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**REVEGETATION TRIALS IN DEGRADED COASTAL MARSHES  
OF THE HUDSON BAY LOWLANDS**

by

Tanya Handa

A thesis submitted in conformity with the requirements  
for the Degree of Master of Science,  
Graduate Department of Botany,  
University of Toronto

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# REVEGETATION TRIALS IN DEGRADED COASTAL MARSHES OF THE HUDSON BAY LOWLANDS

Tanya Handa

Degree of Master of Science

Graduate Department of Botany, University of Toronto, 1998

## ABSTRACT

Intense foraging by an increasing population of lesser snow geese, *Anser caerulescens caerulescens* L., has led to the conversion of former salt-marsh swards, dominated by *Puccinellia phryganodes* and *Carex subspathacea* to hypersaline mudflats, and the conversion of former fresh-water sedge meadows, dominated by *Carex aquatilis*, to moss carpets. This study reports the potential for natural and assisted revegetation by the dominant graminoids of the former plant communities at La Pérouse Bay, Manitoba in the absence of goose foraging. Natural recolonization by *P. phryganodes* was observed within five years where edaphic conditions were suitable. Transplants of *P. phryganodes* established readily in an intertidal marsh, and growth was enhanced by amelioration treatments of peat mulch and fertilizer to the soil surface. Natural recolonization by *Carex subspathacea* was not observed. Transplants of the sedge did not establish readily in an inland marsh and amelioration treatments showed no effect. In fresh-water areas, tillers of *Carex aquatilis* established readily in moss carpets and growth was not enhanced by fertilizer application. The potential for revegetation is discussed within the context of vegetational succession and the ongoing degradation processes.

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## CHAPTER 1: INTRODUCTION

### 1.1 Opening Statement

Humans have induced change to the structure and function of ecosystems on Earth that has resulted in decreases to global biodiversity, alterations to global biogeochemical cycles and has led to land transformation (Vitousek *et al.* 1997). Land degradation (decline in species diversity, primary production and an increase in soil erosion) has been one of the more extreme transformations that has resulted primarily from long term, chronic effects of agriculture, forestry, animal grazing and industrial activities (Dobson *et al.* 1997). Recent estimates suggest that a total of 43% of the Earth's vegetated surfaces have been affected adversely by activities that have resulted in soil degradation, loss of vegetation in drylands and loss of vegetation in tropical moist forests (Daily 1995). Functionally, such transformations are frequently mediated by changes in the abundance of species, all of which, influence water and nutrient dynamics, disturbance regimes and trophic interactions (Chapin *et al.* 1997). For example, an estimated 35% of all soil degradation is a direct result of intense grazing pressure by domesticated or semi-domesticated animals (Daily 1995).

Herbivores exert a strong influence on the structure and function of plant communities (Crawley 1983). Depending on plant growth rate and herbivore density (plant consumption rate), herbivores can alter the vegetation state towards one of several equilibria (Noy-Meir 1975, May 1977). When grazing pressure exceeds the vegetational carrying capacity of the ecosystem, shifts can be rapid and catastrophic leading to changes in the abiotic environment and ultimately to the loss of vegetation (Rietkerk *et al.* 1996, van de Koppel *et al.* 1997). In the Sahelian grasslands of the semi-arid African belt, intense grazing by livestock coupled with climatic stress has resulted in desertification (human-induced loss of vegetation and subsequent soil erosion; Sinclair and Fryxell 1985, Graetz 1991). Overstocking in arid and semi-arid rangelands of the western United States (Hess and Holechek 1995, Whiteford *et al.* 1995), Australia (Ludwig and Tongway 1995) and South Africa (Milton and Dean 1995, Kerley *et al.* 1995) has led to the

replacement of grass-dominated systems by unpalatable shrub or small-tree dominated systems. In the Republic of Kalmykia, Russian Federation, livestock grazing, coupled with wind erosion and salinization has led to the transformation of semishrub and grass pastures to desert (Zonn 1995). Similar threshold responses have been observed in arctic ecosystems; intense foraging by increased populations of reindeer on the Yamal peninsula in western Siberia (Vilchek 1997) and on St. Matthew Island in the Bering Sea (Klein 1987), by the rivière George caribou population in northern Quebec (Manseau *et al.* 1996), by sheep in Greenland (Jacobsen 1987) and Iceland (Arnalds 1987, Runolfsson 1987, Magnússon 1997) and by geese on the Hudson Bay lowlands (Bazely and Jefferies 1996, Srivastava and Jefferies 1996, Jano *et al.* 1998), has shifted systems in a rapid, non-linear manner towards alternate, degraded vegetation states.

It has become an increasing priority to understand the recolonization processes of degraded ecosystems in order to assess their potential for restoration (Cairns *et al.* 1995, Daily 1995, Dobson *et al.* 1997, Urbanska *et al.* 1997). Restoration (*sensu* Bradshaw 1997a), involves bringing a degraded ecosystem back to its previous condition with the emphasis on restoring ecosystem function. The recolonization of degraded land is a slow process, and thus restoration efforts require assistance in enabling adequate numbers of individuals of plant, animal and microbial species to establish in degraded substrates (Bradshaw 1997b). Restoration efforts also necessitate an understanding of the role of different ecosystem components in the functioning of the system (Bradshaw 1997b). In systems damaged by grazing, restoration is seldom as simple as lowering levels of herbivory, because degradation is frequently the consequence of secondary feedbacks in the abiotic environment which cannot be easily reversed (Westoby 1980, Bazely and Jefferies 1996, Rietkerk and van de Koppel 1997, van de Koppel 1997).

With these general considerations in mind, this study examined natural and assisted revegetation processes in degraded coastal marshes at La Pérouse Bay, Manitoba, where the intense foraging activity of lesser snow geese, (*Anser caerulescens caerulescens* L.), has led to the destruction of beach ridge, coastal salt-marsh and fresh-water sedge meadow habitats.

## 1.2 Disturbance in polar and alpine areas

The scale of natural disturbance patterns in arctic tundra, based on a spatial hierarchy framework of Delcourt and Delcourt (1988), can range from disturbances at the micro-scale ( $10^{-1}$ - $10^6$  m<sup>2</sup>), such as periglacial activity, to those at the macro-scale ( $10^{10}$ - $10^{12}$  m<sup>2</sup>), such as glaciation (Walker and Walker 1991). Anthropogenic disturbances are often microscale phenomena, but the cumulative impact can affect mesoscale ( $10^6$ - $10^{10}$  m<sup>2</sup>) and macroscale regions (Walker and Walker 1991, Walker 1997). Direct anthropogenic disturbances associated with the oil industry in the Arctic include the construction of exploratory drill sites, the disposal of drilling and other waste, vehicular traffic from seismic operations, the placement of gravel fill for road beds, drill pads, pipelines and air strips, the associated excavation and placement of overburden from gravel pits, and the physical damage to soils and vegetation from accidental oil, diesel and other chemical spills (McKendrick and Mitchell 1978, McKendrick 1987, 1991, McKendrick et al. 1992, Jorgenson and Joyce 1994, Jorgenson 1997, McKendrick 1997, Walker 1997, Vilchek 1997). Other disturbances associated with development include mine spoils (Elliott *et al.* 1987, Densmore 1994), borrow pits (Kershaw and Kershaw 1987, Harper and Kershaw 1996), vehicular tracks (Forbes 1993, Kevan *et al.* 1995, Harper and Kershaw 1996, Strandberg 1997) and the expansion of human settlements and military activity (Jorgenson 1997). In alpine regions, vegetation disturbance has resulted from the exploitation of mineral, water and fossil fuel reserves, road construction, sport and recreational activities and the use of off-road vehicles (Chambers 1997, Urbanska 1997a,b).

Some disturbances are not the result of direct human activity, but the consequence of human influence on components of the ecosystem. In Iceland, extensive macro-scale soil erosion has resulted from the clearing of woodland vegetation, its subsequent replacement by grasslands, and from grazing activity by domestic livestock (Magnússon 1997). These erosion processes have been accelerated by climatic change and volcanic activity (Magnússon 1997). Similar macro-scale disturbances brought about by humans are evident in the threshold-response examples from the Arctic previously discussed that

result from increased herbivory. In the Antarctic, increases in populations of fur seals following the cessation of commercial hunting, the reduction of whaling and the consequent increase in available krill, have led to the loss of vegetation through excessive trampling and nutrient fecal input into the system (Lewis-Smith 1988).

### **1.3 Topics associated with revegetation efforts in arctic and alpine regions**

To date, many efforts to revegetate degraded tundra regions have focused on re-establishing a closed canopy of vegetation without the goal of restoring former ecosystem function (Elliott *et al.* 1987, McKendrick 1987, McKendrick *et al.* 1992, Younkin and Martens 1987, Younkin and Martens 1994, Magnússon 1997, McKendrick 1997). Such efforts can be classified as “reclamation” efforts (*sensu* Bradshaw 1997a), that is efforts with the goal of bringing land back to a “proper” state, but without the implication of “restoration”, which is the return of the land to an original state. At present, the focus of research appears to be changing as better restoration procedures are established (McKendrick 1997, Forbes and Jefferies 1999). However, regardless of the goal, all northern revegetation efforts must deal with the constraints of arctic environments as well as those of degraded environments.

Recovery from natural disturbances (in undegraded areas) is a slow process in arctic and alpine systems due to the severity of physical, climatic and evolutionary constraints (Svoboda and Henry 1987, Billings 1992, Chambers 1997). The dominant plant reproduction mode is asexual and seed production can be highly variable between years, thus limiting dispersal opportunities (Chambers 1989, Urbanska 1997b). When disturbance occurs at the micro-scale among clonally reproducing plants, revegetation can occur through the lateral growth of ramets, however, this strategy is not effective at a larger scale (Forbes and Jefferies 1999). Plant establishment and successional processes are constrained by frequent periglacial disturbances (Svoboda and Henry 1987, Crawford 1997, Forbes and Jefferies 1999), lack of moisture in space and time (Urbanska 1997a), slow rates of decomposition and nutrient turnover (Nadelhoffer *et al.* 1992, Shaver *et al.* 1997), low energy, a short growing season and high winds (Billings 1987, 1992, Bliss and



Peterson 1992). In the High Arctic, Svoboda and Henry (1987) have suggested that the environment is 'marginal' and succession is not a matter of species replacement, but rather of species establishment and survival. Temperatures and precipitation can be extremely variable (Rapport *et al.* 1997), thereby magnifying the severity of disturbances and further limiting re-establishment (Chambers 1997). Oksanen and Virtanen (1997) have cautioned against the "vulnerable Arctic" view claiming that particularly in the Middle and High Arctic, secondary impacts can vary and natural recolonization is not always a challenge. Nevertheless, they recognize that in the Low Arctic and tussock tundra, when heavy disturbance initiates secondary changes that are likely to persist on a long time scale, recolonization rates are severely impeded.

In addition to the constraints of the arctic environment, plant growth is impeded in degraded areas as a result of changes in physical and chemical factors to the soil environment (Bradshaw 1997b). Such changes include alteration of soil texture, structure, stability, water supply, surface temperature, nutrient content, acidity, toxicity or salinity (Bradshaw and Chadwick 1980). Amelioration treatments to remedy chemical imbalances, ensure adequate levels of organic matter, water retention capacity and nutrient supply have become important components of revegetation schemes (Bloomfield *et al.* 1982, Good *et al.* 1985, Bradshaw 1997b). In restoration efforts on former agricultural lands, nutrient supply may be too high (Marrs and Gough 1989, Marrs 1993). In arctic areas, however, nutrient supply often limits plant growth (Cargill and Jefferies 1984, Jonasson 1992, Chapin *et al.* 1995), and the lack of sufficient organic matter slows the recovery process (Cargill and Chapin 1987, Chambers 1997). Several arctic and alpine revegetation schemes have included amelioration treatments of fertilizer additions (Densmore *et al.* 1987, Chambers 1997, Magnússon 1997, McKendrick 1997). Mulch additions, which reduce soil erosion (Ungar 1996), increase water retention capacity (Bradshaw 1997b) and alter the soil surface temperature (Rosenberg *et al.* 1983, Oke 1995), have been used also in arctic (Densmore *et al.* 1987) and alpine (Ferchau 1988) revegetation schemes.

Assuming the degraded soil environment can be improved so that plant establishment can occur, the question of the ability of plants to immigrate to the sites

remains. Although natural immigration may occur in instances where source populations exist in close proximity, often immigration must be assisted either through normal agricultural seeding, or through more labour intensive hand seeding and planting (Bradshaw 1997b). Many plants in arctic and alpine environments reproduce asexually, or do not set regular seed (see references above) thus making assistance challenging. Furthermore, in arctic and alpine environments, the total pool of species available for recolonization is limited (Forbes and Jefferies 1999). At a global scale, vascular plant diversity is low, estimated at 1500 species in arctic systems, and 8000-10,000 species in alpine systems (Billings 1992, Körner 1995). At local scales, the pool of species is limited even further, since only a fraction of these total species occur. Given these constraints, many revegetation efforts in the Arctic have resorted to the use of non-native species, or a combination of native and non-native species; the primary goal is preventing erosion by the establishment of a vegetation “template” (Elliott *et al.* 1987, Younkin and Martens 1987, Younkin and Martens 1994, Magnússon 1997, McKendrick 1997). However, native plants are often superior at establishing in disturbed sites because they are adapted to the natural constraints of the local environment (Johnson 1987, Urbanska 1997a). In Alaska, colonization of barren saline soil was much more successful with indigenous species such as *Puccinellia langanea*, *Dupontia fisheri* and *Arctophila fulva* than it was with seeded cultivars of *Poa glauca*, *Festuca rubra* and *Arctagrostis latifolia* (McKendrick 1997). In another study, native plants of *Eriophorum vaginatum* were more successful at establishing in a bulldozed site than commercially available seeded cultivars (Chapin and Chapin 1980). When the goal of a revegetation scheme includes the restoration of a particular community structure and function, the use of native species is more likely to prevent later successional changes that are unrepresentative of the area (Bradshaw 1989). Although in some schemes, a vegetation template of non-native plants has been facilitative in the establishment of native plants (McKendrick 1997), exotic species can curtail the invasion of native species through competitive interactions (Younkin and Martens 1987, Martens 1995, McKendrick 1997).

Alternative revegetation schemes have used vegetative dispersal strategies to assist immigration. Herbs and graminoids have been transplanted from seedlings and

from clones in high altitude revegetation efforts (Tschurr 1990, Urbanska 1997a,b) and in vehicle damaged areas in the High Arctic (Forbes 1993). Willow seedlings have been transplanted to restore moose habitat destroyed through gravel mining in Alaska (Densmore *et al.* 1987, Cargill and Chapin 1989a). Some graminoid species such as *Puccinellia phryganodes*, *Carex subspathacea*, *Arctophila fulva* and *Leymus mollis* have the ability to develop roots from the above-ground portion of the shoot system (Chou *et al.* 1992, McKendrick 1993, 1997) and have been used in restoration schemes (Ritchie and Gimmingham 1989, Greipsson and Davy 1994, Magnússon 1997, McKendrick 1997). Sod transplants, sometimes referred to as community or habitat translocation, are another increasingly common restoration technique (Harris *et al.* 1996, Bullock *et al.* 1998). One advantage of transplanting soil from a donor site is that the potential for restoring soil microflora and mycorrhizal fungi, which is increasingly recognized to be important in restoration schemes so as to create a sustainable ecosystem (Perry and Amaranthus 1990, St. John 1990, Haselwandter 1997), is there. Sod transplants have been used with success in arctic (Shirazi *et al.* 1998) and alpine systems (May *et al.* 1982, Urbanska 1997b). However, such a technique must be used with caution such that transplanting does not adversely affect donor populations (Urbanska 1997b).

In developing a revegetation scheme, particularly with the intent of restoring ecosystem function, restoration must be understood as a “moving target” since ecosystems exist in dynamic equilibrium (Inouye 1995, Parker and Pickett 1997). Restoration schemes are often most effective if mechanisms of natural succession are understood (Cargill and Chapin 1987). However, the application of successional models to restoration is not simple, since some examples exhibit well documented successional changes and others do not (Harris *et al.* 1996). In the Arctic, successional models can be complicated by interactions among processes controlling successional change (Walker and Chapin 1987), and the ‘marginal’ environment factor that pushes succession away from species replacement to species establishment and survival (Svoboda and Henry 1987). Consequently, understanding the natural successional scheme within the ecosystem prior to disturbance (Cargill and Chapin 1987), as well as documenting the natural post-disturbance recolonization and succession (Kershaw and Kershaw 1987,

Densmore 1994, Harper and Kershaw 1996, Jorgenson 1997), are invaluable in restoration and revegetation schemes.

#### **1.4 Site description of La Pérouse Bay**

La Pérouse Bay (58°44'N, 94°28'W) is located in the Hudson Bay lowlands, 32 km east of Churchill, Manitoba and approximately 20 km north of the treeline (Fig. 1.1). Since the retreat of the Wisconsin ice sheet 7300-8000 years ago (Craig 1968), the shoreline has been emerging as a result of isostatic uplift at an estimated rate of 0.5 to 1.2 cm/yr (Andrews 1973). The bedrock in the lowlands is Paleozoic in origin and consists primarily of limestone, dolomite, shale and sandstone (Glooschenko 1980). Permafrost is continuous in the Churchill region (Rouse *et al.* 1997) and in salt-marsh sites at La Pérouse Bay occurs at approximately 25-30 cm below the surface in mid-summer (Wilson 1993). The mineral soils of the lowlands are made up of marine silts, clays, washed tills and subglacial deposits from the post-glacial Tyrell sea (Glooschenko and Martini 1978, Riley 1982). The combination of generally impermeable sediment substrates, the slight slope of the land (0.5-1 metres per km in coastal areas) and the presence of beach ridges resulting from isostatic uplift, have provided suitable conditions for the formation of extensive wetlands (Riley 1982).

The physiography of La Pérouse Bay has been described in detail by Jefferies *et al.* (1979). La Pérouse Bay occurs where the Mast river forms a braided estuary as it enters Hudson Bay. Tidal and estuarine marshes have developed on the surrounding tidal flats and in the brackish waters of the delta, and are the breeding grounds for many migratory birds including lesser snow geese, Canada geese and a variety of shorebirds (Cooke *et al.* 1995, Rockwell *et al.* 1999). The topography of the land is flat with minor relief (< 2 m) resulting primarily from the frost-heaving of unconsolidated sediments in the estuary and open tidal flats. The delta contains numerous islands, 2-30 m in diameter, resulting from frost-heave. These islands influence the hydrology of the land surrounding the delta by impeding drainage, thus causing flooding, deepening of existing channels, and the cutting of new channels. The intertidal flats and the coastal marshes beyond the

limit of extreme tides are characterized by an inverse salinity gradient where high soil salinities have been recorded at the landward end of the continuum, as a consequence of impeded drainage (Glooschenko and Martini 1978, Jefferies *et al.* 1979, Price and Woo 1988a,b). Marshes in the lowlands receive fossil salt from underlying marine sediments deposited during the post-glacial Tyrell sea (Price and Woo 1988a,b). Microrelief occurs as a consequence of freeze-thaw phenomena, and ephemeral streams and ponds that develop following snow melt or heavy precipitation events. Foraging geese in the early spring accelerate the formation of ponds by grubbing at the roots and rhizomes of the vegetation on the pond edges thus damaging vegetation which leads to the enlarging of ponds the following season (Jefferies 1988a,b).

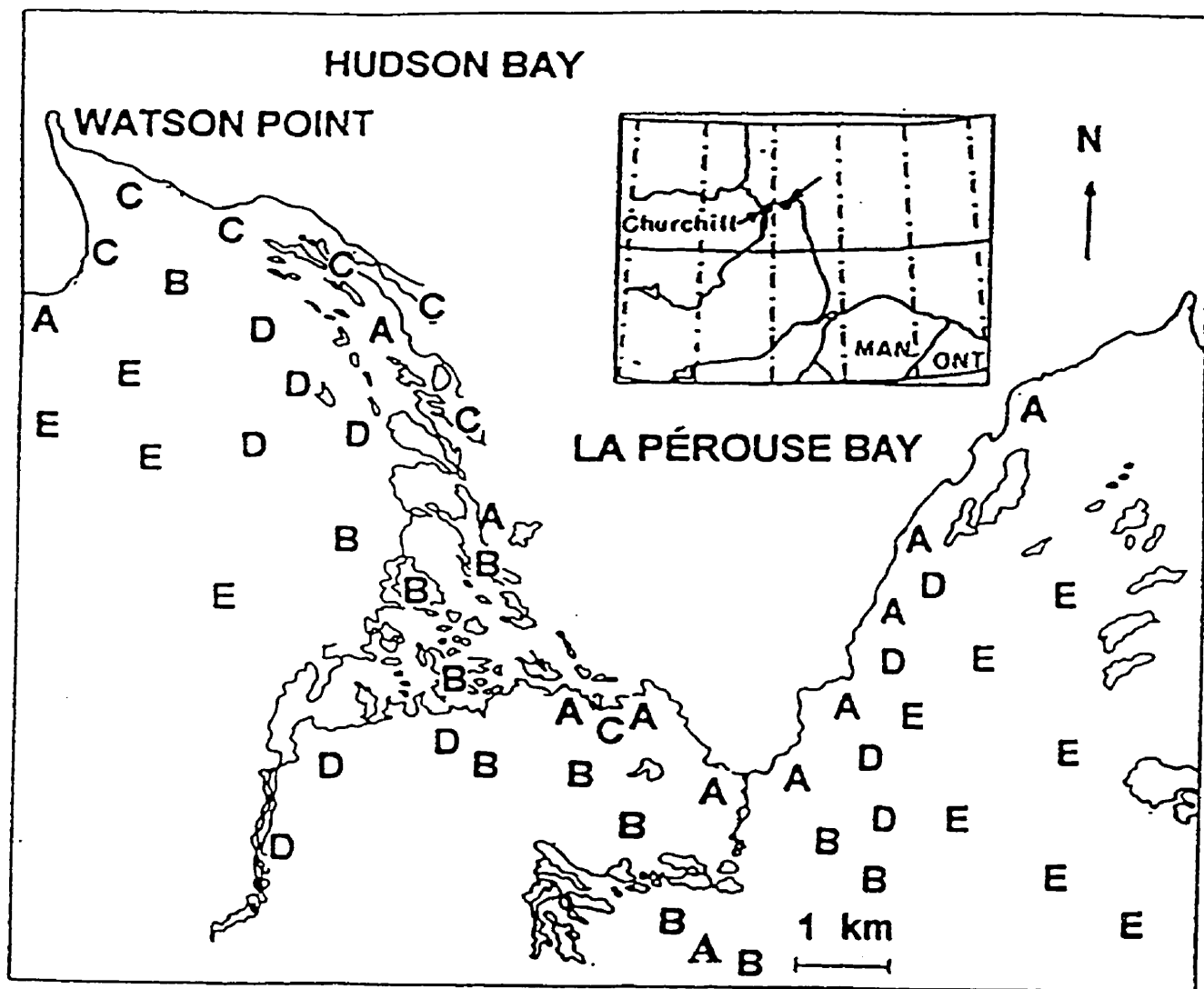
Snowmelt at La Pérouse Bay usually occurs sometime between May 15 and June 15 (Skinner *et al.* 1998) when the Arctic Front moves north, followed by a sharp rise in air temperature as it is replaced by a warmer continental air mass (Scott 1992). With the exception of the heat released by the freezing soils in early winter (end of October), the most significant energy fluxes in the Churchill region occur during the four months from early June to early October (Rouse *et al.* 1997). Although solar radiation is plentiful in April and May, net radiation is weak because of the high albedo of the snow (Rouse *et al.* 1997). The presence of Hudson Bay as an extension of the polar ocean, is a strong influence on the surface climate of the lowlands (Rouse *et al.* 1997). Ice cover remains on the Bay until the end of July (Danielson 1969). The resulting advective effects are pronounced, and the moist, cold characteristics of the overlying air can be carried up to 600 km inland creating cool conditions for approximately half the summer (Rouse 1991).

## 1.5 Vegetation description of La Pérouse Bay

Tidal salt-marshes occur on the flats on the east side of the Bay (Fig 1.1:A). In intact areas, the dominant graminoids are *Puccinellia phryganodes* (Trin) Scribn. & Merr., a stoloniferous grass, and *Carex subspathacea* Wormskj, a rhizomatous sedge<sup>1</sup>.

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<sup>1</sup> Nomenclature follows Porsild and Cody (1980).



**Figure 1.1** 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. Vegetation types are indicated as follows: A, intertidal or secondary salt-marshes dominated by *Puccinellia-Carex* swards; B, willow-grassland tundra; C, beach-ridge vegetation including *Leymus mollis*; D, high willows; E, fresh-water sedge meadows dominated by *Carex aquatilis*. Modified with permission from Jano *et al.* 1998.

Dicotyledenous plants present at low frequency include *Potentilla egedii* Wormsk., *Plantago maritima* L., *Ranunculus cymbalaria* Pursh., and *Stellaria humifusa* Rottb.. Salt marshes also occur on islands in the drainage channels and in the upper reaches of the estuary where drainage is impeded and marine sediments are exposed (Jefferies *et al.* 1979). In drainage channels, pools and in areas of high salinity along the periphery of the river system, where erosion of the thin veneer of organic matter has occurred exposing the underlying marine sediments, *Salicornia borealis* Wolff & Jeff., and *Triglochin palustris* L. grow in degraded *Puccinellia-Carex* swards.

Where the elevation is higher, in the upper levels of the intertidal salt-marsh or on the frost-heave hummocks, *Puccinellia-Carex* communities are replaced by a ground cover of two caespitose grasses, *Festuca rubra* L. and *Calamagrostis deschampsoides* Trin.. In addition, low lying willow bushes of *Salix brachycarpa* Nutt. and *Salix myrtifolia* Anderss. establish with time (Hik *et al.* 1992, Fig 1.1:B). Other graminoids that establish in these communities include *Leymus mollis* (Trin) Pilger, *Carex glareosa* Wahlen., and *Hierchlöe pauciflora* R. Br.. Associated dicotyledenous plants include *Chrysanthemum arcticum* L., *Potentilla egedii*, *Parnassia palustris* L., and *Stellaria longipes* Muhl. On the lower periphery of frost-heave hummocks, *Primula stricta* Hornem. and *Matricaria ambigua* (Ledeb.) Kryl. often grow in the presence of high densities of the moss *Bryum inclinatum*.

On the east side of the Bay, a high willow community (>3 m) (Fig. 1.1:D) dominated by *Salix candida* Flüg., *Salix planifolia* Pursh, *Salix lanata* L., and associated species, *Betula glandulosa* Michx., *Myrica gale* L. and *Empetrum nigrum* L. fringes the tidal flats. Within the willow assemblages and landward of them, extensive fresh-water sedge meadows dominated by *Carex aquatilis* L. occur in standing water and permanently saturated ground (Fig. 1.1:E). Smaller *Carex* species that grow in carpets of saturated moss (primarily *Drepanocladus* and *Aulacomnium* moss species) include *C. atrofusca* Schk., *C. capillaris* L., *C. x flavicans* Nyl., *C. microglochin* Wahlen., *C. rariflora* (Wahlen.) Sm., and *C. vaginata* Tausah (Kotanen and Jefferies 1997). *C. aquatilis* dominated communities are also found in standing water and saturated moss carpets on islands in the Mast river. Other species associated with such islands include *Eriophorum*

*angustifolium* Honck., *Dupontia fisheri* R. Br., *Petasites sagittatus* (Banks) A.Gray, *Cardamine pratensis* L. and *Potentilla palustris* (L.) Scop..

A beach ridge extends for about 3 km along the north-west coast of the Bay towards Watson Point. Formerly, extensive stands of *Leymus mollis* grew along the dunes on the ridge (Fig 1.1:C). Within the estuary, the initial colonizer of unconsolidated sediment is *Hippurus tetraphylla* L. f. (Jefferies *et al.* 1979). Other species that establish in the estuarine marsh, in a depth of standing water >10 cm (Srivastava 1993), include *Eleocharis acicularis* (L.) R. & S., *Myriophyllum exalbescens* Fern., *Ranunculus aquatilis* L., *Ranunculus purshii* Rich., and *Potamogeton filiformis* Pers.. In the subtidal regions seaward of the tidal and estuarine marshes, beds of *Zostera marina* L. grow.

## **1.6 Degradation of intertidal and freshwater coastal marshes in the Hudson Bay lowlands**

The mid-continent lesser snow goose population breeds in the coastal areas of the Hudson Bay lowlands with colonies scattered from Moosonee, north to Southampton Island and to south-western Baffin Island. Since the mid-1970s, the entire wintering population has nearly doubled, increasing exponentially at a steady rate of 7% per annum to almost 4.5 million birds by 1996 (Abraham *et al.* 1996). The size of the colony at La Pérouse Bay has increased concurrently from 1300 breeding pairs in 1968 (Cooke *et al.* 1995) to an estimated 45 000 breeding pairs in 1997 (K.F. Abraham, R.F. Rockwell and K. Ross, unpublished aerial survey). Agricultural intensification this century has had strong biological consequences through the alteration of patterns in resource availability (Matson *et al.* 1997). The snow goose population increase is attributed primarily to the high quality, agricultural food subsidy (crops such as rice and corn) that is available to the geese during the winter and migration periods (Abraham *et al.* 1996). Other factors thought to contribute to the population growth include increased refugia along the Central and Mississippi flyway routes, reduced harvest rates, and climate amelioration of early springs, leading to a greater reproductive success, and a southern shift of the nesting range (Francis *et al.* 1992, Abraham *et al.* 1996).



Coupled biotic and abiotic threshold responses resulting from intense activity by the geese have resulted in habitat degradation visible at the landscape level throughout the breeding grounds (Jano *et al.* 1998). The mechanism of degradation (described below) is a consequence of grubbing (Jefferies 1988a,b), shoot pulling of forage plants (Kerbes *et al.* 1990, Kotanen and Jefferies 1997) and heavy grazing pressure (Srivastava and Jefferies 1996, 1995a), which, in turn, have led to a self-amplifying positive feedback, destroying existing plant communities and prompting a terrestrial trophic cascade (*sensu* Carpenter *et al.* 1985; Bazely and Jefferies 1996). The loss of ecosystem “health” in these areas is evident through decreases in the rates of net primary production and nutrient cycling, and in the loss of species diversity (Jefferies 1997). Total nitrogen, exchangeable nitrogen and net mineralization rates are significantly reduced in degraded sites (Wilson and Jefferies 1996). Studies also show a reduction in the community diversity of plants (Srivastava 1993), invertebrates (Milakovic 1998) and shorebirds that breed in the area (Rockwell *et al.* 1999). Multitemporal analysis of LANDSAT data shows that the extent of habitat degradation at La Pérouse Bay currently exceeds 2500 ha (Jano *et al.* 1998).

Degradation mechanisms are as follows. In the early spring, immediately after snow-melt, staging and breeding geese grub for roots and rhizomes of graminoid plants in the intertidal salt-marsh creating patches of damaged vegetation that increase in circumference each season (Jefferies 1988a,b, Kerbes *et al.* 1990). When grubbing occurs proximal to the willow community, the removal of the insulating mat of plant litter and ground vegetation results in increased thermal gradients in the soil, a substantial increase in soil salinity as the summer progresses, and the subsequent death of the salt-sensitive willow stands (Iacobelli and Jefferies 1991). On dunes and in the fresh-water sedge meadows, geese pull up graminoid shoots before their new growth begins (Jefferies 1988a,b). Typical of arctic herbivores exploiting nutrient pulses in space and time (Jefferies *et al.* 1994), the geese in early spring consume the swollen bases of the shoots, rich in soluble carbohydrates and total nitrogen (Gadallah and Jefferies 1995), and discard the remainder (Kerbes *et al.* 1990, Kotanen and Jefferies 1997). The intensive shoot-pulling has led to the death of the majority of the *Leymus mollis* stands along the beach

ridge (Ganter *et al.* 1996, Jefferies 1997). In the fresh-water sedge meadows, the dead *C. aquatilis* stands have been replaced by extensive moss carpets in which seedlings do not appear to re-establish (Kotanen and Jefferies 1997). Such moss carpets have been observed at the McConnell River snow goose colony on west Hudson Bay (Kerbes *et al.* 1990) and in the High Arctic, at the greater snow goose colony on Bylot Island (Gauthier *et al.* 1996). As the season progresses, the moss carpets can dry out, break and blow away leaving exposed peat barrens.

On average, geese at the La Pérouse Bay colony initiate nesting on May 29 and the goslings hatch on June 23 (Skinner *et al.* 1998). Following hatch, the grazing pressure exerted on the system is substantial; goslings grow from about 80 g at hatch to 1500 g in less than 8 weeks, and adults regain up to 40% of their body weight lost during brood rearing (Cooke *et al.* 1995). In the salt-marsh, *P. phryganodes* and *C. subspathacea* are the preferred forage of the geese, in part, because of their high nutritive quality (Gadallah and Jefferies 1995). Both plants are tolerant of grazing due to their basal meristem and both plants produce new leaves continuously throughout the season (Kotanen and Jefferies 1987, Bazely and Jefferies 1989a). However, when grazing pressure is heavy, the reduced vegetation cover leads to increased soil evaporation rates (Srivastava and Jefferies 1995a). The increase in evaporation draws inorganic salts from the underlying marine sediments to the surface layers of the soil rooting zone, subsequently killing the dominant salt-marsh plants as a result of hypersalinization (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1995b). The death of plants in hypersaline patches further reduces graminoid biomass thus prompting a self-amplifying, positive feedback coupled with secondary feedbacks (Srivastava and Jefferies 1996). In the former intertidal marsh on the east shore of La Pérouse Bay, the result has been the transformation of intact salt-marsh swards into extensive bare mudflats devoid of vegetation. In the former inland marshes and on the upper levels of the intertidal marshes, *Salicornia borealis* and *Atriplex patula* var. *hastata* L., annual halophytes, which are not eaten by the geese have colonized the mudflats, but no recolonization by the former vegetation has been observed.

## 1.7 Issues in a revegetation scheme for La Pérouse Bay

Soil aging or maturation processes (“soil ripening” *sensu* Pons and Zonneveld 1965) occurs together with species replacement in the natural successional sequence within coastal salt-marshes (Packham and Willis 1997). The degradation in both the salt-marsh and the fresh-water sedge meadows at La Pérouse Bay, presents a discontinuity in the natural successional sequence of these habitats; the soil has matured to a particular state despite the fact that the vegetation has been completely removed. Consequently, the desired goal of the assisted revegetation trials was to re-establish the dominant, native vegetation that existed in the soils prior to degradation, while taking into account the hypersaline condition of the soil. In the salt-marsh, destruction has occurred in the *Puccinellia-Carex* swards (Srivastava and Jefferies 1996), as well as in the *Festuca-Calamagrostis* communities (Iacobelli and Jefferies 1991). Both *P. phryganodes* and *C. subspathacea* are capable of withstanding intermediate levels of salt stress (Srivastava and Jefferies 1995b). However, *Festuca-Calamagrostis* communities are generally restricted to soils at a higher elevation and which have a greater organic content, but less salt content than soils at a lower elevation. It was assumed that *F. rubra* and *C. deschampsoides* could not establish directly in the degraded soil given their lower salt tolerance (this assumption was tested and is discussed in Chapter 6). Based on the successional sequence observed on the east shore of La Pérouse Bay by Hik *et al.* (1992), it was also assumed that within the areas that *Festuca-Calamagrostis* communities could potentially occur, a *Puccinellia-Carex* template would be necessary for their establishment. *P. phryganodes* and *C. subspathacea* were selected for revegetation trials in this study as the dominant representatives of the salt-marsh community. In the degraded fresh-water sedge meadows, *C. aquatilis* was selected as the target species as it was a former dominant within the system (Kotanen and Jefferies 1997).

Given this choice of species and the prevalent issues discussed above in arctic revegetation schemes, the following topics were examined in this study:

- (1) In the absence of goose grazing, can *P. phryganodes* and *C. subspathacea*, the native dominant graminoids, re-establish in degraded salt-marsh sites; and if so, to what

extent can amelioration treatments of fertilizer and/or organic mulch enhance the establishment process (Chapter 2)?

- (2) How is the microclimate within the soil environment altered by organic mulch treatments and what is the effect of such alterations on the establishment of *P. phryganodes* (Chapter 3)?
- (3) How do differences in climate between the growing seasons of 1996 and 1997 influence the establishment of *P. phryganodes* (Chapter 3)?
- (4) In the absence of goose grazing, how do growth rates of *P. phryganodes* in assisted revegetation trials compare to those in natural revegetation trials (Chapter 4)?
- (5) In the absence of goose grazing, can tillers of *C. aquatilis* re-establish in moss carpets; can fertilizer applied to the moss carpet surface be taken up by *C. aquatilis*, and if so, to what extent does fertilization enhance the establishment process (Chapter 5)?
- (6) Can patterns of successional vegetation change be detected in the presence and absence of goose grazing from 1986-1997 (Chapter 6)?

Based on the results, the potential for revegetation in La Pérouse Bay coastal habitats is discussed (Chapter 7).

## CHAPTER 2: ASSISTED REVEGETATION TRIALS IN THE SALT-MARSH AT LA PÉROUSE BAY

### 2.1 Introduction

The objective of the assisted revegetation trials was to examine whether the two dominant salt-marsh graminoids, *P. phryganodes* and *C. subspathacea*, could re-establish in degraded salt-marsh soils if (a) immigration into the soils was assisted and if (b) the soil environment was ameliorated to assist establishment. Immigration was assisted by the transplanting of small sod cores (plugs) taken from an intact donor site. Plant establishment was assisted by soil amelioration treatments that included the application of fertilizer and/or peat mulch (see review of general techniques in arctic revegetation schemes in Section 1.6, description of specific methodology in Section 2.2.1). The rationale for selecting this approach to assist both plant immigration and establishment was based on prior knowledge of the system at La Pérouse Bay, as outlined below.

#### 2.1.1 Immigration of graminoids into degraded sites

The reproductive biology of *P. phryganodes* and *C. subspathacea* is such that immigration of plants of these graminoid species could be assisted only through vegetative means. Both species flower infrequently at La Pérouse Bay (Jefferies and Gottlieb 1983, Chou *et al.* 1992). *P. phryganodes* is recognized as a sterile triploid in North America (Bowden 1961), which has been confirmed at La Pérouse Bay (Sadul 1987), and seed set has never been observed (Jefferies and Gottlieb 1983). Seed set by *C. subspathacea* has been reported at other arctic sites (Polunin 1959), but not in mixed *Puccinellia-Carex* swards or swards dominated by *C. subspathacea* at La Pérouse Bay because of heavy grazing of inflorescences (Chou *et al.* 1992). Both species form extensive swards that result from asexual reproduction (stoloniferous growth in *P. phryganodes* and rhizomatous growth in *C. subspathacea*). Both species can also establish from single leaves and other plant fragments generated by goose grazing (Chou *et al.* 1992). Chou *et al.* (1992) have suggested that the random assortment of these plant fragments, in addition to an increase in the number of microsites available for

recolonization as a result of goose foraging activity, may account for the high levels of genetic variability observed in populations of *P. phryganodes* at La Pérouse Bay (Jefferies and Gottlieb 1983). The selection of sod transplants as an immigration assistance technique was largely influenced by these reproductive constraints.

### **2.1.2 Issues of soil degradation at La Pérouse Bay**

Dobson *et al.* (1997) argue that restoration of an ecosystem should be possible because primary succession is possible; an ecosystem can develop over time where no previous soil exists. However in the case of degradation, soil from the previous vegetation state exists, and the properties of the existing degraded soil environment must be understood, so that restoration schemes, when based on a suitable choice of plant species, can be successful (Bradshaw 1997b). Approaches for dealing with degraded soil include soil remediation prior to revegetation, or the selection of stress-tolerant species that can establish, grow and reproduce in a seemingly inhospitable environment (Good *et al.* 1985).

One of the most significant changes to the abiotic environment in the degraded salt-marshes of La Pérouse Bay is the hypersalinity of the soil (Srivastava and Jefferies 1996). Hypersaline soils in degraded agricultural lands have been remediated through the application of sufficient water to leach and flush salts (Oster *et al.* 1996). When soils are sodic (exchangeable sodium >15%), reclamation through equilibrations with successive dilutions of saline water (Reeve and Bower 1960, Reeve and Doering 1966), or the application of gypsum (Keren 1996), can be used so that the exchangeable sodium is replaced by a less harmful cation, such as calcium. However, such reclamation efforts require irrigation, drainage and a place for salt disposal, and can have the significant environmental consequence of making the soil better in one place while exhausting soil and water resources elsewhere (Oster *et al.* 1996). In Alaska, remediation attempts as a result of the application of a calcium nitrate solution to saline soil (caused by seepage from the oil drilling level) were entirely ineffective (McKendrick 1997). Because of the complicated infrastructure needed for reclaiming hypersaline soil, and the risk of remediation attempts being ineffective, the transplanting of soils from intact swards as

part of the sod core, was a more practical strategy in dealing with the hypersalinity of the soils.

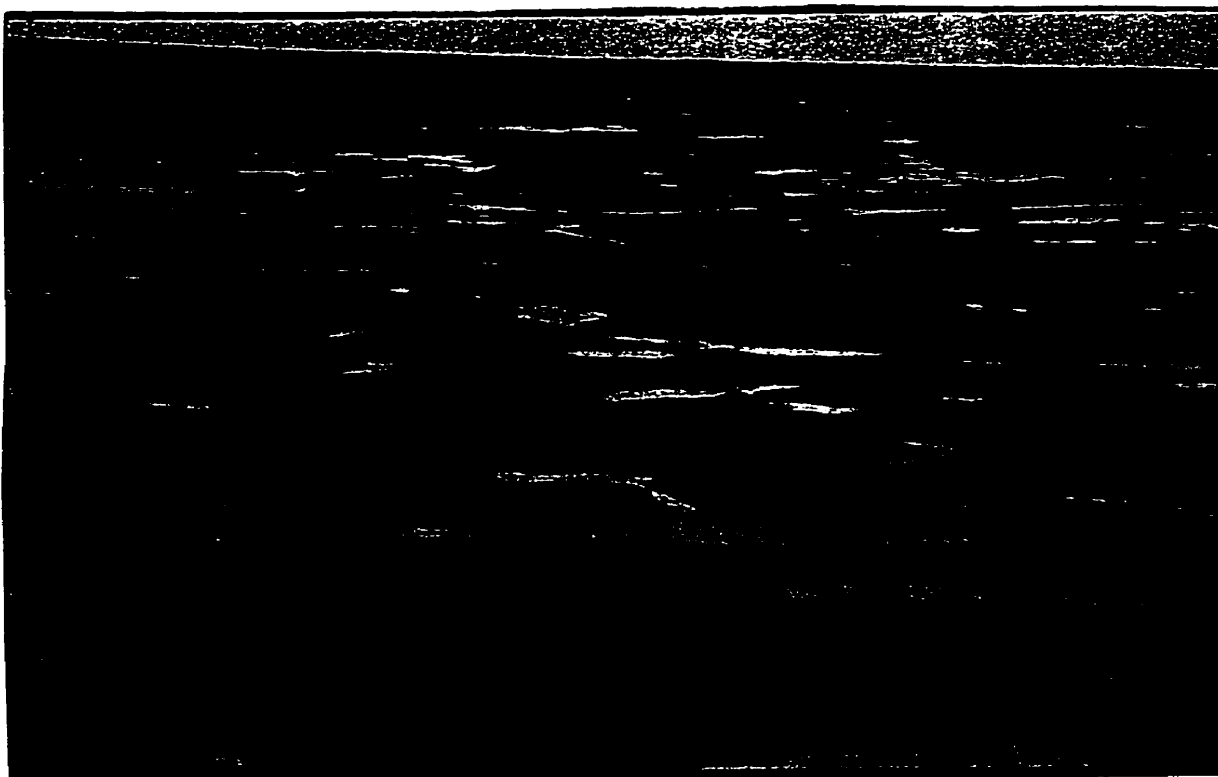
The reduced nutrient cycling rates in degraded sites, that are evident as reduced levels of total nitrogen, exchangeable nitrogen and net mineralization rates, indicate another aspect of soil degradation at La Pérouse Bay (Wilson and Jefferies 1996). Furthermore, Cargill and Jefferies (1984) have shown that exchangeable and soluble inorganic nitrogen is limiting to net primary production of *Puccinellia-Carex* swards at La Pérouse Bay. These results both made the addition of fertilizer a logical choice as an amelioration treatment to the soil environment. Another consequence of the degradation in the intertidal marsh, is the loss of the thin veneer of organic soil that exists at the surface layer of the profile. Since the lack of sufficient organic matter can slow the vegetational recovery process (Cargill and Chapin 1987), the application of a layer of organic mulch at the soil surface was chosen as a second amelioration treatment. Peat mulch on the soil surface increases water infiltration (which is reduced by hypersaline conditions; Ungar 1996), decreases the surface albedo, and provides insulation, thereby raising soil temperatures (Rosenberg *et al.* 1983, Oke 1995).

## 2.2 Methods

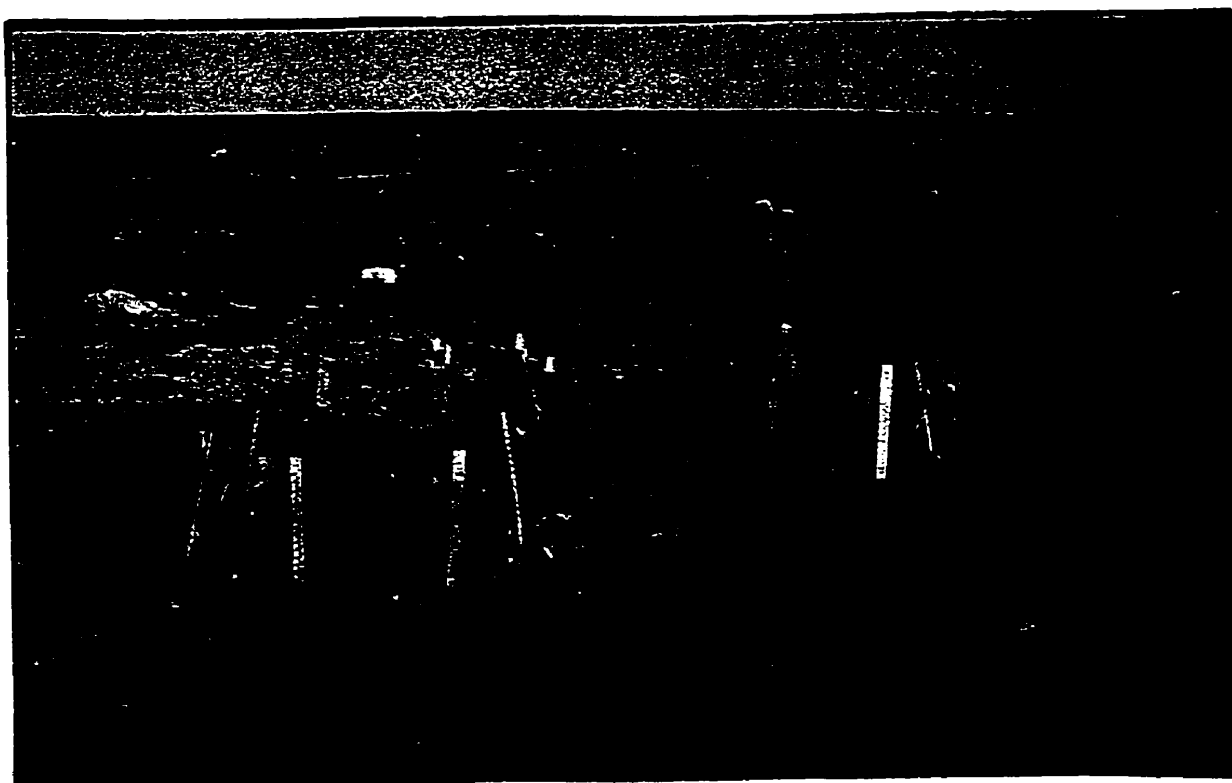
### 2.2.1 Experimental Design

In order to control adequately for the transplanting factor within experiments, it was necessary to select sites where both intact and degraded patches were present in close proximity to one another. Sites that met this requirement were extremely limited. Experimental plots were established where partial degradation has led to a fragmented vegetational mosaic at a scale of a few metres or less (Fig. 2.1a,b; see Srivastava and Jefferies 1995a for discussion of mosaics). Sites were selected so that the graminoid transplanted was the dominant plant in the remnant sward of intact patches. *P. phryganodes* has a higher salinity tolerance than *C. subspathacea* (Srivastava and Jefferies 1995b). Consequently, it is typically the dominant species in intertidal areas. Three sites on the east shore of La Pérouse Bay, separated by a distance of 75-100 m,

a)

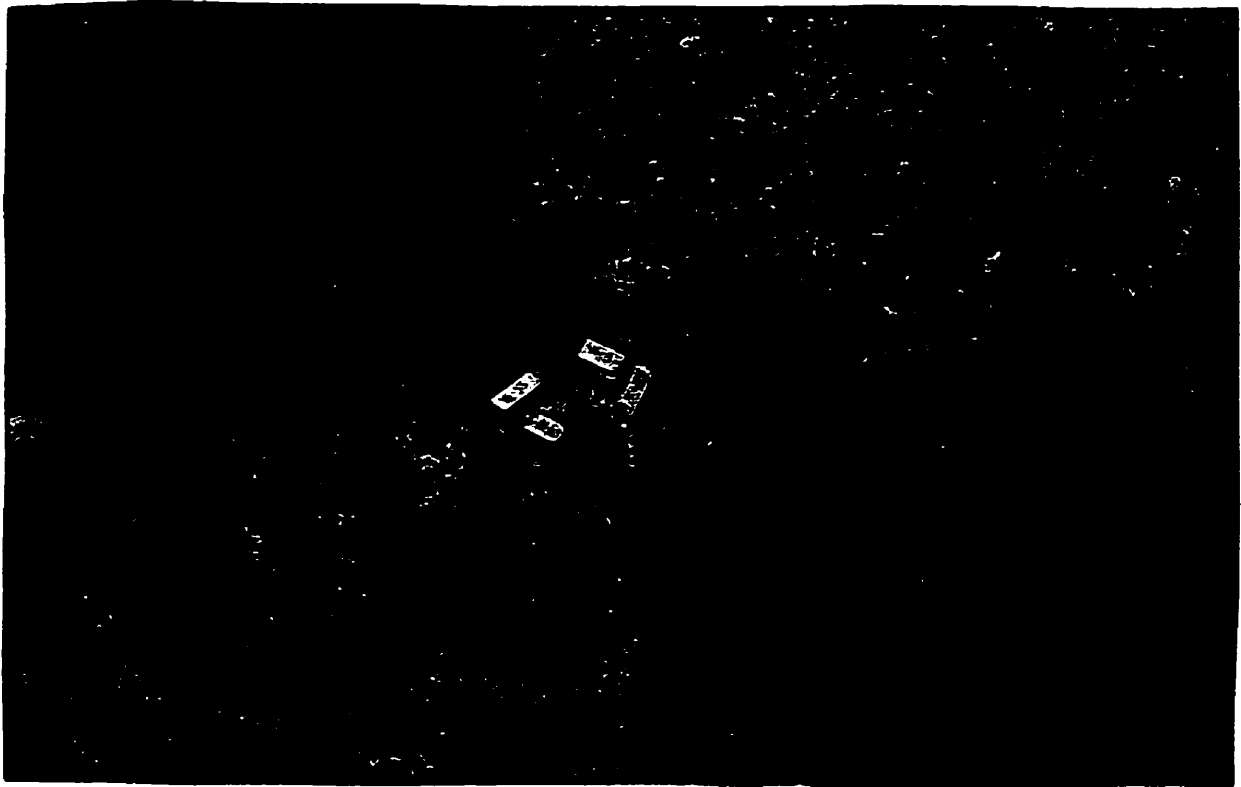


b)





c)



**Figure 2.1** Photographs taken of the assisted revegetation trials in the intertidal marsh on the east shore of La Pérouse Bay. Photographs depict (a) the landscape mosaic of intact and degraded patches, (b) a pair of 1 m x 1 m exclosures with transplants of *Puccinellia phryganodes* erected on a degraded patch (left) and an intact patch (right), and (c) circular plugs of *P. phryganodes* and the four treatment plots; fertilizer and mulch addition (top left), no addition (top right), fertilizer addition (bottom left) and mulch addition (bottom right). The cyanobacteria crust on the soil surface is evident in the bare and fertilizer addition treatments.

were selected for the transplant trials of *P. phryganodes*. *C. subspathacea* tends to be abundant further inland, or where there is some fresh-water input from small streams flowing onto the intertidal marsh. The three study sites selected for *C. subspathacea* were in a supratidal marsh, 3 km inland from the coast.

At each of the three sites in both the intertidal and supratidal marshes, each of four replicated pairs of 1 m x 1 m exclosures were erected at approximately 15-20 m distance. Each pair consisted of an exclosure on a degraded patch proximal (<5 m) to one on an intact patch (Fig. 2.1b). Degraded patches were chosen where an undisturbed cyanobacteria crust occurred (Fig. 2.1c). Some species of cyanobacteria have been shown to be important nitrogen fixers in arctic systems (Getsen *et al.* 1997), and the inclusion of nitrogen fixers within revegetation schemes has been encouraged by a number of authors (Skeffington and Bradshaw 1980, Perry and Amaranthus 1990, St. John 1990). At La Pérouse Bay, the cyanobacteria typically colonize bare sediments on the mudflats (Bazely and Jefferies 1989b), particularly in the early spring directly after snowmelt, and form a continuous algal crust (1-2 mm) on the sediment surface (Wilson 1993, Srivastava 1993). As the summer progresses, however, the crust dried out, blisters and cracks, and is carried away by the wind, thus arresting succession on degraded sediments.

Care was taken to choose patches at roughly equal elevation and on level ground so as to control for differences in snowmelt and water drainage, but patches were still subject to considerable spatial and temporal variability (e.g. microscale differences in relief, thermal regime, moisture content, salinity, redox potential) both within and among patches. In choosing intact patches, swards with a heavy presence of moss (mostly *Bryum inclinatum*) were avoided as they often indicated the early stages of habitat deterioration (Jefferies 1988a,b). The inland marsh, where the *C. subspathacea* plots were located, was in a substantially more advanced state of degradation and selected sites were only separated by 25-50 m.

Transplant material was cored from a single intact patch (5 m x 5 m) in order to minimize genotypic variation (Jefferies and Gottlieb 1983). Each cored plug, which included both plant and soil material, was 22 mm in diameter x 40 mm in depth, and typically consisted of 3-5 tillers of *P. phryganodes* or *C. subspathacea*. The rooting zone

for these graminoids was in the top 5 cm of the soil (Wilson 1993). Each treatment plot was planted with 42 plugs (7 columns x 6 rows), and each plug was separated from adjacent plugs by 7 cm. The 22 plugs on the perimeter in each treatment plot acted as a buffer zone. The remaining 20 plugs which occurred in the inner 5 x 4 matrix were designated as experimental plants to be scored for rates of growth and senescence during the season. Plugs of *P. phryganodes* and *C. subspathacea* were planted on June 17-21, 1996 and June 25-28, 1996 respectively.

Five treatments were applied to each replicated enclosure pair. The intact treatment involved transplanting plugs into exclosed intact swards to ensure that the transplanting itself did not cause death of plants. Each enclosure in a degraded area was subdivided into four plots and each plot was randomly assigned one of the following treatments: (1) bare (no amelioration), to see if plants could survive in the degraded edaphic conditions, and to provide a control in order to compare the effect of amelioration in treatment plots, (2) nitrogen and phosphorus fertilizer addition, (3) peat mulch addition and (4) a combination of nitrogen and phosphorus fertilizer and peat mulch additions (Fig. 2.1c). Fertilizer was sprinkled evenly across the plots as inorganic salts based on amounts used in agriculture ( $40.20 \text{ g of NH}_4\text{Cl/ m}^2$  and  $22.32 \text{ g of NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O/ m}^2$ ) that previously have been demonstrated to enhance the growth of these and other halophytes (Jefferies and Perkins 1977, Cargill and Jefferies 1984). The peat mulch consisted of fully decomposed surface organic material that was excavated from under *Salix* bushes growing on frost-heave hummocks in the supratidal marsh (inundated with tidal water once every 2-3 years). All living moss, large roots and rhizomes were removed from the mulch and a 5 mm layer was applied uniformly on a treatment plot.

### **2.2.2 Monitoring of above-ground biomass**

Following the establishment of both experiments (i.e. the *Puccinellia* and *Carex* transplants), plants were monitored for growth, senescence and death in order to assess the effect of the amelioration treatments during the growing seasons of 1996 and 1997. The above-ground biomass of plugs of *P. phryganodes* was scored on July 11, 20, 29,

1996 and June 25, July 6, 17, 29 and August 12, 1997. Similarly, plugs of *C. subspathacea* were scored on July 10, 19, 28, 1996 and June 26, July 10, July 23, August 2 and 13, 1997.

Senescence of plants was included as part of the above-ground monitoring, in order to detect any adverse effects associated with transplanting in the early stage of the experiments. It was possible that there might have been a time delay before shoots of the transplanted plugs began to grow and that some leaf senescence might have been associated with the effects of transplanting. The senescence and death of the plants were scored as an index of “greenery” (0-5) based on shoot appearance within each plug. Categories followed a scale whereby 0= death, 1= a yellow appearance with faint traces of green, 2= a yellow appearance with 1-2 shoots entirely green, 3= a mixed yellow-green appearance with 2-3 shoots entirely green, 4= a green appearance with 4-7 shoots entirely green, only faint traces of yellow and 5= a green appearance with 8 or more shoots entirely green. For the purpose of analysis, categories were pooled, such that plants were considered “yellow” in categories 1 and 2, “yellow-green” in category 3 and “green” in categories 4 and 5.

Plant growth was measured by monitoring the radial extension of shoots from the plug “circle” (Fig. 2.1c). On the first two scoring events in 1996 (July 10, 11, 19 and 20), eight of the twenty plugs in each plot were randomly subsampled and five length measurements were made which included the length of the longest shoot (measured from plug centre to shoot tip) and four measurements from the plug centre along the cardinal axes from which a mean was calculated to estimate average radial growth. By July 28, this scoring technique was no longer satisfactory as it became clear that plant growth involved both “guerilla” and “phalanx” growth strategies (Lovett Doust 1981). In order to incorporate the degree of infilling (phalanx growth) into the growth estimates of the tillers, the basal area of growth was measured based on a system of concentric circles which extended outwards at increments of 11 mm. For each plug, the mean radial extension (to the nearest 11 mm), the length of the longest shoot (to the nearest 11 mm) and a percent cover (within the mean radial extension circle) were estimated visually. Basal area of plant growth (A) was calculated by using the formula  $A = (\% \text{ cover}) * \pi r^2$ ,

where  $r$  = the radius of the mean radial extension circle. This technique was used to measure the twenty plugs for each treatment on July 28, 29 and all sampling dates in 1997. For analyses purposes, radial growth measurements from July 10, 11, 19 and 20, 1996 were rounded to the nearest 1 mm and compared to those made on July 28 and 29, 1996.

In order to support the subjective measurements of basal area of plants with a more objective measurement of above-ground primary production, all living above-ground biomass was quantified on June 21, July 19 and August 10, 1997 (*P. phryganodes*) and June 27, July 24 and August 15, 1997 (*C. subspathacea*). Turves (12 cm x 4 cm), that contained two established plugs, were collected from the buffer zone of all treatment plots in three of the four exclosures at each site. The above-ground biomass from these turves was clipped into standing water to remove dirt and dead biomass, dried at 50°C for one week and then weighed on a Mettler analytical balance to the nearest milligram.

### **2.2.3 Monitoring of environmental variables**

In addition to measuring plant responses, soil variables were monitored carefully, in order to see if establishment and growth of plants could be affected by differences in the soil environment. In June 1996, a 40 cm x 60 cm plot of each of the bare, mulched and intact vegetation treatments was established adjacent to nine of the twelve paired exclosure replicates, in order to monitor the edaphic environment at both the intertidal and supratidal sites ("edaphic plots"). Bare and mulch plots were established 2 m or more away from each exclosure in the degraded site. Plots also were established inside each exclosure in which the sward was intact; these plots were adjacent to the treatment plots. Soil samples were collected by cutting blocks (10 cm x 5 cm x 5cm) within each of these plots. In 1997, in addition to the samples taken outside of the treatment exclosures, samples were also taken from inside three of the four treatment exclosures at each site as well as from intact swards. These samples were collected from the edges of the buffer zone, in order to avoid destruction to the transplanted plants present in the inner matrix.

Plots at the intertidal marsh were sampled in 1996 on July 3 (bare and mulch treatments only), July 11, 20, and 29 (bare, mulch and intact vegetation treatments). In 1997, intertidal plots were sampled on June 21, 1997 (within exclosure treatments: i.e. bare, +N/P, +mulch, +N/P+mulch plots and plots with intact vegetation), July 7 (permanent edaphic plots: i.e. bare and mulch treatment plots and plots with intact vegetation), and July 19 and August 10 (all plots, both within exclosure treatment plots and adjacent edaphic plots). In 1996, salinity, gravimetric soil moisture content and redox potential were measured on all dates given above, and, in addition, total soil carbon and nitrogen were measured on July 22. In 1997, salinity measurements were made on all dates listed above, and, gravimetric soil water content was measured on July 7 and August 10, and soil redox potential was measured on July 7 and 19.

Plots at the inland marsh were sampled in 1996 on July 3 (bare and mulch treatments only), July 10, 19, and 28 (bare, mulch and intact vegetation treatments). In 1997, inland plots were sampled on June 27 (within exclosure treatments: i.e. bare, +N/P, +mulch, +N/P+mulch plots and the intact vegetation plot), July 10 (permanent edaphic plots: i.e. bare, mulch and intact vegetation plots), and July 24 and August 15 (all plots, both within exclosure treatment plots and adjacent edaphic plots). In 1996, salinity, gravimetric soil moisture content and soil redox potential were measured on all dates and total soil carbon and nitrogen were measured on July 19. In 1997, salinity measurements were made on all dates. Gravimetric soil water content was measured on July 10, 24 and August 15, and soil redox potential was measured on July 10, 24 and August 15.

The soil profile was described for each soil block down to a depth of 4 cm. A soil sample of known dimensions was weighed, dried at 50° C for five days, and re-weighed in order to calculate the bulk density (expressed as grams of dry soil per cm<sup>3</sup> of wet soil). Bulk density was calculated for soil depths at both 0-2 cm and 2-4 cm. Gravimetric soil water content was determined by the same drying procedure based on approximately 10 g of fresh soil taken from the top 2 cm of the soil profile. Water content was expressed as grams of water (calculated as the difference between fresh and dry weights) per gram of dry soil. Redox potential ( $E_h$  values) of a freshly cut soil surface was measured with a platinum electrode (Ag/AgCl reference) and a portable Fisher meter. The meter was

calibrated with ZoBell's solution (0.003 M potassium ferricyanide, 0.003 M potassium ferrocyanide and 0.1 M potassium chloride) which has an  $E_h$  value of +430 mV at 25 °C (Howes *et al.* 1981). Because redox values varied over distances less than 1 cm, a series of values were obtained ( $n=10$ ) by inserting the electrode perpendicular to the soil surface and the range of values was recorded. In 1996, measurements were taken in the top 4 cm of a soil block. In 1997, measurements were taken at a depth of 0-2 cm and 2-4 cm.

Water for salinity determination was extracted from the top 4 cm of soil. On dates when it was possible, soil water was extracted by squeezing the soil. However, when soils became too dry, soil was pressed into 5 ml syringe casings, which in turn were placed in 20 ml centrifuge tubes, and centrifuged for 5 minutes at 7000 x g. Salinities of soil water extracted by different techniques have been shown to be similar (Srivastava and Jefferies 1995a). On the first two dates in 1996, salinity of the soil solution was measured with the use of a portable Yellow Springs salinity meter. On the last date in 1996 and on all dates in 1997, soil water was frozen and later analyzed for its sodium content with the use of a Perkin-Elmer atomic absorption spectrophotometer (model 3110, Rexdale, Ontario, Canada) in flame-emission mode. Standard sodium chloride solutions were used to calibrate the instrument, samples were diluted to fall within the range of 0.2-1.0 mg/L, and repeated measures on the same samples were taken to ensure that the error was less than 2 %. Sodium concentration in soil solutions has been shown previously to stay in fairly constant proportion to all other dissolved ions in samples at La Pérouse Bay, thus it made the results a reasonable index of soil salinity (Srivastava 1993, Srivastava and Jefferies 1995a). Salinity measurements that were made on the first two dates in 1996 were converted to sodium concentration based on a linear regression model of salinity versus sodium concentration ( $r^2=0.96$ ) developed by Srivastava (1993).

In 1996, dried soil samples were transported to the University of Toronto to determine the proportions of sand, silt and clay, as well as total carbon, total nitrogen and the C:N ratio at all sites. Proportions of sand, silt and clay were measured using the hydrometer method of particle size distribution (Sheldrick and Wang 1993). Only soils from the intertidal marsh were analysed, as inland soils were predominantly organic. Total amounts of soil carbon and nitrogen were determined with the use of a LECO

Series 600 CHN analyzer (St. Joseph, Missouri, U.S.A.) and amounts of these elements expressed as percent of dry weight of soil.

Soil surface temperatures and evaporation of bare, mulch and intact treatments were measured at intertidal sites. Temperature was measured in bare, mulch and intact plots on July 19 and August 17, 1997 with the use of a fine thermistor wire inserted in soil to a depth of 0.5 cm and attached to a precalibrated voltmeter. Relative soil surface evaporation was measured in bare, mulch and intact plots on June 20, July 7 and July 18, 1997 by sinking 1.5 ml microcentrifuge tubes (39 mm long, 9 mm diameter at the top tapering to 5 mm diameter at the bottom) filled with de-ionized water into the soil surface for 24 hours (the trial on July 7, 1997 was prolonged to 67 hours due to logistical difficulties). Tubes were weighed before and after the trial, and evaporation was expressed as the percent of evaporated water. The technique is unlikely to give an accurate measurement of actual rates of evaporation, because of the edge effect of the tube. Nevertheless, as a relative index of evaporation, the technique allows for a comparison of soil surface evaporation in the different treatments.

The elevation of all the exclosures, relative to a Department of National Defense benchmark (set to an arbitrary zero), was determined using a quick-set level and surveying staff.

#### **2.2.4 Statistical Methods**

Analyses of estimates of the above-ground growth of plugs, plant senescence and plant death were analyzed using the S-PLUS statistical software (Mathsoft Inc., version 3.3, 1995). Estimates of the above-ground growth of plugs were analyzed by analysis of variance techniques based on a mixed model split-plot factorial design (Kirk 1982) with site, and exclosure nested within site, crossed with treatment. Treatment was defined as a fixed factor, while site and exclosure were defined as random factors. A mean for each plot was calculated based on the values recorded for the living ( $n \leq 20$ ) plugs within the plot in order to avoid pseudoreplication (Hurlbert 1984). Data of plant death and senescence were analyzed by the use of a general linear model (McCullagh and Nelder 1983) in which treatment and site were incorporated as factors. The models were



generated with a binomial “family” specification and subsequently tested for significance with a chi-square test that used a likelihood ratio argument (Venables and Ripley 1997).

Environmental data were analyzed with the MINITAB statistical software (Minitab Inc., version 10.2, 1994) based on a mixed model two-factor ANOVA (Kirk 1982) for treatment (fixed) crossed by site (random). “Exclosure” was not treated as a factor in the environmental analyses because the edaphic samples were not as spatially concentrated as the above-ground growth measurements that were taken from within a 1 m<sup>2</sup> area. For the soil redox data of 1997 at both the intertidal and supratidal marshes, the midpoint of the recorded range was used for the analysis. The redox data from the intertidal marsh in 1996 were not amenable to ANOVA techniques because of unequal variances and non-parametric distributions. Although Kruskal-Wallis tests also assume equal variances (Underwood 1997), they were used as a non-parametric alternative to analyze the redox data collected on each date at all three sites (test statistic = H). Although all experiments were originally established with a balanced design, difficulty in extracting soil water from samples, as well as sodium contamination led to the loss of some replicates. In such cases, a general linear model, in which equal importance was assigned to each treatment mean, was used (Neter *et al.* 1990).

Homogeneity of variance for all analysis of variance tests was verified ( $p > 0.05$ ) based on Bartlett’s test statistic for normal data (Zar 1984) and Levene’s test statistic for data with slight deviations from normality (MINITAB reference manual, 1994). Slight deviations from normality were tolerated as analysis of variance techniques are robust to such deviations (Underwood 1997). Some transformations were necessary to correct for heteroscedasticity. Data of gravimetric soil water content at the intertidal marsh in 1996, and soil sodium contents in 1996 and 1997, at both intertidal and supratidal marshes, were transformed by taking the natural logarithm. Data of above-ground biomass from the intertidal marsh and basal area of plants for the supratidal marsh were transformed by taking the square-root of values. Unplanned pairwise comparisons for testing differences among means were done based on Tukey’s contrasts (controlling for experiment-wise error) with appropriate modifications for the design in question (Kirk 1982).

### 2.3 Growth of transplants of *Puccinellia phryganodes* in the intertidal marsh

In order to facilitate the reading of the detailed results from the intertidal marsh, as outlined below, the following summary is given:

- (1) Soils in degraded sites lacked an organic layer, had significantly higher bulk densities, clay content, soil surface temperatures, evaporation rates, salinities, and significantly lower soil water content than soils in sites where swards were intact.
- (2) Plants of *P. phryganodes*, transplanted with a plug of soil from where the vegetation was intact established in degraded sediments. The overall death of plants was low; at the end of the second growing season, 8 of the 48 plots had > 75% mortality of which the majority was concentrated in plots of 2 of the 12 exclosures.
- (3) Plant growth measured as radial growth and basal area of plants varied significantly with treatment, site and exclosure (on all dates). Plant growth measured as clipped above-ground biomass varied significantly only with treatment (on all dates).
- (4) All three growth estimation techniques showed that plants that received an amelioration treatment had significantly higher growth rates than those that were planted in bare sediments. Estimates of radial growth indicated that among the three amelioration treatments, plants treated with the combined fertilizer-mulch treatment had higher growth rates than plants treated with fertilizer only (on all dates in 1996 and 1997) and also plants treated with mulch only (on all dates in 1997).
- (5) Although treatment effects were the same at all three sites, the magnitude of plant growth varied. On all dates, plants at site two had significantly higher growth rates than those in site one and significantly higher or equal growth rates than those in site three. These growth differences were supported by significant differences in the edaphic environment where variation in sand content, soil moisture, salinity and total carbon and nitrogen was recorded between sites.

### 2.3.1 Monitoring of above-ground biomass

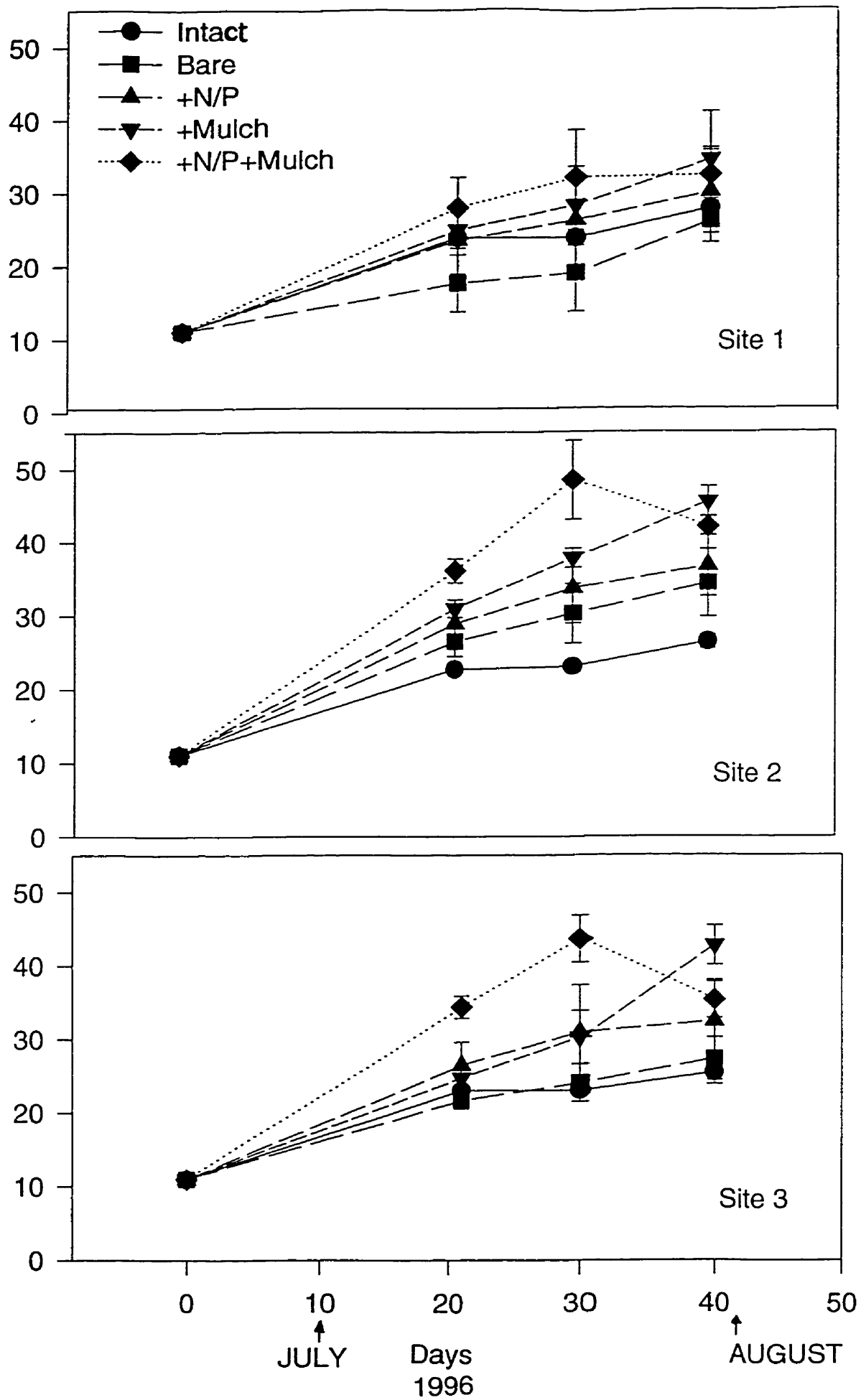
#### 2.3.1.1 Above-ground growth estimates

In 1996, radial growth estimates (Figure 2.2) varied significantly with treatment ( $F_{4,8}=10.33, 13.57, 12.75$ ;  $p<0.01$ ), site ( $F_{2,8}=7.47, 8.48, 7.18$ ;  $p<0.05$ ) and exclosure ( $F_{9,36}=6.26, 8.32, 4.36$ ;  $p<0.01$ ) on July 11, 20 and 29 respectively. Contrasts (restricted to site and treatment factors) revealed that plants in site two had significantly higher radial growth values than those in site one on July 11 ( $p<0.05$ ) and 29 ( $p<0.01$ ) and than those in sites one ( $p<0.01$ ) and three ( $p<0.05$ ) on July 20. On all dates in 1996, plants that received no amelioration treatment had significantly lower radial growth than plants that received fertilizer ( $p<0.05$ , except on July 29, 1996 when the contrast was insignificant), mulch ( $p<0.05$ ) and fertilizer+mulch ( $p<0.01$ ). Among the amelioration treatments, plants that were given only fertilizer showed significantly lower growth than those that were given fertilizer+mulch ( $p<0.01$ , on all dates) and mulch only ( $p<0.01$  on July 11 and 29, 1996). Finally, plants in intact plots showed significantly lower growth than plants that received fertilizer ( $p<0.05$  except on July 11, 1996 when the contrast was insignificant), mulch ( $p<0.05$ ) and fertilizer+mulch ( $p<0.01$ ) on July 11, 20 and 29, 1996.

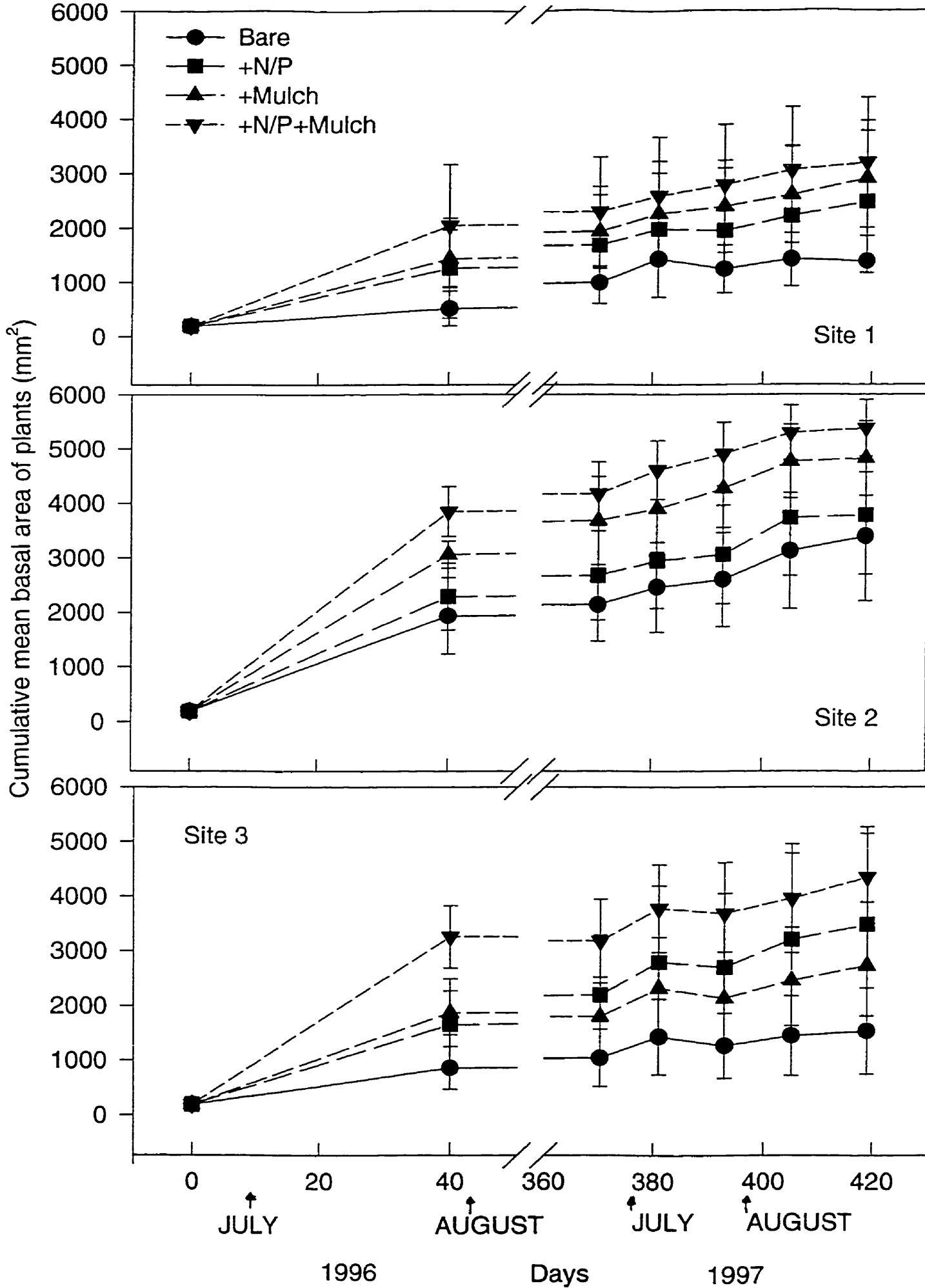
On July 29, 1996 and June 25, July 6, 17, 29 and August 12, 1997, the basal area of plants (Figure 2.3) varied significantly with treatment ( $F_{3,6}=33.33, 13.97, 3.13, 18.98, 18.8, 17.6$ ;  $p<0.01$ ), with site ( $F_{2,6}=31.14, 19.25, 16.45, 16.30, 22.4, 12.6$ ;  $p<0.01$ ) and exclosure ( $F_{8,26}=9.66, 21.14, 17.88, 20.20, 18.1, 17.6$ ;  $p<0.001$ ). On all dates, plants with no amelioration had a significantly lower basal area than plants that received amelioration treatments ( $p<0.05$ ). Plants that were given the fertilizer or mulch amelioration treatments (the growth of which were not significantly different from one another) had significantly lower values of growth than those plants that received the combined fertilizer+mulch treatment ( $p<0.05$  to  $p<0.001$  for all comparisons). On all dates, plants from site one had significantly lower basal areas than comparable values for plants at site two ( $p<0.001$  to  $p<0.01$ ) and than plants in site three on July 29, 1996 and July 6, 1997 ( $p<0.05$ ). Plants from site three had significantly lower basal areas than plants in site two ( $p<0.01$  for all sampling dates).

**Figure 2.2** Mean cumulative radial growth of *P. phryganodes* during the growing season of 1996 at the intertidal marsh on the east shore of La Pérouse Bay. Planting was completed on June 20, 1996 and plants were scored on July 11, 20 and 29. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The plotted points show the mean (error bars show one standard error of the mean) per treatment per site (n=4 except on July 29, where due to plot mortality, n=3 for the bare treatment in site one).

Cumulative mean radial growth of plants (mm)



**Figure 2.3** Mean cumulative basal area of plants of *P. phryganodes* during the growing seasons of 1996 and 1997 at the intertidal marsh on the east shore of La Pérouse Bay. Planting was completed on June 20, 1996 and plants were scored on July 29, 1996 and June 25, July 6, 17, 29, and August 12, 1997. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The plotted points show the mean (error bars show one standard error of the mean when  $n \geq 3$ ) per treatment per site ( $n=4$  except, due to plot mortality, on July 29, when  $n=3$  for the bare treatment in site one, and on all dates in 1997, when  $n=2$  for the bare treatment in site one, and  $n=3$  for the fertilizer addition treatment in sites one and three).



Values of clipped above-ground biomass in 1997, shown in Table 2.1, were not significantly different by site or exclosure, but showed significant differences in response to treatment on June 27 ( $F_{4,7}=10.16$ ,  $p<0.01$ ), July 24 ( $F_{4,8}=14.66$ ,  $p<0.001$ ), and August 15 ( $F_{4,8}=22.04$ ,  $p<0.001$ ). On all three dates, plants in plots of intact vegetation (exclosed in 1996) showed significantly higher biomass than those from the other treatments ( $p<0.01$ ). In addition, on July 24, plants that received no amelioration had significantly lower biomass than those that were given fertilizer, mulch or fertilizer+mulch treatments ( $p<0.01$  for all contrasts).

### **2.3.1.2 Above-ground senescence of plants**

Death of plants of *P. phryganodes* (Figure 2.4) was restricted to particular plots (plot mortality is shown in Table 2.2) although mortality of plants did not vary significantly by treatment or site on any dates. Plant senescence (Figure 2.5) differed significantly in relation to treatment on July 11, 1996 in the “green” plug analysis ( $p<0.05$ ). On all other dates, plant senescence condition did not show significant variation by treatment or site.



**Table 2.1** Clipped above-ground biomass at (a) the intertidal (east shore of La Pérouse Bay) and (b) the inland supratidal marsh at La Pérouse Bay. Each entry shows a mean for each treatment (expressed in grams per m<sup>2</sup> ± s. e. m.), pooled over all three sites (n≤9).

(a)				
Treatment	June 21, 1997	July 19, 1997	August 10, 1997	
Bare soil	29.4 ± 15.9	77.4 ± 44.1	98.8 ± 56.4	
Intact vegetation	136.8 ± 19.0	141.6 ± 24.1	141.6 ± 19.2	
+N/P	47.1 ± 26.5	108.3 ± 47.1	122.3 ± 58.5	
+Mulch	44.5 ± 16.5	91.6 ± 30.9	77.7 ± 25.5	
+N/P+mulch	84.5 ± 34.1	134.9 ± 49.0	178.2 ± 67.4	

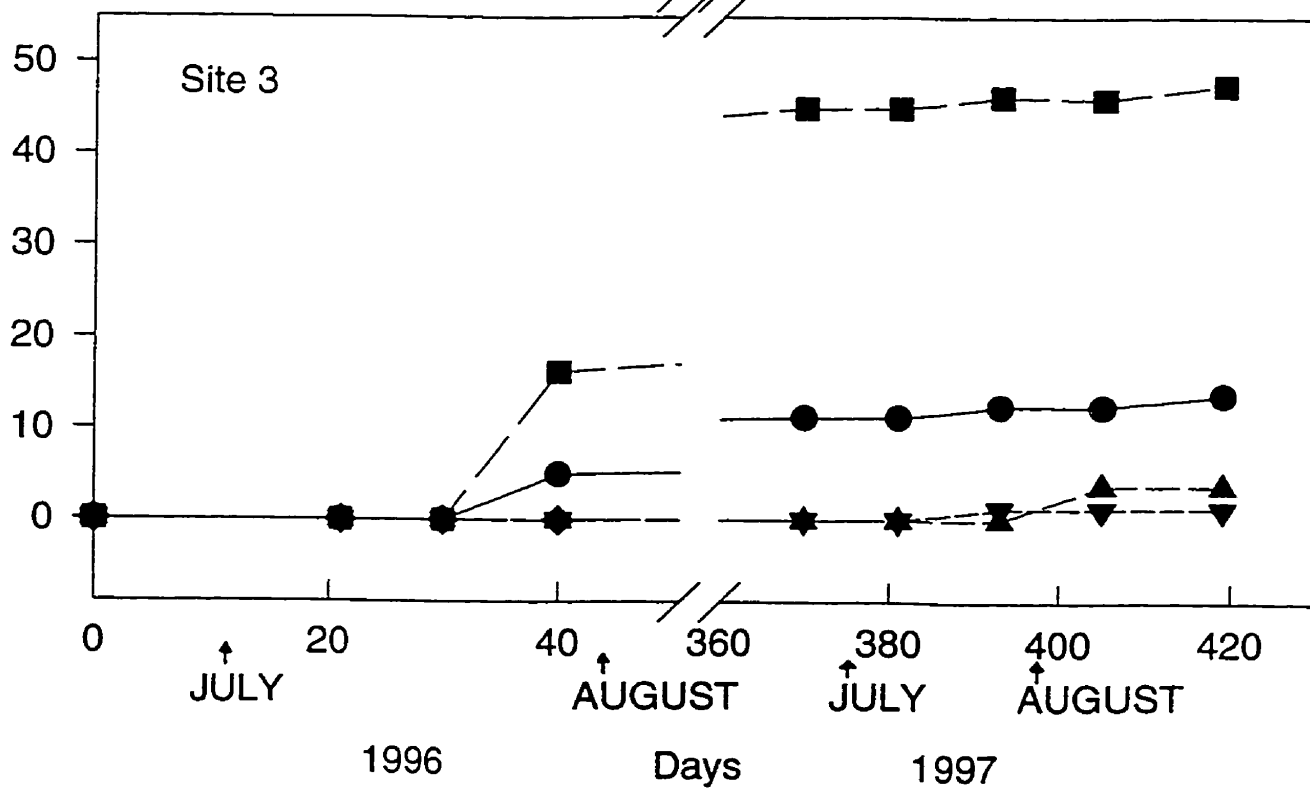
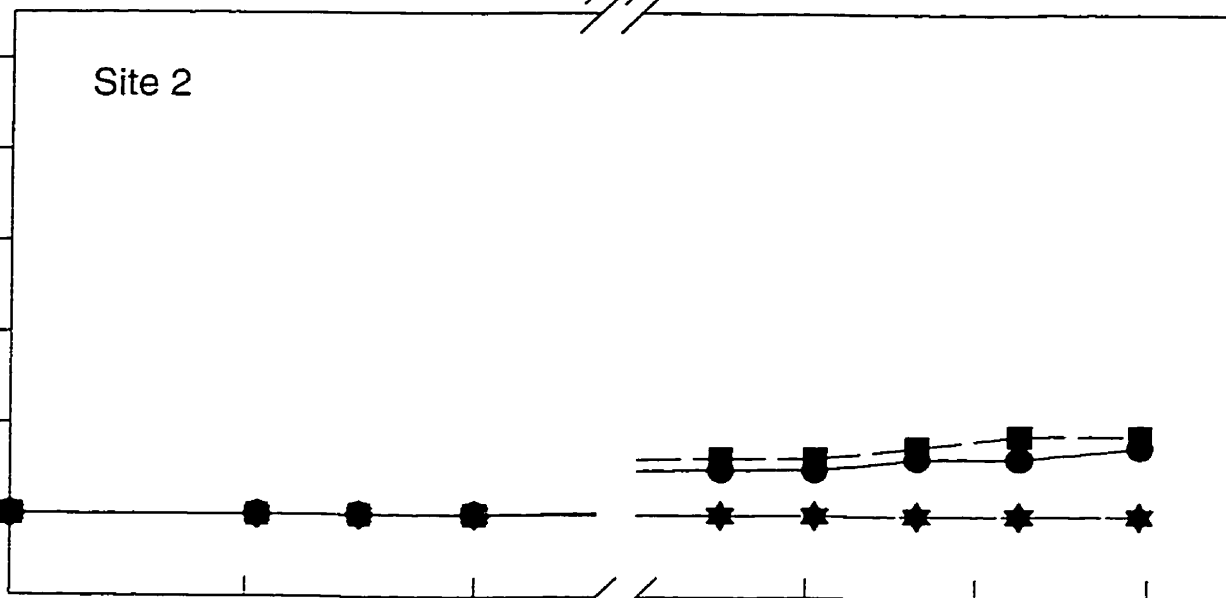
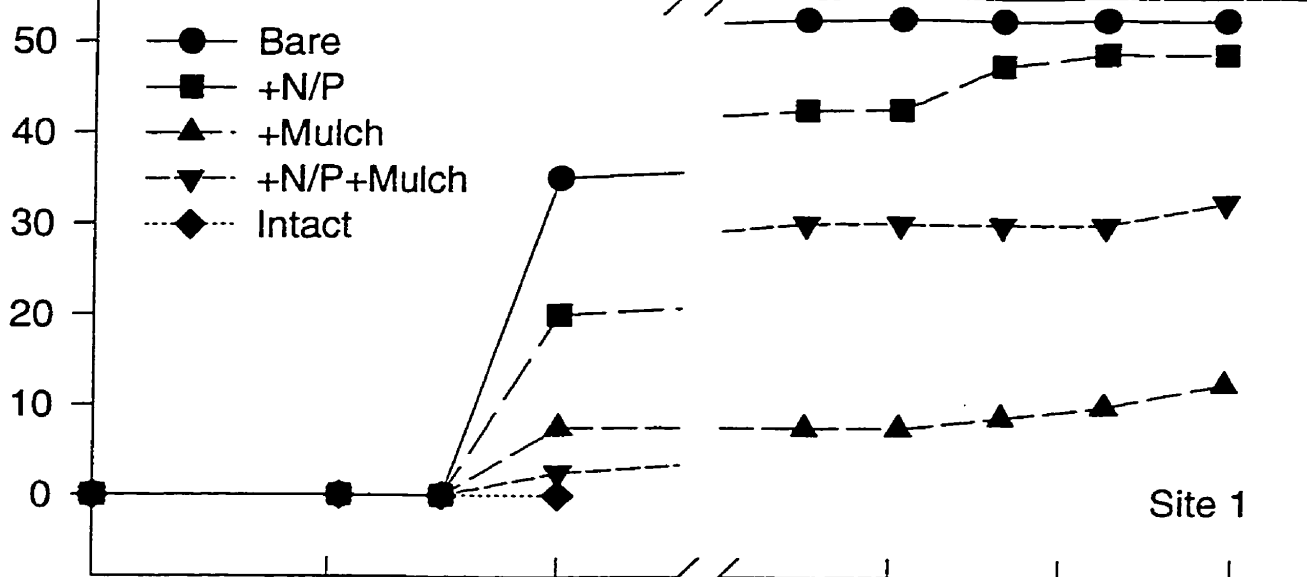
(b)				
Treatment	June 27, 1997	July 24, 1997	August 15, 1997	
Bare	0.54 ± 0.17	0.72 ± 0.31	3.24 ± 1.33	
Intact	83.4 ± 21.2	120.6 ± 16.2	137.9 ± 27.0	
+N/P	2.72 ± 1.28	29.4 ± 12.0	4.38 ± 1.85	
+Mulch	2.27 ± 0.89	34.7 ± 11.0	3.97 ± 1.86	
+N/P+Mulch	0.98 ± 0.31	25.5 ± 8.23	3.49 ± 1.22	

**Table 2.2** Plot mortality at (a) the intertidal and (b) the supratidal sites at La Pérouse Bay during the growing seasons of 1996 and 1997. Each entry name refers to one of the four enclosure replicates, one of the three site numbers and one of the five treatments (bare soil, intact vegetation, +N/P, +mulch, +N/P+mulch to bare soil). E.g. “C-3-mulch” is enclosure replicate “C” in site three and treated with mulch).

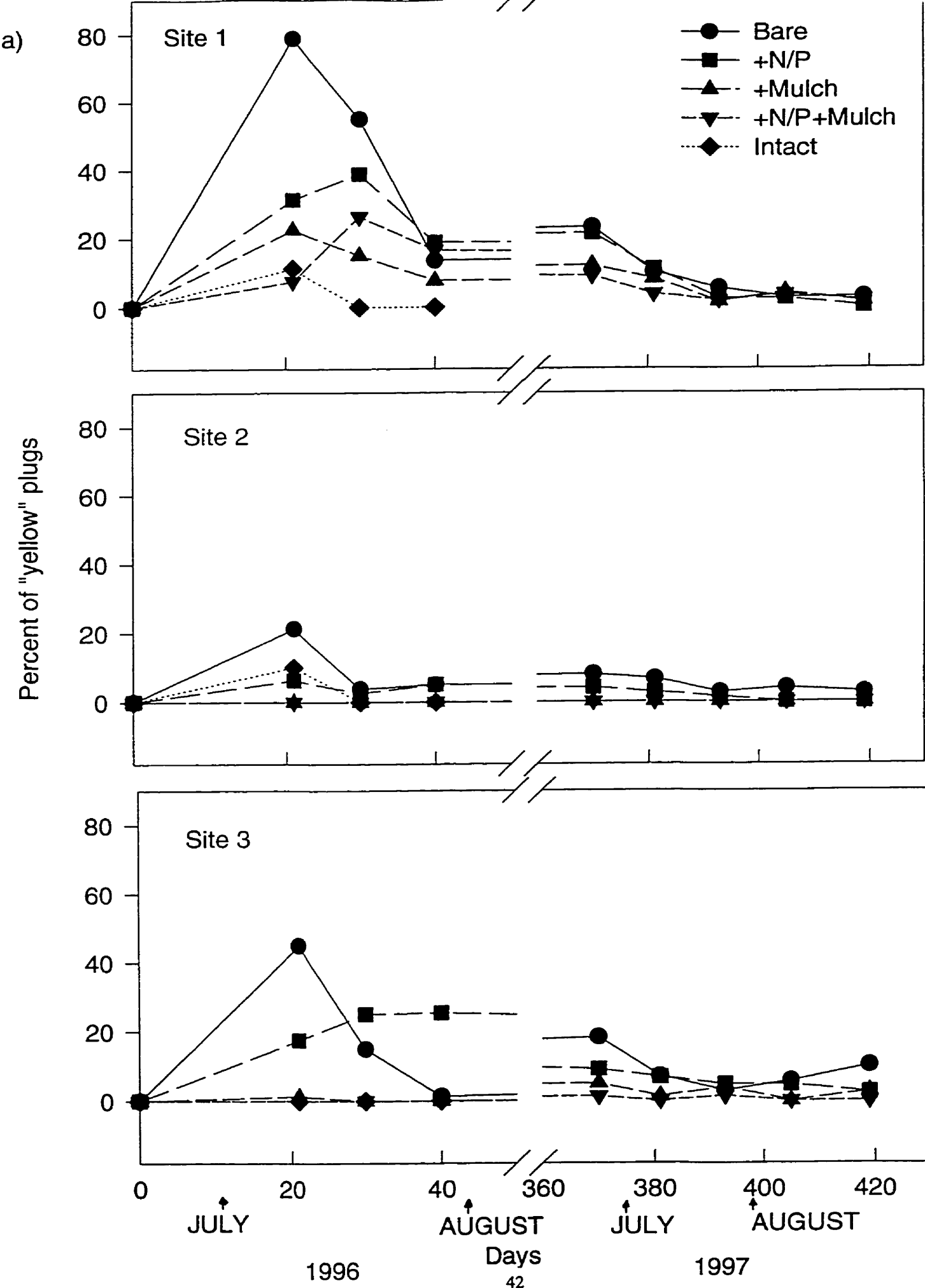
(a)		
Date	Plots showing 100% mortality	Plots showing >75% mortality
11/07/96	none	none
20/07/96	none	none
29/07/96	B-1-bare	none
25/06/97	B-1-bare, B-1-N/P, C-1-bare, A-3-N/P	B-1-mulch, B-1-N/P+mulch, C-1-N/P, C-1-N/P+mulch
06/07/97	as on 25/06/97	as on 25/06/97
17/07/97	as on 25/06/97	as on 25/06/97
29/07/97	as on 25/06/97	as on 25/06/97
12/08/97	as on 25/06/97	as on 25/06/97
(b)		
Date	Plots showing 100% mortality	Plots showing >75% mortality
10/07/96	none	none
19/07/96	none	none
28/07/96	A-1-all treatments except intact B-1-all treatments except intact B-3-all treatments except intact	C-2-N/P
26/06/97	as on 28/07/96, and, in addition, B-2-all treatments except intact C-2-N/P D-2-bare, D-2-N/P, D-2-mulch D-3-bare, D-3-N/P, D-3-mulch	C-2-mulch D-2-N/P+mulch A-3-bare
10/07/97	as on 26/06/97	as on 26/06/97
23/07/97	as on 26/06/97, and, in addition, D-3-N/P+mulch	as on 26/06/97
02/08/97	as on 23/07/97	as on 26/06/97
13/08/97	as on 23/07/97	as on 26/06/97, and, in addition, A-3-N/P

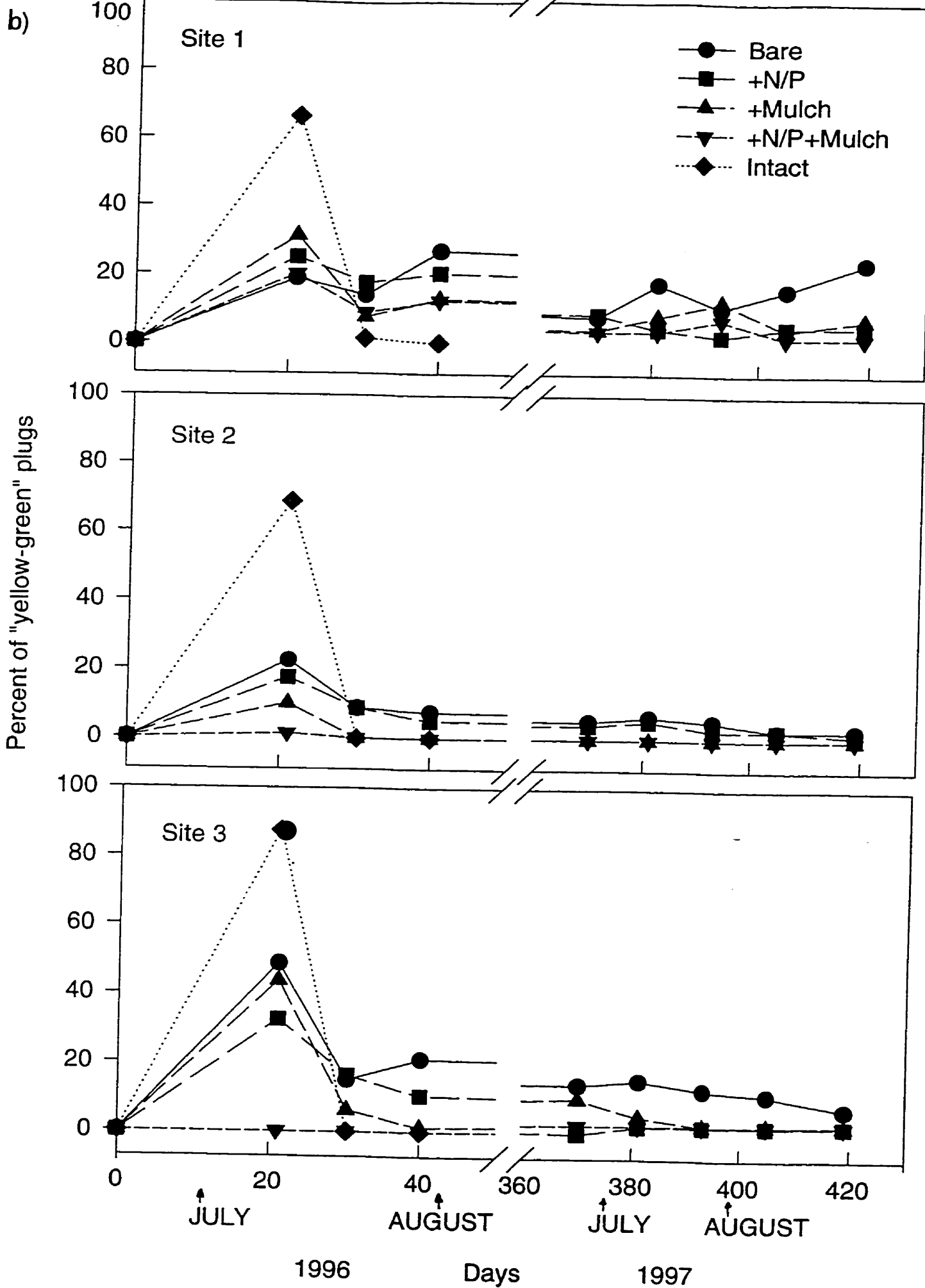
**Figure 2.4** Death of plants of *P. phryganodes* during the growing seasons of 1996 and 1997 at the intertidal marsh on the east shore of La Pérouse Bay. Planting was completed on June 20, 1996 and plugs were scored in 1996, on July 11, 20, 29 and in 1997, on June 25, July 6, 17, 29, and August 12. Each point shows the total number of plugs devoid of live plants divided by the total number of planted plugs (n=80 per treatment per site) and expressed as a percentage. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments shown are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The intact vegetation treatment was monitored in 1996 only.

Percent of plugs with dead plants

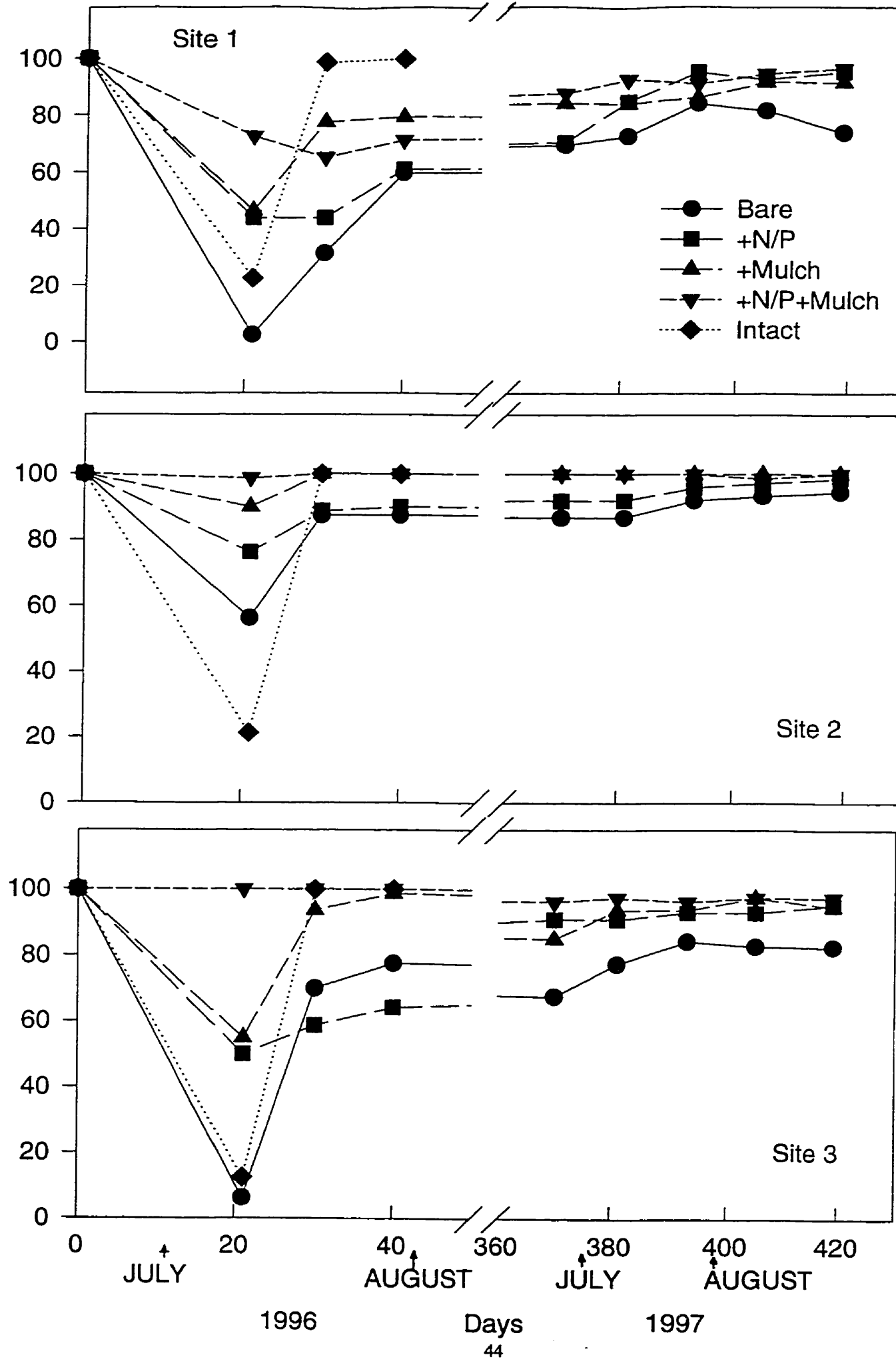


**Figure 2.5** Percent of plugs with senescing plants of *P. phryganodes* during the growing seasons of 1996 and 1997 at the intertidal marsh on the east shore of La Pérouse Bay. Planting was completed on June 20, 1996 and plugs were scored for plant senescence in 1996, on July 11, 20, 29 and in 1997, on June 25, July 6, 17, 29, and August 12. Each graph shows the proportion of (a) “yellow”, (b) “yellow-green” and (c) “green” plugs (see Section 2.2.2 for index of “greenness”). The plotted points show the number of plugs in each senescence category divided by the total number of living plugs ( $n \leq 80$  plugs per treatment per site). Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The intact vegetation treatment was monitored in 1996 only.





c)





## **2.3.2 Monitoring of environmental variables**

### **2.3.2.1 Description of the soil profile**

The soils sampled on the east shore of La Pérouse Bay resembled other intertidal soils previously described at a site <2 km away and classified as regosolic static cryosols (new soils, predominantly mineral, with permafrost within 1 m of the surface and no marked cryoturbation; Wilson 1993). In intact sites, the depth of the organic layer was 1-3 mm, 5-8 mm and 2-4 mm in sites one, two, and three respectively. Degraded soils, devoid of vegetation, lacked an organic layer. In both intact and degraded soils, beneath the 2-3 mm layer of cyanobacteria at the soil surface, a C<sub>g</sub> horizon occurred characterized by a light grey mineral soil with intermittent striations of organic matter (2-3 mm) and occasional dark grey bands (0-33 mm). The dark bands indicated periods of intense reduction, while the organic striations were likely the result of tidal inundation that deposited organic-rich sediment (Wilson 1993).

### **2.3.2.2 Bulk density**

Bulk density was calculated in intact and degraded soils at each site at depths of 0-2 cm and 2-4 cm. In degraded and intact soils respectively, mean bulk density ( $\pm$  s. e. m.) was  $0.60 \pm 0.03$  and  $0.46 \pm 0.03$  at 0-2 cm,  $0.56 \pm 0.04$  and  $0.44 \pm 0.04$  at 2-4 cm ( $n=9$  per treatment at each depth). Bulk density did not vary with site, but was significantly greater in degraded soils than in intact soils at both 0-2 cm in depth ( $F_{1,14}=10.60$ ,  $p<0.01$ , Tukey,  $p<0.05$ ) and at 2-4 cm in depth ( $F_{1,14}=6.14$ ,  $p<0.05$ , Tukey,  $p<0.05$ ).

### **2.3.2.3 Particle size**

Sand, silt and clay contents are shown in Table 2.3 for each of the three sites on the intertidal marsh on the east shore of La Pérouse Bay. The percentage of sand ( $F_{2,12}=8.34$ ,  $p<0.01$ ) and silt ( $F_{2,12}=6.98$ ,  $p=0.01$ ) varied significantly with site. Site one had significantly more sand and less silt than sites two (Tukey,  $p<0.01$ ) and three (Tukey,  $p<0.05$ ). Clay content did not vary significantly with site, but did vary significantly with treatment ( $F_{1,14}=7.24$ ,  $p<0.05$ ). Degraded soils had roughly 3% more clay than intact

**Table 2.3** Percent of sand, silt and clay analysed in degraded and intact soils of the intertidal marsh on the east shore of La Pérouse Bay in July 1996. Mean percent values are shown for each site with the standard error of the mean (n=3 per treatment per site).

Particle type	Degraded			Intact		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
Sand	41.1 ± 1.5	31.7 ± 2.1	37.9 ± 2.8	45.3 ± 1.8	34.4 ± 2.6	37.6 ± 3.6
Silt	45.1 ± 2.7	56.1 ± 1.5	50.2 ± 2.2	46.0 ± 2.0	53.6 ± 3.8	54.3 ± 2.5
Clay	14.2 ± 1.1	12.2 ± 0.7	11.9 ± 0.9	8.7 ± 0.4	12.0 ± 2.4	8.1 ± 1.6

**Table 2.4** Mean total carbon, total nitrogen (expressed as % dry weight) and the C:N ratio from soils collected on July 22, 1996 at the intertidal marsh on the east shore of La Pérouse Bay. Values are pooled over the three treatments (n=9 per site) and are shown by site with the standard error of the mean.

Site	% C	% N	C:N
1	11.45 ± 0.30	0.58 ± 0.03	19.99 ± 0.65
2	12.15 ± 0.33	0.65 ± 0.04	18.91 ± 0.73
3	10.78 ± 0.28	0.52 ± 0.04	21.49 ± 1.29

**Table 2.5** Median ranges of soil redox potentials (mV) pooled over the three sites in soils from bare, mulch treated and intact vegetation treatments during the growing season of 1996 at the intertidal marsh on the east shore of La Pérouse Bay (n=9 per treatment).

Date	Bare soil	Mulch treated	Intact vegetation
03/06/96	180-220	180-220	-
07/06/96	-	-	240-290
10/06/96	260-290	260-290	260-290
22/06/96	240-260	280-300	290-310
29/06/96	290-310	280-300	330-350

soils at comparable depths below the surface (Tukey,  $p < 0.05$ ), although these do not represent identical chronological stages.

#### **2.3.2.4 Total carbon and nitrogen**

Results of total carbon and total nitrogen of soils are shown in Table 2.4. Total carbon and nitrogen did not vary significantly by treatment, but did vary significantly by site ( $F_{2,18}=6.91$ ,  $p < 0.01$  for carbon;  $F_{2,18}=5.42$ ,  $p < 0.05$  for nitrogen). Soils in site two had greater amounts of total carbon than those in site one and greater total carbon and nitrogen than those in site three (Tukey,  $p < 0.05$  for carbon,  $p < 0.01$  for nitrogen). Although the mean C:N value ( $\pm$  s.e.m.) for the mulch treatment ( $21.5 \pm 0.8$ ) was slightly higher than comparable values for soils from bare sites ( $19.7 \pm 1.0$ ) and sites where the vegetation was intact ( $19.2 \pm 1.0$ ), C:N values did not vary significantly by treatment or by site.

#### **2.3.2.5 Redox potential**

Ranges of soil redox potential for 1996 are shown in Table 2.5. There was no significant difference between treatments on July 3 or 10. On July 22 at site one, bare plots showed significantly lower redox potentials than intact or mulched plots ( $H_2=5.85$ ,  $p=0.05$ ). On July 29 at all three sites, soils from intact swards showed significantly higher redox potentials (40-50 mv) than those of bare or mulch soils ( $H_2=7.58$ ,  $7.78$ ,  $7.09$   $p < 0.05$  for sites 1, 2 and 3 respectively). Analyses also indicated that redox values at site three were, on average, 50 mv less than those in sites one and two on July 10 and 22.

Redox measurements were made at depths of 0-2 cm and 2-4 cm on July 7 (permanent edaphic plots), and July 19, 1997 (permanenent edaphic plots and within exclosures). Analyses on both dates, at both depths and in both sets of plots indicated no significant treatment effects. Median redox potential values typically ranged from 250-270 mV. Site was a significant factor in the analysis on July 7, 1997 at a depth of 2-4 cm ( $F_{2,18}=3.28$ ,  $p=0.06$ , Tukey  $p < 0.05$  for site one vs. site two contrast). The median redox potential values on that date were 310, 270 and 280 mV at sites one, two and three respectively.

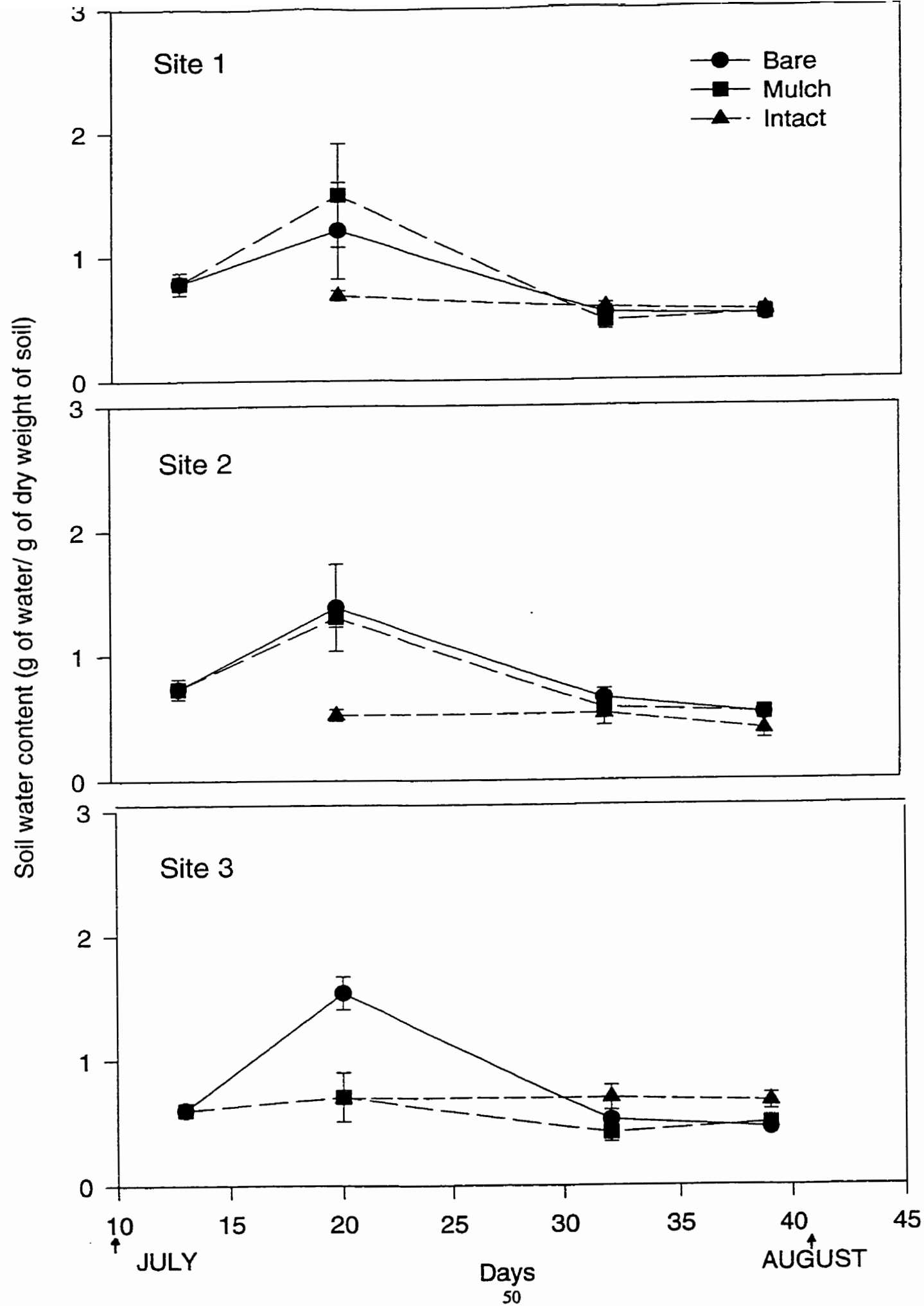
### 2.3.2.6 Gravimetric soil water content

Soil moisture content did not differ significantly by treatment or by site on any date in 1996 ( $n=3$  per treatment per site). Mean soil water content generally varied between 0.48-0.78 g of water/ g dry weight of soil with the exception of July 11, 1996 when mean values calculated for some bare and mulch treatment plots exceeded 1 g of water/ g dry weight (Figure 2.6). In 1997, soils sampled on July 7 from bare plots just missed showing a significantly lower water content than soils from intact vegetation or mulched plots ( $F_{2,4}=4.97$ ,  $p=0.08$ ), and values did not vary significantly by site. Mean values for bare and mulch plots and plots with intact vegetation were  $0.469 \pm 0.014$ ,  $0.543 \pm 0.029$  and  $0.561 \pm 0.020$  respectively ( $n=9$  per treatment). On August 10 (Table 2.6), soils measured at a depth of 0-2 cm in the permanent plots were not significantly different by treatment or site, however, soils measured at a depth of 2-4 cm had significantly less water in site one than corresponding values at site three ( $F_{2,18}=4.71$ ,  $p<0.05$ ; Tukey  $p<0.05$  for site one vs site three). Soil water content measured inside the enclosure plots did not vary by treatment, but varied strongly by site ( $F_{2,24}=60.75$ ,  $p<0.0001$ ) with site one showing significantly drier values than those in sites two and three (Tukey,  $p<0.001$  for both contrasts).

### 2.3.2.7 Salinity

Figure 2.7 shows the sodium content of soil water from plots measured in both years. There was no significant difference by treatment or by site for samples from bare and mulch plots on July 3, 1996. Intact plots were significantly less saline than bare and mulch plots on July 11 ( $F_{2,4}=136.62$ ,  $p<0.0001$ , Tukey,  $p<0.01$ ), July 22 ( $F_{2,4}=95.27$ ,  $p<0.0001$ , Tukey,  $p<0.01$ ) and July 29, 1996 ( $F_{2,4}=13.33$ ,  $p<0.05$ , Tukey,  $p<0.05$ ). Soil sodium content also varied significantly with site on July 29, 1996 ( $F_{2,18}=6.16$ ,  $p<0.01$ ); site one was significantly more saline than site two ( $p<0.01$ ) and site three ( $p<0.05$ ). Sodium content varied significantly with treatment ( $F_{4,8}=10.43$ ,  $p<0.01$ ) on June 21, 1997. Soils with intact vegetation were significantly less saline than soils from all

**Figure 2.6** Mean gravimetric soil moisture content during the growing season of 1996 shown by site at the intertidal marsh on the east shore of La Pérouse Bay. Error bars show one standard error of the mean (n=3 per treatment per site).



treatments within degraded exclosure plots (Tukey,  $p < 0.05$  for all contrasts). On July 7, 1997, sodium content did not vary significantly by site, but did vary significantly by treatment ( $F_{2,4} = 30.38$ ,  $p < 0.01$ ). Again, soils with intact vegetation were significantly less saline than bare soils or soils to which mulch was added ( $p < 0.01$  for both contrasts). On July 19, both treatment ( $F_{6,12} = 40.72$ ,  $p < 0.0001$ ) and site ( $F_{2,42} = 4.84$ ,  $p < 0.05$ ) were significant. Multiple contrasts showed that soils with intact vegetation were significantly less saline than bare and mulch treated soils from permanent plots ( $p < 0.05$ ), and that site three was significantly more saline than site one ( $p < 0.01$ ). On August 10, sodium content varied significantly with treatment ( $F_{6,12} = 4.10$ ,  $p < 0.05$ ). Samples from bare plots and plots to which mulch was added outside of the exclosure were significantly more saline than corresponding values for soils from intact vegetation ( $p < 0.01$ ), than bare and fertilizer+mulch addition plots ( $p < 0.001$ ), than fertilizer addition plots ( $p < 0.05$ ) and than mulch treated plots ( $p < 0.05$  for contrast vs. bare plots only). Inside exclosures, plots which received fertilizer or mulch additions were significantly more saline than bare and fertilizer+mulch treated plots ( $p < 0.05$  to  $0.01$  for all contrasts).

#### **2.3.2.8 Elevation**

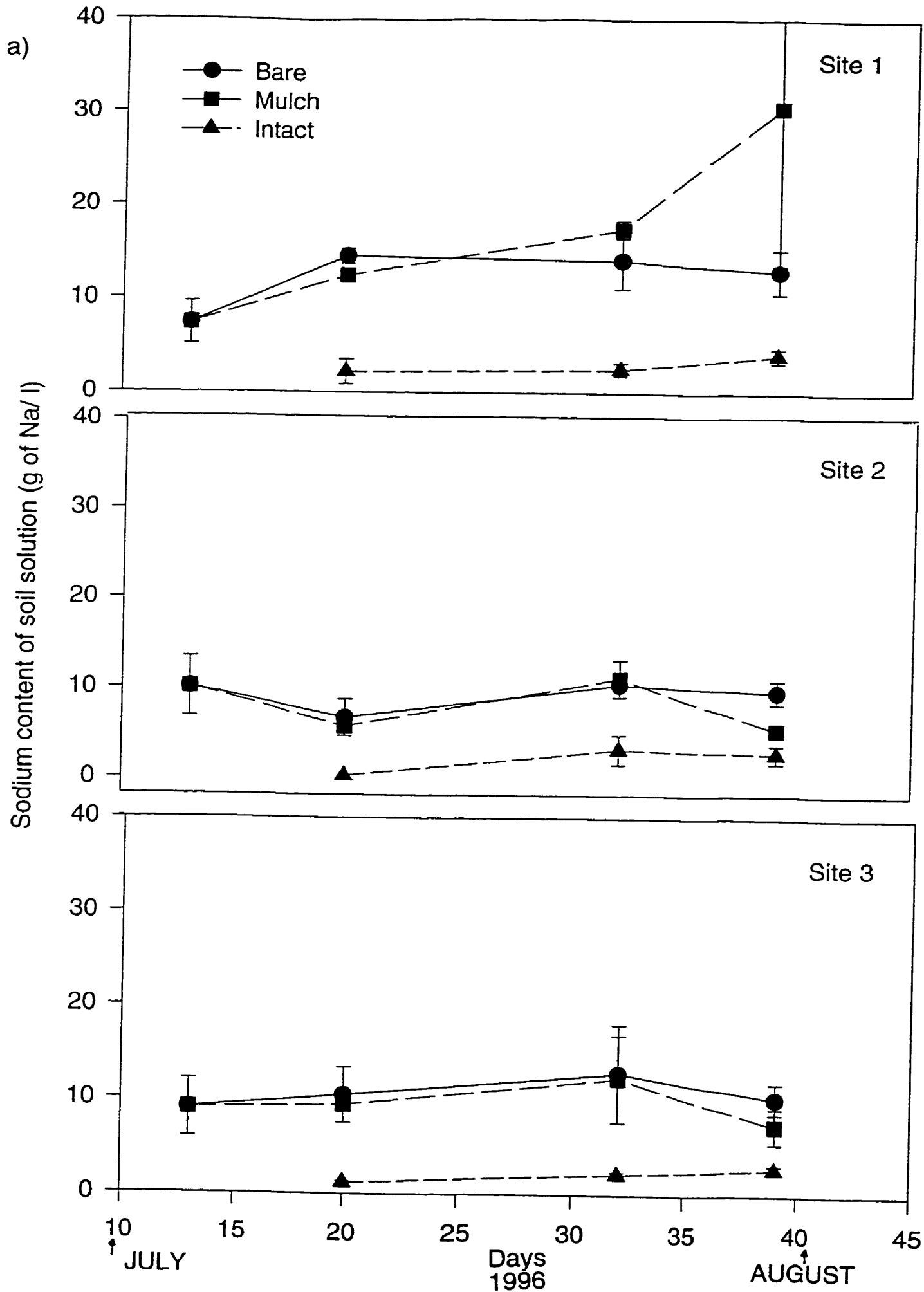
On average ( $\pm$  s.e.m.), intact exclosures ( $-0.165 \pm 0.015$  m) were surveyed as 3 cm higher than degraded exclosures ( $-0.131 \pm 0.008$ ). Elevation differences, however, were not significant between treatment (degraded or intact) or between sites ( $n = 4$  per treatment per site).

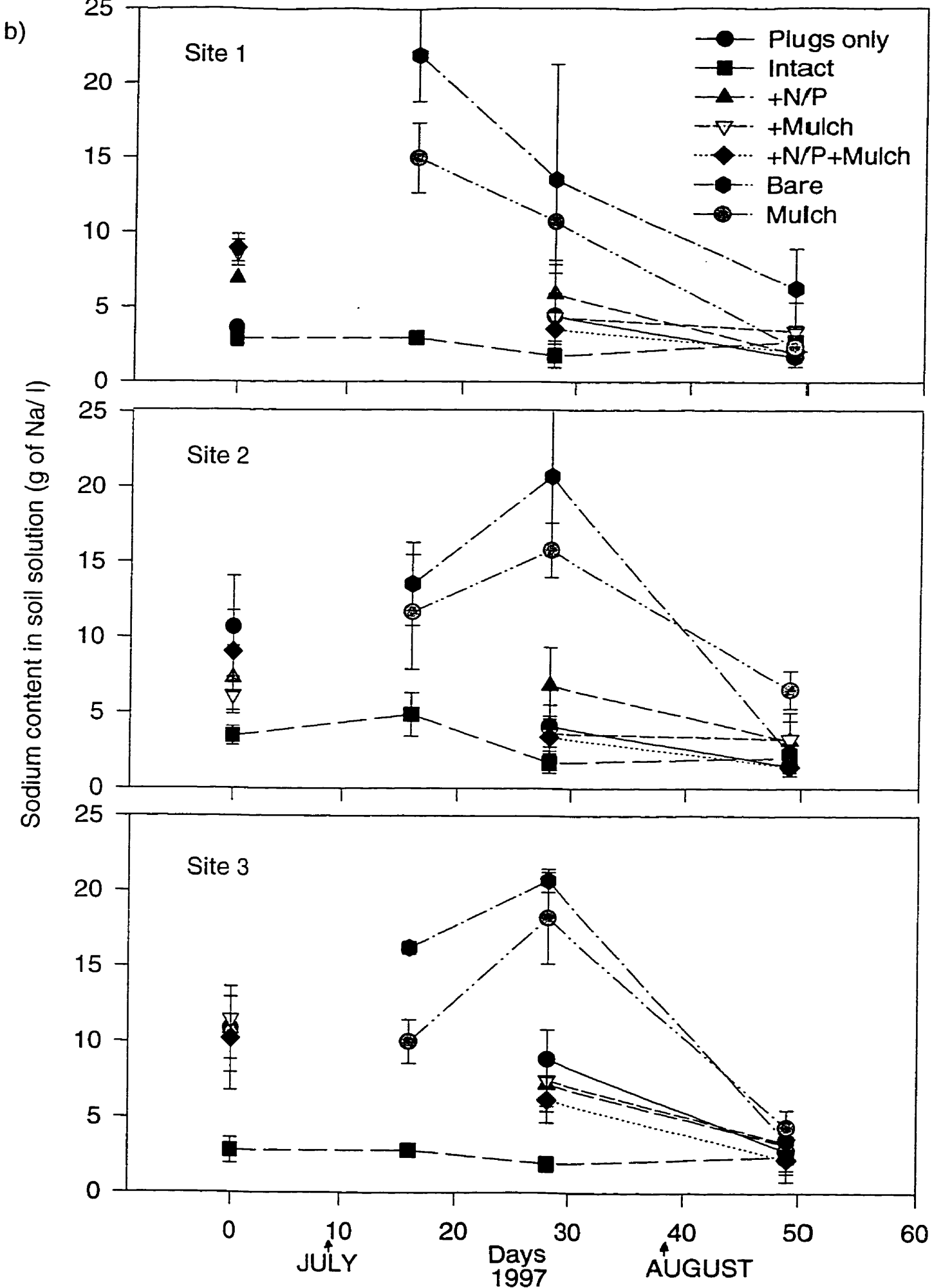
#### **2.3.2.9 Evaporation and temperature**

Evaporation measurements (Table 2.7) did not vary significantly by site, but varied significantly by treatment on July 19, 1997 ( $F_{2,4} = 24.43$ ,  $p < 0.01$ ) and values were marginally non-significant on June 20, 1997 ( $F_{2,4} = 5.00$ ,  $p = 0.08$ ). Bare and mulch treated soils had higher relative evaporation rates than corresponding values for soils with intact vegetation on both dates (Tukey,  $p < 0.05$  for both contrasts on July 19). Relative evaporation rates in bare and mulch treated plots sampled on July 7, 1997 were not significantly different.

**Figure 2.7** Sodium content of soils in (a) 1996 and (b) 1997 shown by site at the intertidal marsh on the east shore of La Pérouse Bay. Error bars show the standard error of the mean for all samples where  $n \geq 3$  ( $n=3$  per treatment per site except where, because of insufficient extracted volume,  $n=2$ ; these cases are July 11, 1996 at site two (mulch and intact treatments) and at sites one and three (mulch treatment), and June 21, 1997 at site one (no addition and N/P addition treatments inside the exclosures) and site three (bare treatment in permanent plots outside the exclosure)).







**Table 2.6** Gravimetric soil water content (g of water/ g of dry weight of soil) measured August 10, 1997 and shown by site at the intertidal marsh on the east shore of La Pérouse Bay. Mean values (shown with one standard error of the mean) are pooled over three treatments in the permanent edaphic plots (n=9 per site) and over four treatments within the exclosure plots (n=12 per site). Soil moisture content in the permanent edaphic plots was measured both at depths of 0-2 cm and 2-4 cm.

Site	Permanent edaphic plots		Within exclosure plots 0-2 cm depth
	0-2 cm depth	2-4 cm depth	
1	0.760 ± 0.046	0.681 ± 0.048	0.431 ± 0.020
2	0.686 ± 0.056	0.560 ± 0.053	0.836 ± 0.023
3	0.695 ± 0.049	0.480 ± 0.040	0.802 ± 0.041

**Table 2.7** Soil evaporation in bare, mulched treated plots and plots with intact vegetation at the intertidal marsh on the east shore of La Pérouse Bay. Table entries show mean percent of evaporated water with standard errors of the mean pooled over the three sites. The trial on July 7 was extended because of logistical difficulties in returning to the site the following day.

Date	Length of trial (hrs)	Sample size	Bare	Mulch	Intact
20/06/97	24	9	15.6 ± 1.3	16.7 ± 1.2	10.2 ± 1.3
07/07/97	67	27	55.3 ± 4.8	47.0 ± 5.1	NA
18/07/97	24	27	30.4 ± 0.8	27.3 ± 0.9	13.8 ± 3.5

**Table 2.8** Soil temperature measured in bare, mulched treated and plots with intact vegetation at the intertidal marsh on the east shore of La Pérouse Bay. Table entries show temperatures (°C) with one standard error of the mean. Temperatures were pooled over the three sites on July 19th (n=9 per treatment). Temperatures were only recorded at site two on August 17th (n=30 per treatment).

Date	Time	Air	Bare	Mulch	Intact
19/07/97	10:45-11:45	n.a.	20.1 ± 0.4	18.8 ± 0.3	16.1 ± 0.6
17/08/97	18:00-18:10	21.0 ± 0.1	18.8 ± 0.1	18.5 ± 0.1	16.5 ± 0.2

Temperature measurements (Table 2.7) varied significantly by treatment on July 19 ( $F_{2,4}=41.8$ ,  $p<0.01$ ) and August 17, 1997 ( $F_{2,6}=10.6$ ,  $p<0.05$ ). On July 19, bare soils had significantly higher values than soils from intact swards, or mulch treated soils (Tukey,  $p<0.05$ ). On August 17, both bare and mulch treated soils had significantly higher values than values from soils with intact vegetation (Tukey,  $p<0.05$ ).

## **2.4 Growth of transplants of *C. subspathacea* in the supratidal marsh**

In order to facilitate the reading of the detailed results from the supratidal marsh, as outlined below, the following summary is given:

- (1) Soils in degraded sites had significantly lower total carbon and nitrogen content, lower soil moisture content (on some dates) and higher soil salinities (on all dates).
- (2) Plants of *C. subspathacea*, transplanted with a plug of soil from an intact site, did not establish readily in degraded sediments. The overall mortality of plants was high; at the end of the second growing season, 28 of the 48 plots had > 75% plant mortality of which the majority were concentrated in 8 of the 12 exclosures.
- (3) Plant growth measured as radial growth varied significantly with site and treatment on July 10 and 19, 1996 respectively and with exclosure on all dates. Plant growth measured as basal area and clipped above-ground biomass did not vary significantly with treatment on any dates, but varied significantly with site (on all dates for basal area measurements, and on August 10, 1997 for clipped above-ground biomass) and with exclosure (on all dates for basal area measurements, and on June 21, 1997 for clipped above-ground biomass).
- (4) The treatment differences that were recorded with the radial growth and clipped above-ground biomass techniques showed that plants planted into intact swards had significantly higher growth than those planted in degraded sediments. There were no treatment differences among any of the treatments in the degraded sediments recorded with any of the growth estimation techniques.

(5) The magnitude of plant growth measured as basal area was greater at sites one and three than at site two on all dates, and greater at site one than at site three on some dates. Although the edaphic data show great variation, significant differences on some dates suggest that the lower basal areas observed at site two may be a consequence of lower soil water content at site two than at sites one and three. Anaerobic conditions at site three may explain the lower basal areas observed at site three than those observed at site one.

## **2.4.1 Monitoring of above-ground biomass**

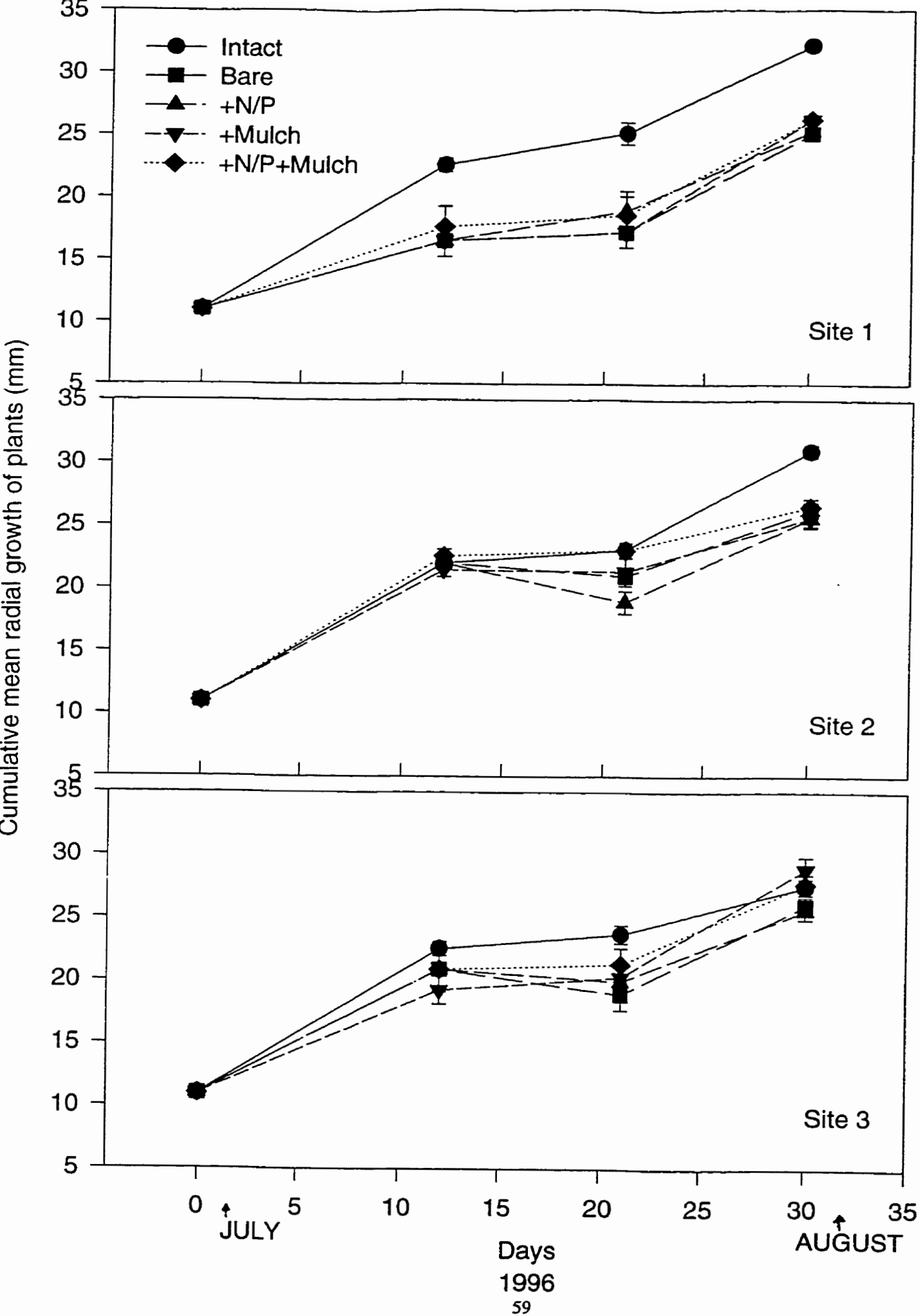
### **2.4.1.1 Above-ground growth estimates**

In 1996, radial growth estimates (Figure 2.8) varied significantly with treatment on July 19 ( $F_{4,8}=5.48$ ,  $p<0.05$ ), with site on July 10 ( $F_{2,8}=12.01$ ,  $p<0.01$ ) and with exclosure on July 10, 19 and 28 respectively ( $F_{9,36}=11.2$ ,  $8.21$  and  $F_{9,28}=11.2$ ;  $p<0.001$ ). Contrasts indicated that plants in sites with vegetation on July 19 had significantly higher radial growth than those without amelioration ( $p<0.01$ ), addition of fertilizer ( $p<0.01$ ) or mulch ( $p<0.01$ ) and addition of fertilizer and mulch ( $p<0.05$ ). On July 10, plants in site one had significantly lower radial growth than those in sites two or three ( $p<0.01$ ).

The basal area of plants (Figure 2.9) did not vary significantly with treatment on any dates. On July 28, 1996 and June 26, July 10, 23, August 2 and 15, 1997, the basal area of plants varied significantly with site ( $F_{2,6}=70.9$ ,  $6.15$ ,  $7.96$ ,  $9.99$ ,  $8.52$ ,  $13.8$  respectively;  $p<0.05$  to  $p<0.001$ ) and exclosure ( $F_{6,18}=27.6$ ,  $F_{2,8}=51.1$ ,  $91.7$ ,  $59.0$ ,  $64.2$ ,  $69.8$ ;  $p<0.001$ ). Site one had plants with significantly greater basal area values than those in sites two ( $p<0.01$  on all dates) and three (significant on July 28, 1996 and June 26, 1997 only;  $p<0.01$ ). Site three had plants with significantly greater basal area values than those in site two ( $p<0.01$  on all dates except June 26, 1997 where  $p<0.05$ ).

Values for clipped above-ground biomass showed a huge variance (Table 2.1). Biomass varied significantly with exclosure on June 21, 1997 ( $F_{5,22}=4.05$ ,  $p<0.05$ ) and site on August 10, 1997 ( $F_{2,8}=6.65$ ,  $p<0.05$ ) with site one having significantly lower biomass than sites two ( $p<0.01$ ) and three ( $p<0.05$ ).

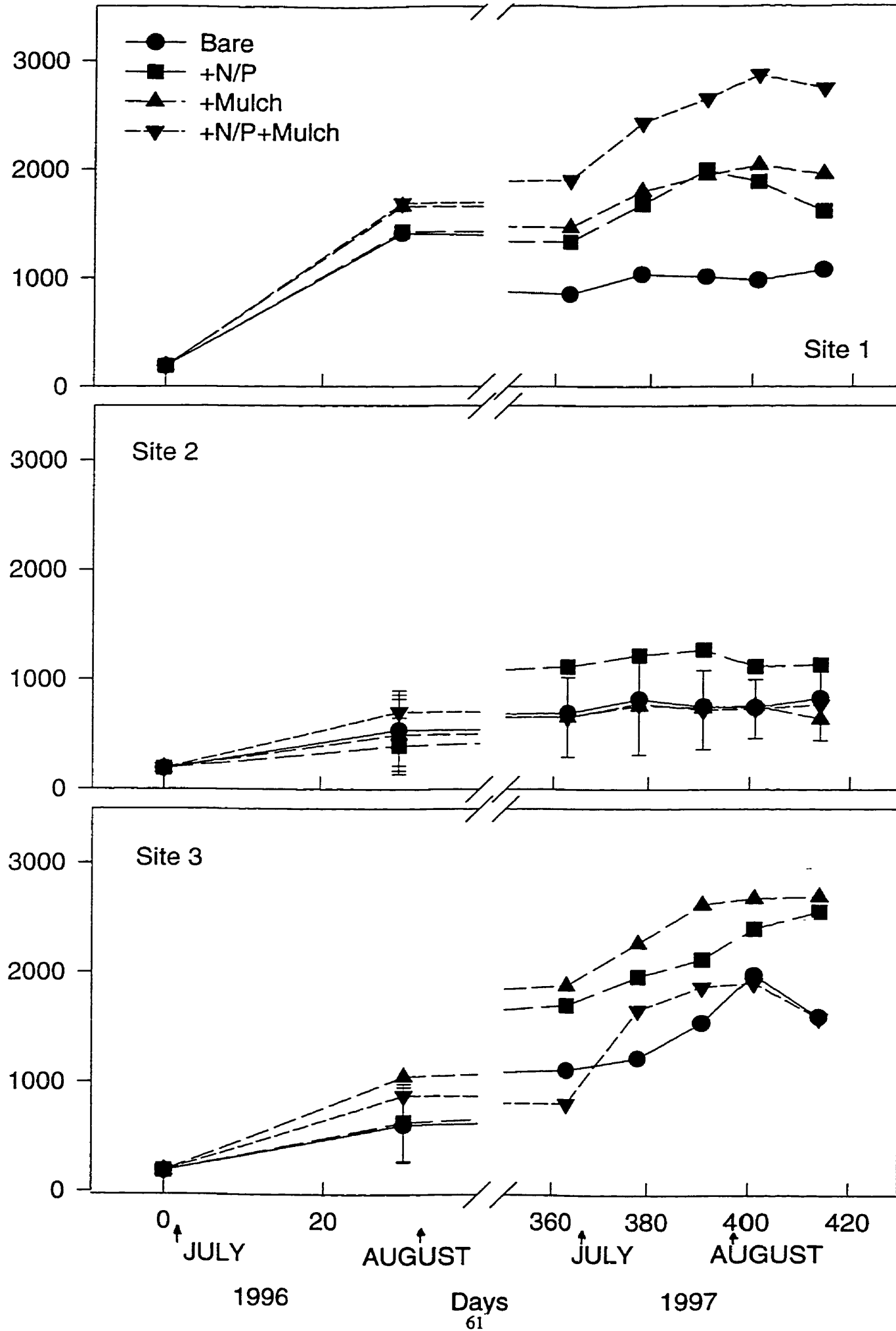
**Figure 2.8** Mean cumulative radial growth of *C. subspathacea* during the growing season of 1996 at the inland supratidal marsh. Planting was completed on June 28, 1996 and plants were scored on July 10, 19 and 28. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The plotted points show the mean (error bars show one standard error of the mean for  $n \geq 3$ ) per treatment per site ( $n=4$  except on July 28, when due to plot mortality,  $n=2$  and  $n=3$  for bare soil, fertilizer addition, mulch addition and combined fertilizer-mulch addition treatments to bare sediments in sites one and three respectively).



**Figure 2.9** Mean cumulative basal area of plants of *C. subspathacea* during the growing seasons of 1996 and 1997 at the inland supratidal marsh. Plugs were planted on June 20, 1996 (mean planting date) and plants were scored in 1996, on July 29, and in 1997, on June 25, July 6, 17, 29, and August 12. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The plotted points show the mean (error bars show one standard error of the mean when  $n \geq 3$ ) per treatment per site. Sample sizes ( $n=4$  per treatment per site) vary due to plot mortality. On July 28,  $n=2$  and  $n=3$  for bare, fertilizer addition, mulch addition and combined fertilizer-mulch addition treatments in sites one and three respectively. On all dates in 1997 except for June 26,  $n=1$  for the fertilizer addition treatment in site two,  $n=2$  for the bare and mulch addition treatments in all sites and for the fertilizer addition and combined fertilizer-mulch addition treatments in sites one and three, and  $n=3$  for the combined fertilizer-mulch addition treatment in site two. On June 26,  $n=3$  for the combined fertilizer-mulch treatment in site three.

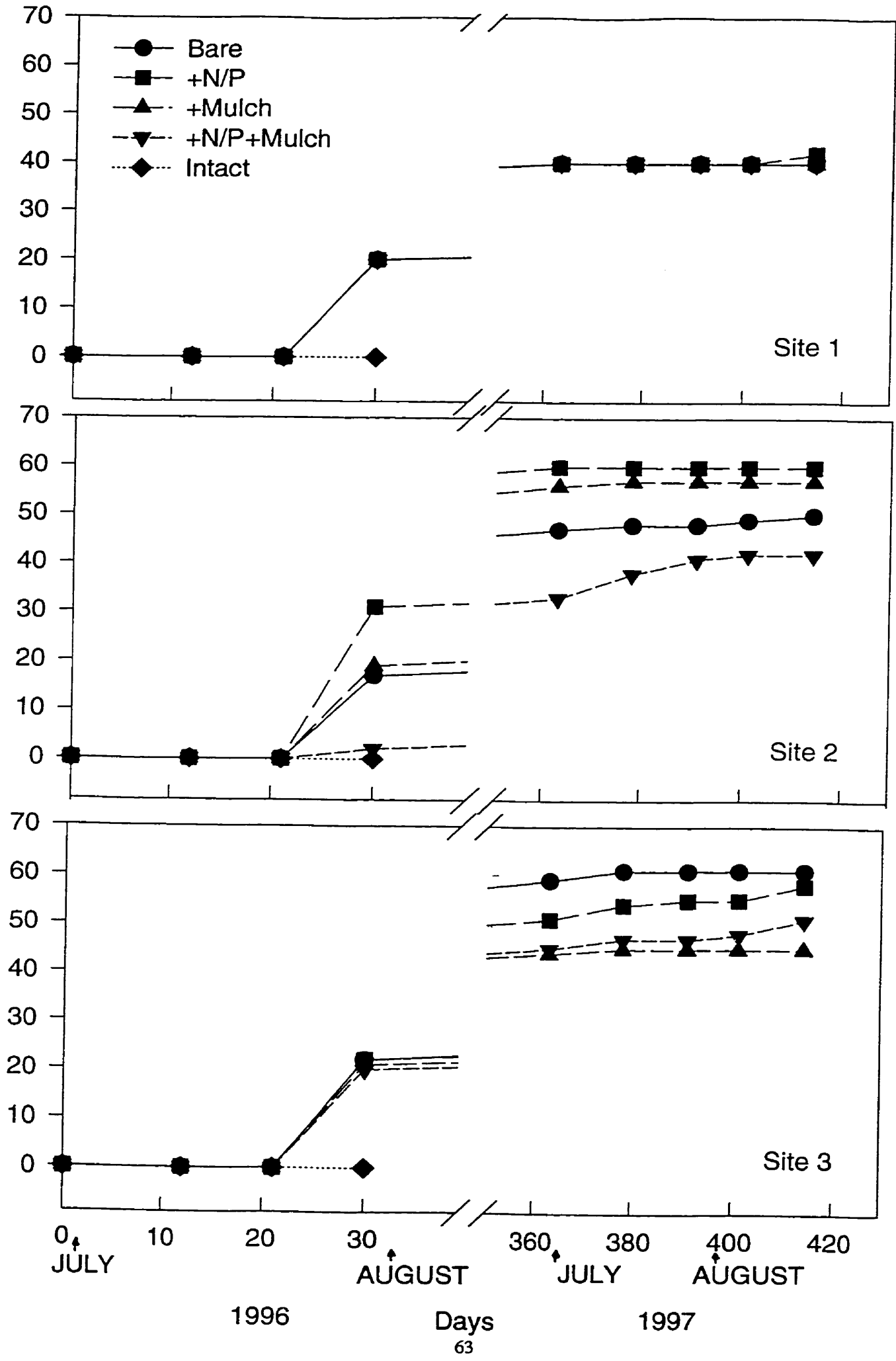


Cumulative mean basal area of plants ( $\text{mm}^2$ )

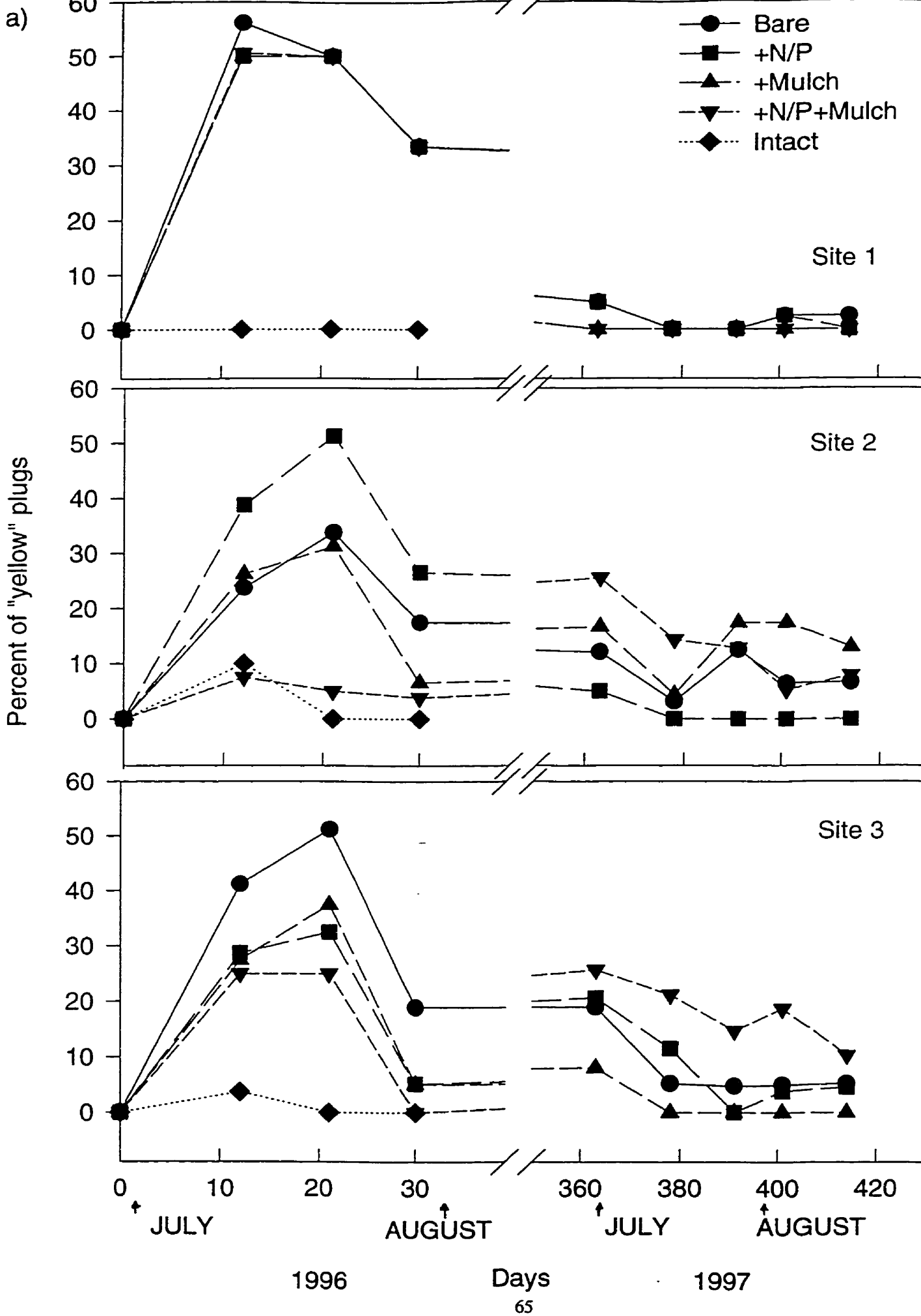


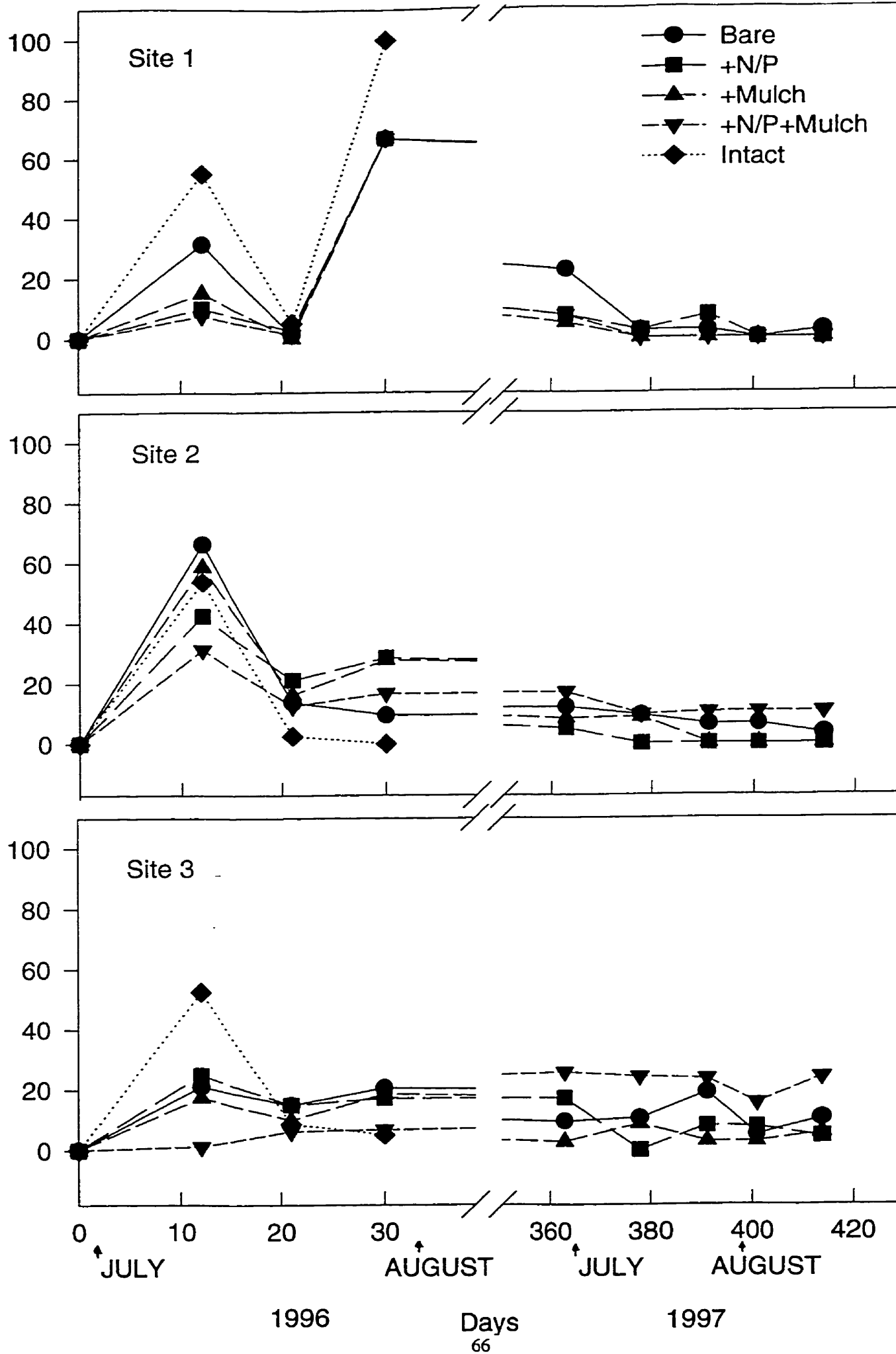
**Figure 2.10** Death of plants of *C. subspathacea* during the growing seasons of 1996 and 1997 at the inland supratidal marsh. Planting was completed on June 28, 1996 and plants were scored in 1996, on July 10, 19, 28 and in 1997, on June 26, July 10, 23, August 2 and 15. Each point shows the total number of plugs devoid of vegetation divided by the total number of planted plugs (n=80) per treatment per site and is expressed as a percentage. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments shown are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The intact vegetation treatment was monitored in 1996 only.

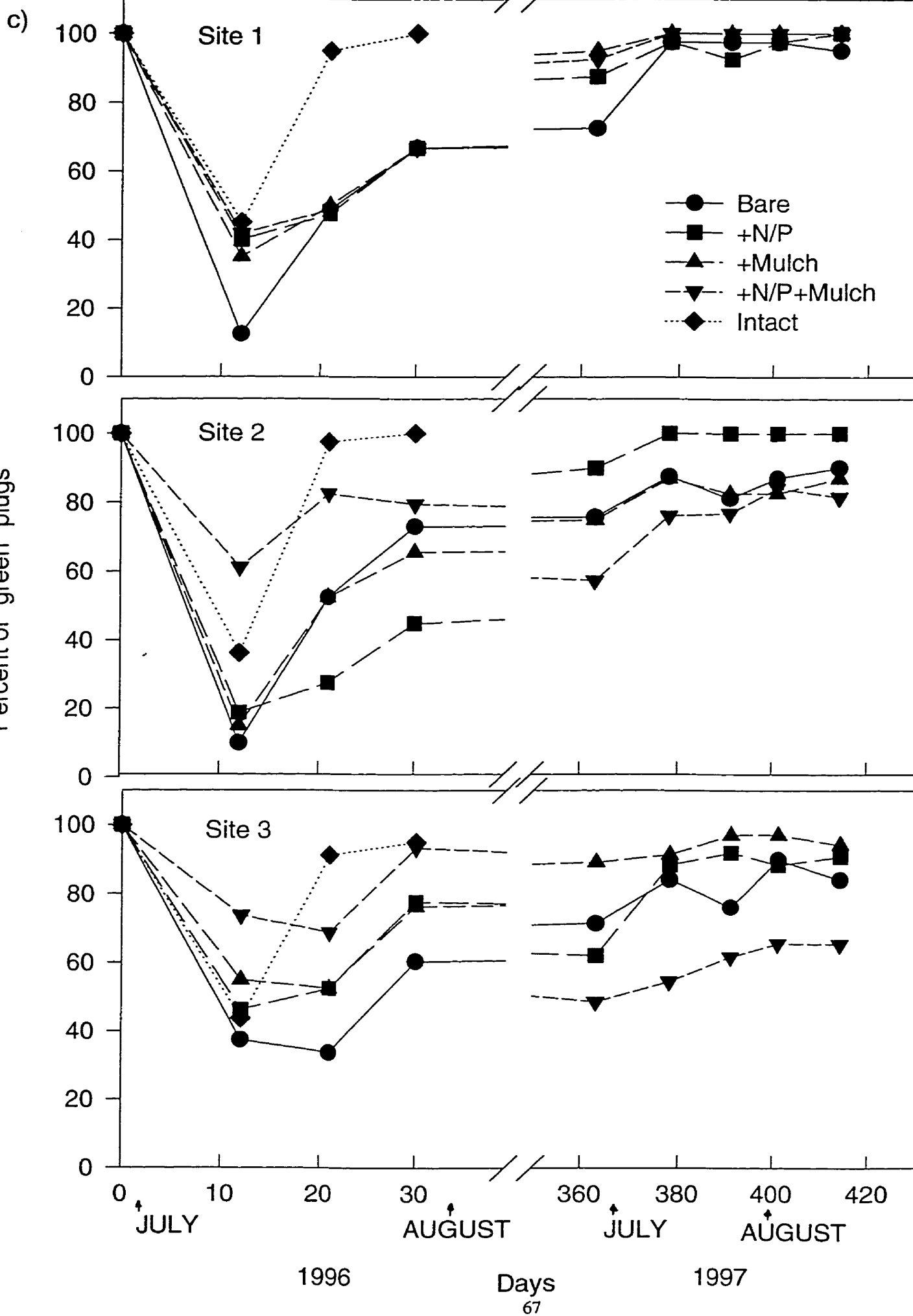
Percent of plugs with dead plants



**Figure 2.11** Percent of plugs with senescing plants of *C. subspathacea* during the growing seasons of 1996 and 1997 at the inland supratidal marsh. Planting was completed on June 28, 1996 and plants were scored in 1996, on July 10, 19, 28 and in 1997, on June 26, July 10, 23, August 2 and 15. Each graph shows the proportion of (a) “yellow”, (b) “yellow-green” and (c) “green” plugs (see Section 2.2.2 for index of “greenness”). The plotted points show the number of plugs in each senescence category divided by the total number of living plugs ( $n \leq 80$  plugs) per treatment per site. Sites one, two and three are shown in the top, middle and bottom graphs respectively. Treatments are intact vegetation, bare soil, fertilizer addition, mulch addition, and combined fertilizer-mulch additions to bare soil. The intact vegetation treatment was monitored in 1996 only.







#### **2.4.1.1 Above-ground senescence of plants**

Death of plants of *C. subspathacea* (Figure 2.10) was highly restricted to particular exclosures (plot/exclosure mortality is shown in Table 2.2). Plot mortality and plant senescence (Figure 2.11) did not vary significantly by treatment or site on any dates.

#### **2.4.2 Monitoring of environmental variables**

##### **2.4.2.1 Description of the soil profile**

The top horizon of soils in the inland marsh was a dark brown, organic horizon, typically 30-35 mm thick below which a light grey mineral horizon occurred. In intact soils, light grey bands, 5-10 mm in thickness, were common and occurred in the top 5-10 mm or at a depth of 30-35 mm. Soils sampled from site three generally were entirely organic in the top 40 mm (no mineral horizon was observed).

##### **2.4.2.2 Bulk density**

Mean bulk densities for exclosures at intact and degraded sites respectively ( $\pm$  s.e.m.,  $n=6$  per treatment) were  $0.80 \pm 0.07$  and  $0.72 \pm 0.10$  at a depth of 0-2 cm, and  $1.11 \pm 0.28$  and  $0.72 \pm 0.08$  at a depth of 2-4 cm. Although bulk density is slightly higher in degraded than intact soils, differences did not vary significantly by treatment or site at either depth.

##### **2.4.2.3 Total carbon and nitrogen**

Results of total carbon and total nitrogen of soils are shown in Table 2.9. Total carbon and nitrogen did not vary significantly by site, but did vary significantly by treatment ( $F_{2,4}=27.0$ ,  $p<0.01$  for carbon;  $F_{2,4}=56.8$ ,  $p<0.01$  for nitrogen). Soils from the intact vegetation had significantly higher total carbon and total nitrogen than soils from bare soils and mulch treated soils (Tukey,  $p<0.01$  for carbon and  $p<0.001$  for nitrogen). C:N values did not vary significantly by treatment or by site.



**Table 2.9** Mean total carbon, total nitrogen (expressed as % dry weight) and the C:N ratio from soils collected on July 19, 1996 at the inland marsh. Values are pooled over the three sites (n=9 per treatment) and are shown with the standard error of the mean.

Element	Bare soil	Mulch treated	Intact vegetation
% C	22.9 ± 2.4	22.3 ± 2.4	32.6 ± 2.4
% N	1.7 ± 0.2	2.5 ± 0.2	1.7 ± 0.2
C:N	13.6 ± 0.7	12.9 ± 0.3	14.0 ± 0.7

**Table 2.10** Ranges of redox potentials (mV) measured during (a) 1996 and (b) 1997 growing seasons at the inland marsh. Ranges are shown (medians are shown in the brackets) and pooled over site and treatment (n=18, 27, 27, 27, 27, 18 and 24 on July 3, 10, 19, 28, 1996 and July 10,24 and August 15, 1997 respectively).

(a)		
Date	Redox potential (mV)	
03/07/1996	-50 to +110	(30)
10/07/1996	-110 to +310	(80)
19/07/1996	-160 to +260	(20)
28/07/1996	-60 to +260	(150)
(b)		
Date	0-2 cm depth	2-4 cm depth
10/07/1997	150 to 310 (260)	190 to 300 (270)
24/07/1997	150 to 320 (260)	100 to 290 (260)
15/08/1997	30 to 260 (190)	70 to 280 (220)

**Table 2.11** Gravimetric soil water content (g of water/ g of dry weight of soil) for (a) the 1996 and (b) the 1997 growing seasons at the inland marsh. Mean values (shown with one standard error of the mean) are pooled over (a) the three sites (n=9 per treatment) and (b) the three treatments (n=9 on July 10 and n=21 on July 24 and August 15).

(a)			
Date	Bare soil	Mulch treated	Intact vegetation
03/07/96	1.868 ± 0.196	1.868 ± 0.196	NA
10/07/96	1.361 ± 0.131	1.494 ± 0.144	2.028 ± 0.140
19/07/96	1.345 ± 0.145	1.309 ± 0.133	1.970 ± 0.151
28/07/96	1.893 ± 0.205	2.302 ± 0.236	1.733 ± 0.268
(b)			
Date	Site 1	Site 2	Site 3
10/07/97	1.150 ± 0.161	1.501 ± 0.096	1.716 ± 0.160
24/07/97	1.234 ± 0.060	1.689 ± 0.178	1.676 ± 0.109
15/08/97	1.620 ± 0.091	1.323 ± 0.064	1.619 ± 0.079

#### **2.4.2.4 Redox potential**

Ranges of soil redox potentials measured during both growing seasons are shown in Table 2.10. Redox potential did not vary significantly by treatment or site with the exception of values measured on July 10, 1996 (by treatment,  $F_{2,4}=11.2$ ,  $p<0.05$ ) and on July 24, 1997 (by site, at a depth of 0-2 cm,  $F_{2,9}=6.24$ ,  $p<0.05$  and at a depth of 2-4 cm,  $F_{2,9}=23.2$ ,  $p<0.001$ ). Contrasts indicated that on July 10, 1996, soils from plots with intact vegetation had significantly lower values than those for bare soils or mulch treated soils ( $p<0.05$ ). On July 24, 1997, contrasts were not significant at a depth of 0-2 cm, but at a depth of 2-4 cm, site one and two had significantly higher redox potentials than values for site three ( $p<0.01$ ).

#### **2.4.2.5 Gravimetric soil water content**

Table 2.11 shows the soil water content measured on dates in 1996 and 1997. In 1996, soil moisture content varied significantly by treatment on July 10 ( $F_{2,4}=48.3$ ,  $p<0.01$ ), and July 19 ( $F_{2,4}=52.1$ ,  $p<0.001$ ) with soils from plots with intact vegetation showing significantly higher values than those from bare soils or mulch treated soils (Tukey,  $p<0.01$  on both dates). Soil moisture content did not vary significantly by site in 1996. In 1997, soil moisture content did not vary significantly by treatment, but did vary significantly by site on July 10 ( $F_{2,18}=4.37$ ,  $p<0.05$ ), July 24 ( $F_{2,40}=4.00$ ,  $p<0.05$ ) and August 15 ( $F_{2,40}=5.11$ ,  $p<0.05$ ). Post-hoc contrasts on all dates, however, were insignificant.

#### **2.4.2.6 Salinity**

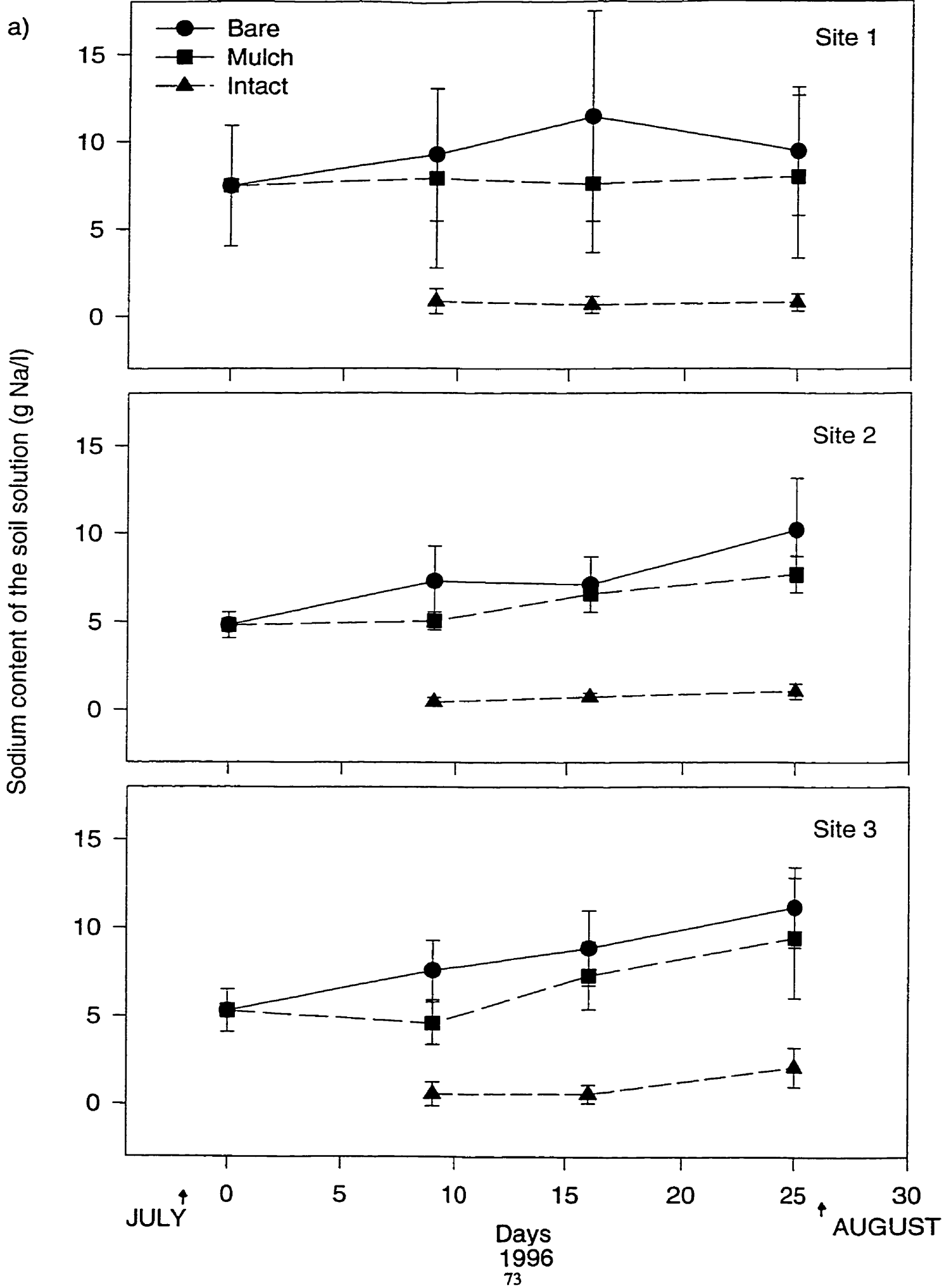
Sodium contents of soils, measured during both seasons, are shown in Figure 2.12. In 1996, sodium content did not vary significantly by site, but varied significantly by treatment on all dates ( $p<0.0001$ ,  $F_{2,4}=689.4$ , 183.9 and 480.8 on July 10, 19 and 28 respectively) except for July 3. On July 10 and 28, values of samples from bare soils were significantly higher than those of soils which were mulch treated ( $p<0.01$  and 0.05), and values for both bare soils and mulch treated soils were significantly higher than those of soils from plots with intact vegetation ( $p<0.001$  on all dates). In 1997, sodium content

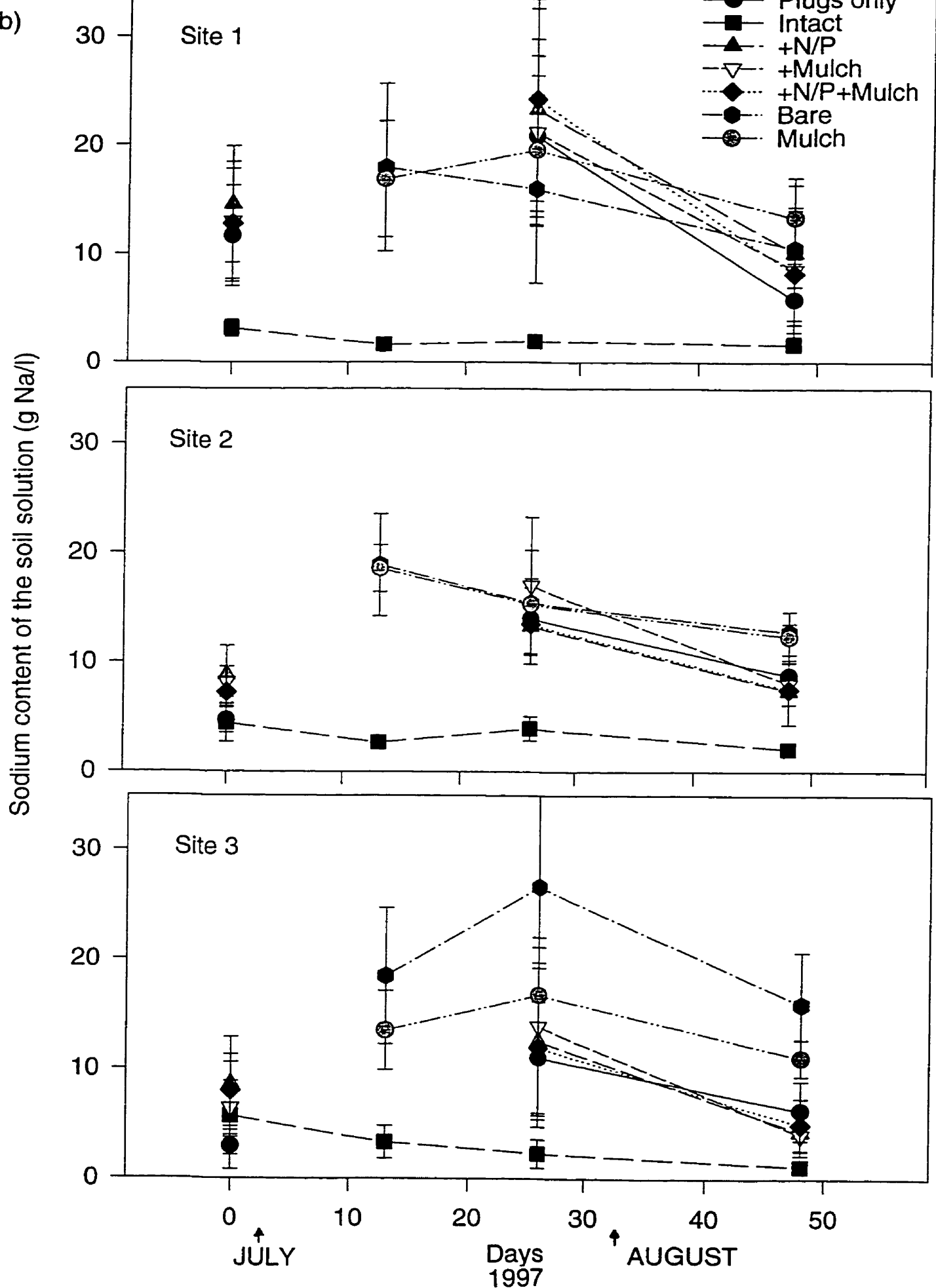
varied significantly by treatment on all dates ( $p < 0.001$ ,  $F_{4,8}=14.2$ ,  $F_{2,4}=101.8$ ,  $F_{6,12}=11.9$ , and  $F_{6,12}=20.9$  on June 27, July 10, 24 and August 15 respectively). Sodium content varied significantly by site on June 27 only ( $F_{2,45}=3.48$ ,  $p < 0.05$ ) with site one and two showing higher salinities than site three ( $p < 0.001$  for site one vs. site three,  $p < 0.01$  for site two vs. site three). Treatment contrasts indicated that sodium content in soils with intact vegetation was significantly less than that measured in all other treatments, both inside and outside the exclosures, on all dates (Tukey,  $p < 0.001$  to  $p < 0.01$ ). On June 27, inside the exclosure, soils with fertilizer addition, mulch addition and fertilizer+mulch addition treatments had significantly higher salinities than soils without additions ( $p < 0.05$  for all contrasts). On August 15, bare soils and mulch treated soils outside of the exclosure had significantly higher salinities than those of soils from treatments inside the exclosures ( $p < 0.001$  for all contrasts). All other treatment contrasts were insignificant.

#### **2.4.2.7 Elevation**

On average, exclosures in intact vegetation were 3-4 cm higher than exclosures on degraded soils, however elevation was not significantly different between treatments. Elevation varied significantly by site ( $F_{2,18}=3.64$ ,  $p < 0.05$ ); exclosures at site three were at a higher elevation than those at site one (Tukey,  $p < 0.05$ ). Mean values (measured in metres  $\pm$  s.e.m.) were  $0.944 \pm 0.020$ ,  $0.982 \pm 0.016$  and  $1.006 \pm 0.150$  for sites one, two and three respectively ( $n=8$  per site).

**Figure 2.12** Sodium content of soils in (a) 1996 and (b) 1997 shown by site at the inland supratidal marsh at La Pérouse Bay. Error bars show one standard error of the mean for all samples where  $n \geq 3$  ( $n=4$  per treatment per site on June 27, 1997,  $n=3$  per treatment per site on all other dates except where, because of damaged samples,  $n=2$ ; these cases are at site two on July 24, 1997 (no addition and combined fertilizer+mulch treatments)).





## 2.5 Discussion

### 2.5.1 Assisted revegetation potential of *Puccinellia phryganodes* at the intertidal marsh

Documenting differences between intact and degraded sites is important in restoration schemes so that so called 'safe site' environments (*sensu* Harper *et al.* 1961) for potential recolonizing plants can be recognized (Harris *et al.* 1996, Urbanska 1997a). Although safe sites are *a posteriori* by definition, a suite of environmental traits may be recognized that are likely to increase the probability of successful establishment. The measurements made of the edaphic environment in both seasons revealed a number of differences between intact and degraded sites. Although not significant, degraded sites were on average at a lower elevation than sites in intact swards, which probably is a consequence of goose grubbing activity (Jefferies 1988a,b) and the subsequent erosion of the organic layer. In mid-summer (late July) 1996, soils from intact vegetated swards had higher redox potentials than those of degraded soils (Table 2.5), a result observed previously on the east shore and elsewhere at La Pérouse Bay (Srivastava 1993, Wilson 1993), and probably due to oxygen diffusion through the roots into the soil (Howes *et al.* 1981). This difference however is unlikely to affect directly plant establishment in the plugs. With the exception of the early season when some soil samples were still waterlogged from snow melt, the majority of redox potentials measured at the intertidal sites were >250 mV in both degraded and intact sites. At these  $E_h$  values, aerobic decomposition of organic matter and nitrification can still occur (Metting 1993). Some of the observed differences in the soil environment, however, are clearly less favourable to plant establishment. Degraded sites had a significantly higher proportion of clay (Table 2.3) and significantly higher bulk densities. Increased bulk density has been observed in other degraded systems, and results in decreased water infiltration (Bradshaw 1983). Furthermore, in comparison to intact vegetated sites, degraded sites had significantly higher soil temperatures in the upper layers (Table 2.8), evaporation rates (Table 2.7), salinities (Fig. 2.7) and significantly lower soil water content (Fig. 2.6, Table 2.6) which

confirmed results previously reported at La Pérouse Bay (Srivastava 1993, Srivastava and Jefferies 1995a, 1996).

Despite the “stresses” of the degraded soil environment, the relatively low mortality observed in the two-year duration of the experiment (Fig. 2.4, Table 2.2a) demonstrated that plants of *P. phryganodes* in cores can successfully establish in bare sites under some circumstances. Most of the plant mortality observed within plugs (Fig. 2.4) was concentrated within particular plots (Table 2.2a); only plants in four plots (out of the forty-eight established plots) had died by the beginning of the second growing season. The death at the beginning of the second growing season was corroborated by the senescence data which showed that plants of several plots appeared weak (a higher percentage of “yellow” plugs in bare and fertilizer addition treatments; Fig. 2.5a) at the end of the first growing season. Mortality appeared to occur in the winter; little mortality (<5% of plugs with live plants) occurred during the growing season (Fig. 2.4). Although plot mortality did not differ significantly between treatments, Table 2.2a suggests that plots receiving mulch as a form of amelioration were less prone to death during the first winter. It also appears that N/P addition may slow growth and lead to the death of plants in some instances (three of the four plots showing high mortality in 1997 received fertilizer, Table 2.2a). Fertilizer when applied as an inorganic salt may increase the salinity stress on plants under low moisture and high salinity conditions (Soliman and Doss 1992).

Early senescence can occur when increasing demands are made upon a plant that lead to an initial destabilization of functions, followed by either normalization and improved resistance or, if the limits of tolerance are exceeded, by permanent damage or death (Larcher 1995). The overall senescence of plants of *P. phryganodes* (Fig. 2.5) indicated that the performance did not change appreciably. The percent of “yellow” (Fig. 2.5a) or “yellow-green” (Fig. 2.5b) plugs was generally <20% of the total living plugs. On July 11, plugs in all treatment plots, except the plots that received fertilizer+mulch, showed a decrease in the percent of “green” plugs (Fig. 2.5c), and a corresponding increase in the percent of “yellow” and “yellow-green” plugs. The fact that plugs planted into the intact swards of vegetation showed this same pattern suggested that the



senescence peak reflected transplant shock during which the plants were acclimating to the new environment. The magnitude of the transplant shock (a reduction in the percent of “green” plugs) varied significantly with treatment in mid-July 1996; Figure 2c indicates that plants of plugs in bare soil and intact vegetation showed higher senescence than those in soils to which fertilizer, mulch and fertilizer+mulch additions were made to bare soil. The percent of “green” plugs was also somewhat, but not significantly, lower in the early season of 1997 (June 25) than it was later on in the season (Fig. 2.5c), which likely reflected the senescence of overwintering leaves of *P. phryganodes* that occurred shortly after spring melt (Bazely and Jefferies 1989a).

Estimates of above-ground growth indicate that on almost all dates, with all three techniques of growth estimation (Fig. 2.2; cumulative mean radial growth, Fig. 2.3; cumulative mean basal area and Table 2.1a; clipped above-ground biomass), plants that received an amelioration showed significantly greater growth rates than those that did not. Of the treatments, estimates of radial growth and basal area indicated that plants treated with the combined fertilizer and mulch treatment showed significantly higher growth rates on all dates than plants that received only a fertilizer treatment. On most dates, plants treated with the combined treatment had significantly higher growth rates than those treated with only a mulch treatment, with the exception of sampling dates in July, 1996 when growth rates were equivalent. Although statistically insignificant, on July 29, 1996, at all sites, a slight decline was observed in the cumulative mean radial growth rate of plants that grew in the fertilizer+mulch treated plugs; the mean value for growth dropped below that of plants from plugs treated with only mulch. This decline may have been a consequence of increasing resource limitation so that high growth rates could no longer be sustained.

The results indicate that both fertilizer and mulch application ameliorate the soil environment for *P. phryganodes*. Wilson and Jefferies (1996) have shown that nitrogen mineralization rates are lower in degraded sites than in sites with intact vegetation. As hypothesized, the application of fertilizer helped enhance the growth of *P. phryganodes* which has previously been shown to be limited by available inorganic nitrogen at La Pérouse Bay (Cargill and Jefferies 1984). Contrasting measurements made of the edaphic

environment between bare and mulch plots revealed that on most dates, there were no significant differences in soil water content, salinity, temperature values or evaporation loss. However, on July 7, 1996, soil moisture content was significantly higher in soils with mulch treatment (Fig. 2.6) and on July 17, 1997, soil temperature measured under the mulch was significantly lower than that in bare soil (Table 2.8). These slight differences suggest that on some days, the mulch can ameliorate the plant environment by increasing the available soil water content and decreasing soil evaporation. The mechanism of plant growth enhancement by the mulch application is discussed in detail in Chapter 3.

There were significant differences in the magnitude of growth of plants (measured as radial growth and basal area) among sites. On all dates, site two had significantly higher growth rates than site one and significantly higher or equal growth rates of plants than those at site three. As well, the percent of “yellow” plugs in 1996 was more pronounced in site one than the corresponding percentages in sites two or three (Fig. 2.5a) and this reflected in the higher mortality that was observed over the winter in site one compared with death of plants at the other two sites (Table 2.2a). The marginality of conditions for plant growth at site one may be attributed to differences in the edaphic environment. Soils in site one had a significantly higher proportion of sand than that in sites two and three (Table 2.3) which may be expected to lead to soils drying out more readily and thus less available water for plants (Dingman 1994, Brady 1996). In addition, on some dates, the lower growth observed at site one is supported by significantly lower soil moisture values (August 10, 1997) and higher soil salinities values (July 29, 1996) than those measured at the other sites. Total carbon was significantly higher in site two than in sites one and three and total nitrogen was significantly higher in site two than in site three (Table 2.4), which might account for the significantly higher growth rates observed in site two. Despite the differences in magnitude of growth observed among sites, the effect of treatment was the same at all three sites (treatment by site interaction term was strongly insignificant on all dates and for all measures of above-ground growth).

### 2.5.2 Assisted revegetation potential of *Carex subspathacea* at the inland marsh

Contrasting edaphic measurements taken from intact and degraded sites at the inland marsh revealed a number of differences. Soils with intact vegetation had a higher occurrence of light grey bands visible in the soil profile, possibly indicative of more gleying than that which occurred in degraded sites. As observed at the intertidal marsh, although not significant, soils from intact vegetated sites had, on average, lower bulk densities, and exclosures were at a higher elevation. On July 10, 1996, samples from vegetated sites had significantly lower redox potentials than those in degraded sites which is likely a consequence of higher water retention abilities of vegetated sites. Soils from degraded sites had significantly lower total carbon and nitrogen contents (Table 2.9), significantly lower soil moisture contents on July 10 and 19, 1996 (Table 2.11), and significantly higher salinities in soils sampled from both inside and outside exclosures than comparable values of soils from vegetated sites on all dates in both years (Fig. 2.12).

Unlike *P. phryganodes*, the high mortality observed during the course of the experiment indicates that cores of *C. subspathacea* establish in degraded sediments with much greater difficulty (Figure 2.10, Table 2.2b). The successful establishment of plugs planted into intact swards (Figure 2.2) indicated that the high mortality was not due to the transplant, but to the conditions in the soil environment. Plants did not survive the first growing season in one quarter of the total plots, and plants in half of the total plots did not survive the first winter (Table 2.2b). As with *P. phryganodes*, mortality during the course of the second growing season was low (<5%), the majority of mortality occurred during the winter (Figure 2.10). "Plug" mortality (Figure 2.10) was concentrated within particular plots (Table 2.2b). Plot mortality did not differ significantly by treatment, but was strongly a function of the location of exclosures. With the exception, of exclosure "C-2", all other plots that showed complete or high mortality of plants were located within particular exclosures (Table 2.2b). Overall, plot mortality did not vary significantly with treatment (as is clearly indicated by the death of plants in entire exclosures). However, plots in exclosures "C-2" and "D-2" which showed high mortality (not complete mortality like the rest of the plots within those exclosures) were plots that received mulch as the amelioration treatment. As well, plants in the two plots in

exclosure “A-3” that showed high levels of mortality (>75%) in 1997 were those that did not receive mulch; the plots within “A-3” to which mulch was added were still showing less than 75% mortality in 1997.

Concurrent with the higher mortality observed in *C. subspathacea*, 20-30% of plugs with live plants were scored as “yellow” or “yellow-green” throughout the growing season (Fig. 2.11a,b). As observed with *P. phryganodes*, an increase in senescence of plants was observed in plugs placed in vegetated sites as well as in plugs which received the other treatments on July 10, 1996 that probably indicated transplant shock. After this date, the percent of “yellow” and “yellow-green” plugs in plots with intact vegetation decreased, however in some of the other treatments, the percent of “yellow” plugs increased further, that led eventually to significant treatment differences on July 19, 1996 (Fig. 2.11a) and the death of plants in twelve plots on July 28, 1996 (Table 2.2b). As with *P. phryganodes*, *C. subspathacea* produces overwintering leaves that senesce shortly after spring melt (Kotanen and Jefferies 1987). In 1997, this change was seen as an increase in “green” plugs after June 26, 1997 (Fig. 2.11c).

On July 19, 1996 and June 21, 1997, estimates of radial growth (Fig. 2.8) and clipped above-ground biomass (Table 2.1b) respectively, showed that plugs planted into intact vegetated sites had significantly higher growth rates than those planted into degraded sites. On all dates, and with all three growth estimation techniques, there were no significant differences between growth rates of plants in plugs that received any of the four treatments that were planted into degraded sites. As at the intertidal site on the east shore of the Bay (Fig. 2.7), on some dates, sodium content of the soil solution at the inland site (Fig. 2.12) exceeded 20 g/l (sodium content of sea water is 12.5 g/l). The edaphic data showed that salinities in plots that received a mulch treatment were lower than those in bare plots on July 10 and 28, 1996 and on June 27, 1997. Results suggested that in spite of the soil core transplanted with the sod, and the amelioration of the soil environment, soil salinities were still too high at many of the selected exclosure sites to allow successful establishment of plants. The lower salt tolerance of *C. subspathacea* in comparison to that of *P. phryganodes* has been documented (Srivastava and Jefferies 1995b), and previous transplants of *C. subspathacea* from high biomass sites into low

biomass sites have shown higher mortality than similar transplants with *P. phryganodes* (Srivastava 1993). The rhizomatous growth strategy of *C. subspathacea* was also likely to make its establishment a slower process. Kotanen and Jefferies (1987) observed that unlike in *P. phryganodes*, grazing disturbance that affected *C. subspathacea* did not result in a burst of shoot production.

Measurements made of the edaphic environment indicated that *C. subspathacea* was able to grow in soils with much lower redox potentials than *P. phryganodes* (Table 2.10). Ranges recorded at sites in 1996 included negative  $E_h$  values and in 1997,  $E_h$  values were  $<200$  mV at which point net nitrification no longer occurs (Metting 1993). Although some arctic plants show anoxic tolerance (Crawford *et al.* 1994, Crawford 1997), and sod transplants can improve soil oxygen by allowing permeation of air through cracks in the sod (Bruns and Gilcher 1995), anoxia may have been a stress at some of the enclosure sites that had a seemingly more favorable water regime.

Among plants that survived the transplanting, there were significant differences between the magnitude of above-ground growth between sites. On July 10, 1996, plants at site one had significantly lower values of radial growth than plants at sites two or three. On August 10, 1997, results from the clipped above-ground biomass technique showed the same trend. However, this latter result must be interpreted with caution as Table 2.1b clearly indicates that peak seasonal biomass occurred around July 24, 1997. Kotanen and Jefferies (1987) have documented previously that *C. subspathacea* shows early seasonal senescence, thus the results from August 10, 1997 may have reflected senescence differences among sites rather than growth difference among sites. The trend, however, was reversed in 1997 when basal area was used as a measure of growth; plants in sites one and three showed greater values on all dates than plants in site two, and plants in site one showed greater values than plants in site three on July 29, 1996 and June 26, 1997. Given the rhizomatous growth strategy of *C. subspathacea*, it is likely that basal area (which incorporates infilling) provides a more accurate growth measure than the radial growth measured in 1996.

The differences in growth among sites may be accounted for by some of the observed differences recorded in the edaphic environment. In 1997, site one had a

significantly lower soil water content than that in site three on July 10, and than those in sites two and three on July 24 (Table 2.11b). On August 15, 1997, both sites one and three had significantly higher soil water content than site two. Site three, that had organic soil in the top 40 mm of the soil profile, had significantly lower redox potentials on July 24, 1997 (Table 2.10b), significantly higher elevation and significantly lower soil salinities on June 27, 1997 than corresponding values for soils at sites one and two (Fig. 2.12b). These characteristics all indicate that site three was more anaerobic than sites one and two. From personal observation, it was also noted that soil samples from site three had a strong sulfur odour which indicated that sulfate reduction was taking place at these low redox potentials (Metting 1993). Thus, it is likely that the higher water content observed in site three was indirectly a stress on plant establishment as it resulted in waterlogged and anaerobic soil conditions.

## CHAPTER 3: POTENTIAL MECHANISMS OF MULCH AMELIORATION AND THE INFLUENCE OF MICROCLIMATE AND WEATHER ON THE ESTABLISHMENT OF *PUCCINELLIA PHRYGANODES*

### 3.1 Introduction

The Earth's surface presents a boundary layer to water and energy and is thus an important interface for their mass exchange and conversion (Oke 1995). Microclimate, refers to the climate in which plants live, occurring at this interface (Rosenberg *et al.* 1983). It is a function of the incoming energy and water from the surrounding macroclimate, and the characteristics of the "active" surface in question, such as its topography, aspect, albedo, roughness and porosity (Oke 1995). Slight changes in surface characteristics can change microclimate, which in turn can influence plant growth (Jones 1992). The sensitivity of plants to microclimate is exploited frequently in agricultural practice by intentional modifications that result in changes in surface temperatures, moisture regimes and protection from frost and wind (Oke 1995). Slight changes to the microclimate can also affect species establishment. For example, differential heat exchange in grass and bare soil, at a spatial scale <1 m, significantly influences the establishment of snow gum seedlings (Ball *et al.* 1997). In restoration efforts in barren ombotrophic peatlands, the re-establishment of *Sphagnum* diaspores is enhanced by altering the surface geometry by creating a microrelief of ridges and furrows (Ferland and Rochefort 1997). In the Arctic, changes in the microclimate facilitate plant colonization, such as the establishment of propagules in partial dead plant cushions that have a low albedo (Urbanska 1997a).

The purpose of mulching is to alter microclimate by placing a moisture or heat barrier over the top of the soil in order to conserve soil moisture, or induce thermal change (Rosenberg *et al.* 1983, Oke 1995). As discussed in Chapter 2, a peat mulch treatment to the soil surface was used in the assisted revegetation trials of *P. phryganodes* and *C. subspathacea*. Results at the end of the first growing season (1996) indicated that plugs of *P. phryganodes* that received one of the mulch treatments had significantly greater above-ground growth than those that received no amelioration or just the addition

of fertilizer (Figure 2.2). These results prompted the question of how the microclimate within the soil environment was altered by the organic mulch, and what the effect of the alterations was on the establishment of *P. phryganodes*. Four hypotheses were formulated in order to explain why mulching enhanced the above-ground growth of *P. phryganodes*.

- (1) Enhancement was not the result of a microclimatic effect but of a nutrient subsidy available to the plants in the peat that was greater than the subsidy that was available from the additions of inorganic fertilizer.
- (2) Enhancement was the result of a microclimatic change that caused an increase in available water as a consequence of decreased soil surface evaporation from the mulch barrier and a higher infiltration capacity of the peat mulch compared to with mineral sediments.
- (3) Enhancement was the result of a microclimatic change that consisted of a decrease in albedo because of the dark colour of the mulch which, in turn, increased soil temperatures that aided establishment in the early growing season.
- (4) Enhancement of above-ground plant growth was the result of enhanced below-ground growth which, in turn, was the result of a more favourable moisture regime provided by the mulch barrier.

Microclimate is a function of the macroclimate, which occurs a few metres beyond the boundary layer (where turbulent air flow replaces laminar air flow), and determines the levels of radiation and water at the Earth's surface (Rosenberg *et al.* 1983). Yearly variation in macroclimate creates variable microclimate conditions that may act differently on the establishment of *P. phryganodes* in degraded sediments compared to the establishment of plants in intact swards, because of differences in albedo and in surface conditions. In addition to the experiments conducted in 1997 to test the four above hypotheses, differences in weather conditions during the growing seasons of 1996 and 1997 also have been examined. These differences are compared to growth data



of plants of *P. phryganodes* in assisted trials conducted in the snow-free seasons of 1996 and 1997.

## **3.2 Methods**

### **3.2.1 Nutrient subsidy hypothesis**

In order to address the nutrient subsidy hypothesis, levels of exchangeable and soluble ammonium and nitrate ions in freshly collected mulch were examined since previous results indicated that plant growth in the intertidal areas at La Pérouse Bay was limited by the available soil nitrogen (Cargill and Jefferies 1984). Mulch was collected on July 5, 29, and August 20, 1997. Ten grams (fresh weight) were added to an Erlenmeyer flask with 50 ml of 1.0 M KCl (potassium and chloride ions exchange with ammonium and nitrate ions respectively). Five replicates of each sample were prepared and the soil was extracted for four hours with occasional swirling of the flask (Allen *et al.* 1986). Blanks of the de-ionized water and of the 1.0 M KCl solution were kept to check for contamination. Samples of the extracts were filtered through washed Whatman 40 filter papers, and the extracts were frozen and analysed at the University of Toronto for ammonium and nitrate concentrations. Amounts of ammonium ions in the extract were determined by the use of the phenol-sodium nitroprusside method, and Marshall's reagent was used to determine concentrations of nitrate (as nitrite), after nitrate was reduced to nitrite with zinc dust (Wilson and Jefferies 1996). In order to calculate the levels of exchangeable and soluble ammonium and nitrate ions present in the total volume of fresh mulch applied to each plot surface (about 1400 cm<sup>3</sup>), the bulk density of the mulch was measured based on the methodology described in Section 2.2.3 (n=3).

### **3.2.2 Improved water regime hypothesis**

Plants of *P. phryganodes* were watered in order to determine whether an increase in water availability affected the establishment and growth of the grass when transplanted into degraded soil and treated with the different amelioration treatments described in Chapter 2. Because of the logistic difficulty of transporting fresh-water, as well as the

time constraint of daily waterings, the experiment was set up at two sites (50 m apart) 0.5 km from the La Pérouse Bay field station and proximal to the Mast river. Each treatment plot was planted with 25 plugs (5 columns x 5 rows) and each plug was separated from adjacent plugs by 7 cm. The 18 plugs on the perimeter of the plot acted as a buffer zone for each treatment. The remaining 9 plugs in the inner 3 x 3 matrix were designated as experimental plants and their growth was monitored during the season. In each 1 m x 1 m enclosure, the same split-plot design described in Chapter 2 was used. The four treatments (bare, +N/P, +mulch, +N/P+mulch) were randomly assigned to each of the four plots within each enclosure. Plugs of plants were obtained from the donor patch on the east shore of La Pérouse Bay that was used in 1996 (plugs were identical in dimensions; see Section 2.2.1). Enclosures were paired (<1 m apart), and on days when the air temperature reached or exceeded 15° C, one designated enclosure in each pair received 6 L of Mast river water that was sprayed uniformly across each plot in the late afternoon (17:00-19:00 hr solar time). Each pair of enclosures was replicated three times at both sites (n=27 plugs per treatment per site). The experiment was started on June 10, 1997 and plugs were scored for plant growth on June 30, July 14, July 23, August 4 and 18, 1997 based on estimates of basal area described in Section 2.2.2.

### 3.2.3 Albedo and temperature regime hypothesis

The effect of a varying thermal and moisture regime on the establishment of *P. phryganodes* was examined by surrounding plants with polystyrene mulch treatments of differing albedos (Figure 3.0). As with the irrigation experiment, *P. phryganodes* plugs were transported from the donor site on the east shore of La Pérouse Bay, planted and enclosed in degraded sites within 0.5 km of the field station. Each plot was planted with 25 plugs (5 columns x 5 rows) and each plug was separated from adjacent plugs by 7 cm. Peat mulch was used as a control treatment, and white, green and black painted styrofoam tiles (10 mm thick) were used to create different thermal treatments within each 1 m x 1 m enclosure. Around the perimeter of each plot, a buffer strip of 10 cm of peat mulch was applied that allowed all 25 plugs within the plot to be scored. Styrofoam tiles were positioned firmly around the plugs. Each enclosure was replicated three times at two sites



**Figure 3.0** Photograph that depicts the three exclosures at one site in the supratidal marsh proximal to the Mast river in the experiment in which the soil surface conditions were altered. In each of the three exclosures, plants of *P. phryganodes* were treated with peat mulch, black, green and white styrofoam treatments.

(75 m apart). The experiment was started on June 18, 1997 and the growth of plants was scored on July 5, 16, 28, August 12 and 23, 1997 based on the estimates of basal area described in Section 2.2.2.

Surface temperature of soils in the plugs was measured during cloudless periods in plots from all four treatments with the use of a fine thermistor probe inserted to a depth of 0.2 cm on August 13 and 23, 1997 and June 4, 5, 7 and 23, 1998. Several individuals helped in collecting the data that resulted in some differences in the protocol. On June 5 and 7, 1998, measurements were made for all plots in one exclosure only ( $n=3$  per treatment). On all other dates, measurements were made for each treatment plot in each of three exclosures ( $n=10$  on August 13 and 23, 1997 and  $n=4$  on June 4 and 23, 1998). Soil surface temperatures were also measured beneath the styrofoam tiles on June 4, 5 and 7, 1998. Evaporation was measured in three exclosures on June 5 and 23, 1998 based on the method described in Section 2.2.3 (tubes were inserted into holes in each treatment so that the top of the tube was flush with the sediment surface,  $n=4$  per treatment per exclosure). Total incoming and reflected short-wave radiation ( $W/m^2$ ), to and from the surface respectively, of the four different surfaces (coloured tiles and peat mulch) was measured with the use of a LICOR pyranometer (Lincoln, Nebraska, U.S.A.) on August 13, 1997, June 5 and 7, 1998 in order to calculate albedo values.

### **3.2.4 Enhanced below-ground biomass hypothesis**

In order to examine whether the application of mulch enhanced below-ground growth of *P. phryganodes*, an experiment similar to the one established on the east shore of La Pérouse Bay in June 1996, was established on June 14-17, 1997 proximal to site two where the highest values of growth of *P. phryganodes* were recorded, as described in Chapter 2. Two treatments per exclosure, (bare soil and mulch-treated soil) were replicated three times (at a distance  $<10$  m from each other), at two sites that were separated by approximately 100 m. Each treatment plot was planted with 42 plugs (7 columns x 6 rows) and each plug was separated from adjacent plugs by 10 cm. Planting protocol was identical to that for the experiments described above. The 22 plugs on the perimeter acted as a buffer zone for each treatment. The remaining 20 plugs which

occurred in the inner 5 x 4 matrix were designated as experimental units. On July 4, 14, 26, August 7 and 17, four plugs per treatment from each exclosure were removed randomly. Seven tillers were selected randomly from each plug and measured after sediment had been removed by gentle washing. Plugs with less than seven tillers were designated as dead. The number of roots on each tiller was counted, and each was classified either as a live root (white and fleshy), or as a dead root (thin, brown, not fleshy). The number of leaves on each tiller also was counted and the lengths of the roots and shoots measured.

### **3.2.5 Contrasting climatic data and growth data of *P. phryganodes* for the growing seasons of 1996 and 1997**

Climatic data consisting of daily rainfall, daily maximum and minimum temperatures, hourly global solar radiation (direct and diffuse short-wave), hourly wind speed and hourly relative humidity data were obtained for the growing seasons of 1996 and 1997 from the Environment Canada weather station at Churchill Airport, Manitoba, 35 km west of the field station. Unfortunately, there were large omissions (several weeks) in the continuity of data of global solar radiation, so the remaining data were deleted from the analyses. Wind speed and relative humidity data were averaged over 24 hours and expressed as daily estimates. Values of mean basal area of *P. phryganodes* recorded on August 4, 1997 in the non-irrigated, bare, +N/P, +mulch and +N/P+mulch treatment plots of the irrigation experiment were contrasted with mean values of basal area recorded on July 29, 1996 in the same treatments at the intertidal sites on the east shore of La Pérouse Bay.

### **3.2.6 Statistical Methods**

Measurements of the basal area of plants from the irrigation experiment for August 18, 1997 and all measurements of roots were analyzed based on the analysis of variance described in Chapter 2 in which a mixed model split-plot factorial design was used (site (random) and exclosure nested within site (random), were crossed with treatment (fixed)). A mean for each plot for the basal area of plants was calculated from

the values recorded for the plugs in which live plants were present ( $n \leq 9$ ). For data of the total root number, total leaf number, root length, shoot length and root:shoot ratio, a mean for each plug was calculated based on the seven measured tillers. Total root number was calculated (live roots + dead roots) and data were transformed subsequently by taking the natural logarithm to reduce heteroscedasticity. All above data were analyzed using the S-PLUS software (Mathsoft Inc., version 3.3, 1995).

High plant mortality within plots at site one of the thermal regime experiment (all plants died in seven out of the twelve plots) prevented the use of site as a factor in the analysis of basal area of plants. Results of mean basal area of plants per treatment for the remaining plots in site one were calculated and are reported below. Analysis of variance was restricted to the data of basal area of plants for August 23, 1997 at site two. A mean value of the basal area for each plot was calculated from the values recorded for each plug in which live plants were present ( $n \leq 25$ ). A mixed model, two factorial design with exclosure (random) crossed with treatment (fixed) was used to analyze the data. The same model was used to analyze soil temperature and evaporation data with the exception of soil temperatures measured on June 5 and 7, 1998. On these dates, the data were analyzed by the use of a one-way analysis of variance, with treatment as a factor. All data associated with the thermal regime experiment were analyzed with the use of MINITAB software (Minitab Inc., version 10.2, 1994).

Unplanned pairwise comparisons for testing differences among means in all analyses of variances were made based on Tukey's contrasts with appropriate modifications for the design in question (Kirk 1982).

### **3.3 Results**

#### **3.3.1 Nutrient subsidy hypothesis**

Measured levels of exchangeable and soluble nitrate and ammonium (in  $\mu\text{g}$  of nitrogen/ g dry soil, the s. e. m. were all less than 0.001 and thus are not shown) were 0.80 and 25 on July 5, 1997, 1.70 and 53 on July 29, 1997, and 0.15 and 75 on August 20,

1997. Bulk density of the mulch was measured (in g of dry wt/ cm<sup>3</sup> ± s. e. m.) as 0.288 ± 0.029. When estimated as the total amount of exchangeable and soluble nitrogen in the volume of fresh mulch applied to each plot, values of nitrogen (calculated as the sum of exchangeable and soluble nitrate and ammonium and expressed in g of N/ m<sup>2</sup>) were 0.074, 0.157 and 0.215 on July 5, 29 and August 20, 1997 respectively. These levels suggest that any nutrient subsidy in the mulch is minor in comparison to the 10.5 g of N/ m<sup>2</sup> that were added to plots that received fertilizer.

### **3.3.2 Improved water regime hypothesis**

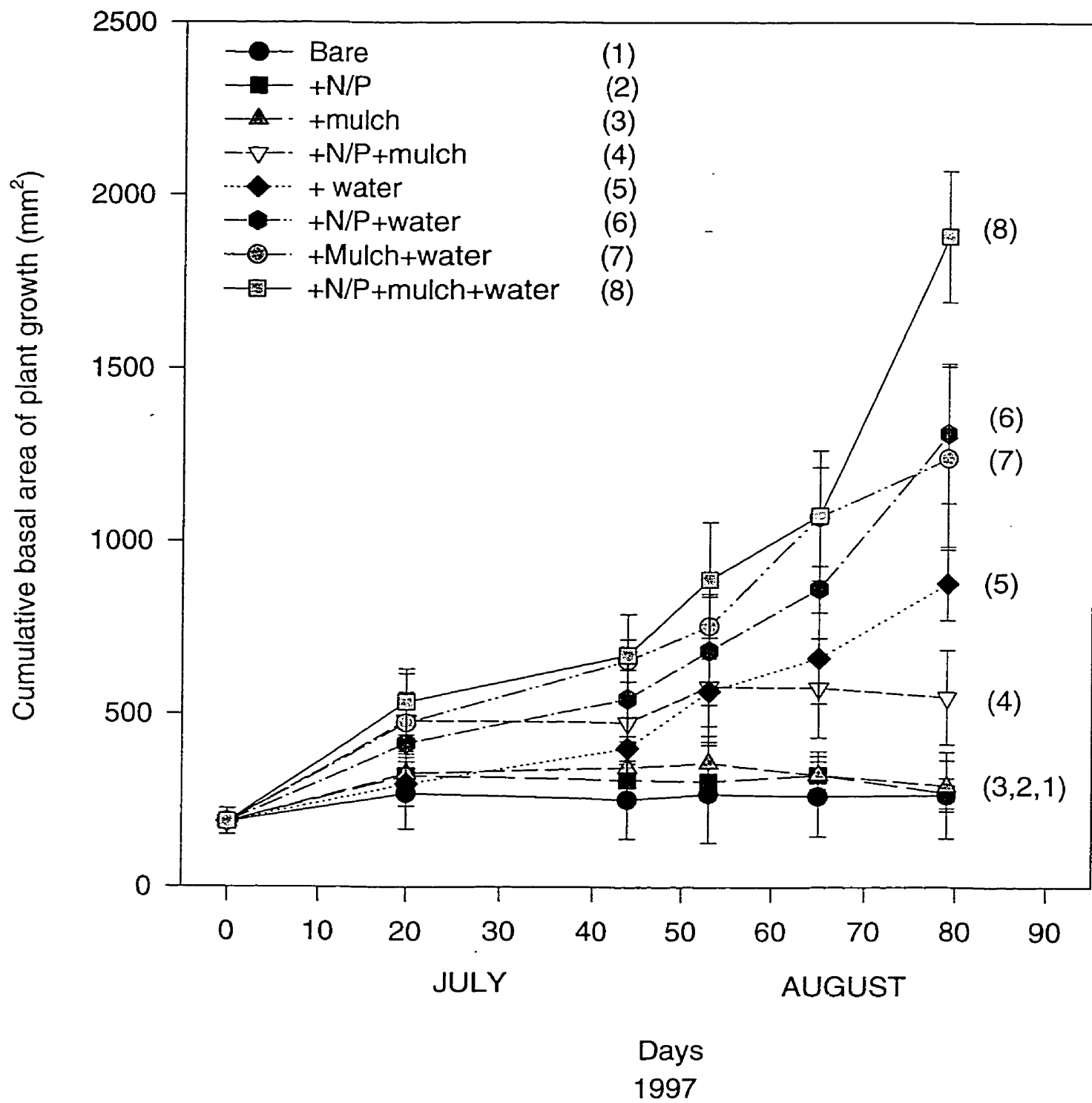
Plants of *P. phryganodes* established successfully in exclosures; no plots showed the death of all plants. The death of plants within plugs was observed in 26 of the 48 plots, but only exceeded 50% of the plugs in a plot in two cases, both of which were plots that did not receive a supplement of water. Mean basal area of plants (Figure 3.1) did not vary significantly with site or exclosure, but did vary significantly with treatment ( $F_{7,7}=12.68$ ,  $p<0.01$ ). With the exception of the contrast between the plants that received a combined fertilizer and mulch treatment without a water supplement and plants that were grown in bare sediments with a water supplement, plants that received all other amelioration treatments with a water supplement had a significantly higher basal area than those that did not receive a water supplement (Tukey,  $p<0.05$ ). Within the four unwatered treatments, the only significant contrast in basal area was between plants that were grown in bare sediment and plants that received a combined fertilizer and mulch addition (Tukey,  $p<0.05$ ). Within the four treatments that were given a supplement of water, there were no significant differences in plant growth.

### **3.3.3 Albedo and temperature regime hypothesis**

As indicated above, *P. phryganodes* established with great difficulty in all exclosures at one of the sites. At this site, the death of all plants was observed in three of the plots that received the peat mulch treatments, two of the plots that received the black

**Figure 3.1** Mean basal area of plants of *P. phryganodes* during the growing season of 1997 for both sites in the experiment to which additions of water were made (n=6 per treatment). Plugs were planted on June 10 and the basal area of plants was scored on June 30, July 14, 23, August 4 and 18, 1997. Error bars show one standard error of the mean.

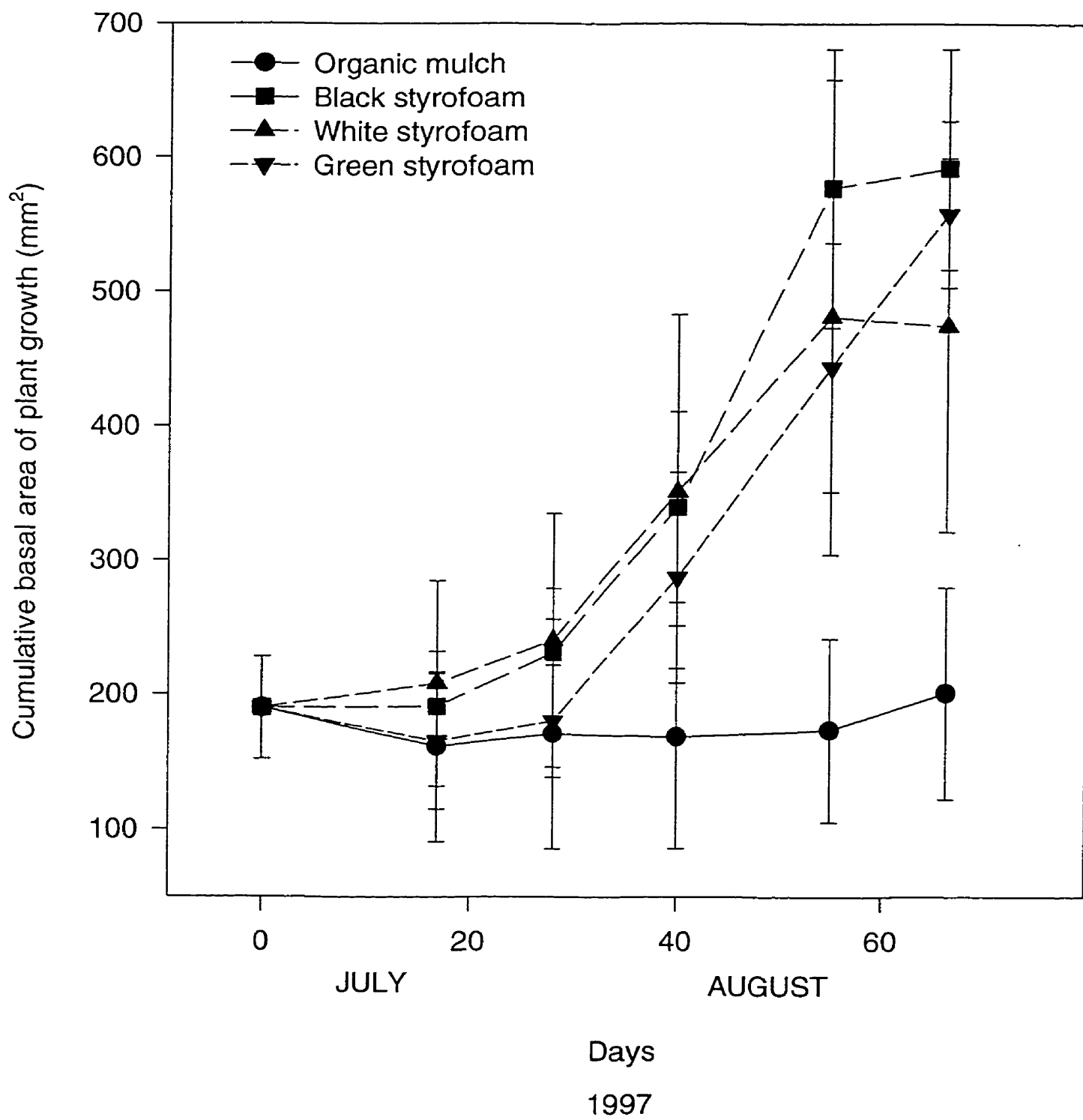




styrofoam treatment and one of each of the plots that received the white and green styrofoam treatments. At site two, high plant mortality (92%) was observed in only one plot treated with peat mulch; some plant mortality was observed in 7 of the 12 plots, however overall mortality was <25%. Values of mean basal area of plant growth ( $\text{mm}^2 \pm \text{s. e. m.}$ ) calculated at site one for the plots with living plants were 210 for the black styrofoam treatment ( $n=1$ ),  $208.2 \pm 113.0$  for the white styrofoam treatment ( $n=2$ ) and  $240.4 \pm 54.2$  for the green styrofoam treatment ( $n=2$ ). Values of mean basal area of plant growth (Figure 3.2) recorded at site two on August 23, 1997 did not vary significantly by treatment or by site. However, mean values were lower, on average, in plots treated with peat mulch than in those treated with styrofoam mulches.

The albedo values of the mulches (reflected radiation/ incoming radiation  $\pm \text{s. e. m.}$ ) were calculated as  $0.48 \pm 0.10$ ,  $0.20 \pm 0.10$ ,  $0.07 \pm 0.02$  and  $0.11 \pm 0.02$  for white, green, black and peat mulches respectively. On all dates in 1997 and 1998, soil temperatures measured in the plugs of *P. phryganodes* (Table 3.1) varied significantly with treatment ( $F_{3,6}=90.98$ ,  $106.1$ ,  $30.83$ ,  $F_{3,8}=138.8$ ,  $F_{3,7}=31.9$ ,  $F_{3,6}=2243$ ,  $p<0.0001$  on August 13, 23, 1997 and June 4, 5, 7 and 23, 1998 respectively) with soil temperatures around plants treated with peat mulch showing significantly higher values than those surrounding plants treated with one of the three coloured styrofoams ( $p<0.001$ ). Contrasts of soil temperatures among the three styrofoam treatments indicated that temperatures measured in black and green plots were significantly greater than those measured in white plots on August 13, 1997 ( $p<0.05$ ), June 5, 1998 ( $p<0.001$ ) and June 23, 1998 ( $p<0.001$ ), temperatures measured in black plots were significantly greater than those measured in white plots on August 23, 1997 ( $p<0.05$ ) and temperatures measured in green plots were significantly greater than those measured in white plots on June 23, 1998 ( $p<0.001$ ). Exclosure was a significant factor on August 13 ( $F_{2,108}=15.06$ ,  $p<0.0001$ ) and August 23, 1997 ( $F_{2,108}=7.60$ ,  $p<0.0001$ ) but insignificant on all dates in 1998. The interaction term between treatment and exclosure was significant on August 23, 1997 ( $F_{6,108}=7.60$ ,  $p<0.0001$ ) and June 4, 1998 ( $F_{3,6}=9.18$ ,  $p<0.001$ ). Soil temperatures measured under the three coloured styrofoam mulches did not vary significantly by

**Figure 3.2** Mean basal area of plants of *P. phryganodes* as a measure of plant growth during the growing season of 1997 at site two in the experiment in which the thermal regime was modified (n=3 per treatment). Plugs were planted on June 18, and the basal area of plants was scored on July 5, 16, 28, August 12 and 23, 1997. Error bars show one standard error of the mean.



**Table 3.1** Soil measurements made in the four mulch addition treatments to bare soil consisting of (a) soil temperature within the plug (°C), (b) soil temperature under the styrofoam mulch (°C) and (c) percent evaporated water. All entries indicate means shown with one standard error of the mean.

(a)		Mulch type	Exclosure # 1	Exclosure # 2	Exclosure # 3
Date and time					
Air temperature (°C)					
Total incoming radiation (W/m <sup>2</sup> )					
13/08/97	17:45-18:00	Peat	13.1 ± 0.1	13.2 ± 0.1	12.7 ± 0.1
Air = 11		Black	12.1 ± 0.1	12.5 ± 0.1	11.9 ± 0.1
Rad. = 800		Green	11.8 ± 0.1	11.9 ± 0.1	11.8 ± 0.1
		White	11.2 ± 0.1	11.2 ± 0.1	11.2 ± 0.1
23/08/97	11:00-11:15	Peat	21.9 ± 0.1	21.9 ± 0.1	21.5 ± 0.2
Air = 23.7		Black	17.4 ± 0.1	18.7 ± 0.1	17.8 ± 0.1
Rad. = not available		Green	17.1 ± 0.1	17.5 ± 0.2	17.5 ± 0.1
		White	16.0 ± 0.1	16.7 ± 0.1	17.0 ± 0.1
04/06/98	16:00-16:15	Peat	8.6 ± 0.1	8.0 ± 0.1	8.1 ± 0.1
Air = 2.5		Black	6.3 ± 0.2	5.5 ± 0.1	6.3 ± 0.1
Rad. = not available		Green	5.7 ± 0.0	6.0 ± 0.1	5.5 ± 0.1
		White	5.0 ± 0.3	5.6 ± 0.2	5.2 ± 0.1
05/06/98	14:30-14:45	Peat	14.0 ± 0.1	---	---
Air = 6.0		Black	10.1 ± 0.2	---	---
Rad = 850		Green	10.4 ± 0.3	---	---
		White	8.4 ± 0.2	---	---
07/06/98	16:30-16:45	Peat	18.6 ± 0.4	---	---
Air = 13.7		Black	15.0 ± 0.2	---	---
Rad = 640		Green	15.0 ± 0.3	---	---
		White	13.7 ± 0.4	---	---
23/06/98	11:45-12:00	Peat	13.1 ± 0.1	13.1 ± 0.1	13.1 ± 0.1
Air = 28.6		Black	12.1 ± 0.1	12.1 ± 0.1	12.1 ± 0.1
Rad= 740		Green	11.8 ± 0.1	11.8 ± 0.1	11.8 ± 0.1
		White	11.2 ± 0.1	11.2 ± 0.1	11.2 ± 0.1

(b)

Date	Styrofoam mulch colour	Exclosure # 1	Exclosure # 2	Exclosure # 3
June 4, 1998	Black	$5.1 \pm 0.0$	$5.0 \pm 0.0$	$5.5 \pm 0.1$
	Green	$5.0 \pm 0.0$	$4.6 \pm 0.1$	$4.3 \pm 0.1$
	White	$4.3 \pm 0.1$	$4.4 \pm 0.1$	$4.6 \pm 0.2$
June 5, 1998	Black	$9.1 \pm 0.2$	---	---
	Green	$7.7 \pm 0.1$	---	---
	White	$8.2 \pm 0.0$	---	---
June 7, 1998	Black	$13.3 \pm 0.1$	---	---
	Green	$13.1 \pm 0.2$	---	---
	White	$12.6 \pm 0.2$	---	---

(c)

Date	Mulch type	Exclosure # 1	Exclosure # 2	Exclosure # 3
June 5, 1998	Peat	$4.1 \pm 0.3$	$3.4 \pm 0.8$	$3.0 \pm 0.4$
	Black	$6.7 \pm 1.1$	$10.2 \pm 1.0$	$4.0 \pm 0.3$
	Green	$8.2 \pm 1.2$	$7.8 \pm 0.2$	$9.2 \pm 0.3$
	White	$4.4 \pm 0.5$	$3.6 \pm 0.5$	$3.5 \pm 0.7$
June 22, 1998	Peat	$18.9 \pm 0.8$	$8.2 \pm 0.7$	$15.3 \pm 0.7$
	Black	$13.7 \pm 1.2$	$13.5 \pm 0.9$	$15.1 \pm 0.9$
	Green	$12.3 \pm 1.3$	$12.8 \pm 0.6$	$14.4 \pm 1.2$
	White	$9.9 \pm 0.4$	$16.7 \pm 0.5$	$10.1 \pm 0.6$

treatment or enclosure on June 4 or 7. Measurements made on June 5, 1998 under the styrofoam mulches (Table 2.1b) varied significantly by treatment; soil temperatures beneath black tiles were significantly higher than corresponding values beneath green tiles, which in turn, were significantly higher than those measured beneath white tiles ( $p < 0.001$  for all contrasts).

The percentage of evaporated water (Table 2.1c) varied significantly by treatment on both June 5 ( $F_{3,6}=5.85$ ,  $p < 0.05$ ) and June 23, 1998 ( $F_{3,6}=17.21$ ,  $p < 0.01$ ). Contrasts on June 5 indicated that evaporation measured in tubes inserted in peat was higher than that measured in holes in green or white styrofoam tiles ( $p < 0.05$ ), and higher in holes in black tiles than those in white tiles ( $p < 0.05$ ). On June 23, 1998, evaporation measured in the peat was higher than in all styrofoam treatments ( $p < 0.05$ ), and measurements made in holes in black and green styrofoam tiles were higher than those made in white styrofoam tiles ( $p < 0.01$ ). "Enclosure" was a significant factor in the analysis of variance model on June 5, 1998 ( $F_{2,36}=3.98$ ,  $p < 0.05$ ) and the treatment by enclosure interaction term was significant on June 5 and 23, 1998 ( $F_{6,36}=6.17$  and  $20.45$ ,  $p < 0.0001$ ).

### **3.3.4 Enhanced below-ground biomass hypothesis**

Plant mortality within sites was relatively low; on all dates only 0-3 plugs (out of the total twelve plugs) per treatment per site were devoid of all live plants. The total number of roots and leaves per tiller did not vary significantly by treatment, site or enclosure on any date. The total number of roots per tiller showed a gradual decline over the growing season. Tillers, on average, had 7-9 roots in the early season and 4-6 roots in the late season (Figure 3.3a). Dead roots were present in the early season, but declined to very low frequencies in the late season. The total number of leaves per tiller showed a gradual increase over the growing season. There were approximately three leaves per tiller in the early season and the number increased to five leaves per tiller in the later season (Figure 3.3b). Although not significant, towards the end of the season, the mean number of leaves per tiller was greater in plants that received mulch than in plants that were grown in bare sediments.

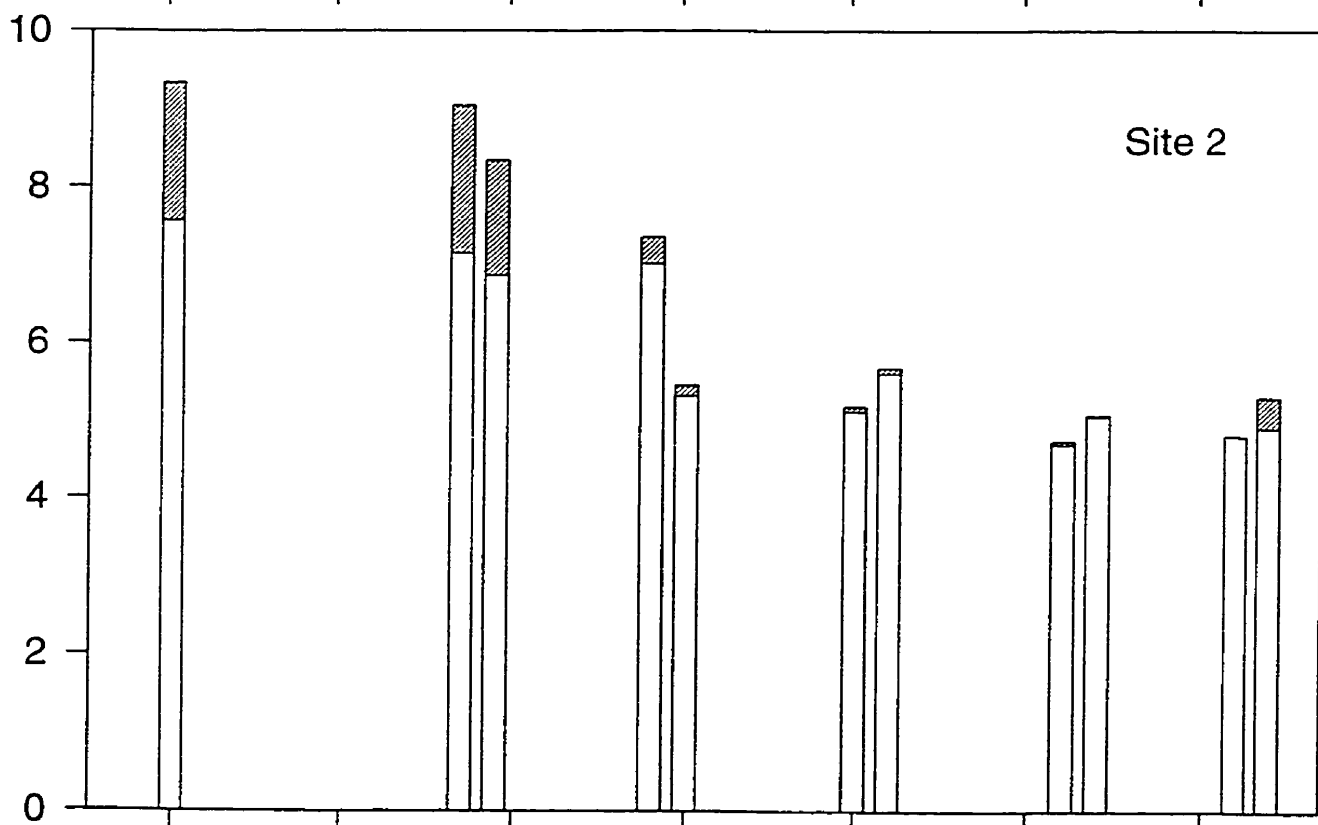
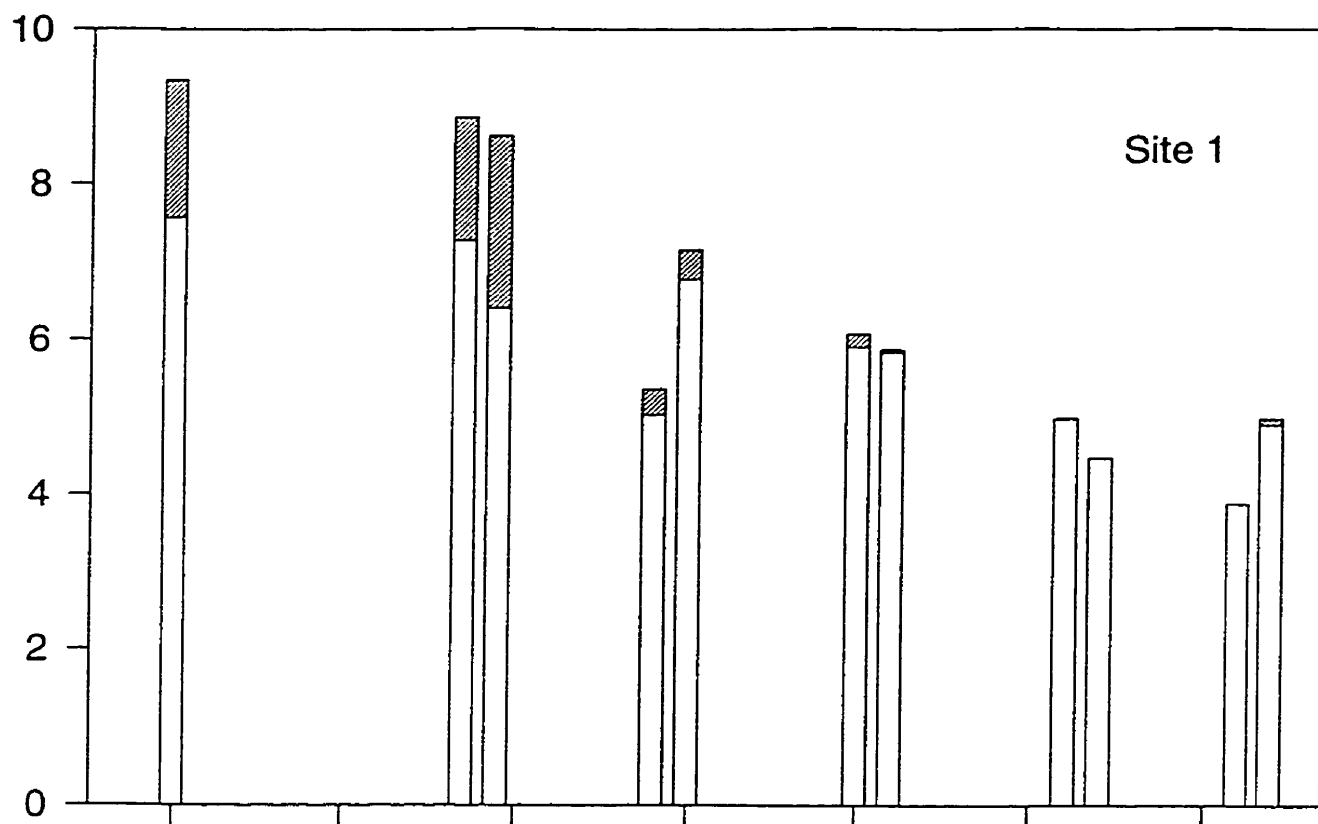
**Figure 3.3** Measurements per tiller of *P. phryganodes* of (a) mean number of roots, (b) mean number of leaves and (c) root to shoot ratio, shown by site, for treatments of bare soil and addition of mulch to bare soil during the growing season of 1997. The experiment to examine root growth was established June 14-17, 1997 and the first solitary column shows measurements made on the planting material collected June 15 (n=15 plugs). The subsequent paired columns show treatments of bare soil (left), and mulch addition to bare soil (right), on July 4, 14, 26, August 7 and 17, 1997 (n≤12 plugs). Comparisons for all measurement types between bare soils and mulch treated soils were insignificant on all dates with the exception of root to shoot ratio measured on August 17, 1997 (p<0.05).



a)

Mean number of roots per tiller

Live roots  
Dead roots

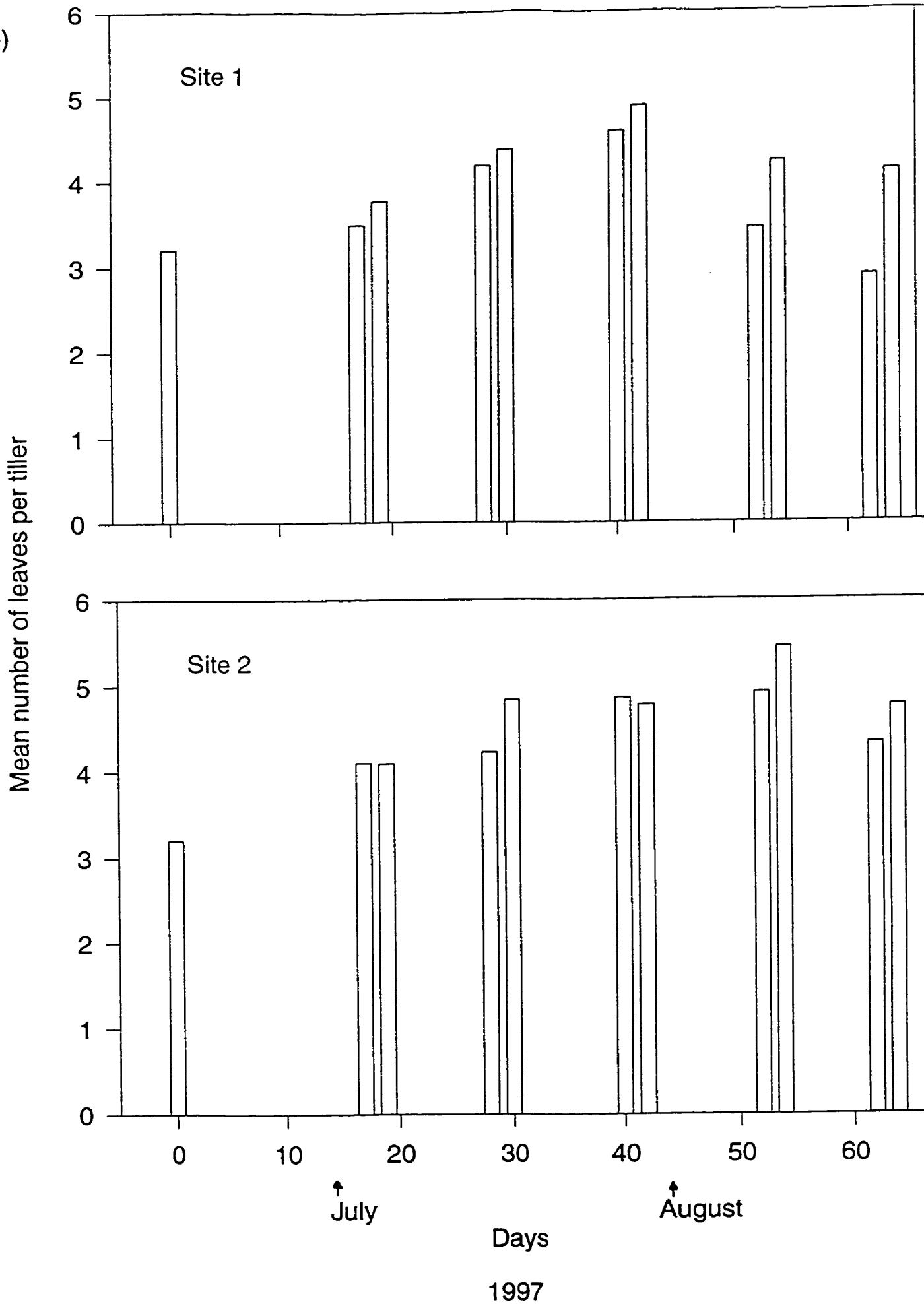


↑  
July

Days  
1997

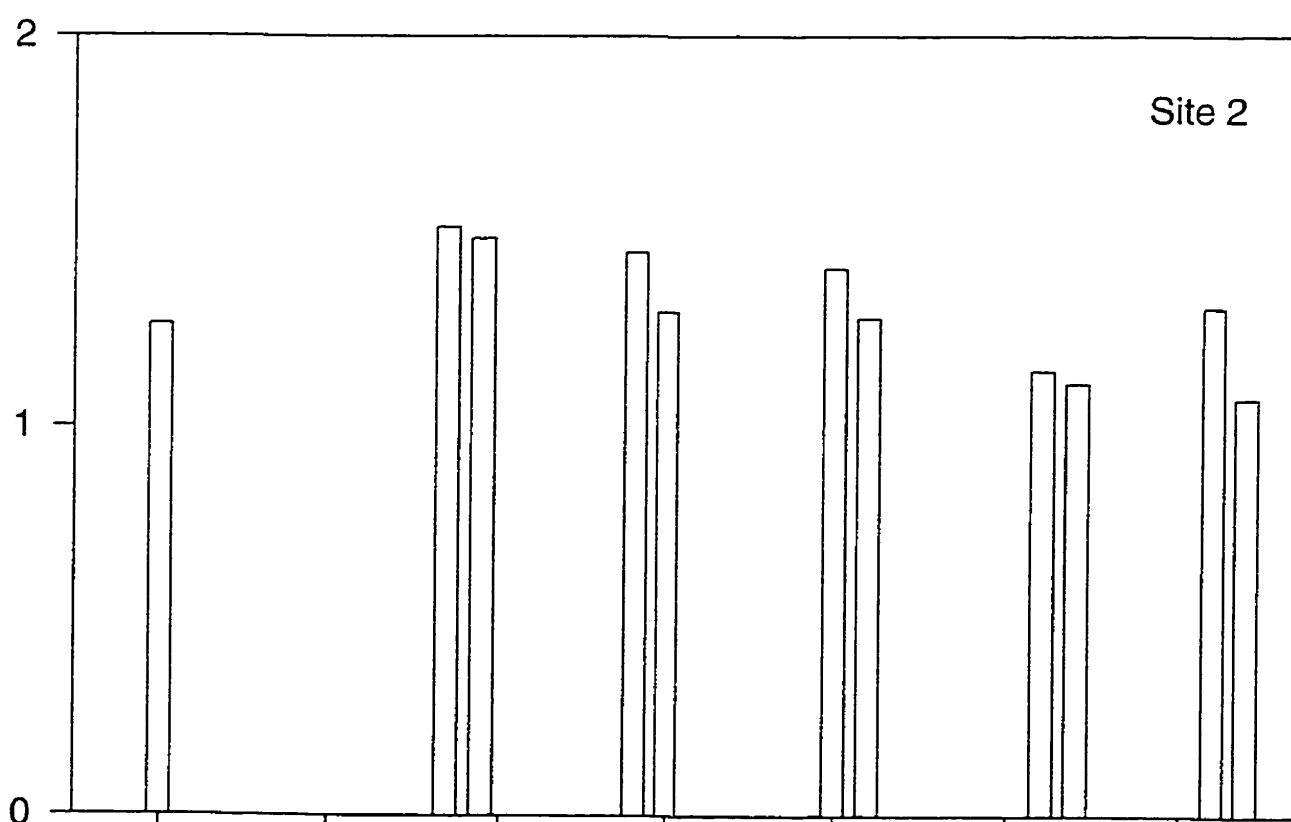
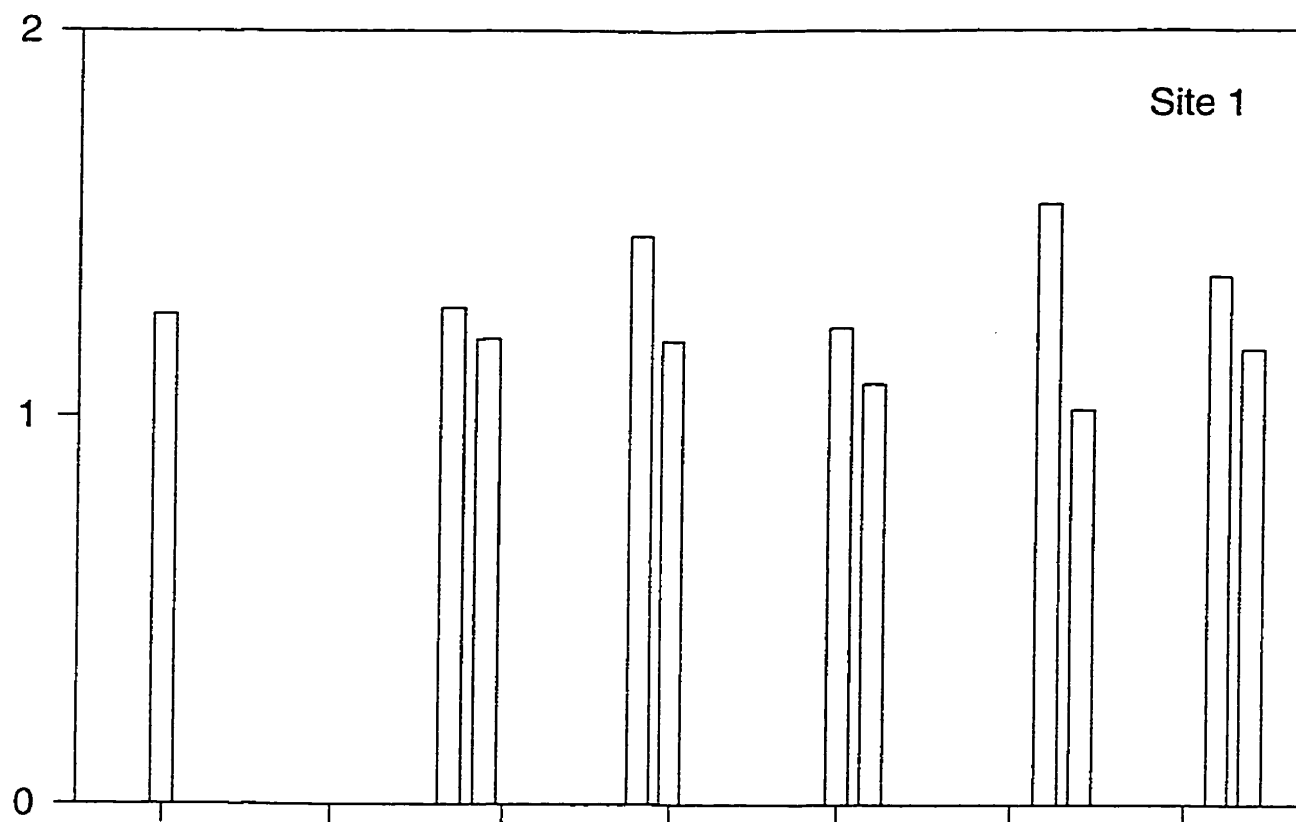
↑  
August

b)



c)

root:shoot ratio



0

10

20

30

40

50

60

↑  
July

↑  
August

Days

1997

Neither root length or shoot length varied significantly with treatment, site or exclosure on any date. The lengths of the roots and shoots of each tiller were between 20-25 mm throughout the season. Root length declined slightly as the season progressed and shoot length was, on average, a few mm shorter in plants grown in bare sediments than in plants treated with mulch. Consequently, the ratio of root to shoot length was, on average, higher for plants grown in bare sediment than for those treated with mulch on most dates (Figure 3.3c) and the difference was statistically significant on August 17, 1997 ( $F_{1,1}=916$ ,  $p<0.05$ ).

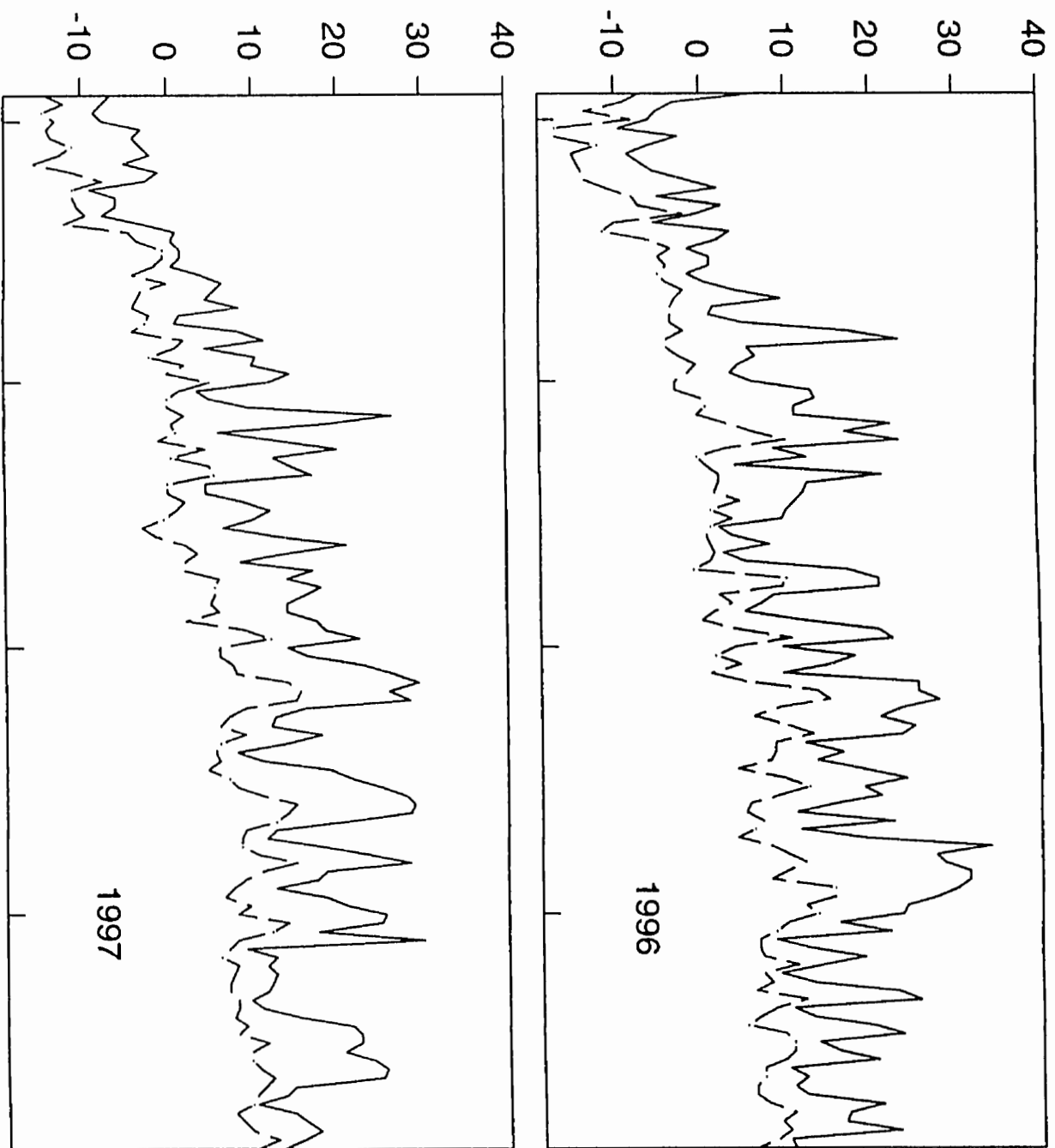
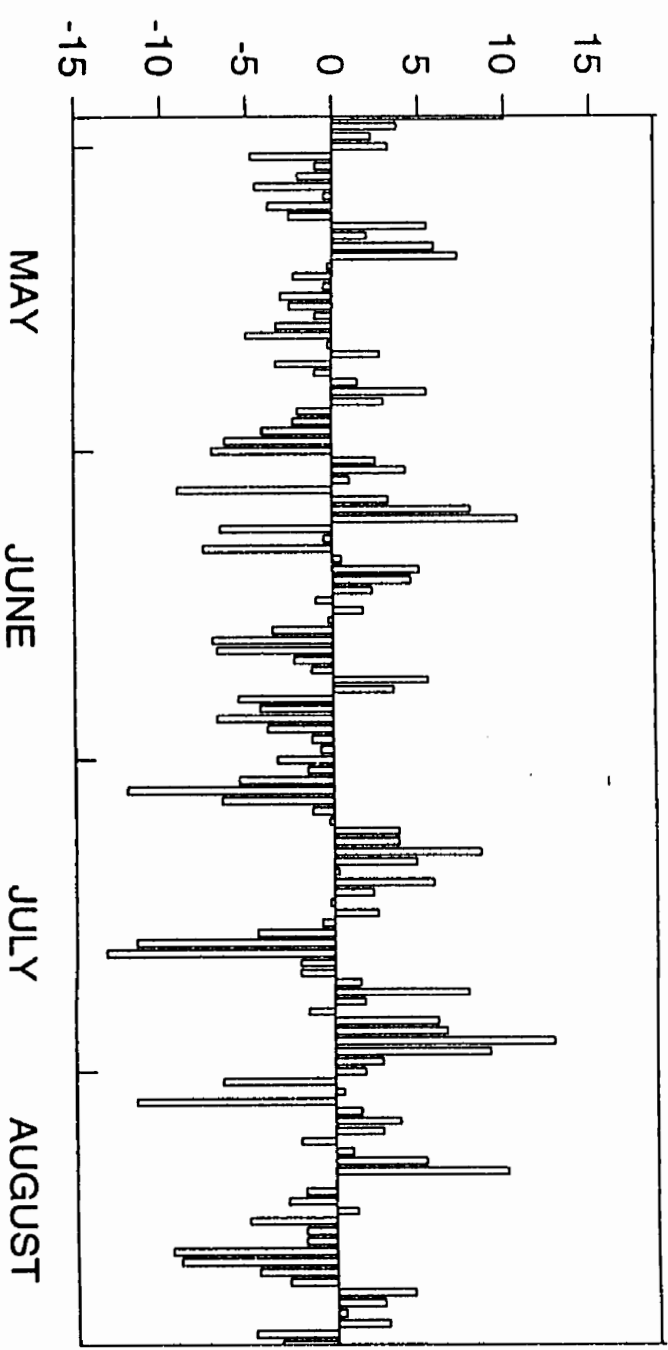
### **3.3.5 Comparing climatic data and growth data of *P. phryganodes* in 1996 and 1997**

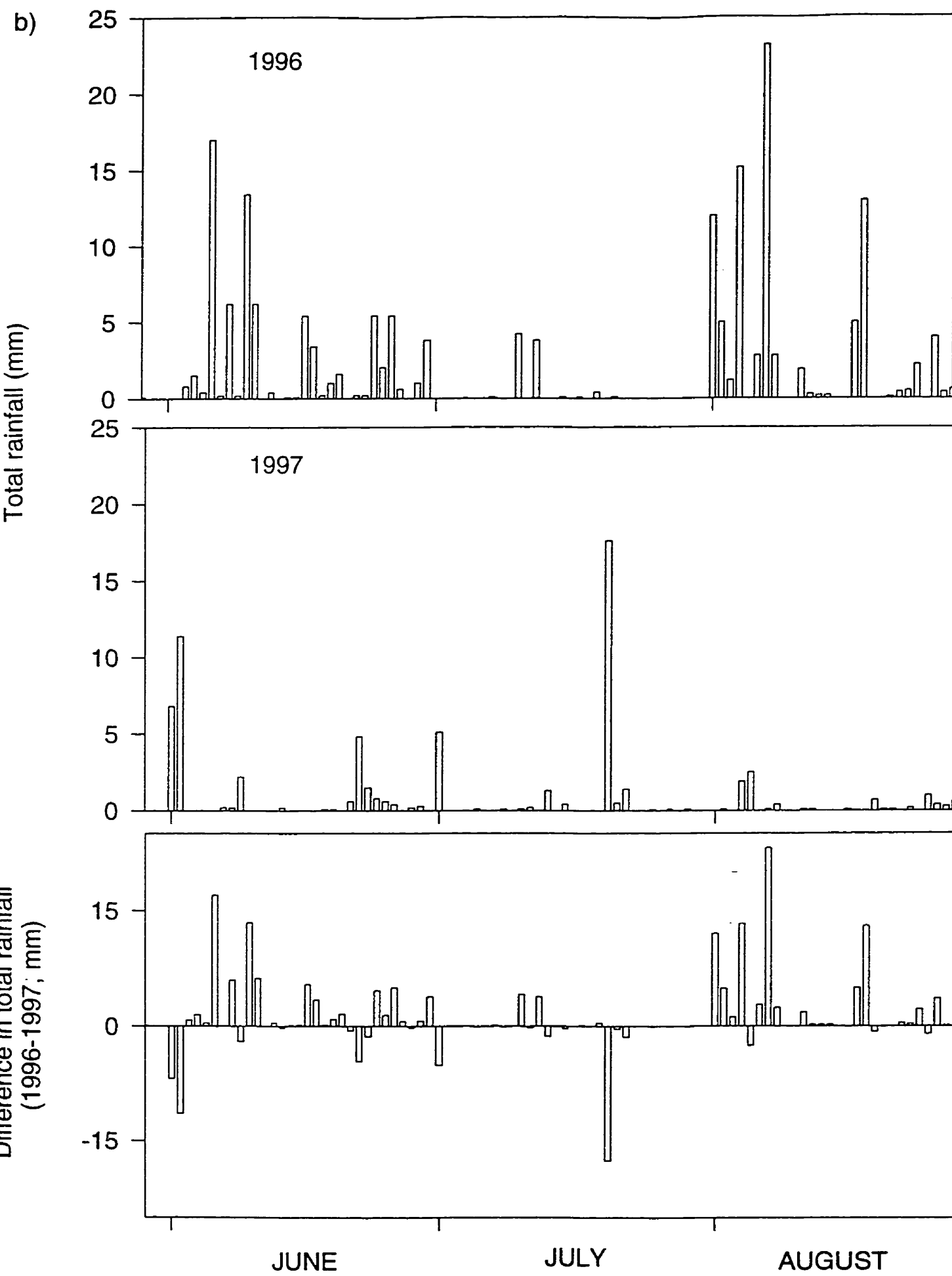
The growing season in 1997 had higher temperatures, less precipitation, lower relative humidity and greater windspeeds than those in 1996 (Figure 3.4). From the period of May 1-September 1, 1997, mean temperature (Fig. 3.4a) and windspeed (Fig. 3.4d) were higher on approximately 10% of the total days with the majority of these days falling during the peak radiation period of late June and early July compared with corresponding data in 1996. Total precipitation in 1996 and 1997, during the period of June 1-September 1, was 175.6 mm and 65.9 mm respectively (Fig. 3.4b). Relative humidity was greater on approximately 15 % of the days in 1996 than in 1997 (frequently on the order of a 20% difference; Fig. 3.4c).

Mean basal areas of plants recorded for all treatments on July 29, 1996 were five to six times greater than those recorded on August 4, 1997. Mean values (measured in  $\text{mm}^2 \pm \text{s. e. m.}$ ) for bare, fertilizer, mulch and fertilizer+mulch treatments respectively were  $1157 \pm 335$ ,  $1730 \pm 437$ ,  $2120 \pm 299$  and  $3047 \pm 462$  in 1996, and  $225 \pm 123$ ,  $253 \pm 32$ ,  $303 \pm 81$  and  $465 \pm 177$  in 1997. Values for plant growth in the plots which received water were also lower than measurements of growth in 1996 when water was not added as a supplement:  $651 \pm 140$ ,  $801 \pm 210$ ,  $1071 \pm 144$  and  $1052 \pm 200$  for bare, +N/P, +mulch and +N/P+mulch treatments respectively.

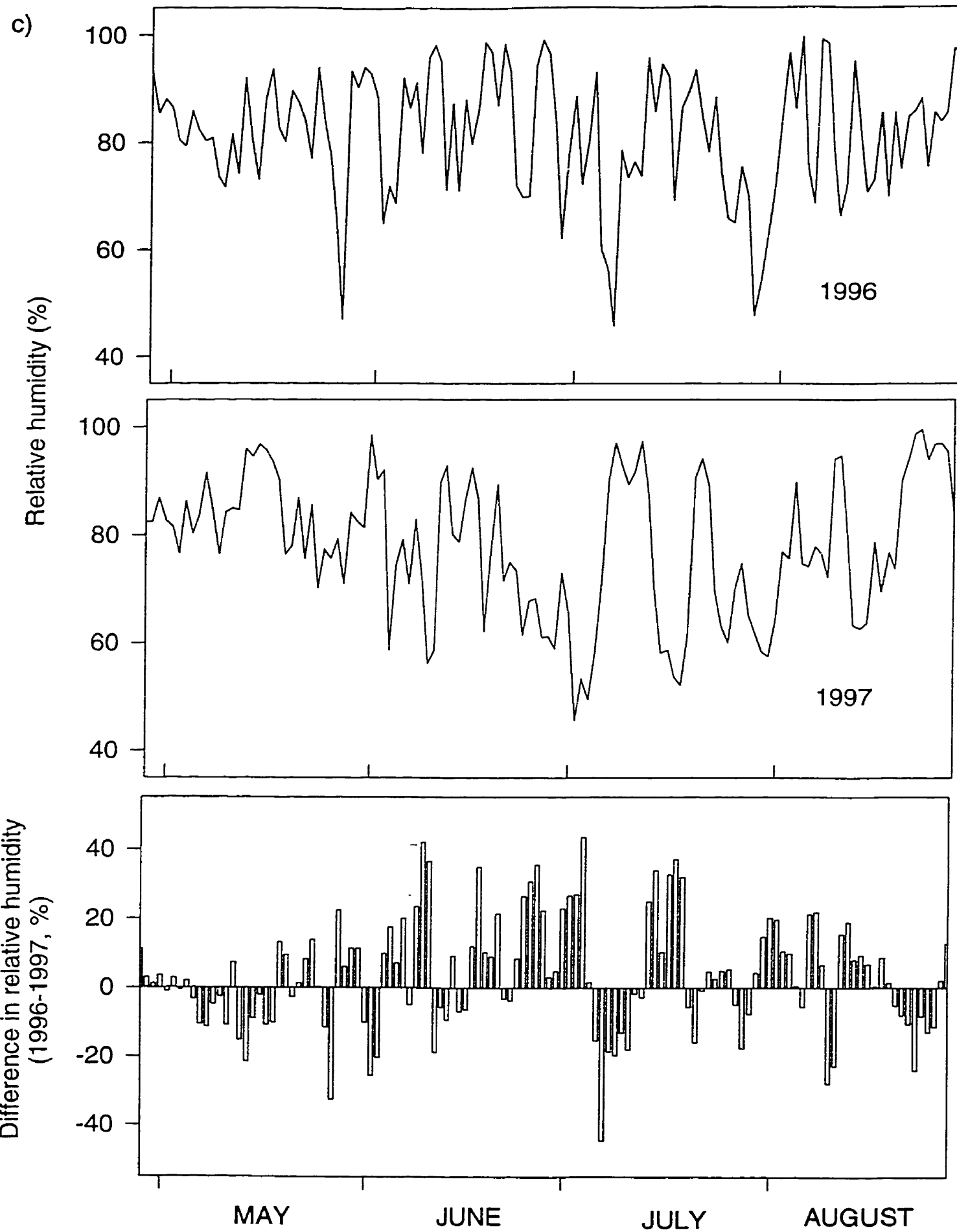
**Figure 3.4** Daily climate variables measured during the growing seasons of 1996 and 1997, consisting of (a) maximum and minimum temperatures, (b) total rainfall, (c) relative humidity and (d) windspeed. With the exception of rainfall that is shown from June 1- September 1, all other measurements are shown from May 1- September 1. Data were measured at the automated Environment Canada Weather Station (Churchill Airport, Manitoba).

a)

Daily maximum and minimum air temperatures  
(degrees C)Difference in mean temperature  
(1996 - 1997, degrees C)

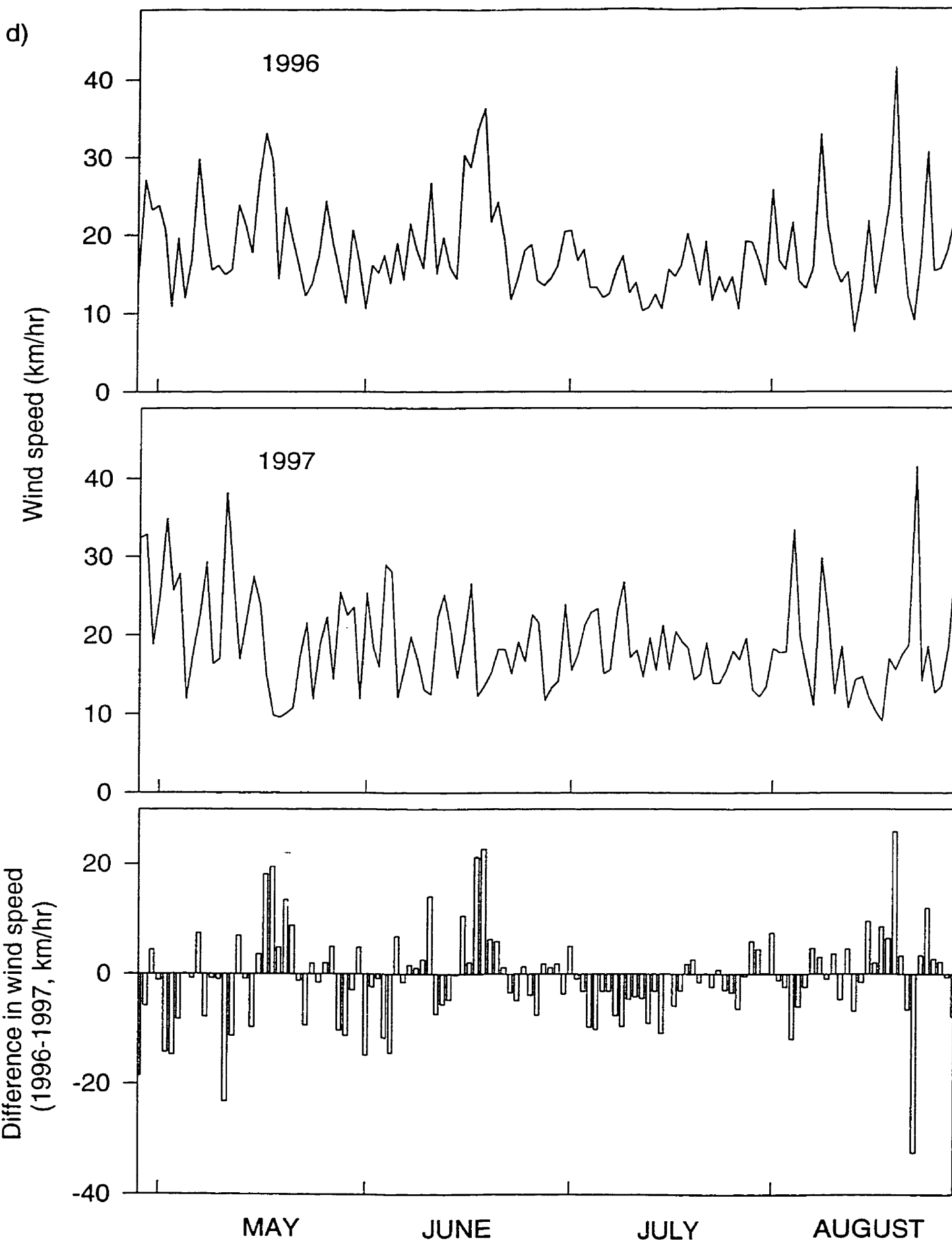


c)





d)



### 3.4. Discussion

In the tussock tundra of Alaska, the naturally occurring organic mat at the soil surface contains most of the stored nutrients in the system (Chapin and Chapin 1980). In the case of recolonization following disturbance, the organic mat provides a continual release of nutrients to colonizers in the growing season, thus making restoration efforts easier when an organic mat is present (Cargill and Chapin 1987). At La Pérouse Bay, however, the low levels of exchangeable ammonium and nitrate ions that were measured in the fresh peat from beneath the willows indicated that the nutrients available to plants in the organic layer of peat mulch that was applied to the soil surface were insignificant in amount in comparison to the inorganic nutrient additions that were made. These measurements suggested that the growth enhancement observed in plants of *P. phryganodes* in response to the mulch treatment was not a function of the nutrient subsidy available in the peat mulch.

As discussed in Chapter 1, manipulating the moisture and thermal regimes have been useful at sites at high altitude (Ferchau 1988, Urbanska 1997a) and in arctic revegetation schemes (Densmore 1994, Shirazi *et al.* 1998), where degradation is directly or indirectly climate-driven, and usually mediated by hydrological change (Walker and Walker 1991). The application of mulch to the soil surface ameliorates the water regime of the soil by providing a barrier to soil surface evaporation (Oke 1995). In addition, the use of organic peat as a mulch increases the infiltration capacity of the soil (Brady 1996). The irrigation experiment indicated that manipulation of the water regime clearly affected the growth of plants of *P. phryganodes* (Fig. 3.1). The higher basal area of plants that received water, in contrast to comparable values of plants in the adjacent, unwatered exclosures indicated that water limited the growth of *P. phryganodes* in 1997. In general, the literature suggests that water limitation of growth of established plants is more prevalent in the High Arctic than in the Low Arctic, although in both environments, plants are highly susceptible to frequent water stress particularly during the establishment phase (Oberbauer and Dawson 1992). However, the effect of water limitation on established plants can be compounded by the adverse effects of increases in the salt

concentrations in sediments. In a study examining the effect of drought on two high arctic grass species (*Puccinellia vaginata* (Lge.) Fern & Weath and *Phippsia algida* (Sol.) R. Br.), Grulke and Bliss (1988) found that although drought conditions induced mortality in both species, *P. vaginata* was more drought tolerant because of its ability to tolerate higher concentrations of salt as the soil dried. The relatively high survival of transplants of *P. phryganodes* in both years suggests that plants of this species can establish and endure drought stress. However, the extreme hypersaline soil conditions that can exist in the degraded sediments in coastal marshes at La Pérouse Bay affect the ability of plants to establish and grow; demography studies on *P. phryganodes* have shown that plants produce new leaves at soil salinity concentrations up to 30 g of dissolved solutes per litre. Above these concentrations, leaf death rate exceeds leaf birth rate that ultimately leads to plant death (Srivastava and Jefferies 1995b).

Measurements made to the soil environment confirmed that the use of the different coloured styrofoam tiles was a successful technique to manipulate the thermal regime. Altering the albedo changes the short and long-wave absorption and sets limits to the surface energy balance and indirectly the water balance in the soil, thus controlling thermal and moisture climates in the adjacent air and soil layers (Oke 1995). The highest albedo was recorded for the white styrofoam tiles, followed by the green tiles, peat mulch and black tiles respectively. Although the lowest albedo was not recorded in the peat mulch, measurements taken from these plots had significantly higher soil temperatures and soil evaporation rates than corresponding values taken from styrofoam tiles. There are several contrasting properties between peat and styrofoam that may account for these differences. Thermal conductivity values for soil are greater than those for air; soils with greater porosity have a lower thermal conductivity (Oke 1995). Although peat has a high porosity, the air space within the peat is substantially less than the air space in the styrofoam thus making the latter a better insulator. Furthermore, the peat was applied to the soil surface without a gap existing between the mulch layer and the degraded sediments. The styrofoam tiles, however, were placed with toothpicks on the soil surface, and because of the roughness of both surfaces, a thin layer of air existed between the styrofoam boundary and the degraded sediment boundary which provided further

insulation. Peat is also more permeable to water than the painted styrofoam surface. Although many holes were cored in the styrofoam tiles to increase their permeability, the lower permeability of the styrofoam likely led to lower evaporative loss from sediment. Among the styrofoam treatments, soil temperature and evaporation rates were inversely correlated with albedo; highest soil temperatures and evaporation rates were observed in black styrofoam treated plots, followed by corresponding values in green and white styrofoam treated plots respectively where the albedo was high.

The effect of the modified thermal and moisture regimes on the plants of *P. phryganodes* was difficult to assess due to the high mortality of plants. Field observations suggested that the bare sediments at site one of the experiment in which the thermal regime was modified were in a more advanced state of degradation (minimal cyanobacterial crust development, no traces of former vegetation) than sediments at site two. The high plant mortality observed in all mulch-treated plots at site one, in addition to the low mean basal area of plants (which showed no significant growth beyond the original basal area of the transplanted plugs) indicated that there might be a threshold of degradation beyond which plants of *P. phryganodes* cannot re-establish. The exclusion of site one from the analysis of variance reduced the statistical power of the analysis which may account for the lack of significance detected among treatments.

Although not statistically significant, basal area of plants at site two was on average 200 mm<sup>2</sup> greater in the styrofoam treatments than in the peat mulch treatment (Fig. 3.2). In considering the water limitation of the plants discussed above, the results suggested that the impermeable nature of the styrofoam provided a better barrier for conserving soil moisture (reducing evaporative loss) than the peat mulch, thus allowing for greater plant growth in the styrofoam treated plots. Among the different coloured styrofoam treatments (when a favorable soil moisture regime was provided), increased temperatures appeared to enhance growth (on August 23, among the styrofoam plots, highest mean basal area was recorded in plants growing in black styrofoam treated plots, followed by green and white styrofoam treated plots respectively). Higher soil temperatures increase productivity in arctic systems by increasing the depth of thaw and promoting nutrient cycling (Chapin 1983, Chapin and Shaver 1985). In a recent

revegetation study in Alaskan oil fields, the establishment of native plants planted into an inactive gravel drill pad was enhanced by increasing soil temperatures with the use of a miniature greenhouse (Shirazi *et al.* 1998).

However, all differences in the plant response and in the environment (measured as soil temperature and evaporative loss) that were noted among the styrofoam treatments must be interpreted with caution; differences were small and sometimes trends were not clear. For example, in July and early August, 1997, plants grown in black and white styrofoam tiles had higher values for basal area than corresponding values for plants grown in green styrofoam tiles. On some dates, the interaction term between treatment and enclosure was significant for both soil temperature and evaporation analyses. The thermal properties of soil are profoundly affected by differences in water content and compaction (Monteith 1990, Oke 1995). The high degree of variability of the soils (see results of edaphic measurements in Chapter 2), differences in water content and bulk density that occur at the microscale (1 cm) are likely to affect soil temperature, evaporation and plant growth.

Measuring soil temperatures in such a way that allows for statistical analysis of different treatments is a challenge. For measurements to be directly comparable, they must all be taken at the same time, since climate factors that influence the soil temperatures, such as radiation or windspeed, can vary over a very short time. Making replicated measurements in four treatment plots, in multiple enclosures at multiple sites during a short time is impossible with a limited number of thermistors. Due to this constraint, measurements were restricted (with exceptions noted above) to three enclosures at one site. As with the basal area data, this approach resulted in a loss of statistical power if a mean is to be calculated for each plot, in order to avoid pseudoreplication (Hurlbert 1984). A mean for each plot was calculated for basal area of plants in order to be consistent with the other plant analyses and because, the response of plants within a plot may be controlled by other factors (e.g. nutrient regime, soil moisture) that may sometimes vary at the scale of the plot. However, it is likely that soil temperature varies at the microscale (large variance within plots), which makes it more likely that each temperature measured within a plot is independent and not a

pseudoreplicate. Based on this reasoning of scale, a mean for each plot was not calculated for the soil temperature data.

When a resource increases in an environment where it was formerly limited, plants often respond by allocating their reserves to acquire the resource (Bloom *et al.* 1985). In a study conducted at the arctic treeline, Landhausser *et al.* (1996) found that increased soil temperature led to a significant increase in root biomass of three subarctic tree species. However, results from the below-ground excavations conducted on plants of *P. phryganodes* indicated that there was no increase in root production (measured as total number of roots and length of root mass) in response to a more favorable water regime provided by the mulch application. The high proportion of dead roots on the established tillers of *P. phryganodes* in the early season (Fig. 3.3a) suggested that plants have roots that overwinter and die once new root production begins (as observed in shoots of *P. phryganodes*; Bazely and Jefferies 1989a). Although not significant, the lower number of leaves and shorter shoots (higher root:shoot ratio) of tillers planted into bare sediments compared with those treated with mulch (Figure 3.3b,c) suggested that the mulch treatment enhanced above-ground growth of *P. phryganodes*, as observed in 1996 (Fig. 2.2). Decreased water availability led to decreased shoots and to increased root:shoot ratios in three subarctic trees as well (Landhausser *et al.* 1996).

Plant growth observed in the assisted revegetation trials on the east shore of La Pérouse Bay in 1996, is not necessarily comparable to that observed in the trials established for the irrigation experiment proximal to the Mast river as the latter site was not an intertidal site. Nevertheless, the soil types are the same and the large variability observed in edaphic conditions within different marshes in the La Pérouse Bay region (Srivastava 1993, Wilson 1993, and previous results described in Chapter 2) suggest that there is just as much variation within a *Puccinellia*-dominated site as there is between sites. Growth rates recorded as basal area were five to six times less in 1997 proximal to the Mast river than they were in 1996 on the east shore of La Pérouse Bay. Furthermore, field observations made on above-ground biomass of plants that were excavated for the root experiment on the east shore of La Pérouse Bay showed that above-ground growth of transplants made in 1997 were also much lower than that observed in 1996. Important

factors influencing plant water relations include solar radiation, air temperature, atmospheric humidity/vapour pressure deficit and wind velocity (Oberhauer and Dawson 1992, Dingman 1994, Burman and Pochop 1994). Evaporation increases with increasing temperature, increasing windspeed and a greater differential between the vapor pressure of the evaporating surface and that of the overlying air (Dingman 1994). It is likely that the lower precipitation (Fig. 3.4b), higher temperatures (Figure 3.4a), lower relative humidity (Fig. 3.4c) and higher windspeeds recorded in 1997 all contributed to increasing evaporative loss from soils, and decreased the growth potential of transplanted plants. The conditions observed in 1997 are likely indicative of changes that may occur in the Arctic in response to global climate change (higher temperatures, lower rainfall; Kane *et al.* 1992, Maxwell 1992, Chapin *et al.* 1995, Keeling *et al.* 1996, Munn and Maarouf 1997, Myneni *et al.* 1997). The lower growth rates and higher mortality observed in trials conducted in 1997 suggest that with such changes in macroclimate, restoration of the salt-marsh at these sites may become increasingly difficult.

## CHAPTER 4: THE RATE OF NATURAL REVEGETATION OF *PUCCINELLIA PHRYGANODES* WITHIN THE COASTAL SALT-MARSH

### 4.1 Introduction

An understanding of the patterns and rates of natural revegetation processes is important in order to predict the long-term impact of disturbances on ecosystems (Kershaw and Kershaw 1987, Harper and Kershaw 1996, Jorgenson 1997, Vilchek 1997). Biological processes often occur on more rapid timescales than pedological processes, such that the rates of natural revegetation on degraded land can be extremely slow where the soil environment has a diminished amount of resources to sustain plant growth (Bradshaw 1997b). Documenting patterns and rates of natural revegetation is also important in order to improve techniques of assisted restoration (Cargill and Chapin 1987, 1989b), as well as to assess the need for assisted restoration schemes (Jorgenson 1997), as they are often costly to implement (Edwards and Abivardi 1997, McKendrick 1997).

At La Pérouse Bay, exclosures have been erected on bare sediments by R.L. Jefferies and colleagues in both an intertidal and supratidal degraded salt-marsh in order to observe any potential natural revegetation. Specifically, a 5 m x 5 m exclosure was erected in 1984 at an inland supratidal site (<1 km from the supratidal site described in Chapter 2) and eight exclosures (2 m x 2 m) were erected in 1992 on the tidal flats proximal to the estuary of the Mast river on the south-west shore of La Pérouse Bay (see Fig. 6.1). Field observations have indicated that to date, no plant cover has established in the supratidal exclosure, except on the perimeter which is an artifact associated with litter accumulation at the base of the wire exclosure. Salinities at this site can exceed 120 g of dissolved solutes per litre (Iacobelli and Jefferies 1991). In contrast, at the intertidal site, which is subject to tidal inundation and also receives fresh water from the braided estuary of the Mast river, vegetation (predominantly colonies of *P. phryganodes*) has established in all eight of the exclosures.

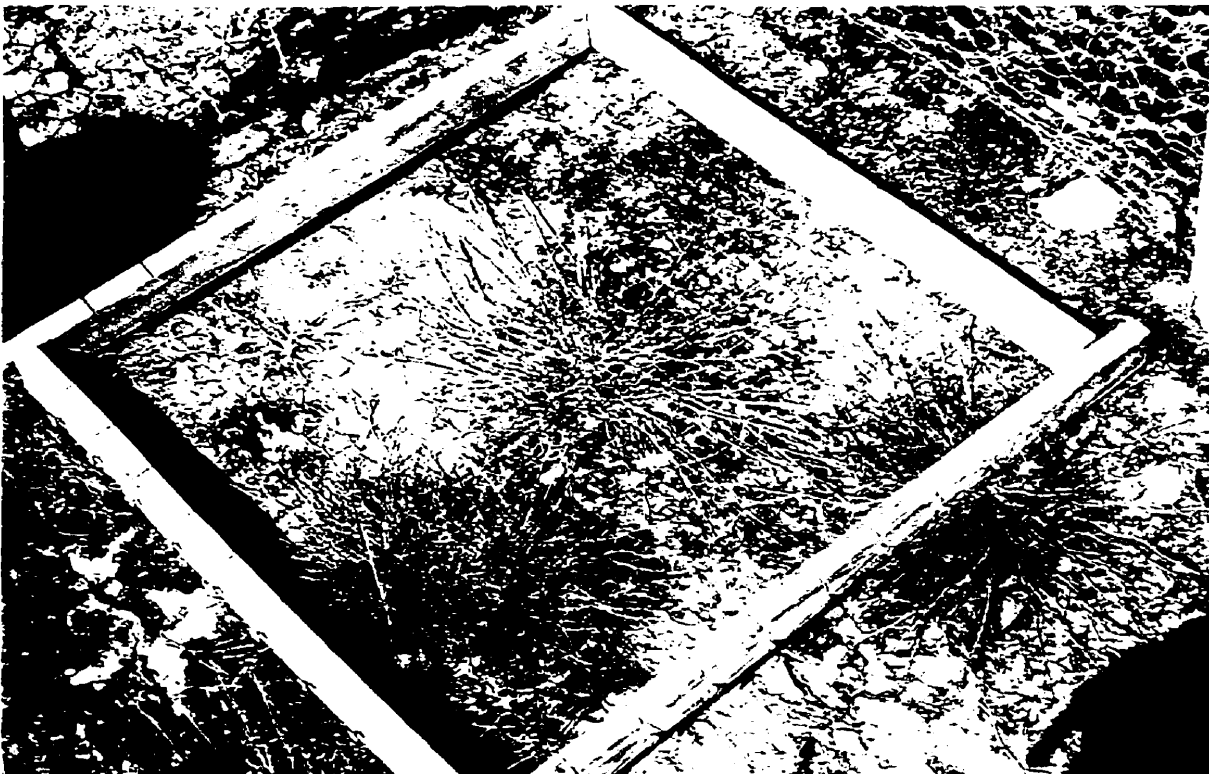


**Figure 4.1** Photographs that show the variation in total plant cover and species diversity among the exclosures undergoing natural revegetation on the south-west shore of La Pérouse Bay. Species that are visible in (a) include *Puccinellia phryganodes*, *Ranunculus cymbalaria* (top right), *Hippurus tetraphylla* (top left) and *Senecio congestus* (bottom left). The circular stoloniferous growth of *P. phryganodes* is shown clearly in (b).

a)



b)



In order to provide a context for the assisted revegetation trials with plants of *P. phryganodes* described in Chapter 2, the vegetation in the exclosures on the south-west shore of La Pérouse Bay made it possible (1) to document the species of plants that have successfully established in the five growing seasons since the exclosures were erected and (2) to contrast the growth rates of colonies of *P. phryganodes* that established naturally on bare sediments to those of plugs of *P. phryganodes* that were planted into bare sediments and exclosed in late June, 1996 (as described in Chapter 2).

## 4.2 Methods

The presence of all species that had established within the eight exclosures that were undergoing natural revegetation were recorded. The colonies of *P. phryganodes* in the exclosures on the south-west shore of La Pérouse Bay showed a similar circular growth pattern (Fig. 4.1b) to that of the transplanted plugs of *P. phryganodes* on the east shore of La Pérouse Bay (Fig 2.1b). On July 27-29, 1996, plots were established within seven of the eight exclosures that were undergoing natural revegetation where individual colonies of *P. phryganodes* could be identified (total cover was approximately 90% in one of the eight exclosures which made the identification of individual colonies impossible). Each colony was mapped by visually estimating the percent cover in 5 cm x 5 cm grid squares to the nearest 5% (Fig. 4.1b). Based on these estimates, the area of *P. phryganodes* cover in each 5 cm x 5 cm square was calculated and areas were summed to give an estimate of the total area of each colony. On August 20-22, 1997, twenty-six of the colonies that were mapped in 1996 that occurred in six of the eight exclosures were relocated and mapped again (the seventh exclosure was destroyed in the winter of 1996-97 and grubbed the following spring). It was not possible to identify all the colonies that were mapped in 1996, as in some plots the total cover had increased considerably and colonies had formed a continuous mat of vegetation.

The basal areas of the colonies of *P. phryganodes* in the assisted revegetation experiment on the east shore of La Pérouse Bay were measured on July 29, 1996 and

August 12, 1997, as described in Section 2.2.2. Due to the design of the experiment, basal area measurements were free to vary between 2 cm<sup>2</sup> (the area of the initial transplant material) and 61 cm<sup>2</sup> (the area of the colony prior to coalescence with adjacent colonies). In two of the original twelve plots, mean basal area dropped to 0 cm<sup>2</sup> due to the death of plants. The mean basal area of colonies in these plots were omitted from the comparison.

The unknown number of days in the growing season after plants were last scored on July 29, 1996 did not make it possible to calculate relative growth rates for the colonies of *P. phryganodes*. As an alternative growth rate measurement, the ratio of the area of the colony measured in August 1997 to the area of the colony measured in June 1996 was used.

### 4.3 Results

After five growing seasons in the absence of grazing, a total of eleven vascular plant species established in the eight exclosures undergoing natural revegetation on the south-west shore of La Pérouse Bay (Table 4.1). Plants of *Puccinellia phryganodes* had established in all eight of the exclosures. Other species that established successfully were *Senecio congestus*, *Ranunculus cymbalaria*, *Hippurus tetraphylla* and *Juncus albens* that were recorded in five, four, three and three of the exclosures respectively.

Colony sizes of *P. phryganodes* measured at the end of July, 1996 ranged from 1.3 to 586 cm<sup>2</sup> in exclosures undergoing natural revegetation and 2.2 to 36.3 cm<sup>2</sup> in exclosures undergoing assisted revegetation. The area of 12 of the 26 colonies on the south-west shore of La Pérouse Bay and the mean colony area in 8 of the 10 plots on the east shore of La Pérouse Bay were less than 20 cm<sup>2</sup> after five and one growing season respectively (Table 4.2). The other 14 colonies in the exclosures undergoing natural revegetation exceeded areas of 20 cm<sup>2</sup>, and 6 of these 14 colonies had areas greater than 100 cm<sup>2</sup>. Colony sizes of *P. phryganodes* remeasured in August, 1997 ranged from 13.8 to 973 cm<sup>2</sup> in exclosures undergoing natural revegetation and 4.2 to 58.4 cm<sup>2</sup> in exclosures undergoing assisted revegetation. Of the areas recorded in 1997, 2 of the 26

**Table 4.1** The presence of species that have colonized bare sediments in eight exclosures after five years at an intertidal site on the south-west shore of La Pérouse Bay.

Species	1	2	3	4	5	6	7	8
<i>Puccinellia phryganodes</i>	x	x	x	x	x	x	x	x
<i>Senecio congestus</i>	x		x	x	x		x	
<i>Ranunculus cymbalaria</i>	x		x	x			x	
<i>Hippurus tetraphylla</i>			x	x	x			
<i>Juncus albens</i>			x	x			x	
<i>Carex subspathacea</i>			x		x			
<i>Ranunculus purshii</i>			x				x	
<i>Salicornia borealis</i>		x						
<i>Salix</i> seedlings			x					
<i>Stellaria humifusa</i>			x					
<i>Triglochin palustris</i>			x					

**Table 4.2** The total number of colonies of *P. phryganodes* (percentage frequency in brackets) per frequency classes of areas of colonies of *P. phryganodes* as recorded on July 27-29, 1996 at intertidal sites in exclosures undergoing natural revegetation on the south-west shore of La Pérouse Bay (n=26), and in exclosures undergoing assisted revegetation on the east shore of La Pérouse Bay (n=10).

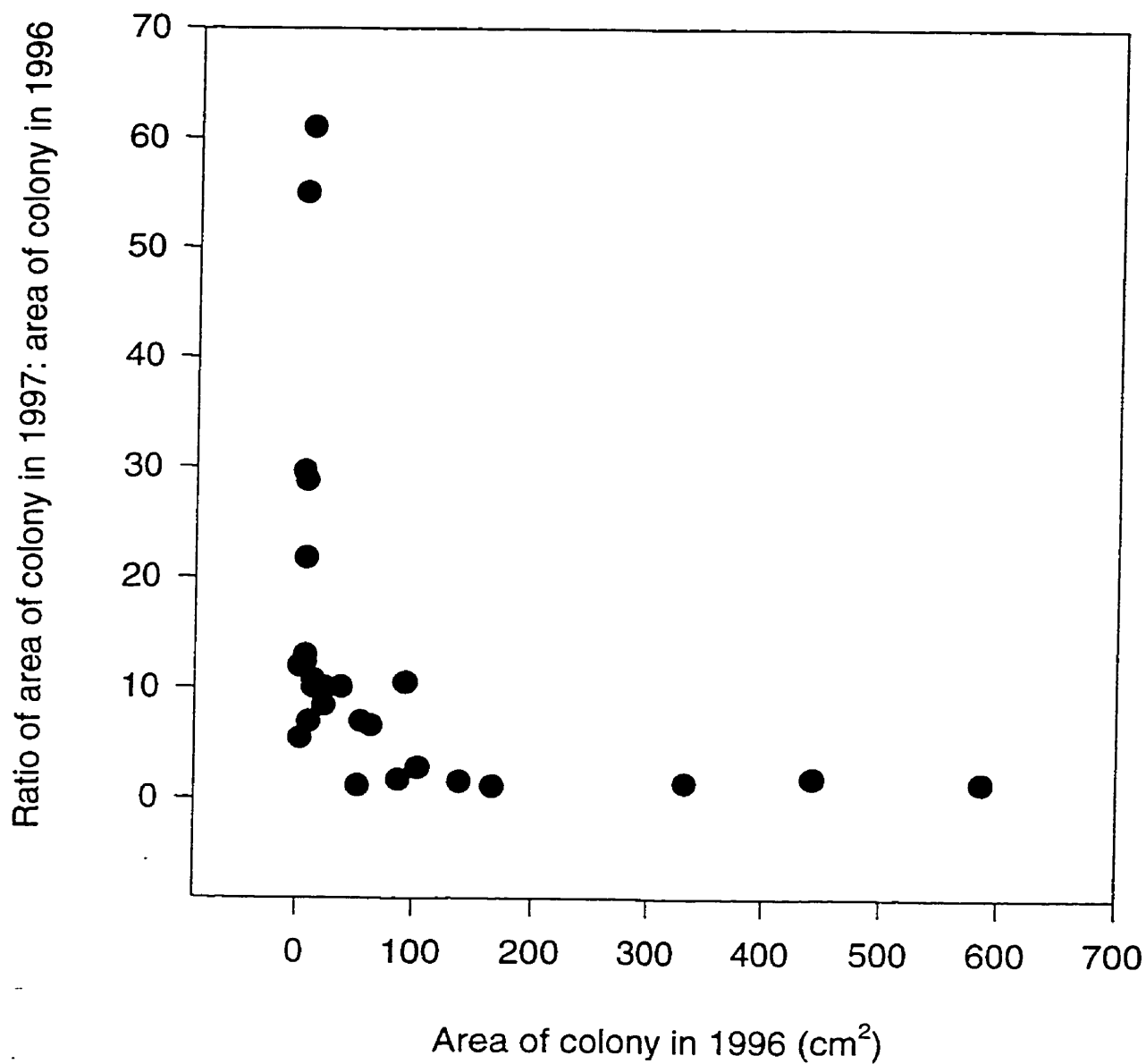
Frequency classes of colony areas (cm <sup>2</sup> )	Total number of colonies on the south-west shore of La Pérouse Bay (natural revegetation)	Total number of colonies on the east shore of La Pérouse Bay (assisted revegetation)
0-10	10 (38.5)	5 (50.0)
11-20	2 (7.7)	3 (30.0)
21-50	3 (11.5)	2 (20.0)
51-100	5 (19.3)	0
101-200	3 (11.5)	0
201-500	3 (11.5)	0

colonies in the exclosures undergoing natural revegetation and 5 of the 10 colonies in the exclosures undergoing assisted revegetation were less than 20 cm<sup>2</sup>.

The growth rate, calculated as the ratio of the colony area measured in 1997 to that measured in 1996, ranged from 1.2 to 61 in exclosures undergoing natural revegetation and 1.1 to 2.2 in exclosures undergoing assisted revegetation. In exclosures undergoing natural revegetation, of the 26 colonies, 14 colonies had ratios less than 10 and the remaining 12 colonies had ratios ranging from 10 to 61 (Table 4.3). In exclosures undergoing assisted revegetation, all 10 colonies had ratios less than 10; 9 of these colonies had ratios less than 2. The relationship between the ratio of areas and the size of the colony as measured in 1996 for the 26 colonies in the exclosure undergoing natural revegetation is a negative exponential function (Fig. 4.2). The large variance of ratios observed in these exclosures is restricted to colonies of *P. phryganodes* that were less than 30 cm<sup>2</sup> in 1996; colonies that were greater than 30 cm<sup>2</sup> showed less variance in growth rate with ratio values ranging from 1.2 to 10.5.

**Table 4.3** The total number of colonies of *P. phryganodes* (percentage frequency in brackets) per frequency class of ratios of areas of colonies of *P. phryganodes* recorded in August 1997 to those recorded in late July 1996. Ratios are shown for colonies at intertidal sites in exclosures undergoing natural revegetation on the south-west shore of La Pérouse Bay (n=26), and exclosures undergoing assisted revegetation on the east shore of La Pérouse Bay (n=10).

Frequency classes of ratios of colony areas in 1997:1996	Total number of colonies on the south-west shore of La Pérouse Bay (natural revegetation)	Total number of colonies on the east shore of La Pérouse Bay (assisted revegetation)
1.0-2.0	7 (26.9)	9 (90.0)
2.1-10.0	7 (26.9)	1 (10.0)
10.1-50.0	10 (38.5)	0
50.0-100.0	2 (7.7)	0



**Figure 4.2** The relationship between the growth rate of twenty-six colonies of *P. phryganodes* (ratio of colony area measured in 1997 to that measured in 1996) and the area of the colony measured in 1996 in exclosures undergoing natural revegetation on the south-west shore of La Pérouse Bay.

#### 4.4 Discussion

The results indicate that the rate of revegetation of *P. phryganodes* varies considerably within the spatial scale of a site (10-100 m) as well as within that of an exclosure (<2 m). As discussed in Chapter 2, the mean basal area of plants of *P. phryganodes* on the east shore of La Pérouse Bay varied significantly with site and exclosure as factors in the analyses on all dates (spatial scales of 10-100 m). At a similar spatial scale, among the eight exclosures undergoing natural revegetation on the south-west shore of La Pérouse Bay, the extent of total plant cover varied from 5 to 90% of the total exclosed area (Fig. 4.1). At the end of July, 1996, in three of these exclosures, some colonies of *P. phryganodes* had begun to coalesce into a continuous mat of vegetation. Based on the variance in areas of colonies of *P. phryganodes*, it is likely that the process of natural revegetation at this site began shortly after the exclosures were erected. The small colonies with areas from 2-10 cm<sup>2</sup> likely established in the growing season of 1996 (all of these colonies were greater than 10 cm<sup>2</sup> when measured again in 1997). Large colonies, such as those greater than 500 cm<sup>2</sup> and those that were not mapped as they have coalesced into a continuous mat of vegetation, established in the previous growing seasons of 1992 to 1995.

A high variance at the micro-scale (10<sup>-1</sup>-10<sup>6</sup> m<sup>2</sup>) has been observed in the rates of vegetation recovery among comparable degraded habitat types in natural revegetation studies in Greenland (Holt 1987, Strandberg 1997), in northwestern Canada (Kershaw and Kershaw 1987, Harper and Kershaw 1996) and in northern Alaska (Jorgenson 1997). The range of growth rates of colonies of *P. phryganodes* was considerably larger in the exclosures undergoing natural revegetation (ratios of 1.2-61) in comparison to growth rates of colonies in exclosures where plugs were planted (ratios 1.1-2.2). The higher rates of growth observed in the former case, can be attributed, in part, to less intraspecific competition between colonies in the former case than in the latter. As illustrated in Figure 4.2, the high ratio values of colonies in the exclosures undergoing natural revegetation corresponded to colonies that were measured as less than 30 cm<sup>2</sup> in late July,



1996. Unlike the situation in the experimental exclosures on the east shore of La Pérouse Bay where all colonies (plugs) were surrounded by four other colonies at ninety degree angles and a distance of 7 cm, small colonies in the exclosures on the south-west shore of the Bay often had 50 to 100 cm of bare sediments around the colony. The shorter distance between colonies in the former case resulted in the coalescence of some plugs by the end of the first growing season and increased the likelihood of intraspecific competition.

In addition, the higher growth rates observed on the south-west shore of La Pérouse Bay may be attributed to the overall, less hostile edaphic environment on the south-west shore than that which occurs on the east shore of the Bay. The former sites are influenced by the braided estuary of the Mast river that has formed many shallow channels where ephemeral streams with brackish water flow throughout much of the growing season. Salinities measured in sediments devoid of vegetation, but close to the edge of such streams, are on the order of 1-2 grams of dissolved solutes per litre, in contrast to those measured on flat plateaus, which are on the order of 25-25 grams of dissolved solutes per litre ( $n=2$ , July 1, 1998). On the east shore of La Pérouse Bay, however, the only source of water is from rainfall (which, as discussed in Chapter 3, can be minimal) or from tidal incursions (which do not occur until the autumn equinox). Salinities measured in bare sediments on all dates during the growing seasons of 1996 and 1997 at sites on the east shore of La Pérouse Bay were consistently greater than 10 grams of dissolved solutes per litre.

## CHAPTER 5: ASSISTED REVEGETATION TRIALS OF *CAREX AQUATILIS* IN MOSS CARPETS OF FORMER FRESH-WATER SEDGE MEADOW HABITATS

### 5.1 Introduction

At La Pérouse Bay in areas where there is standing fresh-water and permanently saturated ground, *Carex aquatilis* dominates the plant assemblages (Kotanen and Jefferies 1997). Such hydrological conditions exist on some small islands in the Mast river, as well as in certain areas landward of the salt-marshes where extensive fresh-water sedge meadows occur (see vegetation description of sedge meadows in Section 1.5). Lesser snow geese use *C. aquatilis* as a forage plant in the post-hatch period. In July and early August, in particular, the geese graze heavily on plants of this species (Jefferies 1988 a,b, Kotanen and Jefferies 1997). However, in the early spring, the foraging behaviour of the geese is more destructive. The birds pull up shoots of plants before the new growth of shoots has begun, consume the swollen bases of the shoots that are rich in soluble carbohydrates and total nitrogen at that time of the year (Gadallah and Jefferies 1995), and discard the remainder of the shoot (Jefferies 1988 a,b, Kerbes *et al.* 1990, Kotanen and Jefferies 1997).

The intense foraging activity by the increasing goose population has led to the death of *C. aquatilis* stands and their replacement by extensive moss carpets (primarily *Drepanocladus* and *Aulacomnium* species; Kotanen and Jefferies 1997). Similar moss carpets have been observed at the former lesser snow goose colony at McConnell River on the west coast of Hudson Bay (Kerbes *et al.* 1990) and in the High Arctic, at the greater snow goose colony on Bylot Island (Gauthier *et al.* 1996). As the growing season progresses, the moss carpets can dry out, break, and blow away, leaving exposed peat barrens (Kerbes *et al.* 1990, Kotanen and Jefferies 1997). Kotanen and Jefferies (1997) have described the extensive moss carpets as an alternate vegetation state (*sensu* Noy-Meir 1975), and have suggested that the failure of the system to revert to its former state is a consequence of the sustained foraging pressure of the geese as well as the resulting abiotic limitations on the establishment of seedlings. Surface winds that blow across

open ponds where stands of *C. aquatilis* formerly occurred, increase the mobility of large amounts of organic matter and peat debris which leads to unstable conditions that appear to restrict the germination and establishment of the wetland plant species (Kotanen and Jefferies 1997).

In order to examine qualitatively the potential for re-establishment of *C. aquatilis* in moss carpets in the absence of goose foraging pressure and with assisted establishment, revegetation trials were conducted during the growing seasons of 1996 and 1997. Tillers of *C. aquatilis* were planted into the moss carpets and a fertilizer treatment was applied to the moss surface in order to see if the addition of N/P nutrients enhanced establishment.

## 5.2 Methods

Although *C. aquatilis* can produce viable seed (Ebersole 1989), seed set is often infrequent. For example at some sites in Alaska (Shaver *et al.* 1979), at the southern limit of its range in the Netherlands (Grootjans and van Tooren 1984), as well as in the High Arctic (Bliss and Grulke 1988), populations of *C. aquatilis* reproduce clonally most years. Although some seed set is observed in stands of this sedge at La Pérouse Bay, seed production can be unpredictable and seedling establishment in the moss carpets is rarely observed (Kotanen and Jefferies 1997). Hence, tillers were used as the transplant material in this experiment. Vegetative transplants of *C. aquatilis* var. *stans* have been used to revegetate successfully vehicle ruts on Devon Island, N.W.T. (Forbes 1993).

Tillers, consisting of one vegetative shoot (10 to 15 cm) with a root system and no rhizomes, were collected by separating clones of several plants in a population of *C. aquatilis* growing in the stream on the island where the La Pérouse Bay Field Station is located (Fig 6.1 shows the location of the Field Station). In order to standardize the variation that existed in the root lengths of the tillers, all long roots were cut to a length of 4 cm (most roots were approximately this length). Each treatment plot was planted with twenty-five tillers (5 columns x 5 rows) separated from adjacent tillers by 7 cm. Two treatment plots were established in diagonal quarters of each 1 m x 1 m enclosure in order

to eliminate the need for a buffer zone. One of the plots was selected randomly for the addition of fertilizer which was sprinkled evenly across the moss layer as inorganic salts (40.20 g of  $\text{NH}_4\text{Cl}$ /  $\text{m}^2$  and 22.32 g of  $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$ /  $\text{m}^2$ ). The two remaining diagonal quadrats, where no tillers were planted, served as controls in order to monitor whether *C. aquatilis* established naturally in the absence of grazing.

Each 1 m x 1 m enclosure was replicated five times (exclosures were separated by a distance of 5 m) at each of three sites. Sites were established in moss carpets on three islands in the Mast river delta: site one was on the island where the Field Station was located, site two was on an island 100 m west of the Field Station and site three was on an island approximately 1500 m north of the Field Station. In some of the moss carpets, low frequencies of plants such as *Potentilla palustris*, *Cardamine pratensis*, *Dupontia fisheri*, *Ranunculus cymbalaria* and *Eriophorum angustifolium* were present. Initially, above-ground shoots of all vascular plants were cleared from the carpets before the tillers of *C. aquatilis* were planted (June 29 to July 3, 1996). Any plants that reappeared were weeded on each date when the plots were scored for the cumulative number of vegetative and flowering shoots of the sedge (July 15, 24 and August 1, 1996 and July 7, 18 and August 19, 1997).

In contrast to the revegetation trials that were conducted in the salt-marshes where individual colonies of *P. phryganodes* and *C. subspathacea* were monitored frequently during the two growing seasons (Chapter 2), the rhizomatous growth habit of *C. aquatilis* made it difficult to associate new shoot production with particular planted tillers, especially in the second growing season. For this reason, the total number of shoots per plot was recorded. Preliminary analyses indicated that shoot production showed little variation among exclosures within a site; this result was attributed to the greater homogeneity among experimental sites in the moss carpet environment, in contrast to the large spatial variation within the experimental sites in the degraded salt-marshes. In view of the similarity among exclosures and the qualitative nature of the objectives, the total numbers of shoots per treatment per exclosure were pooled to calculate the total number of shoots per treatment per site.

### 5.3 Results

Table 5.1 summarizes the total shoot production of *C. aquatilis* for the growing seasons of 1996 and 1997. Tillers of *C. aquatilis* established successfully in the moss carpets and produced new vegetative shoots in 1996 and 1997. Shoot production showed no substantial variation between treatments, but did vary with site (Table 5.1). Site one was the most productive and produced approximately 50% and 100% of the original number of planted shoots as new shoots (n=125 tillers per treatment per site) in 1996 and 1997 respectively. Sites two and three were less productive; in 1996 and 1997 respectively, site two produced approximately 15% and 50%, and site three produced approximately 10% and 25%, of the original number of planted shoots.

As in many arctic plants, most of the differentiation in flower primordia of *C. aquatilis* takes place at least one season prior to anthesis (Shaver and Kummerow 1992). Although care was taken to avoid the selection of flowering shoots when the planting material was collected, approximately 10% of the shoots in each site produced inflorescences in 1996 (Table 5.1). In 1997, <1% of the plants produced inflorescences likely as a consequence of the transplant shock in 1996.

### 5.4 Discussion

The success of the transplants indicated that in the absence of goose grazing, tillers of *C. aquatilis* can re-establish in the moss carpets and obtain sufficient resources to maintain growth and development. Emers *et al.* (1995) have indicated that the different investigators who have examined the varying resistance and resilience of tundra plant communities to disturbance in the Arctic agree that although wetter vegetation types often are impacted more severely by physical disturbance than plant communities of dry soils (due to looser substrate in the wet soils), the vegetation can recover faster. The rapid recovery is attributed to greater nutrient fluxes in hydric soils (Chapin *et al.* 1988)

**Table 5.1.** Summary of shoot production of *C. aquatilis* during the growing seasons of (a) 1996 and (b) 1997. Table entries show the cumulative total number of vegetative shoots with the cumulative number of new vegetative shoots in brackets recorded on each date. The last row shows the cumulative total of flowering shoots recorded at each site and treatment during each respective growing season. Treatment symbols (-) and (+) refer to the bare and N/P addition treatments respectively (n=125 planted tillers/ treatment/ site).

(a)						
Site	1		2		3	
Treatment	-	+	-	+	-	+
15/07/96	125 (0)	129 (4)	125 (0)	125 (0)	125 (0)	125 (0)
24/07/96	153 (28)	154 (29)	130 (5)	130 (5)	129 (4)	127 (2)
01/08/96	192 (67)	186 (61)	144 (19)	140 (15)	136 (11)	129 (4)
Total # of flowering shoots	16	10	9	16	21	16

(b)						
Site	1		2		3	
Treatment	-	+	-	+	-	+
07/07/97	224	217	163	179	112	127
18/07/97	232	232	172	191	134	131
19/08/97	281	262	183	200	154	150
Total # of flowering shoots	0	0	0	2	0	0

and the dominance of vegetatively reproducing species (Jonasson 1992), such as *C. aquatilis*. Although not conducted in moss carpets, several studies have documented the natural and assisted establishment of *C. aquatilis* following different disturbances. On the Tuktoyaktuk Peninsula, N.W.T., Hernandez (1973) showed that six years after disturbance from the construction of summer seismic lines where the top soil was bladed to the permafrost and the mineral soil exposed, basal plant cover was 30 to 50% of the soil surface, and *C. aquatilis* was one of the codominant graminoids. Thirty years after disturbance by construction and drilling activity on the Alaskan arctic coastal plain, complete vegetation cover had established at some sites (Ebersole 1987, 1989); *C. aquatilis* was codominant in the wetter sites and showed a strong presence in the germinable soil seedbank (Ebersole 1989). On Alaska's North Slope, phosphorus fertilization encouraged *C. aquatilis* and *D. fisheri* to recolonize and replaced seeded *Puccinellia borealis* where crude-oil damage had occurred fourteen years earlier (McKendrick 1987). As well, on Devon Island, N.W.T., tillers of *C. aquatilis* var. *stans* were used to revegetate vehicle ruts, and after eighteen years, plots showed 20 to 50% total basal plant cover (Forbes 1993).

The lack of a fertilizer effect on the shoot production of the planted tillers of *C. aquatilis* at La Pérouse Bay suggests that (1) above-ground primary production was not limited by available nitrogen and phosphorus or (2) the tillers of *C. aquatilis* were not able to take up the fertilizer. As discussed in Chapters 1 and 2, previous studies in the intertidal and supratidal marshes at La Pérouse Bay on *P. phryganodes* and *C. subspathacea* have indicated that the net above-ground primary production (NAPP) is limited by available soil nitrogen (Cargill and Jefferies 1984, Bazely and Jefferies 1989). Results from experimental trials have indicated that grazed swards of *P. phryganodes* and *C. subspathacea* when compared to ungrazed swards showed an increase in NAPP and in the nitrogen content of plant shoots, as a result of nutrients that leached from goose faeces (Bazely and Jefferies 1985, 1989, Hik and Jefferies 1990, Wilson and Jefferies 1996). However, other studies conducted at La Pérouse Bay on *Festuca rubra* and *Calamagrostis deschampsoides* (Zellmer *et al.* 1993) and at Bylot Island, N.W.T. on *Dupontia fisheri* and *Eriophorum scheuchzeri* (Gauthier *et al.* 1995, Beaulieu *et al.* 1996)

failed to show enhanced NAPP in response to addition of goose faeces. In the latter studies on Bylot Island, the *Eriophorum* and *Dupontia* plants grew in a moss-peat matrix (primarily *Drepanocladus*, *Caliergon*, *Meesia* and *Sphagnum* moss species) to a depth of 15 to 25 cm (Gauthier *et al.* 1995). Gauthier *et al.* (1995) and Beaulieu *et al.* (1996) have suggested that the lack of NAPP enhancement in response to goose grazing may be because the nutrients leached from goose faeces (e.g.  $\text{NH}_4$  ions) are first absorbed by mosses which have a higher surface ion-exchange capacity than that of vascular plants (Clymo 1963, Graigie and Mass 1966).

Clearly, the ability of the tillers of *C. aquatilis* to establish and produce new vegetative and flowering shoots (Table 5.1) indicated that inspite of any potential competitive interactions, vascular plants were able to obtain sufficient resources to maintain growth and development. However, in order to determine whether or not the applied fertilizer treatment had an effect on the establishment of the sedge, it is necessary to show that the fertilizer was taken up by the *C. aquatilis* plants (i.e. that the moss species did not outcompete the *C. aquatilis* tillers for the nutrient supplement). In late June 1998, a pilot experiment ( $n=4$ ) that used the stable isotope of nitrogen ( $^{15}\text{N}$ ) as a tracer was conducted over 48 hours in order to determine the extent of incorporation of nitrogen into the vascular plant tissue of *C. aquatilis* and the surrounding moss tissue. The experiment, which measured the accumulation of  $^{15}\text{N}$ , injected as a solution of ammonium chloride onto the moss surface, indicated that both plants of *C. aquatilis* and moss (sampled at a distance of 2.5 cm from the point source) were capable of rapidly accumulating the isotope (peak  $\delta^{15}\text{N}$  values were observed after 24 hours for the sedge and after 48 hours for the moss). Overall values of  $\delta^{15}\text{N}$  were higher for the moss samples than those for the sedge which suggests that some of the fertilizer applied in June 1996 may have been utilized by the moss prior to uptake by the transplanted tillers of *C. aquatilis*. In a study in which the growth responses of *Dupontia fisheri* and *Eriophorum scheuchzeri* to different fertilizer regimes in polygon fens were examined on Bylot Island (1 and 10 g N/  $\text{m}^2$ , 0.6 and 3 g of P/  $\text{m}^2$ , combinations of both nutrients, and goose faeces), Pineau *et al.* (1997) found that the above-ground biomass of graminoids responded to fertilization only when at least 10 g/  $\text{m}^2$  of nitrogen was applied alone or in



combination with phosphorus; the application of faeces or the addition of lower amounts of nitrogen did not influence growth.

In summary, the studies at La Pérouse Bay indicated that tillers of *C. aquatilis* were capable of growing and developing ramets in the absence of the addition of fertilizer. The preliminary results of the pilot experiment suggest that tillers of *C. aquatilis* were capable of taking up appreciable quantities of the isotope in the presence of a moss carpet. However, the greater quantities of the isotope taken up by the moss plants may indicate that in the short term, the moss carpet acted as a barrier to the full acquisition of nutrients by the sedge.

## CHAPTER 6: REVEGETATION AND ITS RELATION TO VEGETATIONAL SUCCESSION IN THE SALT-MARSH OF LA PÉROUSE BAY

### 6.1 Introduction

The successful restoration of plant communities to their former state depends on an appreciation that they exist in dynamic equilibrium (Inouye 1995, Parker and Pickett 1997). Hence, an understanding of directional vegetational change in species assemblages over time (succession), is an important basis for the development of both restoration and revegetation programmes (Cargill and Chapin 1987). The term 'succession' implies a directional change in plant species assemblages over time at a site, which differs from vegetational 'fluctuations' in species abundances around some vegetational state, as described by Watt (1947) in his paper on pattern and process of vegetation change. Although this distinction is widely used, the difference between 'succession' and 'fluctuation' can seem arbitrary depending on the choice of a temporal scale (Glenn-Lewin and van der Maarel 1992). The rate of successional processes is influenced by the dispersal and establishment of the species within a system, the abiotic environment, biotic interactions among established plant species (e.g. facilitation, competition) and among trophic levels (e.g. herbivory, parasitism), and lastly, the stage, type, frequency and intensity of disturbances within the system (Walker and Chapin 1987, Glenn-Lewin and van der Maarel 1992, van Andel *et al.* 1993, Parker and Pickett 1997).

Grazing of vegetation can retard successional processes (Bakker 1985, Bazely and Jefferies 1986, Dublin *et al.* 1990, Hik *et al.* 1992, Prins and van der Jeugd 1993 but see Pastor *et al.* 1988). In the Netherlands and northern Germany, grazing by livestock in salt-marshes increases the species richness of the upper marsh by 'retrogressive succession', that is enhancing the success of establishment of the early successional species that dominate the lower marsh (Bakker 1985, Andresen *et al.* 1990, Berg *et al.* 1997). Hik *et al.* (1992) have shown that in the upper salt-marsh close to the strand line on the east shore of La Pérouse Bay, grazing of *Puccinellia-Carex* swards (standing crop ca. 40 g/m<sup>2</sup>) by geese, retards the development of the willow-grassland assemblage, at

least over short time scales of ten years or less (Hik *et al.* 1992). When exclosures are established, plant litter accumulates which results in the build-up of a thin layer of organic soil. If the elevation of the soil is high enough (due to isostatic uplift and frost heave), a vegetational change is observed after a few years towards a willow-grassland species assemblage characterized by the presence of *Salix brachycarpa*, *Festuca rubra* and *Calamagrostis deschampsoides* (Bazely and Jefferies 1986, Hik *et al.* 1992). This vegetational state is particularly characteristic of the supratidal marsh in which tidal flooding occurs approximately once every two to three years. At high foraging pressure (standing crop < 20 g/ m<sup>2</sup>), as discussed previously, the grubbing activity and hypersalinity shift both *Puccinellia-Carex* swards and the willow-grassland assemblages to degraded states where the soil is essentially devoid of vegetation (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996, Jefferies 1997).

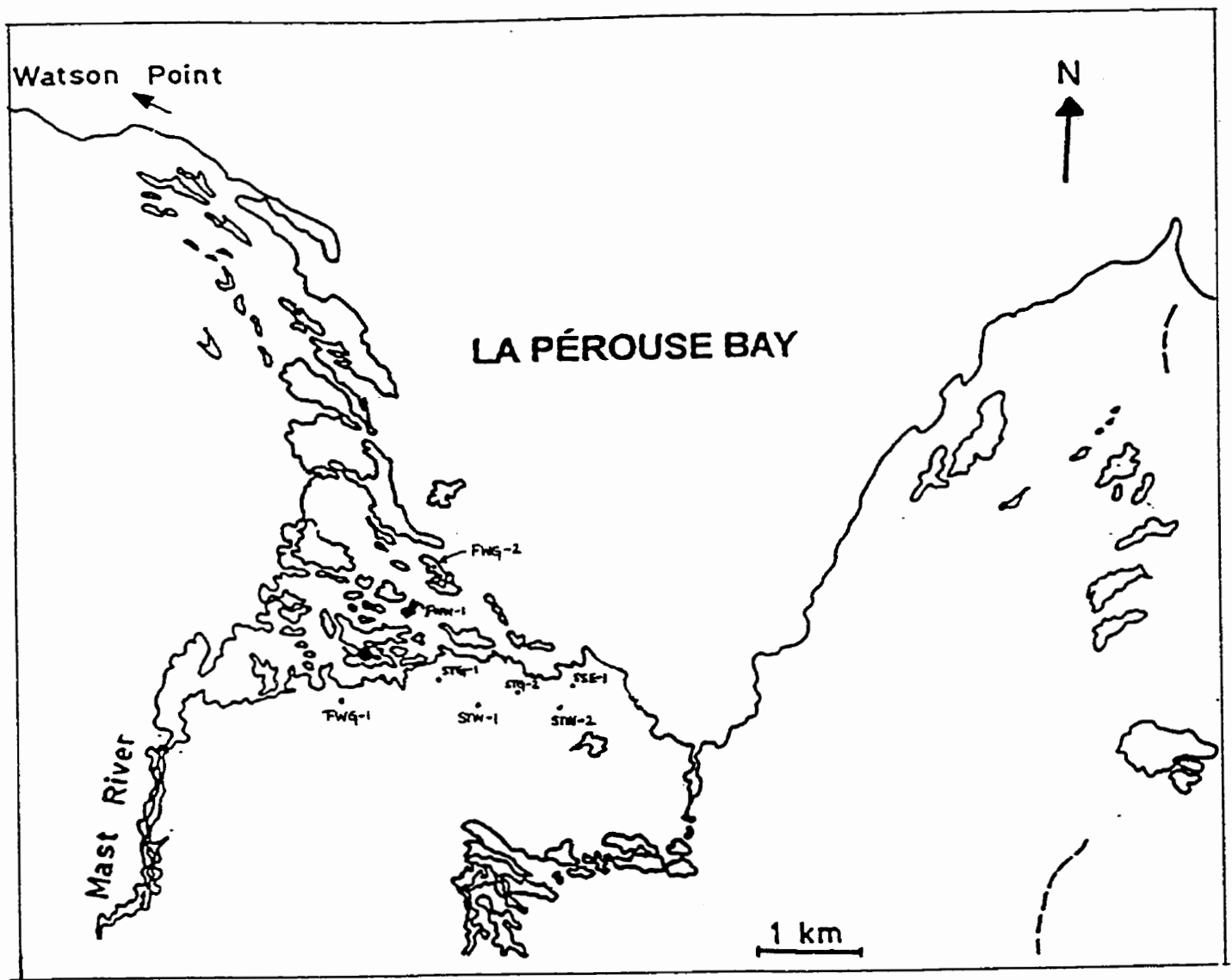
The destruction of the vegetation presented a major discontinuity in the natural successional sequence of the coastal system at La Pérouse Bay. The desired goal of the assisted revegetation scheme described in Chapter 2 was to focus on the re-establishment of the dominant, native vegetation which existed prior to degradation in soils that were hypersaline. Based on the evidence of the observed sequence of vegetational change in which *Puccinellia-Carex* swards preceded willow-grassland assemblages (Bazely and Jefferies 1986, Hik *et al.* 1992), and the knowledge that both *P. phryganodes* and *C. subspathacea* could tolerate at least intermediate levels of salt stress (< 30 g of dissolved solutes per litre in the soil solution; Srivastava and Jefferies 1995b), the *Puccinellia-Carex* assemblage was selected as a target for the revegetation trials (Chapter 2). The studies described below were carried out to evaluate further the successional processes that occurred within the coastal system in the presence and absence of grazing, in order to assess the suitability of selecting the *Puccinellia-Carex* assemblage as a target assemblage for a revegetation scheme of the upper intertidal and supratidal marshes at La Pérouse Bay. Specifically, (1) a comparison of vegetation data collected in 1986, 1992 and 1997 in long-term grazed and ungrazed vegetation plots was made and (2) transplants of *F. rubra* and *C. deschampsoides* from the willow-grassland supratidal marsh were made into degraded soils of the upper salt-marsh.

## **6.2 Methods**

### **6.2.1. Long-term vegetation records**

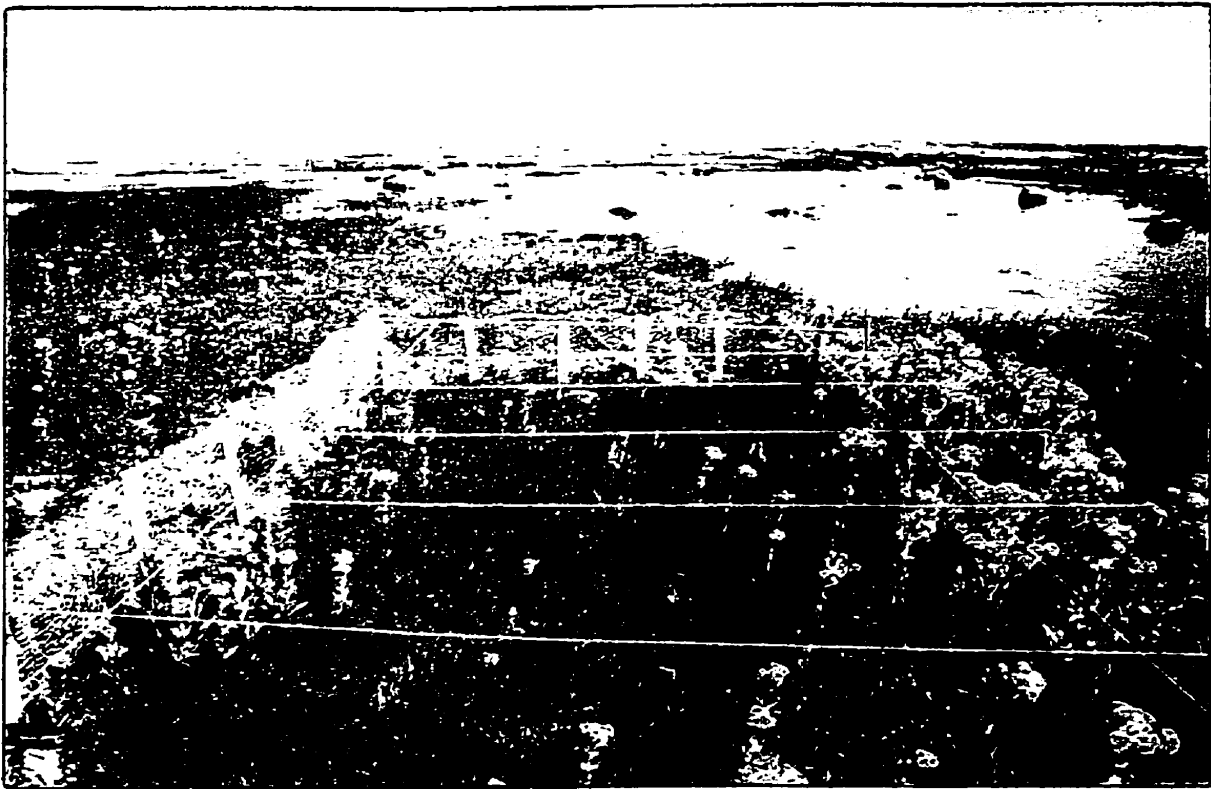
Eight exclosures (5 m x 5 m) were erected by Dr. R. Harmsen (Queen's University) during the summers of 1982 to 1986 in order to study long-term changes in plant species assemblages in the presence and absence of goose grazing. Exclosures were established in a variety of habitat types (Fig. 6.1): soft sediment estuarine marsh of the Mast River delta (SSE), fresh-water brackish marsh that occurred on the islands within the Mast River (FW) and supratidal marsh that occurred at coastal sites within 1 km of the Mast river (ST). Exclosure sites were selected by Dr. Harmsen to include an apparent successional gradient of plant species assemblages which represented vegetation communities at both low elevations (G, graminoid swards) and high elevations (W, willow-grassland assemblages) in the intertidal, supratidal, and riverine complexes (Fig. 6.2). The eight exclosures were named as follows (with year of establishment indicated in brackets): SSE-1 (1982); FWG-1, FWG-2 and FWW-1 (1982, 1983 and 1986 respectively); and STG-1, STG-2, STW-1 and STW-2 (all established in 1982). The vegetation composition of all exclosures is shown in detail in Table 6.1.

In 1986, fifteen contiguous 50 cm x 50 cm plots were established by Dr. R. Harmsen inside and outside all exclosures, with the exception of exclosures FWG-1 and STG-1 where only two plots were established. The vegetation in these plots was scored by recording the living plant which was rooted closest to each of eighty-one wire crosspoints in a 50 cm x 50 cm quadrat strung at 5 cm intervals. If no plant was rooted in the 5 cm x 5 cm square surrounding the point, the point was recorded as bare. Species that were present in the plot and were not recorded at any of the eighty-one points were assigned a percent frequency of <1 %. Plots were scored every summer by Dr. R.

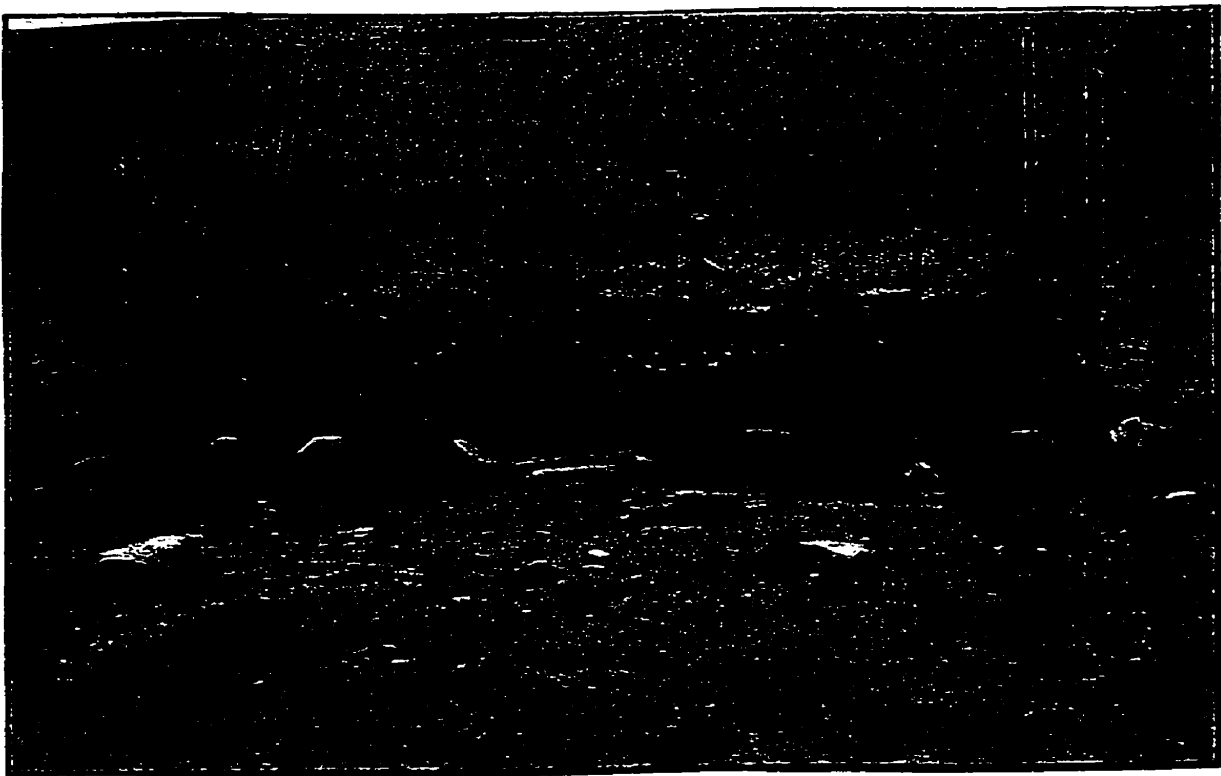


**Figure 6.1** Map of La Pérouse Bay on which the location of the eight enclosures erected by Dr. Harmsen during the summers of 1982-1986 are indicated. Enclosures are named according to the vegetation assemblage and habitat type: soft sediment estuarine marsh (SSE-1), fresh-water graminoid swards (FWG-1,2), supratidal graminoid swards (STG-1,2), fresh-water willow-grassland assemblages (FWW-1) and supra-tidal willow-grassland assemblages (STW-1,2).

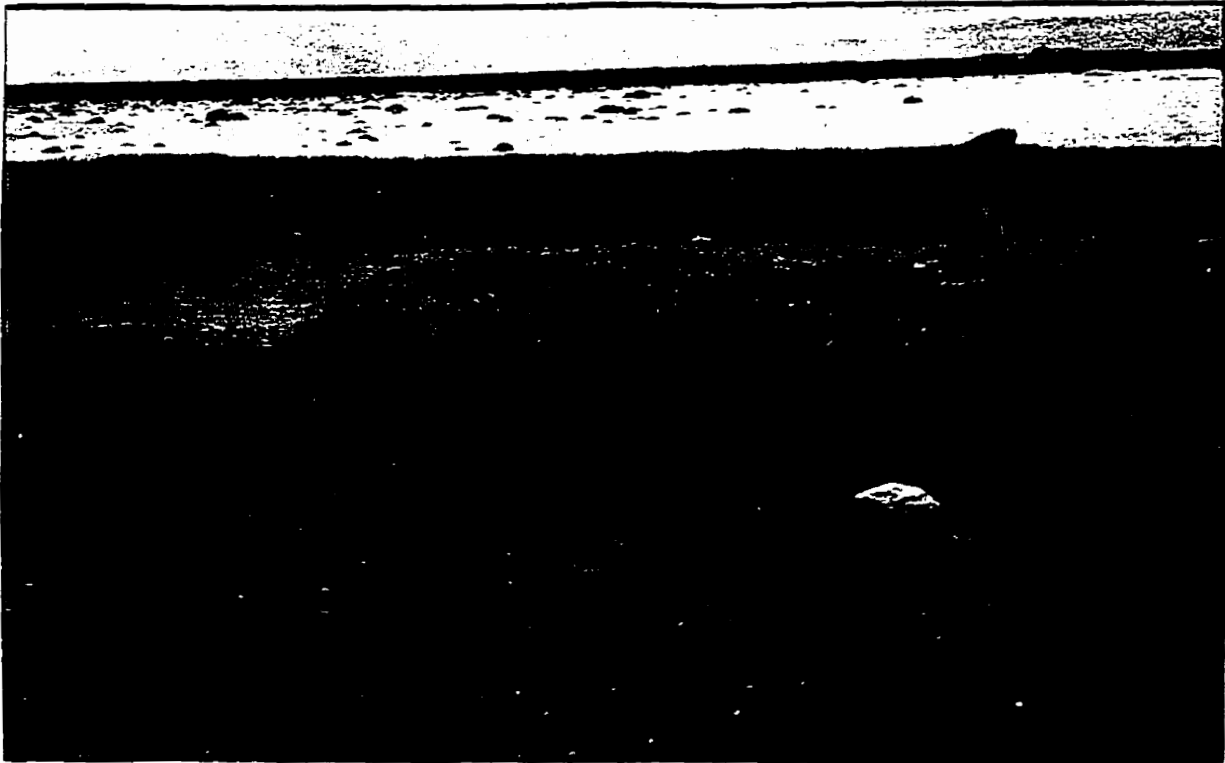
a)



b)



c)



**Figure 6.2** The three types of vegetational assemblages that were selected by Dr. Harmsen to include an apparent successional gradient. Photographs depict (a) exclosure SSE-1, the soft sediment estuarine marsh (July 1996), (b) exclosure FWG-2, the fresh-water graminoid sward (July 1998), and (c) FWW-1, the fresh-water willow-grassland assemblage (July 1998). The latter two photographs were taken by Curtis Vacek.

Harmsen from 1986-1990 and 1992, and by the author in 1997 based on the above technique. In 1992, a severe winter storm damaged enclosure FWG-2 and several of the permanent plots were lost both inside and outside the enclosure. The enclosure was rebuilt around the undamaged parts and in 1997, five and eight of the remaining permanent plots were scored inside and outside the enclosure respectively.

### **6.2.2. Transplant trials of *Festuca rubra* and *Calamagrostis deschampsoides* in hypersaline mudflats devoid of vegetation**

In order to test the assumption that *F. rubra* and *C. deschampsoides* could not establish directly in degraded hypersaline soil, a transplant experiment was performed. Transplant material was cored from a single intact donor patch of a mixed *Festuca-Calamagrostis* sward (2 m x 2 m) that occurred among the low-lying willow fringe in the supratidal marsh on the east shore of La Pérouse Bay. Each cored plug, which included both plant and soil material, was 22 mm in diameter x 40 mm in depth. Plugs were planted on June 17, 1997 into vegetated control plots of *Festuca-Calamagrostis* swards proximal to the donor patch, and into plots in degraded sediments on the east shore of La Pérouse Bay, proximal to site two where the highest values of growth of plants of *P. phryganodes* were recorded (as described in Chapter 2). Plots were exclosed and replicated three times (each replicate was <10 m from the others) at two sites that were separated by approximately 100 m. Each treatment plot was planted with 25 plugs (5 columns x 5 rows), and each plug was separated from adjacent plugs by 7 cm. Plants were scored for survival and senescence on July 2, 14, 26, August 7 and 17, 1997.

### **6.2.3. Statistical methods**

The data from the years 1986, 1992 and 1997 were used to contrast the long-term changes in plant species assemblages in the presence and absence of grazing. A percent frequency was calculated for each plot based on the eighty-one observations. Since the group of plots in each treatment at each enclosure site were not independent, in order to avoid pseudoreplication (Hurlbert 1984), a mean percent frequency was calculated for



each exclosure site ( $n=15$  for all treatments, except those at exclosure sites FWG-1 and STG-1 where  $n=2$ ). Kendall's rank correlation coefficient ( $\tau$ ), a non-parametric statistic (Sokal and Rohlf 1995), was used to contrast species abundances in the presence and absence of grazing in all three years, and to contrast species assemblages between 1986 and 1992, 1992 and 1997 and 1986 and 1997 within each respective grazing treatment. Species which were rare or infrequent (percent frequencies  $<5\%$  in all years and treatments) were omitted from the analyses.

## **6.3 Results**

### **6.3.4. Long-term vegetation records**

Tables 6.1 and 6.2 show, respectively, the mean percent frequencies of all species in the grazed and ungrazed plots at the eight exclosure sites, and the correlation coefficient between comparisons of species composition in grazed and ungrazed plots over time. Significant correlations ( $p<0.05$  when the comparison indicated that there was no difference between the ranked abundances of the compared treatments) were observed at exclosure site STW-1 (supratidal, willow-grassland coastal marsh) in the comparisons of grazed and ungrazed plots in 1986, and of grazed plots between 1986 and 1992, and at exclosure site STW-2 in a comparison of grazed plots between 1992 and 1997 (Table 6.2). However, since the comparisons were not corrected for multiple tests, it is possible that these significant differences may be the result of chance. All other comparisons, notably comparisons made of the rank order of species at ALL sites between grazed and ungrazed plots in 1997, those made of the rank order of species in grazed plots between 1986 and 1997 and those made of the rank order of species in ungrazed plots between 1986 and 1997 were NOT significantly correlated, i.e. indicating differences in species composition and the rank order of species between the compared grazing treatments and the time periods.

In the grazed graminoid-dominated plots in the supratidal and brackish marshes (STG-1,2, FWG-1,2), all correlation coefficients comparing vegetation in 1986 to 1997 had values  $<0.500$  (Table 6.2). Grazing has led to a notable loss of diversity over time

**Table 6.1.** Percent frequencies ( $\pm$  s.e.m.) of species in grazed and ungrazed plots measured at eight sites in 1986, 1992 and 1997 at La Pérouse Bay. Exclosures STG-1,2 and FWG-1,2 show the vegetation composition at low elevations in the supratidal and brackish marshes; exclosures STW-1,2 and FWW-1 show the vegetation at higher elevations in the supratidal and brackish marshes; and exclosure SSE-1 shows the vegetation in the soft sediments of the Mast river estuary.

Supratidal marsh, graminoid swards (STG-1)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Puccinellia phryganodes</i>	50.6 $\pm$ 6.2	61.7 $\pm$ 1.2	51.9 $\pm$ 11.1	41.4 $\pm$ 1.9	19.1 $\pm$ 6.8	3.7 $\pm$ 2.5
<i>Salicornia borealis</i>	31.5 $\pm$ 11.7	26.5 $\pm$ 0.6	13.0 $\pm$ 1.9	45.7 $\pm$ 7.4	1.2 $\pm$ 1.2	0
<i>Stellaria humifusa</i>	9.9 $\pm$ 5.0	0	0	6.8 $\pm$ 6.8	25.9 $\pm$ 6.2	2.5 $\pm$ 0.0
<i>Carex subspathacea</i>	3.7 $\pm$ 1.2	0	0	<1	6.8 $\pm$ 0.6	17.3 $\pm$ 6.2
<i>Plantago maritima</i>	1.9 $\pm$ 1.9	0	<1	<1	30.3 $\pm$ 1.9	54.3 $\pm$ 2.5
<i>Potentilla egedii</i>	<1	0	0	0	9.9 $\pm$ 0.0	9.9 $\pm$ 4.9
<i>Puccinellia nuttaliana</i>	0	0	0	0	4.3 $\pm$ 3.1	<1
<i>Festuca rubra</i>	0	0	0	0	<1	8.6 $\pm$ 0.0
<i>Ranunculus cymbalaria</i>	0	0	0	0	1.2 $\pm$ 1.2	<1
<i>Triglochin palustris</i>	0	0	0	0	0	<1
<i>Triglochin maritima</i>	0	0	0	0	0	<1
<i>Salix brachycarpa</i>	0	0	0	0	0	<1
<i>Chrysanthemum arcticum</i>	0	0	0	0	0	<1
<i>Calamagrostis</i>	0	0	0	0	0	<1
<i>deschampsoides</i>						
<i>Bare</i>	1.8 $\pm$ 0.6	11.7 $\pm$ 0.6	34.6 $\pm$ 9.9	3.7 $\pm$ 3.7	<1	0

Supratidal marsh, graminoid swards (STG-2)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Puccinellia phryganodes</i>	56.5 $\pm$ 3.2	0	0	35.6 $\pm$ 3.8	87.8 $\pm$ 4.5	79.3 $\pm$ 2.5
<i>Carex subspathacea</i>	31.8 $\pm$ 3.0	0	0	47.9 $\pm$ 3.1	0	0
<i>Potentilla egedii</i>	8.1 $\pm$ 1.8	0	0	8.2 $\pm$ 1.9	0	<1
<i>Plantago maritima</i>	<1	0	0	3.8 $\pm$ 0.7	0	1.2 $\pm$ 0.5
<i>Stellaria humifusa</i>	<1	0	0	<1	0	0
<i>Salicornia borealis</i>	0	0	0	0	1.6 $\pm$ 0.7	5.2 $\pm$ 1.7
<i>Triglochin maritima</i>	<1	0	0	0	0	0
<i>Puccinellia nuttaliana</i>	0	0	0	0	0	6.5 $\pm$ 2.2
<i>Bare</i>	2.9 $\pm$ 1.0	100	100	3.8 $\pm$ 1.2	10.8 $\pm$ 4.6	<1

Fresh-water, brackish marsh, graminoid swards (FWG-1)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Carex subspathacea</i>	42.0±7.4	61.1±9.3	95.1±3.7	34.6±9.9	31.5±1.9	29.0±6.8
<i>Festuca rubra</i>	15.4±0.7	0	0	11.7±1.9	1.2±1.2	21.0±6.2
<i>Calamagrostis</i> <i>deschampsoides</i>	10.5±5.6	0	0	<1	0	0
<i>Triglochin maritima</i>	7.4±1.2	0	0	12.3±0.0	19.8±3.7	11.7±1.9
<i>Plantago maritima</i>	0	0	0	20.4±6.8	21.6±0.6	14.2±5.6
<i>Potentilla egedii</i>	20.4±3.1	0	<1	21.0±4.9	24.1±1.9	17.9±3.1
<i>Ranunculus cymbalaria</i>	<1	0	<1	0	0	0
<i>Puccinellia phryganodes</i>	0	1.8±0.6	3.1±1.9	0	1.9±1.9	<1
<i>Senecio congestus</i>	0	0	<1	0	0	0
<i>Calamagrostis stricta</i>	0	0	0	<1	0	0
<i>Parnassia palustris</i>	0	0	0	0	0	4.3±3.1
<i>Stellaria humifusa</i>	0	0	0	0	0	<1
<i>Salix brachycarpa</i>	0	0	0	0	0	1.2±1.2
<i>Bare</i>	4.3±3.1	37.0±9.9	0	0	0	0

Fresh-water, brackish marsh, graminoid swards (FWG-2)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Carex subspathacea</i>	35.2±5.8	16.8±5.3	6.6±3.2	32.8±3.5	6.9±2.0	0
<i>Puccinellia phryganodes</i>	47.3±8.0	3.9±1.5	2.9±1.2	10.7±1.8	18.2±4.1	0
<i>Plantago maritima</i>	2.4±0.8	<1	0	24.0±3.8	9.1±2.3	7.7±3.6
<i>Potentilla egedii</i>	<1	<1	0	21.9±1.7	24.9±5.9	24.2±2.5
<i>Ranunculus cymbalaria</i>	3.6±1.2	<1	<1	1.1±0.3	1.2±0.4	0
<i>Calamagrostis</i> <i>deschampsoides</i>	<1	0	0	2.2±1.4	1.2±0.7	6.2±2.7
<i>Triglochin palustris</i>	<1	<1	1.7±1.2	0	<1	0
<i>Juncus bufonius</i>	<1	0	0	0	0	0
<i>Puccinellia nuttalliana</i>	0	0	0	1.6±0.5	1.6±0.6	0
<i>Stellaria humifusa</i>	0	0	0	1.5±0.3	<1	<1
<i>Chrysanthemum arcticum</i>	0	0	0	<1	1.2±0.6	5.2±0.9
<i>Festuca rubra</i>	0	0	0	<1	4.4±2.5	55.8±5.9
<i>Dupontia fisheri</i>	0	0	0	0	0	<1
<i>Salix brachycarpa</i>	0	0	0	<1	0	0
<i>Parnassia palustris</i>	0	0	0	<1	0	0
<i>Bare</i>	9.9±1.9	78.2±6.8	85.5±4.5	1.7±0.4	30.6±9.0	0

Supratidal marsh, willow-grassland assemblage (STW-1)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Festuca rubra</i>	46.5±1.6	30.4±2.6	22.1±3.3	32.7±1.7	55.6±1.8	40.6±2.8
<i>Carex subspathacea</i>	29.8±1.4	46.1±2.8	49.6±3.7	42.3±2.6	30.6±2.7	14.3±2.8
<i>Calamagrostis</i>	15.8±1.1	8.2±1.6	1.9±0.8	13.7±1.7	3.9±0.8	4.2±1.2
<i>deschampsoides</i>						
<i>Carex glareosa</i>	0	0	0	0	<1	31.7±2.5
<i>Potentilla egedii</i>	1.8±0.4	6.5±1.0	8.8±1.1	3.8±0.6	1.9±0.4	0.9±0.4
<i>Chrysanthemum arcticum</i>	1.0±0.2	0	<1	<1	<1	<1
<i>Parnassia palustris</i>	1.5±0.2	0	<1	2.3±0.5	<1	0
<i>Dupontia fisheri</i>	<1	<1	0	<1	<1	0
<i>Salix brachycarpa</i>	1.1±0.3	0.7±0.2	8.7±0.9	1.9±0.5	5.8±1.4	3.0±0.5
<i>Stellaria longipes</i>	1.3±0.3	<1	0	1.6±0.3	<1	<1
<i>Primula stricta</i>	<1	0	0	<1	0	0
<i>Galium palustre</i>	<1	0	0	0	0	0
<i>Rhinanthus borealis</i>	<1	0	0	<1	0	<1
<i>Puccinellia phryganodes</i>	0	2.9±0.7	4.4±1.8	0	0	0
<i>Stellaria humifusa</i>	0	<1	2.3±0.9	0	0	<1
<i>Salicornia borealis</i>	0	<1	<1	0	0	0
<i>Ranunculus cymbalaria</i>	0	<1	1.5±0.6	0	0	0
<i>Plantago maritima</i>	0	<1	<1	0	0	0
<i>Euphrasia arctica</i>	0	0	<1	0	0	<1
<i>Triglochin palustris</i>	0	0	<1	0	0	0
<i>Bare</i>	0	2.1±0.7	0	0	0	3.1±1.3

Supratidal marsh, willow-grassland assemblage (STW-2)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Festuca rubra</i>	66.6±1.8	74.5±1.8	60.7±2.1	57.7±1.1	61.8±2.0	56.6±4.5
<i>Calamagrostis</i> <i>deschampsiioides</i>	12.4±1.3	2.2±0.6	1.6±0.4	16.7±1.1	8.4±3.5	4.0±1.0
<i>Leymus mollis</i>	7.8±1.4	13.7±1.1	18.9±2.2	6.2±0.6	17.7±1.1	13.6±3.1
<i>Stellaria longipes</i>	5.8±0.7	3.3±0.7	6.3±0.7	10.4±1.0	7.4±1.1	17.6±2.9
<i>Carex subspathacea</i>	2.1±0.8	0	<1	2.0±0.5	0	0
<i>Chrysanthemum arcticum</i>	<1	1.2±0.4	3.6±0.8	2.4±0.4	<1	<1
<i>Parnassia palustris</i>	1.7±0.5	1.1±0.4	2.6±0.7	1.9±0.6	<1	<1
<i>Potentilla egedii</i>	2.8±0.6	2.4±0.6	2.3±0.7	2.1±0.4	<1	<1
<i>Salix brachycarpa</i>	<1	1.2±0.5	2.6±0.7	<1	2.8±1.1	4.6±1.8
<i>Lomatogonium rotatum</i>	<1	<1	0	0	0	0
<i>Rhinanthus borealis</i>	<1	0	<1	<1	0	0
<i>Dupontia fisheri</i>	0	<1	<1	0	0	0
<i>Euphrasia arctica</i>	0	0	<1	0	0	0
<i>Ranunculus cymbalaria</i>	0	0	<1	0	0	<1
<i>Triglochin palustris</i>	0	0	<1	<1	<1	0
<i>Rumex occidentalis</i>	0	0	0	<1	0	<1
<i>Bare</i>	<1	0	<1	<1	0	1.6±0.6

Fresh-water, brackish marsh, willow-grassland assemblage (FWW-1)<sup>1</sup>

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Calamagrostis deschampsoides</i>	61.2±1.1	8.0±1.1	1.5±0.8	43.4±2.6	17.5±3.5	2.5±0.7
<i>Carex subspathacea</i>	16.5±1.3	78.2±1.8	87.2±2.1	34.7±2.3	19.8±1.9	<1
<i>Dupontia fisheri</i>	9.3±1.4	1.2±0.4	3.6±0.8	6.9±1.0	5.2±1.1	73.9±2.8
<i>Festuca rubra</i>	6.4±1.1	5.7±1.2	0	10.0±1.4	45.2±3.6	2.9±1.0
<i>Puccinellia phryganodes</i>	0	<1	4.4±0.9	0	0	0
<i>Potentilla egedii</i>	1.7±0.5	<1	<1	1.9±0.5	3.3±0.6	1.6±0.6
<i>Chrysanthemum arcticum</i>	1.3±0.3	0	0	<1	2.8±1.0	6.5±1.0
<i>Salix brachycarpa</i>	<1	<1	<1	<1	3.6±1.1	4.9±0.8
<i>Ranunculus cymbalaria</i>	<1	<1	<1	<1	0	1.2±0.6
<i>Parnassia palustris</i>	1.4±0.4	0	<1	<1	<1	<1
<i>Triglochin palustris</i>	0	1.8±0.5	1.6±0.5	0	<1	0
<i>Stellaria humifusa</i>	1.1±0.4	0	<1	<1	0	<1
<i>Stellaria longipes</i>	0	0	0	0	<1	2.5±0.9
<i>Potentilla palustris</i>	0	0	0	0	<1	2.1±0.5
<i>Cochlearia officinalis</i>	<1	0	0	0	0	0
<i>Galium palustre</i>	<1	0	0	0	0	<1
<i>Senecio congestus</i>	0	0	<1	0	0	<1
<i>Primula stricta</i>	0	0	0	<1	<1	<1
<i>Hippurus vulgaris</i>	0	0	<1	0	0	0
<i>Rhinanthus borealis</i>	0	0	0	0	<1	0
<i>Salicornia borealis</i>	0	0	0	0	0	0
<i>Cardamine pratensis</i>	0	0	0	0	0	<1
<i>Lomatogonium rotatum</i>	0	0	0	0	0	<1
Bare	0	3.1±0.8	0	0	0	0

<sup>1</sup> Figure 6.2c suggests to the eye that the percent frequency of *Salix brachycarpa* should be higher than the values presented in the above table. The apparent lower values are a consequence of the technique that was used to score the plots, i.e. recording the living plant which was rooted closest to each of the eighty-one crosspoints in the quadrat (Section 6.2.1). Under most of these willow bushes, there was a continuous cover of graminoid-dominated vegetation.

## Soft sediment estuarine marsh (SSE-1)

Species	GRAZED			EXCLOSED		
	1986	1992	1997	1986	1992	1997
<i>Carex subspathacea</i>	19.3±4.7	9.1±2.6	4.8±0.8	8.3±2.2	33.5±4.5	44.9±1.9
<i>Puccinellia phryganodes</i>	8.4±2.3	7.7±1.9	10.9±1.9	24.1±2.7	19.8±2.4	9.6±2.5
<i>Hippurus tetraphylla</i>	20.2±2.5	41.4±2.4	24.9±2.2	23.5±2.7	31.0±3.5	18.4±1.5
<i>Eleocharis acicularis</i>	1.8±0.3	13.9±3.1	23.6±4.4	12.6±1.7	3.1±0.9	<1
<i>Triglochin palustris</i>	9.4±1.0	15.7±2.5	11.9±1.6	4.2±4.2	3.7±0.7	5.8±0.8
<i>Ranunculus cymbalaria</i>	7.3±1.3	6.7±0.9	10.6±2.3	10.0±2.0	7.8±1.5	13.3±0.9
<i>Myriophyllum exalbescens</i>	0	<1	0	0	0	0
<i>Potentilla egedii</i>	0	<1	<1	0	0	<1
<i>Ranunculus aquatilis</i>	0	<1	<1	<1	0	<1
<i>Senecio congestus</i>	0	0	7.5±1.3	0	<1	1.2±0.4
<i>Dupontia fisheri</i>	0	0	3.1±0.7	0	0	2.4±0.7
<i>Ranunculus purshii</i>	0	0	1.8±1.1	0	<1	2.1±1.1
<i>Stellaria longipes</i>	0	0	<1	0	0	<1
<i>Potamogeton filiformis</i>	0	0	0	<1	0	0
<i>Calamagrostis</i>	0	0	0	<1	0	0
<i>deschampsoides</i>						
<i>Bare</i>	33.5±5.3	5.0±1.4	0	20.7±4.9	0	0

**Table 6.2.** Summary of Kendall's rank correlation coefficients ( $\tau$ ) for comparisons between plots of vegetation in the presence and absence of grazing recorded in 1986, 1992 and 1997 at La Pérouse Bay. Correlations are shown between (a) grazed and ungrazed plots in 1986, 1992 and 1997, (b) vegetation in grazed plots in 1986 and 1992, 1992 and 1997 and 1986 and 1997, (c) vegetation ungrazed swards between 1986 and 1992, 1992 and 1997 and 1986 and 1997. Significant values (\*,  $p < 0.05$ ) are indicated when the null hypothesis, that states that the variates in both samples are arrayed at random with respect to each other, is rejected.

(a)

Exclosure	1986	1992	1997
STG-1	0.786	0.171	0.377
STG-2	0.533	0.067	0.133
FWG-1	0.428	0.237	0.132
FWG-2	0.143	0.286	0.536
STW-1	0.867 *	0.600	0.067
STW-2	0.667	0.667	0.667
FWW-1	0.800	0.600	0.100
SSE-1	0.286	0.143	0.071

(b)

Exclosure	1986 - 1992	1992 - 1997	1986 - 1997
STG-1	0.643	0.714	0.214
STG-2	0.143	0.286	0.119
FWG-1	0.385	0.459	0.431
FWG-2	0.102	0.684	0.154
STW-1	0.867 *	0.733	0.600
STW-2	0.333	1.000 *	0.333
FWW-1	0.600	0.500	0.700
SSE-1	0.286	0.642	0.071

(c)

Exclosure	1986 - 1992	1992 - 1997	1986 - 1997
STG-1	0.071	0.321	0.679
STG-2	0.036	0.133	0.500
FWG-1	0.683	0.750	0.829
FWG-2	0.048	0.190	0.428
STW-1	0.600	0.467	0.333
STW-2	0.333	0.333	0.333
FWW-1	0.400	0.400	0.600
SSE-1	0.143	0.642	0.286



(1986 to 1997) at all four of the sites (from six to three species at STG-1, six to zero species at STG-2, six to four species at FWG-1 and eight to four species at FWG-2). Several of the species that disappeared were dicotyledenous plants and included *Potentilla egedii* (STG-2, FWG-1,2), *Plantago maritima* (STG-1,2, FWG-2), *Stellaria humifusa* (STG-1,2) and *Ranunculus cymbalaria* (FWG-1). At sites STG-1, STG-2 and FWG-2, there was a concurrent decrease in the total vegetation cover in grazed plots (respectively 35%, 100% and 86% of the cover recorded as devoid of vegetation). The disappearance of *C. subspathacea* and *P. phryganodes* at site STG-2 and their respective decline to <15% of the total vegetation at site FWG-2 indicated that heavy grazing has caused a shift towards bare mudflats. At site STG-1, the abundance of *P. phryganodes* remained constant from 1986 to 1997, however, *C. subspathacea* disappeared from plots. At site FWG-1, intense grazing led to a > 50% increase in the abundance of *C. subspathacea* and the appearance of *P. phryganodes* (3%). These species have replaced *F. rubra* and *C. deschampsoides* which had frequencies of 15% and 11% respectively in 1986, but both had disappeared by 1997.

In the absence of grazing, changes in species composition of graminoid-dominated plots of the supratidal and brackish marshes between 1986 and 1997 were also evident ( $\tau$  values ranged from 0.428-0.679; Table 6.2c). At site STG-1, the frequencies of *P. phryganodes* and *S. borealis* decreased by 37% and 46% respectively, while the frequencies of *C. subspathacea* and *F. rubra* increased by 16% and 9% respectively. In contrast, at site STG-2, the frequencies of *P. phryganodes* and *S. borealis* increased by 44% and 5% respectively while the frequencies of *C. subspathacea* decreased by 48%. At sites FWG-1 and FWG-2, the presence of *C. subspathacea* decreased by 6% and 33% respectively, while that of *F. rubra* increased by 9% and 55% respectively. With the exception of site STG-2, increased or unchanging frequencies of dicotyledenous plants such as *Plantago maritima* (except site FWG-2), *Potentilla egedii*, *Parnassia palustris* and *Chrysanthemum arcticum* were observed. As well, seedlings of *Salix brachycarpa* established in enclosure FWG-1.

In grazed plots at the willow-grassland sites (STW-1,2 and FWW-1), between 1982 and 1992, the surveys showed a decrease in the presence of *F. rubra* (25%, 6% and 6% respectively) and of *C. deschampsioides* (14%, 60% and 10% respectively). At sites STW-1 and FWW-1, results of surveys indicated an increase in the presence of *C. subspathacea* (20% and 71% respectively), and at site STW-2, an increase in the presence of *Leymus mollis* (11%). The frequencies of *S. brachycarpa* increased at both supratidal sites (2% and 8% respectively). As well, *P. phryganodes* established at sites STW-1 and FWW-1 (4%) where it had not been recorded previously. Values of dicotyledonous plants such as *Chrysanthemum arcticum*, *Parnassia palustris*, *Stellaria longipes* and *Potentilla egedii* remained stable over the eleven years at frequencies <5%.

In the absence of grazing, species surveys of the willow-grassland sites showed changes in the dominant graminoids within plots. Surveys indicated a respective decrease in the abundance of *C. deschampsioides* (10%, 12% and 38%) at sites STW-1,2 and FWW-1 and of *C. subspathacea* (28% and 33%) at sites STW-1 and FWW-1. Increases in the presence of graminoid species included a 32% increase in the abundance of *Carex glareosa* at site STW-1, an 8% increase in the abundance of *Leymus mollis* at site STW-2 and a 67% increase in the frequency of *Dupontia fisheri* at site FWW-1. Frequency values of *F. rubra* showed minor fluctuations but with little change. The presence of *Salix brachycarpa* increased over the 11 years, but frequency values were less than 5% of all records. Some dicotyledonous species, such as *Stellaria longipes* (STW-2) and *Chrysanthemum arcticum* (FWW-1), showed increases above frequencies of 5%, however, most dicotyledonous species remained at frequencies below 5%.

The weakest correlation coefficients ( $\tau < 0.300$ ) for comparisons of species present in plots in the presence and absence of grazing from 1986 to 1997, were observed at the soft-sediment estuarine site. In grazed plots, a 14% decrease in the presence of *Carex subspathacea* and a 33% increase in the total vegetation cover were observed. Correspondingly, increased frequencies (increase quantified in brackets) were observed in *Eleocharis acicularis* (22%), *Hippurus tetraphylla* (5%), *P. phryganodes* (4%) and *Triglochin palustris* (3%). In the absence of grazing, the species composition showed a reverse trend with a 37% increase in the presence of *C. subspathacea*, coupled with an

11% decrease in the frequency of *Eleocharis acicularis* and a corresponding 5% decrease of *Hippurus tetraphylla*. *Ranunculus cymbalaria* was present at a frequency of approximately 10% in grazed and ungrazed plots. As well, other plant species were present at frequencies <5% (several of which were not present formerly in 1986, see Table 6.1). They included *Senecio congestus*, *Dupontia fisheri*, *Ranunculus purshii*, *Ranunculus aquatilis*, *Potentilla egedii* and *Stellaria longipes*.

### **6.3.2. Transplant trials of *Festuca rubra* and *Calamagrostis deschampsoides* in hypersaline mudflats devoid of vegetation**

Transplanted plugs of *Festuca-Calamagrostis* vegetation did not establish successfully in bare sediments. On July 2, 1997, within two weeks of planting, all plants were dead at site one and >50% of plants were recorded as dead in all plots at site two. Plants that were recorded as living were in fact senescing. By July 14, 1997, all plants that were transplanted into bare sediments were dead. In contrast, plants in plugs that were transplanted into intact *Festuca-Calamagrostis* swards showed low mortality: no mortality of plants was observed on July 2 and mortality of 11% was observed in plants in half the plots on July 14, 26 and August 7, 1997. On August 17, 1997, mortality of plants ranged from 11% to 22% of the all plants.

## **6.4 Discussion**

Primary succession of salt-marshes is typically considered to lead to a series of vegetation zones parallel to the coast which represent a chronosequence with the youngest zone at the seaward end and the oldest zone at the top of the shore (Packham and Willis 1997). Plants growing in the lower marsh are typically those that can establish and tolerate abiotic factors such as salinity, wave action and frequent tidal inundation, but are thought to be poor competitors with plants that dominate the upper marsh (Bertness 1991a,b). Although the species composition of salt-marshes around the world differ, there is a remarkable consistency in the dominant genera associated with apparent zonation patterns (Ranwell 1972, Long and Mason 1983, Packham and Willis 1997). In

western Europe, New Zealand and California, *Salicornia* species are often the primary colonizers of the lower marsh (Long and Mason 1983). In these systems, the *Salicornia* zone is usually followed by a mixed zone of salt-tolerant dicotyledons (*Aster*, *Limonium*, and *Armeria* species), followed by a zone of salt-tolerant grasses such as *Spartina* or *Puccinellia* species and a higher salt-marsh grass zone of *Festuca*-dominated vegetation, which may be replaced by woody plants (some *Atriplex* and *Salix* species), rushes (*Juncus* and *Scirpus* species), reeds (*Phragmites australis*) and grasses, at the landward end (*Leymus* species; Long and Mason 1983, Bakker 1985, Andresen *et al.* 1990, Packham and Willis 1997).

Elsewhere, grasses are the primary colonizers of the lower marsh, such as *Spartina alterniflora* on the east coast of North America (Ranwell 1972, Long and Mason 1983, Bertness 1991b), *Spartina* or *Puccinellia* species in north-west Europe (Long and Mason 1983, Packham and Willis 1997) and predominantly *Puccinellia phryganodes* in northern Canada (Kershaw 1976, Jefferies 1977, Jefferies *et al.* 1979, Glooschenko and Martini 1982, Riley 1982). *Salicornia* species are present within these temperate and subarctic (but not arctic) marshes and act as opportunistic colonizers when bare patches are created (Ellison 1987, Jefferies 1988a,b). Within these marshes, which are located within different climatic regimes, grasses (*Spartina*, *Distichlis*, *Agrostis*, *Dupontia* species) and sedges (*Carex* and *Scirpus* species) often dominate the middle zones, and reeds, rushes, woody plants (genera as described above) and other graminoids (*Carex*, *Festuca*, *Leymus* and *Calamagrostis* species) occur at the higher, landward end (Kershaw 1976, Jefferies 1977, Jefferies *et al.* 1979, Glooschenko and Martini 1982, Riley 1982, Long and Mason 1983, Bertness 1991a,b, Packham and Willis 1997).

Although some zonation is visible in the salt-marsh at La Pérouse Bay, (*Puccinellia-Carex* swards occur at the seaward end and *Salix* species usually fringe the strand line), the pattern is not a simple chronosequence. A mosaic landscape occurs in response to goose foraging activity (Srivastava and Jefferies 1995a). Vegetation patterns are also influenced by inverse salinity gradients (Glooschenko and Martini 1982) and frost-heave hummocks that can develop as islands in the salt-marsh and in river delta (Jefferies *et al.* 1979). Processes influencing successional development of the salt-marsh

at La Pérouse Bay have been explained primarily as isostatic uplift, soil aging, frost-heave action and the foraging activity of the geese (Jefferies *et al.* 1979, Bazely and Jefferies 1986, Hik *et al.* 1992). Following the colonization of bare sediments by diatoms and cyanobacteria, *P. phryganodes* is the initial plant to colonize the emerging tidal flats, followed by *Carex subspathacea* and *Ranunculus cymbalaria*. The presence of *C. subspathacea* early in the colonization is highly dependent on the availability of fresh-water or frequent coverage by the brackish tidal waters. Once *Puccinellia-Carex* swards are well developed, dicotyledenous plants such as *Potentilla egedii*, *Stellaria humifusa*, *Plantago maritima* var. *juncoides* and *Chrysanthemum arcticum* establish. As the elevation of the ground increases as a result of isostatic uplift and frost-heave, soils become better drained, less saline and *Festuca rubra* and *Calamagrostis deschampsoides* establish together with *Salix brachycarpa* and *Salix myrtifolia*.

Hik *et al.* (1992) have argued that the *Puccinellia-Carex* and *Festuca-Calamagrostis* plant assemblages are examples of stable vegetation states (*sensu* Noy-Meir 1975) that shift asymmetrically in response to grazing pressure and uplift. Their observations suggest that: (1) in areas of higher elevation, when grazing pressure on intact *Puccinellia-Carex* swards is removed, a shift towards the *Festuca-Calamagrostis* state occurs, but that in areas of lower elevation, the removal of grazing will not cause the *Puccinellia-Carex* state to shift in the short term (<5 years), (2) when swards of *Festuca-Calamagrostis* are grazed, the state will not easily revert to a *Puccinellia-Carex* sward and (3) a change in both the *Festuca-Calamagrostis* and *Puccinellia-Carex* state may occur as a consequence of the degenerative positive feedback which shifts both states to bare mudflats.

In order to validate the selection of the *Puccinellia-Carex* state as a target state for the first step of a revegetation scheme, it is necessary to show that (1) a *Festuca-Calamagrostis* sward cannot develop directly on bare sediments in the upper intertidal mudflats that have resulted from the loss of vegetation (in contrast to *Puccinellia-Carex* swards that may develop over time), and (2) a *Festuca-Calamagrostis* sward can only develop from a former *Puccinellia-Carex* sward. The former requirement was clearly supported by the inability of transplanted plugs of *Festuca-Calamagrostis* grasses to

establish in bare sediments. In contrast to the successful establishment of transplanted plugs of *P. phryganodes* into bare sediments (Chapter 2), mortality of transplants of *Festuca* and *Calamagrostis* into bare intertidal mud indicated that they cannot shift directly to an alternate state of a *Festuca-Calamagrostis* sward. The latter result was supported by the long-term surveys which also indicated this constraint described previously at La Pérouse Bay (Bazely and Jefferies 1986, Hik *et al.* 1992).

The results of the long-term surveys reported in this study showed that in the presence of heavy grazing and grubbing, *Puccinellia-Carex* swards are replaced by bare mudflats. All grazed *Puccinellia-Carex* swards showed a decrease in total species richness, particularly a decline in the abundance of dicotyledenous plants which are unable to tolerate heavy grazing (Bazely and Jefferies 1986, Sadul 1987). In plots at three of the four low elevation marsh sites, a marked decrease in the total vegetation cover was observed that indicated a loss of the *Puccinellia-Carex* sward and its replacement by bare mudflats (the plots outside the exclosure site STG-2 were completely devoid of vegetation by 1992). The changes inside the exclosure at site STG-2 showed that a similar shift had taken place in the absence of grazing which was likely due to the degradation in the area around the exclosure. The frequency of *Carex subspathacea* decreased from 48% to 0%, and the frequencies of plants with a higher salt tolerance such as *Puccinellia phryganodes* and *Salicornia borealis* increased. In the other three exclosures, in the absence of grazing, the *Puccinellia-Carex* swards (STG-1, FWG-1,2) showed a shift towards an increased frequency of *Festuca* and *Calamagrostis*. In exclosures FWG-1 and STG-1, the shift was slight (a 9% increase in the presence of *F. rubra*), while in exclosure FWG-2, the shift was more pronounced, (a 56% increase in the abundance of *F. rubra*). In both of the fresh-water exclosures, the increase in *F. rubra* was coupled with a concurrent decrease in *C. subspathacea*. In contrast, in exclosure STG-1, an increase in the abundance of *C. subspathacea* was observed, a trend which has been documented previously by Bazely and Jefferies (1986).

In contrast to the observations of Hik *et al.* (1992), when the goose population was appreciably lower in number than that in 1997, grazing has led to changes in the species composition of *Festuca-Calamagrostis* swards. In grazed plots at all three of the

high elevation willow-grassland sites (STW-1, STW-2, FWW-1) and at site FWG-1 (a lower elevation graminoid site without willows, but with the former presence of *F. rubra* and *C. deschampsoides* in 1986), foraging activity has led to a decrease in abundance of *F. rubra* and *C. deschampsoides*. At three of these sites, the decreases have been coupled with increases in the abundance of *C. subspathacea* (STW-1, FWW-1, FWG-1) which suggests that it may be possible for the *Festuca-Calamagrostis* state to revert to the *Puccinellia-Carex* state if the foraging activities of the geese are intense. Jano *et al.* (1998) have estimated that 1026 ha and 1428 ha of vegetation cover has decreased in the decades of 1973 to 1983 and 1984 to 1993 respectively. Based on this estimated rate of change, in the last six years since Hik *et al.* (1992) made their observations, an additional 500-750 ha have been degraded, during which time the snow goose colony has continued to increase at a rate of 7% per annum (Abraham *et al.* 1996). Given the increased foraging pressure and the reduction in the available *Puccinellia-Carex* swards, it is likely that *Festuca-Calamagrostis* swards are being grazed more intensively. Potentially, this increased grazing pressure, the removal of live vegetation and the loss of the thin veneer of soil organic matter, have given a competitive advantage to *C. subspathacea*. In the absence of grazing at the three willow-grassland sites, a decrease in the abundance of *C. deschampsoides* occurred in all three exclosures, and the *Festuca-Calamagrostis* sward changed towards an assemblage of *F. rubra* and other dominant graminoids. Exclosures STW-1, STW-2 and FWW-1 showed respectively increases in *Carex glareosa*, *Leymus mollis* and *Dupontia fisheri*.

Unfortunately, since only one site was established originally in the estuarine marsh, it is impossible to make generalizations. According to Jefferies *et al.* (1979), *Hippurus tetraphylla*, *Hippurus vulgaris* and *Myriophyllum exalbescens* are the primary colonizers of the soft sediments in the estuary of the Mast river. Once the sediments stabilize, the aquatic plants are replaced by *Carex subspathacea* which can colonize semi-soft sediments. Other species associated with the brackish marsh include *Triglochin maritima*, *Triglochin palustris*, *Plantago maritima* var. *juncooides*, *Potentilla egedii* and *Ranunculus cymbalaria*. As elevation increases, *Carex subspathacea* is replaced by other graminoids such as *Carex glareosa*, *Dupontia fisheri* and *Calamagrostis neglecta*. The

results of the surveys at site SSE-1 indicated that in the absence of grazing, the abundance of *C. subspathacea* increased and the abundance of *Eleocharis acicularis* decreased. In the presence of grazing, the reverse trend was observed. Although the plants associated with the *Hippurus* state are not the preferred forage of the geese, as food resources have become increasingly scarce in the last decade at La Pérouse Bay, the geese have been observed grazing the aquatic vegetation, particularly the tips of plants of *Hippurus tetraphylla* and *Potamogeton filiformis* (R.L. Jefferies, personal observation). The decrease in the abundance of *C. subspathacea* in the presence of grazing indicates another instance where grazing is retarding the successional process.



## CHAPTER 7: GENERAL DISCUSSION

### 7.1 The potential for revegetation of plant community assemblages at La Pérouse Bay

The occurrence of alternate stable vegetation states in terrestrial grazing systems depends on herbivore density, plant growth rate and plant consumption rate (Noy-Meir 1975). Stable vegetation states are characterized by resilience to small perturbations, but when subject to large perturbations, such as intense grazing, the states change rapidly and often irreversibly (May 1977, Rietkerk *et al.* 1996, van de Koppel *et al.* 1997). The changes brought about by herbivores can trigger secondary changes in the soil conditions, such that even if herbivores are removed from the system, the vegetation state will not revert to its former condition (Rietkerk and van de Koppel 1997). In addition to the alternate vegetation states of *Puccinellia-Carex* and *Festuca-Calamagrostis* assemblages maintained by the geese at La Pérouse Bay (Hik *et al.* 1992), Srivastava (1993) and Kotanen and Jefferies (1997) have proposed, respectively, that the extensive bare mudflats and moss carpets that result from the goose foraging activity represent a third and fourth stable vegetation state in this coastal system. Consequently, the revegetation trials that have been described in this study, which were conducted in the absence of goose foraging in both bare mudflats (Chapters 2 to 4) and moss carpets (Chapter 5), can be considered a test of the irreversibility of these proposed stable states.

Clearly, the present levels of goose foraging activity at La Pérouse Bay are preventing any reversal of vegetation states; no natural revegetation has been observed outside of exclosed areas, and the degradation processes continue to accelerate. The incremental area of vegetational decline at La Pérouse Bay was greater between 1984 and 1993 than from 1973 to 1984 (Jano *et al.* 1998) which indicates that the rate of vegetation decline is increasing concurrently with the increase in the number of breeding pairs of lesser snow geese. Furthermore, results of long-term monitoring (twelve years) of fixed plots in grazed *Puccinellia-Carex* swards have shown a loss of species diversity and an increase in the total area devoid of vegetation cover (Chapter 6). Although some plants may successfully recolonize patches of bare sediments where the salinity and moisture

regimes are adequate for establishment and growth, plants cannot survive the current grazing pressure in combination with a degraded soil environment (soils that are hypersaline, have an increased bulk density and lower total carbon and nitrogen content; Chapter 2). Thus, the intense foraging activity of the geese continually resets the “successional clock” by preventing revegetation and by continuing to trigger the degenerative positive feedback process.

Nevertheless, in the absence of goose foraging, the results show that some revegetation can occur in both bare mudflats (Fig. 2.2, 4.1) and in moss carpets (Table 5.1). In areas in the younger intertidal marsh formerly dominated by *Puccinellia phryganodes*, short-term observations (<5 years) indicate that *Puccinellia phryganodes* can re-establish naturally in bare sediments shortly after geese are excluded from plots (Fig. 4.1). The assisted trials in the intertidal marsh on the east shore of La Pérouse Bay also indicates that over 75% of the transplants of *P. phryganodes* (as plugs) can establish in the degraded sediments when soils have adequate moisture regimes and soil salinity levels for plant growth (Table 2.2a). The growth of *P. phryganodes* increases significantly when single and combined additions of peat mulch and inorganic nitrogen and phosphorus are made to the soil surface. Plants that receive the combination of treatments show the highest growth. However, when only single additions are made, additions of peat mulch enhance growth more than additions of fertilizer (Fig. 2.2). Experiments in which a water supplement is given to plants suggest that enhancement as a consequence of the mulch treatment is largely due to an increase in available water due to decreased soil surface evaporation (Fig. 3.1) and lower salinities (Fig. 2.7). Based on these results, and the previous results that have documented the death of plants of *P. phryganodes* in response to hypersaline conditions (Srivastava and Jefferies 1995b, 1996), it is likely that the sites in which the transplanted plugs of *P. phryganodes* do not survive are those where there is insufficient water and high soil salinities.

The successful re-establishment of a continuous patch of *P. phryganodes* appears to facilitate the recolonization of other salt-marsh species associated with the *Puccinellia-Carex* vegetation state by acting as a “nurse” species. Urbanska (1997a) has documented the role of “nurse” plants in high alpine revegetation processes, whereby healthy clonal

structures (e.g. cushions) are frequently colonized by later arrivals. A continuous patch of *P. phryganodes* can act as “nurse” plants and trap seed and vegetative fragments from the strandline, from snowmelt and from the seed rain, and thus facilitate the establishment of other graminoids and dicotyledenous plants. Seed input from the strandline is considered an important seed source for salt-marsh plants (Ranwell 1972, Packham and Willis 1997) and has been shown to influence the seedbank at a site 30 km from La Pérouse Bay (Staniforth *et al.* 1998). After five years, in the exclosures which are undergoing natural revegetation on the south-west shore of La Pérouse Bay, ten other vascular plant species have established successfully in addition to *P. phryganodes* (Table 4.1). The highest species diversity was observed in exclosures with the greatest amount of *Puccinellia* cover. As well, three years after the assisted revegetation trials in bare sediments on the east shore of La Pérouse Bay were started, dicotyledenous plants such as *Potentilla egedii*, *Ranunculus cymbalaria* and *Stellaria humifusa* were recorded inside the exclosures in mats of *Puccinellia*.

The “template” of *P. phryganodes* makes the edaphic environment more hospitable for plant establishment. In a New England salt-marsh, Bertness (1991) showed that the colonization of bare saline patches by *Spartina patens* and *Distichlis spicata* decreased soil salinities and facilitated the colonization of *Juncus gerardii*. The salinity measurements made from soils inside exclosures on the east shore of La Pérouse Bay (1997) were significantly lower than those of soils outside of exclosures. This difference suggested that the vegetation inside the exclosure reduced the evaporative loss from the soil and hence the salinity (Chapter 2). Similarly, Srivastava (1993) showed that exclosure of *Puccinellia-Carex* swards led to lower soil salinities in soils sampled inside the exclosures than in those sampled outside the exclosures. These lower soil salinities appeared to facilitate the establishment of plants that were not as salt tolerant as *P. phryganodes*. For example, in one of the exclosures on the south-west shore of La Pérouse Bay, a 25% cover of *C. subspathacea* was recorded. The lower soil salinities may have provided suitable conditions for the germination of seeds in the soil seedbank whose germination was depressed by hypersaline conditions (E. Chang, unpublished data).

The reversal of the bare mudflat state to the *Festuca-Calamagrostis* state is only possible through an intermediate state of the *Puccinellia-Carex* assemblage. Transplanted plugs of *Festuca* and *Calamagrostis* plants cannot establish in bare, saline sediment (Section 6.3.2). When, as a result of isostatic uplift and frost heaving, the sediments are elevated beyond the height of most tidal inundations and there is an absence of grazing, litter of plants of *Puccinellia* and *Carex* accumulates and forms a thin veneer of organic soil that facilitates the colonization of *Festuca* and *Calamagrostis* (Hik *et al.* 1992). Long-term observations (12 years) described in this study indicate that in the absence of grazing, *Puccinellia-Carex* swards show a shift towards the willow-grassland community with increased establishment of *Festuca* and *Calamagrostis* grasses. In the exclosed willow-grassland assemblages, with time, other graminoids such as *Carex glareosa* in the supratidal marsh, or *Dupontia fisheri* in the estuarine marsh colonize exclosed plots. These results suggest that if a *Puccinellia-Carex* “template” can establish in degraded sediments, the willow-grassland assemblage is likely to re-establish as well.

Although *P. phryganodes* established in bare sediments, there was a huge temporal and spatial variation in the success and rate of plant establishment. Differences in weather conditions between the growing seasons led to a greater success of the establishment of plants in transplanted plugs of *P. phryganodes* in 1996 than in 1997 (Fig. 3.4). In the exclosures that were undergoing natural revegetation on the south-west shore of La Pérouse Bay, total plant cover of the 2 m x 2 m exclosures ranged from 5% to 90%. In the assisted revegetation trials on the east shore of La Pérouse Bay, plants in all the plugs in some exclosures died in the first growing season (Table 2.2a). As well, in the former *Puccinellia*-dominated marsh proximal to the Mast river, plants in all of the plugs at one site chosen for the experiment where soil surface conditions were manipulated with styrofoam also died in the first growing season (Section 3.2.3). Among plants that survived on the east shore of La Pérouse Bay, rates of establishment differed among all the exclosures within a site (a spatial scale of 10-15 m) as well as among sites (a spatial scale of 100-200 m; Chapter 2). The large spatial variation in the establishment rates of *P. phryganodes* reflected edaphic variation; differences in salinity, nutrient availability, bulk density and particle size that influenced soil water availability for plant growth.

Although some of the edaphic measurements recorded between sites (at a spatial scale of 100-200 m) on the east shore of La Pérouse Bay were significant, many of the measurements showed greater within-site variance (at a spatial scale <15 m; Chapter 2). It is likely that most of this edaphic variance is associated with the temporal and spatial components of the degradation processes that create an edaphic mosaic. The edaphic variance is very fine grained. Soils in patches that have been devoid of vegetation for a longer period of time will have decreased bulk densities, decreased amounts of available nutrients and will develop higher salinities during the growing season than soils that have recently lost their vegetation cover. Srivastava (1993) showed that soil salinity increased with the size of a bare soil patch. Based on these results, it is likely that the potential for recovery of a bare patch is related to its size, which may reflect the time since vegetation was removed.

In the older, supratidal marsh, formerly dominated by *Carex subspathacea*, the potential for reversing the bare mudflat state to the former sedge community in the absence of grazing is poor. Long-term observations (14 years) in an enclosure erected in a 25 m<sup>2</sup> bare patch have indicated that no recolonization by the former vegetation has occurred. Less than half of the transplanted plugs of *C. subspathacea* survived the first growing season, and the mortality within plots continued to increase in the second growing season (Table 2.2b). Total plant cover was not enhanced by fertilizer and/or mulch amelioration (Fig. 2.9). The lack of enhancement to the soil water regime by the application of the mulch is likely a consequence of the long-term soil ripening process (>1000 years; Scott 1995) that has led to a thicker surface organic layer in the inland marsh. Although the clayey, silt mineral soils (typical of the younger, intertidal marsh) have a lower porosity than organic soils, unlike organic soils, they are able to bind water molecules to their matrix more readily (Brady 1996), which is an advantage under the dry conditions of recent summers. Soils in the inland marsh have extremely high salinities (Iacobelli and Jefferies 1991), and *C. subspathacea*, unlike *P. phryganodes*, has a low tolerance of hypersaline conditions (Srivastava and Jefferies 1995b). In addition, the slight changes in the elevation of the land (1 m drop every 3 km) have impeded drainage in the inland marsh and led to anaerobic conditions just below the surface of the soil.

While *C. subspathacea* can grow in soils with negative redox potentials (Table 2.10), *P. phryganodes* does not establish under such conditions. Thus, despite its higher salt tolerance, it is unlikely that *P. phryganodes* would be a suitable species to revegetate the hypersaline, anaerobic sediments of the inland marsh.

In the absence of goose foraging, the successful establishment of tillers of *Carex aquatilis* suggests that the moss carpet can revert to sedge meadow. Unlike the situation in the salt-marsh, where in the absence of grazing, the degraded soil presents a serious limitation on the recolonization process, the soils of the former sedge meadows still have adequate nutrients to sustain plant growth. Although the results of the pilot experiment on nutrient uptake suggest that the moss species compete with the sedges for nutrients, clearly, this competition is not preventing revegetation. It is likely that the limitation on revegetation in these areas is dispersal. While *C. aquatilis* can rapidly revegetate areas by lateral growth of ramets when the disturbance is small (Forbes and Jefferies 1999), when the disturbance is large, the lateral growth is not rapid enough. As well, seedlings do not appear to establish readily in moss carpets. It is important to note that the moss carpets on the islands where these trials were conducted present a more hospitable environment than that in the extensive sedge meadows. In these areas at La Pérouse Bay, and further north along the west coast of Hudson Bay at McConnell River (Kerbes *et al.* 1990), moss carpets have dried out, and due to the high winds, blown away leaving exposed peat barrens. It is possible that if the system continues to shift towards a state of peat barrens, the soil environment may be altered and tillers of *C. aquatilis* may not establish as readily.

## **7.2 The revegetation potential at La Pérouse Bay in relation to other arctic and alpine revegetation studies.**

Unlike most studies in arctic and alpine regions to date, this study has used vegetative transplants to assist immigration of plants in degraded sites. As discussed in Chapter 1, the use of non-native, commercially available cultivars alone, or in combination with native seed, has been a common strategy (Elliott *et al.* 1987,

McKendrick 1987, Younkin and Martens 1987, McKendrick *et al.* 1992, Younkin and Martens 1994, Martens 1995, Magnusson 1997). However, the competitive dominance of non-native species in some of these trials (Younkin and Martens 1987, Martens 1995) and the superior establishment of native species compared with non-native species in other trials (Chapin and Chapin 1980, McKendrick 1997, Krautzer and Lassacher 1998) have led to increased interest in the use of indigenous species. Seed of indigenous species have been collected in the field (McKendrick 1997) or in some instances, propagated in nurseries (Magnusson 1997, Krautzer and Lassacher 1998). However, Urbanska (1997b) has pointed out that the mentality that the use of seedlings is the only approach to restoring degraded land must be overcome as in some instances, such as in this study, the reproductive biology of the native plants dictates that alternative methods need to be used.

Transplants in other small scale, experimental studies have proven to be useful in revegetating disturbed areas with native species (Tschurr 1990, Forbes 1993, Urbanska 1997a,b, Shirazi *et al.* 1998). Although the use of transplants is considerably more labour-intensive than sowing seeds, the technique has other benefits. For example, transplants allow greater control of the density and spatial organization of plants at a site. This spatial control may help avoid the problem observed in some seeded revegetation trials where high densities of plants in graminoid stands have prevented the colonization of later successional species (Densmore 1992, Chambers 1997, McKendrick 1997). Transplants also allow for greater control in the species composition of revegetated patches which can potentially accelerate the establishment of later successional species. Urbanska (1997a) has argued that the creation of small, diverse patches can act as “safety islands”, that is patches with a high density of “safe sites”. As discussed above, the establishment of dicotyledenous plants in some patches of *P. phryganodes* may indicate this facilitation.

The inclusion of native soil as part of the transplant technique offers other advantages. It is likely from the results of the transplants of *P. phryganodes* that the soil core may help the acclimatization of plants to the hypersaline “stress” in their new environment (although in some of the transplants of *P. phryganodes* and in most of the

transplants of *C. subspathacea*, the “stress” was still too large). A transplanting of soil to the degraded site may also transfer seed from the donor soil seedbank and facilitate seedling emergence. At La Pérouse Bay, for example, recent studies have shown that the seedbank sampled from soils in intact patches has a much higher diversity of plants than that sampled from degraded patches approximately 10 m away (E. Chang, unpublished data). As well, the soil in the core helps maintain the native thermal regime (Shirazi *et al.* 1998) and may promote nutrient cycling by restoring the microbial and mycorrhizal communities (Haselwandter 1997). Although the technique of transplanting plugs of native plants has a limited applied value in large scale revegetation projects, (especially in a case such as this study where there exists the added constraint of excluding geese in order for any revegetation to occur), Chambers (1997) has pointed out that the lack of detailed autoecological studies on the establishment ecology of native species has limited the successful restoration of damaged arctic and alpine plant communities. Thus, small scale transplant experiments on native species, are important in building a sound scientific base for restoration efforts.

The large spatial and temporal variability in successful establishment evident in this study and other arctic studies (Kershaw and Kershaw 1987, Holt 1987, Harper and Kershaw 1996, Jorgenson 1997, Strandberg 1997) indicates the need to establish which factors limit recovery. One approach is to document carefully the plant environment at a spatial scale that reflects the variability in the establishment success of plants. Jorgenson (1997) used this approach in monitoring the natural recovery on land disturbed by oil development in northern Alaska. However, this approach presents challenges in an experimental study, such as this one, where the spatial variability of the edaphic environment must be estimated accurately at the time experiments are initiated. When this study was initiated, it was thought that within an area of approximately 100 m<sup>2</sup>, differences in edaphic conditions would be minimal. However, variation in successful establishment of plants between exclosures that were separated by less than 10 m was consistent with differences in the soil environment between edaphic plots and nearby exclosures. The fine spatial scale of the variation was evident at the end of the first growing season, and the soils inside exclosures were sampled subsequently in the second



growing season. While these measurements were valuable in indicating how the edaphic environment was altered once the plants established (e.g. plant cover reduced soil salinities), the alterations to the edaphic environment did not make it possible to describe soil conditions prior to planting. This study would have been strengthened had the edaphic environment been characterized at the spatial scale of every 1 m<sup>2</sup> patch prior to the transplanting of plugs.

Nonetheless, by the use of manipulative experiments, the results of this study provided some explanation of the effect of factors that influence establishment success. The results of the assisted trials in the salt-marsh with *P. phryganodes* was consistent with the results of other arctic studies that have shown that fertilizer enhanced the recovery process (McKendrick and Mitchell 1978, McKendrick 1987, Chapin and Chapin 1980, Chambers 1997, Magnusson 1997, McKendrick 1997). The results also indicated that the application of peat mulch to the soil surface was more effective at enhancing growth than the application of fertilizer alone. This latter result supports the arguments that have been made by several other authors on the importance of organic soil and the manipulation of the microclimate to ensure adequate soil moisture for plant growth in revegetation trials (Cargill and Chapin 1987, Ferchau 1988, Chambers 1989, McKendrick 1997).

### **7.3 Long-term predictions of the ecosystem at La Pérouse Bay**

Studies on the effect of insect pests on revegetation schemes have demonstrated that herbivores can constrain the rate of revegetation, if not prevent it outright (Louda 1994, 1995). In arctic and alpine revegetation studies that have been conducted in lands degraded by activities associated with the oil industry, by vehicle passage, by recreational activity, or the grazing activity of domesticated livestock, there exists the possibility of direct anthropogenic control over the cause of the disturbance. Once restoration work begins, and vegetation cover is established, it is possible for natural succession to occur. However, at La Pérouse Bay, the disturbance to the system is still ongoing and difficult to control as the population of geese continues to increase. Observations at La Pérouse Bay

indicate that although the vegetation is rapidly being depleted, the breeding pairs are continuing to show site fidelity and the foraging pressure on the vegetation is continuing to increase, thus preventing any natural revegetation in the degraded salt-marsh and wetland habitats.

As the plant species which are the preferred forage of the geese decrease in abundance (e.g. *Puccinellia phryganodes* and *Carex subspathacea*), the geese have expanded their forage selection to include other species such as *Hippurus tetraphylla* and *Potamogeton filiformis* in the aquatic community assemblages, and *Festuca rubra* and *Calamagrostis deschampsoides*, in the willow-grassland community assemblages. The long-term surveys in grazed plots within these communities indicate that the grazing activity continues to retard succession (Table 6.1). The results show that grazing of the *Hippurus*-dominated plant assemblage caused a decreased abundance of *Carex subspathacea*, a plant with a rhizome network that further consolidates sediments and facilitates the development of the estuarine marsh. Heavy grazing of the *Festuca* and *Calamagrostis* plants led to “retrogressive succession” evident in the increased abundances of *Puccinellia* and *Carex* plants. Grazing of the *Puccinellia* and *Carex* plants led to an increase in bare ground devoid of vegetation. In an extreme case (Table 6.1; STG-2), even in the absence of grazing for twelve years, the *Puccinellia* and *Carex* system showed a considerable loss of diversity and an increase in *Salicornia borealis*, that indicated that the degradation of the soil which surrounded the enclosure was influencing the plant dynamics inside the enclosure.

This latter example is important as it suggests that even if the grazing pressure is reduced in the system, the degradation of the soil environment may reach the point where the existing vegetation simply cannot tolerate the prevailing salinity and other soil conditions. This scenario was also evident in the enclosures in which *P. phryganodes* was unable to establish on the east shore of La Pérouse Bay (Chapter 2). It is possible that the soils in which these clones died are in an older state of degradation than those in which plants were able to establish. At present, some natural and assisted revegetation is possible as there still exists some vegetation in the vicinity to act as a dispersal source. However, as degradation continues, vegetation patches in the landscape mosaic will die,

and the potential for plant fragments of *P. phryganodes* to disperse will be limited. In addition, soil salinity will increase. It is likely that once the system loses its mosaic nature and becomes uniform mudflats, revegetation of *P. phryganodes* will not be possible.

The lack of revegetation observed in the long-term enclosure (14 years) of the inland marsh, (with the exception of under the wire where litter accumulated; Chapter 4) in addition to the low establishment success of transplants of *C. subspathacea* (Chapter 2) suggest that even in the absence of goose foraging, the older marshes will not revert to their former vegetation states. In the hypersaline, organic soils of the older marshes, a new vegetation state has established. The annual, *Salicornia borealis* is present at high frequencies together with low frequencies of plants of *Atriplex patula* var. *hastata* and *Senecio congestus*. Although the geese have begun to consume the latter species in recent years (young shoots are pulled in the early spring), *Salicornia borealis*, which is extremely abundant in the seedbank of degraded soils (E. Chang, unpublished data), is not consumed by the geese.

As Hobbs (1994) has pointed out, when vegetation dynamics involve rapid, catastrophic shifts, the long-term ecosystem response to environmental change is a challenge to predict. Nonetheless, it is likely that the herbivore population will decrease eventually. Over a very long timescale, isostatic uplift will expose fresh sediments where primary succession potentially can occur. However, the results of this study suggest that the present marshes will not revert to the former vegetation states. The only possible mechanism of recovery is indicated by the narrow fringe of vegetation that has developed on litter which has accumulated along the base of the perimeter under the wire of the long-term enclosure in the inland marsh. Plants are able to establish on this litter base which lies above, and is out of immediate contact with the underlying hypersaline sediments. Away from the fence, however, the carpets of *Salicornia borealis* are washed or blown away each winter and no litter accumulates. Under these conditions, revegetation is not possible and the loss of a “seral” stage will be maintained.

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