Soil carbon in a grazed and ungrazed tidal marsh in the St. Lawrence Estuary

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Abstract

Soil carbon storage is an important ecosystem service of tidal salt marshes, but is this service maintained under an agricultural use? Sheep grazing on Quebec's Île Verte, in the upper estuary of the St. Lawrence River, provided an opportunity to examine whether seven summers of grazing negatively affected soil carbon storage in high latitude tidal salt marshes. I compared plant biomass and soil properties in grazed and ungrazed sections. Above- and below-ground production was assessed through plant litter, end-of-season standing crop, and roots and rhizomes in ingrowth core measurements. Edaphic properties were measured from 10 cm soil cores. The grazed marsh had higher soil carbon density and belowground biomass, yet lower aboveground biomass. Greater soil carbon density was attributable to grazing, as at this latitude, marsh soil remained frozen through April. Greater solar exposure of grazed soils during spring and summer allowed for warmer soils and thus a longer growing season for belowground growth.

Résumé

Le stockage de carbone dans les sols est un service important dans l'écosystème des marais salants, mais ce service est-il maintenu lors de l'utilisation agricole? Des moutons broutant sur l'Île Verte, dans l'estuaire supérieur du fleuve du Saint Laurent, nous donnent l'occasion de mesurer si sept étés de broutage ont négativement affecté le stockage de carbone de sol des marais salants de latitude élevée. J'ai comparé des biomasses et des propriétés de sol dans les sections broutés et intactes. La production à la surface et souterraine de la litière végétale sont évaluées par la récolte à la fin de la saison, et les racines et rhizomes dans des mesures d'échantillons de sols. Des propriétés édaphiques ont été mesurées à partir d'échantillons de sol de 10 cm. Le marais brouté avait une densité plus élevée de carbone de sol et de biomasse souterraine, mais une baisse de biomasse en surface. Une plus grande densité de carbone de sol était attribuable au pâturage, comme à cette latitude, le sol de marais reste gelé jusqu'en avril. Pendant le printemps et l'été, une plus grande exposition solaire des sols réchauffe les sols et apporte une plus longue période de croissance végétale.

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Table of Contents

List of Tables

List of Figures

List of Appendices

1. Introduction

Humans derive many benefits from the natural environment, termed ecosystem services. Daily (1997) defined ecosystem services as "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life." This concept of ecosystem services has since been elaborated as the multifaceted indirect and direct benefits that people receive from ecosystem functions of natural and semi-natural ecosystems (e.g., Costanza et al., 1997; Wilson and Carpenter, 1999; de Groot et al., 2002; Farber et al., 2002; Wilson and Howarth, 2002).

Tidal salt marshes, wetlands flooded by saline waters, provide many ecosystem services such as nutrient cycling, flood mitigation, and aesthetics (Sather and Smith, 1984; Keddy, 2000; Mitsch and Gosselink, 2000). Vegetation uptakes nutrients (Comin et al., 1997), dampens wave intensity (Christiansen et al., 2000; Leonard and Reed, 2002), and provides habitats for nesting and migratory birds (Reed and Moisan, 1971; Weller, 1999). Tidal salt marsh soils are sinks for metals (Giblin et al., 1980; Baars et al., 1987; Bricker, 1993; Hung and Chmura, 2006; Chmura and Hung, 2007) and carbon (Connor et al., 2001; Chmura et al., 2003) and release minimal methane, a greenhouse gas commonly released from terrestrial soils and freshwater wetlands (Bridgham et al., 2006). The purpose of this study is to document soil carbon density in a Quebec salt marsh on the St Lawrence River estuary, and examine the impact of sheep grazing on the density of soil carbon in that marsh.

1.1. Primary productivity in tidal salt marshes

Tidal flooding is the primary control of the abiotic conditions in a salt marsh. Tides contribute and remove nutrients for plant growth (Valiela et al., 1978; DeLaune et al.,

1981). The sediment deposited from flooding tides and organic matter accumulation drive vertical accretion, keeping marsh elevations in step with sea level rise (Chmura et al., 2001; Chmura and Hung, 2004). Sediment deposition varies among marshes due to differences in the sediment load in tidal water and hydroperiod. Stem density of vegetation also affects sedimentation rates (Christiansen et al., 2000). Both tidal inputs of nutrients and sediment burial of vegetation that sequesters nutrients affect marsh production (Craft et al., 1988). Hydroperiod varies with elevation, thus vegetation varies with elevation within a tidal salt marsh. On the Atlantic coast of North America, *Spartina alterniflora* dominates the lower elevations (low marsh) and in many regions is bordered by *Spartina patens* at higher elevations (high marsh).

Murphy and Moore (*in preparation*) recently reviewed wetland productivity and noted that salt marshes have the highest belowground production of all wetlands. Without the inclusion of the belowground component, studies on salt marsh productivity and hence soil carbon storage is greatly underestimated.

The majority of salt marsh productivity studies have focused on the *S. alterniflora* zone (e.g. Nixon, 1980; Chambers et al., 1992; Odum, 2000); yet *S. patens* dominates many tidal salt marshes north of 42°N (Silander and Antonovics, 1979). Understanding the ecological processes influencing *S. patens*' productivity is important for a more complete assessment of carbon storage potential of tidal salt marshes. Several initial studies of *S. patens* production report only the aboveground component (Linthurst and Reimold, 1978; Hopkinson et al., 1978; White et al., 1978). An exception is the study by Valiela et al. (1976), who reported that 80% of *S. patens*' annual production in Massachusetts was belowground. Later studies of other marshes did consider the belowground component: Schubauer and Hopkinson (1984) in Georgia, Connor and

Chmura (2000) in New Brunswick, and Windham (2001) in New Jersey. Belowground production varied widely with climatic conditions and porewater chemistry, particularly salinity, NH_4-N, PO_4-P, sulfides, and pH (Burdick et al., 1989). Studies on Bay of Fundy salt marshes demonstrate the variability that exists. Belowground biomass of the high marsh was 45% of total live plant biomass near the mouth of the Bay (Connor and Chmura, 2000) to 86% near the head of the Bay (Gordon et al., 1985).

Root distribution reflects nutrient availability and soil water conditions (Gregory, 2006). The formula, $Y = 1-\beta^d$, where Y is the proportion of roots between 0 and 1, d is the depth from soil surface, and β is the fitted coefficient, produces an index that reflects vertical distribution of belowground biomass (Gale and Grigal, 1987; Jackson et al., 1996). The magnitude of the β value increases as the proportion of roots at depth increases. In northern climates, low soil temperatures at depth along with anaerobic conditions limit nutrient availability and hence root growth. The majority of *S. patens* roots concentrates in the top 10 cm with few live roots found below 30 cm depth (Connor and Chmura, 2000).

Saline soils present a stress to growth. The challenge of osmoregulation in saline soils is thought to drive plant demand for nitrogen (Crain, 2007) because nitrogen-based amino acids play a critical role in this process (Jefferies, 1981). Thus, increasing nitrogen availability would aid in salinity tolerance and should increase production. Aboveground growth of *S. patens* increased with nitrogen fertilization, but not with phosphorus fertilization (Wigand et al., 2004; Crain, 2007). Valiela et al. (1976) observed that *S. patens* root biomass decreased with nitrogen fertilization, while a later study by Wigand

et al. (2004) did not detect a significant difference with either nitrogen or phosphorus addition.

Salt marsh primary productivity is further limited by nitrogen (Valiela and Teal, 1979; Jefferies and Perkins, 1977; Kiehl et al., 1997; Crain, 2007) because high sulfide concentrations in anaerobic sediments inhibits NH_4-N uptake (Koch and Mendelssohn, 1989; Koch et al., 1990). The nitrogen mineralization rate is controlled by levels of oxygen, pH, and soil temperature (Keddy, 2000). At a given level of oxygen and threshold temperature, generally 5ºC (Rabenhorst, 2005), soil microbial communities are stimulated to decompose organic matter, which releases nutrients into soil water (porewater) for plant use (Pregitzer and King, 2003).

Biomass turnover contributes to the nutrients needed for production and the above- and belowground biomass turnover rates decrease with latitude (Linthurst and Reimold, 1978; Gallagher and Plumley, 1979). In contrast, tissue nitrogen appears to increase with latitude, which could be attributed to a multitude of climatic factors including a short growing season that requires faster uptake of available nitrogen, porewater salinity, and herbivory (Siska et al., 2002). Low soil nitrogen pools resulting in low decomposition rates and trapping nitrogen in peat could also contribute to nitrogen concentration in biomass. Wilson and Jefferies (1996) showed that the standing crop from soils with a low total nitrogen pool had higher percent of nitrogen than the standing crop in soils with high total nitrogen.

1.2. Impacts of vertebrate grazing on salt marshes

Research on vertebrate grazing of salt marshes has had three primary foci: 1) herbivore's plant selectivity and resultant changes in plant community composition and productivity,

2) modifications to soil processes, and 3) changes to nutrient cycling. Herbivores preferentially consume some species and influence a plant species' ability to compete with changes in light and nutrient levels (Drent and van der Wal, 1999; Huisman et al., 1999). Changes in plant community structure factor into rates of carbon and nutrient cycling. As a result, much research had been devoted to understanding the role of herbivores in salt marsh primary production (e.g., Jefferies et al., 1979; Cargill and Jefferies, 1984; Bazely and Jefferies, 1986; Hik et al., 1992; Morris and Jensen, 1998; van Wijnen et al., 1999; Kiehl et al., 2001; Jefferies and Rockwell, 2002; Bakker et al., 2004; Kuijper and Bakker, 2005; Jefferies et al., 2006). Simultaneous above- and belowground production measurements are few, partly because of methodology limitations. Many studies only focused on the observable aboveground component, even though herbivory affects above- and belowground processes.

Most research on livestock herbivory has been based in Europe because of the long history of using salt marshes as pastures there (Ranwell, 1961; Gray, 1972; Ranwell, 1972; Bakker, 1978; Bakker et al., 1993). Light to moderate sheep and cattle grazing was suggested as a conservation strategy to maintain a desired landscape for migratory geese habitat and species diversity (Bakker, 1985; Pehrsson, 1988; Bakker et al., 1993; Bernhardt and Koch, 2003; Bouchard et al., 2003; Bos et al., 2005). Herbivory-induced changes in plant community and species diversity were suggested to be manifestations of changes in plant canopy heterogeneity from a decrease in dominant species and litter reduction (Ranwell, 1961; Jensen, 1985; Bakker and de Vries, 1992; Kiehl et al., 1996; Berg et al., 1997; Olofsson and Oksanen, 2002; Person and Ruess, 2003; Tessier et al., 2003). Disturbance by sheep was less than cattle because of their grazing behaviour (Jensen, 1985). Sheep graze selectively, leading to plant canopy micropatterns

(differences in plant heights), while cattle are generalists often uprooting plants from the soft substrate. Without grazing, the tall canopy of dominant species prevents colonization of annual species that require light provided in bare patches (Bakker, 1985; Bakker and de Vries, 1992; van der Wal et al., 2000). The percentage of light reaching the soil surface positively correlated to the amount of standing crop consumed. Geese preferred to graze in areas of less dense vegetation because high light competition in dense biomass areas resulted in the dominance of tall less palatable species over smaller more palatable species (Huisman et al., 1999; van Oene et al., 1999).

Geese grazing in arctic and sub-arctic salt marshes of North America has been fairly well studied (e.g., Cargill and Jefferies, 1984; Bazely and Jefferies, 1986; Ruess et al., 1989; Hik and Jefferies, 1990; Srivastava and Jefferies, 1996; Wilson and Jefferies, 1996; Person and Ruess, 2003; Jefferies et al., 2006). While geese can deplete biomass of preferred species, geese grazing has been shown to increase net aboveground primary productivity (NAPP), which was approximately 80% higher in plots grazed by lesser snow geese, *Chen caerulescens caerulescens* (Cargill and Jefferies, 1984). One rationale for a higher total NAPP in grazed *Puccinellia phryganodes* was the maintenance of the early-season percent nitrogen in the grazed plant biomass throughout the growing season; while the percent nitrogen in the ungrazed biomass declined (Hik and Jefferies, 1990; Hik et al., 1991). Yet, the ability of *P. phryganodes* to maintain a high nitrogen content depended on grazing starting date, period, duration, frequency, and recovery intervals between grazing periods. Belowground production was not affected (Cargill and Jefferies, 1984) unless geese grubbing occurred before shoot production. The latter resulted in a decline in primary productivity (Srivastava and Jefferies, 1995, 1996). Hik

and Jefferies (1990) also found that geese grazing early in the growing season resulted in a spike of belowground biomass, which tampered off as grazing continued.

Studies of grazing by other wild vertebrates centred on the impacts of non-native species, such as nutria (Nyman et al., 1993; Taylor et al., 1994; Taylor and Grace, 1995; Ford and Grace, 1998a,b; Gough and Grace, 1998a,b) and feral horses (Turner, 1987, 1988; Hay and Wells, 1991; Furbish and Albano, 1994; Reader and Craft, 1999). The authors of these studies suggested that grazing was detrimental to salt marsh production and stability. However, these studies did not measure the influence of grazing on porewater chemistry, including salinity, which is one of the most important constraints on salt marsh production (Ranwell, 1972; Adam, 1990). By removing a large amount of aboveground cover, grazing increases light penetration to the soil, lowers soil moisture, and thus increasing soil salinity (Srivastava and Jefferies, 1996; Ford and Grace, 1998a; Person and Ruess, 2003). Hypersaline conditions, resulting from a combination of naturally saline soil, infrequent inundation, and high evapotranspiration, can occur in high and low latitude salt marshes. While a sparse plant cover would lower transpiration and thus reduce soil salinity at depth, high surface soil salinity could deter plant colonization. In a Massachusetts salt marsh, bare patches had 2-3 times higher soil surface salinity (0-2 cm) and 30% higher soil salinity at 5 cm depth than vegetative plots (Bertness et al., 1992). The amount of solar exposure decreased by passive shading is a considerable factor in moderating soil salinity.

Salinity was not measured in studies involving nutria and lesser snow geese, even though their grubbing and grazing behaviour, which creates “eat-outs,” reduced the survivability of salt marsh plants and decreased primary production of *S. patens* (Lynch et al., 1947; Taylor et al., 1994; Taylor and Grace, 1995; Johnson and Foote, 1997; Evers et

al., 1998; Gough and Grace, 1998a,b; Ford and Grace, 1998b). Unless documented during the study, the impact of grazing on environmental parameters in various marshes, which affects primary productivity, as opposed to a direct influence on primary productivity is difficult to ascertain. For instance, nutria grazing on a *S. patens*-dominated marsh in Louisiana reduced the belowground biomass by over 40% (Ford and Grace, 1998a). However, the belowground biomass of a geese-grazed *S. patens* salt marsh in North Carolina was 172% higher than the ungrazed marsh (Smith and Odum, 1981).

Above- and belowground responses can differ with species and grazing regime. *Spartina alterniflora* rhizome concentration in the top 10-cm of soil was not significantly lower in feral horse grazed plots examined by Turner (1987), but moderate grazing and trampling resulted in lower live and dead *S. alterniflora* aboveground biomass. In contrast, Gough and Grace (1998a) found that *S. patens* aboveground biomass was ~25% more in grazed plots, while a separate study conducted at the same marsh detected ~75% less in grazed plots (Ford and Grace, 1998a). The greater amount of live aboveground biomass found in grazed *S. patens* plots by Gough and Grace (1998a) could be the result of a lower amount of dead biomass, which increases light availability. Morris and Jensen (1998) reported a grazing intensity of 0.5 sheep ha^{-1} and 0.5 cattle ha^{-1} on a Danish salt marsh resulted in 330 g m^{-2} more *S. anglica* belowground biomass to a depth of 60 cm, but the difference was not significant. Reader and Craft (1999) detected a significant decrease in both aboveground and belowground biomass of a feral horse-grazed *S. alterniflora* marsh in North Carolina with over 80% reduction in the belowground biomass. Feral horse grazing of *S. patens* on sand dune flats on Assateague Island, Maryland, did reduce aboveground, but not belowground biomass (Seliskar, 2003). The

lack of significance at $\alpha = 0.05$ resulted from a lack of power (n= two paired plots), even though belowground biomass in the grazed plots was ~20% of ungrazed plots.

The impact of grazing varies depending on whether grazing occurs in the low or high marsh. At lower elevations, a decrease in plant canopy could reduce the ability of vegetation to trap sediments. As sediments are sources of nutrients (DeLaune and Patrick, 1979; DeLaune et al., 1990), a lower rate of sedimentation would decrease available nutrients (van Wijnen and Bakker, 1999). A cessation of grazing, which leads to increasing rates of sedimentation in the low marsh, is attributed to salt marsh seaward development in a cattle-grazed salt marsh on the North Sea coast of Germany (Andresen et al., 1990) and a *S. alterniflora* marsh in North Carolina (Hays and Wells, 1991). Correspondingly, fewer roots could contribute to lower soil elevation if not balanced by greater soil accretion (Ford and Grace, 1998a). Roots maintain soil structure and decrease erosion. Lower belowground biomass means lower rooting zone thickness, and greater subsidence could occur. However, Andresen et al. (1990) found that various grazing intensities did not affect sedimentation rates for the high marsh.

1.3. Human influences on tidal salt marshes

As coastal environments with grassland-like characteristics, tidal salt marshes have long been used for agriculture (Ranwell, 1961; Reimold et al., 1975; Jensen, 1985; Bakker et al., 1993; Hatvany, 2003). When Europeans colonized North America, they made extensive use of tidal salt marshes, using them as pastures or harvesting them for livestock fodder and hay (Burkholder, 1956; Reimold et al., 1975). In eastern Canada, extensive areas of marsh were transformed to conventional terrestrial agricultural systems

by draining and constructing dikes to prevent tidal flooded (Ganong, 1903; Hatvany, 2003). While the direct economic value is derived from farming a diked marsh, many ecosystem services are lost (Valiela, 2006).

Large expanses of salt marsh have been diked along the St. Lawrence River estuary. One exception is the island of Île Verte in Quebec. Instead of converting a salt marsh into terrestrial agricultural land, recently, sheep grazing was introduced to a functioning tidal salt marsh. Though many salt marshes were formerly grazed, a quantitative relationship of herbivory impact on a marsh's carbon sink is scarce (Ford and Grace, 1998a; Morris and Jensen, 1998; Reader and Craft, 1999). No research had been conducted before on the impact of livestock grazing on carbon storage of a tidal salt marsh in Canada.

My research addresses this gap by studying the impact of sheep grazing on the salt marsh of Île Verte, specifically on how grazing impacts the potential for soil carbon storage. I measured soil carbon inputs in a high latitude salt marsh and impacts of grazing on soil carbon inputs. Both aboveground and belowground plant components will be collected because both components are needed to depict herbivory impact. Many studies about the effect of herbivory neglected to include the belowground component because of time constraints and accuracy of methodological techniques on assessment of production.

2. Study area

Approximately 1600 ha of salt marshes bordering the St. Lawrence River (Létourneau and Jean, 2005) are located mainly on the south shore of the upper estuary with the highest concentration near the town of Isle Verte, Quebec (Environment Canada, 1985).

In this region of the St. Lawrence River, tides are semi-diurnal and have an amplitude of 3.4 m (Canadian Hydrographic Service, 2007). Water salinity ranges from 17-20‰ (Gauthier, 1982). Salinity of tidal water measured on July 30, 2008 at the La Richardière port, Île Verte was 25‰. The area has a mean annual temperature of 3.6ºC and a growing season of 1469 growing degree days (Environment Canada, 2004). Cumulative rainfall during the week before sampling date was 29.2 mm in June, 62.0 mm in July, 12.2 mm in August, and 49.4 mm in September (Environment Canada, 2007).

Vegetation of the region's salt marshes has been described in reports by Reed and Moisan (1971) and Environment Canada (1985). *S. alterniflora* dominates the lower elevations of the tidal marshes. At higher elevations, dominant vegetation includes the grasses *S. patens, Spartina pectinata, Hierochloe odorata*, *Hordeum jubatum;* sedge *Eleocharis sp.*; and a lower abundance of a variety of forbs such as *Atriplex sp., Glaux maritima, Limonium nashii, Plantago sp., Ranunculus cymbalaria*, *Salicornia europaea, Suaeda maritima, Spergularia canadensis,* and *Triglochin maritima*. Also common in the high marsh are pools with the submerged aquatic *Ruppia maritima* and salt pannes, where poor drainage and hypersaline soils severely limit plant growth (Reed and Moisan, 1971).

During the spring and autumn migrations, tens of thousands of Canada Goose (*Branta canadensis*), Greater Snow Goose (*Chen caerulescens atlantica*), and Brent Goose (*Branta bernicla*) can be found grazing and grubbing on *Bolboschoenus maritimus* (Gauthier et al., 1984; Gauthier et al., 2005). These marshes also are major breeding grounds for the American Black Duck (*Anas rubripes*) (Belanger et al., 1998; Reed and Moisan, 1971).

The only inhabited island in the upper estuary of the St. Lawrence, Île Verte (48º02'N, 69º26'W), is ~ 4 km from the south bank of the St. Lawrence River (Fig. 1).

On the central portion of the island's eastern shore lies a 110 ha salt marsh. Inspired by sheep grazing on the salt marshes of Mont-St. Michel, France, islanders introduced seasonal sheep grazing to stimulate agro-tourism. Between 2000 and 2006, about 100 lambs grazed for at least six hours per day for 90 days. An experienced sheepherder rotated them among thirty ~80 x 80 m paddocks. Paddocks were restricted to the high marsh and the herd was shifted to minimize impacts on soil and vegetation.

3. Methods

3.1. Fieldwork

Research was conducted between May and October 2007, as ferry access was restricted to the period between thaw and freezing of sea ice. Station selection was made from a 19.2 ha grazed and 0.9 ha ungrazed area of the salt marsh. Approximately 0.5 km separated the two treatments. In early May, 10 stations were located within the grazed and ungrazed areas. The 10 stations in the grazed area were located in paddocks that were continuously grazed throughout the previous six summers and in the middle marsh where grazing was most regular (evidenced by fecal remains and short, lawn-like sections). Stations in the ungrazed area were chosen to conform to elevations and vegetation of the grazed stations. Pools, patches dominated by *Salicornia sp.* or *Bolboschoenus maritimus,* were excluded in an attempt to sample similar vegetation zones.

Each station was one m^2 and subdivided into nine 30 cm x 30 cm plots, laid out in a grid (Fig. 2). The four corner subplots were used for litter and aboveground biomass samples. The four remaining edge subplots were used for collection of soil and belowground biomass samples. The elevation of the soil at station centers differed by no more than 20 cm, determined by conventional surveying.

Porewater and water table depth were monitored in the center of each station. Piezometers were constructed from 1.7 cm inner diameter PVC pipes with thirty uniform and evenly spaced holes perforating the lower 15 cm of each pipe. The perforated end, which was inserted into the ground, was covered with a piece of duct tape. The other end was capped, but not so tight as to prevent equilibration with atmospheric pressure differences. Piezometers were inserted to a depth of 21.5 to 48.5 cm belowground in the grazed area and 27.8 to 53.3 cm in the ungrazed area. Depth to water table and porewater chemistry were measured each month during neap tides (June 21, July 21, August 19, and September 14) generally during the ebbing tide. On these dates, the tidal amplitudes ranged from 1.2 to 4.1 m (Canadian Hydrographic Service, 2007). At each plot (N=80), soil temperature at 10 cm depth was taken with a dial thermometer on June 21. Temperature readings were measured at least ten minutes after insertion. Environment Canada (2007) reported a minimum air temperature of 9.4ºC and a maximum of 18.4ºC on this date.

Depth to water table was measured by inserting a thin metal pipe with plastic tubing on one end into a piezometer while blowing into the plastic tubing. The sound of bubbling indicated the presence of water. Some piezometers were dry when measurements were taken, thus the depth to water table was probably underestimated in some cases. Piezometers with a water table above the soil surface have a positive water table depth measurement.

Soil porewater samples were collected after measurement of water table depth. The sampler was constructed from 1 cm-diameter x 50.8 cm-long PVC tube (Robinet tube). A 10 cm-length of one end was perforated with evenly spaced 2 mm holes. This end of the tube was stoppered with silicon gel to prevent clogging when inserted into the

soil. The top was attached to a 30 cm-length of plastic Tygon tubing, which in turn was connected to a three-way valve and a 30 mL syringe attached to the valve was used to suction water through the sipper. After the sipper was inserted 15 cm into the soil, ~15 mL of porewater was drawn into the syringe to rinse the sipper and syringe, then discarded, before drawing 30 mL of porewater for sulfide and nutrient analyses. About 2.5 mL was siphoned into a 5 mL syringe attached to the third port of the valve. The water was then transferred to a vial holding the same quantity of prepared sulfide buffer solution, ~2.5 mL. The remaining sample in the 30 mL syringe was passed through a 0.45 μm nylon filter and into an acid-washed glass vial for nutrient analyses. A final porewater sample of ~15 mL was withdrawn and transferred to a third vial for pH and salinity measurements. All samples were chilled immediately and nutrient samples were frozen within hours after collection.

Soil cores were removed with a 5 cm-diameter, 58 cm-long sharpened pipe with a plumber's valve attached. The pipe was gently twisted to 10 cm depth, then a plumber's valve was inserted to create a vacuum, allowing the soil to be withdrawn. This portion was used for laboratory analyses. The pipe was twisted to an additional 20 cm depth and the soil discarded. Soil was collected on May 5 and 6 from all grazed stations and three stations in the ungrazed section of the salt marsh. At the remaining ungrazed stations, soil was frozen to the surface and prevented coring. Soil collection was completed on May 23, when the soil was still frozen at 20 cm depth at six stations and at 10-15 cm depth at one station.

Ingrowth cores, for determination of below ground production, were inserted immediately after soil was removed. These are mesh bags packed with finely ground *Sphagnum* peat. Cores are 5 cm-diameter and ~30 cm long. All 79 ingrowth cores

(ungrazed area only had 39 cores installed) were removed on October 20-21 and stored under refrigeration upon return to the lab.

Litter, standing dead from previous growing seasons, was collected May 5 - 6 from all stations, providing 80 samples. Green biomass was observed and was avoided as much as possible while clipping. End-of-season standing crop, dead and alive, was harvested October 20 - 21 from the same plots clipped in the spring, providing 79 samples from 20 stations because one ungrazed sample was lost.

3.2. Laboratory analyses

Soil was freeze-dried to make grinding easier (salt marsh soils harden with warm drying). Inspection of samples revealed that some cores still had damp centers. Any questionable cores were placed in a drying oven at 70ºC until drying was complete. Dried soils were weighed and then ground with a small food processor. Percent organic matter was determined by loss-on-ignition (LOI). Approximately 1 g samples of ground soil were placed into pre-weighed crucibles and combusted in a muffle furnace, heated for 1 hr at 350ºC when temperature was increased to 550ºC for a minimum of 4 hr. Crucibles were cooled in a dessicator then reweighed. Two replicates were run for each sample. If difference between replicates was greater than 10%, then a third replicate was run. Percent organic matter was converted to percent organic carbon using a formula published by Craft et al. (1991).

Aboveground biomass (litter and end-of-season) was washed and dried at 70ºC. Any green biomass was removed from litter samples. Samples were weighed to the nearest 0.01 g. Total carbon and nitrogen were determined from ground samples using a

Carlo Erba Na-1500 CNS Elemental Analyzer in the laboratory of the Department of Earth and Ocean Sciences at the University of British Columbia.

Various techniques to determine belowground productivity include sieving soil cores (Gallagher and Plumley, 1979; Scholand et al., 1991), removing soil cores and replacing with mud (Gallagher et al., 1984) or sand (Valiela et al., 1976), and installing ingrowth cores (Persson, 1983; Steen, 1991). While less accurate than sieving of soil cores, ingrowth cores are appropriate for comparing the relative amount of root growth between treatments (Steen 1991). Since net primary productivity will not be addressed, the ingrowth bag method is suitable for this experiment. The ingrowth core method used is similar to that employed in other studies of salt marshes belowground production (Persson, 1983; Gallagher et al., 1984; Symbula and Day, 1988; Neill, 1992).

Ingrowth cores were made and processed following an unpublished protocol by McKee and Herbert (n.d.) by lightly packing moist finely milled *Sphagnum* peat (Berger Blonde Golden) into 5 cm-diameter x 30 cm-long bags of 2.5 mm nylon mesh (Kane Supply Corp.). The length of each core was measured, biomass and debris outside the mesh bag removed, and cores divided into 10 cm sections measured from the top of the core. Due to difficulty in installation and irregularities in bag construction, some cores were less than 30 cm deep. The biomass of the bottom section was normalized to 10 cm. Statistical analyses were performed on both the 20 cm and normalized 30 cm of belowground biomass.

Peat from the ingrowth cores was washed over a 1-mm sieve. Live belowground biomass, roots and rhizomes, identified by their pale colour, turgidity and ability to float, were separated from the peat. Belowground biomass, herein termed roots, was separated into coarse (>2 mm) and fine (≤2 mm) size fractions. Cleaned roots were blotted on

paper towels before their volume was measured by displacement using a graduated cylinder. Each subsample was placed in a paper coin envelope and placed in an oven at 70ºC until dry. Mass of dry roots was measured to the nearest 0.001 g.

Porewater sulfides, NH_4^+-N, PO_4^{-3}-P, salinity, and pH were measured at different periods post field sampling. Sulfides were measured within 24 hr, salinity and pH within 48 hr, and frozen nutrient samples analyzed within months. Salinity was determined with a hand-held refractometer (Fisherbrand), and pH with an Oyster 10 pH meter.

The sulfide procedure follows a standard operating procedure developed by McKee et al. (1988) of the United States Geological Survey National Wetlands Research Center. Reagents for sulfide analyses were prepared with deoxygenated water to prevent oxidation of H_2S and HS^- and containers were kept capped when not in use to minimize oxidation. Deoxygenated water was made by bubbling nitrogen gas into 1 L of distilled water for 10 min. An antioxidant buffer was made by dissolving 62.5 g of sodium salicylate, 21.3 g of sodium hydroxide, and 16.3 g of ascorbic acid in 150 mL of deoxygenated water. Once chemicals were completely dissolved, more deoxygenated water was added to the antioxidant buffer to make up to 250 mL, which was divided into two portions of 125 mL. Both portions were deoxygenated again for several minutes. One half was used to fix soil pore water samples in the field, while the other half was for standards. For use in the field, 8 mL each of the buffer and deoxygenated water was added to a 20 mL plastic vial. Standards of 1000, 100, 10, 1, 0.1 ppm were prepared by adding 25 mL of the antioxidant buffer to 100 mL volumetric flasks. A washed 0.75g pellet of $Na_2S•9H_2O$ was added to the 1000 ppm flask, dissolved and brought to volume with deoxygenated water. The remainder of the standard series was made by a 1:10 serial dilution. These standards were kept refrigerated in 50 mL centrifuge tubes until needed

for analysis. Sulfides were measured with a sulfur electrode (LAZAR Micro Mono Ion ISM-146S). Procedure for operating the LAZAR sulfide electrode followed that outlined in their operating manual. Millivolt readings were converted to micromoles.

Ammonium analyses followed colorimetric protocols for seawater outlined by Parsons et al. (1984) with several modifications. For accuracy, standards for each run were made anew from a 10 mM stock solution. July samples were analyzed with a $(NH_4)_2SO_4$ stock solution directly following Parsons et al. (1984). A different stock solution made with NH_4Cl was used for August and September samples to conform with an unpublished U.S. Geological Survey Standard Operating Protocol (Nagel, 2007). Vials were covered to prevent light exposure of the mixture as phenol is photosensitive. After some trials, standard concentrations adopted were 0 (blank), 0.1, 1, 4, 5, 10, 20, 30, 50, 100, and 200 ppm. Standards were reanalyzed after every 20 samples. Samples were stored either overnight (< 24 hr) or incubated for at least 4 hr before measuring in the spectrophotometer. Nutrient concentrations were determined colorimetrically with a Thermo Electron Corp. Genesys 10 uv spectrophotometer.

Phosphate analyses closely followed the PO_4-P protocol of Parsons et al. (1984). A 1000 μmol KH_2PO_4 stock solution was used to make 0.1, 1, 5, 10, 20, 30, 50, 100 ppm standards. Two sets of standards, one set of standards for every 10 samples, and mixed regent were made fresh for each run. Samples were held 30 min before concentrations were measured with the spectrophotometer.

3.3. Statistical analyses

Statistical analyses were performed with SPSS 15.0. A two-level, mixed model, nested, one-way ANOVA was used to test for differences in properties of grazed and ungrazed

stations (Table 1). To determine the effect of porewater on treatment differences, a three-level, mixed model, nested one-way ANOVA was used (Table 2). Student's t-test was used to test for treatment difference within a given month (Table 3). Parameters with missing samples were analyzed according to the guidelines of Sokal and Rohlf (1995). The main problem with unequal sample sizes is testing the significance of difference in upper levels of a.nested ANOVA. This problem was dealt with through the application of the Satterthwaite approximation of the groups' mean square. Adjusted F values and degrees of freedom are reported.

Besides assumptions of random selection of sampling units (stations) and independence, the two key assumptions to be met before application of analysis of variance (ANOVA) are homogeneity of variance and normality (Underwood, 1997). The term homogeneity of variance instead of homoscedescity will be used as defined by Tabachnick and Fidell (2001) because a nested experimental design was used. Homogeneity of variance was assessed with Levene's test of equal means at $\alpha = 0.05$ and graphically with cell plots. Normality was determined graphically by normal Q-Q plots, skewness and kurtosis values, and the Shapiro-Wilks' statistic at $\alpha = 0.05$. Both test of homogeneity and normality were assessed with station averages of four replicates (grazed n=10 and ungrazed n=10) to avoid violation of independence and randomness assumptions (Underwood, 1999). Appendix 1 and 2 tabulate the results of normality and homogeneity of variance. Test of homogeneity for end-of-season standing crop, roots, litter, root:shoot ratio and total biomass was based on the mean. Homogeneity of variance in volume of roots soil and porewater chemistry was based on the median because there were missing samples (Tabachnick and Fidell, 2007).

Violation of homogeneity of variance is considered of greater influence on the resulting ANOVA test than violation of normality because many environmental variables have nonnormal distribution (Sokal and Rohlf, 1995; Underwood, 1999). While various transformations on porewater parameters decreased nonnormality, no transformation resulted in a normal distribution for these parameters without lowering homogeneity of variance. Thus, porewater parameters were not transformed despite highly nonnormal data. Likewise, transformations that converted a heterogeneous, normal data set to an acceptable homogeneous, but highly nonnormal data was not necessarily selected. For instance, neither total belowground biomass nor root:shoot ratios from 20 and 30 cm depths were transformed because heterogeneity of plant growth was expected. The marginal heterogeneity of percent organic matter and organic carbon was considered insignificant. Due to the small sample size and unbalanced design, *p*-values for the homogeneity of variance may actually be higher (Weinberg and Abramowitz, 2008). Transformation was chosen according to recommendations by Tabachnick and Fidell (2001). However, data in figures are non-transformed. Appendix 1 tabulated the results of normality and homogeneity of variance results. Despite the persistence of nonnormality, depth to water table data was log-transformed because nonnormality decreased and homogeneity of variance improved. Inverse transformation of NH_4-N samples improved normality and homogeneity of variance. The best transformation to meet both normality and homogeneity of variance for the PO_4-P variable was $\log_{10}$, even though homogeneity of variance was not attained.

4. Results

4.1. Environmental variation between the grazed and ungrazed tidal salt marsh

Soil temperature on June 21 averaged 13.5ºC in the grazed area and 10.9ºC in the ungrazed area. The average depth to water table in each month was significantly ($F_{1,4}$ = 15.5, p = 0.017) lower in the grazed area than the ungrazed area (Table 3, Fig. 3). At several stations in the grazed marsh, the water table was below the bottom of the piezometers, yet above the marsh surface in the ungrazed marsh on the same day.

With the exception of salinity, there was no significant difference in pore water chemistry between grazed and ungrazed salt marsh. Sulfides, PO_4-P, and pH exhibited significant monthly variation during the monitoring period, while all porewater chemistry was spatially variable within a station (Table 2). In contrast, salinity was the only porewater parameter without treatment effect at each monthly sampling (Table 3). Monthly differences were not detected ($F_{6,72}$ = 0.4, p=0.844), possibly because of heavy rainfall events in the preceding 5 days (Table 5). Averaged over the growing season, salinity was 12‰ and 9‰ in grazed and ungrazed marsh, respectively (Table 4).

Sulfide concentrations varied significantly over the study period (Fig. 4). In the grazed area, sulfide levels were highest (0.53 mM) in June and lowest in July when concentrations fell below the detection limit in many samples. Sulfide concentration in the grazed area was higher than ungrazed for the month of June ($t_{0.05, 20}$ = 0.038). The difference among months was less in the ungrazed area, where the highest concentrations occurred in August (0.27 mM). Levels were similarly low in July (0.01 mM) when only one out of ten ungrazed stations had both replicates within detection limits.

No difference was detected between grazed and ungrazed in any month, but there was temporal variability. NH_4-N concentrations in July cannot be compared to August and September because the analytical protocol was different. Although average

September levels were twice that of August for the grazed area (Fig 5), the difference was not significant. July levels for both treatments were similar.

Average PO_4-P concentrations significantly varied by month ($F_{6,72} = 3.8$, $p=0.003$). PO_4-P concentrations were significantly higher in June (29.0 ppm). Lowest levels occurred in September (5.8 ppm). Average PO_4-P concentrations were more constant throughout the sampling period in the ungrazed area, where they ranged from 3.4 ppm in September and 10.5 ppm in August. Average PO_4-P concentrations in the grazed area were consistently higher than the ungrazed area (Fig. 6), although differences were not significant ($F_{1,6} = 2.2$, $p=0.186$).

The pH increased steadily from June to August then decreased in September (Fig. 7). Average pH was lower in the grazed area for all months except June and pH levels for these months were significantly higher in the ungrazed area than grazed (Table 3).

Grazed soils had a higher bulk density, but this difference is not significant ($F_{1,17} = 1.3$, $p=0.271$). The percent organic matter and organic carbon of ungrazed marsh soil is 25% and 10%, respectively. The grazed soil is slightly lower, 23% and 9%, respectively (Fig. 8). In contrast, soil carbon density of the grazed soils (0.032 g C cm^{-3}) was significantly higher than in ungrazed soils (0.025 g C cm^{-3}).

4.2. Biomass in the grazed and ungrazed tidal salt marsh

The mass of litter collected in May was significantly lower ($F_{1,18}= 25.3$, $p<0.001$, Fig. 9) in the grazed than ungrazed marsh (124 and 322 g m^{-2}, respectively). Treatment effect explained 58.1% of the variance. Litter from the grazed area appeared more decomposed and shorter than that from the ungrazed area. Litter amounts varied greatly among stations within a treatment ($F_{18,60}= 4.0$, $p< 0.001$).

End-of-season standing crop (EOST) harvested in mid-October was significantly lower in the grazed area than the ungrazed area ($F_{1,17} = 21.3$, $p < 0.001$, Fig. 9). The ungrazed area held nearly one-third more EOST than the grazed. Significant spatial heterogeneity among stations within a treatment was detected ($F_{18,59} = 5.6$, $p<0.001$). Percent carbon was higher in the end-of-season standing crop from the grazed area ($F_{1,8} = 6.244$, $p = 0.022$) Average nitrogen and carbon content of aboveground biomass from the grazed area (3.5 g N m^{-2} and 127.2 g C m^{-2}) was significantly lower than ungrazed samples (4.8 g N m^{-2} and 186.5 g C m^{-2}). However, there was no difference in C:N ratio ($F_{1,8} = 0.007$, $p=0.933$).

Total belowground biomass in 30 cm depth was nearly 130% greater in the grazed than the ungrazed area. Treatment effect for 20 cm compared to a normalized 30 cm length core did not differ (Table 1). Cumulative belowground production to either 20 or 30 cm depth in the grazed salt marsh (487 and 524 g m^{-2}) was more than twice that in the ungrazed area (223 and 229 g m^{-2}), respectively. This treatment effect for belowground biomass was detected also for each 10-cm interval (Fig. 10). Average cumulative root volume to the 30 cm depth was also significantly higher in the grazed area (8 cm^{-3}) than ungrazed area (3 cm^{-3}) ($F_{1,16} = 18.6$, $p=0.001$), with root volume to 20-cm depth similarly significant. This volume of roots comprises 1.3% of grazed soil volume to depth of 30 cm compared to 0.51% in the ungrazed soil.

Roots and rhizomes were not separated, but it is likely that the coarse root fraction (> 2 mm in diameter) was rhizomes and those with diameter ≤ 2 mm were true roots. Coarse roots were concentrated in the top 10 cm and were not found below 20 cm (Fig. 11a). The averaged mass of coarse roots was almost five times higher in grazed (54 g m^{-2}) than ungrazed marsh (11 g m^{-2}), but high spatial variability prevents detection of

significance ($F_{17,59}$ = 3.9, p< 0.001). The mass of coarse roots at grazed stations ranged from 0 to 552 g m^{-2}. Although the percentage of dry weight of coarse roots in the 0-10 cm section was higher in the grazed than ungrazed area; proportionally, the ungrazed area appeared to have slightly more coarse roots in the 10-20 cm below soil surface.

Fine roots in the ungrazed area were 82% and 15% of the total belowground biomass in 0-10 cm and 10-20 cm, respectively compared to 69%, and 23% for the grazed area (Fig. 11b). Cumulative coarse root production was not significantly different between the treatments ($F_{1,17}$ =2.3, p=0.148), but there were more fine roots in the grazed area ($F_{1,17}$ = 14.5 p=0.001). As a proportion of total belowground biomass, the ungrazed area had almost 10% more belowground biomass in the top 10 cm of soil (Fig. 12). Correspondingly, the β value for the ungrazed area was lower at 0.83 compared to β=0.87 at the grazed area.

The total dry weight plant production (end-of-season standing crop and 30 cm of roots) was not significantly different between grazed and ungrazed areas ($F_{1,18}$ = 2.8, p=0.113). However, differences in root to shoot ratios were significant. The root to shoot ratio of the grazed marsh is 2.0 and only 0.5 in the ungrazed marsh ($F_{1,18}$ =23.2, p< 0.001).

5. Discussion

5.1. The ungrazed salt marsh at Île Verte

Climate influences aboveground production of salt marshes. Turner (1976) showed that end-of-season standing live crop (EOSL) and total end-of-season standing crop (EOST) of *S. patens* along the eastern coast of North America increased with decreasing latitude,

as greater solar radiation and higher temperatures lead to a longer growing season. Aboveground production at Île Verte fits this trend (Table 6). The belowground component of the ungrazed salt marsh at Île Verte has a β value of 0.83 and is within the range Murphy and Moore (*in preparation*) reported for North American salt marshes (Table 7). The reported values for above- and belowground biomass represent *S. patens* primary production at its northernmost range (Rousseau, 1974; Groupe Fleurbec, 1985). Furthermore, a review of soil carbon density in the world's salt marshes also revealed a climatic gradient in *S. patens* marshes. Chmura et al. (2003) surmised that increased rates of decomposition driven by higher temperatures at lower latitudes overcome the high rates of biomass production thus, soil carbon density decreased with decreasing latitudes (Chmura et al., 2003). My results from Île Verte expand that global database as it has a colder climate than any *Spartina*-dominated marsh where carbon density has been reported. Re-evaluation of the relationship between soil carbon density and average annual temperature of *S. patens* marshes by including soil carbon density from Île Verte produces a higher correlation than that calculated by Chmura et al. ($R = -0.61$, $p < 0.001$, Fig. 13).

5.2. Differences between grazed and ungrazed marsh

At Île Verte, grazing likely initiated a negative feedback cycle that increased soil carbon density (Fig. 14). The decreased aboveground growth and litter allowed more light to reach the soil surface, which increased soil temperature, depth and period at which soil was unfrozen – driving increased belowground production. Increased temperatures are known to increase nutrient availability (Pregitzer and King, 2003), which could enhance

production. Yet, evapotranspiration and soil salinity (Bertness et al., 1992) increase plant stress and nitrogen demands (Crain, 2007). The larger rhizosphere in the soil would increase oxidation of the soil further enhancing nitrogen availability and reducing the concentrations of soil toxins such as hydrogen sulfide and ethanol, phytotoxins produced during anaerobic metabolism (Koch and Mendelssohn, 1989, Koch et al., 1990), although sulfides were equally low in both treatments.

The response of soil temperature to grazing is not unique to Île Verte. Meyer et al. (1995) found that, on the Wadden Sea, where grazing intensity is similar to Île Verte (3-5 sheep ha^{-1}), marsh soil temperatures at 5 cm below soil surface were 0.5 to 4ºC higher in grazed marsh. At Île Verte, the average difference in soil temperatures on June 21 between the grazed and ungrazed stations was 2.5ºC, and differences were as great as 9 ºC. Generally, soil temperatures were lower at ungrazed stations despite the measurements taken in the afternoon compared to soil temperature measured at the grazed stations in the morning of the same day.

Although no treatment difference was detected in available nutrients in soil porewater, concentration of PO_4-P in the grazed area was higher than ungrazed in June. Additional phosphorus could have influenced the difference in *S. patens* belowground biomass observed even though the aboveground biomass did not show a difference (Wigand et al., 2004; Crain, 2007). In a *S. alterniflora* marsh in Louisiana, Darby and Turner (2008a) detected less live belowground biomass, but no change in aboveground biomass with the addition of 6 g m^{-2} of orthophosphate. Nutrient addition has been shown to affect root distribution and decrease rooting depth (Gregory 2006). The ungrazed area had almost 10% more total belowground biomass in the top 10 cm of soil than the grazed area (Fig. 12), reflected in its lower β value. Though not detected in this

experiment, phosphorus fertilization causing a decrease in belowground biomass could have significant repercussions on marsh vertical accretion (Darby and Turner, 2008a,b).

Soil salinity was significantly higher in grazed soils. However, porewater salinity in grazed soils (11.7‰) was less than half the levels recorded for Dipper Harbour, Bay of Fundy (~27‰) and Kouchibouguacis, Gulf of St. Lawrence (24‰), where salt marsh production is comparable (Beaumier, unpublished data). Other studies of grazing in Canadian "salt" marshes reported negative impacts on vegetation due to increased soil salinity. Jefferies and colleagues worked in arctic "salt" marshes where higher evapotranspiration rates under goose grazing resulted in soil salinities that limited plant growth (Iacobelli and Jefferies, 1991; Srivastava and Jefferies, 1995, 1996). Increased soil salinity in these Hudson Bay marshes was due to upward movement of salts from subsurface fossil salt (Price and Woo, 1988a,b). Two of the dominant species in the Hudson Bay marshes, *Puccinellia phryganodes* and *Carex subspathacea* are not commonly found where soil salinities are >15.4‰. They likely are less salt tolerant than *S. patens,* which is regularly found at salinities greater 25‰ (e.g. Pezeshki and DeLaune, 1991, 1997).

The larger rhizosphere present in the grazed marsh would increase oxidation of the wetland soil (Howes et al., 1981). Since nitrification occurs in oxidized soil, nitrogen availability would increase (Reddy and D'Angelo, 1994) because an expanding oxidized zone caused by roots produces a concentration gradient, in which NH_4-N diffuses upwards from the reduced soil (Keddy, 2000). Windham-Myers (2005) detected an inverse relationship between belowground biomass and porewater NH_4-N concentration in a marsh in the Hudson River estuary. Greater belowground biomass can lower NH_4-N levels through increased uptake. In contrast, high NH_4-N levels in the soil can lead to a

decrease in belowground biomass because a decrease in nitrogen limitation meant less energy will be devoted to belowground growth. Caffery et al. (2007) found higher bacterial populations in soil with nitrogen fertilization and determined there were higher numbers of nitrogen-fixing bacteria making nitrogen more available. *S. patens* belowground biomass at 10 cm depth at the Hudson River site was 545 g m^{-2} compared to 191 g m^{-2} at Ile Verte. Correspondingly, August porewater NH_4-N concentration at 10 cm depth was 1.5 ppm and 20.0 ppm at the Hudson River and Îsle Verte, respectively. Greater belowground biomass and soil aeration could have influenced the low levels of sulfides at this marsh, thereby lessening the inhibition of NH_4-N uptake.

Sheep grazing on Île Verte the previous summer resulted in 117% more belowground biomass. Although no significant difference was detected for NH_4-N concentration between the porewater samples from grazed and ungrazed areas, a higher concentration of NH_4-N in September could be indicative of increased availability. In comparison, lower NH_4-N in the grazed area in August could be the result of increased uptake during the peak growing period despite a lower depth to water table. Results for June concentration of NH_4-N were significantly higher in the grazed area, but were not shown because of a discrepancy in protocol. This increase in porewater NH_4-N and PO_4-P early in the growing season may be an influence on belowground production.

The grazed area with higher belowground biomass and percent carbon in the end-of-season standing crop contributed to higher soil carbon density and soil volume. These results are unexpected based upon observations elsewhere on the northwestern Atlantic. Grazing in a Georgia low marsh resulted in 51-72% decrease of *S. alterniflora* belowground biomass and a decrease in carbon input and accumulation (Reader and Craft 1999). In Louisiana, Ford and Grace (1998a) reported that grazing resulted in nearly 50%

reduction in *S. patens* belowground biomass, which meant that the root zone thickness was reduced from 6.67 to 1.86 mm. This decrease in rooting zone has a larger influence on marsh elevation than sediment deposition. Although sediment deposition was over a third greater in grazed plots, surface elevation was 71% lower. Seliskar (2003) indicated that a decrease in above- and belowground biomass of *S. patens* from feral horses grazing on Assateague Island would result in marsh erosion. Thus, inputs of organic matter are a positive factor in salt marsh accretion (DeLaune et al., 1990; Nyman et al., 1993; Turner et al., 2001; Chmura and Hung, 2004) contributing to the stability of salt marshes subjected to rising sea levels (Seliskar, 2003).

6. Implications for marsh sustainability

Greater carbon sequestration in salt marshes with an agricultural use could be a powerful economic incentive. Enhanced, nutrient availability from grazing can enhance productivity, which will be both economically and ecologically advantageous. The use of salt marshes for grazing creates a high value product that optimizes economic potential of an ecosystem such as the tidal salt marsh and at Île Verte. It also increases an ecosystem service by storing more carbon.

In Europe, light grazing on salt marshes was shown to increase plant species diversity and recommended as a conservation tool (Bakker and Ruyter, 1981; Bakker et al., 1983; Bakker et al., 1993; Bouchard et al., 2003). Livestock grazing on the Wadden Sea marshes facilitated grazing by migratory geese (Bos et al., 2005) and contributed to the maintenance of a desired landscape.

Sequestration of carbon through plant production is one of the most important ecosystem services provided by salt marshes. Efforts to mitigate greenhouse warming

have lead to the development of carbon markets (e.g., Chicago Climate Exchange) and if grazing can lead to an increase in soil carbon storage, then this ecosystem service gains in economic value. For perspectives on modified tidal salt marshes' role as carbon sinks, an understanding of salt marsh plant production and the disturbances affecting the productivity, especially human modifications, is necessary.

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Table 1- ANOVA results studying the effect of six years of grazing on salt marsh biomass and soil parameters. A nested design was used to avoid pseudo-replication. Boldface denotes significance.

	SS	df	MS	F	*p*	SS	df	MS	F	*p*
	Between treatments					Among stations within a treatment				
Biomass										
Litter (g m^{-2})	786326	1	786326	25.3	**<0.001**	559135	18	31063	4.0	**<0.001**
End-of-season crop (g m^{-2})	470163	1	470163	21.3	**<0.001**	396968	17	22110	5.6	**<0.001**
All belowground biomass (20 cm, g m^{-2})	1364042	1	1364042	15.3	**0.001**	1602513	17	89270	7.7	**<0.001**
Coarse (>2 mm)	35814	1	35814	2.3	0.148	280178	17	15602	3.9	**<0.001**
Fine (≤2 mm)	957806	1	957806	13.7	**0.002**	1255891	17	69966	9.4	**<0.001**
All belowground biomass (30 cm, g m^{-2})	1704363	1	1704363	15.2	**0.001**	2007199	17	111823	9.7	**<0.001**
Coarse (>2 mm)	35814	1	35814	2.3	0.148	280178	17	15602	3.9	**<0.001**
Fine (≤2 mm)	1246050	1	1246050	14.5	**0.001**	1544015	17	86017	9.2	**<0.001**
Root volume (20 cm, cm^3)[1]	17	1	17	18.1	**0.001**	16	16	0.9	4.3	**<0.001**
Root volume (30 cm, cm^3)[1]	18	1	18	18.1	**0.001**	17	17	1.0	3.6	**<0.001**
Root:shoot ratio 20cm	36	1	36	22.2	**<0.001**	29	18	2	8.3	**<0.001**
Root:shoot ratio 30cm	43	1	43	23.2	**<0.001**	33	18	2	7.9	**<0.001**
Total live biomass (20cm, g m^{-2})	241255	1	241255	2.1	0.168	2104031	18	116891	11.5	**<0.001**
Total live biomass (30cm, g m^{-2})	397296	1	397296	2.8	0.113	2575074	18	143060	12.2	**<0.001**
Soil										
Bulk density (g cm^{-3})	0.07	1	0.07	1.3	0.271	1	17	0.06	7.9	**<0.001**
Percent Organic Matter	83	1	83	0.4	0.536	3572	17	207	14.5	**<0.001**
Percent Organic Carbon	13	1	13	0.4	0.535	575	17	33	14.6	**<0.001**
Carbon density	0.0008	1	0.0008	25.1	**<0.001**	0.0006	16	0	0.9	0.551

[1]Square root transformation

Table 2- ANOVA results studying the effect of six years of grazing on depth to water table and porewater chemistry. A nested design was used to separate the treatment effect from monthly and spatial variation. For NH_4-N, a different protocol was used between July and August and September, so the effect of months was not tested for the entire period. Boldface denotes significance.

	SS	df	MS	F	*p*
Between treatments					
Depth to water table[1] (cm)	0.36	1	0.36	15.5	**0.017**
Salinity (‰)	336	1	336	6.2	**0.048**
Sulfides (mM)	0.54	1	0.54	0.9	0.371
NH_4-N: all (ppm)	0.398	1	0.398	0.001	0.983
NH_4-N[1]: August and September (ppm)	0.002	1	0.002	0.03	0.869
PO_4-P[2] (ppm)	0.6	1	0.6	2.2	0.186
pH	2.1	1	2.1	1.6	0.257
Among months within a treatment					
Depth to water table[1] (cm)	0.09	4	0.02	0.8	0.519
Salinity (‰)	327	6	55	0.4	0.844
Sulfides (mM)	3.4	6	1	2.8	**0.015**
NH_4-N[1]: August and September (ppm)	0.104	2	0.052	1.259	0.296
PO_4-P[2] (ppm)	2	6	0.3	3.8	**0.003**
pH	8	6	1	6.5	**0.000**
Among stations within a treatment					
Salinity (ppt)	8746	72	121	30.8	**0.000**
Sulfides (‰)	14.5	72	0.2	2.7	**0.000**
NH_4-N: August and September[1] (ppm)	1.490	36	0.041	5.8	**0.000**
PO_4-P[2] (ppm)	5.5	72	0.1	7.8	**0.000**
pH	14.9	72	0.2	2.6	**0.000**

[1] $\log_{10}$ transformation [2] inverse transformation

Table 3- Student's independent samples t-test results for treatment effect on depth to water table and porewater chemistry within a month. Boldface denotes significance. Underline means that the t-test was conducted with unequal variances.

	Month	t	df	*p*
Depth to water table (cm)	July	1.172	18	0.256
	August*	2.903	18	**0.009**
	September	2.142	18	**0.046**
Salinity (‰)	June	0.410	36	0.684
	July	1.716	38	0.094
	August	1.357	38	0.183
	September	1.281	38	0.208
Sulfides (ppm)	June	2.217	20	**0.038**
	July	1.170	38	0.249
	August	0.404	30	0.689
	September	0.233	38	0.817
NH_4-N (ppm)	July	0.251	38	0.803
	August	-1.252	30	0.221
	September	0.684	38	0.498
PO_4-P (ppm)	June	3.604	26	**0.001**
	July	0.827	38	0.414
	August*	1.040	31	0.306
	September	1.534	34	0.135
pH	June	1.002	36	0.323
	July	-2.609	38	**0.013**
	August	-3.298	38	**0.002**
	September	-2.705	38	**0.010**

* $\log_{10}$ transformation

Table 4- Median, mean, and standard deviation of biomass, soil, water table, and porewater chemistry parameters.

	Grazed			Ungrazed		
	Median	Mean	SD	Median	Mean	SD
Biomass						
Litter (g m^{-2})	137	124	70	333	322	103
End-of-season crop (g m^{-2})	256	285	72	435	440	77
All belowground biomass (20 cm, g m^{-2})	539	487	197	220	223	76
Coarse (>2 mm)	14	54	88	11	11	10
Fine (≤2 mm)	485	433	173	213	212	71
All belowground biomass (30 cm, g m^{-2})	579	524	222	226	229	80
Coarse (>2 mm)	14	54	88	11	11	10
Fine (≤2 mm)	518	470	193	219	218	76
Root volume (20 cm, cm^3)	7	7	3	3	3	1
Root volume (30 cm, cm^3)	8	8	3	3	3	1
Root:shoot ratio 20cm	2	2	0.9	0.6	0.5	0.2
Root:shoot ratio 30cm	2	2	0.9	0.6	0.5	0.2
Total live biomass (20 cm, g m^{-2})	775	772	200	674	663	135
Total live biomass (30 cm, g m^{-2})	820	810	229	679	669	139
Soil						
Bulk density (g cm^{-3})	0.36	0.36	0.08	0.23	0.29	0.15
Percent Organic Matter	24	23	4	29	25	9
Percent Organic Carbon	10	9	2	12	10	4
Carbon density (g cm^{-3})	0.031	0.032	0.004	0.025	0.025	0.003
Water table and porewater chemistry						
Depth to water table (cm)	10.00	14.60	11.86	6.10	6.35	7.02
Salinity (‰)	10.75	11.71	6.40	5.00	8.72	8.70
Sulfides (mM)	0.02	0.26	0.43	0.07	0.15	0.21
NH_4-N: all (ppm)	4.82	16.44	26.97	5.18	16.32	21.84
NH_4-N: July (ppm)	2.83	12.95	22.04	3.13	11.32	16.57
NH_4-N: August and September (ppm)	5.43	18.18	29.51	6.14	18.82	24.05
PO_4-P (ppm)	7.93	16.24	18.57	3.55	6.83	8.09
pH	6.31	6.25	0.35	6.39	6.47	0.42

Table 5- Rainfall levels for 5 days before porewater sampling. An asterix denotes sampling day (Canadian Hydrographic Service, 2007).

2007	Rainfall (mm)	2007	Rainfall (mm)
16 June	0.0	16 July	0.0
17 June	3.8	17 July	0.2
18 June	0.0	18 July	missing
19 June	0.0	19 July	0.2
20 June	25.4	20 July	61.4
21 June*	0.0	21 July*	0.2
Sum	29.2	Sum	62.0

2007	Rainfall (mm)	2007	Rainfall (mm)
14 August	0.2	9 September	0.0
15 August	9.4	10 September	0.0
16 August	2.2	11 September	42.0
17 August	0.0	12 September	7.2
18 August	0.0	13 September	0.2
19 August*	0.4	14 September*	0.0
Sum	12.2	Sum	49.4

Table 6- High marsh end-of-season standing total (EOST) biomass. Though not necessarily restricted to *Spartina patens*, most studies below are values for a *Spartina patens* marsh.

Latitude	Location	g m^{-2}	Reference
48.0ºN	Quebec, Canada	440	This study
45.5ºN	Nova Scotia, Canada	403	Gordon et al., 1985
45.1ºN	New Brunswick, Canada	379	Connor and Chmura, 2000
43.3ºN	Maine[1], USA	550	Crain, 2007
41.4ºN	Rhode Island, USA	667	Wigand et al., 2004
41.2ºN	Connecticut, USA	804	Turner, 1976
40.4ºN	New York, USA	503	Turner, 1976
39.6ºN	New Jersey, USA	674	Turner, 1976
39.3ºN	New Jersey, USA	694	Windham, 2001
38.8ºN	Delaware, USA	608	Linthurst and Reimold, 1978
37.9ºN	Maryland, USA	521	Selikar, 2003
35.5ºN	North Carolina, USA	1227	Turner, 1976
31.2ºN	Georgia, USA	744	Linthurst and Reimold, 1978
31.1ºN	Louisiana, USA	2194	White et al., 1978
31.1ºN	Louisiana, USA	2466	Cramer et al., 1981
29.3ºN	Mississippi, USA	1242	Turner, 1976

[1] Estimated from graphs

Table 7- Range of β values, an indication of root distribution, for salt marshes in North America. The β coefficient is calculated from the equation $Y=1-\beta^d$, where Y is the cumulative proportion of roots at d depth (Gale and Grigal, 1987). Higher β value means higher proportion of roots at depth. Modified table from Murphy and Moore (*in preparation*).

Location	β	d (cm)	Reference
Île Verte, Quebec	0.83[a]	30	This study
Dipper Harbour, New Brunswick	0.91[b]	30	Connor and Chmura, 2000
Great Sippewissett Marsh, Massachusetts	0.77[a]	20	Valiela et al., 1976
Hog Island, Virginia	0.89[b]	50	Windham, 2001

[a] high marsh, *S. patens* dominated
[b] *S. patens*

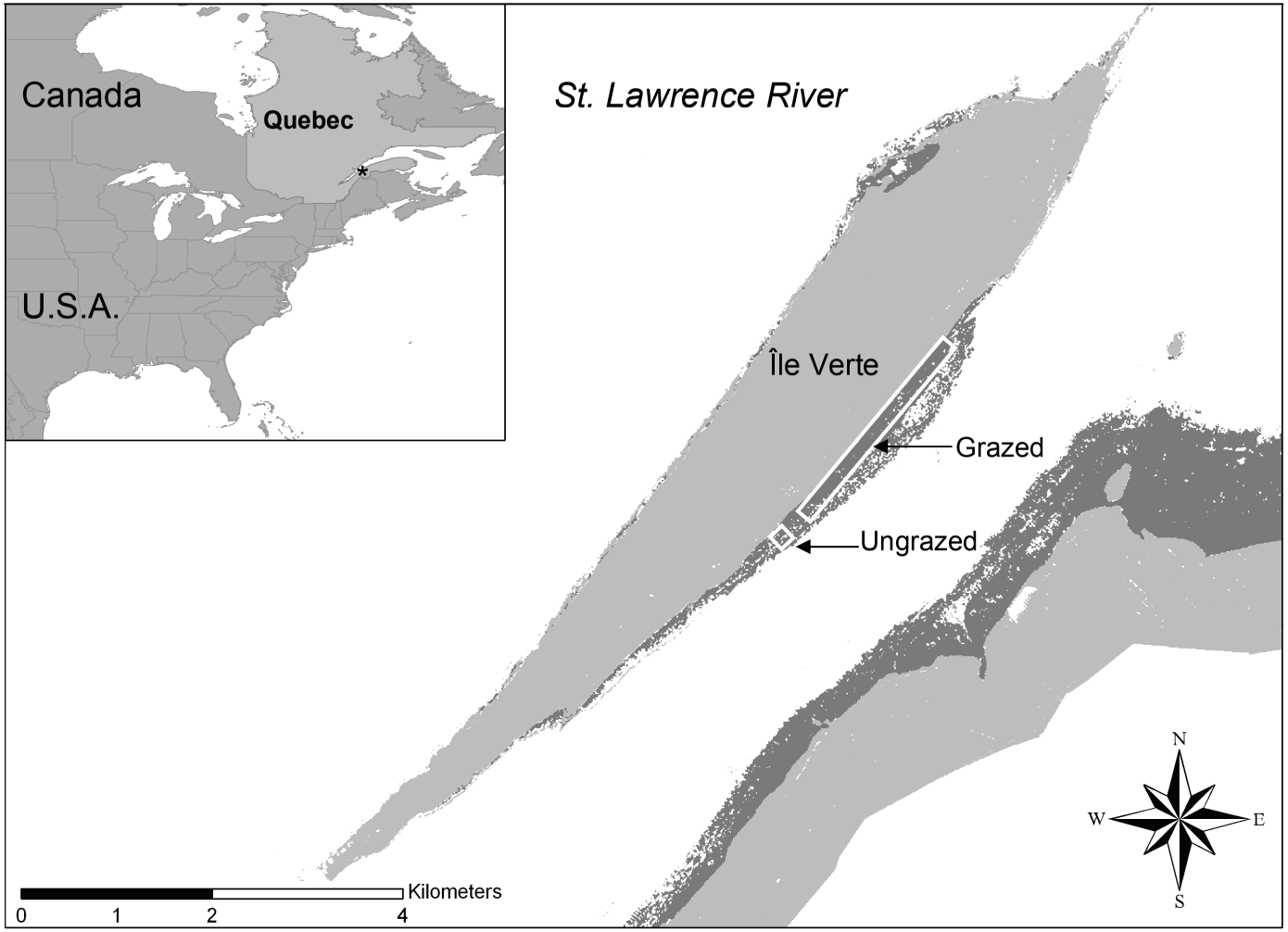

Fig. 1- Inset map depicts the location of Île Verte, denoted by a star (Natural Resources Canada 2003). The larger map shows distribution of salt marsh, in dark gray, around the island and neighboring mainland with location of grazed and ungrazed areas noted (adapted from 1990-1991 vegetation map series of Létourneau and Jean 2005).

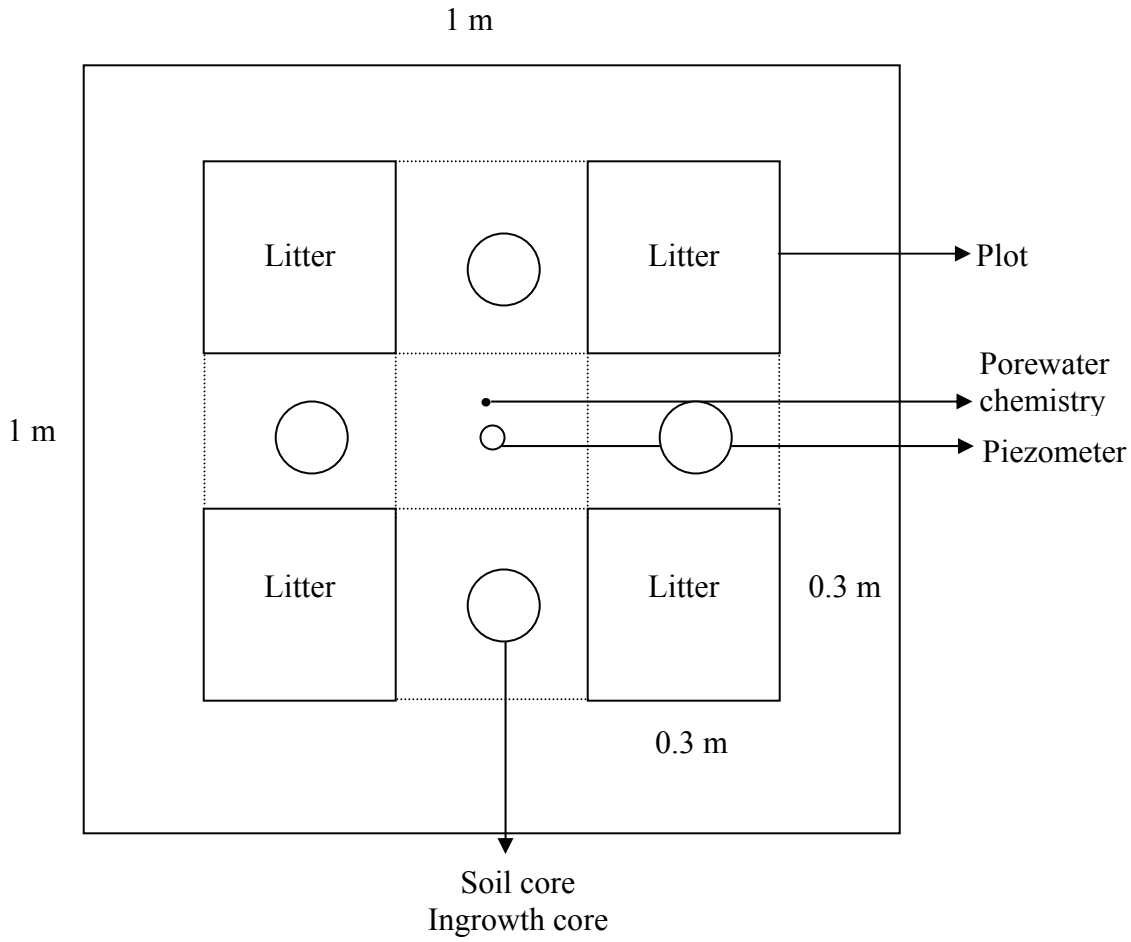

Fig. 2 - Schematic layout of one experimental unit (station). Plots were nested within a station. End-of-standing crop were collected from litter plots.

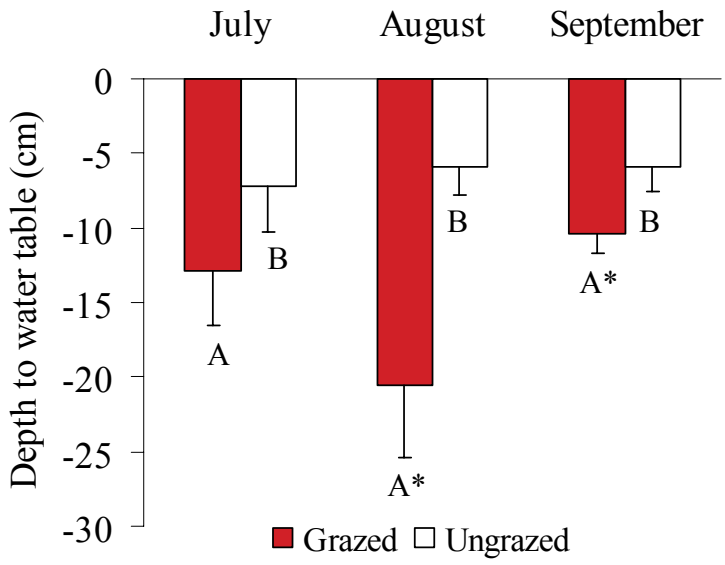

Fig. 3 - Depth to water table (+SE) in grazed and ungrazed areas of the high marsh. Different letter represents overall treatment effect. Asterix represents treatment effect within a month.

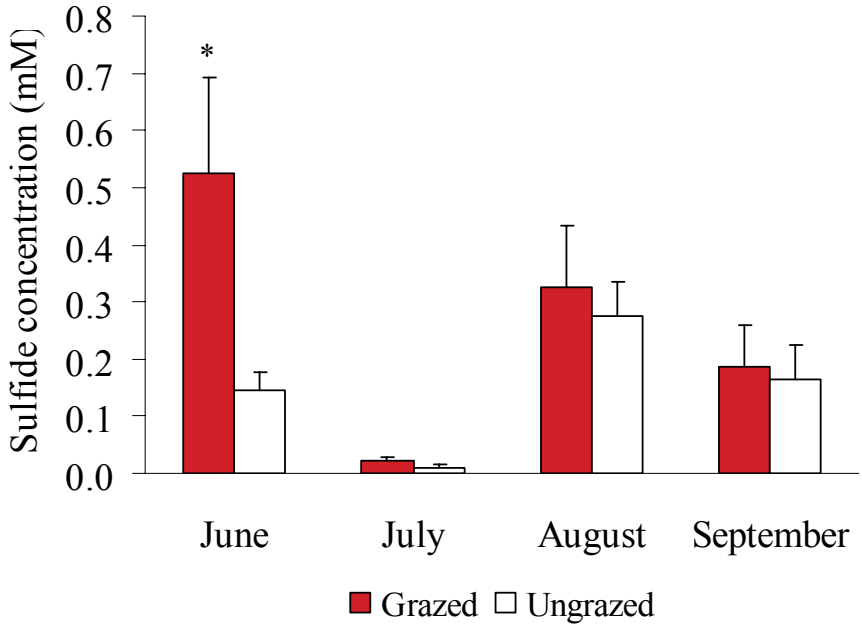

Fig. 4 - Average monthly sulfide concentration (+SE) in porewater. Asterix represents treatment effect within a month.

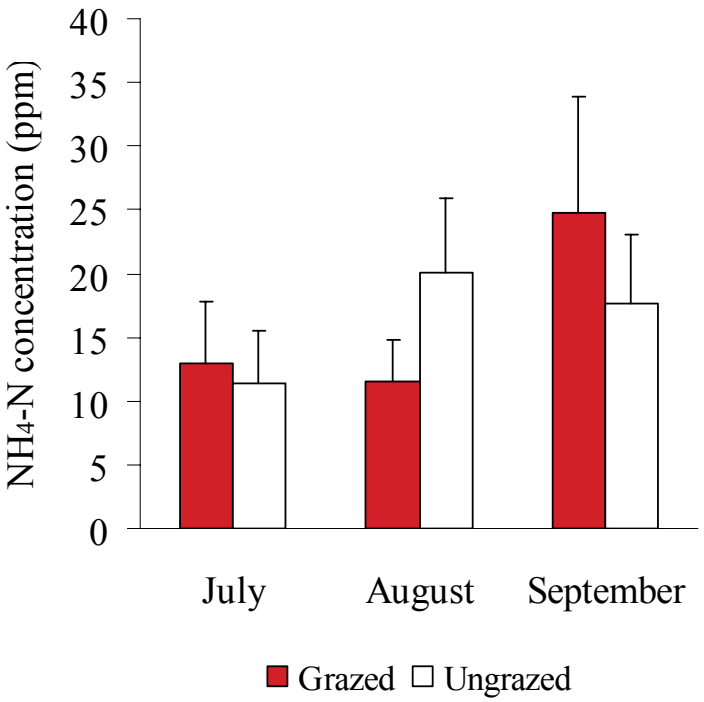

Fig. 5 - Average monthly ammonium concentration (+SE) in porewater. July samples were analyzed differently from August and September because of a change in protocol.

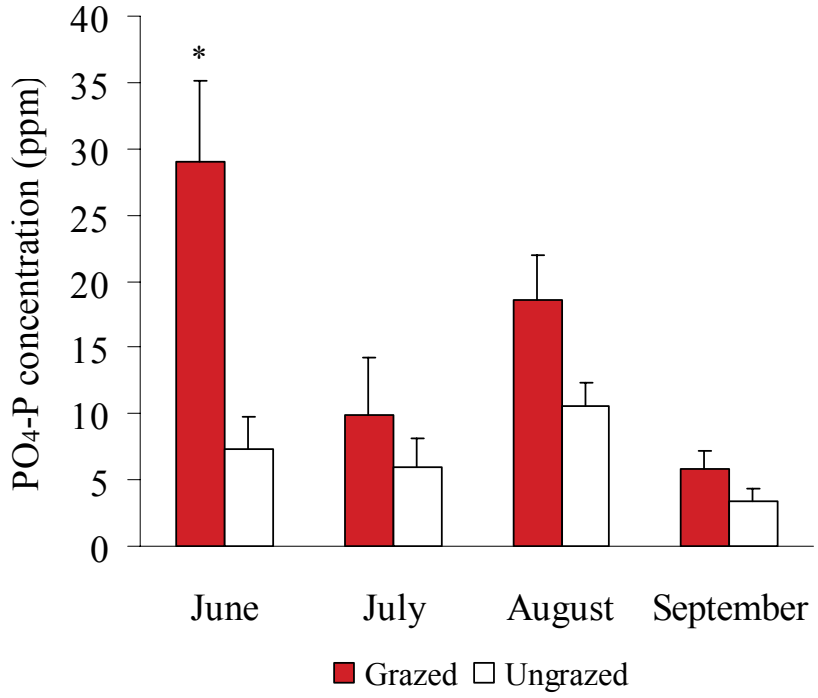

Fig. 6 - Average monthly phosphate concentration (+SE) in porewater. Asterix represents treatment effect within a month.

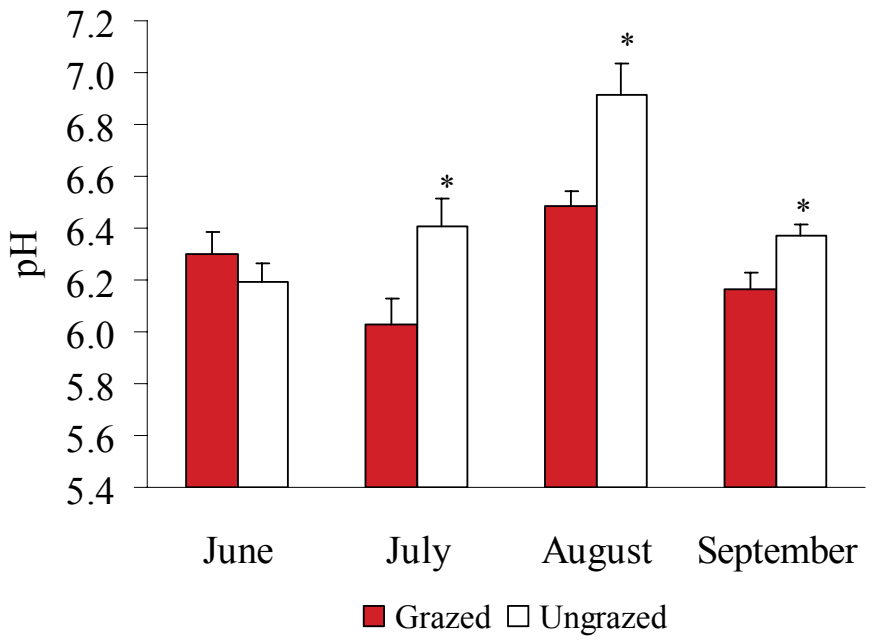

Fig. 7 - Average monthly pH concentration (+SE) in porewater. Asterix represents treatment effect within a month.

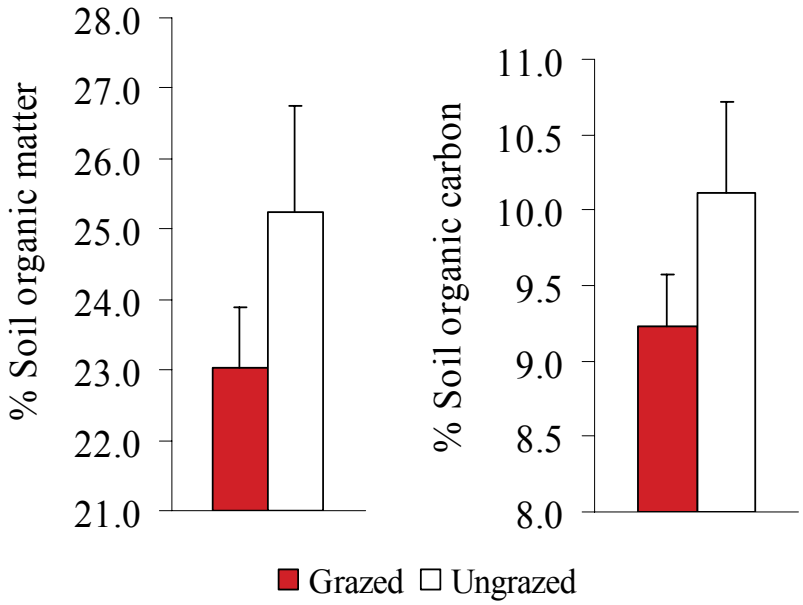

Fig. 8 - Percent of soil organic matter and soil organic carbon (+SE) for 0-10 cm soil cores.

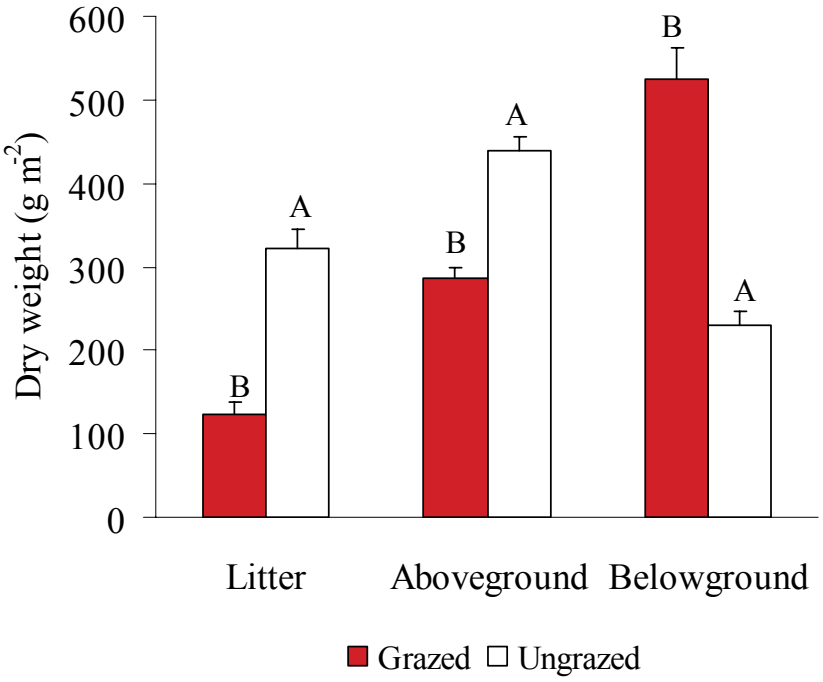

Fig. 9 - Average litter, aboveground (end-of-season standing crop) and belowground (30 cm) dry weight biomass (+SE). Different letter represents overall treatment effect.

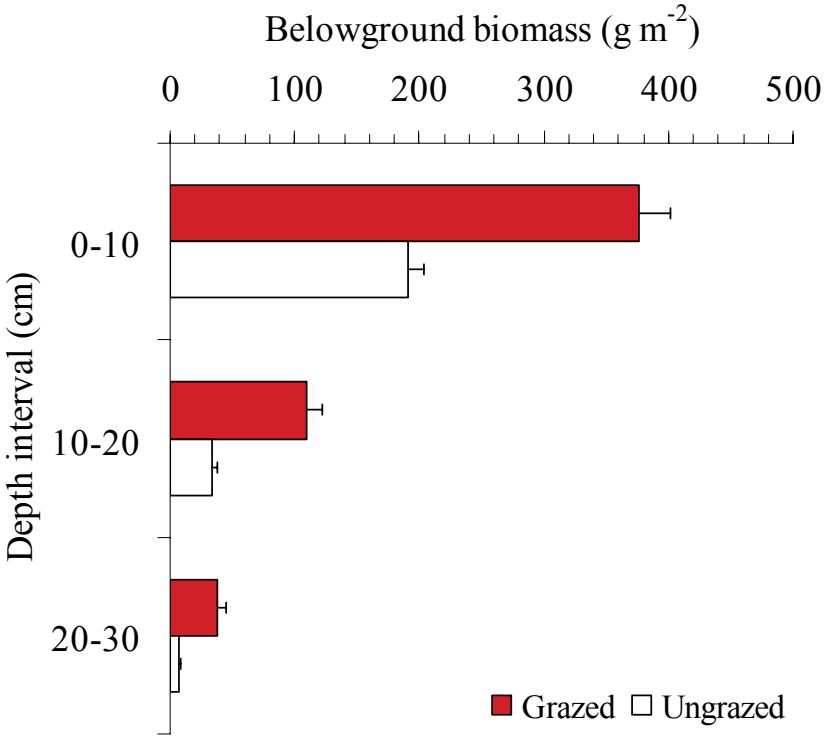

Fig. 10 – Cumulative belowground biomass (+SE) in each 10 cm interval. The 20-30 cm interval was normalized.

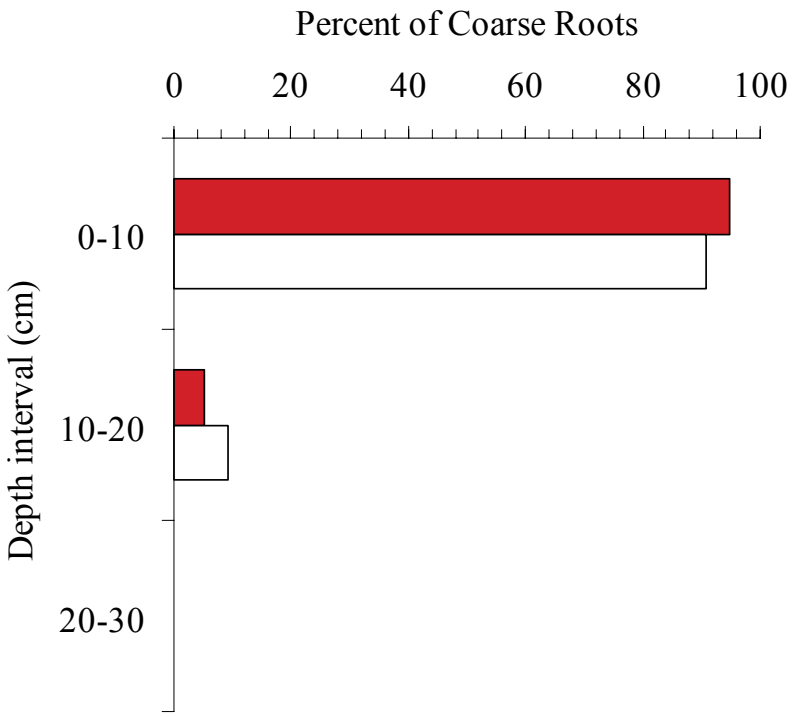

Fig. 11a- Percent of coarse roots by dry weight in each depth interval.

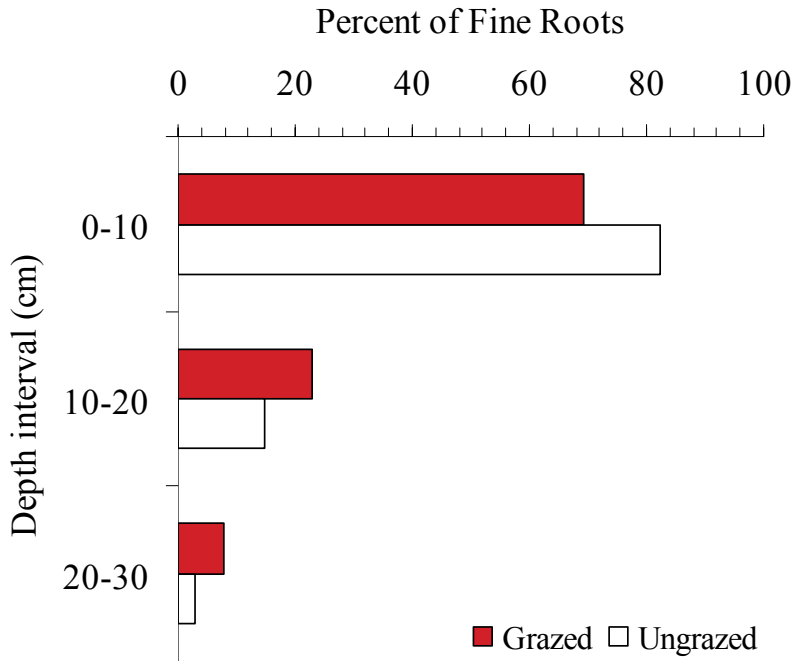

Fig. 11b.- Percent of fine roots by dry weight in each depth interval.

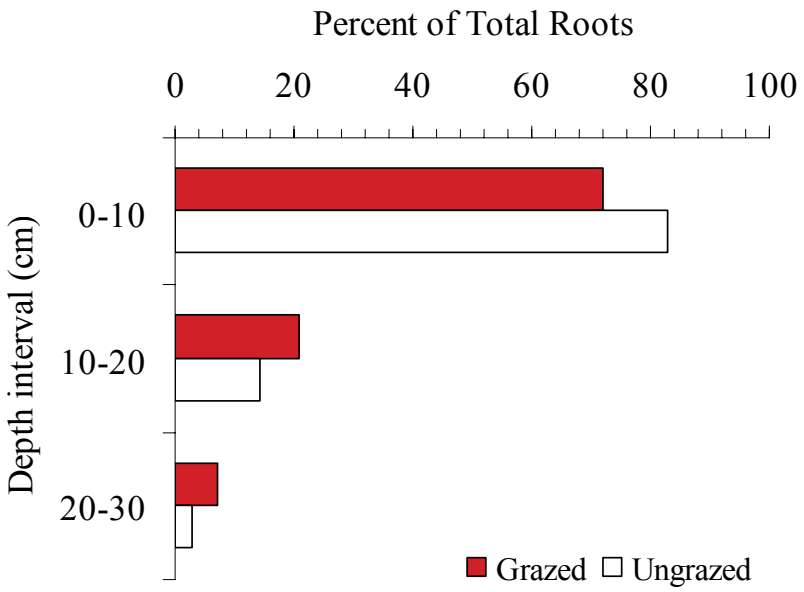

Fig. 12- Percent of total dry weight belowground biomass by depth interval.

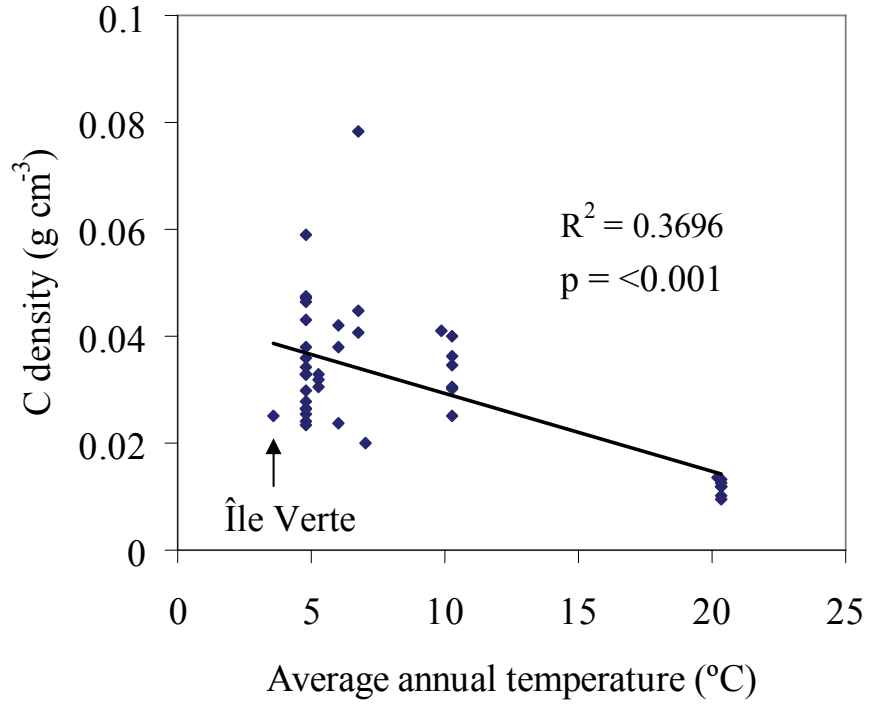

Fig. 13- Simple linear regression of average annual temperature and soil carbon density of *Spartina patens* marshes. Data from Chmura et al. (2003).

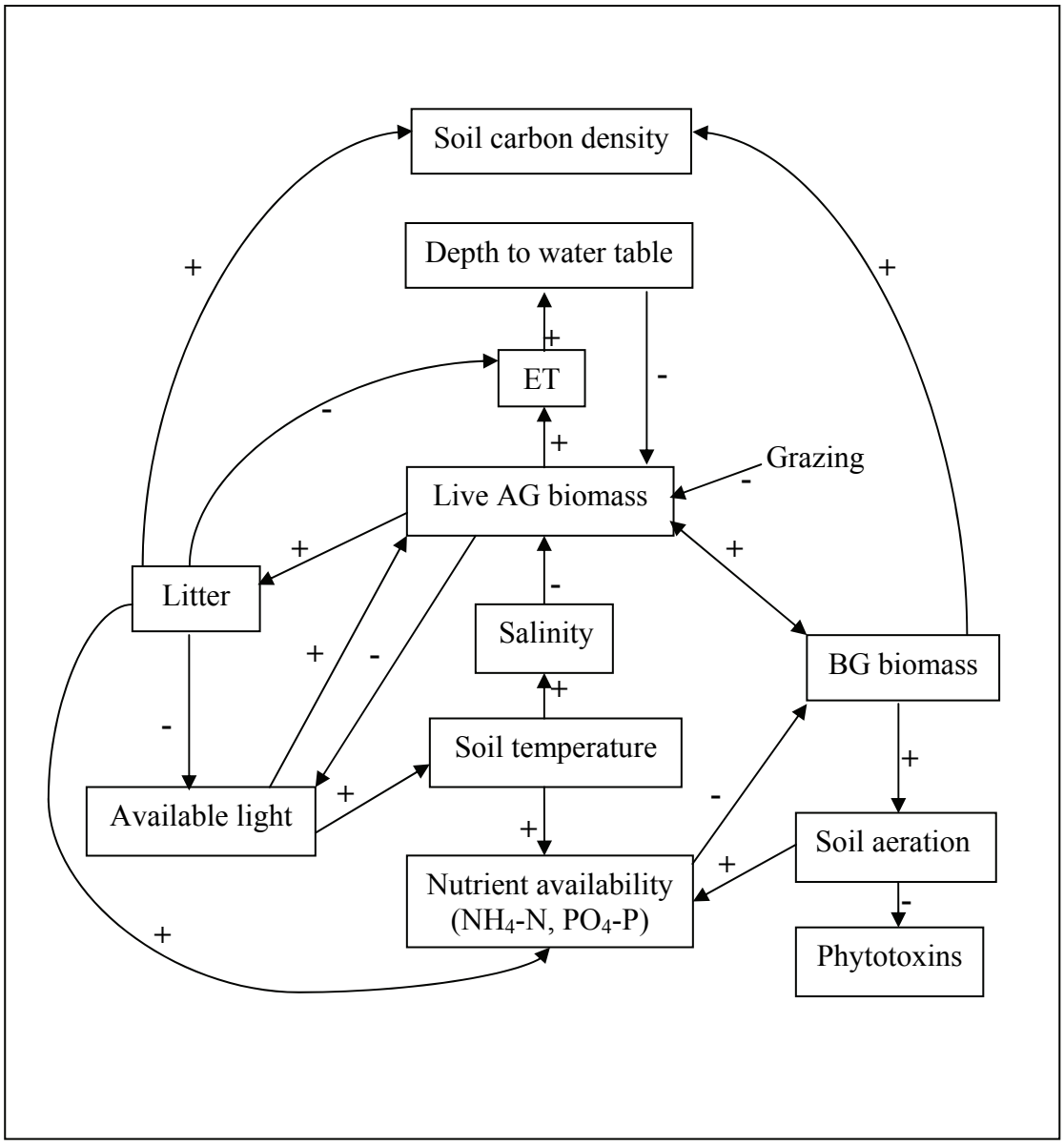

Fig. 14- Potential feedback cycle initiated by grazing.

Appendix 1. Normality and homogeneity of variance values for biomass and soil parameters. The robustness of an ANOVA test relies on normal and homogeneous data. Boldface denotes significance.

	Normality				Homogeneity of variance[a]	
	Grazed		Ungrazed			
	Shapiro -Wilks	*p*	Shapiro -Wilks	*p*	Levene	*p*
Biomass						
Litter (g m^{-2})	0.953	0.698	0.880	0.131	*0.898*	*0.356*
End-of-season crop (g m^{-2})	0.828	**0.032**	0.964	0.832	*0.001*	*0.977*
All belowground biomass (20 cm, g m^{-2})	0.877	0.122	0.976	0.944	*7.833*	***0.012***
Coarse (>2 mm)	0.635	**0.000**	0.901	0.224	2.102	0.164
Fine (≤2 mm)	0.948	0.647	0.968	0.868	3.546	0.076
All belowground biomass (30 cm, g m^{-2})	0.880	0.131	0.981	0.970	*9.445*	***0.007***
Coarse (>2 mm)	0.635	**0.000**	0.901	0.224	2.102	0.164
Fine (≤2 mm)	0.917	0.330	0.965	0.845	4.285	0.053
Root volume (20 cm, cm^3)	0.964	0.841	0.982	0.975	4.827	**0.042**
Root volume (20 cm)[1]	0.948	0.668	0.987	0.993	1.527	0.233
Root volume (30 cm, cm^3)	0.961	0.813	0.975	0.936	4.187	0.057
Root volume (30 cm)[1]	0.937	0.547	0.985	0.985	1.088	0.312
Root:shoot ratio (20cm)	0.901	0.223	0.921	0.364	*14.606*	***0.001***
Root:shoot ratio (30cm)	0.859	0.073	0.909	0.277	*17.391*	***0.001***
Total live biomass (20cm, g m^{-2})	0.944	0.595	0.973	0.914	*1.232*	*0.282*
Total live biomass (30cm, g m^{-2})	0.949	0.659	0.973	0.913	*1.689*	*0.210*
Soil						
Bulk density	0.848	0.055	0.770	**0.006**	0.356	0.558
Percent Organic Matter	0.874	0.111	0.874	0.112	4.449	**0.049**
Percent Organic Carbon	0.874	0.111	0.874	0.112	4.457	**0.049**
Carbon density (g m^{-3})	0.815	**0.022**	0.975	0.933	0.124	0.729

[1]Square root transformation

[a] Homogeneity of variance is based on the median, except for italics, in which the test is based on the mean.

Appendix 2. Normality and homogeneity of variance values for water table and porewater chemistry. The robustness of an ANOVA test relies on normal and homogeneous data. Boldface denotes significance.

	Normality				Homogeneity of variance[a]	
	Grazed		Ungrazed			
	Shapiro -Wilks	*p*	Shapiro -Wilks	*p*	Levene	*p*
Depth to water table	0.851	**0.001**	0.874	**0.002**	2.577	0.114
Depth to water table[1]	0.921	**0.029**	0.909	**0.014**	0.015	0.903
Porewater chemistry						
Salinity (‰)	0.951	0.084	0.850	**0.000**	1.431	0.235
Sulfides (mM)	0.666	**0.000**	0.698	**0.000**	3.300	0.073
NH_4-N: all* (ppm)	0.582	**0.000**	0.679	**0.000**	0.001	0.981
NH_4-N: all[2]	0.935	0.068	0.925	**0.036**	0.004	0.947
NH_4-N: July (ppm)	0.587	**0.000**	0.618	**0.000**	0.042	0.840
NH_4-N: July[2]	0.947	0.635	0.953	0.706	0.019	0.892
NH_4-N: August and September (ppm)	0.561	**0.000**	0.696	**0.000**	0.009	0.926
NH_4-N: August and September[2]	0.936	0.203	0.921	0.103	0.210	0.649
PO_4-P (ppm)	0.805	**0.000**	0.734	**0.000**	9.969	**0.002**
PO_4-P[1]	0.961	0.180	0.986	0.899	4.484	**0.037**
pH	0.973	0.443	0.915	**0.005**	0.082	0.776

[a] Homogeneity of variance is based on the median.
* July to September
[1]$\log_{10}$ transformation
[2]inverse transformation