

Stability of a subarctic saltmarsh: Plant community resistance to tidal inundation¹

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Abstract: We investigated the effects of tidal inundation and grazing pressure on soil carbon and nitrogen mineralization and plant community characteristics in the predominant plant communities used by breeding black brant (*Branta bernicla nigricans*) in southwestern Alaska. Three plant communities dominate the outer coastal zone, the lowest in elevation being *Carex subspathacea* grazing lawns, the next being *C. ramenskii* meadows, and the highest being a slough levee community. We flooded each of these communities in the field with tidal waters (mean total dissolved salts $28.3 \pm 0.7 \text{ g L}^{-1}$) at different frequencies for two growing seasons. Relative to controls, treatments that were flooded weekly had soils that had two-, three-, and six-fold increases in salinity in the *C. subspathacea*, *C. ramenskii*, and slough levee communities, respectively. We detected no effect of flooding on either soil carbon or nitrogen mineralization, nor any effect on live plant standing biomass and net aboveground primary productivity in the most coastal communities, those dominated by *C. subspathacea* and *C. ramenskii*. Biomass in the slough levee community was lower in plots that had soil salinities six times higher than the ambient soil salinity. This effect resulted from an 83% decline in woody vegetation. Grass biomass, predominately *Poa arctica* and *Deschampsia caespitosa*, increased in these plots, however, and maintained the productivity of this community relative to controls. Geese reduced the biomass of a preferred forage species (*Triglochin palustris*) by 50% over two growing seasons within the slough levee community. *Carex subspathacea* compensated for the loss of over 95% of its production by geese, even in soils that had twice the ambient salinity. The *C. subspathacea* and *C. ramenskii* communities are resistant to short-term tidal inundation and elevated soil salinities, and grazing by geese is responsible for maintaining their community boundaries. Elevated soil salinity and tidal inundation restricts the development of woody vegetation in the slough levee community, but graminoids compensate for the reduction in woody biomass and maintain the overall productivity of this community.

Keywords: Alaska, climate change, geese, herbivory, salinity, trophic dynamics.

Résumé : Nous avons cherché à connaître les effets de la marée et du broutement de la végétation sur la minéralisation du carbone et de l'azote, ainsi que sur les caractéristiques des principales communautés végétales utilisées par la Bernache cravant (*Branta bernicla nigricans*) pendant la période de reproduction dans le sud-ouest de l'Alaska. Trois communautés végétales dominent la zone côtière. La plus basse est composée de près de *Carex subspathacea*. Au-dessus de celle-ci, on trouve une communauté de *C. ramenskii*. Dans la zone la plus élevée, on trouve essentiellement un marécage dont l'eau est retenue par une digue. Nous avons inondé chacune de ces communautés végétales avec des eaux de marée (en moyenne $28,3 \pm 0,7 \text{ g l}^{-1}$ de sels totaux dissous) à différentes fréquences pendant deux saisons de croissance. Par rapport aux secteurs témoins, le sol des secteurs ayant été inondés chaque semaine présentait une salinité deux fois plus grande dans la communauté de *C. subspathacea*, trois fois plus grande dans la communauté de *C. ramenskii* et six fois supérieure dans le marécage. Les inondations n'ont engendré aucun changement au niveau de la minéralisation du carbone et de l'azote. Elles n'ont pas non plus eu d'effet sur la biomasse de la végétation et sur la productivité primaire (au-dessus de la surface du sol) chez la plupart des communautés côtières dominées par *C. subspathacea* et *C. ramenskii*. La biomasse dans le marécage était plus faible dans les parcelles au sol à salinité six fois supérieure que dans les secteurs témoins. On y a observé, en effet, une baisse de 83 % de la biomasse ligneuse. La biomasse des Poacées, en particulier de *Poa arctica* et *Deschampsia caespitosa*, s'est toutefois accrue dans les mêmes parcelles, ce qui a permis le maintien de la productivité de la communauté. Dans le marécage, le broutement des oies a résulté en une baisse de biomasse de 50 % chez *Triglochin palustris* après deux saisons de croissance. Le *C. subspathacea* a pu compenser la perte de plus de 95 % de sa production primaire causée par le broutement des oies, même sur les sols deux fois plus salins. Les communautés de *C. subspathacea* et *C. ramenskii* sont résistantes aux inondations de courte durée et à l'accroissement du taux de salinité du sol; le broutement des oies est, pour sa part, responsable de leur répartition spatiale. Les inondations et une salinité élevée nuisent au développement de la végétation ligneuse. Toutefois, la perte de végétation ligneuse peut être compensée par la croissance accrue de certaines Poacées, ce qui permet le maintien de la productivité végétale à un niveau similaire.

Mots-clés : Alaska, changements climatiques, dynamique trophique, herbivorie, oie, salinité.

Nomenclature: Hultén, 1990.

Introduction

Cyclonic storm events in the Bering Sea region are predicted to increase in response to climate change

(Walsh, Chapman & Shy, 1996; Serreze, Maslanik & Key, 1997). Increased frequency of storm events, combined with melting of ice reserves, is predicted to increase the extent and frequency of tidal flooding in the coastal zone of the Yukon-Kuskokwim (YK) Delta in southwestern Alaska (Wise, Cominsky & Becker, 1981;

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Sallenger, 1983). Increased tidal flooding would likely elevate soil salinities and decrease the redox potential of soils. Plant biomass, community diversity, and nutrient uptake by plants can decline under these conditions (Rozema & Blom, 1977; Bradley & Morris, 1991; Chambers, Mozdzer & Ambrose, 1998; Gough & Grace, 1998). Reduction of aboveground biomass would likely impact consumers in this system. The YK Delta supports some of the largest and most diverse breeding populations of waterfowl in the circumpolar Subarctic, including four species of herbivorous geese (Nudds, 1992). Because the nutritional environment experienced by goslings affects their final body size, recruitment rate, and future fecundity (Cooch *et al.*, 1991; Larsson & Forslund, 1991; Sedinger, Flint & Lindberg, 1995), we investigated the effect that increased tidal inundation would have on edaphic and plant community characteristics by flooding three plant communities known to be important as a food source to geese breeding in this area.

Increased tidal flooding can affect soil processes and plant community characteristics by elevating soil salinities and by causing the depletion of oxygen in flooded soils by plants and soil microbes (Ponnamperuma, 1984). Both salinity and inundation pressures can lead to a reduction in soil nitrogen and carbon mineralization rates (Ponnamperuma, 1984; Wilson & Jefferies, 1996) and decreased efficiency of nutrient uptake by plants (Bradley & Morris, 1991; Chambers, Mozdzer & Ambrose, 1998). Similarly, decreased plant growth and survival result from stomatal closure in response to saline conditions. Thus, a trade-off between plant-water loss and photosynthetic rate occurs under saline soil conditions (Jackson & Drew, 1984; Wainwright, 1984; Neumann, 1997). Some plants can adjust to these changes in environmental conditions as a result of morphological and physiological acclimation of individuals (Brown & Hellebust, 1977; Story & Wyn Jones, 1977; Jackson & Drew, 1984; Jefferies & Rudmik, 1991) or population changes in response to selective pressures (Wainwright, 1984; Neumann, 1997). However, while plants growing in inland (*e.g.*, less tidally influenced) communities are more likely to be negatively affected by tidal inundation, the increased plant diversity of inland communities (Bertness, 1991; Bertness, Winkler & Chatkupt, 1992) is likely to buffer productivity at the community level (Tilman & Downing, 1994; Chapin *et al.*, 1997).

Soil salinity and the frequency of tidal inundation decrease with subtle increases in elevation away from the coast of the YK Delta, and patterns of plant community zonation are correlated with soil salinity (Kincheloe & Stehn, 1991). It has been suggested that graminoids growing along tidally influenced rivers 30 km inland from the coast of the YK Delta are salt tolerant (Kincheloe & Stehn, 1991). However, patterns of saltmarsh zonation may not reflect optimal growth conditions for plants inhabiting particular communities, and predictions about the response of communities to increased tidal inundation require experimental testing (Snow & Vince, 1984; Gough & Grace, 1998). We hypothesized that rates of soil carbon and nitrogen mineralization and plant diversity and productivity would be negatively affected by increased tidal inundation of inland communities, but that soil

processes and vegetation growing in the more coastal environments of this marsh would not be affected by tidal inundation. These hypotheses were tested by flooding three plant communities with tidal water at different frequencies throughout the growing seasons of 1994 and 1995.

Methods

STUDY AREA

Experiments were conducted at the Tutakoke River black brant (*Branta bernicla nigricans*) goose colony located on the coast of the Bering Sea in southwestern Alaska. The population of black brant (hereafter brant) nesting at the Tutakoke River colony decreased from 7,400 to 1,100 breeding pairs between 1981 and 1986 (Sedinger *et al.*, 1993), but has since increased to an estimated 7,400 pairs (Anthony, 2001). The size of goslings is sensitive to the quality and availability of forage due, in part, to digestive processing rates (Sedinger & Raveling, 1988; Sedinger & Flint, 1991). Smaller goslings have lower survival rates, and those that do survive develop as smaller adults that have both decreased recruitment and fecundity (Sedinger, Flint & Lindberg, 1995). Thus, the potential negative effect of flooding on plant growth and community composition could impact the species of geese that rely on the vegetation in this system.

Plant communities within the colony area are less than 50 cm above mean tidal range (MTR) (Kincheloe & Stehn, 1991). We examined the effect of increased tidal inundation on the *Carex subspathacea*- and *C. ramenskii*-dominated meadows and a slough levee community. These are the predominant plant communities in the outer coastal zone of the YK Delta, and they have important life history implications for breeding brant (Mulder, Ruess & Sedinger, 1996; Person *et al.*, 1998; Person, 2001). Community zonation is not strictly ordinal with respect to the coast, and we refer to the communities with the lowest elevation as the most coastal communities. *Carex subspathacea* is the lowest in elevation of the three communities included in this study; it occurs in monospecific swards that constitute the interface between coastal and riparian mudflats (Figure 1). Swards of *C. subspathacea* form grazing lawns that are inundated several times diurnally during monthly high tide phases. The *C. ramenskii*-dominated meadow typically occurs along the inland side of the *C. subspathacea* community. These meadows are the most prevalent of the three communities contained in the Tutakoke colony area and are widely distributed throughout the coastal region (Kincheloe & Stehn, 1991). Brant typically nest in this community, which is *ca* 5 cm above MTR (Kincheloe & Stehn, 1991). The *C. ramenskii* meadow is inundated by storm surges of the Bering Sea infrequently (2-3 times per decade) during the growing season (B. T. Person, pers. observ.). Herbivory is patchy in this community, governed ostensibly by snowmelt patterns, proximity to nesting areas, and variation in brant density (Ruess *et al.*, 1997; Person, 2001). Slough levees dissect the Tutakoke landscape and are *ca* 25 cm above MTR. Like the *C. ramenskii* meadow, the slough levees are inundated by storm surges 2-3

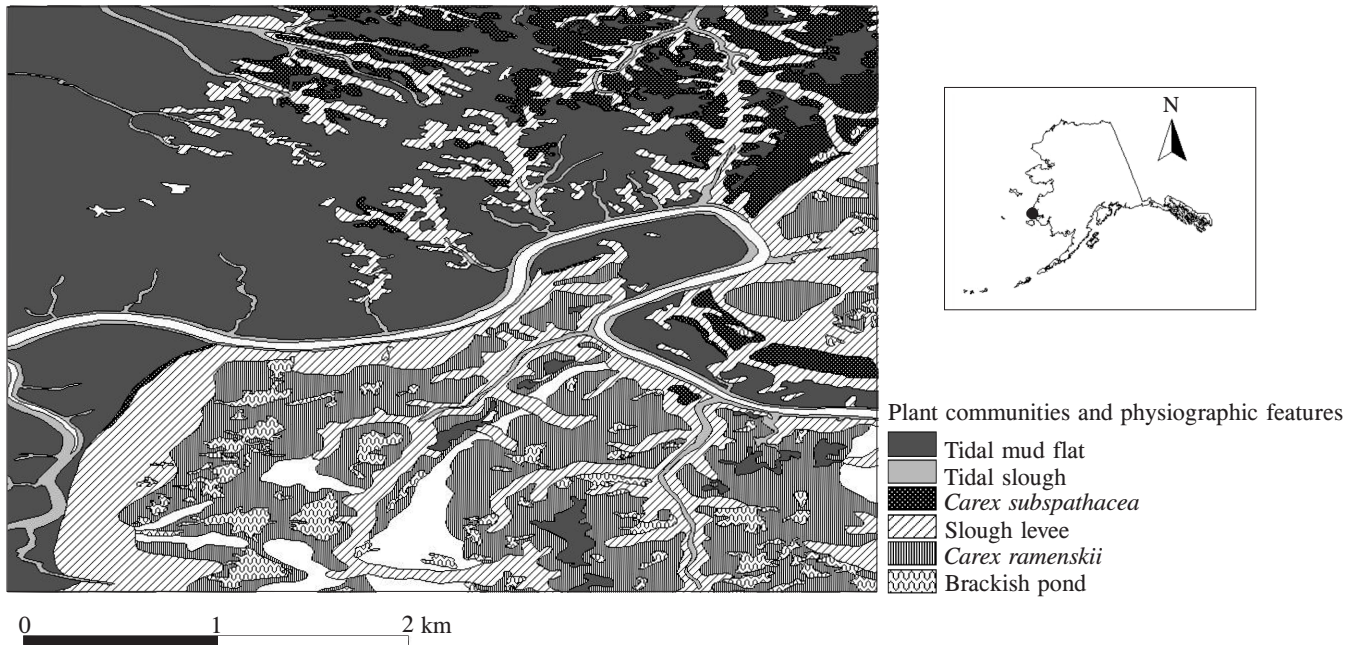


FIGURE 1. Map of physiographic features and the predominant plant communities in the central Tutakoke River black brant colony ($61^{\circ} 20' N$, $165^{\circ} 38' W$). The *Carex subspathacea* community is *ca* 1-3 cm above mean tidal range (MTR) and is flooded during the growing season on monthly high tides; hence, we consider it the most coastal of the three communities. The *Carex ramenskii*-dominated community is *ca* 5 cm above MTR and is flooded infrequently (2-3 times per decade) during the growing season from storm surges of the Bering Sea. The slough levee community experiences the same frequency of tidal inundation as does the *C. ramenskii* community and is *ca* 25 cm above MTR. Map is modified from Jorgenson (2000).

times per decade. This community has the highest plant species richness of the three communities in the Tutakoke area (Kincheloe & Stehn, 1991; Mulder, Ruess & Sedinger, 1996). The grasses *Elymus arenarius*, *Poa arctica*, and *Deschampsia caespitosa* dominate the community. Geese selectively forage on *Triglochin palustris* because of its high concentration of protein relative to cell wall content (Sedinger & Raveling, 1988; Mulder & Ruess, 1998). Slough levee soils are well drained and have lower soil salinities compared with the other plant communities included in this study, and we consider this community the most inland of the three communities.

EXPERIMENTAL DESIGN

We flooded 2-m diameter plots with tidal waters at three different frequencies throughout the growing seasons of 1994-1995. Treatments included plots flooded 1 (F1), 2 (F2), and 4 (F4) times monthly. A brackish-water treatment (BW; frequency: 2 times per month) was included to distinguish the potential effects of salt from those of soil waterlogging on edaphic and vegetation parameters. Together with untreated controls (CT), these five treatments were replicated 3 times within each of the three plant communities previously described. Replicate plots were spatially separated by a minimum distance of 0.5 km throughout the Tutakoke River colony. Plots were flooded with tidal and brackish waters using a gasoline-powered pump and 100 m of collapsible hose. Water for saline treatments was obtained either from the Tutakoke River or from an adjoining tidal slough (total dissolved salts [TDS] $28.3 \pm 0.7 \text{ g L}^{-1}$, $\bar{x} \pm \text{SE}$). Fresh water was transported in 200-litre plastic barrels via a skiff from a freshwater lake 15 km upriver and mixed with tidal waters

for the BW treatments (TDS: $9.9 \pm 1.4 \text{ g L}^{-1}$). Five hundred ± 50 L of water was held on all plots for 1 h during each treatment application by temporarily inserting a 3.25-m-diameter by 40-cm-high Teflon dam into the soil to a depth of 8 ± 3 cm. In both the 1994 and 1995 growing seasons plots were flooded 16 times (F4), 8 times (F2 and BW), and 4 times (F1).

In order to study the interaction between herbivory and flooding, a 0.5 m-diameter permanent enclosure was centred in each plot, in addition to small (15 cm \times 15 cm) temporary enclosures distributed throughout the unenclosed portion of each plot (Table I). Geese could freely graze in the open section of the plots except when we established a temporary dam for 1 hour each time we flooded plots. Permanent enclosures were established to study the bi-annual effects of removing grazing pressure on community growth and composition. Short-term enclosures were used to estimate more precisely plant growth in the *C. ramenskii* and *C. subspathacea* communities because grazing pressure on these communities can be high. We estimated net aboveground primary productivity (NAPP) as the difference between biomass in short-term enclosures and unprotected biomass sampled from independent sites approximately 21 days earlier, divided by the number of days during the interval (McNaughton *et al.*, 1996). We did not establish movable enclosures in the slough levee community, but measured NAPP annually as the difference between biomass within long-term enclosures and biomass within the unenclosed portion of each plot divided by the number of days that vegetation was protected from geese. Geese have little effect on the total standing crop biomass of the slough levee communi-

TABLE I. Sampling dates (day/month) of aboveground biomass. Number of 10-cm × 10-cm turves sampled is in parenthesis.

Community Year	<i>Carex subspathacea</i>		<i>Carex ramenskii</i> meadow		Slough Levee	
	1994	1995	1994	1995	1994	1995
Treatment						
Unexclosed	19/6 (1) 13/7 (1) 3/8 (1)	20/6 (1) 15/7 (1) 1/8 (2)	20/6 (1) 11/7 (2) 2/8 (2)	18/6 (2) 12/7 (2) 30/7 (2)	31/7 (3)	21/6 (2) 14/7 (2) 31/7 (2)
Short-term exclosure	13/7 (1) 3/8 (1)	15/7 (1) 1/8 (1)	11/7 (2) 2/8 (2)	12/7 (2) 30/7 (2)		
Long-term exclosure	19/6 (1) 13/7 (1) 3/8 (1)	20/6 (1) 15/7 (1) 1/8 (1)	20/6 (1) 11/7 (1) 2/8 (2)	18/6 (1) 12/7 (1) 30/7 (1)	30/7 (3)	21/6 (2) 14/7 (2) 31/7 (2)

ty since they selectively feed on *T. palustris*, which comprises only a small proportion (<2%) of the total biomass (Mulder *et al.*, 1996; Mulder & Ruess, 1998). Consequently, short-term exclosures were not used in this community.

EDAPHIC MEASUREMENTS

In situ soil redox profiles were measured using platinum electrodes inserted vertically into the soil to a depth of 3 cm. Measurements were made every 30 min for 1 h before- and 6 h post-flooding treatment application. Platinum electrodes were acid-etched and calibrated using ZoBell reference solutions (100%, 50%, 25% concentrations) prior to measuring each profile (ZoBell, 1946). Values were collected using a hand-held voltmeter and transformed to redox potentials by adding the potential of a Ag^+/AgCl reference probe (+187 mV). Soil pH was measured using a hand-held pH meter on a slurry of soil by adding 25 mL double distilled water (DDO) to a small soil core that had been dried at 60°C. Soil pH in all communities was similar (mean pH 6.5 ± 0.2 ; overall *P*-value >0.6); therefore, we did not adjust redox potentials for soil pH. We averaged redox values measured from three probes inserted in each flooded and non-flooded plot. Our level of replication was at the treatment level (two flooded plots and three non-flooded plots). We could not sample all blocks and replicates at the same time due to logistic constraints. Some of the non-flooded plots in this analysis had been flooded a week prior to making the redox profiles; therefore, we assumed that any effects of flooding on redox potential from the week before were ephemeral. This assumption is likely valid (see RESULTS-EDAPHIC RESPONSES). Soil water content was measured gravimetrically and is expressed as a percentage of wet mass. Soil- and tide-water salinities were measured using a hand-held salinity meter and are presented as total dissolved salts. Soil salinity was measured from a small soil core (2 cm diameter × 5 cm depth) taken from each grazed and exclosed portion of each plot at the end of the 1995 growing season. Wet soils were weighed to the nearest 0.01 g and then dried at 60°C in a field laboratory. Soil total dissolved salts (TDS) was measured by adding 25 mL DDO to create a soil slurry and values were adjusted for soil mass.

At the end of the experiment, we collected one soil core (5 cm diameter × 10 cm depth) from each exclosed and grazed plot to be used for estimating soil carbon and nitrogen mineralization rates. Soil cores were stored in polyethylene bags in a portable cooler and sent to Fairbanks

within 36 h. Aboveground biomass was re-moved down to a depth of 0.25 cm below the soil surface, and soil cores were cut in half vertically; one half was used for soil incubations and the other for initial mineral nitrogen extraction (see below). Fifty ± 3 g of moist soil was incubated in a 497 mL mason jar in the dark at 12°C for 21 days. Soil respiration was measured every 7 d using a Shimadzu 8A gas chromatograph (Kyoto, Japan). Jar atmosphere was allowed to equilibrate to atmospheric CO_2 after each measurement. Respiration rates ($\mu\text{g CO}_2 - \text{C g dwt soil}^{-1} \text{d}^{-1}$) were calculated as the sum of all 7 d fluxes divided by the 21 interval days. Net N mineralization rate ($\mu\text{g N g dwt}^{-1} \text{d}^{-1}$) was calculated as the difference in mineral N ($\text{NH}_4^+ + \text{NO}_3^-$) extracted with 2N KCl on days 21 and 0 of the incubation.

VEGETATION SAMPLING AND ANALYSIS

Aboveground biomass was measured 3 times each season with the exception of the slough levee community where, in 1994, biomass was only sampled at the end of the growing season (Table I). All biomass contained in randomly thrown 10-cm × 10-cm quadrats was clipped to the soil surface, washed in fresh water, sorted to species and standing dead (Hultén, 1990), and dried at $60 \pm 5^\circ\text{C}$ in a field laboratory. Aboveground biomass was redried and weighed to the nearest 0.001 g upon return from the field. We refer to live standing crop biomass as standing crop biomass hereafter. The forage species *C. subspathacea* and *C. ramenskii* were each ground in a size 20 mesh Wiley Mill and analyzed for carbon and nitrogen content using a LECO CNS 2000 autoanalyzer (St. Joseph, Michigan, U.S.A.). All grass species within a community, except *Elymus arenarius*, which is not a forage species, were combined before grinding, and the pooled material was analyzed for its carbon and nitrogen content. Therefore, we do not present data of the nutrient content of individual species of grasses. Species richness is defined as the number of species within each turf sampled within each treatment plot. Species diversity (*H'*) was estimated using the Shannon-Weiner index, where species biomass was used to calculate the proportion of each species within each sample. Statistical analyses were performed on indices calculated from standing crop biomass harvested at the end of the growing season of 1995.

STATISTICAL PROCEDURES

We used a nested split-plot design where replicates (blocks) were nested within each community. Each block

consisted of treatments representing five levels of flooding, and each of these plots was split into three levels (sub-plot) of grazing (grazed, short-term, and long-term enclosures). Live standing crop biomass was averaged if several turves were sampled in order to avoid pseudoreplication (for number of turves sampled see Table I). All analyses were performed using SAS Institute (1990) software. We entered year, time of harvest, flooding treatment, block (replicate), and sub-plots (grazing treatments) as class variables in our ANOVA (PROC GLM) models. *F*-tests for overall treatment variation associated with grazing were tested using the treatment mean squared error (MSE_{graze}) divided by the enclosure \times block \times treatment interaction MSE. *F*-tests for treatment variation associated with flooding were calculated using the treatment mean squared error (MSE_{flood}) divided by the block \times treatment interaction MSE. We partitioned effects of significant interactions ($P < 0.05$) by limiting analyses to a single community type. If an overall treatment effect was significant (at $\alpha < 0.05$), we used Tukey's Honest Significant Difference (HSD) multiple comparisons to examine treatment differences. Model assumptions of variance homogeneity were met by transforming data, $\log_{10}(x + 1)$, where necessary. Percent soil water data were square root transformed to meet model assumptions.

Redox profiles were analyzed using a repeated measures design (PROC MIXED). Treatment and community were entered as fixed effects. Treatment by time interactions were included to test for an overall treatment effect, followed by linear contrasts between flooded and non-flooded treatments if a significant treatment \times time interaction was detected. Within-subject correlation structure was modeled as a compound symmetry (CS) process, and we evaluated this model against other correlation structures using Akaike's Information Criterion. All data presented in text represent the $\bar{x} \pm 1$ SE of non-transformed data.

Results

EDAPHIC RESPONSES

Flooding significantly increased the concentration of dissolved salts in soils of all plant communities (overall treatment effect: $F_{4,8} = 34.5$; $P < 0.0001$). At the end of the growing season of 1995, plots that were flooded weekly (F4) had soils that had two-, three-, and six-fold increases in the concentrations of TDS when compared to control plots in the *C. subspathacea* lawn, *C. ramenskii* meadow, and slough levee communities, respectively (Figure 2). Herbivory exacerbated these effects (overall enclosure effect: $F_{1,24} = 8.9$; $P = 0.007$) in the *C. subspathacea* community, where soils in enclosed F4 plots had a mean TDS concentration of 15.0 ± 0.4 in contrast to 27.8 ± 3.1 g g H_2O^{-1} g dwt soil $^{-1}$ in grazed soils.

Flooding tended to decrease the redox potential of soils, although this effect was not significant in the overall model (linear contrast: $F_{1,185} = 3.5$; $P = 0.064$). However, flooding had a strong effect on the redox potential of soils in the slough levee community (linear contrast: $F_{1,58} = 20.3$; $P < 0.0001$) (Figure 3). Although redox potentials were highest in the slough levee community, we caution readers that community differences may exist, because

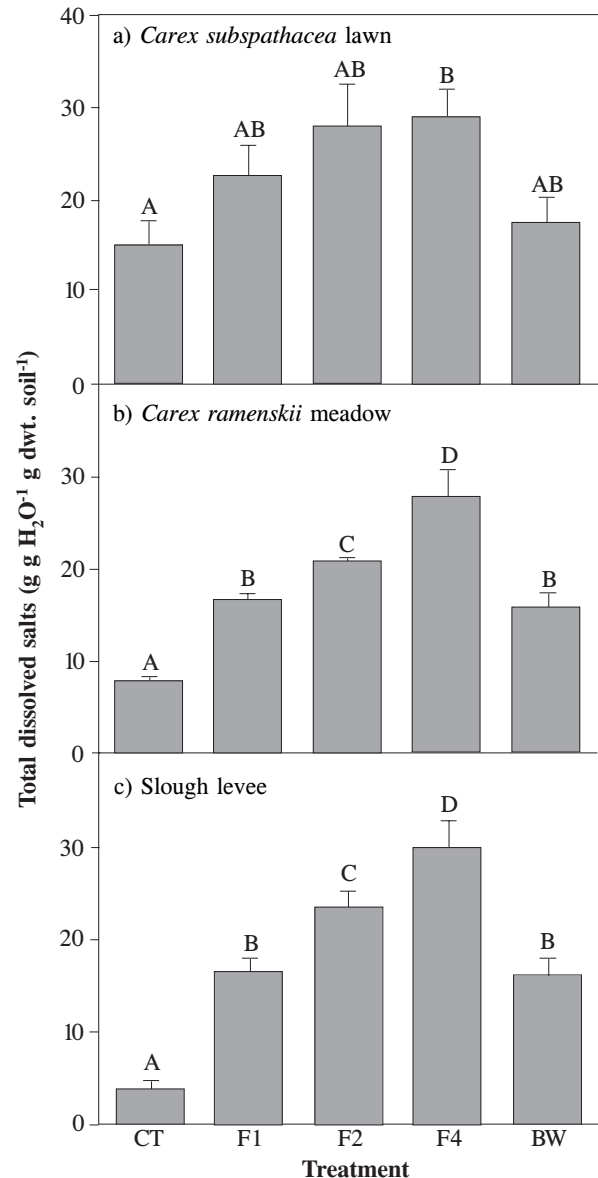


FIGURE 2. The effect of artificial tidal flooding on soil salinity on a) *Carex subspathacea* grazing lawns, b) *C. ramenskii*-dominated meadows, and c) a slough levee community. Treatment abbreviations are as follows: control (CT); flood 1 time mo⁻¹ (F1); flood 2 times mo⁻¹ (F2); flood weekly (F4); and flood 2 times mo⁻¹ with brackish water (BW). Data represent $\bar{x} \pm$ SE. Total dissolved salts differed among treatments (overall treatment effect: $F_{4,8} = 34.5$; $P < 0.0001$). Treatments with the same letter are not significantly different at $\alpha > 0.05$ (Tukey's HSD).

profiles were not made among communities at the same time of the growing season because of logistical constraints. Thus, community differences may represent seasonal differences in soil redox potentials. Nevertheless, apparent community differences in redox potentials are consistent with the patterns of soil moisture. Percent soil water content was not affected by flooding treatments one week following treatment application ($P > 0.7$). Similarly, protection from herbivores did not affect soil water content ($P > 0.7$). Percent soil water content in control plots was lowest in the slough levee community ($58.3 \pm 3.5\%$), intermediate in the *C. subspathacea* community ($61.1 \pm 5.5\%$),

and highest in the *C. ramenskii* meadow ($63.4 \pm 5.3\%$) (community effect: $F_{2,89}=6.2$; $P=0.078$).

Soil respiration rates did not significantly differ among flooding treatments (overall treatment effect: $F_{4,24}=0.1$; $P>0.9$) (Table II). Soils incubated from control plots in the *C. ramenskii* meadow had the highest respiration rates ($80.3 \pm 3.3 \mu\text{g CO}_2\text{-C g dwt soil}^{-1} \text{d}^{-1}$) (community effect: $F_{2,89}=7.6$; $P=0.0014$). Respiration of soils from control plots within the *C. subspathacea* ($37.7 \pm 13.2 \mu\text{g CO}_2\text{-C g dwt soil}^{-1} \text{d}^{-1}$) and slough levee communities ($29.1 \pm 8.4 \mu\text{g CO}_2\text{-C g dwt soil}^{-1} \text{d}^{-1}$) were similar. We did not detect an overall grazing effect on soil respiration rates ($P=0.14$). However, soils collected from long-term exclusions in the *C. subspathacea* community had higher ($80.2 \pm 13.8 \mu\text{g CO}_2\text{-C g dwt soil}^{-1} \text{d}^{-1}$) respiration rates than soils from grazed plots when averaged across all treatments ($55.6 \pm 8.1 \mu\text{g CO}_2\text{-C g dwt soil}^{-1} \text{d}^{-1}$) ($F_{1,4}=4.79$; $P=0.094$).

We detected a small difference in nitrogen mineralization rates between plant communities ($F_{2,89}=3.24$; $P=0.049$). Nitrogen mineralization rates were highest in the *C. subspathacea* and slough levee communities (0.23 ± 0.04 and $0.21 \pm 0.03 \mu\text{g N g dwt soil}^{-1} \text{d}^{-1}$, respectively) and lowest in the *C. ramenskii* meadow ($0.13 \pm 0.01 \mu\text{g N g dwt soil}^{-1} \text{d}^{-1}$). Neither flooding nor

grazing had an effect on nitrogen mineralization within a community (P -values >0.7).

ABOVEGROUND RESPONSES

Flooding had no effect on standing crop biomass in the *C. subspathacea* or *C. ramenskii* communities (Figure 4a,b). However, weekly flooding reduced standing crop biomass in the slough levee community relative to other treatments (Figure 4c) (treatment effect: $F_{4,28}=3.77$; $P=0.024$). Standing dead biomass was greater in both the slough levee and *C. ramenskii* F4 treatment plots when compared to CT plots at the end of the growing season of 1995. Standing dead in F4 and CT treated plots averaged 264 and 152 g dwt m^{-2} in the slough levee community and 291 and 147 g dwt m^{-2} in the *C. ramenskii* meadow. No treatment differences in NAPP were detected in any of the three communities in 1995 (overall treatment effect: $F_{4,8}=1.7$; $P=0.24$). NAPP varied significantly among the three communities ($F_{2,119}=9.7$; $P=0.0002$). NAPP of *C. ramenskii* meadows averaged 2.1 g dwt $\text{m}^{-2} \text{d}^{-1}$ and differed from the productivity of *C. subspathacea* lawns, which averaged 0.47 g dwt $\text{m}^{-2} \text{d}^{-1}$. NAPP of the slough levee community did not differ from those of the other two communities and averaged 1.3 g dwt $\text{m}^{-2} \text{d}^{-1}$.

The negative effect of flooding on the slough levee community resulted from a decline of woody vegetation, predominantly *Salix ovalifolia*, which averaged 23.7 ± 8.5 g dwt m^{-2} in F4 plots, compared to 138.7 ± 22.1 g dwt m^{-2} in control plots in 1995. Thus, the proportion of woody to total biomass decreased in the F4 treatment (0.19) relative to CT plots (0.63). However, the biomass of grass in F4 plots increased (76.0 ± 18.2 g m^{-2}) when compared to controls (55.8 ± 16.9 g m^{-2}). Neither this trend nor treatment effects on the slough levee community were apparent by the end of the growing season of 1994.

Flooding did not affect the plant species richness of any community ($P=0.225$); however, species diversity of the slough levee community varied among flooding treatments ($F_{4,59}=7.1$; $P=0.026$), tending to be greater at higher soil salinities. Changes in community diversity likely represent a shift in the evenness of the slough levee community. We detected no effect of flooding on the species diversity of *C. ramenskii* meadows ($F_{4,59}=1.4$; $P=0.25$), and the *C. subspathacea* community was monospecific.

Grazing significantly reduced standing crop biomass in the *C. subspathacea* community (exclusion effect: $F_{2,28}=179.4$; $P<0.0001$). Following protection from grazing for two growing seasons, standing crop biomass

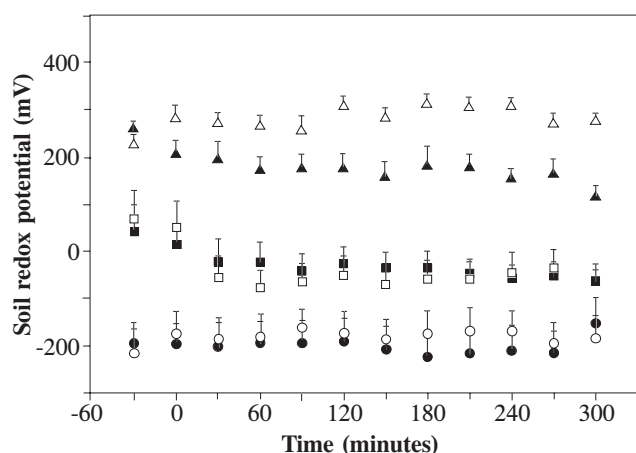


FIGURE 3. Differences in redox potential (mV) profiles between flooded and non-flooded soils. Open symbols represent non-flooded soils and closed symbols flooded soils. Symbols represent redox profiles from the slough levee community (triangles); *C. ramenskii*-dominated meadows (squares); and *C. subspathacea* lawns (circles). Measurements were made 30 minutes prior to flooding plots (-30), while plots were flooded (0), and every 30 minutes for 5 hours after water was released from the temporary dams. Bars represent 1 SE.

TABLE II. Soil respiration rates ($\mu\text{g CO}_2\text{-C g dwt soil}^{-1} \text{d}^{-1}$) from 21-day laboratory incubation of soils sampled from field plots after 2 years of artificial tidal flooding and protection from grazing. Treatments are as follows: flood monthly (F1), flood bi-weekly (F2), brackish water (BW), flood weekly (F4), and control (CT). No differences among flooding treatments ($F_{4,89}>0.1$; $P=0.94$) or between soils from grazed and excluded treatments were found ($F_{1,89}=1.9$; $P=0.18$). Data represent the $\bar{x} \pm \text{SE}$.

Community Treatment	<i>Carex subspathacea</i>		<i>Carex ramenskii</i>		Slough Levee	
	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded
F1	66.2 \pm 21	77.3 \pm 50	60.5 \pm 15	56.2 \pm 6	38.1 \pm 19	36.0 \pm 5
F2	68.7 \pm 13	68.7 \pm 38	43.5 \pm 6	69.7 \pm 16	28.6 \pm 4	41.1 \pm 11
BW	54.3 \pm 20	70.6 \pm 21	42.6 \pm 8	57.7 \pm 13	43.1 \pm 17	57.2 \pm 9
F4	51.1 \pm 27	88.7 \pm 34	52.0 \pm 8	59.1 \pm 12	32.2 \pm 11	32.4 \pm 8
CT	37.7 \pm 13	95.8 \pm 28	80.3 \pm 3	42.5 \pm 13	29.1 \pm 8	28.9 \pm 7

of *C. subspathacea* did not differ from that of *C. ramenskii* meadows ($F_{1,28}=0.53$; $P=0.47$). We could detect no overall enclosure effect on either the *C. ramenskii* or slough levee

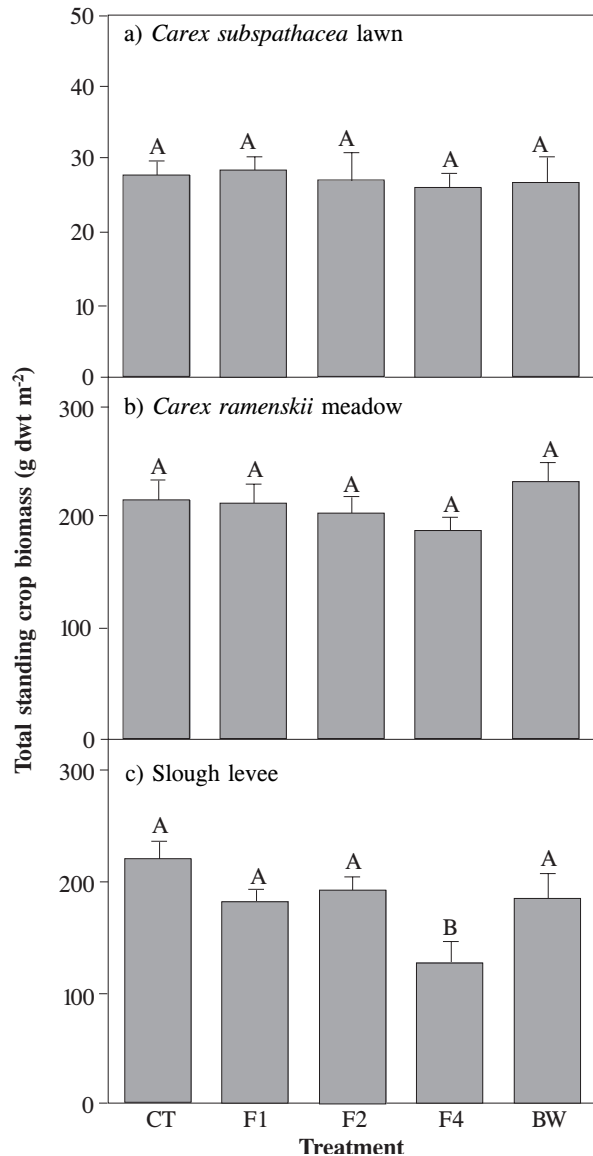


FIGURE 4. Standing crop biomass following two growing seasons of treatment application. Biomass represents that harvested at the end of the growing season of 1995. Treatment abbreviations follow those used in Figure 2a-c. Standing crop biomass differed among treatments within the slough levee community (treatment effect: $F_{4,28}=3.77$; $P=0.024$). Treatments with the same letter are not significantly different at $\alpha=0.05$ (Tukey's HSD). Please note axis-scale differences between Figures 3a-c.

communities. However, *T. palustris* biomass within long-term enclosures in the slough levee community averaged 8.1 ± 1.0 g dwt m⁻² compared to 3.9 ± 0.5 g dwt m⁻² in unprotected plots. It is noteworthy that human trampling around plots in *C. ramenskii*-dominated meadows induced a character state of *C. ramenskii* that made it indiscernible from *C. subspathacea*. This likely reduced grazing pressure on our *C. ramenskii* plots because geese foraged selectively on the surrounding trampled vegetation (B. T. Person, pers. observ.).

Flooding affected both the nitrogen concentration and carbon to nitrogen ratio (C:N) of aboveground tissues of *C. ramenskii* and *C. subspathacea* collected from their respective communities and of grass species collected from within the slough levee community (all treatment P -values < 0.04). The nitrogen content of these graminoids was highest when they were growing in saline soils (Table III). Similarly, C:N ratios were lower in saline treatments. Grazed *C. subspathacea* had increased nitrogen content ($F_{2,8}=236.4$; $P<0.0001$) and a decreased C:N ratio ($P<0.0001$) compared to protected vegetation. This effect reflects differences between vegetation in long-term enclosures and unprotected *C. subspathacea* lawns.

Discussion

The structural and functional characteristics of plant communities that we focused on in this experiment are resistant to short-term effects of changes in tidal inundation. We did not detect a reduction of aboveground biomass until soil salinity was increased to over six times that of ambient salinity. This response occurred in only one of three communities studied and resulted largely from a reduction in *S. ovalifolia*, which occurs as a prostrate (5 ± 2 cm high) stoloniferous plant. Iacobelli and Jefferies (1991) reported the death of *S. brachycarpa* stands in response to increased soil salinity, and our results also suggest that the distribution of *Salix* spp. within salt marshes is limited by soil salinity. However, the slough levee community partially compensated for reduced standing biomass through an increase in the biomass of grasses, suggesting that NAPP of communities containing grasses is resilient to short-term increases in tidal inundation. Our results are likely representative of changes that would occur following long-term increases in flooding frequency. Acute salinity stress leads to both a rapid reduction in standing biomass of glycophytes and a rapid loss of salt-intolerant species from a community (Jackson & Drew, 1984; Wainwright, 1984). However, over several growing seasons these effects are

TABLE III. Nutritional characteristics of key forage species of geese and grass pooled from the slough levee community following 2 years of artificial tidal flooding. Treatments are as follows: flood monthly (F1), flood bi-weekly (F2), brackish water (BW), flood weekly (F4), and control (CT). C:N represents the carbon to nitrogen ratio of foods and is presented as an index of the fibre content. Letters shared within columns are not significantly different at $\alpha > 0.05$, Tukey's HSD method.

Species	<i>Carex ramenskii</i>		Grasses		<i>Carex subspathacea</i>	
	% N	C:N	% N	C:N	% N	C:N
F1	1.2 ± 0.05 ab	35.9 ± 1.7 ab	1.02 ± 0.06 ab	42.2 ± 2.9 ab	2.6 ± 0.1 ab	14.8 ± 0.7 a
F2	1.3 ± 0.05 b	33.3 ± 1.3 ab	1.01 ± 0.06 ab	42.5 ± 3.0 ab	2.6 ± 0.1 ab	16.9 ± 1.8 a
BW	1.3 ± 0.03 b	33.0 ± 0.8 a	0.87 ± 0.03 b	49.8 ± 2.0 a	2.4 ± 0.1 b	18.9 ± 1.7 a
F4	1.5 ± 0.07 c	29.0 ± 1.4 b	1.23 ± 0.04 a	34.5 ± 1.3 b	3.0 ± 0.2 a	13.7 ± 0.9 b
CT	1.1 ± 0.05 a	38.0 ± 2.0 ab	0.86 ± 0.09 b	49.9 ± 3.4 a	2.6 ± 0.1 ab	16.6 ± 1.1 a

often reversed in species that survive acute saline stress, potentially through selection for salt-resistant ecotypes (Wainwright, 1984; Neumann, 1997).

Communities with a diverse assemblage of functional groups are likely to be buffered against disturbances (Tilman & Downing, 1994; Chapin *et al.*, 1997; Hooper & Vitousek, 1997). We cannot attribute the reduction in woody biomass to salt intolerance versus changes in competitive interactions with grasses for light and nutrients, because the scope of our experiment did not investigate competitive interactions among species within the three communities studied. Inland marsh communities are structured through competitive interactions (Bertness, 1991; Bertness, Gough & Shumway, 1992; Pennings & Callaway, 1992), and competition between woody and grass vegetation for nutrients and light may have contributed to the decreased performance of *S. ovalifolia* in addition to its apparent salt intolerance. Dormann, Van Der Wal and Bakker (2000) found that the distribution and production of some species inhabiting late-successional communities were limited by light competition. We do not believe that competition for light led to a reduction in *S. ovalifolia* because this species persists beneath the grass canopy. Thus, if competition for light reduced its performance one would predict an overall increase in the NAPP of the F4 plots (*i.e.*, overcompensation) rather than a compensatory response by grasses. We suggest that the compensatory response by grasses, predominately *Poa arctica* and *Deschampsia caespitosa*, occurred from reduced competition with *S. ovalifolia* for nutrients. The efficiency of ammonium uptake by plants growing in inland saltmarsh communities is often inhibited by saline soils (Bradley & Morris, 1991; Chambers, Mozdzer & Ambrose, 1998). Graminoid life history traits enable a rapid response to and exploitation of changes in resource availability because the growth rates of graminoids are higher than those of woody plants (Grime, 1977). Grasses growing under the most saline treatments likely responded to changes in nutrient competition following the reduction of *S. ovalifolia*. Thus, variation in the life history characteristics among functional groups within the slough levee community stabilized the productivity of this community.

Aboveground tissues of graminoids growing in the most saline treatments had higher nitrogen concentration than tissues of graminoids growing at lower salinity. Increased leaf nitrogen content can result from differences in plant allometry or from the accumulation of osmotic solutes (Brown & Hellebust, 1977; Story & Wyn Jones, 1977; Jefferies & Rudmik, 1991; Ruess *et al.*, 1997). We controlled for differences in aboveground allometry by entering standing biomass as a covariate in our ANCOVA model and still detected an increase in N content in these tissues. Ruess *et al.* (1997) attributed increased nitrogen content of *C. ramenskii* tissues grown in saline soils to the accumulation of nitrogen-based osmoregulatory molecules. Thus, graminoids likely acclimated to salinity stress through a physiological response.

Biomass turnover may have been greater in *C. ramenskii* meadows that experienced the most saline treatments. For example, there was 112 g m⁻² more standing dead biomass in slough levee F4 plots when compared to the CT plots; this accounts for the treatment differences

in live biomass observed in this community. However, standing dead biomass in *C. ramenskii* F4 plots was 144 g m⁻² greater than that in CT plots, and standing live biomass did not differ between these two treatments (Figure 4b). This suggests that NAPP was higher in F4 plots, although our estimates of NAPP conflict with this finding. If leaf life-span is shorter in this community, we may have underestimated NAPP following our sampling interval protocol (Bakker & Loonen, 1998). Younger leaf tissues have both higher nitrogen concentrations and higher water-use efficiencies (Kotani & Jefferies, 1987; Oosterheld & McNaughton, 1991), and increased leaf turnover suggests that the resilience of this community may be high. Increased leaf turnover offers an additional mechanism through which community productivity is maintained under increased tidal inundation. This stand-level response could lead to an increase in the flow of nutrients to herbivores because young tissues have higher nutritive values, and NAPP may have been higher in the *C. ramenskii* F4 plots than our measurements reflect (Reich, Walters & Ellsworth, 1992; Cebrián & Duarte, 1994).

Neither soil respiration nor nitrogen mineralization was influenced by flooding treatments, suggesting either that microbial populations were resistant to changes in soil salinity and redox potential or that changes in microbial community structure led to stabilizing effects on soil carbon and nitrogen processing rates. Higher quality litter has been shown to decompose more rapidly, and had we followed aboveground inputs from the growing season of 1995 one would predict that respiration and N mineralization rates would have been higher in F4 plots, because the nitrogen concentration was increased in aboveground graminoid tissues (Ruess, Hik & Jefferies, 1989). Our results differ from those of Van Wijnen, van der Wal, and Baker (1999), who found decreased carbon and nitrogen mineralization rates following herbivory in a temperate salt marsh. We could detect no effect of grazing on either of these parameters following grazing.

Although we detected a decrease in soil redox potential following our flooding treatments (Figure 3), we believe the aboveground responses occurred as a result of increased soil salinity. Soil salinity in our BW and F1 treatments did not differ (Figure 2). Linear contrasts between these two treatments provided a basis for decoupling the potential effects of soil waterlogging versus increased salinity on above- and belowground processes, because soil salinity did not differ between these treatments and soils in BW plots were inundated twice as often as were F1 plots. We detected no differences between these two treatments in any two variable we measured. However, when tidal surges occur they inundate soils for up to 6 hours, and these soils remain waterlogged for several days following such events (B. T. Person, pers. observ.). Thus, the potential effect of soil waterlogging associated with storm surges remains largely untested at the intensity that occurs naturally.

Herbivory decreased the availability of key forage species in the slough levee community and maintained the *C. subspathacea* community as a grazing lawn. Protection from herbivores over 2 years allowed *T. palustris* biomass to double. *Triglochin palustris* biomass was greater in F4

plots ($4.3 \pm 0.3 \text{ g m}^{-2}$) than in CT plots ($3.2 \pm 0.5 \text{ g m}^{-2}$), although this effect was not statistically significant. This likely reflects changes in resource competition with neighbouring plants, rather than a positive effect on growth or recruitment associated with increased soil salinity or waterlogging. Grazing removed over 95% of annual NAPP of the *C. subspathacea* community, while protection from herbivores dramatically changed the structure of this community (Figure 5). *Carex subspathacea* within long-term exclosures more closely resembled *C. ramenskii* than unexclosed *C. subspathacea*. Person *et al.* (2003) present ecological evidence that *C. ramenskii* and *C. subspathacea* are conspecifics whose morphology is controlled by grazing pressure. They describe “grazed hot-spots” of the *C. ramenskii* community that metastasize into grazing lawns that favour the growth, recruitment, and fecundity of young geese in this population. The reason brant select these forage sites is poorly understood but may be tied to spring snow break-up patterns (Ruess *et al.*, 1997). We suggest that hypersalinization of soils may also be a contributing factor influencing food selection. We found elevated leaf nitrogen content of graminoids growing in saline soils, and we know geese selectively graze forage high in nitrogen content (Sedinger & Raveling, 1988). Because flooding did not have an effect on standing crop biomass of *C. ramenskii* meadows we suspect that herbivory may be the primary force that limits its lower zonation. This conclusion is contrary to descriptive studies that concluded these community boundaries were maintained by a salinity gradient (Kincheloe & Stehn, 1991). *Carex ramenskii* meadow diversity, aboveground biomass, and NAPP were not affected by a three-fold increase in soil salinity.

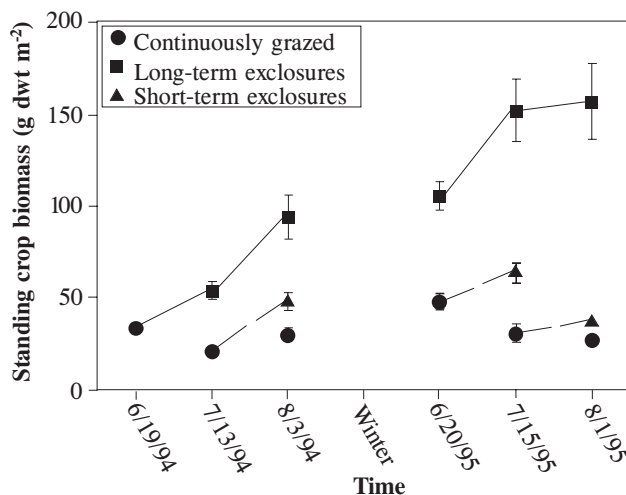


FIGURE 5. Aboveground biomass of *C. subspathacea* swards over two growing seasons of natural goose grazing pressure. Symbols represent continuously grazed swards (circles); standing biomass following *ca* 21 days of protection from herbivores (triangles); and biomass within long-term exclosures (squares). $\bar{x} \pm \text{SE}$.

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