POPULATION DIFFERENTIATION IN *CAREX LYNGBYEI* FROM THREE PUGET TROUGH WETLANDS

by

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Population Differentiation in Carex Lyngbyei From Three

Puget Trough Wetlands.

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ABSTRACT

Population differentiation was examined in *Carex lyngbyei* from the Squamish River delta (49°41'N, 123°10'W), the Skagit River delta (48°18'N, 122°24'W) and the Nanaimo River delta (49°11'N, 123°54'W). A field survey was performed to determine how much morphological variation in *C. lyngbyei* and how much variation in *C. lyngbyei* habitat existed among and within these river deltas. A reciprocal field transplant experiment lasting for one growing season and a germination experiment were carried out to determine whether any variation found in morphology and/or germination requirements was genetically-based or due to plastic responses to environmental conditions.

The field survey demonstrated that the morphological characteristics of the Squamish, Skagit and Nanaimo *C. lyngbyei* varied in response to environmental heterogeneity on the meso-scale between river deltas and on the micro-scale within each delta. Generally, shoot height and biomass per shoot decreased, while shoot density increased, with increased soil water salinity.

The reciprocal transplant experiment indicated that variation in shoot height, shoot density, aboveground biomass and biomass per shoot is primarily ecophenic, as these characters were modified by the environment of the transfer site. Differences in these variables were attributable to interactions among the salinity and submergence regimes of the native and transfer sites. In a few instances, plants maintained their morphological characteristics after transplantation. This suggests that genetic divergence has occurred in a few discrete *C. lyngbyei* populations. A transplantation experiment run over several growing seasons is needed to determine whether this response was influenced by buffering by underground reserves.

The germination experiment was run in two phases. The germination response of the sample populations was examined during exposure to 0, 5, 10, 15, and 30 ppt saline solutions for 47 days in Phase I, and then during exposure to fresh water for a further 61 days in Phase II. It showed that seeds from all the *C. lyngbyei* sample populations exhibited maximum germination in fresh water, reduced germination in 5 ppt and virtually no germination in salinities ≥ 10 ppt. When the seeds subjected to high salinity treatments were returned to fresh water, percent germination increased to levels equivalent or just below the original fresh water treatments. The germination of the Squamish seeds in fresh water after exposure to higher salinities was significantly later than that of the Skagit seeds. This response is consistent with the salinity regimes of the native wetlands. Germination would occur in both river deltas when the probability of encountering low salinities is highest. Ecotypic differentiation appears to have occurred with respect to the speed of germination in fresh water, but not in terms of percent germination at any salinity level.

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CHAPTER I

INTRODUCTION

Plant species often vary genetically and/or plastically in response to a heterogeneous environment. The variation may be morphological, anatomical and/or physiological.

Genetic differentiation occurs when environmental gradients produce selection pressures which act on individual organisms such that the relative frequency of genotypes with a net superiority (the greatest ability to develop and reproduce in a given habitat) will increase. As particular environmental factors vary in intensity from place to place, over time different populations may become characterized by different gene frequencies. In this way they become adapted to particular habitats and the species differentiates into numerous genetically distinct populations, each characterized by reduced fitness in other habitats occupied by the species as a whole. If sharp gradients exist, this variation may occur on a small-scale in closely adjacent populations experiencing considerable gene flow (Jain and Bradshaw 1966; Snaydon 1970). Such habitat-correlated genetic differentiation has been termed ecotypic variation.

Alternatively, differentiation may not be fixed genetically. Instead, the morphological, anatomical and/or physiological expressions of a genotype may be modified by its immediate growing conditions. This type of variation has been termed ecophenic variation.

Intertidal wetlands provide a suitable environment in which to study population differentiation. Because they are geographically isolated from one another, these wetlands form discrete sites between which there may be considerable environmental contrast and little gene flow. Intertidal wetlands "lie on the interface zone between totally marine and totally terrestrial environments. As the zone is traversed the influence of one environment increases or lessens in respect to the influence of the other, thus generating broadly linear patterns of variation in habitat factors" (Gray 1974). In addition, local changes in elevation and substrate

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characteristics result in mosaics of environmental variation within any given zone. Intertidal wetlands, like the salt marshes described by Davy and Smith (1985), "are heterogeneous in space but they vary in a cyclic, largely predictable, manner in time". Hence, while environmental factors may vary within and among marshes, on a local scale they exhibit a similar annual pattern. Population differentiation is likely to occur in such conditions (Davy and Smith 1985).

Intertidal wetlands also form promising study sites because many of the emergent plant species occupying these areas reproduce vegetatively, producing long-lived clones. They provide large amounts of experimental material which has been exposed to selection pressures for many years. This means that many samples from one population exposed to the same growing conditions for years, when transplanted to several different sites, may provide a significant comparison of the performance of that population in many of the environments occupied by the species as a whole.

Genetically-based population differentiation has been documented in several intertidal wetland or coastal plant species. Turesson (1920, 1922) popularized the concept of the ecotype with work on *Hieracium umbellatum* (among others), while Gregor (1930, 1938) found evidence for ecotypic variation in *Plantago maritima*. Boucaud (1962, 1970, 1972) reported physiological tolerance and germination requirement contrasts in *Suaeda maritima*, and Silander (1979) found considerable divergence among adjacent dune, swale and salt marsh populations of *Spartina patens*. Shaver *et al.* (1979) and Chapin and Chapin (1981) demonstrated ecotypic variation in *Carex aquatilis* with respect to growth processes, nutrient uptake and metabolism, while Antlfinger (1981) found that physiological characters associated with water use in *Borrichia frutescens* exhibited a high degree of genetic determination.

Although genetic differentiation has been observed in numerous coastal plant species, it is not necessarily the rule. Shea *et al.* (1975) found that variation in *Spartina alterniflora* is

ecophenic rather than ecotypic. Seliskar (1985) came to a similar conclusion for *Deschampsia caespitosa, Distichlis spicata, Grindelia integrifolia, Jaumea carnosa* and *Salicornia virginica* with respect to morphology and anatomy.

The northwest coast of North America contains numerous small pockets of saline and brackish intertidal wetlands. MacDonald and Barbour (1974) listed 78 vascular plant species as common inhabitants of these wetlands, of which 14 were wide-ranging on both sides of the international border. Only one study (Seliskar 1980) has examined plant population differentiation in this region. That study was limited to a single saline wetland in Netarts Bay, Oregon. The more productive brackish wetlands have not been examined in this light.

The purpose of this study was to examine population differentiation in *Carex lyngbyei* Hornem. *Carex lyngbyei* (sea sedge) (Figure 1) is a clonal, perennial sedge that reproduces vegetatively or sexually. Its triangular culms arise singly or in small clumps from well-developed rhizomes. Its leaves are elongate, flat or nearly so, and generally equal or surpass the inflorescence, which usually consist of 3 to 7 loosely aggregated spikes. The uppermost 1 or 2 spikes are staminate, the others are pistillate or the upper androgynous. The lower lateral spikes are loose or nodding on elongate peduncles (Hitchcock *et al.* 1969).

Carex lyngbyei occupies estuarine marshes of the North American Pacific coast from Marin County in northern California (Mason 1957) to the Seward Peninsula in Alaska, which borders the Bering Strait (Murray 1984). This broad latitudinal range means that at its northern extent *C. lyngbyei* experiences a mean annual air temperature of $-3.3°C$ and a mean duration of sunshine of 1884 hours, while at the southern end it encounters a mean annual air temperature of $13.8°C$ and a mean duration of sunshine of 2959 hours (Müller 1982). *C. lyngbyei* is dominant in diverse salinity and submergence conditions within these wetlands from Oregon to subarctic Alaska (Eilers 1975; Levings and Moody 1976; Disraeli and Fonda 1979; Dawe and White 1982; Ewing 1982; Kistritz *et al.* 1983; Vince and Snow

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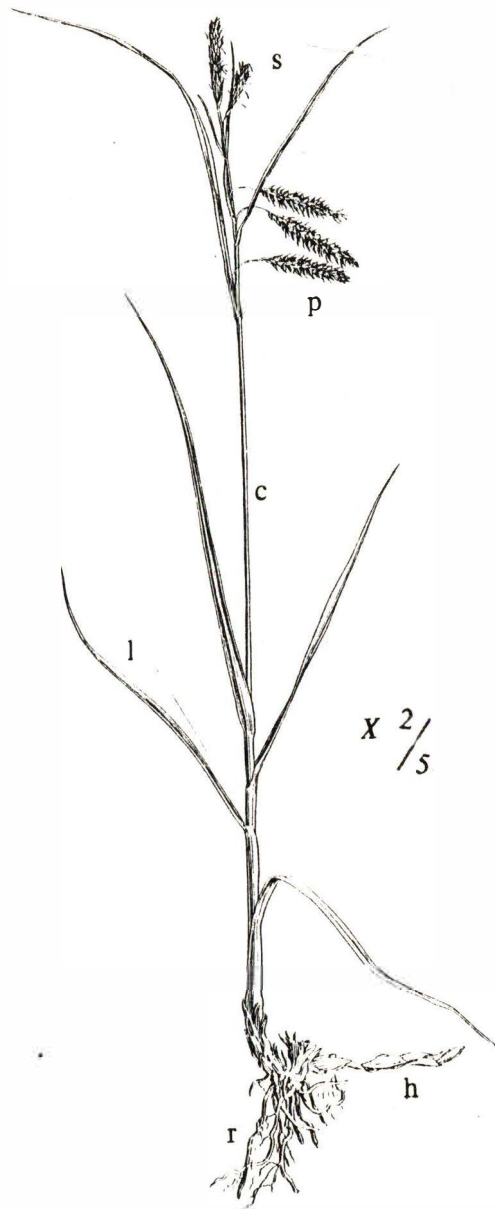
Figure 1. Diagram of *Carex lyngbyei* showing salient features of the species: drooping pistillate spikes (p) and erect staminate ones at apex (s), flat leaf blades (l), triangular culm (c), roots (r) and rhizome (h). (Source: Mason 1957).

1984), and thus has a wide ecological amplitude. In terms of aerial biomass, it is the most productive emergent plant species of the northwest coast estuaries (Keefe 1982; Hutchinson 1986). Ecologically, sea sedge seems to be the nearest Pacific counterpart to *Spartina alterniflora* Loisel of the Atlantic Coast (Hutchinson 1986).

Intertidal wetlands provide cover and food for many invertebrates and higher organisms inhabiting estuaries. The Pacific estuarine environment provides juvenile salmonids with a rearing area and a refuge from predators (Dunford 1975; Dorcey *et al.* 1978; Levy *et al.* 1979; Levy and Northcote 1982; Healey 1982; Simenstad *et al.* 1982). It serves as a staging area for migratory waterfowl on the Pacific flyway, and provides nesting cover for ducks and geese and valuable cover for wildlife (Burgess 1971; Hunter and Jones 1982; Eamer 1985). As the dominant emergent plant species, *C. lyngbyei* is an important component of this habitat. In addition, sea sedge plays an essential role in the energetics and food-web dynamics of the Pacific estuaries. Its high productivity and slow decay provide plant leachates for export during the spring months which enhance microbial activity. The release of detritus through the autumn and winter months seemingly provides a constant, nutritious food source for detritivores (Kistritz *et al.* 1983). Besides providing food indirectly as detritus to fish and aquatic birds (Healey 1982; Dawe *et al.* 1986), *C. lyngbyei* produces large numbers of seeds which are consumed directly by waterfowl, songbirds and other estuarine animals (Burgess 1971; Snow 1982; Dawe *et al.* 1986). Its shoots and rhizomes are consumed by seasonally resident lesser snow geese *(Anser caerulescens)* before spring migration (Burton 1977).

For these reasons, *C. lyngbyei* is a critical plant species in marsh rehabilitation and creation projects designed to enhance wildlife and fish habitat. In British Columbia most mitigation projects involve the transfer of this species because it is so dominant along the coast, and hence, forms abundant, nearby donor material (K. Conlin, personal communication). *C. lyngbyei* has also been used extensively as donor material in Oregon (eg. Ternyik 1978). Little published information is available from Washington (Kentula 1986), however, an

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indication of the importance of *C. lyngbyei* is that 15,000 of 18,000 plant culms transfered to a Puyallup marsh creation project were of *C. lyngbyei* (Thom 1986). The success of *C. lyngbyei* transplants may rest upon an understanding of the genecology of the species.

OBJECTIVES

The objective of the present study was to determine whether local populations of *Carex lyngbyei* have diverged in terms of morphology and/or germination requirements in response to large environmental gradients in the estuarine intertidal zone. A subsequent objective was to determine whether any variation found was genetically-based, or due to plastic responses to environmental conditions. To implement the first objective, populations of *C. lyngbyei* from different areas within and between contrasting estuarine wetlands were examined in a field survey. The subsequent objective was addressed in a reciprocal transplantation experiment and a germination experiment.

The potential selection pressures operating in this environment and the status of knowledge of the test species are discussed in the next chapter. Based upon this, the rationale for the sampling scheme, the experimental design and the methods employed in this study are presented in Chapter 3. The results of the field survey, and the transplant and germination experiments are reported in Chapter 4. Chapter 5 contains a discussion of the results and suggestions for further research. Concluding statements are made in Chapter 6.

CHAPTER II

A FRAMEWORK FOR THE INVESTIGATION

SELECTION IN THE INTERTIDAL ENVIRONMENT

The intertidal, estuarine environment contains substantial spatial and temporal environmental variation, and consequently, strong selection pressures. Many of the environmental variables are linked together in a complex web of interrelationships.

The size, shape and nature of estuarine wetlands are controlled by interactions among drainage basins, ocean basins, and river mouth morphologies. Fresh water and sediment flow from a drainage basin to the ocean where they are mixed with, and transported by, tidal waters. Salinity gradients perpendicular to river distributaries are formed as a result. The delta morphology, itself a product of ocean/drainage basin relations, interacts with the local tidal regime to control sediment accretion or erosion. This influences the delta topography which in turn affects submergence/emergence ratios as lower elevations experience higher inundation frequencies and durations. The substrate texture interacts with the topography such that fine-grained substrates that are subjected to long periods of inundation may be waterlogged, and hence, anaerobic. Elevation gradients may also produce salinity gradients in response to penetration by a salt wedge and/or to evapotranspiration at higher levels. As many of these factors vary both spatially and temporally, growing conditions vary among and within estuarine marshes. Although they vary through the year, these conditions have a relatively consistent annual periodicity.

A detailed review of the chemical changes occurring in frequently inundated substrates may be found in Patrick and DeLaune (1977). A discussion of the factors which may limit plant growth in salt marshes and sand dunes is provided in Rozema *et al.* (1985*a*). The following review of potential selection pressures, therefore, is limited to a brief discussion of

the factors known to have led to population differentiation in intertidal plant species. Results from numerous studies indicate that variation in salinity, nutrient status and interspecific competition are important factors in this environment. These may have different effects on growth and development at different stages in a plant's life-cycle.

Salinity

In the intertidal estuarine environment, inundating waters vary from fresh to saline temporally in response to river discharge, and spatially as a function of distance from river distributaries. Population differentiation in response to salinity variation is apparently common at the germination stage. Dewey (1960) reported different germination responses to salinity in populations of *Agropyron intermedium*, and Kingsbury *et al*. (1976) found that southern California populations of *Lasthenia glabrata* showed greater sensitivity to salinity at the germination stage than the northern populations which have evolved in areas of lower salinity. After germination, plants growing in saline conditions must acquire essential nutrients from a medium with an unfavorable ionic mix and acquire water from an external medium of high osmotic pressure. At the same time, they must maintain an internal ionic balance despite excess concentrations of certain ions in the external medium (Queen 1975). This may induce differentation at the post-germination phase among populations proximal and distal to river distributaries or in estuaries of contrasting salinity regimes. Rhebergen and Nelissen (1985) reported such ecotypic differentiation within *Festuca rubra* populations in response to variation in substrate salt concentration.

Nutrient Status

Among the 16 nutrients essential for plant growth and development, nitrogen, sulphur and iron have been found most often associated with inter- or intraspecific differentiation in coastal wetlands (Rozema *et al*. 1985*a*). In general, the availability of these three elements seems to be linked to the substrate aeration status, and hence, to elevation. Periodic flooding

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may thus act as an effective selective force to bring about the evolution of populations in frequently inundated habitats which are better able to grow on waterlogged soils than are those populations from free-draining soils (Davies and Singh 1983).

Experimental evidence suggests that variation in nitrogen availability can produce genetic divergence. Jefferies *et al.* (1981) examined growth rates of *Salicornia europea* and found that low growth rates of high marsh populations of this species were not altered by the addition of water and nitrogen. This was suggested to be a genetically fixed adaptation to the low nitrogen availability in the upper marsh.

Variation in sulphide concentration across elevation gradients may be an important selective factor in intertidal estuarine habitats. Havill *et al.* (1985) showed that the metabolism of *Atriplex patula* and *Festuca rubra* from the upper-marsh and *Puccinellia maritima* from the lower-marsh was disrupted dramatically by concentrations of sulphide equivalent to that in some salt marsh sediments, while the metabolism of *Salicornia europaea* (frequently associated with sulphide-rich sediments) was not.

Potential iron toxicity selection pressures also follow elevation gradients. Rozema *et al.* (1985*b*) presented evidence from nutrient solution experiments suggesting that low marsh halophytes are more tolerant of high iron and manganese concentrations than are their high marsh counterparts. Waisel (1972) and Adams (1963) found that low marsh species exhibited iron-deficiency when grown in aerobic upper marsh sediments. Adams (1963) reported that upper marsh species are adapted to low iron availability, and suggested that *Spartina alterniflora* is limited to the low marsh by its high iron requirements.

Interactions

There appear to be important interactions among aeration, salinity and nutrient uptake. Morris and Dacey (1984) found that nitrogen uptake in this species was stimulated by increased O_2 in the rhizosphere. DeLaune *et al.* (1983) suggested that sulphide may prevent nitrogen uptake and root development in *S. alterniflora*.

Interspecific Competition

Biotic selection pressures are induced by competition with other species. Experimental evidence from Watson (1969) suggests that populations of *Potentilla erecta* have differentiated in response to diversifying selection imposed by *Molinia* and *Agrostis*.

STATUS OF KNOWLEDGE OF CAREX LYNGBYEI

Since MacDonald and Barbour (1974) pointed out that the Pacific Coast wetlands were poorly known, several studies from this region have been published, many of which included data on *C. lyngbyei*. The type of information contained in this literature is summarized in Table 1 by author. The studies are listed roughly in order of decreasing latitude. This table illustrates that much of this research has been phytosociological. Although most studies have provided *C. lyngbyei* community descriptions and many have reported cover estimates or productivity measurements, few have included habitat information. Consequently, they have done little to increase our knowledge of sea sedge. The inundation, salinity, substrate texture and chemistry, and growth and development information that can be gleaned from these publications is summarized below.

Table 1. Summary of *Carex lyngbyei* literature.

Researcher:	Community Descriptions:	Percent Cover:	Productivity:	Succession:	Life History:	Growth Forms:	Plant/ Environment Interactions:	Detritus Flux/ Nutrient Cycling:	Elevation:	Salinity:	Substrate Texture:	Drainage/ Substrate Characteristics:
Frohne (1953)	*									*		*
Stephens & Billings (1967)	*	*							*		*	*
Sparks *et al.* (1977)	*	*							*	*		
del Moral & Watson (1978)	*	*							*	*		
Stone (1984)	*								*	*	*	
Crow (1968)	*								*			
Thilenius (1986)	*								*			
Snow (1982)	*	*	*		*				*	*		*
Campbell (1986)	*	*							*			
Kennedy (1982)	*	*						*	*			*
Lim & Levings (1973)	*											
Levings & Moody (1976)	*		*			*			*	*		
Dawe & White (1982)	*		*						*			
Dawe & White (1986)	*		*						*			
Moody (1978)	*			*	*							
Hutchinson (1982)	*	*		*			*		*	*	*	*

(cont'd)

Researcher:[1]	Community Descriptions:	Percent Cover:	Productivity:	Succession:	Life History:	Growth Forms:	Plant/ Environment Interactions:	Detritus Flux/ Nutrient Cycling:	Elevation:	Salinity:	Substrate Texture:	Drainage/ Substrate Characteristics:
Bradfield & Porter (1982)									*			*
Kistritz et al. (1983)					*			*				
Yamanaka (1975)	*		*									
Hillaby & Barrett (1976)	*											
Burg et al. (1980)	*		*		*	*			*			
Disraeli & Fonda (1979)	*								*		*	*
Ewing (1982, 1983, 1986)	*		*		*	*				*	*	*
Eilers (1975)	*		*	*	*	*			*	*		
Jefferson (1975)						*	*		*	*		
Frenkel et al. (1981)									*			
Gallagher & Kibby (1981)			*			*		*				

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Habitat Occupance

Inundation

The range of inundation through which *C. lyngbyei* grows is difficult to pin-point because different units of measurement and methods of presentation have been utilized by virtually every researcher Further, Canadian and United States Chart Datum are based upon lowest normal tides and mean lower low water, respectively. Despite these problems, it is apparent that *C. lyngbyei* grows across a wide elevational range. This species has been reported to dominate in tide flat areas and at the lowest vegetated elevations (Stephens and Billings 1967; Sparks *et al.* 1977; del Moral and Watson 1978; Burg *et al.* 1980; Snow 1982; Stone 1984; Thilenius 1986), channel banks (Crow 1968; Bradfield and Porter 1982; Stone 1984), and in the supratidal high marsh (Burg *et al.* 1980). Eilers (1975) reported *C. lyngbyei* growing from supratidal levels to elevations subjected to 9.3 hour growing season submergence periods. Jefferson (1975) found it exposed 55 to 100% of the growing season. Disraeli and Fonda (1979) found it dominated at elevations not submerged at all between May and October. Sea sedge was found at elevations equivalent to inundation durations of 0 to 50% of the active growing season daylight hours (Dawe and White 1982) and from annual tidal inundation durations of 0 to 60% (Hutchinson 1982). Campbell (1986) found *C. lyngbyei* to be wide-ranging in elevation, although it generally occupied intermediate zones. It formed low elevation communities only in fresh water to brackish conditions. Ewing (1986) also found *C. lyngbyei* to be absent from low elevation, saline areas.

Salinity Tolerance

C. lyngbyei survives across a broad range of salinity (Frohne 1953; Eilers 1975; Jefferson 1975; Snow 1982; Ewing 1982, 1983, 1986). Levings and Moody (1976) reported *Carex* growing within the Squamish River delta in inundating waters with salinities ranging from 0 to 28 ppt. Hutchinson and Smythe (1986) found that different populations of *C.*

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lyngbyei have different percent germination responses to salinity treatments. They reported that *C. lyngbyei* seeds which are exposed to high salinities in the field before spring germination exhibited diminished germination percentages when not exposed to pre-germination high salinities in the laboratory. In contrast, seeds not subjected to pre-germination high salinities in natural conditions were not stimulated by similar high salinity laboratory treatments.

Substrate Texture and Drainage

C. lyngbyei exists over a wide range of substrate textures and drainage conditions. It grows on gravelly-loamy sands and stratified gravels and sands (Stephens and Billings 1967), fine-grained or silty substrates (Disraeli and Fonda 1979; Hutchinson 1982; Stone 1984), clays (Ewing 1982), and peat to organic muck (Dawe and White 1982, 1986). Drainage conditions vary from relatively well-drained (Bradfield and Porter 1982; Hutchinson 1982) to anaerobic (Kennedy 1982; Snow 1982).

Substrate Chemistry

Some information on *C. lyngbyei* rhizosphere soil characteristics has been reported by Stephens and Billings (1967), Crow (1968), Ewing (1982) and Snow (1982). This, however, only allows a comparison of pH (which ranged from 5.8 to 8.0) and total cations (which ranged from 2.7 to 47.6 meq l^{-1}). The dearth of substrate nutrient data makes comprehensive comparison of substrates and plant vigor impossible.

Growth and Development

The timing of various *C. lyngbyei* life-stages has been reported by several researchers. This information is summarized in Table 2. In general, most shoots begin growth in late summer or early fall, overwinter as short shoots and resume growth in late winter to early spring. Second or third year shoots begin flowering in May to June and set seed by late

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Table 2. Summary of *Carex lyngbyei* phenology information.

Researcher:	Overwintering Shoots Formed:	Shoot Elongation:	Peak Aboveground Biomass:	Seed Production:	Seed Set:	Senescence:
Eilers (1975)	Fall	Early February	July		August to September	July
Burg *et al.* (1980)	Fall		July	Late May		
Ewing (1986)		Mid–April	Mid– to late–June			
Levings and Moody (1976)	September		Late July to early August			September
Kistritz *et al.* (1983)	August	Mid–April	June	May	June	Summer months
Dawe and White (1982, 1986)			June (tall) Late July (short)			
Snow (1982)	Late August	Spring	Mid-July	June	Mid-August	

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summer, by which time senescence has occurred (Eilers 1975; Jefferson 1975; Levings and Moody 1976; Burg *et al.* 1980; Gallagher and Kibby 1981; Dawe and White 1982, 1986).

Two growth forms have been recognized in several studies. These are distinguished on the basis of habitat, growth at maturity, net aerial productivity and signature on aerial photography (Eilers 1975). The habitat occupance by the two growth forms and the factors to which the height differences have been attributed are outlined in Table 3. These factors range from aeration, salinity and continuous soil renewal to differences in underground photosynthate reserve quantity and release patterns.

Implications for this Study

The research summarized above has revealed two important facts:

1.   that *C. lyngbyei*, because it occupies diverse habitats and therefore is exposed to different selection pressures throughout its geographic range, exists in circumstances conducive to population differentiation, and

2.   that morphological variation within the species, which may be a visible manifestation of genetic differentiation, has been recognized.

C. lyngbyei has a wide ecological amplitude; it grows across broad ranges of latitude, salinity, elevation and aeration. As stated previously, from the northern to southern limits of its range the mean annual air temperature ranges from $-3.3^{\circ}C$ to $13.8^{\circ}C$ while the mean annual duration of sunshine hours increases from 1884 to 2959. The life-histories that have been reported by Eilers (1975), Burg *et al.* (1980), Snow (1982) and Kistritz *et al.* (1983) suggest that the timing of shoot elongation and seed production in *C. lyngbyei* vary with latitude. This variation could be either genotypic or phenotypic. *C. lyngbyei* occupies sites inundated by waters ranging in salinity from 0 to 28 ppt. This strong gradient alone, or in conjunction with temporal variation in response to river discharge, may favor genetic

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Table 3. Summary of *Carex lyngbyei* growth form information.

Researcher:	Growth Forms Recognized by:	Tall Form Description:	Short Form Description:	Height Differences Attributed to:
Eilers (1975)	Habitat, growth at maturity, net aerial productivity, signature on aerial photography	Well-drained sections of low marsh -eg. major creek levees and levee-like margins of an island	a) Low elevations, invading unvegetated mudflat, and in b) Back levee sites in the low marsh	Proximity to deep creek channels characterized by rapid drainage and continuous soil removal
Jefferson (1975)	Height differences	Low in the intertidal zone in considerably "diluted", saturated soils	Pure stands in the inland edge of the high marsh on saline soils associated with summer evaporation	Salinity differences
Levings and Moody (1976)	Height differences	Less saline West, Central and East portions of the Squamish River delta	More saline Mamquam portion of the Squamish River delta	Salinity differences
Burg *et al.* (1980)	Height differences	Monotypic stands along slough banks	Away from slough banks	
Gallagher and Kibby (1981)	Differences in biomass and net annual aerial primary productivity	Streamside stands	Backmarsh stands	Differences in the amount, and timing of mobilization, of underground photosynthate reserves
Dawe and White (1982, 1986)	Height differences	Saturated, anaerobic channel edges	Slopes and elevated flats	Flushing of nutrients from higher levels to channels

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divergence at the germination and/or post-germination phases. *C. lyngbyei* grows over a range in tidal inundation of 0 to 60% and in coarse- to fine-grained substrates. At lower elevations in poorly-drained substrates, solar radiation and CO_2 are reduced so photosynthesis is limited, and iron and sulphide toxicity may be problematical. The high marsh, on the other hand, may be characterized by low nitrogen availability and evapotranspiration. These divergent growing conditions may favor population differentiation. Recognition of this wide ecological amplitude led Ewing (1982) to question whether the *C. lyngbyei* populations occupying diverse habitats in the Skagit River delta were composed of a single genotype of great plasticity or a series of genetically distinct populations or ecotypes.

Two growth forms analogous to those of *Spartina alterniflora* (Shea *et al.* 1975; Valiela *et al.* 1975) have been recognized in *C. lyngbyei* in studies from Oregon, Washington and southern British Columbia. Jefferson (1975) noted that where these height forms grew in adjacent stands, their distinctly different appearance could not be related to environmental heterogeneity and suggested that they may represent two common ecotypes.

These points raise several questions:

1. How much variation exists among *C. lyngbyei* populations?

2. Is the variation habitat-correlated?

3. Does the variation occur spatially on the macro-, meso-, or micro-scale?

4. Is the variation clinal?

5. Is the variation genotypic or phenotypic?

6. Is the variation morphological, anatomical and/or physiological?

7. What selection factors account for this variation?

8. Are the bimodal height forms associated with this variation?

BASIS FOR THE PRESENT STUDY

To test for population differentiation in a species such as *C. lyngbyei*, a research project could range across gradients of latitude, elevation and salinity. To paraphrase Gregor and Watson (1961), however, population differentiation established on the basis of one genotype–environment relation might occur again with new boundaries on the basis of different criteria. For this reason it is beyond the scope of any one study to examine more than a small portion of the variation within a species. This study focusses on the local scale. Population differentiation in response to the inundation and salinity conditions that vary substantially within each estuary, and often dramatically among local estuaries is examined.

Genetic variation within a species is often detected using reciprocal transplants and/or gel electrophoresis of enzymes. Ideally, both techniques are used, however, biological constraints (eg. study organisms with long regeneration times) or logistical constraints may limit the study to one approach. Transplantation is advantageous because genetic variation may be shown to be adaptive. Gel electrophoresis allows a detailed picture of variation in genotypes between and within different populations to be seen, but this method alone cannot determine whether the variation is adaptive. In the present study reciprocal transplant methods alone were employed.

Within the scope of this study, four of the questions posed above are addressed. The results will indicate whether *C. lyngbyei* populations vary on a meso–scale between local river deltas, and on a micro–scale within local river deltas as a result of salinity differences at the germination phase and/or as a result of salinity and inundation differences at both germination and post–germination phases. If variation is found to be habitat–correlated, it will be attributed to either genetic or plastic responses. If two growth forms are found to exist in the sampling areas, their relation to ecotypic or ecophenic variation will be examined.

CHAPTER III

METHODS

SAMPLING STRATEGY

The study sampling scheme was designed to incorporate populations of *C. lyngbyei* which collectively spanned gradients of important abiotic selection factors. As sampling across a broad latitudinal range was not attempted, the study was limited to the local scale. For the results to have meaning for other *C. lyngbyei* populations, it was necessary to establish trends by either sampling several estuarine wetlands occupying different positions an environmental continuum, or by sampling replicate wetlands of contrasting environmental character.

For this study, three nearby wetlands with different physical characteristics were chosen on the basis of a study by Hutchinson (1988). The wetlands were selected from distinct groupings revealed by a cluster analysis of the variation in the physical characteristics of the deltas of the Puget Trough. The three areas, the Squamish, Skagit and Nanaimo River deltas, border the Strait of Georgia in southwest British Columbia and Puget Sound in northwest Washington (Figure 2). Although there is some variation in the regional climate among these deltas, the major environmental contrasts derive from differences in the seasonal discharge patterns of the contributing rivers. Because of these differences, the Squamish River delta is basically fresh to oligohaline (0.5 to 5 ppt salt) during the growing season, the Skagit River delta is oligohaline to mesohaline (5 to 18 ppt salt), and the Nanaimo River delta is essentially polyhaline (18 to 30 ppt salt). On a smaller-scale, salinities vary across each delta front with distance from river distributaries.

Within each delta, sampling was carried out along gradients of the physical variables deemed to be the abiotic factors with the greatest influence on plant growth - salinity and
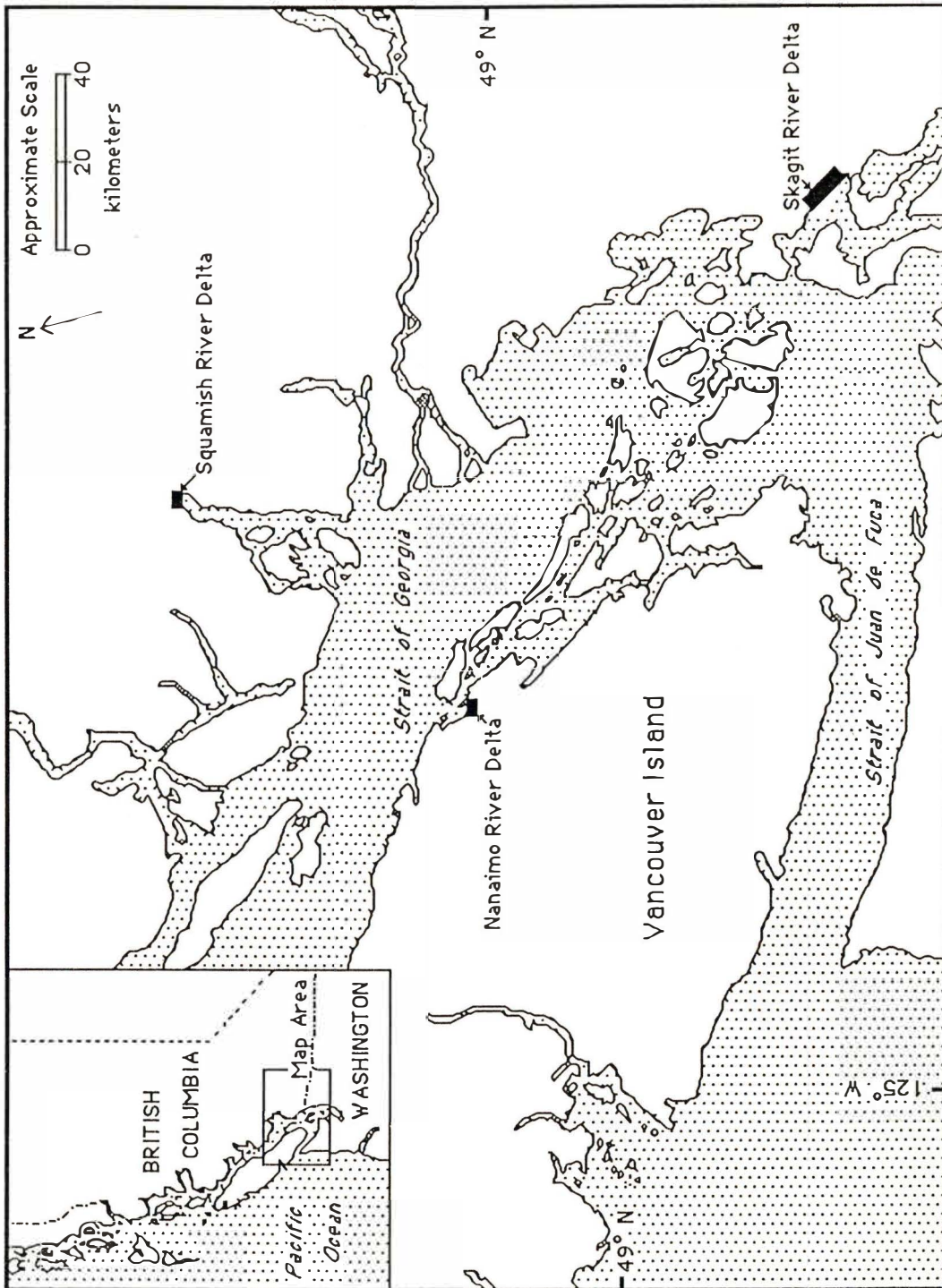
Figure 2. Location of the study river deltas.

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elevation. In the initial field survey, sites from all topographic "micro-environments" present within the deltas were sampled. These are illustrated in Figure 3. Channel edge, levee, and foreshore-, intermediate- and elevated flats categories were not present in all deltas. In consequence, the number of samples sites within each delta are unequal. These 50 sites are denoted by codes such as SQF4, representing the fourth sample site in the relatively fresh water section of the Squamish River delta. During this field survey, categories common to all the deltas were identified as sampling sites for the transplantation and germination experiments.

The sampling scheme for the two experiments involved a subset of the field survey sites (four sites from each of the three river deltas). It was based upon a factorial arrangement with populations from three marshes (i.e. three different salinity regimes), from two zones within each marsh (characterized by different salinity levels - proximal and distal to river channels), and from two elevation levels. The resultant sampling scheme and the codes for these 12 sample sites are illustrated in Figure 4. As the southern, relatively freshwater portion of the Skagit River delta examined in the field survey was inaccessible when the transplant material was collected, other comparable sites were selected. There are referred to only as SKFH and SKFL.

FIELD SURVEY

Study Areas

The Squamish River delta (49° 41'N, 123° 10'W) is located at the head of the fjord forming Howe Sound. The mean annual air temperature of the area is 8.7° C and the mean annual precipitation is 2247 mm (Environment Canada 1981). The delta measures approximately 2 km in width at the seaward edge. It is dissected by current and relic
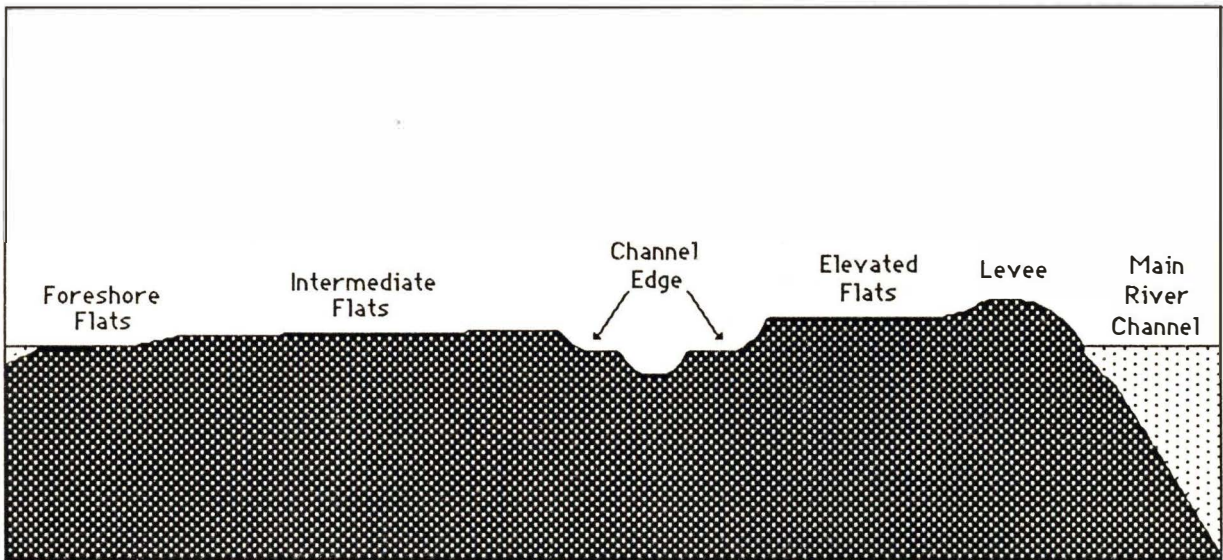
Figure 3. Diagram of the marsh platform categories identified in this study.
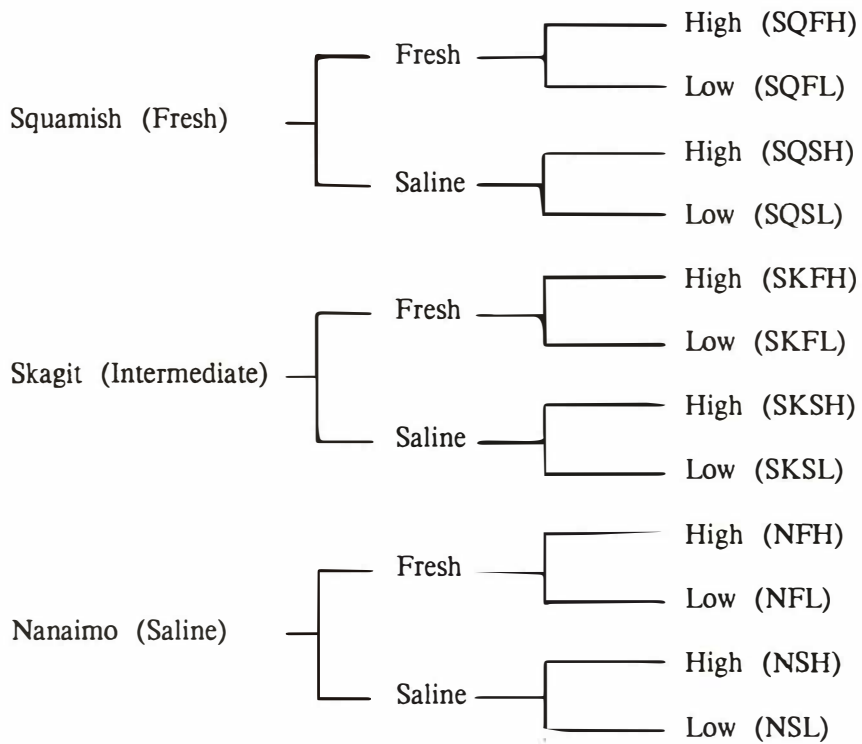
Figure 4. Study sampling scheme and the codes by which the 12 sample sites are referred to in the thesis.

distributaries into the West, East, Central, and Mamquam deltas. In total, these contain 1.25 km² of intertidal marsh, 0.77 km² of which is dominated by *C. lyngbyei* (Squamish Habitat Work Group Final Report 1981).

The significant morphological changes to the estuary in the last 65 years have been discussed by Clague and Luternauer (1982). Before catastrophic flooding diverted Mamquam flow to the Squamish main channel in 1921, both the Squamish and Mamquam Rivers drained directly into Howe Sound. Most of the Squamish River discharge flowed through the highly sinuous eastern distributary until flood–control ditching connected it to the western distributary in 1945. This, combined with the 1972 construction of the British Columbia Railway river training dyke, resulted in the eastern distributary silting up and becoming virtually cut off from the main channel.

The estuarine surface salinities mirror the discharge pattern of the Squamish River shown in Figure 5. Salinities decrease slightly with heavy winter rains, but decrease dramatically in the spring and summer months as snowmelt contributes to a pronounced summer discharge. Levings and Moody (1976) monitored seasonal and spatial variations in surface salinity across the delta front during 1974. Their findings illustrate the contrast in salt concentration across the delta with distance from the main river channel. Salinities on the West delta adjacent to the main channel were less than 8 ppt and dropped to less than 2 ppt during the summer months. In contrast, the Central and East deltas experienced salinities ranging up to 28 ppt in the winter months, dropping to between 2 to 4 ppt in the summer. The Mamquam delta was characterized by a similar pattern but with less extreme values.

The sample areas at the Squamish River delta were selected to reflect the salinity gradient across the delta front and to minimize disturbance from the morphological changes that have occurred over the last several decades. The West and East deltas were chosen
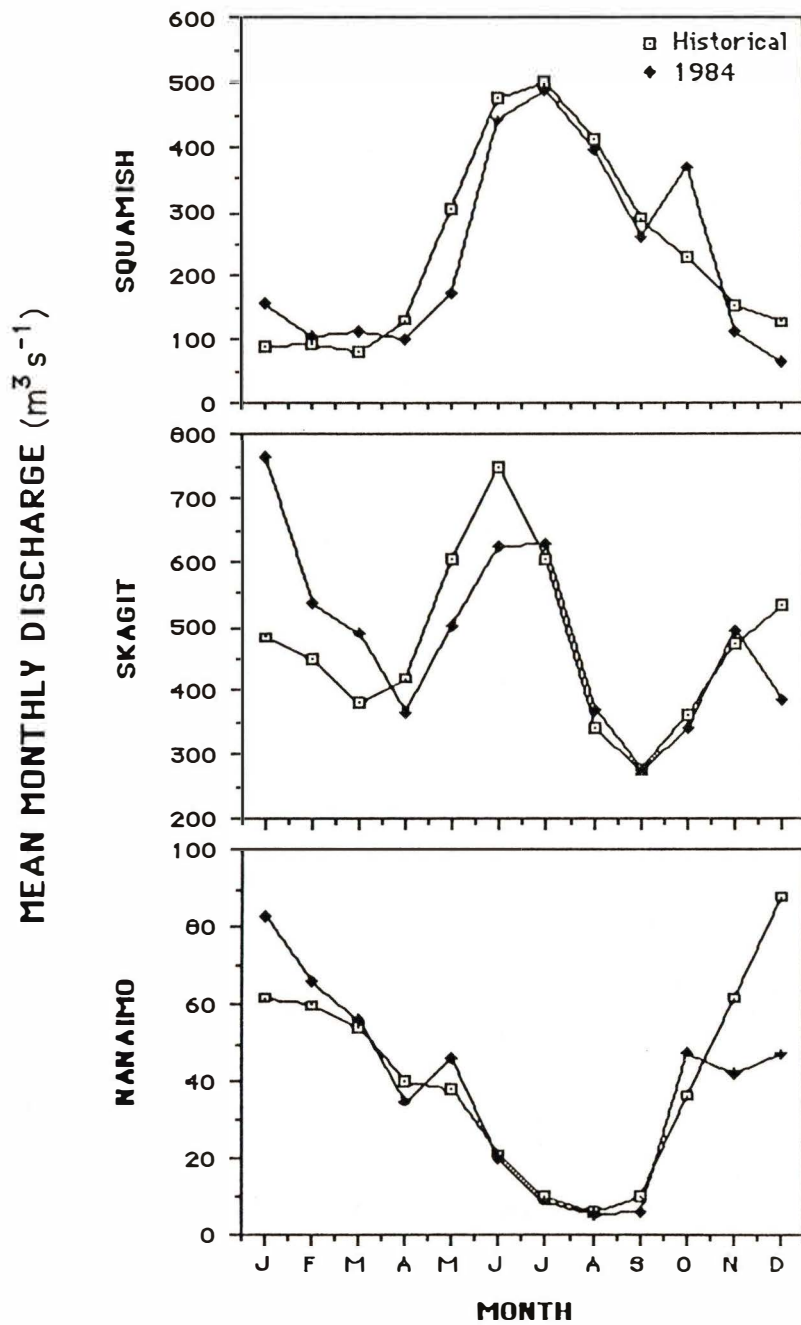
Figure 5. Historical and 1984 mean monthly discharges for the Squamish, Skagit and Nanaimo Rivers. (Sources: Environment Canada 1983, 1985, data for the Squamish River near Brackendale and the Nanaimo River near Cassidy; McGavock *et al.* 1984, data for the Skagit River near Mount Vernon.)

(Figure 6).

The Skagit River delta (48°18'N, 122°24'W), located just southwest of Mount Vernon, Washington, is surrounded by Fidalgo, Whidbey and Camano Islands. The mean annual air temperature is 9.8°C. The mean annual precipitation is 450 mm (National Oceanic and Atmospheric Administration 1982). The seaward edge of the delta spans approximately 23 km and contains 41 km² of wetlands, 14.4 km² of which are vegetated and tidally influenced (Shapiro *et al* 1978; Brewer 1980). These cover a 0.5 to 2 km wide band along the Skagit Bay shoreline (Ewing 1983).

The annual flow of the Skagit River, in response to winter rains and spring/summer snowmelt, is almost equally divided between winter and summer months (Figure 5). Salinities generally increase with distance from major river channels, varying seasonally as a reflection of the amount of freshwater discharged by the Skagit River.

Sample areas chosen to capture salinity changes alongshore were located in the southern portion (Figure 7) of the delta where *C. lyngbyei* stands were abundant and where salinity contrasts had been reported by Ewing (1983). The first, near Freshwater Slough, the major southern distributary of the Skagit River, experienced surface salinity levels of 3–5 ppt in winter, and 0 to 4 ppt in spring and summer. Salinity levels at the second area, north of Wiley Slough, vary from 6 to 12 ppt in winter to 1 to 7 ppt in summer. These two areas correspond roughly to Ewing's first and second transects.

The Nanaimo River delta (49°11'N, 123°54'W) is located on the east coast of Vancouver Island just south of the City of Nanaimo. At the seaward edge, the delta is about 2.7 km wide. The mean annual precipitation of the area is 930 mm and the mean annual air temperature is 10.3°C. The intertidal area covers approximately 8.2 km² (Bell and Kallman 1976), with an emergent plant zone of about 0.53 km² (Hutchinson 1988). At the apex of the delta, the river divides into two channels, the easternmost of which is restricted

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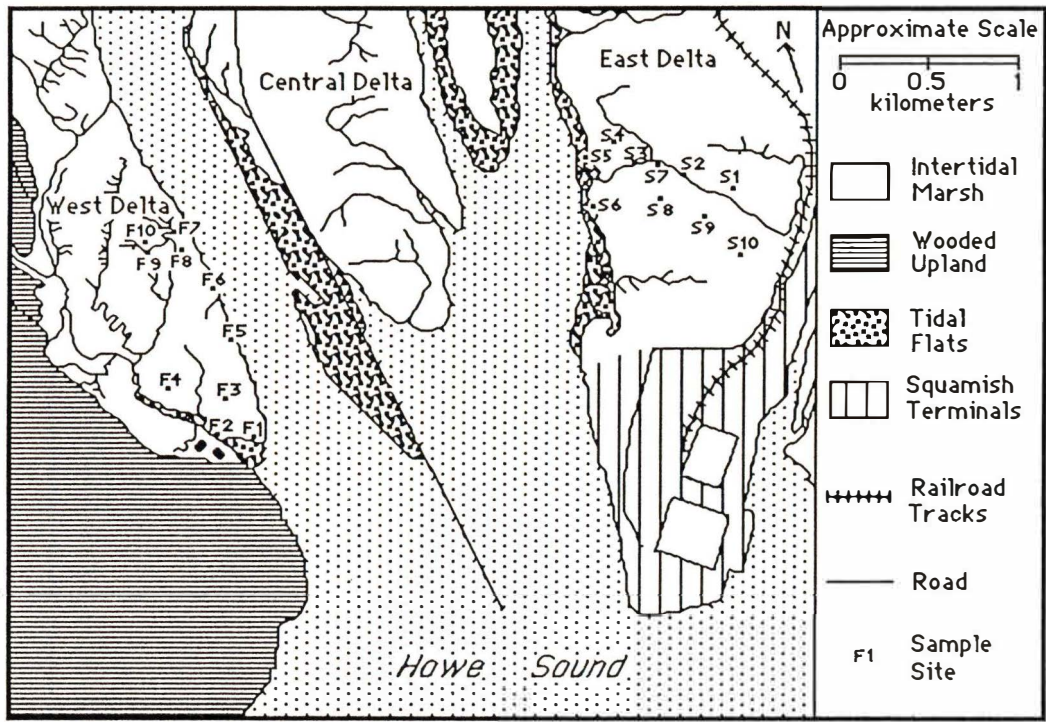
Figure 6. Location of the Squamish sample sites on the relatively fresh water West delta (samples F1-F10) and the more saline East delta (samples S1-S10).
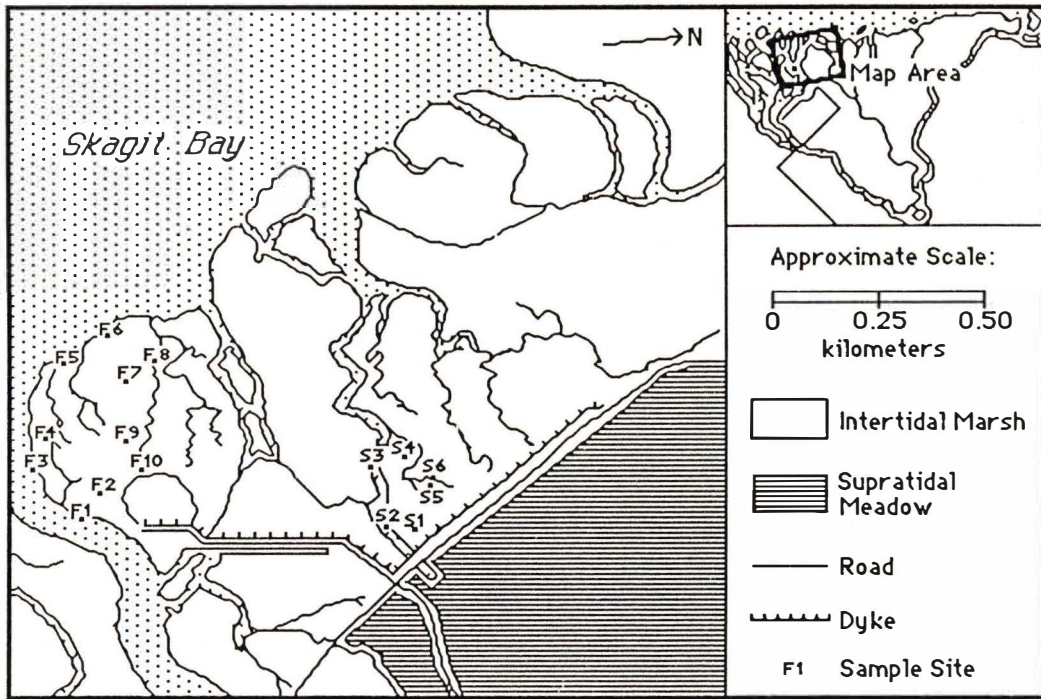
Figure 7. Location of the Skagit sample sites near Freshwater Slough (samples F1–F10) and in the more saline area to the north (samples S1–S6).

by a large gravel bar.

Maximum discharge in the Nanaimo River occurs in the winter (Figure 5), thus surface salinities increase through the spring and summer. Data presented by Kask and Sibert (1976) indicate that surface salinities in Nanaimo Bay increase to the east, away from the main river channel. The values range from 3 to 27 ppt, increasing through the summer. To account for this trend in the sampling scheme, the study areas were located adjacent to the restricted river channel and toward the eastern margin of the delta (Figure 8).

Location of Sample Sites

Within the more fresh water and saline sections of each delta, individual sites were located in all marsh platform categories present (eg. elevated flats, foreshore flats). This was accomplished by establishing a temporary benchmark in each wetland using a theodolite. Individual sites were selected by locating an appropriate zone (ie., channel edge or elevated flats) and then surveying from the benchmark to the site. A replicate for each site was established across channels from the original sites by surveying from the benchmark to the first concordant elevation in appropriate zones. The sampling sites are marked in Figures 6 to 8.

Vegetation Sampling

A pilot study performed prior to the field survey demonstrated that the indicators of plant vigor measured in this study (shoot height, shoot density, aboveground biomass, biomass per shoot and flowering shoots per unit biomass) could be reliably estimated for each population by examining a random sample of four 0.25 m² quadrats. Further, the pilot sampling showed that shoot height could be estimated from a randomly selected subsample of 30 shoots per quadrat. As the vegetation at each site was relatively uniform, the samples
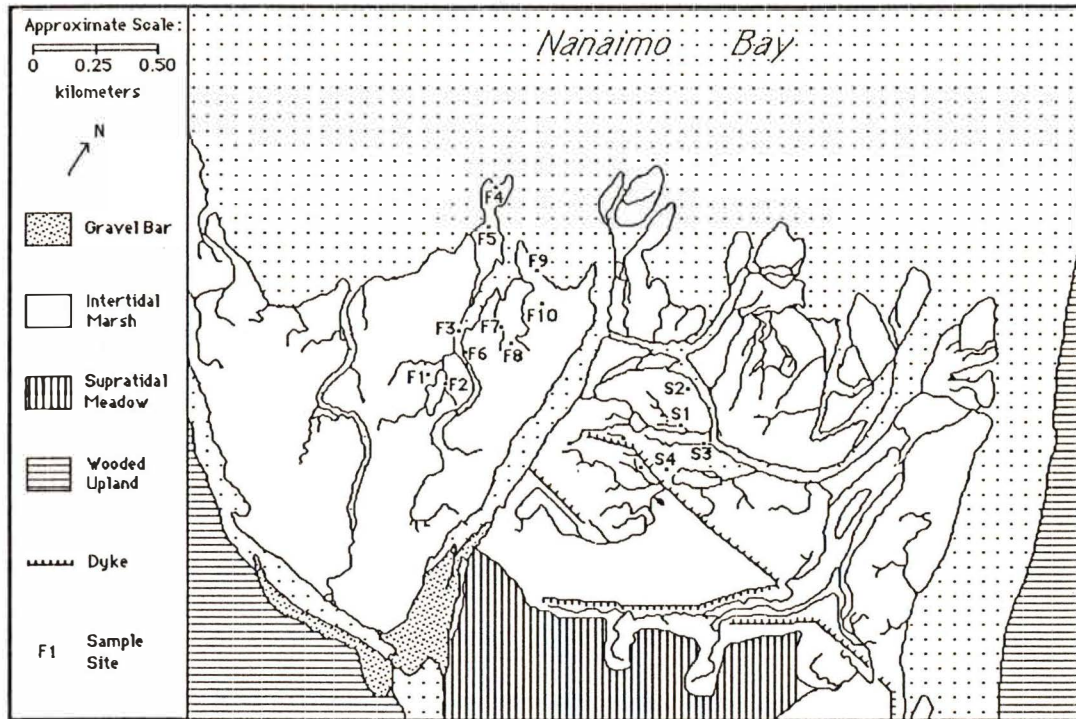
Figure 8. Location of the Nanaimo sample sites on the relatively fresh water island between river distributaries (samples F1–F10) and in the more saline eastern delta (samples S1–S4).

were located by the common "over-the-shoulder-toss" method. No attempt was made to obtain peak aerial biomass measurements. Instead, sampling was carried out over as short a time span as possible so that comparable life-stages would be measured. In late July and August 1984, all plants within each quadrat were clipped to ground level. Shoot heights were measured as the distance from sediment to tallest leaf in millimeters while shoot density was calculated as the number of shoots per quadrat. Aboveground live biomass was determined by separating and discarding dead tissue, placing the shoots in narrow-mesh wash bags, and carefully rinsing with tap water, repeating the procedure until the rinse water was clear. The plant tissue was then dried at 70°C for 72 hours and the dry weight determined to 0.1 g. The flowering shoots per unit biomass and the biomass per shoot variables were calculated from the number of shoots, the number of flowering shoots and the biomass values. Attempts to obtain belowground biomass estimates were met with tenacious opposition from roots and root hairs of *C. lyngbyei* and other entwined species. Even when the majority of the soil was removed from the plant tissue by 72 hours of soaking and massaging in water, the sea sedge roots could not be extracted from those of other species with reliability within a reasonable time. Hence, belowground biomass measurements were discontinued.

Environmental Measurement

An environmental survey was carried out synchronously with the vegetation sampling. Geodetic elevations were converted to chart data. Percent annual submergence estimates were then made for each site using historical tide data and instruction from the Tidal Chiefs at the Pacific Biological Station, Nanaimo, British Columbia, and the National Oceanic and Atmospheric Administration, Rockville, Maryland. The submergence values provide a rough estimate of annual submergence durations and allow a comparison between Canadian and American study areas.

Soil cores were removed from each site using a golf course cup cutter (length = 170 mm, radius = 52 mm). Substrate salinity was measured using a YSI portable salinometer by allowing interstitial water to collect in the hole formed when each soil core was removed. Sediment texture was determined by oven drying the samples for 24 hours at $105°C$ and wet sieving the soil to separate sand ($>63\mu m$) from silt and clay. Organic matter was then removed with 50% hydrogen peroxide, and the fine particles were analyzed for silt and clay proportions using a Micromeritics Sedigraph Particle Size Analyzer. Sediment organic matter was measured using a loss-on-ignition method where oven dried samples were weighed, placed in a muffle furnace at $450°C$ for 4 hours, cooled and reweighed. The organic matter was calculated as a percentage.

Data Analysis

The relationships between the plant growth variables (dependent) and the environmental variables (independent) were examined using a MIDAS multiple stepwise regression procedure. To stabilize the variance the shoot height, shoot density, aboveground biomass and submergence variables were subjected to a square root transformation. The biomass per shoot, flowering shoots per unit biomass, summer salinity, winter salinity and organic matter variables were transformed to $\log_{10}$ prior to analysis (Sokal and Rohlf 1969).

TRANSPLANTATION EXPERIMENT

Plant material was collected in February 1985 from the sample sites at high and low elevations in the saline and fresh water areas of each marsh. Using the golf course cup cutter, sixteen cores were removed in a random fashion from the clones at each sample site. Each core was placed in a labelled pot (length = 170 mm, radius = 75 mm, 4 holes in base for drainage) for transplantation.

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Four replicates from each of the 12 sample populations were transfered to four transfer sites: high and low elevation sites at the Nanaimo east delta (the most saline sample area) and the Squamish west delta (the most fresh water sample area). Vegetation native to each site was thus potted in a manner identical to the alien samples and so formed the controls. At each location the pots were placed in two 170 mm deep pits large enough to accommodate six rows of pots, each composed of the four replicates from one sample site (Figure 9).

Plant Growth

The transplants were monitored for shoot density and substrate salinity at monthly intervals beginning in May and ending in August when the plants were harvested. Five variables were measured for each pot at harvest:

1.   shoot height,

2.   shoot density,

3.   ,   aboveground biomass (dry weight),

4.   biomass per shoot

5.   flowering shoots per unit biomass.

Means and standard errors were calculated from the four replicates of each population. The measurements were made utilizing the same methods employed in the field survey, except that stem mortality had to be taken into consideration. Stems without any green tissue were assumed to be dead, and hence were discarded.

Figure 9. The Nanaimo high transfer site in May 1985, approximately one month after the transplanted *Carex lyngbyei* shoots had begun to elongate. Each transfer site was comprised of two pits which accomodated six rows of pots, each composed of four replicates from one sample site. The pot surfaces were level with the surrounding sediment.

Data Analysis

To examine differences in growth response among sea sedge populations in terms of salinity and elevation, analysis of variance (ANOVA) and Student–Newman–Keul's (SNK) multiple–range tests were used. A two–way ANOVA (BMDP7D) was used to assess shoot density changes in each population over the growing season, while an N–way ANOVA (BMDP2V) was used to examine the relationship between the abiotic variables and plant measurements.

The streamchannel bank adjacent to the Squamish low transfer site slumped during the course of the experiment. A thick layer of silt was deposited on several pots; shoots did not emerge from them in consequence. These were treated as missing data in the analyses so that the results were not biased by misleadingly low shoot numbers and aboveground biomass from this site.

GERMINATION EXPERIMENT

Plant Material

Carex lyngbyei seeds were collected at the time of the field survey within each of the three study marshes, from both high and low elevations in relatively fresh and saline sample sites. Plant material from the two replicates of each type of habitat was pooled wherever possible so that a random sample, perhaps of several genotypes, would be obtained for the experiment. Since flowering percentages were low in four of the zones, "Nanaimo fresh low" and "Skagit saline low" seeds were not available for use in the experiment. Low seed production in the Nanaimo saline high (NSH) and Nanaimo saline low (NSL) populations meant that the number of replicates in these samples had to be reduced.

All *C. lyngbyei* seeds were stored outside over the winter in containers filled with tapwater. In April the seeds were cleaned, rinsed in a 1:4 dilution of household bleach to distilled water for 1 minute, then rinsed three times with distilled water and stored dry for 2 to 3 days.

The germination tests were carried out on two sheets of Whatman No. 1 filter paper in 100 mm petri dishes. Fifty seeds were placed in each dish; four replicate dishes were used per population, except where the Nanaimo salt replicates had to be reduced to two. Initially, each population was exposed to five salinity treatments (0, 5, 10, 15, 30 ppt) produced by adding distilled water to seawater obtained from Burrard Inlet. Salinity levels were checked using a YSI salinometer. Five ml of solution were added to each dish. During this first phase, the dishes were examined 4, 7, 10, 13, 20, 27, 34 and 41 days after the experiment was initiated. At these times, seeds that had germinated (defined as emergence of the radicle or plumule) were counted and removed, and filter paper was replaced to prevent salinity build-up through evaporation. Water loss was corrected twice a week. All dishes were placed in growth cabinets set on a 12 hour photoperiod and a $20°C/10°C$ thermoperiod. Light was produced by cool-white fluorescent tubes emitting approximately 12 Wm^{-2} at plant height.

After 47 days (there had been no germination since day 41) the seeds were rinsed in distilled water and transfered to new filter paper in clean petri dishes. Each dish was then treated with 5 ml of distilled water. The dishes were inspected 4, 8, 12, 17, 20, 26, 33, 40, 47, 54, and 61 days after this second, fresh water phase was initiated.

The germination response of the 12 sample populations of *C. lyngbyei* to the different salinity levels were examined using a Survival Analysis technique. The methods are described in Appendix II.

CHAPTER IV

RESULTS

FIELD SURVEY

The three estuarine marshes sampled in this study are environmentally diverse. In consequence, the 50 *Carex lyngbyei* populations sampled occupy and reflect these contrasting growing conditions. The field survey data are presented in Tables 4 and 5 where the environmental conditions and plant vigor variables that were measured in the study are listed for each individual site. The sites from which donor material for the transplant and germination experiments was removed are identified in both these tables. The field survey data are summarized below.

Environmental Conditions

Elevation/Submergence

Although the elevation range through which *Carex lyngbyei* was sampled was relatively small (eg. from 1.742 to 0.418 m geodetic at Nanaimo, or from 1.378 to -0.337 m geodetic at Squamish), the range in percent annual submergence represented by these elevations large. At the Squamish West delta (fresh), the sample sites were inundated from 55 to 95% of the time annually while at the Squamish East delta (saline) they were covered from 10 to 70% of the time. Submergence values in the Skagit south area (fresh) ranged from 3 to 30% and in the Skagit north area (saline) from 3 to 55%. At the Nanaimo Island area (fresh) submergence levels ranged from 0 to 25%; in the more eastern area (saline) from 10 to 35%.

Table 4. Environmental measurements for the 50 sites sampled in the field survey plus two other sites from the Skagit River delta used in the transplantation and germination experiments.

Site	Transplantation Material	Germination Material	Topographic Category	% Annual Submergence	Soil Water Salinity (ppt)			Texture			% Organic Matter
					April	July	January	% Sand	% Silt	% Clay	
SQF1			Foreshore flats	95	1.5	0	2.0	18.1	79.9	2.0	1.6
SQF2			Foreshore flats	95	1.5	0	2.0	25.2	74.8	0	1.6
SQF3		SQFL	Intermediate flats	75	–	0	2.0	70.9	29.1	0	1.5
SQF4			Intermediate flats	75	–	0	2.0	30.6	69.4	0	3.5
SQF5		SQFH	Levee	60	–	0	1.0	66.5	26.5	7.0	1.3
SQF6			Levee	55	–	0	1.0	62.2	34.4	3.4	2.4
SQF7	SQFL		Channel edge	75	1.5	0	2.0	53.0	47.0	0	2.3
SQF8	SQFH		Elevated flats	60	1.5	0	1.0	20.5	70.8	8.7	2.7
SQF9			Channel edge	70	–	0	2.0	43.4	50.7	5.9	3.8
SQF10			Elevated flats	60	–	0	1.0	30.0	58.8	11.2	1.6
SQS1	SQSL	SQSL	Channel edge	40	11.0	8.0	17.0	16.5	76.8	6.7	4.7
SQS2			Channel edge	70	11.0	8.0	17.0	20.1	74.5	5.6	3.1
SQS3			Channel edge	70	11.0	6.0	17.0	45.7	47.0	7.3	2.5
SQS4	SQSH		Elevated flats	10	–	5.0	17.0	23.1	74.6	2.3	4.3
SQS5			Foreshore flats	50	–	6.0	17.0	17.5	79.6	2.9	2.5
SQS6			Foreshore flats	60	–	6.0	17.0	24.9	72.1	3.0	2.9
SQS7			Intermediate flats	15	10.5	6.0	17.0	8.4	91.6	0.0	5.8
SQS8			Elevated flats	10	–	5.0	17.0	11.3	82.5	6.2	5.7
SQS9			Intermediate flats	20	–	5.0	17.0	5.6	71.5	22.9	5.8
SQS10		SQSH	Intermediate flats	20	–	6.0	17.0	7.1	92.9	0.0	7.7

(cont'd)

Site	Transplantation Material	Germination Material	Topographic Category	% Annual Submergence	Soil Water Salinity (ppt)			Texture			% Organic Matter
					April	July	January	% Sand	% Silt	% Clay	
SKF1		SKFH	Levee	3	0	3.0	2.0	59.5	37.7	2.8	2.9
SKF2			Elevated flats	4	0	3.0	2.0	58.1	38.5	3.4	2.1
SKF3			Intermediate flats	17	0.5	3.0	2.0	84.7	14.6	0.7	4.2
SKF4		SKFL	Channel edge	12	0.5	3.0	2.0	32.2	62.4	5.4	4.6
SKF5			Channel edge	24	0	3.5	2.0	37.3	59.6	3.1	3.8
SKF6			Channel edge	30	0	4.0	3.0	67.1	32.6	0.3	3.6
SKF7			Intermediate flats	17	1.0	4.0	3.0	35.3	57.3	7.4	2.3
SKF8			Channel edge	21	1.0	4.0	3.0	–	–	–	–
SKF9			Elevated flats	7	1.0	4.0	3.0	16.2	58.7	25.1	6.7
SKF10		SKFH	Levee	5	1.0	4.0	3.0	20.8	71.3	7.9	6.2
	SKFH		Elevated flats	–	–	–	–	–	–	–	–
	SKFL		Channel edge	–	–	–	–	–	–	–	–
SKS1			Channel edge	30	1.0	7.0	12.0	4.3	79.4	16.3	4.8
SKS2			Elevated flats	3	1.0	7.0	12.0	45.2	34.0	20.0	4.4
SKS3			Channel edge	46	1.0	7.0	6.0	31.2	62.6	6.2	5.8
SKS4			Levee	8	1.0	6.5	6.0	24.1	67.2	8.7	3.1
SKS5	SKSH		Levee	11	1.0	7.0	4.0	15.6	72.6	11.8	6.7
SKS6	SKSL		Channel edge	55	1.0	6.0	4.0	–	–	–	–

(cont'd)

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Site	Transplantation Material	Germination Material	Topographic Category	% Annual Submergence	Soil Water Salinity (ppt)			Texture			% Organic Matter
					April	July	January	% Sand	% Silt	% Clay	
NF1		NFH	Levee	0	12.0	17.0	12.0	35.7	58.7	5.6	34.6
NF2			Channel edge	20	12.0	17.0	12.0	29.4	55.1	15.5	12.9
NF3			Channel edge	20	12.0	20.0	7.0	15.0	73.1	11.9	17.8
NF4			Foreshore flats	25	7.0	19.0	7.0	32.6	61.3	6.1	4.7
NF5			Elevated flats	5	–	19.0	7.0	52.6	42.9	4.5	17.0
NF6			Channel edge	15	–	19.0	12.0	24.2	64.4	11.4	24.6
NF7			Channel edge	10	–	15.0	12.0	42.8	45.2	12.0	10.8
NF8	NFH		Elevated flats	0	–	19.0	12.0	34.0	56.1	9.9	30.3
NF9	NFL		Foreshore flats	25	–	20.0	7.0	46.0	47.2	6.8	5.2
NF10			Elevated flats	0	–	20.0	12.0	15.4	49.1	35.5	23.9
NS1		NSL	Channel edge	35	13.0	20.0	7.0	28.6	63.5	7.9	6.2
NS2			Elevated flats	20	15.0	22.0	7.0	33.2	61.5	5.3	13.2
NS3	NSL	NSL	Channel edge	35	13.0	19.0	7.0	57.1	39.9	3.0	9.8
NS4	NSH	NSH	Elevated flats	10	15.0	22.0	7.0	44.7	49.2	6.1	14.8

Table 5. Field survey plant growth measurements – mean (±1 SE) shoot height, shoot density, aboveground biomass, biomass per shoot and flowering shoots per unit biomass measurements for the 50 sites sampled in the field survey plus two other sites from the Skagit River delta used in the transplantation and germination experiments. Multispecific species composition refers to sites composed of ≤95% *Carex lyngbyei*

Site	Transplantation Material	Germination Material	Topographic Category	Shoot Height (mm)	Shoot Density (shoots m⁻²)	Aboveground Biomass (g)	Biomass per Shoot (g shoot⁻¹)	Flowering Shoots per Unit Biomass	Species Composition
SQF1			Foreshore flats	567±34	224±84	152±56	.68±.11	.004±.004	Multispecific
SQF2			Foreshore flats	635±70	252±84	172±32	.79±.12	0	Multispecific
SQF3		SQFL	Intermediate flats	854±19	508±72	454±38	.90±.07	.33±.03	Multispecific
SQF4			Intermediate flats	932±13	560±64	428±51	.77±.03	.13±.03	Multispecific
SQF5		SQFH	Levee	835±34	480±56	560±56	1.20±.13	.05±.03	Multispecific
SQF6			Levee	1080±72	312±28	432±36	1.43±.20	.11±.02	Multispecific
SQF7	SQFL		Channel edge	1229±35	320±68	528±80	1.73±.18	.18±.04	Monospecific
SQF8	SQFH		Elevated flats	432±27	60±20	20±6	.40±.08	1.40±.38	Multispecific
SQF9			Channel edge	938±40	436±28	536±52	1.23±.05	.36±.02	Monospecific
SQF10			Elevated flats	542±16	372±52	128±18	.33±.06	.57±.19	Multispecific
SQS1	SQSL		Channel edge	928±54	704±40	558±64	.81±.10	.45±.08	Monospecific
SQS2			Channel edge	580±37	532±44	153±20	.36±.11	.92±.20	Monospecific
SQS3			Channel edge	1151±76	664±52	608±60	.93±.10	.08±.03	Monospecific
SQS4	SQSH		Elevated flats	714±110	2012±148	133±13	.46±.16	.24±.12	Multispecific
SQS5			Foreshore flats	849±43	564±52	382±44	.68±.06	.66±.41	Monospecific
SQS6			Foreshore flats	704±67	484±88	330±143	.68±.14	.47±.11	Monospecific
SQS7			Intermediate flats	661±70	688±116	446±130	.60±.12	.40±.12	Monospecific
SQS8			Elevated flats	707±32	132±72	54±17	.72±.35	.20±.12	Multispecific
SQS9			Intermediate flats	1042±50	532±84	500±30	1.00±.13	.15±.05	Monospecific
SQS10		SQSH	Intermediate flats	753±54	652±28	560±35	.86±.06	.15±.03	Monospecific

(cont'd)

Site	Transplantation Material	Germination Material	Topographic Category	Shoot Height (mm)	Shoot Density (shoots m⁻²)	Aboveground Biomass (g)	Biomass per Shoot (g shoot⁻¹)	Flowering Shoots per Unit Biomass	Species Composition
SKF1		SKFH	Levee	491±30	311±92	71±26	.20±.03	1.06±.39	Multispecific
SKF2			Elevated flats	1183±60	592±80	506±27	.88±.06	.05±.02	Monospecific
SKF3			Intermediate flats	847±55	258±51	231±60	.84±.11	.003±.003	Multispecific
SKF4		SKFL	Channel edge	1035±40	186±25	145±34	.75±.08	.08±.02	Multispecific
SKF5			Channel edge	689±31	870±88	261±8	.31±.04	.84±.39	Monospecific
SKF6			Channel edge	761±18	771±77	299±29	.41±.06	1.11±.36	Monospecific
SKF7			Intermediate flats	1373±24	588±80	861±102	1.30±.14	.09±.02	Multispecific
SKF8			Channel edge	1116±31	731±1643	458±61	.81±.08	.04±.01	Monospecific
SKF9			Elevated flats	1288±33	383±55	533±57	1.44±.19	.01±.01	Multispecific
SKF10		SKFH	Levee	1411±42	569±38	692±73	1.22±.10	.11±.03	Multispecific
	SKFH		Elevated flats	1076±123	90±15	150±25	1.67±.00	.05±.03	Monospecific
	SKFL		Channel edge	885±107	66±14	107±4	1.71±.41	0	Multispecific
SKS1			Channel edge	1097±129	571±23	608±25	1.07±.01	.05±.01	Monospecific
SKS2			Elevated flats	947±22	53±23	97*	1.62*	0	Multispecific
SKS3			Channel edge	1137±90	341±128	433±142	1.40±.15	.01±.01	Multispecific
SKS4			Levee	1014±76	623±140	556±120	.93±.06	.09±.03	Multispecific
SKS5	SKSH		Levee	1227±104	427±123	1081±268	2.56±.11	.044±.003	Multispecific
SKS6	SKSL		Channel edge	821±27	340±10	252±4	.74±.04	.024±.006	Monospecific

(cont'd)

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Site	Transplantation Material	Germination Materal	Topographic Category	Shoot Height (mm)	Shoot Density (shoots m^{-2})	Aboveground Biomass (g)	Biomass per Shoot (g shoot^{-1})	Flowering Shoots per Unit Biomass	Species Composition
NF1		NFH	Levee	580±23	521±20	188±4	.38±.01	.06±.02	Monospecific
NF2			Channel edge	671**	925**	359**	.39**	.01**	Monospecific
NF3			Channel edge	802±26	883±48	472±59	.54±.08	0	Monospecific
NF4			Foreshore flats	382±64	378±180	73±42	.15±.07	0	Multispecific
NF5			Elevated flats	904±25	410±85	322±63	.79±.04	.08±.02	Multispecific
NF6			Channel edge	627±37	283±62	151±36	.58±.15	.02±.01	Multispecific
NF7			Channel edge	653±35	745±145	321±42	.53±.04	.11±.03	Monospecific
NF8	NFH		Elevated flats	702±25	1349±80	604±46	.45±.02	.30±.03	Monospecific
NF9	NFL		Foreshore flats	463±27	602±74	226±36	.38±.04	0	Multispecific
NF10			Elevated flats	858±30	251±106	159±60	.73±.09	.11±.05	Multispecific
NS1			Channel edge	656±25	1118±164	578±74	.52±.02	.13±.03	Monospecific
NS2			Elevated flats	390±12	9±5	4±2	.40±.04	0	Multispecific
NS3	NSL	NSL	Channel edge	626±36	1294±156	438±82	.33±.03	.20±.04	Monospecific
NS4	NSH	NSH	Elevated flats	508±61	263±76	80±30	.28±.06	.09±.05	Multispecific

*Measurements based on one 0.5 m² sample. **Measurements based on one 1.0 m² sample.

Soil Water Salinity

Soil water salinity decreased during the growing season at the Squamish and Skagit sites, particularly at the former area, and increased during the spring and summer months at the Nanaimo stations. Soil water salinity generally increased with distance from river distributaries. It did not vary substantially with elevation. The spring, summer and winter salinities measured at each site are listed in Table 4. The highest salinities measured were 22 ppt in July at the high elevation Nanaimo east sites; the lowest measured were 0 ppt in July at the Squamish West delta. The greatest salinity range from summer to winter (22 to 7 ppt) occurred at the Nanaimo east sites.

Soil Texture

The sand, silt and clay proportions of the soil sampled from each site can be found in Table 4. In general, the most coarse–grained soils were found at low elevations near river distributaries. The Squamish West delta sites were composed of sandy loams near the river bank and creek channels, and silt loams in inter–channel and foreshore flats. The Squamish East delta sites were mostly silt loams with a few silts and one sandy loam. The Skagit south area was composed of sandy loams at channel edges and silt loams between channels, while the Skagit north sample sites were mainly silt loams. The Nanaimo River delta differed from the other two deltas in composition. Silt and sand layers interspersed with gravels and cobbles were overlain, for the most part, by silt loams and sandy loams which occasionally contained cobbles.

Soil Organic Matter

The organic matter percentage of dry soil weight tended to increase with increased elevation. The organic matter proportion was generally highest at Nanaimo, particularly in the elevated flats where it reached 34.6%. In the Skagit River delta organic matter levels ranged

between 2.1 to 6.7%; at Squamish it varied from 1.3 to 7.7%.

Plant Growth

Shoot Height

The shoot height of different *Carex lyngbyei* populations sometimes varied dramatically, over very short distances. On the Squamish West delta, for instance, channel edge shoots attained a height of 1229 ± 35 mm while elevated flats shoots only 0.5 m away grew to just 432 ± 27 mm (Figure 10). The photograph in Figure 11 illustrates a similar situation in early June on the Squamish Central delta. These distinctly different shoots growing in close proximity to one another were the closest approximation to the described tall and short growth forms seen in this study. They were found only in specific situations in the Squamish River delta where tall shoots grew in channel edges and short shoots grew in elevated flats. In the Skagit and Nanaimo River deltas, shoot heights varied in a more continuous manner such that obviously "tall" or "short" shoots were not found. In the Skagit River delta the tallest shoots were found in inter-channel platforms and occasionally on levees (eg. 1227 ± 104 mm), while the smallest shoots grew in channel edges and in tussocks within the channels (eg. 821 ± 27 mm). The Nananimo shoots tended to be smaller, and never exceeded 910 mm in height. In some areas the tallest shoots were found in elevated flats.

Generally, the tallest shoots occurred in salinities of less than 10 ppt and where the organic matter content was less than 8%. The stepwise multiple regression procedure indicated that approximately 56% of the variance in shoot height is attributable to variation in summer soil water salinity (Table 6). The relationship was negative; shoot heights declined as soil water salinity increased.
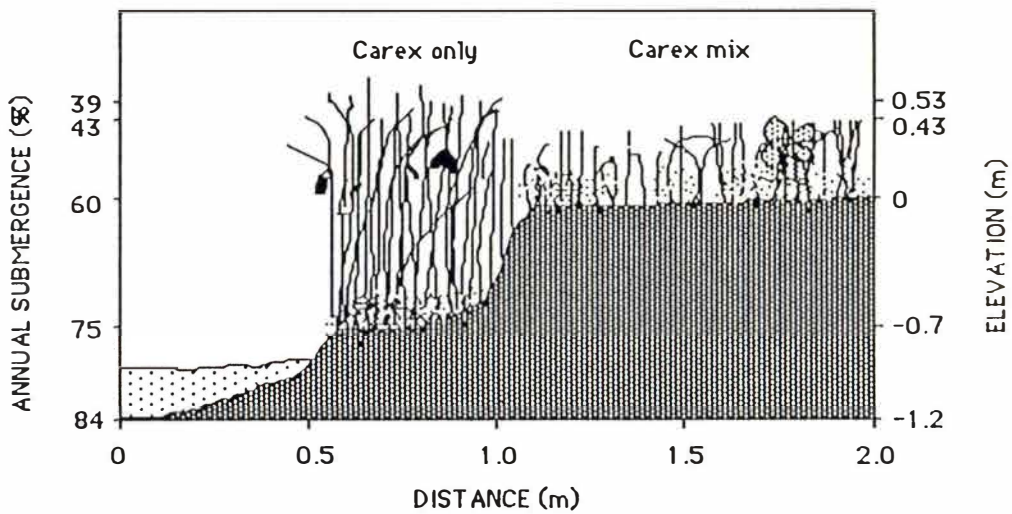
Figure 10. Native channel edge and elevated flats *Carex lyngbyei* at the Squamish West delta (the Squamish high and low elevation transfer sites). This picture depicts one-half of a cross-section of the streamchannel. The opposite bank had a similar arrangement. The channel edge shoots reached approximately 1230 mm in height while the elevated flats shoots reached approximately 432 mm.

Figure 11. *Carex lyngbyei* in the Squamish Central delta, early June, 1984. The channel edge shoots measured approximately 800 mm in height, while the elevated flats shoots reached approximately 400 mm. Height differences became more pronounced later in the growing season. This is the best expression of distinct tall and short growth forms encountered in this study. Shoots commonly varied in height in a more continuous manner.

Table 6. Significant results of multiple stepwise regression of *Carex lyngbyel* plant growth.

Dependent variable:	Independent variables entered into the regression equation at the α = 0.05 significance level:	Independent variables not entered into the regression equation at the α = 0.05 significance level:	Partial:	R²	Sig.
Shoot height	Summer salinity			.55963	
		Percent submergence	-.74808		.0000
		Winter salinity	-.14391		.4320
		Percent sand	-.13175		.4723
		Percent organic matter	-.04548		.8048
			.18040		.3231
Biomass per shoot	Summer salinity			.39583	
		Percent submergence	-.62915		.0001
		Winter salinity	-.15220		.4057
		Percent sand	.06071		.4057
		Percent organic matter	-.19476		.2854
			.23688		.1918
Flowering shoots per unit biomass	Winter salinity			.15916	
		Percent submergence	.39895		.0355
		Summer salinity	.10609		.5984
		Percent sand	-.27901		.1587
		Percent organic matter	-.06764		.7375
			-.36194		.0636

Shoot Density

Shoot density varied widely among the Nanaimo and Skagit samples (9.2 ± 5.2 to 1349.2 ± 80.0, and 53.0 ± 23.0 to 879.0 ± 88.0 shoots m^{-2}, respectively) and to a lesser extent among the Squamish samples (59.0 ± 19.5 to 702.0 ± 40.8 shoots m^{-2}). Shoot density was not strongly associated with the abiotic variables measured in this study, as not one of the dependent variables was entered into the stepwise multiple regression procedure at the α = 0.05 significance level. The shoot densities of near, or totally-monotypic *Carex lyngbyei* stands, however, did increase at the more saline Nanaimo River delta (Table 5).

Aboveground Biomass

Aboveground biomass measurements ranged from just above 0 to about 600 g m^{-2} in both the Squamish and Nanaimo samples. Similar values were recorded for the Skagit samples, although three exceeded 600 g/m^2 and one reached 1080.6 ± 268 g m^{-2}. The highest values occurred in relatively high elevations and low salinities in substrates containing little organic matter. Again, no independent variables were entered into the regression equation at the α = 0.05 level.

Biomass per Shoot

The biomass per shoot values for the Nanaimo samples were lower than those of the Skagit and Squamish samples. The Nanaimo values ranged from 0.15 ± 0.07 to 0.79 ± 0.04 g stem^{-1}. The Squamish measurements rose from 0.33 ± 0.06 to 1.73 ± 0.18 g stem^{-1} while the Skagit values ranged from 0.2 ± 0.03 to 2.56 ± 0.11 g stem^{-1}. High biomass per shoot values did not occur at elevations subjected to frequent inundation, nor in areas with high summer salinities. The regression analysis indicated that approximately 40% of the variation in biomass per shoot is attributable to variation in summer soil water salinity. Biomass per shoot decreased with increased salinity.

The flowering shoots per unit biomass values were lowest in the Nanaimo samples (0 to 0.13 ± 0.03 flowering shoots/unit biomass), but ranged to higher levels in the Skagit and Squamish samples (0 to 1.11 ± 0.36, and 0 to 1.40 ± 0.38 flowering shoots/unit biomass, respectively). High measurements of this variable did not occur in areas characterized by high summer salinities. Samples with high shoot densities tended to have a low flowering shoot/ unit biomass ratio.

The multiple stepwise regression analysis indicated that approximately 16% of the variation in flowering shoots per unit biomass was attributable to variation in winter soil water salinity. As winter salinities increased, so did the number of flowering shoots per unit biomass.

TRANSPLANTATION EXPERIMENT

The sites from which plant material was collected for the transplantation and germination experiments were, as stated previously, in either relatively saline or fresh water, and either relatively high or low elevations within each marsh. The plant material was transfered to elevated flats (high) and channel edge (low) sites in the Squamish West delta and the eastern portion of the Nanaimo delta.

The Squamish high site (SQH), had an annual submergence duration of 60%. Soil water salinity there varied over the sampling period from 1.5 ppt in May, to 0 ppt in July and 1.0 ppt in August. The site was composed of a silt-loam substrate on which the native, untransplanted sea sedge grew in a mixed stand to a height of 432 ±27 mm. The adjacent Squamish low site (SQL) was composed of sandy loam. It was characterized by an annual submergence duration of 75% and by soil water salinities that did not vary appreciably from

those of the Squamish high site. The native, untransplanted sea sedge grew to a height of 1229 ± 35 mm in a monotypic stand. The Nanaimo high site (NH) experienced an annual submergence duration of 10% and soil water salinities ranging from 15 ppt in May to 21.5 ppt in June, 22 ppt in July and 23 ppt in August. The native *Carex lyngbyei* grew on sandy loam substrates in a mixed stand to a height of 508 ± 61 mm. The Nanaimo low site (NL) was inundated annually 35% of the time. Soil water salinities varied from 13 ppt in May to 19 ppt in June, 20 ppt in July and 22 ppt in August. The native *C. lyngbyei* attained a height of 626 ± 36 mm in a monotypic stand on sandy loam substrates.

The means and standard errors of the shoot height, shoot density, aboveground biomass, biomass per shoot and flowering shoots per unit biomass variables at harvest in August are illustrated in order of most exposed/fresh water to most submerged/saline transfer sites in Figures 12 – 16, respectively. The controls (native vegetation transplanted back into their home sites) are marked by an asterisk. SNK range-test information is omitted from the graphs for the sake of clarity. Instead, it is presented in Figure 17. Significant interactions from the N-way ANOVA are given in Table 7.

Shoot Height

The heights of the transplanted *Carex lyngbyei* (with the exception of the Nanaimo samples at the Squamish low site) were lower than those of the untransplanted donor material described in the field survey. The shoot heights of the Squamish populations ranged from 147 ± 23 to 734 ± 165 mm. In general, the shoots were taller at Squamish (particularly at the Squamish low site) than at Nanaimo. The Squamish low shoots were significantly taller than their Squamish high counterparts except in two instances: once at the Squamish low site, where no shoots were produced, and once at the Nanaimo low site, the most submerged, saline site. The Skagit populations ranged in height from 223 ± 5 to 716 ± 101 mm. The shoot heights of the Nanaimo populations ranged from 186 ± 23 to 680 ± 98
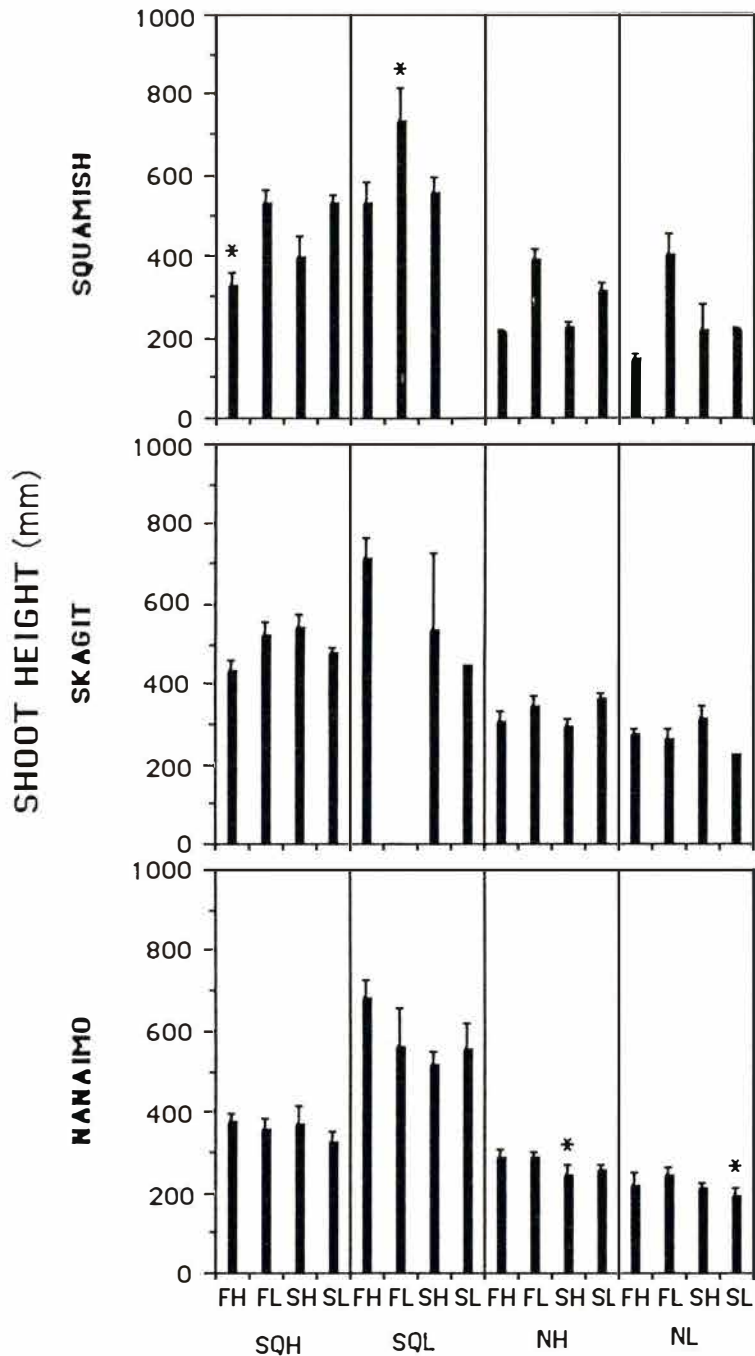
Figure 12. Mean (±1 SE) shoot height responses of 12 populations of *Carex lyngbyei* from relatively fresh water (F) and saline (S), high (H) and low (L) sites in the Squamish, Skagit and Nanaimo River deltas after transfer to four field plots – high and low elevation sites at both the Squamish West (SQH, SQL) and the eastern Nanaimo (NH, NL) River deltas – for 6 months. Data are from August, 1985. The asterisks denote the controls (native vegetation transplanted back into their home sites).
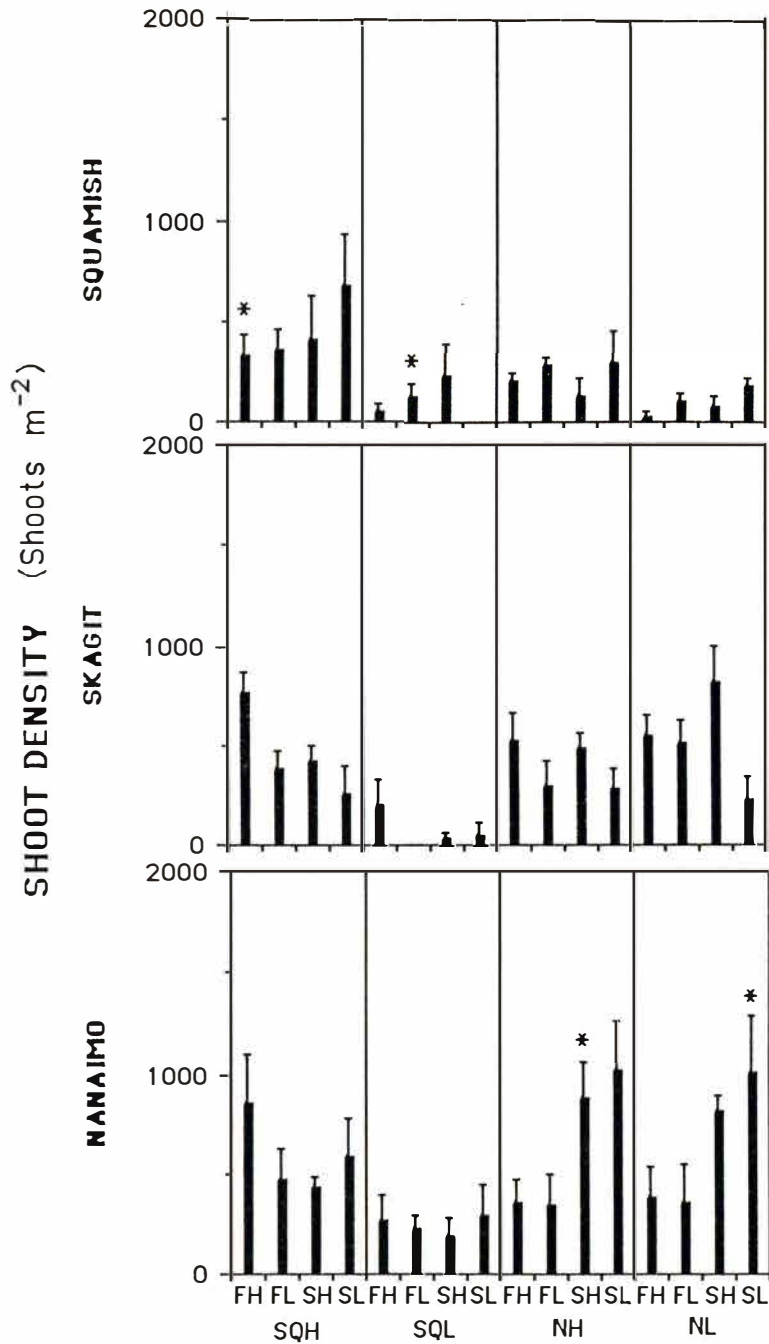
Figure 13. Mean (±1 SE) shoot density responses of 12 populations of *Carex lyngbyei* from relatively fresh water (F) and saline (S), high (H) and low (L) sites in the Squamish, Skagit and Nanaimo River deltas after transfer to four field plots – high and low elevation sites at both the Squamish West (SQH, SQL) and the eastern Nanaimo (NH, NL) River deltas – for 6 months. Data are from August, 1985. The asterisks denote the controls (native vegetation transplanted back into their home sites).
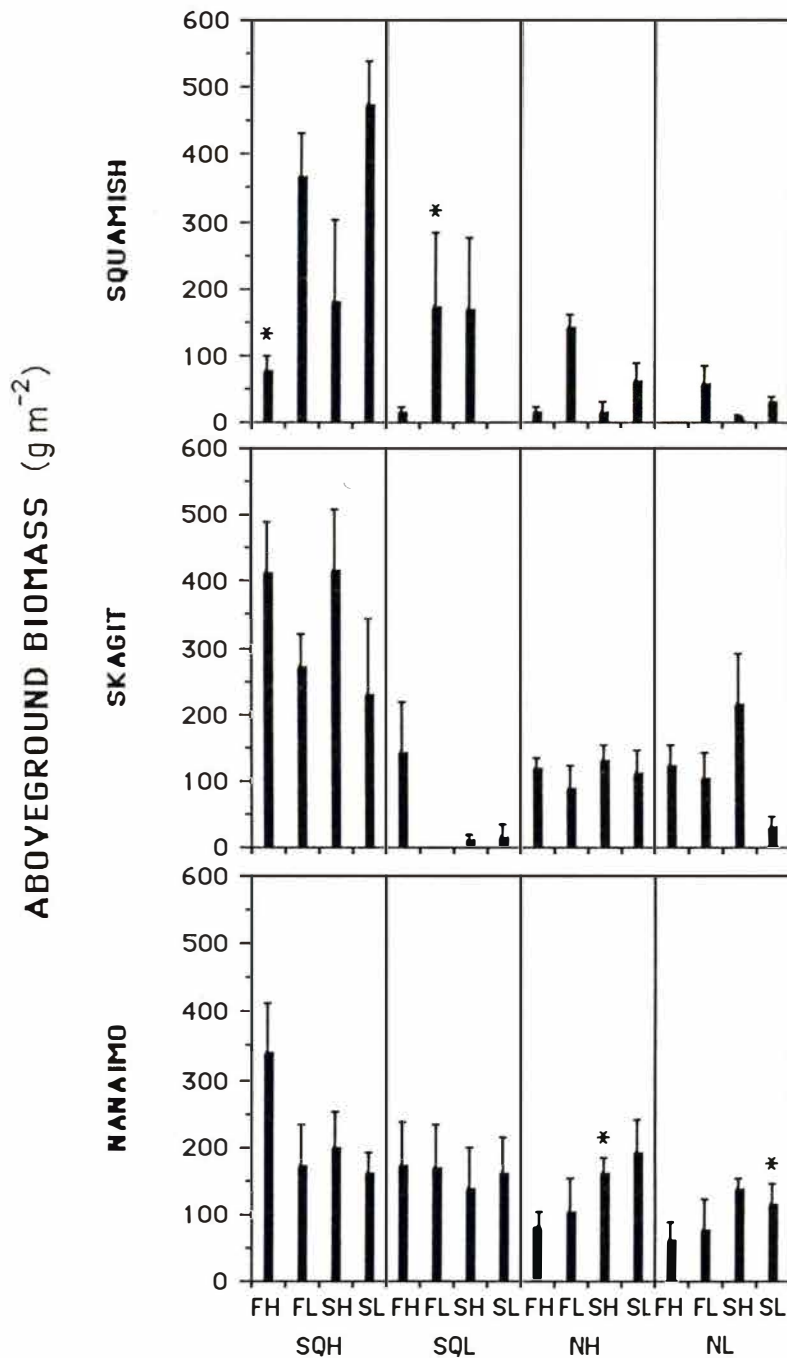
Figure 14. Mean (±1 SE) aboveground biomass responses of 12 populations of *Carex lyngbyei* from relatively fresh water (F) and saline (S), high (H) and low (L) sites in the Squamish, Skagit and Nanaimo River deltas after transfer to four field plots − high and low elevation sites at both the Squamish West (SQH, SQL) and the eastern Nanaimo (NH, NL) River deltas − for 6 months. Data are from August, 1985. The asterisks denote the controls (native vegetation transplanted back into their home sites).

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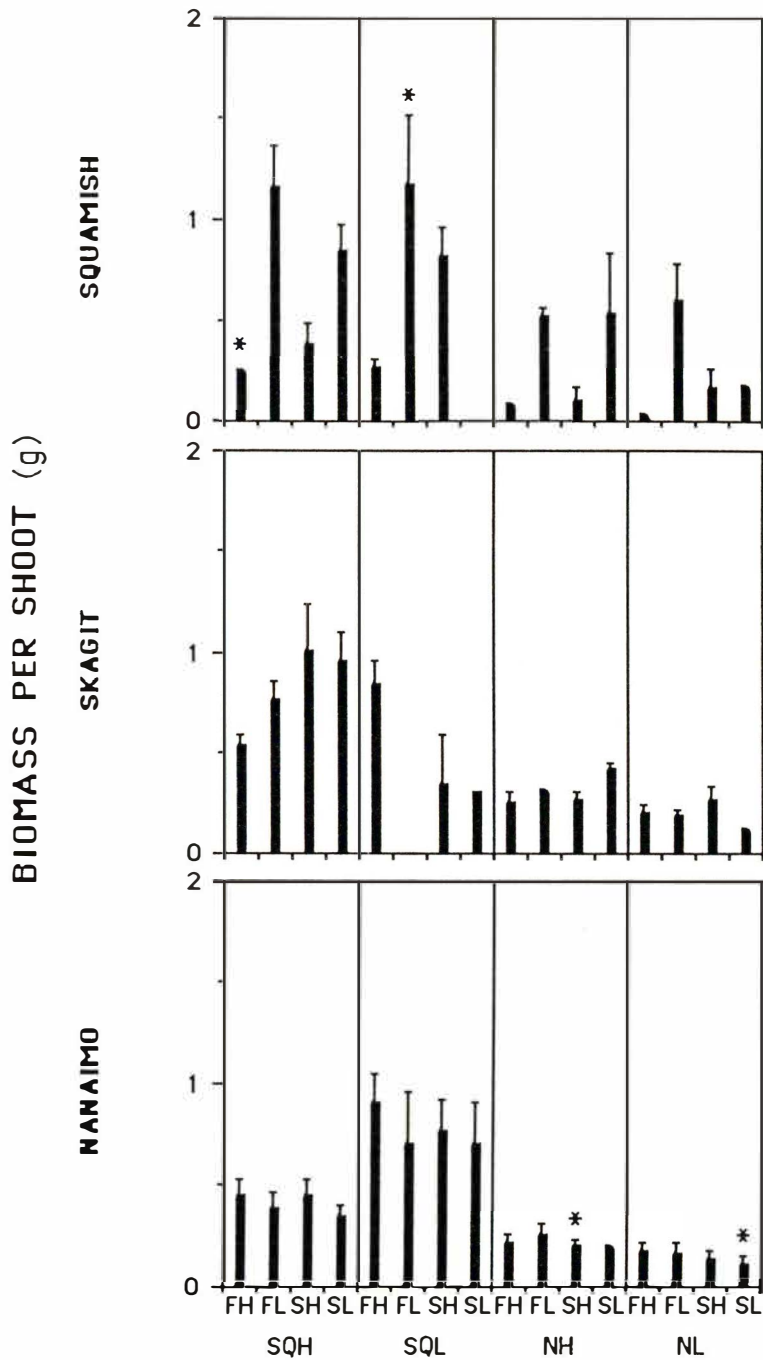
Figure 15. Mean (±1 SE) biomass per shoot responses of 12 populations of *Carex lyngbyei* from relatively fresh water (F) and saline (S), high (H) and low (L) sites in the Squamish, Skagit and Nanaimo River deltas after transfer to four field plots – high and low elevation sites at both the Squamish West (SQH, SQL) and the eastern Nanaimo (NH, NL) River deltas – for 6 months. Data are from August, 1985. The asterisks denote the controls (native vegetation transplanted back into their home sites).
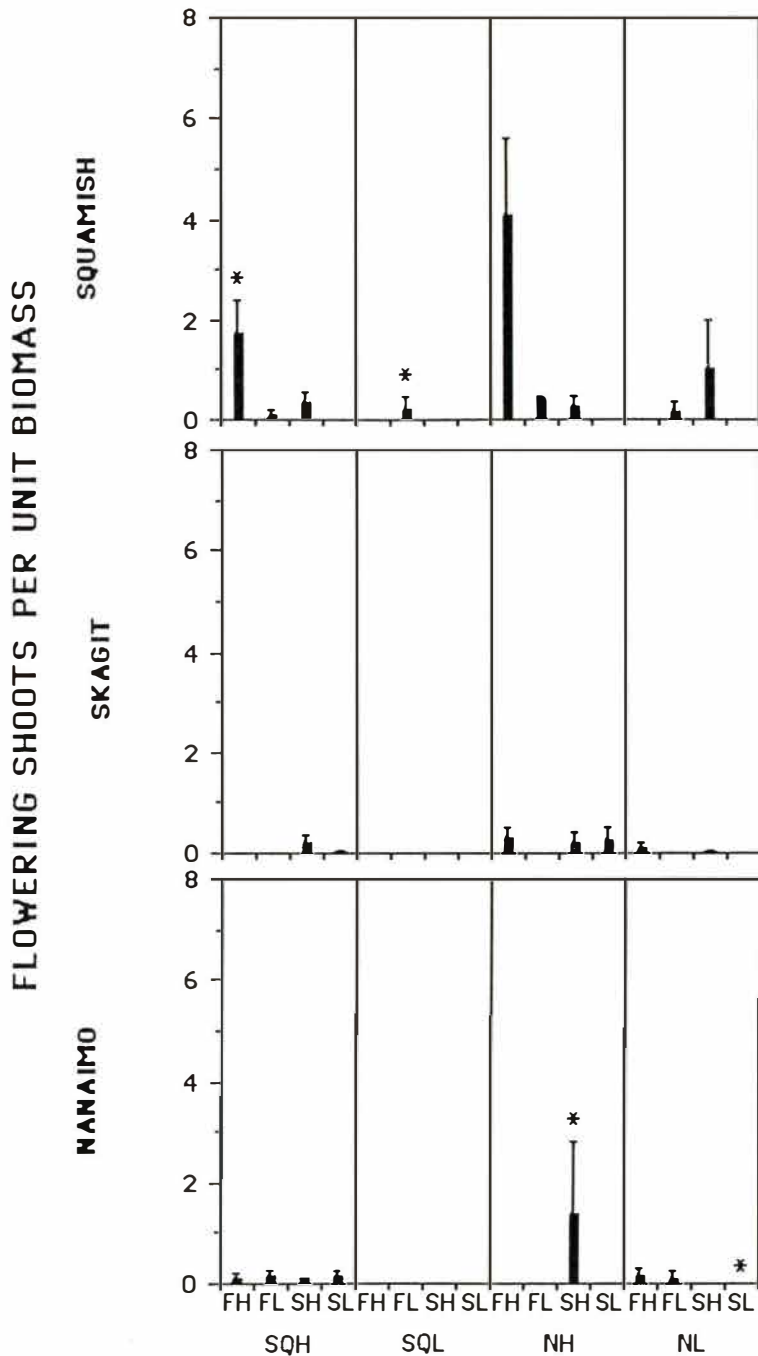
Figure 16. Mean (±1 SE) flowering shoot per unit biomass responses of 12 populations of *Carex lyngbyei* from relatively fresh water (F) and saline (S), high (H) and low (L) sites in the Squamish, Skagit and Nanaimo River deltas after transfer to four field plots – high and low elevation sites at both the Squamish West (SQH, SQL) and the eastern Nanaimo (NH, NL) River deltas – for 6 months. Data are from August, 1985. The asterisks denote the controls (native vegetation transplanted back into their home sites).

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Shoot Height

```
N-NL
N-NH
SK-NL
SK-NH
N-SQH
SQ-NH
SQ-SQH
SQ-NL
SK-SQH
N-SQL
SQ-SQL
SK-SQL
```

Aboveground Biomass

```
SQ-NL
SK-SQL
SQ-NH
SQ-SQL
N-NL
SK-NH
SK-NL
N-NH
N-SQL
N-SQH
SQ-SQH
SK-SQH
```

Shoot Density

```
SQF-N
SQS-N
SKS-SQ
SQF-SQ
SQS-SQ
SKF-SQ
NF-N
NS-SQ
SKS-N
NF-SQ
SKF-N
NS-N
```

Biomass per Shoot

```
N-NH
N-NL
SK-NL
SK-NH
N-SQH
SQ-SQH
SK-SQH
N-SQL
SQ-NH
SQ-NL
SQ-SQL
SK-SQL
```
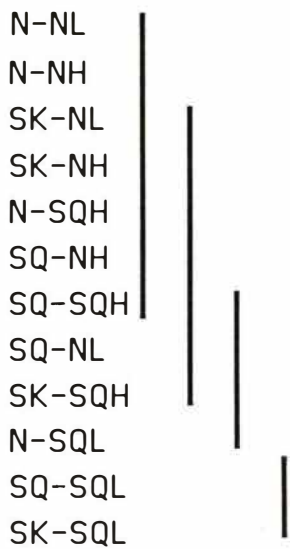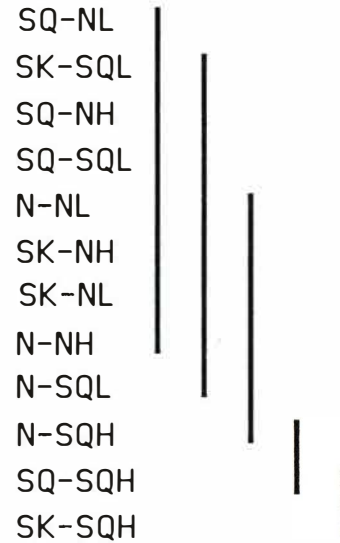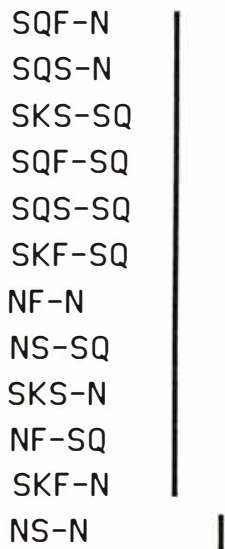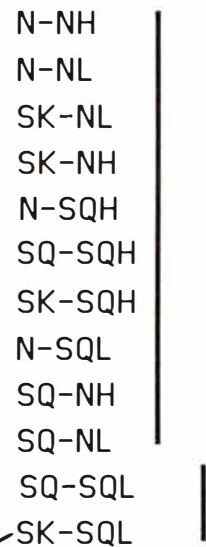
eg. The Skagit populations at the Squamish low site

Figure 17. Student–Newman–Keul's multiple range test information for shoot height, shoot density, aboveground biomass and biomass per shoot responses of 12 populations of *Carex lyngbyei* from high (H) and low (L) elevations of relatively fresh water (F) and saline (S) portions of the Squamish (SQ), Skagit (SK) and Nanaimo (N) River deltas after transfer to four field plots – high and low elevation sites at both the Squamish West (SQH, SQL) and the eastern Nanaimo (NH, NL) River deltas – for 6 months. Data are from August, 1985.

Table 7. Summary of significant ANOVA results.

Plant Growth Variable	Native River Delta X Native Site Salinity X Transfer River Delta Interaction	Native River Delta X Transfer River Delta X Transfer Site Elevation Interaction	Native Site Salinity X Transfer River delta X Transfer Site Elevation Interaction	Native Site Salinity X Native Site Elevation X Transfer River Delta X Transfer Site Elevation Interaction	Native River Delta X Native Site Salinity X Native Site Elevation X Transfer River delta X Transfer Site Elevation Interaction
Shoot Height	NS	***	**	NS	*
Shoot Density	**	NS	NS	NS	NS
Aboveground Biomass	NS	**	NS	NS	NS
Biomass per Shoot	NS	***	NS	**	NS

NS, not significant; *, P < 0.05; **, P < 0.01; ***, P < 0.001

mm. The shoots were significantly taller at the Squamish low site.

Generally, shoot heights increased from the Nanaimo sites to the Squamish sites. In particular, shoot heights increased at the the Squamish low site,where in the field survey native channel edge shoots were three times taller than nearby elevated flats shoots. Shoots were marginally shorter at the Nanaimo low site than at the Nanaimo high site. Shoot heights increased at the Squamish high site, and increased substantially at the Squamish low site.

The ANOVA identified two 3-way interactions and one 5-way interaction as influences on shoot height. The first involved interactions among the native river delta, the transfer river delta and the transfer site elevation. The second involved interactions among the native site salinity, the transfer river delta and the transfer site elevation. The 5-way interaction involved the native river delta, the native site salinity, the native site elevation, the transfer river delta and the transfer site elevation. The SNK range-test indentified 4 homogeneous subsets for the native river delta, transfer river delta and transfer site elevation interaction. These are illustrated in Figure 15.

Shoot Density

Shoot densities were monitored monthly from May to August. However, the Squamish transfer sites were inaccessible for a month, hence, the June data for those sites are missing. No significant interaction between the donor and transfer wetlands was found. The Squamish shoots declined in number as salinities increased over the summer at the Nanaimo sites, but increased slightly in number at the Squamish sites as salinities dropped and stabilized around 0 ppt. The Skagit and Nanaimo shoot numbers remained basically static over the summer at all transfer sites.

At the time of harvest in August, the densities of the transplanted shoots were often greater than those of the untransplanted donor material. The Squamish material was generally the least dense, varying from 0 to 679 ± 247 shoots m^{-2}. In general, the highest densities occurred at the Squamish high site; the lowest at the Nanaimo low site. Shoot densities of the Skagit populations ranged from 0 to 764 ± 97 shoots m^{-2}, were lowest at the Squamish low site, but remained at similar densities at the Squamish high and both Nanaimo sites. The Nanaimo shoots generally exhibited the greatest densities, ranging from 184 ± 81 to 1019 ± 238 shoots m^{-2}. The NSH and NSL samples were significantly more dense than their fresh water counterparts at the Nanaimo sites. Their densities decreased at Squamish, particularly at the Squamish low site. The Nanaimo fresh samples did not vary significantly from site to site.

The ANOVA indicated that variation in shoot density is attributable to interactions among the native river delta, the salinity of the native site, and the transfer river delta. The Student–Newman–Keul's multiple range test indentified 2 homogeneous groups shown in Figure 15.

Aboveground Biomass

The aboveground biomass of the transfered plant material was lower than that of the untransplanted donor material. The aboveground biomass of the Squamish populations ranged from 0 to 473.2 ± 64.2 g m^{-2}. Tha values were greatest at the Squamish high site, lowest at the Nanaimo low site. Values of the Skagit populations ranged from 0 to 418.3 ± 90.8 g m^{-2}, and were greatest at the Squamish high site, while lowest at the Squamish low site. The Nanaimo population ranged from 62.3 ± 24.6 to 341.9 ± 71.0 g m^{-2}. Their aboveground biomass was greater at the Squamish sites than at the Nanaimo sites.

Generally, the biomass values were greatest at the Squamish high site and lowest at the Nanaimo sites, particularly for the Squamish samples. The biomass of the Squamish and

Skagit samples was reduced at the alien, relatively saline Nanaimo sites. The Nanaimo samples were slightly more productive in the alien fresh water environment of the Squamish sites. The shoot height differences maintained between the high and low Squamish samples were reflected in their aboveground biomass measurements. The tall channel edge shoots (SQFL, SQSL) had greater aerial biomass than their elevated flats counterparts (SQFH, SQSH) in each transfer environment, with the exception of the problematical Squamish low site.

ANOVA demonstrated that variation in aboveground biomass was attributable to interactions among the native river delta, transfer river delta and the transfer site elevation. The multiple range test detected 5 homogeneous subsets which are presented in Figure 15.

Biomass per Shoot

The biomass per shoot values of transplanted material were lower than those of the untransplanted donor material, with the exception of the Nanaimo shoots at the Squamish sites. The biomass per shoot for all samples decreased with increased salinity, as the values diminished from the Squamish sites to the Nanaimo sites. The Nanaimo samples indicate that the biomass per shoot values were greatest at the Squamish low, channel edge transfer area.

The biomass per shoot levels over which the Squamish populations ranged are from 0.03 ± 0.01 to 1.17 ± 0.34 g stem^{-1}. The biomass per shoot values of the Squamish low populations was consistently, and significantly greater than those of the Squamish high populations except for one case out of 8, at the most submerged, saline Nanaimo site. The Skagit populations varied from 0.11 ± 0.02 to 1.01 ± 0.22 g stem^{-1} values were greatest at the Squamish sites. The Nanaimo populations varied from 0.11 ± 0.01 to 0.91 ± 0.13 g stem^{-1} Values were greater at the Squamish sites than at the Nanaimo sites, particularly at the Squamish low site.

ANOVA indicated that variation in biomass per shoot is attributable to two different interactions, firstly among the native river delta, the transfer river delta and the transfer site elevation, and secondly among the salinity and the elevation of the native site, the transfer river delta and the elevation of the transfer site. The multiple range test identified 2 homogeneous subsets for the native river delta, the transfer river delta and the transfer site elevation interaction. These are shown in Figure 17.

Flowering Shoots per Unit Biomass

The flowering shoots per unit biomass of the Squamish populations ranged from 0 to 40.7 ± 1.53, the Skagit populations varied from 0 to 0.31 ± 0.18, and the Nanaimo populations varied from 0 to 1.39 ± 1.39. No trends are apparent, and the variation is not attributable to any of the independent variables measured. In fact, the flowering shoots per unit biomass results were so variable that meaningful interpretation is impossible. Under natural growing conditions, Snow (1982) found that second, or perhaps, third year shoots flower. As clones spread, .shoots of the same age may occur close together, and hence, flowering shoots may be clumped. This clumping was observed in the field. The cup-cutter used to obtain donor plant material may have been too small to capture a representative sample of flowering shoots in a clone, and instead, may have captured either mainly young shoots which would not flower, or mainly second-year shoots which would flower. This would explain the sporadic results. Critical examination of this variable may require that at least 0.25 m² sample sods are transplanted.

The flowering shoots per unit biomass measurements varied in a direct relationship with winter soil water salinity. This seems to be more a statistical artifact than a plant growth response to environmental variation. There is no reason to suspect that flowering should be associated with events that occur during the winter.

GERMINATION EXPERIMENT

The percent germination response of *Carex lyngbyei* seeds from the Squamish, Skagit and Nanaimo test populations to immersion in various salinity treatments in Phase I of the germination experiment, and then to further immersion in fresh water in Phase II is presented in Table 8. The number of Squamish, Skagit and Nanaimo seeds which germinated in each salinity treatment within each counting period in Phase I and Phase II are presented in Appendix I.

Seeds from the Squamish, Skagit and Nanaimo *Carex lyngbyei* samples exhibited similar percent germination response patterns but different percent germination magnitudes after exposure to various salinities. The timing of their germination responses were significantly different.

All the sample seeds exhibited maximum germination in fresh water, decreased germination at 5 ppt and virtually no germination at salinities $\geq$ 10 ppt. The overall percent germination response of all the samples was not enhanced by exposure to the phase I high salinities prior to the phase II immersion in fresh water. Moreover, because the seeds in high salinities remained dormant until exposed to fresh water in Phase II, they were not damaged by 47 days of exposure to high salinities.

The Squamish samples produced abundant seed such that all four populations were fully represented in the experiment. The Squamish high seeds had a much greater germination response in fresh water than the Squamish low seeds. SQFH seed germination percentage diminished after exposure to salinities $\geq$ 10 ppt. The Skagit study samples were represented in the experiment by only three populations, as the SKSL population produced few seeds in the field, and so was not available for examination. The SKFH seeds generally exhibited lower germination percentages than the other Skagit samples. In the field, the Nanaimo

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Table 8.—The mean (±1 SE) percent germination response of 10 *Carex lyngbyei* populations to various salinities for 47 days (Phase I) prior to immersion in fresh water for 61 days (Phase II).

Parent Site	Phase	Salinity Treatments				
		0 ppt	5 ppt	10 ppt	15 ppt	30 ppt
SQFH	I	76.0 ± 5.0	13.0 ± 5.2	0	0	0
	II		69.5 ± 14.7	50.5 ± 5.4	54.0 ± 6.2	45.0 ± 9.9
SQFL	I	55.5 ± 11.2	2.0 ± 2.0	0	0.5 ± 0.5	0
	II		64.0 ± 6.9	24.5 ± 3.3	62.0 ± 9.0	44.5 ± 3.9
SQSH	I	83.5 ± 1.7	0	0.5 ± 0.5	0	0
	II		88.5 ± 3.3	74.5 ± 5.5	40.0 ± 7.4	82.0 ± 5.2
SQSL	I	36.0 ± 3.7	2.5 ± 1.5	0	0	0
	II		37.5 ± 7.6	29.0 ± 6.0	26.5 ± 7.9	25.0 ± 7.3
SKFH	I	40.0 ± 5.3	22.0 ± 4.8	0	0.2 ± 0.2	0.5 ± 0.5
	II		41.5 ± 9.4	34.5 ± 5.7	28.7 ± 9.5	29.5 ± 12.2
SKFL	I	65.0 ± 5.7	22.5 ± 10.2	1.5 ± 1.0	0	0.5 ± 0.5
	II		47.5 ± 20.7	53.0 ± 7.4	44.0 ± 8.2	55.5 ± 10.1
SKSH	I	76.5 ± 6.9	26.5 ± 6.9	0	0	0
	II		76.5 ± 13.7	68.5 ± 4.2	64.5 ± 10.8	62.5 ± 11.8
NFH	I	6.5 ± 1.5	0.5 ± 0.5	0	0	0
	II		0.5 ± 0.5	9.5 ± 2.8	13.5 ± 2.6	9.0 ± 2.4
NSH	I	7.0 ± 7.0	1.0 ± 1.0	0	0	0
	II		1.0 ± 1.0	10.0 ± 0	4.0 ± 4.0	11.0 ± 7.0
NSL	I	0	0	0	0	0
	II		0	0	0	0

populations, generally, produced little seed material. The only population fully represented in the experiment was the NFH. The NSH and NSL shoots produced few seeds, allowing only two replicates for each treatment, while the NFL material did not produce enough seed to be represented at all. The NFH and NSH seeds had a very low percent germination response, while not one NSL seed germinated.

The timing of the germination response of all seeds during exposure to various salinities in phase I and then during exposure to fresh water in phase II was examined in the survival analysis procedure. This indicated that during the first phase, the Squamish and Skagit seeds (which were not significantly different in this context), had statistically significant earlier germination than the Nanaimo seeds.

The mean germination time increased with increased treatment salinity, and increased with winter salinity and decreased with summer salinity, while spring salinity had no effect. No significant interactions were detected between winter and summer salinities. After immersion in fresh water during phase II, the Squamish seeds had significantly longer mean germination times than did the Skagit and Nanaimo seeds.

CHAPTER V

DISCUSSION

Study Findings

The field survey demonstrated that *Carex lyngbyei* populations in the Squamish, Skagit and Nanaimo River deltas grew across broad ranges of salinity and percent annual submergence. Considerable variation in aboveground growth was found in different populations in relation to this heterogeneous environment.

In general, shoot height and biomass per shoot decreased slightly from the low salinity Skagit River delta to the basically fresh water Squamish River delta, and decreased substantially at the more saline Nanaimo River delta. Aboveground biomass, however, did not diminish dramatically with increased salinity because shoot densities (in monotypic stands) increased at the Nanaimo sites. This suggests that as shoots decreased in height and biomass at the Nanaimo River delta, the loss of photosynthetic area was offset by increased shoot densities. Thus, although morphological differences among *C. lyngbyei* populations from different deltas were apparent, overall aboveground production did not vary substantially.

Morphological variation in *C. lyngbyei* within a single delta was often considerable, even over short distances. The Squamish River delta channel edge and elevated flats populations provided the most dramatic contrasts. The channel edge shoots were three times taller and had over four times more biomass per shoot than did the adjacent elevated flats shoots. Despite these differences, the distinct tall and short growth forms recognized by several researchers were not found in this study. Within each delta, shoot height varied in a complex manner. Mean shoot height was correlated with marsh platform morphology rather than with elevation. In the Squamish West delta, shoots from low elevation channel edge sites grew to approximately the same height as shoots on high elevation levees. They were

slightly taller than shoots on intermediate flats and were substantially taller than shoots from low elevation foreshore flats and high, elevated flats. Distinct tall and short growth forms were recognized only where channels cut through elevated flats such that particularly tall shoots grew adjacent to particularly short shoots. The tall and short growth forms may be distinguished only when small areas (several square meters) of marsh are examined. Over tens of square meters, so many intermediate stages may be found that this terminology is not applicable.

The field survey also revealed that in fresh water, *C. lyngbyei* grew at elevations with an annual submergence of 95%, but in more saline conditions did not extend below annual submergence levels of 35%. These data suggest that sea sedge can withstand either prolonged inundation in fresh water, or short inundation periods in higher salinities.

The transplantation experiment results showed that most of the characters examined were modified by the environment of the transfer sites such that they more closely resembled the vegetation native to each site. Only occasionally did particular samples either maintain their morphological characteristics or show significantly less growth after transplantation. For these reasons, morphological variation in the Squamish, Skagit and Nanaimo sea sedge populations is interpreted as primarily ecophenic.

Generally, the shoot height, aboveground biomass and biomass per shoot values of the transferred material decreased from the fresh water Squamish sites to the more saline Nanaimo sites. The shoot height and dry weight per shoot findings were in accordance with the field survey results; the aboveground biomass findings were not. The latter discrepancy may be attributed to two particular responses. Firstly, the Squamish samples were unable to produce many shoots at the Nanaimo transfer sites, hence, their aboveground biomass decreased at Nanaimo. Secondly, the Nanaimo shoots attained greater heights when transferred to the Squamish River delta. This translated into increased aboveground biomass there. The

result of these two responses was a greater discrepancy in aboveground biomass between the Squamish and Nanaimo sites in the transplant experiment than was evident in the field survey.

The shoot densities of the transfered sea sedge did not mimic those of the native vegetation. Rather than having greater densities at Nanaimo than at Squamish, the transplanted *C. lyngbyei*, with two notable exceptions, had comparable densities at both deltas. The first exception involved the Squamish shoots, which became less dense when transferred to the Nanaimo sites. This suggests that the Squamish material (from an oligohaline/fresh water environment) was unable to produce many shoots in the polyhaline environment of the Nanaimo delta. These Squamish samples had particularly low densities in the Nanaimo low site where they faced longer inundation by the relatively saline waters. The second exception involved the saline Nanaimo samples (NSH, NSL). They were significantly more dense at both Nanaimo sites (where they were native) than were their Nanaimo fresh counterparts (NFH, NFL). Their densities decreased to levels equivalent to those of the Nanaimo fresh samples in the alien, fresh water Squamish sites.

The transplantation experiment results demonstated that, for the most part, aboveground biomass, shoot height, biomass per shoot and, to a lesser extent, shoot density varied with site. This essentially plastic response to environment indicates that variation in these characters is primarily ecophenic. Three cases, involving populations from either the fresh water or saline extremities of the study sites, ran contrary to this trend.

The first exception occurred when the Squamish low samples retained greater shoot heights, aboveground biomass and biomass per shoot values than did the Squamish high samples in virtually all transfer situations. The differences occurred between channel edge and elevated flats populations from both the "fresh water" and "saline" sections of the Squamish River delta. This suggests two possibilities. Either larger underground reserves in the channel

edge samples than in the elevated flats samples buffered the alien site conditions until the end of the six month experiment, or genetic differentiation has occurred in these four populations. Such genetic differentiation would be in response to environmental differences between the elevated flats and channel edge sites rather than in response to noticeable salinity differences between the Squamish West ("fresh water") and East ("saline") deltas. Because diking changes begun in the late 1940's diverted most of the river discharge from the eastern to the western distributary, the East delta has become more saline over the last 30 years, while the West delta has perhaps become more fresh. The long-lived, perennial Squamish sea sedge may still be adjusting to these changes, and thus may not have diverged in response to salinity.

It is surprising that genetically-fixed differences exist between the high and low elevation Squamish shoots since it seems likely that *C. lyngbyei* from higher elevations would be transfered to channel edges as the channel banks slumped with lateral erosion. The results, however, indicate that environmental differences between the two habitats may have been strong enough to induce genetic divergence.

The second exception to the overall pattern of ecophenic variation again involved Squamish plant material. The Squamish populations, generally, had lower densities than the others at the Nanaimo transfer sites. This suggests that in the relatively saline Nanaimo River delta, they had a lower ability to produce new shoots than did the Skagit and Nanaimo populations. This reduced vigor in an alien environment indicates limited plasticity and points to a narrow, genetically-fixed response to a salinity regime.

The third exception involved the more saline Nanaimo populations. The NSH and NSL samples were significantly more dense at their native Nanaimo sites than were their Nanaimo fresh counterparts. Their densities decreased substantially in the alien, freshwater Squamish River delta. These results are difficult to interpret since equally high shoot densities were

found in one Nanaimo fresh site in the field survey. The transplant results could be a reflection of sampling variability at the time of transplantation, but consistent results in both Nanaimo transfer sites make that unlikely. Moreover, the dense samples were from both an elevated flats (multispecific) and a channel edge (monospecific) area where natural *Carex lyngbyei* densities are different. That these transplanted samples produced comparable shoot numbers in both sites suggests that they were less stressed than the Nanaimo fresh samples and, therefore, were able to produce more shoots. This greater vigor in their native environment suggests genetic divergence in this character between the Nanaimo fresh water and Nanaimo saline samples.

The morphology results were obtained from a transplant experiment lasting only 6 months. As Snow (1982) pointed out, however, strong trends exhibited one growing season are not likely to be reversed the next. The heights, aboveground biomass and biomass per shoot of the transplanted material were less than those of the natural material in the field, but shoot densities were slightly higher. There was no evidence at harvest that the plants were root bound, hence, their performance was not limited by confinement to small pots. The slightly reduced growth seen in the transplant experiment is probably due to minor transplant shock.

The germination experiment showed that the Squamish, Skagit and Nanaimo sea sedge differed substantially in terms of viable seed production. *C. lyngbyei* from the relatively fresh water Squamish River delta developed abundant seed which germinated in the laboratory in large numbers. The Skagit populations of *C. lyngbyei* produced similar seed material, except in low/saline sites, where few seeds were found. The percent germination in the laboratory of these Squamish and Skagit samples was relatively high, despite the unsophisticated pre-germination storage. In contrast, the mesohaline to polyhaline Nanaimo sea sedge produced small numbers of small, thin seeds, most of which did not germinate in the growth chambers. Although seed production in the field may vary from year to year with

environmental conditions, seed output at Nanaimo in the second field season of this study was no more extensive than in the first. This indicated that the Nanaimo plants have low vigor with respect to seed production, probably in response to higher ambient salinities.

Seeds from the Squamish, Skagit and Nanaimo test populations all exhibited maximum germination in fresh water, decreased germination at 5 ppt and no germination at salinities ≥ 10 ppt. When transfered to fresh water after exposure to higher salinities, seeds from these populations germinated in numbers equal to or just below those of fresh water only treatments. The percent germination in fresh water, therefore, was neither augmented nor diminished by exposure to high salinities. The *C. lyngbyei* seeds from the Squamish, Skagit and Nanaimo River deltas did not require salt for germination, regardless of a high probability of exposure to salt by the native populations. As the seeds of all populations had similar percent germination patterns, no genetic divergence among populations has occurred with respect to this characteristic.

The percent germination response exhibited by the test populations is well suited to springtime conditions at the Squamish and Skagit River deltas. At the time of spring germination, the soil water salinity of the SQFH and SQFL sites falls from 2 ppt to 0 ppt, while the soil water salinities of the SQSH and SQSL populations drops from approximately 12 ppt to approximately 6 ppt. At this time the SKFH and SKFL populations are subjected to soil water salinities of 0 ppt, while the SKSH and SKSL samples experience salinities of 1 ppt. Salinities in the Skagit River delta are lowest in the spring, increase in summer, and increase yet again in the winter. The advantages of this germination response are twofold: seeds are inhibited from germination while floating with no anchorage in seawater, and germination at reduced salinities allows developing seedlings (whose shallow roots may encounter high soil surface salinities) greater probability of survival (Ungar 1982).

The seeds from the Squamish East delta (SQSH, SQSL) experience a substantial drop in salinity in the field at the time of germination, and might be expected to have increased percent germination in fresh water after exposure to high salinities. Such behavior was not found in this study.

Seeds in the Nanaimo River delta do not encounter reduced soil water salinities in the spring except during periods of prolonged precipitation. In the Nanaimo River delta, soil water salinities rise from spring levels of 12 ppt to 16 ppt in early summer at the NFH and NFL sites, and from 13-15 ppt to approximately 19 ppt at the NSH and NSL sites. The maximum germination of these seeds in fresh water in the experiment is not consistent with field conditions. The Nanaimo *C. lyngbyei*, because they seemingly produced few, viable seeds, which germinated best in fresh water, have a germination pattern that is not well suited to the higher salinities found in the Nanaimo River delta.

The germination experiment demonstrated that the timing of germination among the Squamish, Skagit and Nanaimo *C. lyngbyei* populations was significantly different. In Phase I, the seeds from the Squamish and Skagit River deltas had significantly earlier germination than those from the Nanaimo River delta. This must be interpreted with caution, as few seeds from Nanaimo germinated. In consequence, this aspect of the analysis may be biased by an unrepresentative response of a few seeds. As low salinities are a temporary phenomenon at the Nanaimo River delta, delayed germination after exposure to fresh water would be of no benefit to the emerging seedlings.

The mean Phase I germination time was increased by high winter, and low summer, salinities. Populations from the Squamish East delta, therefore, had relatively delayed germination. This behavior would be advantageous in field conditions because seedlings emerging there some time after a first exposure to fresh water would have a low probability of encountering damaging high salinities.

The Phase II timing of germination in fresh water after exposure to high salinities was significantly different between seeds from the Squamish and Skagit River deltas. The longer germination times of the Squamish (compared to the Skagit) seeds again would ensure emerging Squamish seedlings a greater probability of encountering low salinities. The Skagit River delta, on the other hand, has the lowest salinities in the spring. Rapid germination when low salinities are first encountered would ensure seedlings of growth in relatively fresh water. The differences between the Squamish and Skagit seeds, then, correlate well with the conditions each encounters in the natural environment.

The germination rate in Phase II was determined to be a function of the submergence regimes of the samples' native habitats. The germination rate increased significantly from 40 to 70% annual submergence, then decreased dramatically with a further increase in submergence. This pulse in germination around the 70% submergence level may simply reflect the vigor of the low elevation Squamish samples.

Comparison with Other Studies

The field survey yielded results similar to those of other studies. An increase in shoot density concurrent with a decrease in shoot height and weight is in accordance with the findings of Ewing (1986) and Karagatzides (1987). Ewing (1986) examined several intertidal plant species in the Skagit River delta. He found that the shoot density of *C. lyngbyei* at the northern (saline) end of the delta was double that at the southern (fresh) end. Biomass per shoot decreased as shoot density increased, indicating less investment per shoot as densities increased. Ewing also reported a similar pattern in *Eleocharis palustris*. Karagatzides (1987) found that *Scirpus maritimus* in the Fraser River delta exhibited a comparable response.

The interaction between salinity and elevation in limiting the expansion of sea sedge to lower elevations was also observed in two other studies on the Pacific coast. Campbell (1986) compared plant species composition in 13 river deltas on the Queen Charlotte Islands, northern Vancouver Island and the northern mainland of British Columbia. She reported that in fresh to brackish areas, *C. lyngbyei* grew in the low marsh, but in more saline areas it was part of the intermediate marsh. Ewing (1986) reported that sea sedge in the Skagit River delta was not present in low elevation, saline sites. Deschenes and Serodes (1985) found a similar response in *Scirpus americanus* growing in the St. Lawrence River.

The transplantation experiment results indicated that *C. lyngbyei* has responded to its heterogeneous environment by plastic modification of the phenotype. Sea sedge, thus, is similar to several other coastal halophytes. Tall and short forms of *Spartina alterniflora*, for instance, were found to be genetically indistinguishable when compared by reciprocal transplantation and gel electrophoresis of enzymes by Shea *et al.* (1975). *Deschampsia cespitosa, Distichlis spicata, Grindelia integrifolia, Jaumea carnosa,* and *Salicornia virginica,* from the upper and lower ranges of each species in Netarts Bay, Oregon, were examined in a reciprocal transplant experiment by Seliskar (1980). The transplanted material assumed the morphological and anatomical characteristics of the vegetation native to the transfer sites. Variation in these 5 species was considered to be ecophenic. High and low elevation *Scirpus americanus* and *S. maritimus* from the Fraser River delta were found to vary ecophenically in terms of morphology in a transplantation experiment by Karagatzides (1987). Day-time exposure period, during which photosynthesis could occur, was found to be the primary factor influencing plant growth. Secondary factors included salinity and soil nitrogen levels.

The *C. lyngbyei* examined in this study differs from these other species in that some genetic differentiation appears to have occurred in the populations from the relatively fresh water Squamish River delta and the relatively saline Nanaimo River delta. In this respect, sea sedge more closely resembles *Salicornia europaea.* Jefferies *et al.* (1981) found that populations

of *S. europaea* from upper and lower portions of an intertidal wetland maintained differences in phenology after reciprocal transplantation. The differences were interpreted as a response to hypersalinity in the upper marsh. Genetic differentiation has been shown to occur more often in coastal plant species that inhabit dune, swale, and saltmarsh areas. Rhebergen and Nelissen (1985) reported genetic differentiation within *Festuca rubra* from these three habitats in terms of salt tolerance and relative growth rate. Silander (1979) found that resident *Spartina patens* had greater survival and fecundity than did alien reciprocal transplants. Density was deemed to be the primary selection pressure.

C. *lyngbyei*, like *Spartina alterniflora* of the Atlantic coast, has been reported to have tall and short growth forms. The *S. alterniflora* growth forms have been determined to be ecophenes rather than ecotypes (Shea *et al.* 1975). Several research projects have been aimed at determining the causes of these height differences. Morris and Dacey (1984) found that nitrogen uptake in *S. alterniflora* in a coastal marsh in Massachusetts was a function of O_2 concentration in the rhizospere. DeLaune *et al.* (1983) suggested from work in Louisiana, that growth of the short *S. alterniflora* ecophene is limited by anoxic substrates containing toxic concentrations of sulphide which prevent nitrogen uptake and root development. Howes *et al.* (1986) found that interactions among sediment oxidation, available nitrogen and interstitial salinity determine the growth form of *S. alterniflora* in a New England salt marsh.

Recognizable *C. lyngbyei* tall and short forms were found in this study only in the Squamish River delta where channels cut through elevated flats. Contrary to the *Spartina* situation, these *C. lyngbyei* shoots retained distinct differences after transfer to four different sites. This may be due to either buffering of alien site conditions by underground reserves or to inherent genetic differences among the channel edge and elevated flats shoots.

The aboveground variation at these Squamish sites may be a response to a complex of factors similar to those reported to influence *Spartina alterniflora* growth. Alternatively, it may

be a function of differences in the quantity and timing of mobilization of underground photosynthate reserves (the "streamside effect") found in *C. lyngbyei* in Siletz Bay, Oregon (Gallagher and Kibby 1981). This latter explanation is supported by modest field evidence from this study. Although belowground biomass measurements were discontinued after soil removal problems became apparent, the preliminary results indicated that the channel edge *Carex lyngbyei* had greater belowground biomass than did the elevated flats material. This observation supports the idea that underground storage organs may have confounded the effects of the transfer sites for the duration of the six month transplantation experiment.

The germination experiment results indicate that sea sedge is similar to many halophytes that avoid germination at low water potentials by remaining dormant until salinities are reduced by increased precipitation or river discharge (Ungar 1982; Schat and Scholten 1985). *C. lyngbyei* fits into the Type 2 category of Woodell (1985), where the germination of species from habitats likely to experience seawater inundation was strongly inhibited by salinities ≥ 15 ppt, but which after transfer to fresh water, rebounded to levels equal to, or just below, those of seeds exposed only to fresh water.

Mooring *et al.* (1971) reported similar percent germination responses in seeds from short, medium and tall forms of *Spartina alterniflora* in North Carolina. She concluded that in terms of germination response, the different *Spartina* growth forms are ecophenes. The present experiment indicates that, as in *S. alterniflora*, the percent germination pattern of different *C. lyngbyei* populations does not vary. In contrast, the timing of that germination response among *C. lyngbyei* populations from different river deltas is different and is genetically-fixed.

Hutchinson and Smythe (1986) found that germination of seeds from the Squamish Central delta was augmented by exposure to high salinities before immersion in fresh water. Similiar behavior might have been expected from seeds from the Squamish East delta, as

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they experience a substantial drop in salinity in the field at the time of germination. These different findings may again reflect river distributary changes since the 1940's. The Squamish East delta (examined in the present study) has likely become more saline, while the salinity regime of the Squamish West delta has remained relatively stable.

The germination experiment also provided other serendipitous information. Virtually all of the leftover seeds not used in the experiment germinated when taken indoors to a warm, dark room. This indicates that temperature, not daylength, triggers germination in *C. lyngbyei*.

Interpretation of the Study Findings

To date, several studies have shown that morphological variation in the intertidal wetlands of the North American Pacific coast is essentially ecophenic. Possible genetically-based population differentiation in this region has been reported only in this study, and here it is limited to a few occurrences. The potential causes of this plastic response to a heterogeneous environment are numerous and may be environmental and/or biological in nature.

The intertidal estuarine environment is characterized both by seasonal changes that occur more frequently than the resident perennial plants' regeneration cycles, and by more unpredictable, long-term changes with recurrence intervals greater than the plants' regeneration cycles. Plasticity may be favored by both conditions (Bradshaw 1965; Gray 1974). Plasticity might enable plants to adjust to salinity changes in response to river discharge fluctuations throughout the growing season, or to uncommonly hot, dry summers when soil salinities rise as a result of low precipitation and high evapotranspiration.

The Squamish and Nanaimo *C. lyngbyei* are exposed to relatively low and high salinities, respectively, each growing season. The morphological genotypic variation found in

this study occurred in these consistently more extreme sites. In contrast, the Skagit *C. lyngbyei* may be exposed to unusually high salinities approaching those of the long-term Nanaimo River delta average during extremely hot, dry years, and to persistent low salinities like those of the Squamish West delta during extremely cold, wet years. Only ecophenic variation was found in the Skagit samples, thus, it appears that in these less extreme, variable sites, flexibility of responses has been selected.

The essentially ecophenic variation exhibited by the Squamish, Skagit and Nanaimo *C. lyngbyei* may be associated with low amounts of recombination, high rates of gene flow, and founder effects. Disruptive selection may not lead to genetic divergence if recombination is low. Results from this research indicate that in the more saline wetlands few *C. lyngbyei* seeds are produced and apparently fewer still germinate. The seedlings that do emerge are faced with high surface soil salinities and may not be able to survive to maturity. Although considerable time was spent examining the sea sedge shoots colonizing the foreshore flats in each wetland during the field survey, not one seedling was observed. *C. lyngbyei* establishment by seed germination seems to be infrequent in foreshore areas and is even less probable at higher elevations where sea sedge and other species have spread by rhizome extension to form a closed stand. The subsequent low levels of recombination mean that few genetic variations are provided to be molded by the forces of selection.

Ecotypic variation may not be common within the Pacific coast wetlands because few genotypes may have colonized each wetland, providing little genetic diversity for selection to act upon. These founder effects may provide an explanation as to why genetic differentation has not occurred on a large-scale within each wetland. Founder effects do not, however, account for the lack of genetically-fixed variation between wetlands. Indeed, these conditions should facilitate genetic divergence at the meso-scale. Likewise, high levels of gene flow may occur within individual wetlands, but are highly unlikely between wetlands. The effects of disruptive selection thus may be mitigated by gene flow on the micro-scale but not on the

meso-scale.

Future Research

Before an understanding of intraspecific variation within *C. lyngbyei* is possible, much research is needed. Crossing experiments and/or gel electrophoresis studies are needed to determine how large *C. lyngbyei* clones are, how many genotypes inhabit each wetland, and how many genotypes inhabit more than one wetland. Such studies may also provide more insight into the importance of founder effects. Pollination studies are needed to provide basic information on *C. lyngbyei* breeding systems. If the species is essentially inbreeding, then recombination levels would be low regardless of low levels of seed germination and seedling survivorship.

Research is needed to further examine the possible genotypic variation between the Squamish channel edge and elevated flats sea sedge revealed in this study. A transplantation experiment lasting several growing seasons would clarify the role of buffering by underground reserves. Detailed substrate chemistry studies would illuminate what environmental factors influence plant growth and so select for the differences between the two populations. Physiological research is needed to delimit the internal processes which account for the outward morphological differences.

A larger scale of investigation may reveal information about the way *C. lyngbyei* has adjusted to climatic differences across its large latitudinal range. Research examining differences in phenology on a latitudinal scale may prove fruitful.

Ramifications for Wetland Restoration and Enhancement

This research has shown that while morphological characteristics vary in *C. lyngbyei* from site to site (ecophenically, for the most part), overall aboveground production is high across a range of salinity and submergence regimes. Sea sedge, therefore, forms abundant, accessible donor material for marsh rehabilitation and creation work in both relatively fresh and brackish wetlands. Plasticity, rather than narrow, genetically-fixed response seems to have been selected for in the Puget Trough wetlands. Hence in most cases, *C. lyngbyei* transplanted without careful attention to the matching of donor and transfer habitats may yield high aerial biomass. Some genetic divergence, however, may occur in individual populations such that particular sea sedge stands may always have greater yields than others. Moreover, *C. lyngbyei* from areas of consistently low salinities may have reduced vigor if transfered to wetlands characterized by substantially higher salinities. Only examination of each population on an individual basis will allow a reliable prediction of vigor after transfer to another site. *C. lyngbyei* seeds from different wetlands may differ in germination response, but since artificial colonization is primarily by rhizome extension, this may not be a consideration of grave importance in wetland rehabilitation projects.

CHAPTER VI

CONCLUSIONS

A field survey demonstrated that the morphological characteristics of the Squamish, Skagit and Nanaimo *Carex lyngbyei* varied in response to environmental heterogeneity on the meso–scale between local river deltas and on the micro–scale within each delta. In natural field conditions, generally, shoot height and biomass per shoot decreased, while shoot density increased, with increased soil water salinity. Loss of aboveground biomass and photosynthetic area was offset by increased shoot densities. As shoot density increased, investment per shoot decreased. Shoot height varied in a complex manner within each wetland such that distinct short and tall growth forms were not often evident. For this reason the tall and short form terminology should be used with caution. Flowering shoots per unit biomass varied unpredictably and was not correlated with any abiotic factors measured in this study.

The truncated reciprocal transplant experiment indicated that variation in shoot height, shoot density, aboveground biomass and biomass per shoot is primarily ecophenic. Differences in these four variables were attributable to interactions among the native wetland, the transfer wetland, and the transfer site elevation.

The Squamish channel edge and elevated flats *C. lyngbyei* differed significantly in height, aerial biomass and biomass per shoot despite being separated by just a few meters. The differences were maintained over the course of the experiment. This suggests that genetic divergence has occurred between these two habitats. A transplantation experiment run over several growing seasons is needed to determine whether this response is influenced by buffering by underground reserves. The height forms recognized by several researchers were associated with genotypic variation in that these channel edge and elevated flats shoots were the only ones readily identifiable as "tall" and "short" forms.

The shoot density pattern seen in the field survey was complicated in the transplantation experiment by the response of all the Squamish shoots and of the Nanaimo salt shoots. Each of these samples had greater densities at their native river delta than at the alien, transfer river delta. This is interpreted as a genetically–fixed response to the environment.

A germination experiment demonstrated that seeds from all Squamish, Skagit and Nanaimo test populations of *Carex lyngbyei* had maximum germination in fresh water, reduced germination in 5 ppt and virtually no germination in salinities ≥ 10 ppt. After a return to fresh water, percent germination rebounded to levels equivalent or just below the original fresh water treatment. The timing of germination of the Squamish and Skagit seeds in fresh water after exposure to higher salinities was significantly different, in that the germination of the Squamish seeds was delayed compared to that of the Skagit seeds. These responses are in accordance with the salinity regimes of the native wetlands. Germination would occur in both river deltas when the probability of encountering low salinities is highest. Habitat–correlated genetic differentiation, thus, seems to have occurred in terms of the speed of germination in fresh water, but not in terms of percent germination at any salinity level.

The results indicate that genetic divergence may occur in discrete *Carex lyngbyei* populations, but the populations in which it may appear cannot be predicted from an examination of the physical environment. Sea sedge transplanted in marsh rehabilitation and creation projects generally will be able to adjust to the environment of the transfer site. If the transplanted material is drawn from populations in which such divergence has occurred, however, low aboveground production and mortality may result. This is likely to happen only when material from deltas with consistently low growing season salinities is transfered to higher salinity sites.

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The raw data from the germination experiment are presented below. The variables represented in the data are as follows:

Column 1:
>   Native River delta:
>   1 = Nanaimo River delta
>   2 = Skagit River delta
>   3 = Squamish River delta

Column 2:
>   Native site elevation:
>   1 = high
>   2 = low

Column 3:
>   Native site salinity:
>   1 = relatively saline
>   2 = relatively fresh

Column 4:
>   Replicate number

Column 6:
>   Salinity treatment:
>   1 = Phase I, 0 ppt salt
>   2 = Phase I, 5 ppt salt
>   3 = Phase I, 10 ppt salt
>   4 = Phase I, 15 ppt salt
>   5 = Phase I, 30 ppt salt
>   6 = Phase II, fresh water after immersion in 5 ppt salt.
>   7 = Phase II, fresh water after immersion in 10 ppt salt.
>   8 = Phase II, fresh water after immersion in 15 ppt salt.
>   9 = Phase II, fresh water after immersion in 30 ppt salt.

Column 8/9: The number of seeds that germinated up to the first counting period.

Column 11/12: The number of seeds that germinated between the first and second counting periods.

Column 14/15: The number of seeds that germinated between the second and third counting periods.

Column 17/18: The number of seeds that germinated between the third and fourth counting periods.

Column 20/21: The number of seeds that germinated between the fourth and fifth counting periods.

Column 23/24: The number of seeds that germinated between the fifth and sixth counting periods.

Column 26/27: The number of seeds that germinated between the sixth and seventh counting periods.

Column 29/30: The number of seeds that germinated between the seventh and eighth counting periods.

Column 32/33: The number of seeds that germinated between the eighth and ninth counting periods.

Column 35/36: The number of seeds that germinated between the ninth and tenth counting periods.

Column 38/39: The number of seeds that germinated between the tenth and eleventh counting periods.

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1111  1  00  00  06  01  00  00  00  00  00  00  00
1112  1  00  00  00  00  00  00  00  00  00  00  00
1121  1  00  00  02  00  03  00  00  00  00  00  00
1122  1  00  00  00  01  01  00  00  00  00  00  00
1123  1  00  00  00  02  00  01  01  00  00  00  00
1124  1  00  00  00  00  01  00  00  01  00  00  00
1211  1  00  00  00  00  00  00  00  00  00  00  00
1212  1  00  00  00  00  00  00  00  00  00  00  00
1111  2  00  00  00  00  00  00  00  02  00  00  00
1112  2  00  00  00  00  00  00  00  00  00  00  00
1121  2  00  00  00  00  00  01  00  00  00  00  00
1122  2  00  00  00  00  00  00  00  00  00  00  00
1123  2  00  00  00  00  00  00  00  00  00  00  00
1124  2  00  00  00  00  00  00  00  00  00  00  00
1211  2  00  00  00  00  00  00  00  00  00  00  00
1212  2  00  00  00  00  00  00  00  00  00  00  00
1111  3  00  00  00  00  00  00  00  00  00  00  00
1112  3  00  00  00  00  00  00  00  00  00  00  00
1121  3  00  00  00  00  00  00  00  00  00  00  00
1122  3  00  00  00  00  00  00  00  00  00  00  00
1123  3  00  00  00  00  00  00  00  00  00  00  00
1124  3  00  00  00  00  00  00  00  00  00  00  00
1211  3  00  00  00  00  00  00  00  00  00  00  00
1212  3  00  00  00  00  00  00  00  00  00  00  00
1111  4  00  00  00  00  00  00  00  00  00  00  00
1112  4  00  00  00  00  00  00  00  00  00  00  00
1121  4  00  00  00  00  00  00  00  00  00  00  00
1122  4_ 00  00  00  00  00  00  00  00  00  00  00
1123  4  00  00  00  00  00  00  00  00  00  00  00
1124  4  00  00  00  00  00  00  00  00  00  00  00
1211  4  00  00  00  00  00  00  00  00  00  00  00
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3224	9	00	00	00	06	04	06	04	00	01	00	00

APPENDIX II

The germination data were analysed using a GLIM Survival Analysis technique. A Weibull distribution with a shape parameter of $\alpha = 1.77216$ was fitted to the Phase I data, and an exponential Weibull model was constructed for the Phase II data.

The fitted models constructed for both phases of the experiment involved 15 estimated coefficients. The models are presented below along with the standard errors of the estimated coeffients. These are followed by an explanation of the coefficient code names.

Phase I fitted model:

$G(t) = 1.72216*\log(t) - 78.64[1] + 90.86*DONM2[2] + 134.6*DONM3[3] \; 0.3607*TSUB[4] +$

$0.04648*TSU2[5] - 0.001802*TSU3[6] + 0.0000151*TSU4[7] \; 0.3838*TSAL[8] - 4.738*SPSA[9] +$

$9.748*SUSA[10] - 12.62*WISA[11] - 0.3774*SPSU[12] + 0.5645*SPWI[13] + 0.5435*SUWI[14]$

where the standard errors are:

[1]38.59, [2]40.09, [3]64.5, [4]0.3541, [5]0.04295, [6]0.001918, [7]0.00001679, [8]0.01434, [9]5.875, [10]4.668, [11]2.518, [12]0.3140, [13]0.3373, [14]0.3789

Phase II fitted model:

$G(t) = 1.000*\log(t) - 5.308[1] + 0.1830*DONM2[2] - 2.737*DONM3[3] + 0.5028*TSUB[4] -$

$0.039*TSU2[5] + 0.0009091*TSU3[6] - 0.000006218*TSU4[7] + 0.008167*D2TS[8] - 0.01391*D3TS[9] -$

$0.1644*SUSA[10] + 0.3087WISA[11]$

where the standard errors are:

[1]0.3122, [2]0.3598, [3]0.6236, [4]0.03081, [5]0.001937, [6]0.00004267, [7]0.0000002872, [8]0.003156, [9]0.002856, [10]0.02826, [11]0.02857

The code names stand for:

TSAL = Treatment salinity (0, 5, 10, 15, or 30 ppt)

TOBS = Time of observation (in days after initiation of Phase I or II)

TSUB = Percent annual submergence

TSU2 = $TSUB^2$

TSU3 = $TSUB^3$

TSU4 = $TSUB^4$

SPSA = Spring salinity

SUSA = Summer salinity

WISA = Winter salinity

SPSU = SPSA*SUSA

SPWI = SPSA*WISA

SUWI = SUSA*WISA

D2TS = DONM2*TSAL

D3TS = DONM3*TSAL

DONM2 = Skagit seed variable – DONM2=1 if from the Skagit River delta, DONM2=0 if

otherwise

DONM3 = Squamish seed variable – DONM3=1 if from the Squamish Riv delta, DONM3=0

if otherwise

The first two files presented below (G1, G2) contain the consolidated data files used in the GLIM analysis. Each contain 9 variables. The first variable is the seeds' native river delta. The second is the treatment salinity, the third is the counting period. The fourth variable is the percent annual submergence level of the native site. The next three variables are the spring, summer and winter salinities of the native sites, respectively. The eighth variable refers to the phase (0 = Phase I, 1 = Phase II). The final variable denotes the number of seeds left ungerminated at that counting period.

The second two files presented below (Phase I, Phase II) contain the elements of the vector X(betahat) which equals $G(t) - 1.72216*\log(t)$ for Phase I and $G(t) - \log(t)$ for Phase

II as the first variable. The coefficients 1.72216 and 1.00 respectively are the fitted shape parameters of the fitted baseline Weibull distribution of germination rate. G(t) is the fitted log(log(1/Prob that germination will occur after t)) Variable two is the estimated standard error of variable one. Variable four is the fitted expected time of germination for each data case; variables three and five are lower and upper 67% confidence limits for variable four, based on variable 1 ± variable 2.

File G1:

1	0	9	10	15	22	7	0	43
1	0	9	10	15	22	7	0	50
1	0	9	0	12	17	12	0	45
1	0	9	0	12	17	12	0	48
1	0	9	0	12	17	12	0	46
1	0	9	0	12	17	12	0	48
1	0	9	35	13	20	7	0	50
1	0	9	35	13	20	7	0	50
1	5	9	10	15	22	7	0	48
1	5	9	10	15	22	7	0	50
1	5	9	0	12	17	12	0	49
1	5	9	0	12	17	12	0	50
1	5	9	0	12	17	12	0	50
1	5	9	0	12	17	12	0	50
1	5	9	35	13	20	7	0	50
1	5	9	35	13	20	7	0	50
1	10	9	10	15	22	7	0	50
1	10	9	10	15	22	7	0	50
1	10	9	0	12	17	12	0	50
1	10	9	0	12	17	12	0	50
1	10	9	0	12	17	12	0	50
1	10	9	0	12	17	12	0	50
1	10	9	35	13	20	7	0	50
1	10	9	35	13	20	7	0	50
1	15	9	10	15	22	7	0	50
1	15	9	10	15	22	7	0	50
1	15	9	0	12	17	12	0	50
1	15	9	0	12	17	12	0	50
1	15	9	0	12	17	12	0	50
1	15	9	0	12	17	12	0	50
1	15	9	35	13	20	7	0	50
1	15	9	35	13	20	7	0	50
1	30	9	10	15	22	7	0	50
1	30	9	10	15	22	7	0	50
1	30	9	0	12	17	12	0	50

1	30	9	0	12	17	12	0	50
1	30	9	0	12	17	12	0	50
1	30	9	0	12	17	12	0	50
1	30	9	35	13	20	7	0	50
1	30	9	35	13	20	7	0	50
2	0	9	7	1	5	6	0	21
2	0	9	7	1	5	6	0	13
2	0	9	7	1	5	6	0	7
2	0	9	7	1	5	6	0	6
2	0	9	3	0	2	3	0	27
2	0	9	3	0	2	3	0	37
2	0	9	3	0	2	3	0	25
2	0	9	3	0	2	3	0	31
2	0	9	9	0	1	2	0	16
2	0	9	9	0	1	2	0	22
2	0	9	9	0	1	2	0	10
2	0	9	9	0	1	2	0	22
2	5	9	7	1	5	6	0	43
2	5	9	7	1	5	6	0	37
2	5	9	7	1	5	6	0	40
2	5	9	7	1	5	6	0	26
2	5	9	3	0	2	3	0	36
2	5	9	3	0	2	3	0	44
2	5	9	3	0	2	3	0	34
2	5	9	3	0	2	3	0	42
2	5	9	9	0	1	2	0	44
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2	10	9	7	1	5	6	0	50
2	10	9	7	1	5	6	0	50
2	10	9	7	1	5	6	0	50
2	10	9	3	0	2	3	0	50
2	10	9	3	0	2	3	0	50
2	10	9	3	0	2	3	0	50
2	10	9	3	0	2	3	0	50
2	10	9	9	0	1	2	0	50
2	10	9	9	0	1	2	0	50
2	10	9	9	0	1	2	0	48
2	10	9	9	0	1	2	0	49
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2	15	9	7	1	5	6	0	50
2	15	9	7	1	5	6	0	50
2	15	9	7	1	5	6	0	50
2	15	9	3	0	2	3	0	50
2	15	9	3	0	2	3	0	49
2	15	9	3	0	2	3	0	50
2	15	9	3	0	2	3	0	50
2	15	9	9	0	1	2	0	50
2	15	9	9	0	1	2	0	50
2	15	9	9	0	1	2	0	50
2	15	9	9	0	1	2	0	50

2	30	9	7	1	5	6	0	50
2	30	9	7	1	5	6	0	50
2	30	9	7	1	5	6	0	50
2	30	9	7	1	5	6	0	50
2	30	9	3	0	2	3	0	50
2	30	9	3	0	2	3	0	50
2	30	9	3	0	2	3	0	49
2	30	9	3	0	2	3	0	50
2	30	9	9	0	1	2	0	50
2	30	9	9	0	1	2	0	50
2	30	9	9	0	1	2	0	49
2	30	9	9	0	1	2	0	50
3	0	9	10	12	5	17	0	6
3	0	9	10	12	5	17	0	10
3	0	9	10	12	5	17	0	8
3	0	9	10	12	5	17	0	9
3	0	9	60	2	0	1	0	13
3	0	9	60	2	0	1	0	6
3	0	9	60	2	0	1	0	18
3	0	9	60	2	0	1	0	11
3	0	9	20	12	6	17	0	33
3	0	9	20	12	6	17	0	27
3	0	9	20	12	6	17	0	32
3	0	9	20	12	6	17	0	36
3	0	9	75	2	0	2	0	19
3	0	9	75	2	0	2	0	8
3	0	9	75	2	0	2	0	33
3	0	9	75	2	0	2	0	29
3	5	9	10	12	5	17	0	50
3	5	9	10	12	5	17	0	50
3	5	9	10	12	5	17	0	50
3	5	9	10	12	5	17	0	50
3	5	9	60	2	0	1	0	44
3	5	9	60	2	0	1	0	47
3	5	9	60	2	0	1	0	47
3	5	9	60	2	0	1	0	36
3	5	9	20	12	6	17	0	50
3	5	9	20	12	6	17	0	47
3	5	9	20	12	6	17	0	50
3	5	9	20	12	6	17	0	48
3	5	9	75	2	0	2	0	46
3	5	9	75	2	0	2	0	50
3	5	9	75	2	0	2	0	50
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3	10	9	60	2	0	1	0	50
3	10	9	20	12	6	17	0	50

3	10	9	20	12	6	17	0	50
3	10	9	20	12	6	17	0	50
3	10	9	20	12	6	17	0	50
3	10	9	75	2	0	2	0	50
3	10	9	75	2	0	2	0	50
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3	15	9	60	2	0	1	0	50
3	15	9	20	12	6	17	0	50
3	15	9	20	12	6	17	0	50
3	15	9	20	12	6	17	0	50
3	15	9	20	12	6	17	0	50
3	15	9	75	2	0	2	0	49
3	15	9	75	2	0	2	0	50
3	15	9	75	2	0	2	0	50
3	15	9	75	2	0	2	0	50
3	30	9	10	12	5	17	0	50
3	30	9	10	12	5	17	0	50
3	30	9	10	12	5	17	0	50
3	30	9	10	12	5	17	0	50
3	30	9	60	2	0	1	0	50
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3	30	9	20	12	6	17	0	50
3	30	9	20	12	6	17	0	50
3	30	9	20	12	6	17	0	50
3	30	9	20	12	6	17	0	50
3	30	9	75	2	0	2	0	50
3	30	9	75	2	0	2	0	50
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3	30	9	75	2	0	2	0	50
1	0	2	10	15	22	7	1	7
1	0	2	0	12	17	12	1	2
1	0	3	0	12	17	12	1	3
1	0	2	0	12	17	12	1	1
1	0	3	0	12	17	12	1	1
1	0	2	0	12	17	12	1	2
1	0	4	0	12	17	12	1	1
1	0	5	0	12	17	12	1	1
1	0	3	0	12	17	12	1	1
1	0	6	0	12	17	12	1	1
1	5	6	10	15	22	7	1	2
1	5	4	0	12	17	12	1	1
2	0	1	7	1	5	6	1	5
2	0	2	7	1	5	6	1	22

2	0	3	7	1	5	6	1	1
2	0	4	7	1	5	6	1	1
2	0	1	7	1	5	6	1	14
2	0	2	7	1	5	6	1	21
2	0	3	7	1	5	6	1	2
2	0	1	7	1	5	6	1	16
2	0	2	7	1	5	6	1	27
2	0	1	7	1	5	6	1	12
2	0	2	7	1	5	6	1	32
2	0	1	3	0	2	3	1	11
2	0	2	3	0	2	3	1	10
2	0	4	3	0	2	3	1	1
2	0	5	3	0	2	3	1	1
2	0	2	3	0	2	3	1	12
2	0	4	3	0	2	3	1	1
2	0	1	3	0	2	3	1	5
2	0	2	3	0	2	3	1	15
2	0	3	3	0	2	3	1	3
2	0	4	3	0	2	3	1	1
2	0	5	3	0	2	3	1	1
2	0	1	3	0	2	3	1	4
2	0	2	3	0	2	3	1	11
2	0	3	3	0	2	3	1	2
2	0	4	3	0	2	3	1	1
2	0	5	3	0	2	3	1	1
2	0	1	9	0	1	2	1	16
2	0	2	9	0	1	2	1	17
2	0	3	9	0	1	2	1	1
2	0	1	9	0	1	2	1	12
2	0	2	9	0	1	2	1	16
2	0	1	9	0	1	2	1	14
2	0	2	9	0	1	2	1	25
2	0	3	9	0	1	2	1	1
2	0	1	9	0	1	2	1	15
2	0	2	9	0	1	2	1	13
2	5	3	7	1	5	6	1	1
2	5	5	7	1	5	6	1	4
2	5	6	7	1	5	6	1	2
2	5	3	7	1	5	6	1	2
2	5	5	7	1	5	6	1	5
2	5	6	7	1	5	6	1	6
2	5	2	7	1	5	6	1	1
2	5	3	7	1	5	6	1	6
2	5	5	7	1	5	6	1	2
2	5	6	7	1	5	6	1	1
2	5	1	7	1	5	6	1	1
2	5	2	7	1	5	6	1	1
2	5	3	7	1	5	6	1	9
2	5	5	7	1	5	6	1	13
2	5	2	3	0	2	3	1	6
2	5	3	3	0	2	3	1	2
2	5	4	3	0	2	3	1	1
2	5	5	3	0	2	3	1	3

2	5	6	3	0	2	3	1	2
2	5	1	3	0	2	3	1	1
2	5	2	3	0	2	3	1	1
2	5	3	3	0	2	3	1	1
2	5	5	3	0	2	3	1	2
2	5	6	3	0	2	3	1	1
2	5	1	3	0	2	3	1	1
2	5	2	3	0	2	3	1	7
2	5	3	3	0	2	3	1	4
2	5	4	3	0	2	3	1	1
2	5	5	3	0	2	3	1	2
2	5	6	3	0	2	3	1	1
2	5	1	3	0	2	3	1	1
2	5	2	3	0	2	3	1	6
2	5	5	3	0	2	3	1	1
2	5	2	9	0	1	2	1	2
2	5	3	9	0	1	2	1	1
2	5	5	9	0	1	2	1	1
2	5	6	9	0	1	2	1	2
2	5	3	9	0	1	2	1	2
2	5	5	9	0	1	2	1	6
2	5	6	9	0	1	2	1	2
2	5	1	9	0	1	2	1	2
2	5	2	9	0	1	2	1	1
2	5	3	9	0	1	2	1	1
2	5	5	9	0	1	2	1	17
2	5	6	9	0	1	2	1	5
2	5	3	9	0	1	2	1	1
2	5	5	9	0	1	2	1	2
2	10	1	9	0	1	2	1	2
2	10	1	9	0	1	2	1	1
2	15	1	3	0	2	3	1	1
2	30	1	3	0	0	0	1	1
2	30	1	9	0	0	0	1	1
3	0	2	10	12	0	0	1	18
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3	0	4	10	12	0	0	1	3
3	0	2	10	12	0	0	1	32
3	0	3	10	12	0	0	1	4
3	0	4	10	12	0	0	1	4
3	0	1	10	12	0	0	1	1
3	0	2	10	12	0	0	1	34
3	0	3	10	12	0	0	1	2
3	0	4	10	12	0	0	1	3
3	0	5	10	12	0	0	1	2
3	0	2	10	12	0	0	1	36
3	0	3	10	12	0	0	1	5
3	0	2	60	2	0	0	1	35
3	0	3	60	2	0	0	1	2
3	0	2	60	2	0	0	1	36
3	0	3	60	2	0	0	1	8
3	0	2	60	2	0	0	1	19
3	0	3	60	2	0	0	1	10

3	0	4	60	2	0	0	1	3
3	0	2	60	2	0	0	1	30
3	0	3	60	2	0	0	1	6
3	0	4	60	2	0	0	1	3
3	0	2	20	12	0	0	1	13
3	0	3	20	12	0	0	1	3
3	0	5	20	12	0	0	1	1
3	0	2	20	12	0	0	1	15
3	0	3	20	12	0	0	1	4
3	0	4	20	12	0	0	1	4
3	0	2	20	12	0	0	1	10
3	0	3	20	12	0	0	1	8
3	0	2	20	12	0	0	1	11
3	0	3	20	12	0	0	1	2
3	0	4	20	12	0	0	1	1
3	0	2	75	2	0	0	1	15
3	0	3	75	2	0	0	1	16
3	0	2	75	2	0	0	1	34
3	0	3	75	2	0	0	1	8
3	0	2	75	2	0	0	1	10
3	0	3	75	2	0	0	1	6
3	0	4	75	2	0	0	1	1
3	0	2	75	2	0	0	1	1
3	0	3	75	2	0	0	1	13
3	0	4	75	2	0	0	1	5
3	0	5	75	2	0	0	1	2
3	5	5	60	2	0	0	1	2
3	5	6	60	2	0	0	1	4
3	5	5	60	2	0	0	1	1
3	5	6	60	2	0	0	1	2
3	5	6	60	2	0	0	1	3
3	5	6	60	2	0	0	1	14
3	5	1	20	12	0	0	1	1
3	5	6	20	12	0	0	1	2
3	5	3	20	12	0	0	1	1
3	5	4	20	12	0	0	1	1
3	5	6	75	2	0	0	1	4
3	10	1	10	12	0	0	1	1

File G2:

1	5	9	10	15	22	7	0	48
1	5	9	10	15	22	7	0	48
1	5	9	0	12	17	12	0	48
1	5	9	0	12	17	12	0	44
1	5	9	0	12	17	12	0	50
1	5	9	0	12	17	12	0	46
1	5	9	35	13	20	7	0	50
1	5	9	35	13	20	7	0	50

1	10	9	10	15	22	7	0	45
1	10	9	10	15	22	7	0	45
1	10	9	0	12	17	12	0	42
1	10	9	0	12	17	12	0	43
1	10	9	0	12	17	12	0	46
1	10	9	0	12	17	12	0	43
1	10	9	35	13	20	7	0	50
1	10	9	35	13	20	7	0	50
1	15	9	10	15	22	7	0	46
1	15	9	10	15	22	7	0	50
1	15	9	0	12	17	12	0	41
1	15	9	0	12	17	12	0	42
1	15	9	0	12	17	12	0	43
1	15	9	0	12	17	12	0	47
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File Phase I:

-5.862	0.3336	22.10	26.82	32.55
-5.862	0.3336	22.10	26.82	32.55
-6.127	0.2676	26.77	31.27	36.52
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-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-14.67	16.19	0.3689	4464.	0.5400E+08

-14.67	16.19	0.3689	4464.	0.5400E+08
-7.781	0.3385	67.14	81.73	99.48
-7.781	0.3385	67.14	81.73	99.48
-8.045	0.2737	81.28	95.28	111.7
-8.045	0.2737	81.28	95.28	111.7
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-16.59	16.19	1.124	0.1360E+05	0.1646E+09
-16.59	16.19	1.124	0.1360E+05	0.1646E+09
-9.700	0.3580	202.3	249.0	306.6
-9.700	0.3580	202.3	249.0	306.6
-9.964	0.2975	244.3	290.3	345.1
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-18.51	16.19	3.424	0.4144E+05	0.5016E+09
-18.51	16.19	3.424	0.4144E+05	0.5016E+09
-11.62	0.3899	605.1	758.8	951.6
-11.62	0.3899	605.1	758.8	951.6
-11.88	0.3353	728.1	884.6	1075.
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-20.43	16.19	10.43	0.1263E+06	0.1529E+10
-20.43	16.19	10.43	0.1263E+06	0.1529E+10
-17.38	0.5341	0.1574E+05	0.2147E+05	0.2927E+05
-17.38	0.5341	0.1574E+05	0.2147E+05	0.2927E+05
-17.64	0.4957	0.1877E+05	0.2503E+05	0.3337E+05
-17.64	0.4957	0.1877E+05	0.2503E+05	0.3337E+05
-17.64	0.4957	0.1877E+05	0.2503E+05	0.3337E+05
-17.64	0.4957	0.1877E+05	0.2503E+05	0.3337E+05
-26.18	16.20	294.3	0.3573E+07	0.4336E+11
-26.18	16.20	294.3	0.3573E+07	0.4336E+11
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
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-3.600	0.9081E-01	6.838	7.208	7.599
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-2.885	0.7854E-01	4.548	4.760	4.983
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-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
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-5.518	0.1055	20.66	21.96	23.35
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-5.518	0.1055	20.66	21.96	23.35
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-4.804	0.8913E-01	13.77	14.51	15.28
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-6.373	0.1348	33.35	36.07	39.01
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-7.437	0.1559	61.14	66.93	73.27
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-7.437	0.1559	61.14	66.93	73.27
-7.437	0.1559	61.14	66.93	73.27
-6.723	0.1414	40.71	44.20	47.98
-6.723	0.1414	40.71	44.20	47.98
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-8.292	0.1997	97.88	109.9	123.4
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-8.292	0.1997	97.88	109.9	123.4
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-9.356	0.2185	179.6	203.9	231.5
-9.356	0.2185	179.6	203.9	231.5
-9.356	0.2185	179.6	203.9	231.5
-9.356	0.2185	179.6	203.9	231.5
-8.642	0.2058	119.5	134.7	151.8
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-8.642	0.2058	119.5	134.7	151.8
-8.642	0.2058	119.5	134.7	151.8
-14.05	0.4083	2453.	3109.	3941.
-14.05	0.4083	2453.	3109.	3941.
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-14.05	0.4083	2453.	3109.	3941.
-15.11	0.4240	4510.	5770.	7380.
-15.11	0.4240	4510.	5770.	7380.
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-15.11	0.4240	4510.	5770.	7380.
-14.40	0.4136	2997.	3810.	4844.
-14.40	0.4136	2997.	3810.	4844.
-14.40	0.4136	2997.	3810.	4844.
-14.40	0.4136	2997.	3810.	4844.
-28.67	13.73	5215.	0.1513E+08	0.4389E+11
-28.67	13.73	5215.	0.1513E+08	0.4389E+11
-28.67	13.73	5215.	0.1513E+08	0.4389E+11
-28.67	13.73	5215.	0.1513E+08	0.4389E+11
-12.88	2.064	476.6	1580.	5237.
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-12.88	2.064	476.6	1580.	5237.
-12.88	2.064	476.6	1580.	5237.
-14.21	10.86	6.228	3420.	0.1878E+07
-14.21	10.86	6.228	3420.	0.1878E+07
-14.21	10.86	6.228	3420.	0.1878E+07
-14.21	10.86	6.228	3420.	0.1878E+07
-24.62	4.128	0.1308E+06	0.1437E+07	0.1580E+08

-24.62	4.128	0.1308E+06	0.1437E+07	0.1580E+08
-24.62	4.128	0.1308E+06	0.1437E+07	0.1580E+08
-24.62	4.128	0.1308E+06	0.1437E+07	0.1580E+08
-30.59	13.73	0.1588E+05	0.4610E+08	0.1339E+12
-30.59	13.73	0.1588E+05	0.4610E+08	0.1339E+12
-30.59	13.73	0.1588E+05	0.4610E+08	0.1339E+12
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-14.80	2.076	1442.	4814.	0.1607E+05
-14.80	2.076	1442.	4814.	0.1607E+05
-14.80	2.076	1442.	4814.	0.1607E+05
-14.80	2.076	1442.	4814.	0.1607E+05
-16.13	10.86	18.98	0.1042E+05	0.5722E+07
-16.13	10.86	18.98	0.1042E+05	0.5722E+07
-16.13	10.86	18.98	0.1042E+05	0.5722E+07
-16.13	10.86	18.98	0.1042E+05	0.5722E+07
-26.53	4.140	0.3957E+06	0.4380E+07	0.4848E+08
-26.53	4.140	0.3957E+06	0.4380E+07	0.4848E+08
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-26.53	4.140	0.3957E+06	0.4380E+07	0.4848E+08
-32.51	13.73	0.4833E+05	0.1405E+09	0.4084E+12
-32.51	13.73	0.4833E+05	0.1405E+09	0.4084E+12
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-32.51	13.73	0.4833E+05	0.1405E+09	0.4084E+12
-16.72	2.091	4356.	0.1467E+05	0.4939E+05
-16.72	2.091	4356.	0.1467E+05	0.4939E+05
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-16.72	2.091	4356.	0.1467E+05	0.4939E+05
-18.05	10.86	57.80	0.3175E+05	0.1744E+08
-18.05	10.86	57.80	0.3175E+05	0.1744E+08
-18.05	10.86	57.80	0.3175E+05	0.1744E+08
-18.05	10.86	57.80	0.3175E+05	0.1744E+08
-28.45	4.154	0.1196E+07	0.1335E+08	0.1489E+09
-28.45	4.154	0.1196E+07	0.1335E+08	0.1489E+09
-28.45	4.154	0.1196E+07	0.1335E+08	0.1489E+09
-28.45	4.154	0.1196E+07	0.1335E+08	0.1489E+09
-34.43	13.74	0.1471E+06	0.4280E+09	0.1246E+13
-34.43	13.74	0.1471E+06	0.4280E+09	0.1246E+13
-34.43	13.74	0.1471E+06	0.4280E+09	0.1246E+13
-34.43	13.74	0.1471E+06	0.4280E+09	0.1246E+13
-18.64	2.108	0.1314E+05	0.4469E+05	0.1520E+06
-18.64	2.108	0.1314E+05	0.4469E+05	0.1520E+06
-18.64	2.108	0.1314E+05	0.4469E+05	0.1520E+06
-18.64	2.108	0.1314E+Q5	0.4469E+05	0.1520E+06
-19.97	10.87	176.0	0.9675E+05	0.5318E+08
-19.97	10.87	176.0	0.9675E+05	0.5318E+08
-19.97	10.87	176.0	0.9675E+05	0.5318E+08
-19.97	10.87	176.0	0.9675E+05	0.5318E+08
-30.37	4.168	0.3615E+07	0.4067E+08	0.4574E+09
-30.37	4.168	0.3615E+07	0.4067E+08	0.4574E+09
-30.37	4.168	0.3615E+07	0.4067E+08	0.4574E+09
-30.37	4.168	0.3615E+07	0.4067E+08	0.4574E+09
-40.18	13.75	0.4139E+07	0.1211E+11	0.3543E+14
-40.18	13.75	0.4139E+07	0.1211E+11	0.3543E+14

-40.18	13.75	0.4139E+07	0.1211E+11	0.3543E+14
-40.18	13.75	0.4139E+07	0.1211E+11	0.3543E+14
-24.39	2.173	0.3581E+06	0.1264E+07	0.4465E+07
-24.39	2.173	0.3581E+06	0.1264E+07	0.4465E+07
-24.39	2.173	0.3581E+06	0.1264E+07	0.4465E+07
-24.39	2.173	0.3581E+06	0.1264E+07	0.4465E+07
-25.72	10.87	4962.	0.2737E+07	0.1510E+10
-25.72	10.87	4962.	0.2737E+07	0.1510E+10
-25.72	10.87	4962.	0.2737E+07	0.1510E+10
-25.72	10.87	4962.	0.2737E+07	0.1510E+10
-36.13	4.218	0.9935E+08	0.1150E+10	0.1332E+11
-36.13	4.218	0.9935E+08	0.1150E+10	0.1332E+11
-36.13	4.218	0.9935E+08	0.1150E+10	0.1332E+11
-36.13	4.218	0.9935E+08	0.1150E+10	0.1332E+11
-5.862	0.3336	22.10	26.82	32.55
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-6.127	0.2676	26.77	31.27	36.52
-7.781	0.3385	67.14	81.73	99.48
-8.045	0.2737	81.28	95.28	111.7
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-2.535	0.7489E-01	3.720	3.885	4.058
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599
-3.600	0.9081E-01	6.838	7.208	7.599

-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-2.885	0.7854E-01	4.548	4.760	4.983
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-4.454	0.8216E-01	11.29	11.84	12.42
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-5.518	0.1055	20.66	21.96	23.35
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28

-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-4.804	0.8913E-01	13.77	14.51	15.28
-6.723	0.1414	40.71	44.20	47.98
-6.723	0.1414	40.71	44.20	47.98
-9.356	0.2185	179.6	203.9	231.5
-0.5025E-02	1.000	0.5002	0.8940	1.598
0.9659E-02	0.9859	0.5000	0.8864	1.571
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.514	0.7715E-01	2.053	2.147	2.245
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.390	0.7539E-01	1.912	1.998	2.087
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.525	0.1140	2.023	2.161	2.309
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427
-1.632	0.9285E-01	2.179	2.299	2.427

-1.632	0.9285E-01	2.179	2.299	2.427
-3.309	0.9828E-01	5.750	6.088	6.446
-3.309	0.9828E-01	5.750	6.088	6.446
-3.309	0.9828E-01	5.750	6.088	6.446
-3.309	0.9828E-01	5.750	6.088	6.446
-3.309	0.9828E-01	5.750	6.088	6.446
-3.309	0.9828E-01	5.750	6.088	6.446
-3.444	0.1337	6.094	6.586	7.118
-3.444	0.1337	6.094	6.586	7.118
-3.444	0.1337	6.094	6.586	7.118
-3.444	0.1337	6.094	6.586	7.118
-3.551	0.1164	6.549	7.007	7.496
-5.351	0.1628	18.13	19.93	21.91
-7.388	0.2329	56.83	65.05	74.47

File Phase II:

-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-6.988	0.1797	905.4	1084.	1297.
-6.988	0.1797	905.4	1084.	1297.
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-6.988	0.1797	905.4	1084.	1297.
-6.988	0.1797	905.4	1084.	1297.
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-6.988	0.1797	905.4	1084.	1297.
-6.988	0.1797	905.4	1084.	1297.
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-6.988	0.1797	905.4	1084.	1297.
-6.988	0.1797	905.4	1084.	1297.

-2.167	0.5647E-01	8.249	8.728	9.235
-2.167	0.5647E-01	8.249	8.728	9.235
-2.167	0.5647E-01	8.249	8.728	9.235
-2.167	0.5647E-01	8.249	8.728	9.235
-3.326	0.7453E-01	25.84	27.84	29.99
-3.326	0.7453E-01	25.84	27.84	29.99
-3.326	0.7453E-01	25.84	27.84	29.99
-3.326	0.7453E-01	25.84	27.84	29.99
-2.663	0.6201E-01	13.48	14.34	15.26
-2.663	0.6201E-01	13.48	14.34	15.26
-2.663	0.6201E-01	13.48	14.34	15.26
-2.663	0.6201E-01	13.48	14.34	15.26
-2.126	0.4862E-01	7.981	8.379	8.796
-2.126	0.4862E-01	7.981	8.379	8.796
-2.126	0.4862E-01	7.981	8.379	8.796
-2.126	0.4862E-01	7.981	8.379	8.796
-3.285	0.6878E-01	24.95	26.72	28.62
-3.285	0.6878E-01	24.95	26.72	28.62
-3.285	0.6878E-01	24.95	26.72	28.62
-3.285	0.6878E-01	24.95	26.72	28.62
-2.622	0.5517E-01	13.03	13.76	14.55
-2.622	0.5517E-01	13.03	13.76	14.55
-2.622	0.5517E-01	13.03	13.76	14.55
-2.622	0.5517E-01	13.03	13.76	14.55
-2.085	0.4513E-01	7.689	8.044	8.415
-2.085	0.4513E-01	7.689	8.044	8.415
-2.085	0.4513E-01	7.689	8.044	8.415
-2.085	0.4513E-01	7.689	8.044	8.415
-3.245	0.6637E-01	24.01	25.65	27.41
-3.245	0.6637E-01	24.01	25.65	27.41
-3.245	0.6637E-01	24.01	25.65	27.41
-3.245	0.6637E-01	24.01	25.65	27.41
-2.581	0.5235E-01	12.54	13.21	13.92
-2.581	0.5235E-01	12.54	13.21	13.92
-2.581	0.5235E-01	12.54	13.21	13.92
-2.581	0.5235E-01	12.54	13.21	13.92
-1.962	0.6358E-01	6.678	7.116	7.583
-1.962	0.6358E-01	6.678	7.116	7.583
-1.962	0.6358E-01	6.678	7.116	7.583
-1.962	0.6358E-01	6.678	7.116	7.583
-3.122	0.8011E-01	20.95	22.69	24.59
-3.122	0.8011E-01	20.95	22.69	24.59
-3.122	0.8011E-01	20.95	22.69	24.59
-3.122	0.8011E-01	20.95	22.69	24.59
-2.459	0.6941E-01	10.91	11.69	12.53
-2.459	0.6941E-01	10.91	11.69	12.53
-2.459	0.6941E-01	10.91	11.69	12.53
-2.459	0.6941E-01	10.91	11.69	12.53
-1.730	0.4949E-01	5.370	5.642	5.929
-1.730	0.4949E-01	5.370	5.642	5.929
-1.730	0.4949E-01	5.370	5.642	5.929
-1.730	0.4949E-01	5.370	5.642	5.929
-2.274	0.5555E-01	9.191	9.716	10.27

-2.274	0.5555E-01	9.191	9.716	10.27
-2.274	0.5555E-01	9.191	9.716	10.27
-2.274	0.5555E-01	9.191	9.716	10.27
-3.138	0.7005E-01	21.50	23.06	24.74
-3.138	0.7005E-01	21.50	23.06	24.74
-3.138	0.7005E-01	21.50	23.06	24.74
-3.138	0.7005E-01	21.50	23.06	24.74
-2.393	0.5633E-01	10.35	10.95	11.58
-2.393	0.5633E-01	10.35	10.95	11.58
-2.393	0.5633E-01	10.35	10.95	11.58
-2.393	0.5633E-01	10.35	10.95	11.58
-1.800	0.4320E-01	5.794	6.050	6.317
-1.800	0.4320E-01	5.794	6.050	6.317
-1.800	0.4320E-01	5.794	6.050	6.317
-1.800	0.4320E-01	5.794	6.050	6.317
-2.343	0.5021E-01	9.907	10.42	10.95
-2.343	0.5021E-01	9.907	10.42	10.95
-2.343	0.5021E-01	9.907	10.42	10.95
-2.343	0.5021E-01	9.907	10.42	10.95
-3.208	0.6608E-01	23.15	24.73	26.42
-3.208	0.6608E-01	23.15	24.73	26.42
-3.208	0.6608E-01	23.15	24.73	26.42
-3.208	0.6608E-01	23.15	24.73	26.42
-2.463	0.5110E-01	11.16	11.74	12.36
-2.463	0.5110E-01	11.16	11.74	12.36
-2.463	0.5110E-01	11.16	11.74	12.36
-2.463	0.5110E-01	11.16	11.74	12.36
-1.870	0.4113E-01	6.226	6.487	6.760
-1.870	0.4113E-01	6.226	6.487	6.760
-1.870	0.4113E-01	6.226	6.487	6.760
-1.870	0.4113E-01	6.226	6.487	6.760
-2.413	0.4863E-01	10.64	11.17	11.73
-2.413	0.4863E-01	10.64	11.17	11.73
-2.413	0.4863E-01	10.64	11.17	11.73
-2.413	0.4863E-01	10.64	11.17	11.73
-3.278	0.6507E-01	24.85	26.52	28.30
-3.278	0.6507E-01	24.85	26.52	28.30
-3.278	0.6507E-01	24.85	26.52	28.30
-3.278	0.6507E-01	24.85	26.52	28.30
-2.533	0.4959E-01	11.98	12.59	13.23
-2.533	0.4959E-01	11.98	12.59	13.23
-2.533	0.4959E-01	11.98	12.59	13.23
-2.533	0.4959E-01	11.98	12.59	13.23
-2.079	0.6015E-01	7.530	7.997	8.493
-2.079	0.6015E-01	7.530	7.997	8.493
-2.079	0.6015E-01	7.530	7.997	8.493
-2.079	0.6015E-01	7.530	7.997	8.493
-2.622	0.6592E-01	12.89	13.77	14.71
-2.622	0.6592E-01	12.89	13.77	14.71
-2.622	0.6592E-01	12.89	13.77	14.71
-2.622	0.6592E-01	12.89	13.77	14.71
-3.487	0.7928E-01	30.20	32.69	35.39
-3.487	0.7928E-01	30.20	32.69	35.39

-3.487	0.7928E-01	30.20	32.69	35.39
-3.487	0.7928E-01	30.20	32.69	35.39
-2.742	0.6670E-01	14.52	15.52	16.59
-2.742	0.6670E-01	14.52	15.52	16.59
-2.742	0.6670E-01	14.52	15.52	16.59
-2.742	0.6670E-01	14.52	15.52	16.59
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
-4.417	0.1101	74.23	82.87	92.52
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-4.417	0.1101	74.23	82.87	92.52
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
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-4.807	0.1866	101.5	122.4	147.5
-4.807	0.1866	101.5	122.4	147.5
-4.417	0.1101	74.23	82.87	92.52
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-4.417	0.1101	74.23	82.87	92.52

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-4.417	0.1101	74.23	82.87	92.52
-2.167	0.5647E-01	8.249	8.728	9.235
-2.167	0.5647E-01	8.249	8.728	9.235
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-3.326	0.7453E-01	25.84	27.84	29.99
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-2.663	0.6201E-01	13.48	14.34	15.26
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-2.126	0.4862E-01	7.981	8.379	8.796
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-2.581	0.5235E-01	12.54	13.21	13.92
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-2.463	0.5110E-01	11.16	11.74	12.36
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-1.870	0.4113E-01	6.226	6.487	6.760
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