THE EFFECTS OF GRAZING BY LESSER SNOW GEESE ON THE VEGETATION OF THE SALT MARSH AT LA PEROUSE BAY, MANITOBA

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SUMMARY

1. Net primary production of salt marsh vegetation, and nitrogen fluxes between vegetation and lesser snow geese (Anser caerulescens caerulescens) have been examined at La Pérouse Bay, Manitoba, during the summers of 1979 and 1980.

2. The geese feed primarily on the aerial parts of Puccinellia phryganodes (Gramineae) and Carex subspathacea (Cyperaceae), the dominant species in the marsh. Ninety percent of the biomass of these plants is below ground.

3. Net primary production is limited by the availability of nitrogen. Estimated values for net above-ground primary production of a mixed Puccinellia phryganodes- Carex subspathacea community between June and August 1979 were 200 gm^{-2} for ammonia treated plots and 90 gm^{-2} for untreated plots. The corresponding values for pure stands of Puccinellia and Carex respectively, measured in 1980, were 165 and 160 gm^{-2} for ammonia treated plots and 41 and 60 gm^{-2} for untreated plots.

4. Above-ground primary production is also increased on sites grazed by geese, in comparison to ungrazed sites. The estimated net above-ground primary production of mixed Puccinellia-Carex swards in 1979 was 149 gm^{-2} on grazed sites and 100 gm^{-2} on ungrazed sites. The corresponding values, from 1980, for pure stands of Puccinellia and Carex respectively, are 103 and 95 gm^{-2} for grazed and 56 and 52 gm^{-2} for ungrazed sites.

5. Grazing resulted in increased total nitrogen content of shoots of both Puccinellia and Carex, in both years, in comparison to ungrazed shoots.

6. Estimates indicate that approximately 80% of the net above-ground primary production was consumed by geese. About 60% of the nitrogen in the plant tissues was assimilated by the geese.
7. The geese represent a major pathway for net primary production, and the nitrogen present in plant tissues. However, the return of nitrogen in faeces, in forms which may be directly or indirectly utilized by the plants, appears to result in an increase in the rate of nitrogen cycling compared to that in ungrazed areas.
8. It is suggested that nitrogen fixation by blue-green algae on the mud surface, early in the season, represents a major source of nitrogen in the grazed marsh system.

INTRODUCTION

The Hudson Bay Lowlands are an important breeding ground for many species of shorebirds and waterfowl, including the lesser snow goose (Anser caerulescens caerulescens), which nests and feeds on the coastal marshes. Since 1968, Dr. F. Cooke and his associates have studied the population biology of a nesting colony of lesser snow geese at La Pérouse Bay, on the Hudson Bay coast about 30 km east of Churchill, Manitoba. (Figure 1) (Cooke et al, 1972, 1975, 1976, 1978). The results provide excellent demographic data on changes in the structure of the population of approximately 3500 breeding pairs of geese.

During the post-hatch brood-rearing period at La Pérouse Bay, the adult geese and goslings feed primarily on the shoots of Puccinellia phryganodes (Gramineae) and Carex subspathacea (Cyperaceae), and to a lesser extent on supplementary items such as the rhizomes of Potentilla egedii and catkins of Salix spp. In early spring, adult birds may also feed on roots and rhizomes of Puccinellia and Carex and other graminoids, and the shoot bases and young leaves of Elymus arenarius. One effect of this grazing is that vegetational development in the salt marsh is retarded, (Jefferies, Jensen and Abraham, 1979) but little is known about the effects of grazing on the growth and physiology of the preferred species.

It is not clear to what extent the availability of nutrients limits net primary production in arctic salt marshes, although there is considerable evidence that nitrogen is a limiting factor in temperate salt marshes. (Valiela and Teal, 1979). Shortage of nitrogen, as well as phosphorus, has also been found to limit net primary production in arctic coastal tundra vegetation. (Ulrich and Gersper, 1978).

Salt marsh plants contain large amounts of soluble nitrogen compounds. In Puccinellia phryganodes, early in the season, much of the soluble nitrogen appears to be proline (Cargill and Jefferies, 1980). Low molecular weight nitrogen compounds such as this serve as osmotic solutes in many halophytes. (Story and Wyn Jones, 1977; Stewart and Lee, 1979; Jefferies et al, 1979). Geese appear to derive most of their nutrients from broken cells, as they do not digest cellulose (Mattocks, 1971), and food passes through the gut in 30 to 90 minutes (Harwood, 1977). Therefore, plants with thin cuticles and indeterminate growth form, which contain high concentrations of soluble nitrogen and carbon, may be particularly valuable as food sources for geese. Kear (1970) suggested that nitrogen was the limiting nutrient in the summer diet of wild geese, and this has been supported by the experimental results of Harwood (1974) and Owen (1975).

In recent years, there has been some concern among management personnel about the continuing capacity of the arctic salt marshes to support the snow goose populations, which have been increasing. At those sites where observations have been made, grazing appears to be extremely heavy. Geese have been accused of damaging vegetation in other habitats (Lynch et al, 1948) and heavy grazing by cattle and sheep has often been found to depress plant growth. (Jameson, 1963). However, in some instances, grazing has been found to increase primary productivity (McNaughton, 1962). No previous information is available about the effects of goose grazing on salt marsh vegetation, or on other tundra graminoid communities. The quantity of vegetation consumed by geese at La Pérouse Bay was estimated by calculating the quantity of droppings produced, and the effects on plant growth examined by comparing the net above-ground primary production of grazed and ungrazed sites in the marsh. Particular attention was paid to the effects of grazing on nitrogen fluxes in the marsh ecosystem, because of the probable importance of this nutrient to both the geese and the marsh plants. This part of the investigation included analysis of the total and soluble nitrogen contents of shoots and roots of Carex and Puccinellia throughout the growing season. Grazed and ungrazed plants of both species were compared. In combination with the data on consumption, and on productivity of grazed vegetation, this allowed calculation of the total nitrogen content of the forage available to the geese, and the portion actually consumed. The amount of nitrogen assimilated by the geese was also calculated, by comparing the amounts consumed and rejected in the faeces.

The objectives of the study were:

1. To estimate the net above ground productivity of vascular plants in the *Puccinellia phryganodes*-*Carex subspathacea* marsh community.
2. To determine whether lack of nitrogen limits net primary productivity in this community.
3. To determine how grazing affects the net primary productivity of the marsh.

4. To determine the total quantity of vegetation consumed by the goose population.
5. To estimate the quantity of nitrogen present in the above-ground net primary production, and what portions of this are consumed by the geese, assimilated by them, and returned to the marsh in droppings.

CHARACTERISTICS OF THE STUDY SITE

A characteristic feature of Hudson Bay is that it is still undergoing isostatic uplift at an estimated rate of 1.0 to 1.5m per century (Hunter 1970). A consequence of this uplift is the presence of numerous beach ridges and sand spits and the occurrence of broad tidal flats on the shores of the Bay which extend seaward for approximately 1.0 km below the upper limit of the tides. Much of the coast of Hudson Bay constitutes one of the longest low gradient (0.5 to 1m/km), emergent shorelines in the world. Salt marshes frequently develop landward of these offshore bars and ridges. In addition estuarine salt marshes are formed at the mouths of some rivers which drain into Hudson Bay. Both types of salt marsh occur at La Pérouse Bay on the southern shore of Hudson Bay, 30 km east of Churchill, Manitoba (Fig. 1). The Mast River forms a braided estuary where it drains into La Pérouse Bay. The vegetation of the coastal strip, which extends between 5 and 7 km inland, is characteristic of low Arctic coastal tundra and is dominated by various species of willow.

La Pérouse Bay supports a breeding colony of lesser snow geese (*Anser caerulescens*). The resident population during the nesting period is approximately 8500 geese, of which perhaps 1500 are nonbreeders; this swells to approximately 18,000 during July and August with the addition of young birds (Cooke et *al*. 1972, 1975, 1976, 1978). In addition to supporting these breeding birds, the Bay is used as a staging area by geese during the spring and fall migrations, and at these times of the year the snow goose population may exceed 30,000. The salt marshes are important feeding grounds for these birds (Cooke & Abraham 1980). The coastal physiography and vegetation of the salt marshes at La Pérouse Bay have been described by Jefferies et al. (1979).

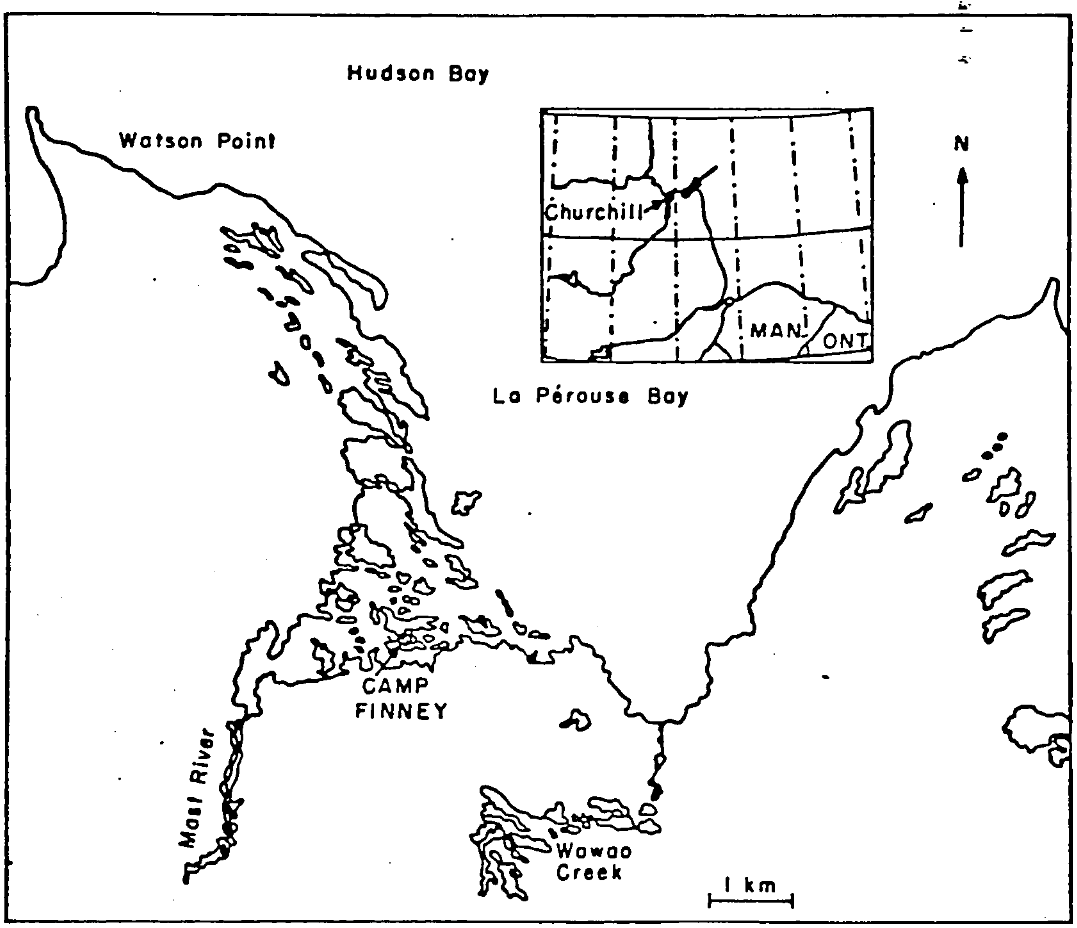

Figure 1

Map of La Pérouse Bay, the position of which on the Hudson Bay coast is indicated by an arrow on the inset map.

Within the delta of the Mast River are a series of islands, some of which have been subject to frost heave. The islands are as much as 15 x 10m in area, and mounds or islands may be raised a metre above the level of the surrounding land by frost action. The frost-heaving alters the drainage pattern in the estuary: new channels are created and existing channels may become blocked with sediment. Within the delta, islands of unconsolidated sediment are colonized by Hippuris tetraphylla. However, the initial colonizer of the surface of the islands is a grass, Puccinellia phryganodes. The species undergoes extensive clonal growth and forms large mats across the surface of the ground. Another species which appears at the initial colonization stage is Carex subspathacea. This sedge is particularly abundant on islands in the delta, where it is codominant with Puccinellia phryganodes (Jefferies et al. 1979). On older islands in the upper reaches of the delta, which are about 1 metre above the level of the surrounding water in summer, Elymus arenarius var. mollis is present. Plant of this species tiller freely and produce numerous horizontal rhizomes. The tops of the mounds are also colonized by Salix brachycarpa.

As indicated above, approximately 18,000 lesser snow geese are resident at La Pérouse Bay in summer, and during spring and autumn migrations, the population may increase to over 30,000. Feeding by the geese is not restricted to any particular area in the Bay; virtually all suitable sites are used at some time during the summer. For most of the summer the birds feed primarily on shoots of Puccinellia phryganodes and Carex subspathacea. Early in the season, when these are not available, the geese eat basal shoots of Elymus arenarius var. mollis. (Heagy & Cooke 1979) and roots and rhizomes of a number of herbaceous species.

Perhaps the most dramatic effect of the geese on the vegetation and surface topography is in the area where willows are colonizing islands. This area is one of the first to be exposed during snow melt in spring and both the breeding and migrant populations of lesser snow geese feed here before other areas are exposed. As discussed by Jefferies _et al_. (1979) the geese strip the turf around the fringes of the ponds in their attempts to feed on underground storage organs of plants. The above-ground vegetation is not in an active stage of growth at this time. This stripping may lead to an increase in the area of ponds. In addition, the geese are responsible for the creation of some ponds. Stripping of vegetation and trampling by the geese leads to the formation of a small depression of exposed sediments, usually less than 1 metre in diameter. The accumulation of water in the depression and the subsequent action of ice enlarges the pool. The findings indicate that a number of pools in the upper levels of the salt marsh may have been produced by goose activity. The role of geese in producing small ponds does not appear to have been reported before in the Arctic. McAtee (1910), McIlhenny (1932) and Lynch _et al_. (1947) have reported that snow geese grub out rhizomes of a number of perennial grasses and sedges on their wintering grounds in Louisiana.

An effect of grazing is to slow down the rate of vegetational development in these plant communities at La Pérouse Bay. Observations and results already published (Jefferies et al. 1979) indicate that, unlike many salt marshes in temperature regions, much of the primary production is utilized by herbivores, and that this probably represents a significant pathway for the export of carbon and nitrogen from the marsh.

METHODS

Measurement of biomass

In 1979, in order to estimate the biomass of the mixed Puccinellia phryganodes-Carex subspathacea sward on which the geese feed, five sites were selected subjectively in the salt marsh. The different sites, which were located on the west side of the estuary, were contained within an area 0.5 x 0.5km. Each site was approximately 25 x 25 m and there was a continuous cover of the two species throughout all sites. The sites were chosen because of the uniform appearance of the vegetation. Within a site, an exclosure (5 x 5m) was erected from which the geese were excluded. Two samples (17.5 x 17.5 x 12.0cm) of turf were taken at random from grazed and ungrazed areas at each site, approximately once every ten days, from 10 June to 23 August 1979. The vegetation was stripped from the turf and live above-ground material was sorted into individual species. Dead above-ground material was not sorted into component species. Below-ground material was also bulked, as it was not possible to recognise root systems of different species or to distinguish between living and dead tissues.

All samples were washed in tap water and dried at 80 C. The results for each component of the biomass are expressed as grams of dry weight per m^2 for each sampling date.

In 1980 the following modifications to the procedure were made. Three sites were selected within pure stands of Puccinellia phryganodes and three in Carex subspathacea stands. At each of the six sites an exclosure (5 x 5 m) was erected. One sample of turf (17 x 17 x 5 cm) was taken at random from grazed and ungrazed areas at each site, approximately every fourteen days from 5 June to 25 August. In order to estimate the below-ground biomass, a sample of soil (5 x 5 x 5 cm) was taken adjacent to the centre of each turf. The 5 cm depth was chosen because, at the beginning of the sampling program, this represented the depth of thaw. Thereafter, it was necessary to continue to use the same standard depth.

Roots were carefully separated into living and dead components on the basis of visual criteria, and the validity of these criteria was determined with the tetrazolium chloride dye test. Roots which had been visually classified as living or dead were placed in a 1% solution of the dye for one hour, whereupon the function of the dye as an electron acceptor for the cytochrome chain caused living roots to take on a bright pink color. The results of this assay indicated that the visual sorting of roots was accurate in most cases, with a slight tendency to over-estimate the proportion of dead roots.

In all other respects the procedure for collection and handling of vegetation samples was identical in 1979 and 1980.

Recovery of vegetation from the effects of grazing

In order to determine whether net primary productivity is enhanced by continual grazing, exclosures were placed in freshly grazed areas at appropriate intervals during the summer, and the subsequent increase in above-ground living biomass was determined. On each occasion, six wire-netting exclosures, 0.5 x 0.5 m, were positioned in swards dominated by either *Puccinellia phryganodes* or *Carex subspathacea*. The positions of the cages in the freshly grazed sites were decided subjectively. The wire cages were left in place for varying periods depending on the prevailing growth rate, but the periods did not exceed 24 days. At the time of harvest, turfs (12 x 12 x 12 cm) were cut from these exclosures and transported to the laboratory. The vegetation was stripped, washed, dried at 80^{o}c and weighed, as described previously. Increments in live above-ground standing crop were expressed in g m^{-2}. Relative growth rates (g g^{-1} wk^{-1}) were calculated from the increments in standing crop.

Response of vegetation to addition of nitrogen fertilizers

In 1979, in order to determine whether net primary production of salt marsh vegetation was limited by the availability of nitrogen, additions of inorganic nitrogen were made to an enclosed area containing a sward of Puccinellia phryganodes and Carex subspathacea. A Latin square experimental plot (5 x 5m) of similar design to that described by Jefferies and Perkins (1977) was set up to examine the effects of additions of nitrogen on the growth of these plants. The plot was designed to give five rows and five columns, and each of the 25 sub-plots was 50 x 50 cm. Between the rows and columns were strips 50 cm wide which allowed access to the plots. From early May to August, mineral salts were applied to designated sub-plots once every 10 to 14 days. Amounts of sodium nitrate or ammonium sulphate added on each occasion were equivalent to those used by Willis (1963), that is 10.05 g and 7.95 g per sub-plot respectively. Two sub-plots in each row or column received sodium nitrate and two received ammonium sulphate; the remaining plot served as a control. Salts were crushed and spread carefully across plots by hand. Once every ten days 5 samples (12 x 12 x 12 cm) were taken at random from plots representative of the different treatments. The vegetation in the five samples for each treatment was sorted and weighed as described earlier. The results for the different components of biomass are expressed as gm^{-2}.

In 1980, the following modifications to the procedure were made. One exclosure (5 x 5 m) was set up in a sward of Puccinellia phryganodes, and another (4 x 4 m) on a site dominated by Carex subspathacea. As before, the exclosures were divided into grids of 50 x 50cm subplots. On the Puccinellia site, four treatments in addition to control were used; ammonium sulphate (7.64 g), soldium nitrate (12.15 g) di-sodium phosphate (8.05), or the ammonium and phosphate treatments combined. All of these except the nitrate addition were also applied to the Carex site. In both exclosures, treatments were assigned in a Latin-square arrangement so that each row and column of the grid contained one of each type of treatment plot, and one control plot. Salts were added by hand about every 21 days, and vegetation samples collected on the same days. A sample of turf (12 x 12 x 2cm) was taken from each subplot on each occasion. Vegetation was clipped, washed, dried and weighed as described earlier.

Measurement of total nitrogen in plant tissue and goose droppings.

Measurements were made on subsamples of the plant material collected for biomass determinations. Samples consisted of either live, above-ground tissue of each species, bulked dead above-ground tissue or bulked below-ground tissue, all of which had been dried at 80^{o}c. Fresh goose droppings were also collected and dried for determination of nitrogen content.

Tissue was digested by the micro-Kjeldahl technique, and the amount of ammonia released was then estimated using a modification of the phenol-hypochlorite method. (Solorzano 1969). The results are expressed as mg of N per g dry weight.

Measurement of total soluble nitrogen in plant tissue and goose droppings.

In order to determine total soluble nitrogen in the ethanol extract, an aliquot was digested using the micro-Kjeldahl technique. The amount of ammonia released was then estimated using a modification of the phenol-hypochlorite method (Solorzano 1969). The results are expressed as mg of N per g dwt.

Estimation of Quantity of Droppings Produced by Geese

Geese were observed from a blind at the edge of the feeding area, on six days during the post-hatch period. The average interval between defaecations was estimated by selecting geese at random, observing them for five minutes or until the cloaca disappeared even momentarily from view, and counting the number of defaecations observed.

For each day (dawn to dusk), the total number of minutes of observations was divided by the number of defaecations observed to estimate the average number of minutes between defaecations. Observations on adults and goslings were treated separately. This method was chosen in preference to attempting to observe entire intervals between successive defaecations in individual birds, in order to avoid biasing the observations toward the shorter intervals. Because defaecation is almost instantaneous, an observation must be discontinued if the cloaca cannot be seen for even one or two seconds. Therefore, it was found in this study that it was virtually impossible to keep a bird in view for more than five minutes, so that attempting to observe whole intervals would tend to underestimate the frequency of defaecation intervals longer than this.

Approximately every ten days throughout the summer, a collection of fresh goose droppings was made, and these were oven dried for 24 hours and weighed, in order to determine the average weight of a dropping. For the first three weeks after hatch, two distinct size classes of droppings occurred, and it was possible to collect the droppings of adults and goslings separately. Thereafter, there was some overlap between the weights of gosling and adult droppings, and no separation of the classes was attempted.

These data were used to estimate the total production of droppings by breeding adults and young during the post-hatch period. Consumption by other classes of geese, and at other times of the season was estimated using observations and data from a number of sources, as described in the Results section.

RESULTS

Primary Productivity

Net primary production of the *Puccinellia* and *Carex* communities is limited by the availability of nitrogen (Figs. 2-3). At the final harvest, on 11 August, 1979, above-ground standing crop in plots treated with nitrate and ammonium salts was approximately 250 gm^{-2}. The corresponding value for untreated plots was 140 gm^{-2}. In mid-August 1980 the above-ground standing crop of the nitrogen-treated plots was also approximately double that of the untreated plots, in both the *Puccinellia* and *Carex* swards. However, it was evident that in these nitrogen-treated plots lack of phosphorus limited production from July onwards. During the first part of the season production in nitrogen- and nitrogen and phosphorus-treated plots was similar but live above-ground standing crop differed thereafter. The final values for above ground biomass in the *Puccinellia* and *Carex* plots treated with both ammonium and phosphate were 520 and 290 gm^{-2} respectively, compared to 215 and 177 gm^{-2} for ammonium only treated plots.

Below ground biomass did not differ between treated and untreated plots in 1979. The fact that living and dead roots were not separated may have obscured any response to nutrient enrichment by below-ground plant parts. Below-ground standing crop was not sampled in 1980.

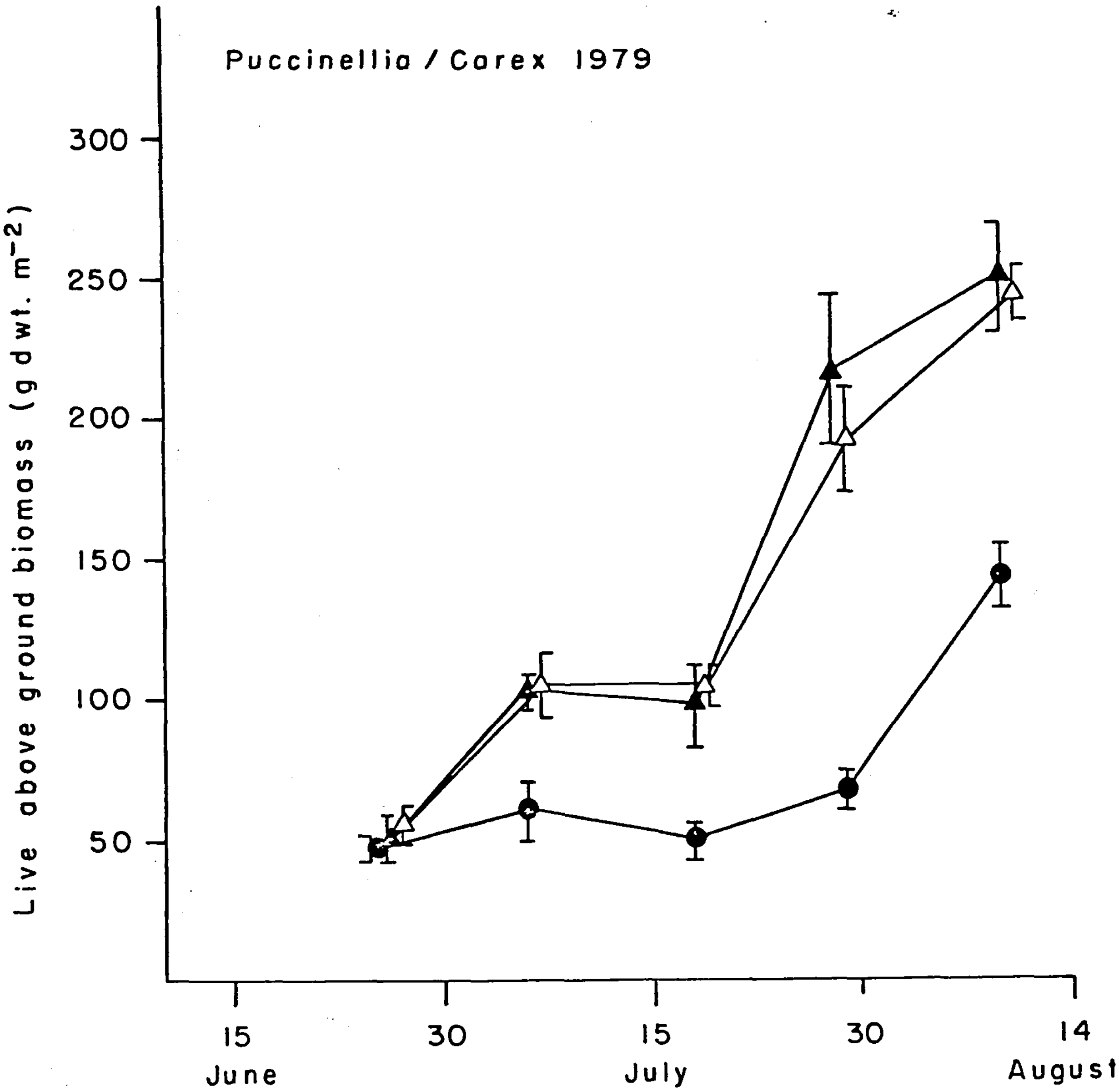

Fig. 2: Live, above-ground standing crop of a mixed sward of Puccinellia phryganodes and Carex subspathacea in response to different nutrient treatments. La Perouse Bay, Manitoba.

NH4 added NO3 added control

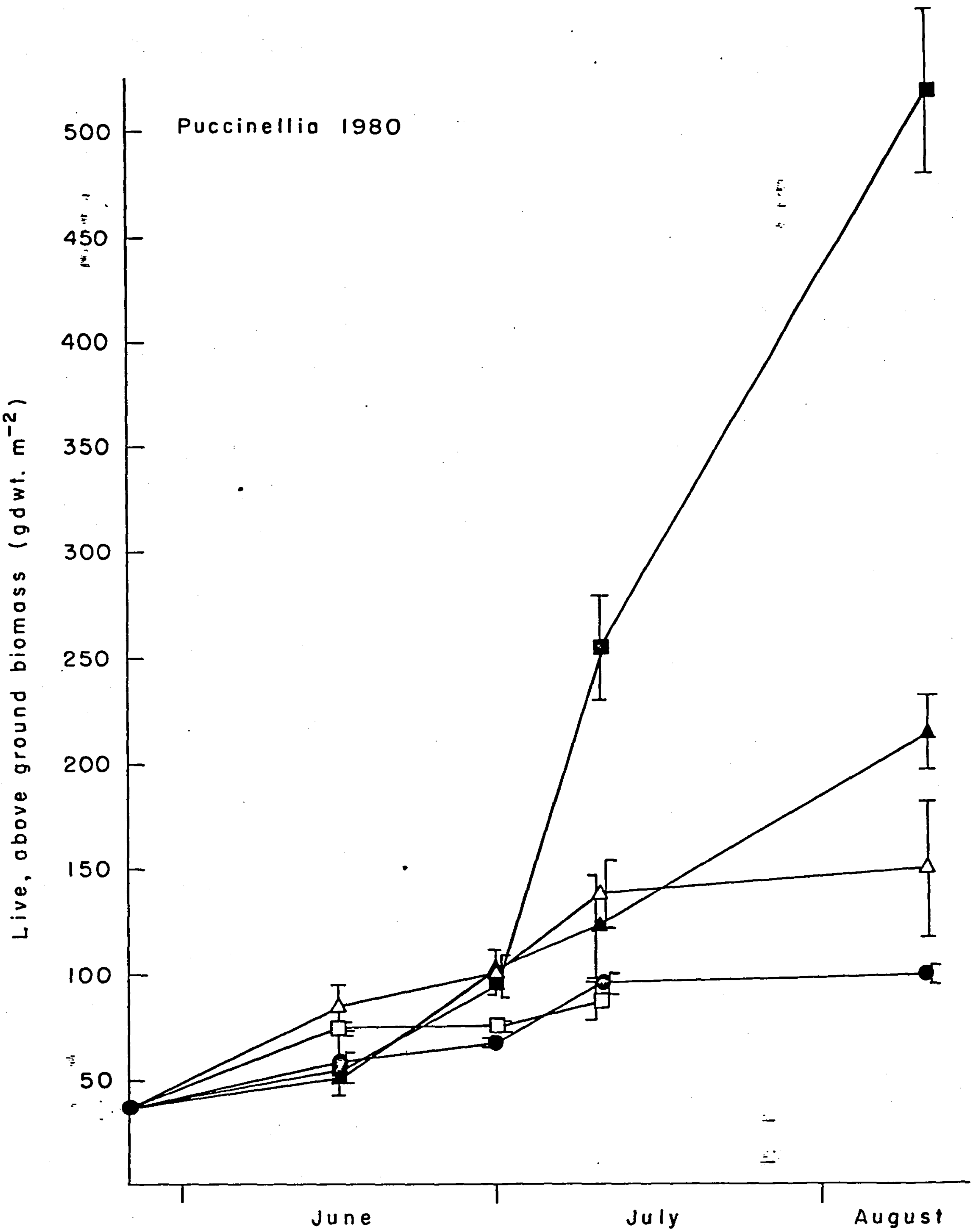

Fig. 3a: Live, above-ground standing crop of a sward of Puccinellia phryganodes in response to different nutrient treatments. La Perouse Bay, Man.
NH4 added PO4 added NO3 added NH4/PO4 added control

Fig. 3b

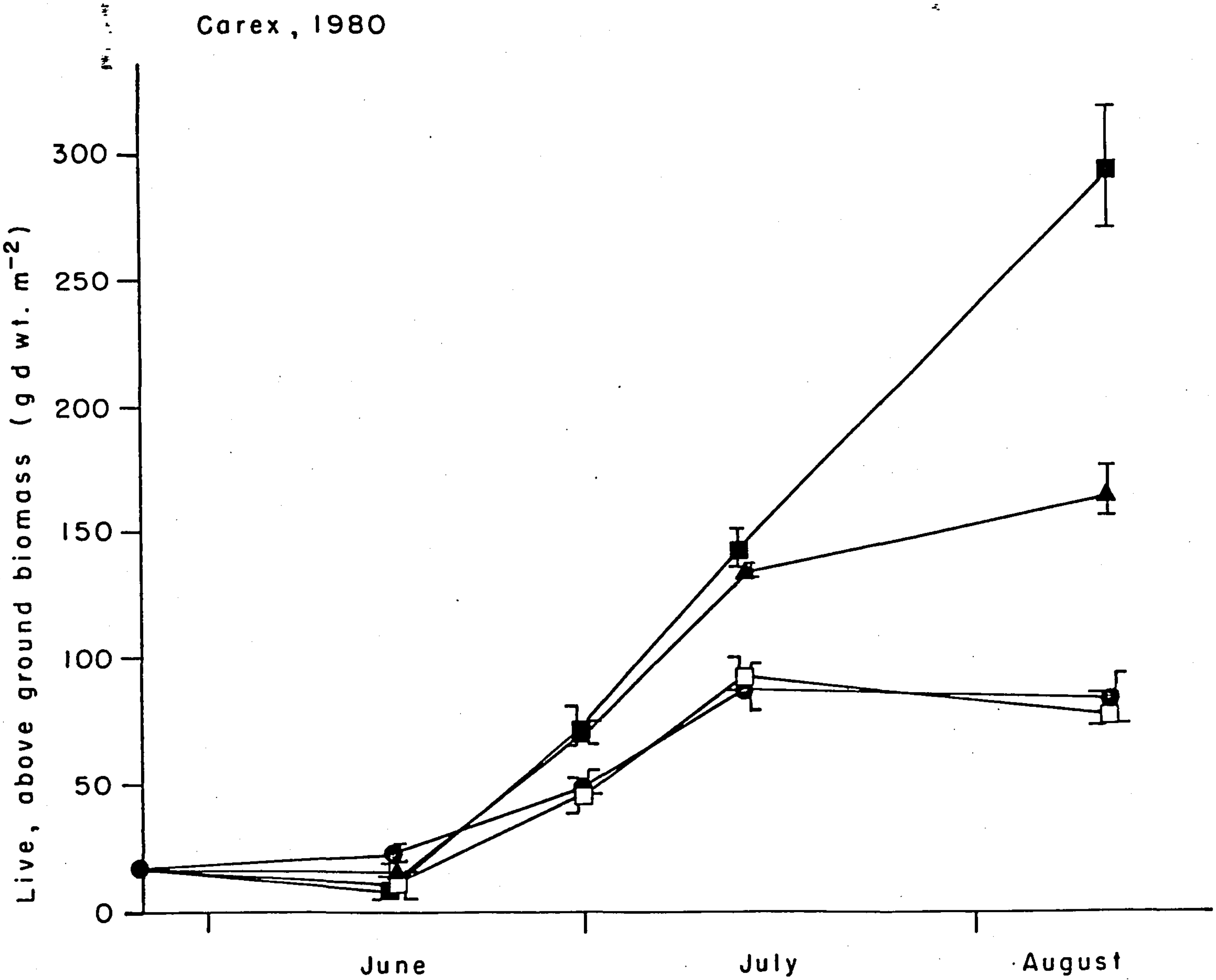

Fig. 3b: Live, above-ground standing crop of a sward of Carex subspathacea in response to different nutrient treatments. La Perouse Bay, Man.
NH4 added PO4 added NH4 and PO4 added control

In 1979, significant increases in the level of above-ground standing crop did not occur until late June or early July. The hatching of the snow goose young also occurred during this period. Before this, air and soil temperatures were low; ice and snow did not disappear from the islands in the estuary until mid June. (Cargill and Jefferies, 1980). In 1980, ice and snow finally disappeared in early June, although there was a period of extensive thaw in April. There was a steady accumulation of above-ground biomass in both grazed and ungrazed plots from early June onward. (Figures 5 and 6) However, the initial rate of production was not maintained in ungrazed swards of either Puccinellia or Carex beyond mid July. As will be discussed later, further production is limited by a shortage of available nitrogen in ungrazed areas. As in 1979, the onset of plant growth in early June coincided with hatching of the snow geese.

During 1979, in areas which were grazed by snow geese, the amount of living above-ground biomass was remarkably constant for much of the summer at about 40 gm^{-2}. (Figure 7) The period of recording the standing crop covered the phases of incubation, hatch, and post-hatch, when there were up to 22,000 geese on the marsh. In 1980, although the standing crop on the Puccinellia sites was approximately 38 gm^{-2} for much of June in grazed areas, the figure rose to about 60 gm^{-2} in July and August. (Figure 8) A similar increase in the level of live above-ground standing crop was recorded in the Carex plots, from an initial value of 17 gm^{-2} to 30 gm^{-2} in July and early August. The results indicate that the grazing pressure may have been less in 1980 than in 1979. Estimates of the population size are 4400 breeding pairs in 1979 and 3500 pairs in 1980. (Cooke et al, unpublished.)

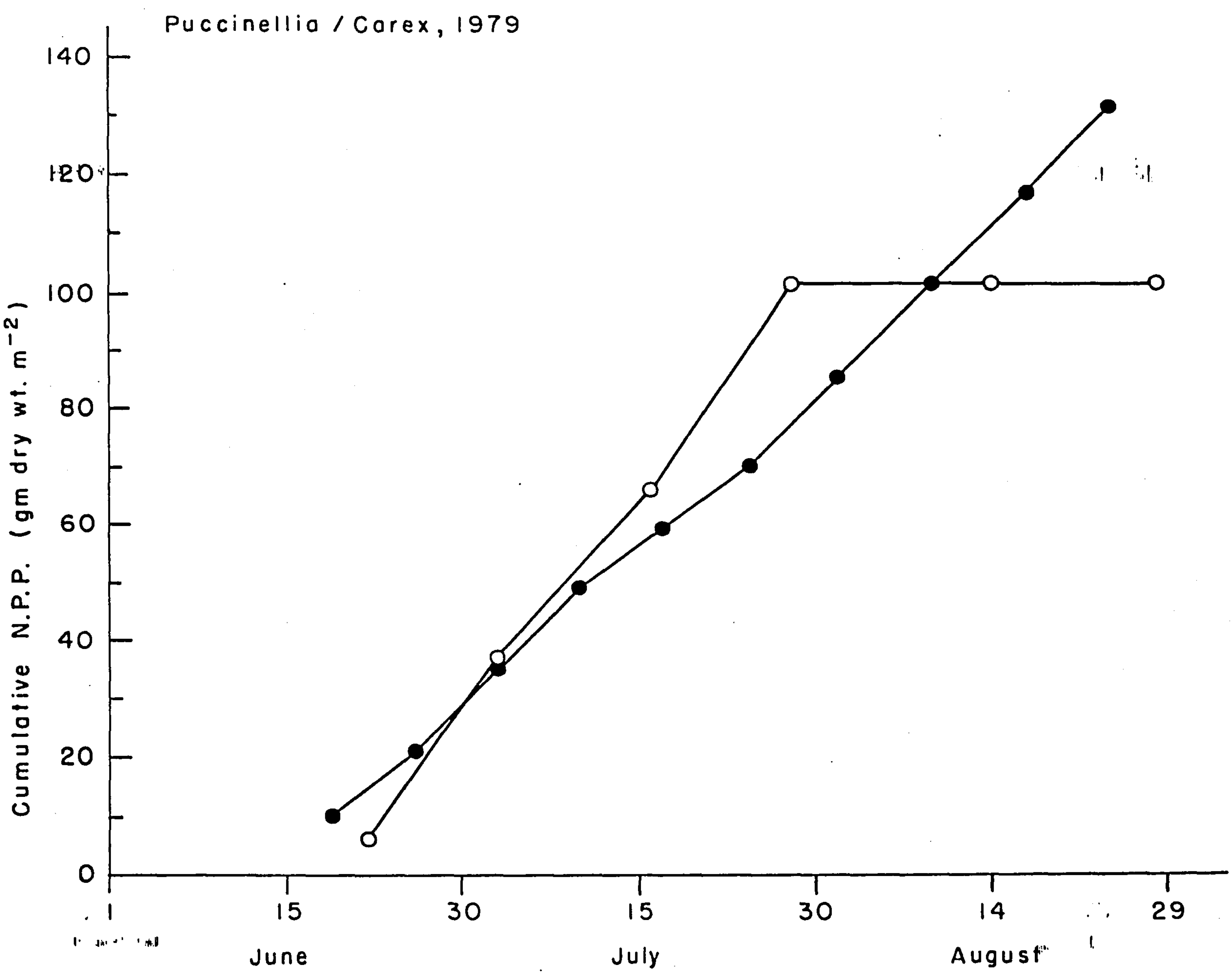

Fig.4: Cumulative net primary production of above-ground biomass in grazed ( ) and ungrazed ( ) mixed swards of Puccinellia phryganodes and Carex subspathacea. La Perouse Bay. Man.

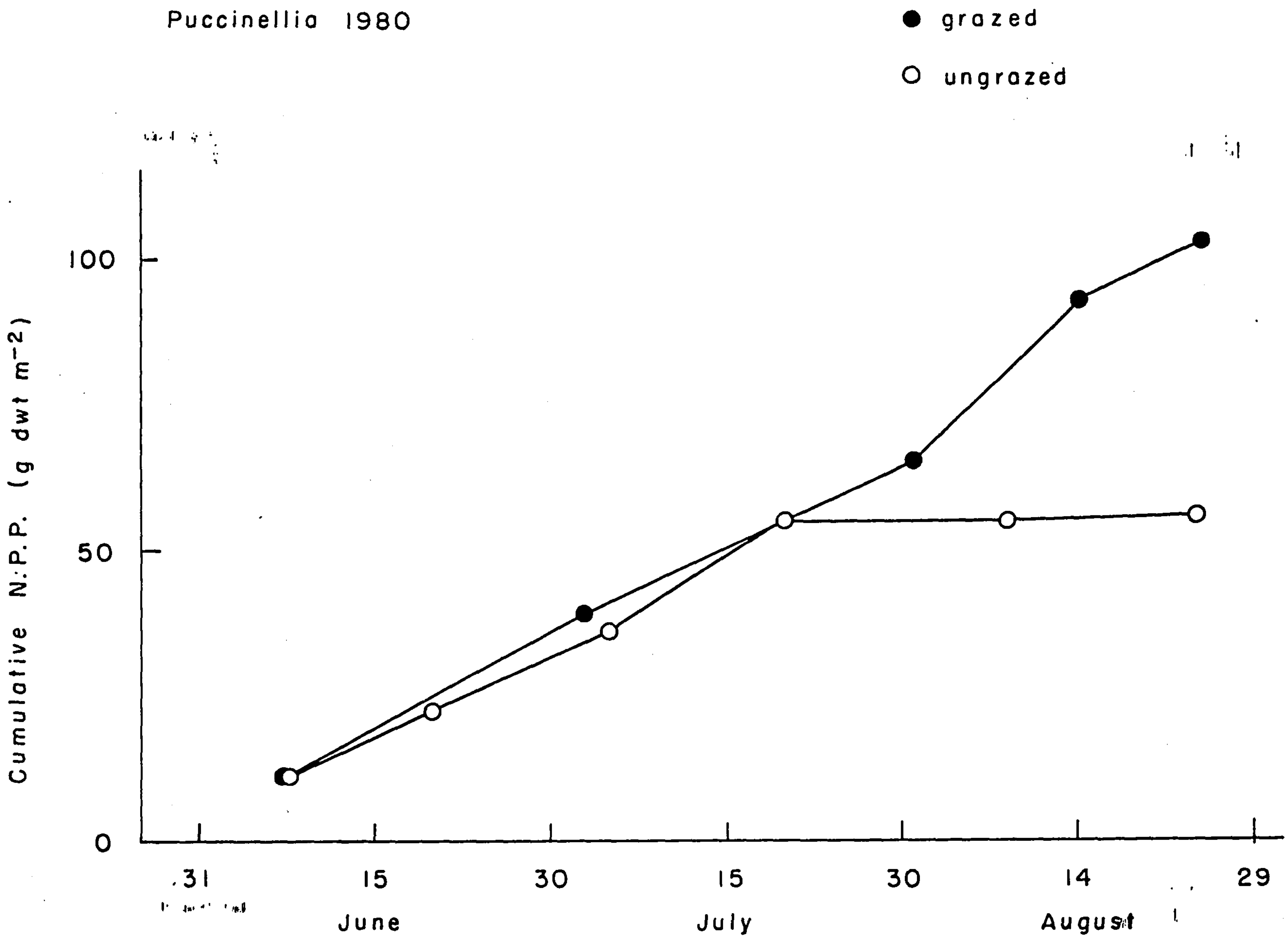

Fig. 5: Cumulative net primary production of above-ground biomass in grazed ( ) and ungrazed ( ) swards of Puccinellia phryganodes at La Perouse Bay, Manitoba.

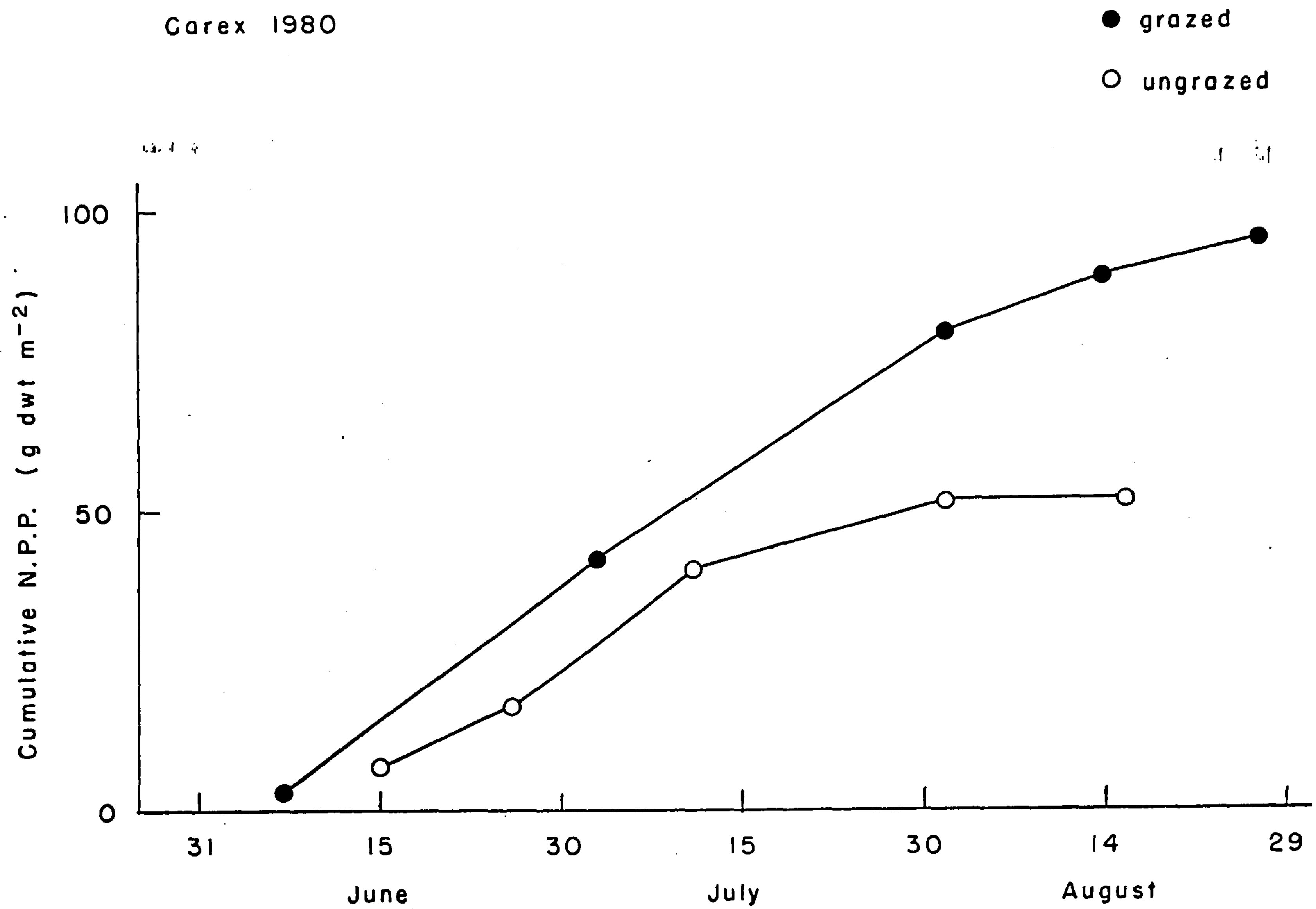

Fig. 6: Cumulative net primary production of above-ground biomass in grazed ( ) and ungrazed ( ) swards Carex subspathacea at La Perouse Bay, Manitoba.

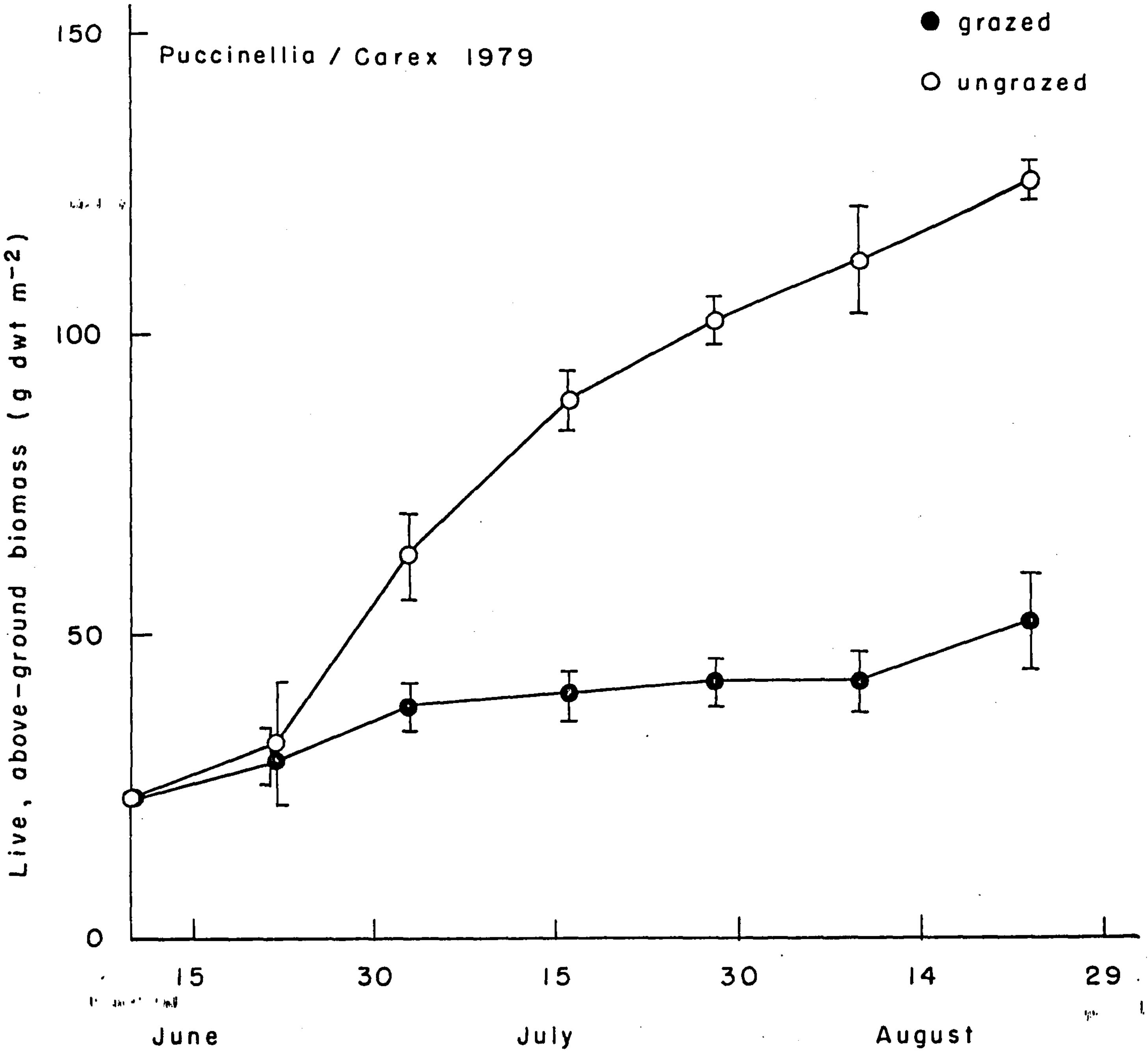

Fig. 7: Live, above-ground standing crop of grazed ( ) and ungrazed ( ) swards of <u>Puccinellia phryganodes</u> at La Perouse Bay, Manitoba.

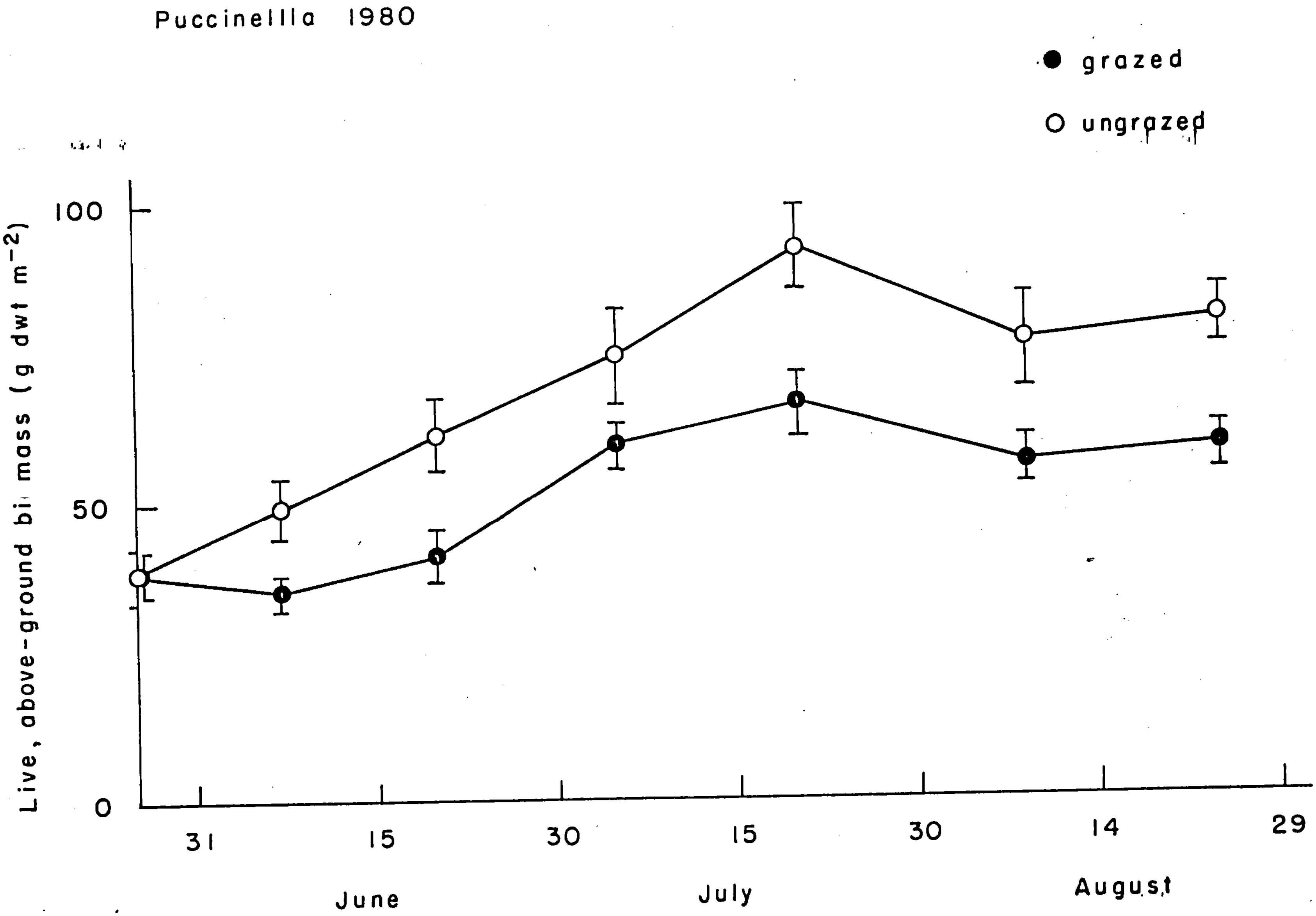

Fig. 8: Live, above-ground standing crop of grazed ( ) and ungrazed ( ) swards of <u>Puccinellia phryganodes</u> at La Perouse Bay, Manitoba.

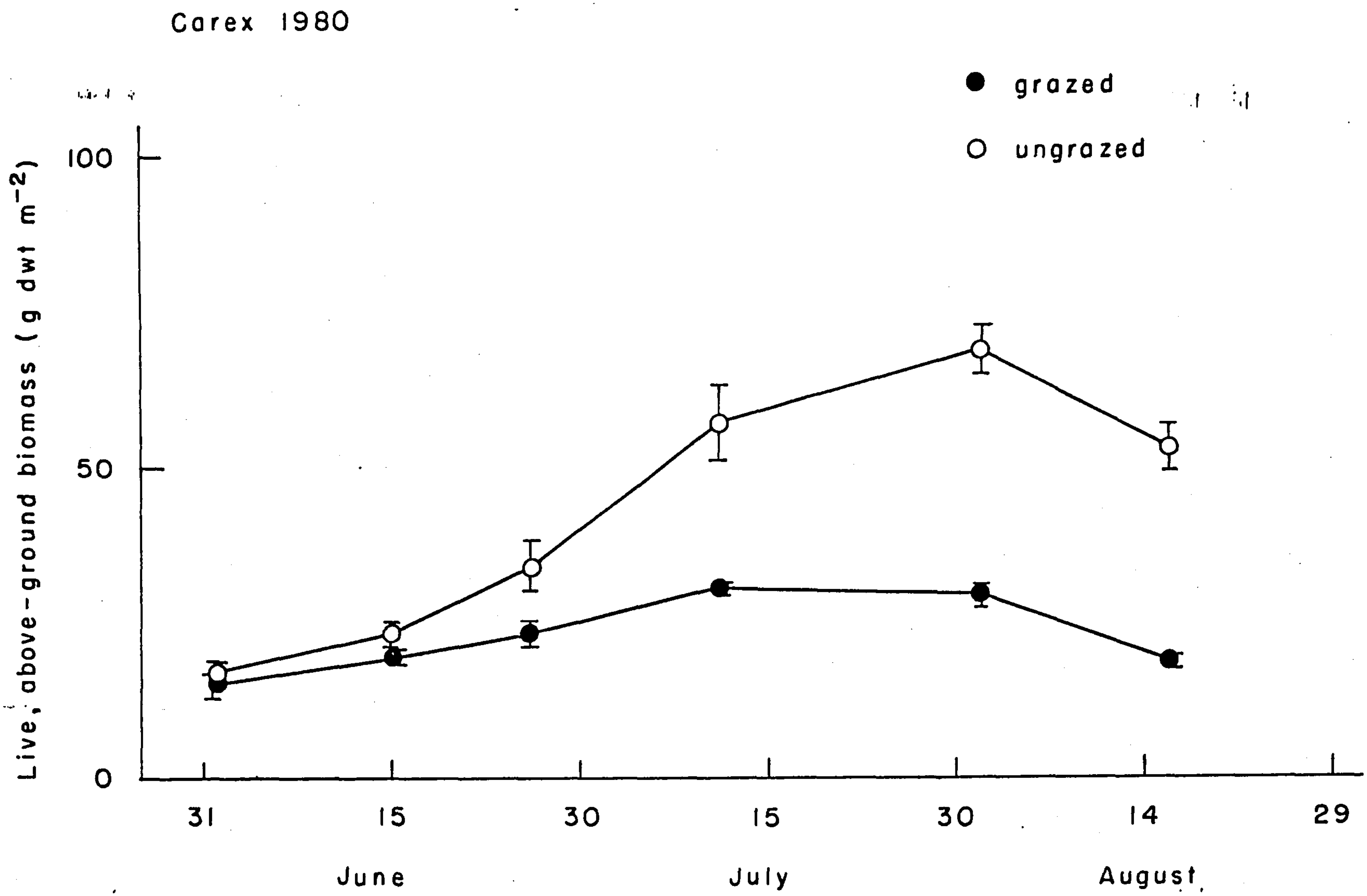

Fig. 9: Live, above-ground standing crop of grazed ( ) and ungrazed ( ) swards of *Carex subspathacea* at La Perouse Bay, Manitoba.

In ungrazed exclosures, standing crop increased throughout the season; above-ground biomass reached 125 gm^{-2} at the end of August 1979, in the mixed Puccinellia-Carex community. Corresponding values for 1980 were 92 and 69 gm^{-2} in Puccinellia and Carex swards respectively.

In 1979, there were no significant differences in below-ground biomass between grazed and ungrazed plots. (Figure 10) In both, the biomass increased from 1050 gm to 3100 gm^{-2} over the course of the growing season. Little reliance is placed on the first harvest on 11 June, as at that time the ground was frozen, making extraction of turf samples very difficult. Living and dead roots were not separated in 1979, thus it is difficult to estimate net below-ground primary productivity.

In 1980 modifications were made to the methods which allowed more precise estimates of the changes in below-ground biomass to be obtained. In both grazed and ungrazed swards of Puccinellia, there was a substantial increase in the quantity of live roots in June. However, this increase was not maintained, and the below-ground standing crop fell during July to about what it had been at the start of the season. Throughout August it remained at this level. (700 gm^{-2}) (Figure 11). The data suggest that below ground production was higher on grazed than on ungrazed sites, but this must be interpreted with caution, because of the relatively high variances associated with the mean below-ground standing crop figures. The below-ground productivity and standing crop values, and the apparent response to grazing, are essentially the same for Carex-dominated sites as for Puccinellia swards. (Figure 12).

The results suggest that there is a substantial annual turnover of roots in this marsh, perhaps moreso in grazed than in ungrazed areas. It is therefore difficult to estimate the net below-ground production,

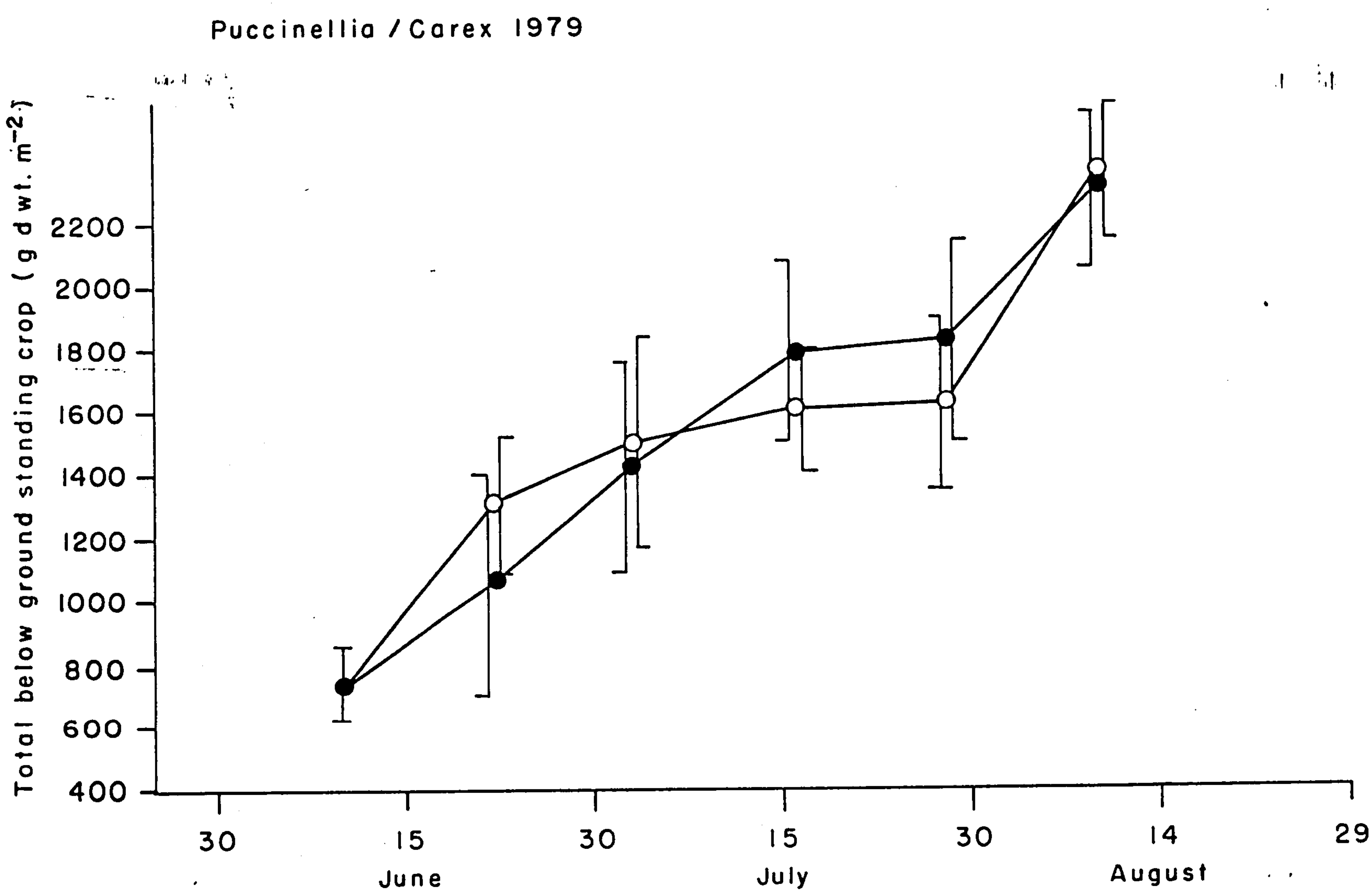

Fig. 10: Seasonal changes in total below-ground biomass at grazed (●) and ungrazed sites (o) in a mixed <u>Puccinellia phryganodes-Carex subspathacea</u> community at La Pérouse Bay, Manitoba. (Mean ± SEM)

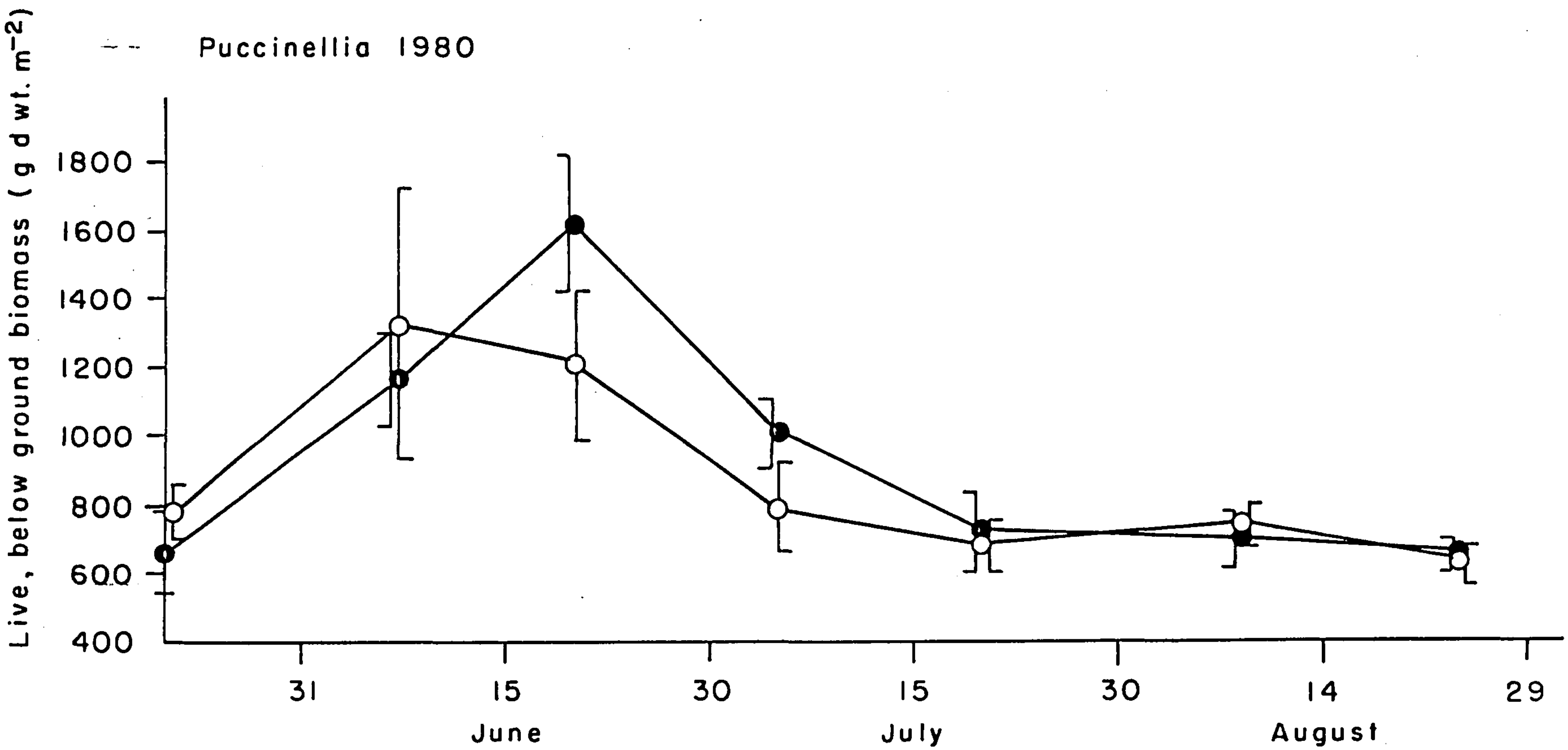

Fig. 11: Seasonal changes in living below-ground biomass at grazed (•) and ungrazed (o) swards of <u>Puccinellia phryganodes</u> at La Pérouse Bay, Manitoba (Mean ± SEM).

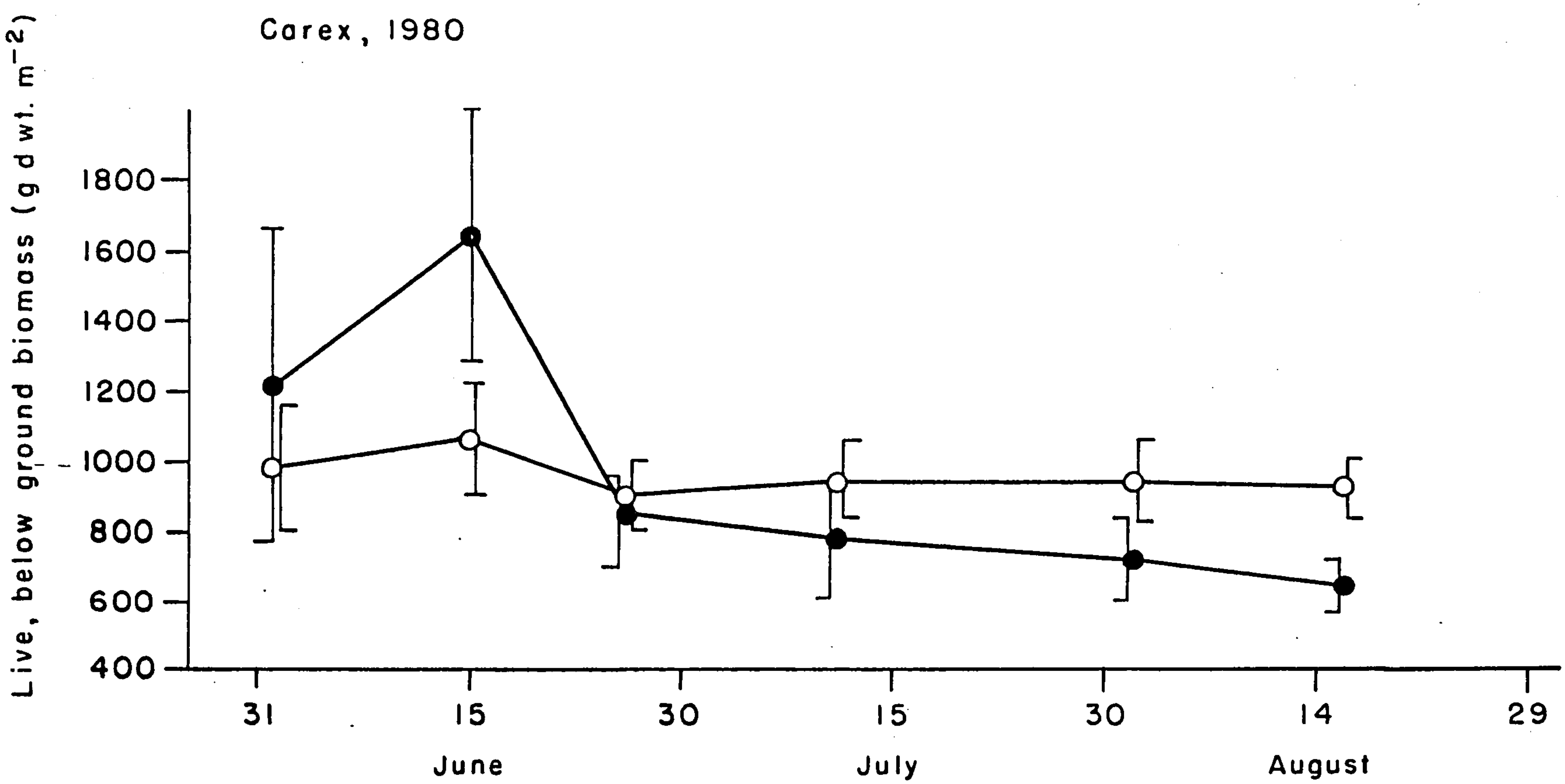

Fig. 12: Seasonal changes in living below-ground biomass at grazed (o) and ungrazed (o) swards of *Carex subspathacea* at La Pérouse Bay, Manitoba (Mean ± SEM).

because of the possibility of turnover of roots during July and August. However, even if it is assumed that no turnover occurred after mid July, the resulting estimates of below-ground production are surprisingly high. (Table 1) The results indicate that not only was the majority of the biomass (80 - 90%) below ground in these Carex and Puccinellia communities, but also approximately 90% of the total net primary production.

In order to examine further the effects of grazing on the growth of Carex and Puccinellia, the relative growth rates of grazed and ungrazed swards of the two species have been compared. The data are based on changes in standing crop obtained from the long- and short- term exclusures.

Mean relative growth rate is defined as:

$$R = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1}$$

where W_2 is the standing crop (g dwt m^{-2}) at time 2, and W_1 is the standing crop at time 1. $T_1 - T_2$ is therefore the interval over which relative growth rate is measured. (14 to 22 days in this study) The units are g g^{-1} wk^{-1}, or simply wk^{-1}. The mean time, in weeks, for the standing crop to double is equal to 0.693 $/\overline{R}$.

The mean relative growth rates in 1979 are given in Figure 13; some figures are for mixed swards and some refer to pure stands of one species or the other. The growth of the ungrazed swards was characterized by a high relative growth rate of above-ground biomass in late June and early July, followed by a decline to very low values for the remainder of the season. When grazed, both species appeared to maintain higher mean relative growth rates throughout the season; they did not exhibit the late

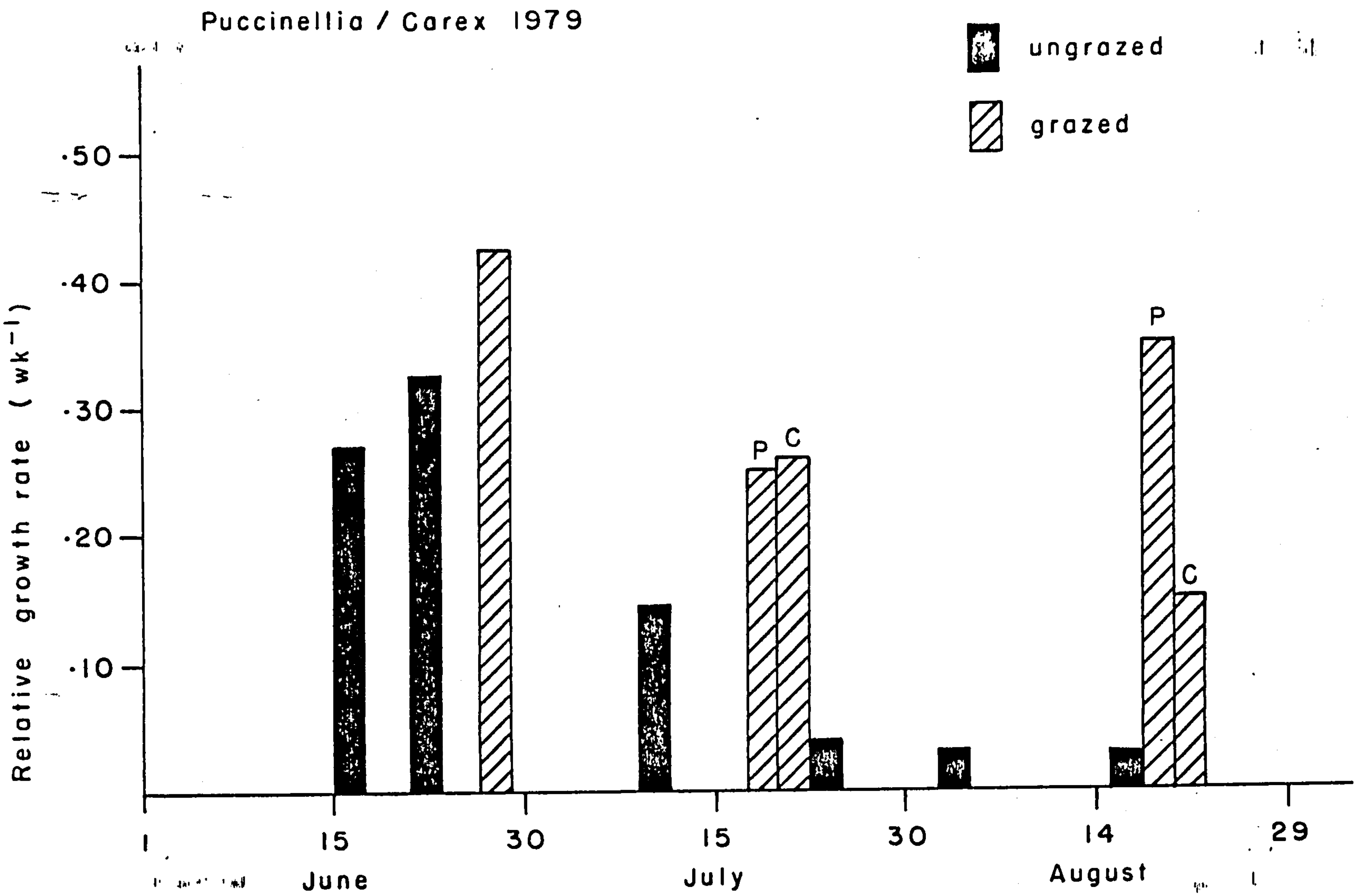

Fig. 13: Mean relative growth rates of grazed and ungrazed above-ground vegetation at La Perouse Bay, Manitoba. Solid bars refer to ungrazed mixed Puccinellia phryganodes - Carex subspathacea communities. Hatched bars refer to either grazed Puccinellia (P) or Carex (C) Swards.

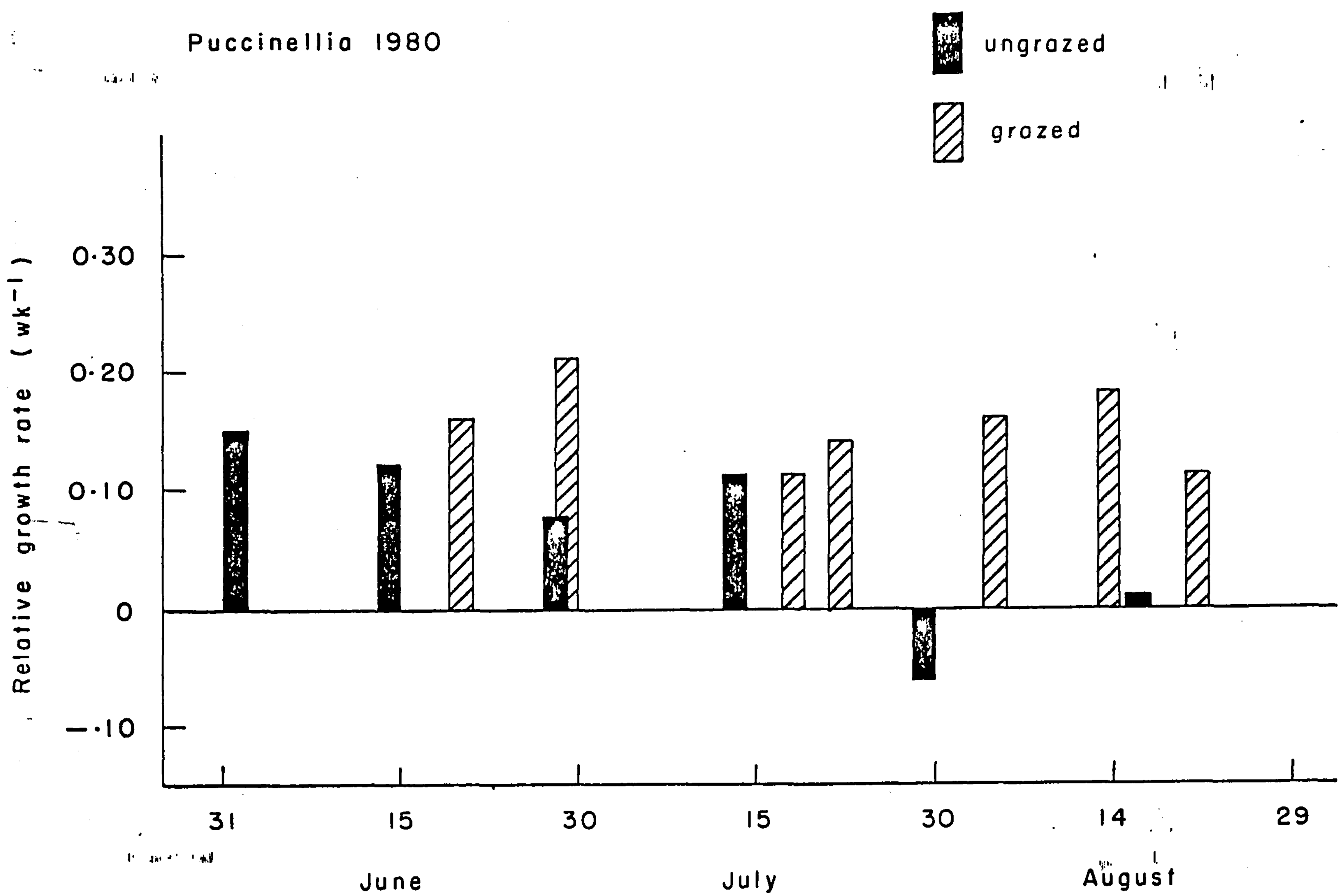

Fig. 14: Mean relative growth rates of grazed and ungrazed swards of Puccinellia phryganodes at La Perouse Bay, Manitoba.

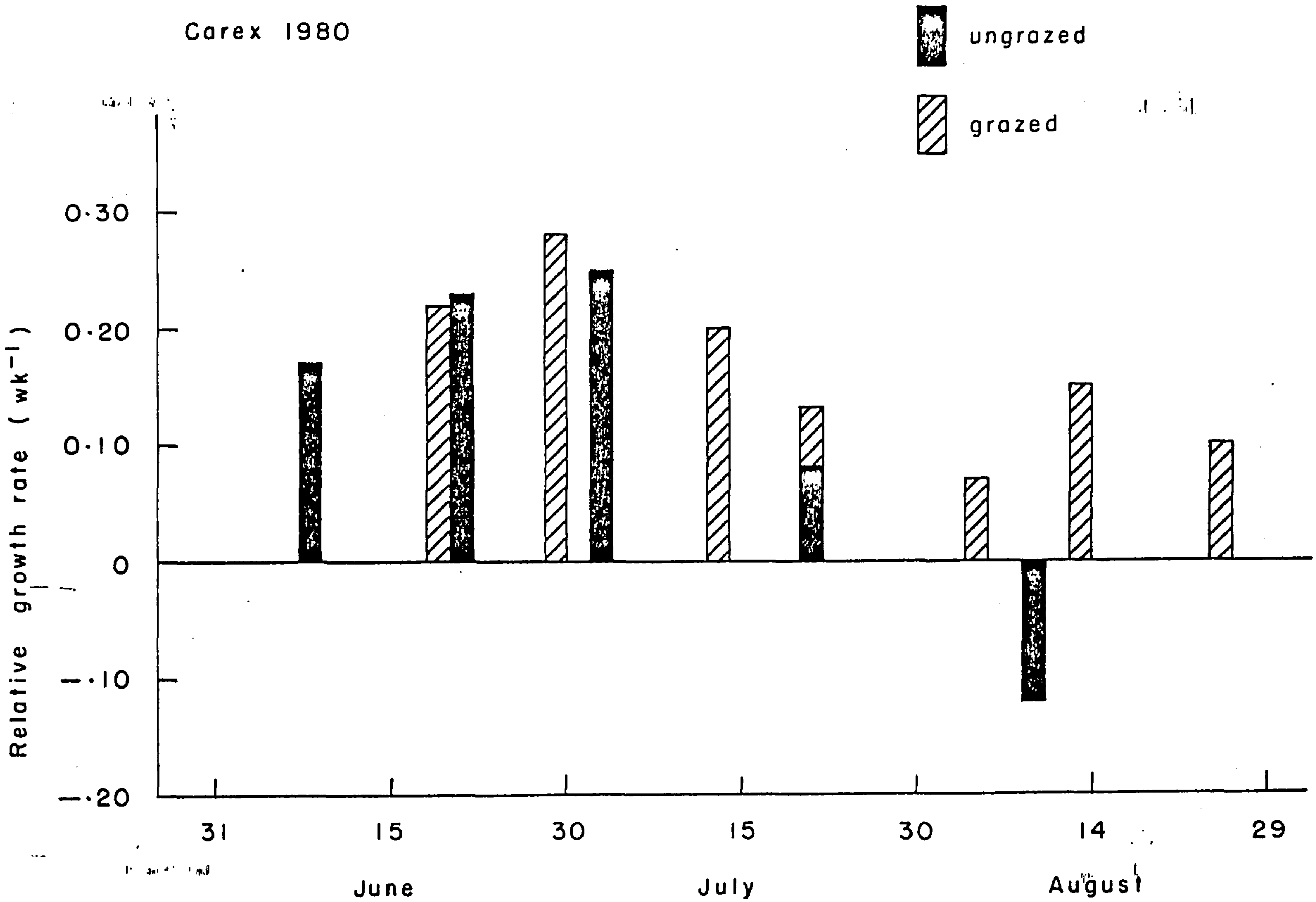

Fig. 15: Mean relative growth rates of grazed and ungrazed swards of Carex subspathacea at La Perouse Bay, Manitoba.

summer decline in growth showed by ungrazed swards. Similar results were obtained in 1980, for pure stands of both Carex and Puccinellia. (Figures 14 and 15) Although continual grazing appears to result in the maintenance of the initial growth rates, even these are low compared to corresponding values for temperate salt marshes. (Jefferies, unpublished)

Total quantities of dead biomass (standing dead and litter) were measured at grazed and ungrazed sites in 1979 and 1980. No seasonal trends were apparent in either year, but the total quantities were consistently higher in 1980 than in 1979. No difference was observed in the between grazed and ungrazed sites with respect to the standing crop of dead tissues.

In estimating total net primary production of Carex and Puccinellia, no allowance was made for the possibility of mortality and decomposition of plant biomass during the season. The lack of variation in the dead component of the total standing crop suggests that this did not cause productivity to be underestimated by very much. The values of net annual primary production for the different community types and treatments in the two years are summarized in Table 1.

Total and soluble nitrogen contents of plant tissues and goose droppings.

Nitrogen contents of shoots and roots of Puccinellia and Carex in 1979 and 1980 are shown in Figures 17 - 20. In Puccinellia, there is very little evidence of seasonal changes in the nitrogen content of either shoots or roots. In both years, the nitrogen content of shoot tissue was between 2 and 3% of the dry weight throughout the growing season, whereas the corresponding value for roots was between 1 and 2%.

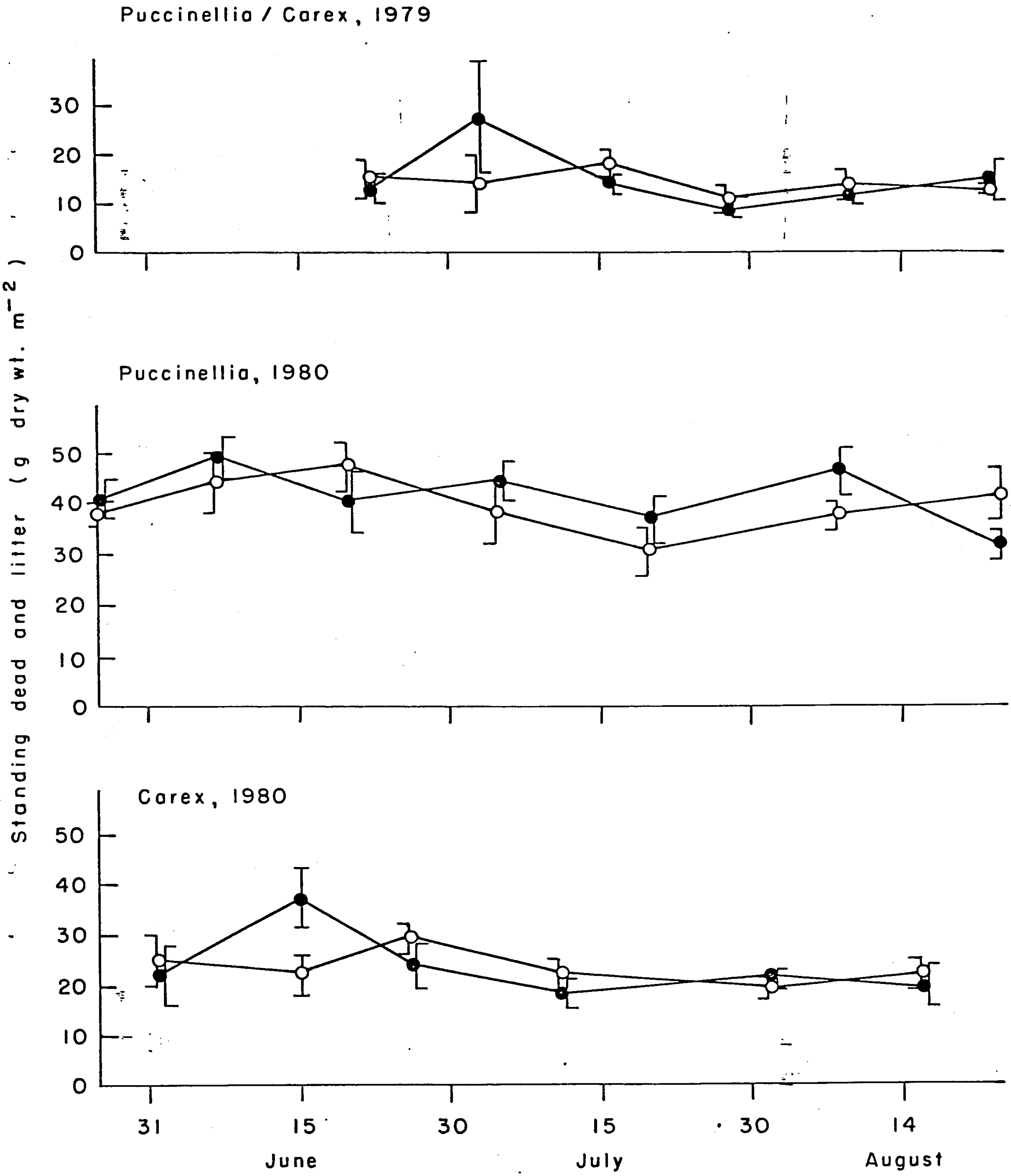

Fig. 16: Total standing crop of dead, above-ground biomass in grazed ( ) and ungrazed ( ) swards if Puccinellia phryganodes and Carex subspathacea at La Perouse Bay, Manitoba.

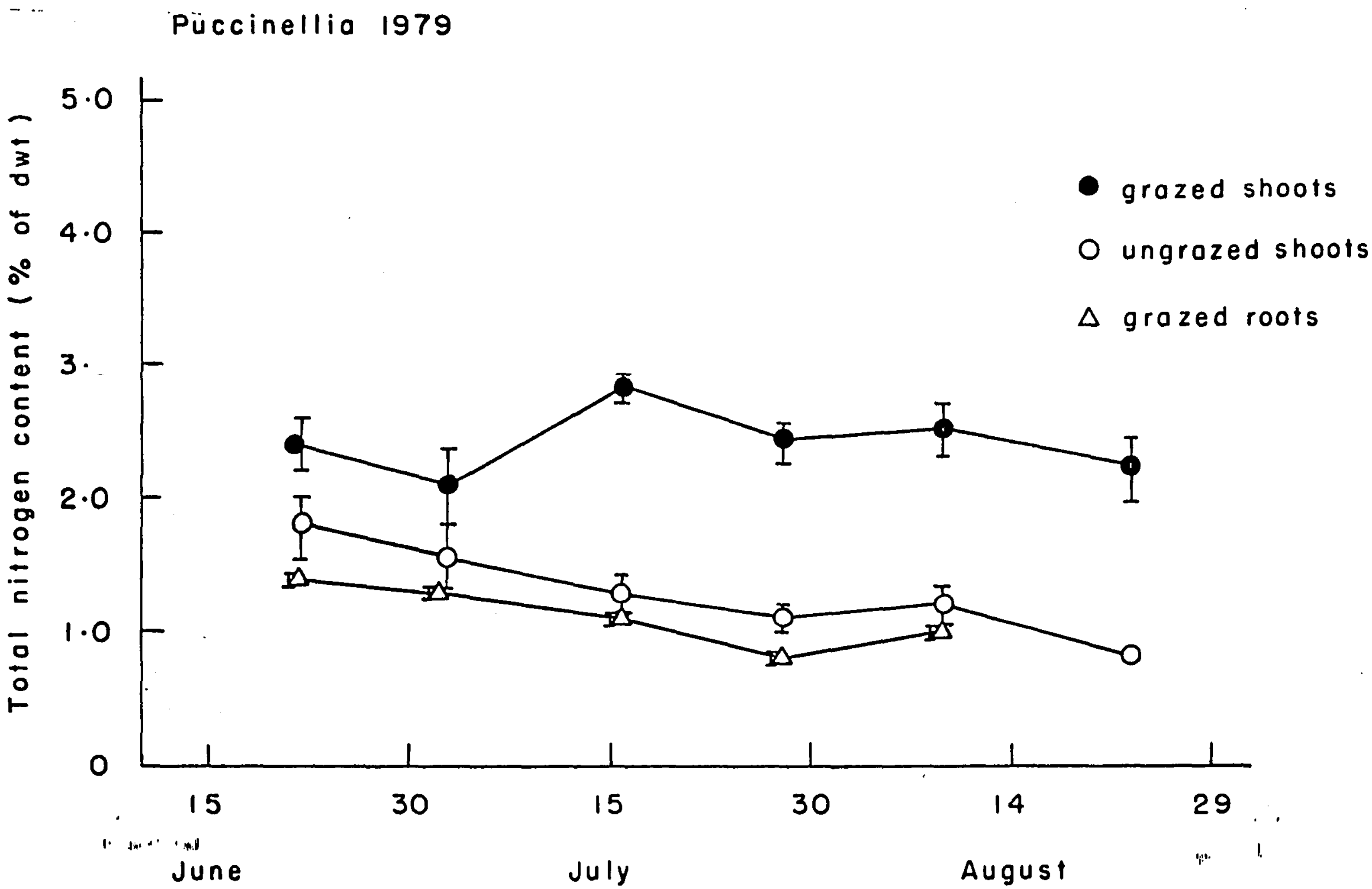

Fig. 17: Seasonal changes in total nitrogen content of above- and below-ground tissues of <u>Puccinellia phryganodes</u>. La Perouse Bay, Manitoba.

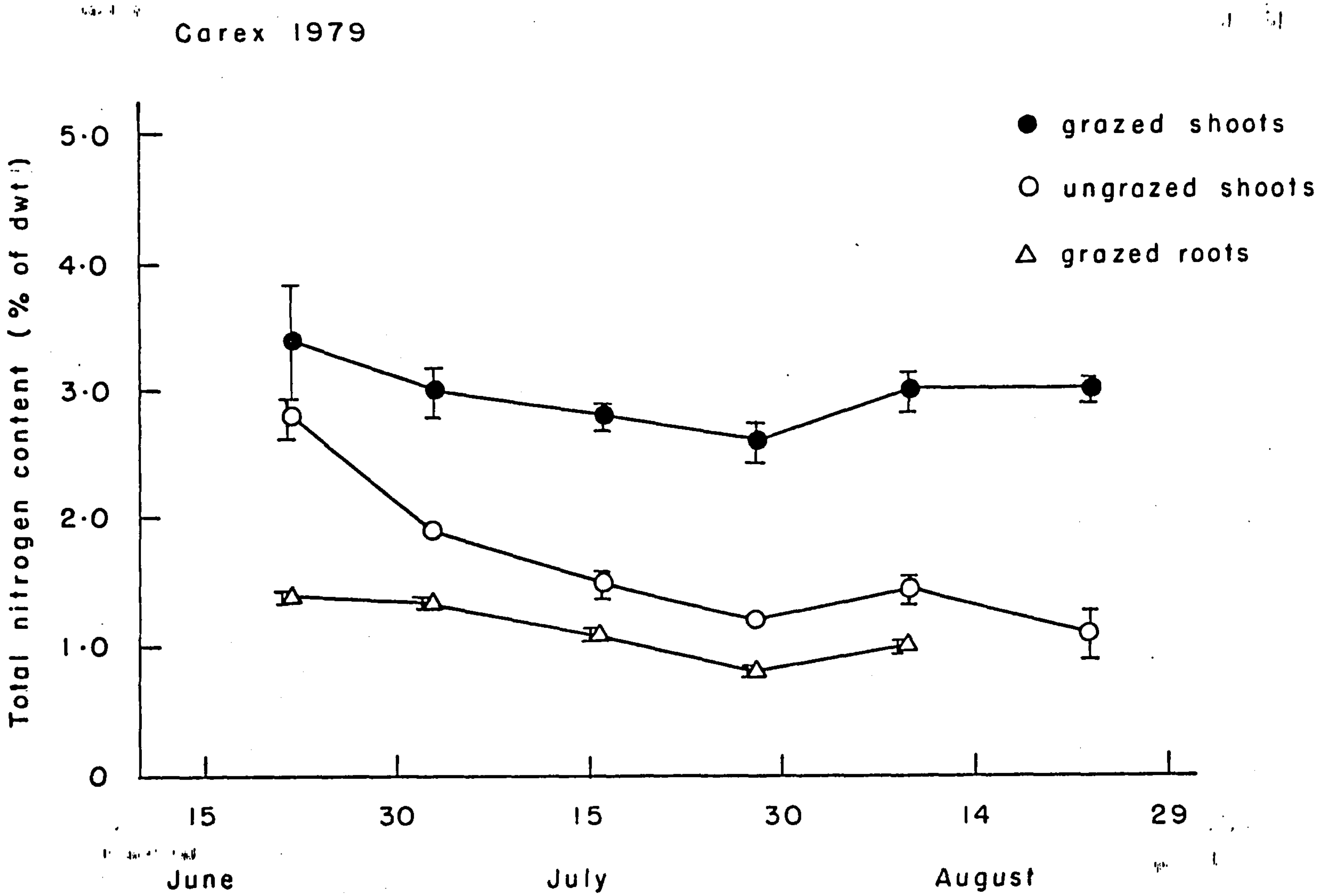

Fig. 18: Seasonal changes in total nitrogen content (% dry weight) of above- and below-ground tissues of *Carex subspathacea*. La Perouse Bay, Manitoba.

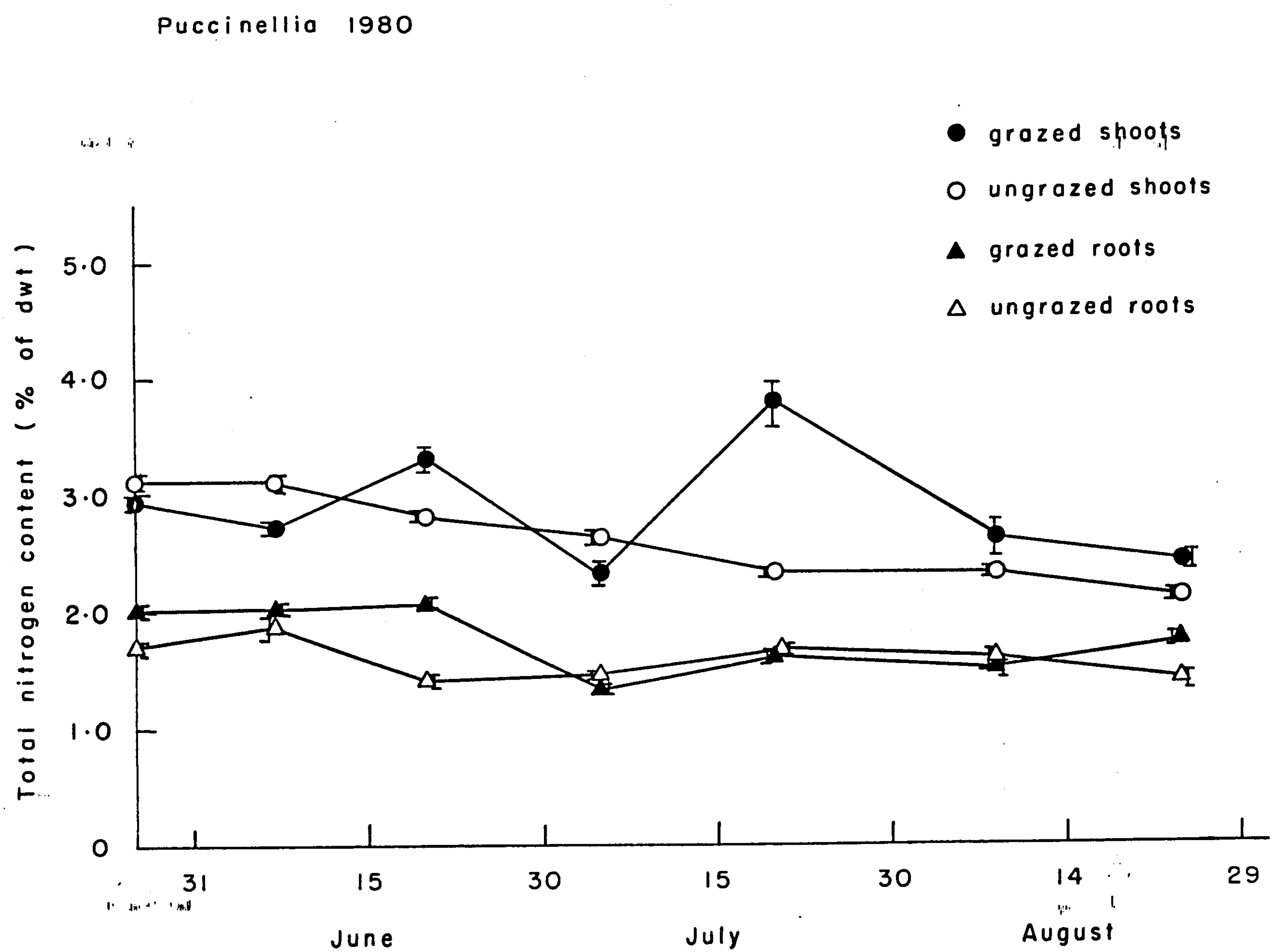

Fig. 19: Seasonal changes in total nitrogen content (% dry weight) of above- and below-ground tissues of Puccinellia phryganodes at La Perouse Bay, Manitoba.

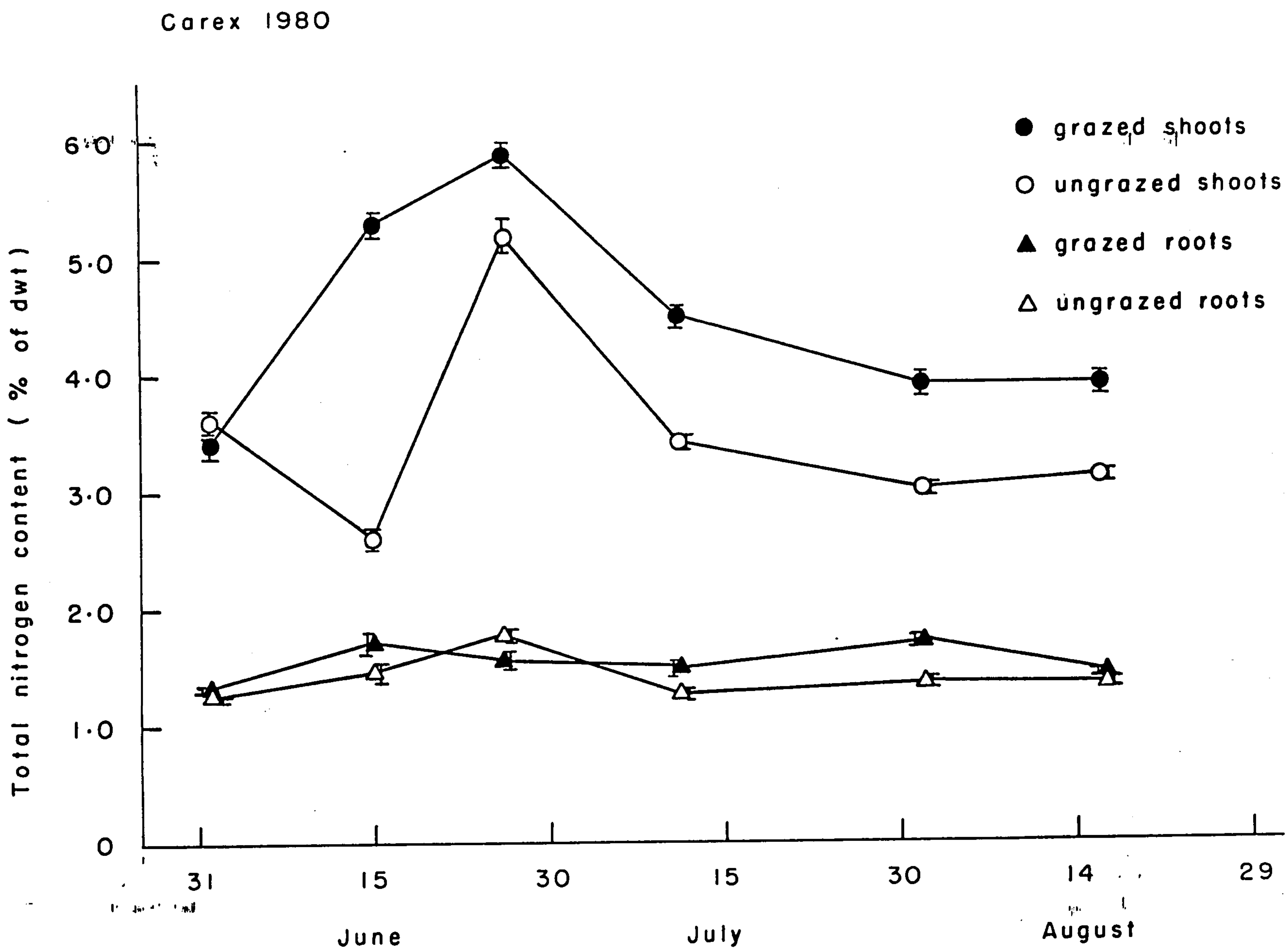

Fig. 20: Seasonal changes in total nitrogen content (% dry weight) of above- and below-ground tissues of *Carex subspathacea*. La Perouse Bay, Manitoba

Table 1. Net primary production of *Puccinellia phryganodes*-*Carex supspathacea* marsh at LaPérouse Bay, Manitoba.

Year	Sward type	Above-ground N.P.P. (gm^{-2})	Below-ground N.P.P. (gm^{-2})
1979	Grazed *Puccinellia*-*Carex*	135	960
1979	Ungrazed *Puccinellia*-*Carex*	100	960
1980	Grazed *Puccinellia*	103	700
1980	Ungrazed *Puccinellia*	56	700
1980	Grazed *Carex*	95	740
1980	Ungrazed *Carex*		
1979	*Puccinellia*-*Carex* (N added)	176	
1980	*Puccinellia* (NH_4 added)	176	
1980	*Puccinellia* (NO_3 added)	111	
1980	*Puccinellia* (PO_4 added)	64	
1980	*Puccinellia* (NH_4/PO_4 added)	482	
1980	*Carex* (NH_4 added)	160	
1980	*Carex* (PO_4 added)	61	
1980	*Carex* (NH_4/PO_4 added)	277	

During the 1979 season, and from mid July on in 1980, the nitrogen content of grazed shoots was higher than that of ungrazed shoots.

The nitrogen content of Carex shoots reached 6% in early summer of 1980; a very high value for plant tissue. Although both grazed and ungrazed tissues contained a high percentage of nitrogen early in the season, the values were not maintained, and fell to between 3 and 4% by August. Root tissue contained between 1 and 2% nitrogen throughout the season. In both years, the nitrogen content of grazed Carex shoots was substantially higher than that of ungrazed shoots.

Figures 21 and 22 illustrate the cumulative totals for the quantity of nitrogen used in shoot production on grazed and ungrazed sites dominated by either Carex or Puccinellia. These values were obtained, by summing, for all between-harvest periods, the net above ground primary production multiplied by the average nitrogen content during that period. For both species, the total quantity of nitrogen used in shoot production is very much higher on grazed sites than on ungrazed sites.

In 1979, the total nitrogen content of goose droppings was about 1.9% of the dry weight until late July, after which it declined to about 1.5%. In 1980, goose droppings contained approximately 1.9% nitrogen by dry weight until the middle of August, when the geese left the area. (Table 2)

Droppings contained a very low percentage of proline (Table 2) which strongly suggests that this compound was absorbed by the gut. The data on the total soluble nitrogen content of droppings refer only to the intestinal wastes, and not the product of the kidneys, probably mostly uric acid. In geese, nitrogenous wastes from the kidney are excreted as a thin layer of white paste adhering to one end of the faecal perlet, and this component was not included in the dropping samples taken for

Fig. 21: Cumulative amount of nitrogen deposited in shoots of grazed ( ) and ungrazed ( ) *Puccinellia phryganodes*. La Perouse Bay, Man.

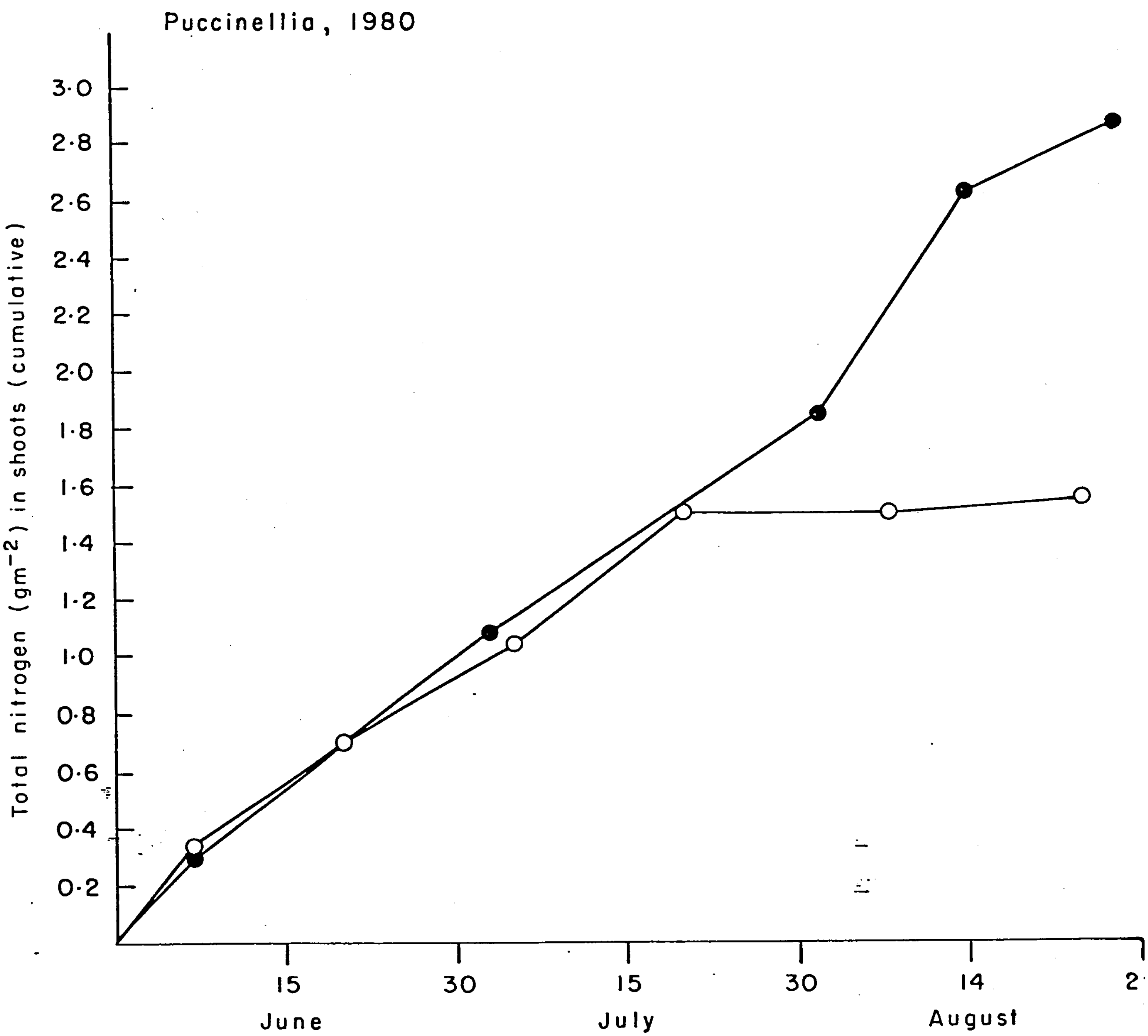

Fig. 22: Cumulative amount of nitrogen deposited in shoots of grazed ( ) and ungrazed ( ) Carex subspathacea at La Perouse Bay, Man.

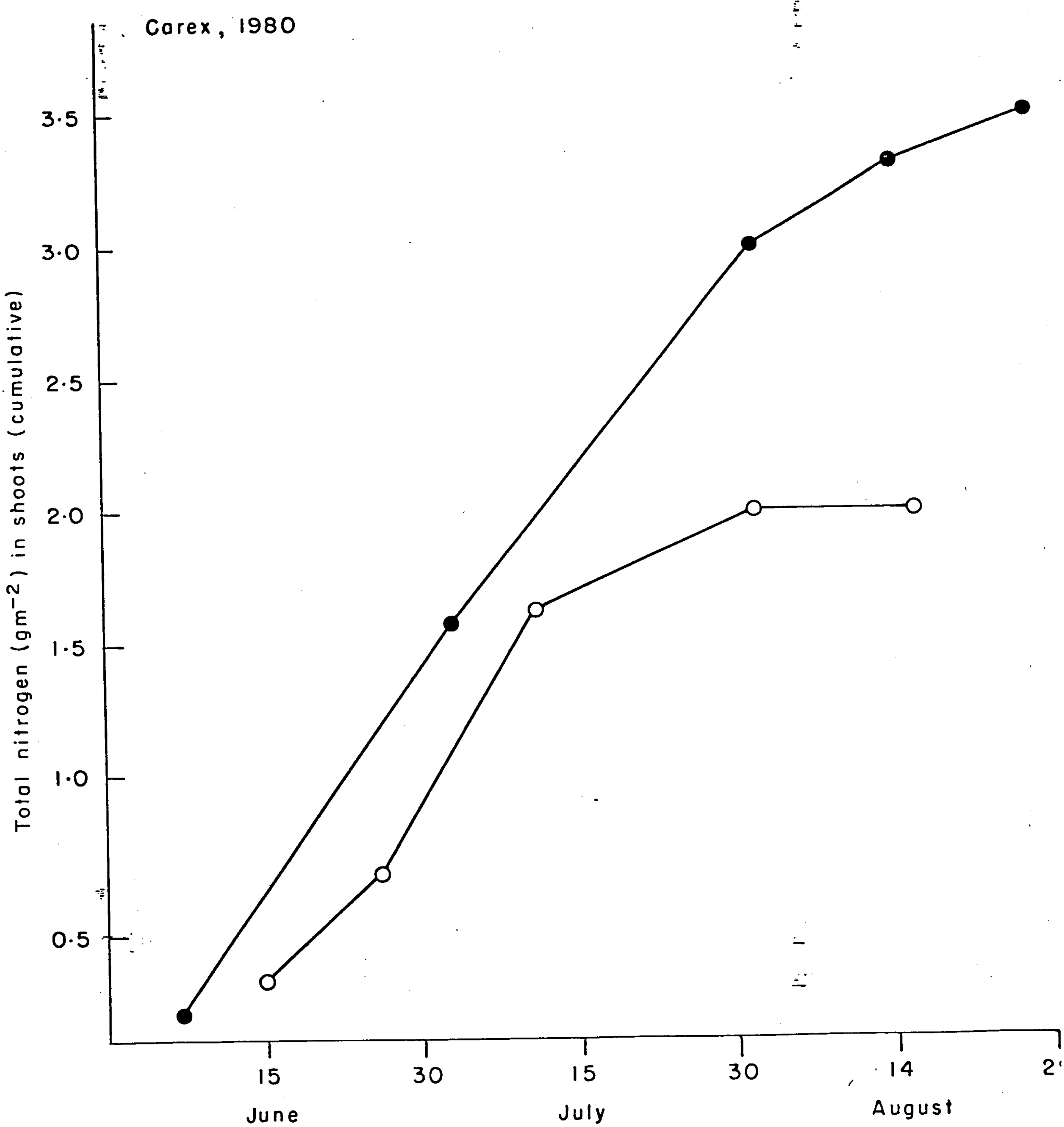

Table 2. Levels of total nitrogen, soluble nitrogen, ammonia and proline in droppings of lesser snow geese.

Date	Total N (1980)	Soluble N (1980)	Total N (1979)	Soluble N (1979)	Ammonia (1979)	Proline (1979)
June 1-10	19.2	5.2	14.2	3.5	3.3	0.7
June 11-20	17.0	--	13.6	4.5	3.1	0.7
June 21-30	18.3	24.3	20.7	16.7	1.9	0.9
July 1-10	18.4	38.7	21.0	18.0	5.0	0.8
July 11-20	19.7	--	--	--	--	--
July 21-31	22.3	--	12.7	1.8	1.6	0.2
Aug. 1-10	19.8	3.1	14.5	4.5	5.1	0.4
Aug. 11-20	21.6	--	--	--	--	--

analysis. The soluble nitrogen content of the faecal material alone averaged approximately 0.3% of the dry weight, or 15 to 20% of the total nitrogen content. Much of the soluble nitrogen in droppings consists of ammonia; the identity of the other constituents is not known.

The efficiency with which nitrogen was absorbed by the geese was calculated by comparing the nitrogen: cellulose ratios of goose droppings to those of plant tissues during the post hatch feeding period. (Table 2) Because cellulose passes through the gut of the goose undigested, it can be used as a marker to relate the quantity of droppings produced to the quantity of forage consumed. Thus, the percentage of nitrogen assimilated from the forage was calculated as follows:

Rp = nitrogen: cellulose ratio of plant tissue

Rd = nitrogen: cellulose ratio of goose droppings.

Percent assimilation (A.E.) = 1 - (Rd/Rp)

It was assumed that the diet consisted of equal quantities of *Carex* and *Puccinellia* shoots.

Estimated values of A.E. are 64% for 1979 and 61% in 1980. These are probably slight overestimates of the actual assimilation efficiency, as the failure to include the kidney wastes in the analysis underestimated the total nitrogen content of the droppings.

Estimation of Budgets

Both the total net above-ground primary productions and the quantity of this consumed by the geese, were estimated in two independent ways. In the first approach, consumption was estimated from the quantity of droppings produced by the goose population, and this estimate was used as a basis for estimating the net primary production. The second method involved estimating net above-ground primary production directly, from the short-term exclosures. Consumption was then calculated from the portion of this production which "disappeared" on grazed plots.

The calculations outlined below are designed to provide tentative answers to the following questions:

1. What is the total net above-ground production of Carex-Puccinellia marsh vegetation at Perouse Bay?
2. What proportion of this production is consumed by the geese?
3. What are the magnitudes of the fluxes of nitrogen between the geese and the vegetation?

Inevitably a number of assumptions have been made in the construction of this preliminary model. Data on numbers of lesser snow geese are based on studies of Cooke and his associates, and our own field observations (see reference list).

In 1980 estimates of the population structure were:

Mean of 500 non-breeding birds present for 21 days in June

500 Migrants present for 10 days in June

3500 pairs of breeding birds

3.0 goslings per pair during post-hatch period.

(A) Estimation of net primary production and forage consumption.

a) Estimage of forage consumption from dropping production

Prehatch period

1) La Pérouse Bay yearlings

500 birds x 100 g dwt x 21 days — 1,050 kg

2) Migrant birds

500 birds x 25 g dwt x 10 days — 125 kg

3) Breeding pairs

7000 birds x 30g dwt x 28 days — 14,700 kg

Late Posthatch period (August)

4) 800 Canada geese x 500g dwt x 14 days — 5,600 kg

Posthatch period

5) Adults weeks 1-3

7000 birds, 346g dwt per day — 50,862 kg

Adults weeks 4-8

7000 birds, 231g dwt per day — 56,595 kg

6) Goslings (12,000)

1st week	65g dwt /day/gosling	150,000 kg
2nd week	129g dwt /day/gosling	
3rd week	220g dwt /day/gosling	
4-8 week	286g dwt /day/gosling	

The cellulose content of the droppings was 50% of the dry weight and that of the plant tissues was 36% of the dry weight. It was assumed that the birds did not break down cellulose (Mattocks 1971); hence the amount of forage consumed is 50/36 of the weight of droppings.

Estimation of forage consumed based on droppings using the conversion factor outlined above the amount of net primary production consumed is 426,000 kg.

b) Estimation of total above-ground production based on consumption by geese.

The total consumption, based on the quantity of droppings produced, was 4.26×10^5 kg, and the area of the marsh was estimated at 5.4 km^2. Therefore, the average quantity of forage consumed over the whole marsh was 78.9 gm^{-2}. Total net above-ground primary production is assumed to equal:

Consumption (C) = Final standing crop - initial standing crop

<u>Puccinellia</u> NAPP = 78.9 + 57.6 - 38.0 = 98.5 gm^{-2}

<u>Carex</u> NAPP = 78.9 + 36.8 - 16.7 = 99.0 gm^{-2}

Assuming equal areas dominated by <u>Carex</u> and <u>Puccinellia</u>;

Total NAPP of the marsh is therefore approximately 99.0 gm^{-2} x 5.4 km^{-2}

Total NAPP of the marsh therefore equals:

$$99.0\ gm^{-2} \times 5.4\ km^{-2} = 535{,}000\ kg$$

c) Estimation of total net above-ground primary production based on short-term exclosures.

The net above-ground primary production of <u>Carex</u> and <u>Puccinellia</u>-dominated sites was estimated at 95.0 and 102.6 gm^{-2}, respectively. The total production of the marsh, assuming equal areas dominated by the two species, is approximately 98.8 gm^{-2} x 5.4 km2 = 534,000 kg.

d) Estimation of forage consumed based on regrowth.

Consumption is assumed to equal:

Initial standing crop + NAPP - final standing crop

Puccinellia C = 38 + 102.6 - 57.0 = 83.8 gm^{-2}

Carex C = 16.7 + 95.0 -36.8 = 74.9 gm^{-2}

Assuming equal areas of Carex and Puccinellia, total forage consumption equals: (83.8 ± 74.9)/2 gm^{-2} x 5.4 km^2 = 428,000 kg

Although the estimate of productivity and consumption are approximations, based on a number of assumptions, the close agreement of the largely independent pairs of estimates indicates that they are fairly good approximations. The total net above-ground production of Carex and Puccinellia was estimated at either 5.34 or 5.35 x 10^5 kg, and the total quantity of forage consumed was estimated at either 4.26 or 4.28 x 10^5 kg, depending on the method of estimation. Thus, the geese appear to be consuming approximately 80% of the total net above-ground primary production.

(B) Estimation of the magnitudes of the fluxes of nitrogen between vegetation and geese.

a) Total nitrogen utilized in shoot production.

Puccinellia 2.86 gm^{-2}

Carex 3.50 gm^{-2}

Assuming that the marsh consists of 50% Carex and 50% Puccinellia total nitrogen utilized in above-ground net primary production is $3.18\ gm^{-2} \times 5.4\ km^2 = 1.72 \times 10^4$ kg.

b) Total nitrogen utilized in root production Puccinellia or Carex.

$950\ gm^{-2} \times 1.5\%\ N = 14.25\ gm^{-2}$ total nitrogen utilized in below-ground net primary production is $14.25\ gm^{-2} \times 5.4\ km = 7.70 \times 10^4$ kg

c) Total nitrogen consumed by the geese.

Puccinellia: 83% of above-ground net primary production consumed

Therefore $2.86\ gm^{-2}$ of nitrogen $\times\ 0.83 - 2.35\ gm^{-2}$

Carex: 79% of above-ground net primary production consumed

Therefore $3.50\ gm^{-2}$ of nitrogen $\times\ 0.79 = 2.77\ gm^{-2}$

Total (assuming 50% Carex, 50% Puccinellia)

is 1.38×10^4 kg for the marsh as a whole.

d) Total nitrogen returned to the marsh in droppings.

Analyses of droppings indicates 61% of the nitrogen is consumed. Of this, at least 15 - 20% is in the form of soluble nitrogen compounds.

Hence - total nitrogen returned	5382 kg
total soluble nitrogen returned	8076 kg
total insoluble nitrogen returned	4575 kg

DISCUSSION AND CONCLUSIONS

The data presented in this report are based on results obtained in two consecutive field seasons. Although conclusions can be drawn, iterative modifications to the budget will necessitate some modifications to the conclusions.

Primary productivity of the salt marsh vegetation at La Pérouse Bay is regulated by the length of the growing season, the availability of nitrogen and, at some sites, the effects of high salinity (cf. Cargill and Jefferies, 1980).

In spite of spring thaw occurring in June in 1979 and April in 1980, daytime temperatures were generally below 0 C until June in both years. Active growth of Puccinellia and Carex also commenced in June, at about the sake date as the young snow geese hatched. Whether hatching coincides with the spring onset of plant growth every year is a question which requires further examination. At present, neither the factors controlling the onset of primary productivity, nor those governing the timing of nesting, are completely understood.

The results of the additions of nutrients to the salt marsh vegetation clearly demonstrated that lack of available nitrogen limited net primary production. (Figs. 2 - 3). There was some evidence, particularly in 1980, the addition of ammonia resulted in a larger increase in NAPP than did the addition of equivalent amounts of nitrate. Some of the nitrate may have been lost as a result of denitrification. At some sites, redox potentials in the sediments approached -100 volts, based on measurements with a hydrogen electrode. (Jefferies and Jensen, unpublished). Further studies are required on the availability of inorganic nitrogen for plant growth in these sediments.

Under conditions prevailing in the marsh, phosphorus did not appear to limit plant growth; only when additions of nitrogen enhanced plant growth did demand for phosphorus exceed supply. (Fig. 3) Even in the plots treated with ammonia, phosphorus did not become limiting for plant growth until later in the season.

As indicated elsewhere (Cargill and Jefferies, 1980), hypersaline conditions may develop in the rooting zone of the sediments, particularly at sites on south-facing slopes, well above the mean high water mark. Measurements made in 1980 indicated that at such sites the salinity of the upper 5 cm may exceed 1.0 M sodium (salinity 84 parts per thousand). (Jefferies and Jensen, unpublished). These sites are in the upper regions of the marsh, along the edges of small ponds or creeks in areas of impeded drainage. They are either unvegetated, or occupied by sparse stands of _Puccinellia phryganodes_ and _Salicornia europaea_ agg.

In midsummer, the sites are dry at the surface, and the sediment is deeply stained with ferric salts. Immediately beneath the surface conditions are highly reduced; the sediments consist of a thick layer of black, anaerobic mud. In the spring of 1980, shallow pools of water covered much of the area. On sunny days, although the air temperature was close to 0 C, the water temperature was between 10 and 20 C. Large mats of filamentous green algae grew in these shallow transient pools. As the season progressed and the pools dried out, mats of dead algae were deposited on top of the _Puccinellia_ sward, which either killed or severely reduced the vigour of the grass. In July, a mat of dead algae and _Puccinellia_ was visible at the surface of the dried-up ponds. It is postulated that this process results in the development of a mosaic of bare areas within the marsh, with impeded drainage and highly reduced conditions in the sediments immediately below the surface.

In 1979, areas of mixed Carex and Puccinellia which were grazed by geese maintained a remarkably constant live, above-ground standing crop for much of the growing season. (c. 40 gm^{-2}). Comparable figures in 1980 were between 50 and 60 gm^{-2} for the Puccinellia sward and between 30 and 35 gm^{-2} for Carex. (Figs. 7-9) The number of breeding pairs of geese declined from 4400 to 3500 in the second year of the study, suggesting that grazing may have been less intense.

In order to examine the effects of grazing on Puccinellia and Carex, mean relative growth rates of grazed and ungrazed swards were compared in both years. At all sites, initial relative growth rates were similar for grazed and ungrazed vegetation. However, these growth rates were not sustained throughout the season in the ungrazed plots. Rates declined from mid July onwards; negative values were recorded in mid August 1980 for ungrazed swards of both Carex and Puccinellia. (Figs. 13-15) In Puccinellia. grazing resulted in the maintenance of the initial growth rates throughout the season, and this is reflected in the cumulative net primary production figures for grazed and ungrazed sites. (Fig. 5) Grazed Carex showed a decline in growth rate in late summer, but this was much less pronounced than in ungrazed swards of the same species. (Fig. 6) It should be noted that even the maximum-growth rates attained by grazed vegetation in the La Perouse Bay marsh are fairly low compared to rates which have been measured in temperate salt marshes. (Jefferies, unpublished) The lower ability of Carex to maintain a high growth rate when grazed, in comparison to Puccinellia, is probably related to inter-specific differences in growth form. Carex spreads by means of underground rhizomes, while Puccinellia tillers freely from above-ground stolons. Demographic studies are planned for 1981 which will explore the influence of growth form on response to grazing, by following the fate of individual shoots and tillers.

The conclusion of this part of the study is that continual grazing of both species results in enhanced net aerial primary production, compared with ungrazed swards. The productivity of grazed and ungrazed sites of differing species composition is summarized in Table 1.

Below-ground biomass amounted to approximately 90% of the total, irrespective of grazing regime or nutrient treatment. As discussed previously, (Cargill and Jefferies, 1980), the inability to differentiate between living and dead roots made it difficult to interpret the results for 1979. However, considerable care was taken in 1980 to separate living and dead below-ground parts, resulting in production estimates of 700 gm^{-2} for Puccinellia and 740 gm^{-2} for Carex. Much of this production was confined to the early part of the season, and live below-ground biomass declined from late June onward in all sward types. The results indicate either that root production ceased at this time, or that heavy mortality of roots masked any subsequent production. Whether the loss of live roots in July and August resulted from death of roots produced in previous years, or those produced earlier in 1980, was not determined. In any event, by the end of the summer, below-ground standing crop had declined to about the same level present at the beginning of the growing season. The considerable mortality and turnover of roots during the summer may have resulted in an underestimate of total production, so that the estimates given in Table 1 are minimal. Little significance is attached to the apparent differences in below-ground biomass between grazed and ungrazed sites, because of high inter-site variability in below-ground biomass, despite the similarity of the sites above-ground. The large quanitity of below-ground biomass represents a major nutrient sink in the marsh ecosystem.

There was little change in the standing crop of dead material during either summer of the study. During 1980, total dead plant material amounted toapproximately 15 g m^{-2} in Puccinellia swards and 25 g m^{-2} in Carex swards, irrespective of grazing. In 1979, mixed communities had about 15 g m^{-2} of dead biomass throughout the growing season (Figs. 13 a-c). The higher litter levels in 1980 probably reflect the high production in 1979, while the smaller quantity of dead biomass in 1979 indicates lower primary production in 1978.

The estimates of net above-ground primary production do not take into account any death and turnover of plant tissue during the growing season, except in relation to goose grazing, and the relative constancy of dead standing crop indicates that this is not likely to be a serious source of error. The question of shoot mortality will be addressed in the 1981 field season, by means of the demographic studies referred to earlier. The information obtained will presumably result in a small upward adjustment of the above-ground productivity estimates.

The total amounts of nitrogen in the shoots and roots of grazed and ungrazed Puccinellia and Carex are shown in Figures 17 - 23. Most values of total nitrogen in grazed Puccinellia shoots were between 2 and 3% of the dry weight. In both 1979 and 1980, ungrazed shoots contained a lower percentage of nitrogen than grazed shoots, from July onward. A similar pattern was observed for Carex, but nitrogen content was generally higher than in Puccinellia. This was particularly noticeable early in in the 1980 season, when total nitrogen content of grazed Carex shoots reached 6% of the dry weight, an exceptionally high value for plant tissues.

Although most of the biomass of these plants is below ground, the proportion of the total standing stock of nitrogen contained in below-ground tissues is lower. The percentage of nitrogen in roots is generally much lower than in shoots; betwen 1 and 2%. Much of the below-ground biomass may consist of storage tissues, which typically have low carbon: nitrogen ratios.

Soluble nitrogen levels in shoots of Puccinellia changed appreciably during the growing season. Early in the season, soluble compounds accounted for approximately 20% of the total nitrogen content, and much of the soluble nitrogen was present as proline. In many herbaceous perennial the shoot acts as a "sink" for nutrients early in the season, insoluble nitrogen compounds in the below-ground storage organs being converted into soluble forms and translocated to the shoots. During the active growing season, the pool of soluble nitrogen can be expected to decrease, as it acts as a source for growth and development, and this trend was apparent in Puccinellia.

The soluble nitrogen content of Carex was low (0.1 to 0.2%) throughout the growing season. The failure to detect an early season peak in soluble nitrogen in this species may indicate that it had already begun active growth before the first collection of samples. Mean relative growth rates were quire high in Carex, so the pool of soluble nitrogne may have been used for growth as fast as it was translocated, keeping the level in the shoots low.

By comparing the nitrogen content of goose droppings with that of plant tissues, it was possible to obtain some idea of the efficiency with which the geese absorbe nitrogen from their forage. The values given for nitrogen content of goose droppings are under-estimates, because they refer only to the nitrogen contained in the faecal material. Urinary nitrogen was not analysed, and would presumably have increased the total nitrogen of the droppings somewhat.

It has previously been suggested that, because food passes through the gut of a goose extremely rapidly (30 to 90 minutes), the major source of nutrients is soluble nitrogen compounds derived from broken cells. However, the dat collected in this study indicate that the geese absorbed approximately 64% of the total nitrogen content of the forage, although only 10% or less of this was in the form of soluble compounds. Furthermore, much of the nitrogen in the droppings is present as ammonia, a metabolic by-product not present in plant tissues. Amino acids and proline are virtually absent from droppings, indicating that these compounds are effectively absorbed by the gut.

Complete data on the frequency of defaecation by the geese are at present only available for the post-hatch period, so accurate estimates of forage consumption are also restricted to that part of the season. During laying and incubation, plant productivity is low, and the birds feed much less than they do after hatch. Approximate estimates of the production of droppings during this period were based on field observations by the authors and the data of Mineau (1978).

An accurate estimate of the area of the Puccinellia phryganodes - Carex subspathacea community at La Perouse Bay is necessary in order to calculate the total amount of forage available to the geese. During the 1980 season, different habitat types were identified, and the total area occupied by each was estimated using maps and aerial photographs. Transects were laid out in each habitat type, and the frequency of the Puccinellia - Carex vegetation zone along each transect recorded. This procedure yielded and estimate of 5.4 km^2 for the total area of the community within La Perouse Bay.

Total net above-ground primary production of the Puccinellia-Carex marsh for 1980 was estimated from the results of the short-term exclosures, and from the quantity of vegetation consumed by the goose population, as estimated from the production of droppings. The two approaches yielded estimates of 5.34×10^5 kg and 5.35×10^5 kg respectively, assuming that Carex - dominated and Puccinellia - dominated sites occupied approximatley equal areas. This assumption was based on extensive field observations over three summers, and is not likely to be in error by more than 10%, In any case, the productivity per unit area was quite similar for the two sward types.

The quantity of vegetation consumed by the goose population was estimated from the production of droppings, and also from the disappearance of vegetation from grazed sites. Again, the two estimates were remarkably similar; 4.26×10^5 and 4.28×10^5 kg. This result indicate that approximately 80% of the NAPP was consumed by the geese, a very high figure compared to other grazing ecosystems (Wiegert and McInnis, 1975).

The total quantity of nitrogen ingested by the geese was about 1.38×10^4 kg, of which about 64% was absorbed and 36% returned directly to the marsh in droppings. Much of this was in the form of soluble compounds, which would be rapidly leached into the marsh sediments. Insoluble nitrogen in droppings was presumably broken down more slowly, and part of this component was lost when autumn storm tides washed the droppings out to sea, or deposited them on the strand line at the edge of the willow zone. In estimating the total loss of nitrogen from the marsh as a result of the activities of geese, it was assumed that all the insoluble nitrogen in the droppings was exported. This is certainly an over-estimate, but it was felt that an estimate of the maximum possible impact of the geese on the nitrogen budget of the marsh would be useful.

Nitrogne export was further over-estimated by the failure to assess urinary nitrogen excretion. Although the geese absorbed 64% of the nitrogen in the forage, some part of this was subsequently returned to the marsh in urine, and this has not been accounted for in the calculation of the quantity of nitrogen exported. Based on these assumptions, the maximum possible total loss of nitrogen attributable to the geese was estimated at 1.07×10^4 kg, or 1.99 g for each sqare meter of marsh.

Although no data are presently available on the rate of nitrogen fication at La Perouse Bay, figures for other tundra ecosystmes suggest that a loss of this magnitude would likely be compensated for by fixation by blue-green algae and bacteria in the marsh sediments. In addition, preliminary data on the rates of nitrogen mineralization in the sediments at La Perouse Bay indicate rates on the order of 10 to 20 g m^{-2} yr^{-1} (Jefferies and Jensen, unpublished). Hence, the annual input of nitrogen into the marsh, and the rate of turnover, are probably adequate to compensate for the quantity removed by the geese. It is possible that grazing results in increased nitrogen fixation by the mats of blue-green algae on the marsh sediments, by keeping the sward open and ensuring that high levels of irradiance reach the algae. Leaf area index on grazed sites selcom exceed 0.7. Blue-green algae will utilize soluble nitrogen, if available, rather than fix nitrogen, so fixation may occur mainly in the pre-hatch period, when nitrogen input from grazing geese is minimal.

The low leaf area index on grazed sites also results in high levels of irradiance reaching the leaves and shoots of *Puccinellia* and *Carex* at all levels of the canopy. It is well known that young shoots and leaves with high protein content have high photosynthetic capacity and can exploit high irradiance levels. Where litter accumulates and reduces irradiance, photosynthesis will be reduced. It is apparent that, at La Perouse Bay, the competitive ability of *Puccinellia* and *Carex* are favoured by the high irradiance in grazed swards. At sites which have been protected from grazing for several years, other species are beginning to invade the sward. Evidently, the maintenance of an open canopy by grazing results in the successional process being retarded, and Puccinellia and Carex persisting in the area longer than they would in the absence of grazing.

The third, and possibly most important effect og grazing on primary production is related to the role of geese in the cycling of nitrogen within the salt marsh ecosystem. In goose droppings, the plant tissues are reduced to tiny fragments, making a large surface area available for the activity of decomposing organisms. In addition, the soluble nitrogen (mainly ammonia) in the droppings may be taken up by the plants, or may serve to stimulate the rates of microbial nitrogen mineralization (Caskey and Tiedje, 1978). Further investigation is planned to determine the quantity of nitrogen released from the droppings to the sediments and its path in the nitrogen budget of the marsh. The data on total amounts of nitrogen assumulated by shoots of Carex and Puccinellia indicate clearly that nitrogen is recycled more rapidly in grazed than in ungrazed areas.

One of the objectives of the study was to estimate the carrying capacity of the marsh for geese. The results to date indicate that this will be a more compex task than was anticipated at first. Because the productivity of the marsh vegetation is affected by grazing, and different levels of grazing pressure can be expected to have different effects, the total quantity of forage available in any season depends on the number of geese present.

Carrying capacity will also be influenced by the weather conditions prevailing in a particular season. A late thaw may result in the plants being subjected to heavy grazing before conditions are optimal for growth, which might reduce their capacity to withstand grazing. In addition, nesting is delayed in a late season, and this in turn delays the departure of the geese from the area in the autumn. This may reduce the opportunity for the plants to accumulate carbohydrates in late summer for translocation to below-ground storage organs. Such reduction of stored carbohydrate reserves could be expected to lead to poor initial shoot growth in the following spring. Two or three successive late seasons, especially combined with high goose populations, might well lead to serious reduction in the potential net primary production of the marsh.

Future investigation will be aimed at developing a model for the interaction of grazing and primary production, using such approaches as experimental grazing regimes of varying intensity, and demographic studies of the fates of individual shoots. This will ultimately allow prediction of the capacity of the marsh to support a goose population of any given size, and the likely consequences of any level of grazing for present and future productivity. The ability to make such predictions is considered an important priority in view of the continuing growth of the continental population of lesser snow geese. Although the actual figures obtained at La Perouse Bay will be specific to the local situation, the overall nature of the relationship between grazing and primary production can be expected to apply in other areas which support goose populations.

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