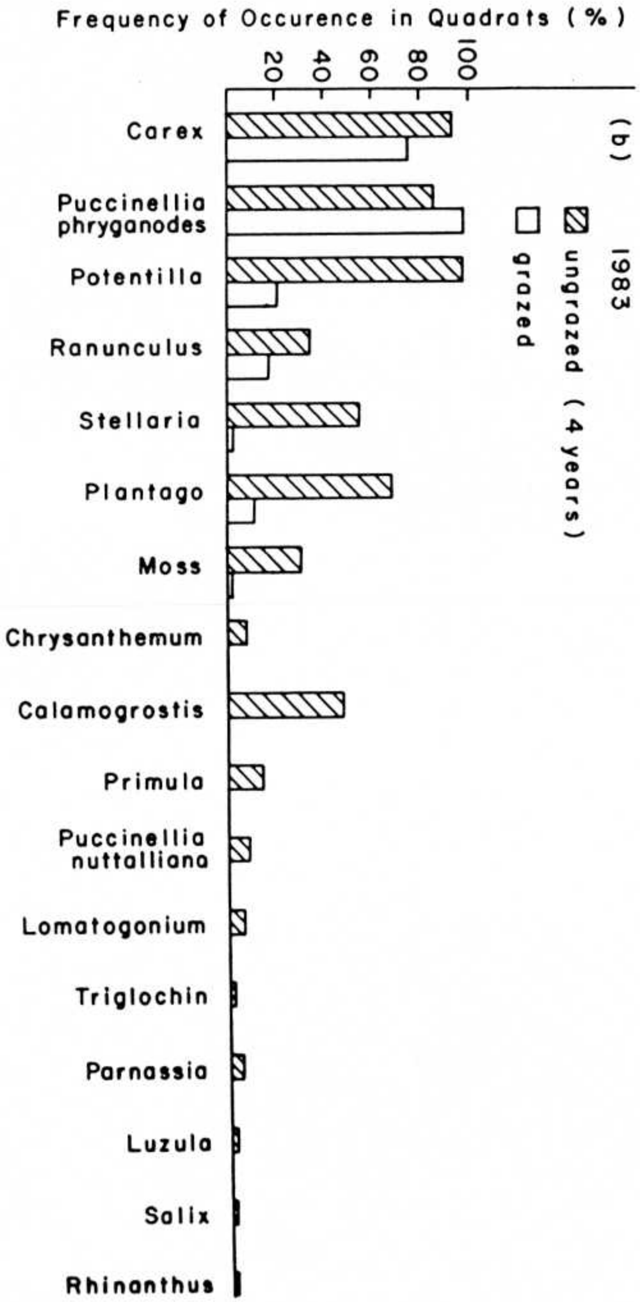
In Exclosure 5, the total number of species present was much higher than in the grazed site. In 1982, when it was three years old, a total of 12 different plant species were scored in the exclosure (Fig. 6-4a), and the following year, when this exclosure was four years in age, a total of 17 plant species were observed in it (Fig. 6-4b). This was ten more species than were recorded in

Figure 6-4. Frequency of occurrence of plant species present in grazed (□) swards dominated by *Puccinellia phryganodes* and in an ungrazed exclosure (▨) erected in 1979 in a sward originally dominated by *P. phryganodes* at La Pérouse Bay. (Absolute frequency based on presence-absence of species in 200, 5cm x 5cm quadrats thrown inside the exclosure, and 200 quadrats thrown in the adjacent grazed site).

a. Absolute frequency in 1982. Exclosure aged three years.

b. Absolute frequency in 1983. Exclosure aged four years.


Frequency of Occurence in Quadrats (%)
20
40
60
80
100
(a)
1982
ungrazed (3 years)
grazed
Carex
Puccinellia
Potentilla
Ranunculus
Stellaria
Plantago
Moss
Chrysanthemum
Calamogrostis
Primula
Lomatogonium
Triglochin


Frequency of Occurence in Quadrats (%)
20
40
60
80
100
(b)
1983
ungrazed (4 years)
grazed
Carex
Puccinellia phryganodes
Potentilla
Ranunculus
Stellaria
Plantago
Moss
Chrysanthemum
Calamogrostis
Primula
Puccinellia nuttalliana
Lomatogonium
Triglochin
Parnassia
Luzula
Salix
Rhinanthus

adjacent grazed site. The additional species found in Exclosure 5 were: Chrysanthemum arcticum, Calamagrostis deschampsioides, Primula egaliksensis, Lomatogonium rotatum and Triglochin palustris. In 1983, the additional species were Puccinellia nuttalliana, Parnassia palustre, Luzula arctica, Rhinanthus borealis and a Salix sp. seedling. All of these species occur in locations to the south of the salt marsh flats, and they also grow on hummocks scattered throughout grazed areas on the edges of the marsh, on which the geese do not graze.

Not only were there increases in the number of plant species present at ungrazed sites, but the relative and absolute frequencies of the species common to both grazed and ungrazed sites also changed Figs. 3-3 and 3-4). In 1982, the relative frequencies of Puccinellia and Carex dropped to 0.20 and 0.21 respectively in Exclosure 5, compared to the corresponding values of 0.46 and 0.32 in the grazed site, while that of Potentilla increased to 0.21 in the exclosure, compared with 0.095 in the grazed site (Fig. 6-3a). This indicated that although the former two species were present in most of the quadrats in the exclosure, there were also many other species commonly observed in the quadrats, and Potentilla was present at the same frequency as Puccinellia and Carex (Fig. 6-4a). Compared with the grazed site, Plantago, Stellaria, Ranunculus and moss were also much more common in the exclosure (Figs. 6-3a and 6-4a).

Table 6-2. Total number of plant species present in grazed sites and exclosures of different ages at La Pérouse Bay, Manitoba, in 1982 and 1983.
Refer to Table 6-1 for explanation of exclosure numbers.

		1982		1983	
Exclosure No.	Date of Erection	No. of Species in Exclosure	No. of Species in Grazed Site	No. of Species in Exclosure	No. of Species in Grazed Site
6	1983	-	-	7	7
7	1982	6	6	6	7
8	1981	7	6	7	6
3	1980	9	9	9	6
5	1979	12	7	17	7

In the exclosures built immediately following thaw in a particular year or which were one or two years of age, the number of species present was either equal to, or greater than, that in the adjacent grazed area. In the three- and four-year old exclosures, there was an increase in the total number of species present.

Although total numbers of species may have been similar in the younger exclosures to those in adjacent grazed areas, the relative frequencies of the different species were very different. Figure 6-5 shows the relative frequencies of the five most common species: Puccinellia, Carex, Potentilla, Ranunculus and Stellaria, in exclosures of different ages, and in the adjacent grazed sites. Overall values for the relative frequency of species in grazed sites were obtained by taking the average of the relative frequencies for each species at each grazed sitee. A decline in the relative frequencies of Puccinellia and Carex with time was observed (Figs. 6-5a and 6-5b). In 1983, the new exclosure had very little Carex growing in it compared with the outside. This was because the sward occupied by the exclosure was dominated by Puccinellia to a much greater extent than the surrounding swards. There was an immediate increase in the relative frequency of Potentilla following the erection of the exclosures, which was evident in older exclosures. However, the exclosure aged one year in 1982, was in a very wet site, which contained little Potentilla compared with the adjacent, grazed, drier sites (Fig. 6-5c). In 1983, when this same exclosure was two-years old, the relative frequency of Potentilla increased by nearly 100%. The relative frequency of Ranunculus increased

Figure 6-5. Relative frequencies of *Puccinellia phryganodes*, *Carex subspathacea*, *Potentilla egedii*, *Ranunculus cymbalaria*, and *Stellaria humifusa* in grazed sites and in exclosures of different ages in 1982 (☐) and 1983 (▨). Relative frequencies are based on presence-absence of species in 200, 5cm x 5cm quadrats thrown inside the exclosures. Relative frequencies for grazed sites are Mean +/-S.E., n=4 or 5; the latter relative frequency values were from 4 or 5 grazed sites at each of which 200 quadrats were thrown).

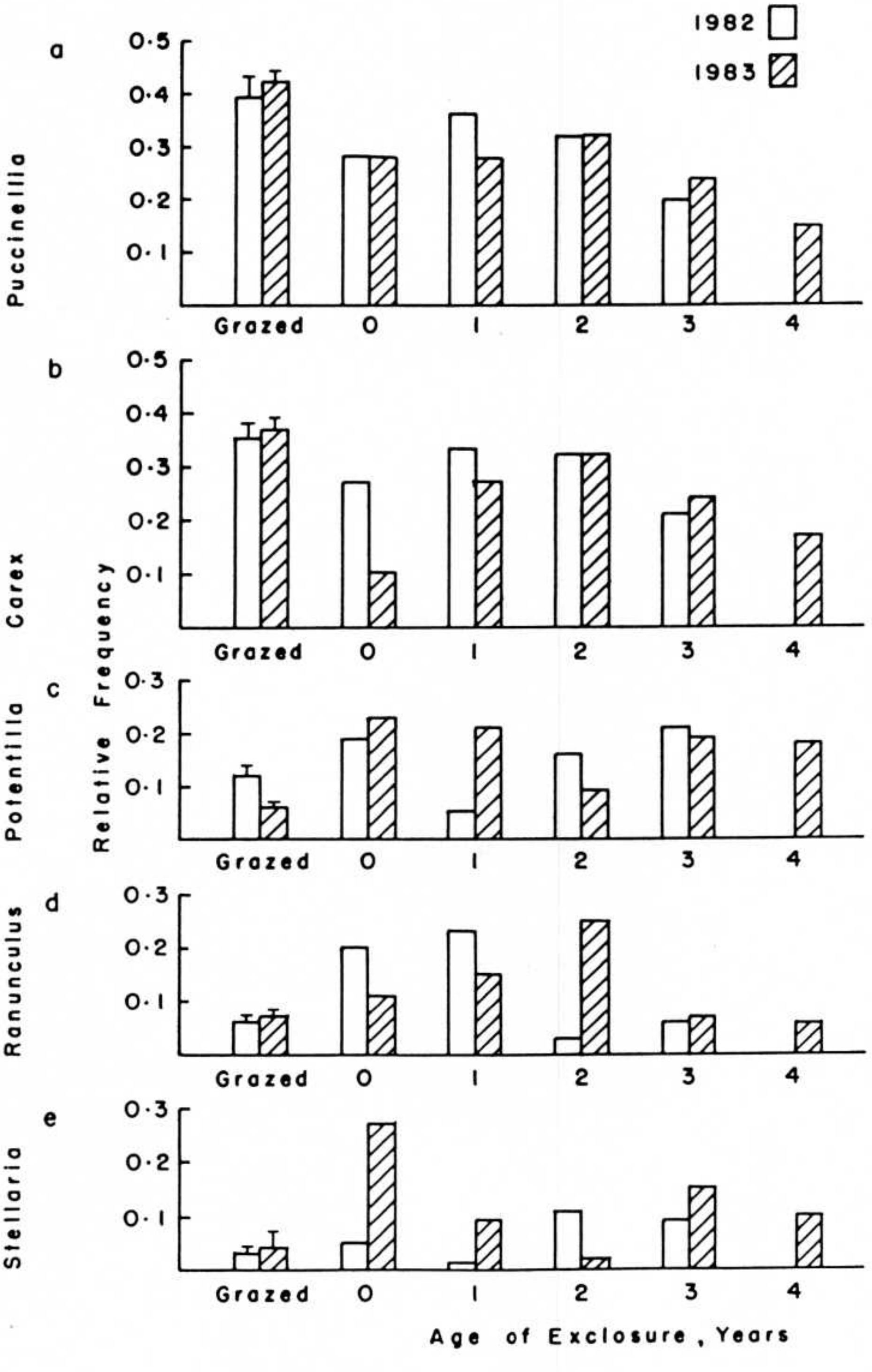
a. *Puccinellia phryganodes*

b. *Carex subspathacea*

c. *Potentilla egedii*

d. *Ranunculus cymbalaria*

e. *Stellaria humifusa*

1982 ☐
1983 ▨
a
Puccinellia
b
Carex
c
Potentilla
d
Ranunculus
e
Stellaria
Relative Frequency
0·5
0·4
0·3
0·2
0·1
Grazed
0
1
2
3
4
Age of Exclosure, Years

immediately after a site was left ungrazed (Fig. 6-5d), whereas in the older exclosures, it has started to decline. The relative frequency of Stellaria increased more slowly in the exclosures. The new exclosure built in 1983 contained a larger number of Stellaria plants than any other site. By comparison, the one-year old exclosure in 1982 contained low levels of Stellaria, but the frequency increased in 1983.

The data on the presence and absence of species in grazed and ungrazed sites, indicate that grazing decreases the number of plant species present, and that Puccinellia and Carex are the most frequently occurring of the species. These data suggest that the ratios of the dry weights of different species obtained in the standing crop measurements should be different for grazed sites and exclosures of different ages. An examination of the contributions made by different species to the total standing crop measurements, indicated that in the three- and four-year old exclosures, species other than Puccinellia and Carex accounted for up to 30% of the total dry weight, while in the grazed sites these latter two species accounted for in excess of 95% of the total dry weight.

6-4 DISCUSSION

The absence of grazing for periods of time longer than one season resulted in the following:

(1) The accumulation of litter and decreasing amounts of live biomass.

(2) An increase in the number of plant species.

(3) The revival of successional processes.

(4) Increases in the variability of sites which had previously appeared homogeneous in their species composition and levels of live standing crop.

Reasons for the fall in net primary production and amounts of live biomass have been discussed in relation to the effects of grazing on growth and the cycling of nitrogen (Chapters 3 and 5). In the absence of snow geese, the availability of nitrogen and net primary production declined after one season because, in part, the source of nitrogen derived from snow goose droppings was absent. The source of nitrogen from diazotrophic blue-green algae was also probably affected. Results in Chapter 5 indicated that in a three-year old exclosure, the input of nitrogen from fixation dropped greatly. An inspection of surface sediment samples from this exclosure revealed that there were no colonies of blue-green algae present in September, 1983. Diazotrophic activity was not tested in younger exclosures, and blue-green algae may have been present on the sediments.

However, even after short term exclusion of geese, there would have been shading of the soil surface as a result of the presence of a higher amount of standing crop. This biomass was not removed by the geese, and after its senescence at the end of summer, it would have remained on the surface and covered up any algal colonies growing on the sediments. During each successive year litter continues to accumulate. The demographic results in Chapter 4 indicate that there is a rapid turnover of leaves on Puccinellia shoots. Thus, litter continually accumulates during the summer. This litter accumulation destroys suitable habitats for surface algal species, and brings about environmental changes in the soil environment which have been discussed in Chapter 5.

There have been few studies of the long term effects of the removal of grazers on the levels of biomass and production in an ecosystem. Kelly and Walker (1976) observed declines of 66% and 80% in seasonal production, after the exclusion of cattle from a savanna grassland for five years. The importance of herbivores in facilitating energy flow by reducing the accumulation of litter in grazed areas, has however been observed by a number of researchers (Kelly and Walker, 1976; McNaughton, 1976, 1979; Rawes, 1981; Coppock, Detling, Ellis and Dyer, 1983). For example, 135 g m^{-2} of litter were present in ungrazed sites compared with 46 g m^{-2} in an old, heavily grazed prairie dog "town" (Coppock, Detling, Ellis and Dyer, 1983). However, none of these researchers investigated the effects of the litter accumulation on nutrient cycling.

The increases in the numbers of plant species in the absence of grazing were unexpected, because the idea that "a grazing animal tends to be a diversifier of a grassland community" prevails in the literature (Harper, 1977; Crawley, 1983). However, Caughley and Lawton (1981) and Crawley (1983, p. 291) do make the point that grazing has been observed to decrease the diversity of plant species when "selective feeding on a dominant species reduces its vigour and allows the spread of less competitive, but more grazing tolerant (or less heavily grazed) plants".

In the Pennines, exclusion of sheep for eight years resulted in a drop from 90 to 67 in the number of plant species present, and this trend continued for a further sixteen years (Rawes, 1981). The intensive grazing activities of rabbits in chalk grasslands have been shown to be important in the maintenance of a high diversity of species and six years after the removal of grazing pressure, the number of plant species had decreased drastically (Harper, 1977). In prairie areas colonized by herbivorous prairie dogs, the diversity of plant species was found to be highest in an area that had been occupied by the animals for three to eight years; it declined to levels similar to those in uncolonized sites in an old dog town site that had been used for 25 years (Coppock, Detling, Ellis and Dyer, 1983). Thus, after very long periods of usage, species diversity did decline as a result of prolonged grazing.

Other, apparently equivocal results relating to the effects of grazing on species diversity were observed by Watt (1981a, 1981b) and by Rice and Westoby (1978). After six years of exclusion of rabbits from Breckland, the number of species present in Watt's (1981a) exclosures dropped. However, during the following 37 years the total number of species increased, although not all species were present at the same time. In a study of plant communities in Curlew Valley, Utah, protected from grazing by jack-rabbits and sheep for between six and fifteen years, there were no significant changes in the numbers or abundances of species over this period (Rice and Westoby, 1978). Therefore, it is difficult to make generalizations about the effects of grazing on plant species richness and diversity. Watt's (1981a,1981b) studies indicate that changes taking place in plant communities following the exclusion of grazers should be studied in detail in order to determine the underlying mechanisms.

In the absence of grazing at La Pérouse Bay, the relative proportions of plant species, other than *Puccinellia* and *Carex*, contributing to the total live biomass production increased and the number of species present increased by over 200% in four years. Two of the dicotyledenous species which increased greatly in abundance in the exclosures were *Potentilla* and *Ranunculus*. They are rosette forming species that are able to reproduce vegetatively by forming stolons. The snow geese prevented their spread in grazed areas by nipping off these stolons H. Sadul and R.L. Jefferies, unpubl.). Rosettes inside a two year-old exclosure had many stolons, while those outside had none. Also, in July of each summer, most of the *Potentilla* and *Ranunculus* rosettes inside the exclosure flowered, while those outside did not. Therefore, the geese must have picked or nibbled flower buds. Bishop and Davy (1984) found that there was a shift to an older age-structure in populations of *Hieracium pilosella* exclosed from rabbits. This was because grazing released the inhibition of flowering, and the onset of flowering triggered increased clonal growth (Bishop and Davy, 1984). In the exclosures fewer rosettes of *Potentilla* flowered, but it seemed to be a larger number, because all of the flowers opened. Unlike geese, the rabbits did not bite off stolons and *H. pilosella* was able to spread in grazed areas (Bishop and Davy, 1984).

Potentilla, *Ranunculus* and other dicotyledonous species which were present in exclosures, were obviously not the preferred forage of the snow geese, which did not feed selectively on them. Harwood (1974) also noted that snow geese at McConnell River avoided such species. They may have done so because their cranial morphology is not adapted to stripping leaves from shrubs, and the leaves have thick leaf cuticles which might resist digestion in the relatively simple gut. In addition the leaves are likely to contain toxic secondary compounds (Harwood, 1974). Since the geese do avoid these species which grow on mounds at the upper edge of the marsh, it is logical to predict a change in the grazed plant community over time similar to that observed in African grasslands. In the latter the seedlings of less palatable woody shrubs are completely avoided by herbivores (Kelly and Walker, 1976; Taylor and Walker, 1976) which allows them to compete successfully with grasses. However, at

La Pérouse Bay, dicotyledenous species present at low frequencies in grazed sites do not grow well, and other species which are not eaten by snow geese fail to establish.

Evidence suggests that two main factors prevent species other than Puccinellia and Carex from competing successfully in grazed areas. First, there are the trampling effects of the geese, which Jefferies, Jensen and Abraham (1979) found to have an impact large enough to lead to the formation of small ponds in some areas. Young seedlings of species such as Plantago, Primula, Stellaria and Lomatogonium would probably not tolerate heavy trampling. Secondly, the feeding habits of the goslings appear to restrict establishment. In 1982, the crops of three adult snow geese were examined in July, and only shoots of Puccinellia and Carex were found, while Potentilla and Hippuris leaves were also found in low quantities in the crops of two goslings collected at the same time. The goslings must learn which plant species are best to eat (Harwood, 1974) and it is possible that in the process, they nibble at other species enought to prevent their growth in grazed areas.

The diversity in the grazed sites may be greater than meets the eye, if it is viewed on a different level. Harper (1977) pointed out that "the diversity of a plant community is inadequately described by the number or abundance of the different species within it". A large amount of species diversity exists at intraspecific levels (Harper, 1977). There is much genetic variability within and between populations of Puccinellia phryganodes in the Arctic, inspite of the fact that this species is thought to only reproduce vegetatively, as it is a sterile triploid (Jefferies and Gottlieb, 1983). Thus, diversity at the genotype level in *Puccinellia* under the influence of grazing may well exist at La Pérouse Bay. Preliminary morphological studies suggest that different phenotypes occur in grazed versus ungrazed sites (H. Sadul and R.L. Jefferies, unpubl.). Gray and Scott (1980) found that tillers of *Puccinellia maritima* from grazed salt marshes in England were smaller and more prostrate than those in ungrazed marshes, and that the former produced tillers faster.

Wiegert and Owen (1981) also stressed the importance of distinguishing between an individual ramet or tiller and genet, which is the evolutionary individual in grasses. In predominantly asexually reproducing perennial grasses such as *Puccinellia phryganodes*, there may be very large, long lived genets or clones, for which the probability of extinction of the genotype decreases as more tillers form, even though other tillers may die (Wiegert and Owen, 1981). This assumption forms part of the basis for the hypothesis that grasses and grazers are co-evolved (Wiegert and Owen, 1981). The survival of these long lived genets was postulated as the chief benefit occuring to grasses in the presence of grazers (Wiegert and Owen, 1981). Silvertown (1982) pointed out that many grasses do grow in the absence of grazers. Even though *Puccinellia* and *Carex* do not compete as well in the absence of the geese, and their biomass declines, it is unlikely that this plant-herbivore interaction has co-evolved. There are many coastal salt marshes in the arctic where *Puccinellia* forms pure swards in the absence of snow geese (Porsild and Cody, 1980).

A further criterion that must be met in order for co-evolution to be considered in a plant-herbivore interaction, is that it must trigger evolutionary changes within the two populations (grazer and grazed populations) (Silvertown, 1982). This is unlikely to be the case at La Pérouse Bay, although the snow geese may act as agents of selection on the different forms of *Pucinellia* occurring in the marsh. The reason for the lack of likelihood of an evolutionary change occurring in *Puccinellia* is related to the successional processes taking place. As the elevation increased and sites became drier due to isostatic, rebound, Jefferies, Jensen and Abraham (1979) observed that *Puccinellia* was present at lower frequencies. Thus, in the natural successional process this species is an initial colonizer and its dominance of the plant community eventually declines. The snow geese do retard the vegetational process and prolong the dominance of *Puccinellia*. However, as environmental constraints overcome those imposed on the plant community by grazing, it is predicted that *Puccinellia* is outcompeted in drier the sites.

The previous points raise the question of the stability of the interaction of the snow geese with the salt-marsh vegetation. The geese have a stabilizing effect on the vegetation in that they reduce the variability of the species present at different sites, which may be environmentally different. For example, one site may be wetter than another, but grazing imposes a stability that results in the same plant species being present at both sites. An example of the heterogeneity between sites which only becomes apparent after the exclusion of geese, was observed in 1983 in two, two year-old exclosures: no. 2 and no. 8. A casual inspection of the former made it clear that it contained two or three more species than the latter, a much wetter site, which still contained only seven species.

Mathematical theories of stability and diversity have often been applied to field studies (McNaughton, 1977; Walker, Ludwig, Holling and Peterman, 1981; Zaret, 1982). In a study of a savanna, Walker, Ludwig, Holling and Peterman (1981) examined the ability of the community to absorb the disturbance by returning to its original state. This is the definition of stability given by Pimm (1984). In this savanna system, grazing was the disturbance, and the stability was defined as an equilibrium between grasses, grazers and woody plants.

Thus, "overgrazing" and plant destruction would require higher numbers of geese. If there was a drastic increase in the population of nesting birds, their forage requirements could be met by grazing in peripheral areas of the marsh dominated by Puccinellia and Carex. In other words, they would expand their feeding grounds, and this is entirely possible at La Pérouse Bay.

May (1974) has shown that plant-herbivore-carnivore interactions may be more stable than plant-herbivore interactions, if there is a long time lag in the recovery of the vegetation compared with the growth rate time of the herbivore population. At La Pérouse Bay, the vegetation apparently has a relatively short recovery rate while being grazed. However, it is important to note that the main population control in the snow goose population is hunter-kill. This does not take place on the breeding grounds but may well be contributing to the stability of the grazing interaction, by fulfilling the role of the "carnivore".

A more serious perturbation to the system may be "undergrazing". As plant species not eaten by the geese invade and dominate the exclosures, they may be permanently lost as forage sites. In 1982, a one year old exclosure was removed, and by the end of the summer, very little grazing had taken place in the exclosure . However, this may have been because it was a 5m x 5m area in a large area of grazed marsh, and was avoided in favour of better forage close by. At least in the short term, heavy grazing by snow geese maintains inputs of nitrogen and high levels of preferred species of forage. Eventually, as isostatic rebound proceeds these areas will be lost, but they could be replaced by new areas of *Puccinellia* marsh emerging from Hudson Bay.

CHAPTER 7

GENERAL DISCUSSION

At the La Pérouse Bay breeding colony, grazing by snow geese results in significant increases in net above-ground primary production compared with ungrazed, exclosed sites. The geese appear to limit the immobilization of nitrogen in plant litter. Snow goose droppings, which contain a high proportion of soluble nitrogen provide an available source of this, otherwise, limiting nutrient (Cargill and Jefferies, 1984a) for plant growth. The export of nitrogen from the marsh by the snow geese in the form of protein may well be compensated for by inputs of nitrogen by diazotrophic blue-green algae. However, the data on acetylene reduction rates and nitrogen-fixing activity do not allow a reliable estimate to be made of the magnitude of nitrogen input to the salt marsh flats. This estimate is necessary in order to assess whether the input of nitrogen from this source is equivalent to the export of nitrogen from the marsh by the geese, which Cargill (1981) estimated to be of the order of 2 g m^{-2}. Questions relating to diurnal fluctuations in ARA, diazotrophic activity in the rhizosphere of the plant species occurring in grazed and ungrazed sites, and changes in the species composition and numbers of suspected diazotrophic blue-green algae growing on sediment surfaces in grazed areas, remain unresolved. Nevertheless, on all sample dates, ARA was higher in grazed than in ungrazed areas.

The mechanism of the increased above-ground production of P. phryganodes in response to grazing is an increased production of axillary shoots. Early results from a demographic study of Carex subspathacea, the other species on which the geese graze heavily, indicate that there is a higher rate of production of leaves in grazed compared with ungrazed swards (P. Kotanen and R.L.Jefferies, unpubl.).

In the absence of grazing, species which occur at low frequencies in grazed sites increase in abundance, and the relative proportions of Puccinellia and Carex contributing to above-ground biomass decline. According to conventional grazing theory, this would suggest that the rarer species in the grazed areas are selectively grazed by the snow geese. However, this is not the case, as these other species - Potentilla egedii, Ranunculus cymbalaria and Stellaria humifusa - are abundant in higher, ungrazed patches in the edges of the grazed flats (ie. they are not grazed). Also, when the crops of six adult snow geese were examined in July 1982, the only plant species found were Puccinellia and Carex. Species of Hippuris and Potentilla were found in addition to the grass and sedge in the crops of two goslings collected at the same time. Thus, it appears that Puccinella and Carex are the preferred foods of the geese, although the goslings may not be as selective as the adults in grazing different species. Grazing increases the abundance of the preferred species at La Perouse Bay, probably because of their graminoid growth habit. The rarer dicotyledenous species do not have the advantage of meristems occurring close to the ground. For example, Potentilla and Ranunculus spread by overground stolons which may be easily nipped off by goslings. This is one reason why grazing decreases rather than increases species diversity.

As stated in the general introduction, optimal foraging theory states that a predator will seek food in a manner that optimizes its fitness. The most obvious advantage gained by a snow goose in the La Pérouse Bay ecosystem, is that since heavy grazing increases NAPP, there is more forage available. As mentioned in Chapter 3, the difference in cumulative NAPP between the grazed and the ungrazed sites became apparent approximately six weeks after hatch in each of four summers of study, inspite of varying interseasonal weather conditions. Were this difference to occur any later, for example after the migration, there would be no immediate advantage to the birds in terms of the availability of food during their post-hatch residence at La Pérouse Bay. Thus, the intensive grazing does not have an immediate effect on the growth of Puccinellia and Carex. The only advantage that an end of summer rise in NAPP of grazed sites, occurring after the departure of the geese, might confer on the latter, would be that grazed shoots would have an opportunity to recover from the loss of photosynthetic tissue. Increased growth at the end of the summer would produce photosynthetic assimilate for translocation to below-ground reserves. Such a period of "recovery" growth was observed in September and October, 1983.

Fortunately, for the snow geese the above scenario is only partly true. In 1979, 1980, 1982, 1983, the snow geese were present on the marsh for one to three weeks following the levelling off of biomass accumulation in exclosures. Thus, they were able to take advantage of the additional forage produced in grazed sites. Evidence also indicates that the quality of the forage in exclosures starts to decline as early as two weeks following the hatch period. Cargill and Jefferies (1984b) observed declines in the total nitrogen content of ungrazed Puccinellia shoots in late June, 1979 and in early July, 1980. In 1983, the decline was observed in mid-July, two weeks after hatch. Although the quantity of biomass may have been similar in both grazed and ungrazed sites up to six weeks following hatch, the quality of the forage, in terms of nitrogen content was not. The soluble nitrogen in the droppings was probably the source of the extra nitrogen. Lotero, Woodhouse and Petersen (1966) showed this type of effect with cattle urine. It would be useful to test the total nitrogen levels in the Puccinellia shoots growing under different treatment conditions in the exclosure fertilised with droppings to determine whether the levels of total nitrogen in the control shoots were lower than those in fertilised shoots.

The coloniality of the snow geese on their breeding grounds appears to be a useful strategy for creating optimal foraging conditions. Harwood (1974) in his study of the grazing strategies of snow geese came to a similar conclusion using a different approach, which involved studying the system from the point of view of the goose rather than the vegetation. He did not document increased NAPP in grazed areas, but he did note the maintenance of high levels of total nitrogen in grazed vegetation compared with ungrazed vegetation (Harwood, 1974). If one assumes that a goose selects its food so as to maximise its nitrogen intake, and given that overall total nitrogen content of ungrazed *Puccinella* shoots falls within two weeks following hatch, then from early on in the summer, a snow goose should be selecting grazed plants over ungrazed plants. Thus, the grazed plants, which are the most attractive to the geese because of their higher total nitrogen content, gain the benefit of the nitrogen from droppings, and continue to be the most attractive forage. Harwood (1974) did find that snow geese fed preferentially in mown areas that had been fertilised, in which the nitrogen content was higher than in adjacent unfertilised plots.

In addition to the short term advantages of heavy grazing, there are long term advantages to be considered. Exclusion of geese from grazed sites results in a slowing down of the rate of recycling of nitrogen and the accumulation of litter. Thus, by grazing heavily, the geese maintain the flow of nutrients through the system. Grazing increases the supply of the preferred forage species, as well as its quality. In the light of this, and the amount of discussion in the literature recently, regarding the co-evolution of grasses and grazers, it is tempting to suggest that the La Pérouse Bay grazed system is such an example. Under heavily grazed conditions, the competitive ability of Puccinellia and Carex is apparently greatly enhanced.

One of the major reasons why this system cannot even be considered as an example of co-evolution is that the La Pérouse Bay colony is at most 20 years old. Previous to this there were no reports of such a colony. Also, the coastline is evolving as a result of isostatic rebound. As new land emerges from Hudson Bay, Puccinellia phryganodes is one of the first species to colonize the sediments (Jefferies, Jensen and Abraham, 1979). The subsequent successional processes are unavoidable, and, although the grazing activities of the snow geese retard succession, the environmental changes, which include increased drainage and the creation of drier sites, will eventually preclude the growth of Puccinellia and Carex. In addition, there are vast areas of coastal salt marsh dominated by Puccinellia phryganodes along the coasts of Hudson and James Bay (Porsild and Cody, 1980; Glooschenko and Harper, 1982) on which lesser snow geese do not feed.

It is likely that the snow geese act as a selective agent on shoots of Puccinellia phryganodes. The demography data indicate that Puccinellia occasionally produces very long prostrate trailing stolons from which ten or more axillary shoots may grow in grazed areas. In the ungrazed populations, a larger proportion of shoots with an upright growth habit which produced fewer axillary shoots was observed. The latter would not be expected to grow as well in grazed areas as they would be nipped off more frequently. It is not known whether the different growth forms that have been observed are genetically different or merely indicative of high phenotypic plasticity in Puccinellia. However, the work of Jefferies and Gottlieb (1983), which revealed a high degree of genetic variation within and between various populations of Puccinellia suggests that this point is worth pursuing. Early results (H. Sadul and R.L. Jeffferies, unpubl.) indicate that there are morphological differences between shoots of Puccinellia from grazed areas and from ungrazed sites in the high willow areas, which are maintained in cultivation.

The La Pérouse Bay ecosystem cannot be regarded as stable in the long term, because the underlying environmental constraints are changing. However, the snow geese will always have new areas of Puccinellia on which to graze, as the land emerges from Hudson Bay. There are also areas of Puccinellia further inland, between the beach ridges which appear to be feeding areas favoured by younger pairs of snow geese which have been forced to nest on the periphery of the colony, further away from the marsh flats. This change in feeding habits has taken place in 1983 and 1984.

The original concerns as to whether overgrazing in this system may occur, appear to be ill-founded. McNaughton (1979), Cargill (1981) and Crawley (1983) point out that grazing pressure must be very high in order for there to be sufficient overcropping of resources so as to lower productivity. The majority of studies concerning overgrazing have taken place in grasslands in temperate or tropical zones, in which introduced cattle have upset the equilibrium between the existing herbivores and their forage species (Kelly and Walker, 1976; Walker, Ludwig, Holling and Peterman, 1981). This is not the case with the snow goose, which appears to have reached a point of equilibrium with the vegetation at La Pérouse Bay. This interaction is stable as long as grazing overcomes the environmental constraints imposed by isostatic rebound.

APPENDIX 3-1

Statistical Analyses

Statistical method used to estimate variances and confidence limits for cumulative net above-ground primary production were as follows:

Assumptions

1. The growth is independant from one regrowth period to the next.

2. For a given period of regrowth, the six small exclosures provide six independant observations of growth.

3. Growth is $N(\mu_i, \sigma^2)$, and we suppose equal variances for each observation period.

Observations

	1st regrowth period..............		7th regrowth period
small exclosure 1:	x_{11}	x_{21}.........	x_{71}
⋮	⋮	⋮	⋮
Small exclosure 6:	x_{16}	x_{26}.........	x_{ij}
	$\overline{X}_1$	$\overline{X}_2$	$\overline{X}_7$

where x_{ij} is the amount of regrowth in small exclosure j during regrowth period i.

The production after the ith period as measured by exclosure j is:

$$x_{ij} + \ldots\ldots + x_{ij} \sim N(\mu_1 + \ldots\ldots + \mu_{ij} \sim \sigma^2)$$

Each mean production value for each regrowth period will have a variance associated with it:

$$\sum_{k=1}^{6}(x_{1k} - \overline{X}_1)^2 + \ldots. + \sum_{k=1}^{6}(x_{7k} - \overline{X}_7)^2 \sim \sigma^2 \chi^2_{35}$$

The production after the ith regrowth period as measured by all cages is:

$$\overline{X}_1 + \dots + \overline{X}_i \sim N(\mu_1 + \dots + \mu_{ij} \quad \frac{\sigma^2}{6})$$

An unbiased estimate of σ^2 or variance (pooled) of the final cumulative production value based on the addition of means for each regrowth period is:

$$\hat{\sigma}^2 = \frac{\sum_{l=1}^{7} \sum_{k=1}^{6} (x_{lk} - \overline{X}_l)^2}{35}$$

A confidence interval for $\mu_1 \dots \mu_i$ can be calculated:

$$\text{C.I. for } \mu_1 : \ \overline{X}_1 \ +/- \ z_{\alpha/2} \sqrt{\frac{\hat{\sigma}^2}{6}}$$

$$\text{C.I. for } \mu_1 + \mu_2 : \ (\overline{X}_1 + \overline{X}_2) \ +/- \ z_{\alpha/2} \sqrt{2 \frac{\hat{\sigma}^2}{6}}$$

$$\text{C.I. for } \mu_1 + \dots + \mu_7 : \ (\overline{X}_1 + \dots + \overline{X}_7) \ +/- \ z_{\alpha/2} \sqrt{7 \frac{\hat{\sigma}^2}{6}}$$

The estimated variance, $\hat{\sigma}_i^2$, for each $\overline{X}_i$ is the variance for each mean divided by 6.

$$\text{i.e. } \hat{\sigma}_1^2 \text{ or } \widehat{V(\overline{X}_1)} = \frac{\sum_{j=1}^{6} (x_{1j} - \overline{X}_1)^2}{5 \cdot 6}$$

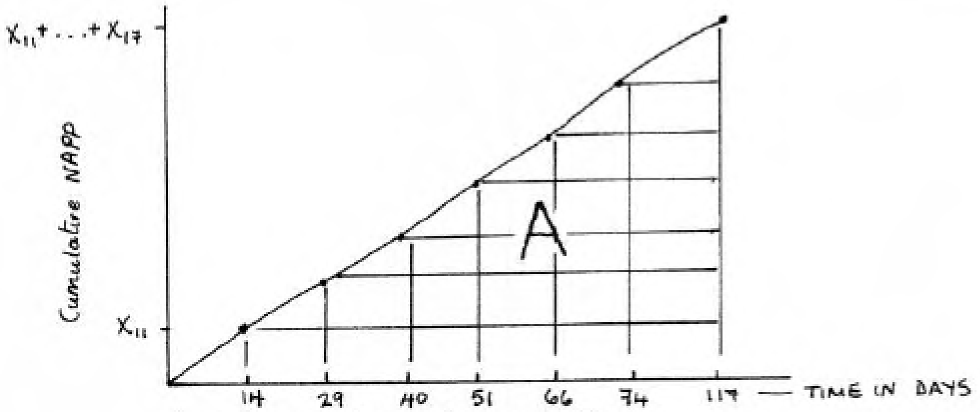
Since each $\hat{\sigma}_i^2$ may be different, they should be summed for each confidence interval estimate:

$$\therefore \sqrt{7 \frac{\hat{\sigma}^2}{6}} = \sqrt{\frac{\hat{\sigma}_1^2 + \dots + \hat{\sigma}_7^2}{6.}}$$

At La Pérouse Bay each x_{ij} was not known for each individual small exclosure, as only final and initial values of standing crop were collected without indicating which initial standing crop value was associated with which final value. Therefore, in matching up initial and final values for each regrowth period for 1982 and 1983, the variance was maximized around each mean regrowth value. The calculations for variance associated with each cumulative NAPP sample point were based on these maximum variance values. "Negative" regrowth, i.e. a drop in standing crop was not allowed, when maximizing the differences between initial and final values.

The following is a proposed test of the difference between final and cumulative NAPP values for grazed and ungrazed sites. It was devised by Martin Bilodeau, who is currently studying for a PhD. in Statistics at the University of Toronto.

<u>Measure of Cumulative Production in Grazed Sites in Small Exclosure 1</u>



A = Area under polygonal lines

$$= 110x_{11} + 99.5x_{21} + 82.5x_{31} + 71.5x_{41} + 58.5x_{51} + 47x_{61} + 21.5x_{71}$$

call $a = \begin{pmatrix} 110 \\ \vdots \\ 21.5 \end{pmatrix}$ $\quad X_1 = \begin{pmatrix} x_{11} \\ \vdots \\ x_{71} \end{pmatrix}$ $\quad A = a' X_1$ $\quad \mu = \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_7 \end{pmatrix}$

$$A \sim N\ (\ a'\mu\ ;\ \sigma^2 a'a\ )$$

If we assume that the variance of growth in the same for grazed and ungrazed areas, σ^2, we have 6 observations of the random variable A for the grazed area.

A further set of 6 (1982) or 3 (1983) observations of a can be calculated for the ungrazed areas.

GRAZED OBSERVATIONS	UNGRAZED OBSERVATIONS
$x_1 \ldots x_6 \sim N(\mu_1, \sigma^2)$	$y_1 \ldots y_2 \sim N(\mu_2, \sigma^2)$

Each x and y is a value of A for the grazed and ungrazed cumulative NAPP curves respectively.

Test $H_0: \mu_1 \leq \mu_2 \quad H_a: \mu_1 > \mu_2$

reject H_0 if $$\frac{\bar{x} - \bar{y}}{S_p \sqrt{\frac{1}{n_x} + \frac{1}{n_y}}} \geq t_{n_x + n_y - 2,\ \alpha}$$

where $$S_p = \sqrt{\frac{\Sigma(x_i - \bar{x})^2 + \Sigma(y_i - \bar{y})^2}{n_x + n_y - 2.}}$$

When a t-statistic was calculated for La Pérouse Bay plant production in 1982 and 1983, there were significant differences between grazed and ungrazed areas for both years at a level of $p < 0.05$, df=10.

APPENDIX 5-1

Calculations used in the Acetylene Reduction Technique

Calculations for converting heights of ethylene peaks on a recorder printout to rates of reduction of acetylene for determination of nitrogenase activity.

1. The peak height obtained from injecting 1 ml of 100 ppm C_1H_4 represented a concentration of 125 ng C_2H_4 per ml. The relationship between peak height and ethylene (C_2H_4) concentration was assumed to be linear.
2. Therefore, the amount of ethylene in 1 ml of gas injected into the chromatograph was:

$$X = \frac{y \times 125}{144}$$

where 125 ng = amount of C_2H_4 per ml of 100 ppm C_2H_4 gas injected

144 mm = mean height of peak for 125 ng of C_2H_4

y = height of peak for unknown amount of C_2H_4

x = amount of C_2H_4 in ml of gas sample from field

3. This value (x) was multiplied by the volume of the plexiglass chamber (1.55 l) to give the amount of ethylene present at specific sample points, for the area (1.54×10^{-4} m^2) covered by the chamber.
4. By calculating the amount of ethylene produced during the twenty minute incubation period and by converting this rate to a m^2 basis, the rate of ethylene production could be converted to moles produced per m^2. This is directly equivalent to moles of acetylene reduced per m^2.

APPENDIX 5-2

Appendix 5-2a - Kjeldahl Acid Digestion of Plant Tissue and Snow Goose Droppings

Reagents:

1. Selenium Powder.
2. Concentrated sulphuric acid (H_2SO_4).
3. Concentrated sodium hydroxide (NaOH) solution - 40% w/v. i.e. 40g NaOH per 100 ml distilled water.

Procedure:

1. Place 10 mg dried plant tissue or goose dropping or 1 ml of resuspended ethanol extract in a test tube.
2. Add two small glass beads to prevent the solution from boiling over.
3. Add approximately 50mg Selenium powder or beads.
4. Add 1 ml of conc. H_2SO_4.
5. Cap the test tube with a glass marble and place on hot plate at 500°C (turn the heat up slowly) for 24 hours or longer if necessary, until the solution is clear. If any selenium volatilizes and sublimes on the walls of the test tube above the solution, carefully resuspend it by shaking or tipping the solution up the test tube until it reaches the selenium deposit.
6. Allow the test tubes to cool completely. Transfer the samples to 25ml volumetric flasks. Add approximately 5ml distilled water and then add 4.3 ml NaOH or enough to bring pH up to 11. Make up solution to 25 ml with distilled water.
7. Carry out ammonium analysis (See Appendix 5-2d).

Appendix 5-2b - Ethanol Extraction of Soluble Nitrogen Fraction of Plant Tissue and Snow Goose Droppings

1. Cut up washed plant shoots weighing at least 1 g fresh weight into fine pieces and place in erlenmeyer flask. If a snow goose dropping is being analysed, take its its fresh weight and place in erlenmeyer flask.
2. Add 60% ethanol (6:4 ratio by volume of absolute ethanol to distilled water) to flask at a ratio of 15 ml ethanol to 1 g fresh weight.
3. Cover flask with parafilm and shake periodically. Break up the dropping with a glass rod.
4. After 24 hours incubation in a cool place, filter the ethanol extract through glass microfibre filter paper (Whatman GF/A) and store in nalgene bottle in freezer.

Frozen samples were transported to Toronto:

1. A known volume of ethanol filtrate is placed in a round-bottomed quick fit flask which is fitted onto a rotary evaporator. (A Brinkmann Rotovapor-R was used). The water bath should be 40°V and the speed, no. 6). The sample is evaporated to dryness.
2. It is resuspended in 1 to 5 ml (known volume) of 0.8M potassium acetate (CH_3COOK), buffered to pH 4.85 with acetate (CH_3COOH).
3. To estimate the nitrogen content in this solution, 1 ml is digested according to the methods in Appendix 5-2a.

Appendix 5-2c - Extraction of KCl - Exchangeable Ammonium Ions from Sediment Samples

Reagent

1. 1 M potassium chloride (KCl) solution.

Procedure

1. Cut soil block to desired dimensions, e.g. 5 cm x 10 cm depth and take its fresh weight.
2. Place soil block in erlenmeyer flask and add potassium chloride solution at a ratio of 5 ml solution to 1 g fresh weight of sediment.
3. Break up soil block with a glass rod and shake flask well. Cover with parafilm and let stand for a minimum of 4 hours, shaking the flask periodically to stir the sediments.
4. Filter KCl-extract through Whatman no. 1 filter paper into clean erlenmeyer flasks. Analyse the extracts as soon as possible for ammonium-nitrogen content according to the procedure outlined in Appendix 5-2d.

Appendix 5-2 d - Estimation of Ammonium-Nitrogen in Acid Digestions or in KCl Extract Solutions (Solorzano, 1969).

Reagents

1. Phenol-sodium nitroprusside solution
   10 g. of phenol are dissolved in about 250 ml. of distilled water in a 500 ml. volumetric flask. 50 mg. of sodium nitroprusside is then added and the flask topped to 500 ml. with distilled water.

2. Sodium hydroxide - sodium hypochlorite solution
   5 g. of sodium hydroxide are dissolved in about 250 ml. of distilled water. 8.4 ml. of sodium hypochlorite (12% w/v) are added and the solution diluted to 500 ml. with distilled water.

Procedure

1. Pipette a 1 ml. aliquot of soil or plant solution into a 25 or 10 ml. volumetric flask. Add distilled water until flask is half-full.

2. Add 1 ml. of phenol nitroprusside solution and shake flask.

3. Add 1 ml. of sodium hydroxide-hypochlorite solution and shake flask.

4. Make up to the mark with distilled water. Incubate flask in a water bath at 30°C for 20 minutes.

5. After allowing 20 minutes for the colour to develop, the absorption is measured at 625 nm.

Standards

1. A standard ammonium chloride solution is made up by dissolving 3.821 g. of ammonium chloride into 2 litres of distilled water (equivalent to 500 mg N l^{-1}). 5 ml. are then taken and diluted to 100 ml. with distilled water to give a final concentration of 25 mg N l^{-1}.

2. A standard curve is prepared by using 0.1 to 1.0 ml. aliquots of the standard solution with any adjustments to 1 ml. made by adding distilled water. The procedure than continues from step #2 given above.

Appendix 5-2e Estimation of Nitrate-Nitrogen in KCl Extract Solutions and Soil Water of Sediments

Reagents

1. 1 gram of sulphanilic acid dissolved in 100 ml. of 2 M HCL over a hot plate (less than or equal to 70°C).
2. 50 mg. N-(1-Napthyl)-ethylenediamine Dihydrochloride dissolved in 100 ml. of distilled water.
3. Zinc dust.
4. 1 M Ammonium hydroxide solution.

Procedure

1. Pipette 2 ml. of plant solution or 1 ml. of soil solution into a centrifuge tube.
2. Add 2 ml. of ammonium hydroxide solution.
3. Add approiximately 50 mg. zinc dust with a spatula.
4. Spin on a shaker for 2 minutes.
5. Centrifuge for 5 minutes at 3000 r.p.m.
6. Pipette 1 ml. of supernatant into a test tube.
7. Add 1 ml. of sulphanilic acid solution and mix.
8. Add 1 ml of napthyl-ethylenediamine solution and mix.
9. The colour becomes stable after 15 minutes, after which the sample can be read at 540 nm. in a spectrophotometer.

Standards

1. A standard solution of 4 mg. N l^{-1} is made up using KNO_3 or Na_2NO_3.
2. A standard curve is prepared by using 0.1 to 1.0 ml. aliquots of the standard solution. The volume in the centrifuge tube is adjusted to 1 ml. with distilled water. The procedure then continues from step #2 as given above.

REFERENCES

Akiyama, T., Takahashi, S., Shiyomi, M. and Okubo, T. 1984. Energy flow at the producer level. The energy dynamics of grazed grassland I. Oikos 42: 129-137.

Alexander, K.I. and Thompson, K. 1982. The effect of clipping frequency on the competitive interaction between two perennial grass species. Oecologia. 53: 251-254.

Alexander, M. 1977. Introduction to Soil Microbiology 2nd Ed. John Wiley and Sons, Toronto.

Alexander, V., Billington, M. and Schell, D.M. 1978. Nitrogen fixation in arctic and alpine tundra. In Vegetation and Production Ecology of an Alaskan Arctic Tundra. ed. L.L. Tieszen. pp. 539-558. Springer-Verlag, New York.

Arber, A. 1934. The Gramineae. Cambridge University Press, Cambridge.

Archer, S. and Tieszen, L.L. 1983. Effects of simulated grazing on foliage and root production and biomass allocation in an arctic tundra sedge (Eriophorum vaginatum). Oecologia. 58: 92-102.

Atlas, R.M. and Bartha, R. 1981. Microbial Ecology: Fundamentals and Applications. Addison-Wesley Publishing Co., Reading, Mass.

Aziz, S.A. and Nedwell, D.B. 1979. Microbial nitrogen transformations in the salt marsh environment. In Ecological Processes in Coastal Environments. ed. R.L. Jefferies and A.J. Davy. pp. 385-398. Blackwell Scientific Publications, Oxford.

Baker, H.R. 1961. The influence of grazing management on grassland production. N.A.A.S. Quarterly Review. 13: 25-29.

Bergersen, F.J. 1970. The quantitative relationship between nitrogen fixation and the acetylene-reduction assay. Australian Journal of Biological Science. 23: 1015-25.

Bews, J.W. 1929. The World's Grasses. Longman's, Green and Company, London.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs. 52: 335-351.

Bishop, G.F. and Davy, A.J. 1984. Significance of rabbits for the population regulation of Hieracium pilosella in Breckland. Journal of Ecology. 72: 273-284.

Bishop, G.F., Davy, A.J. and Jefferies, R.L. 1978. Demography of Hieracium pilosella in breck grassland. Journal of Ecology. 66: 615-629.

Bleken, E. and Ugland, K.I. 1984. The empirical study of coevolution: a critique of Stenseth. Oikos. 43: 125-126.

Brady, N.G. 1974. The Nature and Properties of Soil 8th Ed. Macmillan Publishing Co., Inc., New York.

Brougham, R.W. 1956. Effect of intensity of defoliation on regrowth of pasture. Australian Journal of Agricultural Research. 7: 376-387.

Cameron, R.E., Knox, A.D. and Morelli, F.A. 1978. The role of algae in tundra soil. In Vegetation and Production Ecology of an Alaskan Arctic Tundra. ed. L.L. Tieszen. pp. 207-228. Springer-Verlag, New York.

Campbell, A.G. 1966. The dynamics of grazed mesophytic pastures. Proceedings of the 10th International Grassland Congress, Helsinki. pp. 458-463.

Cargill, S.M. 1981. The effects of grazing by lesser snow geese on the vegetation of an arctic salt marsh. M.Sc. Thesis. University of Toronto.

Cargill, S.M. and Jefferies, R.L. 1984a. Nutrient limitation of primary production in a sub-arctic salt marsh. Journal of Applied Ecology. In Press.

Cargill, S.M. and Jefferies, R.L. 1984b. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology. In Press.

Carpenter, E.J., Van Raalte, C.D. and Valiela. I. 1978. Nitrogen fixation by algae in a Massachusetts salt marsh. Limnology and Oceanography. 23: 318-327.

Caughley, G. and Lawton, J. 1981. Plant-herbivore systems. In Theoretical Ecology 2nd Ed. ed. R. May. pp. 132-166. Blackwell Scientific Publications, Oxford.

Chapman, S.B. 1976. Production ecology and nutrient budgets. In Methods in Plant Ecology. ed. S.B. Chapman. pp. 157-228. Blackwell Scientific Publications, Oxford.

Charnov, E.L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist. 110: 141-151.

Christiansen, M.S. 1979. Grasses, Sedges and Rushes in Colour. Blandford Press, Poole, Dorset.

Cooke, F.C., Abraham, K., Davies, J.C., Findlay, C.S., Healey, R.F., Sadura, A. and Sequin, R.J. 1982. The La Pérouse Bay Snow Goose Project - A 13-Year Report. Dept. of Biology, Queen's University, Kingston, Ontario.

Coppock, D.L., Detling, J.K., Ellis, J.E. and Dyer, M.I. 1983. Plant-herbivore interactions in a north American mixed-grass prairie. I. Effects of Black-Tailed Prairie Dogs on intraseasonal above-ground plant biomass and nutrient dynamics and plant species diversity. Oecologia. 56: 1-9.

Crawley, M.J. 1983. Herbivory: The Dynamics of Animal-Plant Interactions. Blackwell Scientific Publications, Oxford.

Davy, A.J. and Taylor, K. 1974. Seasonal patterns of nitrogen availability in contrasting soils in the Chiltern Hills. Journal of Ecology. 62: 793-807.

Denmead, O.T., Simpson, J.R. and Freney, J.R. 1974. Ammonia flux into the atmosphere from a grazed pasture. Science. 185: 609-610.

Dennis, J.G., Tieszen, L.L. and Vetter, M.A. 1978. Seasonal dynamics of above- and below-ground production of vascular plants at Barrow, Alaska. In Vegetation and Production Ecology of an Alaskan Arctic Tundra. ed. L.L. Tieszen. pp. 113-140. Springer-Verlag, New York.

Desikachary, T.V 1959. Cyanophyta. Indian Council of Agricultural Research Monograph, New Delhi.

Dore, W.G. and McNeil, J. 1980. Grasses of Ontario. Agriculture Canada Monograph 20, Ottawa.

Dyer, M.I. and Bokhari, U.G. 1976. Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57: 762-772.

Etherington, J.R. 1982. Environment and Plant Ecology 2nd Ed. John Wiley and Sons, Ltd., New York.

Evans, G.C. 1972. The quantitative analysis of plant growth. Studies in Ecology, Volume 1. Blackwell Scientific Publications, Oxford.

Fay, P. 1983. The Blue-Greens. Studies in Biology #160. Edward Arnold, London.

Flanagan, P.W. and Bunnell, F.L. 1980. Microflora activities and decomposition. In An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. U.S. IBP Synthesis Series 12. ed. J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell. pp. 291-334. Dowden, Hutchinson and Ross Inc. Pennsylvania.

Floate, M.J.S. 1970a. Decomposition of organic materials from hill soils and pastures. II. Comparative studies of the mineralization of carbon, nitrogen, and phosphorus from plant materials and sheep faeces. Soil Biology and Biochemistry. 2: 173-185.

Floate, M.J.S. 1970b. Decomposition of organic materials from hill soils and pastures. IV. The effects of moisture content on the mineralization of carbon, nitrogen and phosphorus from plant materials and faeces. Soil Biology and Biochemistry. 2: 275-283.

Fletcher, G.M. and Dale, J.E. 1974. Growth of tiller buds in barley: effects of shade treatment and mineral nutrition. Annals of Botany. 38: 63-76.

Frame, J. 1966. The evaluation of herbage production under cutting and grazing regimes. Proceedings of the 10th International Grassland Congress, Helsinki. pp. 291-7.

Freyman, S. 1980. Quantitative analysis of growth in southern Alberta of two barley cultivars grown from magnetically treated and untreated seed. Canadian Journal of Plant Science. 60: 463-71.

Futuyma, D.J. 1979. Evolutionary Biology. Sinauer Associates Inc., Sunderland, Mass.

Gallagher, J.L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of Spartina alterniflora and Juncus roemerianus. American Journal of Botany. 62: 644-648.

Gallagher, J.L. 1983. Seasonal patterns in recoverable underground reserves in Spartina alterniflora. Loisel. American Journal of Botany. 70: 212-215.

Glooschenko, W.A. and Harper, N. 1982. Net aerial primary production of a James Bay, Ontario, salt marsh. Canadian Journal of Botany. 60: 1060-1067.

Glooschenko, W.A. and Martini, I.P. 1978. Hudson Bay Lowlands Baseline Study. In Coastal Zone '78: Proceedings of the Symposium on the Technolgical; Environmental, Sociological and Regional Aspects of Coastal Zone Management. A.S.C.E., California. pp. 663-679.

Godfrey, E.J. 1966. The Birds of Canada. Bulletin #203. National Museum of Canada, Ottawa.

Gould, F.W. and Shaw, R.B. 1983. Grass Systematics 2nd Ed. Texas A and M University Press, Texas.

Granhall, U. and Selander, H. 1973. Nitrogen fixation in a subarctic mine. Oikos. 24: 8-15.

Grant, S.A., Barthram, G.T. and Torvell, L. 1981. Components of regrowth in grazed and cut Lolium perenne swards. Grass and Forage Science. 36: 155-168.

Gray, A.J. and Scott, R. 1980. A genecological study of Puccinellia maritima Huds. (Parl.) I. Variation estimated from single-plant samples from British populations. New Phytologist. 85: 89-107.

Haag, R.W. 1974. Nutrient limitations to plant production in two communities. Canadian Journal of Botany. 52: 103-116.

Hansen, J.I., Henriksen, K. and Blackburn, T. 1981. Seasonal distribution of nitrifying bacteria and rates of nitrification in coastal marine sediments. Microbial Ecology. 7: 297-304.

Hardy, R., Holsten, R., Jackson, E. and Burns, R. 1968. The acetylene-ethylene assay for N_2 fixation: Laboratory and field evaluaton. Plant Physiology. 43: 1185-1207.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London.

Harwood, J. 1974. The grazing strategies of Blue Geese Anser caerulescens. Ph.D. Thesis. University of Western Ontario.

Harwood, J. 1977. Summer feeding ecology of Lesser Snow Geese. Journal of Wildlife Management. 41: 48-55.

Haynes, R.J. and Goh, K.M. 1978. Ammonium and nitrate nutrition of plants. Biological Reviews. 53: 465-510.

Heal, O.W., Flanagan, P.W., French, D.D. and MacLean, Jr., S.F. 1981. Decomposition and accumulation of organic matter in tundra. In Tundra Ecosystems: a Comparative Analysis. ed. L.C. Bliss, O.W. Heal and J.J. Moore. pp. 587-636. Cambridge University Press, Cambridge.

Henriksen, K. and Jensen, A. 1979. Nitrogen mineralization in a salt marsh ecosystem dominated by Halimione portulacoides. In Ecological Processes in Coastal Environments. ed. R.L. Jefferies and A.J. Davy. pp. 373-384. Blackwell Scientific Publications, Oxford.

Henzell, E.F. and Norris, D.O. 1962. Processes by which nitrogen is added to the soil/plant system. In A Review of Nitrogen in the Tropics with Particular Reference to Pastures. Commonwealth Bureau of Pastures and Field Crops, Bulletin #46 pp. 1-18. (cited in Simpson and Stobbs, 1981).

Herrera, C.M. 1982. Grasses, grazers, mutualism and co-evolution: a comment. Oikos. 38: 254-257.

Hodgson, J. 1979. Nomenclature and definitions in grazing studies. Grass and Forage Science. 34: 11-18.

Hopkinson, C.S. and Schubauer, J. 1984. Static and dynamic aspects of nitrogen cycling in the salt marsh graminoid Spartina alterniflora. Ecology. 65: 961-969.

Howes, B., Howarth, R., Teal, J. and Valiela, I. 1981. Oxidation-reduction potentials in a salt marsh: spatial patterns and interactions with primary production. Limnology and Oceanography. 26: 350-360.

Hubbard, C.E. 1984. Grasses 3rd Ed. revised by J.C.E. Hubbard. Penguin Books, Middlesex.

Hulten, E. 1968. Flora of Alaska and Neighbouring Territories. Stanford University Press, Stanford, California.

Hunt, R. 1982. Plant Growth Curves: the functional approach to plant analysis. Edward Arnold, London.

Hussey, A. and Long, S.P. 1982. Seasonal changes in weight of above and below ground vegetation and dead plant material in a salt marsh at Colne Point, Essex. Journal of Ecology. 70: 757-772.

Jefferies, R.L. 1977. The vegetation of salt marshes at some coastal sites in Arctic North America. Journal of Ecology. 65: 661-672.

Jefferies, R.L. 1984. The phenotype: its development, physiological constraints and environmental signals. In Perspectives on Plant Population Ecology. ed. R. Dirzo and J. Sarukhan. pp. 347-358. Sinauer Associates Inc., Sunderland, Mass.

Jefferies, R.L. and Gottlieb, L.D. 1983. Genetic variation within and between populations of the asexual plant Puccinellia X phryganodes. Canadian Journal of Botany. 61: 774-779.

Jefferies, R.L., Jensen, A. and Abraham, K.F. 1979. Vegetational development and the effect of geese on vegetation at La Perouse Bay, Manitoba. Canadian Journal of Botany. 57: 1439-1450.

Jefferies, R.L., Jensen, A. and Bazely, D. 1983. The biology of the annual, Salicornia europaea agg. at the limits of its range in Hudson Bay. Canadian Journal of Botany. 61: 762-773.

Johnsgard, P.A. 1978. Ducks, Geese and Swans of the World. University of Nebraska Press, Lincoln, Nebraska and London.

Jones, K. 1974. Nitrogen fixation in a salt marsh. Journal of Ecology. 62: 553-565.

Jones, M.B., Collett, B. and Brown, S. 1982. Sward growth under cutting and continuous stocking managements: sward canopy structure, tiller density and leaf turnover. Grass and Forage Science. 37: 69-73.

Jordan, D.C., McNicol, P.J. and Marshall, M.R. 1978. Biological nitrogen fixation in the terrestrial environment of a high arctic ecosystem (Truelove Lowland, Devon Island, N.W.T.). Canadian Journal of Microbiology. 24: 643-649.

Kays, S. and Harper, J.L. 1974. The regulation of plant and tiller density in a grass sward. Journal of Ecology. 62: 97-106.

Kelly, R.D. and Walker, B.H. 1976. The effects of different forms of land use on the ecology of a semi-arid region in south eastern Rhodesia. Journal of Ecology. 64: 553-576.

Kenyon, C.N., Rippka, R. and Stanier, R.Y. 1972. Fatty acid composition and physiological properties of some filamentous blue-green algae. Archiv fur Mikrobiologie. 83: 216-236.

Kerbes, R.H. 1975. Lesser snow geese in the eastern Canadian Arctic: Canadian Wildlife Service Report Series #35. Ministry of the Environment, Ottawa.

King, J., Lamb, W.I.C., and McGregor, M.T. 1979. Regrowth of rye grass swards subject to different cutting regimes and stocking densities. Grass and Forage Science. 34: 107-118.

Knowles, R. and Denike, D. 1974. Effect of ammonium-, nitrite- and nitrate-nitrogen on anaerobic nitrogenase activity in soil. Soil Biology and Biochemistry. 6: 353-358.

Krebs, J.R. and McCleery, R.H. 1984. Optimization in behavioral ecology. In Behavioural Ecology: An Evolutionary Approach 2nd Ed. ed. J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford.

Langer, R.H.M. 1979. How Grasses Grow 2nd Ed. Studies in Biology #34. Edward Arnold, London.

Lawrie, A.C. 1981. Nitrogen fixation by native Australian legumes. Australian Journal of Botany. 29: 143-57.

Linthurst, R. and Reimold, R. 1978. An evaluation of methods for estimating the net aerial primary productivity of estuarine angiosperms. Journal of Applied Ecology. 15: 919-931.

Lomnicki, A., Bandola, E. and Jankowska, K. 1968. Modification of the Wiegert-Evans method for estimation of net primary production. Ecology 49: 147-149.

Lotero, J., Woodhouse, W. and Peterson, R. 1966. Local effect on fertility of urine voided by grazing cattle. Agronomy Journal. 58: 262-265.

MacArthur, R.H. 1955. Fluctuation of animal populations, and a measure of community stability. Ecology. 36: 533-536.

Mattheis, P.J., Tieszen, L.L. and Lewis, M.C. 1976. Responses of Dupontia fisheri to simulated lemming grazing in an Alaskan arctic tundra. Annals of Botany, New Series. 40: 179-197.

Mattocks, J.G. 1971. Goose feeding and cellulose digestion. Wildfowl. 22: 107-113.

May, R.M. 1972. Will a large complex system be stable? Nature. 238: 413-414.

May, R.M. 1974. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, New Jersey.

McNaughton, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science. 191: 92-94.

McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. American Naturalist. 111: 515-525.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist. 113: 691-703.

McNaughton, S.J. 1983. Compensatory growth as a response to herbivory. Oikos. 40: 329-336.

Miller, P.C., Webber, P.J., Oechel, W.C. and Tieszen, L.L. 1980. Biophysical processes and primary production. In An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. U.S. IBP Synthesis Series 12. ed. J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell. pp. 66-101. Dowden, Hutchinson and Ross Inc. Pennsylvania.

Muc, M. 1977. Ecology and primary production of Sedge-moss Meadow communities, Truelove Lowland. In Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. ed. L.C. Bliss. pp. 157-184. University of Alberta Press, Edmonton.

Muller, R.A. and Oberlander, T.M. 1974. Physical Geography Today 2nd Ed. Random House, Toronto.

Nowak, R.S. and Caldwell, M.M. 1984. A test of compensatory photosynthesis in the field: implications for herbivory tolerance. Oecologia: 61: 311-318.

Orians, G.H. 1975. Diversity, stability and maturity in natural ecosystems. In Unifying Concepts in Ecology. ed. W.H. Van Dobben and R.H. Lowe-McConnell. pp. 139-150. Dr. W. Junk, The Hague, Netherlands.

Ott, L. 1977. An Introduction to Statistical Methods and Data Analysis. Wadsworth Publishing Co., Inc. Belmont, California.

Owen, D.F. 1980. How plants may benefit from the animals that eat them. Oikos. 35: 230-235.

Owen, D.F. and Wiegert, R.G. 1976. Do consumers maximize plant fitness? Oikos. 27: 488-492.

Owen, D.F. and Wiegert, R.G. 1981. Mutualism between grasses and grazers: an evolutionary hypothesis. Oikos. 376-378.

Owen, D.F. and Wiegert, R.G. 1982a. Reply: Grasses and grazers: is there a mutualism? Oikos. 38: 258-260.

Owen, D.F. and Wiegert, R.G. 1982b. Beating the walnut tree: more on grass/grazer mutualism. Oikos. 39: 115-116.

Owen, D.F. and Wiegert, R.G. 1983. Darwin's "abominable mystery" and the need for speculation in evolutionary ecology. Oikos. 41: 154-155.

Owen, M. 1980. Wild Geese of the World. B.T. Batsford Ltd., London.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist. 100: 65-74.

Parsons, A.J., Leafe, E.L., Collett, B. and Stiles, W. 1983. The physiology of grass production under grazing. I. Characteristics of leaf and canopy photosynthesis of continuously grazed swards. Journal of Applied Ecology. 20: 117-126.

Parsons, A.J., Leafe, E.L., Collett, B., Penning, P.D. and Lewis, J. 1983. The physiology of grass production under grazing. II Photosynthesis, crop growth and animal intake of continuously grazed swards. Journal of Appled Ecology. 20: 127-139.

Patriquin, D.G. and Keddy, C. 1978. Nitrogenase activity (acetylene reduction) in a Nova Scotian salt marsh: its association with angiosperms and the influence of some edaphic factors. Aquatic Botany. 4: 227-244.

Patriquin, D.G. and McClung, G.R. 1978. Nitrogen accretion and possible significance of nitrogen fixation (acetylene reduction) in a Nova Scotian Spartina alterniflora stand. Marine Biology. 47: 227-242.

Petelle, M. 1982. More mutualisms between consumers and plants. Oikos. 38: 125-127.

Pimm, S.L. 1984. The complexity and stability of ecosystems. Nature. 307: 321-326.

Polunin, N. 1940. Botany of the Canadian Eastern Arctic Part I: Pteridophyta and Spermatophyta. National Museum of Canada Bulletin #92 in Biological Series #24, Ottawa.

Porsild, A.E. and Cody, W.J. 1980. Vascular Plants of Continental Northwest Territories, Canada. National Museum of Canada, Ottawa.

Postgate, J.R. 1982. The Fundamentals of Nitrogen Fixation. Cambridge University Press, Cambridge.

Prevett, J.P., Marshall, I.F. and Thomas, V.G. 1979. Fall foods of lesser snow geese in the James Bay region. Journal of Wildlife Management. 43: 736-742.

Ranwell, D.S. 1972. Ecology of Salt Marshes and Sand Dunes. Chapmsn and Hall, London.

Rawes, M. 1981. Further results of excluding sheep from high-level grassland in the North Pennines. Journal of Ecology. 69: 651-669.

Reid, D. 1959. Studies on the cutting management of grass-clover swards. Journal of Agricultural Science. 53: 299-312.

Reuss, R.W., McNaughton, S.J. and Coughenour, M.B. 1983. The effect of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an east African sedge. Oecologia. 59: 253-261.

Rice, B. and Westoby, M. 1978. Vegetative responses of some Great Basin shrub communities protected against Jack-rabbits or domestic stock. Journal of Range Management. 31: 28-34.

Ritchie, J.C. 1956. The native plants of Churchill, Manitoba, Canada. Canadian Journal of Botany. 34: 269-320.

Ritchie, J.C. 1957. The vegetation of Northern Manitoba II. A prisere on the Hudson Bay lowlands. Ecology. 58: 429-435.

Robertson, J.H. 1933. Effect of frequent clipping o the development of certain grass seedlings. Plant Physiology. 8: 425-447.

Rockwell, R.F. and Cooke, F. 1977. Gene flow and local adaptation in colonially nesting dimorphic birds: the Lesser Snow Goose Anser caerulescens caerulescens, American Naturalist. 11: 91-97.

Sandford, B.V., Norris, A. and Bostock, H. 1968. Geology of the Hudson Bay Lowlands. Geological Survey of Canada Paper, Ottawa. pp. 67-60.

Sarukhán, J., Martinez-Râmos, M., and Piñero, D. 1984. The analysis of demographic variability at the individual level and its populational consequences. In Perspectives on Plant Population Ecology. ed. R. Dirzo and J. Sarukhan. pp. 83-106. Sinuauer Associations Inc., Sunderland, Mass.

Schultz, A.M. 1969. A study of an ecosystem: the arctic tundra. In The Ecosystem Concept in Natural Resource Management. ed. G.M. van Dyne. pp. 77-93. Academic Press, New York.

Scoggan, H.J. 1959. The native flora of Churchill. National Museum of Canada, Ottawa.

Shaver, G.R. and Chapin, F.S. 1980. Response to fertilization by various plant growth forms in an Alaska tundra: nutrient accumulations and growth. Ecology. 61: 662-675.

Silvertown, J.W. 1982. No evolved mutualism between grasses and grazers. Oikos. 253-254.

Simpson, J.R. and Stobbs, T.H. 1981. Nitrogen supply and animal production from pastures. In Grazing Animals. ed. F.H.W. Morley. pp. 261-287. Elsevier, Amsterdam.

Sims, R.A., Riley, J.L. and Jeglum, J.K. 1979. Vegetation, flora and vegetational ecology of the Hudson Bay Lowlands: A literature review and annotated bibliography. Canadian Forsetry Service, Department of the Environment Report 0-X-297, Ottawa.

Skoog, D.A. and West, D. 1980. Principles of Instrumental Analysis 2nd Ed. Saunders College, Philadelphia.

Smalley, A.E. 1960. Energy flow of a salt marsh grasshopper population. Ecology. 41: 672-677.

Smith, D.L., McLachlan, J. and Patriquin, D.G. 1979. Nitrogen fixation, as determined by acetylene reduction, in two salt marshes of Minas Basin. Proceedings of the Nova Scotia Institute of Science. 29: 381-392.

Sokal, R.F. and Rohlf, F.J. 1981. Biometry 2nd Ed. W.H. Freeman and Co., San Francisco.

Solorzano, L. 1969. Determination of ammonium in natural waters by the phenol hypochlorite method. Limnology and Oceanography. 14: 799-801.

Sprent, J.I. 1979. The Biology of Nitrogen-Fixing Organisms, McGraw-Hill Book Company, London.

Stenseth, N.C. 1978. Do grazers maximize individual plant fitness? Oikos. 31: 299-306.

Stenseth, N.C. 1983. Grasses, grazers, mutualism and co-evolution: a comment about handwaving in ecology. Oikos. 41: 152-153.

Stenseth, N.C. 1984. Testing evolutionary predictions: a reply to Bleken and Ugland. Oikos. 43: 126-128.

Stewart, W.D.P. 1980. Some aspects of structure and function in nitrogen fixing cyanobacteria. Annual review of Microbiology. 34: 497-536.

Stewart, W.D.P. 1982. Nitrogen fixation - its current relevance and future potential. Israel Journal of Botany. 31: 5-44.

Stewart, W.D.P. and Lex, M. 1970. Nitrogenase activity in the blue-green alga _Plectonema_ _boryanum_ strain 594. Archives of Microbiology. 73: 250-260.

Stewart, W.D.P., Fitzgerald, G.P. and Burris, R.H. 1967. _In_ _situ_ studies on N_2 fixation using the acetylene reduction technique. Proceedings of the National Academy of Science, U.S.A. 58: 2071-8.

Stutz, R.C. 1977. Biological nitrogen fixation in high arctic soils, Truelove Lowland. In Truelove Lowlands, Devon Island, Canada: A High Arctic Ecosystem. ed. L.C. bliss. pp. 301-314. University of Alberta Press, Edmonton.

Swift, M.J., Heal, O.W. and Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. Studies in Ecology, Volume 5. Blackwell Scientific Publications, Oxford.

Taylor, R.D. and Walker, B.H. 1978. A comparison of vegetation use and condition in relation to herbivore biomass on a Rhodesian game and cattle ranch. Journal of Applied Ecology. 15: 565-581.

Thomas, H. 1980. Terminology and definitions in studies of grassland plants. Grass and Forage Science. 35: 13-23.

Thomas, V.G. and Prevett, J.P. 1980. The nutritional value of arrow-grasses to geese at James Bay. Journal of Wildlife Management. 44: 830-836.

Thompson, K. and Uttley, M.G. 1982. Do grasses benefit from grazing? Oikos. 39: 113-115.

Tiezen, L.L., lewis, M.C., Miller, P.C., Mayo, J., Chapin, F.S. and Oechel, W. 1981. An analysis of processes of primary production in tundra growth forms. In Tundra Ecosystems: A Comparative Analysis. ed. L.C. Bliss, O.W. Heal and J.J. Moore. pp. 285-356. Cambridge University Press, Cambridge.

Valiela, I. and Teal, J. 1974. Nutrient limitation in salt marsh vegetation. In Ecology of Halophytes. ed. R.J. Reimold and W.H. Queen. pp. 547-563. Academic Press, London.

Valiela, I., Teal, J.M. and Sass, W.J. 1975. Production and dynamics of salt marsh vegetation and effect of sewage contamination on biomass production and species composition. Journal of Applied Ecology. 12: 973-982.

Vine, D.A. 1983. Sward structure changes within a perennial ryegrass sward: Leaf appearance and death. Grass and forage Science. 38: 231-242.

Walker, B.H., Ludwig, D., Holling, C.S. and Peterman, R.M. 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology. 69: 473-498.

Watson, D.J. 1947. Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. Annals of Botany, New Series. 11: 41-76.

Watt, A.S. 1981a. A comparison of grazed and ungrazed Grassland A in East Anglian Breckland. Journal of Ecology. 69: 499-508.

Watt, A.S. 1981b. Further observations on the effects of excluding rabbits from Grassland A in East Anglian Breckland: the pattern of change and factors affecting it (1936-73). Journal of Ecology. 69: 509-536.

Webber, P.J. 1978. Spatial and temporal variation of the vegetation and its productivity. In Vegetation and Production Ecology of an Alaskan Arctic Tundra. ed. L.L. Tieszen. pp. 37-112. Springer-Verlag, New York.

Weeda, W.C. 1967. The effect of cattle dung patches on pasture growth, botanical composition and pasture utilization. New Zealand Journal of Agricultural Research. 10: 150-159.

Westoby, M. 1980. Relations between genet and tiller population dynamics: survival of Phalaris tuberosa tillers after clipping. Journal of Ecology. 68: 863-869.

Whidden, P. 1977. Microbiology and decomposition on Truelove Lowland. In Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem ed. L.C. Bliss. pp. 505-530. University of Alberta Press, Edmonton.

White, J. 1980. Demographic factors in plant populations. In Demography and Evolution in Plant Populations. ed. O.T. Solbrig. pp. 21-48. Blackwell Scientific Publications, Oxford.

Wiegert, R.G. and Evans, R. 1964. Primary production and the disappearance of dead vegetation on an old field. Ecology. 45: 49-63.

Wiegert, R.G. and Evans, F.C. 1967. Investigations of secondary productivity in grasslands. In Secondary Productivity in Terrestrial Ecosystems Volume II. ed. K. Petrusewicz. pp. 499-518. Polish Academy of Science, Institute of Ecology.

Wielgolaski, F.E. 1981. Introduction to Part III: Plant production components and processes. In Tundra Ecosystems: a Comparative Analysis. eds. L.C. Bliss, O.W. Heal and J.J. Moore. pp. 183-186. IBP 25, Cambridge University Press, Cambridge.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J. and Doyle, G. 1981. Primary production of tundra. In Tundra Ecosystems: a Comparative Analysis eds. L.C. Bliss, O.W. Heal and J.J. Moore. pp. 187-226. IBP 25, Cambridge University Press, Cambridge.

Zaret, T.M. 1982. The stability/diversity controversy: a test of hypotheses. Ecology. 63: 721-731.