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**LA THÈSE A ÉTÉ
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DORMANCY AND GERMINATION RESPONSES TO VARIOUS WATER
LEVELS AND THEIR RELATIONSHIP TO SPECIES DISTRIBUTIONS
IN A LAKESHORE PLANT COMMUNITY

by

Dwayne R.J. Moore

submitted in partial fulfilment of the requirements for the degree
of Master of Science at
University of Ottawa
Ottawa, Canada

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ABSTRACT

Seed dormancy and germination represent critical stages in the life cycle of a plant and the factors that affect them are important in determining the abundance and distribution of a species. This study examined how different water levels affected both seed dormancy and germination in lakeshore plants. The results were then related to the adult distributions of those plants.

The first part of this study was undertaken: (i) to determine the effects of different moisture conditions during cold storage on the germination capacity of six species of lakeshore plants, and (ii) to test whether there was an interaction between moisture levels during the storage period and germination responses to a water depth gradient. Seeds were stored under five moisture conditions: 25%, 50%, 75%, and 100% saturated sand and distilled water. The seeds were then either placed in petri-dishes to measure germination capacity or sown along a three-level water depth gradient to determine if storage conditions could affect germination responses to a water depth gradient. It was found that different moisture conditions during stratification significantly affected the germination capacity of some species, but had little effect on which water level produced maximum germination. As well, there was no relationship between the moisture level that stimulated maximal germination in a species and the field

distribution of that species along a water depth gradient.

The objectives of the second part of this study were: (i) to determine the germination responses of many lakeshore species to a water depth gradient, (ii) to test whether these responses were similar or different among species (i.e., shared or distinct germination responses), and (iii) to test whether germination responses were related to adult distributions. Germination responses were determined in a greenhouse by sowing seeds of twenty-four lakeshore species along an artificial water depth gradient using two substrate types (sand and high organic content soil). Those species showing significant treatment effects were then tested for shared or distinct germination responses using Kendall's coefficient of concordance. On the sand substrate, species had shared germination responses ($n = 5$; $p = 0.02$), while on the organic substrate, species had distinct germination responses ($n = 7$; $p > 0.50$). The correlation between mean depth of germination, and the mean depth of occurrences of adults of the same species along a water depth gradient in the field, was significant ($r = 0.81$; $p = 0.01$). This suggests that seeds do have a germination response to the water depth gradient and, in the case of distinct germination responses, germination responses are similar to adult distributions.

ABSTRAIT

La dormance de la graine et sa germination représentent des étapes critiques dans le cycle vital d'une plante et les facteurs affectant ceux-ci sont des déterminants importants ayant un effet sur l'abondance et la distribution des espèces. Cette étude examine comment différents niveaux d'eau affectent l'un comme l'autre la dormance et la germination chez les plantes lacustres.

La première partie de cette étude fût entreprise: (i) pour déterminer les effets qu'ont différentes conditions d'humidité pendant le stockage au froid sur la capacité de germination de six espèces lacustres, et (ii) pour vérifier si il y a interaction entre le taux d'humidité durant l'entreposage et la réponse germinative en fonction de la profondeur de l'eau. Les graines furent mises en réserve sous cinq différentes conditions d'humidité dans du sable saturé à 25%, 50%, 75% et 100% d'eau, ainsi que dans de l'eau distillée. Les graines furent ensuite placées ou dans des boîtes de pétri pour mesurer la capacité germinative ou semées suivant un gradient de profondeur d'eau à trois niveaux pour déterminer si le traitement de stockage affecte le mode de germination. Il fût trouvé que différentes conditions d'humidité pendant la stratification affectent significativement la capacité germinative de certaines espèces mais n'ont que peu d'effet si le niveau d'eau produit une germination maximale. De même il n'y a aucune

relation entre le taux d'humidité qui stimule une germination maximale chez une espèce, et le champs de distribution de cette espèce le long d'un gradient de profondeur d'eau.

Les objectifs de la seconde partie de cette étude sont: (i) de décrire la répartition de la germination de plusieurs espèces lacustres en fonction de la profondeur de l'eau, (ii) de tester si ces répartitions sont semblables ou différentes (i.e., si les réponses germinatives sont partagées ou distinctes), et (iii) de vérifier si ces répartitions sont similaires à la distribution des plantes adultes. La réponse germinative fût mesurée en semant, dans une serre, les graines de vingt-quatre espèces lacustres sur deux types de substrats (du sable ou un sol organique riche) offrant un gradient de profondeur d'eau. Les espèces présentant des effets de traitement significatifs furent testées pour la réponse germinative partagée ou distincte en utilisant le test de Kendall sur le coefficient de concordance. Sur le substrat sablonneux, les espèces ont une germination partagée ($n = 5$; $p = 0,02$), tandis que sur le substrat organique, les espèces ont une germination distincte ($n = 7$; $p > 0,50$). La corrélation entre la profondeur moyenne de germination, et la profondeur moyenne de la fréquence des plantes matures le long du gradient de profondeur de l'eau sur le terrain est significative ($r = 0,81$; $p = 0,01$). Cela suggère que les jeunes plants répondent au gradient de profondeur de l'eau et, dans le cas

de la réponse germinative distincte, que les répartitions
germinatives sont similaires à la distribution des adultes.

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will remember one.

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GENERAL INTRODUCTION

There is a vast literature indicating a close relationship between the biology of juvenile plants and their establishment success in different habitats (Cook 1979). Grubb (1977) proposed that differentiation among plant species during the regeneration stage may explain co-existence in species-rich communities. Since most mortality occurs at the regeneration stage in a plant's life cycle (Harper 1977, Cook 1979), there are likely intense selection pressures on seeds to recognize and respond to environmental factors that can affect the suitability of a site for germination, establishment, growth and reproduction (Barber 1965, Harper et al. 1961, Sheldon 1974). The purpose of this study is to examine how factors such as storage conditions, moisture availability and soil organic content affect germination of a large number of lakeshore plant species. I will then test whether past selection pressures have been of sufficient intensity to shape germination requirements in relation to adult distributions.

The most important environmental factor affecting the suitability of a site for germination is moisture availability (Cook 1979). On lakeshores there is a well defined vertical moisture availability (or water depth) gradient (Hutchinson 1975, Spence 1982). Correlated with water depth are many other environmental factors such as oxygen concentration, light intensity and quality,

temperature fluctuations and duration of submergence. (see Appendix 2)(Hutchinson 1975, Spence 1982) which can all have a major influence on seed dormancy (Barton 1961, Lang 1965, Stokes 1965), germination (Angevine and Chabot 1979), and survival and reproduction of adults. Because so many environmental factors are correlated with one another on this gradient, it is possible to quantify species' germination responses and adult distributions in relation to water depth without the risk of excluding other equally important factors. As well, previous studies have shown: (1) that seedling regeneration is important in many wetlands (see Appendix 1) (Keddy and Reznicek 1982, Salisbury 1970, van der Valk 1981), and (2) that water levels affect germination (Harper and Sagar 1953, Keddy and Ellis 1985, Pemadesa and Lovell 1975). Therefore, the lakeshore plant community is an ideal experimental system for studying the relationship between the seedling regeneration stage and the adult stage of a plant's life cycle.

Moisture availability not only affects germination but can also affect the dormancy condition of a seed. In Chapter 1 of this thesis I investigate how different moisture conditions during cold storage affects the germination capacity (i.e., percentage of seeds capable of germination under favourable conditions; Lang 1965) of six lakeshore plant species, as well as their germination responses to a water depth gradient. The relationship between the moisture level that stimulates maximal

germination in a given species and the field distribution of that species is then examined.

In Chapter 2, species' germination responses to a water depth gradient and the relationship between their responses and their respective adult distributions are investigated. This experiment was done on two substrates varying in organic content in order to simulate gradients on a sandy shore (low organic content) and in a sheltered bay (high organic content). This additional factor was included because substrate organic content varies in the field and could affect germination responses to a water depth gradient.

The experiments measuring the effects of different moisture levels on seed dormancy and germination were done in the greenhouse. To determine whether greenhouse environmental conditions paralleled those in nature (see Diamond 1983, Hicks 1964), I measured five environmental factors both in the greenhouse and at Axe Lake where the seeds for this study had been collected and adult distributions determined. The results of these measurements are discussed in Appendix 2.

The general discussion at the end of this thesis brings together the experimental results and considers several questions that arose during this study.

CHAPTER 1

GERMINATION OF SIX LAKESHORE PLANT SPECIES:

EFFECTS OF DIFFERENT MOISTURE CONDITIONS DURING
COLD STRATIFICATION

In temperate zone plant species, the most common requirement for breaking seed dormancy is a period of cold stratification (i.e., storage in a moist medium at low temperature) (Crocker and Barton 1957). This has been demonstrated for a wide variety of plant species including: aquatic plants (Justice 1944), woodland herbs (Baskin and Baskin 1982, 1984, Threadgill et al. 1981), and shrubs and trees (Crocker and Barton 1957). The effective range of temperature during cold stratification for breaking dormancy is from 0°C to 10°C with the optimal temperature occurring from 4°C to 6°C (Stokes 1965). Although this has been established for several decades, the effective range of moisture conditions during cold stratification is unknown. Few studies have even addressed this question. This is especially critical when one considers species that may be exposed to a broad range of moisture conditions in their natural habitat during stratification. For example, many wetland species have seeds that are dispersed along a water depth gradient (van der Valk and Davis 1978, van der Valk 1981, Parker and Leck 1985) or are exposed to varying yearly water levels (Keddy and Reznicek 1982). The first objective of this chapter is to determine the optimal and effective

range of moisture conditions during stratification that will stimulate germination in six species of lakeshore plants.

An implicit assumption of previous germination studies (e.g., Keddy and Ellis 1985, Grime et al. 1981, Baskin and Baskin 1982, 1984) has been that different moisture levels during cold storage do not affect germination responses. However, this assumption has never been critically tested. This point takes on added significance when many species are simultaneously screened for their germination requirements (e.g., Grime et al. 1981, Keddy and Constabel 1985). For such screening, we need to know how dependent the comparisons are upon prior storage treatment. Therefore, the present study was also designed to test whether different moisture levels during cold storage affect germination responses to a water depth gradient.

METHODS

Seed Collection and Storage

The seeds of six species (Glyceria canadensis (Michx.) Trin., Juncus militaris Bigel., Lobelia Dortmanna L., Triadenum Fraseri (Sach.) Gl., Viola lanceolata L. and Xyris difformis Chapman) (nomenclature follows Gleason and Cronquist (1963), except X. difformis which follows Randall and Keddy (1983)) were collected at Axe Lake, Ontario, Canada (45° 23'N, 79° 30'W) from 23 to 25 September 1983. These species represent both high and low shoreline species (Keddy 1980). The word seed is used here to mean a propagule containing a single embryo. Seeds were air-dried at 20°C for one month before being transferred to plastic containers and kept dry and in darkness at 4°C for 45 days. This period of cold dry storage parallels natural conditions encountered by seeds before dispersal takes place. This protocol was used previously by Keddy and Ellis (1985) and Keddy and Constable (1985). On 9 December 1983 the seeds were transferred to nylon bags and placed into one of five cold stratification treatments: (1) distilled water, (2) 100% saturated sand (i.e., water table at substrate surface), (3) 75% saturated sand, (4) 50% saturated sand, and (5) 25% saturated sand. Percent saturation in the last three treatments was calculated as a percentage of the mass of distilled water added to treatment two. Each treatment was maintained in sealed plastic containers (height = 12 cm,

diameter = 12 cm) wrapped in aluminum foil at 4°C for the duration of the storage period. The nylon bags with seeds were placed in the above containers approximately 6 cm from the bottom. Personal observations suggest that treatments two to five remained uniformly moist throughout the storage period.

Germination Capacity

Seven thousand five hundred seeds were placed in petri-dishes over a five-day period (one block per day; a block is defined as a random arrangement of all possible treatments each replicated once (Sokal and Rohlf 1981)) beginning 11 February 1985. Therefore, the seeds had been in cold storage for at least 429 days. The experiment included five storage treatments, six species and five replicates arranged in a complete randomized block design with 50 seeds placed in each dish. Each petri-dish had two Whatman #4 filter papers wetted with 7.5 mL distilled water. The dishes were sealed with petri-dish seals and placed in the University of Ottawa greenhouse for 28 days. From 11 to 15 March petri-dishes were opened (one block per day) and the seeds that had germinated (i.e., those having a radicle and/or a green shoot) were counted.

The data analyses consisted of a two-factor ANOVA (species, storage treatment) followed by one-factor ANOVAs for each species. For these analyses, data were arcsine transformed and further transformed using $\log x$ when

necessary to meet the assumption of homogeneity of variances.

Germination Responses

This experiment was designed to test if different moisture conditions during cold storage affected where species germinated on a water depth gradient. The storage conditions during cold stratification were the same as previously described.

The water depth gradient included three treatments in which water levels were maintained above (-10 cm), at (0 -cm), or below (+10 cm) the substrate surface. The substrate used was topsoil mixed with sand (loss on ignition at 500°C = 3.12%). The gradient was produced in the University of Ottawa greenhouse using three plexiglass aquaria (57.5 x 30.5 x 26 cm). The experiment consisted of five blocks with the water levels assigned at random in each block. Each plexiglass aquarium was fitted with a tray containing 32 inserts (7 x 6.5 x 6 cm) with their bottoms removed and sunk into the substrate one cm below the surface. Two of the inserts were used to inspect and adjust water levels daily or twice daily.

Twenty-two thousand five hundred seeds were sown over a five-day period (one block per day) beginning 26 of June 1984. Therefore, seeds had been in cold storage for at least 201 days. Fifty seeds of each species were sown in

each treatment. The seeds were counted out 24 hours prior to sowing and stored dry in petri-dishes in the dark at 4°C until sown. The seeds were then randomly assigned to an insert, scattered over the substrate surface, and covered with approximately 0.25 cm of substrate. Water levels were then raised to the required depth.

In this experiment, germination refers to early recruitment (i.e., germination and subsequent emergence). A seed was deemed to have germinated when a green shoot appeared above the substrate surface (User's definition of germination; Lang 1965). Recruited seedlings were counted and either removed (small seedlings) or clipped below the hypocotyl (large seedlings) weekly. The experiment continued for six weeks (26 June to 10 August).

To test whether there was a significant storage x depth interaction term, a two-factor ANOVA (storage treatment, depth) was performed for each species that had at least ten percent total germination in at least one treatment. Data from treatments with no germination were not included in the analyses because a violation in the assumption of homogeneity of variances would have resulted. Data were arcsine transformed and further transformed using log x when necessary.

RESULTS

Germination Capacity

Mean percent germination after each storage treatment for each species is shown in Figure 1. This figure and Table 1 show that storage treatment had a significant effect on the germination capacity of Juncus militaris, Lobelia Dortmanna and Viola lanceolata ($p < 0.05$). Triadenum Fraseri was not included in the analyses because of insufficient germination. There was no single storage treatment favoured by all species. For example, after storage in distilled water, some species (Viola lanceolata and Glyceria canadensis) achieved maximum germination whereas others (Juncus militaris and Lobelia Dortmanna) exhibited lowest germination.

Germination Responses

Of the four species that had enough germination to be included in the analyses (Glyceria canadensis, Juncus militaris, Lobelia Dortmanna and Viola lanceolata), only Viola lanceolata had a significant storage x depth interaction term ($p < 0.05$). However, even in this case, maximum germination occurred at the same depth regardless of storage treatment (Figure 2).

Figure 1. Mean percent germination (\pm 95% C.I.) in petri-dishes after storage for at least 429 days under five moisture regimes at 4 ° C (n = five replicates). Each p value is from a one-factor ANOVA that tested for significant storage treatment effects. The storage treatments included: 25%, 50%, 75%, 100% water saturated sand and distilled water (P.W.).

Mean Percent Germination

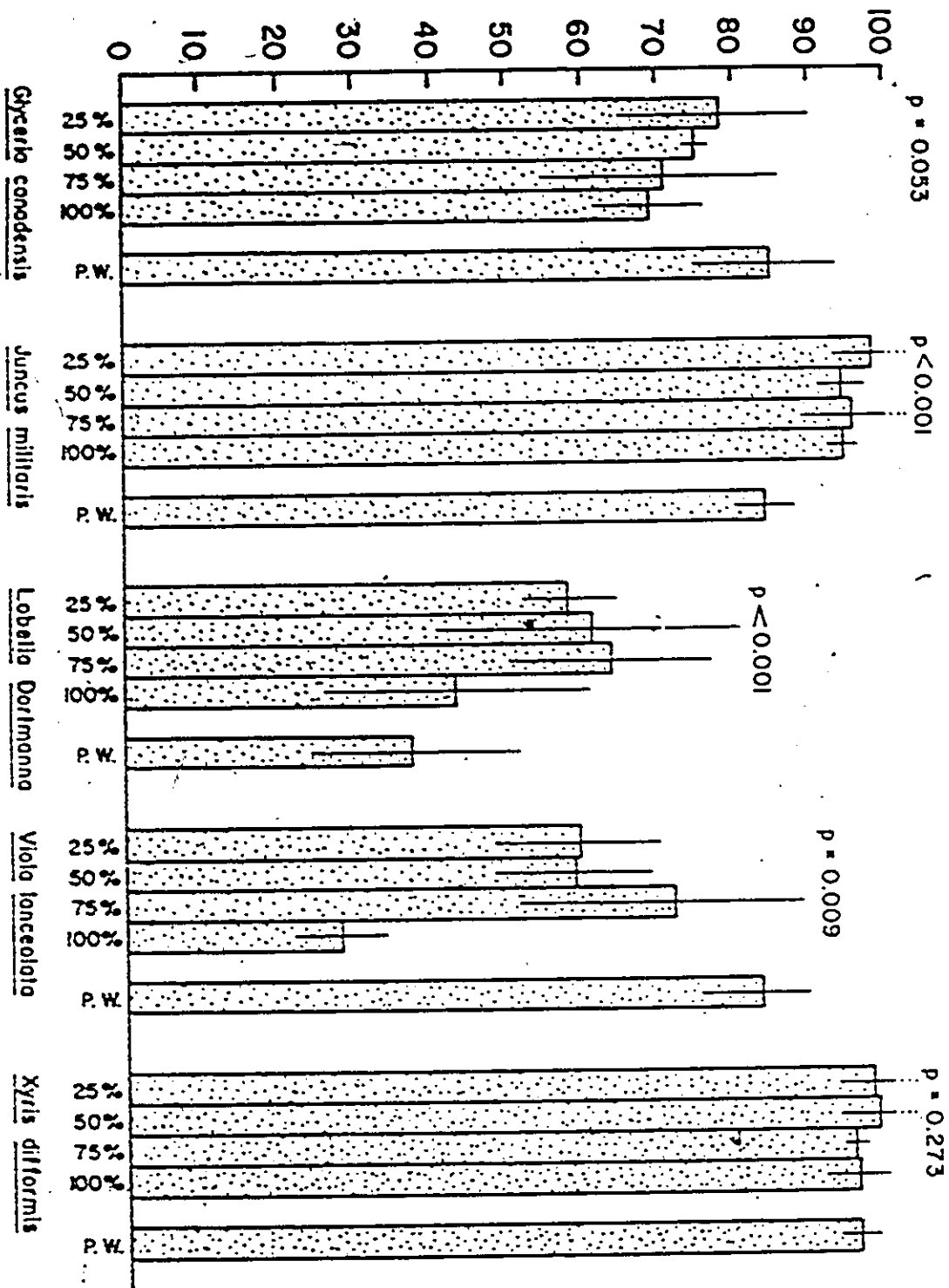
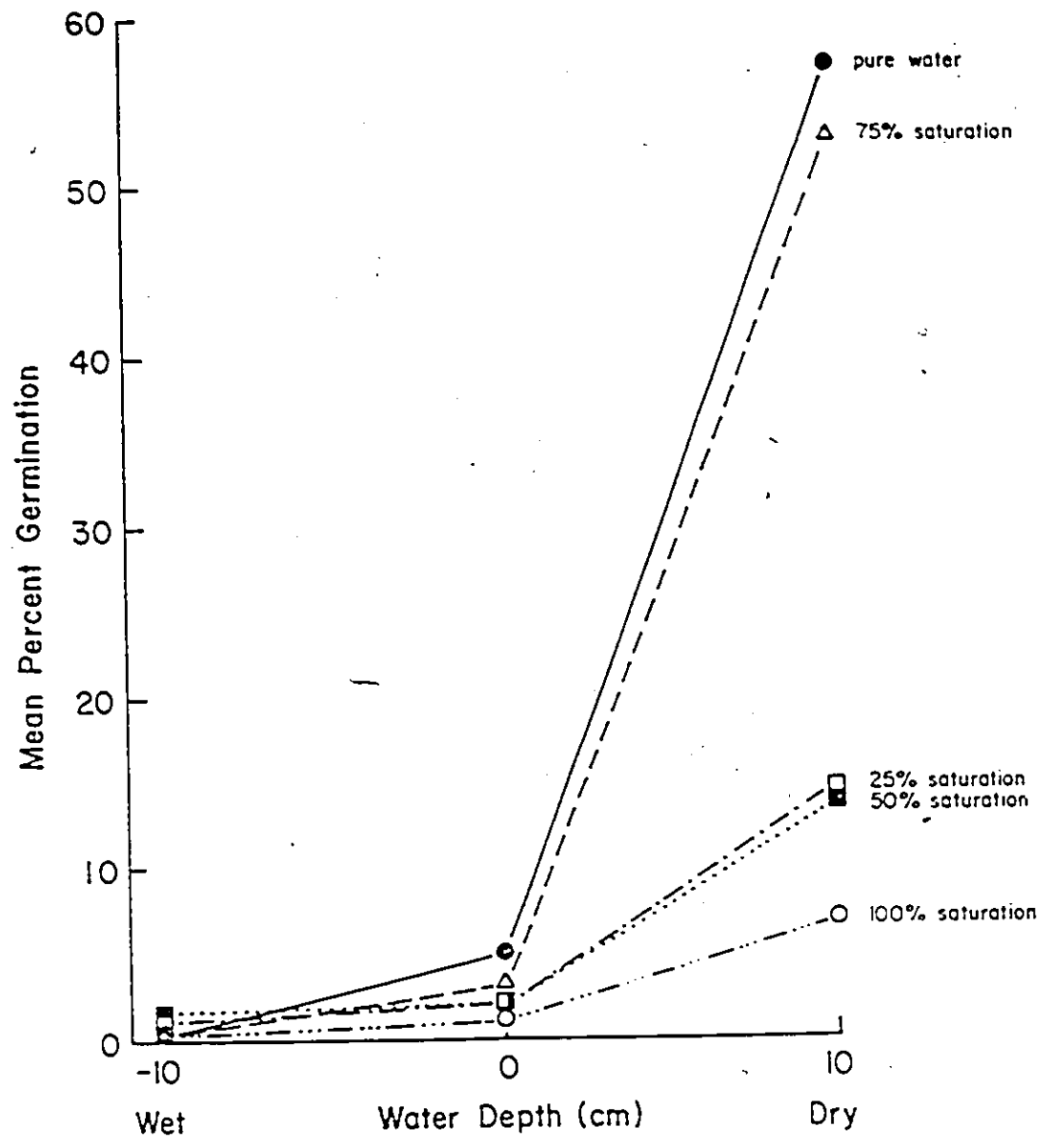


Table 1. Two-factor ANOVA table where the variable is percent germination measured for five lakeshore plant species after storage under five different moisture regimes at 4°C for at least 429 days. Data were arcsine transformed.

Source of Variation	Sum of Squares	D.F.	Mean Square	F	Significance Level
Species	21435.36	4	5358.84	162.15	<0.001
Storage	1239.74	4	309.94	9.38	<0.001
Storage x Species	4045.27	16	252.83	7.65	<0.001

Figure 2. Mean percent germination plotted against water depth for Viola lanceolata, comparing the germination responses after cold stratification under five moisture regimes (n = 5). Storage x depth interaction term for two-factor ANOVA is $p = 0.017$.



DISCUSSION

Several studies have shown that seeds stored dry during cold storage are incapable of germinating afterwards. For instance, Justice (1941, 1944) found that seeds of Polygonum amphibium, P. coccineum and P. hydropiperoides did not germinate after cold storage if stored dry, but did germinate after storage in moist sand or water. Similarly, Farmer (1978) found that seeds of Gentiana crinita were incapable of germinating after dry storage at 3°C, but did germinate when stored under moist conditions. Therefore, it is likely that moisture is necessary during cold storage to break seed dormancy (see Stokes 1965). Based on my results, it appears that there is a wide effective moisture range during cold stratification for lakeshore plants.

Of those species that were significantly affected by different moisture conditions during cold stratification (Figure 1), there was no single treatment that uniformly produced optimal germination. This is not surprising given that Barton (1941, 1961) found no relationship between the amount of water absorbed by a seed and its germinability. This may be a result of the variable physiological effects moisture has on different seeds during stratification (Lang 1965). In some species, immersing seeds in water leaches out metabolic inhibitors allowing increased germination (Koller and Negbi 1959), whereas in other species, the same treatment leaches out growth promoters resulting in

decreased germination (Esashi et al. 1976, Eyster 1940). Thus, it is unlikely that an optimal moisture treatment exists for all species.

One assumption of several studies that examined germination responses to an environmental gradient (e.g., Keddy and Ellis 1985, Keddy and Constabel 1985) was that germination responses are unaffected by storage treatment. My results indicate that this assumption is reasonable, although more testing is required for other plant associations.

Moisture level optima within a given species during stratification appears to be unrelated to its adult distribution along the water depth gradient. Juncus militaris and Lobelia Dortmanna had lowest germination after storage in water (Figure 1), yet the adults of both species are normally submersed. Conversely, Glyceria canadensis and Viola lanceolata had highest germination after storage in water (Figure 1), yet the adults of both species occur higher on shorelines.

In conclusion, varying moisture conditions during cold stratification affected the germination capacity of some shoreline plant species. There was, however, no optimal storage treatment for all species. Storage treatment had little effect on germination responses to different water depths, nor did it bear any relationship to the environment occupied by adults.

CHAPTER 2

GERMINATION RESPONSES TO A WATER DEPTH GRADIENT:

THEIR ROLE IN DETERMINING PLANT DISTRIBUTIONS

There are four life history stages that control the abundance and distribution of plants: (i) the distribution of viable seeds, (ii) germination, (iii) growth and mortality after germination, and (iv) production of viable seeds. Each of these stages has been studied extensively. For instance, there is a wealth of information on the composition and distribution of seeds in seed banks in such habitats as salt marshes (Irwin and Riehl 1980), prairie marshes (van der Valk and Davis 1976, 1978, van der Valk 1981), lakeshores (Keddy and Reznicek 1982), grasslands (Major and Pyott 1966) and forests (Olmstead and Curtis 1947). Similarly, the germination requirements of a wide range of species in various habitats have been studied (e.g., Crocker and Barton 1957, Grime et al. 1981, Baskin and Baskin 1974, 1982, 1984). As well, the effects of various events on growth and reproduction have been documented (e.g., competition, Fowler 1981, 1982, Grace and Wetzel 1981; herbivory, Tilman 1983; disturbance, White 1979, Klemow and Raynal 1983, Wilson and Keddy 1985). However, little is known of the relationships between these four stages particularly in entire associations of species (Grubb 1977, but see Harper and White 1974, Raynal and Bazzaz 1973). In this chapter, I will test whether there

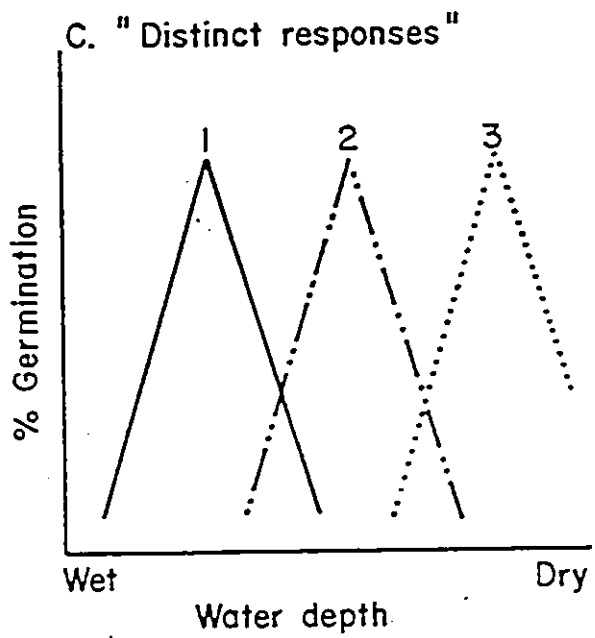
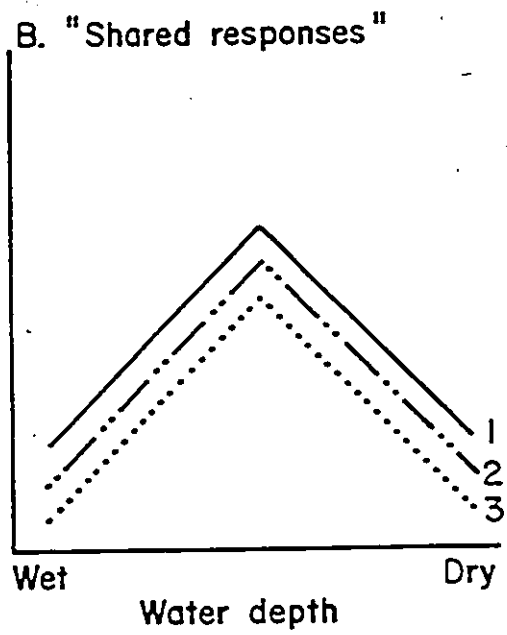
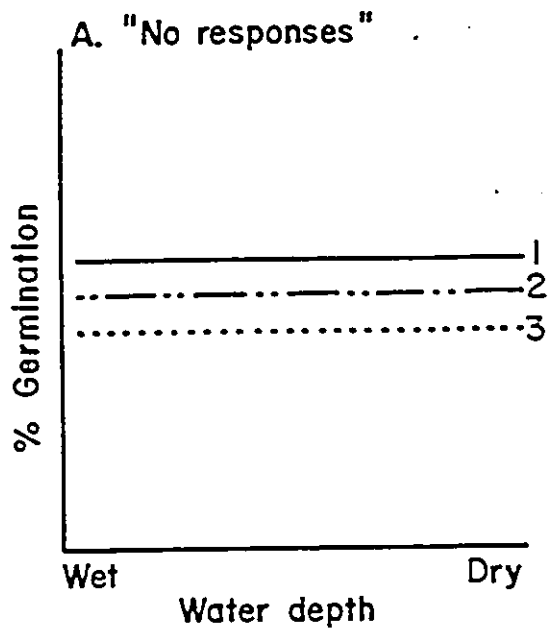
has been sufficient selection pressure on species' germination requirements to maximize the probability that a given seed will germinate in a habitat where it can successfully reproduce. To answer this question, I will test whether germination varies along a water depth gradient and, if so, test whether seedling germination responses to the water depth gradient are correlated with adult distributions.

If seeds of three hypothetical plant species are sown along a gradient, there are three possible outcomes (Figure 3), only one of which is consistent with a positive relationship between germination responses and adult distributions: (i) germination of the three species does not change with water depth (no responses), (ii) the three species have similar germination responses (shared responses), or (iii) the three species have different germination responses (distinct responses). Combinations of the above outcomes are also possible but cannot be tested for. If the species exhibit no germination response to varying water depths or if the species exhibit shared responses, then it must be concluded that other forces (e.g., competition, herbivory, stress, disturbance) after the germination stage are present in determining the abundance and distribution of adults in this community. However, in the case of distinct responses where germination maxima are correlated with adult distributions, it is possible that differences in germination requirements are

sufficient to produce the adult zonation patterns observed on lakeshores. The latter case would also suggest that species could coexist by partitioning the environment as seedlings (Grubb 1977) possibly to reduce intense competitive interactions (May 1981, Werner 1979, MacArthur 1972, Schoener 1983) or to exploit differing sets of environmental conditions (Connell 1980).

To determine plant germination responses, seeds of twenty-four lakeshore plant species were sown along a water depth gradient and the germination response of each was measured. I tested among the three alternatives in Figure 3 on each of two substrates, to examine the generality of the observed responses to the water depth gradient. The distributions of adults and seedlings along a water depth gradient were then quantitatively compared.

Figure 3. Possible germination responses of three species sown along a water depth gradient: (A) Percent germination of all three species does not change over the gradient, (B) All three species share germination maxima at an intermediate water depth, and (C) Germination maxima are distinct from one another.



METHODS

Seed Collection and Storage

The seeds of twenty-four species (Table 2) were collected from Axe Lake, Ontario, Canada (45 ° 23'N, 79 ° 30'W) and an adjacent beaver pond from 23 to 25 September 1983. The word seed is used to mean a propagule containing a single embryo. Seeds were air-dried at 20°C for one month before being transferred to dry plastic containers which were kept at 4°C in the dark. From 9 to 14 December 1983 the seeds were transferred to nylon bags in plastic containers filled with moist sand (75% by mass water saturated) and were kept in the dark at 4°C.

The Gradient

The water depth gradient included treatments in which water levels were above (-20, -10, -5, -2 cm), at (0 cm), or below (+2, +5, +10 cm) the substrate surface. This gradient was created on two substrates: sand (loss on ignition at 500°C = 0.59%) and high organic content (organic) soil (loss on ignition at 500°C = 3.12%). The gradients were produced in the University of Ottawa greenhouse using eight plastic containers (56.5 x 37 x 35 cm). The experiment consisted of five blocks with the water levels randomly assigned within each block and each container having both substrates. Each half of the plastic containers was divided into twenty-four sections (5 x 7 cm) with 0.25 cm thick plexiglass strips and

each container was divided into two by a 0.5 cm thick plexiglass insert (37 x 35 cm). The containers were filled to a level of 13 cm with either commercially obtained sand or organic soil (topsoil mixed with sand). Plexiglass strips were sunk into the substrate to a level of 1.5 cm. Water levels were adjusted daily or twice daily.

Germination Responses

Ninety-six thousand seeds were planted over a five day period (one block per day) beginning 4 June 1984. Fifty seeds of each species were sown in each treatment. The seeds had been counted out two weeks prior to sowing and had been stored dry in petri-dishes in the dark at 4°C until sown. The seeds were then randomly assigned to a section, scattered over the substrate surface, and covered with approximately 0.25 cm of substrate. Water levels were then raised to the required depth. On 16 of June 1984 an algicide, Cutrine Plus (< 0.2 Cu ppm), was added to the underwater treatments to minimize algal growth.

In this study, germination refers to early recruitment (i.e., germination and subsequent emergence) and a seed is deemed to have germinated when a green shoot appears above the substrate surface. Recruited seedlings were counted and either removed (small seedlings) or clipped below the hypocotyl (large seedlings) weekly. The experiment continued for ten weeks (4 of June 1984 to 17 of August 1984).

At the conclusion of this experiment, four environmental factors (oxygen concentration, moisture content, organic content and light intensity) were measured in some or all treatment replicates. Daily temperature fluctuations in several treatments had also been measured during the experiment. These measurements are compared with similar measurements taken at Axe Lake, Ontario in Appendix 2.

Data Analysis

For species that had at least ten percent total germination in at least one treatment, a three-factor ANOVA (water depth, substrate type, species) was performed to determine: (i) if there was more germination at some depths than at others, (ii) if substrate type had an effect on germination responses, and (iii) if there were differences among species in their response to the water depth gradient. For this analysis, percent data were arcsine transformed and further transformed using $\log x$ to reduce (but not eliminate) a problem with the assumption of homogeneity of variances. Friedman's non-parametric test (Siegel 1956) was then performed for each species on each substrate to test for the equality of means among the eight water depths. Depths were ranked according to level of germination; the rankings were done separately for each block.

Those species showing a significant response to water depth were compared using Kendall's coefficient of concordance (Siegel 1956). Two tests were done, one for

each substrate. The null hypothesis was that the species' germination responses (on each substrate) were not concordant (distinct responses) with the alternative hypothesis being that the responses were concordant (shared responses) (Siegel 1956).

Field Distributions

The distributions of sixty-five species along a water depth gradient at Axe Lake, Ontario were determined in December 1979. Presence/absence of each species was recorded at 20 relative heights (beginning 0.5 m underwater and extending to 0.5 m above water) along each of twenty-five transects (Keddy 1983). The number of times a species was found at a particular depth over the twenty-five transects was then calculated for each species.

A Pearson correlation was performed between the mean depth of germination on the experimental depth gradient, and the mean depth of occurrences of adults along the water depth gradient in the field. The correlation included only those species that showed a significant germination response to water depth in the experiment.

Table 2. The 24 lakeshore species used in this study*.

Species**	Family	Monocotyledonae (M) or Dicotyledonae (D)
<u>Bidens cernua</u> L.	Asteraceae	D
<u>Cladium mariscoides</u> (Muhl.) Torr.	Cyperaceae	M
<u>Drosera intermedia</u> Hayne.	Droseraceae	D
<u>Dulichium arundinaceum</u> (L.) Britt.	Cyperaceae	M
<u>Eleocharis palustris</u> (L.) R. and S.	Cyperaceae	M
<u>Glyceria canadensis</u> (Michx.) Trin.	Poaceae	M
<u>Hypericum boreale</u> (Britt.) Sicken.	Hypericaceae	D
<u>Hypericum ellipticum</u> Hook.	Hypericaceae	D
<u>Juncus brevicaudatus</u> (Engelm.) Fern.	Juncaceae	M
<u>Juncus canadensis</u> J. Gay.	Juncaceae	M
<u>Juncus militaris</u> Bigel.	Juncaceae	M
<u>Lobelia Dortmanna</u> L.	Lobeliaceae	D
<u>Lycopus uniflorus</u> Michx.	Labiatae	D
<u>Muhlenbergia uniflora</u> (Muhl.) Fern.	Poaceae	M
<u>Myrica Gale</u> L.	Myricaceae	D
<u>Rhexia virginica</u> L.	Melastomataceae	D
<u>Rhynchospora fusca</u> (L.) Ait. f.	Cyperaceae	M
<u>Sagittaria latifolia</u> L.	Alismataceae	M
<u>Scirpus Torreyi</u> Olney.	Cyperaceae	M
<u>Triadenum Fraseri</u> (Sach.) Gl.	Hypericaceae	D
<u>Typha latifolia</u> L.	Typhaceae	M
<u>Utricularia cornuta</u> Michx.	Lentibulariaceae	D
<u>Viola lanceolata</u> L.	Violaceae	D
<u>Xyris difformis</u> Chapman	Xyridaceae	M

* all species are perennials, except B. cernua which is an annual

** nomenclature follows Gleason and Cronquist (1963), except X. difformis which follows Randall and Keddy (1983)

RESULTS

Statistical Analyses

The three-factor ANOVA (Table 3) indicates that all three factors and all possible interactions between the factors except the substrate by depth interaction were significant ($p < 0.05$). The most important results of this analysis are: (i) there is significantly more germination at some depths than at others, (ii) some species have significantly more germination on one of the substrates, and (iii) there are significant differences among species in their response to the water depth gradient. However, because the assumption of homogeneity of variances was violated in this analysis, non-parametric tests were used in the remaining analyses.

Of the ten species analyzed individually with Friedman's non-parametric test, nine demonstrated a significant difference ($p < 0.05$) in recruitment along the water depth gradient on one or both substrates (Figure 4). Therefore, one possible outcome, that of no response to the gradient, can be rejected.

Because species' germination responses to the water depth gradient differ between the two substrates, Kendall's coefficient of concordance was performed separately for each substrate to test for shared or distinct germination responses. Using only species that had a significant

response to the water depth gradient in each analysis, it was found that species had a significantly concordant response on the sand substrate (Kendall's $W = 0.48$, $k = 5$, $df = 7$, $p = 0.02$) whereas on the organic substrate species did not have a significantly concordant response (Kendall's $W = 0.11$, $k = 7$, $df = 7$, $p > 0.50$). Therefore, on the sand substrate species had a shared germination response with maximal germination occurring at intermediate water depths (Figure 4) while on the organic substrate species had distinct germination responses.

There was a significant correlation ($r = 0.81$, $df = 6$, $p = 0.01$) between mean depth of germination and mean depth of occurrence of adults. Thus, germination responses are similar to adult distributions (Figure 5). In this analysis, data from both substrates for both adults and seedlings were combined to increase sample sizes.

Figure 4. Mean percent germination ($n = 5$) versus water depth for lakeshore plant species which demonstrated a significant response to the gradient, comparing the overall responses on a sand and an organic substrate (Kendall's coefficient of concordance).

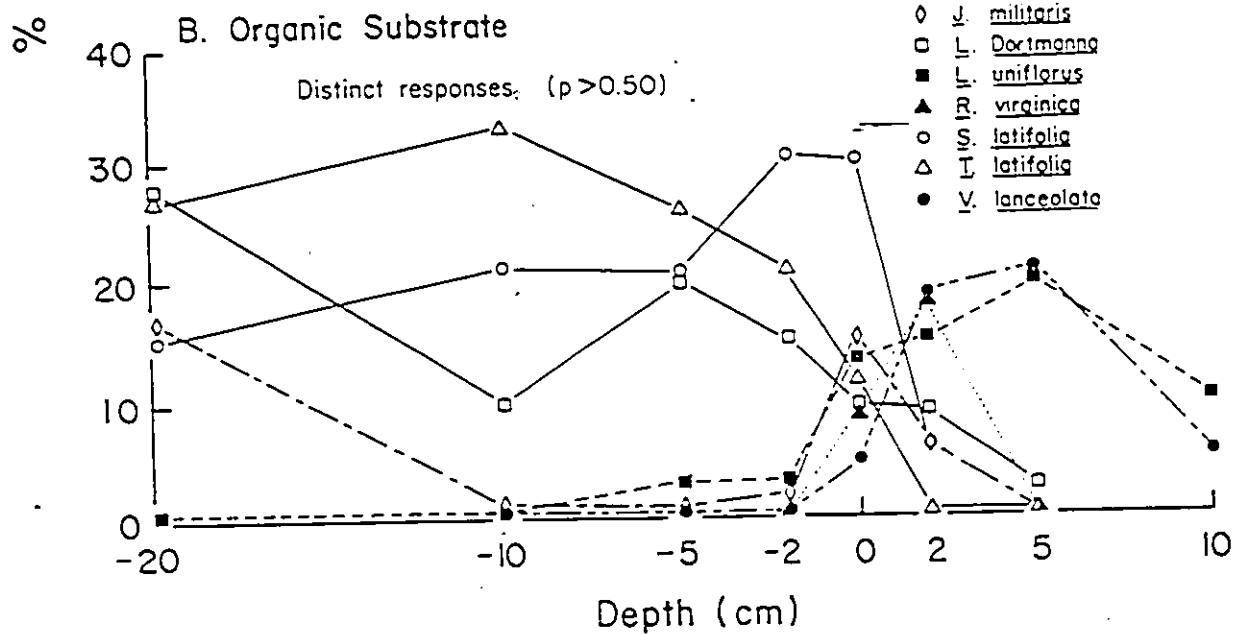
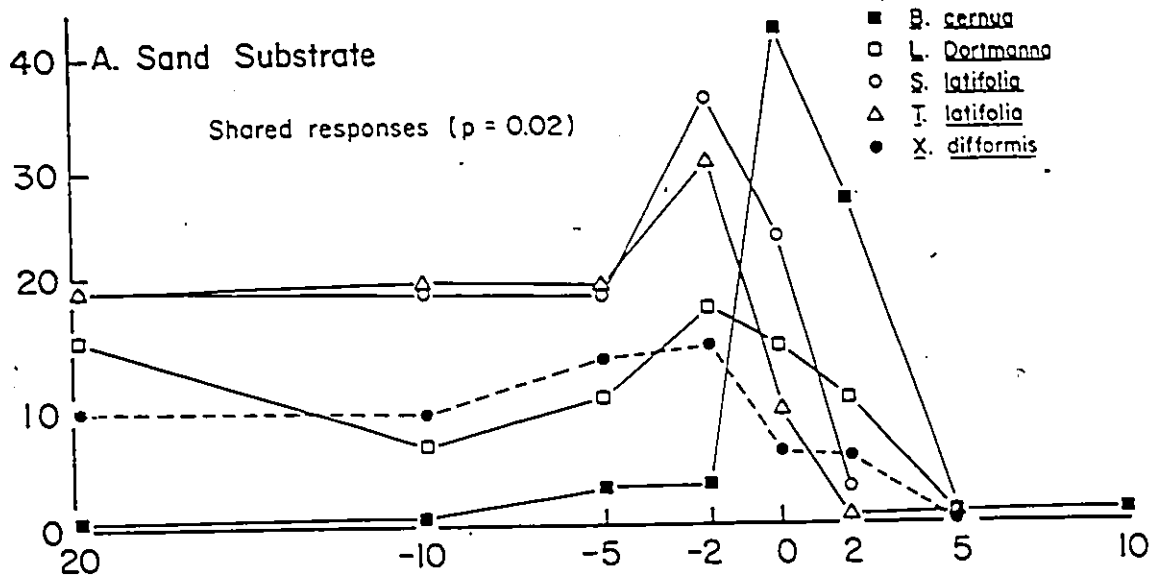


Figure 5. Mean depth of germination (\pm 95% C.I.) in the greenhouse versus mean depth of adult occurrences at Axe Lake for seven lakeshore plant species. Mean depth of germination was calculated by averaging germination responses from sand and organic substrates. r value calculated using Pearson correlation. Species #1 is Bidens cernua, species #2 is Rhexia virginica, species #3 is Lycopus uniflorus, species #4 is Viola lanceolata, species #5 is Xyris difformis, species #6 is Lobelia Dortmanna, and species #7 is Juncus militaris.

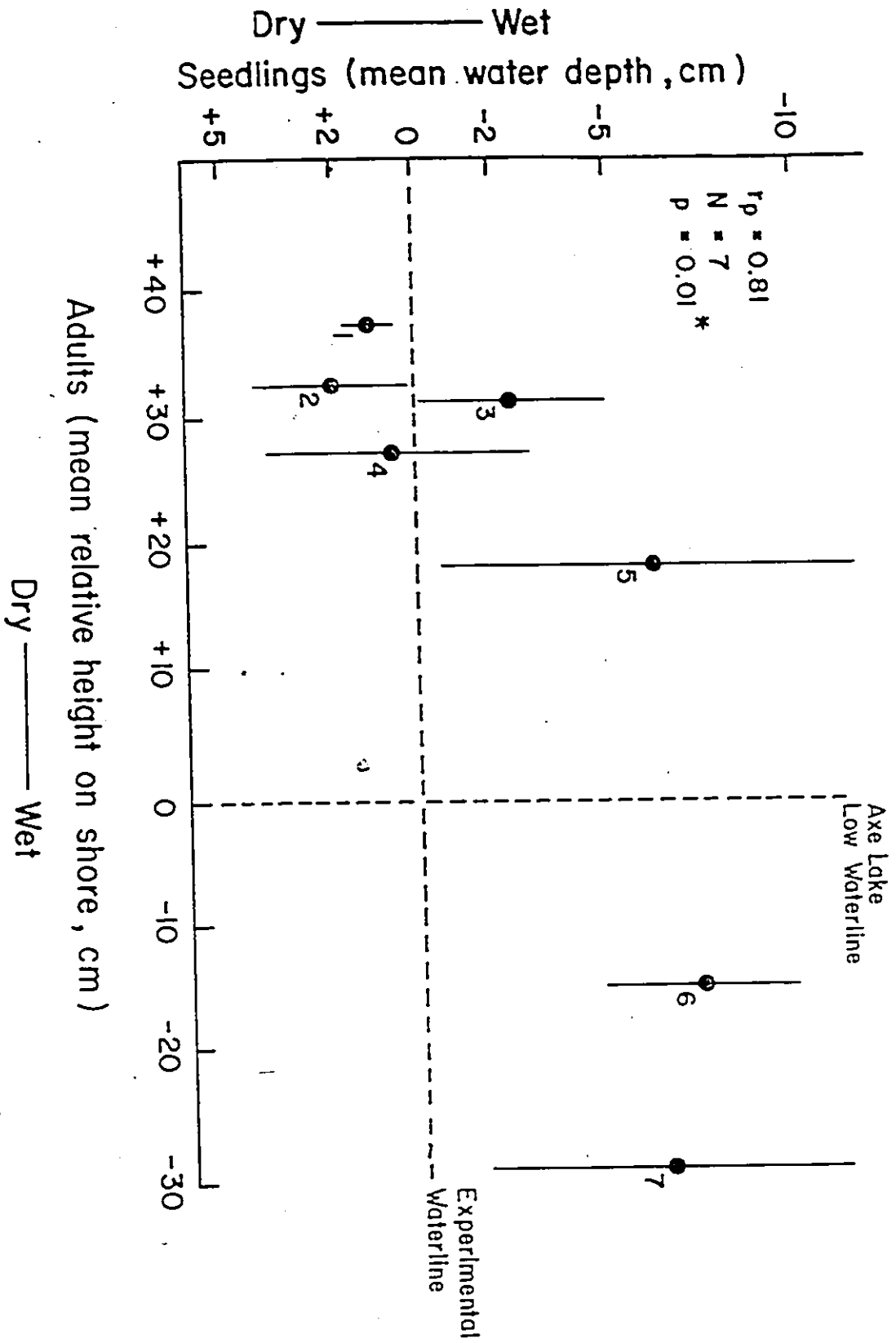


Table 3. Three-factor ANOVA table where the variable is percent germination measured for ten lakeshore species across an eight level water depth gradient on two substrates (sand and organic).

There were five replicates of each treatment and the data were log arcsine transformed.

Source of Variation	Sum of Squares	D.F.	Mean Square	F	Significance Level
Substrate	1.25	1	1.25	11.38	<0.001
Depth	17.05	7	2.44	22.26	<0.001
Species	35.81	9	3.98	36.35	<0.001
Substrate x Depth	1.01	7	0.14	1.32	0.239
Substrate x Species	8.37	9	0.93	8.50	<0.001
Depth x Species	64.05	63	1.02	9.29	<0.001
Subs. x Depth x Sp.	11.39	63	0.18	1.65	0.002

DISCUSSION

In this study many species failed to germinate regardless of water depth; this may be because of the hardened seed coats or pericarps characteristic of many wetland species (Sculthorpe 1967, Hook 1984, Hutchinson 1975). These species may require special pre-treatments (e.g., mechanical breaking, bacterial activity, drying; Hook 1984, Sculthorpe 1967) to stimulate germination (i.e., the seeds are in an innate dormancy state; Harper 1977). The moisture regime during cold storage may also be important to several species (Bannister 1976; see Chapter 1) enhancing or retarding germination.

The Gradient

If an artificial water depth gradient was created of sufficient length to include both very dry treatments and deep water treatments, and germination responses of xerophytes and hydrophytes were observed, distinct germination responses would be found. However, the outcome is not nearly so obvious along shorter gradients within particular plant associations. The question of shared or distinct germination responses is most relevant to species that can potentially interact; therefore, I included only species found between the shrub and floating plant zones on lakeshores. Within this shoreline association, I found shared germination responses on the sand substrate and distinct germination responses on the organic gradient.

Germination Responses: Other Studies

Several studies of recruitment along an environmental gradient have also found shared germination responses. For instance, Harper and Benton (1966) found that of twelve species sown on a water tension gradient, nine had maximal germination at the wettest end, two had no response to the gradient, and one did not germinate. Similarly, Keddy and Constabel (1985) sowed eleven wetland plants along a particle size gradient to test whether different sized seeds germinated best on substrates with specific particle sizes. They found shared responses with maximal germination occurring on small particle substrates, irrespective of the seed size sown. Germination tests on twelve halophytic species on a six-level salinity gradient (ranging from tap water to 10% NaCl) revealed that all twelve species had maximal germination in tap water, and only one species, Salicornia stricta, had any germination under extreme saline conditions (Chapman 1974). The selective advantages of shared germination responses have not been investigated. However, it may be that on stress gradients (e.g., a salinity gradient), seedlings cannot survive high stress conditions, and thus seeds germinate only in areas of low stress or at times of low stress (avoidance strategy, Angevine and Chabot 1979).

Distinct germination responses on environmental gradients have also been demonstrated. Keddy and Ellis (1985) found

that of eleven species from the Ottawa River sown on a water depth gradient, six had distinct germination responses, while the other five had no response. Harper and Sagar (1953) found that three species of Ranunculus that coexist in ridge and furrow grassland have distinct germination responses to a moisture gradient with maximal germination for R. bulbosus occurring at the dry end, R. acris in the middle, and R. repens at the wet end. In California deserts, it has been shown on a temperature gradient that summer annuals have maximal germination at high temperatures, whereas winter annuals have maximal germination at lower temperatures (Went 1949).

It is not apparent why in some situations plants have shared responses while in others, plants have distinct responses. A comparison of which environmental gradients produce shared or distinct germination responses (Table 4) fails to yield any important generalizations. In fact, the same gradient can elicit both shared and distinct responses in different plant associations (e.g., moisture gradients). Similarly, the same plant association can also elicit shared or distinct germination responses on different environmental gradients (e.g., forest and prairie annuals). Future research needs to be directed at determining which environmental gradients or plant associations are likely to be characterized by either shared or distinct germination responses and why.

Germination Responses and Adult Distributions

Figure 5 shows a positive relationship between germination maxima and adult distributions on the water depth gradient. On lakeshores, plants often occur in distinct zones perpendicular to the water depth gradient. This study indicates that the recruitment stage may be important in determining the zonation patterns observed. Previous discussions of zonation on lakeshores (e.g., Spence 1982, Hutchinson 1975) had not considered the importance of recruitment. Several other studies that have found distinct germination responses have also found a positive relationship between germination responses and adult distributions. The best known of these is Harper and Sagar's (1953) study which found that the germination responses of three Ranunculus species on a moisture gradient paralleled their field distributions in ridge and furrow grassland. Similarly, Keddy and Ellis (1985) noted that the distinct germination responses of six Ottawa River species were related to adult distributions. In contrast, Rabinowitz (1978) found that zonation of four genera of mangroves in mangrove swamps could not be attributed to distinct germination responses because seedlings often germinated best in zones occupied by adults of other mangrove genera.

It is apparent that there is often a relationship between seedling and adult distributions, although it varies among

different habitats and different species. A strong relationship between these two stages is important because it indicates that the selection pressures operating at different times in an individual's life cycle are similar in their effects. This has two consequences: (i) a minimum number of seeds will germinate in areas where adults cannot survive, and (ii) species can co-exist by partitioning their environment during the germination stage of their lifecycle.

Table 4. A sampling of studies which have examined germination responses of two or more species along environmental gradients.

Gradient	Plant Association	Germination	References
Moisture	<u>Ranunculus</u> spp.	Distinct*	Harper and Sager (1953)
Moisture	Successional — Field spp.	Shared	Pickett and Bazzaz (1978)
Moisture	Sand Dune Annuals	Shared*	Pemadasa and Lovell (1975)
Water Potential	Forest and Prairie Annuals	Shared*	Raynal and Bazzaz (1973)
Water Tension	Range Grasses	Shared*	Knipe and Herbal (1960)
Water Tension	Various Herbs	Shared*	Harper and Benton (1966)
Water Depth	River Shoreline Herbs	Distinct	Keddy and Ellis (1985)
Tidal Freshwater	Marsh Herbs	Distinct*	Garbisch and Coleman (1978)
Saltwater Depth**	Mangrove spp.	Distinct	Rabinowitz (1978)
Salinity	Halophytes	Shared*	Chapman (1974)
Particle Size	Wetland Herbs	Shared	Keddy and Constabel (1985)
Soil Type	Forest and Prairie Annuals	Distinct*	Raynal and Bazzaz (1973)
Temperature	Old Field spp.	Shared*	Shontz and Oosting (1970)
Temperature	Desert Annuals	Distinct	Went (1949)

* determined by visual inspection of the data

** adults were present throughout this study

GENERAL DISCUSSION

Two unresolved questions, one from each chapter, arose during this study: (i) Why was there no relationship between 'preferred' storage conditions and the adult distribution of a given species, and (ii) Why do lakeshore plant species have shared germination responses on the sandy substrate? The rest of this discussion will deal with these questions and suggest possible answers. However, it is suggested that further research is required to resolve the above questions.

Two Unresolved Questions

(1) In Chapter 1 of this thesis, I reported that there was no relationship between the moisture level during stratification which stimulated maximal germination in a species and the adult distribution of that species along a water depth gradient. This was unexpected, since species' differences in one stage of a plant's life cycle (e.g., germination requirements) should be reflected by species' differences in other life cycle stages (e.g., dispersal in space, storage treatment requirements) (Grubb 1977). It is possible, in a situation where seeds are dispersed only to the habitat in which they are likely to germinate, that there has been no selection pressure to recognize and respond to different storage conditions. However, this possibility seems unlikely for two reasons: (i) seeds of many wetland species are dispersed over a wide portion of the water depth gradient (Keddy and Reznicek 1982, Leck and

Graveline 1979, Parker and Leck 1985), and (ii) in this study, some species did respond to moisture level differences during storage.

Alternatively, natural storage conditions in many lakes may be quite uniform because of high water levels in the fall (personal observations) again precluding any selection pressure towards specific storage treatment requirements. However, in this situation all species should have had maximal germination after storage in distilled water which was not the case.

No reasonable hypothesis for why there is no relationship between 'preferred' storage moisture conditions and adult distributions is known to this author. Perhaps the significant effects of storage moisture conditions on the germination capacity of some species are, in nature, biologically insignificant. Figure 1 does indicate that treatment effects on species' germination capacities are relatively small. These 'small' differences may not be important in situations where high density dependent mortality occurs during germination and establishment. In this situation, there is also not likely to be any selection towards 'preferred' storage conditions that are related to adult distributions.

(2) Several mechanisms could produce shared germination responses. For example, the seeds may be physiologically incapable of germinating and establishing on some portion of

a gradient. In this case, selection pressures for distinct germination requirements would be outweighed by the inability of seeds to exploit unoccupied habitats, and shared germination responses would result. This seems most likely on stress gradients such as one of increasing salinity (see Chapman 1974). However, on lakeshores, it is

— Not known whether such a stress gradient exists.

— Alternatively, all species may germinate over a wide portion of the gradient. This is most likely in stressed and/or disturbed habitats where selection pressures for distinct germination requirements are outweighed by selection for wide environmental tolerances such that species can opportunistically exploit any habitat in which there is an opening; this situation parallels that of weeds whose germination requirements are often fulfilled in many environments (Baker 1974). On lakeshores, sandy shores are characterized by a high degree of stress and disturbance whereas sheltered bays (high organic content substrate) are not. However, before accepting the results of this study as evidence of the above scenario, two problems must be considered. First, species should have wide germination ranges and little, if any, response to the water depth gradient. Figure 4 indicates that Bidens cernua has a very strong response to the water depth gradient on the sandy substrate. Second, to properly assess the likelihood of the above scenario, one would have to measure the germination responses of species typical of sandy shores on a sandy

substrate and repeat the process for species typical of sheltered bays on an organic substrate. This step could not be taken in this study because of the small number of species that had a germination response to the water depth gradient on the sandy substrate.

Conclusions

- (1) The germination capacity of some lakeshore species is affected by varying moisture conditions during cold stratification. There is no optimum moisture level for all lakeshore species nor is there any relationship between the optimal moisture level for each species and their respective adult distributions.
- (2) Moisture levels during cold stratification have little effect on where lakeshore species germinate on a water depth gradient.
- (3) Lakeshore species have shared germination responses to a water depth gradient with a low organic content substrate.
- (4) Lakeshore species have distinct germination responses to a water depth gradient with a high organic content substrate.
- (5) Germination responses along the water depth gradient are correlated with adult distributions.
- (6) These results indicate that lakeshore species can respond to differences in moisture levels during cold stratification and germination.
- (7) By responding to moisture level differences, plants can

determine where on the water depth gradient germination will take place.

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APPENDIX 1
 PLANT SPECIES FOUND
 AS SEEDLINGS AT AXE LAKE¹

Species	Abundance and Distribution
<u>Aster</u> sp.	-common near washline ²
<u>Cladium mariscoides</u>	-rare
<u>Drosera intermedia</u>	-very common anywhere above waterline ³
<u>Dulichium arundinaceum</u>	-patchy distribution
<u>Eleocharis</u> sp.	-infrequent along washline
<u>Eriocaulon septangulare</u>	-near washline
<u>Glyceria canadensis</u>	-near washline
<u>Hypericum boreale</u>	-very common anywhere above waterline
<u>Juncus canadensis</u>	-patchy distribution along washline
<u>Lobelia Dortmanna</u>	-common between waterline and washline
<u>Lycopus uniflorus</u>	-occurring in clumps above washline
<u>Myrica Gale</u>	-common between washline and shrubs
<u>Panicum lanuginosum</u>	-common near washline
<u>Rhexia virginica</u>	-common near shrubs on open beach
<u>Scirpus</u> sp.	-infrequent along washline
<u>Spiraea latifolia</u>	-common between washline and shrubs
<u>Triadenum Fraseri</u>	-common at washline and above
<u>Viola lanceolata</u>	-very common anywhere above water
<u>Xyris difformis</u>	-common underwater, uncommon above

¹seedlings which could not be identified are not included

²highest point on beach subject to wave action; much debris deposited here

³as determined when lake was calm

APPENDIX 2

A COMPARISON OF FIVE ENVIRONMENTAL FACTORS
AT AXE LAKE AND IN THE GREENHOUSE

In Chapter 1 and 2, species' germination responses to a water depth gradient produced in a greenhouse were measured, and then subsequently related to adult distributions in the field. Before extrapolating these results to the field, one must first determine the 'realism' (i.e., the degree to which conditions in the greenhouse resemble those in the field; see Harper 1982) of this experiment, since laboratory (or greenhouse) experiments often suffer from a failure to consider important environmental factors (Diamond 1983). Four factors (oxygen concentration, soil moisture content, soil organic content, and light intensity) were measured in all treatment replicates (unless otherwise stated) in the greenhouse and compared to measurements made at Axe Lake, Ontario. As well, preliminary measurements of daily temperature fluctuations were taken in two treatments both at Axe Lake and in the greenhouse. The measurements at Axe Lake were made on both a sandy beach with low substrate organic content and in a sheltered bay with relatively high substrate organic content. Five randomly chosen transects running perpendicular to the shoreline were set up at both Axe Lake sites and measurements were taken at each of eight water depths (corresponding to the depths used in the greenhouse experiment). Measurements or samples (to be

analyzed later) were taken from 16 to 19 July 1984 at Axe Lake and from 15 to 20 August 1984 in the greenhouse. The data from the oxygen concentration, moisture content and light intensity measurements were analyzed to test for significant differences along each water depth gradient on each substrate at each location (one-factor ANOVAs), to test for significant differences among substrate types at each of Axe Lake and in the greenhouse (two-factor ANOVAs), and to test for differences between the Axe Lake and greenhouse locations (three-factor ANOVA). Data were log transformed when necessary to meet the assumption of homogeneity of variances.

Oxygen Concentration

A Model 53 Clark oxygen electrode was used to determine oxygen concentrations in the water in all underwater (i.e., substrate surface below water surface) treatments and the zero depth treatment. Ten mL samples were taken just above the substrate surface with a 10 mL syringe previously flushed with N_2 . This method could not be used for treatments above water.

Mean underwater oxygen concentrations varied significantly between water depths at Axe Lake and in the greenhouse on the sand substrate ($p < 0.005$; one-factor ANOVAs). Figure 6 indicates that underwater oxygen concentrations were at a minimum at the zero water depth treatment for both locations on the sand substrate.

Underwater oxygen concentrations were significantly depressed ($p < 0.001$; two-factor ANOVAs) on the organic substrate at both Axe Lake and in the greenhouse (Figure 6). This is expected since eutrophic waters (i.e., high nutrient status) are generally characterized by increased oxygen deficits (Wetzel 1975).

Underwater oxygen concentrations were also significantly lower ($p < 0.001$; three-factor ANOVA) in the greenhouse when compared to Axe Lake. It should be noted, however, that the assumption of homogeneity of variances was violated in this analysis. Overall, the results (Figure 6) indicate that the underwater oxygen concentration gradients are similar in shape at both Axe Lake and in the greenhouse. If one includes above water treatments (where oxygen availability is greatly increased) the oxygen concentration gradient in the greenhouse has a greater range than occurs at Axe Lake.

Soil Moisture Content

Surface soil samples (upper 1.0 cm) were taken for all above water (i.e., substrate surface above water surface) treatments and the zero depth treatment to determine soil moisture contents. The soil was dried at 110°C for over 48 hours and percent moisture content was calculated.

Mean above water moisture contents varied significantly ($p < 0.001$; one-factor ANOVAs) between water depth treatments in the greenhouse on each substrate. Moisture

content measurements taken from the organic site at Axe Lake, however, showed a high degree of association between moisture content and soil organic content. Since the latter was quite variable, moisture content means tended to have a large amount of variance (Figure 7). Thus, any moisture gradient that might exist at the organic Axe Lake site is likely obscured by the variable soil organic contents characteristic of this site.

At both Axe Lake and in the greenhouse, soil moisture content was significantly ($p < 0.001$; two-factor ANOVAs) lower on the sandy substrate than on the more organic substrate.

There were significant differences between moisture contents at Axe Lake and in the greenhouse ($p < 0.001$; three-factor ANOVA). It should be noted, however, that the assumption of homogeneity of variances was violated in the latter analysis. In summary, Figure 7 indicates that moisture contents of the sand substrate at both locations are similar but a much more defined gradient is present in the greenhouse. The moisture content gradients on the organic substrate are similar in orientation at both locations but the gradient in the greenhouse is likely more characteristic of a less productive site than the one chosen at Axe Lake. More productive sites would have higher soil organic contents and, hence, higher soil moisture contents than found in the organic substrate used in the greenhouse.

Soil Organic Content

Ten cm soil cores were taken for all treatments at both Axe Lake and in the greenhouse. Soil organic contents were determined by measuring mass loss on ignition (500°C, 18 hours) after drying (60°C, 48 hours) (Dean 1974).

Since soil organic content was kept as a constant along the water depth gradients in the greenhouse, no attempt was made to test for differences along any of the water depth gradients. Soil organic content in the sandy substrate in the greenhouse (Mean \pm 95% C.I. = 0.586 \pm 0.074%) was very close to the soil organic content value on the sandy shoreline at Axe Lake (Mean \pm 95% C.I. = 0.784 \pm 1.795%) although the latter was quite variable. Soil organic content in the organic substrate in the greenhouse (Mean \pm 95% C.I. = 3.115 \pm 0.471%) was more characteristic of a less productive site than the one chosen at Axe Lake (Mean \pm 95% C.I. = 6.011 \pm 7.714%).

Light Intensity

Light intensity readings were taken with a light meter for all treatments both at Axe Lake and in the greenhouse. All readings were taken on a sunny day between 1300 and 1400 hrs and were made at the substrate surface.

At both Axe Lake and in the greenhouse, the light intensity gradient on the sand substrate was not steep with only a slight increase occurring from deep water to above

water. Of these two gradients, only the one at Axe Lake had significant treatment differences ($p < 0.001$; one-factor ANOVAs). The light intensity gradients on the organic substrate at Axe Lake and in the greenhouse increased more rapidly from deep water to above water, although much more so at Axe Lake ($p < 0.001$) than in the greenhouse ($p < 0.05$; one-factor ANOVAs)(Figure 8).

There were significant ($p < 0.005$; two-factor ANOVAs) differences in light intensity between substrates at both Axe Lake and in the greenhouse. In both locations, light intensity was reduced on the organic substrate especially in deep water.

There were significant ($p < 0.001$; three-factor ANOVA) differences in light intensity between the two locations. Overall, Figure 8 indicates that on all four water depth gradients, light intensity increases from deep water to above water with this increase being most pronounced on the organic substrate at Axe Lake. As well, light intensities were lower in the greenhouse when compared to Axe Lake except in the case of deep water treatments on the organic substrate where the situation was reversed.

Daily Temperature Fluctuations

Daily maximum/minimum temperatures were recorded from 13 June to 11 July 1984 in the greenhouse and from 16 July to 21 July 1984 at Axe Lake. Daily temperature fluctuations

were recorded in two treatments: deep water (-20 cm) and above water (+10 cm). At each location, substrate differences were averaged with one daily recording of each.

In deep water, mean daily temperature fluctuations were small both in the greenhouse (Mean \pm 95% C.I. = $6.80 \pm 2.46^\circ\text{C}$; $n = 28$) and at Axe Lake (Mean \pm 95% C.I. = $4.45 \pm 3.32^\circ\text{C}$; $n = 6$). Conversely, daily temperature fluctuations were much greater above water both in the greenhouse (Mean \pm 95% C.I. = $16.3 \pm 4.3^\circ\text{C}$) and at Axe Lake (Mean \pm 95% C.I. = $12.9 \pm 6.7^\circ\text{C}$). These preliminary results indicate that temperature fluctuations are greater above water than below water at Axe Lake and in the greenhouse.

Summary

In general, the shape and direction of changes in five environmental factors along water depth gradients in the greenhouse and at Axe Lake were similar, although differences did occur in the magnitude of these changes. The results also indicate that the water depth gradient on the organic substrate in the greenhouse is more characteristic of an Axe Lake site of intermediate productivity rather than one of high productivity.

As with any greenhouse or laboratory study, 'realism' is invariably lost because field conditions can never be duplicated (Diamond 1983, Harper 1982). However, greenhouse studies are, in general, more precise than field studies

(Diamond 1983; Harper 1982). This study opted for more precision while attaining as much 'realism' as possible.

Figure 6. A comparison of oxygen concentrations (mg/L) (Mean \pm 95% C.I.) along water depth gradients on two substrates at Axe Lake and in the greenhouse.

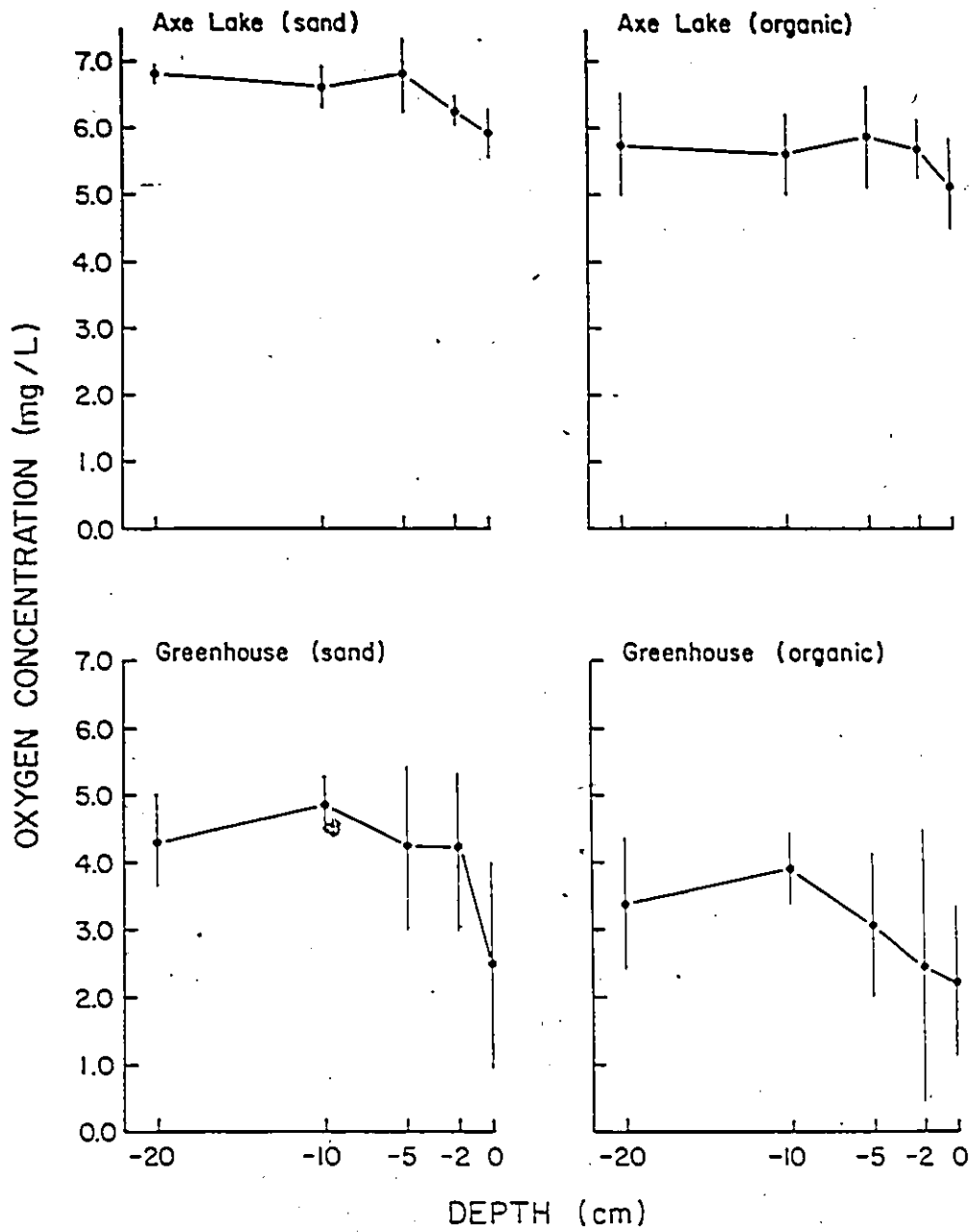
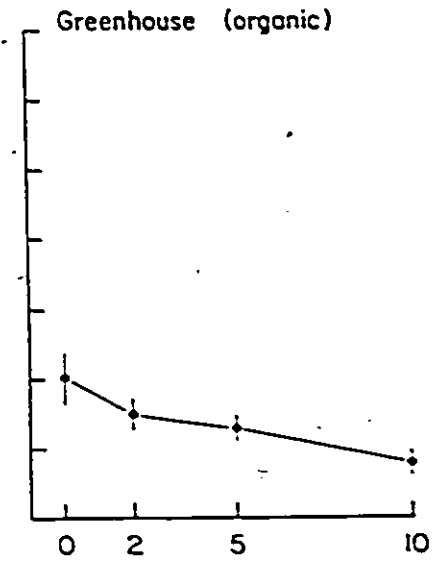
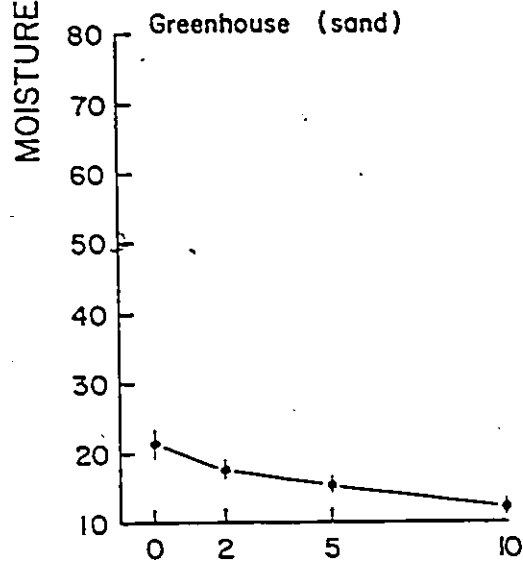
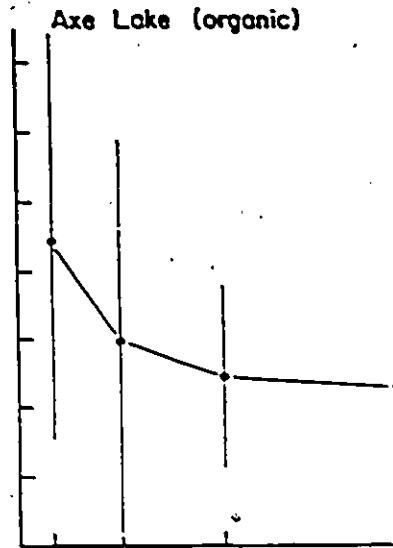
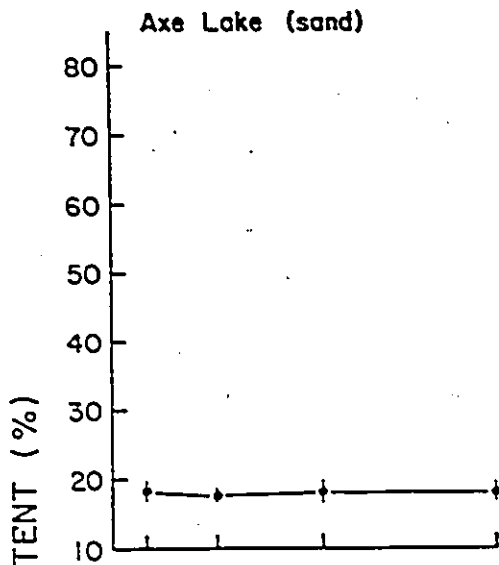
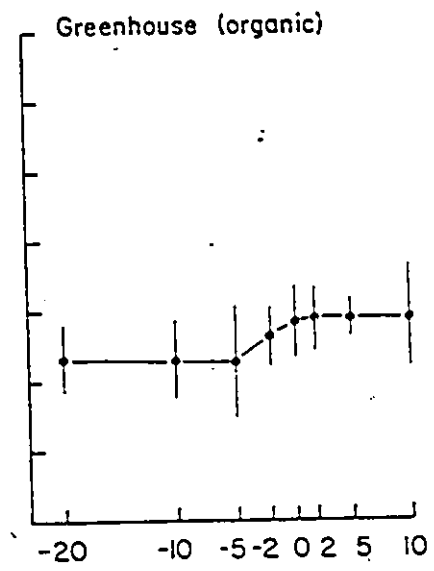
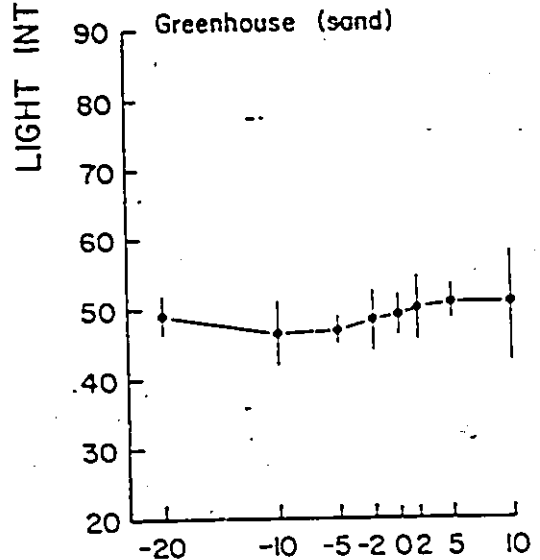
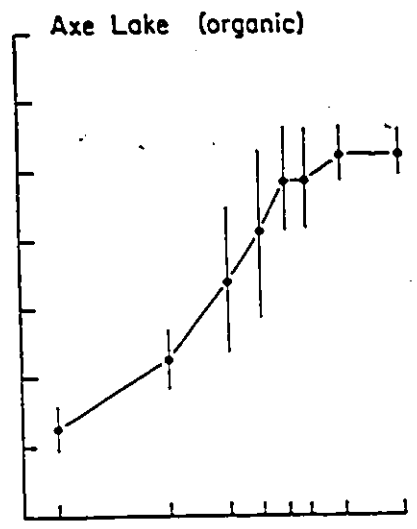
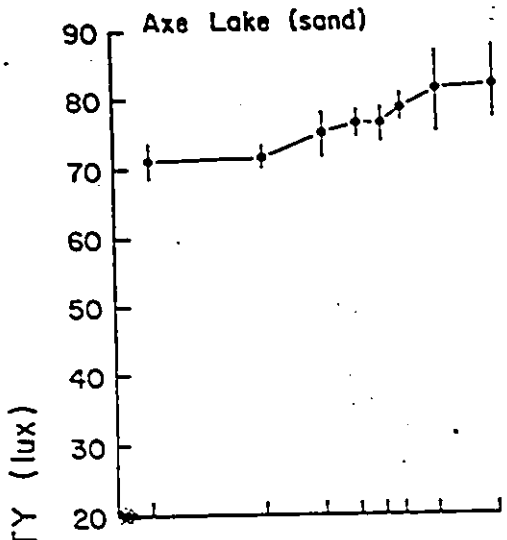


Figure 7. A comparison of soil moisture contents (%) (Mean \pm 95% C.I.) along water depth gradients on two substrates at Axe Lake and in the greenhouse.



DEPTH (cm)

Figure 8. A comparison of light intensities (lux)(Mean \pm 95% C.I.) along water depth gradients on two substrates at Axe Lake and in the greenhouse.



DEPTH (cm)

APPENDIX 3A

Mean percent germination (n = 5 replicates of 50 seeds each) of 24 lakeshore species at eight water depths on a sandy substrate.

Species	Depth (cm)							
	-20	-10	-5	-2	0	2	5	10
<u>Bidens cernua</u>	0.8	0.4	2.4	4.0	42.8	26.4	2.0	2.8
<u>Cladium mariscoides</u>	0	0	0	0	0	0	0	0
<u>Drosera intermedia</u>	0	0	0	0	0.8	1.2	0	0
<u>Dulichium arundinaceum</u>	0	0	0.4	0	1.6	1.6	0.4	1.2
<u>Eleocharis palustris</u>	0.8	0.4	0.4	0.8	2.8	2.8	0.4	0.4
<u>Glyceria canadensis</u>	0	0	0.4	1.2	0.8	2.0	0.8	2.0
<u>Hypericum boreale</u>	0	0.4	0	0.4	0	0	0	0
<u>Hypericum olliopicum</u>	0	0	0	0	0	0	0	0
<u>Juncus brevicaudatus</u>	0	0.4	0	0.8	0	0	0	0
<u>Juncus canadensis</u>	0.8	0	0.8	2.8	2.4	2.8	0.4	0
<u>Juncus militaris</u>	1.6	0.4	0.4	4.0	1.2	0.8	0.4	0
<u>Lobelia Dortmanna</u>	16.8	6.0	12.8	18.8	14.8	10.8	0.8	0
<u>Lycopus uniflorus</u>	33.6	26.4	12.0	10.0	21.2	28.8	20.8	14.0
<u>Muhlenbergia uniflora</u>	0	0	0	0	0	0.8	0	0
<u>Myrica Gale</u>	0	1.2	0.4	0.8	3.6	3.6	4.0	1.6
<u>Rhexia virginica</u>	3.2	1.2	2.0	2.0	8.4	12.0	8.0	9.2
<u>Rhynchospora fusca</u>	0.4	0	0.4	0	0.8	0	0	0
<u>Sagittaria latifolia</u>	18.0	18.8	19.2	36.8	24.8	3.6	0.4	0
<u>Scirpus Torreyi</u>	0	0.4	0	0.4	0	0	0	0
<u>Triadenum Fraseri</u>	0	0.8	0	0	0	0.8	0	1.2
<u>Typha latifolia</u>	19.2	21.2	20.4	32.0	9.6	1.6	2.0	0
<u>Utricularia cornuta</u>	0.8	0	0.8	0	0	0	0	0
<u>Viola lanceolata</u>	4.0	5.6	9.6	3.2	16.4	21.2	12.8	2.4
<u>Xyris difformis</u>	10.8	8.0	14.0	14.4	6.8	6.0	0	0

APPENDIX 3B

Mean percent germination (n = 5 replicates of 50 seeds each) of 24 lakeshore species at eight water depths on an organic substrate.

Species	Depth (cm)							
	-20	-10	-5	-2	0	2	5	10
<u>Bidens cernua</u>	0.4	0	0	1.6	8.8	8.8	5.6	2.8
<u>Cladium mariscoides</u>	0	0	0	0	0	0	0	0
<u>Drosera intermedia</u>	0	0	0	0	0	0	0	0
<u>Dulichium arundinaceum</u>	0	0	0	0	1.2	6.4	0	0
<u>Eleocharis palustris</u>	0	1.2	2.4	2.8	0	0	0	1.2
<u>Glyceria canadensis</u>	0	0	0	0	10.0	8.8	2.4	1.6
<u>Hypericum boreale</u>	0	0	0	0	0	0	0	0
<u>Hypericum ellipticum</u>	0	0.4	0	0	0	0	0	0
<u>Juncus brevicaudatus</u>	0.8	0	0.4	0	0.4	0	0.4	0
<u>Juncus canadensis</u>	3.2	0.4	7.2	6.8	5.6	8.0	0	0.8
<u>Juncus militaris</u>	16.8	0.4	1.6	2.8	14.4	6.0	0	0
<u>Lobelia Dortmanna</u>	27.6	10.8	21.2	16.0	12.4	10.4	2.4	0
<u>Lycopus uniflorus</u>	0.4	0.8	2.8	2.8	12.8	14.4	19.2	9.6
<u>Muhlenbergia uniflora</u>	0	0	0	0	0	0.8	0	0
<u>Myrica Gale</u>	0	0	0	0	3.2	2.8	0.4	1.6
<u>Rhexia virginica</u>	0	0.4	0	0.4	8.8	18.0	0	2.8
<u>Rhynchospora fusca</u>	0	0	0	0	0	0	0	0
<u>Sagittaria latifolia</u>	14.8	21.2	19.6	31.6	32.0	4.8	0	0
<u>Scirpus Torreyi</u>	0	1.2	1.6	0.4	0	0	0.4	0
<u>Triadenum Fraseri</u>	0	0	0	0	0	0.8	0	0.4
<u>Typha latifolia</u>	27.2	34.8	26.4	21.6	12.0	2.8	1.2	0
<u>Utricularia cornuta</u>	0.4	1.2	0	0	0.4	0	0	0
<u>Viola lanceolata</u>	0	1.2	0.8	0.8	8.8	17.6	19.6	4.4
<u>Xyris difformis</u>	3.2	2.0	9.6	7.2	12.4	2.8	0	0