EXPERIMENTAL STUDIES OF THE EFFECTS OF GRAZING BY CAPTIVE GOSLINGS OF THE LESSER SNOW GOOSE ON THE VEGETATION OF A SUBARCTIC SALT MARSH

by

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SUMMARY

1. The effects of grazing by captive goslings of the Lesser Snow Goose on the vegetation of the La Pérouse Bay salt marsh were investigated. Goslings fed on swards of *Puccinellia phryganodes*; net above-ground primary production (NAPP) and forage quality (amounts of nitrogen and carbon) were measured over the course of the season.

2. Grazing early in the season resulted in increased NAPP of swards of *Puccinellia*, as predicted by the herbivore-optimization model. The greatest enhancement of production occurred at low to moderate levels of grazing compared to production in ungrazed swards. At higher levels of grazing production was reduced. Enhancement of NAPP following grazing was detected only early in the season; the ability of the plants to recover from the effects of grazing decreased later in the season.

3. Repeated grazing episodes on the same swards of *Puccinellia* over the course of the summer demonstrated that swards could maintain high rates of production, and high nitrogen content of shoots even when they were grazed late into the season. Swards of *Puccinellia* grazed at approximately 24 day intervals throughout the summer and swards grazed at approximately 12 day intervals on four occasions had the largest increase in NAPP compared to ungrazed swards. Increases in NAPP were achieved over a wide range of grazing periods and intervals between grazing episodes.

4. NAPP was 30 to 40% less in swards of *Puccinellia* where faeces were removed compared to corresponding values for swards where the faeces remained. Faeces provided a source of soluble nitrogen that could be readily taken up by plants. However, the amount of nitrogen contributed by the faeces to the total amount of nitrogen accumulated in the above-ground biomass of grazed swards of *Puccinellia* was less than 10%. Up to 44% of total nitrogen accumulated in the above-ground biomass of grazed swards could not be accounted for.

5. Nitrogen mineralisation processes which occur in goose faeces may be important in maintaining the nitrogen balance of the salt marsh. Rates of microbial respiration and the net mineralization of nitrogen in fresh faeces from gosings grazing *Carex subspathecea* were higher than corresponding values for faeces derived from *Puccinellia phryganodes* and *Calamagrostis deschampsiodes*. However the mineralisation efficiency (net mineralisation rate / respiration rate) was similar in faeces derived from *Carex* and *Puccinellia*. The ratios were considerably higher than the corresponding rates in faeces derived from *Calamagrostis*. The digestibility of *Calamagrostis* shoots was considerably lower than that of *Carex* and *Puccinellia* shoots based on analysis of acid-detergent fibre.

6. The interactive and dynamic processes of nitrogen cycling between plants, geese, sediments and microbes lead to enhanced primary production in this grazed system. A suite of interactions exist which extend the influence of

plant-herbivore interactions beyond the immediate participants, and involve all trophic levels in this grazing system.

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ANOVA:	analysis of variance
NAPP:	net above-ground primary production
Puccinellia:	*Puccinellia phyrganodes*

CHAPTER 1: GENERAL INTRODUCTION - THE PROCESS OF HERBIVORY

1.1 Introduction to herbivory

Herbivory has been pervasive in determining the structure and dynamics of plant and animal communities, populations and individuals (Crawley 1983; Howe and Westley 1988). The effects of herbivory are evident at all levels of biological organization. Herbivory affects primary and secondary production, energy flow, nutrient cycling, and the structure and composition of plant communities (Harper 1969, 1977; Crawley 1983; Vitosek 1984). A suite of processes exist, which extend the influence of plant-herbivore interactions beyond the immediate participants to other members of the community (see Owen-Smith 1987; Ruess and McNaughton 1987). The effects of the interactions are evident at both evolutionary and ecological time scales.

It is estimated that at least 10% of the net above-ground primary production of terrestrial ecosystems is consumed by vertebrate and invertebrate herbivores. (Odum, Connell and Davenport 1962; Teal 1962; Chew and Chew 1970; Chew 1974; Crawley 1983). In some communities (eg. grazing systems) this proportion may be considerably higher, approaching 100% (Dyer _et_ _al_. 1982; Cargill and Jefferies 1984b; Coley, Bryant and Chapin 1985; McNaughton 1985). There is a paucity of research on below-ground herbivory, but estimates of the consumption of plant biomass range from 6% to 30% of net below-ground production (Andersen 1987). It is unlikely that any plant is completely immune from the effects of herbivory.

Herbivores and plants have shared a long *evolutionary history (Friis, Chaloner and Crane 1987).* Herbivory has probably been a strong selection force on the patterns of leaf growth that have evolved in plants (Mooney and Gulmon 1982). Virtually all leaves have traits which, to some degree, reduce the intensity of herbivory (eg. lignification, silification, secondary compounds, reduced palatability). Similarly, herbivores display a wide range of feeding morphologies and behaviours, which have probably evolved in response to the evolution of their forage plants. From the time of the Cretaceous when the herbivore community was dominated by dinosaurs that were generalists in their foraging behaviour, browsing has been a common form of herbivory. It was not until the mid- to late Eocene (45 mybp), following world-wide cooling of climate and the radiation of annual or biennial reproductive strategies in plants and the presence of plants with perenating buds at or below ground level, that large mammalian grazers became common (Stebbins 1981; Wing and Tiffney 1987).

The graminoid (grasses and sedges) plant form, in particular, is believed to have coevolved with large ungulate grazers (Webb 1977, 1978; Stebbins 1981; Mack and Thompson 1982; Coughenour 1985; Herrera 1985; Wing and Tiffney 1987). Many graminiods possess morphological traits that permit them to tolerate repeated or partial defoliation (Hyder 1972; Dahl and Hyder 1977; Briske 1986). Grasses and sedges usually have their shoot apical meristems located at or below ground level and have leaves which elongate from intercalary meristems. These characteristics protect meristems from herbivore damage and allow regrowth of clipped leaves to occur (Mack and Thompson 1982; Crawley 1983; Coughenour 1985).

The question of whether or not herbivory is "good" for plants is a controversial issue in ecology (McNaughton 1983, 1986a,b; Westoby 1985, 1986; Belsky 1986a, 1987; Crawley 1987). Compensatory growth responses of plants following defoliation by herbivores may result in increases in fitness, or more often, in net primary production (McNaughton 1986). The effects of herbivory at the level of the individual, population, community and ecosystem, and interactions between these levels of organization will in turn influence the outcome of a particular plant-herbivore interaction.

Herbivores act as agents of natural selection, leading to differential performance of plant genotypes in response to herbivory. Plants in grazed graminoid communities frequently have prostrate leaves and shoots, shortened internodes, and increased rates of leaf production and of tillering (Turesson 1922; Stapleton 1928; McNaughton 1979a; Gray and Scott 1980; Crawley 1983; Detling and Painter 1983; Sadul 1987; Waisel 1987; Jefferies 1988a). This implies modification of the genetic structure of the population in response to the overall effects of herbivory. Intensive herbivory is likely to increase the mortality of the more suseceptible genotypes, leading to an increase in the frequency of grazing-tolerant or resistant genotypes (see Wilbur 1976; Snaydon 1980). Few studies have shown an increase in the genetic fitness of individual plants following defoliation (Belsky 1986a, 1987), and most claims of an increase in genetic fitness are unconvincing (for example see Owen 1978; Boscher 1979; Boucher and Sork 1979). Paige and Whitham (1987) have recently shown that individuals of Ipomopsis aggregata browsed by deer or elk have nearly 2.5 times the relative fitness of intact, ungrazed plants based on seed output, but the mechanism is unclear.

From the point of view of the herbivore, enhancement of forage availability and of the nutritional quality of forage following grazing is a desirable attribute of grazed swards. In grasses where propagation is achieved primarily by vigorous vegetative clonal growth, fitness measured in terms of seed production may be mostly irrelevant (Crawley 1983). Changes in net above-ground primary production may have the greatest influence on plant-grazer interactions in these systems.

1.2 Positive feedbacks and nutrient cycling in grazing ecosystems

Feedback processes can regulate the flow of materials and the effect of various physical and biotic processes in ecosystems (DeAngelis, Post and Travis 1986). When a population or ecological community is perturbed slightly from "equilibrium", the balance of positive and negative feedback mechanisms in the system act to counteract the perturbation and restore the system to "equilibrium" (assuming a stable equilibrium in the first place) (DeAngelis, Post and Travis 1986). Alternatively, feedback mechanisms may cause the system to change, if the balance between positive and negative influences is upset. The magnitude of various feedback processes in the ecosystem determine the outcome, and as in most processes involving more than one step, the one which is rate-limiting is often the most important.

Nutrient cycling in ecosystems is often thought of as a feedback process. In terrestrial ecosystems, herbivores accelerate rates of nutrient mineralization above those in their absence (Arman, Hopcraft and McDonald 1975; Woodmansee 1978; Schowalter, Hargrove and Crossley 1986; Ruess and McNaughton 1987). Nutrient limitations on plant growth can be offset by the rapid recycling of essential elements within an ecosystem and these processes may be enhanced by herbivores. The uptake of mineral nutrients by plants is often limited by the rate of mineralization processes in the soil.

Nitrogen is a critically limiting nutrient for plant growth (Lee, Harmer and Ignaciuk 1983; Stewart et al. 1983; Sprent 1987). Many studies have shown that it is the most important nutrient limiting growth in tundra ecosystems (Ulrich and Gersper 1978; Shaver and Chapin 1980), and in salt marshes (Pigott 1969; Stewart, Lee and Orebamjo 1973; Valeila and Teal 1974; Cargill and Jefferies 1984a).

A large number of processes are involved in nitrogen inputs, transfers and losses in natural ecosystems (Clark 1981; Sprent 1987). Pathways of nitrogen cycling involve all trophic levels, including live and dead plant biomass, microbes (bacteria, actinomycetes, fungi), soil animals (arthropods, nematodes, protozoans), invertebrate grazers (grasshoppers), vertebrate grazers (large and small mammals, birds), and chemical processes in the soil and atmosphere. These processes include the mineralization of nitrogen from dead organic matter (eg. plant litter, animal faeces and carcasses), to ammonia (ammonification) or nitrate (nitrification). Ammonium ions (NH_4^+) may be in either an exchangable or soluble form, and depending upon conditions of temperature, pH and moisture may volatilized as a gas (NH_3). Ammonia volatilization and denitrification of nitrate to gaseous nitrogen (N_2 and N_2O) consitute pathways of nitrogen loss from ecosystems. Leaching of organic and and inorganic nitrogen following rainfall or snowmelt may also result in losses from the system. Nitrogen may be immobilized by the uptake of ammonium and nitrate by plants and soil micro-organisms. In addition, free-living or symbiotic cyanobacteria may fix atmospheric nitrogen.

A close coupling of the activities of the soil microflora and the growth and nutrition of plants in natural ecosystems exists (Fenchel and Blackburn 1979; Lee, Harmer and Ignaciuk 1983). In fact, most plants are dependent on the microbial breakdown of soil organic matter for their nitrogen supply. Microbial activity determines the rate of release of ammonium and nitrate to higher plants, and any environmental factor which affects the microorganisms will indirectly determine the availability of these ions for plant growth. For example, factors such as low temperatures, high soil acidity (low pH), and anaerobic conditions may depress nitrification (Aziz and Nedwell 1979; Fenchel and Blackburn 1979; Lee, Harmer and Ignaciuk 1983).

1.3 Responses of Plants to Grazing

Grazing by animals affects the structure of plant populations (Crawley 1983). In a series of mostly discussion papers published in Forum in Oikos, Owen (1980), Owen and Wiegert (1976, 1981, 1982a,b, 1983) and Petelle (1982) suggested that there are a wide variety of coevolved mutualisms between plants and herbivores. They suggest that plants exploit consumers and that the outcome of this arrangement is an increase in the genetic fitness of plants. However, this hypothesis was challenged on the grounds that most theoretical and experimental evidence did not support it (Stenseth 1978, 1983; Silvertown 1982; Thompson and Uttley 1982; Herrera 1982, 1985; Belsky 1986a; Dirzo 1984; Lam and Dudgeon 1985).

There is a considerable body of "suggestive" evidence which supports the general idea that herbivory results in increased net primary production, but there are few studies which provide "real" evidence demonstrating that this increase occurs, and also provide evidence of the mechanism which accounts for this regrowth following grazing. Collectively however, the evidence suggests that increases in production may occur following grazing under some circumstances in both terrestrial (Cook, Stoddart and Kissinger 1958; Vickery 1972; Dyer 1975; McNaughton 1976, 1979; Prins, Ydenburg and Drent 1980; Cargill and Jefferies 1984b), and aquatic algal and coral ecosystems (Bjorndahl 1980; MacDonald 1985; Bergquist and Carpenter 1986; Sterner 1986; Carpenter 1986; Power 1987). On the other hand, plants also produce a wide variety of secondary chemicals in response to herbivory (Rhoades and Cates 1976; Rhoades 1979, 1983, 1985; Feeny 1980; Harborne 1982; Crawley 1983). Therefore, the responses of plants to herbivory may be considered under two general, operational headings; 1) structural, phenological and chemical defenses, and 2) production and growth responses. These responses are not mutually exclusive (see Westoby 1980; Bryant 1987; Coley 1988; Georgiadis and McNaughton 1988; van der Meijden, Wijn and Verkaar 1988), however one type of response generally dominates in a particular species.

A broad distinction between the two responses, based on differences in the morphology between woody shrubs or herbs which are generally characteristic of browsing systems, and graminiods which dominate terrestrial grazing systems, can be made. Graminoids have evolved a number of defenses to grazers including secondary chemicals, but they are generally more tolerant of grazing than woody shrubs or herbs (Coughenour 1985).

The terms "defensive" and "tolerance" need to be treated with some degree of caution because their definitions can be interpreted a number of ways. Defenses may have a negative impact on consumers, or they may actually reduce net losses in terms of tissue biomass or fitness (Schultz 1988). Defenses can be considered avoidance mechanisms that reduce the probability of defoliation, while tolerance mechanisms facilitate regrowth following defoliation (Briske 1986). Tolerance does not necessarily imply increased production or fitness as a consequence of herbivory.

1.3.1 Plant defenses to the effects of herbivory

Defenses have important influences on the feeding preferences of herbivores (Harper 1969, 1977; Rosenthal and Janzen 1979; Crawely 1983; Sinclair and Smith 1984; Robbins et al. 1987). Structural defences function by making herbivory difficult, damaging or energetically expensive. In graminoids common structural defences include large amounts of silica, and indigestible lignins and cellulose (McNaughton and Tarrants 1983; Coughenour 1985). These defences may also reduce the concentrations of nutrients in plant tissues relative to the amount of structural material (Mattson 1980; Crawley 1983). Other avoidance mechanisms include reduced tissue accessibility (ie. decreased leaf length and angle, and leaf/culm ratio), awns or spines of the inflorescence, and changes in leaf tensile strength at the individual level (Briske 1986), and interspecific associations with less palatable species within the community (McNaughton 1978). Feeny

(1976, 1980) and Rhoades and Cates (1976) have also suggested that ephemerality or rarity may reduce damage to individual plants by herbivores. Asynchrony between the phenology of plant growth and forage demand may limit the size of a herbivore population within an area (Crawley 1983; Drent and Prins 1987).

Many plants produce antiherbivore chemicals (Fraenkel 1959; Harborne 1982; Crawley 1983). Plants or tissues with a slow growth rate tend to be protected with high concentrations of "quantitative" defences, such as tannins and polyphenols, which act in a dosage-dependent manner by inhibiting digestion (Feeny 1976, 1980; Rhoades and Cates 1976; Coley 1988). "Quantitative" defenses tend to be carbon-based and are not very labile (Coley, Bryant and Chapin 1985). Plants or tissues with rapid growth rates tend to be protected with low concentrations of "qualitative" defences, such as alkaloids, cyanogenic glycosides and terpenes. These toxins are usually nitrogen-based and turn over rapidly (Feeny 1976, 1980; Rhoades and Cates 1976; Harborne 1982; Coley, Bryant and Chapin 1985)

Different patterns of phytochemistry have been explained in terms of resource availability (Mooney and Gulmon 1982; Coley, Bryant and Chapin 1985; Bazzaz et al. 1987). Resource-limited plants with slow growth rates and long lived tissues tend to develop "quantitative" defences. Although these compounds are initially expensive to produce, maintenance costs are low. Plants that are not resource limited, which are fast-growing, and have short-lived tissues tend to be protected with low concentrations of "qualitative" defences. The most obvious exception to these generalizations are graminoids which are depauperate of defensive chemicals (Crawley 1983; Coughenour 1985). Jung, Batzli and Seigler (1979), in a survey of the phytochemistry of arctic graminoids, found that alkaloids were present only in small concentrations (< 1 ppt); tannins, saponins, cyanogens and anthraquinones were not detected.

Induced chemical defences generally are produced in response to tissue damage (Rosenthal and Janzen 1979; Crawley 1983; Coley, Bryant and Chapin 1985). These generally are "qualitative" defences, and are usually restricted to damaged areas. Induced "quantitative" defences (tannins and resins) may also appear more gradually (Rhoades 1979). Induced chemical defenses are a form of phenotypic plasticity of plants, in response to the effects of herbivory. Georgiadis and McNaughton (1988) have shown that defoliation can induce cyanogenisis in _Cynoden_ _plectostachyus_, an African C_4 grass, and suggest that this trait evolved as a herbivore deterent.

Carroll (1988) has suggested that fungal endophytes may protect host plants from herbivores which are poisoned by the mycotoxins produced by the endophytes. In particular, many grasses are infected by fungal endophytes which produce physiologically-active alkaloids in the tissues of their host (Clay 1988). These fungal endophytes are of the genus _Acremonium_ (mainly in C_3 grasses) or _Balansia_ (mainly in C_4 grasses, but also some C_3 grasses). Their hyphae occur intercellularly in leaf and stem and root tissue, and they produce no external morphological changes to the host plant (Clay 1988).

Many infected grasses are known to be toxic to livestock, however the effects of endophyte-infected grasses on the foraging and diets of nondomestic and insect grazers are generally unknown (Clay 1988). Greater growth and seed production of infected plants has been reported for perennial ryegrass and tall fescue in the absence of grazing (Latch, Hunt and Musgrave 1985; Clay 1987). The outcome of the interactions between chemical defenses, fungal endophytes, herbivory, and intrinsic and extrinsic compensatory growth mechanisms may have profound consequences not just for the individual plant but also for the structure and composition of the plant community.

1.3.2 Productivity and growth rate of plants in relation to herbivory

The growth responses of plants to defoliation as a result of grazing can be grouped into three categories: 1) negative response, or undercompensation; 2) exact compensation; and 3) enhancement, or overcompensation (the herbivore optimization model; see Fig. 1-1). The type of response observed depends upon the intensity and frequency of grazing, the timing of grazing during the season, and the phenology of plant growth (McNaughton

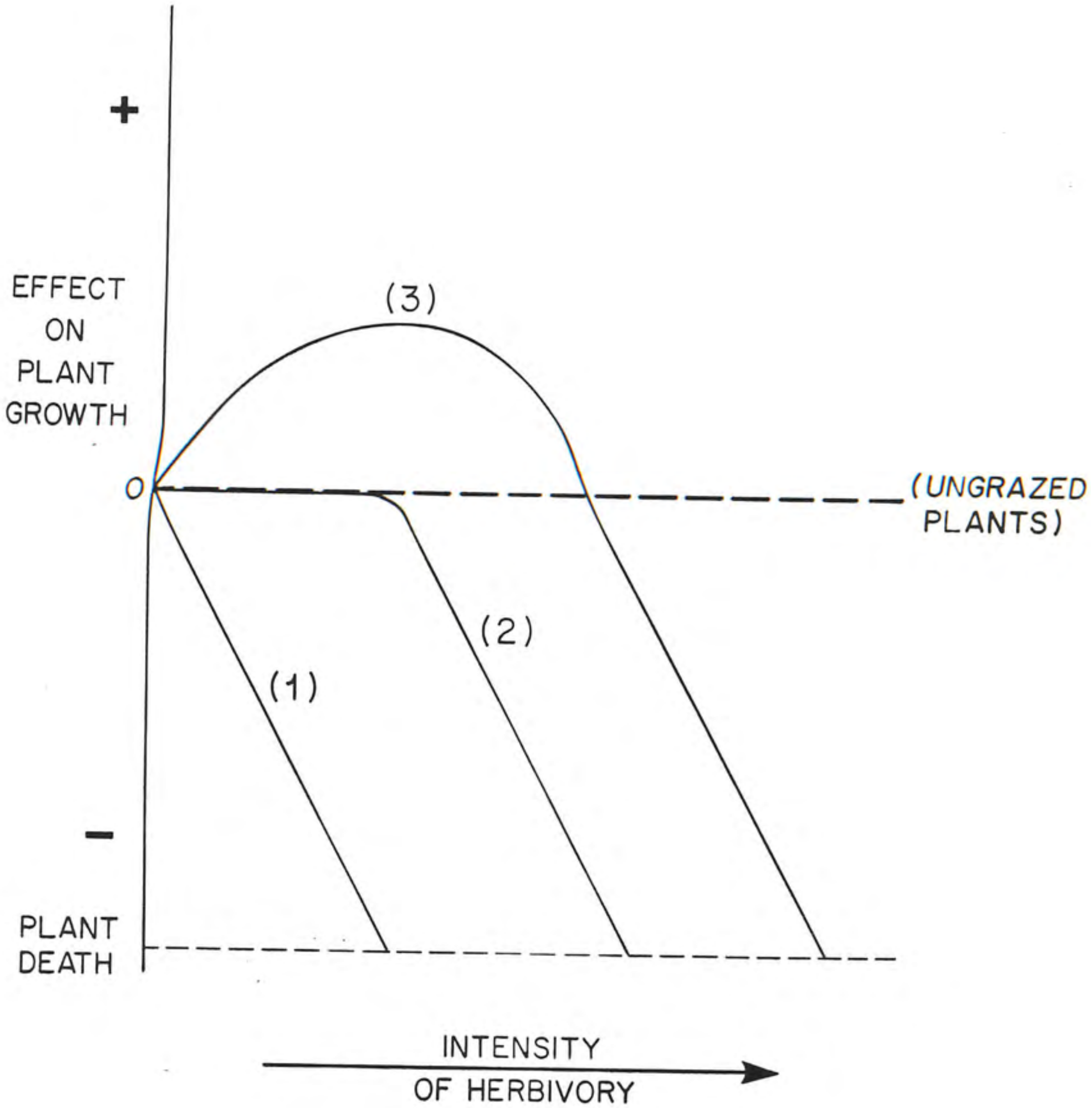
1979a; Dyer et al. 1982; Jefferies 1988a). Grazing can affect both above- and below-ground production of grazed plants. Clipping by itself is almost always detrimental (Dahl and Hyder 1977; Lee and Bazzaz 1980; Sadul 1987), but compensatory morphological and physiological responses may enhance above-ground production. These responses include changes in photosynthesis, transpiration, nutrient uptake and translocation, and rates of tissue turnover. All of these processes may interact with each other.

A difference exists in the type of growth responses observed between grazing and browsing systems, (Bryant, Chapin and Klein 1983). The regrowth of woody plants (browsing systems) is often limited by the availability of resources and by the destruction of apical meristems. There is a heavy reliance on chemical (usually carbon-based) defences. In comparison, regrowth in many graminoids (grazing systems) is much faster, since growth rates and turnover rates of leaves are much faster and meristems are generally protected from damage.

1.4 Compensatory Responses

A critical assumption of the herbivore optimization model (Fig. 1-1) is that some plant species possess a strong potential for compensatory regrowth following grazing. A variety of mechanisms may account for increased primary production following grazing. Intrinsic mechanisms that operate at the level of

Fig. 1-1. Three possible effects of herbivory on plant growth (or fitness). 1) a decline as the intensity of herbivory increases; 2) compensation up to a threshold level of herbivory, after which growth declines with increasing herbivory; 3) enhancement of growth at moderate levels of herbivory above that of ungrazed plants. At higher intensities growth declines. This is the herbivore optimization curve (after McNaughton 1979, 1983a; Dyer *et al*. 1982; Jefferies 1988a).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individual plants and extrinsic mechanisms that involve processes at the community or ecosystem level have been proposed to account for an increase in production (McNaughton 1983a,b).

1.4.1 Intrinsic Mechanisms

1.4.1.1 Photosynthesis

Photosynthetic CO_2 assimilation by leaves is affected by the nutrition of the plant, the light regime during growth, leaf age, water stress and many other environmental and physiological factors. Both an increase and a decrease in photosynthetic rates in tissue remaining or produced after grazing have been observed (King, Wardlaw and Evans 1967; Gifford and Marshall 1973; Detling, Dyer and Winn 1979; Caldwell *et al*. 1981; Painter and Detling 1981; Detling and Painter 1983; Nowak and Caldwell 1984; von Caemmerer and Farquhar 1984; Wallace, McNaughton and Coughenour 1985). In *Bouteloua gracilis*, Detling, Dyer and Winn (1979) measured both increased net photosynthetic rates within three days of defoliation, and an increase in the proportion of new photosynthate allocated to the production of leaves. Gifford and Marshall (1973) suggested that decreases in mesophyll resistance to CO_2 diffusion in leaves of *Lolium* remaining after partial defoliation may lead to increased photosynthetic rates. A more likely explanation is that partial defoliation causes a proportional increase in both ribulose-1,5-bisphosphate (RuBP) carboxylase-oxygenase activity, and RuBP regeneration capacity (von Caemmerer and Farquhar 1984). These authors measured a significant increase in CO_2-assimilation rate of leaves of Phaseolus vulgaris eight days after partial defoliation, which was accompanied by an increase in chlorophyll concentration per unit leaf area and by an increase in in-vitro RuBP-carboxylase activity.

A number of graminoid species show enhanced photosynthetic rates when partial defoliation occurs (Caldwell et al. 1981; Wallace, McNaughton and Coughenour 1985). However, Detling and Painter (1983) found no difference in photosynthetic rates or stomatal conductances between two ecotypes (one from grazed sites, one from an exclosed site) of Agropyron smithii following clipping. Similarly, Nowak and Caldwell (1984) did not record a difference in gas exchange rates in clipped and unclipped leaves of the same age of plants of A. desertorum and A. spicatum. The overall significance of increased rates of photosynthesis in leaves following grazing in relation to compensatory growth is unclear.

1.4.1.2 Resource Allocation

Herbivory frequently alters patterns of resource allocation. A number of studies have reported that the proportion of photosynthate allocated to the production of new leaf area increases after grazing (Ryle and Powell

1975; Detling, Dyer and Winn 1979; Detling *et al*. 1980). Richards (1984) reported an increase in allocation of current photosynthate from roots to shoots. While foliage herbivory often increases upward translocation of assimilates at the expense of root growth, grazing of roots may reverse this pattern (Crawley 1983; Andersen 1987). However, the ability of plants to support above-ground production with below-ground reserves, and *vice versa*, is not entirely clear (see Section 1.4).

A distinction must be made between carbon (carbohydrate) and nutrient (particularly nitrogen and phosphorus) limitation of growth. Although well fertilized plants may be carbon-limited, under natural conditions plant growth is frequently limited by nutrient availability (Harper 1977). This is particularly pronounced in nutrient-deficient habitats. The regrowth of leaves following defoliation requires substantial quantities of mineral nutrients and carbohydrates. Calculations of nutrient budgets of tundra graminoids at Barrow, Alaska, suggest that leaf regrowth following defoliation depletes plant nitrogen and phosphorus reserves more rapidly than carbohydrate reserves (Chapin 1977).

Herbivory often results in increases in the quality of forage. Translocation of stored nutrients from the below-ground biomass and increased uptake of inorganic nutrients can lead to high concentrations of nitrogen and other nutrients and soluble (non-structural) carbohydrates in the developing leaves of grazed plants (Ydenberg and Prins 1981; Cargill and Jefferies 1984b;

McNaughton and Chapin 1985; but see Ruess 1984). However, while grazing may result in changes in resource allocation patterns, new growth cannot be sustained if a resource is limited. Eriophorum vaginatum and other graminoids frequently grow in nutrient-limited habitats in the Arctic. Sequential leaf development is associated with the movement of nutrients from senescing leaves to developing leaves, thereby minimizing annual nutrient requirements from the soil (Jonasson and Chapin 1985). Under these conditions removal of leaves by herbivores restricts further leaf development. The nutrient pool has to be replenished (by fertilization), and the plants must be able to assimilate these nutrients at a rate proportional to the grazing intensity, or else new growth will cease.

1.4.1.3 Morphological Plasticity

Grazing is known to increase rates of tillering in graminoids (Stapleton 1928; Peterson 1962; Younger 1972; Laude 1972; Belsky 1986; Kotanen and Jefferies 1987; Bazely and Jefferies 198N). These responses could be due to the removal of apical dominance if the herbivore has removed the apical bud. At the community level, defoliation results in the opening of the canopy and increased light penetration which leads to rapid changes in the growth rates of the surrounding plants as they exploit the light gaps. In grasslands, these responses are related to the morphology of graminoids, which protect meristems from damage during grazing (Hyder 1972; Dahl and Hyder 1977; Briske 1986).

At the level of the individual tiller the probability of defoliation may be reduced as a result of the existence of a number of so called avoidance mechanisms (Branson 1953). In species where shoots are not erect, so that the apical meristems are close to the ground or else are surrounded by vegetative tillers, the meristems are not likely to be destroyed and hence plant growth can be sustained following defoliation. Growth is likely to be most rapid from intercalary meristems, followed by newly developed leaf primordia, and least rapid from newly initiated axillary buds (Briske 1986). Leaf replacement following grazing is largely a function of the number, source and location of meristems of each plant. In Puccinellia phryganodes, grazing by Lesser Snow Geese resulted in twice as many axillary tillers produced per main tiller in grazed plants compared to the number in ungrazed plants (Bazely and Jefferies 198N). The clonal growth of graminoid vegetation permits rapid regrowth following grazing. Morphological plasticity is an important mechanism by which grazed plants can sustain production when grazed.

1.4.2 Extrinsic mechanisms

1.4.2.1 Water-use efficency

McNaughton (1979, 1983a,b, 1985) has suggested that grazing leads to the conservation of soil moisture by reducing transpirational water losses, because of reduced leaf area of grazed plants. The validity of this observation has been questioned by Belsky (1986a), based on the results of studies by Younger (1972) and Ellison (1960). Hodgkinson and Baas Becking (1977) have shown that defoliation during periods of low water availability accelerate plant death, because root growth is impaired as a result of lack of assimilates, and new roots cannot extend into the lowered water table. Detling and Painter (1983), and Nowak and Caldwell (1984) found no difference in photosynthetic water-use efficency between defoliated and unclipped plants. Cox, Parr and Plant (1988) found that frequent clipping reduced water-use efficiency of plants of Lolium perenne in the first year but that clipping had no effect on established swards. These contradictory results suggest that grazing has a very unpredictable influence on water- use efficency at the level of the individual and community, and that this is not likely to be an important compensatory mechanism, except perhaps in arid regions. Since the response of plants is linked to plant architecture, any generalizations are difficult.

1.4.2.2 Salivatory hormones

The stimulatory effects of salivatory hormones on grasses has been investigated as a possible compensatory mechanism (Reardon 1972; Dyer and Bokhari 1976; Dyer 1980; Dyer et al. 1982; McNaughton 1985). Classes of chemicals recognized as growth factors or regulators in plants which are involved in molecular, cellular, and physiological activities may be transfered across trophic levels from herbivores to plants. Experiments with thiamine and bovine saliva suggested that direct application of saliva stimulates plant growth (Reardon, Leinweber and Merrill 1972). However, in a subsequent publication (Reardon, Leinweber and Merrill 1974), no stimulation of plant growth was reported. Johnson and Bailey (1972) showed that saliva did not promote the growth of two _Festuca_ species, and Detling _et al_. (1980, 1981) found that bison saliva did not lead to an increase in plant growth or photosynthetic physiological activity of _Avena sativa_ and _Bouteloua gracilis_.

McNaughton (1985) detected increased growth of thiamine treated leaves of the unclipped grasses, _Sprobolus iocládos_ and _S. pyramidalis_, but thiamine did not promote the growth of defoliated plants beyond that of ungrazed plants. Thiamine application also resulted in a decreased concentration of leaf nitrogen (McNaughton 1985). In summary, the influence of salivatory hormones on the growth of grazed plants resulting in enhanced production is not established as a compensatory mechanism.

1.4.2.3 Fertilization

Perhaps the most important extrinsic factor responsible for the enhancement of plant growth following grazing is the effect of fertilization from faeces and urine (see Section 1.2). Herbivores play an important role in nutrient cycling in most ecosystems (Mattson and Addy 1975; Bjorndal 1980; McNaughton, Coughenour and Wallace 1982; Ruess and McNaughton 1984; Bazely and Jefferies 1985; Schowalter, Hargrave and Crossley 1986). Excretion of soluble nutrients by herbivores accelerates the availability of nutrients that normally would be limited by the rate of plant litter decomposition. This accelerated transfer of nutrients is essential to sustain the growth of grazed swards (McKendrick <u>et</u> <u>al</u>. 1980; Coppock <u>et</u> <u>al</u>. 1983; Jefferies 1988a). It is likely to be of particular significance in systems which are intrinsically nutrient-limited. Grazers may also indirectly affect the balance between the net mineralization and immobilization of nutrients in soils by altering the dynamics of the soil microbial processes (Ruess and McNaughton 1987; Chapter 5).

Nutrient availability affects the suitability of plants as forage for herbivores. Most plants generally experience nutrient flushes early in the growing season and the have highest uptake capacity at that time (Chapin 1980). Because grazing is coincident with the return of nutrients to the soil from faeces and urine, plants may be able to maintain a high rate of uptake of nutrients for a long period during the growing season. In addition uptake rates of nutrients may be considerably higher in grazed plants, than those in ungrazed plants (see Ruess, McNaughton and Coughenour 1983).

A number of authors have recently suggested that the effects of fertilization are "blatantly group selectionist" (Belsky 1987; Crawley 1987). This arguement is based on the observation that the effects of defoliation affect only some of the plant species in the community, while nutrients recycled in faeces are available to all plants. However, in grazing systems very few plants on a "grazing lawn" escape defoliation (McNaughton 1984; Jefferies 1988a). Effects of herbivory evident at one level of organization (ecosystems, communities, populations or individuals), may not be as obvious at another level. Fertilization by faeces and urine has effects at the level of the individual plant as well as at the level of the entire grazing ecosystem. All of the effects of fertilization need to be considered before concluding that this mechanism has no influence on individual selection.

1.5 Grazing and Below-Ground Biomass and Production

Grazing may have effects on root growth and the activities of roots (Milthorpe and Davidson 1977; Andersen 1987). Root growth is reduced in many plants following clipping of above-ground tissue (Crider 1955; Hodgkinson and Baas Becking 1977; Detling, Dyer and Winn 1979). Excessive grazing causes a dramatic decline in root growth, and the rate of shoot development is reduced. However, clipping of culms only affected root growth of individual ramets (Crider 1955). Since selective clipping is typical of the natural grazing patterns of many animals (Stephens and Krebs 1986), these results suggest that the effects of grazing on root growth are more complicated (and possibly not as severe) as many studies might indicate.

In many tundra plants there is a large source of fixed carbon, energy and nutrients below-ground. This source is available for plant growth following herbivory. Chapin and Slack (1979) suggest that defoliation of increasing intensity produces the following responses: 1) decreased root growth, 2) decreased activity of existing roots, and finally 3) increased root mortality. However, in perennial plants which have large below-ground reserves, root function may diminish only after below-ground nutrient reserves are depleted. This emphasizes the need for nutrient input following grazing if production is to be sustained in nutrient-limited environments.

In two tundra graminoids, *Eriophorium vaginatum* and *Carex aquatilis*, moderate experimental defoliation stimulated root respiration and phosphate absorption (Chapin and Slack 1979). The was the result of lowered root phosphorus levels following defoliation, as nutrient reserves were reallocated to support shoot growth. However, the investigators noted that *Carex aquatilis* has a large perennial root system and is less sensitive to defoliation than *Eriophorum* which produces a new set of roots each season.

Cargill and Jefferies (1984b) did not detect a difference in the below-ground biomass of grazed plants of *Puccinellia phyrganodes* and *Carex subspathecea* compared to ungrazed plants. However, this does not imply that the rate of turnover of biomass between grazed and ungrazed sites is not different. Measurement of small changes in live below-ground biomass is very complicated because it is difficult to separate live and dead roots. The extensive root systems of established plants may contain sufficient carbohydrates to support root growth and maintenence following grazing, until enough photosynthate is produced and translocated below-ground.

Below-ground herbivory is also likely to be important but its effects are poorly understood (Andersen 1987; Seartedt, Ramundo and Hayes 1988). Some plants respond to the removal of root tissue by increasing the growth rate of the remaining roots and by initiating new roots (Andersen 1987). Because there is often a simultaneous decrease in shoot growth proportional to the degree of root loss, below-ground herbivores may have a major role in determining the energy and nutrient flow through the community (Andersen 1987). In a recent study of the dynamics of the interactions between soil arthropods and the prairie grass, Andropogon gerardii, Seartedt, Ramundo and Hayes (1988) have shown a strong positive correlation between the intensity of above-ground herbivory and the density of below-ground herbivores. The results of these recent experiments re-enforces the concept that the effects of herbivory are evident at all levels of community organization.

1.6 Principle Objectives

The general goal of this study was to investigate the response of Puccinellia phyrganodes, a stoloniferous salt marsh grass, to different levels of grazing by captive goslings of the Lesser Snow Goose (Chen caerulescens caerulescens). The effect of goose faeces on nitrogen cycling and rates of nitrogen mineralization in faeces were also examined. Previous studies of the effects of snow geese on production, nutrient cycling and composition of the grazed salt marsh at La Pérouse Bay, Manitoba, since 1978, provided the framework for conducting experiments in this study (see Jefferies 1988a for an overview). The herbivore optimization model, which predicts that grazing may lead to the enhancement of net primary production under certain conditions, provided the conceptual framework (see McNaughton 1979, 1983a,b; Hilbert et al. 1981; Dyer et al. 1982; Jefferies 1988a). The major objectives and rationale for these experiments are listed below.

1. An experimental test of the prediction of the herbivore optimization model, that moderate levels of herbivory lead to the greatest enhancement of NAPP of Puccinellia phryganodes grazed by geese.

Cargill and Jefferies (1984b) found that grazing by Lesser Snow Geese led to increases in NAPP of grazed Puccinellia under field conditions. However the relationship between the length of the grazing period and the increase in NAPP could not be established. This can be accomplished by controlling the duration of grazing on swards of Puccinellia in experimental plots by using captive goslings.

2. An examination of the effects of the timing of grazing within a season and the interval between grazing events, on the type of response exhibited by swards of Puccinellia.

The ecological time frame over which enhanced NAPP occurs in response to grazing is rarely discussed (Jefferies 1988a). The capacity of the plants to recover from the effects of grazing is dependent upon the timing and intensity of herbivory during the season, and the phenology of plant growth. A number of experiments were conducted to examine the capacity of swards of Puccinellia to recover from grazing at different times during the summer. In particular, the effects of repeated partial defoliation at different intervals during the season were examined.

3. The determination of the relative effects of clipping and fertilization by goose faeces on the NAPP of swards of Puccinellia.

Fertilization by goose faeces is essential for the increase in NAPP of Puccinellia following grazing (Bazely and Jefferies 1985). The relative effects of clipping and fertilization at different levels of grazing may change the type of growth response observed. Grazing experiments where faeces either remained or were removed from grazed swards of Puccinellia were conducted to examine this question.

4. An examination of microbial-mediated nitrogen mineralization processes in goose faeces derived from three graminoid forage species, Puccinellia phryganodes, Carex subspathacea and Calamagrostis deschampsiodes.

Soluble nitrogen of goose faeces is rapidly leached to the sediments within 48 hours and is taken up by plants (Bazely and Jefferies 1985). The microbial biomass present in goose faeces may also contribute to the net nitrogen balance in the marsh as a result of the net mineralization of organic nitrogen present in faeces. Rates of net nitrogen mineralization and microbial respiration in fresh goose faeces derived from goslings grazing on three forage species were measured on three occasions during the summer.

CHAPTER 2: DESCRIPTION OF STUDY SITE AND SPECIES

2.1 Description and History of the La Pérouse Bay Grazing System

La Pérouse Bay is located on the west coast of Hudson Bay, approximately 25 km east of Churchill, Manitoba (58′, 24′ N, 94°, 24′ W) (Fig. 2-1). It lies within the belt of coastal tundra that extends along Hudson Bay in this region. The treeline is approximately 10 km inland. The duration of the snow-free period averages four months, from the end of May until the end of September. Snow melt usually occurs in late May, at which time the entire area is flooded. Minimum temperatures are consistently greater than 0° C in June, July, August and September (Fig. 2-2; Table 2-1). Maximum temperatures average 10° to 15° C, but can vary from below 0° C to 30° C, within the same 24 h period. Annual precipitation is approximately 450 mm, of which approximately 60% falls during the snow-free period. Over 50% of the total number of hours of bright sunshine occur during this period (Table 2-1).

The La Perouse Bay colony of Lesser Snow Geese (*Chen caerulescens caerulescens* (L.) Gundl.) currently numbers about 8000 nesting pairs, although tens of thousands of migrants pass through the area each spring and autumn. Snow Geese are the dominant and most important herbivore of graminoid vegetation at La Pérouse Bay. Canada Geese (*Branta canadensis*) are also resident during part of the summer, but at much lower numbers (< 100). Mammalian herbivores which occur infrequently in the area are

Fig. 2-1. Map of of Hudson Bay showing the location of La Pérouse Bay, Manitoba.

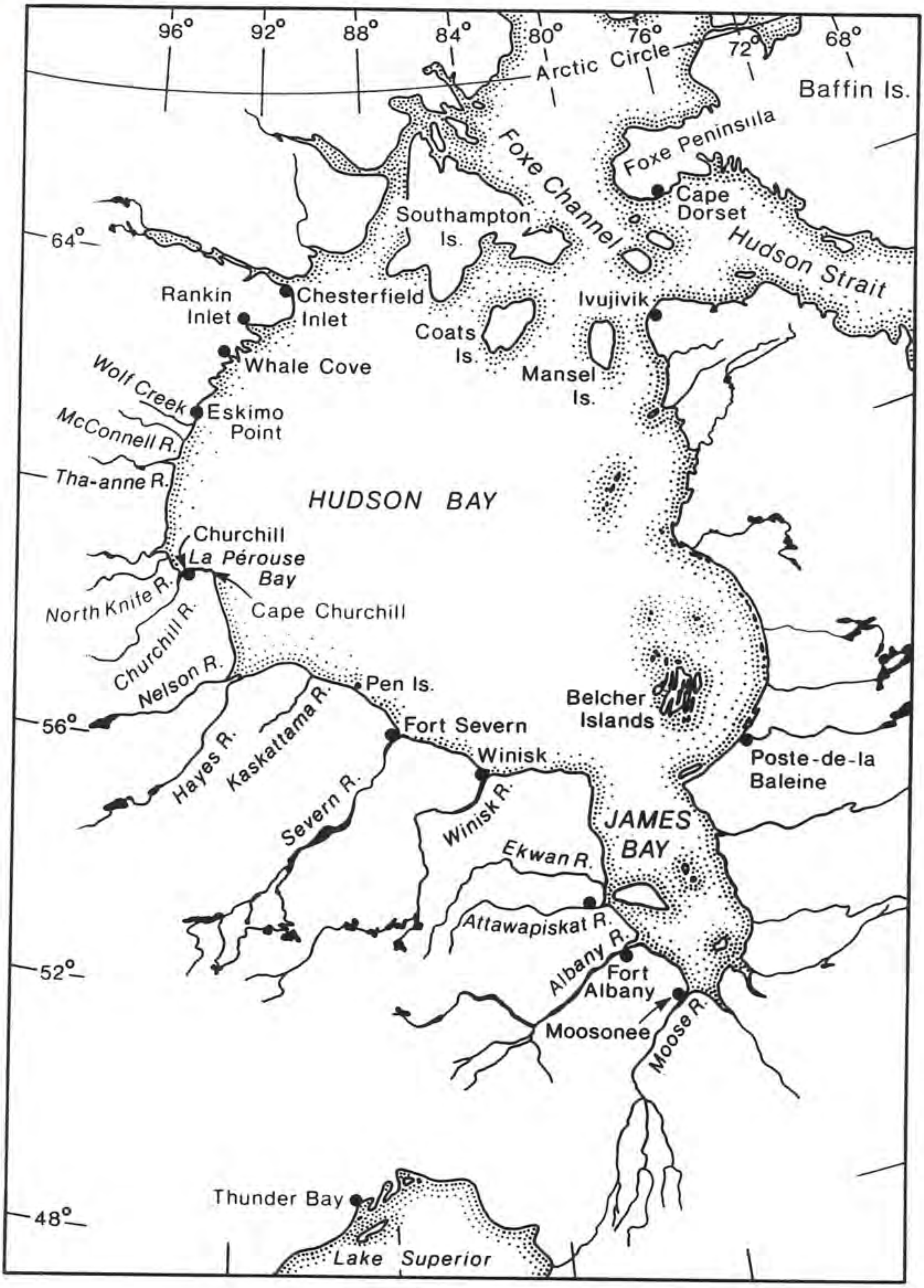
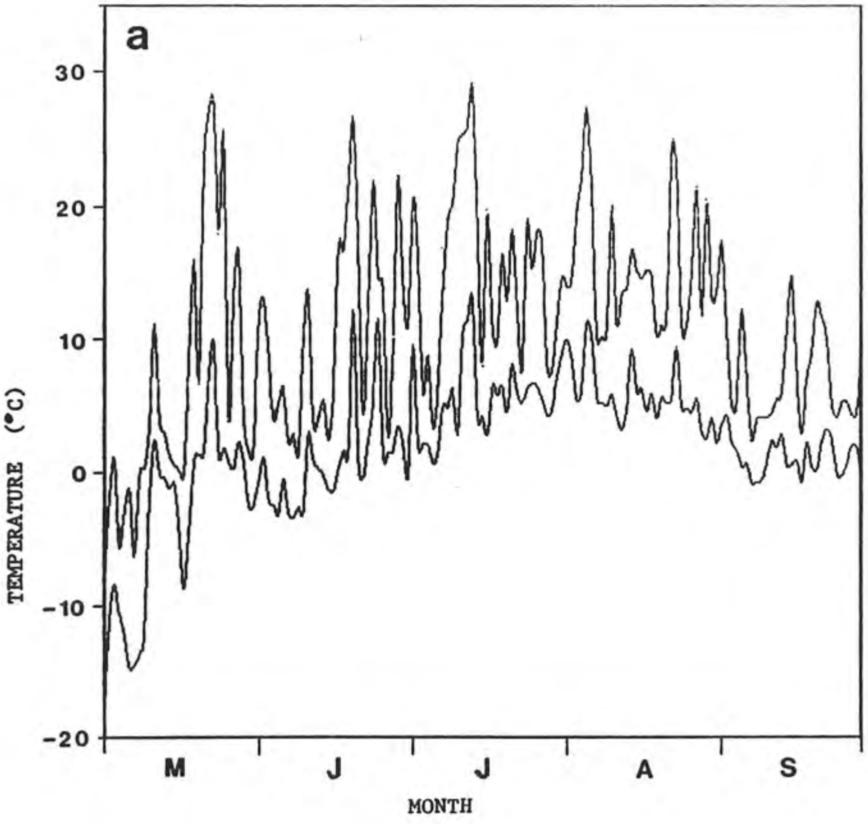

96°
92°
88°
84°
80°
76°
72°
68°
Arctic Circle
Baffin Is.
Foxe Peninsula
Foxe Channel
Cape Dorset
Hudson Strait
Southampton Is.
64°
Rankin Inlet
Chesterfield Inlet
Coats Is.
Ivujivik
Mansel Is.
Whale Cove
Wolf Creek
Eskimo Point
McConnell R.
Tha-anne R.
HUDSON BAY
Churchill
La Pérouse Bay
Cape Churchill
North Knife R.
Churchill R.
Nelson R.
Pen Is.
Belcher Islands
56°
Hayes R.
Kaskattama R.
Fort Severn
Winisk
Poste-de-la Baleine
Severn R.
Winisk R.
JAMES BAY
Ekwan R.
Attawapiskat R.
52°
Albany R.
Fort Albany
Moosonee
Moose R.
Thunder Bay
48°
Lake Superior

Fig. 2-2. Daily maximum and minimum temperatures at Churchill, Manitoba during the summer of 1986 (a) and 1987 (b).


a
30
20
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-10
-20
TEMPERATURE (°C)
M
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J
A
S
MONTH

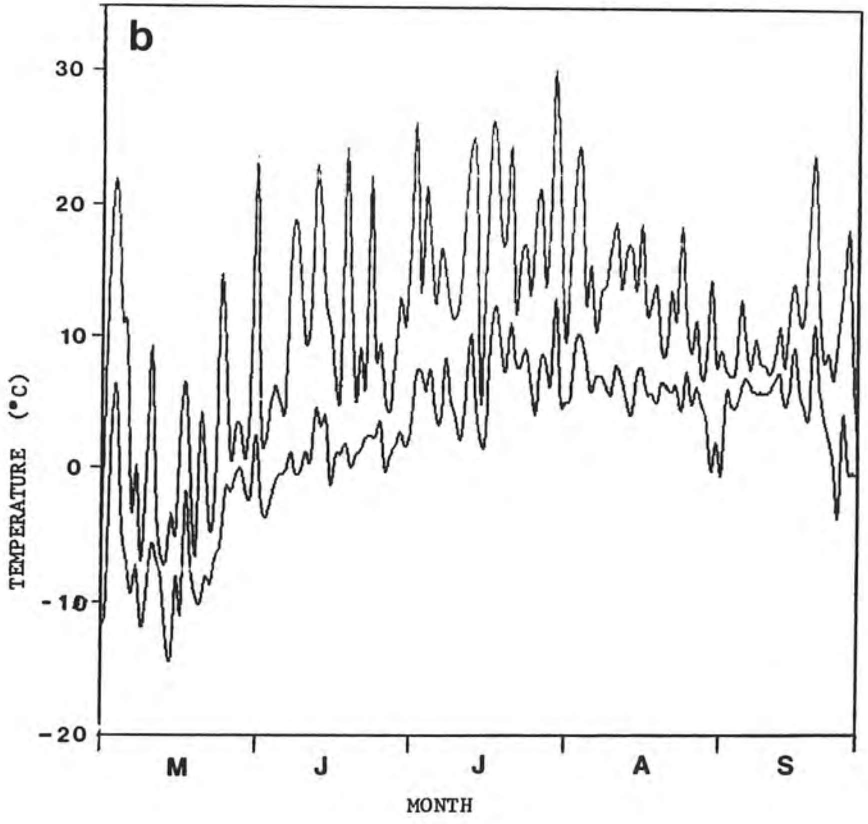

b
30
20
10
0
-10
-20
TEMPERATURE (°C)
M
J
J
A
S
MONTH

TABLE 2-1. Summary of precipitation (rainfall and snowfall water equivalent), bright sunshine hours, and mean high and low temperatures for May, June, July, August and September in 1986 and 1987, and yearly totals. Data compiled from Churchill, Manitoba monthly climatological summary (Environment Canada, Churchill Weather Office).

	1986					
	MAY	JUNE	JULY	AUG.	SEPT.	YEAR TOTAL
Precipitation (mm)						
Rainfall	29.6	103.0	48.8	74.7	40.8	306.0
Snowfall Water Equivilent	0	15.3	0	0	2.4	191.9
Bright Sunshine Hours	287.9	223.6	247.0	233.1	73.7	1821.8
Mean High (°C)	6.0	10.5	14.9	15.6	7.5	
Mean Low (°C)	-3.7	1.0	5.3	6.0	1.2	

	1987					
	MAY	JUNE	JULY	AUG.	SEPT.	YEAR TOTAL
Precipitation (mm)						
Rainfall	3.6	58.7	37.0	66.0	42.0	225.3
Snowfall Water Equivilent	65.4	0.9	0	0	0.2	204.8
Bright Sunshine Hours	196.7	251.0	339.6	233.5	76.0	1831.9
Mean High (°C)	1.7	10.9	17.6	13.8	10.1	
Mean Low (°C)	-6.2	0.9	6.6	5.9	4.3	

caribou (Rangifer tarandus) and meadow voles (Microtus pennsylvanicus). A few species of birds also feed on graminiod vegetation for short periods (both residents (eg. Willow Ptarmigan, Lagopus lagopus albus) and migrants (eg. Snow Buntings, Plectrophenax nivalis nivalis)) (see Savory 1976; Bazely 1987).

Salt marshes, such as those at La Pérouse Bay, are a common physiographic feature along the southern and western coastlines of Hudson Bay. The rate of isostatic uplift along this coast is estimated to be between 0.5 and 1.2 m per century (Hunter 1970; Andrews 1974; Hansel et al. 1983; Scott, Hansel and Fayle 1987). This high rate of uplift combined with the flatness of the land (0.5 to 1.0 m in elevation per km) results in the appearance of an estimated 100 m to 200 m of new shoreline every decade (Martini 1982). In many areas this newly emergent land is utilized by breeding geese (Gaston et al. 1987).

The vegetation of these extensive intertidal flats and emergant sediments at La Pérouse Bay is dominated by Puccinellia phyrganodes (Trin.) Scribn. and Merr., a stoloniferous arctic salt marsh grass. In less saline sites and where freshwater drainage streams dissect the tidal flats Carex subspathecea Wormsk., a rhizomatous sedge, dominates the vegetation, and often Puccinellia and Carex occur in mixed swards. These two species acccount for over 90% of the above-ground standing crop (Bazely and Jefferies 1986). Other species present at low frequencies are Triglochin palustris L., and a number of dicotyledonous species including Potentilla egedii Wormsk., Ranunculus cymbalaria Pursh., Stellaria humifusa

Rottb., and *Plantago maritima* L. The soft sediments of freshwater streams are dominated by *Hippuris tetraphylla* L.. The total area of the salt marsh is about 5.4 km^2 (Cargill and Jefferies 1984b).

Inland from the intertidal flats the vegetation is dominated by several species of willow (especially *Salix brachycarpa* Nutt. and *Salix phylicifolia* L. ssp. *planifolia* (Pursh) Hiitonen), shrub birch (*Betula glandulosa* Michx.), and *Myrica gale* *L.* which establish on frost-heave mounds. Ground cover is composed of *Elymus mollis* Trin., *Carex subspathecea*, *Festuca rubra* L., *Calamagrostis deschampsiodies* Trin., *Dupontia fisheri* R. Br., and a number of other graminoids and herbs (see Jefferies, Jensen and Abraham 1979). Low-lying ground and small pools in this zone are often very saline (Jefferies, Jensen and Abraham 1979; Iacobelli and Jefferies unpublished), and may be colonized by the halophyte *Salicornia borealis* Wolff and Jefferies (Wolff and Jefferies 1987). The willow areas are the primary zone of nesting of Lesser Snow Geese (Hik 1986; Jackson, Hik and Rockwell 1988).

Further inland freshwater ponds and sedge meadows are dominated by *Carex aquatilis* Wahl., *Carex* X *flavicans* Nyl. and *Eriophorum angustifolium* Honck.. Many other graminoids also occur in these fresh-water habitats. Saturated carpets of moss (mainly *Drepanocladus uncinatus* (Hedw.) Warnst.) surround the edges of many ponds. This zone is also used by nesting and feeding geese, although not as heavily as the saltmarsh.

Growth of salt marsh graminiod species is strongly nitrogen- limited (Cargill and Jefferies 1984a; Frey 1988). The accelerated cycling of nitrogen via goose faeces bypasses normal decomposition processes, and provides a renewable source of nitrogen for plant growth during the summer. Fertilization by goose faeces increased the net above-ground primary production of _Puccinellia_ by up to 105%, compared to ungrazed swards; approximately 80% of the annual NAPP was consumed by the geese (Bazely 1984; Cargill and Jefferies 1984b; Bazely and Jefferies 1985). Grazing also prevents the accumulation of litter and limits the formation of a canopy. Because of this, nitrogen-fixing cyanobacteria are able to colonize the surface of the sediment between grazed shoots, thereby increasing the absolute input of nitrogen and replacing nitrogen which the geese export south at the end of each summer (Bazely and Jefferies 1988). Grazing by the geese also retards changes in community compositition, which becomes evident when salt-marsh vegetation is protected from grazing by the erection of exclosures (Bazely and Jefferies 1986).

In spring, before the onset of above-ground plant growth, geese grub for roots and rhizomes of graminiod plants in the salt marsh (mainly _Puccinellia_ _phyrganodes_), which creates patches of disturbed sediments (Jefferies 1988a,b). Approximately 40% of the shoots of _Puccinellia_ are removed by the geese. Small patches are generally recolonized by the remaining plants. Large patches on the other hand, may be seriously and irreversibly damaged by secondary erosion (Jefferies 1988a,b). Grubbing of the graminoids under and around willow vegetation leads to the rapid death of willows by exposing their roots (Iacobelli and Jefferies, unpublished). In the freshwater sedge meadows geese eat the swollen basal portions of shoots of carices in spring. Up to 1600 shoots per m2 may be removed (Kotanen 1987, 1988). Intensive shoot pulling of developing shoots of Carex aquatilis by geese in the spring has been implicated in the production of moss carpets (Jefferies and Kerbes 1985; Kotanen 1987; Jefferies 1988a,b). Leaves of plants of both salt and fresh water marshes are grazed during the summer.

The La Pérouse Bay Snow Goose colony is one of the most southerly breeding grounds and was probably established only recently. Small numbers of geese were first documented nesting in the area during the summers of 1953 (Wellein and Newcomb 1953) and 1957 (Foster 1957). In 1943 no geese were observed nesting in the area (Lumsden, cited in Cooke 1981), and there was no evidence of nesting in previous centuries (Cooke 1981). Hanson et al. (1972) reported no nesting in 1962, but at least 2500 pairs of geese nested in 1963, and successful nesting by large numbers of geese has been documented every year since then. This large increase in 1963 may be explained by a group of nesting birds, destined for breeding colonies further north, which were forced to nest at La Pérouse Bay due to adverse weather conditions (see Geramita and Cooke 1982 for recent documentation of a similar immigration). This original group of immigrants formed the nucleus of the colony which continued to persist as their offspring returned. This is a consequence of strong female natal philopatry (Abraham 1980; Cooke and Abraham 1980). Between 1968 and 1987 the colony increased in size from 1200 to 8000 breeding pairs, reaching a peak of 9700 in 1983. Recent estimates of colony size have been confounded by the geographic expansion of nesting areas beyond the boundaries of the traditional colony. Detailed studies of the breeding biology, behaviour, genetics and ecology of Lesser Snow Geese at La Pérouse Bay have been conducted continuously since 1968 (see Cooke *et al*. 1982), and of the interactions between geese and local plant communities since 1978 (see Jefferies 1988a).

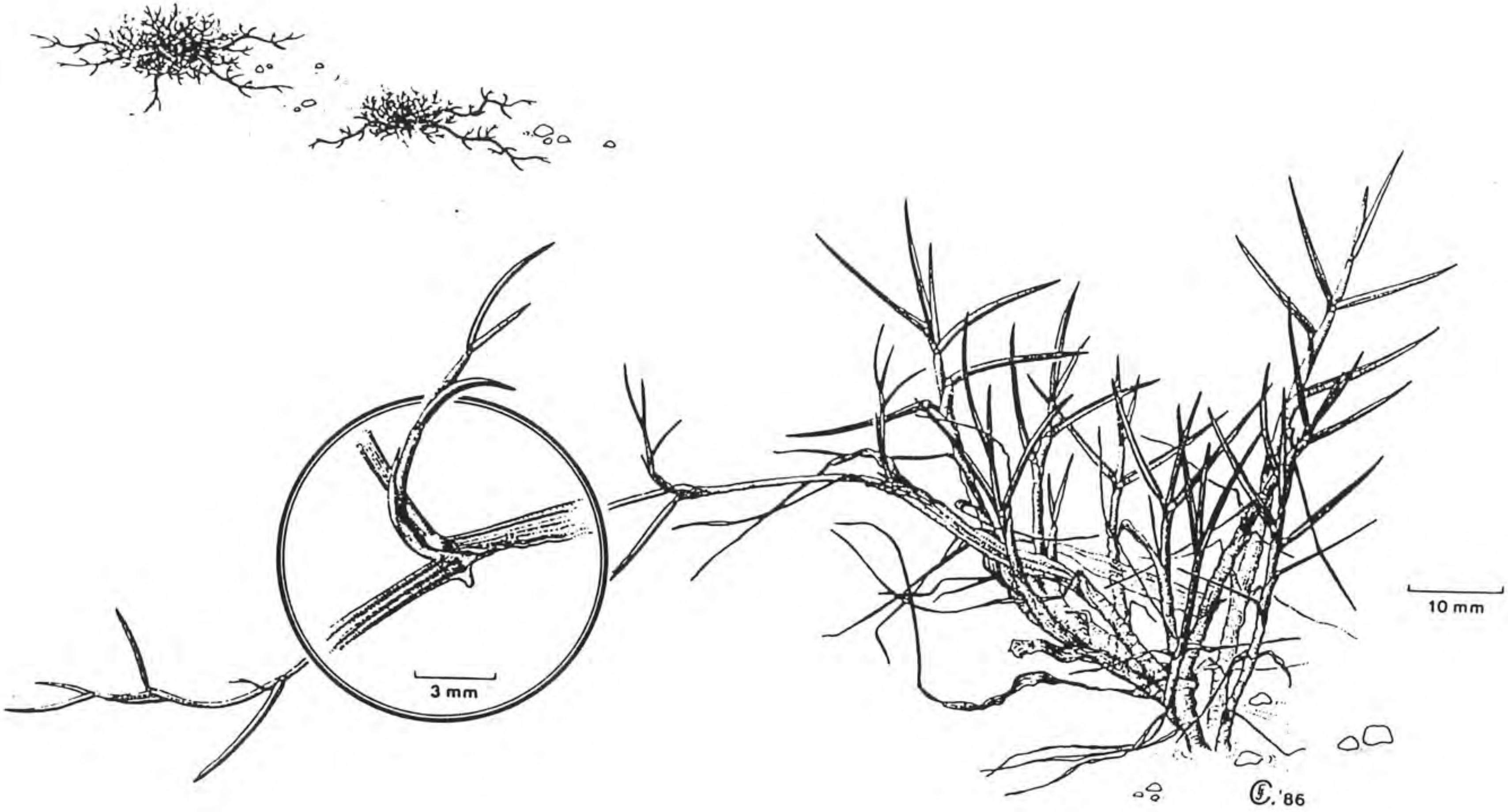
2.2 Biology of *Puccinellia phyrganodes*

Puccinellia phryganodes (Trin.) Scribn. and Merr. is the dominant grass species on the salt marsh flats at La Pérouse Bay. The *Puccinellia* genus contains generally caespitose or stoloniferous, yellowish-green, smooth grasses found in alkaline or saline environments (Porsild and Cody 1980). *P. phryganodes* is a halophyte that dominates arctic and sub-arctic coastal marshes and it has a circumpolar distribution (Polunin 1940; Hulten 1968; Porsild and Cody 1980). It is the primary colonist of intertidal mud flats and unconsolidated silt in arctic coastal areas (Jefferies 1977).

P. phryganodes is a stoloniferous species that forms caespitose or densely tufted mats (Fig. 2-3). It often occurs in pure swards, or in association with another common graminoid, Carex subspathacea Wormskj., a rhizomatous sedge. Grazed swards of P. phyrganodes at La Pérouse Bay rarely exceed 2 cm in height (Cargill 1981), although ungrazed plants may grow to 15 cm (Polunin 1940; personal observation). Typical of many grasses, the apical meristem is close to the ground in Puccinellia. This highly active region of growth produces leaf primordia, which eventually form nodes, on opposite sides, just beneath the meristem (Langer 1979). Each primordium is completely meristematic at the beginning of its development, but soon is restricted to an intercalary meristem at its base. Puccinellia forms extra-axillary (extravaginal) shoots which act as stolons and have the capability of rooting at their nodes. Puccinellia contains low amounts of crude fiber and silica, no known secondary defensive compounds and has a high concentration of nitrogen in its tissue (Cargill and Jefferies 1984b). Thus it is particularly high quality goose forage.

P. phryganodes is a sterile triploid (2n = 21) in the Hudson Bay region, which rarely flowers and is not known to set seed (Polunin 1940; Bowden 1961; Dore and McNeill 1980; Jefferies and Gottlieb 1983; Sadul 1987). Pollen is sterile. P. phryganodes reproduces vegetatively by extensive clonal propagation, however dispersal mechanisms are effective. Ice rafting, tidal action and spring runoff all are means by which pieces of the plant are transported around the saltmarsh. Broken shoots and leaves of P. phryganodes are able to root in soft sediments and rapidly colonize soft sediments and

Fig. 2-3. Diagram of the growth habit of of <u>Puccinellia phryganodes</u> (Trin.). Scribn. and Merr. The positioning of an axillary shoot is magnified.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disturbed sites (Jefferies, unpublished).

Sadul (1987) has detected considerable electrophoretic variation amoung plants from La Pérouse Bay. This variation in the population appears to be maintained by frequent abiotic and biotic disturbances, followed by recolonisation (Sadul 1987; Jefferies 1988a). There is also considerable morphological variation among individuals. This variation may reflect the fact the there is selection for genets with slow growth rates in ungrazed sites and selection for genets with faster growth rates under grazed conditions (also see Gray and Scott 1980).

2.3 Biology of Lesser Snow Geese

2.3.1 Distribution

Snow geese are members of the tribe Anserini, in the family Anatidae, the ducks, geese and swans. Currently two subspecies of snow geese are recognized: the Lesser Snow Goose (<u>Chen</u> <u>caerulescens</u> <u>caerulescens</u> (L.) Gundl.) and the Greater Snow Goose (<u>C.</u> <u>c.</u> <u>atlantica</u> Kennard) (Godfrey 1979; Owen 1980). The two subspecies are distinguished on the bases of their sizes and distribution. In addition, Lesser Snow Geese display a conspicuous "white" or "blue" plumage polymorphism. The blue phase is rarely observed in the Greater Snow Goose

(Cooke and Cooch 1968). The Lesser Snow Goose is the subspecies occuring at La Pérouse Bay, Manitoba.

The eastern Arctic population of Lesser Snow Geese numbers about two million birds (Boyd, Smith and Cooch 1982). This population has been increasing rapidly over the past two decades (MacInnes and Kerbes 1987; Cooch 1988). The geese winter on the Gulf coast of Texas and Louisiana, and are becoming increasingly common in grain fields in the midwest States along the Central and Missisippi flyways. These geese nest in colonies in the south and west coasts of Hudson Bay, the southwest coast of Baffin Island, Southhampton Island, and the smaller islands in the Foxe Basin and Hudson Bay (Gaston et al. 1987).

Snow geese are usually monogamous and females return with their mates to their natal colonies to breed (Cooke, MacInnes and Prevett 1975). The consequences of this female natal philopatry on the genetic structure of the La Pérouse Bay population is approximately 50% gene flow (from males) each generation (Rockwell and Cooke 1977; Rockwell and Barrowclough 1987). Female snow geese display strong local philopatry at La Pérouse Bay, generally nesting within 500 m of their previous nest site (Abraham 1980; Cooke et al. 1983; Hik 1986).

2.3.2 Reproduction and growth

The arrival of snow geese on the colony is generally coincident with snow melt (Abraham 1980; Davies and Cooke

1983). Females begin to lay eggs soon after arriving. Nests are generally located on snow-free willow hummocks (Abraham 1980; Jackson, Hik and Rockwell 1988). Modal clutch size is four, however there has been a systematic decline in clutch size (about 0.5 egg) over the past 15 years (Cooch _et_ _al_. 198N). The duration of the incubation period is approximately 23 days and goslings hatch in late June or early July. During this period incubating females may lose up to 20% of their body weight (approx. 400 g; Ankney and MacInnes 1978). Hatching is synchronous, occurring at all nests within a two week period (Findlay and Cooke 1982). Following hatch, adults and goslings graze intensively on the salt-marsh vegetation. At this time the population of geese on the colony may exceed 30,000. Both adults and goslings are flightless during this period. Their demand for forage is very high. In a six week period the goslings increase in weight from 80 g to over 1500 g, and females regain weight lost during incubation. By fledging (six weeks) the size of each brood has been reduced to approximately two goslings (Cooke _et_ _al_. 1985; Rockwell, Findlay and Cooke 1987), a consequence of predation by jaegers, gulls, Arctic foxes, wolves and polar bears, and disease. Obtaining sufficient quantities of high quality forage may also be a problem in some years, leading to increased gosling mortality.

2.3.3 Foraging behaviour and digestive physiology

The diet of Snow Geese is dominated by graminoids. On the wintering grounds and on the migration flyways their diet consists primarily of the roots and rhizomes of plants of coastal marshes. The most important forage plants include species of Scirpus, Spartina, Distichlis, and Typha (Lynch, O'Neil and Lay 1947; Burton, Hudson and Bragg 1979; Owen 1980; Smith and Odum 1981; Smith 1983; Bedard, Nadeau and Gauthier 1986). In the past decade waste rice and corn, and cereal stubble on farmland along the flyway and Gulf coast have become important sources of forage during the migrations and during the winter months (Reed 1976; Bedard, Nadeau and Gauthier 1986). Grubbing for forage during this time of year is often destructive (Lynch, O'Neil and Lay 1947; Smith and Odum 1981; Smith 1983). In spring this destructive grubbing also occurs on the breeding grounds, as the geese often arrive prior to melt and the commencement of plant growth (Jefferies 1988a,b).

Many studies have indicated that the critical factor determining the success of breeding is the amount of food available to parents for building up body reserves prior to breeding (see Perrins 1970; Sinclair 1977; Teunissen, Spaans and Drent 1985). Thus forage aquisition during the spring migration is critical for breeding Snow Geese (see Wypkema and Ankney 1979; Davies and Cooke 1983; Hamman, Andrews and Cooke 1986). The preferred foods during this time include the roots, rhizomes and young shoots of marsh plants. Prevett, Marshall and Thomas (1979, 1985) found that migrating geese in James Bay consume about equal proportions of below- and above-ground tissue of grasses (mainly Puccinellia phryganodes), sedges, Triglochin spp. and Equisetum spp.. Geese feed selectively on the parts of plants which have the highest nitrogen content (Thomas and Prevett 1980, 1982).

During the summer at La Pérouse Bay geese feed primarily on two saltmarsh graminoids, Puccinellia phryganodes and Carex subspathacea. Calamagrostis deschampsiodies is also frequently eaten. In freshwater areas Carex X flavicans and Carex aquatilis are common forage sedges. These areas are intensively used from the end of June following hatch until mid-August when the birds begin their southward migration. Although goose families are initially limited to feeding areas within a few kilometers of their nest, as the goslings increase in size families may travel further (up to 50 km) in search of forage (McLaren and McLaren 1982; R.F. Rockwell, unpublished data for LPB).

Geese spend 70-80% of their time feeding during the summer (Sedinger and Raveling 1986; Lessels 1987; Rockwell, unpublished data), and are characterised as having continuous flow digestive systems (Sibly 1981; Penry and Jumars 1987). Geese have small gut capacities and relatively high metabolic rates and thus must maintain high rates of forage intake to meet their metabolic requirements (Demment and Van Soest 1983). Survival and reproductive success is critically dependent on a continual supply of energy and nutrients. Geese tend to choose food that is relatively easy to digest, and which has few mechanical or biochemical defences against herbivory. The optimal strategy for geese apparently is to maximise the rate of intake of energy or more often, some limiting nutrient (Sibly and Calow 1986).

The daily intake of an adult goose weighing 1500 to 1800 g is estimated to be 350-520 g dry weight of forage (Cargill and Jefferies 1984b). The throughput time (or rate of passage) in geese is estimated to be 30 to 150 minutes (Owen 1975; Burton, Hudson and Bragg 1979), and adult geese defecate about every 5 minutes (Cargill and Jefferies 1984a). One consequence of this rapid throughput is that the efficency of digestion is poor (Mattocks 1970; Demment and Van Soest 1983). Buchsbaum, Wilson and Valiela (1986) estimate that Brant and Canada Geese digest 36-39% of organic matter and 28% of cellulose. These values are similar to estimates for Lesser Snow Geese which retain 34% of the dry weight of forage (Cargill and Jefferies 1984a). Protein digestion is considerably higher (61-80%), however geese, like most herbivores, have difficulty obtaining sufficient nitrogen in their diet (Mattson 1980; Buchsbaum, Wilson and Valiela 1986; Sedinger and Raveling 1986).

Feeding preferences of geese are correlated with forage digestability and the nitrogen content of forage (Harwood 1974, 1977; Owen 1975, 1976; Owen, Nugent and Davies 1977; Boudewijn 1984; Sedinger and Raveling 1984, 1986). Buchsbaum, Valiela and Swain (1984) report that Canada Geese avoided feeding on plants with a high phenolic content. It is generally agreed that the digestive physiology and feeding behaviour of geese maximizes protein intake at the expense of digestive efficiency (Sibly 1981; Sibly and Calow 1986; Buchsbaum, Wilson and Valiela 1986), however food intake is still limited by the processing rate (Sedinger and Raveling 1988).

A number of potentially pathogenic parasites (associated with feeding) are also prevelent in Lesser Snow Geese at La Pérouse Bay (Wobeser 1981; Gajadhar, Cawthorn and Rainnie 1982; Rainnie 1982). These include renal coccidia (Eimeria spp.), gizzard nematode infections, typhlitis infections and a blood protozoan parasite (Leucocytozoon simondi). These diseases are important in the context of food resources because the first three are transmitted via faeces. Contamination of the limited snow free area by infected birds arriving on the colony in spring, combined with increased susceptability to infection at this time may result in the increased prevalence of disease in the population (Rainnie 1982). The population dynamics of snow geese are influenced by these parasites, which in turn are dependent upon the colonial feeding habits of the geese.

2.4 The use of captive goslings in experimental studies

Pattern and process in natural ecosystems can only be understood by experimentally manipulating various components of the system. This is particularly true of grazing systems where there are many levels of interactions at all trophic levels. The experiments discussed in the following chapters were conducted using captive goslings. This permitted control of the level of grazing on specific plots of vegetation and control of nutrient input from faeces.

Goslings were collected within hours of hatch from the nests of wild geese. The goslings were returned to the camp and raised in captivity. Guidelines for the experimental handling of animals in research issued by the University of Toronto, and permit requirements for migratory waterfowl issued by the Canadian Wildlife Service were strictly adhered to. Goslings were raised on a diet of Puccinellia and Carex aquatilis, supplemented by Purina 8815 Duck Growena or dry dog food. Diet was not supplemented on the day prior to experiments.

Goslings double in weight approximately every 7 days (Fig. 2-4). Asymtopic weight of about 1600 g is reached about six weeks after hatch. Differences in the growth rate of wild and captive raised goslings have been observed in other studies (Aubin, Dunn and McInnes unpublished), but the composition of body tissues and the feeding behavior of wild and captive goslings does not appear to differ. Pecking rates of wild goslings are not significantly different than those measured for captives (Fig. 2-5). Similar seasonal patterns in growth and pecking rate were observed by Sedinger and Raveling (1988). Captive goslings behave much like wild goslings in most respects, however they are much easier to manipulate experimentally.

Fig. 2-4. Growth of captive goslings of the Lesser Snow Goose at La Pérouse Bay in 1987. Increases in mean weight (mg) of between 40 and 8 goslings were determined on a number of occasions following hatch (23 June 1987).

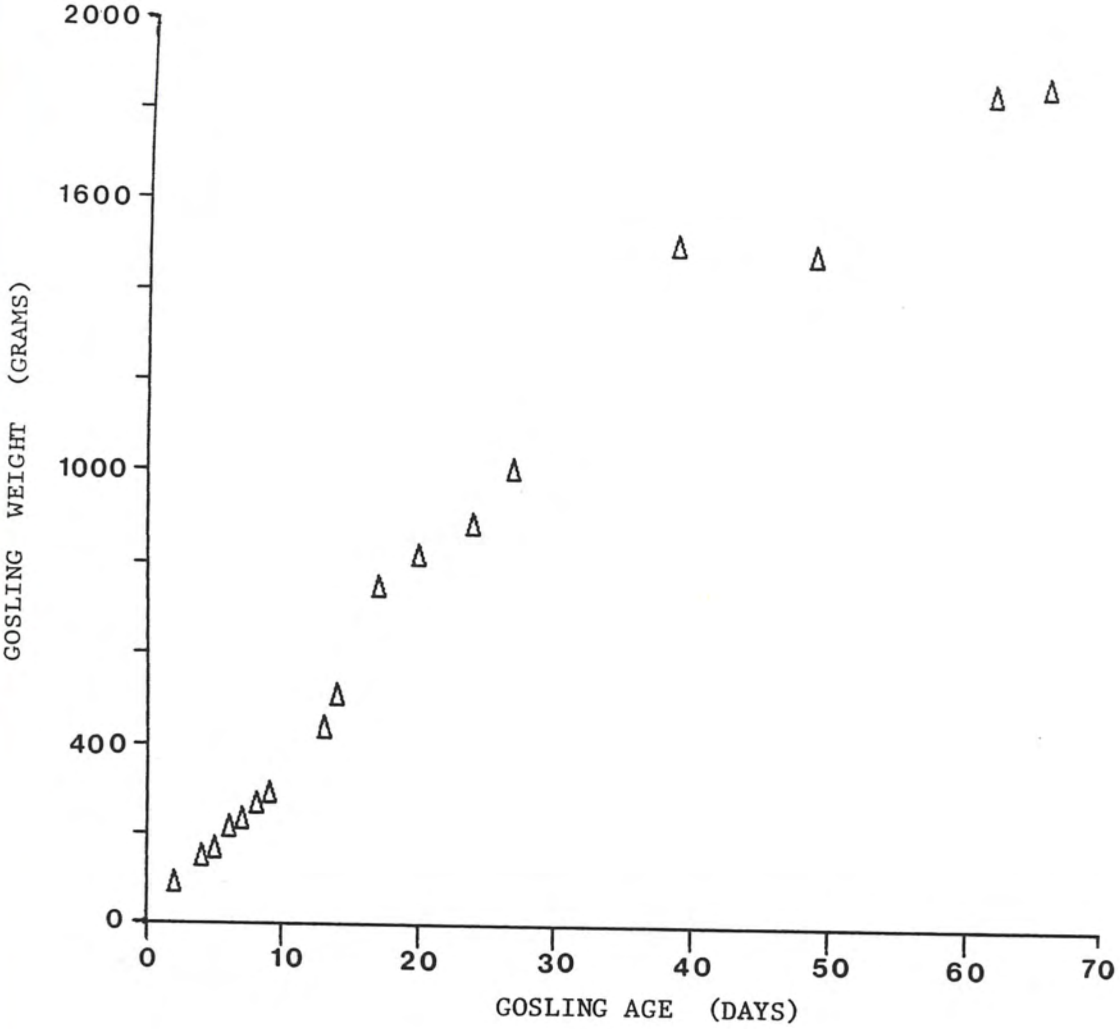
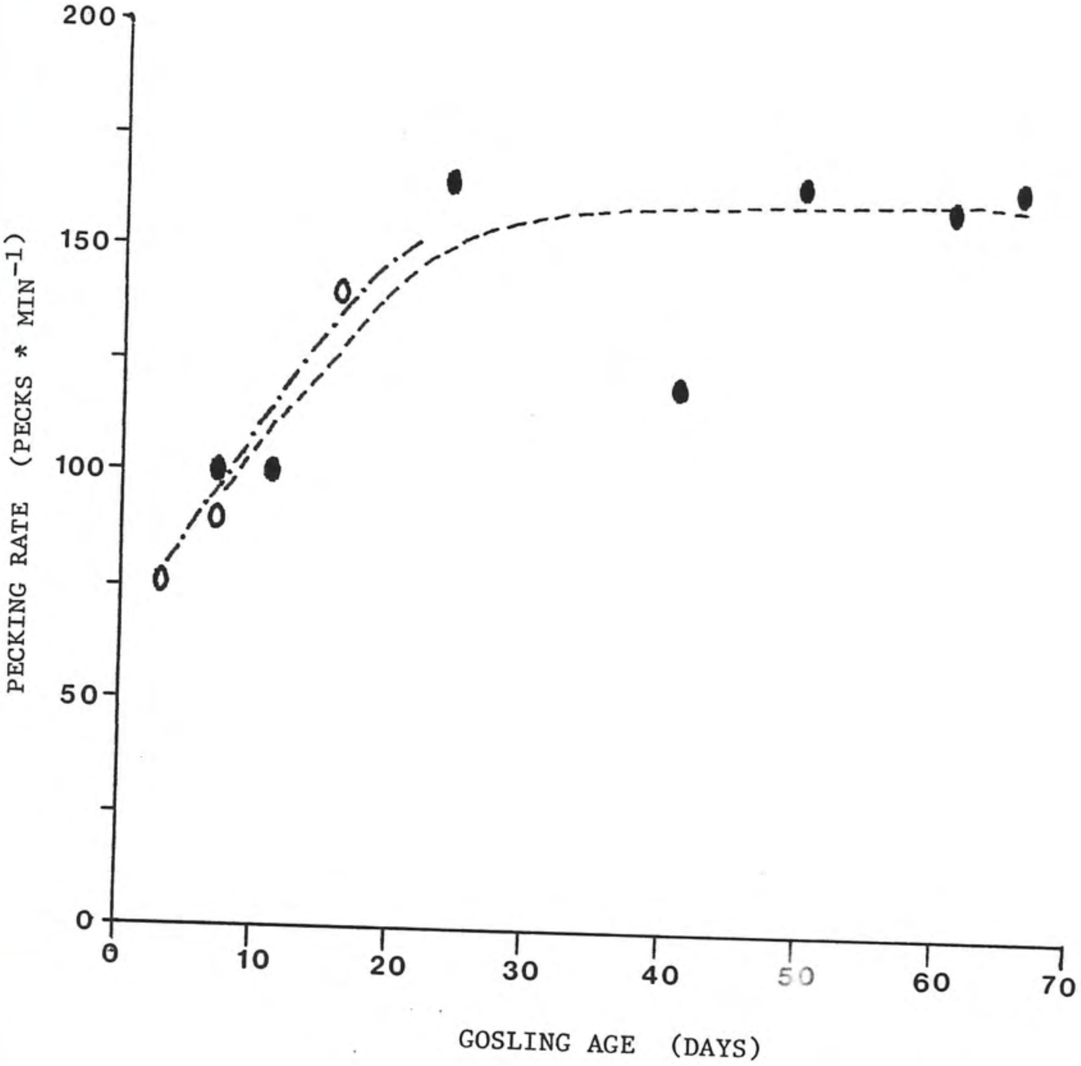

2000
1600
1000
400
0
GOSLING WEIGHT (GRAMS)
0
10
20
30
40
50
60
70
GOSLING AGE (DAYS)

Fig. 2-5. Comparison of pecking rate of wild (o) and captive (●) goslings at La Pérouse Bay. Pecking rates for captive goslings were determined for Puccinellia vegetation during the summer of 1987. Rates for wild goslings were measured on mixed Puccinellia-Carex sward (see Lessels 1987). Lines fitted by eye.


PECKING RATE (PECKS * MIN^{-1})
200
150
100
50
0
0
10
20
30
40
50
60
70
GOSLING AGE (DAYS)

CHAPTER 3: WITHIN SEASON INCREASES IN THE NET ABOVE-GROUND PRIMARY PRODUCTION OF A SALT MARSH FORAGE GRASS: A TEST OF THE HERBIVORE-OPTIMIZATION MODEL

3.1 INTRODUCTION

Plant-herbivore interactions cannot be considered in isolation from the ecosystems in which they occur. Herbivores affect primary and secondary production, energy flow and nutrient cycling, and the structure and composition of plant communities (Harper 1969; Crawley 1983; Vitousek 1984). The herbivore optimization model (Dyer 1975, McNaughton 1979, 1983a,b; Hilbert *et al*. 1981; Dyer *et al*. 1982; Jefferies 1988a), predicts that one of the effects of herbivory on plant production is the enhancement of net primary production of forage plants above that of ungrazed plants, at moderate levels of herbivory. Circumstantial evidence in support of this prediction has come primarily from studies of the responses of terrestrial graminoid communities (McNaughton 1976, 1979; Prins, Ydenburg and Drent 1980; Cargill and Jefferies 1984b) and aquatic algal and coral communites (Ogden and Lobel 1978; Bjorndahl 1980; Bergquist and Carpenter 1986; Carpenter 1986; Power, 1987) to herbivory. The generally applicability of these results remains highly controversial (Stenseth 1978, 1983; Belsky 1986a, 1987; McNaughton 1986a; Crawely 1987).

Intrinsic mechanisms that operate at the level of individual plants and/or extrinsic mechanisms that involve processes at the ecosystem level have been proposed to account for the increase in net primary production of forage plants at moderate intensities of herbivory (McNaughton 1983a,b). These include photosynthetic *compensation, reallocation of resources for growth*, changes in morphology and leaf turnover rates, and fertilization by faeces and urine.

We conducted a critical test of the herbivore optimization model using captive goslings of the Lesser Snow Goose (Chen caerulescens caerulescens L.) which grazed on graminoid vegetation of a sub-arctic salt marsh. Plant growth in this marsh is strongly nitrogen-limited (Cargill and Jefferies 1984a). Previous studies have shown that grazing by snow geese significantly increased the net above-ground primary production (NAPP) of a stoloniferous salt-marsh grass, Puccinellia phryganodes (Trin.) Scribn. and Merr., and a rhizomatous sedge, Carex subspathacea Wormsk., from 30% to 105%, depending upon the year, compared to corresponding values in ungrazed swards of these two species (Cargill and Jefferies 1984b; Bazely 1984). A consequence of the intense grazing is that plant tissue is converted into either goose biomass or faeces, instead of accumulating as live plant biomass or litter. Nitrogen released from goose faeces accelerates the supply of this element to the sediments. In addition, patches of sediment (0.5 cm diameter) are colonized by cyanobacteria that contribute to the long-term input of nitrogen, as a result of nitrogen fixation (Bazely and Jefferies 1988).

Detailed demographic studies have shown that plants of *Puccinellia phryganodes* are capable of increasing the production of shoots and leaves in resonse to grazing (Bazely and Jefferies 198N). In contrast, plants of *Carex subspathacea* increase leaf production following grazing (Kotanen and Jefferies 1987). The persistence of the grazed graminoid swards is strongly dependent on the colonial feeding behaviour of the geese (Bazely and Jefferies 1986). There is selection for biotypes of *Puccinellia* with faster growth rates under grazed conditions (Sadul 1987). The ability of both *Puccinellia* and *Carex* to show rapid growth responses within the season compensates for the adverse effects of defoliation *per se* on net above-ground primary production (Sadul 1987; Jefferies 1988a). A continual supply of high quality forage is produced during a period when it is most required by the geese.

Although it is evident that grazing by snow geese leads to enhanced NAPP of the grazed sward, interrelationships between intensity of clipping, fertilization from faecal nitrogen, and forage regrowth and quality, can only be determined experimentally under controlled conditions. We have used captive goslings to investigate the dynamics of the overall effects of grazing (grazing, addition of faeces, trampling) on plant production on the salt marsh flats at the La Pérouse Bay. In this study the following questions have been addressed.

1. What is the effect of increasing periods of grazing (grazing intensity) on NAPP and forage quality?

2. Does grazing affect NAPP and forage quality in the same way throughout the summer?

3. If grazing results in the enhancement of NAPP what mechanism(s) account for this, and how is this related to the intensity of herbivory? Faeces may be either left on or removed from the grazed plots to assess the importance of nutrients in faeces to the regrowth of vegetation following grazing.

3.2 METHODS

3.2.1 Study site

Over 8000 pairs of Lesser Snow Geese breed each summer at La Pérouse Bay, 25 km east of Churchill, Manitoba, Canada, (58°, 24′ N, 94°, 24′ W), on the west coast of Hudson Bay. Following the hatch of goslings in late June or early July, the geese forage intensively on the vegetation of the intertidal salt marsh, dominated by either *Puccinellia phryganodes*, a stoloniferous grass, or *Carex subspathacea*, a rhizomatous sedge which is abundant in less saline areas. The intertidal grazing lawn is about 2.5 cm high. There are over 4000 shoots of these species per square meter and very few shoots (< 5%) escaped the effects of grazing (Kotanen and Jefferies 1987; Bazely and Jefferies 198N). By the second week of August the geese begin their autumn migration and leave the salt marsh. Permanent snowfall and the cessation of plant growth occurs in late September. A complete description of the study area is provided in Jefferies, Jensen and Abraham (1979) and Jefferies (1988a).

3.2.2 Experimental trials

All experiments were conducted using captive goslings. The goslings were removed from nests of wild geese within 24 hours of hatching and were raised in captivity in the research camp. Goslings were fed a diet of natural foods (mainly Puccinellia phryganodes and Carex aquatilis), supplemented with a daily ration of Purina 8815 Duck Growena, or dry dog food, except on the days prior to an experiment. Prior to each experiment the weight of the goslings was determined (Table 3-1). Depending upon the number of goslings required for each experiment, those which were greater than 1 S.E. (larger or smaller) than the mean in weight were excluded from the grazing trials.

Experimental plots were established prior to each experiment on selected areas of saltmarsh vegetation dominated by Puccinellia. Each plot was 1m x 1m. Four replicates for each grazing treatment were established in a completely randomized block design. On the morning of the experiment, goslings were randomly assigned to a plot and allowed to graze for a specific period. The number of goslings per plot and the period of grazing was adjusted during the season as the goslings increased in weight and their foraging efficency increased (Table 3-1). Grazing times varied from 0 to 150 minutes at intervals of 15 or

TABLE 3-1. Dates on which grazing experiments were conducted at La Pérouse Bay, Manitoba and mean gosling weights and number of goslings grazed per plot for each experiment.

Experiment	date	mean gosling wt (g)	goslings per plot
1	23/6/86	130	4
2	2/7/86	371	4
3	13/7/86	539	3
4	1/8/86	1273	3
5	10/8/86	1420	2
6/7	1/7/87	247	4
8/9	11/8/87	1478	2

30 minutes. The extreme grazing levels (120 and 150 minutes) exaggerated the overall effects of grazing well beyond natural levels. At the end of the grazing trials all plots were exclosed with chicken wire to prevent further grazing by wild geese.

Five experiments were conducted in 1986 (23 June; 2, 17 July; 4, 11 August). The feeding activity of the goslings was monitored at intervals of 10 or 15 minutes during each experiment. Goslings spent at least 90% of their time feeding. In 1987 Experiments 6/7 and 8/9 were conducted on 1 July and 12 August respectively. Paired plots (1m x 1m) were established on a Puccinellia sward. Both sets of plots received identical grazing treatments, however in one set of plots faeces were removed at intervals of ten minutes during the experiments. This was to ensure that nitrogen was not transfered from the faeces into the plants or sediments. At the end of the experiments the number of faeces deposited on each plot was counted, and some of these were randomly selected, and returned to the laboratory for determinations of their water content and dry weight, and amounts of soluble and total nitrogen present in individual droppings.

3.3.3 Sampling and data analysis

Above-ground biomass was sampled by removing a 7.5 x 7.5 cm turve at random from each of the plots before grazing, after grazing, and at intervals of approximately 12 days for the duration of the summer. The above-ground biomass was removed by clipping the sward at ground level. Since approximately 90% of the biomass was live, dead material was not removed prior to biomass or nitrogen determinations. The plant material was washed and then dried at 60-80°C for 24 hr. Dry weights of the material were determined using a Mettler (PK-300) electronic balance. Determinations of amounts of carbon and nitrogen present in dried faeces and plant tissues were made using a LECO series 600 CHN autoanalyser (St. Joseph, MI., USA). All material was ground (20 mesh size) in a Wiley mill and appropriate quantities (approx. 100 mg) were preweighed before combustion in the analyser. Soluble nitrogen of fresh goose faeces was determined in 1987 using the phenol-sodium hypochlorite method (Solorzano 1969) after extraction over 12 h with a solution of 1 M KCl. Approximately 6 g of fresh goose droppings were suspended in 40 ml of solution.

Analysis of Variance (ANOVA) was used to assess all treatment effects. Data sets were transformed prior to analysis if variance was heterogenous. Significant interaction terms of two-way ANOVA's were investigated using trend analysis (Kirk 1982). Using this approach, the between-group sum of squares can be partitioned into a number of trend components (linear, quadratic, cubic) reflecting orthogonal trend contrasts. The efficacy of the trend components was measured by $\hat{\omega}^2$, the strength of association. This statistic was calculated in conjunction with the trend analyses (Kirk 1982; Keppel 1982). The magnitude of the effect measured by $\hat{\omega}^2$ is considered to be large when $\hat{\omega}^2 > 0.15$, and moderate when $\hat{\omega}^2 > 0.06$ (Keppel 1982).

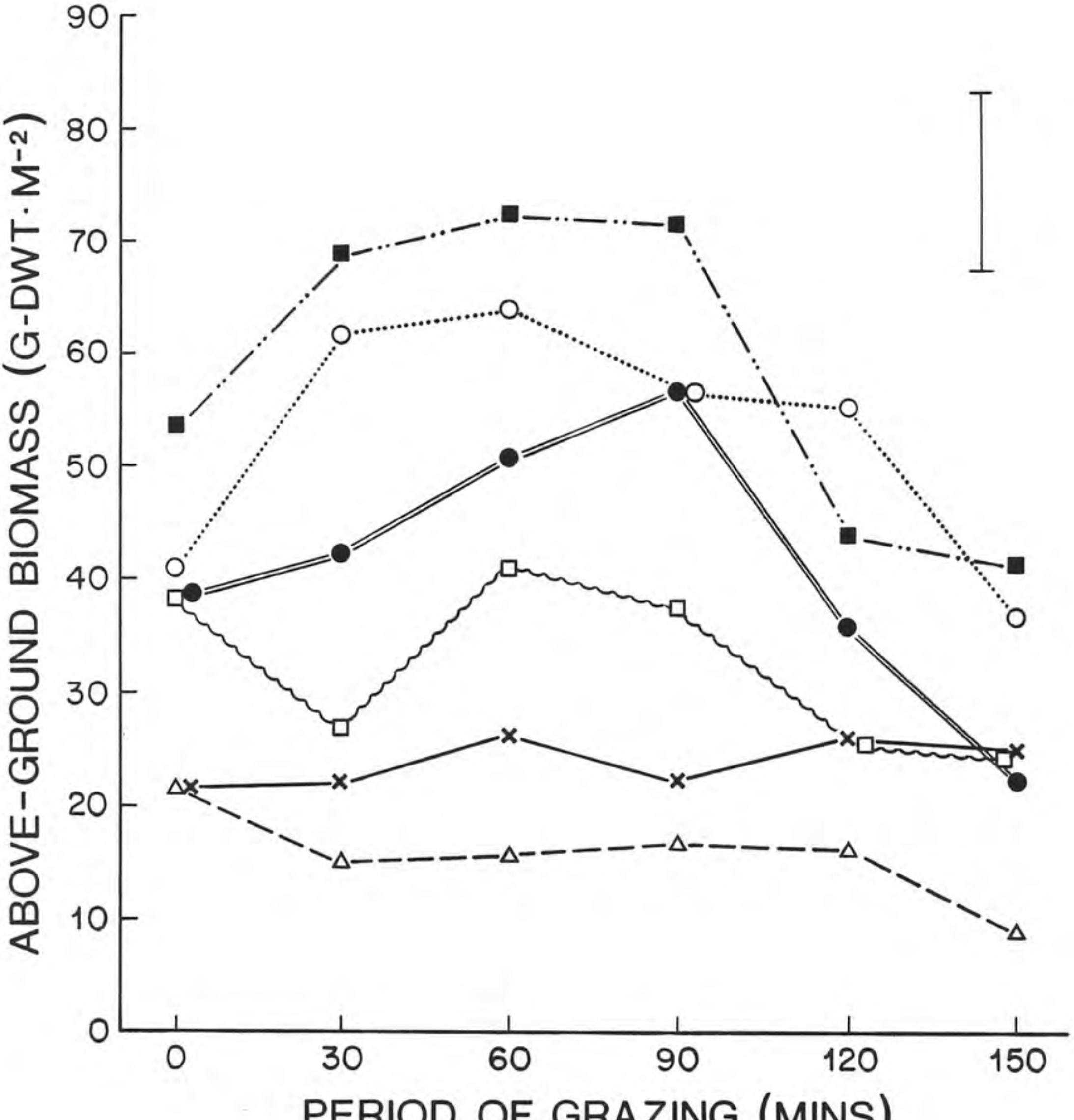
3.3 RESULTS

3.3.1 Changes in above-ground biomass following grazing

The ability of Puccinellia swards to regrow following grazing late in the spring (23 June 1986) is shown in Fig. 3-1. At 30, 60 and 90 minutes of grazing significant increases in above-ground biomass compared to that of ungrazed plots were detected after 24, 36 and 48 days of regrowth. At the extreme grazing levels (120 and 150 minutes), no enhancement of growth is evident, possibly because of damage to meristems as a result of grazing and trampling. The results of a two-way ANOVA indicate that both main effects are significant (harvest time: $F[5,108] = 66.98$, $p < 0.001$; grazing treatment: $F[5,108] = 11.76$, $p < 0.001$). In addition the time x treatment interaction is significant ($F[25,108] = 2.15$, $p < 0.004$). This interaction can be explained by the change in the shape of the growth response curves from a linear to an approximate quadratic function 24, 36 and 48 days after grazing. Over half of the variance of an a posteriori trend analysis (Kirk 1982) can be explained by a quadratic term after 24, 36 and 48 days of regrowth (71%, 85% and 53% respectively; $\hat{\omega}^2 > 0.15$).

The ability of Puccinellia to recover from the effects of grazing apparently decreases over the course of the summer (Fig. 3-2). With each successive experiment the maximum amount of regrowth of the Puccinellia sward occurs in plots which have received shorter periods of grazing. In Experiment 2 (2 July) the greatest amount of

FIG. 3-1. Increase in above-ground biomass of _Puccinellia phryganodes_ following grazing on 23 June, 1986 by goslings of the Lesser Snow Goose in Experiment 1 (mean values of 4 plots). Each plot was 1 m2 in which four goslings grazed. Error bar is Tukey's honestly significant difference. Before grazing (x); after grazing (△); 12 days regrowth (□); 24 days regrowth (●); 36 days regrowth (o); 48 days regrowth (■).


ABOVE-GROUND BIOMASS (G-DWT·M-²)
0
10
20
30
40
50
60
70
80
90
0
30
60
90
120
150
PERIOD OF GRAZING (MINS)

regrowth of vegetation occurred in plots which had been grazed for 15, 30 and 60 minutes, whereas in Experiment 3 (17 July), the standing crop was highest in the plots grazed for 15 and 30 minutes. As in Experiment 1, the time, treatment and interaction terms of the ANOVA are significant for both these experiments (Table 3-2). Although there is tendency for the curves of above-ground biomass to become unimodal, the quadratic term is not significant for any interval following grazing in Experiments 2 and 3. The proportion of the variance explained by a quadratic term in Experiment 2 after 24 and 36 days regrowth is only 14% and 18% respectively ($\hat{\omega}^2 = 0$). In Experiment 3 the variance explained by the quadratic term after 24 and 48 days regrowth is 12% and 18% respectively ($\hat{\omega}^2 = 0$).

Significant regrowth of the Puccinellia in excess of values for the standing crop of ungrazed vegetation was not detected for grazing Experiments 4 and 5 conducted in August 1986. Although in these two Experiments the plots were sampled only at 12 and 24 days, the last harvest was taken just two or three weeks before "freeze-up", consequently further significant increases in biomass were unlikely to have occurred. In Experiments 4 and 5, the time x treatment interaction term is not significant, although both the main effects (time treatment) show significant differences (Table 3-2). These results reflect the amount of biomass consumed by grazing and not the regrowth of Puccinellia following grazing.

FIG. 3-2. Incease in above-ground biomass of _Puccinellia phryganodes_ following grazing by goslings in Experiment 2, 2 July 1986 (a); Experiment 3, 13 July 1986 (b); Experiment 4, 1 August 1986 (c); Experiment 5, 10 August 1986 (d). Values shown are mean values of 4 plots for Experiments 2, 3, 4 and 3 plots for Experiment 5. Each plot was 1 m^2, in which 4 goslings grazed in Experiment 2, 3 goslings grazed in Experiments 3 and 4, and 2 goslings grazed in Experiment 5. Error bar is Tukey's honestly significant difference. Before grazing (x); after grazing (△); 12 days regrowth (□); 24 days regrowth (●); 36 days regrowth (o); 48 days regrowth (■); 60 days regrowth (▽).

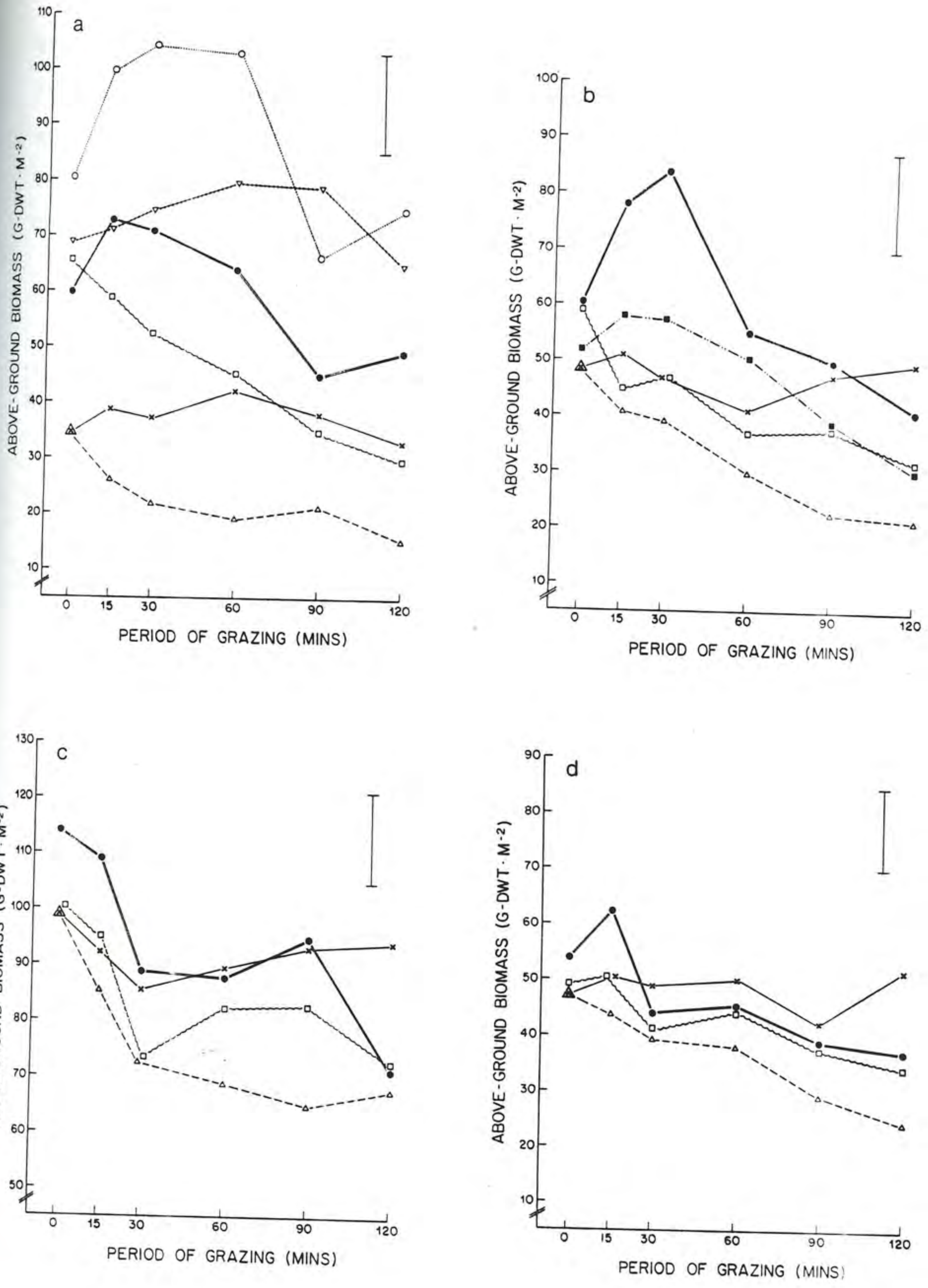

a
ABOVE-GROUND BIOMASS (G-DWT · M-2)
110
100
90
80
70
60
50
40
30
20
10
0
15
30
60
90
120
PERIOD OF GRAZING (MINS)
b
ABOVE-GROUND BIOMASS (G-DWT · M-2)
100
90
80
70
60
50
40
30
20
10
0
15
30
60
90
120
PERIOD OF GRAZING (MINS)
c
ABOVE-GROUND BIOMASS (G-DWT · M-2)
130
120
110
100
90
80
70
60
50
0
15
30
60
90
120
PERIOD OF GRAZING (MINS)
d
ABOVE-GROUND BIOMASS (G-DWT · M-2)
90
80
70
60
50
40
30
20
10
0
15
30
60
90
120
PERIOD OF GRAZING (MINS)

TABLE 3-2. Summary of results of a two-way ANOVA for increases in above-ground biomass in Experiments 2, 3, 4, and 5 (Fig. 3-2). Main effects are harvest times during the summer (T), and grazing treatment (G), and the time x treatment interaction (TG).

	Effect	F-ratio	df	P
Exp 2	T	135.66	5,108	<.001
	G	12.94	5,108	<.001
	TG	2.79	25,108	<.001
Exp 3	T	25.02	4,90	<.001
	G	17.60	5,90	<.001
	TG	2.10	20,90	<.020
Exp 4	T	8.20	3,72	<.001
	G	7.91	5,72	<.001
	TG	1.12	15,72	>.353
Exp 5	T	11.23	3,48	<.001
	G	11.43	5,48	<.001
	TG	1.87	15,48	>.051

3.3.2 Increase of NAPP of swards of Puccinellia following grazing

Cumulative NAPP of Puccinellia phryganodes for each grazing treatment was calculated by summing positive increments of above-ground biomass between harvests for each of the five experiments. There were significant increases in the NAPP of the swards following grazing, in Experiments 1, 2, and 3 (Table 3-3). In Experiment 1 the greatest increases in NAPP occurred in plots which were grazed for 30, 60 and 90 minutes. Cumulative NAPP in these plots was approximately 40% greater than that in the ungrazed plots. Corresponding values for NAPP in plots which were grazed for 120 or 150 minutes were less than the mean value for ungrazed plots.

A similar pattern of increases of NAPP is evident in Experiment 2, in which the largest increases occurred where plots were grazed for 15, 30 and 60 minutes (35-45% greater than that of ungrazed plots). There were no significant increases in NAPP beyond 36 days, irrespective of the grazing treatment. In Experiment 3 the greatest increase was evident in plots grazed for 15 and 30 minutes (the values were approximately 70% greater than the value of ungrazed plots). The NAPP of grazed swards was not significantly greater than that of ungrazed swards in Experiments 4 and 5 after 24 days of regrowth.

TABLE 3-3. Cumulative net above-ground primary production (g DWT * m^{-2}) for each harvest of experimental plots in Experiments 1 to 5. Calculated as positive increases in dry weight of above-ground biomass between successive harvests. Significant differences in total NAPP between that of ungrazed plots (control) and values for grazed plots for each treatment ($p < 0.05$) are indicated (*).

Harvest (days)	Period of grazing (min)						
	0	15	30	60	90	120	150
EXP 1 12	16		12	26	21	9	16
24	16		27	36	40	20	16
36	19		47	48	40	39	28
48	32		54*	57*	55*	39	32
EXP 2 12	30	33	32	28	14	15	
24	30	46	51	46	25	34	
36	46	73	83	76	45	60	
60	46	73*	83*	76*	57	60	
EXP 3 12	9	4	8	13	15	8	
24	11	37	45	25	26	19	
48	11	37*	45*	25	26	19	
EXP 4 12	1	9	0	17	20	6	
24	15	23	13	19	29	6	
EXP 5 12	1	7	1	4	9	10	
24	7	19	5	5	9	13	

3.3.3 Forage quality and nitrogen content of shoots

Grazing early in the season (Experiment 1) not only resulted in increased NAPP at intermediate grazing treatments, but also led to higher amounts of nitrogen present in above-ground tissue compared to corresponding values for ungrazed plots. Fig. 3-3a indicates that the nitrogen content of above-ground biomass was significantly higher in the grazed plots than in ungrazed plots. Although the nitrogen content of plant tissue declined over the course of the summer (from about 4.5% to 2.8%), the rate of decline in shoots from grazed plots was less than that for shoots from the ungrazed plots, mainly because no decline occurred in the first 12 days following grazing. Statistical analysis revealed no significant interaction between sampling time and grazing treatment (Table 3-4), but both of the main effects were significant. Carbon content of plant tissues did not change over the course of the season, and there were no differences in the amounts of carbon in tissues between swards subject to the various grazing treatments (Fig. 3-3a).

The pattern of changes in amounts of nitrogen and carbon as a percentage of the dry weight for the different treatments in Experiments 2 and 3 were similar to those for Experiment 1 (Fig. 3-3b,c). However, the nitrogen contents of the shoots, prior to grazing, declined throughout the season (4.5%, 2.8%, 2.5% for Experiments 1, 2, and 3 respectively). In Experiment 2 neither of the main effects were significant (Table 3-4).

FIG. 3-3. Total nitrogen (% N) and carbon (% C) content as a percentage of the dry weight of above-ground biomass of Puccinellia phryganodes following grazing by goslings in Experiments 1 (a), 2 (b), 3 (c), 4 (d), and 5 (e), (mean values are shown, n = 3 for Experiment 1; n = 2 for Experiments 2 to 5). Above-ground biomass with a nitrogen content significantly greater than that from ungrazed swards at each harvest are circled ($P < 0.05$; SNK multiple range test). Control (ungrazed): 0 mins grazing (○); 15 mins grazing (▽); 30 mins grazing (□); 60 mins grazing (●); 90 mins grazing (▲); 120 mins grazing (■); 150 mins grazing (+).

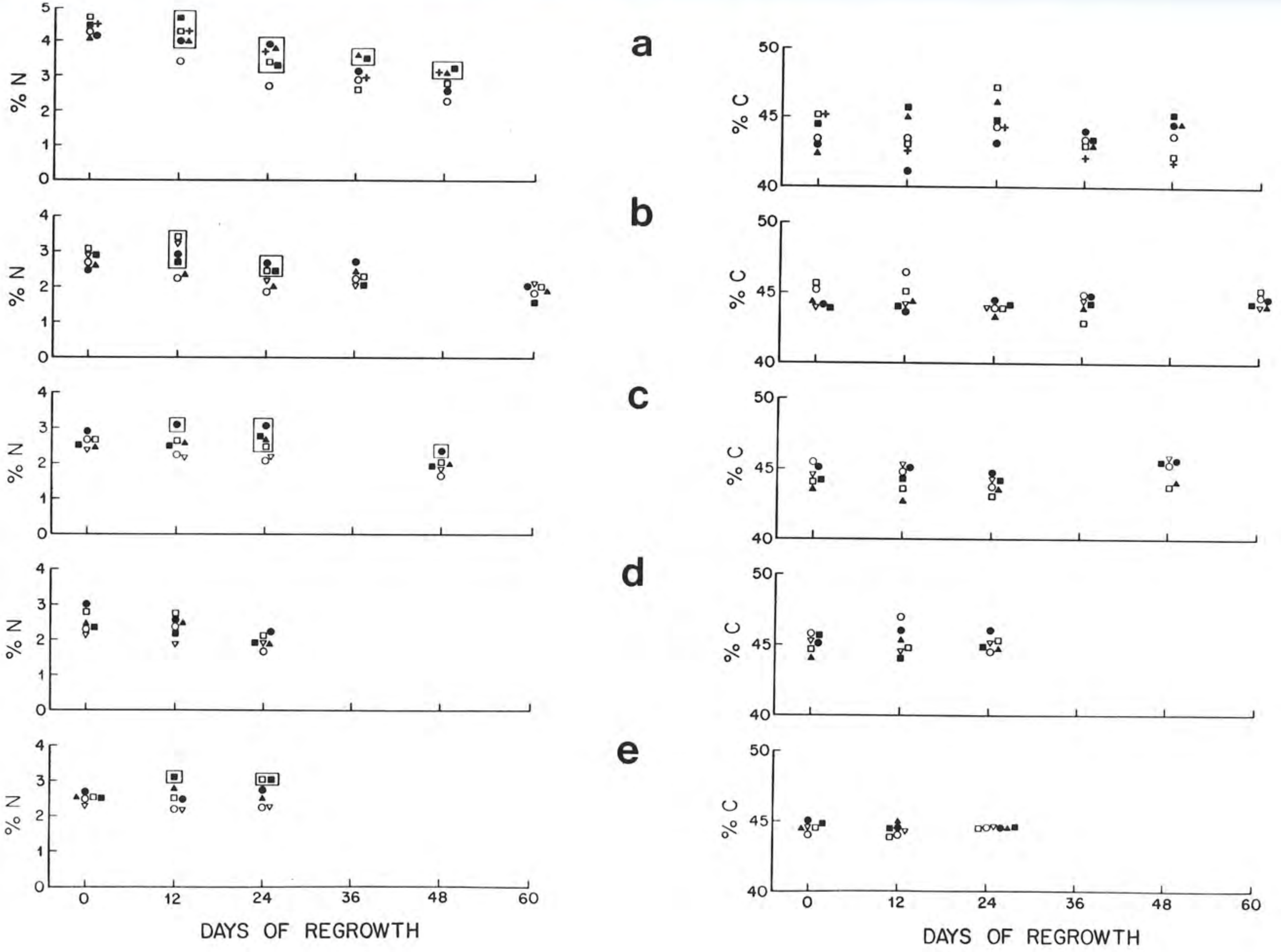

a
b
c
d
e
% N
% C
0
1
2
3
4
5
40
45
50
0
12
24
36
48
60
DAYS OF REGROWTH
DAYS OF REGROWTH

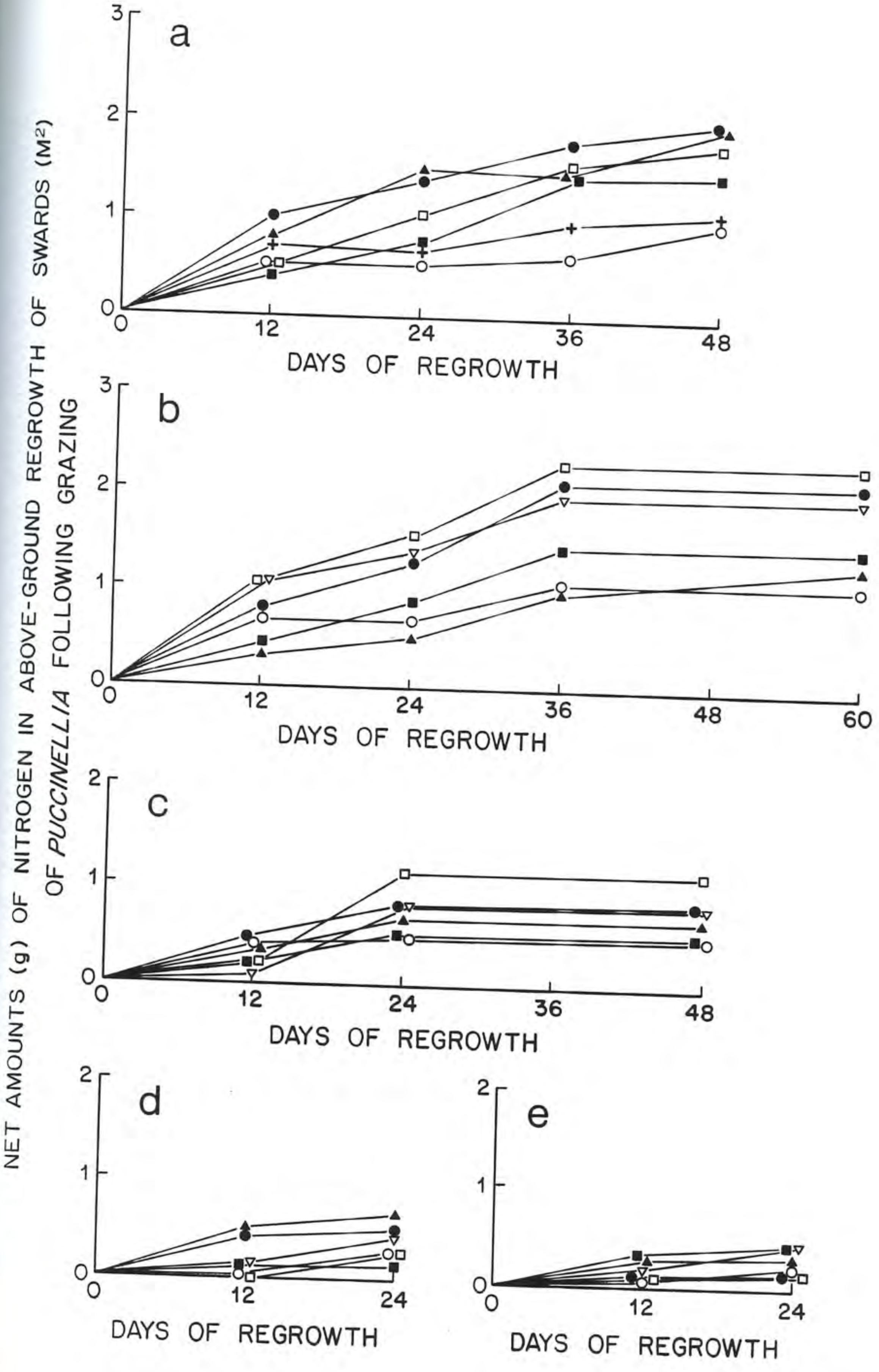
TABLE 3-4. Summary of results of a 2-way ANOVA of amounts of nitrogen expressed as a percentage (%N) of the dry weight of above-ground biomass in Experiments 1 to 5 (Fig. 3-3). Main effects are harvest times during the summer (T), and grazing treatment (G), and the time x treatment interaction (TG).

	Effect	F-ratio	df	P
Exp 1	T	20.06	4,60	<.001
	G	2.59	5,60	<.035
	TG	0.83	20,60	>.672
Exp 2	T	1.67	4,30	>.183
	G	1.26	5,30	>.308
	TG	0.82	20,30	>.679
Exp 3	T	20.06	3,24	<.001
	G	2.59	5,24	<.035
	TG	0.83	15,24	>.672
Exp 4	T	24.29	2,18	<.001
	G	9.02	5,18	<.001
	TG	1.08	10,18	>.428
Exp 5	T	1.09	2,18	>.360
	G	4.39	5,18	>.009
	TG	1.17	10,18	>.372

In Experiment 4 there were slight declines in amounts of nitrogen as a percentage of the dry weight in shoots in all plots during the course of the Experiment, but the decrease was relatively small (0.5%) (Fig. 3-3d). In Experiment 5 no differences in the amounts of nitrogen present in shoots from swards subject to a particular grazing treatment were evident (Fig. 3-3e; Table 3-4). The nitrogen content of the above-ground biomass averaged about 2.5% of the dry weight in both Experiments 4 and 5. Amounts of carbon as a percentage of the dry weight showed no significant time, treatment or interaction effects for any Experiment (2-way ANOVA; $p > .20$). Carbon content of tissue averaged approximately 45% of dry weight throughout the season in all experiments.

The cumulative net amounts of nitrogen present in above-ground biomass from the different plots are shown in Fig. 3-4 for Experiments 1 to 5. These results were obtained by multiplying the increment of live, above-ground biomass for each interval between successive harvests by the average nitrogen content of above-ground biomass during that period. In general, the cumulative net amounts of nitrogen were greatest in shoots from plots which received the intermediate grazing treatments. Late in season (Experiments 4 and 5) the rate of accumulation of nitrogen in shoots was lower than that measured earlier in the season for comparable periods (Experiments 1 and 2). In those treatments in which the goslings grazed the swards for 120 and 150 minutes the swards contained low amounts of nitrogen, because the NAPP in these plots was low (Table 3-3).

FIG. 3-4. Net amounts of nitrogen (g * m^{-2}) accumulated in the regrowth of above-ground biomass of swards of Puccinellia phryganodes following grazing in Experiment 1 (a); Experiment 2 (b); Experiment 3 (c); Experiment 4 (d); and Experiment 5 (e). Control (ungrazed): 0 mins grazing (○); 15 mins grazing (▽); 30 mins grazing (□); 60 mins grazing (o); 90 mins grazing (▲); 120 mins grazing (■); 150 mins grazing (+).


NET AMOUNTS (g) OF NITROGEN IN ABOVE-GROUND REGROWTH OF SWARDS (M²)
OF *PUCCINELLIA* FOLLOWING GRAZING
a
b
c
d
e
0
1
2
3
0
12
24
36
48
60
DAYS OF REGROWTH

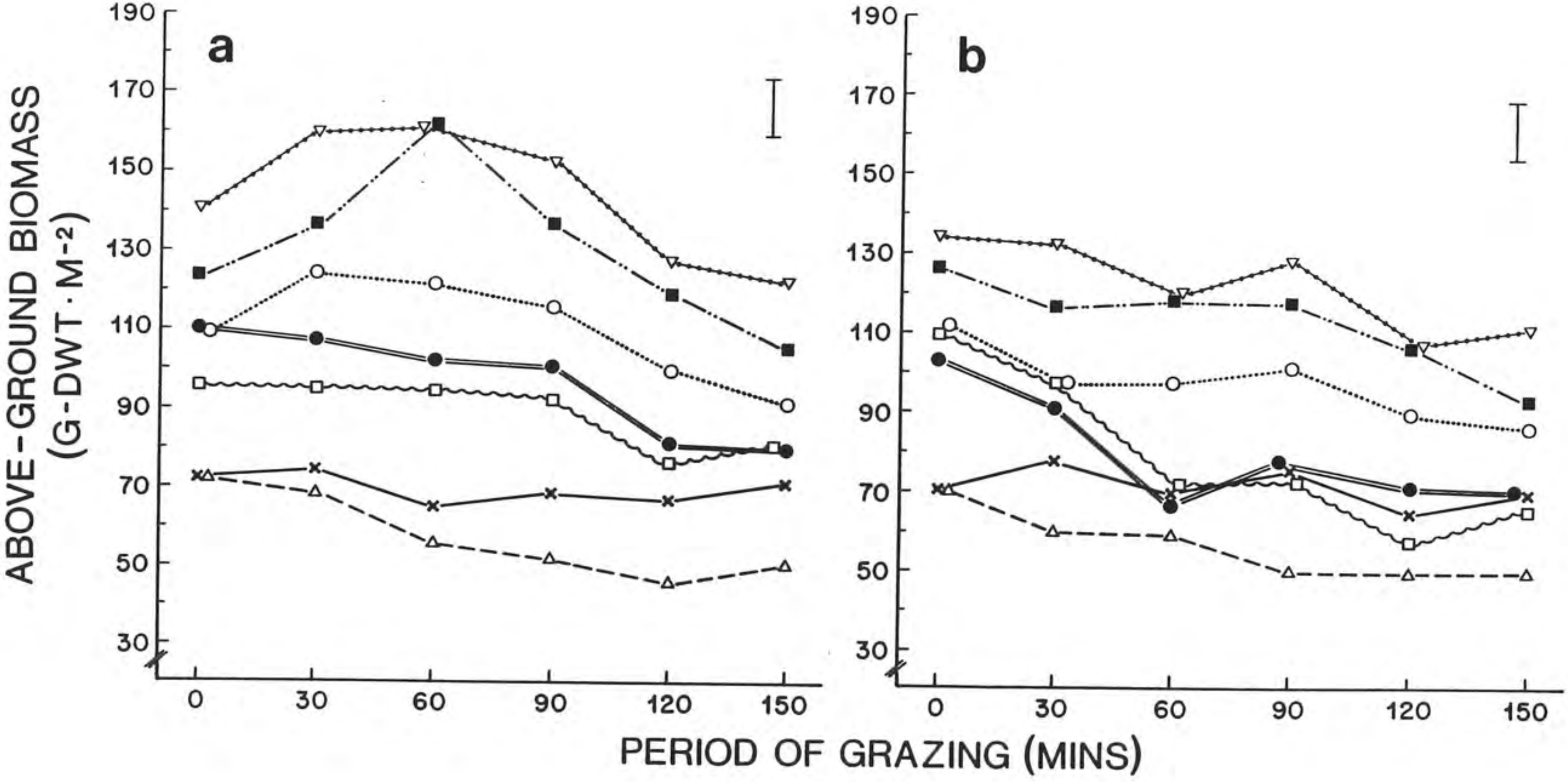
The amount of nitrogen available in above-ground biomass per unit area from moderately grazed plots after 36 and 48 days was almost twice that of ungrazed (control) plots in Experiments 1 and 2 (Fig. 3-4a,b). This difference was smaller in the other Experiments (Fig. 3-4c,d,e).

3.3.4 Effect of faeces on the growth of swards of Puccinellia following grazing

Although the overall effects of grazing can significantly increase the subsequent growth of Puccinellia (Fig. 3-1 and 3-2), the experimental design and the results do not allow the separation of the relative effects on plant growth of the addition of nutrients from faeces or those caused by clipping. On 1 July 1987 two further grazing Experiments were conducted. The two Experiments were similar, except that while the geese were grazing faeces were removed from one set of plots every ten minutes (Experiment 7). In the adjacent group of paired plots the faeces remained (Experiment 6). The results show that clipping without the concomitant deposition of faeces did not lead to increased growth evident when faeces remained in plots (Fig. 3-5, Table 3-5a). Clipping alone did not result in increases in production beyond that of ungrazed plots. This is most clearly indicated by the significant faeces x treatment interaction ($p < .017$; Table 3-5a).

After 60 days of regrowth following grazing the standing crop in Experiment 6 was approximately 160 g DWT

FIG. 3-5. Increase in above-ground biomass of *Puccinellia phryganodes* following grazing by goslings of the Lesser Snow Goose in Experiment 6 with faeces remaining (a), and Experiment 7 with faeces removed (b) (mean value for four plots (1 m2) grazed by 4 goslings). Error bar is Tukey's honestly significant difference. Before grazing (x); after grazing (△); 12 days regrowth (□); 22 days regrowth (●); 37 days regrowth (○); 48 days regrowth (■); 60 days regrowth (▽).


a
b
ABOVE-GROUND BIOMASS
(G-DWT · M-2)
190
170
150
130
110
90
70
50
30
0
30
60
90
120
150
PERIOD OF GRAZING (MINS)

* m^{-2} in plots which were grazed for 30, 60 and 90 minutes, compared to a corresponding value of approximately 130 g DWT * m^{-2} in Experiment 7. The curve of standing crop of Puccinellia for the different treatments in Experiment 6, 48 days after grazing (Fig. 3-5a), approximates to a quadratic form ($\hat{\omega}^2 > 0.09$). This type of growth response occurred 24 days later than that measured in the previous year (Fig. 3-1). The difference in the timing of response is most probably due to seasonal and site differences.

On 11 August 1987 a similar grazing Experiment with faeces present (Experiment 8) and faeces removed (Experiment 9) was conducted. The results indicated only a slight increase in the growth of swards of plots that were grazed for 15, 30 and 45 minutes, compared with growth in corresponding plots from which faeces were removed (Fig. 3-6; Table 3-5b). The difference (95 g DWT * m^{-2} compared to 85 g DWT * m^{-2}) was not significant. After 65 days following grazing (mid-October) the above-ground biomass had decreased by almost 30%. The faeces x treatment interaction was not significant ($p > .281$; Table 3-5b), hence the onset of winter precluded the establishment of significant differences in the growth of swards with respect to the different treatments.

3.3.5 Effect of faeces on NAPP

The NAPP of plots with faeces (Experiment 6) showed significant increases compared to values for plots from which faeces were removed (Experiment 7; Table 3-6). At

FIG. 3-6. Increase in above-ground biomass of Puccinellia phryganodes following grazing by goslings of the Lesser Snow Goose in Experiment 8 with faeces remaining (a), and Experiment 9 with faeces removed (b) (mean value of 4 plots (1 m2) grazed by 2 goslings). Error bar is Tukey's honestly significant difference. Before grazing (x); after grazing (△); 12 days regrowth (□); 24 days regrowth (●); 65 days regrowth (+).

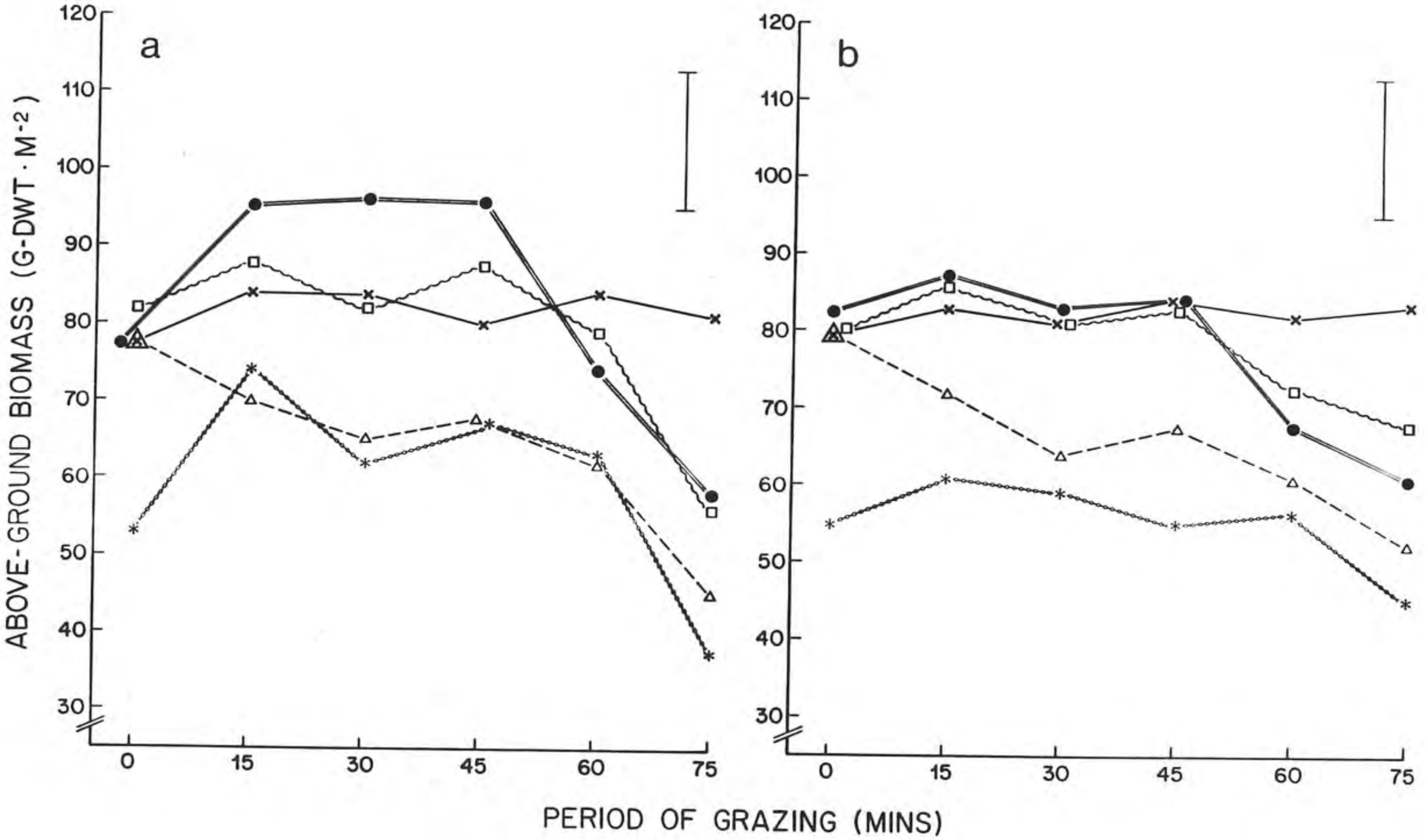

a
b
ABOVE-GROUND BIOMASS (G-DWT · M-2)
120
110
100
90
80
70
60
50
40
30
0
15
30
45
60
75
PERIOD OF GRAZING (MINS)

TABLE 3-5b. Summary of results of 3-way and 2-way ANOVA of changes in above-ground biomass of Puccinellia phryganodes following grazing in Experiments 8 and 9 (Fig. 3-6). Main effects are faeces (F), harvest time (T), and grazing treatment (G).

	Effect	F-ratio	df	P
Exp 8/9	F	1.56	1,180	>.211
	T	31.23	4,180	<.001
	G	13.27	5,180	<.001
	FT	0.65	4,180	>.634
	FG	1.26	5,180	>.281
	TG	1.71	20,180	<.025
	FTG	0.24	20,180	>.999
Exp 8	T	7.95	4,72	<.001
	G	6.19	5,72	<.001
	TG	1.22	20,72	>.279
Exp 9	T	8.44	4,72	<.001
	G	4.78	5,72	<.002
	TG	1.16	20,72	>.326

intermediate grazing levels NAPP was 30 to 40% greater in Experiment 6; the highest values for NAPP were detected in plots where the goslings grazed for 30, 60 and 90 minutes. The values were approximately 35% greater than that for ungrazed swards. The values of NAPP of swards subject to the different grazing treatments in Experiment 7 were not significantly different from each other, or from the NAPP of ungrazed plots after 60 days of regrowth (Table 3-6). There were no differences between the NAPP of plots in Experiments 8 and 9, irrespective of the treatment. In both of these experiments, however, NAPP was largest for swards which had been grazed, and lowest for ungrazed plots (Table 3-6).

3.3.6 Nitrogen content of above-ground biomass following grazing in the presence and absence of faeces

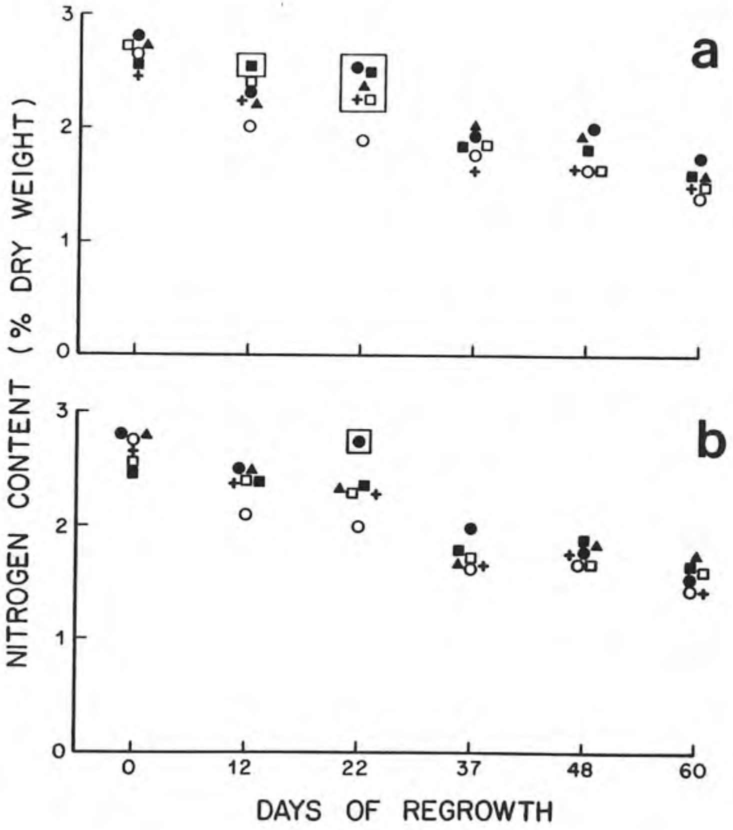
There were no significant differences in the nitrogen (or carbon) content of above-ground biomass of grazed plants in the presence or absence of faeces (Experiments 6 and 7; Fig. 3-7; Table 3-7). As in Experiment 1, the rate of decrease in the amount of nitrogen as a percent of the dry weight was least in tissue from grazed plots where faeces remained. Nevertheless, no significant differences in the amount of nitrogen as a percent of the dry weight in plant tissues from Experiments 6 and 7 were detected ($p > .713$; Table 3-7). Initial amounts of nitrogen, which were about 2.8%, decreased to about 1.5% after 60 days.

TABLE 3-6. Cumulative net above-ground primary production (g DWT * m^{-2}) for each harvest of grazed plots in Experiments 6 and 7, and 8 and 9. Significant differences in total NAPP between the ungrazed (control) plots and plots which received the different grazing treatments ($p < .05$) are indicated (*).

Harvest (days)		Period of grazing (min)					
		0	30	60	90	120	150
EXP 6	12	24	26	38	40	31	30
	22	38	39	46	48	35	30
	37	39	56	65	64	54	42
	48	51	68	106	85	74	55
	60	67	91*	106*	101*	82	72
EXP 7	12	39	29	13	23	8	16
	22	39	29	13	27	21	20
	37	42	29	38	51	39	37
	48	56	48	59	67	57	44
	60	64	64	61	78	57	61

		Period of grazing (min)					
		0	15	30	45	60	75
EXP 8	12	5	23	16	19	17	11
	24	5	25	30	27	17	12
	65	5	25*	30*	27*	17	12
EXP 9	12	1	14	22	14	11	15
	24	3	14	24	15	11	15
	65	3	14	24*	15	11	15

FIG. 3-7. Total nitrogen and carbon content as a percentage of the dry weight of above-ground biomass of Puccinellia phryganodes following grazing by goslings in Experiments 6 (a,c) and 7 (b,d), (mean values given, $n = 2$). Above-ground biomass with a nitrogen content significantly greater than that from ungrazed swards at each harvest are circled ($p < 0.05$; SNK multiple range test). Control (ungrazed): 0 mins grazing (o); 30 mins grazing (□); 60 mins grazing (●); 90 mins grazing (▲); 120 mins grazing (■); 150 mins grazing (+).


a
b
NITROGEN CONTENT (% DRY WEIGHT)
0
1
2
3
0
12
22
37
48
60
DAYS OF REGROWTH

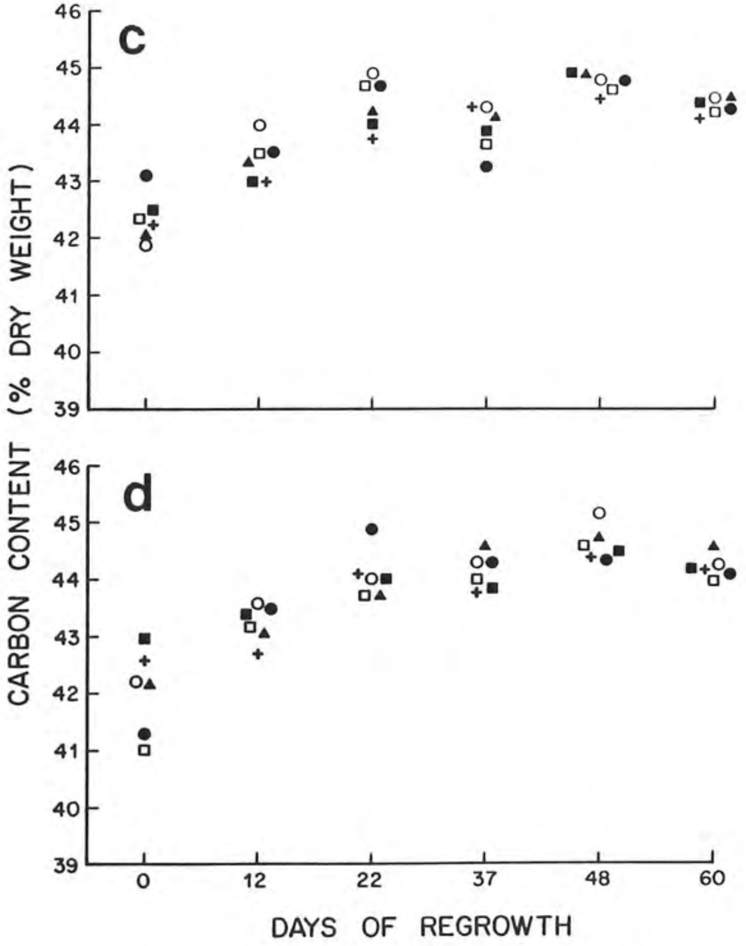

c
d
CARBON CONTENT (% DRY WEIGHT)
39
40
41
42
43
44
45
46
0
12
22
37
48
60
DAYS OF REGROWTH

TABLE 3-7. Summary of results of 3-way and 2-way ANOVA of amounts of nitrogen expressed as a percentage of the dry weight of above-ground biomass of Puccinellia phryganodes for Experiments 6 and 7. Main effects are faeces (F), harvest time (T), and grazing treatment (G).

	Effect	F-ratio	df	P
Exp 6/7	F	0.14	1,72	.713
	T	121.63	5,72	<.001
	G	7.67	5,72	<.001
ALL INTERACTION TERMS NON-SIGNIFICANT (p > .60)				
Exp 6	T	70.56	5,36	<.001
	G	6.52	5,36	<.001
	TG	0.83	25,36	.689
Exp 7	T	54.65	5,36	<.001
	G	2.43	5,36	.054
	TG	0.62	25,36	.897

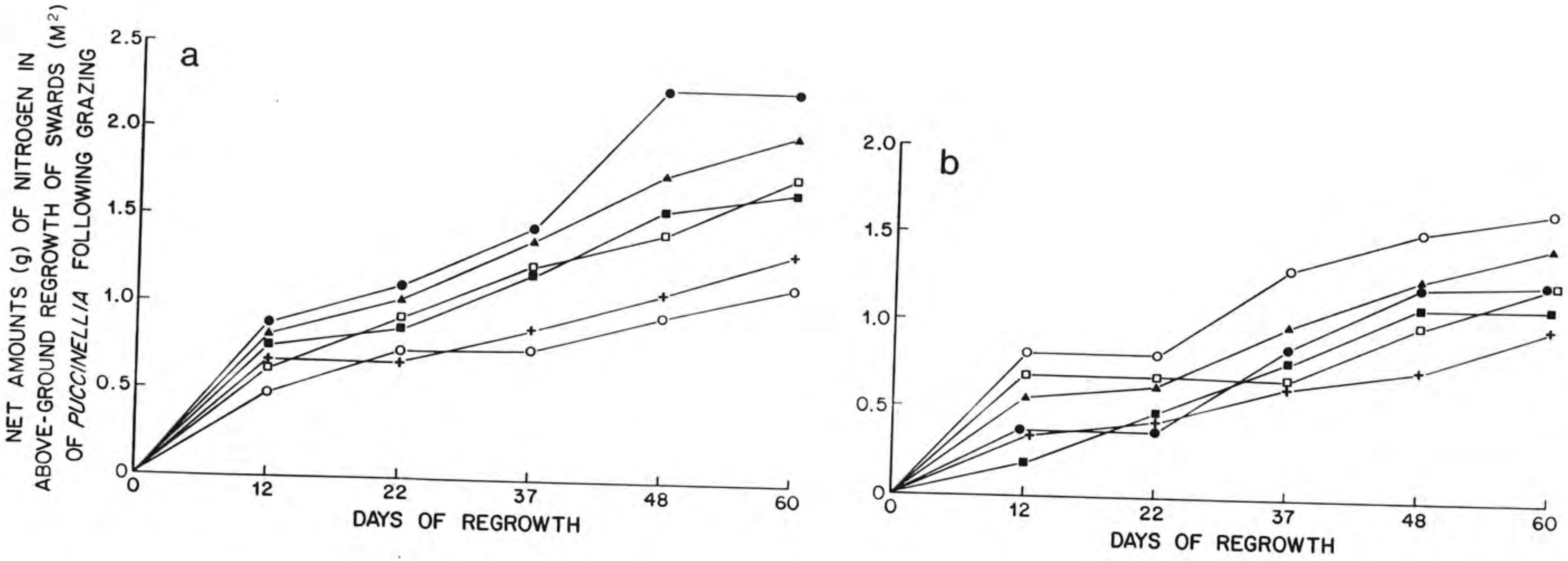
The amount of carbon in the tissues increased slightly from 42.5% to 44.5% of the dry weight after 60 days.

The amount of nitrogen deposited in the above-ground biomass in Experiments 6 and 7 was calculated by multiplying the increment of live, above-ground biomass in each interval between successive harvests by the average total nitrogen content of above-ground biomass during that period (Fig. 3-8). In both experiments the amount of nitrogen accumulated in the above-ground biomass in the ungrazed control after 60 days was approximately 1.5% of the dry weight. In the presence of faeces all swards accumulated more nitrogen per unit area than the corresponding value for ungrazed swards (Fig. 3-8a). In the absence of faeces the total amount of nitrogen per unit area present in grazed swards was less than that for ungrazed swards (Fig. 3-8b).

3.3.7 Accounting for nitrogen accumulated in shoots

The amount of above-ground biomass consumed by the grazers was not linearly related to the length of the grazing period (Fig. 3-9a). The amount of above-ground biomass consumed by the geese (% offtake) levelled off at about 28% of the initial standing crop after 90 minutes of grazing. Continued grazing and trampling probably damaged meristems. The input of nitrogen from faeces in the Experimental plots was significantly and positively related to the length of the grazing period and the amount of live biomass comsumed (% offtake) (Fig. 3-8a;

FIG. 3-8. Net amounts of nitrogen (g * m^{-2}) accumulated in the regrowth of biomass of swards of <u>Puccinellia phryganodes</u> following grazing in Experiment 6 (a), and Experiment 7 (b). Control (ungrazed): 0 mins grazing (○); 30 mins grazing (□); 60 mins grazing (●); 90 mins grazing (▲); 120 mins grazing (■); 150 mins grazing (+).


NET AMOUNTS (g) OF NITROGEN IN ABOVE-GROUND REGROWTH OF SWARDS (M^2) OF *PUCCINELLIA* FOLLOWING GRAZING
a
b
0
0.5
1.0
1.5
2.0
2.5
0
12
22
37
48
60
DAYS OF REGROWTH
DAYS OF REGROWTH

$r = 0.856$, $p < 0.001$), and ranged from 32 mg N - g DWT * m^{-2} to 192 mg N - g DWT * m^{-2}.

The amount of nitrogen was 1.71 ± .10% of the dry weight of faeces. Approximately 34.4% was in a soluble form (mainly NH_4^+ -N). It is possible to calculate the total input of faecal nitrogen into each grazed plot based on the number of faeces deposited during the grazing period, the dry weight of faeces, and the nitrogen content of faeces. The net amount of nitrogen which is incorporated in above-ground biomass (g * m^{-2}) directly from faecal nitrogen, or from the translocation of nitrogen from below-ground reserves or as a result of nitrogen fixation by cyanobacteria on the sediment surface, can be calculated (Experiment 6). From these values the corresponding values of the total amount of nitrogen accumulated in above-ground biomass (g * m^{-2}) in plots where all these sources of nitrogen are available, except the presence of faeces (Experiment 7), can be subtracted. If the amounts of nitrogen (g * m^{-2}) in swards where faeces remained are in excess of the values for amounts in swards in the absence of faeces the difference may be balanced by the nitrogen supplied in the faeces (Table 3-8). In fact, the differences in amount are in excess of that predicted from assuming that all the nitrogen in faeces is available for plant growth (Table 3-8). The values of of amounts of nitrogen unaccounted for range from 1.1% to 44.3% of the nitrogen deposited in the above-ground biomass in Experiment 6 (14 to 1016 mg N * m^{-2}).

FIG. 3-9. Relationship between length of the grazing period and the amount of above-ground biomass removed as a percentage of the initial amount present (% offtake) (a). Bars are mean ± SEM, n = 2); and the relationship between % offtake and the amount of nitrogen present in faeces (mg N * m^{-2}) deposited on plots (b).

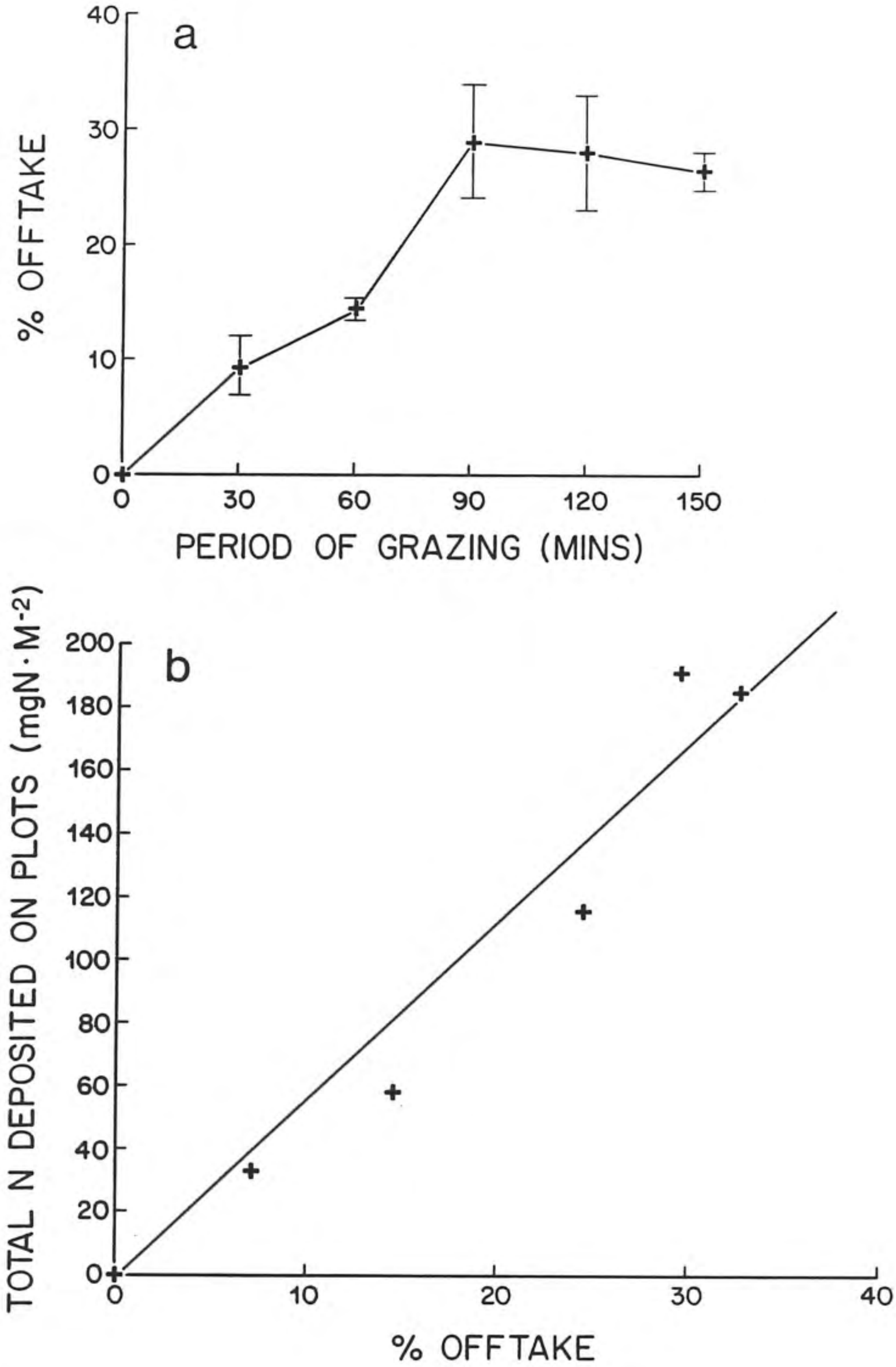

a
% OFFTAKE
0
10
20
30
40
0
30
60
90
120
150
PERIOD OF GRAZING (MINS)
b
TOTAL N DEPOSITED ON PLOTS (mgN·M-2)
0
20
40
60
80
100
120
140
160
180
200
0
10
20
30
40
% OFFTAKE

TABLE 3-8. Summary of net amounts of nitrogen accumulated in above ground biomass of swards of <u>Puccinellia phryganodes</u> in Experiments 6 and 7 (Fig. 3-8) and calculation of the proportion of nitrogen available from a number of sources to account for the total nitrogen accumulated after 60 days of regrowth.

A) Total N deposited in above-ground biomass (Experiment 6 with faeces remaining).

B) Total N available from faeces (assuming 100% mineralization and no ammonia volatilization).

C) Total N deposited in above-ground biomass (Experiment 7 with faeces removed); attributable to below-ground reallocation and N fixation at the sediment surface and net mineralisation of organic nitrogen in the sediments in the absence of faeces.

D) Amount (and percentage) of nitrogen (A) unaccounted for by (B) and (C).

	mg N * m^{-2} at each grazing treatment					
	0	30	60	90	120	150
A)	1144	1759	2296	2042	1751	1328
B)	0	33	58	107	185	191
C)	1673	1270	1222	1557	1160	1123
D)	0 (0%)	456 (26%)	1016 (44%)	378 (19%)	406 (23%)	14 (1%)

3.4 DISCUSSION

The main conclusions of these Experiments are, 1) that grazing by goslings of the Lesser Snow Goose leads to an increase of NAPP at low to moderate levels of grazing early in the season, compared to that of ungrazed swards; 2) that the ability of the plants of regrow following grazing declines as the season progresses; 3) that moderate levels of grazing maintain forage quality (amount of nitrogen as a percentage of the dry weight of tissue) during the season compared to the corresponding percentages for ungrazed plants; 4) that the increase in NAPP at moderate grazing levels above that of ungrazed swards is dependent upon goose faeces; without faeces there is no increase; and 5) the input of nitrogen from faeces is insufficient to account for the accumulation of nitrogen (g * m^{-2}) in swards which have regrown following grazing. The presence of faeces probably influences microbial growth and rates of net mineralization of nitrogen in sediments (Chapter 5). This conclusion is based on the magnitude of the difference in the amount of nitrogen (g * m^{-2}) in above-ground biomass between grazed swards in which faeces remained, and similar swards where the faeces were removed. This difference is greater than the amount of nitrogen supplied as faeces.

Early in the season, grazing by goslings leads to the enhancement of above-ground growth of swards of *Puccinellia phryganodes* in a pattern consistent with the predictions of the herbivore optimization model. To our knowledge this is the first experiment conducted in a terrestrial system where the results provide a critical test of the model. The mechanisms which appear to account for the regrowth of Puccinellia are the addition to the sediments of soluble nitrogen from faeces which is rapidly taken up and used by the plants (Bazely and Jefferies 1985), and the net mineralization of nitrogen in faeces and sediments which results in the further release of inorganic nitrogen for plant growth (Chapter 5). The reduced ability of the vegetation from heavily grazed plots to show increased NAPP is likely to be a consequence of the severe damage to meristems from excessive grazing and trampling, and to inputs of soluble nitrogen (largely as ammonium ions) from fresh faeces, which may approach toxic levels (Bazely 1984).

Grazing late in the summer failed to produce results which support the herbivore optimization model (Fig. 4-2c,d). Rather, grazing resulted in amounts of NAPP similar to amounts measured in the ungrazed swards. The results appear to indicate that enhancement of NAPP was generally limited to swards which were grazed early in the season when there was still sufficent time for regrowth to take place during the remainder of the season relative to the growth phenology of the plants. The patterns of growth may have precluded high rates of regrowth late in the season. This decline in growth is coincident with the southward migration of the geese, possibly reflecting the lower nitrogen content of the above-ground tissue by this time. In August, plants may have already begun to store carbohydrates and nutrients in below-ground tissue, rather than produce new above-ground tissue. Nevertheless, grazing in the late season does stimulate some production of new tissue. In Experiments 8 and 9, the NAPP of swards in grazed plots was greater than that of swards of ungrazed (control) plots after only 24 days of regrowth (Table 3-6), even though the total above-ground biomass was considerably less, compared to earlier in the season.

Our results, and those of Cargill and Jefferies (1984b) demonstrate increased production of *Puccinellia* swards. Similar results have been obtained in experimental studies when leaves of individual shoots of plants of this grass which have been grown in pots are clipped and/or nutrients are added to the soil (Sadul 1987). The collective experimental evidence demonstrates the importance of an adequate supply of nitrogen in order to achieve enhanced production of swards of *Puccinellia* following grazing. It is also clear, however, that the efficient cycling of nitrogen necessary to sustain plant growth in this system involves a number of processes well removed from the immediate plant-herbivore interaction.

Previous studies have suggested that grazing by Lesser Snow Geese results in the selection for genets of *Puccinellia* which have higher growth rates than plants which grow in ungrazed sites (Sadul 1987). While fertilization from faeces may be required in order to enhance production, clipping by itself also may stimulate production in *Puccinellia*, by selecting for plants with faster growth rates that would be inherently more tolerant of grazing. There is some evidence for this, particularly in Experiments conducted late in the growing season (Experiment 8 and 9; Fig. 3-6), where grazing both in the presence and in the absence of faeces increased NAPP above that of ungrazed swards.

Not all plant species have the ability to respond to herbivory as rapidly or effectively as *Puccinellia phryganodes*. This response is dependent upon the ability of *Puccinellia* to rapidly take up nutrients from the sediments. The stolons are on the surface of the sediments and the majority of the root system is confined to the top five centimeters of sediment, hence nutrients which are leached from faeces are likely to be rapidly absorbed by the roots or stolons. Nitrogen applied on the surface of the sediments is rarely available for uptake by deeper roots, but is rapidly taken up at the surface (Marion, Miller and Black 1987). Plants of *Carex subspathacea* begin to senesce earlier in the season compared to *Puccinellia* (Kotanen 1987), which precludes regrowth following grazing except early in the summer (see Cargill and Jefferies 1984b). Swards of two coarser, turf-forming grasses common in willow sites in the upper marsh, *Calamagrostis deschampsiodes* and *Festuca rubra*, do not show increases in growth, within the season, following grazing (Frey 1988), possibly because they are not able to utilize nutrients available in faeces as rapidly as *Puccinellia*.

In swards of *Puccinellia* 90% of the total plant biomass is below-ground (Cargill and Jefferies 1984b). However, Cargill and Jefferies (1984b) detected no differences in below-ground biomass between grazed and ungrazed swards. This does not imply that the rates of turnover were the same. The differences in above-ground biomass and NAPP shown in Fig. 3-5 and Table 3-6 also indicate that the redistribution of biomass from below- to above-ground alone cannot account for the enhanced growth of grazed shoots. The presence of faeces was essential in order to achieve the response.

The results of Experiment 6 and 7 provide critical evidence that the faeces are essential for the herbivore optimization model to operate at La Pérouse Bay. There are no differences in the amounts of nitrogen as a percentage of the dry weight of shoots from the different treatments, however there are significant differences in NAPP, and thus in the total amount of nitrogen accumulated in above-ground tissue ($g * m^{-2}$). Thus the total amount of high quality forage available to the geese is twice as high in the presence of faeces compared to swards where faeces were removed.

In a few other grazing systems similar increases in NAPP have been reported. In the Serengeti, McNaughton and his collegues have demonstrated that grazing by large ungulates leads to increases in NAPP (McNaughton 1979, 1984, 1985a,b; McNaughton, Coughenour and Wallace 1982; McNaughton, Wallace and Coughenour 1983; Ruess, McNaughton and Coughenour 1983; Coughenour, McNaughton and Wallace 1985b). The recycling of nutrients from faeces and urine in this system appears to be essential for regrowth to occur (Ruess and McNaughton 1984, 1987, 1988). In coral reef systems grazing by herbivores may also lead to increases in production at moderate levels of herbivory (Carpenter 1986). Coral reefs are highly productive systems surrounded by seas low in nutrients, thus tight nutrient cycling is imperative (Carpenter 1986; Sprent 1987). Herbivores (sea urchins, limpets, fish) graze intensively on "algal turf" communities which dominate the surface of reefs. These algae are one of the primary producers in the reef ecosystem (Odum and Odum 1955). Herbivores excrete nitrogen into waters surrounding the reefs, which provides a readily available source of ammonium to support the growth of algae and cyanobacteria. Grazing by sea urchins in particular increases the overall rate of reef productivity by facilitating the flow of nutrients required for growth (Carpenter 1986).

Goose faeces are essential for the regrowth of Puccinellia following grazing. Goose faeces differ from some other types of herbivore faeces in that they generally have no adverse effects on the vegetation they are deposited on. Cow pads, for example, provide a source of nutrients for grazed plants, but represent a local disaster, leading to death, for the plants they bury (Harper 1977). Goose faeces may also have effects on the nitrogen budget of the salt marsh other than the direct contribution of nitrogen. These processes are critical to the sustained regrowth of Puccinellia following grazing, and will be discussed in the greater detail in the following Chapters.

CHAPTER 4: NET ABOVE-GROUND PRIMARY PRODUCTION OF PUCCINELLIA PHRYGAONODES IN RESPONSE TO MULTIPLE GRAZING EPISODES BY LESSER SNOW GEESE: THE IMPORTANCE OF THE TIMING OF GRAZING DURING THE SUMMER

4.1 INTRODUCTION

The response of plants to grazing depends upon the phenology of plant growth in relation to the season, and the frequency and the severity of defoliation of the grazed sward. Experimental evidence suggests that regrowth of graminoid plants following grazing, and therefore the longevity and persistence of a particular plant-herbivore interaction, depends upon the rapid return of nutrients to the soil via faeces and urine (Petersen, Lucas and Woodhouse 1956; McKendrick _et al_. 1980; McNaughton 1983a,b; Ruess and McNaughton 1984, 1987; Bazely and Jefferies 1985, 1988). The phenology of plant growth may be altered by the timing of grazing during the summer, and the ability of plants to respond to inputs of nutrients following defoliation (Chapin 1980).

There is considerable interest in a model of grazing responses which suggests that, at moderate levels of herbivory, net above-ground primary production of forage plants may be increased compared to that of ungrazed plants (the herbivore optimization model; McNaughton 1979, 1983a,b; Hilbert _et al_. 1981; Dyer _et al_. 1982; Jefferies 1988a). Evidence in support of the type of response predicted by the model comes mainly from studies of grazing of terrestrial graminoid communities and aquatic algal and coral communities (McNaughton 1976, 1979; Prins, Ydenburg and Drent 1980; Cargill and Jefferies 1984b; Ogden and Lobel 1978; Bergquist and Carpenter 1986; Carpenter 1986; Power 1987; Chapter 3). This model predicts the overall effects of grazing intensity on production but does not address the outcome of the interaction between the frequency and severity of defoliation over the course of the season on plant regrowth.

A number of models of the stability of plant-grazer systems exist (Noy-Meir 1985; Parsons, Johnson and Harvey 1988), and these have been of value in managed agricultural grazing systems where the objective is to find the "optimum" balance between stocking density, the duration of the period of grazing (continuous or intermittent), and plant regrowth (Stoddart and Smith 1955; Parsons, Johnson and Harvey 1988). In natural grazing systems the conditions necessary for increases in plant growth to occur following grazing are not well understood (Jefferies 1988a).

Seasonal effects in relation to the phenology of plant growth and the timing of the foraging activities of grazers are extremely important in determining the outcome of plant-grazer interactions. In the Arctic, the foraging patterns of a number of herbivores shows a strong seasonal pattern. Many grazers are migratory (geese, caribou) and the production of plant biomass is limited to a brief period during the summer. At other times of the year most plant biomass is frozen and buried beneath snow. Nevertheless, consumption of total net above-ground primary production (NAPP) in these environments can be in excess of 80% of the available biomass (Cargill and Jefferies 1984b; Bliss 1986).

Plant growth in the subarctic La Pérouse Bay salt marsh is strongly nitrogen-limited (Cargill and Jefferies 1984a). Previous studies have shown that grazing by Lesser Snow Geese (Chen caerulescens caerulescens L.) significantly increased the net above-ground primary production of a stoloniferous salt-marsh grass, Puccinellia phryganodes (Trin.) Scribn. and Merr., and a rhizomatous sedge, Carex subspathacea Wormsk., from 30 to 105%, depending upon the year, compared to corresponding values for ungrazed swards of these two species (Cargill and Jefferies 1984b; Bazely 1984). A consequence of the intense grazing is that plant tissue is converted into either goose biomass or faeces, instead of accumulating as live plant biomass or litter. Nitrogen released from goose faeces accelerates the supply of this element to the sediments. In addition, patches of sediment between grazed shoots (0.5 cm diameter) are colonized by cyanobacteria that contribute to the long-term input of nitrogen, as a result of nitrogen-fixation (Bazely and Jefferies 1988).

Detailed demographic studies have shown that plants of Puccinellia phryganodes are capable of increasing the production of shoots and leaves in response to grazing (Bazely and Jefferies 198N). There is selection for biotypes of Puccinellia with faster growth rates under grazed conditions (Sadul 1987). The ability of both Puccinellia and Carex to show rapid growth responses within the season compensates for the adverse effects of defoliation per se on above-ground net primary production (Sadul 1987; Jefferies 1988a). A continual supply of high quality forage is produced during a period when it is most required by the geese.

As discussed previously in earlier experiments (Chapter 3), the foraging activities of the goslings of Lesser Snow Geese resulted in increased NAPP of Puccinellia phryganodes early in the season, but as the season progressed the ability of grazed swards to recover declined. Nitrogen from faeces was responsible, in part, for these increases in NAPP and for maintaining the high nitrogen content of grazed swards relative to ungrazed swards (Chapter 3). In this study captive goslings have been used to examine the effects of multiple grazing bouts on swards of Puccinellia phryganodes throughout the growing season. Swards were grazed on 12 or 24 day cycles at the same intensity of grazing (proportion of above-ground biomass removed), in order to examine the effects of the (seasonal) timing of grazing and of the interval between successive grazing bouts on NAPP, the phenology of plant growth and the quality of forage.

4.2 METHODS

4.2.1 Study site

Over 8000 pairs of Lesser Snow Geese breed each summer at La Pérouse Bay, 25 km east of Churchill, Manitoba, Canada, (58°, 24' N, 94°, 24' W), on the west coast of Hudson Bay. Following the hatch of goslings in late June or early July, the geese forage intensively on the vegetation of the intertidal salt marsh for 6 to 8 weeks before migrating south. The vegetation is dominated by Puccinellia phryganodes and Carex subspathacea, which is abundant in less saline areas. The intertidal grazing lawn is approximately 2 cm high and very few shoots (< 5%) escape the effects of grazing (Kotanen and Jefferies 1987; Bazely and Jefferies 198N). There are over 4000 shoots of these species per square meter. After the geese leave the marsh, plant growth continues in September before the arrival of permanent snow. A complete description of the study area is provided in Jefferies, Jensen and Abraham (1979) and Jefferies (1988a).

4.2.2 Experimental trials

All experiments were conducted using captive goslings. The goslings were removed from nests of wild geese within 24 hours of hatching and were raised in captivity in the research camp. Goslings were fed a diet of natural foods (mainly Puccinellia phryganodes and Carex aquatilis), supplemented with a daily ration of Purina 8815 Duck Growena, or dry dog food, except on the days prior to an experiment. Prior to each experiment the weight of the goslings was determined (Table 4-1). Experimental plots were established at the beginning of the summer on selected areas of saltmarsh vegetation dominated by Puccinellia phryganodes. The plots were exclosed with chicken wire to prevent any grazing by wild geese. Each plot was 1.1 m x 1.1 m. Four replicates for each of the ten grazing treatments were established in a completely randomized block design. On the morning of the grazing bouts (6, 18 July; 3, 12, 23 August; 3 September 1987), goslings were taken to the grazing site and allowed to "acclimate" to the vegetation in holding pens for 1 h. They were then randomly assigned to a plot and allowed to graze for a specific period. This process was repeated until all plots had been grazed. Fresh water was provided in small plastic bowls during the grazing bouts.

Grazing bouts were conducted at approximately 12 day intervals (Table 4-1). The number of goslings per plot and the period of grazing was adjusted over the season, as the goslings increased in weight and their rate of intake of vegetation increased, in order to achieve the removal of approximately 25% of above-ground biomass (% offtake) during each grazing bout. Grazing times varied over the course of the summer from 45 to 15 minutes and 4 to 2 goslings were placed in a plot (Table 4-1). Faeces remained in the plots and were counted at the end of each experiment. Two days before an experiment was conducted, goslings were allowed to graze plots of similar vegetation, in order to determine the conditions necessary (ie. number of birds, length of grazing peroid) to achieve a 25% offtake.

Swards of Puccinellia were grazed at intervals of approximately 12 or 24 days (Table 4-1). For the 12 day cycle, plots were grazed on 1, 2, 3, 4, 5, or 6 occasions.

Table 4-1. Days on which experimental plots containing swards of Puccinellia phryganodes were grazed and/or sampled during 1987 at La Pérouse Bay, Manitoba, on a 12 day cycle, 24 day cycle and late season only grazing schedule. The mean weight of goslings (g), length of the grazing bout, and number of goslings grazed per plot is also shown. Grazed plots were sampled before and after grazing bouts.

Treatment (# of bouts) (of grazing)	Dates grazed and sampled (g) or sampled (s)						
Date	6/7	18/7	3/8	13/8	23/8	3/9	15/10
12 day cycle							
6	g	g	g	g	g	g	s
5	g	g	g	g	g	s	s
4	g	g	g	g	s	s	s
3	g	g	g	s	s	s	s
2	g	g	s	s	s	s	s
1	g	s	s	s	s	s	s
0	s	s	s	s	s	s	s
24 day cycle							
3	g	s	g	s	g	s	s
2	g	s	g	s	s	s	s
late season							
3	s	s	s	g	g	g	s
mean weight (g)	499	880	1200	1478	1841	1876	
grazing time (mins)	45	30	40	25	20	15	
# goslings per plot	4	3	2	2	2	2	

For the 24 day cycle, plots were grazed on 1, 2, or 3 occasions (Table 4-1). The same plots for the "ungrazed control" and for those plots where one bout of grazing occurred were used in the comparisons for both the 12 and 24 day cycles. One further treatment was established where grazing by goslings was not initiated until 13 August (late season schedule). Grazing was continued in these plots until the end of the season (3 September) at 12 day intervals. Swards in plots which were grazed on 23 August and 3 September extended the period of grazing up to 3 weeks after wild geese had left the marsh, exaggerating the overall effects of grazing on the vegetation beyond levels observed under natural conditions.

4.3.3 Sampling and data analysis

Above-ground biomass was sampled by removing a 7.5 x 7.5 cm turve at random from each of the plots before grazing, and after grazing from the grazed plots. The above-ground biomass was removed by clipping the sward at ground level. The plant material was washed and then dried at 60-80°C for 24 hr. Since 90% of all material was live, standing dead biomass was not removed prior to weighing. A number of fresh faeces were collected from the gosling holding pen adjacent to the experimentsl plots for determination of their dry weight and their carbon and nitrogen contents. Dry weights were determined using a Mettler (PK-300) electronic balance. Determinations of amounts of carbon and nitrogen present in dried faeces and plant tissues were made using a LECO series 600 CHN autoanalyser (St. Joseph, MI., USA). All material was ground (20 mesh size) in a Wiley mill and appropriate quantities (approx. 100 mg) were preweighed before combustion in the analyser. All above-ground tissue was pooled for the analyses; leaves and shoots were not separated. Analysis of Variance (ANOVA) was used to assess the effects of the treatment.

4.3 RESULTS

4.3.1 Changes in NAPP of swards of _Puccinellia phryganodes_ in response to grazing

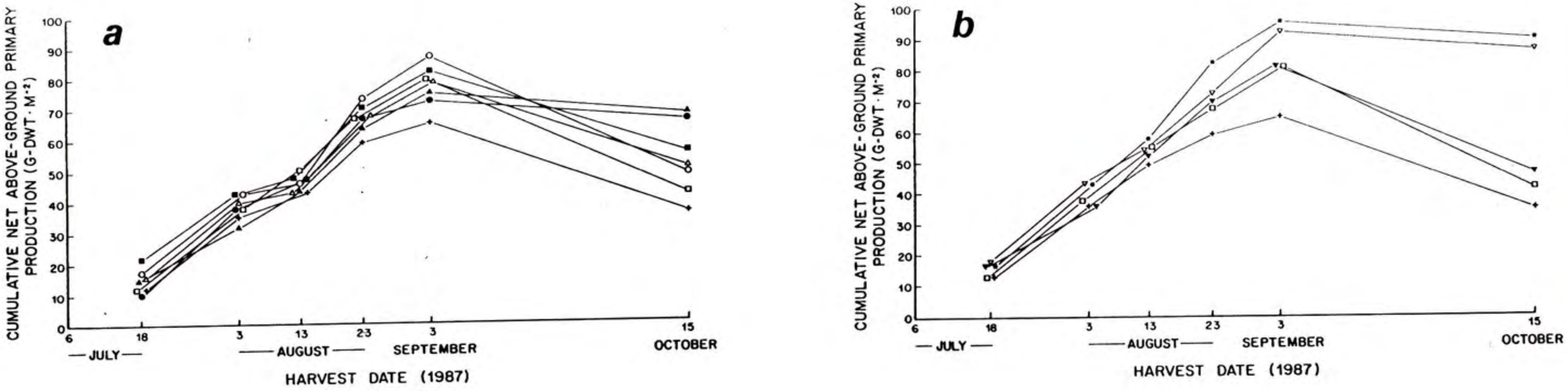
Net above-ground primary production of plots of grazed swards of _Puccinellia phryganodes_ was influenced by the number and timing of the grazing bouts during the season (Fig. 4-1). Where swards of _Puccinellia_ were grazed approximately once every 12 days (Fig. 4-1a), those grazed on 3 or 4 occasions had a higher total NAPP than the ungrazed (control) swards or swards grazed on 1 or 2, or 5 or 6 occasions (2-way ANOVA: $F = 2.388$, df = 6,105, $p < 0.033$). The cumulative NAPP of all swards increased significantly over the course of the summer ($F = 132.730$, df = 4,105, $p < 0.001$), but the interaction between season and treatment was not significant ($F = 0.344$, df = 24,105, $p > 0.998$). No significant differences in cumulative NAPP among the grazing treatments were apparent until 23

August. By the end of the summer (3 September) ungrazed swards had a lower value for cumulative NAPP than all grazed swards (Fig. 4-1a).

For plots grazed on a 24-day cycle (Fig. 4-1b), the cumulative NAPP of the sward grazed on three occasions was significantly greater than that of swards grazed on 1 or 2 occasions, and the ungrazed sward ($F = 4.578$, $df = 3,60$, $p < 0.006$). Increases in cumulative NAPP between treatments over the course of the season were significant ($F = 106.830$, $df = 4,60$, $p < 0.001$), but the interaction between season and treatment was not ($F = 0.638$, $df = 12,60$, $p < 0.802$). In the sward which was left ungrazed until 13 August (late season schedule), the cumulative NAPP was similar to the plot grazed on 3 occasions at 24-day intervals earlier in the season.

The initial amount of above-ground biomass present in all plots at the beginning of the experiment (6 July) was 54.6 ± 3.5 g DWT * m^{-2}. By the end of the summer (3 September) the mean above-ground standing crop in the seven treatments for the swards on the 12-day grazing cycle varied significantly (116.5, 119.3, 111.2, 103.1, 82.7, 58.8, 61.6 g DWT * m^{-2} for swards grazed on 0 (control), 1, 2, 3, 4, 5 and 6 occasions respectively). For the 24-day grazing cycle and the plots grazed late in the season the mean above-ground biomass on 3 September was 116.5, 119.3, 106.4, 88.6, and 78.9 g DWT * m^{-2} respectively for swards grazed on 0 (control), 1, 2 and 3 occasions, and those grazed late in the season. The above-ground biomass of swards in plots sampled on 15 October was lower than that sampled in early September for

Fig. 4-1. Cumulative net above-ground primary production of swards of *Puccinellia phryganodes* grazed by goslings of the Lesser Snow Goose for each treatment during the summer of 1987 (mean value of 4 plots; each plot was 1.1 x 1.1 m). a) NAPP of swards grazed at approximately 12 day intervals. Ungrazed control (+); one grazing bout (□); two grazing bouts (△); three grazing bouts (o); four grazing bouts (■); five grazing bouts (▲); six grazing bouts (●). b) NAPP of swards grazed at approximately 24 day intervals and only late in the season. Ungrazed control (+); one grazing bout (□); two grazing bouts (▼); three grazing bouts (▽); three grazing bouts late in the season (*).


a
CUMULATIVE NET ABOVE-GROUND PRIMARY PRODUCTION (G-DWT·M⁻²)
0
10
20
30
40
50
60
70
80
90
100
6
18
3
13
23
3
15
— JULY —
—— AUGUST ——
SEPTEMBER
OCTOBER
HARVEST DATE (1987)
b
CUMULATIVE NET ABOVE-GROUND PRIMARY PRODUCTION (G-DWT·M⁻²)
0
10
20
30
40
50
60
70
80
90
100
6
18
3
13
23
3
15
— JULY —
—— AUGUST ——
SEPTEMBER
OCTOBER
HARVEST DATE (1987)

all treatments. However, the reduction in above-ground biomass compared with the biomass present on 3 September was least in the swards grazed late in the summer, and greatest in the ungrazed swards and in swards grazed only 1 or 2 times earlier in the summer (Fig. 4-1). The largest number of new leaves evident in October was in the plots where swards were grazed late in the summer, but unfortunately quantitative records were not made.

The amount of above-ground biomass consumed by goslings over the summer and during each bout of grazing is shown in Table 4-2. This was calculated by subtracting the amount of above-ground biomass immediately following grazing from the amount of above-ground biomass present before grazing. The amount of biomass consumed averaged 12 to 13 g DWT * m^{-2} during each grazing bout for each experiment (about 25% of above-ground biomass), except in the plots which were grazed only late in the season where the initial amount of biomass was higher. However, the percentage of biomass removed was still approximately 25%.

In general, the percentage of the total NAPP consumed by the goslings during the experiments increased with the number of grazing bouts, from 14.7% in the swards grazed twice during the summer, to over 75% in the swards grazed 5 or 6 times for the 12 day cycle (Table 4-2). The percentage of the NAPP consumed by the goslings in the 24 day grazing cycle was highest in the swards grazed on 3 occasions (42%). Biomass consumed by the goslings during the first bout of grazing (6 July) is not included in the estimate of the percentage of the total NAPP consumed, since measurements of NAPP only began at this time.

Table 4-2. Amount of above-ground biomass of swards of <u>Puccinellia</u> <u>phryganodes</u> consumed by goslings of the Lesser Snow Goose in experimental plots in 1987. The proportion of the total NAPP measured (Fig. 4-1), which was consumed by the goslings during the summer is also shown (these values do not include biomass consumed on 6 July).

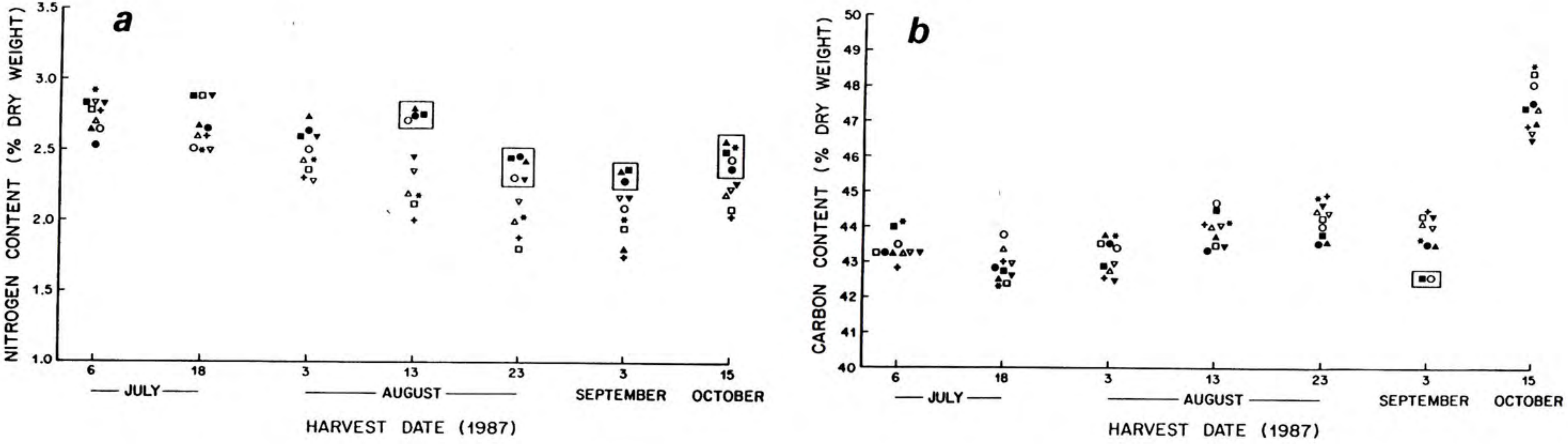
Treatment (# of bouts) (of grazing)	Amount of above-ground biomass consumed (g DWT * m^{-2})						% total NAPP consumed
	6/7	18/7	3/8	12/8	23/8	3/9	
12 day cycle							
6	5.9	13.4	14.3	18.3	9.6	1.6	78.9
5	18.3	11.4	16.4	18.0	12.8	0	76.1
4	17.1	13.7	13.9	8.5	0	0	44.6
3	17.2	12.8	12.5	0	0	0	29.2
2	10.1	12.1	0	0	0	0	14.7
1	11.4	0	0	0	0	0	0
0	0	0	0	0	0	0	0
24 day cycle							
3	12.8	0	11.3	0	26.9	0	41.7
2	16.0	0	10.5	0	0	0	13.3
late season							
3	0	0	0	24.7	27.7	11.2	67.4

4.3.2 Amounts of nitrogen and carbon in above-ground biomass of Puccinellia phryganodes

The amount of nitrogen in the above-ground biomass, as a proportion of the dry weight was initially (6 July) about 2.7% for all treatments, but decreased to approximately 1.75% in the ungrazed (control) plots by the beginning of September (Fig. 4-2a). In the grazed plots on the 12 day cycle the amount of nitrogen as a percentage of the dry weight did not decrease significantly over the course of the season, but remained above 2.3% even in September (2-way ANOVA; time: $F = 9.925$, $df = 6,49$, $p < 0.001$; treatment: $F = 6.143$, $df = 6,49$, $p < 0.001$; time x treatment interaction: $F = 0.784$, $df = 36,49$, $p > 0.775$). The amount of nitrogen in the shoots of both grazed and ungrazed swards increased slightly between the beginning of September and the middle of October. After the third bout of grazing (3 August) the amount of nitrogen in the shoots of Puccinellia from plots grazed 4, 5, and 6 times during the summer were significantly higher than the amounts of nitrogen in shoots from the ungrazed swards. This difference was maintained for the remainder of the summer (Fig. 4-2a).

In the plots grazed on a 24 day cycle and those grazed late in the season, the amounts of nitrogen in shoots as a percentage of the dry weight were generally less than that in shoots from plots grazed on the 12 day cycle (Fig. 4-2a). The plots grazed on 2 and 3 occasions and the plots grazed late in the season had amounts of nitrogen in the shoots greater than corresponding values for shoots from ungrazed

Fig. 4-2. Total nitrogen (a) and carbon (b) content as a percentage of the dry weight of above-ground biomass of <u>Puccinellia phryganodes</u> during the summer of 1987 (mean values are shown; n = 2). Above-ground biomass with a nitrogen content significantly greater than that from the ungrazed swards at each harvest are circled ($p < 0.05$; SNK multiple range test). Ungrazed control (+); Swards grazed on 12 day cycle: one grazing bout (□); two grazing bouts (△); three grazing bouts (o); four grazing bouts (■); five grazing bouts (▲); six grazing bouts (●). Swards grazed on 24 day cycle and late in the season only: two grazing bouts (▼); three grazing bouts (▽); three grazing bouts late in the season (*).


a
NITROGEN CONTENT (% DRY WEIGHT)
3.5
3.0
2.5
2.0
1.5
1.0
6
18
3
13
23
3
15
JULY
AUGUST
SEPTEMBER
OCTOBER
HARVEST DATE (1987)
b
CARBON CONTENT (% DRY WEIGHT)
50
49
48
47
46
45
44
43
42
41
40
6
18
3
13
23
3
15
JULY
AUGUST
SEPTEMBER
OCTOBER
HARVEST DATE (1987)

swards and from swards which were grazed only once (2-way ANOVA; time: $F = 9.630$, $df = 6,28$, $p < 0.001$; treatment: $F = 2.946$, $df = 3,28$, $p < 0.050$; time x treatment interaction: $F = 0.580$, $df = 18,28$, $p > 0.885$). Shoots from swards grazed late in the season generally had a lower amount of nitrogen as a percentage of the dry weight of tissue.

The amount of carbon, as a percentage of the dry weight of the above-ground biomass, averaged approximately 44% for all treatments, including the ungrazed control, and for all harvests in July, August and September (Fig. 4-2b). In October the amount of carbon in swards from all grazing treatments increased to approximately 47.5% of the dry weight of shoots (Fig. 4-2b).

4.3.3 Nitrogen accumulated in above-ground biomass of Puccinellia phryganodes

The amount of nitrogen accumulated in the above-ground biomass is shown in Fig. 4-3. These values are calculated by multiplying successive increments of biomass between harvests for each grazing treatment by the amount of nitrogen in the shoots as a percentage of the dry weight during this period. Since the amount of nitrogen is determined for total above-ground biomass and not just the leaves, these estimates are average values of the net accumulation of nitrogen in above-ground biomass. The nitrogen content of the pooled above-ground biomass is probably less than the nitrogen content of new leaves alone. Although new growth was evident in October (personal observation), and the nitrogen content of above-ground biomass was marginally higher than that in September (Fig. 4-2a), there were no increases in biomass, therefore it is not possible to calculate the net amount of nitrogen taken up by the shoots late in the season using this method.

For the 12 day grazing cycle (Fig. 4-3a), the net amount of nitrogen accumulated in the above-ground biomass was similar for all grazing treatments up to 13 August. After this time the nitrogen deposited in ungrazed swards was less than for the grazed swards (Fig. 4-3). The highest amounts of nitrogen accumulated by 3 September were in the swards from plots which were grazed on 3, 4, and 5 occasions by the goslings. For the plots grazed on a 24 day cycle, the amounts of nitrogen accumulated in above-ground biomass were greatest in swards which were grazed on 2 and 3 occasions (Fig. 4-3b). Significant differences in amounts of nitrogen in the biomass of ungrazed (control) and grazed swards were evident by 23 August. In general, the swards grazed late in the season accumulated larger amounts of nitrogen than the ungrazed swards.

The amount of nitrogen deposited as faeces on the grazed plots (g N * m^{-2}) is shown in Table 4-3. There is a positive linear relationship between the number of grazing bouts and the amount of nitrogen deposited in faeces. These values range from 0.127 g N * m^{-2} in plots grazed only once, to 0.823 g N * m^{-2} for plots grazed on 6 occasions for the 12 day grazing cycle. The amount of

Fig. 4-3. Net amounts of nitrogen (g N * m^{-2}) accumulated in the regrowth of above-ground biomass of swards of *Puccinellia phryganodes* during the summer of 1987. a) NAPP of swards grazed at intervals of 12 days. Ungrazed control (+); one grazing bout (□); two grazing bouts (△); three grazing bouts (o); four grazing bouts (■); five grazing bouts (▲); six grazing bouts (●). b) NAPP of swards grazed at 24 day intervals and only late in the season. Ungrazed control (+); one grazing bout (□); two grazing bouts (▼); three grazing bouts (▽); three grazing bouts late in the season (*).

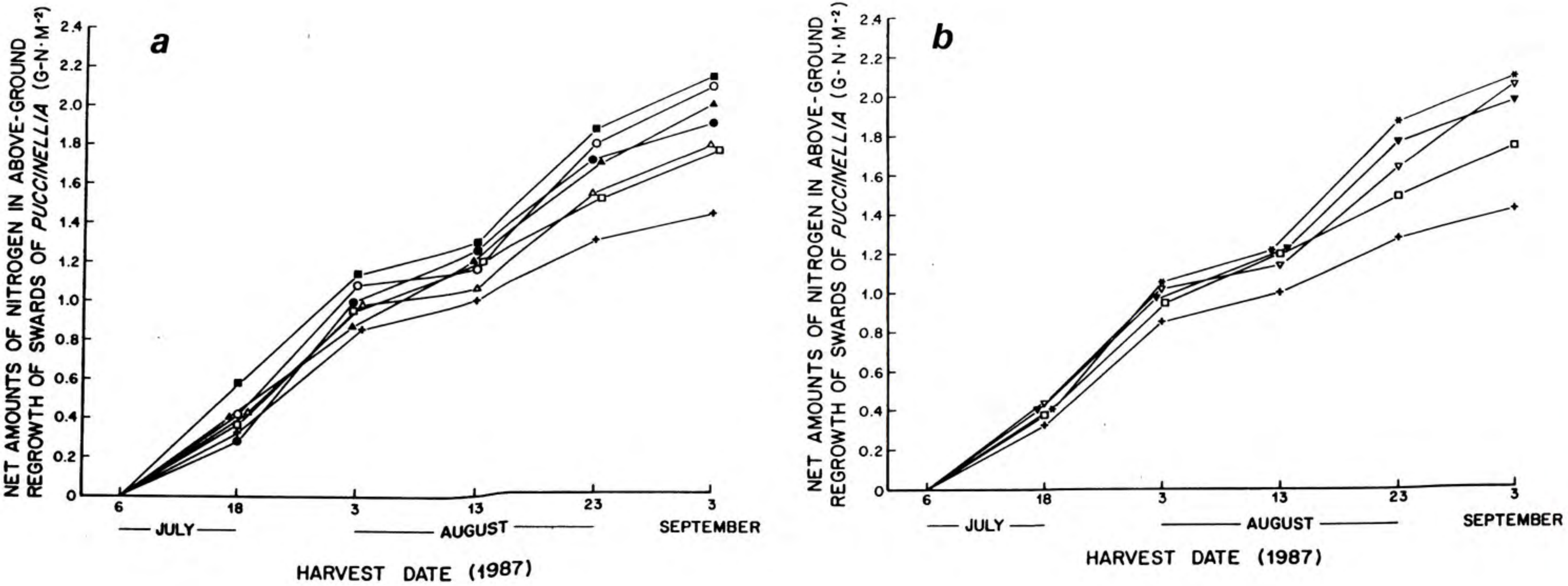

a
b
NET AMOUNTS OF NITROGEN IN ABOVE-GROUND REGROWTH OF SWARDS OF *PUCCINELLIA* (G·N·M⁻²)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
6
18
3
13
23
3
JULY
AUGUST
SEPTEMBER
HARVEST DATE (1987)

Table 4-3. Amount of nitrogen (g N * m^{-2}) in faeces of goslings of Lesser Snow Geese deposited on grazed swards of *Puccinellia phryganodes* in experimental plots in 1987.

Treatment (# of bouts) (of grazing)	Amount of nitrogen deposited (g N * m^{-2})						Total
	6/7	18/7	3/8	12/8	23/8	3/9	
12 day cycle							
6	.119	.148	.183	.147	.147	.111	.823
5	.118	.161	.174	.145	.116	0	.714
4	.149	.135	.180	.141	0	0	.605
3	.140	.139	.189	0	0	0	.468
2	.125	.137	0	0	0	0	.262
1	.127	0	0	0	0	0	.127
0	0	0	0	0	0	0	0
24 day cycle							
3	.116	0	.163	0	.098	0	.377
2	.124	0	.131	0	0	0	.255
late season							
3	0	0	0	.142	.112	.084	.338

nitrogen in faeces deposited on swards grazed on the 24 day cycle or grazed late in the season was less than 0.4 g N * m^{-2} (Table 4-3).

4.4 DISCUSSION

The results show that the regrowth of swards of *Puccinellia phryganodes* is dependent on the time of grazing during the season and the interval between successive grazing bouts, relative to the phenology of plant growth. Swards grazed until the beginning of August showed a higher NAPP compared to above-ground production of ungrazed swards, of swards grazed only at the beginning of the season, and of swards grazed approximately every 12 days throughout the summer. By comparison, plots grazed on 3 occasions once every 24 days, and those grazed on 3 occasions only at the end of the season, had a higher total NAPP than plots grazed on one or two occasions at an interval of 24 days. However, for plots subject to either the 12 or 24 day interval between grazing bouts, the decrease in the above-ground biomass between September and October was least for swards grazed late in the season (Fig. 4-1). Inputs of nitrogen in faeces apparently were essential for sustaining NAPP and the levels of nitrogen in the above-ground biomass of grazed swards. The amounts of nitrogen accumulated by plants in the above-ground biomass were greatest in swards grazed on 3 and 4 occasions, based on a grazing interval of 12 days.

The results of this experiment support the predictions of the herbivore-optimization model (Chapter 3), that intermediate levels of grazing result in increases in the NAPP of grazed swards. Unlike earlier tests of the herbivore optimization model (see Chapter 3) in which the effects of different periods of grazing on the regrowth of the vegetation were investigated, this study examined the regrowth of swards of Puccinellia subjected to an increasing number of grazing bouts at different intervals. The amount of biomass removed during each grazing bout was kept relatively constant at about 25% of the total. The importance of both seasonal effects and the phenology of plant growth on the regrowth of vegetation following grazing were evident. NAPP of grazed swards up to early September was highest when grazing was limited to the period of peak plant growth (mid to late July), although decreases of above-ground standing crop in October compared with values in early September were least in plots which were grazed on 3 occasions in the latter half of the summer. The reasons for this are not entirely clear, but nitrogen provided in faeces at this time may prime or activate microbial growth, and thus the net mineralization of nitrogen in sediments at a time when sediment temperatures are high (Bazely 1984). The resulting net mineralization of nitrogen and release of inorganic nitrogen may have been sufficient to sustain growth until late in the season. In addition, the photosynthetic leaf surface area, which remained intact in the absence of defoliation for much of the summer, may have enabled leaves and stems to build up reserves of carbohydrates necessary for regrowth once defoliation occurred. Usually the geese leave the marsh in early August after the swards have been heavily grazed, so that both the type of growth response reported above and its timing in relation to the season are at variance with the growth patterns of grazed swards under natural conditions.

The total amount of nitrogen present in faeces deposited in plots (g * m^{-2}), as a percentage of the cumulative net amounts of nitrogen (g * m^{-2}) present in the NAPP can be calculated. These calculations assume that 100% of the nitrogen in the faeces is mineralized and that there are no volatilization losses (see Ruess, Hik and Jefferies 198N; Chapter 5). For the 12 day grazing cycle this proportion is largest in swards of plots grazed on 6 occasions (38%), and 5 occasions (36%), and least in plots grazed only once (7%) or twice (15%). The nitrogen present in faeces as a percentage of the net amounts of nitrogen accumulated in the NAPP of plots grazed on 3 and 4 occasions are 22% and 28% respectively.

The second step in this calculation is to recalculate these percentages after the amount of nitrogen that is incorporated in the NAPP of ungrazed (control) swards is subtracted from these values of amounts of nitrogen present in the NAPP of grazed swards. In swards that were grazed on 1, 2, 3, and 4 occasions the cumulative amounts of nitrogen (cumulative N of grazed swards - faeces N - cumulative N of ungrazed swards) that <u>cannot</u> be accounted for is between 7% and 13%. All of the nitrogen accumulated in the above-ground biomass of the swards grazed on 5 and 6 occasions could be accounted for based on these calculations.

In the other experiments, nitrogen present in faeces accounted for 18% and 13% respectively, of the total nitrogen accumulated in above-ground biomass of swards grazed on 3 and 2 occasions at intervals of 24 days. The corresponding percentage where swards were grazed late in the season was 16%. When the cumulative amount of nitrogen present in the above-ground biomass of ungrazed swards is subtracted, these percentages become 57%, 45% and 48% respectively. This second set of estimates indicates that values of the nitrogen content of faeces in these experiments (24 day cycle and late season grazing) are insufficient to account for the cumulative amounts of nitrogen in grazed plots over and above that in the biomass of ungrazed swards. The deficits are 43%, 55% and 52% respectively for swards grazed on 3 and 2 occasions, and those grazed late in the season. Whether the nitrogen released from faeces in these grazed plots primes, or activates microbial growth leading to further net mineralisation of nitrogen in sediments which accounts for the deficit remains to be established. In any event, as mentioned above, this priming may occur in sediments of all grazed plots where faeces are deposited, in which case supplies of nitrogen are more than adequate to meet the growth demands of *Puccinellia* following defoliation, particularly in those experiments where plants are grazed once every 12 days.

In agricultural systems, in particular, there is interest in "optimizing" net primary production under continuous grazing. Maximum net above-ground primary production per meter is often achieved in a grazed sward by maintaining a relatively low Leaf Area Index (area of leaves per unit area of ground beneath the canopy). Under such conditions high rates of photosynthesis per unit leaf area are achieved. Of course, the total amount of photosynthesis per m2 of sward, and the standing crop at a given time are low at sites where the Leaf Area Index (LAI) is low compared with corresponding values in ungrazed swards (Parsons, Johnson and Harvey 1988). However, the relatively low amount of standing crop and the low LAI under the influence of grazing ensures that little attenuation of irradiance occurs through the canopy, so that maximum rates of photosynthesis per unit leaf area can be sustained at all levels within the canopy. This enables the forage plants to achieve high relative growth rates ($g\ g^{-1} * wk^{-1}$) where the sward is grazed.

At the La Pérouse Bay salt marsh the Leaf Area Index of grazed and ungrazed swards of <u>Puccinellia</u> does not exceed 1.5 (Bazely 1984). Such values are unlikely to result in attenuation of irradiance through the canopy. This usually occurs where the LAI is in excess of 3.0 (Brougham 1956). Hence the difference in NAPP between ungrazed and grazed swards cannot be the result of changes in irradiance, as occurs in some stands of crop plants when they are thinned. Nutrient cycling within the system provides the most acceptable answer to account for the increase in NAPP of the vegetation observed under the influence of grazing.

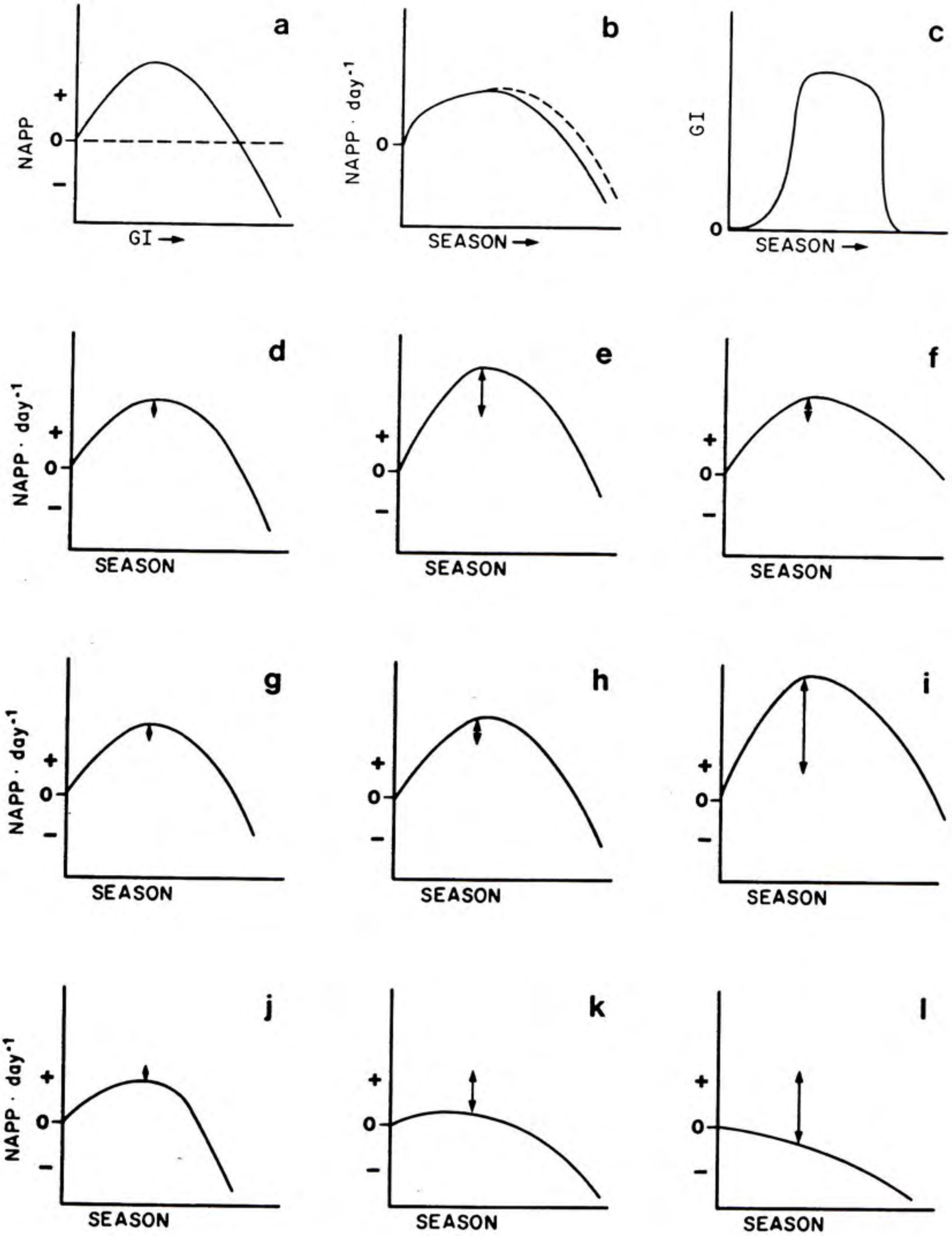
A number of models have been put forward to describe grazing systems as a whole. Noy-Meir (1975) presented an analysis of the stability of grazing systems based on Lotka-Volterra predator-prey type relations. His analyses considered simple interactions between plant growth and herbivore consumption, and assumed that the number of species (plant and herbivore) is small, that environmental heterogeneity within a system is low, and that the movement of the animals is controlled. While these assumptions are valid in managed agricultural grazing systems (Parsons and Penning 1988; Parsons, Johnson and Harvey 1988; Grant et al. 1988), stabilty in natural grazing systems may be easily upset by disturbance, such as habitat degradation or immigration of herbivores. In his models Noy-Meir (1975) also assumes that production is unaffected by grazing. As Johnson and Parsons (1985) demonstrate, considerable errors are incurred by ignoring the effects of defoliation on subsequent sward production.

While there is some debate as to whether continuous or intermittent grazing patterns lead to the greatest increases in production, in both cases, growth rate and digestibility of ryegrass (Lolium perenne) tend to be "optimized" when the interval of regrowth of vegetation between grazing bouts is between 14 and 28 days (Parsons and Penning 1988; Parsons, Johnson and Harvey 1988; Grant et al. 1988). This period is slightly longer than the 12 day period between repeated defoliations observed for salt marsh grasses and sedges at La Pérouse Bay (Bazely and Jefferies 198N), but corresponds approximately to the period of regrowth which led to the highest values of NAPP in the experiments reported here. However, these results only apply to one fixed period of grazing for each grazing bout. At a higher grazing intensity the responses of the swards may be different.

The effect of grazing intensity and frequency of grazing over the season on plant growth, can be modelled in the context of the herbivore-optimization model for the La Perouse Bay grazing system. Characteristic response curves for the rate of NAPP (g DWT * m^{-2} * day^{-1}) across the season can be constructed for each combination of grazing intensity (period of grazing) and frequency. The curves shown in Fig. 4-4(b,d-l) can be thought of as cross-sections through a three dimensional graph of NAPP, the stage of the growing season, and grazing intensity (period of grazing; GI) or grazing frequency. The herbivore optimization model is shown in Fig. 4-4a; NAPP is increased at moderate levels of grazing (GI) compared to ungrazed or heavily grazed swards. The rate of growth (NAPP * day^{-1}) changes over the season, with the most rapid growth occurring in early summer, and decreasing later in the season (Fig. 4-4b). The rate of NAPP of ungrazed swards (solid line) generally begins to decline earlier in the season than that of grazed swards (broken line). The intensity of grazing (GI) on the Puccinellia sward at La Pérouse Bay is greatest immediately following hatch of goslings, and then declines until the geese leave the site in mid-August (Fig. 4-4c).

Fig. 4-4d,e,f graphically display the effects of increasing the number of grazing bouts on the rate of NAPP for the 12 day grazing cycle, assuming a constant grazing

Fig. 4-4. Responses of NAPP to increases in grazing intensity and the changes in the interval between successive grazing bouts. The herbivore optimization model (a); Seasonal patterns of rates of NAPP (g DWT * m^{-2} * day^{-1}) (solid line: ungrazed sward; broken line: grazed sward) (b); seasonal pattern of grazing intensity (GI) and use of salt marsh forage by geese (c); seasonal patterns of rates of NAPP in swards where 25% of above-ground biomass is removed during each grazing bout (GI = 0.25) and grazed once every 12 days on 2 occasions (d); on 4 occasions (e); and on 6 occasions (f); Seasonal pattens of rates of NAPP in swards where 25% of above-ground biomass is removed during each grazing bout (GI = 0.25) and grazed once every 24 days where applicable: on 1 occasion (g); on 2 occasions (h); and on 3 occasions (i); Seasonal patterns of rates of NAPP of swards where grazing intensity and/or the frequency of grazing bouts is increasing (eg. GI = 0.4 (j); GI = 0.6 (k); GI = 0.8 (l)). The vertical arrows indicate the difference in NAPP * day^{-1} compared to ungrazed swards.


a
+
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NAPP
GI →
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intensity of 25% offtake (d: 2 bouts; e: 4 bouts; f: 6 bouts). The vertical arrows indicate the increase in the rate of NAPP compared to the ungrazed sward (Fig. 4-4b). Fig. 4-4g,h,i show the effects of grazing at 24 day intervals on 1 (g), 2 (h) and 3 (i) occasions, at a constant grazing intensity of 25% offtake. Two trend are apparent for both the 12 and 24 day grazing cycle. Firstly, the rate of NAPP depends upon the number of grazing bouts. Secondly, as grazing continues later into the season the decline in the rate of NAPP is delayed compared to that of the ungrazed sward. As grazing intensity or the frequency of grazing bouts increases, these response curves would most likely be depressed, representing poor growth of these swards (Fig 4-4j,k,l respectively).

The effects of grazing by the geese on the vegetation may not be entirely evident until the geese leave the salt marsh on their southward migration in early August. Although grazing does not result in significant increases in the NAPP of grazed swards compared to that of ungrazed swards in July, significant differences are realized in August (Fig. 4-1). However, grazing by the geese does maintain the amounts of nitrogen in the above-ground biomass, which is utilized by the geese at a time when they require large amounts of high quality forage (Fig. 4-3). During this flightless moult period and before the goslings have fledged, the geese rely heavily upon the vegetation of the salt marsh for their nutritional requirements. The departure of the geese in mid-August provides a period of approximately six weeks for plants to recover from the effects of grazing. The regrowth of grazed swards which occurs in late August may be essential for the plants to acquire sufficient nutrient and carbohydrate reserves to overwinter and to support growth the following season. This period is important for the laying down of carbohydrate reserves in below-ground biomass in arctic graminoids (Billings and Mooney 1968; Bliss et al. 1973; Shaver and Billings 1975; Johnson and Tiezen 1976; Ulrich and Gersper 1978; Archer and Tiezen 1980; Shaver and Chapin 1980). Swards grazed in late August and early September would not have as long to do this before "freeze-up" occurred.

The persistence of the grazed graminoid swards is strongly dependent on the colonial feeding behaviour of the geese (Bazely and Jefferies 1986). Rapid changes in species composition are evident in the absence of grazing. Graminoid species are displaced by dicotyledonous species which are not suitable forage for the geese (Bazely and Jefferies 1986), because they are not capable of regrowth within the season once the apical meristems are destroyed by grazing. The geese are also able to maintain the quality of their forage and increase NAPP compared to that of grazed swards by grazing early in the season (Fig. 4-2a). Continued grazing late in the summer does not affect the nitrogen content of the above-ground tissue, but does affect NAPP during this period.

These results raise the question of why the geese leave the salt marsh at the beginning of August, during a time when the food supply still is of high quality and is plentiful. The answer likely has nothing to do with the quality or availability of the forage, but rather with inate migration responses associated with decreasing photoperiod and migration tradition (Baker 1978). Also, since the snow goose is a relatively long-lived species and the parent-offspring bond is maintained for one year (Prevett and MacInnes 1980), exploration of the flyway and staging areas once the goslings are able to fly may be important for subsequent survival. The indirect consequence of this behaviour is a period of recovery for the vegetation. Further sampling of experimental plots during the summer of 1988 will provide some insights into the long-term effects of late season grazing on plant growth, and the stability of the snow goose-salt marsh grazing system. Even if the patterns of foraging by the geese and the phenology of plant growth are complimentary and the interaction can be maintained successfully over a long time, the effects of spring grubbing by the geese and localized disturbance caused by ice-scouring and algal mats on the salt marsh vegetation are slowly degrading this grazing system and forcing the geese to find new foraging sites (Jefferies 1988a,b).

CHAPTER 5: MICROBIAL NITROGEN MINERALIZATION PROCESSES IN A GRAZED SALT MARSH - POSITIVE FEEDBACKS BETWEEN SNOW GOOSE FORAGING AND NITROGEN CYCLING

5.1 INTRODUCTION

In terrestrial ecosystems plant growth is dependent on the flow of nitrogen from the soil to the plant and also the return of this element to the soil. It is in the soil that nitrogen compounds are converted into forms which may be taken up by plants (Floate 1981; Sprent 1987). Growth of plants is often limited by the rate of net mineralization of organic nitrogen in litter or in excreta. Only some of the nitrogen in plant tissue is removed from a habitat by animals; a large proportion of the nitrogen in plants which are grazed is returned to the habitat in urine and faeces.

Herbivores may act as mineralizing agents by processing and recycling nutrients present in plant biomass, thereby bypassing the rate-limiting step of the release of nutrients from dead plant material (litter) (McNaughton 1983a,b,c; Bazely and Jefferies 1985). This recycling is frequently essential in natural habitats if the regrowth of grazed swards is to be sustained, as plant growth in these habitats is nitrogen-limited (McKendrick et al. 1980, Floate 1981; Coppock et al. 1983; Jefferies 1988a). In addition to their direct effects on nutrient recycling, herbivores may also indirectly affect the nutrient budgets and decomposition processes of ecosystems by promoting microbial mineralization processes (Botkin et al. 1981; Naiman and Melillo 1984; Ruess and McNaughton

1987; Bazely and Jefferies 1988; Ruess, Hik and Jefferies 198N). The annual flux of nutrients through the microbial biomass may be several times greater than that taken up by plants (Ruess and McNaughton 1987). The soil microbial biomass functions as both a net nutrient source and as a sink for nutrients.

The extent and persistence of the nutrient coupling between plants, herbivores and microbes may also be dependent upon the foraging behaviour of the grazers (McNaughton 1984). Many microbial- mediated mineralization-immobilization processes, which occur in the sediments, are dependent upon such factors as water content of the soil, pH of the soil and the C:N ratio of the substrate. Since these properties vary among different soil and forage types (Clark and Rosswell, 1981), forage selection may influence the efficacy of nitrogen cycling in natural ecosystems. Nitrogen cycling in grazed graminoid communities is strongly linked to the deposition of faeces on the grazed sward. In sites where the grazing sward is spatially separated from "latrine" sites, plant growth cannot be sustained by recycling of nutrients from faeces (see Gibson and Phillipson 1983).

Plant growth on the salt marsh at La Pérouse Bay on the western coast of Hudson Bay where there is a breeding colony of Lesser Snow Geese (Chen caerulescens caerulescens L.) is strongly nitrogen-limited (Cargill and Jefferies 1984a). Previous studies have shown that grazing by Lesser Snow Geese significantly increased the net above-ground primary production (NAPP) of a stoloniferous salt-marsh grass, Puccinellia phryganodes

(Trin.) Scribn. and Merr., and a rhizomatous sedge, Carex subspathacea Wormsk., by over 100% compared to corresponding values in ungrazed swards of these two species (Cargill and Jefferies 1984b; Bazely 1984). A consequence of the intense grazing is that plant tissue is converted into either goose biomass or faeces, instead of accumulating as live plant biomass or litter. Nitrogen released from goose faeces accelerates the supply of this element to the sediments. Although as much as 2 g N * m^{-1} from the marsh may be incorporated into goose biomass each year (Cargill and Jefferies 1984b), much of this export is probably counterbalanced by the fixation of atmospheric nitrogen by cyanobacteria living on the surface of the sediments. The rate of fixation is significantly higher in grazed swards compared to that in ungrazed swards (Bazely and Jefferies 1988). The ability of Puccinellia and Carex to show rapid growth responses within the season compensates for the adverse effects of defoliation per se on production (Kotanen and Jefferies 1987; Sadul 1987; Bazely and Jefferies 198N). A continual supply of high quality forage is produced during a period when it is most required by the geese.

It is evident that grazing by the snow geese leads to enhanced NAPP of the Puccinellia sward by accelerating the supply of nitrogen available to plants. In this study faecal decomposition, net mineralization of nitrogen and the dynamics of microbial growth in fresh faeces from goslings of the Lesser Snow Goose which grazed three types of forage were determined, in order to examine the link between foraging behaviour and nutrient cycling and plant growth on the tidal flats at La Pérouse Bay. The results indicate the relative importance of the three forage species in relation to the release of inorganic nitrogen from faeces derived from these three plants.

5.2 METHODS

5.2.1 Study site

Over 8000 pairs of Lesser Snow Geese breed each summer at La Pérouse Bay, 25 km east of Churchill, Manitoba, Canada, (58°, 24′ N, 94°, 24′ W), on the west coast of Hudson Bay. After the hatch of goslings in late June or early July, up to 30,000 adults and goslings forage intensively on the vegetation of the tidal salt marsh. The vegetation of the salt marsh is dominated by *Puccinellia phryganodes* and *Carex subspathacea* which is abundant in less saline areas (Jefferies, Jensen and Abraham 1979). There are over 4000 shoots of these species per square meter and very few shoots (< 5%) are unaffected by grazing (Kotanen and Jefferies 1987; Bazely and Jefferies 198N). The intertidal grazing lawn is about 2.5 cm high. Approximately 80% of the above-ground primary production of the salt marsh is consumed by the geese (Cargill and Jefferies 1984b). In the upper marsh, beyond the high tide level, shrub willows (mainly *Salix brachycarpa* Nutt.) and birch (*Betula glandulosa* Michx.) dominate the vegetation. The most common grass in these willow sites is *Calamagrostis deschampsiodes*. This coarser, turf-forming grass is grazed by the geese when supplies of other sources of forage are limited (Jefferies 1988a,b).

5.2.2 Experimental trials

All experiments were conducted using captive goslings during the summer of 1987. The goslings were removed from nests of wild geese within 24 hours of hatching and were raised in captivity in the research camp. Goslings were fed a diet of natural foods (mainly *Puccinellia phryganodes* and *Carex aquatilis*), supplemented with a daily ration of Purina 8815 Duck Growena, or dry dog food, except on the days prior to an experiment. Before each experiment the weight of the goslings was determined.

A number of experimental plots were established on selected areas of salt-marsh vegetation dominated by either *Puccinellia phryganodes*, or *Carex subspathacea*, or *Calamagrostis deschampsiodes*. Each plot was approximately 3m x 3m. Experiments were conducted on three occasions in 1987 (Experiment 1: 13 July; Experiment 2: 13 August; Experiment 3: 28 August).

The goslings were allowed to "acclimate" to the vegetation for 8 to 10 hours prior to the collection of faeces. Fresh water was provided regularly. The goslings were moved to new plots containing ungrazed vegetation approximately every 2 hours. In Experiment 1 (13 July) six goslings grazed on swards of each of the three species (*Puccinellia*, *Carex*, *Calamagrostis*) in the experimental plots. Only four goslings were used (12 total) in the last two experiments (13, 28 August). Pecking rates and defecation rates were determined on at least two occasions during each experiment. Since pecking rates are low and defecation rates are generally high when forage plants contain a high percentage of their dry weight as fiber, measurement of these two indicators provides indirect evidence of the digestibility of the three forage types. Fresh faeces were collected between 2000 h and 2100 h, after the goslings had been grazing for the previous 8 to 10 hours. Above-ground biomass of each of the species was collected and dried at 80°C for 24 hr. The nitrogen and carbon contents of these plant tissues and amounts of inorganic ions present in the material were determined as described below.

5.2.3 Measurement of rates of microbial respiration rates and rates of nitrogen mineralization in fresh faeces

Fresh faeces collected from the plots grazed by goslings were returned to the laboratory. Determinations of faecal water content and pH for each type of forage were made at the begining of the experiment. Approximately 15 - 20 g of fresh faeces from each type of forage were weighed and placed on a moistened sponge in a 0.8 litre glass jar. Two replicates of each of the three treatments (<u>Puccinellia</u>, <u>Carex</u> and <u>Calamagrostis</u>) and one control jar (no faeces present) were set up during each experiment. Incubations for all three experiments were conducted at a constant temperature of 19.2 ± 0.1°C.

15 ml of 1N NaOH in a 20 ml glass scintillation vial was placed inside the sealed jars to trap CO_2, derived from microbial respiration. These chambers were incubated for 24 h in the dark. The NaOH traps were changed after 12 h. The amount of CO_2 trapped by NaOH during each 12 h period was determined by titrating a dilute (1:6) sample with 0.05 N HCl (Fisher Accumet Model 156 pH meter). The conversion from millilitres of titrant used to change the pH from 8.3 to 3.7 to the amount of CO_2 respired is:

$$\text{mg } CO_2\text{-C/g DWT faeces} = (\text{ml titrant} * 0.6 * 6)/\text{g DWT faeces}$$

This expression is based on standard conversions for determination of microbial biomass (Jenkinson and Ladd 1981).

5.2.4 Determination of soluble nitrogen

Soluble ammonium present in faeces was measured at the start of the experiment and after 24 h; the difference was a measure of net nitrogen mineralization. Soluble nitrogen of fresh goose faeces was determined using the phenol-sodium hypochlorite method (Solorzano 1969), after extraction for 12 hours with a solution of 1 M KCl. Approximately 6 g of fresh goose droppings were suspended in 40 ml of solution. The absorbance of filtered extracts at 625 nm was determined using a field spectrophotometer (mini Spec-20). New standard solutions of ammonium chloride were prepared for each new phenol-hypochlorite solution.

5.2.5 Carbon and nitrogen determinations

Measurements of amounts of carbon and nitrogen as a percentage of the dry weight of samples of dried faeces and plant tissues were made using a LECO series 600 CHN autoanalyser (St. Joseph, MI., USA). All material was ground (20 mesh size) in a Wiley mill and a subsample (approx. 100 mg) was preweighed before combustion in the analyser. Samples were burned at 950°C; elemental nitrogen was measured by the use of a thermal conductivity cell; carbon was detected by an infrared cell.

5.2.6 Neutron activation analysis

Dried samples of faeces and plants were analysed for amounts of magnesium, sodium, potassium, chloride, and calcium (μmole * g DWT^{-1}) using instrumental neutron activation analysis (INAA). The SLOWPOKE reactor at the University of Toronto was used for all irradiations. Each INAA sample was packaged in a small (2.5 x 1.1 cm) polyethylene vial. Samples were irradiated by a neutron flux of 1 x 10^{11} neutrons * cm^{-2} * s^{-1} for 3 minutes at 2 kW. After a delay time of 8 minutes following irradiation for faecal samples, and 2 minutes for plant samples, the gamma rays emitted by the artificially produced radioisotopes were counted for 200 seconds using a gamma-ray spectrometer (Canberra Ge(Li) detector, 8100 series, Meriden, Connecticut). The intensities of the gamma-ray peaks were determined by automatic analyser integration of manually selected spectral regions. To convert radiation counts to chemical concentrations, elemental standards were prepared and analysed by the methods described above.

Radiation counts were converted to concentrations by the formula;

$$\text{concentration} = (P-B) / (\text{sample mass} \times K)$$

where P is the peak reading and B is the background reading of the spectrometer for the gamma rays being measured, and K is a conversion factor specific for each element, as derived by comparing the number of counts with the number obtained from the standards. All counts were corrected for half-life decay of the respective isotopes between irradiation and counting.

5.2.7 Acid detergent fibre analyses

Quantities of acid detergent fibre (Demment and Van Soest 1983) of dried faeces and plant samples were analysed by Agri-Food Laboratories, Ontario Ministry of Agriculture and Food, Guelph, Ontario. Calculations of digestibility were based on the ratio of acid detergent fibre (ADF) in plants compared to faeces (Buchsbaum, Wilson and Valiela 1986). The expression used to calculate digestibility was:

$$\%\ \text{digestibility} = [1-(\%\ \text{plant ADF} / \%\ \text{faecal ADF})] \times 100$$

5.2.8 Statistical analysis of data

Data were analyzed using standard statistical procedures (Sokal and Rohlf 1981). Because the number of samples was low in a few of the experiments, the power of the statistical tests was low. The likely presence of Type I and II errors in certain of the ANOVA's does not affect the main conclusions of this study.

5.3 RESULTS

5.3.1 Feeding behavior of goslings

Gosling weight averaged 775, 1494 and 1842 g respectively for the three experimental periods; there were no significant differences in the weight of goslings of the three groups selected at random to graze on each forage type for each experiment (Table 5-1). Goslings feeding on Calamagrostis had lower pecking rates compared to goslings grazing on Carex or Puccinellia in all three experiments (Table 5-1). Observations indicated that goslings had difficulty biting the stiff, erect stems and blades of Calamagrostis. Pecking rates did not change significantly over the course of the season for any treatment (Table 5-1). Rates of defecation were significantly higher for goslings grazing on Calamagrostis compared to rate for Carex or Puccinellia in the first two experiments (Table 5-1). There were no significance differences in defecation rates across the season.

Table 5-1. Gosling weight (a), pecking rate (b), and defecation rate (c) of goslings of the Lesser Snow Goose feeding on three forage types (*Puccinellia phryganodes*, *Carex subspathacea* and *Calamagrostis deschampsiodes*), in three feeding experiments (Exp. 1 - 13 July; Exp. 2 - 13 August; Exp. 3 - 28 August). F values, based on one-way ANOVA's, are given for data across rows and down colums (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

a) gosling weight (g)

Exp.	*Carex*	*Puccinellia*	*Calamagrostis*	
1	760	861	701	F2,15 = 2.03
2	1517	1583	1383	F2,6 = 1.29
3	1913	1737	1875	F2,6 = 0.45
	F2,10 = 38.22***	F2,10 = 70.45***	F2,10 = 161.52***	

b) pecking rate (pecks * min^{-1})

Exp.	*Carex*	*Puccinellia*	*Calamagrostis*	
1	114.0	100.8	74.8	F2,15 = 20.79***
2	123.5	125.5	77.7	F2,6 = 4.05
3	113.7	114.3	79.3	F2,9 = 10.11**
	F2,10 = 0.60	F2,10 = 9.06**	F2,10 = 0.82	

c) defecation rate (faeces * h^{-1})

Exp.	*Carex*	*Puccinellia*	*Calamagrostis*	
1	9.1	6.7	9.0	F2,9 = 9.90**
2	8.9	7.7	11.5	F2,11 = 4.10*
3	7.4	7.5	9.9	F2,5 = 1.10
	F2,11 = 1.22	F2,6 = 0.26	F2,8 = 3.30	

5.3.2 Chemical composition of plants of *Puccinellia phryganodes*, *Carex subspathacea* and *Calamagrostis deschampsiodes*

Significant differences were found in the chemical composition of the three plant species used in the feeding experiments (Table 5-2). *Puccinellia* had the highest amounts of nitrogen as a percentage of the dry weight compared to values for *Carex* and *Calamagrostis* in all three experiments. Nitrogen content decreased over the season in *Carex* and *Puccinellia*, but increased in Experiment 2 for *Calamagrostis*. *Carex* contained the highest amounts of carbon as a percentage of the dry weight compared to corresponding values for *Puccinellia* or *Calamagrostis* (Table 5-2). Amounts of carbon as a percentage of the dry weight tended to increase during the course of the season. The C:N ratio was highest in *Calamagrostis* in Experiments 1 and 3. In *Carex* and *Puccinellia* the C:N ratio was lowest in Experiment 1, but increased by 37% between Experiments 1 and 2 (Table 5-2).

Amounts of sodium and chloride are greatest in *Puccinellia* and least in *Calamagrostis* throughout the season (Table 5-2). Amounts of potassium and magnesium were similar in all three species. Although there was considerable variation in the results, no consistent trend in the amounts of these elements for the three species was evident in the three experiments. Amounts of calcium present in the above-ground biomass of *Carex* and *Puccinellia* were similar, and the values were almost twice as large as those for *Calamagrostis* (Table 5-2).

Table 5-2. Elemental composition of the above-ground biomass of *Puccinellia phryganodes*, *Carex subspathacea* and *Calamagrostis deschampsiodes* forage consumed by goslings in the three grazing experiments. C and N values are reported as a percentage of the dry weight of the above-ground biomass; values for other elements expressed as μmol * g DWT^{-1}. (n = 2 for C and N; n = 1 for all other elements). F values, based on one-way ANOVA's, are given for data across rows and down colums (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Values presented are mean (1 SEM).

Element	Exp.	*Carex*	*Puccinellia*	*Calamagrostis*	
C	1	43.8 (.21)	42.7 (.78)	39.2 (.27)	F2,4 = 23.98**
	2	44.2 (.24)	43.9 (.07)	42.2 (.15)	F2,3 = 44.03**
	3	44.1 (.63)	43.0 (.33)	43.4 (.44)	F2,3 = 1.44
		F2,3 = 0.16	F2,3 = 1.76	F2,4 = 32.04**	
N	1	3.32 (.01)	3.59 (.06)	1.80 (.14)	F2,3 = 185.22***
	2	2.12 (.07)	2.33 (.06)	2.32 (.28)	F2,3 = 0.48
	3	2.14 (.08)	2.23 (.04)	2.03 (.13)	F2,3 = 1.34
		F2,3 = 133.69***	F2,3 = 236.87***	F2,3 = 2.52	
C:N	1	13.22	11.88	21.76	
	2	20.84	18.85	18.17	
	3	20.61	19.36	21.39	
Na	1	209	607	162	
	2	147	404	99	
	3	214	445	173	

Table 5-2 continued

Element	Exp.	Carex	Puccinellia	Calamagrostis
Cl	1	361	622	317
	2	393	437	295
	3	235	518	229
K	1	843	714	535
	2	585	456	634
	3	565	387	535
Mg	1	104	160	113
	2	104	160	123
	3	187	75	104
Ca	1	214	252	126
	2	291	351	146
	3	262	175	155

5.3.3 Chemical composition of faeces from goslings grazing on Puccinellia phryganodes, Carex subspathacea and Calamagrostis deschampsiodes

Significant differences were found in the chemical composition of the faeces from the goslings grazing on the three plant species used in the feeding experiments (Table 5-3). The highest amount of nitrogen as a percentage of the dry weight was in faeces derived from Carex and Puccinellia forage compared to the value in faeces from birds which fed on Calamagrostis. The nitrogen content of faeces also increased significantly over the course of the season irrespective of the forage source. The decrease in the amount of nitrogen as a percentage of the dry weight in faeces compared to the amount in the above-ground plant tissue (Table 5-2 above) is a rough indicator of how much nitrogen was retained by the goslings. Averaged over all three experiments these values were 22% for Carex, 29% for Puccinellia and 17% for Calamagrostis.

The highest amounts of carbon were found in faeces derived from Puccinellia compared to corresponding results for faeces from goslings which fed on Carex or Calamagrostis, but this difference was not significant (Table 5-3). There was a increase in the amount of carbon over the course of the season in faeces derived from plants of all three species. The C:N ratio of the faeces was generally largest for Calamagrostis, except for Experiment 2 (Table 5-3).

Amounts of sodium and chloride ions were largest in faeces derived from *Puccinellia* forage, and lowest in faeces of goslings which fed on *Calamagrostis* (Table 5-3). Amounts of potassium, magnesium and calcium were also greatest in faeces derived from *Carex* compared with the amounts in faeces of goslings which fed on *Puccinellia* and *Calamagrostis* (Table 5-3).

The water content of the faeces derived from each of the three forage species did not differ significantly over the course of the summer, however there were significant differences in the water content of the faeces derived from the three species (Table 5-3). The water content of *Calamagrostis* was, on average, 4% lower than the contents of *Carex* or *Puccinellia*. The amounts of soluble nitrogen (NH_4^+ -N * g DWT^{-1}) in faeces derived from the three forage types were not significantly different (Table 5-3). The pH of the faeces was only measured for the first two experiments, and varied between 6.4 and 7.4 (Table 5-3).

5.3.4 Microbial respiration and nitrogen mineralization during the incubation of faeces

The rates of microbial respiration over a 12 hour and a 24 hour period respectively were, on average, 50% and 74% higher in faeces from goslings which fed on *Carex*, than in faeces from goslings which grazed *Puccinellia* or *Calamagrostis* (Table 5-4a,b). There were no significant differences in rates of microbial respiration over 24 hours in faeces derived from *Puccinellia* or *Calamagrostis*, however in the first 12 hours of the faecal incubations faeces from *Puccinellia*

Table 5-3 Elemental composition of faeces of goslings grazing on *Puccinellia phryganodes*, *Carex subspathacea* and *Calamagrostis deschampsiodes* forage in the three grazing experiments and amounts of H2O (%) and NH_4^+ -N (mg NH_4^+ -N * g DWT^{-1} faeces), and pH of faeces determined for fresh faeces at the beginning of the incubations. C and N values are reported as a percentage of the dry weight of the above-ground biomass; values for other elements expressed as µmol * g DWT^{-1}. (n = 2 for C and N; n = 1 for all other elements; n = 3 for %H2O, NH_4^+ -N, and pH). F values, based on one-way ANOVA's, are given for data across rows and down colums (*, p < 0.05; **, p < 0.01; ***, p < 0.001). Values presented are mean (1 SEM).

Element	Exp.	*Carex*	*Puccinellia*	*Calamagrostis*	
C	1	39.3 (.17)	41.3 (.68)	39.9 (.05)	F2,3 = 6.21
	2	41.8 (.09)	41.9 (.18)	41.8 (.20)	F2,3 = 0.21
	3	40.6 (.03)	42.9 (.99)	41.9 (.09)	F2,3 = 0.34
		F2,3 = 125.27***	F2,3 = 0.64	F2,3 = 80.78**	
N	1	1.92 (.01)	1.67 (.08)	1.26 (.01)	F2,3 = 57.01**
	2	1.91 (.22)	1.72 (.04)	2.16 (.10)	F2,3 = 2.44
	3	2.08 (.06)	2.39 (.04)	1.68 (.06)	F2,3 = 24.56**
		F2,3 = 0.54	F2,3 = 28.30**	F2,3 = 44.41**	
C:N	1	20.51	24.86	31.68	
	2	22.15	24.37	19.42	
	3	19.52	17.93	24.94	

Table 5-3 continued

Element	Exp.	*Carex*	*Puccinellia*	*Calamagrostis*	
Na	1	325	351	152	
	2	293	427	115	
	3	225	276	99	
Cl	1	776	1042	404	
	2	459	728	300	
	3	399	710	437	
K	1	854	716	535	
	2	486	456	486	
	3	406	278	436	
Mg	1	349	258	94	
	2	217	227	151	
	3	349	129	104	
Ca	1	175	136	97	
	2	136	58	146	
	3	184	97	49	
%H2O	1	88.2 (.28)	87.6 (.35)	85.8 (.22)	F2,6 = 19.54**
	2	89.9 (3.1)	86.9 (.19)	84.1 (.10)	F2,6 = 2.60
	3	88.0 (.40)	88.0 (.49)	84.3 (1.0)	F2,6 = 9.48*
		F2,6 = 0.32	F2,6 = 2.32	F2,6 = 2.25	
NH_4^+	1	1.79 (.34)	2.93 (.55)	2.46 (.51)	F2,6 = 1.47
	2	2.58 (.16)	2.85 (.30)	2.38 (.16)	F2,6 = 0.37
	3	2.37 (.44)	4.07 (.51)	3.14 (.10)	F2,6 = 4.78
		F2,6 = 1.51	F2,6 = 2.17	F2,6 = 1.82	

Table 5-3 continued

Element	Exp.	*Carex*	*Puccinellia*	*Calamagrostis*
pH	1	7.34 (.10)	7.22 (.17)	7.16 (.11)
	2	7.23 (.26)	6.57 (.12)	6.60 (.17)

plants consistently had lower rates of respiration than faeces of goslings which fed on Calamagrostis (Table 5-4a). Rates of respiration based on 24 hours were more than double the rates recorded for the first 12 hours of incubation, suggesting that autolysis of cells occurred which led to rapid microbial growth as respiratory substrates were released. No significant seasonal effects (between the three Experiments) on rates of microbial respiration were detected (Table 5-4a,b).

Net nitrogen mineralization rates of faeces based on incubations that lasted 24 hours ranged from 1.31 to 2.52 to 4.97 mg NH_4^+ -N * g DWT $faeces^{-1}$ * 24 h^{-1} respectively for faeces from goslings grazing on Calamagrostis, Puccinellia, and Carex, averaged over the three experiments (Table 5-4c). This is equivalent to a mineralization rate of 7.7%, 13.6% and 25.2% respectively of the total nitrogen of faeces derived from Calamagrostis, Puccinellia and Carex. Rates of net nitrogen mineralization were generally highest for faeces collected late in the season (Experiment 3), and lowest for faeces collected in July (Experiment 2) (Table 5-4c).

The amount of nitrogen mineralized per unit of CO_2 respired (nitrogen mineralization efficiency) was, on average, twice as high in faeces derived from Carex or Puccinellia compared to faeces derived from Calamagrostis (Table 5-4d).

Table 5-4. Microbial respiration between 0 and 12 h (a), and 0 and 24 h (b), net nitrogen mineralization between 0 and 24 h (c), and mineralization efficiency (mineralization/respiration) (d), of faeces of goslings grazing on Puccinellia phryganodes, Carex subspathacea and Calamagrostis deschampsiodes forage during incubations for the three grazing experiments (1, 2, 3). F values, based on one-way ANOVA's, are given for data across rows and down colums (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Values presented are mean (1 SEM).

a) Respiration (to - t12) (mg CO_2 * g DWT faeces^{-1} * 12 h^{-1})

Exp.	Carex	Puccinellia	Calamagrostis	
1	3.65 (0.92)	1.76 (0.37)	1.83 (0.18)	F2,3 = 3.39
2	4.99 (0.12)	1.09 (0.01)	2.94 (0.13)	F2,3 = 384.73***
3	4.11 (0.05)	1.52 (1.01)	2.39 (0.26)	F2,3 = 4.82
	F2,3 = 1.63	F2,3 = 0.30	F2,3 = 7.76	

b) Respiration (to - t24) (mg CO_2 * g DWT faeces^{-1} * 24 h^{-1})

Exp.	Carex	Puccinellia	Calamagrostis	
1	22.12 (3.87)	17.37 (1.45)	9.92 (1.24)	F2,3 = 6.10
2	27.08 (1.34)	8.51 (0.64)	15.19 (0.89)	F2,3 = 99.96***
3	21.20 (2.28)	13.87 (2.78)	16.27 (0.41)	F2,3 = 3.20
	F2,3 = 1.37	F2,3 = 5.85	F2,3 = 13.86*	

Table 5-4 continued

c) Nitrogen mineralization (mg NH_4^+ -N * g DWT $faeces^{-1}$ * 24 h^{-1})

Exp.	Carex	Puccinellia	Calamagrostis	
1	6.27 (1.34)	2.03 (0.08)	0.97 (0.34)	F2,3 = 12.17*
2	2.57 (0.40)	1.25 (0.02)	0.67 (0.08)	F2,3 = 17.13*
3	6.07 (0.11)	4.29 (0.36)	2.29 (0.57)	F2,3 = 23.05*
	F2,3 = 6.57	F2,3 = 53.32**	F2,3 = 5.01	

d) Nitrogen mineralization efficiency (Nmin/Resp)
(mg NH_4^+ -N * mg CO_2^{-1} * g DWT $faeces^{-1}$ * 24 h^{-1})

Exp.	Carex	Puccinellia	Calamagrostis
1	0.30 (0.11)	0.12 (0.01)	0.09 (0.02)
2	0.09 (0.01)	0.15 (0.01)	0.04 (0.003)
3	0.29 (0.04)	0.33 (0.09)	0.14 (0.04)

5.3.5 Digestibility of the three forage types

Estimates of forage digestibility are based upon the analysis of amounts of acid detergent fibre present in faeces compared to that in plant tissues. In general, digestibility is highest in Puccinellia compared to Carex and Calamagrostis (Table 5-5). In all three species there appears to be a decline in digestibility over the season, however no estimate of digestibility of Calamagrostis could be made in Experiment 3. It must be emphasised that these estimates of digestibility are only crude estimates based upon the total fibre of one sample, and these values were not corrected for the influence of other factors which might affect apparent digestibility, such as the amount of silica present (Demment and van Soest 1983).

5.4 DISCUSSION

Significant differences in the chemical composition of the three forage species affected the feeding behaviour of the goslings, the digestibility of the forage and the dynamics of microbial growth and rates of net nitrogen mineralization in fresh faeces. To some extent the results of these experiments represent processes taking place in an artificial system and therefore extrapolations to the conditions in the natural system should be made with care. The captive goslings may have a different

Table 5-5. Digestibility of _Puccinellia_ _phryganodes_, _Carex_ _subspathacea_ and _Calamagrostis_ _deschampsiodes_ forage based on estimates of the ratio of acid detergent fibre of above-ground biomass of plants and faeces produced by goslings of the Lesser Snow Goose grazing on these plants (n = 1).

	% digestibility		
	Puccinellia	_Calamagrostis_	_Carex_
Exp. 1	33.6	21.8	24.0
Exp. 2	27.4	13.4	10.1
Exp. 3	15.3	-	9.5
Mean	25.4	17.6	14.5

microbial gut flora than wild geese not exposed to supplemental food. The conditions under which the goslings were raised may have contributed to the differences in microbial respiration, nitrogen mineralization and forage digestibility. However, there is no reason to doubt that the overall trends in microbial activity detected in faeces derived from these three species do occur under natural conditions when wild geese feed on these species.

Wild geese at La Pérouse Bay are subject to changes in diet over relatively short periods of time which may affect their digestive physiology. During the day they forage extensively on Carex-Puccinellia swards, but during the evening they move into less exposed sites, where Calamagrostis is common. Some geese also move frequently between salt- and fresh-water marshes during the brood-rearing period following hatch (Hik 1986). Increases in caecal volume (the site of bacterial breakdown of cellulose) has been reported for ducks adapted to high fibre diets (Malone 1965; Miller 1975), and there may also be corresponding changes in the composition of gut flora. Seasonal changes in the length of the small intestine and weights of gizzards of Lesser Snow Geese on their wintering grounds may represent an adaptation which results in the efficient utilization of food containing high amounts of fibre (Burton, Hudson and Bragg 1979). Similar anatomical and physiological changes may occur in geese at La Pérouse Bay, as they utilize different forage types during the season.

The large nutritional requirements of geese, coupled with their rapid processing of food, characterized by relatively short throughput times (Sibly 1981), provides an explanation for the very selective feeding behaviour of geese (Lieff 1973; Owen 1976; Owen, Nugent and Davies 1977; Prins, Ydenburg and Drent 1980; Thomas and Prevett 1980; Sedinger and Raveling 1984; Buchsbaum and Valiela 1987). Selection of forage by geese probably involves a compromise between meeting nutritional requirements and avoiding foods containing high amounts of fibre, silica or secondary metabolites. During the summer period when the rapid growth of forage species occurs, the tissues contain large amounts of nitrogen compared to carbohydrate. It is likely that this type of forage will be preferred compared to forage low in nitrogen and high in carbohydrates (Harwood 1974, 1977; Buchsbaum, Valiela and Swain 1984; Buchsbaum and Valiela 1987). At La Pérouse Bay Carex and Puccinellia are preferred over Calamagrostis (Jefferies 1988a,b). However, at the McConnell River (250 km north of La Pérouse Bay, near Eskimo Point, NWT), Calamagrostis deschampsiodes is used extensively in the absence of the more preferred forage species (Kerbes, Kotanen and Jefferies 198N). Geese may be able to effectively utilize this forage by increasing the amount of time spent foraging (see Sedinger and Raveling 1988). Alternatively, changes in anatomy of the gastrointestinal tract in response to increases in dietary fibre may compensate for the decrease in forage quality, as noted above.

Differences in the elemental composition of above-ground plant tissue and faeces from each of the three forage species suggests that the most important elements retained by the geese are nitrogen, carbon, calcium, and potassium. In general, there were increases in the amounts of sodium, chloride ions and magnesium contained in faeces compared to values in plant tissue. Retention of large amounts of nitrogen and calcium reflect the importance of these elements in protein metabolism and bone structure during the short period of rapid gosling growth.

The quality of the substrate (faeces from different forage species) appears to affect microbial growth. No differences were found in the concentrations of soluble ammonium ions in faeces from goslings which grazed on *Carex*, *Calamagrostis* or *Puccinellia*. Microbial immobilization may have reduced the concentrations of soluble nitrogen in faeces from goslings which grazed *Carex*. This was associated with a high respiration rate. Despite the higher digestibility of *Puccinellia* compared with *Carex*, rates of the net nitrogen mineralization in faeces derived from *Puccinellia* were significantly less than corresponding values derived form *Carex*. The cause of this difference is unknown, but it may be associated with the higher amounts of sodium and chloride in faeces derived from *Puccinellia* forage which may restrict microbial activity. Also, relatively few cells of the grass may be broken during passage through the gut of the gosling, so that hydrolases and proteases which can act on the cellular contents and provide substrates for microbial growth are not released.

The rates of net nitrogen mineralization were low in faeces derived from *Calamagrostis* forage, reflecting nitrogen-limited microbial growth on a poor quality substrate. The relatively low nitrogen content of the tissue, the low retention time during gut passage, the high C:N ratio and the low digestibility of tissue of *Calamagrostis* compared to corresponding values for the other two forage species, suggest that this plant is of low quality as a food resource for geese. Pecking rates of goslings were relatively low on *Calamagrostis*, but defecations rates were high. This inverse relationship between passage rate and forage digestibility is often observed in herbivores feeding on forage of poor quality (Demment and Van Soest 1983).

A significant portion of the soluble faecal nitrogen unaccounted for by Bazely and Jefferies (1985) after 48 h in their experiments was likely immobilized by microbes present in the fresh faeces, rather than lost as ammonia to the atmosphere (volatilized) (Ruess, Hik and Jefferies 198N). Laboratory incubations of fresh faeces indicate that at 15°C microbial respiration and nitrogen mineralization rates would be 12.9 mg CO_2 * g DWT^{-1} * 24 h^{-1}, and 2.3 mg NH_4^+ -N * g DWT^{-1} * 24 h^{-1} respectively, representing the potential for a significant net increase in the concentration of inorganic nitrogen in faeces (Ruess, Hik and Jefferies 198N). This measure is probably an underestimate since it does not include nitrification. Nitrifiers in sediments are probably severely substrate-limited, making their detection difficult. Nitrate was rapidly produced in the sediments if they were primed with ammonium ions (Jefferies 1988a). However, the physical-chemical conditions in fresh faeces are suitable for nitrification, and nitrate generated in faeces may provide a significant source of nitrate for plant growth. However, under nutrient limiting conditions, mineral nitrogen may be immobilized by microbes (Bosatta and Berendse 1984; Ruess and McNaughton 1987). The growth of soil microbes may also be stimulated by the high levels of microbial acitivity in goose faeces, which in turn may contibute to increased net nitrogen mineralization on the salt marsh, and the availability of inorganic nitrogen for plant growth (Ruess and McNaughton 1987).

The selection of high quality forage by the geese has effects beyond the level of herbivore nutrition which affect both the pathways and rates of nitrogen fluxes in the system. Forage of high quality promotes faecal decomposition and nitrogen mineralization by microbes. Since plant growth is limited by the availability of nitrogen (Cargill and Jefferies 1984a), any process which increases the rate of availability of this element for plant growth will be significant in the overall nitrogen balance of the salt marsh. Mineralization of organic faecal nitrogen represents an essential link in the maintenance of the flow of nitrogen into the sediments, and supports the regrowth of grazed vegetation at a time when most required by the geese.

The colonial foraging behaviour of the geese on their breeding grounds is also necessary for maintaining optimal foraging conditions. Harwood (1974, 1977) and Cargill and Jefferies (1984b) have documented that higher amounts of nitrogen are deposited in grazed vegetation compared to ungrazed vegetation. Since foragers apparently select food to maximize nitrogen intake (Sibly and Calow 1986; Stephens and Krebs 1986), the maintenence of high amounts of nitrogen and increased net above-ground primary production in grazed swards results in the geese continually selecting it over ungrazed plants. Thus the effects of grazing are of potential benefit to both plants and geese, since rapid net mineralization of nitrogen by microbes in fresh faeces facilitates the return of this element to the sediments, before the faeces are removed by tides or winds. Where forage quality is poor (eg. *Calamagrostis*) mineralization of nitrogen by microbes is reduced, possibly exacerbating net losses of nitrogen from the system on these sites.

CHAPTER 6: GENERAL DISCUSSION - HERBIVORY AS AN ECOSYSTEM PROCESS AND COEVOLUTION IN GRAZING SYSTEMS

6.1 Overview of results

The main results of these experiments are 1) that moderate levels of grazing by goslings of the Lesser Snow Goose led to increases in NAPP of swards of Puccinellia phryganodes early in the season, but that the ability of the vegetation to recover from the effects of grazing declined as the season progressed (Chapter 3). 2) Grazing maintained the nitrogen content of the swards at higher amounts than that in ungrazed swards, which resulted in the production of forage of high nutritional quality during the period when it was most required by the geese (Chapters 3 and 4). 3) Swards of Puccinellia grazed on 3 or 4 occasions at intervals of 12 days showed high cumulative values of NAPP compared to that of ungrazed swards. Swards grazed on three occasions at intervals of approximately 24 days showed even larger increases in NAPP above that of ungrazed swards (Chapter 4). 4) The amount of nitrogen accumulated in the above-ground biomass of grazed swards could not be accounted for by nitrogen deposited in faeces on the swards. The amount of nitrogen accumulated was significantly greater than the amount in the above-ground biomass of swards that were grazed but from which the faeces were removed (Chapter 3). 5) The amount of nitrogen mineralized from faeces derived from goslings which fed on Carex subspathecea was larger than the corresponding amounts from faeces derived from Puccinellia phryganodes or Calamagrostis deschampsiodes (Chapter 5). Microbial nitrogen mineralization in faeces and the sediments may provide additional sources of nitrogen to sustain plant growth following grazing.

6.2 The limitations of perturbation experiments

The advantages of using captive goslings in experimental studies were discussed in Section 2.4, but the limitations of this approach have not been considered. The ability to control the level of grazing (amount of biomass removed and input of nitrogen from faeces) on swards of vegetation provides many obvious advantages when studying the effects of herbivory. Nevertheless, there are three major difficulties associated with the use of captive goslings in these experiments.

1. The effects of grazing by goslings on the vegetation may not be the same as those which result from the foraging activies of wild geese (adults and goslings). Goslings differ from adult geese in their foraging behaviour. Goslings tend to have higher defecation rates (Cargill and Jefferies 1984b) and spend more time feeding (Rockwell unpublished) than adult geese. The effects of goslings on the vegetation tend be evident on a smaller spatial scale since they are smaller than adults, although by the end of summer goslings are effectively

adult size. The faeces of goslings may also contain lower amounts of soluble nitrogen compared to adults (Ruess, Hik and Jefferies 198N). In addition, the number of goslings per adult following hatch is approximately 2:1; this ratio decreases to approximately 1:1 by the time the goslings fledge six weeks later (Cooke et al. 1982). Therefore, even though the results of experiments using captive goslings provide no direct evaluation of the effects of grazing by adult geese on the vegetation, there is no reason to believe that similar responses of the vegetation would not be detected if the experiments had been conducted using adult geese.

2. Captive goslings may behave differently from wild goslings and have a different digestive physiology than that characteristic of wild goslings. Differences in pecking rates of wild and captive goslings were not detected (Section 2.4), however differences may exist between the digestive physiology of wild and captive goslings. The reason for this is that the diet of captive goslings was supplemented by artificial foods that contain high amounts of nutrients and less fibre than natural forage. This may result in modification in the digestive tract compared to that of wild birds (Demment and Van Soest 1983). This problem raises concerns about the results of physiological experiments involving captive goslings, but it is unlikely to lead to significant changes in foraging behaviour.

3. Extrapolation of results obtained from these experiments to the natural conditions must be done with

care. This is a general problem in experimental biology. The experiments reported above were conducted using captive goslings in experimental plots, because the questions which were being addressed could not be answered using wild geese. The conditions used in the experimental treatments may occur under natural conditions but it is very difficult to obtain reliable information from field observations. It must be emphasised that this project involves a study of the responses of the vegetation to grazing; it is not a study of the foraging behaviour of the snow goose. At the risk of grossly oversimplifying the experimental approach, the goose is used as a mowing machine and a bag of NPK in order to study the responses of plants to defoliation and the application of fertilizer.

6.3 Ecosystems as dynamic units

Ecosystems cannot be conceptualized as simple collections of species and habitats, but must be viewed from a holistic standpoint (O'Neill et al. 1986). Although ecosystems processes, such as nutrient cycling, can be reduced to the level of nutrient flow between individuals or populations, higher order levels of integration must also be considered. "Simple" biological interactions may be complex at larger spatial and temporal scales.

The concept of stability usually refers to the tendency of a system to remain near an equilibrium point or to return to it after a disturbance (Orians 1975). Many interaction processes in ecology exhibit some form of cyclical stability and oscillate around some central point (ie. predator-prey systems). The amplitude of the region over which a system is stable is important in determining both the size of the disturbance required to upset stability, and the rate with which a system returns to its former state following disturbance. Systems which are resilient, persistent or constant tend to be able to compensate for disturbance and remain relatively stable. They give the appearence of an equilibrium state (Orians 1975).

Often it is impractical to consider the ecosystem as an "equilibrium" system, since data collected over a long period are required to prove equilibrium stability (Connell and Sousa 1983). Ecosystems change as climate and other environmental variables change; consequently different scales of disturbance influence our perception of stability. Current ecological theory does not support the concept of "equilibrium" community, however it remains a useful descriptive term to describe situations where the balance between positive and negative feedbacks result in a system that is relatively unchanging and resilient to disturbance (DeAngelis, Post and Travis 1986; O'Neill et al. 1986).

6.4 Ecosystem responses to herbivory and disturbance

The effects of herbivory upon the composition and diversity of natural communities will depend upon the behaviour of the herbivores, the growth response of the various species of plants to herbivory, and the prevailing abiotic conditions (Harper 1969, McNaughton 1983). Herbivores may alter the composition of plant communites, reduce (or stimulate) growth and reproduction of plants, aid in the effective dispersal of plant propagules, or alter the competitive abilities of the component plant species (Harper 1969, 1977; Crawley 1983).

At the community level, direct effects of herbivory (ie. removal of tissue) may be of secondary importance to indirect effects (ie. fertilization). Indirect effects may have positive or negative effects on other organisms in the community. For example, Seartedt, Ramundo and Hayes (1988) have shown that above-ground herbivores change the magnitude of the plant-soil-microbial interactions in a manner that benefits soil animals. The immobilisation of inorganic nitrogen in the soil by microbes colonizing senescent roots following grazing (see Aber and Melillo 1980), may be responsible for the increase in arthropod numbers by increasing the amount of nitrogen available to these below-ground herbivores. Thus, interactions between above-ground and below-ground herbivory, soil micro-organisms, environmental factors and other processes are responsible for increases the quality of forage available to below-ground herbivores. Interactions of this type are probably not uncommon (see Chapter 5), however it is important to distinguish between responses to herbivory at the community, population and individuals.

Herbivores can modify the net primary production of plant communities, and the species composition in many communities, and these modifications affect ecosystem processes (Smith 1983; Bergquist and Carpenter 1986; Bazely and Jefferies 1986). Even in communities where the total amount of primary production consumed is small, herbivores can have an important impact on ecosystem processes. For example, Shachak, Jones and Granot (1987) report that grazing by snails on rock containing endolithic lichens contributes to the process of soil formation at a rate similar to windborne dust deposition.

Disturbance by herbivores is an important source of vegetational heterogeneity in many habitats (Sousa 1984; Pickett and White 1985; Chesson and Chase 1986; Jefferies 1988a,b). Although disturbance often leads to habitat destruction (Wharton and Mann 1981; Kerbes, Kotanen and Jefferies 198N), it may also retard succession (Bazely and Jefferies 1986), and may create patches which provide opportunities for recolonization (Jefferies 1988a) or replacement of species (Crawley 1983; Pickett and White 1985). Herbivory represents a form of disturbance for the plant which is consumed. In order to characterise this disurbance, important variables include the frequency with which a patch is grazed and the amount of biomass removed. Since most herbivores are relatively mobile and different herbivores may not use the same types of forage within one community, a mosaic of patches that experience levels of grazing varying in frequency and intensity are likely to exist.

As mentioned earlier, disturbance in grazing systems may be associated with either positive or negative feedback process. Concomitant with clipping (grazing) and fertilization are the effects of treading and trampling on vegetation. Despite the existence of potential compensatory mechanisms which may lead to increases in production following grazing (positive feedback mechanisms; Section 1.4), the trampling effects of large grazers on the production of swards and survival of individual plants are almost always negative. Wind and Schothorst (1967) report that the bulk densities of the surface layer of moist soils increased due to compaction by grazers. Also treading where soil moisture is high (ie. salt marshes) often leads to the loss of soil structure and the development of anoxic conditions in the sediments (Jensen 1985). In some cases the sward is cratered and the roots cannot develop fully. In these situations there is a reduced volume of soil available for the plants to acquire nutrients (Charles 1979). Edmond (1964) reports that treading by sheep reduced the growth of 10 pasture species between 9% and 77% of that of the control plants, probably due to reduced tiller survival.

These studies suggest that the severity of trampling effects may determine the outcome of the plant-herbivore interaction, even in the presence of suitable compensatory mechanisms such as fertilization. However, not all trampling effects may be negative. Belsky (1986b) showed that trampling by African ungulates increased the root-crown diameter of Andropogon greenayi and forced its tillers into the ground, where they rooted and enabled the plants to form clonal mats (also see Georgiadis and McNaughton 1988). Nevertheless, the most severe effects of trampling are probably caused by large ungulate herbivores. Smaller grazers, such as geese, probably have a limited trampling effect on most types of vegetation. Trampling by geese may even temporarily reduce the angle of the most accessable leaves, thus making them unavailable as forage for a short time (< 60 mins) (M. Loonen, personal communication). Such a response does not result in an adverse, long-term effect on growth.

On an evolutionary scale disturbance is also extremely important. Wing and Tiffney (1987) suggest that plant predation and vegetational disturbance by large herbivorous tetrapods during the Cretaceous favoured the individual success of weedy angiosperms and simultaneously tended to create conditions where weedy plants could prosper (also see Owen-Smith 1987). This highly productive type of vegetation in turn favoured the continued success of large herbivores. Similarly in the Late Eocene-Oligocene the world-wide cooling of the climate led to the spread of grasses, which allowed a rapid radiation of large, mammalian grazers (Stebbins 1981).

6.5 Nutrient cycling in grazing ecosystems

Nutrient cycling in ecosystems is often thought of as a positive feedback process (O'Neill _et al_. 1986). In terrestrial systems the activities of herbivores result in an acceleration of rates of nutrient mineralization above the rates which occur in their absence (Arman, Hopcraft and McDonald 1975; Woodmansee 1978; Ruess and McNaughton 1987). Nutrient limitations on plant growth can be offset by the rapid and efficient recycling of essential elements within an ecosystem which results from the activities of herbivores.

The data from Chapter 3 show that even in swards of _Puccinellia_ which were subjected to the longest period of grazing, less than 10% of the nitrogen incorporated into the new tissue over the course of the season could have come directly from faecal sources (Table 3-8). Even this estimate of 10% assumes no loss of nitrogen from faeces due to ammonia volatilization, and that all the available nitrogen in faeces is mineralized. Since neither of these assumptions is fully valid (Chapter 5), other sources of nitrogen must be available for plant growth only when faeces are present. These sources could include below-ground reserves, available nitrogen for plant growth in the sediments, net mineralization of organic nitrogen in sediments as a result of microbial processes, and nitrogen fixation either in the rhizosphere or on the surface of sediments (Bazely and Jefferies 1988).

Nitrogen mineralization-immobilization processes which occur in soils are strongly affected by the addition of faeces where grazing occurs (Bosatta and Berendse 1984; Ladd and Paul 1984; Ruess and McNaughton 1987; Chapter 5). Evidence from La Pérouse Bay indicates the presence of a substantial microbial biomass in goose faeces (Ruess, Hik and Jefferies 198N; Chapter 5). The release of inorganic nitrogen into the soil as a result of the net mineralization of nitrogen in faeces may be important in enabling the soil microbial flora to develop in sediments where nitrogen amounts are low and the C:N ratio is high. The C:N ratio of sediments at La Pérouse Bay is greater than 20 (Bazely and Jefferies 1988; Jefferies and Jensen unpublished). At such ratios it is likely that most of the nitrogen which is mineralized is immobilized by microbes. The role of faeces as a primer of the soil microbial flora (ie. lowering of the C:N ratio so that net mineralisation rather than immobilization occurs) is known to operate elsewhere, and ultimately results in a net mineralization of nitrogen in soils (Ruess and McNaughton 1987). If this priming of soil microbial activity occurs at La Pérouse Bay, as the results suggest, it implies that the timing of the grazing episodes by the geese are not critical for achieving increases in the NAPP of grazed swards, above that of ungrazed swards, provided sufficient faeces are deposited on the sward early in the season. The results of Chapter 4 suggest that, over a wide range of grazing intensities and numbers of grazing episodes, the values of cumulative NAPP are broadly similar, irrespective of the treatment. The geese do not have to follow a precise pattern of foraging behaviour, (ie. return time to a particular patch) in order for the swards to achieve high NAPP. The resilience of the system to the effects of grazing by Lesser Snow Geese appears to depend to a large extent on the ability of the soil microbial biomass to release nutrients for the growth of the graminoid swards under a wide range of grazing conditions.

Nutrient feedback in coral reef systems show many similarities to feedback processes at the La Pérouse Bay salt marsh. Tight nutrient cycling is essential, so that nutrients are not lost to the ocean (Carpenter 1986). This is achieved in a number of ways as far as nitrogen is concerned. Most corals host symbiotic xooanthellae (non-motile stages of dinoflagellates) that utilize ammonium excreted by the host coral and may also assimilate ammonium from outside the coral. Corals lacking xooanthellae tend to show net ammonium excretion which is lost from the system (Burris 1983). In addition, nitrogen-fixing cyanobacteria and green algae on the surface of reefs are actively grazed by herbivores (invertebrates and fishes). Excreted ammonium ions may be used by green algae (Sprent 1987), which are the most important primary producers in these systems. Nitrogen for the growth of the coral reef comes either directly from fixation by cyanobacteria, or from the efficient uptake of ammonium ions in excreta following grazing. Just like the grazed salt marsh, the pool of nitrogen available for biological growth is limited and feedback processes between the component organisms result in the efficient recycling of a limited resource.

6.6 Arctic breeding geese and community structure

The foraging activities of Lesser Snow Geese modify the structure and composition of vegetation of coastal wetlands in the eastern Canadian Arctic (Jefferies 1988b). As mentioned above, these activities can be considered in terms of positive or negative feedbacks. Jefferies (1988b) has interpreted the patterns of vegetational development of these coastal areas in relation to the interaction between effects of Lesser Snow Goose foraging, isostatic uplift of the Hudson Bay lowlands, and climatic change on vegetation.

Arctic breeding geese require large quantities of high quality forage. There are a number of ways that they can accomplish this. The first is to breed in areas where food is plentiful. The second is to manipulate the quality of the forage they use. The third is to continually move to new food resources. Geese are not highly mobile during the summer so their abilty to move over large distances is limited (see McLaren and McLaren 1980). In general, Lesser Snow Geese display strong female natal philopatry and tend to return to the same nesting colony and nest site each year (Abraham 1980; Hik 1986). Therefore, snow geese must breed in areas where food availability is high, and where they can manipute both forage availability and its quality during periods when they are not mobile (options 1 and 2 above).

The results of the experiments reported above support the suggestion that the foraging activities of the geese results in a continual supply of high quality forage during the summer. The patterns of grazing also provide a mechanism for the continued production of forage in subsequent years. The departure of the geese in mid-August allows the vegetation to recover from the effects of intenive grazing earlier in the summer. The ecological significance of this period for the growth of the forage plants and the maintenance of the grazing sward has yet to be determined, however during this period nutrient and carbohydrate reserves are laid down, which support growth the following season. Continued grazing late in the season may depress the ability of the plants to grow the following season.

There is often an asymmetry in the relationship between the size and movements of the herbivore populations and their food supply (Drent and Prins 1987). Often interactions between different species of herbivores using the same resource creates problems for sustained plant growth. The movement of different animal populations may affect the ability of plants to recover from grazing, and therefore influence the quality of the vegetation for subsequent grazers. For example, the "grazing succession" of generalist ungulate herbivores on the Serengeti grasslands (McNaughton 1976, 1985) is facilitated by the different feeding behaviours and the morphologies of the ungulate grazers. Increases in amounts of biomass of grass available for red deer (_Cervus elaphus_ L.) following winter grazing by cattle (_Bos taurus_ L.) on the island of Rhum (Gordon 1988) also provides an example of how temporal separation of the use of forage by different grazers can "benefit" both the forage species and the grazers. In another example grazers of the same species utilize different plant parts over the course of the season as forage. The diet of geese (Anser anser) in the Netherlands shifts from seeds of Agrostis stolonifera in the fall to leaves in spring (van Eerden et al. 1984; Drent and Prins 1987), in order to make use of the forage which is both readily available and of high quality at different seasons. Prins and Ydenburg (1985) have reported similar seasonal shifts in grazing patterns of Barnacle geese between different habitat types.

6.7 Coevolution in grazing systems

Mutualisms involve interactions between two populations where the growth or genetic fitness of both populations is enhanced as a result of the interaction. Although mutualisms are a common type of organism-to-organism interaction (Janzen 1985), herbivory is not normally included in this category. However, depending upon the definition of mutualism used this may not always be the case (see Starr 1975; Lewis 1985). Nevertheless, there is no reason to believe that trophic interactions, such as herbivory, necessarily become mutualistic in evolutionary time (Oksanen 1988). Ecologically stable or quasi-stable interactions between populations are to be expected in natural ecosystems. As noted above however, the influence of these interactions may extend to all levels of the community. Coevolution is a process that can be thought of as a positive feedback process which may result in mutualistic associations between populations. Many features of mutualistic systems can be explained by examining positive feedback loops in ecosystems (DeAngelis, Post and Travis 1986). At the level of the community these types of interactions between groups of species are considered to be examples of "diffuse" coevolution (Herrera 1985b).

Herbivory is a process which has had a profound influence on the evolution of both plants and animals (Section 1.1). For example, there is little doubt that graminoid growth form and herbivores have shared a long evolutionary history, and this is often used as an example of diffuse coevolution. Wing and Tiffney (1987) have shown that there has been a strong reciprocal interaction of vertebrate herbivores and angiosperms in the Cretaceous and Tertiary. During the Cretaceous, plant predation and disturbance by large herbivores simultaneously favoured the individual success of weedy angiosperms and created conditions where weedy angiosperms could prosper as mentioned above. In the Tertiary, vegetational structure militated against the diversification of large herbivores, until climatic change brought about changes in angiosperm physiognomy and reproductive biology (Wing and Tiffney 1987). In this case the potential for the evolution of large mammalian herbivores appears to be restricted by the diversification of the grasses.

Ecosystems can be viewed as a diffuse web of feedbacks, as suggested above. These interactions may promote the efficiency and stability of the system as a whole (Patten and Odum 1981). Processes which lead to greater stability within ecosystems and communities may do so by dampening the effects of disturbance on populations and individuals. While natural selection is normally assumed to act on the level of the individual, selection between groups of interacting species, or whole ecosystems may possibly occur. Mechanisms have been proposed that involve competition between positive feedback loops to account for evolution at higher levels of organization (ie. community, ecosystem) (Wilson 1976, 1980; Patten and Odum 1981). In these systems it remains to be determined whether internal feedbacks dominate in shaping the course of ecosystem evolution, or whether the extraneous factors of chance disturbance are more significant over the long term.

It could be argued that coevolution in the Lesser Snow Goose - salt marsh system is evident at the community level, but not at the level of the population. However there is no real evidence for "trait group" selection (see Wilson 1976, 1980), but rather of tight coupling of nutrient cycling among various levels of organization. This results in a system where plant and herbivore have had a profound influence on each other and upon other components of the system. The integration of the whole is greater than the sum of each component part in determining the stability of the system, but this does not necessarily imply coevolution. In fact, in this system, given the relatively short period it has existed (approximately 30 years), the view that coevolution has occurred is untenable. However, snow geese and coastal vegetation in the Arctic have probably co-existed for a long time. The resilience of these systems can be attributed to the tight coupling of nutrient cycling between various levels of organization, the morphology of Puccinellia, and the timing of grazing by the geese.

The interactive and dynamic processes of nitrogen cycling between plants, geese, sediments and microbes lead to enhanced primary production in this grazed system. Emphasis must be placed on the plurality of the effects of grazing and the necessity of including studies of nutrient cycling in investigations of plant-herbivore interactions (Jefferies 1988a). A suite of interactions exist, which extend the influence of plant-herbivore interactions beyond the immediate participants, to different trophic levels. This tight coupling of ecosystem and community level processes provides a basis for the interpretation of a grazing system which exibits a high degree of constancy (sensu Orians 1975), and which is extremely resilient to the effects of summer grazing by Lesser Snow Geese.

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