Competitive Processes and Spatial Patterning of Plant Species in Boreal Saline Habitats

by

Geoffrey Brent Jones

A thesis presented to the University of Manitoba in partial fulfillment of the requirements for a degree Master of Science in the Faculty of Graduate Studies

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Contents

Abstract

Patterning of vegetation into mono-dominant, discrete zones is a common feature of inland boreal saline sites. This discontinuous vegetation gradient cannot be totally accounted for by gradients in soil factors, especially salinity, which tend to be continuous at these sites. Inter-relationships between a variety of environmental factors and the vegetation of four saline sites located in the Overflow Bay area of Lake Winnipegosis, Manitoba, was examined. Reciprocal transplant experiments using field and greenhouse material were employed at each site to determine the effects of salinity and competition on the performance of dominant species. The experimental design involved placing vegetation plugs from each zone into cleared (salinity effects only) and uncleared (competition and salinity effects) plots of each other zone within each site. Controls were also established in each plot. The transplant experiment and soil-vegetation monitoring was conducted over two consecutive growing seasons (1989 and 1990). Results indicate that interspecific competition and salinity are important factors influencing the patterning of vegetation at these sites.

Acknowledgements

I thank the following individuals who contributed their expertise and advice towards the research, experimental design, data collection and analysis, and ecological interpretation contained within this thesis.

First of all, I thank my advisory committee, Drs. T. Booth, J. Shay, and B. Hann for providing me with direction and guidance through this process. I especially thank my immediate advisor, Dr. N. C. Kenkel, for his support and encouragement.

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Finally, I thank my wife Deanna for her love, patience, and encouragement during the course of this study. She was also very helpful in providing me with a swift kick in the ass when I needed it (which was, at times, often).

Well, that's about it. Thank you. (This one's for you Nicholas!).

List of Tables

List of Figures

Study Objectives

The objectives of this study were two-fold:

1) to identify and describe the relationship between the soil and vegetation of inland boreal saline habitats through periodic soil and vegetation sampling, gradient analysis, and seed bank surveys.

2) to assess the relative role of edaphic factors and competition in the creation and maintenance of the vegetation zonation in inland boreal saline habitats.

Chapter 1 - Introduction and Literature Review

Section 1.1 - Introduction

Ecological studies of the vegetation of coastal saline habitats are numerous and geographically diverse (Chapman 1960; Waisel 1972; Odum 1988). Studies have been conducted on coastal marshes of Hudson Bay (Jefferies *et al.* 1983; Zbigniewicz 1985) and James Bay (Glooschenko 1978; Ewing *et al.* 1989); British Columbia (Dawe & White 1986); Alaska (Snow & Vince 1984); New England (Shea *et al.* 1975; Bertness & Ellison 1987; Ellison 1987; Niering & Warren 1980); the southeastern United States (Statler & Batson 1969; Nestler 1977; Wiegert 1979); California (Pearcy & Ustin 1984); Oregon (Gallagher & Kirby 1980; Seliskar 1985); England (Adam 1978; Jefferies *et al.* 1979, 1981; Davy & Smith 1985; Hutchings & Russel 1989); The Netherlands (Joenje 1979; Groenendijk & Vink-Lievaart 1987); Australia (Clarke & Hannon 1969); and New Zealand (Partridge & Wilson 1987). Inland saline sites have not received as much attention.

Plants of both inland and coastal saline habitats must adapt to high levels of salt in their environment (Burchill 1991). The concentration and composition of ions in the soil solution directly influences the types of plants that can occur in saline habitats. However, other environmental factors which also influence plant life often differ between coastal and inland saline habitats (Ungar 1974(a)). For example, regular tidal inundation and wrack disturbance affect coastal areas, but are not present at most inland sites. Drought conditions often occur in inland habitats, but are virtually absent in coastal regions. Furthermore, the salinity levels and ion composition of inland saline habitats tend to be variable. Coastal saline habitats, which are regularly inundated by tidal saltwater, experience more constant salinity levels and ion composition (Ungar *et al.* 1979).

North American inland saline sites are generally located in arid to semi-arid areas of the mid-western United States and western Canada. While some of these sites have

developed under natural conditions, the majority are the result of poor irrigation, dry land fallowing, and other agricultural activities (McKell *et al.* 1986). A number of ecological studies have investigated the vegetation composition, patterning, dynamics, and vegetation-soil relationships of sites in western Canada (e.g.: Keith 1958; Dodd *et al.* 1964; Dodd & Coupland 1966(a); Guy *et al.* 1986) and the mid-western United States (e.g.: Flowers 1934; Ungar 1968, 1970, 1974(a), 1987; Williams & Ungar 1972; Skougard & Brotherson 1979; Ungar *et al.* 1979; Shupe *et al.* 1986; Ungar & Riehl 1986; Ungar & Khan 1986). Waisel (1972) presents a review of studies on inland saline sites found in North America, Europe, and the Mediterranean Australasian regions.

Recent ecological studies by Burchill (1991) and Burchill & Kenkel (1991) have been conducted on the plant communities found at boreal inland saline sites of the Lake Winnipegosis region in west-central Manitoba. However, detailed research into the underlying mechanism of species' spatial distribution and vegetation patterning at these northern sites is lacking.

Section 1.2 - Description of the Lake Winnipegosis Saline Sites.

Section 1.2.1 - Introduction

The Lake Winnipegosis saline sites of this study belong to a series found along the western shoreline of Lake Winnipegosis in west-central Manitoba, Canada (Figure 1.1). The geographical range of the sites is from 51° 20' N to 53° 8' N, along the lake's western shoreline. I visited 25 sites of this series during this study (Figure 1.2). The southern sites (i.e. those of the Camperville-Winnipegosis area) tend to be highly disturbed by agricultural activity (e.g. pasture). The northern sites, located in the Dawson Bay and Overflow Bay areas appear to be less disturbed. However, there is evidence from aerial photos that logging and road construction have taken place in the vicinity of some sites.

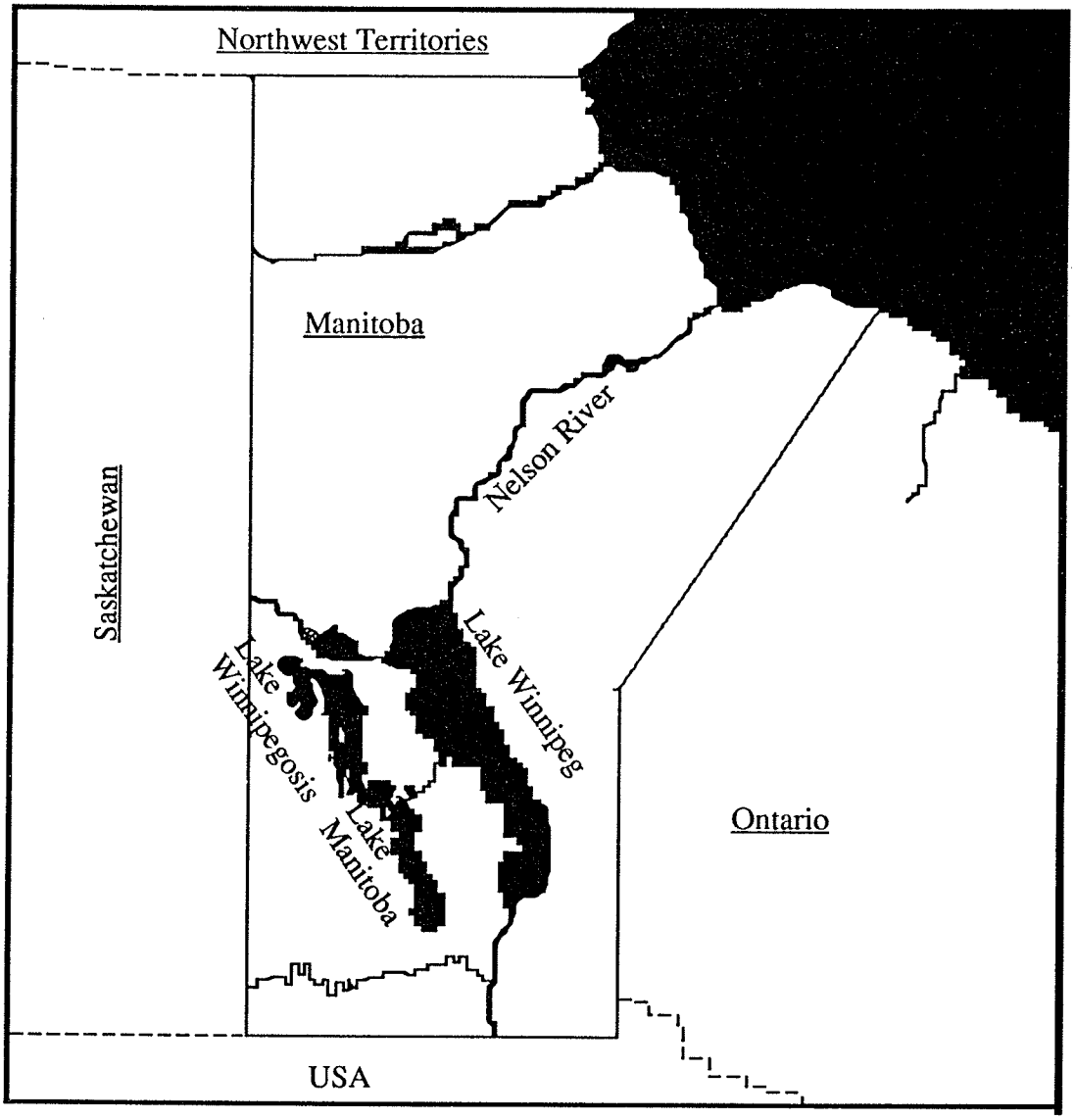


Fig. 1.1. Map of Manitoba, Canada. 1 cm = 100 km.

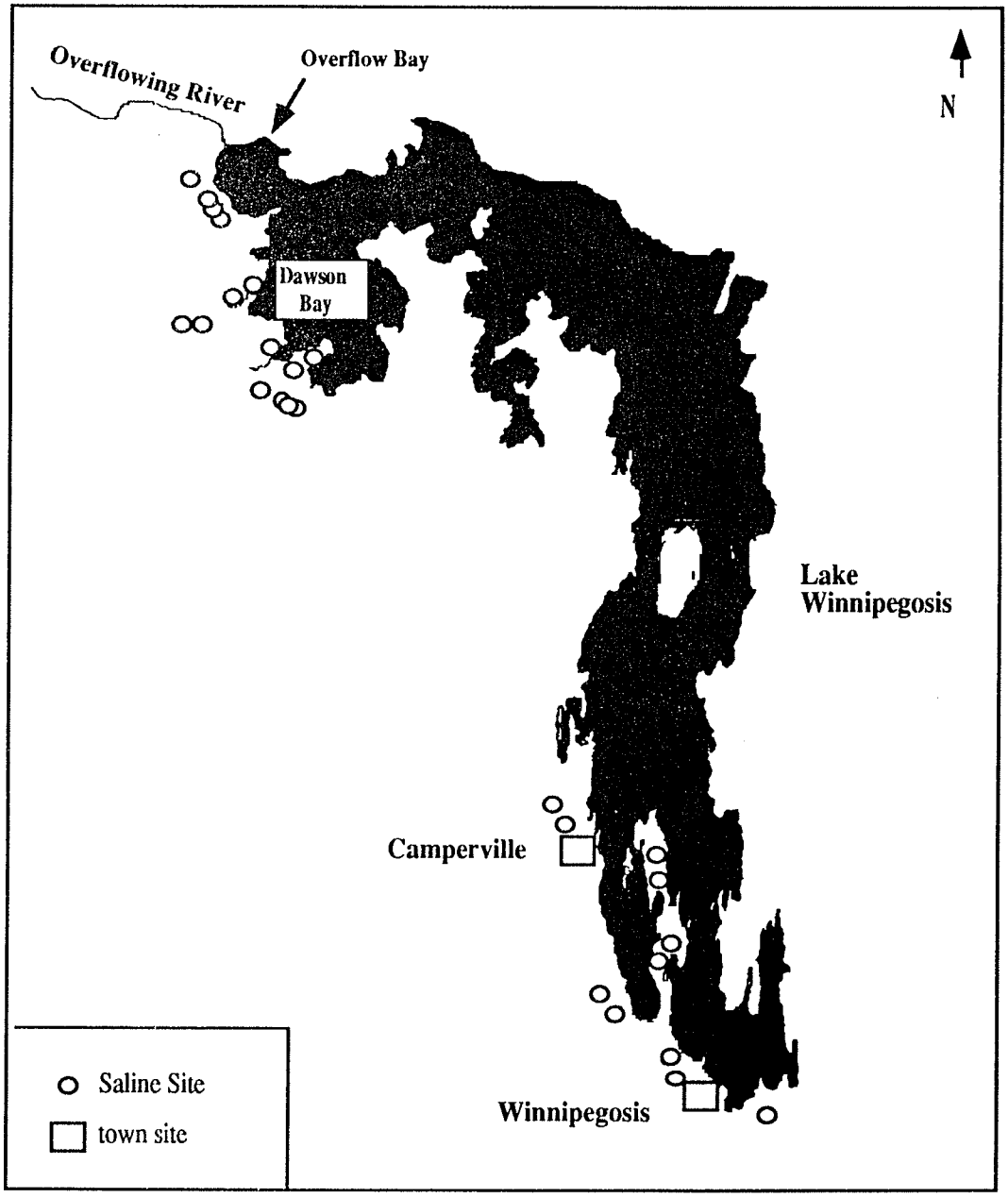


Figure 1.2. Map of Lake Winnipegosis with location of saline sites visited during the study (1989-1990). 1 cm = 7.5 km.

Section 1.2.2 - Geography

The Lake Winnipegosis and area is situated in the Manitoba Lowlands (Rowe 1972), which is a sub-division of the larger Interior Plains physiographic region (Rowe 1972). The Manitoba Lowlands is a lake plain containing the remnants of Glacial Lake Agassiz in the form of Lakes Winnipeg, Manitoba, and Winnipegosis. The region is bounded on the west by the Manitoba Escarpment, on the north by the The Pas Moraine, and on the east by the Canadian Shield. Raised beach ridges composed of glacio-fluvial material deposited by the stepwise recession of glacial Lake Agassiz are common throughout the region (Nielson 1987). However, the area generally has very low relief with elevations ranging from 305 meters in the west to 218 meters in the northeast (van Everdingen 1971). This results in drainage of the region in an easterly to northeasterly direction. A number of streams and rivers flow into the region from the Manitoba Escarpment. The majority of these empty into Lake Winnipegosis and Lake Manitoba, and then into Lake Winnipeg. Lake Winnipeg is drained by the Nelson River system, which eventually carries the water of the Manitoba Lowlands across the Canadian Shield to the Hudson Bay coast.

Section 1.2.3 - Geology

Lake Winnipegosis and environs are underlain by Devonian Period limestone and dolomite bedrock (Geological Survey of Canada 1987). This bedrock extends from approximately 50° 25' N to 53° 30' N. On average the deposit is 60-70 km wide, with its greatest width of 90-100 km attained in the northeast corner of the Lake (refer to Figure 1.3). The Devonian bedrock of this region is divided into six north-south oriented rock Formations. Moving from the bottom to the top of this Devonian deposit the following formations are encountered: the Ashern Formation; the Elm Point Formation; the Winnipegosis Formation; the Prairie Evaporite Formation; the Dawson Bay Formation; and

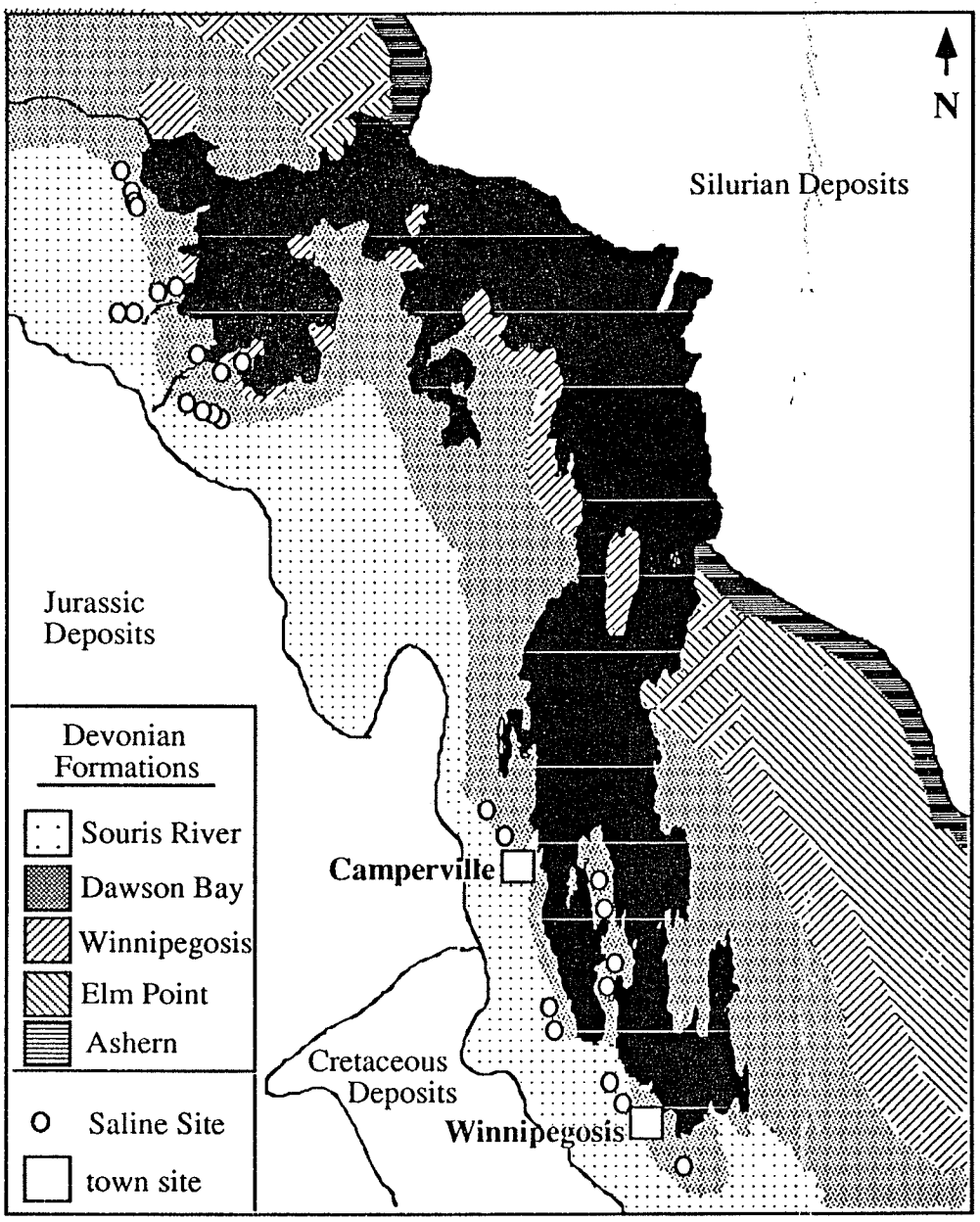


Figure 1.3. Map of Lake Winnipegosis region, showing location of underlying Devonian bedrock Formations and saline sites (Modified from Geological Survey of Canada 1987). 1 cm = 7.5 km.

the Souris River Formation (Geological Survey of Canada 1987). The Ashern Formation contains deposits laid down during the late Silurian and early Devonian Periods (Kent 1967), and thus contains the oldest rocks of this Devonian system. The Souris River Formation, located at the top of this stratum, contains the most recent deposits. Sporadic outcrops of this Devonian bedrock occur in the Lake Winnipegosis and Lake Manitoba regions, with the Ashern Formation reaching the surface in the extreme east where it meets Silurian deposits. The Souris River Formation is exposed in the west at the base of the Manitoba Escarpment (i.e.: Jurassic-Cretaceous deposits; Kent 1967). Outcrops of the Prairie Evaporite Formation, situated between the Winnipegosis and Dawson Bay Formations, do not occur.

The Ashern Formation, consists mainly of dolomitic shale and argillaceous dolomite. The Elm Point Formation consists of high-calcium limestone, upper member-thin interreef dolomitic and calcareous bituminous laminites, and thick reefal dolomite, and gradually grades into lower member dolomite and platform facies of the Winnipegosis Formation. The Prairie Evaporite Formation consists mainly of halite, with traces of clay and anhydrite (Kent 1967). On the northeast extreme of the Formation anhydrite and dolomite inclusions are evident. The Dawson Bay Formation forms the western shoreline of Lake Winnipegosis and is composed of basal red shale, bituminous dolomite, high-calcium micritic limestone, calcareous shale, coral-stromatoporoid high-calcium limestone, and dolomite. The Souris River Formation consists of basal red shale, argillaceous and high-calcium limestone, and dolomite. The presence of sedimentary rocks (e.g. dolomite, limestone, and halite), reef structures, and marine fossils in the bedrock indicates that the Lake Winnipegosis region was subject to intermittent marine transgressions during Devonian times.

The geological stratigraphy of the Manitoba Lowlands plays a prominent role in determining the distribution of the Lake Winnipegosis saline springs and seeps. Geologists postulate that the salt solutions are derived from subterranean waters originating below the

Devonian bedrock (see van Everdingen 1971; Wadien 1984; Geological Survey of Canada 1987). This water percolates up through the permeable reef deposits of the Winnipegosis Formation and into the halite-rich Prairie Evaporite Formation. The water, now containing dissolved salts, flows through the Dawson Bay Formation and is discharged at the surface.

Section 1.2.4 - Soils

When not exposed at the surface, the Devonian bedrock is overlain by a mixture of glacial till and till-derived sand, silt, clay, and gravel (Geological Survey of Canada 1987). Glacial till constitutes the parent material of the majority of the soils of the Lake Winnipegosis region. This material is highly calcareous as it was derived primarily from Devonian carbonate rocks (Weir 1983).

The soils of the western shoreline of Lake Winnipegosis are divided into three Great Soil Groups (Weir 1983). The soil of the Camperville-Winnipegosis region is classified as a Dark Gray Chernozem. It is characterized by a loamy texture with a relatively high stone content and good horizontal drainage (Clayton *et al.* 1977). The tendency for carbonate leaching of the B horizon and deposition in the C horizon suggests that the soil is Orthic (Clayton *et al.* 1977). The pH ranges from neutral to slightly alkaline.

The soil to the north and northeast of the Camperville- Winnipegosis area belongs to the Eutric Brunisol Great Soil Group (Weir 1983). As in the Dark Gray Chernozems, this soil is derived from calcareous parent material, is medium-loamy in texture, and ranges from neutral to alkaline. However, it is distinguished from the Dark Gray Chernozems by poor horizon development due to a lack of recognizable zones of mineral leaching and accumulation (Weir 1983) in the profile.

The third soil type associated with the Lake Winnipegosis region is the Mesisolic Organic Soil (Clayton *et al.* 1977). These organic soils are situated in the Overflow Bay and Dawson Bay area at the northwest corner of the Lake. Mesisolic soils are derived from partially decomposed herbaceous fen material and boreal forest peat (Clayton *et al.* 1977).

Organic matter content of this soil is >30% (Weir 1983) and the soils are thus acidic (Brady 1974).

Soil moisture of the Lake Winnipegosis area is classed as sub-humid to humid, with moisture deficits often occurring in the southern regions, but rare in the north (Clayton *et al.* 1977).

Although these three soil types predominate, minor inclusions of other soil types do occur. In Saskatchewan, Dodd *et al.* (1964) found that the main soil types were Saline Gleysols, Saline Chernozems, and Saline Regosols. Most soils specifically associated with the saline sites of the Winnipegosis shoreline exhibit characteristics of Saline Regosols. A Regosol is a mineral soil with a thin organic layer at the surface and no horizon development below (Clayton *et al.* 1977). Thus, the characteristics of the parent material dominate the entire profile. The parent material of Saline Regosols is always saline, and usually calcareous (Clayton *et al.* 1977). These are two characteristics common to the Winnipegosis sites (Burchill 1991). A few of the saline sites of the Dawson Bay and Overflow Bay are characterized by soils high in organic matter.

Section 1.2.5 - Climate

According to the Koppen-Geiger classification scheme (deBlij 1981), the climate of the Lake Winnipegosis region is humid and cold, with short, cool summers, long, cold winters, and no discernible dry periods. On average the area experiences a frost-free period of 100 days, from 25-30 May to 10-15 September (Weir 1983). Temperature ranges from an average low of -26.7 °C in January, to an average high of 23.9 °C in July, with a mean annual temperature of -0.3 °C (Rowe 1972). The mean temperature over the growing season (May to September) is 13.8 °C. Average annual precipitation is 557 mm, with approximately 250 - 280 mm falling as rain from May to September (Rowe 1972; Weir 1983).

Section 1.2.6 - Vegetation

Lake Winnipegosis lies in the Manitoba Lowlands Section of the Boreal Forest Vegetation Region (Rowe 1972). The area is essentially a transition zone between the broad-leaf Aspen-Oak Section to the south, and the Northern Coniferous Section to the north and east. The southern half of the Lake area is dominated by *Populus tremuloides*, with *Picea mariana* occurring in wet depressions, and *Picea glauca* on gravel ridges (Weir 1983). The northern area of Lake Winnipegosis, including Dawson and Overflow Bays, is dominated by *Picea mariana* and *Picea glauca. Populus tremuloides, Populus balsamifera, Betula papyrifera,* and *Larix laricina* are common, with *Pinus banksiana* occurring on outcrop areas and low ridges (Rowe 1972). *Sphagnum* bogs and sedge meadows are also common in depressions in the northwest.

Annual halophytes (mainly Chenopodiaceae) along with perennial halophytic graminoids (including members of Juncaginaceae, Juncaceae, and Poaceae) and composites (Asteraceae) characterize the vegetation of the saline sites. The sites are often surrounded by stands of *Picea glauca* located on elevated gravel ridges (Burchill 1991). Appendix I presents a list of species found at the saline sites visited in this study.

Section 1.2.7 - Saline Sites

The saline sites of Lake Winnipegosis range from actively flowing springs (Figure 1.4) to more passive saline seeps (Figure 1.5). Chemical analysis of the soil and water of these sites has indicated that sodium and chloride are the dominant ions (van Everdingen 1971; Burchill 1991). Sulphate, carbonate, calcium, and magnesium ions also occur, but at far lower concentrations (van Everdingen 1971). The concentration and composition of ions in the soil of the Winnipegosis sites differs appreciably from that of other North American inland saline sites to the south and west. These other sites tend to be dominated by sodium and/or magnesium cations and sulphate anions (Keith 1958; Dodd *et al.* 1964; Dodd & Coupland 1966(a); Ungar 1970).

The soil associated with active springs is generally very hard-packed and stony. The area immediately surrounding the springs lacks vegetation, although cyanobacteria and members of Bacillariophyceae (diatoms) can proliferate in the run-off from the springs. A number of active springs occur on gravel beaches of the lake shore. These discharge into the lake and thus influence aquatic macrophyte and algal populations.

Submerged springs also occur throughout Lake Winnipegosis itself (Nielson *et al.* 1987). This results in localized regions of saltwater in an otherwise freshwater body (Wadien 1984).

The majority of the saline sites are passive saline seeps. In such sites actively flowing springs are absent, although evidence of past springs, in the form of cauldron-like domes, may be present. Saline seeps consist mainly of a highly saline, unvegetated central pan or "playa" surrounded by roughly concentric bands or zones of vegetation. The concentration of soil salts decreases away from the pan. The elevation tends to rise slightly as one moves from the pan outward, giving the seep sites a shallow "bowl-shape". This results in water drainage into the pan area following rainfall and snow-melt. Soil salinity results from capillary movement of dissolved salts from the underlying groundwater (Burchill 1991). Analysis of soil samples collected from the pans of 20 seeps in 1989 indicated that the soil salt concentration varies between sites (Table 1.1). These differences may be due to small scale local variation in environmental factors such as drainage and weather from site to site.

Burchill (1991), in a detailed discussion of the ecology of saline sites in the Overflow Bay area, compared the Overflow Bay sites to other inland saline sites at nine different geographic locations in North America (Nebraska, Kansas, Oklahoma, Colorado, Utah, California, North Dakota, South Dakota, and Saskatchewan). A sum of squares cluster analysis algorithm was used to delineate the sites into four main groups based on the presence/absence of 37 vascular plant species. The results (Figure 1.6) show that the

Figure 1.4 Photograph of actively flowing saline spring, Dawson Bay, Lake Winnipegosis, Manitoba.

Figure 1.5 Photograph of passive saline seep area, Dawson Bay, Lake Winnipegosis, Manitoba.

Overflow Bay sites are distinct. This is likely due to differences in climate and soil ionic composition between the Overflow Bay sites and the other sites addressed.

Table 1.1. Results of preliminary salinity analysis of salt pan soil from 20 saline sites. Mean soil salinity analysis was done by the author, while chlorine ion concentration is based on data collected by McKillop (1989, personal communication). NA = information not available. n = 3.

Saline Site	Mean Soil Salinity (mg salt/ml of soil)	[Cl-] in Soil Water (ppm)
1	15.48 ±6.29	12500
2	29.27 ±0.74	11750
3	31.24 ±0.56	18000
4	29.41 ±4.98	11000
5	30.24 ±2.08	30500
6	31.15 ±2.78	32000
7	17.44 ±6.53	27800
8	20.27 ±4.28	30750
9	19.81 ±0.73	12500
10	29.34 ±5.50	NA
11	33.46 ±2.88	33750
12	55.96 ±0.17	NA
13	47.28 ±0.91	NA
14	54.33 ±6.53	35500
15	55.02 ±36.91	NA
16	16.47 ±4.91	NA
17	39.06 ±1.67	NA
18	37.73 ±2.2	NA
19	27.99 ±1.15	NA
20	38.95 ±4.11	NA

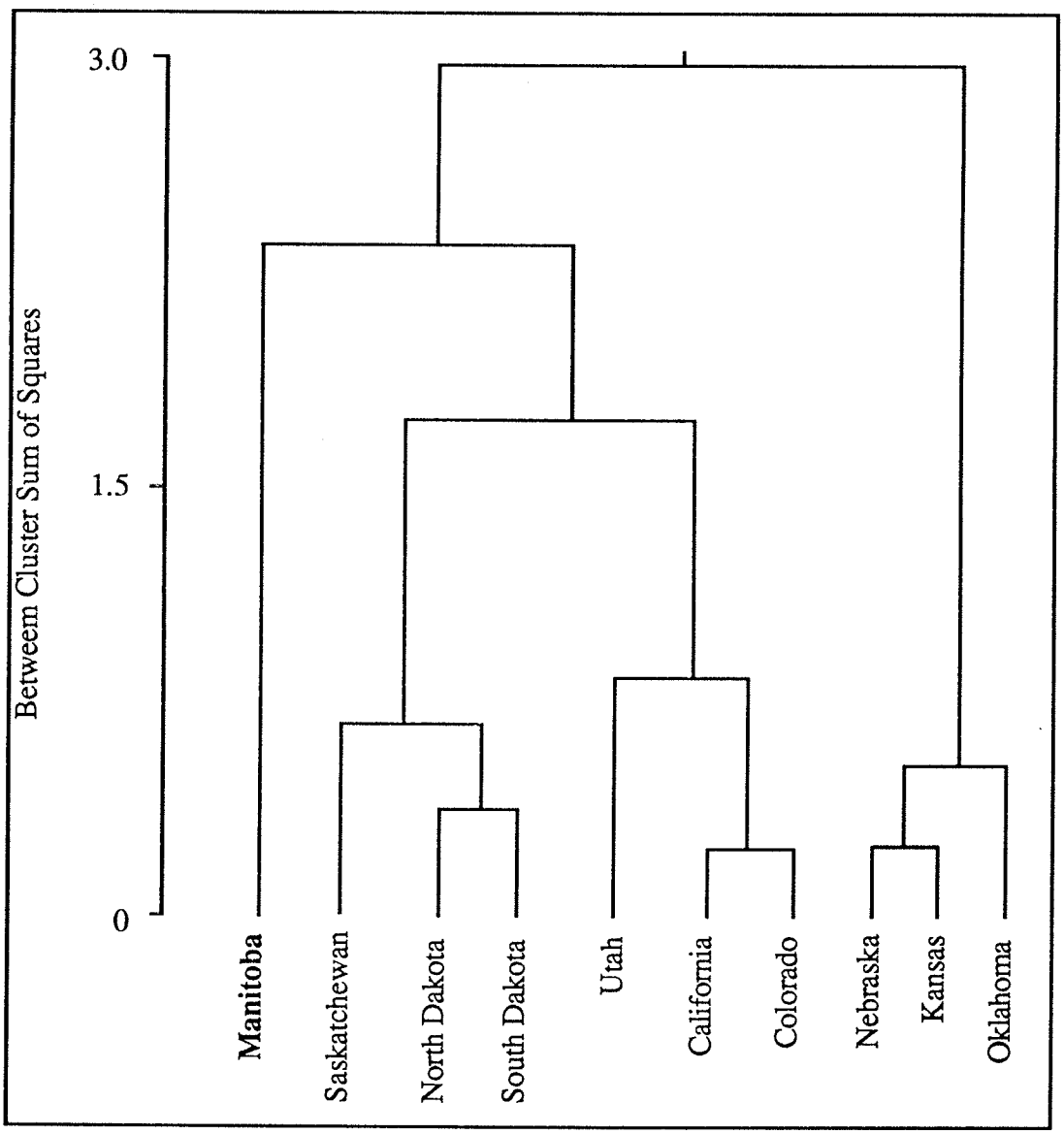


Fig. 1.6. Cluster analysis results based on presence/absence of 37 vascular plant species of saline sites in ten geographic locations in North American. Note relative uniqueness of Manitoba sites indicated by the dendrogram. (Modified from Burchill 1991).

Section 1.3 - Vegetation Zonation

Section 1.3.1 - Introduction

The distribution of plant species in discrete vegetation zones has been reported in many studies of coastal saline marshes (for reviews see Waisel 1972; Odum 1988). Vegetation zonation also occurs in inland saline habitats (reviewed by Ungar 1974(a)), and is apparent at the Lake Winnipegosis sites. Burchill (1991), working at Overflow Bay, identified eight distinct vegetation zones. Moving from most saline to least saline (i.e. from playa or pan outward) the zones are: (1) Salt Pan (Salicornia); (2) Puccinellia; (3) Triglochin; (4) Hordeum-Distichlis; (5) Spartina; (6) Agropyron; (7) Calamagrostis; and (8) Rosa. (Figure 1.7). (Note that henceforth non-italicized genera names refer to vegetation zones).

Section 1.3.2 - Vegetation Zones

The Salt Pan zone soil has the highest salinity. Where vegetation is present, it is dominated by *Salicornia rubra.* Other associated species are *Spergularia marina, Triglochin maritima,* and *Plantago maritima.* The Puccinellia zone is almost solely occupied by *Puccinellia nuttalliana,* with *Suaeda depressa* co-occurring at far lower cover values. The Triglochin zone is dominated by *Triglochin maritima* with minor occurrences of *Plantago maritima, Puccinellia nuttalliana, Suaeda depressa, Distichlis stricta,* and *Hordeum jubatum.* The Triglochin zone is followed by the Hordeum-Distichlis zone, co-dominated by *Hordeum jubatum* and *Distichlis stricta.* The next zone, the Spartina zone, is dominated by *Spartina gracilis* with a few associated species such as *Hordeum jubatum, Distichlis stricta, Grindelia squarrosa, Aster pauciflorus,* and *Triglochin maritima.* The Agropyron zone is dominated by *Agropyron trachycaulum* with *Aster pauciflorus* and *Sonchus arvensis* also present. Following the Agropyron zone is the Calamagrostis zone which is dominated by *Calamagrostis inexpansa.* Associated species in the Calamagrostis

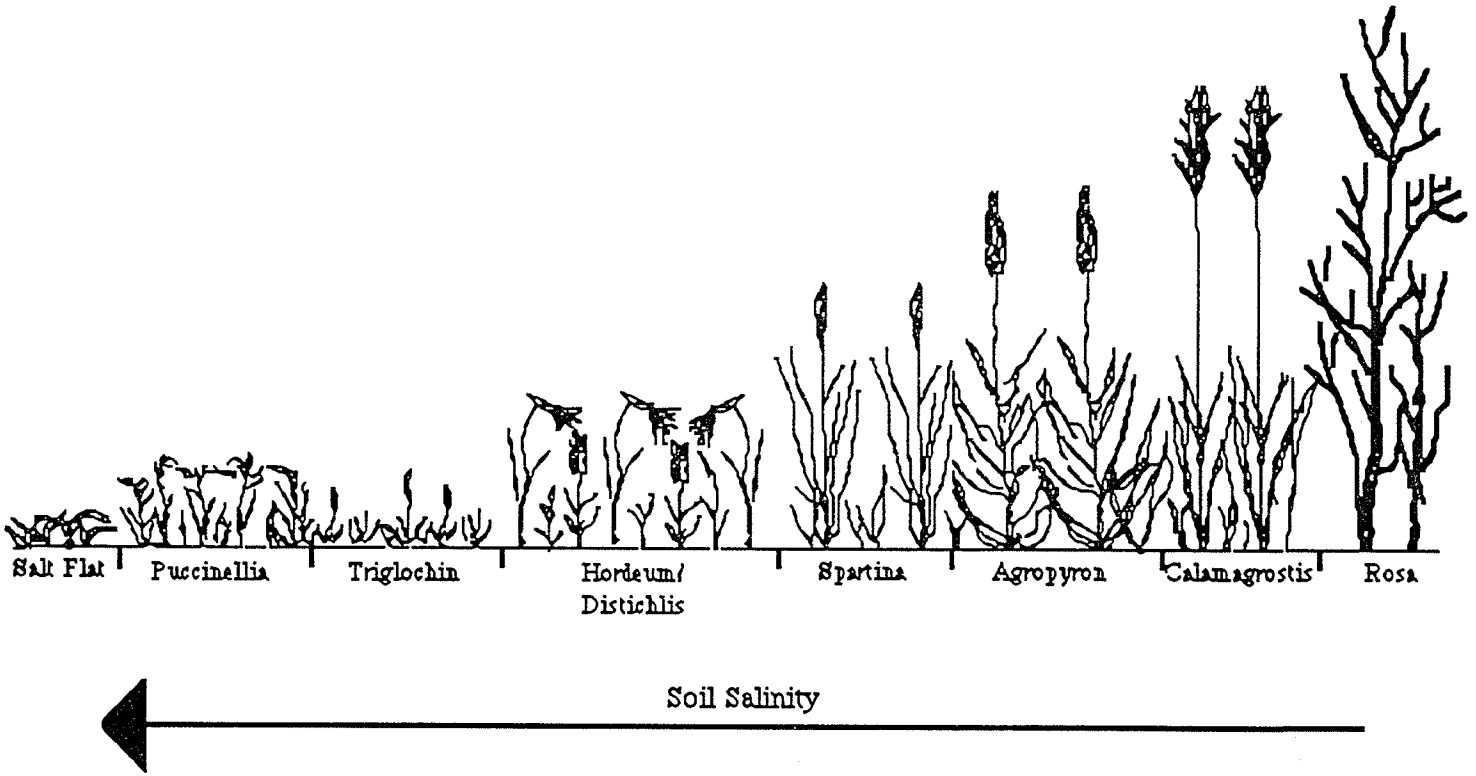


Fig. 1.7 Diagram showing an idealized zonation in vegetation from the hypersaline salt pan zone to the low salinity Rosa zone. Note increase in relative height of dominants with decreasing salinity. (Modified from Burchill, 1991).

zone include *Agropyron trachycaulum, Aster pauciflorus, Sonchus arvensis*, and *Juncus balticus.*

The final and least saline zone of this sequence is the Rosa zone. It is dominated by the shrub *Rosa acicularis*, with a number of relatively salt intolerant composites such as *Helianthus maximiliani, Sonchus arvensis*, and *Solidago* sp. This zone is located adjacent to *Picea glauca* dominated gravel ridges which surround the saline sites.

Section 1.3.3 - Soil Gradients

Burchill (1991) described a number of soil gradients which run from the pan outward. Soil salinity decreases gradually from a high of 20 mg/ml of soil to a low of 3.9 mg/ml in the Rosa zone. Relative surface elevation (elevation of the soil surface in relation to the lowest point in the site) increases gradually from the salt pan zone (0 cm) to the Rosa zone (+45 cm). This results in a drainage pattern from the Rosa zone toward the pan. The soil pH gradient is inversely related to salinity, with the salt pan area having a pH of 8.8, and the Rosa zone a pH of 7.5. In general, bulk density and carbonate content of the soil decreases from the salt pan outward, while soil organic matter increases. Potassium, nitrogen, and phosphorus were analyzed by Burchill (1991). Only phosphorus showed a clear gradient across the vegetation zones. Quantities ranged from a low of 11.8 ppm in pan soil to a high of 53.4 ppm in Rosa soil. The lowest and highest readings for both potassium and nitrogen can be found in the salt pan and Rosa zones respectively.

Canonical correlation analysis by Burchill (1991) on eight environmental factors indicated that salinity was the soil factor influencing vegetation distribution (Table 1.2). Other factors of importance include soil pH, relative surface elevation, and bulk density. However, the discontinuous vegetation gradient (i.e. zonation) cannot be described as being directly reflective of continuous edaphic gradients. Thus, some other factor(s) must be involved in the creation and maintenance of vegetation zonation. Factors

may include soil parameters not measured in Burchill's study, such as moisture content, or biotic factors such as interspecific competition.

Table 1.2 Results of canonical correlation analysis applied to saline site soil data. Note salinity, pH, and relative elevation have the highest correlation values (from Burchill 1991).

Soil Factor	Canonical Correlation	
	Axis I	Axis II
Salinity	-0.813	0.415
pH	-0.756	-0.101
Relative Elevation	0.643	-0.026
Bulk Density	-0.488	0.456
Potassium	-0.44	0.328
Phosphorus	0.22	-0.132
Nitrogen	-0.17	-0.18
Organic Matter	0.145	0.301

Section 1.4 - Salinity and Its Effects on Plants

Section 1.4.1 - Introduction

Soils of saline habitats contain salts in such excess as to adversely affect the normal growth and development of plants. Effects on plants result from decreased osmotic potentials in the root zone due to the presence of dissolved salts (Bernstein 1975). This disrupts the water potential gradient and can lead to loss of turgor pressure and eventually wilting. Plants of saline soils can take in water only if they can produce and maintain an osmotic potential lower than the surrounding soil (Larcher 1980). They also suffer toxic effects of ions in the soil solution (Bernstein 1975; Jefferies & Pitman 1986). Low concentrations of salts in rooting media are not directly toxic to plants (Yeo & Flowers

1977). This indicates salt toxicity is more a function of concentration than of the types of ions present in the rooting medium. At higher concentrations, however, the actual composition of ions involved increases in importance (Yeo & Flowers 1977). High salinity can also influence the availability of nutrients directly, by competing for and occupying sites on soil micelles, and indirectly, by altering soil pH (Brady 1974) and reducing the uptake of water-nutrient solutions (Bernstein & Hayward 1958). The short-term, rapid fluctuations in salinity which occur in saline habitats can also be detrimental to plant growth (Dainty 1979). Some species are more susceptible than others, and the mechanisms involved in resisting the effects of salinity often differ between species (Jefferies & Rudmik 1984).

Section 1.4.2 - Salt Resistance

Introduction

Larcher (1980, p.187) defines salt resistance as "the ability of a plant to withstand the presence of excess salts without serious impairment of vital functions". He defines salt tolerance as "a property of the protoplasm that enables it to tolerate ... the changed ionic ratios associated with salt stress and the toxic and osmotic effects associated with increased ion concentration". These definitions harken back to Levitt (1972) who distinguished salt tolerance mechanisms from those of salt avoidance (regulation), and put both strategies as subcategories of salt resistance. According to Levitt, avoidance or regulation refers to the ability of a plant to avoid or exclude the stress agent (i.e. salt), while tolerance refers to the ability of a plant to survive an internal stress brought about by external salts. Both salt tolerance and salt resistance have been used interchangeably (Shannon 1984), and there are arguments for and against using each term. For the purposes of this thesis I will refer to the definitions provided by Larcher. Thus, the ability of a plant to regulate the uptake of

excessive external ions, coupled with its ability to tolerate and adjust internally to changes in external osmotic pressures, constitute its degree of salt resistance.

There are a number of mechanisms employed by plants to counter the effects of salinity (see Levitt 1972, and Flowers *et al.* 1977 for detailed reviews). These mechanisms (Figure 1.8) fall into two main categories: (1) osmotic tolerance, including the accumulation of organic solutes and inorganic ions to maintain a low osmotic potential, and (2) salt regulation, including exclusion, storage and elimination, and dilution.

Osmotic Tolerance

By increasing the solute concentration in both the cell vacuole and cytoplasm, plants can lower their osmotic potential relative to the soil solution, and create a favorable osmotic gradient such that turgor pressure is maintained (Jefferies 1981; Jefferies *et al.* 1981; Ewing *et al.* 1989). Organic osmotic solutes (osmotica) include: (i) nitrogenous compounds such as proline, glycinebetaine (Stewart & Lee 1974; Storey & Wyn Jones 1975; Cavalieri & Huang 1979; Rozema 1979; Jefferies 1981; Ewing *et al.* 1989;), homobetaine (Stewart *et al.* 1979), and choline (Storey & Wyn Jones 1975), (ii) carbohydrate compounds including reducing sugars such as sucrose (Jefferies *et al.* 1979; Rozema 1979; Briens & Larher 1982; Ewing 1989), and (iii) various polyols (Ewing *et al.* 1989) such as sorbitol and mannitol (Ahmad *et al.* 1979; Jefferies *et al.* 1979). Glycinebetaine appears to gradually accumulate with increasing salinity, while production of proline does not appear to increase until a certain salinity is reached (Ewing *et al.* 1989). Proline production has also been shown to be effective as a means of drought resistance in xerophytes (Stewart & Lee 1974). The relative importance of carbohydrates and polyols in osmoregulation is poorly understood (Jefferies *et al.* 1979; Briens & Larher 1982; Ewing *et al.* 1989). Plants under saline conditions will often employ a combination of these compounds for osmotic adjustment (Stewart *et al.* 1979; Ewing *et al.* 1989).

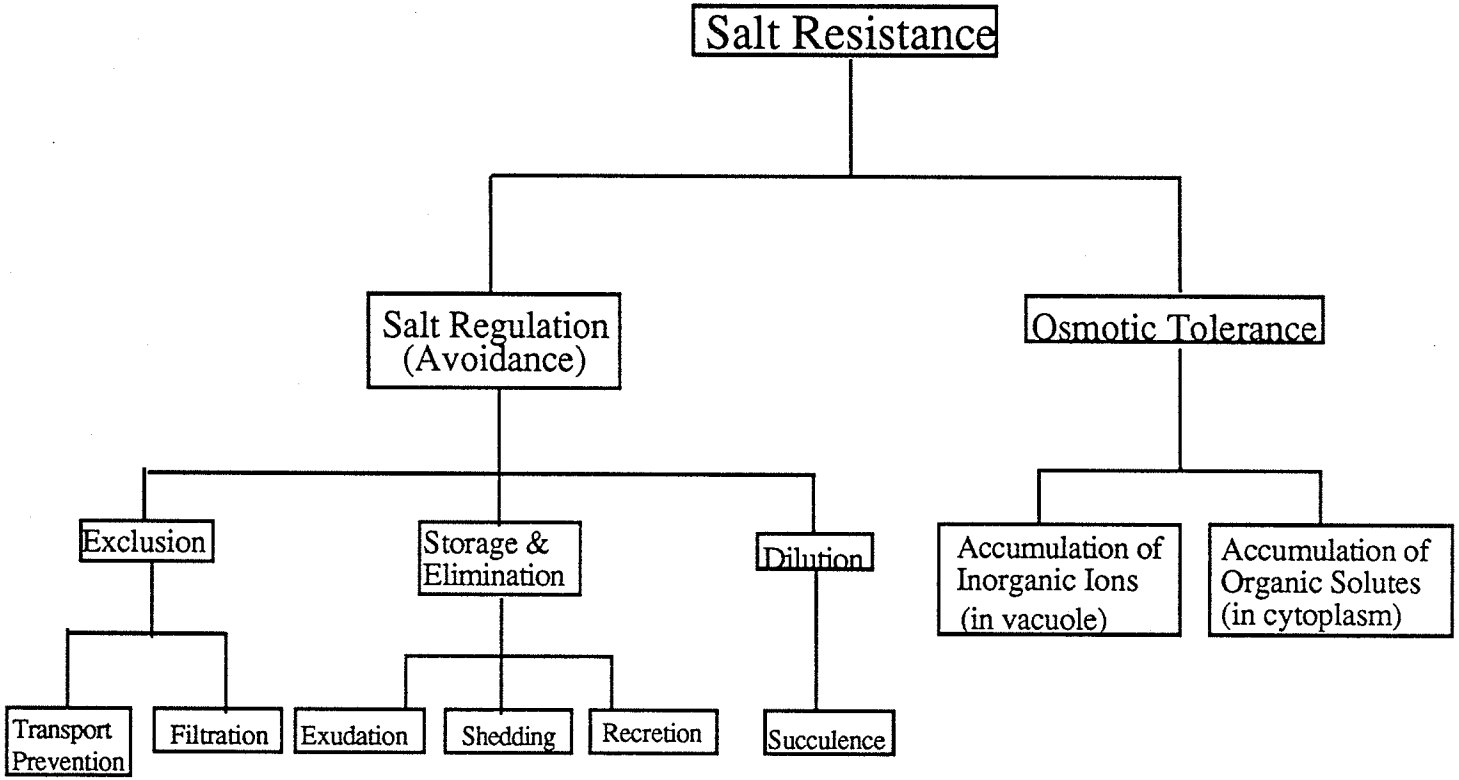


Figure 1.8. Diagrammatic representation of relationship between salt resistance mechanisms (modified from Levitt 1972 and Larcher 1980).

Studies have shown that accumulation of nitrogenous organic compounds in the plant does not disrupt normal enzymatic activity (Guy *et al.* 1984; Jefferies & Pitman 1986). Because of this, nitrogenous compounds are accumulated in the cytoplasm. However, their increased production in response to salinity is energy consumptive (Dainty 1979), resulting in reallocation of photosynthate and a subsequent reduction in growth rate, flowering, and seed production (Bernstein 1961; Dainty 1979; Jefferies *et al.* 1979; Jefferies 1981; Ewing *et al.* 1989). Because increasing salinity often limits the availability of soil nitrogen (Jefferies *et al.* 1979), the accumulation of nitrogenous organic compounds as a primary means of osmotic adjustment tends to be more prevalent in plants of relatively low to moderate salinity (Stewart *et al.* 1979). These plants, referred to as glycohalophytes (Bernstein 1975), tend to be long-lived, perennial graminoids and composites (Rozema 1979; Ewing *et al.* 1989). They are capable of storing nitrogen in below-ground organs during periods of low salinity (i.e. in spring) and later, during periods of high salinity (i.e. summer), they can access this nitrogen and use it in osmotica production (Jefferies *et al.* 1979; Jefferies *et al.* 1981). This is not an exclusive property, as proline is present in a number of highly salt resistant, non-graminoids such as *Spergularia marina, Plantago maritima, Salicornia europaea, Suaeda maritima,* and *Glaux maritima* (Stewart & Lee 1974). The degree to which proline aids in salt tolerance in these latter species is unknown. However, since they live in hypersaline conditions, it is likely that another mechanism, in combination with proline, aids in salt resistance.

As with organic solute accumulation, inorganic osmotica lower the osmotic potential in the plant and thus maintain turgor. Plants relying on inorganic osmotica are called euhalophytes by Bernstein (1975). Greenway & Munns (1980) and Jefferies & Pitman (1986) indicate that this may be the main means of osmotic adjustment employed by halophytes. Studies on coastal and inland halophytes reveal that dicotyledons tend to accumulate Na^+ and Cl^- (Albert 1975; Riehl & Ungar 1982; Jefferies & Pitman 1986), while graminoids accumulate K^+ and Cl^- (Jefferies & Pitman 1986). Studies by Jefferies

et al. (1979) indicate that some form of compartmentation may occur in halophytes. This would involve segregation of accumulated ions, thus limiting their influence on the activity of enzymes. Studies have shown that most inorganic ions are stored in the cell vacuole (e.g. Yeo 1981; Riehl & Ungar 1982.). This appears to maintain hydrostatic equilibrium within the cell (Jefferies & Pitman 1986), as well as protecting enzymes in the cytoplasm from toxic effects of inorganic ions. However, this accumulation of inorganic ions does have a limit, beyond which further ion intake will adversely affect metabolic processes (Jefferies and Pitman 1986). This threshold differs from species to species, and is a measure of a species' salt tolerance. This means of osmotic adjustment consumes energy, and thus is accompanied by decreased plant growth and development (Haines & Dunn 1985).

Some halophytes, such as members of the Chenopodiaceae, accumulate Na^+ even when external concentrations are low (Jefferies & Rudmik 1984). Because of this, Storey & Wyn Jones (1977) suggested a classification of salt resistant plants into two groups: (1) osmoregulators and (2) osmoconformers. Osmoregulators are plants which maintain a low osmotic potential throughout the season by constantly taking in ions regardless of external fluctuatons in concentration. This may be an adaptive feature to counter the effects of external salinity fluctuations. This group would include many of the succulents such as species of *Halimione, Salicornia,* and *Suaeda*, which are generally shallow rooted annuals, and as such are subjected to high, rapid fluctuations in salt concentration. By constantly accumulating salts, these species are prepared for periods when the external salinity increases. Osmoconformers adjust their internal water potential in line with changes in the external water potential. Most are deep rooted perennials, with their rooting zone well below that of annuals, and as such, tend to experience relatively low, non-fluctuating salinity levels.

Salt Regulation

The second main category of salt resistance involves treatment of the salt solution in such a way as to minimize intake and maximize protection of plant tissues from the toxic effects of ions (Larcher 1980). One way plants can do this is through exclusion (Waisel 1972), involving selective impermeability of roots to specific ions (Caldwell 1974; Yeo 1983) and/or the retention of ions (particularly Na^+) in the roots and lower stem (Larcher 1980), thereby preventing ions from reaching the leaves. Transportation of salts out of the roots and back into the soil can also occur in halophytes (Waisel 1972) via a process known as recretion (Larcher 1980). Example species include *Salicornia europaea* and *Suaeda monoica* (Waisel 1972). The salt content of these plants peaks in the late morning and late afternoon, with significant decreases occurring in the early afternoon and at night, suggesting that salts are being transported back into the soil. Recretion is poorly understood (Waisel 1972), but may be related to fluctuations in the salt content of the soil solution near the roots. Diurnal temperature fluctuations at the soil surface cause capillary movement of the soil solution (Brady 1974). This could cause the vertical movement of salts into and out of the root zone. Periods of draw-down (i.e. night) would result in a lower concentration of salts in the root zone than in the roots, allowing diffusion of salts from roots into the soil.

Another mechanism of salt regulation involves the uptake and excretion of excess salts (Jennings 1976; Flowers *et al.* 1977; Ewing *et al.* 1989). This is accomplished through specialized salt glands (Waisel 1972), the structure of which differs from species to species (Anderson 1974), or through accumulation of salts in senescing leaves (Waisel 1972; Larcher 1980). Salt-excreting glands have been observed in *Spartina alterniflora, Spartina patens, Limonium* spp., *Distichlis spicata* (Anderson 1974), *Glaux maritima,* and *Atriplex* spp. (Larcher 1980), however, they are not necessarily present in all halophytes (Anderson 1974). Waisel (1972) stated that salt excretion through glandular structures is mainly a mechanism employed by non-succulent halophytes.

The energetics of salt excretion through specialized glands is poorly understood (Haines & Dunn 1985). However, it is advantageous as it prevents accumulation of harmful ions (e.g. Cl^- and Na^+), without affecting the uptake and balance of nutrients (Waisel 1972). Many salt-excreting species also employ recretion and exclusion (Waisel 1972).

The discarding of salt-saturated leaves has been observed in *Salicornia* spp. (Waisel 1972), *Plantago maritima*, *Triglochin maritima*, and *Aster tripolium* (Larcher 1980). This mechanism may be a response to hormonal activity brought about by exposure to high salinity. Mizrahi *et al.* (1971) observed that increased salinity led to a decrease in the transport of kinetin from the roots to the shoots and leaves, accompanied by an increased concentration of abscisic acid in the leaves. Such changes decrease the stomatal aperture and thus prevent water loss through transpiration (Mizrahi *et al.* 1971). Kinetin promotes cell elongation and delays senescence, while abscisic acid promotes senescence and leaf abscission (Abercrombie *et al.* 1981). Decreased kinetin and increased abscisic acid levels in response to high salinity may result in loss of salt saturated leaves, thus lowering the salt load of the plant. Whatever the precise role of kinetin and abscisic acid may be in salt resistance, it appears that it is only temporary, as re-establishment of normal hormone levels takes place once osmotic adjustment has occurred (Bernstein 1975).

The third main mechanism of salt regulation in halophytic species involves the retention of relatively large volumes of water in cells (Larcher 1980), a phenomenon termed succulence. The main problem encountered by plants is not the quantity of salt present per gram dry weight of tissue, but the concentration of these salts in the cell sap solution. Thus, by increasing the amount of water in its cells, a plant is able to dilute the salts to an acceptable concentration (Jennings 1968; Larcher 1980). Succulence is characterized by an overall reduction in plant size, increased leaf thickness, enlargement of cells with increased elasticity of the cell wall, low chlorophyll content, and decreased size and number of stomata (Waisel 1972). Identification of the controlling mechanism behind

succulence has received considerable attention. Strogonov (1962) suggested that Cl^- plays a prominent role in increasing elongation of the palisade layer, thus leading to increased succulence. Later research indicated that succulence likely depends more on the concentration of Na^+ in the root zone and plant tissues (Jennings 1968), and involves the operation of an ATP-driven sodium pump which deposits ions into the cell vacuole. This indicates that succulence is closely tied to inorganic solute accumulation in cells as a means of osmotic tolerance. Succulence has been observed in halophytes, particularly the family Chenopodiaceae, and in a number of xerophytes (Larcher 1980). Plants which regulate their salt content by excretion tend to be non-succulent (Waisel 1972; Anderson 1974).

Section 1.4.3 - Effects of Salinity on the Plant Life Cycle

Introduction

As mentioned above, the direct effects of salinity on plants are osmotic and toxic, while indirect effects include limitation of nutrient uptake and assimilation. The ability of a species to tolerate high salinity is a function of its salt resistance and the timing of events in its life-cycle. A species' susceptibility to hypersaline conditions varies at different stages of its life-cycle. Many halophytes have evolved specific life-history strategies to cope with hypersaline habitats.

Germination and Seedling Establishment

High salinity decreases germination and seedling establishment in many inland halophytes including *Salicornia rubra* (Ungar *et al.* 1979), *Suaeda depressa* (Williams & Ungar 1972), *Distichlis stricta* (Ungar 1974(a)), *Puccinellia nuttalliana* (Macke & Ungar 1971), and *Hordeum jubatum* (Ungar 1974(b)). Experiments have found that seeds of some species remain dormant until subjected to periods of high moisture and low salinity (Ungar 1974(a); Ungar 1978), such as occur in spring and early summer, and seeds

subjected to high salinity conditions remained viable after salinity was lowered, indicating that the effect of salinity on the seeds is osmotic rather than toxic. This externally imposed dormancy allows a population to persist as seeds over periods of high salinity, and under conditions which seedlings and mature plants would not normally survive (Ungar 1978; McMahon & Ungar 1978; Ungar & Riehl 1980). Release from seed dormancy is likely related to the activity of endogenous hormones in reaction to changes in external osmotic potential, temperature, and light (Ungar 1978).

Seed dimorphism has been observed in a number of annual halophyte and non-halophyte species (Philipupillai & Ungar 1984). As a rule, this phenomenon has evolved as a mechanisms of survival in "weedy" or "ruderal" species found in unpredictable, harsh habitats (Harper *et al.* 1970). *Salicornia europaea* (Ungar 1979; Philipupillai & Ungar 1984) and *Atriplex triangularis* (McMahon & Ungar 1978; Ungar & Riehl 1980) produce two types of seeds which vary in size and length of dormancy: large seeds germinate in the spring when salinity levels are relatively low, and smaller seeds persist in the seed bank and may germinate later in the summer if conditions are optimal. This seed dimorphism and staggered period of germination aids in assuring the survival of the population. The success of seed germination, seedling establishment, growth, and reproduction is largely dependent on environmental conditions. Seedling establishment is hindered by drought, excessive rainfall, and flooding, which may result in the demise of the population. Seed dimorphism offers a solution to this problem by ensuring that some seeds are available for re-establishment of the population later in the growing season should conditions change and become more suitable.

Most halophytes are perennials (Jefferies & Pitman 1986; Odum 1988), and have extensive rhizome systems or robust tap-roots. In rhizomatous graminoids and composites sexual reproduction occurs, but the main method of propagation is by tillering and fragmentation of rhizomes (Waisel 1972; Odum 1988). These features aid in the survival

of populations under stressful conditions because allocation of large quantities of photosynthate and energy to seed production is not required.

General Growth Rate and Photosynthesis

Excess salinity is responsible for decreased growth rates in plants (Larcher 1980), as observed in most glycophytes at low salinities, and halophytes at higher salinities (Waisel 1972). Some annual halophytes such as *Salicornia europaea* and *Spergularia maritima*, and perennials such as *Triglochin maritima*, actually display stimulated growth in response to moderate increases in salinity under laboratory conditions (Caldwell 1974; Jefferies & Pitman 1986). Such growth enhancement is only temporary, as continued increases in salinity will lead to an eventual decline in growth rate (Jefferies & Pitman 1986). Decreased growth rate can result directly from the disruption of the physical structure of soil, decreased water intake, increased water loss, toxic effects of ions on enzymatic activity and plasma membranes, and reduced nutrient availability (Waisel 1972). Indirectly, growth rate suffers as a result of the reallocation of photosynthate and energy to operating salinity resistance mechanisms (Yeo 1983; Odum 1988).

Pearcy & Ustin (1984) indicate that increasing salinity has a negative impact on photosynthesis and relative growth rate. They suggest that as salinity increases, the ability of *Scirpus robustus* and *Spartina foliosa* to photosynthesize decreases. Both species close stomata in response to increasing salinity in an effort to conserve water. This results in a decrease in CO_2 intake, which then decreases the rate of photosynthesis. They found that salinity had a greater effect on relative growth rate than photosynthesis. This suggests that much of the photosynthate produced is allocated to salt resistance rather than to vegetative growth. Guy *et al.* (1980, 1986) also point out that photosynthesis in halophytes is affected by increasing salinity, which they suggest may be due to the decrease in available water brought about by high salinity.

Nutrient Limitations

The main limiting macro-nutrients in inland saline sites are available nitrogen and phosphorus (Jefferies & Pitman 1986). In such habitats the availability of nutrients for plant growth and development is limited directly by excess soil salts and indirectly through reallocation of nutrients to maintaining salinity resistance. Inorganic phosphates ($H_2PO_4^-$ and HPO_4^{-2}) are the main sources of phosphorus for plants. Both phosphates are available to plants at a soil pH range of 6.0 - 7.0, however, saline soils tend to be alkaline, with pH levels usually in excess of 7.0 (Brady 1974). At pH levels above 7.0 $H_2PO_4^-$ becomes bound to cations in the soil (e.g. Ca^{+2}) forming insoluble compounds, and only HPO_4^{-2} is available (Waisel 1972). Thus, an increase in salinity creates an increase in soil pH, which can adversely affect phosphorus availability and uptake by plants.

Pigot (1969), Valiela & Teal (1974), and Jefferies & Perkins (1977) have demonstrated through fertilizer application experiments that nitrogen is a limiting factor in coastal saline marshes. There are three main forms of nitrogen in soils (Brady 1974): (1) organic nitrogen associated with soil humus; (2) ammonium nitrogen which is bound to certain clay materials; and (3) nitrogen compounds dissolved in the soil solution. Only the latter form of nitrogen is readily available to plants. Soluble nitrogen compounds include ions of inorganic ammonium and nitrates. Plants take up nitrate directly, and ammonium ions indirectly through the process of nitrification, a two step process carried out by nitrobacteria. First, ammonium ions are converted to nitrous acid (nitrites), and are subsequently oxidized into nitrates that can be used by plants. *Nitrosomonas* is responsible for converting ammonium to nitrite, while *Nitrobacter* oxidizes nitrite to nitrate. Energy is also a by-product of these conversions, and is used by the bacteria for metabolic processes. Nitrification is rapid and keeps the concentration of nitrites in the soil low, thus minimizing acidic affects on microbial activity. Soluble nitrogen seldom constitutes more than 1-2 percent of the total nitrogen content of soil (Brady 1974).

Major inputs of soluble nitrogen in salt marshes include: (1) fixation of atmospheric nitrogen by blue-green algae and bacteria; (2) inflow of ground water containing dissolved nitrate, nitrite, and ammonium ions; (3) deposition of dissolved nitrogen compounds in precipitation; and (4) inflow from tidal inundation (in the case of coastal marshes). Major losses of nitrogen result from: (1) extraction of nitrogen compounds and detrital material by out-flowing tidal waters; (2) denitrification, in which microbial activity converts nitrates to nitrogen gas which escapes into the atmosphere; (3) volatization of ammonia and its release into the atmosphere; and (4) leaching of compounds deep into the sediment and beyond the reach of plant roots. Valiela & Teal (1979) state that the inputs and outputs of nitrogen to the salt marsh ecosystem result in a net loss of available nitrogen, and thus nitrogen deficiency for plants. McClung & Frankenberger (1985) indicate that microbial enzymatic activity is reduced by increasing salt ions, particularly Cl^-, in the soil, leading to a decrease in nitrification. They also suggest that increasing salinity leads to increased volatization of ammonia.

There are few studies of inland salt marsh nitrogen budgets. The absence of tidal influence on inland habitats makes direct comparisons of inland and coastal marsh nitrogen budgets invalid. Loveland & Ungar (1983) found that growth of *Salicornia europaea* in an inland marsh increased dramatically with the application of nitrogen. This suggests that populations of *Salicornia europaea* are normally limited by nitrogen. Application of nitrogen to *Hordeum jubatum* and *Atrilplex triangularis* populations had no significant effect (Loveland & Ungar 1983). This lack of response may indicate that *Hordeum jubatum* and *Atriplex triangularis* are not limited by nitrogen. Alternatively, these results may indicate an error in the experimental design. For instance, the application of fertilizer may have been improperly timed with the plants' life-cycles. The soil in which the latter two species grow is less saline than that of the *Salicornia europaea* population. This lower salinity may allow near optimal amounts of available nitrogen for growth of *Hordeum jubatum* and *Atriplex triangularis*.

Results from a preliminary nutrient experiment, conducted at Overflow Bay in 1989 (Burchill 1990 personal communication), suggest that growth of vegetation in the Hordeum-Distichlis zone is initially limited by available nitrogen and then by available phosphorus. This experiment involved using a random block design with three fertilizer treatments (nitrogen, phosphorus, and nitrogen-phosphorus) and a control. The treatments and control were replicated four times. Plant response to treatment was based on biomass accumulation over the growing season. Burchill (1990 personal communication) found that increase in growth was very evident in the nitrogen fertilizer treatments, but was insignificant in the phosphorus treatments. The greatest increase in growth was observed in the nitrogen-phosphorus treatments ($p = 0.0099$). This indicates that vegetation in the Hordeum-Distichlis zone will readily assimilate nitrogen until it is limited by available phosphorus. A similar experiment was conducted on vegetation of the salt pan zone. Results were inconclusive as the vegetation of this zone died in the early spring due to drought.

Inland halophytic perennials have adapted to nitrogen limitation by redistributing nitrogen between their leaves and rhizomes (Jefferies *et al.* 1979). They are able to store nitrogen in their rhizomes during periods of high salinity and later access this supply for continued growth during periods of low salinity, when nitrogen in the soil becomes more available.

Root and Leaf Growth

Studies into the effects of salinity on root growth are few (Groenendijk & Vink-Lievaart 1987), probably because roots are inaccessible for study, especially under field conditions. Williams & Ungar (1972) showed that root biomass in *Suaeda depressa* declined when plants were grown in media with >1.0 % NaCl. Decreased root biomass with increased salinity has also been observed in *Salicornia europaea* (Ungar *et al.* 1979; Riehl & Ungar 1982), *Suaeda monoica* (Storey & Wyn Jones 1979), *Spergularia maritima*

(Yeo & Flowers 1977), *Atriplex spongiosa* (Storey & Wyn Jones 1979), *Hordeum jubatum* (Kenkel *et al.* 1991), and *Puccinellia nuttalliana* (Kenkel *et al.* 1991). Cooper (1982) studied the effects of waterlogging and salinity on the growth of eight salt marsh halophytes. *Festuca rubra, Juncus gerardii, Armeria maritima, Plantago maritima, Aster tripolium,* and *Triglochin maritima* showed the greatest decrease in shoot and root growth under the combined conditions of high salinity and poor soil aeration (i.e. waterlogging). *Plantago maritima* showed greatest above-ground and below-ground biomass reduction under conditions of high salinity alone. *Salicornia europaea* shoot and root growth reduction was greatest under poor aeration conditions. *Salicornia europaea* actually showed an increase in growth of shoot and roots on saline soil compared with non-saline soil. Thus, its growth rate was more affected by soil aeration than salinity. While the overall growth rate of plants declines with increasing salinity, the decline in growth rate of glycophyte roots is greater than shoots (Larcher 1980). Thus, there is a pronounced increase in the shoot:root ratio in glycophytes with increasing salinity. This increase in the shoot:root ratio does not appear to be as pronounced in halophytes (Waisel 1972; Cooper 1982; Kenkel *et al.* 1991). Groenendijk & Vink-Lievaart (1987) found that the below ground biomass of *Elymus pycnanthus, Halimione portulacoides, Spartina anglica,* and *Triglochin maritima* was significantly higher than the above-ground biomass and that most of the below-ground biomass was concentrated in sediment 20 - 60 cm deep. This would be advantageous because concentrating energy and photosynthate on root development allows halophytes to extend roots deeper into the soil where the salinity is usually lower.

Salinity has both toxic and osmotic effects on leaf development. High salinity leads to development of succulence in the most highly salt resistant halophytes (e.g. *Salicornia* spp. (Poljakoff-Mayber 1975), *Suaeda* spp. (Waisel 1972), and *Atriplex* spp. (Waisel 1972)). If the salinity in leaf cells becomes too high, salts become toxic. Toxic effects on leaves tend to result from disruption of enzyme activity. Leaves of salt-affected plants usually become darker green, and may take-on a deep bluish-green hue (Bernstein 1975)

due to increased cuticle thickness. I observed this coloration in *Hordeum jubatum* and *Puccinellia nuttalliana.* Eventually leaf chlorosis and necrosis occurs, followed by leaf abscission and death (Levitt 1972), a sequence observed in *Spartina* spp. (Nestler 1977) under conditions of high salinity.

Flowering and Fruiting

Flowering and fruiting of both glycophytes and halophytes is dependent on photoperiod, temperature, light intensity, and plant maturity (Waisel 1972). Although many studies are available for crop plants (see Bernstein & Hayward 1958), literature addressing the effect of salinity on flowering and fruit development in halophytes is lacking. However, one would expect that flowering and fruiting would be delayed or reduced in the presence of high salinity. This would likely result from a decrease in the allocation of photosynthate to sexual reproduction. As mentioned above, halophytic perennials are able to counter this decrease by concentrating on asexual propagation through rhizome fragmentation and tillering. Annual halophytes, on the other hand, do not produce vegetative propagules. Williams & Ungar (1972), in a study on growth and development of *Suaeda depressa,* found that flower and fruit production declined as salinity levels increased to >1.0 %. This decrease was correlated with decreases in leaf, shoot, and root growth. They also found that flowering was induced by a short photoperiod treatment, and discouraged during the long photoperiod treatment. This reliance on photoperiod for induction of flowering could be a strategy to counter high salinity. A short photoperiod corresponds with field conditions in late summer and early fall, at which time salinity levels in the soil tend to be low due to decreased temperature and increased rainfall. Thus, the delayed flowering and fruiting in annual halophytes may be a strategy for improved reproductive success.

Summary

In summary, salinity may stimulate a variety of responses in halophyte growth and development. A plant's response to saline conditions is dependent on the level and composition of ions present, its innate salt resistance mechanisms and life-history traits, and its life-cycle stage.

Section 1.5 - Competition and Distribution of Halophytes

Section 1.5.1 - Definitions and Discussion

The concept of competitive interactions and the effects of these interactions on organisms have been of interest to biologists since the writings of Darwin in the mid-1800's (Turkington & Aarssen 1984). Darwin (1859) states "we have reason to believe that species in a state of nature are limited in their ranges by competition of other organic beings". This early recognition of competitive interactions between species led to definitions describing competition as "the struggle for existence", and is often referred to as the Darwinian approach to competition (Harper 1977).

Early studies concentrated on quantifying the observable results of interactions between pairs of species (see Volterra 1931; Lotka 1932; Gause 1932). These studies, conducted under controlled laboratory conditions, resulted in the first series of working models of competition. The models, often referred to as Lotka-Volterra Models, led to the formulation of a general phenomenological-based definition of competition, namely that "...two species compete when an increase in the density of one leads to a decrease in the density of the other, and vice versa" (Tilman 1987). The impacts of these early models on the study of competition were immense and, according to Tilman (1987), they play a significant role in the design and interpretation of competition experiments to this day.

There are several problems with the Lotka-Volterra interpretation and definition of competitive interaction. First, it is unlikely that the models, which were developed for the

pair-wise interactions of two species, apply to the natural situation where many species interact. Levine (1976) stated that in natural situations, interactions between species are both direct and indirect. The Lotka-Volterra model breaks down when there are more than two species, because one species may influence the performance of a second species, indirectly or directly, through its influence on the remaining species (Tilman 1987). Secondly, this approach to defining competition omits consideration of the mechanisms underlying interactions, and thus relegates competitive interactions to the category of observable, but not predictable, responses.

According to Weaver & Clements (1938), the struggle for plant existence occurs between each plant and its habitat, and competition is one of the factors characterizing a plant's habitat. They defined competition as a decrease in the amount of water, nutrients, or available light for each individual plant. Furthermore, they state that competition between two or more plants always occurs where and when individuals require resources in excess of supply, and is therefore greatest between species or individuals which make similar demands on the same resource at the same time. Weaver & Clements also recognized the importance of species composition and phenological development in plant competition (Kershaw & Looney 1985).

Donald (1963) defined competition as a phenomenon that occurs when two organisms attempt to satisfy their needs for a certain element when the total amount of a resource available is less than the sum of their requirements. Waisel (1972) stated that "...competition usually refers to all types of allelopathy or mutual inhibition and, in a strict sense, its existence is difficult to prove".

Milne (1961) proposed the following definition of animal competition: "competition is the endeavor of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)". Attempts have been made to extend this to include plants by simply substituting 'animals' with 'individuals' (Pielou 1978). This creates a problem as it is difficult to

designate individuality in plants, which often reproduce vegetatively. Pielou suggests that the term 'individual' should be replaced by the term 'population' when considering a definition of competition in plants. In this way the word 'population' can refer to a single individual, a group of separate individuals, or all or part of a clonal population. Pielou's (1978) definition is thus: "competition takes place when the growth of a biological population, or any part of it, is slowed because at least one necessary factor is in short supply".

Harper (1977) suggests that the word 'competition' be abandoned and replaced with a more general term that he calls 'interference'. He states that the presence of a plant changes the environment of its neighbors, thus altering their growth rate and form, and these changes in the environment brought about by the proximity of individuals may be regarded as interference. Interference not only incorporates the Weaver-Clements concept of competition (i.e. consumption of resources in limited supply by two or more individuals or species), but also includes other plant interactions such as allelopathy, changes in conditions such as protection from wind, and influences on the behavior of predators (Harper 1977). Interference therefore incorporates both direct and indirect interactions that occur between neighboring plants and between theses plants and the rest of their environment. The response of plants to interference can take a number of forms including reduced growth rate of individuals, reduced growth or death of certain parts of individuals, and increased death rate of entire individuals. According to Harper (1977), the ability of an individual or species to cope with interference is not a measure of its competitive ability, but is rather an indication of its adaptability to environmental change. Harper does not, however, attempt to define how environmental changes may occur.

Harper's view is useful in that it does away with the colloquiallism inherent in the term competition. It is also useful in that it introduces two main mechanisms underlying interactions between plants: consumption of resources and production of toxins. Harper is quick to point out that there is still little proof that allelopathy (i.e the production and release

of toxins by plants to harm or kill their neighbors) is anything but a laboratory artefact, and thus, plant interactions have generally concentrated on resource consumption and availability .

Grime (1979a) defined the competitive ability of a plant as its ability to compete with its neighbors for necessary limiting resources. "Competitive ability" is difficult to measure quantitatively, and therefore should be thought of as a relative term. The ability of a plant to compete successfully, and thus acquire necessary resources, is a function of the area, activity, and spatial-temporal distribution of the surfaces through which resources are absorbed (Weaver & Clements 1938). Grime (1979a) expands this concept, stating that the competitive ability of a plant depends on morphological, anatomical, and physiological characteristics, including type and efficiency of storage organs, stature, extent of lateral spread, phenology, growth rate, and response to stress and disturbance. For the purpose of this paper I will use the definition of 'stress' offered by Grime (1977)--"the external constraints which limit the rate of dry-matter production of all or part of the vegetation". Burdon (1982) and Tilman (1988) state that disease resistance and morphological plasticity, respectively, are also important in influencing a species' ability to compete.

The Mechanistic Approach

The mechanisms underlying competition or interference have largely been overlooked in the preceding definitions that addressed competition more in phenomenological terms based on the 'outcome' of the interaction between two or more competing individuals or species. The mechanistic approach attempts to define competition on the basis of the mechanisms that cause individuals of one species to influence individuals of that and/or another species (Tilman 1988). Both 'phenomenological' and 'mechanistic' approaches imply that all plants involved in competition are affected, though not necessarily equally; the interaction is reciprocal, but may not be symmetrical

(Silvertown 1987). Silvertown (1987) noted that the immediate effect of competition is to decrease individual performance and not plant density. The closer two plants are spatially, the more depressed their growth rate since they interfere with each other's efforts to acquire the same resource(s) (Watkinson 1986), leading to mortality or at least reduced seed and ramet production.

Grime (1979a) states that plants (the same or of different species) growing in close proximity exhibit differences in growth, seed production, and mortality. He does not refer to this response as competition, but rather indicates that one cause of this response is competition. Grime further emphasizes that to define competition we must distinguish it from other processes which also influence vegetation, such as allelopathy, pathogenicity, environmental stress, natural disturbance, and selective predation. In this way his view differs from Harper's, which attempted to lump all interactions between plants under the term interference. Grime believes that competition works with, and is influenced by, other events in nature, and that all of these together determine species composition, distribution, and (ultimately) community structure.

Taking the mechanistic approach, Grime (1979a) defined competition as "the tendency of neighboring plants to utilize the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space". Accordingly, Grime believes competition refers only to the capture of resources by plants, and is only one of many mechanisms by which a plant may affect the performance of a neighbor. This definition is helpful as it allows us to classify the means by which plants become successful in crowded environments, and also allows analysis of situations, such as in disturbed or resource-poor habitats, in which dominance of vegetation is achieved by plants that have relatively low rates of resource acquisition (Grime 1979a). The use of the word 'tendency' makes the definition somewhat vague, as well, the definition implies that neighboring plants are able to utilize precisely the same resource at the same time, which is not possible. Neighboring plants may place

similar demands on an available resource, but only one individual (i.e. the one with the highest competitive ability) in any given interaction will take-in and use that resource.

Tilman (1986, 1987, 1988) also presents a mechanistic approach to competition. He defines competition as an interaction between plants in which increases in the population density of one brings about a decrease in the per capita growth rate and density of another (Tilman 1986). Tilman he states further that in order to be mechanistic, a definition must include both the process by which competition occurs, and information concerning the physiology, morphology, and behavior (i.e. life-history) of the species or individuals involved. A change in the population density of one plant species affects the amount of resources available for growth of another. Tilman (1988) refers to this as resource competition, and indicates that the mechanism driving the inhibition of one plant population (or individual) by another lies in both consuming a resource that is in limited supply. A resource is a factor required by plants, which, when readily available, leads to an increase in growth rate as it is consumed (Tilman 1980). However, the availability of one resource can affect the availability of, and the population's response to, other resources. According to Tilman (1986) a resource can be considered limiting if an increase in its availability brings about an increase in plant growth rate.

Competition for a single limiting resource can be illustrated by the following hypothetical example. Suppose we have two neighboring plants, (A) and (B), that are limited at different levels of the same resource (R), with plant (A) requiring a lower concentration of (R), and plant (B) requiring a higher concentration for its survival. If the two plants compete for the resource, plant (A), which requires less of (R), will eventually displace plant (B) because plant (A) can reduce (R) below the level required to sustain plant (B). This rather simplified illustration shows that plants do not directly affect each other in competition, but do so indirectly by affecting the availability of (R). This is somewhat different from the model proposed by Grime (1979a), who felt that when two species

attempt to obtain the same limiting resource, the one that is able to obtain the resource the quickest will displace the other, regardless of the concentration of that resource in nature.

Tilman (1982) contrasts his resource competition model with that of the more classical models developed by Lotka-Volterra. Although he demonstrates that his model of resource competition can actually be reworked to mirror the Lotka-Volterra model, he emphasizes that the Lotka-Volterra model equations, unlike his model, do not consider the mechanisms involved in the interaction, but rather show only the outcome of the interaction. Tilman points out that the competition coefficients (i.e the effects of species A on species B (α) and the effects of species B on species A (β)) and the carrying capacity for each species (i.e. K_A and K_B), both integral to the Lotka-Volterra model, change along with changes in the type of resource, its availability, and the consumptive characteristics of the species involved. Therefore, it is difficult to predict competitive coefficients without thorough knowledge of the mechanisms (i.e. resource consumption) of the interaction. He states that using the Lotka-Volterra model for illustrating cases of resource competition along a gradient is invalid because "it is difficult to know which mechanisms of competition are reflected in a given pattern of change of the competition coefficents and carrying capacities along the gradient"(Tilman 1982 p. 204).

Plants, of course, take up and assimilate a number of different resources simultaneously. Tilman (1985) has applied his concept of competitive interactions to competition for a number of limiting resources, resulting in the formulation of a resource-ratio hypothesis. Referring back to the hypothetical example, recall that species (A) out-competed species (B) for the available resource (R). However, according to Tilman, a point will be reached at which further up-take and assimilation of (R) will level-off because of limitation by, and thus competition for, another resource (R2). This can be illustrated as follows. Suppose we have two resources: nitrogen and phosphorus. Species (A) may out-compete species (B) for available nitrogen because it requires lower levels of the nutrient in the soil. However, a point will be reached when use of nitrogen by species (A) becomes

limited by the availability of phosphorus. For increased growth, species (A) may have to compete for available phosphorus with another species, perhaps species (C). Tilman's concept of competitive interactions emphasizes the importance of concentration and availability of resources and the variation in physiological requirements of different species.

The views of Grime and Tilman, although both mechanistic in approach, describe varying roles for competition in the life-history strategies of plants (McGraw & Chapin 1989). Grime, in his C-S-R (Competitor-Stress Tolerator-Ruderal) strategy theory (Grime 1977, 1979a, 1979b), proposes that a plant's competitive ability is important in determining its survival in nutrient-rich, undisturbed habitats. In stressed environments, however, the competitive ability of a plant is secondary to its ability to tolerate the stress factor(s) of the environment. According to Grime, competitive plants are able to take in nutrients more rapidly than non-competitive plants. Under stressed conditions, when the availability of resources is restricted, stress-tolerant plants are able to retain the resources they acquire for longer period of time, through slow growth and low turnover. Ruderal plants are able to preside in unstable or periodically disturbed habitats by out-reproducing plants that are adapted to nutrient-rich or stressful habitats. Thus, there are trade-offs between adaptations for survival (stress- tolerators), growth (competitors), and reproduction (ruderals) (McGraw & Chapin 1989). The C-S-R theory depends on a strict allocation of photosynthate to certain plant parts at certain phenological stages. This allocation is influenced directly by the external environment. In conclusion, Grime's theory implies that because highly developed tolerance to low resource availability (i.e. stress-tolerance) and a high competitive ability are in direct opposition, these two traits cannot be highly developed at the same time in any one individual or species. Grime (1979b) presents a review of the morphological, physiological, and life history characteristics of competitive, stress-tolerant, and ruderal plants.

Tilman (1982, 1985), in his resource-ratio hypothesis, states that a species is adapted to a range of resource ratios, with each species having its own optimum resource

ratio. At this ratio of available resources, a species is competitively superior, and it becomes less competitive when this ratio is not optimum. This contrasts with Grime's theory, as it suggests that the relative competitive abilities of species change in accordance with environmental changes or along gradients. This suggests that competitive interactions are still present and are of importance in disturbed or stressful environments.

The degree of a competitive interaction often differs between shoots and roots. Grime (1979a) states that during colonization of a new area by plants, a higher degree of competition occurs below-ground between roots and rhizomes than on or above the surface. As the canopy increases, above-ground competition increases. Below-ground competition influences the ability of a plant to compete above-ground, and vice versa (Grime 1979a). The relative importance of below-ground and above-ground competition is considered by Grime to be a function of the 'maturity' of the vegetation.

Summary

In summary, the competition theories of Grime and Tilman, although both mechanistic, differ on a number of points (Grace & Clark 1990). First, Grime's theory infers that competitively superior species are able to rapidly take up and utilize resources, while Tilman's theory states that superiority is a condition of a species' resource ratio requirements, and not necessarily its rate of resource uptake. Secondly, Grime contends that a species' ability for rapid uptake is positively correlated with all available resources and thus, the rapid assimilation of an available resource will facilitate the rapid uptake and use of other resources. On the other hand, Tilman believes that the uptake of one resource by a species is dependent on the availability (ratio) of other resources, and thus resource uptake may be negatively correlated. In otherwords, a species may be competitively superior for one resource(s), but not for other resources. Grime's 'life-history traits strategy' model also states that species can be classified according to their ability to compete. Tilman, however, stresses that a species' competitive ability is very dependent

on environmental conditions. Thus, a species that is a 'good' competitor in one habitat may be inferior in another habitat. Tilman emphasizes that the term 'competitive ability' is inherently vague. 'Competitive ability' is a relative term, and is influenced by temporal and spatial fluctuations in the biotic and abiotic environment. Species may be considered competitively superior at a given time and place, but making sweeping generalizations of species' overall competitive ability in a number of habitats may not be valid. Grime also contends that competition plays a minimal role in community structure in unproductive, disturbed, or 'stressed' habitats. Tilman counters that the importance of competition may not decrease in such habitats, and that other factors, such as the ability of a species to tolerate the harsher environmental conditions actually increase in importance. As pointed out by Grace & Clark (1990), some of the apparent contradictions between the two theories are a question of interpretation and semantics.

To date, neither theory has been entirely proven nor rejected, and further research is required to test their prediction capability. For this thesis I will define competition as a general term used to describe the direct or indirect interaction that occurs between two or more individuals that have the same or similar requirements for a resource that is limited. This interaction is driven by the availability of the resource and by the relative ability of the individuals involved to take up this resource. The individual(s) in the interaction that can best acquire the resource (usually to the detriment of the other individual(s)) can be considered the superior competitor. The ability of an individual to compete with others is influenced by its response to other environmental conditions (e.g. stress, disturbance, and the availability of other resources) and may change with the life-history stage of the individual or its neighbors. The interaction generally results in decrease in the growth of the competitive inferior, and a maintenance or increase in the growth of the competitive superior.

Since its inception as a biological concept, competition, although difficult to define, has been recognized as being important at all levels of ecological organization. Competition

influences or plays a role in: (1) plant form by eliciting a response of morphological plasticity (Weaver & Clements 1938; Bell 1985; White 1985; Lovell & Lovell 1985); (2) phenology (Jefferies *et al.* 1981; Grubb *et al.* 1982); (3) community patterning and zonation (Grubb 1985; Tilman 1988); (4) niche differentiation and species evolution (Burdon 1982; Turkington & Aarssen 1984); (5) species diversity, composition, and dominance (Tilman 1988); (6) and successional processes (Weaver & Clements 1938; Peet & Christensen 1987).

Section 1.5.2 - Types of Competition

Competitive interactions can be categorized according to their operating mechanisms or according to the number of individuals or species involved. Mechanistically there are two classes of competition -- exploitative and interference (Schoener 1983; Tilman 1987). Exploitative competition occurs when certain individuals (or species) take up available resources and thus deprive other individuals of those resources. Interference competition is more direct and involves the inflicting of physical 'harm' on an individual(s) by another individual(s).

Exploitative competition can be consumptive or preemptive. Consumptive competition occurs when resources are consumed by one individual(s) at the expense of another individual(s). Preemptive competition occurs when an individual(s) occupies a space and prevents another individual(s) from gaining the resources located within that space, even though the occupying individual(s) may not be using all the available resources. Consumptive and preemptive competition terminology can be applied to both plants and animals (sessile animals in the case of preemptive competition).

Interference competition can be allelopathic, in which chemical toxins are released by an individual(s), resulting in damage to surrounding individuals, or it can be confrontational, in which case harm occurs due to physical combat, death by predation, or theft of food supply. Allelopathic competition occurs mainly in sessile organisms such as

plants, while confrontational or encounter competition is more characteristic of non-sessile animal interactions.

Two other types of competition, which can be either consumptive or interference, include overgrowth competition and territorial competition (Schoener 1983). Overgrowth competition occurs when an individual(s) grows over or upon another individual(s), and in doing so deprives it of resources (e.g. light, in the case of plants, and access to food, in the case of filter feeding sessile marine animals) and causes physical damage as a consequence of contact (e.g. abrasion). Territorial competition is strictly an animal characteristic and occurs when an individual(s) actively defends, or, by signal, shows that it intends to defend its territory against encroachment by another individual(s).

Competition that occurs between two individuals of the same species is the simplest scenario of competitive interactions (Weaver & Clements 1938). Such competition leads to variation in characteristics such as root penetration, leaf shape, and plant height between individuals of the same species (Weaver & Clements 1938). This response is a reflection of the phenotypic/genotypic plasticity of individuals of a given species and has certain implications in evolutionary taxonomy. Generally, the more 'plastic' a plant the better it is able to cope with the effects of competition, and thus adapt to changes in its environment (Tilman 1988). A competitive interaction which takes place between two individuals or populations of different species is called interspecific competition (Tilman 1986). According to Silvertown (1987) interspecific interactions in the field are generally more dependent on the size of the individuals than on the actual species involved. This is due to the concept that the relative size of a plant and the phenological stage of it, or its competitors (whether they be seedlings, juveniles, or larger), has a great bearing on its ability to compete successfully. Watkinson (1985) states that intraspecific and interspecific competition are basically different aspects of the same general phenomenon of competition between plants, although they have generally been studied in isolation from each other.

Competition in the field rarely occurs between only two individuals or populations of the same or different species. Populations of plant species, with the exception of cases involving extreme mono-dominance, are usually interspersed in nature, and interact with several other populations. This has been called diffuse competition. A number of possible definitions for diffuse competition have been proposed (Moen 1989). However, I think the definition suggested by MacArthur (1972) describes the concept best: "a cluster of competitors may much more easily out-compete one species than can a single competitor. It has been suggested that competition by a constellation of species be called 'diffuse competition'" (his quotation marks). Silvertown (1987) reworked this definition slightly, defining diffuse competition as: "the interference effects on a species which derive indiscriminantly from all or many of the other species in a community". Both definitions assume that the individual competitive interactions between a certain species and its neighboring species are relatively weak, but that the total affects the performance of a given species in the community (Moen 1989). Such competition is likely omnipresent in communities, with more severe competitive interactions occurring between individuals and species that require the same limiting resource (Silvertown 1987). Diffuse competition has received little study (Wilson & Keddy 1986), probably due to the difficulty in developing adequate experimental designs and methods of data analysis, and in distinguishing it from other intraspecific and interspecific forms of competition (Mitchley 1987). We should be reminded that the term 'diffuse' is not a reference to 'distance', but means multifaceted (both direct and indirect) and multi-species.

Experiments have shown that in extreme cases, competition may ultimately lead to the elimination of the least competitive individuals/species. This is known as the Competitive Exclusion Principle or Gause's Principle (Silvertown 1987). For this to occur the competing species must have the same or very similar requirements for a limiting resource, in other words they have the same or very similar niches. This proposition raises several questions. Why then do we observe situations in which many species, some rare

and some abundant, live together in a given area? If competition is taking place, why are rare species not totally excluded by dominant species? Finally, does this lack of total exclusion indicate that each species in a community occupies its own discrete niche? Also, problems arise in determining whether a species is being competitively excluded or whether it is actually invading a community. In nature, complete annihilation of a species' population by a superior competitor is rare. Rather, poor competitors are excluded to the periphery of their fundamental niche, thus establishing their realised niche, where they are better adapted than the superior competitors (Grime 1979a). This implies that species do not occupy precisely the same niche, but where fundamental niche overlap occurs, the competitively superior species will exclude the competitively inferior species to the inferior species' realized niche.

Pontin (1982) and Turkington & Aarssen (1984) assert that species are inherently different from each other, and that these differences allow them to coexist. However, recent literature on the subject of coexistence suggests that niche differentiation may only be one mechanism behind coexistence of species (see Silvertown 1987; Aarssen 1989). Silvertown (1987) presents a number of equilibrium (coexistence) models in an attempt to offer a more complete explanation for the occurrence of species coexistence. The models are addressed briefly below.

Model 1 - The competitive exclusion principle and the niche model suggests that in a strict sense coexistence does not occur. Rather, the *apparent* coexistence is actually the result, in part, of the competitive exclusion of inferior species by superior species to their realized niches. This *apparent* coexistence is maintained by a number of processes, including competition, disturbance, and allelopathy. For example, suppose we have two plant species, A and B, existing in the same habitat, with A competitvely excluded by B to slightly drier sites in the habitat. During periods of high soil moisture, the niche of species B would expand to occupy a larger area at the expense of the niche of species A, while the

reverse would be the case during periods of low soil moisture. Thus, the area (geographically) occupied by the two species would be constantly changing depending on the environmental conditions. If the dry and wet sites were numerous and dispersed throughout the habitat, it would appear, at any one-moment in time, that the two species were coexisting. This implies the concept of dynamic species' niches which differentiate temporally and spatially. The remaining models a variants of this niche differentiation theme.

Model 2 - The guilds and niches model deals with differences between the fundamental niche and the realized niche. The fundamental niche of a species is the 'space' it would occupy in the absence of competition, and is determined by the species' ability to grow over ranges of various environmental factors. The realized niche is the 'space' occupied by a species in the presence of other species. The realized niche is smaller than the fundamental niche, and its size relative to its fundamental niche is positively correlated with its competitive ability. This indicates that a number of species may have very similar fundamental niches, but their realized niches will be dependent on their relative competitive abilities under given conditions.

Model 3 - The regeneration niche model takes into account differences in phenology and life-history strategies between species. It suggests that coexistence between species may be possible because the competitive ability of species is different at different phenological stages in its life-cycle. For example some species have rapid rates of growth, flowering, and fruit-set, which allows them to complete their life-cycle early, thus avoiding competition with competitively superior species which develop later in the growing season. These strategies are characteristic of ruderal plants as described by Grime (1979a).

Model 4 - The resource ratio hypothesis model suggests that competition for resources occurs in coexisting species, but that competition intensity is reduced. Resources are rarely distributed homogeneously throughout a community. Their patchy distribution results in spatial variation in resource concentrations. Areas where concentrations are low

favour species that have adapted efficient methods for resource use or deficiency tolerance, while areas of high resource concentration favour species which can compete well for light in productive vegetation. It should be emphasized that these spatial variations in resources can be on a very small-scale, resulting in the *apparent* coexistence of species.

Model 5 - **The aggregation model** is based on the idea that increasing intraspecific competition leads to a reduction in interspecific competition. This model agrees with the Lotka-Volterra model of competition, which states that competing species will stably coexist, at high density, because each will inhibit, or be inhibited by, its own population more than that of its competitors. This idea can be traced back to early discussions of competition theory (e.g. Weaver & Clements 1938). One expects that individuals of the same species will require the same types and amounts of resources, and thus, that intraspecific competition will be more intense.

Model 6 - **The density and distance-dependent predation and disease model** suggests that the density of individuals and their distance from each other influences predation and pathogenicity. This may promote coexistence by decreasing the competitive ability of dense plant populations.

These models emphasize that niche differentiation alone does not fully account for coexistence. We must account for various life-history strategies of species and the role of factors in the environmental, besides competition, in order to fully understand coexistence.

Section 1.5.3 - Competition Experiments

Although the literature on plant competition experiments is extensive (for reviews see Connell 1983; Schoener 1983; Aarssen & Epp 1990), the interpretation and usefulness of results from most of these experiments is questionable. Problems arise because it is difficult to distinguish plant responses to competition from responses to other environmental factors (Kershaw & Looney 1985). Most competition experiments performed to date deal with pair-wise combinations of species, and are often conducted

under controlled conditions. Both of these characteristics make the extrapolation of experimental results to the natural system difficult.

According to Tilman (1987) " a study of competition requires a multifaceted approach that is both observational and experimental". Such a study should include tests to determine which mechanisms lie behind the interaction, the limiting resource(s) involved, and the role of density effects. Once mechanisms have been identified, information on species' life-history, morphology, and physiology should be incorporated. Experiments (both laboratory and field) should be designed to test the predictive power of the results.

According to Silvertown (1987), there are three main types of experimental design used in competition experiments: (1) *replacement series* experiments; (2) *additive* experiments; and (3) *additive series* experiments.

The *replacement series* design involves a series of mixtures of two species in which the proportions of the two are varied, but the total density is kept constant (e.g. 0:100, 25:75, 50:50, 75:25, 100:0 %). From this, one determines the relative performance (yield) of each species at various proportions and then compares the results with their performance in monoculture. Presumably, the difference between the performance of a species in the proportional mixtures from that of its performance in monoculture will be due to competition with the other species. The replacement series has problems for a number of reasons (Silvertown 1987). First, it does not provide much information about how composition and yield behave in mixtures in which density is not held constant; this is the situation most commonly found in the field. Secondly, the performance of the plants involved is assessed relative to a monoculture control of each species. These controls are at arbitrary densities, and thus a choice of different monoculture densities as reference points may produce different performance values and subsequently lead to different interpretations. Thirdly, the constant density used presents problems in that it may not reflect actual densities in the field. For instance, if the constant density used in the experiment is higher than that found in the field, the experimental

results may falsely suggest that competition is actually taking place between the two species. In this case the experiment may be 'inducing' competitive interaction. The reverse may occur if the constant density chosen for the experiment is too low. Thus, prior knowledge of field densities is an important requirement for replacement series experiments.

The second type of design is the *additive* experiment. In this case the density of one species is kept constant while that of the other species is varied (e.g. 100:0, 100:50, 100:100, 100:150, 100:200 individuals). As in the replacement series design, plant responses are compared to monoculture controls. One control would be established for the 'constant' species, and a number of monoculture controls would be established for the 'varied' species, corresponding to each of the density values used. This design is useful in that it illustrates the real life situation of a plant species existing at a fixed density being invaded by another species (Silvertown 1987). According to Mack (1985), experiments which simulate plant invasions can be very helpful in studying competition as few verifiable and demonstrable examples of competition exist in nature.

The third type is the *additive series* experiment. This design is basically a combination of the two previous designs and involves mixtures of two species grown over a range of densities and proportions. This type of design comprehensively explores plant responses to a range of densities and proportions of two competitors and, therefore, better reflects the natural situation (Silvertown 1987).

These designs can be modified to incorporate varying levels of resources (e.g. nutrient addition) or other environmental factors (e.g. salt addition). This allows testing of the effects of selected environmental factors and resource limitation on the performance of the species, and may shed some light on the mechanisms underlying competitive interactions.

A recurring problem with these experimental designs is they are generally restricted to pair-wise studies of interspecific competition and, therefore, do not address the question

of diffuse competition. Also, because they require controlled conditions, they are usually carried out in artificial environments, producing results which are of limited practical use when applied to the field situation.

Connell (1983) lists four main criteria for designing a successful field competition experiment. First, replication is extremely important. Not only should controls and treatments be sufficiently replicated within an experiment, but the entire experiment should be conducted at different times in a number of similar sites in order to increase the predictability of results. A second important decision is that the densities used in treatments should reflect those found in nature. Densities, especially those far in excess of the natural situation, are of little use. In order to determine what densities to use, preliminary surveys of the natural vegetation are required. Another criterion for a successful field experiment is to ensure that the results can be applied to the natural situation. This is less a problem in vegetation studies than animal studies, because of the sessile habit of plants. However, one must take into account characteristics of the species involved, including their physiology, morphology, and life-history (Tilman 1987). Finally, data analysis methods to be used for interpreting the data must be considered in the design. One must be aware that manipulation of the natural vegetation may alter (enhance or reduce) the indirect effects of other species and/or environmental factors and thus influence the performance of the target species. As Connell (1983) states, these indirect effects should not be dismissed as simply anomalous as they may give important information about interactions which occur naturally in vegetation. They do, however, complicate the situation by making predictions and identification of mechanisms difficult. A way around this problem is to incorporate, or at least be aware of, these indirect effects in the experiment design. This may lead to a more complex design with several types of controls, but this is necessary to increase the likelihood of reaching realistic conclusions.

Field experiments for studying competition involve the manipulation of natural vegetation, usually through changes in density or morphology, to expose the presence of

competitive interactions. Aarssen & Epp (1990) present an up-to-date summary of vegetation manipulation experimental designs. They found that there were three basic designs: (1) *introduction* experiments; (2) *trenching* experiments; and (3) *removal* experiments.

Introduction experiments involve the transplantation of individuals or placement of propagules into existing vegetation. This design was used to test the response of plants to competition in different habitat types (for examples see Aarssen & Epp 1990). It has also been used extensively to distinguish species' ecotypes and species' phenotypic plasticity (e.g. Statler & Batson 1969; Shea *et al.* 1975; Jefferies *et al.* 1981; Jefferies *et al.* 1983; Seliskar 1985). Resource addition (e.g. nutrient fertilization) can also be incorporated into the experimental design.

Trenching is often used to study the effects of root competition in plants. This involves digging a trench around an individual plant or population in a plot to severe roots and confine them to the plot. The plot can then be manipulated (e.g. resource additions/deletions) and the response of species determined. This design is not used much as it is very labour intensive and the validity of results may be poor due to difficulties in ensuring that deep roots have been severed.

Removal experiments are the most common design (Aarssen & Epp 1990), and follow three basic variations. First, whole plant groups such as grasses or broad-leaf herbs may be removed, either by clipping, excavation, or selective herbicide application. Second, particular species or group of species may be removed, with the removal method dependent on the species involved. Third, removal of all species with the exception of a target species (i.e. the species of interest) may occur. Again, this can be accomplished through clipping, excavation, or selective herbicide applications. In all cases responses of the remaining plants are measured and compared with untreated control plots. Differences between treatments and controls are inferred as being attributable to competition. Unfortunately, the removal method used may itself result in unnatural disturbance to the

remaining vegetation. Also, one cannot be assured of complete removal of below-ground overwintering organs; periodic maintenance of plots is therefore necessary to prevent introduction of propagules from outside of the plot or regrowth of persistent organs in the soil.

Section 1.5.4 - Factors Influencing Vegetation Zonation

The main physical factors influencing the distribution of coastal species are: salinity level of the growth medium, water level, and wave and wrack disturbance (for examples see: Adams 1963; Kershaw 1975; Jefferies *et al.* 1979; Niering & Warren 1980; Cooper 1982; Snow & Vince 1984; Dawe & White 1985; Zbigniewicz 1985; Ewing & Kershaw 1986; Bertness & Ellison 1987). These factors are directly related to tidal inundation and relative surface elevation (Adams 1963).

Although early studies emphasized the role of abiotic factors, they did not totally discount the importance of biotic factors in influencing plant zonation. Reed (1947) concluded that the distribution of North Carolina salt marsh species was limited along the seaward border by tidal inundation, high salinity, and poor soil aeration, and along the landward periphery by competition with competitively superior species. Statler & Batson (1969), in one of the first reciprocal transplant experiments on salt marsh vegetation, also concluded that interspecific and intraspecific competition, along with abiotic factors, were important in creating zonation. However, the design of their experiment did not allow them to actually assess the relative importance of abiotic and biotic factors. Work by Pielou & Routledge (1976), Barbour (1978), Bertness & Ellison (1987), and Ellison (1987) suggests that interspecific competition may play an important role in the distribution of vegetation within coastal salt marshes. The pretext of their argument is the observed disparity between the ecological optimum (realized niche) and the physiological optimum (functional niche) of a species, particularly in harsh habitats (Barbour 1978). Bertness & Ellison (1987), in a study of a New England salt marsh, concluded that competitively

superior species occupied the most favorable sites, forcing competitively inferior, but more salt-resistant species to more saline areas.

Flowers (1934) and Hull & Martin (1939) found that the distribution of a number of salt-resistant species of inland saline habitats correlated highly with the salt content of the soil. The importance of soil salinity in influencing the distribution of plants in inland saline areas was further emphasized by Gates *et al.* (1956). Keith (1958) agreed, but suggested that soil pH plays an important role in species' distribution once a certain salinity is attained. The idea that soil salinity is the main factor determining vegetation distribution in inland saline habitats relates to a long-held belief that the plants of such habitats are obligate halophytes. However, studies of the salt tolerance of saline species (see Ungar 1966) have shown that most species occupied very wide salinity ranges, but tended to grow best at low salinity. This indicates that most plants of saline habitats are facultative halophytes, and very few, if any (Barbour 1970), are actually obligative. Ungar (1968, 1970) stated that extremely salt resistant species such as *Salicornia rubra, Suaeda depressa,* and *Sesuvium verrucosum* are likely relegated to high salinity soils because of their poorly developed root systems, their requirement for large amounts of water (related to succulent habit), and their inability to compete with rapid-growing glycophytes. Ungar (1974(a)) stated that the distribution of inland halophytes is most directly determined by soil salinity, with climate, soil moisture, topography, and biotic factors playing accessory roles. According to Ungar "species appear to be selected out by the highly saline environment in a gradient from the most to the least salt tolerant". Competition, leading to exclusion of poor competitors to the limits of their tolerance, is likely one of the 'selection' factors involved.

Experiments by Szwarcbaum & Waisel (1973) involving the halophyte *Hordeum marinum* and the glycophyte *Triticum vulgare* showed that under non-saline conditions growth of *Hordeum marinum* declined in the presence of *Triticum vulgare.* However, under saline conditions *Triticum vulgare* declined while *Hordem marinum* flourished.

They suggest that the glycophyte out-competed the halophyte under non-saline conditions, but that in the presence of salinity the competitive ability of the glycophyte declined, allowing increased growth of the halophyte. They concluded that halophytes are poor competitors relative to glycophytes, and are thus normally relegated to saline soils.

Reciprocal transplantation of the halophytes *Atriplex triangularis* (McMahon & Ungar 1978) and *Salicornia europaea* (syn. *rubra*) (Ungar *et al.* 1979; Ungar 1987) into soil of cleared and uncleared plots of less saline vegetation zones resulted in the plants generally performing best in cleared plots and worst in the uncleared plots of these lower saline zones. These results indicated that interspecific competition, along with soil salinity, were important in determining the distribution of these species on inland salt flats. This suggests that high salt levels are not necessarily physiologically required by halophytic species. Rather such species are relegated to high salinity soils because they cannot compete with faster growing, taller glycophytes.

The effects of herbivory by waterfowl, rodents, and insects on salt marsh species distribution have also been studied (Jefferies *et al.* 1979; Joenje 1979; Ellison 1987). However, according to Ellison (1987), much study is still needed in order to gain an understanding of the specifics of these interactions.

Chapter 2 - Study Site Descriptions and Experimental Plot Design

Section 2.1 - Introduction

The four saline sites of the study are located 12-14 km south of Overflowing River in the Overflow Bay area of Lake Winnipegosis (53°05'N and 101°07'W). Sites were chosen because they are easily accessible, relatively undisturbed, and have distinct vegetation zonation. All four sites are saline seeps, and are surrounded by gravel ridges of boreal vegetation. Four sites were selected in order to study differences between sites and to increase the predictability of the results (i.e. decrease the chance of site-specific anomalies).

Section 2.2 - Local Geography

An aerial photograph of the sites (Figure 2.1) shows their location relative to each other, Overflow Bay, and Provincial Highway #10. Sites 1 and 2 (Figure 2.2) are large with a minimum of four distinct zones of vegetation, while sites 3 and 4 (Figure 2.3) are smaller, with three distinct vegetation zones. Sites 2 and 4 are located within 1 km of the shoreline of Overflow Bay. Sites 1 and 3 are situated further inland from the lake, and are separated from sites 2 and 4 by Provincial Highway #10.

Although sites 2 and 4 are located adjacent to the lake shore, they are rarely inundated by lake water (Burchill 1991). The water level of the lake has been high enough to cover the lowest reaches of the salt flats 19 times in the last 20 years, with 18 of these inundations occurring in 1974. Four years of observation by Burchill and myself (1987 - 1990) indicated that the lake water and wrack disturbance has reached the lakeward edge of these salt flats, but never came in contact with the vegetated areas of the sites. Sites 2 and 4 experience exposure to winds off the lake.

Sites 1 and 3 are located inland from the lake and are, therefore, more sheltered than sites 2 and 4. Logging has occurred in the vicinity of sites 1 and 3, but the sites

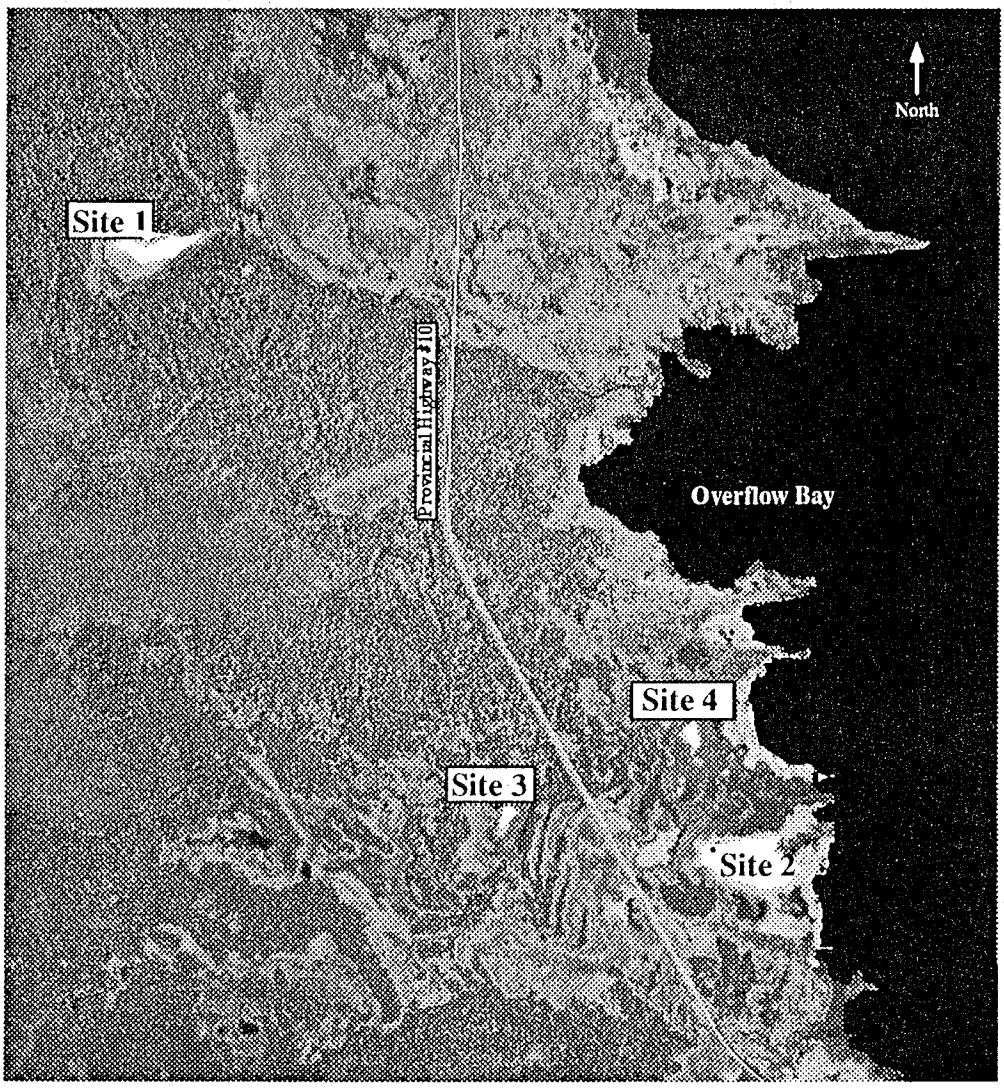
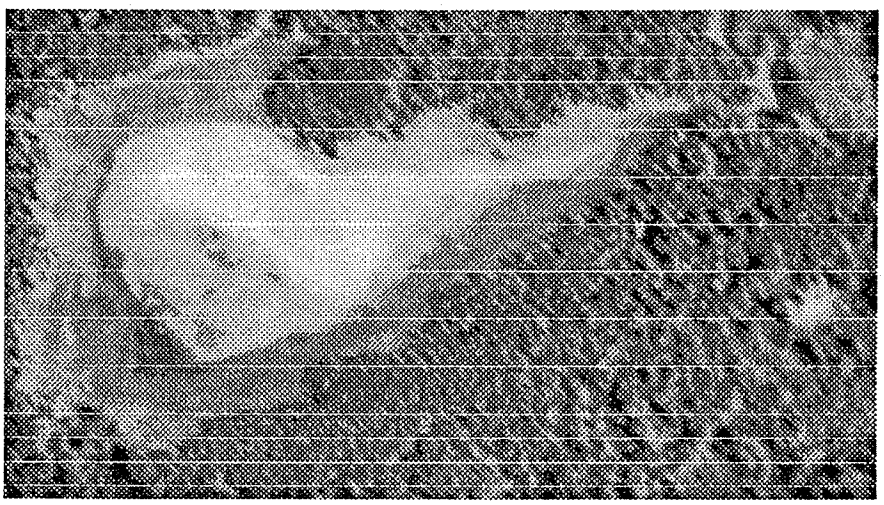


Fig. 2.1. Aerial photo of Overflow Bay shoreline with study sites. 1cm = 500 m.

Site 1



Site 2

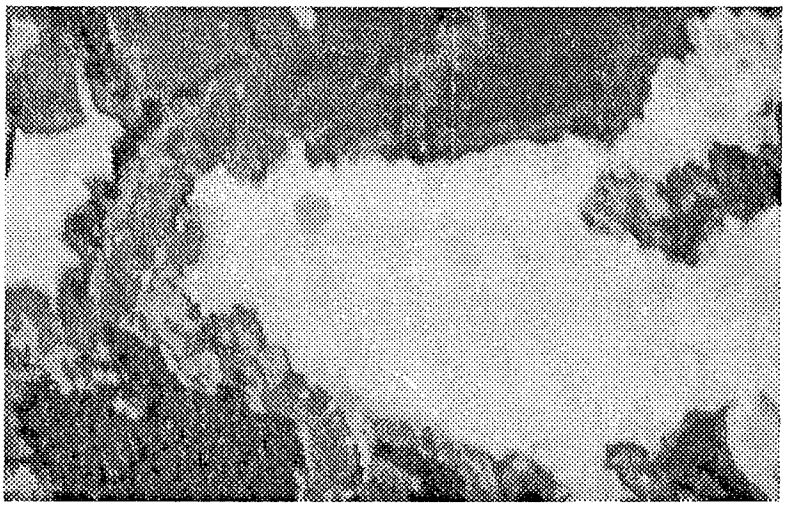
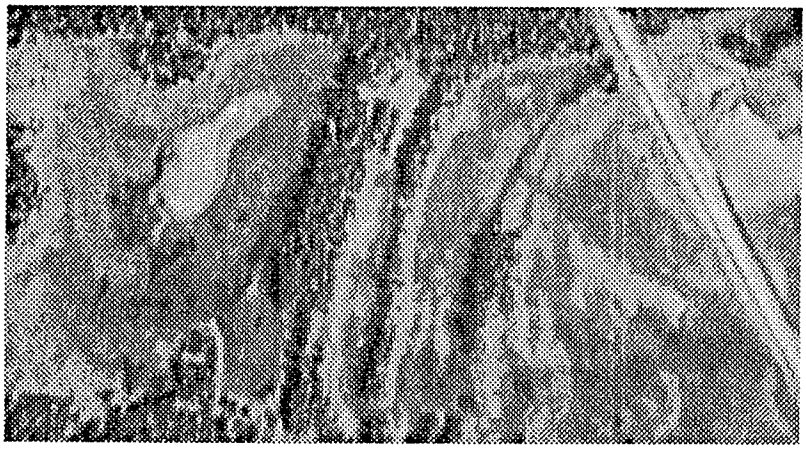


Fig. 2.2 Aerial photographs of sites 1 (top) and 2 (bottom). Note unvegetated salt flat (white), surrounding halophytic vegetation zones (light to medium gray), and boreal vegetation (dark gray to black). 1cm = 75 m.

Site 3



Site 4

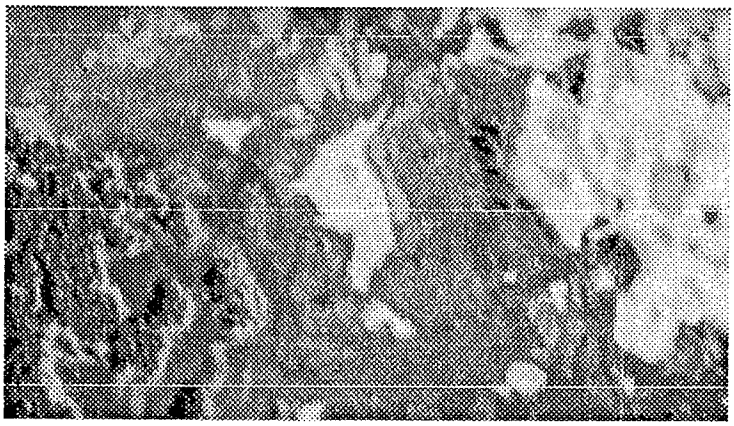


Fig. 2.3 Aerial photographs of sites 3 (top) and 4 (bottom). Note unvegetated salt flat (white), surrounding halophytic vegetation zones (light to medium gray), and boreal vegetation (dark gray to black). 1cm = 75 m.

themselves have been left essentially untouched. I was concerned as to whether the construction of Provincial Highway #10 had had any adverse effects on sites 1 and 3. The highway was first built in 1939, and upgraded in 1960 (Burchill 1991). Comparison of aerial photos taken prior to and following construction indicates that the basic shape of the salt sites, and possibly the vegetation zones themselves, have not been altered by highway building (Burchill 1991).

Section 2.3 - Geology and Soil

The four saline sites are located within 3 km of each other. The underlying bedrock for all sites belongs to the Dawson Bay Formation. Although bedrock geology is the same, field observations indicated differences in surface deposits and soil types. Sites 1, 2 and 4 are characterized by Saline Regosols and have a hard-packed, gravelly to stony, high salinity salt pan. Moving out from the salt pan the soil becomes less calcareous and more silt-laden, and there is a surface layer of organic matter. The thickness of the organic matter layer differs between vegetation zones both within and among sites.

The soil of site 3 differs considerably from the other sites. The salt pan of site 3, although having a relatively high salinity, is a silt-clay-organic matter mixture, and does not contain significant amounts of gravel, sand, or stone. The organic matter content of the vegetation zones surrounding the salt pan of site 3 is also high; the soil has a dark-brown to black, peaty appearance.

Section 2.4 - Climate

Climatic data for the 1989 and 1990 growing seasons are presented in Figures. 2.4 and 2.5. The 1989 records are from the village of Overflowing River, 14 km north of the sites. In 1990 the climatic data were not collected at Overflowing River, therefore data from the station at Mafeking, Manitoba, 40 km to the south are presented in Figure 2.5. The region experienced relatively low precipitation in spring and mid- summer of 1989.

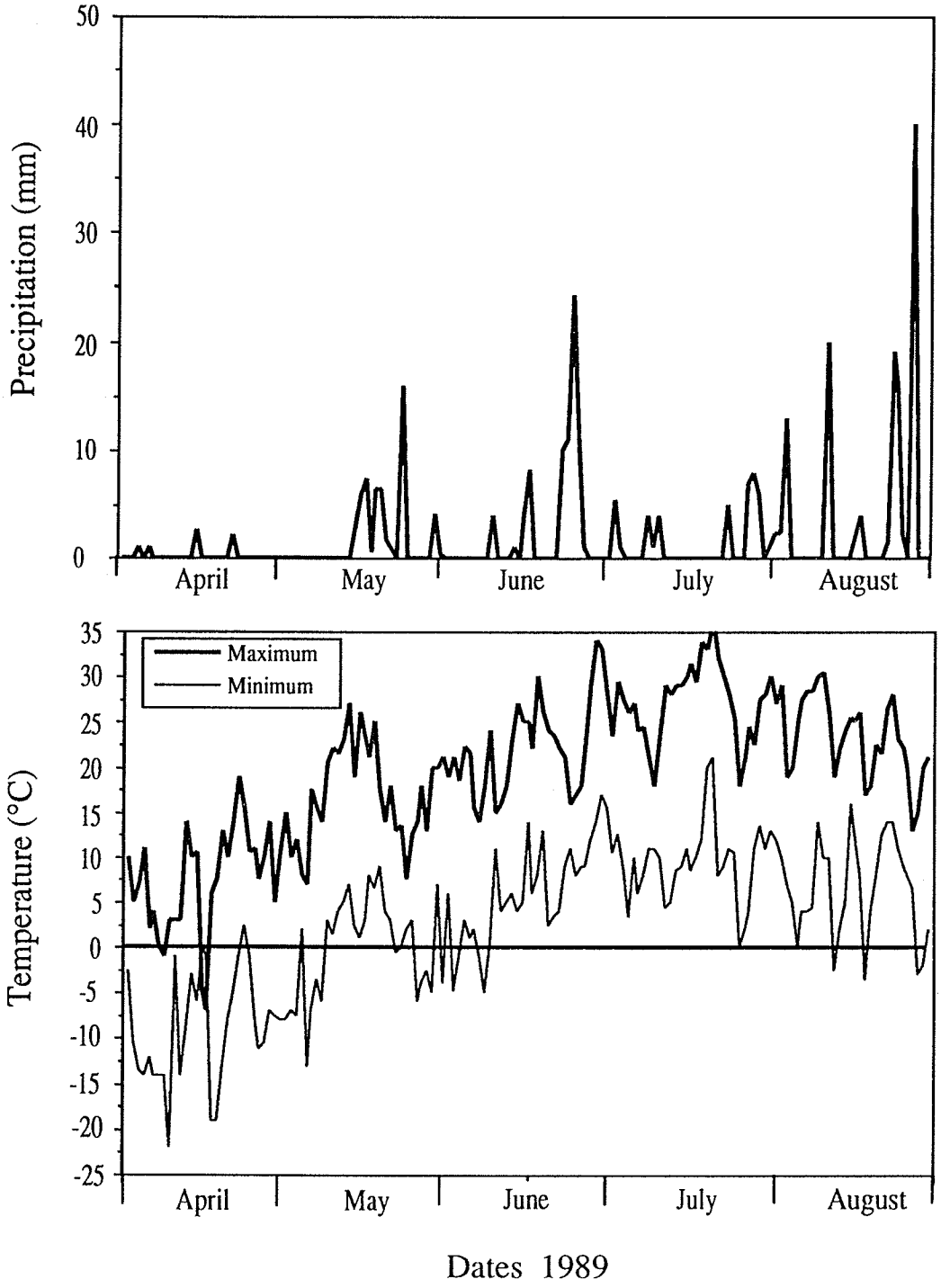


Fig. 2.4 Total daily precipitation (mm) and maximum/minimum daily temperature over the 1989 field season (1 April - 31 August). Data obtained from Environment Canada climate monitoring station, Overflowing River, Manitoba.

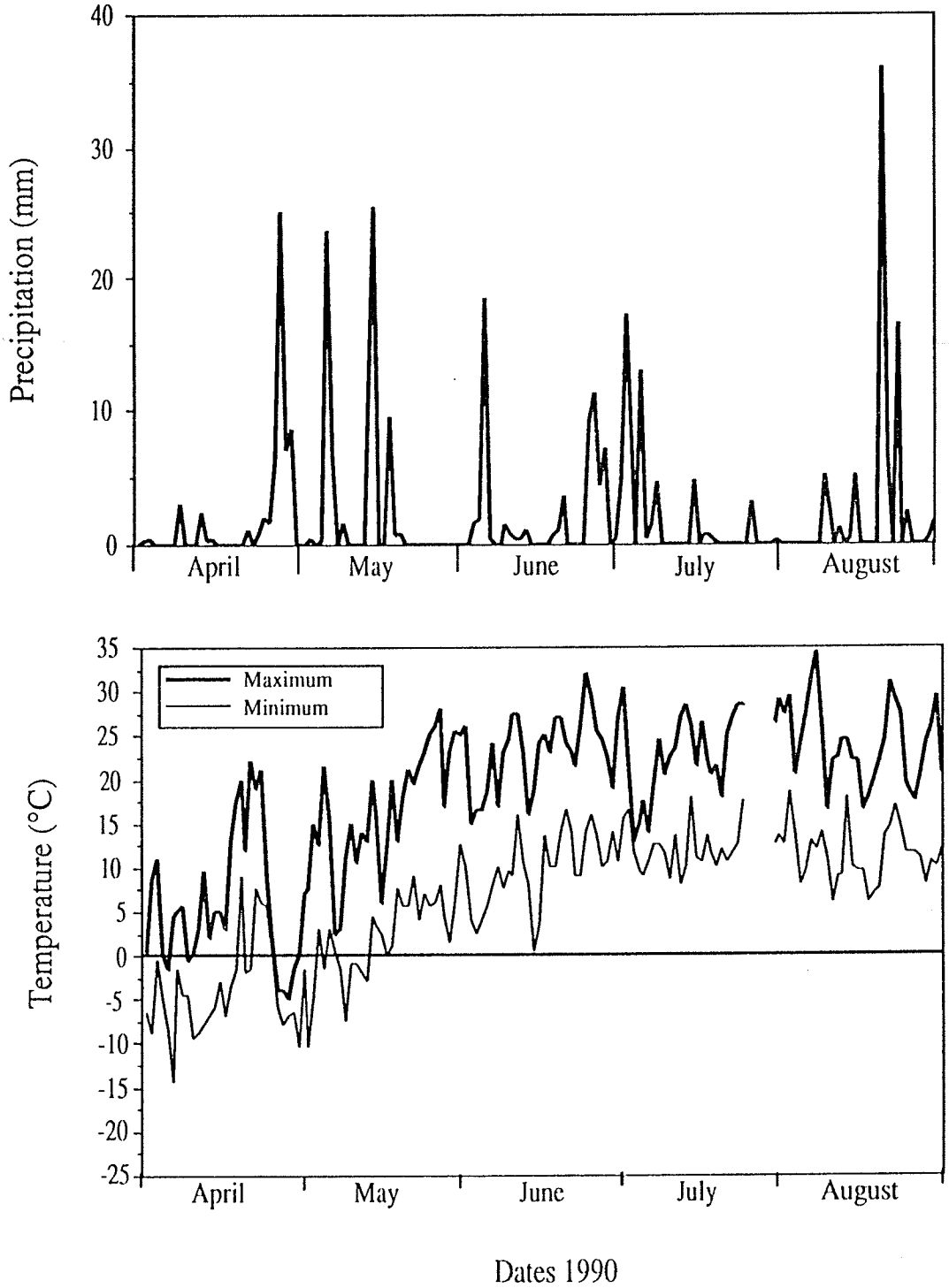


Fig. 2.5 Total daily precipitation (mm) and maximum/minimum daily temperature over the 1990 field season (1 April - 31 August). Data obtained from Environment Canada climate monitoring station, Mafeking, Manitoba. (Note no temperature data was available for the last few days of July).

This, coupled with high daily temperatures, created drought-like conditions similar to those experienced in southern Manitoba. The 1990 data indicate that precipitation was considerably higher during the 1990 growing season than in the previous year; particularly during the spring and early summer.

The salt flats of sites 1, 2, and 4 experienced extreme drying conditions during 1989, manifested by the deposition of a thin, crystalline layer of salt at the soil surface. The salt flat zone of site 3, however, did not experience the degree of drying that occurred at other sites in 1989. The significantly higher organic matter content of site 3 soils probably provided greater water holding capacity, thus reducing the effects of evapotranspiration.

The salt pans and some of the adjacent vegetation zones of all sites experienced flood-like conditions in spring 1990. The salt pans of sites 1, 2, and 4 were submerged until late June, while the pan of site 3 was submerged until late July.

Section 2.5 - Vegetation

The four sites support vegetation typical of Lake Winnipegosis saline sites generally. All study sites displayed distinct vegetation zonation (Table 2.1). Vegetation zones are named by the genus of their dominant species (dominance as % cover). Burchill (1991) referred to the 'salt pan' zone as a distinct vegetation type. However, only the periphery of the salt pan is commonly vegetated. This vegetation consists of the most salt resistant plants of the sites, and is dominated by the annual *Salicornia rubra* (Burchill 1991). In this thesis I refer to the vegetated part of Burchill's 'salt pan' vegetation type as the Salicornia Zone.

Table 2.1. List of dominant and associated species present in vegetations zones at each study site. The species were recorded during the 1989 season.

Site	Vegetation Zone	Dominant Species	Associated Species
1	Calamagrostis	*Calamagrostis inexpansa*	*Triglochin maritima* *Aster pansus* *Sonchus arvensis* *Potentilla anserina* *Achillea millefolium* *Hierchloe odorata*
	Hordeum	*Hordeum jubatum*	*Triglochin maritima* *Puccinellia nuttalliana* *Atriplex patula* *Glaux maritima*
	Puccinellia	*Puccinellia nuttalliana*	*Glaux maritima* *Triglochin maritima* *Hordeum jubatum* *Suaeda depressa*
	Salicornia	*Salicornia rubra*	*Suaeda depressa* *Triglochin maritima* *Spergularia marina*
2	Calamagrostis	*Calamagrostis inexpansa*	*Aster pansus* *Sonchus arvensis* *Atriplex patula* *Hordeum jubatum* *Distichlis stricta* *Ambrosia psilostachys* *Agropyron trachycaulum*
	Hordeum/Distichlis	*Hordeum jubatum* & *Distichlis stricta*	*Atriplex patula* *Aster pansus* *Grindelia squarrosa* *Spartina gracilis*
	Puccinellia	*Puccinellia nuttalliana*	*Suaeda depressa* *Triglochin maritima*
	Salicornia	*Salicornia rubra*	*Suaeda depressa* *Spergularia marina*

Table 2.1. (continued)

Site	Vegetation Zone	Dominant Species	Associated Species
3	Calamagrostis	*Calamagrostis inexpansa*	*Aster pansus* *Sonchus arvensis* *Atriplex patula* *Hordeum jubatum* *Triglochin maritima* *Grindellia squarrosa* *Aster pauciflorus* *Aster simplex*
	Hordeum	*Hordeum jubatum*	*Triglochin maritima* *Atriplex patula* *Aster pansus* *Grindellia squarrosa* *Sonchus arvensis*
	Salicornia	*Salicornia rubra*	*Triglochin maritima*
4	Calamagrostis	*Calamagrostis inexpansa*	*Aster pansus* *Sonchus arvensis* *Achillea millefolium* *Aster laevis*
	Distichlis	*Distichlis stricta*	*Hordeum jubatum* *Triglochin maritima* *Atriplex patula* *Suaeda depressa* *Grindellia squarrosa*
	Salicornia	*Salicornia rubra*	*Suaeda depressa* *Distichlis stricta*

In 1989 germination and seedling establishment in Salicornia Zone of sites 1,2, and 4 occurred in late-May. By the end of June to early July the vegetation died. This was probably due to lack of moisture and high salinity levels. In contrast, vegetation of the Salicornia Zone in site 3 flourished. It appears that the soil moisture content of this zone was high enough, and the salinity low enough, to permit growth and development.

In 1990, Salicornia Zone vegetation was present at sites 1, 2, and 4, but was virtually nonexistent at site 3. Presumably the wet conditions in late spring and early summer at sites 1, 2, and 4 promoted the germination and establishment of Salicornia Zone vegetation. The Salicornia Zone of site 3, however, experienced prolonged submergence, which likely hindered germination and seedling establishment.

Section 2.6 - Experimental Plot Design

For the sake of convenience, the study sites were numbered 1 - 4. Ten plots (75cm x 150cm) were established in each vegetation zone of the two large sites (1 and 2), while six plots were delineated in each zone of sites 3 and 4, because zones were narrower and less accommodating. A total of 116 plots were used in the entire study; 40 in each large site, and 18 in each smaller site. Each plot of each zone was designated with a number/letter code. For example, plots in the Salicornia Zone of site 1 were given the number code 1-A through 1-J. The numeral refers to the vegetation zones of the site, while the letter refers to plots within zones. Zones were numbered in order of decreasing salinity. Thus,the plots of the Puccinellia zone of site 1 would be designated as plots 2-A through 2-J. The lay-out of the plots for each site is illustrated in Figures 2.4 - 2.7. Plots were used for soil sampling and transplantation experiments. The experiment was designed to run for two consecutive growing seasons in 1989 and 1990. Appendix II provides a schedule of activities carried out at the saline sites in 1989 and 1990.

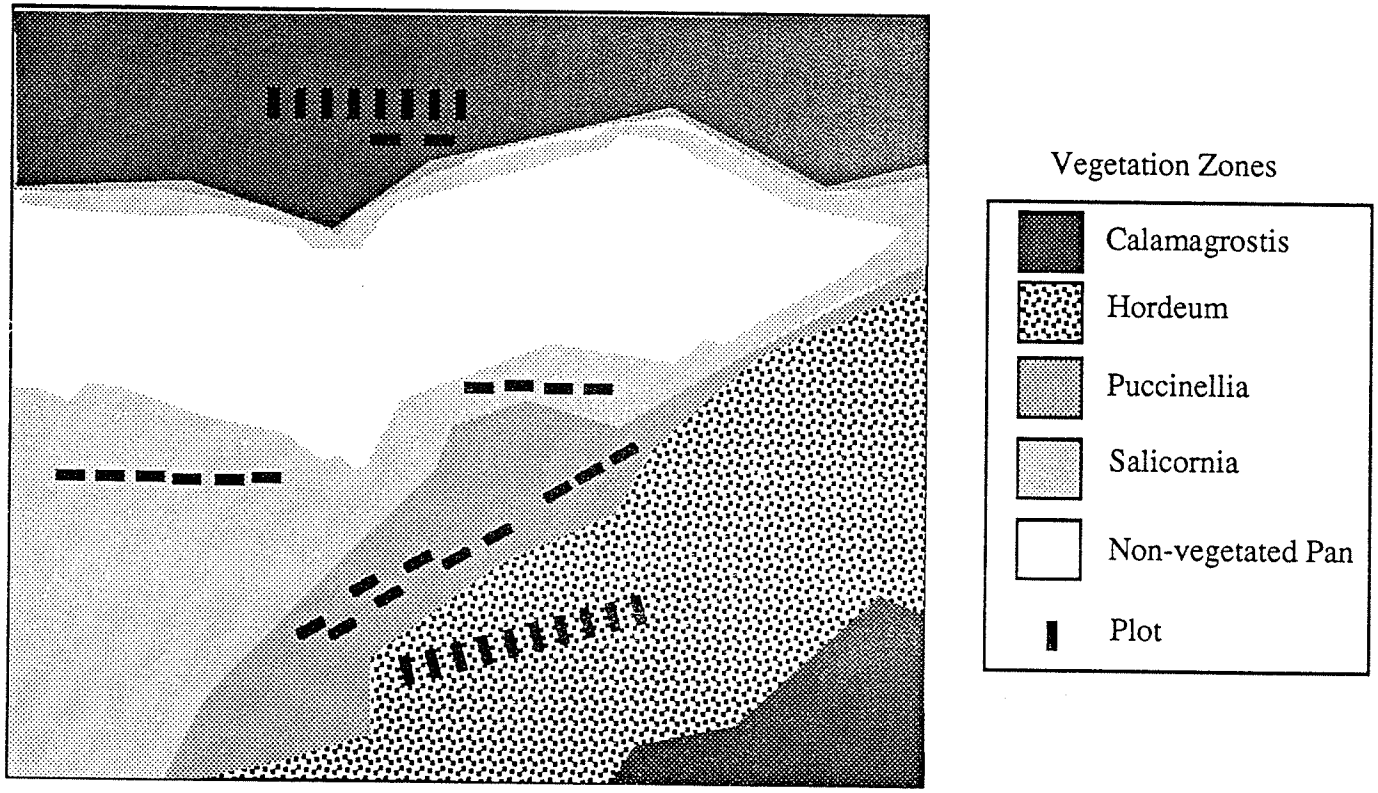


Figure 2.6 Diagram of site 1 showing plot lay-out in vegetation zones. Scale: 1 cm = 10 m.

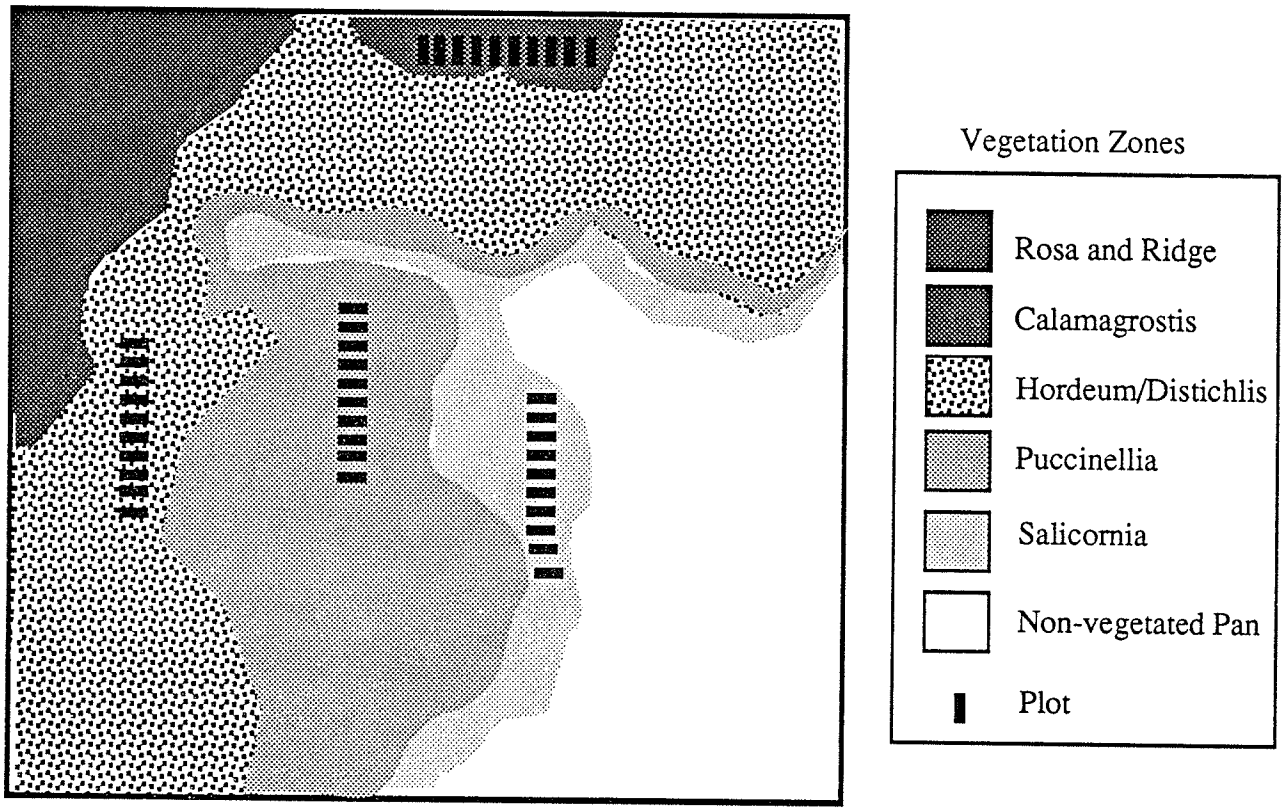


Figure 2.7 Diagram of site 2 showing plot lay-out in vegetation zones. Scale: 1 cm = 15 m.

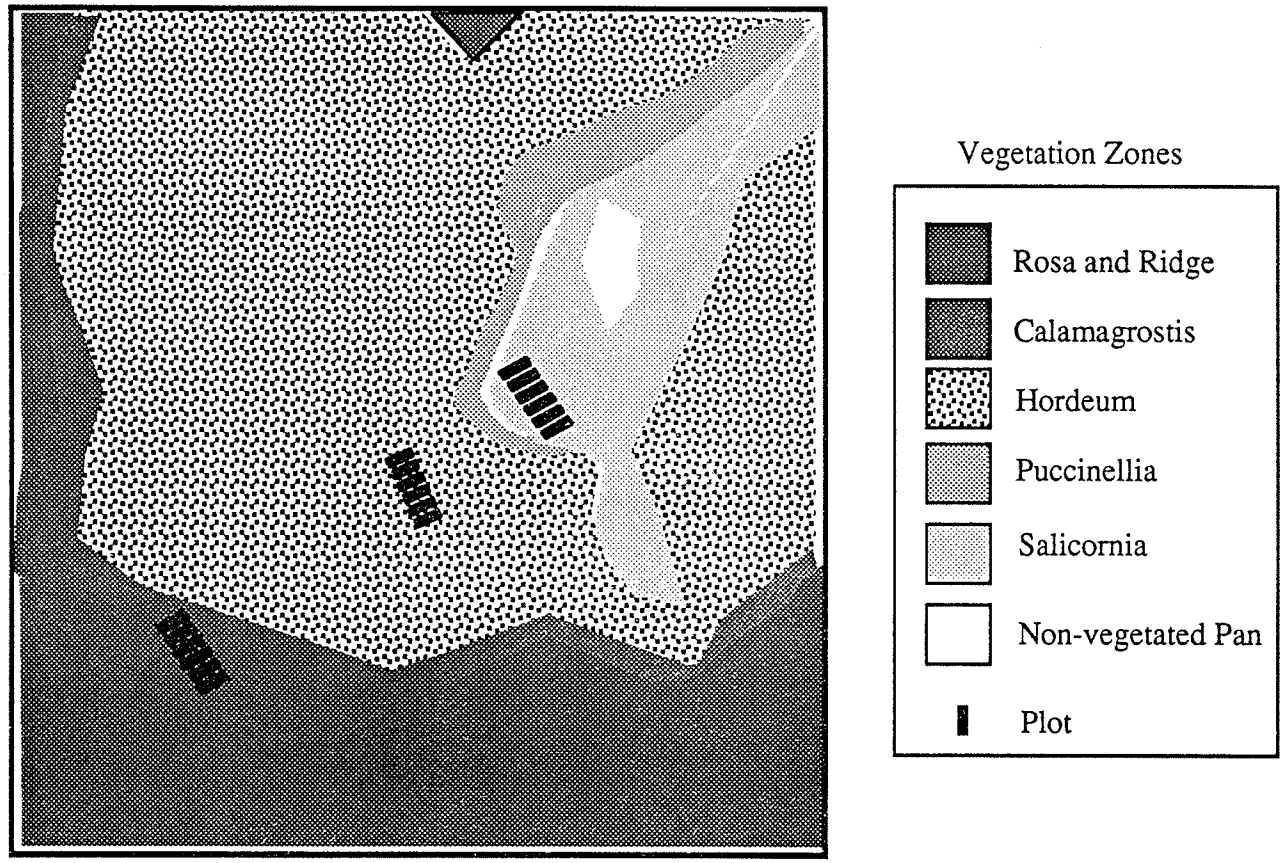


Figure 2.8 Diagram of site 3 showing plot lay-out in vegetation zones. Scale: 1 cm = 25 m

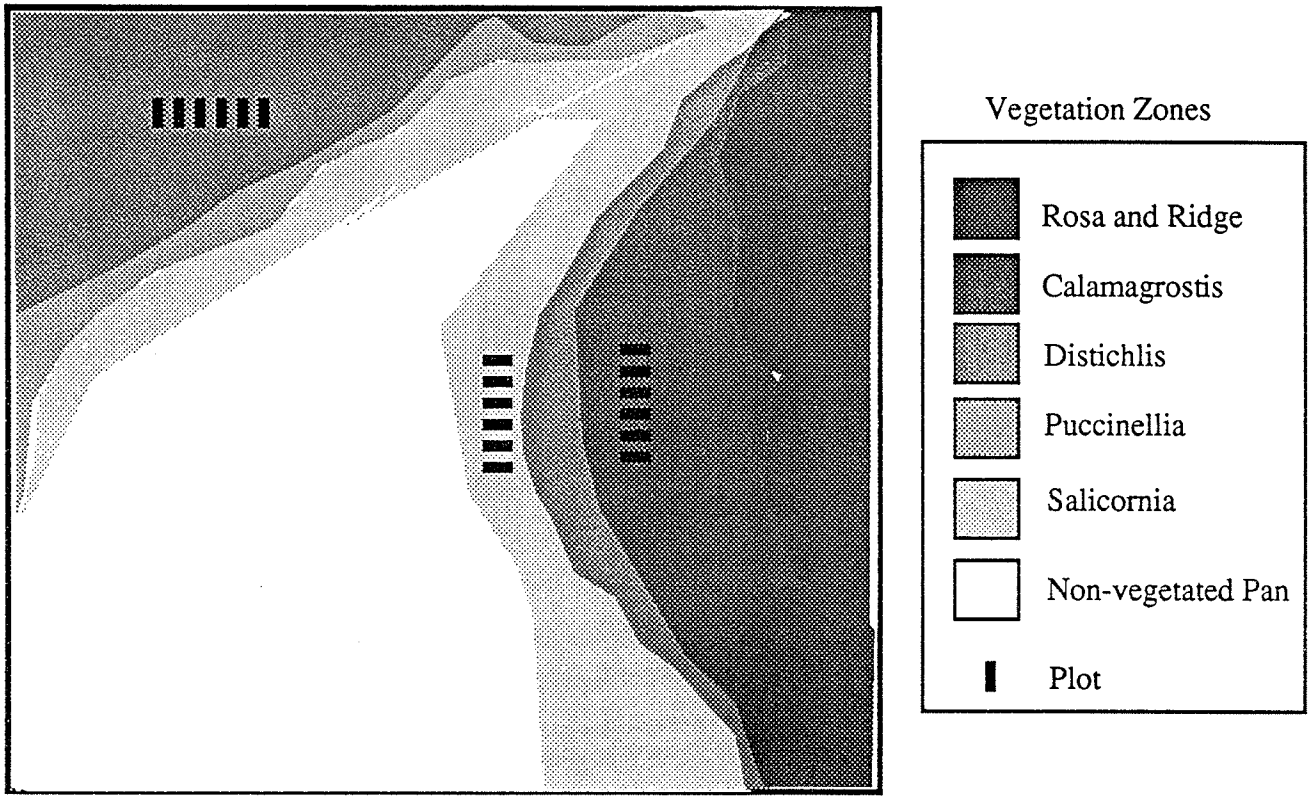


Figure 2.9 Diagram of site 4 showing plot lay-out in vegetation zones. Scale 1 cm = 10 m

Chapter 3 - Soil Factors

Section 3.1 - Introduction

Soil cores were extracted from experimental plots using a metal soil corer to a depth of 10 cm (unless otherwise specified). This depth was chosen because the majority of the underground biomass of the plants of these sites is found within the top 10 cm of soil (Burchill 1991). The use of a soil corer allows the extraction of a known volume of soil, making possible the analysis of soil factors (e.g. salinity) on a per volume basis. Relating soil factors to a volume of soil often provides more informative results than using the more traditional dried soil mass method (Gosselink *et al.* 1984), since the underground biomass of a plant occupies and interacts with a certain volume of soil (Brady 1974). It is the concentration and composition of materials in this soil volume that directly influences plant response.

Section 3.2 - Methods and Analysis

Section 3.2.1 - Plot Variation and Monitoring

On 2 June 1989, a 5 cm diameter corer was used to extract two soil cores from each experimental plot. Cores were then analyzed to determine pH, soil salinity (mg of NaCl/ml of soil), bulk density, and organic matter content. Two cores were taken from each plot to test for within-plot variation.

After determining variation within plots, monitoring of soil pH, salinity, and moisture content was conducted periodically over 1989 and 1990 (see Appendix II). Analysis for these factors did not require large amounts of soil, therefore, a smaller soil corer (2.5 cm in diameter x 10 cm deep) was employed. At all monitoring dates one core was extracted from each plot of each site. Cores were frozen and transported to the University of Manitoba where they were air-dried prior to analysis.

Section 3.2.2 - Bulk Density

The bulk density of soil was measured on each sampling date in the various vegetation zones. Bulk density of the cores was determined by taking the dry mass of each sample and dividing by the sample volume (McRae 1988) as follows:

$$\frac{\text{mass of dry soil (g)}}{\text{volume of sample(ml)}} = \text{mass of dry soil (g)/ml}$$

Section 3.2.3 - Organic Content

Soil organic content was determined by the combustible carbon method (Davies 1974; McRae 1988). Approximately 10 grams of air-dry, ground soil was taken from each soil core and placed in labelled beakers and dried at 105°C for 24 hours. The dry soil was then placed into preheated, pre-weighed ceramic crucibles. The crucibles containing the soil were placed into a muffle furnace and fired at 430 °C for 18 hours. I was initially concerned about the high $CaCO_3$ content of the soil of these sites (Burchill 1991) and the effect this may have on the final organic content determinations (McRae 1988). However, Davies (1974) states that, by following this temperature and time regime, the loss of carbon due to combustion is not affected by the presence of $CaCO_3$. After firing, the crucibles and their contents were placed into a desiccator, cooled, and massed. The amount of organic matter of each sample was presented as a percentage value using the following calculation (McRae 1988):

$$\frac{(\text{mass of pre-fired soil (g)} - \text{mass of fired soil (g)})}{\text{mass of pre-fired soil (g)}} \times 100 = \% \text{ organic matter}$$

Section 3.2.4 - Soil Particle Analysis

One soil sample (5 cm in diameter x 10 cm deep) was collected at random from half of the plots in each zone of each site. These samples were air dried in the lab and subjected to the Stoke's Law of soil particle size analysis (McRae 1988). The method involved three

main steps: (1) elimination of organic matter from the soil by hydrogen peroxide digestion, followed by dispersion of particles in a water column; (2) removal of sand by sieving; and (3) determination of silt and clay contents by pipette sampling at appropriate times.

Section 3.2.5 - Soil Salinity

Introduction

Methods used to determine soil salinity are numerous, and more precise methods are constantly being developed (Rhoades & Corwin 1984). A number of factors should be considered when choosing a method to measure soil salinity. Soil salinity is often spatially and temporally variable. A large number of soil samples are generally required to get an accurate measurement even within a small land area (Rhoades & Corwin 1984). This problem can usually be solved by resampling the same spot in the field. However, care should be taken that the sampling process does not alter the actual soil itself. This can be accommodated by the use of small soil corers. Although *in situ* methods have been developed, soil salinity is most often determined in the laboratory by measuring the conductivity of soil sample extracts (Rhoade & Corwin 1984). The dilution factor employed in extracting the salts from the soil sample depends on the type of salt present in the soil, as different salts often have different solubilities (Bernstein 1975). Soil extract methods involve removal of soil from the field, grinding, sieving, and dilution with water (Rhoades & Corwin 1984). Thus, the measured salinities may not be representative of actual field conditions. If the method employed in assessing salt content is consistently applied, however, comparable soil salinity measures are generated (Rhoades & Corwin 1984; Jacober & Sandoval 1971; Bernstein 1975).

The Case for the Dilution Extract

The electrical conductivity of a soil is related to the its salt content. Soil salinity levels are usually determined by measuring the electrical conductivity of an aqueous soil extract, followed by extrapolation to yield ionic concentration (Rhoades & Corwin 1984). Sonneveld & Van den Ende (1971) found that the ratio of soil:water used in obtaining an extract solution was dependent on the types of salt present, and the organic content of the soil. A 1:5 soil:water (by weight) extract method was found to be adequate for soil salinity determination in my study for a number of reasons. First, some salts (e.g. NaCl) are highly soluble in water, while others (e.g. salts of sulphate and calcium) are less so (Chang *et al.* 1983). Because of these differences in solubility, a soil saturation extract (paste) is not recommended, as it may lead to an underestimation of the actual salt content of the soil , especially if the soil being studied contains a variety of salts (Chang *et al.*. 1983). Chang *et al.* (1983) found that a 1:10 extract was suitable for extraction of salts in sulphate dominated soils. However, as NaCl was found to be the dominant salt of the Overflow Bay saline sites (Burchill 1991), a 1:5 dilution was deemed adequate for salt extraction (Agarwal *et al.* 1961). Secondly, although a soil saturation extract could have been used, the high soil organic matter content of the sites would have necessitated the collection of relatively large soil samples (Sonneveld & Van den Ende 1971). The use of the 1:5 dilution allowed for the collection of small samples which could easily be carried from each site and transported to the lab. Finally, when relative measures (such as those between vegetation zones of the study sites) are of more concern than absolute values, salinity determination using a fixed extract dilution is acceptable (Rhoades 1978).

Methodology Using the Dilution Extract

When sodium chloride predominates in the soil, the conversion factor:

Total Dissolved Salts (mg/ml) = 0.64 mg/ml/S x Electrical Conductivity (S)

can be used to estimate soil salinity (Richards 1954; Bernstein 1975).

Ten grams of dry, ground soil and 50 ml of distilled water were placed into numbered 125 ml Erlemeyer flasks. The flasks were placed on a mechanical shaker for one hour to allow soil salts to dissolve. The contents of each flask were then vacuum filtered through Whatman Number 1 paper filters to extract the salt water solution. The soil particles caught by the filter were discarded. The conductivity of each extract solution was determined using a Conductance/TDS meter (Analytical Instrument Science, Ser No. COND72485) and platinum electrode (Radiometer Electrodes). This value was then used to determine the amount of salt per ml of soil using the following calculations (modified from Richards 1954, to incorporate soil density and the dilution of the extract):

(1) electrical conductivity (S) x 0.64 mg/ml/S = salt (mg/ml)
(2) salt (mg/ml) x 50/10 g soil = mg of salt/10 g of soil
(3) (mg of salt/10 g of soil)/10 g = mg of salt/g of soil
(4) (mg of salt/ g of soil) x soil density (g/ml) = mg of salt/ml of soil

The four steps can be summarized in the following equation:

3.2 mg/ml/S x electrical conductivity (S) x soil density (mg/ml) = mg salt/ml soil.

Section 3.2.8 - Soil pH

Saline soils are alkaline (Brady 1974) and may have pH values as high as 9.0, and possibly higher (Agarwal *et al.* 1961). This can create nutritional problems for plants since the availability of some macronutrients (namely Ca, Mg, and P) and micronutrients (e.g. Fe, Mn, Zn, Co, and Cu) decrease as pH increases (Brady 1974). Therefore, knowledge of soil pH is important when dealing with saline soils. Agarwal *et al.* (1961) determined the pH of highly saline soils using a 1:5 extract, and compared their results with those obtained from a saturation extract of the same soils. Their comparison showed that the correlation of pH values obtained from the 1:5 extract to those obtained from a saturation extract was approximately $r = 0.98$. I determined soil pH by immersing a pH probe (Fisher, Model No. 229) into the same 1:5 extract as was used in salinity determination. pH was monitored over both field seasons (see Appendix II).

Section 3.2.7 - Nutrient Analysis

On 30 May 1990 one soil core (5 cm in diameter and 10 cm in depth) was obtained from each plot at each site and used for soil nutrient determinations. The samples were placed in labelled plastic bags and kept in cold storage until ready for processing. Analysis for available nitrogen, potassium, and phosphorus was performed by the Manitoba Provincial Soil Testing Laboratory, University of Manitoba, Winnipeg, Manitoba. Available nitrate (nitrogen) and phosphorus were determined using the sodium bicarbonate ($NaHCO_3$) extraction technique. Filtered extracts (Whatman No.30 paper) from a shaken mixture of 2.5 grams of soil, 1.0 gram of activated charcoal, and 50 ml of 0.5M $NaHCO_3$ were analyzed using a Tecnicon Auto Analyzer system. Available potassium was determined through the exchangeable ammonium acetate (NH_4OAc) method. An extract was obtained by filtering (Whatman No.1 paper) a shaken solution containing 2.5 grams of soil in 25 ml of neutral 1N NH_4OAc. The extract was then subjected to flame photometry to yield the potassium concentration. All values were expressed in parts per million (ppm) dry soil.

Section 3.2.8 - Soil Moisture

Soil moisture content was calculated as a percentage of loss of mass of field soil when dried at 105 ^{o}C for 24 hours (Brady 1974). The calculation is as follows:

$$\frac{\text{(mass of wet soil (g) - mass of dry soil (g))}}{\text{mass of wet soil (g)}} \times 100 = \%\ \text{soil moisture}$$

As it is important to prevent water loss due to evaporation, samples were kept cool or frozen immediately after collection.

Section 3.2.9 - Soil Water Salinity

Rhoades and Corwin (1984) state that total salt concentration in soil water is a particularly useful measure, since it is the concentration of solute in the soil solution to

which plants are directly exposed. They recommended the use of *in situ* salinity sensors, which make the collection and extraction of soil samples unnecessary. However, the use of *in situ* plot monitoring in the present study would have required a very large number of salinity sensors, which was not economically or logistically feasible. I therefore calculated soil water salinity on the basis of the measured soil water content. This involved determining the concentration of salts in the 1:5 soil extract, and then using soil moisture content data to calculate the concentration of salts in the soil water. This method assumed that the majority of the salts were in solution in the field. Since sodium chloride is highly soluble in water, this assumption is tenable. The following steps were used to determine soil water salinity.

(1) Determine amount of water in the original soil sample.

$$\text{g of water/g of dry soil} = \frac{\text{mass of wet soil (g) - mass of dry soil (g)}}{\text{mass of dry soil (g)}}$$

$$\text{g of water/g of dry soil} = \text{ml of water/g of dry soil}$$

(2) Determine salt concentration in the 5:1 extract solution.

$$\text{mg salt/ml extract} = \text{conductivity(S)} \times 0.64 \text{ mg/ml/S}$$

(3) Determine the amount of salt in the water of the original soil sample (soil water salinity), taking into consideration the ratio of the amount of water in the extract to the amount of water in the original sample, and multiplying by the salinity of the extract.

$$\text{mg salt/ml water} = \frac{5 \times \text{mass of dry soil (g)} \times \text{mg salt/ml extract}}{\text{mass of wet soil (g) - mass of dry soil (g)}}$$

The advantage of using soil water salinity as a measure is that it does not require information on soil density . If measures incorporating soil density are used, extreme care must be taken to obtain identically sized samples at each sampling date, and from one sampling date to the next. Even so, soil density may vary spatially within a given plot, and even a slight variation could result in very different salinity values per volume of soil. Measures based on soil water salinity are therefore useful in comparing soil samples both spatially and temporally.

In order to test the reliability of the 1:5 dilution extract method, results of soil salinity (mg salt/ml soil) and soil water salinity (mg salt/ml soil water) determinations were compared with those obtained from other salinity measurement methods. Linear regression analysis was used to examine the relationship between the 1:5 extract method and salinity readings obtained from: (1) soil saturation extracts, (2) evaporation of filtrate, and (3) a variety of soil:water ratios (extract dilutions). The results, which are presented in Appendix III, confirmed the validity of using the 1:5 dilution extract method.

Section 3.2.10 - Soil Depth Cores

Soil depth cores were extracted in order to examine gradients in soil water salinity and moisture content with increasing depth in the soil profile. Burchill (1991) conducted similar investigations using soil pits, but only on a single occasion at a single site.

Three replicate soil cores were extracted from each vegetation zone at each site. When possible soil cores were extracted to a depth of 60 cm. However, the presence of stones and high soil density (due to compaction of mineral particles) in some zones allowed only shallow soil penetration at some sites. Soil core depths therefore ranged from 10 to 60 cm, depending on the vegetation zone and the site sampled. After extraction, each soil core was divided into 10 cm lengths and frozen. Samples were then transported back to Winnipeg where soil moisture and soil water salinity were determined.

Evapotranspiration leads to a decrease in soil water content. However, the total amount of salt remains more or less constant (Rhoades & Corwin 1984), and as a result, the concentration of salts in the remaining soil water increases. Also, the dynamic nature of salts in soil (i.e. tendency for movement vertically in the soil profile as a result of precipitation, run-off, evaporation, and evapotranspiration), leads to changes in profile gradients that are reflective of changes in environment and vegetation conditions (Brady 1974; Rhoades *et al.* 1976). In order to obtain some indication of soil depth gradient

variability, cores were collected on two separate occasions for each site during the 1990 field season: under wet conditions and early vegetation (end of May) and drier conditions with more mature vegetation (early July for site 3 and 4, and late August for sites 1 and 2).

Section 3.2.11- Data Analysis

Paired t-tests ($\alpha = 0.01$) were used to indicate if there was significant variability within plots. Tukey Box-Plots (see Figure 3.1) of bulk density, organic matter, pH, soil salinity, and soil nutrients were used to illustrate variation both within and between vegetation zones. Mean values and standard errors were calculated for soil moisture and soil water salinity measurements. ANOVA and Scheffe's multiple comparison test ($\alpha = 0.05$) were used to determine if significant differences existed between zones and sites.

Section 3.3 - Results

Section 3.3.1- Plot Variation

Results of paired t-tests on soil bulk density, pH, and salinity (Table 3.1) indicated that within-plot soil variation was not significant for the three factors tested ($p > 0.01$).

Table 3.1 Results from paired t-test analysis performed on three soil factors.

Saline Site	Vegetation Zone	Bulk Density (g/ml)	pH	Salinity (mg salt/ml soil)
1	Calamagrostis	0.82	0.15	0.17
1	Hordeum	0.35	0.22	0.73
1	Puccinellia	0.66	0.14	0.71
1	Salicornia	0.67	0.62	0.54
2	Calamagrostis	0.12	0.25	0.46
2	Hordeum/Distichlis	0.93	0.98	0.89
2	Puccinellia	0.04	0.58	0.09
2	Salicornia	0.07	0.36	0.54
3	Calamagrostis	0.09	0.08	0.06
3	Hordeum	0.71	0.71	0.49
3	Salicornia	0.45	0.44	0.52
4	Calamagrostis	0.27	0.09	0.73
4	Distichlis	0.57	0.31	0.84
4	Salicornia	0.39	0.89	0.49

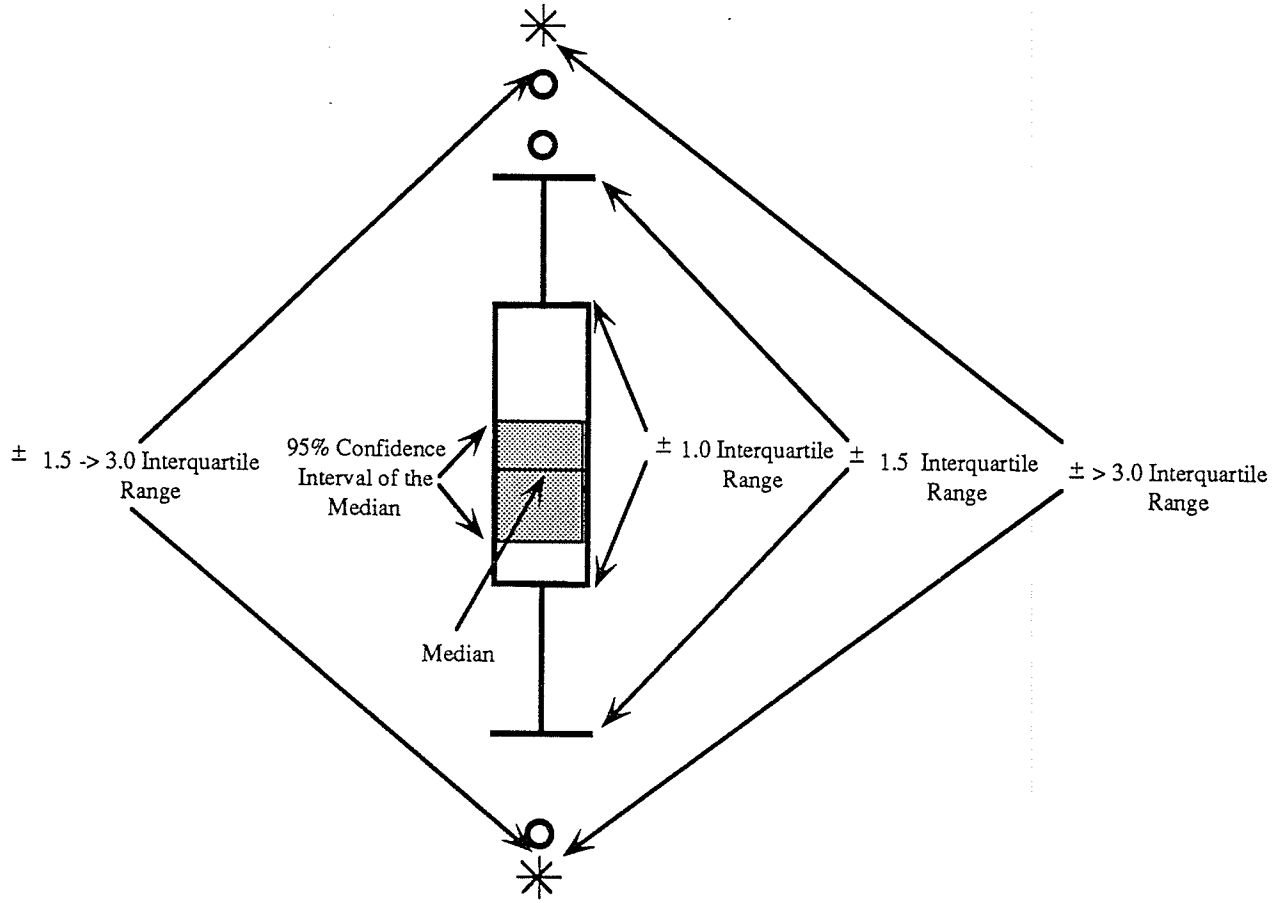


Fig. 3.1 Diagram of Tukey Boxplot with explanation. The rectangular box represents ± interquartile range, with the median indicated by the horizontal line, and the shaded area representing the 95% confidence interval of the median. T's extend from the box to the nearest point within ± 1.5 interquartile range. Circles and stars represent outliers within and beyond ± 3.0 interquartile range respectively. (from Emerson & Strenio 1983).

Section 3.3.2 - Soil Density, Salinity, pH, and Particulate Matter

Results of soil density, salinity, pH, and particulate matter analysis for each site are presented in Tables 3.2 - 3.5. Distinct trends were observed in these soil factors across vegetation zones. Soil salinity increased from the Calamagrostis through to the Hordeum, or Hordeum/Distichlis, or Distichlis, Puccinellia, and Salicornia zones (specific zones are dependent on site). A similar gradient was observed in soil bulk density, with lowest densities occurring in the least saline zones and highest densities in the Salicornia zone. In general, the lower salinity zones were more acidic than the Salicornia zone. However, the trend in pH was not as distinct as that observed in the other soil factors. Soil of the Calamagrostis and Hordeum zones had higher organic content levels than that of the Salicornia zone. The soils of the Calamagrostis and Hordeum zones of site 3, and the Hordeum and Puccinellia zones of site 1 were particularly high in organic matter. The soil of the remaining zones and sites (i.e. Calamagrostis and Salicornia zones of site 1, the Salicornia zone of site 3, and all zones of sites 2 and 4) were predominantly mineral in nature.

Based on these soil analysis results, the sites can be roughly classified into three types. Sites 2 and 4 are similar, both possessing highly saline mineral soils with high pH values. These sites are similar as they are located in close proximity to each other. On the other hand, site 3 soil is less saline overall, somewhat acidic, and predominantly organic. Site 1 fits between these two groupings. The Puccinellia and Hordeum zone soils of site 1 are similar to the Hordeum zone soil of site 3, while the Calamagrostis and Salicornia zone soil have characteristics in common with the Calamagrostis and Salicornia zones of sites 2 and 4.

Table 3.2 Results of analysis for selected soil factors from vegetation zone soils of site 1. Values are means ± SE. n = 20 for salinity, density, pH, and organic matter. n = 5 for mineral particles.

Soil Factor	Vegetation Zones			
	Calamagrostis	Hordeum	Puccinellia	Salicornia
Salinity (mg salt/ml soil)	2.81 ±0.17	10.70 ±0.39	18.21 ±1.05	39.59 ±0.88
pH	7.59 ±0.16	6.41 ±0.18	6.84 ±0.15	7.83 ±0.04
Bulk Density (g/ml)	0.96 ±0.04	0.26 ±0.01	0.44 ±0.04	1.48 ±0.04
Organic Content (% of dry soil)	15.99 ±2.64	64.84 ±2.76	43.90 ±6.01	8.41 ±1.95
Gravel (% of dry soil)	1.30 ±0.27	0.00	0.43 ±0.43	1.61 ±0.44
Sand (% of dry soil)	16.31 ±1.75	2.96 ±0.50	4.06 ±0.95	35.30 ±7.99
Silt (% of dry soil)	43.61 ±3.47	7.73 ±1.35	18.11 ±3.85	39.63 ±5.66
Clay (% of dry soil)	11.03 ±1.68	9.33 ±0.92	12.72 ±1.77	8.84 ±1.66

Table 3.3 Results of analysis for selected soil factors from vegetation zone soils of site 2. Values are means ± SE. n = 20 for salinity, density, pH, and organic matter. n = 5 for mineral particles.

Soil Factor	Vegetation Zones			
	Calamagrostis	Hordeum/ Distichlis	Puccinellia	Salicornia
Soil Salinity (mg salt/ml soil)	6.59 ±0.42	9.20 ±0.46	15.31 ±0.46	27.62 ±0.95
pH	7.55 ±0.09	7.76 ±0.06	7.95 ±0.06	8.00 ±0.06
Bulk Density (mg/ml)	0.55 ±0.02	0.61 ±0.02	0.99 ±0.03	1.34 ±0.04
Organic Content (% dry soil)	25.19 ±1.62	18.44 ±1.44	11.61 ±1.31	9.40 ±1.05
Gravel (% of dry soil)	1.03 ±0.13	0.60 ±0.22	0.24 ±0.12	14.56 ±3.84
Sand (% of dry soil)	26.00 ±2.56	11.45 ±1.03	19.01 ±2.38	30.98 ±2.42
Silt (% of dry soil)	40.99 ±1.37	51.92 ±2.71	56.74 ±3.29	39.21 ±1.73
Clay (% of dry soil)	7.74 ±0.93	12.07 ±0.96	9.07 ±0.49	4.24 ±0.73

Table 3.4 Results of analysis for selected soil factors from vegetation zone soils of site 3. Values are means ± SE. n = 12 for salinity, density, pH, and organic matter. n = 3 for mineral particles.

Soil Factor	Vegetation Zones		
	Calamagrostis	Hordeum	Salicornia
Salinity (mg salt/ml soil)	6.00 ±0.30	6.14 ±0.44	25.23 ±1.02
pH	6.37 ±0.06	6.74 ±0.20	7.37 ±0.12
Bulk Density (mg/ml)	0.14 ±0.01	0.15 ±0.00	0.49 ±0.024
Organic Content (% dry soil)	79.17 ±0.39	75.85 ±1.46	14.10 ±1.22
Gravel (% of dry soil)	0.00	0.00	0.00
Sand (% of dry soil)	5.95 ±0.82	4.46 ±1.16	4.16 ±1.16
Silt (% of dry soil)	3.07 ±1.64	5.23 ±1.12	48.58 ±3.72
Clay (% of dry soil)	5.85 ±0.25	8.08 ±0.58	28.63 ±3.75

Table 3.5 Results of analysis for selected soil factors from vegetation zone soils of site 4. Values are means ± SE. n = 12 for salinity, density, pH, and organic matter. n = 3 for mineral particles.

Soil Factor	Vegetation Zones		
	Calamagrostis	Distichlis	Salicornia
Salinity (mg salt/ml soil)	4.87 ±0.46	10.55 ±0.65	43.20 ±3.08
pH	7.66 ±0.10	7.75 ±0.07	7.99 ±0.05
Bulk Density (mg/ml)	0.68 ±0.05	0.55 ±0.04	1.49 ±0.03
Organic Content (% dry soil)	18.58 ±2.29	22.48 ±1.47	10.53 ±0.79
Gravel (% of dry soil)	0.75 ±0.03	0.54 ±0.29	1.07 ±0.39
Sand (% of dry soil)	25.11 ±0.93	7.63 ±1.39	27.48 ±2.92
Silt (% of dry soil)	53.11 ±3.28	57.05 ±10.34	57.92 ±2.52
Clay (% of dry soil)	2.91 ±1.00	10.89 ±2.26	3.34 ±0.48

Section 3.3.3 - Soil Nutrients

Results from soil analysis for nitrogen, phosphorus, and potassium content are presented in Tables 3.6 - 3. 9. Nitrogen content did not show a clear across-zone gradient, with the possible exception of site 4, which showed a trend of decreasing nitrogen levels from the Calamagrostis zone through to the Salicornia zone. The lowest levels were consistently found in the Salicornia zone soils. In general, less saline soils had higher nitrogen levels. Site 3 soils had the highest nitrogen levels when compared with corresponding zones of the other sites. This is probably due to the lower salinities in these soils, which provides a better habitat for nitrogen-fixing organisms (Brady 1974). Across-zone gradients in phosphorus were more apparent than gradients in nitrogen. In general, the sites showed a gradual decrease in phosphorus content of soils from the low salinity Calamagrostis zone to the high salinity Salicornia zone. This gradient in decreased phophorus availability may have occurred indirectly through increasing salinity and subsequent increases in pH. As with nitrogen, site 3 soils generally had the highest mean phosphorus content compared with corresponding zones of the other sites. Potassium was relatively high in all zones of all sites. No clear gradient was evident for potassium content, although the lowest levels were consistently recorded in the Salicornia zone soils. Again, site 3 soils had the highest potassium levels, and actually exceeded the maximum detectable amount for the scale employed in analysis (700 ppm).

Table 3.6 Nutrient content (ppm) of soil from experimental plots in vegetation zones of site 1. Values are means ± SE. n = 10.

Nutrient (ppm)	Vegetation Zones			
	Calamagrostis	Hordeum	Puccinellia	Salicornia
Nitrogen	44 ±5.9	61.8 ±17.1	255 ±67.1	5.7 ±2.3
Phosphorus	10 ±1.1	57.4 ±1.5	39.7 ±3.2	8.8 ±1.8
Potassium	448 ±53.3	699 ±1.0	685 ±12.5	326 ±40.1

Table 3.7 Nutrient content (ppm) of soil from experimental plots in vegetation zones of site 2. Values are means ± SE. n = 10. Data is not available for the potassium content of the Salicornia zone soil

Nutrient (ppm)	Vegetation Zones			
	Calamagrostis	Hordeum/ Distichlis	Puccinellia	Salicornia
Nitrogen	104 ±9.6	90.7 ±14.9	92.2 ±13.8	2.3 ±0.3
Phosphorus	28.8 ±2.8	20.2 ±2.1	12.2 ±1.0	4.4 ±0.5
Potassium	497 ±32.6	513 ±27.2	401 ±14.4	N/A

Table 3.8 Nutrient content (ppm) of soil from experimental plots in vegetation zones of site 3. Values are means ± SE. n = 6. Values for potassium in the Calamagrostis and Hordeum zones exceeded the maximum detectable amount.

Nutrient (ppm)	Vegetation Zones		
	Calamagrostis	Hordeum	Salicornia
Nitrogen	175 ±71.2	291 ±121	40.2 ±8.7
Phosphorus	58.8 ±0.8	57.8 ±2.2	43.5 ±2.9
Potassium	700+	700+	410 ±17.3

Table 3.9 Nutrient content (ppm) of soil from experimental plots in vegetation zones of site 4. Values are means ± SE. n = 6.

Nutrient (ppm)	Vegetation Zones		
	Calamagrostis	Distichlis	Salicornia
Nitrogen	65.8 ±9.0	30.9 ±16.0	5.8 ±1.4
Phosphorus	79.7 ±43.8	24.4 ±4.9	10.2 ±1.4
Potassium	360 ±40.1	449 ±32	184 ±13.4

Section 3.3.4 - Comparison of Corresponding Zones between Sites

The previous section presented the soil analysis results on a site by site basis. This section addresses the same data, but in such a way as to allow comparison of corresponding vegetation zones between sites. The results are presented graphically using

Tukey boxplots. Horizontal lines on the x-axis of each graph connect sites between which the particular vegetation zones are not significantly different (Scheffe' $\alpha = 0.05$).

Calamagrostis Zones (Sites 1 - 4)

Soils of the Calamagrostis zone of site 1 had the highest density and the lowest organic matter content (Figures 3.2 and 3.3). Sites 2 and 4 soils had similar densities and similar amounts of organic matter, while soils of the Calamagrostis zone of site 3 were significantly lower in density and higher in organic matter than the other three sites. Calamagrostis zone soil salinity ranged from a low of about 2 mg/ml in site 1, to a high of just under 9 mg/ml in site 2. Soil salinity levels were similar between the Calamagrostis zones of site 2,3, and 4. The salinity of the Calamagrostis zone soil of site 1 was lower than that of sites 2 and 3, but not significantly different from that of site 4. Soil pH hovered around 7.5 in the Calamagrostis zones of the study sites, with the exception of site 3, The soils of site 3 were somewhat more acidic, probably due to the presence of organic acids resulting from the soil's high organic matter content.

There was no significant difference in available nitrogen and phosphorus in the Calamagrostis zone soils between sites. However, the values obtained from site 3 soils had a wide range, and if more cores had been collected they might have shown significantly higher levels of nitrogen and phosphorus in the soil than that of the other study sites. The Calamagrostis soil of sites 1,2, and 4 had similar levels of potassium, with site 3 soil levels being significantly higher.

Hordeum Zones (Sites 1 and 3)

Hordeum zones were present in sites 1 and 3. The soil of the Hordeum zone in site 1 was significantly more dense, had less organic matter, and was more saline (Figure 3.4) than that of site 3. Salinity levels in the Hordeum zone in site 1 were 10 - 11 mg/ml, while in site 3 they were between 5 and 7 mg/ml. The soil pH of the Hordeum zones of the

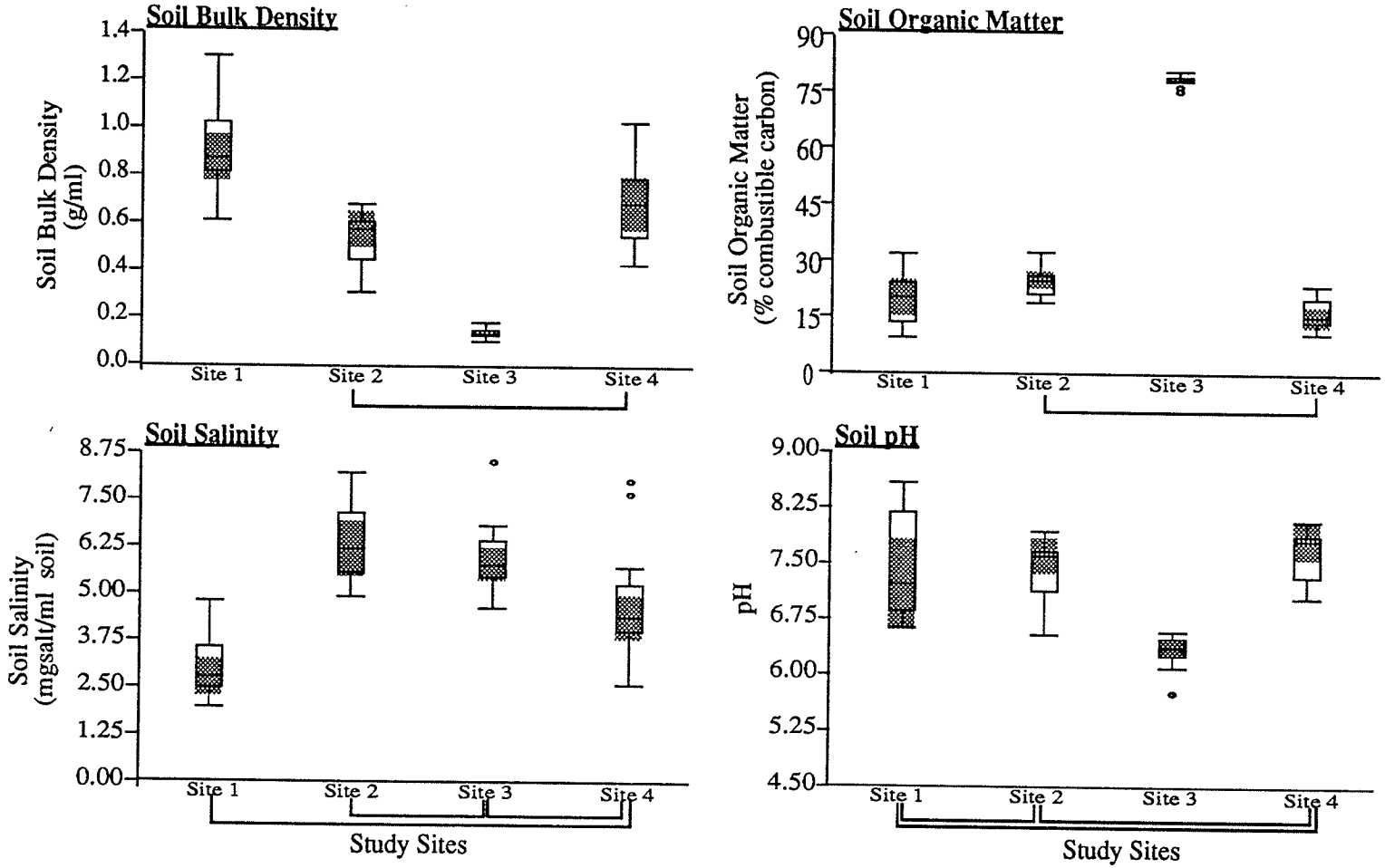


Fig. 3.2 Comparison of soil factors between Calamagrostis zones of study sites 1 - 4. Brackets join sites in which the Calamagrostis zones are not significantly different (Scheffé $\alpha = 0.05$). n = 20 for sites 1 & 2, and n = 12 for sites 3 & 4.

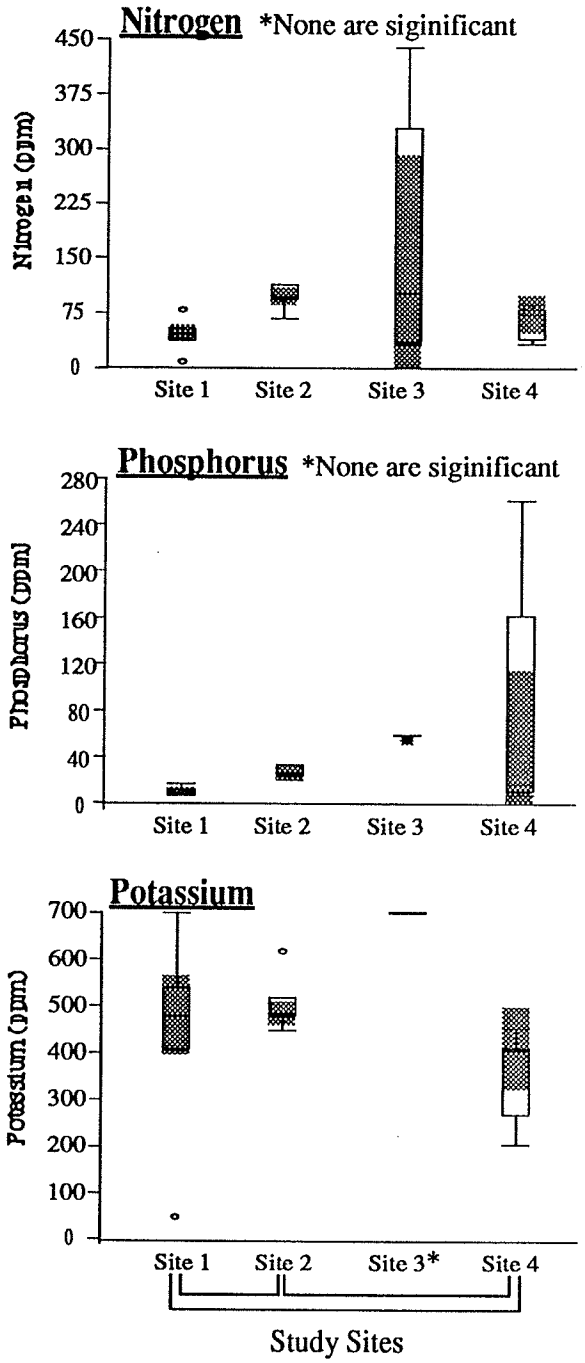


Fig. 3.3 Comparison of selected soil macronutrients between Calamagrostis zones of study sites 1 - 4. Brackets join sites between which the Calamagrostis zones are not siginificantly different (Scheffé $\alpha = 0.05$). n = 10 for sites 1 & 2, and n = 6 for sites 3 & 4. *Note the potassium value for site 3 exceeded the maximum of the detection scale, and was significantly different from the other sites.

two sites was, for the most part, slightly below neutral, and did not differ significantly between sites (Figure 3.4).

Soil nitrogen content was significantly higher in the Hordeum zone soil of site 3 than in site 1 (Figures 3.5). No significant difference was found between the amount of available phosphorus between sites 1 and 3. Both sites showed maximum detectable levels for soil potassium.

Hordeum/Distichlis and Distichlis Zones (Sites 2 and 4)

No significant differences in soil factors were found between the Hordeum/Distichlis zone of site 2 and the Distichlis zone of site 4 (Figures 3.6 and 3.7), with the exception of nitrogen, which was significantly higher in the Hordeum/Distichlis zone than the Distichlis zone soil, .

Puccinellia Zones (Sites 1 and 2)

Analysis of the soil from the Puccinellia zones of sites 1 and 2 indicated that the Puccinellia zones of the two sites were significantly different for all the soil factors investigated (Figures 3.8 and 3.9). The Puccinellia zone soil of site 1 is less dense, has more organic matter, a slightly higher salinity, and a lower pH than that of site 2. Nutrient content was consistently highest in the site 1 soils.

Salicornia Zones (Sites 1 - 4)

Salicornia zones were present at all the study sites. Soil bulk density was lowest in the Salicornia zone of site 3, and highest in the corresponding zone of site 4 (Figure 3.10). Bulk density values of the Salicornia zone soil of sites 1 and 2 were not significantly different. Organic matter content of the Salicornia zone soil was significantly higher in site 3 than the other sites. Soil salinity was lowest in sites 2 and 3, and significantly higher in

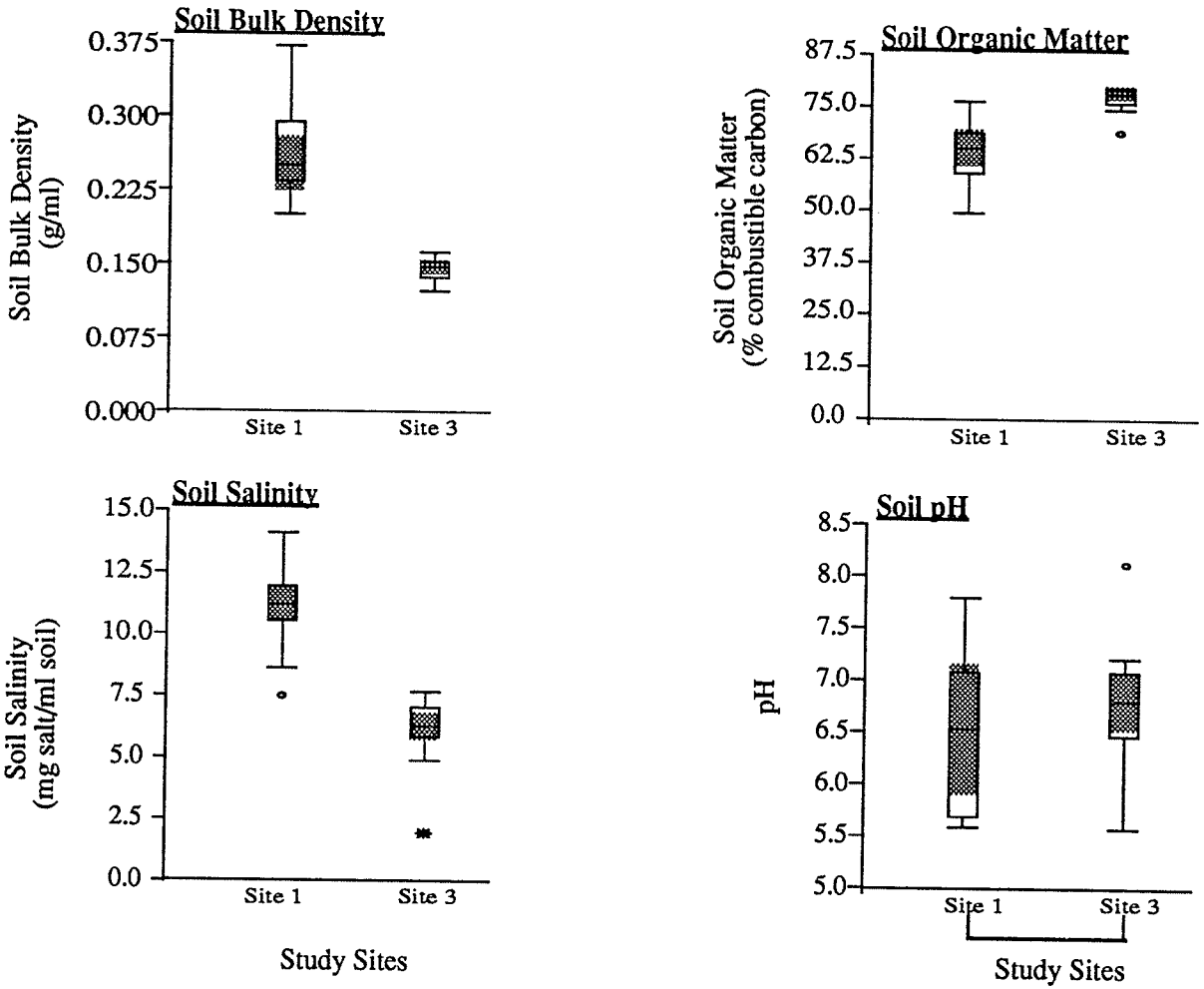


Fig. 3.4 Comparison of soil factors between Hordeum zones of study sites 1 and 3. Brackets indicate the zones are not significantly different (ANOVA $p \leq 0.05$). n = 20 for site 1, and n = 12 for site 3.

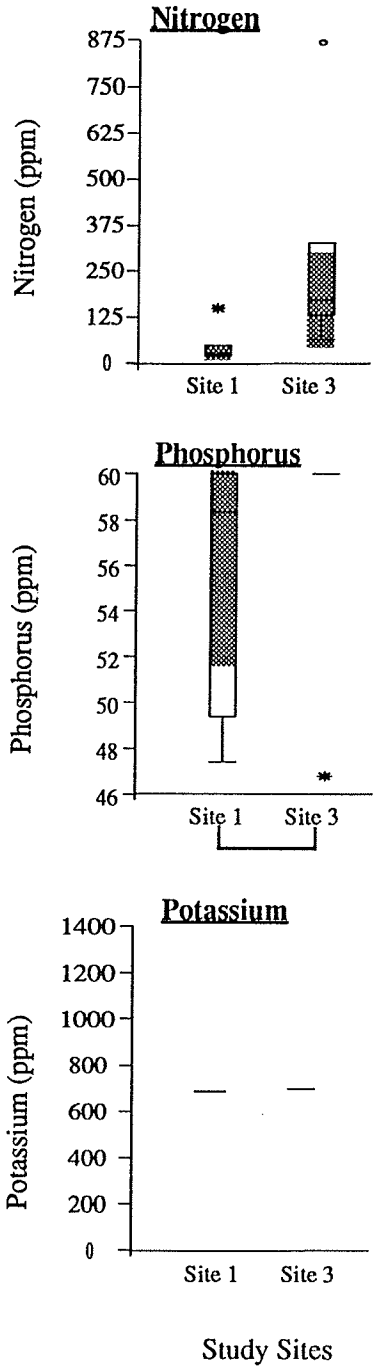


Fig. 3.5 Comparison of selected soil macronutrients between Hordeum zones of study sites 1 and 3. Brackets join sites between which the Hordeum zones are not siginificantly different (ANOVA $p \leq 0.05$). $n = 10$ for site 1, and $n = 6$ for site 3. (Note that the potassium levels in sites 1 and 2 exceeded the maximum (700 ppm) of the detection scale and thus were not subjected to ANOVA).

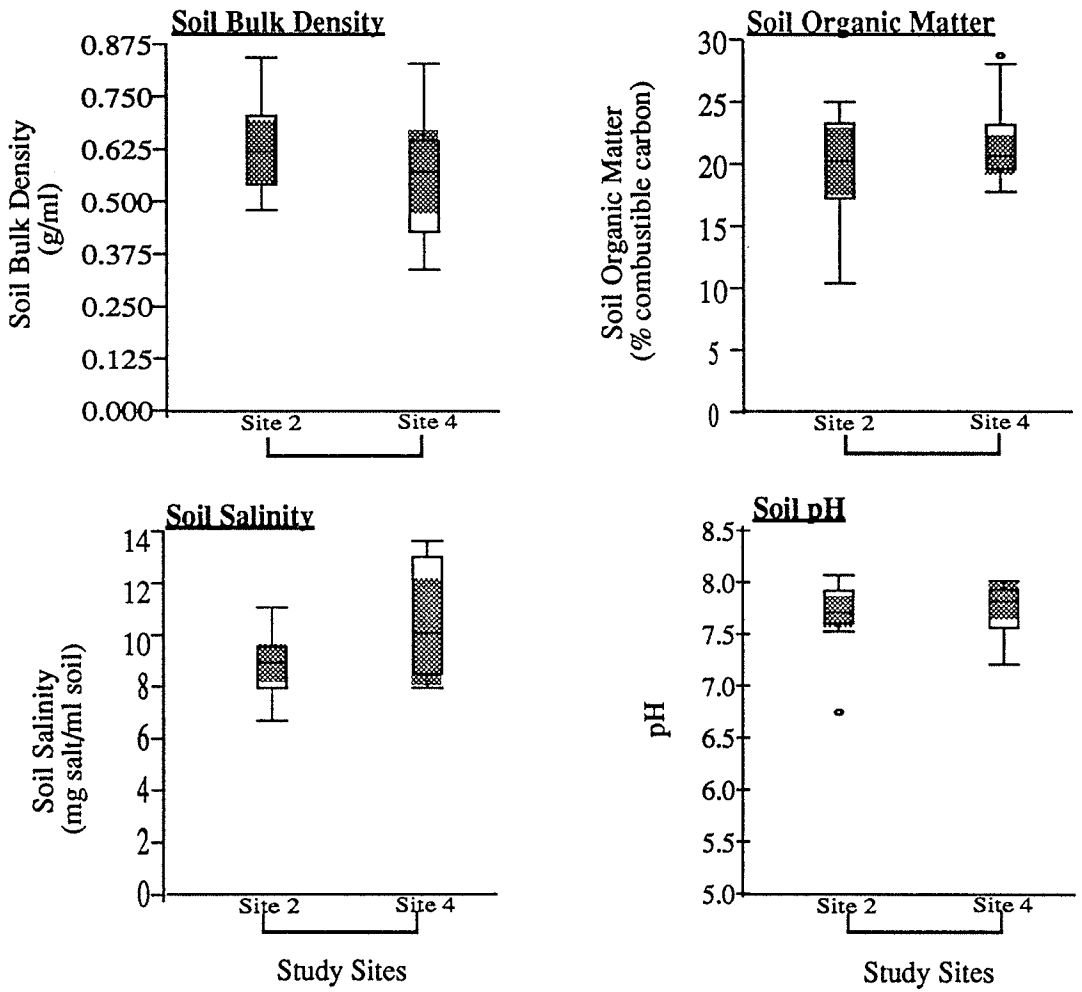


Fig. 3.6 Comparison of soil factors between Hordeum/Distichlis zone of site 2 and the Distichlis zone of site 4. Brackets join sites in which the zones are not significantly different (ANOVA $p \leq 0.05$). n = 20 for site 2, and n = 12 for site 4.

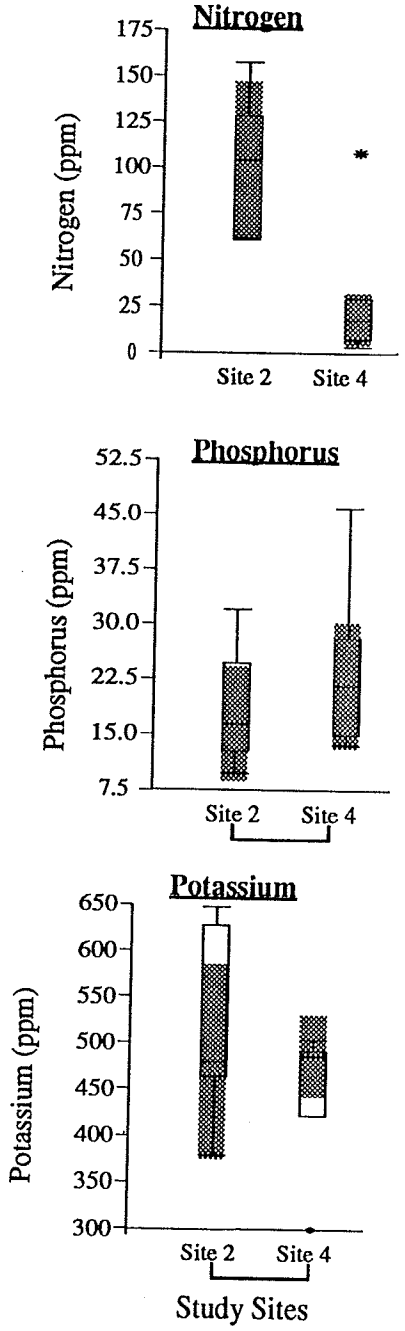


Fig. 3.7 Comparison of selected soil macronutrients between the Hordeum/ Distichlis zone of site 2 and the Distichlis zone of site 4. Brackets join sites between which the zones are not significantly different (ANOVA $p \leq 0.05$). $n = 10$ for site 2, and $n = 6$ for site 4.

sites 1 and 4. Soil pH was significantly lower in the Salicornia zone of site 3 compared with the other sites. Soil nitrogen and phosphorus concentration were highest in the Salicornia zone soil of site 3 (Figure 3.11). Nitrogen and phosphorus content were not significantly different between sites 1, 2, and 4. Levels of potassium in the Salicornia zones were high, with no significant difference between the sites. (Potassium content for the Salicornia zone soil of site 2 was not available due to lost samples).

Section 3.3.5 - Soil Moisture and Soil Water Salinity

The initial soil analysis agenda did not address moisture as a soil factor. However, as facilities in the field became available (i.e use of a refrigerator to keep samples cool), soil moisture determinations became possible. Incorporating soil moisture readings into salinity determinations allowed for the calculation of soil water salinity. As stated in the introductory chapter, plant growth is directly affected by the ionic composition of the soil solution (i.e. soil water). Soil water salinity was therefore deemed to be the best measurement of salt concentration in the site soils.

Soil moisture and soil water salinity were monitored over both field seasons. The mean results are presented graphically by site in Figures 3.12 - 3.15. Soil moisture is influenced by rainfall, temperature, evapotranspiration, soil density, and surface topography. For purposes of comparison, the precipitation regime for the area during both field seasons appears at the top of each Figure.

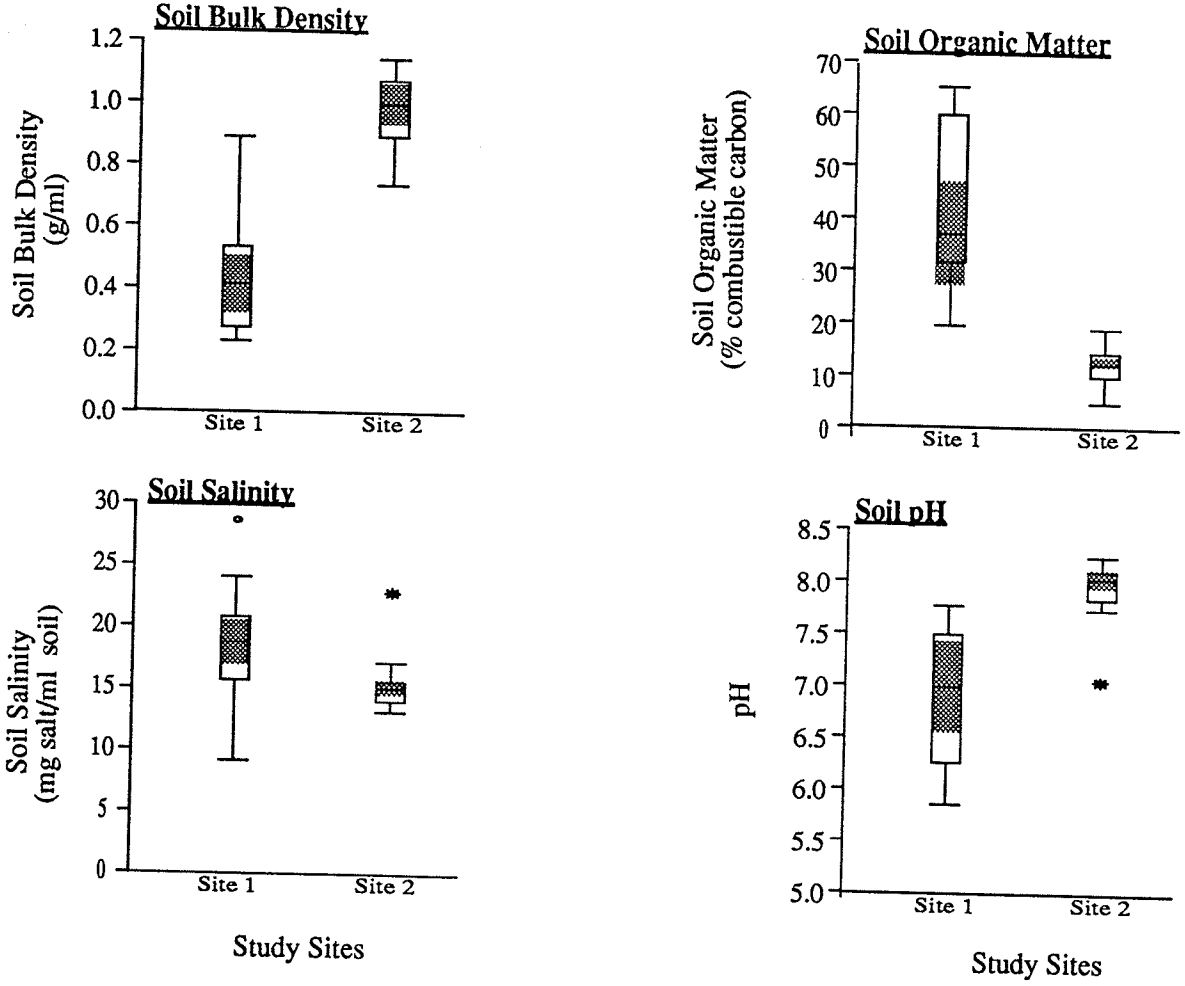


Fig. 3.8 Comparison of soil factors between Puccinellia zones of study sites 1 and 2. The zones were significantly different between sites for each soil factor (ANOVA $p \leq 0.05$). $n = 20$.

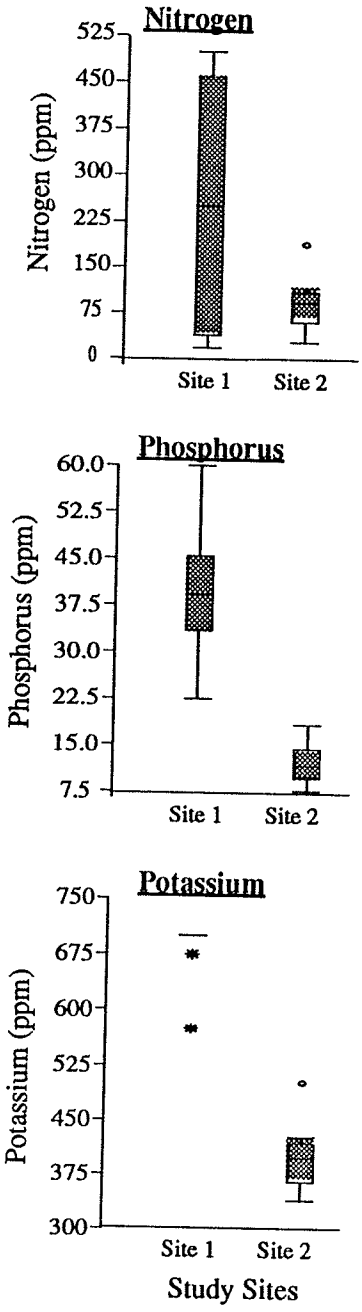


Fig. 3.9 Comparison of selected soil macronutrients between Puccinellia zones of study sites 1 and 2. Note, all three nutrients were signficantly different between sites (ANOVA $p \leq 0.05$). $n = 10$.

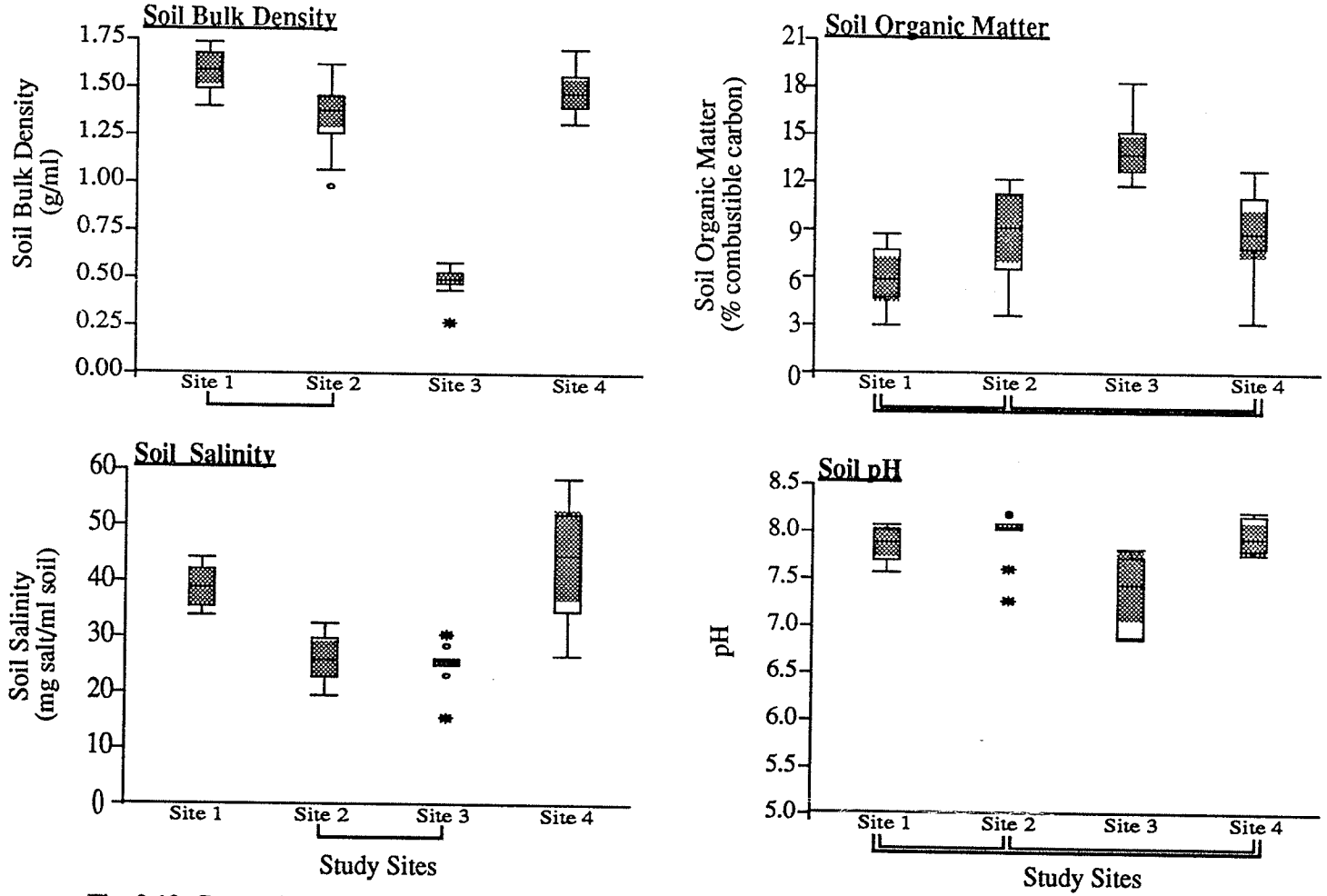


Fig. 3.10 Comparison of soil factors between Salicornia zones of study sites 1 - 4. Brackets join sites in which the Salicornia zones were not significantly different (Scheffé α=0.05). n = 20 for sites 1 & 2, and n = 12 for sites 3 & 4.

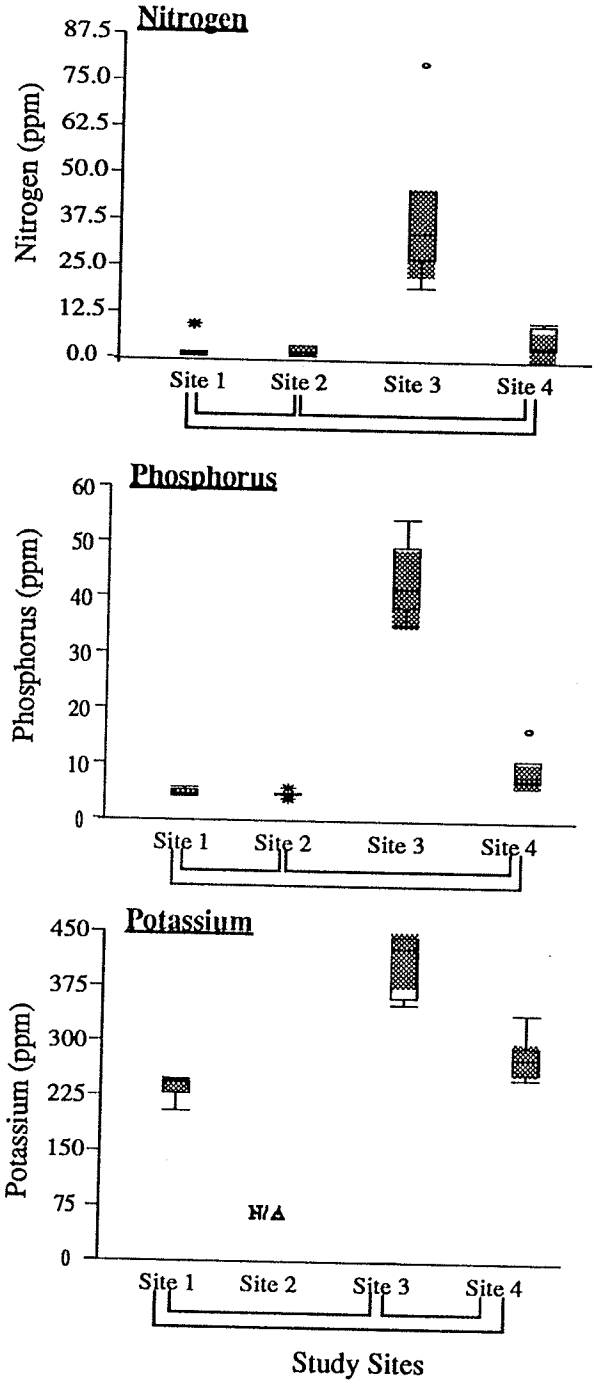


Fig. 3.11 Comparison of selected soil macronutrients between Salicornia zones of study sites 1 - 4. Brackets join sites between which the Salicornia zones were not significantly different (Scheffé $\alpha = 0.05$). n = 10 for sites 1 & 2, and n = 6 for sites 3 & 4.

Site 1

In site 1 (Figure 3.12) the mean soil moisture of each zone increased over the monitoring period during the 1989 field season. Initially the soil was relatively dry due to low precipitation in the early spring. This was followed by a rather sharp increase in late June and a slight decrease or levelling-off (depending on the zone) by mid-summer. Moisture again increased following rainfall in the month of August. During 1990 mean soil moisture was fairly constant in the Puccinellia and Salicornia zones, and showed a gradual increase of between 10% and 20% in the Calamagrostis and Hordeum zones. The mean soil moisture of the Hordeum zone was consistently higher than the other zones at each sampling date over both growing seasons. The Puccinellia zone had the next highest mean soil moisture content, followed by the Calamagrostis and Salicornia zones. Note that while the mean soil moisture of one zone may have overlapped with that of an adjacent zone during the growing season, no overlaps occurred on the same sample date. For example, in 1989, the highest moisture reading for the Salicornia zone occurred in late August, which overlapped with the soil moisture content present in the Calamagrostis zone in June and July. Thus the soil moisture gradient across the vegetation zones, although subject to fluctuations, was maintained over both growing seasons.

Mean soil water salinity also fluctuated during both field seasons. During 1989 the least saline zone was Calamagrostis, followed by Hordeum and Puccinellia. During periods of steady precipitation and subsequent high moisture conditions (such as occurred in August of 1989 and over the 1990 season) the mean soil water salinity of these zones tended to overlap considerably. The reverse was true during periods of low rainfall, such as the late spring and early summer of 1989. The Salicornia zone was the most saline zone and experienced the greatest range in mean soil water salinity over the two field seasons.

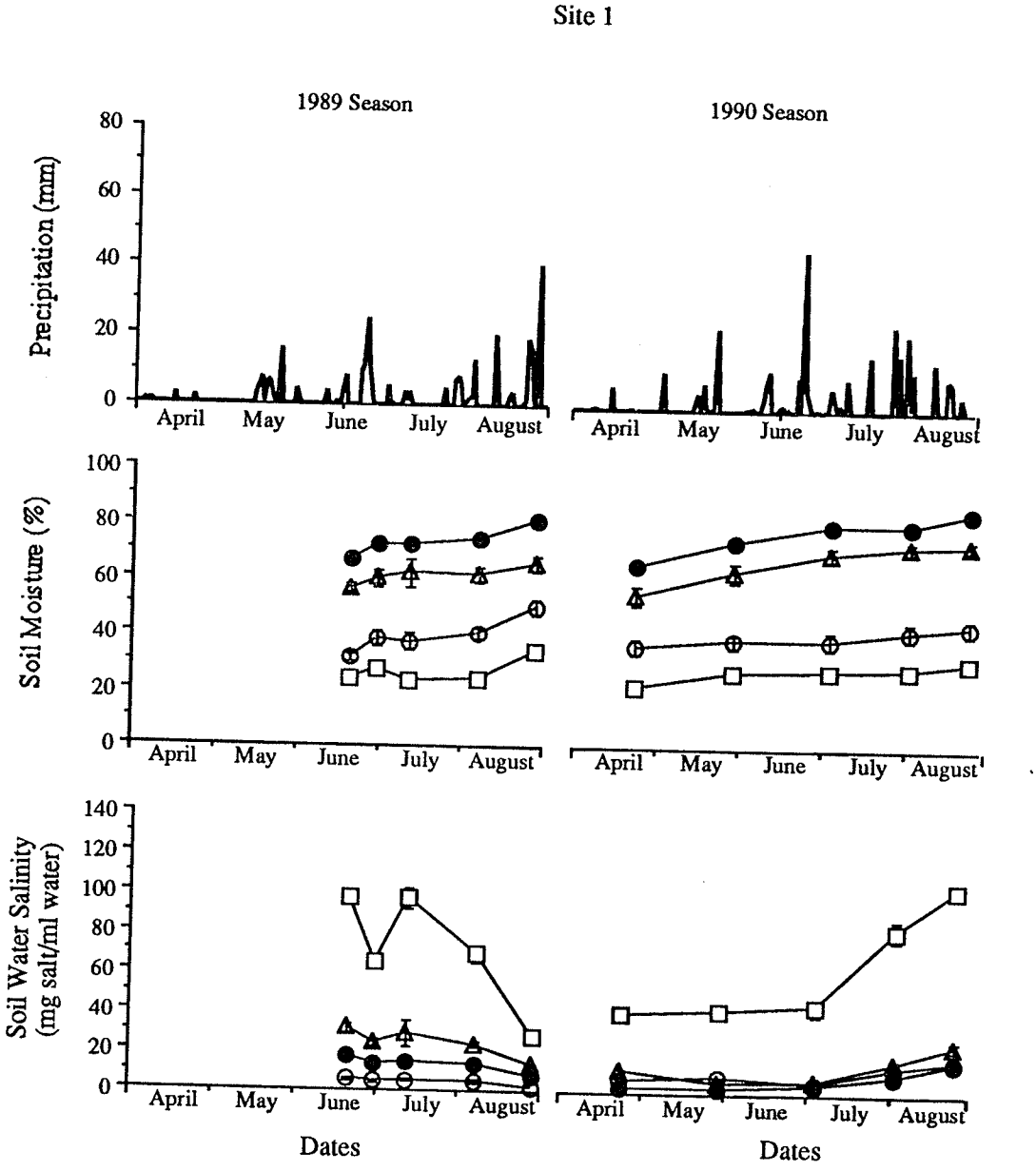


Fig. 3.12 Total daily precipitation regime and soil moisture and soil water salinity of each vegetation zone of site 1 during the 1989 and 1990 field seasons. Vegetation zones are as follows: —○— Calamagrostis, —●— Hordeum, —△— Puccinellia, —□— Salicornia. Values for soil moisture and soil water salinity are mean values (n = 10) ± SE.

Site 2

Unlike site 1, the Calamagrostis and Hordeum/Distichlis zones of site 2 had similar soil moisture values (Figure 3.13). Mean values overlapped on a number of occasions throughout the two field seasons. The soil of the Puccinellia zone was generally drier than the previous two zones. The Salicornia zone soil had the lowest mean moisture values over both seasons, with the exception of early spring, 1990; at this time its moisture content was equal to that of the Puccinellia zone.

In 1989 the general trend in soil moisture over the season involved an initial increase in June followed by a slight decline or steady state (depending on the zone) during July and another increase towards the end of August. This was reflective of the percipitation regime for the season, which began with a dry spring, a short period of rainfall in late June, low rainfall from July to mid-August, concluding with a relatively high amount of precipitation during the end of August. The 1989 trend at site 2 was similar to that of site 1. However, the 1990 trend was quite different. Rather than a gradual increase, the soil moisture content of the site 2 vegetation zones gradually decreased over the field season. This difference may be related to the topography and drainage pattern of the sites.

Trends in mean soil water salinity of site 2 were similar to those in site 1, with a gradual decrease over 1989 season, and a gradual increase over the 1990 season. However, mean salinities were generally higher in the vegetation zones of site 2 than their corresponding zones in site 1. In periods of increased precipitation the mean salinity of the Calamagrostis, Hordeum, and Puccinellia zones overlapped. The mean salinity of the Salicornia zone was consistently higher than the other vegetation zones. One exception to this occurred in April of 1990, when the mean soil water salinity of all four zones was similar.

Site 2

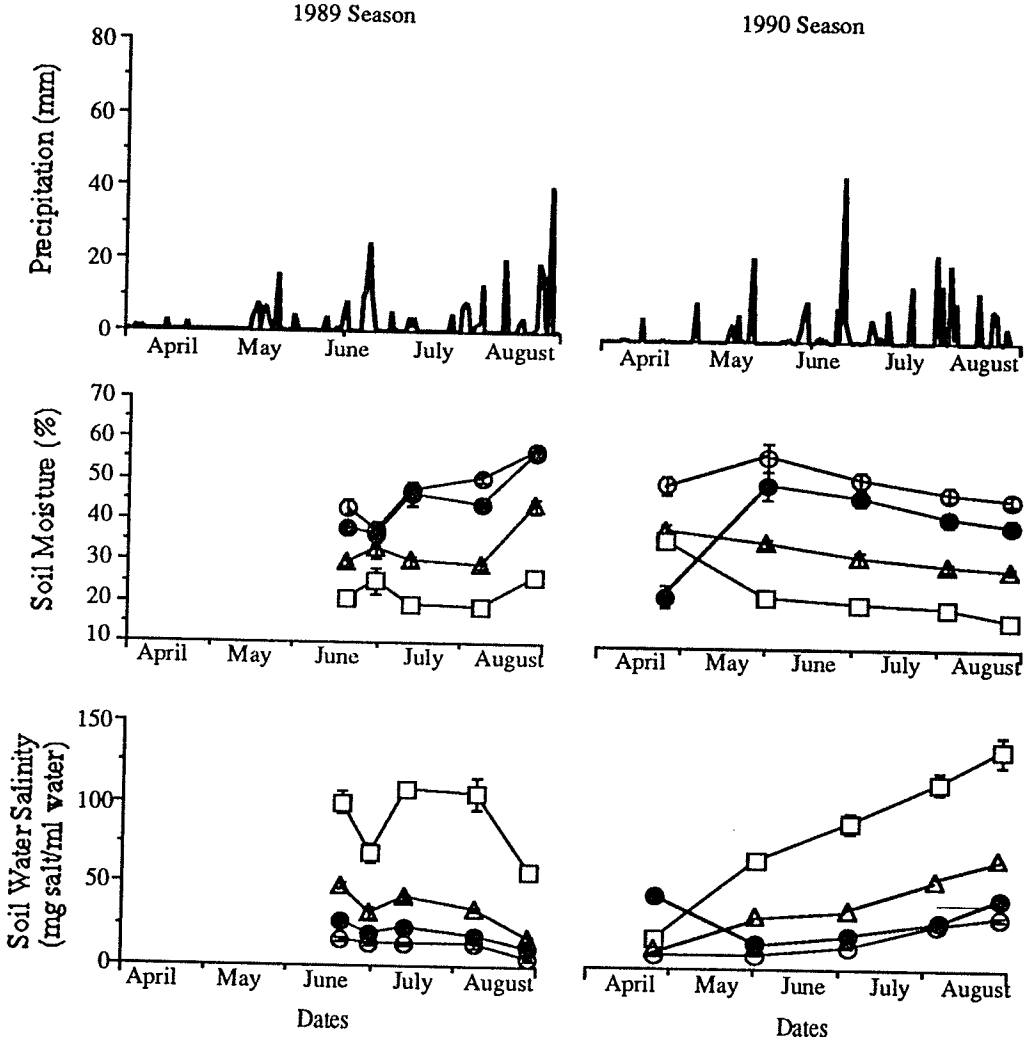


Fig. 3.13 Total daily precipitation regime and soil moisture and soil water salinity of each vegetation zone of site 2 during the 1989 and 1990 field seasons. Vegetation zones are as follows: —○— Calamagrostis, —●— Hordeum/Distichlis, —△— Puccinellia, —□— Salicornia. Values for soil moisture and soil water salinity are mean values (n = 10) ± SE.

Site 3

The mean moisture content and soil water salinity of site 3 soils (Figure 3.14) showed trends similar to site 2. The Salicornia zone was the driest and most saline, while the Hordeum and Calamagrostis zones were significantly wetter and lower in soil water salinity. Mean moisture content fluctuated between 80 and 90% for the Hordeum and Calamagrostis zones, and was essentially the same at each sample date over both seasons. Salinity also differed little between the two zones.

Site 4

Trends in the mean soil moisture and soil water salinity of site 4 were basically the same as in sites 2 and 3. Again, the wettest zones -- Calamagrostis and Distichlis -- were also the least saline. The mean soil moisture content readings were very similar over the 1989 growing season. In 1990, the soil moisture of the Distichlis zone was slightly higher than that of the Calamagrostis zone. In 1989 the mean salinity of the Distichlis zone was higher than Calamagrostis, even though their moisture content was essentially the same. By the end of the 1989 season, the salinity readings for the two zones had decreased and became equilibrated. This corresponded with an increase in soil moisture for both zones.

The soil water salinity of the Distichlis and Calamagrostis zones in 1990 were almost identical over the entire season. All zones showed an increase in mean soil moisture content and a decrease in mean soil water salinity over the 1989 season. This trend was reversed in 1990, with a decrease in moisture and an increase in salinity over the season.

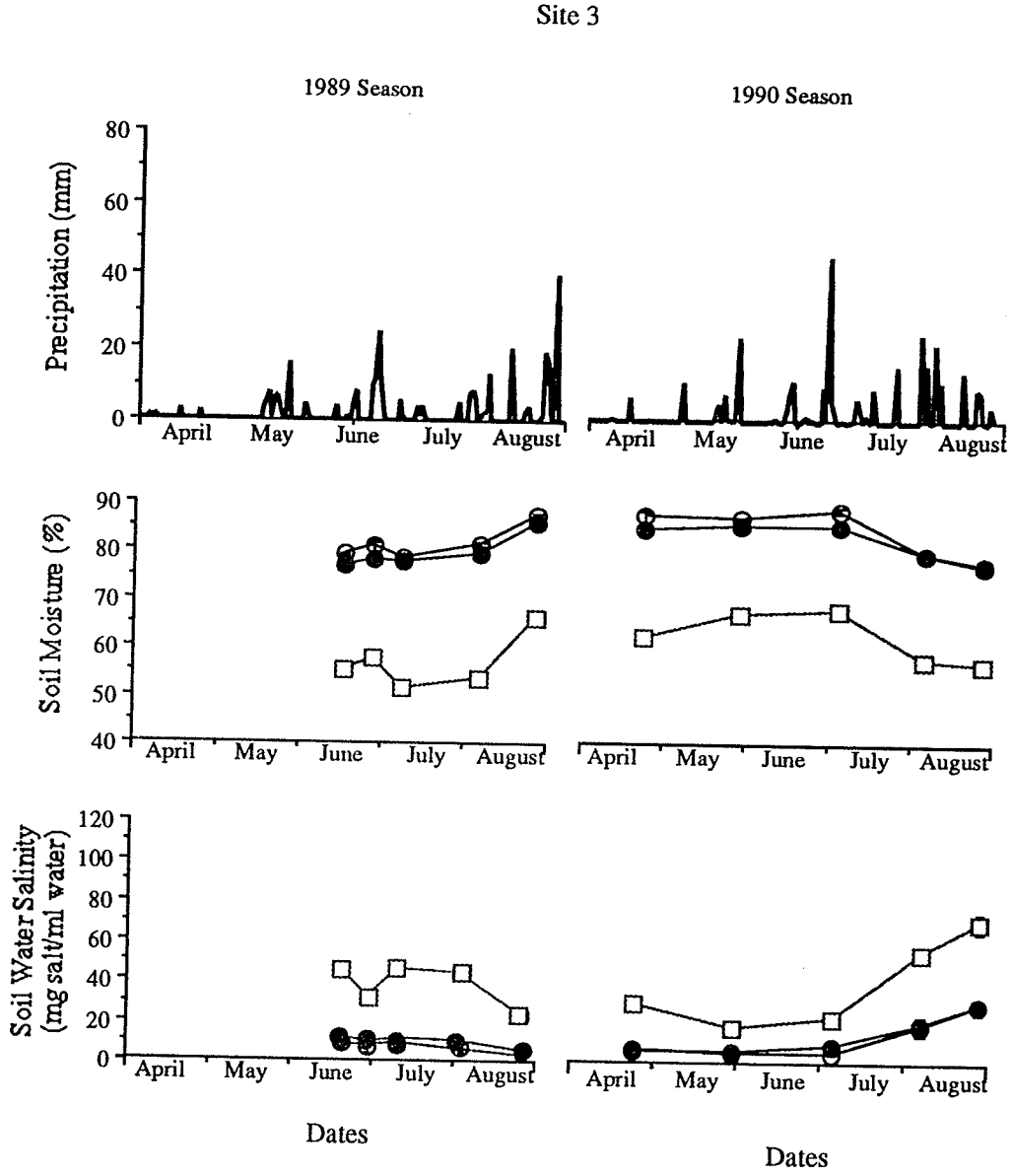


Fig. 3.14 Total daily precipitation regime and soil moisture and soil water salinity of each vegetation zone of site 3 during the 1989 and 1990 field seasons. Vegetation zones are as follows: —○— Calamagrostis, —●— Hordeum, —□— Salicornia. Values for soil moisture and soil water salinity are mean values (n = 6) ± SE.

Site 4

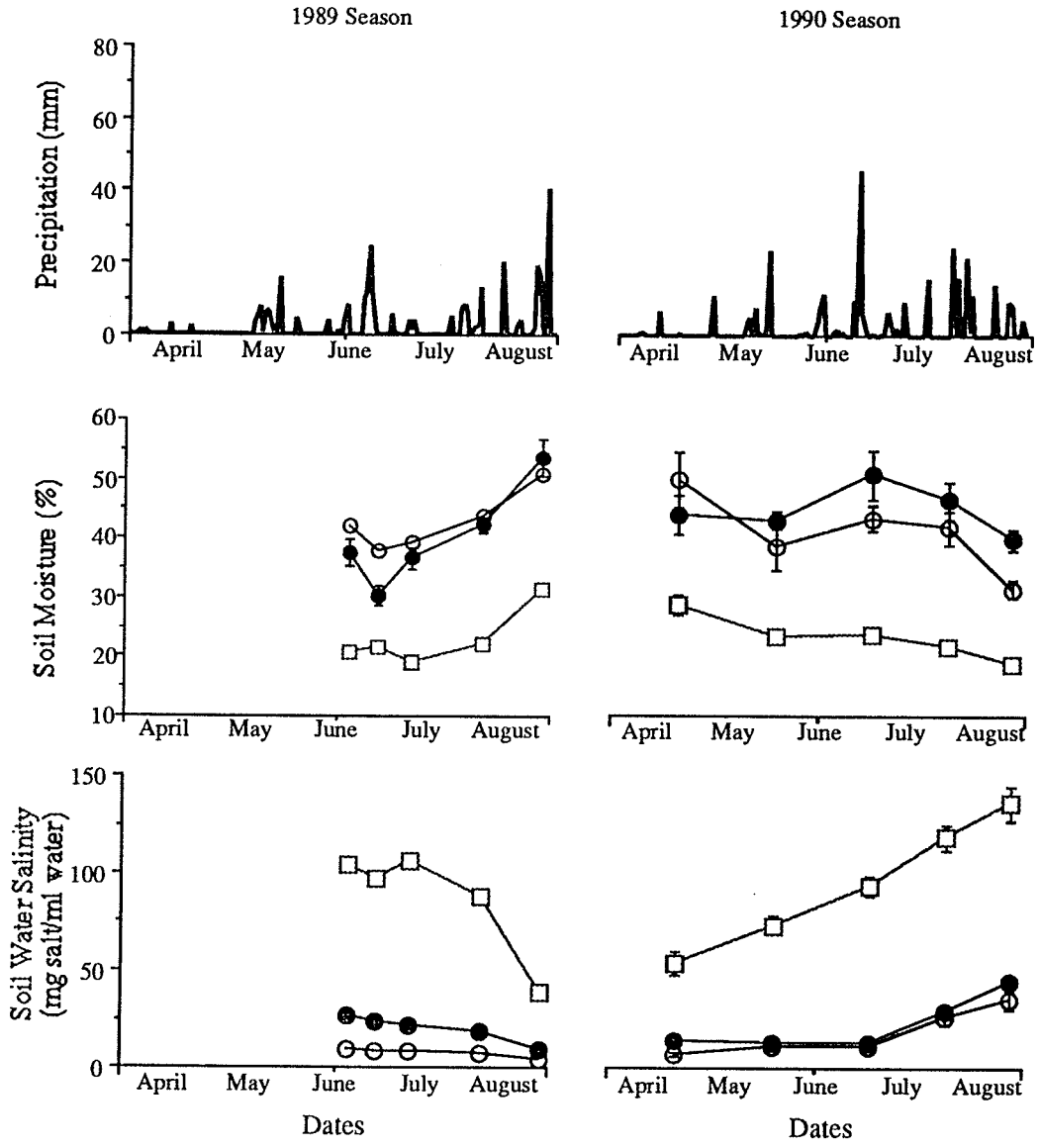


Fig. 3.15 Total daily precipitation regime and soil moisture and soil water salinity of each vegetation zone of site 4 during the 1989 and 1990 field seasons. Vegetation zones are as follows: —○— Calamagrostis, —●— Distichlis, —□— Salicornia. Values for soil moisture and soil water salinity are mean values (n = 6) ± SE.

Summary

In summary, sites 2,3, and 4 showed similar trends of increasing soil moisture and decreasing soil salinity over the 1989 season. In 1990 the trend was reversed, with soil moisture declining, and soil salinity increasing, over the season. Site 1 showed a similar trend for 1989, but in 1990 the soil moisture of site 1 increased rather than decreased. The soil salinity in 1990, however, showed the same decreasing trend observed in the other study sites. Salicornia zone soils at all four sites were the driest and most saline. Generally, the next highest salinity levels were found in the Puccinellia zone soils. The soils of the Calamagrostis, Hordeum, Hordeum/Distichlis, and Distichlis zones were the least saline and often showed similar moisture contents. The mean salinity values of these zone were indistinguishable at a number of sampling dates over the two seasons. Mean moisture and soil water salinity levels varied between corresponding zones from site to site. Overall, sites 1 and 3 were the wettest and least saline of the four sites.

Section 3.3.6 - Soil Depth Cores

Introduction

Soil moisture content and soil water salinity were measured on cores taken at various depths in the soil profile. The results are presented by site in the following series of graphs (Figures 3.16 - 3.19). Each graph incorporates mean soil moisture (top axis), mean soil water salinity (bottom axis), and soil depth (left axis). Two sample periods are presented for each site; 29 and 30 May 1990 (wet period) and 2 July or 22 August 1990 (dry period). Vegetation zones are presented from the top of the Figure to the bottom in order of increasing salinity for each site. Note that the moisture and salinity scales may change from zone to zone and between sites, and that only the depth scale is constant.

Site 1

On both sample dates soil moisture showed a dramatic decrease with depth in all the vegetation zones of site 1. Data from 30 May indicates that a mean moisture content of between 10 and 20 % was maintained in all the zones for a depth of 20 - 60 cm. On 22 August only the Hordeum zone could be fully sampled because of increased compactness of the soil with drying conditions. However, it appears that the same 10 - 20 % soil moisture level was maintained. This happened even though the mean surface (0 - 10 cm) moisture content differed between zones and sample dates.

The increases in moisture in the Calamagrostis zone at a depth of 50 - 60 cm in May, and in the Puccinellia zone at a depth of 30 - 40 cm in August, are difficult to explain. They may be due to sampling error, or localized pockets of moisture in the underlying clay.

In the May samples, the mean soil water salinity gradient was basically the inverse of the soil moisture depth gradient. However, with the exception of the Salicornia zone, the salinity continued to increase even though the soil moisture stayed the same. In Salicornia, the salinity increased slightly from 0 - 30 cm in depth, and then remained essentially the same. In August the surface (0 - 10 cm) salinities of the Salicornia and Puccinellia zones varied considerably from those of the previous sample date, while the Hordeum zones surface salinity appeared to decrease. That of the Calamagrostis zone remained virtually unchanged from the previous date. The Calamagrostis and Hordeum zones showed a distinct increase in soil water salinity with depth, while the Puccinellia zone remained the same. In the Salicornia zone, there was a decrease with depth towards the levels recorded in May.

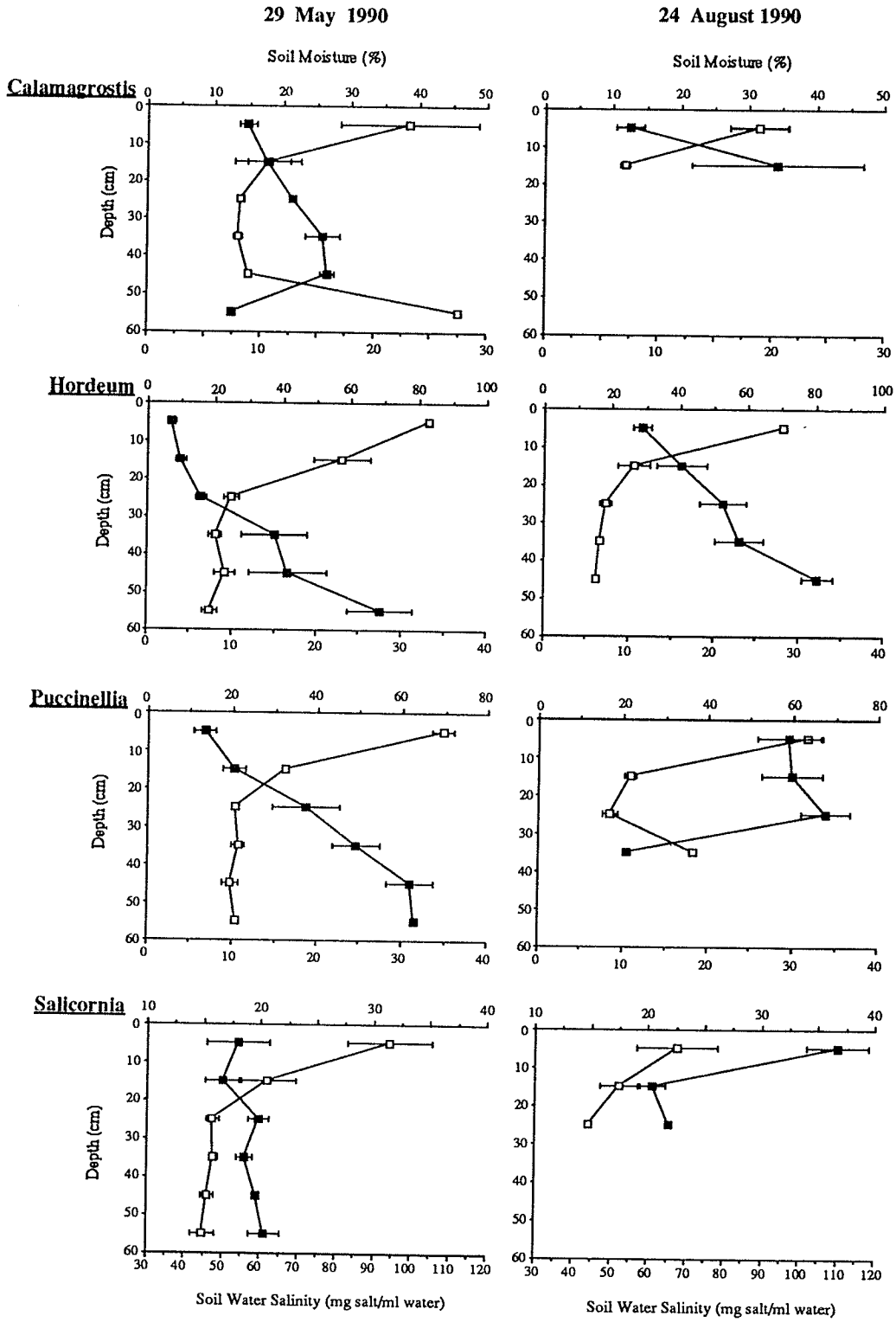


Fig. 3.16 Changes in soil moisture (—□—) and soil water salinity (—■—) with soil depth in each vegetation zone of site 1. Note results are presented for two dates: 29 May (wet period) and 24 August (dry period). Values are means ± SE. n = 3.

Site 2

As in site 1, the mean soil moisture content in site 2 decreased with depth during the May sampling period (Figure 3.17) but, the decrease was not as substantial. The moisture levels remained around the 20 - 25 % level from a depth of 10 - 60 cm in the Calamagrostis, Hordeum/Distichlis, and Puccinellia zones. This occurred despite the fact that all three zones had different levels of soil moisture at the surface. The soil moisture of the Salicornia zone decreased from 20 % to fluctuate around 15 % . Salinity increased gradually with depth in the Calamagrostis and Hordeum/Distichlis zones to a level of 30 mg salt/ml water. The Puccinellia zone also showed an increase in soil water salinity with depth. However, once a depth of 20 - 30 cm was reached, the mean salinity levelled at between 35 and 42 mg/ml for the rest of the profile. Mean soil water salinity in the Salicornia zone decreased in May from a surface reading of 62 mg salt/ml water to 40 - 50 mg for depths 20 - 60 cm.

In August, the zones of site 2 differed from each other in levels of moisture in their surface soils. Also, the mean soil moisture content of the surface soil of each zone had dropped about 10 % from the May sample date. At a depth of 10 - 20 cm the moisture levels in the Calamagrostis, Puccinellia, and Hordeum/Distichlis zones had decreased to approximately 15 - 20 %. This level of moisture was maintained throughout the rest of the soil profile in the Hordeum/Distichlis and Puccinellia zones to a depth of 50 - 60 cm and 40 - 50 cm respectively. Sampling in the Calamagrostis zone was only possible to a depth of 20 - 30 cm. The mean soil moisture content in the Salicornia zone fluctuated between 15 - 19 % to a depth of 40 cm. Further depth sampling was not possible due to impermeability of the soil.

Mean soil water salinity at the soil surface (0 - 10 cm) also varied between zones, and had increased from the previous sampling date. Soil water salinity in the Calamagrostis zone dropped from 50 mg salt/ml water at the surface to 40 mg between 10 - 30 cm in depth. The Hordeum/Distichlis zone's salinity increased from around 25 mg/ml

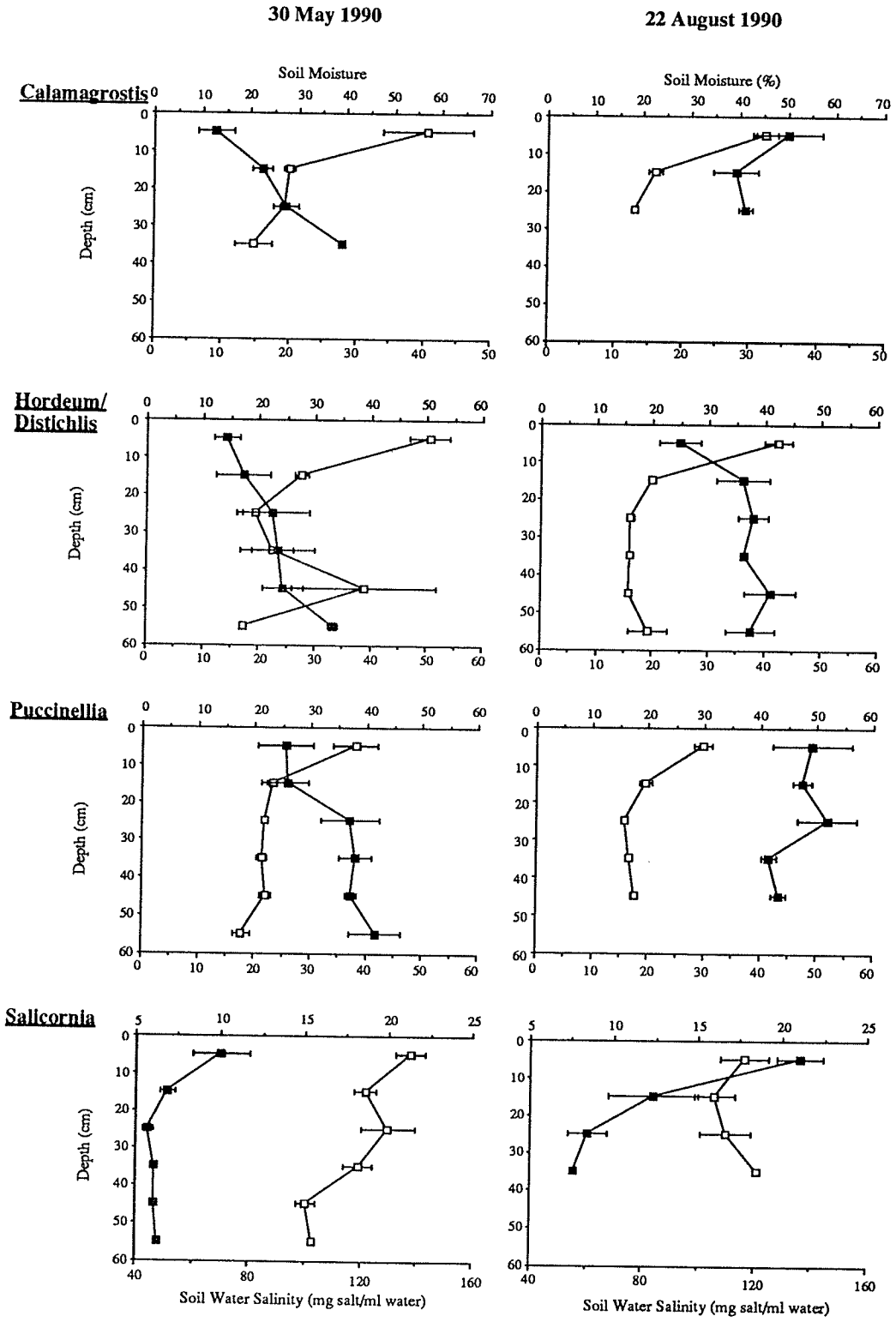


Fig. 3.17 Changes in soil moisture (—□—) and soil water salinity (—■—) with soil depth in each vegetation zone of site 2. Note results are presented for two dates: 30 May (wet period) and 22 August (dry period). Values are means ± SE. n = 3.

at the surface to level-off at between 35 and 40 mg/ml from 10 - 60 cm in depth. The Puccinellia zone's salinity remained fairly level, fluctuating between 40 and 50 mg/ml as depth increased. The Salicornia zone experienced a sharp decline in mean salinity from a high exceeding 130 mg/ml at the surface, to a low of about 55 mg at a depth of 30 -40 cm.

Site 3

The general trend of decreasing soil moisture and increasing soil water salinity with soil depth was repeated on both sampling dates in site 3 (Figure 3.18). In May, soil moisture in the Calamagrostis zone remained above 80 % from 0 - 40 cm, after which it declined sharply to about 15 % at a depth of 50 - 60 cm. Mean soil moisture in the Hordeum zone remained above 80 % to a depth of 10 - 20 cm. It then decreased to 20 % at a depth of 30 - 40 cm and remained at that level to 50 - 60 cm. The Salicornia zone experienced a steady decrease in mean soil moisture from a high of 65 % at the surface, to a low of about 15 % at 40 - 50 cm in depth. Soil water salinity increased steadily down the soil profile in the Calamagrostis zone from 5 mg/ml to 17 mg/ml. The soil of the Hordeum zone experienced a more rapid increase in salinity, and tended to level-off at 17 - 22 mg/ml at 30 - 60 cm in depth. The Salicornia zone recorded an initial increase in mean salinity between 0 - 20 cm in depth. This was followed by a gradual decrease to about 22 mg/ml at a depth of 40 - 50 cm.

The general trends observed in the May sampling period were repeated on 3 July, when the moisture content of the surface soil of the three zones had not changed from the previous sample date. The surface soil moisture content for the Calamagrostis and Hordeum zones remained above 80 %, while that of the Salicornia zone hovered around 65 - 70 %. As depth increased, the Calamagrostis soil moisture content dropped to 20 % at 50 - 60 cm. The Hordeum zone also experienced decreased moisture with depth. However, rather than a rapid decline to 20 %, as in May, the moisture content in July remained above

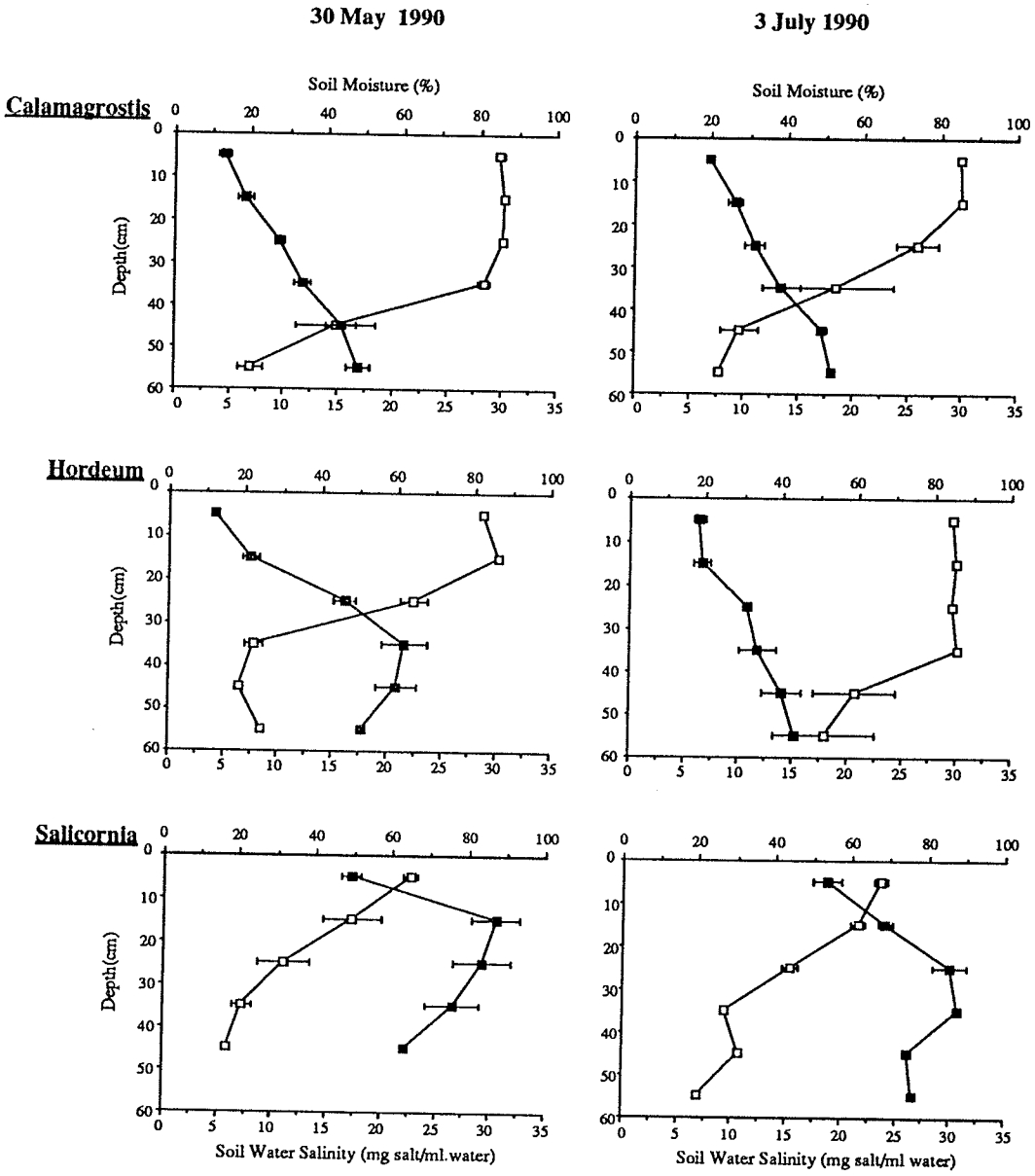


Fig. 3.18 Changes in soil moisture (—□—) and soil water salinity (—■—) with soil depth in each vegetation zone of site 3. Note results are presented for two dates: 30 May (wet period) and 3 July (dry period). Values are means ± SE. n = 3.

80 % from 0 - 40 cm, and then decreased to 50 % at 50 - 60 cm. The Salicornia zone showed a steady decline in moisture content to a low of 15 % at a depth of 50 - 60 cm.

While the mean soil water salinity at the surface increased in the Calamagrostis and Hordeum zones over that of the previous sampling date, the surface salinity of the Salicornia zone remained unchanged. The Calamagrostis and Hordeum zones experienced a gradual increase in salinity from around 7 - 8 mg salt/ml water to 15 - 17 mg/ml at a depth of 50 - 60 cm. The salinity in the Salicornia zone had an initial increase to over 30 mg/ml between 20 and 40 cm, followed by a decrease to 27 mg/ml at a depth of 50 - 60 cm.

Site 4

Site 4 was the most difficult site to sample for depth core gradients because of the highly compacted nature of the underlying clay. It was not possible to obtain deep cores from the Salicornia and Calamagrostis zones. However, the soil of the Distichlis zone was less dense, and allowed for deeper penetration of the soil corer. In May, the Distichlis zone experienced a decrease in soil moisture content from about 44 % at the surface to 25 % at a depth of 10 - 20 cm (Figure 3.19). The moisture content then rose slightly to fluctuate around the 30 % mark for 20 - 50 cm. Mean salinity in May increased from 14 mg/ml to about 20 mg/ml at a depth of 10 - 20 cm, and then fluctuated between 17 and 20 mg salt/ml water for the remaining 30 cm of the profile.

July 2 sampling showed that the moisture content of the surface soil in the Distichlis zone remained unchanged from the 29 May sampling. However, the soil water salinity concentration had risen by about 10 mg/ml. The soil moisture content decreased with depth to 17 % at a depth of 30 - 40 cm. The salinity increased slightly from 31 mg/ml at the surface to 36 mg/ml over the same depth.

Section 3.4 - Discussion

Section 3.4.1 - Soil Gradients and Trends in Sites and Vegetation Zones

The soil analysis results indicated that the sites had a number of soil factor gradients in common. In general, soil bulk density increased with increasing soil salinity. The soils of the outer vegetation zones (i.e. Calamagrostis, Hordeum, and Distichlis) tend to contain more organic matter and less sand, silt, and clay than the inner zones (i.e. Puccinellia and Salicornia), and are therefore less dense. Ungar (1970), in a study of saline sites in South Dakota, noted a gradient of increasing soil organic matter from the salt pan outward to the less saline vegetation zones, with maximum soil organic matter content in the Hordeum/Distichlis zone. This was similar to my findings. However, organic values exceeding 50 % were not uncommon in my study sites, whereas the maximum soil organic matter content recorded by Ungar was 14.7 %. Greater productivity in inland boreal saline sites, along with the persistence of organic matter in the soil (especially in site 3) may account for the higher organic content readings at my sites.

Gradients in soil pH were not as well defined as those of density and organic matter. No gradient in pH was readily apparent in sites 1 and 2, while results from sites 3 and 4 indicated a gradient of increasing pH from the Calamagrostis zone towards the Salicornia zone. Dodd *et al.* (1964) and Ungar (1970) assessed soil pH at a number of inland saline sites in Saskatchewan and South Dakota respectively. Dawe & White (1986) investigated soil pH at a coastal marsh in British Columbia. All three studies found comparable gradients of decreasing pH from the Salicornia zone outward to the peripheral vegetation zones. Soil pH is related to organic matter (Brady 1974), with more acidic soil having a higher organic matter content .

Mean soil salinity (mg salt/ml soil) showed a general gradient of increase sequentially from the Calamagrostis to the Hordeum, Hordeum/Distichlis, Distichlis,

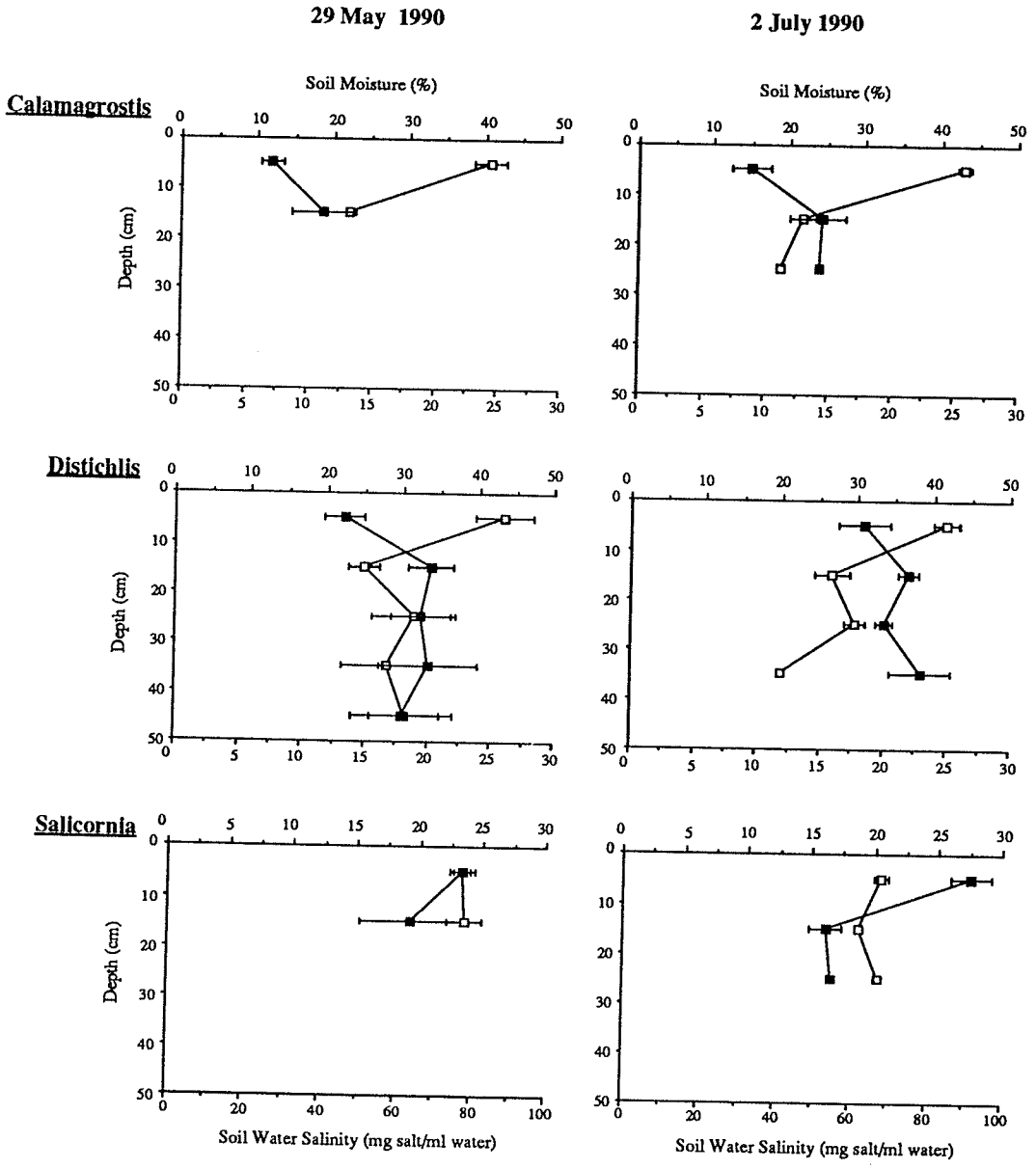


Fig. 3.19 Changes in soil moisture (—□—) and soil water salinity (—■—) with soil depth in each vegetation zone of site 4. Note results are presented for two dates: 29 May (wet period) and 2 July (dry period). Values are means ± SE. n = 3.

Puccinellia, and the Salicornia zone. This gradient has been reported in a number of studies on inland saline habitats in North America, and is apparent regardless of the ionic composition of the soil (Dodd *et al.* 1964; Ungar 1966; Ungar 1970; Ungar 1974(a); McMahon & Ungar 1978; Ungar *et al.* 1979; and McGraw & Ungar 1981). More detailed comparison of the salinity values from my results with those of past studies was difficult due to differences in the methods of determination and the units employed.

Gradients in soil nutrients were not as distinct as those of salinity. Nitrogen was highest in the low salinity zones, which may reflect a higher level of microbial activity. Phosphorus showed a gradient of decreasing availability with increasing salinity, and corresponding increases in pH likely played a part in this relationship (Brady 1974). Potassium content often surpassed the maximum level of detection, and exceeded the requirement necessary for plant growth (Burchill 1990). Levels of potassium were consistently lowest in the Salicornia zone of each site.

Comparison of corresponding vegetation zones between sites revealed that although the species composition of each zone was the same or very similar, soil factors often varied. This indicates that each dominant species is able to grow under a wide range of edaphic factors. It also suggests that a species' distribution within a specific site, although strongly influenced by the soil characteristics, is also governed by the presence of other species.

Section 3.4.2 - Seasonal Fluctuations and Extremes in Moisture and Salinity

Trends in soil moisture and soil water salinity over the field season were similar between sites. In general, increased soil moisture content in the dilution of the salts in the soil solution, and thus lower salinity levels. The reverse was true during periods of low moisture content. This fluctuation in moisture and salinity over the season is largely dependent on precipitation. The data show that dramatic differences in salinity and moisture can occur during the growing season, as well as from one season to the next.

This dynamic characteristic of saline soils has been readily observed in other studies (e.g. McMahon & Ungar 1978; Ungar *et al.* 1979; and McGraw & Ungar 1981). Soil moisture is dependent on a number of variables, and one-time sampling of soil often yields little useful information. However, periodic monitoring of soil moisture, and interpretation in relation to climatic conditions, can prove helpful in saline habitat research. McMahon & Ungar (1978) monitored the soil moisture of four vegetation zones over a single growing season and found that soil salinity and vegetation growth fluctuated with changes in soil moisture, which was in turn influenced by precipitation and temperature. Seasonal variation in soil salinity with soil moisture has also been documented by Beadle *et al.* (1957), Waisel (1972), Sharma (1973), and Ungar (1974(b)).

The use of soil water salinity as a measure of salt concentration in saline sites is not common. As mentioned earlier, most studies tend to measure salinity on the basis of the conductivity of a soil saturation extract or soil paste. The conductivity readings are then converted to give salt concentrations based on the mass of dried soil. Units such as milliequivalents, percentages, parts per million, and grams per kilogram have been used (Burchill 1991). Soil water salinity has been used in some laboratory based experiments (Bradley & Morris, 1991; Ewing *et al.* 1988; Kenkel *et al.* 1991), as well in the field (Haines & Dunn 1985). It has generally been expressed in grams of salt per litre of water. The soil water salinities determined from Salicornia zone soils at my study sites were comparable with those reported by Haines & Dunn (1985) for similar vegetation in a coastal salt marsh.

The results have shown that salt concentrations in the soil solution fluctuated with soil moisture. During periods of low soil moisture the salt concentration in each zone usually increased and the salinity levels between zones became more widely separated and rarely overlapped. During periods of heavy rainfall and low temperatures the soil water salinity levels of the zones tended to overlap or became equal. If either of these situations were maintained over a long enough period, it could cause a shift in the vegetation zone

boundaries towards, or away from, the central salt pan. However, as aerial photographs of the study sites failed to reveal any movement of vegetation zones over the last 64 years, it is likely that such vegetation changes would require a very prolonged period of non-normal precipitation and temperature regimes.

Mean values of the data (± standard error) were used to illustrate the relationship between soil salinity and soil moisture. However, as pointed out by Burchill (1991), the actual extremes in salinity (and perhaps moisture) are probably more important from the 'plant's point of view' than mean levels. Variability in salinity exists within each vegetation zone and between corresponding zones of different sites. In addition, the soil water salinity is constantly fluctuating with the external environment, and the vegetation must have the ability to rapidly adapt its physiology to the extremes of these fluctuations in order to survive. Figures 3.20 - 3.23 present the ranges in soil moisture and soil water salinity for the vegetation zones of each site over the 1989 and 1990 growing seasons. Table 3.10 combines the moisture and salinity data collected over both seasons and shows the extremes, means, and median values for each vegetation zone.

Table 3.10 Summary of overall soil moisture and soil water salinity data for each vegetation zone. Data were compiled from all sites over both seasons.

Vegetation Zone	Soil Moisture (%)			
	Spread	Mean (± SE)	Median	n
Calamagrostis	18.3 - 91.8	51.2 ±1.0	47.1	320
Hordeum	50.0 - 88.7	77.4 ±0.5	77.8	160
Hordeum/Distichlis	20.0 - 68.2	44.0 ±1.1	44.1	100
Distichlis	26.6 - 71.5	43.0 ±1.2	41.6	60
Puccinellia	18.4 - 82.5	48.6 ±1.3	44.4	200
Salicornia	15.5 - 73.0	31.2 ±0.8	24.6	320
Vegetation Zone	Soil Water Salinity (mg/ml)			
	Spread	Mean (± SE)	Median	n
Calamagrostis	1.4 - 49.4	11.3 ±0.5	8.6	320
Hordeum	2.3 - 35.1	10.5 ±0.5	10.1	160
Hordeum/Distichlis	5.8 - 51	23.9 ±1.1	21.4	100
Distichlis	6.1 - 52.4	21.4 ±1.4	18.9	60
Puccinellia	3.6 - 70.8	26.6 ±1.1	24.5	200
Salicornia	11.4 - 199.0	71.9 ±2.0	68.9	320

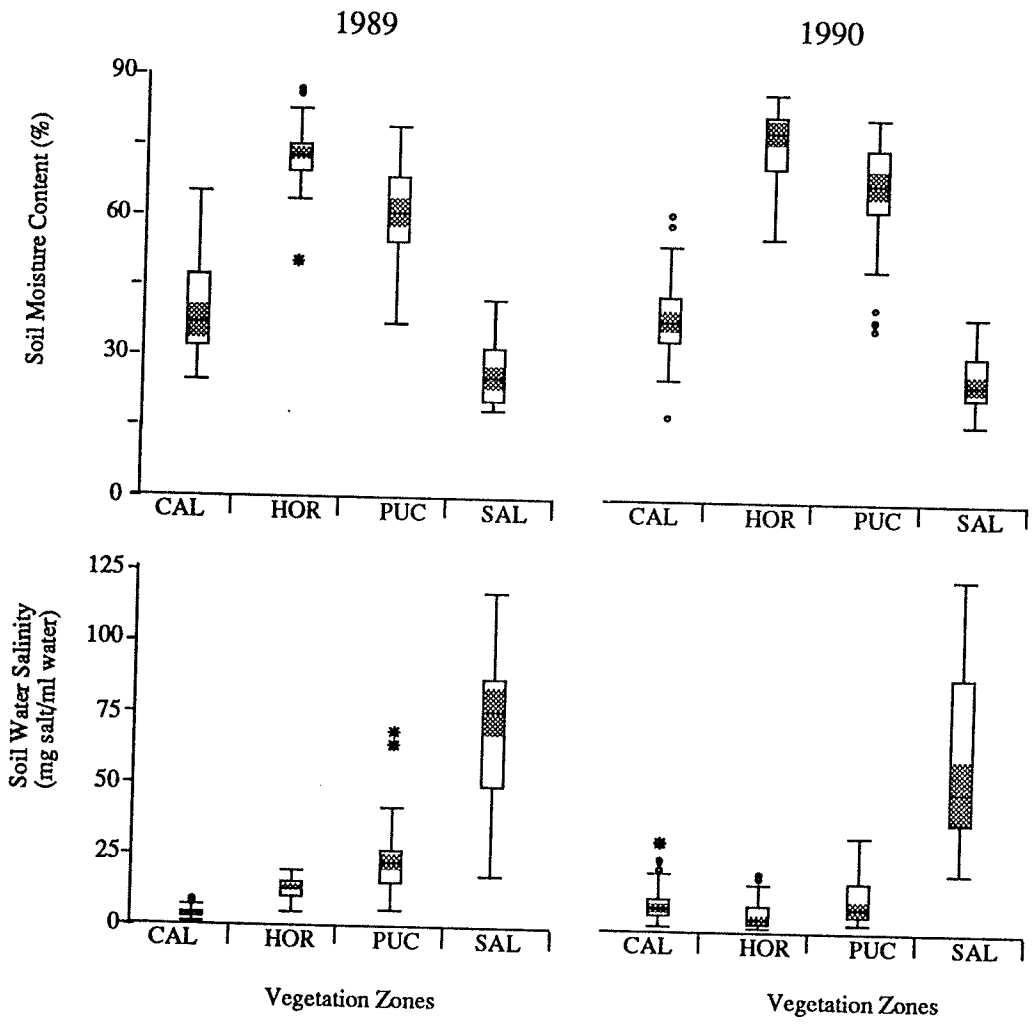


Fig. 3.20 Range of soil moisture and soil water salinity in vegetation zones of site 1 for each field season. n = 50. Vegetation zones are Calamagrostis (CAL), Hordeum (HOR), Puccinellia (PUC), and Salicornia (SAL).

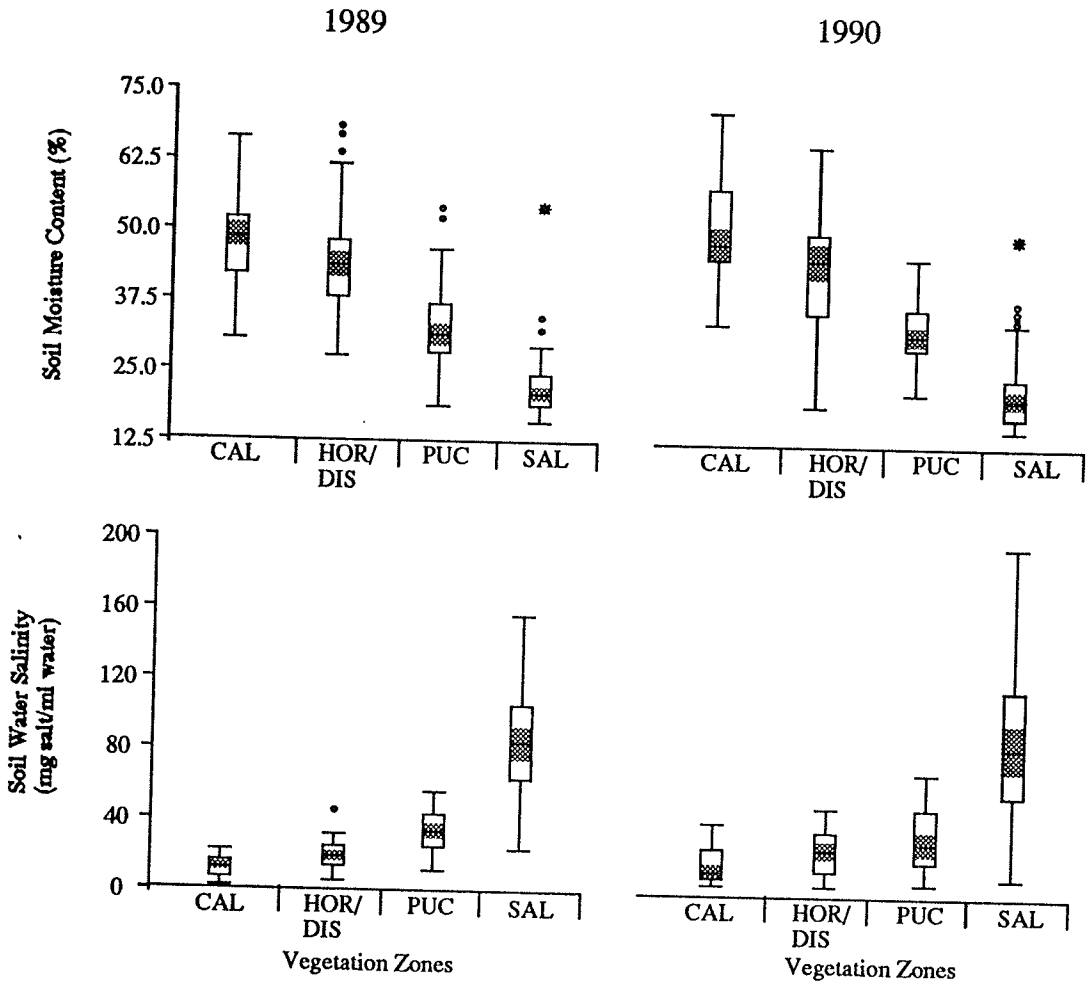


Fig. 3.21 Range of soil moisture and soil water salinity in vegetation zones of site 2 for each field season. n = 50. Vegetation zones are Calamagrostis (CAL), Hordeum/Distichlis (HOR/DIS), Puccinellia (PUC), Salicornia (SAL).

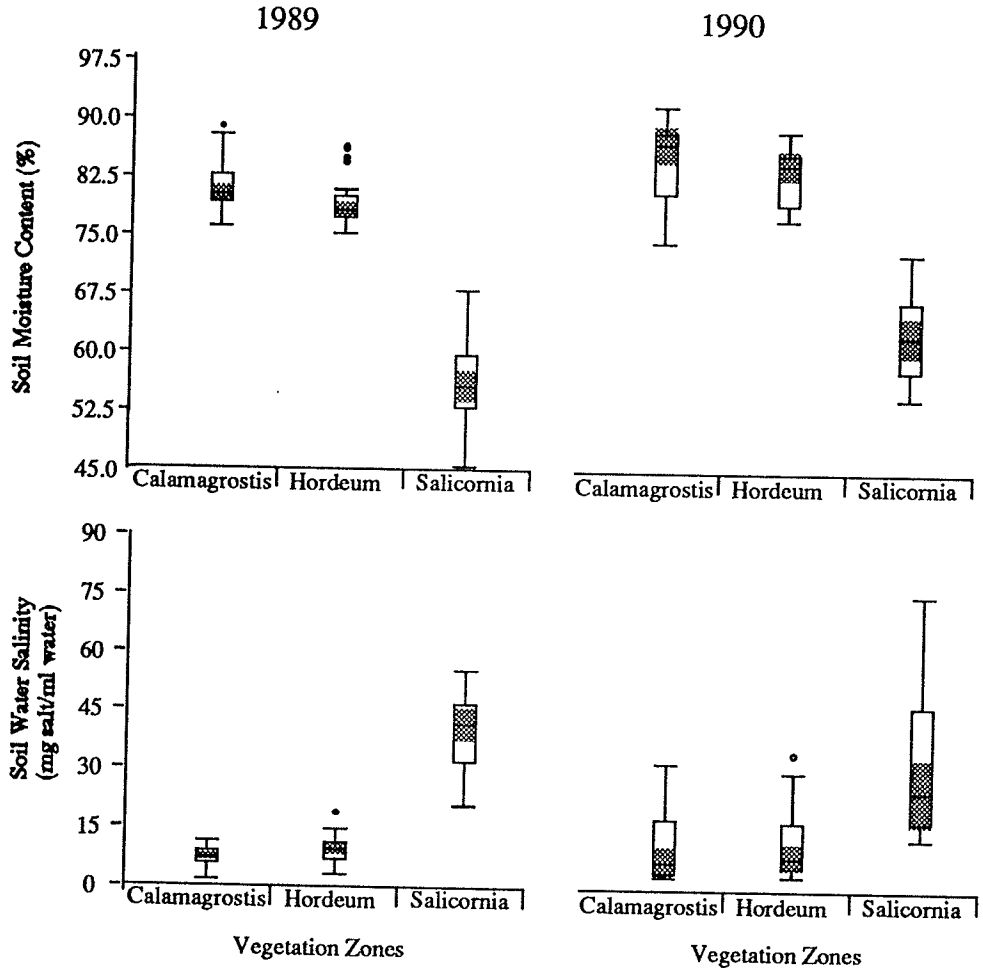


Fig. 3.22 Range of soil moisture and soil water salinity in vegetation zones of site 3 for each field season. n = 30.

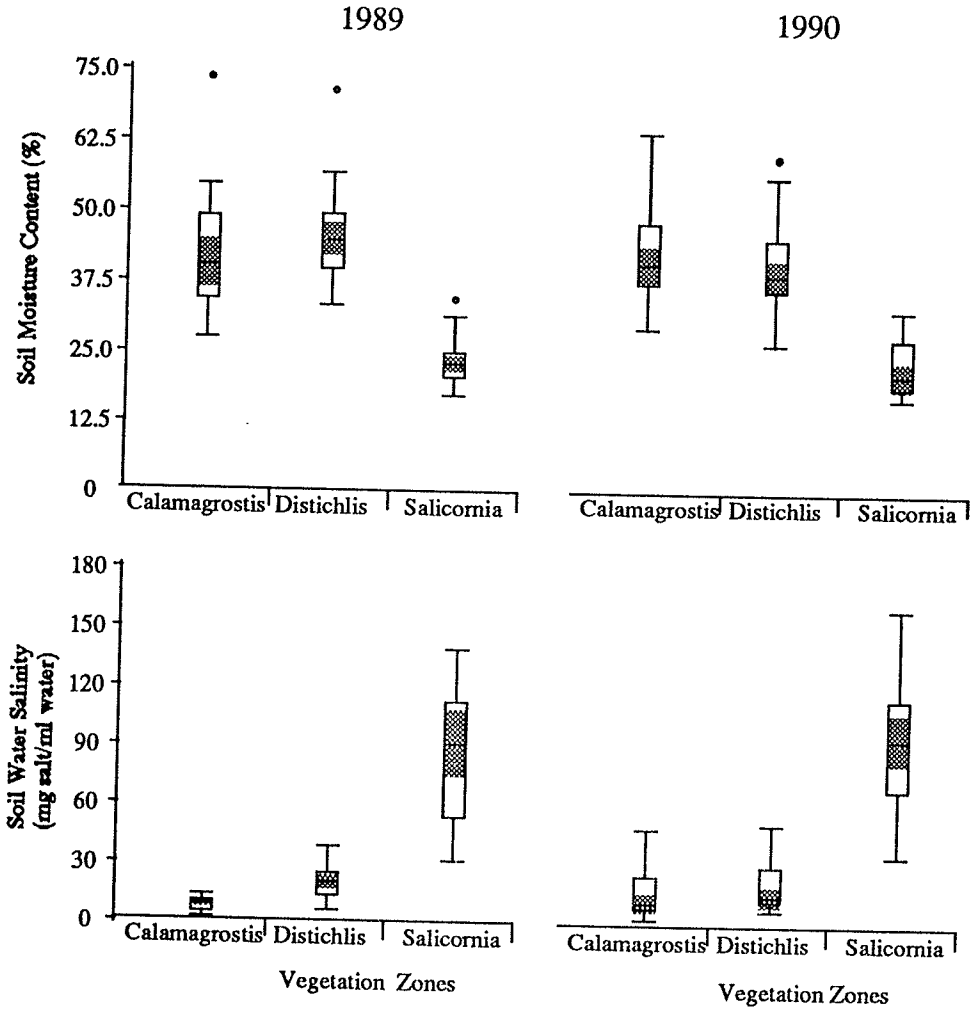


Fig. 3.23 Range of soil moisture and soil water salinity in vegetation zones of site 4 for each field season. n = 30.

Section 3.4.3 - Soil Depth Gradients

Visual inspection of the soil depth cores indicated that the amount of organic matter decreased with depth, while the silt-clay particles increased. This resulted in a gradient of increasing soil density with increasing depth in the soil profile. Increasing soil density is related to compaction of soil particles and greater impermeability of the soil. The gradient of increasing soil density with depth differed between vegetation zones and sites. In general, the density gradient reflected a decreasing gradient of soil moisture to a certain depth in all zones. Soil water salinity tended to increase to a certain depth in the low salinity zones and remain the same or decrease in the high salinity Salicornia zone. Similar changes in soil salinity with depth have been reported by Dodd *et al.* (1964) and Ungar (1966). Studies by Flowers (1934) and Bolen (1964) found that salinity of the subsurface soil was often less than that recorded at the surface.

The moisture and soil water salinity gradients often levelled-off at a certain depth in the soil profile. In the Calamagrostis, Hordeum, and Hordeum/Distichlis zones soil moisture tended to level-off at 10 - 20% and soil water salinity at 30 mg/ml. The Distichlis zone soil decreased to a constant moisture content of between 30 - 35 %, and a salinity level of about 20 mg/ml. The Puccinellia zone maintained a moisture content fluctuating around the 20 % mark, and a salinity level of between 30 - 50 mg/ml. The high salinity Salicornia zones showed a decrease in moisture to a level of 10 - 20 %. The concentration at which salinity reached an equilibrium with depth varied between sites. In sites 1 and 2 salinity equilibrated to between 40 - 60 mg/ml, while in site 3 it increased with depth to a plateau of 20 - 30 mg/ml. For all zones, the depth at which this levelling-off occurred varied between vegetation zones and sites, probably because of differences in soil density gradients. Although the surface soil varied considerably between zones, sites, and sampling dates, the depth at which the soil moisture and soil water salinity levelled-off was generally maintained. This suggests that only the top 10 or 20 cm of the soil profile is directly influenced by external environmental factors such as climate, evapotranspiration,

and topography. This may be important in the growth strategies and distribution of halophytic species. Those species that are capable of only shallow root penetration, such as annual members of the Chenopodiaceae, must be able to adapt rapidly to changes in the surface soils. On the other hand, species capable of deeper root penetration, such as long-lived perennials, may be able to by-pass the upper soil profile completely, and establish their root systems at a greater depth, where soil factors are more static.

Chapter 4 - Vegetation Factors

Section 4.1 - Introduction

The interrelationships between soil and vegetation gradients in an inland boreal saline region at Overflow Bay have been discussed in detail by Burchill (1991) and Burchill & Kenkel (1991). However, these authors examined conditions at only two adjacent sites (one of which was site 2 in this study) in the Overflow Bay area; no research has been conducted on the other three sites of my study. My observations of vegetation zone species composition and detailed soil collection and analysis indicated that a number of similarities and differences existed between zones within each site and between corresponding zones of different sites. Investigations into the density, growth rate, phenology, and seed dispersal of dominant species is lacking. This chapter will address these vegetational aspects and relate them to environmental factors.

Section 4.2 - Methods and Analysis

Section 4.2.1 - Vegetation-Soil Gradients

Burchill's study (1991) of two adjacent Overflow Bay sites involved the use of transects to sample soil and vegetation. His results showed a continuous gradient of increasing salinity from the periphery to the central salt pan of each site. Associated with this salinity gradient was a discontinuous vegetation gradient, resulting in zonation of salt tolerant species near the salt pan, and less tolerant species around the periphery.

Figures 2.6 - 2.9 show that the experimental plots in one vegetation zone are spatially separated from those of adjacent zones in each study site. The soil data and species composition of these plots indicated the existence of between zone trends in soil factors and vegetation. However, they failed to conclusively demonstrate that continuous soil gradients and discontinuous vegetation gradients are present at all my study sites.

Furthermore, although each site displayed discrete vegetation zonation, the species composition of corresponding vegetation zones between sites was often not consistent. For example, the Puccinellia zone of sites 1 and 2, although dominated in both cases by *Puccinellia nuttalliana*, had different associated species. In site 1 *Suaeda depressa, Spergularia marina, Triglochin maritima,* and occasionally *Hordeum jubatum*, were associated with *Puccinellia nuttalliana.* However, in site 2, *Suaeda depressa* was the only species generally associated with *Puccinellia nuttalliana* . The width of respective vegetation zones also differed between sites. For example, the Hordeum/Distichlis zone of site 2 is approximately 10 - 20 m in width, while the corresponding Hordeum zone of site 3 is well over 50 m wide. It was hypothesized that these between-site differences in vegetation were probably the consequence, at least in part, of soil and topographic (i.e. drainage) differences between sites. In order to gain some insight into these differences and to be assured that continuous soil and discontinuous vegetation gradients existed, a line transect survey was conducted at each of my study sites.

Transects were laid down across each site perpendicular to the vegetation zones. The transects were positioned to incorporate the area of each zone in which experimental plots had been placed. Transects were aligned parallel with one another, and separated by a distance of 5 m. The length, positioning, and number of transects employed varied between sites. This was reflective of between-site differences in the extent and relative location of vegetation zones (see Figures. 2.6 - 2.9)

Figure 4.1 shows the placement of sampling transects in each study site. In site 1 four parallel transects, each 75 m in length, were established. Each transect extended across the entire site and incorporated the four main vegetation zones. In site 2, four transects, each 70 m in length, were established across the Salicornia, Puccinellia, and Hordeum zones. The portion of the Calamagrostis zone used in site 2 is separated from the other zones. For the Calamagrostis zone three shorter transects, each 25 m in length, were employed.

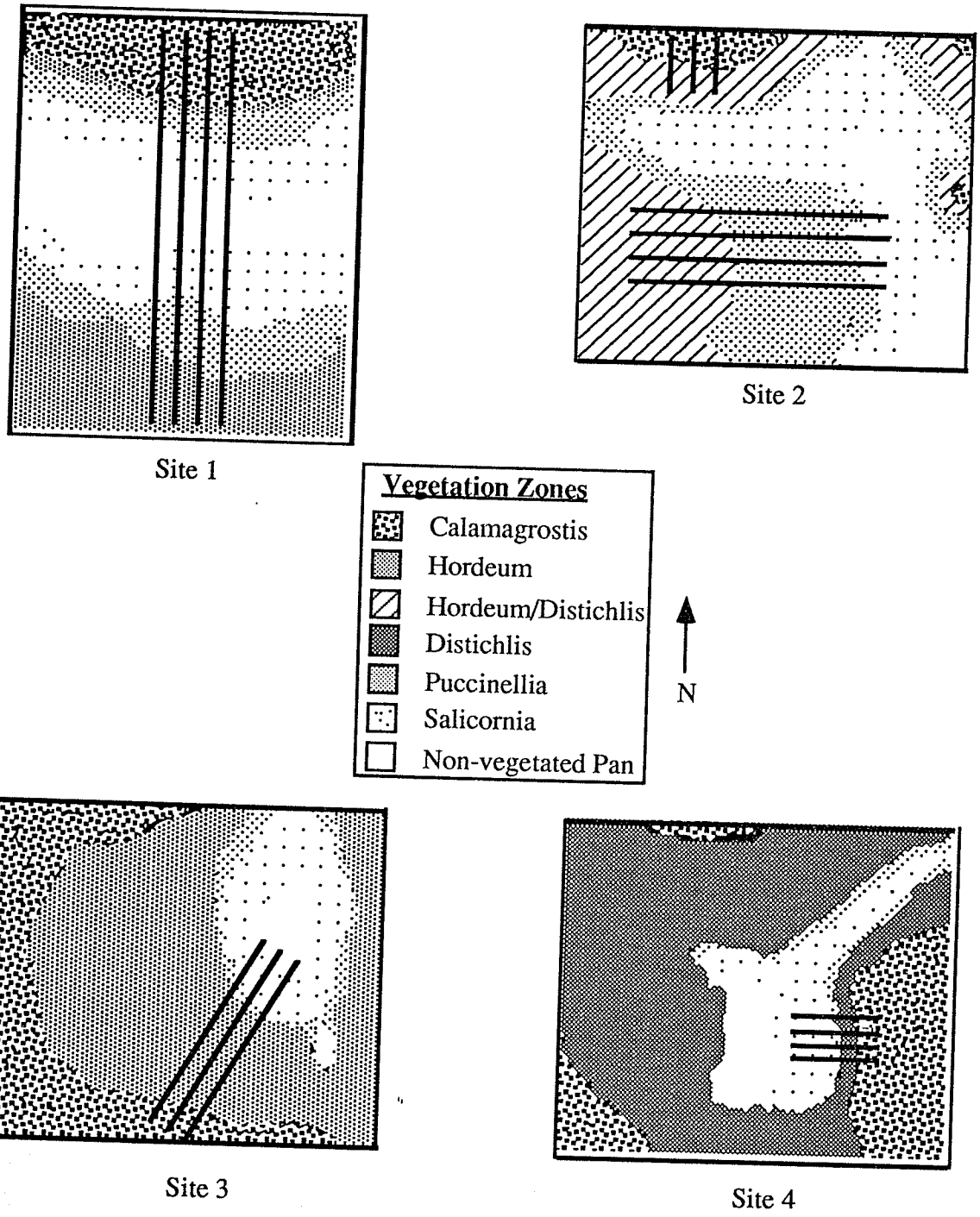


Fig. 4.1 Diagram of each study site showing vegetation zonation and approximate position of transects for vegetation-soil gradient sampling. Scale varies according to site.

Three 100 meter long transects were laid down across the vegetation zones of site 3 . In site 4, four transects, 15 m in length, were established to survey the Salicornia, Distichlis, and Calamagrostis zones. The portion of the Distichlis zone sampled by the transects is relatively narrow, and did not include the area of that zone where the experimental plots were located.

Transect sampling was conducted on 23 April 1990. Elevation data were recorded every 5 m along each transect, and more often when observable changes in elevation were encountered. When a vegetation boundary was encountered elevations were taken at the boundary, and 50 cm on either side of the boundary. The dominant vegetation was noted and a soil core was extracted at each elevation point. Cores were placed into a labelled bag and frozen for transportation back to the lab. Soil cores were analyzed for water content (%) and soil water salinity (mg salt/ml soil water). At site 4 the pH of each transect soil core was also determined.

Section 4.2.2 - Species' Density, Growth, and Phenology

In order to obtain a better understanding of the natural growth and development of the vegetation of the study sites, a phenology survey was conducted over the 1990 growing season. At each sampling date throughout the 1990 season the above-ground biomass of each vegetation zone at each site was randomly sampled using an 8 cm x 8 cm quadrat. All above-ground plant material was removed and transported back to the lab where the phenology, density, and biomass were determined for each species. Ten quadrats were used to sample zones at sites 1, 2, and 3, and five quadrats at site 4. The sampling schedule allowed the monitoring of only general phenological categories including seed germination, vegetative growth, flowering, and seed set.

Section 4.2.3 - Seed Bank Experiments

A simple germination experiment was conducted to determine if the seed banks of the study sites were transient or persistent, and to examine whether the seed bank of each vegetation zone reflected the zones' current species composition. On 23 April, three soil samples, each 2 cm in depth and 10 cm in diameter, were collected randomly from each vegetation zone at each site. The samples were placed in labelled bags and transported back to the lab. In the lab the three samples of each zone were combined and placed into a 0.2 mm sieve. The soil was then washed thoroughly with water to remove salts. The washed soil from each zone was spread evenly over the surface of plastic flats which had been previously filled with approximately 5 cm of sterilized potting soil. Each flat was labelled by zone and site of origin, placed on tables in the greenhouse, and flooded with water to simulate field moisture conditions. The flats were watered regularly to maintain a high soil moisture content, and emerging seedlings were identified to species. The flats were monitored for two months, at which time seedling emergence had ceased.

Section 4.2.4- Data Analysis

Transect data were entered into a computer graphics programme to produce three-dimensional images of the gradients present at the four sites. Mean values were calculated for species' density and biomass data. Density was expressed as the mean number of culms (individuals for non-grasses) per square meter, and biomass as the mean dried biomass (grams) per individual or culm. The phenological data and seed bank experiment results were not quantitative, and therefore were not subject to statistical analysis.

Section 4 3 - Results

Section 4.3.1 - Transect Results

Site 1

Transects for site 1 were oriented in a north-south direction. The graphs of the results (Figure 4.2 - 4.4) show an oblique view in a west-to-east direction across the transected area. The highest surface elevations and soil moisture readings were in the Hordeum zone (Figures 4.2 and 4.3). Soil surface elevations and moisture levels decreased through the Puccinellia zone and into the Salicornia zone and the salt pan, where they remained relatively constant, before rising slightly in the Calamagrostis zone. All the zones sloped in an eastward direction. Surface water flowed down from the Hordeum, Puccinellia, and Calamagrostis zones and into the Salicornia zone and the salt pan. It then drained into a small stream at the eastern edge of the site. Soil water salinity was low in the Hordeum zone and gradually increased through the Puccinellia zone (Figure 4.4). Highest readings were obtained in the Salicornia zone and the salt pan. Salinity showed a number of peaks and troughs through both the Salicornia zone and the salt pan. It decreased toward the Calamagrostis zone, where the lowest salt concentrations were reached.

Site 2

Figures 4.5 - 4.7 present results from transect sampling of the Salicornia, Puccinellia, and Hordeum/Distichlis zones of site 2. Transects were oriented in an east-west direction and the graphs show a view looking northward across the zones. Figures 4.8 - 4.10 present results from the Calamagrostis zone transects. In this case, the transects were laid north-to-south, and the view presented in the graphs is west-to-east.

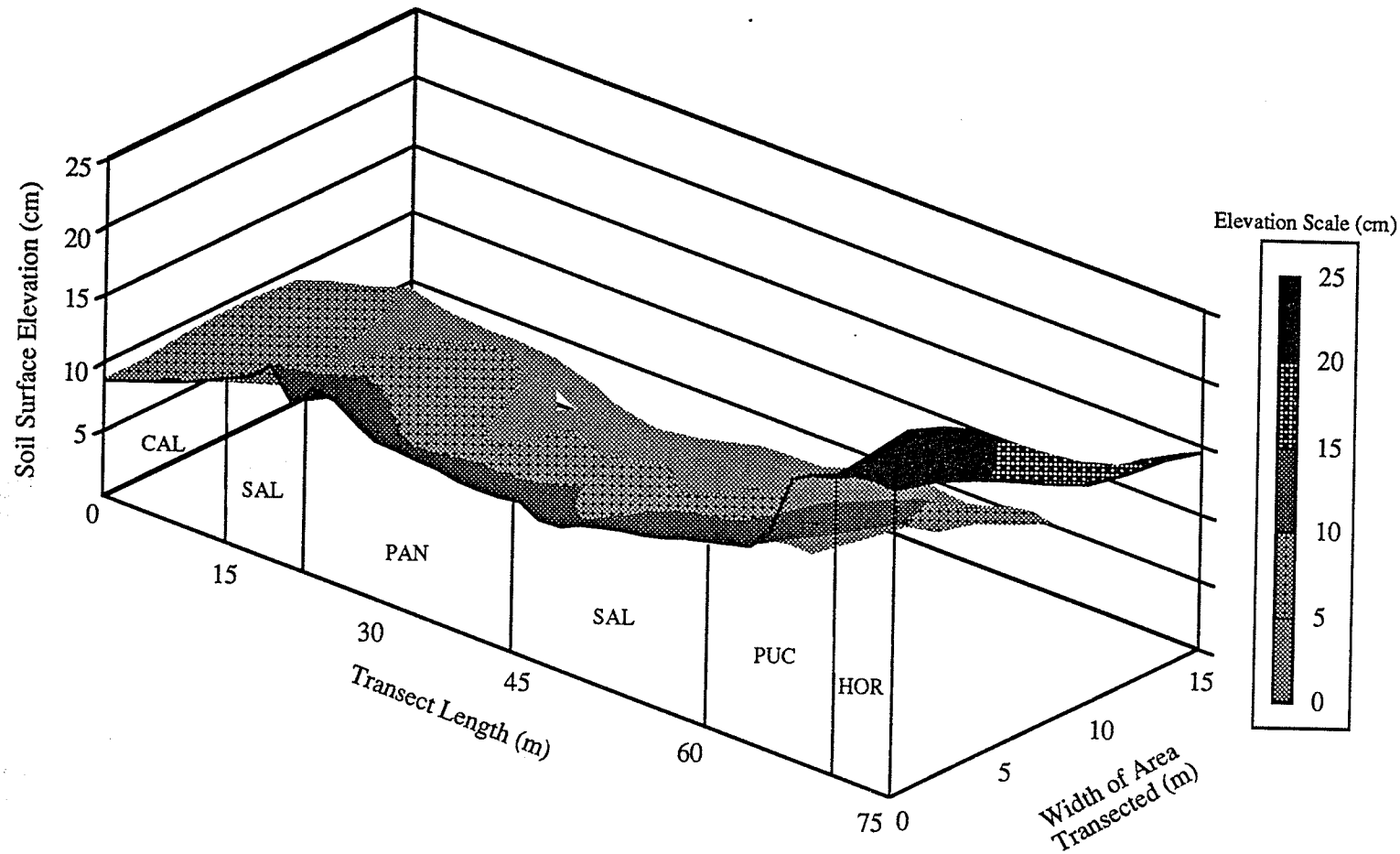


Fig. 4.2 Three dimensional representation of soil surface elevation data obtained from transect sampling of site 1, April 1990. Vegetation zones are: Calamagrostis (CAL), Hordeum (HOR), Puccinellia (PUC), Salicornia (SAL), and the unvegetated salt pan (PAN).

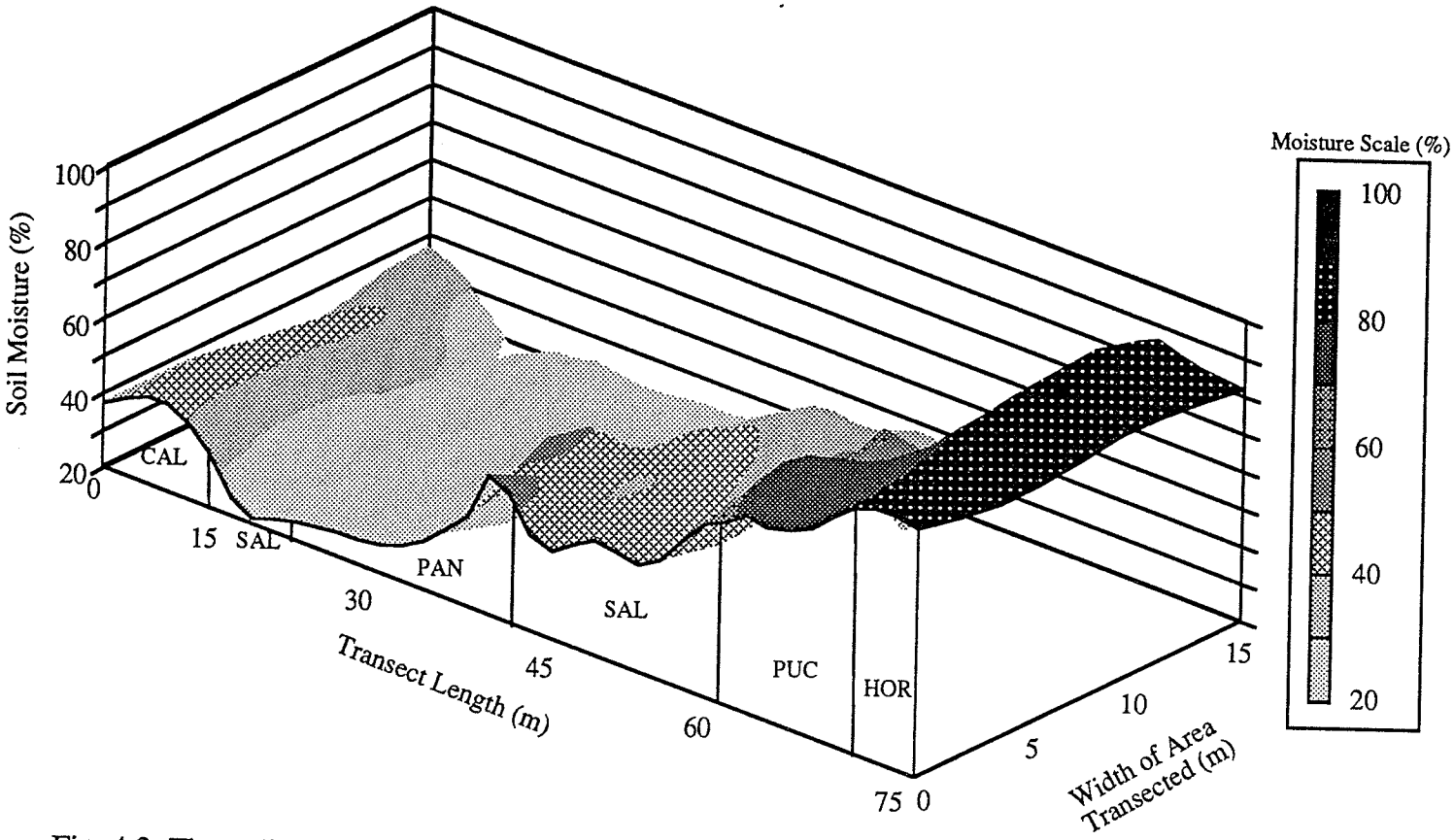


Fig. 4.3 Three dimensional representation of soil moisture data obtained from transect sampling of site 1, April 1990. Vegetation zones are: Calamagrostis (CAL), Hordeum (HOR), Puccinellia (PUC), Salicornia (SAL), and the unvegetated salt pan (PAN).

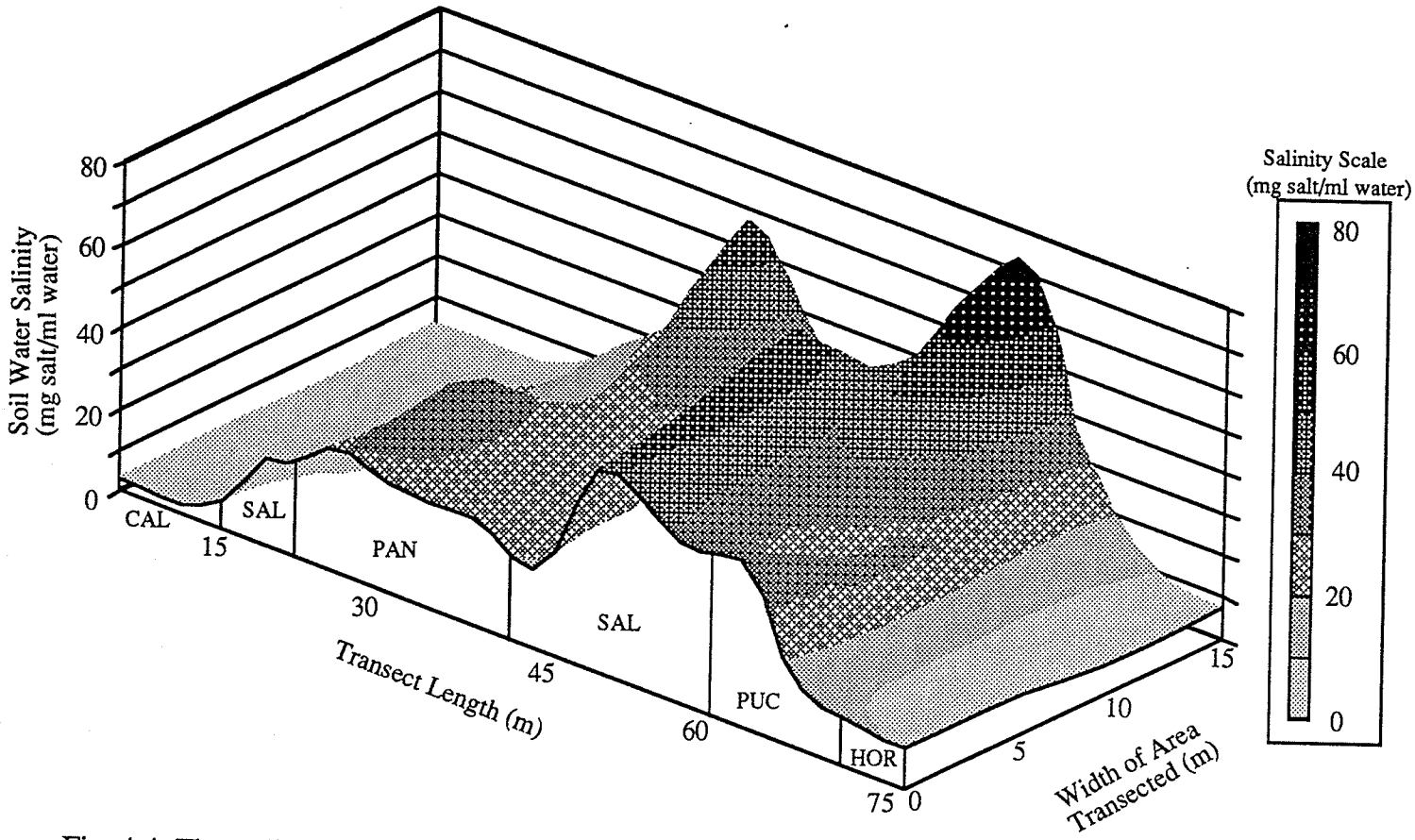


Fig. 4.4 Three dimensional representation of soil water salinity data obtained from transect sampling of site 1, April 1990. Vegetation zones are: Calamagrostis (CAL), Hordeum (HOR), Puccinellia (PUC), Salicornia (SAL), and the unvegetated salt pan (PAN).

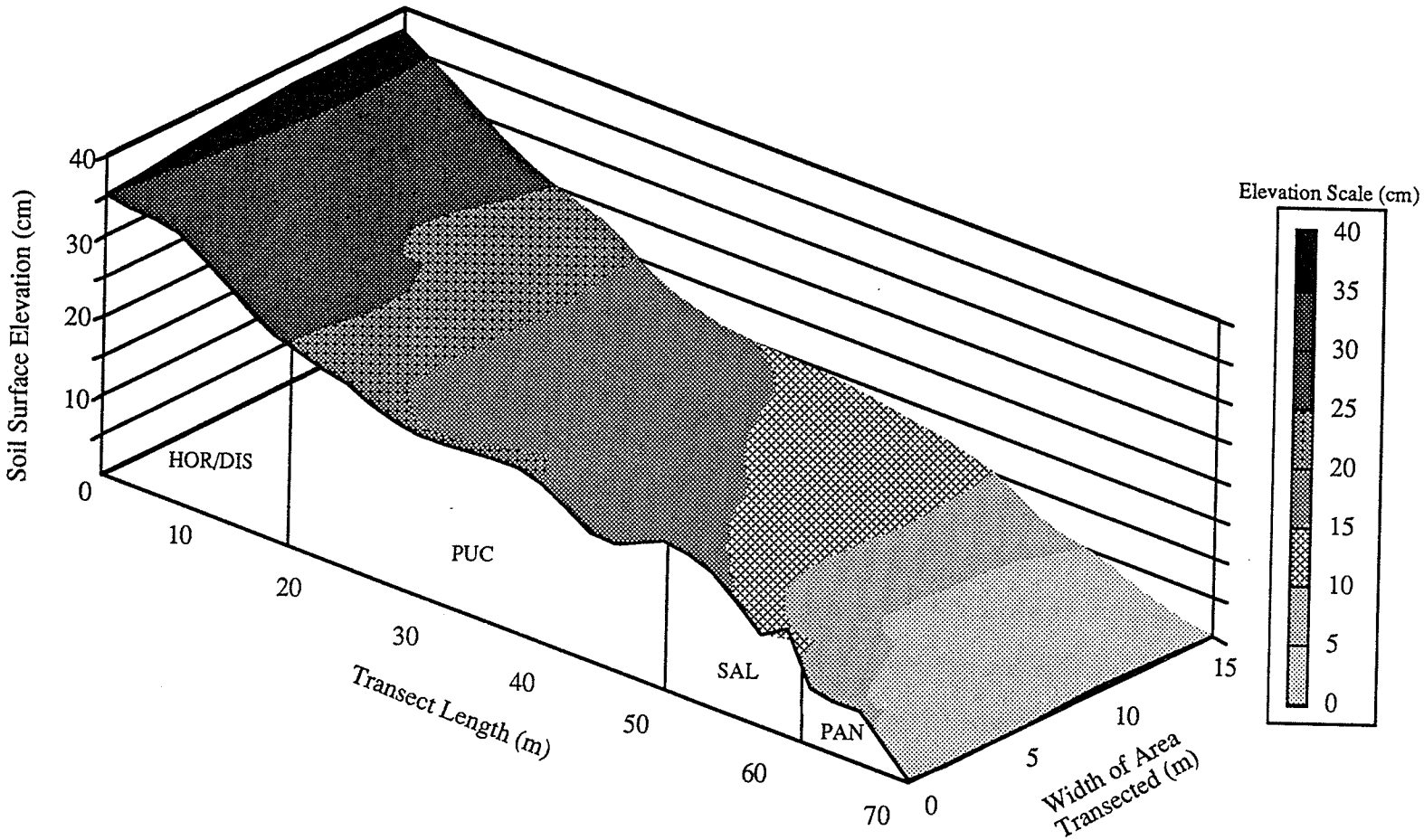


Fig. 4.5 Three dimensional representation of soil surface elevation data obtained from transect sampling of site 2, April 1990. Vegetation zones are: Hordeum/Distichlis (HOR/DIS), Puccinellia (PUC), Salicornia (SAL), and the unvegetated salt pan (PAN).

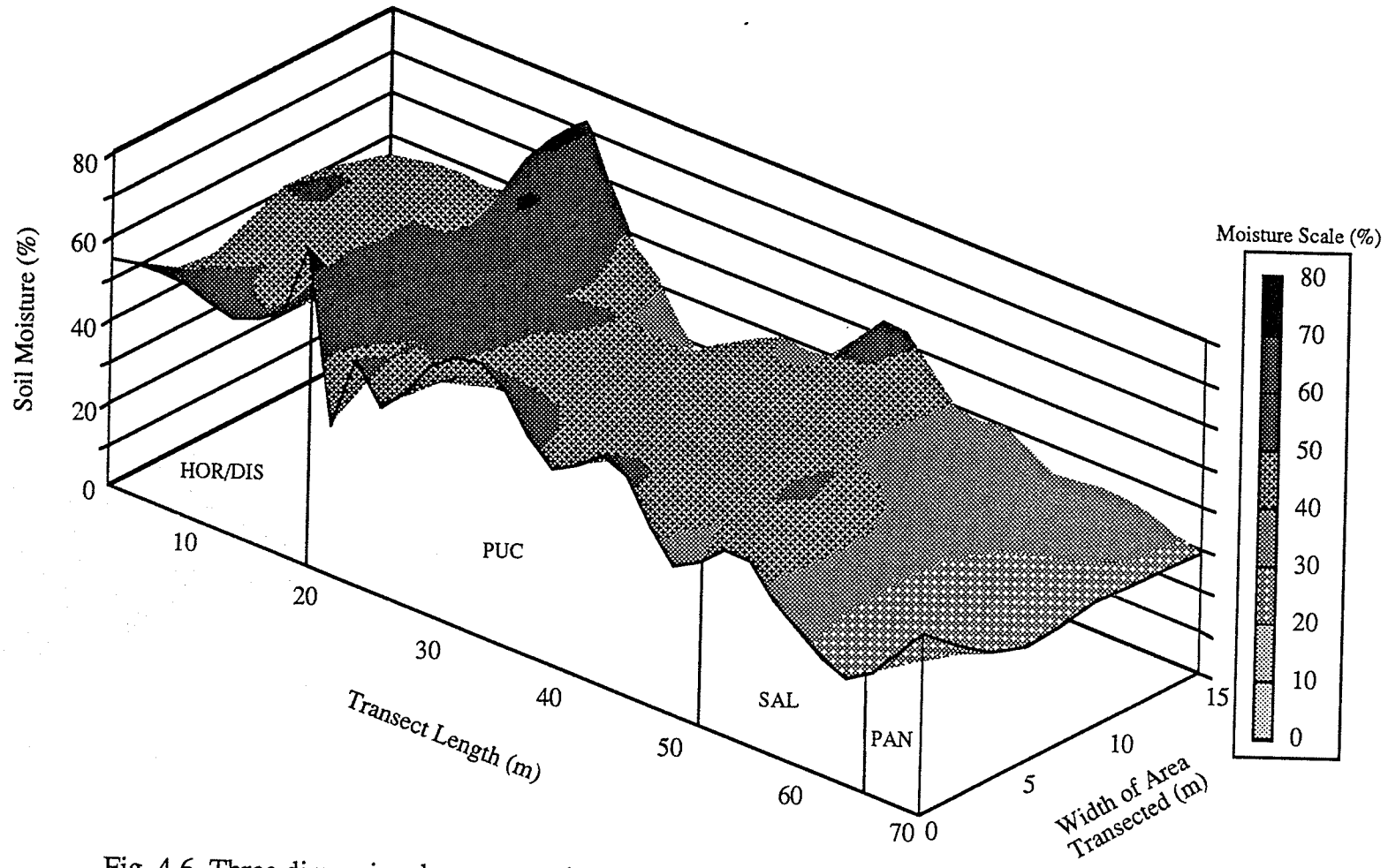


Fig. 4.6 Three dimensional representation of soil moisture data obtained from transect sampling of site 2, April 1990. Vegetation zones are: Hordeum/Distichlis (HOR/DIS), Puccinellia (PUC), Salicornia (SAL), and the unvegetated salt pan (PAN).

There was a definite increase in elevation from the Salicornia zone through the Puccinellia and Hordeum/Distichlis zones (Figure 4.5). Soil moisture also showed an increasing gradient across the Salicornia and Puccinellia zones (Figure 4.6). Moisture levels peaked near the western extent of the Puccinellia zone, and then decreased slightly into the Hordeum/Distichlis zone. The moisture gradient was not as linear as that of elevation. Soil moisture was subject to fluctuation across the Puccinellia and Hordeum/Distichlis zones, and resulted in the presence of peaks and valleys in the graphical representation. Drainage of the zones was in a eastward direction towards the salt pan.

The gradient in soil water salinity was in general the reverse of the moisture gradient (Figure 4.7). Salinity was high in the Salicornia zone and then gradually decreased to the Hordeum/Distichlis zone. The Puccinellia zone experienced spatially fluctuating levels of salt, which is reflective of fluctuations in soil moisture.

Elevation increased gradually from the Hordeum/Distichlis zone to the Calamagrostis zone (Figure 4.8). Soil moisture was highest in the Hordeum/Distichlis zone and decreased towards the Calamagrostis zone (Figure 4.9). Once in the Calamagrostis zone the soil moisture began to increase again. Soil water salinity was highest at the southern edge of the area transected (Figure 4.10). This was followed by decreasing peaks and troughs through the Hordeum/Distichlis zone towards the Calamagrostis zone. With nearness to the Calamagrostis zone the gradient became more linear, and continued to the northern extent of the sampled area.

Site 3

The transects of site 3 were oriented in a northeast-southwest direction. The view across the transected area, presented in Figures 4.11 - 4.13, is in a southwest direction. Gradients of increasing elevation and soil moisture were apparent from the unvegetated salt pan to the Calamagrostis zone (Figures 4.11 and 4.12). The elevation and moisture

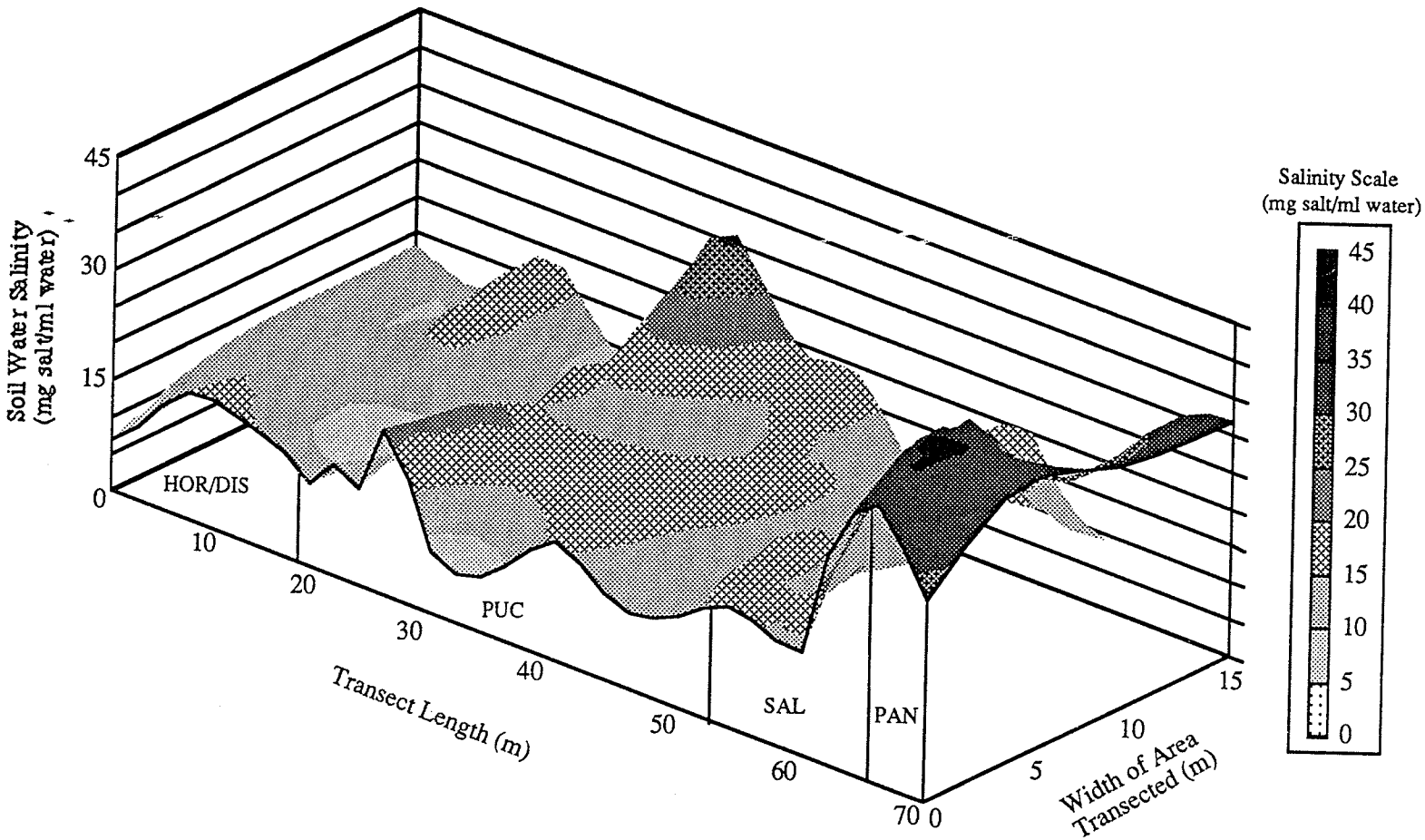


Fig. 4.7 Three dimensional representation of soil water salinity data obtained from transect sampling of site 2, April 1990. Vegetation zones are: Hordeum/Distichlis (HOR/DIS), Puccinellia (PUC), Salicornia (SAL), and the unvegetated salt pan (PAN).

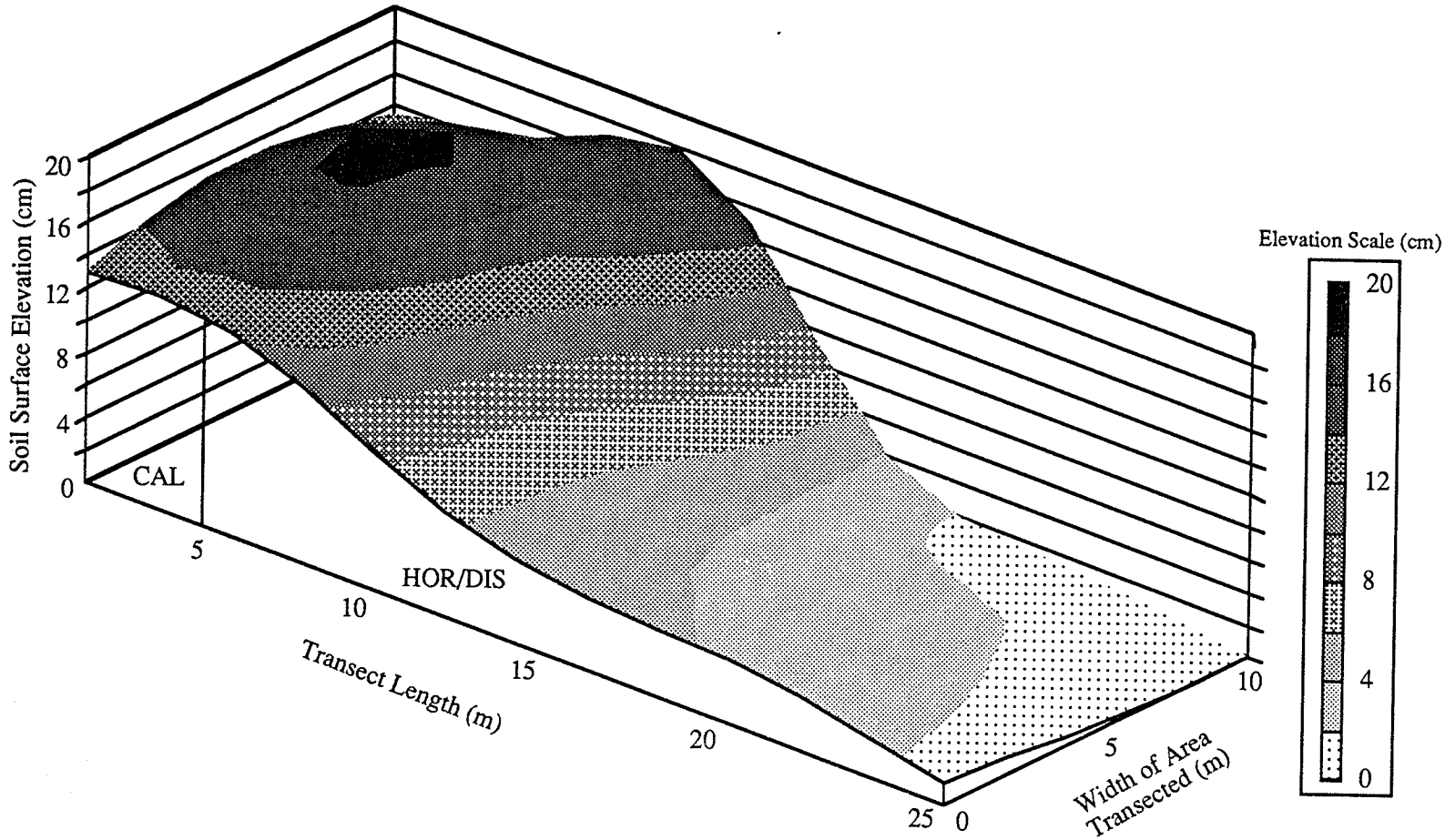


Fig. 4.8 Three dimensional representation of soil surface elevation data obtained from transect sampling of the Hordeum/Distichlis (HOR/DIS) and Calamagrostis (CAL) zones of site 2, April 1990.

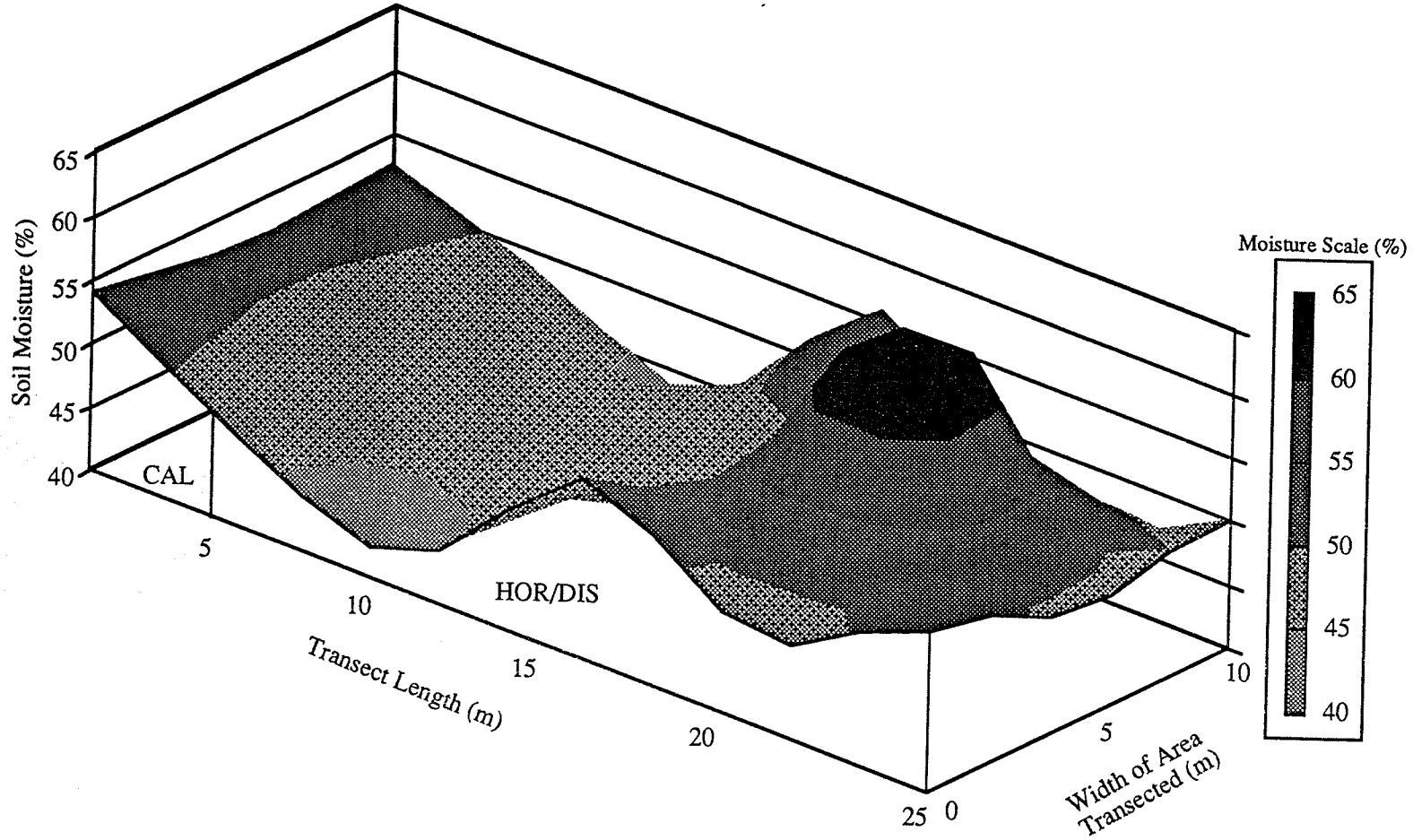


Fig. 4.9 Three dimensional representation of soil moisture data obtained from transect sampling of the Hordeum/Distichlis (HOR/DIS) and Calamagrostis (CAL) zones of site 2, April 1990.

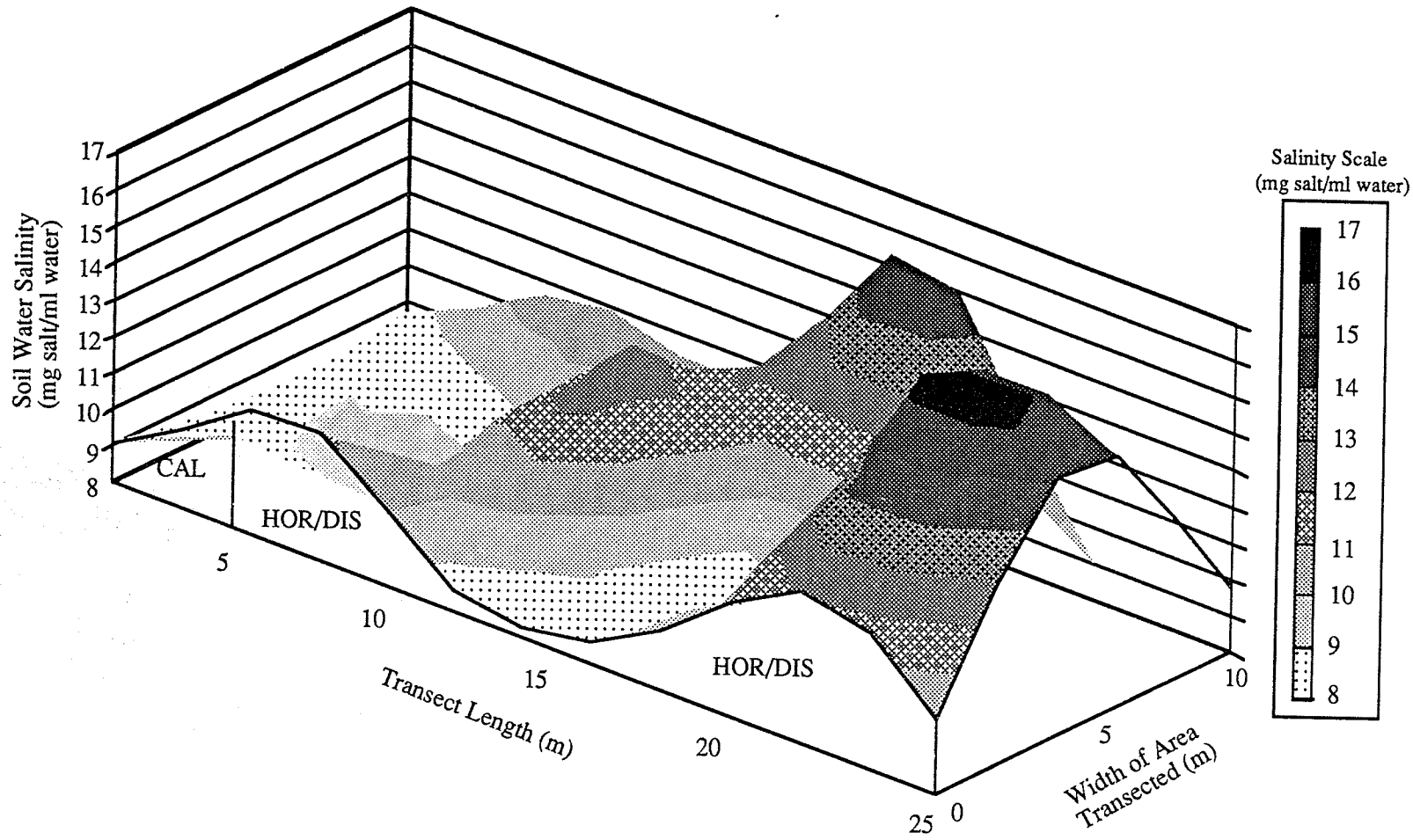


Fig. 4.10 Three dimensional representation of soil water salinity data obtained from transect sampling of the Hordeum/Distichlis (HOR/DIS) and Calamagrostis (CAL) zones of site 2, April 1990.

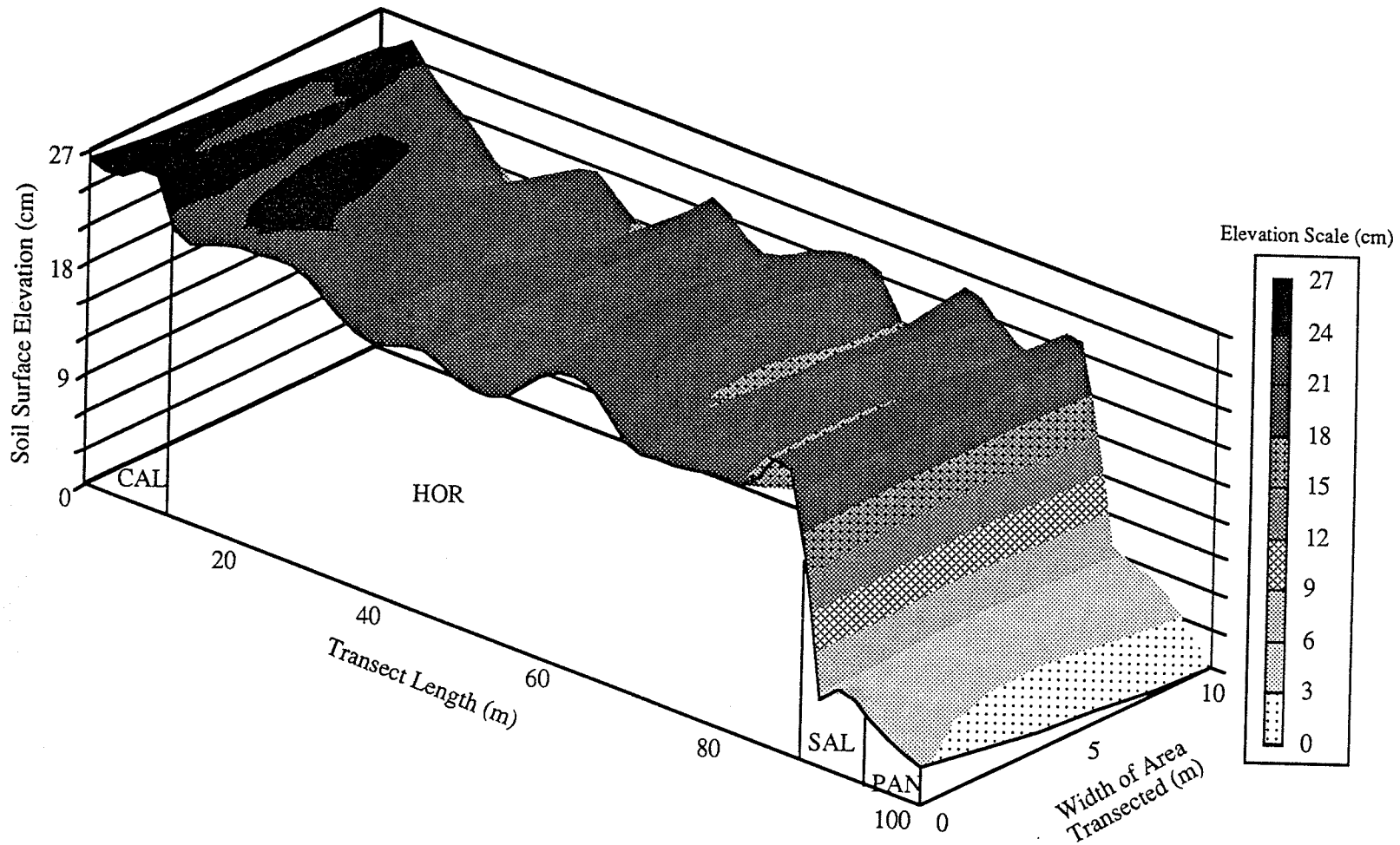


Fig. 4.11 Three dimensional representation of soil surface elevation data obtained from transect sampling of site 3, April 1990. Vegetation zones are: Calamagrostis (CAL), Hordeum (HOR), Salicornia (SAL), and the unvegetated salt pan (PAN).

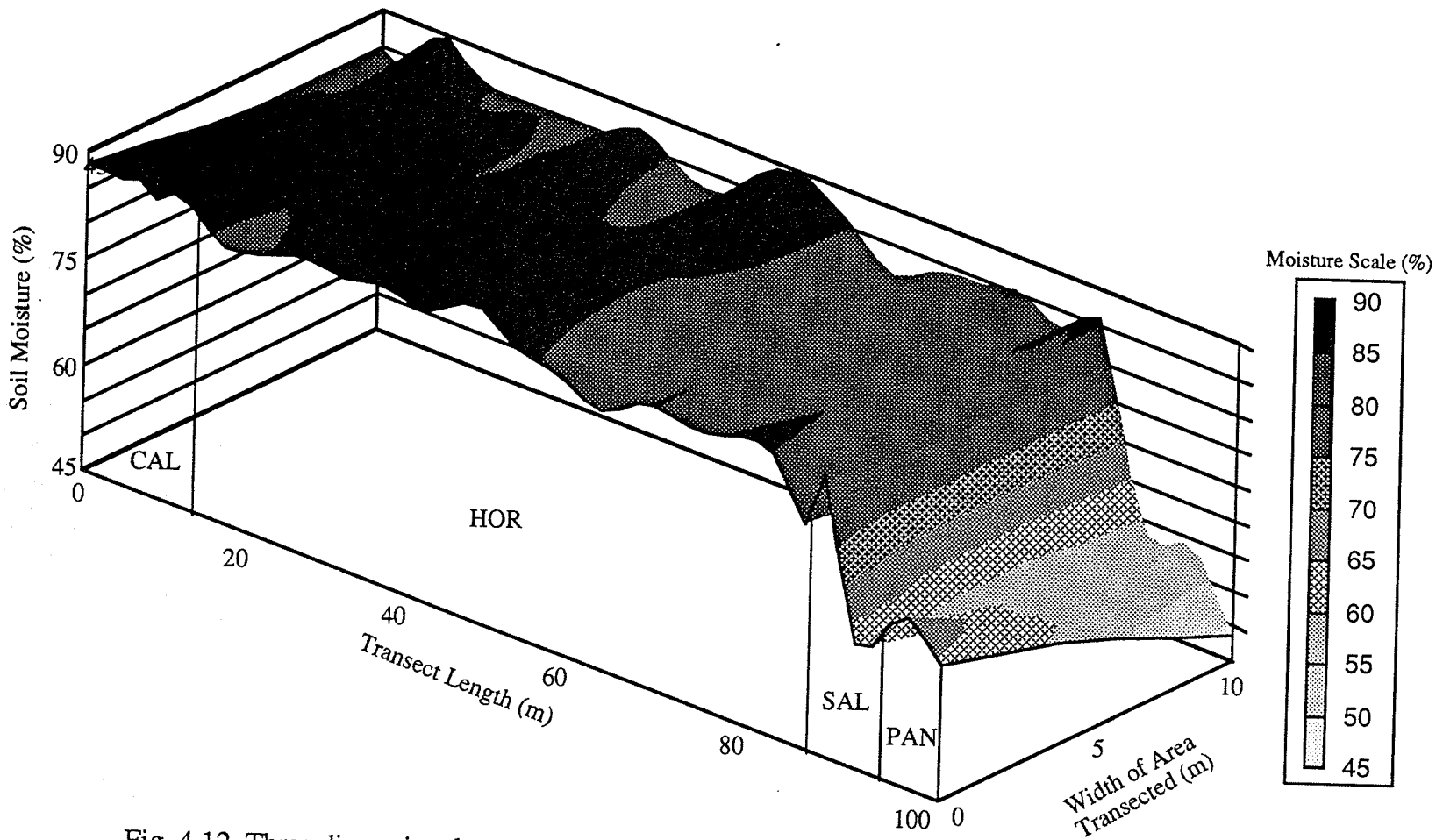


Fig. 4.12 Three dimensional representation of soil moisture data obtained from transect sampling of site 3, April 1990. Vegetation zones are: Calamagrostis (CAL), Hordeum (HOR), Salicornia (SAL), and the unvegetated salt pan (PAN).

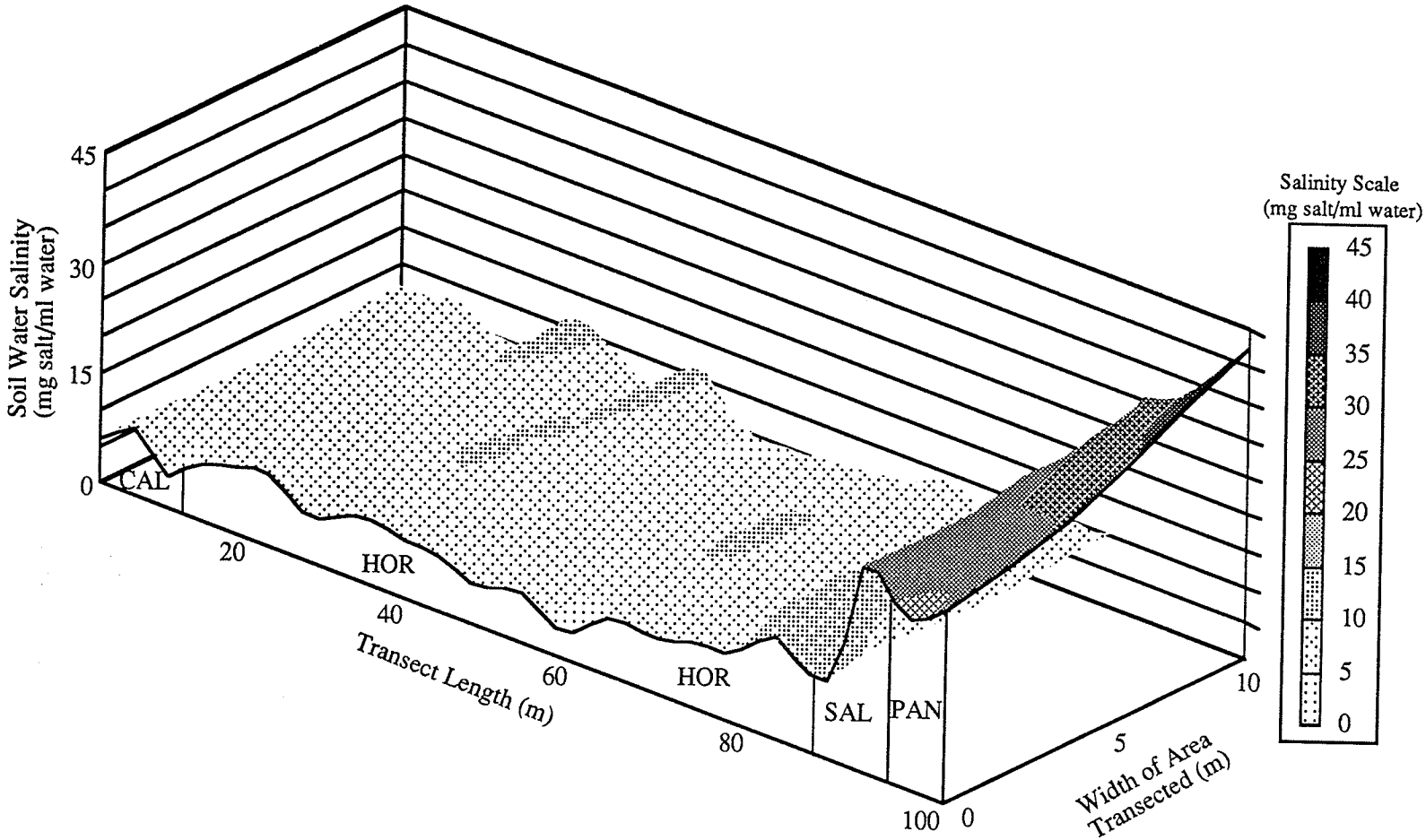


Fig. 4.13 Three dimensional representation of soil water salinity data obtained from transect sampling of site 3, April 1990. Vegetation zones are: Calamagrostis (CAL), Hordeum (HOR), Salicornia (SAL), and the unvegetated salt pan (PAN).

increased rapidly through the Salicornia zone. The increase then became more gradual over the Hordeum and Calamagrostis zones. The peaks and valleys in elevation and moisture through the Hordeum and Calamagrostis zones reflected the hummock/hollow topography of the site, which resulted from the high organic, peat-like nature of the soil. The gradient in soil water salinity was the reverse of the moisture and elevation gradients. Salinity decreased quickly from the salt pan to the Hordeum zone (Figure 4.13). It then remained fairly level across the Hordeum and Calamagrostis zones. Surface water tended to drain towards the salt pan, although site drainage was generally poor due to the pooling of water in small hollows in the Hordeum and Calamagrostis zones.

Site 4

Results from transect sampling of site 4 are presented in Figures 4.14 - 4.17. Transects were established in an east-west direction and the view presented in the Figures is from north to south across the width of the transected area. Soil surface elevation and moisture showed a gradient of increase from the Salicornia zone, across the Distichlis zone, and into the Calamagrostis zone (Figures 4.14 and 4.15). Highest surface elevations were found in the southeast corner of the Calamagrostis zone, while the lowest elevation was in the northwest corner of the Salicornia zone. Surface water flowed off the vegetation zones and onto the salt pan and then exited the site via a small stream in a northeastern direction. Soil water salinity decreased rapidly through the Salicornia and Distichlis zones and gradually leveled-off in the Calamagrostis zone (Figure 4.16). Soil pH remained relatively level across the zones, but rapidly decreased at the eastern extreme of the Calamagrostis zone (Figure 4.17).

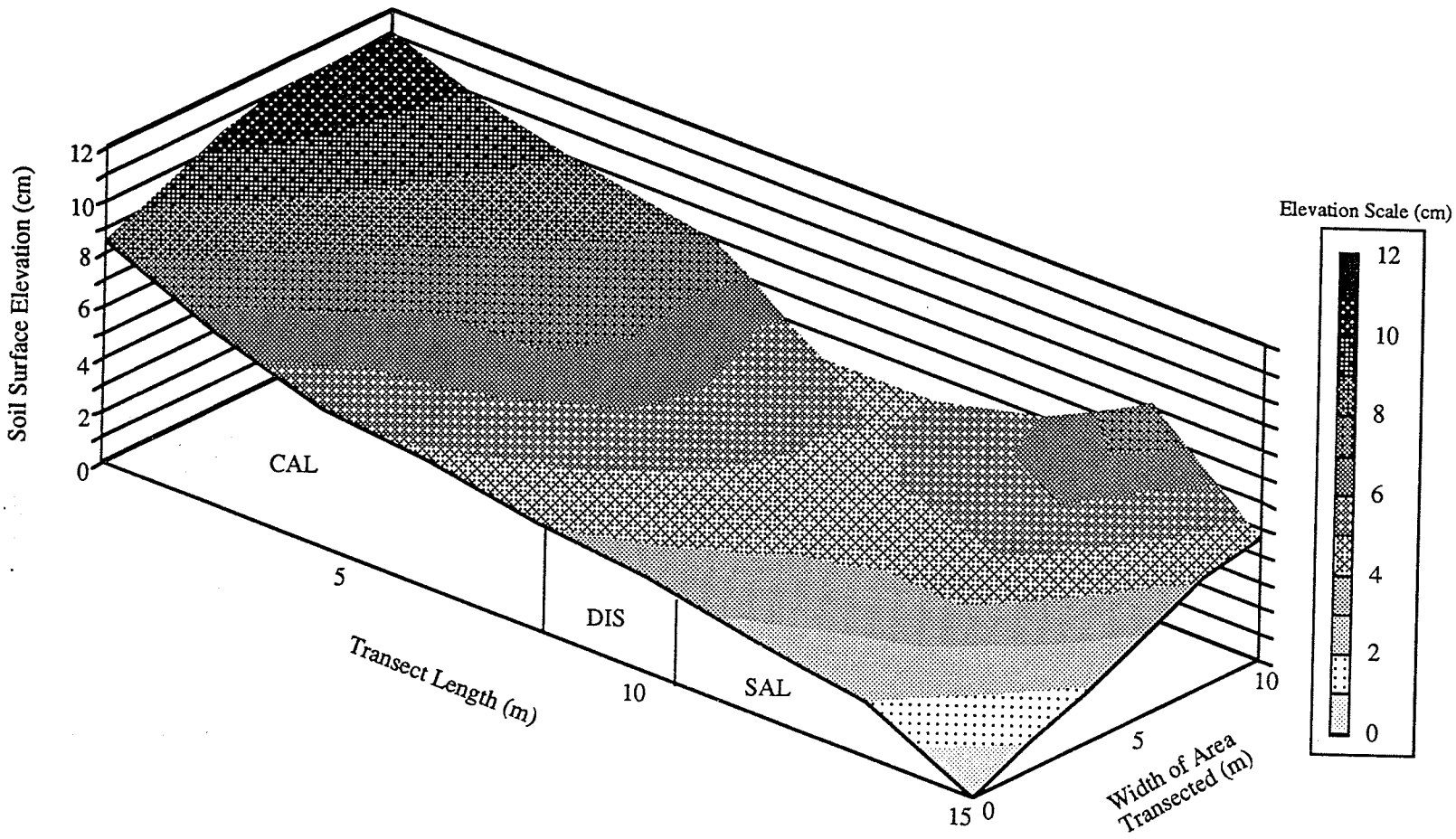


Fig. 4.14 Three dimensional representation of soil surface elevation data obtained from transect sampling of site 4, April 1990. Vegetation zones are: Calamagrostis (CAL), Distichlis (DIS), and Salicornia (SAL).

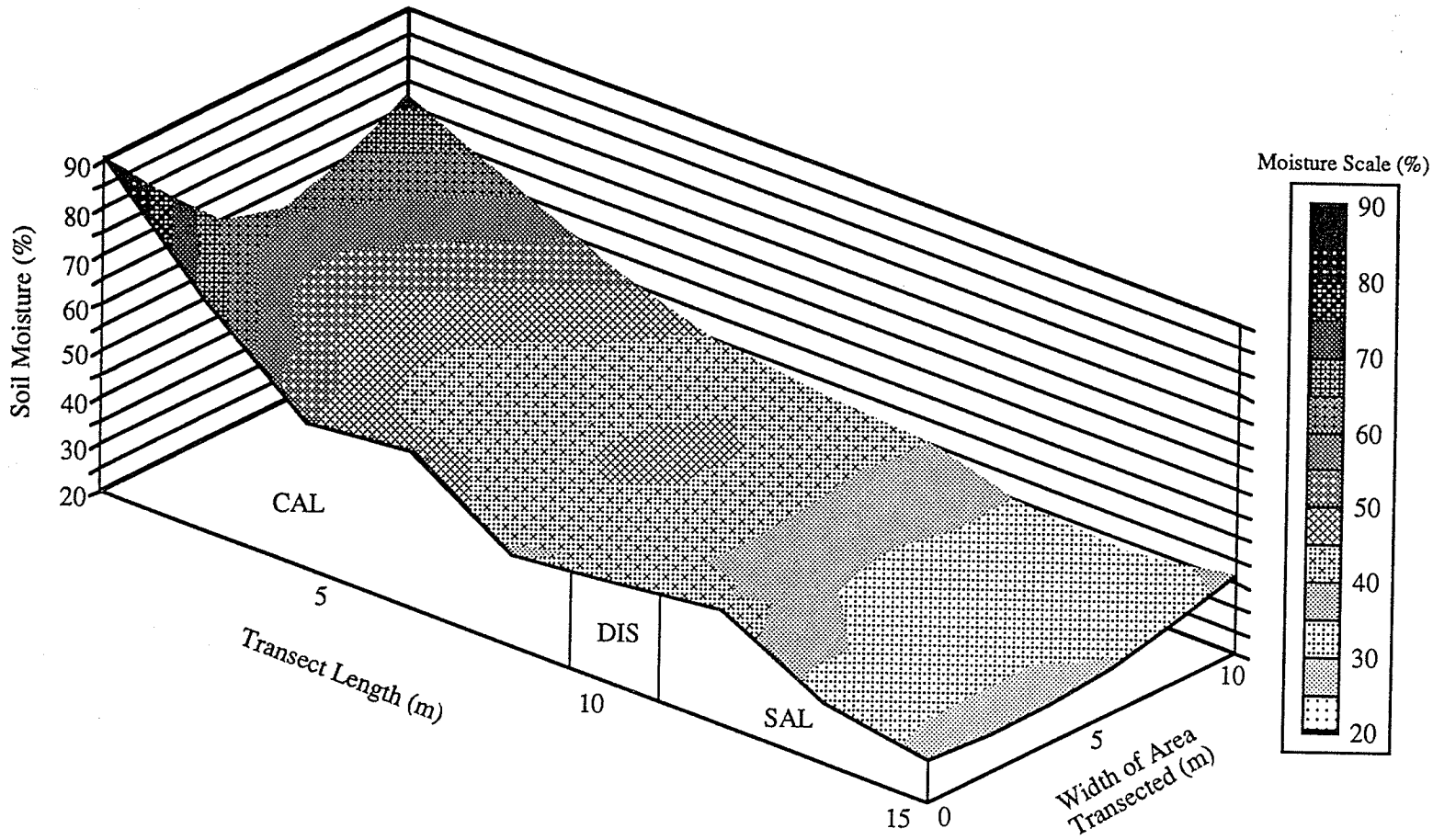


Fig. 4.15 Three dimensional representation of soil moisture data obtained from transect sampling of site 4, April 1990. Vegetation zones are: Calamagrostis (CAL), Distichlis (DIS), and Salicornia (SAL).

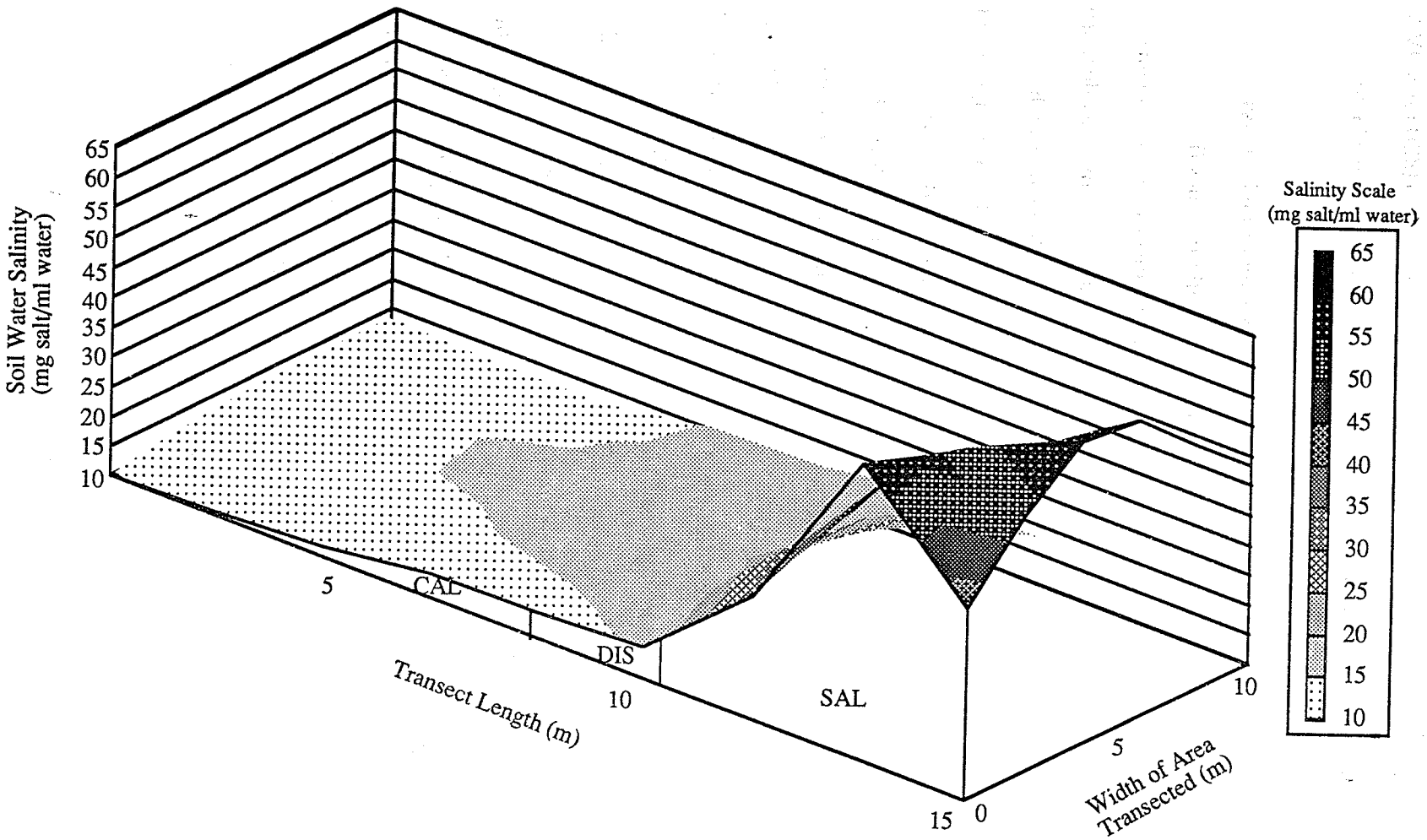


Fig. 4.16 Three dimensional representation of soil water salinity data obtained from transect sampling of site 4, April 1990. Vegetation zones are: Calamagrostis (CAL), Distichlis (DIS), and Salicornia (SAL).

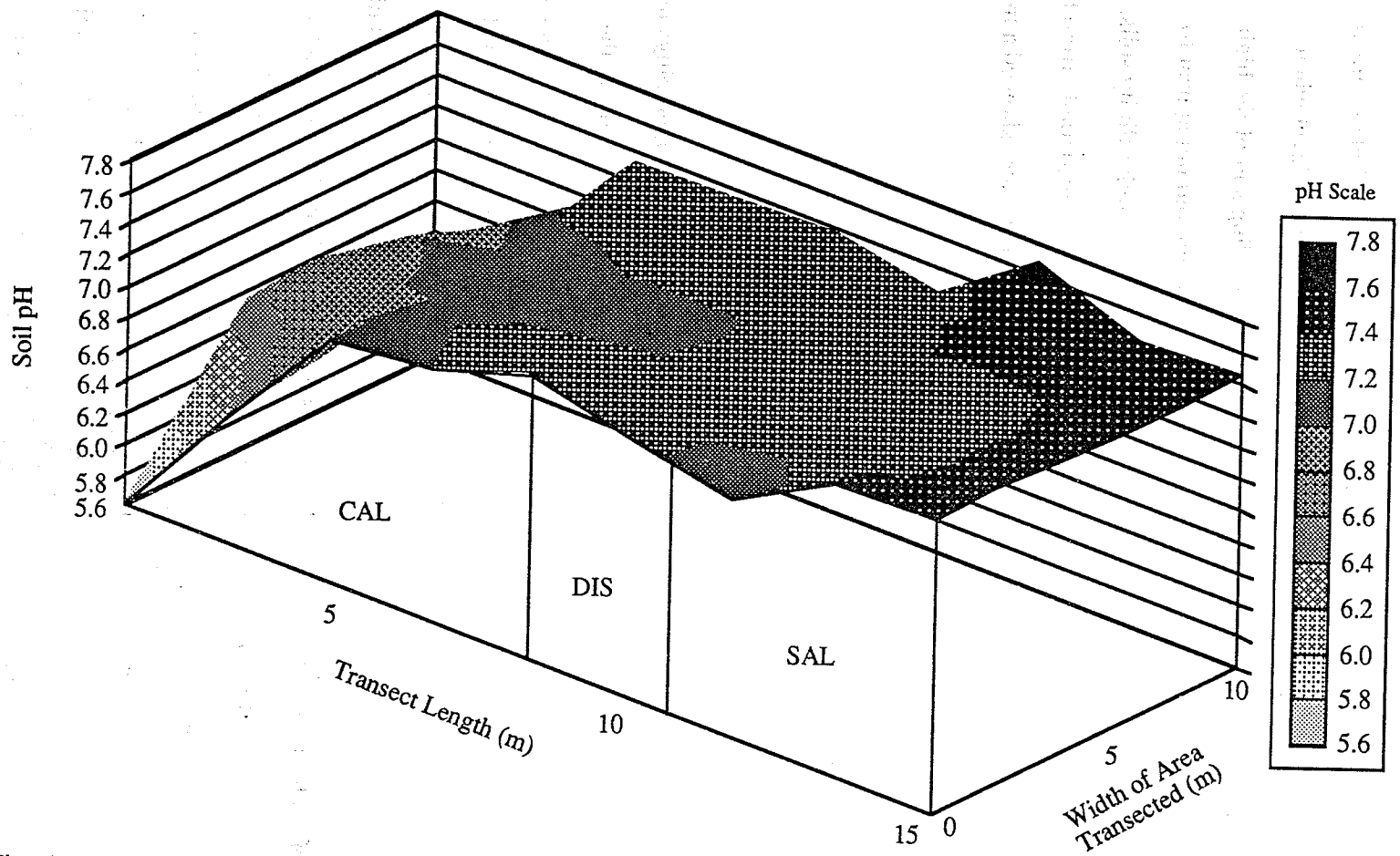


Fig. 4.17 Three dimensional representation of soil pH data obtained from transect sampling of site 4, April 1990. Vegetation zones are: Calamagrostis (CAL), Distichlis (DIS), and Salicornia (SAL).

Section 4.3.2 - Density, Growth, and Phenology

Calamagrostis inexpansa

Calamagrostis inexpansa (Table 4.1) experienced a general trend of decreasing culm density over the season. Individual culm biomass generally increased over the season. Culms in sites 1 and 2 showed a general increase in biomass at each sample period until late August. When a significant decrease in culm biomass occurred. The decrease may have resulted from biomass loss due to seed dispersal at these two sites. Culms of *Calamagrostis inexpansa* in sites 3 and 4 continued to show an increase in biomass during the season. There was close correspondence in the phenological stages between sites 1 and 2. Culm density was highest, and phenological development was most rapid in sites 3 and 4.

Hordeum jubatum

In general the density of *Hordeum jubatum* (Table 4.2) in sites 2 and 3 increased in the early summer, and then decreased later in the season. Initially site 3 experienced the densest growth, but later in the season declined to the densities observed in site 2. *Hordeum jubatum* density in site 1 showed an initial increase in early summer, followed by a sharp decline at the beginning of August. Density then increased again towards the end of August. The decline at the beginning of August is difficult to explain, and may be the result of an error in sampling (e.g. sample size). Initial biomass of individuals was the same between sites. Biomass then increased until the late August sampling period, where there was a decline in individual biomass. The most robust plants were found in site 1. Phenology of *Hordeum jubatum* showed little variation between sites. Fruit development was commonly observed by early August. The decline in individual biomass by late August corresponded with seed dispersal, and was likely a precursor to plant senesence.

Table 4.1 Mean frequency, individual biomass, density, and phenology/growth stage of *Calamagrostis inexpansa* over the 1990 growing season. Biomass and density refers to individual culms. n = 10 for site 1, 2, and 3, n = 5 for site 4.

Site	Sample Date	Frequency of Occurrence (%)	Individual Biomass (mg)	Density (individuals/m^2)	Phenology/Growth Stage
1	29 May	90	41.0	500.0	Vegetative
	5 July	90	106.0	390.6	Vegetative
	2 August	80	234.0	390.6	Flowering
	24 August	90	202.0	375.0	Seed Set
2	30 May	30	13.2	265.6	Vegetative
	2 July	50	43.1	234.4	Vegetative
	31 July	90	265.4	734.4	Flowering
	22 August	60	171.2	406.3	Seed Set
3	30 May	100	59.1	1359.4	Vegetative
	5 July	90	211.2	1250.0	Vegetative & Flowering
	31 July	90	299.8	968.8	Seed Set
	23 August	100	383.9	1109.4	Seed Set
4	29 May	100	34.2	843.8	Vegetative
	2 July	100	153.8	1031.3	Vegetative
	1 August	100	192.3	1250.0	Flowering & Seed Set
	21 August	100	330.0	968.8	Seed Set

Table 4.2 Mean frequency, individual biomass, density, and phenology/growth stage of *Hordeum jubatum* over the 1990 growing season. Biomass and density refers to individual culms. n = 10.

Site	Sample Date	Frequency of Occurrence (%)	Individual Biomass (mg)	Density (individuals/m^2)	Phenology/Growth Stage
1	29 May	100	21.0	1171.9	Vegetative
	5 July	100	90.0	3218.8	Flowering
	2 August	100	69.0	1437.5	Seed Set
	24 August	100	50.0	4156.3	Seed Set
2	30 May	80	21.4	1546.9	Vegetative
	2 July	70	37.2	1140.6	Flowering
	31 July	100	42.6	2984.4	Seed Set
	22 August	100	37.7	2203.1	Seed Set
3	30 May	100	22.1	3968.8	Vegetative
	5 July	100	57.0	6390.6	Vegetative & Flowering
	31 July	80	59.1	2859.4	Seed Set
	23 August	100	47.0	2890.6	Seed Set

Distichlis stricta

The biomass of *Distichlis stricta* individuals increased steadily over the 1990 season (Table 4.3), without the decline in biomass at the end of the sampling period that was observed in *Hordeum jubatum* and *Calamagrostis inexpansa* individuals. Density of culms showed an initial increase until mid-summer. It then decreased by early August and remained fairly constant until the end of the sample period. Plants were generally more robust, but less dense in site 4. Phenological development varied little between sites, although individuals appeared to set seed earlier in site 4.

Puccinellia nuttalliana

The density of *Puccinellia nuttalliana* was higher in site 1 than in site 2 at the start of the sample period. Density in site 1 then decreased dramatically by the second sample date. It remained essentially unchanged through the third sample date and then increased by the final sample date in late August. Density in site 2 showed a distinct increase from one date to the next over the growing season. Biomass of individuals in site 1 was low at the start of the season and then increased steadily until the beginning of August, whereupon it began to decline until the last sample date in late August. The low individual biomass and high density values for the early season in site 1 are reflective of the phenology of the population. At this time a large proportion of the population was still in the germination stage of development. In site 2 individuals showed an initial increase in biomass at the start of the season. After the 2 July sample the biomass remained the same for the rest of the season. In general, the highest densities and most rapid maturation of *Puccinellia nuttalliana* occurred in site 2. Plants in site 1 were not as dense, but appeared to be more robust.

Table 4.3 Mean frequeny, individual biomass, density, and phenology/growth stage of *Distichlis stricta* over the 1990 growing season. Biomass and density refers to individual culms. n = 10 for site 2, n = 5 for site 4.

Site	Sample Date	Frequency of Occurrence (%)	Individual Biomass (mg)	Density (individuals/m^2)	Phenology/Growth Stage
2	30 May	60	9.5	328.1	Vegetative
	2 July	90	50.2	1078.1	Flowering
	31 July	90	60.8	812.5	Flowering & Seed Set
	22 August	90	64.3	765.6	Seed Set
4	29 May	60	11.9	375.0	Vegetative
	2 July	100	53.6	1593.8	Flowering
	1 August	60	59.8	437.5	Seed Set
	21 August	60	83.5	593.8	Seed Set

Table 4.4 Mean frequency, individual biomass, density, and phenology/growth stage of *Puccinellia nuttalianna* over the 1990 growing season. Biomass and density refers to individual culms. n = 10.

Site	Sample Date	Frequency of Occurrence (%)	Individual Biomass (mg)	Density (individuals/m^2)	Phenology/Growth Stage
1	29 May	100	6.7	5453.1	Germination &Vegetative
	5 July	100	40.3	3546.9	Flowering
	2 August	100	52.2	3296.9	Seed Set
	24 August	100	36.5	7000.0	Seed Set
2	30 May	90	12.4	3921.9	Vegetative
	2 July	100	25.2	4796.9	Flowering & Seed Set
	31 July	100	27.9	7046.9	Seed Set
	22 August	100	26.0	7703.1	Seed Set

Salicornia rubra

Salicornia rubra individuals showed a distinct trend in increasing biomass over the growing season. Biomass accumulation was similar between populations from sites 1 and 4. Greatest biomass accumulation occurred in plants from site 2. Density of individuals increased in sites 1 and 4, and then decreased by the final sample date. Density of individuals was low in site 3, while in site 2 the population appeared to maintain a constant density after seedling establishment. Overall highest densities were recorded at site 4. Phenology was similar between sites 1, 2, and 4. Development of the site 3 population was hindered by standing water in the early summer. Flowering was not observed at any site until early August, and fruit development was common by the final sample date later that month.

Section 4.3.3 - Seed Bank Investigations

The seed bank experiment results (Tables 4.6 - 4.9) indicate that the vegetation zones not only had a seed bank reflective of their native vegetation, but also contained seeds of a number of species from adjacent zones. For example, in site 1 (Table 4.6) the Salicornia zone soil contained seeds from species normally found only in the Puccinellia zone. A number of species normally restricted to the Salicornia and the Hordeum zones were found germinating in soil taken from the Puccinellia zone. Following this trend, the Hordeum zone soil contained seed from Puccinellia and Calamagrostis zone species, but no seed from Salicornia zone species. Finally, the Calamagrostis zone soil yielded species native to its own zone, as well as two species normally restricted to the other vegetation zones of the site. This trend was also observed at sites 2, 3, and 4.

Table 4.5 Mean frequeny, individual biomass, density, and phenology/growth stage of *Salicornia rubra* over the 1990 growing season. Biomass and density refers to individuals plants. n = 10 for sites 1, 2, and 3, n = 5 for site 4.

Site	Sample Date	Frequency of Occurrence (%)	Individual Biomass (mg)	Density (individuals/m^2)	Phenology/Growth Stage
1	29 May	50	2.0	1781.3	Germination
	5 July	100	13.0	1656.3	Germination &Vegetative
	2 August	100	18.0	2718.8	Flowering
	24 August	70	33.0	750.0	Seed Set
2	30 May	0	0.0	0.0	none
	2 July	100	10.9	1078.1	Vegetative
	31 July	100	29.6	968.8	Flowering
	22 August	100	58.6	1218.8	Seed Set
3	30 May	0	0.0	0.0	none
	5 July	0	0.0	0.0	none
	31 July	0	0.0	0.0	none
	23 August	60	37.8	140.6	Vegetative & Flowering
4	29 May	100	3.6	3875.0	Germination
	2 July	100	13.8	6437.5	Vegetative
	1 August	100	17.9	3250.0	Flowering
	21 August	100	28.9	2343.8	Seed Set

Table 4.6 Results from preliminary seed bank investigations in site 1. Germinating species are indicated by '*' or '+'. An '*' indicates species that are normally found in the particular vegetation zone, while a '+' indicates species normally found in other zones.

Species Germinated	Vegetation Zones			
	Calamagrostis	Hordeum	Puccinellia	Salicornia
Calamagrostis inexpansa	*			
Sonchus arvensis	*			
Aster pansus	*	+		
Aster pauciflorus		*		
Atriplex patula			*	
Hordeum jubatum	+	*	*	
Triglochin maritima	*	*	*	*
Puccinellia nuttalliana		+	*	+
Spergularia marina			+	*
Suaeda depressa			+	*
Salicornia rubra			*	*

Table 4.7 Results from preliminary seed bank investigations in site 2. Germinating species are indicated by '*' or '+'. An '*' indicates species that are normally found in the particular vegetation zone, while a '+' indicates species normally found in other zones.

Species Germinated	Vegetation Zones			
	Calamagrostis	Hordeum/Distichlis	Puccinellia	Salicornia
Hierchloe odorata				+
Calamagrostis inexpansa	*			
Sonchus arvensis	*	+	+	
Aster pansus	*	*		
Grindelia squarrosa		*		
Atriplex patula		*		
Hordeum jubatum		*		
Distichlis stricta	+			
Triglochin maritima			*	
Puccinellia nuttalliana	+	+	*	+
Spergularia marina			+	*
Suaeda depressa	+	+	*	*
Salicornia rubra			+	*

Table 4.8 Results from preliminary seed bank investigations in site 3. Germinating species are indicated by '*' or '+'. An '*' indicates species that are normally found in the particular vegetation zone, while a '+' indicates species normally found in other zones.

Species Germinated	Vegetation Zones		
	Calamagrostis	Hordeum	Salicornia
Typha sp.	+	+	+
Juncus balticus	*		
Calamagrostis inexpansa	*		
Sonchus arvensis	*		
Aster laevis	*		
Aster pansus	+		
Atriplex patula	*	*	
Glaux mariana		+	
Hordeum jubatum	+	*	+
Triglochin maritima	*	*	
Puccinellia nuttalliana	+	+	+
Suaeda depressa		+	
Salicornia rubra		+	*

Table 4.9 Results from preliminary seed bank investigations in site 4. Germinating species are indicated by '*' or '+'. An '*' indicates species that are normally found in the particular vegetation zone, while a '+' indicates species normally found in other zones.

Species Germinated	Vegetation Zones		
	Calamagrostis	Distichlis	Salicornia
Polygonum sp.			+
Typha sp.		+	+
Rumex occidentalis			+
Juncus balticus	*		
Calamagrostis inexpansa	*		
Achillea millefolium	*		
Sonchus arvensis	*	+	
Aster pansus	*	+	+
Stellaria longifolia		+	
Ranunculus cymbalaria	+	+	
Atriplex patula		*	
Grindelia squarrosa		*	
Hordeum jubatum		*	
Triglochin maritima			+
Puccinellia nuttalliana	+	+	+
Suaeda depressa	+	*	*
Salicornia rubra			*

Section 4.4 - Discussion

Section 4.4.1 - Soil and Vegetation Gradients

The relationship between plant distribution and soil gradients in inland saline habitats have been studied extensively (e.g. Keith 1958; Dodd & Coupland 1966a,b; Ungar 1966; 1968; 1970; 1974; McMahon & Ungar 1978; Badger & Ungar 1990; Burchill 1991; Burchill & Kenkel 1991). These studies emphasize the existence of a continuous gradient of decreasing soil salinity from the salt pan towards the peripheral vegetation zones, and concluded that this gradient was a major influence on species distribution within inland saline habitats. Ungar (1978), in a study of Ohio salt pan soil-vegetation relationships, found that this gradient was maintained even though soil salinity fluctuated over the growing season. Although salinity gradients described in these studies were continuous, vegetation gradients were not. Instead, the vegetation was patterned into distinct vegetation zones dominated by a single species or pair of species.

Relationships between vegetation distribution and soil surface elevation, soil moisture, and soil pH have not received as much attention as soil salinity. Keith (1958) and Ungar (1968; 1970) found *weak* trends in soil pH at the saline sites they studied. The salt pan often had the highest soil pH, while the soil pH on the outer periphery of the site was generally the lowest. Soil pH values of the zones in between these two extremes often overlapped. Burchill (1991) reported a correlation between soil pH and vegetation distribution, but this correlation was considerably weaker than that between vegetation and soil salinity. Keith (1958), Ungar (1968; 1970), and McMahon & Ungar (1978) described the existence of a soil moisture gradient across saline sites, and found that it was generally negatively correlated with soil salinity. They found that an increase in soil moisture generally resulted in a corresponding decrease in soil salinity. Ungar (1970), in a study of sulphate dominated soil of South Dakota, found a direct correlation between soil moisture and soil organic matter content. Generally the two factors increased along a

gradient away from the salt pan. Presumably the higher a soil's organic matter content the greater its moisture holding capacity, which would lead to a decreased concentration of salts in the soil solution. The influence of elevation gradients on species distributions in coastal saline marshes has been well documented (Adams 1963; Neiring & Warren 1980). Descriptions of elevation gradients in inland saline habitats are generally lacking, although, Burchill (1991) discovered an increasing gradient of relative surface elevation away from the salt pan and across the vegetation zones. The gradient was generally linear and resulted in the drainage of surface waters from the periphery of the sites toward the salt pan. Salinity analysis of the surface waters from inland sites has not been reported in the literature. However, it is likely that salts are transported in the run-off of surface water from the higher to the lower zones. This may play a role in maintaining a soil salinity gradient across a site.

Results from transect sampling of my study sites were similar to those reported in the literature. Continuous gradients in elevation, soil moisture, and soil water salinity, and discontinuous gradients in vegetation were present at each site. The vegetation zones met to form distinct boundaries at which there was little mixing of species. Sample cores taken on both sides of a vegetation boundary, and on the actual boundary itself, failed to indicate a discontinuity in the soil factors analyzed. Some small-scale fluctuations in soil factors within vegetation zones occurred, but these were probably the result of localized differences in soil texture, elevation, and water holding capacity.

The width of vegetation zones differed between sites, but the extent of zones was found to correspond well with the slope of the soil gradients. Gradual gradients in soil factors, as occurred in site 3, resulted in wide vegetation zones. Presumably the soil factors fell within the dominant species' tolerance ranges over a larger spatial area. In site 4 the soil gradients were steeper, which led to rapid changes in soil factors over a short distance, and resulted in relatively narrow vegetation zones.

Section 4.4.2 - Growth of Dominant Species

Calamagrostis inexpansa

Calamagrostis inexpansa is a native North American perennial grass usually inhabiting slightly saline, moist areas and marshes (Budd & Best 1964). A search of the literature revealed little information about the growth and development of *Calamagrostis inexpansa* in inland saline habitats. The only exception to this is in Burchill (1991), who describes *Calamagrostis inexpansa* as a tall rhizomatous grass forming a loose sod and dense standing litter. He found that the species was the least salt tolerant dominant grass commonly found at the Overflow Bay sites. While the Calamagrostis zones of all sites had the lowest salinity levels, *Calamagrostis inexpansa* growth was considerably more robust and denser at sites 3 and 4 than at sites 1 and 2. An explanation for this difference is difficult because of the present lack of information about the species' physiological and ecological requirements.

Hordeum jubatum

Hordeum jubatum is a short lived perennial bunch-grass commonly found in waste places, pastures, and saline habitats throughout North America (Cords 1960; Ungar 1974(b)). The salinity tolerance of *Hordeum jubatum* has been described as moderate by Badger & Ungar (1990). However, its ability to complete its life-cycle in the absence of salts (Ungar 1974(b)) and its prevalence in non-saline habitats indicate that it is not an obligate halophyte. Badger & Ungar (1990) reported that phenological development and growth of the species was concentrated in late spring and early summer. This was probably the result of long exposure to sunlight which encouraged growth (Ungar 1974b). Cords (1960) reported that seed dispersal occurred in mid-summer and by late summer seeds germinated, which allowed the plants to overwinter as seedlings. He suggested that

this overwintering habit was a survival strategy, as seed viability was found to be reduced by prolonged periods of cold temperature. Findings by Ungar (1974(b)), however, indicated that seeds may retain their viability over long periods of time, and attributed Cords' results to ecotypic variation or some form of secondary seed dormancy induced by low temperatures.

At the first sampling date in 1990 I observed that individuals of *Hordeum jubatum* were in the vegetative phase of growth, with no germinating individuals present, which tends to support Cords view (see above). However, germination and seedling establishment may have occurred prior to my first sample date. My observations indicated that growth and maturation of *Hordeum jubatum* was relatively rapid, as most individuals flowered by the end of June and set seed during the month of July. Plants continued to accumulate biomass until early August. The decline in biomass after this date probably resulted from seed dispersal; my findings are thus in close agreement with those of Badger & Ungar (1990).

Studies by Ungar (1974(b)) and Badger & Ungar (1990) indicate that *Hordeum jubatum* is most susceptible to high salinity during the seedling establishment phase of its life-cycle. Thus, soil salinity is important in limiting the distribution of *Hordeum jubatum* in saline habitats. These studies also found that soil moisture was correlated with the species' distribution. From this they concluded that salinity effects on seedling development were therefore likely osmotic rather than toxic. Badger & Ungar (1990) suggested that competition, along with physiological tolerance, also played an important role in the distribution of *Hordeum jubatum*. This will be discussed in more detail in the next chapter.

Distichlis stricta

Distichlis stricta is a shallow-rooted, rhizomatous perennial. It occurs throughout the western United States and western Canada, but is generally restricted to saline soils in

these regions (Ungar 1974a). It is often associated with other species such as *Hordeum jubatum* and *Puccinellia nuttalliana* (Ungar 1974a), and may, under suitable conditions of salinity and moisture, become a co-dominant with these species, or even form pure stands.

The range of salt tolerance of *Distichlis stricta* overlaps with that of *Puccinellia nuttalliana* at the upper extreme and *Hordeum jubatum* at the lower (Ungar 1974(a)). This probably plays a major role in its apparent coexist with both these species. Apparent coexistence of *Diostichlis stricta* and *Hordeum jubatum* was readily observed in site 2 of my study. Soil moisture requirements for *Distichlis stricta* are less than those of *Hordeum jubatum*. This, along with its wide range of salinity tolerance, may have enabled it to coexist with *Hordeum jubatum*. Observations on Hordeum/Distichlis communities in the midwestern United States (Ungar 1974a) indicate that on a micro-topographical scale *Hordeum jubatum* was often found in moist depressions while *Distichilis stricta* occupied the drier ridges. Differences in phenological development between *Distichlis stricta* and *Hordeum jubatum* may also aid in coexistence of the two species. Growth of *Hordeum jubatum* is most active in the spring and early summer (Ungar 1974a), while other species, *Distichlis stricta* among them, tend to reach full maturity later in the summer. Bolen (1964) observed that *Distichlis stricta* began growth at the same time as *Hordeum jubatum*, but did not flower and set seed until at least a month after *Hordeum jubatum*. These latter observations coincide with results I obtained of *Distichlis stricta* growth and development at sites 2 and 4. Plants of *Distichlis stricta* continued to increase in biomass throughout the course of the 1990 season, unlike *Hordeum jubatum*, which showed a decline in individual biomass over the month of August. Phenological observations indicate that in site 2, where coexistence with *Hordeum jubatum* occurred, the majority of *Distichlis stricta* was still flowering while *Hordeum jubatum* had already developed seeds. In site 4, where *Distichlis stricta* formed mono-dominant stands, phenological development followed a similar regime as in mono-dominant stands of

Hordeum jubatum at the other sites. This suggests that *Distichlis stricta* may be able to modify its phenological development in order to coexist with *Hordeum jubatum.*

Puccinellia nuttalliana

Dodd & Coupland (1966a) have described *Puccinellia nuttalliana* as the most salt tolerant grass species in saline soils of Saskatchewan. The species is perennial and is found on alkaline, saline soils throughout the interior plains of western North America (Ungar 1974a). Soil texture does not appear to have a major influence on *Puccinellia nuttalliana* distribution (Dodd *et.al.* 1964). The species has been found under a wide range of soil moisture conditions (Ungar 1974a), but probably requires wet periods for successful germination. Ungar (1970) found that *Puccinellia nuttalliana* completed its life-cycle under a wide range of soil salinities, and concluded that it should not be considered an obligate halophyte. In study sites 1 and 2 *Puccinellia nuttalliana* dominated the vegetation between the Salicornia zone and the Hordeum/Distichlis or Hordeum zone. Individuals of *Puccinellia nuttalliana* often appeared sporadically in the Hordeum and Hordeum/Distichlis zones, and germinating individuals were observed in the Salicornia zone of site 3 during the early spring of 1990, when salt levels were low and soil moisture levels were high. These seedlings died after the onset of drying conditions in the summer. Macke & Ungar (1971) suggested that the species' wide salt tolerance allows it to occupy highly saline areas where few competitors occur. Presumably it cannot compete with *Hordeum jubatum* and *Distichlis stricta* under low salinities, but is able to out-compete Salicornia zone species under conditions of high salinity up to the limits of its physiological tolerance (Macke & Ungar 1971).

Phenological development of *Puccinellia nuttalliana* at study sites 1 and 2 was similar to that of *Hordeum jubatum.* Germination and vegetative growth occurred in the early spring, while flowering and seed production were observed by early July.

Laboratory experiments by Macke & Ungar (1971) found that rapid growth and development of *Puccinellia nuttalliana* was a function of photoperiod. Long days (14 hours of light) promoted vegetative growth and flowering, and are in accordance with conditions in the late spring and early summer.

Macke & Ungar (1971) also found that seeds of *Puccinellia nuttalliana* remained viable over periods of high salinity and germinated when conditions ameliorated. Although they found that salinity inhibited germination, the level at which salts became inhibitory was higher for *Puccinellia nuttalliana* than for *Hordeum jubatum.*

Salicornia rubra

Salicornia rubra is a succulent, annual halophyte, and a member of the Chenopodiaceae (Scoggan 1957). The species is found across the western United States and British Columbia and the prairies provinces of Canada (Ungar 1974 (a)). The taxonomic classification of *Salicornia rubra* remains uncertain and often has been considered synonymous with, or a subspecies of, the more widespread *Salicornia europaea*. Studies specific to the growth and development of *Salicronia rubra* (*Salicornia europaea*) in inland saline habitats are numerous (Tiku 1976; Ungar *et.al.* 1979; McGraw & Ungar 1981; Riehl & Ungar 1982; Philipupillai & Ungar 1984; Guy *et al.* 1986; Ungar 1987). The various literature sources agree that *Salicornia rubra* is likely *the* most salt tolerant species found in inland saline sites. This high tolerance is instrumental in its ability to exist on and dominate the edge of the unvegetated salt pan. However, studies, such as Ungar *etal.* (1979), have shown that plant growth and development was enhanced under less saline conditions. Despite this, the species normally occurred only under highly saline conditions. Presumably interspecific competition with less saline tolerant species limits the distribution of *Salicornia rubra.*

Salicornia rubra requires a wet spring for successful seed germination (Ungar 1974(a)). High soil moisture is probably required to dilute the concentration of salts in the

soil, thus creating osmotic conditions favorable to the breaking of seed dormancy. Seed dispersal by *Salicornia rubra* is usually very localized, and seeds were usually observed germinating on and around the previous season's growth. Germination of *Salicornia rubra* was apparent a sites 1 and 4 in late April, and continued through May. The Salicornia zones of sites 2 and 3 were inundated with standing water in the early spring. This period of soil saturation appeared to limit germination. Germination eventually occurred at these sites once the standing water was no longer present. Also, the germination of new seedlings was observed throughout the season, and appeared to be correlated with periods of high soil moisture (however, not to the point of saturation). Germination of *Salicornia rubra* later in the season may be a function of seed dimorphism and an ability of the seed to maintain viable during periods of unfavorable environmental conditions (Philipupillai & Ungar 1984). Flowering occurred during July, and seed development over the month of August.

Jefferies *et al.* (1979) and Ungar (1987) found that the primary response of *Salicornia rubra* to increasing salinity was a reduction in plant growth and eventual death if salinity exceeded the species' tolerance. They found no evidence for intraspecific competition, and concluded that density-dependent mortality was limited or non-existent in populations of *Salicornia rubra*, and that the main factors controlling populations were abiotic. However, I found that *Salicornia rubra* individuals continued to increase in size until the end of the season. This was accompanied by a decrease in density in sites 1 and 4 and a maintenance of density in site 2. Increasing size of individuals does not suggest excessive stress from salinity, but a simultaneous decrease in density suggests intraspecific competition. My results are somewhat preliminary; clearly more detailed monitoring of *Salicornia rubra* populations is required in order to address the problem more completely.

Section 4.4.3 - Seed Banks

Hutchings & Russell (1989) studied the seed bank of a coastal salt marsh in Chichester Harbour, Sussex, England in order to determine if seedbanks of such habitats were transient or persistent, and if there was a correlation between seed bank species and existing vegetation. Their findings showed that the seed bank of their salt marsh was more transient than persistent. They suggested that the main reasons why such seedbanks were not persistent related to wave and tidal action, which removed the majority of the seeds before they became secured in the sediment. To counter this, plants of the tidal zone tend to grow rapidly, be prolific seed producers, and thus are able to replenish the seed bank annually. Conversely, those species of less disturbed zones (at high tide), tend to be rhizomatous perennial grasses.

Seed bank studies on inland saline habitats have been conducted by Ungar (1974(b), 1978) and Ungar & Riehl (1980). Inland saline sites such as those of my study are not influenced by wave or tidal disturbances, as are coastal marshes. Thus, one would expect the establishment of a persistent seed bank within each vegetation zone of each site. Results from preliminary seed bank investigations within vegetation zones revealed that each zone does in fact contain seed reserves reflective of the naturally occurring vegetation, as well as seeds of species from adjacent vegetation zones. Similar findings are reported by Ungar & Riehl (1980) in a study of the seed bank of an inland saline habitat near Rittman, Ohio. Their study site contained four vegetation zones -- Hordeum, Atriplex, tall Salicornia, and dwarf Salicornia -- and a sparsely vegetated salt pan. They found that seed from each of the zones was present in each of the other zones, and concluded that the zonal distribution of species in inland salt sites is not due to the segregation of seed or the absence of seed from the seed bank of the vegetation zones. Salinity appeared to be the main factor controlling germination. Seeds of low salt tolerant species such as *Hordeum jubatum* and *Calamagrostis inexpansa* will not germinate in Puccinellia or Salicornia zone soils until the concentration of salts is reduced. This explains why these species are

restricted from the Puccinellia and Salicornia zones. However, it does not explain why individuals of salt tolerant species such as *Puccinellia nuttalliana*, *Salicornia rubra*, and *Distichlis stricta* are rarely, if ever, found in the Hordeum and Calamagrostis zones, even though the soil of these zones contains their seed. The next chapter will deal with this problem.

Chapter 5 - Transplant Experiments

Section 5.1 - Introduction

Chapters 3 and 4 described in detail interrelationships between the soil and vegetation gradients at the four study sites. Soil gradients were shown to be continuous and vegetation gradients discontinuous. Burchill (1991) showed that salinity was the most important soil factor influencing the distribution of species. It is likely, from looking at my results, that soil moisture and salinity act in concert to influence the species present and their distribution within the study sites. Although salinity and moisture are very important in species distribution, they cannot totally account for the vegetation zonation pattern observed. Thus, some other factor such as interspecific competition may be important in the creation and maintenance of zonation. In order to assess the relative roles of salinity and interspecific competition, a reciprocal transplant experiment was conducted. The design of the experiment was modified from that used by McMahon & Ungar (1978), Ungar *et al.* (1979), Ungar (1987), and Bertness (1991).

Section 5.2 - Methods and Analysis

Section 5.2.1 - Field Transplants

The reciprocal transplant experiment involved transplanting uniform plugs of vegetation and soil from each zone into experimental plots of each other zone at each site.

In order to distinguish between the effects of salinity alone, and the combined effects of salinity *and* competition on transplants, the vegetation in half of the experimental plots was removed by herbicide application. The use of herbicides in vegetation manipulation experiments is relatively common, and has been reviewed by Aarssen & Epp (1990). A 2% solution of Roundup™ herbicide was applied to half of the plots (selected at random) in each zone at each site to kill the vegetation. A 25 cm buffer zone was also

sprayed around each of these plots. Sprayed plots are referred to as 'cleared plots'. Roundup™ is a glyphosate herbicide and must be applied to photosynthesizing vegetation in order to be effective (Duke 1988), therefore, application took place in early June of 1989, when plants were actively growing. This herbicide was chosen because it is non-selective, it is quickly absorbed by the vegetation, and it rapidly binds to soil particles to become inert within about seven days of application (Duke 1988). In order to be certain that the herbicide was no longer active, cleared plots were left for a period of two weeks before transplantation of vegetation plugs. The dead plant material that resulted from the herbicide application was left in place in order to provide a ground cover and minimize evaporation of soil moisture in cleared plots. Uncleared plots were used to gauge the response of transplanted vegetation to salinity *and* interspecific competition, while transplants placed into cleared plots were used to gauge the response of vegetation to salinity alone.

To extract vegetation/soil plugs for transplanting, a 10 cm diameter stainless steel tube was forced into the ground to a depth of 10 cm. The corer was then twisted to break the soil and vegetation within the tube free of the surrounding soil. The corer and contents were then removed from the ground and the transplant plug pushed out the end of the tube. The majority of the underground biomass was located within 10 cm of the soil surface (Burchill 1991). Each transplant plug contained uniformly monodominant vegetation and soil representative of the zone from which it was extracted.

In uncleared plots, plugs were taken from within the boundary of the plot. In cleared plots, plugs were extracted from just outside the buffer zone. Plugs were then transplanted into corresponding plots of each other zone within each site. For example plugs from plot A of the Salicornia zone were transplanted into 'A plots' of each other zone in the site. Thus, the origin of each transplanted plug was known. Placement of plugs within plots was randomized.

Two types of control plugs were established in each plot. In uncleared plots, one plug of native vegetation was extracted and then replanted into the same hole. In cleared

plots a plug was extracted from just outside the buffer zone of each plot and placed into that plot. In both cleared and uncleared plots this type of control was called a *cut-and-replace* control. The other type of control plug involved delineating a circular area of vegetation with a diameter of 10 cm within each plot. This type of control plug was left untouched and was called a *non-transplanted* control. The *cut-and-replace* control plugs of each zone were compared with *non-transplanted* control plugs to assess the disturbance effects of transplantation. *Cut-and-replace* controls allowed comparison of the response of vegetation transplanted into experimental plots of foreign zones relative to its response in experimental plots of its native zone.

The field experiment was designed to run for two consecutive growing seasons, and required that two complete series of plugs to be established in each plot of each site. In sites 1 and 2 five plugs were used per season, for a total of ten plugs per plot. These plugs consisted of two each of: (a) *non-transplanted* controls; (b) *cut-and-replace* controls; and (c) vegetation plugs transplanted from each of the other vegetation zones of the site. The total number of plugs used in each large site was 400. The two smaller sites required 144 plugs per site. The total number of plugs over all the sites for the duration of the experiment was 1088. All were established in mid-June of 1989.

Cleared plots were periodically weeded to keep them clear of recolonizing vegetation. A schedule of monitoring periods is given in Appendix II. Figure 5.1 shows an example of a cleared plot and an uncleared plot containing transplanted vegetation, and control plugs. Figure 5.2 is a photograph taken in July 1989 of the experimental plot lay-out with transplanted plugs in the Salicornia zone of site 3.

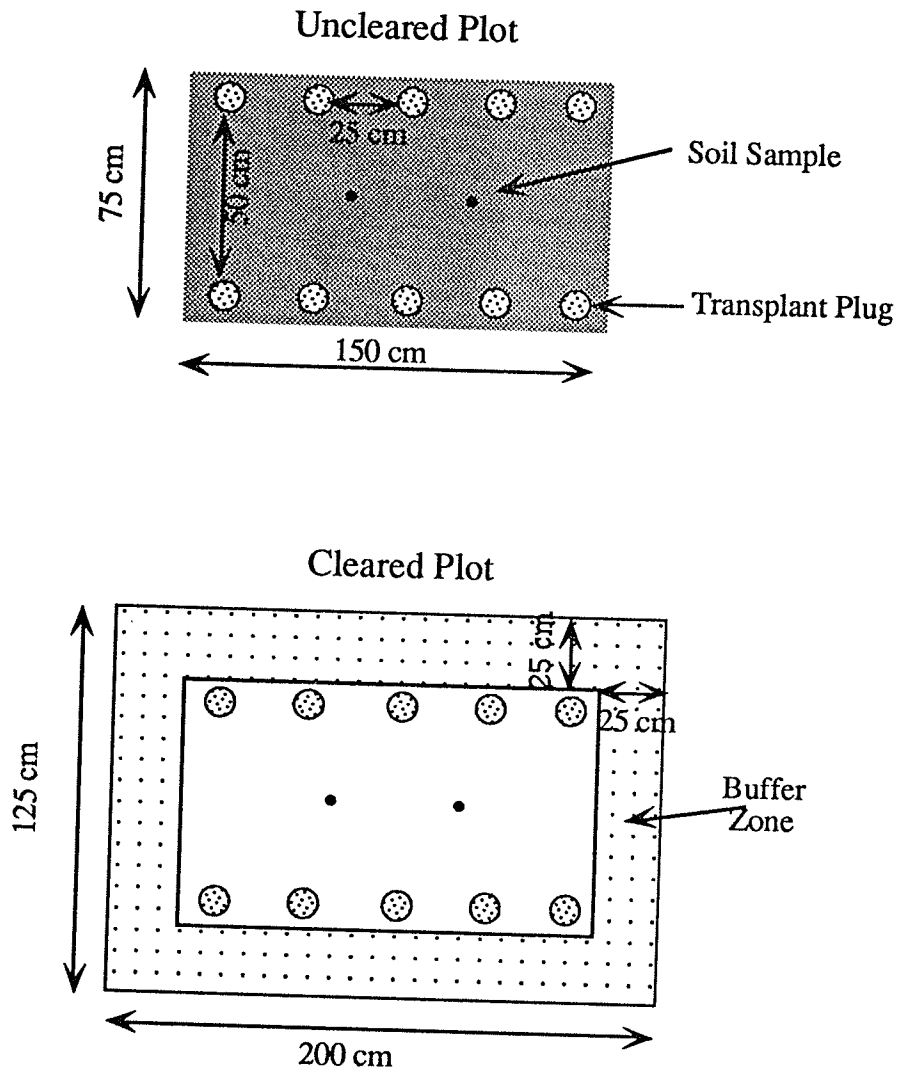


Figure 5.1 Diagram of uncleared (top) and cleared (bottom) plots with transplant plugs from a site containing four vegetation zones. Note the buffer zone around the cleared plot.

Figure 5.2 Photograph of experimental plots in the Salicornia zone of site 3, 1989.

One series of plugs was chosen at random and designated for the 1989 harvest. With the exception of site 3 plugs, the above-ground biomass of each plug of this series was harvested during the final week of August, 1989. The remaining series was harvested during the third week of August, 1990, which, according to the growth and phenology study (see Chapter 4) represented the period of maximum biomass accumulation for the species involved. In each case the biomass of each plug was clipped, placed in plastic bags, labelled, and frozen. The 1989 biomass harvest of site 3 involved the extraction of the entire vegetation plug (including soil) from each plot. The plugs were then placed in labelled plastic bags and frozen. The entire plug was removed in order to determine below-ground biomass. The 1989 harvest results were used to assess the progress of the experiment. Only the 1990 transplant data will be presented and discussed in this thesis.

One soil core sample was also removed from each harvested plug to determine soil water salinity, moisture content, and pH. Soil samples were frozen to preserve moisture. Biomass and soils were then transported to the University of Manitoba for processing.

Above-ground plant material was thawed, separated by species, and dried at 90 ^{o}C for 24 hours. Material was massed and biomass recorded. Species' density was recorded for the 1990 series. Plugs extracted from site 3 in 1989 (for below-ground biomass determinations) were treated as above, and then the soil was washed on a 2mm sieve to removal soil particles from the below-ground material. An attempt was made to separate live material from dead and decaying material. This involved separating roots on the basis of color (live material being whiter, and dead being off-white to brown). The below-ground material was dried, and biomass determined and recorded. No attempt was made to separate below-ground biomass by species because of the difficulty of doing so, and the probable inaccuracy of the results obtained. Results of the below-ground biomass measurements are presented in Appendix IV (1989 harvest data).

Section 5.2.2 - Growth Chamber Transplants

Transplant experiments can also be conducted by growing plants under controlled conditions (such as in a greenhouse or growth chamber) and then transplanting them into the field. This method of transplantation allows more control over the density and uniformity of species being transplanted. *Salicornia rubra, Hordeum jubatum,* and *Calamagrostis inexpansa* --the three dominant species of each vegetation zone of site 3 -- were grown at known densities in a growth chamber and later transplanted into cleared and uncleared plots of site 3.

Seeds of the three species were placed in pots in the growth chamber under conditions favorable for germination (following Kenkel *et al.* 1991). Twenty four pots were used per species, while 10 control pots were established in which no seeds were placed. The control pots allowed analysis of soil moisture, soil water salinity, and pH of the potting medium prior to transplantation. This amounted to a total of 72 species pots and 10 controls. The pots were 10 cm in diameter x 10 cm deep (the same size as the field transplant plugs). A sterilized potting soil mix of 1 part peat: 1 part sand: 2 parts loam was used. Thirty seeds of each species were placed in the pots for germination, and the pots, including the seedless controls, were watered daily to maintain high soil moisture and humidity. After two weeks germination had ceased and seedlings were then removed to establish the following densities for each species: *Salicornia rubra* - 3 plants/pot; *Hordeum jubatum* - 5 plants/pot; *Calamagrostis inexpansa* - 4 plants/pot. Plants were grown for six weeks. At the end of May 1990, the pots were then transported to site 3 and the entire contents of each pot (plants and soil) was placed into the transplant plug holes left from by the previous seasons above/below ground biomass harvest. Four pots of each species were placed into the cleared plots and four into the uncleared plots of each zone. The plants in the plugs were then clipped to conform in height with each other and the surrounding vegetation. The control pots were not transplanted into the site.

The above-ground plant material of the growth chamber transplants was harvested at the same time and in the same manner as the 1990 field transplants. A soil core was also collected from each transplant soil for purposes of soil water content, soil water salinity, and pH determinations.

Section 5.2.3 - Transplant Data Analysis

Means (± SE) of biomass were determined for the dominant species transplanted into cleared and uncleared plots of each zone, as well as for the control plugs in cleared and uncleared plots of each zone. Mean values (± SE) were also calculated for the soil moisture, soil water salinity, and pH of transplanted and control plug soils in each zone. Biomass values for species in field transplanted plugs were calculated relative to their corresponding *cut-and-replace* controls (i.e. biomass (g) of transplanted plug - biomass (g) of the control = net gain or loss of biomass (g) due to transplantation). A two-factor ANOVA ($\alpha = 0.05$) with interaction was used to determine if there were significant differences in biomass accumulation between cleared and uncleared plots within each zone, and between cleared plots from one zone to the next, for each species transplanted. In a number of cases the vegetation died as a result of transplantation. When this occurred in both cleared and uncleared plots of a particular zone, the data were excluded from the ANOVA. T-tests using the pooled estimate of variance ($\alpha = 0.05$) were used to indicate whether significant differences existed between the biomass of species in *non-transplanted* controls and *cut-and-replace* controls in order to determine effects of transplantation on the dominants. The t-test was also used to determine if significant differences existed between soil factors (salinity, moisture, and pH) of cleared versus uncleared plots, in order to determine if the soil of plots had been altered by herbicide application. ANOVA and Dunnett's test ($\alpha = 0.05$) for comparing a control mean with each other group mean were used to determine whether soil factors of plugs (groups) were significantly different from those of the plots (controls) into which they were transplanted.

Only the 1990 biomass accumulation results are presented and discussed in the following sections. The biomass accumulation results for 1989 are presented in Appendix IV. The 1989 results allowed assessment of the experiment's progress over the first season. Density can be used as a measure of a species' growth response, however, biomass accumulation was deemed to be the better indicator of overall plant production in the transplanted plugs. The results from density data for the 1990 harvest, although not dealt with in the following sections, are presented in Appendix V.

Section 5.3 - Results

Section 5.3.1 - Soil Factors of Cleared and Uncleared Plots

It was important for the success of the transplant experiment that the effect of the herbicide application on soil factors be minimal. In other words, the soil characteristics of cleared plots should not differ appreciably from those of uncleared plots within the same zone. I was concerned that the removal of vegetation in cleared plots may have led to changes in evaporation rates, and thus altered the soil moisture, pH, and salinity of the cleared plots. In order to determine if this occurred, the soil pH, soil moisture content, and soil water salinity of cleared and uncleared plots from each zone of each site were compared to determine if significant differences existed . Figures 5.3 - 5.5 present a series of graphs showing the relationship between cleared and uncleared plots for the three soil factors analyzed.

The specific data tested for soil moisture and soil water salinity were collected on the final sample date of 1989, and the first and last sample dates of 1990. Data for comparison of soil pH are from the 1990 season only. These dates were chosen because they are periods between which climatic conditions differed. Results of this analysis indicated that, for the most part, soil pH, moisture, and water salinity were not significantly

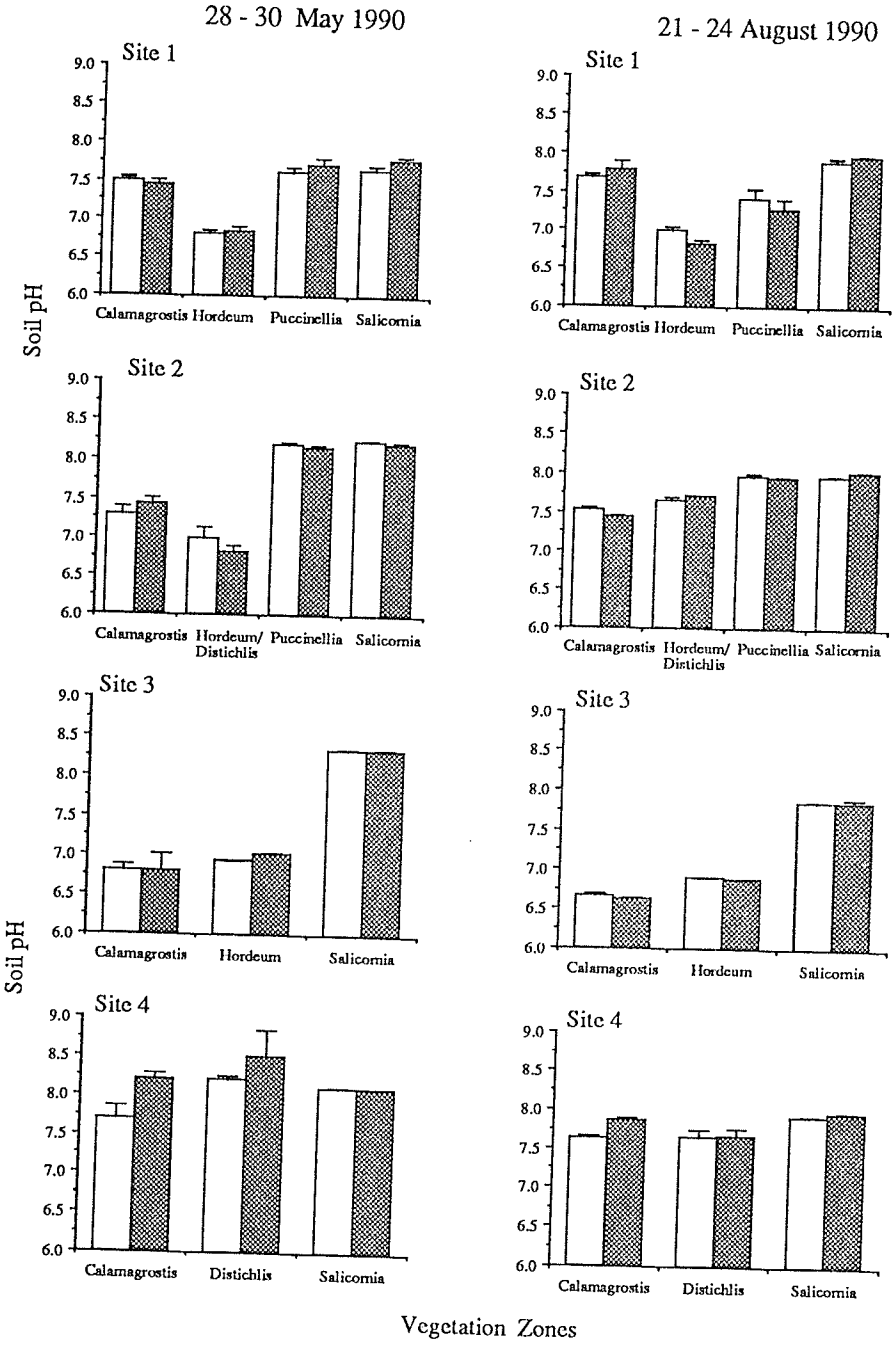


Fig. 5.3 Comparison of soil pH between cleared (□) and uncleared (▨) plots in vegetation zones of each study site. pH levels are presented for the second sample date in 1990 (pH was not recorded for the first sample date of 1990) and the last sample date in 1990. (n = 5 for sites 1 and 2, n = 3 for site 3 and 4). Values are means, ± S.E.

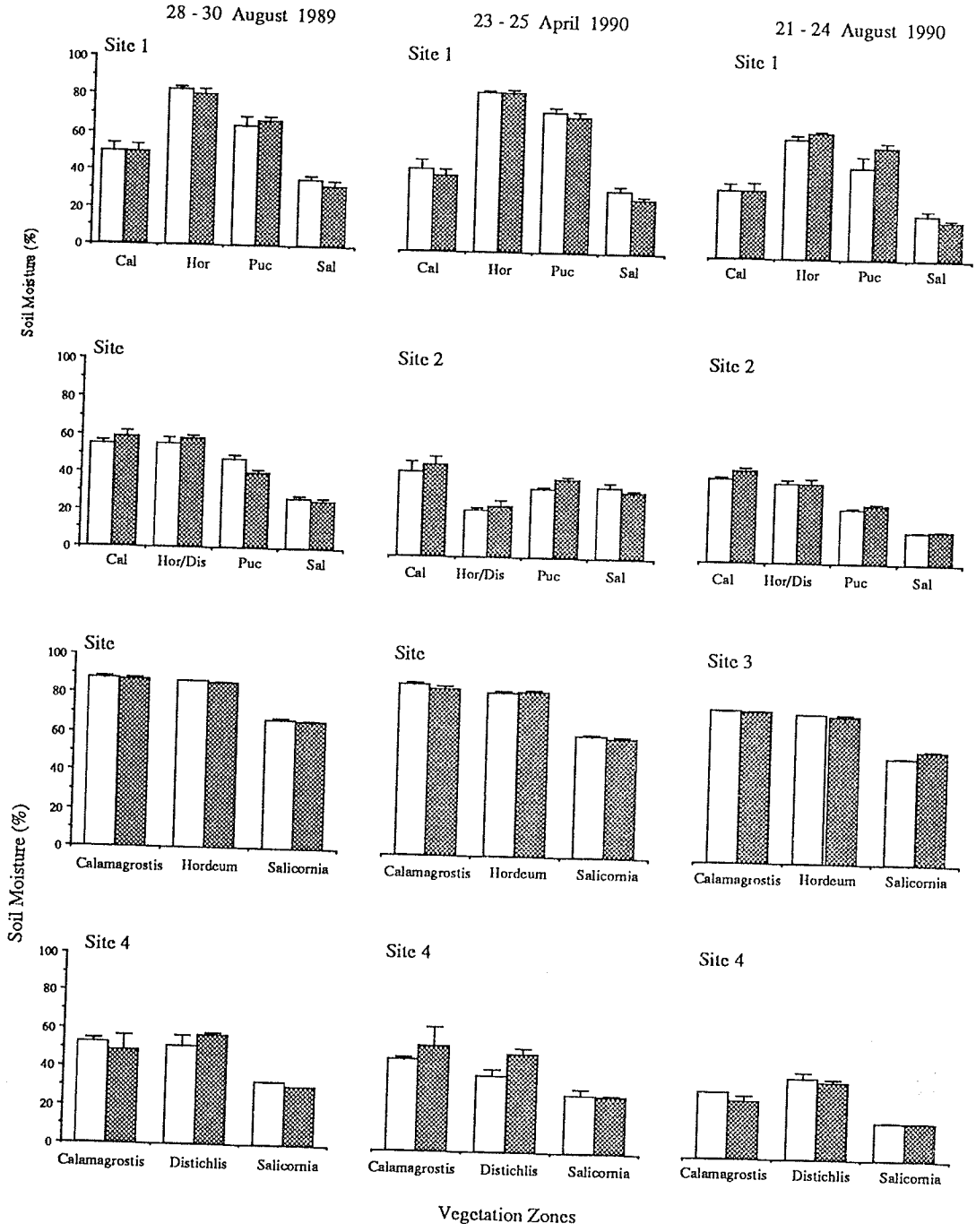


Fig. 5.4 Comparison of soil moisture percentages between cleared (□) and uncleared (▨) plots in vegetation zone soils of each study site. Moisture levels are presented for the last sample date in 1989, the first sample date in 1990, and the last sample date in 1990. n = 5 for sites 1 and 2, n = 3 for sites 3 and 4. Values are means, ± S.E.

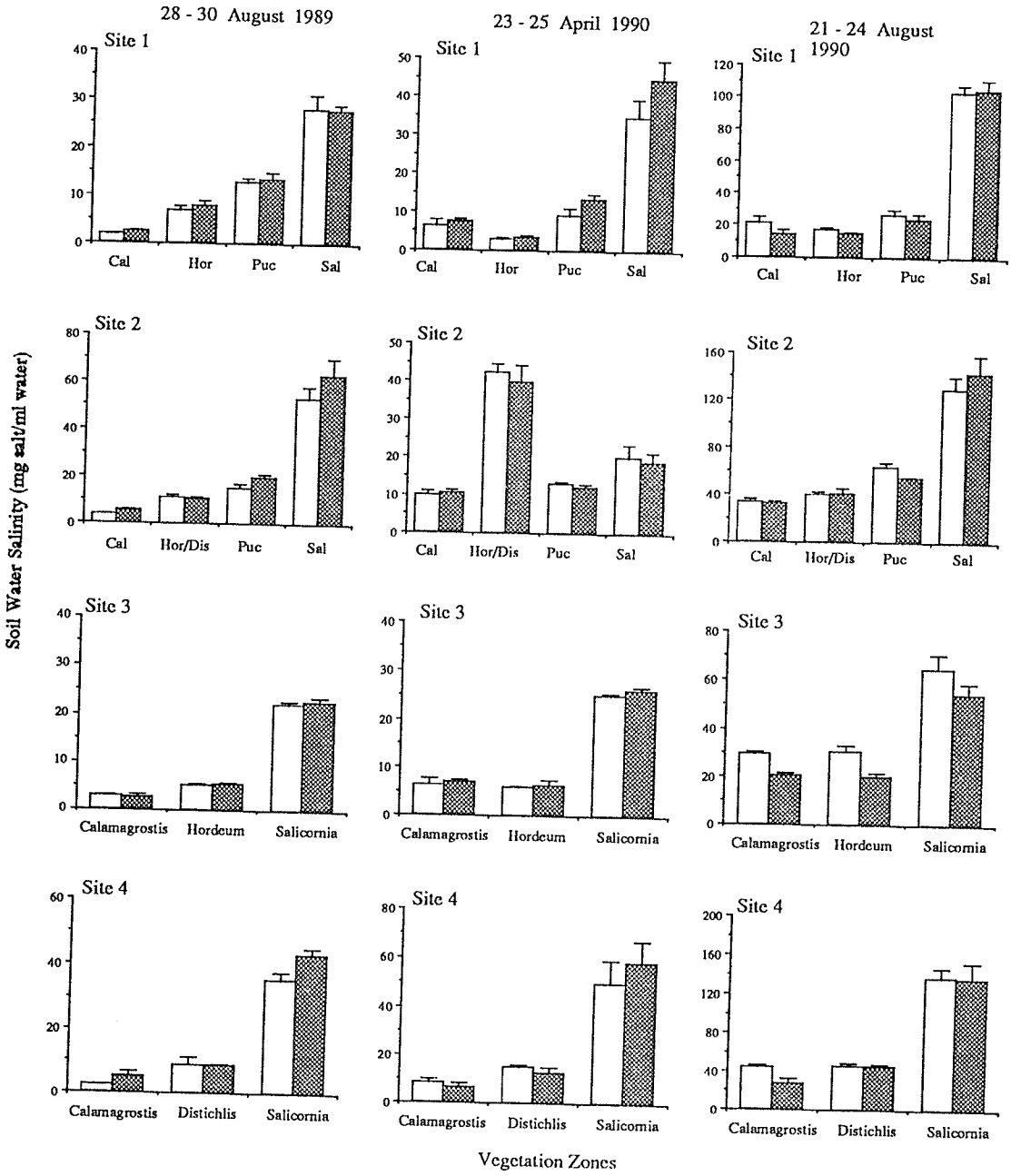


Fig. 5.5 Comparison of soil water salinity levels between cleared (□) and uncleared (▨) plots in vegetation zone soils of each study site. Salinity levels are presented for the last sample date in 1989, the first sample date in 1990, and the last sample date in 1990. n = 5 for sites 1 and 2, n = 3 for site 3 and 4. Values are means, ± S.E.

different between cleared and uncleared plots. A few exceptions to this are listed in Table 5.1.

Table 5.1 List of occurrences by date, site, and vegetation zone in which soil pH, soil moisture, and soil water salinity differed significantly between cleared and uncleared plots. (t-test $\alpha = 0.05$).

Soil Factor	Sample Date	Site	Vegetation Zone
pH	21-24 Aug 1990	1	Hordeum
	21-24 Aug 1990	4	Calamagrostis
Soil Moisture	28-30 Aug 1989	2	Puccinellia
	28-30 Aug 1989	4	Salicornia
	23-25 Aug 1990	2	Calamagrostis
Soil Water Salinity	28-30 Aug 1989	1	Calamagrostis
	28-30 Aug 1989	2	Calamagrostis
	21-24 Aug 1990	3	Calamagrostis
	21-24 Aug 1990	3	Hordeum

Although there were, on occasion, significant differences between cleared and uncleared plots, these differences were relatively small. The soil factors within the plots (whether cleared or uncleared) of a particular zone, still remained within the general tolerance range for the zone's dominant species. Thus, herbicide application and eradication of vegetation did not appear to adversely affect or alter the soil of the cleared plots.

Section 5.3.2 - Soil Factors of Plots and Transplanted Vegetation Plugs

A second important condition for the success of the experiment was the need for conformity between the soil of the transplanted vegetation plugs and the soil of the plots into which they were placed. For example, the soil of vegetation plugs extracted from the Salicornia zone plots and transplanted into the Calamagrostis zone plots should have decreased in salinity and pH, and increased in soil moisture to levels found in the soil of the Calamagrostis zone plots.

Graphs comparing the soil of experimental plots and transplant plugs are presented in Figures 5.6 - 5.11. The data for transplant plug soils are from soil cores collected from

the 1990 biomass harvest period. Data for plot soils were obtained from soil cores collected in the plots at the same time as plug harvesting.

Soil pH of transplant plugs was collected from site 2 only (Figure 5.6). Note that each graph represents the transplanted plugs from a specific zone, while the bottom axis lists the vegetation zones into which the plugs were transplanted. The black bars represent the values obtained from transplant plug soils while the shaded bars represent levels reported for the plot soils.

The format of the graphs used to present the moisture and salinity data (Figures 5.7 - 5.11) differs from that used to present the pH data (Figure 5.6), in that each Figure compares the soil of a particular type of transplant plug with the soil of each zone at each site into which it was placed. Both soil moisture and soil water salinity are presented in each Figure. For example, Figure 5.7 is a series of graphs comparing the soil of *Calamagrostis inexpansa* transplant plugs to the soil of each zone of each site. Soil moisture is shown on the left side of the page, while soil water salinity is on the right. The left axis of each graph represents the scale for each soil factor. Note that this scale may differ between sites. The bottom axis represents the vegetation zones into which, in the case of Figure 5.7, transplant plugs containing *Calamagrostis inexpansa* were placed. Black bars represent the soil of the transplant plugs, while shaded bars represent the soil of the experimental plots.

The results of the statistical analysis are presented in Appendix VI. It was discovered that the majority of the transplanted soils were significantly higher or lower in soil moisture, soil water salinity, and soil pH than the soils into which they were placed. Thus, the degree of conformity between transplant plug soils and experimental plot soils was less than optimal. However, by looking at the graphed results, a trend approaching conformity is apparent. In general the soil water salinity of transplant plugs

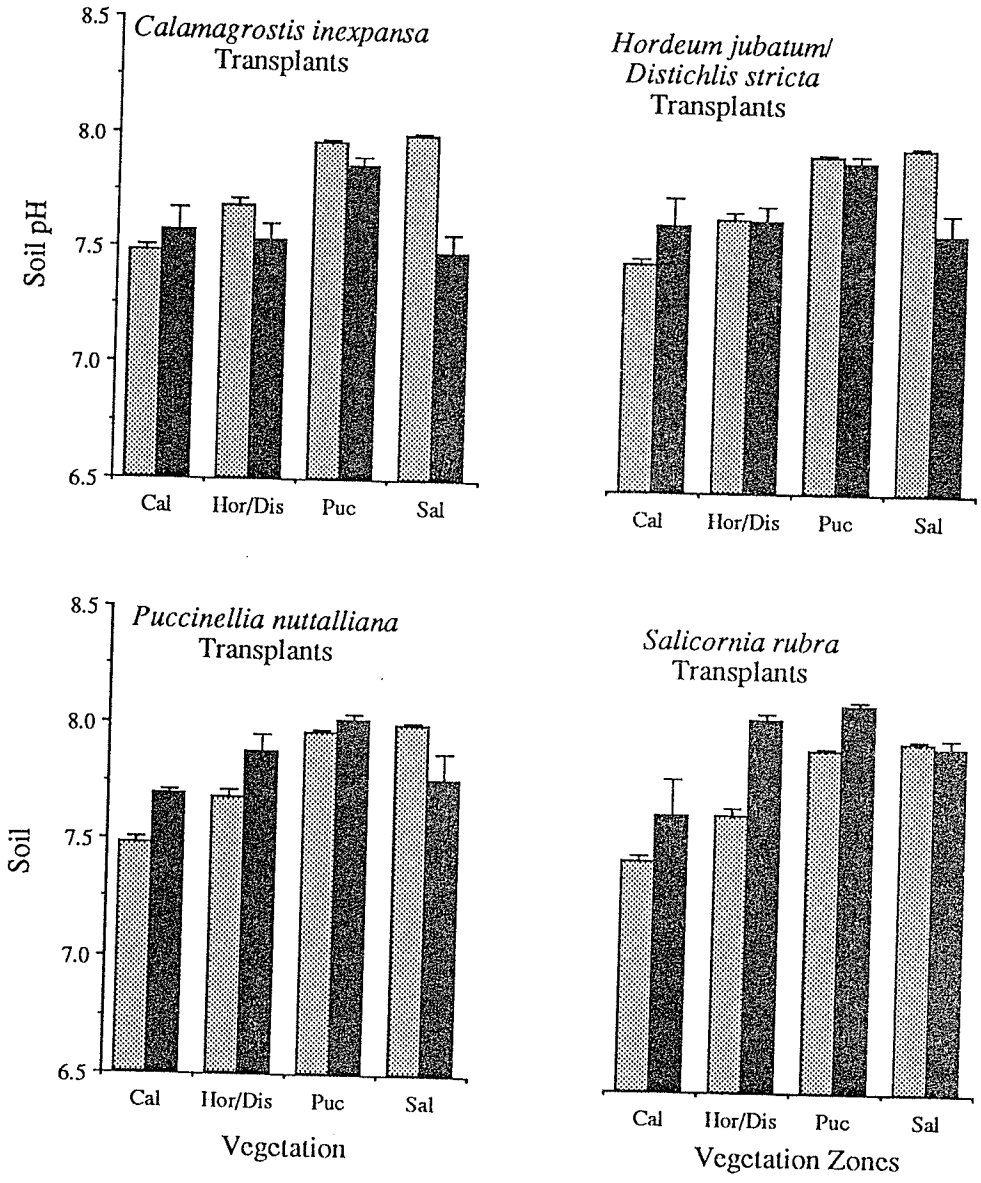


Fig. 5.6 Soil pH of transplant plugs (■) and experimental plots (▨) in each vegetation zone of site 2. Vegetation zones are: Calamagrostis (Cal); Hordeum (Hor); Distichlis (Dis); Puccinellia (Puc); and Salicornia (Sal). Data is from the 1990 harvest/soil collection. n = 10. Values are means, ± S.E.

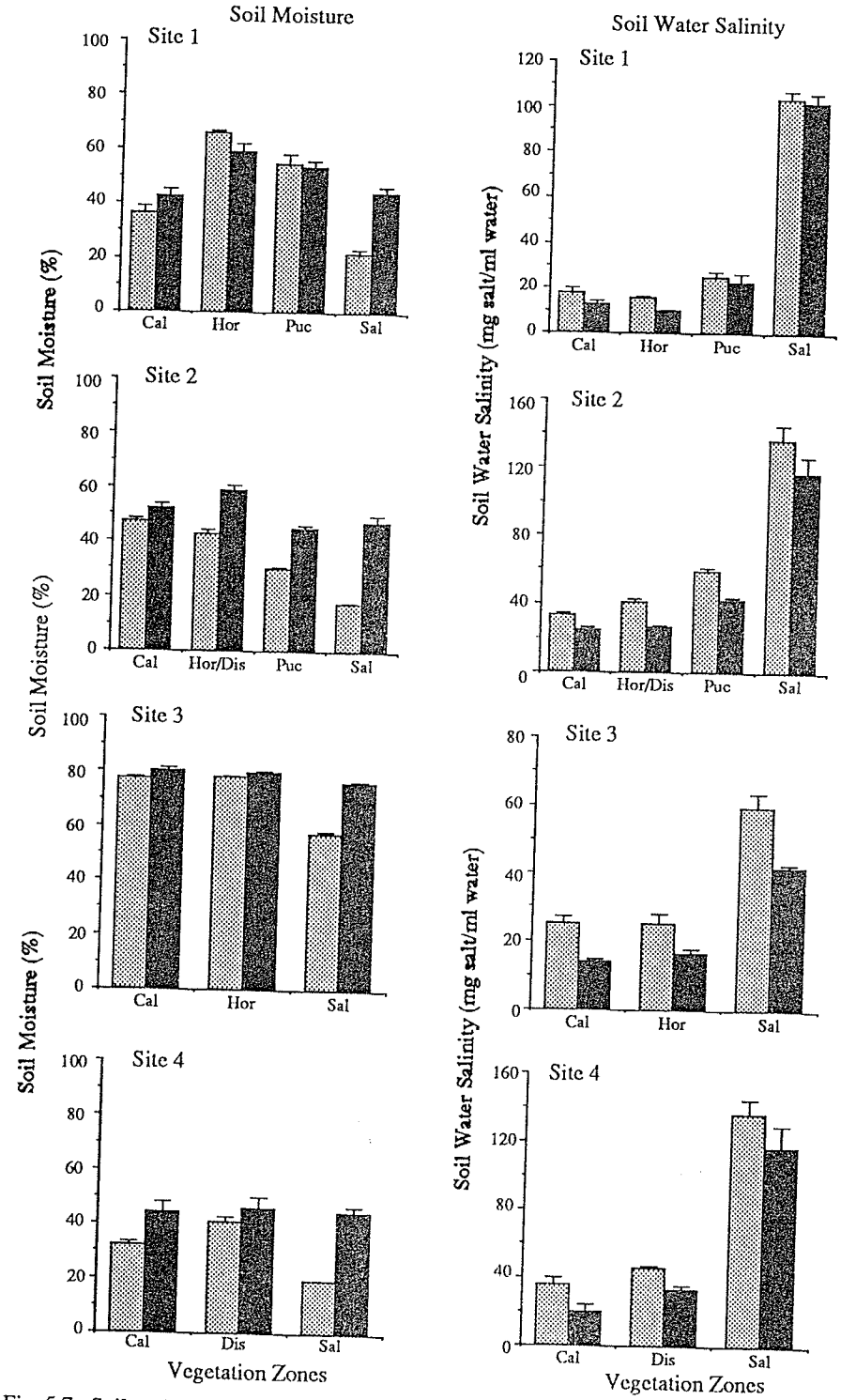


Fig. 5.7 Soil moisture and soil water salinity of Calamagrostis transplant plugs (▩) and experimental plots (▨) of each vegetation zone of each site. Vegetation zones are: Calamagrostis (Cal); Hordeum (Hor); Distichlis (Dis); Puccinellia (Puc); and Salicornia (Sal). Data is from the 1990 harvest/soil collection. n = 10 for site 1 and 2, n = 6 for sites 3 and 4. Values are means, ± S.E.

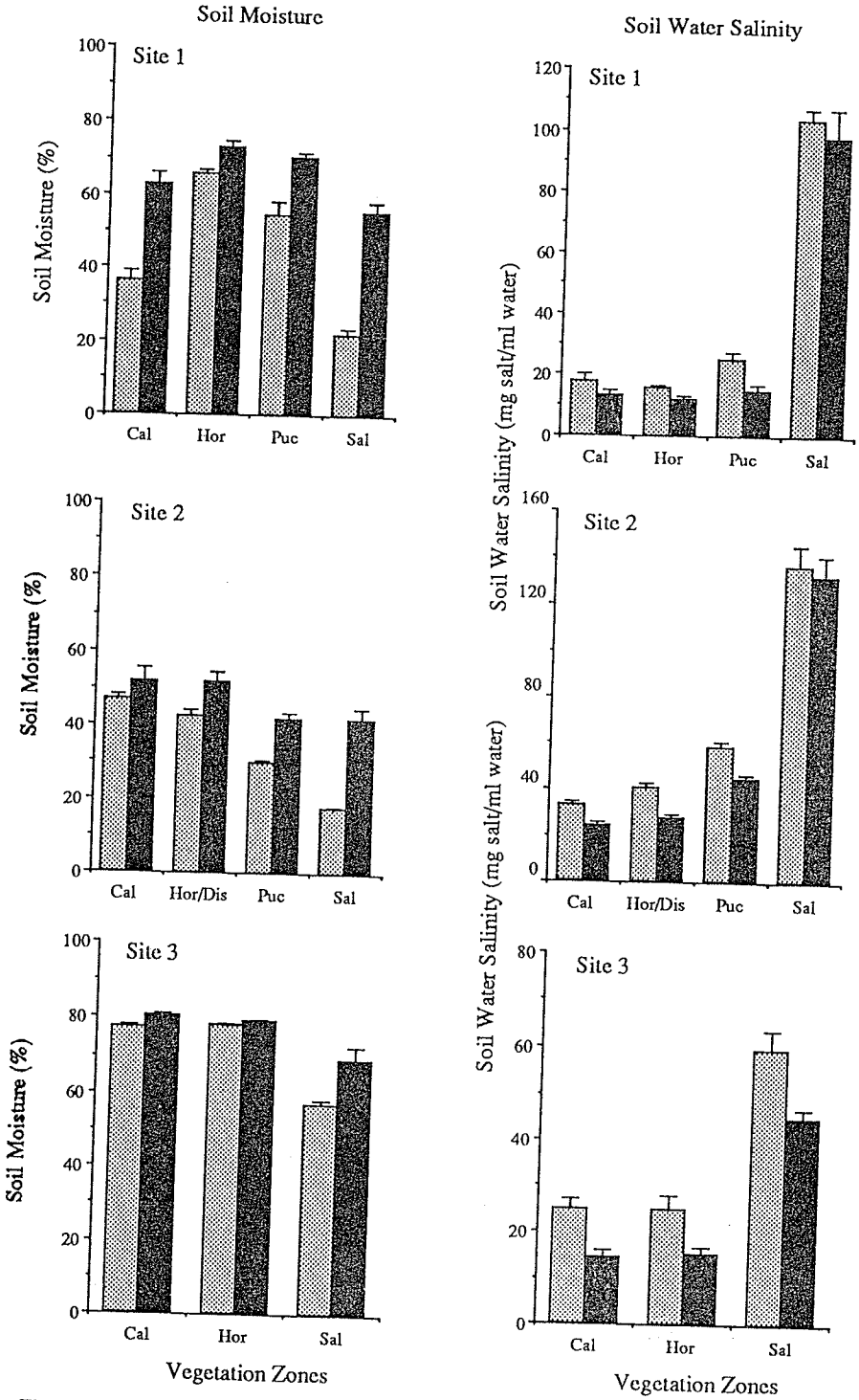


Fig. 5.8 Soil moisture and soil water salinity of Hordeum transplant plugs (■) and experimental plots (▩) of each vegetation zone of each site. Vegetation zones are: Calamagrostis (Cal); Hordeum (Hor); Distichlis (Dis); Puccinellia (Puc); and Salicornia (Sal). Data is from the 1990 harvest/soil collection. n = 10 for sites 1 and 2, n = 6 for site 3. Values are means, ± S.E.

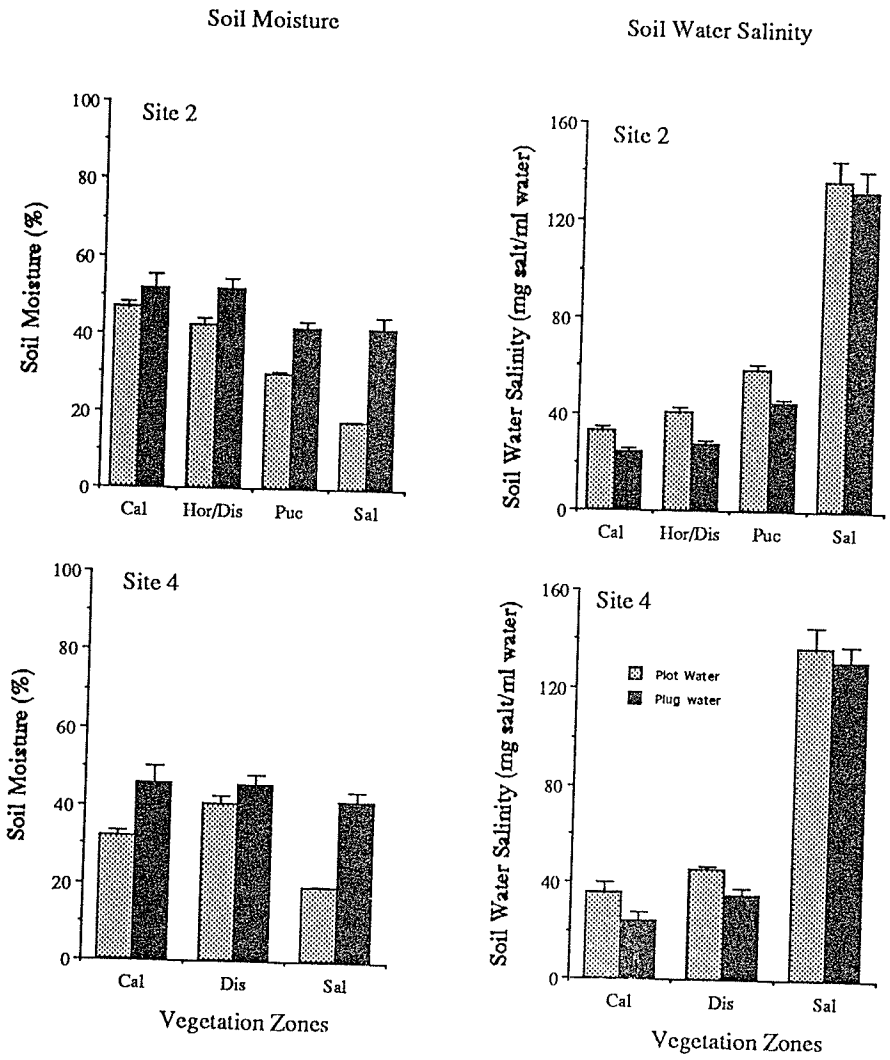


Fig. 5.9 Soil moisture and soil water salinity of Distichlis transplant plugs (▩) and experimental plots (▨) of each vegetation zone of each site. Vegetation zones are: Calamagrostis (Cal); Hordeum (Hor); Distichlis (Dis); Puccinellia (Puc); and Salicornia (Sal). Data is from the 1990 harvest/soil collection. n = 10 for site 2, n = 6 for site 4. Values are means, +/- S.E.

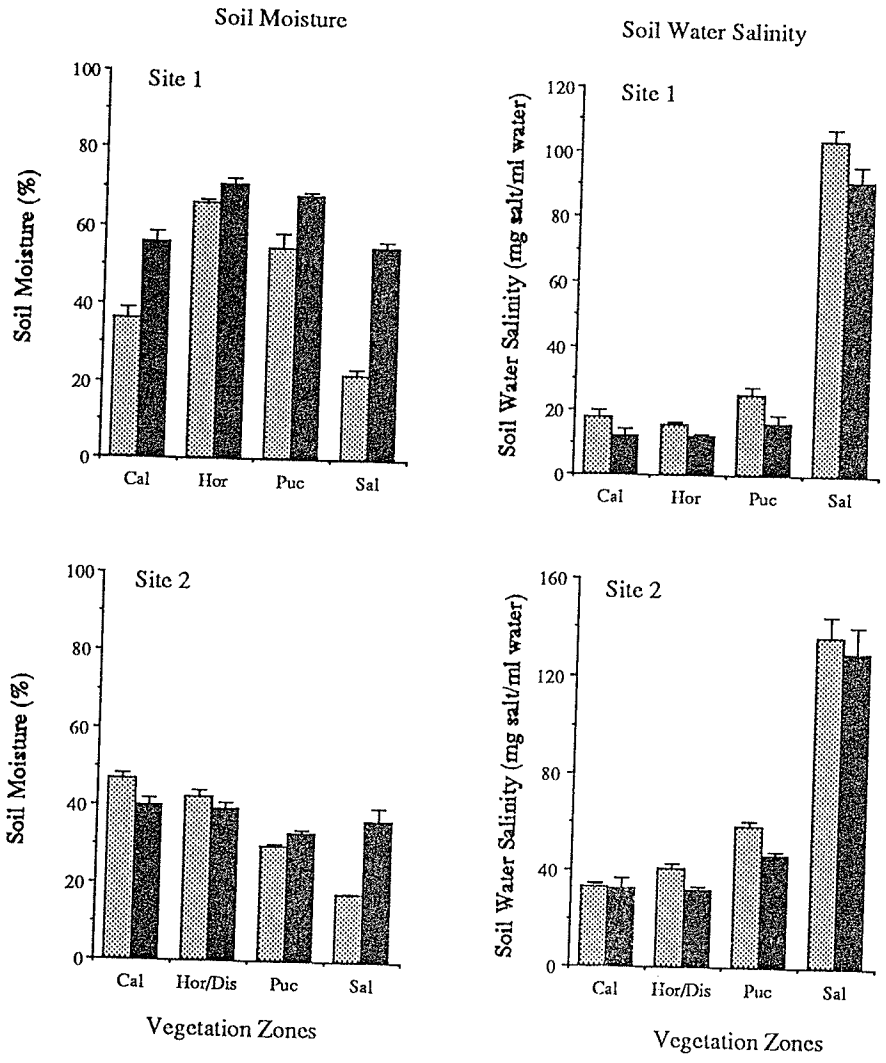


Fig. 5.10 Soil moisture and soil water salinity of Puccinellia transplant plugs (▩) and experimental plots (▨) of each vegetation zone of each site. Vegetation zones are: Calamagrostis (Cal); Hordeum (Hor); Distichlis (Dis); Puccinellia (Puc); and Salicornia (Sal). Data is from the 1990 harvest/soil collection. n = 10. Values are means ± S. E.

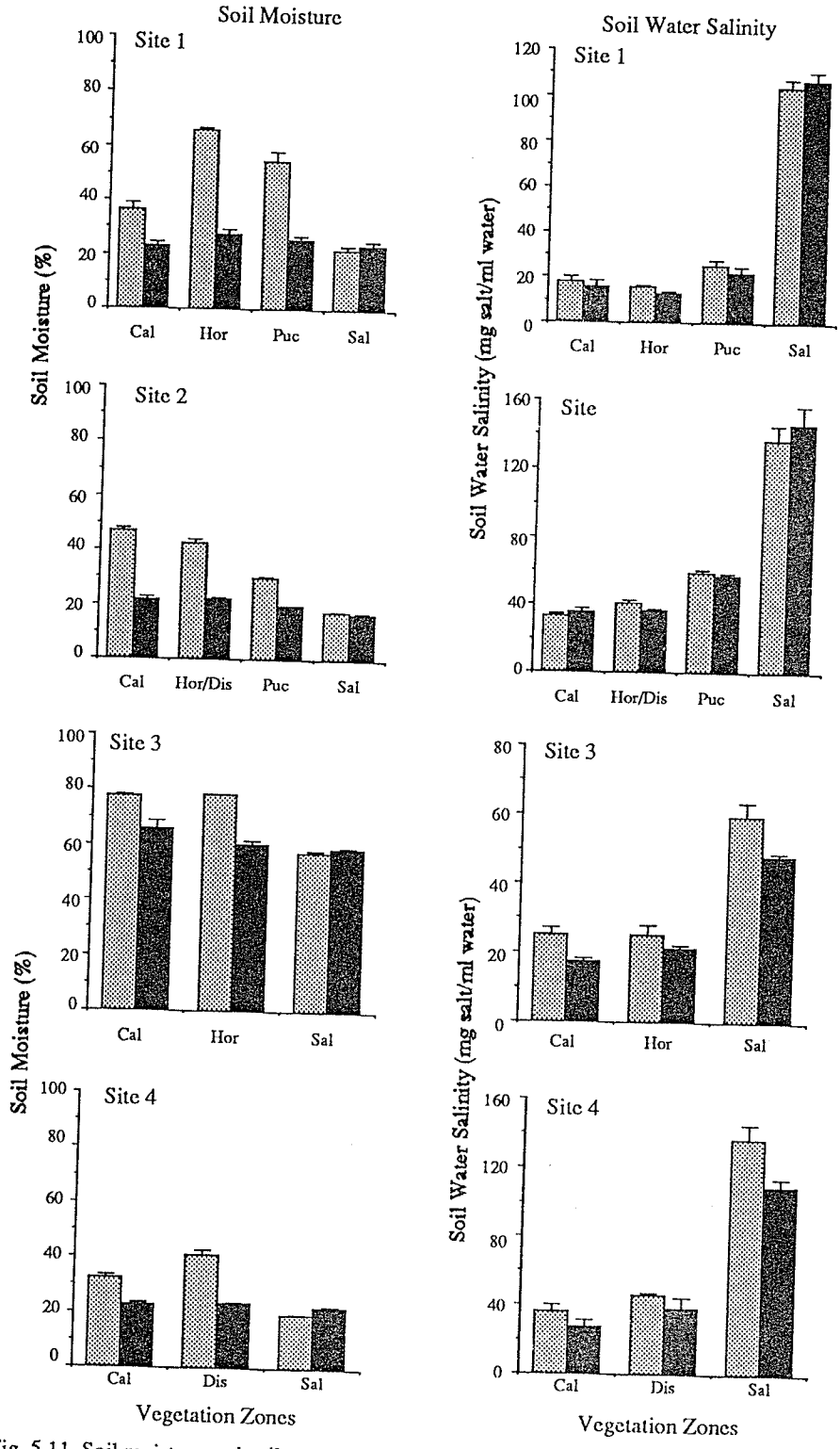


Fig. 5.11 Soil moisture and soil water salinity of Salicornia transplant plugs (■) and experimental plots (□) of each vegetation zone of each site. Vegetation zones are: Calamagrostis (Cal); Hordeum (Hor); Distichlis (Dis); Puccinellia (Puc); and Salicornia (Sal). Data is from the 1990 harvest/soil collection. n = 10 for site 1 and 2, n = 6 for sites 3 and 4. Values are means, ± S. E.

from low salinity vegetation zones increased when placed into the higher saline zones. The expected reverse trend in soil moisture did not occur. Soil moisture of transplant plugs showed the least amount of change and conformity to zone soils. Moisture content is strongly influenced by the amount of organic matter in the soil. Thus, the soil in plugs from low salinity zones, such as Hordeum and Calamagrostis, which tend to be high in organic matter, maintained a high soil moisture level when transplanted into the high salinity zones, even though the surrounding soil of the high salinity zones was low in moisture. This retention of soil moisture did not appear to radically hinder soil water salinity from increasing in plugs put into high salinity soils. Thus, the proportion of water in the transplant plugs often differed significantly from the amount in the surrounding soil, but the concentration of salts in that water showed a trend towards conformity.

Section 5.3.4 - Field Transplant Experiment

Introduction

The previous section dealt with the soil characteristics of transplanted plugs in relation to the soil of experimental plots of each zone. This section will compare the response of the transplanted species to that of the *cut-and-replace* control plugs of uncleared plots. First, the mean biomass (± SE) for each dominant species transplanted into cleared and uncleared plots in each zone of each site was calculated. Secondly, the mean biomass (± SE) of the dominant species in the *cut-and-replace* control plugs from uncleared plots in each zone of each site was determined. The means of the transplanted dominants were then standardized to that of the *cut-and-replace* controls for each species. Figures 5.12 - 5.16 present the results of this data manipulation. Each Figure represents the biomass results for a specific dominant. For example, Figures 5.12 presents the response (as relative biomass accumulation) of *Calamagrostis inexpansa* (i.e. the plugs that originated from the Calamagrostis zone) to transplantation into cleared and uncleared

plots of each zone in each study site. The 1990 seasonal range of salinity for each zone is presented in parenthesis along the x-axis of each graph. The horizontal line across each graph which intercepts the y-axis at zero represents the *cut-and-replace* control to which the transplant plugs are compared. Values occurring above the horizontal line represent cases where growth was greater than that of the control, while values below the line signify cases in which growth declined below the control. For example, in the site 3 graph of Figures 5.12, the maximum growth of *Calamagrostis inexpansa* occurred when it was transplanted into cleared plots of its native zone, while it decreased in growth when transplanted into the Hordeum zone, and died in the plots of the Salicornia zone.

The data were also subjected to a two-factor ANOVA ($\alpha = 0.05$) with interaction. The questions asked of the analysis were:

(1) Was there a significant effect on the growth of the dominant species when they were transplanted into different vegetation zones? Did an increase or decrease in salinity significantly affect the growth response of the transplanted species?

(2) Was there a significant effect on the response of transplanted dominant species due to treatment of plots? In other words, did a species' response to transplantation into cleared plots, with no competition, differ significantly from its response to transplantation into uncleared plots, where competition was present?

(3) Was there any interaction between the two variables (competition and salinity) on the growth response of transplanted species? That is, if both the effects of competition and salinity proved significant, was the effect of competition the same between different salinity levels (no interaction), or did the effect of competition differ from one zone to the next (interaction present).

Calamagrostis inexpansa

Transplants of *Calamagrostis inexpansa* showed the best growth when placed into their native zone (Figure 5.12, Table 5.2), and died when transplanted into plots of the

Salicornia zones of sites 1 - 4, the Puccinellia zones of sites 1 and 2, and the Hordeum, Hordeum/Distichlis, and Distichlis zones of sites 1, 2, and 4 respectively. In sites 3 and 4, *Calamagrostis inexpansa,* as well as showing best growth in its native zone, showed a distinction between treatments, performing better in cleared plots than in the uncleared plots of its native zone ($p < 0.05$ ANOVA). It is also interesting to note that when transplanted into the Hordeum zone of site 3, where soil factors between the Hordeum and Calamagrostis zones were very similar, the species also performed better in cleared plots as opposed to uncleared plots.

Table 5.2 Results of two-factor ANOVA ($\alpha = 0.05$) conducted on biomass data of *Calamagrostis inexpansa* transplants at each site. The two factors are: vegetation zones (soil water salinity) ($n = 10$ for sites 1 and 2, $n = 6$ for sites 3 and 4); and plot treatment (presence or absence of neighbors) ($n = 5$ for sites 1 and 2, $n = 6$ for site 3, $n = 3$ for site 4). N/A indicates non-applicability due to death of the transplanted individuals in each zone except the Calamagrostis zone.

Saline Site	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
1	N/A	0.8709	N/A
2	N/A	0.4588	N/A
3	0.0671	0.0132	0.7965
4	N/A	0.0395	N/A

The graphs and the ANOVA results indicate that the main factor influencing the performance of transplants in sites 1 and 2 was soil water salinity (vegetation zones). ANOVA indicated that differences between transplants placed into the Calamagrostis zone and those placed into the Hordeum zone in site 3 were less significant ($p = 0.0671$).

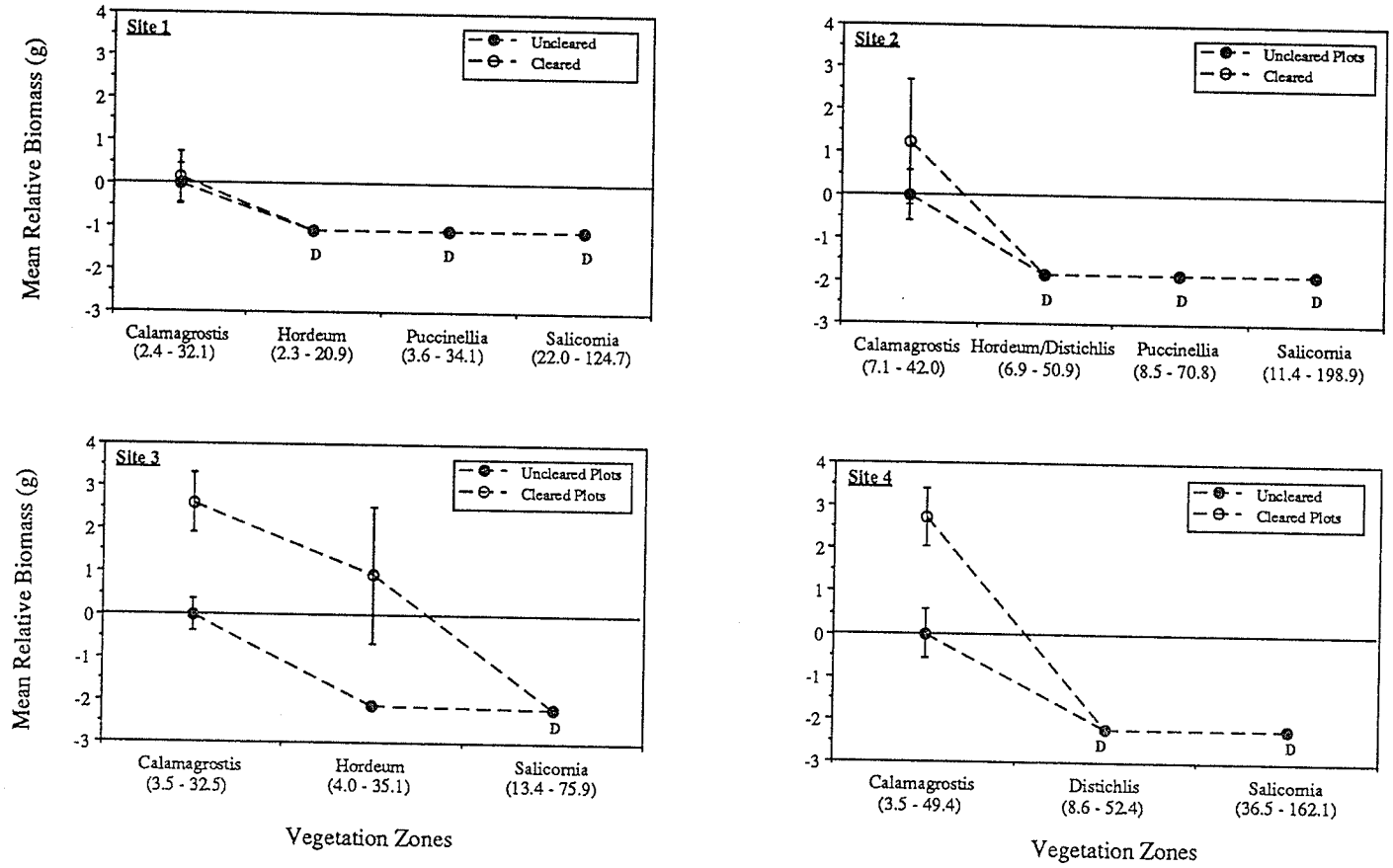


Fig. 5.12 Response of *Calamagrostis inexpansa* in vegetation plugs taken from the Calamagrostis zone and transplanted into each vegetation zone at each site. Response is measured bybiomass accumulation per transplant plug relative to the Calamagrostis zone cut-and-replace control plugs. Biomass values are means ± S.E. (n = 5 for sites 1 and 2, n = 3 for sites 3and 4). Values in parentheses are soil water salinity ranges for the 1990 season. The letter **D** indicates that the vegetation in the transplant plug was dead prior to harvesting.

However, the presence or absence of neighbors (plot treatment) played a significant role in determining the response of these surviving transplants ($p = 0.0132$). In Site 4 salinity strongly influenced the performance of the transplants, while ANOVA results indicate a significant difference ($p = 0.0395$) between plot treatments for the transplants that survived in the the Calamagrostis zone.

Hordeum jubatum

Trends in the performance of *Hordeum jubatum* transplants in sites 1 - 3 are not as evident as those expressed in the case of *Calamagrostis inexpansa* transplants (Figure 5.13). Results tended to vary somewhat between sites. However, some similarities can be observed. In all three sites *Hordeum jubatum* died when transplanted into plots of the Salicornia zone. The vegetation also died in plugs transplanted into the Puccinellia zone plots of site 2, while those placed into the Puccinellia zone plots of site 1 showed a decline in mean biomass accumulation. Placement of *Hordeum jubatum* into uncleared plots of the Calamagrostis zone of site 1 also resulted in death. Transplantations into uncleared plots in the Calamagrostis zones revealed no change in growth in site 2, and a decline in growth in site 3 relative to the *cut-and-replace* controls.

In zones in which transplants survived, the highest mean biomass accumulations were recorded in the cleared plots as opposed to the uncleared plots. ANOVA results (Table 5.3) indicate that the response of the surviving plants appeared to be influenced more by plot treatment than by salinity levels in sites 1 and 2 ($p < 0.05$).

The growth response of surviving *Hordeum jubatum* transplants in site 3 differed somewhat from that of sites 1 and 2. Both the zone and the treatment were found to significantly affect the species' response ($p = 0.0001$), and significant interaction between the two variables was evident ($p = 0.0002$). Figure 5.13 shows that in site 3 the

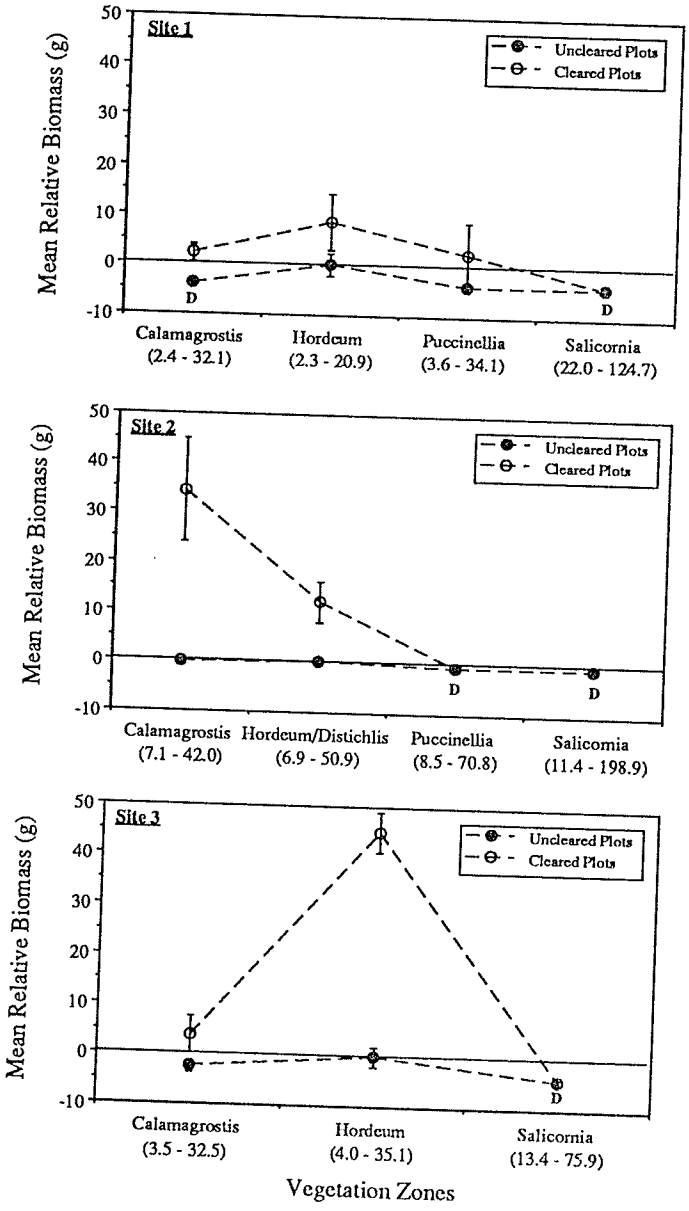


Fig. 5.13 Response of *Hordeum jubatum* in vegetation plugs taken from the Hordeum and Hordeum/Distichlis zones and transplanted into each vegetation zone at each site. Response is measured by biomass accumulation per transplant plug relative to the Hordeum or Hordeum/Distichlis zone cut-and-replace control plugs. Biomass values are means ± S.E. (n = 5 for sites 1 and 2, n = 3 for site 3). Values in parentheses are soil water salinity ranges for the 1990 season. The letter **D** indicates that the vegetation of these plugs died prior to harvesting.

performance of *Hordeum jubatum* was highest for transplants placed into cleared plots of its native zone. When transplanted into cleared plots of the Calamagrostis zone, biomass accumulation did not differ from than that of the *cut-and-replace* controls in the Hordeum zone.

Table 5.3 Results of two-factor ANOVA ($\alpha = 0.05$) conducted on biomass data of *Hordeum jubatum* transplants at each site. The two factors are: vegetation zones (soil water salinity) (n = 10 for sites 1 and 2, n = 6 for site 3); and plot treatment (presence or absence of neighbors) (n = 15 for site 1, n = 10 for site 2, n = 6 for site 3).

Saline Site	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
1	0.2861	0.0263	0.9239
2	0.0667	0.0008	0.0651
3	0.0001	0.0001	0.0002

Distichlis stricta

In site 2, *Distichlis stricta* growth was negligible when transplanted into the Puccinellia zone, and death resulted from transplantation into the Salicornia zone (Figure 5.14). The species survived transplantation into plots of the Hordeum/Distichlis zone and the Calamagrostis zone. However, the biomass of the transplants did not differ between these latter zones. The ANOVA results for site 2 (Table 5.4) indicate that there was no significant difference due to plot treatment for biomass accumulation (p = 0.9528 ANOVA), but there was a significant difference due to vegetation zones (p = 0.0074) for the surviving transplants.

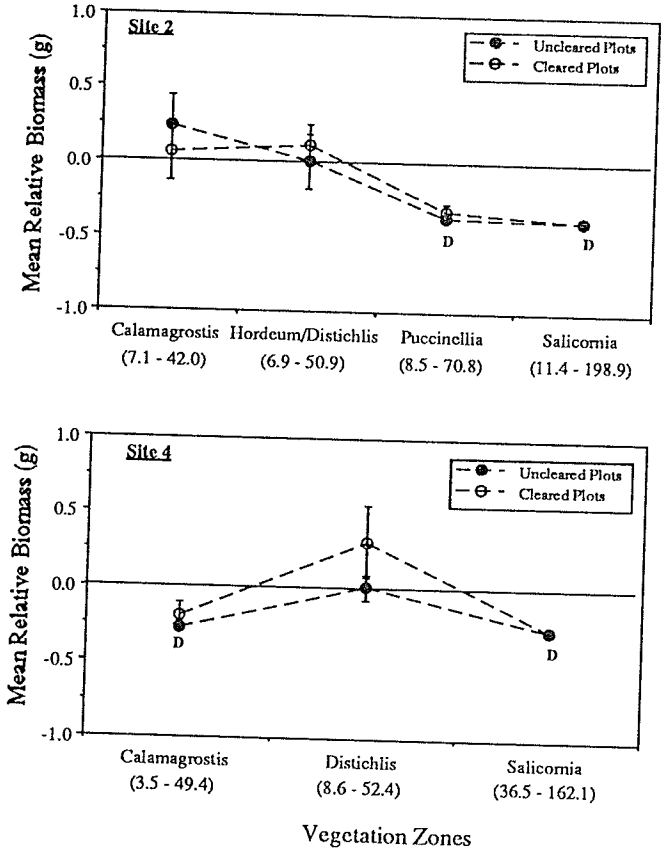


Fig. 5.14 Response of *Distichlis stricta* in vegetation plugs taken from the Hordeum/Distichlis and Distichlis zones and transplanted into each vegetation zone at sites 2 and 4. Response is measured by biomass accumulation per transplant plug relative to the Distichlis or Hordeum/Distichlis zone cut-and-replace control plugs. Biomass values are means ± S.E. (n = 5 for site 2, n = 3 for site 4). Values in parentheses are soil water salinity ranges for the 1990 season. The letter **D** indicates that the vegetation of these plugs died prior to harvesting.

Table 5.4 Results of two-factor ANOVA ($\alpha = 0.05$) conducted on biomass data of *Distichlis stricta* transplants at each site. The two factors are: vegetation zones (soil water salinity) (n = 10 for site 2, n = 6 for site 4); and plot treatment (presence or absence of neighbors) (n = 15 for site 2, n = 6 for site 4).

Saline Site	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
2	0.0074	0.9528	0.6089
4	0.0196	0.1836	0.4292

The trend in the growth response of *Distichlis stricta* to transplantation in site 4 differed considerably from that of site 2. As in site 2, plants died when placed into the Salicornia zone. However, unlike site 2, transplantation into uncleared plots of the Calamagrostis zone of site 4 also resulted in the death of the plants. Mean biomass of *Distichlis stricta* also decreased below the *cut-and-replace* control when transplanted into cleared plots of the Calamagrostis zone. Transplantation into cleared plots of its own zone in site 4 resulted in an increase in mean biomass. Excluding the transplants placed into the Salicornia zone, ANOVA indicates that biomass was significantly different between the remaining zones ($p = 0.0196$), but was not significantly different for the plot treatments ($p = 0.1836$).

Puccinellia nuttalliana

Transplantation of *Puccinellia nuttalliana* plugs was conducted in sites 1 and 2 only. The biomass accumulation of *Puccinellia nuttalliana* in transplant plugs showed some similarities between the two sites (Figure 5.15). In both sites the species died when placed into the Salicornia zone plots, and plants either died (site 1) or biomass was greatly reduced (site 2) with transplantation into the uncleared plots of the Calamagrostis zone.

The graph of site 1 results shows that the mean biomass of transplants placed into cleared plots of the Puccinellia zone and cleared and uncleared plots of the Hordeum zone differed little from that of the *cut-and-replace* controls, but mean values tended to be higher in the cleared plots. When placed into cleared plots of the Calamagrostis zone the mean biomass decreased slightly relative to the control, but remained higher than the biomass of plugs placed into uncleared plots of this zone. In site 1, ANOVA was conducted only on those transplants placed into the Calamagrostis, Hordeum, and Puccinellia zones. The ANOVA results indicate that while there was no significant difference between plot treatments ($p = 0.1357$) on the growth response of surviving the *Puccinellia nuttalliana* individuals in site 1, the difference between vegetation zones was approaching significance ($p = 0.0898$).

Table 5.5 Results of two-factor ANOVA ($\alpha = 0.05$) conducted on biomass data of *Puccinellia nuttalliana* transplants at sites 1 and 2. The two factors are: vegetation zones (soil water salinity) ($n = 10$); and plot treatment (presence or absence of neighbors) ($n = 20$).

Saline Site	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
1	0.0898	0.1357	0.8923
2	0.3772	0.0005	0.7419

In site 2 the accumulated biomass values of *Puccinellia nuttalliana* transplanted into cleared plots of the Puccinellia, Hordeum/Distichlis, and Calamagrostis zones, were not only similar to each other, but were considerably higher than that of the uncleared plots for

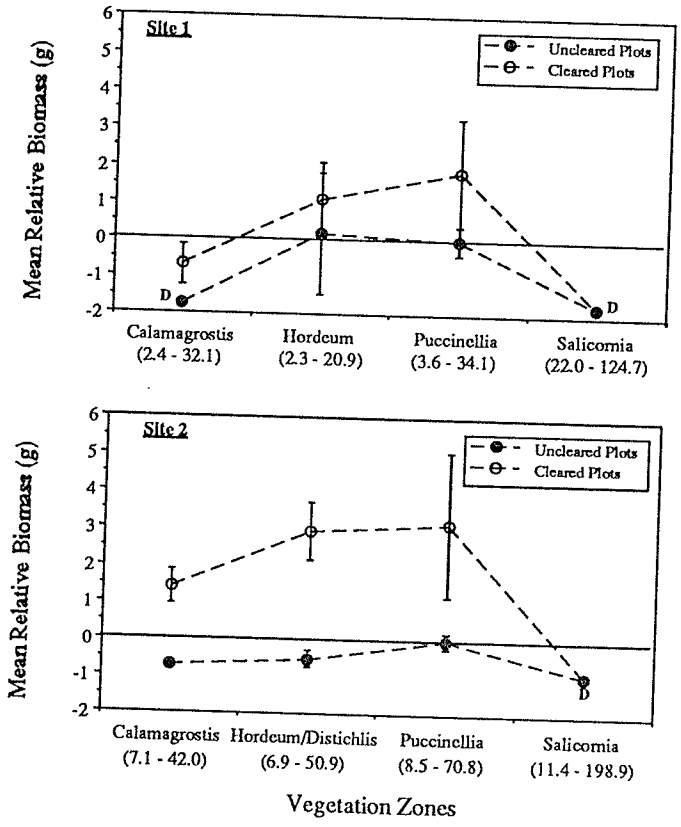


Fig. 5.15 Response of *Puccinellia nuttalliana* in vegetation plugs taken from the Puccinellia zones and transplanted into each vegetation zone at sites 1 and 2. Response is measured by biomass accumulation per transplantplug relative to the Puccinellia zone cut-and-replace control plugs. Biomass values are means ± S.E. (n = 5). Values in parentheses are soil water salinity ranges for the 1990 season. The letter **D** indicates that the vegetation of these plugs died prior to harvesting.

each zone. Placement into uncleared plots of the Calamagrostis and Hordeum/Distichlis did not result in total eradication of *Puccinellia nuttalliana* , but biomass accumulation was reduced relative to the control. ANOVA results from the site 2 transplants (excluding those placed into the Salicornia zone) indicate that competition had a significant effect on the growth of *Puccinellia nuttalliana.* ($p = 0.0005$), while no significant difference was apparent due to salinity ($p = 0.3772$)

Salicornia rubra

Transplantation of *Salicornia rubra* into each vegetation zone was conducted at all four study sites (Figure 5.16). Individuals of *Salicornia rubra* survived transplantation into cleared plots of each vegetation zone. Thus, values for biomass accumulation, although often very low, were available from each vegetation zone in each site. Because of this, all the data on *Salicornia rubra* transplants were included in the ANOVA testing.

Table 5.6 Results of two-factor ANOVA ($\alpha = 0.05$) conducted on biomass data of *Salicornia rubra* transplants at each site. The two factors are: vegetation zones (soil water salinity) ($n = 10$ for sites 1 and 2, $n = 6$ for sites 3 and 4); and plot treatment (presence or absence of neighbors) ($n = 20$ for sites 1 and 2, $n = 9$ for sites 3 and 4).

Saline Site	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
1	0.0001	0.1297	0.9
2	0.3329	0.0018	0.1244
3	0.0037	0.0001	0.0032
4	0.0196	0.0023	0.0057

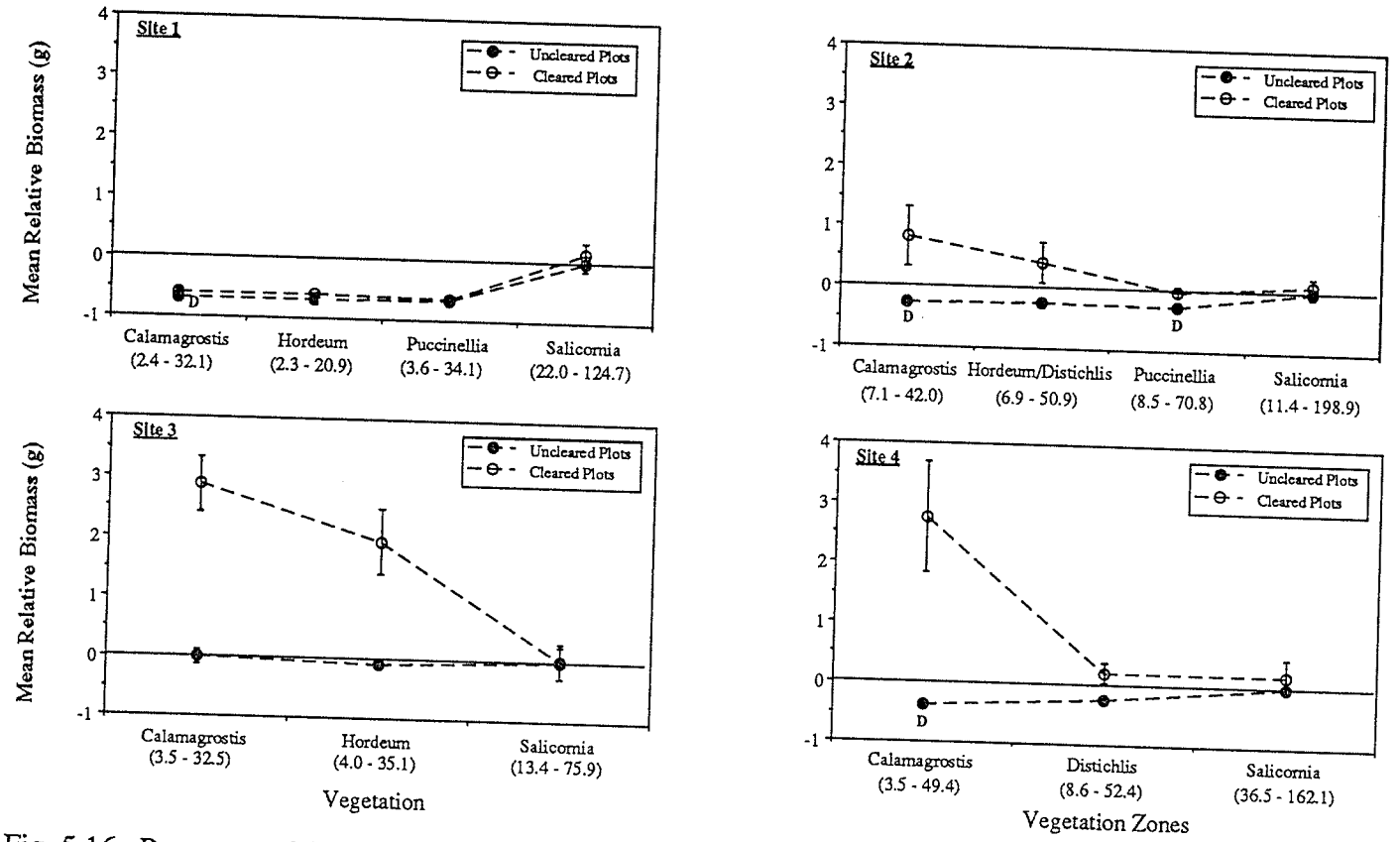


Fig. 5.16 Response of *Salicornia rubra* in vegetation plugs taken from the Salicornia zones and transplanted into each vegetation zone at each site. Response is measured by biomass accumulation per transplant plug relative to the Salicornia zone cut-and-replace control plugs. Biomass values are means ± S.E. (n = 5 for sites 1 and 2, n = 3 for sites 3 and 4). Values in parentheses are soil water salinity ranges for the 1990 season. The letter **D** indicates that the vegetation of these plugs died prior to harvesting.

In site 1, the biomass of *Salicornia rubra* decreased from that of the control when placed into cleared and uncleared plots of the Hordeum and Puccinellia zones, and the cleared plots of the Calamagrostis zone. Plants placed into uncleared plots of the Calamagrostis zone died. ANOVA (Table 5.6) indicates this decrease in biomass is significant ($p = 0.0001$). ANOVA also indicates that there was no significant difference between *Salicornia rubra* transplants placed into cleared and uncleared plots in each zone ($p = 0.1297$).

The graph of site 2 results shows a trend towards increasing mean biomass accumulation between transplants in cleared plots of the lower salinity zones (i.e. Calamagrostis and Hordeum/Distichlis) and the Puccinellia and Salicornia zones. Plants placed into the uncleared plots of the Puccinellia and Calamagrostis zones died, while those in the uncleared plots of the Hordeum/Distichlis zone exhibited very limited growth. ANOVA indicates that this different response to cleared and uncleared plots was significant ($p = 0.0018$), while differences between zones were not significant ($p = 0.3329$)

The results from site 3 show a trend of increasing biomass of *Salicornia rubra* with decreasing soil salinity in cleared plots. ANOVA results indicate that there was a significant difference between vegetation zones ($p = 0.0037$) and between plot treatments ($p = 0.0001$), and that interaction ($p = 0.0057$) existed between these two factors. *Salicornia rubra* performed best in the cleared plots of the Hordeum and Calamagrostis zones, where salinity was low and competition greatly reduced. No difference in biomass accumulation was observed between the control and transplants placed into uncleared plots of each zone.

Results from transplantation of *Salicornia rubra* in site 4 are similar to those of site 3. In site 4 *Salicornia rubra* performed best in cleared plots, but died in the uncleared plots, of the Calamagrostis zone. Mean biomass decreased for plants placed into uncleared plots of the Distichlis zone. Plants placed into cleared plots of the Distichlis and Salicornia zones showed no difference with regards to biomass accumulation. ANOVA indicates that

biomass accumulation differed significantly due to vegetation zones ($p = 0.0196$) and plot treatment ($p = 0.0023$), with interaction occuring between the two variables ($p = 0.0057$).

Section 5.3.5 - Effects of Plug Extraction

The main purpose of the reciprocal transplant experiment was to show the singular and combined effects of competition and salinity on the dominant species. However, the data did not show the effect that the physical extraction of vegetation plugs (for transplantation) might have had on the dominant species of the plugs. The process of extraction would inevitably result in the severing of plant rhizomes and roots, and thus, may have had a negative affect on the performance of the vegetation following transplantation. In order to determine if the vegetation of the transplants was adversely affected by the plug extraction process, the accumulated biomass of *cut-and-replace* controls and *non-transplanted* controls, both from uncleared plots, were compared using a pooled estimate of variance t-test ($a = 0.05$). No significant difference in biomass accumulation between the two controls could be interpreted as a sign of minimal disturbance due to plug extraction. Biomass results from both the 1989 and 1990 harvests were used to see if there were any between-season differences.

The results of this comparison are presented in Figures 5.17 - 5.21. Each Figure presents the biomass accumulation from both seasons for a specific dominant species. For example, Figure 5.17 presents the biomass for *Calamagrostis inexpansa* controls, Figure 5.18 the results for *Hordeum jubatum*, and so on for the five dominant species of the four study sites. The mean biomass of the control plugs is presented along the y-axis, while the study sites are found along the x-axis. The presence of square brackets (along the x-axis) indicates that the controls were not significantly different ($\alpha = 0.05$) for a particular site.

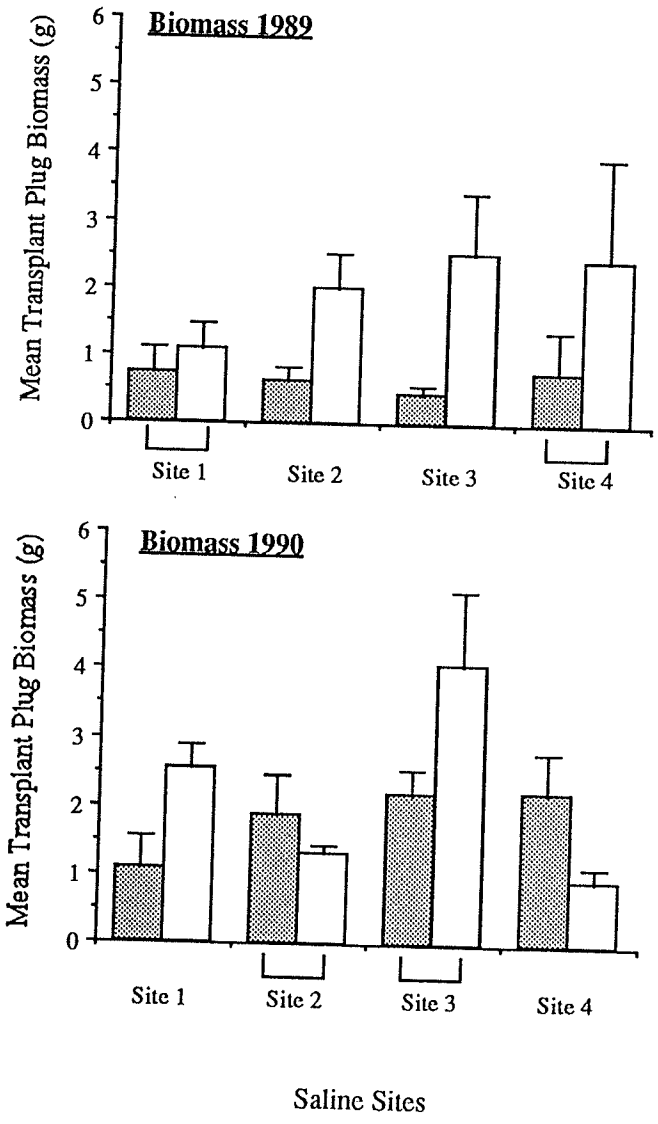


Fig. 5.17 Biomass of *Calamagrostis inexpansa* in *cut-and-replace* control plugs (▩) and *non-transplanted* control plugs (□) at each site. Values are means ± SE. (n = 5 for sites 1 and 2, n = 3 for sites 3 and 4). Brackets join controls that are not significantly different ($\alpha = 0.05$ t-test).

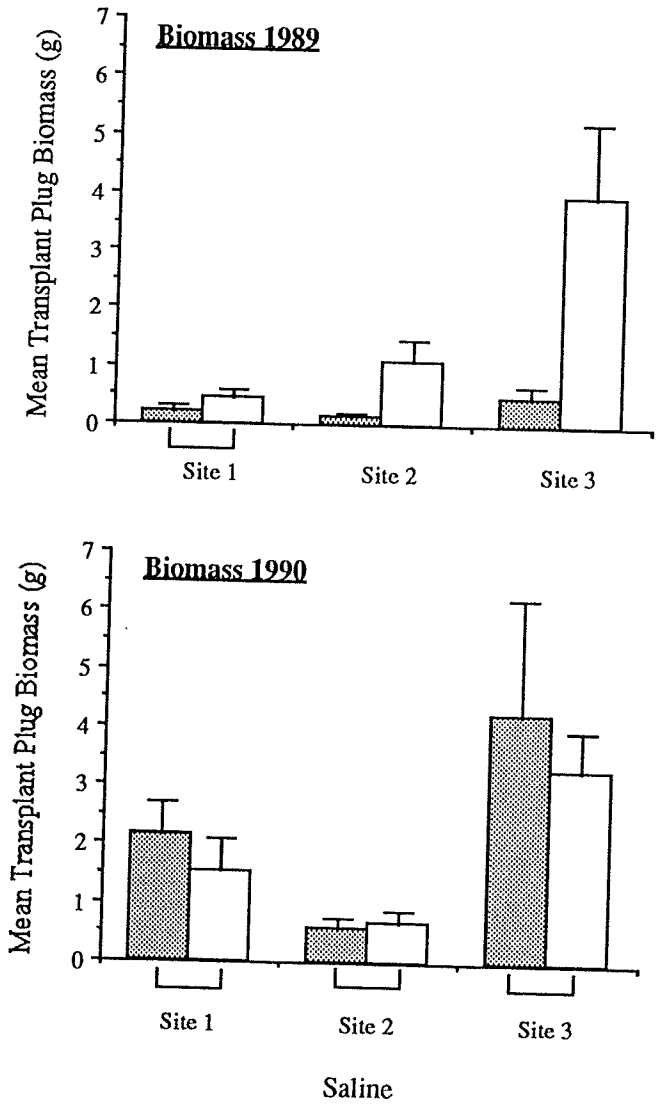


Fig. 5.18 Biomass and density of *Hordeum jubatum* in *cut-and-replace* control plugs (▩) and *non-transplanted* control plugs (□) at each site. Values are means ± SE. (n = 5 for sites 1 and 2, n = 3 for site 3). Brackets join controls that are not significantly different ($\alpha = 0.05$ t-Test)

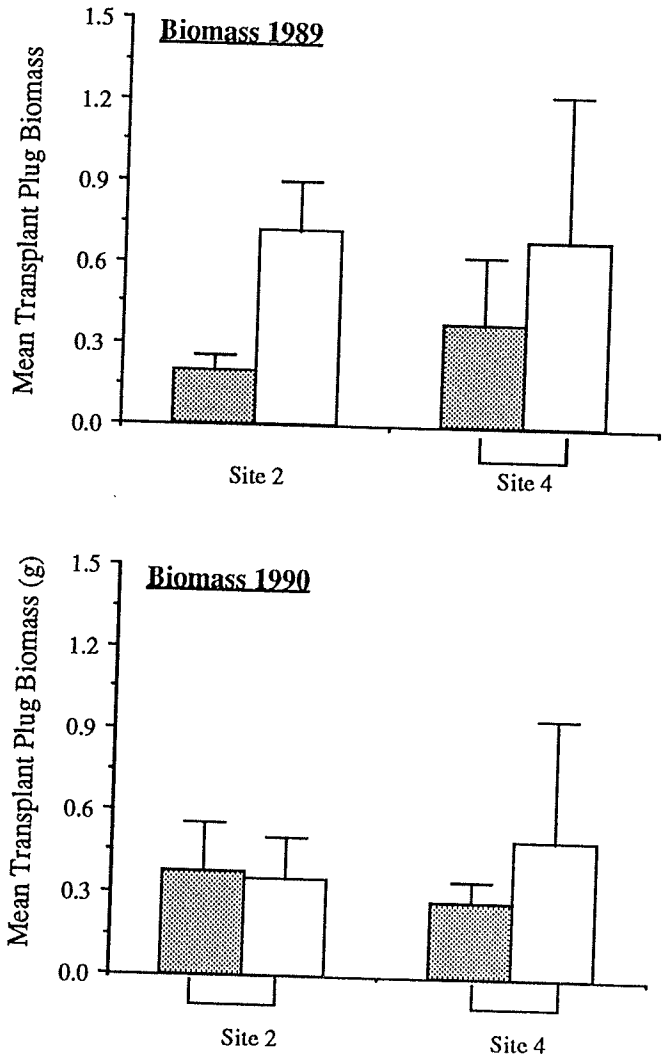


Fig. 5.19 Biomass and density of *Distichlis stricta* in *cut-and-replace* control plugs (▩) and *non-transplanted* control plugs (□) at each site. Values are means ± SE. (n = 5 for site 2, n = 3 for site 4). Brackets join controls that are not significantly different ($\alpha = 0.05$ t-Test).

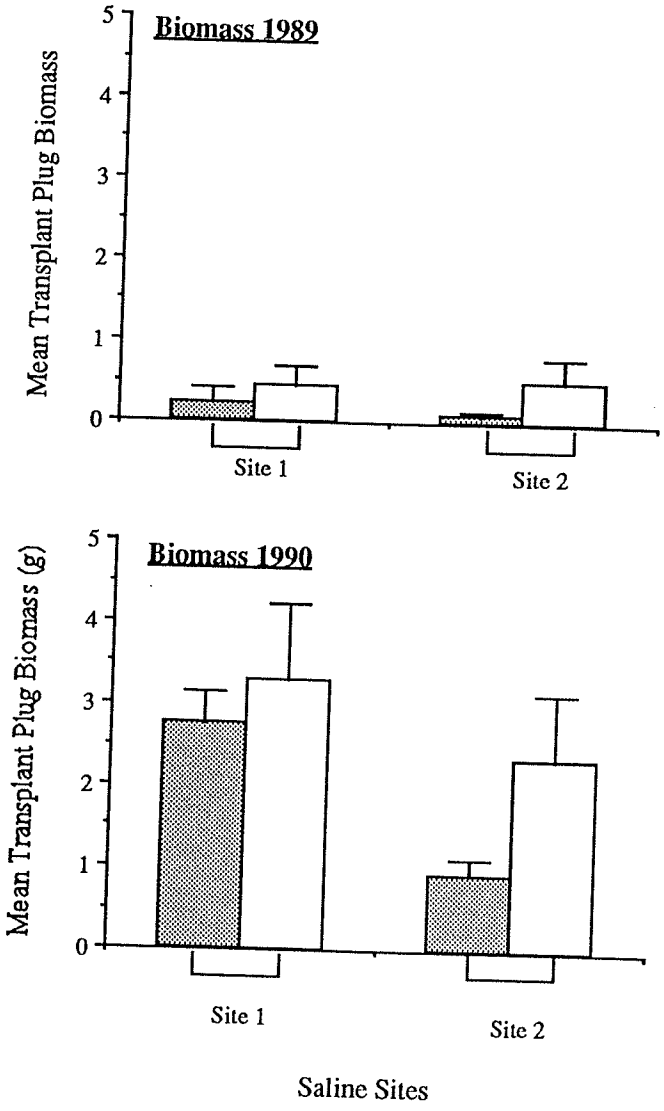


Fig. 5.20 Biomass and density of *Puccinellia nuttalliana* in *cut-and-replace* control plugs (▨) and *non-transplanted* control plugs (□) at each site. Values are means ± SE. (n = 5). Brackets join controls that are not significantly different ($\alpha = 0.05$ t-Test).

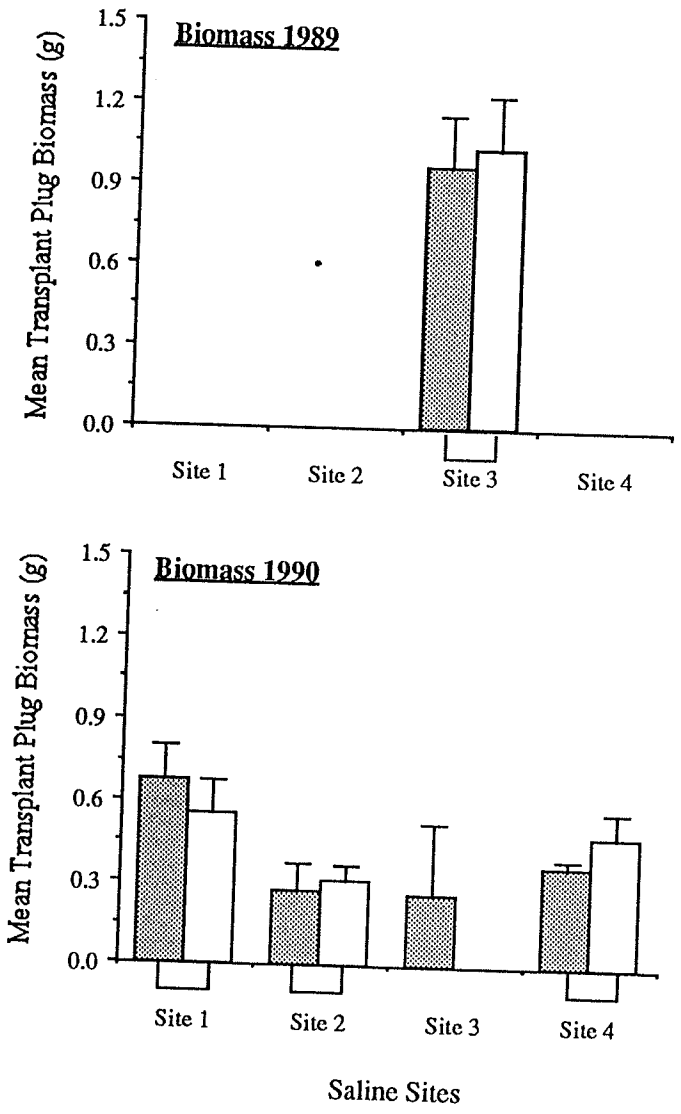


Fig. 5.21 Biomass and density of *Salicornia rubra* in *cut-and-replace* control plugs (▩) and *non-transplanted* control plugs (□) at each site. Values are means ± SE. (n = 5 for sites 1 and 2, n = 3 for sites 3 and 4). Brackets join controls that are not significantly different (α = 0.0 5 t-Test).

The results indicate that the biomass of species in the *cut-and-replace* controls tended to conform to that of the *non-transplanted* controls over the course of the two growing seasons. *Salicornia rubra* and *Puccinellia nuttalliana* appear to have been the least affected by the extraction process. Biomass accumulation of *Distichlis stricta* and *Hordeum jubatum* was significantly lower in *cut-and-replace* controls than in *non-transplanted* controls in the 1989 season. This decline in growth may have been due to damage resulting from plug extraction. However, the 1990 results suggest that the vegetation had recovered by the end of the second field season. Results from the 1989 *Calamagrostis inexpansa* controls indicates that the extraction process may have caused damage to vegetation in plugs of sites 2 and 3, but not to those of site 1 and 4. The 1990 results suggest that the vegetation in plugs of sites 2 and 3 had recovered by the second field season.

Section 5.3.6 - Growth Chamber Transplants

Soil Factors

As with the field transplant experiments, it was important that the soil of the growth chamber transplants conform to the soil of the plots into which they were placed. Comparisons were made between the transplanted soils and the plot soils to determine if the soil pH, soil moisture content, and soil water salinity had been altered by placement into the experimental plots. These comparisons are presented graphically in Figures 5.22 - 5.24. Note that each Figure presents the three soil factors for a particular transplanted species in separate graphs. Each graph is divided into three sections; one for each vegetation zone of site 3. The scale for the soil factor is located on the y-axis, and does not differ between Figures. This allows easy comparison between transplanted species. Plot treatment

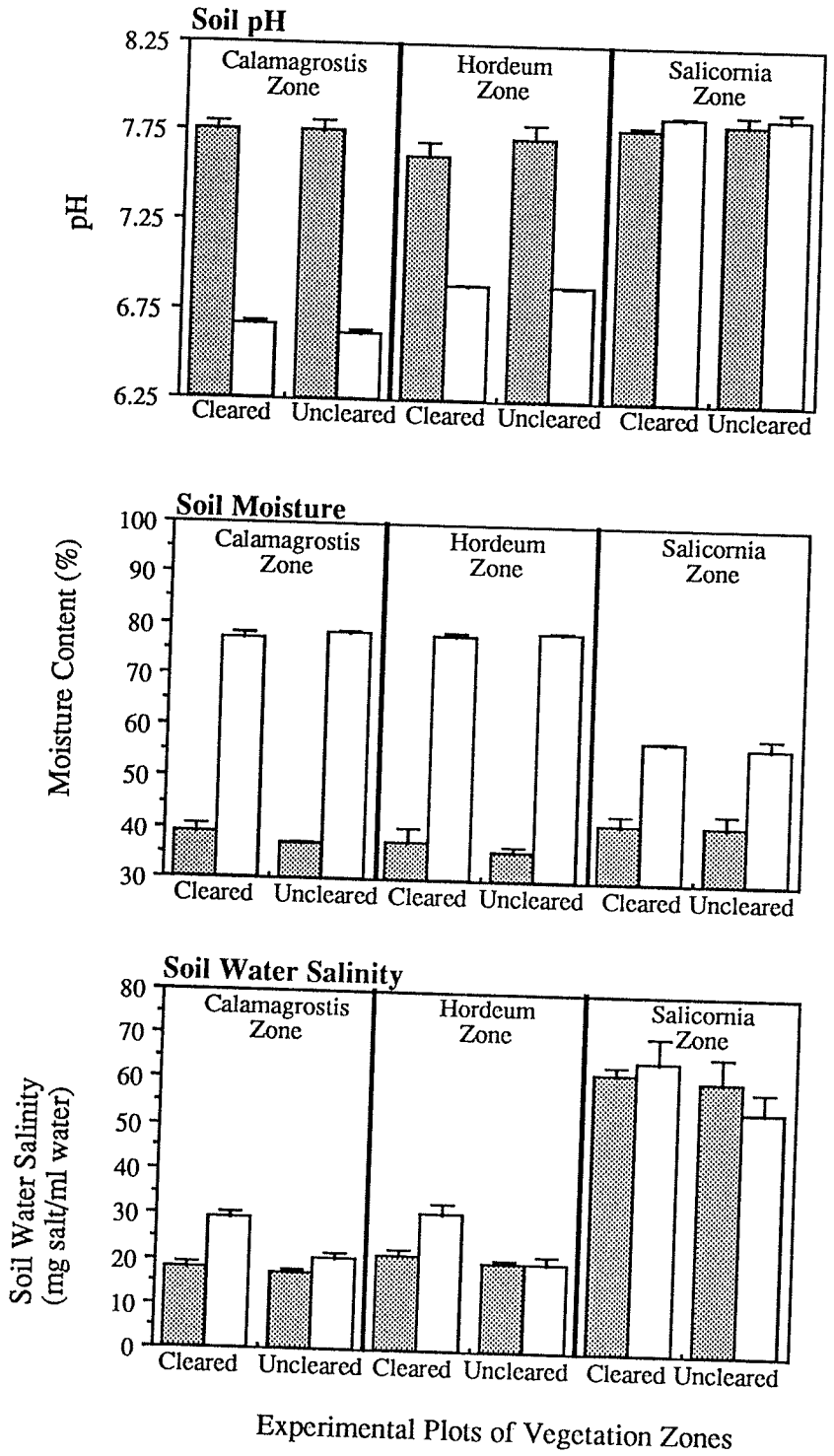


Fig. 5.22 Comparison of pH, moisture content, and water salinity of soil in *Calamagrostis inexpansa* transplant plugs (▨) to that in cleared and uncleared plots (□) of each vegetation zone in site 3. Values are means ± SE. (n = 4 for plugs; n = 3 for plots).

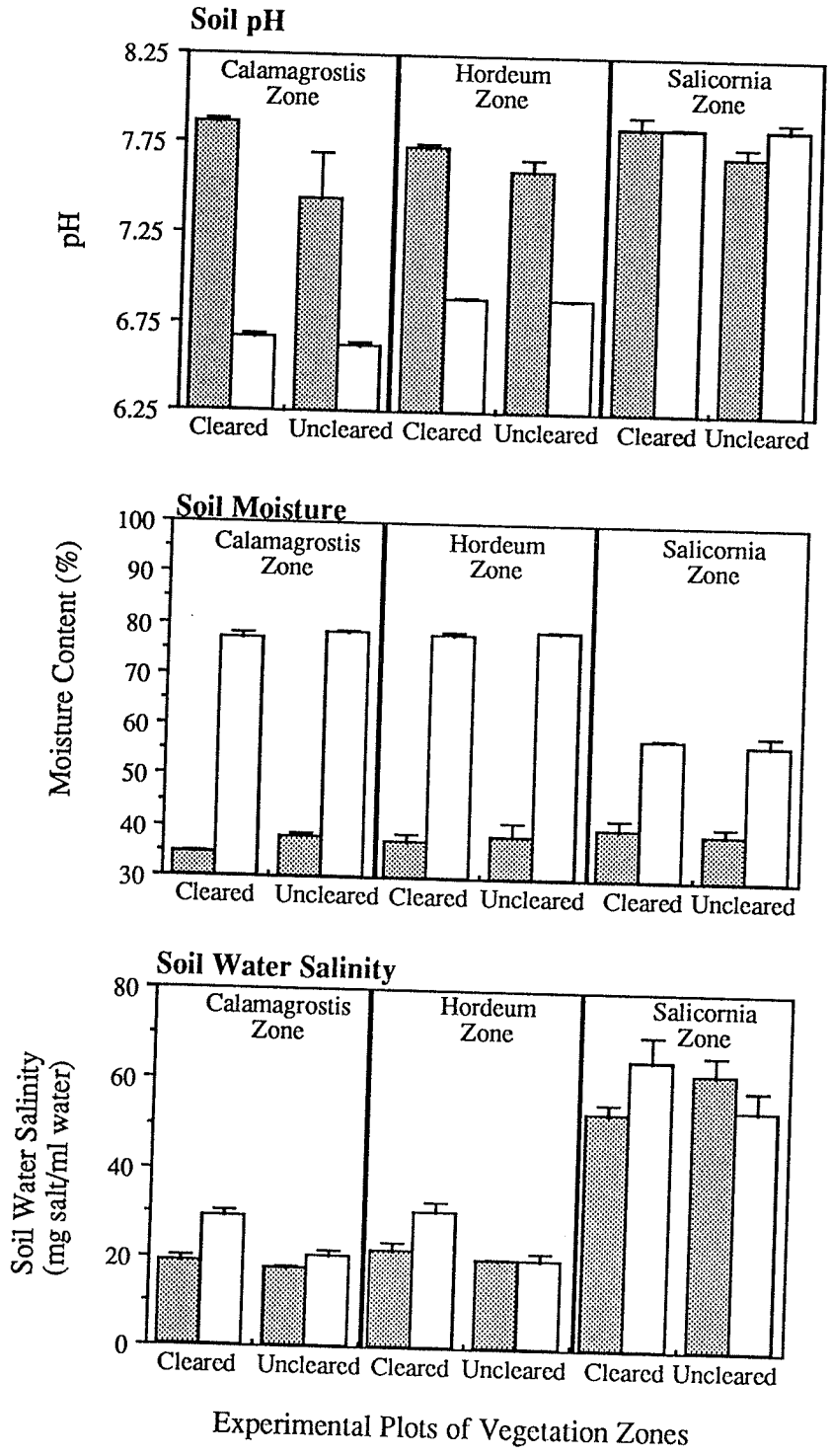


Fig. 5.23 Comparison of pH, moisture content, and water salinity of soil in *Hordeum jubatum* transplant plugs (▩) to that in cleared and uncleared plots (□) of each vegetation zone in site 3. Values are means ± SE. (n = 4 for plugs; n = 3 for plots).

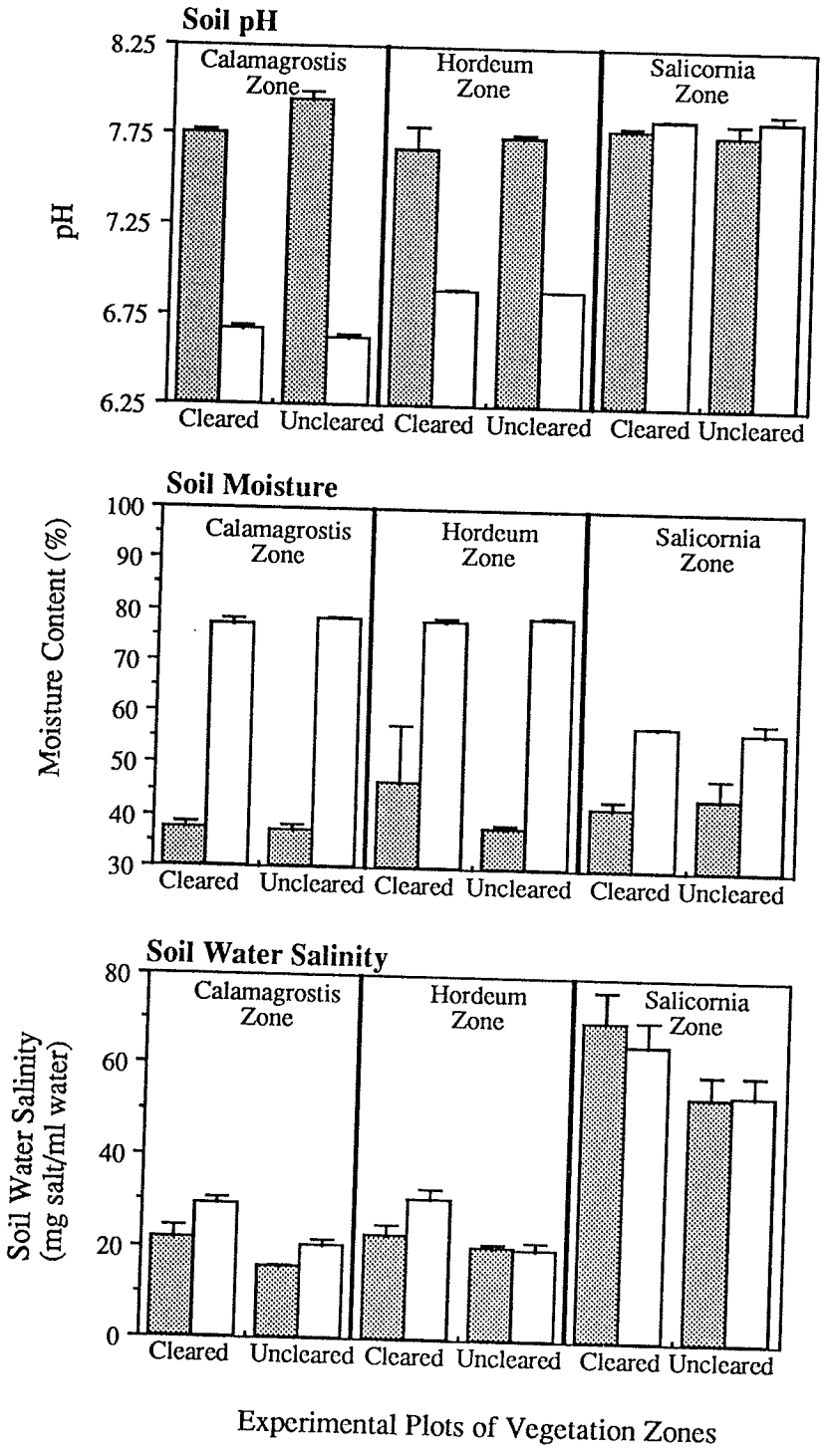


Fig. 5.24 Comparison of pH, moisture content, and water salinity of soil in *Salicornia rubra* transplant plugs (▨) to that in cleared and uncleared plots (□) of each vegetation zone in site 3. Values are means ± SE. (n = 4 for plugs; n = 3 for plots).

categories (cleared or uncleared) are listed along the x-axis. Note that there is a cleared treatment and an uncleared treatment for each vegetation zone. This arrangement allows comparisons to be made between the plug and plot soils in cleared and uncleared plots within a particular zone, as well as between vegetation zones of the site.

Based on soil analysis of the growth chamber controls, the mean soil pH of the transplant plugs prior to transplantation was 7.57 ± 0.02, while the mean moisture content was $67.1 \pm 1.1\%$, and the mean soil water salinity was 0.67 ± 0.06 mg/ml. The soil pH of transplant plugs increased slightly when placed into the plot soils. Conformity of pH in plugs to that of plots occurred only in the Salicornia zone. The pH of plugs placed into the Hordeum and Calamagrostis zones did not decrease to levels present in the plot soils of these zones, but rather increased slightly above the pre-transplantation levels. There appeared to be little difference between the pH of plug soils with regards to plot treatment. The soils of the Hordeum and Calamagrostis zone are fairly acidic because of their extremely high organic matter content. The growth chamber transplant plug soils were only about 25% organic matter (peat), and thus the pH of these plug soils remained slightly basic, and were not influenced by the surrounding plot soils.

Soil moisture content of transplanted plugs did not conform to the moisture of the plot soils into which they were placed. As mentioned in the previous paragraph, the organic matter content of the vegetation zones was considerably higher than that of the plug soils. This probably allowed greater water retention in the plot soils compared with the transplant plug soils, resulting in lower moisture content levels in the plug soils. In general the soil moisture content of the plugs ranged between 35 and 45 % at the time of plug biomass harvesting. Like the moisture content in field soils, it is probable that the moisture in the plugs fluctuated over the growing season in concert with the precipitation and temperature regimes. The soil moisture of the plug soils showed little variation between cleared and uncleared plots and between vegetation zones.

Unlike soil pH and moisture, the soil water salinity of the transplant plugs tended to increase to levels present in the plot soils of the three vegetation zones. Soil pH and soil moisture were roughly equal in all the transplant plugs regardless of the plot treatment or vegetation zone into which they had been placed. The soil water salinity levels of the transplanted plugs, although apparently not influenced by plot treatment, were dependent on the vegetation zone soils into which they had been transplanted.

Species Transplants

The biomass accumulation results for transplanted plugs containing *Calamagrostis inexpansa*, *Hordeum jubatum*, and *Salicornia rubra* are presented graphically in Figure 5.25. A two-way factorial ANOVA with interaction was also conducted on the biomass data. The results of the ANOVA are presented in Table 5.7. In situations in which plants died in both cleared and uncleared plots of a particular zone, the data were excluded from the ANOVA. Note that the graphs in Figure 5.25 differ somewhat from the field transplant graphs. Each graph presents the biomass accumulation for a single transplanted species, however, the graphs use histograms to illustrate biomass accumulation, and the values are absolute, rather than relative to a *cut-and-replace* control. Biomass values (means ± SE) from cleared plots are represented by white bars, while shaded bars represent uncleared plots.

Calamagrostis inexpansa

Calamagrostis inexpansa died when placed into the plots of the the Salicornia zone. Mean biomass accumulation of *Calamagrostis inexpansa* was lower in uncleared plots compared with cleared plots of the Calamagrostis and Hordeum zones. Also, there was a slight decrease in biomass in the *Calamagrostis inexpansa* placed into the cleared plots of the Hordeum zone compared with cleared plots of the Calamagrostis zone. ANOVA (Table 5.7), however, indicates that these differences in means were not significant ($p > 0.05$).

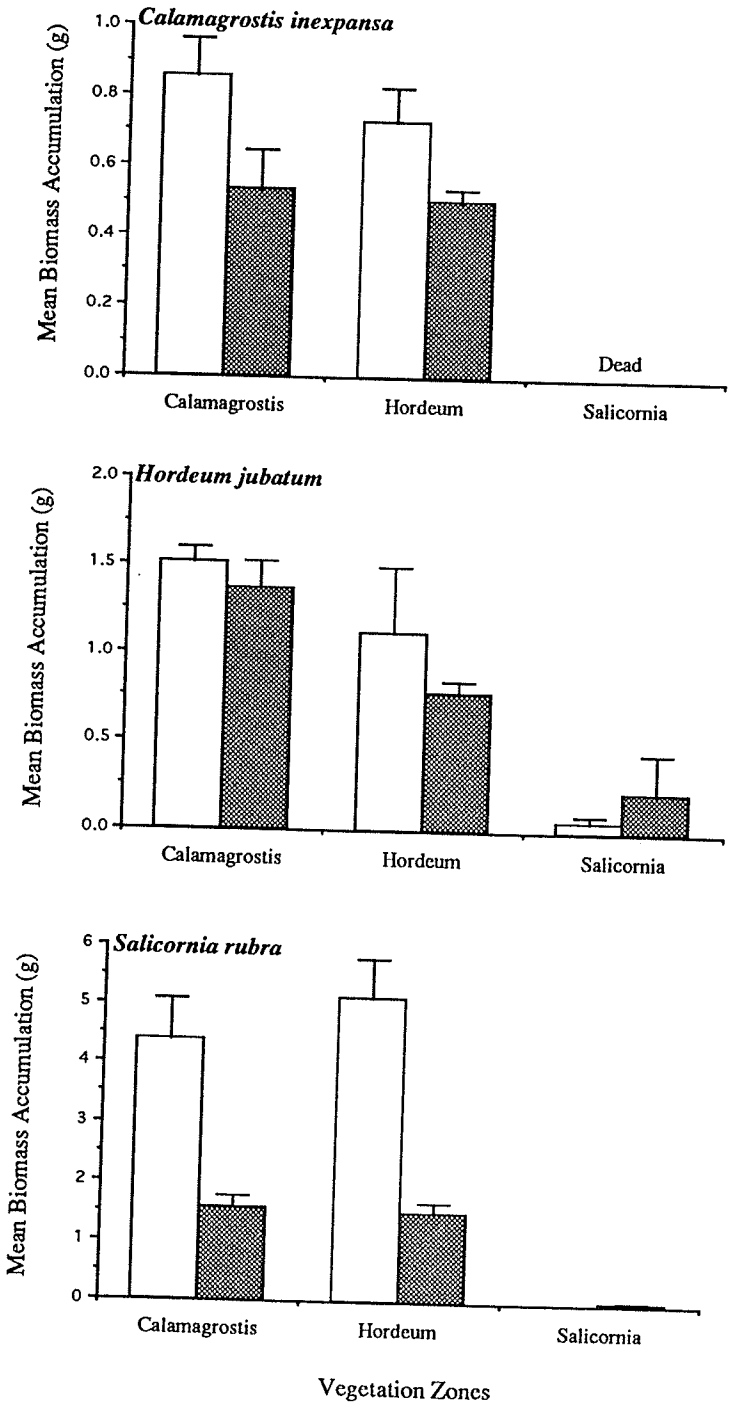


Fig. 5.25 Mean biomass accumulation of species in growth chamber transplant plugs placed into cleared (□) and uncleared (▩) plots in the vegetation zones of site 3. Values are means ± SE. n= 4

Table 5.7 Results of two-factor ANOVA ($\alpha = 0.05$) conducted on biomass data of growth chamber transplants. The two factors are: vegetation zones (soil water salinity) (n = 8); and plot treatment (presence or absence of neighbors) (n = 8 for *C. inexpansa*, n = 12 for *H. jubatum* and *S. rubra*).

Transplanted Species	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
Calamagrostis inexpansa	0.4291	0.126	0.625
Hordeum jubatum	< 0.0001	0.5065	0.4478
Salicornia rubra	< 0.0001	< 0.0001	0.0007

Hordeum jubatum

Individuals of *Hordeum jubatum* survived transplantation into all of the vegetation zones (Figure 5.25). However, biomass was greatly reduced due to transplantation into plots of the Salicornia zone. ANOVA (Table 5.7) indicates that there was no significant difference due to plot treatment ($p = 0.5065$), but there was a siginificant difference due to zones ($p < 0.0001$) for transplants of *Hordeum jubatum*.

Salicornia rubra

Salicornia rubra did not survive transplantation into cleared plots of the Salicornia zone, and growth was negligible in uncleared plots of the same zone. The graph clearly illustrates that the species performed considerably better in cleared plots of the Hordeum and Calamagrostis than in uncleared plots of these two zones, and in experimental plots of the Salicornia zone. ANOVA indicates significant differences due to plot treatment ($p < 0.0001$) and zones ($p < 0.0000$), with interaction ($p = 0.0007$).

Section 5.4 - Discussion

Section 5.4.1 - Introduction

Three main conditions were important for the success of the transplant experiments. First, the effect of vegetation removal with herbicide on the soil factors in cleared plots should have been minimal. Second, the soil of the transplanted plugs should have shown conformity with that of the experimental plots into which the plugs were placed. Third, the effect of plug extraction on the transplanted vegetation should have be minimal.

Significant differences between soils from cleared and uncleared plots were few, suggesting that the effects of vegetation removal were minor. Although the soil factors of the plugs were sometimes significantly different from the soil factors of the plots, there appeared to be a general trend in conformity in the soil water salinity factor. The soil moisture and soil pH of the transplant plugs appeared to be strongly influenced by organic material. Because of this, the soil moisture and soil pH of plugs from zones high in soil organic matter did not conform to the soil of plots in zones of low soil organic matter and vice versa. Soil water salinity appeared unaffected by organic matter content. This was best revealed in the results from the growth chamber transplant plug soils. Thus, although the soil moisture in plugs and plots may have differed, the salt concentration in the soil water of the plugs compared to that of the plots was similar. As salinity is likely the most important soil factor governing the distribution of species in these saline sites (Burchill 1991), the soils data results were positive. Biomass data from the transplant experiment control plugs showed that some species, such as *Puccinellia nuttalliana*, appeared unaffected by extraction, while others, such as *Hordeum jubatum*, suffered damage the first year, but appeared to have recovered by the second season. Thus, the three conditions outlined in the previous paragraph were attained, and permit further discussion of the transplant experiment results.

Section 5.4.2 - Use of ANOVA for Data Analysis

The ANOVA method for determining significant differences assumes that the data have a normal distribution and that the sample means of the data have equal variances. The biomass accumulation data from the field and growth chamber transplant experiments did not fully meet these assumptions. In some situations the transplanted species died when placed into uncleared plots and into high salinity soils. This generated a number of zero values and, consequently, led to non-normality and unequal variances. In an attempt to counter this problem, cases in which there were no surviving transplants in both cleared and uncleared plots of a particular zone (e.g. placement of *Calamagrostis inexpansa* into the Salicornia zone) were excluded from the ANOVA. This data manipulation was not totally successful, however it did somewhat increase the normality and equalize the variances of the data.

Normal probability plots of the data residuals indicated that in most cases there were too many extremes or outlying points to be considered normal. This resulted in a non-linear relationship between the residual scores and the normal scores of the data. A linear relationship between residuals and normal scores indicates normality in a data set. In order to determine how close to normal the data were, I subjected the residual and normal scores to the Pearson product-moment correlation. Tables 5.8 and 5.9 presents the correlation coefficients (r' - values) for the transplanted species of each site, where $r = 1.00$ indicates a positive correlation and normality in the data. In my data the r - values, although less than 1.00, were relatively high and thus indicate that the data, for the most part, were close to normal.

Zar (1984) states that the robustness of the ANOVA allows operation even with considerable heteroscedasticity (heterogeneity of variances) as long as the sample sizes are equal. He states further that the analysis, because of its robustness, is not affected

dramatically by even considerable deviations from normality such as skewness and/or kurtosis. Thus, although the data did not entirely fit the assumptions of the ANOVA, I decided that ANOVA was the most appropriate method for determining significant differences, and that, coupled with the graphical representation of the data, would provide the desired information for proper interpretation of the transplant results.

Table 5.8 Correlation coefficients results from Pearson product-moment correlation between residuals and normal scores of the biomass accumulation data from field transplant experiments.

Transplanted Species	Saline Site	Correlation Coefficient (r)
Calamagrostis inexpansa	1	0.960
	2	0.988
	3	0.950
	4	0.982
Hordeum jubatum	1	0.905
	2	0.910
	3	0.945
Distichlis stricta	2	0.957
	4	0.947
Puccinellia nuttalliana	1	0.942
	2	0.861
Salicornia rubra	1	0.867
	2	0.833
	3	0.974
	4	0.875

Table 5.9 Correlation coefficients results from Pearson product-moment correlation between residuals and normal scores of the biomass accumulation data from growth chamber transplant experiments.

Transplanted Species	Correlation Coefficient (r)
Calamagrostis inexpansa	0.960
Hordeum jubatum	0.988
Salicornia rubra	0.950

Section 5.4.3 - Effects of Salinity and Competition on Transplanted Species

Calamagrostis inexpansa

With the exception of the Hordeum zone of site 3, *Calamagrostis inexpansa* died when placed into zones of higher salinity, regardless of the plot treatment. It was unable to tolerate high soil salinities, and thus, was excluded from the Salicornia, Puccinellia, Distichlis, Hordeum/Distichlis, and Hordeum zones. The species survived transplantation into the Hordeum zone of site 3. However, growth of plants in uncleared plots was considerably less than that of the *cut-and-replace* controls and the transplants placed into cleared plots. The soil salinity of the Hordeum zone of site 3 was similar to that of the adjacent Calamagrostis zone, and *Calamagrostis inexpansa* was able to tolerate the slightly higher salinities under conditions of no competition (i.e. in cleared plots). ANOVA revealed that when transplanted into plots of its own zone, the response of *Calamagrostis inexpansa* was significantly higher in cleared plots than in uncleared plots in sites 3 and 4. This suggests that in these sites the growth of *Calamagrostis inexpansa* within its native vegetation zone was influenced to a degree by intraspecific competition. No interaction

was found between plot treatments and vegetation zones for surviving transplants in site 3. This indicates that the effect of competition is the same regardless of the salinity level.

The growth chamber transplant results for *Calamagrostis inexpansa* were similar to those of field transplants in site 3 in that individuals died when placed into the high salinity soils of the Salicornia zone. However, unlike the field transplant results, growth chamber transplants of *Calamagrostis inexpansa* showed no significant difference in growth between cleared and uncleared plots or between the Hordeum and Calamagrostis zones. However, the mean biomass values were lower in uncleared plots than in cleared plots, and if left to grow for another season significant differences in growth between plot treatments might have developed.

Hordeum jubatum

Field transplants of *Hordeum jubatum* died when placed into cleared and uncleared plots of the Salicornia zones in each site, and the Puccinellia zone in site 2. Obviously the salinity in these zones exceeded its tolerance levels. Death or reduced growth also occurred in transplants placed into uncleared plots of the Calamagrostis zones in sites 1 and 3, while mean biomass accumulation increased for individuals placed into the cleared plots of this zone. This indicates that *Hordeum jubatum* was competitively excluded from the uncleared plots, but was able to thrive in situations where competition was absent. This increased growth in cleared plots therefore was due to a lack of competition and lower soil water salinity levels. Transplants placed into cleared plots of its native zone in sites 2 and 3 showed increased growth over the *cut-and-replace* controls from uncleared plots, indicating that intraspecific competition was prevalent in these *Hordeum jubatum* populations. ANOVA indicated significant interaction between the biomass accumulation in transplants placed into the Hordeum and Calamagrostis zones of site 3. Thus, the effects of competition on the *Hordeum jubatum* transplants differed depending on the level of salinity.

Results from growth chamber transplants indicated that there was a major influence from salinity on the growth of *Hordeum jubatum* transplants. The species was able to survive in all the vegetation zones, although growth was considerably reduced in the Salicornia zone. The species was probably able to survive in the Salicornia zone because of high soil moisture levels which created relatively low salinity levels throughout most of the 1990 season. According to the ANOVA, competition did not play a significant role in the response of these *Hordeum jubatum* transplants. However, the mean biomass accumulation results indicate a trend to increased growth in cleared plots over uncleared plots in the Hordeum and Calamagrostis zones. Also, the mean biomass accumulation in the cleared plots of the Calamagrostis zone was higher than that in both cleared and uncleared plots of the Hordeum zone. Clearly *Hordeum jubatum* grows best in situations of low salinity and low competition. These trends might have become more apparent if the transplants had been left in the field for a second season.

Distichlis stricta

The death of transplants in the Salicornia zone of sites 2 and 4, and decreased growth in transplants placed into the Puccinellia zone of site 2 indicates that *Distichlis stricta* could not tolerate the high salinity levels prevalent in these soils. Thus, *Distichlis stricta* was restricted to soils with lower salinities. There was no significant difference between transplants placed into cleared and uncleared plots, suggesting that *Distichlis stricta* was not strongly affected by the presence or absence of neighbors. Bertness and Ellison (1987) examined the response of *Distichlis spicata* to transplantation into the various vegetation zones of a coastal salt marsh. They found that the species was primarily associated with disturbed areas, and suggested its guerrilla growth form was competitively inferior to the phalanx growth form of other marsh species (Bertness & Ellison 1987). The same may be true for *Distichlis stricta* , which also has a guerrilla type of growth form and was found to inhabit relatively dry soils with moderate salinity levels.

Puccinellia nuttalliana

As in the case of the previous species, *Puccinellia nuttalliana* transplants died when placed into the high salinity soils of the Salicornia zone. Death also occurred in transplants placed into the uncleared plots of the Calamagrostis zone in site 1, and growth declined in transplants placed into the uncleared plots of the Hordeum/Distichlis and Calamagrostis zones of site 2. ANOVA conducted on the transplants in site 1 (excluding those in the Salicornia zone) indicated that the growth of *Puccinellia nuttalliana* was not significantly affected by plot treatments or changes in salinity. However, death occurred in transplants placed into uncleared plots of the Calamagrostis zone. This was likely a response to competition; the vegetation of the Calamagrostis zone being competitively superior to *Puccinellia nuttalliana*. ANOVA results from site 2 support this conclusion. The ANOVA indicated that there was a significant difference in biomass accumulation due to plot treatment for surviving transplants, and *Puccinellia nuttalliana* performed better in cleared plots, where competitors were absent and salinity was tolerable, than in the uncleared plots, where competitors were present. Thus, *Puccinellia nuttalliana* could not tolerate the high salinity levels of the Salicornia zone, nor the competition of the Hordeum/Distichlis and Calamagrostis zones. Increased growth in cleared plots of its own zone indicates that intraspecific competition plays a role in limiting the growth of the species in its native zone.

Salicornia rubra

In site 1, transplants of *Salicornia rubra* died or showed considerable decline in growth when transplanted into the other vegetation zones. ANOVA indicated that there was no effect due to plot treatment. I expected that following transplantation into cleared plots of the lower salinity zones the performance of the species would increase relative to the *cut-and-replace* controls. There is a possible explanation for these results. When the

cleared plots were sprayed with herbicide the dead plant material was not removed, but rather, it was left lying in the plots. This dead plant material was quite extensive in cleared plots of the Puccinellia, Hordeum, and Calamagrostis zones in site 1, and likely resulted in the shading of *Salicornia rubra* transplants, thus reducing their growth. This response suggests that availability of light is the limiting resource at these sites, and that competitive superiority is directly related to a species' stature. This is further supported by the vegetation gradient at each site, which shows a discontinuous increase in plant stature from the high salinity Salicornia zone through to the low salinity Calamagrostis.

Dead plant material was packed down around transplanted plugs in an attempt to minimize shading of transplants by dead material in cleared plots. The results suggest that this practice was more successful in site 2,3, and 4 than in site 1. The ANOVA and the graph of results from site 2 show that *Salicornia rubra* transplants were out-competed in uncleared plots of the Puccinellia, Hordeum/Distichlis, and Calamagrostis zones, but survived well, and even showed an increase in mean biomass accumulation in cleared plots of these zones; the lack of competition and lower salinity levels in these plots providing better conditions for growth. This trend was repeated in sites 3 and 4. However, unlike the site 2 results, ANOVA of the data from sites 3 and 4 indicated significant interaction between the factors, suggesting that the degree of competition differed depending on the vegetation zone into which the species was transplanted. Presumably, competition was most severe in the Calamagrostis zone because the plants of this zone were relatively large and created the greatest amount of shade.

Trends in biomass accumulation of growth chamber transplants of *Salicornia rubra* were similar to those of the field transplants in sites 3 and 4. ANOVA indicated that salinity and competition influenced the response of the species to transplantation, and that the level of competition differed from one zone to the next.

Section 5.4.4 - Competitive Exclusion and Physiological Tolerance

Bertness & Ellison (1987) and Bertness (1991 a,b) in a series of studies at a coastal salt marsh concluded that interspecific competition was an important component in determining vegetation patterns in these habitats. Through transplant experiments they found that the competitively superior species occupied the most favorable habitats, and the non-competitive species were relegated to less desirable areas which were often subjected to inundation, wrack disturbance, and higher salinity levels. Similar conclusions have been reached by Wilson & Keddy (1986) and Snow & Vince (1984).

Reciprocal transplant studies on specific inland halophytes, such as *Atriplex triangularis* (McMahon & Ungar 1978), *Salicornia rubra* (Ungar *et. al.* 1979), and *Hordeum jubatum* (Badger & Ungar 1990), concluded that competition *and* salinity tolerance were important factors influencing the growth and distribution of species in inland saline habitats. This conclusion was also reached in controlled growth chamber experiments studying competition and salinity tolerance between two halophytes (*Puccinellia nuttalliana* and *Hordeum jubatum*) and a glycophyte (*Poa pratensis*) (Kenkel *et. al.* 1991).

Observations of abiotic and biotic factors at my study sites revealed that the gradients of decreasing soil water salinity and increasing plant stature (not actually measured, but generally observed) outward from the salt pan were constant from one site to the next, while gradients in other soil factors such as moisture, organic matter, mineral particulate matter, bulk density, and pH differed between sites. The fact that the soil salinity and vegetation gradients were the only constants between the sites suggests that soil salinity and plant stature are the main factors influencing the distribution of species in these sites. Results from transplant experiments showed that the most salt resistant (tolerant) species, such as *Salicornia rubra* and *Puccinellia nuttalliana* , often performed better in cleared plots of the lower salinity zones than in uncleared plots in these zones and their native zone. Conversely, the results also showed that transplantation of low salt

tolerant species, such as *Calamagrostis inexpansa* and *Hordeum jubatum* into high salinity soils resulted in reduced growth or death. These results, coupled with the gradient observations indicate that under natural conditions species in these sites are distributed according to their competitive ability (stature) and the upper limits of their physiological tolerance.

Calamagrostis inexpansa is the largest species, but has a low tolerance to salinity, thus it dominates soils with the lowest salinities on the periphery of the sites. *Hordeum jubatum* has a wider range of tolerance than *Calamagrostis inexpansa*. However, being smaller than *Calamagrostis inexpansa*, it is competitively inferior, and is relegated to more saline soils in which it can survive, but which prohibit the growth of *Calamagrostis inexpansa* . In the same manner, *Hordeum jubatum* competitively excludes *Puccinellia nuttalliana* to the upper limits of its salt tolerance, and *Puccinellia nuttalliana* excludes *Salicornia rubra* to the limits of its salt tolerance.

Chapter 6 - Modeling and Summary Discussions

Section 6.1 - Introduction

Inland boreal saline habitats are characterized by distinct vegetation zonation. The purpose of this study was to investigate the vegetation and soil characteristics of such habitats in order to determine which factors are important in the creation and maintenance of this zonation. Past studies (see Chapter 1 for review) have shown that the relationship between soil salinity and the physiological tolerance of species is important in determining the distribution of species in saline habitats. In this study, as expected, high salt tolerant species were found at the upper end of the salinity gradient, while less tolerant species occurred at the lower end of the gradient. However, controlled experiments with inland halophytes have shown that species normally found in high salinity soils actually perform significantly better when grown in soils of reduced salinity. That is, species with a high tolerance to salinity are able to grow under a wide range of salinity, but appear to be restricted in the field to the upper extent of this range. This restricted distribution indicates that some other factor must be involved in creating and maintaining the vegetation zonation.

Both soil salinity and interspecific competition have been shown to be important factors in determining the distribution of vegetation at inland boreal saline sites, and the salinity tolerance and competitive ability of a species determines its position, relative to other species, along a salinity gradient. The salinity tolerance of a species appears to be inversely related to its ability to compete. Thus, a species with a high tolerance to salinity is less capable of competing successfully with a species exhibiting lower tolerance under conditions of reduced salinity. Transplantation of salt tolerant species species such as *Salicornia rubra* and *Puccinellia nuttalliana* into uncleared plots in the low salinity soils of the Hordeum and Calamagrostis zones resulted in a decline in growth. On the other hand, transplantation of these species into cleared plots of these same zones, where competition

was absent and salinity low, resulted in a general increase in growth. Thus, there is a restriction of high salt tolerant species to the upper extent of their tolerance range by less salt tolerant, but competitively superior species.

Section 6.2 - Modeling the Results

Kenkel *et al* (1991) conducted an experiment dealing with the interactions of three species along a salinity gradient. Their study included two halophyte grasses (*Puccinellia nuttalliana* and *Hordeum jubatum*) and a glycophyte grass (*Poa pratensis*). When grown in monoculture along the gradient, results indicated that *Puccinellia nuttalliana* was the most salt tolerant, followed by *Hordeum jubatum*, and finally *Poa pratensis*. All species showed the best growth response under conditions of low salinity. When grown in mixture, results indicated that each species had an advantage over the others at different salinity levels. Thus, when grown in mixture at high salinities, *Puccinellia nuttalliana* out-performed *Hordeum jubatum* and *Poa pratensis* , while when grown in mixture at low salinities, *Poa pratensis* proved more successful than the other two species. *Hordeum jubatum* appeared to be at an advantage over the other two species in mixtures grown at intermediate salinities. They concluded that competition from competitively superior, low salt tolerant species, leads to the exclusion of salt-tolerant species to the limits of their tolerance range. These results are in agreement with my results obtained from field and growth chamber transplants.

Soil salinity and interspecific competition exert a combined influence on the species that results in the vegetation zonation pattern. The position of vegetation boundaries along the salinity gradient, where the growth of one dominant species ends and another begins, are determined by the relative salinity tolerance and relative competitive ability of the two species. Figure 6.1(A, B, and C) presents a model to illustrate this step-wise exclusion of competitively inferior species, high salt tolerant species by competitively superior, low tolerant species.

Figure 6.1 (A) illustrates the relative potential growth of four hypothetical species when grown separately (i.e. no competition) along a gradient of increasing salinity. In the model , the four species differ with respect to their salinity tolerance, with species **A** having the narrowest tolerance range, and species **D** having the broadest tolerance range. All species reach their highest level of growth at the low end of the salinity gradient. As salinity increases the relative potential growth of each species begins to decline in accordance with its range of salt tolerance.

Figure 6.1 (B) illustrates the relative potential growth of the four species when grown together (i. e. competition present) along the salinity gradient. The low end of the salinity gradient is occupied by species **A**; the top competitor under low salinity conditions. As one moves along the salinity gradient, from low salinity to high salinity, there is a point at which the competitive ability of species **A** declines to that of species **B**. Beyond this point growth of species **A** ceases, allowing for the dominance of species **B**. Species **A** can no longer tolerate the high salinity soils and simultaneously maintain its competitive advantage over the more salt tolerant species **B.** The same set of circumstances prevail between species **B** and **C**, and species **C** and **D**, as one moves further along the salinity gradient. The decline in competitive ability with increased salinity results in the creation of vegetation boundaries and the zonation pattern observed.

Note that in Figure 6.1 (B) the curves for species **B**, **C**, and **D** indicate that the species are not able to attain their maximum growth potential when grown together. This occurs because competition with a superior competitor relegates the more salt tolerant species to the higher end of its tolerance range, where the competitor is excluded by salinity. However, conditions inherent at the upper end of each species' tolerance range are suboptimal, resulting in a growth response that is less than the maximum potential growth for the species.

Figure (A)

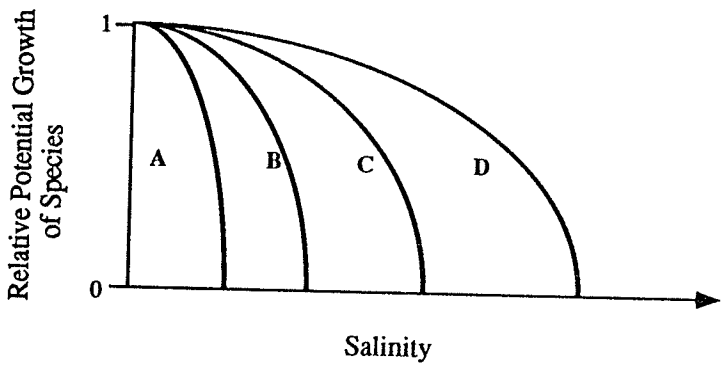


Figure (B)

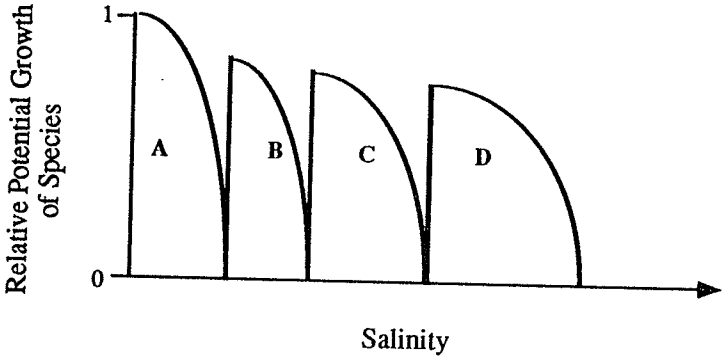


Figure (C)

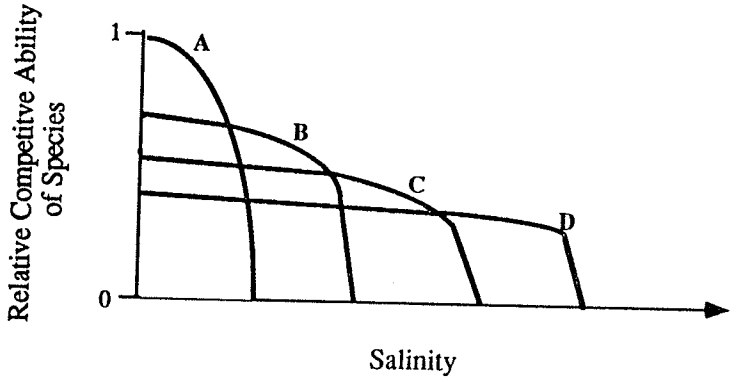


Figure 6.1 Model illustrating relationship between four species differing in salinity tolerance and competitive ability. Figure (A) shows potential growth under conditions of no competition. Figure (B) shows potential growth when competitors are present. Figure (C) illustrates the relative competitive abilities of the four species along the gradient (derived in part from Kenkel *et. al.* 1991 and Burchill 1991)

Figure 6.1 (C) is derived from Figure 6.1 (B) and illustrates the decline in competitive ability of each species as salinity increases. Each dominant species has a specific range of salinity along the gradient within which it is competitively superior over other species. This relationship between relative competitive ability and salinity tolerance creates and maintains the vegetation zonation.

The model in Figure 6.1 has implications with regards to the concept of the niche. Each species curve in Figure 6.1 (A) represents the boundary of the fundamental niche for a particular species. Thus, when grown in the absence of neighboring species (i.e. transplants placed into cleared plots of each vegetation zone) the size of the fundamental niche is proportional to the salt tolerance of the species. It follows that the wider a species' physiological tolerance, the larger its fundamental niche. Figures 6.1 (B) and (C) represents the response of species along the salinity gradient in the presence of competitors (i.e. transplants placed into uncleared plots in each vegetation zone). The species curves represents the boundary of the realized niche for each species. The model indicates that the size of a species' realized niche, relative to its fundamental niche, is related to its competitive ability, as well as its tolerance to salinity.

According to Grime's (1977, 1979a,b) C-S-R strategy theory, in resource-poor habitats competition between species is less intense, and therefore less important with regards to species distribution, than in resource-rich habitats. The theory infers that under conditions of low resource availability plant growth declines, resulting in a reduced chance for competitive interactions to take place, but under conditions of high resource availability the growth of species increases, resulting in increased occurrence of competition (Reader & Best 1989). This implies that competitive ability and wide physiological tolerance are two characteristics that cannot both be highly developed in a single species. A further implication of the theory is that for a given plant species there must be a trade-off between its ability to compete, through rapid growth, with other species, and its ability to tolerate abiotic conditions within its environment (Smith & Huston 1989). Presumably species

adapt to resource-poor habitats by developing mechanisms to tolerate the sub-optimal conditions. Often these tolerance mechanisms are energy consumptive, and consequently the growth of tolerators relative to competitors is inhibited. In habitats characterized by limited resources, the ability of species to effectively retain and efficiently use the resources they acquire, through slow growth and low-turnover rates (stress tolerators), is advantageous over the rapid up-take and utilization of resources characteristic of species (competitors) in resource-rich habitats.

If a competitor and stress-tolerator (Grime 1979a,b) were allowed to compete along a resource gradient, the stress-tolerator would occupy the lower end of the gradient, while the competitor would occupy the upper end of the gradient. As pointed out by McGraw & Chapin (1989) the relationship between tolerance and competitive ability, as put forth by Grime, suggests that there would be no reversal of the interaction, over the short term, if the resource gradient was changed. That is, according to the C-S-R theory, to make resources more available will not increase the stress-tolerator's competitive ability relative to that of the competitor species, because the competitor species is able to more rapidly take up and utilize the resources, and thus it will continue to exclude the stress-tolerator to lower end of the gradient.

Tilman's resource-ratio hypothesis (see Tilman 1982, 1985) infers that because resource-poor habitats provide only a limited supply of resources, competition for the resources should be intense (Reader & Best 1989). According to McGraw and Chapin (1989), the Tilman approach suggests that the competitive ability of a species can be altered by altering the environment, which implies that the outcome of competitive interactions between species is a function of the environment and the adaptations of the species involved. This also implies that the competitive abilities of species may reverse along a resource gradient.

My results agree only partially with both Grime's and Tilman's approaches. They indicate that competitive ability of species declines with increasing salinity. However, they

also indicate that competitive interactions are not only present under conditions of salinity stress (stress as defined by Grime), but also play a prominent role in the distribution of plant species throughout inland boreal saline habitats. It is important to remember that Grime and Tilman formulated their theories on the basis of competition along resource gradients. My experiment involved the competitive interactions of species along a gradient of salinity (NaCl), which can not be considered a resource according to Tilman's definition (see Chapter 1). Therefore, neither Grime's nor Tilman's models are fully appropriate in illustrating species interactions along a stress gradient, in this case salinity.

Section 6.3 - Areas of Future Research

The inland boreal saline sites of west central Manitoba are very unique to the province and are currently in the process of being designated 'ecologically significant' areas by the Government of Manitoba. The fact that they are easily accessible, relatively simple systems, make such sites excellent candidates for ecological research. Knowledge gleaned from such studies can then be extrapolated to larger, more complex systems. The sites may also be useful in 'island ecology' research, as they are essentially isolated from each other by boreal forest vegetation. Some specific suggestions for future research include:

1) Research should be conducted to address the role of competition in plant zonation at sites varying in age. Age classes could be determined based on the presence or absence of springs and unvegetated salt pans, and the concentration of salt along the salinity gradient. Presumably sites with active springs would be the youngest sites, while sites with little or no salt pan, and low overall salinity would be the oldest. Transect sampling and multivariate analysis methods (as described in Burchill 1991) could be employed to determine the degree of continuity/discontinuity of soil and vegetation gradients in each age class. Transplant experiments could be used to determine if competition is occurring, and

if the intensity of the competitive interactions is related to the age of sites. This investigation may provide criteria to enable one to age saline sites on the basis of their salinity, species composition, and vegetation patterning.

2) Further research should be conducted into the life-history strategies of the dominant species. Numerous studies have been conducted on the growth and distribution of *Salicornia rubra*, however, parallel studies on the other dominant species of inland saline sites are few.

3) My results indicate that soil characteristics often differed between corresponding zones of different sites, however, the vegetation composition remained very similar between sites. A study involving reciprocal transplantation of vegetation into corresponding zones of different sites may yield information regarding ecotypic variation and plasticity within the dominant species.

4) Studies addressing the stability and resiliency of the vegetation zonation are lacking. Research should be conducted to determine how stable the zone boundaries are, and if the position of the boundaries changes over time with fluctuations in salinity and incidences of disturbance. This could have implications with regards to environmental influences on competitive interactions.

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Appendices

Appendix I - List of Vascular Plant Species

Appendix I(A): Vascular plants recorded in the saline meadows around saline flats: Overflow Bay (Lake Winnipegosis). (Nomenclature according to Scoggan. 1957). (Collected and identified by C. Burchill, May - August 1987).

Achillea millefolium
Agropyron trachycaulum
Alnus rugosa
Ambrosia psilostachya var. coronopifolia
Amelanchier alnifolia
Arenaria lateriflora
Aster laevis
Aster pansus
Aster pauciflorus
Aster simplex
Atriplex patula var. hastata
Betula occidentalis
Bromus ciliatus
Calamagrostis inexpansa
Calamagrostis neglecta
Campanula rotundifolia
Carex aurea
Carex lanuginosa
Carex viridula
Castilleja miniata
Circium arvense
Commandra richardsonii
Distichlis stricta
Dodecatheon media
Eleocharis palustris
Eleocharis pauciflora
Epilobium angustifolium
Erigeron philadelphicus
Festuca saximontana
Fragaria virginiana
Galium boreale
Glaux maritima
Grindelia squarrosa
Helianthus maximilliannii
Heracleum lanatum
Hierchloe odorata
Hordeum jubatum
Juncus balticus var. littoralis
Juncus compressus
Juniperus communis
Lathyrus palustris
Lilium philadelphicum

Luzula sp.

Appendix I(A) (continued)

Melilotus officinal
Phragmites communis
Picea glauca
Plantago maritima
Poa compressa
Poa palustris
Populus tremuloides
Potentilla anserina
Primula mistassinica
Puccinellia nuttalliana
Ranunculus cymbalaria
Ribes oxyacanthoides
Rosa acicularis
Salicornia rubra
Scirpus americanus
Scirpus paludosus
Senecio integeriumus
Shepherdia canadensis
Sisyrinchium montanum
Smilacina stellata
Solidago canadensis
Sonchus arvensis
Spartina gracilis
Spergularia marina
Sphenopholis obtusata
Stellaria longifolia
Suaeda depressa
Symphoricarpos albus
Thalictrum dasycarpum
Triglochin maritima
Viola sp.
Zizia aptera
Zygadenus elegans

Appendix I(B): Vascular plants found on the spruce dominated ridges around the salt flats of Overflow Bay (Lake Winnipegosis). (Nomenclature follows Scoggan, 1957). (Collected and identified by C. Burchill, August 1988).

Achillea millefolium
Agropyron sp.
Alnus rugosa
Antennaria parviflora
Aralia nudicaulus
Arctium lappa
Arctostaphylos uva-ursi
Aster laevis
Betula glandulifera
Betula papyrifera
Carex spp.(two species)
Commandra richardsiana

Cornus alba

Appendix I(B) (continued)

Cornus canadensis
Crepis sp.
Cypripedium calceolus
Epilobium angustifolium
Equisetum arvense
Fragaria virginiana
Galium boreale
Galium trifidum
Habenaria sp.
Juncus balticus
Juniperus communis
Lathyrus sp.
Linnaea borealis
Maianthemum canadense
Moneses uniflora
Monotropa uniflora
Oxycoccus quadripetalus
Petasites palmatus
Pyrola rotundifolia
Pyrola secunda
Ribes oxyacanthoides
Rosa acicularis
Rubus idaeus
Rubus pubescens
Shepherdia canadensis
Solidago sp.
Symphoricarpos alba
Taraxacum sp.
Thalictrum venulosum
Trientalis borealis
Vaccinium sp.
Vibernum rafinesquianum
Vicia sp.
Viola sp.

Appendix II - Field Activity Schedule 1989 & 1990

The study sites were visited six times in 1989 (2-3 June, 20-21 June, 30 June, 12-13 July, 7 August, and 28-30 August) and five times in 1990 (23-25 April, 28-30 May, 2-5 July, 31 July -2 August, and 21-24 August). Table II(A) provides a schedule of field work activities (data collection and monitoring) conducted during the 1989 and 1990 growing seasons.

Table II(A). Research activity schedule for 1989 and 1990 field seasons.

Subject	1989 Season	1990 Season
Soil Density	All	All
Soil Organic Matter	2-3 June	
Soil pH	2-3 June	All, except 23-25 April
Soil Salinity (volume dry soil)	2-3 June	
Soil Moisture	All, except 2 June	All
Soil Water Salinity	All, except 2 June	All
Particle Size Analysis		28-30 May
Nutrient (N,P,K) Analysis		28-30 May
Salinity Methods Tests		28-30 May
Soil Depth Gradients		28-30 May & 2-5 July

Table II(A) (continued).

Subject	1989 Season	1990 Season
Site Transects		23-25 April
Vegetation Sampling		All, except 23-25 April
Seed Bank Collection		23-25 April
Experimental Design Setup	2-3 June	
Herbicide Application	2-3 June	
Vegetation Transplantation	20- 21 June	
Growth Chamber Transplantation		28-30 May
Weeding of Plot	All, except 2 June	All
Seed Collection for Lab Experiments	28-30 August	21-24 August
Harvesting & Soil Sampling of Field Transplants	28-30 August	21-24 August
Harvesting & Soil Sampling of Growth Chamber Transplants		21-24 August

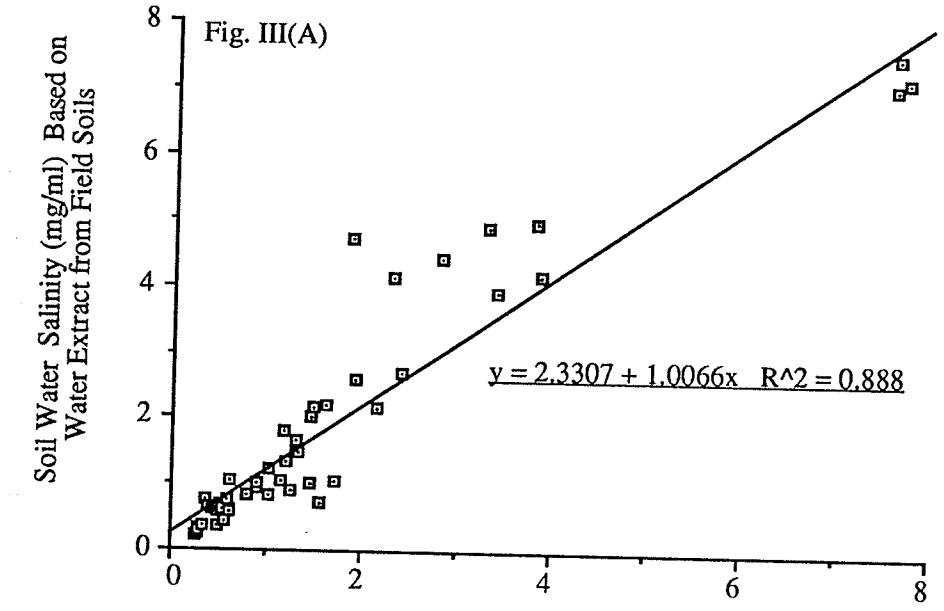
Appendix III - Salinity Method Tests

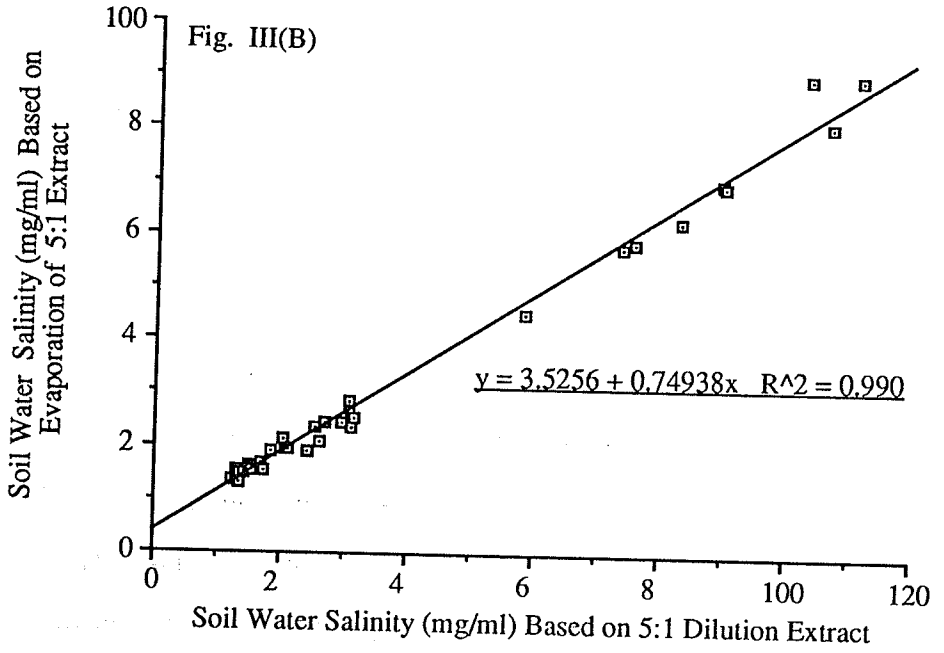
Three variations for determining salinity concentration were conducted in order to test the relevance of the 5:1 (water:dry soil by mass) dilution extract method used in the methods (see Chapter 3).

First, 45 large soil cores were collected from plots at the study sites and transported frozen back to the lab. The conductivity of extracted field water from these large soil samples was measured. This conductivity reading was then converted to mg of salt/ml of soil water, based on the soil water content of the samples. The results were then compared, using linear regression analysis, with results obtained from another set of core samples that had been collected at the same time and place, but had been subjected to the 5:1 dilution extract method. Figure III(A) presents the results of the regression. We see that the salinity measurements obtained from the two methods are highly related (R^2= 0.888; Slope = 1.0066) .

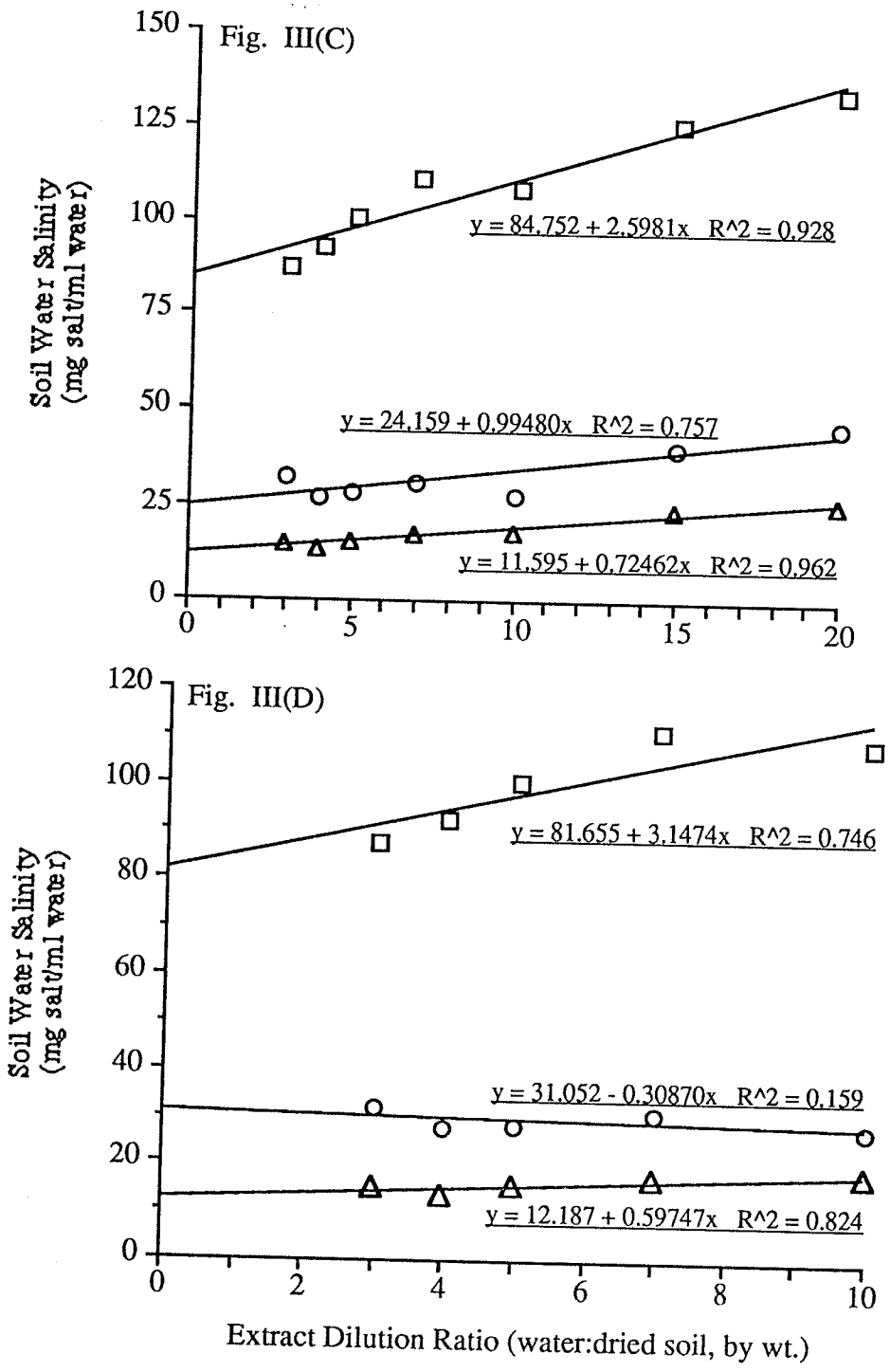
To further test the method, the soil water salinity of 36 soil samples from various zones of site #2 was determined using the 5:1 dilution extract method. The flasks containing the extracts were then placed in a drying oven to allow evaporation. The mass of the precipitate was recorded and converted to mg/ml of soil water based on the soil water content of the original sample cores. A comparison of results obtained from the two methods is presented in Figure III(B). Regression analysis was used to illustrate the strength of the relationship between the two data sets. As in figure III(A), the regression shows that the results from the two methods are closely related (R^2=0.99). The slope of the line is lower than that of Figure III(A), indicating that the results from the 5:1 dilution method are higher than those obtained from the evaporation method. However, the high R^2 value indicates that this discrepancy is consistent throughout the samples. The difference in results may be due to error in the conductivity meter.

The final test of the 5:1 dilution extract method involved collecting a number of soil samples from each zone of site 4, and subjecting them to a variety of dilution ratios. The ratios (ml water: g dry soil) used included: 3:1; 4:1; 5:1; 7:1; 10:1; 15:1; and 20:1. The soil water salinity values obtained from each dilution are presented graphically in figures III(C) and III(D). In general the salinity levels were similar for the 3:1 up to the 10:1 dilution extract. Dilutions above the 10:1 extract tended to yield increased levels of salinity, especially in the Salicornia zone samples. These high salinity values (with high dilutions) likely represent an increased presence of low soluble salts in the extract solution, and thus, do not accurately represent the NaCl content of the soil salinity. The 5:1 dilution was found to be the best for my purposes, as it required relatively small amounts of soil, and provided ample extract solution for salinity determination, as well as pH testing.





Figs. III (A) & (B) Graphs comparing the 5:1 dilution extract method of salinity determination with results obtained from (A) water extracted directly from field samples (n = 45), and from (B) evaporation of the 5:1 extract (n = 36).



Figs. III (C) & (D) Graphs showing soil water salinity determinations using different extract dilution ratios: 3:1, 4:1, 5:1, 7:1, 10:1, 15:1, and 20:1 (water:dry soil by wt.). Figure (C) includes all dilution ratios, while figure (D) omits 15:1 and 20:1. Soils sampled were collected from the Calamagrostis (Δ), Distichlis (O), and Salicornia (□) zones of site 4, 1990.

Appendix IV - 1989 Transplant Results

The 1989 season biomass accumulation results for the transplanted dominant species are presented in Figures IV(A) - IV(E). The graphs follow the same format as those of the 1990 season harvest (Figures 5.12 - 5.16, Chapter 5). ANOVA was conducted as described in Chapter 5. The results of the ANOVA are presented below in Table IV(A).

Table IV(A) ANOVA results (p - values) from biomass accumulation data of dominant transplanted species from the 1989 season harvest.

Dominant	Saline	ANOVA	Results	(p values)
Species	Site	Zone	Treatment	Interaction
Calamagrostis inexpansa	1	0.0014	0.5519	0.5791
	2	0.0017	0.0078	0.0556
	3	0.737	0.0797	0.5224
	4	0.1233	0.3466	0.6157
Hordeum jubatum	1	0.1856	0.023	0.487
	2	0.1073	0.0435	0.1478
	3	0.8673	0.0173	0.7598
Distichlis stricta	2	0.9738	0.3862	0.2165
	4	0.1719	0.5631	0.1614
Puccinellia nuttalliana	1	0.0345	0.2113	0.4876
	2	0.1129	0.0032	0.4674
Salicornia rubra	1	0.178	0.1064	0.178
	2	All Dead		
	3	0.0001	0.0001	0.0015
	4	0.0004	0.0000	0.0004

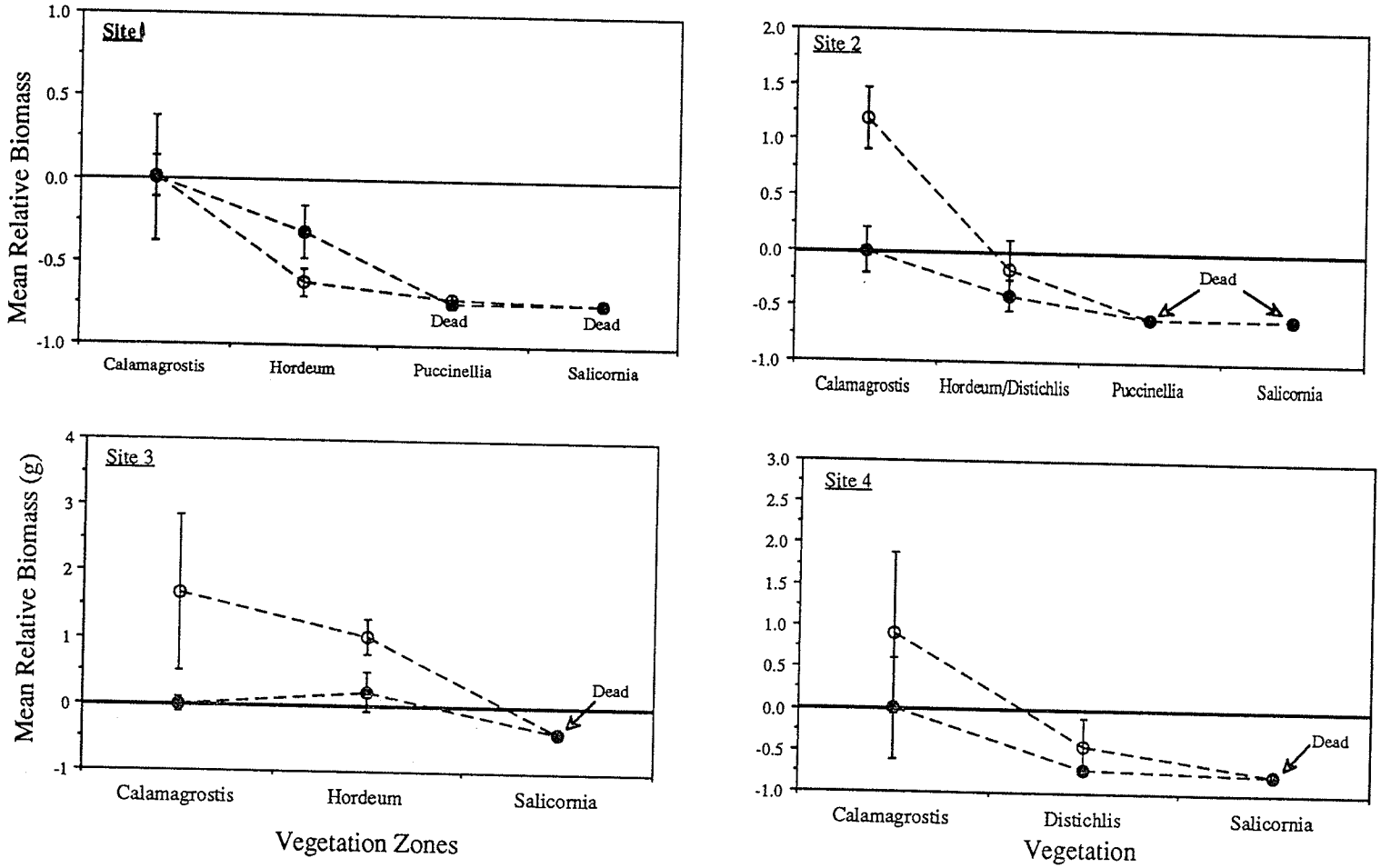


Fig. IV(A) Mean relative biomass accumulation of *Calamagrostis inexpansa* in field transplant plugs placed into cleared (○) and uncleared (●) plots in each vegetation zone of sites 1 - 4, 1989 season. Values are means ± SE. n= 5 for site 1 and 2, n = 3 for sites 3 and 4.

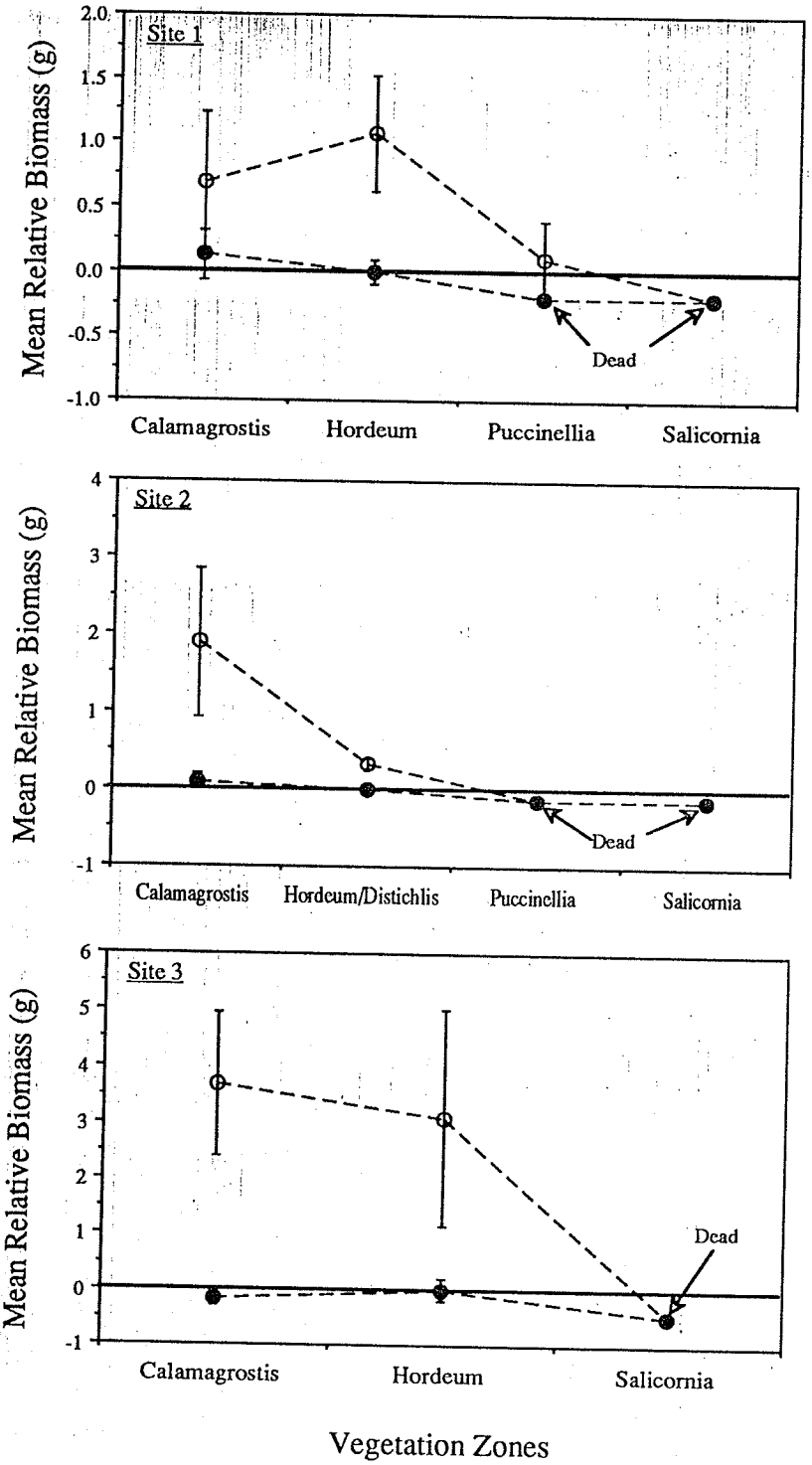


Fig. IV(B) Mean relative biomass accumulation of *Hordeum jubatum* in field transplant plugs placed into cleared (O) and uncleared (●) plots in each vegetation zone of sites 1 - 3, 1989 season. Values are means ± SE. n= 5 for sites 1 and 2, n = 3 for site 3.

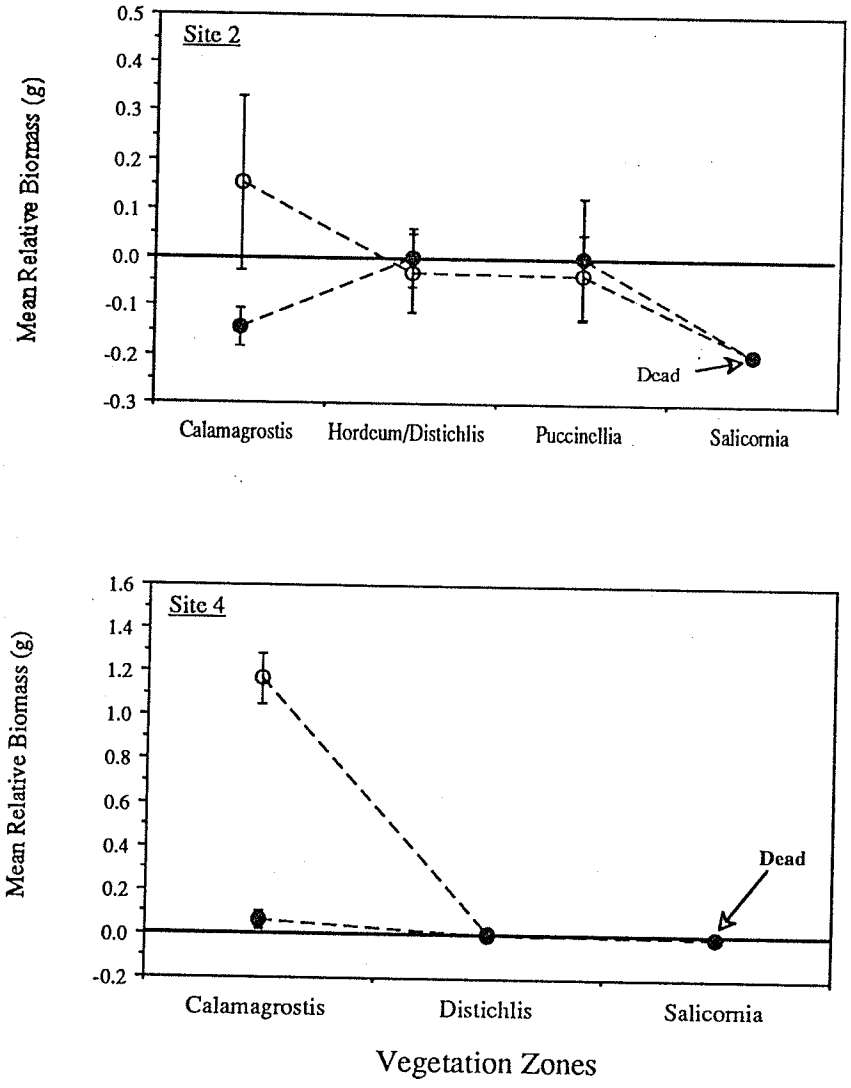


Fig. IV(C) Mean relative biomass accumulation of *Distichlis stricta* in field transplant plugs placed into cleared (O) and uncleared (●) plots in each vegetation zone of sites 2 and 4, 1989 season. Values are means ± SE. n= 5 for site 2, n = 3 for site 4.

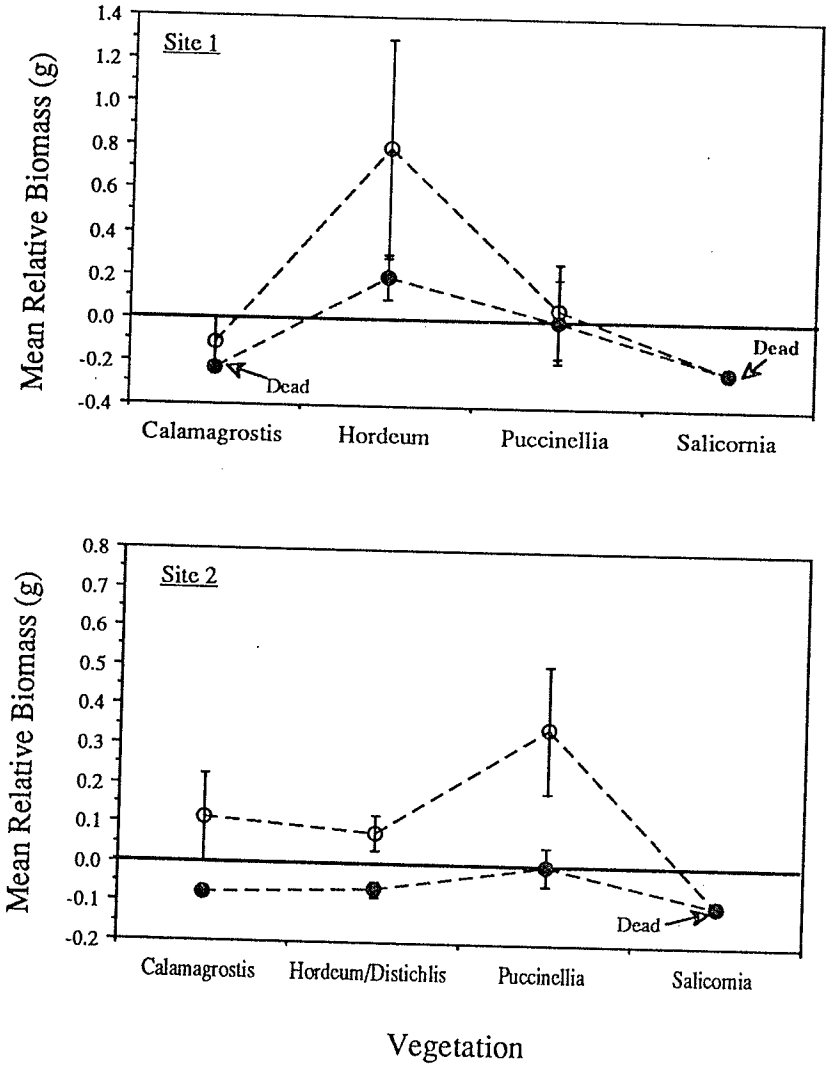


Fig. IV(D) Mean relative biomass accumulation of *Puccinellia nuttalliana* in field transplant plugs placed into cleared (O) and uncleared (●) plots in each vegetation zone of sites 1 and 2, 1989 season. Values are means ± SE. n= 5.

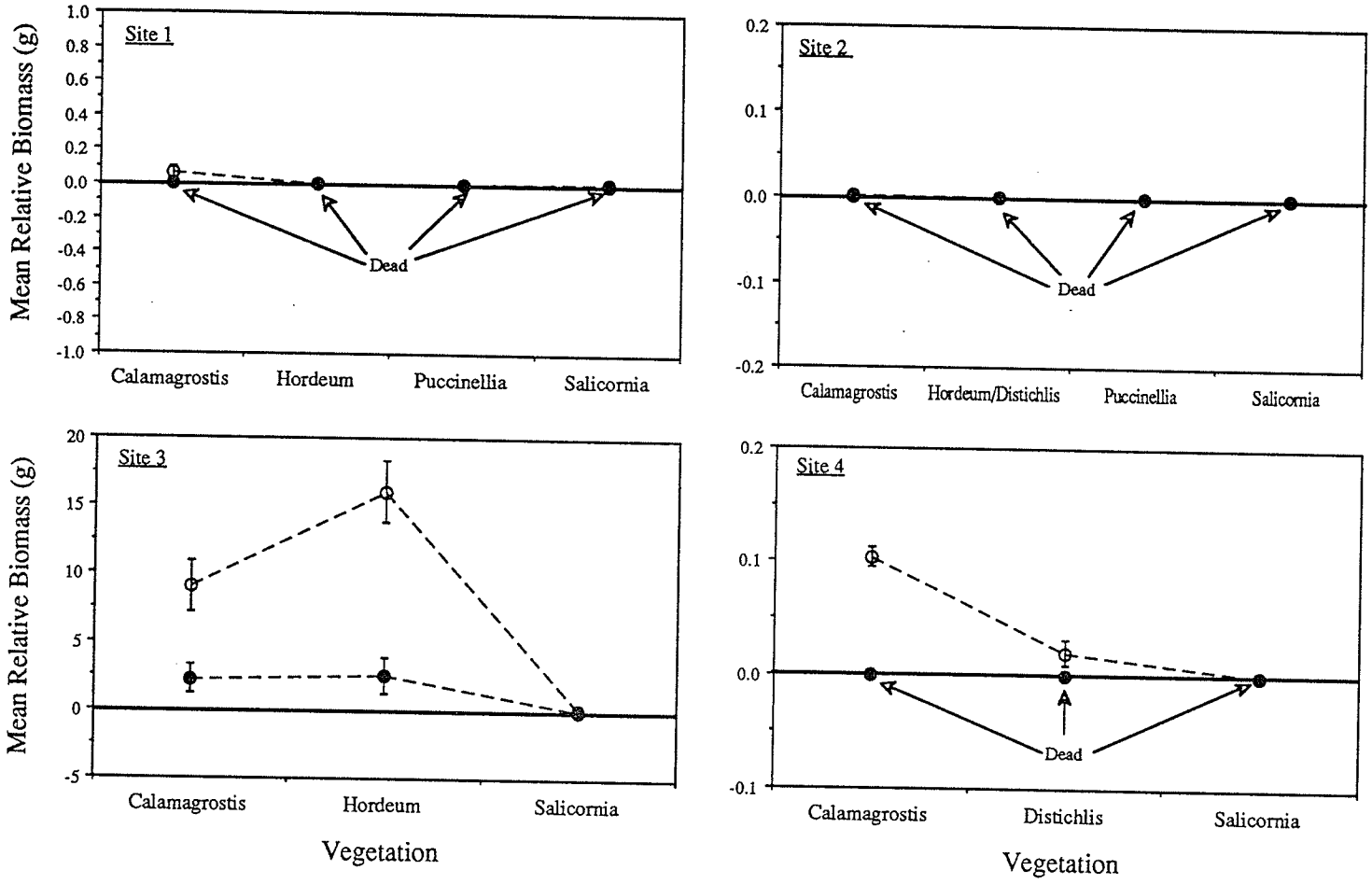


Fig. IV(E) Mean relative biomass accumulation of *Salicornia rubra* in field transplant plugs placed into cleared (○) and uncleared (●) plots in each vegetation zone of sites 1 - 4, 1989 season. Values are means ± SE. n= 5 for sites 1 and 2, n = 3 for sites 3 and 4.

Results from determination of below-ground biomass in transplants at site 3 (1989 season) are presented graphically in Figure IV(F). ANOVA of the below-ground biomass data is presented below, in Table IV(B).

Table IV(B). Results of two-factor ANOVA (a = 0.05) conducted on below ground biomass data of dominant species transplanted into vegetation zones of site 3, 1989.

Dominant Species	ANOVA Results (p values)		
	Vegetation Zone	Plot Treatment	Interaction
Calamagrostis inexpansa	0.6889	0.3814	0.024
Hordeum jubatum	0.2835	0.0595	0.5701
Salicornia rubra	0.0936	0.0386	0.3944

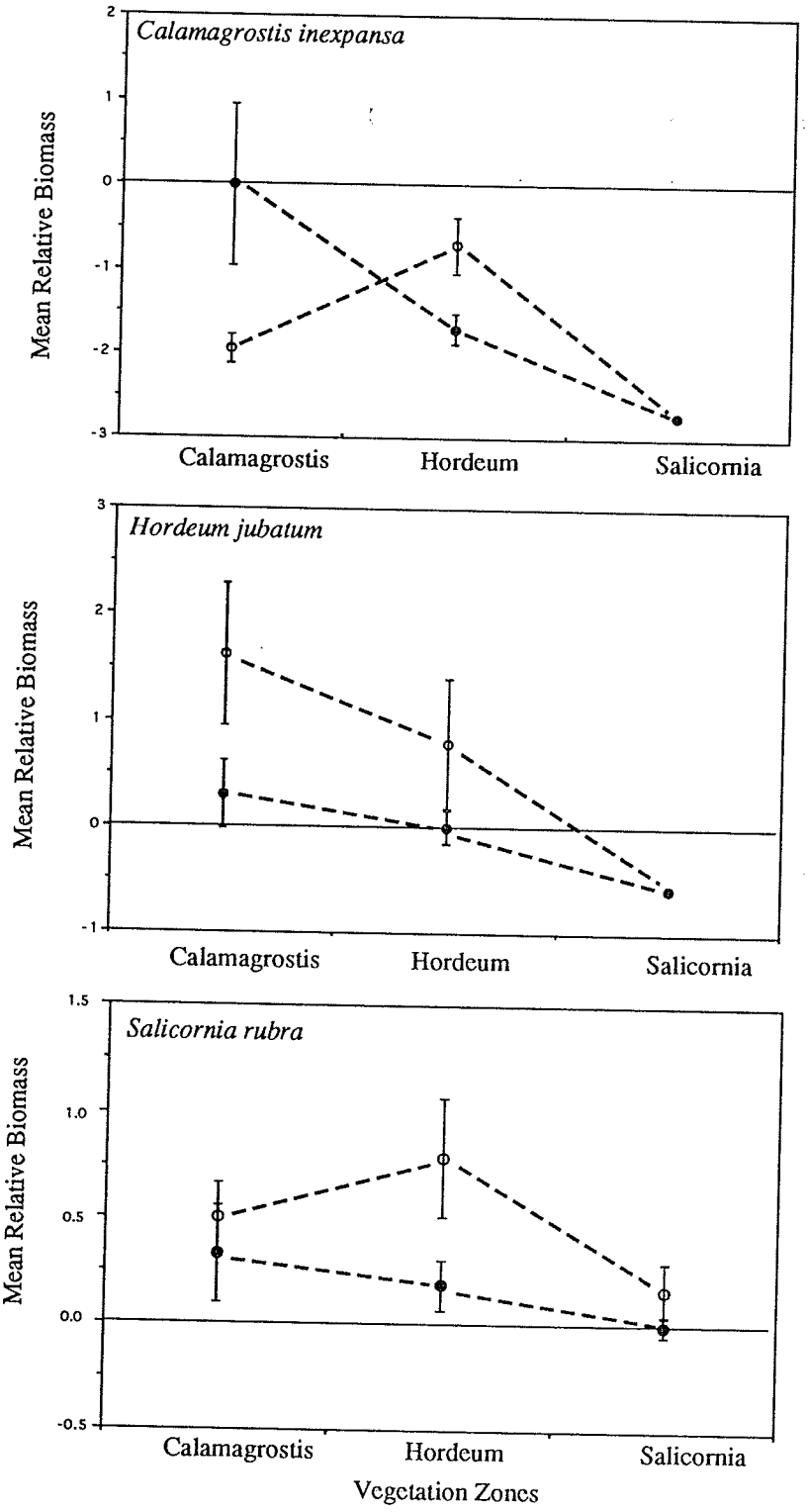


Fig. 5.25 Mean below-ground biomass accumulation of species in transplant plugs placed into cleared (□) and uncleared (▩) plots in the vegetation zones of site 3. Values are means ± SE. n = 3. Horizontal line at zero represents the control to which the transplants are compared.

Appendix V - 1990 Density Results

The 1990 season density results for the transplanted dominant species are presented in Figures V(A) - V(E). The graphs follow the same format as those of the 1990 season biomass accumulation results (Figures 5.12 - 5.16, Chapter 5). ANOVA was conducted as described in Chapter 5. The results of the ANOVA are presented below in Table V(A).

Table V(A) Results of two-factor ANOVA (a = 0.05) conducted on density data of dominant species transplanted into vegetation zones at each site, 1990.

Dominant Species	Saline Site	ANOVA Results (p values)		
		Vegetation Zone	Plot Treatment	Interaction
Calamagrostis inexpansa	1	N/A	0.9454	N/A
	2	0.0039	0.8251	0.6913
	3	0.0287	0.0004	0.0000
	4	N/A	0.0191	N/A
Hordeum jubatum	1	0.3485	0.0284	0.9805
	2	0.2108	0.0002	0.1053
	3	0.0276	0.0178	0.6022
Distichlis stricta	2	0.0124	0.9013	0.9844
	4	0.0888	0.5037	0.4306
Puccinellia nuttalliana	1	0.0000	0.0023	0.1723
	2	0.2879	0.0002	0.8439
Salicornia rubra	1	0.0001	0.0611	0.9186
	2	0.0799	0.0005	0.1723
	3	0.0002	0.0001	0.0022
	4	0.0293	0.0036	0.0550

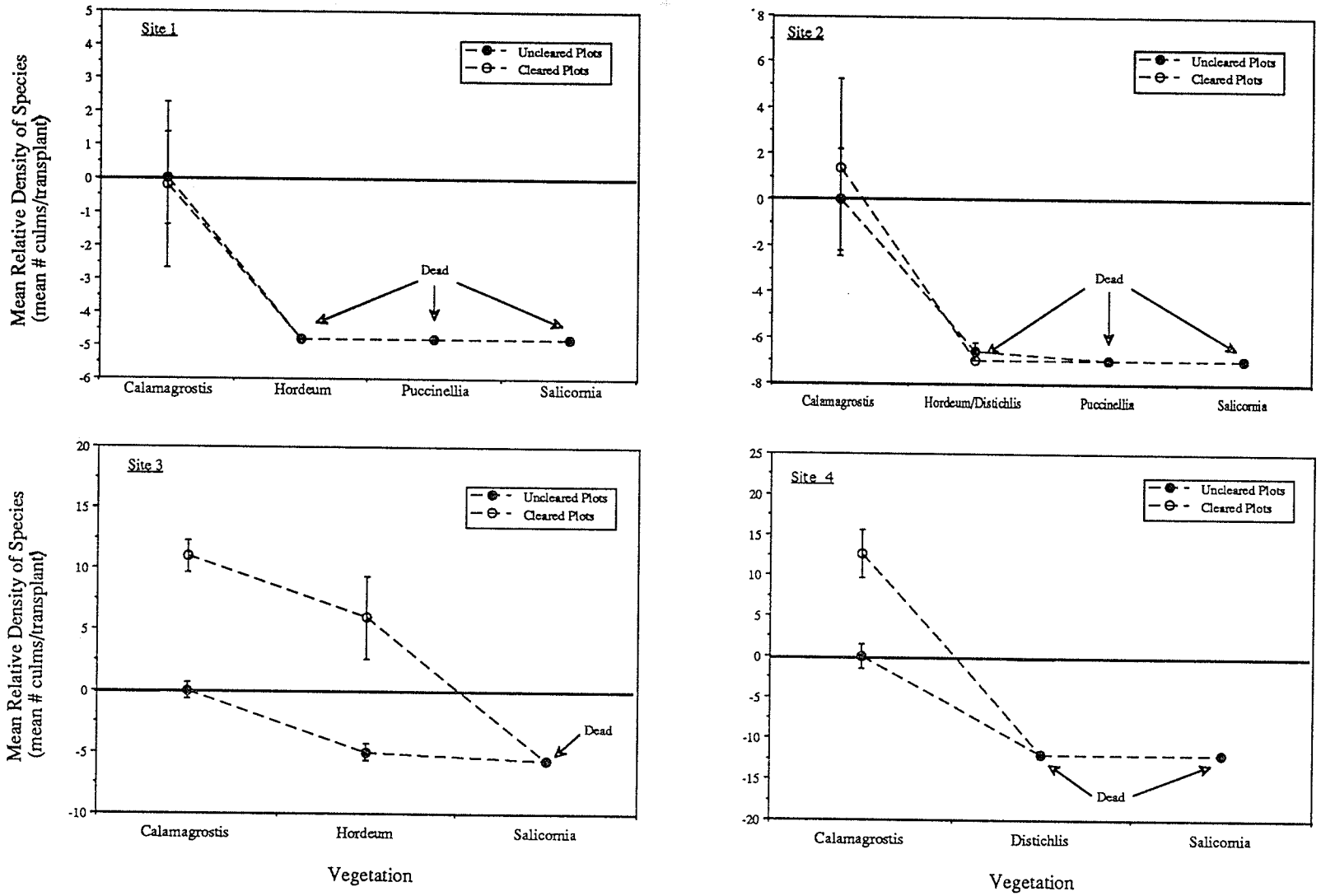


Fig. V(A) Response of *Calamagrostis inexpansa* in vegetation plugs taken from the Calamagrostis zone and transplanted into each vegetation zone at each site. Response is measured by density of culms per transplant plug relative to the Calamagrostis zone cut-and-replace control plugs. Density values are means ± S.E. (n = 5 for sites 1 and 2, n = 3 for sites 3and 4).

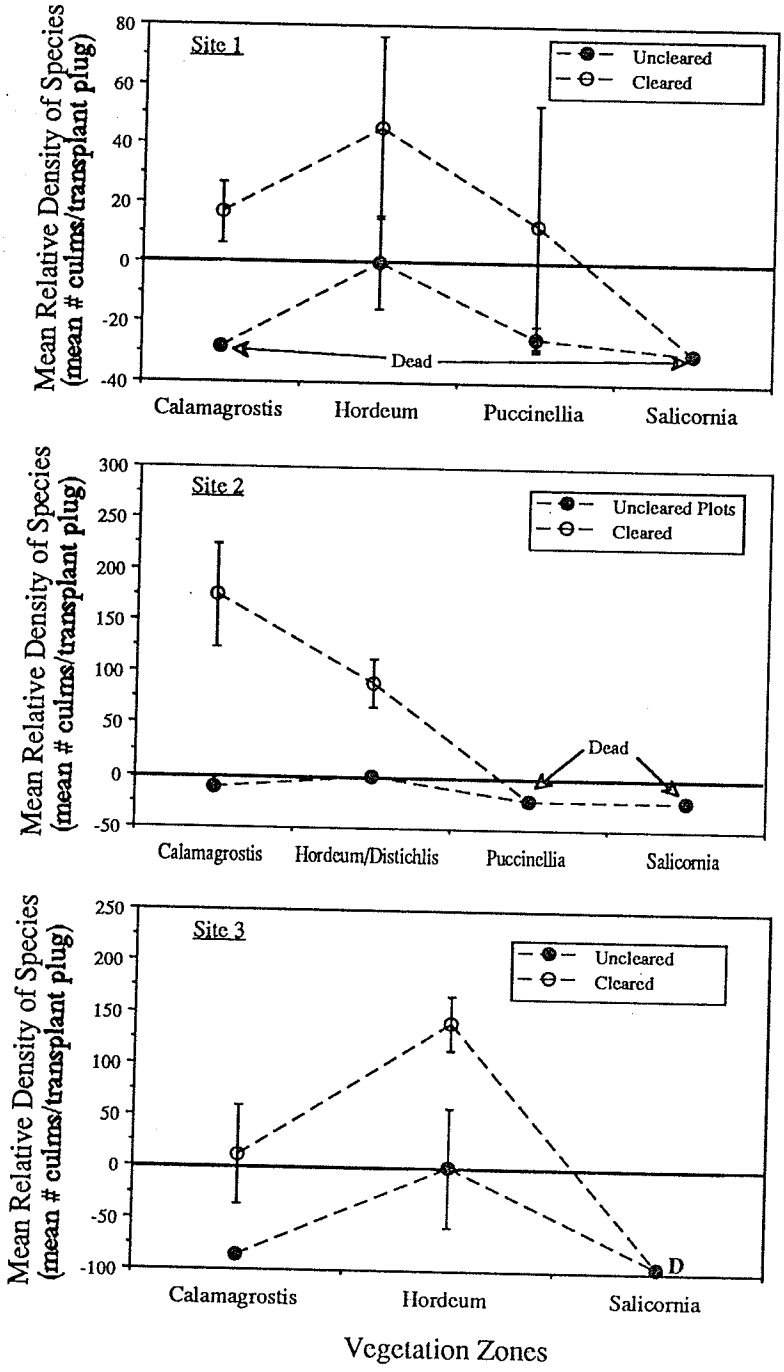


Fig. V(B) Response of *Hordeum jubatum* in vegetation plugs taken from the Hordeum and Hordeum /Distichlis zones of sites 1, 2, and 3, and transplanted into each vegetation zone. Response is measured by density of culms per transplant plug relative to the Hordeum or Hordeum/Distichlis zone cut-and-replace control plugs. Density values are means ± S.E. (n = 5 for sites 1 and 2, n = 3 for site 3).

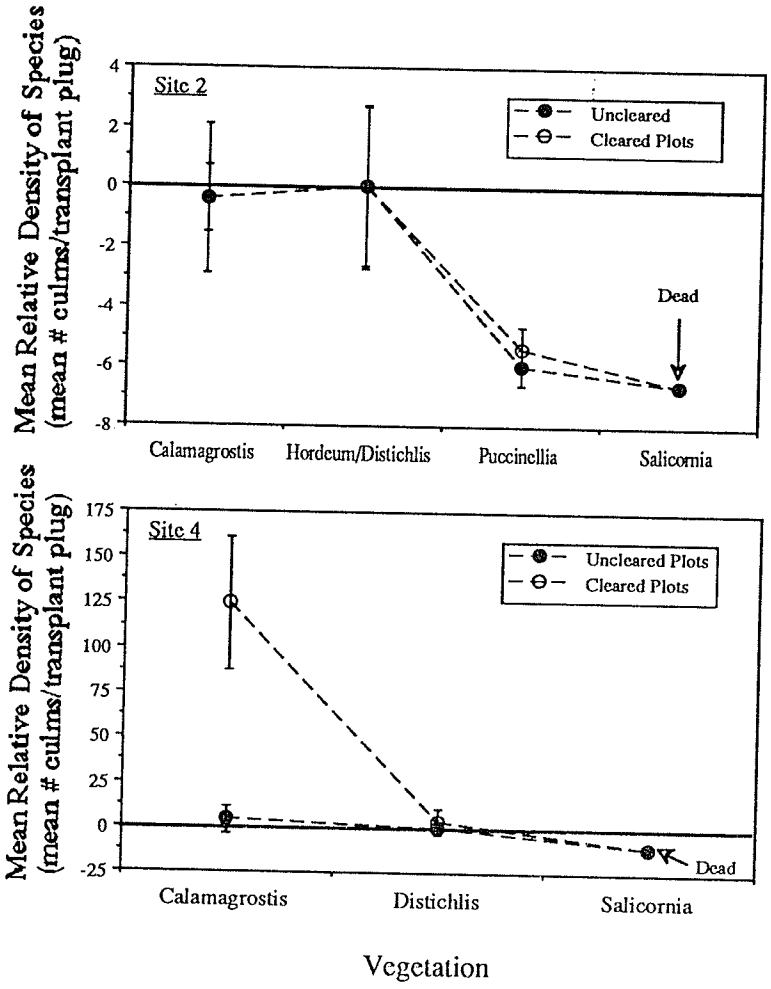


Fig. V(C) Response of *Distichlis stricta* in vegetation plugs taken from the Hordeum/Distichlis zone of site 2 and the Distichlis zone of site 4, and transplanted into each vegetation zone. Response is measured by density of culms per transplant plug relative to the Hordeum/Distichlis and Distichlis zones cut-and-replace control plugs. Density values are means ± S.E. (n = 5 for site 2, n = 3 for site 4).

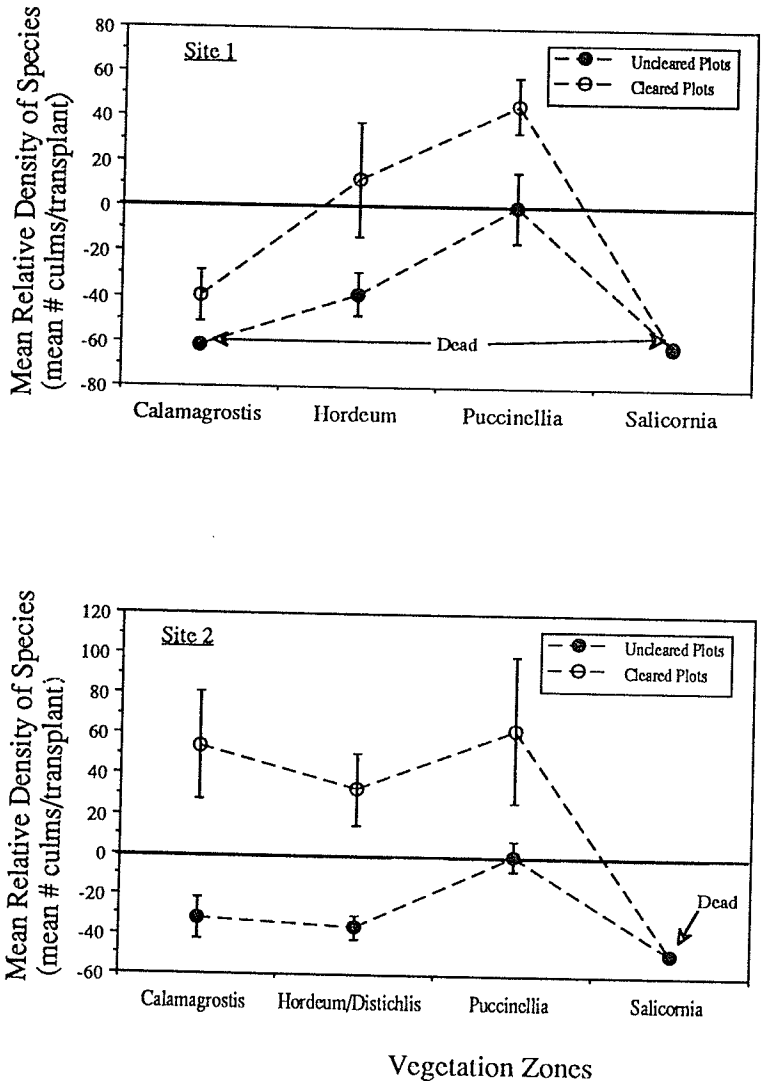


Fig. V(D) Response of *Puccinellia nuttalliana* in vegetation plugs taken from the Puccinellia zones of sites 1 and 2, and transplanted into each vegetation zone. Response is measured by density of culms per transplant plug relative to the Puccinellia zone cut-and-replace control plugs. Density values are means ± S.E. (n = 5).

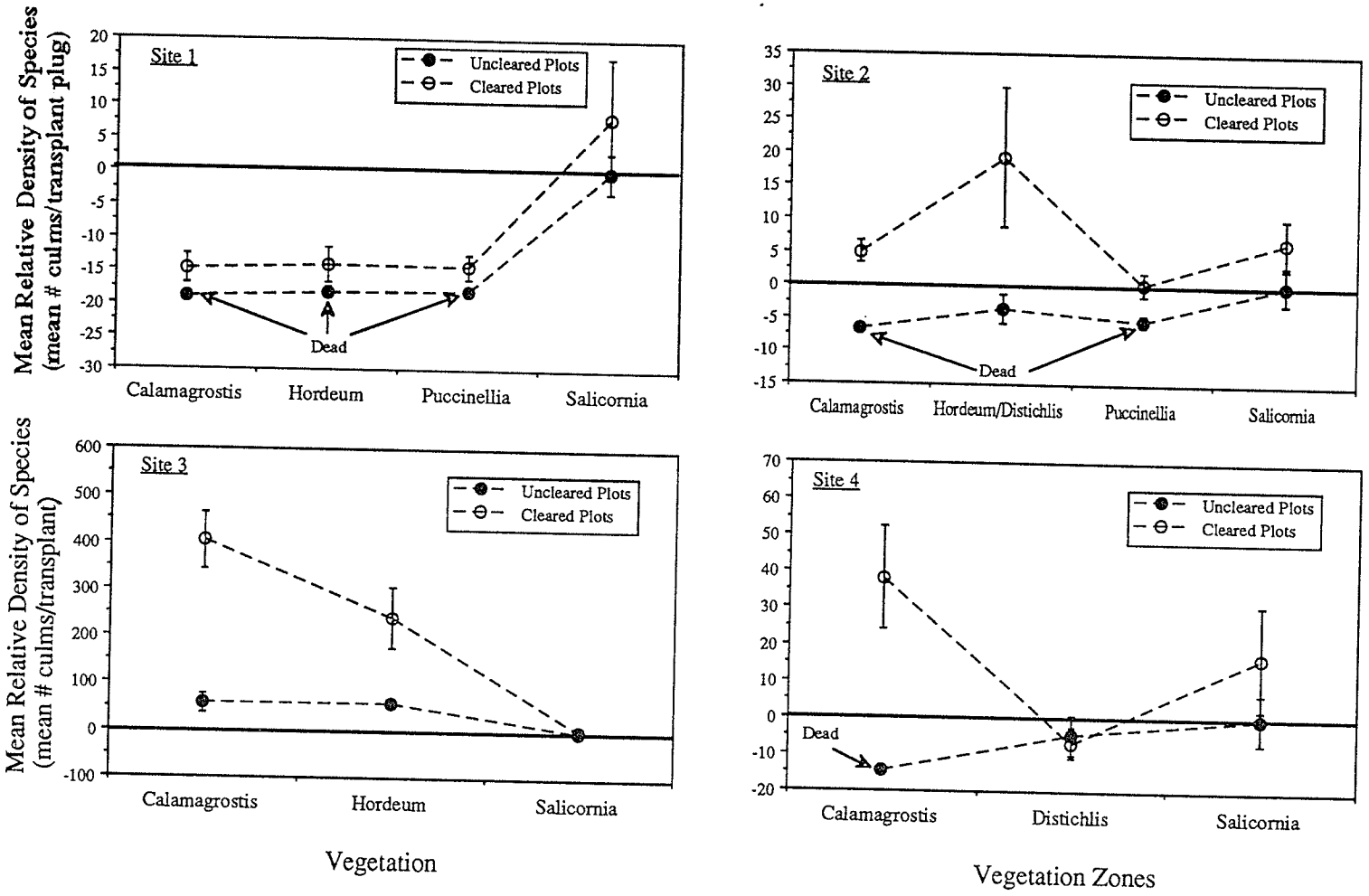


Fig. V(E) Response of *Salicornia rubra* in vegetation plugs taken from the Salicornia zones of sites 1 - 4, and transplanted into each vegetation zone at each site. Response is measured by density of culms per transplant plug relative to the Salicornia zone cut-and-replace control plugs. Density values are means ± S.E. (n = 5 for sites 1 and 2, n = 3 for sites 3 and 4)).

Appendix VI - t-Test Results of Plug Soils vs Plot Soils, 1990.

Table VI(A). Results of t-Test analysis ($\alpha = 0.05$) used in comparing the soil pH of transplant plugs and vegetation zones. Situations in which the pH of the plugs was significantly higher than that of the vegetation zones is indicated by '*', and by '+' if the plug soil was significantly lower.

Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
Cal ine	Calamagrostis	
	Hordeum/Distichlis	
	Puccinellia	+
	Salicornia	+
Hor jub/Dis str	Calamagrostis	*
	Hordeum/Distichlis	
	Puccinellia	
	Salicornia	+
Puc nut	Calamagrostis	*
	Hordeum/Distichlis	*
	Puccinellia	
	Salicornia	+
Sal rub	Calamagrostis	
	Hordeum/Distichlis	*
	Puccinellia	*
	Salicornia	

Table VI(B). Results of t-Test analysis ($\alpha = 0.05$) used in comparing the soil moisture of transplant plugs and vegetation zones. Situations in which the moisture of the plugs was significantly higher than that of the vegetation zones is indicated by '*', and by '+' if the plug soil was significantly lower.

Saline Site	Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
1	*Cal ine*	Calamagrostis	
		Hordeum	+
		Puccinellia	
		Salicornia	*
2		Calamagrostis	*
		Hordeum/Distichlis	*
		Puccinellia	*
		Salicornia	*
3		Calamagrostis	
		Hordeum	
		Salicornia	*
4		Calamagrostis	*
		Distichlis	
		Salicornia	*
1	*Hor jub*	Calamagrostis	*
		Hordeum	*
		Puccinellia	*
		Salicornia	*

Table VI(B) (continued).

Saline Site	Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
2	*Hor jub*	Calamagrostis	
		Hordeum/Distichlis	*
		Puccinellia	*
		Salicornia	*
3		Calamagrostis	*
		Hordeum	
		Salicornia	*
2	*Dis str*	Calamagrostis	
		Hordeum/Distichlis	*
		Puccinellia	*
		Salicornia	*
4		Calamagrostis	*
		Distichlis	
		Salicornia	*
1	*Puc nut*	Calamagrostis	*
		Hordeum	*
		Puccinellia	*
		Salicornia	*
2		Calamagrostis	+
		Hordeum/Distichlis	
		Puccinellia	*
		Salicornia	*

Table VI(B) (continued).

Saline Site	Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
1	*Sal rub*	Calamagrostis	+
		Hordeum	+
		Puccinellia	+
		Salicornia	
2		Calamagrostis	+
		Hordeum/Distichlis	+
		Puccinellia	+
		Salicornia	
3		Calamagrostis	+
		Hordeum	+
		Salicornia	
4		Calamagrostis	+
		Distichlis	+
		Salicornia	*

Table VI(C). Results of t-Test analysis ($\alpha = 0.05$) used in comparing the soil water salinity of transplant plugs and vegetation zones. Situations in which the salinity of the plugs was significantly higher than that of the vegetation zones is indicated by '*', and by '+' if the plug soil was significantly lower.

Saline Site	Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
1	*Cal ine*	Calamagrostis	
		Hordeum	+
		Puccinellia	
		Salicornia	
2		Calamagrostis	+
		Hordeum/Distichlis	+
		Puccinellia	+
		Salicornia	
3		Calamagrostis	+
		Hordeum	+
		Salicornia	+
4		Calamagrostis	+
		Distichlis	+
		Salicornia	
1	*Hor jub*	Calamagrostis	
		Hordeum	+
		Puccinellia	+
		Salicornia	

Table VI(C) (continued)

Saline Site	Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
2	*Hor jub*	Calamagrostis	+
		Hordeum/Distichlis	+
		Puccinellia	+
		Salicornia	
3		Calamagrostis	+
		Hordeum	+
		Salicornia	+
2	*Dis str*	Calamagrostis	
		Hordeum/Distichlis	+
		Puccinellia	+
		Salicornia	
4		Calamagrostis	
		Distichlis	+
		Salicornia	
1	*Puc nut*	Calamagrostis	
		Hordeum	+
		Puccinellia	+
		Salicornia	

Table VI(C) (continued)

Saline Site	Transplanted Plug	Vegetation Zone (plug destination)	Significant Difference (plug higher '*' plug lower '+')
2	*Puc nut*	Calamagrostis	
		Hordeum/Distichlis	+
		Puccinellia	+
		Salicornia	
1	*Sal rub*	Calamagrostis	
		Hordeum	+
		Puccinellia	
		Salicornia	
2		Calamagrostis	
		Hordeum/Distichlis	
		Puccinellia	
		Salicornia	
3		Calamagrostis	+
		Hordeum	
		Salicornia	+
4		Calamagrostis	
		Distichlis	
		Salicornia	+