VEGETATION MOSAICS, PATCH DYNAMICS AND ALTERNATE STABLE STATES IN AN ARCTIC INTERTIDAL MARSH

by

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Degree of Master of Science

Graduate Department of Botany, University of Toronto, 2003

Abstract

Soil degradation occurs following loss of vegetative cover at both the landscape and individual patch scale at La Pérouse Bay, Manitoba. At the landscape scale, soils from vegetated patches had a higher infiltration rate, and higher moisture, organic content and nitrogen content, but lower salinity and bulk density, than comparable values for exposed mineral soils. These differences in soil properties resulted in higher establishment success of the forage grass, *Puccinellia phryganodes,* in vegetated than in mineral soils. At the patch scale, similar to the landscape scale, soil conditions became more adverse for plant growth with increasing patch size (2.5 to 40 cm diameter) following experimental grubbing, resulting in a decrease in the re-colonization potential of *Puccinellia.* Localized vegetation removal by geese limits plant-soil interactions resulting in areas of intact intertidal salt marsh changing to an alternate stable state of exposed mud flats, where soil conditions offer little possibility of re-vegetation.

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Chapter 1: General Introduction

1.1. Land and soil degradation and the impacts of herbivores

Roughly 43% of the Earth's vegetated land has been affected adversely by recent impacts of land use resulting in loss of vegetation and soil degradation (Daily 1995). This land degradation (declines in species diversity and primary production, and increases in soil erosion) has been one of the more long-term, chronic effects of agriculture, forestry, and industrial activities on landscapes (Dobson *et al.* 1997). In particular, soil degradation (a loss or reduction of soil functions, or soil uses (Blum 1998)) has been particularly severe: the extent of soil degradation induced by human activity since 1945 is about 17% of the Earth's vegetated land (Daily 1995). Changes in soil properties may be a general measure of the changes in ecosystem function that underlie various forms of degradation, including desertification (Schlesinger *et al.* 1990).

Soil degradation is often a consequence of herbivory (Daily 1995). Herbivores strongly influence both the structure and function of plant communities (Crawley 1983). Besides their direct effects on vegetative cover, herbivores also influence soil-vegetation interactions (Schlesinger *et al.* 1990, Graetz 1991, Van de Koppel *et al.* 1997, Jefferies 1999). Intense grazing pressure by domesticated and semi-domesticated animals accounts directly for 35% of all soil degradation worldwide (Daily 1995). As a result, high densities of grazers, particularly in semi-arid systems, frequently lead to vegetation collapse (Schlesinger *et al.* 1990). Herbivores may trigger rapid and irreversible vegetation changes in grazing systems resulting in large-scale vegetation loss and soil degradation (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Van de Koppel and Rietkerk 2000).

This study focuses on degradation resulting from increases in a population of lesser snow geese (*Anser caerulescens caerulescens* L.). In the coastal marshes of Hudson Bay, increases in the number of geese have resulted in large-scale vegetation loss, as well as adverse changes in soil conditions. In this chapter I discuss the conceptual framework on which the study was based. I discuss the topics of alternate stable states and vegetation mosaics, disturbance patch dynamics and patch re-colonization, and facilitation in stressful environments. I conclude by introducing the study system, the intertidal marsh at La Pérouse Bay, Manitoba, and how the vegetation mosaic in this system relates to the above topics.

1.2. Alternate stable states and vegetation mosaics

The idea that ecosystems under very similar environmental conditions may exist in two (or more) contrasting stable states originated from work on theoretical models (Holling 1973, May 1977). Natural systems respond to environmental change in different ways (Fig. 1.1). They may respond to steady environmental change in a gradual manner (Fig. 1.1a). Others may not respond over a certain range of conditions but then respond more strongly when conditions approach a critical threshold (Fig. 1.1b). In other situations, the ecosystem response curve is ‘folded’ backwards producing non-linear changes (Fig. 1.1c) implying that the ecosystem has two alternative stable states, separated by an unstable equilibrium (Scheffer *et al.* 2001).

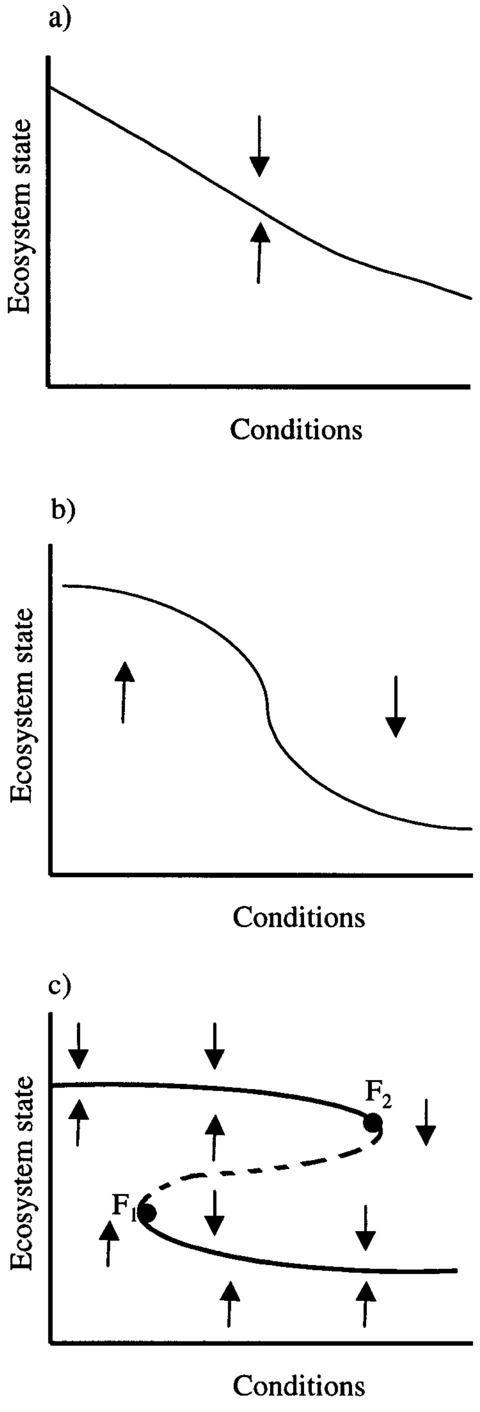


Figure 1.1. Possible ways in which ecosystems may respond to environmental change. Solid lines represent equilibria and arrows represent direction of chage. A system may only contain one equilibrium (a,b). If the equilibrium curve is folded backwards (c), three equilibria can exist for a single situation. The dashed middle section is unstable, however, and represents the border between the two alternative states on the upper and lower ends. Modified from Scheffer (2001)

The stability of a system lies in its ability to return to the current, equilibrium state, after a disturbance (Holling 1973). A system is considered to be in a stable state if it returns to the same point after being disturbed (i.e., the system has high resilience) (Sutherland 1974). However, in addition to the original state, an alternative stable state may exist. After small perturbations, a system may return to its original state, however, large perturbations may result in a threshold being reached and the system passes to another stable state (May 1977). Once the system has arrived in the new stable state, simply restoring environmental conditions that existed prior to the collapse (F_2 on Fig. 1.1) may be inadequate to switch back to the original state. Conditions that existed further back in time (F_1 on Fig. 1.1), before the original state collapsed, may be needed before the system can revert to the original state (Scheffer *et al.* 2001). Hence, alternate stable states are essentially irreversible, at least in ecological time (order of decades).

After results from theoretical models predicted the existence of alternate stable states, examples of real communities with alternate stable states were discussed (Sutherland 1974, May 1977). These examples, however, were criticized strongly (Connell and Sousa 1983) and debate has continued on the topic ever since (Peterson 1984, Sousa and Connell 1985, Sutherland 1990, Scheffer *et al.* 2001). Proof of the existence of multiple stable states can be difficult to demonstrate. Observing a large shift in ecosystem properties is not sufficient, as non-linear responses to gradual change can occur in a system, even if there are no alternative stable states (Scheffer *et al.* 2001). Additionally, simply demonstrating the existence of a positive feedback, that could potentially maintain a system in an alternate state, is again insufficient proof (Scheffer *et al.* 2001). The strongest evidence for the existence of a multiple stable state comes from a combination of these approaches, such as observations of repeated shifts, the presence of feedback mechanisms that maintain the different states, and field data that are consistent with the theoretical models of alternative stable states (Scheffer *et al.* 2001).

Despite these difficulties, more recently there have been examples in natural systems of the existence of multiple-stable states. Cultural eutrophication has resulted in shifts between alternate stable states in shallow lakes with a loss of water transparency and vegetation (Scheffer *et al.* 1993, Scheffer *et al.* 1997). Nutrient loading past a critical threshold results in an abrupt shift from clear water to a turbid system. This clear state is self-stabilizing below the nutrient threshold: water clarity is maintained by plants, thus enhancing their own growing conditions (Scheffer 1990). Woody and grassy open landscapes are considered alternate stable states (Dublin *et al.* 1990). These landscapes can be kept open by herbivores because they easily remove seedlings of woody plants. If herbivore numbers drop, however, grasslands may convert to woodlands, which are stable, because adult trees cannot be destroyed by herbivores (Dublin *et al.* 1990). There is evidence that vegetated and bare states in deserts represent alternate stable states based on plant-soil feedback processes (Van de Koppel *et al.* 1997). Perennial vegetation cover allows precipitation to infiltrate into the topsoil, but once this cover is removed, infiltration rate decreases, runoff increases, and water is lost from the system (Graetz 1991). This creates a hostile environment for plant re-establishment, resulting in the maintenance of an alternate, stable, non-vegetated state. (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997). Alternate stable states have been shown in models of tidal flats, where high diatom cover and low levels of erosion characterize one state and high levels of erosion and low diatom cover characterize the other (Van de Koppel *et al.*

2001). Additionally, experimental evidence has supported the assumptions and predictions of this model (Van de Koppel *et al.* 2001).

1.2.1. Vegetation mosaics

In arid and semi-arid regions vegetation commonly occurs in a two-phase mosaic composed of patches of vegetation alternating with patches of (almost) exposed soil (termed "vegetation mosaic" in this study) (Montana 1992, Bromley *et al.* 1997, Rietkerk *et al.* 2000, HilleRisLambers *et al.* 2001) which may represent two alternate stable states (Wilson and Agnew 1992). Vegetation mosaics in these ecosystems are often characterized by the shape, size and spatial distribution of the patches with dense vegetative cover (Aguiar and Sala 1999). Patches of low cover (or exposed patches of soil) are usually considered as a matrix in which the vegetated patches are distributed (Aguiar and Sala 1999). Vegetation mosaic patterning can influence the re-distribution of resources as well as the movement and persistence of organisms (Pickett and Cadenasso 1995). In semi-arid systems vegetation patches may maintain ecosystem productivity by concentrating the limiting resources in areas that are still vegetated (Adler *et al.* 2001).

In general, there are two main types of vegetation mosaics that can be recognized. These examples are based on studies in semi-arid areas. In some ecosystems, patches form bands or stripes ("tiger vegetation mosaic") and in others the dense vegetation patches are irregular in shape ("leopard vegetation mosaic") (Aguiar and Sala 1999). In semi-arid regions, tiger vegetation mosaics often occur on hillsides and the more irregular mosaic or leopard vegetation mosaics occur on flat ground (Klausmeier 1999). Generally, studies have focused on the tiger vegetation mosaic due to its distinct appearance

(Klausmeier 1999), even though leopard vegetation mosaics sometimes appear in the immediate vicinity of the tiger vegetation mosaics (Couteron and Lejeune 2001).

1.2.1.1. Vegetation mosaic formation and its maintenance

Formation of both of these vegetation mosaics has been ascribed to a large number of causes and no consensus has been reached on the processes that account for the mosaics in these semi-arid areas. Hypotheses include variation in the texture of the soil-parent material (Boaler and Hodge 1962), wind (Puigdefabregas *et al.* 1999), selective grazing by herbivores (Kellner and Bosch 1992), soil sodicity and salinity (Belsky 1986), and creation of patches by the actions of termites, or by grazing or fire (Bromley *et al.* 1997). Changes in hydrology on slopes in relation to soil types may explain the formation of striped vegetation mosaics, but irregular mosaics are most likely caused by a slight variation in topography (Klausmeier 1999), or spatial differences in abiotic characteristics, such as soil type (Van de Koppel *et al.* 2002).

The processes that create a vegetation mosaic, however, may not be the same mechanisms that maintain a mosaic (Petraitis and Latham 1999). Vegetation mosaics are often maintained through interactions between plant communities and their environment (Wilson and Agnew 1992). These interactions occur when a plant assemblage brings about a change in the environment in which it exists that provides a more suitable environment for the community (Wilson and Agnew 1992). Plant-environment interactions alter development of vegetation along different pathways that diverge into alternate stable states (Wilson and Agnew 1992). These alternate states are stable in space and time, but intermediate stages between the states are not.

Interactions between plants and their environments are numerous. For example, plants promote water infiltration into soil (Elwell and Stocking 1976, Box and Bruce 1996), reduce erosion (Elwell and Stocking 1976), prevent salt accumulation (Srivastava and Jefferies 1996), and reduce nutrient loss (Aguiar and Sala 1999), all of which encourage plant growth and the persistence of species. There is empirical evidence supporting the persistence of vegetation mosaics as a result of these plant-soil interactions that stabilize edaphic conditions and lead to alternate stable states (Rietkerk *et al.* 2000).

In semi-arid areas the persistence of vegetation mosaics may be linked to the hydrological regime and to plant-water relations. Increased infiltration where vegetative cover exists can increase water availability for vegetation, which may result in increased biomass, and increased vegetation mass may, in turn, increase water availability. Studies of savanna systems indicate that in these ecosystems, vegetation mosaics are caused or maintained by changes in infiltration rate (Wilson and Agnew 1992, HilleRisLambers *et al.* 2001). Theoretical models also show that differing infiltration rates within the mosaic can lead to regular patterns of vegetation alternating with exposed soil (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Klausmeier 1999, HilleRisLambers *et al.* 2001).

Accordingly, a common feature of semi-arid areas that exhibit vegetation mosaics is the strong interaction between vegetative cover and water infiltration. With increased vegetative cover, more water infiltrates into the soil as vegetation intercepts raindrops (Box and Bruce 1996, Anderson and Hodgkinson 1997), and root channels act as conduits for water and leaves funnel water to the soil (Glover *et al.* 1962). In contrast, rain falling on exposed patches, on which there may be a biotic crust, barely infiltrates the soil and runs off where it may be lost from the system (HilleRisLambers *et al.* 2001). Examples of infiltration interactions with vegetation that help maintain patches of vegetation that are surrounded by exposed (or nearly exposed) soil are the Serengeti grasslands (Belsky 1986), rangelands of Africa, Australia and the United States of America (Wilson and Agnew 1992, Van de Koppel *et al.* 1997), and hillslopes of semi-arid areas in Africa (Aguiar and Sala 1999, Seghieri and Galle 1999).

In addition to a reduced infiltration rate in exposed areas, other factors may cause decreased growth in areas with a low standing crop (Van de Koppel *et al.* 1997). Little attention has been paid to nutrient cycling in vegetation mosaics, although nutrient availability is a frequent constraint on plant growth (Guillaume *et al.* 1999). Areas that are bare or have low plant density in a vegetation mosaic frequently have lower levels of soil organic matter and mineral nutrients than areas with dense vegetation (Aguiar and Sala 1999), because vegetation protects the soil against erosion (Elwell and Stocking 1976) and creates plant litter (Aguiar and Sala 1999) leading to higher rates of nutrient retention (Rietkerk and Van de Koppel 1997). Additionally, nutrient and water dynamics in vegetation are not necessarily independent. Soil particles, organic matter, nutrients, and litter may be carried to vegetated areas with surface run-off (Anderson and Hodgkinson 1997, Rietkerk *et al.* 2002) and the vegetation may retain some of these resources (Rietkerk and Van de Koppel 1997).

Recently, it has been proposed that vegetation mosaics, rather than being formed strictly by positive plant-soil interactions, may be solely the outcome of interactions between plants (Lefever and Lejeune 1997, Lejeune *et al.* 1999, Couteron and Lejeune 2001). The propagation-inhibition model (Lefever and Lejeune 1997) states that vegetation mosaics occur particularly when short-range dispersal leads to facilitative interactions between species during establishment. In contrast, where there are inhibitory interactions between propagules at the local scale, populations are dependant on long-range dispersal of propagules (Lejeune *et al.* 1999, Couteron and Lejeune 2001). This model provides a possible alternative explanation of mosaics based only on intrinsic vegetation dynamics (Lefever and Lejeune 1997). Numerous mechanisms can explain differences in the intensity of the competition and facilitation between species that account for the different vegetative components of the mosaics. Seeds accumulate near adult plants, which can increase seedling survival by providing a favourable microenvironment for growth (Aguiar and Sala 1999). In other developmental stages, however, adult plants can reduce seedling survival because of competition for light, water and nutrients (Franco and Nobel 1988).

1.2.2. Grazing and alternate stable states

Herbivores may trigger rapid, irreversible vegetation changes in grazing systems resulting in alternate stable states, often characterized by a loss of vegetation (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Van de Koppel and Rietkerk 2000). Evidence for the existence of alternate vegetation states that result from threshold effects in grazing systems were presented over two decades ago (Noy Meir 1975, May 1977). These types of "catastrophic" vegetation dynamics most often occur in systems with low plant productivity, such as in savanna or tundra systems (Van de Koppel *et al.* 1997). Increasing grazing in these systems can result in continuous vegetative cover changing first into patterned vegetative cover (vegetation mosaic) and then to exposed soil

(Klausmeier 1999). Altering the spatial structure of these ecosystems as a result of grazing can have a large effect on ecosystem functions (Adler *et al.* 2001), as the vegetation changes are often coupled to changes in abiotic conditions (Bazely and Jefferies 1986, Rietkerk and Van de Koppel 1997) that are frequently irreversible (Sinclair and Fryxell 1985, Friedel 1991, Laycock 1991).

Vegetation collapse resulting from a high concentration of grazers occurs frequently in semi-arid systems (Sinclair and Fryxell 1985, Schlesinger *et al.* 1990). In the Sahel region, Schleisinger (1990) found that in years with low rainfall, increasing grazing pressure led to a collapse of herbaceous vegetation. Vegetation collapse following changes in grazing pressure also has been reported for Arctic salt marshes in the Hudson Bay lowlands (Jefferies 1988a, b). Both of these examples show two characteristics of alternate stable states: 1. Increasing the grazing pressure resulted in an irreversible shift between vegetation states. Reducing herbivore numbers has had little effect in restoring the vegetation in the Sahel region (Van de Koppel *et al.* 1997) and exclosures in Arctic salt marshes show little recovery of vegetation (Handa *et al.* 2002). 2. Two-phase mosaics have been found in both the Sahel (Schlesinger *et al.* 1990) and the Arctic (Hik *et al.* 1992, Srivastava and Jefferies 1995, Handa *et al.* 2002) which also may indicate that these phases (vegetated and non-vegetated soils) are part of multiple-stable states (Wilson and Agnew 1992).

Irreversible vegetation shifts and alternate stable states resulting from grazing have been modelled in a variety of ways. Originally, these systems were based on herbivore dynamics without reference to possible soil feedbacks resulting from changes in grazing pressure and they also were based on saturation kinetics of herbivore number

(Noy Meir 1975, May 1977). More recently, models of these grazing systems have been created that do not involve herbivore saturation, in which alternate stable states arise solely due to plant-soil interactions (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Van de Koppel and Rietkerk 2000). Models that combine both herbivory and plant-soil interactions, however, describe equilibria different from models based solely on herbivore dynamics (Rietkerk and Van de Koppel 1997, Rietkerk *et al.* 1997). These herbivore-plant-soil feedback models place different constraints on herbivore numbers (Klausmeier 1999, Van de Koppel and Rietkerk 2000, HilleRisLambers *et al.* 2001, Van de Koppel *et al.* 2002).

Vegetation models based solely on herbivore dynamics were developed by Noy Meir (1975) using predator-prey models created earlier by Rosenzweig and MacArthur (1963). Noy Meir's (1975) models produced different equilibria, based on the levels of herbivory present in the system (Fig. 1.2). Where herbivore saturation occurs, a level of herbivores, H, is maintained at a constant density, and sustained by vegetation which has a biomass of V (May 1977). Where H and V intersect based on a graphical solution, a set of equilibria of herbivore density and vegetation biomass exists (Noy Meir 1975). The equilibrium can be stable, to which the system returns after a disturbance, or an unstable equilibrium (or turning-point) may exist from which the system diverges with even a slight change in herbivore numbers (Noy Meir 1975). When no herbivore is present, the rate of change of vegetation biomass (dV/dt) increases as vegetative biomass (V) increases, but as V continues to increase, dV/dt decreases as shading and competition

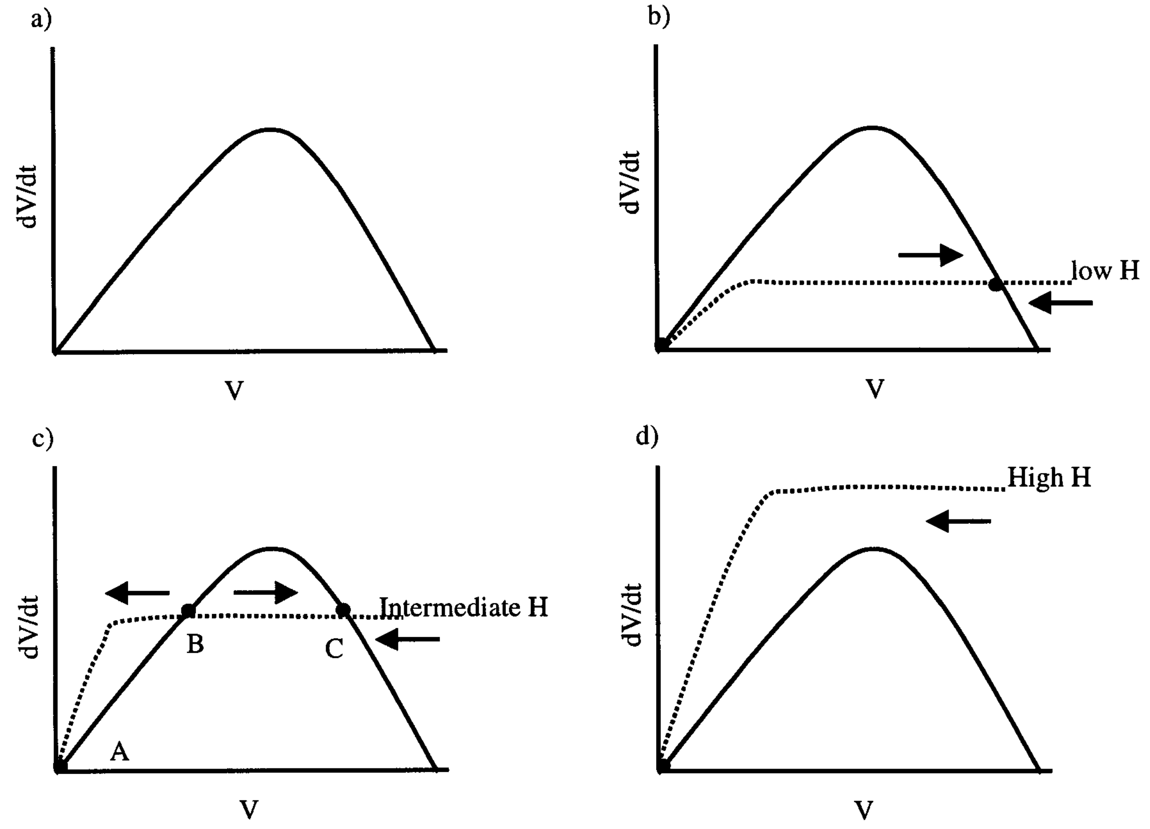


Figure 1.2. The rate of change of vegetation biomass, dV/dt is shown as a function of vegetation biomass, V. The solid curve is the natural, ungrazed vegetation growth rate. The dashed curves are loss rates due to grazing at b) low, c) intermediate and d) high herbivore densities. The points of intersection of the curves, marked by a solid circle, corresponds to possible equilibrium points. Arrows represent the direction of the net growth rate: where the solid curve lies above the dashed one, the net growth rate is positive (and arrow points towards higher values of V), where the solid curve lies below the dashed one, the net growth rate is negative (and arrow points towards lower values of V). For further discussion, see text. Modified from May (1977) and Noy Meir (1975).

become increasingly important (Fig. 1a). At low levels of herbivory, (Fig. 1.2b) there are two equilibria, a stable one with vegetation and an unstable one without. As herbivory increases, a threshold may be crossed, whereupon three equilibria exist: a single unstable point at intermediate plant density (B on Fig. 1.2c), and two stable points (A and C on Fig. 1.2c), one with a high plant density and one without vegetation (Fig. 1.2c). Even at the equilibrium where a high plant density exists, if an environmental event decreases the plant density to below a threshold value, the system will collapse (Rietkerk and Van de Koppel 1997). At very high levels of herbivory there is only a single equilibrium where vegetation is no longer present (Fig. 1.2d). At this equilibrium, resource levels are insufficient for plants to compensate for herbivore consumption and the system collapses (Rietkerk and Van de Koppel 1997).

These early theoretical studies emphasized saturation of herbivore density to explain catastrophic behavior of semi-arid grazing systems, but more recent theoretical studies indicate that multiple-stable states and catastrophic behavior can be solely the outcome of plant-soil interactions (Van de Koppel *et al.* 1997, Van de Koppel and Rietkerk 2000). Models have been created that contain two alternate stable states in grazed systems which do not involve herbivore saturation (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997): one with no vegetation because of adverse soil characteristics, and one with vegetation where edaphic conditions are suitable for plant growth and which allow plants to compensate for losses due to grazers (Van de Koppel *et al.* 1997). These theoretical models of grazing in semi-arid areas indicate that an interaction between plant standing crop and rates of water infiltration can induce vegetation mosaics in semi-arid grasslands (Klausmeier 1999, HilleRisLambers *et al.*

2001) associated with multiple-stable states and catastrophic changes (Van de Koppel *et al.* 1997). In areas without vegetation most of the rainfall is lost as surface run-off, resulting in lower water and nutrient availability, and this creates a positive feedback that leads to loss of vegetative cover (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997).

Although these plant-soil interactions may lead to collapse of vegetation, even without increased herbivory, herbivory may accelerate the plant-soil feedbacks. Herbivory reduces vegetation cover resulting in soil degradation that further increases plant losses. This leads to loss of resources within the plant and this resource loss limits the ability of plants to cope with further soil degradation (Charney *et al.* 1975, Rietkerk and Van de Koppel 1997, Rietkerk *et al.* 1997, Van de Koppel *et al.* 1997). Models that contain both herbivore dynamics and plant-soil interactions describe equilibria similar to those that contain herbivore dynamics alone. At low levels of herbivory, there are two equilibria, one stable with vegetation and one stable without, as in Noy Meir's model (1975) that does not include plant-soil interactions. At intermediate levels of herbivory, there are again three equilibria, an unstable one at intermediate plant density and two stable ones, one with high plant density and one with no vegetative cover (Rietkerk and Van de Koppel 1997). Finally, at very high levels of herbivory there is only a single equilibrium: the equilibrium where vegetation is lost (Rietkerk and Van de Koppel 1997). This is where the primary difference between herbivore saturation models and models that combine both herbivore-saturation and plant-soil interaction lies. In herbivore-saturation models, at high levels of herbivory, the system is overgrazed, and lowering the level of herbivory can result in recovery of the vegetation. However, if herbivore saturation and plant-soil interactions are combined, high levels of herbivory result in a stable degraded state, where lowering herbivory levels has no effect on cover (Rietkerk *et al.* 1997).

Combination herbivore-plant-soil interaction models put a variety of constraints on herbivore numbers, with differing results. In models created by Klausmeier (1999) and HilleRisLambers (2001), herbivore presence is even across the landscape and the output from the model can only explain collapse of primary production on the scale of patches (HilleRisLambers *et al.* 2001) with the spatial re-distribution of rainwater preventing irreversible vegetation collapse on a larger scale (Van de Koppel *et al.* 2002). If both herbivores and water, however, are re-distributed in the model, coarse-scale degradation and vegetation collapse can be explained (Van de Koppel *et al.* 2002). If vegetative cover is reduced either by herbivory or lack of soil moisture or both, herbivores graze on remaining patches, which may ultimately lead to large-scale vegetation collapse (Van de Koppel *et al.* 2002). The models assume that the herbivore and vegetation dynamics are not coupled, the herbivore population size remains constant as vegetation density changes dramatically (Van de Koppel and Rietkerk 2000). This may be realistic for managed systems but does not describe natural populations. However, irreversible vegetation losses may also occur in systems in which herbivore numbers are affected by plant density: at a low plant standing crop severe soil degradation may prevent recovery, even after food shortages have caused herbivore numbers to collapse (Van de Koppel and Rietkerk 2000). Models that couple herbivore numbers to plant density suggest that multiple-stable vegetation states can also exist in systems where the herbivore population size fluctuates, but these states are less evident than in systems in which herbivore population size is stable (Van de Koppel and Rietkerk 2000).

Thus, grazing in semi-arid systems can result in a vegetation mosaic or vegetation collapse, depending on the effect of the soil-plant interactions, especially when changes in infiltration rate occur (Van de Koppel *et al.* 2002). Run-off from bare patches can result in increased water availability in vegetated patches in catchment areas (Montana 1992, Bromley *et al.* 1997) and may allow the patches to survive under increased grazing (Van de Koppel *et al.* 2002). In other systems, however, re-distribution of water may have little effect and the degradation results in the collapse of the system (Van de Koppel *et al.* 2002). These overgrazed systems cannot be restored on a practical time scale simply by lowering herbivore impact (Friedel 1991).

1.3. Disturbance, patch dynamics and patch re-colonization

Disturbance is a ubiquitous process in communities and ecosystems (Keddy 2000). A disturbance is a short-lived event (with a duration shorter than the life-span of the organisms involved) that causes a measurable change in a community (Keddy 2000), and often results in loss of biomass (Sousa 2001). Disturbance results in changes in the structure of the physical environment as well as the distribution of organisms within that environment (Wiens 2000). Disturbances can increase the availability of limiting resources for survivors and for new colonists, but it can also increase mortality by removing the ameliorating effects of previous residents (Sousa 2001). A disturbance can be characterized by its magnitude (both the intensity and the severity), duration, frequency, predictability, rotation period and by the size of the disturbed areas ("patches") produced (Levin and Paine 1974, Sousa 1984b, Keddy 2000).

Heterogeneity within ecosystems is often the result of disturbance. Many types of disturbance are highly localized which creates open spaces in discrete patches or gaps within a background assemblage of organisms (Sousa 1984a, Pickett and White 1985, Sousa 1985). Landscapes become a heterogeneous mixture composed of discrete patches of disturbance (Pickett and Cadenasso 1995). There is spatial and temporal variation in the formation of patches in landscapes, which leads to a shifting mosaic of patches. Patch dynamics consists of the spatial pattern of patches in combination with the changes in conditions within these patches (Pickett and Cadenasso 1995).

Much of the work on patch dynamics is based on forest studies, yet the processes are important in all ecosystems (Keddy 2000). Abiotic factors create patterns of disturbance: patches may be created by wind-throw or fire in forests (Frelich and Reich 1995), patches are created in salt marshes by deposition of wrack (Bertness and Ellison 1987) and frost-heave in Arctic environments creates disturbance (Nylehn and Totland 1999). However, organisms themselves also create or influence abiotic heterogeneity either directly or indirectly (Stewart *et al.* 2000). For example, by intercepting and trapping rainfall plants can create soil moisture gradients (Wilson 2000), and animals maintain vegetation heterogeneity as a result of their grazing, trampling and burrowing (Stewart *et al.* 2000).

There are four mechanisms by which plant populations re-establish in disturbed patches (Sousa 2001): (1) vegetative re-growth of individuals within the patch that survived the disturbance; (2) recruitment of propagules from within the patch that survived the disturbance; (3) lateral inward encroachment from the surrounding undisturbed assemblage by clonal growth; (4) recruitment from dispersing propagules.

The rate and pattern of re-colonization of a disturbed patch depends on the following conditions (Sousa 1984b):

1. Traits (both morphological and reproductive) of species present when the disturbance occurs.
2. The traits of species which are not present when the disturbance occurs, but that have previously occupied the disturbed site, or live within dispersal distance of it.
3. Characteristics of the disturbed patch including:
    a) the intensity and severity of the disturbance that created it
    b) its size and shape
    c) its location, including the degree of isolation from colonists
    d) the heterogeneity of its internal environment
    e) the time it was created
    f) the presence of corridors between patches, which may affect plant-animal interactions, that, in turn, affect dispersal patterns (Tewksbury *et al.* 2002)

These traits, and their interactions (c.f. "regeneration niche" Grubb 1977), must be considered in order to predict processes of regeneration and succession in patches (Shumway and Bertness 1994).

Patch size and shape, in particular, can be useful predictors of the type of regeneration within patches, primarily due to the alteration of the circumference to area ratio (Forbes *et al.* 2001). This ratio increases as patch size decreases, which has a number of consequences for re-colonization (Sousa 1984b). Within a patch, the physical and biological environment also can vary with patch area (Sousa 1984b) which can affect re-colonization.

The organisms that surround a disturbed patch can have both positive and negative effects on recruitment. The direction and strength of these effects vary with patch size and shape, as well as with the characteristics of neighbours and the environmental conditions (Sousa 2001). Neighbours can affect recruitment by influencing the availability of propagules in the centre. Where plants are present on the perimeter of small patches there is a short distance to the centre of the patch, resulting in a potentially high availability of propagules. In addition, species that reproduce clonally and those whose propagules only disperse over short distances may have denser settlement and a more rapid recruitment in small patches than in large ones (Sousa 2001).

Secondly, neighbours can affect recruitment by changing the within-patch environment. A smaller clearing may have more shading or a depletion of the local nutrient supply compared with larger patches where there are fewer neighbours per unit area (Sousa 1985). Alternatively, neighbouring organisms may ameliorate harsh physical conditions that are often associated with removal of vegetation (Sousa 2001). This amelioration will be greater in small patches than in large patches due to the proportion of the patch that is shaded or covered by the neighbouring canopy. (Sousa 1984b, 2001)

1.4. Facilitation in stressful environments

Although positive interactions have long been recognized as an important driver of community structure and succession (Connell and Slatyer 1977), early work on processes that structure plant communities focused on competition (Connell 1983, Schoener 1983, Goldberg and Barton 1992). Positive interactions can be broadly defined as all non-consumer (non-predatory) interactions among species that positively affect at least one of the species involved (often both), and include facultative and obligatory facilitations and mutualisms (Bertness and Callaway 1994). Facilitation, in particular, occurs when one species enhances the survival, growth or fitness of another (Callaway 1997). Recently, there has been renewed interest in how facilitation influences community processes (Hunter and Aarssen 1988, Bertness and Callaway 1994, Callaway 1995, Callaway *et al.* 1996, Callaway 1997, Callaway and Walker 1997, Hacker and Gaines 1997, Callaway *et al.* 2002). This interest has been incited by the growing evidence that facilitation is probably as ubiquitous as competition among organisms (Hacker and Bertness 1996).

1.4.1. Factors affecting the balance between competition and facilitation

Facilitation is rarely the only effect of one species on another. Plants that benefit from the presence of neighbours are also likely to compete with them (Hunter and Aarssen 1988). Plants grow in close proximity of each other and thus there is the potential for both resource competition and amelioration of the abiotic environment to occur simultaneously. The same species often have co-occurring facilitative and competitive effects (Hay 1986, Aguiar *et al.* 1992, Callaway 1994, Chapin *et al.* 1994, Callaway *et al.* 1996, Pugnaire *et al.* 1996, Brooker and Callaghan 1998, Stachowicz 2001), but factors that influence how the balance between the two effects shifts are poorly understood (Callaway and Walker 1997).

Processes that affect this balance include plant-life stage (Chapin *et al.* 1994, Pugnaire *et al.* 1996), indirect interactions between other community members (Miller 1994) and the intensity of abiotic stress (Bertness and Callaway 1994). A large number of recent studies have examined the effect of abiotic stress on the balance between facilitation and competition (Bertness and Callaway 1994, Casper 1996, Greenlee and Callaway 1996, Brooker and Callaghan 1998, Goldberg *et al.* 1999, Choler *et al.* 2001, Pugnaire and Luque 2001, Tewksbury and Lloyd 2001, Callaway *et al.* 2002). Bertness and Callaway (1994) assert that facilitation should be particularly common in communities that have either high physical stress or high levels of herbivory, but that in those relatively benign environments where there is little herbivory and resources are less limiting for growth, competitive interactions should dominate (Bertness and Callaway 1994). In stressful environments, physical conditions, such as temperature, may limit plant growth more than resource availability and amelioration of these stressful conditions by neighbours may favour growth of a species in the presence of neighbours (Callaway *et al.* 2002).

A number of field experiments have supported the Bertness-Callaway hypothesis across both spatial and temporal gradients of stress (Bertness and Shumway 1993, Bertness and Hacker 1994, Greenlee and Callaway 1996, Choler *et al.* 2001, Pugnaire and Luque 2001, Tewksbury and Lloyd 2001, Callaway *et al.* 2002) but, no conclusive relationship was found in a recent meta-analysis between competition, facilitation and productivity (Goldberg *et al.* 1999), although there was a consistent restriction of facilitation between plants to poor environments with limited resources (Goldberg *et al.* 1999). However, not all studies indicate facilitation in stressful environments where resources are limiting. Negative influences between plants were found in a high alpine environment associated with disturbance (Olofsson *et al.* 1999). Although this study does not necessarily contradict the Bertness-Callaway hypothesis, as plant interactions were not examined across a gradient of abiotic stresses but only at one extreme site, it does emphasize that despite the evidence for high levels of facilitation in stressed environments, negative interactions between plants still occur, altering the balance between facilitating and competitive mechanisms.

1.5. Population increases in lesser snow geese, vegetation loss and soil degradation at La Pérouse Bay, Manitoba

The North American Mid-Continent population of lesser snow geese (*Anser caerulescens caerulescens* L.) has increased in recent decades at a rate of 5-7% per year (Abraham *et al.* 1996). This population, which uses the North American Central and Mississippi flyways and breeds in the eastern Canadian Arctic, has increased from 1.2 million to over 5 million birds between 1963 and 1997 (Abraham and Jefferies 1997). At La Pérouse Bay, on the coast of the Hudson Bay in northern Manitoba, the breeding colony of lesser snow geese has increased in size from 1300 pairs in 1968 to an estimated 44,500 pairs in 1997 (Cooke *et al.* 1995, Abraham, Rockwell & Ross, unpubl. aerial survey in 1997). This increase in population size is thought to be linked to the conversion of natural habitats to croplands and the increased use of nitrogen on agricultural lands (Jefferies 2000). This represents an increased energy and nutrient subsidy to the geese on their wintering grounds and along the flyways (Jefferies 2000). In addition, the presence of refugia along flyways provides the geese with protection as well as food supplements

(Alisaukas and Ankney 1992, Abraham *et al.* 1996, Jefferies 2000, Jefferies *et al.* 2002). Other factors that may be contributing to the population growth are the possibility of reduced harvest rates of geese, and early springs, which has resulted in greater reproductive success of the geese (Francis *et al.* 1992, Abraham *et al.* 1996).

The increased foraging on salt-marsh vegetation at coastal Arctic breeding sites by the increased number of geese has led to vegetation loss and soil degradation. Removal of vegetation by the geese results in loss of plant cover, erosion of organic-rich surface sediments and increased soil surface temperatures and evapotranspiration rates that produce hypersaline conditions (Srivastava and Jefferies 1996, Bazely and Jefferies 1997). This degradation is due both to increased number of geese feeding on the marshes, as well as their foraging habits. At La Pérouse Bay geese usually begin nesting in late May and early June and the goslings hatch in late June or very early July (Cooke *et al.* 1995) The grazing pressure exerted on the intertidal marshes during the post-hatch phase is substantial. Goslings increase their weight by about a factor of 20, from 80 g at hatch to approximately 1500 g, in less than 9 weeks and adults regain body weight lost during brood rearing, often up to 40% of their body weight (Cooke *et al.* 1995).

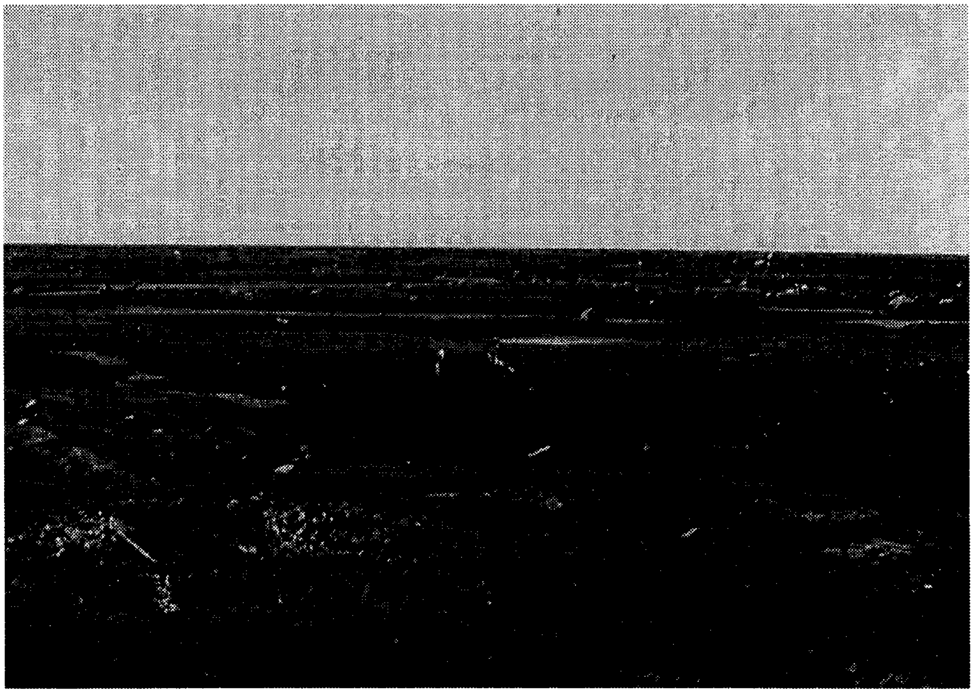
During the growing season, geese primarily graze *Puccinellia phryganodes* and *Carex subspathacea* (Cargill and Jefferies 1984a, b). These plants are both well-adapted to grazing due to their basal meristem and their ability to produce new leaves throughout the season (Kotanen and Jefferies 1987, Bazely and Jefferies 1989). However, the birds arrive in the marshes in early spring, at or just before snow melt, and start feeding before the onset of above-ground growth (Kerbes *et al.* 1990, Hik *et al.* 1992). They grub for roots and rhizomes of the graminoid plants, removing the entire graminoid plant from the ground. As a result of "grubbing" by the geese, the thin veneer of organic matter and plant litter above the sediment is removed as well (Hik *et al.* 1992). This destructive form of feeding produces patches of disturbed sediment in the intertidal marsh, resulting in the loss of graminoid swards and summer forage.

The removal of vegetation by the geese leads to increased soil evaporation rates (Srivastava and Jefferies 1995) which draws inorganic salts from the underlying marine sediments to the surface layers of the soil (Iacobelli and Jefferies 1991). These high soil surface salinities limit growth and survival of plants, further reducing above-ground biomass. The increases in evaporation and soil salinity can produce hypersaline soil in exposed areas (Srivastava and Jefferies 1996).

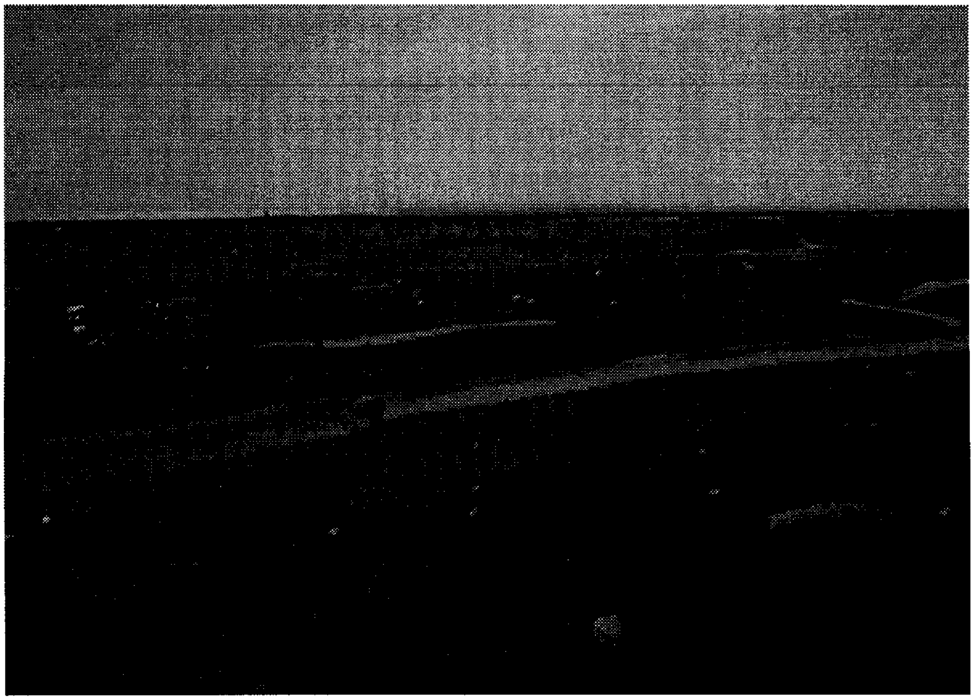
In the former intertidal marsh at La Pérouse Bay, the hypersalinization and soil degradation has resulted in the transformation of intact salt-marsh swards into large areas of exposed sediment devoid of vegetation (Plate 1.1.). Small patches may be re-colonized by inward growth of plants from the perimeter (Hik *et al.* 1992), but the grubbing has resulted in extensive exposed sediment in which re-colonization is difficult. The vegetation losses in this area are severe in recent decades; they can be detected by the use of multi-temporal analysis of LANDSAT data (Jano *et al.* 1998). Over 2500 ha of coastal habitat at La Pérouse Bay showed a decline in vegetation cover in 20 years between 1973 and 1993 (Jano *et al.* 1998). This degradation resulting from shoot pulling of forage plants (Kerbes *et al.* 1990, Kotanen and Jefferies 1997), heavy grazing pressure (Srivastava and Jefferies 1995, 1996) and grubbing (Jefferies 1988a, b) that have destroyed existing plant communities and prompted an “apparent trophic cascade” on

Plate 1.1. Photos of intertidal salt marsh at La Pérouse Bay. a) West marsh prior to extensive damage by lesser snow goose foraging and b) East Bay marsh after intensive foraging by geese.

a)



b)



intertidal vegetation and soils leading to large-scale ecosystem changes (Jefferies and Rockwell 2002).

1.6. Alternate stable states, vegetation mosaics and patch dynamics at La Pérouse Bay, Manitoba

The large-scale ecosystem changes are the result of the existence of alternate stable states in this intertidal marsh. As described earlier, the intertidal marsh has at least two alternate stable states. Firstly, foraging pressure by geese has resulted in an irreversible shift between vegetation states: herbivore exclosures show little recovery of vegetative cover (Handa *et al.* 2002). Secondly, the two-phase mosaic that is present in this system (Hik *et al.* 1992, Srivastava and Jefferies 1995, Handa *et al.* 2002), may be part of a set of multiple stable states (Wilson and Agnew 1992). Swards of salt-marsh vegetation are interspersed with areas in which the vegetation has been lost by the action of geese (Handa *et al.* 2002), resulting in a "leopard vegetation mosaic" in the intertidal marsh.

Vegetation mosaics may be maintained through a variety of plant-soil interactions. Previous work has shown that plant-soil feedbacks initiated by goose feeding may cause vegetation collapse in localized areas, because of a self-amplifying positive feedback between vegetation loss and soil salinity (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996). Other soil variables may be involved in the maintenance of the vegetation mosaic. Soil under vegetated areas has been found to have both a higher soil moisture (Iacobelli and Jefferies 1991, Wilson and Jefferies 1996) and a greater total soil nitrogen content (Wilson and Jefferies 1996). These, and other soil characteristics may differ between the vegetated and non-vegetated states that maintain the mosaic.

An objective of this study was to determine soil characteristics that maintain and characterize the vegetation mosaic at La Pérouse Bay and how these soil properties affect the potential for *Puccinellia phryganodes* to re-colonize non-vegetated soils (Chapter 2). In particular, I examined differences in water infiltration rate between components of the mosaic. I also examined numerous other soil properties that may contribute to the maintenance of the mosaic. These included soil moisture, bulk density, salinity, penetration strength, organic content, total nitrogen, and exchangeable nitrogen. Finally, I examined the ability of *Puccinellia* transplants to grow and survive in the different components of the mosaic.

The processes that create, rather than maintain, vegetation mosaics at La Pérouse Bay, however, may operate at smaller spatial scales. By removing vegetation cover and exposing underlying soil at small spatial scales, geese in the intertidal marshes, create a mosaic of swards and localized patches of exposed soil. Over time, these localized patches may develop into larger areas as a result of further grubbing, creating a large-scale vegetation mosaic described above (Jefferies and Rockwell 2002). The size and shape of these patches may determine both the soil dynamics within the patch, as well as restrict the type of regeneration that is possible within the patch, primarily due to the alteration of the ratio of the circumference to the area (Forbes *et al.* 2001). Thus, the size of the patch may also determine whether there is the potential for complete regeneration of vegetation in the patch over ecological time

A second objective of this study was to examine the influence of patch size on both soil dynamics within the patch, as well as on the ability of *Puccinellia* to re-colonize exposed sediment (Chapter 3). Patches simulating goose grubbing were experimentally created at a variety of patch sizes (ranging from 2.5 to 40 cm in diameter) and soil properties of sediment within the patch were determined over two growing seasons. The size and shape of a patch has a number of consequences for the patterns and rates of patch re-colonization (Sousa 1984b, Forbes *et al.* 2001). The re-growth of *Puccinellia* in the patches was monitored during the second and third growing seasons after patch establishment.

The final chapter of the thesis (Chapter 4) synthesizes the results of both the study of the mosaics as well as the study of patch dynamics in the intertidal marsh. I discuss how similar soil processes may operate on small and large spatial and temporal scales in maintaining vegetation mosaics and controlling patch dynamics. The potential for natural re-colonization of disturbed areas is discussed, as well as the dependence of this re-colonization on the spatial extent of goose damage. I discuss how processes that occur at small spatial scales (removal of vegetation by grubbing) may result in changes to spatial patterns at the landscape level.

Chapter 2: Vegetation patterning and soil degradation by lesser snow geese in an intertidal salt marsh at La Pérouse Bay, Manitoba.

2.1. Introduction

The Mid-Continent population of lesser snow geese (*Anser caerulescens caerulescens* L.) in North America has been increasing at a rate of approximately 7% per year (Abraham *et al.* 1996). At La Pérouse Bay, on the coast of the Hudson Bay in northern Manitoba, a breeding colony that is part of this population has increased from 1300 pairs to an estimated 44,500 pairs between 1968 and 1997 (Cooke *et al.* 1995, Abraham, Rockwell & Ross, unpubl. aerial survey in 1997). As a result, there has been increased foraging on the salt-marsh vegetation resulting in the degradation of large areas of the intertidal marsh. Former areas of intact salt marsh have been transformed into a vegetation mosaic of intact swards and exposed marine sediments (vegetation removed both by goose foraging and abiotic processes) (Handa *et al.* 2002) and at some locations only exposed sediment is present (Jefferies and Rockwell 2002).

Where resources are limiting, vegetation often occurs in a two-phase mosaic where patches of vegetation alternate with patches of exposed soil that are low in resources for plant growth (Montana 1992, Bromley *et al.* 1997, Rietkerk *et al.* 2000, HilleRisLambers *et al.* 2001). The resulting mosaic influences the distribution of resources and the movement and persistence of organisms (Pickett and Cadenasso 1995). It may maintain ecosystem productivity by concentrating limiting resources in areas that are still vegetated (Adler *et al.* 2001). Examples of systems exhibiting these vegetation mosaics are grasslands in the Serengeti (Belsky 1986), African rangelands (Wilson and

Agnew 1992, Van de Koppel *et al.* 1997), the slopes of semi-arid areas in Africa (Aguiar and Sala 1999, Seghieri and Galle 1999) and the intertidal vegetation and exposed sediment at La Pérouse Bay (Handa *et al.* 2002, Jefferies and Rockwell 2002).

Although the cause of these mosaics is still under debate (Boaler and Hodge 1962, Belsky 1986, Kellner and Bosch 1992, Bromley *et al.* 1997, Puigdefabregas *et al.* 1999), the maintenance of vegetation mosaics is commonly attributed to the existence of plant-soil interactions (Graetz 1991, Wilson and Agnew 1992, Aguiar and Sala 1999, Klausmeier 1999, HilleRisLambers *et al.* 2001). In particular, plant-soil interactions that maintain vegetation mosaics are thought to be primarily driven by differences in infiltration rate between different components of the mosaic (Graetz 1991, Wilson and Agnew 1992, Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Klausmeier 1999, HilleRisLambers *et al.* 2001). Rain falling on vegetated areas of the mosaic will infiltrate more easily than that on bare areas, as vegetative cover increases infiltration (Glover *et al.* 1962, Box and Bruce 1996, Anderson and Hodgkinson 1997). Rain falling on the non-vegetated component of the vegetation mosaic will barely infiltrate and run off where it may accumulate in vegetated patches or be lost from the system (Graetz 1991, HilleRisLambers *et al.* 2001).

Although rates of infiltration are considered to be a primary factor controlling vegetation mosaics, at least in tropical and sub-tropical ecosystems, numerous other soil variables may be involved in plant-soil interactions that also contribute to the maintenance of vegetation mosaics. Despite the potential existence of additional interactions between vegetation and nutrient availability, little attention has been paid to nutrient cycling influencing the spatial characteristics of vegetation mosaics (Guillaume *et al.* 1999). Nutrient and water dynamics in vegetation patterns are closely linked. Soil particles, organic matter, nutrients, and litter are carried to vegetated areas with surface run-off (Graetz 1991, Anderson and Hodgkinson 1997, Rietkerk *et al.* 2002) and the vegetation retains at least some of these resources (Rietkerk and van de Koppel 1997).

These types of plant-soil interactions, that are facilitative interactions, are common in many ecosystems, especially those characterized by severe stress, such as salt marshes and Arctic tundra (Holmgren *et al.* 1997). Positive interactions between plants in stressful environments generally occur through the amelioration of the abiotic environment by a modification of microclimate and soil properties (Hunter and Aarssen 1988). Microclimate modification is often provided by shade from canopies of large plants, which may protect seedlings from temperature extremes and reduce water evaporation (Callaway 1995). Shade may also reduce evaporation from soils under canopies in salt marshes, resulting in lower soil salinities (Bertness *et al.* 1992, Bertness and Hacker 1994, Hacker and Gaines 1997). Plants can promote water infiltration into soil (Elwell and Stocking 1976, Box and Bruce 1996), reduce erosion (Elwell and Stocking 1976), prevent salt accumulation (Srivastava and Jefferies 1996), and reduce nutrient loss (Aguiar and Sala 1999). All of these examples indicate the role of plants in modifying extreme abiotic conditions.

Although these plant-soil interactions may both cause and maintain vegetation mosaics, even in the absence of herbivory, intense herbivory may strengthen plant-soil interactions. The reduction in vegetative cover by herbivory may result in soil degradation, in addition to the direct loss of plant mass, which results in a loss of resources within plants. This loss of resources limits their ability to cope with further herbivory and soil degradation (Charney *et al.* 1975, Rietkerk and van de Koppel 1997, Rietkerk *et al.* 1997, Van de Koppel *et al.* 1997). Models of semi-arid grazing systems indicate that as herbivore impact increases, vegetation changes occur that include loss of complete plant cover, to areas of spatial patterning (vegetation mosaics) at intermediate levels of herbivory to areas of exposed soil devoid of plants, where there is a high impact of foraging (Klausmeier 1999, Rietkerk *et al.* 2000). The models assume that plant dispersal is low at short time scales (<10 years) (HilleRisLambers *et al.* 2001). The vegetation changes are often coupled with changes in abiotic conditions (Bazely and Jefferies 1986, Rietkerk and Van de Koppel 1997) and thus they are often irreversible (Sinclair and Fryxell 1985, Friedel 1991, Laycock 1991).

In the intertidal salt marsh at La Pérouse Bay, Manitoba, a trend similar to that described above has developed with intact salt marsh changing to a marsh with a well developed vegetation mosaic, and in some areas only exposed sediment remains- the outcome of intense goose foraging pressure. (Jefferies 1988b, a, Handa *et al.* 2002) Because of plant-soil interactions, herbivores may trigger rapid, irreversible vegetation changes in grazing systems resulting in an alternate stable states, often characterized by a loss of vegetation (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Van de Koppel and Rietkerk 2000). Previous work has shown that plant-soil feedbacks initiated by goose feeding may be the cause of the vegetation collapse at La Pérouse Bay through a self-amplifying positive feedback between vegetation loss and soil salinity (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996). The positive feedback has resulted in the formation of an alternate stable state of large areas of hypersaline exposed sediment in which plant regeneration is rare or infrequent (Hik *et al.* 1992, Handa *et al.* 2002).

Plant-soil interactions, other than those described for salinity, may be contributing to the formation of a vegetation mosaic at La Pérouse Bay and to the further degradation of this system to large areas of exposed sediment. Vegetation mosaics, such as those seen in the intertidal marsh at La Pérouse Bay, are often predicted to be maintained primarily through differences in infiltration rates between the components (vegetated and non-vegetated areas) of the mosaic. However, these predictions are primarily based on studies in semi-arid systems. Both semi-arid systems and Arctic salt marshes have low productivity, but productivity is limited by different factors in each system and thus vegetation mosaics may be maintained by different processes. Consequently, the first objective of this study was to examine if differences existed in infiltration rates between the components of the vegetation mosaic in the intertidal salt marsh at La Pérouse Bay, similar to patterns of infiltration in semi-arid systems.

In studies of vegetation mosaics in semi-arid systems, often soil properties other than infiltration rate are ignored, although these soil characteristics may contribute to the maintenance of vegetation patterns. Thus, the second objective of this study was to determine if there were other soil properties (including physical soil characteristics and nutrient availability) that may be contributing to existence of the mosaic at La Pérouse Bay.

Finally, models have predicted that in systems where plant dispersal is low, under high levels of herbivory a mosaic may progress into a stable degraded state of soil devoid of plants. Large areas of intertidal marsh at La Pérouse Bay, that have been subject to high foraging pressure by lesser snow geese, are moving from a vegetation mosaic to an alternate stable state of large areas of exposed sediment, as predicted by the models.

Thus, the third objective of this study was to determine the potential for dispersal of *Puccinellia phryganodes* into exposed sediment. This grass is the dominant graminoid and the primary forage species for snow geese at this site. The overall objective of this study, therefore, was to determine the soil characteristics that maintain and characterize the mosaic created by snow goose foraging at La Pérouse Bay, and how the soil properties affected the potential for *Puccinellia* to re-colonize exposed saline sediment.

2.2. Materials and Methods

2.2.1. Site description

Study sites were located in the intertidal flats at La Pérouse Bay, Manitoba (58°44'N, 94°28'W). Isostatic uplift has resulted in extensive coastal flats at La Pérouse Bay, and elsewhere in this region (Hansell *et al.* 1983). The topography of the coastal lowland displays only minor surface relief that results from frost heaving of unconsolidated sediments and the presence of ephemeral streams and ponds that develop during spring melt and run-off (Handa and Jefferies 2000). In the intact, vegetated areas of the intertidal salt marshes the dominant graminoids are *Puccinellia phryganodes* (Trin.) Scribn. & Merr. , a stoloniferous grass, and *Carex subspathacea* Wormskj., a rhizomatous sedge. An area of low willow (1 metre high) extends inland from the flats for approximately 2 km (Iacobelli and Jefferies 1991). The supratidal marsh is flooded infrequently by tidal water (< 2 innundations every three years). Permafrost is continuous in the Churchill region (Rouse *et al.* 1997) and it is present approximately 25-30 cm below the surface of sediment in mid-summer in salt-marsh sites at La Pérouse Bay

(Wilson 1993). The snow-free season usually extends from mid June to late September, although snow can fall in any month.

In this study, soil properties were examined along a soil ripening (aging) gradient that was associated with the rise in land elevation from the sea landwards to the upper limit of the intertidal marsh. In recent decades, land has emerged from the Hudson Bay at a rate of about 0.80 metres per 100 years in the Churchill region (Hansell *et al.* 1983). This is equivalent to approximately 200 metres of new shoreline every decade (Glooschenko and Martini 1978). There is a change in soil properties as the sediments age (termed "soil ripening") (Pons and Zonneveld 1965, Packham and Willis 1997) that occurs along a geographical gradient extending from the coast inland. At La Pérouse Bay, the change in soil properties is not associated with a change in the plant species as the two graminoid species mentioned above are dominant in the entire intertidal marsh.

The study area used in this study extended over a distance of approximately one kilometre in the intertidal marsh along which soil properties changed between the more immediate coastal sites and the more inland sites. Three sites were selected within the experimental area; they were located in the low marsh, mid-marsh and high marsh (Plate 2.1) which differ in age since the land has emerged from Hudson Bay. The fore marsh represents the youngest site and the high marsh, which is close to the willow fringe at the landward limit of the intertidal marsh, the oldest. The sites, which were approximately 100m x 100m, were selected because intact swards were still present. Elsewhere, the effects of grubbing by geese have led to loss of vegetation. Unconsolidated sediments in the fore marsh (seaward of the low marsh) were also examined. These included sediments

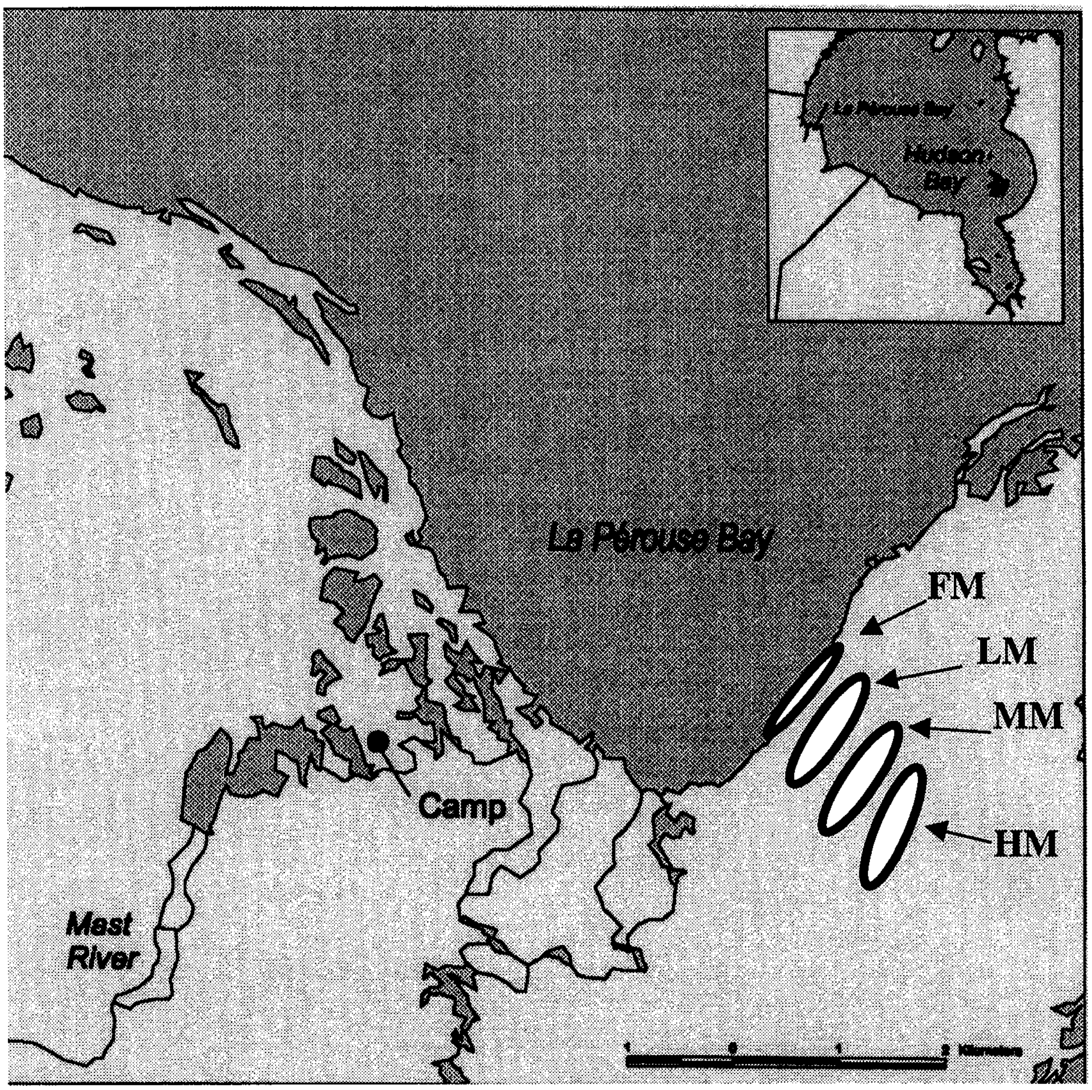


Plate 2.1. Map of La Pérouse Bay, Manitoba and the coastal zone, the position of which, on the Hudson Bay coast, is indicated by an arrow on the inset of the map. Sites along a soil ripening gradient associated with rise in land elevation from the sea landwards across which components of the vegetation mosaic were examined are the fore marsh (FM), low marsh (LM), mid-marsh (MM) and the high marsh (HM). The low marsh represents the youngest site, the high marsh, close to the willow fringe, the oldest. The fore marsh, seaward of the low marsh, consists of unconsolidated sediments.

that emerged recently from Hudson Bay but have not been colonized by vegetation and sites where secondary deposition of eroded materials has occurred.

2.2.2. Soil analysis

Soil analysis was carried out on soils in the intertidal salt marsh at La Pérouse Bay at sites where the vegetative cover was incomplete (i.e.,a vegetation mosiac of vegetated swards and exposed sediments was present, Plate 2.2). The four types of vegetative cover recognized were: (1) intact swards of *Puccinellia phryganodes* (vascular plant vegetative cover); (2) black algal mat growing on the soil surface that is devoid of vascular vegetation (non-vascular vegetation cover); (3) white algal mat growing on the soil surface that is devoid of vascular vegetation (non-vascular vegetation cover); (4) exposed mineral soil devoid of plant cover (Plate 2.3). Each of these four soil types defined in terms of their associated vegetative cover was examined at each of three sites in the intertidal salt marsh at La Pérouse Bay, and on unconsolidated sediments (fore marsh).

Soil characteristics examined at sites included: infiltration rate; soil moisture content; bulk density; salinity; penetration strength; organic content; nitrogen content of dry soil; exchangeable inorganic nitrogen. Soil samples for each variable were haphazardly selected at each site from beneath areas of a minimum 1 m^2 of each vegetation class described above. Replicate samples (see below) were collected from different patches of a particular soil, located at a minimum distance of 20 m apart.

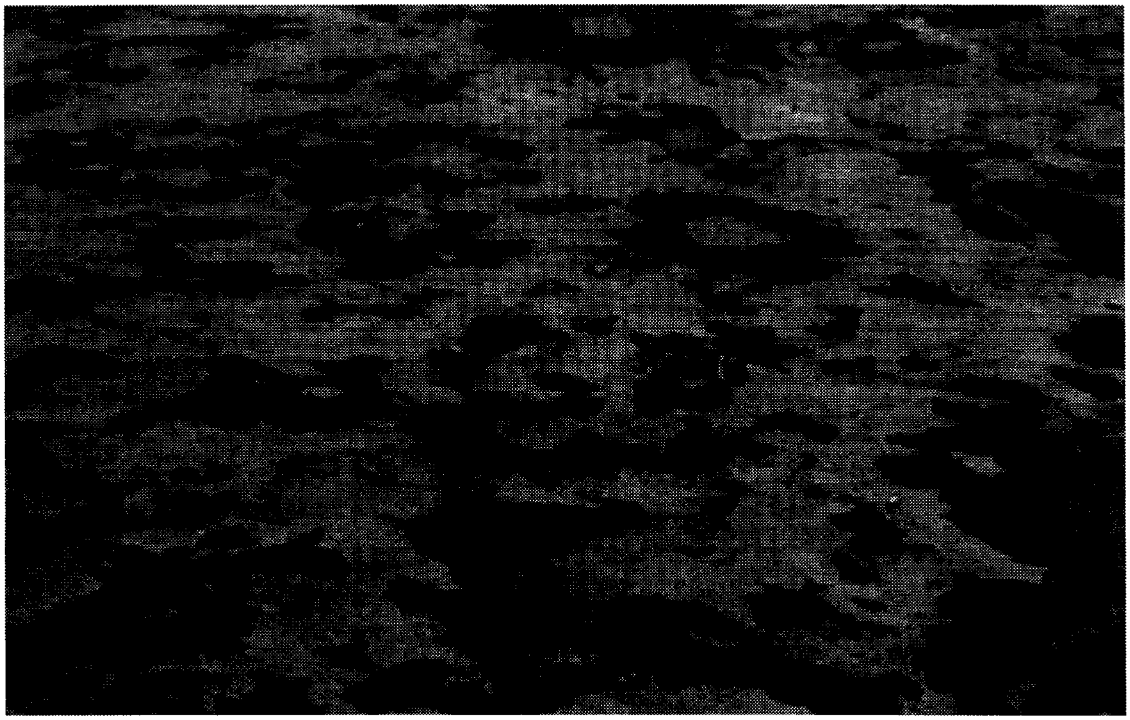


Plate 2.2. Vegetation mosaic in the intertidal salt marsh at La Pérouse Bay, Manitoba. Green areas are continuous swards of *Puccinellia phryganodes*, the primary forage grass in the salt marsh. The light areas are exposed sediment where vegetation has been removed as a result of grubbing by lesser snow geese.

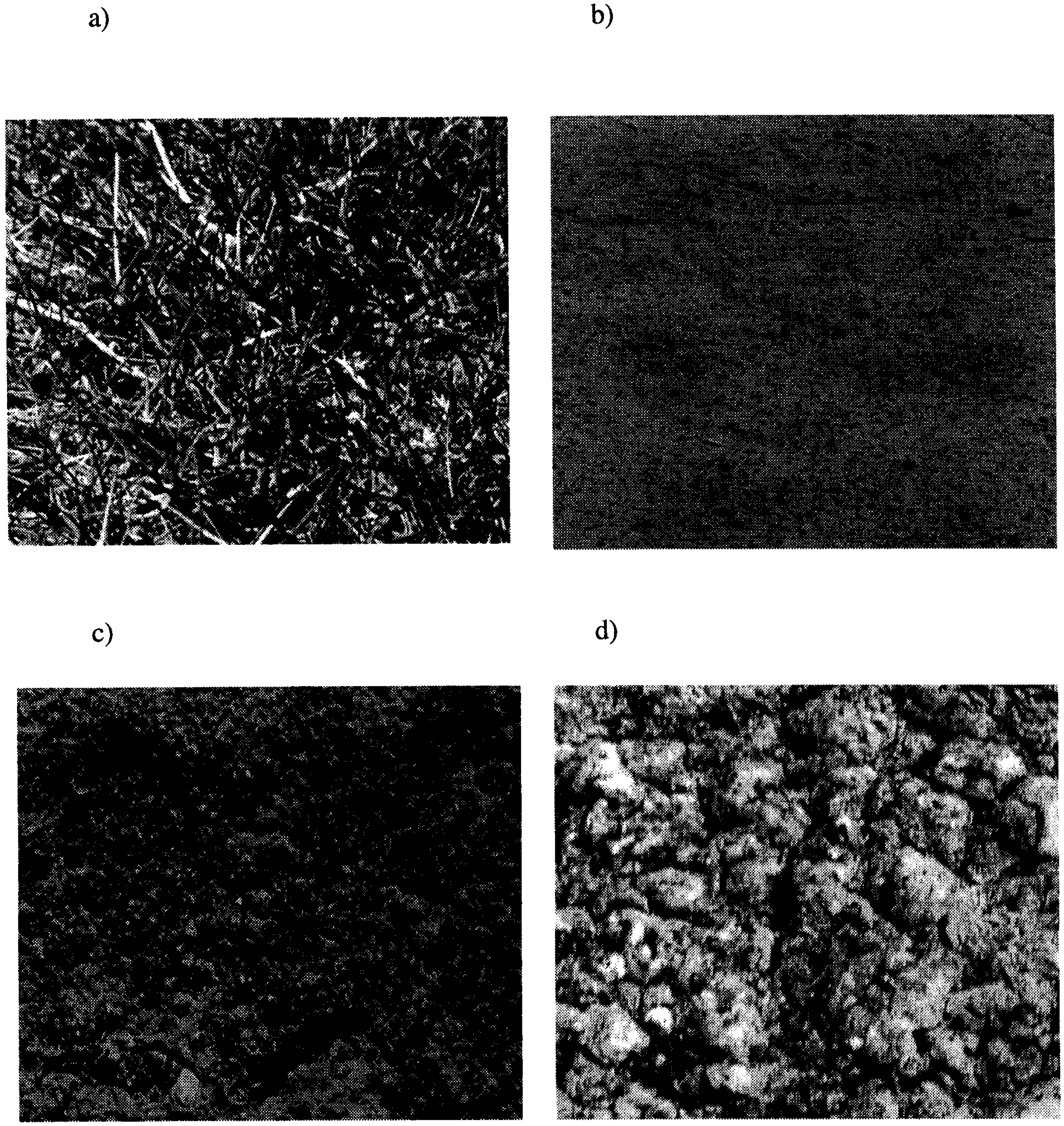


Plate 2.3. The four types of vegetative cover examined in the vegetation mosaic in the intertidal salt marsh at La Pérouse Bay, Manitoba: a) intact swards of *Puccinellia phryganodes* (vascular plant vegetative cover); b) exposed mineral soil devoid of plant cover c) black algal mat growing on the soil surface that is devoid of vascular vegetation (non-vascular vegetation cover); d) white algal mat growing on the soil surface that is devoid of vascular vegetation (non-vascular vegetation cover).

2.2.2.1. Determination of infiltration rate

Infiltration rate was measured in July 2001 on soils beneath all four types of vegetation cover at the three sites and on unconsolidated sediment from the fore marsh (n = 3 for each type per site). Infiltration rate was measured using a Turf-Tec Infiltrometer (Forestry Supplies, Inc.) on a 5 cm thick layer of turf and soil that was removed from the ground and placed on a wire mesh. Infiltration rate could not be measured *in situ* because of the presence of a permafrost layer under the active layer of the soil that would have impeded infiltration. Infiltration was measured as the amount of water that entered the soil (measured in cm) every minute for a period of 20 minutes. This procedure was repeated on the same turf until three trials of similar infiltration rates were obtained and data from the final trial were used in the analysis. The repeated measures of rate were needed to ensure that the soil was saturated (i.e., the soils were at field capacity) before infiltration rates were determined, so that only the steady-state infiltration rate was examined (Shainberg and Levy 1996).

2.2.2.2. Determination of soil moisture

The soil moisture content of the top 3 cm of the soil profile (the majority of *Puccinellia* roots occur within this depth) was measured using the gravimetric method in late June and late July of 2001 on the soil types from each site and from the unconsolidated sediment (n=5). A soil sample was weighed, dried at about 50°C for approximately one week, and re-weighed to calculate soil moisture content (expressed as grams of water per gram of dry soil).

2.2.2.3. Determination of bulk density

The bulk density of the top 3 cm of the soil profile was measured in late June and late July of 2001 on the soil types from each site and from the unconsolidated sediment (n=5). A soil sample of known volume was weighed, dried at about 50°C for approximately one week, and re-weighed to calculate bulk density (expressed as grams of dry soil per cm^3 of the wet soil volume).

2.2.2.4. Determination of soil salinity

Soil salinity was measured in late June and late July of 2001 on soils from each site (n=5 for each soil type at each site). The first series of salinity measurements were determined using the same procedure as Iacobelli and Jefferies (1991). The soil solution from the top 5 cm of the soil profile was extracted by manually squeezing the soil by hand (covered with latex gloves). This solution was filtered through Whatman No. 1 filter paper and then diluted with deionized water. Salinity was measured as grams of solute per litre of solution ($^{0}/_{00}$ S) using a portable Yellow Springs Instrument Salinity Meter (Ohio, USA). At the second sampling, the soil was too dry to extract soil water by this method. Soil was then pressed into 5 ml plastic syringe casings, which were placed in 20 ml centrifuge tubes and centrifuged at 7000 x g for 5 minutes. Salinities of soil water extracted by the different techniques have been shown to be similar (Srivastava and Jefferies 1995b). Soil water was then frozen and later analyzed for its sodium content using a Perkin-Elmer atomic absorption spectrophotometer (model 3110) (Rexdale, Ontario) in flame-emission mode. Standard sodium chloride solutions were used to calibrate the instrument and then samples were diluted to fall within the readable range of 0.2-1 milligrams of sodium per litre.

Soil salinity as measured by the use of the spectrophotometer is read as the concentration of sodium ions in the solution (g litre $^{-1}$), whereas salinity as measured by the salinity meter measures total solute content. However, data using the two methods are comparable; all values were converted to salinity using the regression equation : Salinity (g. diss. solids/l) = 3.59 * $[Na^+]$ g/l + 3.850 (r^2=0.96) (Srivastava and Jefferies 1995) where $[Na^+]$ is the concentration of sodium ions in the solution.

2.2.2.5. Determination of surface penetration strength

Penetration strength of each soil surface at a site was measured using a plate-type penetrometer (EFFEGI, Alfonsine, Italy). Ten replicate measurements were obtained (measurements made in unconsolidated sediments only in 2001) on 3 dates during the growing season of 2000 (13 July, 26 July, 8 August) and on two dates during the growing season of 2001 (12 June, 23 July).

2.2.2.6. Determination of soil organic content

Organic content of dry soil was measured in soil collected in July 2000 from the top 3 cm of the soil profile (n = 5 for each soil type at each site). This soil (about 1g per sample) was weighed in a porcelain crucible, placed in the muffle furnace at 500°C for 3 hours and then reweighed after cooling (loss on ignition). Organic content as a percentage by weight in the soil was then calculated as (dry soil weight - ash weight)/ dry soil weight.

2.2.2.7. Determination of total nitrogen content of soil

Similar to the measurements of organic content, total nitrogen content of soil was measured in soil samples collected from the top 3 cm of the soil profile for each of the four soil types at each site as well as in the unconsolidated sediments (n = 5 for each) using a LECO, CHN Analyser (St Joseph, Missouri) in July 2000, June 2001 and July 2001. The results are expressed on a mass basis as %N per gram of dry weight of soil.

2.2.2.8. Determination of cumulative exchangeable inorganic nitrogen

Available soil nitrogen for plant growth was also estimated using resin bags (made from nylon stocking bags (3 cm by 3 cm)), each containing 10g mixed-bed ion-exchange resin (anionic and cationic, M8157 Sigma-Aldrich, USA) buried approximately 4 cm below the soil surface in each soil type at each site and in the unconsolidated sediments (n = 5 per soil type, per site). Bags were buried in early June 2001 after snow-melt and retrieved after 7 weeks burial in late July. Resin bags were immediately frozen and transported to the Department of Botany, University of Toronto for analysis. Resin bags were air dried for two days before the resin was removed. Mineral ions were extracted in 50 mL of 2 molar KCL for 120 minutes. The elutant was frozen until analysis. Ammonium and nitrate were analyzed using an auto-analyzer (Pulse Instrumentation LTD, Saskatoon, Saskatchewan, Canada). Ammonium was determined using the phenol-sodium nitroprusside colometric method (Solorzano 1969). Nitrate ions in the elutant were analyzed by reducing nitrate to nitrite, in the presence of cadmium, followed by a colorimetric assay of nitrite using Marshall's reagent (N-(1-Napthyl)-ethylenediamine dihydrochloride) (Morris and Riley 1963).

2.2.3. Vegetation analysis

2.2.3.1. Determination of transplant vigour of *Puccinellia phryganodes*

Plants of *Puccinellia phryganodes* were transplanted and monitored during the growing season of 2001 to determine their growth potential in each of the four soil types at a site. Four exclosures were established in each vegetation cover type at each site in June 2001 and an additional four exclosures were established in the unconsolidated sediments in June 2001. In each exclosure, five rows of four transplants of *Puccinellia phryganodes* (i.e., 20 transplants) and surrounding soil (2 cm diameter, 4 cm depth) were transplanted into the soil with a minimum 15 cm between each transplant. Transplants were taken from an area of intact *Puccinellia* within 5m of the exclosure (and thus, at the same site). In the case of transplants placed in *Puccinellia* swards, transplants were removed from intact swards within an exclosure, left exposed for the same length of time as soil cores of *Puccinellia* transplanted into other soil types (ca. 10 minutes), and then the selected cores were transplanted back into intact vegetation within an exclosure. Transplants placed in unconsolidated sediment located seaward of the low marsh, were taken from the low marsh.

Transplants remained in place for the growing season and shoots present in late July 2001 were scored for their state of growth, termed transplant vigour. Each transplant was given a score between 0 and 10, with a score of 0 indicating all *Puccinellia* tillers in the transplant had died, a score of 1 indicating 10% of tillers in the transplant in late July 2001 were alive (green) and each point indicated an additional 10% increment up to a maximum score of 10, indicating 100% of tillers in the transplant were green. Where the soil was undisturbed and exclosed, *Puccinellia* had an average score of 9 at this stage of the season.

Scores of the fate of the 20 transplants inside each exclosure were averaged and average scores for each exclosure were used for the statistical analyses (n=4).

2.2.3.2. Determination of above-ground biomass

Above-ground biomass was determined in late July 2001 by clipping turves (7.5 cm x 7.5 cm) taken from intact swards (n=5) of *Puccinellia phryganodes* at each site (low marsh, mid-marsh and high marsh). Turves were clipped at soil level into trays of water and the living (floating) biomass was separated from the dead (sinking). The living biomass was dried at 50°C for approximately 1 week and weighed.

2.2.4. Statistical analysis

Statistical analyses on soil and vegetation variables were carried out using fixed-effects ANOVAs (Zar 1999). Three-factor (sampling date, site and soil type based on vegetative cover (all factors are nominal variables)) fully-crossed ANOVAs were used to examine differences between soil types at three sites in an intertidal marsh at La Pérouse Bay, Manitoba (low marsh, mid-marsh and high marsh). When there was only one sampling date, the ANOVA model contained only two factors (site and soil type based on vegetative cover). In order to examine differences between exposed mineral soil at four sites (fore marsh, low marsh, mid-marsh and high marsh), a two-factor (date and site) fixed effects ANOVA was used for each soil variable, except when there was only one sampling date when a single-factor (site) ANOVA was used. In most of the overall

ANOVA models, two- or three-way interaction terms were significant, and thus soil variables were examined independently for each site and each date. All statistics were calculated with JMP 4.0 (SAS Institute 2000).

2.3. Results

2.3.1. Soil analysis

2.3.1.1. Effects of the type of vegetation cover on infiltration rate

Results of infiltration rate indicated that there was an interaction between site and soil type (two-factor fixed effects ANOVA, Table 2.1). There was a significant effect of soil type in the low marsh (Fig. 2.1a, $F_{3,8}=51.93$, $p\leq0.001$), the mid-marsh (Fig. 2.1b, $F_{3,8}=33.99$, $p \leq0.001$) and the high marsh (Fig. 2.1c, $F_{3,8}=26.22$, $p \leq 0.001$). Across all sites, the infiltration rate was lowest for exposed mineral soil (BM) and highest in the intact swards of *Puccinellia* (Fig. 2.1). Infiltration rates for exposed mineral soil were generally very low at all sites and increased with distance from the coast (Fig. 2.1d, $F_{3,8}=8.99$, $p=0.006$). There was a negative relationship between infiltration rate and bulk density (Fig. 2.2, $r^2=0.37$, $p\leq0.001$) when data from all sites and soil types were combined.

Table 2.1. Two-factor fixed-effects ANOVA used to analyze the effect of SITE and SOIL TYPE on infiltration rates in 2001 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Site	2	0.004	4.93 *
Soil Type	3	0.107	93.76 ***
Site * Soil Type	6	0.011	4.74 **

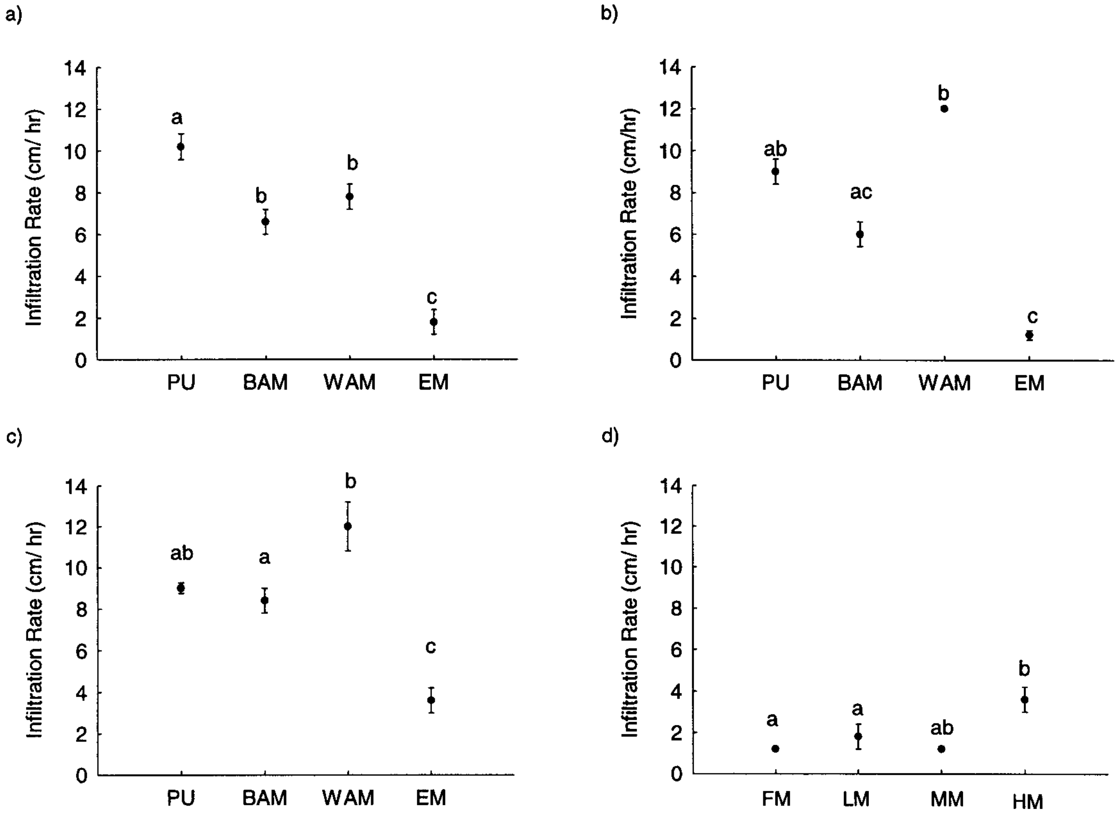


Figure 2.1. Rate of water infiltration (cm/ hr) in four soil types based on types of vegetative cover (PU-*Puccinellia*, BAM-Black Algal Mat, WAM-White Algal Mat, and EM-Exposed Mineral soil) in the a) Low Marsh, b) Mid-Marsh and c) High Marsh. d) Rates of water infiltration through exposed mineral soil at each of four sites (Fore Marsh (FM), Low Marsh (LM), Mid-Marsh (MM) and High Marsh (HM) in an intertidal marsh at La Pérouse Bay, Manitoba. Mean water infiltration is displayed +/- SEM (n = 3 for each soil type at each site). Different letters indicate significant differences between means (Tukey's comparison of all means, $p < 0.05$).

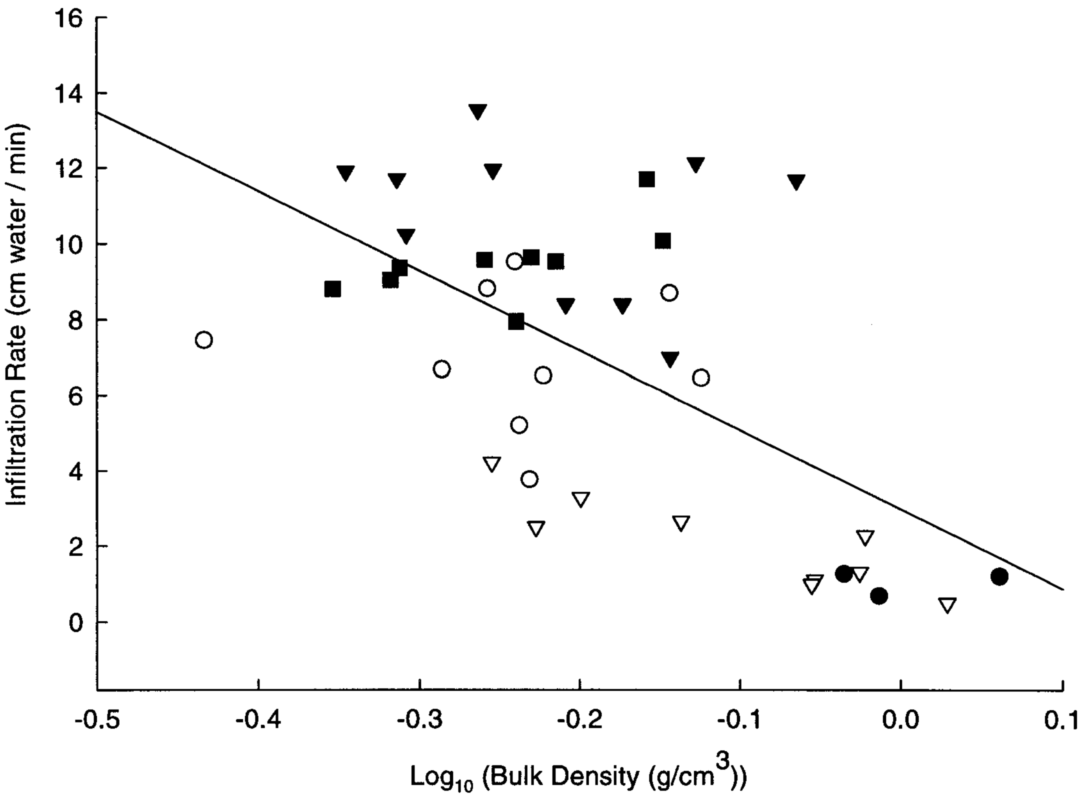


Figure 2.2. Rate of water infiltration (cm/ hr) plotted against $\log_{10}$ bulk density of samples from all soil types based on types of vegetative cover across all sites (Fore Marsh, Low Marsh, Mid-Marsh and High Marsh) in an intertidal marsh at La Pérouse Bay, Manitoba. $y = -0.350x + 0.050$, $r^2 = 0.37$, $p<0.001$. Closed circles represent soils from unconsolidated sediments, open circles black algal mat covered soil, closed inverted triangles white algal mat covered soils, open inverted triangles exposed mineral soil and closed squares *Puccinellia* covered soils.

2.3.1.2. Effects of the type of vegetation cover on soil moisture

Results of soil moisture indicated that there was a three-way interaction between sampling date, site and soil type (three-factor fixed effects ANOVA, Table 2.2). Significant effects of soil type on soil moisture were found in the low marsh (20 June 2001: Fig. 2.3a, $F_{3,16}=38.88$, $p \leq 0.001$; 21 July 2001: Fig. 2.3b, $F_{3,16}=4.15$, $p=0.024$), the mid-marsh (20 June 2001: Fig. 2.3c, $F_{3,16}=18.80$, $p \leq 0.001$; 21 July 2001: Fig. 2.3d, $F_{3,16}=3.49$, $p=0.041$), and the high marsh (20 June 2001: Fig. 2.3e, $F_{3,16}=7.99$, $p=0.0018$; 21 July 2001: Fig. 2.3f, $F_{3,16}=7.20$, $p=0.0028$). The moisture content of soil was generally lower in exposed mineral soil than in soils at all sites on all dates from either intact swards of *Puccinellia* or areas with non-vascular vegetation (Fig. 2.3).

In exposed mineral soil there was an interaction between sampling date and site with respect to soil moisture (two-factor fixed effects ANOVA, Table 2.3). Soil moisture in exposed mineral soil generally increased with distance from the coast on both dates (20 June 2001:Fig. 2.4a, $F_{3,16}=8.35$, $p=0.0020$; 21 July 2001: Fig. 2.4b, $F_{3,16}=11.80$, $p \leq 0.001$).

2.3.1.3. Effects of the type of vegetation cover on bulk density

Results of bulk density indicated that there was a three-way interaction between sampling date, site and soil type (three-factor fixed effects ANOVA, Table 2.4). Significant effects of soil type on bulk density were found in the low marsh (20 June 2001: Fig. 2.5a, $F_{3,16}=12.98$, $p \leq 0.001$; 21 July 2001: Fig. 2.5b, $F_{3,16}=6.05$, $p=0.0059$), the mid-marsh (20 June 2001: Fig. 2.5c, $F_{3,16}=20.90$, $p \leq 0.001$; 21 July 2001: Fig. 2.5d, $F_{3,16}=7.49$, $p=0.0024$), and the high marsh (20 June 2001: Fig. 2.5e, $F_{3,16}=3.66$, $p=0.035$;

Table 2.2. Three-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE, SITE and SOIL TYPE on soil moisture in 2001 in low, mid- and high marsh sites at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	0.296	8.61 **
Site	2	5.002	72.86 ***
Sampling * Site	2	0.335	4.88 **
Soil Type	3	3.330	32.34 ***
Sampling * Soil Type	3	0.951	9.23 ***
Site * Soil Type	6	0.424	2.06
Sampling * Site * Soil Type	6	0.518	2.52 *

Table 2.3. Two-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE and SITE on soil moisture of exposed mineral sediments in 2001 in fore, low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	0.079	3.95
Site	3	0.935	15.57 ***
Sampling * Site	3	0.256	4.26 *

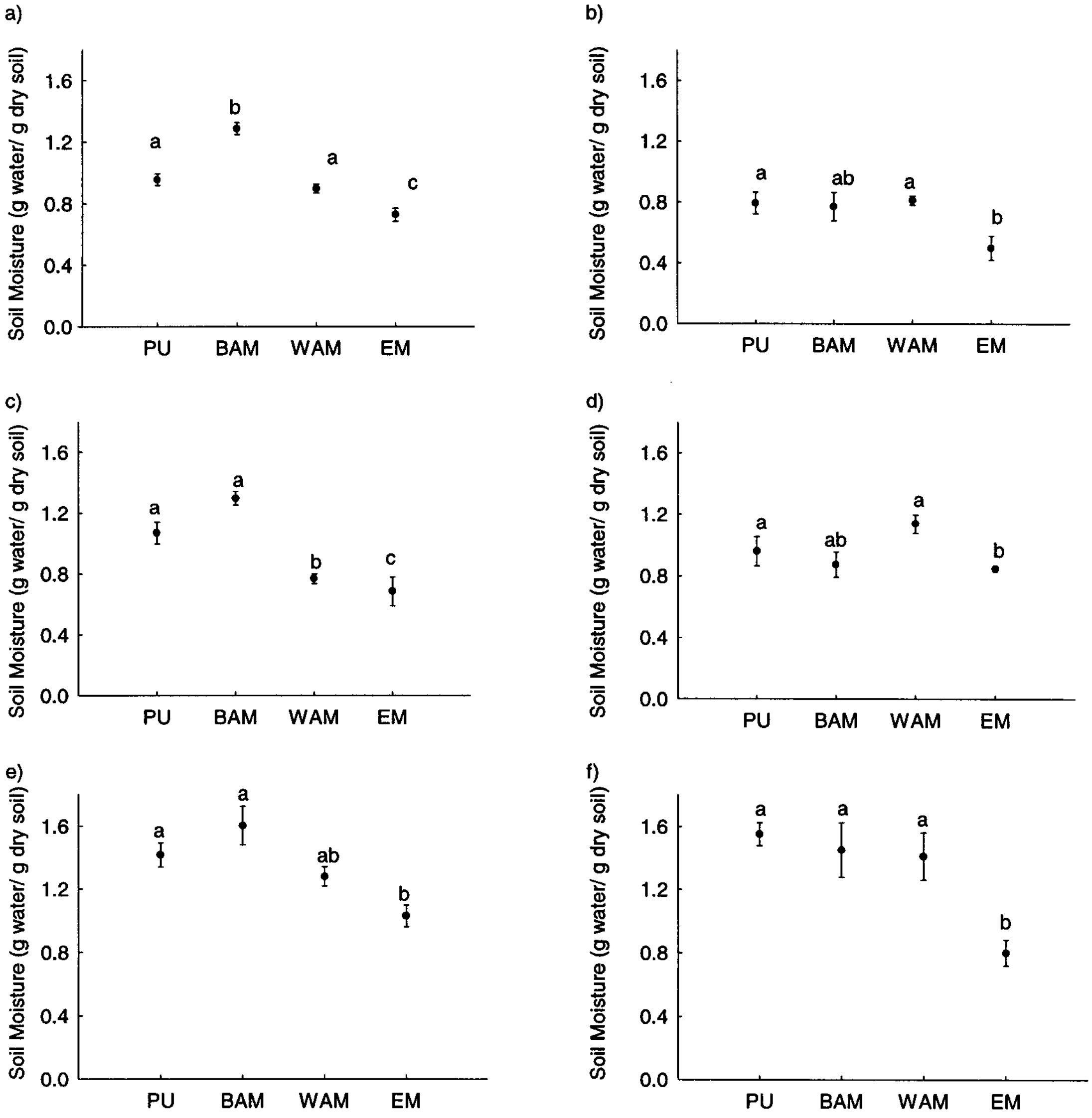


Figure 2.3. Soil moisture (g water / g dry soil) of four soil types based on types of vegetative cover (PU- Puccinellia, BAM- Black Algal Mat, WAM- White Algal Mat, EM- Exposed Mineral soil) for the Low Marsh, (a) 20 June 2001 b) 21 July 2001) Mid-Marsh, (c) 20 June 2001 d) 21 July 2001) and High Marsh (e) 20 June 2001 f) 21 July 2001) in an intertidal marsh at La Pérouse Bay, Manitoba. Soil moisture is displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters above means indicate significant differences between soil types (Tukey's comparison of all means, p< 0.05).

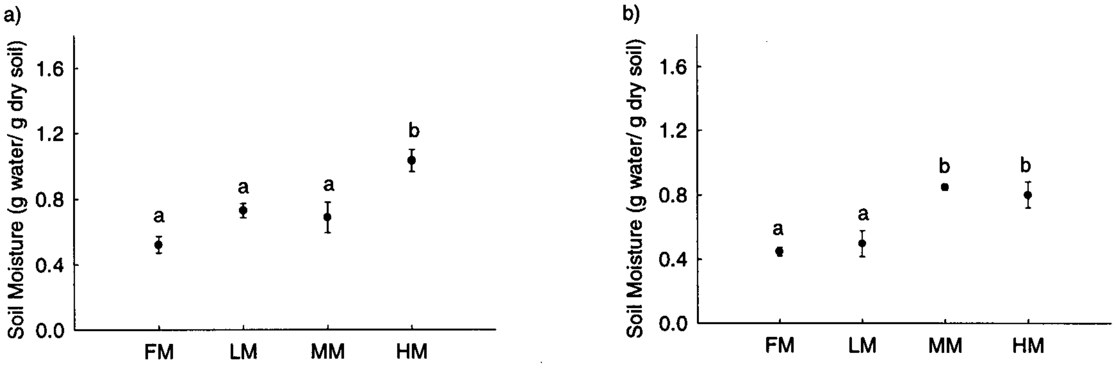


Figure 2.4. Soil moisture (g water/ g dry soil) for exposed mineral soil across four sites (FM- Fore Marsh, LM-Low Marsh, MM- Mid-Marsh, HM- High Marsh) in an intertidal marsh at La Pérouse Bay, Manitoba on a) 20 June 2001 and b) 21 July 2001. Soil moisture is displayed as mean +/- SEM (n = 5 for each site). Different letters above means indicate significant differences between sites (Tukey's comparison of all means, $p < 0.05$).

Table 2.4. Three-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE, SITE and SOIL TYPE on bulk density in 2001 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (data $\log_{10}$ transformed to improve normality) (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Sampling	1	0.259	11.08 **
Site	2	1.620	34.7 ***
Sampling * Site	2	0.525	11.24 ***
Soil Type	3	2.998	42.81 ***
Sampling * Soil Type	3	0.398	5.68 **
Site * Soil Type	6	0.116	0.83
Sampling * Site * Soil Type	6	0.579	4.13 ***

Table 2.5. Two-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE and SITE on bulk density of exposed mineral sediments in 2001 in fore, low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (data $\log_{10}$ transformed to improve normality) (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Sampling	1	0.032	1.2
Site	2	0.399	7.42 **
Sampling * Site	2	0.566	10.53 ***

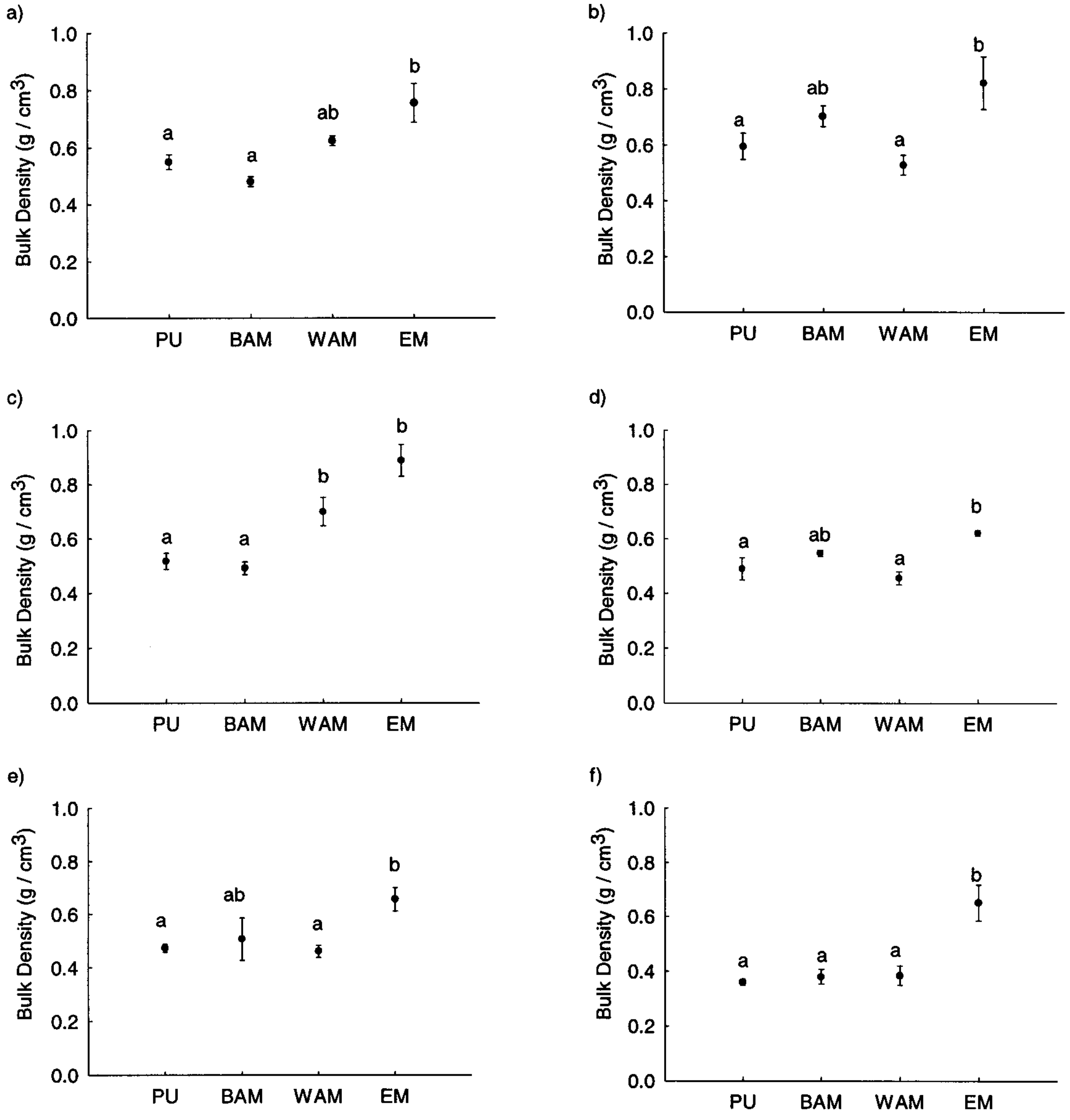


Figure 2.5. Bulk density (g/ cm^3) of soil from four soil types based on types of vegetative cover (PU-Puccinellia, BAM- Black algal mat, WAM-White Algal Mat, EM-Exposed Mineral soil) in the Low Marsh (a) 20 June 2001 b) 21 July 2001), Mid-Marsh (c) 20 June 2001 d) 21 July 2001) and High Marsh (e) 20 June 2001 f) 21 July 2001) in an intertidal marsh at La Pérouse Bay, Manitoba. Bulk density is displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters above means indicate significant differences between soil types (Tukey's comparison of all means $p<0.05$).

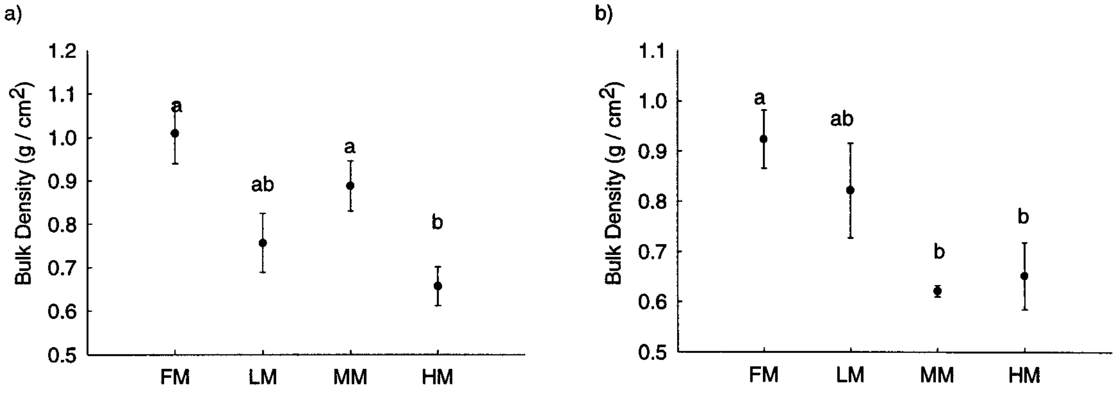


Figure 2.6. Bulk density (g/ cm^3) of soil from exposed mineral soil in each of four sites in an intertidal marsh at La Pérouse Bay, Manitoba (FM-Fore Marsh, LM-Low Marsh, MM-Mid Marsh, HM-High Marsh) on a) 20 June 2001 and b) 21 July 2001. Bulk density is displayed as mean +/- SEM (n = 5 for each site). Different letters above means indicate significant differences between sites (Tukey's comparison of all means $p<0.05$). Note y-axis does not begin at 0.

21 July 2001: Fig. 2.5f, $F_{3,16}=13.59$, $p \leq 0.001$). The bulk density was generally higher in exposed mineral soil than in soil beneath *Puccinellia* swards at all sites (Fig. 2.5). Areas with non-vascular vegetation had bulk densities similar to exposed mineral soil and soil beneath intact *Puccinellia* swards, depending on date and site (Fig. 2.5).

In exposed mineral soil, there was an interaction between sampling date and site with respect to bulk density (two-factor fixed effects ANOVA, Table 2.5). Bulk density in exposed mineral soil generally decreased with distance from the coast, with the fore marsh consistently having a higher bulk density than the high marsh on both dates (20 June 2001: Fig. 2.6a, $F_{3,16}=5.81$, $p=0.0085$; 21 July 2001: Fig. 2.6b, $F_{3,16}=5.63$, $p=0.0079$).

2.3.1.4. Effects of the type of vegetation cover on salinity

Results of salinity indicate that there was a three-way interaction between sampling date, site and soil type (three-factor fixed effects ANOVA, Table 2.6). Significant effects of soil type on salinity were found in the low marsh (13 June 2001: Fig. 2.7a, $F_{3,16}=18.40$, $p \leq 0.001$; 20 July 2001: Fig. 2.7b, $F_{3,16}=157.45$, $p \leq 0.001$), the mid-marsh (13 June 2001: Fig. 2.7c, $F_{3,16}=45.94$, $p \leq 0.001$; 20 July 2001: Fig. 2.7d, $F_{3,16}=219.67$, $p \leq 0.001$), and the high marsh (13 June 2001: Fig. 2.7e, $F_{3,16}=6.01$, $p=0.006$; 20 July 2001: Fig. 2.7f, $F_{3,16}=26.64$, $p \leq 0.001$). The salinity was generally higher in exposed mineral soil than in soil beneath *Puccinellia* swards at all sites (Fig. 2.7). Areas with non-vascular vegetation had salinities similar to exposed mineral soil and soil beneath intact *Puccinellia* swards, depending on date and site (Fig. 2.7).

Table 2.6. Three-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE, SITE and SOIL TYPE on salinity in 2001 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	20831.249	319.82 ***
Site	2	1991.505	15.29 ***
Sampling * Site	2	488.419	3.75 *
Soil Type	3	32075.761	164.15 ***
Sampling * Soil Type	3	4347.213	22.25 ***
Site * Soil Type	6	1854.088	4.74 ***
Sampling * Site * Soil Type	6	1309.732	3.35 **

Table 2.7. Two-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE and SITE on salinity of exposed mineral sediments in 2001 in fore, low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	16429.185	120.02 ***
Site	3	2889.970	7.04 ***
Sampling * Site	3	1567.715	3.82 *

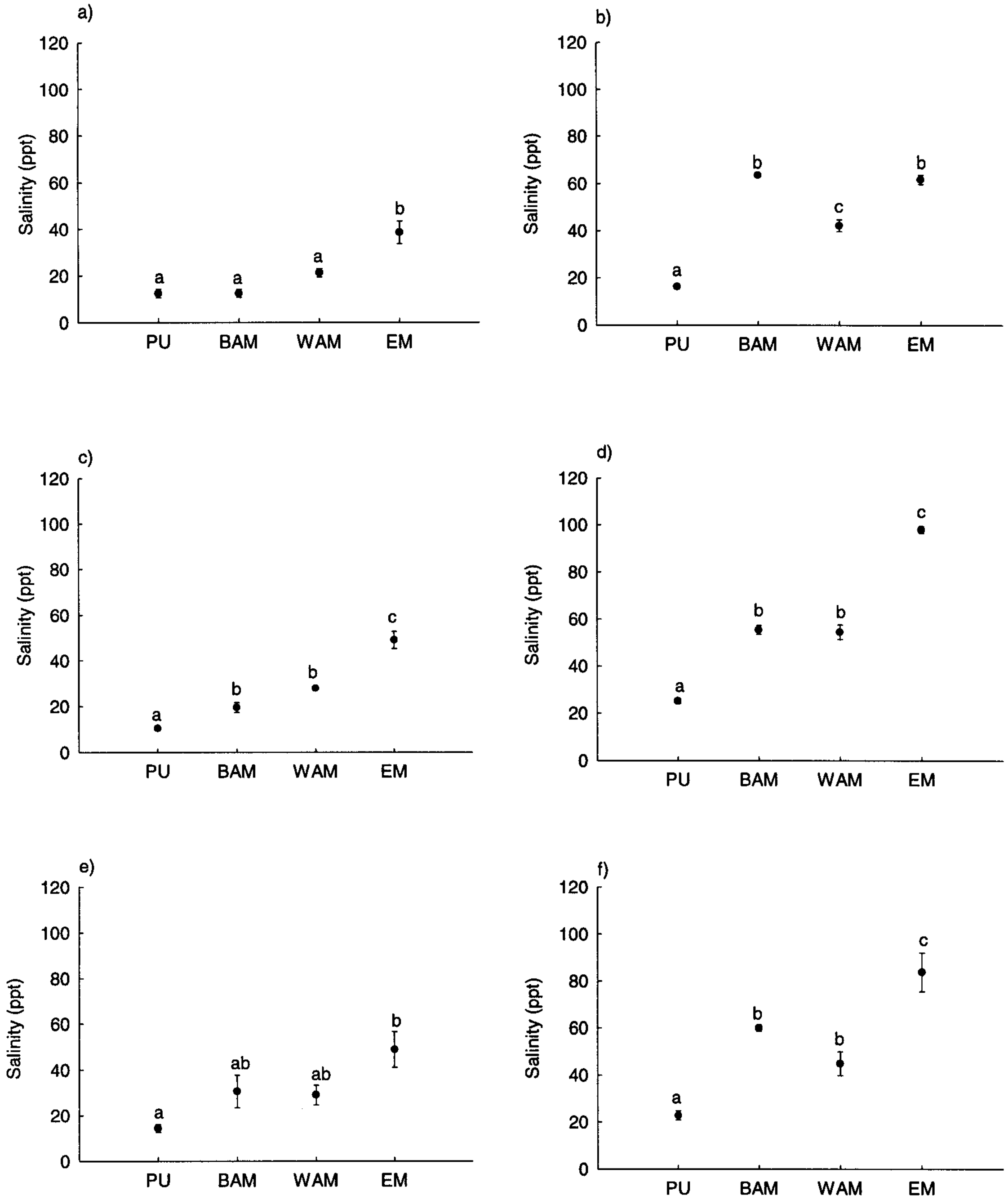


Figure 2.7. Salinity (ppt) of soil from four soil types based on types of vegetative cover (PU-*Puccinellia*, BAM- Black algal mat, WAM-White Algal Mat, EM-Exposed Mineral soil) in the Low Marsh (a)13 June 2001 b) 20 July 2001), Mid-Marsh (c) 13 June 2001 d) 20 July 2001) and High Marsh (e) 13 June 2001 f) 20 July 2001) in an intertidal marsh at La Pérouse Bay, Manitoba. Salinity is displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters above means indicate significant differences between soil types (Tukey's comparison of all means p<0.05).

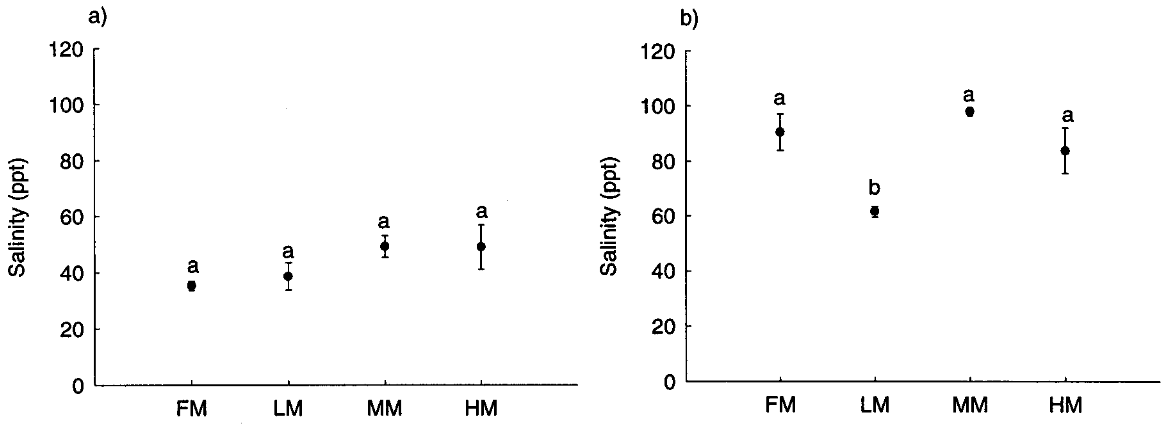


Figure 2.8. Salinity (ppt) of soil from exposed mineral soil in each of four sites in an intertidal marsh at La Pérouse Bay, Manitoba (FM-Fore Marsh LM-Low Marsh, MM-Mid Marsh, HM-High Marsh) on a)13 June 2001 and b) 20 July 2001. Salinity is displayed as mean +/- SEM (n = 5 at each site). Different letters above means indicate significant differences between sites (Tukey's comparison of all means $p<0.05$).

In exposed mineral soil there was an interaction between sampling date and site with respect to salinity (two-factor fixed effects ANOVA, Table 2.7). Salinity did not differ consistently between dates at the four sites (13 June 2001: Fig. 2.8a, $F_{3,16}=1.99$, $p=0.155$; 20 July 2001: Fig. 2.8b, $F_{3,16}=8.40$, $p\leq 0.001$).

2.3.1.5 Effects of the type of vegetation cover on penetration strength

Results of penetration strength indicated that there was a three-way interaction between sampling date, site and soil type (three-factor fixed effects ANOVA, Table 2.8). Penetration dates for only 2 August 2001 are shown for clarity (Fig. 2.9).

Significant effects of soil type on penetration strength were found in the low marsh (13 July 2000: $F_{3,36}=64.09$, $p\leq 0.001$; 26 July 2000: $F_{3,36}=68.60$, $p\leq 0.001$; 2 August 2000: Fig. 2.9a, $F_{3,36}=111.36$, $p\leq 0.001$; 12 June 2001: $F_{3,36}=57.17$, $p\leq 0.001$; 23 July 2001: $F_{3,36}=15.01$, $p\leq 0.001$). On all five dates, penetration strength was lower in the exposed mineral soil than in the soil beneath the *Puccinellia* swards. Additionally, on all five dates, soil covered by algal mats (WAM and BAM) had a lower penetration strength than that of soils of the *Puccinellia* swards. Penetration strengths of the algal mats varied: algal mat covered soil had a penetration strength higher than or equal to that of exposed mineral soil, and the penetration strength of the white algal mat was higher than or equal to that of soil covered by black algal mat.

Significant effects of soil type on penetration strength were also found in the mid-marsh (13 July 2000: $F_{3,36}=16.44$, $p\leq 0.001$; 26 July 2000: $F_{3,36}=3.74$, $p=0.019$; 2 August 2000: Fig. 2.9b, $F_{3,36}=40.10$, $p\leq 0.001$; 12 June 2001: $F_{3,36}=64.63$, $p\leq 0.001$; 23 July 2001: $F_{3,36}=21.44$, $p\leq 0.001$). On all dates, penetration strength was lower in the exposed

Table 2.8. Three-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE, SITE and SOIL TYPE on penetration strength in 2001in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	4	7.882	60.8 ***
Site	2	3.223	49.72 ***
Sampling * Site	8	3.779	14.58 ***
Soil Type	3	46.540	478.65 ***
Sampling * Soil Type	12	5.788	14.88 ***
Site * Soil Type	6	5.253	27.01 ***
Sampling * Site * Soil Type	24	7.479	9.62 ***

Table 2.9. Two-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE and SITE on penetration strength of exposed mineral sediments in 2001 in fore, low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	0.502	21.91 ***
Site	3	1.130	16.42 ***
Sampling * Site	3	0.163	2.37

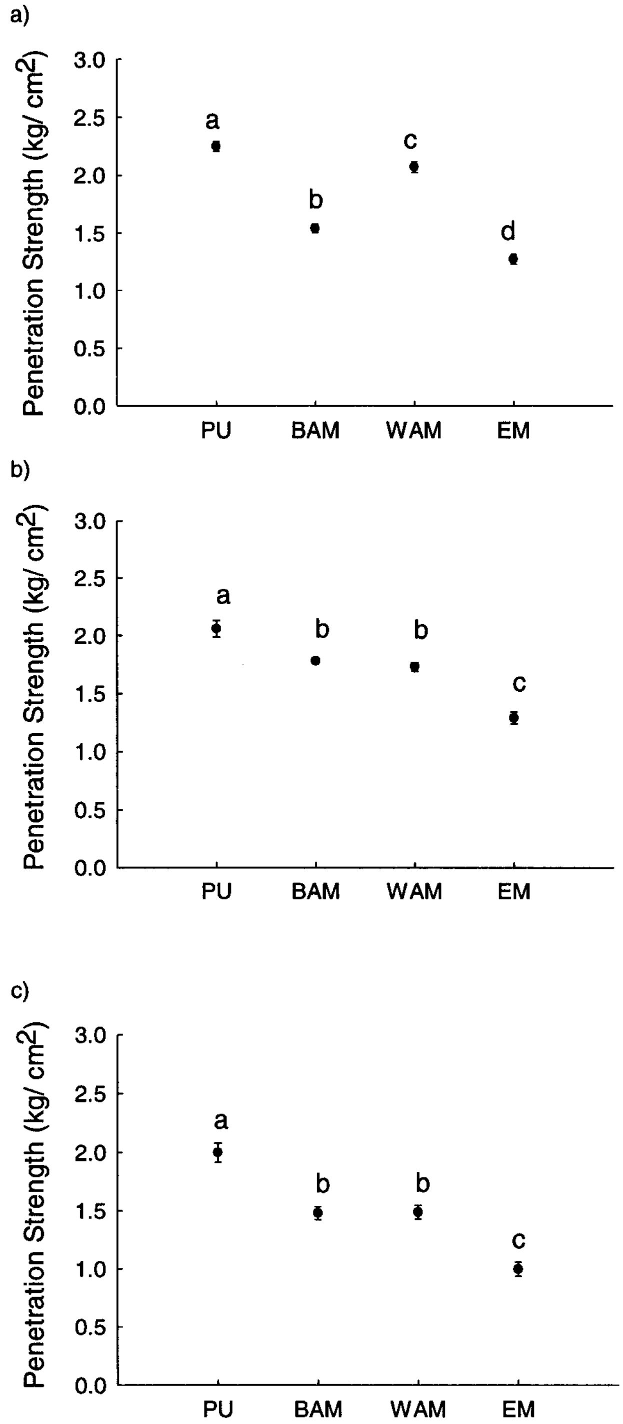


Figure 2.9. Penetration strength (kg/ cm^2) on 2 August 2000 for each of 4 soil types based on types of vegetative cover (PU- *Puccinellia*; BAM- Black Algal Mat; WAM- White Algal Mat; EM- Exposed Mineral soil) from the a) Low Marsh b) Mid-Marsh and c) High Marsh in an intertidal marsh at La Pérouse Bay, Manitoba. Penetration strength is displayed as mean +/- SEM (n = 10 for each soil type at each site). Different letters above means indicate a significant difference between treatments (Tukey's comparison of all means, $p < 0.05$).

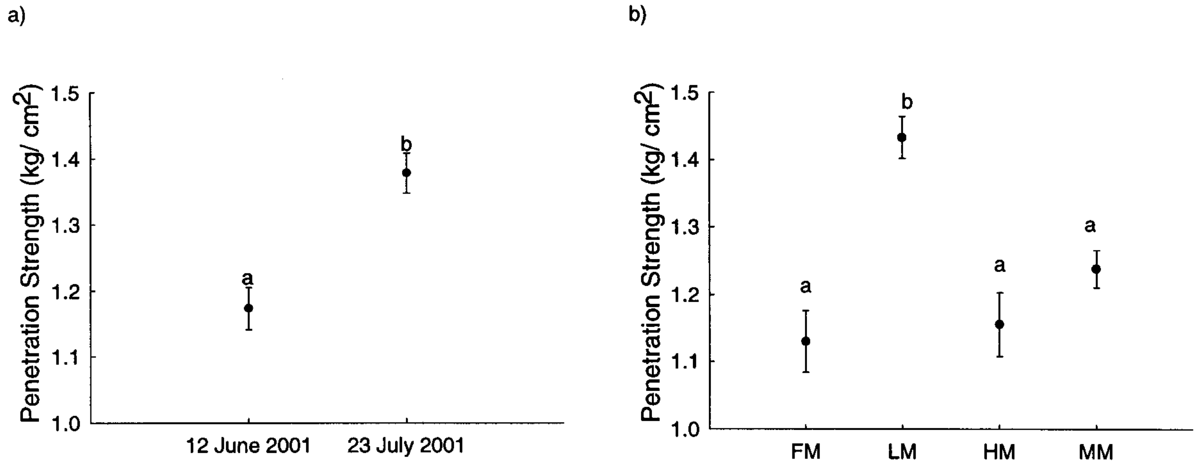


Figure 2.10. a). Penetration strength (kg/ cm^2) of soil surface for exposed mineral soil on 2 dates sampled in 2001(12 June 2001 and 23 July 2001). Data from all four sites (FM-Fore Marsh; LM- Low Marsh; MM- Mid-Marsh; HM - High Marsh) in an intertidal marsh at La Pérouse Bay, Manitoba are combined. Penetration strength is displayed as mean +/- SEM (n = 40 on each date). Different letters above means indicate sites are significantly different (Least Square Mean Tukey's comparison of all means, $p < 0.05$). Note y-axis does not begin at 0. b) Penetration strength of soil surface for exposed mineral soil for each of four sites in an intertidal marsh at La Pérouse Bay, Manitoba (FM-Fore Marsh; LM- Low Marsh; MM- Mid-Marsh; HM - High Marsh). Data from 12 June 2001 and 23 July 2001 are combined. Penetration strength is displayed as mean +/- SEM (n = 20 for each site). Different letters above means indicate sites are significantly different (Least Square Mean Tukey's comparison of all means, $p < 0.05$). Note y-axis does not begin at 0.

mineral soil than in soils from *Puccinellia* swards (except 26 July 2000 when the penetration strengths of the two soil types were equal). Soil covered by algal mats (WAM and BAM) had a lower penetration strength than those of *Puccinellia* swards on all dates (except 26 July 2000 where the penetration strengths of the two soil types were equal). Penetration strengths of the algal mat soils varied. Algal mat covered soil had a penetration strength higher than or equal to that of exposed mineral soil, except 13 July 2000 when the black algal mat soil had a penetration strength less than that of bare mineral soil. The penetration strength of the soil from the white algal mat was higher than or equal to that of the black algal mat soil.

Significant effects of soil type on penetration strength were also found in the high marsh (13 July 2000: $F_{3,36}$=48.30, $p \leq 0.001$; 26 July 2000: $F_{3,36}$=28.33, $p \leq 0.001$; 2 August 2000: Fig. 2.9c, $F_{3,36}$=38.86, $p \leq 0.001$; 12 June 2001: $F_{3,36}$=98.55, $p \leq 0.001$; 23 July 2001: $F_{3,36}$=12.43, $p \leq 0.001$). On all dates, penetration strength was lower in the exposed mineral soil than that beneath *Puccinellia* swards. Soil covered by algal mats (WAM and BAM) had a lower penetration strength than soils from *Puccinellia* swards on all dates (except 26 July, 2000 where the penetration strengths of the two soil types were equal). Penetration strengths of algal mats varied: algal mat covered soil had a penetration strength higher than or equal to that of exposed mineral soil, depending on sampling date. The penetration strength of the white algal mat was higher than or equal to black algal mat soil, depending on sampling date.

In exposed mineral soil there was a significant effect of date and site but no significant interaction with respect to penetration strength (two-factor fixed effects

ANOVA, Table 2.9) and thus data for sites were pooled to examine the effects of date. Penetration strength was significantly higher on 23 July 2001 than on 12 June 2001 (Fig. 2.10a). Similarly, data for dates were pooled to examine the effects of site. Penetration strength was higher for exposed mineral soil in the low marsh than for comparable values for soils at other sites (Fig. 2.10b).

2.3.1.6. Effects of the type of vegetation cover on soil organic content in dry soil

Results of soil organic content indicate that there was an interaction between site and soil type (two factor fixed effects ANOVA, Table 2.10). Organic content did not differ between soil types in the low marsh (Fig. 2.11a, $F_{3,16}=1.69$, $p=0.209$). In the mid- marsh, the organic contents of soils beneath *Puccinellia* swards and the white algal mat were significantly higher than that of soils with black algal mats and the exposed mineral soil (Fig. 2.11b, $F_{3,16}=89.32$, $p\leq 0.001$). In the high marsh, the organic content of exposed mineral soil was significantly lower than that of all other soil types (Fig. 2.11c, $F_{3,16}=25.32$, $p\leq 0.001$).

2.3.1.7. Effects of the type of vegetation cover on total nitrogen content in dry soil

Results of total nitrogen content in dry soil indicate that there was a three-way interaction between sampling date, site and soil type (three-factor fixed effects ANOVA, Table 2.11). Significant effects of soil type on nitrogen content in dry soil were found in the low marsh (13 July 2000: Fig. 2.12a, $F_{3,16}=8.14$, $p=0.002$; 25 June 2001: Fig. 2.12b, $F_{3,16}=16.45$, $p\leq0.001$; 21 July 2001: Fig. 2.12c, $F_{3,16}=14.85$, $p\leq0.001$), the mid-marsh (13

Table 2.10. Two-factor fixed-effects ANOVA used to analyze the effect of SITE and SOIL TYPE on organic content in 2000 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Site	2	0.100	62.58 ***
Soil Type	3	0.123	51.15 ***
Site * Soil Type	6	0.104	21.74 ***

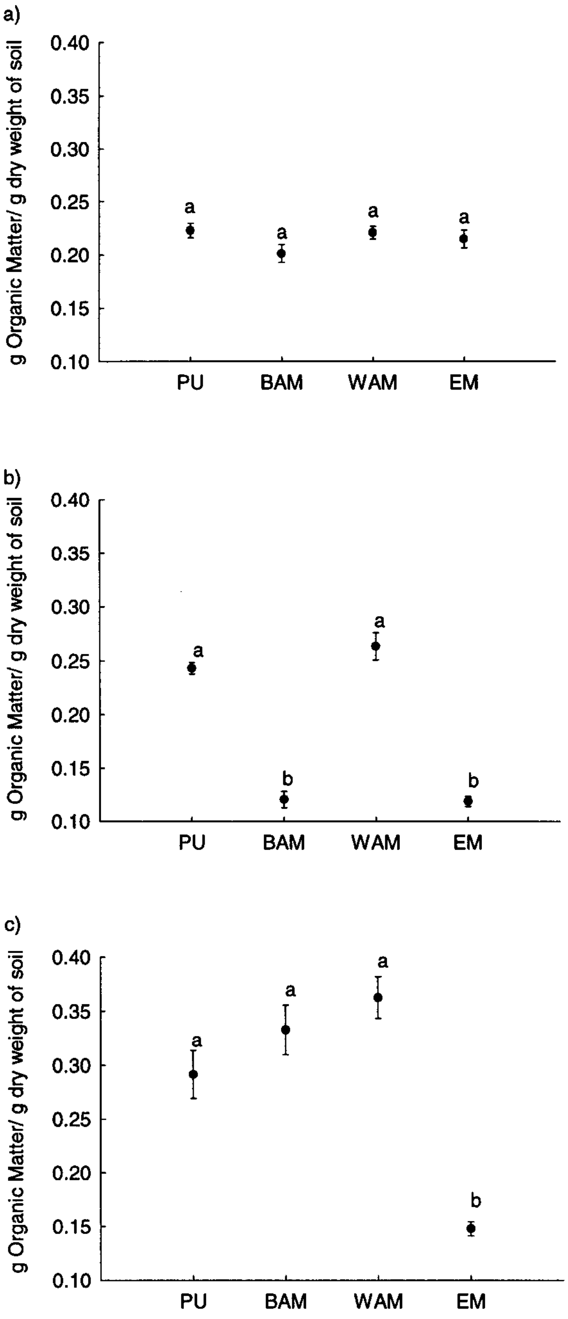


Figure 2.11. Organic content (g organic matter/ g dry soil) in July 2000 across four soil types based on types of vegetative cover (PU-*Puccinellia*, BAM- Black Algal Mat, WAM- White Algal Mat, EM- Exposed Mineral Soil) in the a) Low Marsh, b) Mid-Marsh and c) High Marsh in an intertidal marsh at La Pérouse Bay, Manitoba. Organic content is displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters above means indicate significant differences between soil types (Tukey's comparison of all means, $p<0.05$). Note y-axis does not begin at 0.

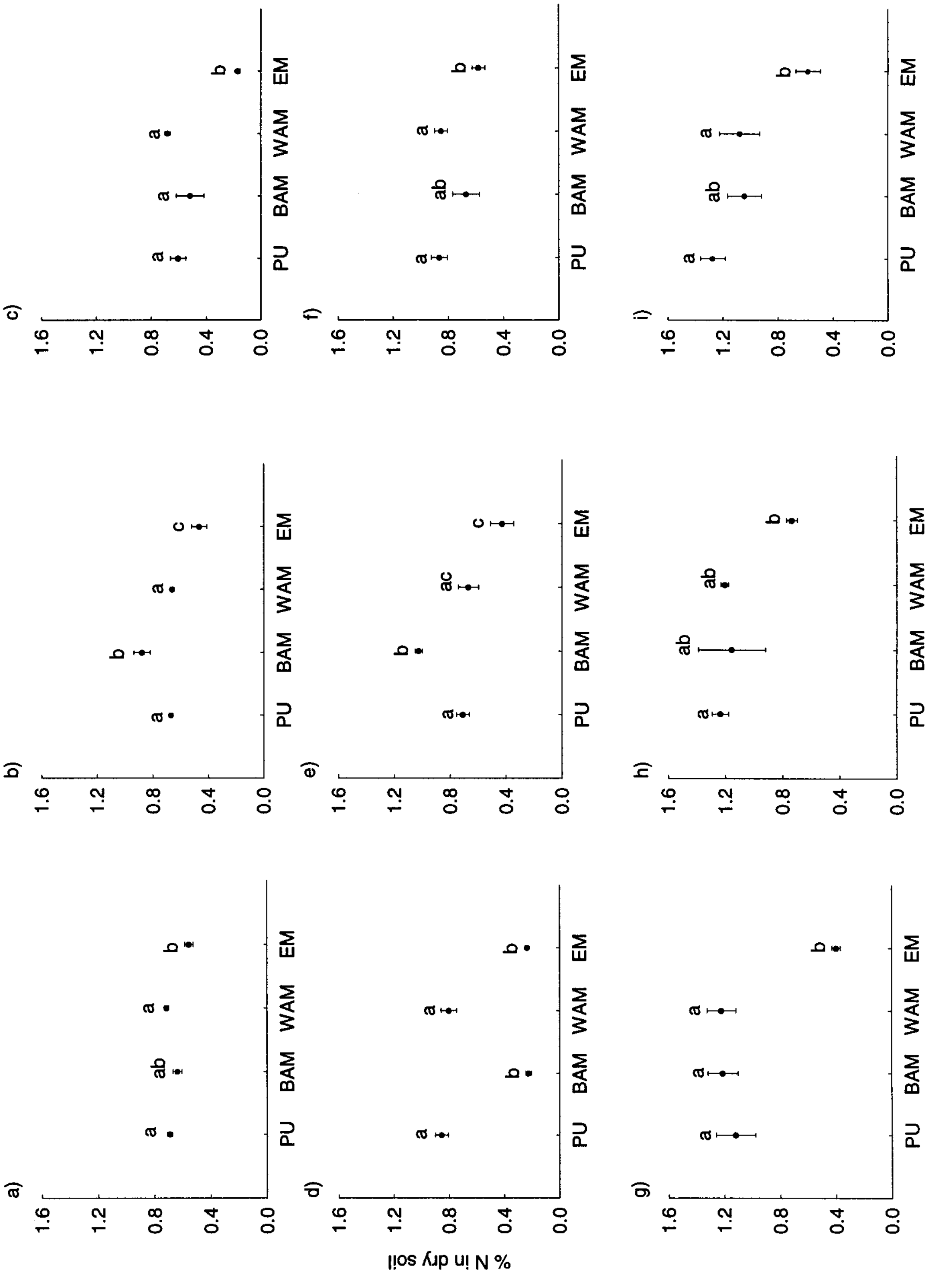
Table 2.11. Three-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE, SITE and SOIL TYPE on total nitrogen content in dry soil in 2000 and 2001in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	0.012	0.29
Site	2	6.034	71.48 ***
Sampling * Site	2	0.695	8.24 ***
Soil Type	3	4.980	39.34 ***
Sampling * Soil Type	3	0.042	0.34
Site * Soil Type	6	0.767	3.03 **
Sampling * Site * Soil Type	6	0.764	3.02 **

Table 2.12. Two-factor fixed-effects ANOVA used to analyze the effect of SAMPLING DATE and SITE on total nitrogen content in dry soil of exposed mineral sediments in 2001 in fore, low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * p<0.05, ** p<0.01, *** p<0.001).

Source	df	SS	F-ratio
Sampling	1	0.053	3.81
Site	3	1.163	27.70 ***
Sampling * Site	3	0.290	6.92 **

Figure 2.12. Total nitrogen (% in dry soil) of soil from four soil types based on types of vegetative cover (PU-*Puccinellia*, BAM- Black algal mat, WAM-White Algal Mat, EM-Exposed Mineral soil) in the Low Marsh (a) 13 July 2000 b) 25 June 2001 c) 21 July 2001), Mid-Marsh (d) 13 July 2000 e) 25 June 2001 f) 21 July 2001) and High Marsh (g) 13 July 2000 h) 25 June 2001 i) 21 July 2001) in an intertidal marsh at La Pérouse Bay, Manitoba. Soil nitrogen is displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters above means indicate significant differences between soil types (Tukey's comparison of all means $p<0.05$).



a)
b)
c)
d)
e)
f)
g)
h)
i)
% N in dry soil
0.0
0.4
0.8
1.2
1.6
PU
BAM
WAM
EM
a
ab
a
b
a
b
a
c
a
a
a
b
a
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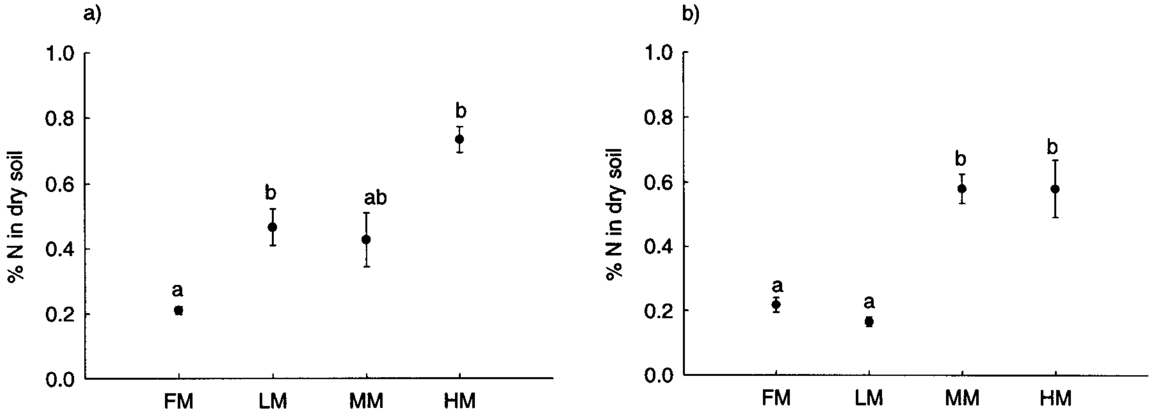


Figure 2.13. Total nitrogen (% in dry soil) of soil from exposed mineral soil in each of four sites in an intertidal marsh at La Pérouse Bay, Manitoba (FM-Fore Marsh LM-Low Marsh, MM-Mid-Marsh, HM-High Marsh) on a) 25 June 2001 and b) 21 July 2001. Soil nitrogen is displayed as mean +/- SEM (n = 5 for each site). Different letters above means indicate significant differences between sites (Tukey's comparison of all means $p<0.05$).

July 2000: Fig. 2.12d, $F_{3,16}$=8.29, p≤0.001; 25 June 2001: Fig. 2.12e, $F_{3,16}$=16.29, p≤0.001; 21 July 2001: Fig. 2.12f, $F_{3,16}$=4.54, p=0.017) and the high marsh (13 July 2000: Fig. 2.12g, $F_{3,16}$=14.57, p≤0.001; 25 June 2001: Fig. 2.12h, $F_{3,16}$=3.62, p=0.036; 21 July 2001: Fig. 2.12i, $F_{3,16}$=6.59, p=0.004). The total nitrogen content of dry soil was higher in soil beneath *Puccinellia* swards than exposed mineral soil at all sites (Fig. 2.12). Areas with non-vascular vegetation had total soil nitrogen contents similar to soil beneath intact *Puccinellia* swards and exposed mineral soil, depending on date and site (Fig. 2.12).

In exposed mineral soil there was an interaction between sampling date and site with respect to total nitrogen content (two-factor fixed effects ANOVA, Table 2.12). Total nitrogen content in dry soil generally increased with distance from the coast, with soil from the fore marsh consistently having a lower total nitrogen content than that from the high marsh on both dates (25 June 2001: Fig. 2.13a, $F_{3,16}$=15.88, p≤0.001; 21 July 2001: Fig. 2.13b, $F_{3,16}$=18.86, p≤0.001).

2.3.1.8. Effects of the type of vegetation cover on cumulative exchangeable inorganic nitrogen

2.3.1.8.1. Effects of the type of vegetation cover on cumulative exchangeable nitrate

Results of exchangeable inorganic nitrogen (as nitrate) indicated that there was an interaction between site and soil type (two-factor fixed effects ANOVA, Table 2.13). Exchangeable nitrate did not differ between soil types in the low marsh (Fig. 2.14a, $F_{3,16}$=2.93, p=0.066). In the mid-marsh, soil on which white algal mats were present had significantly higher exchangeable nitrate than corresponding values for all other soil

Table 2.13. Two-factor fixed-effects ANOVA used to analyze the effect of SITE and SOIL TYPE on cumulative exchangeable nitrate in 2001 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Soil Type	3	91.468	11.88 ***
Site	2	33.844	6.6 **
Soil Type * Site	6	69.186	4.49 **

Table 2.14. Two-factor fixed-effects ANOVA used to analyze the effect of SITE and SOIL TYPE on cumulative exchangeable ammonium ions in 2001 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Site	2	1.042	2.79
Soil Type	3	4.995	8.92 ***
Site * Soil Type	6	2.803	2.5 *

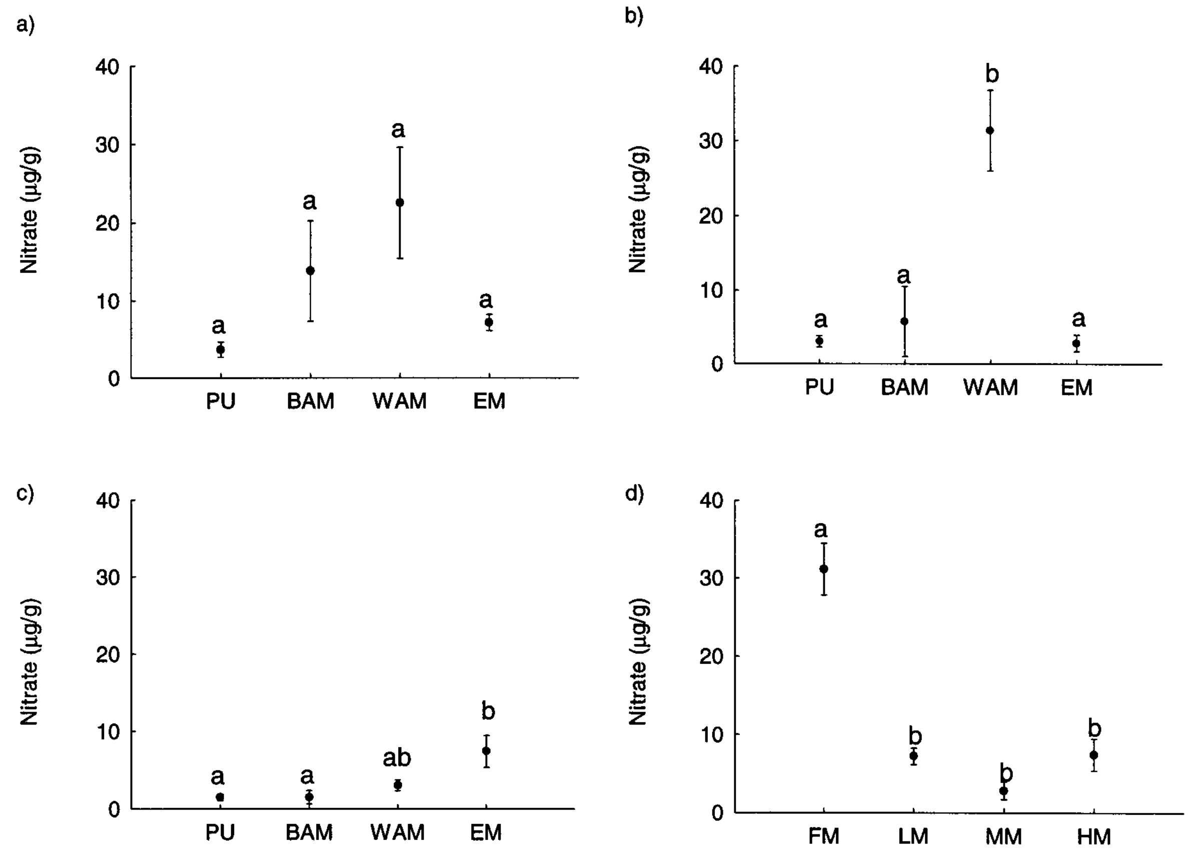


Figure 2.14. Cumulative nitrate concentrations (µg nitrate/g resin) from field-collected resin for four soil types based on types of vegetation cover (PU- *Puccinellia*, BAM- Black Algal Mat, WAM- White Algal Mat, EM- Exposed Mineral soil) for the a) Low Marsh, b) Mid-Marsh and c) High Marsh in an intertidal marsh at La Pérouse Bay, Manitoba. d) Cumulative nitrate concentrations (µg nitrate/g resin) from field-collected resin from exposed mineral soil at four sites in an intertidal marsh at La Pérouse Bay, Manitoba. (FM- Fore Marsh, LM- Low Marsh, MM- Mid-Marsh, HM-High Marsh). Nitrate concentration displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters indicates a significant difference between means (Tukey's comparison of all means, $p < 0.05$).

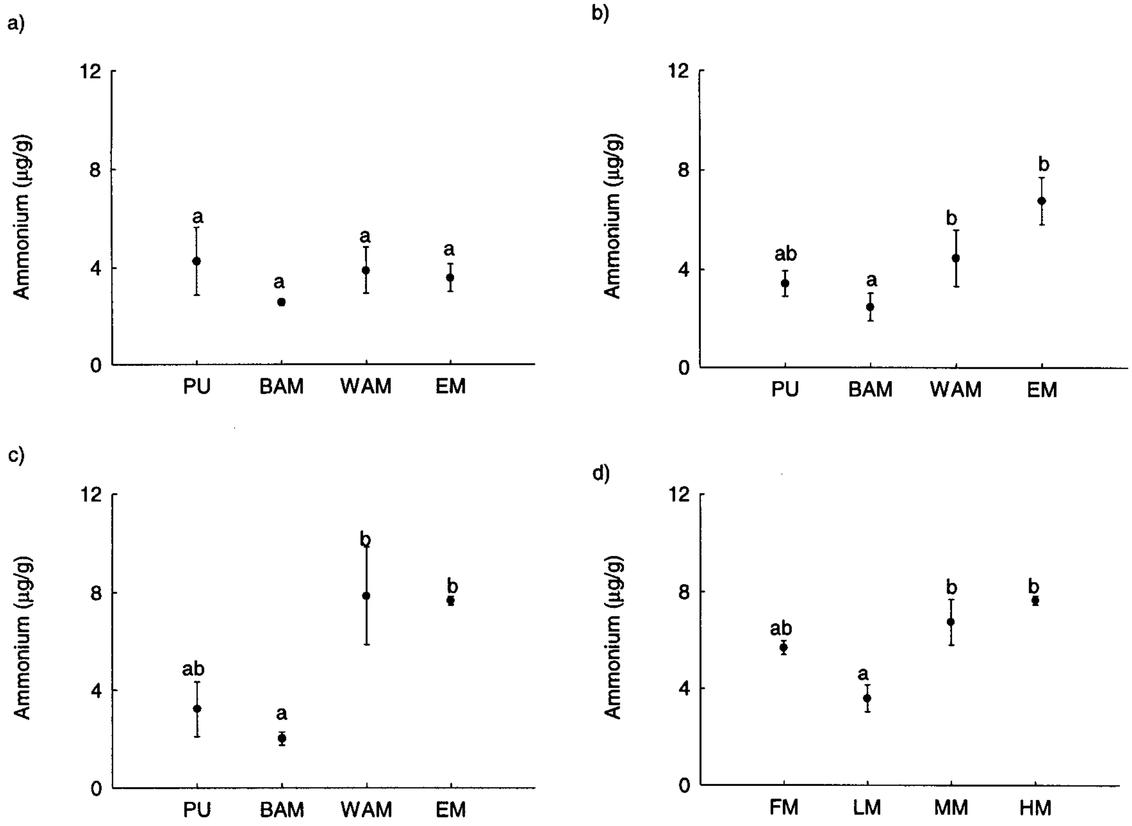


Figure 2.15. Cumulative ammonium concentrations (µg ammonium/g resin) from field-collected resin for four soil types based on types of vegetation cover (PU- *Puccinellia*, BAM- Black Algal Mat, WAM- White Algal Mat, EM- Exposed Mineral soil) for the a) Low Marsh, b) Mid-Marsh and c) High Marsh in an intertidal marsh at La Pérouse Bay, Manitoba. d) Cumulative ammonium concentrations (µg ammonium/g resin) from field-collected resin from exposed mineral soil at four sites in an intertidal marsh at La Pérouse Bay, Manitoba. (FM- Fore Marsh, LM- Low Marsh, MM- Mid-Marsh, HM-High Marsh) Ammonium concentration displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters indicates a significant difference between means (Tukey's comparison of all means, $p < 0.05$)..

types (Fig. 2.14b, $F_{3,16}=14.12$, $p\leq 0.001$). Soil type also had a significant effect on exchangeable nitrate in the high marsh (Fig. 2.14c, $F_{3,16}=5.62$, $p=0.0080$). In exposed mineral soil cumulative exchangeable nitrate was significantly higher in the fore marsh than corresponding values for the soils at all other sites (Fig. 2.14d, $F_{3,16}=37.46$, $p\leq 0.001$).

2.3.1.8.2. Effects of vegetation cover type on cumulative exchangeable ammonium ions

Results of exchangeable inorganic nitrogen (as ammonium ions) indicated that there was an interaction between site and soil types (two-factor fixed effects ANOVA, Table 2.14). Exchangeable ammonium amounts did not differ between soil types in the low marsh (Fig. 2.15a, $F_{3,16}=0.66$, $p=0.59$). Soil type had a significant effect on exchangeable ammonium in both the mid-marsh (Fig. 2.15b, $F_{3,16}=4.90$, $p=0.013$) and the high marsh (Fig. 2.15c, $F_{3,16}=6.82$, $p=0.0036$). Amounts of exchangeable ammonium ions in exposed mineral soil were significantly lower in the low marsh than at all other sites (except the fore marsh with which there was no difference) (Fig. 2.15d, $F_{3,16}=9.19$, $p\leq 0.001$).

2.3.2. Vegetation analysis

2.3.2.1. Effects of the type of vegetation cover on vigour of *Puccinellia* transplants

Results of vigour of transplants indicated that there was an interaction between site and soil type (two-factor fixed effects ANOVA, Table 2.15). There was a significant effect of soil type on transplant vigour in the low marsh (Fig. 2.16a, $F_{3,12}=20.10$, $p\leq 0.001$), mid-marsh (Fig. 2.16b, $F_{3,12}=50.81$, $p\leq 0.001$) and the high marsh (Fig. 2.16c,

Table 2.15. Two-factor fixed-effects ANOVA used to analyze the effect of SITE and SOIL TYPE on transplant vigour in 2001 in low, mid- and high marsh sites of an intertidal marsh at La Pérouse Bay, Manitoba (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Site	2	42.950	19.3 ***
Soil Type	3	395.368	118.42 ***
Site * Soil Type	6	30.822	4.62 **

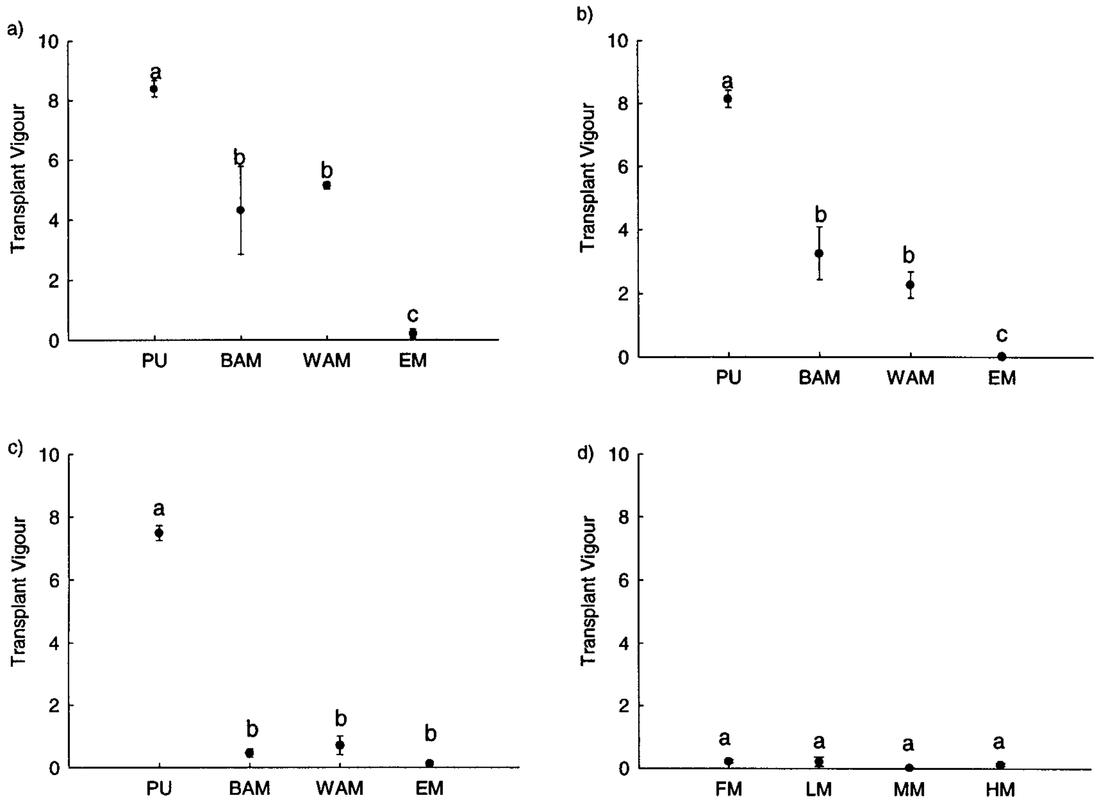


Figure 2.16. Transplant vigour in four soil types based on type of vegetative cover (PU- *Puccinellia*, BAM- Black Algal Mat, WAM- White Algal Mat, EM- Exposed Mineral soil) in the growing season of 2001 in the a) Low Marsh, b) Mid-Marsh and c) High Marsh in an intertidal marsh at La Pérouse Bay, Manitoba. A vigour score of 0 indicates no tillers of *Puccinellia* were alive at the end of one growing season after transplant, a score of 1 indicates 10% of tillers were alive and each point incrementally adds 10% survival to a maximum score of 10, or all tillers were alive at the end of a single growing season after transplant. Transplant vigour is displayed as mean +/- SEM (n = 5 for each soil type at each site). Different letters above means indicate a significant difference between soil types (Tukey's comparison of all means, $p < 0.05$) d) Transplant vigour in exposed mineral soil across four sites in an intertidal marsh at La Pérouse Bay, Manitoba (FM- Fore Marsh, LM- Low Marsh, MM- Mid-Marsh, HM- High Marsh) in the growing season of 2001. Transplant vigour is displayed as mean +/- SEM (n = 5 for each site). Different letters above means indicate a significant difference between sites (Tukey's comparison of all means, $p < 0.05$).

$F_{3,12}=300.24$, $p \leq 0.001$). In the low marsh and mid-marsh, *Puccinellia* transplanted into intact *Puccinellia* swards had the highest vigour, and those planted in exposed mineral soil the lowest. Transplants in soils with non-vascular vegetation displayed vigour midway between these extremes (Fig. 2.16a,b). In the high marsh, the vigour of *Puccinellia* transplanted into intact swards was higher than the vigour of transplants planted in the all other soil types, which otherwise were not significantly different (Fig. 2.16c). In the full model comparing algal mats (combined BAM and WAM), *Puccinellia*-covered soil and exposed mineral soil, vigour of transplants planted in *Puccinellia*-covered soil was not significantly different between sites, but the vigour of transplants planted in the algal mat covered soil (BAM and WAM) was significantly different between sites (Least Square Means Differences Tukey's Comparison of All Means, $p< 0.05$). In exposed mineral soil, *Puccinellia* had a very low vigour at all sites and again results were not significantly different between sites (Fig. 2.16d, $F_{3,12}=1.29$, $p=0.323$).

2.3.2.2. Above-ground biomass

There was a significant effect of site on above-ground biomass (Fig. 2.17, $F_{2,12}=20.38$, $p \leq 0.001$). Biomass in the high marsh sites was over two-fold higher than biomass in either the mid-marsh or the low marsh, which were not significantly different from each other.

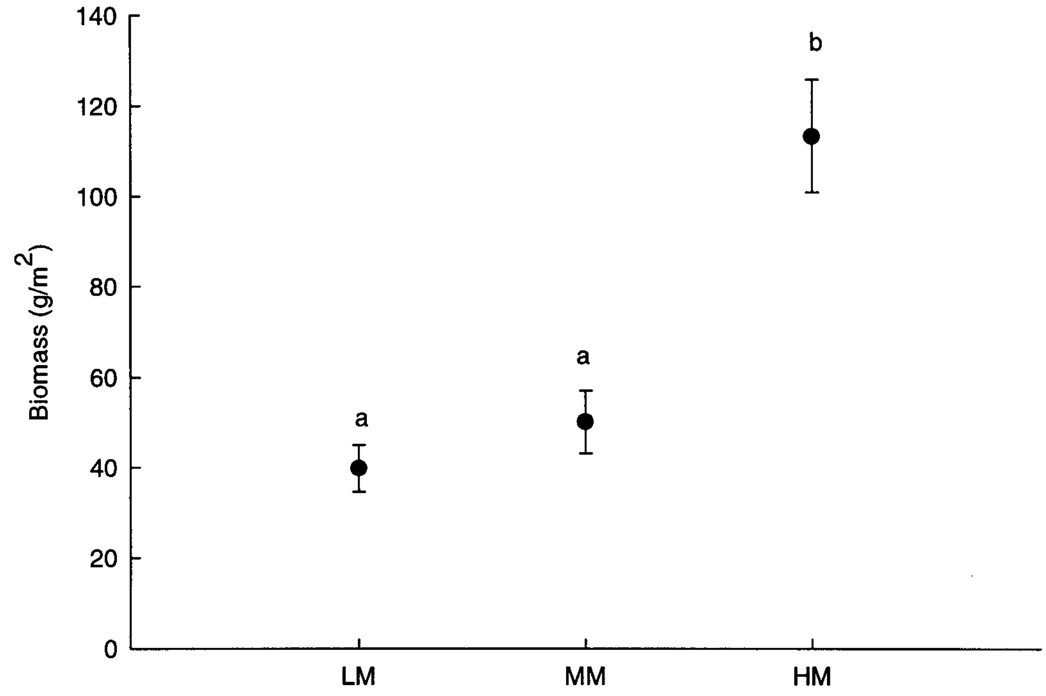


Figure 2.17. Above-ground biomass in three sites (LM- Low Marsh, MM- Mid-Marsh, HM- High Marsh) in 2001 in an intertidal marsh at La Pérouse Bay, Manitoba. Biomass is displayed as mean +/- SEM (n = 5 at each site). Different letters above means indicate a significant difference between sites (Tukey's comparison of all means, $p < 0.05$).

2.4 Discussion

Processes involving plant-soil interactions are often thought to lead to the development and maintenance of vegetation mosaics (Van de Koppel *et al.* 1997, Klausmeier 1999, HilleRisLambers *et al.* 2001). In addition to differences in infiltration rate, I found differences in soil moisture, bulk density, salinity, penetration strength, organic content, total nitrogen, and exchangeable nitrogen between different components of the vegetation mosaic at La Pérouse Bay, Manitoba. These differences in soil properties result in different establishment success of *Puccinellia phryganodes* in the different structural components of the mosaic, which, in combination with high levels of herbivory, may result in the movement of this system towards an alternate stable state of large areas of exposed sediment, devoid of vegetation (HilleRisLambers *et al.* 2001).

Across all sites, soil covered with *Puccinellia phryganodes* had a higher infiltration rate than exposed mineral soil (Fig. 2.1). Increasing plant density is often found to promote water infiltration into soil (Elwell and Stocking 1976, Box and Bruce 1996, Anderson and Hodgkinson 1997) as a result of the interception of raindrops by grasses (Box and Bruce 1996), increased water capture by grasses (Anderson and Hodgkinson 1997), the forming of root channels and funnelling of water by leaves (Glover *et al.* 1962). In contrast, working in a bunch-grass system Glover *et al.* (1962) found that vegetated soil had a lower infiltration rate than non-vegetated soil. This conflicting result is likely due, however, to the extremely high density of shoots within the grass bunches (Glover *et al.* 1962). Across all soil types, infiltration rate was negatively correlated with bulk density (Fig. 2.2), resulting in differences in infiltration rate between soil types. Soil compaction has been found previously to decrease water infiltration, and thus increase runoff and erosion (Hakansson and Voorhees 1998).

Higher infiltration rates in vegetated sites compared with exposed sediments of a vegetation mosaic, as seen above, is a consistent pattern found in different habitat types including the Serengeti (Belsky 1986), African rangelands (Wilson and Agnew 1992, Van de Koppel *et al.* 1997) and the slopes of semi-arid areas in Africa (Aguiar and Sala 1999, Seghieri and Galle 1999). The formation and maintenance of vegetation mosaics is almost always attributed to differences in infiltration rates between the different soil components that give rise to the pattern (Wilson and Agnew 1992, HilleRisLambers *et al.* 2001). Additionally, theoretical models have shown that differences in infiltration rate between soil types can induce regular patterns of vegetation alternating with exposed soil (Rietkerk and Van de Koppel 1997, Van de Koppel *et al.* 1997, Klausmeier 1999, HilleRisLambers *et al.* 2001). Rain falling on bare patches, which may be covered by a biotic crust, will barely infiltrate and run off where it may accumulate in vegetated patches (HilleRisLambers *et al.* 2001) or be lost from the system. The accumulation of water in vegetated patches may result in the maintenance of these patches in a system that overall is water-limited (Bromley *et al.* 1997).

The maintenance of vegetation mosaics is primarily attributed to differences in infiltration rate (Wilson and Agnew 1992, HilleRisLambers *et al.* 2001), and little attention is paid to other soil characteristics, despite the numerous other soil properties that may negatively affect plant growth in exposed sediment. Despite the close links between other physical soil properties, such as bulk density and infiltration rate (Hakansson and Voorhees 1998), and the evidence that physical soil properties can affect plant growth, these other soil physical characteristics are rarely examined. In addition, nutrient cycling in vegetation mosaics has been largely ignored. Non-vegetated areas in vegetation mosaics often have lower soil organic matter and a lower availability of nutrients for plant growth (Aguiar and Sala 1999) because vegetation offers protection against erosion (Elwell and Stocking 1976) and generates plant litter (Aguiar and Sala 1999) that promotes higher nutrient retention (Rietkerk and Van de Koppel 1997).

Other soil properties, in addition to infiltration rate, varied between components of the vegetation mosaic at La Pérouse Bay, Manitoba. Soil moisture was consistently higher and bulk density lower in *Puccinellia*-covered soil than in exposed mineral soil across all sites and dates (Fig. 2.3 and 2.5 respectively). Salinity was lower in *Puccinellia*-covered soil than in exposed mineral soil (Fig. 2.7). *Puccinellia*-covered soil had a higher soil organic matter content than that in exposed mineral soil at two out of three sites (Fig. 2.11) and the total nitrogen content of soil was higher in *Puccinellia* covered soil than in the exposed mineral soil (Fig. 2.12). Cumulative available nitrogen (in the forms of exchangeable nitrate and ammonium ions), however, generally did not vary between soil types (Fig. 2.14 and 2.15 respectively).

Aside from low infiltration rates, the soil characteristics of exposed mineral soil may be detrimental to plant growth in other ways. Low soil moisture can cause reduced plant growth in systems limited by water. Compacted soils (soil with higher bulk densities) can lead to lower nutrient uptake in plants (Arvidsson 1999) resulting in lower plant growth (Masle and Passioura 1987). Although weakly saline conditions are favorable for the growth of most marsh halophytes (Adam 1990) including *Puccinellia phryganodes*, this grass species has been shown to be negatively affected by high soil salinities (Srivastava and Jefferies 1995a). Finally, nutrient availability is a frequent constraint on plant growth (Guillaume *et al.* 1999). The impact of these characteristics of exposed soil on *Puccinellia phryganodes* survival may, in addition to the effects of infiltration rate, contribute to the maintenance of the vegetation mosaic at La Pérouse Bay, Manitoba and the absence of *Puccinellia* from these mineral soils.

The two algal mat-covered soils generally had soil properties similar to those of *Puccinellia*-covered soil, or else the properties were mid-way between *Puccinellia* covered soil and exposed mineral soil. The algal mat cover maintains infiltration rate (Fig. 2.1), soil moisture (Fig. 2.3), bulk density (Fig. 2.5), soil salinity (Fig. 2.7), and organic (Fig. 2.11) and total nitrogen contents (Fig. 2.12) at levels generally above those of exposed mineral soil. By maintaining favorable soil characteristics, the microbiotic crusts may be acting as a facilitator to *Puccinellia* re-growth by slowing the rate of soil degradation after the removal of *Puccinellia* by geese.

The two algal mat-covered soils generally did not differ in their effects on soil properties for most of the variables examined. For these soil characteristics, algal mat presence was more important that the identity of the algal mat. Algal mats were differentiated based solely on mat colour, which may be a dynamic property of the mat. Black algal mats, as the season progresses and temperatures increase, dry out and change colour, becoming white algal mats. This transition may be very rapid, or occur slowly throughout the season, and may occur multiple times during a single growing season. During the transplant vigour experiment, black algal mats exclosed at the beginning of the season, often appeared white at the end of the season. Thus, the algal mats represent a 'moving target' and the transition between black and white algal mats may occur at different rates both within a season, for mats that are spatially separated, and between seasons depending on climatic conditions.

Microbiotic crusts can produce soil conditions that can have both negative and positive effects on plant growth (Prasse and Bornkamm 2000). One of the most important effects that microbiotic crusts can have on ecosystem dynamics is the stabilization of soil surfaces (Evans and Johansen 1999). Soil crusts can, however, have numerous other effects. Microbiotic crusts affect soil hydrology, although the direction of this effect is not consistent between studies. Microbiotic crusts have been found to increase the rate of water infiltration into the soil (Fletcher and Martin 1948, Loope and Gifford 1972). In contrast, other studies have found that removal of crust increases infiltration (Graetz and Tongway 1986), infiltration rates are lower in crust-covered soil than vegetated soil (Maestre *et al.* 2002), and further that there is a negative relationship between cyanobacteria cover and infiltration rate (Maestre *et al.* 2002). The effect of microbiotic crusts on infiltration rate may depend on local soil properties and crust composition (for example, in this study, white algal mat covered soil had an infiltration rate different from black algal mat covered soil in two of the three sites (Fig. 2.1)).

In addition to effects on soil hydrology, the presence of soil microbiotic crusts has been found to increase soil salinity (Anderson *et al.* 1982) and decrease soil moisture (Franco and Nobel 1988). Crusts have been found to lower nutrient availability for plants (Evans and Johansen 1999), but also to increase nutrient availability in some studies (Johansen 1993, Gold and Bliss 1995, Belnap 1996, Belnap and Gillette 1998, DeFalco *et al.* 2001). Crust presence can result in decreased seedling emergence (Johansen 1993, Prasse and Bornkamm 2000) and decreased germination (Zaady *et al.* 1997), although germination may be promoted under certain conditions (Zaady *et al.* 1997). Thus, crusts can have both positive and negative effects on plants through their effects on soil characteristics, that enable the crusts to act as both a facilitator (by maintaining favourable soil conditions) and a competitor (Franco and Nobel 1988).

Although plant-soil interactions may lead to both to the maintenance of mosaics and vegetation collapse without herbivory, herbivore presence in these systems may accentuate these plant-soil interactions. Vegetation collapse resulting from a high density of grazers frequently occurs in semi-arid systems (Jefferies 1988b, a, Schlesinger *et al.* 1990). Grazing in semi-arid systems can result in either a vegetation mosaic or vegetation collapse, depending on the nature of the plant-soil interactions (Van de Koppel *et al.* 2002). These interactions can result in increased resource availability in the remaining vegetated patches (Montana 1992, Bromley *et al.* 1997), allowing the vegetated patches to survive under increased grazing (Van de Koppel *et al.* 2002). In other systems, however, the plant-soil interactions may have little effect and the degradation from grazing results in the collapse of net primary production (Van de Koppel *et al.* 2002). Models describing semi-arid grazing systems predict that provided the rate of vegetation dispersal is low, an increase in the level of herbivory may lead to vegetation changes from closed vegetation cover, to a state with spatial vegetation patterning (vegetation mosaics), to a state of exposed soil without vegetation (Rietkerk *et al.* 2000, HilleRisLambers *et al.* 2001).

As the numbers of snow geese have increased at La Pérouse Bay, resulting in an increase in the levels of herbivory on salt-marsh vegetation, a trend in vegetation structure in the salt marsh has occurred similar to that described above. Vegetation has changed from continuous grazing lawns to a system with a mosaic of exposed sediment and vegetation (Handa *et al.* 2002). Additionally, large areas have progressed further to hypersaline exposed sediment, devoid of vegetation (Jefferies and Rockwell 2002). According to the model created by (HilleRisLambers *et al.* 2001), plant-soil interactions involving feedbacks may be unable to maintain vegetated patches when the levels of herbivory is as high as it is at La Pérouse Bay, especially if the dispersal rates of *Puccinellia* are low.

Numerous factors may lead to a low dispersal rate in *Puccinellia phryganodes.* This grass is a sterile triploid (Bowden 1961) and thus there is no seed bank for re-establishment of *Puccinellia* (Chang *et al.* 2001). It therefore must rely on clonal growth for re-establishment in damaged areas (Jefferies and Rockwell 2002). The grass can establish from leaf fragments in soft sediments (Chou *et al.* 1992). The numerous residual leaf fragments resulting from goose grazing, and movement of these fragments by wind or water and by biotic agents (i.e., geese) may increase the dispersal potential of *Puccinellia.* However, although there is potential for high dispersal rates of *Puccinellia,* also required is the ability of *Puccinellia* to survive in the sediment of other components of the mosaic in order for this dispersal to result in successful establishment.

In order to test the ability of *Puccinellia* to establish in the different components of the mosaic, plugs of *Puccinellia* were transplanted into each component and transplant vigour monitored. Transplants showed high survival in all plots covered with *Puccinellia* and very low survival in exposed mineral sediments (Fig. 2.16). Thus, dispersal within a vegetated patch may be possible, but successful establishment in other components of the mosaic is likely to be a rare event. This low rate of establishment, in combination with high levels of herbivory, may result in the transition of continuous swards of *Puccinellia* to a vegetation mosaic of *Puccinellia* interspersed with exposed areas, to large areas of exposed sediment, devoid of vegetation, as described in the recent model of HilleRisLambers *et al.*(2001).

Algal mat cover (black or white) negatively affected transplant vigour of *Puccinellia* compared with the vigour of *Puccinellia* in intact swards. In some cases, vigour was as low as that in exposed mineral soil (Fig. 2.16). By maintaining soil characteristics at a level either equal to that of *Puccinellia*-covered soil, or at least generally more favourable for plant growth than exposed mineral soil, the algal mats may be acting as a facilitator for *Puccinellia* re-establishment. However, transplant vigour is not as high in algal mat-covered soil as in *Puccinellia*-covered soil, which may be due to less favourable soil conditions under algal mats, or due to competition between the algal mats and *Puccinellia,* resulting in lower establishment success of the grass. Transplant vigour in algal mat-covered soil varied between sites (for example, vigour was much lower in high marsh sites than in low or mid-marsh sites (Fig. 2.16)) and thus the relative importance of facilitation and competition of the crusts may be changing, depending on the conditions existing at each site.

Bertness and Callaway (1994) formulated a hypothesis predicting how the balance between facilitation and competition might vary with environmental conditions. Increased levels of physical stress or consumer pressure may lead to positive interactions by neighbours, driven by the amelioration of these potentially limiting stresses (Bertness and Callaway 1994). In a harsh environment, which may restrict plants from acquiring resources, growing in close association with neighbors may favour growth by ameliorating harsh conditions so that the negative competitive effects of the close association are negated. In less harsh environments, however, the negative effects of competing with neighbors would likely outweigh any small effects that the neighbours may show in ameliorating environmental conditions (Bertness and Callaway 1994, Callaway 1997, Olofsson *et al.* 1999). Numerous field experiments have supported this hypothesis (Bertness and Shumway 1993, Bertness and Hacker 1994, Greenlee and Callaway 1996, Choler *et al.* 2001, Tewksbury and Lloyd 2001, Callaway *et al.* 2002). However, Casper (1996) found no evidence of an increase in facilitation under increasing water stress. Also, no conclusive relationship between competition or facilitation and productivity was found in a recent meta-analysis (Goldberg *et al.* 1999), although there was a consistent restriction of facilitation to poor environments (Goldberg *et al.* 1999).

Defining a gradient of stress across an environment can be difficult because the definition of stress varies between species (Choler *et al.* 2001), and because favourable and non-favourable environments for growth may be difficult to determine if numerous soil variables are considered. For example, soil moisture (Fig. 2.3), organic content (Fig. 2.11) and nitrogen content (Fig. 2.12) were generally higher in the high marsh than the low marsh, indicating a more favourable environment for growth (and thus less stressful environment) in the high marsh. However, salinity was higher in the high marsh than the low marsh (Fig. 2.7), indicating a more stressful environment in the high marsh. Callaway (1998) used Grime's (1979) definition of stress: "the external constraints which limit the rate of dry matter production of all or part of the vegetation" to define more and less stressed sites, and thus he used biomass of an individual species at each site as a measure of stress. According to this definition of stress, as biomass is higher in the high marsh than the other two sites (Fig. 2.17), the high marsh is a less stressful site than either the mid- or the low marsh.

In addition to levels of stress, sites also vary with the degree of facilitation offered by the algal mats to *Puccinellia* transplants. When comparing soil beneath algal mats from different sites, one can assume that because there was no difference in survival of transplants in *Puccinellia*-covered soil, that a higher level of transplant vigour in algal mat soil indicates a higher proportion of facilitation offered by the mat, as opposed to competition. Levels of transplant vigour in algal mat-covered soil decreased from the low marsh to the high marsh, indicating a higher level of facilitation in the low marsh than in the high marsh sites. This is consistent with the Bertness- Callaway (Bertness and Callaway 1994) hypothesis that more stressful sites should have higher levels of facilitation that ameliorate abiotic stress.

Few differences in soil characteristics were exhibited between the exposed mineral soil at the different sites, regardless if the soil had previously been colonized by vegetation (fore marsh sites are unconsolidated sediments that have not previously been colonized) (Fig. 2.4, 2.6, 2.8, 2.13). At the furthest point examined along the soil ripening gradient (high marsh sites), in the exposed mineral soil, soil moisture was higher (Fig. 2.4), bulk density was lower (Fig. 2.6) and total nitrogen content of dry soil was higher (Fig. 2.13) than values from other sites. As the high marsh is further along the soil ripening gradient, it emerged from Hudson Bay at an earlier date than the other sites and thus has been accumulating soil organic matter for a longer period of time. Despite the removal of the thin organic veneer at this site by grubbing in exposed areas, there is still a higher organic content in the underlying mineral sediment, resulting in the higher soil moisture content, a lower bulk density and a higher total nitrogen content than the other sites. However, this does not result in a higher vigour of transplants in exposed mineral soil at this site compared with elsewhere. Transplant vigour in exposed mineral soil did not differ between sites (Fig. 2.16d) and was extremely low at all sites. Presence of other *Puccinellia* plants exhibiting self-facilitation is required to allow successful establishment of *Puccinellia* transplants and thus establishment in exposed soil, regardless of the site or its previous history of colonization.

In summary, plant-soil interactions exist at La Pérouse Bay that may maintain the existence of vegetated patches in a vegetation mosaic. However, high levels of herbivory and low levels of dispersal by *Puccinellia*, may be triggering the movement of this system from a state with continuous vegetative cover to a vegetation mosaic to an alternative stable state of hypersaline, large areas of exposed sediment, devoid of vegetation. There are differing degrees of degradation in components of the mosaic, with the algal mats being the intermediate point between vegetated patches and exposed mineral soil. In sites with high stress, these algal mats may ameliorate soil conditions, allowing partial re-establishment of *Puccinellia*. As the degradation of algal mat soils progresses, however, towards exposed mineral soil, the possibility of successful re-vegetation of these areas decreases and the system moves towards complete vegetation collapse.

Chapter 3: Disturbance, patch dynamics, soil change and rate of vegetation re-colonization in an intertidal salt marsh at La Pérouse Bay, Manitoba.

3.1. Introduction

Disturbance can alter both the structure and the distribution of organisms within an environment resulting in increased environmental heterogeneity (Wiens 2000). A disturbance is damage to the environment, caused by abiotic or biotic factors, which results in the displacement or mortality of individuals (Sousa 2001). Disturbances can be highly localized, creating open space in discrete patches within a background assemblage of organisms (Sousa 1984a, Pickett and White 1985, Sousa 1985). Patches that are the result of disturbance may coalesce to form contiguous areas where the resident organisms have been removed or are highly reduced in numbers (Sousa 2001). At a larger spatial scale, landscapes are a mosaic of discrete patches, characterized by differences in biotic and abiotic structures between patches (Pickett and Cadenasso 1995).

Abiotic factors, such as frost-heave or wind-throw can create gaps in an otherwise continuous distribution of organisms (Stewart *et al.* 2000). Organisms themselves may also create heterogeneity in an otherwise uniform environment. (Stewart *et al.* 2000, Wiens 2000, Wilson 2000, Sousa 2001). In particular, animals may create and maintain heterogeneity through their grazing behavior, trampling and burrowing (Stewart *et al.* 2000). Foraging animals can alter vegetation structure, growth, production, species composition, and nutrient dynamics at multiple scales, resulting in a heterogeneous environment (Wiens 2000).

Re-colonization of disturbed patches, either through vegetative re-growth or recruitment from dispersing propagules, can be affected by numerous biotic and abiotic factors (Sousa 2001). Depending on the type and severity of the disturbance, both the biological and physical environment of the patch can be altered, which may strongly influence patterns of re-colonization (Sousa 2001). Re-colonization of the patch depends both on traits of species that have the potential to colonize the now exposed patch, but also on the characteristics of the disturbed patch itself (Sousa 1984b). These characteristics include variables such as the intensity and severity of the disturbance that created the patch, the time and location in which it was created, as well as the size and shape of the patch (Sousa 1984b). All of these traits, and interactions between them, will determine the pattern of patch regeneration (Shumway and Bertness 1994).

In particular, patch size and shape greatly influence patterns of patch regeneration, primarily due to the alteration of the ratio of the circumference to the area of the patch (Forbes *et al.* 2001). As the patch size increases, the perimeter to area ratio decreases, which has consequences for rates of re-colonization, due to changes in the physical and biological environment within the patch, as well as the density of reproductive adults near the patch (Sousa 1984b). Small patches have a greater patch perimeter to area ratio, and thus the number of reproductive adults in undamaged areas closest to the center of the patch will often be much larger per unit area of patch than the number for large patches. For species that reproduce clonally and for those whose propagules have a low dispersal potential, this may result in a denser settlement and a more rapid recruitment for small patches than for large ones (Sousa 2001).

The organisms that surround a disturbed patch can have both positive and negative effects on recruitment. The direction and strength of these effects varies with patch size and shape as well as with characteristics of the neighbours and the prevailing environmental conditions (Sousa 2001). A high perimeter to area ratio can promote regeneration by providing an easy access of the patch to a supply of propagules, but can also indirectly inhibit regeneration because of alteration of the within-patch environment (Sousa 2001). A smaller clearing may have increased shading or depletion of the local nutrient supply compared to the situation in larger patches where the distance to the patch center is greater (Sousa 1985). Alternatively, neighbouring organisms may ameliorate harsh physical conditions that are often associated with the removal of cover (Sousa 2001). This amelioration will be greater in small patches than in large patches due to the proportion of the patch that is shaded or covered by the neighbouring canopy. (Sousa 1984b, 2001).

In stressful environments, such as salt marshes and Arctic ecosystems, facilitation may be a prevalent force in patch regeneration. Harsh environments are often characterized by the presence of facilitative interactions that ameliorate stressful environmental conditions (Bertness and Callaway 1994, Holmgren *et al.* 1997, Brooker and Callaghan 1998). Plants on the perimeter of the patch may have positive effects on the internal patch environment through such mechanisms as reducing evaporation rates (Srivastava and Jefferies 1995b), increasing oxygen diffusion (Armstrong 1979) and increasing nutrient availability (Müller 1953, Callaway 1995). In particular, in salt marshes shade from vegetative cover often reduces evaporation from soils under plant canopies resulting in lower soil salinities (Iacobelli and Jefferies 1991, Bertness *et al.*

1992, Bertness and Hacker 1994, Srivastava and Jefferies 1996, Hacker and Gaines 1997). Because of its effects on the proximity of neighbouring plants relative to the disturbed sediment, variation in patch size may determine the overall impact of facilitative mechanisms in controlling patch regeneration.

The reproductive strategy of the plants surrounding the patch may also have large impacts on the patterns and processes involved in re-colonization (Sousa 1984b). Plants that do not undergo sexual reproduction, such as asexual clonal plants (e.g. *Puccinellia phryganodes*), do not generate a seedbank from which regeneration can occur, and thus must re-colonize disturbed patches by vegetative in-growth from the patch perimeter or through the establishment of ramets from plant fragments. In stressful environments, a clonal growth strategy may put a plant at a competitive advantage. In Arctic and alpine environments the clonal growth strategy is widespread and is often the dominant fraction of biomass (Körner 1999, Jónsdóttir 1996)

Although the production of ramets is both energy and nutrient demanding, it may provide a competitive advantage in harsh environments (Jónsdóttir *et al.* 1996), especially when nutrients can be translocated from older ramets during establishment (Callaghan 1984), as connected ramets may "help each other out" during disturbance (e.g. herbivory) or when resources are patchy (Körner 1999). This is because offspring resulting from clonal growth are more likely to be successful in the local environment than offspring from sexual reproduction, as clonal offspring tend to be larger resulting in higher survival. Hence, resources invested in asexual reproduction are less likely to be wasted (Jónsdóttir *et al.* 1996), which can be of ecological significance in a nutrient-limited environment. The lateral spread of plants from clonal growth can also be advantageous in a nutrient-limited environment, as clonal growth provides a searching mechanism where new resource patches can be entered (Hutchings and de Kroon 1994).

Within the clonal growth habit, there are two growth patterns that are alternative strategies to improve resource acquisition in resource-limited habitats (Harper 1985). The two growth patterns, spreading, with large distances between ramets, and caespitose, with short distances between ramets, are termed guerilla growth and phalanx growth respectively (*sensu* Lovett Doust 1981). Guerilla growth allows a continuous search for new patches to exploit (Harper 1985, Jónsdóttir *et al.* 1996) and plants invade "free" space rapidly (Bertness and Ellison 1987). Alternatively, the ramets of the phalanx growth pattern are confined to limited area and are thus forced to use resources efficiently (Harper 1985, Jónsdóttir *et al.* 1996) and invade bare space more slowly with a dense front of rhizomes, roots and tillers (Bertness and Ellison 1987).

The foraging activity of the lesser snow goose (*Anser caerulescens caerulescens* L.) creates a mosaic of vegetated swards with localized patches of exposed soil in the intertidal marsh of La Pérouse Bay, Manitoba. The intertidal marsh is colonized primarily by the graminoids, *Puccinellia phryganodes* and *Carex subspathacea*, and it is within swards of these two vegetation types that exposed patches are created. Exposed patches of sediment are created by a type of foraging termed "grubbing" that occurs early in the season, before the onset of above-ground vegetative growth (Jefferies *et al.* 1979, Kerbes *et al.* 1990, Hik *et al.* 1992). In spring, geese grub for roots and rhizomes of the graminoid plants, removing both the entire graminoid plant from the ground as well as the thin veneer of organic matter and plant litter above the sediment (Hik *et al.* 1992).

This destructive form of feeding results in patches of disturbed sediment of different size surrounded by intact salt-marsh vegetation.

The objectives of this study were to determine the influence of patch size on both soil dynamics within a patch, as well as on the ability of *Puccinellia phryganodes* to re-colonize the exposed sediment. In order to examine soil dynamics after disturbance, patches simulating grubbing were experimentally created at a variety of patch sizes. Soil properties of the sediment were determined in the various patches after creation of the patch and over the two subsequent growing seasons. Secondly, as patch size can largely influence patch re-colonization (Sousa 1984b, Forbes *et al.* 2001), the re-growth of *Puccinellia* into exposed patches was followed in the second and third growing seasons after establishment of the patch. The overall objective of this experiment was to determine if influences of patch size on sediment properties and vegetative re-growth create a threshold patch size above which regeneration of a sward is inhibited.

3.2. Materials and Methods

3.2.1. Site Description

Experimental sites were located in the intertidal flats at La Pérouse Bay, Manitoba (58°44'N, 94°28'W) where isostatic uplift has resulted in extensive coastal flats (1 m rise per 3 km) (Jefferies *et al.* 1979). The surface topography of the coastal zone displays only minor relief that results from frost heaving of unconsolidated sediments and the presence of ephemeral streams and ponds that are active during spring melt, or when heavy precipitation occurs during summer (Handa and Jefferies 2000). In the intact, vegetated areas of the intertidal salt marsh, the dominant graminoids are *Puccinellia* *phryganodes* (Trin.) Scribn. & Merr. , a stoloniferous grass, and *Carex subspathacea* Wormskj., a rhizomatous sedge. An area of low willow (1 metre high) extends inland from the salt marsh for approximately 1 km (Iacobelli and Jefferies 1991). Permafrost is continuous in the Churchill region (Rouse *et al.* 1997) and in salt-marsh sites at La Pérouse Bay it is present approximately 25-30 cm below the surface of sediment in mid-summer (Wilson 1993). The snow-free season usually extends from mid-June to late September, although snow can fall in any month of the year.

In this study, soil properties were examined along a soil ripening (aging) gradient that was associated with the rise in land elevation from the sea inland to the upper limit of the intertidal marsh. Land is emerging from the Hudson Bay at a rate of about 80 cm per 100 years in the Churchill region (Hansell *et al.* 1983). This is equivalent to approximately 200 metres of new shoreline every decade (Glooschenko and Martini 1978). There is a change in soil properties as the sediments age (termed "soil ripening") (Pons and Zonneveld 1965, Packham and Willis 1997) that occurs along a geographical gradient that extends from the coast inland. At La Pérouse Bay, the change in soil properties is not associated with a change in the plant species as the two graminoid species mentioned above are dominant throughout the intertidal flats. The experimental area extends over a distance of approximately one kilometre along which soil properties change between the immediate coastal sites and the more inland sites in the intertidal marsh. Three sites were selected within the experimental area; they were located in the low marsh, mid-marsh and high marsh (Plate 2.1) which differ in the age since the land has emerged from the Hudson Bay. The low marsh represents the youngest site and the

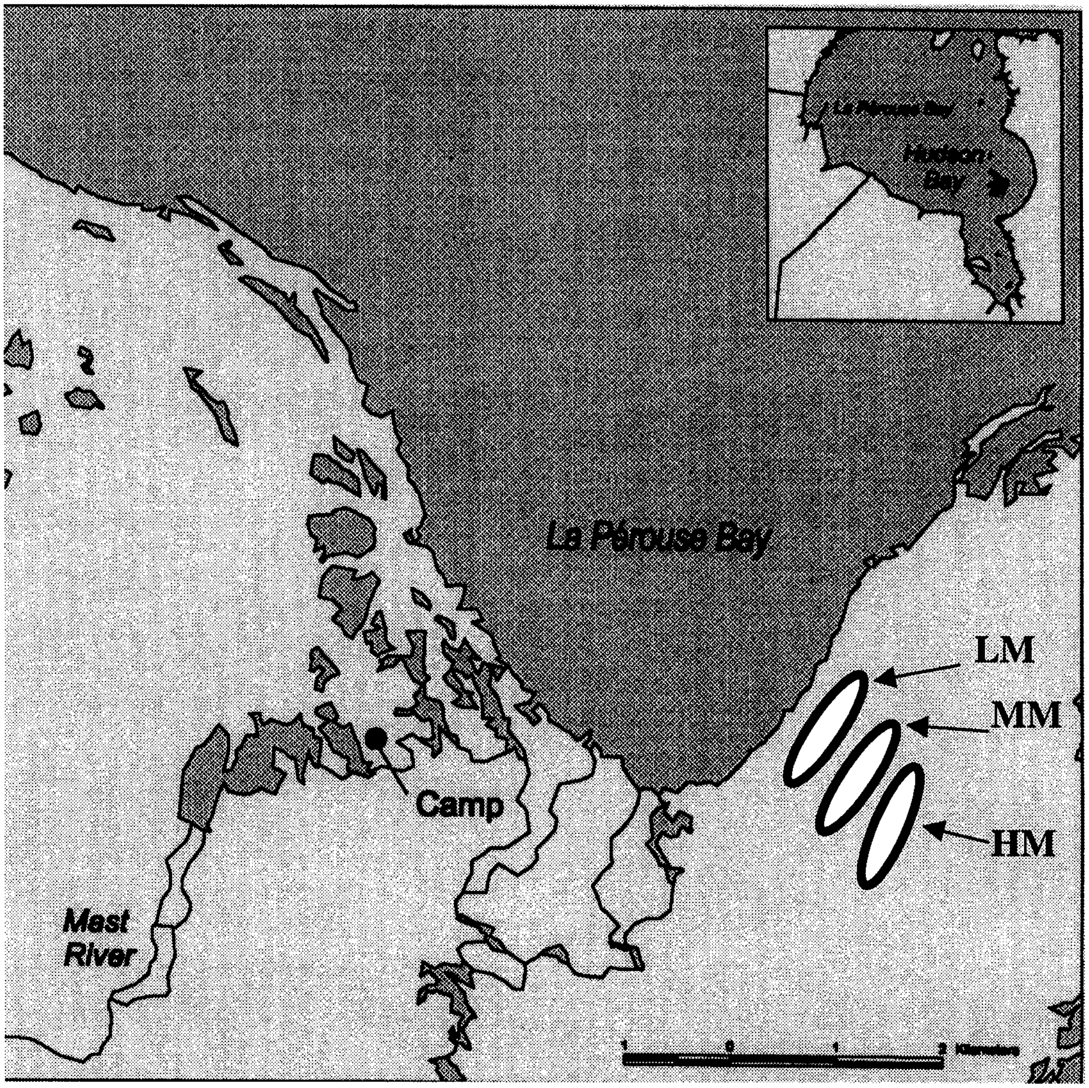


Plate 3.1. Map of La Pérouse Bay, Manitoba and the coastal zone, the position of which, on the Hudson Bay coast, is indicated by an arrow on the inset of the map. Sites along a soil ripening gradient associated with rise in land elevation from the sea landwards across which experimental patches were created are the low marsh (LM), mid-marsh (MM) and the high marsh (HM). The low marsh represents the youngest site, the high marsh, close to the willow fringe, the oldest.

high marsh, close to the willow fringe at the landward limit of the intertidal marsh, the oldest. The sites were approximately 100m x 100m and were selected because some intact swards were still present within each site. Elsewhere, the effects of grubbing by geese has led to loss of vegetation.

3.2.2. Experimental Design

Experimental plots (1m x 1m) were established in June, 2000 at the three sites. Different patch sizes of exposed sediment (diameters of 2.5 cm, 5 cm, 10 cm, 20 cm, and 40 cm) that simulated grubbing were prepared by removing vegetation and litter along with the top layer (ca. 1cm) of soil. Smaller patch sizes were replicated (5 cm patch replicated 3 times, 2.5 cm patch replicated 6 times) within a plot to ensure sufficient soil was available for sampling. Otherwise, one replicate of each patch size (10, 20, 40 cm) was present in a plot. Sufficient area was left undisturbed in each plot to allow sampling where the sward was still intact that provided a vegetated control area. Each plot, therefore, contained all sizes of grubbed patches (Plate 3.2, Plate 3.3), and it was surrounded by a chicken-wire exclosure to restrict the geese from further grubbing or grazing the vegetation. Thirty-five plots were created at each site that were separated by at least 5 metres. Plots at each site were used to examine changes in soil properties and vegetation re-growth with respect to patch size.

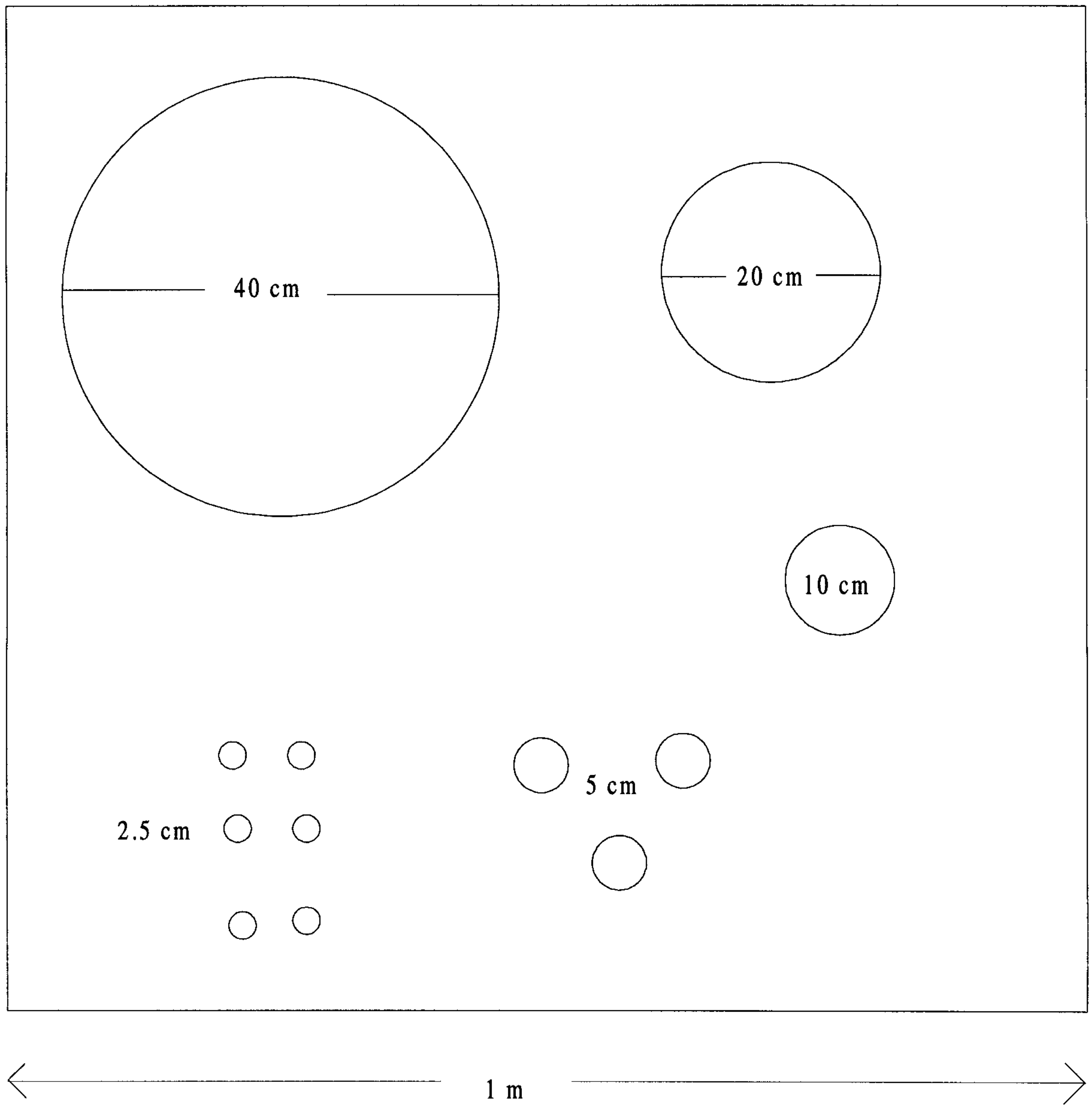


Plate 3.2. Graphical representation of experimental plot design. Solid square surrounding circles represents chicken-wire goose exclosure. Each circle represents one artificially grubbed patch of the diameter indicated. Patches were arranged as shown.

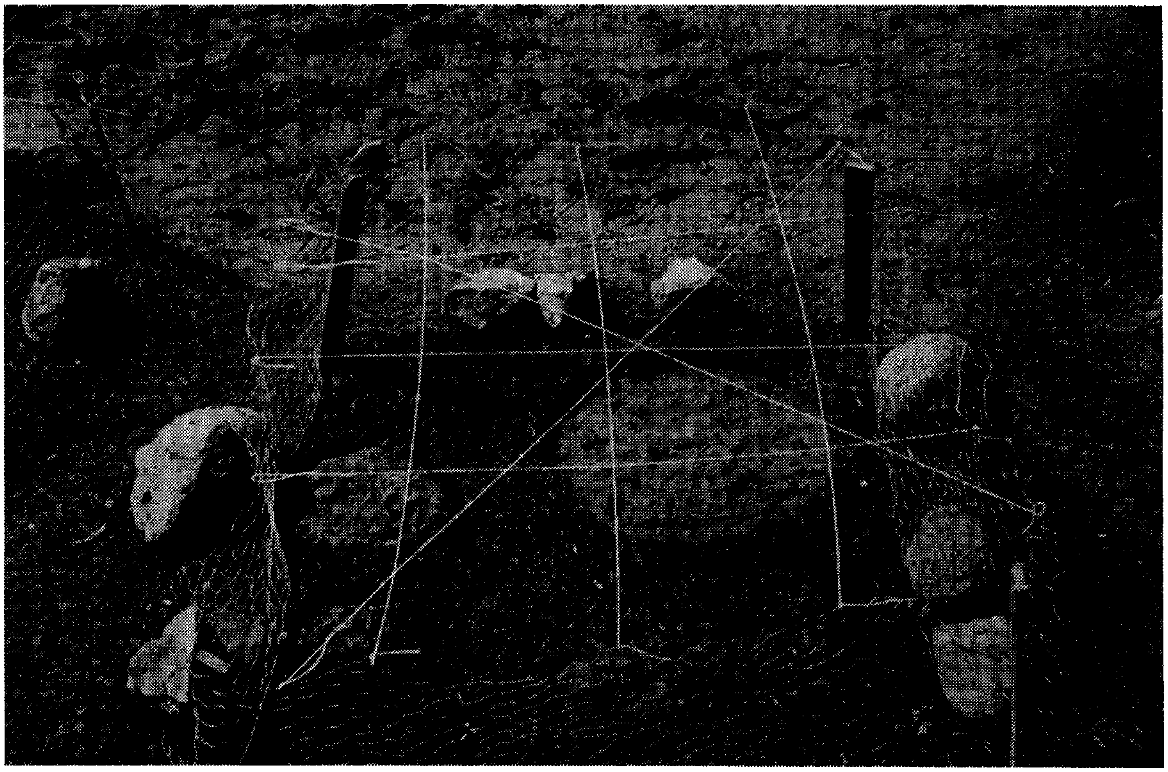


Plate 3.3. Photo of experimental plots. Cleared circles within *Puccinellia* sward are experimentally grubbed patches (ranging between 40 cm and 2.5 cm in diameter. Plots were exclosed to prevent further damage by geese.

3.2.3. Soil variables

Soil characteristics were recorded during the establishment of plots and then twice during the growing season (mid- July and early August) in 2000 and twice during the growing season (mid-July and early August) in 2001. At each site, three plots were sampled destructively on each date in 2000 and four plots were sampled on each date in 2001. Soil properties examined included: salinity; bulk density; soil moisture content; redox potential.

3.2.3.1 Determination of soil salinity

Salinity was measured when the experiment was initiated and then in mid-July and early August in 2000, but only mid-July in 2001. All salinity measurements, except the last sampling in 2000, were determined using the same procedure as Iacobelli (1991). The soil solution from a block of soil within the disturbed patches was extracted by manually squeezing the soil by hand (wearing latex gloves), this solution was filtered through Whatman No. 1 filter paper and then diluted with deionized water. Salinity was measured as grams of solute per litre of solution ($^{0}/_{00}$ S) using a portable Yellow Springs Instrument Company Salinity Meter (Ohio, USA). At the last sampling in 2000, the soil was too dry to extract soil water by this method. Therefore, soil was pressed into 5 ml plastic syringe casings, which were placed in 20 ml centrifuge tubes and centrifuged at 7000 x g for 5 minutes. Salinities of soil water extracted by the different techniques have been shown to be similar (Srivastava and Jefferies 1995b). Soil water was then frozen and later analyzed for sodium content using a Perkin-Elmer atomic absorption spectrophotometer (model 3110) (Rexdale, Ontario) in flame-emission mode. Standard sodium chloride solutions were used to calibrate the instrument and then samples were diluted to fall within the readable range of 0.2-1 milligrams of sodium per litre. Repeated measurements were done on each sample (n =3, average CV = 6.0%).

Soil salinity as measured by the use of the spectrophotometer is read as the concentration of sodium ions in the solution (g $litre^{-1}$) whereas salinity as measured by the salinity meter measures total solute content per litre. However, data of the two methods are comparable; all values were converted to salinity using the regression equation: Salinity (g. diss. solids/l) = 3.59 * $[Na^+]$ g/l + 3.850 (r^2=0.96) (Srivastava and Jefferies 1995b), where $[Na^+]$ is the concentration of sodium ions in the solution.

3.2.3.2. Determination of soil moisture

Soil moisture content was measured in the upper 3 cm of soil (the bulk of *Puccinellia* and *Carex* roots occur at this depth) in each patch in each plot. Soil in undisturbed patches was taken from the upper 3 cm of the sediment profile after removal of vegetation. All soil sampling occurred within the organic-rich soil horizon. A soil sample was weighed, dried at about 50°C for approximately one week, and re-weighed to calculate soil moisture, expressed as grams of water per gram of dry soil.

3.2.3.3. Determination of bulk density

Similar to soil moisture, bulk density was measured in the upper 3 cm of soil in each patch in each plot. Soil in undisturbed patches was taken from the upper 3 cm of the sediment profile after removal of vegetation, as indicated above. A soil sample of known volume was weighed, dried at about 50°C for approximately one week, and re-weighed. Bulk density was expressed as grams of dry soil per cm^3 wet soil volume.

3.2.3.4. Determination of soil redox potential (mV)

Redox potential of a freshly cut soil surface was measured with a platinum electrode (Ag/AgCl reference) and a portable Fisher pH meter in the mV mode for each patch size. The instrument was calibrated with the use of ZoBell's solution (0.003 M potassium ferricyanide, 0.003 M potassium ferrocyanide and 0.1M potassium chloride) which has a redox potential of +430 mV at 25°C (Howes *et al.* 1981). Redox values were obtained by inserting the electrode perpendicular to the soil surface and measurements were taken every 1 cm of the upper 5 cm of the soil sample. Soil from undisturbed patches was taken from the surface 5 cm of soil directly beneath the vegetation. Three measurements were made at each depth and averaged for analysis.

3.2.3.5. Determination of total soil nitrogen

A second set of 6 experimental plots, identical to those described above, were established at each site (low marsh, mid-marsh and high marsh) in June 2001. These plots were sampled for total soil nitrogen content of soil on five occasions during the growing season of 2001. Total nitrogen was sampled in the upper 5cm of the soil profile using a LECO, CHN Analyser (St Joseph, Missouri). The results are expressed on a mass basis as %N per gram of dry weight of soil.

3.2.4. Vegetation variables

3.2.4.1. Determination of re-growth of *Puccinellia phryganodes* expressed as basal cover

Vegetative re-growth from the patch perimeter into exposed sediment was measured during the growing season of 2001(approximately 1 year after patch establishment) and again during the growing season of 2002 (approximately 2 years after patch establishment). Tillers of *Puccinellia phryganodes* that were present within a patch 2 weeks after the creation of a patch were weeded to ensure complete removal of vegetation within the patch. Re-growth from the perimeter was estimated as percentage cover of vegetation in each of the patches in 12 plots at each site each year.

Estimates of plant cover within a patch were determined as follows. For the 10, 20 and 40 cm patch sizes, a clear polyethylene sheet with concentric rings 1 cm apart was laid on top of the exposed sediment. For each quadrant of a plot (divided into quadrants along the four cardinal directions) percentage cover for each section of a concentric ring was estimated subjectively, beginning with the outermost ring that marked the boundary of the patch. This procedure was repeated for each sector of a ring progressively moving to the centre of a patch until the estimate of cover fell below 5%, at which point the number of tillers in a particular sector of a ring were counted. For the patches 2.5 and 5 cm in diameter, a single patch from the replicate patches inside each exclosure was randomly chosen for measurement. The 5 cm patch was divided into 4 quadrants (as described above) and percentage cover was estimated for each entire quadrant. Cover in the selected 2.5 cm patch in each plot was determined for the entire patch.

3.2.4.1. Determination of biomass of the re-growth of *Puccinellia phryganodes* in a patch

Biomass of the re-growth of the grass was determined for each of the above patches in August 2001 and July 2002. All above-ground biomass of *Puccinellia* that fell within the disturbed patch (rooted or not) was clipped for each quadrant of a patch (except for 2.5cm patches which were not divided), dried at approx. 50°C for 1 week and weighed. The grass was the only vascular plant present. Aspect did not have an effect on re-growth rate in terms of cover or biomass (ANOVA: $F=0.40$, $p>0.05$), so data from all quadrants in 2001 were pooled for each patch for statistical analyses. Biomass collected during the growing season of 2002 was pooled for each patch upon collection.

3.2.5. Statistical analysis

Statistical analyses on soil and vegetation variables were carried out using general linear models treating sampling date and site as nominal variables and patch size as a continuous variable (Zar 1999). In most of the overall models, two- or three-way interaction terms were significant, and thus the effect of patch size was examined independently for each site and each date. All statistics were calculated with JMP 4.0 (SAS Institute 2000).

3.3. Results

3.3.1. Soil variables

3.3.1.1. Effects of patch size on salinity

For salinity there was an interaction between sampling date and patch size (Table 3.1) due to the increasing effect of patch size on salinity over time. Salinity generally increased with increasing patch size, with this effect becoming more pronounced with time since the patches were created (Fig. 3.1). Additionally, the values of r^2 increased as the season progressed (Fig. 3.1). There was no significant effect of patch size on the first sampling date (19 July 2000) (Fig. 3.1 a-d). On the latter sampling in 2000 (27 July 2000) the effect of patch size on salinity was highly significant across all sites (Fig. 3.1e, $F_{1,43}=17.82$, $p\leq0.001$) as well as independently for the low marsh (Fig. 3.1f, $F_{1,13}=8.53$, $p=0.012$), mid-marsh (Fig. 3.1g, $F_{1,13}=6.53$, $p=0.024$) and high marsh (Fig. 3.1h, $F_{1,13}=5.76$, $p=0.032$). On the last sampling date (15 July 2001), the effect of disturbance was highly significant across all sites (Fig. 3.1i, $F_{1,58}=50.51$, $p\leq0.001$) and independently for the low marsh (Fig. 3.1j, $F_{1,18}=13.63$, $p=0.002$), mid-marsh (Fig. 3.1k, $F_{1,18}=17.99$, $p\leq0.001$) and high marsh (Fig. 3.1l, $F_{1,18}=20.01$, $p\leq0.001$).

3.3.1.2. Effects of patch size on soil moisture

For soil moisture, the effect of sampling date, site and patch size were significant, but there was no significant interaction term (Table 3.2). When the effect of patch size on soil moisture (g of water per g dry weight of soil) was significant, soil moisture decreased with patch size (Fig. 3.2). On the first sampling date (11 July 2000), there was no significant relationship between patch size and soil moisture (Fig. 3.2 a-d),

Table 3.1. General linear model used to analyze the effect of SAMPLING DATE, SITE and PATCH SIZE on salinity in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2000 and 2001. The effect of PLOT nested within SITE is blocked. Levels of significance are * p<0.05, ** p<0.01, *** p<0.001.

Source	df	SS	F-ratio
Sampling	2	24.471	130.76 ***
Site	2	0.619	3.31
Sampling * Site	4	0.162	0.43
Patch Size	1	3.726	39.82 ***
Sampling * Patch Size	2	0.717	3.83 *
Site * Patch Size	2	0.029	0.16
Sampling * Site * Patch Size	4	0.442	1.18
Block	27	1.57	0.62

Figure 3.1. Salinity of soil water in ppt (g of solute per litre of soil water) (Log_{10} transformed) in soil from patches of different size that simulated goose disturbance on 19 July 2000 (a-d), 27 July 2000 (e-h) and 15 July 2001 (i-l) for the low marsh (b,f,j), mid-marsh (c,g,k,) and high marsh (d,h,l) and data pooled from all sites (a,e,i) in an intertidal marsh at La Pérouse Bay, Manitoba. Open circles are mean soil salinity from undisturbed patches (+/- SEM) and closed circles are mean soil salinity of disturbed patches of different sizes (+/- SEM). For each patch size at each site, n = 3 in 2000 and n = 4 in 2001. Regression lines are calculated based only on disturbed patches. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.

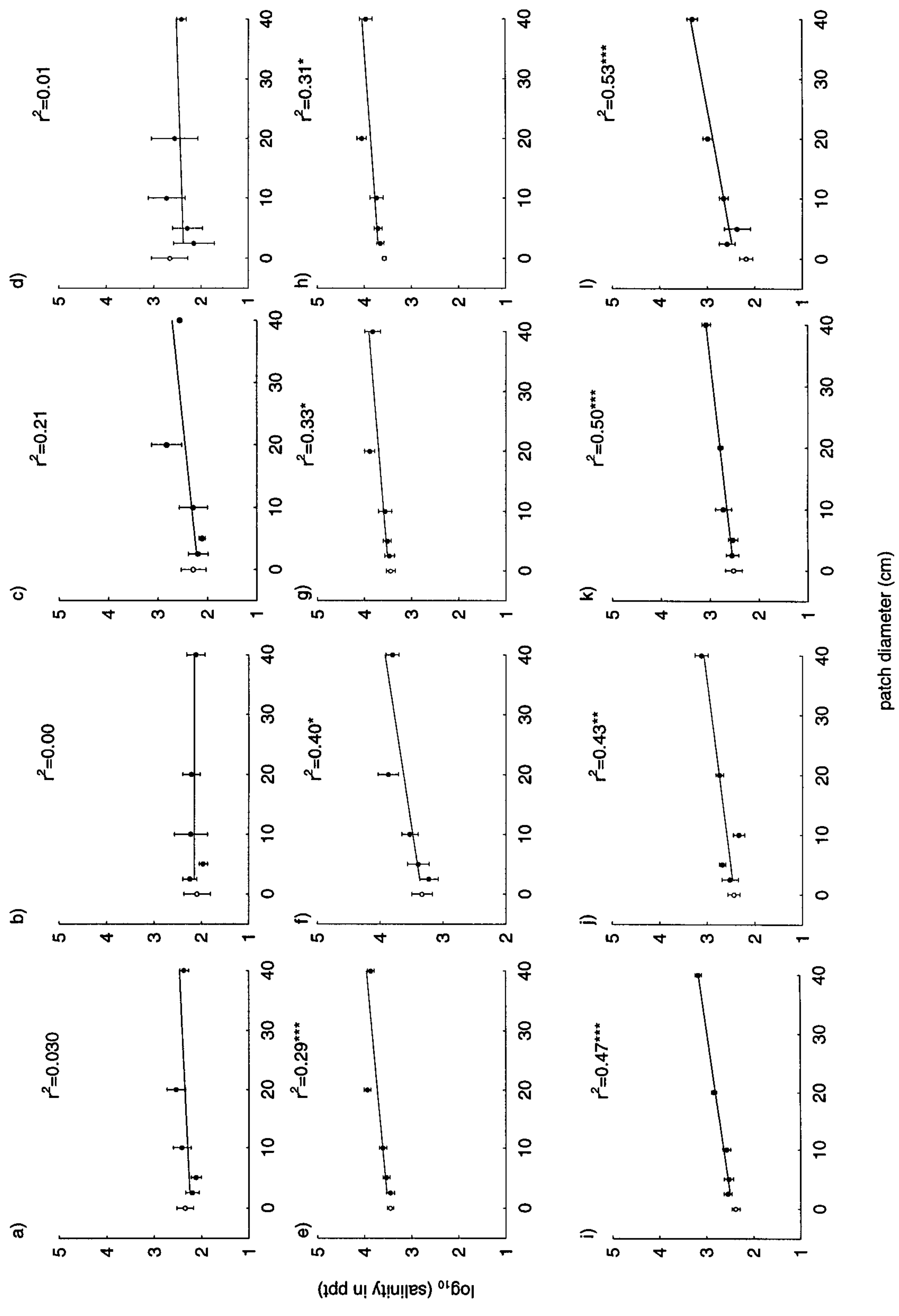
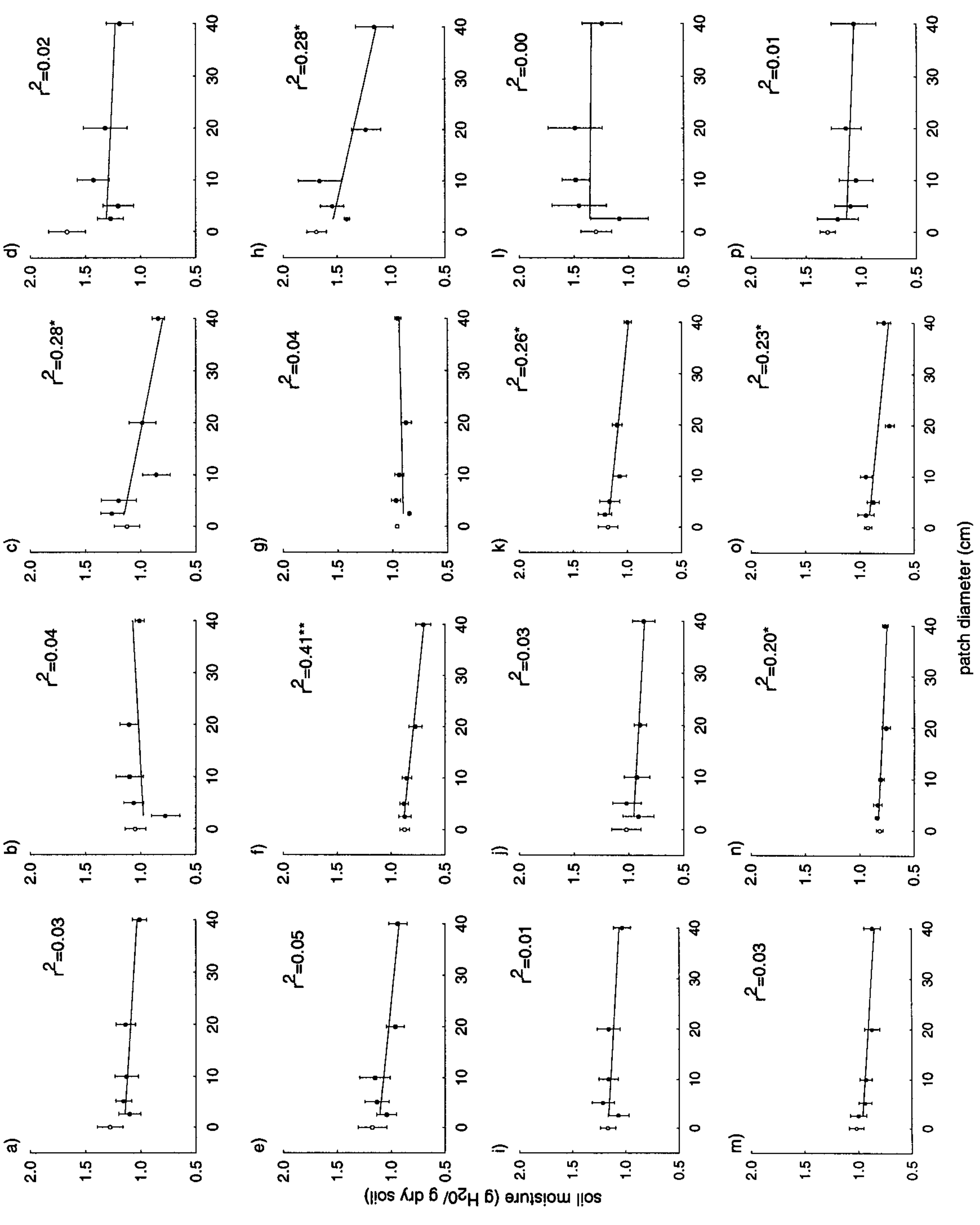

a)
r²=0.030
b)
r²=0.00
c)
r²=0.21
d)
r²=0.01
e)
r²=0.29***
f)
r²=0.40*
g)
r²=0.33*
h)
r²=0.31*
i)
r²=0.47***
j)
r²=0.43**
k)
r²=0.50***
l)
r²=0.53***
1
2
3
4
5
0
10
20
30
40
log₁₀ (salinity in ppt)
patch diameter (cm)

Table 3.2. General linear model used to analyze the effect of SAMPLING DATE, SITE and PATCH SIZE on soil moisture in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2000 and 2001. The effect of PLOT nested within SITE is blocked. Levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Source	df	SS	F-ratio
Sampling	3	1.659	10.75 ***
Site	2	5.608	54.52 **
Sampling * Site	6	0.583	1.89
Patch Size	1	0.297	5.78 *
Sampling * Patch Size	3	0.001	0.01
Site * Patch Size	2	0.093	0.91
Sampling * Site * Patch Size	6	0.339	1.10
Block	3	0.302	1.96

Figure 3.2. Soil moisture (g H_2O/ g dry soil) in soil from patches of different size that simulated goose disturbance on 11 July 2000 (a-d), 27 July 2000 (e-h), 13 July 2001 (i-l), 25 July 2001 (m-p) for the low marsh (b,f,j,n), mid-marsh (c,g,k,o) and high marsh (d,h,l,p) and data pooled from all sites on each date (a,e,j,m) in an intertidal marsh at La Pérouse Bay, Manitoba. Open circles are mean soil moisture from undisturbed patches (+/- SEM) and closed circles are mean soil moisture of disturbed patches of different sizes (+/- SEM). For each patch size at each site, n = 3 in 2000 and n = 4 in 2001. Regression lines are calculated based only on disturbed patches. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.


a)
r^2=0.03
b)
r^2=0.04
c)
r^2=0.28*
d)
r^2=0.02
e)
r^2=0.05
f)
r^2=0.41**
g)
r^2=0.04
h)
r^2=0.28*
i)
r^2=0.01
j)
r^2=0.03
k)
r^2=0.26*
l)
r^2=0.00
m)
r^2=0.03
n)
r^2=0.20*
o)
r^2=0.23*
p)
r^2=0.01
2.0
1.5
1.0
0.5
0
10
20
30
40
soil moisture (g H_20/ g dry soil)
patch diameter (cm)

except in the mid-marsh (Fig. 3.2c, $F_{1,13}$=5.04, p=0.043). On the final sampling date in 2000, soil moisture decreased with patch size in the low marsh (Fig. 3.2f, $F_{1,13}$=9.13, p=0.010) and in the high marsh (Fig. 3.2h, $F_{1,13}$=4.99, p=0.044). On the earlier sampling date in 2001 (13 July 2001), there was no significant relationship between patch size and soil moisture (Fig. 3.3 i-l), except in the mid-marsh where soil moisture decreased with increasing patch size (Fig. 3.2k, $F_{1,13}$=6.24, p=0.022). On the last sampling date in 2001 (25 July 2001), soil moisture decreased with increasing patch size in the low marsh (Fig. 3.2n, $F_{1,13}$=4.47, p=0.049) and the mid-marsh (Fig. 3.2o, $F_{1,13}$=5.26, p=0.034).

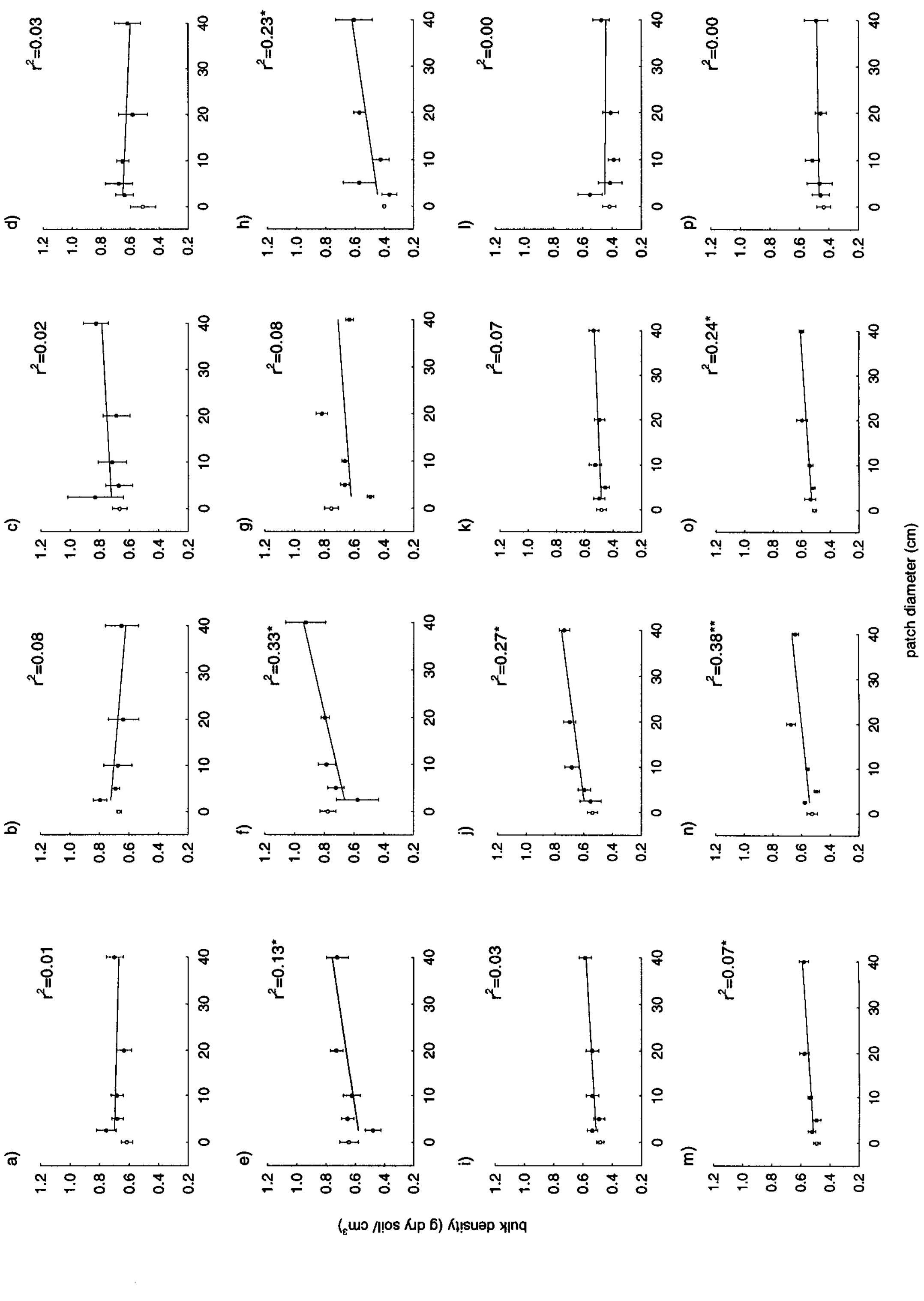
3.3.1.3. Effects of patch size on bulk density

For bulk density (g of dry soil per cm^3 of soil volume) there was an interaction between sampling date and site and between sampling date and patch size (Table 3.3), as the effect of bulk density was more marked on the final sampling date in both 2000 and 2001. Whenever the effect of patch size on bulk density was significant, bulk density increased with patch size (Fig. 3.3). On the first sampling date (11 July 2000) there was no effect of patch size on bulk density (Fig. 3.3 a-d). On the last sampling date in 2000 (27 July 2000) the combined effect of patch size on bulk density for all sites was significant (Fig. 3.3e, $F_{1,43}$=6.43, p=0.015) but the mid-marsh alone failed to indicate a significant effect of patch size on bulk density (Fig. 3.3g, $F_{1,13}$=1.12 p=0.31). In contrast, results for the low marsh (Fig. 3.3f, $F_{1,13}$=6.37, p=0.025) and the high marsh (Fig. 3.3h, $F_{1,13}$=4.86, p=0.042) were significant. On the earlier sampling date in 2001 (13 July 2001), there was no effect of patch size on bulk density (Fig. 3.3 i-l) except in the low marsh (Fig. 3.3j, $F_{1,18}$=6.80, p=0.018). At the last sampling in 2001 (25 July 2001) the

Table 3.3. General linear model used to analyze the effect of SAMPLING DATE, SITE and PATCH SIZE on bulk density in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2000 and 2001. The effect of PLOT nested within SITE is blocked. Levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Source	df	SS	F-ratio
Sampling	3	0.493	11.88 ***
Site	2	0.759	27.44 *
Sampling * Site	6	0.288	3.48 **
Patch Size	1	0.127	9.15 **
Sampling * Patch Size	3	0.132	3.18 *
Site * Patch Size	2	0.022	0.79
Sampling * Site * Patch Size	6	0.078	0.94
Block	3	0.163	3.92 **

Figure 3.3. Bulk density (g dry soil/ cm^3) in soil from patches of different size that simulated goose disturbance on 11 July 2000 (a-d), 27 July 2000 (e-h), 13 July 2001 (i-l) and 25 July 2001 (m-p) for the low marsh (b,f,j,n), mid-marsh (c,g,k,o) and high marsh (d,h,l.p) and data pooled from all sites on each date (a,e,j,m) in an intertidal marsh at La Pérouse Bay, Manitoba.. Open circles are mean bulk density from undisturbed patches (+/- SEM) and closed circles are mean bulk density of disturbed patches of different sizes (+/- SEM). For each patch size at each site, n = 3 in 2000 and n = 4 in 2001. Regression lines are calculated based only on disturbed patches. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.


a)
r^2=0.01
b)
r^2=0.08
c)
r^2=0.02
d)
r^2=0.03
e)
r^2=0.13*
f)
r^2=0.33*
g)
r^2=0.08
h)
r^2=0.23*
i)
r^2=0.03
j)
r^2=0.27*
k)
r^2=0.07
l)
r^2=0.00
m)
r^2=0.07*
n)
r^2=0.38**
o)
r^2=0.24*
p)
r^2=0.00
1.2
1.0
0.8
0.6
0.4
0.2
0
10
20
30
40
bulk density (g dry soil/ cm³)
patch diameter (cm)

combined effect of patch size on bulk density was significant across all sites (Fig. 3.3m, $F_{1,58}$=4.48, p=0.039) as well as for the low marsh (Fig. 3.3n, $F_{1,18}$=10.83, p=0.004) and mid-marsh (Fig. 3.3o, $F_{1,18}$=5.81, p=0.027).

3.3.1.4. Effects of patch size on soil redox potential (mV)

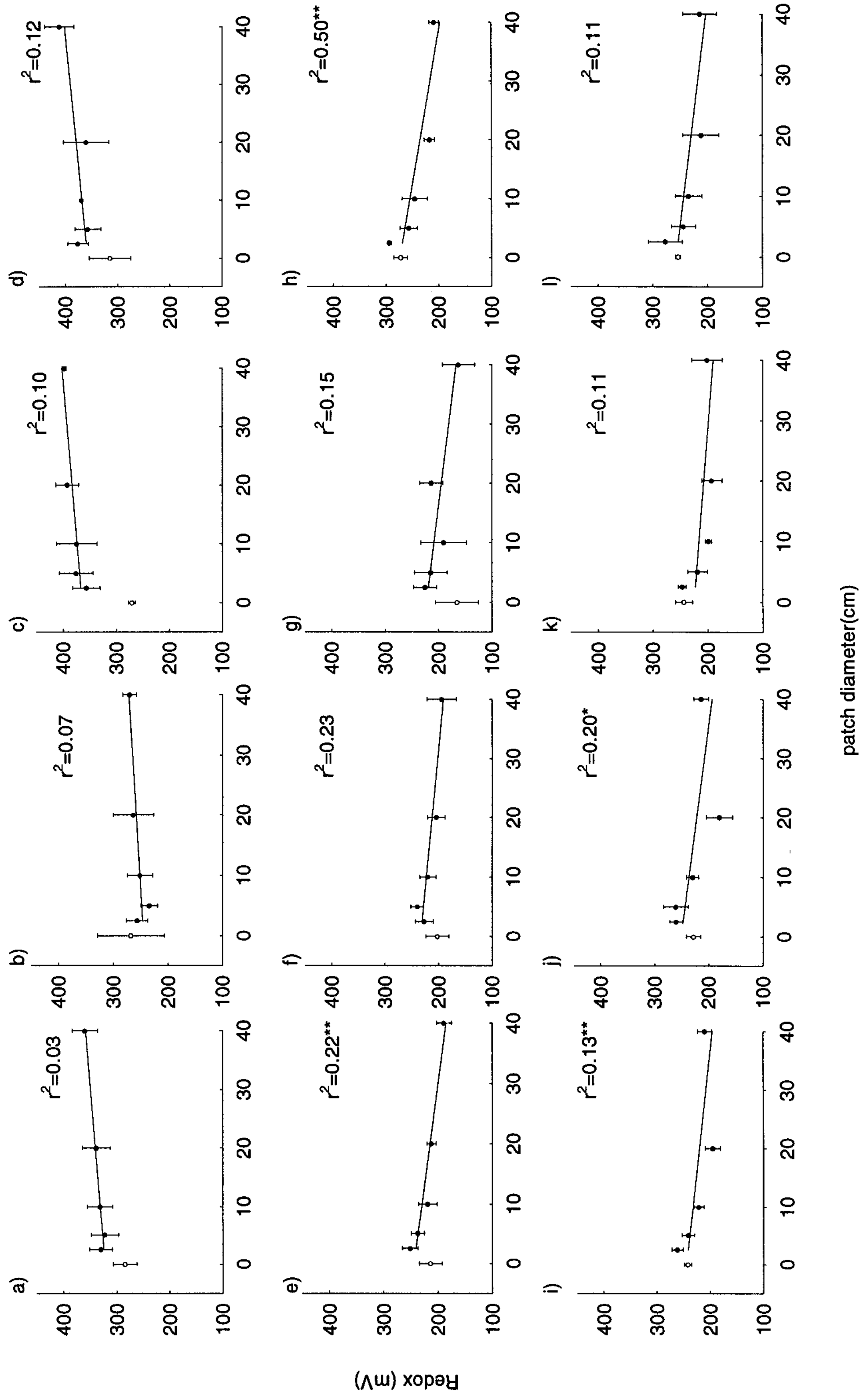
The overall general linear model of soil redox potential contained numerous significant interaction terms (Table 3.4). Patch size was analyzed independently in relation to soil depth (surface soil redox potential, and soil redox potential averaged across the upper 5 cm of the soil profile), sampling date and site. On the first sampling date (12 July 2001), there was no significant relationship between patch size and surface soil redox potential (Fig. 3.4 a-d). On the last soil sampling date in 2000 (29 July 2001), surface soil redox potential significantly decreased with increasing patch size across all sites (Fig. 3.4e, $F_{1,42}$=11.74, p=0.001), but was only significant in the high marsh (Fig. 3.4h, $F_{1,13}$=13.23, p=0.003) when sites were analyzed independently. On 13 July 2001, surface soil redox potential significantly decreased with increasing patch size across all sites (Fig. 3.4i, $F_{1,58}$=8.46, p=0.005), but it was only significant in the low marsh (Fig. 3.4j, $F_{1,18}$=4.59, p=0.046) when sites were analyzed independently.

The soil redox potential of soil from the upper 5 cm of the soil profile (sub-surface soil redox potential) was not significantly related to patch size when all sites were analyzed together (Fig. 3.5 a,e), except on the last sampling date (Fig. 3.5i, $F_{1,58}$=5.63, p=0.021) when sub-surface soil redox potential decreased with increasing patch size. There was no significant relationship between sub-surface soil redox potential and patch size on any sampling date when sites were analyzed independently (Fig. 3.5 b-d, f-h, j-l).

Table 3.4. General linear model used to analyze the effect of SAMPLING DATE, SITE, PATCH SIZE and SOIL DEPTH on soil redox potential in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2000 and 2001. The effect of PLOT nested within SITE is blocked. Levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

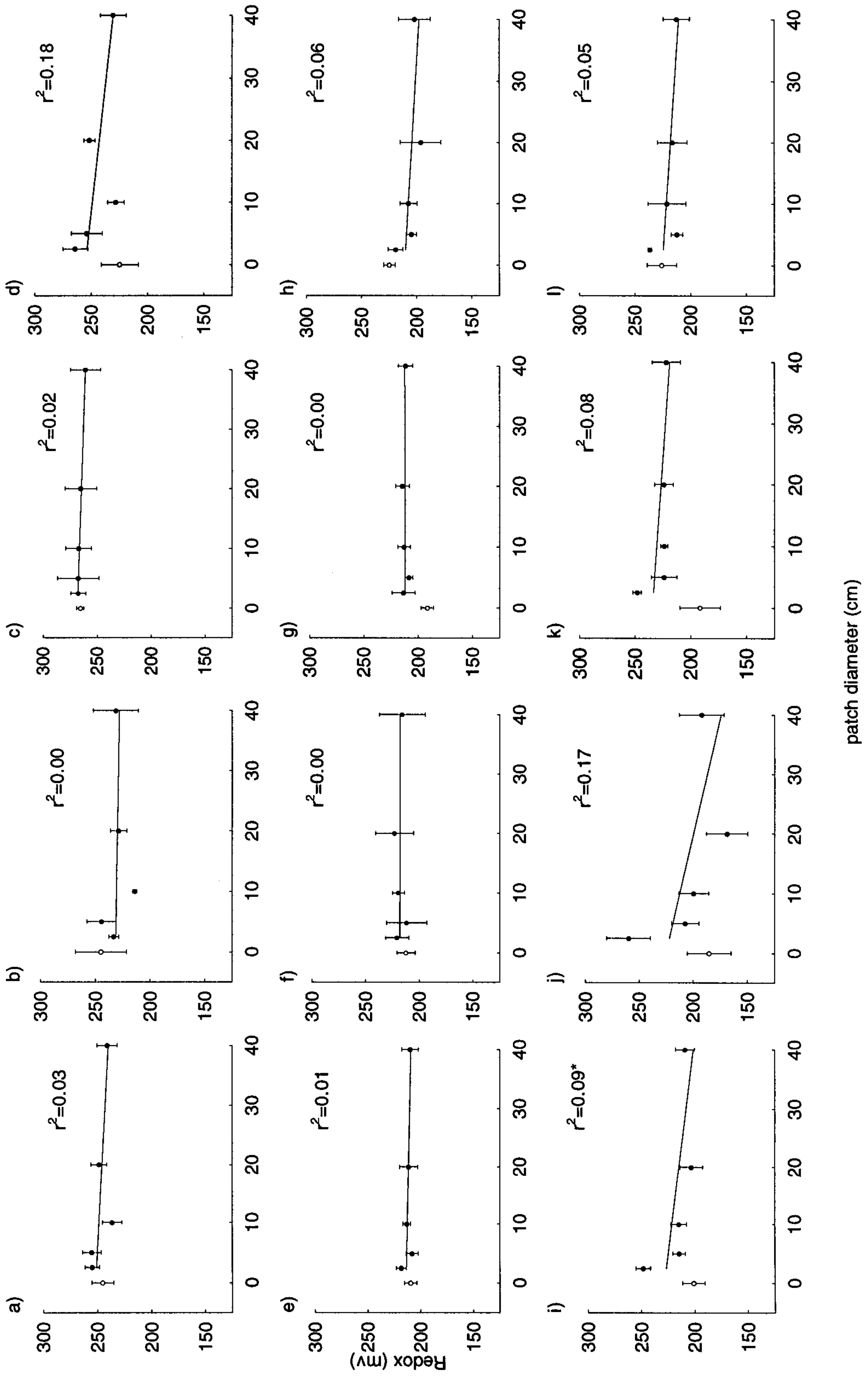
Source	df	SS	F-ratio
Sampling	1	156779.736	106.76 ***
Site	2	61427.921	20.91 *
Sampling * Site	2	101867.028	34.68 ***
Patch Size	1	16011.641	10.90 **
Sampling * Patch Size	1	14015.290	9.54 **
Site * Patch Size	2	570.153	0.19
Sampling * Site * Patch Size	2	931.998	0.32
Soil Depth	1	78614.609	53.53 ***
Sampling * Soil Depth	1	79092.353	53.86 ***
Site * Soil Depth	2	22572.463	7.60 ***
Sampling * Site * Soil Depth	2	41213.805	14.03 ***
Patch Size * Soil Depth	1	986.709	0.67
Sampling * Patch Size * Soil Depth	1	6083.538	4.14 *
Site * Patch Size* Soil Depth	2	97.035	0.03
Sampling * Site * Patch Size * Soil Depth	2	1284.954	0.44
Block	3	57734.503	13.10 ***

Figure 3.4. Redox (mV) of soil immediately below the surface in soil patches of different size that simulated goose disturbance on 12 July 2000 (a-d), 29 July 2000 (e-h) and 13 July 2001 (i-l) for the low marsh (b,f,j), mid-marsh (c,g,k,) and high marsh (d,h,l) and for data pooled from all sites on each date (a,e,i) in an intertidal marsh at La Pérouse Bay, Manitoba. Open circles are mean soil redox from undisturbed patches (+/- SEM) and closed circles are mean soil redox of disturbed patches of different sizes (+/- SEM). For each patch size at each site, n = 3 in 2000 and n = 4 in 2001. Regression lines are calculated based only on disturbed patches. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.



a)
r^2=0.03
b)
r^2=0.07
c)
r^2=0.10
d)
r^2=0.12
e)
r^2=0.22**
f)
r^2=0.23
g)
r^2=0.15
h)
r^2=0.50**
i)
r^2=0.13**
j)
r^2=0.20*
k)
r^2=0.11
l)
r^2=0.11
Redox (mV)
100
200
300
400
0
10
20
30
40
patch diameter(cm)

Figure 3.5. Redox (mV) of soil from the top 5 cm of the soil profile (measurements taken every 1cm and averaged across depth) in soil patches of different size that simulated goose disturbance 12 July 2000 (a-d), 29 July 2000 (e-h) and 13 July 2001 (i-l) for the low marsh (b,f,j), mid-marsh (c,g,k,) and high marsh (d,h,l) and for data pooled from all sites on each date (a,e,i) in an intertidal marsh at La Pérouse Bay, Manitoba. Open circles are mean soil redox from undisturbed patches (+/- SEM) and closed circles are mean soil redox of disturbed patches of different sizes (+/- SEM). For each patch size at each site, n = 3 in 2000 and n = 4 in 2001. Regression lines are calculated based only on disturbed patches. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.



a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)
r^2=0.03
r^2=0.00
r^2=0.02
r^2=0.18
r^2=0.01
r^2=0.00
r^2=0.00
r^2=0.06
r^2=0.09*
r^2=0.17
r^2=0.08
r^2=0.05
300
250
200
150
0
10
20
30
40
Redox (mV)
patch diameter (cm)

3.3.1.5. Effect of patch size on total soil nitrogen

For soil nitrogen there was an interaction between site and patch size and between site and sampling date (Table 3.5). Total soil nitrogen was not significantly related to patch size when all sites were analyzed together (Fig. 3.6 a,e,i,m), nor when sites were analyzed independently on each sampling date (Fig. 3.6 b-d, f-h, j-l, m-p). Each site was analyzed with a general linear model of total soil nitrogen. The low marsh and mid-marsh analysis contained a significant effect of sampling date, but no significant effect of patch size and no significant interaction. The high marsh analysis contained a significant effect of both patch size and sampling date, but no significant interaction term (Table 3.6). The significant effect of patch size is a result of the decrease in total soil nitrogen with increasing patch size on all dates (Fig. 3.6 d,h,l,p).

3.3.2. Vegetation variables

3.3.2.1. Effects of patch size on the re-growth of *Puccinellia phryganodes* as basal cover

Proportion of patches covered by the re-growth of *Puccinellia phryganodes* in July 2001 (1 year after patch initiated) and 2002 (2 years after the patch was initiated) generally decreased with increasing patch size and the extent of basal cover followed a curvilinear pattern (Fig. 3.7). Area (cm^2) of the disturbed patch covered by *Puccinellia* in July 2001 and July 2002 increased with patch size in a curvilinear pattern (Fig. 3.8). The distance of the re-growth of *Puccinellia* from the perimeter of a patch (Fig. 3.9 a-c) and the area of re-growth standardized for total circumference of a patch (Fig. 3.10 a-c) in July 2001 both increased with patch size to approximately the patch size of 20 cm, where the rate of

Table 3.5. General linear model used to analyze the effect of SAMPLING DATE, SITE and PATCH SIZE on soil nitrogen as a percent of dry weight in low, mid- and high marsh sites of intertidal salt-marsh at La Pérouse Bay, Manitoba in 2001. The of PLOT nested within site is blocked. Levels of significance are $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Source	df	SS	F-ratio
Sampling	1	1.729	46.34 ***
Site	2	0.941	12.61 ***
Sampling * Site	2	0.702	9.41 ***
Patch Size	1	0.158	4.23 *
Sampling * Patch Size	1	0.000	0.01
Site * Patch Size	2	0.527	7.07 ***
Sampling * Site * Patch Size	2	0.045	0.60
Block	17	6.160	9.71 ***

Table 3.6. General linear model used to analyze the effect of SAMPLING DATE and PATCH SIZE on soil nitrogen as a percent of dry weight in the high marsh site of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2001. The effect of PLOT is blocked. Levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

Source	df	SS	F-ratio
Patch Size	1	0.676	7.89 **
Sampling	1	2.060	24.05 ***
Patch Size * Sampling	1	0.008	0.09
Block	5	5.064	11.82 ***

Figure 3.6. Percent nitrogen content in dry soil in soil patches of different size that simulated goose disturbance on 28 June 2001 (a-d), 8 July 2001 (e-h), 17 July 2001 (i-l), 28 July 2001 (m-p) for the low marsh (b,f,j,n), mid-marsh (c,g,k,o) and high marsh (d,h,l.p) and data pooled from all sites on each date (a,e,j,m) in an intertidal marsh at La Pérouse Bay, Manitoba. Open circles are mean soil moisture from undisturbed patches (+/- SEM) and closed circles are mean soil moisture of disturbed patches of different sizes (+/- SEM). n = 6 for each patch site on each date. Regression lines are calculated based only on disturbed patches. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.

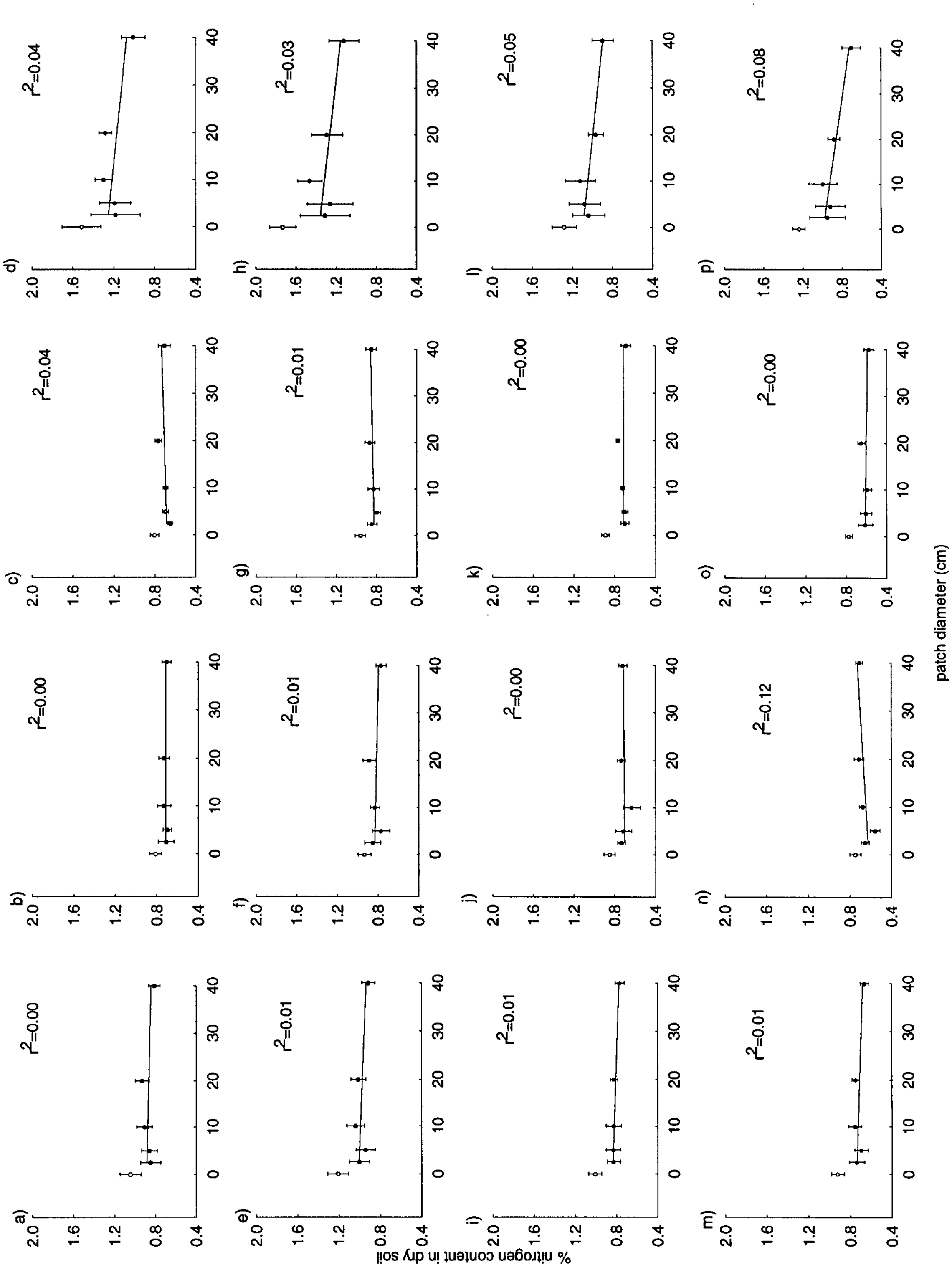

a)
r^2=0.00
b)
r^2=0.00
c)
r^2=0.04
d)
r^2=0.04
e)
r^2=0.01
f)
r^2=0.01
g)
r^2=0.01
h)
r^2=0.03
i)
r^2=0.01
j)
r^2=0.00
k)
r^2=0.00
l)
r^2=0.05
m)
r^2=0.01
n)
r^2=0.12
o)
r^2=0.00
p)
r^2=0.08
2.0
1.6
1.2
0.8
0.4
0
10
20
30
40
% nitrogen content in dry soil
patch diameter (cm)

Figure 3.7. Proportion of the area of patches of different size that simulated goose disturbance covered by *Puccinellia phryganodes* (basal cover) in July 2001 (a-c) and July 2002 (d-f). Cover is shown as mean proportion +/- SEM for the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.

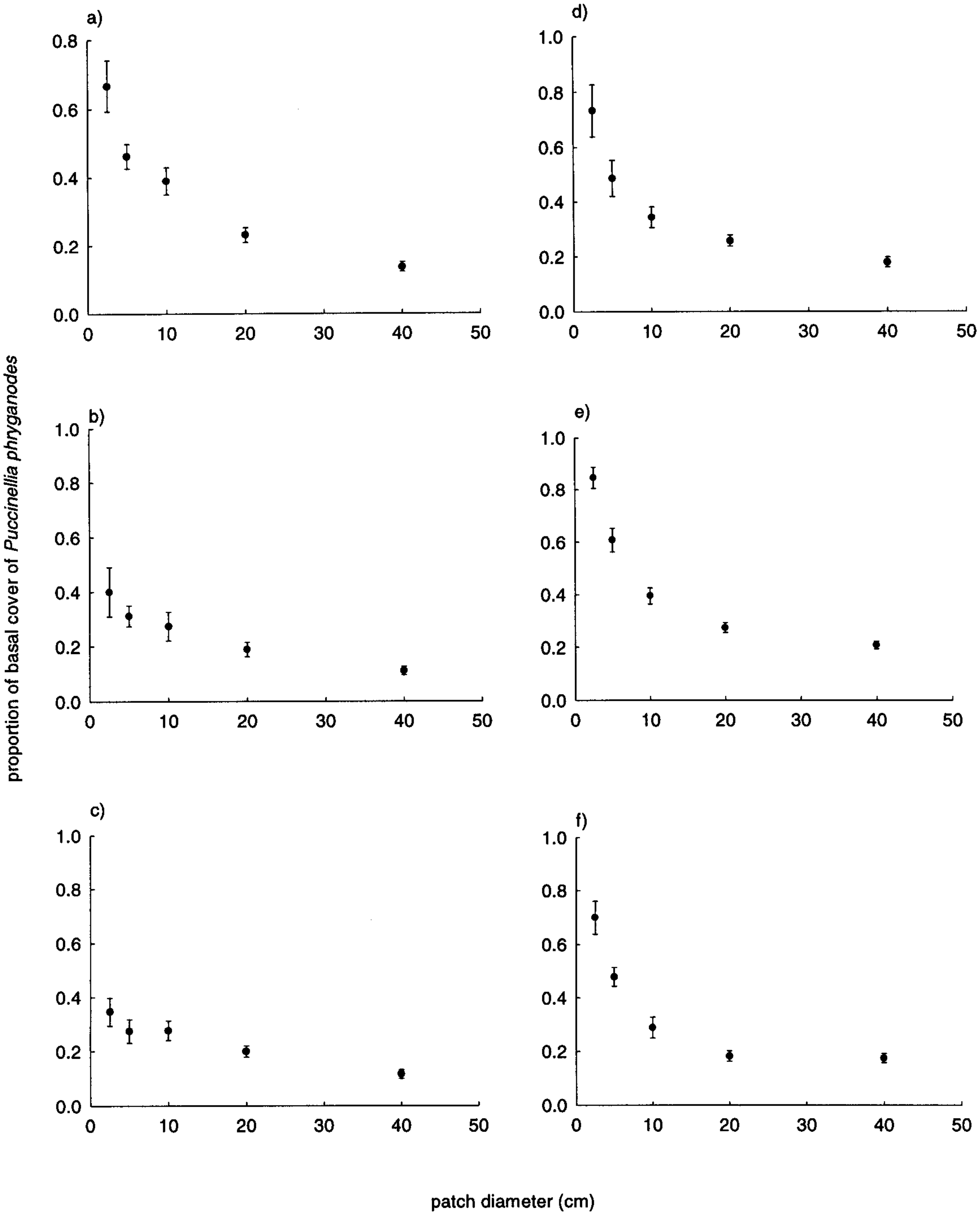

a)
d)
b)
e)
c)
f)
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
proportion of basal cover of *Puccinellia phryganodes*
patch diameter (cm)

Figure 3.8. Area (cm^2) of patches of different size that simulated goose disturbance covered by *Puccinellia phryganodes* in July 2001 (a-c) and July 2002 (d-f). Mean area cover is shown +/- SEM in the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.

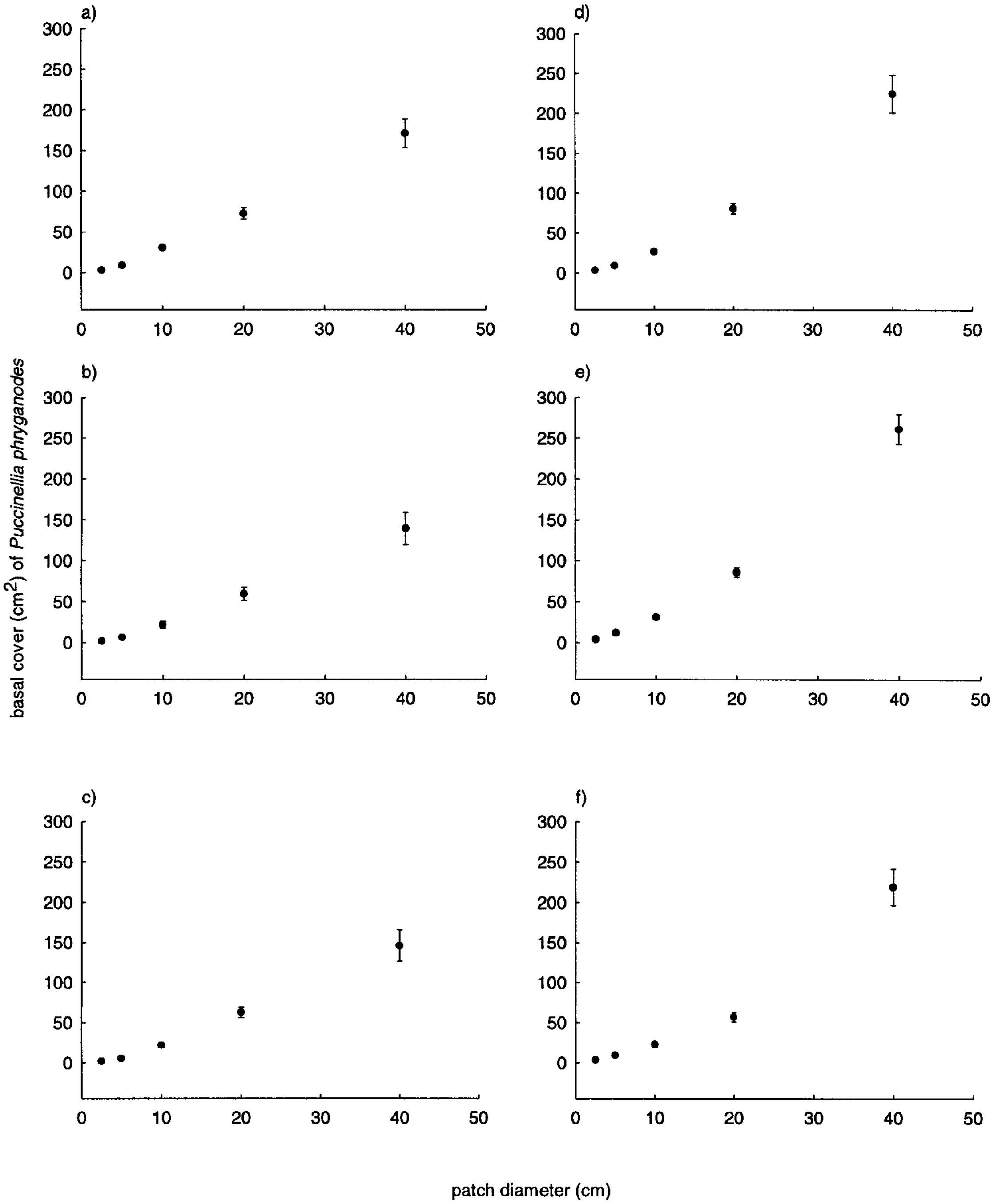

a)
b)
c)
d)
e)
f)
300
250
200
150
100
50
0
0
10
20
30
40
50
basal cover (cm^2) of *Puccinellia phryganodes*
patch diameter (cm)

Fig. 3.9. Inward radial growth (cm) of *Puccinellia phryganodes* from perimeter patches of different size that simulated goose disturbance in July 2001 (a-c) and July 2002 (d-f). Mean distance is shown +/- SEM in the low marsh (a,d), mid marsh (b,e) and high-marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.

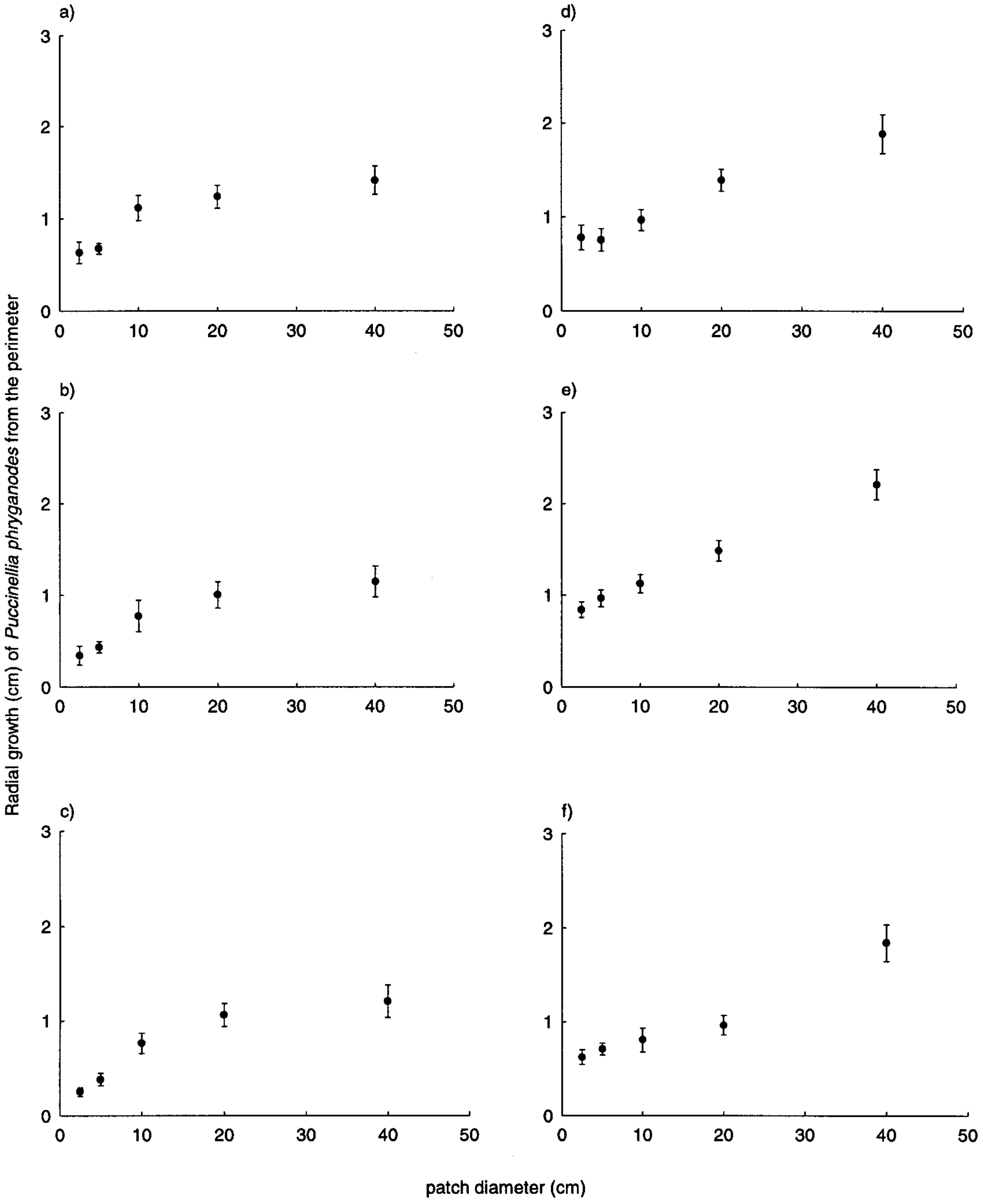
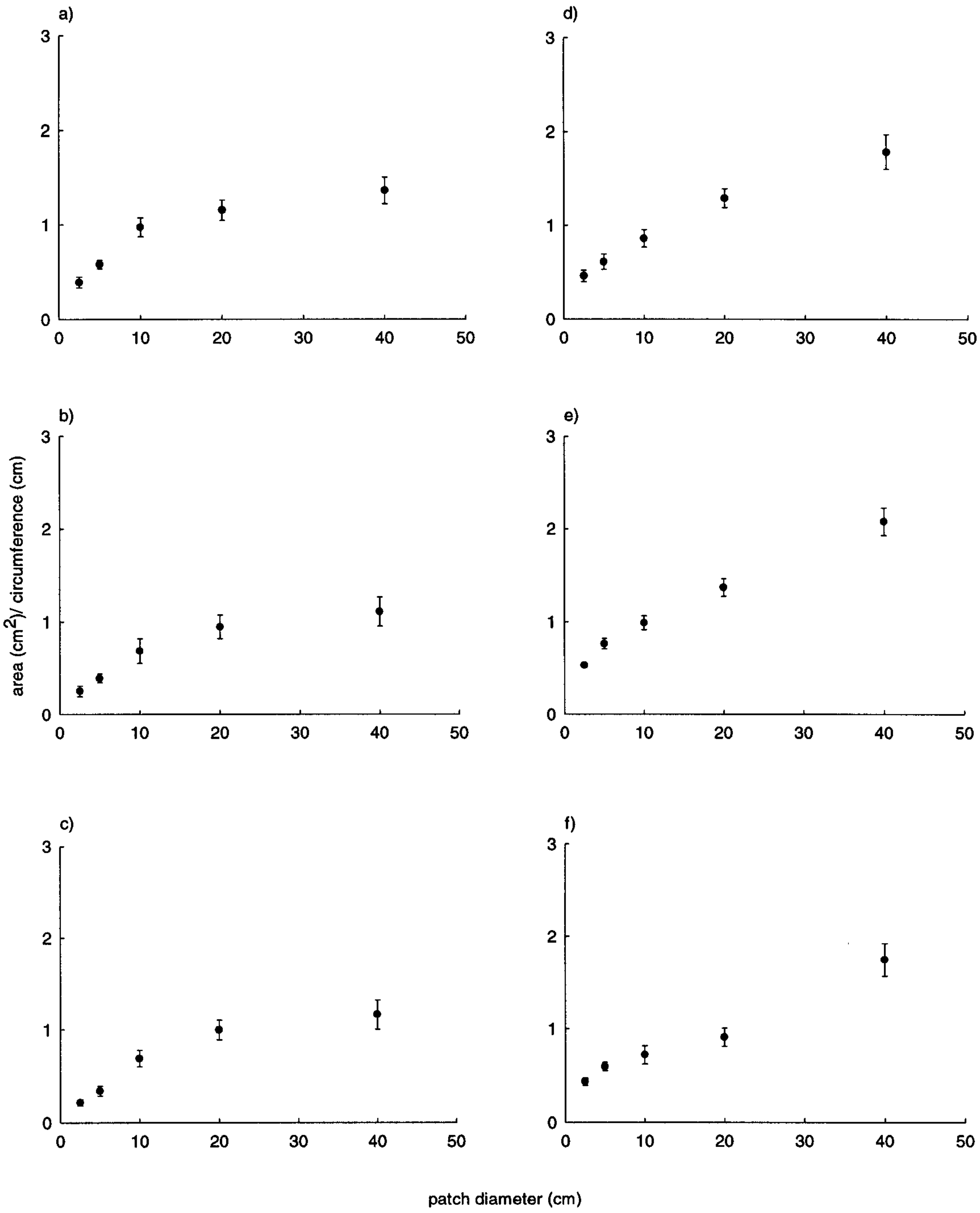

a)
b)
c)
d)
e)
f)
0
1
2
3
0
10
20
30
40
50
Radial growth (cm) of *Puccinellia phryganodes* from the perimeter
patch diameter (cm)

Fig. 3.10. Area (cm^2) of patch covered by *Puccinellia phryganodes* re-growth (standardized for patch circumference) for patches of different size that simulated goose disturbance in July 2001 (a-c) and July 2002 (d-f). Mean area (cm^2)/ circumference (cm) is shown +/- SEM in the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.


a)
b)
c)
d)
e)
f)
area (cm^2)/ circumference (cm)
patch diameter (cm)
0
1
2
3
0
10
20
30
40
50

increase declined. In July 2002, the relationships of the linear re-growth of *Puccinellia* from the perimeter of a disturbed patch to the centre (Fig. 3.9 d-f) and the area of re-growth standardized for total circumference of disturbed patch (Fig. 3.10 d-f) and patch size were similar to results from the previous year, 2001.

Of the cover variables listed above, statistical analysis was performed only on area of re-growth standardized for circumference of patch size. For statistical analysis of data from 2001, patch size was log-transformed in order to "linearize" the data. The overall general linear model contained a significant effect of both site and the covariate, patch size, but there was no significant interaction term (Table 3.7). There was a significant positive relationship between area of re-growth (standardized for patch size circumference) and $\log_{10}$ patch size in the low marsh (Fig. 3.11a, $F_{1,58}=70.40$, $p \leq 0.001$), the mid-marsh (Fig. 3.11b, $F_{1,58}=42.22$, $p \leq 0.001$) and high marsh (Fig. 3.11c, $F_{1,58}=69.60$, $p \leq 0.001$). In 2002, both patch size and area covered were log-transformed to "linearize" the data. The overall general linear model contained a significant effect of the covariate, patch size, but no significant interaction term (Table 3.8). There was a significant positive relationship between area of re-growth and $\log_{10}$ patch size in the low marsh (Fig. 3.11d, $F_{1,58}=57.89$, $p \leq 0.001$), the mid-marsh (Fig. 3.11e, $F_{1,58}=216.77$, $p \leq 0.001$) and high marsh (Fig. 3.11f, $F_{1,58}=68.54$, $p \leq 0.001$).

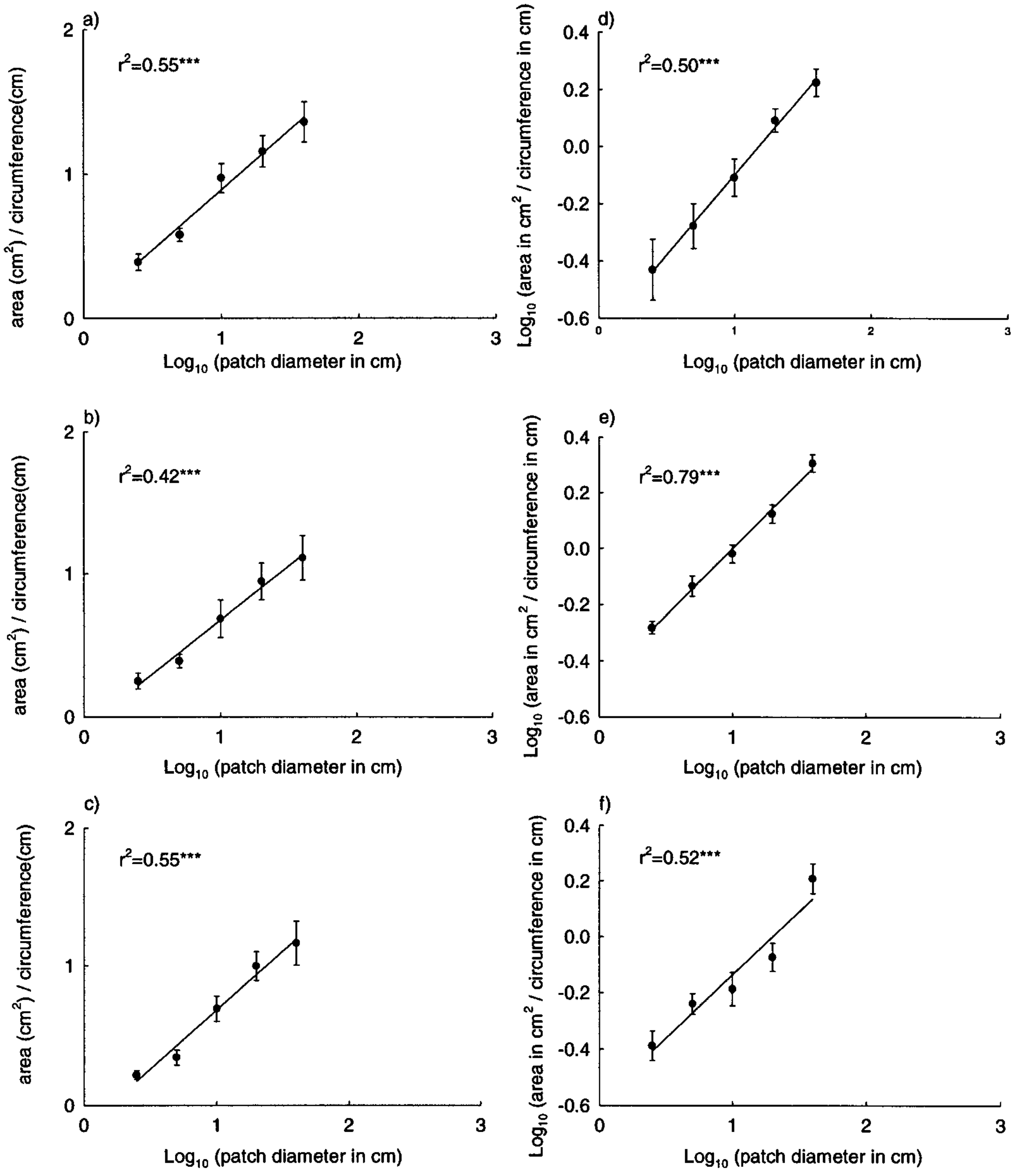
Table 3.7. General linear model used to analyze the effect of SITE and PATCH SIZE (data $\log_{10}$ transformed) on area of regrowth of *Puccinellia phryganodes* adjusted for patch circumference in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2001. The effect of PLOT nested within SITE is blocked. Levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Source	df	SS	F-ratio
Site	2	0.753	3.88 *
Patch Size	1	21.542	222.19 ***
Site* Patch Size	2	0.055	0.28
Block	33	4.403	1.38

Table 3.8. General linear model used to analyze the effect of SITE and PATCH SIZE (data $\log_{10}$ transformed) on area of regrowth of *Puccinellia phryganodes* adjusted for patch circumference in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2002. The effect of PLOT nested within SITE is blocked. Levels of significance are* $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Source	df	SS	F-ratio
Site	2	0.1	2.8
Patch Size	1	8.22	459.53 ***
Site * Patch Size	2	0.069	1.93
Block	34	3.059	5.03 ***

Fig. 3.11. Area (cm^2) of patch covered by re-growth of *Puccinellia phryganodes* (standardized for patch circumference in cm) for patches of different size that simulated goose disturbance (log_{10} transformed) in July 2001 (a-c) and July 2002 (d-f). Values for 2002 are log_{10} transformed to a linear function. The standardized relationship between area and circumference are shown as mean +/- SEM in the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

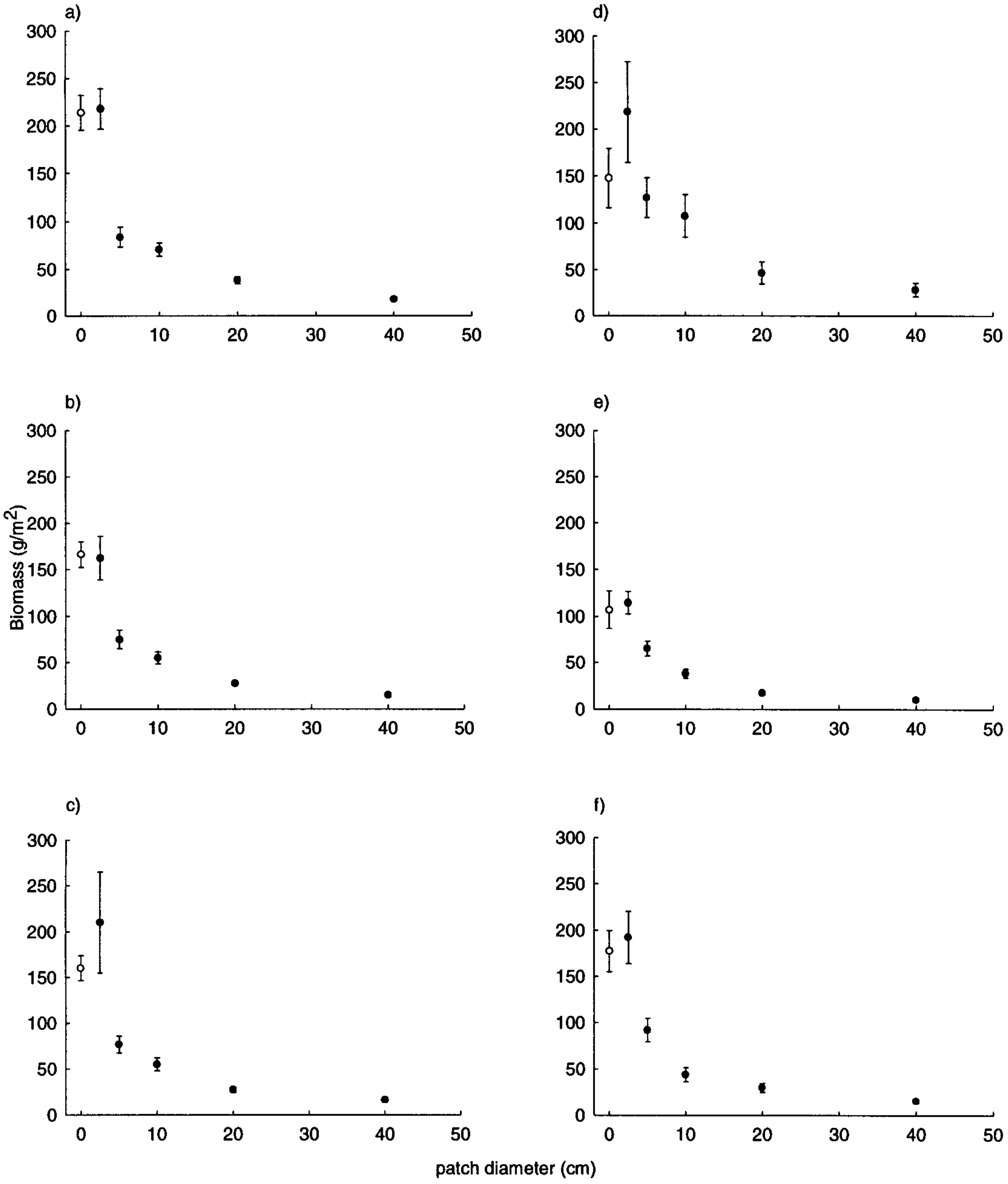

a)
r²=0.55***
area (cm²) / circumference(cm)
0
1
2
0
1
2
3
Log₁₀ (patch diameter in cm)
d)
r²=0.50***
Log₁₀ (area in cm² / circumference in cm)
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
1
2
3
Log₁₀ (patch diameter in cm)
b)
r²=0.42***
area (cm²) / circumference(cm)
0
1
2
0
1
2
3
Log₁₀ (patch diameter in cm)
e)
r²=0.79***
Log₁₀ (area in cm² / circumference in cm)
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
1
2
3
Log₁₀ (patch diameter in cm)
c)
r²=0.55***
area (cm²) / circumference(cm)
0
1
2
0
1
2
3
Log₁₀ (patch diameter in cm)
f)
r²=0.52***
Log₁₀ (area in cm² / circumference in cm)
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
1
2
3
Log₁₀ (patch diameter in cm)

3.3.2.2. Effects of patch size on biomass of the re-growth of *Puccinellia phryganodes* in a patch

Biomass of the re-growth of *Puccinellia phryganodes* inside patches (per m^2 of patch) in July 2001 (1 year after patch initiated) and 2002 (2 years after patch initiated) decreased with increasing patch size and it followed a curvilinear pattern (Fig. 3.12). Similarly, when biomass was adjusted for the area of a patch covered by re-growth of *Puccinellia*, biomass decreased with increasing patch size generally and followed a log-linear pattern (Fig. 3.13), indicating that re-growth in smaller patches is denser than in larger patches. This effect was more pronounced in 2001 (Fig. 3.13 a-c) than in 2002 (Fig. 3.13 d-f).

Statistical analysis was performed only on biomass adjusted for the area of a patch covered by re-growth of *Puccinellia*. For statistical analysis of the data of 2001, biomass (g per m^2 of re-growth of *Puccinellia*) was log-transformed to "linearize" the data. The overall general linear model of biomass contained a significant effect of the covariate, patch size, but no significant interaction term (Table 3.9). There was a significant negative relationship between $\log_{10}$ biomass and patch size in the low marsh (Fig. 3.14a, $F_{1,58}=15.77$, $p \leq 0.001$), the mid-marsh (Fig. 3.14b, $F_{1,58}=18.82$, $p \leq 0.001$) and high marsh (Fig. 3.14c, $F_{1,58}=19.62$, $p \leq 0.001$). In 2002, no transformation was required to "linearize" the data, however, biomass was log-transformed to improve normality. The overall general linear model of biomass contained a significant effect of site and the covariate, patch size, but no significant interaction term (Table 3.10). There was a significant negative relationship between $\log_{10}$ biomass and patch size in the low marsh (Fig. 3.14d, $F_{1,58}=9.85$, $p=0.003$), the mid-marsh (Fig. 3.14e, $F_{1,58}=38.76$, $p \leq 0.001$) and high marsh (Fig. 3.14f, $F_{1,58}=39.32$, $p \leq 0.001$).

Fig. 3.12. Biomass of re-growth of *Puccinellia phryganodes* per m^2 of patch for patches of different size that simulated goose disturbance in July 2001 (a-c) and July 2002 (d-f). Open circles represent average biomass +/- SEM from undisturbed patches and closed circles represent average biomass +/- SEM from disturbed patches in the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.



a)
d)
b)
e)
c)
f)
300
250
200
150
100
50
0
0
10
20
30
40
50
Biomass (g/m^2)
patch diameter (cm)

Fig. 3.13. Biomass of re-growth of *Puccinellia phryganodes* per m^2 of re-growth for patches of different size that simulated goose disturbance in July 2001 (a-c) and July 2002 (d-f). Open circles represent average biomass +/- SEM from undisturbed patches and closed circles represent average biomass +/- SEM from disturbed patches in the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date.

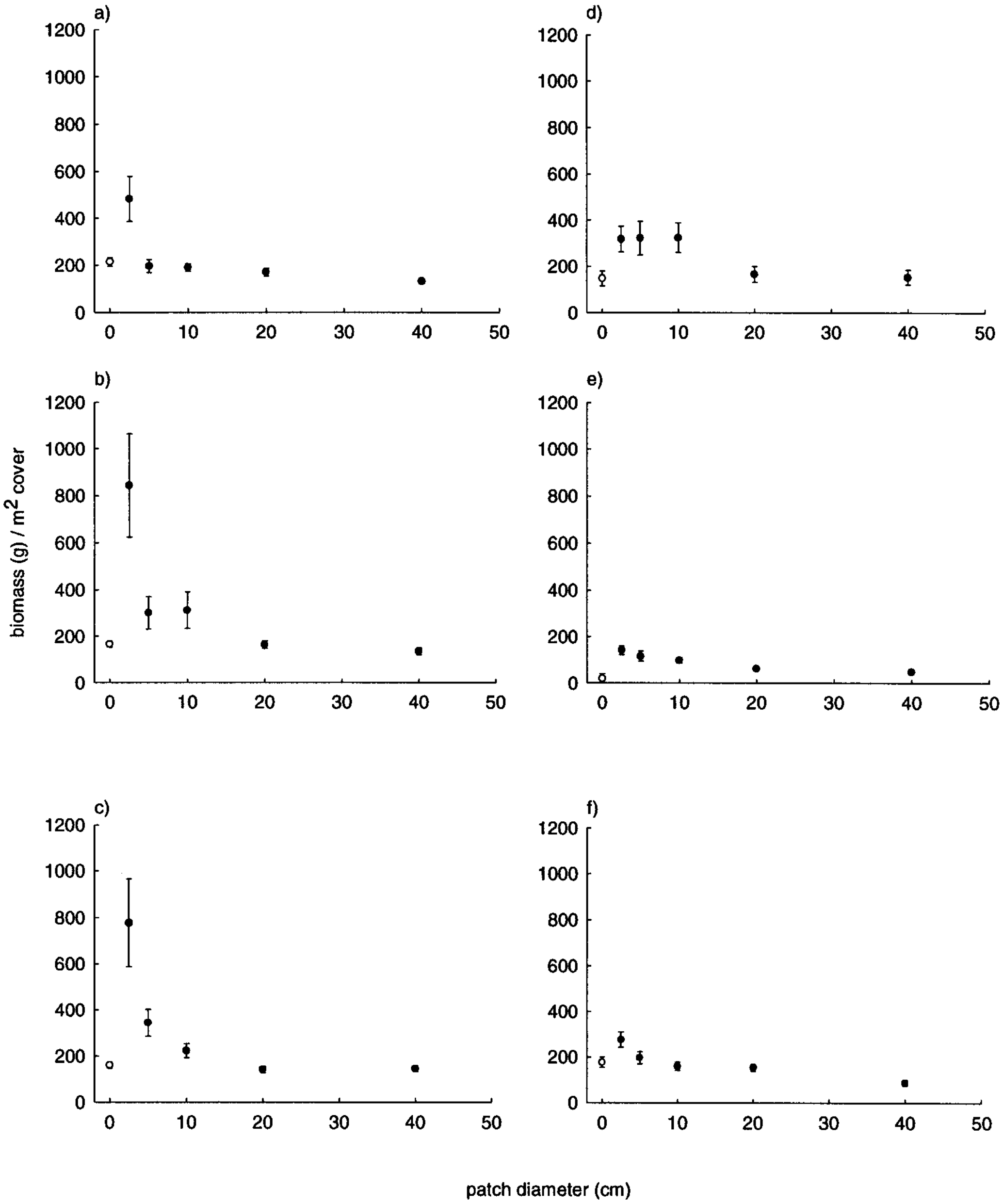

a)
b)
c)
d)
e)
f)
1200
1000
800
600
400
200
0
0
10
20
30
40
50
biomass (g) / m2 cover
patch diameter (cm)

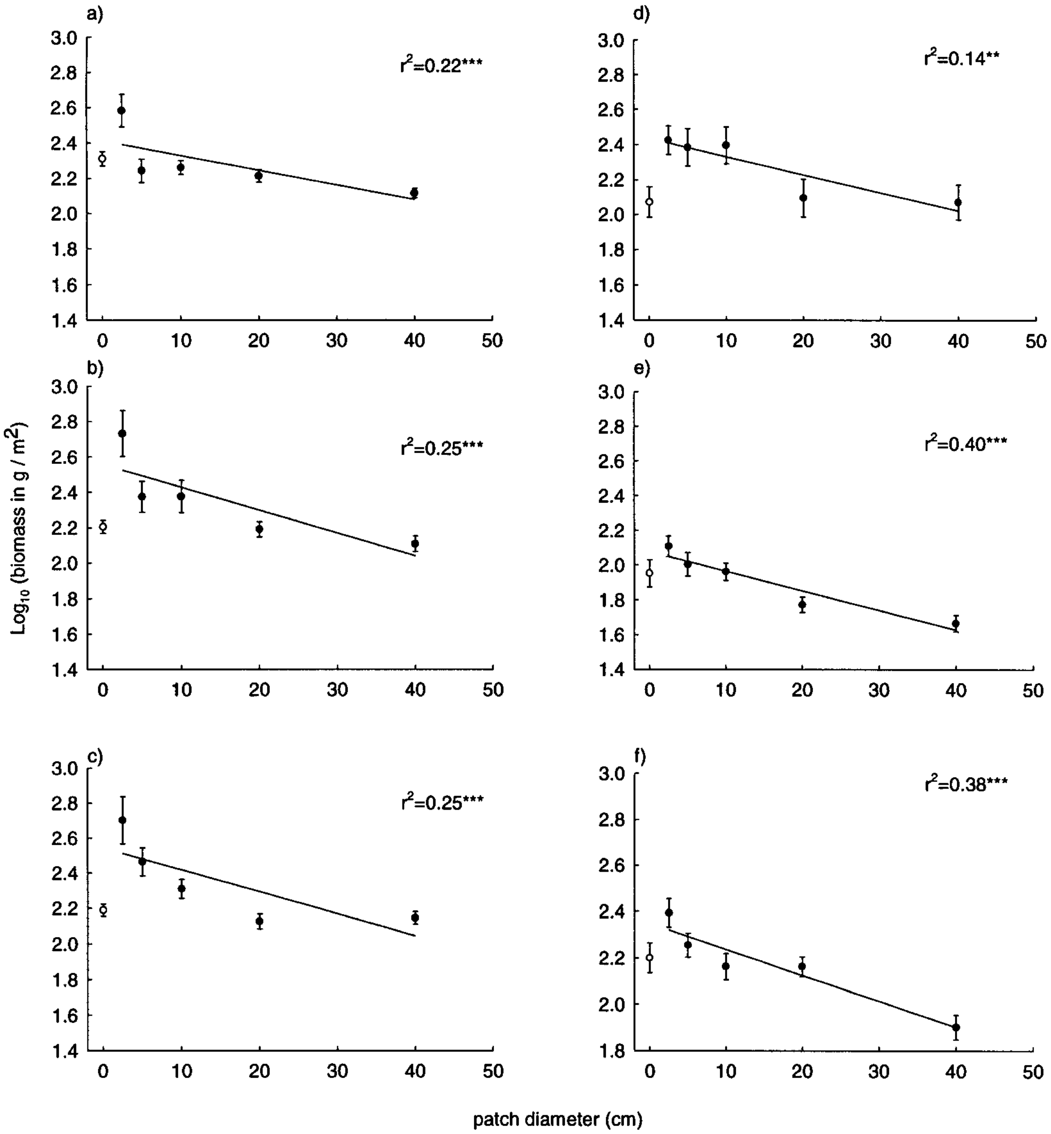
Table 3.9. General linear model used to analyze the effect of SITE and PATCH SIZE on biomass of regrowth of *Puccinellia phryganodes* standardized for area regrowth in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2001.The effect of PLOT nested within SITE is blocked. Levels of significance are * p<0.05, ** p<0.01, *** p<0.001.

Source	df	SS	F-ratio
Site	2	0.137	0.94
Patch Size	1	4.222	57.94 ***
Site* Patch Size	2	0.139	0.95
Block	33	1.009	0.42

Table 3.10. General linear model used to analyze the effect of SITE and PATCH SIZE on biomass of regrowth of *Puccinellia phryganodes* standardized for area regrowth in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2002.The effect of PLOT nested within SITE is blocked. Levels of significance are * p<0.05, ** p<0.01, *** p<0.001.

Source	df	SS	F-ratio
Site	2	0.964	12.73 ***
Patch Size	1	4.061	107.26 ***
Site* Patch Size	2	0.006	0.08
Block	34	4.672	3.63 ***

Fig. 3.14. Biomass of re-growth of *Puccinellia phryganodes* per m^2 patches of different size that simulated goose disturbance ($\log_{10}$ transformed) in July 2001 (a-c) and July 2002 (d-f). Open circles represent average biomass +/- SEM from undisturbed patches and closed circles represent average biomass +/- SEM from disturbed patches in the low marsh (a,d), mid-marsh (b,e) and high marsh (c,f) sites of an intertidal marsh at La Pérouse Bay, Manitoba. n = 12 for each patch size at each site on each date. The r^2 values with a significance level are indicated on each graph (levels of significance are * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Note ordinate axis does not start at zero.


a)
r²=0.22***
b)
r²=0.25***
c)
r²=0.25***
d)
r²=0.14**
e)
r²=0.40***
f)
r²=0.38***
Log₁₀ (biomass in g / m²)
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
0
10
20
30
40
50
patch diameter (cm)

3.4. Discussion

Soil conditions became less favourable for plant growth with increasing patch size following experimental grubbing in an intertidal salt marsh at La Pérouse Bay, Manitoba. Soil salinity increased (Fig. 3.1), soil moisture decreased (Fig. 3.2), bulk density increased (Fig. 3.3), redox of surface soils decreased (Fig. 3.5) with increasing patch size. Total soil nitrogen decreased with patch size, especially in the high marsh (Fig. 3.6). The harsher conditions in larger patches results in a switch of the growth strategy of *Puccinellia phryganodes* between phalanx growth at small patch sizes to guerilla growth at large patch sizes (*sensu* Lovett Doust 1981). As soil conditions in cleared patches worsen progressively over time and space with increasing patch size, re-colonization by *Puccinellia* of large cleared patches becomes increasingly more difficult as the soil conditions deteriorate for plant growth.

Soil salinity increased with increasing patch size across all sites on the final sampling date in 2000 and in 2001 (Fig. 3.1). High soil salinities are often limiting for plant growth in salt marshes, but plants can act as facilitators for other plants by shading soil surfaces and thus lowering soil salinity (Bertness and Hacker 1994). At La Pérouse Bay, soil salinity has been found to be inversely related to above ground biomass (Srivastava and Jefferies 1996). Removal of vegetation from this system leads to increases in soil evaporation rates (Srivastava and Jefferies 1995b) which draws inorganic salts from the underlying marine sediments to the surface layers of the soil (Iacobelli and Jefferies 1991). These high soil surface salinities limit growth and survival of plants, further reducing above-ground biomass. This further increases in evaporation and soil salinity, as a result of this positive feedback, can lead to hypersaline conditions in exposed areas (Srivastava and Jefferies 1996).

Removal of vegetation can also lead to higher soil salinities in other salt-marsh systems. Similar to La Pérouse Bay, passive shading by the plant canopy limits surface evaporation and maintains soil salinity at relatively low levels in New England salt marshes (Bertness *et al.* 1992, Bertness and Hacker 1994, Callaway 1994, Bertness and Leonard 1997). In areas where vegetation is removed, soil salinity is elevated due to the direct exposure of soil to solar radiation leading to increased evaporation which may limit re-colonization of exposed sediment (Bertness 1991). In New England salt marshes, closure of exposed patches can occur via facilitated succession where initial colonizers reduce soil salinity by shading the patch surface, leading to the invasion of less salt-tolerant competitive dominants into the patch (Bertness 1991, Bertness and Shumway 1993). In contrast, at La Pérouse Bay exposed sediments are maintained as a result of the positive feedback described above, which leads to large areas of hypersaline exposed sediment (Srivastava and Jefferies 1996).

Previously, soil salinity has been found to be positively related to patch size in both Arctic salt-marsh systems (Srivastava and Jefferies 1995b) and New England salt marshes (Bertness 1991). Larger patch sizes have a greater exposed surface for evaporation and less shading from edge plants, resulting in higher salinities in larger patches. These higher salinities may, in turn, further restrict plant re-establishment, resulting in the maintenance of these large patches of exposed sediment.

Soil moisture decreased with increasing patch size and the effect of patch size on soil moisture was more pronounced in the latter portion of each growing season (Fig.

3.2). Vegetation often reduces the evaporative water loss from surface soils (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1995b) and thus removal of vegetation results in lower soil moistures. Soil moisture has previously been shown to be lower under naturally grubbed soils than vegetated soil (Wilson and Jefferies 1996), and soil moisture tended to be lower under artificially grubbed surfaces (Iacobelli and Jefferies 1991), although the difference was not statistically significant. Similar to salinity, the larger exposed surface for evaporation and less shading from edge plants, results in higher rates of evaporation and lower soil moisture in large patches.

Bulk density increased with increasing patch size and, again, the effect of patch size on bulk density was more pronounced at the end of each growing season (Fig. 3.3). Previous studies found no difference in bulk density between naturally grubbed areas and vegetated areas in the same system (Wilson and Jefferies 1996). Grubbing by snow geese removes the thin veneer of organic matter and plant litter above the sediment (Hik *et al.* 1992). As organically rich soil has a lower bulk density than the deeper marine sediments, removal of the organic veneer will increase the bulk density of the soil. Further, larger patches may be exposed to greater erosion, resulting in a greater loss of organic material than that that occurs in small patches. This results in a larger increase in bulk density in the soils in these larger patches.

Surface soil redox potential decreased with increasing patch size (Fig. 3.4). Sub-surface redox potential, however, did not change with patch size (Fig. 3.5). Redox potential is a measure of the conditions when oxidative processes supplant reduction processes (Hacker and Bertness 1999). Redox potential of naturally grubbed sites tend to be lower than that in vegetated sites (although this trend was not significant) (Srivastava and Jefferies 1995b). Redox values may decrease with grubbing as oxygen can diffuse from live roots into sediment (Armstrong 1979) when a sward is present and removal of plants reduces the potential for this diffusion. Large patches may be more affected than small patches due to the increased distance oxygen must diffuse through the soil from roots of live plants at the patch edge.

In contrast to the other soil variables, overall, total soil nitrogen did not change with patch size within the one-year period (Fig. 3.6). There was a significant decrease, however, in total soil nitrogen with increasing patch size in the high marsh, when data was pooled among dates. Results from earlier studies of soils in the supratidal marsh (<2 inundations of tidal water every 3 years) indicated significantly greater total soil N under intact swards than grubbed swards (Wilson and Jefferies 1996). In agreement with this study, total nitrogen was generally lower in experimentally grubbed patches than in control patches (Fig. 3.4). A decrease in total soil nitrogen with increasing patch size occurred only in the high marsh. Total soil nitrogen is strongly affected by the amount of organic matter in the soil. The one-year period over which nitrogen loss was examined may not be long enough for significant differences in organic matter loss to be detected in younger sites (such as the low marsh and mid-marsh) where accumulation of organic matter is low. In the high marsh, however, total nitrogen levels are approximately two times higher than in the other, younger sites. In these sites, the area of soil exposed directly to solar radiation increases with patch size, which would likely result in higher temperatures in large patches and thus higher rates of oxidation of organic matter (Schlesinger 1991). Oxidation of organic matter may, in turn, result in volatilization of both the carbon and nitrogen from the soil, decreasing both the total soil carbon and nitrogen.

Soil conditions may be detrimental to plant growth, especially in the prevailing conditions found in larger patches. High soil salinities have been shown to adversely affect the growth of *Puccinellia phryganodes*, the dominant plant in the intertidal marsh at La Pérouse Bay (Srivastava and Jefferies 1995a). Low soil moisture also may limit plant growth and plants growing in soils with high bulk densities have low nutrient uptake (Arvidsson 1999), resulting in poor growth (Masle and Passioura 1987). Finally, anoxic conditions can result in low net rates of nitrification (Wilson and Jefferies 1996) and lower nutrient availability for growth.

Soil deterioration in larger patches generally occurred at a faster rate than that in smaller patches, producing conditions in larger patches that are more inimical to plant growth. The differences in soil properties between different patch sizes are likely due to differences in edge effects between patches (smaller patches have a greater edge to area ratio than larger patches). Plants have positive effects on all of the soil variables described. Vegetative cover can reduce surface evaporation rates (Srivastava and Jefferies 1995b) which in turn can lead to higher soil moisture and lower soil salinities (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1995b). Increased organic matter retention and formation of root channels due to plant presence can decrease bulk density. Oxygen can diffuse into soil from live roots, resulting in higher redox potentials (Armstrong 1979, Wilson and Jefferies 1996). In small patches, the close proximity to living plants at the patch edge may reduce the negative changes in soil properties associated with grubbing, as edge plants can alleviate some of the microclimate changes associated with vegetation removal. As patches become larger, however, the distance from the patch center to the living plants at the patch edge also increases, and decreases the potential for these plants to facilitate re-colonization through alleviation of the inimical soil conditions.

In addition to spatial differences in the amount of soil degradation, there were also temporal differences. Soil conditions became harsher over the growing season in both 2000 and 2001 (e.g. the relationship between soil moisture and patch size (Fig. 3.2) and bulk density and patch size (Fig. 3.3) was stronger in the latter portion of both growing seasons) and also over the entire experimental period (e.g. the r^2 values for the relationship between salinity and patch size (Fig. 3.1) increased over the 2-year period). As temperatures increased over the season, the rate of evaporation from the exposed soil likely increased as well, resulting in lower soil moistures and higher salinities. Thus, as time since disturbance increased, the soil conditions become more adverse for plant growth, decreasing the probability of re-colonization of the patches by *Puccinellia*, especially in large sized patches.

In "stressful" environments, such as those found in grubbed patches at La Pérouse Bay, a clonal (as opposed to sexual) reproductive strategy may put a plant at a competitive advantage (Jónsdóttir *et al.* 1996). Clonal plants are those which produce new offspring (termed ramets) that can complete a life cycle without going through the sexual cycle, including various modes of vegetative spread such as stolons and rhizomes (Jónsdóttir *et al.* 1996). In the Arctic and sub-Arctic, the clonal growth strategy is widespread (Jónsdóttir *et al.* 1996). *Puccinellia phryganodes*, for example, the dominant vegetation in the intertidal salt marsh at La Pérouse Bay is an entirely clonal plant, as the grass is a sterile triploid (Bowden 1961) and thus must rely on vegetative growth to re-colonize damaged areas (Jefferies and Gottlieb 1983) or, alternatively, may re-colonize new areas through the establishment of leaf fragments in exposed sediment (Chou *et al.* 1992).

The production of ramets may provide a competitive advantage in harsh environments (Jónsdóttir *et al.* 1996), especially when nutrients can be translocated from older ramets during establishment (Callaghan 1984). The lateral spread of plants from clonal growth can be advantageous in a nutrient-limited environment, as clonal growth provides a searching mechanism for new resources (Hutchings and de Kroon 1994).

Proportion of the cleared patch covered by the re-growth of *Puccinellia phryganodes* decreased as patch size increased (Fig. 3.7). Area of the patch covered by the re-growth of *Puccinellia* increased with patch size (Fig. 3.8). These general patterns would be expected if the *Puccinellia* colonized the bare area at a constant rate regardless of patch size. For example, if *Puccinellia* grew in from the patch edge at a rate of 1cm per year after a specified period of time, the larger patch would have a lower proportion covered by *Puccinellia*, but also would have a greater area covered, due to the larger circumference in larger patches. Consequently, for a given patch shape, the perimeter or the perimeter to area ratio often matters more than the area of the disturbance (Miller 1982).

The area of re-growth, when adjusted for the patch perimeter, increases with patch size, to approximately the patch size of 20cm, where the rate of increase declines (Fig. 3.10). *Puccinellia* colonizing larger patches may be exploiting more of a guerilla, as opposed to a phalanx, growth strategy (*sensu* Lovett Doust 1981), which allows a faster invasion of free space (Bertness and Ellison 1987), and exploits more of the available area. *Puccinellia* colonizing small patches, alternatively, may be exploiting a phalanx growth strategy, proliferating more within a specific area as opposed to spreading over large areas. The soil within the small patches is more favourable for growth than that within the large patches, and thus the plants may use the phalanx growth strategy to efficiently exploit the resources available in these patches, rather than search for more favourable patches.

The increased lateral spreading of the guerilla growth habit with increased patch size (and thus less favourable growth conditions) does not occur indefinitely. *Puccinellia* reaches its maximum growth response (in terms of area covered) at approximately a patch size of 20cm. This appears to be the maximum amount of growth possible for *Puccinellia* within the time frame of the study. *Puccinellia* may have the potential for further areal coverage, but the soil conditions in the larger patches become too adverse to permit further encroachment into the exposed soil in the larger patch sizes. Biomass of *Puccinellia* that has re-colonized the patches decreases with increasing patch size, when adjusted for the area of the patch covered by re-growth of *Puccinellia* (Fig. 3.13). Thus, re-growth of *Puccinellia* was denser in smaller patches than in larger patches. This is consistent with a phalanx growth strategy at small patch sizes and guerilla growth strategy at large patch sizes.

Puccinellia is currently re-colonizing the experimental bare patches at a rate of approximately 1 cm per year, depending on patch size (Fig. 3.10). Although this growth rate appeared constant between 2001 and 2002, re-colonization is not likely to continue at this rate indefinitely. Soil conditions within the experimental patches became more extreme with time, both within season (Fig. 3.2, 3.3) and between seasons (Fig. 3.1) and, in turn, re-colonization by *Puccinellia* may become more difficult. This will be more evident in larger patches than smaller patches. Both edge plants, and plants that have re-colonized the patch, may ameliorate the adverse conditions within the patch, self-facilitating re-colonization, but under the deteriorating soil conditions full re-growth in large patches is likely to take many decades, and some large patches may not fully recover from disturbance.

Re-colonization of both natural and experimental large exposed patches at La Pérouse Bay has been shown to be an extremely slow process. Re-vegetation has not yet begun to occur on exposed surfaces resulting from goose grubbing (4 m x 4 m) in the supratidal marsh that have been exclosed to prevent further damage by geese for over twelve years (Jefferies, unpublished data). Further, areas that were experimentally cleared (50 cm x 50 cm) ten years ago in the intertidal marsh have not been colonized to date (Srivastava, unpublished data). Re-vegetation of large exposed surfaces of consolidated sediments in the intertidal marsh at La Pérouse Bay is expected to be negligible.

In summary, soil degradation, resulting from grubbing by lesser snow geese, in the intertidal salt marsh at La Pérouse Bay, becomes more severe with both size of grubbed patch and time since grubbing. Soil salinity and bulk density both increase, while soil moisture and soil redox potential decrease with patch size, resulting in less favourable growing conditions in larger patches. Additionally, these soil property changes become more severe with time, both within and between seasons. In small patches, with more favourable conditions, *Puccinellia* exhibits phalanx growth, resulting in dense re-growth of *Puccinellia*. As patch size increases, however, and soil conditions become more adverse, *Puccinellia* switches to a guerilla growth form, more effectively searching for an environment more hospitable for growth. Although the basal cover of re-growth of *Puccinellia* is higher (although less dense) in large patches, there is a threshold patch size, of about 20cm diameter, beyond which the rate of areal expansion does not increase further. In these large patches, the slow rate of colonization of *Puccinellia*, in addition to the worsening soil conditions with time, may create an environment in which re-colonization by *Puccinellia* cannot occur.

Chapter 4: General Discussion

4.1. Soil degradation following loss of vegetative cover at La Pérouse Bay, Manitoba

Removal of vegetative cover as a result of the foraging activities of geese has resulted in changes in soil properties at La Pérouse Bay both on the long-term, at a large spatial scale (vegetation mosaics, Chapter 2) and on the short-term, at a small spatial scale (patch dynamics, Chapter 3). The different types of vegetative cover in the mosaic are on the scale of metres (or tens of metres), whereas non-vegetated components have been devoid of vascular vegetation for an extended period of time (> 5 years) and some of these extend over hundreds of metres. In contrast, the spatial scale of the experimental cleared patches was much smaller: patches ranged between 2.5 cm and 40 cm in diameter, and the vegetation cover had been removed for only two years. Despite these differences in both temporal and spatial scales, the soil processes examined were comparable in both studies. In the absence of vegetative cover similar soil properties deteriorated with increasing patch size in the small experimental patches, as were observed in the exposed soil of the vegetation mosaics that represent the outcome of changes at larger spatial and temporal scales.

A number of soil properties changed with loss of vegetative cover, both at the landscape level and at the individual patch level. Infiltration rate was higher in soil covered with vegetation (Fig. 2.1). Vegetation cover is known to increase infiltration rate (Elwell and Stocking 1976, Box and Bruce 1996, Anderson and Hodgkinson 1997), resulting in higher soil water availability for plants. In addition to the physical characteristics of plants that promote water capture (Anderson and Hodgkinson 1997), effects of vegetation on soil characteristics may also influence the rate that water can infiltrate into soil. Soil under vegetated swards, which had a higher infiltration rate than bare soil, also had a lower bulk density than exposed soil (Fig. 2.5). In addition, infiltration rate was negatively correlated with bulk density across all soil types (Fig 2.2). In the patch-size experiment (Chapter 3), infiltration rate was not measured in patches of different size due to methodological constraints. However, bulk density increased with patch size (Fig. 3.3), and as bulk density was correlated with infiltration rate in this study, as well as in other studies (Hakansson and Voorhees 1998), the infiltration rate of soils likely decreased with increasing patch size. As a result of the direct effects of vegetation on infiltration rate through water capture, and the indirect effects that result from modification of soil properties, vegetation removal produces a lower infiltration rate in exposed soils, which may limit re-growth of plants.

Soil moisture and salinity both changed with loss of vegetative cover. At the landscape scale, exposed soil had lower soil moisture (Fig. 2.3) and higher salinity (Fig 2.7) than comparable values for soil with vegetative cover. At the individual patch scale, the same trends were present with soil moisture decreasing (Fig. 3.2) and salinity increasing (Fig. 3.1) with increasing patch size. The rise in salinity is closely linked to the loss of soil water. Removal of vegetation in this system (Srivastava and Jefferies 1995b) and other salt-marsh systems (Bertness *et al.* 1992, Bertness and Hacker 1994, Callaway 1994, Bertness and Leonard 1997) result in increased soil evaporation rates. In the intertidal marshes of the Hudson Bay Lowlands, this increased evaporation draws inorganic salts from the underlying marine sediments to the surface layers of the soil (Iacobelli and Jefferies 1991).

Finally, total nitrogen content was affected by the presence of vegetative cover. In the vegetation mosaics, exposed mineral soil had significantly lower total soil nitrogen than soil covered by *Puccinellia* (Fig. 2.12). In experimental patches in the high marsh, total soil nitrogen decreased with increasing patch size, but the other sites examined showed no relation between soil nitrogen and patch diameter (Fig. 3.6). In the low marsh and the mid-marsh, however, large areas of exposed soils that have had no vegetation cover for a long period of time have undergone significant soil nitrogen loss. Differences between sites of the effect of vegetation removal on total nitrogen are likely the result of differences in the initial soil nitrogen content between sites at the start of the experiment. The high marsh soil has approximately twice as much nitrogen (Fig. 3.4) and contained more organic matter (Fig. 2.11) than the other sites. Soil at this site is further along the soil-ripening gradient (*sensu* Pons and Zonneveld 1965) and has been accumulating organic matter for a longer period of time. In the less developed sites (low marsh and mid-marsh), the one year over which nitrogen loss was examined may not be a long enough time to be able to detect a decrease in nitrogen in these soils due to their initially low nitrogen contents. Because soils where vegetation has been removed from a large area, or for a long period of time, have undergone significant nitrogen loss (as in the exposed mineral soil), if the experimental patches are not re-colonized, soils in these patches will likely eventually show a large loss of nitrogen, similar to exposed soils in the high marsh.

Differences in soil properties between vegetated and non-vegetated components of the mosaic at La Pérouse Bay may be accentuated by the inability of plants to re-colonize non-vegetated soils. The differences in soil properties between the components of the mosaic are a result of plant-soil interactions. They are often thought responsible for the development and maintenance of vegetation mosaics (Van de Koppel *et al.* 1997, Klausmeier 1999, HilleRisLambers *et al.* 2001). Vegetation has numerous positive effects on soil; plant presence in soil can increase nutrient availability (Müller 1953, Callaway 1995) and reduce nutrient loss (Aguiar and Sala 1999), promote water infiltration (Elwell and Stocking 1976, Box and Bruce 1996), reduce erosion (Elwell and Stocking 1976), prevent salt accumulation (Srivastava and Jefferies 1996), and increase oxygen diffusion (Armstrong 1979). The maintenance of favourable soil conditions by vegetation cover in a harsh environment allows vegetation to persist by concentrating resources in areas where plants are present (Adler *et al.* 2001). In soil not covered by vegetation, however, soil conditions deteriorate to the point where establishment of vegetation is difficult, as seen by the low transplant survival of *Puccinellia* in areas not already covered by the grass (Fig. 2.16).

Large exposed areas may be maintained by adverse soil conditions, but soil conditions resulting from vegetation loss at a smaller scale may also result in maintenance of exposed patches, if the spatial extent of the vegetation loss is beyond a threshold size. Soil conditions deteriorated rapidly in patches with experimental removal of vegetation, and changes in soil properties were evident, in some cases, within a single growing season. The changes in soil conditions became more rapid as patch size increased, resulting in more adverse soil conditions in large exposed patches than in smaller patches. Although conditions in smaller patches may be ameliorated by edge plants (see discussion in following section), in larger patches the soil conditions may prevent re-growth into the patches. The result is a mosaic of *Puccinellia* and exposed patches of soil, similar to the vegetation mosaic described in Chapter 2, only at a smaller spatial scale.

4.2. Facilitation and vegetation re-colonization at La Pérouse Bay, Manitoba

Facilitation by salt-marsh vegetation will likely play a large role in the re-colonization of disturbed sediment at La Pérouse Bay. Facilitation is common in systems characterized by severe stress (Holmgren *et al.* 1997), and is recognized as an important process driving salt-marsh community processes in non-Arctic environments (Bertness *et al.* 1992, Bertness and Hacker 1994, Callaway 1994, Bertness and Leonard 1997). Facilitation is also likely an important processes in Arctic environments due to the prevailing physical conditions, such as low temperature, limited nutrient supply and destructive processes affecting soil movement (Brooker and Callaghan 1998). In these systems, the environmental factors that constrain plant growth may be alleviated by the presence of other plants, which ameliorate environmental conditions (Brooker and Callaghan 1998). For example, the conditions in soil exposed by the foraging activity of geese may be ameliorated by the presence of *Puccinellia* or algal mats, enhancing the capacity for vegetative re-growth in the system.

Facilitation often involves amelioration of the abiotic environment, which includes modification of the microclimate and of soil properties (Hunter and Aarssen 1988, Stachowicz 2001). A plant may modify the microclimate for other organisms that share the same location by altering temperature, wind flow, light intensity, and soil moisture availability (Hunter and Aarssen 1988, Stachowicz 2001). For example, canopy shade may protect seedlings and other smaller plants from temperature extremes, reducing evaporation from soil and increasing water availability to plants (Callaway 1995). The most common examples of facilitation result from amelioration of the soil environment (Hunter and Aarssen 1988). For example, the nutrient regime under canopies often has large facilitative effects on understory plants; frequently there are higher levels of nutrients in soils below a canopy than in adjacent open areas (Callaway 1995).

4.2.1. Facilitation and vegetation mosaics at La Pérouse Bay, Manitoba

Vegetated patches in mosaics are maintained by self-facilitative processes in systems with patterned vegetation, including La Pérouse Bay. Plant-soil interactions result in soil conditions in vegetated areas that are amenable for plant growth and maintenance. Vegetation increases water infiltration into the soil (Glover *et al.* 1962, Elwell and Stocking 1976, Box and Bruce 1996, Anderson and Hodgkinson 1997), resulting in higher water availability for plant growth. Higher water infiltration under vegetated patches compared with non-vegetated patches has been found in a variety of semi-arid and saline systems (Belsky 1986, Wilson and Agnew 1992, Van de Koppel *et al.* 1997, Aguiar and Sala 1999, Seghieri and Galle 1999) including the intertidal marsh at La Pérouse Bay (Fig. 2.1), and may be partially responsible for the maintenance of vegetated patches within the mosaic as well as the inability of the exposed patches to re-vegetate.

Although most attention has been paid to differences in infiltration, self-facilitative processes that maintain vegetated patches may involve other soil variables (Van de Koppel *et al.* 1997). Other studies have found higher soil organic matter and mineral nutrients in vegetated patches compared with non-vegetated patches (Aguiar and Sala 1999). At La Pérouse Bay, vegetated swards had a higher soil moisture (Fig. 2.3), lower bulk density (Fig. 2.5), lower salinity (Fig. 2.7), higher soil organic matter content (Fig. 2.11) and higher total soil nitrogen content (Fig. 2.12) than comparable values for exposed mineral soil, resulting in a more positive environment for plant growth where vegetation cover is already present. The effects of vegetation on these soil variables, in addition to their effects on infiltration, result in the maintenance of vegetated patches within a matrix of non-vegetated soil in the intertidal marsh at La Pérouse Bay. Transplants of *Puccinellia* growing in *Puccinellia*-covered soil had much higher transplant vigour than those in soil not covered in vascular vegetation, likely as a result of these self-facilitative processes.

In addition to self-facilitative processes maintaining vegetated patches, facilitative processes may also enable *Puccinellia* to disperse successfully to areas of the mosaic not covered in vascular vegetation. For example, algal crusts may be an important facilitator for vascular plant growth in the intertidal salt marshes at La Pérouse Bay. After one growing season, transplants of *Puccinellia* in soil covered by algal mats had a higher transplant vigour than transplants planted in exposed mineral soil, in two out of three sites, although vigour was still lower than that in *Puccinellia*-covered soil (Fig. 2.6).

In many ecosystems, especially those limited by water, microbiotic crusts can have large facilitative effects on vascular plant growth (Evans and Johansen 1999). Soil crusts can potentially influence both the establishment and growth of vascular plants, because crusts modify soil properties and resource availability close to the soil surface, where most vascular plant roots are located (DeFalco *et al.* 2001). Most reviews conclude that the effects of algal crusts are positive (Prasse and Bornkamm 2000), although there is evidence of both negative and positive effects of algal crusts on vascular plant growth (Evans and Johansen 1999).

Although the presence of algal mats may improve transplant growth above that of exposed soil, at least at some sites, the effects of algal mats at these sites is not entirely facilitative. These algal mats, that are composed of cyanobacteria, diatoms and green algae, develop only on peaty soil surfaces where vascular plant cover has been removed recently by goose grubbing (Jefferies and Rockwell 2002, Srivastava and Jefferies 2002). In this study, algal mats ameliorate soil conditions compared with exposed mineral soil. Although the results show the potential for facilitation by algal mats for transplanted *Puccinellia*, this effect may be of little consequence for natural re-vegetation. The facilitation is only effective if the grass can establish naturally in the mat. Developing shoots of *Puccinellia phryganodes* and *Carex subspathacea*, may be unable to penetrate the hard algal crust which dries out in summer (Jefferies and Rockwell 2002, Srivastava and Jefferies 2002). Additionally, leaf fragments of *Puccinellia,* which can be transported to these surfaces, and have the potential to root in exposed sediments (Chou *et al.* 1992), may not be able to establish on the hard microbiotic crust. Thus, although there may be potential positive effects of algal mats on re-vegetation of the intertidal exposed soils, these may not be realized because of the drying out of the sediment surface in summer.

4.2.2. Facilitation and patch dynamics at La Pérouse Bay, Manitoba

Facilitation may also play a role in re-colonization of exposed sediment at a small scale, in addition to that observed at the landscape level. Plants have positive effects on most of the soil variables examined in the patch-size experiment (Chapter 3). This potentially could result in self-facilitation by *Puccinellia* and play a large role in re-colonization, similar to the role self-facilitation plays in maintenance of vegetated patches. The differences in soil properties between different experimental patch sizes (Figs. 3.1, 3.2, 3.3, 3.4, 3.6) are likely a consequence of differences in edge effects between patches associated with the potential for amelioration of soil conditions by plants growing at the perimeter. There is the potential for self-facilitation of vegetative re-growth through amelioration of soil conditions, as plant cover has positive effects on all of soil variables described. Vegetative cover reduces surface evaporation rates (Srivastava and Jefferies 1995b) leading to higher soil moisture and lower soil salinities (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1995b). Bulk density may be decreased by plant presence through increased organic matter retention and formation of root channels. Oxygen diffusing into soil from live roots may result in higher redox potentials (Armstrong 1979, Wilson and Jefferies 1996).

The potential for these facilitative effects is higher in small patches than in large patches. The changes in soil properties resulting from grubbing may not be as high for soil in close proximity to surviving plants, due to ameliorating effects of plants. Thus, in small patches, the close proximity of the center of the disturbed patch to living plants at the patch edge may result in a fewer adverse soil changes. As the patches become larger, however, so does the distance of the center of the patch to the nearest plant, and the potential for these plants to facilitate re-colonization is decreased.

This type of facilitation through amelioration of adverse soil conditions is particularly common in salt marshes (Bertness and Hacker 1994) and the reduction of soil salinity through plant presence has been well described. Bare patches in New England salt marshes often have elevated soil salinities due to the direct exposure of soil to solar radiation and resultant high rates of evaporation that may limit re-colonization (Bertness 1991). The salinity of these patches can be affected by rainfall, patch size and their location in the marsh (Bertness 1991). Growth of marsh plants can be facilitated by alleviation of this salinity stress. Passive canopy shading limits surface evaporation and the accumulation of salts in the upper layers of soil (Bertness *et al.* 1992, Bertness and Hacker 1994, Callaway 1994, Bertness and Leonard 1997). Closure of bare patches occurs via facilitated succession where initial colonizers can reduce soil salinity by shading the patch surface, and this leads to the invasion of less salt-tolerant competitive dominants into the patch (Bertness 1991, Bertness and Shumway 1993).

High soil salinities can also limit plant growth in Arctic salt marshes. At La Pérouse Bay, canopy plants maintain low soil salinities because shading of the soil surface and the presence of a soil organic layer restricts evaporation of water from soil (Srivastava and Jefferies 1995b). Removal of vegetation results in increased soil evaporation rates (Srivastava and Jefferies 1995b) that draws inorganic salts from the underlying marine sediments to the surface layers of the soil where the roots of vascular plants occur, killing plants (Iacobelli and Jefferies 1991). The death of plants, as a result of hypersalinization, reduces plant biomass, via a self-amplifying positive feedback coupled with secondary feedbacks (Srivastava and Jefferies 1996). The result has been the transformation of intact salt-marsh swards into extensive areas of hypersaline exposed sediment, where re-colonization by salt-marsh vegetation is very slow. With the addition of fertilizer and mulch (as an evaporative barrier facilitating low soil salinities) in protected exclosures, re-vegetation of dominant salt-marsh graminoids can occur (Handa and Jefferies 2000) but is likely to be a rare event in the absence of this amelioration and the continual presence of geese.

4.2.3. Impacts of facilitation on natural re-vegetation at La Pérouse Bay, Manitoba

Facilitation is likely to be an important process in the re-colonization of exposed surfaces at La Pérouse Bay, from the individual patch scale to the landscape scale. Natural re-vegetation, however, is likely only tenable on the scale of the individual patch. At the landscape scale, I found low survival of transplants in soils that did not already have *Puccinellia* cover, and as described earlier, the facilitative mechanisms of algal mat presence is likely not effective due to the difficulties of *Puccinellia* establishment in the crust in summer. At the patch scale, however, natural re-colonization by *Puccinellia* is likely, although it depends on the spatial extent of the damage. I found that the rate of re-colonization increased with patch size, until a threshold size (about 20 cm diameter) at which the rate of increase slowed (Fig. 3.10). In addition, the re-colonization of the exposed patches is not likely to continue at the same rate indefinitely. As the soil conditions in the disturbed patches progressively worsens over time, the plants are re-colonizing a 'moving target', and eventually the soil may degrade to the point where re-colonization is impossible. This is more likely to occur in larger patches than in small patches that may become completely re-colonized before soil degrades to this point.

4.3. Re-colonization potential of *Puccinellia* across a soil-ripening gradient

Sites for both the vegetation mosaic study (Chapter 2) and the patch-size experiment (Chapter 3) were established along a soil ripening (aging) gradient in the intertidal marsh on the coastal flats at La Pérouse Bay. The coastal flats, both at La Pérouse Bay and elsewhere along the Hudson Bay coast, are the result of isostatic uplift (Hansell *et al.* 1983). Isostatic uplift has resulted in a rise in land elevation from the sea landwards to the upper limit of the intertidal marsh, with soils closest to the sea emerging from the Hudson Bay more recently. There is a change in soil properties as these sediments age (time since emergence from the Hudson Bay), termed "soil ripening" (Pons and Zonneveld 1965, Packham and Willis 1997) that occurs along a geographical gradient extending from the coast inland. At La Pérouse Bay, the change in soil properties is not associated with a change in plant species as in vegetated areas *Puccinellia phryganodes* and *Carex subspathacea* are dominant across the entire gradient.

Four sites were examined over the soil ripening gradient: they were located in the fore marsh, low marsh, mid-marsh and high marsh. These sites extend over about a kilometre, and differ in age since the land has emerged from the Hudson Bay. The fore marsh represents the youngest site and the high marsh, which is close to the willow fringe at the landward limit of the intertidal marsh, the oldest. The fore marsh is unconsolidated sediments that have not yet been colonized by vegetation.

Numerous soil characteristics varied over the soil ripening gradient in sites that have been colonized by vegetation (low marsh, mid-marsh and high marsh) (Figs. 2.3, 2.5, 2.7, 2.11, 2.12). Many of the differences in soil variables between sites are likely a result of the accumulation of organic matter at the site over time, with older sites accumulating more organic matter than younger sites. The increase in salinity with site age is due to the inverse salinity gradient at La Pérouse Bay; the intertidal flats and coastal marshes beyond the tidal limits are characterized by an inverse salinity gradient where soil salinities are highest at the landward end of the continuum of marshes (Glooschenko and Martini 1978, Jefferies *et al.* 1979, Price and Woo 1988b, a).

In addition to differences in soil properties along the soil-ripening gradient, patterns of re-growth of *Puccinellia* in exposed soil differed between sites. The variation in transplant growth between sites in the vegetation mosaic depended on the type of soil into which *Puccinellia* was transplanted (Fig. 2.16). Transplant vigour was extremely low in exposed mineral soil, regardless of site. Transplant vigour decreased with increasing site age in soil covered with an algal mat and, to a lesser degree, in soil in which a sward of *Puccinellia* was present. In the patch-size experiment, re-growth occurred at a faster rate in younger sites (low marsh) than in older sites (mid-marsh and high marsh) (Figs. 3.7, 3.9, 3.10). Thus, the potential for re-colonization of exposed sediments is likely higher in younger than older sites, although the re-colonization potential is low across all sites.

Handa and Jefferies (2002) also found better establishment of vegetation in degraded soils in younger sites than at older sites at La Pérouse Bay across a more extreme age gradient (from a younger site in the intertidal marsh to an older site in the supratidal marsh). Transplants of *Puccinellia phryganodes* in the intertidal marsh established in degraded sediments, whereas transplants of *Carex subspathacea* in the supratidal marsh did not establish readily in degraded sediments (Handa *et al.* 2002).

However, the differences in establishment in this experiment may not be due solely to transplant location. The difference may be due, in part, to the higher salt tolerance of *Puccinellia phryganodes* than that of *Carex subspathacea* (Srivastava and Jefferies 1995a, Handa *et al.* 2002) and to the greater seasonal shoot production in *Puccinellia* plants than in *Carex* plants (Kotanen and Jefferies 1987, Bazely and Jefferies 1989).

The potential for re-colonization of exposed soil by *Puccinellia* was also examined in unconsolidated sediments, seaward of the low marsh. In the fore marsh, the youngest of all sites examined, transplant vigour was extremely low (Fig. 2.16d). Re-colonization of disturbed patches was not examined at this site, as no previous colonization by *Puccinellia* has occurred in the fore marsh. Previous studies have suggested that unconsolidated sediments may provide an environment in which colonization of *Puccinellia* could occur (Handa and Jefferies 2000, Handa *et al.* 2002). Field observations indicated that erosion followed by the accumulation of unconsolidated sediment may provide suitable conditions for re-vegetation (Handa and Jefferies 2000). The fore marsh site examined in this study differs from the previously described unconsolidated sediment, however, as it has not been previously covered by vegetation, and thus has not undergone erosion followed by sediment accumulation.

Alternatively, direct establishment of *Puccinellia* in these sites may not be possible without the presence of an early successional species. Bare consolidated sediments, resulting from the degradation of the marsh, undergo erosion and create unconsolidated sediments in which a *Hippuris*-dominated community can establish (Handa *et al.* 2002). The *Hippuris* community may be a necessary precursor for *Puccinellia* establishment, through the modification of the soil environment either by living *Hippuris* plants or by accumulating litter. Bertness (1991) has previously found in New England salt marshes that colonization of exposed sediment by a salt tolerant early colonizer reduces substrate salinity by shading the surface, facilitating the invasion of *Juncus* plants. The potential for direct re-colonization of unconsolidated sediments is low, but may be more likely if the sediment is previously colonized by a species that can grow under the prevalent soil conditions.

4.4. Long-term implications of soil degradation at La Pérouse Bay

Small-scale removal of vegetation by lesser snow geese will likely eventually result in the formation of large-scale mosaics of intact swards of salt-marsh vegetation interspersed with exposed sediment (vegetation mosaics). Soil deterioration occurred within only a short period of time (< 2 years) in small experimentally grubbed patches of sediment (Chapter 3). The developing soil properties in exposed areas inhibit regeneration of *Puccinellia* in this sediment, as soil properties become more adverse to plant growth over time. This progression is especially evident in large (20 cm and 40 cm diameter) patches in which soil conditions may prevent the eventual complete re-colonization of patches that may occur in the smaller diameter patches.

The rate of re-colonization into exposed patches decreases in the larger sized patches (Fig. 3.9, 3.10), even under conditions where further goose impact is removed by exclosure of damaged patches. In naturally formed patches, which are not exclosed from further damage, re-colonization of large patches becomes even more unlikely. New growth from the edge of patches results in the amelioration of soil conditions inside the damaged patch, promoting further re-growth (Sousa 1984, Sousa 1985, Bertness and

Callaway 1994, Holmgren *et al.* 1997, Brooker and Callaghan 1998, Sousa 2001). If grazing by geese removes the re-growth into exposed patches, this results in the removal of the agent that leads to amelioration of soil conditions, and may lead to inhibition of plant re-growth as the soil deteriorates.

In addition to inhibiting re-colonization of existing patches, further foraging by geese creates new exposed areas of sediment. These new exposed areas and the existing patches may coalesce to form large areas of exposed sediment, under foraging pressure by geese. The result of this coalescence is large patches, with the resultant high rates of soil degradation, further inhibiting vegetative re-growth. These patch dynamics eventually produce a vegetation mosaic of isolated intact small swards of *Puccinellia* (3 m x 3 m) interspersed with large areas of exposed sediment, as seen currently at La Pérouse Bay (Handa *et al.* 2002).

The vegetation mosaic at La Pérouse Bay is likely to progress further towards an alternate stable state of large areas of hypersaline exposed sediment, devoid of vegetation. This prediction is based on theoretical models of grazing systems that indicate that as herbivore impact increases, vegetation mosaics will progress towards systems without vegetative cover, provided that plant dispersal is low (HilleRisLambers *et al.* 2001). As this progression involves changes in vegetation coupled with changes in abiotic conditions (Bazely and Jefferies 1986, Rietkerk and Van de Koppel 1997), the formation of a non-vegetated state is often irreversible (Sinclair and Fryxell 1985, Friedel 1991, Laycock 1991).

The progression from vegetation mosaics to large areas of exposed sediment is already occurring in areas of La Pérouse Bay, in accordance with the model of

HilleRisLambers (2001). The assumptions of the model are supported in this salt marsh. *Puccinellia phryganodes*, the primary graminoid present on the marshes, has a low dispersal potential. The grass is a sterile triploid (Bowden 1961), with no seed bank for re-establishment (Chang *et al.* 2001) and must rely on clonal growth for re-establishment in damaged areas (Jefferies and Rockwell 2002). The grass can establish from leaf fragments in soft sediments (Chou *et al.* 1992) but transplant experiments (Fig. 2.16) have shown that establishment is low in soils without *Puccinellia* cover. The combination of these factors results in low dispersal potential of *Puccinellia*, an assumption in the model of HilleRisLambers (2001). Consequently, large areas have progressed from a vegetation mosaic to hypersaline exposed sediment, devoid of vegetation at La Pérouse Bay (Jefferies and Rockwell 2002).

The above long-term implications of soil degradation at La Pérouse Bay are represented in a conceptual model of vegetation change (Fig 4.1). This model begins with an intact salt marsh at La Pérouse Bay where there is complete vegetative cover. Within the salt-marsh vegetation, small exposed patches are created as a result of grubbing by geese. As a result of a feedback between soil degradation in localized areas of exposed sediment and the slow re-colonization of this exposed sediment by plants(Chapter 3), these exposed patches are not rapidly re-colonized and they frequently coalesce to form larger patches of exposed sediment as a result of the cumulative impact of grubbing. Eventually this results in a vegetation mosaic of swards of *Puccinellia* within a matrix of exposed sediment. Within the exposed areas of the vegetation mosaic there is a feedback between adverse soil conditions in areas lacking vegetative cover and poor *Puccinellia* survival (Chapter 2). This feedback may result in the transformation of the vegetation

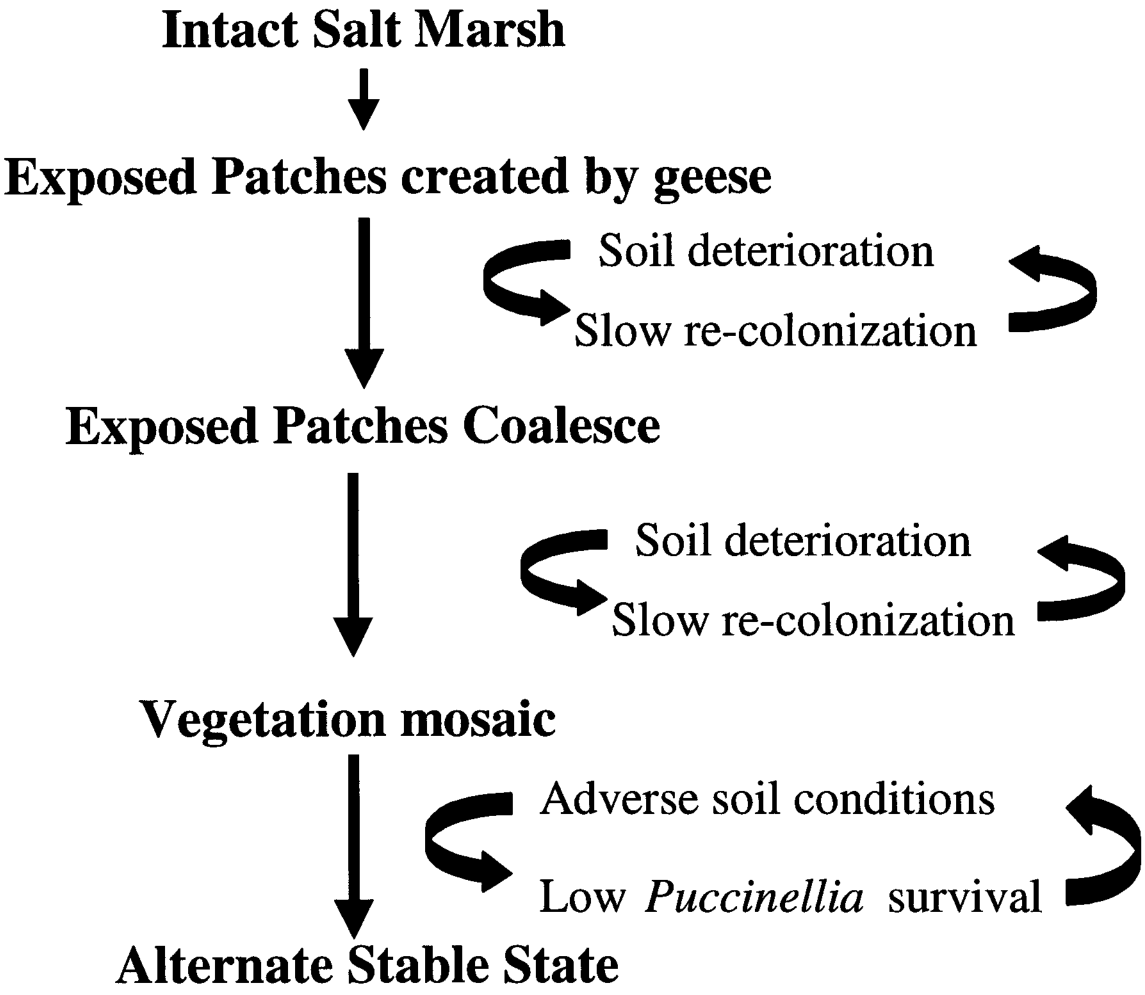


Fig. 4.1. Conceptual model of vegetation change in the intertidal salt marsh at La Pérouse Bay, Manitoba. Within intact salt marsh, localized exposed patches of sediment are created as a result of grubbing by snow geese. This results in disruption of plant-soil interactions and the initiation of feedbacks both between soil deterioration and slow vegetation re-colonization in localized exposed patches and also between adverse soil conditions and low survival of *Puccinellia phryganodes* in large areas of exposed sediment. As a result of these positive feedbacks between soil conditions and vegetation re-colonization, vegetation proceeds from intact salt marsh to a system with vegetation mosaics and further degrades to an alternate stable state of extensive areas of exposed sediment, devoid of vegetation.

mosaic to an alternate stable state of extensive areas of exposed sediment, devoid of vegetation, with adverse soil characteristics that offer little possibility for re-vegetation to occur.

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