A COMPARISON OF THE GROWTH RESPONSES OF THREE SEDGES

TO

FORAGING BY LESSER SNOW GEESE

by

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SUMMARY

1. The responses to herbivory of above-ground organs of the sedges Carex subspathacea and Carex X flavicans were investigated at La Pérouse Bay, Manitoba. Demographic techniques were used to compare the production and turnover of leaves and shoots and the elongation of leaves between plants of swards on which Lesser Snow Geese fed and plants of swards from which geese were excluded. The effects of herbivory on the shoot demography of Carex aquatilis were also studied.

2. Patterns of foraging by the geese varied seasonally. Following their arrival at La Pérouse Bay, the geese fed by pulling shoots of carices and by grubbing the roots and rhizomes of graminoids. After the hatch of the goslings, the geese fed by clipping the leaves of grasses and sedges.

3. Within one summer, grazing increased the cumulative production of leaves of Carex subspathacea and of Carex X flavicans. Though the geese removed few leaves, leaves of shoots of both species in grazed plots had shorter lifespans than leaves of shoots in ungrazed plots. Grazing also increased the total number of leaves per shoot which died during the growing season.

4. The rates of elongation of leaves of shoots of Carex subspathacea and Carex X flavicans in grazed plots did not consistently differ from the rates of elongation of leaves of shoots in ungrazed plots.

5. Herbivory by geese did not consistently alter the production of shoots of Carex aquatilis, Carex subspathacea, or Carex X flavicans.

6. The increased production of leaves is the primary response of above-ground organs of these carices to herbivory by geese. The unresponsiveness of shoot production suggests that these carices are more vulnerable to damage from the loss of shoots than from the clipping of leaves.

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LIST OF ABBREVIATIONS

ANOVA:	analysis of variance
C. aquatilis:	Carex aquatilis
C. caerulescens:	Chen caerulescens
C. c. atlantica:	Chen caerulescens atlantica
C. c. caerulescens:	Chen caerulescens caerulescens
C. X flavicans:	Carex X flavicans
C. subspathacea:	Carex subspathacea
MDCA:	multidimensional contingency analysis
NAAPP:	net annual above-ground primary production
NAPP:	net above-ground primary production

CHAPTER 1: GENERAL INTRODUCTION

1.1. General information

1.1.1 Herbivory

Herbivory is a process of ecological and evolutionary significance. The need for adequate supplies of food of high quality has influenced almost every aspect of the behaviour, morphology, and physiology of herbivores. Conversely, animals are among the most important agents of natural selection on plants, acting as predators (by removing seeds or killing individuals), as parasites (by removing or damaging tissue), or as mutualists (by promoting growth or reproduction) (Crawley 1983). These interactions have strongly affected the evolution of plants, resulting in a wide range of morphological, developmental, and physiological responses of plants to herbivory (Harper 1977; Rosenthal and Janzen 1979; Crawley 1983). It is unlikely that any species of plant completely escapes phytophagy. On average, over 10% of the above-ground net primary production of natural communities is consumed by herbivores; in grasslands, this proportion may be much greater (McNaughton 1976, 1979a,b; Dyer et al. 1982; Coley et al 1985; McNaughton 1985). Plant-herbivore interactions are important in many natural communities as modifiers of species diversity. They affect the physical environment, the flow of energy and nutrients, and primary production (Harper 1969; Mattson and Addy 1975; Harper 1977; Crawley 1983). The action of the herbivore often results in the development of vegetational heterogeneity (Harper 1969; Paine and Levin 1981; Sousa 1984; Pickett and White 1985).

Attempts to produce a general theory of plant-herbivore interaction have

met with limited success, in part, because of the complexity of the processes involved. The response of an individual plant to damage by a herbivore is likely to depend as much upon the physical and biological characteristics of its local environment as upon the intrinsic properties of the plant and the herbivore; feedback loops and complex interactions often extend the influence of plant-herbivore relationships far beyond the immediate participants. As a consequence of this complexity, individuals, populations, and communities often exhibit contrasting responses which can only be reconciled if the nonequivalent nature of similar processes operating at these different levels of organization is recognized. Studies of the production or stability of grazed communities tell us little about the production or survival of grazed individuals; these are questions which require investigation at the level of the individual. Research primarily concerned with the individual is required if we are to understand either the nature of the selective pressures exerted upon plants by herbivores or the abilities of individual plants to withstand herbivory.

The general goal of this study was to investigate the changes in the growth of three sedges (Carex subspathacea Wormsk.[*], Carex aquatilis Wahl., Carex X flavicans Nyl.) in response to herbivory by Lesser Snow Geese (Chen caerulescens caerulescens (L.) Gundl.), in an effort to understand the morphological basis of their tolerance to grazing. The responses of sedges are of particular interest, since these are plants which are both very important to grazers and very tolerant of herbivory (Sections 1.2.2, 2.2.1.). The study location, the Snow Goose colony of La Pérouse Bay, Manitoba, provided an excellent opportunity to explore the responses of grazed individuals within the framework of a well-studied system. Research conducted at this location since 1968 by Dr. F.

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[*] Nomenclature of vascular plants follows Scoggan (1978).

Cooke and his associates has provided much information on the biology of the geese themselves (Sections 2.1, 2.3.1.). The intensive botanical studies which began at La Pérouse Bay in 1978 have provided detailed information on the effects of the geese upon the production, nutrient cycling, and composition of the grazed salt marsh communities (Section 2.3.1.).

Following a brief account of the application of demographic techniques to botanical ecology (Section 1.1.2.), I will provide a background for my own research by presenting a summary of some of the effects of herbivory at different levels of biological organization. Section 1.3 will then provide a more detailed statement of the aims of this study. The ecology of my study organisms and the locations where the study was conducted will be described in Chapter 2.

1.1.2. Demography of clonal organisms

Almost all species of plants may be considered to be populations of repeated units, or modules (Harper and White 1974; Harper 1977; Harper and Bell 1979). As a result of clonal growth, a genetic individual (genet) becomes a set of fragmented, potentially or actually independent modules (ramets); for example, the rhizomatous or stoloniferous growth habits of some grasses and sedges results in a network of ramets (Harper and White 1974; Harper 1977; Harper and Bell 1979; Noble et al. 1979). Ramets are themselves composed of repeating units, each consisting of a leaf with its axillary bud (Harper and White 1974; Harper 1977; Harper and Bell 1979). Modules have their own life histories and population dynamics (Harper 1977; Harper and Bell 1979). For many herbaceous perennials, including sedges, genets are rarely distinguishable; ramets are the largest units which are practical for

demographic study (Noble et al. 1979). However, the consideration of populations of modules instead of populations of genets is more than a convenient abstraction. Modular construction is a characteristic strategy of plants, allowing flexibility in morphology and patterns of growth; conversely, the success of a genet depends upon the success of its modules (Harper 1977; Harper and Bell 1979). The ecology of both herbivores and plants themselves are usually more strongly influenced by interactions with ramets than by interactions with genets; the abundance and sizes of the ramets which are present are much more important to a herbivore searching for food, or to an unrelated plant competing for resources, than the number of genets to which those ramets belong.

Plasticity of plants is primarily the result of changes in numbers of modular units, rather than changes in their sizes or shapes (Harper 1977, Harper and Bell 1979). Consequently, plasticity may be studied as the demography of modules. Though the study of changes in below-ground morphology is not conveniently approached in this manner, it may be argued that the important component of primary production in plant-herbivore studies is that which is actually available to the herbivores. As such, below-ground production is important to grazers only if it affects above-ground production. In graminoids, the growth and the replacement of above-ground tissues lost to herbivory is a plastic response of three nested sources: axillary, apical, and intercalary meristems (Section 1.2.3.2.). Axillary meristems develop into new tillers. Apical meristems produce new leaves and culms on existing tillers. Intercalary meristems lead to the elongation of existing leaves. Together, the behaviour of these three populations of meristems and their products determine the success of a grazed individual. Leaves lost to herbivory and senescence must be replaced from intercalary and apical meristems; shoots must be replaced from

axillary meristems. In this study, the demography of these meristems and their products was investigated in order to accurately describe the character of the morphological responses to herbivory of Carex aquatilis, Carex subspathacea, and Carex X flavicans.

1.2. Important effects of herbivory

1.2.1. The plant community

1.2.1.1. Composition of communities

Herbivores may alter the composition of a plant community by destroying plants of a species, by reducing their rates of growth, by suppressing their reproduction, or by unfavourably altering their competitive abilities (Harper 1969, 1977; Crawley 1983; Hawkins and Hartnoll 1983). Alternatively, plants of some species may be favoured as herbivores open up space for colonization, aid in the effective dispersal of propagules, stimulate growth or flowering, or alter competitive conditions (Harper 1969, 1977; Crawley 1983; Hawkins and Hartnoll 1983). Many of the most dramatic examples of herbivore-induced changes in the abundances of plants of different species within plant communities come from environments disturbed by human activity. Examples include changes in plant communities following the introduction of domestic herbivores (Harper, 1977; Mack and Thompson 1982; Crawley 1983), the biological control of Opuntia stricta Haw. in Australia (Harper 1969, 1977), and the destruction of vegetation during outbreaks of phytophagous insects (May 1976; Harper 1977; Strong et al. 1984; Rhoades 1985). However, herbivores also play much subtler, yet important, roles in determining the species composition

of natural communities of plants (Harper 1977). Removal of herbivores from an area in which they have few obvious effects on the species structure of the vegetation may result in important changes in species composition (e.g. Bazely and Jefferies 1986).

It is difficult to generalize about the effects of herbivory upon the composition and diversity of natural communities, since these effects depend upon the behaviour of herbivores, the growth responses of individual plants to herbivory, and the prevailing conditions in both the physical and the biotic environment (Harper 1969; Lubchenko and Gaines 1981; McNaughton 1983c). The degree of dietary specialization of the herbivore and the ability of each species of plant to recover from damage are particularly important. While an animal foraging upon infrequent species may reduce the diversity of species in a community, one feeding preferentially upon a competitively dominant species may allow the invasion of plants which are competitively inferior, but which are resistant to damage, or not utilized as forage. Conversely, intense herbivory, especially if non-selective, may cause diversity to decline, as the original community is replaced by an assemblage of herbivore-resistant species (Harper 1969; Gray and Scott 1977; McNaughton 1979a,b; Hawkins and Hartnoll 1983; Bergquist and Carpenter 1986; Section 2.3.1). These relationships may explain the frequent observation that intermediate intensities of grazing often increase species diversity (Harper 1969; Lubchenko and Gaines 1981; Crawley 1983). For example, Coppock et al. (1983) found that the species diversity of plants initially increased following invasion of an area by Prairie Dogs, but as the colony became established and its numbers increased, the diversity of plant species declined.

As a consequence of their direct and indirect influences upon the abundances of plants, herbivores commonly alter the successional trajectories

of the communities which they exploit. For example, herbivores may exclude
species of plants that would become important in the successional development
of the community if herbivory were absent (Harper 1969; Lubchenko and Gaines
1981; Crawley 1983; Section 2.3.1.). At La Pérouse Bay, Manitoba, the
accumulation of litter and the invasion of dicotyledons over several years
converted swards from which grazing geese had been excluded into communities
distinctively different from the grazed graminoid communities which dominated
the surrounding salt marsh (Bazely and Jefferies 1986). Disturbance by
herbivores is an important source of vegetational heterogeneity in many habitats
(Hawkins and Hartnoll 1983; Sousa 1984; Pickett and White 1985; Section 2.3.1.).
Heterogeneity may be the result of the direct destruction of vegetation or of
herbivores preferentially utilizing patches of vegetation which are a consequence
of environmentally-generated pattern (Sousa 1984; Belsky 1986b). Disturbance may
retard succession, thereby maintaining the species diversity of a community, by
continually providing opportunities for recolonization (Sousa 1984;
Pickett and White 1985; Jefferies 1987). Conversely, disturbance may lead to
an acceleration of successional processes by providing more frequent
opportunities for species replacement (Connell and Slayter 1977; Crawley 1983).
Some herbivores, including geese, are capable of destroying the communities
which they inhabit (Section 2.3.2.). For example, the removal by man of their
chief predators is thought to have led to abnormally large populations of sea
urchins which have destroyed vast areas of kelp forest on both the east and
west coasts of North America (Duggins 1980; Wharton and Mann 1981). Though
catastrophes of this magnitude are rarely reported from habitats not disturbed
by man, their apparent rarity, in part, may be a consequence of their transient
nature (Harper 1977).

1.2.1.2. Production of communities

The alteration of community composition by herbivory may result in changes in net primary production associated with changes in the abundance of species with different rates of growth (Bergquist and Carpenter 1986; Carpenter 1986). This type of change is an indirect and complex function of herbivory, and is probably best considered as a facet of species change (Section 1.2.1.1.). Herbivores also can modify the net primary production of plant communities more rapidly than changes in species composition alone can explain. The reduction of net primary production without large changes in community composition is a common observation (Harper 1977; Crawley 1983; Belsky 1986a), but whether herbivory can sustainably increase production is a very contentious issue (Belsky 1986a; McNaughton 1986). Most of the support for this claim comes from either terrestrial graminoid communities (McNaughton 1976, 1979a,b, 1983a; Bazely 1984; Cargill and Jefferies 1984a,b; McNaughton 1984, 1985; Section 2.3.1.) or from aquatic algal communities (McDonald 1985; Bergquist and Carpenter 1986; Sterner 1986). These examples are similar in that they all involve some mechanism, mediated by the herbivores, which more than compensates for the loss of plant tissue by herbivory.

The effects of herbivory per se are probably always detrimental to individual survival and reproduction. Herbivores often activate responses intrinsic to the damaged individuals which temporarily increase production. Examples include increased photosynthetic rates of residual tissue, activation of surviving meristems, and decreased mortality of leaves (McNaughton 1979a, 1983a,b). However, for increased net primary production to be sustained, there appears to be a requirement for a herbivore-mediated extrinsic mechanism, which supplies materials necessary to support plant growth. Examples include

accelerated cycling of nutrients, reduced evapotranspiration, and decreased competition for light or other resources (McNaughton 1979a, 1983a,b; Cargill and Jefferies 1984a; Bazely and Jefferies 1985, 198Na, 198Nb; Mooney and Gulmon 1982; Section 2.3.1.). Such extrinsic mechanisms may more than compensate for the accompanying damage, at least until the amount of damage reaches some critical upper threshold; consequently, production may be maximized at intermediate intensities of herbivory (Dyer 1975; McNaughton 1976,1979a,b; Dyer et al. 1982; Hilbert et al. 1981; McNaughton 1983a; Section 2.3.1.). There is little reason to believe that herbivory generally increases the net primary production of plant communities; however, there is every reason to believe that such increases occur when the activities of the herbivore supply increased amounts of a critically limiting resource.

1.2.2. The plant population

1.2.2.1 Defences

Plants are protected from herbivores by a wide variety of structural, phenological, and chemical defences. These defences have important influences on the feeding preferences of herbivores (Harper 1969, 1977; Rosenthal and Janzen 1979; Crawley 1983; Strong et al. 1984).

Structural defences include the presence of spines, trichomes, and tough inedible coverings of seeds and fruits. High amounts of abrasive silica or indigestible lignins and cellulose in tissues are among the few types of defence commonly found in graminoids (Crawley 1983; Coughenour 1985). Most of these defences function by making herbivory difficult, damaging, or expensive in terms of time or energy. Cellulose, lignin, and other substances

indigestible to most herbivores may also act as deterrents by diluting the concentrations of nutrients in tissues of plants to unprofitable levels (Mattson 1980; Crawley 1983).

Many morphological characteristics reduce damage not by actively deterring herbivores, but by making vulnerable tissues inaccessible or better able to regrow. For example, grasses and sedges usually have their vulnerable shoot apical meristems at or below the ground surface, out of the reach of large grazers (Harper 1977; Crawley 1983; Coughenour 1985; Mack and Thompson 1982). Graminoids also have leaves which elongate from basal (intercalary) meristems, allowing rapid regrowth of damaged leaves (Harper 1977; Crawley 1983; Coughenour 1985). Though it is uncertain that these characters originated in response to herbivory (Coughenour 1985), they certainly confer considerable resistance to grazing (Harper 1977; Mack and Thompson 1982; Crawley 1983). On a microevolutionary scale, the defoliation of graminoids commonly selects for prostrate leaves and shoots, shortened internodes, and increased rates of leaf production and of tillering (Warwick and Briggs 1978a,b; McNaughton 1979a; Crawley 1983; Detling and Painter 1983; McNaughton 1984; Jefferies 1987; Sadul 1987).

The timing of growth and reproduction of many plants may reduce damage by herbivores. Ephemerality or rarity may reduce herbivory by specialist herbivores by limiting their ability to locate food plants, or by limiting the size of a herbivore population (Feeny 1976; Rhoades and Cates 1976; Feeny 1980). In the case of common perennials, if critical periods of growth are confined to brief or irregular intervals this may have a similar effect on the herbivore population. The vulnerable periods of growth may end before significant damage occurs to the plants (Feeny 1976; Rhoades and Cates 1976; Feeny 1980).

The great variety of antiherbivore chemicals produced by plants represent the most widely discussed class of defences of plants against herbivory (Rosenthal and Janzen 1979; Harbourne 1982; Crawley 1983). Slowly growing plants and tissues tend to be protected with large concentrations of "quantitative defences," such as tannins, lignins, and polyphenols; these act in a dosage-dependent manner, inhibiting digestion or reducing the quality of food in proportion to their concentrations in food (Feeny 1976; Rhoades and Cates 1976; Feeny 1980). Most quantitative defences are carbon-based, and most turn over very slowly within the plant (Coley et al. 1985). In contrast, seeds and rapidly growing tissues are often protected with small amounts of toxins, such as alkaloids, cyanogenic glycosides, and terpenes. These "qualitative defences" are effective at very low concentrations but turn over rapidly; they are often nitrogen-based (Feeny 1976; Rhoades and Cates 1976; Feeny 1980; Coley et al. 1985).

Feeny (1976, 1980) and Rhoades and Cates (1976) report that quantitative defences are favoured in species likely to be utilized by specialist herbivores, since they are difficult for all herbivores, including specialists, to detoxify. If rarity or ephemerality prevent specialists from locating plants of a species, qualitative defences are likely to be favoured, since these toxins are needed in only small amounts to be effective against most generalists. Unfortunately, many predictions of this "apparency" theory have not held up well to close scrutiny. Consequently, an alternative theory based upon resource availability has been developed to explain observed patterns of phytochemistry (Mooney and Gulmon 1982; Coley et al. 1985; Bazzaz et al. 1987). Severely resource-limited plants, such as many late-successional species, tend to exhibit slow rates of growth. Tissue lost to herbivores is replaced slowly, and only if sufficient resources are available; consequently, effective herbivore deterrents are

favoured. Since quantitative defences, though initially expensive, incur few maintenance costs, these are expected to be employed in the long-lived tissues of these plants. In contrast, plants which are not severely resource-limited (e.g. many weedy annuals) tend to be fast-growing and to have short-lived tissues; material lost to herbivores may be rapidly replaced. Consequently, the diversion of resources from growth into expensive defences is not favoured. Instead, plants may be protected with low concentrations of qualitative defences, since their maintenance costs will be small in short-lived tissues. Neither of these theories seems particularly successful in explaining the depauperacy of chemical defences among graminoids (Coughenour 1985; Section 2.2.1.).

It has been repeatedly suggested that some plants, primarily graminoids, may have coevolved mutualistically with herbivores (Owen and Wiegert 1976; Owen 1980; Owen and Wiegert 1981), encouraging phytophagy in exchange for stimulated growth or reproduction (Section 1.2.1.2). Though herbivores and plants may in some cases be mutually beneficial, the existence of an evolved mutualism seems unlikely (Herrera 1982; Silvertown 1982; Thompson and Uttley 1982; Coughenour 1985; McNaughton 1985, 1986). The mutualistic hypothesis seems to confuse community responses with individual responses. Sustainable increases in production usually require an extrinsic mechanism which more than compensates for the loss of tissue (Section 1.2.1.2.); however, most extrinsic mechanisms equally affect all individuals and not just those which are grazed. As a result, individuals which avoid grazing receive the same benefits as grazed individuals, without suffering the loss of tissue. This implies that co-operation with herbivores is an easily invaded, unstable strategy unlikely to be favoured by evolution (Stenseth 1978; Hererra 1982; Stenseth 1983). Of course, graminoids and many other plants exhibit characteristics which minimize

damage by herbivores and which allow regrowth, but tolerance of grazing does not necessarily imply either mutualism (McNaughton 1983a, 1985) or coevolution (Coughenour 1985).

1.2.3. The individual plant

1.2.3.1. Physiological responses

Many individual plants produce or translocate defensive chemicals in response to herbivory (Levin 1976; Rosenthal and Jarzen 1979; Crawley 1983; Denno and McClure 1983; Coley et al. 1985). These "induced" or "facultative" defences generally appear in response to the damage of tissue within the same individual, though damage in nearby plants has also been reported to produce responses in undamaged plants (Denno and McClure 1983; Rhoades 1983a,b). Induced defences may appear within minutes of damage; such responses generally involve qualitative defences, and may be restricted to the damaged area (Rhoades 1979; Denno and McClure 1983). Induced defences may also appear much more gradually, but affect the entire plant for years; this class of responses frequently involves quantitative defences, notably tannins and resins (Rhoades 1979; Haukioja 1980; Crawley 1983). In species with such persistent defences, frequent herbivory may lead to a progressive decline in the quality of forage (Haukioja 1980; Bryant et al. 1983).

In addition to changes in defensive chemistry, herbivory can produce a wide range of effects relating to carbon and mineral content and metabolism. For example, herbivory can increase photosynthetic rates by both extrinsic mechanisms, such as increasing supplies of nutrients, water, and light, and by intrinsic alterations involving increases in concentrations of carboxylating

enzymes, alterations in hormone levels and in source-sink relationships, and by the removal of senescing tissue (McNaughton 1979a; Crawley 1983; McNaughton 1983a,b; Section 1.2.1.2.). As a consequence of these changes, photosynthetic rates often increase following partial defoliation (Harper 1977; Dyer et al. 1982; Crawley 1983), though exceptions are very common (Wallace 1981; Wallace et al. 1985). Even in plants in which photosynthetic rates increase following clipping, rates generally decline within those leaves actually suffering damage (Dyer et al. 1982). Increased photosynthetic rates (on a leaf area basis) may not translate into increased fixation of carbon if defoliation has excessively reduced leaf area, or if resources become too depleted to allow the maintenance of photosynthetic mechanisms (McNaughton 1979a; Crawley 1983; McNaughton 1983a).

Following an episode of herbivory, rates of respiration often increase and carbohydrate and nutrient reserves decline as plants replace lost tissue (Mattheis et al. 1976; Crawley 1983). Even if photosynthetic rates increase, they may not be able to meet the increased respiratory demands. Alternatively, carbohydrates or other essential substances may accumulate if regeneration is limited by another factor. For example, the concentration of non-structural carbohydrates may increase if damage by herbivores limits regrowth by reducing the uptake of nitrogen (Crawley 1983). Herbivory also frequently alters patterns of allocation of resources. Defoliation often increases upward translocation at the expense of the growth of roots; grazing of roots can reverse this pattern (Caldwell et al. 1981; Dyer et al. 1982; Crawley 1983). In arid regions, the removal of transpiring tissue can result in important reductions in water stress at the level of both the individual and the community (McNaughton 1979a, 1983a,b, 1985; Archer and Detling 1986). Similarly, herbivores can affect the uptake of mineral nutrients both by increasing their community-wide availability (Sections 1.2.1.2, 2.3.1.) and by

altering the rates of uptake of individual plants by affecting the growth of roots, source-sink relationships, or other aspects of the plant's physiology (Chapin and Slack 1979; Ruess 1984; McNaughton and Chapin 1985).

One effect of these complex physiological responses is that herbivores often increase the quality of their forage. Both intrinsic mechanisms (replacement of senescing tissue with nutritious young tissue, translocation of stored nutrients, increased uptake of nutrients) and extrinsic mechanisms (acceleration of nutrient cycling, amelioration of the physical environment) can lead to increased concentrations of nitrogen, non-structural carbohydrates, or other nutrients in the accessible tissues of grazed plants (Ydberg and Prins 1981; Cargill and Jefferies 1984b; Bazely and Jefferies 1985; McNaughton 1985; McNaughton and Chapin 1985).

1.2.3.2. Morphological responses

The tolerance of a plant to herbivory may be considered synonymous with its capacity to replace lost tissues and to maintain growth and reproduction. Consequently, morphological responses of reproductive and vegetative organs to herbivory may be thought of as providing a biologically meaningful integration at the level of the individual of all extrinsic and intrinsic influences on the performance of grazed plants.

Herbivores have complex effects upon the fecundity of plants. Seed predation and defloration generally depress fecundity: in some cases, seed predators may destroy close to 100% of the annual seed crop (Janzen 1976; Harper 1977; Crawley 1983). The indirect effects of phytophagy are less predictable. By reducing the availability of essential resources, defoliation and grazing of roots often reduce the production of seeds; however, enhanced

seedset is also frequently observed (Crawley 1983). The mechanisms by which increases occur are poorly understood, but both extrinsic community processes and intrinsic alterations of source-sink relationships have been implicated (Crawley 1983).

Though excessive defoliation can lead to reduced production of shoots by severely depleting resources (Dyer et al. 1982), both moderate defoliation and the removal of active meristems can have the opposite effect by releasing axillary buds from apical dominance (Caldwell et al. 1981; Crawley 1983; McNaughton et al. 1983; Coughenour 1985). However, the removal of buds can severely limit the potential for future growth (Harper 1977). In woody plants, browsing frequently modifies the growth form as terminal shoots are destroyed and lateral shoots are activated (Harper 1977; Sinclair and Norton Griffiths 1979; Crawley 1983). Though the shoot apical meristems of graminoids are well protected, they are certainly not immune to herbivory. If an apex is killed by grubbing or close cropping the affected tiller will die, since continued growth is impossible. Whether it is replaced depends upon the availability of suitable meristems and sufficient resources for growth (Mattheis et al. 1976; Crawley 1983).

Though studies of the effects of herbivory on the total biomass of leaves are common, demographic studies of changes in the rates of production of leaves in response to herbivory are rare, presumably because of the practical difficulties involved in following individual leaves. The production of new leaves commonly increases following moderate defoliation, as one might expect of a plant which is successfully replacing lost biomass (Harper 1977; Crawley 1983; Kotanen and Jefferies 1987; Bazely and Jefferies 198Nb). Following intense defoliation, production may be reduced (Harper 1977; Crawley 1983). In graminoids, the increased elongation of existing leaves from their intercalary

meristems can also be an important source of new leaf tissue following grazing (Archer and Tiezen 1980; McNaughton et al. 1983; Coughenour 1985; Wallace et al. 1985).

Though longevities of leaves are often decreased by herbivory (Crawley 1983), lifespans of leaves may also increase in grazed graminoids in response to both intrinsic factors and changes in the external environment, such as reductions in leaf area index (McNaughton 1983a,b). Increased longevity may be advantageous if it allows the increased internal recycling of nutrients, the maintenance of photosynthesis, or increased total leaf elongation (Archer and Tiezen 1980; McNaughton 1983a; Coley et al. 1985; Jonasson and Chapin 1985).

1.3. Objectives of this study

The purpose of this study was to use demographic techniques in order to determine the aboveground morphological responses of Carex subspathacea, Carex aquatilis and Carex X flavicans to herbivory by Lesser Snow Geese. The design was based upon comparisons of plants exposed to natural grubbing and grazing with plants protected by exclosures from the geese. The most important objectives are listed below, along with some of the significant issues arising from them.

(1) The documentation of the patterns of growth of Carex aquatilis, Carex subspathacea, and Carex X flavicans, and of patterns of foraging by the geese.

Though extensive investigations of this sort have been conducted during previous summers at La Pérouse Bay in the salt marshes inhabited by C. sub-

spathacea (Section 2.3.1), very little information exists on seasonal shifts in feeding behaviour by the geese or on the ecology of grazing by geese in the freshwater areas inhabited by C. aquatilis and C. X flavicans.

(2) The description of changes which herbivory produces in the demography of organs of these carices, including:

a. the production and turnover of leaves

b. the production and turnover of shoots

c. the elongation of leaves.

Any of these processes might be an important element in the responses of these sedges to herbivory (Sections 1.1.2., 1.2.3.2.). Bazely and Jefferies (198Nb) found that the increased net annual above-ground primary production of grazed Puccinellia phryganodes at this location (Section 2.3.1.) could be attributed primarily to the production of new axillary shoots. Is the increased production of shoots also responsible for the enhancement of net annual above-ground primary production which grazing by geese produces in swards of C. subspathacea (Sections 2.2.3., 2.3.1.)? Do the other two carices exhibit the ability to increase their production of new tissue in response to herbivory?

(3) The comparison among these carices of their growth responses to herbivory.

These carices are morphologically similar and very closely related (Section 2.2.). Do they also share similar responses to herbivory? If not, can these differences be ascribed to variation in the behaviour of the geese or to differences among the habitats where the different species occur (Section 2.3.1.)?

(4) The prediction of the fates of heavily exploited individuals and communities.

Are the morphological responses of individuals (Objective 2) sufficient to compensate for the loss of tissue to geese?   The vegetation of the McConnell River Snow Goose colony is thought to have been destroyed by excessive herbivory (Section 2.3.2.). Does evidence exist for damage at La Pérouse Bay? Could this be reconciled with the evidence that the geese enhance the production and stability of the salt marsh (Section 2.3.1.)?

In subsequent chapters, each of these objectives will be discussed with reference to other studies and to some of the broad issues outlined in the preceding sections. Specific experimental hypotheses and questions of interest other than those listed above will be considered where appropriate.

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CHAPTER 2: STUDY ORGANISMS AND LOCATIONS[*]

2.1. Biology of Snow Geese

2.1.1. Taxonomy and distribution

Two subspecies of Snow Goose are currently recognized: the Lesser Snow Goose (Chen caerulescens caerulescens (L.) Gundl.) and the Greater Snow Goose (C. c. atlantica Kennard) (Godfrey 1979; Owen 1980). Chen. c. caerulescens includes both "white" and "blue" individuals, a plumage polymorphism which is almost absent from the predominantly white Greater Snow Goose (Cooke and Cooch 1968; Godfrey 1979; Owen 1980; Anon. 1981). The two subspecies are distinguished primarily on the bases of their sizes and distribution; they are similar in their behaviour and dietary habits (Owen 1980). Chen. c. caerulescens is the subspecies occurring at La Pérouse Bay and in the West Hudson Bay colonies (Kerbes 1975).

Snow Geese nest in a restricted number of colonies primarily located in the Canadian Arctic. Greater Snow Geese nest in the High Arctic Islands; the largest colonies occur on northern Baffin Island and Bylot Island (Godfrey 1979; Anon. 1981). The total winter population currently numbers about 200 000 (Anon. 1981). Lesser Snow Geese are more southern and western in their breeding distribution. Kerbes (1975) divided Lesser Snow Geese into three summer populations. The eastern Arctic population totals at most about 2 000 000 birds, (yearlings or older) nesting on the southern and western coasts of Hudson Bay.

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[*] Nomenclature of vascular plants follows Scoggan (1978). Nomenclature of mosses follows Ireland et al. (1980).

It includes both La Pérouse Bay and the West Hudson Bay colonies. Birds of this population also nest on southern Baffin and Southampton Islands (Kerbes 1975; Boyd et al. 1982). The central North American population is the smallest, numbering about 25 000 birds nesting in the area of the Queen Maud Gulf (Kerbes 1975). The western North American population totals about 600 000 birds nesting on Banks Island and in the Mackenzie and Anderson River deltas, and on Wrangel Island in the U.S.S.R. (Kerbes 1975, 1983, 1986).

Greater Snow Geese winter on the Atlantic coast of the United States from New Jersey to South Carolina (Owen 1980; Anon. 1981). During both spring and fall migration, this subspecies flies through Quebec, staging for around one and a half months near Cap Tourmante on the St. Lawrence Estuary (Godfrey 1979; Owen 1980; Anon. 1981). The eastern population of Lesser Snow Geese primarily winters on the American coast of the Gulf of Mexico (Kerbes 1975). The central population also winters in this general area, but some birds also winter in Mexico (Kerbes 1975). The eastern population migrates through the American Midwest, Manitoba, and Western Ontario, staging at numerous locations in the central U.S.A., southern Manitoba, and on the Hudson and James Bay coasts (Blokpoel 1974; Kerbes 1975; Cooke et al. 1982). Most of the central population takes a more westerly route, staging in Saskatchewan and Alberta (Bellrose 1976; McLaren and McLaren 1982). The western breeding population winters primarily in the interior of California, though smaller groups winter on the Pacific coast as far north as British Columbia, and inland as far as New Mexico and Arizona (Kerbes 1975; Bellrose 1976; Godfrey 1979; Owen 1980).

Numbers of both Greater and Lesser Snow Geese are unusually high at present (Owen 1980; Anon. 1981; Boyd et al. 1982; McLaren and McLaren 1982; Jefferies 1987). The reasons for these large populations are probably related to a decline in hunting mortality as wintering areas have shifted toward

greater use of agricultural land (Bellrose 1976; Reed 1976; Boyd et al. 1982; Jefferies 1987; Section 2.1.3).

2.1.2. Reproductive biology

Snow Geese are usually monogamous for life (Cooke et al. 1975a; Cooke and Sulzbach 1978). Paired females return with their mates to their natal colonies to breed (Cooke et al. 1975a; Cooke and Sulzbach 1978). The establishment of nesting territories occurs as soon as suitable bare ground is exposed; nests are generally built near sites used by the same pair in previous years, on slightly raised ground (Kerbes 1975; Harwood 1977; Heagy and Cooke 1979; Cooke and Abraham 1980). About 4 eggs are laid and incubated for approximately 3 weeks (Harvey 1971; Owen 1980; Findlay and Cooke 1982a,b). Hatching is synchronous, occuring at about 90% of all nests within 2 weeks (Findlay and Cooke 1982a,b). Within 24 hours of hatch, the adults and their precocial goslings leave the nest for their summer feeding areas, where the adults temporarily become flightless following wing moult (Cooke and Abraham 1980). By fledging, surviving families contain about 2-3 goslings (Findlay and Cooke 1982b; Giroux et al. 1984; Cooke et al. 1985). Most of the loss of young between laying and fall migration is the result of the predation of both eggs and goslings by gulls, jaegers, and Arctic Foxes (Harvey 1971; Abraham et al. 1977).

Families remain together during fall migration. Hunting is the major source of post-fledging mortality; survivors return north in the spring (Sulzbach and Cooke 1979; Cooke and Abraham 1980; Boyd et al. 1982). Yearlings do not breed; they remain in the parental colony during incubation, but disappear before moult (Cooke and Abraham 1980; Cooke et al. 1982). The first

pairings occur during the young birds' second winter; many 2-year old birds and most 3-year old birds breed (Cooke and Abraham 1980; Cooke et al. 1982). Snow geese are long-lived, commonly exceeding 10 years of age (Sulzbach and Cooke 1979; Rockwell et al. 1983).

2.1.3. Feeding and nutrition

In all seasons, the diet of Snow Geese is dominated by graminoids; both subspecies are similar in their feeding habits (Owen 1980).

During the winter, Snow Geese feed primarily by grubbing the roots and rhizomes of plants of coastal marshes. Important forage plants of the coasts of the Atlantic and the Gulf of Mexico include species of Scirpus, Spartina, Distichlis, and Typha (Lynch et al. 1947; Smith and Odum 1981; Smith 1983). Scirpus spp. are also important foods in British Columbia and the St. Lawrence Estuary (Lemieux 1959a; Burton 1977 in Burton et al. 1979; Owen 1980; Bédard et al. 1986). In recent years, the use of farmland by geese in winter has been increasing (Bellrose 1976; Reed 1976; Bédard et al. 1986). Waste corn and rice have become important as food sources during migration and during winter on the Gulf coast (Glazener 1946; Reed 1976). Feeding by migrating Greater Snow Geese on plants of hayfields and pastures has recently increased in importance in Quebec (Bédard et al. 1986). In California, nearly all winter feeding occurs in grasslands and in cereal stubble (Bellrose 1976; Owen 1980).

The winter feeding of Snow Geese is capable of denuding large areas of marsh, producing extensive "eat outs" (Lynch et al. 1947; Smith and Odum 1981; Smith 1983). Recolonization of these areas by vegetation may be very slow, especially if the erosion of sediment or continued disturbance by geese occur (Lynch et al. 1947).

In spring, Snow Geese arrive on their breeding grounds before food becomes readily available (Harvey 1971; Reed 1976; Owen 1980). Consequently, many of the resources required for the production of eggs, incubation, and territorial defence must be brought with the geese in a stored form; the loss of weight is dramatic through incubation, especially in females (Harvey 1971; Ankney and MacInnis 1978; Davies and Cooke 1983). Spring reserves of nutrients are important determinants of clutch size and breeding success (Ankney and MacInnis 1978). Snow Geese gain weight by feeding during spring migration (Wypkema and Ankney 1979). Preferred foods during early spring migration include the roots, rhizomes, and young shoots of marsh plants; in recent years, waste corn, green pasture vegetation, and sprouting wheat have also become important (Owen 1980; Davies and Cooke 1983; Bédard et al. 1986). When the geese reach their staging areas at James Bay and Hudson Bay, green vegetation is scarce; nonetheless, Prevett et al. (1979) found that migrating geese at these locations consumed about equal proportions of "root" and "shoot" tissue, mostly provided by grasses (especially Puccinellia phryganodes Trin. Scribn. and Merr.), sedges, Triglochin spp., and Equisetum spp.. Much of the shoot tissue consumed probably was composed of developing bases of shoots, rather than brown overwintering foliage. Northbound migrants at La Pérouse Bay intensively pull shoots of Carex aquatilis Wahl. and Carex X flavicans Nyl. for their succulent bases (Section 2.3.1.).

The feeding habits of Snow Geese on their breeding grounds vary throughout the summer. Upon their arrival, geese circumvent the lack of green tissue by continuing to feed primarily by grubbing for roots, rhizomes, and by pulling shoots (Owen 1980). After incubation commences, females feed very little, though males may continue to grub for the roots and shoots of graminoids in the vicinity of the nest (Harvey 1971; Ankney 1977; Jefferies et al. 1979). After the eggs hatch, adults and goslings abandon their nests for summer feeding areas

located either on the coast or further inland. These feeding areas may be within a kilometre or so of the nesting areas, as they are at La Pérouse Bay. Conversely, families may travel up to 50 km in search of forage (Cooch 1958 in Kerbes 1975; Kerbes 1975; McLaren and McLaren 1982; R.F. Rockwell, unpublished data for 1985). Adults and goslings feed intensively during this period; adults must regain the weight lost during breeding (Harvey 1971; Ankney and MacInnis 1978), while goslings must rapidly grow to adult size. At La Pérouse Bay, goslings grow from 80 g to 1500-1800 g in just 7 weeks (Bazely and Jefferies 1985). The primary food of both adults and goslings during this period consists of the foliage of both fresh-water and salt-water graminoids (Kerbes 1975; Harwood 1977; Owen 1980; Kerbes 1982; Cargill and Jefferies 1984a,b; Giroux et al. 1984; Bazely and Jefferies 1986), though grubbing for herbs such as Polygonum viviparum L. may be important in more northern colonies (Lemieux 1959b; Drury 1961). By the fall, the diet has begun to shift back to the grubbing and pulling of shoots (P.M. Kotanen, pers. obs.). Intense herbivory on the breeding grounds may lead to the degradation of habitat on a large scale (Sections 2.3.1., 2.3.2.).

Snow Geese feed extensively during their fall migration, replacing reserves used during breeding and accumulating the fat needed for long-distance travel (Harvey 1971; Wypkema and Ankney 1979; Owen 1980). In staging areas on James Bay and Hudson Bay, sedges, grasses, Triglochin spp. and Equisetum spp. are again the most frequent foods; shoots, roots and seeds of these plants are all important, with the proportion of roots increasing as the season progresses (Prevett et al. 1979; Thomas and Prevett 1980, 1982; Prevett et al. 1985). Further south, the diet shifts toward the winter diet of roots, rhizomes, shattered rice, and corn (Lemieux 1959a; Owen 1980; Anon. 1981).

Because of their small gut capacities and relatively high metabolic rates,

small herbivores such as geese are constrained to intake forage at high rates
in order to meet their metabolic requirements (Demment and Van Soest 1983).
Cargill and Jefferies (1984b) estimated that an adult goose weighing 1500-1800g
ingests 350-520 g dry weight of forage per day in the 8 weeks following hatch.
Such high intake rates, coupled with a small digestive system, result in very
rapid throughput. Food passes through the digestive system of Snow Geese in
30-150 minutes (Burton et al. 1979); adults defaecate about once every 5 minutes
(Cargill and Jefferies 1984b). Such rapid processing tends to reduce the
efficiency of digestion (Demment and van Soest 1983). Buchsbalm et al. (1986)
found that Brant and Canada Geese could digest 36-39% of organic matter and 28%
of cellulose; Cargill and Jefferies (1984b) estimated that Lesser Snow Geese
retained about 34% of the dry weight of the forage that they consumed. These
figures are low for vertebrate herbivores (Demment and van Soest 1983;
Buchsbalm et al. 1986). Digestion of protein (61-80%) is closer to the average
for other herbivores (Buchsbalm et al. 1986), though droppings still are rich in
soluble nitrogen (Cargill and Jefferies 1984a; Bazely and Jefferies 1985,
198Na). Nonetheless, it seems likely that Snow Geese, like most herbivores,
have difficulties in obtaining sufficient nitrogen for growth and reproduction
(Ankney and MacInnis 1978; Wypkema and Ankney 1979; Mattson 1980), especially
since at least some of their breeding habitats are strongly nitrogen-limited
(Cargill and Jefferies 1984a). Choice of food by geese has occasionally been
shown to be correlated with digestibility or nutritional value (Owen 1975, 1976;
Harwood 1977; Owen et al 1977; Boudewijn 1984). For example, Owen (1975) found
that geese preferred fertilized patches of vegetation, though factors other than
nutritional quality might account for this preference (Owen 1975, 1976; Owen
et al. 1977). In Canada Geese, Buchsbalm et al. (1984) found that feeding
preferences were most strongly (negatively) correlated with phenolic content.

It may be that digestive physiology and feeding behaviour of geese are adjusted so as to maximize intake of protein, at the expense of digestive efficiency, given that tough or unpalatable species are initially avoided (Owen 1976; Buchsbalm et al. 1984, 1986).

2.2. Biology of carices

2.2.1 General information

Sedges (Cyperaceae) are very widely distributed, both ecologically and geographically, but are especially important in Arctic-alpine habitats (Billings and Mooney 1968; Bliss et al. 1973). Sedges resemble grasses in many features of their physiology, morphology, and ecology. Like grasses, sedges have few known chemical or morphological deterrents, but are very tolerant to grazing (Coughenour 1985). Sedges are both very abundant and very heavily grazed in many habitats; many "grasslands" actually have a large component of members of the Cyperaceae.

Carex is a large genus of world-wide distribution (Fernald 1970; Scoggan 1978). Plants of this genus are perennial, highly clonal herbs producing leafy shoots and culms from subterranean rhizomes (Fernald 1970; Scoggan 1978). Shoot apical meristems tend to be at or below the ground surface, and the elongation of leaves occurs from intercalary meristems near their bases, conferring considerable resistance to grazing and allowing rapid regrowth (Sections 1.2.2.1., 1.2.3.2.; Coughenour 1985). Plants are monoecious or dioecious, with the very reduced flowers arranged in spikes; fruits are hard achenes enclosed in sacs (perigynia) (Fernald 1970; Scoggan 1978).

The three taxa with which this study is primarily concerned are Carex

aquatilis, Carex subspathacea, and their hybrid, Carex X flavicans. These
species are morphologically similar species of wet habitats, differing most
noticeably in size. Much more information is available on the biology of C.
aquatilis than on that of the other two taxa. A brief review of the biology of
each species is presented below.

2.2.2. Carex aquatilis Wahl.

C. aquatilis (Figure 2.1.) is a sedge of damp to wet ground and shallow
fresh water (Scoggan 1978). Scoggan (1978) recognizes three varieties in Canada:
var. altior (Rydb.) Mack., var. aquatilis, and var. stans (Drej.) Root.. C.
aquatilis var. aquatilis is circumpolar. In North America, it is primarily
a sedge of boreal, Low Arctic, and alpine regions (Hultén 1968; Scoggan 1978).
Var. aquatilis is replaced by var. stans to the north and by var. altior to
the south (Hultén 1968; Fernald 1970; Scoggan 1978; Porsild and Cody 1980).
Var. aquatilis is the common variety at La Pérouse Bay and in the West
Hudson Bay region, though var. stans is also found at both locations.

The following paragraph is based upon descriptions in Hultén (1968),
Fernald (1970), Scoggan (1978), Shaver et al. 1979, Porsild and Cody (1980), and
personal observations. C. aquatilis var. aquatilis is a tufted perennial with
cord-like horizontal subterranean rhizomes. Leaves are up to 5 mm broad and 1 m
tall, though they are more commonly around half this height in the Low Arctic.
Plants tend to be largest in especially wet, protected habitats. Culms are
tall and erect (to 0.9 m), with 1-2 staminate spikes overtopping 3-5 pistillate
spikes.

Other authors have interpreted the morphology of C. aquatilis (Figure 2.1.)
as consisting of two types of shoots: sympodial "clumping" tillers and

Figure 2.1. Diagram of the general morphology of <u>Carex</u> <u>aquatilis</u>.
Clumping and spreading tillers are illustrated; the
irregular line represents the surface of the ground.
From Shaver and Billings (1975) (Figure 8).

0   5   10 cm

c = clumping tillers
s = spreading tillers
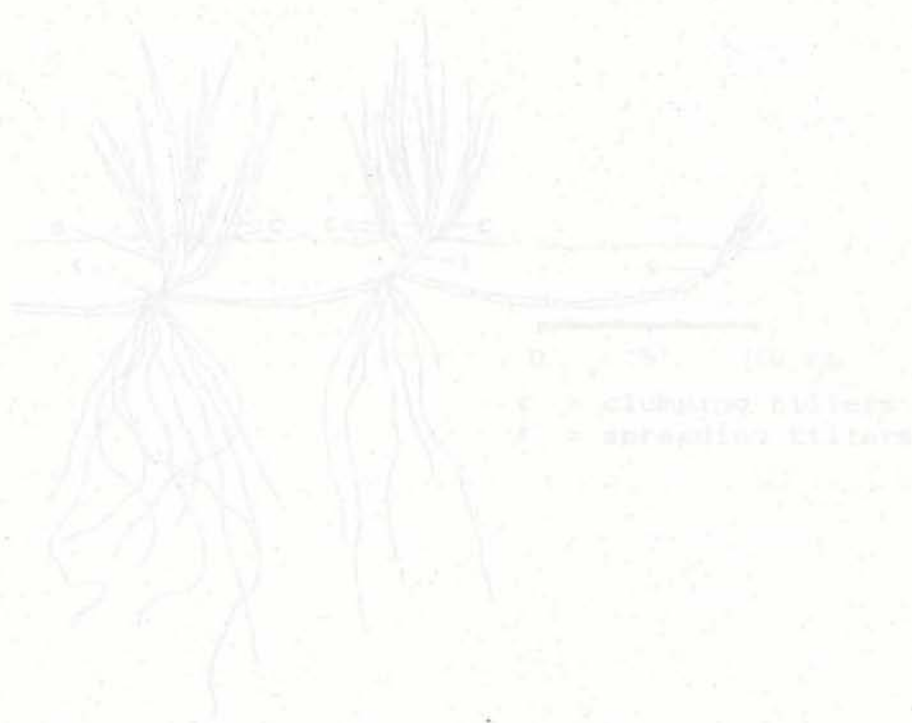
monopodial "spreading" tillers (Shaver and Billings 1975; Billings et al. 1978;
Shaver et al. 1979). The following account is based upon descriptions provided
by these authors; excavation of rhizome systems at La Pérouse Bay supported
their general interpretation. Spreading tillers are produced at the ends of
long (15-30 cm) rhizomes and give rise to most of the roots. Clumping tillers
are produced at the end of short (0-10 cm) rhizomes; these tillers rarely
produce roots. They remain dependent on their parental tillers for supplies of
water and nutrients. New clumping and spreading tillers are produced from
older spreading tillers; clumping tillers rarely produce daughter tillers.
There are generally several clumping tillers per spreading tiller, which
accounts for the tufted growth form.

Carex aquatilis commonly grows in near-monocultures, especially in shallow
standing water. Densities of shoots may be very high, with figures over 600 m^{-2}
being commonly reported (Gorham and Somers 1973; Shaver and Billings 1975).
Plants also may be tussock-forming, although at La Pérouse Bay tillers are
commonly evenly dispersed. In some locations, the proportion of shoots
flowering may approach 50% (Gorham and Somers 1973), although figures on the
order of a few per cent are more typical (Shaver et al. 1979; Chapin 1981).
Flowering ends the life of a tiller (Gorham and Somers 1973). It is likely
that successful sexual reproduction is quite rare at northern locations; most
new shoots are clearly products of clonal growth (P.M. Kotanen, pers. obs.).

Working in the Rocky Mountains of Alberta, Gorham and Somers (1973)
identified two annual peaks of shoot production. One population of shoots
was produced in late summer and flowered and died in about 12 months; the
second population was produced in winter and spring, and lived about 15
months before flowering and death. Rates of turnover of shoots in more
northern locations are considerably slower, although two annual peaks of shoot

production may still exist. Chapin and Chapin (1981) reported tillering rates of 0.2 new tillers per tiller per year for plants from a muskeg population. Lifespans of shoots at northern latitudes have been estimated to range from 2 to 8 years, with averages around 2 to 3 years (Shaver and Billings 1975; Chapin and Chapin 1981).

Leaves turn over slowly. Estimates of production range from 1-2.5 leaves per tiller per year (Chapin and Chapin 1981) to 3-6 leaves per tiller per year (Shaver and Billings 1975). Leaves are long lived; estimates range from 85 growing season days (Johnson and Tiezen 1976) to as long as 2-3 years (Chapin and Chapin 1981). Individual leaves may take 2 months to fully elongate (Johnson and Tiezen 1976; Archer and Tiezen 1980). Many leaves overwinter; these typically wither at the tips but can still elongate from their green bases (P.M. Kotanen, pers. obs.).

Root to shoot ratios are large, commonly on the order of 10:1 (Muc 1977). Roots may not be produced until the second year of a spreading tiller's life, and the production of new roots by a tiller may continue for only 2-3 years (Shaver and Billings 1975; Shaver et al. 1979). However, roots and rhizomes are long-lived (5-10 years), supplying nutrients to clumping tillers even after their parental tillers have died (Shaver and Billings 1975; Billings et al. 1978).

Carex aquatilis is used as forage by a wide range of herbivores (Shaver and Billings 1979; Archer and Tiezen 1980). Archer and Tiezen (1980) found that the longevity of leaves was increased by defoliation, though the production of new leaves was depressed in the following season. Chapin and Slack (1979) found that the initiation, elongation, and mortality of roots were not affected by moderate levels of defoliation.

There is some evidence of antiherbivore chemistry in C. aquatilis.

Joachim et al. (1979) reported alkaloids in foliage. Rhoades (1979) reported 35% increases in phenolics and 45% increases in proanthocyanins in undamaged tissue following partial defoliation. In addition, mature foliage is tough and probably abrasive, as is true of many graminoids (Section 1.2.2.1.). Reported concentrations of nutrients in above-ground tissues are unremarkable: 1-3% N and 0.1% P by dry weight (Chapin et al. 1975; Shaver et al. 1979). Concentrations of N and P peak in green above-ground tissues shortly after snowmelt; "dilution" by growth and translocation to below-ground storage organs reduce concentrations as the summer progresses (Chapin et al. 1975).

2.2.3. Carex subspathacea Wormsk.

Carex subspathacea (= Carex salina Dew. var. subspathacea (Wormsk.) Tuckerm.) is a sedge of damp to wet soils in saline coastal areas and intertidal marshes (Hultén 1968; Fernald 1970; Scoggan 1978; Porsild and Cody 1980). A circumpolar species, in North America it is restricted to coastal sites in the High and Low Arctic and in the St. Lawrence Estuary (Hultén 1968; Fernald 1970; Scoggan 1978; Porsild and Cody 1980; Cayouette and Morisset 1986a).

C. subspathacea is a dwarf turf-forming species which produces very short leafy shoots from creeping rhizomes (Hultén 1970; Scoggan 1978). Plants range from about 3 cm to about 2 dm in height. Culms are erect, with 1 staminate spike overtopping 2-3 pistillate spikes (Hultén 1970; Scoggan 1978). In its vegetative morphology, C. subspathacea resembles a tiny C. aquatilis (Figure 2.1.); the main difference is that its spreading rhizomes, which may reach lengths of 20 cm, are less easily distinguishable from its clumping rhizomes, which usually range between 0.5 and 10 cm in length.

C. subspathacea seems to avoid the most saline sites, tending to be commonest near the high-tide mark and along brackish drainage channels in salt marshes (Kershaw 1976; Jefferies et al. 1979; Bazely and Jefferies 1986). Though flowering is common in lightly grazed areas, it seems likely that most reproduction is vegetative, as in C. aquatilis. On the heavily grazed salt marshes at La Pérouse Bay, very few seeds are set before flowers are removed by geese. Root to shoot ratios are high, ranging from 2:1 to 10:1 (Jefferies 1977; Cargill and Jefferies 1984b).

At La Pérouse Bay, grazing by Lesser Snow Geese increases the net annual above-ground production of C. subspathacea by 60-80% (Cargill and Jefferies 1984b; Section 2.3.1.). This same study did not demonstrate any significant effects of grazing on belowground biomass, though very high between-site variance reduced the power of the comparisons. The nitrogen contents of above-ground tissues in salt-marsh plants of this species range from 0.4% to about 6%, tending to be highest at the beginning of the season (Jefferies et al. 1979; Cargill and Jefferies 1984b). Grazing by the geese and their associated activities tend to increase concentrations of nitrogen in the bulk tissues (Cargill and Jefferies 1984b).

2.2.4. Carex X flavicans Nyl.

Carex X flavicans (= Carex X halophila nm. flavicans (Nyl.) Boivin) is a rarely reported hybrid between C. aquatilis and C. subspathacea (Scoggan 1978; Cayouette and Morisset 1985). It is generally found in coastal areas within the geographic ranges of its parental species; most Canadian records come from Hudson Bay, James Bay, and the St. Lawrence Estuary (Scoggan 1978; Cayouette and Morisset 1985). C. X substans Lepage, a hybrid of C.

aquatilis var. stans and C. subspathacea, is also known from the High Arctic (Scoggan 1978).

Carex x flavicans is intermediate in general appearance between its parents, tending to more closely resemble C. X subspathacea in above-ground morphology (Cayouette and Morisset 1985); plants tend to be 15-30 cm tall. In its below-ground morphology, C. X flavicans resembles C. aquatilis, with well differentiated spreading shoots (produced by rhizomes with lengths of around 15 cm) and clumping shoots (produced by rhizomes with lengths of 0.5-5.0 cm). Plants range from densely turf-forming in shallow water and in the wet areas between ponds to sparsely tufted along the edges of ponds.

Flowers are frequent at La Pérouse Bay, and do set seed if they escape herbivory, but whether seeds are viable is unknown (Cayouette and Morisset 1985). Stainabilities of pollen at La Pérouse Bay and elsewhere ranged from 10-79%, as compared with 92% for C. aquatilis and 90% for one specimen of C. subspathacea (Cayouette and Morisset 1985; J. Cayouette, pers. comm.). For specimens from the Quebec shore of Hudson Bay, Cayouette and Morisset (1985) cited a diploid chromosome complement of 2N=79; numbers of chromosomes in pollen grains were variable. For plants from the same site, Cayouette and Morisset (1985) report diploid numbers of 2N=83 for C. subspathacea and 2N=78 for C. aquatilis. Aneuploid series exist in both of these species, as is typical of Carex, but the phenomenon does not necessarily imply sterility (Grant 1981; Cayouette and Morisset 1985, 1986a,b).

Very little is known of the ecology of C. X flavicans. At La Pérouse Bay, this hybrid occurs in wet peats in fresh-water areas, where it often grows as dense monocultures. It also grows sparsely interspersed in the moss carpets which surround many fresh-water ponds. Reproduction appears to be primarily or exclusively clonal, a suspicion shared by Cayouette and Morisset

(1985), who felt that the morphological uniformity of this hybrid implied vegetative reproduction by F_1's or the occasional backcross. Though its known distribution is rather spotty, it is possible that C. X flavicans might better be considered as a "stabilized hybrid or as a species of hybrid origin" (J. Cayouette, pers. comm.).

2.3. Study Locations

2.3.1. La Pérouse Bay

La Pérouse Bay is located on the Hudson Bay coastline, about 25 km east of Churchill, Manitoba (Figure 2.2.). Lying within the Hudson Bay Lowland, this area is very flat and poorly drained, dominated inland by fresh-water marshes and along the coast by lagoons, salt marshes, and tidal flats.

This area is undergoing isostatic uplift at a rate of 0.5-1.2 m per 100 years (Hunter 1970; Weber et al. 1970). Since the coastline rises very slowly from the sea (0.5-1.0 m in elevation per km inland: Jefferies et al. 1979), this rate of uplift exposes about 10-20 m of new land per year (Martini 1982). Numerous beach ridges extend far inland at many locations; along with eskers and other glacial landforms, these provide most of the relief (Jefferies et al. 1979).

The area of La Pérouse Bay is deeply covered with glacial till and with fresh-water and marine sediments. Intertidal soils are mixtures of sand and silt, scattered with numerous large rocks; where vegetation has colonized successfully, the soil may have a large organic component, contributed primarily by microbial and root litter (Jefferies et al. 1979). Sediments are saturated and may be anoxic; if vegetated, they may have C:N ratios in

Figure 2.2. Map of the Hudson Bay region, showing La Perouse Bay
and the McConnell River. From Jefferies and Kerbes
(1985).

96° 92° 88° 84° 80° 76° 72° 68°

Arctic Circle

Baffin Is.

Foxe Channel

Foxe Peninsula

Cape Dorset

Hudson Strait

Southampton Is.

64°

Rankin Inlet

Chesterfield Inlet

Ivujivik

Coats Is.

Whale Cove

Mansel Is.

Wolf Creek

Eskimo Point

McConnell R.

Tha-anne R.

HUDSON BAY

Churchill

La Pérouse Bay

North Knife R.

Churchill R.

Cape Churchill

Nelson R.

Pen Is.

Belcher Islands

Hayes R.

Kaskattama R.

Fort Severn

56°

Winisk

Poste-de-la Baleine

Severn R.

Winisk R.

JAMES BAY

Ekwan R.

Attawapiskat R.

Albany R.

52°

Fort Albany

Moosonee

Moose R.

Thunder Bay

48°

Lake Superior

excess of 15:1 (Bazely and Jefferies 198Na). In fresh-water areas, surficial deposits are generally wet or saturated peats; mineral soils are exposed only in some ponds and near streams.

La Perouse Bay includes the braided deltas of two major drainage systems: the Mast River and Wawao Creek. Along with other, smaller drainage systems, these rivers flood the entire area each spring. Noticeable tides do not occur until most of the ice has disappeared from Hudson Bay; the salt marshes are not regularly flooded until mid-July to late July. The salinity of the inshore regions of Hudson Bay is low where runoff and melting ice have a strong influence (Jefferies 1977; Jefferies et al. 1979).

The climate in the area of Churchill is Subarctic (Low Arctic) (Scoggan 1959). Though Churchill lies on the treeline, La Perouse Bay is within the belt of coastal tundra which fringes Hudson Bay; the treeline lies about 10 km inland. Snowmelt generally extends over two weeks beginning in mid-May to late May; daytime minimum temperatures consistently exceed 0 C from early June (Bazely 1984). From late June to mid-August, typical daytime maxima are in the order of 10-15 C, though maxima above 30 C can occur, and minima around 3 C are not uncommon (Bazely 1984; Cargill and Jefferies 1984a). Daily minima drop below 0 C in mid-September, and snow begins to accumulate in October (Cargill and Jefferies 1984a). Snow may fall in any month, but is rare from mid-June to late August; the snow-free period averages around 4 months (Cargill and Jefferies 1984a). Annual precipitation totals about 400 mm, of which 2/3 falls in the summer (Cargill and Jefferies 1984a).

The vegetation within the study areas at La Perouse Bay forms 3 distinct belts: the salt marshes, a transition zone, and the fresh-water marshes. The extent of each of these zones varies along the coast. The salt-marsh community extends inland to a maximum of about 1.5 km inland near the

centre of the Bay, but to only a few hundred metres near its periphery. The transition zone is a belt of vegetation which is generally narrower than 500 m, which also reaches its maximum width near the centre of the Bay. The fresh-water communities, interspersed with beach ridges and other well-drained areas, continue to the treeline.

The salt marshes extend over 5.4 km^2 (Cargill and Jefferies 1984a). These marshes are dominated by the grass, Puccinellia phryganodes (Trin.) Scribn. and Merr. and the sedge Carex subspathacea Wormsk., which together account for over 90% of the total above-ground standing crop; the remainder is composed of herbs such as Potentilla egedii Wormsk., Ranunculus cymbalaria Pursh, Plantago maritima L., Stellaria humifusa Rottb., Triglochin palustris L., and Hippuris tetraphylla L.f., and the mosses Bryum inclinatum (Brid.) Bland. and Campylium stellatum (Hedw.) C. Jens. (Jefferies et al. 1979; Cargill and Jefferies 1984a,b; Bazely and Jefferies 1986). Though Puccinellia phryganodes and Carex subspathacea often grow in even mixtures, P. phryganodes is also the primary colonizer of newly exposed foreshore mudflats while C. subspathacea, like Hippuris tetraphylla, is more abundant in depressions and along fresh-water streams through the salt marsh (Jefferies et al. 1979; Cargill and Jefferies 1984a,b; Bazely and Jefferies 1986).

Inland of the salt marsh is a transition zone of frost-heave mounds and small pools which are flooded by runoff in the spring and by very high tides in the fall. Many of these pools become much more saline than Hudson Bay as evaporation progresses over the summer (Jefferies et al. 1979; Glooschenko and Harper 1982). The vegetation in this zone resembles that of the tidal flats in lowlying areas, often with additional halophytes such as Salicornia borealis Wolff and Jefferies (Wolff and Jefferies 1987). Hummocks are dominated

with a more glycophytic vegetation in which prominent species include willows
(especially Salix brachycarpa Nutt.), Betula glandulosa Michx., and the grass
Elymus mollis Trin.. The ground cover is composed of Carex subspathacea,
grasses such as Calamagrostis deschampsioides Trin., Festuca rubra L.,
Dupontia fisheri R. Br., and many dicotyledonous herbs (Jefferies et al. 1979).

Above the high tide mark, the vegetation gives way to fresh-water pools
separated by slightly higher ground dominated by shrubs, including Salix
phylicifolia L. ssp. planifolia (Pursh) Hiitonen, Betula glandulosa, and Myrica
gale L.. Edges of ponds and lowlying areas are dominated by a variety of
graminoids. Carex aquatilis Wahl. is widespread, but is commonest in
standing water and in the wet areas surrounding ponds and streams. Carex
X flavicans is often dominant in shallow standing water and in the saturated
carpets of moss (mostly Drepanocladus uncinatus (Hedw.) Warnst.) which surround
many ponds. Many other graminoids, such as Eleocharis spp., Juncus spp.,
Calamagrostis spp., Dupontia fisheri, Scirpus caespitosus L., Carex spp.,
and numerous creeping dicotyledons such as Potentilla palustris (L.) Scop.,
also occur in these fresh-water communities.

The La Pérouse Bay colony of Lesser Snow Geese currently numbers about
7000 pairs, nesting primarily in the transition zone (Jefferies 1987). Each
spring, the La Pérouse Bay area also briefly supports tens of thousands of
migrants; smaller numbers of migrants use the area in the fall. Together with
their goslings, Snow Geese are by far the most important herbivores at this
location.

The age of this colony is uncertain, but it is probably quite young.
Though nesting at this location has been reported intermittantly since 1953,
continuous use by the geese may have begun as recently as the early 1960's
(Cooke et al. 1975b; Kerbes 1975). In 1968, when a team led by Dr. F. Cooke

began intensive studies at this site, the colony numbered only about 1200 pairs (Cooke et al. 1975b).

Both residents and migrants arrive in mid-May, before snowmelt. At this time of year, little green above-ground tissue is available; the geese avoid brown overwintered tissue. Instead they grub on the salt marsh for roots and rhizomes, stripping many areas of Carex subspathacea and Puccinellia phryganodes to bare patches of sediment extending over a few square metres; similar behaviour occurs along edges of ponds and streambanks in the transition zone (Jefferies et al. 1979; Jefferies 1987). As consequences of this behaviour, the geese enlarge pre-existing ponds and denude areas of vegetation, which may take years to recover (Jefferies et al. 1979; Jefferies 1987). During the spring, the geese also forage intensively in fresh-water areas where they pull the developing shoots of Carex X flavicans and especially those of Carex aquatilis, consuming their succulent, swollen bases and discarding the remainder (Jefferies 1987; P.M. Kotanen pers. obs.). This pulling of shoots may be very intense, with hundreds of shoots per square metre being destroyed. It is possible that this grubbing leads to the elimination of these carices at the local scale, which results in the production of the moss carpets. Geese have been implicated in the production of moss carpets at other tundra locations (Tikhomirov 1959; Jefferies and Kerbes 1985; Jefferies 1987; Section 2.3.2.). Less intensive grubbing also occurs in both fresh-water and salt-water habitats at the beginning of the fall migration in August.

Grubbing and shoot pulling are almost exclusively spring and fall phenomenona; between hatch in mid-June and the departure of the geese in mid-August, adults and goslings feed almost exclusively by clipping the leaves of graminoids. Throughout this period, the average ratio of goslings to adults is about 1.7:1, which implies a total size of over 30 000 geese for the colony

at La Pérouse Bay (Cargill and Jefferies 1984b).

Post-hatch feeding occurs primarily on the salt marsh. Here, the vegetation is uniformly reduced to 2.5 cm or less in height; however, this grazing is relatively nondestructive. Comparisons between grazed areas and areas protected from the geese by exclosures indicate that the geese increase the net annual above-ground primary production of the salt marsh by 30-110%, depending upon the year (Cargill and Jefferies 1984b; Bazely 1984; Bazely and Jefferies 198Nb). This increased production is not a product of grazing per se, but is a consequence of the geese increasing the availability of nitrogen in this strongly nitrogen-limited environment (Cargill and Jefferies 1984a; Bazely and Jefferies 1985, 198Na). The geese remove about 80% of the annual above-ground primary production, converting it into droppings rich in soluble nitrogen rather than slowly decomposing litter; the net effect is an increased supply of nitrogen available for regrowth (Cargill and Jefferies 1984a,b; Jefferies et al. 1984; Bazely and Jefferies 1985, 198Na). By preventing the buildup of litter and limiting the leaf area index, geese also promote the colonization of the sediment by nitrogen-fixing cyanobacteria, increasing the absolute input of nitrogen and replacing the nitrogen which the geese export south with them in the fall (Bazely and Jefferies 198Na).

As well as enhancing its production, the geese maintain the salt-marsh community. Protecting the salt-marsh vegetation from grazing results in rapid changes in species composition, with Carex subspathacea increasing in frequency at the expense of Puccinellia phryganodes (Bazely and Jefferies 1986). Geese prevent these changes by excluding species not resistant to grazing or trampling, and by preventing changes in the composition and salinity of the soil associated with the accumulation of litter (Bazely and Jefferies 1986).

During the summer, the geese also graze in fresh-water areas. Though

this grazing is patchier, less intense, and less continuous than that on the salt marsh, it is frequent enough to be an important source of food for the colony, especially when poor weather or disturbance by people or Polar Bears force the geese from the tidal marshes. The most intensely grazed fresh-water species is C. X flavicans; grazing lawns of this species are maintained in the moss carpets around the margins of ponds. The vegetation in these carpets is limited to about 5 cm in height by frequent clipping. Leaves of Carex aquatilis are also eaten, but where this occurs is patchy, and the consumption of the leaves is less intense and declines through the summer. If the La Pérouse Bay colony continues to grow, the importance of foraging in fresh-water areas may be expected to increase, especially if the salt marshes are already near their carrying capacity, as Cargill (1981) suggests.

2.3.2. The West Hudson Bay colonies

Approximately 300 000 Lesser Snow Geese currently nest on 5000 km^2 of the coastal plain in the vicinity of Eskimo Point, Northwest Territories (Kerbes 1982). Though on the Canadian Shield, this area is very flat and wet, and the Shield is deeply buried beneath glacial till. In contrast to the Churchill area, extensive vegetated tidal flats are scarce. Most nesting and feeding occur in the sedge meadows which are the dominant vegetation inland of Hudson Bay.

The vegetation of the West Hudson Bay region is similar to that of La Pérouse Bay, though of a distinctly more northern character. Where salt marshes exist, they are largely composed of Carex subspathacea and Puccinellia phryganodes. Inland, there are extensive fresh-water meadows of Carex aquatilis, Carex spp., Eriophorum spp., Calamagrostis spp., Dupontia

fisheri, and many other grasses and sedges, together with Betula glandulosa, Salix spp. and other shrubs which dominate in slightly elevated areas. Mosses are very important in the ground cover of these areas; soils are generally wet organic peats. Eskers, glacial moraines, and beach ridges are common, and support a more xerophytic vegetation.

The largest of the West Hudson Bay colonies is located at the mouth of the McConnell River, south of Eskimo Point (Figure 2.2.) (Kerbes 1975). This colony has existed since at least 1910; it has been studied intensively by various researchers since 1954 (Kerbes 1982). Other important colonies in the West Hudson Bay region are located on the Tha-anne River, Wolf Creek, and the Maguse River (Kerbes 1975).

Geese in the West Hudson Bay region forage in spring by grubbing for shoots and rhizomes; after hatch, foraging shifts to the grazing of leaves of graminoids (Harvey 1971; Ankney 1977; Harwood 1977; Kerbes 1982). Following hatch, families do not confine themselves to the immediate area of the colony, as most do at La Pérouse Bay, but may wander tens of kilometres in search of food (MacLaren and MacLaren 1982).

Between 1941 and 1973, the McConnell colony may have grown as much as 30-fold (Kerbes 1975); however, between 1973 and 1980, the colony declined in size from 163 000 pairs to 115 400 pairs, and also moved outward from its original centre (Kerbes 1975, 1982, pers. comm.; Jefferies 1987). Excessive herbivory may be the cause of these changes (Harwood 1977; Kerbes 1982; Jefferies and Kerbes 1985; Jefferies 1987). In 1985 and 1986, ground surveys of the vegetation near the former centre of the colony indicated that the heavily grazed sedge communities which were formerly abundant in this area have been destroyed and degraded (Jefferies and Kerbes 1985; Jefferies 1987; Jefferies, Kerbes, and Kotanen, unpublished data). In the coastal salt marsh,

only isolated clumps of vegetation remain. Within fresh-water communities, the graminoid cover has been almost completely removed, exposing bare peat; only species not eaten by the geese survive, such as <u>Betula glandulosa</u>, <u>Salix</u> spp, and <u>Potentilla palustris</u>. In some areas, even the peat has eroded, exposing mineral soil. Whether these communities will regain their original character is uncertain; if recolonization is slow, isostatic uplift may fundamentally alter the physical environment before recovery can occur (Jefferies and Kerbes 1985).

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**CHAPTER 3: THE LEAF AND SHOOT DEMOGRAPHY OF GRAZED AND UNGRAZED PLANTS OF
CAREX SUBSPATHACEA**[*]

3.1. Introduction

Carex subspathacea[+] Wormsk., a rhizomatous sedge, is widespread in arctic
coastal salt marshes (Hultén 1968). Plants frequently form a dense turf on
intertidal sediments. On the foreshore of La Pérouse Bay, Manitoba, this
species and the grass, Puccinellia phryganodes (Trin.) Scribn. and Merr., are
abundant, and both are grazed intensively by a breeding colony of 7000 pairs of
Lesser Snow Geese (Chen caerulescens caerulescens (L.) Gundl.) and their
goslings. Other migratory populations of Lesser Snow Geese also use the site
as a staging area.

Grazing by the geese significantly increased net above-ground primary
production (NAPP) of mixed swards of the two species by 35% in 1979 and 80% in
1980 (Cargill and Jefferies 1984b). In 1980, NAPP of grazed swards of pure
stands of Carex was 60 to 80% higher than that of ungrazed swards (Cargill and
Jefferies 1984b).

A consequence of grazing is that plant tissue, rather than accumulating as
live biomass or litter, is converted into goose biomass or faeces. Since geese
defaecate approximately 200 times a day and most of the nitrogen is present in
a soluble form in faeces, the addition of this nitrogen to a Carex sward
increases plant production in this nitrogen deficient environment (Cargill and
Jefferies 1984a,b). When fresh faeces are added to experimental plots at

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[*]This chapter is based upon Kotanen and Jefferies (1987).

[+]Nomenclature follows Scoggan (1978)

densities comparable to those recorded in the salt marsh, significant increases in standing crop occur compared with values for untreated plots (Bazely and Jefferies 1985). These graminoid species can increase above-ground net primary production in response to the addition of nutrients during the same growing season, unlike some arctic sedges which may show a more delayed response (Cargill and Jefferies 1984a; Henry, Freedman and Svoboda 1987). The ability of preferred forage species to show rapid growth responses to an available nutrient source (i.e., within the breeding season) more than compensates for any adverse effects of defoliation on production.

The purpose of this study was to determine the changes in the growth of shoots that enabled plants of Carex subspathacea to achieve a significant increase in NAPP when grazed. Using demographic techniques, we have measured the production and turnover of shoots and leaves of Carex in swards subjected to grazing and in which faeces accumulated. Corresponding demographic changes that occurred in swards protected from grazing likewise have been measured.

3.2. Materials and Methods

3.2.1. The site

The extensive tidal flats at La Pérouse Bay, 25 km east of Churchill, are covered by spring tides from late July or early August each year until "freeze-up" in October or early November. Besides Carex and Puccinellia, the flats are colonized by Potentilla egedii Wormsk., Plantago maritima L., Ranunculus cymbalaria Pursh., and Stellaria humifusa Rottb., although the latter four species are present at a much lower frequency than the

graminoid species. In excess of 7000 pairs of geese nest in the coastal lowlands immediately inland from La Pérouse Bay. Within 24 hours of hatching, which occurs in late June, goslings and their parents graze intensively on the tidal flats during daylight hours. The geese leave in mid-August to begin their southward migration.

Each year the geese crop the vegetation of the tidal flats to 2.5 cm or less in height. It appears that the existence of the community in its present form is strongly dependent on herbivory. When exclosures are erected rapid changes in the species composition of the sward occur during successive seasons, and standing crop increases five-fold within two seasons (Bazely and Jefferies 1986).

A detailed description of the salt marsh at La Pérouse Bay and the vegetational zones has been presented elsewhere (Jefferies, Jensen and Abraham 1979; Cargill and Jefferies 1984b).

3.2.2. The growth habit of Carex subspathacea

The species is strongly rhizomatous; there is an iterative production of sympodial shoot modules resulting in a dense sward of shoots. The aerial shoots, although clustered, are produced from either long or dwarf branches, as in Carex arenaria L. (Noble, Bell and Harper 1979). The diagrams (2c and 2d) of the basic morphology of the rhizome axis of Carex arenaria (Noble, Bell and Harper 1979) describe the growth habit of Carex subspathacea. Clustered aerial shoots are separated from each other by about 0.5 cm. The length of the rhizome between clusters of aerial shoots is about 10 cm; branching of the rhizome at the nodes is rare, and no shoots develop from intervening nodes. The sward is composed of a mosaic

of rhizomes produced by different ramets. Flowering is a rare event in both grazed and ungrazed swards.

The overall pattern of growth of this sedge is similar to that described for other species (Johnson and Tieszen 1976; Noble, Bell and Harper 1979; Callaghan and Collins 1981; Fetcher and Shaver 1983; Robertson and Woolhouse 1984).

3.2.3. Demographic methods

In mid-June, 1984, a few days after thaw, three pairs of plots (0.5 X 0.5 m) were established in an area of marsh dominated by Carex subspathacea, which had been frequently grazed by Lesser Snow Geese in 1983. Wire netting was used to construct an exclosure (0.6 X 0.6 X 0.5 m) around one plot of each pair; the remaining three plots were left open to grazing. Shoots of Carex were located in each plot with the aid of a 0.5 X 0.5 m metal quadrat strung with thin wire at intervals of 5 cm. The shoot closest to each of the 81 intersections of the crosswires was marked and subsequently identified by a small ring of thin, coloured telephone wire, located close to the sediment at the base of the shoot. Demographic changes of the population of leaves on marked shoots were recorded on six occasions between mid-June and early September (Table 3.1.). Where necessary, the average date of sampling is given, since the sampling of all plots often took several days to complete. At each sampling date, the corners of the metal quadrat were placed over four permanent pegs. All leaves on a designated shoot were recorded as being alive, dead, partially grazed or removed. Leaves present at the start of the season and all new leaves were marked with a distinctive pattern of small India ink dots applied with a camel hair brush, so that they could be

Table 3.1.

Dates on which leaves and shoots of _Carex subspathacea_ were examined.

Leaves were recorded in 1984, shoots in 1985.

Leaves		Shoots	
Date	Average interval (days)	Date	Average interval (days)
June 11-16————|		June 16————————|	
	|- 13.0		|- 16.0
June 26-27————|		July 2————————|	
	|- 18.0		|- 19.0
July 14-15————|		July 21————————|	
	|- 17.5		|- 13.0
July 30-Aug 4——|		August 3————————|	
	|- 13.5		|- 8.0
August 14-15———|		August 11———————|	
	|- 19.0		|- 21.0
Sept. 2-3————|		Sept. 1————————|	

identified again. This technique allowed the patterns of leaf development and senescence to be determined for each shoot during the summer of 1984. In spite of the burial of rings beneath silt, 77 and 80 shoots respectively from grazed and ungrazed plots were located with their rings intact in the spring of 1985, so that it was possible to determine their survivorship over the winter. Similar data of changes in leaf number were based on a small sample of 13 grazed and 21 exclosed living shoots, which possessed identifiable marked leaves.

A further six plots of similar size were established in the same area soon after thaw in June, 1985. These plots were set up in order to obtain additional information on the demography of grazed and ungrazed shoots, as preliminary results obtained in 1984 indicated a low turnover of shoots. As before, three were exclosed and three were grazed. One of the latter plots was abandoned early in the season because of the deposition of sediment from pack ice and spring melt. Within each of the five remaining plots three (2 X 2 cm) subplots were chosen at random, and a total of 169 shoots for all subplots were marked with a toothpick sunk into the sediment adjacent to the shoot; only 1 mm of the toothpick protruded above the sediment. Shoots were examined approximately once every 15 days from mid-June until early September (Table 3.1.). On each sampling date, toothpicks associated with dead or missing plants were removed and new shoots were marked. The data were used to estimate the numbers of births and deaths of shoots within the plots and the survivorship of shoots.

3.2.4. Statistical methods

Unless otherwise stated, all statistics of births and deaths of leaves were based upon cumulative births and deaths for each of the 178 grazed and 205 ungrazed (exclosed) shoots that survived the season. Analyses of variance of the number of leaves produced, the number of leaf deaths, and the standing numbers of leaves were the most important exceptions; these were based upon 52 randomly selected shoots per plot. This truncation of sample size was necessary in order to avoid the unequal sample sizes associated with differential mortalities of shoots in plots during 1984. The statistical design was a factorial ANOVA with sites crossed with grazing treatments, which allowed a separation of effects due to site differences and those due to treatments (Kirk 1982). In no such analysis did a significant interaction term occur. Cumulative births and deaths were also compared using a split-plot factorial ANOVA design (Kirk 1982). When necessary, data were transformed so as to pass the F_{max} test for homogeneity of variance (Kirk 1982). Calculations of births and deaths of leaves over the winter were based on data pooled from either grazed or ungrazed plots, in order to increase sample size in exchange for the loss of measures of heterogeneity between plots.

Wherever possible, $\hat{\omega}^2$ or $\hat{\rho}_I$ was calculated. These very similar statistics are analogous to r^2 in a regression, giving a measure of the "importance" or "strength of association" of a treatment; that is, how much of the variance in a set of data is explained by a treatment (Keppel 1982; Kirk 1982). Both range from 0 to 1, with values over 0.15 considered "strong" effects (Cohen 1977; Keppel 1982); $\hat{\omega}^2$ is used for a "fixed" treatment, such as grazing treatment (levels of treatment selected by

experimenter), while $\hat{\rho}_I$ is used for a "random" treatment, such as plot effect (Kirk 1982). These statistics are valuable companions for any F- or t-test, in that a significant F or t merely indicates that a treatment is responsible for some of the experimental variance, while giving no indication of how strong an effect the treatment has produced.

Expected leaf lifespans and grazing schedules within the field season of 1984 were calculated from data of the survivorship of all marked leaves. This required a computer life-table program for right-censored survivorship data; that is, data including individuals surviving or remaining ungrazed at the end of the sampling season (S.P.S.S.X, Anon. 1986). Because survivorship of leaves differed between plots experiencing the same treatment, the results of each plot were considered separately. Since dates of birth, death, and grazing were known only approximately (i.e., within a sampling interval), values were adjusted for this source of bias by assuming all events occurred at the midpoint of the appropriate interval. In order to obtain large and representative samples for the estimation of lifespans, survivorship data were pooled for cohorts of leaves produced at different times throughout the season. Such an approach combines features of cohort and current life tables, and is valid only if the populations so treated are stationary (Pielou 1969). As indicated below, this assumption is approximately true for leaf lifespans but not for grazing schedules; consequently, the age of leaves at the time of their first grazing were calculated separately for each sampling interval. Comparisons of survivorship of leaves between plots and treatments were made using the Lee-Desu modification of the Wilcoxon test (Lee and Desu 1972). This statistic, symbolized by "D", approximates χ^2 with (k-1)df, where k is the number of comparisons involved.

Analyses were carried out on the entire data set from the pooled grazed

plots, in order to determine if leaves of any particular age were more heavily grazed than random selection of leaves predicted. This involved the use of G-tests (Sokal and Rohlf 1981) of the independence of leaves' ages, and the proportion of leaves being first grazed within a given sampling interval. It is assumed that, if leaves are randomly grazed, the proportion of previously ungrazed leaves being grazed for the first time in an interval equals the proportion of all leaves that are grazed in the same interval, irrespective of the number of times that any given leaf has been grazed. Since it is much easier to record the first grazing of a leaf than to monitor any subsequent grazings, this procedure gives the most accurate estimate possible that is still consistent with the null hypothesis of randomness. Again, proportions were adjusted for the bias of events occurring between sampling dates.

In the statistical analysis of the data of the demography of shoots, numbers of shoot births and deaths for each plot were expressed as proportions of the total number of shoots observed during the season. This procedure compensated for unequal initial shoot densities and small sample sizes, and made the data more closely analogous to cumulative leaf births and deaths. After ensuring that plots within each treatment were statistically homogeneous, plots subject to each treatment were pooled so that the numbers of births and deaths of shoots could be compared between treatments by the use of G-tests.

3.3. Results

3.3.1. Demography of leaves

Between 11 June and 3 September, 1984, shoots in grazed plots produced an average of 8.2 new leaves, compared with an average of 5.7 leaves per shoot in ungrazed plots (Fig. 3.1.). Production between 3 September 1984 and 16 June, 1985 added only an average of 0.31 leaves to grazed shoots and 0.76 leaves to ungrazed shoots (Table 3.2.). Although the latter difference is significant ($p < 0.05$; Kruskal-Wallis test), the small values involved indicated that production of leaves from June to September represents by far the greatest part of the annual leaf production. The within-season production was significantly greater in grazed plots than in ungrazed plots ($F_{1,2} = 63.70**$). Significant between-plot variation also existed ($F_{2,306} = 10.18**$). The effects of treatment and between-plot variation respectively explained large ($\hat{\omega}^2 = 0.339$) and medium ($\hat{\rho}_I = 0.052$) proportions of the variance. Coefficients of variation derived from the complete, untransformed set of data were similar in grazed and ungrazed plots (coefficients of variation and 95% confidence intervals were 0.256 +/- 0.027 and 0.240 +/- 0.024, respectively). Rates of leaf production were higher in grazed plots than in ungrazed plots; in both treatments, rates declined over the season (Fig. 3.2.).

In 1984, 8.0 and 5.7 leaves per shoot died respectively in grazed and ungrazed plots (Fig. 3.1a.). As a result, cumulative deaths in grazed plots significantly exceeded those in ungrazed plots ($F_{1,2} = 105.00**$). Significant between-plot variation also existed ($F_{2,306} = 4.97**$). The effects of treatment and between-plot variation again explained large ($\hat{\omega}^2 = 0.245$) and small ($\hat{\rho}_I = 0.021$) proportions of the experimental variance. Coefficients of variation

Figure 3.1.   Changes from June to September, 1984, in numbers of

leaves of grazed (solid lines) and ungrazed (broken lines)

plants of <u>Carex</u> <u>subspathacea</u> at La Pérouse Bay, Manitoba.

(a) Cumulative births (●); cumulative deaths (○),

including deaths of leaves produced before the first

sampling, and change (births minus deaths) in number of

live leaves (△).

(b) Standing numbers of live leaves, which includes, if

applicable, those produced before the first sampling (●);

standing number of dead leaves, which includes, if

applicable, those produced before the first sampling (○).

DAYS FROM INITIAL SAMPLING
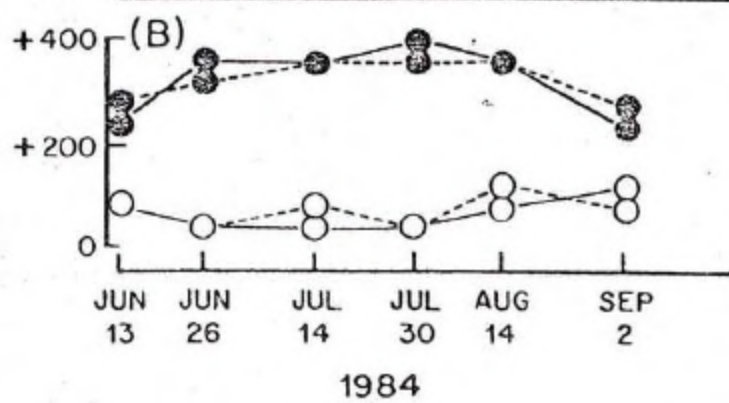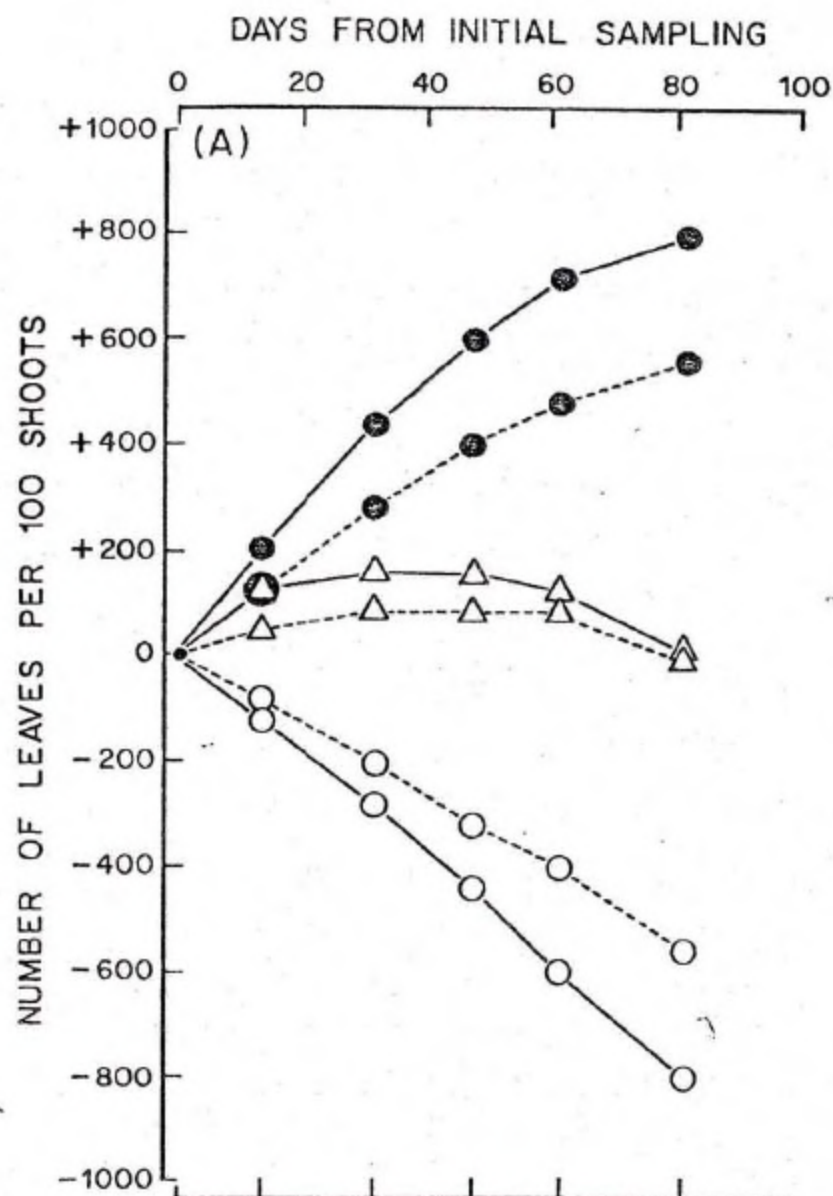
Table 3.2.

Changes in the numbers of leaves of <u>Carex</u> <u>subspathacea</u> between September, 1984 and June, 1985. Data are pooled for plots subjected to the same grazing treatment and are compared between treatments (Kruskal-Wallis tests).

parameter	treatment	n^a (shoots)	mean (leaves/shoot)	level of significance
births	grazed	13	0.31	$-\mid$
	ungrazed	21	0.76	$\mid- H = 4.049^*$, 1df $-\mid$
deaths	grazed	13	1.00	$-\mid$
	ungrazed	21	1.81	$\mid- H = 7.302^{**}$, 1df $-\mid$
survival	grazed	13	1.69	$-\mid$
	ungrazed	21	1.38	$\mid- H = 1.620$ ns, 1df $-\mid$

[a] These values are small, since ink marks on most shoots disappeared over the winter.

ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$

Figure 3.2.   Approximate natality (a) and mortality (b) of leaves of

grazed (●) and ungrazed (○) plants of <u>Carex</u>

<u>subspathacea</u> at La Pérouse Bay, Manitoba from June to

September, 1984.

NATALITY OF LEAVES

DAYS FROM INITIAL SAMPLING

(A)

LEAVES SHOOT^{-1} DAY^{-1} X 10^3

JUN 13 · JUN 26 · JUL 14 · JUL 30 · AUG 14 · SEP 2

MORTALITY OF LEAVES

DAYS FROM INITIAL SAMPLING

(B)

LEAVES SHOOT^{-1} DAY^{-1} X 10^3

JUN 13 · JUN 26 · JUL 14 · JUL 30 · AUG 14 · SEP 2

1984
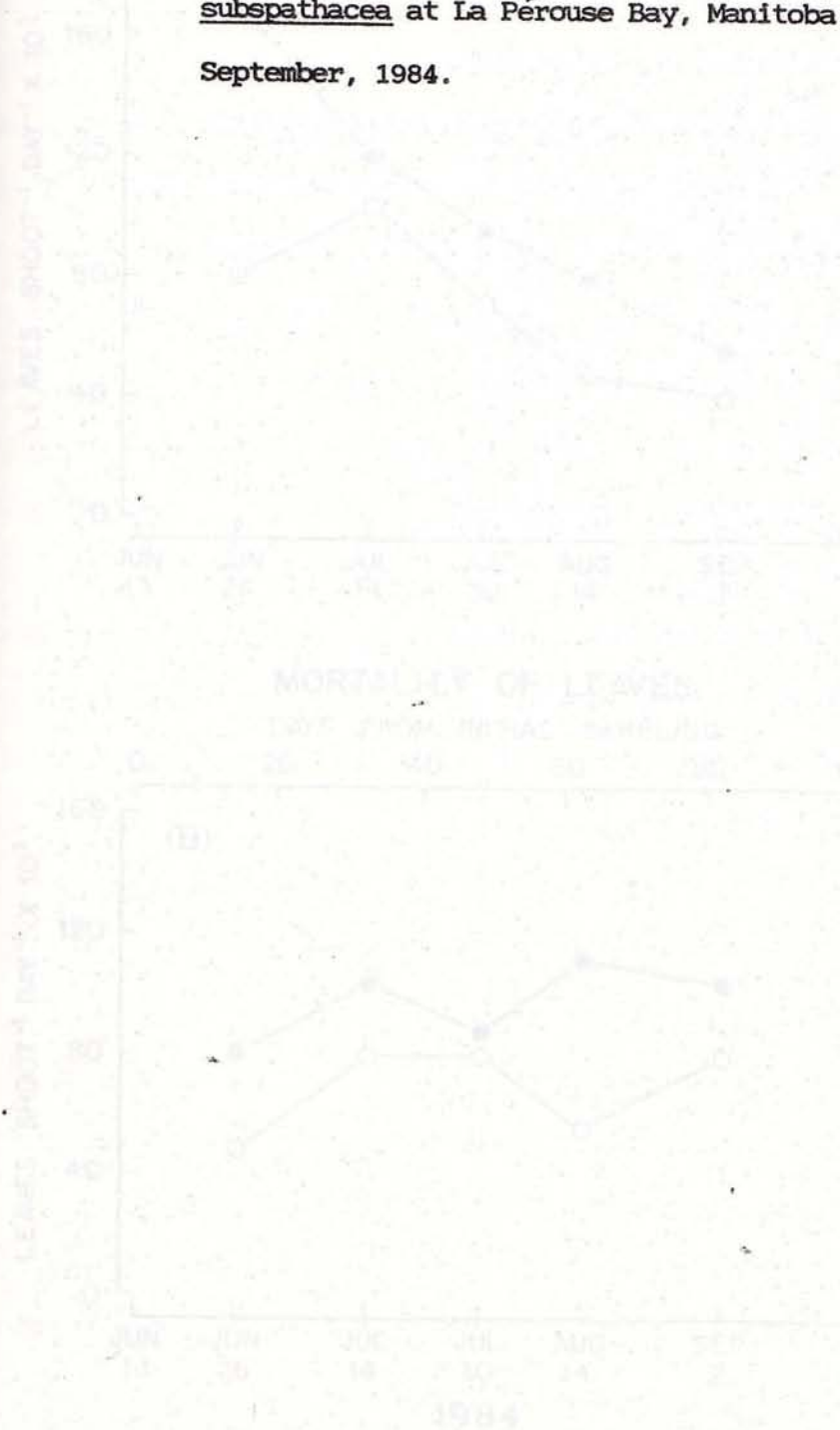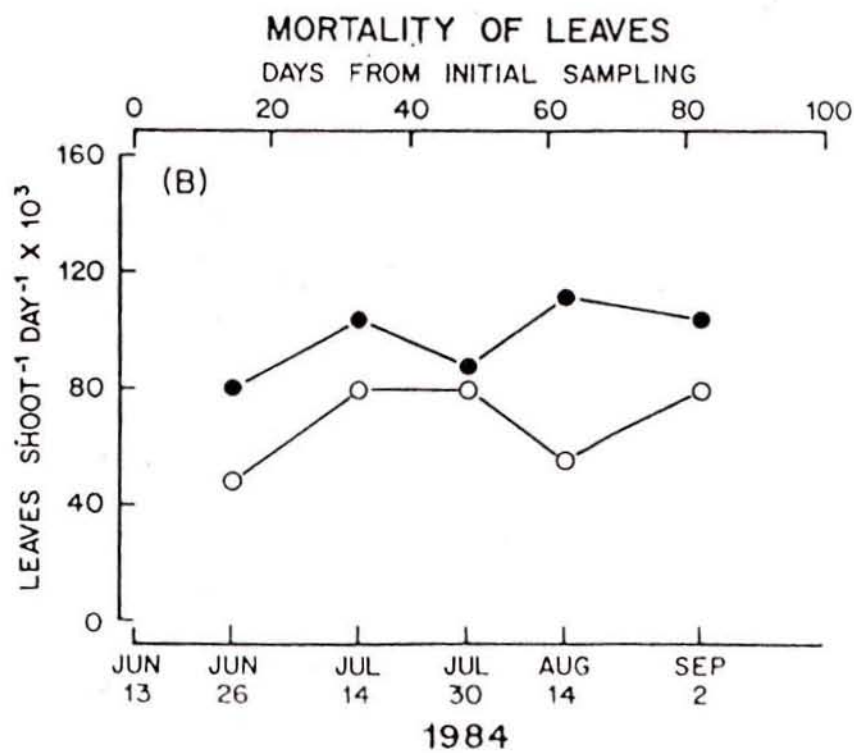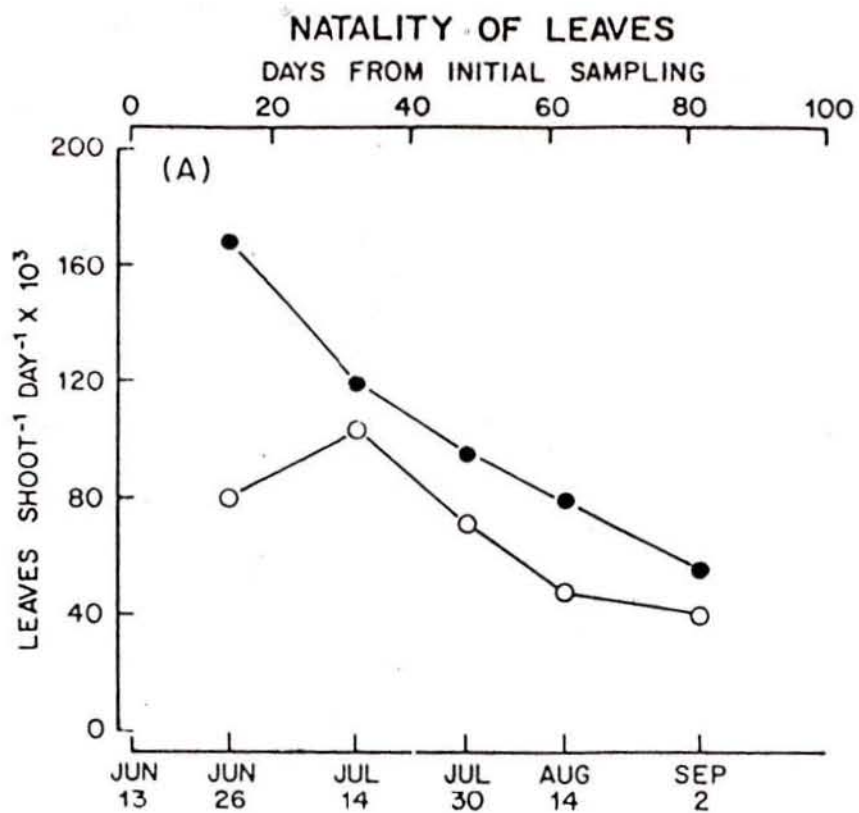
derived from the complete, untransformed set of data differed significantly between treatments, thereby providing additional evidence that grazing modified survivorship of leaves (coefficients of variation and 95% confidence intervals were 0.265 +/- 0.028 and 0.212 +/- 0.021 respectively for grazed and ungrazed treatments). Rates of leaf death were greater in grazed plots than in ungrazed plots; no seasonal trends were evident (Fig. 3.2.).

Cumulative births within the season did not significantly exceed deaths in either grazed or ungrazed plots ($F_{1,2}$ = 12.7 and 0.5 respectively; split-plot design). As a result, the net number of live leaves did not change substantially over the season in either treatment (Fig. 3.1b.), although on the final sampling date, this value was significantly greater for ungrazed sites (2.8 vs 2.5 leaves per shoot; $F_{1,2}$ = 18.99*, $\hat{\omega}^2$ = 0.04). The net number of dead leaves per shoot also changed little during the season (Fig. 3.1b.); on the final sampling date, this figure did not differ significantly between treatments (about 1 leaf per shoot, $F_{1,2}$ = 0.309). The number of leaves per shoot that died over the winter in ungrazed plants significantly exceeded the number in grazed plots (1.8 vs 1.0; p<0.05, Kruskal-Wallis test: Table 3.2.); however, the small size of the difference involved implies that this result may not be biologically important. The number of leaves per shoot surviving the winter did not differ significantly between treatments (p>0.05, Kruskal-Wallis test; Table 3.2.).

Because death rates (Fig. 3.2.) and standing numbers of live leaves (Fig. 3.1b.) did not vary markedly over the season, it was felt safe to assume a stationary population and to pool different cohorts of leaves in order to produce survivorship estimates. The suitability of this approach is indicated by the fact that estimates of life expectancies based on the first (most complete) cohort and pooled data were very similar (Table 3.3.). Leaves of shoots

Table 3.3.

Future life expectancies of zero-aged leaves of grazed and ungrazed plants of Carex subspathacea in 6 plots. Values are based on data collected between June and September 1984, pooled over all cohorts. A significant value of "D" indicates that survivorships differ within the comparison being made. Estimated life expectancies for grazed and ungrazed leaves in grazed plots, based on data pooled for the 3 grazed plots, are also given.

treatment	plot	estimated [a] life expectancy (days)	n	Lee-Desu "D" (2df) comparing plots	Lee-Desu "D" (1df) comparing treatments
grazed	1	29.80 (27.13)	581 —|		
	2	35.50 (31.86)	454	|— 53.312***	—|
	3	33.16 (31.69)	414 —|		
					|— 394.934***
ungrazed	1	47.18 (42.85)	426 —|		
	2	46.27 (45.86)	338	|— 1.410 ns	—|
	3	45.08 (43.79)	393 —|		
grazed leaves — in grazed plots		33.28	733 —|		
					0.043 ns
ungrazed leaves — in grazed plots		34.22	715 —|		

[a] Values in parenthesis are obtained from the analysis of only the first cohort and are provided strictly for comparison with the estimates based on data pooled over all cohorts.

ns p>0.05, * p<0.05, ** p<0.01

from grazed plots had estimated life expectancies between 29.8 and 35.5 days, as opposed to life expectancies of about 46 days for shoots in ungrazed plots (Table 3.3.). Very few deaths of leaves produced in 1984 occurred in the first 13 days of sampling grazed plots, or in the first 31 days of sampling ungrazed plots. When similarly treated plots were pooled, survivorships differed significantly between treatments ($p<0.001$; Lee-Desu test: Table 3.3.). When treated separately, each grazed plot differed significantly from each ungrazed plot ($p<0.001$ or better; Lee-Desu tests). Leaf survivorship also differed significantly among grazed plots ($p<0.01$; Lee-Desu test: Table 3.3.). Grazed and ungrazed leaves on shoots in grazed plots both had estimated life expectancies of 33.5 days, and survivorships that did not differ significantly (Table 3.3.). Although, strictly speaking, life expectancies are underestimated if any subjects survive the entire sampling period (Berkson and Gage 1950), the fact that less than 0.2% of leaves fall into this category implies that this is a very minor source of bias in these estimates.

Although about 50% of the leaves produced in 1984 in grazed plots were clipped by geese before their death or the final sampling date in September (Table 3.4.), only 3% of all leaves were completely removed. Since the geese annually leave the area in mid-August, it is unlikely that a significant amount of grazing occurred after the final sampling date. In early August, before the geese departed, leaves averaged 19 days old at the time they were first grazed, an average age that was slightly younger than that of the entire population of leaves at the same time (Table 3.4.). Corresponding ages at earlier dates could not be calculated since too many leaves of unknown age still survived from before the first sampling. This apparent preference of geese for young leaves is misleading, since, if grazing intensity is sufficiently great, it is probable that a leaf will be first grazed while very young, even

Table 3.4.

Mean ages and mean ages at the time of first grazing of leaves of <u>Carex</u> <u>subspathacea</u> at La Pérouse Bay, Manitoba between 30 July and 15 August, 1984. Mean age is estimated for the midpoint of this time interval (7 August). "Cumulative proportion grazed" refers to the proportion of leaves grazed at least once between June and the death of the leaf or the termination of the experiment in September.

treatment	plot	mean age (days +/- S.D.)	mean age at first grazing (days +/- S.D.)	cumulative [a] proportion grazed
grazed	1	19.57 +/- 12.46 (n = 234.5)	15.51 +/- 8.20 (n = 91)	0.558 (n = 586)
	2	23.25 +/- 12.98 (n = 211.5)	21.41 +/- 10.39 (n = 43)	0.452 (n = 456)
	3	24.02 +/- 12.74 (n = 198.5)	24.67 +/- 11.10 (n = 38)	0.417 (n = 414)
	Overall	22.15 +/- 12.85 (n = 644.5)	19.01 +/- 10.18 (n = 172)	0.485 (n = 1456)
ungrazed	1	26.62 +/- 13.19 (n = 250)	----	----
	2	25.85 +/- 12.70 (n = 220.5)	---	----
	3	24.79 +/- 12.38 (n = 251.5)	---	----
	Overall	25.75 +/- 12.77 (n = 728)	----	----

[a] These figures refer only to leaves produced between June and September 1984. If leaves produced before the first sampling date (11 June) but alive on the first sampling date are included, values of the cumulative proportion grazed for each plot drop to 0.431, 0.382 and 0.374 respectively, as a consequence of the low incidence of grazing in the early spring.

if grazing is random with respect to age. A series of G-tests of independence (Table 3.5.) demonstrated no clear preference of geese for the youngest available leaves; similar results were obtained whether or not all grazed plots were pooled.

3.3.2. Shoot demography

Between June and September 1985, cumulative shoot production, expressed as shoots produced/total shoots observed, did not differ significantly among the grazed or among the ungrazed plots (G_{adj} = 0.8 with 1df and 1.8 with 2df respectively). This allowed data from plots subject to a similar grazing treatment to be pooled. An analysis of the pooled data indicated that the observed cumulative shoot production did not differ significantly between the grazed and ungrazed treatments (G-test: Table 3.6.). Data of cumulative deaths, expressed in a similar manner, were also homogeneous among grazed and ungrazed plots (G_{adj} = 1.6 with 1 df and 0.2 with 2df, respectively). Based on pooled data, cumulative shoot deaths in grazed plots exceeded those in ungrazed plots (Table 3.6.). Shoot deaths exceeded births only in grazed plots (p<0.001; G_{adj} = 11.1 with 1df). An accurate measurement of mortality of shoots during the winter has still to be made, but there may be a significant loss in this season. Of the 157 shoots marked in 1984 that were identified in June 1985, a minimum of 8% had died (Table 3.7.). Shoot deaths over the winter did not differ significantly between grazed and ungrazed plots (Table 3.7.).

In some areas at the seaward edge of the salt marsh, deaths of shoots may be much more frequent than in other areas where a well-developed sward has established. About 97% of 127 shoots in five plots, each containing a low density of shoots (<10 shoots per 2 X 2 cm) died during the summer in such

Table 3.5.

Results of G-tests of independence (Sokal and Rohlf 1981) of the ages of

leaves of <u>Carex</u> <u>subspathacea</u> at La Perouse Bay, Manitoba and the proportions

of leaves grazed for the first time within each sampling interval. A

significant value of G indicates that these two factors are correlated.

Data were pooled for all grazed plots; similar results were obtained if each

of the three grazed plots was treated separately.

sampling interval	trend [a]	n	G_{adj}
11 June – 27 June	Not calculable	194.50	not calculable
27 June – 15 July	Y > M	495.25	6.31, 1 df
15 July – 4 August	Y < M > O	450.50	17.41, 2 df*
4 August –15 August	Y < M = O	473.25	11.92, 2 df*
15 August – 3 September	Y < M > O	303.00	6.18, 2 df

* Trend is significant at better than the 1% level. This level of
significance was used in order to reduce the possibility of a significant
result arising because of cumulative error in this series of tests.

[a] Y < M > O should be interpreted as meaning proportionally fewer younger and
older leaves grazed than middle-aged leaves. Because the lengths of
sampling intervals varied, the exact definition of these age-classes
differed among G-tests. However, all young leaves were younger than 20
days; all middle-aged leaves were younger than 34 days.

Table 3.6.

The proportions of all marked shoots of grazed or ungrazed plants of Carex
subspathacea that either were produced or else died between June and
September 1985. Data are pooled for plots subject to the same treatment.
Proportions are compared with G-tests of independence (Sokal and Rohlf 1981).

treatment	n	proportion produced in 1985	G_{adj}	proportion that died in 1985	G_{adj}
grazed	60	0.13 –|		0.40 –|	
			0.392 ns, 1 df		8.44, 1 df**
ungrazed	141	0.17 –|		0.20 –|	

ns p>0.05, ** p<0.01

Table 3.7.

The proportions of marked shoots of <u>Carex</u> <u>subspathacea</u> at La Pérouse Bay, Manitoba located in June 1985 that had died since September 1984. Because of very low frequencies, plots could not be treated separately; data are pooled for plots subjected to the same grazing treatment. Proportions are compared with a G-test of independence (Sokal and Rohlf 1981).

treatment	n^a	proportion dying in winter	G_{adj}
grazed	77	0.078 —|	
			0.044 ns 1 df
ungrazed	80	0.088 —|	

[a] These values are small, since many of the rings used to mark shoots were buried under silt during the winter, and could not be relocated.

ns $p > 0.05$

areas. Because two of the plots were exclosed and because little or no grazing were observed in the other three plots, the deaths were assumed to be caused by edaphic conditions. A combination of a heavy deposition of silt, the effects of exposure and the drying out of the surface of sediment probably accounted for the large number of deaths.

3.4. Discussion

Sedge-meadow communities in both fresh- and salt-water environments in the Arctic are an important source of forage for geese (Chapter 2). Because the densities of geese in these marshes are frequently high, the herbivores exert a profound effect on the structure and composition of the plant communities - a fact which has largely gone unrecognized.

At La Perouse Bay, grazing by Lesser Snow Geese significantly increased net above-ground primary production of a sward of Carex subspathacea (Cargill and Jefferies 1984b). The geese consumed approximately 80% of the NAPP. In the absence of grazing rapid changes in the composition of the plant community occur, leading to a decline in the abundance of some of the preferred forage species. The intensive grazing by the geese appears to be essential to maintain the community in its present state (Bazely and Jefferies 1986). The purpose of this study was to determine the changes in the growth of shoots that enabled plants of Carex subspathacea to achieve a significant increase in NAPP when grazed.

Although there was little change during the growing season in the net population of leaves in either grazed or ungrazed swards, new leaves were produced and leaves died throughout the season. Immediately after "spring thaw" there was a loss of live leaves which had been born the previous year and

which had survived the winter, so that by 30 July all leaves from this cohort were dead. Concurrent with this mortality was the production of new leaves. The birth rate exceeded the death rate of leaves of these cohorts in the early part of the season, and the birth rate also exceeded the death rate of overwintering leaves, leading to an increase in the net number of leaves in both grazed and ungrazed swards (Figs. 3.1b., 3.2.). At the end of the season the relationship was reversed. Death rates in both treatments exceeded birth rates which had declined progressively throughout the season, whereas death rates had shown little change. The large difference between treatments in the rate of leaf production at the start of the season is unexplained. It seems unlikely that it can be attributed to differences in treatment, since little foraging occurred before the end of the first sampling interval. It is also unlikely that the presence of chicken-wire exclosures could depress leaf production, particularly after such a short interval. The most likely explanation is that the disappearance of a high proportion of ink dots, because of extremely wet conditions, contributed to an inaccurate estimate of leaf production. As the estimates based on the initial sample period make only a small contribution to cumulative estimates, this initial inaccuracy is of minor importance to other calculations of leaf demography.

Many of the leaves produced in August were alive in early September, approximately ten days before the initial snowfall. In spite of the onset of winter, a few shoots produced a further leaf (Table 3.2.). Although some of the leaves from the later cohorts survived the winter, leaves died between the sampling dates of early September 1984 and June 1985. The overall seasonal pattern of demographic changes in leaf numbers is not only similar for plants from grazed and ungrazed swards, but it is also similar to that reported for other sedges (Johnson and Tieszen 1976; Robertson and Woolhouse 1984).

Perhaps the most striking result is the rapid turnover of leaves in this species. The life expectancy of leaves in ungrazed plots is between 45.1 and 46.3 days, depending on the plot (Table 3.3.). Each year the growing season lasts approximately 110-120 days. The rapid turnover of leaves of plants from this arctic salt marsh exceeds that reported for plants of Eriophorum vaginatum L. growing in arctic or sub-arctic environments (Johnson and Tieszen 1976; Fetcher and Shaver 1983; Robertson and Woolhouse 1984). Although leaves are produced continuously throughout the season in the latter species, most leaves of the early cohorts survive the growing season.

The geese appear to be selective in their grazing habits. The number of entire shoots which were destroyed by geese was less than 20% of the total population of marked shoots; in addition the geese removed less than 3% of all leaves. Although large numbers of leaves were grazed (41.7 to 55.8% depending on plot, Table 3.4.), few basal meristems were destroyed. This pattern of foraging ensured continued growth of partially grazed leaves, continued growth of existing shoots and the production of new leaves throughout the season.

Grazing resulted in a marked increase in the production of new leaves. In grazed plots an average of 8.2 new leaves per shoot were produced compared with 5.7 leaves per shoot in ungrazed plots - a 44% increase. The greater production of leaves in grazed plants, together with the associated leaf sheath growth, appears to account for the increase in net primary production in grazed swards (Cargill and Jefferies 1984b). If a linear relationship holds between cumulative births and cumulative net primary production, the increase of 44% in number of leaves produced by grazed shoots is in good agreement with the increase of between 35 and 80% in NAPP reported for grazed swards of Puccinellia and Carex by Cargill and Jefferies (1984b) for two successive years. The higher number of births of leaves resulted in a significant

increase in deaths of leaves later in the season in grazed plots, not a net increase in the number of live leaves (Fig. 3.1.). The increased production of leaves was associated with a decrease in life expectancy of leaves from 45.1 - 47.2 days in ungrazed plots to 29.8 - 35.5 days in grazed plots (Table 3.3.). Pooled data indicated no significant difference between the life expectancies of partially grazed (33.3 days) and ungrazed (34.2 days) leaves in grazed plots.

The salt marsh at La Pérouse Bay is nitrogen-deficient (Cargill and Jefferies 1984a). Addition of this element via faeces to experimental plots at densities comparable to those recorded in the salt marsh resulted in significant increases in standing crop, and the nitrogen content of shoots was also higher (Bazely and Jefferies 1985). Cargill and Jefferies (1984b) also showed that the nitrogen content of grazed shoots of Carex subspathacea was higher than that of ungrazed shoots. The addition of mobile nitrogen from faeces enhanced the growth of the graminoid species and resulted in better quality forage. A feedback model accounts for the effects of the geese in regulating the growth of their forage.

Jonasson and Chapin (1985) have suggested that in Eriophorum vaginatum and other graminoids characteristic of nutrient-poor sites, sequential leaf production increases the possibility of nutrient recycling among leaves and minimizes the annual nutrient requirements from the soil. In ungrazed swards, the continuous production of new leaves may well be dependent upon movement of nutrients from senescing leaves to developing leaves. However, in nutrient-deficient habitats removal of leaves by herbivory will restrict further leaf development if new leaves are strongly dependent on efficient recycling of resources from existing leaves. In grazed areas, faeces provide a readily available supply of ammonium ions for growth (Cargill 1982; Bazely and Jefferies 1985). The source of nitrogen not only replaces that lost to

herbivory, but also enables leaf production to exceed that of ungrazed shoots.

As indicated, a large proportion of leaves are grazed (Table 3.4.). Are leaves selected at random, independent of leaf age? When the data are expressed on a proportional basis (Table 3.5.), the overall results show that fewer younger and older leaves are clipped compared with middle-aged leaves. Protein and nitrogen contents of leaves tend to be highest at the stage when leaves reach maturity and are fully expanded. Thereafter, the protein and nitrogen contents decline. The results suggest that the geese graze leaves that provide the maximum intake of nutrients per bite, and that are likely to be the most nutritious.

In spite of the apparent uniformity of much of the marsh, the results indicate that there are plot-to-plot differences in numbers of births and deaths of leaves, life expectancies of leaves (Table 3.3.), and in the proportion of leaves grazed (Table 3.4.). Although this does not affect the overall conclusions of the study, differences in the leaf demography of plants between plots subject to the same treatment indicate that complex vegetational mosaics occur within the marsh that influence and are influenced by the geese. Why geese graze more frequently in some parts of the marsh is not known. Similar results have been reported by MacNaughton (1985) in relation to plant productivity and herbivory in the Serengeti plains.

Grazing fails to lead to the production of more shoots of Carex subspathacea. No significant difference in the number of shoots produced per live shoot was detected between grazed and ungrazed swards (Table 3.6.). The proportion of shoots dying over the winter was not significantly different between treatments (Table 3.7.). However, the difference in shoot deaths between the two treatments during the summer (Table 3.6.) should be treated with caution. The results of the demography of shoots indicate that the turnover of shoots is

exceedingly slow compared with that of leaves. A season is too short a period
to allow the detection of an overall difference in the pattern of mortality,
given the longevity of shoots and the slow birth rate. The fate of shoots
needs to be monitored over several years. When large amounts of inorganic
fertilizer (400 kg ha^{-1} of N) are applied to swards of Carex arenaria, turnover
of shoots increases dramatically within a season (Noble et al. 1979). At La
Pérouse Bay, the maximum annual input of nitrogen from all sources approaches
only 5% of this amount (Bazely and Jefferies 1987). Whether plants of Carex
subspathacea show the same response as the sand sedge to this quantity of
fertilizer is unknown.

The results show that there is no burst of shoot production and turnover
in Carex subspathacea in response to grazing, as occurs in the other important
forage species, Puccinellia phryganodes, which grows in the salt marsh (Bazely
1984). Instead, adjustment within a season involves changes in the leaf
population rather than in the population of shoots.

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CHAPTER 4: THE LEAF DEMOGRAPHY OF GRAZED AND UNGRAZED PLANTS

OF CAREX X FLAVICANS

4.1. Introduction

Grasses and sedges are among the plants most tolerant of defoliation (Harper 1977; Crawley 1983); they are also among the most heavily grazed of different groups of plants. Regrowth of above-ground tissues following herbivory results primarily from three processes: the elongation of both ungrazed and partially grazed leaves, the production of new leaves, and the production of new leafy shoots. Together with changes in the longevities of above-ground organs, these processes determine whether a grazed individual is successful in maintaining its photosynthetic surface area in spite of herbivory.

Carex X flavicans Nyl.[*] is a rarely reported hybrid of the sedges Carex aquatilis Wahl. and Carex subspathacea Wormsk. (Scoggan 1978; Cayouette and Morisset 1985). At La Pérouse Bay, Manitoba, this hybrid is a common component of fresh-water habitats. C. X flavicans is heavily grazed during the summer by a breeding colony of Lesser Snow Geese (Chen caerulescens caerulescens (L.) Gundl.).

The purpose of this study was to determine the changes in the production and the longevity of leaves of C. X flavicans which occur in response to grazing. Using demographic techniques, we compared plants in plots subjected to grazing with plants in plots from which geese were excluded. The effects of grazing on the elongation of leaves and the production of shoots of this hybrid have also been investigated (Chapters 5,6). Together, these data

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[*] Nomenclature follows Scoggan (1978).

provided a complete description of the short-term changes in the demography
of above-ground organs of this hybrid brought about by the geese. The results
were compared with the responses of plants of C. aquatilis and C. subspathacea
to grazing, which have also been studied at this same location. These
investigations provided evidence of the ability of C. X flavicans to
tolerate herbivory, and on the circumstances likely to lead to the persistence
or destruction of sedges when utilized by the geese as forage.

4.2 Materials and Methods

4.2.1. The site

La Pérouse Bay is located on the Hudson Bay coastline about 25 km east of
Churchill, Manitoba. This area is very flat and is deeply covered with
terrestrial and marine sediments and glacial till. Isostatic uplift is very
rapid in the region, exposing 10-20 m of new land per year (Martini 1982).

Adjacent to the coast are extensive tidal flats dominated by Carex
subspathacea and the grass Puccinellia phryganodes (Trin.) Scribn. and Merr..
Further inland, numerous fresh-water ponds and areas of saturated peat cover
most of the landscape. The most important components of the tundra between
ponds are shrubs, notably Salix phylicifolia L. ssp. planifolia (Pursh)
Hiitonen, Betula glandulosa Michx., and Myrica gale L.. In the ponds and wetter
areas, graminoids predominate. Carex aquatilis forms dense near-monocultures in
standing water and permanently saturated ground. Carex X flavicans frequently
predominates in shallow standing water and in the saturated carpets of moss
(mostly Drepanocladus uncinatus (Hedw.) Warnst.) which surround many ponds.
Other important species co-occurring with these fresh-water carices include

other graminoids such as Dupontia fisheri R. Br., Calamagrostis deschampsioides Trin., Calamagrostis neglecta (Ehrh.) Gaertn., Mey. & Scherb., and Carex spp., and creeping dicotyledons, such as Potentilla palustris (L.) Scop..

The Lesser Snow Goose is by far the most important herbivore at La Pérouse Bay. When both resident and migrant geese arrive in mid-May, little green vegetation is available as forage; consequently, most feeding in both fresh-water and salt-water habitats involves grubbing of grasses and sedges for their roots and rhizomes and eating the bases of overwintering shoots of these plants. Within a couple of weeks of their arrival, northbound migrants leave the area while about 7000 pairs remain to nest. Following the hatching of about 30 000 goslings in late June, adults and goslings feed almost exclusively by clipping the leaves of graminoids. The primary grazing areas are the intertidal marshes, where the geese help to maintain the graminoid-dominated community (Bazely and Jefferies 1986). They also increase the net annual above-ground primary production of the intertidal plant community by increasing the availability of nitrogen for growth (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985, 198Na, 198Nb). Freshwater areas are important as secondary sources of food. They are used continuously by small numbers of geese and by much of the remainder of the colony when bad weather or predators force the geese off the tidal flats. Carex X flavicans is the most frequently grazed species in these habitats. Though very patchy, herbivory of sedges can be intense in the moss carpets around ponds, where the vegetation may be maintained at a height of less than 5 cm. The geese leave La Pérouse Bay in mid-August.

More information on the vegetation and climate of La Pérouse Bay and on the biology of Lesser Snow Geese may be found in Jefferies et al. (1979), Cooke et al. 1982, Cargill and Jefferies (1984a), and Kotanen (198N).

4.2.2.   The growth habit of Carex X flavicans

Carex X flavicans is intermediate in general appearance between its two parental species (Section 2.2). Below-ground morphology closely resembles that described for C. aquatilis by Shaver and Billings (1975), Billings et al. (1978), and Shaver et al. (1979) (Figure 2.1.); the terminology used by these authors is adopted below. Like C. aquatilis, C. X flavicans is strongly rhizomatous. Leafy shoots are produced from clusters of 3-5 dwarf rhizome branches (clumping rhizomes) which develop from a central tiller. A new cluster develops from a long rhizome branch (spreading rhizome), spreading away from its parental cluster. Clumping rhizomes do not often produce daughter rhizomes. Spreading rhizomes are usually produced by other spreading rhizomes. In Carex X flavicans, spreading rhizomes are about 15 cm long, while clumping rhizomes are 0.5-5 cm long. Swards are mosaics of rhizomes produced by different ramets. Tillers are leafy and upright, reaching heights of 15-30 cm in ungrazed areas. New leaves are produced sequentially from an apical meristem located near ground level at the centre of the tiller. Some leaves overwinter, dying back at the tips but resuming growth from their green bases in the spring. Flowering occurs from late June to early July from primordia which were probably initiated in the previous fall. The growth of a tiller is terminated after flowering. Flowering is not uncommon, but whether the seed produced by this hybrid is fertile is unknown (Cayouette and Morisset 1985). Reproduction from seed is probably very rare; no seedling was observed at La Pérouse Bay in the two years that this hybrid was studied.

4.2.3. Demographic methods

In mid-June of 1985, a few days after snowmelt, 3 pairs of permanent
0.5 X 0.5 m plots were established in the moss carpets surrounding 3 fresh-water
ponds. These sites were chosen as random representatives of the most heavily
grazed sites of fresh-water areas. They appeared to have been intensely and
uniformly grazed in the previous year. The vascular flora of these 3 sites was
dominated by a moderate density of shoots of C. X flavicans. Wire netting was
used to construct 0.5 X 0.5 X 0.5 m exclosures around one plot of each pair; the
remaining plots were left open. Shoots were chosen for study using a removable
0.5 X 0.5 m metal quadrat strung with 2 sets of 5 intersecting wires at
intervals of 10 cm. The quadrat was positioned with the aid of 4 permanent
corner pegs. The shoot closest to each of the 25 intersections was permanently
marked at its base with a ring of coloured wire anchored deep in the moss, giving
an initial sample of 25 grazed and 25 ungrazed (exclosed) shoots per plot. Plots
were examined 8 times between June and September (Table 4.1.); when necessary,
the average date of sampling is reported, since the examination of all plots took
1-3 days to complete. At each visit, after ringed shoots were located using the
quadrat, all leaves on each shoot were classified as live or dead and grazed or
ungrazed, and were marked using a fine brush with distinctive patterns of
small ink dots. These techniques allowed the patterns of leaf development
and senescence to be determined for each shoot.

In spite of the senescence of leaves and the loss of wire rings and ink
dots over the winter, 23 grazed and 59 exclosed shoots with identifiable
markings were located in June of 1986, allowing the determination of their
overwinter production and deaths of leaves. Consequently, data exist for
one complete annual cycle.

Table 4.1.

Dates in 1985 and 1986 on which the status of leaves of <u>Carex</u> X <u>flavicans</u>
was recorded.[*]

Mean Date	Average Interval (days)
June 14.5, 1985	
	10.0
June 24.5, 1985	
	10.5
July 5, 1985	
	12.0
July 17, 1985	
	11.0
July 28, 1985	
	10.0
August 7, 1985	
	7.0
August 14, 1985	
	17.0
August 31, 1985	
	290.0
June 17, 1986	

[*] Some samplings took several days. Average sampling dates are reported.

4.2.4. Statistical methods

Unless otherwise stated, all statistics of the production and deaths of leaves in 1985 are based upon cumulative births and deaths for each of the 68 ungrazed and 48 grazed shoots that survived the season without flowering; flowering shoots were discarded because of their determinate growth. Analyses of variance of the production, deaths, and standing numbers of leaves are the most important exceptions. These were based upon 14 randomly-selected shoots per plot, in order to avoid the problems of analysis associated with the unequal sample sizes caused by the differential mortalities of demographic shoots in different plots (Kirk 1982). Though this reduction of sample size reduced the power of the ANOVAs, it should not lead to the spurious significance of any test (Kirk 1982). In all cases, similar results were also obtained without this convenient truncation. Statistics of the overwinter demography of leaves were based upon the entire available sample.

Where possible, statistics are based upon factorial ANOVAs or multidimensional contingency analyses (MDCAs) incorporating both site and grazing treatment as experimental factors. Unlike tests comparing pairs of plots one site at a time, these designs greatly reduce the dangers of pseudoreplication (Hurlbert 1984).

For the ANOVAs, grazing treatment was considered a fixed factor while site was treated as a random factor (Kirk 1982). Data were transformed so as to pass the F_{max} or Cochran's C test for homogeneity of variance (Kirk 1982). Whenever appropriate, $\hat{\omega}^2$ or $\hat{\rho}_I$ was calculated; these "strength of association" statistics are analogous to r^2 in a regression, reflecting the proportion of the experimental variance explained by significant fixed or random factors respectively (Kirk 1982; Kotanen and Jefferies 1987;

Chapter 3). Values greater than about 0.15 are indicative of "strong" treatment effects (Cohen 1977; Keppel 1982). In factorial designs, it should be noted that both $\hat{\rho}_I$ and the mean square for the interaction term will be inflated if plots within one site differ from one another in characteristics other than grazing treatment; similar considerations apply to the 3-way term of the MDCAs. In order to minimize this source of error, plots within sites were chosen to be as similar as possible; in any case, this source of error should not have made tests of other treatment effects less conservative.

When it was possible to express data as proportions, MDCAs were employed. All 2-way and 3-way interaction terms were tested, excluding the grazing treatment x site interaction which was fixed by the design in this context and hence was not meaningfully testable (Fienberg 1980). The values of G^2 which are presented are those associated with the deletion of the term being tested. As such, they test the significance of each term separately, rather than the significance of lack of fit of the implied model. Statistics are presented without corrections for continuity (Fienberg 1980; Sokal and Rohlf 1981) since these were of small magnitude and did not effect the general outcome of the tests. In some cases, MDCA data were expressed for convenient analysis as the proportions of values falling above or below the sample mean. Though this procedure formally violates the assumption of independent classification, the effects of this violation were considered to be small because sample sizes were large. Such an approach is similar to the treatment of residuals in a regression analysis (Neter et al. 1985).

4.3. Results

Shoots in both grazed and ungrazed plots initially supported an average of 3.1 leaves per shoot (Figure 4.1.); there was no significant difference between treatments (Table 4.2.), which supported the assumption that plots were initially similar. Between this first sampling and 31 August, 1985, vegetative shoots in grazed plots produced an average of 6.0 new leaves, as opposed to 4.1 new leaves per shoot in ungrazed plots (Figure 4.1.; Table 4.3.). This difference was significant with a large $\hat{\omega}^2$; however, the presence of a significant interaction precluded simple interpretation of the results (Figure 4.2.; Table 4.2.). Although at all 3 sites, mean numbers of leaves produced were greater in the grazed plot of each pair of plots (Figure 4.2.), independent one-way analyses of variance indicated that the difference was significant at only Sites 2 and 3 (p<0.001). A multidimensional contingency analysis performed on the full set of data indicated that the proportion of shoots with greater than average total production of leaves was significantly increased by grazing (Table 4.4.).

The production of new leaves between 31 August, 1985 and 17 June, 1986 added an average of 1.2 leaves per shoot in grazed plots and 1.8 per shoot in ungrazed plots (Table 4.3.). At all sites, the production of leaves in ungrazed plots exceeded that in grazed plots (Figure 4.3.). Though very unequal sample sizes precluded the use of a satisfactory factorial ANOVA, both Mann-Whitney U tests and one-way ANOVAs demonstrated a significant difference between shoots from grazed and ungrazed plots at only Site 1 (p<0.05). An MDCA also indicated that the proportion of shoots with greater than average winter production was significantly greater in ungrazed plots than in grazed plots (Table 4.4.). In any case, it appears that more than 75% of the annual

Figure 4.1.   Changes from June to September, 1985, in numbers of
leaves of grazed (solid lines) and ungrazed (broken lines)
plants of <u>Carex</u> X <u>flavicans</u> at La Pérouse Bay, Manitoba.
(a) Cumulative births (●); cumulative deaths (O),
including deaths of leaves produced before the first
sampling, if applicable, and change (births minus deaths)
in number of live leaves (△).
(b) Standing numbers of live leaves, which includes, if
applicable, those produced before the first sampling.
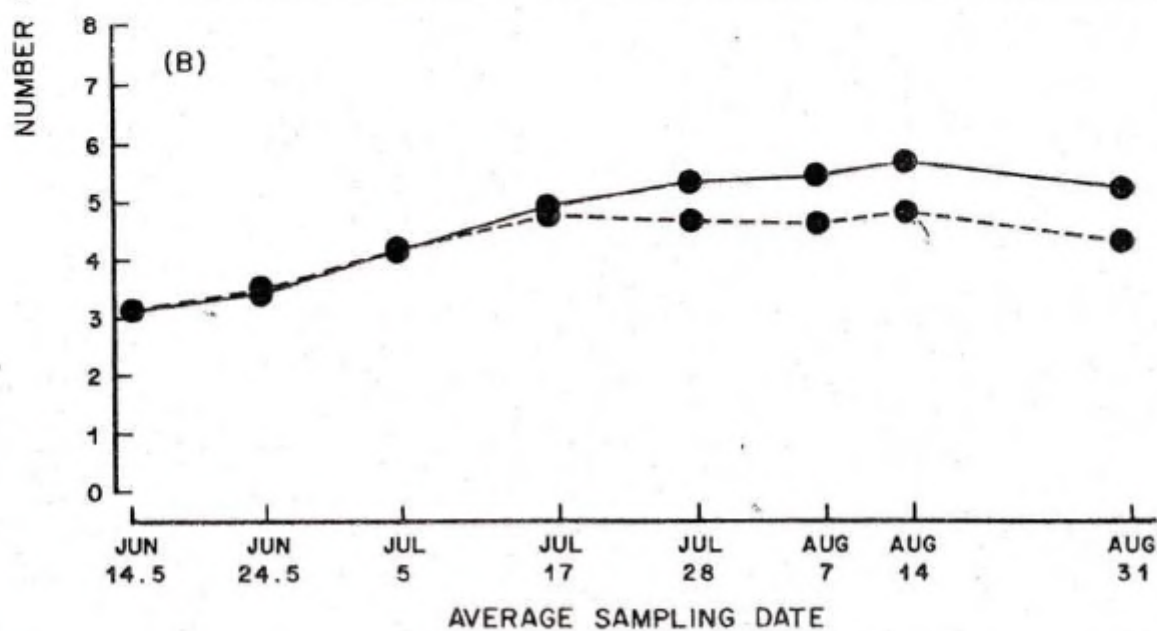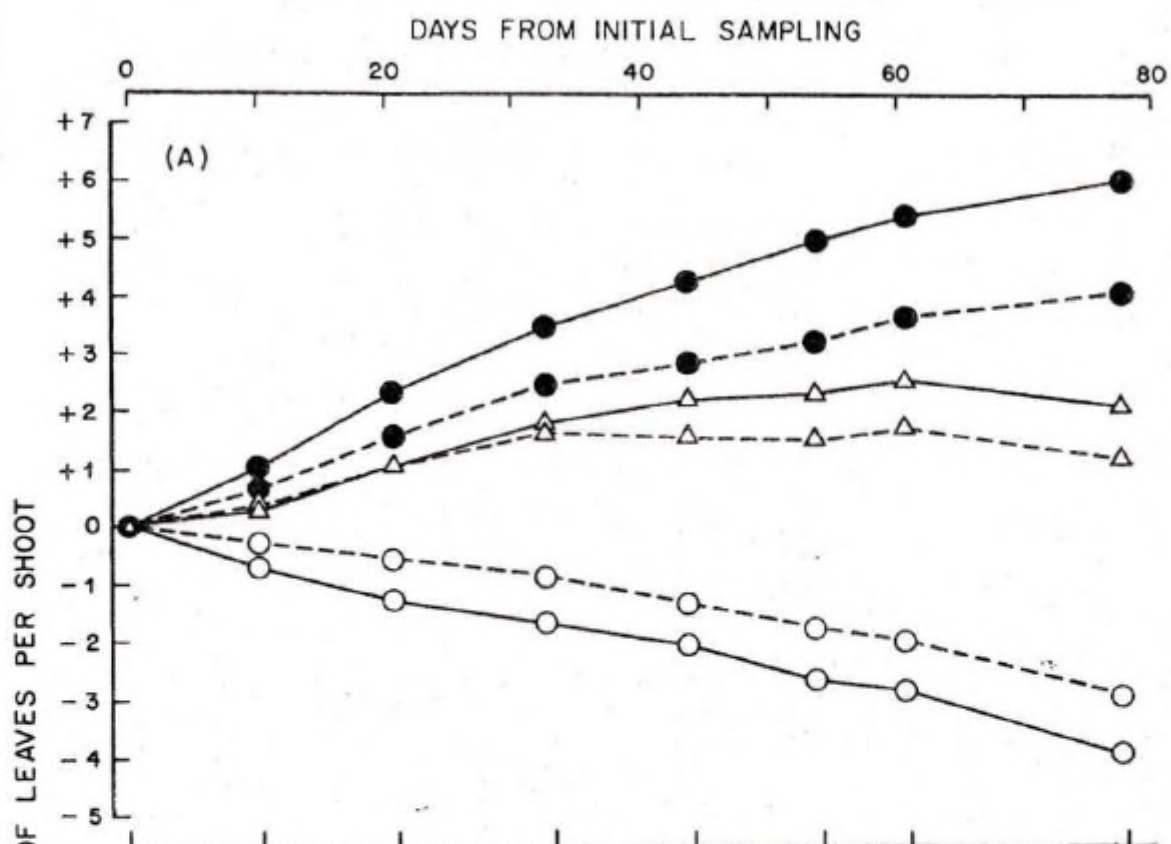
Table 4.2.

Two-factor ANOVAs of the effect of grazing treatment and site

on leaf demographic parameters of <u>Carex</u> X <u>flavicans</u>.

source of variation	df	Mean squares[a]			
		initial number of live leaves	summer production of leaves	summer deaths of leaves	number of live leaves at final sampling
treatment	1	0.00 (0%)	90.11* (23%)	0.044 (5%)	23.05 (4%)
site	2	0.46 (0%)	12.19** (8%)	0.019 (6%)	4.44 (1%)
treatment x site	2	1.39 (1%)	9.00* (11%)	0.012 (6%)	8.66 (8%)
residual	78	0.62	2.44	0.006	3.74

[a] "Treatment" was tested over the interaction term; "site" was tested over the residual term. Strength of association ($\hat{\omega}^2$ for "Treatment" and $\hat{\rho}_I$ for the other terms) is given in parentheses.

* p<0.05, ** p<0.01

Table 4.3.

Means and one standard error unit (SEM) of leaf demographic statistics

of <u>Carex</u> X <u>flavicans</u>, pooled over sites.

parameter	grazed plots	ungrazed plots
leaves produced in summer	6.00 +/- 0.31 (n=48)	4.06 +/- 0.15 (n=68)
leaves produced over winter	1.22 +/- 0.20 (n=23)	1.80 +/- 0.13 (n=59)
leaves dying in summer	3.92 +/- 0.27 (n=48)	2.90 +/- 0.12 (n=68)
leaves dying over winter	3.83 +/- 0.41 (n=23)	2.90 +/- 0.15 (n=59)

Figure 4.2. Mean numbers of leaves produced between 14 June, 1985 and 31 August, 1985 by shoots of <u>Carex</u> X <u>flavicans</u> in grazed (●) and ungrazed (○) plots at three study sites at La Pérouse Bay, Manitoba.
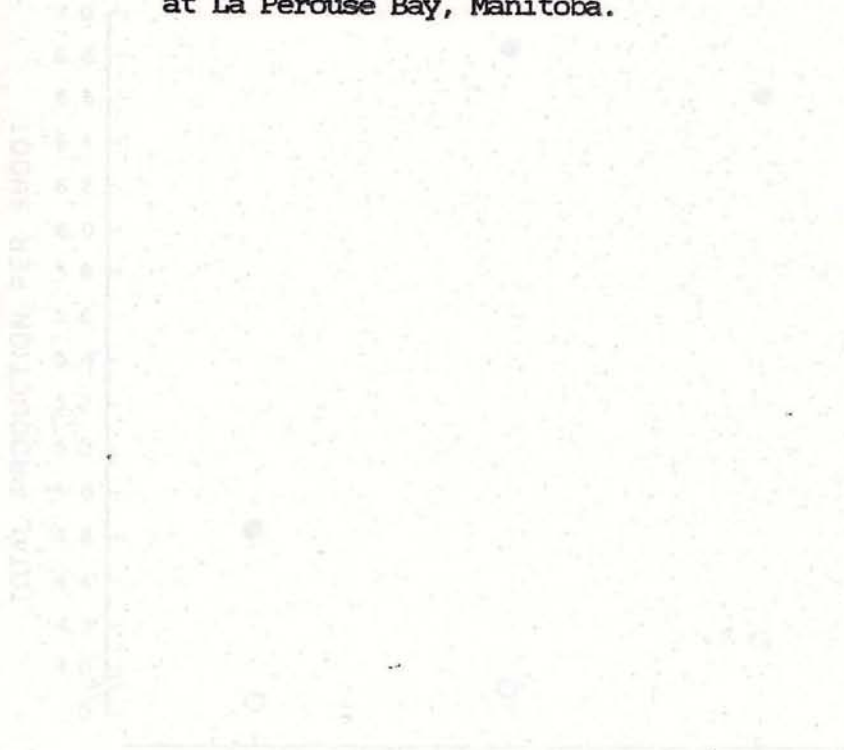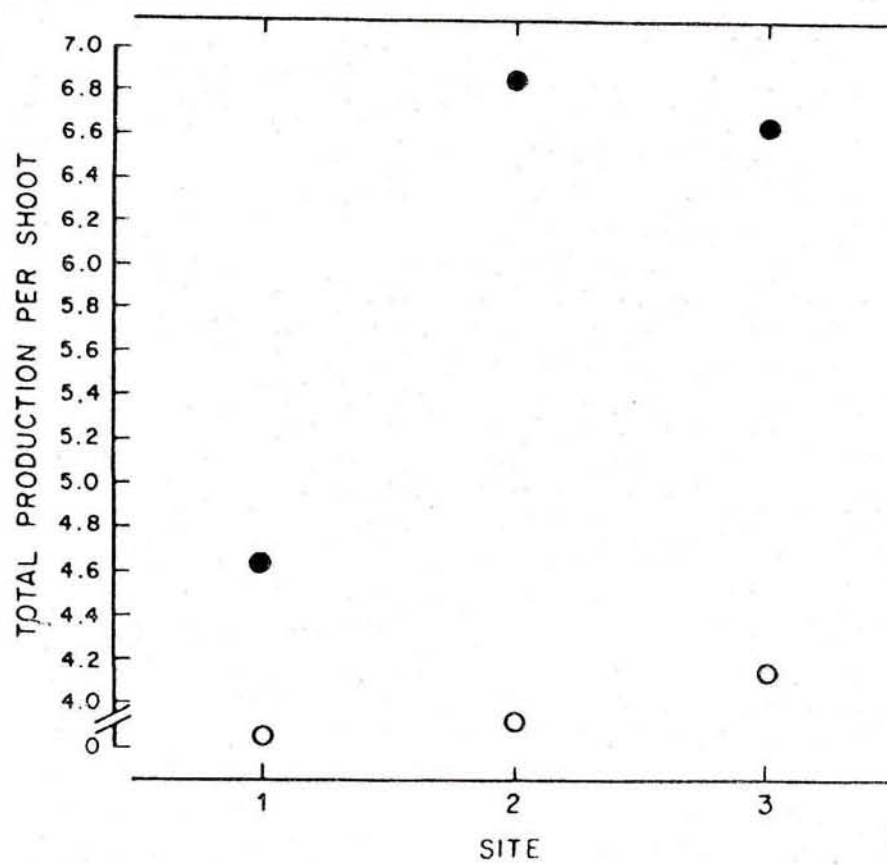
Table 4.4.

Multidimensional contingency analyses examining the influence of grazing
treatment and site on the proportion of shoots of _Carex_ X _flavicans_
with greater than average production or deaths of leaves.

effect [a]	df	G^2 summer production	summer deaths	winter production	winter deaths
proportion x treatment	1	23.81***	13.60***	10.85**	6.55*
proportion x site	2	9.63**	5.62	9.57**	2.06
proportion x treatment x site	2	0.13	0.08	0.34	8.27*

[a] The treatment x site interaction was fixed by the experimenter and hence was
not tested.

* p<0.05, ** p<0.01, *** p<0.001

Figure 4.3.   Mean numbers of leaves produced between 31 August, 1985

and 17 June, 1986 by shoots of <u>Carex</u> X <u>flavicans</u> in

grazed (●) and ungrazed (O) plots at three study sites at

La Pérouse Bay, Manitoba.

TOTAL PRODUCTION PER SHOOT

2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0

1   2   3

SITE
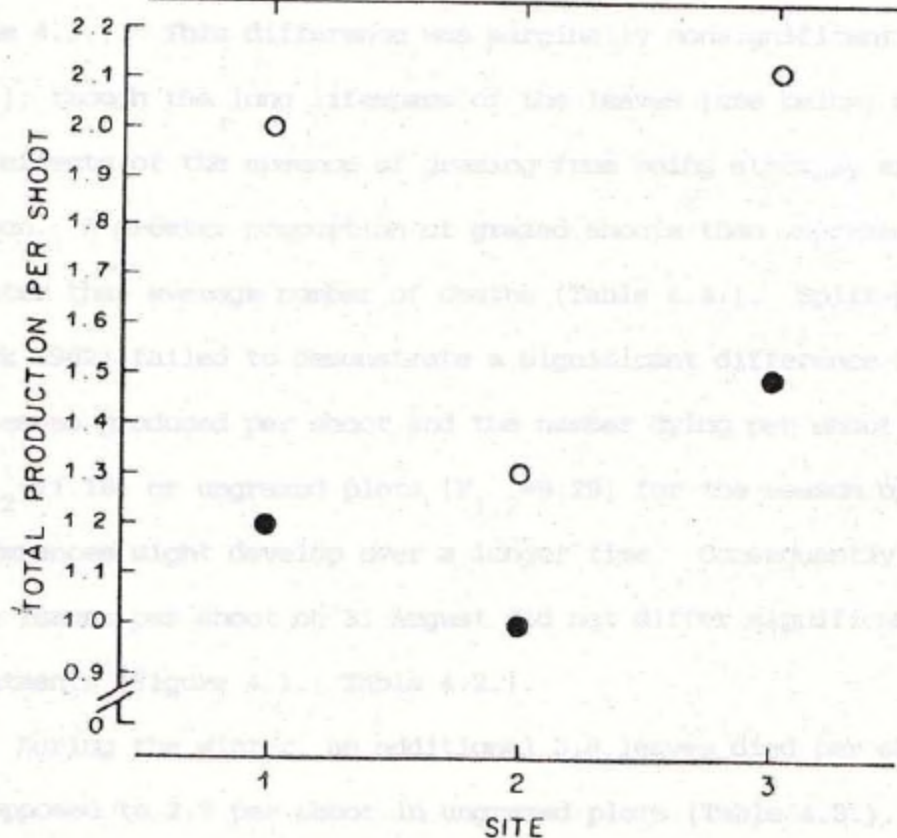
production of leaves occurred in the summer.

From June to August of 1985, an average of 3.9 leaves died per shoot in grazed plots, as compared with 2.9 per shoot in ungrazed plots (Figure 4.1.; Table 4.3.). This difference was marginally nonsignificant (Figure 4.4.; Table 4.2.), though the long lifespans of the leaves (see below) may have prevented the effects of the absence of grazing from being strongly expressed within one season. A greater proportion of grazed shoots than ungrazed shoots suffered a greater than average number of deaths (Table 4.4.). Split-plot factorial ANOVAs (Kirk 1982) failed to demonstrate a significant difference between the number of leaves produced per shoot and the number dying per shoot in either grazed $(F_{1,2}=11.18)$ or ungrazed plots $(F_{1,2}=9.29)$ for the season of 1985, though such differences might develop over a longer time. Consequently, the number of live leaves per shoot on 31 August did not differ significantly between treatments (Figure 4.1.; Table 4.2.).

During the winter, an additional 3.8 leaves died per shoot in grazed plots, as opposed to 2.9 per shoot in ungrazed plots (Table 4.3.). Though winter deaths per shoot in grazed plots exceeded those in ungrazed plots at Sites 2 and 3 (Figure 4.5.), Mann-Whitney U tests indicated a significant difference only at Site 3 (p<0.01). An MDCA of the proportion of shoots with a greater than average number of winter deaths was difficult to interpret, since there was a significant 3-way interaction (Table 4.4.). Independent X^2 tests for each site revealed that grazing significantly increased the proportion of shoots with above-average numbers of leaves dying only at Site 3 (p<0.01).

Leaves were long-lived: about 87% (n=564) of all leaves produced after 14 June survived past the termination of sampling in August, implying a mean lifespan in excess of one growing season. Precise life expectancies were impossible to calculate, since many leaves survived the entire sampling period

Figure 4.4.   Mean numbers of leaves dying between 14 June, 1985 and 31
August, 1985 on shoots of _Carex_ X _flavicans_ in grazed
(●) and ungrazed (○) plots at three study sites at La
Pérouse Bay, Manitoba.
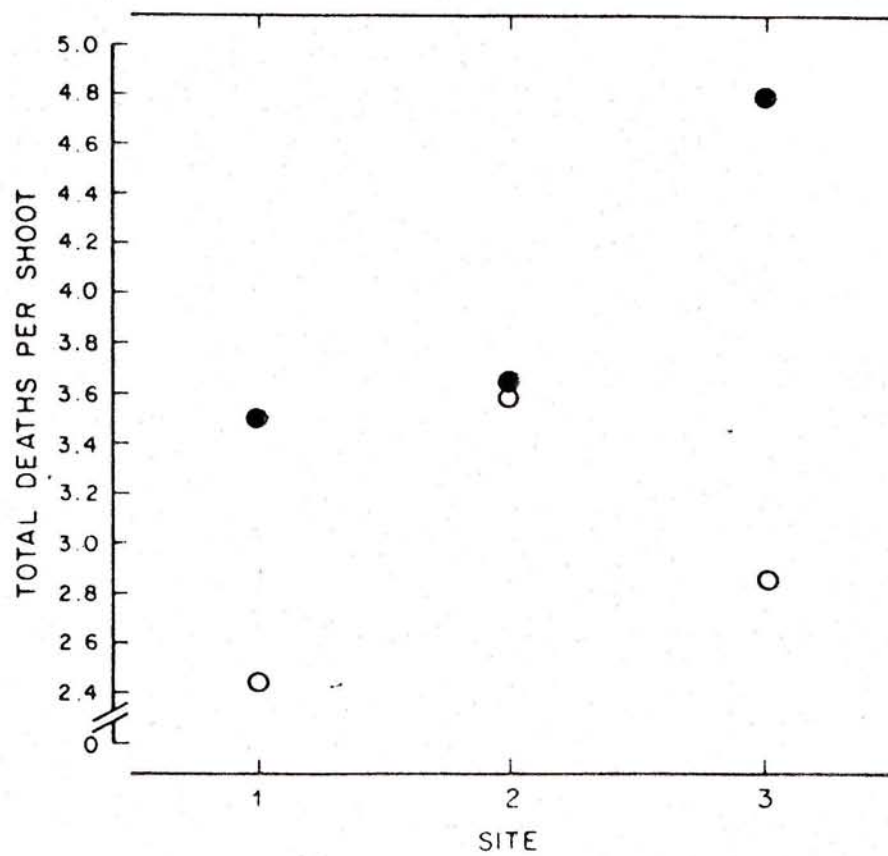
Figure 4.5. Mean numbers of leaves dying between 31 August, 1985 and 17 June, 1986 on shoots of <u>Carex</u> X <u>flavicans</u> in grazed (●) and ungrazed (○) plots at three study sites at La Pérouse Bay, Manitoba.

TOTAL DEATHS PER SHOOT

5.4
5.2
5.0
4.8
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6

1   2   3
SITE

(Berkson and Gage 1950); however, the effects of grazing on life expectancy could still be tested indirectly. For example, an MDCA (Table 4.5.) indicated that the proportion of those leaves produced after 14 June which survived the summer was significantly smaller for shoots in grazed plots (81%; n=288) than for shoots in exclosed plots (93%; n=276) (Figure 4.6.). An MDCA based upon only the first cohort of leaves (those produced between 14 June and 25 June) produced similar results (Table 4.5.). Of those leaves produced during the summer which were still alive on the 31 August sampling, about 32% (n=380) survived until 17 June 1986 (Figure 4.7.); this proportion was not significantly influenced by the grazing treatment (Table 4.5.).

About 76% (n=288) of all leaves produced after 14 June in grazed plots had been grazed by 31 August; Site 2 was most heavily grazed (80%) while Site 1 was least grazed (72%) (Figure 4.8.); these proportions did not differ significantly $(G^2_{2df}=1.50)$. The corresponding proportion in ungrazed plots was only 3% (n=276) (Figure 4.8.). If all leaves alive on 14 June were included instead, the proportions for grazed and ungrazed plots changed to 69% (n=438) and 14% (n=489) respectively. In this case, the percentages for grazed plots ranged from 62% for Site 1 to 76% for Site 2, and were statistically inhomogeneous $(G^2_{2df}=6.53, p<0.05)$, though each of the grazed plots was much more heavily grazed than any exclosed plot.

4.4. Discussion

Shortly after melt, both the production of new leaves and the elongation of leaves which had survived the winter began to replace the green tissue lost by shoots of C. X flavicans since the previous fall (Figure 4.1.). The pools typically inhabited by C. X flavicans thawed long before the surrounding

Table 4.5.

Multidimensional contingency analyses examining the influence of grazing treatment and site upon the proportion of leaves of <u>Carex</u> X <u>flavicans</u> surviving the specified season.

effect [a]	df	G^2 all leaves (summer)	leaves of first cohort (summer)	all leaves alive on 31 Aug. (winter)
proportion x treatment	1	17.78***	8.82**	2.76
proportion x site	2	2.62	3.34	0.39
proportion x treatment x site	2	3.71	2.99	1.95

[a] The treatment x site interaction was fixed by the experimenter and hence was not tested.

** $p<0.01$, *** $p<0.001$

Figure 4.6.   The proportions of those leaves of _Carex_ X _flavicans_

produced after 14 June, 1985, which survived until 31

August, 1985 in grazed plots (●) and in ungrazed plots (○).
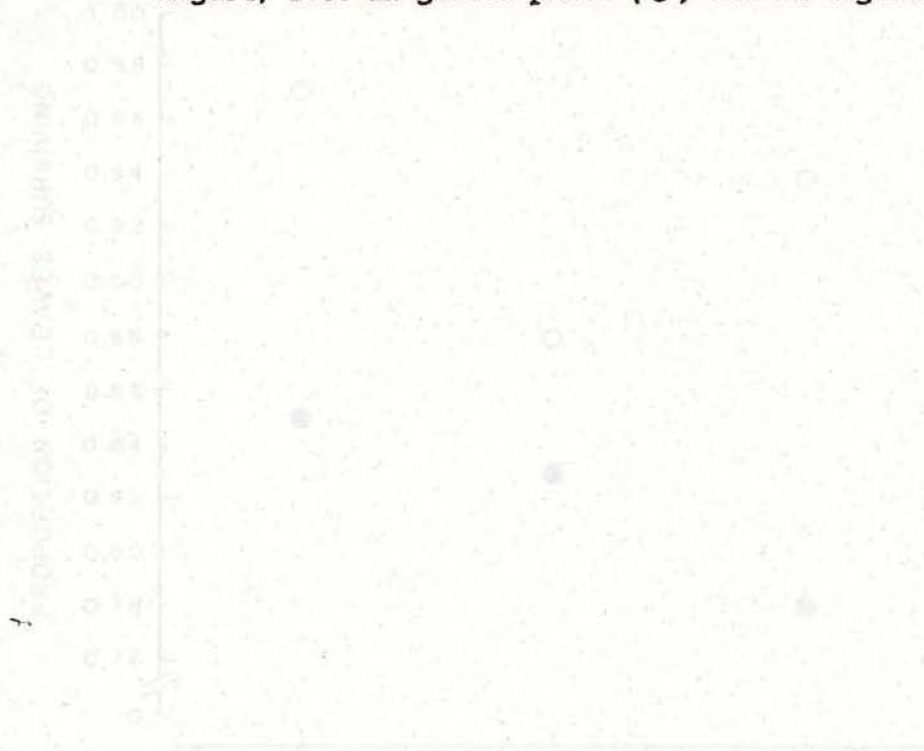
Figure 5.?   The proportions of those leaves of *Carex* X *flavicosa* produced after 14 June, 1983 and alive on 21 August, [...] in burned plots [...] and in unburned plots (●).
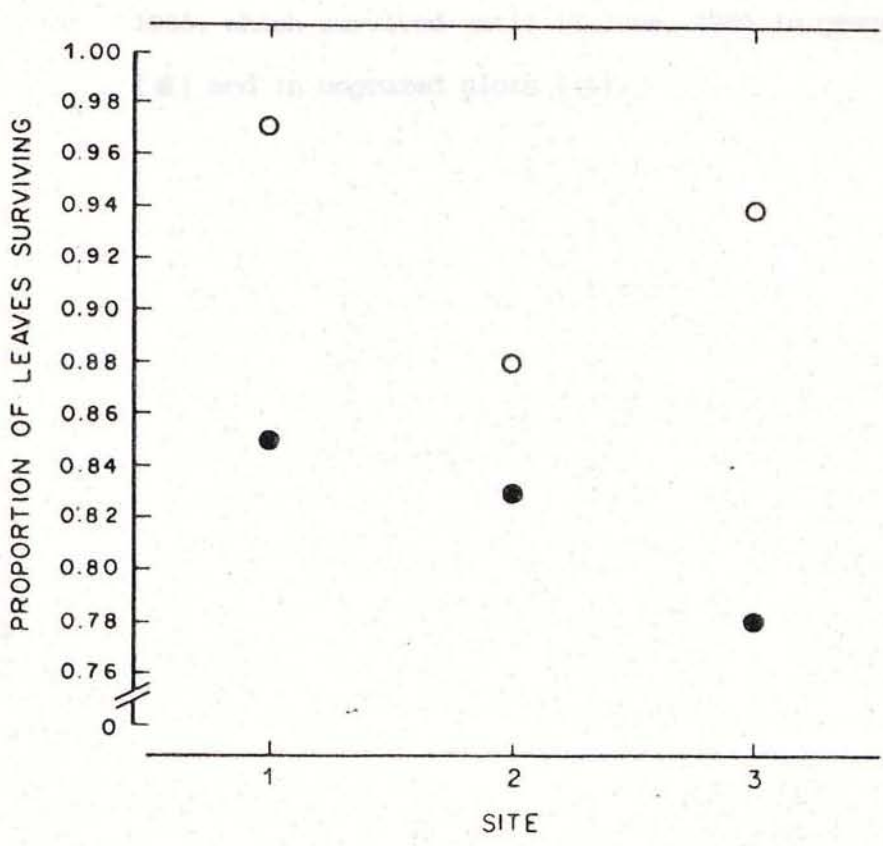
Figure 4.7.   The proportions of those leaves of <u>Carex</u> X <u>flavicans</u>

produced after 14 June, 1985 and alive on 31 August,

1985, which survived until 17 June, 1986 in grazed plots

(●) and in ungrazed plots (O).

Figure 4.8. The proportions of those leaves of *Carex* x *flavicans* produced after 14 June, 1985, which were grazed by 31 August 1985 in gazed plots (●) and in exposed plots (○).

Figure 4.8.   The proportions of those leaves of <u>Carex</u> X <u>flavicans</u>

produced after 14 June, 1985, which were grazed by 31

August 1985 in grazed plots (●) and in ungrazed plots (○).

PROPORTION OF LEAVES GRAZED

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0

1   2   3

SITE
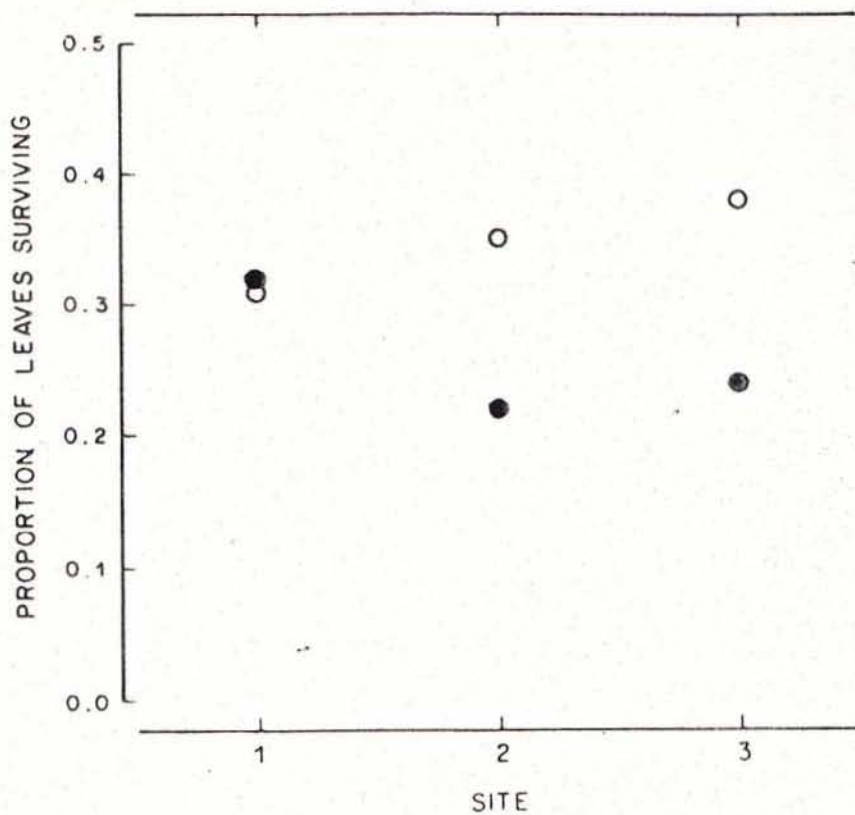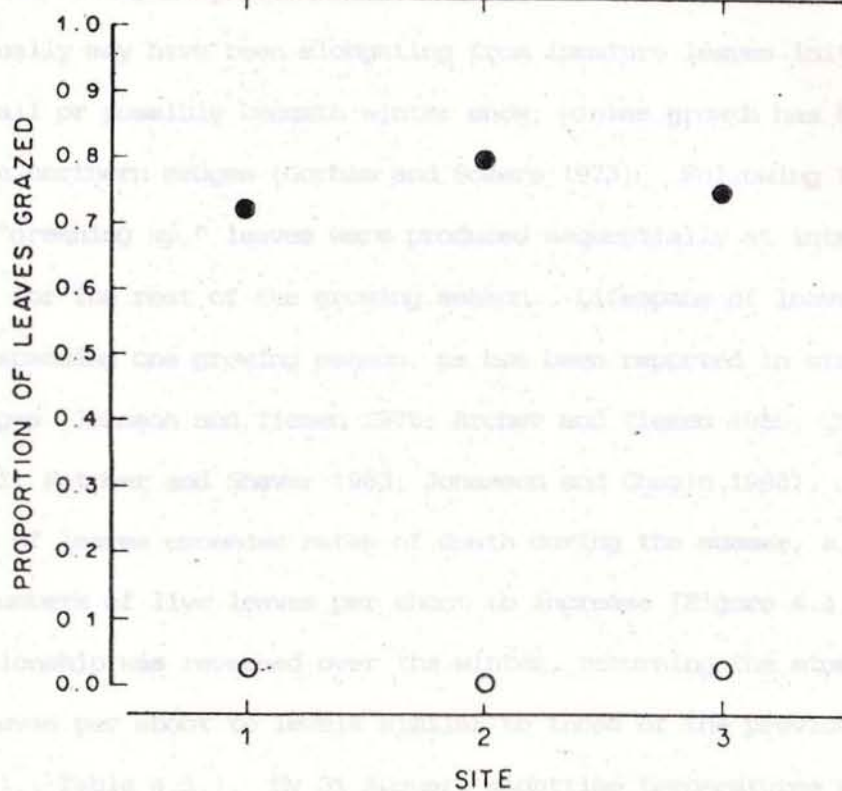
tundra; vigorous growth was already occurring by 14 June. Because leaves are concealed within the centre of the tiller until they elongate sufficiently to be visibly exserted, many of the leaves recorded as being "produced" in early spring actually may have been elongating from immature leaves initiated in the previous fall or possibly beneath winter snow; winter growth has been reported in northern sedges (Gorham and Somers 1973). Following this spring period of "greening up," leaves were produced sequentially at intervals of 10-20 days for the rest of the growing season. Lifespans of leaves were long, commonly exceeding one growing season, as has been reported in studies of other Arctic sedges (Johnson and Tiezen 1976; Archer and Tiezen 1980; Chapin and Chapin 1981; Fetcher and Shaver 1983; Jonasson and Chapin 1985). Rates of production of leaves exceeded rates of death during the summer, allowing the standing numbers of live leaves per shoot to increase (Figure 4.1.; Table 4.3.). This relationship was reversed over the winter, returning the standing numbers of live leaves per shoot to levels similar to those of the previous spring (Figure 4.1.; Table 4.3.). By 31 August, nighttime temperatures were dropping below freezing, though sunny weather may have allowed some additional growth at least until the first permanent snow in October. Growth in this late fall period may have been sufficient to account for the additional 1-2 leaves that most shoots produced between August and June; alternatively, growth may have occurred under winter snow or during spring thaw. These patterns of development were qualitatively similar for shoots in both grazed and exclosed plots, and resembled those described for other arctic and alpine carices (Gorham and Somers 1973; Shaver and Billings 1975; Johnson and Tiezen 1976; Shaver et al. 1979; Archer and Tiezen 1980; Chapin and Chapin 1981; Kotanen and Jefferies 1987; Chapter 2).

For a brief period after the arrival of the geese in mid-May, the feeding

of both residents and migrants on C. X flavicans is dominated by the pulling of shoots, though some clipping of leaves may also occur. In 1985, this phase ended between 14 June and 25 June; during this period, the grazing of leaves replaced grubbing as the primary form of foraging in areas dominated by this hybrid. Grazing was very intense: 76% of leaves produced in 1985 were grazed before their deaths or the departure of the geese in mid-August. Plants were reduced from a potential height of 20-30 cm to around 5 cm in heavily exploited areas. Though leaves were often clipped very close to their bases, very few were completely removed, and shoot apical meristems probably were damaged only rarely. Consequently, regrowth of grazed leaves and shoots readily occurred, as is typical of graminoids (Harper 1977; Crawley 1983).

Grazing significantly increased the production of new leaves. During the summer, shoots in grazed plots produced an average of 6.00 new leaves, as compared with 4.06 in exclosed plots (Tables 4.2., 4.3.) - a 48% increase. During the winter, this trend was reversed: shoots in exclosures produced an average of 1.8 leaves while shoots in grazed plots produced only 1.2 (Tables 4.3., 4.4.). Because winter production amounted to only 30% of summer production, grazed shoots still produced 23% more leaves on an annual basis. This increased production in grazed plots was associated with increased numbers of deaths of leaves in both summer and winter (Tables 4.2., 4.3., 4.4.). Grazing also increased the probability that a leaf would die in the season in which it was produced (Table 4.5.), implying shorter lifespans of leaves. Within the space of one year, C. X flavicans did not respond to herbivory with an increased production of new shoots, or with an increased elongation of existing leaves (Chapters 5,6). Consequently, it appears that the major short-term compensatory responses of above-ground organs of this hybrid to grazing are the increased production and turnover of leaves and the

decreased longevities of leaves.

Demographic studies examining changes in the production and longevities of leaves in response to herbivory are scarce, probably because of the practical difficulties involved in following individual leaves for extended periods. The production of new leaves commonly increases after moderate defoliation, as one might expect if a plant replaces the removed above-ground tissue, but production of leaves after severe defoliation may be reduced (Harper 1977; Crawley 1983). Kotanen and Jefferies (1987; Chapter 3) found that, in contrast to shoots from ungrazed plots, the cumulative numbers of leaves produced and the number of leaves that died were greater in shoots of C. subspathacea growing in the tidal marshes of La Pérouse Bay that were exposed to the foraging activities of the geese. The life expectancies of leaves from these plants were shorter than corresponding values for ungrazed plants within the exclosures. Bazely and Jefferies (198Nb) found that geese also increased the number of leaves produced by axillary shoots and decreased the longevity of leaves of Puccinellia phryganodes at the same location, though the primary response of this species to grazing was the production of new axillary shoots.

The increased production of leaves of C. X flavicans in response to grazing does not necessarily imply that this species is successful in completely replacing the above-ground tissues lost to the geese. It is possible that this increased production is achieved only by sacrificing some other component of above-ground production. In C. X flavicans, decreased elongation of leaves often accompanies grazing (Chapter 6), though the magnitude of this decline is small. Even if net above-ground production is increased, it is possible that this enhancement is being achieved at the expense of reserves or below-ground tissues, leading to an eventual decline in above-ground growth (Belsky 1986). Unlike the salt-marsh communities at La Pérouse Bay, insufficient information is

known of the history of grazed fresh-water communities to state with authority that they successfully persist under regular summer grazing; it is possible that the moss carpet communities containing the sampling sites are the outcome of severe herbivory (both grazing and pulling of shoots) where the geese are progressively destroying the dominant graminoids (Jefferies 1987; Kotanen 198N; Chapters 6,7). The development of moss carpets at other Arctic locations has been attributed to destruction of sedge communities by geese (Tikhomirov 1959; Jefferies and Kerbes 1985; Jefferies 1987). Alternatively, it is possible that the observed increases in production of leaves represent a real, sustainable increase in net above-ground primary production, as has been demonstrated for grazed plants of Carex subspathacea and Puccinellia phryganodes on the salt marshes at La Pérouse Bay (Cargill and Jefferies 1984b). Such sustainable increases usually require modification of the external environment of the grazed plants that enables the development of new tissue to occur, which compensates for the damage that herbivores inflict (McNaughton 1983). In the salt marshes at La Pérouse Bay, this external change is the amelioration of nitrogen limitation through the accelerated cycling of nitrogen by the geese and through the increased fixation of nitrogen by cyanobacteria in grazed areas (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985,198Na); similar mechanisms might operate in fresh-water areas where the grazing is not so intense as to outweigh the advantages of an increased availability of nutrients.

Longevities of graminoid leaves are not always decreased by grazing. For example, Archer and Tiezen (1980) found that lifespans of leaves of Eriophorum vaginatum L. increased following experimental defoliation; McNaughton et al. (1983) achieved similar results with the tropical sedge Kyllinga nervosa Steud.. Increased longevities may reduce the costs of losing tissue to herbivores by allowing more efficient recycling of scarce

nutrients within the plant, or by maintaining carbon fixation by reducing the loss of photosynthetic tissue to senescence (Archer and Tiezen 1980; McNaughton 1983; Coley et al. 1985, Jonasson and Chapin 1985). Conversely, herbivores may reduce lifespans of leaves simply by damaging them, making their retention impossible or unprofitable (Crawley 1983). Bazely and Jefferies (198Nb) found that partially grazed leaves of Puccinellia phryganodes had shorter life expectancies than undamaged leaves in grazed plots. Neither of these theories successfully accounts for the demographic leaf patterns in C. subspathacea, in which lifespans are equally reduced in both grazed and undamaged leaves within grazed plots (Kotanen and Jefferies 1987; Chapter 3). In this case, perhaps the nitrogen that the geese make available for regrowth reduces the value of conserving resources by recycling nutrients within plants in favour of the continuous production of new, rapidly photosynthesizing tissue. Unfortunately, sufficiently precise lifespans could not be calculated to determine whether leaves of C. X flavicans behaved in a similar manner.

In summary, these results indicate that the strongest short-term responses of the above-ground organs of C. X flavicans to grazing by geese include the increased production and turnover and the decreased lifespans of leaves. Whether these responses result in enhanced production or persistence of this plant is unknown, but they certainly suggest that C. X flavicans may have the ability to appropriately modify its leaf demography in response to foraging by geese.

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CHAPTER 5: THE SHOOT DEMOGRAPHY OF GRAZED AND UNGRAZED PLANTS

OF CAREX AQUATILIS, CAREX X FLAVICANS, AND CAREX SUBSPATHACEA

5.1. Introduction

The sedges Carex aquatilis Wahl. and Carex subspathacea Wormsk. are
widespread throughout the North American Arctic (Hultén 1968; Scoggan 1978).
Their hybrid, Carex X flavicans Nyl., is infrequently reported, but may
be locally abundant within the range of its parental species (Section 2.2.4.;
Cayouette and Morisset 1985). At La Pérouse Bay, Manitoba, these three species
are used as forage by a breeding colony of 7000 pairs of Lesser Snow Geese (Chen
caerulescens caerulescens (L.) Gundl.) and their goslings. In spring, thousands
of migrating Snow Geese also feed upon these sedges while staging at La Pérouse
Bay.

In the vicinity of the colony, feeding by the geese upon these sedges is
intense. When the geese arrive in spring, little green vegetation is available
as forage; most feeding consists of the pulling of developing shoots and the
grubbing of roots and rhizomes. Following the hatch of the goslings, feeding
shifts to the clipping of leaves (grazing), although the pulling of shoots
occurs infrequently. Comparisons of grazed and ungrazed plots in 1980
indicated that geese increased net above-ground primary production of swards
of Carex subspathacea by 60 to 80% (Cargill and Jefferies 1984b). This
increase was a consequence of the geese accelerating the cycling of nitrogen in
this nitrogen-deficient environment (Cargill and Jefferies 1984a,b). By conver-
ting plant tissue into droppings rich in soluble nitrogen and by preventing

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* Nomenclature follows Scoggan (1978).

the accumulation of litter, the geese make more nitrogen available for plant growth (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985, 198Na; Jefferies 1987). Much of the additional net above-ground primary production of Carex subspathacea comes from the increased production and turnover of leaves (Kotanen and Jefferies 1987; Section 2.3.1; Chapter 3). Both the production and the turnover of leaves of Carex X flavicans are also increased by grazing (Chapter 4).

Increased tillering of graminoids is commonly reported as another response to herbivory (Caldwell et al 1981; Crawley 1983; Coughenour 1985; Belsky 1986; Bazely and Jefferies 198Nb). Tillering a process by which some carices are able to replace the photosynthetic tissue removed by geese. Tillering also is essential for the replacement of shoots lost to senescence and grubbing. Even if the production of leaves is enhanced by grazing, the pulling of shoots may cause the collapse of an intensely exploited community, if rates of tillering are insufficient to replace lost shoots. For example, the pulling of shoots of grasses and sedges by geese may be destroying patches of vegetation at La Pérouse Bay (Jefferies 1987; Section 2.3.1).

The purpose of this study was to determine whether Carex aquatilis, Carex subspathacea, and Carex X flavicans respond to grubbing and grazing by Lesser Snow Geese by rapid changes in the the number of shoots that are produced by these plants. Using demographic techniques, the production and turnover of shoots have been measured in plots from which geese were excluded, and compared with the production and turnover of shoots in plots exposed to grazing in which the accumulation of faeces occurred.

5.2. Materials and methods

5.2.1. The site

La Pérouse Bay is located on the Hudson Bay coastline about 25 km east
of Churchill, Manitoba. The extensive tidal flats at this location are
dominated by the grass Puccinellia phryganodes (Trin.) Scribn. and Merr., and by
Carex subspathacea. Above the high tide mark, the landscape is covered with
fresh-water ponds, areas of saturated moss, and graminoid communities. Carex
aquatilis often forms dense stands in shallow water and permanently saturated
ground. Carex X flavicans also forms dense stands in shallow water and is
present in the saturated carpets of moss (mostly Drepanocladus uncinatus
(Hedw.) Warnst.) which surround many ponds. Between ponds, the tundra
vegetation is dominated by shrubs, such as Salix spp., Betula glandulosa
Michx. and Myrica gale L..

Following their arrival in mid-May, both resident and migrant geese strip
away salt-marsh vegetation, exposing patches of bare sediment which are usually
a few square metres in size (Jefferies 1987). In fresh-water areas, developing
shoots of C. aquatilis and C. X flavicans are intensively pulled and their
succulent bases consumed; the remainder of the shoot is discarded. Within
a couple of weeks of the arrival of the geese, northbound migrants depart, and
feeding by the 7000 resident pairs declines as nesting begins. After the hatch-
ing of the 30 000 goslings in late June, families feed primarily by grazing the
leaves of graminoids. The areas most heavily used for feeding are located in
the salt marshes, where the geese crop the vegetation to 2.5 cm or less in
height. Grazing in fresh-water areas is much patchier, but may be locally
intense: around the margins of ponds, C. X flavicans is frequently

maintained at 5 cm in height. Intense grazing of C. aquatilis is uncommon.
Shortly before the departure of the geese in mid-August, scattered grubbing and
pulling of shoots resume. The Lesser Snow Goose is by far the most important
herbivore at La Pérouse Bay.

More information on the vegetation and climate of La Pérouse Bay and the
biology of Lesser Snow Geese may be found in Jefferies et al. (1979), Cooke et
al. 1982, Cargill and Jefferies (1984a), Kotanen (198N) and Section 2.3.1..

5.2.2. The growth habits of the species studied

The morphology of Carex aquatilis, C. subspathacea, and C. X flavicans
(Figure 2.1.) resemble that described for C. aquatilis by Shaver and
Billings (1975), Billings et al. (1978), and Shaver et al. (1979). Leafy shoots
are produced in loose clusters from dwarf rhizome branches which develop from a
central tiller. A new cluster develops from a long rhizome branch spreading
away from its parental cluster. Though C. aquatilis may be tussock-forming, at
La Pérouse Bay all three species more commonly grow in swards composed of
mosaics of subterranean rhizomes produced by different ramets. Flowering occurs
in all three species, but little evidence of successful reproduction from seed
was observed during three years of study; most shoots in established swards were
vegetatively produced.

These carices differ most noticeably in their sizes. Vegetative tillers of
C. subspathacea may reach 2 dm in height in ungrazed areas, though plants
growing on the tidal marshes are dwarfed to less than 3 cm; long branches of
rhizomes range to about 10 cm in length. Tillers of C. aquatilis often exceed
5 dm in height; long rhizome branches may extend to 2 dm.. C. X flavicans is
intermediate in size between its two parents, reaching heights of 1.5-3.0 dm.

More information on the morphology of these species may be found in Shaver and Billings (1975), Billings et al. 1978, Shaver et al. 1979, Cayouette and Morisset (1985, 1986a,b) Kotanen and Jefferies (1987) and Sections 2.2., 3.2.2., and 4.2.2..

5.2.3. Demographic methods

5.2.3.1. Carex subspathacea

On 25-26 May, 1986, within 3 days of the first foraging by large groups of geese on the salt marsh, 5 pairs of permanent 0.5 X 0.5 m plots were established at 5 sites in an area of salt marsh which had been grazed frequently by Lesser Snow Geese in previous years. Plots were chosen so that they contained intact swards of C. subspathacea, and so that members of a pair of plots were initially as similar as possible. Wire netting was used to construct a 0.5 X 0.5 X 0.5 m exclosure around one plot of each pair; the remaining plot was left open. Within each plot, five (2.5 X 2.5 cm) subplots were chosen at random and permanently delimited with a securely anchored wire perimeter set into the sediment. All shoots in each subplot were marked with a toothpick sunk into the ground adjacent to the shoot so that only the tip protruded, giving an initial sample size of 659 shoots. Plots were examined three times before September (Table 5.1.). On each sampling, toothpicks associated with dead or missing shoots were removed, and new shoots were marked. These techniques were used to estimate the numbers of births and deaths of shoots, and the survivorships of shoots.

In 1985, similar techniques had been used in a pilot experiment based upon 3 pairs of plots (Kotanen and Jefferies 1987; Chapter 3; Table 5.1.). The results

Table 5.1.

Dates in 1985 and 1986 on which the status of shoots was recorded for <u>Carex</u> <u>subspathacea</u>, <u>Carex</u> X <u>flavicans</u>, and <u>Carex</u> <u>aquatilis</u>.[a]

Plots established in 1985

<u>Carex</u> <u>subspathacea</u>		<u>Carex</u> X <u>flavicans</u>	
Mean Date	Mean Interval (days)	Mean date	Mean Interval (days)
June 16, 1985 ———|		June 14.5, 1985 ————|	
	|– 16.0		|– 10.0
July 2, 1985 ———|		June 24.5, 1985 ————|	
	|– 19.0		|– 10.5
July 21, 1985 ———|		July 5, 1985 ————|	
	|– 13.0		|– 12.0
Aug 3, 1985 ———|		July 17, 1985 ————|	
	|– 8.0		|– 11.0
Aug 11, 1985 ———|		July 28, 1985 ————|	
	|– 21.0		|– 10.0
Sept 1, 1985 ———|		August 7, 1985 ————|	
	|– 296.0		|– 7.0
June 24, 1986 ———|		August 14, 1985 ————|	
			|– 17.0
		August 31, 1985 ————|	
			|– 290.0
		June 17, 1986 ————|	

Plots established in 1986

<u>Carex</u> <u>subspathacea</u>		<u>Carex</u> X <u>flavicans</u>		<u>Carex</u> <u>aquatilis</u>	
Mean Date	Mean Interval (days)	Mean Date	Mean Interval (days)	Mean Date	Mean Interval (days)
May 25.5, 1986 –|		June 21.5, 1986 –|		June 18.5, 1986 –|	
	|– 48.5		|– 20.5		|– 21.5
July 13, 1986 —|		July 12, 1986 ——|		July 10, 1986 ——|	
	|– 42.0		|– 44.5		|– 48.0
Aug. 24, 1986 —|		Aug. 25.5, 1986 –|		Aug. 27, 1986 ——|	

[a] In some cases, samplings took several days. Average dates are reported.

of this experiment, obtained from the two pairs of plots which survived the
season, have been reanalyzed in order to conform with the methods used in this
paper and are presented below for purposes of comparison. These plots contained
an initial total of 95 marked shoots. Both of these pairs of plots were located
and examined in June of 1986 (Table 5.1.), providing information on the
demography of shoots over the winter.

On 13 June, 1986, after the spring grubbing of salt-marsh vegetation had
ceased, 0.5 X 0.5 X 0.5 m exclosures were erected at 5 sites where C.
subspathacea had been stripped away by geese; an undamaged area within 5 m of
each grubbed plot was also exclosed to act as a control. A turf measuring
9 X 9 cm was removed from each plot on 13 June and on 14 August. For each
species of plant present, shoot density was determined from 6 randomly placed
2 X 2 cm quadrats per turf. Comparisons between grubbed and ungrubbed plots
allowed the description of the intensity of grubbing, and the degree to which
grubbed plots recovered within one growing season.

5.2.3.2. Carex X flavicans

The demography of shoots of C. X flavicans was investigated using methods
similar to those described for C. subspathacea. On 14 June, 1985, the day that
the first goslings hatched, three pairs of 0.5 X 0.5 m plots were established
in carpets of moss surrounding 3 fresh-water ponds; one plot in each pair was
surrounded with a 0.5 X 0.5 X 0.5 m exclosure. These sites were chosen because
they were uniformly vegetated with shoots of C. X flavicans which showed signs
of having been intensely grazed in the previous year. Within each plot, a
subplot approximately 15 X 15 cm in size was chosen for permanent study,
providing an initial sample of 160 shoots. At each sampling, subplots were

located and delimited using the crosswires of a removable metal frame which was placed over the corner pegs of the plot. All shoots within each subplot were encircled with small rings of colored wire which were anchored and concealed in the moss. Plots were sampled approximately every 15 days until September (Table 5.1.). Rings of dead or missing shoots were removed and new shoots were marked with rings of a different colour at each sampling, in order to aid the identification of separate cohorts. These plots were again located in June 1986, allowing the description of the "overwinter" (i.e. September to June) patterns of shoot demography.

In 1986, a larger experiment of essentially the same design was established. Five pairs of plots were set in moss carpets dominated by Carex X flavicans on 23 May, the day after the intensive pulling of shoots by geese began in fresh-water areas. Ten 5 X 5 cm subplots were randomly chosen in each plot and permanently delimited with a wire perimeter set into the moss. All shoots in each subplot were marked with wire rings, giving an initial sample of 463 shoots. Sampling was performed on 3 occasions before September (Table 5.1.).

On 10-11 June, 1986, a few days before the intensive spring pulling of shoots by geese had ended, 94 (0.5 X 0.5 m) quadrats were randomly thrown in areas where the grubbing of shoots had occured. Shoots of Carex X flavicans within each quadrat which had been discarded by the geese after their bases had been consumed were counted. These data were used to estimate the numbers of shoots which had been pulled and destroyed.

5.2.3.3. Carex aquatilis

On 23 May, 1986, the day after intensive pulling of shoots by geese began in fresh-water areas, 5 pairs of plots were established in nearly pure

stands of <u>Carex</u> <u>aquatilis</u> growing in shallow ponds which had been heavily exploited by geese in the previous year. One plot in each pair was protected with a 1.5 X 1.5 X 1.5 m exclosure. Within each plot, a permanent 25 X 25 cm subplot was established and delimited with a wire perimeter set into the sediment. These subplots initially contained 457 shoots. All shoots in each subplot were ringed and their fate recorded as described for <u>C</u>. X <u>flavicans</u> (Section 5.2.3.2.); recording was done on three sampling dates between June and early September (Table 5.1.).

On 10-11 June, 1986, a few days before the intensive spring pulling of shoots by geese had ended, 70 (0.5 X 0.5 m) quadrats were randomly thrown in areas in which intensive grubbing of tillers of <u>C</u>. <u>aquatilis</u> had occurred. Shoots within each quadrat which had been discarded after their bases had been consumed were counted, in order to provide an estimate of the numbers of shoots destroyed by the geese.

5.2.4. Statistical methods

Unless otherwise stated, statistics of the births and deaths of shoots were based upon cumulative values. Whenever possible, the statistical method employed was a factorial analysis of variance (ANOVA), or a multidimensional contingency analysis (MDCA), incorporating both site and grazing treatment as experimental factors. For the MDCAs, the values of G^2 which are presented are those associated with the deletion of the term being tested. Details of the use of these techniques may be found in Sections 3.2.4. and 4.2.4., and in Kotanen and Jefferies (1987).

Half lives were calculated for the shoots initially present using a modification of the formula of Bishop and Davy (1984):

$$\text{half life in days} = t\,(\ln 2)\,/(\ln a - \ln b), \qquad (1)$$

where "t" represents the total sampling interval in days, "a" represents the number of shoots present at the beginning of this interval, and "b" represents the number of these shoots surviving until the end of this interval.

This formula assumes that the fates of all shoots are known. Unfortunately, in this study, some marked shoots vanished during winter: their designating toothpick or wire ring could not be located in the spring. These shoots cannot simply be ignored, since this would mean that sample size would change over the winter; likewise, assuming that these shoots died or survived also biases the resulting half life. When this problem was encountered, Formula 1 was modified by replacing "a" with :

$$\text{effective } a = a\,(b + d)/f \qquad (2)$$

where "a" represents the number of shoots initially marked, "f" represents the number of these shoots still alive in the fall, "b" represents the number of initially marked shoots known to be alive in the next spring, and "d" represents the number of initially marked shoots known to have died over the winter. "Effective a" approaches "a" as the number of missing shoots declines.

Half lives are strictly calculable only for exponentially decaying populations. There is no reason to believe that this assumption is true for any of the species studied; consequently, half lives are reported here strictly for purposes of comparison, not as statistically valid estimates of longevity.

5.3. Results

5.3.1. Carex subspathacea

On 16 June 1985, grazed plots initially contained an average of 8.7 shoots per 2 X 2 cm subplot in grazed plots, as compared with 7.2 shoots per subplot in exclosed plots. These figures are equivalent to about 24 450 shoots m^{-2} and to 15 005 shoots m^{-2}, respectively. Between 16 June, 1985 and 1 September, 1985, an average of 0.15 shoots was produced per initial shoot in grazed plots, as opposed to 0.21 per initial shoot in ungrazed plots (Table 5.2.; Figure 5.1.). The proportion of all shoots observed over the summer that had been produced in the same season was not significantly affected by the grazing treatment (Table 5.3.; Figure 5.1.). In the same interval, 0.46 shoots died per shoot in grazed plots, as opposed to 0.26 per shoot in exclosed plots (Table 5.2.). The proportion of all shoots observed in the summer that died before 1 September was significantly increased by grazing (Table 5.3.).

In grazed plots, 11% of those shoots alive on 1 September, 1985, died before 24 June 1986; the corresponding proportion in exclosed plots was 15%. The effect of grazing upon these proportions was difficult to interpret, since there was a significant 3-way interaction (Table 5.4.). Because of small sample sizes, independent G-tests for each site were not possible. When all sites were pooled, a G-test failed to demonstrate a significant effect of grazing treatment ($p < 0.05$). In grazed plots, an average of 0.14 shoots were produced over the winter for each shoot present in the fall; in exclosed plots this figure was 0.02 shoots per shoot (Table 5.2.; Figure 5.2.). The proportion of shoots present in the spring that had been produced over the winter was significantly greater in grazed plots than in ungrazed plots (Table 5.4.; Figure 5.2.). Over an entire

Table 5.2.

Shoot demographic statistics and sample sizes for <u>Carex</u> <u>subspathacea</u>

in 1985 and 1986, pooled over sites.

parameter	grazed plots	n	ungrazed plots	n
summer production of shoots per initial shoot (1985)	0.18	60	0.21	52
winter production of shoots per fall shoot (1985-1986)	0.14	40	0.02	42
summer production of shoots per initial shoot (1986)	0.78	581	0.73	575
summer deaths of shoots per initial shoot (1985)	0.46	60	0.26	52
winter deaths of shoots per fall shoot (1985-1986)	0.11	35	0.15	41
summer deaths of shoots per initial shoot (1986)	0.15	581	0.16	575

Figure 5.1. The average production of shoots of <u>Carex</u> <u>subspathacea</u>
between 16 June, 1985 and 1 September, 1985 in grazed plots
(●) and in ungrazed plots (○), expressed as the number of
shoots produced divided by the number of shoots present in
each plot at the initial sampling.
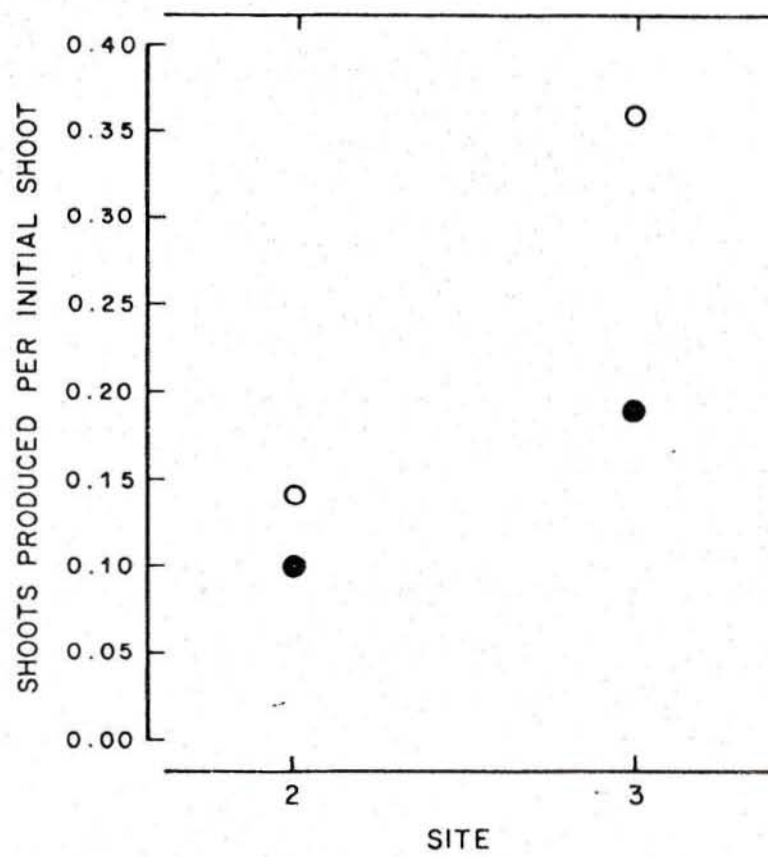
Table 5.3.

Multidimensional contingency analyses examining the influence of grazing
treatment and site on the proportion of shoots of <u>Carex</u> <u>subspathacea</u> observed
between 16 June, 1985 and 1 September, 1985 which were produced or died in the
same interval.

effect[a]	df	G^2	
		production	deaths
proportion x treatment	1	0.92	5.52*
proportion x site	1	2.13	0.93
proportion x treatment x site	1	0.08	0.51

[a] The treatment x site interaction was fixed by the design and hence was not
tested.

Table 5.4.

Multidimensional contingency analyses of the proportion of shoots of Carex subspathacea alive on 1 September, 1985 that died before 24 June, 1986, and of the proportion of shoots alive on 24 June, 1986 that had been produced since 1 September, 1985.

effect[a]	df	G^2 production	deaths
proportion x treatment	1	5.55*	0.04
proportion x site	1	5.12*	0.46
proportion x treatment x site	1	0.12	8.84**

[a] The treatment x site interaction was fixed by the design and hence was not tested.

* p<0.05, **p<0.01

Figure 5.2. The average production of shoots of <u>Carex</u> <u>subspathacea</u>
between 1 September, 1985 and 24 June, 1986 in grazed plots
(●) and in ungrazed plots (○), expressed as the number of
shoots produced divided by the number of shoots present in
each plot on 1 September, 1985.

SHOOTS PRODUCED PER INITIAL SHOOT

0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00

2   3

SITE
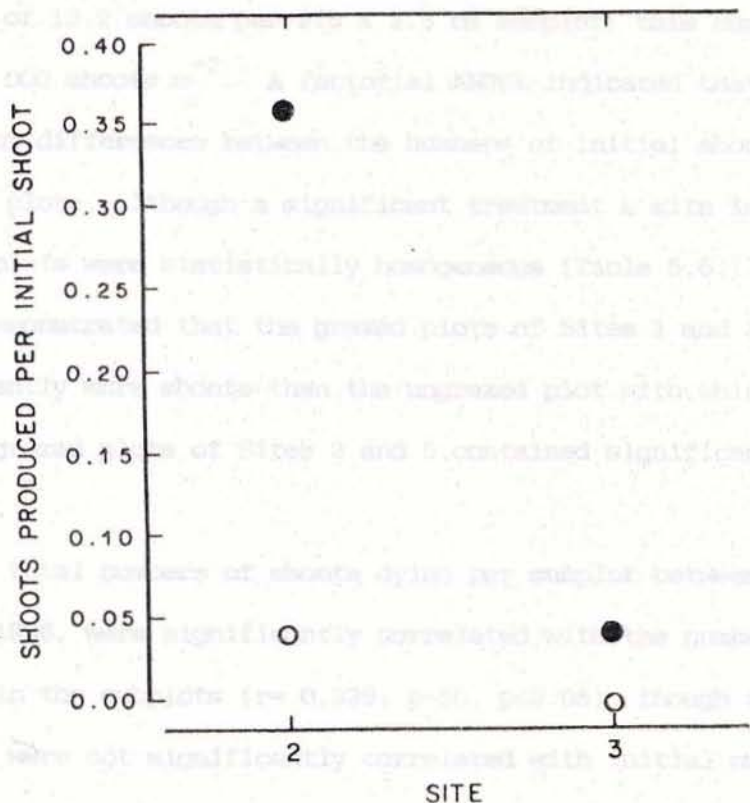
year, from 16 June, 1985 to 24 June, 1986, grazing did not significantly alter
the proportion of shoots produced or dying (Table 5.5.).

On 14 June, 1986, both grazed and ungrazed plots initially supported
averages of 13.2 shoots per 2.5 X 2.5 cm subplot; this number translates to
about 21 000 shoots m^{-2}. A factorial ANOVA indicated that there were not
consistent differences between the numbers of initial shoots in grazed and
exclosed plots, although a significant treatment x site interaction implied that
not all plots were statistically homogeneous (Table 5.6.). Independent one-way
ANOVAs demonstrated that the grazed plots of Sites 1 and 3 initially contained
significantly more shoots than the ungrazed plot with which they were paired,
but the grazed plots of Sites 2 and 5 contained significantly fewer shoots
$(p<0.05)$.

The total numbers of shoots dying per subplot between 14 June, 1986 and 24
August, 1986, were significantly correlated with the numbers of shoots initially
present in the subplots $(r= 0.339; n=50, p<0.05)$, though the numbers of shoots
produced were not significantly correlated with initial numbers $(r=0.136; n=50,$
$p>0.05)$. One would expect correlations with the initial shoot population as a
because larger populations would be likely to have greater absolute numbers of
births and deaths. However, the influence of initial population size was
considered undesirable, since numbers of shoots present at the beginning of the
experiment were unlikely to reflect the effects of excluding the herbivore.
Consequently, statistics of the births and deaths of shoots are presented below
in two forms: as raw data, and divided by the number of shoots initially
present. It was hoped that expressing births and deaths on a per initial shoot
basis would remove some of the biases associated with differing initial
populations of shoots in different plots.

Between 14 June, 1986 and 24 August, 1986, subplots within grazed plots

Table 5.5.

Multidimensional contingency analyses of the proportion of shoots of Carex subspathacea observed between 16 June, 1985 and 24 June, 1986 that were produced or died in the same interval.

effect[a]	df	G^2	
		production	deaths
proportion x treatment	1	0.00	1.89
proportion x site	1	0.08	0.56
proportion x treatment x site	1	1.21	1.17

[a] The treatment x site interaction was fixed by the design and hence was not tested.

Table 5.6.

Two factor ANOVAs of the effect of grazing treatment and site on shoot demographic parameters of _Carex subspathacea_ between 14 June, 1986 and 24 August, 1986.

source of variation	df	mean squares [a]				
		initial number of live shoots	shoots produced during the summer	ratio of shoots produced: initial shoots	shoots dying during the summer	ratio of shoots dying: initial shoots
treatment	1	0.001	3.380	0.000	0.500	0.002
site	4	0.027*	27.830	0.028**	2.830	0.016
treatment x site	4	0.104***	73.930**	0.048***	6.250*	0.017
residual	40	0.008	17.460	0.007	1.650	0.011

* p<0.05, **p<0.01, ***p<0.001

produced an average of 10.2 shoots, while subplots in ungrazed plots produced 9.7; these figures are equivalent to 0.78 shoots produced per initial shoot and 0.73 shoots per initial shoot, respectively (Table 5.2.; Figure 5.3.). An ANOVA indicated that the number of shoots produced per initial shoot did not differ significantly between grazing treatments, though a significant treatment x site interaction prevented simple interpretation (Table 5.6.); independent one-way ANOVAs performed for each site indicated that the number of shoots produced per initial shoot was significantly increased by grazing at Sites 4 and 5 and significantly decreased at Site 3 ($p < 0.05$) (Figure 5.3.). An ANOVA based on the raw data, examining the effects of grazing and site upon the production of shoots, also produced a significant interaction, though when one-way ANOVAs were performed for the data from each site, the only significant effect was a reduction in production at Site 2 ($p < 0.05$) (Table 5.6.). As another approach to investigating production, an MDCA was employed to determine whether grazing treatment affected the proportion of all shoots observed over the summer which had been produced between 14 June and 24 August (Table 5.7.). This analysis also indicated a significant 3-way interaction involving both site and treatment. G-tests performed independently for each site indicated that grazing significantly increased the proportion of shoots produced during the summer at Sites 4 and 5 and significantly decreased it at Sites 1 and 3 ($p < 0.05$).

Between 14 June and 24 August, 1986, an average of 2.0 shoots died per subplot in grazed plots, as opposed to 2.2 deaths per subplot in exclosed plots. These figures are equivalent to about 0.15 deaths per initial shoot in grazed plots and 0.16 deaths per initial shoot in exclosed plots (Table 5.2.); there were no significant effects of grazing treatment on the number of deaths per initial shoot (Table 5.6.). An MDCA detected no significant effects of grazing

Figure 5.3.   The average production of shoots of <u>Carex</u> <u>subspathacea</u>
between 25 May, 1986 and 24 August, 1986 in grazed plots
(●) and in ungrazed plots (○), expressed as the number of
shoots produced divided by the number of shoots present in
each plot at the initial sampling.
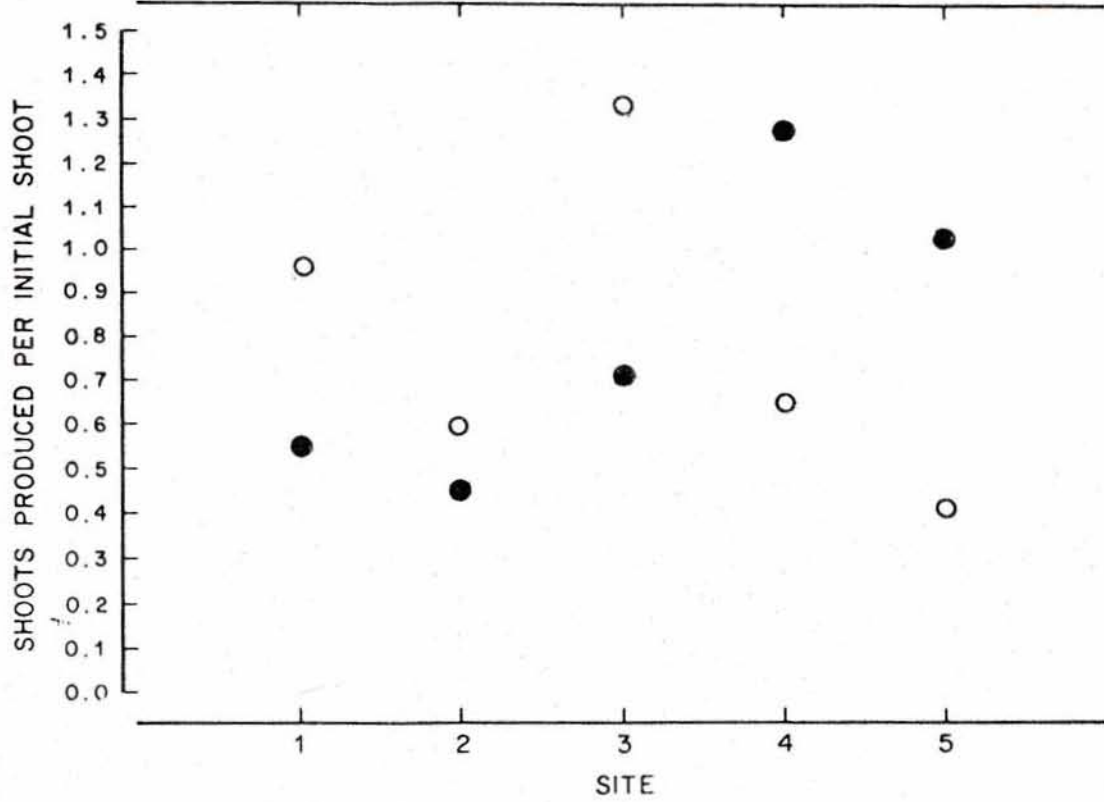
Table 5.7.

Multidimensional contingency analyses of the proportion of shoots of <u>Carex</u> <u>subspathacea</u> observed between 14 June, 1986 and 24 August, 1986 that were produced or died in the same interval.

effect [a]	df	G^2	
		production	deaths
proportion x treatment	1	0.03	0.10
proportion x site	4	11.86*	8.25
proportion x treatment x site	4	29.62***	9.49

[a] The treatment x site interaction was fixed by the design and hence was not tested.

* p<0.05, *** p<0.001

upon the proportion of all shoots that died between 14 June and 24 August (Table 5.7.).

In June, 1984, 486 shoots were ringed as part of a leaf demography experiment described elsewhere (Kotanen and Jefferies, 1987) and in Chapter 3. These shoots were followed until June of 1985, allowing the calculation of half lives based upon one complete annual cycle. Half lives ranged between 3 and 4 years. In grazed plots, the half life for the entire initial sample of shoots was estimated at 1113 days; in exclosed plots the equivalent half life was estimated at 1507 days (Table 5.8.).

Samples taken from grubbed areas on 13 June, 1986 contained an average of 0.06 shoots of Carex subspathacea per square centimeter (Table 5.9.). Swards in adjacent intact swards contained an average of 1.96 cm^{-2} (Table 5.9.). On 14 August, 1986, these values had increased to 2.6 cm^{-2} and 0.11 cm^{-2}, respectively (Table 5.9.). These increases amounted to 0.37 shoots per shoot in ungrubbed areas and 0.83 shoots per shoot in grazed areas.

Flowering was extremely infrequent. Between 1984 and 1986, only 2 culms flowered, out of a total of 1486 shoots. Flowering was locally common in sheltered areas adjacent to the grazing flats.

5.3.2. Carex X flavicans

On 14 June, 1985, grazed plots initially supported about 1200 shoots m^{-2}, as compared with 1800 m^{-2} in ungrazed plots. Between this date and 31 August, 1985, an average of 0.71 shoots were produced per initial shoot in grazed plots, as opposed to 0.52 per initial shoot in exclosed plots (Table 5.10.; Figure 5.4.). The proportion of all shoots observed over the summer that had been

Table 5.8.

Half lives in days and sample sizes for shoots of <u>Carex</u> <u>subspathacea</u>, based upon data collected between 16 June, 1985 and 24 June, 1986.

site	grazed plot	exclosed plot
1	757	2845
2	1879	1755
3	1227	960
pooled	1113	1507

Table 5.9.

Densities of shoots of <u>Carex</u> <u>subspathacea</u> per 2 X 2 cm quadrat in grubbed and intact swards on 13 June, 1986.

	grubbed plots			intact plots		
site	mean	variance	n	mean	variance	n
1	8.67	18.27	6	0.00	0.00	6
2	10.00	10.80	6	0.00	0.00	6
3	5.67	3.07	6	1.00	1.60	6
4	4.67	5.07	6	0.17	0.17	6
5	9.50	18.30	6	0.00	0.00	6
overall	7.70	14.29	30	0.23	0.46	30

Figure 5.4.   The average production of shoots of <u>Carex</u> X <u>flavicans</u>
between 14 June, 1985 and 31 August, 1985 in grazed plots
(●) and in ungrazed plots (○), expressed as the number of
shoots produced divided by the number of shoots present in
each plot at the initial sampling.

Table 6.10

Shoot demographic statistics and sample sizes for *Carex* ? *lyngbaei*
in 1985 and 1986 (by all data given.)

SHOOTS PRODUCED PER INITIAL SHOOT

SITE

parameter	grazed plots	n	enclosed plots	n
summer production of shoots per initial shoot (1985)	0.77	135	0.80	165
winter production of shoots per fall shoot (1985-1986)	0.65	121	0.18	130
summer production of shoots per initial shoot (1986)	0.19	270	0.19	270
summer deaths of shoots per initial shoot (1985)	0.50	135	0.19	165
winter deaths of shoots per fall shoot (1985-1986)	0.13	163	0.11	147
summer deaths of shoots per initial shoot (1986)	0.90	270	0.19	270
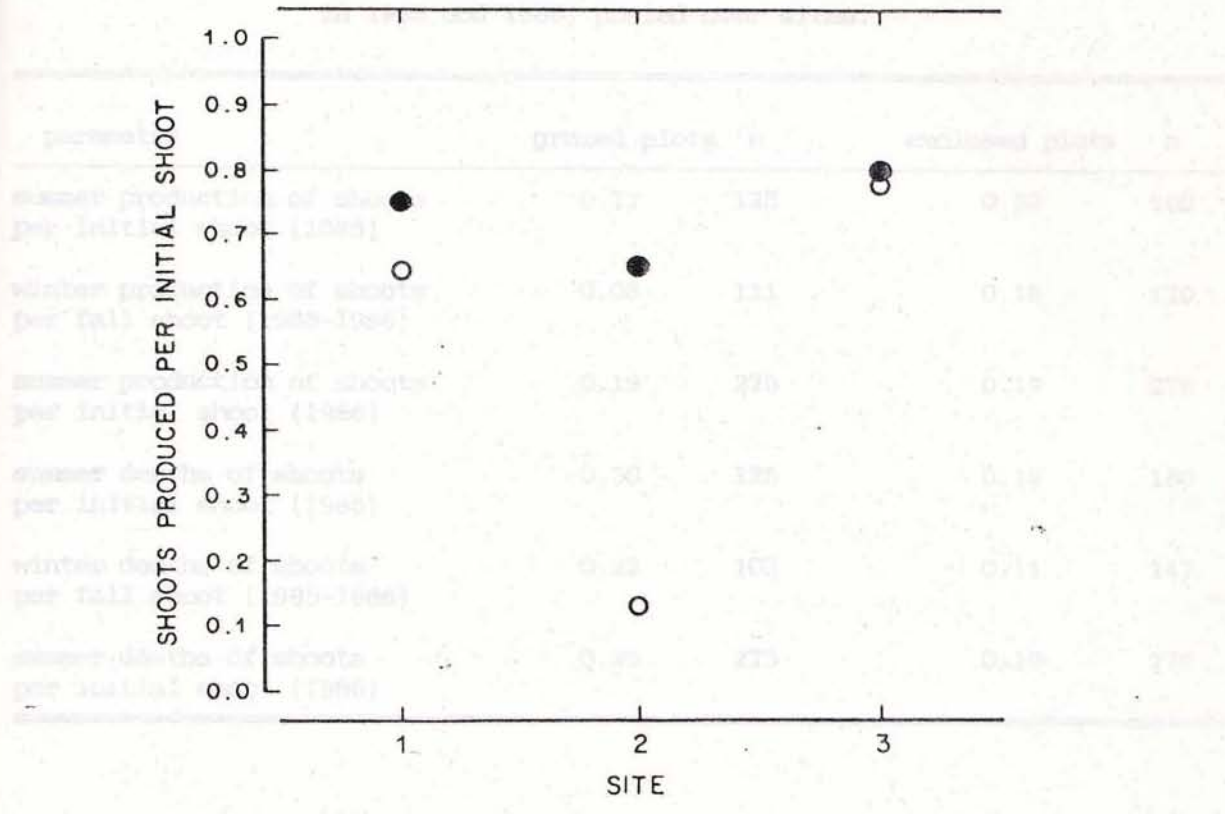
Table 5.10.

Shoot demographic statistics and sample sizes for <u>Carex</u> X <u>flavicans</u>

in 1985 and 1986, pooled over sites.

parameter	grazed plots	n	exclosed plots	n
summer production of shoots per initial shoot (1985)	0.71	125	0.52	160
winter production of shoots per fall shoot (1985-1986)	0.08	111	0.16	170
summer production of shoots per initial shoot (1986)	0.19	275	0.19	276
summer deaths of shoots per initial shoot (1985)	0.30	125	0.12	160
winter deaths of shoots per fall shoot (1985-1986)	0.22	103	0.11	147
summer deaths of shoots per initial shoot (1986)	0.29	275	0.18	276

produced in the same season was not significantly increased by grazing
(Table 5.11.; Figure 5.4.). In the same interval, deaths amounted to 0.30 and
0.12 per initial shoot in grazed and ungrazed plots respectively (Table 5.10.).
The proportion of all shoots observed over the summer that died before 31 August,
1985 was significantly increased by grazing (Table 5.11.).

In grazed plots, 22% of those shoots alive on 31 August, 1985 died before
17 June, 1986; the corresponding proportion in exclosed plots was 11% (Table
5.10.). These proportions were significantly different (Table 5.12.). The
proportion of shoots present in the spring that had been produced over the
winter did not differ significantly between grazing treatments (Table 5.12.;
Figure 5.5.). In grazed plots, about 0.08 shoots were produced over the winter
for each shoot present in the fall, while winter production in ungrazed plots
amounted to about 0.16 shoots per fall shoot (Table 5.10.; Figure 5.5.). Over
the entire year, from 14 June, 1985 to 17 June, 1986, grazing increased the
proportion of shoots dying, but did not affect the proportion of shoots
produced (Table 5.13.).

On 20 June, 1986, both grazed and exclosed plots initially supported
averages of 4.6 shoots per 5 X 5 cm subplot; this figure is equivalent to about
1840 shoots m^{-2}. The proportion of subplots with more than this number of
shoots did not differ significantly between treatments (Table 5.14.). The total
numbers of shoots produced and dying between 20 June and 26 August were both
significantly correlated with the numbers of shoots initially present ($r=0.41$
and $r=0.52$, respectively; $n=100$, $p<0.05$). Consequently, statistics of the
births and deaths of shoots are presented below in two forms: as raw data, and
as divided by the number of shoots initially present.

Between 20 June and 26 August, 1986, subplots within both grazed and
exclosed plots produced averages of 0.88 new shoots per subplot; these

Table 5.11.

Multidimensional contingency analyses of the proportion of shoots of Carex X flavicans observed between 14 June, 1985 and 31 August, 1985 that were produced or died in the same interval.

effect[a]	df	G^2 production	deaths
proportion x treatment	1	3.65	4.67*
proportion x site	2	8.16*	3.89
proportion x treatment x site	2	6.00	1.66

[a] The treatment x site interaction was fixed by the design and hence was not tested.

* $p < 0.05$

Table 5.12.

Multidimensional contingency analyses of the proportion of shoots of <u>Carex</u> X <u>flavicans</u> alive on 31 August, 1985 that died before 17, June 1986, and of the proportion of shoots alive on 17 June, 1986 that had been produced since 31 August, 1985.

		G^2	
effect[a]	df	production	deaths
proportion x treatment	1	3.22	8.27**
proportion x site	2	0.37	4.04
proportion x treatment x site	2	5.98	0.18

[a] The treatment x site interaction was fixed by the design and hence was not tested.

** $p < 0.01$

Figure 5.5.   The average production of shoots of <u>Carex</u> X <u>flavicans</u>

between 31 August, 1985 and 17 June, 1986 in grazed plots

(●) and in ungrazed plots (O), expressed as the number of

shoots produced divided by the number of shoots present in

each plot on 31 August, 1985.
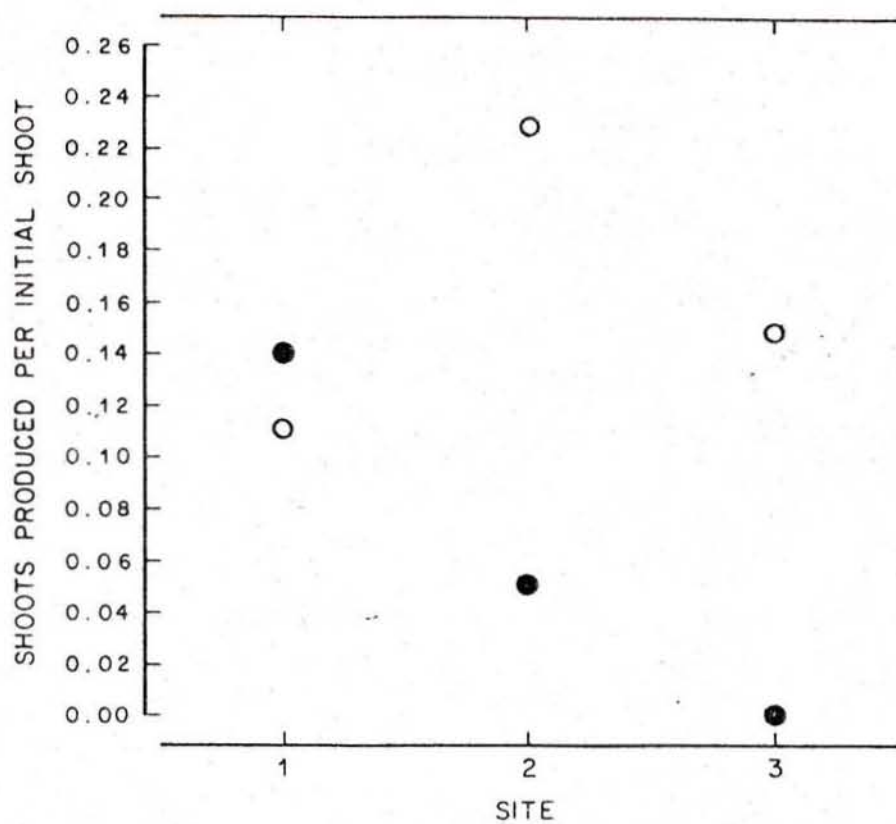
Table 5.13.

Multidimensional contingency analyses of the proportion of shoots of <u>Carex</u> X <u>flavicans</u> observed between 14 June, 1985 and 17 June, 1986 that were produced or died in the same interval.

effect[a]	df	G^2 production	G^2 death
proportion x treatment	2	0.90	15.01***
proportion x site	2	5.61	4.47
proportion x treatment x site	1	1.90	0.15

[a] The treatment x site interaction was fixed by the design and hence was not tested.

*** p<0.001

Table 5.14.

Multidimensional contingency analyses of the effects of grazing treatment and site upon demographic parameters of shoots of Carex X flavicans. Tests examine effects on the proportion of subplots with more than the average initial number of shoots, and effects on the proportion of shoots observed between 20 June, 1986 and 26 August, 1986 which were produced or died in this interval.

| | | G^2 | | |
effect[a]	df	initial number of shoots	production of shoots	death of shoots
proportion x treatment	1	1.57	3.80	10.75**
proportion x site	4	7.74	6.45	51.93***
proportion x treatment x site	4	1.13	0.01	14.16**

[a] The treatment x site interaction was fixed by the design and hence was not tested.

** p<0.01, *** p<0.001

figures are equivalent to about 0.19 shoots produced per initial shoot in both grazed and exclosed plots (Table 5.10.; Figure 5.6.). The proportion of shoots observed between 20 June and 26 August, 1986 that were produced during this period was not significantly affected by grazing (Table 5.14.; Figure 5.6.).

Between 20 June and 26 August, 1986, an average of 1.36 shoots per subplot died in grazed plots, as opposed to an average of 0.84 per subplot in exclosed plots. These figures are equivalent to about 0.29 deaths per initial shoot in grazed plots and about 0.18 deaths per initial shoot in exclosed plots (Table 5.10.). The proportion of shoots observed in the summer that died before 26 August is difficult to interpret because of a 3-way interaction (Table 5.14.). When pooled because of zero values in some plots, grazed plots differed significantly from exclosed plots in the proportion of shoots dying during the summer ($G_{1df}=7.86**$).

By 10-11 June, 1986, pulling of shoots by geese had removed about 28.4 shoots m^{-2} (Table 5.15.) in the most intensely used areas. In the fall, the geese removed about 2.7 shoots m^{-2}.

Based upon the data collected from the plots established in 1985, the half life of all shoots initially present in grazed plots was about 368 days, as compared with 1515 days for shoots in exclosed plots (Table 5.16.).

In 1985, 11% of the shoots initially present in grazed plots and 5% of the shoots initially present in ungrazed plots flowered. When pooled over sites because of small sample size, these proportions did not differ significantly ($G^2_{1df}=0.22$). In 1986, culms totalled 3% of the shoots initially present in grazed plots and 5% of the shoots initially in ungrazed plots; when pooled over sites, this difference was nonsignificant ($G^2_{1df}=2.09$). Geese removed many culms before their seeds matured.

Figure 5.6. The average production of shoots of <u>Carex</u> X <u>flavicans</u>
between 21 June, 1986 and 26 August, 1986 in grazed plots
(●) and in ungrazed plots (○), expressed as the number of
shoots produced divided by the number of shoots present in
each plot at the initial sampling.
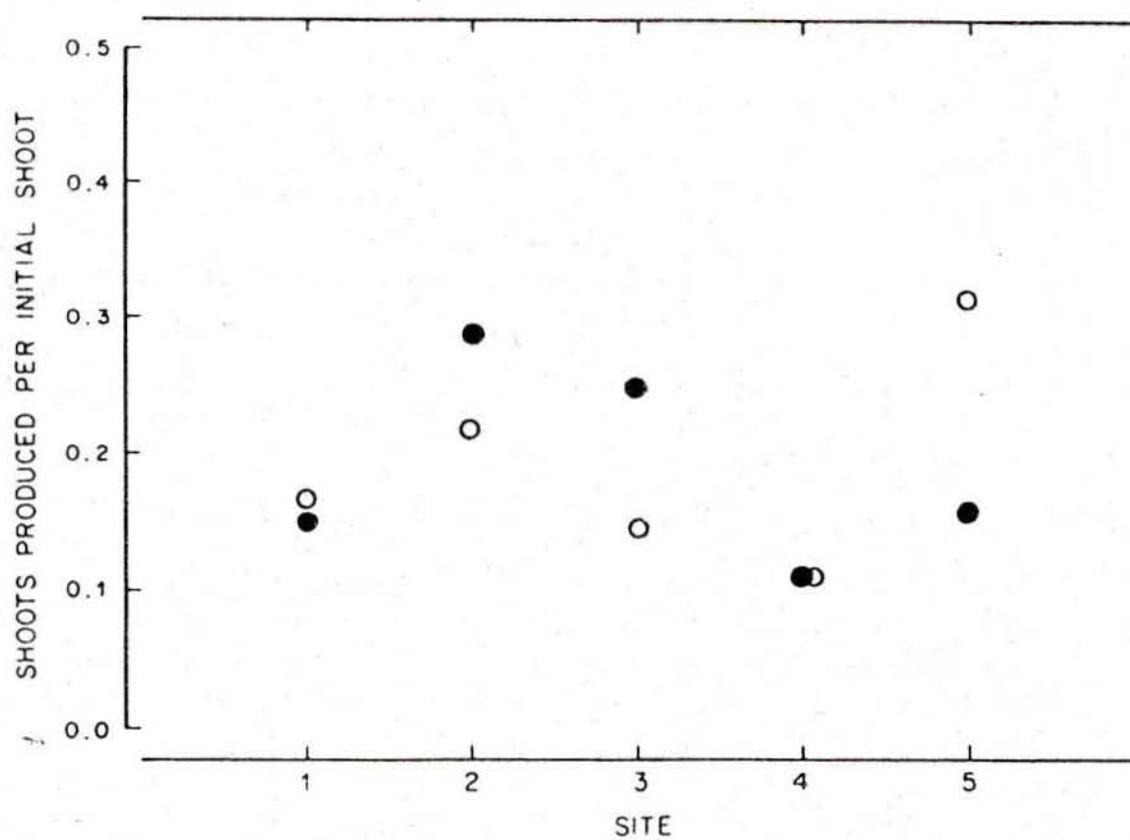
Table 5.15.

Means and standard errors of the loss of shoots of Carex X flavicans and Carex aquatilis per 0.25 m^2 quadrat to pulling by geese in the spring of 1985.

Carex X flavicans			Carex aquatilis		
site	shoots pulled	n	site	shoots pulled	n
A	41.70 +/- 5.04	10	A	28.20 +/- 7.81	10
B	4.30 +/- 0.88	10	B	46.10 +/- 7.17	10
C	12.30 +/- 3.44	10	C	19.50 +/- 4.81	10
D	2.10 +/- 1.18	10	D	49.80 +/- 4.31	10
E	0.21 +/- 0.12	14	E	42.90 +/- 5.75	10
F	0.10 +/- 0.10	10	F	66.30 +/- 14.28	10
G	0.90 +/- 0.46	10	G	53.60 +/- 8.84	10
H	1.50 +/- 0.45	10			
I	3.60 +/- 1.86	10			

Table 5.16.

Half lives in days for shoots of Carex X flavicans, based upon data collected between 14 June 1985 and 17 June 1986.

site	grazed plot	exclosed plot
1	293	1397
2	491	1971
3	314	1286
overall	368	1515

5.3.3. Carex aquatilis

On 18 June, 1986, grazed plots contained an average of 42.2 shoots per 25 X 25 cm subplot, while exclosed plots contained an average of about 49.2 shoots. These values respectively are equivalent to 650 and 768 shoots m^{-2}. Between 18 June, 1986 and 23 August, 1986, neither total production nor total deaths were significantly correlated with the numbers of shoots initially present ($r=$ -0.282 and $r= 0.344$ respectively; $n=10$, $p>0.05$).

Between 18 June and 23 August, 1986, an average of 18.6 shoots were produced per subplot in grazed plots, as compared with an average of 16.2 in exclosed plots. These figures translate to about 0.44 new shoots per initial shoot in grazed plots and 0.33 new shoots per initial shoot in exclosed plots (Table 5.17.; Figure 5.7.). The effect of grazing upon the proportion of all shoots observed during the summer that had been produced in the same season was difficult to interpret, as a consequence of a significant 3-way interaction (Table 5.18.). Independent G-tests for each site indicated that this proportion was significantly increased by grazing at 2 of 5 sites; no significant effects were detected at the other sites (Figure 5.7.).

Between 18 June and 28 August, 1986, an average of 6.2 shoots died per grazed subplot, compared with 5.2 per exclosed subplot. These figures respectively equal about 0.15 deaths per initial shoot in grazed plots, and about 0.11 deaths per initial shoot in exclosed plots (Table 5.17.). The proportion of all observed shoots that died during this period was not affected by grazing (Table 5.18.).

By 10-11 June 1986, grubbing had removed an average of 175 shoots m^{-2} in the most heavily exploited areas (Table 5.15.). By 29 August, 1986, fall shoot pulling had removed only about 15 shoots m^{-2}.

Table 5.17.

Shoot demographic statistics and sample sizes for <u>Carex aquatilis</u>

in 1986, pooled over sites.

parameter	grazed plots	n	exclosed plots	n
summer production of shoots per initial shoot (1986)	0.44	304	0.33	327
summer deaths of shoots per initial shoot (1986)	0.15	304	0.11	327

Table 5.18.

Multidimensional contingency analyses of the proportion of shoots of <u>Carex</u>

<u>aquatilis</u> observed between 18 June, 1986 and 23 August, 1986 which were produced

or died in the same interval.

effect [a]	df	G^2 production	deaths
proportion x treatment	1	3.21	0.84
proportion x site	4	11.23*	8.23
proportion x treatment x site	4	18.70***	3.95

[a] The treatment x site interaction was fixed by the design and hence was not tested.

* p<0.05, *** p<0.001

Figure 5.7. The average production of shoots of <u>Carex</u> <u>aquatilis</u>
between 18 June, 1986 and 27 August, 1986 in grazed plots
(●) and ungrazed plots (O), expressed as the number of
shoots produced divided by the number of shoots present in
each plot at the initial sampling.

SHOOTS PRODUCED PER INITIAL SHOOT

1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0

1   2   3   4   5
SITE
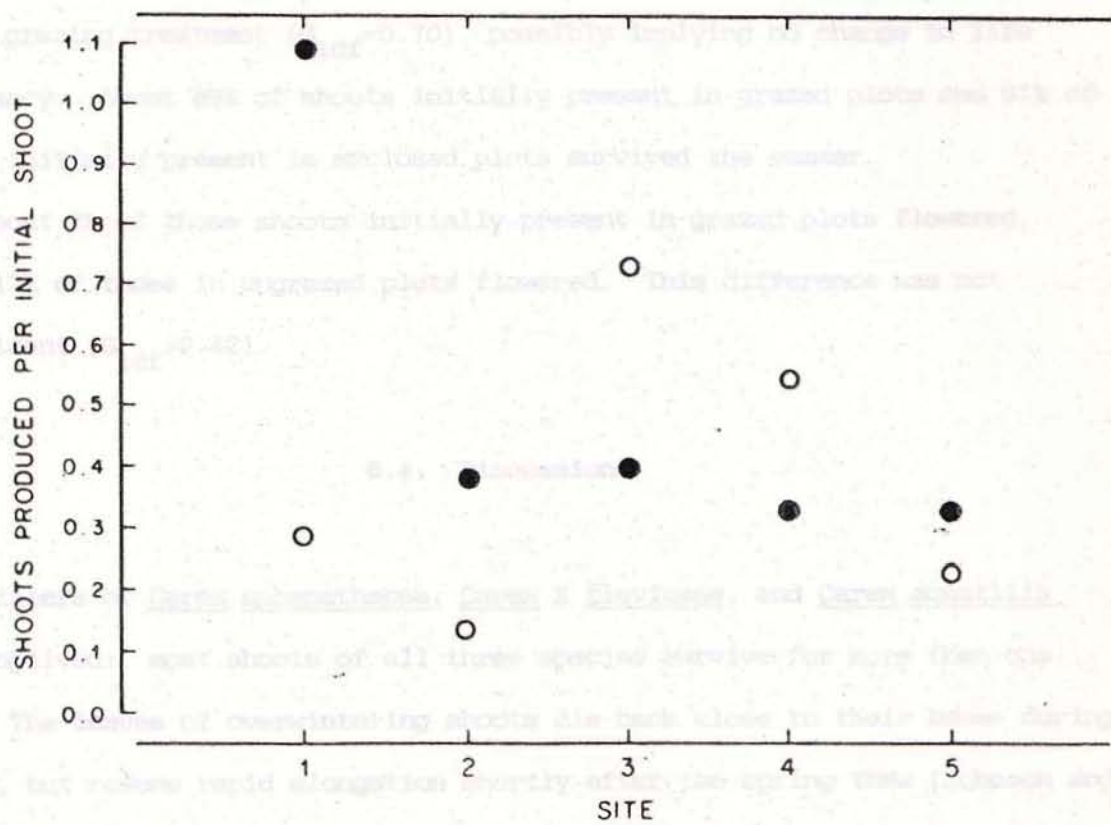
Without data for a complete annual cycle, meaningful half lives were not calculable. However, the proportion of shoots present on the first sampling that died before the end of the year was not significantly affected by the grazing treatment (G_{1df}=0.70), possibly implying no change in life expectancy. About 89% of shoots initially present in grazed plots and 91% of shoots initially present in exclosed plots survived the summer.

About 7% of those shoots initially present in grazed plots flowered, while 12% of those in ungrazed plots flowered. This difference was not significant (G_{1df}=2.42).

5.4. Discussion

Tillers of Carex subspathacea, Carex X flavicans, and Carex aquatilis are longlived: most shoots of all three species survive for more than one year. The leaves of overwintering shoots die back close to their bases during winter, but resume rapid elongation shortly after the spring thaw (Johnson and Tiezen 1976; Archer and Tiezen 1980; Chapin and Chapin 1981; Kotanen and Jefferies 1987; Chapters 2,3,4,6). At La Pérouse Bay in 1985 and 1986, both the elongation of old leaves and the production of new leaves by "overwintering" shoots of all three carices were well underway by mid-June (Kotanen and Jefferies 1987; Chapters 3,4,6). The fresh-water pools inhabited by Carex aquatilis and Carex X flavicans thawed before the surrounding tundra; early spring growth was especially rapid in these species.

Because many shoots survived for more than the entire sampling period, detailed information on the forms of the depletion curves of shoots was not available. As well, half lives based on depletion curves do not generally equal either half lives based on survivorship curves, or mean life expectancies.

Consequently, the half lives reported in Tables 5.8. and 5.16. must be considered to be rough indications of the longevities of shoots. In exclosed plots, shoots of Carex subspathacea and Carex X flavicans both had estimated half lives of about 4 years (1500 days) (Tables 5.8., 5.16.). Half lives could not be calculated for Carex aquatilis, but 91% of the shoots initially present in exclosed plots survived beyond the final sampling on 23 August, indicating a half life in excess of one summer. Tillers of Carex aquatilis growing at high latitudes have been estimated to have lifespans ranging from 2 to 8 years, with averages of 2 to 3 years (Shaver and Billings 1975; Chapin and Chapin 1981). However, lifespans vary among locations: in the Rocky Mountains of Alberta, shoots of Carex aquatilis survived for only 12 to 15 months (Gorham and Somers 1973). Though no published figures are available for lifespans of shoots of Carex subspathacea or Carex X flavicans, lifespans in excess of one year have been reported for at least some cohorts of shoots of other carices (Gorham and Somers 1972; Bernard 1975; Noble et al. 1979).

The production of new shoots by Carex aquatilis, C. X flavicans, and C. subspathacea occurred throughout the year, but rates of shoot production of all three species were greatest in spring and fall. This production probably reflected an increase in the activation of subterranean buds in the late summer and early fall; some of these buds emerged from the ground as new shoots in fall, while others overwintered beneath the ground surface and emerged in the subsequent spring. Although night-time temperatures began to drop below 0 C by the beginning of September, it is possible that warm days may have allowed some growth between the termination of sampling and the first permanent snow in October. Shoots recorded as having been produced in the winter may have emerged in this period, or possibly beneath winter snow or during the spring thaw, as has been reported elsewhere for Carex aquatilis (Gorham and Somers 1973). These

seasonal patterns of growth are similar to those described for carices at other northern locations (Gorham and Somers 1973; Bernard and Macdonald 1974; Bernard 1975).

In exclosed plots in both summer and winter, the total production of shoots and the total number of deaths of shoots of each species amounted to less than 1 tiller per tiller (Tables 5.2., 5.10., 5.17.), as might be expected from the observation that most shoots survive for more than a year. Chapin and Chapin (1981) also reported tillering rates which ranged between 0.1 and 0.9 tillers tiller^{-1} year^{-1} for ramets from different populations of Carex aquatilis transplanted into different habitats. In the summer of 1985, the production of shoots of Carex X flavicans greatly exceeded the production recorded in the summer of 1986 (Table 5.10.). Though it is possible that these figures accurately represent year-to-year variation, another explanation for this discrepancy may be that as a result of the slightly shorter sampling season in 1986 (Table 5.1.) some of the shoot production in spring and fall may have been missed. In contrast, in Carex subspathacea, production per initial shoot in the summer of 1986 exceeded that of the summer of 1985 (Table 5.2.). In this case, it may be that the later date on which the experiment was begun in 1986 (Table 5.2.) allowed geese to remove more shoots before the first scoring. This loss would reduce the initial number of shoots, and thus inflate the ratio of production to initial shoots. This would also explain why fewer shoots of Carex subspathacea apparently died in 1986 (Table 5.9.).

Flowering of all of the study species occurred from late June to mid-July. Flowering resulted in the termination of the growth of a shoot, though some culms of Carex X flavicans survived to the following year. Culms probably developed from primordia initiated in the previous fall. Flowering of all three species generally was uncommon within the study plots, though culms of Carex

subspathacea and Carex X flavicans were more frequent in areas more sheltered than those chosen for study. Successful reproduction from seed was probably rare in all of the study species; most of the shoots observed in this study were probably of vegetative origin. No seedling of C. subspathacea or C. flavicans was identified in three years of study. Though seedlings of Carex aquatilis were observed, all perished while very young; no successful establishment was noted in the study plots.

For a short period after their arrival at La Pérouse Bay in mid-May, feeding by both resident and migrant geese is characterized by the pulling of shoots in fresh-water habitats and by the grubbing of roots and rhizomes on the salt marshes (Jefferies 1987). In 1985 and 1986, this pattern of feeding by the geese ended between 12 June and 25 June. During this period, the grazing of leaves of Carex subspathacea and, to a lesser extent, the grazing of leaves of Carex X flavicans replaced grubbing and shoot pulling as the most important form of foraging (Kotanen and Jefferies 1987; Chapters 3,4). Grazing by adults and goslings remained the predominant type of feeding until the geese leave the area in mid-August, although some grubbing and shoot pulling resumed shortly before the departure of the geese.

Assuming that densities of shoots in grubbed and ungrubbed areas were initially similar, data given in Table 5.9. indicate that 97% of shoots of Carex subspathacea were removed from patches of salt-marsh vegetation grubbed by geese in the early spring. In swards that escaped grubbing, losses of shoots were much smaller in both summer and winter (Table 5.2.). Losses of shoots from all causes were significantly greater in grazed plots than in exclosed plots in the summer of 1985 (Table 5.3.), although not in the following winter (Table 5.4.) or when the results are expressed on an annual basis (Table 5.5.). Grazing did

not significantly increase deaths of shoots in the summer of 1986 (Tables 5.6., 5.7.).

Although the spring pulling of shoots of Carex X flavicans was widespread, even among the most heavily pulled areas only about 28 shoots m^{-2} were destroyed (Table 5.15.). Assuming that the densities of shoots per square metre prior to pulling equalled those initially recorded in demography plots in 1986, the average proportion of shoots removed by spring grubbing was only 0.02; this proportion is small, compared to the loss of shoots in the remainder of the year (Table 5.10.). In contrast, geese grubbed an average of 175 shoots of Carex aquatilis per square metre (Table 5.15.); assuming initial shoot densities equal to those of ungrazed plots, this amounted to a loss of about 0.23 shoots per initial shoot. This proportion exceeded the losses during the rest of the summer (Table 5.17.). Grubbing of both C. aquatilis and C. X flavicans in the fall removed only about a tenth of the shoots removed in the spring. Deaths of shoots of C. X flavicans from all causes in grazed plots significantly exceeded deaths in exclosed plots in both summer and winter (Tables 5.11., 5.12., 5.13., 5.14.). There was no significant difference between the proportion of shoots of C. aquatilis which died during the summer in grazed plots, compared to the proportion in exclosed plots (Table 5.18.).

The exclosure of swards of these carices from the geese did not consistently affect the half lives of shoots of Carex subspathacea or Carex aquatilis, but increased half lives of shoots of Carex X flavicans by a factor of 4, as might be expected from the strong effect that grazing has on the survival of shoots of this hybrid.

Increased tillering is a response of many graminoids to herbivory (Caldwell et al. 1981; Humphreys 1981; Dyer et al. 1982; Crawley 1983; McNaughton et al. 1983; Coughenour 1985; Belsky 1986). Even in tundra

habitats, the rapid production of additional shoots may occur; Bazely and Jefferies (198Nb) found that the grass _Puccinellia_ _phryganodes_ growing on the salt marshes at La Pérouse Bay responded to grazing within one summer with a significantly increased production of axillary shoots. In contrast to these examples, neither _Carex_ _aquatilis_ nor _Carex_ X _flavicans_ nor _Carex_ _subspathacea_ showed consistent increases in tillering in response to herbivory within the duration of this study.

Although the date on which each experiment was first scored may affect the accuracy of estimates of total production and deaths of shoots, it should not bias comparisons of grazed plots with exclosed plots. In contrast, the loss of shoots after exclosures were erected, but before scoring began, would be expected to inflate the ratio of the number of shoots produced to the number of shoots initially present for grazed plots, but not for exclosed plots. In spite of this bias, few comparisons suggested that foraging by geese significantly increased the production of new shoots in any of the species studied. Grazing did not affect the production of shoots of _Carex_ _subspathacea_ in the summer of 1985 or 1986 (Tables 5.3., 5.6., 5.7.). Though the production of shoots of this species over the winter of 1985-1986 was greater in grazed plots than in exclosed plots (Table 5.4.), grazed plots did not have significantly greater production shoots on an annual basis (Table 5.5.). Foraging by geese did not significantly increase production of shoots of _Carex_ X _flavicans_ in any season (Tables 5.11., 5.12., 5.14.), or on an annual basis (Table 5.13.). The production of shoots of _Carex_ _aquatilis_ also failed to respond within one season to foraging by geese (Table 5.18.). Changes in the demography of leaves represented the most important short-term compensatory responses of at least _C_. _subspathacea_ and _C_. X _flavicans_ to herbivory by geese (Chapters 5.3., 5.4.).

Even if grazed plants successfully maintained their NAPP, production of aerial shoots would be essential for the replacement of shoots lost to herbivory and senescence. A clone which was unable to keep pace with these losses would eventually disappear. It is suggestive that all of the carices considered in this study suffered significant losses of shoots to geese, but that none responded with increased rates of shoot production. It appears that these carices were not able to keep pace with the loss of shoots during the period of the study, at least in the most intensively grubbed areas. Circumstantial evidence suggests that this interpretation may provide an explanation of plant-herbivore relations at La Pérouse Bay. Despite the fact that NAAPP is increased in by grazing in areas of intact salt-marsh vegetation (Cargill and Jefferies 1984b), grubbing on the salt marsh leads to the development of bare areas which are only slowly recolonized by plants (Jefferies et al. 1979; Jefferies 1987; Section 2.3.1.). In fresh-water areas the moss carpets which frequently surround ponds at sites heavily exploited by the geese may similarly be the result of the local elimination of shoots of carices (Tikhomirov 1959; Jefferies and Kerbes 1985; Jefferies 1987; Sections 2.3.1., 2.3.2.), even though the production of leaves may be increased by grazing among the sparse population of shoots of Carex X flavicans that remain. Though further study is needed to confirm these speculations, they serve to emphasize the importance of explicitly considering the patchiness of foraging behaviour in ecological studies of real systems.

5.5. References

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CHAPTER 6: THE ELONGATION OF LEAVES OF GRAZED AND UNGRAZED SHOOTS OF <u>CAREX</u>

<u>SUBSPATHACEA</u> AND <u>CAREX</u> X <u>FLAVICANS</u>

6.1. Introduction

Much of the resistance of grasses and sedges to the deleterious effects
of grazing is attributable to characteristics of graminoid morphology which
protect vulnerable meristems from damage by herbivores. These meristems
enable regrowth to occur following defoliation (Harper 1977; Mack and Thompson
1982; Crawley 1983; Coughenour 1985). The basal (intercalary) meristem of
graminoid leaves is located close to the shoot; this meristem often escapes
damage by grazers, so that rapid regrowth of clipped leaves is possible (Harper
1977; Crawley 1983; Coughenour 1985). In many grasses and sedges, elongation
of leaves following grazing is one of the most important responses determining
whether a tiller regenerates its photosynthetic surface area after grazing
(McNaughton <u>et</u> <u>al</u>. 1983; Coughenour 1985; Wallace <u>et</u> <u>al</u>. 1985).

The sedges <u>Carex</u> <u>subspathacea</u> Wormsk.[*] and <u>Carex</u> X <u>flavicans</u> Nyl.
respectively occur in saline and fresh-water habitats at La Pérouse Bay,
Manitoba. Both of these species are heavily grazed during the summer by a
breeding colony of 7000 Lesser Snow Geese (<u>Chen</u> <u>caerulescens</u> <u>caerulescens</u> (L.)
Gundl.) and their offspring. In 1980, comparisons of grazed and ungrazed plots
indicated that the foraging activities of the geese increased the net annual
above-ground primary production of <u>Carex</u> <u>subspathacea</u> by 60% to 80% (Cargill
and Jefferies 1984b). This increase was a consequence of the geese increasing
the availability of nitrogen for plant growth in this nitrogen-deficient

[*] Nomenclature follows Scoggan (1978)

environment (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985, 198N;
Jefferies 1987; Section 2.3.1.). Much of this increased production is a
consequence of the increased production and turnover of leaves; significant
changes in the demography of shoots did not occur in response to grazing (Kotanen
and Jefferies 1987; Chapters 3,5). Carex X flavicans also responded to
grazing during the season with increased production of leaves, but not of
shoots (Chapters 4,5).

The purpose of this study was to determine whether Carex subspathacea and
Carex X flavicans also show increased elongation of leaves when grazed.
Rates of elongation of leaves were compared between plants in plots subjected
to grazing and plants in plots from which geese were excluded. Together with
investigations at the same location of the effects of grazing upon the shoot
and leaf demography of these species (Kotanen and Jefferies 1987; Chapters
3,4,5), these data completed the description of the short-term responses of
above-ground organs of these sedges to grazing by geese.

6.2. Materials and Methods

6.2.1. The site

La Pérouse Bay is located on the coast of Hudson Bay, about 25 km east
of Churchill, Manitoba. The extensive tidal flats at this location are
dominated by the grass Puccinellia phryganodes (Trin.) Scribn. & Merr. and by
Carex subspathacea. Above the high-tide mark, the landscape consists of
fresh-water ponds and areas of saturated moss, separated by shrub tundra
vegetation. Carex X flavicans, a hybrid of Carex subspathacea and Carex
aquatilis Wahl., often predominates in shallow fresh water and in the moss

carpets which surround many ponds.

For a few weeks following their arrival at La Pérouse Bay in mid-May, Lesser Snow Geese feed primarily by grubbing roots and rhizomes, and by pulling the developing shoots of carices in both fresh-water and intertidal habitats. About 7000 pairs of geese nest at this location. After the hatching of the 30 000 goslings in late June, families feed on the leaves of graminoids. The areas which are most intensively used for feeding are the intertidal marshes, where the geese uniformly crop the vegetation to 2.5 cm or less in height. Freshwater areas are continuously used by small numbers of geese, and frequently by much of the remainder of the colony when bad weather or predators force the birds off the tidal flats. Carex X flavicans is the most frequently grazed species in fresh-water habitats. Though very patchy, herbivory by geese can be intense in the moss carpets around ponds where open swards of C. X flavicans may be maintained at a height of less than 5 cm. The geese leave La Pérouse Bay in mid-August.

More information on the vegetation and climate of La Pérouse Bay and on the biology of Lesser Snow Geese may be found in Jefferies et al. 1979, Cooke et al. 1982, Cargill and Jefferies 1984a, Kotanen 198N, and in Section 2.3.1..

6.2.2. The growth habits of the species studied

The morphology of Carex subspathacea and Carex X flavicans resemble that described for Carex aquatilis by Shaver and Billings (1975), Billings et al. (1978), and Shaver et al. (1979) (Figure 2.1.). Leafy shoots are produced in clusters from subterranean rhizomes. Vegetative tillers of C. subspathacea may reach 2 dm in height in ungrazed areas, though plants growing on the tidal marshes are dwarfed (less than 3 cm in height). Ungrazed tillers of Carex

X <u>flavicans</u> are commonly 1.5-3.0 dm tall. Throughout the summer, leaves
develop sequentially from an apical meristem that is concealed at the centre of
each shoot near the ground surface. Even after a young leaf elongates
sufficiently to be visibly exserted from the centre of a tiller, its base remains
concealed by the bases of the older leaves which surround it. Leaves of <u>Carex</u>
<u>subspathacea</u> live for 30-45 days (Kotanen and Jefferies 1987, Chapter 3). The life
expectancy of a leaf of <u>C</u>. X <u>flavicans</u> is in excess of one year (Chapter 4).
Many leaves of both species survive the winter. Flowering occurs in both
species, but successful reproduction from seed is rare; most shoots in
established swards are produced vegetatively. Swards of both species consist
of mosaics of rhizomes produced by different ramets.

More information on the morphology and ecology of these species may be
found in Cayouette and Morisset (1985, 1986), Kotanen and Jefferies (1987), and
Sections 2.2.2, 3.2.2, and 4.2.2.

6.2.3. Demographic methods

6.2.3.1. <u>Carex</u> <u>subspathacea</u>

On 25-27 May, 1986, about 3 weeks before the beginning of hatch, two
pairs of 0.5 X 0.5 m plots were established in an area of salt marsh that had
been frequently grazed by Lesser Snow Geese in previous years. One additional
pair of plots was established in a heavily grazed area of the salt marsh on 4
June in order to increase the sample size of leaves. Wire netting was used to
construct a 0.6 X 0.6 X 0.5 m exclosure around one plot of each pair (the
"ungrazed" plot); the remaining ("grazed") plots were left open.

After the unexclosed plots had been heavily grazed by adult geese and

goslings in June, immediately after hatch, experimental shoots were selected within each plot with the aid of a removable 0.5 X 0.5 m metal quadrat strung with thin wire at intervals of 10 cm. The shoot closest to each of the 25 intersections of the crosswires was marked and subsequently identified with a small ring of thin, coloured wire set inconspicuously into the sediment. All leaves on each shoot were marked with distinctive patterns of small dots of ink in order to allow their re-identification. The length of each leaf was then measured to the nearest millimetre from its tip to the surface of the sediment. Both grazed and ungrazed plots were then exclosed to prevent geese from removing tissue before the next examination; this procedure was necessary in order to allow the accurate estimation of leaf elongation.

After one week, all plots were re-examined. Shoots were again located using the quadrat, and their leaves were measured. In order to preclude unconscious biases, re-measurement of leaves was done blind; that is, without the person doing the measurement being told the values obtained in the previous week. The measurer was told he was producing inaccurate results only if the values obtained obviously indicated a correctible error, such as measurement of the wrong shoot.

After re-measurement was complete, new grazed plots were established. Shoots were chosen and ringed in each of these plots, and their leaves were marked and measured. These plots were then exclosed until the next sampling. The grazed plots from the previous week were abandoned, but the ungrazed plots were retained. This procedure was repeated 5 times before the end of August at intervals of 6-10 days (Table 6.1.). On the fifth occasion, only 15 shoots per plot were sampled because of time constraints. One pair of plots was abandoned before the last sampling date because of damage by caribou.

Table 6.1.

Dates in 1986 on which lengths of leaves of <u>Carex</u> <u>subspathacea</u> and <u>Carex</u> X <u>flavicans</u> were recorded in open and exclosed plots at La Pérouse Bay.[a]

<u>Carex</u> <u>subspathacea</u>				<u>Carex</u> X <u>flavicans</u>			
Site 1	Site 2	Site 3	Number of sampling	Site 1	Site 2	Site 3	Number of sampling
July 8	July 9	–	–| 1	July 2	–	–	–| 1
July 16	July 16	–	–|	July 14	–	–	–|
July 16	July 16	–	–| 2	July 14	July 15	–	–| 2
July 22–23	July 22	–	–|	July 24	July 24	–	–|
July 23–24	July 22	July 25	–| 3	July 24	July 24	July 25	–| 3
Aug. 1	Aug. 1	Aug. 1	–|	Aug. 10	Aug. 9	Aug. 9	–|
Aug. 1	Aug. 1	Aug. 1	–| 4	Aug. 10	Aug. 9–10	Aug. 9–10	–| 4
Aug. 7	Aug. 7	Aug. 7	–|	Aug. 28	Aug. 28	Aug. 28	–|
–	Aug. 13	Aug. 13	–| 5				
–	Aug. 23	Aug. 23	–|				

[a] In cases where one sampling took 2 days, samplings were timed so that the interval between samplings was shorter for the grazed plot of the pair. This procedure should lead to a slightly more conservative test of the hypothesis that grazing increases leaf elongation.

These techniques allowed the determination of leaf elongation over short intervals for shoots in both plots which previously had been exclosed and plots which previously had been grazed. Elongation of each leaf was calculated as the increment in its measured length between samplings. Comparisons of lengths of senescent leaves between samplings suggested measurements were accurate to within 1-2 mm for a 10-20 mm leaf. Though this uncertainty is relatively great, it permitted the detection of differences in elongation large enough to be of ecological significance.

6.2.3.2. Carex X flavicans

The methods employed in the investigation of leaf elongation in Carex X flavicans were closely analogous to those used for C. subspathacea. On 23 May, 1986, one pair of 0.5 X 0.5 m plots was established at the edge of a fresh-water pond in a moss carpet containing a moderate density of shoots of C. X flavicans; one of these plots was exclosed. This site had been heavily grazed by geese in 1985. On 15 July, 1986, after grazing had begun, 25 shoots per plot were chosen with the aid of the removable quadrat and marked with wire rings. At intervals of 9-19 days, leaves on each shoot were marked and measured from the moss surface, and new grazed plots were established, as described above. Four samplings were performed before September (Table 6.1.).

In order to increase sample size, 2 additional pairs of plots were established in grazed moss carpets at the beginning of July, following hatch. Sampling began for one of these pairs in mid-July, and for the other in early August (Table 6.1.). It was hoped that this delay between the initial exclosure of the "ungrazed" plots and the first sampling would allow differences in rates of leaf elongation to develop between the grazed and exclosed treatments.

The accuracy of measurement was in the order of 2-3 mm for a 20-30 mm leaf.

6.2.4. Statistical methods

The elongation of a leaf was calculated as the increment in its length during a sampling interval. Leaves which had been grazed in exclosed plots before the exclosures were erected, or which were damaged following exclosure were excluded from all analyses. However, undamaged leaves which apparently decreased in length between samplings were included in order to allow the unbiased estimation of average elongation. The magnitude of such negative elongations rarely exceeded 2 to 3 mm. Leaves which appeared between samplings were not considered in the analyses, since their initial length was unknown. The initial length of such leaves was not likely to have been zero, since all leaves were concealed within their shoot until they became long enough to be visibly exserted (Section 2.2.). Leaves which died between samplings were also excluded from the analyses.

Since different pairs of plots were established at different times, since sampling intervals varied in duration, and since sample sizes were variable, data for each site and for each sampling interval were considered separately, rather than being unrealistically treated as replicates. Since rates of elongation varied with the age of the leaf, leaves were grouped into age classes; each age class was also considered separately. In each analysis, Class 1 consisted of the youngest leaf of each shoot at the beginning of a sampling interval. Class 2 consisted of the leaves which had been produced immediately before Class 1 leaves, as indicated by their position on the shoot. Similarly, leaves were placed in older age classes on the basis of their positions on each shoot. Since leaves of the older age classes elongated very

little, these were lumped together into Class 3 for $\underline{C}$. subspathacea and Class 4 for $\underline{C}$. X flavicans. Excluding overwintering leaves, the mean ages of successive classes of leaves differed by 10-14 days for $\underline{C}$. subspathacea and by 13-19 days for $\underline{C}$. X flavicans. On the first sampling, some Class 2 and possibly some Class 1 leaves had been produced in both species during the previous year. Following this initial sampling, all leaves placed in these respective classes had probably been produced in 1986.

The elongation of leaves of shoots in previously grazed plots was compared statistically with the elongation of leaves of shoots in previously ungrazed plots for each site, age class, and sampling interval. No attempt was made to distinguish between grazed and ungrazed leaves in grazed plots, since this would have made analysis very complex, and since the behaviour of grazed tillers was considered to be of greater interest than the behaviour of grazed leaves. If data could be transformed so as to approach a normal distribution and to pass the F_{max} test for homogeneity of variance, a one-way analysis of variance (ANOVA) was used. Otherwise, the nonparametric Wilcoxon test was employed (corrected for ties) (Sokal and Rohlf 1981). Other statistical tests were employed when required.

Cumulative error is a problem when conducting multiple tests of significance: when $\underline{c}$ independent statistical tests are performed, each at the $\underline{a}$ level of significance, the probability that at least one test will be spuriously significant is $1-(1-a)^C$ (Kirk, 1982). Consequently, among the multiple tests described below, isolated significant results should be treated with suspicion. Highly significant results (P<0.001) and consistent trends in significance are more useful in the interpretation of collections of multiple statistical tests.

6.3 Results

6.3.1. Carex subspathacea

Rates of elongation of leaves of $\underline{C}$. subspathacea declined with age in both grazed and exclosed plots (Tables 6.2., 6.3., 6.4., 6.5., 6.6.). Average rates of elongation for the youngest leaf on each shoot at the beginning of a sampling interval (the "Class 1" leaf) ranged between 0.5 and 1.7 mm day^{-1} during the subsequent 6-10 days, depending upon the plot, sampling date, and treatment. The average rates of elongation between samplings for the next youngest class of leaves ("Class 2" leaves) ranged between 0.1 and 1.0 mm day^{-1}. Average rates of elongation of older leaves ("Class 3" leaves) were generally less than 0.3 mm day^{-1}, leading to total elongations less than the margin of error of measurement. Consequently, elongation of a leaf was essentially complete by the time it was considered as Class 3; that is, by an age of about 30 to 42 days. Leaves produced between samplings probably elongated at rates comparable to those of Class 1 leaves, though their elongations could not be measured (Section 6.2.4).

Grazing did not have consistent effects upon the elongation of leaves. Out of a total of 36 comparisons of paired plots, in 4 cases the elongation of leaves in grazed plots significantly exceeded the elongation in ungrazed plots; in 5 cases, this trend was significantly reversed (Tables 6.2., 6.3., 6.4., 6.5., 6.6.). Only 1 of the cases in which grazing apparently increased elongation occurred in Class 1 leaves; the other 3 occurred in Class 2 and Class 3 leaves, in which the absolute difference between treatments was relatively small. Of the cases in which grazing significantly decreased elongation, 4 occurred in Class 1 leaves.

Table 6.2.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> <u>subspathacea</u> between 8 July and 16 July, 1986 (the first sampling interval) in open and exclosed plots in an intertidal marsh at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which have been used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

		site 1	site 2
class	treatment	mean SEM n	mean SEM n
1	grazed	8.4 +/- 0.6 (23)	7.3 +/- 0.5 (24)
	ungrazed	11.0 +/- 0.6 (24)	7.5 +/- 0.7 (23)
	comparison	$F_{1,45} = 8.57^{**}$	$F_{1,45} = 0.05$
2	grazed	2.5 +/- 0.8 (24)	3.1 +/- 0.5 (25)
	ungrazed	3.5 +/- 0.8 (22)	2.9 +/- 0.5 (24)
	comparison	$F_{1,44} = 0.76$	$F_{1,47} = 0.07$
3	grazed	-0.4 +/- 0.4 (20)	0.4 +/- 0.2 (35)
	ungrazed	-1.1 +/- 0.4 (24)	0.9 +/- 0.3 (35)
	comparison	$F_{1,42} = 1.73$	$F_{1,68} = 2.66$

Table 6.3.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> <u>subspathacea</u> between 16 July and 23 July, 1986 (the second sampling interval) in open and exclosed plots in an intertidal marsh at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which have been used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 1 mean SEM n	site 2 mean SEM n
1	grazed	6.1 +/- 0.7 (23)	4.3 +/- 0.3 (24)
	ungrazed	7.8 +/- 0.5 (25)	4.2 +/- 0.4 (25)
	comparison	$F_{1,46} = 3.81$	$F_{1,47} = 0.01$
2	grazed	1.8 +/- 0.7 (22)	1.9 +/- 0.3 (24)
	ungrazed	2.2 +/- 0.7 (24)	1.3 +/- 0.3 (22)
	comparison	$F_{1,44} = 0.16$	$F_{1,44} = 2.18$
3	grazed	-0.5 +/- 0.3 (37)	0.4 +/- 0.1 (53)
	ungrazed	0.2 +/- 0.3 (34)	0.2 +/- 0.2 (38)
	comparison	$F_{1,69} = 2.56$	$t_s = 1.30$

Table 6.4.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> <u>subspathacea</u> between 22 July and 1 August, 1986 (the third sampling interval) in open and exclosed plots in an intertidal marsh at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which have been used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 1 mean SEM n	site 2 mean SEM n	site 3 mean SEM n
1	grazed	6.8 +/- 0.6 (25)	6.5 +/- 0.7 (25)	4.9 +/- 0.4 (23)
	ungrazed	9.8 +/- 0.9 (22)	7.2 +/- 0.6 (24)	6.0 +/- 0.4 (24)
	comparison	$F_{1,45} = 8.37^{**}$	$F_{1,47} = 0.51$	$F_{1,45} = 4.10^{*}$
2	grazed	2.2 +/- 0.7 (25)	3.0 +/- 0.8 (24)	0.6 +/- 0.5 (25)
	ungrazed	3.0 +/- 0.8 (25)	0.8 +/- 0.3 (22)	3.0 +/- 0.5 (23)
	comparison	$F_{1,48} = 0.64$	$t_s = 2.14^{*}$	$F_{1,46} = 11.89^{**}$
3	grazed	-0.1 +/- 0.4 (29)	0.1 +/- 0.3 (35)	-0.8 +/- 0.3 (26)
	ungrazed	-0.2 +/- 0.4 (29)	-0.1 +/- 0.4 (22)	-0.4 +/- 0.4 (33)
	comparison	$F_{1,56} = 0.06$	$F_{1,55} = 0.17$	$F_{1,57} = 0.93$

Table 6.5.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> <u>subspathacea</u> between 1 August and 7 August, 1986 (the fourth sampling interval) in open and exclosed plots in an intertidal marsh at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which have been used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 1 mean SEM n	site 2 mean SEM n	site 3 mean SEM n
1	grazed	10.4 +/- 0.8 (24)	6.2 +/- 0.4 (25)	7.0 +/- 0.4 (25)
	ungrazed	8.3 +/- 0.9 (22)	6.8 +/- 0.9 (24)	9.3 +/- 0.4 (23)
	comparison	$F_{1,44} = 3.24$	$t_s = 0.54$	$F_{1,46} = 15.67***$
2	grazed	6.1 +/- 0.6 (24)	2.1 +/- 0.4 (25)	2.8 +/- 0.6 (24)
	ungrazed	2.1 +/- 0.7 (24)	1.5 +/- 0.5 (24)	3.6 +/- 0.7 (24)
	comparison	$F_{1,46} = 18.82***$	$F_{1,47} = 0.85$	$F_{1,46} = 0.66$
3	grazed	1.6 +/- 0.3 (51)	0.3 +/- 0.3 (32)	1.2 +/- 0.4 (34)
	ungrazed	0.5 +/- 0.3 (40)	0.9 +/- 0.4 (31)	1.4 +/- 0.2 (26)
	comparison	$F_{1,89} = 7.33**$	$F_{1,61} = 1.32$	$t_s = 0.98$

Table 6.6.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of Carex subspathacea between 13 August and 23 August, 1986 (the fifth sampling interval) in open and exclosed plots in an intertidal marsh at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which were used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 2 mean SEM n	site 3 mean SEM n
	grazed	7.5 +/- 0.5 (14)	8.9 +/- 1.1 (14)
1	ungrazed	4.7 +/- 0.5 (15)	7.1 +/- 1.1 (15)
	comparison	$F_{1,27} = 15.52$***	$F_{1,27} = 1.25$
	grazed	3.3 +/- 0.4 (12)	3.7 +/- 0.6 (13)
2	ungrazed	2.5 +/- 0.7 (13)	3.3 +/- 1.0 (14)
	comparison	$t_s = 1.27$	$F_{1,25} = 0.12$
	grazed	0.7 +/- 0.2 (10)	2.3 +/- 1.0 (9)
3	ungrazed	0.2 +/- 0.5 (18)	1.6 +/- 0.4 (10)
	comparison	$t_s = 1.07$	$t_s = 0.38$

If all sites at all sampling intervals were treated as replicates, it was possible to perform independent Friedman Rank tests for each age class of leaves. These tests examined the null hypothesis that the mean elongations of leaves in grazed plots did not differ from the mean elongations in the ungrazed plots with which they were paired. These three tests did not demonstrate any significant difference between grazed and ungrazed plots for any age class of leaves (P>0.05 in each test).

6.3.2. Carex X flavicans

Rates of elongation of leaves of C. X flavicans declined with age in both grazed and ungrazed leaves (Tables 6.7., 6.8., 6.9., 6.10.). Average rates of elongation for Class 1 leaves ranged between 0.6 and 3.5 mm day^{-1}, depending upon the plot, sampling date, and treatment. Average rates of elongation ranged between 0.5 and 2.5 mm day^{-1} for Class 2 leaves and between 0.0 and 0.6 mm day^{-1} for Class 3 leaves. Older leaves (Class 4) elongated very little: averages were less than 0.3 mm day^{-1}. Consequently, the elongation of a leaf extended over at least 52 to 76 days. Leaves produced between samplings probably elongated at rates comparable to those of Class 1 leaves, though their elongations could not be measured (Section 6.2.4.).

Grazing did not have consistent effects upon the elongation of leaves. Out of a total of 36 comparisons of paired plots, in 4 cases the elongation of leaves in grazed plots significantly exceeded the elongation in ungrazed plots; in 7 cases, this trend was significantly reversed (Tables 6.7., 6.8., 6.9., 6.10.). Only 2 of the cases in which grazing increased elongation involved Class 1 leaves or Class 2 leaves; the others involved Class 3 or 4 leaves, in which the absolute differences between treatments were relatively small. Of

Table 6.7.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> X <u>flavicans</u> between 2 July and 14 July, 1986 (the first sampling interval) in open and exclosed plots beside fresh-water ponds at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which were used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

site 1

class	treatment	mean	SEM	n
	grazed	38.1 +/- 2.0 (25)		
1	ungrazed	41.8 +/- 1.5 (25)		
	comparison	$F_{1,48} = 2.17$		
	grazed	29.7 +/- 2.2 (25)		
2	ungrazed	28.1 +/- 2.3 (25)		
	comparison	$F_{1,48} = 0.24$		
	grazed	4.7 +/- 1.8 (25)		
3	ungrazed	3.6 +/- 0.6 (25)		
	comparison	$t_s = 0.40$		
	grazed	0.5 +/- 0.4 (22)		
4	ungrazed	1.2 +/- 0.4 (22)		
	comparison	$F_{1,42} = 1.82$		

Table 6.8.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> X <u>flavicans</u> between 14 July and 24 July, 1986 (the second sampling interval) in open and exclosed plots beside fresh-water ponds at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which were used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 1 mean SEM n	site 2 mean SEM n
1	grazed	24.2 +/- 1.2 (25)	14.7 +/- 1.2 (25)
	ungrazed	28.7 +/- 1.5 (23)	18.2 +/- 1.7 (25)
	comparison	$F_{1,46} = 5.52$*	$F_{1,48} = 2.94$
2	grazed	16.0 +/- 2.1 (24)	10.3 +/- 1.6 (24)
	ungrazed	16.0 +/- 2.1 (25)	13.7 +/- 1.7 (15)
	comparison	$F_{1,47} = 0.00$	$F_{1,37} = 1.35$
3	grazed	2.3 +/- 0.4 (24)	1.3 +/- 0.4 (24)
	ungrazed	0.8 +/- 0.6 (25)	0.7 +/- 0.6 (6)
	comparison	$t_s = 2.72$*	$F_{1,28} = 0.74$
4	grazed	1.4 +/- 0.2 (38)	2.5 +/- 0.6 (22)
	ungrazed	-0.6 +/- 0.5 (27)	1.4 +/- 0.5 (5)
	comparison	$t_s = 3.81$*	$t_s = 0.89$

Table 6.9.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> X <u>flavicans</u> between 24 July and 9 August, 1986 (the third sampling interval) in open and exclosed plots beside fresh-water ponds at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which were used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 1 mean SEM n	site 2 mean SEM n	site 3 mean SEM n
1	grazed	22.7 +/- 2.6 (25)	17.6 +/- 1.8 (23)	25.0 +/- 2.4 (22)
	ungrazed	34.6 +/- 2.3 (25)	26.1 +/- 2.2 (23)	29.3 +/- 1.8 (23)
	comparison	$F_{1,48} = 11.67**$	$F_{1,44} = 9.31**$	$F_{1,43} = 2.03$
2	grazed	12.3 +/- 2.9 (24)	10.7 +/- 2.0 (24)	8.6 +/- 2.0 (24)
	ungrazed	18.6 +/- 2.2 (25)	14.6 +/- 2.8 (17)	23.9 +/- 2.5 (20)
	comparison	$F_{1,47} = 3.08$	$F_{1,39} = 1.36$	$F_{1,42} = 23.8***$
3	grazed	0.7 +/- 0.7 (21)	0.7 +/- 0.8 (20)	1.9 +/- 1.4 (21)
	ungrazed	0.6 +/- 0.5 (25)	0.0 +/- 0.8 (8)	8.9 +/- 1.7 (10)
	comparison	$F_{1,44} = 0.01$	$F_{1,26} = 0.26$	$F_{1,29} = 8.85**$
4	grazed	0.3 +/- 0.7 (24)	-0.2 +/- 1.1 (12)	1.3 +/- 1.2 (14)
	ungrazed	-0.3 +/- 0.4 (29)	0.0 +/- 0.9 (6)	2.0 +/- 1.0 (2)
	comparison	$t_s = 0.32$	$F_{1,16} = 0.01$	$t_s = 0.79$

Table 6.10.

Means, one standard error (SEM), and sample sizes (n) of the measured elongation of leaves of <u>Carex</u> X <u>flavicans</u> between 9 August and 28 August, 1986 (the fourth sampling interval) in open and exclosed plots beside fresh-water ponds at La Pérouse Bay. Also indicated are the results of analyses of variance (F values) or Wilcoxon rank tests (t_s values), which were used to compare data from previously grazed plots with corresponding data from previously ungrazed plots.

class	treatment	site 1 mean SEM n	site 2 mean SEM n	site 3 mean SEM n
	grazed	23.2 +/- 1.7 (22)	11.5 +/- 1.6 (25)	30.2 +/- 2.7 (22)
1	ungrazed	18.3 +/- 1.0 (25)	17.5 +/- 1.5 (23)	17.1 +/- 1.3 (23)
	comparison	$F_{1,45} = 6.91*$	$F_{1,46} = 7.05*$	$F_{1,43} = 7.42**$
	grazed	12.9 +/- 2.0 (22)	9.8 +/- 1.6 (20)	19.4 +/- 2.7 (22)
2	ungrazed	15.5 +/- 1.4 (25)	15.3 +/- 1.3 (22)	14.6 +/- 1.4 (22)
	comparison	$F_{1,45} = 1.20$	$F_{1,40} = 7.57**$	$F_{1,42} = 0.69$
	grazed	7.0 +/- 1.0 (18)	5.7 +/- 1.3 (11)	6.8 +/- 1.4 (17)
3	ungrazed	6.5 +/- 1.0 (23)	6.2 +/- 1.1 (14)	6.3 +/- 1.0 (18)
	comparison	$F_{1,39} = 0.13$	$F_{1,23} = 0.08$	$F_{1,33} = 0.08$
	grazed	5.3 +/- 0.5 (21)	4.0 +/- 1.9 (15)	4.7 +/- 0.6 (15)
4	ungrazed	3.6 +/- 0.7 (45)	3.5 +/- 0.9 (11)	4.2 +/- 0.7 (10)
	comparison	$t_s = 1.90$	$t_s = 0.34$	$F_{1,23} = 0.31$

the cases in which grazing significantly decreased elongation, all but 1 involved Class 1 or 2 leaves.

If all sites at all samplings were treated as replicates, it was possible to perform Friedman Rank tests for each age class of leaves. These four tests failed to demonstrate a significant difference between grazed plots and ungrazed plots for any age class of leaves ($P>0.05$ in each test).

6.4. Discussion

The rates of elongation of leaves of both Carex subspathacea and Carex X flavicans declined rapidly as leaves aged. Growth of leaves of the oldest age classes was small when compared to the rapid elongation of young leaves (Tables 6.2., 6.3., 6.4., 6.5., 6.6., 6.7., 6.8., 6.9., 6.10.). Based upon the positions of the growing leaves on each shoot, leaves of C. subspathacea continued to elongate measureably for about 30 to 42 days following their exsertion. Assuming that the average lifespan of leaves of C. subspathacea ranges from 30 days to 47 days (Kotanen and Jefferies 1987; Chapter 3), this result implies that elongation continued at a diminishing rate through most of the life of each leaf. Based upon similar criteria, leaves of C. X flavicans were estimated to elongate for even longer periods: at least 52 to 76 days. The result suggests that leaves of C. X flavicans produced as early as the beginning of July, only a few weeks after thaw, were still actively elongating at the return of sub-zero daytime temperatures in September. Such a long period of growth is consistent with the observation that the average lifespan of a leaf of this hybrid is in excess of one growing season (Chapter 4). There is circumstantial evidence that leaves produced late in the summer continued to elongate during the following summer, as "mature" leaves present at the first

sampling date continued to elongate during July and August. These patterns of growth resemble those described for leaves of other arctic carices. For example, the first cohort of leaves of _Eriophorum vaginatum_ L. produced in the spring in northern Alaska elongated for about 3 months before senescence began; later cohorts overwintered and resumed elongation in the spring (Jonasson and Chapin 1985). Leaves of _Carex aquatilis_ Wahl. shared a similar pattern of development (Johnson and Tiezen 1976; Archer and Tiezen 1980).

Although the effects upon the vegetation of foraging by geese tend to be unevenly distributed in both space and time (Jefferies 1987; Kotanen 198N; Chapter 2), all study sites were intensely grazed between the hatch of the goslings in late June and the departure of the geese in mid-August. About 49% of the leaves of _C. subspathacea_ which were produced at nearby sites on the salt marsh in 1984 were clipped by the geese before their deaths or before the final sampling date in September (Kotanen and Jefferies 1987; Chapter 3). The corresponding figure for leaves of _C._ X _flavicans_ in 1985 was 76% (Chapter 4). On average, leaves of _C. subspathacea_ were grazed at about 19 days of age in 1984, while rapid elongation must have been still occurring (Kotanen and Jefferies 1987; Chapter 3). Although the equivalent figure is not available for _Carex_ X _flavicans_, the long duration of elongation of leaves of this hybrid suggests that most of these leaves were grazed while they were still extending. Since the geese rarely destroyed the intercalary meristems, leaves continued to expand following grazing, re-establishing their photosynthetic surface areas. However, unless the average rates of elongation of leaves were greater in grazed shoots than in shoots which escaped herbivory, this regrowth of leaves would not in itself maintain the photosynthetic surface area of a grazed tiller at the same value as that of an ungrazed tiller.

Most comparisons indicated that grazing had no significant effect upon the

elongation of leaves. In a few cases, the elongation of leaves of shoots in a grazed plot was significantly greater than or less than the elongation of leaves of shoots in the accompanying ungrazed plot; however, no consistent trends were apparent. These conclusions were not altered if only the plots established before hatch were considered. Although study sites were chosen to be as initially similar as possible, the few significant differences which occurred may in part have been spurious products of uncontrolled environmental differences between paired plots. In addition, one in twenty statistical tests might have been expected to be significant at the 5% level, even if grazing truly had no effects upon elongation. In any case, grazing did not consistently affect the elongation of leaves of either species within the period of study.

If a plant is to survive in spite of frequent grazing, it must replace the photosynthetic tissues lost to its herbivores. In some species of grasses and sedges, the increased elongation of leaves in response to herbivory is important in this replacement of grazed tissue. For example, a series of studies of the tropical graminoids Kyllinga nervosa Steud., Panicum coloratum L., and Themeda triandra L. have consistently revealed significantly increased rates of elongation of the leaves of these species in response to simulated grazing (Wallace 1981; McNaughton et al. 1983; Coughenour 1985; Wallace et al. 1985). In contrast, this study indicates that grazed shoots of Carex subspathacea and Carex X flavicans must replace lost tissue without similar stimulation of growth. Although the ability of leaves to regrow from their basal meristems may reduce the damage done by herbivores to these sedges (Coughenour 1985), the key response which can allow individuals of these species to maintain their photosynthetic surface areas in spite of grazing is the increased production of leaves (Kotanen and Jefferies 1987; Chapters 3,4).

In summary, shoots of neither Carex subspathacea nor Carex X flavicans

respond to herbivory by geese within one season with increased rates of elongation of leaves.   Instead, replacement of aboveground tissue removed by geese primarily occurs through the enhancement of rates of production of new leaves (Kotanen and Jefferies 1987; Chapters 3,4).

[illegible bibliography entries]

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CHAPTER 7:   GENERAL DISCUSSION

7.1.   Reprise of Objectives

As stated in Section 1.4., the primary objectives of this study were as follows:

(1) The documentation of the patterns of growth of Carex aquatilis, Carex subspathacea, and Carex X flavicans, and of patterns of foraging by the geese

(2) The description of changes which herbivory produces in the demography of organs of these carices, including:

    a. the production and turnover of leaves

    b. the production and turnover of shoots

    c. the elongation of leaves

(3) The comparison among these carices of their growth responses to herbivory

(4) The prediction of the fates of heavily exploited individuals and communities.

In the following discussion, the results of this study and their implications are summarized for each of these objectives in turn.

7.2.   Patterns of growth and patterns of foraging

Shoots of Carex aquatilis, Carex subspathacea, and Carex X flavicans were perennial, probably living for several years (Chapter 5). All three species were

strongly clonal, producing new tillers from their subterranean rhizomes. Rates
of emergence of new shoots were greatest in the spring and fall, though some
emergence occurred throughout the year (Chapter 5). Growth of shoots following
melt was rapid, especially in plants of Carex aquatilis and Carex X flavicans
which were growing in fresh-water pools. Flowering of all three species
occurred from late June to mid-July, but generally was uncommon within the
study areas (Chapter 5). Flowers probably developed from primordia initiated
in the previous fall. Although flowering terminated the growth of a shoot, it
was not frequent enough in Carex subspathacea or Carex X flavicans to be as
important a form of mortality as the loss of vegetative shoots to geese and to
senescence (Chapter 5). In Carex aquatilis, the greater frequency of flowering
suggested a greater contribution to the mortality of shoots (Chapter 5). Most
new shoots were probably vegetative in origin.

Shortly after spring melt, overwintered leaves resumed elongation from
their green bases, and the production of new leaves commenced (Kotanen and
Jefferies 1987; Chapters 3,4). A newly produced leaf elongated through most of
its life, which ranged from 30 to 45 days for Carex subspathacea to over a year
for the other two species (Kotanen and Jefferies 1987; Chapters 3,4,6). Leaves
were produced at regular intervals throughout the growing season (Kotanen and
Jefferies 1987; Chapters 3,4).

These overall patterns of growth were similar for plants of both grazed and
ungrazed swards, and resembled those described for other arctic sedges (Shaver
and Billings 1975; Johnson and Tiezen 1976; Billings et al. 1978; Shaver et al.
1979; Archer and Tiezen 1980; Chapin and Chapin 1981; Fetcher and Shaver 1983;
Robertson and Woolhouse 1984; Jonasson and Chapin 1985). Most of the species
discussed in these studies are also clonal perennials with continuous production
of leaves and prolonged elongation of leaves. The most unusual feature of the

growth of the carices investigated in this study was the extremely short lifespan of leaves of Carex subspathacea – only 45 to 46 days in ungrazed plots (Kotanen and Jefferies 1987; Chapter 3). This rate is exceptional among arctic sedges, in which leaves typically survive for more than one year (Johnson and Tiezen 1976; Archer and Tiezen 1980; Chapin and Chapin 1981; Fetcher and Shaver 1983; Jonasson and Chapin 1985), although shoots of the grass Puccinellia phryganodes growing at La Pérouse Bay have leaf lifespans of 25–43 days (Bazely and Jefferies 198Nb). It has been suggested that long lifespans of leaves allow the efficient recycling of nutrients from senescing tissues to younger, rapidly growing tissues (Coley et al. 1985; Jonasson and Chapin 1985). If the short lifespans of leaves of C. subspathacea are not simply an intrinsic characteristic of this species, an explanation for the short life of leaves may lie in the nitrogen made available on the salt marsh by the geese, which reduces the the need for the efficient internal recycling of nutrients and the long life of leaves (Cargill and Jefferies 1984a; Bazely and Jefferies 1985, 198Na; Section 2.3.1.).

The foraging behaviour of the geese changed during the season. Upon their arrival at La Pérouse Bay in mid-May, before snowmelt, little green above-ground plant tissue was available. At this time of year, both resident geese and the thousands of migrants which stage in this area fed primarily on roots, rhizomes, and shoot bases of graminoids (Chapter 2). Areas of Carex subspathacea on the salt marsh were stripped, exposing patches of the under-lying sediment (Section 2.3.1.). In fresh-water areas, shoots of Carex aquatilis and Carex X flavicans were pulled, their succulent bases consumed, and the remainder of the shoot discarded. Feeding by breeding birds declined during incubation, but resumed following the hatch of the goslings in mid-June (Chapter 2). Following hatch, the grazing of leaves was the most common form

of feeding. Although the most intensive feeding occurred on C. subspathacea on the salt marsh, where the vegetation was maintained at a height of around 2 cm, heavily grazed swards of Carex X flavicans were also evident around fresh-water ponds (Chapter 2). Leaves of Carex aquatilis were grazed to a much lesser extent. Grazing of leaves remained the major form of feeding until the departure of the geese in the fall, although shoot pulling and grubbing resumed as the above-ground tissues of the sedges began to senesce, shortly before the departure of the geese, (Chapter 2).

Earlier studies of herbivory at La Pérouse Bay have emphasized the post-hatch feeding of the geese on the salt marsh (Jefferies et al. 1979; Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985, 1986, 198Na, 198Nb). This study provides the first detailed description of patterns of feeding before hatch, and of the feeding on the vegetation of fresh-water habitats (Chapter 2). Grubbing of shoots and rhizomes in early spring and in the fall is probably of considerable importance to both resident and migrant geese, allowing migrants to arrive on their breeding grounds with sufficient stored resources for successful reproduction, and providing residents with a source of food at a time of year when green tissue is scarce but when the metabolic demands upon the breeding geese are great (Sections 2.1.2., 2.1.3.). Although grazing on the salt marshes of La Pérouse Bay is undoubtably the most important source of forage for the colony following hatch, grazing in fresh-water habitats plays a significant secondary role. Small numbers of geese continually graze in these habitats throughout the summer, and much of the remainder of the colony forages in these areas while taking refuge from foul weather or predators. Since 1968, the La Pérouse Bay colony has grown from about 1200 pairs to about 7000 pairs (Section 2.3.1.). If this trend continues, foraging by the expanding colony in fresh-water areas may become increasingly prevalent, especially if the salt

marshes are already near their carrying capacity as suggested by Cargill (1981).

7.3. Responses to herbivory of above-ground organs of the species studied

The photosynthetic tissues of carices which are removed by herbivores may be replaced from three sources: intercalary meristems, shoot apical meristems, and the axillary meristems of rhizomes (Sections 1.1.2., 1.2.3.2.). Growth from these sources respectively leads to the elongation of existing leaves, the production of new leaves, and the production of new leafy shoots. Following grazing, increased rates of elongation of leaves and rates of production of leaves and shoots have been reported for many graminoids (Section 1.2.3.2.). For example, Bazely and Jefferies (198Nb) found that rates of both the production of axillary shoots and the production of leaves on axillary shoots were greater in swards of Puccinellia phryganodes which were grazed by Lesser Snow Geese than in swards which were protected from grazing, although the life expectancies of leaves of grazed shoots were also reduced. In contrast, in this study, neither C. subspathacea nor C. X flavicans nor C. aquatilis responded within one year to herbivory with an increased production of shoots (Chapter 5). Although geese rarely removed entire leaves of these sedges, grazing did diminish the life expectancies of leaves of both Carex subspathacea and Carex X flavicans (Kotanen and Jefferies 1987; Chapters 3,4), but failed to consistently increase their rates of elongation (Chapter 6). Consequently, the only component of the above-ground production of these carices which was significantly increased by herbivory by the geese was the production of leaves of C. subspathacea and C. X flavicans (Kotanen and Jefferies 1987; Chapters 3,4).

This conclusion should be treated with some caution. The failure to

detect any consistently significant effects of herbivory upon the rates of elongation of leaves or the production of shoots does not necessarily demonstrate that such effects were absent (Popper 1959). However, there is reason to believe that even if such effects occur, they may be relatively unimportant responses within a season. The large sample sizes involved in the statistical tests (generally hundreds of shoots) imply that the statistical power of these tests was generally high. Consequently, any undetected effects that herbivory might have had upon the elongation of leaves or upon the production of shoots probably were too small to be ecologically significant.

It is possible that the effects of herbivory upon the production of shoots and the elongation of leaves may be expressed too slowly to have become apparent within the duration of these experiments. For example, the minimal time required for a dormant bud on a rhizome to be activated and to grow sufficiently to emerge from the ground is unknown. It is likely to be in the order of months. Similarly, if plants which were previously used as forage are protected from herbivory, changes in their rates of production of shoots or in the rates of elongation of their leaves may not occur immediately, if these changes reflect gradual alterations in the availability of resources for growth. For example, changes in the size of the internal carbohydrate pool of the plant, the availability of nitrogen, and the availability of light occur gradually following the exclosure of a sward. Consequently, differences between grazed plots and newly exclosed plots may be slow to develop. The "indirect" effects of herbivory are important in determining the growth responses of grazed plants (Sections 1.2., 2.3.1.). Delayed responses of individual plants to herbivory may be important in an explanation of differences between the growth of plants from communities with different histories of grazing. Such responses may also be important in determining whether plant communities can

persist despite the activities of herbivores (Sections 1.2.1., 7.5.). However, these processes are not directly responsible for the rapid replacement by individual plants of the photosynthetic tissues consumed by the geese.

Experimental procedures often manipulate the indirect effects of herbivore activity, including the correlated changes in light, water, and nutrient regimes which herbivory can produce, as well as the direct effects of the removal of tissue by herbivores (Section 1.2.). Previous studies at La Perouse Bay have demonstrated that the foraging activities of the geese significantly increase the net above-ground primary production (NAPP) of Carex subspathacea (Cargill and Jefferies 1984b) in comparison with the NAPP of exclosed plots. The enhanced production of leaves is the only morphological response of grazed plants which could be responsible for this increase. Natural examples of herbivory increasing the NAPP of plant communities are unusual, and generally involve an indirect effect of herbivore activity which compensates for the damage which herbivory does to the plants (Section 1.2.1.2.). For example, the accelerated cycling of nutrients has been implicated in aquatic algal communities in which herbivory stimulates production (McDonald 1985; Bergquist and Carpenter 1986; Sterner 1986). Increased production in grassland communities of the Serengeti plains which are grazed by large ungulates may be related to a variety of mechanisms, including the accelerated cycling of nutrients and the reduction of evapotranspiration (McNaughton 1976, 1979a,b, 1983, 1984, 1985). Similarly, the enhancement of NAPP by geese at La Perouse Bay is not a product of grazing per se, but a result of the geese accelerating the cycling of nitrogen and promoting nitrogen fixation by cyanobacteria in this nitrogen-deficient environment (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985, Jefferies 1987; Bazely and Jefferies 198Na; Section 2.3.1.). When shoots of Puccinellia phryganodes are clipped without the addition of

nutrients, their leaf production is significantly reduced (Jefferies 1987; Sadul 1987). It is not known whether the increased production of leaves by shoots of Carex X flavicans when grazed is a product of similar goose-mediated changes in the availability of nitrogen, or whether it also leads to an increased NAPP in grazed fresh-water habitats. Densities of droppings rivalling those of the intertidal flats occur in these grazed areas, which suggests that processes similar to those that occur on the salt marshes may be taking place in the fresh-water habitats used by the geese.

A general problem for the interpretation of demographic data lies in the difficulty of extrapolating the results to the level of the population or the community. The failure to recognize that individuals, populations, and communities at the same location often respond in contrasting ways to herbivory has frequently led to confusion; it is important to recognize that processes at one of these levels of biological organization often cannot easily be inferred from processes at any of the other levels (Crawley 1983; Belsky 1987; Section 1.1.1.). For example, Carex aquatilis, C. subspathacea, and C. X flavicans growing at La Pérouse Bay were all strongly clonal; no evidence was found for successful sexual reproduction in any of these species (Section 2.2.). The age and extent of clones of these species is unknown, but graminoid clones may extend over hectares and be hundreds of years old (Harper 1977); it is certainly conceivable that all of the shoots at each study site represented only one genotype. The existence of extensive clones would suggest that some of the site-to-site variability detected in this study may have actually been genotype-to-genotype variability, but such a finding would not demand any important modifications of other conclusions. However, the presence of large clones would necessitate much careful experimental design before demographic data could be applied to the study of the population biology of these sedges.

For example, the degree to which different genotypes differ in their morphology or production cannot currently be assessed.

Extrapolation of demographic data to the level of the community is even more difficult. Though grazing increased the production of leaves of Carex X flavicans (Chapter 4), this need not necessarily translate to an increased net above-ground primary production even for monocultures of this species. Production of leaves may occur at the expense of decreased production of other tissues, leading to less overall production of biomass (Belsky 1986,1987). Since neither the elongation of leaves nor the production of shoots significantly declined in grazed plots (Chapters 4,5,6), it seems likely that grazing may at least increase the above-ground component of production. Little information exists on the effects of grazing by geese on the below-ground tissues of any of the carices studied; it is possible that increased leaf production might occur at the expense of the production of roots or rhizomes, ultimately leading to a decline in above-ground production as well. Although Cargill and Jefferies (1984b) did not detect such an effect in Carex subspathacea, the growth of roots of other species of graminoids is commonly inhibited by grazing (Belsky 1986, 1987). The growth of below-ground tissues is an important component of the responses of plants to herbivory; however, it may be argued that the critical component of primary production in studies of plant-herbivore interactions is that which is actually available to the herbivore. In this view, the responses of below-ground tissues to herbivory are important to this study only through their contribution to the more easily measured responses of above-ground tissues.

7.4. Comparisons among the study species of responses to herbivory

Carex aquatilis, Carex subspathacea, and Carex X flavicans are morphologically similar and closely related (Cayouette and Morisset 1985; Section 2.2.). The responses of these three species to herbivory were also qualitatively very similar, though the lack of information about the demography of leaves of C. aquatilis precludes a complete comparison. There were small quantitative differences between the effects of grazing on the leaf production of Carex subspathacea and of Carex X flavicans. The enhancement of the leaf production of Carex subspathacea was relatively greater, more highly significant, more strongly associated with grazing, and more consistent among sites than corresponding values of leaf production for C. X flavicans (Kotanen and Jefferies 1987; Chapters 3,4). Together, these differences suggest that the responses of C. X flavicans to herbivory were weaker and less predictable than those of Carex subspathacea. Since the habitats of these species differed in many environmental characteristics, and since they were investigated in different years with slightly different methods, there is no reason to believe that these small differences were attributable solely to the interactions between these species and the geese. However, differences between patterns of foraging by the geese in intertidal and fresh-water habitats may have produced these different responses. On the salt marshes, the increased production of leaves of C. subspathacea in grazed swards was a consequence of the additional nitrogen which the geese made available for plant growth (Sections 2.3.1, 7.3.). Even if the geese played a similar role in fresh-water communities, the relatively small numbers of birds which regularly foraged in fresh-water areas may have been insufficient to have increased the availability of nitrogen, and their relatively patchy foraging may have

resulted in less consistent stimulation of the growth of plants (Kotanen 198N; Section 2.3.1.). When the geese did make significantly more nutrients available in fresh-water areas, the greater longevities of leaves of Carex X flavicans imply the demographic responses of leaves would have been more sluggish in the case of this species than in the case of C. subspathacea (Kotanen and Jefferies 1987; Chapters 3,4). Additional research is required before any of these hypotheses can be rejected.

7.5. The fates of heavily exploited individuals and communities

Sedge communities at La Pérouse Bay appear to be maintained by the activities of grazing geese. The net annual above-ground primary production of Carex subspathacea is increased by the grazing of leaves (Section 2.3.1., 7.3.). The production of leaves by shoots of both C. subspathacea and C. X flavicans is significantly greater in grazed plots than within exclosures (Kotanen and Jefferies 1987; Chapters 3,4; Section 7.3.). Grazing by the geese leads to the exclusion or elimination of invading species of plants from intertidal communities, retarding succession and maintaining the grazing flats (Cargill and Jefferies 1984b; Bazely and Jefferies 1986; Section 2.3.1.); the low numbers of species per unit area of grazed swards in fresh-water areas may be a similar product of "weeding" by geese. However, Lesser Snow Geese also locally destroy areas of forage species within both fresh-water and intertidal communities (Jefferies 1987; Section 2.3.1.). Despite the difficulties in extrapolating between levels of biological organization (Crawley 1983; Belsky 1987; Section 7.3.), the morphological responses of forage plants to herbivory by the geese may provide clues to some of the factors determining whether a plant community persists or collapses as a consequence of herbivory by geese.

The ability of a grazed shoot of Carex subspathacea or Carex X flavicans to increase its production of leaves in response to grazing allowed plants of these species to rapidly replace the photosynthetic tissues removed by grazing geese (Kotanen and Jefferies 1987; Chapters 3,4; Section 7.3.). However, neither of these carices, nor Carex aquatilis, increased its rate of shoot production in response to herbivory (Chapter 5, Section 7.3.), suggesting that the shoots pulled by the geese are replaced slowly, if at all. Consequently, these sedges seem better able to compensate for the grazing of leaves than for the grubbing of shoots. Since large numbers of shoots of each sedge are destroyed by grubbing in the early spring, and lesser numbers by the pulling which is associated with grazing throughout the year (Chapter 5), the unresponsiveness of shoot production suggests that the pulling of shoots is more likely to destroy sedge communities than is the grazing of leaves.

Even if they were eventually replaced, the loss of shoots might be expected to be a more serious cost to a plant than the loss of leaves. In comparison with shoots, leaves turn over relatively quickly (Kotanen and Jefferies 1987; Chapters 3,4,5). This suggests that the loss of potential photosynthate incurred between the grazing of a leaf and its replacement is small compared with the longer lasting reduction of photosynthetic production which would occur before the replacement of a shoot. Since much grubbing of shoots takes place in the early spring, the loss of shoots might be expected to significantly diminish total annual production.

Spring grubbing was patchily distributed. On the salt marshes, the geese tended to grub around the edges of ponds and small hummocks, creating numerous bare patches, each of which typically extended over a few square metres (Jefferies et al. 1979; Jefferies 1987; Kotanen 198N; Section 2.3.1.; Chapter 5). Although Puccinellia phryganodes was the most heavily grubbed salt marsh species,

swards of C. subspathacea were also commonly stripped away. The intensity of grubbing in fresh-water communities varied greatly from pond to pond, possibly reflecting the order in which these ponds thawed, or the order in which their water depths fell sufficiently to allow the geese to forage efficiently. Intensive grubbing in fresh-water communities may eliminate the graminoid flora, leading to the formation of the moss carpets which surround many fresh-water ponds (Section 2.3.1.); small mossy areas also develop on frost-heave mounds in heavily grubbed areas of the salt marshes (Jefferies 1987). Herbivory by geese has been implicated in the production of similar bryophyte communities in other arctic locations (Tikhomirov 1959; Jefferies and Kerbes 1985; Jefferies 1987; Chapter 2). Intensities and patterns of grubbing in both fresh-water and intertidal communities at La Perouse Bay differed between one year and the next, probably reflecting variations in the patterns of snowmelt and in the timing of the migration of the geese (Jefferies 1987; Kotanen 198N). This between-year variation may imply that any responses of plants to shoot pulling are likely to be often inappropriate if they are not expressed before the following year.

The length of time likely to be required for a grubbed area to be recolonized is unknown, but circumstantial evidence indicates that areas of a few square metres from which the salt marsh vegetation has been removed do not recover for several years (Jefferies 1987). Recolonization of a larger grubbed area by Carex subspathacea may occur more slowly, since this species rarely reproduces from seed; establishment in grubbed areas occurs primarily through the vegetative growth of surrounding plants (Chapters 2,5). Colonization by Puccinellia phryganodes is likely to be faster, since fragments of shoots of this species root readily after being dispersed by geese or tides (Jefferies 1987). The first colonists of these disturbed areas are often opportunists, such as Senecio congestus and Salicornia borealis (Jefferies 1987).

Species avoided as food by the geese, such as <u>Hippuris vulgaris</u>, <u>Potentilla palustris</u> and <u>Petasites sagittatus</u> are among the few vascular plants found in moss carpets in fresh-water areas frequented by large numbers of geese (Jefferies 1987). Recolonization of grubbed fresh-water areas is probably at least as slow as for intertidal communities. Isostatic rebound may set an upper limit on the length of time over which a grubbed community may recover; insufficiently rapid regeneration may result in a different community replacing the grubbed community, as the rapid uplift alters drainage patterns and the physical characteristics of the area (Bazely 1984; Jefferies 1987).

The local destruction of fresh-water and intertidal communities by grubbing by the geese does not contradict the evidence of enhanced production in areas grazed by the geese. Grazing and grubbing are different processes which may be expected to have different effects upon plant communities. In areas of intact vegetation, grazing does little damage and may perhaps benefit the plant community. In areas grubbed by the geese, the vegetation is destroyed, but may recover. As in many intertidal algal communities (Pickett and White 1984; Sousa 1984), the behaviour of the grazed plant communities of La Pérouse Bay may best be considered as a dynamic cycle of disturbance and recovery , with the geese acting both as sources of disturbance and as sources of consistency in different circumstances.

Very great densities of geese seem able to tip this balance in favour of disturbance, either by increasing the frequency of grubbing or by increasing the intensity of grazing to the point where accelerated nitrogen cycling can no longer compensate for the damage done by the removal of tissue. Following several decades of rapid growth, the McConnell River colony of Lesser Snow Geese declined from 163 000 pairs in 1973 to 115 400 pairs in 1980, and also moved outward from its former centre (Kerbes 1975, 1982, pers. comm.; Jefferies 1987;

Section 2.3.2.). Excessive herbivory by birds of this very large colony may
have been the cause of these changes (Harwood 1977; Kerbes 1982; Jefferies and
Kerbes 1985; Jefferies 1987; Section 2.3.2.). Ground surveys of the vegetation
of this area in 1985 and 1986 indicated that the sedge communities which were
formerly located near the centre of this colony have been destroyed, and the
habitats degraded (Jefferies and Kerbes 1985; Jefferies 1987; Section 2.3.2.).
Some isolated clumps of graminoids remain in the coastal salt marshes, but the
original graminoid cover of the fresh-water communities has been almost
completely removed, exposing bare peat. It is not known whether these
communities will recover their former nature before isostatic uplift
prohibitively alters the local drainage patterns and physical environment.
Most cases of extensive destruction of vegetation by herbivores have been
reported from systems which have been seriously perturbed by man (Harper 1977).
For example, the overfishing of lobsters and other predators of sea urchins is
thought to have led to an explosion in the sea urchin population of the
northeastern coast of North America (Wharton and Mann 1981; Section 1.2.1.1.).
Grazing by large numbers of sea urchins has now eliminated macrophytes from a
500 km stretch along the coastline of Nova Scotia (Wharton and Mann 1981).
Snow geese, like sea urchins, may currently be increasing in numbers as a
consequence of human activities. Numbers of Lesser Snow Geese have risen
sharply in the last few decades, apparently as a consequence of changes in
agricultural and management practices on their wintering grounds (Jefferies
1987; Section 2.1.). Although "boom and bust" cycles regulated by the supplies
of food may have always been intrinsic to colonies of Snow Geese, it also may be
that the decline of the McConnell colony is an indirect result of the increased
survival of wintering geese. It is entirely possible that habitats at La
Pérouse Bay may be degraded in a similar fashion if the current trend of the

growth of the colony continues.

7.6. References

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