

Soluble carbohydrate content of shoots of Arctic wetland plants that are consumed by lesser snow geese

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Abstract: We recorded seasonal changes in the total amounts of soluble carbohydrates in shoots of salt- and fresh-water coastal plants at La Pérouse Bay, northern Manitoba, to determine whether adult snow geese and their goslings selected forage rich in soluble carbohydrates during the breeding season. The selection of forage plants in spring and summer by adults and goslings was strongly linked to the presence of high amounts of soluble carbohydrates in tissues: on the order of $100 \text{ mg}\cdot\text{g}^{-1}$ dry mass. When the content fell as a result of shoot development or leaf senescence, the geese switched to alternative sources of forage. The extent to which individual shoots rich in soluble carbohydrates of the primary freshwater forage species are grazed depends on the local density of breeding geese at the study site, which has fallen in the last decade as a result of the earlier destruction of much of the coastal vegetation by foraging geese.

Key words: Arctic salt- and fresh-water marshes, Hudson Bay coast, pre- and post-hatch feeding, graminoid and herbaceous forage species.

Résumé : Afin de déterminer si les oies des neiges adultes et leurs oisons sélectionnent un fourrage riche en glucides solubles au cours de la saison de reproduction, les auteurs ont enregistré les fluctuations saisonnières des quantités totales de glucides solubles dans les tiges de plantes côtières d'eau douce et d'eau salée. La sélection des plantes alimentaires au printemps et à l'été par les adultes et les oisons montre une forte relation avec la présence de grandes quantités de glucides solubles dans les tissus, de l'ordre de $100 \text{ mg}\cdot\text{g}^{-1}$ en poids sec. Lorsque la teneur diminue suite à la maturation de la tige ou de la sénescence des feuilles, les oies passent à une source alternative de fourrage. Le degré d'utilisation d'espèces de fourrage primaire d'eau douce dont les individus sont riches en glucides solubles dépend de la densité locale d'oies en reproduction sur le site étudié, laquelle a diminué au cours de la dernière décennie comme conséquence d'une destruction hâtive d'une forte proportion de la végétation côtière par le broutage des oies.

Mots-clés : marais arctique d'eau douce et d'eau salée, côtes de la Baie d'Hudson, alimentation pré- et post-éclosion, espèces de fourrage graminoides et herbacées.

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Introduction

Soluble carbohydrates in forage plants are an important energy and nutrient source during the pre- and post-hatch phases of the reproductive cycle of Arctic breeding geese, which are largely herbivorous in their feeding preferences (Owen 1980). Food passes rapidly through the gut of geese, in as little as 30–45 min, and the soluble nutrients that are released from fractured plant cells are readily absorbed in the gut and make a substantial contribution to the diet of the birds (Owen 1975). Geese will often select patches of plants that are high in nitrogen (Lieff 1973; Harwood 1975; Buchsbaum et al. 1984, 1986), but this pattern of selection of forage plants is not always consistent (Lieff et al. 1970; Owen et al. 1977; Buchsbaum et al. 1984). Owen (1980) has suggested that the choice of particular species is also related to the extractable energy content of the plants, as well

as their protein levels, although choices also may be modified by the presence of secondary chemical compounds in plant tissues that deter geese.

Generalist plant consumers must continuously sample a broad spectrum of available foods to monitor changes in food quality and to meet daily energy and nutritional requirements (Robbins 1983). These interactions between food availability and foraging strategies can be related to the marginal value theorem (Charnov 1976; Stephens and Krebs 1986), in which the forager continually assesses the instantaneous rate of gain when foraging in a patch, and leaves when this rate drops to the average rate of energy intake for the overall habitat.

Although there has been a number of nutritional studies (mainly nitrogen and phosphorus) relating the growth and nutritional quality of forage species to the reproduction of adult snow geese and growth of their goslings at La Pérouse Bay on the Hudson Bay coast (cf. Jefferies et al. 2003 and references therein), amounts of soluble carbohydrates in plant tissues of different forage species during the snow-free season have not been determined at this location. However, there are some studies of the levels of soluble carbohydrates in forage species eaten by geese in sub-Arctic and Arctic environments (Sedinger and Raveling 1984;

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Coleman and Boag 1987; Beaulieu et al. 1996; Hupp et al. 2001). In addition, Thomas and Prevet (1980, 1982) showed that the arrow grasses (*Triglochin maritima* L. and *Triglochin palustris* L.) and horsetails (*Equisetum* spp.), which are eaten by lesser snow geese, contained high levels of soluble carbohydrates and crude protein (nomenclature follows Porsild and Cody 1980). Amounts of soluble carbohydrates in plants from temperate salt marshes and the digestibility of these organic compounds by brant (*Branta bernicla* L.) and Canada (*Branta canadensis* L.) geese have been investigated thoroughly (Buchsbaum et al. 1984, 1986; Buchsbaum and Valiela 1987). This limited amount of information for northern plant species is surprising in relation to the ongoing debate whether Arctic-breeding geese are “capital” (depend on endogenous reserves for reproduction) or “income” breeders (acquire exogenous reserves on the breeding grounds for reproduction) (cf. Drent 2006; Klaassen et al. 2006).

The geometric increase in the size of the Mid-Continent population of lesser snow geese of between 5%–7% per annum in recent decades (Cooke et al. 1995; Abraham et al. 1996) has led to changes in the selection of different wetland species as forage in coastal areas of the Hudson Bay Lowland and elsewhere during the post-hatch phase, when the demand for high-quality forage from both goslings and adults is high. This switching is because of the extensive loss of intertidal vegetation as a result of the grubbing of roots and rhizomes of the dominant graminoids (*Puccinellia phryganodes* (Trin.) Scribner & Merrill and *Carex subspathacea* Wormsk.) in thawed ground by increasing numbers of geese in early spring before aboveground growth has started. Only isolated relict patches (1–4 m²) of these graminoids remain in former salt marshes along much of the coast of the Hudson Bay Lowland, which were formerly grazed intensively in summer (Abraham et al. 2005). As a result, the snow geese have modified their foraging behaviour and forage in both spring and summer in brackish marshes and in freshwater calcareous or mesotrophic mires (wet sedge meadows) inland from the coast, which are dominated by *Carex aquatilis* Wahl.

We undertook a study of amounts of total soluble carbohydrates in tissues of the preferred Arctic forage species of the lesser snow goose (*Chen caerulescens caerulescens* L.) in both intertidal and freshwater marshes during the pre- and post-hatch phases at a breeding colony on the coast of the Hudson Bay Lowland. The objective was to examine whether the foraging behaviour of the geese during the breeding cycle was linked to seasonal changes in the soluble carbohydrate content of tissues of forage plants. Because the geese have altered their foraging behaviour over the course of the study, measurements of soluble carbohydrates in selected forage plants have been made on different occasions.

Site characteristics, forage species, and goose foraging behaviour

The study site is located at La Pérouse Bay (58°43'N, 94°26'W), about 30 km east of Churchill, Manitoba, in Wapusk National Park. Extensive intertidal flats occur on the shore of the bay as a result of isostatic uplift, which in the Cape Churchill region is about 0.8 cm·a⁻¹ (Hansell et al. 1983) and shallow braided channels of the Mast River flow

into the bay across the western marsh. The exposed flats away from drainage channels were formerly covered with swards of the stoloniferous grass, *P. phryganodes*, and the rhizomatous sedge, *C. subspathacea*, in which *Potentilla egedii* Wormsk. ex Hornem., *Plantago juncooides* Lam., and *Stellaria humifusa* Rottb. were present (Jefferies et al. 1979). Geese eat the aboveground biomass of all of these species in summer when available, but spring grubbing results in the removal of belowground tissues and exposure of sediment. The vegetation in the low-lying areas of the freshwater calcareous mires immediately inland from the tidal marshes is dominated by *C. aquatilis*. This sedge is also well established along the banks of the shallow, braided tributaries of the Mast River that drain into the bay. Shoot-pulling of this sedge species is widespread in spring where the ground is thawed. The geese eat the basal swollen white section and discard the remainder of the shoot. However, shoot-pulling ceases in late spring when the aboveground growth of intertidal and beach-ridge graminoids starts, just before hatch. When surviving shoots are well developed, adult geese and goslings of age 15 d or more graze the leaf tips of sedges. Occasionally, the mid-portion of the leaf blade may also be taken, as occurs on Akimiski Island in James Bay (K.F. Abraham and R.L. Jefferies, personal observations, 2001).

In most years, breeding and staging lesser snow geese arrive in mid-May on the Hudson Bay coast in thawed brackish and freshwater sites where they also eat the base of emerging leaves of the locally distributed *Senecio congestus* (R.Br.) DC. (Arctic ragwort), which develop soon after melt. As in the case of *C. aquatilis*, the geese eat the fleshy swollen base of the leaves and discard the remainder.

Materials and methods

Sampling

During the pre-hatch phase in early spring, between three and five entire plants of *S. congestus* were collected on six sampling occasions over a 10 d period in June 2000, one from each site over a total area of 500 m × 500 m. Each site was at least 50 m from its nearest neighbour and contained up to 15 plants. Development of the basal rosette of leaves of plants at the sites was broadly synchronous and the few plants that sprouted after the initial harvest were not sampled. In the case of *C. aquatilis*, plants were collected in 2004 from up to six stations, which were at least 30 m apart, in a wet sedge meadow on the Cape Churchill peninsula. During spring and summer, shoots that developed at the start of the season in early June (i.e., this excludes juvenile shoots that may develop later in the season) were harvested on nine occasions between early June and mid-August 2004 from at least three stations. The shoots were pulled up gently, so that the basal white portion which was embedded in moss or fine sediment was included. This action is comparable to shoot-pulling by the geese.

We also recorded, intermittently, during 11 seasons from 1991 to 2007, the annual cumulative percentage of *C. aquatilis* shoots that were grazed by geese during summer at 12 to 20 stands along the Mast River and its braided shallow tributaries, to assess the use of this species as a forage source following the loss of salt-marsh swards in

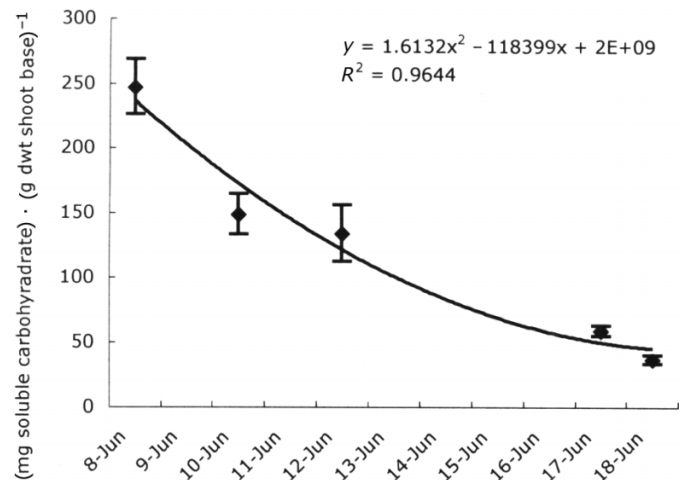
the early 1990s. Within this river wetland and intertidal areas, populations of microtines were very low and were not responsible for the levels of shoot grazing recorded. Snow geese were frequently observed feeding on shoots of *C. aquatilis*, which were often 50 cm or more in height. Depending on river flow, the stands were delineated early in the season and were located in area approximately 600 m × 600 m. Each stand, which was at least 30 m from its nearest neighbour, had a minimum of 20 shoots at the start of the season. The minimum total number of shoots that was counted each year was at least 400, and in most years it exceeded 700, and the cumulative number of grazed shoots as a percentage of the total number of shoots at each of the stands was recorded at intervals during the summer. The most complete record of this cumulative percentage for the different years was based on data collected during the week of 14–21 July and these results are shown. This includes the period of intense foraging by adults and goslings during the first 2–3 weeks of July, approximately 2 weeks after hatch.

Grazed shoots of *P. phryganodes* and *C. subspathacea* are less than 1 cm in height. Six turves (10 cm × 10 cm) of each species for analyses of soluble carbohydrates in shoot tissue were taken at random from the intertidal flats on each sampling occasion (at least once every 10 d, but mostly once a week) during the summers of 1997 and 1998. The distance between samples was not less than 15 m. In July 2007 we also collected leaf material from individual plants of forage and nonforage species to determine whether the levels of soluble carbohydrates in nonforage species were similar to those of forage species. Leaf tissue for analysis was collected from four individual plants that were growing at least 20 m apart. All plant tissue was prepared for extraction of soluble carbohydrates within an hour from the time of collection.

Sample preparation and extraction and measurement of soluble carbohydrates

The basal white fleshy portion was cut from the leaves of three to five plants of *S. congestus* and the leaf bases of each plant were washed in water for 30 s before they were drained using a sieve and gently blotted with filter paper (Whatman No. 1) to remove residual surface water. Just prior to extraction of carbohydrates, the basal portions were cut into small pieces (ca. 0.3 cm³). In the case of shoots of *C. aquatilis*, the white basal portion was separated from the shoot, the tips of the oldest leaf on each shoot were cut at the point where the leaf blade no longer tapered, and the flat central portion of the blade was separated from each shoot. It was only possible very early in the season to recognize the white shoot base and the developing shoot tip. Each type of material was pooled for each station, washed in water for 30 s, drained, and blotted free of surface water with filter paper. The tissues were cut into small pieces before extraction. The aboveground biomass from the six turves of *P. phryganodes* and *C. subspathacea* was cut close to the surface of the turves and the shoots floated in a tray of deionised water. Soil particles sank to the base of the tray and we used forceps to remove dead leaves, shoots of other species, and insects. The shoots were scooped up from the tray with an aquarium cheese cloth net stretched tightly

Fig. 1. Changes in the amounts of soluble carbohydrates in the leaf bases of plants (expressed as mg·g⁻¹ dry mass ± SEM of material) of *Senecio congestus* collected from disturbed freshwater or brackish habitats at La Pérouse Bay, Manitoba, immediately after thaw in early June 2000 ($n = 3-5$). (Fitted partial quadratic curve using linear regression: $R^2 = 0.8304$; $P < 0.001$).



over a metal frame, transferred to filter paper, and blotted to remove residual surface water.

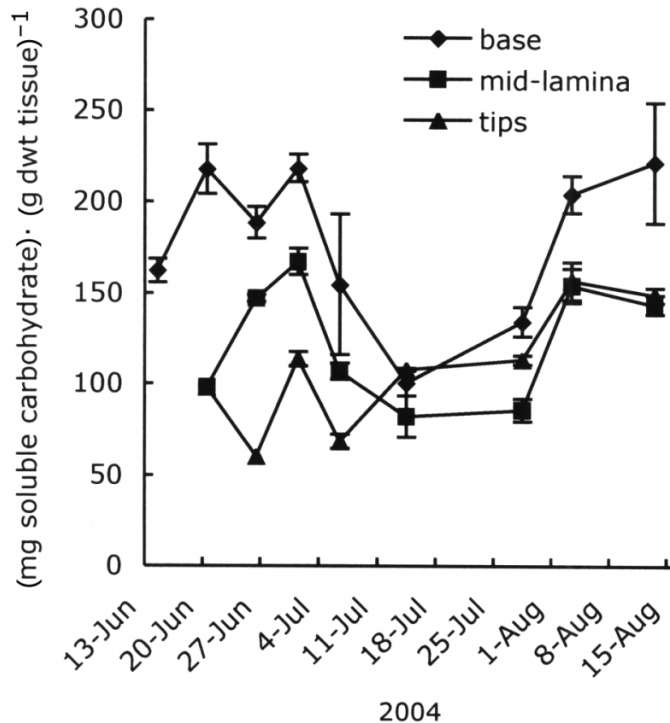
One gram (fresh mass) of plant tissue of samples of the different species was placed in 20 mL of a mixture of ethanol and deionised water (60:40, respectively, v/v) for 24 h with frequent stirring for at least 16 h at room temperature (ca. 20–25 °C) under darkened conditions. The contents of the flask were filtered through Whatman GF/A glass filter paper. This extract contained soluble hexoses and pentoses, oligosaccharides and polysaccharides, and their derivatives. We used the phenol – sulphuric acid reaction to determine amounts of sugars and related substances based on the colorimetric method described by Dubois et al. (1956). We used glucose as the standard and the colorimetric reaction was linear when up to 70 µg of this reducing sugar added to a boiling tube in 2 mL of solution. The results are expressed as glucose equivalents per gram dry mass of tissue. The fresh mass – dry mass ratio was determined by drying a known mass of plant tissue for 72 h at 55 °C.

Results

The soluble carbohydrate content was approximately one quarter of the dry mass of the swollen leaf bases of *S. congestus*, based on glucose equivalents. It fell dramatically during a 10 d period following emergence of leaves in early June (Fig. 1). The adult nesting and staging lesser snow geese did not pull up the basal leaves of this species beyond mid-June. At that stage, leaf development in surviving plants occurred very rapidly and the white fleshy base was no longer a major source of soluble carbohydrates. The birds ignored the green leaves of *Senecio* at all times and only foraged on the white bases in early spring.

In Fig. 2, changes in amounts of soluble carbohydrates during the spring and summer are shown for the different leaf and shoot components of *C. aquatilis*. In spring, the swollen shoot base on which the geese feed also contained

Fig. 2. Seasonal changes in the amounts of soluble carbohydrates (expressed as $\text{mg}\cdot\text{g}^{-1}$ dry mass \pm SEM of material) in the tips, bases, and laminae of leaves of *Carex aquatilis* growing in a fresh-water marsh on the Cape Churchill peninsula, Manitoba, from June to August 2004. Leaf material collected at each sampling site was pooled. ($n = 3\text{--}5$ sites).



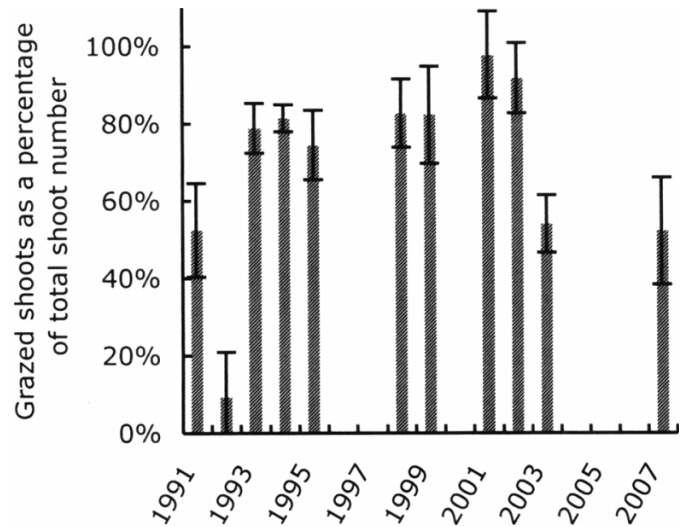
high amounts of soluble carbohydrates (ca. 20% of the dry mass), but values declined to about 50% of the initial values by mid-summer, before rising again in late summer and early autumn. Shoot tips maintained levels of soluble carbohydrates in excess of 100 mg glucose equivalents per gram dry mass of tissue during July when heavy grazing of tips occurred. Levels of soluble carbohydrates in the leaf blade were low during July, but rose in late summer; however, observations of clipped shoots indicated that the leaf blade was rarely grazed.

The cumulative number of shoots of *C. aquatilis* grazed by 21 July for the different years, as a percentage of the total number of shoots, is shown in Fig. 3. The results indicate that during most of the 1990s and the early part of the 2000s between 70% and 95% of all shoots were grazed. By mid-August these values approached 100% in years when data were collected (data not shown).

The lower values in the early 1990s indicate that there was less dependency on the use of this species as a source of forage, likely because areas of intact swards of *P. phryganodes* and *C. subspathacea* on the intertidal flats still remained and provided forage for family groups. In addition, the low value in 1992 reflects the effect of eruption of Mount Pinatubo on the local weather and the phenology of the vegetation in that year and also the low reproductive output of the geese.

With the loss of vegetation in the coastal area in general over the last two decades, the geese no longer forage in

Fig. 3. The cumulative number of grazed shoots of *Carex aquatilis* \pm SEM expressed as a percentage of the total number of shoots that were present between 14–21 July in 11 years from 1991 to 2007. No data indicate the absence of recordings in those years. The shoots were monitored in stands ($N = 12\text{--}20$ sampling stations depending on the year and water flow in the river) of this sedge located along the shallow braided tributaries of the Mast river at La Pérouse Bay, Manitoba. At least 20 shoots were present at each sampling station.

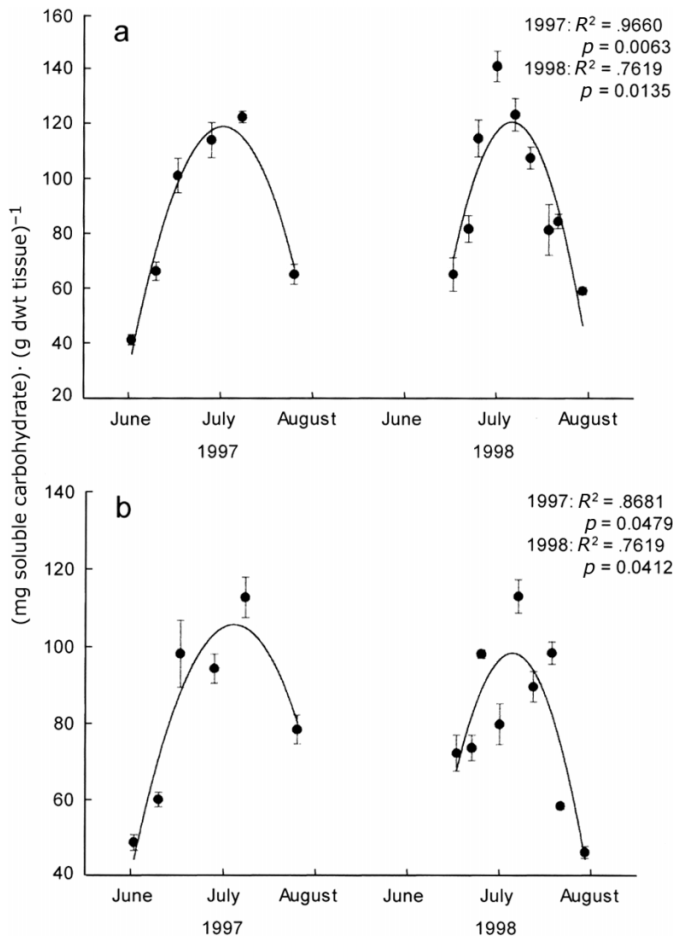


large numbers in the vicinity of La Pérouse Bay during the post-hatch period, and the decline in the proportion of shoots of *C. aquatilis* grazed since 2003 is an indirect measure of the low density of family groups within the area.

The soluble carbohydrate amounts in shoot tissue of the two preferred salt-marsh forage graminoids, *P. phryganodes* and *C. subspathacea*, during the spring and summer months of 1997 and 1998 are shown in Figs. 4a and 4b, respectively. Before the intertidal swards were destroyed by grubbing and the subsequent changes in edaphic conditions, the family groups foraged intensively on these graminoids in the post-hatch period. The graphs indicate that the maximum levels of soluble carbohydrates occurred in July and early August, coincident with the period of intensive grazing and maximum weight gain of the goslings (Gadallah and Jefferies 1995b). Amounts of reducing sugars in shoot tissues in July and early August are similar for both species and also similar to that in the tips of *C. aquatilis*. Of note is the steepness of the curves, reflecting large changes in the levels of these sugars in the shoots of these salt-marsh graminoids between mid-June and late August. The high levels of soluble carbohydrates in the shoots were maintained for only 5–6 weeks.

Finally, on 21 July 2007 we measured the amounts of soluble carbohydrates per gram dry mass in the leaves of nine common coastal forage and nonforage species at La Pérouse Bay (Table 1). Although some nonforage species, such as *Rumex occidentalis* S. Watson and *Salix myrtilifolia* Andersson, had relatively low levels of soluble reducing sugars in their leaves, other nonforage species, including *Potentilla palustris* (L.) Scop. and *Betula glandulosa* Michx.

Fig. 4. Amounts of soluble carbohydrates in grazed shoots of (a) *Puccinellia phryganodes* (mg·g⁻¹ of dried tissue ± SEM) (fitted quadratic curves using linear regression for 1997, $R^2 = 0.8681$; $P = 0.0479$, and for 1998, $R^2 = 0.7619$; $P = 0.0135$) and (b) *Carex subspathacea* (fitted quadratic curves for 1997, $R^2 = 0.8681$; $P = 0.0479$, and for 1998, $R^2 = 0.7619$; $P = 0.0412$) during the period June to August 1997 and 1998. Turves were collected from the intertidal salt marsh at La Pérouse Bay, Manitoba ($n = 5$).



produced large amounts of sugars in their leaves. Leaves of different birch species are known to produce phenols in response to mechanical damage (Haukioja and Niemaliä 1976).

Discussion

The results indicate that lesser snow geese are able to track changes in the amounts of soluble carbohydrates in plant tissues to meet their energetic and nutritional demands during the pre-and post-hatch phases of the breeding cycle. The demand for forage is high, particularly during the post-hatch period. Adult female snow geese may lose up to 32% of their body weight during incubation (Ankney and MacInnes 1978) and goslings increase their weight from 85 g at hatch to between 1500 and 1800 g 7 weeks later, at the start of the autumn migration (Gadallah and Jefferies 1995a, 1995b). There was a correlation between forage selection and soluble carbohydrate patterns in tissues during

the snow-free season. When the concentration of soluble carbohydrates falls below 50 mg·g⁻¹ dry mass of tissue, the tissue is rarely eaten and the birds move elsewhere as predicted by the marginal-value theorem (Charnov 1976).

Although shoots of *C. aquatilis* are pulled up and the bases are eaten by the geese when the soil thaws in spring, leaf tips are not consumed until shoots are well developed. This is usually in early July, soon after hatch. Prior to this, the developing shoots of *C. aquatilis* are silvery-grey/green in appearance and are avoided by geese. There are reports of high amounts of phenolic compounds present in *C. aquatilis* (Jung et al. 1979; Rhoades 1983) and concentrations of these and other secondary chemical compounds maybe high during the early stages of shoot development. Alternatively, as the young shoots are hard and stiff, possibly they are indigestible. Alkaloids of the pyrrolizidine type have been reported in the leaves of close relatives of *S. congestus* (*Senecia vulgaris* L. and *Senecio jacobaea* L., Harborne 1982), which may explain why the green leaves, in contrast to the leaf bases of the Arctic ragwort, are uneaten by the geese in spite of the high levels of soluble carbohydrates in the leaves (Table 1).

As a result of the loss of salt-marsh graminoids, family groups during the post-hatch phase are increasingly foraging in calcareous and mesotrophic mires (wet sedge meadows). However, young goslings under 15 to 20 d of age are unable to reach the leaf tips of well developed *C. aquatilis*, which is often a tall plant (ca. 50 cm high). In addition, they lose weight even when fed chopped whole leaves of this sedge in feeding trials (Gadallah and Jefferies 1995b). Analysis of gizzard content indicates that in the early days of life, the goslings feed on two species in the wet sedge meadows inland from La Pérouse Bay, namely *Triglochin palustris* L. and *Equisetum variegatum* Schleich. ex F. Weber & D.M.H. Mohr. Plants of these species and closely related species are rich in nitrogen and phosphorus and contain high levels of soluble carbohydrates (Thomas and Prevet 1980, 1982; Table 1). The earlier investigations showed that these nutritious plants were an important food source for adults and goslings in the James Bay lowlands during the entire snow-free season. After 15–20 d of life, the goslings at La Pérouse Bay are capable of eating the leaf tips of *C. aquatilis*, which are much more abundant in wet sedge meadows than the species mentioned above (E. Horrigan, unpublished data, 2007).

When feeding in intact intertidal salt marshes, the birds are strongly colonial with large numbers of family groups foraging together. The preferred graminoids are not only rich in nutrients, but produce new leaves approximately once every 11–13 d during the growing season allowing the birds to exploit the new growth throughout the summer (Kotanan and Jefferies 1987; Bazely and Jefferies 1989). Although individual shoots are ca. 1–1.5 cm in height, the density of shoots in the swards is very high and provides a continual supply of good quality forage (Gadallah and Jefferies 1995b). In contrast, shoots of *C. aquatilis* are often 50 cm or more in height, and occur at much lower densities and ongoing shoot production throughout the season is very limited. As a result, family groups when feeding are more dispersed in the wet sedge meadows

Table 1. Amounts of soluble carbohydrates ($\text{mg}\cdot\text{g}^{-1}$ dry mass) in leaves of forage and nonforage plants collected on 21 July 2007 in supratidal and freshwater coastal marshes at La Pérouse Bay, Manitoba ($n = 4$ individual plants collected at least 20 m apart).

Forage species	Mean \pm SE	Nonforage species	Mean \pm SE
<i>Plantago juncooides</i>	31.91 \pm 2.96	<i>Betula glandulosa</i>	98.66 \pm 21.11
<i>Potentilla egedii</i>	71.95 \pm 4.32	<i>Potentilla palustris</i>	132.03 \pm 4.83
<i>Triglochin maritima</i>	89.22 \pm 8.44	<i>Rumex occidentalis</i>	51.18 \pm 3.17
<i>Triglochin palustris</i>	88.10 \pm 9.33	<i>Salix myrtilifolia</i>	61.24 \pm 8.93
		<i>Senecio congestus</i>	97.70 \pm 10.81

than in the intertidal salt marshes and goslings feed on alternative species as discussed above.

There are different cues in addition to the level of soluble carbohydrates that lead to intensive foraging by lesser snow geese on plant tissues rich in soluble carbohydrates. For example, the highest nitrogen levels in shoots of *P. phryganodes* (4.3% of the dry mass) and *C. subspathacea* (4.6% dry mass) also occur at the time of hatch in late June and in the post-hatch period in early July (Gadallah and Jefferies 1995a). Thereafter, values fall to 2.5% and 2.6%, respectively, by early August. Similarly, the nitrogen content as a percentage of the dry mass of tissue is highest in the swollen leaf bases of *C. aquatilis* prior to hatch and in the leaf tips approximately 15 d after hatch (Gadallah and Jefferies 1995a). The levels remain high in the tips from early July until at least mid-August. Hence, soluble levels of carbohydrates and the nitrogen contents of leaves of these graminoid plants peak during the immediate post-hatch period when there is a demand for high quality forage.

The digestibility of soluble carbohydrates in geese is decreased when the fibre content of plant tissue is high (Thomas and Prevet 1980). Marriott and Forbes (1970) showed that Cape Barren geese (*Cereopsis novaehollandiae* Latham) could utilize only 56% of the soluble carbohydrate in alfalfa, because the tissue contained high levels of hemicellulose and pectin. This may provide an explanation why the mid-section of the leaf blade of *C. aquatilis* is rarely grazed by snow geese. Nevertheless, amounts of these reducing sugars (as glucose equivalents) in tissues of the preferred forage species of the geese appear to be a sensitive ecological indicator of forage quality within this coastal wetland on the sub-Arctic – Arctic boundary. This variability in the chemical constituents of plants strongly affects the food choices of herbivores as shown in earlier studies (Denno and McClure 1983; Buchsbaum and Valiela 1987). The high soluble carbohydrate intake in spring and summer as a result of foraging on a range of species at different times allows adult birds to meet energy demands for reproduction and daily activities and both adults and goslings need to build up energy reserves for the autumnal migration.

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