CANADIAN THESES ON MICROFICHE

THÈSES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

Canada

NL 339 (r. 85/09)

National Library of Canada
Bibliothèque nationale du Canada

Ottawa, Canada
K1A 0N4

TC –

ISBN 0-315-31[illegible]-0

CANADIAN THESES ON MICROFICHE SERVICE – SERVICE DES THÈSES CANADIENNES SUR MICROFICHE

PERMISION TO MICROFILM – AUTORISATION DE MICROFILMER

• Please print or type – Écrire en lettres moulees ou dactylographier

AUTHOR – AUTEUR

Full Name of Author – Nom complet de l'auteur
[illegible]

Date of Birth – Date de naissance
[illegible]

Canadian Citizen – Citoyen canadien
☐ Yes Oui ☐ No Non

Country of Birth – Lieu de naissance
[illegible]

Permanent Address – Residence fixe
[illegible]

THESIS – THÈSE

Title of Thesis – Titre de la these
[illegible]
[illegible]

Degree for which thesis was presented
Grade pour lequel cette these fut presentee
[illegible]

Year this degree conferred
Annee d'obtention de ce grade
[illegible]

University – Universite
[illegible]

Name of Supervisor – Nom du directeur de these
[illegible]

AUTHORIZATION – AUTORISATION

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to **microfilm** this thesis and to **lend** or **sell copies of the film.**

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission

L'autorisation est par la presente accordee a la BIBLIOTHEQUE NATIONALE DU CANADA de **microfilmer** cette these et de **prêter** ou de **vendre des exemplaires du film.**

L'auteur se reserve les autres droits de publication ni la these ni de longs extraits de celle-ci ne doivent être imprimes ou autrement reproduits sans l'autorisation ecrite de l'auteur

ATTACH FORM TO THESIS – VEUILLEZ JOINDRE CE FORMULAIRE A LA THESE

Signature

Date
[illegible]

NL 91 (r. 84/03)

Canada

THE UNIVERSITY OF ALBERTA

"An autecological study of *Ruppia occidentalis* S. Wats. in three lakes of different salinities"

by

Brian C. Husband

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

IN

Plant Ecology

Botany

EDMONTON, ALBERTA

Spring 1985

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR	Brian C. Husband
TITLE OF THESIS	"An autecological study of *Ruppia occidentalis* S. Wats. in three lakes of different salinities"

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED Spring 1985

(SIGNED) ....

PERMANENT ADDRESS:

....

....

....

DATED 19

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "An autecological study of *Ruppia occidentalis* S. Wats. in three lakes of different salinities" submitted by Brian C. Husband in partial fulfilment of the requirements for the degree of Master of Science in Plant Ecology.

Michael Hickman
Supervisor

Charles Schweger
Mark Dale

Date 19 April 1985

Abstract

An ecological study was undertaken of the chemical constraints on the ecological distribution of *Ruppia occidentalis* S.Wats. The effects of solute source (substratum *versus* overlying water) and solute concentration on growth were investigated in a field survey and in measurements of biomass over one growing season in three lakes, Pigeon, Buffalo, and Miquelon, listed in order of increasing salinity. Field studies were supplemented with laboratory experiments. Also, plants were reciprocally transplanted and grown in controlled environmental conditions in the laboratory to identify the genetic component of variation observed in the field.

Growth among populations from three lakes was positively correlated with salinity. Individuals from the freshwater lake exhibited characters associated with moderate chemical deficiency, including decreased growth rate, decreased reproductive output and high root:shoot ratios. The frequency of occurrence and percentage cover of *Ruppia* within each lake reflects its growth and reproduction.

Solute concentration also influenced the major site of nutrient absorption in *Ruppia* individuals. Growth corresponded to the concentrations of the limiting solute (sulphate) in the water until at low concentrations; then growth increased due to absorption by the roots. Within-lake distributions of *Ruppia* became increasingly

substratum-specific with decreasing solute concentrations in the water. Colonization of a freshwater site was enhanced using solute-rich sediments. These trends support the hypothesis that the substratum becomes relatively more important in solute-poor water.

Differences in *Ruppia* growth between freshwater-lake and saline-lake populations grown in common environments indicate that variation among lakes may be, in part, genotypic. Significant differences occur, not in chemical tolerance, but in response to substratum salinity. Freshwater-lake plants exhibit root-dominated absorption, relative to saline-lake plants, and are consequently more successful in freshwater, with the appropriate substratum.

Acknowledgements

I express my deepest gratitude to Dr. Hickman for his guidance and support during these past years, and for the opportunity to become involved with aspects of his own research interests. Also I thank Drs. M. Dale, G. La Roi and C. Schweger for their constructive comments and suggestions.

This project would have been impossible without Kelly Ford, Jennifer Shamess and David Wiley who assisted in the field work and accompanied me while I was diving. I also thank Marianne Klemka for her field assistance as well as her valuable advice in the laboratory, and Rick Haag for the opportunity to work on the macrophyte survey and for permission to analyze portions of the results.

A special thankyou to those mentioned above and to friends such as Louise McBain, Stephen Downie, Larry Flanagan, Helen Kubiw, Pat Mash and Craig Richter for much support at various stages of the thesis.

Table of Contents

List of Tables

List of Figures

1. Introduction

Ecology is "...the scientific study of the interactions that determine the distribution and abundance of organisms" (Krebs 1978). Interactions such as between the abiotic and biotic factors of the environment and the organisms, which influence the four demographic processes of a species; birth, death, migration and immigration. Although changes in distributions occur through demographic changes, mechanisms explaining these demographic processes are best sought in the ecological and evolutionary traits of the individual. Therefore, changes in the distribution and numbers of any taxa largely depend on its genetic and physiological constraints.

Historically, studies of the distribution and abundance of taxa have been primarily descriptive (Harper 1982). Without looking outside the existing ecological range, researchers record observations about the taxa and the environment; then correlate what has been described. However, through the course of evolution, selective forces tend to restrict the physiological processes in an organism (Harper 1982). This has a restricting effect on its distribution. For this reason, Harper suggests asking the question, "what are the nature of constraints or limitations that prevent a plant from living elsewhere?" rather than, "what attributes of an organism enable it to live where it does?" Such an approach becomes an exercise in genetics as well as ecology since it accounts for a particular distribution rather than merely recording it.

A species distribution can be limited or enhanced by evolutionary differentiation. Individuals of a species may be genetically narrow based but widely tolerant (plastic), so when transplanted into a different habitat they grow the same as individuals native to that site (Harper 1982). Some weeds are known to have such all purpose genotypes (Baker 1961). At the other extreme, individuals may have narrow tolerances where the species consists of many localized genotypes, as in the metal-tolerant populations of *Agrostis tenuis* (Antonovics et al 1971). Species of wide ecological amplitude generally exhibit a high degree of genetic differentiation. Evidence suggests that the ecological amplitude is determined, in part, by the ability to differentiate (Bradshaw 1984).

In this study, ecological and genetic methods were used to examine the chemical constraints on the distribution of *Ruppia occidentalis* S.Wats., a submersed vascular plant (hydrophyte). The analyses were designed specifically to examine limits in freshwater, the lower margin of its ecological range.

The genus *Ruppia* inhabits temporary or permanent water bodies and has a cosmopolitan distribution (Verhoeven 1979). *Ruppia occidentalis* S. Wats. is a perennial species occurring in permanent water bodies having high solute concentrations. Scientifically, *Ruppia* has two interesting features. First, *Ruppia* is a dominant submerged hydrophyte in the pollen records of sediment cores from Alberta lakes (Hickman et al 1982, Hickman and Klarer 1981, Hickman at al 1984, Schweger, unpublished data). Pollen from most other aquatic species apparently degrades or is inconspicuous in numbers relative to the rain of terrestrial pollen. *Ruppia* pollen is most conspicuous in the sediment cores where other variables (chemistry, diatoms, terrestrial pollen) indicate more arid conditions, lower water levels, and thus higher salinities. For palaeoecologists the question is whether *Ruppia* is a good indicator of saline lake habitats. Although extant European and Australian species are closely associated with a wide range of salinities (Verhoeven 1979, Brock 1982), few studies exist that identify the ecological requirements and chemical tolerances of *R. occidentalis*. That *Ruppia* has been occassionally collected in freshwater adds further impetus to this study.

The second interesting feature is that *Ruppia* is a rooted submerged hydrophyte. With the exception of free-suspended species, submerged species are anchored to the sediment by their roots with their shoots suspended in water, thereby gaining access to two independent sources of solutes. Which organ, root or shoot, dominates in absorption is somewhat controversial (Denny 1980). Recent experimental evidence using biphasic culture methods indicates that roots are as capable of uptake as shoots. In some cases root absorption is dominant, particularly when solute concentrations in the water are low (Nichols and Keeney

1976b, Barko and Smart 1979. Barko 1982, Huebert and Gorham 1983). Westlake (1971) and Denny (1972b) suggested that some plants are flexible in their mode of uptake, depending on the solute concentrations of the water and sediment. Because concentrations of available salts are higher in the sediment interstitial water compared to the overlying water, such a dual absorption system may have important ecological consequences.

Aquatic plants have received less attention than terrestrial plants, largely because they are difficult subjects with which to work. Whole plants subject to experimentation require delicate handling, and cultures are prone to algal contamination. Axenic culture techniques (Gerloff and Krombolz 1966) are unsuitable for large plants or long term experiments. In the field, only recently has SCUBA (self contained underwater breathing apparatus) been recognized as essential for accurate sampling. Even then, sampling by SCUBA in one locality disrupts ~~the~~ substratum after a short duration so as to reduce visibility. Also, fragments of harvested plants float away before they can be collected. It is also difficult to randomize field samples. Consequently there is a lack of field studies and experiments under controlled conditions.

Considering these features, laboratory and field studies in this project were undertaken to 1) determine the within-lake distribution and growth patterns of *Ruppia* in three chemically different lakes, 2) test the ecological prediction that root absorption is dominant in solute-poor water, and 3) distinguish the genetic and environmental bases for variation in chemical tolerances among populations.

2. Growth and Biomass Allocation of <u>Ruppia</u> <u>occidentalis</u> S. Wats. in Three Lakes, Differing in Salinity

2.1 Introduction

Ruppia is an important genus in submersed hydrophyte ecology because of its broad physiological tolerances and cosmopolitan distribution (Verhoeven 1979, Brock 1982, Brock and Shiel 1983). Researchers have reported an ecological range equivalent to 217‰ TDS (parts per thousand, total dissolved solids) and tolerance of fluctuations over 50‰ TDS by some annuals (Brock 1979, Verhoeven 1979). Perennials such as *R. megacarpa* Mason and *R. cirrhosa* Petag (Grande) also occur over broad salinity ranges (5-46‰ TDS, 1.5-60‰ Cl, respectively), and still may not inhabit their entire physiological ranges (Verhoeven 1979, Brock 1982).

The extent of *Ruppia* in low salinities appears to be limited by co[illegible]ion from freshwater macrophytes (Verhoeven 19[illegible]hoeven and Van Vierrson 1978a, Howard-Williams [illegible]iptrot 1980, Verhoeven 1980). For example, Verhoe[illegible] [illegible]served *Potamogeton pectinatus* L., excluding *Rupp*[illegible] [illegible]n ponds diluted below 9‰ Cl (Verhoeven 1980), [illegible] surveys [illegible] encountered *Ruppia*-dominated communities only between 9 and 14‰ Cl. However, in culture, salinities of 3.8‰ Cl were most favorable for growth. Verhoeven suggests that constraints at low salinity are biological rather than chemical. Yet, *Ruppia* has been collected from some freshwater habitats (Rawson and Moore 1944, Higgonson 1965, Hamilton 1980, Haag and Noton 1981b).

In Alberta *Ruppia occidentalis* S. Wats. has been collected from large freshwater lakes (Mitchell 1979, Hamilton 1980, Haag and Noton 1981b) where, in the last study, it is a dominant in a community of 19 hydrophytes. Therefore, a study was undertaken to quantify by field examination the chemical constraints on *Ruppia occidentalis* . Populations from 3 lakes, of different salinities, were examined to 1), establish whether freshwater populations are limited by salinity, in the absence of competition, and 2) relate differences in growth to the distributions in each lake.

2.2 The Genus *Ruppia*

Ruppia , of the family Potamogetonaceae, is a cosmopolitan genus occurring primarily in brackish water and inland saline waters (Verhoeven 1979 and references within, Brock 1982). Although species occur in both temporary and permanent water bodies, perennial forms such as *Ruppia occidentalis* S. Wats. are restricted to the latter. The perennial species in Europe (*R. cirrhosa* (Petagna) Grande) and Australia (*R. megacarpa* Mason) are similar in morphology, growth habit and chemical tolerance to *R.*

occidentalis, the North American counterpart. All species are associated with saline water to some degree; some annuals occur over salinity ranges larger than that reported for any other angiosperm (Brock 1982). This is attributed, in part, to proline accumulations in the cytoplasm to compensate for high external solute concentrations (Brock 1982). The perennial species also have broad ecological ranges (0.2 - 20%. TDS ,*R. occidentalis*; 5 - 46%. TDS, *R. megacarpa*; 1.5 - 60%. Cl , *R. cirrhosa*)(Rawson and Moore 1944, Verhoeven 1979, Brock 1982) and *R. cirrhosa* has been described as "sediment indifferent" (Verhoeven 1979).

Ruppia perennials colonize new sites by seeds, turions (compact leaves at shoot apex) and vegetative fragments; however, seedling establishment is rarely observed in nature (Brock 1982). Growth in spring is initiated in overwintering plants at a mean water temperature of 10°C. Initially, *Ruppia* colonizes the lake bottom through the production of tillers from lateral meristems (horizontal expansion). In mid-season (mean temperature 17°C.) horizontal growth is replaced by the upward expansion (vertical growth) of the apical meristem and inflorescences and turions are produced. The inflorescence consists of two flowers (2 sessile stamens and 4 pistils each) and is borne on a peduncle of variable length. Pollination occurs at the water surface when the flower-bearing peduncle extends upwards into the floating pollen grains. Nevertheless, fruit set is very low, seedling establishment is rarely observed perhaps because seed germination requirements appear to be much different than the growth requirements of the adult plant (Brock 1982). Thus local colonization by *Ruppia* occurs primarily by turion and shoot fragment dispersal and by cloning. Therefore, if the distribution of *R. occidentalis* is constrained by chemical factors, it will be largely the result of interactions between the environment and vegetative propagules.

2.3 Methods

2.3.1 Study Sites

All field work was conducted in Pigeon, Buffalo and Miquelon Lakes which are located in central Alberta (Fig. 1). These lakes were chosen because they spanned a large chemical range (Table 1).

2.3.2 Macrophyte Survey

Field studies, conducted during July and August 1982, were part of a macrophyte survey of Buffalo and Pigeon Lakes (Haag and Noton 1981a,b). Divers sampled by swimming the circumference of about a 4m diameter circle. Percentage cover, recorded in logarithmic abundance classes, was measure as a fraction of this 0.5m wide circular path. This comprised one sampling point. Sampling points were located at 0.75-1.0m depth intervals along a transect orientated

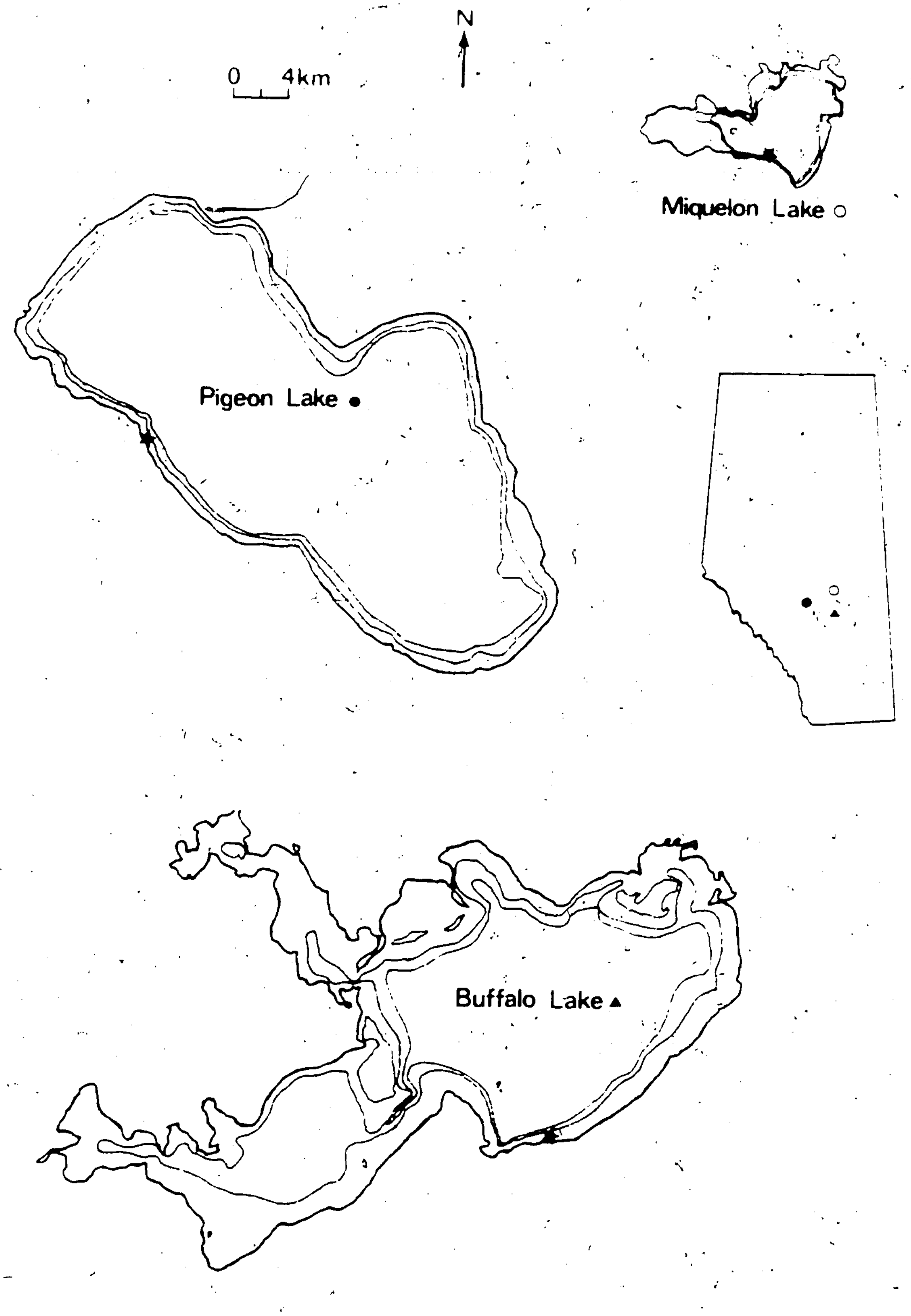

Fig. 1. Morphometry of Miquelon, Pigeon and Buffalo Lakes.
★-transect sites, contours indicate the 1.52 and 3.04m depths.

Table 1. A comparison of the major chemical and physical characteristics of Pigeon, Buffalo (Main Bay), and Miquelon Lakes; chemical concentrations in mg/l unless otherwise stated; * as reported in Haag and Noton (1981); Zc - maximum depth of hydrophytes.

Parameter	Pigeon	Buffalo	Miquelon
Location (lat./long.)	53°01',114°02'	52°50',112°50'	53°15',112°53'
Surface Area (km^2)	*96.4	*83.1	8.76
Max. Depth (m)	10.0	6.4	6.0
Zc (m)	4.5	3.0	3.0
June Ext. Coefficient	1.24	1.09	1.01
Conductivity (μmhos/cm)	285 - 330	2300 - 2450	5300 - 6900
TDS	*250	*2400	6200
Alkalinity (CaCO$_3$)	*147.5	*961.7	-
pH	*8.5	*9.2	9.5
SO$_4$	2.7	426.0	2300
N (total kjeldahl)	*2.03	*3.7	-
P (total)	*0.07	*0.04	-
Ca	23.5	11.0	11.5
Number of Hydrophyte Species (submerged)	19	9	2

perpendicular to shore. The survey comprised 90 and 81 transects, placed near identifiable landmarks around Buffalo and Pigeon Lakes, respectively, for a total of 822 sampling points. Similar methods for percentage cover were used on a separate survey the following summer on Miquelon Lake using 10 transects.

Frequency of occurrence (the fraction of sampling points in a given depth interval occupied by *Ruppia*) and percentage cover was compared between and within lakes. In calculating geometric means, to remove the dependence of variance on the mean, an increment of 1 was added to each cover class value.

2.3.3 Growth and Biomass Allocation

A time series analysis of growth pattern, standing dry weight, and biomass allocation was conducted in 1982 on populations of *Ruppia* in Buffalo, Pigeon and Miquelon Lakes. Samples and field measurements were obtained biweekly, from May to September, from a permanent transect on each lake. Each transect location had a northern exposure, a slope of less than 10% and a percentage cover of *Ruppia* similar to the mean of its respective lake (as determined by survey data). Coincidently, all transects were on exposed shorelines. Interspecific competition was assumed to be unlikely because population densities were low due to turbulence and low light. Each transect was divided into 3, 1m depth intervals (sites) to account for effects of the water depth gradient on growth. Percentage cover at depths greater than 3 meters decreased in Buffalo and Miquelon Lakes.

Physical measurements and samples of the plants were taken at each depth interval. Both temperature and electrical conductance were measured at the sediment water interface with a TC-2 Hydrolab Conductivity meter directly from the boat. Dissolved oxygen (measured on a 54YSI meter) and PAR (photosynthetically active radiation) transmittance (LiCor Quantum Sensor) was recorded at 0.5m depth intervals. Two, 1 liter water samples were collected at 0-0.25m above the sediment with a 3 liter Van Dorn bottle and immediately filtered through Whatman GF/A filters before preserving with 2 ml nitric acid and stored in the dark in a cooler. Four to eight surficial sediment samples (0-10cm, about 75 ml each) were scooped from each interval, combined in a 1 liter pail and allowed to air dry.

Since accurate navigation of the boat was difficult, randomization of plant harvests within each site was achieved by diving at random distances off both sides of the anchored boat. Where possible intact plants were collected from the centre of a sward each time they were encountered on a dive. In total 30 - 50 plants were collected from each depth interval and stored in plastic bags to prevent desiccation. Plants were transported to the laboratory in a cooler and stored at 6°C for a maximum of 72 hours.

In the laboratory 10 plants were randomly selected from each collection to measure growth attributes (shoot height, rhizome length,number of roots and shoots) and dry weight partitioning (dried 48hrs. at 80°C). Variability was great but 10 samples ensured a standard error of 10 - 15% of the mean. Logarithmically-transformed growth data were used in all statistical tests to remove the dependence of the variance on the mean and were summarized as geometric means in figures and tables. Remaining plants were included for phenological documentation. Water samples were analyzed for sulphate-sulfur (turbidimetric method)(Standard Methods 1974), calcium, magnesium (Atomic Absorption spectrophotometer) potassium, sodium (Flame Photometer, Model 143) and electrical conductance (at 22°C). Sediment interstitial water was extracted from 10g of saturated sediment, in a 7:1 w/w water:sediment ratio, by centrifugation and analyzed for sodium, magnesium, potassium (A.A.), sulphate (turbidimetric method) and electrical conductance (Standard Methods 1974). Duplicate sediment samples were taken from a pooled sample of each depth interval.

2.4 Results

2.4.1 Macrophyte Survey

Morphometrically and chemically the three lakes studied are dissimilar (Fig. 1, Table 1). Miquelon Lake is about 1/10 the surface area of Buffalo and Pigeon Lakes; therefore, it is likely the least turbulent. Pigeon Lake has as large a surface area as Buffalo Lake but is deeper, and its shoreline is less dissected. Collectively, the lakes span the known ecological range of salinity for *Ruppia* in Alberta (.3 - 6.2 ‰ TDS)(Table 1). Nitrogen and Phosphorus concentrations in the water, measured by Chemical and Geological Laboratories, are similar in Pigeon and Buffalo Lakes. Lakes with increasing salinity in Alberta and Saskatchewan, have a progressively larger proportion of sulphate and smaller proportion of calcium (Fig. 2), but Alberta lakes tend to have lower sulphate and higher sodium+potassium proportions than Saskatchewan lakes of equivalent salinity (Rawson and Moore 1944). A freshwater inlet creates a strong chemical gradient from the northeastern to the southwestern bay within Buffalo Lake. All data reported here were collected from the most saline, northeast bay. Biologically, the increasing number of hydrophyte species with decreasing salinity may have implications for *Ruppia* establishment in low salinities (Table 1).

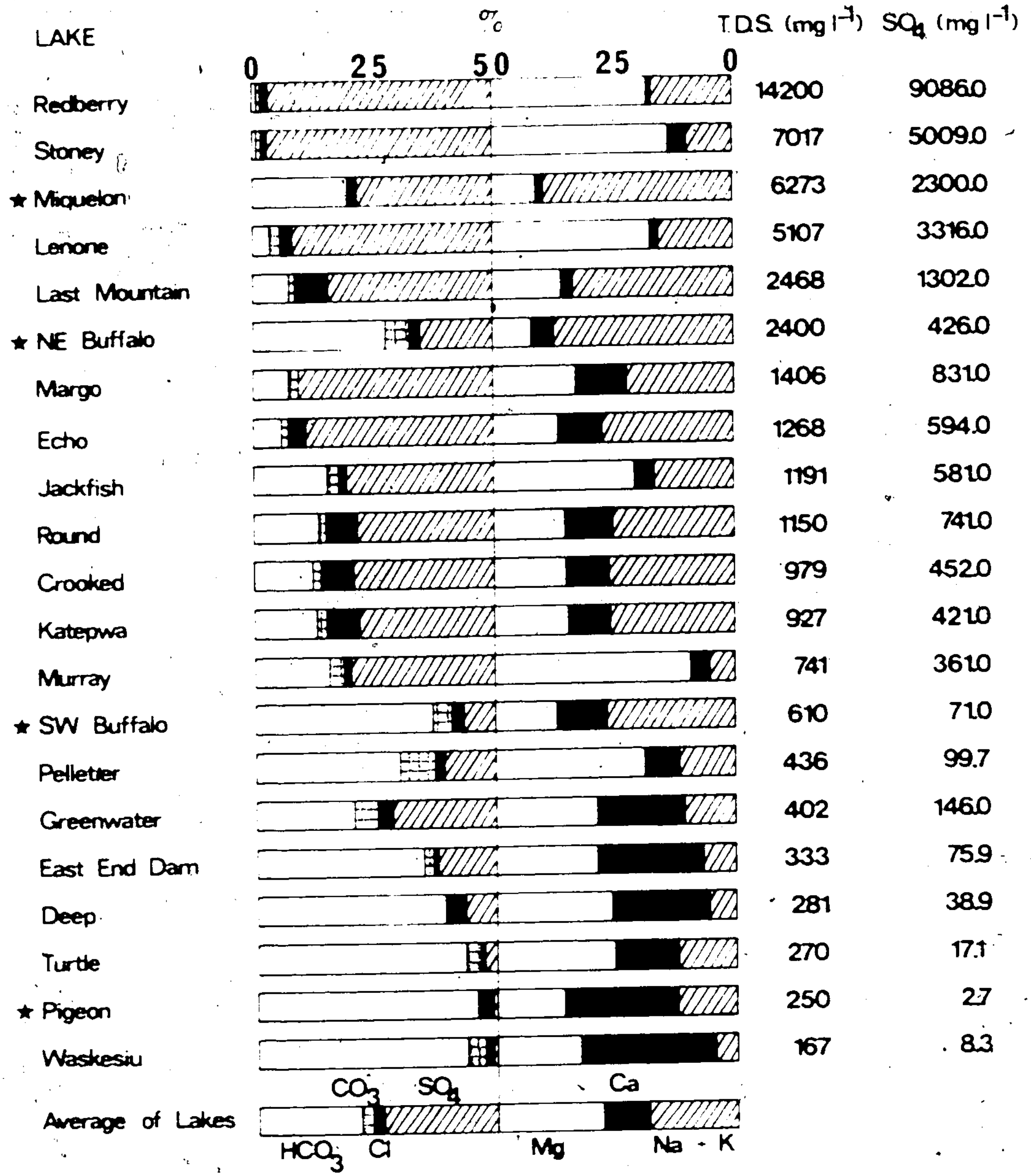

Fig. 2. Percent milliequivalents of the major ions along a salinity gradient in Alberta and Saskatchewan Lakes (★ - from present study in Alberta; all others from Rawson and Moore (1944) in Saskatchewan).

Densities, as measured by frequency of occurrence and percentage cover, increase with salinity (Fig. 3, 4). *Ruppia* is most abundant at greater depths even in the absence of interspecific competition (on exposed shorelines) in Pigeon Lake whereas in the saline lakes its frequency is uniform over most depth intervals. The low frequency at the 0 -.4m depth interval in Pigeon Lake is due to a lack of sampling points for this interval. Sites occupied by *Ruppia* alone, although rare in freshwater, are restricted to greater depths (Fig. 3). Also, the mean percentage cover, represented by logarithmic abundance classes , increases, while depth of maximum percentage cover decreases with increased salinity (Fig. 4).

2.4.2 Seasonal Growth

Within a transect, the seasonal mean temperature did not vary significantly (p>0.05) among sites (depth intervals) due to mixing. Differences between transects were not significant (p>0.05)(Table 2) but the smaller lake volume may have caused seasonal variation to be more extreme in Miquelon Lake. Differences in maximum temperature among lakes did not exceed 3.2^{o}C and number of days suitable for exponential growth (> 10^{o}C) and reproduction (> 16^{o} C)(Verhoeven 1979, this study) was similar among lakes, but least in Pigeon Lake. Differences among lakes in mean percentage Photosynthetically Active Radiation (PAR) transmitted decreased with depth (Table 2, Fig. 5).

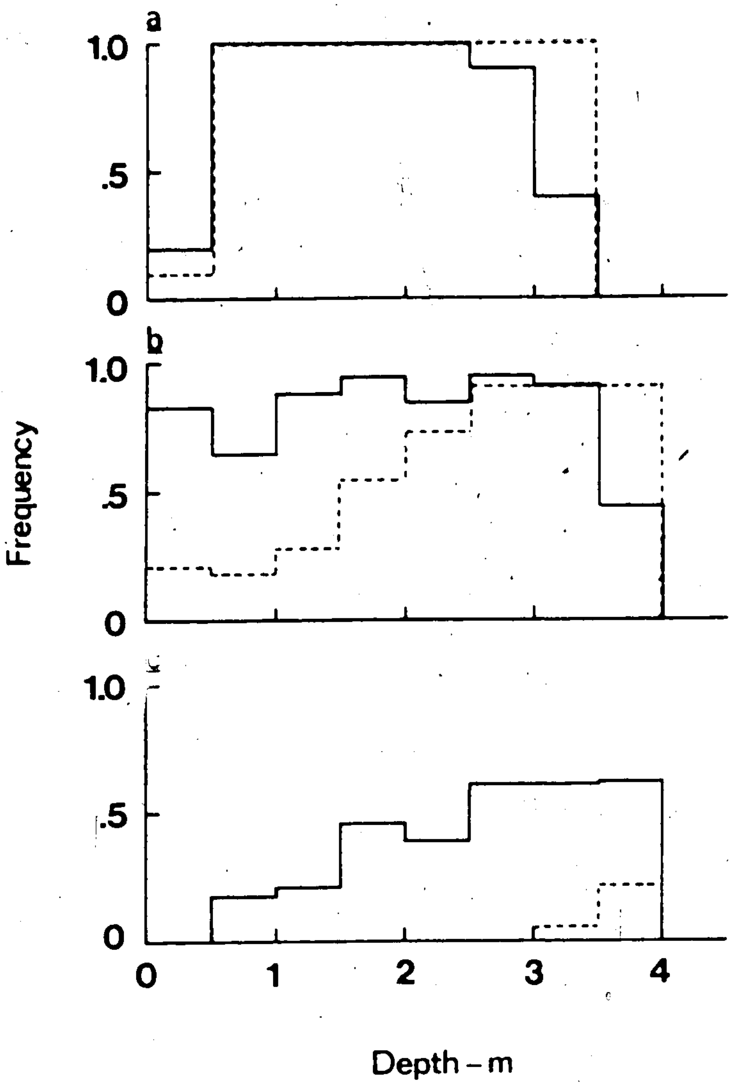

Fig. 3.(———) Frequency of occurrence of <u>Ruppia occidentalis</u> S. Wats. within each 0.5 m depth interval. (---------) Proportion of occupied sites with no other vascular hydrophytes. <u>a</u> Miquelon Lake, <u>b</u> Buffalo Lake - Main Bay, <u>c</u> Pigeon Lake.

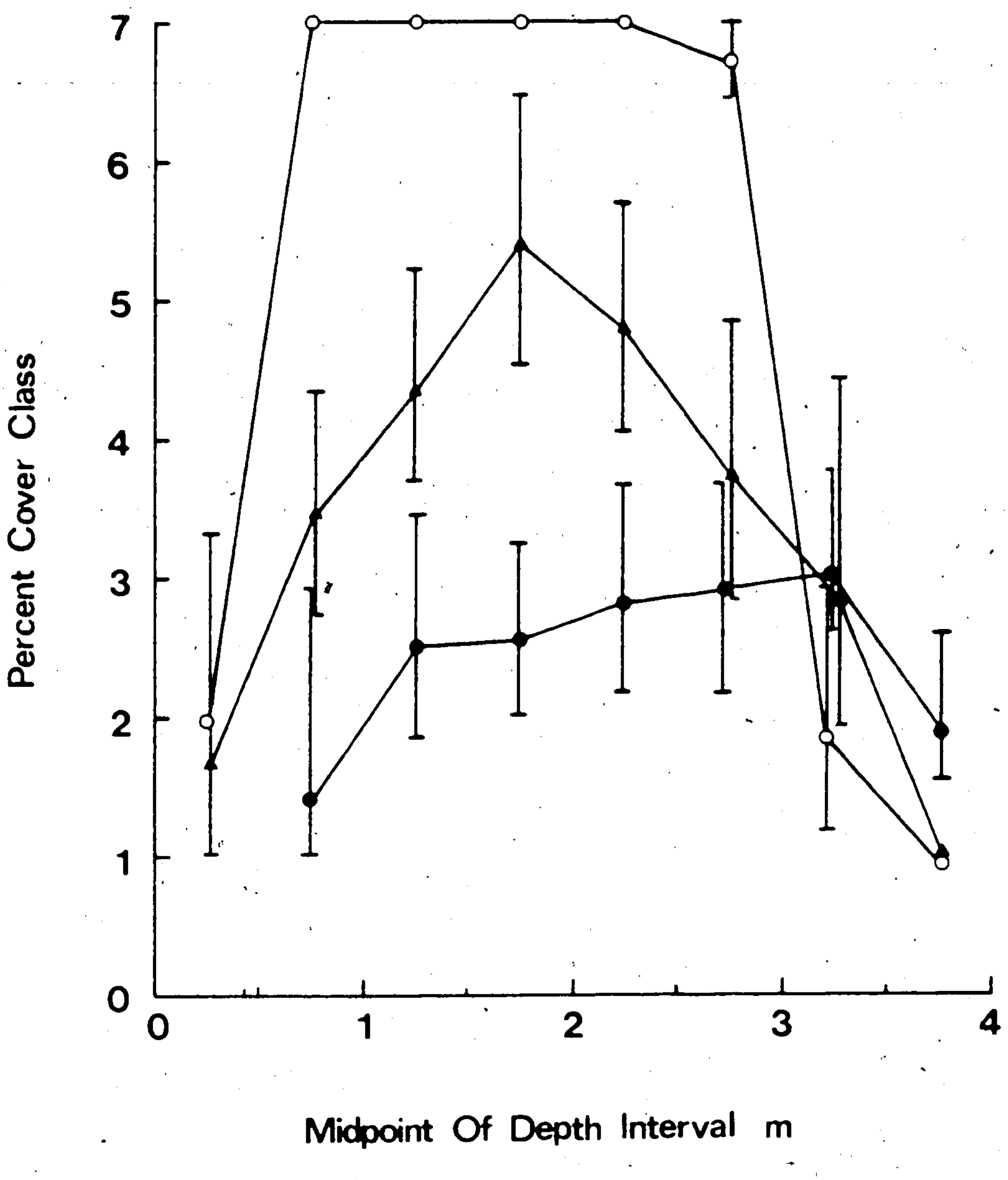

Fig. 4. Mean percentage cover ± 95 percent C.I. of Ruppia in Miquelon (○—○), Buffalo (▲—▲) and Pigeon (●—●) Lakes. Cover classes: 1 <1%, 2 1-5%, 3 6-15%, 4 16-30%, 5 31-50%, 6 51-75%, 7 76-100%.

Table 2. Comparisons of temperature variations and percentage transmission of Photosynthetically Active Radiation (PAR) among sites and lakes. Temperature data was pooled within each lake because site differences were not significantly different ($p \geq 0.05$).

Parameter	Pigeon	Buffalo	Miquelon
	Temperature		
Maximum (C°)	17.8(Aug 6)	21(Aug 7)	20.2(July 29)
Days above 10 C°	114	115	123
Days above 16 C°	67	79	76
Seasonal Mean (C°)	14.7	16.7	15.6
	Mean PAR Transmission (%)		
0 - .9m depth interval	51.6	32.2	72.0
1.0 -1.9m	25.3	20.6	23.8
2.0 - 2.9m	8.4	8.2	9.8

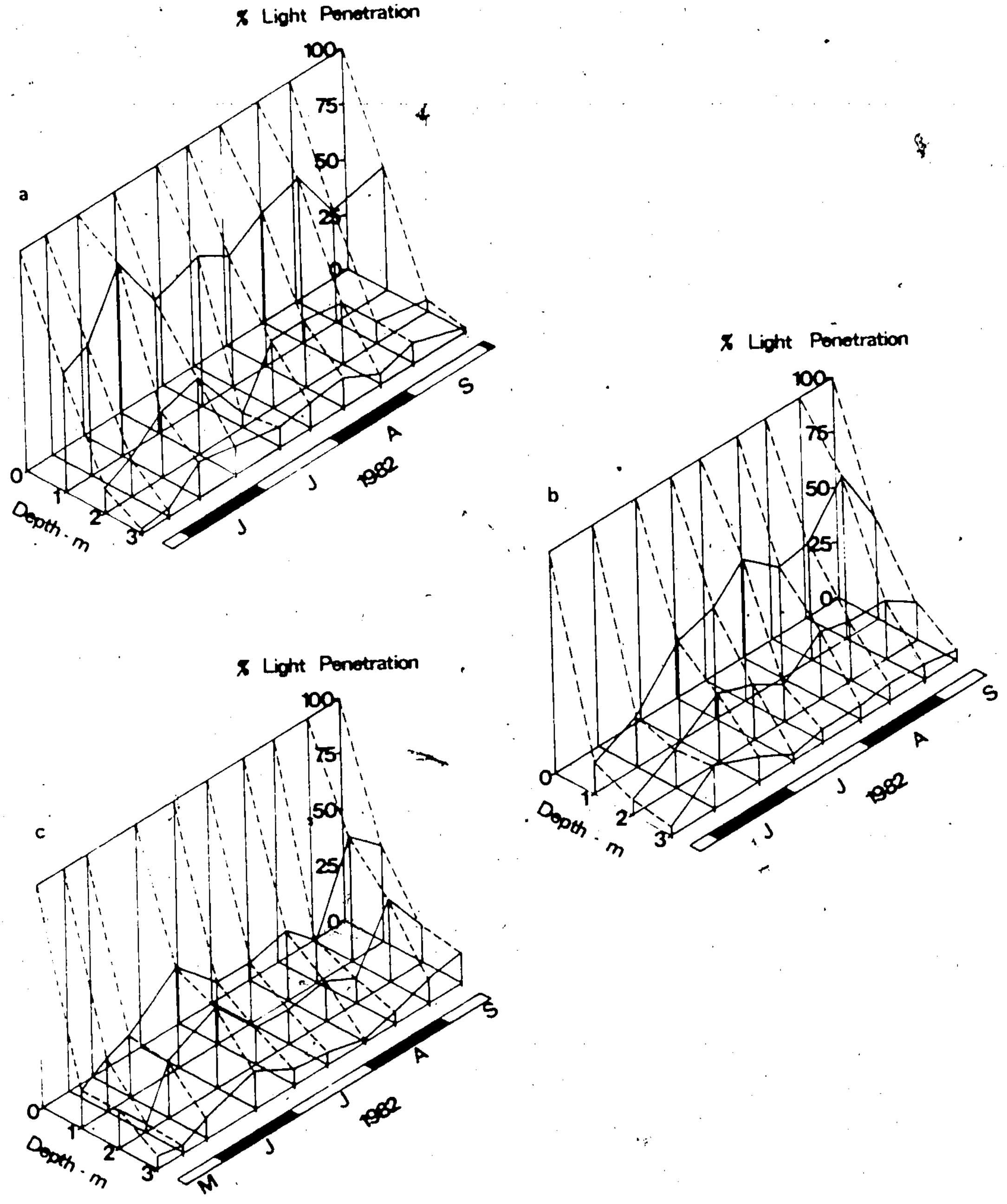

Fig. 5. Percentage transmission of photosynthetically active radiation(PAR)in a-Miquelon. b-Buffalo and c-Pigeon Lakes.

Therefore, lake comparisons of *Ruppia* at the 2 - 3.0m depth interval were least confounded by light differences. Increasing transmission of PAR throughout the season in Buffalo Lake, is likely due to a decreasing frequency of wave induced turbulence. Although light transmission in Pigeon Lake is influenced by turbulence, the early summer and late summer peaks likely reflect the spring and summer maxima of phytoplankton, typical of eutrophic lakes (Hickman 1973, Hickman and Jenkerson 1978, Hickman 1979). PAR transmittance was high and constant in Miquelon Lake, reflecting the lack of turbulence and a supressed phytoplankton biomass, common in high salinities (Hickman 1978, Hammer 1981, Hammer, Shamess and Haynes 1983)(Fig. 5). Seasonal changes in the concentration of major ions were small in all lakes, but an increase throughout the summer was evident in Miquelon Lake (see Table 1 for the range of electical conductance). Mixing was sufficient in all lakes to prevent any significant chemical differences in the water among sites from establishing (Table 3); however, sediment interstitial water was significantly more concentrated at the intermediate depth interval ($p<0.05$)(Table 4). Interestingly, the concentration of solutes in soil water relative to the overlying water is highest and most variable in freshwater (Table 5).

The seasonal maximum of biomass per plant compared at each site was significantly different among lakes ($p<0.05$)(Fig. 6a,b,c) and greatest in Miquelon Lake.

Table 3. Comparison of ion concentrations (mean ± SD) in the three depth intervals (sites) located along the permanent transect in each lake; concentrations reported as mg/l. Analysis of variance indicated no significant differences among sites.

Ion	Site 1(0 - .9m)	Site 2(1 - 1.9m)	Site 3(2 - 2.9m)
Pigeon Lake (n=10)			
SO_4	6.35± 1.11	6.23±1.52	6.37± 1.42
Na	17.43± 2.01	17.11±1.74	17.48± 1.09
K	2.59± 0.13	2.62±0.19	2.61± 0.13
Mg	10.01± 0.59	10.30±0.47	10.25± 1.06
Ca	23.49± 1.54	23.05±1.65	23.93± 1.38
Buffalo Lake (n=9)			
SO_4	257.33± 23.60	254.78± 25.11	257.11± 28.49
Na	461.49± 63.53	476.38± 45.54	489.83± 65.12
K	35.22± 6.02	33.20± 11.89	38.33± 5.83
Mg	51.03± 6.33	52.61± 4.97	53.62± 7.76
Ca	10.67± 1.40	11.05± 1.31	11.39± 1.65
Miquelon Lake (n=10)			
SO_4	1706.00± 106.87	1733.50± 91.04	1791.50± 163.89
Na	1406.70± 123.64	1404.40± 162.11	1473.20± 142.45
K	88.24± 8.22	85.57± 14.44	94.78± 4.41
Mg	130.55± 13.15	129.65± 20.72	139.50± 6.62
Ca	11.33± 0.79	11.35± 1.51	21.48± 14.83

Table 4 . Ion concentrations in soil water extracted from a saturated soil paste; concentrations reported as mg/l ± SD. (n=2). Significant differences determined by an analysis of variance are indicated by *($p<0.05$) and **($p<0.01$).

Ion	Site 1	Site 2	Site 3	
		Pigeon Lake		
SO_4	477.15± 38.40	997.40± 0	398.90± 26.45	**
Na				
Mg	56.92± 15.53	224.69± 0	60.52± 44.80	*
Ca	13.57± 0.95	31.50± 0	13.43± 2.29	**
		Buffalo Lake		
SO_4	1582.45± 19.45	3248.05± 1133.00	2752.45± 618.65	ns
Na	1941.61± 773.59	4028.03± 1210.30	2825.51± 75.82	ns
Mg	1211.38± 121.99	2442.83± 390.76	2321.71± 459.58	$p<0.10$
Ca	731.93± 61.89	2112.69± 228.18	2112.30± 752.34	$p<0.10$
		Miquelon Lake		
SO_4	7284.15± 1002.32	9515.70± 401.50	5659.20± 181.58	**
Na	105109.32± 757.24	148052.18± 6292.37	90968.37± 1257.08	**
Mg	27580.82± 1433.65	36763.77± 898.54	23108.55± 543.18	**
Ca	13870.10± 1462.49	26329.43± 567.35	12663.24± 284.24	**

Table 5 . Soil water/ open water sulphate concentration ratio of each site (depth interval) in each lake.

Lake	Site 1	Site 2	Site 3
Pigeon	75.1	160.1	62.6
Buffalo	6.2	12.8	10.7
Miquelon	4.3	5.5	3.2

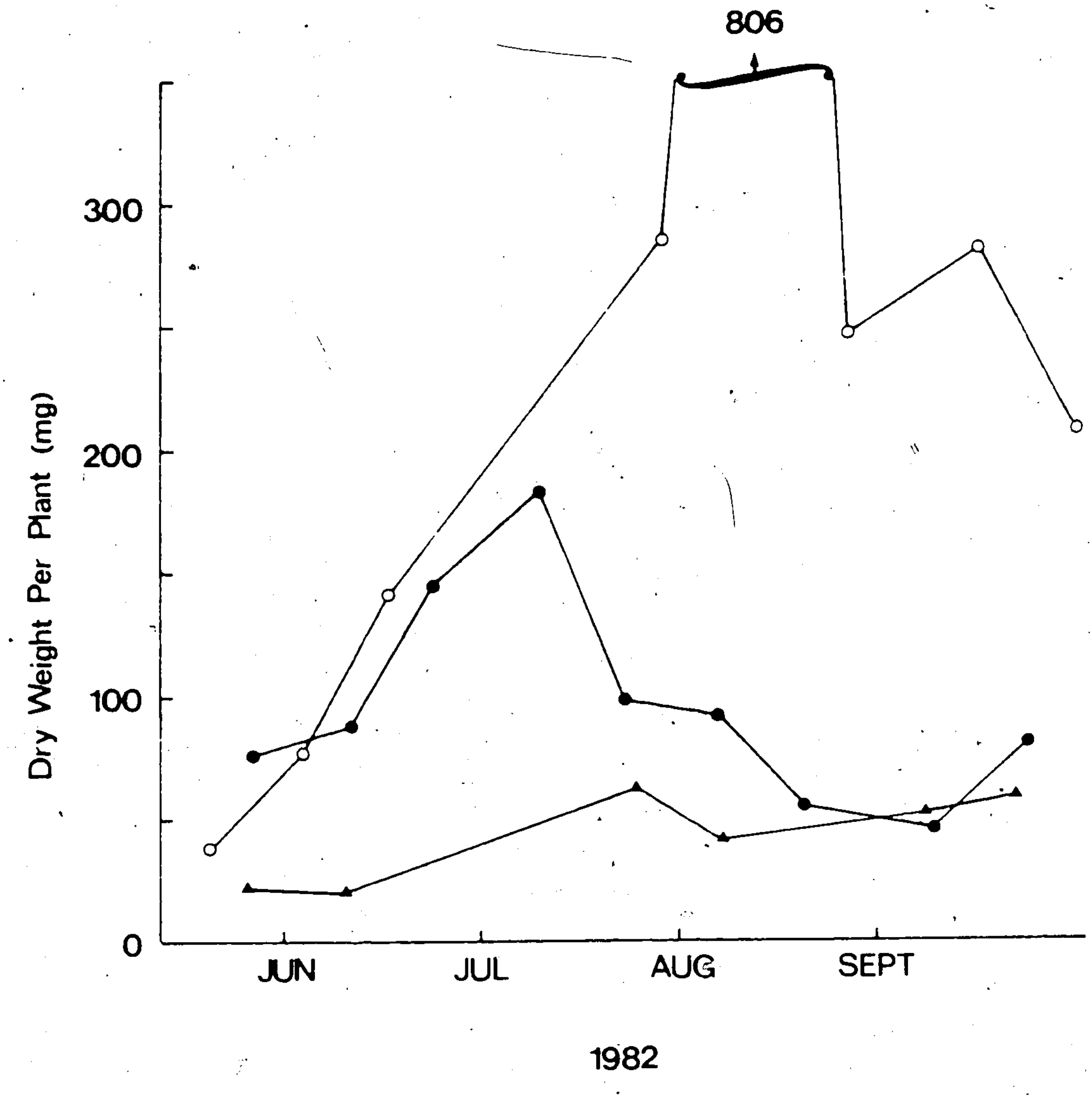

Fig. 6a. Seasonal variation of dry weight per plant in Miquelon-○-○, Buffalo-▲-▲ and Pigeon-●-● Lakes; site 1, 0-.9m.

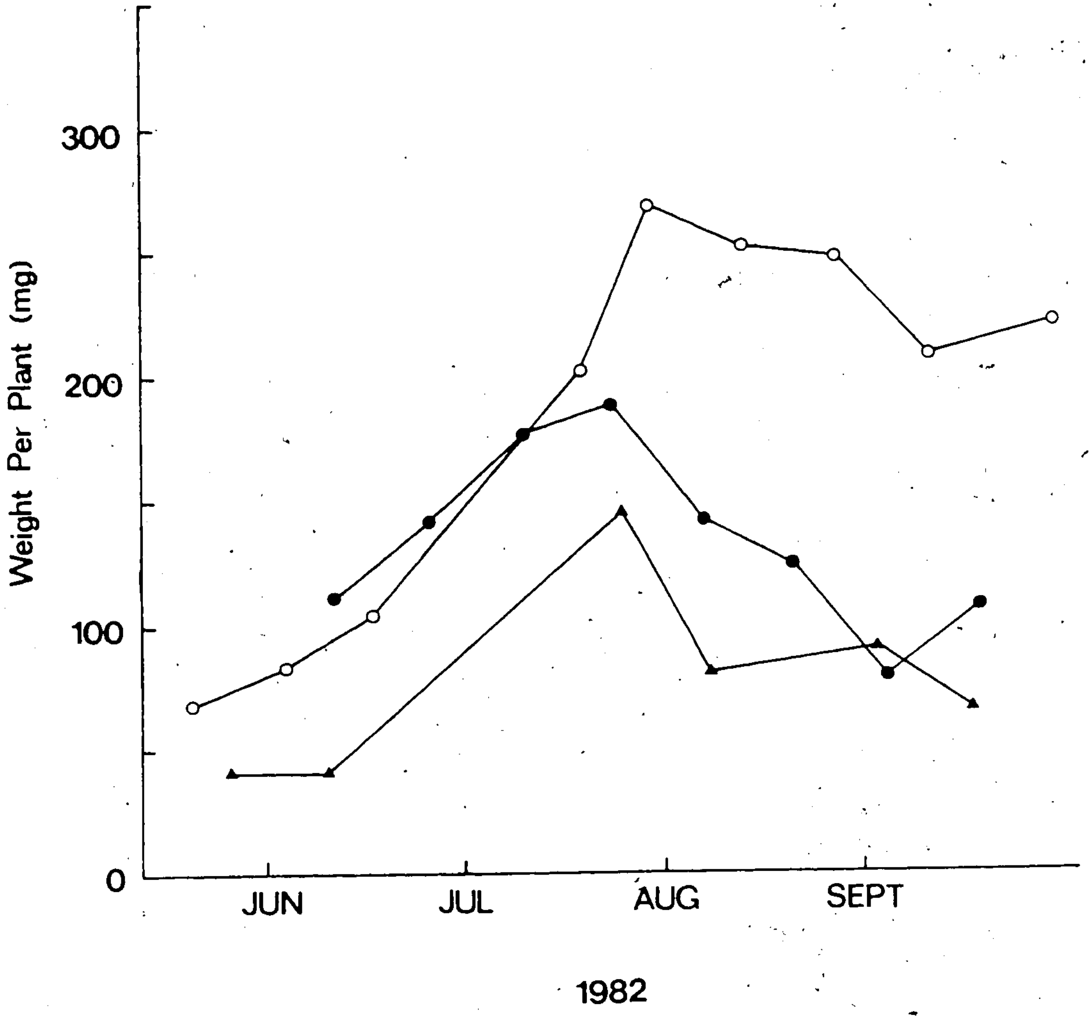

Fig. 6b. Site 2, 1.0–1.9m.

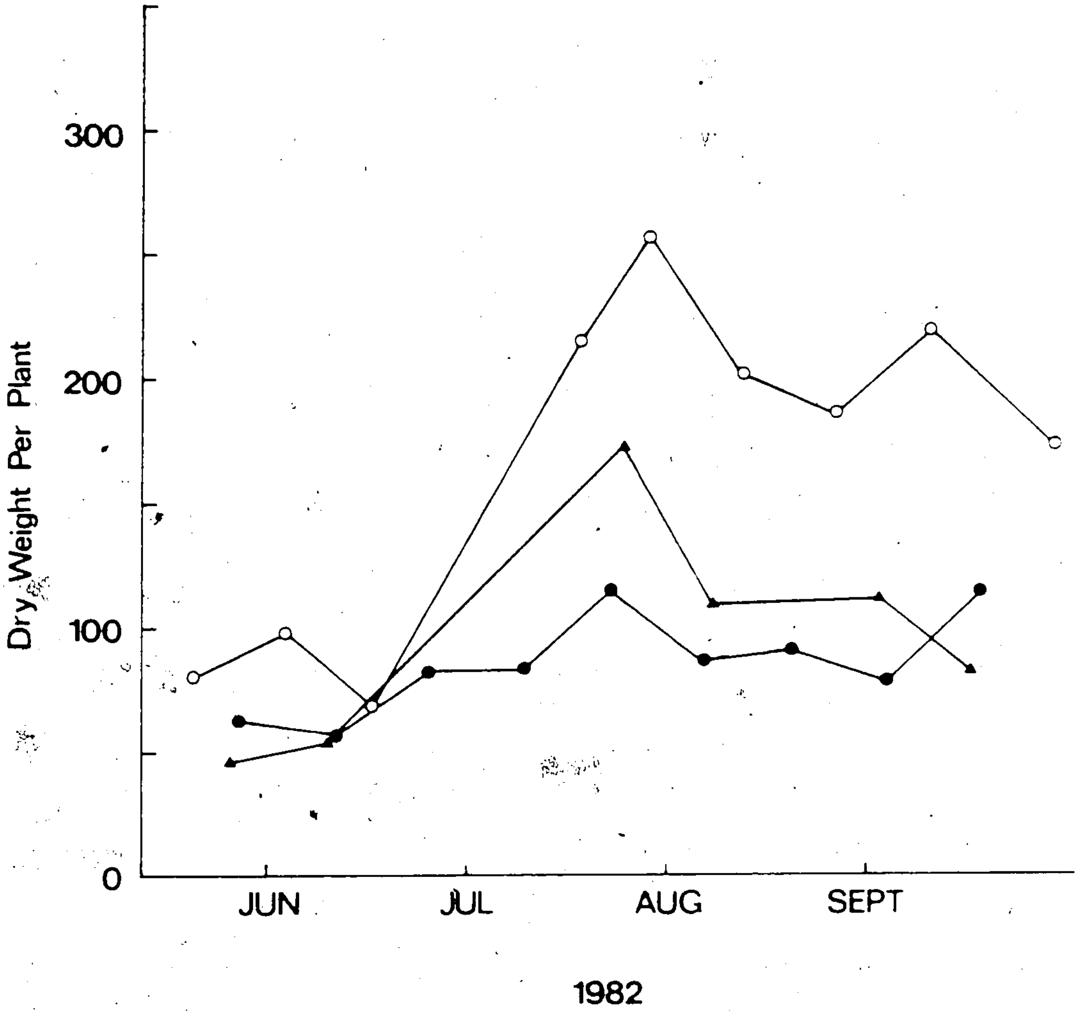

Fig. 6c. Site 3. 2.0 - 3.0m.

Table 6. Differences in growth rates of individuals among the three lakes. S.L. - significance level of lake differences from a oneway ANOVA; **,$p<0.01$; *,$p<0.05$; ns, not significant. Treatments with the same superscript are not significantly different as determined by a Student-Newman-Keuls Test.

Growth Attribute	Pigeon L.	Buffalo L.	Miquelon L.	S.L.
		Site 1		
Rel. Growth Rate (/week)	0.17^a	0.12^a	0.52^b	**
Rhiz. Rel. Extension Rate (/week)	0.20^a	0.16^a	0.17^a	ns
		Site 2		
Rel. Growth Rate	0.05^a	0.16^b	0.15^b	**
Rhiz. Rel. Ext. Rate	0.17^a	0.18^a	0.23^a	ns
		Site 3		
Rel. Growth Rate	0.08^a	0.19^b	0.22^b	**
Rhiz. Rel. Ext. Rate	0.24^a	0.33^b	0.20^a	**

Although biomass in freshwater was greater than in moderately saline water (Buffalo Lake) at sites 1 and 2, the relative growth rate increased significantly with salinity at all 3 sites (Table 6). Rhizomes in freshwater elongate as fast as those in saline water at all depths (Table 6). After the midsummer maximum, rhizomes fragment forming smaller individuals and older shoots decompose at the base. *Ruppia* does not appear to have an innate dormancy; instead, it resumes growth after fragmenting in mid-summer, until low temperatures force quiescence. Even during the quiescent period, the rhizome may continue producing short internodes. The second decomposing event usually occurs immediately upon ice-break (personal observation) but was not documented here.

Dry weight per shoot is seasonally variable and increases with salinity (Fig. 7) . The terminal shoot, if no other, extends vertically in some individuals in all lakes, but extends least and produces fewest leaves in freshwater (Fig. 7)(Table 7).

Miquelon Lake plants produce more live shoots than plants from Buffalo and Pigeon Lakes in site 1 and 3, but, in site 2 shoot production is highest in Pigeon Lake plants (Fig. 8a,b,c). The number of shoots correlates with solute concentration in soil water at the freshwater transect only. The timing and extent of shoot mortality is similar in all lakes.

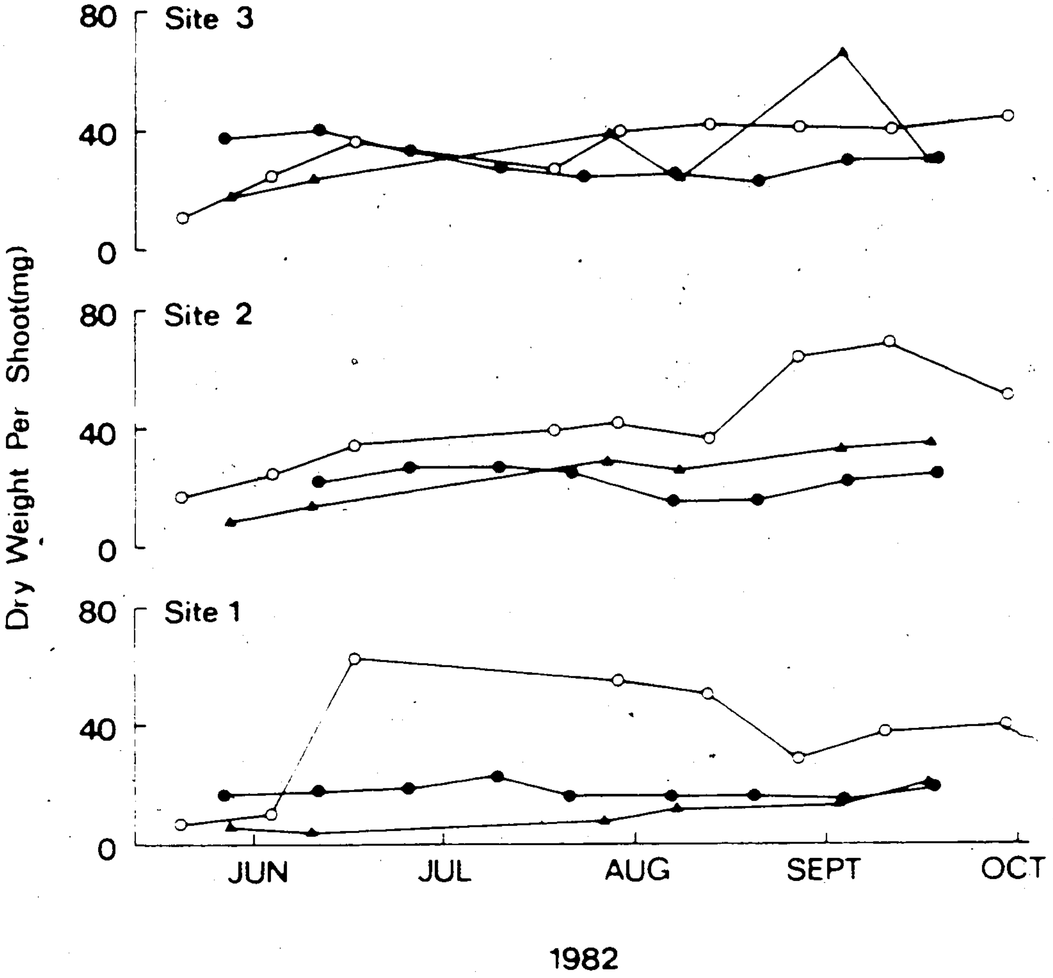

Fig. 7. Differences in mean dry weight per shoot among Miquelon -○-, Buffalo -▲- and Pigeon -●- Lakes.

Table 7. Mean growth and biomass allocation per plant at the summer maximum, N = 10; percentage of plants reproducing or in a vertical growth phase, N = 30 - 50.

	Pigeon L.			Buffalo L.			Miquelon L.		
				Sites					
Growth attributes	1	2	3	1	2	3	1	2	3
Dry weight (mg)	198	206	121	71	153	185	850	309	288
Weight Allocation									
% shoot	61.6	64.5	65.8	59.4	70.8	78.4	73.9	76.1	73.8
% root	17.5	15.2	12.1	15.0	8.0	4.4	5.5	5.4	6.3
% rhizome	20.9	20.3	22.1	25.6	21.2	17.2	20.6	18.5	19.9
Root-Rhiz.:Shoot Ratio	0.62	0.56	0.59	0.69	0.42	0.38	0.36	0.31	0.37
Height of Apical Bud (cm)	0.4	1.0	2.3	1.8	3.0	14.5	7.5	11.4	3.3
Individuals Flowering(%)	20	-	-	-	-	4.3	80	-	-
Individuals with Turions(%)	-	13.9	4.8	26.9	22.9	17.6	80.0	30.0	10.0
Indiv. in Vertical Phase(%)	50.0	50.0	52.0	28.0	73.0	35.0	100.0	50.0	35.3

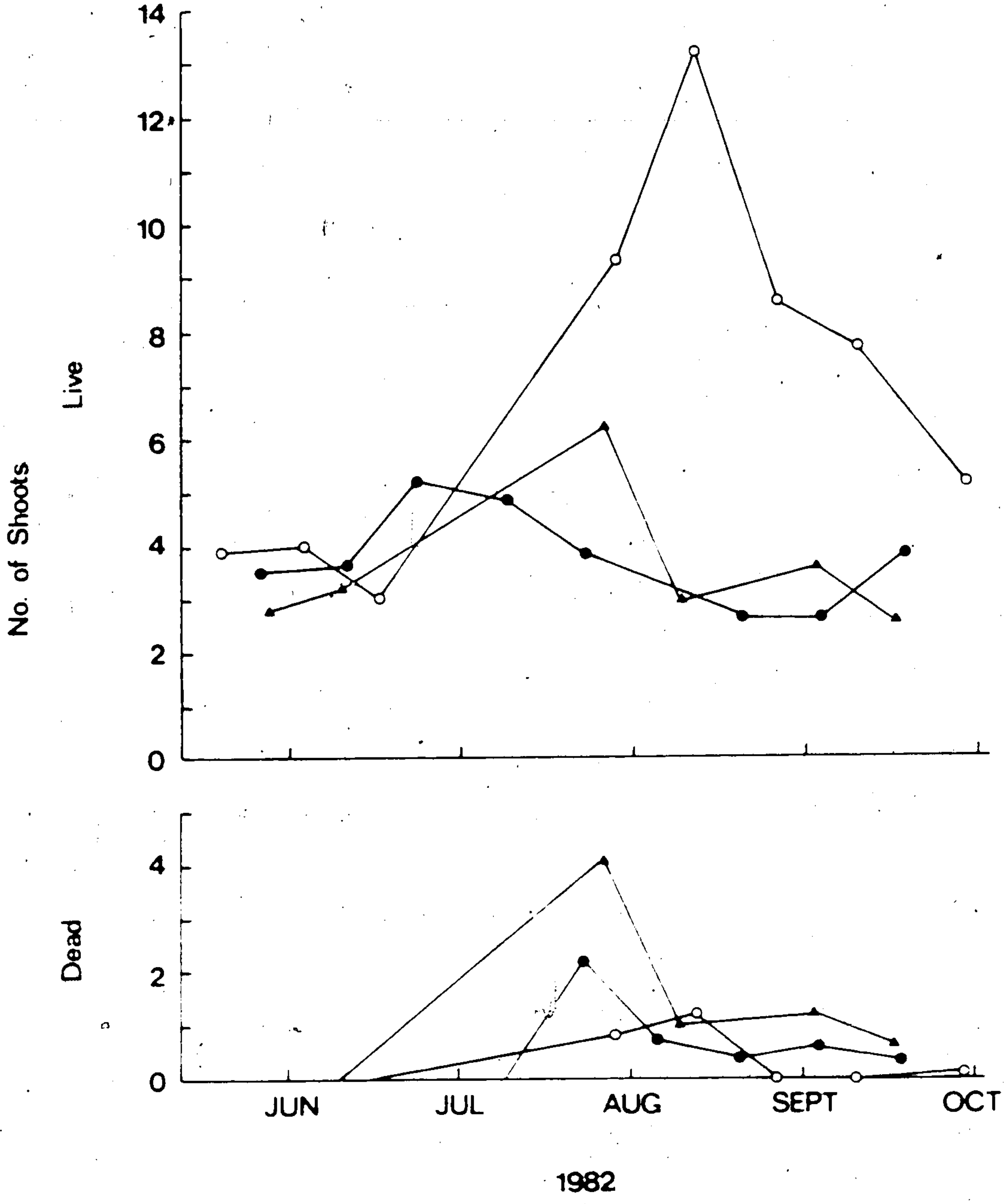

Fig. 8a. Seasonal variation in shoot number per plant; site 1, 0-.9m.
○Miq. L., ▲Buff. L., ●Pig. L.

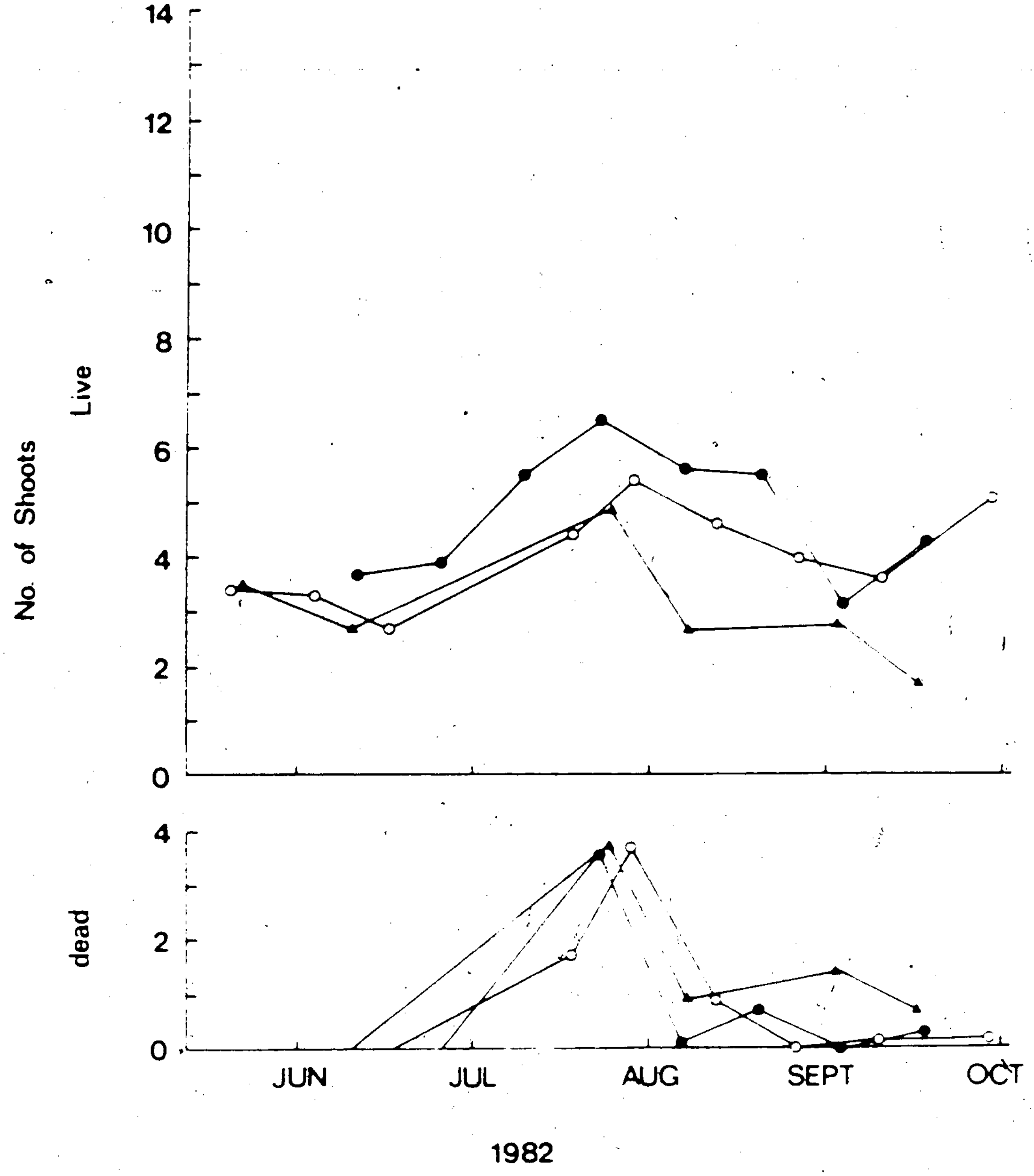

Fig. 8b. Site 2. 1.0 – 1.9m.

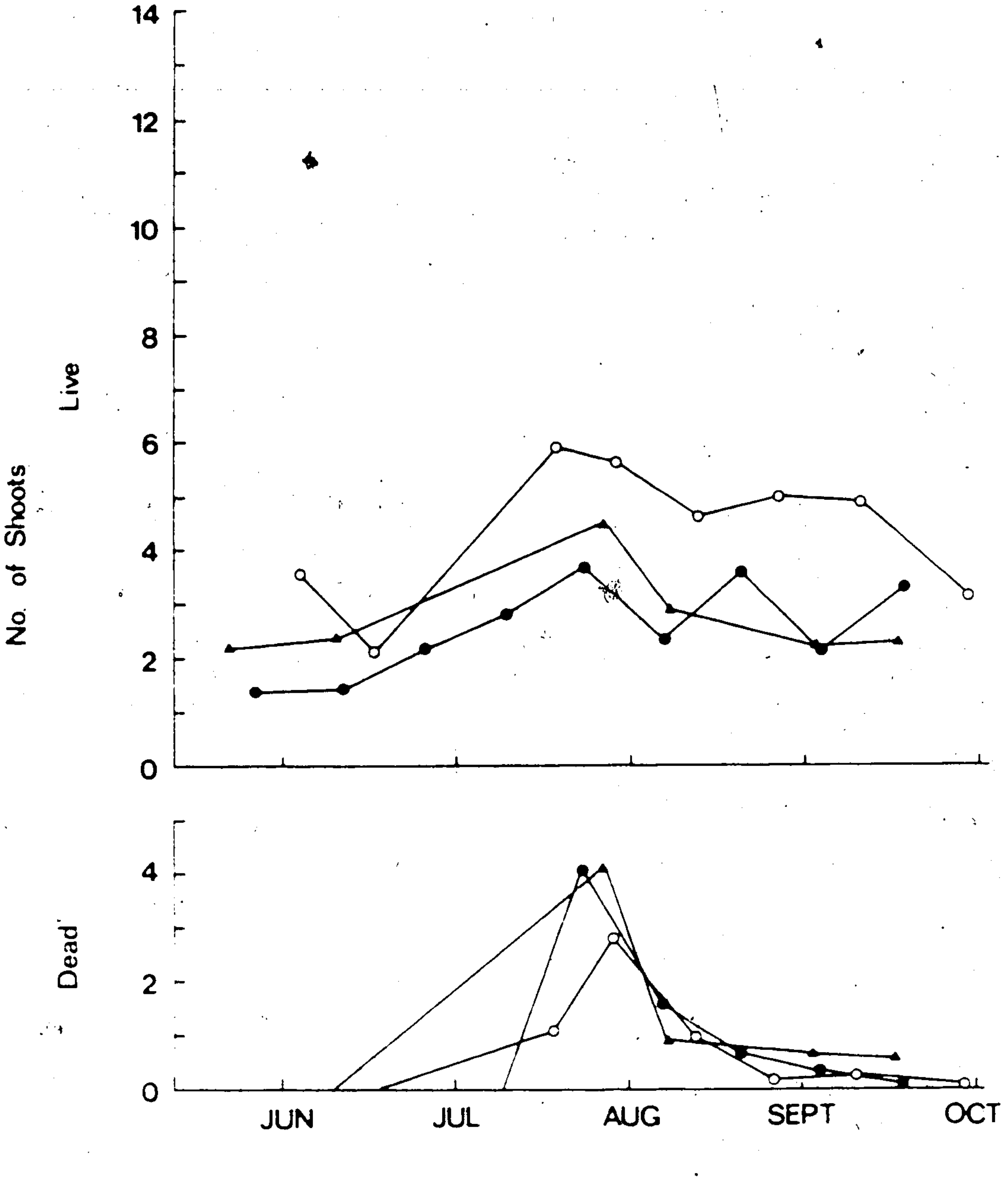

Fig. 8c. Site 3. 2.0 - 3.0m.

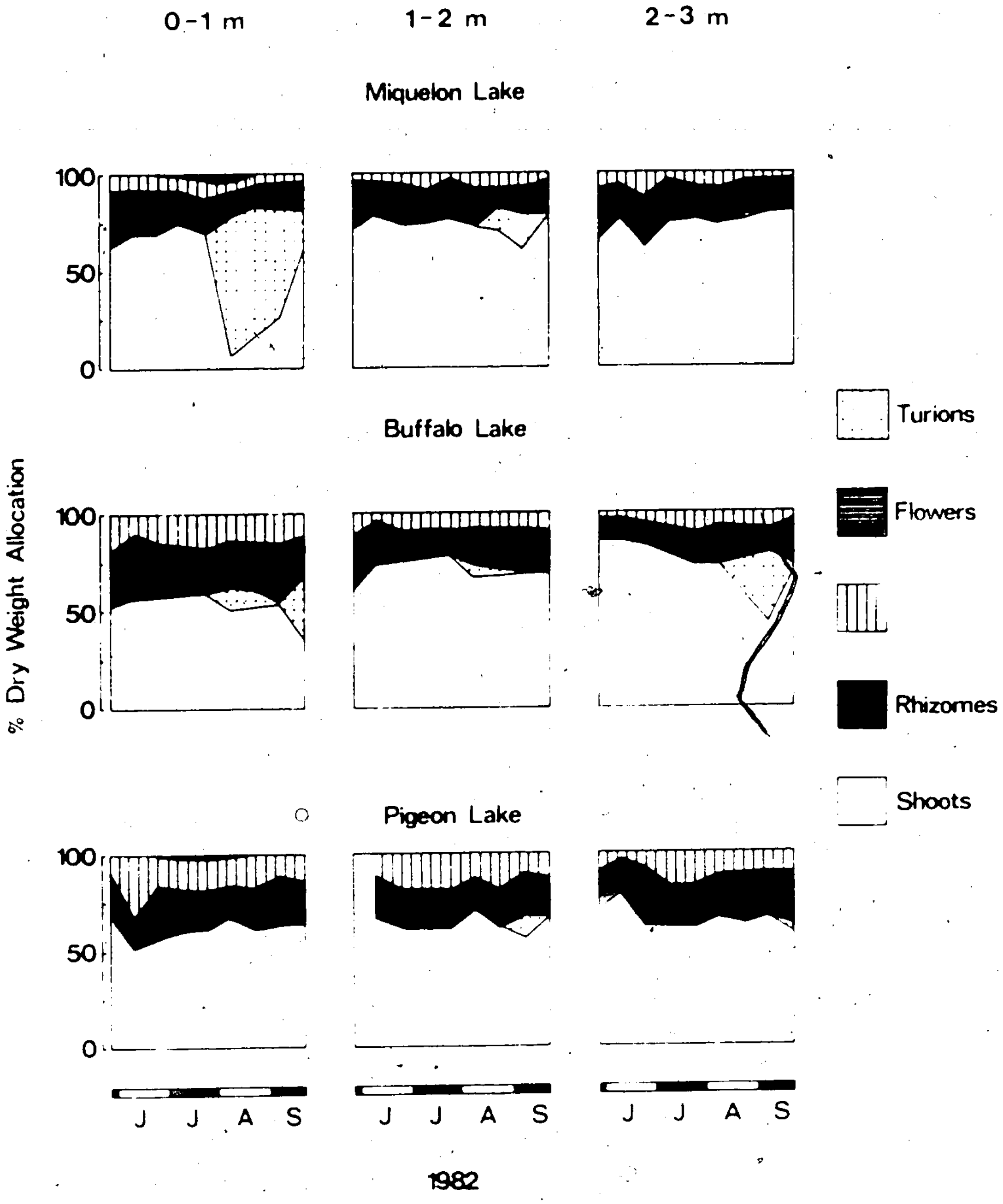

Fig. 9 Seasonal variation in dry weight allocation

Table 8. Percentage of dry weight (mean + range) allocated to sexual (flowers, fruit, peduncles) and asexual (turions) reproduction in reproducing individuals only.

	Pigeon L.	Buffalo L.	Miquelon L.
Asexual	66.0 (61.6-70.3)	55.8 (25.3-88.6)	76.2 (34.0-93.8)
Sexual	2.0 (0.5-3.5)	---	2.3 (0.6-6.2)

Three to six percent of the total net assimilate is allocated to sexual reproductive parts (reproductive effort) and the remaining portion to vegetative growth. The proportion of dry weight allocated to rhizomes does not vary significantly (Fig. 9, Table 8) but percent allocation to shoots is positively and to roots negatively correlated with salinity. That is, the weight of roots relative to shoots decreases with increasing salinity.

Allocation of dry weight to sexual and especially asexual reproduction increases with lake salinity (Fig. 9). Reproductive effort in flowering individuals is less variable (no data from Buffalo Lake) among lakes (Table 8); however, the proportion of plants flowering increases at high salinities (Table 7). Few seeds were collected because wave-action often removes the flowering peduncles prematurely, and no seedlings were ever found in this study. The number of turions per individual (presented as a percentage of the total weight) and the number of plants producing turions are both positively correlated with salinity. Dry weight allocation in relation to total dry weight rather than by season is shown in Fig. 10. Though little sexual reproduction occured, the individuals producing most of the flowers were larger than the maximums presented in Figure 10 and were not included because of the lack of replicates in these size classes. As presented, flower production and turion development are size-specific while vegetative allocation is invariable.

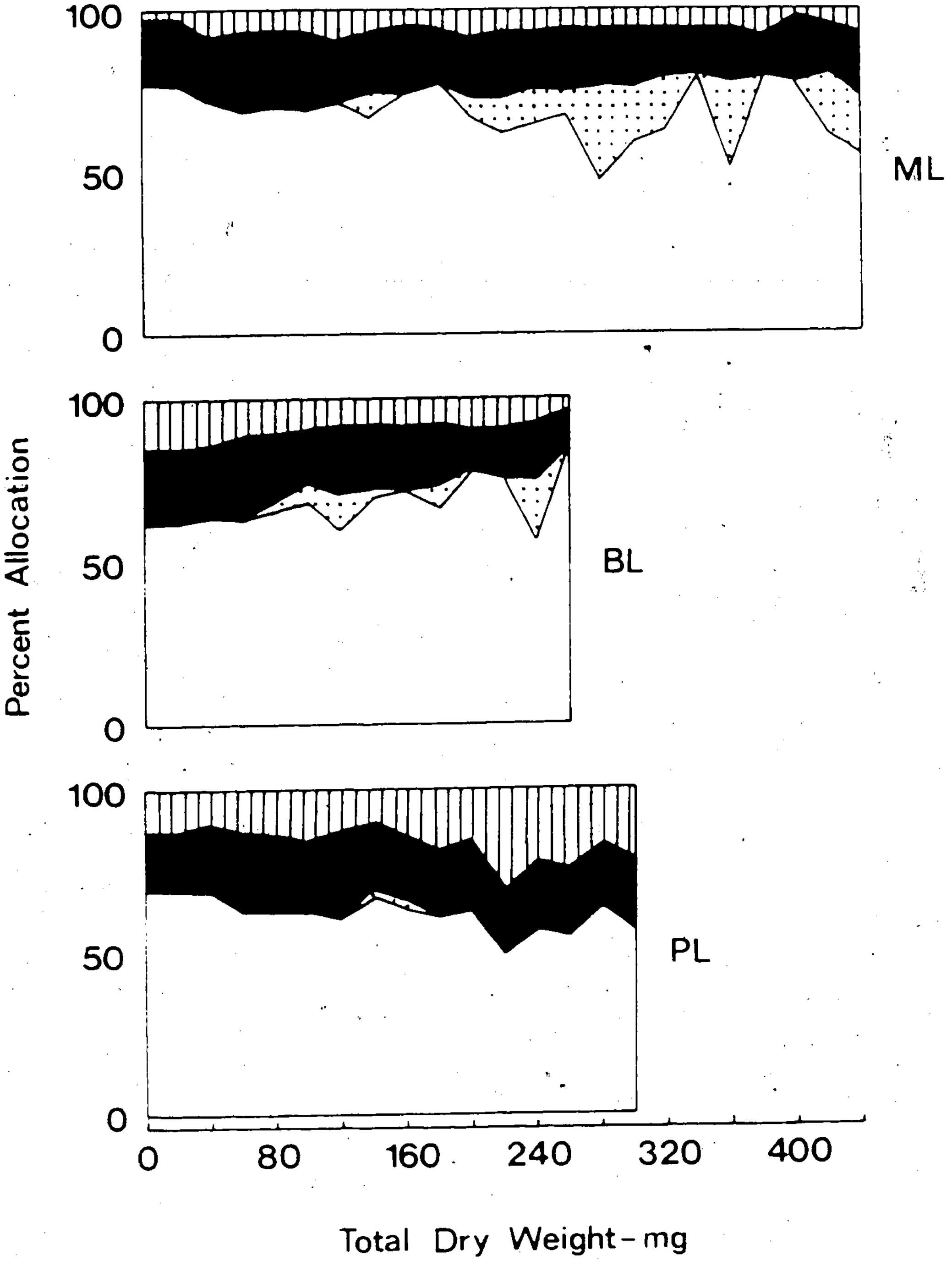

Fig. 10. Dry weight allocation in relation to total plant weight: see Figure 9 for legend.

2.5 Discussion

The relative growth rate of *Ruppia* individuals increased with lake salinity throughout the chemical range studied; however, no such relationship with solute concentrations in the sediment interstices, within lakes, was observed. Considering the magnitude of the growth differential between freshwater and saline lake plants, *Ruppia* appears limited in freshwater. No single limiting factor was identified nor were symptoms of a specific nutrient deficiency observed. However, the fact that levels of cytoplasmic proline are correlated with salinity suggests that osmotic effects are as important as any particular ion (Brock 1979). Surveys demonstrate *Ruppia*'s affinity for high concentrations of solute regardless of the major ions (Rawson and Moore 1944, Moyle 1945, Clapham et al 1968, Moore 1973, Davis and Tomlinson 1974, Moore and Goodall 1974, Reynolds and Reynolds 1975, Verhoeven 1979, Brock 1982). Locally, sulphate concentrations are the most variable over the gradient studied, and may be the primary solute.

Variations in growth rate, reproductive output and allocation of net assimilate in *Ruppia* along the chemical gradient were characteristic of other wild perennial plants under moderate nutrient stress (Chapin 1980 and references within). These symptoms include decreased growth rate, reproductive effort and, to maximize nutrient intake, increased root:shoot ratios (Specht and Groves 1966, Clarkson 1967, Rorison 1968, Dennis and Johnson 1970, Christie and Moorby 1975, Grime 1977, Grime 1979). The similarity between relative growth rates (in sites 2 and 3) of the two saline lakes indicates that the most favorable salinity for vegetative growth is not substantially different than in Miquelon Lake. The salinity of this lake (6.2‰ TDS) is similar to the most favorable salinity for *Ruppia* cultured in Europe (3.8‰ Cl or 6.8‰ S)(Verhoeven 1979), despite the differences in ion proportions. The different osmotic effect, however, of the dominant salt may account for differences in maximum salt tolerance (Reynolds and Reynolds 1975). For example, the negative effect of $MgSO_4$ is only half of the equivalent amount of NaCl (Verhoeven 1979).

Although sexual and vegetative reproduction are highest in the most saline lake (Miquelon), estimates of reproduction in general are very low in all lakes. The effects of solute concentration on sexual reproduction are as reported by Harper and Ogden (1970) and Andel and Vera (1977). That is, reproductive effort (production of peduncles, flowers and fruits as a proportion of the total plant weight) was similar in all flowering individuals while the number of individuals flowering increased with increasing mineral supply. Because of slow growth rates, plants from infertile water grow vegetatively for a long time before accumulating enough reserves to reproduce (Grime 1979). The proportion of net assimilate allocated to sexual reproduction, in individuals that flowered, was similar to *R. megacarpa* , as reported by Brock (1982). Vegetative reproduction was more plastic and prolific than sexual reproduction. It is also important to recognize the seasonal variability of reproduction in such environments, not accounted for in this study.

Within-lake distributions of *Ruppia* reflect the growth and reproduction of individuals in each lake. Turions and plant fragments are likely most important in colonizing sites within each lake. Sexual reproduction, on the other hand, because of a late and prolonged developmental phase, is susceptible to interruption by turbulence prior to fructification. Also, floral production is restricted by low light levels to shallow sites and seeds have different requirements than vegetative fragments for growth (Brock 1982). This may explain why almost no seeds were collected and no seedlings were observed in this study. Consequently, the entire lake population may comprise clones or ramets of just a few genotypes or genets. Low frequency of occurrence of *Ruppia* in the shallow waters of Pigeon Lake (where an annual growth strategy may be well suited to the exposed shorelines) may be the result of low seed production in freshwater. Infrequent and site-specific occurrence of *Ruppia* in freshwater reflect then not only the physical suitability of the lake but also the reproductive and growth capabilities of individuals within the population. Whereas growth and germination of vegetative propagules in freshwater appeared retarded unless anchored to the substratum, propagules in saline lakes produced roots and new shoots while suspended. Site specificity and correlation of certain growth variables with sediment salinity in the freshwater population suggest the sediment could be an important nutrient source particularly in infertile water.

Since each permanent transect is on an exposed shoreline, results from this study represent the most and least favorable growth, respectively, for freshwater and saline lakes. Therefore, results from this field season are likely conservative.

Unexpectedly, variation in shoot production (ramets) did not correspond to variation in dry weight of *Ruppia*. While relative growth rate is positively correlated with salinity, shoot production and relative rhizome growth rate are not, between and within lakes. Anderson (1978) also observed differences between shoot and dry weight production of *Potamogeton pectinatus* on various sediment treatments. However, in studying the effects of light and temperature on hydrophyte growth, Barko et al (1982) reported a close relationship between shoot density and biomass. Watson (1984) suggests from her analysis of *Eichornia* (1984) that those ramets stimulated to initiate flowers and thus convert to vertical shoot extension commit many lateral meristems, otherwise allocated to ramet production to production of continuation shoots on the vertical stem. While *Ruppia* does not grow as fast in freshwater as in saline water perhaps less frequent vertical growth in freshwater and, therefore, allocation of available photosynthate to ramets may account for increased shoot production in freshwater. The concommitant increase in roots with increased ramet production may also explain greater root allocation in low salinity.

In addition, and contrary to saline-lake plants, freshwater-lake plants that do flower initiate little or no vertical growth: just a flower on a peduncle. Kiørboe (1980) also observed little vertical extension in *Ruppia cirrhosa* in a low salinity fjord. Interestingly, freshwater individuals retain this character when grown in saline water (personal observation). Consequently, lateral meristems are continually allocated to ramet production instead of vertical extension. This decrease in shoot production and compensatory increase in leaf production, in the form of ramets, maybe a response to increased interspecific competition for light as hypothesized by Abrahamson and Gadgil (1973).

So, why does *Ruppia* not occur more frequently in low salinity lakes? Verhoeven (1979,1980) observed that *Ruppia* was competitively excluded from salinities most favorable for growth. This study suggests that *Ruppia* in Alberta is an obligate halophyte, and limitation at low salinities is, in part, chemically based. Granted, slow growth rates render *Ruppia* susceptible to exclusion by fast vertically-growing freshwater hydrophytes, particularly in sheltered ponds.

However, success in infertile water may, in part, be determined by sediment mineral content and the extent of root uptake at low salinities.

3. Some Ecological Consequences of Biphasic Mineral Nutrition in a Submersed Hydrophyte, *Ruppia occidentalis* S.Wats.

3.1 Introduction

Rooted hydrophytes (emergent, floating leaved, and submerged) experience two chemically different and somewhat independent environments simultaneously, the water and sediment phases. Many hydrophytes are able to absorb nutrients from both these phases to varying degrees. Absorption from the water phase by the shoots becomes increasingly important with the greater degree of plant submergence (Denny 1972a, Cowgill 1973a,b, 1974).

Within the submersed hydrophyte group (Sculthorpe 1967), roots as well as shoots are an important site for nutrient absorption, but studies to locate the primary absorption site for various species conflict (Denny 1980). Some studies suggest that the major site for absorption may vary throughout the life cycle of the plant. Less is known about what factors determine the major absorption site.

Denny (1980) hypothesized that the major site of absorption and direction of translocation depends on factors such as the anatomy and morphology of the plant, the solute in question, the need for distribution and the physiological state of the plant. Earlier Denny (1972a) suggested the concentration of solutes in the water and sediment phases may influence the primary location of absorption. Recent experiments have corroborated this hypothesis by demonstrating the importance of root uptake in nutrient-deficient water. Nichols and Keeney (1976) demonstrated that nitrogen uptake by shoots of *Myriophyllum spicatum* was twice that by roots, but when the plant was grown in nitrogen-deficient water, nitrogen uptake by the roots could supply all the nitrogen requirements for normal growth. In long-term studies, submersed hydrophytes have been shown capable of mobilizing not only nitrogen but also phosphorus, sulphur and micronutrients from the sediment when the nutrients were absent from the water phase, such that all growth requirements were satisfied (Barko and Smart 1979, Barko 1982, Huebert and Gorham 1983).

The interaction between the major absorption site and water fertility, and its ecological implications were examined for *Ruppia occidentalis* S. Wats. This hydrophyte is found predominantly in the saline lakes of Alberta, and only occasionally in freshwater (range of total dissolved solids 1.2 - 23.0 ‰). The paucity of *Ruppia* in freshwater has been attributed to competitive exclusion (Verhoeven 1979), but the chemical constraints have yet to be fully investigated. Field studies show that *Ruppia* is limited in freshwater by low solute concentrations (Chapter 1) but the importance of solute source (sediment *versus* open water) is unknown.

Therefore, the effect of water and sediment chemistry on the major site of absorption (root *versus shoot*) was examined in *Ruppia occidentalis*. Ecological predictions, suggested by the hypothesis that sediment becomes a more important solute source in freshwater were then tested in the field.

3.2 Methods

3.2.1 Hypothesis

Because roots and transport systems are poorly developed it was once believed that submerged plants absorbed salts primarily from the water through the shoots. However, those nutrients that are less soluble (and thus less available) in an aerobic environment (nitrogen, phosphorus) or soluble ions present in low concentrations are not readily available from the water. In these cases the nutrition of hydrophytes rooted in the substratum, where nutrient solubility and concentration are enhanced, will depend on both root and shoot absorption. Thus, absorption in infertile water will be root-dominated, relative to shoot absorption. There are several important assumptions of this hypothesis, which have been tested previously. It has been shown that solute concentrations in the interstitial water of the substratum are greater (more than 50 times greater) than in the overlying water (Lee 1970 in Kangasniemi 1975, Chapter 1). In Wisconsin lakes very little relationship was found between solute concentrations in the sediment and overlying water. Recent studies have also shown that hydrophytes are capable of absorbing solutes (available in either aerobic or anaerobic water) such as nitrogen, phosphorus, sulfur, potassium and micronutrients from the roots (Nichols and Keeney 1976, Barko and Smart 1979, 1980, 1981, Huebert and Gorham 1983). Nichols and Keeney (1976) and Bole and Allan (1978) have also confirmed the condition that elemental composition of the shoots increases with increasing solute concentrations in the water. However, the capability of absorbing sulphate by shoots and roots must be demonstrated in *Ruppia* before any ecological predictions of this hypothesis can be tested.

3.2.2 Site Description

All plants used in the laboratory experiment were collected from Miquelon Lake (53°15' N, 112°53' W) in central Alberta. Miquel Lake, being moderately saline (6.3 ‰ TDS, parts per thousand total dissolved solids), is considered to be an ecologically central habitat for *Ruppia*. A field survey of *Ruppia* was conducted in Miquelon, Buffalo (52°50' N, 112°50' W) and Pigeon (53°01' N, 114°02' W) Lakes, listed in order of decreasing salinity (6.3 - 0.25 ‰ TDS). All three habitat types are common in Alberta. A transplant experiment was conducted in a small pond of the Devonian Botanic Gardens (53°24' N, 113°46' W) located 16 km southwest of Edmonton. The pond has no *Ruppia* but the water is chemically similar to Pigeon Lake. Therefore it is considered to be an ecologically marginal habitat. The substratum is organic, underlain by clay. Also, additional sediment, needed for culturing, was collected from one site in Wabamun Lake (53°30 N, 114°40 W), a large freshwater lake, and has been described chemically by Huebert and Gorham (1983).

3.2.3 Root Uptake

Ruppia was collected from one site in Miquelon Lake. All individuals likely originated from the same genet because the plant is rhizomatous. In the laboratory, the plants were stored at 6°C under a 24 hour low light regime.

Using two sediment types (Wabamun and Miquelon Lakes substrata) and four sulphate treatments we tested whether the sediment and water were viable sources of sulphate. Sulphate concentrations of 0, 3.5, 75, and 230 mg l in a water medium similar to the freshwater Pigeon Lake were used (Table 9). Phosphorus and micronutrients were not added to the water phase because it has been shown that uptake of these solutes from the sediment is sufficient to satisfy all growth requirements of other species as well as *Ruppia* (Barko and Smart 1979, Huebert 1983, unpublished data on *Ruppia occidentalis*), and will not affect the uptake of another solute (Barko 1982). Algal production in the water phase is thereby reduced.

Table 19. Chemical characteristics of each sulphate treatment. Chemical results reported as mg/l. Percentage transmission of photosynthetically active radiation (PAR) is also reported.

Parameter[1]	1	2	3	4
Sulphate added	230.0	75.0	3.5	0.0
Alkalinity $CaCO_3$	130	140	120	130
pH	8.9	8.8	8.8	8.8
Sulphate Dec 21	162.0	58.0	5.0	0.0
Jan 4	177.0	53.9	7.5	6.8
Jan 19	168.0	55.0	14.0	7.2
PAR Transmission [illegible]	26.0	30.0	37.0	26.0
Conductivity µmhos cm^{-1}	660	470	385	310
Basal Medium				
Na_2SO_4	167.1	-	-	-
Mg_2SO_4	70.5	70.5	2.8	-
$CaCl_2$	54.7	54.7	54.7	
KCl	15.0	15.0	15.0	15.0
$NaHCO_3$	150	150	150	150
$NaNO_3$	0.105	0.105	0.105	0.105
$MgCl_2 \cdot 6H_2O$	83.4	83.4	83.4	83.4

Each plantlet (roots and shoots attached to one rhizome node), stored at 6°C, was randomly selected from newly rooted individuals to ensure viability and each was placed in a 1 litre polyethylene pail containing 600 ml of sediment. Two centimeters of acid-washed silica sand (20-30 mesh, Ottawa grade) were added to the surface of the sediment [illegible] the free exchange of ions between the water and [illegible] phases (Hynes and Grieb 1970). Plants were [illegible]our 750 litre tanks (69cm X 114cm X 103cm high) made of epoxy-coated fibreglass. The large water:sediment volume ratio minimizes the effect of sediment leakage on water treatments (Barko and Smart 1979, Barko 1982, Huebert 1983). Water treatments were randomized among the 4 tanks. Sediment treatments, replicated 6 times per tank, were also randomized within each tank. The experiment was conducted in a controlled environment chamber under constant temperature (24°C) and light (8 dark:16 light, 350 μEinsteins $m^{-2}sec^{-1}$) and weekly chemical monitoring. After seven weeks plants were harvested, measured (rhizome and shoot length), dried (48hrs., 80°C.) and weighed. Results were analyzed by a two-way ANOVA and Student-Newman-Keul multiple comparison of the water treatments after a F-max test for homogeneity of variances (Sokal and Rohlf 1981).

3.2.4 Substrate Affinities

According to the biphasic nutrition hypothesis, the sediment interstices will become the limiting source of solutes for hydrophytes in nutrient-poor water. Therefore, the distribution of *Ruppia* will be expected to be sediment-dependent in freshwater, relative to saline water.

The dependence of *Ruppia* occurrence on substratum type was examined using survey data acquired by diving at 0.5-0.75 m intervals along transects orientated perpendicular to shore. At each interval, cover and composition of hydrophytes along a circular belt, 4m in diameter and 0.5m wide was estimated (as in Chapter 1). circular transect was estimated (as in Chapter 1). A tactular (hand) estimate of substratum texture accompanied each cover estimate. Duplicate sediment samples from 30 sites were analyzed using a modified hydrometer method and compared to tactular estimates of the same sample with a Sign Test (Sokal and Rohlf 1981). To test the hypothesis that sediment affinity interacts with water solute concentration, the distribution of freshwater and saline lake populations were compared in relation to substratum. However, sediments were uniform in Miquelon Lake; therefore, only data from Pigeon Lake and two large bays, of high but different salinities, in Buffalo Lake were compared (Table 10). The contingency of *Ruppia* occurrence on substratum type was compared to the random expectation by a X^2 Goodness of Fit test of a 2X6 contingency table (6 sediment classes).

There are reasons other than nutrient requirements to expect greater sediment affinities in infertile water. Greater species richness in freshwater may result in

Table [illegible]. Summary of the chemical differences among the three water bodies (from Haag and Noton 1981a,b). Ion concentrations reported in mg/l; TDS = total dissolved solids.

Parameter	Pigeon L.	Buffalo L. Secondary Bay	Buffalo L. Main Bay
TDS	174.8	1557.0	2165.0
SO_4	2.7	376.0	419.0
Conductivity (μmhos cm^{-1})	265.4	1985.0	2453.0
N (soluble Kjeldahl)	1.0	2.0	2.5
P (total soluble)	0.034	0.005	0.010

competitive exclusion of *Ruppia* from certain substrata. Consequently, it was attempted to distinguish sediment affinities from the effects of competition in the freshwater site. Using the same data set, the cumulative frequency distribution of canopy cover-classes on coarse to fine sediments and examined the effect of fine *versus* coarse sediment on the percentage cover of *Ruppia* along a range of canopy cover-classes was compared. Canopy cover comprised the sum of the cover of all vascular plants and *Chara*. The cumulative distribution of sediment types was compared using a Kolmogorov-Smirnov Two Sample Test (Sokal and Rohlf 1981).

3.2.5 Transplants

An additional ecological prediction of the hypothesis is that the colonization of marginal freshwater habitats by *Ruppia* may be determined by the substratum, not the water chemistry.

The effect of sediment on colonization in freshwater was tested experimentally. *Ruppia* from Pigeon and Miquelon Lakes was transplanted into a small freshwater pond located in the Devonian Botanic Gardens. Transplants were introduced in 1 litre polyethylene pails with 1 of 2 sediment treatments (Miquelon L. and Pigeon L. sediments) or a control sediment(from the Botanic Gardens). Each sediment treatment was replicated 10 times, 5 replicates for individuals of each lake population.

3.3 Results

3.3.1 Root Uptake

In a two-way analysis of variance sediment and water treatments significantly effected shoot (tiller) production. Significant differences in yield among sulphate treatments were restricted to the sixth and seventh week (Fig. 11). The number of shoots produced in the 3mg/l sulphate treatment was significantly less ($p<0.05$) than in 230mg/l SO4 when on either freshwater or saline substratum (Table 11). Regardless of sediment type, growth in a medium lacking sulphate was not significantly different than either 3 or 75 mg/l SO4 and no deficiency symptoms were observed. In fact, mean growth in water lacking sulphate exceeded growth at 3 mg/l sulphate (Fig. 11). Such a trend was evident throughout the 7 week experiment (Fig. 11). Although this trend is not statistically significant it is consistent on both sediment types and in two other experiments prior to this. It is significant in that the 0 sulphate treatment is the only one where growth differences correspond to sediment sulphate differences. Although the resurgance of growth in the minus-sulphate treatment was evident in both sediment types, the increase, relative to 230 mg/l sulphate was greatest on the saline-lake substratum from Miquelon Lake (Fig 11, Table 11). Horizontal growth of the rhizome was more variable among treatments than tiller production but exhibited the

Table 11. Differences in various growth attributes among plants from each sulphate treatment; expressed as mean± SE. Growth on saline sediment (M) and freshwater sediment (W) within each water treatment is reported (n = 8). All measurements taken after 4 weeks.

		Sulphate Concentration			
Growth Parameter		0.0	3.5	75.0	230.0
Shoot number	M	5.0±0.58	3.4±0.6	4.9±1.16	5.0±0.6
	W	5.6±1.25	5.2±0.90	7.0±1.05	9.1±1.7
Shoot number (% of 230mg/l trmt.)	M	100	68	97	100
	W	61	57	77	100
Vertical growth (% of plants)	M	37.5	37.5	25.0	12.5
	W	12.5	12.5	-	12.5
Height of apical bud (cm)	M	8.26	5.37	5.22	2.80
	W	2.25	2.36	2.70	2.60
Rhizome length (cm)	M	20.2±2.2	7.9±2.0	25.6±8.1	17.0±4.8
	W	36.3±13.4	32.5±9.2	38.3±7.7	72.0±16.8

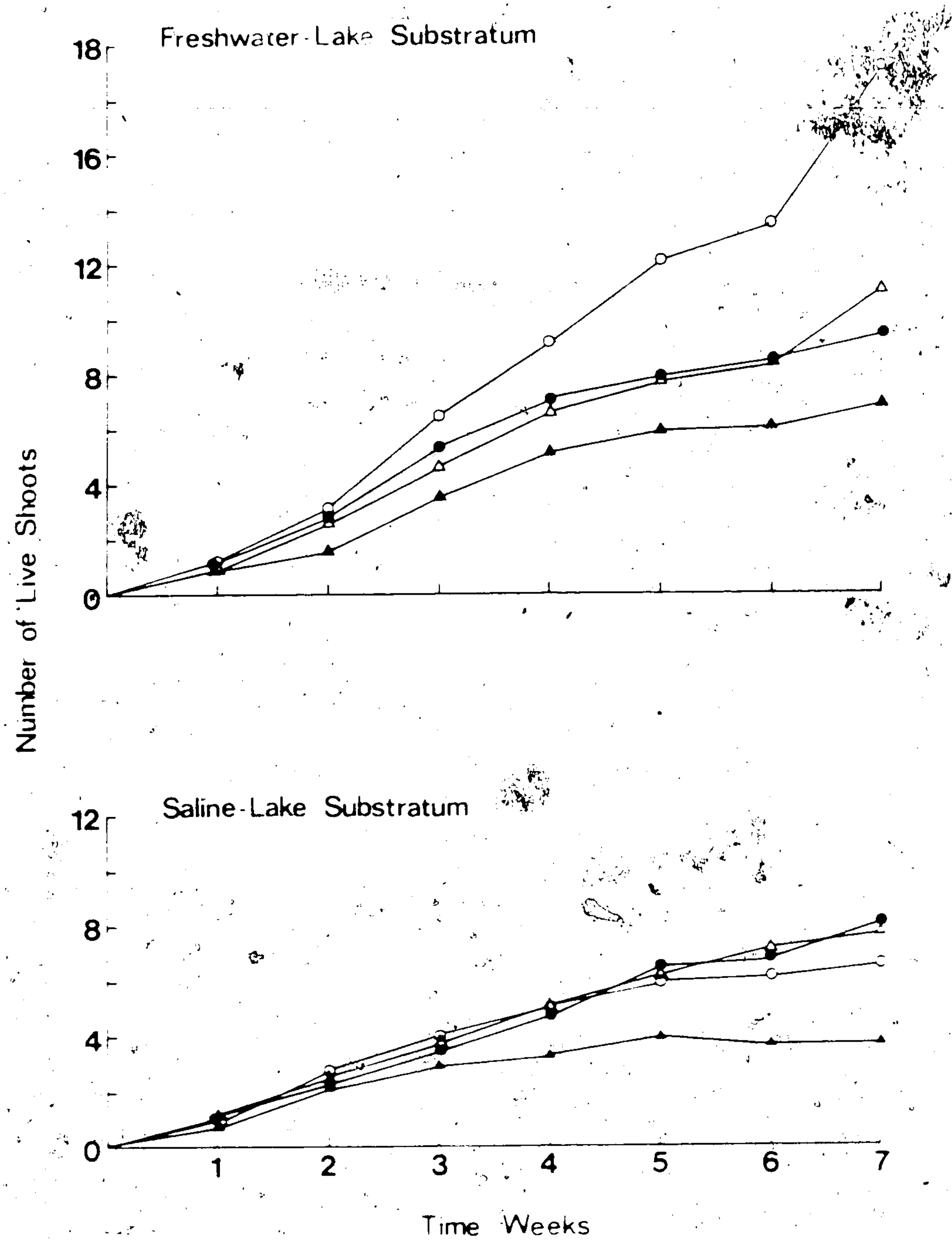

Fig 11 Mean shoot production at 4 sulfate concentrations 230mg l^{-1} —— 75mg l^{-1} ●—● 3.5mg l^{-1} ▲—▲ 0mg l^{-1} ——

same trends (Table 11). With the exception of the sulphate-lacking treatment, more plants in the saline-lake sediment than the freshwater-lake sediment exhibited vertical growth, a precursor to flower development.

Shoot production and rhizome growth were both highest on freshwater-lake mud at all sulphate treatments, particularly the 230mg/l sulphate treatment.

3.3.2 Substrate Affinities

A sign test on paired texture analyses of bulk sediment samples indicates that tactular estimates were not significantly different ($p>0.05$) from laboratory determinations for Pigeon Lake samples. Tactular estimates tended to underestimate coarseness in Buffalo Lake samples. However, combining sands with sandy loams and silts with silt loams minimized the bias in Buffalo Lake field estimates.

Substratum affinities were not uniform throughout the salinity gradient. *Ruppia* exhibits a substrate specificity significantly greater ($p<0.05$) than the random expectation, in the freshwater lake only (Table 12). In both saline lakes, sediment types were colonized in proportions similar to their availability (Fig. 12). Despite their chemical differences there were no differences between the two saline lakes in sediment specificity. Within each saline lake *Ruppia* is sediment indifferent. Not only does sediment affinity vary among lakes but so does the optimum sediment

Table 12. Percent occurrence of *Ruppia* on [illegible] sediment types in three lakes; *, p<0.05.

		Rock	Gravel	Sand	Silt	Clay	Marl	[illegible]
Pigeon Lake		43	30	43	[illegible]	[illegible]	[illegible]	[illegible]
	n	13	27	159	4[illegible]	[illegible]	[illegible]	[illegible]
Buffalo Lake		-	-	[illegible]	[illegible]	[illegible]		
Secondary Bay	n	-	-	[illegible]	[illegible]	22	[illegible]	
Buffalo Lake		[illegible]	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Main Bay	n	14	-	[illegible]	4[illegible]	[illegible]	[illegible]	

Table 13. Mean [illegible] types in three lakes; ** [illegible] among sediment types.

	Gravel	Rock	[illegible]	Sand	[illegible]
Pigeon [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Buffalo [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Buffalo [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

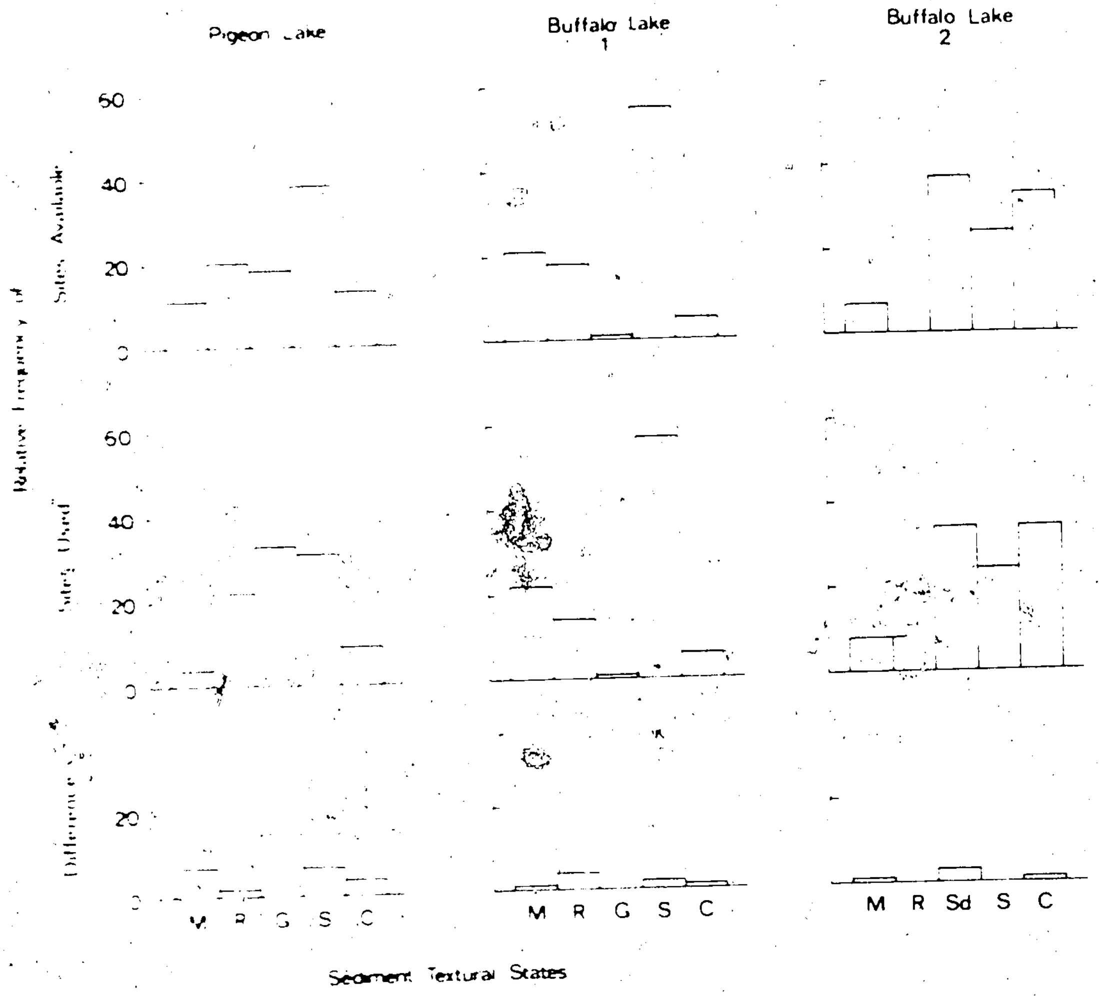

Fig.12. Proportional similarity of substrate sites used and sites available. M-marl R-rock G-Gravel S-silt. Sd-sand. C-clay.

texture. This reversal in textural optima, from coarse to fine sediments, in freshwater and saline lakes, respectively, indicates it is not simply a physical preference (Table 12). In fact coarse sediments, commonly occupied by *Ruppia* in freshwater, are physically least favorable for the growth of such a turbulence-intolerant hydrophyte.

Percentage cover is significantly different among sediment classes ($p<0.05$) within each lake and varied similarly among texture classes in all three lakes (Table 13).

As expected, Pigeon Lake plants experience greater extremes in canopy cover than Buffalo Lake plants. Within Pigeon Lake, the cumulative distribution of fine sediment habitats was not significantly different ($p>0.05$) from coarse sediments along a gradient of canopy cover. (Fig. 13). That is, the probability of encountering another species was equal on coarse and fine sediment sites, in Pigeon Lake. Also, the success of *Ruppia* at any given canopy coverclass , measured as percentage occurrence, is influenced by sediment type (Fig. 13b). In Pigeon Lake, occurrence of *Ruppia* is generally higher on coarse sediments, even where no other hydrophytes occur (percentage occurrence becomes erratic above 45 percent canopy cover because of low number of samples (eg., $n< 6$ in all sizeclasses greater than 45 percent).

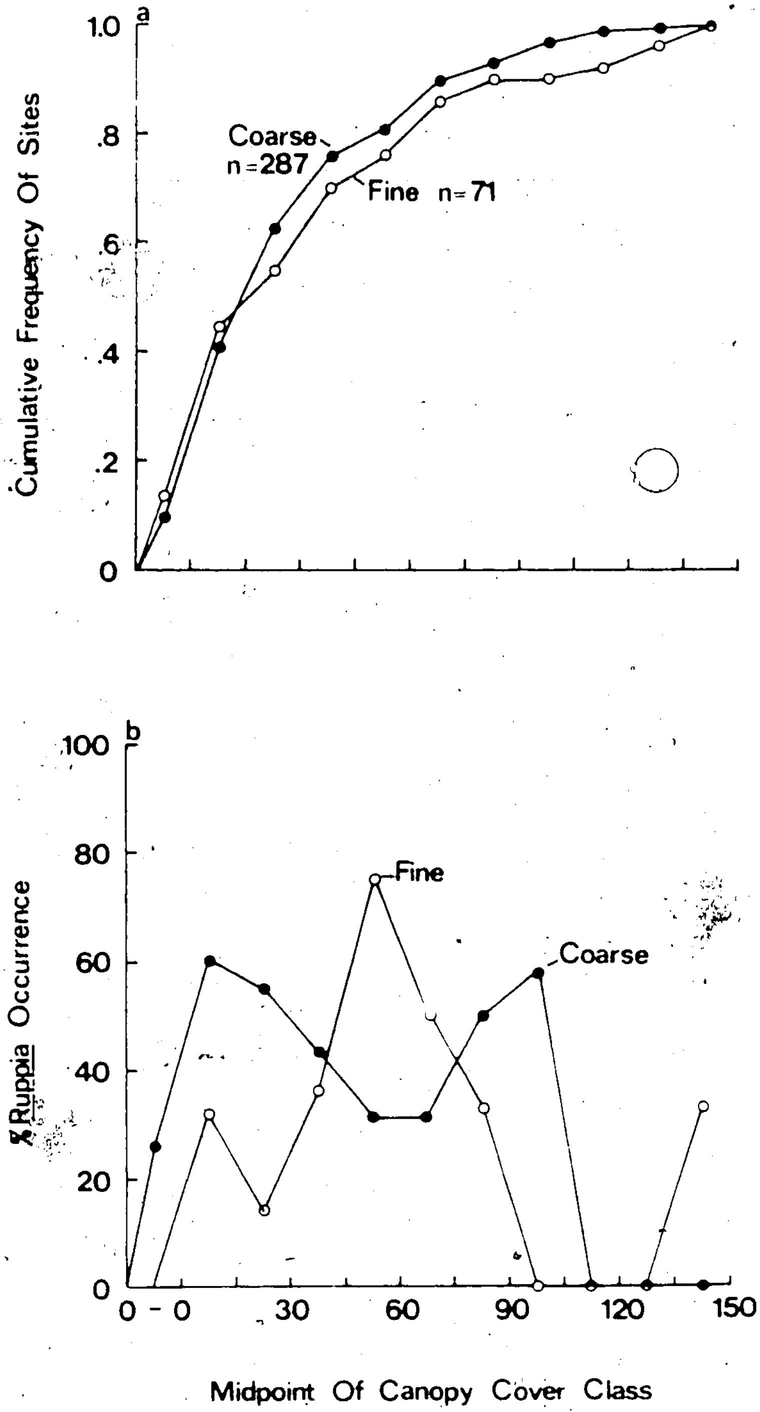

Fig.13. The distribution of fine and coarse substrates of Pigeon Lake on a gradient of canopy percentage cover: b the effect of substrate on Ruppia abundance along a canopy-cover gradient.

3.3.3 Transplants

Unexpected herbivory on shoots reduced the data collection to percentage survivorship of transplants. *Ruppia*, after 6 weeks had experienced lower mortality on the two sediment treatments than on the control (Fig. 14). Though its statistical significance is unknown, mortality was lower on the saline-lake than the freshwater-lake substratum. Also, plants from Pigeon and Miquelon Lakes had similar survivorship.

3.4 Discussion

Roots and shoots of *Ruppia* do not absorb sulphate at a constant rate throughout the range of treatments examined. The mean growth , measured as tiller production, was correlated with sulphate concentrations in the water within the 3 - 230mg l sulphate range. Absorption by roots within this range, if present, is masked by shoot absorption. Where no sulphate was added to the aqueous phase, growth was similar to, and greater than that at 3 mg l sulphate on the freshwater sediment, and,as great as the 230 mg l treatment on the saline sediment. This suggests that *Ruppia* is capable of mobilizing sulphate from the sediment phase, at least when it is lacking from the aqueous phase. Therefore the sediment is a available source of sulphate, the dominant anion in many saline lakes in Alberta. *Potamogeton pectinatus* L., a related species, has also been reported to mobilize sulphate from the sediment (Huebert and Gorham

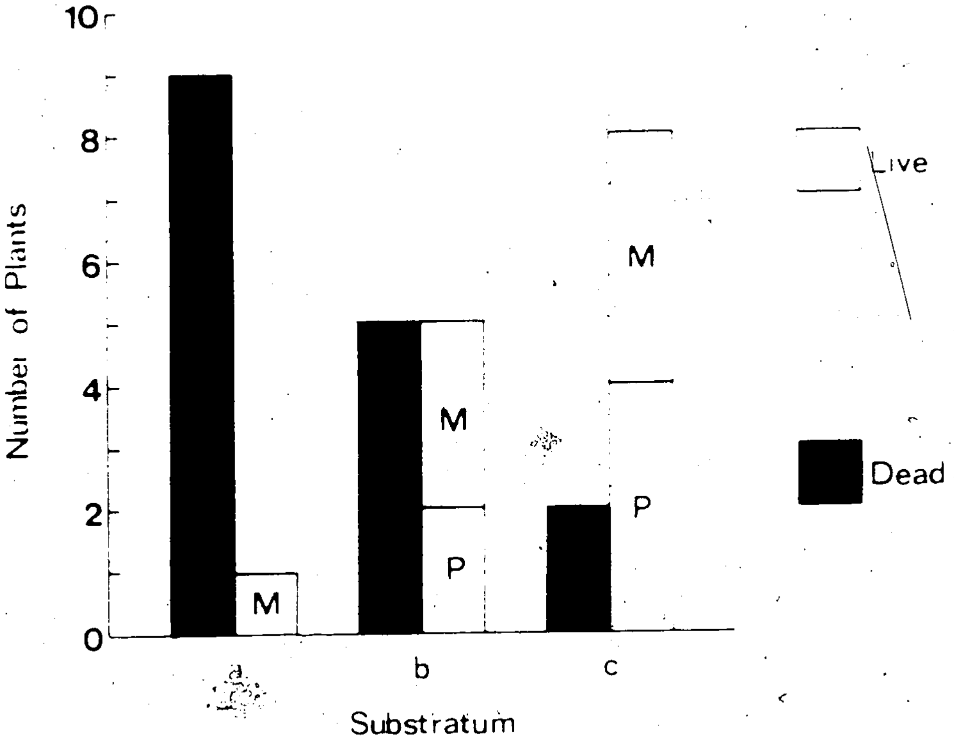

Fig.14 Success of Miquelon and Pigeon Lake transplants into a freshwater pond with: a host sediment. b Pigeon Lake sediment. c Miquelon Lake sediment.

1983) and in similar studies phosphorus uptake by roots satisfied all the growth and reproductive requirements in both P. pectinatus and *Ruppia occidentalis* (Huebert and Gorham 1983, Hubbard and Huebert, unpublished data).

When *Ruppia* was grown in the saline sediment and an aqueous phase without sulphate, growth was greater than in the 1 mg/l treatment, even though the sediment source was identical. This suggests that root absorption dominates in interstitial water not only because of relatively higher solute concentrations in the sediment but also because of the increased capacity of the roots to absorb sulphate. If *Ruppia* utilized [illegible] from the sediment a[illegible]stant rate independent of concentration found in the water or of plant demand, then the growth response over a range of sulphate concentrations would be buffered by a sulphate-rich sediment. Results from this study do not support that prediction. There is no evidence in the literature for changes in the rate of root uptake in hydrophytes. In fact, Bole and Allan (1978) reported that different concentrations of phosphorus surrounding the shoots of *Myriophyllum spicatum* did not affect the amount of phosphorus absorbed from the substratum while higher concentrations in the water raised the concentration of total phosphorus in the plants. However, research with terrestrial plants provides evidence for compensatory changes in root absorption capacity in response to shoot nutrient status (Hoagland and Broyer 1936, Lindgren, Gabelman and Gerloff 1977, Chapin 1980). Whether root uptake rate fluctuates or not, the sediment solute concentrations will be a limiting factor to *Ruppia* in infertile water.

Field results show that *Ruppia* grows on a wide textural range of sediments as Verhoeven (1979) observed. However, substratum specificity is not constant throughout the water-chemical range encompassed in this study. In saline lakes, *Ruppia* occurs on sediments in proportions similar to their availability while, in freshwater, it does not. *Ruppia* occurrence is more sediment indifferent, colonization is more uniform with depth (Chapter Three), and plants thrive without rooting in saline lakes. *Ruppia* is distributed more sediment-specifically when solute concentrations in the open water are low. Although there is no previous ecological evidence for the interaction between the primary source of nutrients and water concentration, Verhoeven (1979) had reported that *Ruppia cirrhosa* was "sediment indifferent" in the saline lakes he examined.

One would also expect *Ruppia* to exhibit similar affinities if measured as percentage cover instead of frequency of occurrence, However, percentage cover among sediment types was significantly different within all three water bodies examined and varied similarly among substratum classes (Gravel<Rock<Clay<Sand<Silt). Variation in percentage cover in all populations (and in frequency in saline lake populations) on different sediment types strongly reflects the physical characteristics of the

substrata and the conditions that created them (highly turbulent, turbid on gravels; sheltered and clear on silts).

In saline water *Ruppia* is dominant, but in freshwater, species interactions may influence hydrophyte distributions. Results in this study suggest that interspecific competition does not significantly affect the spatial organization of *Ruppia* in Pigeon Lake. The probability of interspecific interactions is not different between coarse and fine sediment sites, and the frequency of *Ruppia* occurrence in various canopy cover-classes increases when on sands and gravels. In such a deep uniform lake as Pigeon, it is not surprising competition among hydrophytes is not significant because population densities are so low due to light limitations and turbulence. However, one cannot exclude the effects of competition in "crunch" years (Wiens 1977) on the present distribution.

In addition to within-lake distributions, biphasic nutrition has important implications on between-lake distributions of aquatic hydrophytes, particularly at its lower margin of chemical tolerance. If sediment solutes become a limiting source, it might be expected that sediment type will affect the extent of colonization in freshwater. In contrast, Moyle concluded (1945) that "water chemistry appears to be the most important single factor influencing the general distribution of aquatic plants in Minnesota" and that "type of bottom soil and the physical nature of the body of water greatly influences the local distribution of species within its range of chemical tolerance". Many studies support Moyle's conclusion (Metcalf 1931, Swindale and Curtis 1957, Spence 1964, 1967, Seddon 1972, Wiegleb 1978). However, preliminary experiments in this [illegible] demonstrate the potential importance of sediment type in expanding the distribution of *Ruppia* into freshwater habitats. Although the physical and chemical attributes of each treatment are confounded, both treatments were sand and the control was highly organic; all are textures that *Ruppia* has been collected on in saline habitats. Assuming that the effect of substratum texture does not change with water salinity, the differential survival of *Ruppia* transplants in the Botanic Garden Pond can be attributed to chemical differences among sediments. likely due to chemical differences among sediments.

Verhoeven's autecological study reveals similar evidence, though circumstantial in nature (Fig. 15). Both modal salinity and the salinity range of *Ruppia* are considerably lower in France than the Netherlands. However, *Ruppia* habitats are not only less saline in France but also larger in surface area and more frequently have coarse substrata. Similarly, in Alberta (Hamilton 1980), large freshwater lakes with coarse sediments appear to most likely contain *Ruppia*. Perhaps the high organic content in sheltered sediments inhibits *Ruppia* from growing in freshwater.

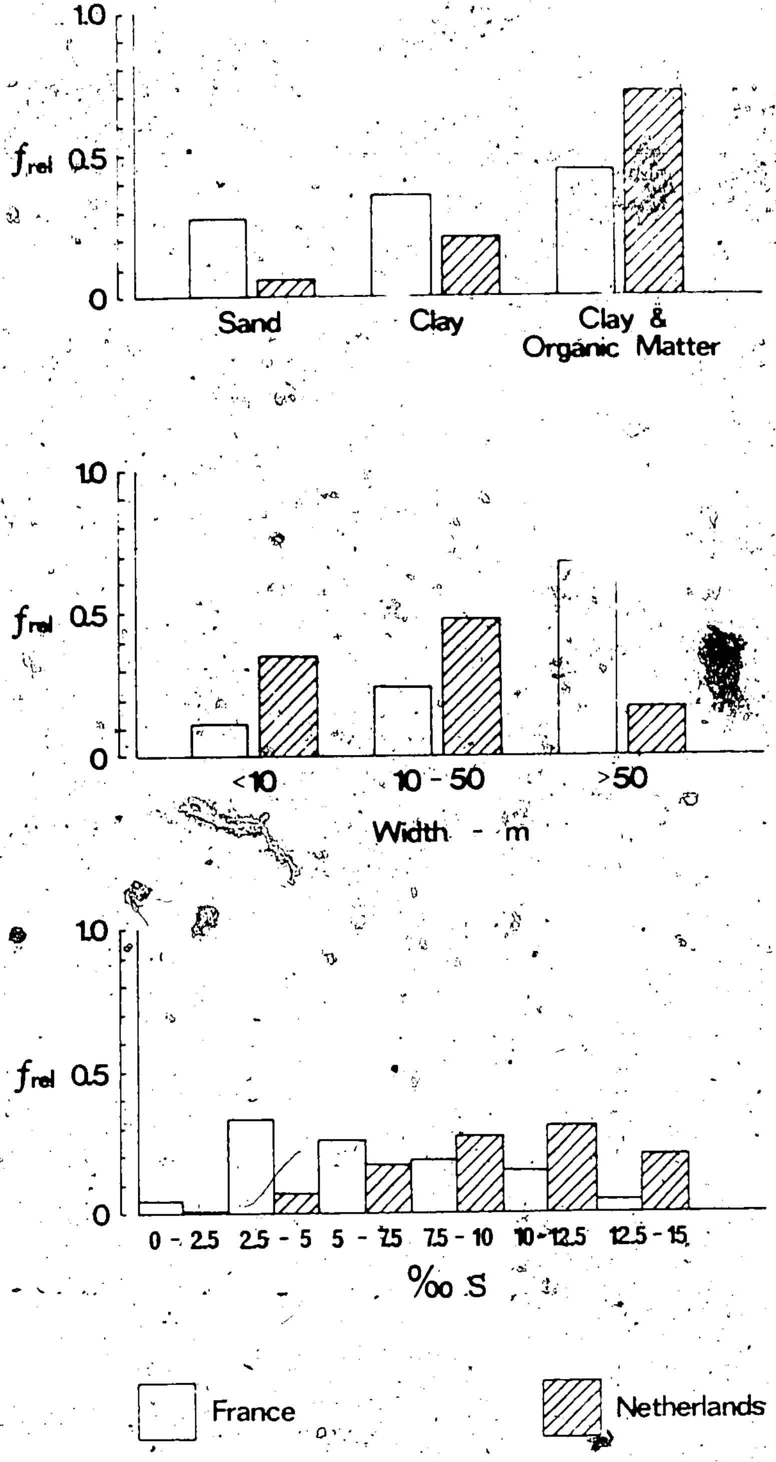

Fig.15: Ruppia habitat distributions in France and the Netherlands (from Verhoeven, 1979).

This study suggests that aquatic plants exhibit considerable plasticity in physiological processes such as bip[illegible] mineral nutrition. From laboratory experiments and field examination, it seems sediment plays a variable role in the distribution of *Ruppia* and has some nutritional basis.

4. Intraspecific Variations in Growth Along Water and Sediment Salinity Gradients in Ruppia occidentalis S. Wats., a Submersed Hydrophyte

4.1 Introduction

Lake chemistry has often been regarded as a dominant factor influencing the distribution and abundance of aquatic plants (hydrophytes; Denny 1980). Chemical differences among lakes result in substantial environmental heterogeneity, and populations in different lakes are subject to various degrees of isolation. Yet, there has been few demonstrations of differentiation and little consideration of the important selective forces in hydrophyte populations. The existence of chemical ecotypes or races associated with distinctive chemical environments is widespread in terrestrial plants (Kruckeberg 1951, Bradshaw 1952, Walker 1954, Kruckeberg 1957, Wilkins 1957, 1960a, 1960b, Antonovics et al. 1971); however, there is little published evidence of genetic differentiation within hydrophyte species. Wooten (1970, 1972) identified nutrient ranges in submersed soils that favoured different ecotypes of *Sagittaria*, an emergent hydrophyte. Pearsall (1920), Misra (1938) and Anderson (1978) all reported that growth of some *Potamogeton* species was greatest on sediments from which the plants had been collected, but no experimental analyses of the relative portance of genetic and environmental effects on population variation [illegible]ophytes have been ignored in the literature.

Rooted submersed hydrophytes can respond differentially to two different sources of solutes, the sediment and the overlying water, through the roots and shoots, respectively. The relative importance of sediment and water solute concentrations, and of root and shoot absorption capacity, has long been studied, but with conflicting results (Denny 1980 and references within). Previous researchers in the past have conducted lake surveys (Metcalf 1931, Swindale and Curtis 1957, Spence 1964, 1967, Seddon 1972, Wiegleb 1978), correlations of plant elemental composition with the environment (Gerloff and Krombholz 1966, Adams et al 1971, Casey and Downing 1976, Welsh and Denny 1976, Denny 1980 and references therein), transplants and cultures (Pond 1905, Denny 1972a, Mayes et al 1977, Barko and Smart 1980, Barko 1982, Huebert 1983), and uptake experiments (Denny 1980 and references within) on species with various degrees of submergence and on related species from different habitats. While these studies have established the importance of both shoots and roots to hydrophyte nutrition, the selective advantages and physiological basis of species differences may be better understood by comparing populations within a species.

Recent studies of naturally occurring lake populations of *Ruppia occidentalis* along a salinity gradient showed [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] water bodies [illegible] correlated with and [illegible] [illegible] species. Previous results (Chapter 3) have also shown that the source of solutes may have important ecological implications. In this study, an ecologically central, saline lake population and a marginal, freshwater population were compared using controlled environment experiments and reciprocal transplants to determine 1) the proportion of observed variation that is genetically imposed, and 2) the relative importance of substratum and water solute concentrations in determining population differences.

4.2 Methods

4.2.1 Study Sites

Plants were collected and transplanted in Miquelon (53° 15' N, 112°53' W) and Pigeon (53°01' N, 114° 02' W) Lakes in central Alberta, Canada. The two lakes are separated by about 85 kilometers. Miquelon Lake is smaller (876 ha compared to 9640 ha), shallower (6.0 m deep compared to 10.0 m) and has a lower species richness (2 compared to 19 hydrophytes) than Pigeon Lake. Most importantly, Miquelon L. has a much higher total ionic content (6200mg/l TDS compared to 250mg/l TDS) then Pigeon L.; the difference being primarily of sodium sulphate. Both lake types are common in Alberta; these two are separated by about 85 kilometers. In the saline site (Miquelon) *Ruppia* is widely distributed, has a high percentage cover, growth rate and reproductive output. In the freshwater lake (Pigeon) *Ruppia* comprises only a small proportion of the total hydrophyte community, and growth rates and reproduction are low. Also, the distribution of *Ruppia* in Pigeon Lake is more site specific and substratum-dependent than in the saline lake. Thus, Miquelon and Pigeon Lakes represent ecologically central and marginal habitats, respectively, for *Ruppia occidentalis*.

4.2.2 Reciprocal Transplants

In mid-June 1983, 8 plants (one plant = the shoot and roots attached to one rhizome node) from each site, equilibrated in tapwater for 4 months, were transplanted in pails into a calm site in 0.5m of water, in each lake. To distinguish the influence of substratum from that of the water 8 additional plants from each site were reciprocally transplanted with the other lake sediment. After 7 weeks, all plants were harvested and surveyed for number of tillers, rhizome length, shoot length and vertical growth, then dried ($80^{\circ}C$, 48hrs.) and weighed. Relative growth rates were calculated to account for differences in initial plant size, using: ln Init. Wt. - ln Final Wt./Time(weeks) (Hunt 1978). Initial weight was estimated using a regression equation of dry weight on leaf number (Pigeon L. Y = 6.9 +

9.6, R^2 0.82, $p < 0.01$; Miquelon L. $Y = 44.7 + 7.56$, $R^2 = 0.90$, $p < 0.01$).

4.2.3 Common Environment Experiment

To test for physiological differences between populations a "common" environment experiment comprising a series of chemical treatments, rather than a single environment, was designed. Plants were collected from southern shorelines in the freshwater and saline lakes in May 1983 and equilibrated in tapwater at 12°C, under low light for 4 months. Plants, each consisting of the shoot and roots at one rhizome node, were randomly selected from those initiating new roots and planted in 1 litre polyethylene pails containing 600 ml of sediment. Four sediment-types, numbered in order of increasing salinity (Table 14) were collected from four different lakes (Buffalo, Miquelon, Pigeon and Botanic Garden Lakes, respectively) to represent the within-lake variations in substratum. Sediments settled for two weeks in the pails while sediment volumes were adjusted and the redox equilibrium reestablished. Once a plant was inserted, a 2cm layer of acid-washed silica sand was spread over the sediment surface to reduce ion leakage into the aqueous phase (Hynes and Grieb 1970). Each sediment treatment was replicated 4 times in each of 4 water-phase treatments in a factorial designed experiment (Sokal and Rohlf 1981). Water treatments spanned the known range of water salinities in which *Ruppia occidentalis* grows (in

Table 14. Chemical characteristics of the four water and four sediment treatments in meq/l unless stated otherwise. Micronutrients (mg/l) in each treatment were the same concentrations.

Parameter	Water Treatments 1	2	3	4
Na	0.77	5.36	20.28	65.30
Ca	1.30	1.59	1.69	1.29
Mg	0.85	2.22	5.34	16.40
K	0.15	0.24	0.64	2.60
SO_4	0.06	1.48	8.82	47.90
HCO_3	2.90	6.90	16.80	32.70
Cl	0.12	0.24	0.64	3.97
CO_3	0.00	0.74	1.69	0.00
TDS(mg/l)	350	800	2600	6000
Conductivity (μmhos/cm)	550	990	2300	6400
pH	8.8	8.8	8.8	8.8
	Sediment Treatments 1	2	3	4
Conductivity (μmhos/cm)	285	1725	5125	7500

Micronutrients

$CoCl_2 \cdot 6H_2O$	8.1	$FeCl_3 \cdot 6H_2O$	2.7g/l	$CuCl_2 \cdot 2H_2O$	8.5
H_3BO_3	0.4	$MnCl_2$	8.8	Edta-Na	2.0
$Na_2MoO_4 \cdot 2H_2O$	0.3	$ZnCl_2$	0.5	K_2HPO_4	0.56g/l

Alberta and each treatment simulated the ionic composition of the Alberta lake of equivalent salinity. A standard phosphorus, nitrogen and micronutrient solution was added to each water treatment since little difference, between field sites, in this respect was measured. Each water treatment was duplicated in two 750 litre fibreglass tanks. The large water:sediment v:v ratio reduced the effect of sediment leakage and ion uptake on the water treatments. The plants were grown at 24°C in a 16hr day: 8hr night photoperiod. Irradiance, measured with a LiCor Quantum Sensor, was 350 Einsteins m s. Throughout the 42 day experiment, conductivity was monitored, tanks were topped up to volume with distilled, deionized water and the pH was regulated to 8.8 by additions of NaOH or HCl. The number of tillers per plant was counted weekly and, after 6 weeks, plants were harvested, dried (80°C, 48 hrs.) and weighed. Although no plants flowered in the 6 week period, extension of the vertical flowering shoot was noted if present. To account for differences in initial weight, relative growth rate was calculated for each plant, using: ln Init. Wt. - ln Final Wt./Time (Hunt 1974). Initial dry weight was estimated using a regression of dry weight on leaf number. Growth attributes from replicate water treatments were pooled and the means were compared in an ANOVA and subsequent unplanned multiple comparisons (Sokal and Rohlf 1981). Results using relative growth rates were similar to results based on dry weight production; therefore only the latter is presented here.

4.3 Results

4.3.1 Reciprocal Transplants

Survivorship in the two lake sites was consistently high for saline-lake (SL) plants, but was variable for freshwater-lake (FL) plants where seven of eight replicates died in the saline-lake site (Table 15). All but one propagule in this treatment was eventually washed away suggesting the importance of root growth and initial establishment. Such high mortality in one treatment prevented a proper two-way analysis of variance of sites and populations from being conducted. Overall, SL plants grew larger than FL plants, and the relative magnitude of population growth in each site indicates a strong site x population interaction (Sokal and Rohlf 1981) (Table 16). This suggests the response to environments differs between populations. Relative growth, root:shoot ratio and shoot (tiller) production within populations was always highest in the "home" (McGraw and Antonovics 1983) site (Table 15). However dry weight and rhizome length (and tiller production in the freshwater site) were not largest in the "home" site (Fig. 16, solid lines). The largest population differences can be attributed to a more plastic response by SL plants to the sites. plastic response to the sites by SL plants. The plasticity in SL plants is manifested in variations in tiller production, not by leaf production per tiller (Fig. 16). The four sediment:population treatment combinations are

Table 15. Reciprocal transplants between Miquelon and Pigeon Lakes: growth expressed as the mean ± SE. FL = plants from Pigeon L. (freshwater), SL = plants from Miquelon L. (saline water).

Lake	Population	N	% Survival	Rt. Sht. Ratio	Rel. Growth Rate week^{-1}	Rel. Shoot Prod. week^{-1}
Miquelon L.	SL	8	75.0	0.32	0.258±.04	0.416±.04
	FL	8	12.5	0.17	0.098±.00	0.116±.00
Pigeon L.	SL	8	87.5	0.13	0.123±.03	0.224±.04
	FL	8	62.5	0.25	0.194±.04	0.224±.03

Table 16. The relative magnitudes of the means of relative growth rate indicating a population x environment interaction.

Lake	Population FL		Population SL	Population	Lake Miq. L.		Lake Pig. L.
Miquelon L.		<		FL		<	
Pigeon L.		>		SL		>	

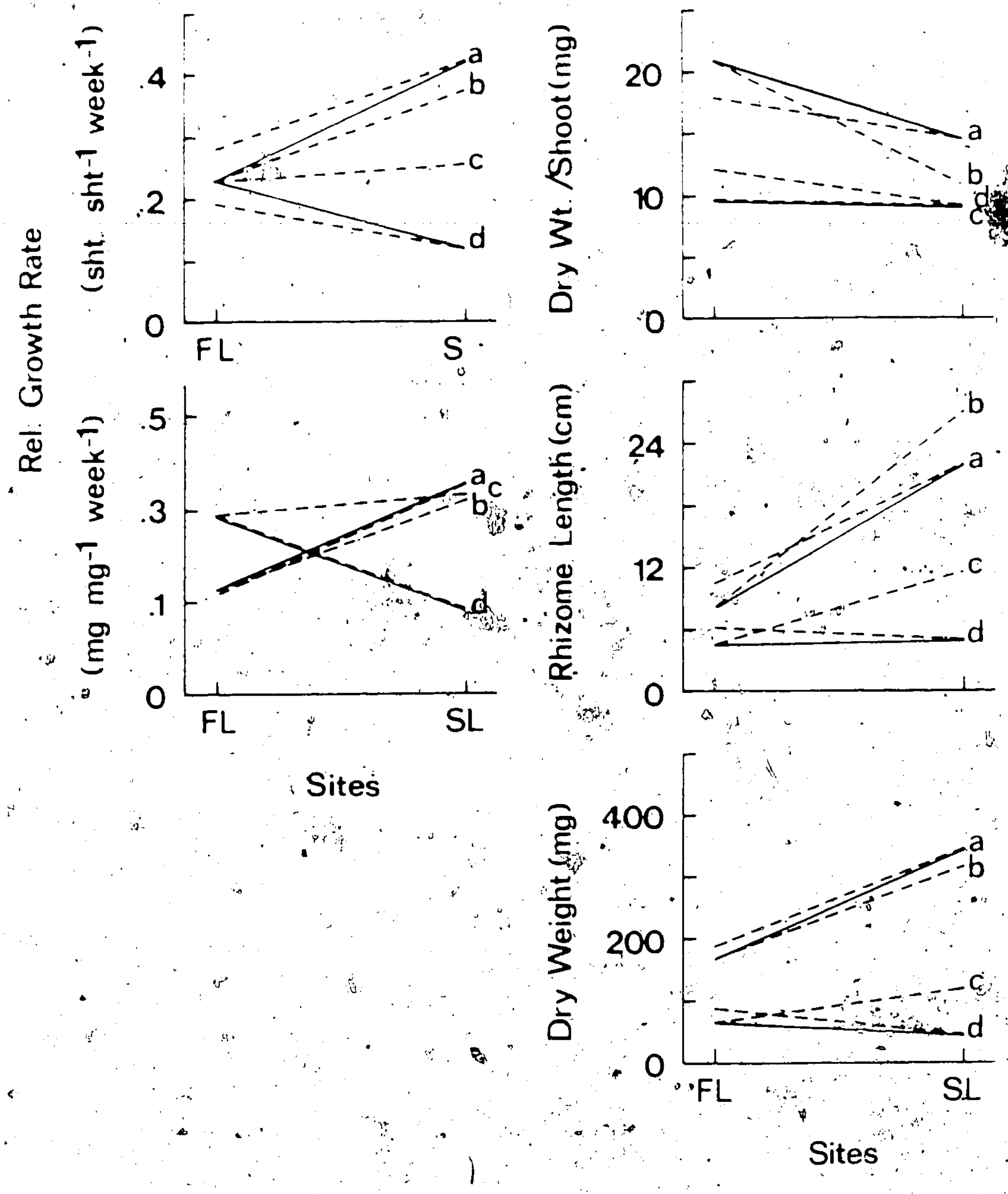

Fig. 16. Growth of a) SL plants on SL substrate, b) SL plants on FL substrate, c) FL plants on FL substrate and d) FL plants on SL substrate transplanted into the freshwater-FL and saline-SL lakes; solid line depicts reciprocal transplants.

also presented in Figure 16 (broken lines). Saline-lake plants have the largest growth difference between sites of the two populations when grown on any one sediment (Table 17). Growth of FL plants differs among sediments as much as SL plants, when in freshwater, but more than SL plants in the saline lake. This trend is evident in both tiller and dry weight production. No flowering or vertical growth was observed within the 7 week period.

4.3.2 Common Environment Experiment

A factorial analysis of variance revealed highly significant main effects of water and sediment ($p<0.01$) on both tiller and dry weight production (Table 18,20). The population effect was highly significant ($p<0.01$) only on dry weight data. However, all interaction terms with the population effects had a significant effect on tiller and dry weight production, suggesting the response to the chemical treatments differed between populations (Table 18,20).

A two-way analysis of variance conducted on tiller data for each population revealed significant differences among water treatments for both populations ($p<0.005$), but significant variation among sediment treatments ($p<0.005$) in the FL plants only (Table 19). The same analysis with dry weights revealed similar relative trends but sediment and sediment-water interaction effects were significant in the SL plants, indicating that water salinity effects depend on

Table 17. Dry weight and shoot (ramet) production differentials between a) sediment treatments and b) lake sites. FL = plants from Pigeon Lake, SL = plants from Miquelon Lake.

a) Lake	Population (shoot prod.) FL	Population (shoot prod.) SL	Population (dry weight) FL	Population (dry weight) SL
Pig. L.	30	56	1	8
Miq. L.	148	41	130	38

b) Lake	Population (shoot prod.) FL	Population (shoot prod.) SL	Population (dry weight) FL	Population (dry weight) SL
Pig. L.	40	151	34	89
Miq. L.	78	136	95	135

Table 18. Analysis of variance of shoot production among individuals from a freshwater lake and a saline lake in response to substrate and water salinity gradients; log-transformed data; $*p<0.05$, $**p<0.01$.

Source of Variation	df	SS	MS	F
Water Treatments	3	25.55	8.52	44.84**
Sediment Treatments	3	6.41	2.14	11.26**
Populations	1	-	-	-
W-S Interaction	9	1.47	0.16	0.84 ns
S-P Interaction	3	3.18	1.06	5.58**
W-P Interaction	3	4.84	1.61	8.47**
W-P-S Inter.	9	4.40	0.49	2.58*
Within Trmts.	32	5.99	0.19	
Total	63			

Table 19. A two-way analysis of variance of shoot production for individuals from the freshwater and the saline lake populations: log-transformed data, *** $p<0.005$, ns not significant.

Source of Variation	df	F -Freshwater	F -Saline
Water Trmts.	3	34.49***	14.19***
Sediment Trmts.	3	2.67***	1.44ns
S-W Interaction	9	1.42ns	2.20ns
Within Trmts.			
Total			

Table 20. Analysis of variance of dry weights among individuals from a freshwater and a saline lake in response to substrate and water salinity gradients; log-transformed data; * $p<0.025$, **<p [illegible]

Source of Variation	df	SS	MS	F
Water Treatments	3	33.87	11.29	37.63**
Sediment Treatments	3	16.15	5.38	17.93**
Populations	1	8.01	8.01	26.70**
W-S Interaction	9	10.83	1.20	4.00**
S-P Interaction	3	3.74	1.24	4.13*
W-P Interaction	3	12.58	4.19	13.97**
W-P-S Inter.	9	8.10	0.90	3.00*
Within Trmts.	32	9.54	0.30	
Total	63			

Table 21. A two-way analysis of variance of dry weights for individuals from the freshwater and the saline lake populations; log-transformed data, *** $p<0.005$, ** $p<0.025$, * $p<0.05$, ns-not significant.

Source of Variation	df	F -Freshwater	F--Saline
Water Trmts.	3	17.27***	6.95***
Sediment Trmts.	3	11.28***	4.21**
S-W Interaction	9	2.16ns	3.27*
Within Trmts.			
Total			

the sediment water treatment (Table 21).

FL plants and SL plants grew largest in the 980 and 2300 µmhos/cm water treatments, respectively, but differences in growth between the two water treatments were not always significant (Fig 17,18, Table 22). Ultimately, neither population grew best in the water treatments most similar to their native habitats. FL plants consistently grew largest on the most saline substratum , but SL plants grew best on 3 of the 4 sediments, depending on the salt concentrations in the water. So, as with water treatments, neither population grew best in its native substratum. In the Botanic Garden sediment, where the effects of substratum are smallest, differences between the populations were small, yet suggested that SL plants were more plastic and had a wider salinity tolerance than FL plants. As substratum salinity increases, FL plants exhibited progressively larger variation in response to water treatments, relative to SL plants. such that growth in the 980 µmhos/cm treatments between populations is significant when grown in the most saline sediment ($p<0.05$,T-Method, unplanned comparison). While overall means do not differ greatly between populations, variation around the mean is greater in FL plants than SL plants, especially in response to sediment treatments (Table 23).

Growth among the water treatments largely reflects changes in solute concentration; its variance is exaggerated or dampered depending of the substratum in which the plant

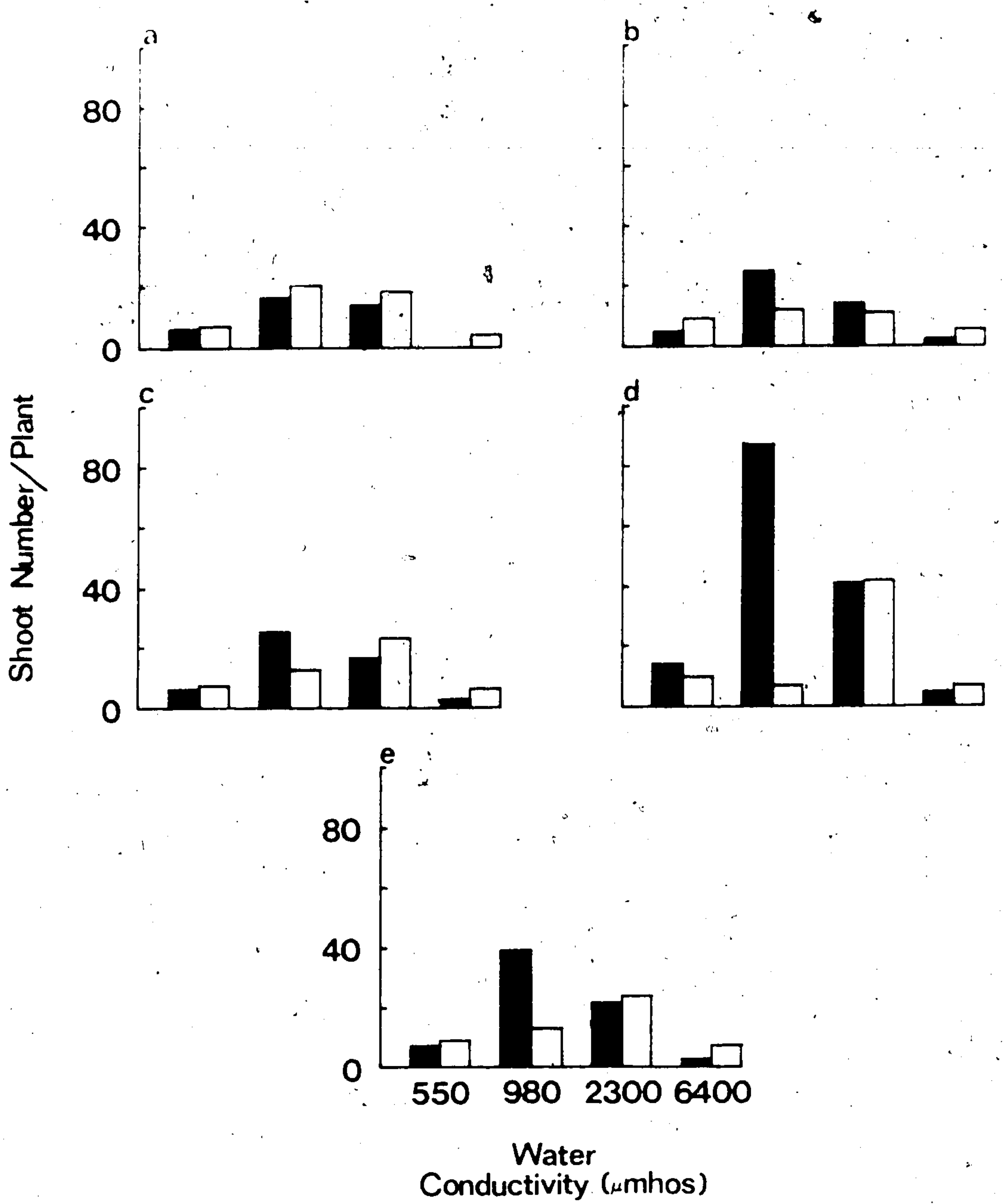

Fig. 17. Shoot production in SL and FL individuals along a water salinity gradient; a Botanic Garden sediment, b Pigeon Lake, c Miquelon L. sediment, d Buffalo L. sediment, e mean response; n=4. FL plant – solid bars.

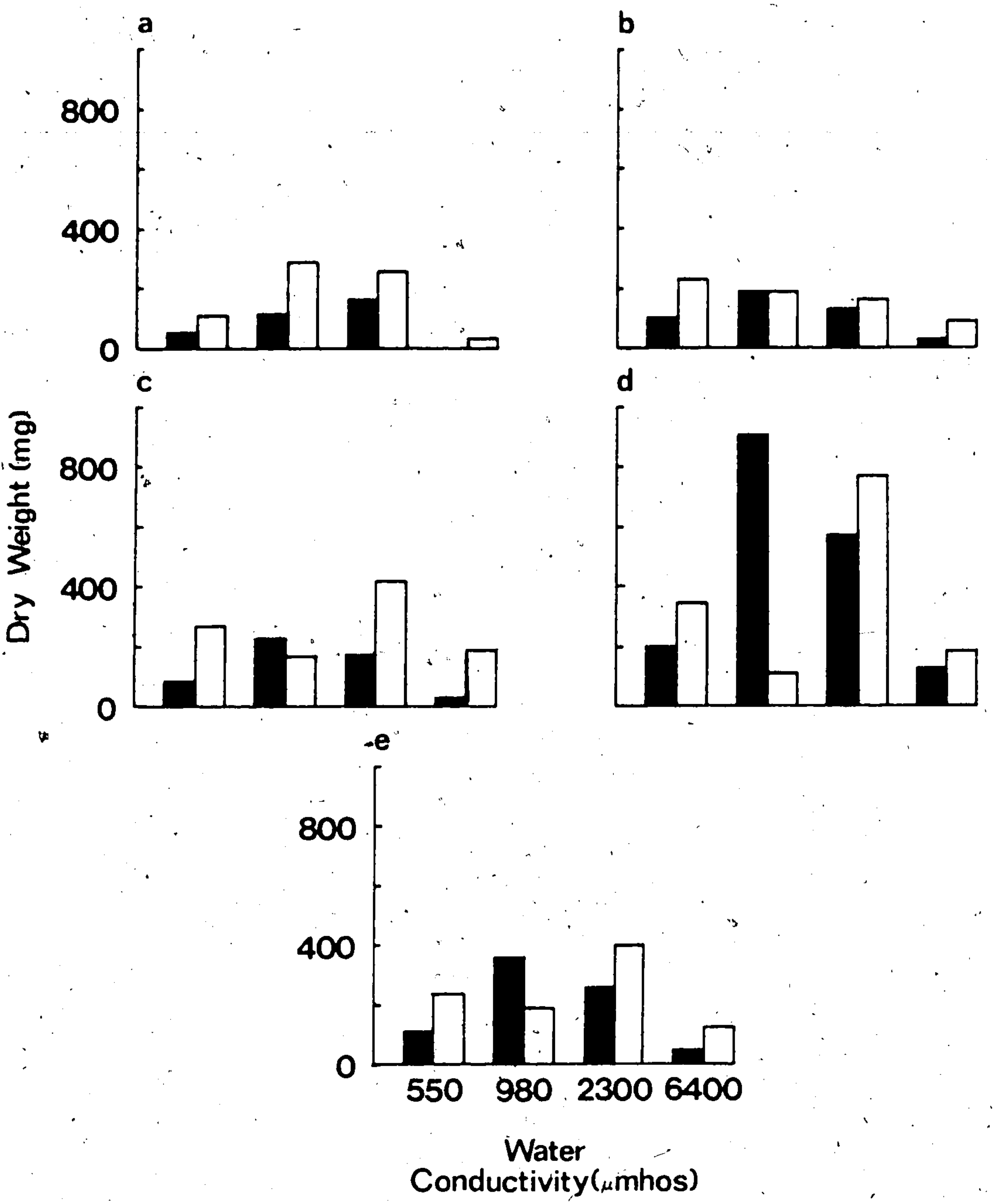

Fig. 18. Dry Weight of SL and FL individuals along a water salinity gradient, on four sediment treatments; a Botanic Garden pond sediment, b Pigeon L. sediment, c Miquelon L. sediment, d Buffalo L. sediment, e mean response; n=4 FL plants-solids.

Table 22. Mean shoot production and dry weight of plants from a freshwater (FL) and a saline (SL) lake grown in four water and four substratum salinities. Means that are not significantly different are labelled with the same letter among water treatments, within populations ($p > 0.05$).

		Water Treatments (µmhos/cm)							
		550		990		2300		6400	
Sediment		FL	SL	FL	SL	FL	SL	FL	SL
Botanic Garden pond (285 µmhos/cm)	No. Shts.	6.0^a	7.0^a	16.7^a	20.0^b	14.0^a	18.5^b	0.0^b	4.0^a
	Weight	58.0^a	114.0^b	117.7^a	292.7^a	161.0^a	258.8^a	0.0^b	37.0^b
Pigeon Lake (1725 µmhos/cm)	No. Shts.	4.8^a	9.0^a	25.0^b	12.0^b	14.0^b	10.3^a	2.0^a	5.3^a
	Weight	94.8^{ab}	231.5^a	191.0^b	193.7^a	132.5^b	162.0^a	26.3^a	92.3^b
Miquelon Lake (5125 µmhos/cm)	No. Shts.	6.0^a	7.5a	25.3^a	12.5^{ab}	16.5^b	23.0^b	2.5^a	6.[illegible]^a
	Weight	84.5^a	269.3^a	222.5^a	169.0a	170.5^a	418.7^b	32.5^b	193.5^a
Buffalo Lake (7500 µmhos/cm)	No. Shts.	14.3^a	10.0^a	87.0^b	7.5^a	41.0^c	41.3^b	4.5^d	6.5^a
	Weight	200.8^{ab}	342.3^{ab}	905.2^c	107.5^a	570.5^{bc}	768.0^b	124.8^a	184.5^a

is growing. Location of response, and specifically the growth in low salinity water is markedly influenced by substratum. In SL plants dry weight production in the low salinity treatment surpasses growth in the 980 μmhos/cm treatment and is not statistically different than the 2300 μmhos/cm treatment if the substratum is solute-rich.

No plants flowered during the 42 day experiment, but vertical extension of the terminal tiller, a precursor to flower production in *Ruppia* , was observed in both populations after 4 weeks. In SL plants the percentage of individuals producing vertical shoots increased with water salinity and occurred on 2 of 4 substrata (Table 24). Vertical growth in FL plants was less variable among water treatments and occurred only on the most saline substratum.

4.4 Discussion

The results revealed significant differences in growth between populations over a range of water and sediment treatments; differences were consistent in reciprocal transplants and controlled environments and are likely a genotypic response. This assumes that previous environmental factors or initial plant size differences (or other maternal affects) did not affect plant growth. Environmental factors can be transferred by seedlings (Heslop-Harrison 1964), and acclimation in plants to high salt concentration has been reported previously (Haller et al 1974, Pip 1979). To account for this, both lake populations were equilibrated in

Table 23. Difference between Miquelon Lake and Pigeon Lake plants in mean, variance and coefficient of variation over A) water treatments and B) sediment treatments.

A)

	Dry Weight (mg)		Shoot Production	
	Miq. L.	Pig. L.	Mic. L.	Pig. L.
Mean	239.7	193.3	12.5	17.5
Variance	13772.4	20167.3	61.0	261.2
Coeff. Var.	49.0	73.5	62.4	92.5
C.V. Difference	24.5		30.1	

B)

	Dry Weight (mg)		Shoot Production	
	Miq. L.	Pig. L.	Miq. L.	Pig. L.
Mean	239.7	193.3	12.5	17.5
Variance	7270.3	29683.3	8.7	166.2
Coeff. Var.	35.6	89.1	23.5	73.8
C.V. Difference	53.5		50.3	

Table 24. Difference between Miquelon Lake (SL) and Pigeon Lake (FL) plants in the percentage of replicates that initiated vertical growth; n = 4.

	Water Treatments (μmhos /cm)							
	550		990		2300		6400	
Sediment Treatments	SL	FL	SL	FL	SL	FL	SL	FL
Buffalo L.	25	-	25	50	25	50	100	25
Miquelon L.	50	-	-	-	25	-	75	-
Pigeon L.	-	-	-	-	-	-	-	-
Botanic Gard. Pond	-	-	-	-	-	-	-	-

common conditions for 4 months. Also, differences between populations in initial plant size, incorporated into calculations of relative growth rates, did not alter results from those using tiller and dry weight measurements.

Jain and Bradshaw (1966) suggest that selection pressures and geneflow characteristics affect the maintenance of genetic differentiation . Both processes are believed to contribute to differentiation in the hydrophyte populations. Most obviously, the habitats are landlocked (except one small outflow in Pigeon Lake), 85 kilometers apart with no known "stepping stone" populations between. The isolated nature of each suitable habitat gives each population the biogeographical properties of an island (Maguire 1963, Keddy 1976). Due to the submerged growth habit and breeding system, gene flow between populations of *Ruppia* is restricted to seeds, turions (dormant shoot apices) and vegetative fragments. However, seed production in *Ruppia* is sporadic and low (Verhoeven 1979, Brock 1982, Chapter 1) as in most perennial, submerged hydrophytes (Sculthorpe 1967). Vegetative fragments and turions are unable to survive out of water for more than about 2 hours (Sculthorpe 1967, Keddy 1976). Nevertheless water birds have been observed carrying vegetative parts (Sculthorpe 1967) and seeds (DeVlaming and Proctor 1968). Since flowers of *Ruppia* never rise completely beyond the water surface (Verhoeven 1979), pollen dispersal between lakes is practically impossible. Ultimately, there are few opportunities for genetic exchange between populations.

One purpose of this study was to determine the relative importance of solute concentrations in the substratum and the overlying water to differences in populations of *Ruppia*. Overall, both water and substratum treatments had significant effects on growth (dry weight and tiller production) as did their respective population interactions. Population differences were most evident in response to sediment treatments, to which FL plants were most variable. Many reports of genetic differentiation in saline, wetland species are known (Jeffries 1977, and references therein), but differentiation among submerged hydrophyte populations, in terms of substratum and water phase salinity has not been reported. However, differences in the relative importance of root absorption and the primary site of absorption do exist among species and are presumably under genetic control (Denny 1980). Within a population, the effect of substratum on growth also varied depending on the solute concentration in the water.

Controlled environment comparisons and reciprocal transplants show the relative importance of genetic and environmental effects on the observed variation in naturally-occurring populations. Overall results indicate that environmentally induced variation is most consistent than genetic effects. Population environment interactions were significant but there were no consistent differences among populations when compared across all treatments.

Variation in growth among water treatments alone was largely environmentally induced, and may sufficiently explain variations in plant growth rate between lake sites. Rather than evolve a reduced growth rate to adverse nutritional conditions as reported by Ernst (1965) and Antonovics et.al (1971), *Ruppia* plants from freshwater exhibit a similar response to water and a greater response to substratum variation, relative to SL plants. The response to substrata is largely genotypic and interacts significantly with growth in response to water salinity.

Differences in growth between FL and SL plants were usually in the direction of each population growing best in the environment from which they came but neither population grew best in the treatment simulating its "native" environment. On saline substrata, FL plants exhibit greater plasticity over the water salinity gradient than SL plants. In low salinity substrata, the growth response of FL plants resembles that of the SL plants or less plastic. Differences in root absorption between populations may explain growth that is considerably greater than what one would predict for a given water salinity. Population differences are consistent with the predictions based on environmentally induced changes.

As stated above, the effect of substratum is partly population specific. Denny (1972a) suggested that uptake by the roots is progressively more important for species of decreasingly submerged growth forms. In this study, all populations were similarly submerged. A major difference between the lake sites is the total solute concentration and the proportions of the major ions (sulphate, sodium,calcium)(Chapter 1). This results in not only a solute deficiency for *Ruppia*, but also a higher substratum:water solute concentration ratio in freshwater (Chapter 1). It is suggested that freshwater habitats, which are ecologically marginal, select for root dominated absorption. Genetic differentiation is conceivable considering the barriers to gene flow and that most Albertan Lakes have been chemically stable for the last 4000-6000 years (Hickman and Klarer 1981, Hickman, Bombin and Bombin 1982a, Hickman et al 1984). One must be cautious in attributing population differences to natural selection as it assumes there is neither selection in the seed or seedling stage nor differentiation due to random genetic events. The first assumption has not been tested, but observations of naturally occurring populations suggest that *Ruppia* colonizes a habitat primarily by vegetative propagules. Therefore, vegetative parts experience many critical selective periods and are under selctive pressure for a longer time than seeds. The second assumption may not be valid because only one or a few genotypes may actually reach and colonize a new habitat. Nevertheless, reciprocal transplants and controlled environment experiments demonstrate that the population differences described have some ecological significance. Increased growth of FL plants in freshwater can be attributed to its "sensitivity" to sediment salt concentrations. It appears that the primary site of absorption is environmentally as well as genetically induced, however the developmental and physiological basis for its plasticity is unknown. Populations respond to concentration of salts similarly, but to source of salts differently. Therefore it is hypothesized that sediment sensitivity in FL plants is due to increased root absorption capacity rather than increased efficiency in which the salts are used. Population differences confirm that *Ruppia* is under definite chemical constraints in freshwater and suggest a physiological mechanism that enables the species to expand its ecological range.

Conclusion

This study indicated that lake chemistry has a significant effect on the ecological range of *Ruppia occidentalis*. Differences among three natural populations from different lakes can be explained by the environmentally-induced and genotypic responses to total ion concentration and to ion source (sediment *versus* overlying water).

Growth rate and biomass per individual increased with salinity. Net assimilate of plants from the saline lake was allocated largely to the vertical growth of shoots, and to reproduction (sexual and asexual). In plants from the freshwater lake a similar proportion of net assimilate was allocated to shoots, but as horizontal growth along the sediment, through ramet or tiller production. Interestingly, tiller mortality and shoot fragmentation were unaffected by salinity. The proportion of reproducing individuals also increased with salt concentration.

The distributions within each lake suggest there is an important interaction between the effects of salinity and both depth and substratum. These interactions are important to understanding the regional distribution of *Ruppia* in freshwater and saline habitats. Being extremely fragile and shallowly rooted, *Ruppia* is susceptible to damage from wave action, ice scouring and sediment erosion. Therefore, in the unpredictable and harsh environment of shallow waters, annuals, or perennials that produce many seeds and tubers, are most likely to dominate. Because *Ruppia* has low reproduction in freshwater, frequency in shallow sites is also low. In saline lakes, plants have higher growth rates and reproduction, thus are able to colonize most depths extensively. Superimposed on this depth distribution, the sediment-dependency of *Ruppia* is not constant over the chemical range studied. In freshwater, *Ruppia* is most often found on coarse substrata. Since coarse substrata are often associated with shallow water, this contradicts the information about depth distributions; however, the the fine, organic substrata in freshwater lakes may inhibit uptake processes in *Ruppia*. Barko (1983) has also indicated that organic content of lake sediments may inhibit certain hydrophytes. Interestingly, *Ruppia* is substrata indifferent in saline water and was not inhibited on highly organic sediments.

Sediment-dependency in freshwater and other experiments from this study indicate that the normal pattern of salt absorption, through the shoots, is altered when solute concentrations are low in the water. This flexibility in absorption is in part a genetic and part a phenotypic response. Increased root absorption likely represents an increase not in the efficiency with which salts are used, but in the rate at which they are taken up. Root absorption capacity may be regulated by internal salt concentration; however, further study is required to confirm this.

These findings provide some ecological support for the belief that aquatic plants are flexible in their mode of uptake, and depending on the respective nutrient levels of the water and sediment, plants may absorb salts " along the path of least resistance " (Westlake 1971). The fact that aquatic plant roots can penetrate into anaerobic sediments, where nutrient solubility is enhanced, makes them particularly well adapted to nutrient (salt)-poor water.

The occurrence of *Ruppia* in freshwater, an infrequent finding, could be attributed to the plant's ability to utilize the salt-rich sediment and to the presence of a suitable sediment in the lake. The variable uptake of nutrients through the root system, and subsequent release of nutrients through excretion or during decomposition of the plant material represents a pathway for nutrient cycling and a natural eutrophication process in aquatic ecosystems.

It is not possible to determine in this study whether, as Verhoeven (1980) suggested, the ecological range of *Ruppia* is constrained by interspecific competition. Indirect evidence gathered from the aquatic plant survey indicated that interspecific competition did not have a significant influence on the spatial distribution of *Ruppia* in the large, wave-disturbed, freshwater lake. However, two factors qualify the general validity of these results. First, *Potamogeton pectinatus*, the main competitor of *Ruppia* in Europe, does not dominate in this lake. Second, Pigeon Lake has a large, wave disturbed shoreline; low light and wave action likely maintain the density of aquatic plants at low levels. *Ruppia* would likely be unable to compete with the dense, fast-growing hydrophytes in small freshwater ponds.

Variation among *Ruppia* populations can be attributed, in part, to a genotypic response to salinity. In general, plants from either freshwater or saline lakes varied significantly among water treatments. However, only plants from the freshwater lake showed significant variation in growth on different sediments. This could be related to the greater importance of substratum as a limiting source of solutes in freshwater. One should recognize that such differences, being interpreted as genetic, may simply be environmental or parent effects retained in the two populations. However, all plants were conditioned for 4 months in tapwater, and second generation clones were used in all experiments to reduce environmental and cytoplasmic effects, but more refined genetic comparisons such as electrophoresis, are required. The only problem with electrophoresis is in the difficulty relating the data to specific ecological traits.

Ruppia's present distribution can also be explained by ultimate causes. *Ruppia occidentalis* is one of only a few hydrophyte species in inland saline water. Most members of the genus *Ruppia* occur in estuarine or coastal habitats. Cytological evidence and aspects of its reproductive biology suggest that *R. occidentalis* arose from the marine form, which is diploid, less robust and has retained hydrophyllous pollination, typical of many seagrasses (Sculthorpe 1967). In light of its history, it might be reasonable to hypothesize that limitations in genetic variability in osmotic requirements have prevented *R. occidentalis* from expanding further into freshwater.

Palaeoecologists make inferences about past ecosystems from reconstructions of past ecosystems using geochemical and fossil remains preserved within the lake sediments. To reconstruct past ecosystems, the palaeoecologist requires knowledge about the ecological requirements and tolerances of the species involved (Birks and Birks 1980) Because of their known ecology and the species with which they are associated, indicator species can be used to indicate past occurrences of present communities. This assumes that there has been little change in the ecological requirements of the species, and that the species are not experiencing more competition now than in the past. The present autecological study suggests that *Ruppia* is a good indicator of saline lake conditions. From its presence, a palaeoecologist may infer a warmer, more arid climate that resulted in salt accumulations due to evaporation. Though its salinity tolerances are broad, *Ruppia*'s association with saline lakes is consistent in all species known (Verhoeven 1979).

Many species comprise a set of ecologically specialized genotypes. Evidence from this study indicates that *Ruppia* consists of several chemical ecotypes, some better suited to freshwater lakes than others. Since ecotypes cannot be recognized in a pollen record, reconstructions of past ecosystems should be made with the entire ecological range of the species in mind. For *R. occidentalis* this would comprise 200 - 30000μmhos/cm Electrcal Conductance, with an optimum of 6300; also recognizing that the tolerance limits may vary with ion composition. The indicator value of *Ruppia* will increase when it is considered with other species in the pollen assemblage whose ecology is also known, or when compared with taxa with similar ecological requirments. The lack of other submerged plants may be as useful an indicator as a complete assemblage since there are few aquatic taxa in saline lakes. A useful step now is to find modern analogues of these past pollen assemblages by comparing the pollen spectra of present aquatic communities to the fossil pollen spectra.

References

Abrahamson,W.G. and M.D. Gadgil. 1973. Growth form and reproductive effort in goldenrods(*Solidago*, Compositae) Amer. Nat. 107:651-661.

American Public Health Association, et al. 1976. Standard Methods for the Examination of Water and Wastewater. 14th Edition. American Public Health Association, Washington, D.C. 1193pp.

Andel, J.Van and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 65:747-758.

Anderson, M.G. 1978. Distribution and production of Sago Pondweed(*Potamogeton pectinatus* L.) on a northern prairie marsh. Ecol. 59:154-160.

Antonovics, J., A.D. Bradshaw and R.G. Turner. 1971. Heavy metal tolerance in plants. Adv. Ecol. Res. 7:1-85.

Antonovics, J. and R.B. Primack. 1982. Experimental ecological genetics in *Plantago*.V1. The demography of seedling transplants of *P. lanceolata*. J. of Ecol. 70:55-75.

Barko, J.W. 1982. Influence of potassium source(sed. vs. open water) and sediment composition on the growth and nutrition of a submersed freshwater macrophyte. Aquatic Botany 12:157-172.

Barko, J.W., D.G. Hardin and M.S. Mathews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Can. J. Bot. 60:877-887.

Barko, J.W. and R.M. Smart. 1979. The role of *Myriophyllum spicatum* in the mobilization of sediment phosphorus. In: Aquatic Plants, Lake Management and Ecosystem Consequences of Lake Harvesting. (Ed. by J.E. Breck, R.T. Prentko, O.L. Louchs). Institute for Environmental Studies, U. of Wisconsin-Madison.

Barko, J.W. and R.M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biol. 10:229-238.

Birks, J.B. and H.H. Birks. 1980. Quaternary Palaeoecology. Edward Arnold, publishers, 289pp.

Bole, J.B. and J.R. Allan. 1978. Uptake of phosphorus from sediment by aquatic plants *Myriophyllum spicatum* and *Hydrilla verticillata*. Water Research 12:353-358.

Bradshaw, A.D. 1952. Populations of *Agrostis tenuis* resistant to lead and zinc poisoning. Nature Lond. 169:1098

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13:115-163.

Bradshaw, A.D. 1984. Ecological significance of genetic variation between populations, in "Perspectives on Plant Population Ecology"(ed. by R. Dirzo and J. Sarukhan). Sinauer Assoc Inc. Publishers, 478pp.

Brock, M.A. 1979. Accumulation of proline in a submerged aquatic halophyte,*Ruppia* L. Oecologia 51:217-219.

Brock, M.A. 1982. Biology of the salinity tolerant genus *Ruppia* L. in saline lakes in S. Australia. I. Morphological variation within and between species and ecophysiology. Aquatic Bot. 13:219-248.

Brock, M.A. and R.J. Shiel. 1983. The comparison of aquatic communities in saline wetlands in Western Australia. Hydrobiologia 105:77-84.

Brown, W.H. 1911. The plant life of Ellis, Great, Little and Long Lakes in North Carolina. Contribution United States National Herbarium 13(10):323-341.

Casey, H. and A. Downing. 1976. Levels of inorganic nutrients in *Ranunculus penicillatus* var. *calcareus* in relation to water chemistry. Aquatic Botany 2:75-79.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.

Christie, E.K. and J. Moorby. 1975. Physiological responses of semi-arid grasses.I. The influence of phosphorus supply on growth and phosphorus absorption. Aust. J. Agric. Res. 26:423-436.

Clapham, A.R., T.G. Tutin and E.F. Warburg. 1968. Excursion flora of the British Isles. Cambridge University Press, London, 2nd Edn., 568pp.

Clarkson, D.T. 1967. Phosphorus supply and growth rate in species of *Agrostis* L. J. Ecol. 55:111-118.

Cowgill, U.M. 1973a. Biogeochemistry of the rare-earth elements in aquatic macrophytes of Linsely Pond, North Branford, Connecticut. Geochemical and Cosmochemica Acta

37(10):2329-2345.

Cowgill, U.M. 1973b. The determination of all detectabe elements in the aquatic plants of Linsley Pond and Cedar Lake (North Branford, Connecticut) by X-ray emission and optical emission spectroscopy. Applied Spectroscopy 27:(1):5-9.

Cowgill, U.M. 1974. The hydrogeochemistry of Linsley Pond , North Branford, Connecticut.Part 2. The chemical composition of the aquatic macrophytes. Archiv fur Hydrobiologie (Supplement band) 45:1-119.

Davis, J.S. and P.B. Tomlinson. 1974. A new species of *Ruppia* in high salinity in Western Australia. J. Arnold Arbor. Harv. Univ. 55:59-66.

Dennis, J.G. and P.L. Johnson. 1970. Shoot and rhizome-root standing crops of tundra vegetation at Barrow, Alaska. Arc. Alp. Res. 2:253-266.

Denny, P. 1972a. Sites of nutrient absorption in aquatic macrophytes . J. Ecol. 60:819-829.

Denny, P. 1980. Solute movement in submerged angiosperms. Biol. Rev. 55:65-92.

DeVlaming,V. and V.W. Proctor. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. Am. J. Bot. 55:20-26.

Durrant, A. 1972. Studies on reversion of induced plant weight changes in flax by outcrossing. Heredity 29:71-81.

Ernst,W. 1965. Uber den Ein fluss des zinks auf die Kermung von Schwermetallpflanzen und auf die Entwicklung der Schwermetallpflanzengesellschaft. Ber. dt.bot. Ges. 78:205-212.

Gerloff, G.C. and P.J. Krombholz. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnology and Oceanography 11:529-537.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-1194.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. N.Y.: Wiley, 222pp.

Haag, R.W. and L.Noton. 1981a. Macrophyte and sediment texture survey of Buffalo Lake. Report to Alberta Environment, Planning Div., 41pp.

Haag, R.W. and L. Noton. 1981b. Macrophyte and sediment texture survey of Pigeon Lake. Report to Alberta Environment, Planning Div., 31pp.

Haller, W.T., D.L. Sutton and W.C. Barlowe. 1974. Effects of salinity on growth of several aquatic macrophytes. Ecol. 55:891-894.

Hamilton, H. 1980. Pine Lake Water Quality Report. Alberta Dept. of Environment, Pollution Control Division, Water Qual. Control Branch. 29pp.

Hammer, U.T. 1981. A comparative study of primary production and related factors in four saline lakes in Victoria, Australia. Int. Revue. ges. Hydrobiol. 66:701-743.

Hammer, U.T., J. Shamess and R.C. Haynes. 1983. The distribution and abundance of algae in saline lakes of Saskatchewan, Canada. Hydrobiologia 105:1-26.

Haller, W.T., D.L. Sutton and W.C. Barlow. 1974. Effects of salinity on growth of several aquatic macrophytes. Ecology 55:891-894.

Harper, J.L. 1980. Plant demography and ecological theory. Oikos 35:244-253.

Harper, J.L. 1982. After Description. In "The Plant as a Working Mechanism" (ed. E.I. Newman). Blackwell Scientific Publications, 128pp.

Harper, J.L. and J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. J. Ecol. 58:681-698.

Heslop-Harrison, J. 1964. Forty years of genecology. Adv. Ecol. Res. 2:159-247.

Hickman, M. 1973. The standing crop and primary production of the phytoplankton of Abbots Pond, north Somerset. J. Ecol. 61:269-287.

Hickman, M. 1978. Ecological studies on the epipelic algal community in five prairie-parkland lakes in central Alberta. C.J.B. 991-1009.

Hickman, M. 1979. Phytoplankton production in a small eutrophic lake in central Alberta, Canada. Int. Revue ges. Hydrobiol. 64(5):643-659.

Hickman, M., E. Bombin and M. Bombin. 1982a. Buffalo Lake-Preliminary paleoenvironmental report to Albert Environment, Planning Division, 22pp.

Hickman, M. and C.G. Jenkerson. 1978. Phytoplankton primary production and population efficiency studies in a prairie-parkland lake near Edmonton, Alberta, Canada. Int. Revue. ges Hydrobiol. 63:1-24.

Hickman, M. and D.M. Klarer.1981. Paleolimnology of Lake Isle, Alberta, Canada (including sediment chemistry, pigments and diatom stratigraphy). Arch. Hydrobiol. 91:490-508.

Hickman,M., C.E. Schweger, and T. Habgood. 1984. Lake Wabamun, Alberta: a paleoenvironmental study. Can. J. Bot. 62:1438-1465.

Hill, J. 1967. The environmental induction of heritable changes in *Nicotiana rustica* parental and selection lines. Genetics 55: 735-754.

Higgonson, F.R. 1965. The distribution of submerged aquatic angiosperms in the Tuggerah Lakes system. Proc. Linn. Soc. N.S.W. 90:328-334.

Hoagland, D.R. and T.C. Broyer. 1936. General nature of the process of salt accumulation by roots with description of experimental methods. Plant Physiology 11:471-507.

Howard-Williams, C. and M.R.M.Liptrot. 1980. Submerged macrophyte communities in a brackish south African Estuarine-Lake System. Aquatic Botany 9:101-116.

Huebert, D.B. and P.R. Gorham. 1983. Biphasic mineral nutrition of the submersed aquatic macrophyte *Potamogeton pectinatus* L. Aquatic Bot. 16:269-284.

Hunt, R. 1974. Plant Growth Analysis. Studies in Biology, No. 96. Edward Arnold, publ., 67pp.

Hynes, H.G.N. and B.J. Grieb. 1970. Movement of phoshate and other ions from and through lake muds. J. Fish. Res. Bd. Can. 27:653-668.

Jain, S.K. and A.D. Bradshaw. 1966. Evolution in closely adjacent plant population.I. The evidence and its theoretical analysis. Heredity 22: 407-441.

Jefferies, R.L. 1977. Growth responses of coastal halophytes to inorganic nitrogen. J.Ecol. 65:847-865. Kangasniemi, B.J. 1975. Lake sediments and rooted macrophytes with particular reference to *Myriophyllum spicatum* in

Okanagan Lake. Water Investigations Branch, British Columbia Water Resources, Department of Lands, Forests and Water Resources.

Keddy, P.A. 1976. Lakes as islands: the distributional ecology of two aquatic plants, *Lemna minor* L. and *Lemna trisulca* L. Ecol. 57:353-359.

Kiørboe, T. 1980. Production of *Ruppia cirrhosa* in mixed beds in Ringkobing Fjord(Denmark). Aquat. Bot. 9:135-143.

Krebs, C.J. 1978. Ecology, The Experimental Analysis of Distribution and Abundance. 2nd ed. Harper and Row, NY. 678pp.

Kruckeberg, A.R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. Am. J. Bot. 38:408-419.

Kruckeberg, A.R. 1954. The ecology of serpentine soils.III. Plant species in relation to serpentine soils. Ecol.35:267-274.

Lindgren, D.T., W.H. Gabelman and G.C. Gerloff. 1977. Variability of phosphorus uptake and translocation in *Phaseolus vulgaris* L. under phosphorus stress. J. Am. Soc. Hort. Sci. 102:674-677.

Maguire, B., Jr. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol Monographs.33:161-185. Mayes, R.A., A.W. McIntosh and J.L. Anderson. 1977. Uptake of cadmium and lead by a rooted aquatic macrophyte (*Elodea canadensis*). Ecology 58:1176-1180.

McGraw, J.B. and J. Antonovics. 1983. Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life--cycle stages of selection. J. of Ecol. 71:879-898.

Metcalf, F.D. 1931. Wild-duck foods of North Dakota lakes. U.S.D.A., Technical Bulletin 221:1-72.

Misra, R.D. 1938. Edaphic factors in the distribution of aquatic plants in the English Lakes. J. of Ecol. 26:411-451.

Mitchel, P. 1979. Skeleton, Garner, Muriel Lakes Water Quality Study. Water Quality Control Branch, Pollution Control Div., Alberta Environment. 106pp.

Moore, D.M. 1973. Additions and amendments to the vascular flora of the Falkland Islands. Bull. Br. Antarctic

Survey 32:85-88.

Moore, D.M. and R.N.P. Goodall. 1974. Further additions to the native vascular flora of Tierra del Fuego. Bot. Not. 127:38-43.

Moyle, J.B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Am. Midl. Nat. 34:402-420.

Nichols, D.S. and D.R. Keeney. 1976a. Nitrogen nutrition of *Myriophyllum spicatum*:variation of plant tissue nitrogen concentration with season and site in Lake Wingra. Freshwater Biol. 6:137-144.

Pearsall, W.H. 1920. The aquatic vegetation of the English Lakes. J. Ecol. 8:163-201.

Pip, E. 1979. Survey of the ecology of submerged aquatic macrophytes in central Canada. Aquatic Botany 7:339-357.

Po[illegible], R.H. 1905. The biological relation of aquatic plants to the substratum. U.S. Commission of Fish and Fisheries Report for 1903, pp485-526.

Primack, R.B. and J. Antonovics. 1981a. Experimental ecological genetics in *Plantago*. Components of seed yield in the ribwort plantain, *Plantago lanceolata* L. Evolution. Lancaster, PA (in press).

Rawson, D.S. and J.F.Moore. 1944. The saline lakes of Saskatchewan. Can J. Res. Dev. 22:141-201.

Reynolds, J.D. and S.C.P. Reynolds. 1975. Aquatic angiosperms of some British Columbia saline lakes. Syesis 8:291-295.

Rickett, H.W. 1922. A quantitative study of the larger aquatic plants of Lake Mendota. Transaction of the Academy of Science, Arts and Letters 20:501-531.
Rickett, H.W. 1924. A quantitative study of the larger aquatic plants of Green Lake, Wisconsin. Transactions of the Academy of Science, Arts, and Latters 21:381-414.

Rorison, I.H. 1968. The response to phosphorus of some ecologically distinct plant species. I.Growth rates and phosphorus absorption. New Phytol. 67:913-923.

Schweger, C.E., T. Habgood and M. Hickman. 1981. Late glacialHolocene climatic changes of Alberta. The record from lake sediments. In Proc. Alberta Climatological Ass. Annual Meeting, Edmonton.

Sculthorpe, C.D. 1967. The biology of aquatic vascular