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16. Abstract (Limit: 200 words)

This report presents the results of a four-year study on techniques for revegetation of native sedges in created basins. Although often the dominant genus in shallow wetlands, sedges (Carex spp.) do not readily recolonize after restoration or creation of the water table. It is unlikely that sedges will naturally establish in created wetlands.

The results of seed germination studies on five Carex species suggest the highest germination rates in fresh seeds – with one exception. Wet/cold storage also can prolong seed viability for at least two-and-a-half years. Dry storage is not recommended for wetland sedge seeds. Short-term wet/cold treatment after prolonged dry storage does not improve germination rates.

Sensitive to deep water, rising water levels, and competition during the establishment year, seedlings grew well across a wide range of water depths in subsequent growing seasons. Both species outcompeted annual weeds within two to three growing seasons, but not Phalaris arundinacea (reed canary grass). The study recommends weed control during the establishment year to prevent the invasion of P. arundinacea.

Wetland soil promotes seedling growth relative to other soils, but does not affect germination rates. Because of the potential for the introduction of undesirable weeds, the study does not recommend the use of donor wetland soil. Instead, study results suggest the potential for the use of organic top-dressings.

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Establishment of Native Sedge Vegetation in Created Wetlands

Final Report

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EXECUTIVE SUMMARY

This final report contains the results of four years of research on techniques for revegetation of native sedges in restored and created basins under Mn/DOT agreement 71 789-72267-1451 Tasks 1-9 "Establishment of Native Sedge Vegetation in Created Wetlands". It was instigated by a desire on the part of both the researchers and funding agency to improve the state of the knowledge for practical application. A list of the Tasks follows this executive summary. The report has five chapters. Each chapter is prefaced with a summary that describes the main results and conclusions of the experiments in that section.

Chapter 1 is a synthesis of the results from Tasks 1-5, which represent the experiments focusing on seed germination and seed storage of five native sedges. The main results of this section indicate that four of the five sedge species have the greatest germination rates when the seeds are fresh and that germination rates decline over time. Storage conditions can influence the rate at which seeds lose the ability to germinate. In general, the combination of wet and cold storage maintained optimum seed viability over time and is recommended as a long-term storage condition for sedge seeds during the entire period between collection and use in the field. Short term stratification (wet cold treatment) of old seeds is not effective in stimulating germination.

Chapters 2 and 3 describe the results from Tasks 6 & 7 for *Carex lacustris* and *Carex stricta*, respectively. Field studies of optimum seedling growth under a variety of controlled environmental conditions were performed in experimental basins at the University of Minnesota's Landscape Arboretum in Chanhassen, MN. Experimental treatments included location of planting along an elevational (water depth) gradient, seasonal water level fluctuations, planting density, and control of competition from weeds. The results indicate that seedlings of both species were sensitive to water fluctuations, particularly at low elevations (deep water) during the establishment year, but were tolerant of a wide range of water depths and fluctuation regimes in subsequent growing seasons. Growth was optimally stimulated by some type of seasonal water fluctuation. Sedges grew more vigorously at upper elevations when competition from weedy species was controlled. When competition was not controlled, growth was suppressed such that plants were uniformly small across all elevations. Although not a design of the study, differences in the weed community affected sedge growth. Both sedges were able to out-compete annual forbs and grasses after two to three growing seasons, but neither were able to out-compete *Phalaris arundinacea* (reed canary grass). Planting density had no affect on the ability of *C. stricta* to out-compete weeds. Higher planting density for *C. lacustris* did reduce the cover of annual weeds, but not *P. arundinacea.* The results of this study suggest that weed control should be a key part of a wetland revegetation design for the first two to three years.

Chapter 4 describes the results of Tasks 8 & 9 in which we investigated the affect of organic rich mineral soil from a former wetland basin on the seed germination and seedling growth of *C. stricta* and *C. lacustris.* Former wetland topsoil was compared to sandy and clayey subsoils. Although donor wetland soil is often advocated for application in newly created basins, this study did not indicate that it had a stimulatory affect on sedge seed germination. Former wetland soil did stimulate seedling growth for both species, but is only cautiously recommended as a top-dressing in created wetlands due to the potential introduction of undesirable weed propagules.

Chapter 5 represents a supplemental experiment in which the results of Tasks 6-9 were applied in a Mn/DOT wetland creation. *Carex stricta* and *Carex lacustris* seedlings were planted at the southeast end of the mitigation wetland for the Shakopee Bypass, Scott county, MN (also known as the J.B. Pond). Seedlings were planted at two elevations and with a variety of site pre-treatments designed to reduce competition from weeds. Experimental plots were treated with herbicide, herbicide and an organic top-dressing (hay), hay only, or no pre-treatment (control). Seedlings of both species displayed greater growth in plots with the hay pre-treatment, but did not respond to the pre-application of herbicide. Application of herbicide early in the season may have reduced its efficacy. We conclude that the organic top-dressing was beneficial to sedge growth, although the mechanism (e.g. moisture retention, nutrient addition, weed exclusion) is not known. We recommend the use of organic top-dressings such as hay (excluding hay made from or including *Phalaris arundinacea* - reed canary grass) in lieu of donor wetland soil. This section is followed by photographs of the plot pre-treatments and planting process at the site.

CHAPTER 1 (Tasks 1-5)

Effects of Moisture, Temperature, and Time on Seed Germination of Five Wetland *Carices*: Implications for Restoration

Rachel A. Budelsky and Susan M. Galatowitsch

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SUMMARY

Successful restoration of sedge meadow wetlands is limited by lack of information regarding reintroduction of sedge (*Carex*) propagules. While restoration from seed is common for prairie restorations, little is known about the germination characteristics of many wetland plants, including sedges. This paper presents the results of a 2.5 year study on seed germination and viability for five species of *Carex* common to sedge meadow and prairie pothole wetlands in temperate North America. Seed storage and germination conditions were investigated to determine the optimum combination for maintaining seed viability and stimulating germination rates over time. Seeds were germinated under seven different temperature and three moisture regimes after storage for 4, 10, and 14 months under one of four different storage regimes (dry/warm, dry/cold, moist/cold, and wet/cold). The efficacy of short-term wet/cold stratification to stimulate germination of 2.5 year old seed after long-term dry storage was also investigated. *Carex stricta, Carex comosa*, and *Carex lacustris* showed the greatest germination response after wet/cold or moist/cold storage while *Carex lasiocarpa* and *Carex rostrata* showed similar rates of germination after either wet/cold or dry/warm storage. Wet/cold long-term storage was associated with a high level of viability in all five species after 2.5 years. Viability and germination rates were reduced in *Carex stricta, Carex comosa*, and *Carex lasiocarpa* after long-term dry/cold storage. Germination rates of seeds stored dry for 2.5 years are not improved by short-term wet/cold treatment in any species tested. *Carex* seeds should be stored under wet/cold conditions to maintain seed viability over time, thus increasing the likelihood of seeding success for sedge meadow restoration.

INTRODUCTION

Sedge meadow wetlands were historically abundant in number and extent in the mid-continental United States prior to agricultural development, but have been disproportionately impacted by conversion and drainage relative to deeper-water wetlands (Galatowitsch & van der Valk 1996b; Detenbeck et al 1998). Although approximately 36,000 ha of wetlands were restored in the prairie pothole region of the United States between 1987 and 1990 as part of federal agricultural incentive programs (Dahl & Johnson 1991), the wetlands typically restored have been deeper water marshes (Galatowitsch & van der Valk 1996b). Thus the combination of wetland loss and subsequent restoration efforts has resulted in a landscape that does not reflect historic wetland diversity (Bedford 1996; Galatowitsch & van der Valk 1996b). While inappropriate basin hydrology is an important limitation to the restoration of sedge meadows, lack of information regarding vegetation re-establishment is equally limiting. In areas where deliberate sedge meadow restoration has been attempted through mitigation, failure rates are high due to revegetation problems (van der Valk et al. 1998).

Unlike many other species of wetland plants that quickly recolonize after reflooding, sedges (members of the genus *Carex*) do not return to isolated wetland restorations (Galatowitsch & van der Valk 1996a). This is likely due to the fragmented nature of the landscape in an agricultural setting, which limits dispersal of water-borne seeds, the depletion of the seedbank that occurs after many years under cultivation (van der Valk & Verhoeven 1988; Wienhold & van der Valk 1989) and the fact that the majority of wetland basins in the agricultural Midwest are restored simply by reflooding and are not planted or seeded. Poor seed set in potential source populations of sedges, and low seed viability may also play a role in limiting recolonization (Bremholm 1993).

To ensure the successful return of sedge meadow wetlands to the landscape, deliberate introduction of propagules to restored wetland basins will be necessary. Seeds are an attractive option for restoration primarily because they are less expensive than the cultivation or acquisition of seedlings or cuttings, but information on seed storage and germination requirements is scant for wetland plants. Such information is readily available for prairie plants (Thompson 1992; Morgan et al. 1995; Packard & Mutel 1997) and forms the baseline from which field germination expectations can be developed. Germination characteristics have been investigated for a number of western U.S. forage and alpine sedges (Bliss 1958; Johnson et al. 1965), but only a handful of studies has provided insight into the germination, storage, and dormancy characteristics of wetland Carices (Larson & Stearns 1990; Bremholm 1993; Baskin et al. 1996). Baskin et al. (1996) investigated Tennessee populations of buried *Carex stricta* (tussock sedge) and *Carex comosa* (bottlebrush sedge) seeds to determine the effect of seasonal temperature cues and flooding on the germination and annual dormancy patterns in these species. Larson and Stearns (1990) examined the effect of dry-warm vs. dry-cold storage on the germination of *Carex scoparia* seeds, and Bremholm (1993) and van der Valk et al. (1998) investigated the effects of seed age, storage conditions, germination moisture, and soil amendments on the viability and germination of a variety of wetland *Carex* seeds.

The current study was initiated to develop criteria that do not presently exist for storage and germination of wetland *Carex* seeds. Such information is critical to the development of field seeding strategies. Specifically we characterize the viability and germination rates of five wetland Carices after different combinations of seed age, storage condition, germination temperature, and germination moisture levels suggested by the work of Bremholm (1993) and Larson and Stearns (1990). Both previous studies point to the potential importance of seed storage condition in promoting *Carex* seed germination and viability, but equivocal results of the effects of specific storage conditions in the study by Bremholm (1993) suggested the need for additional work on optimal storage conditions.

We hypothesize that seeds stored under saturated conditions will maintain consistently higher viability and germination rates over time than seeds stored dry. We are particularly interested in the potential influence of storage condition and duration (seed history) on seed response to different germination conditions. This study is unique in considering the effects of storage condition, storage duration, germination temperature, and germination moisture simultaneously for *Carex* seeds to determine the optimum treatment combination for maintaining viability and stimulating germination.

We consider the germination and storage response characteristics of the following wetland species: *Carex stricta* Lam., *Carex lasiocarpa* Ehrh. (wire grass), *Carex lacustris* Willd.

(lake sedge), *Carex comosa* Boott, and *Carex rostrata* Stokes (beaked sedge). These perennial species were chosen because they are abundant and widespread in temperate North America (Wheeler 1981), making them likely candidates for restorations. *Carex stricta* and *Carex comosa* are tussock-forming species (Bernard 1990). *Carex lacustris*, *Carex lasiocarpa* and *Carex rostrata* are spreading rhizomatous mat formers (Bernard 1990) with relatively hard achenes. As is the case for most Carices, all five species are wind pollinated (Bernard 1990, Ball 1990).

The proximate implications of this research include recommendations for seed producers regarding the best storage conditions for maintaining seed viability after collection, the efficacy of short term stratification on germination of stored seed, optimum conditions for growth chamber or greenhouse germination, and timing of seed dispersal in restorations and creations. The ultimate contribution of this research is to facilitate the restoration of sedge meadows in temperate North America.

METHODS

General Overview

The objectives of this study were to: 1) characterize the optimum germination conditions for five wetland Carices, 2) characterize change in germination and viability over time, 3) test the hypothesis that wet/cold storage maintains seed viability over time at a higher rate than other storage regimes, and 4) test the hypothesis that a short wet/cold treatment can stimulate germination in older seeds. Wet/cold "stratification" is a commonly recommended procedure for breaking dormancy (Agrawal 1980). Tetrazolium analysis was used to independently confirm the viability/dormancy status of seeds stored under different conditions (Grabe 1970). Thus, the study consisted of three complementary parts: 1) germination/storage experiment, 2) short-term wet/cold "stratification" experiment, and 3) tetrazolium viability analysis.

The germination/storage experiment combined seven germination temperatures, three germination moisture conditions, four storage conditions, and four storage durations, into one incomplete factorial design consisting of 84 treatment combinations per species. A full factorial experiment, in which every combination of treatment levels would be used (273 total), was not practical due to time and space constraints. The incomplete factorial design considered all combinations of storage regime, storage duration, and germination temperature for each species, while germination moisture was systematically assigned to combinations of the first three factors. Two replicates of fifty seeds each were used for all treatment combinations for all species.

Changes in germination rates over time were investigated by comparing the pre-storage germination rate obtained from newly collected seeds (storage duration: 0 months) to the germination rates obtained after three subsequent storage durations.

Collection

Seeds were collected from sedge meadow wetlands and fen communities in east-central Minnesota at the University of Minnesota's Cedar Creek Natural History Area (CCNHA) (45° 24' N, 93° 12' W). *Carex stricta, C. lacustris, C. rostrata,* and *C. comosa* were collected from wetlands with Frigid Typic Endoquall (wet mineral) and Frigid Typic Medisaprist (wet organic) soils (Grigal et al. 1974). *Carex lasiocarpa* seeds were collected from floating mats in poor fen communities. Seeds were collected during June and July (*C. stricta, C. lasiocarpa,* and *C. lacustris*) and October (*C. comosa* and *C. rostrata*), 1994. Seed collections were made from multiple wetlands (n = number of wetlands) for each species: *C. stricta* (n=3), *C. lasiocarpa* (n=3), *C. lacustris* (n=3), *C. comosa* (n=2) and *C. rostrata* (n=2). Seeds from each wetland were stored separately throughout the experiment and an equal proportion of seeds was used from each wetland for each species in all experiments.

After collection, chaff was removed with an air-column seed separator. Only full achenes were used in the experiment. Perigynia were not removed for storage or germination experiments. Seed cleaning and counting occurred over a four to six week period during which time the seeds were stored at room temperature, 23° C, in open plastic bags.

Storage

Seeds of each species were placed under four different storage regimes: dry/23° C (dry/warm), dry/4° C (dry/cold), moistened/4° C (moist/cold), and saturated/4° C (wet/cold). The storage temperature and moisture conditions were suggested from experiments conducted by Bremholm (1993), Larson and Stearns (1990), Baskin and Baskin (1978), and Washitani and

Masuda (1990). Seeds in the dry storage regimes were stored loose and dry in sealed plastic bags and were not exposed to any further drying procedures after the initial four to six week exposure to a relative room humidity of 20-30% during cleaning and sorting. Seeds stored in the moistened and saturated storage regimes (100% humidity) were wrapped in steam-sterilized cheese-cloth, packed with fresh *Sphagnum* moss, and placed in sealed plastic bags. Storage in thin plastic bags permitted slow diffusion of oxygen to the seeds (King & Roberts 1979). Deionized water (pH 5.0) was added to the moistened bags until the cheese-cloth seed packages and *Sphagnum* moss were saturated. Water that pooled in the bottom of the bag was decanted. Seed packages in the saturated storage regime were submerged in deionized water. Seeds stored warm (23°C) were kept in a laboratory drawer while those stored cold (4°C) were kept in a temperature-controlled walk-in cold room with a relative humidity of 85-95%. Although seeds were stored in darkened locations, they were occasionally exposed to light during storage when subsamples were removed for experiments.

Germination

Temperature controlled growth chambers were used for the germination experiments. The seeds of all five species (except *C. lacustris*) were placed under germination conditions immediately after cleaning to obtain the baseline germination rate. (Preliminary experiments with fresh seeds of *C. lacustris* produced no germination. The assumption that germination = 0 was used for the baseline for this species). Five different static and diurnally fluctuating temperature regimes were used for the baseline germination experiment: 25°C, 20/15°C, 25/20°C, 30/25°C, and 35/30°C. Additional 20°C and 30°C temperature regimes were added in subsequent experiments as additional growth chambers became available. A separate growth chamber was used for each temperature regime. Diurnal temperature fluctuations corresponded to a 14 hour day (higher temperature) / 10 hour night (lower temperature) light regime provided by fluorescent and incandescent bulbs (*ca.* 200 - 300 μmol s^{-1} m^{-2}). Light has been shown to be a germination requirement for a number of *Carex* species including *C. stricta* and *C. comosa* (Johnson et al. 1965; Larson & Stearns 1990; Baskin et al. 1996), therefore no germination experiments were conducted in the dark. Fluctuating temperatures have been shown to stimulate the highest germination in a number of wetland Cyperaceae (Baskin & Baskin 1978; Thompson & Grime 1983; Larson & Stearns 1990; Baskin et al. 1996). The temperature fluctuations chosen were based upon the average monthly temperatures for central Minnesota in May through September, with the addition of one higher-than-average temperature (35/30°C).

Batches of seeds (1,750 seeds per species) were removed from each of the four storage regimes after four, ten, and fourteen months for *C. stricta*, *C. lasiocarpa*, and *C. lacustris*. *Carex comosa* and *C. rostrata* seeds were removed from storage after six, ten, and fourteen months. The difference in storage duration for the two groups of species was a consequence of different collection dates: *C. comosa* and *C. rostrata* were collected in the early fall, so their baseline germination experiment was run at the same time as the four month experiment for the other three species. The six month storage duration for *C. comosa* and *C. rostrata* then occurred at the same time as the 10 month germination experiment for the other three species, and so on.

Prior to the germination experiments, seeds were surface disinfected for fungus using a 50:50 solution of 5.25% sodium hypochlorite and deionized water for ten minutes (*C. stricta* was soaked for five minutes) then rinsed with deionized water for ten minutes. The duration and concentration of bleach solution used in this study were greater than commonly recommended (Abdul-Baki & Moore 1979) in order to control the relatively high degree of fungal infection found on the perigynia. Preliminary studies showed higher germination rates for all five species in high vs. dilute bleach treatments (R.A. Budelsky, unpublished data). Surface sterilized seeds were plated out into covered 6.0 x 1.5 cm petri dishes (50 seeds/dish) lined with blotter paper and immediately placed in the growth chambers.

Three germination watering regimes were used: moistened, saturated and dry/saturated. The alternating dry/saturated regime was suggested by Baskin and Baskin (1984) as a way to break physically imposed dormancy in hard-coated seeds by cracking the pericarp through expansion and contraction. Approximately 1.5 grams (1.40g +/- 0.27g) of deionized water were used to initially saturate the petri dish blotter paper in the moistened regime. Approximately 3.5 grams (3.39g +/- 0.59g) of water were used in the saturated regime, which produced a thin film of standing water in the bottom of the petri dish. The dry/saturated dishes were initially watered as saturated dishes, but were allowed to dry until the edges of the blotter paper curled before re-watering. Saturated and moistened dishes were watered daily and dry/saturated dishes were watered every four to ten days, depending upon the rate of evaporation from each dish. Dishes were checked daily for germination.

Viability Analysis

Viability was determined from tetrazolium analysis (following Grabe 1970) soon after seeds were collected (baseline measurement) and on batches of seeds taken from storage at 23 and 31 months for all species from each wetland where seeds were collected. Fifty firm achenes were tested from each storage regime/wetland collection site combination for each species. Seeds were removed from the perigynia and nicked with a razor to expose the endosperm. Scarified seeds were soaked in a solution of 0.5% 2,3,5-triphenyltetrazolium chloride (unbuffered) for 24 hours, after which they were bisected longitudinally and the degree of embryo staining was evaluated. The results of this independent viability analysis are compared to the germination results.

Short duration wet/cold stratification treatment

Wet/cold stratification treatments were initiated on seeds stored dry/cold and dry/warm at thirty months for all species except *C. rostrata* for which there were no longer enough seeds. Batches of seeds were exposed to wet/cold (4°C) stratification lasting 4, 8, and 12 weeks. Treatment durations were based upon ranges suggested in horticulture and nursery propagation literature for a variety of species (Hartmann & Kester 1983). At the end of the 4, 8, and 12 week treatment periods, the stratified seeds were germinated along with unstratified seeds from the same long-term storage condition. Seeds that had been stored wet/cold for the entire thirty months were germinated for comparison. Seeds were incubated at 25/20°C with a 14/10 hr day/night light regime under moistened conditions. Six replicates of 50 seeds were used for each species/storage regime/stratification combination. Germination was allowed to proceed for nine weeks.

Statistical Analysis

The results of the germination/storage experiment were analyzed for statistical significance using a General Linear Model analysis of variance (ANOVA) from the Statistical Analysis

Software package for personal computer (SAS institute, Inc. 1988). Percent germination data were arcsine square-root transformed prior to analysis. Arcsine transformed means and standard errors were backtransformed for graphic presentation. Multiple comparisons of means were made using Tukey tests. A log-linear model was used to analyze the tetrazolium viability count data (Siegel 1985). Differences in germination rates from the short duration wet/cold experiment were analyzed for statistical significance using the ANOVA statistic described above. Unless otherwise noted, a significance level of alpha = 0.01 was used for all statistical analyses.

RESULTS

Germination rates in this study ranged from 0-71% for *Carex stricta*, 0-96% for *Carex comosa*, 0-43% for *Carex lasiocarpa*, 0-60% for *Carex rostrata*, and 0-36% for *Carex lacustris*. Significant differences in germination rates were observed between storage duration, storage condition, germination condition, and combinations of these treatments. Statistical results of the germination experiments (F and p values) are shown in Table 1.1.

The number of full achenes (i.e. 'live fill') per gram was determined for each species/wetland collection. The range of full achenes per gram (n = number of wetlands) is as follows: *C. stricta* (1010-3148/g; n=3), *C. lasiocarpa* (529-570/g; n=3), *C. lacustris* (280-347/g; n=3), *C. comosa* (1046-1105/g; n=2), and *C. rostrata* (295-764/g; n=2).

Carex stricta

Germination was highest in fresh seeds (0 month storage) when exposed to diurnally fluctuating germination temperatures (Fig. 1.1a). Overall germination rates declined over time. Germination rates were highest at 20/15°C (46%) averaged over all germination moisture regimes. Fewer than 1% of fresh seeds germinated at the 25°C static germination temperature (the only static temperature tested at 0 storage for this species). After four and 10 months of storage, seeds germinated at static temperatures, but at substantially lower rates than fluctuating temperatures. Generally, static and fluctuating temperatures stimulated germination at similar rates at 14 months.

Seeds stored under dry conditions showed declining germination over time while those stored moist or wet maintained a high germination rate (Fig. 1.2a). When diurnally fluctuating temperatures were used for germination, this difference between seeds stored moist and wet versus dry was even greater (Fig. 1.3a).

Regardless of storage condition, storage duration, or germination temperature, *C. stricta* seeds germinated at significantly higher rates in moistened (25%) and saturated (24%) germination moisture conditions than in alternating dry/saturated conditions (18%) (Fig. 1.4a). Highest germination rates (53%) were achieved at 20/15°C with a moistened water regime using fresh seeds.

When 2.5 year old seeds that had been stored dry/warm and dry/cold were given a short duration wet/cold stratification treatment to stimulate germination in potentially dormant seeds, the results were clear (Fig. 1.5a). Regardless of the stratification period (4, 8, or 12 weeks), seeds stored dry/warm and dry/cold for 2.5 years did not show enhanced rates of germination with a brief wet/cold treatment. Seeds that had been stored wet/cold for the entire 2.5 years had approximately a four-fold higher germination rate than seeds stored dry/cold or dry/warm, whether or not they received a wet/cold stratification treatment.

Viability analysis using tetrazolium tests indicated that *C. stricta* seeds maintained the highest viability under moist/cold and wet/cold storage (Table 1.2). In fact, *C. stricta* seeds stored moist/cold began germinating after 2.5 years while still in storage at 4°C in the dark. Seeds stored dry/warm maintained approximately half of baseline viability and seeds stored dry/cold fared the worst with only 3% viability after 2.5 years of storage. A comparison of viability and germination rates for 2.5 year old seeds is shown in Table 1.3. Conservative interpretation of the tetrazolium analysis may have contributed to viability rates that are lower than germination rates in some instances.

Carex comosa

Like the seeds of *C. stricta*, *Carex comosa* seeds initially germinated best under diurnally fluctuating temperatures (Fig. 1.1b). Unlike *C. stricta* seeds, *C. comosa* seeds germinated at higher rates after storage across all germination temperatures. As seeds aged, higher temperatures stimulated greater germination. Peak germination rates for *C. comosa* seeds occurred at 74% at 20/15°C after six months, 78% at 25/20°C after 10 months, and 46% at 30/25°C after 14 months.

The storage condition explained some of the variability observed in germination rates over time (Fig. 1.2b). Seeds stored wet/cold had significantly higher germination rates than seeds stored dry/cold or dry/warm at all three storage durations. Moist/cold stored seeds had germination rates similar to those stored wet/cold at six and 14 months.

Seeds germinated under moistened or saturated conditions at higher rates (38% and 37%, respectively) than did seeds under alternating dry/saturated conditions (28%) (Fig. 1.4b). The optimal conditions for *C. comosa* germination occurred at either 25°C (96%) or 25/20°C (93%) under a moistened water regime after six months of moist/cold storage.

Short-term wet/cold stratification of 2.5 year-old dry/warm and dry/cold seeds had either no effect or a slightly negative effect on germination of *C. comosa* seeds (Fig. 1.5b). *Carex comosa* seeds maintained fairly uniform viability under all storage regimes after 2.5 years of storage (Table 1.2). Seeds stored wet/cold had the highest viability (60%) and dry/cold storage was associated with the lowest viability (44%). Seeds stored moist/cold and dry/warm both maintained intermediate rates of viability. A high percentage of seeds germinated out of the percent determined to be viable for *C. comosa* (Table 1.3).

Carex lasiocarpa

Fluctuating diurnal temperatures were required for germination of fresh *C. lasiocarpa* seeds (Fig. 1.1c). Little or no germination occurred at static temperatures regardless of storage duration (with one exception at 25°C after 10 months). Germination occurred equally well at all fluctuating temperatures except 35/30°C. Overall, germination rates were lower than either *C. stricta* or *C. comosa*. For fresh seed, the highest germination rate occurred at 20/15°C (10%) in a saturated moisture regime. The greatest average germination rate occurred at 20/15°C (19%) after four months storage, at 30/25°C (18%) after 10 months, and at 25/20°C (24%) after 14 months.

The condition under which seeds were stored was highly significant in explaining germination rates over time. Seeds stored dry/cold had significantly lower germination than moist/cold seeds at four and 10 months. The trend was the same at 14 months, although not significant. Overall, seeds stored moist/cold, wet/cold, and dry/warm had similar germination rates (Fig. 1.2c). The exception occurred at 10 months storage when the average germination rates of moist/cold (10%) and wet/cold (11%) seeds exceeded that of dry/warm seeds (4%).

Storage condition and temperature together provide additional insight into the factors influencing germination (Fig. 1.3b). At static germination temperatures, germination rates were uniformly low, regardless of storage condition. Under diurnally fluctuating temperatures, germination rates were generally higher, except for seeds stored under dry/cold conditions. The difference in germination rates was significant at 25/20°C and 30/25°C between seeds stored dry/cold and all other storage conditions. More seeds germinated under moistened and saturated water regimes than under alternating dry/saturated conditions (Fig. 1.4c).

Peak germination rates for *C. lasiocarpa* occurred at 20/15°C (29%) under moistened germination conditions after four months of moist/cold storage, at 30/25°C (31%) under saturated conditions after 10 months of wet/cold storage, and at 25/20°C (43%) under moistened conditions after 14 months of dry/warm storage. Germination rates increased significantly over time, apparently independently of storage regime and germination temperature.

Short-term wet/cold stratification of 2.5 year old seeds had no significant effect on the germination rate of *C. lasiocarpa* seeds (Fig. 1.5c). Seeds stored dry/warm and wet/cold had the highest germination rates. Dry/cold storage was associated with the lowest germination rates.

Viability analysis indicated that seeds stored dry/warm maintained the highest percent of baseline viability (approximately half) after 2.5 years, followed closely by wet/cold storage (Table 1.2). Out of the proportion of seeds estimated as viable, fifty percent or fewer seeds germinated after 2.5 years of storage under dry/cold or wet/cold conditions (Table 1.3).

Carex rostrata

Germination rates were highest in fresh *C. rostrata* seeds when exposed to diurnally fluctuating temperatures, with maxima at 20/15°C (28%) and 25/20°C (22%) (Fig. 1.1d). Fresh seeds incubated under static temperatures did not germinate. Storage did not significantly improve germination rates at static temperatures. For seeds exposed to diurnally fluctuating temperatures, there was a gradual shift in germination response to higher temperatures as seeds aged, similar to that described for *C. comosa*.

Storage condition over time was also significantly associated with germination rates (Fig. 1.2d). The highest germination rates occurred after six and 10 months of storage with wet/cold or dry/warm conditions. After 14 months, germination was highest after moist/cold storage. Overall, dry/cold storage had the lowest germination rates of any storage regime over time. Germination rates of seeds stored moist/cold and wet/cold were similar across all storage durations. Within a particular storage regime, germination rates did not differ significantly over time except for seeds stored dry/warm, which were lower at 14 months.

Saturated and moistened germination water regimes were associated with similar average rates (10% and 8%, respectively) (Fig. 1.4d). Both had significantly greater rates than the alternating dry/saturated germination water regime (4%). The combination of storage and germination conditions that produced the highest rate (60%) was 25/20°C germination temperature with a saturated germination water regime using fresh seeds.

Although the effects of short-term wet/cold stratification were not obtained for *C. rostrata* due to an inadequate supply of seeds, the viability analysis indicates that seeds stored wet/cold and dry/cold maintained the highest percent of baseline viability (Table 1.2). Moist/cold storage maintained approximately half of the baseline viability and dry/warm storage was associated with the lowest % viability (22%) after 2.5 years.

Carex lacustris

No germination data were collected on fresh seeds. After four months storage, seeds exposed to static germination temperatures did not germinate (Fig. 1.1e). Average germination rates were significantly higher at 20/15°C (22%) and 25/20°C (18%) than at any other germination temperature. After 10 months, rates were higher than at four months for static germination temperatures, although rates were still less than 10%. Germination at 20/15°C and 25/20°C was significantly lower than it had been at four months storage. Germination after 10 months storage was similar across all temperatures, static and fluctuating alike. At 14 months, germination rates were significantly higher at 25/20°C (22%) and 30/25°C (18%) than at any other temperature. Like *C. comosa* and *C. rostrata*, *C. lacustris* showed higher germination rates as seeds aged at higher temperatures.

Storage condition was significantly associated with changes in germination rates over time (Fig. 1.2e). Germination rates for seeds stored dry/warm and dry/cold were significantly lower at 10 months than at either of the other two storage durations. There was no difference in germination rates across storage duration time for seeds stored moist/cold or wet/cold. A comparison of germination rates within each time period across storage regimes revealed additional information. While germination rates did not differ significantly after four months storage among any of the treatments, by 10 months, seeds stored wet/cold (14%) and moist/cold (9%) had significantly higher germination rates than did those stored dry/warm (1%) or dry/cold (<1%). At 14 months, wet/cold stored seeds had significantly higher germination rates than those stored dry/cold. Moisture available for germination was also significantly associated with germination rates. Germination rates were much higher under a saturated germination water regime than under moistened or dry/saturated conditions (Fig. 1.4e).

Short-term wet/cold stratification had no significant effect on dry/cold and dry/warm storage (Fig. 1.5d). Germination rates were similar or slightly depressed after wet/cold stratification. Long-term wet/cold storage had the highest germination rate, although the difference was not significant.

Wet/cold storage maintained the highest percent viability of all the storage conditions for *C. lacustris* (74%) (Table 1.2). Dry/cold storage and dry/warm storage were associated with 46% and 39% viability, respectively, while moist/cold storage maintained the lowest viability (26%) after 2.5 years. Of those seeds confirmed viable, 50% or fewer seeds germinated after 2.5 years of storage under all storage conditions (Table 1.3).

DISCUSSION

Overall germination rates obtained in our controlled environment study of seeds collected and stored under known conditions were comparable with those observed by Baskin et al. (1996) in seed burial studies and Bremholm (1993) using commercially available seeds. The maximum germination rates obtained for fresh *C. stricta* (53%) and *C. comosa* (36%) seeds in this study are similar to those obtained for *C. stricta* (61%) and *C. comosa* (39%) in Baskin et al.'s (1996) study of annual dormancy characteristics in Tennessee populations. Dormancy loss for *C. comosa* after moist/cold or wet/cold treatment is also similar to both studies. Similarly, the germination rates from this study for *C. stricta* after 10 months of dry/warm (13%), dry/cold (19%), and wet/cold (37%) storage closely resemble rates obtained by Bremholm (1993) after dry/warm (10%), dry/cold (20%), and moist/cold (40%) storage for four months followed by five months storage at 4°C. Rates for *C. lacustris* in this study after 10 months of dry/warm (2%), dry/cold (2%), and wet/cold (23%) storage showed greater variation when compared to those of Bremholm (1993) after dry/warm (10%), dry/cold (2%) and moist/cold (5%) storage.

Similarities in germination rates between our study and other studies indicate that different populations of these species respond in like manner to similar germination temperature and storage conditions. Our study shows that the combined effects of germination temperature, storage condition and duration significantly affect seed viability and germination. Specifically, our results indicate that storage condition and duration influence subsequent seed response to germination temperature and that short-term wet/cold conditions do not stimulate germination in seeds previously stored dry for a prolonged period.

Storage Condition and Viability

The viability and germination results from the present study indicate that storage condition is influential in maintaining or reducing seed viablity for all five species considered. The storage condition that promoted or reduced viability differed among species, as did the magnitude of the effect, but two patterns emerged. First, wet/cold storage was associated with a high level of viability in all five species after 2.5 years (Table 1.2). This level of viability was equaled in *C. rostrata* by dry/cold storage and exceeded in *C. lasiocarpa* by dry/warm storage. *C. stricta* showed a higher rate of viability under moist/cold than wet/cold storage, but moist/cold seeds of *C. stricta* germinated during storage, reducing the usefulness of this storage condition.

Germination results mirrored the viability results with few exceptions. *C. stricta, C. comosa*, and *C. lacustris* showed the greatest germination response after wet/cold or moist/cold storage (Fig. 1.2), while *C. lasiocarpa* and *C. rostrata* showed similar rates of germination after either wet/cold or dry/warm storage. Only the germination rates of *C. rostrata* were somewhat inconsistent with the viability results (highest for wet/cold and dry/cold storage), which may be an artifact of low overall rates of germination observed for this species. Secondly, both viability and germination rates were reduced after long-term dry/cold storage in three of the five species: *C. stricta, C. comosa, and C. lasiocarpa.* The viability of *C. stricta* was severely impacted by long-term dry/cold storage (Table 1.2).

Efficacy of short-term wet/cold stratification

Germination of 2.5 year old seeds stored dry/cold and dry/warm is not improved by short-term wet/cold treatment in any of the four species tested (Fig. 1.5). These results combined with the viability analysis done at 2.5 years suggests that poor seed germination in *C. stricta* and *C. comosa* after storage is primarily due to loss of viability over time (germination rates equal or exceed viability rates with one exception), while poor germination in *C. lasiocarpa* and *C. lacustris* is the result of both reduced viability and dormancy (viability rates exceed germination rates; Table 1.3). In *C. stricta* and *C. comosa*, wet/cold stratification did not improve germination of 2.5 year-old seed (although it is initially important in young *C. comosa*), and in *C. lasiocarpa* and *C. lacustris*, it was apparently insufficient to break dormancy.

Optimum germination conditions and the timing of seed dispersal in the field

Germination was highest in fresh seeds of *C. stricta* and *C. rostrata*, and increased over initial rates after four (six) months of age in *C. comosa*, *C. lasiocarpa*, and *C. lacustris*. All species initially germinated best under fluctuating germination temperatures, but only *C. stricta, C. comosa*, and to a lesser extent, *C. lacustris*, gained the ability to germinate at non-fluctuating temperatures with time when all previous storage conditions were considered together. Germination rates for *C. stricta and C. lasiocarpa* were enhanced by prior wet/cold and moist/cold storage (as well as dry/warm storage for *C. lasiocarpa*) when seeds were placed under fluctuating temperatures (Fig. 1.3). Furthermore, *C. stricta* germinated at significantly higher rates after wet/cold and moist/cold storage under non-fluctuating temperatures. This combination of wet/cold and moist/cold storage and fluctuating germination temperatures provides the optimum stimulation for *C. stricta* and *C. lasiocarpa*.

Germination results generally fell into two groups, those species with relatively high germination rates (*C. stricta* and *C. comosa*) and those with low overall germination rates (*C. lasiocarpa, C. rostrata*, and *C. lacustris*). The low germination rates in the second group were exceeded by their viability rates (Table 1.3) indicating that these species have an incompletely broken dormancy, perhaps due to physical or chemical constraints of their hard seed coats. Moistened or saturated germination conditions were associated with the highest rates in all species, although *C. stricta* and *C. comosa* were more tolerant of dry conditions than the other species (Fig. 1.4). Maintaining high humidity in the petri dishes appears to be important in stimulating earlier germination in all species and is recommended in greenhouse and field settings where humidity control is possible.

Based on the observations that *Carex* seedlings are rare in the field (Costello 1936) and emergence is poor in greenhouse seedbank assays (Galatowitsch & van der Valk 1996c; Galatowitsch & Biederman 1998), it is likely that germination in these taxa is triggered by a narrow set of environmental conditions. Germination responses observed in this study may provide insight into both the germination phenology and life history of these five species. The temperature response of fresh seeds of all species to either 20/15°C or 25/20°C suggests late spring or fall germination. Only *C. comosa* demonstrated initial conditional dormancy that was released by wet/cold storage, suggesting that seeds may over-winter before germinating the following spring. Such a pattern is reasonable, given the late summer and early fall seed production exhibited by this species, and is supported by the dormancy study of Baskin et al. (1996). *Carex rostrata* seeds also mature in late summer in east-central Minnesota and may over-winter before germination, although initial wet/cold stratification was not necessary to stimulate germination in this species. Both *C. comosa* and *C. rostrata* seeds responded to higher germination temperatures as they aged suggesting the ability to germinate later and later into the summer of subsequent growing seasons. *Carex stricta* had the highest initial germination rates of all five species and these rates were not improved by wet/cold storage. These results, combined with the steady decrease in seed viability and germinability over time in this species, suggest that *C. stricta* may germinate soon after dispersal from the parent plant in June and early July in east-central Minnesota.

Restoration Recommendations

Improper seed storage can lead to reduced seed viability. The ramifications of a poor seed supply to restoration efforts are substantial. As viability rates are reduced, recommended seeding rates must be increased. Because the availability of sedge seeds is often limited by yearly, seasonal, and site variability (Galatowitsch et al. 1998; R.A. Budelsky personal observation) obtaining sufficient seed supply may be difficult and the associated costs prohibitive. In addition, the risk of weed invasion will likely increase if the proportion of nonviable seeds is high and it is not feasible to increase the seeding rate to compensate. Such limitations can seriously compromise the goal of successfully restoring sedge meadow wetlands in the landscape.

The standard recommended seed storage procedure for the majority of agricultural crop varieties is dry/cool storage at 10-15 % moisture content (Harrington 1972; Bewley & Black 1982), although Schramm (1978) strongly recommends cold-damp storage to maintain seed viability in prairie grasses. Seed producers specializing in wetland plants are largely following the standard agricultural model. An informal survey of seed producers in Minnesota and Wisconsin indicates that wetland seeds are usually allowed to air dry and are stored dry in unheated buildings for one or two years until they are sold. The results of this research indicate that dry seed storage is not appropriate for three species of wetland *Carex* (*C. stricta*, *C. comosa*, *and C. lacustris*). Of all the species, only *C. stricta* should definitely not be stored under dry/cold conditions due to the extreme loss of viability. Several other wetland graminoids (*Zizania aquatica* (wild rice), *Glyceria striata* (fowl meadow grass), and *Spartina angelica* (cordgrass)) have been shown to lose viability if seeds are allowed to dry beyond a certain high moisture content (King & Roberts 1979; Roberts et al. 1984; Probert & Longley 1989). Although *Carex* seeds do not appear to be “recalcitrant” as defined by Roberts et al. (1984), they do lose viability at a faster rate when stored dry than when stored wet. These results support the suggestion made by Bremholm (1993) that wet storage showed promise for maintaining germinability in wetland *Carex*.

The logistics of wet/cold storage are straightforward. Small batches of seeds are easily stored in thin walled plastic bags that permit gas exchange. Larger batches of seeds can be stored in plastic tubs of sufficient size with snap lids fitted with a hole or groove to allow introduction of an aeration device as used for fish tanks. Seeds should be stored in deionized or distilled water as soon as possible after collection. Fungal and bacterial infection of seeds occurred less often during our study when seeds were surface sterilized and stored in standing water. Because wetland *Carex* seeds float, they must be forced under water squeezing the air out of the top of the storage bag. This tendency to float also has implications for the location and timing of sowing. Further work is required to develop seeding criteria for properly stored seeds to ensure germination in the field.

ACKNOWLEDGEMENTS

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Table 1.1. A summary of analysis of variance (ANOVA) on the effects of temperature and moisture during storage and at germination for *C. stricta*, *C. lasiocarpa*, *C. lacustris*, *C. comosa*, and *C. rostrata*. F-value and p-value statistics for Type III sums of squares are shown for four main effects and six two-way interactions (shown with *). The alpha value for this study is 0.01.

	C. stricta		***C. lasiocarpa***		***C. lacustris***		***C. comosa***		***C. rostrata***	
Variable	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Germination temperature	37.24	0.0001	39.37	0.0001	39.29	0.0001	36.96	0.0001	22.03	0.0001
Germination moisture	13	0.0001	15.44	0.0001	25.84	0.0001	8.23	0.0005	16.95	0.0001
Germination temperature*germination moisture	1.61	0.1151	4.15	0.0001	2.87	0.0036	2.74	0.005	3.8	0.0002
Storage duration	6.38	0.0025	4.85	0.0099	1.04	0.3562	37.84	0.0001	9.46	0.0002
Storage duration*germination temperature	5.27	0.0001	12.38	0.0001	11.47	0.0001	4.33	0.0001	4.05	0.0001
Storage duration*germination moisture	2.23	0.1127	2.14	0.1234	9.28	0.0002	2.3	0.1053	0.33	0.717
Storage condition	72.87	0.0001	12.03	0.0001	14.19	0.0001	110.96	0.0001	9.92	0.0001
Storage condition*storage duration	5.43	0.0006	4.68	0.0017	8.65	0.0001	9.72	0.0001	4.6	0.0019
Storage condition*germination temperature	2.6	0.0021	3.22	0.0002	1.39	0.1632	2.01	0.019	2.04	0.0168
Storage condition*germination moisture	1.1	0.3634	2.84	0.028	2.4	0.0557	1.52	0.2025	1.78	0.139

Table 1.2. Mean percent baseline viability and mean percent viability at 31 months for five *Carex* species after four different long term storage conditions: dry/23° C (dry/warm), dry/4° C (dry/cold), moistened/4° C (moist/cold), and saturated/4° C (wet/cold). The mean percent viability values shown here are not directly comparable to germination rates in this form.

	Baseline % Viability	% Viability After Storage for 2.5 Years			
	no storage	dry / warm	dry / cold	moist / cold	wet / cold
C. stricta	57	33	3	53	43
C. comosa	79	54	44	54	60
C. lasiocarpa	85	43	28	32	38
C. rostrata	70	22	47	38	48
C. lacustris	79	39	46	26	74

Table 1.3. Mean percent viability and germination in 2.5 year old seeds in four species of *Carex* after saturated/4° C (wet/cold), dry/23° C (dry/warm), and dry/4° C (dry/cold) storage. No data were available for *Carex rostrata* for this experiment.

	Long-Term Storage Regime								
	wet/cold			dry/warm			dry/cold		
	% viability	% germination	% of viable that germinated	% viability	% germination	% of viable that germinated	% viability	% germination	% of viable that germinated
C. stricta	43	71	>100	33	14	42	3	3	100
C. comosa	60	73	>100	54	43	80	44	58	>100
C. lasiocarpa	38	19	50	43	32	74	28	5	18
C. lacustris	74	28	38	39	19	49	46	8	17

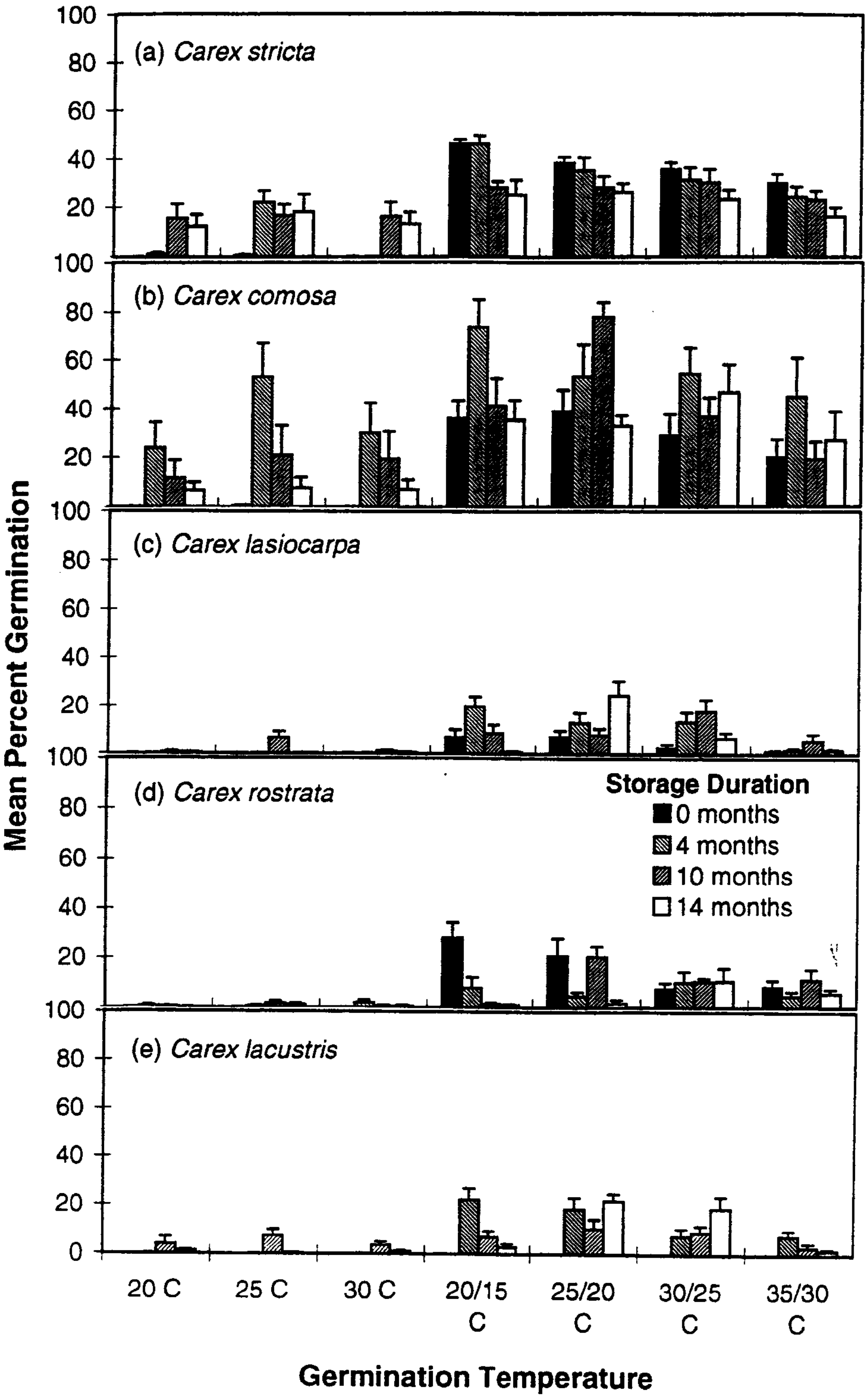

Figure 1.1. Mean percent germination (+ standard error) by storage duration and germination temperature for five *Carex* species (averaged over all storage conditions and germination moistures). Percent germination was arcsine square-root transformed for statistical analysis and calculation of standard error. Back-transformed data are presented.

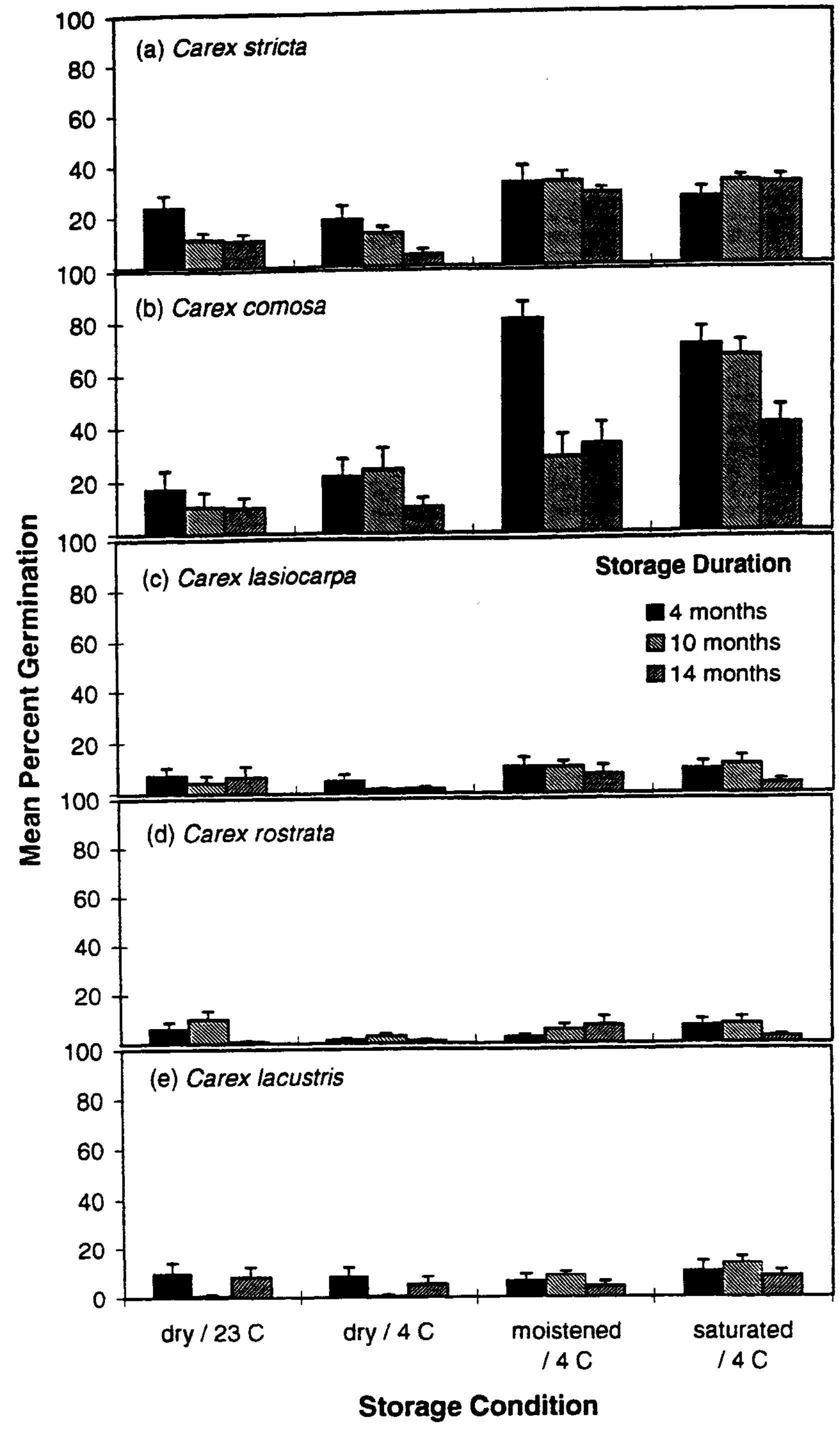

Figure 1.2. Mean percent germination (+ standard error) by storage duration and storage condition for five *Carex* species (averaged over all germination temperatures and germination moistures). Storage conditions dry/23°C (dry/warm), dry/4°C (dry/cold), moistened/4°C (moist/cold), and saturated/4°C (wet/cold) are shown along the horizontal axis. Percent germination was arcsine square-root transformed for statistical analysis and calculation of standard error. Back-transformed data are presented.

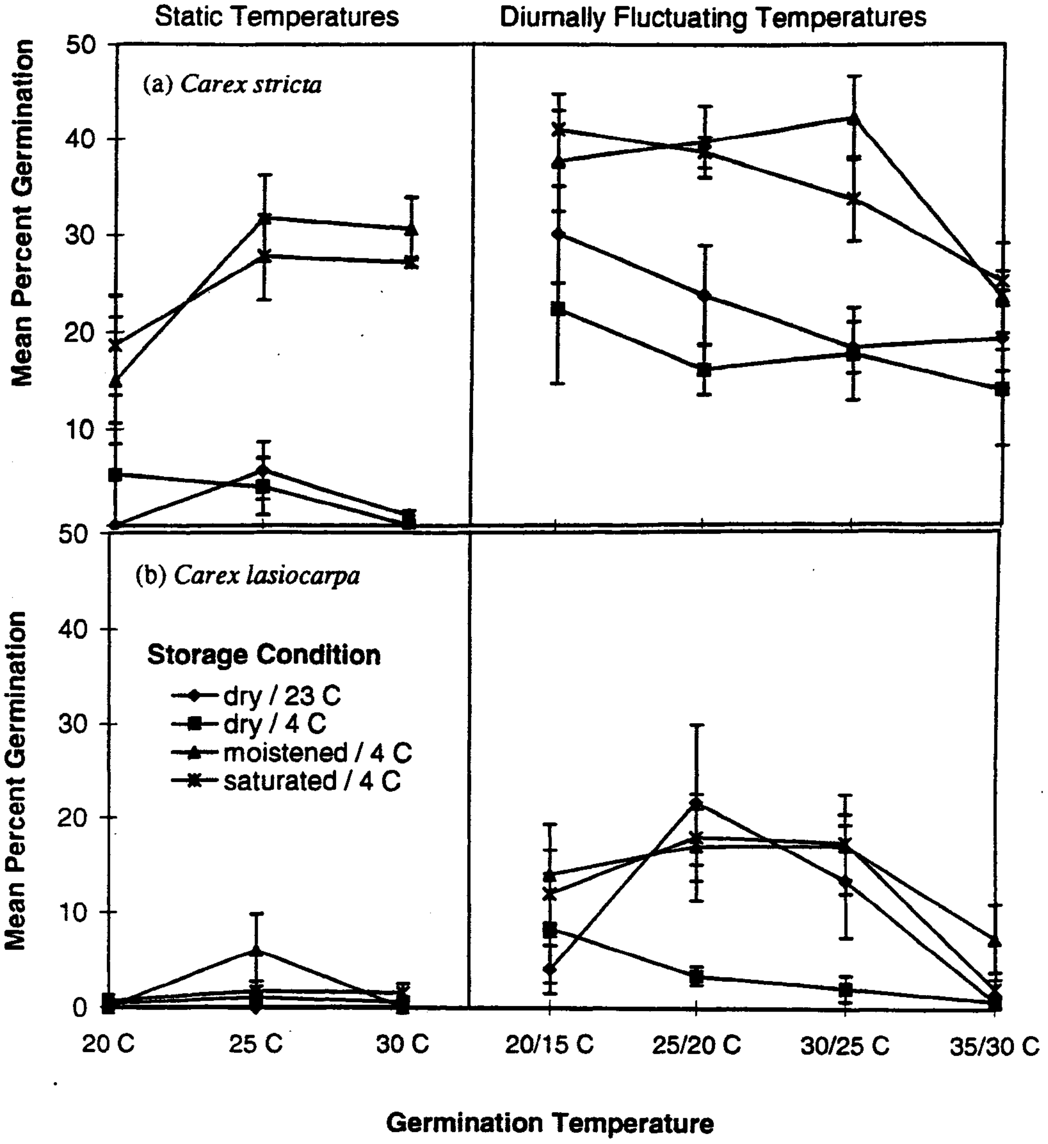

Figure 1.3. Mean percent germination (+/- standard error) by storage condition and germination temperature for *Carex stricta* and *Carex lasiocarpa* (averaged over all storage durations and germination moistures). Only these two species show statistically significant patterns in germination results. Percent germination was arcsine square-root transformed for statistical analysis and calculation of standard error. Back-transformed data are presented.

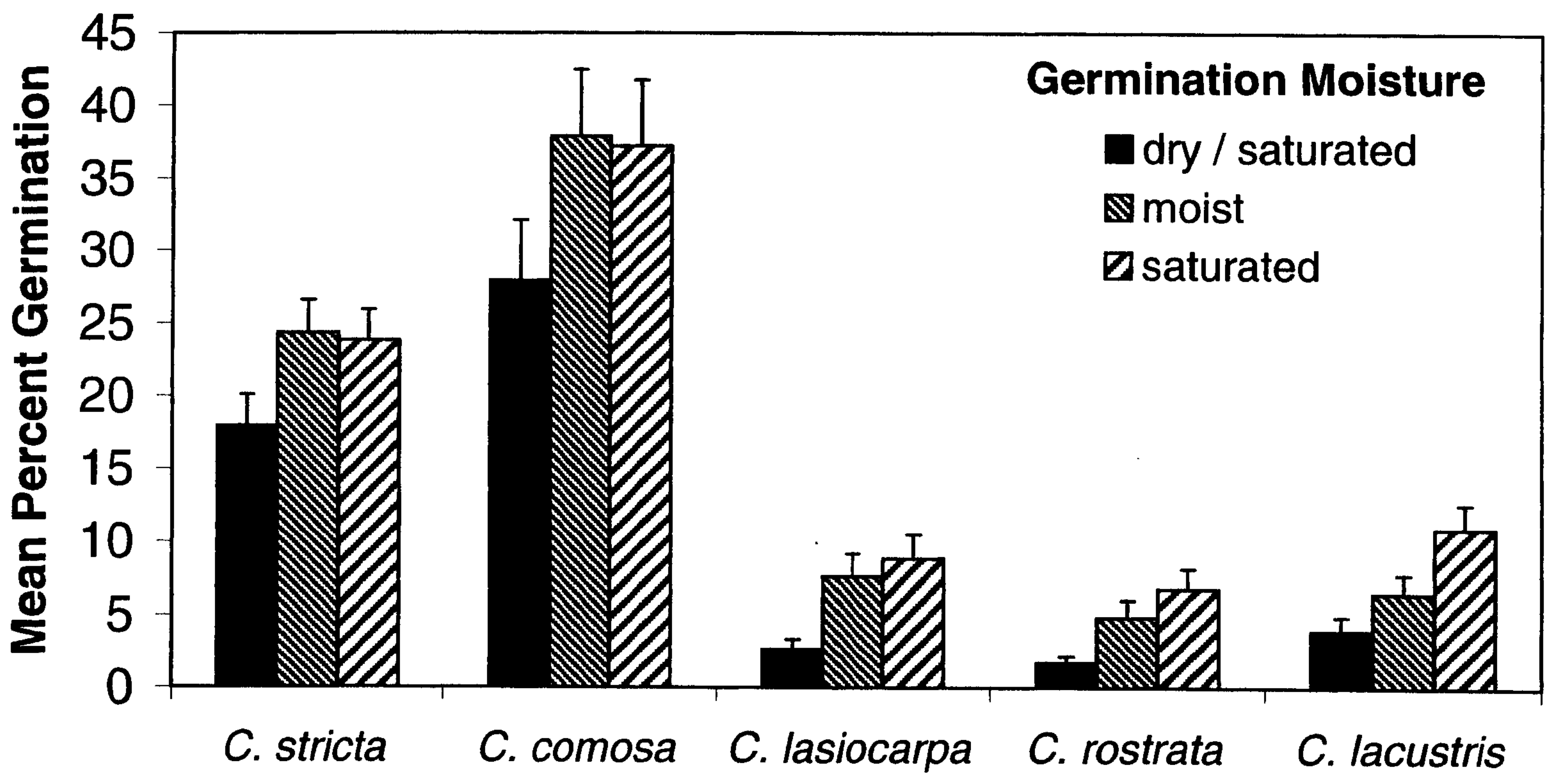

Figure 1.4. Mean percent germination (+ standard error) for five *Carex* species averaged by germination moisture across all germination temperatures, storage conditions, and storage durations. Percent germination was arcsine transformed for statistical analysis and calculation of standard error. Back-transformed data are presented.

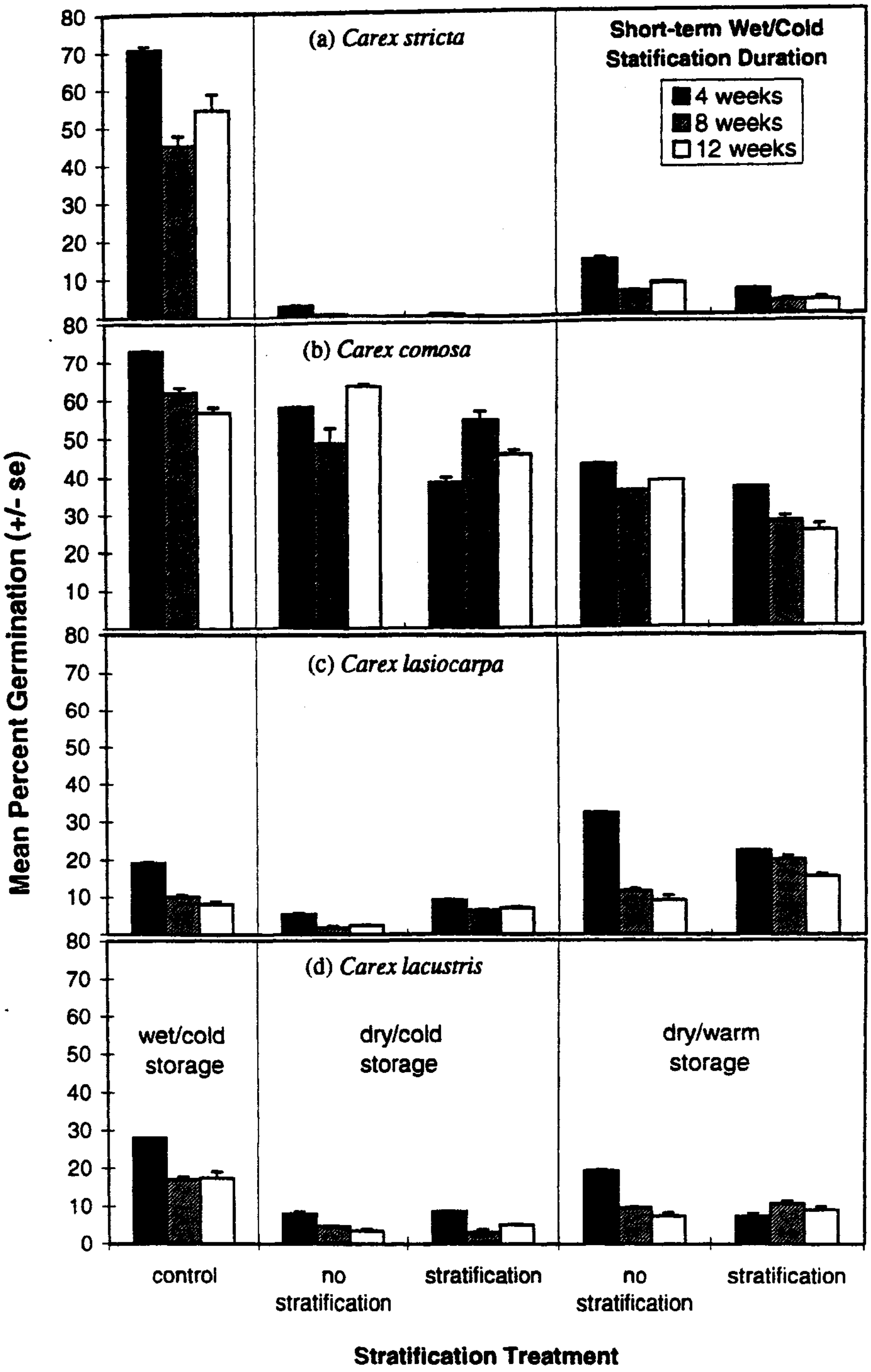

Figure 1.5. Mean percent germination (+ standard error) for seeds stored dry/cold, dry/warm and wet/cold for 2.5 years, with and without a 4, 8, or 12 week wet/cold stratification treatment following removal from long-term storage. Percent germination was arcsine square-root transformed for statistical analysis and calculation of standard error. Back-transformed data are presented. No seeds were available for *Carex rostrata* for this experiment.

CHAPTER 2 (Tasks 6-7: *Carex lacustris*)

Effects of Biotic and Abiotic Factors on the Establishment of *Carex lacustris* in Experimental Wetlands

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SUMMARY

Typical wetland restoration in the mid-western United States and Canada involves reflooding formerly drained basins without artificial revegetation. The assumption that native vegetation will establish on its own does not hold for members of the genus *Carex* (sedges). Criteria for establishment of native sedges do not currently exist because environmental constraints are not well understood. *Carex lacustris* seedlings were planted along an elevational gradient in three experimental wetland basins to determine the effects on seedling survival and stand development of: timing and duration of water-level fluctuation, water depth, initial planting density, and interspecific competition from naturally recruited vegetation. Effects were followed for three growing seasons. Seedling mortality in the first year was greatest at the lowest elevations in the falling and static water regimes. Mortality was < 5% in the second and third growing seasons. Above-ground biomass, tiller density, tillering rate, and tiller height were significantly greater in the rising water regime than in either the static or falling water regimes during the first growing season. By the end of year three, biomass and tiller density were greatest in the falling water regime and tillering rate and tiller height were no longer significantly different between water regimes. Above-ground biomass, biomass growth rates, tiller density and tillering rates were greatest at the highest elevations and declined with increasing water depth in all three years. Interspecific competition was greatest in the upper elevations, particularly in the rising water regime. Competition significantly constrained the potential habitat of *C. lacustris*. Because *C. lacustris* seedlings had the highest mortality and growth rates during the first growing season, environmental control will be most necessary then to ensure appropriate conditions for successful stand establishment.

INTRODUCTION

Most freshwater wetland restorations in the prairie pothole region of the United States and Canada rely on natural plant recolonization after basin hydrology is restored (Galatowitsch & van der Valk 1996a, NRC 1992). Natural recolonization appears to be an appropriate revegetation strategy for species whose propagules are with easily dispersed or have long-lived seedbanks. However, in a survey of recently restored wetlands in northern Iowa, southern Minnesota, and southeastern South Dakota, Galatowitsch & van der Valk (1996b) concluded that sedge meadow species, including sedges, do not readily re-establish after hydrological restoration. Members of the genus *Carex* (sedges) are common, and often dominant, in temperate freshwater wetlands. Their slow natural recolonization may be due to limited dispersal and increased isolation resulting from agricultural drainage (van der Valk & Verhoeven 1988); limited seed longetivity in the seedbank (Wienhold & van der Valk 1989); poor seed set in potential source populations; and low seed viability (Bremholm 1993). Consequently, it is unlikely that sedges will reappear quickly, if at all, in their former habitats, or in newly created wetlands, without artificial establishment.

When native plants are deliberately introduced to a restoration, the initial establishment phase is critical to successful colonization. Seedlings may be more sensitive than mature plants to biotic (e.g. invasive species) and abiotic (e.g. moisture availability) environmental factors (Grubb 1977, Harper 1977). Moreover, at the seedling stage the potential for the development of alternative successional pathways is greatest (Schramm 1990, Wilson & Agnew 1992, Hobbs 1994). Because relatively little is known about the initial successional stages of most wetland communities and about the environmental conditions that promote their development, restorationists must currently make arbitrary decisions about the starting conditions for restorations. Basic information on the growth and survival of desired species is needed to apply existing ecological theories to restoration in a practical way.

In this study, the establishment requirements of *Carex lacustris* (lake sedge) were investigated to identify the factors limiting recolonization. Seedlings were planted along elevational gradients in three experimental wetlands in which water depth, water-level fluctuation, initial planting density, and competition from naturally recruited weeds were experimentally manipulated. Such control, coupled with the relatively simple community structure of sedge meadows, provided an excellent opportunity to investigate the multiple environmental factors that may influence the development of this system. Our objectives were to determine: 1) how seedling survivorship and growth may be influenced by location along a water-level gradient, 2) if differences in seasonal timing of water-level fluctuations will reduce or augment seedling growth, 3) if sedge seedling growth will exceed that of competitive species recruited from the seedbank, and 4) how intraspecific competition may influence sedge growth in higher versus lower density plantings.

Study Site

The study site is on the grounds of the University of Minnesota Landscape Arboretum in Chanhassen, Carver county, Minnesota, USA (44°51'45"N, 93°36'00"W). The regional climate is north temperate with maximum and minium temperatures (averaged 1961-1990) ranging from 27.3-27.8 °C to 13.9-15.1 °C in the summer (June - August) and -2.6--1.9 °C to -12--13.3 °C in the winter (December - February) (Garwood 1996). Annual rainfall (averaged over 30 years) in Carver county is 77.2 cm. The experimental basins are in the shallow depression of a former wetland of approximately 0.8 hectares (2 acres). The basins have a thick black surface horizon of silty clay loam with hydric soil features in the dark gray clay loam sub-horizon. Prior to this study, the depression was divided into four research basins by two earthen dikes that cross through its center. Each basin has a flat rectangular bottom and four shallow side slopes with a 20:1 elevational gradient. The side slopes were re-graded during the summer of 1994 and were flooded through the fall and winter prior to the initiation of this study to retard weed invasion.

The basins are equipped with water-control structures that allow independent water-level manipulation. All four basins are fed through underground irrigation pipes from an electrically driven well pump. Flow control valves permit independent filling of each basin. Water can be drained by raising or lowering a flexible pipe located in the center of each basin. Shore-based control of drain pipes is facilitated by a pole and pulley system.

METHODS

Four elevational treatments were established along the east-facing slope of three of the wetland basins described above. The four rows were identified by their vertical height above or below the mean seasonal water-level: +22.5 cm, +7.5 cm, -7.5 cm, and -22.5 cm. The greatest water depth was associated with the lowest elevation. The elevational treatments were designed to evaluate the effect of water availability (and depth) on seedling survival and growth. Rows were separated by buffers1 m wide. Eight 5m^2 rectangular plots (2.5 m by 2 m) were established in each row with the long dimension parallel to the contour lines of the slope. Plots within the rows were separated uniformly by the remaining available slope width which varied by basin from 0.75 m to 0.25 m.

Treatments within the each row consisted of eight combinations of two planting densities and two competition levels for each of the two species. Sedge seedlings were planted in bare soil plots in late May 1995, at either a high (45 seedlings: 9 plants m^{-2}) or low (10 seedlings: 2 plants m^{-2}) initial density. Plots were either weeded to maintain monocultures (no competition) or not weeded, allowing natural recolonization of weeds from the seedbank (competition plots). The species composition and abundance of naturally recruited vegetation was not controlled in the competition plots.

A different water regime was established in each of the three basins to assess the effect of water-level changes on seedling establishment. The first was a static water-level regime, in which the water-level was maintained at the mean level throughout the growing season. The soil surface was exposed in the upper two rows and inundated in the lower two rows of plots for the duration of the study. The maximum water depth for the static regime was 30 cm, which occurred at the bottom edge of plots in the lowest elevation. A rising water-level regime was established in the second basin. The water-level was set at the bottom edge of the lowest row of plots at the beginning of the growing season and was raised five vertical centimeters every two weeks until the upper row of plants was inundated by the end of the growing season. The third basin was assigned a falling water-level regime. In this regime, all rows were inundated and were gradually exposed throughout the growing season at a rate of 5 cm per two weeks. The rising and falling water regimes experienced a similar range of inundation depths, but at different times and for different durations throughout the growing season. The maximum seasonal water depth for the rising and falling basins was 60 cm, which occurred at the bottom edge of plots in the lowest elevation. Water-level changes were initiated mid-May and ended mid-October in all years. Water-levels in the changing regimes were returned to May conditions at the end of the growing season in two stages over a three-week period. Basins over-wintered in their spring water regime condition.

Seedlings of both species were germinated from seed collected in sedge meadow wetlands at the Cedar Creek Natural History Area in east-central Minnesota, USA (45°24' N, 93°12' W). Seedlings were 8 to 11 weeks old and approximately 25-30 cm tall with one or two tillers (shoots) when they were transplanted into the field plots. A total of 1,320 seedlings of each species were transplanted.

Sedge seedlings in all plots were measured monthly for the following demographic data: survival, tiller height, and above-ground tiller number m^{-2}. Tillering rates were calculated from the tiller numbers by dividing the number of tillers counted in one sampling period by the number in the subsequent period. The spreading growth of *C. lacustris* made it impossible to identify individual genets by two months post-planting, therefore all tillers within the sample area were measured and mean tiller number m^{-2} per plot was calculated. Tiller height was averaged over all tillers measured in the sub-sample strip.

Species diversity and abundance were scored monthly for the vegetation in each competition plot by the Braun-Blanquet cover/abundance scale (Mueller-Dombois & Ellenberg 1974). Above-ground biomass was collected during the last two weeks of August 1995, 1996, and 1997 from sub-sample strips 83 cm wide (approximately one-third of the original plot width) and 2 m long. Biomass was sorted by species and dried at 65° C for a minimum of 48 hours in a drying oven. Only sedge biomass results will be presented. Mean above-ground dry-weight biomass m^{-2} was calculated for each plot. Soil seedbank samples were also collected from each of the basins and analyzed for species diversity, but the data were inconclusive and are not presented here.

Water depth was measured monthly in each plot to ensure proper levels and water was added or subtracted as needed. When the water-level was below the soil surface, ground water observation wells in the center of each row were used to determine depth to water table.

A full factorial design was used in which all combinations of all treatment levels were run. One replicate of each treatment combination was used to maximize the number of treatments and the area over which each treatment was run. We assumed that significant three- and four-way interactions between the four treatments (water-level change, elevation, competition, and planting density) would not occur. This assumption allowed us to estimate random error from the combined mean squares of the higher order interaction terms (Montgomery 1991).

Data on percent survival per plot were arcsine square-root transformed before analysis. Tiller densities and tiller heights were log-transformed to standardize variance between measurement dates before a repeated measures analysis of variance was run. The alpha value for significance was set at 0.01. A conservative p-value (Greenhouse-Geisler) was calculated by which to assess the significance of tillering rates (rates violate the ANOVA assumption of statistical independence). Statistical Analysis Software (SAS) was used to run the analyses (SAS 1992).

RESULTS

Stand response to the four experimental treatments -- seasonal water-level regime (basin), elevation (row), competition, and initial planting density -- are presented below. Synergistic (interacting) combinations of treatments are described under one of the individual treatment headings. Each of the variables used to measure stand response -- survival, above-ground biomass, mean and maximum tiller height, mean tiller number and tillering rates -- are discussed under each treatment section.

Response to water regime

Seedling mortality was greatest during 1995 and was highly correlated with water regime ($p = 0.0023$). Mean percent mortality was significantly lower in the rising water-level regime (3%) than in either the static (17%) or the falling (18%) water regimes averaged across all elevations. Comparatively little mortality occurred in subsequent growing seasons (<5% in 1996 and <1% in 1997), and it was not significantly correlated with any of the treatment variables.

Significant differences in mean above-ground dry-weight biomass m^{-2} per plot were also associated with water regime for *C. lacustris* in 1995 ($p=0.0011$) and 1997 ($p=0.0005$). The rising water regime had a greater mean above-ground dry weight biomass m^{-2} (57.3 +/- 17.77 g) than either the static water (28.6 +/- 8.63 g) or the falling water (19.8 +/- 5.15 g) regimes in 1995 ($p<0.01$). Water regime was not significant in 1996. By 1997, biomass collected in the falling water regime (952.8 +/- 122.28 g) surpassed that of either the rising (572.5 +/- 120.68 g) or the static water regime (535.7 +/- 67.94 g).

In general, the mean tiller density increased over the 1995 and 1996 field seasons ($p=0.0001$) and decreased slightly, although not significantly ($p=0.0839$), during the 1997 field season (Fig. 2.1a). Water regime was significantly associated with mean tiller number m^{-2} in June (p=0.0009) and July/August (p=0.0005) of the first growing season, but it was not significant thereafter. Tillering rates during the June - July/August period of 1995 and the June-July period of 1996 were also significantly associated with water regime (p=0.0001 and p=0.0051, respectively). Monthly tillering rates were highest in 1995 (2.9 - 1.5), dropping to 1.5 - 0.8 by 1997 (Fig. 2.1b). At the end of 1995, there was a greater mean number of tillers m^{-2} per plot in the rising water-level regime (97.1 +/- 26.88), than in the falling (71.3 +/- 21.32) or static (59.6 +/- 14.09) water-level basins. This trend continued into the 1996 season until July at which point the number of tillers in the falling water regime exceeded that of both other water regimes (Fig. 2.1a). The number of tillers in the falling water-level regime continued to exceed that observed in the other two water regimes until the study ended.

As might be expected, the mean tiller height increased over time (p=0.0001). Both the mean tiller height and the maximum tiller height per plot were significantly associated with water regime in July/August and September 1995, May 1996 (mean height only), and May 1997 (p<0.01) (Fig. 2.2). Two months after seedlings were transplanted, the mean and maximum tiller heights were greater in the rising water-level basin than either of the other two water regimes (p=0.0030). By 1997, the rising water regime had the lowest average and maximum heights at the beginning of the season. The falling water regime had consistently greater maximum tiller heights than the other two regimes throughout 1996 and 1997 (Fig. 2.2b).

Response to elevation

During the first growing season, survival rates in the upper three elevations were significantly greater than at the lowest elevation, averaged over all water regimes (p<0.0031) (Fig. 2.3). The greatest mortality (63%) occurred in the lowest elevation of the falling water regime, followed by 40% and 19% mortality in the lowest elevations of the static and rising water regimes, respectively. Mortality was unrelated to elevation in 1996 and 1997.

Elevation was significantly correlated with differences in mean above-ground dry weight biomass m^{-2} per plot in 1995 (p=0.0081), 1996 (p=0.0029), and 1997 (0.0004). In all three years, biomass was highest in the upper two elevations, and declined toward the lower elevations (Table 2.1). Growth rates between the first and second seasons were significant (p=0.0039), responding to elevation in a similar manner as the absolute mean biomass. Growth rates were lower between the second and third growing seasons and were not significantly correlated with elevation. Neither maximum nor mean tiller heights were significantly associated with elevation.

The mean number of tillers m^{-2} per plot was significantly associated with elevation within each growing season; 1995 (p=0.0008), 1996 (p=0.0007), and 1997 (p=0.0036). In general, the number of tillers was highest at the upper elevations and decreased toward the lower elevations with the lowest elevation (-22.5 cm below mean seasonal water-level) having significantly fewer tillers than the upper three elevations (Fig. 2.4a). The number of tillers increased significantly between the beginning and the end of the first growing season (p=0.0001), but not during the second growing season (p= 0.1519). In the third growing season, tillers decreased over time, but not significantly (p=0.0448). Tillering rates were significantly associated with elevation during May-June (p=0.0006), June-July/August (p=0.0001), and September-October (p=0.0005) sampling periods in 1995. During these periods, tillers grew at a significantly lower rate in the -22.5 cm elevation than in the upper three elevations (Fig. 2.4b).

The interaction of elevation and water regime was highly correlated with tillering rate during June-July/August (p=0.0074) and September-October (p=0.0071) sampling periods in 1995. In the rising water regime, seedlings in all elevations grew at a similar rate, but in the static and falling water regimes, seedlings in the -22.5 cm elevation had significantly fewer tillers than did those in the upper two elevations (Fig. 2.5). The -22.5 cm elevation of the falling water regime had a negative growth rate during all but the July/August-September sampling periods in 1995. Between June and July/August 1996, the number of tillers in the -22.5 cm elevation of the falling and static water regimes increased, exceeding that of the rising regime at the same elevation. The interaction of water regime and elevation was not significant in 1996 or 1997.

Response to planting density

Planting density was significantly correlated with biomass (p=0.0001) and tiller number (p=0.0001). Had density lost significance with time, it would have represented a convergence of biomass and tiller number from plots with initial low and high planting densities. Density was significant across all years (p<0.01) as initially greater tiller numbers (and biomass) in the high density plots were maintained over those in low density plots over time. Although the absolute number of tillers remained greater in the high-density plots, there was a notable increase in the growth rate for the lower density plots during the May-June 1996 (p=0.0195) and the October 1996 - May 1997 (p=0.0066) growth periods.

Mortality was not associated with planting density. Mean tiller height was significantly correlated with density over time during the 1995 growing season only (p=0.0037). Mean tiller height was greater in high-density than in low-density plantings by the end of the first growing season.

Response to competition

The effect of competition on sedge growth was more complex than that of the treatments described above because the competing vegetation was itself affected by water regime and elevation. The results presented below include multiple interactions between competition and the abiotic treatments. A brief characterization of the vegetation found in each basin is first provided.

The floristic composition of the +22.5 cm and +7.5 cm elevations was qualitatively different in the three basins. The rising water-level basin contained a primarily perennial grass community that was dominated by *Phalaris arundinacea* L., *Phleum pratense* L., and *Polygonum sp.* The falling water basin contained an annual grass community dominated by *Echinochloa muricata* (P. Beauv.) Fern., *Polygonum sp.,* and *Setaria glauca* (L.) P. Beauv. The static water-level basin contained a roughly equal mixture of annual grasses and forbs including *Setaria glauca*, *Hordeum jubatum* L., *Alopecurus aequalis* Sobol, *Trifolium sp.,* and *Rumex crispus* L. The -7.5 cm and -22.5 cm elevations in all the basins were dominated by *Typha sp.*, *Alisma subcordatum* Raf., and *Eleocharis sp.* During the subsequent two growing seasons, the annual grass assemblage in the falling water regime was greatly reduced in cover class ratings, height, and biomass while competitive vegetation in the other two basins remained substantially the same.

Competition was significantly associated with differences in the mean above-ground dry weight biomass m^{-2} for *C. lacustris* seedlings in 1995 (p=0.0001), 1996 (p=0.0002), and 1997 (p=0.0004) (Table 2.2). Biomass was significantly higher in plots without competition than in plots with competition. While competition within each year was significantly correlated with biomass, its explanatory value was highest during the first two years and decreased during the third growing season (p=0.0045).

Similarly, the mean number of tillers was also associated with inter-specific competition in 1995 (p=0.0001) and 1996 (p=0.0002), but not in 1997 (p=0.1271). As early as one month after planting, seedlings showed a greater mean number of tillers m^{-2} in plots without competition than in plots with competition (p<0.01) (Fig. 2.6a). The mean difference in tillering rates between plots with and without competition over time is illustrated in Fig. 2.6b. Tillering rates were significantly different during the May-June (p=0.0008) and June-July/August, 1995 (p=0.0002) sampling periods only, although the absolute number of tillers (Fig. 2.6a) continued to reflect the effects of this earlier growth event.

Mean tiller height was also significantly associated with presence or absence of competition in 1995 during the peak period of growth in July/Aug only (p=0.0009). Seedlings were taller in plots with competitors than in plots where competitors were weeded out. The difference was not significant after 1995.

The interaction of competition with water regime was significant for biomass in 1995 (p=0.0009) and 1996 (p=0.0067), but not in 1997 (p=0.0217). In 1995, biomass was highest in competition-free plots in the rising water-level basin, but lowest under the same water regime when competition was not controlled (Table 2.3). By 1997, biomass was greatest in the falling water regime in competition-free plots. The difference in biomass between competition and competition free for the falling water regime plots was insignificant in 1997.

Plots without competition had greater sedge biomass than plots with competition in the upper two elevational rows (p<0.01), but biomass in the lower two rows was uniformly low, irrespective of competition levels (Table 2.4). Mean biomass m^{-2} was highest in the +22.5 cm elevation when competition was removed, but when competition was not controlled, plots in the highest elevation had the lowest or second lowest above-ground biomass. When competition was not controlled, there was no significant difference in biomass collected between elevations. This pattern held true for all years.

Tillers m^{-2} per plot were also correlated with the interaction of competition and elevation in 1995 (p=0.0033) and 1996 (p=0.0066), but not in 1997 (p=0.0228). As with biomass (Table 2.4), the presence or absence of competition was most significant in the upper two elevations (p<0.01), but had a non-significant effect in the lower two elevations (Table 2.5). Tillering rate was not significantly correlated with the interaction of competition and elevation.

DISCUSSION

Three clear patterns emerge from the results of this study of *C. lacustris* establishment under different environmental treatments. First, the response of seedlings to water regime in the first growing season was not indicative of the outcome of mature stand development by the end of three growing seasons. Second, sedge growth varied significantly with water depth in the absence of competition, but showed no significant difference across elevation in plots with competition. Third, competition reduced sedge growth to different degrees in the rising versus falling and static water regimes. The results illustrate the sensitivity of *Carex lacustris* seedlings to abiotic and biotic influences during the first growing season after planting.

Establishment year

During the first growing season, a rising water regime promoted the greatest growth and was associated with the lowest seedling mortality of all three water regimes. The falling water regime was associated with the least favorable seedling response, particularly at the lowest elevations where seedlings were over-topped by deep water early in the growing season. A similar pattern was observed in parallel studies of *C. lacustris* rhizome and *C. stricta* seedling survival under the same environmental conditions (Yetka & Galatowitsch 1998, R.A. Budelsky, unpublished data). In the present study, tiller heights in the rising water regime increased at a rate sufficient to ensure that some minimum proportion of the seedling's biomass remained above the water's surface. Differential establishment as a result of seasonal timing of water-level has also been shown to be important in the survival and growth of *Scirpus lacustris* and *Scirpus maritimus* seedlings (Merendino & Smith 1991).

Water depth is considered by many authors to be the most significant factor controlling the establishment of wetland species (van der Valk 1985, Spence 1982). In this study, water depth was clearly the deciding factor in seedling survival. Seedling growth, however, was affected by both water depth and competition. The synergistic effect of water depth and competition together created one of the most interesting growth responses in this study (Tables 2.4 and 2.5). Clearly the significant difference in seedling growth between upper and lower elevations can be attributed to water depth alone in the non-competition plots. In competition plots, the difference in sedge seedling growth was insignificant across all elevations, despite the observation that competitive plant density was greater at upper elevations. We conclude that the establishment of *C. lacustris* seedlings was limited at lower elevations by water depth and at upper elevations by competition. Our results are consistent with Grime (1979) and studies by Wilson & Keddy (1986a, 1986b) in which differences in seedling survival and growth along an elevational gradient are attributed to the combination of water depth and competition.

Water regime and competition also exhibited a synergistic effect on sedge biomass. The difference in biomass between competition and non-competition plots was greater in the rising water regime than the other two water regimes. Competition from dense biomass produced by *Phalaris arundinacea* in the rising water-level regime at the end of the first growing season may have been responsible for this pattern. *P. arundinacea* is thought to be indigenous to the temperate regions of all five continents (Marten & Heath 1985), but has been cultivated for forage for two centuries (Alway 1931). Selective breeding has resulted in a species with aggressive vegetative growth, abundant seed production, and tolerance for a wide range of water conditions (Galatowitsch, Anderson & Ascher, in press). It is characterized as wetland invader and poses a threat to native vegetation because of its rapid growth and difficult removal (Apfelbaum 1987).

Second and third growing seasons

If seedlings survived the first year, mortality in the next two years was low under all water regimes and water depths. Reduced mortality indicates the end of the establishment period and is typically followed by a period of increased biomass production accompanied by a change in the floristic structure known as maturation (van der Valk 1985). In discussing sedge growth response in the second and third years, it is useful to initially consider non-competition and competition plots separately. In non-competition plots in the second growing season, sedge biomass collected from the rising water regime was no longer significantly greater than biomass from the falling water regime (Table 2.3). By the third growing season, rising water regime biomass was significantly lower than that in the falling water regime. The change in biomass production paralleled similar changes in tiller production (Fig. 2.1a). It is likely that new tiller initiation that occurs in the fall for *C. lacustris* was negatively impacted by the rising water-level regime. Grace (1989) suggests that the primary limitation effecting emergents in deeper water is light extinction. Water clarity was not measured in this study, but the water was typically turbid with suspended soil particles.

The static water regime was characterized by the lowest biomass in the last two years. The disparity in biomass between the static water regime and the two fluctuating water regimes appeared to be a consequence of low biomass in the upper two elevations of the static water regime (always above the mean standing water-level). Water fluctuation that produces standing water at some time during the growing season appears to be necessary for optimum *C. lacustris* growth.

Tiller number and biomass continued to differ along the elevational gradient in non-competition plots although tillering rate did not differ significantly in the second and third years. This lingering effect of earlier differential growth rates continued to distinguish the upper three elevations from the lowest elevation into the third growing season. Hultgren (1988) and Squires & van der Valk (1992) found similar results in their experimental studies of water depth effects on mature *Carex rostrata* and *Carex atheroides*, respectively.

The growth patterns in competition plots show differences that illustrate the important interactions of competition and abiotic factors. In contrast to the first growing season, the effect of elevation on sedges in competition plots was not significant across water depths in the second and third growing seasons. Sedges remained limited by competition at the uppermost elevations and water depth at the lowest elevations. Seabloom, van der Valk & Moloney (1998) concluded that water depth alone was sufficient to sort four wetland species according to their adult niche along an elevational stress gradient. They also noted that their experiment did not run long enough to detect the effects of competition. The results of the present study suggest that the adult niches of other wetland species are likely to be constrained by competition at the upper elevations as well. The pattern observed in this study may lead to "competitive displacement" along a water-level gradient as has been shown for *Typha* species (Grace & Wetzel 1981).

Sedges in competition plots in the falling water regime produced greater biomass than sedges in competition plots in the other two regimes in both the second and third growing season. The difference was significant by the third growing season. Because the pattern is identical to that seen in the non-competition plots, differences in plot biomass among competition plots can be explained by the effect of water regime alone. If, however, non-competition and competition plots are compared across water regimes, an interesting pattern appears that cannot be explained by abiotic factors alone. The difference between competition and non-competition plots in the rising water regime is significantly different in all years, whereas the difference between competition and non-competition plots in the static and falling water regimes is insignificant in all years. This suggests that the intensity of competition in the rising water regime is greater than in the other two basins. As described in the results, the rising water basin contained primarily the perennial grass, *Phalaris arundinacea*, in the upper two elevations, whereas the other two basins contained primarily annuals. Although this study was not designed to evaluate the effects of floristic differences in competition on sedge seedlings, the results suggest that sedge seedlings grown in plots with perennials experienced more intense competition than seedlings grown in plots with annuals. This result appears to represent a 'positive feedback switch' (*sensu* Wilson & Agnew 1992) in which *Phalaris*, once established, continues to produce conditions inhospitable for *Carex* seedling growth.

Our own experiments in influencing competition by manipulating sedge seedling density did not affect the invasion of *Phalaris arundindacea*. However, in plots with primarily annual competitors, high density plantings were associated with greater sedge cover estimates than low density plantings. This suggests that by the second growing season, high density plots produced sufficient cover to reduce the germination of shade-intolerant annuals. This was the only significant effect of sedge planting density in this study.

Both water regime and competition have been implicated in the development of coenoclines (*sensu* Whittaker 1967) or vegetation zones in wetlands (Spence 1982, van der Valk & Welling 1988, Wilson & Keddy 1986a,1986b). Zonation patterns of adult plants are presumed to result from conditions at establishment (van der Valk & Welling 1988, Grubb 1977). In the present study, the development of sedge stands diverged depending upon the seasonal water regime experienced, the elevation at which seedlings were planted (in non-competition plots), and the combination of competition and elevation (in competition plots). The intensity of competition provided by annual versus perennial vegetation may also play a role in the development of sedge stands. These results do not support the assertion that appropriate water regime alone (self-design *sensu* Mitch and Cronk 1992) will be sufficient for *Carex* establishment.

Restoration recommendations

The period of seedling recruitment and establishment is presumed to be most critical for the development of species diversity (Grubb 1977, Harper 1977, van der Valk & Welling 1988).

The results of this experimental study confirm the sensitivity of sedge seedlings to both abiotic and biotic conditions in the first growing season, underlining the value of maintaining the greatest environmental control during the establishment year. *C. lacustris* stands had a greater tolerance for a broader range of abiotic and biotic conditions after the establishment year, thus less environmental control is necessary in subsequent years.

The establishment and maturation of sedge stands along a water depth gradient involves a series of tradeoffs between resource exploitation and stress tolerance (Grime 1977, Tilman 1990), regardless of the origin of the propagules and the history of the wetland basin. Thus seedlings artificially introduced to a restored wetland face a similar set of environmental challenges as do seedlings recruited from the seedbank in a native wetland. Wetland restorationists are in a unique position to intervene in succession by manipulating some of the environmental factors that determine the development of vegetation patterns.

Given limits to the control that can be exerted in a restoration, the challenge is to choose the set of environmental conditions that has the greatest potential for growth of desired vegetation and the least potential for death or competitive exclusion. For *Carex lacustris* transplants, a rising water regime is most conducive to low initial mortality rates, but it is accompanied by the potential for invasion of undesirable aggressive species that may exclude sedge seedlings. A falling water regime is ultimately better for growth once sedges are established, but it is associated with higher initial mortality in the establishment year in the deeper water. Ideally, the decision of how best to balance these tradeoffs should come in the restoration planning stage when the potential for establishing control is greatest.

Regardless of whether water control structures exist at the restoration site, intensive weed control during the establishment year is strongly recommended. Because dispersal of weedy propagules from other sites is likely to be continual, the goal of a well-planned restoration should be to re-establish dense stands of native vegetation before aggressive perennials can preempt the site (Galatowitsch, Budelsky, & Yetka 1998). Well-established native vegetation has a greater chance of excluding subsequent invasions (Johnstone 1986). Suggestions for specific weed control interventions can be found in Galatowitsch & van der Valk (1994) and Solecki (1997). Given the potential for undesirable weeds to recruit from the seedbank and displace seedlings, restorationists should be wary of using donor soil unless it is clear the soil does not contain propagules of aggressive weeds. Site preparation strategies such as tillage, herbiciding, or other weed control methods that deplete the seedbank of undesirable species are recommended for two to three years prior to sedge planting (Galatowitsch, Budelsky, & Yetka 1998). If water control structures that allow drawdown are in place, restorationists have the option of maintaining a low water-level in the first growing season during sedge seedling establishment and then allowing the basin to refill.

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Table 2.1. Mean above-ground dry-weight biomass (g m^{-2}) averaged by elevation from the 1995, 1996, and 1997 growing seasons (± SE). Means are compared within years across elevations. Means with the same letter are not significantly different ($p<0.01$).

Elevation above or below mean seasonal water level	Year									Rate of growth over time			
	1995			1996			1997			1995-1996		1996-1997	
	x	SE		x	SE		x	SE					
+22.5 cm	47.4	18.7	a	432	110	a	840	153	a	9.12	a	1.94	a
+7.5 cm	46.7	17.0	ab	424	118	a	875	127	a	9.08	a	2.06	a
-7.5 cm	29.1	10.0	ab	288	60.8	ab	722	109	a	9.91	a	2.50	a
-22.5 cm	17.7	7.68	b	109	22.6	b	312	74.2	b	6.18	b	2.85	a
Overall significance of elevation in the analysis of variance	p=0.0081			p=0.0029			p=0.0004			p=0.0039		p=0.5360	

Table 2.2. Mean above-ground dry-weight biomass (g m^{-2}) averaged by competition regime for 1995, 1996, and 1997 (± SE).

	Without Competition		With Competition		Overall significance of competition in the analysis of variance
Year	x	SE	x	SE	
1995	54.9	12.6	15.6	3.09	$p = 0.0001$
1996	462	72.5	165	39.5	$p = 0.0002$
1997	847	95.2	527	81.4	$p = 0.0004$

Table 2.3. Mean above-ground dry-weight biomass (g m^{-2}) averaged by the interaction between competition and water regime (± SE).

Year	Competition	Water regime						Overall significance of the interaction between competition and water regime in the analysis of variance
		Rising		Static		Falling		
		x	SE	x	SE	x	SE	
1995	No	99.6	20.1	41.3	11.1	23.7	5.98	p=0.0009
	Yes	15.0	3.92	15.9	3.57	16.0	5.98	
1996	No	618	124	290	39.7	478	72.2	p=0.0067
	Yes	57.5	8.62	150	30.1	287	69.2	
1997	No	855	129	615	63.6	1070	128	p=0.0217
	Yes	290	56.2	457	70.4	834	116	

Table 2.4. Mean above-ground dry-weight biomass (g m^{-2}) averaged by the interaction between competition and elevation (+ SE).

		Elevation (cm)								
		+22.5		+7.5		-7.5		-22.5		Overall significance of the interaction between competition and elevation in the analysis of variance
Year	Competition	x	SE	x	SE	x	SE	x	SE	
1995	No	80.9	22.9	77.5	20.5	37.9	13.0	23.1	10.7	p=0.0076
	Yes	13.9	4.60	15.8	4.15	20.3	6.08	12.4	3.05	
1996	No	707	90.5	661	124	352	39.7	129	29.4	p=0.0074
	Yes	158	60.2	187	61.7	225	75.9	89.7	13.6	
1997	No	1160	90.6	1070	102	886	87.2	272	95.4	p=0.0073
	Yes	519	150	678	131	558	114	351	52.0	

Table 2.5. Mean tiller number m^{-2} averaged by the interaction between competition and elevation (± SE).

		Elevation (cm)								Overall significance of the interaction between competition and elevation in the analysis of variance
		+22.5		+7.5		-7.5		-22.5		
Year	Competition	x	SE	x	SE	x	SE	x	SE	
1995	No	56.9	18.7	58.4	17.8	35.9	9.91	18.9	4.50	p=0.0033
	Yes	16.2	4.87	21.4	5.41	25.4	7.41	14.2	3.47	
1996	No	331	55.0	290	52.8	166	23.4	48.2	14.2	p=0.0066
	Yes	81.7	29.3	85.3	20.5	98.7	27.4	46.3	12.7	
1997	No	331	54.0	328	46.4	210	40.8	79.0	28.0	p=0.0228
	Yes	183	25.9	175	42.3	151	20.2	99.4	25.8	

Table 2.6. Mean above-ground dry-weight biomass (g m^{-2}) averaged by the interaction between competition and initial planting density (± SE).

		Initial Planting Density				Overall significance of the interaction of competition and initial planting density in the analysis of variance
		High		Low		
Year	Competition	x	SE	x	SE	
1995	No	88.1	14.9	21.7	3.79	p=0.0030
	Yes	27.5	2.51	3.60	0.87	
1996	No	567	86.9	357	49.5	p=0.9555
	Yes	267	47.1	62.3	9.06	
1997	No	947	96.3	747	93.6	p=0.0542
	Yes	733	91.8	320	39.4	

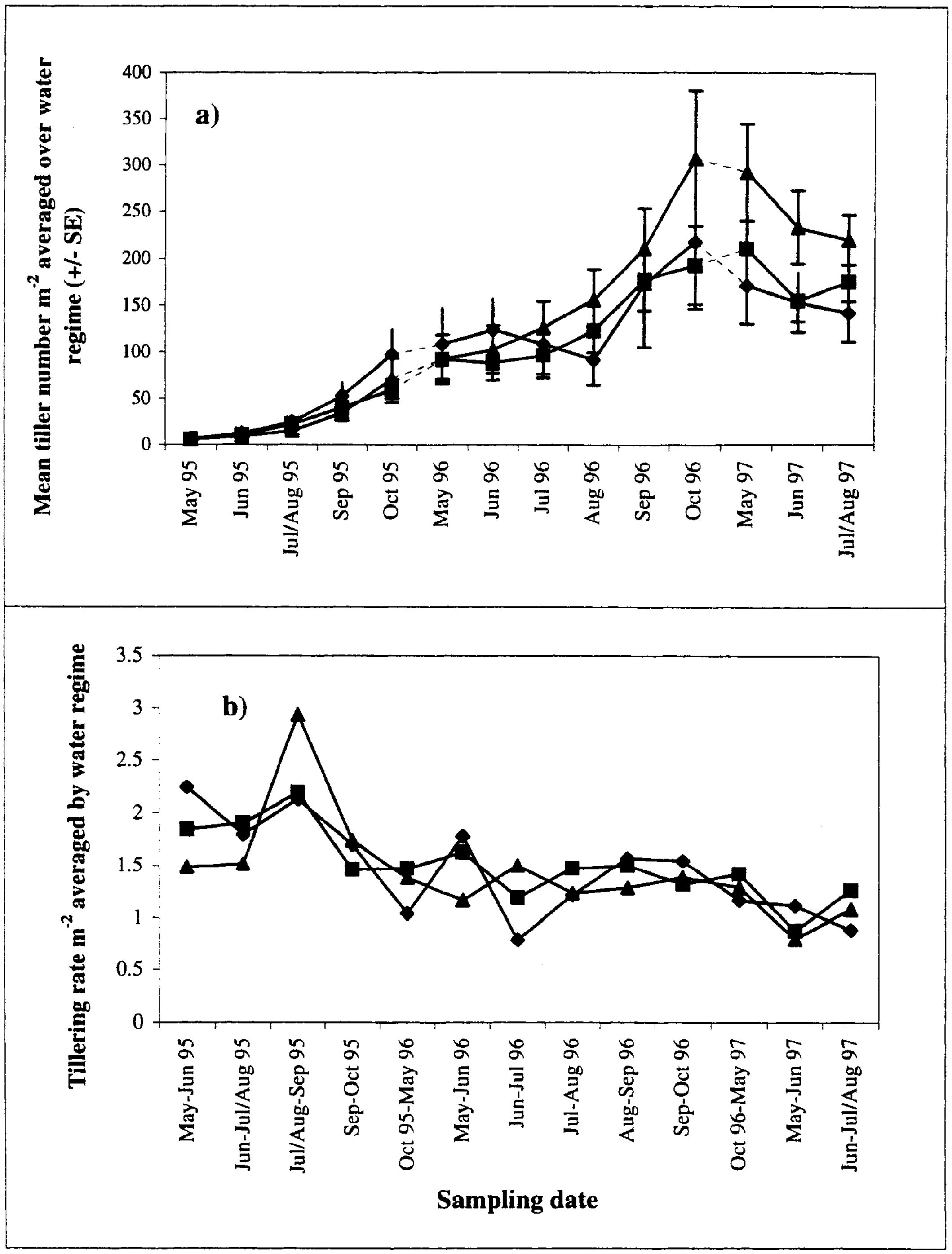

Figure 2.1. Mean tiller number (a) and tillering rates (b) for *Carex lacustris* seedlings averaged by rising (-◆-), static (-■-), and falling (-▲-) water regimes.

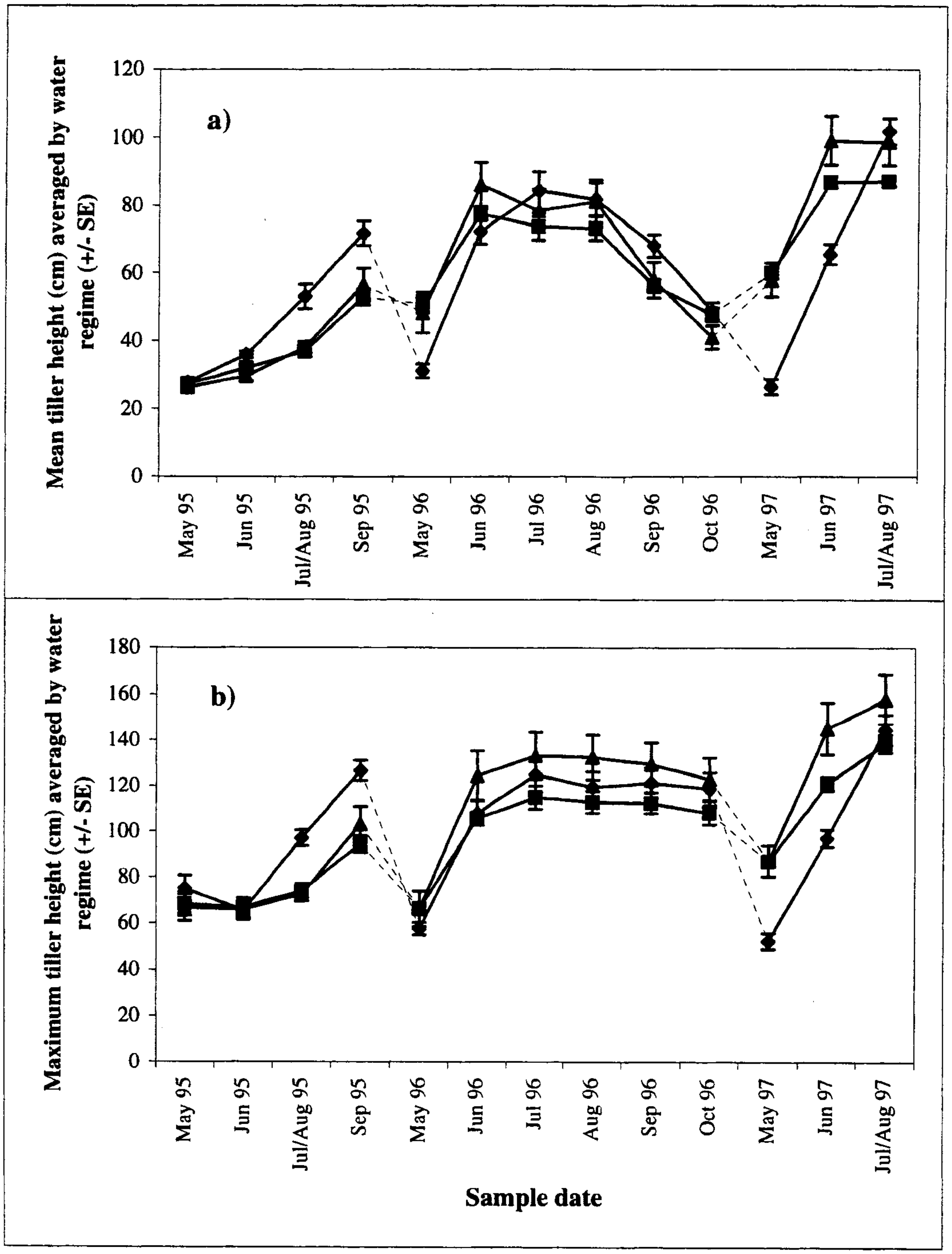

Figure 2.2. Mean tiller height (a) and maximum tiller height (b) for *Carex lacust* seedlings averaged by rising (-◆-), static (-■-), and falling (-▲-) water regimes

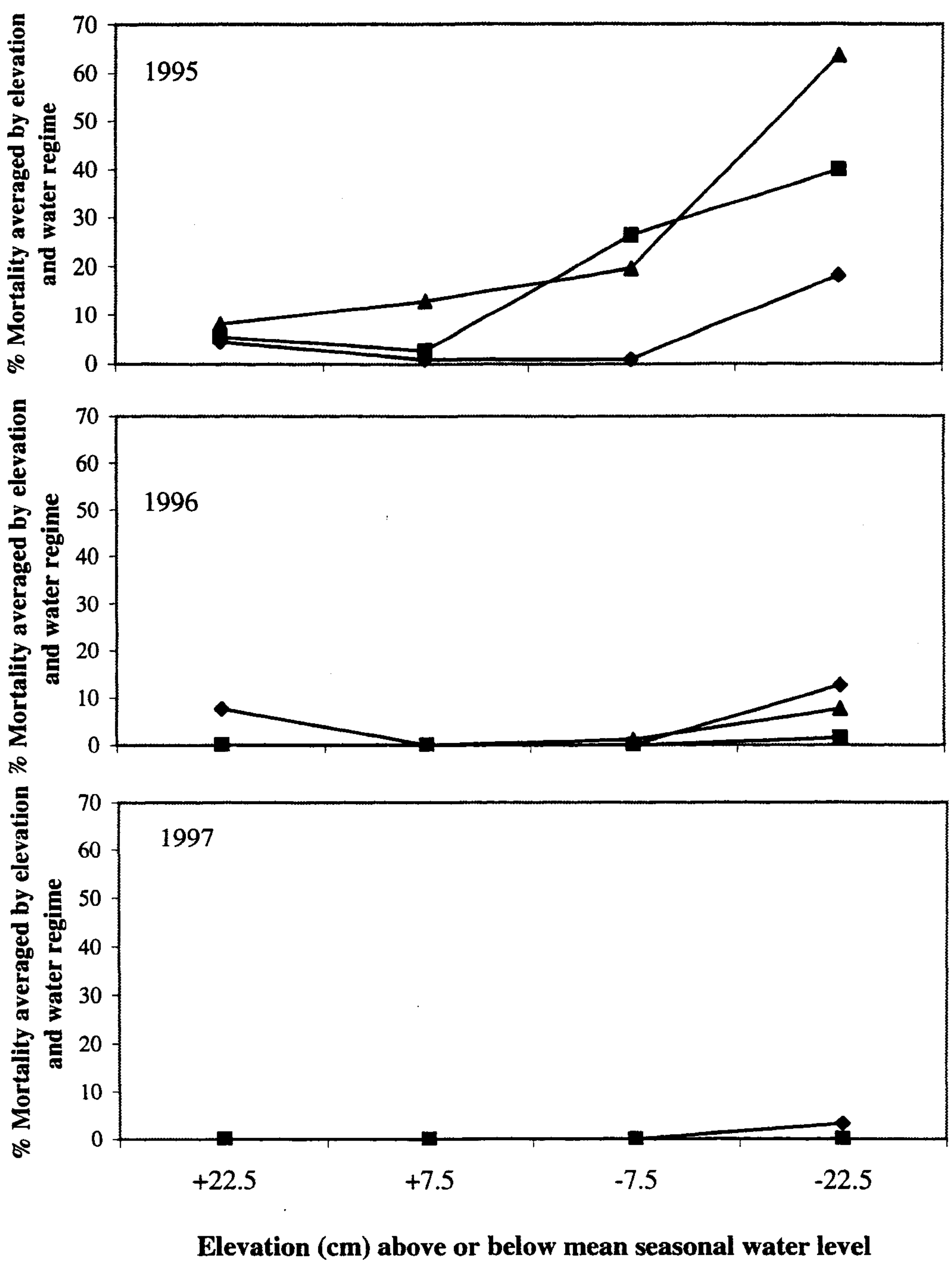

Figure 2.3. Mean percent mortality for *Carex lacustris* seedlings in the first (a), second (b), and third (c) year of establishment. Mortality is averaged by rising (-◆-), static (-■-), and falling (-▲-) water regimes.

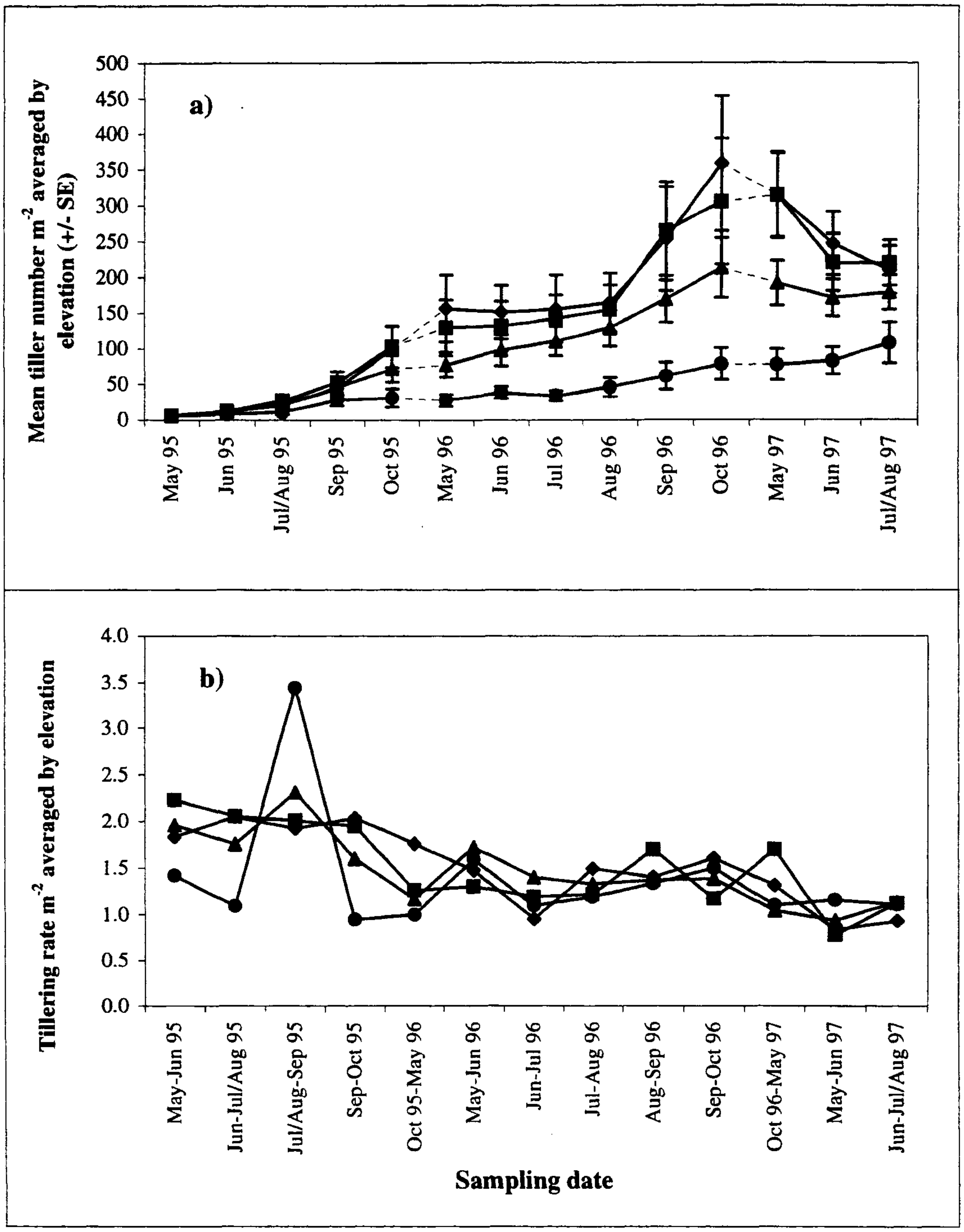

Figure 2.4. Mean tiller number (a) and tillering rates (b) for *Carex lacustris* seedlings averaged by +22.5 cm (-◆-), +7.5 cm (-■-), -7.5 cm (-▲-) and -22.5 cm (-●-) soil elevation above or below mean seasonal water level along a water depth gradient.

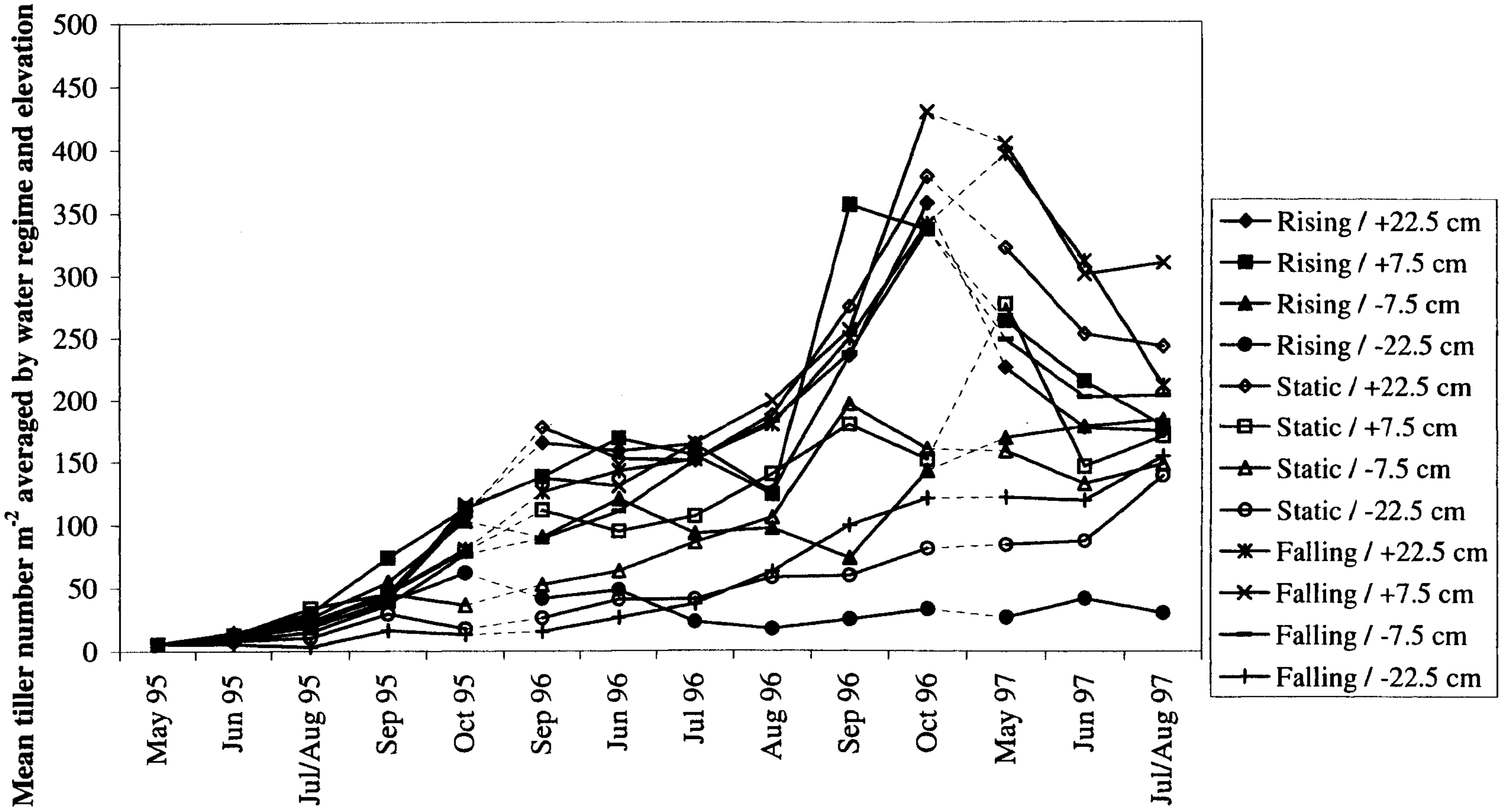

Figure 2.5. Mean tiller number for *Carex lacustris* seedlings averaged by water regime and elevation

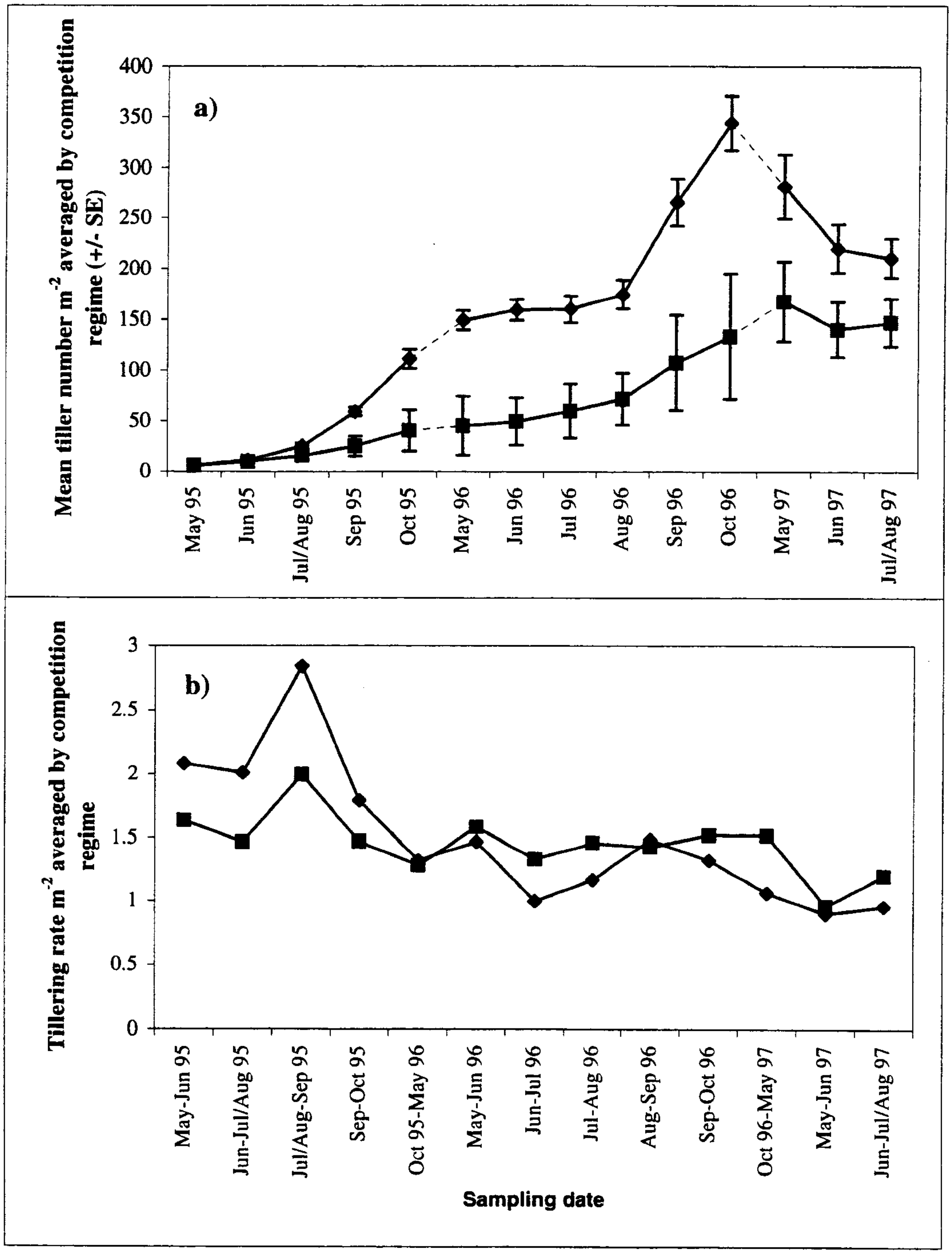

Figure 2.6. Mean tiller number (a) and tillering rates (b) for *Carex lacustris* seedlings averaged by absence of competition (-◆-) and presence of competition (-■-).

CHAPTER 3 (Tasks 6-7: *Carex stricta*)

Establishment of *Carex stricta* seedlings in Experimental Wetlands with Implications for Restoration

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SUMMARY

The loss of sedge meadow wetlands due to agricultural drainage in the glaciated midcontinent of North America has been extensive. The lack of natural *Carex* recruitment in wetland restorations and the failures of revegetation attempts underscore the need for information on the establishment requirements of wetland sedges. In this study, seedlings of *Carex stricta* Lam. were planted in three experimental wetlands in east-central Minnesota, USA to investigate the environmental limitations to establishment. Seedlings were planted along a water-depth gradient to assess the effects of water availability on seedling survival and growth. A different water-level fluctuation regime was assigned to each of the experimental wetlands to assess seedling tolerance for seasonal water-level changes. The effects of seedling planting density and interspecific competition on seedling survival and growth were also studied. The experiment was followed for three growing seasons.

The results of this study indicate that *C. stricta* seedlings have the physiological capacity to establish across a fairly wide range of soil moisture conditions. Seedlings were sensitive to the timing and duration of inundation during the first growing season but, once established, plants tolerated a broad range of seasonal drying and flooding conditions. Competition appeared to be the factor that most limited seedling growth during the first two years. *C. stricta* was able to outcompete annual weeds, but not the aggressive perennial *Phalaris arundinacea* L., by the third growing season. Differences between the growth response of *C. stricta* and other sedges suggest that growth form may affect competitive ability. The rapid growth of *C. stricta* seedlings under optimum conditions indicates that a successful revegetation strategy must control competition during the first two to three years after planting.

INTRODUCTION

It is estimated that more than half of the wetland acreage that existed in the continental United States at the time of European settlement has been drained for development and agriculture (Dahl and Johnson, 1991). Many wetlands in the prairie pothole region of the Midwest once formed extensive hydrologically connected complexes. Today these wetlands exist as isolated basins in the landscape. Sedge meadow wetlands have been disproportionately impacted by conversion and drainage in the midwest relative to deeper-water wetlands (Prince, 1997). Historically, sedge meadow communities were approximately seven times as abundant as open-water wetlands (by area), occurring in shallow groundwater-fed depressions and along the margins of the deeper wetlands (Galatowitsch and van der Valk, 1996b). Sedge meadows are dominated by members of the genus *Carex*. The combination of two life history traits in wetland Carices - clonal growth and water-borne fruits - contributes to reduced opportunities for dispersal in the current landscape. Dispersal limitations have been linked to the absence of sedge meadow communities in wetland restorations that rely upon natural recolonization for reestablishment of native vegetation (Galatowitsch and van der Valk, 1996a).

Despite the historical abundance of sedge meadows, sedge meadow restorations are uncommon. This is due in part to the difficulty of establishing both an appropriate water regime and native species, especially *Carex* (Galatowitsch and van der Valk, 1996b). Where sedge meadow revegetation has been attempted, the success rate is low (e.g. Bremholm, 1993). Simply replicating environmental conditions found in natural sedge meadows does not appear adequate for the recolonization of sedges. For wetlands in general, the environment of adult plants is not necessarily the environment required for establishment (Grubb, 1977; ter Heerdt and Drost, 1994; de Swart et al., 1994). In addition, the life history traits of adult wetland emergent species do not necessarily correlate well with the juvenile or germination traits of those species (Shipley et al., 1989).

Information specifically relevant to establishment is needed to develop an effective restoration strategy for sedge meadows. For example, subtle differences in moisture and temperature result in differential germination of several wetland Carices (Budelsky and Galatowitsch, 1998). Thus, spring planting is advised for seeds that germinate under cool moist conditions, whereas summer planting is adequate for seeds with higher germination temperature requirements. In the absence of studies on establishment criteria, the success of restoration attempts depends upon chance rather than reliable prediction.

Several recent studies focusing on the establishment of wetland sedges in experimental wetlands point to the potential importance of growth form in restoration success (Yetka and Galatowitsch, 1998; Budelsky, 1998). Yetka and Galatowitsch (1998) observed that the mat-forming *C. lacustris* Willd. established from detached rhizomes under a wide range of moisture conditions, whereas the tussock forming *C. stricta* Lam. had a low survival rate under all conditions. The response of *C. lacustris* seedlings to a variety of water regimes in a parallel study confirmed that *C. lacustris* is successful in a broad range of moisture conditions (as well as competition from annuals) during establishment (Budelsky, 1998). The difference in growth form between *C. lacustris* and *C. stricta* may partly responsible for their different responses to establishment from rhizomes.

Tussock-forming and mat-forming *Carices* have been observed to respond differently to moisture and competition gradients in native sedge wetlands (Phillips, 1993). In Phillips' (1993) reciprocal transplant study, both the tussock-forming *C. haydenii* Dewey (a close relative of *C. stricta*) and the spreading *C. lacustris* had a high tolerance for a wide range of moisture conditions. In contrast, *C. haydenii* appeared more sensitive to competition than *C. lacustris*. Phillips' results for mature plants of *C. lacustris* agree remarkably with the establishment of rhizomes and seedlings of that species observed by Yetka and Galatowitsch (1998) and Budelsky (1998). However, Phillips' results for *C. haydenii* cannot be applied to *C. stricta* because of the high mortality observed for *C. stricta* rhizomes (Yetka and Galatowitsch, 1998).

In this study, I investigated the establishment requirements of *Carex stricta* seedlings to begin developing a restoration strategy for this species. I planted *C. stricta* seedlings under the same conditions as those used in the study of *C. lacustris* seedlings, allowing the comparison of establishment characteristics between the two species. *C. stricta* was chosen because of its broad distribution and abundance in temperate wetlands (Gleason and Cronquist, 1991; Wheeler, 1981). I predicted that the response of *C. stricta* seedlings to water conditions and competition would be similar to that of *C. haydenii*. The study was designed to answer the following questions:

1) How does seedling location along an elevational (water availability) gradient affect its survival and growth?

2) How does the timing of water level changes affect survival and growth?

3) To what degree does competition from naturally recruited weeds affect sedge survival and growth?

4) Do the abiotic factors change sedge response to competition?

5) Does initial planting density influence sedge survival and growth?

MATERIALS AND METHODS

Study species

Carex stricta is a perennial graminoid with circumboreal distribution (Curtis, 1959). In North America its range extends from Nova Scotia across central Manitoba and southward as far as Virginia and Texas (Gleason and Cronquist, 1991). It commonly occurs in central and northern Minnesota on soils with high organic matter such as those found in wet meadows, marshes, and along the margins of ponds, lakes, streams, and bogs (Costello, 1936; Wheeler, 1981). The tussocky growth habit of the species results from short rhizomes growing vertically from the plant's base (Bernard, 1990). Spreading rhizomes are also occasionally formed, and these initiate new tussocks away from the parent plant (Costello, 1936). Tussocks may reach heights of over 1 m and diameters of greater than 0.75 m (Costello, 1936).

Study site

The study was conducted at the University of Minnesota's Landscape Arboretum in Chanhassen, Minnesota, USA (44°51'45"N, 93°36'00"W) for three growing seasons beginning May 1995 and ending September 1997. The experiment was established in a former wetland basin that had been drained for irrigation. Several years prior to the start of this experiment, the basin had been divided into four smaller basins by the construction of two earthen dikes that crossed in the center. Each of the smaller basins is approximately 0.2 ha (one quarter acre) in size. The soil is characterized by a thick black surface horizon of silty clay loam with hydric features in the dark gray clay loam sub-horizon.

In the fall immediately prior to the start of this experiment, each basin was regraded to create a flat bottom and four shallowly sloping sides with an elevational gradient of 20:1. The basins were then flooded to retard weed recruitment before the study began. Each of the basins was connected to buried irrigation lines that allowed the addition of water from a ground water well. Each basin was also equipped with a centrally located drainpipe that allowed water removal. Water level could be adjusted independently in each basin.

Experimental design

C. stricta seedlings were planted in bare soil plots on the east-facing slope of three basins in May 1995. Seedlings were grown from seed in the greenhouse and were transplanted at approximately ten weeks of age. Seedlings were approximately 25 cm (± 10 cm) tall with one to three above-ground tillers.

Four rows of four 5 m^2 (2.5 m x 2 m) plots were established along the elevational gradient to create four water depth treatment levels. In each basin, the rows (elevations) corresponded to +22.5, +7.5, -7.5, and -22.5 vertical centimeters above (+) or below (-) the mean seasonal water level. The elevational gradient was designed to evaluate the effect of water availability (and depth) on seedling survival and growth.

A different water regime was assigned to each of the three basins to determine the effect of water depth fluctuation at different times in the growing season. At the beginning of the growing season (May), the water level in the rising water regime was below the lowest elevation and all four elevations were exposed. The water level was gradually increased over the growing season at a rate of five vertical centimeters every two weeks until, at the end of the season (September), plots in the uppermost elevation were inundated. The falling water regime began the season with the water's edge at the top of the plots in the uppermost elevation. Over the growing season, the water level fell at a steady rate (5 vertical cm / 2 weeks) until plots in the lowest elevation were exposed. Thus the water depth treatments along the elevational gradient were similar in both the rising and falling basin, but the seasonal timing of exposure and inundation differed. In the static water regime, the water level was maintained between the +7.5 and -7.5 cm elevations, corresponding to the mean seasonal water depth in the other two water regimes. In this basin, the soil surface was always exposed in the upper two elevations and always inundated in the lower two elevations.

Seedlings were planted at either a high density (45 plants: 9 plants m^{-2}) or low density (10 plants: 2 plants m^{-2}) to assess the relative degree of intra-specific competition and to determine if planting density conferred a competitive advantage against recruited vegetation.

Competition was controlled in half of the plots by hand weeding all non-sedge vegetation. In the other plots, vegetation was allowed to recruit from propagules in the seedbank. The type of vegetation that established in the competition plots was not experimentally controlled. Thus, the treatment was designed to determine the effect of the presence or absence of naturally recruited vegetation on sedge growth and survival.

Field measurements

The experimental unit in this study was the plot. Measurements taken from each plant within plots were averaged. Seedling response to the experimental treatments described above was assayed with the following measurements by plot: percent survival, mean plant height (soil surface to tip of longest leaf), maximum height, mean above-ground biomass per plant, mean tiller number per plant, mean tillering rate per plant, mean number of flowering stems per plant, and percent cover.

Percent survival and mean number of flowering stems were summarized at the end of each season from monthly observations. Above-ground biomass was collected each year from sub-sample strips 0.85 m wide (one-third the width of the plot) in mid-August at the peak of biomass production. Biomass was sorted by species, dried in a drying oven for a minimum of 48 hours at 65° C, and weighed. Only biomass results for *C. stricta* will be presented here. Height and tiller measurements were collected monthly throughout the growing seasons. Percent cover in plots with competition was measured three times in 1995 and twice each in 1996 and 1997 using the Braun-Blanquet floristic cover analysis technique (Mueller-Dombois and Ellenberg, 1974).

Water depth was measured monthly in each plot to ensure proper levels and water was added or subtracted as needed. When the water level was below the soil surface, ground water observation wells in the center of each row were used to determine depth to water table.

Analysis

A full factorial design was used in which all combinations of all treatment levels were run. One replicate of each treatment combination was used to maximize the number of treatments and the area over which each treatment was run. We assumed that significant three- and four-way interactions between the four treatments (water level change, elevation, competition, and planting density) would not occur. This assumption allowed us to estimate random error from the combined mean squares of the higher order interaction terms (Montgomery, 1991).

Survival data were arcsine square-root transformed before analysis. Height and tiller measurements were log transformed to standardize variance over time. Repeated measures analysis of variance was run on height and tiller measurements across all years. Biomass, survival, and number of flowering stems were analyzed separately each year using an analysis of variance. The alpha value for significance was set at 0.01. SAS Release 6.12 for Microsoft Windows was used for the analysis (SAS Institute, 1996).

RESULTS

The response of *C. stricta* to experimental treatments: water regime (basin), elevation along a water depth gradient, competition, and planting density, are presented below. The results are organized by treatment, but there are many instances of synergistic effects from combinations of the individual treatments. These synergistic effects are described under one of the individual treatment headings. Each of the variables used to measure plant response - percent survival, mean plant height, above-ground biomass per plant, mean tiller number per plant, and mean tillering rate per plant - are discussed under each treatment section. Mean values are followed by (± SE).

Maximum plant height per plot and the average number of flowering stems per plant were not significantly associated with any of the treatment variables and are not discussed. Mortality during the second year was statistically significant for several treatments, but it had little biological meaning given the fraction of a plant represented by each percentage point. Mortality was not significant in the third growing season for any variable. Therefore, mortality is only discussed, where significant, for the first growing season.

Response to water regime

Seedling mortality was significantly correlated with water regime for *C. stricta* in the first growing season (p=0.0020). Mortality was higher in the falling water regime (20%) and the static (13%) than in the rising (2%) water regime. Differences in mean above-ground biomass per plant per plot were associated with water regime in the second growing season only (p=0.0038). The mean above-ground dry weight biomass per plant was greater in the falling water regime (64.2 g +/- 13.6 g) than in either the rising water regime (47.2 g +/- 13.4 g) or the static water regime (36.0 g +/- 7.7) regimes. The trend was similar in the third year, but was not significant.

Although mean tiller number increased over the course of each season, it was not significantly associated with water regime. Tillering rate was correlated with water regime between May and June, 1995 and June and July/August, 1995. Growth between May and June was greatest in the rising water regime (3.23 +/-0.15), followed by the static water regime (2.56 +/- 0.22), and finally the falling water regime (2.12 +/- 0.29). Growth between June and July/August was greatest in the falling water regime (3.04 +/- 0.31), followed by the static (2.35 +/- 0.22) and rising (1.76 +/- 0.16) water regimes. The pattern indicates that sedge growth was greatest early in the season in exposed plots in the rising water level regime and that growth rate declined as water level increased. Likewise, growth in the falling water regime was slow until water levels dropped between June and July/August. Tillering rate was not associated with water regime in the second or third growing season.

Response to elevation

Elevation was significantly associated with mortality of *C. stricta* seedlings in the first year (p=0.0004). Mortality was greatest in the lowest elevation (-22.5 cm below mean seasonal water depth), followed by the second lowest elevation (-7.5 cm) (Fig. 3.1). The upper two elevations (+22.5 and +7.5 cm) experienced the least mortality.

Elevation was correlated with differences in mean above-ground biomass for *C. stricta* (p=0.005) in the second growing season only. Mean biomass was greatest at the +22.5 cm and +7.5 cm elevations (67.0 g +/- 17.9 g and 66.5 g +/- 16.1 g, respectively) and lowest at the -22.5 cm elevation (21 g +/- 6.7).

The number of tillers differed between elevations in first and third growing seasons. In both years, tiller number was greater in the upper three elevations than in the lowest elevation ($p<0.01$) (Fig. 3.2a). The pattern was similar in the second growing season, but was not significant. Tillering rate was also associated with elevation in the first year (Fig. 3.2b). In May-June, tillering rate was greatest in the upper two elevations and, in June-July tillering rate was greatest in the -7.5 cm elevation. Tillering rate was uniformly low in the lowest -22.5 cm elevation.

In addition to their individual effects on growth, elevation and water regime together also significantly affected tiller number in June ($p=0.0001$) and July/August ($p=0.0056$) of the first year (Fig. 3.3). Seedlings produced an equal number of tillers across all elevations in the rising water regime, but had greater tiller numbers at the middle two elevations for the static water regime and the upper two elevations in the falling regime. Tillering rate was also affected by the synergistic effect of elevation and water regime during the growth period from May to June in the first year ($p=0.0001$). Tillering rate was uniform across all elevations in the rising water regime, and greatest at the upper two elevations of the static and falling water regimes.

Response to Planting Density

Planting density was not significantly associated with any growth measurement in the first growing season. In the second year, planting density was correlated with biomass ($p=0.0029$). *C. stricta* tussocks had greater biomass in low-density plots (59.0 g +/- 11.8 g), on average, than did tussocks in high-density plots (39.3 g +/- 6.89 g) ($p=0.0029$). These data correspond to 117 g +/- 25.7 g m^{-2} and 300 g +/- 58.5 g m^{-2} for low and high-density plantings calculated by area, respectively. In addition, biomass per plant was linked to the interaction of planting density and elevation in the second growing season (Table 3.1). In the upper two elevations, per plant biomass values in low-density plots were almost twice those in high-density plots. Biomass did not differ between low and high-density plantings in the lower two elevations. Plant height, tiller number, and tillering rate were not associated with planting density in any year.

Response to competition

C. stricta biomass was correlated with competition in all three growing seasons ($p<0.01$) (Table 3.2). Biomass per plant was greater in plots without competition than with competition. In addition, the interaction of competition and elevation created one of the most interesting growth patterns observed in the first two growing seasons (Table 3.3). Biomass was reduced in the upper two elevations in the presence of competition, but there was no difference in biomass production between plots with or without competition at the lower two elevations.

The number of tillers was also linked to competition regime in the first and second growing seasons ($p<0.01$). Tiller number per plant was greater in plots without competition than plots with competition. By the end of the third growing season, the mean tiller number per plant in plots without competition was 197 +/- 36.4 and 110 +/- 22.4 in plots with competition. Tiller number was associated with elevation and competition combined at the end of the first growing season and the beginning of the second growing season ($p<0.01$) (Fig. 3.4). In a pattern similar to the results observed for biomass, tiller number was greater in the upper two elevations in plots without competition than plots with competition. Tiller number at the lower two elevations did not differ for plots with and without competition. Tillering rate was not associated with competition regime.

The combination of water regime and competition also influenced tiller production (Fig. 3.5). In the absence of competition, there was no significant difference in tiller number between water regimes although sedges in the static water regime had consistently fewer tillers than did sedges in the rising and falling water regimes. The pattern differed in the presence of competition. Sedges in the rising water regime had fewer tillers than did sedges in the falling and static water regimes. This difference was significant in the third growing season. Thus, there was little difference in tiller production when the effects of water regime was considered alone, but when the biotic component was added, sedges produced more tillers in the falling and static water regimes.

Characterization of vegetation in the three basins

The floristic composition of the competition plots in the +22.5 cm and +7.5 cm elevations was qualitatively different in the three basins. The type of vegetation recruited in each basin was not directly controlled in this study, although it is possible that differences in water regime affected recruitment. During the first year, the rising water-level basin contained a perennial grass community that was dominated by *Phalaris arundinacea* L., *Phleum pratense* L., and *Polygonum sp.* The falling water level basin contained an annual grass community dominated by *Echinochloa muricata* (P. Beauv.) Fern, *Polygonum sp.* and *Setaria glauca* (L). P. Beauv. The static water level basin contained annual grasses and annual forbs including *Setaria glauca*, *Hordeum jubatum* L., *Alopecurus aequalis* Sobol., *Trifolium sp.* and *Rumex crispus* L. The lower two elevations of all three basins were dominated by *Alisma subcordatum* Raf., *Typha sp.* and *Eleocharis sp.*

In the first growing season, the annual grass assemblage in the falling water level basin developed a simple closed canopy of *Echinochloa muricata* plants from 0.5 to 1 m tall, a thin canopy of other annual grasses and forbs from 0.25 to 0.5 m tall, and relatively bare ground below. The annual grass and forb assemblage in the static water regime grew to approximately 0.5 m. It had multiple canopy layers, relatively open, with a higher diversity of forb species than in the falling water regime. The rising water regime with the perennial weed assemblage produced dense stands of grasses up to 2 m tall. By the end of the first growing season, a compact thatch layer, 5 - 15 cm thick, had developed in these plots. A thatch layer did not develop under the annual canopies.

In the subsequent two growing seasons, the annual graminoid assemblage in the falling water regime decreased in height, biomass, and percent cover. *Phalaris arundinacea* cover in the rising water regimes remained the same across all three growing seasons while the percent cover and presence of other species declined. The vegetation in the static water regime remained largely the same.

DISCUSSION

The response of *C. stricta* seedlings to the treatments used in this study permits several conclusions that relate directly to revegetation strategies. First, *C. stricta* seedlings have the physiological capacity to establish across a fairly wide range of soil moisture. Second, both the duration and the timing of inundation during the first growing season influence establishment. Once established, plants tolerated a broad range of seasonal drying and flooding conditions.

Third, competition appears to limit seedling growth most during the first two years. Fourth, differences between the response of *C. stricta* and studies of other sedges suggest that growth form may affect competitive ability. Finally, the rapid growth of *C. stricta* seedlings under optimum conditions suggests that a successful revegetation strategy must explicitly consider competition control during the first two to three years after planting.

The broad range of *C. stricta* seedling tolerance to moisture during establishment is consistent with germination characteristics of *C. stricta* observed in the laboratory (Budelsky and Galatowitsch, 1998). Seeds germinated readily under all moisture conditions (after wet-cold stratification), suggesting that the potential establishment niche (Grubb, 1977) is equally broad at both life stages. Seedling establishment patterns are not consistent with the establishment results of *C. stricta* from detached rhizomes (Yetka and Galatowitsch, 1998). In their study, rhizome survival was an order of magnitude lower than that observed for seedlings in our study. The authors concluded that cut rhizomes had low tolerance for dehydration and flooding. Seedlings appear to be more appropriate than rhizomes for establishment of *C. stricta* and possibly other tussock-forming sedges.

The effect of water depth on seedling survival and growth in this study is similar to observations made by Costello (1936), Wilcox et al. (1985), and Sjoberg and Danell (1983) for adult *C. stricta* in native wetlands. *C. stricta* tussocks were sensitive to water depths exceeding 45-61 cm (Costello, 1936) and died under prolonged exposure to flooding (Wilcox et al., 1985; Sjoberg and Danell, 1983). Seedling survival and growth relative to water levels and fluctuation regimes are also similar to the parallel study of *C. lacustris* (Budelsky, 1998). The difference in growth forms does not apparently affect sensitivity to abiotic conditions.

Despite its physiological breadth, the realized establishment niche (Grubb, 1977) of *C. stricta* is narrower than its potential niche as a consequence of sensitivity to competition. The effects of competition were greatest at the upper elevations. The pattern corroborates studies of seedling survival and growth of a variety of wetland plants along a water level gradient in the presence of competition (*sensu* Grime, 1979) (Wilson and Keddy, 1986a; 1986b). Parallel observations of reduced growth along an elevational gradient due to competition have been observed by Phillips (1993) for *C. haydenii*, a species with a similar phalanx growth form as *C. stricta*. The pattern of competitive displacement (Spence, 1982; Grace and Wetzel, 1981) at upper elevations and water depth limitation at lower elevations is also similar to that observed for the spreading *C. lacustris* (Budelsky, 1998).

The growth disparity observed in competition plots among the three water regimes is most likely due to the type of competitors in each basin. This conclusion is supported by the fact that there was no difference in growth between the three water fluctuation regimes when competition was controlled. Although this study was not designed to assess qualitative differences in competition, several observations can be made. While the competition vegetation in the falling and static basins was composed primarily of annual grasses and forbs, the vegetation in the rising basin was dominated by the aggressive perennial, *Phalaris arundinacea.* The annual grasses and forbs posed a similar degree of competition as *P. arundinacea* in the first two growing seasons. However, by the third growing season *C. stricta* appeared to out-compete the annuals. *C. stricta* was not able to out-compete *P. arundinacea* in the rising water regime. A similar pattern was observed in a parallel study of water regime and competition effects on the establishment of *C. lacustris* seedlings, except that *C. lacustris* appeared to be able to out-compete the annuals by the second growing season (Budelsky, 1998).

The difference in competitive ability between *C. stricta* and *C. lacustris* is likely due to differences in their growth forms. *C. stricta* produces primarily short vertical rhizomes whereas *C. lacustris* produces long rhizomes that have the potential to extend outside of the most intense areas of competition. With its shorter rhizomes, *C. stricta* migrates much more slowly. Although *C. stricta* has the potential to produce longer, advantageous rhizomes (Bernard, 1990; Costello 1936), the environmental conditions that stimulate their production have not been documented.

Despite the greater length of time required for *C. stricta* to out-compete annual weeds, the rapid growth and establishment of this species under optimum conditions suggests that competition-sensitive species need not be avoided in revegetation attempts. At upper elevations in the absence of inter-specific competition, *C. stricta* seedlings attained a size within three growing seasons that was similar to plants observed in native wetlands estimated to be several decades old (Costello, 1936). Costello (1936) states that adult *C. stricta* plants appear to be excellent competitors in full sunlight when the water level is no greater than 46-61 cm (18-24 inches) above or below the soil surface. This suggests that once *C. stricta* tussocks attain adult size, their likelihood of long-term persistence increases, particularly if the water level does not dramatically increase or decrease for prolonged durations.

The results indicate that slightly different restoration strategies may be appropriate for clonal sedges with different growth forms. While the same abiotic conditions appear advantageous for both *C. stricta* and *C. lacustris* (Budelsky, 1998), a different degree of competition control may be necessary for the two species in the first few growing seasons. Galatowitsch et al. (1998) suggest the use of an annual cover crop to discourage the establishment of aggressive perennials such as *Phalaris arundinacea*. Although this may be appropriate for spreading species such as *C. lacustris*, it may be problematic for tussock formers such as *C. stricta*, given its greater sensitivity to competition from annuals. In addition, the results of different planting densities in this study do not support the use of increased planting densities to discourage weedy recruitment. The higher planting density was not associated with reduced establishment of either annuals or perennial weeds. Higher planting densities also had negative consequences for intra-specific growth. In contrast, high density plantings of *C. lacustris* did exclude annual weeds more effectively than low density plantings (Budelsky, 1998). Results from this study suggest that any type of weed control that reduces or prevents shade from other vegetation is likely to be most successful for *C. stricta*. For example, the application of a ground cover in association with sedge plantings might be considered. An aggressive weed eradication program prior to planting (Galatowitsch and van der Valk 1994) is recommended for both species if propagules of *Phalaris arundinacea* are suspected to be in the propagule bank.

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Table 3.1. Mean above-ground dry weight biomass (g) per plant averaged by elevation and initial planting density (± SE). Overall significance of the interaction between elevation and initial planting density in the analysis of variance is shown in the last column as p-values.

Year	Initial Planting Density	Elevation (cm)								P-value
		+22.5		+7.5		-7.5		-22.5		
		x	SE	x	SE	x	SE	x	SE	
1995	high	7.50	2.74	7.90	1.62	5.00	1.02	3.30	1.16	p=0.4337
	low	10.9	4.57	7.20	1.06	5.40	1.58	4.80	11.9	
1996	high	48.4	17.0	43.6	15.6	40.1	13.2	25.2	10.3	p=0.0088
	low	85.6	31.4	89.4	26.3	44.1	8.95	16.7	9.25	
1997	high	85.9	23.4	102	26.2	103	23.6	70.2	12.1	p=0.1307
	low	226	83.8	216	76.7	128	18.5	45.0	18.6	

Table 3.2. Mean above-ground dry weight biomass (g) per plant for *C. stricta* averaged by competition regime for 1995, 1996, and 1997 (± SE).

	Without competition		With competition		Overall significance of competition in the analysis of variance
Year	x	SE	x	SE	
1995	8.9	1.37	4.10	0.56	p=0.0014
1996	77.7	10.6	20.5	3.35	p=0.0001
1997	169	28.5	75.3	13.2	p=0.0066

Table 3.3. Mean above-ground dry-weight biomass (g) per plant averaged by the interaction between competition and elevation (± SE

		Elevation (cm)								
		+22.5		+7.5		-7.5		-22.5		Overall significance of the interaction between competition and elevation in the analysis of variance
Year	Competition	x	SE	x	SE	x	SE	x	SE	
1995	No	15.8	3.48	9.90	0.84	5.90	1.23	3.80	1.82	p=0.0049
	Yes	2.50	0.79	5.20	0.92	4.53	1.36	4.30	1.32	
1996	No	119	17.5	103	23.0	56.5	12.2	32.6	11.6	p=0.0012
	Yes	15.3	6.20	29.8	8.63	27.7	5.04	9.40	3.30	
1997	No	231	72.9	234	68.9	143	22.4	66.3	21.3	p=0.1872
	Yes	80.8	44.3	82.7	28.7	88.8	13.2	49.0	8.56	

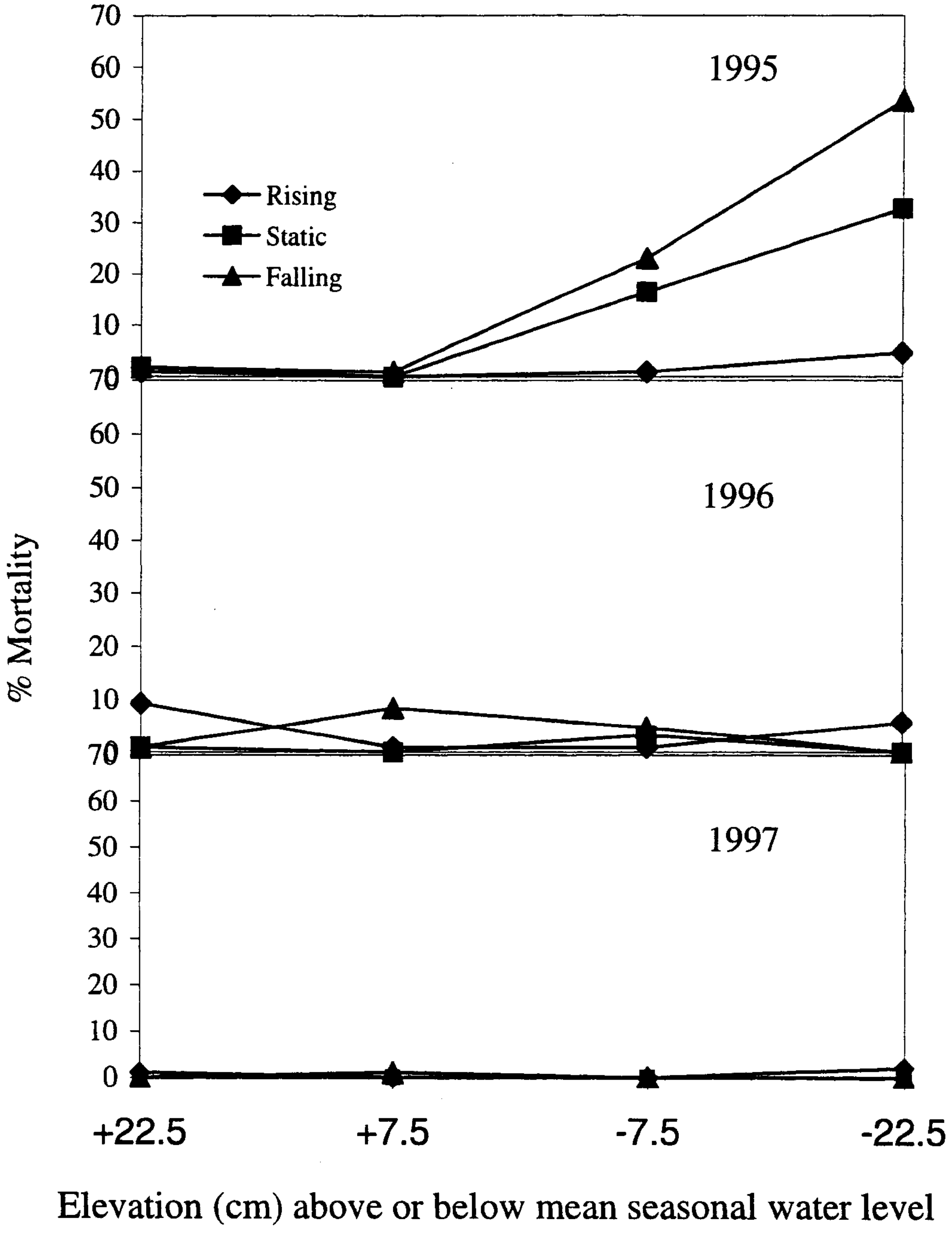

Figure 3.1. Percent mortality across elevational gradients for *Carex stricta* seedlings in the first (1995), second (1996), and third (1997) year of establishment. Mortality is averaged by elevation for rising (-◆-), static (-■-), and falling (-▲-) water regimes.

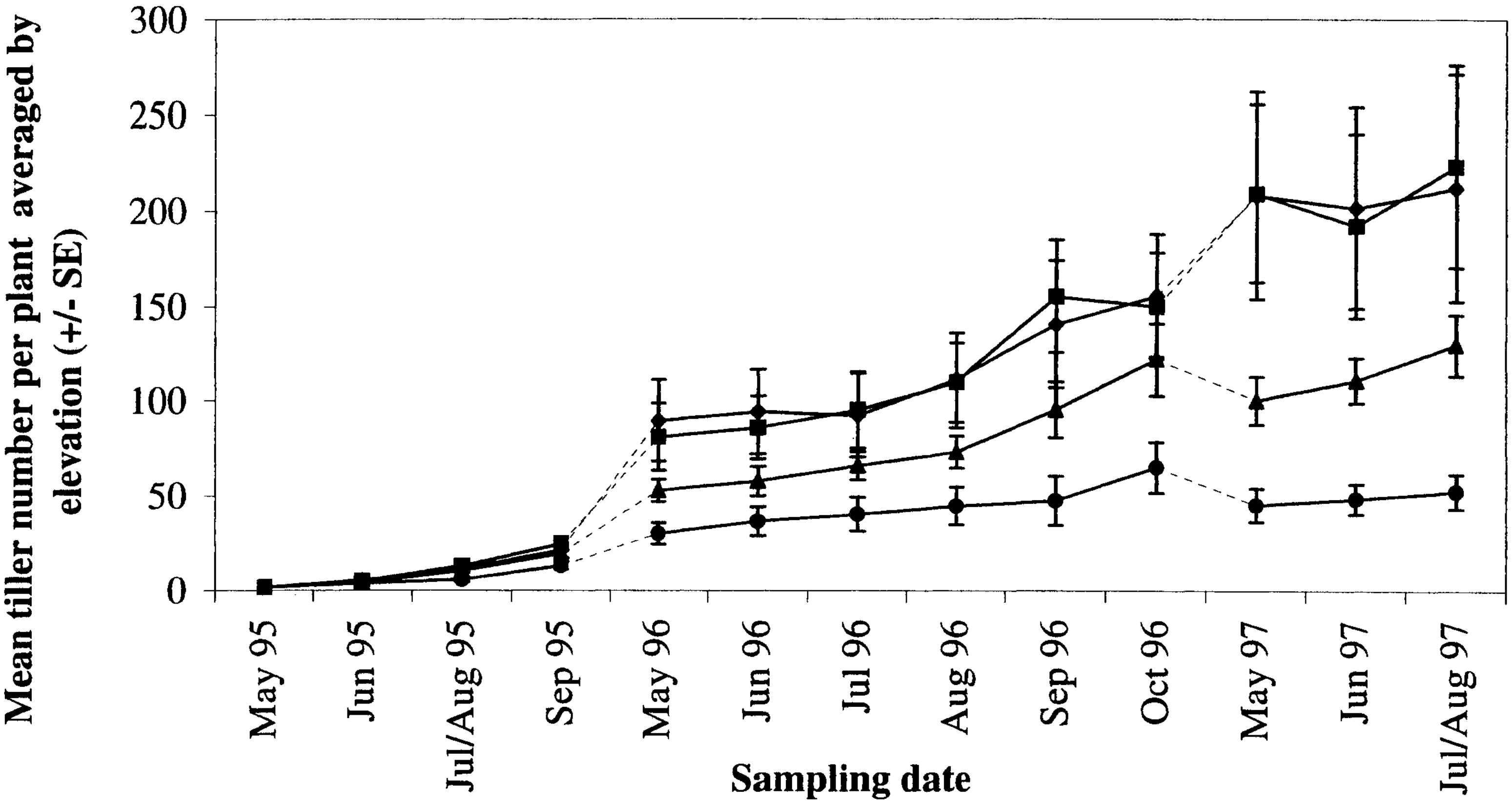

Figure 3.2a. Mean tiller number for *Carex stricta* per plant averaged by elevational treatments along a water level gradient (± SE). Soil elevations are given in vertical centimeters above (+) or below (-) mean seasonal water level. Four elevational treatments were used: +22.5 cm (-◆-), +7.5 cm (-■-), -7.5 cm (-▲-), and -22.5 cm (-●-).

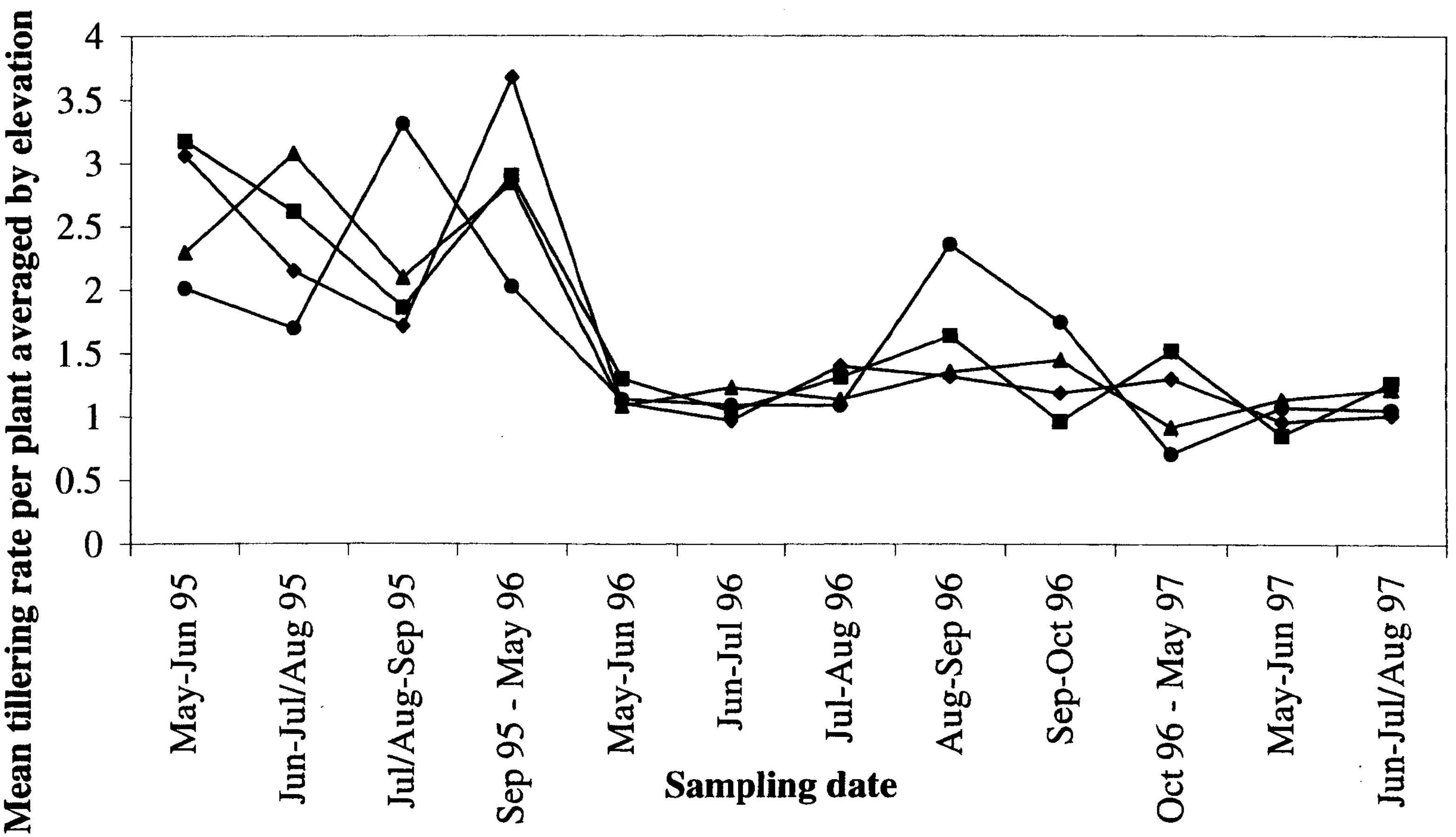

Figure 3.2b. Mean tillering rate for *Carex stricta* per plant averaged by elevational treatments aloing a water level gradient. Soil elevations are given in vertical centimeters above (+) or below (-) mean seasonal water level. Four elevational treatments were used: +22.5 cm (-◆-), +7.5 cm (-■-), -7.5 cm (-▲-), and -22.5 cm (-●-).

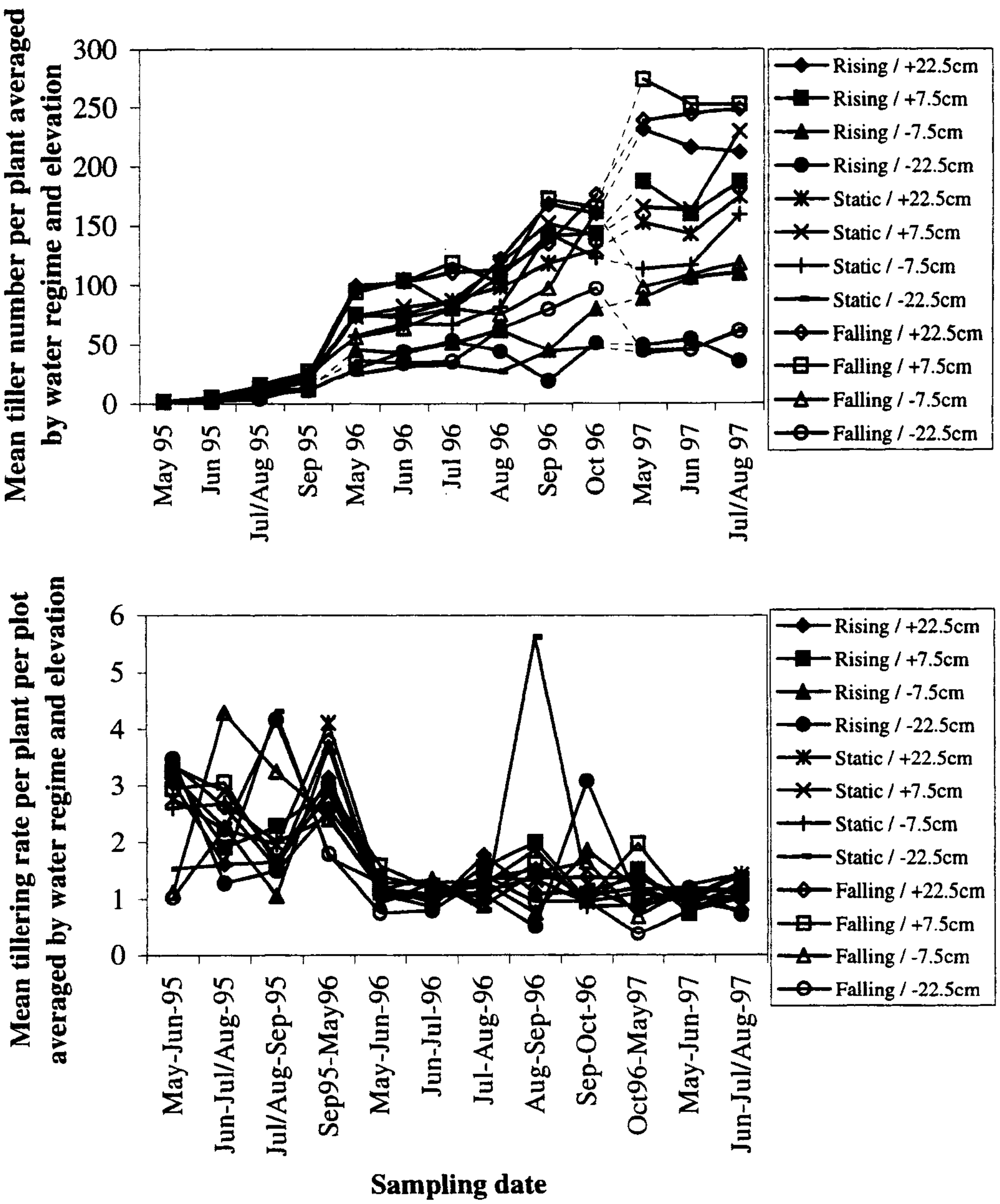

Figure 3.3. Mean tiller number (a) and tillering rates (b) for *Carex stricta* per plant averaged by the interaction of water regime and elevational treatments along a water level gradient.

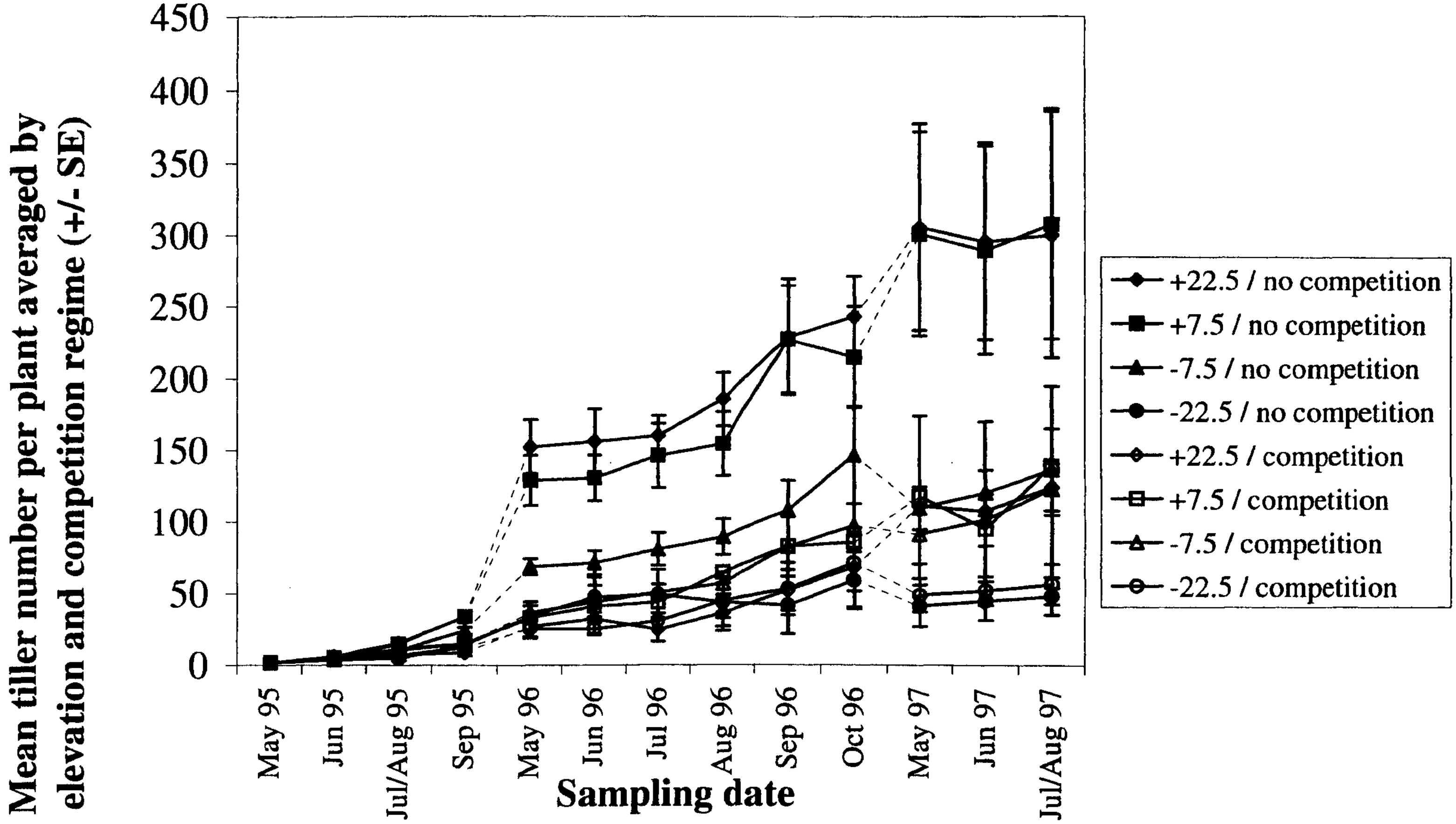

Figure 3.4. Mean tiller number for *Carex stricta* per plant averaged by elevation and competition regime. Symbol shapes represent soil elevation in vertical centimeters above (+) or below (-) mean seasonal water level:+22.5 cm (-◆-), +7.5 cm (-■-), -7.5 cm (-▲-), and -22.5 cm (-●-). Solid symbols represent data from plots without interspecific competition and open symbols represent data from plots in the presence of competition.

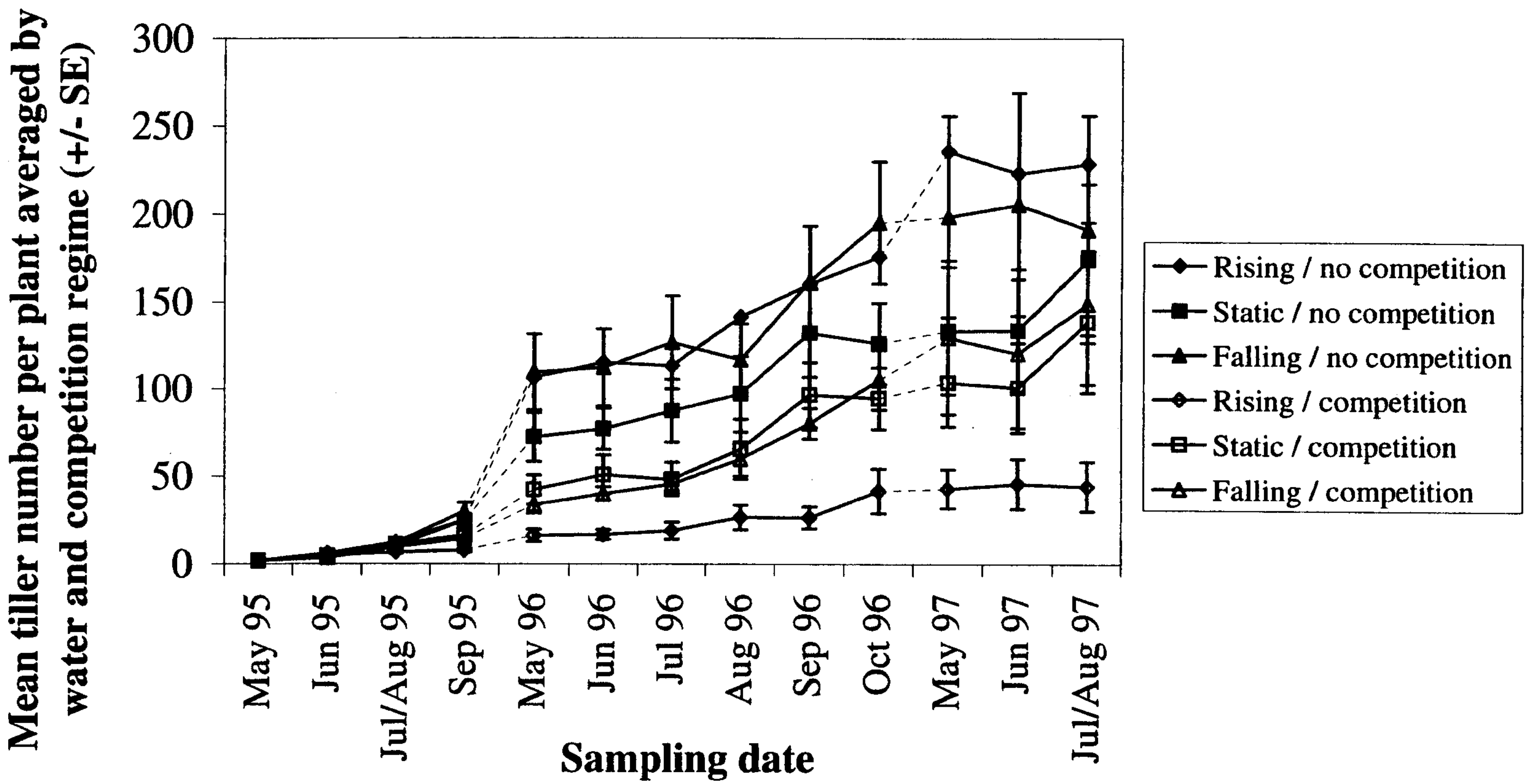

Figure 3.5. Mean tiller number for *Carex stricta* per plant averaged by water and competition regimes (± SE). Symbol shapes represent the rising (-◆-), static (-■-), and falling (-▲-) water regimes. Solid symbols represent data from plots without interspecific competition and open symbols represent data from plots with competition.

CHAPTER 4 (Tasks 8 & 9)

Effect of Soil Type and Water Depth on Survival and Growth of *Carex lacustris* and *Carex stricta*

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Submitted to: *Wetlands*

SUMMARY

This report presents the results of a study on the effect of soil type on the germination, growth, and survival of two wetland sedges, *Carex stricta* (tussock sedge) and *Carex lacustris* (lake sedge). The response of sedges to three soil types (wetland soil, clayey subsoil, and sandy subsoil) was compared to determine if wetland soil stimulated greater germination, growth, and survival than the other two soils. The use of wetland soil has been advocated to enhance growing conditions in created and restored basins where topsoil has been removed. The germination results are the subject of Task 8 and the growth and survival results are summarized in Task 9. The germination experiment on the efficacy of wetland soil to stimulate germination in *Carex* seeds (Task 8) was conducted on a flooded bench in a lighted heated greenhouse on the University of Minnesota St Paul campus. Replicate trays of all three soil types were given either moist or saturated conditions and germination response was measured for 9 weeks. Growth and survival experiments for Task 9 were conducted at the University of Minnesota Landscape Arboretum in Chanhassen, MN. Seedlings were planted in five-gallon containers filled with one of three soil types. Buckets were placed in four rows along an elevational gradient in the experimental wetlands to determine the affect of water availability on seedling survival and growth in different soil types. Three experimental wetlands were used, each with a different seasonal water fluctuation regime (falling, rising, static) to determine the effect of seasonal differences in water level on seedling survival and growth in different soil types. Experiments were followed for one growing season. Seeds of both species germinated best under saturated moisture conditions. Seeds also germinated better on sandy subsoil than on clayey subsoil or

wetland soil, but this was an artifact of humidity conditions that were not controlled in the study. We conclude that wetland soil did not increase germination rates for either *Carex* species used in the study. Planting location along the elevational gradient in each basin was consistently important in limiting or encouraging *C. stricta* survival and growth. Planting location and water regime were most influential in *C. lacustris* survival and growth. The survival and growth response of *C. lacustris* seedlings was lowest in the -22.5 cm elevation of the falling regime only, whereas *C. stricta* growth and survival were reduced in the lowest elevation of all water regimes. The greatest growth occurred at the end of the growing season for both species. In general the results of this portion of the study were similar to the results observed in Tasks 6 & 7. *C. stricta* seedlings had greater survival and growth in wetland soil or clayey subsoil than in sandy subsoil, with one exception. Mean longest leaf length was greater in wetland soil than the other two soils at the lowest elevation (-22.5 cm). Seedling growth was greatest for *C. lacustris* in wetland soil, regardless of elevation or water regime. Survival was not affected by soil type for *C. lacustris*. Results suggest that a soil characteristic other than water holding capacity is responsible for the differences observed in sedge growth between soil types. Nutrient or microbial differences may have played a role. Wetland soil does not appear to increase germination in *Carex* seeds. Water availability is more important in stimulating germination than soil type and may be improved by the use of humidity increasing plastic covers in the greenhouse and organic top-dressing in the field. The use of wetland soil to improve sedge growth is only cautiously recommended. Evidence from previous studies (Tasks 6 & 7) indicate that competition from weedy species, partiuclarly *Phalaris arundinacea* (reed canary grass) can reduce or eliminate the chances of successful sedge establishment. Weedy species such as *P. arundinacea* may be stimulated by application of nutrient-rich wetland soil or may be brought in with the donor soil. The use of wetland soil in wetland restorations and creations should be accompanied by an aggressive weed control program.

INTRODUCTION

Restoration and creation of wetlands typically involves altering water availability at a project site to reflood the wetland basin for all or some portion of the year. Drainage tiles and ditches are removed or broken, dikes may be built, and basins may be excavated to allow water to accumulate. The majority of restorations in the upper mid-west do not involve deliberate revegetation, although seeding of desired wetland species is sometimes done (Galatowitsch and van der Valk 1996a, NRC 1992). It is assumed that plants or seeds introduced or dispersed naturally to the area will eventually establish and that the (re) introduction of water to the site is the primary pre-condition for establishment (Hammer 1992, Hollands 1989). There are few published evaluations of revegetation success under these conditions. Galatowitsch and van der Valk (1996b) have concluded that native sedges and other members of sedge meadow wetland communities do not appear to recolonize naturally in restorations in southern Minnesota, northern Iowa, and eastern South and North Dakota. Dispersal limitations are a likely explanation for the lack of recruitment of these plants and potentially other species as well (van der Valk and Verhoeven 1988).

The use of soil from donor wetlands has been advocated as a way to introduce wetland plant propagules to restored or created sites (Hammer 1992; McKnight 1992, van der Valk, Pederson and Davis 1992). While obtaining the seedbank contained in the donor soil may be the primary goal, the potential for the introduction of nutrients, beneficial microorganisms, and desirable soil water-holding characteristics associated with donor soils has also been postulated (Galatowitsch and van der Valk 1994). Wetland creations and restorations that require soil excavation can result in the exposure of subsoil that is thought to be less hospitable for plant growth (Hammer 1992, Mitsch and Gosselink 1993). In addition, existing seedbanks (in the case of restorations) may be removed or buried with extensive landscaping activity. Organic material, which is often associated with beneficial nutrients, soil texture, and soil architecture, is highest in the upper soil layers removed in such excavation (Allen 1989).

Substantial financial and logistical issues are involved in the collection, transportation, storage and application of excavated wetland soil (often referred to as organic "muck"). In the face of these challenges, unanswered questions regarding the efficacy of donor soil reduce enthusiasm for implementation. Chief among these questions are the following: Does allowing the soil to dry before excavation or transportation negatively affect the seedbank or other desirable chemical and physical characteristics of the soil? How should donor soil be stored? What is the likelihood of introducing seedbank of undesirable species or pathogens? Most importantly, does donor soil improve the likelihood of successful establishment of desirable species?

Because seedbanks vary greatly between wetlands, as well as within wetlands (Galatowitsch and Biederman 1998, van der Valk, and Davis 1979), it is difficult to design a study that would answer these questions universally. However, what differentiates the straightforward introduction of seeds or other propagules to a created wetland and the introduction of wetland donor soil are the characteristics of the soil itself. At the most basic level, information is needed on the effects of soil texture, nutrients, and microorganisms on the germination, survival, and growth of desired wetland species. In the two studies described below, we investigated the differences in the germination (Task 8) and growth (Task 9) of two native wetland sedges on three soil types: surface soil from a former wetland basin, clayey subsoil, and sandy subsoil. Differences in soil nutrients and texture were analyzed and described in this study, but were not manipulated. We were particularly interested in the potential for interaction between soil texture and water holding capacity at different elevations along a water level gradient. Our study of sedge seedling growth under different moisture conditions on silty clay loam (MN/DOT 71789-72267-145: Tasks 6 & 7) indicates that water depth and fluctuation are important factors in sedge survival and growth. The present study duplicates the water depth and water fluctuation treatments used in Tasks 6 & 7 to allow comparison of results between the two studies.

The value of this study to MN/DOT includes: 1) documentation of differences (if any) in wetland sedge germination, survival, and growth on different soil types, 2) recommendations for use of particular soils in restorations and creations, 3) planting suggestions based upon tolerance limits observed for seedlings grown in different soils along a water depth (elevational) gradient, 4) planting suggestions based upon tolerance limits observed for seedlings grown in different soils under different water fluctuation regimes, and 5) suggestions for further investigation.

Study Species

We considered the germination and growth characteristics of *Carex lacustris* Willd. (lake sedge) and *Carex stricta* Lam. (tussock sedge). These species were chosen because they are abundant and widespread in Minnesota (Wheeler 1981) as well as in the upper mid-west of the

United States and the southern portion of Manitoba and Saskatchewan. Both species are perennials. *Carex stricta* has short underground rhizomes (stems) that produce tillers (above ground tillers) close to the parent plant, resulting in the characteristic tussock growth form of the species. *Carex lacustris* has long stout rhizomes that produce tillers up to a meter from the parent plant (Bernard 1990). Previous experiments with these species (MN/DOT 71789-72267-145: Tasks 1 - 7) provide baseline information on germination rates and favorable growth conditions.

Task 8: Germination study

METHODS

Soil Treatments and Analyses

The germination experiment was conducted in the Horticultural Sciences greenhouse on the St. Paul campus of the University of Minnesota from January 23 to March 27, 1997. Three soils were used as germination medium: surface soil from a former wetland basin at the University of Minnesota Landscape Arboretum in Chanhassen, Minnesota (wetland soil), clay subsoil collected from a depth of approximately four to six feet below the surface in the same former wetland basin (clayey subsoil), and washed sand brought into the site from a sand mine southwest of the Twin Cities metro (sandy subsoil). Five (approximately 50 g) samples of each soil type were collected by hand from the source and homogenized. Analyses of texture, total nitrogen, total organic carbon, pH, phosphorous, and potassium were made prior to the initiation of the study for each of the soils (Table 4.1). Analyses of soil chemistry were performed at the Research Analytical Laboratory, Department of Soil and Water and Climate, University of Minnesota. Textural analysis was done at MVTL Laboratories, Inc., New Ulm, MN.

Soil moisture (as a percent of soil dry weight) was determined at 1.5, 1.0, 0.03, and 0.01 (for sand only) MPa using a pressure plate for all three soil types. Soil moisture retention influences the ability of plant roots to extract water from the soil. The field capacity (0.01 MPa) and the permanent wilting point (1.5 MPa) define the range of available soil moisture (Killham 1994). In general, the larger the soil particles, the less tightly water is held. Soils with larger particles become depleted of available water from gravity, plant use, and evaporation more quickly than do those soils with smaller particles. Field capacity and permanent wilting point vary between soils and plant types, but can be estimated by observing the inflection points on a soil moisture release curve. The soil moisture release curves for the wetland soil and clayey subsoil are shown in Fig. 4.1 and for sand in Fig. 4.2. Pressure plate analyses were performed in the University of Minnesota's Soil Characterization Laboratory in the Department of Soil, Water, and Climate.

Experimental Design

Each soil type was placed into 24 20 cm x 20 cm square plastic pots with holes in the bottom (72 pots in total) to a depth of 4 cm. Soil-filled pots were placed on a rubber-lined bench flooded with tempered municipal tap water. Half of the trays were placed on risers such that the water level was 2 cm below the soil surface ("moist" treatment) while the other half were flooded to the soil surface ("saturated" treatment). Soil was allowed to absorb water for several days prior to the beginning of the germination experiment. The combination of three soil types and two water levels produced six water soil germination treatments. Twelve additional trays were filled with soil and placed under moist and saturated conditions, but were not seeded. Half of the trays were removed after four days and the other half after three weeks. Trays were weighed, dried, and weighed again to determine the percent water holding capacity for of each soil type. At the end of the nine-week experiment, twelve trays additional trays used in the experiment were weighed and percent water was calculated. Results are shown in Table 4. 2.

C. lacustris and *C. stricta* seeds were collected from the University of Minnesota's Cedar Creek Natural History Area (45° 24' N, 93° 12'W) from native fen and sedge meadow wetlands in July, 1996. The soils in these wetlands are Frigid Typic Endoqualls (wet mineral) and Frigid Typic Medisaprists (wet organic) (Grigal et al. 1974). Seeds of both species were stored dry at room temperature in the dark for 16 months until November 19, 1997 at which time they were placed into cold/moist storage. Seeds were stratified under these conditions for sixty days prior to the start of the germination experiment. Two hundred seeds of a single species were placed on the soil surface of each of thirty-six pots. Seeds were pressed into the soil to improve seed to soil contact, but seeds were not covered with soil as light is necessary for germination of these species (Johnson et al. 1965, Larson and Stearns 1990, Baskin et al. 1996). The greenhouse bench was illuminated with two large 1000-watt metal halide lamps with an intensity of approximately 1500-1800 ueinsteins m^{-2} s^{-1} at bench level. Light was provided on a 14 / 10 hour day/night schedule. The temperature in the greenhouse was maintained at 24/13°C day/night, which approximates the temperature that stimulated greatest germination of these species in previous germination experiments (Tasks 1-5). Humidity was not controlled. Pots were checked for germination every two to three days and germinated seeds were removed. Germination was defined by the emergence of a tiller. The experiment was terminated after 9 weeks on March 27, 1998.

Percent germination was arcsine square-root transformed prior to analysis. An analysis of variance (ANOVA) was run on the transformed germination values as well as on the number of days elapsed until first germination was observed. The alpha value for significance was set at 0.05. All results presented are significant unless otherwise stated. Statistical Analysis Software (SAS) version 6.12 was used to run the analyses (SAS 1996).

RESULTS

C. stricta and *C. lacustris* seeds germinated on all soil types and under both moist and saturated water conditions. Overall percent germination (± standard error) for *C. stricta* and *C. lacustris* was 51.2 ± 3.2 and 3.8 ± 0.45, respectively. The average number of days to first germination (± standard error) was 5 days ± 0.3 for *C. stricta* and 18 days ± 2.3 for *C. lacustris.*

C. stricta had highest germination rates under saturated conditions. Seeds on saturated soil germinated at a rate of 51% ± 4.5. Seeds on moist soil germinated at a rate of 43% ± 4.7. Percent germination was not affected by soil type. The number of days to first germination was not affected by water regime or soil type.

Unlike *C. stricta, C. lacustris* germination was not affected by water availability. Instead, germination rates varied by soil type. Percent germination was highest on sandy subsoil (6% ± 0.8), with next highest percent germination on clayey subsoil (3% ± 0.7) and the lowest germination on wetland soil (2% ± 0.4). Germination was significantly different between sandy subsoil and wetland soil. Sandy subsoil did not differ from clayey subsoil and clayey subsoil did not differ from wetland soil. The number of days to first germination was not affected by soil type or water availability.

DISCUSSION

Germination rates observed in this study are consistent with rates obtained from the larger germination study (Tasks 1-5) for the age of the seeds and the conditions under which they were germinated. *C. stricta* germination in the previous study did not differ between saturated and moist germination conditions as they did in this study. The disparity between studies is likely the result of humidity differences during germination between the two studies. Humidity was relatively high in the petri dishes used for germination in Tasks 1-5, whereas humidity was low in this greenhouse study, making water availability from below more important constraint. The pattern observed in the greenhouse is more likely to reflect germination conditions in the field.

In general *C. lacustris* has relatively low rates of germination (Budelsky and Galatowitsch, in press). Dormancy of some type, most likely due in part to hard seed coats, prevents otherwise viable *C. lacustris* seeds from germinating. Viability analyses of germinated seeds were not performed on these seeds, however, based on previous experiments (Tasks 1-5) it is likely that viability was substantially higher than the 5 % germination observed in this study. The differential germination of *C. lacustris* seeds on different soil types is intriguing, but is likely due to an artifact of this study and not the result of differences in the soils types. In this study, sandy subsoil was associated with the greatest *C. lacustris* germination. The surface of the sandy subsoil was expected to be drier than the surface of the clayey subsoil and wetland soil, particularly under moist conditions, because the degree of capillary rise in soil with large particles is lower than soil with small particles. Although the percent water (relative to soil weight) for sandy subsoil was less than the other two soils (Table 4.2), the surface of the sandy subsoil in pots was clearly wetter under the moist and saturated water conditions than the surface of either of the clayey subsoil or the wetland soil. The disparity is due to three factors associated with the experiment. First, the rate of evaporation in the heated greenhouse was high as a result of low humidity and strong air currents from the fans used for circulation. Secondly, there was poor soil to water contact as a result of two few and too small holes in the bottom of the pots used. Finally, the clayey subsoil and wetland soil lost pore structure when the soils were homogenized and spread into the pots, further reducing the water holding and wicking characteristics of the soils. Thus, the heavier soils dried out from the top and water was drawn up slowly, if at all, through the 4 cm deep soil to replace lost water at the surface. Differences in water availability, not soil type, are most likely the factor that favored germination on sandy soil.

The results of this experiment are informative, nonetheless. It is likely that the germination conditions observed in the greenhouse study are more similar to what would occur in a field setting than those in petri dishes (Tasks 1-5). Because both *C. stricta* and *C. lacustris* require light for germination, seeds cannot be buried in the soil to take advantage of water deeper in the soil strata. In the absence of humidity-holding ground cover, surface drying of soils is likely to a greater problem for germination in the field than the choice of soil type. This is particularly the case if a donor wetland soil is brought to the site and spread over subsoil. Poor soil to soil contact and compaction of the donor soil from heavy equipment could produce results similar to those observed in this greenhouse study. The higher organic content of the wetland soil used in this study (Table 4. 1) did not demonstrate superior water-holding capacity (relative to the subsoils) although greater organic content, as well as undisturbed soil structure might have improved results. Other characteristics associated with wetland soil such as higher nutrient content also did not stimulate greater germination under the given moisture conditions.

CONCLUSIONS

The results indicate that water availability is of greater importance for the germination of *C. stricta* and *C. lacustris* than soil type. Whereas wetland soil has characteristics that may be beneficial for seedlings, once germinated, this study does not indicate that the use of donor wetland soil with the characteristics used in this study is warranted for stimulating sedge germination. Soil with a higher organic content than that used in this study may be more beneficial for its water holding capabilities. However, compaction of soil during collection, storage, and application in a restored or created wetland has the potential to reduce or eliminate the beneficial water holding characteristics. Because soil and air moisture appear to be important in stimulating germination in both species, the use of organic mulch as a top-dressing in restored or created wetlands should be considered, either alone or in combination with donor soil, to maintain humid moist conditions for germination.

Task 9: Growth study

METHODS

Study Site

The study took place at the University of Minnesota's Landscape Arboretum in Chanhassen, Carver county, Minnesota, USA (44°51'45"N, 93°36'00"W). The experimental basins used for the study are located in the shallow depression of a former wetland basin. The soil is a black silty clay loam with hydric soil features in the dark gray clay sub-horizon. Two clay dikes were built through the center of the basin prior to this study, creating four experimental basins. The basins are approximately 0.1 hectares (1/4 acre) in size. Each basin has a flat rectangular bottom and four shallow slopes with a 20:1 elevational gradient.

The basins are equipped with water-control structures that allow independent water level manipulation. All four basins are fed through underground irrigation pipes from an electrically driven well pump. Flow control valves permit independent filling of each basin. Water can be drained by raising or lowering a flexible pipe which is located in the center of each basin. Shore-based control of drain pipes is facilitated by a pole and pulley system.

The experiment was run from June to November, 1996 for *Carex stricta* and from May to November, 1997 for *Carex lacustris.*

Soil Treatments and Analyses

The growth experiments were established in 72 five-gallon plastic buckets for *C. stricta* (1996) and for *C. lacustris* (1997). New buckets and soil were used in 1997. The buckets were 33 cm in diameter and 35 cm tall. Prior to use, the bottom of each bucket was sawed off and approximately 20 3/8 inch holes were drilled in the sides to facilitate water flow. Twenty-four buckets were placed in each of three experimental basins along the south-facing slope. Buckets were set 10 cm deep into the basin substrate and then filled to the top with one of three soil types: wetland soil, clay rich subsoil (clayey subsoil), or washed sand (sandy subsoil). Each bucket contained approximately 0.02 m^3 of experimental soil. The wetland soil was collected within 100 meters of the experimental basins in the shallow depression of a former wetland basin. The clayey subsoil was also excavated near the experimental basins from a trench four to six feet deep. The sandy subsoil was hauled to the site.

Five (approximately 50 g) samples of each soil type were collected by hand from the source and homogenized. Analyses of texture, total nitrogen, total organic carbon, pH, phosphorous, and potassium were made prior to the initiation of the study for each of the soils (Table 4.4.1). At the end of the first growing season, soil from each of the buckets was collected and analyses run for the following soil characteristics: potassium, calcium, magnesium, sodium, hydrogen, action exchange capacity (C.E.C.) and percent base saturation (Table 4.3). Values differed by soil, but were not affected by either of the treatment variables (water regime and elevation); therefore the data are not elaborated upon in the results. Analyses of soil chemistry were performed at the Research Analytical Laboratory, Department of Soil and Water and Climate, University of Minnesota. Textural analysis was done at MVTL Laboratories, Inc., New Ulm, MN.

Soil moisture was calculated as a percentage of soil dry weight at 1.5, 1.0, 0.03, and 0.01 (for sandy subsoil only) MPa using a pressure plate for all three soil types. Soil moisture retention influences the ability of plant roots to extract water from the soil. The field capacity (0.01 MPa) and the permanent wilting point (1.5 MPa) define the range of available soil moisture (Killham 1994). In general, the larger the soil particles, the less tightly water is held. Soils with larger particles become depleted of available water from gravity, plant use, and evaporation more quickly than do those soils with smaller particles. Field capacity and permanent wilting point vary between soils and plant types, but can be estimated by observing the inflection points on a soil moisture release curve. The soil moisture release curves for the wetland soil and clayey subsoil are shown in Fig. 4.1 and for sandy subsoil in Fig. 4.2. Pressure plate analyses were performed in the University of Minnesota's Soil Characterization Laboratory in the Department of Soil, Water, and Climate.

Elevation and Water Regime Treatments

Four elevational treatments were established along the slope in each basin. Six buckets (two replicates of each soil type) were placed in each of four rows corresponding to the four elevational treatments. The four rows were identified by the height of the soil surface in the buckets above or below the mean seasonal water level: +22.5 cm, +7.5 cm, -7.5 cm, and -22.5 cm. The lowest elevation was associated with the greatest water depth. The elevational treatments were designed to evaluate the effect of water availability (and depth) on seedling survival and growth.

A different water regime was established in each of the three basins to assess the effect of water-level changes on seedling establishment. The water level in the static water regime was maintained at the mean level throughout the growing season. The soil surface was exposed in the upper two rows and inundated in the lower two rows for the duration of the study. The maximum water depth for the static regime was 22.5 cm, which occurred at the lowest elevation. The rising water regime was established such that the water level was set at the lowest elevation at the beginning of the growing season. The water level was raised five vertical centimeters every two weeks until the upper row of buckets was inundated by the end of the growing season. The third basin was assigned a falling water regime. All rows were inundated at the beginning of the growing season and were gradually exposed at a rate of 5 vertical cm per two weeks. The rising and falling water regimes experienced a similar range of inundation depths, but at different times during the growing season. The maximum seasonal water depth for the rising and falling basins was 45 cm, which occurred at the lowest row of buckets. Water-level changes were initiated mid-May and ended mid-October both years.

Seedlings of both species were germinated from seed collected in sedge meadow wetlands at the Cedar Creek Natural History Area in east-central Minnesota, USA (45°24'N, 93°12'W). Seedlings were approximately 7-10 weeks old. The mean longest leaf length for *C. stricta* seedlings was 29 cm ± 5 cm and the mean tiller (tiller) height per plant for *C. lacustris* was 57 cm ± 7 cm at the time the seedlings were transplanted. Three seedlings were planted in each bucket. Weeds were removed from the buckets on a weekly basis. Seedlings that disappeared or died from transplant shock were replaced during the first week after planting.

Seedlings were measured monthly for survival, tiller height, and tiller number. The spreading growth habit of *C. lacustris* made it impossible to identify the parent plant to which individual tillers belonged two months post-planting, therefore the total number of tillers per bucket were averaged by the number of living plants. Data for both species are presented per plant per bucket.

Above and below ground biomass was collected in November for both species. Soil was cleaned from the roots and rhizomes with a high-pressure hose. *C. lacustris* below ground biomass was subdivided into roots and rhizomes. Biomass was dried at 65° C for a minimum of 48 hours in a drying oven.

Water depth was monitored regularly in each row and water levels adjusted accordingly. Ground water wells were used to assess the depth to water table when water levels dropped below the soil surface.

A full factorial design was used in which all combinations of all treatment levels were run. Percent survival values were arcsine square-root transformed prior to analysis. Tiller numbers and heights were log transformed to standardize variance over time before a repeated measures analysis of variance was run on each of the data sets. The alpha value for significance was set at 0.01. Statistical Analysis Software (SAS) version 6.12 was used to run the analyses (SAS 1996).

RESULTS - *C. stricta*

Effect of Water Regime and Elevation on Plant Parameters

Survivorship - *C. stricta* seedlings had the greatest percent survival in the upper three treatment elevations used in the study (Fig. 4.3). In general, survival was highest at the top elevation (+22.5 cm) with a reduction in survival occurring at each lower elevation. The lowest elevation (-22.5 cm), corresponding with deepest water, had the highest mortality. Survival in the lowest elevation (23%) was significantly lower than survival at the next highest elevation (74%). Water regime (fluctuating water levels) did not affect survival of *C. stricta* seedlings.

Biomass - Mirroring the trend observed for survivorship, mean above ground biomass was greatest in the upper three elevations and least in the lowest elevation (Fig. 4.4). Above ground biomass did not differ significantly between the upper three elevations, but was substantially less in the deepest water elevation. Mean aboveground biomass was also affected by the presence of ducks perching on the buckets where the seedlings were planted. The buckets that were occasionally visited by ducks had plants with a higher above ground biomass ($x = 5.6$g;

sterr=0.38, n=16) than plants in buckets without ducks (x = 2.7g, sterr=1.7, n=56). There was no statistical correlation between any of the experimental treatments (water regime, elevation, or soil type) and the use of particular buckets by ducks. Water regime did not affect above ground biomass.

Below ground biomass was affected by a unique combination of water regime and planting location along the elevational gradient (Fig. 4.5). In the falling water regime, mean below ground biomass was greatest at the uppermost elevation (+22.5 cm), with reduced biomass occurring at each of the lower elevations. The upper elevation of the falling water regime also had greater biomass than that collected at the same elevation in the rising and static water regimes. In the rising and static water regimes, the effects of elevation on below ground biomass were small and were not significant.

Tiller number - The number of tillers (above ground tillers) produced by *C. stricta* seedlings over the growing season was affected by planting location along the elevational gradient (Fig. 4.6). The lowest elevation had consistently fewer tillers than the other three elevations in all basins. Whereas tiller number increased over the growing season for seedlings planted at the upper three elevations, tiller number in the lowest elevation remained unchanged over time. The number of tillers was not affected by water regime.

Longest leaf - Elevation, together with soil type, was important in explaining differences in the mean *C. stricta* longest leaf length (Fig. 4.7). For seedlings planted in wetland soil, mean longest leaf length did not change over the course of the growing season and differences associated with planting location along the elevational gradient were not significant. However, for seedlings planted in either clayey subsoil or sandy subsoil, elevation did significantly influence longest leaf length. Within one (sandy subsoil) or two (clayey subsoil) months after planting, seedlings at the lowest elevation showed substantial reduction in height. In contrast, seedlings planted in the same soil type in the upper three elevations remained constant, neither increasing nor decreasing over the growing season. There was no difference in seedling heights in the upper three elevations when compared across soil types. Seedlings in the lowest elevation that were planted in wetland soil were significantly taller than seedlings planted in either clayey subsoil or sandy subsoil at the same elevation. Water regime was not important in explaining differences in longest leaf lengths.

Rhizome number - Mean rhizome number was influenced by planting location along the elevational gradient (Fig. 4.8). Seedlings in the lowest elevation had significantly fewer rhizomes than did seedlings planted at any of the upper three elevations. Rhizome number was highest at the -7.5 cm elevation. Mean rhizome number was not affected by water regime.

Effect of Soil Type on Plant Parameters

Survivorship - *C. stricta* seedling survival was influenced by soil type. The highest percent survival was observed for seedlings planted in wetland soil (Fig. 4.9). Seedling survival in wetland soil (83%) was significantly greater than survival in sandy subsoil (60%) but did not differ substantially from seedlings planted in clayey subsoil (69%).

Biomass - *C. stricta* seedlings had greater above ground and below ground biomass when planted in wetland soil than in sandy subsoil (Fig. 4.10). However, biomass (both above and below ground) did not differ significantly between wetland soil and clayey subsoil. Above ground sedge biomass was greater in clayey subsoil than in sandy subsoil, but there was no difference between the two soil types for below ground biomass.

Tiller number - Soil type was important in influencing the number of tillers produced by C. stricta seedlings (Fig. 4.11). The number of tillers was consistently higher when seedlings were planted in wetland soil than in sandy subsoil. There was no notable difference in tiller number between plants grown in wetland soil and those grown in clayey subsoil across the growing season, with the exception of the July sampling date. Tiller number did not differ between seedlings planted in clayey subsoil and those planted in sandy subsoil except for the July sampling date.

Longest leaf - As described previously (Fig. 4.7), soil type and elevation together affected the average longest leaf length such that the plants in clayey subsoil and sandy subsoil were shorter at the lowest elevation than those at the upper three elevations. Seedlings planted in wetland soil were not affected by elevation.

Rhizome number - The mean rhizome number for *C. stricta* was greatest when seedlings were planted in wetland soil or clayey subsoil (Fig. 4.12). Although there was no substantial difference in rhizome numbers between wetland soil and clayey subsoil or between clayey subsoil and sandy subsoil, plants grown in wetland soil had greater rhizome numbers than did plants grown in sandy subsoil.

RESULTS - *C. lacustris*

The number of rhizomes did not vary with water regime, elevation, or soil type and therefore is not mentioned below.

Effect of Water Regime and Elevation on Plant Parameters

Survivorship - Mean percent survival for *C. lacustris* seedlings at the end of the growing season depended upon both the water regime and the elevation at which the seedlings were planted (Fig. 4.13). In the falling water regime, survival was lowest at the lowest (-22.5 cm) elevation. Seeding survival in the upper three elevations did not differ substantially. The low survival rate in the lowest elevation of the falling water regime was also significantly less than survival at the same elevation in the rising and static water regimes. Seedling survival was not affected by elevation in the rising and static water regimes.

Biomass - Above-ground biomass for *C. lacustris* was also correlated with water regime and elevation. The plants had a unique response across elevations in each water regime (Fig. 4.14). In the falling water level regime, above-ground biomass was lowest at the bottom elevation (corresponding to deeper water) and highest at the uppermost elevation. In the rising water regime, tiller biomass was the inverse of that described above for the falling regime. The greatest biomass occurred at the lowest elevation and least biomass was observed at the uppermost elevation. And in the static water regime, plants fared equally poorly at the uppermost and lowermost elevations with the greatest biomass at the middle two elevations.

Although below ground biomass did not vary across water regimes, the location along the elevational gradient did result in different average rhizome biomass (Fig. 4.15). *C. lacustris* rhizome biomass was greatest at the +7.5 cm (second highest) elevation and lowest at the -22.5 cm (bottom-most) elevation. Root biomass did not vary significantly between water regimes or across elevations.

Rhizome length - Mean, maximum, and total rhizome lengths were greater in the middle two elevations (+7.5 and -7.5 cm) elevations than at the lowest elevation (Fig. 4.16). Rhizome lengths in the at the uppermost elevation were not different than those of the lowest elevation, nor were they different than those of the middle two elevations. Rhizome length was not affected by water regime.

Tiller number - The water regime and elevation together affected the number of tillers produced (Fig. 4.17). The effect appeared near the end of the growing season as seedlings went through a period of increased tiller production. In the falling water regime, seedlings planted in the lowest elevation had fewer tillers than seedlings at the upper three elevations. In the rising water regime, tiller production was lowest at the uppermost elevation, and in the static water regime, the difference in tiller number between elevations was not significant.

Mean tiller height - Mean height was shortest in the lowest elevation of the falling water regime at the end of the growing season (Fig. 4.18). In contrast, tillers in the rising and static regimes were not significantly different across elevation. Mean tiller height in the lowest elevation of the falling water regime was also lower than the mean tiller height in the lowest elevation of the other two basins.

Effect of Soil Type on Plant Parameters

Survivorship - In this study, differences in soil type did not affect survival for *C. lacustris*.

Biomass - The type of soil in which seedlings were planted had a significant effect on plant biomass (Fig. 4.19). Above-ground tillers and below-ground rhizomes had the greatest biomass when *C. lacustris* was planted in wetland soil. Biomass was uniformly low when plants were grown in clayey subsoil or sandy subsoil. Root biomass was highest when plants were grown in wetland soil or sand. Clayey subsoil was associated with the lowest root biomass.

Rhizome length - The mean rhizome length of plants grown in wetland soil or clayey subsoil was greater than that of plants grown in sandy subsoil (Fig. 4.20). However, the mean maximum and the mean total rhizome lengths were greatest in wetland soil, followed by clayey subsoil, and finally sandy subsoil.

Tiller number - The mean number of tillers per plant per bucket was affected by soil type near the end of the growing season (Fig. 4.21). While the mean tiller number for plants grown in clayey subsoil and sandy subsoil did not differ, seedlings grown in wetland soil had a significantly greater number of tillers when compared to the other two soils.

Mean tiller height - Soil type did not affect *C. lacustris* tiller heights in this study.

DISCUSSION

Two summary observations can be made on the basis of these results. First, the two species responded somewhat differently to the experimental treatments. Planting location along the elevational gradient greatly affected *C. stricta* seedling survival and growth, whereas water fluctuation regime did not. *C. lacustris* survival and growth were affected by the combination of water regime and elevation. Second, soil type affected the growth of both species in a similar way. The use of wetland soil stimulated greater sedge growth than did either clayey or sandy subsoil.

Results obtained in this study were remarkably consistent across survival and growth parameters for each species. *C. stricta* seedlings were most sensitive to inundation in deep water. All plant parameters measured indicate that seedlings fared most poorly at the lowest elevation (-22.5 cm below mean seasonal water depth) in all basins, despite differences in absolute water depth, inundation duration, and seasonal timing of inundation between water regimes. Seedling survival and growth in the next highest elevation (-7.5 cm) were consistently greater than at the lowest elevation, which suggests that -7.5 cm is the maximum elevation at which 7-10 week old *C. stricta* seedlings should be planted.

C. lacustris seedlings were influenced by the combination of planting location and water regime. Like *C. stricta*, *C. lacustris* seedlings were sensitive to deep water at the lowest elevation (-22.5 cm), but this response was seen only in the falling water regime. This indicates that *C. lacustris* seedlings have a greater tolerance for deep water than do *C. stricta* seedlings of the same age. Although the mean initial height for *C. lacustris* seedlings (57 cm ± 7 cm) was greater than *C. stricta* seedlings (29 cm ± 5 cm) at planting, *C. lacustris* seedlings experienced transplant shock such that their mean height one month after planting was 22 cm (± 7 cm) (see Fig. 4.18). *C. stricta* mean heights did not decrease (or increase) during this period (Fig. 4.7). Thus a height difference that might have conveyed an advantage in deeper water cannot be evoked as an explanation for survival and growth differences between the two species.

Despite the greater tolerance for deep water observed for *C. lacustris*, this species showed a reduced growth response at the uppermost elevation of the rising water regime (Fig. 4.14 & 4.17), indicating that this species is limited at +22.5 cm above mean seasonal water level.

In general, the results observed in this container study are similar to the results obtained for the same species in the first season of an experiment established in plots along a similar elevational gradient in wetland soil only (Tasks 6 and 7). Growth parameters for *C. lacustris* were affected by water regime and those for *C. stricta* were not. In the previous study, *C. stricta* and *C. lacustris* survival was also tied to water regime. In the current study, only *C. lacustris* survival was influenced by water regime (in combination with elevation). For all cases in which water regime was important, the greatest mortality and poorest growth occurred in the falling water regime (during the first growing season). Elevation was tied to survival for both species in both the plot study and the current study with the lowest survival and growth parameters occurring at the lowest elevation.

The similarity of results between studies serves mainly to set the stage for the soil aspect of the current study. Overall, both *C. stricta* and *C. lacustris* seedlings had higher survival and grew better in wetland soil or clayey subsoil than in sandy subsoil (all measures except mean longest leaf). The greatest disparity between growth in different soil types occurred at the lowest elevation. Growth (mean longest leaf) was greatest when seedlings were planted in wetland soil versus clayey subsoil or sand. It is unclear why the seedlings did more poorly in sandy subsoil and clayey subsoil, particularly at the lowest elevations.

This study indicates that differences in soil type can influence sedge seedling survival and growth. The reason for the different response to wetland soil versus the other subsoil soils was not investigated in this study, but several observations can be made. It does not appear that differences in water holding capacity between the soils (see Figures 4.1 & 4.2) can explain differences in sedge seedling growth and survival. First, water availability was not limiting for either species at the lowest elevation, yet seedling height was greatest in the lowest elevation for *C. stricta* when seedlings were planted in wetland soil. Reduced seedling growth at the upper elevation seen for *C. lacustris* was likely due to limited water availability, but it was not associated with soil type. This suggests that at +22.5 cm above mean seasonal water level, neither species experienced an advantage in soil moisture-holding capacity from the use of wetland soil. Such an advantage cannot be ruled out, however, for wetland soil applied at a higher elevation or for a wetland soil that contained greater amounts of organic matter. These observations also suggest that nutrient or microbial differences in the soils may have influenced seedling growth rates and thus survival. Seedlings able to grow rapidly as a consequence of higher nutrient availability could explain the differences in seedling height for *C. stricta* at the lowest elevation in different soils. Taller seedlings are better able to withstand inundation.

Although the results of this study on different soil types suggest that wetland soil is an advantageous medium in which to establish sedge seedlings, further study is warranted. If indeed greater nutrient content is the reason for increased growth in the sedge seedlings, it is also probable that it would have a similar effect on other species. In this study, all plants except sedges were removed from the study containers as they appeared. Caution and careful consideration should be taken prior to instigating nutrient enrichment studies without appropriate control for the effect such nutrients would have on undesirable weedy species. The results of the study reported in Tasks 6 & 7 indicate that competition from weeds, particularly reed canary grass (*Phalaris arundinacea*), can greatly reduce the establishment of sedge plantings. The negative influence of competition from reed canary grass cannot be overstated. Reed canary grass is more likely to invade successfully under high nutrient conditions (Galatowitsch et al. 1999).

CONCLUSIONS and RECOMMENDATIONS

The response of seedlings to water regime and elevational effects on sedge growth in the first year must be applied with some caution given that the growth patterns observed in the first growing season of the plot study (Task 6 & 7) were not indicative of optimal growth in subsequent years. Thus the recommendations offered here are somewhat based upon the later years of the plot study as well as the results of seedling growth and survival on different soils obtained from this study.

This study indicates that seedlings of both species have the greatest survival and growth patterns when planted in wetland soil. The difference in plant growth between wetland soil and clayey subsoil and sandy subsoil is greatest in the lowest elevation, suggesting that the use of wetland soil will slightly increase the depth at which *C. stricta* seedlings are planted and can be expected to live and grow. Where wetland soil is not available, *C. stricta* seedlings should not be planted at greater than 10 cm below the mean seasonal water level. Conversely, if the mean annual water level cannot be estimated, the use of wetland soil may enhance the survival and growth of *C. stricta* seedlings at depths up to -22.5 cm below mean annual water level. In addition, if water fluctuation patterns cannot be estimated it is better to err on the dry side by planting *C. stricta* at a slightly higher elevation.

As a rule of thumb, seedlings of both species should not be planted at elevations that would result in inundation of greater than 50 % of their height for more than a month during the first growing season. This recommendation is calculated from the inundation regime experienced by seedlings at the -7.5 cm elevation in this study. *C. lacustris* has a higher tolerance for deep water, but shows a decreased growth response at the upper elevation (+22.5 cm) under a rising or static water regime during the first growing season. This suggests that *C. lacustris* seedlings can be planted slightly deeper than *C. stricta* seedlings. Although *C. lacustris* seedlings do not grow as well at +22.5 cm above mean seasonal water level than at lower, wetter elevations, in the first year, survival at the upper elevation is not reduced. As *C. lacustris* plants mature, they have the ability to migrate toward more favorable water regimes through directional production of long underground rhizomes.

Table 4.1. Summary characteristics of soil used in the study. Samples homogenized prior to analysis.

	Texture	Total N %	T.O.C %	pH	P (ppm)	K (ppm)
wetland soil	silty-clay-loam	0.46	6.28	7.3	1	150
clayey subsoil	clay-loam	0.09	2.04	7.3	1	251
sandy subsoil	sand	<0.01	0.19	7.4	2	12

Table 4.2. Water weight calculated as a percentage of soil dry weight from pots used in the greenhouse germination study.

Soil Type	Moisture Condition	Percent Water Weight		
		4 days	3 weeks	9 weeks
wetland soil	saturated	65	58	64
	moist	58	47	55
clayey subsoil	saturated	43	38	41
	moist	31	36	31
sandy subsoil	saturated	17	21	20
	moist	17	15	18

Table 4.3. Summary analyses for soil samples collected at the end of the 1996 growing season (n= 12). Values are shown in milliequivalents of the total cation exchange capacity (C.E.C.).

	K		Ca		Mg		Na		H		C.E.C		% base saturation	
	x	stdev	x	stdev	x	stdev	x	stdev	x	stdev	x	stdev	x	stdev
wetland soil	0.29	0.02	18.88	2.29	4.53	0.67	0.19	0.04	12.11	3.46	35.99	4.40	66.87	6.68
clayey subsoil	0.58	0.09	23.45	5.64	8.89	1.37	0.26	0.07	2.91	3.96	36.09	7.52	92.41	8.56
sandy subsoil	0.04	0.00	7.61	0.95	1.26	0.23	0.06	0.02	4.32	6.23	12.79	6.29	81.45	26.38

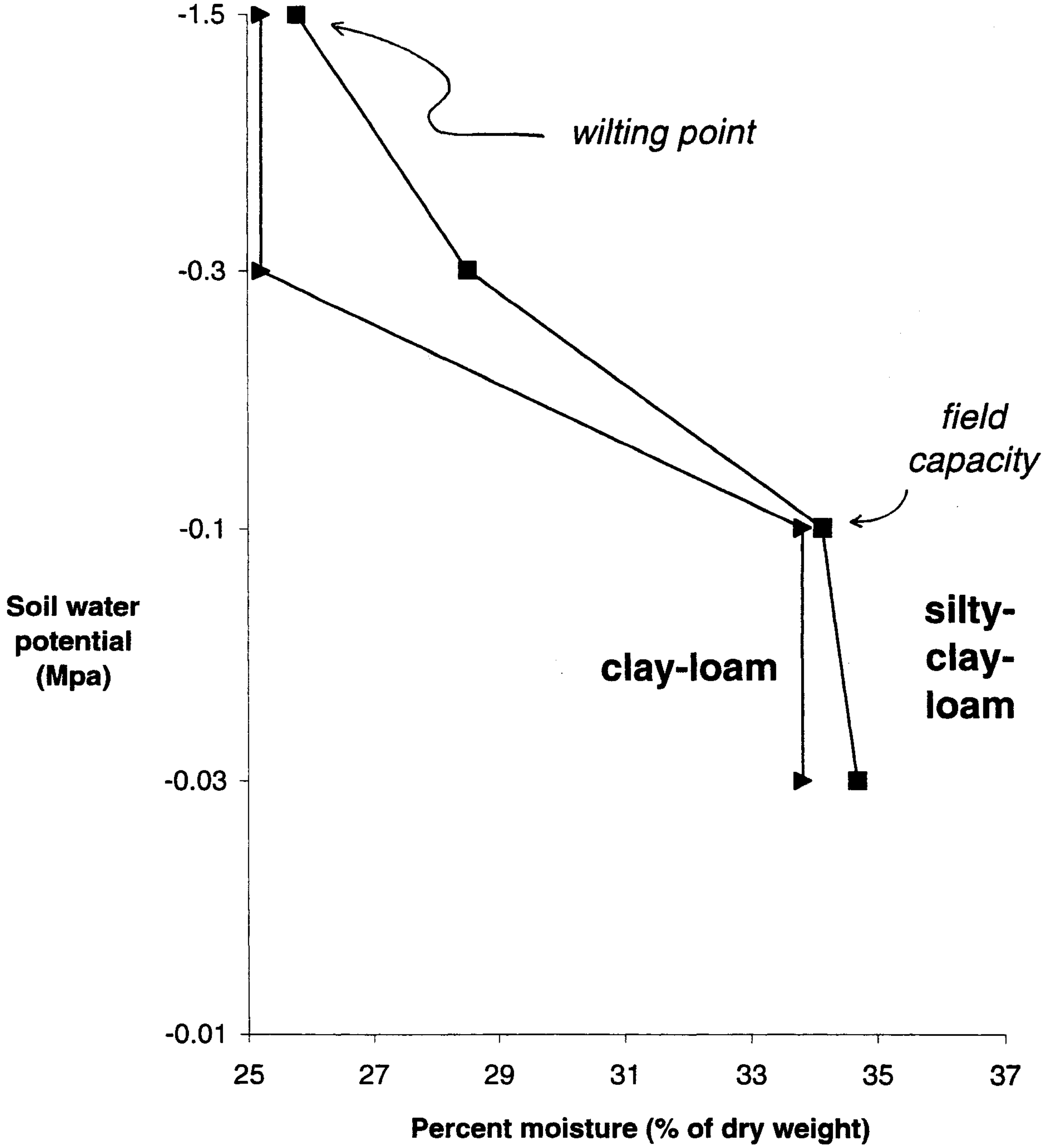

Figure 4.1. Moisture release curves for silty-clay-loam (wetland soil) and clay-loam(clayey subsoil).

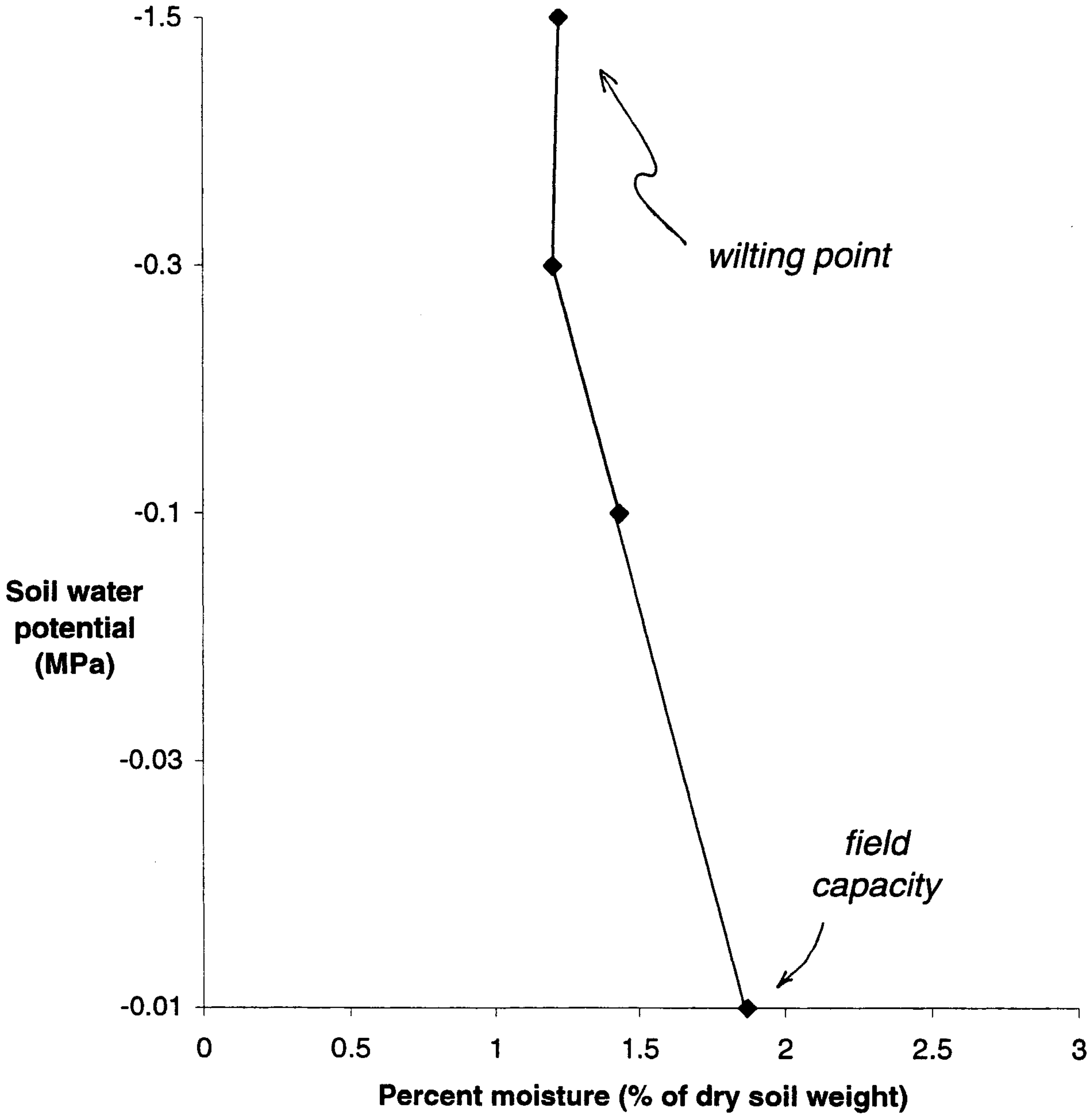

Figure 4.2. Moisture release curve for sandy subsoil.

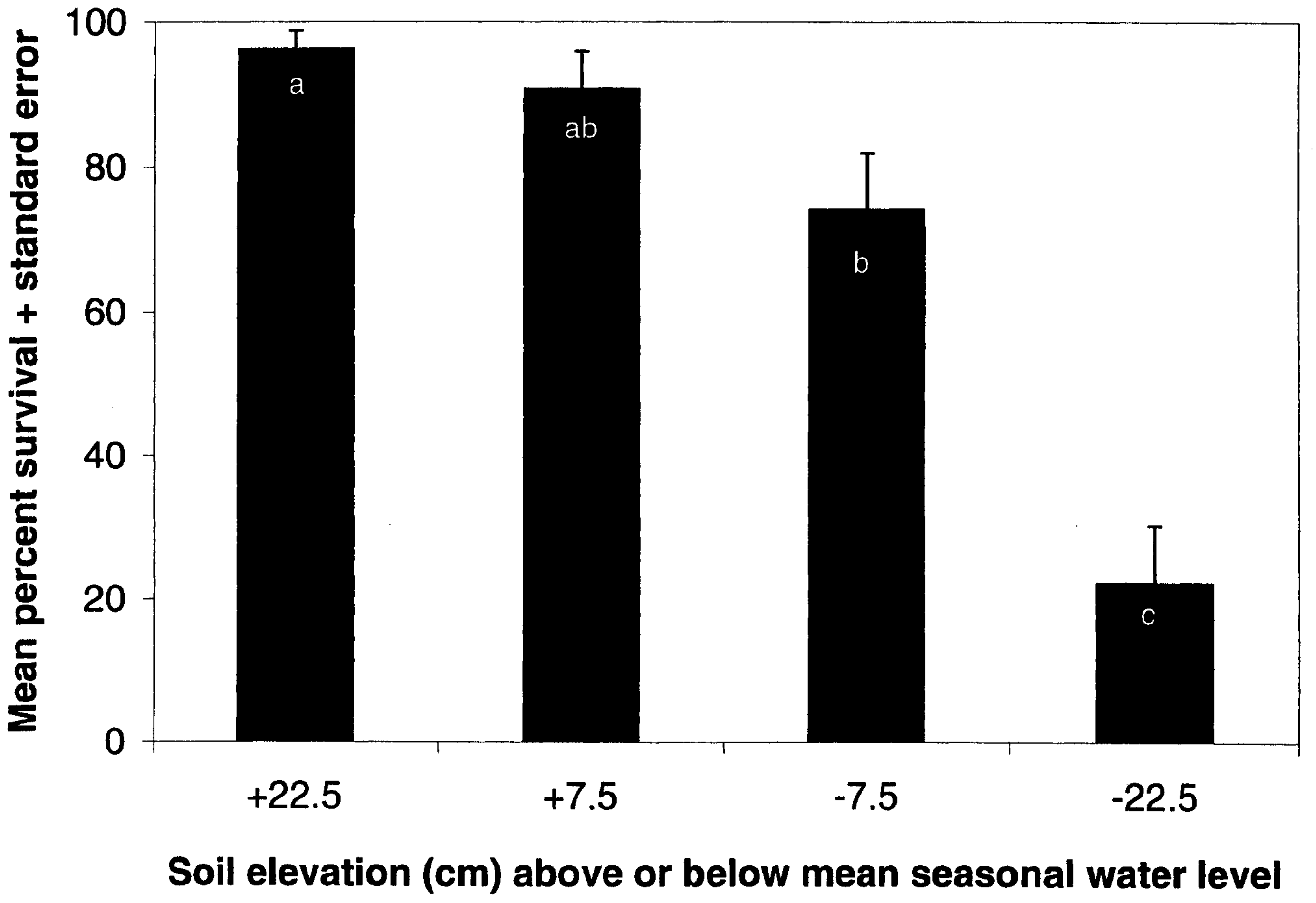

Figure 4.3. Mean percent survival at the end of the first growing season for *C. stricta* seedlings averaged by elevation across all water regimes and soil types. Means with the same letter are not significantly different (alpha = 0.01).

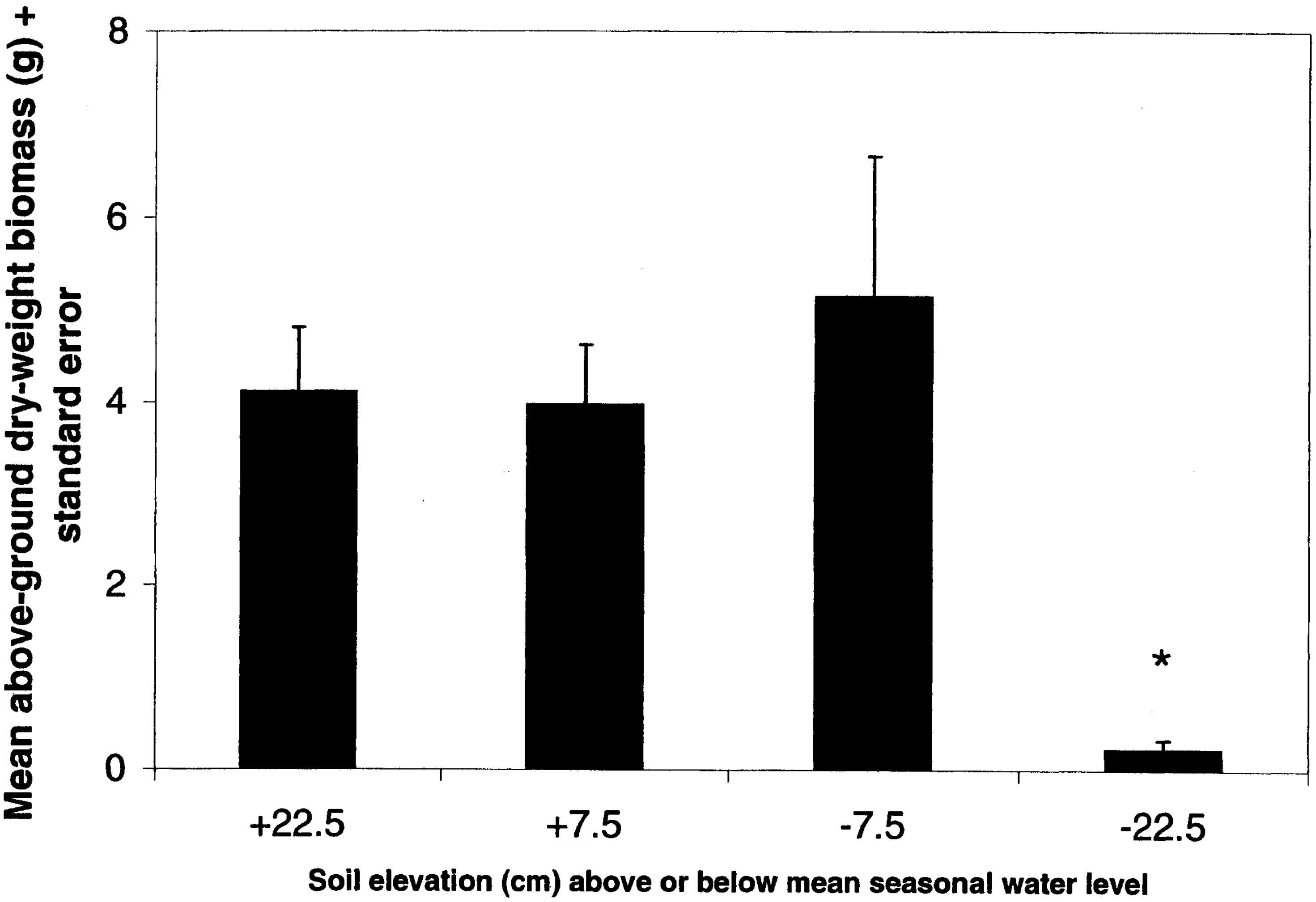

Figure 4.4. Mean above-ground dry-weight biomass (g) for *C. stricta* averaged by elevation across all water regimes and soil types. The asterix indicates a mean that is significantly different (alpha = 0.01).

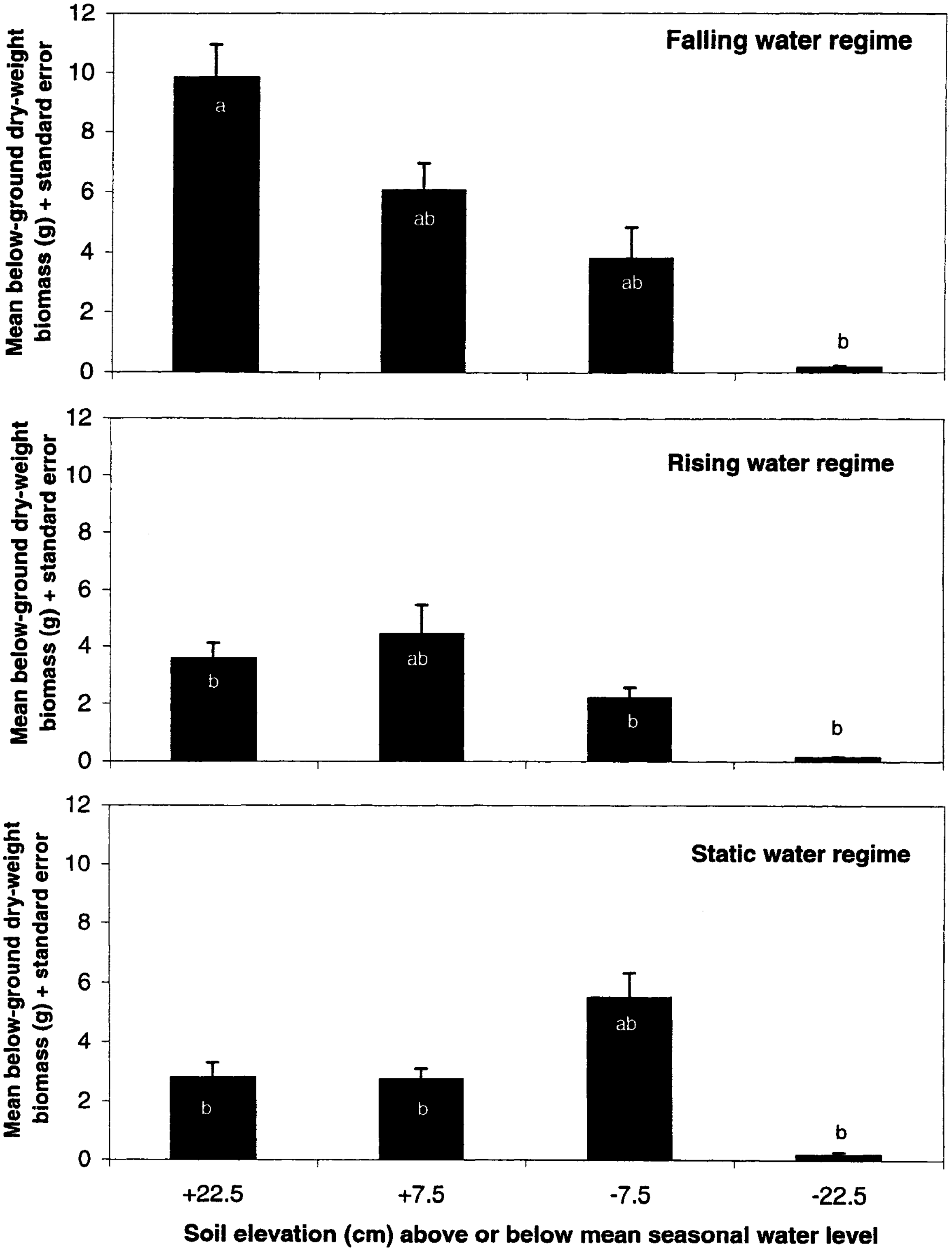

Figure 4.5. Mean below-ground dry-weight biomass (g) for *C. stricta* averaged by water regime and elevation across all soil types. Means with the same letter are not significantly different (alpha = 0.01). Comparison of means can be made across all water regimes and elevations.

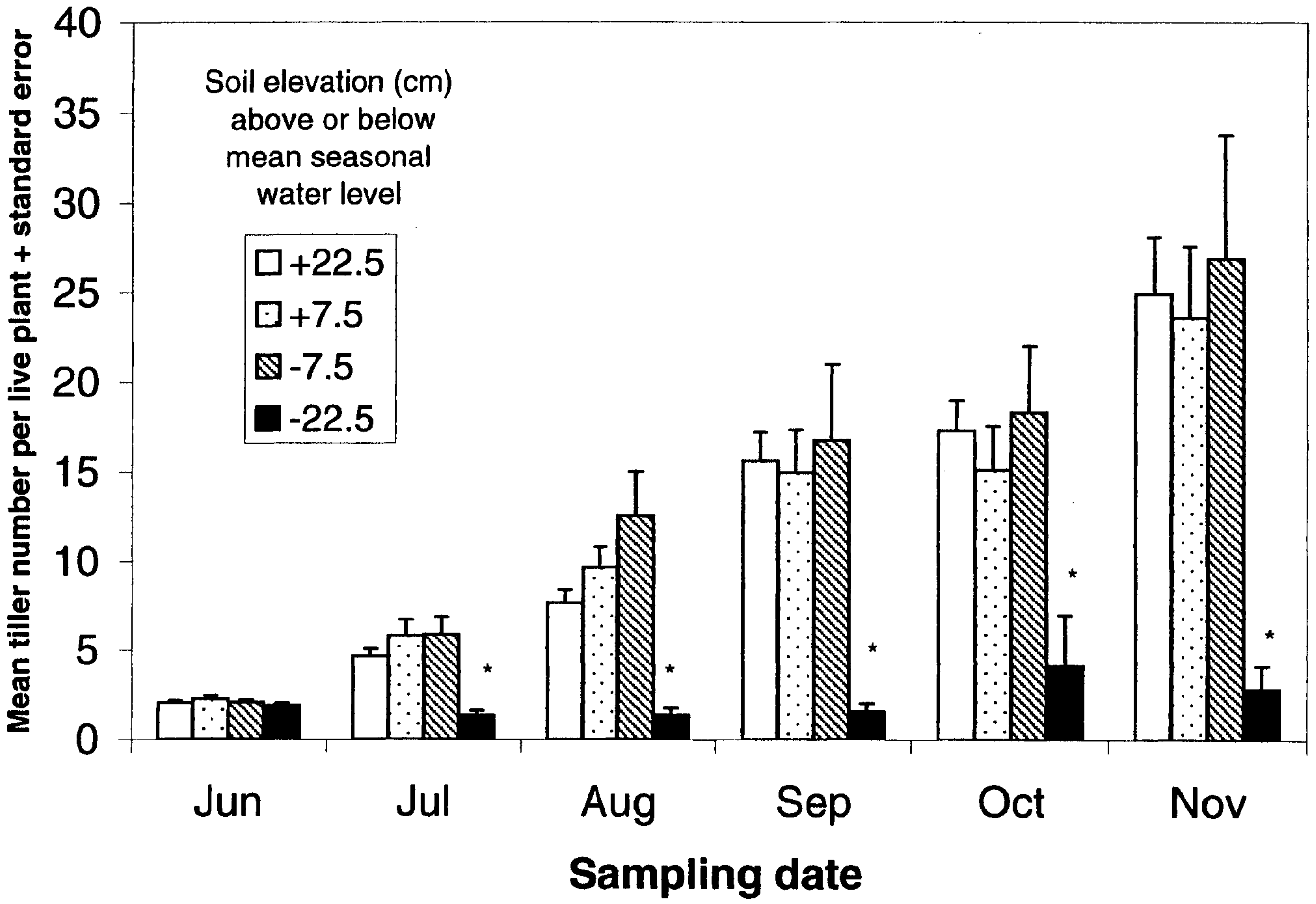

Figure 4.6. Mean tiller number per live plant per container for *C. stricta* averaged by elevation and sampling date across all water regimes and soil types. Means with an asterix are significantly different than other means within the same sampling date (alpha = 0.01).

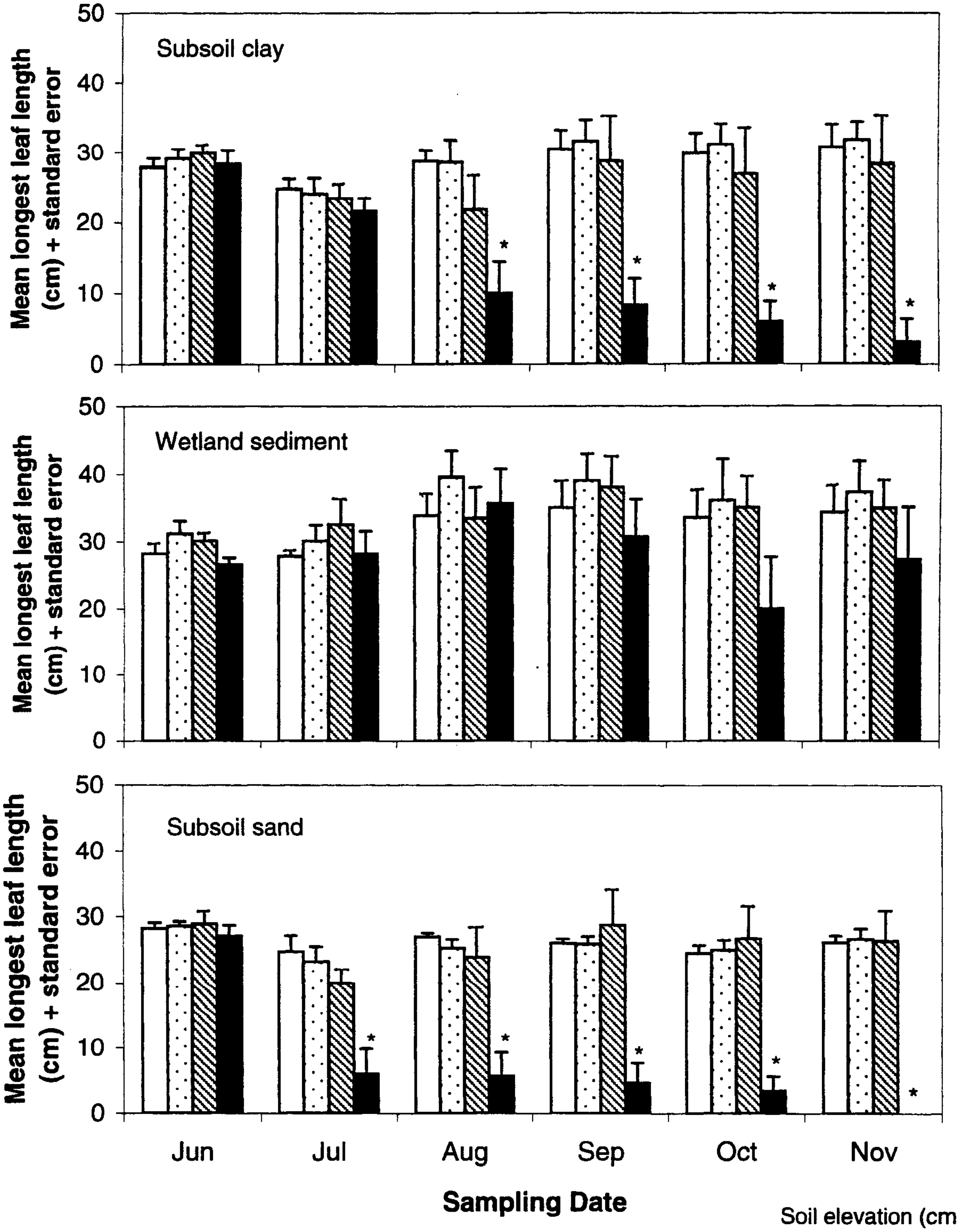

Figure 4.7. Mean longest leaf length per plant per container for *C. stricta* averaged by soil type, elevation, and sampling date across all water regimes. Patterned bars represent the soil elevation above or below mean seasonal water level. Means with an asterix are significantly different than other means within sampling dates (alpha = 0.01). Comparison of means can be made across all soil types and elevations.

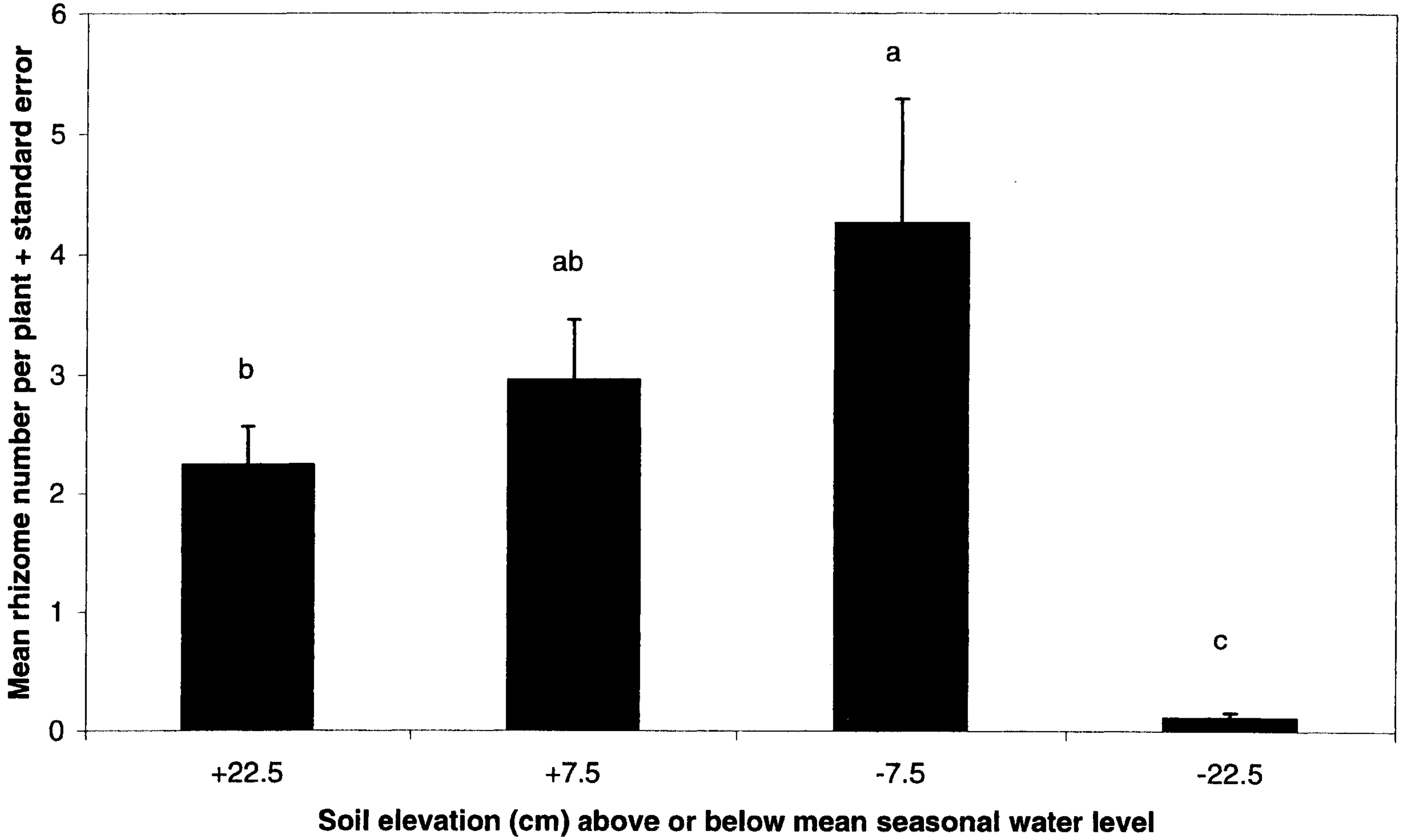

Figure 4.8. Mean rhizome number per plant per container for *C. stricta* averaged by soil elevation across all water regimes and soil types. Means with the same letter are not significantly different (alpha = 0.01).

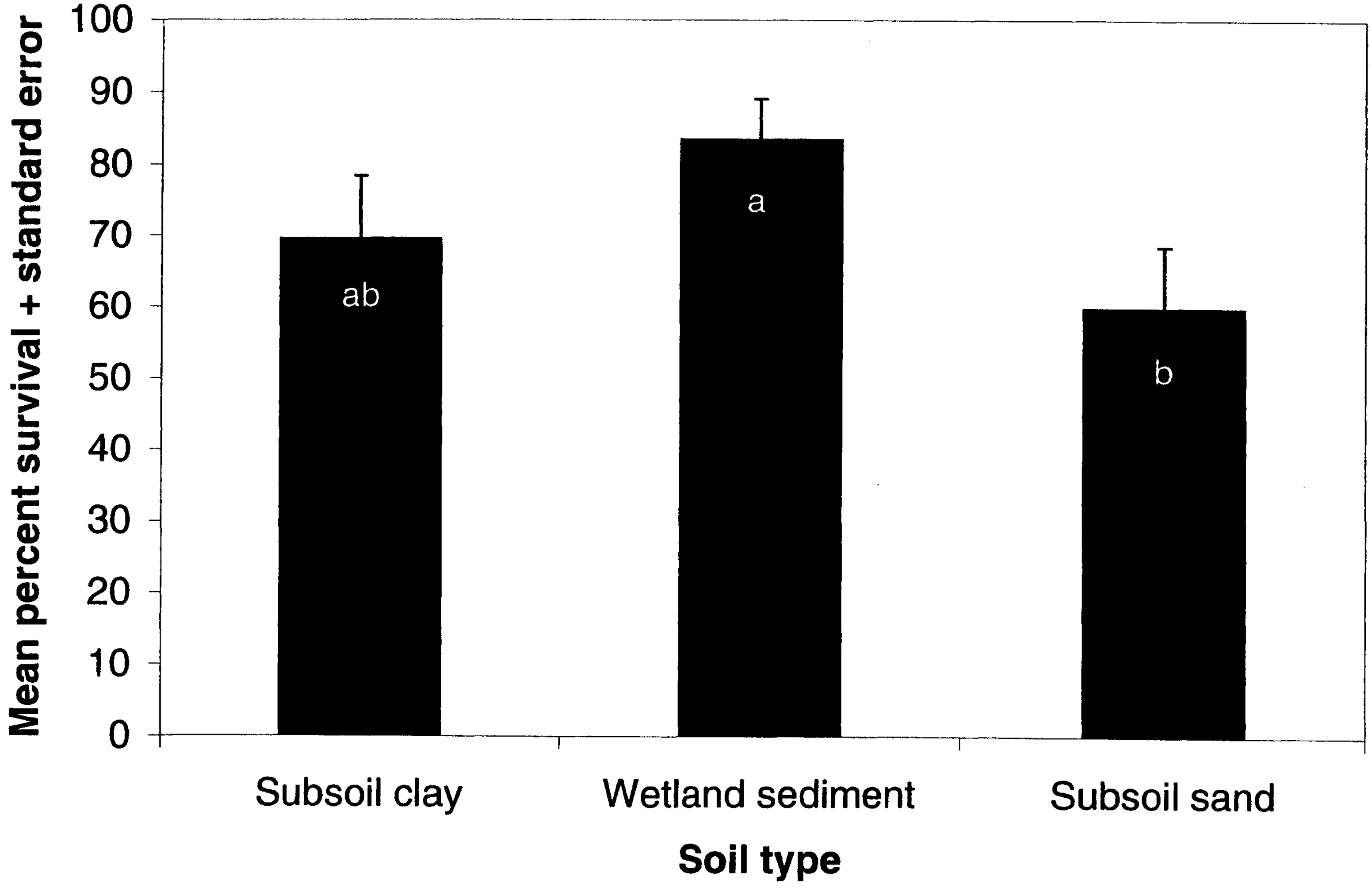

Figure 4.9. Mean percent survival at the end of the first growing season for *C. stricta* seedlings averaged by soil type across all water regimes and elevations. Means with the same letter are not significantly different (alpha = 0.01).

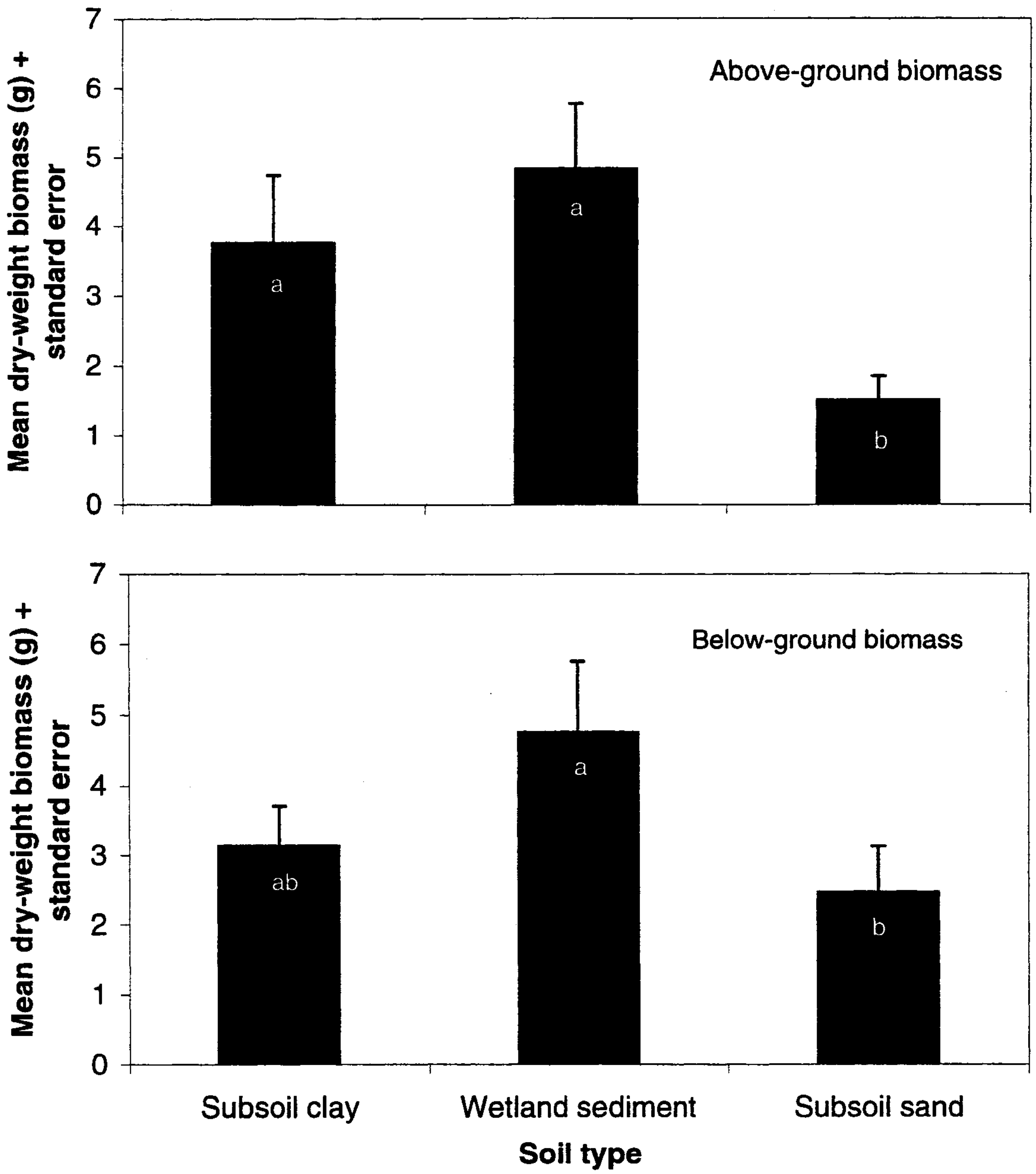

Figure 4.10. Mean above- and below-ground dry-weight biomass (g) for *C. stricta* averaged by soil type across all water regimes and elevations. Means with the same letters are not significantly different (alpha = 0.01). Means can be compared within above-ground or below-ground biomass.

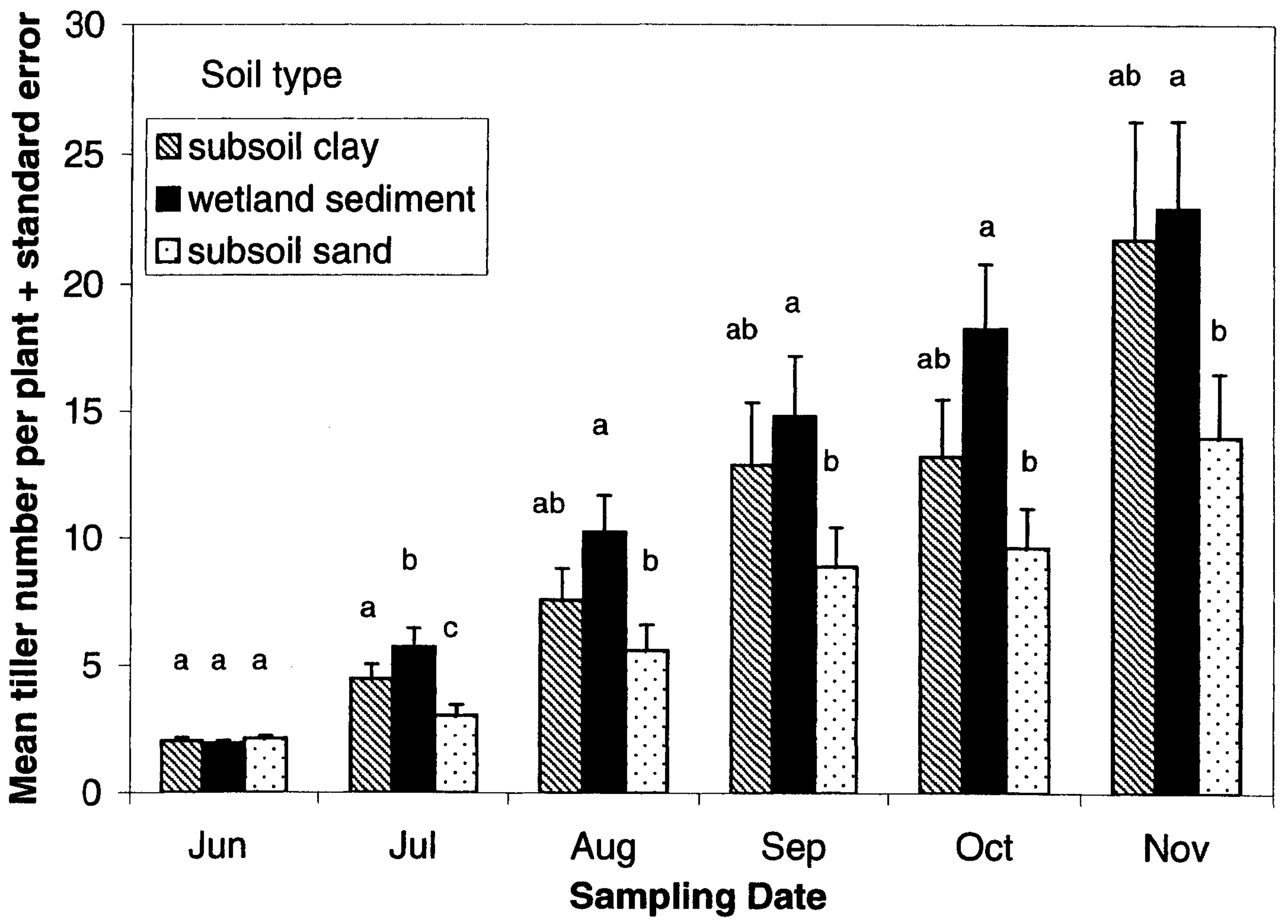

Figure 4.11. Mean tiller number per plant per container for *C. stricta* averaged by soil type and sampling date across all water regimes and elevations. Means with the same letter are not significantly different (alpha = 0.01). Means should be compared only within a sampling date.

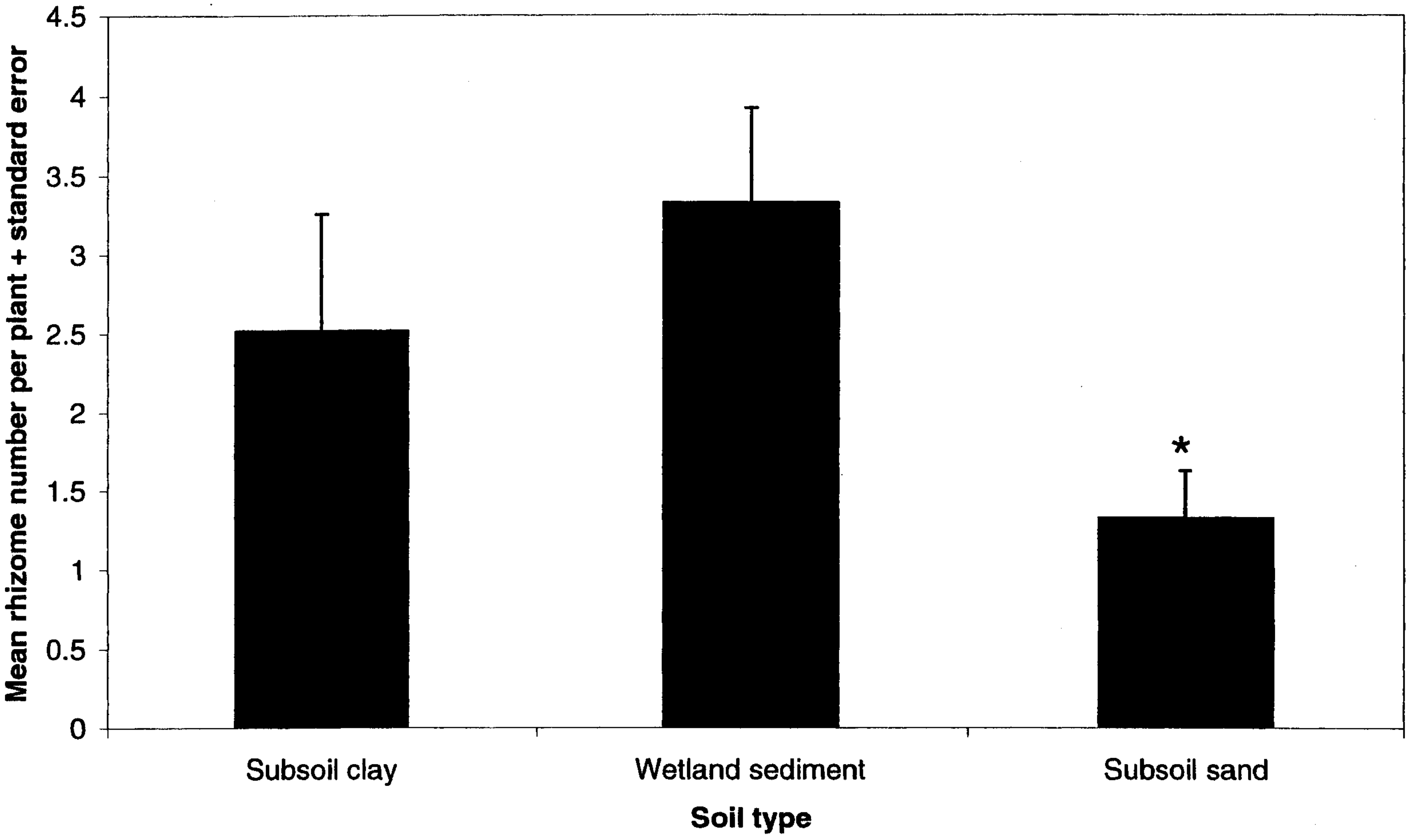

Figure 4.12. Mean rhizome number per plant per container for *C. stricta* averaged by soil type across all water regimes and elevations. The asterix indicates a mean that is significantly different at alpha = 0.01.

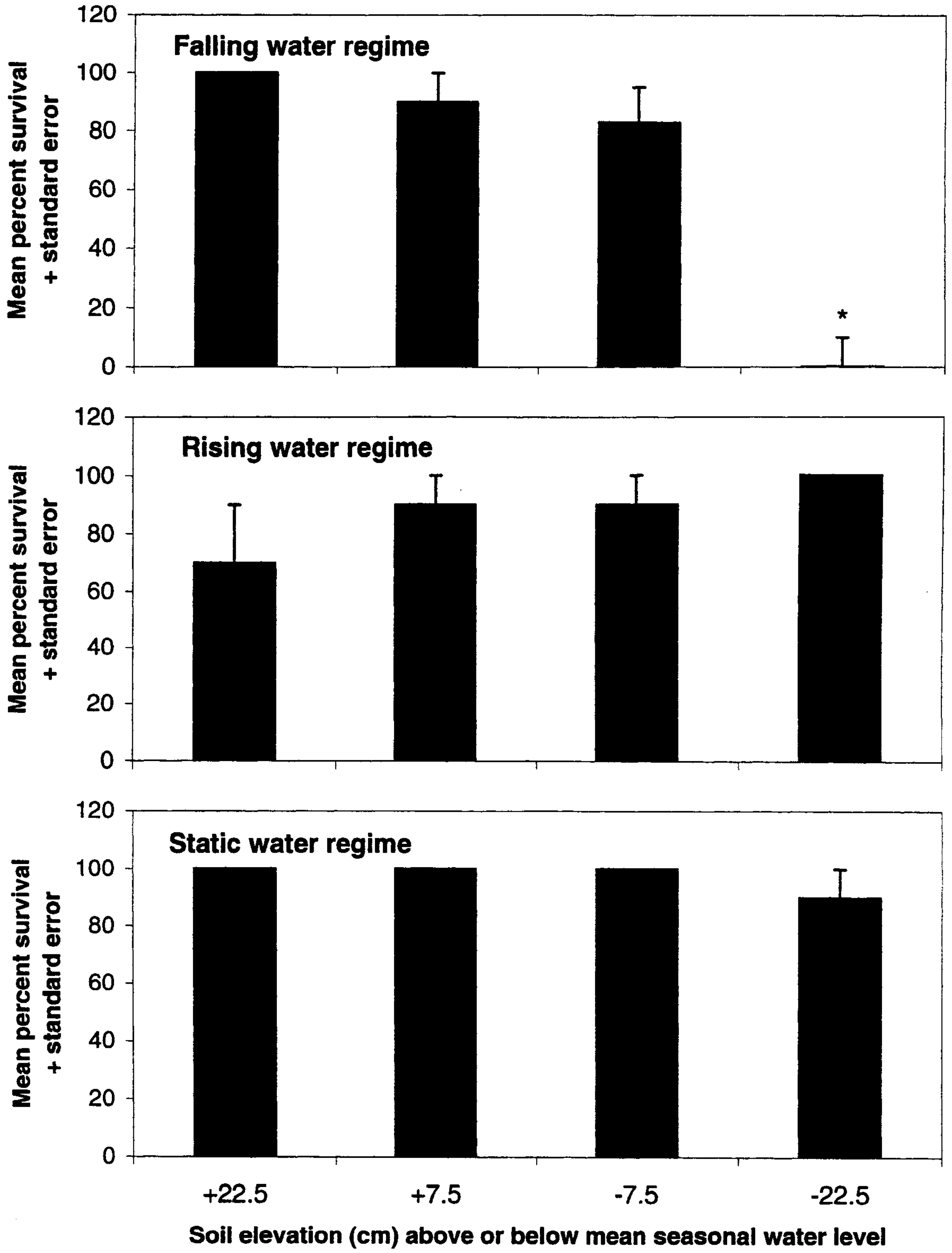

Figure 4.13. Mean percent survival at the end of the first growing season for *C. lacustris* seedlings averaged by elevation across all water regimes and soil types. The asterix indicates a mean that is significantly different (alpha = 0.01).

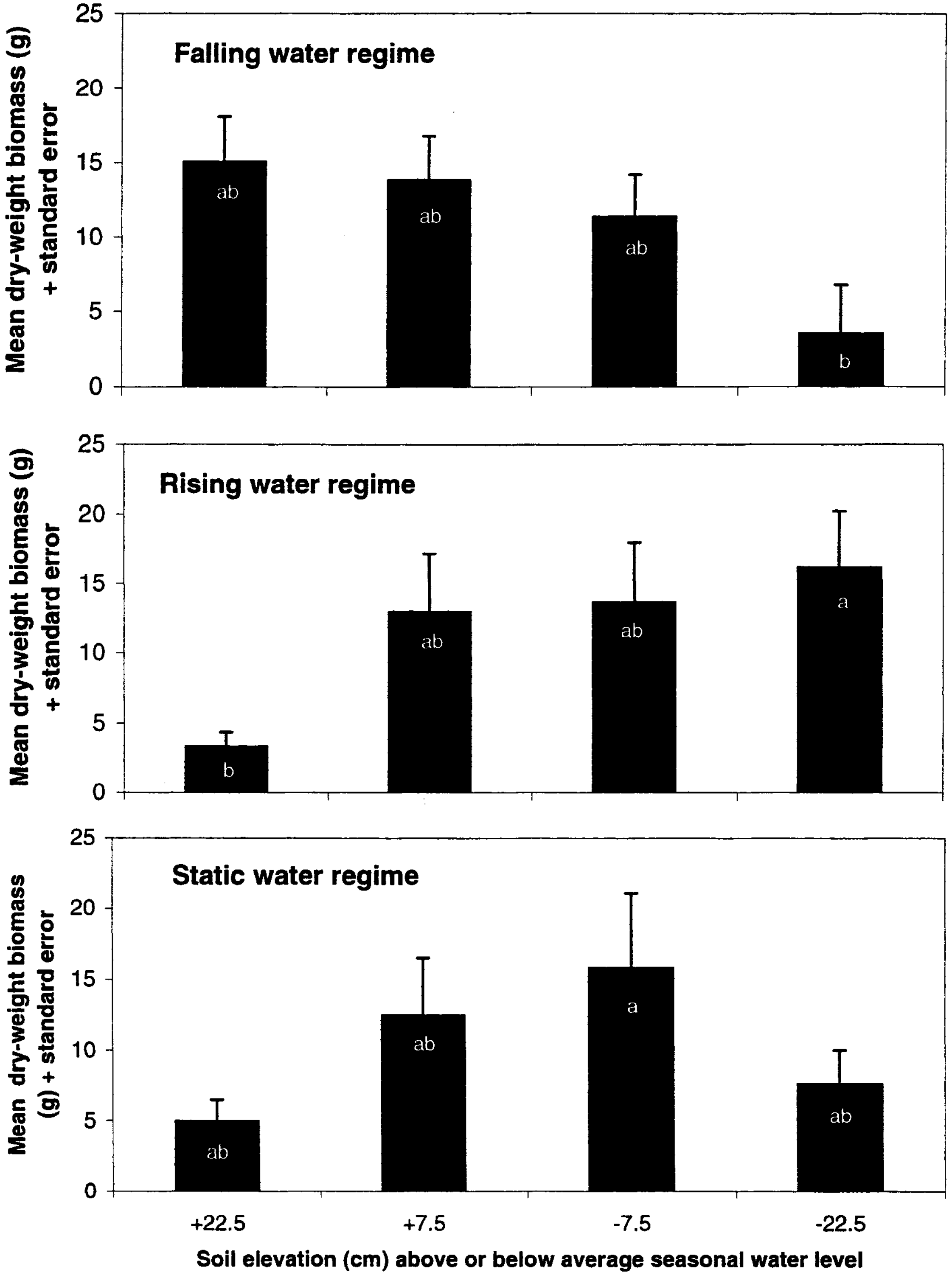

Figure 4.14. Mean above-ground dry-weight biomass for *C. lacustris* averaged by elevation and water regime across all soil types. Means with the same letter are not significantly (alpha = 0.01). Means can be compared across water regime and elevation.

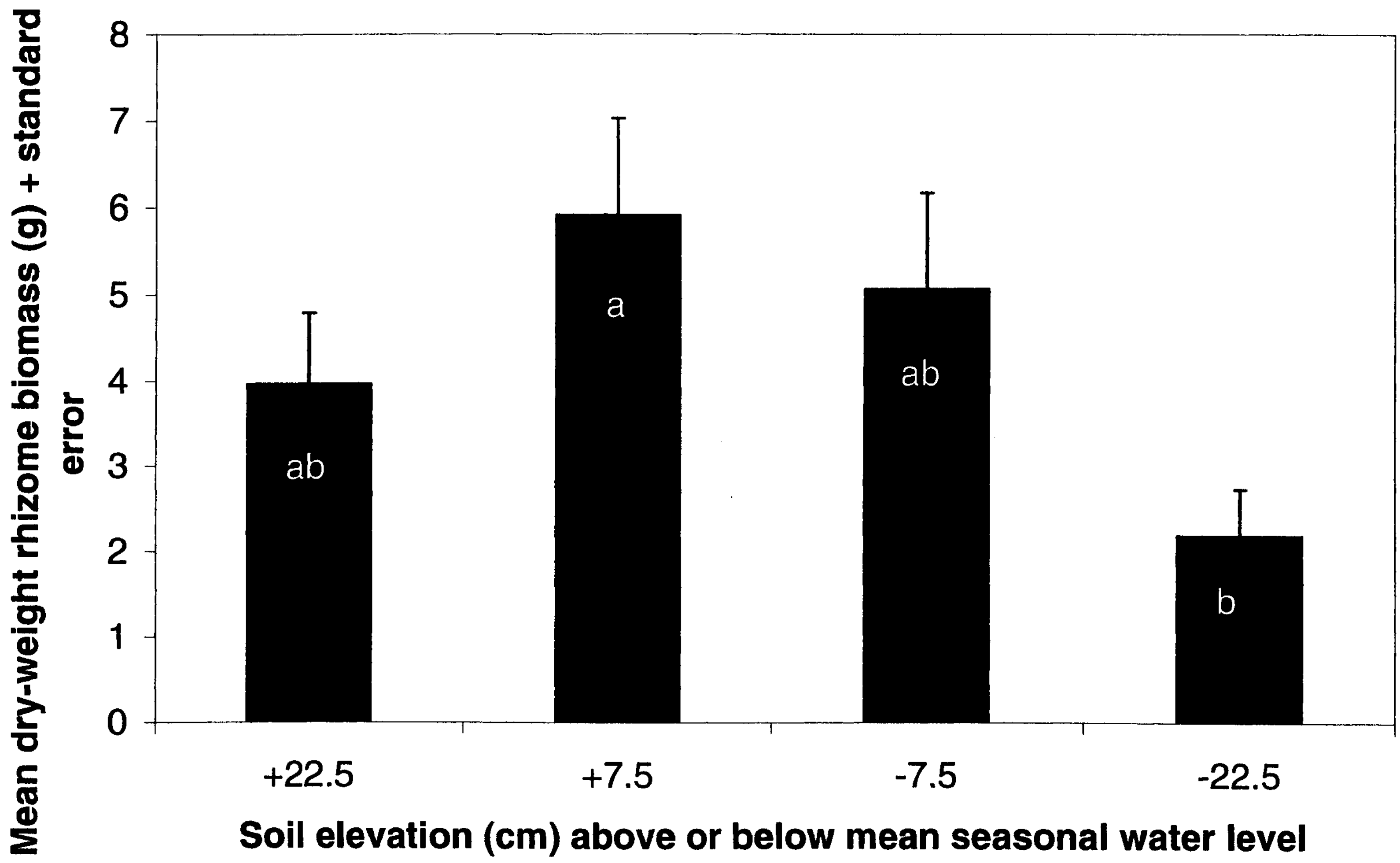

Figure 4.15. Mean dry-weight rhizome biomass for *C. lacustris* averaged by elevation across all water regimes and soil types. Means with the same letter are not significantly different (alpha = 0.01).

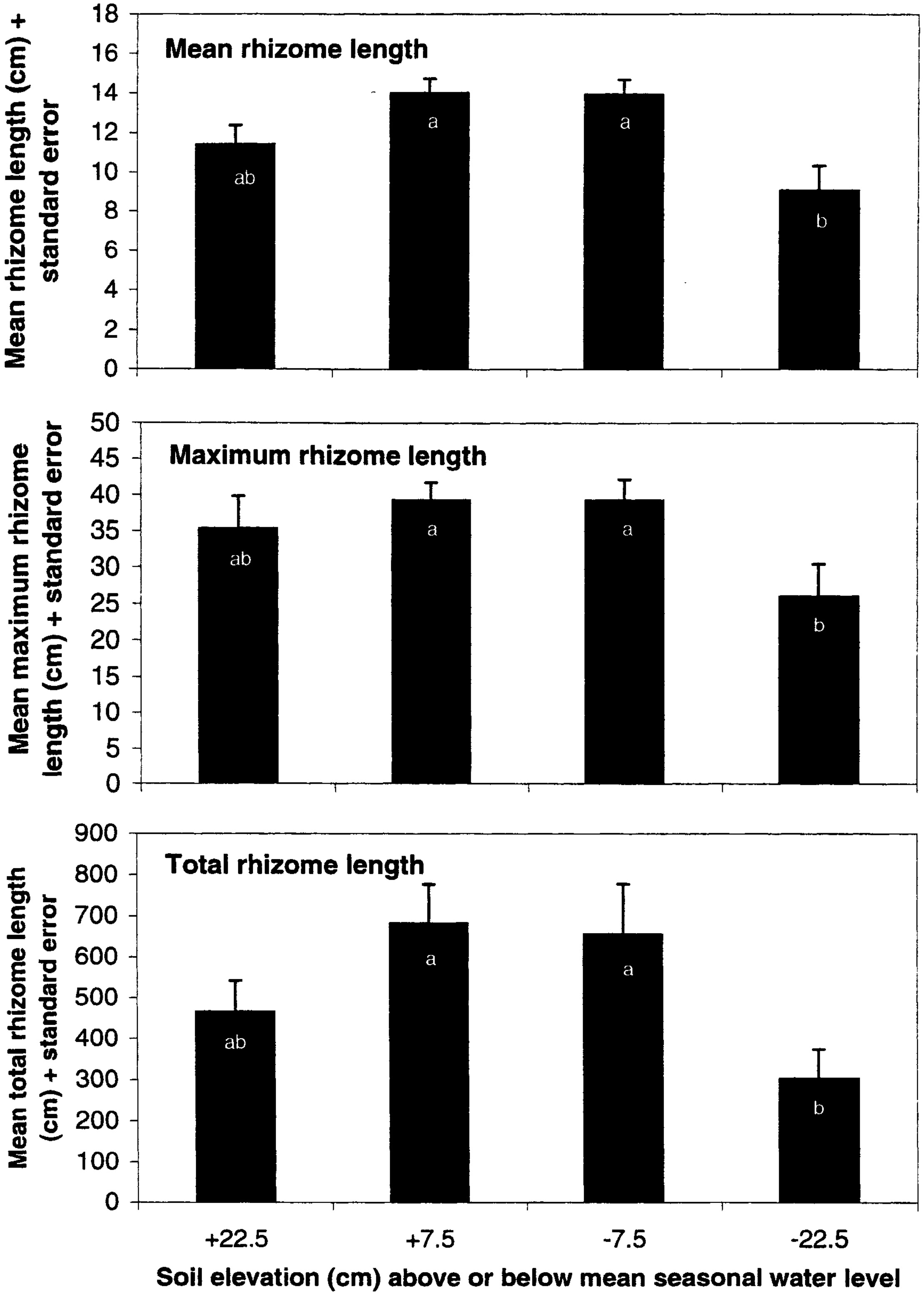

Figure 4.16. Mean, maximum, and total rhizome length for *C. lacustris* averaged by elevation across all water regimes and soil types. Means with the same letter are not significantly different (alpha = 0.01).

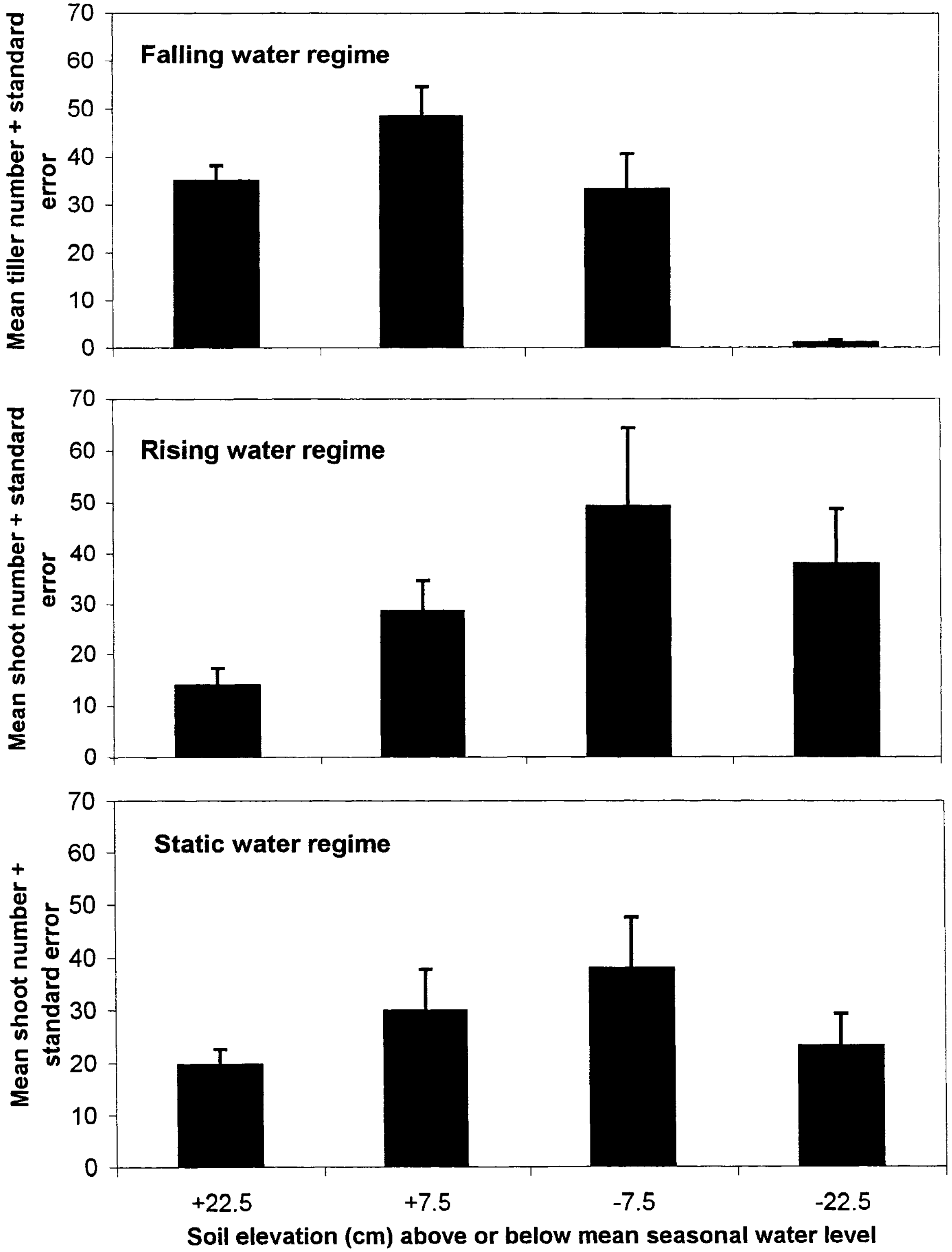

Figure 4.17. Mean tiller number for *C. lacustris* seedlings averaged by water regime and elevation across all soil types.

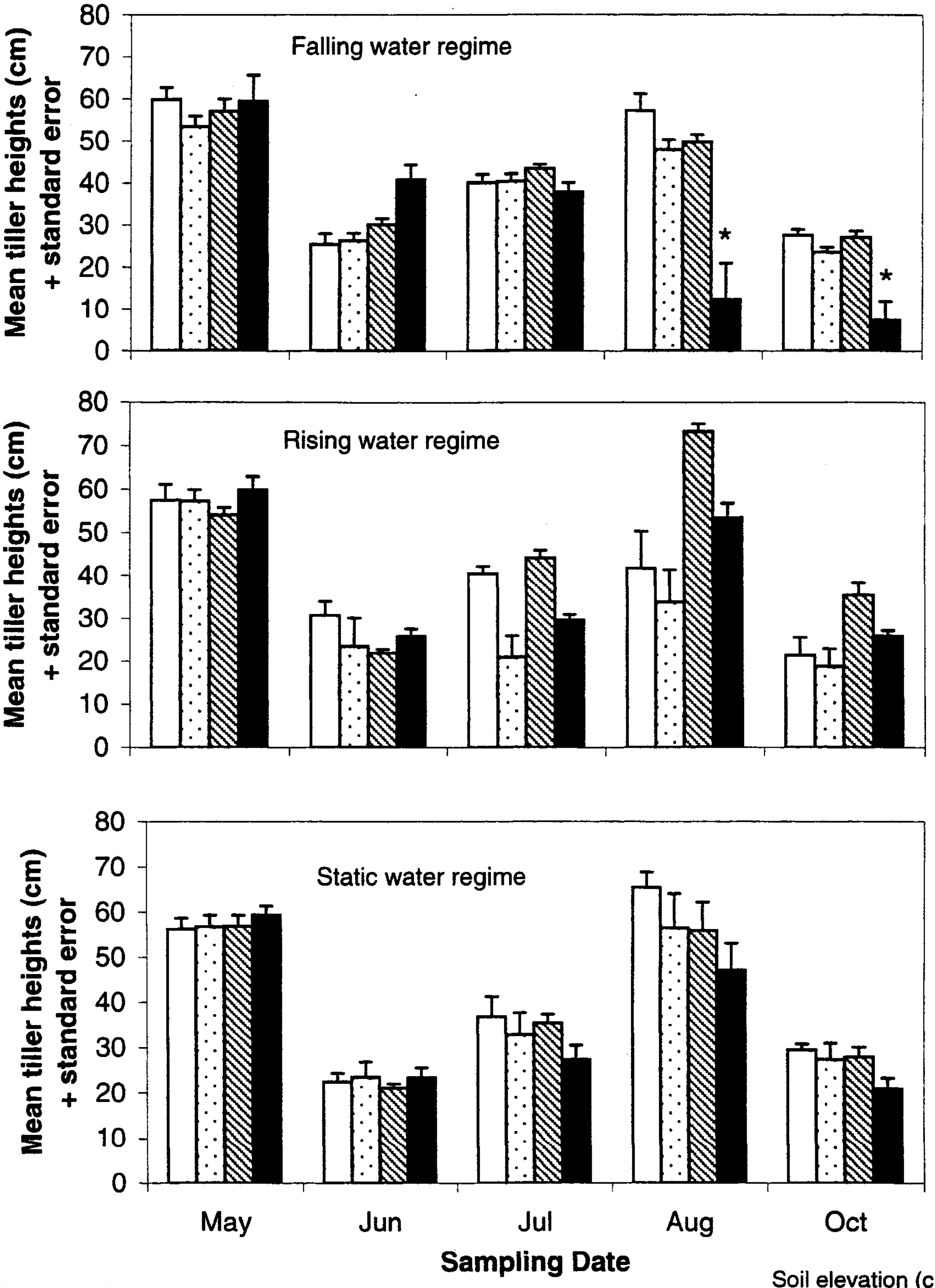

Figure 4.18. Mean tiller heights for *C. lacustris* averaged by water regime, elevation, and sampling date over all soil types. Patterned bars represent the soil elevation above or below mean seasonal water level. Means with an asterix are significantly different than the other means within a sampling period and across water regimes.

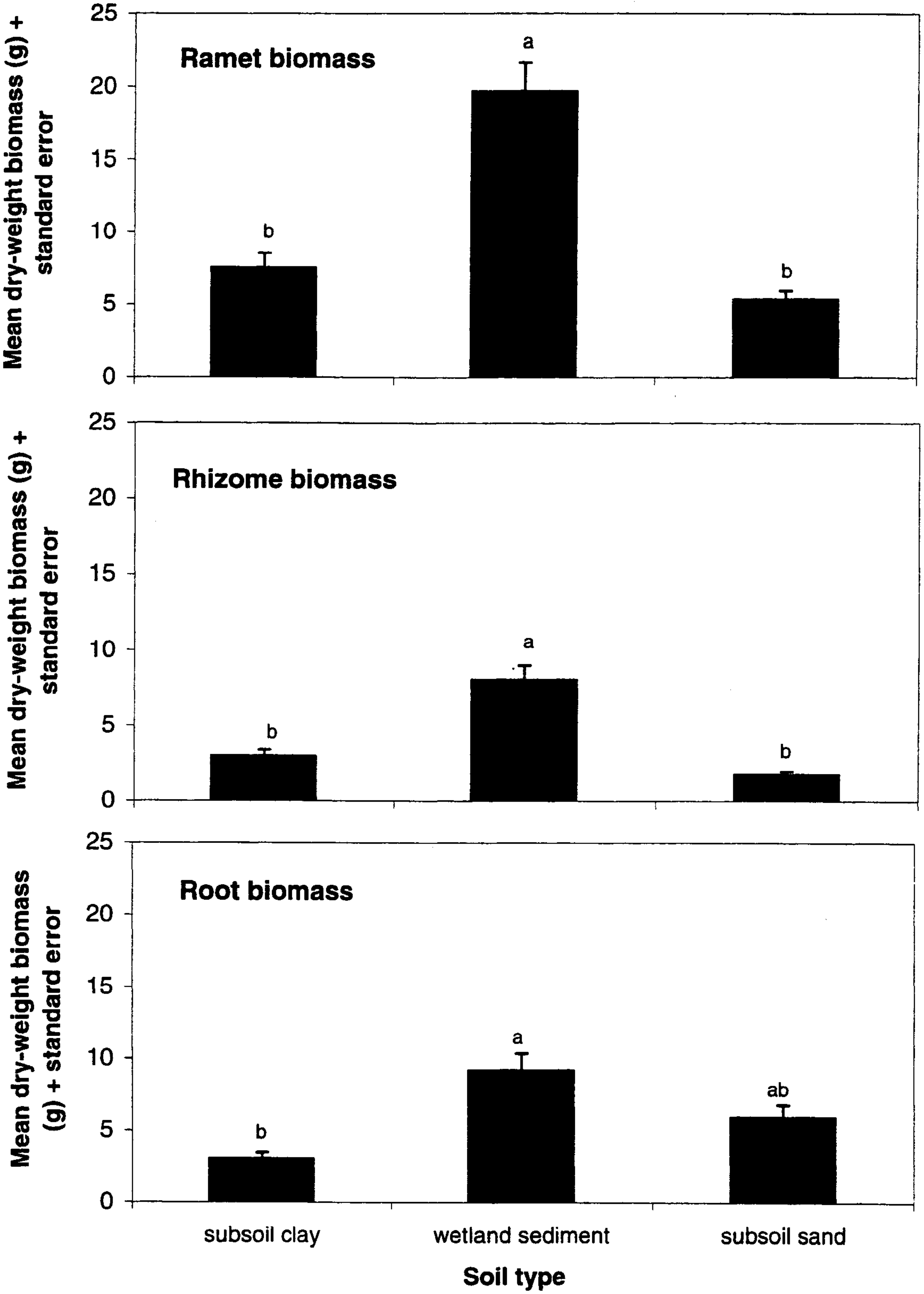

Figure 4.19. Mean dry-weight ramet, rhizome, and root biomass for *C. lacustris* seedlings averaged by soil type across all water regimes and elevations. Means with the same letter are not significantly different (alpha = 0.01).

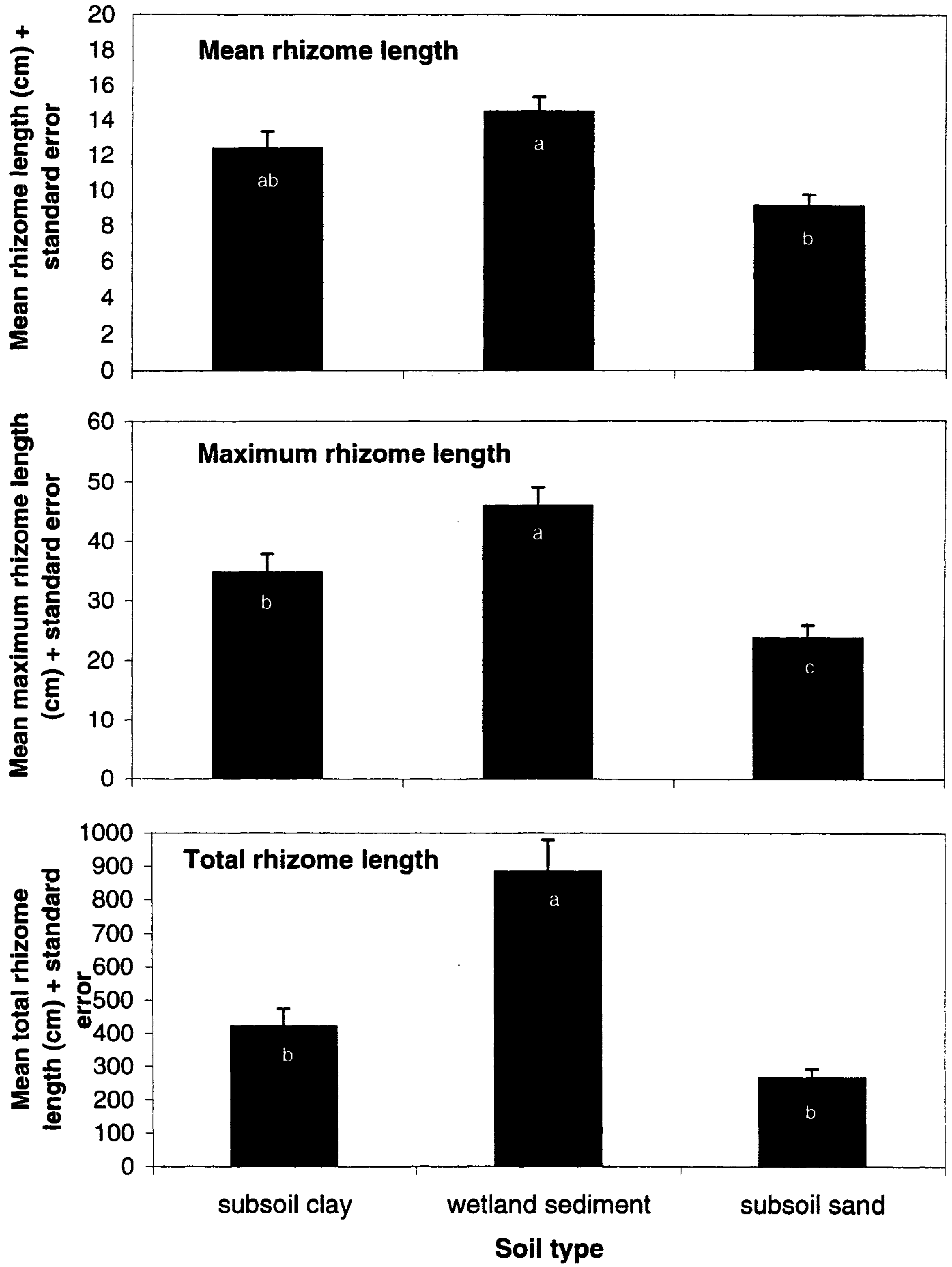

Figure 4.20. Mean, maximum, and total rhizome length for *C. lacustris* averaged by soil type across all water regimes and elevations. Means with the same letter are not significantly different (alpha = 0.01).

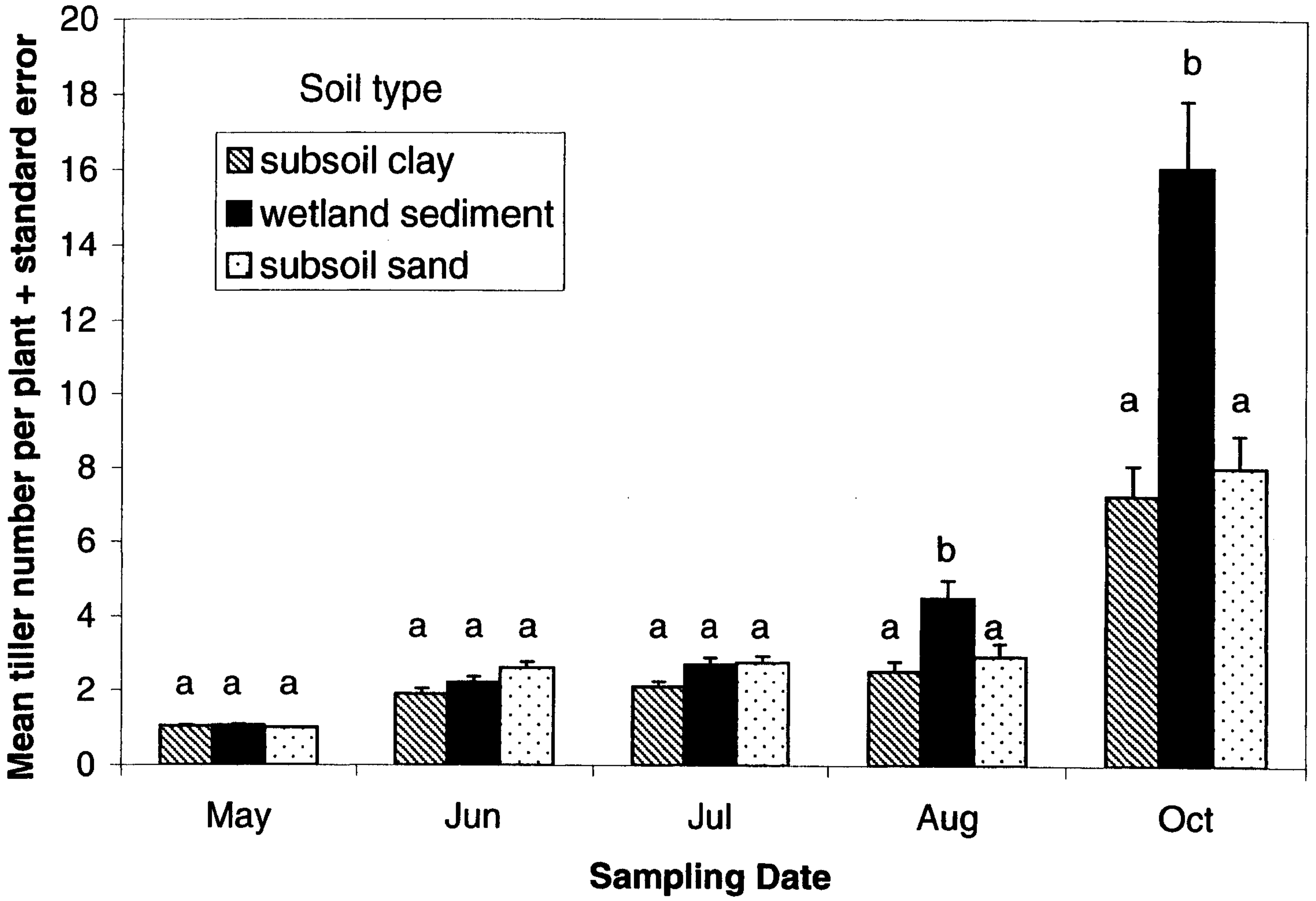

Figure 4.21. Mean tiller number per plant per container for *Carex lacustris* averaged by soil type and sampling date across all water regimes and elevations. Means with the same letter are not significantly different (alpha = 0.01).

CHAPTER 5

Field Application of Results from Tasks 6-9 at the Shakopee Bypass Wetland Creation (J.B. Pond)

Submitted to: *Wetlands*

SUMMARY

The experiment described below is a field application of the formal experiments conducted in Tasks 6-9 (Mn/DOT 71 789-72267-1451). We tested the use of site pre-treatments for controlling weedy competition and for promoting sedge survival and growth at the Shakopee wetland creation (J.B. Pond). Four pre-treatments were used: herbicide-only, herbicide-plus-hay, hay only, and control plots. Two elevations were also considered. *Carex stricta* and *Carex lacustris* were planted after the pre-treatment top-dressings were applied. The results indicated that the application of Sudan grass hay to the experimental plots increased the survival (*C. stricta* only) and growth (both species) of the sedges in this study. The mechanism by which the hay increased growth (e.g. reduction of competitors, retention of soil moisture, nutrient or humic acid augmentation) is unknown. Growth and survival were also greatest in plots with an elevation of 6-20 vertical cm above the mean seasonal water level. We recommend the application of an organic top-dressing such as hay as a pre-treatment in created wetlands for promoting sedge seedling survival and growth in the first growing season. The hay used should not include *Phalaris arundinacea* (reed canary grass).

INTRODUCTION

The experiment described below was undertaken to test the efficacy of site pre-treatments in promoting the survival and growth of native sedge seedlings in a wetland creation. Previous studies (Tasks 6-7) indicated that sedge seedlings were negatively impacted by competition from weeds that naturally recruited from the seedbank, particularly *Phalaris arundinacea* (reed canary grass). The weed control measures used in the well-controlled experiments at the University of Minnesota's Landscape Arboretum rice paddy basins are too time and labor intensive to make them practicable in a typical wetland restoration or creation. Therefore we were interested in finding a feasible weed control alternative to hand weeding.

The same studies also indicated that the application of a donor wetland soil increased the growth and survival of sedge seedlings, although the soil characteristic(s) that promoted sedge growth is unknown. We hypothesized that the application of an organic top-dressing (e.g. hay), alone or in combination with an herbicide, might reduce the germination and growth of unwanted species by shading. If initial moisture loss after planting was important in seedling survival, the top-dressing might also provide a humidity barrier for the seedlings to prevent desiccation under dry conditions. The previous studies (Tasks 6-9) also provided information on ideal water regimes for seedling growth that was used in the design of this experiment.

Site description

The revegetation experiment was conducted in a created wetland built by the Minnesota Department of Transportation (Mn/DOT) as mitigation for wetland impacts associated with the Shakopee Bypass in Shakopee, MN. Within Mn/DOT, it is referred to as the J.B. Pond and is located on the south side of Highway 101 and east of Bridge 70008 near the Shakopee Savage border (N 44° 46' W 93° 24') in Scott county, MN. The wetland was built in the spring of 1995 and was flooded by the spring of 1997. The long axis of the wetland runs approximately east - west with shoreline contouring on the south side. The revegetation experiment was set up on the far southeast bay of the wetland (Fig. 5.1).

METHODS

Soil analysis was performed on a homogenized surface sample collected from three locations along the southeast end of the basin near the shoreline where the planting was to take place (Table 5.1). These data were collected for purposes of comparing the soil characteristics of this site to soil characteristics of other sites where similar revegetation research has been conducted.

Twenty-four 4 m x 2.5 m treatment plots (4.4 yards x 2.7 yards) were established along 96 m (105 yards) of shoreline in the southeast bay of the J.B. Pond (Fig. 5.2). Four top-dressing treatments were used: control (no treatment), herbicide only, hay only, and herbicide with hay. Treatments were assigned randomly to the plots within replicate blocks. Six replicates of each treatment were used. Each plot was subdivided into four 1.5 m x 1 m rectangular plots in which one of two sedge species (*Carex stricta* or *Carex lacustris*) was planted in monoculture. The outer 0.5 m (1.6 feet) edge of the treatment plot was retained as a buffer strip. No sedges were planted in the buffer strip. One meter separated the sedges in one treatment from the nearest sedges in the neighboring treatment plot.

Each species was planted at a "high" and a "low" elevation within the block of four subplots. A white PVC water depth pole was established in the center of the southeast bay of the J.B. Pond for water depth reference. Water depth measurements were taken at the pole approximately once a month from May to October 1997 (Table 5.2). The elevation of the water depth pole and each of the subplots was surveyed in November, 1997 at the end of the first growing season to establish the mean seasonal water depth in each subplot (Table 5.3). The slope angle for the twenty-four plots ranged from 5 to 20 degrees (median slope: 9 degrees, mean slope: 10 ± 3.6 degrees). Plots along the northeast slope of the planting had relatively shallow slopes and plots on the northwest slope had steeper slopes.

Small shrubs, dead plant material, and large weeds were removed from each of the flagged plots on April 18 1997. All plots were raked to smooth minor topographic differences. The corners of the plots were flagged with orange flags and the corners of the subplots were flagged with pink flags. Blue flags were placed in the center of the control plots. Treatments were applied to the plots prior to planting. Herbicide (Glyphicide - Rodeo 3% mix) was spot sprayed on May 8 and again on May 10 in the herbicide-only and herbicide-plus-hay plots. Sudan grass hay was applied by hand in large flakes to the hay-only plots on May 6 1997 and the herbicide-plus-hay plots on May 15 1997 to a depth of approximately 10 - 15 cm (4 to 6 inches). Roughly two bales of hay were used per treatment plot (10 m^2).

The seedlings used for the experiment were approximately 5 (*C. stricta*) and 3 (*C. lacustris*) months old. Seedlings of both species were between 30 - 50 cm (12 - 20 inches) tall with one to three tillers (shoots) at planting. Seedlings were grown in a greenhouse on the University of Minnesota campus and moved to the Mn/DOT site on May 13 and 15 1997. Fourteen seedlings were planted by hand in each subplot through the hay top-dressing on May 16 1997 (see Appendix photos). Planting and watering was accomplished by nine people in approximately six hours. In total 1344 seedlings were planted.

Seedlings were germinated from seeds on a greenhouse bench in flat trays filled with a commercially available germination mix soil. Seeds were spread over the surface of the moistened soil and were not buried. Trays were covered with a transparent plastic lid to prevent seedling desiccation. The seeds used were collected at the University of Minnesota's Cedar Creek Natural History Center (45° 24' N, 93° 12'W) in June (*C. stricta*) and July (*C. lacustris*) 1994 and stored in a dark cold room (4°C or 36°F) under moist conditions until December 1996. The majority of *C. stricta* seeds germinated within three weeks of providing germination conditions whereas *C. lacustris* seeds required four weeks before germination was observed. Germinated seeds were replanted in 13 cm (5 inch) long Ray Leach brand 'conetainers' filled with the same soil used for germination and hung in 30 cm by 60 cm (12 inch by 24 inch) racks. Each rack held 90 cones. The conetainers are of the type frequently used to grow tree seedlings and are superior for growing sedges due to their space saving size, the ease of maintaining appropriate water conditions, and convenience of extracting seedlings from the cones when replanting in a restoration. The racks were set in lined greenhouse benches flooded to a depth such that the water level came midway up the length of the conetainers.

Canopy cover of species in the plots was estimated in each of the plots on September 30 and October 1 1997 using the Braun-Blanquet cover analysis method. The extent of open water and bare or thatch covered ground was also estimated at this time.

The number of sedge tillers (shoots) produced was collected at the end of the growing season from October 3 to October 10 1997. Percent survival and the number of shoots produced per plant were estimated for *C. stricta* tussocks. Because of the spreading growth form of *C. lacustris*, the number of shoots by area (m2) was calculated in each subplot. It was not possible to distinguish to which parent plant the shoots of *C. lacustris* plants belonged at the end of the growing season, therefore it was not possible to accurately calculate survival for this species. The height of seedlings was not collected because previous studies (Tasks 6-7) indicated that height is not a reliable measure of plant health for these species. Percent survival data for *C. stricta* were arcsine square-root transformed prior to analysis. A one-way analysis of variance (ANOVA) was run on all the survival and tiller number data to determine if there were any correlation between seedling survival and growth and soil pre-treatment and elevation. All results are significant at alpha = 0.01 unless otherwise noted.

RESULTS

C. stricta had greater survival (± standard error) at the uppermost elevation (88% ± 3%) than at the lower elevation (65% ± 6%). Survival was not affected by plot pre-treatment.

Seedlings had greater mean tiller numbers in the upper elevation (11.2 ± 0.9) than the lower elevation (6.5 ± 0.6). Mean tiller number was greatest in hay-only, herbicide-plus-hay, and control pre-treatments and lowest in the plots in which only herbicide was used (Fig. 5.3).

In addition, the replicate block (location along the shoreline) also affected *C. stricta* tiller number per plant (Table 5.4). The greatest number of tillers per plant occurred in blocks on the eastern side of the bay with the lowest tiller numbers observed in block six at the far western edge of the planting.

C. lacustris also had a greater number of tillers at the upper elevation (25.7 ± 2.6) than at the lower elevation (20.6 ± 1.8). In addition, the type of plot pre-treatment affected the number of tillers produced (Fig. 5.4). The tiller density was greatest in the herbicide-plus-hay and hay-only plots and lowest in the herbicide-only and control plots.

As with *C. stricta*, the replicate block affected tiller density for *C. lacustris*. Tiller number was greatest at the northeast corner of the planting (replicate block 1) and gradually dropped as the replicate number increased (Table 5.1).

Estimates of weed canopy cover and ground cover taken in late September were not correlated with *C. stricta* or *C. lacustris* tiller numbers or survival.

DISCUSSION

The elevation of the high and low subplots in this study correspond roughly to elevations of the upper two and lower two treatment rows, respectively, used in the seedling study performed at the University of Minnesota Landscape Arboretum (Tasks 6 & 7). The pattern of reduced survival and tiller number at lower elevations was similar in both studies. The similarity of results between the previous study and this one, conducted in a created wetland with less experimental control, confirm the importance of planting location in the survival and growth of seedlings during the establishment year. The slopes along which seedlings were planted in this study had a range of 5 to 20 degree slopes in contrast to the 5 degree slopes in the previous study at the Arboretum. The acceptable planting zone for greatest survival and growth was narrower (2.5 m) in this experiment than the Arboretum study (7 m) because of the greater slope angle along which seedlings were planted in this study. The results support the construction of flatter slopes for a wider planting zone.

The most interesting outcome of this experiment was the observation that application of Sudan grass hay improved the growth of both *Carex* species. The application of the herbicide pre-treatment alone did not improve sedge growth, nor were the herbicide-plus-hay results significantly different than hay alone. The early date of herbicide application may explain the lack of influence. Few weeds had germinated by the early part of May and seedlings that were sprayed may have been rinsed clean of the contact herbicide by subsequent rain events.

The mechanism by which the organic ground cover improved growth is not known. It is likely that it facilitated moisture retention at the soil surface and it may also have reduced the germination of weed seeds in the plots. The cover analysis of vegetation and ground cover did not reveal lower weed estimates in plots with Sudan grass top-dressing. However it is possible that October was not the optimum time of year to collect cover analysis data. Data were collected at that time because early fall marks a period of increased growth for *Carex* plants (cool season growth). The seedlings in control and herbicide-only plots may have experienced greater competition from warm season vegetation that had largely senesced by October. More frequent surveys of vegetation throughout the growing season may have revealed such an interaction. Additionally, it is possible that as the hay decayed, it may have contributed nutrients or humic acids to the soil that enhanced plant growth.

Differences in growth between replicate blocks were likely due to differences in slope angle that varied from one side of the bay to the other. Such variance is to be expected in a created site where environmental factors such as elevation are more difficult to control than in experimental basins such as those used in Tasks 6-7. In general, the steeper the slope, the narrower the optimal growth zone. The statistical significance of the replicate blocks does not change the significance of the treatment results.

RECOMMENDATIONS

The use of Sudan grass or other organic top-dressing as a site pre-treatment is recommended for promoting the growth of sedge seedlings in wetland revegetation projects. It is also recommended that hay or other top-dressing be used in lieu of donor wetland soil. The potential for introducing non-desirable weed seeds in donor soil, in combination with the logistic difficulties associated with moving donor soil are too great relative to the observed benefit at this time (Task 9). One important caveat is that *Phalaris arundinacea* absolutely should not be used as hay for top-dressing a wetland creation. *Phalaris arundinacea* is grown for forage in Minnesota and may be available for sale as hay. Once this species has been introduced into a wetland, it is very difficult to remove.

The use of Sudan grass or other wide bladed grass hay is recommended over the use of oat straw. The Sudan grass remained relatively immobile after application despite heavy rains and wind. We attribute its lack of displacement even after high water events to its wide leaves that held together well. A more brittle oat straw would most likely have been widely dispersed under the conditions that occurred in this experiment.

Table 5.1. Characteristics of soil collected along the SE shoreline of the Shakopee wetland restoration planting (J.B. Pond), Shakopee, MN. Soil was collected on Nov 1 1996.

Soil texture	Sandy loam
Cation Exchange Capacity*	37.06
K	0.08
Ca	23.49
Mg	3.09
Na	0.17
H	10.24
% Base saturation	72.37
pH (0.01 M CaCl^2)	7.1
Total N (w/ NO3 Reduction)	0.08
Bray-P (ppm)	5
K (ppm)	34
Total Organic Carbon (%)	2.56

* C.E.C. by summation (milliequivalents)

Table 5.2. Water depth readings taken at the centrally located water depth pole at the J.B. Pond during the 1997 growing season. Multiple water depths were taken in July to monitor the water fluctuation that occurred after a large rain event.

Sampling date	Water depth (cm)
15-May	48
2-Jun	44
1-Jul	36
15-Jul	44
30-Jul	80
20-Aug	54
30-Sep	50.5
10-Oct	44

Average water depth: 50 cm +/- 13.2 stdev
Median water depth: 46
Mode water depth: 44

Table 5.3. Mean soil elevation (cm) above (+) or below (-) mean seasonal water depth for high and low elevation subplots. Means are averaged across all treatments within a replicate block.

	High elevation		Low elevation	
Replicate Block	Mean	SE	Mean	SE
1	12	2.7	-2.5	1.6
2	6	1.5	-9.5	2.9
3	11	0.8	-15.0	-0.7
4	20	2.3	-2.5	3.3
5	20	1.8	-7.8	3.5
6	16	3.3	-10.5	2.1

Table 5.4. Mean tiller number per plant for *C. stricta* averaged by replicate block. Data are from the Shakopee wetland revegetation experiment at the southeast end of the J.B. Pond and were collected at the end of the first growing season in October 1997. Means with the same letter are not significantly different (alpha = 0.01).

Mean tiller # per plant		SE	Replicate Block	
11.2	±	1.7	3	a
10.0	±	1.7	1	a b
8.9	±	2.1	2	a b
8.8	±	1.0	4	a b
7.3	±	1.4	6	a b
6.8	±	1.0	5	b

Table 5.5. Mean tiller number m^{-2} for *C. lacustris* averaged by replicate block. Data are from the Shakopee wetland revegetation experiment at the southeast end of the J.B. Pond and were collected at the end of the first growing season in October 1997. Means with the same letter are not significantly different (alpha = 0.01).

Mean Tiller # per m^2		SE	Replicate Block	
30.0	±	5.5	1	a
26.4	±	4.8	2	a b
24.3	±	4.7	3	a b
23.5	±	2.1	4	a b
17.3	±	2.1	5	b
17.3	±	1.5	6	b

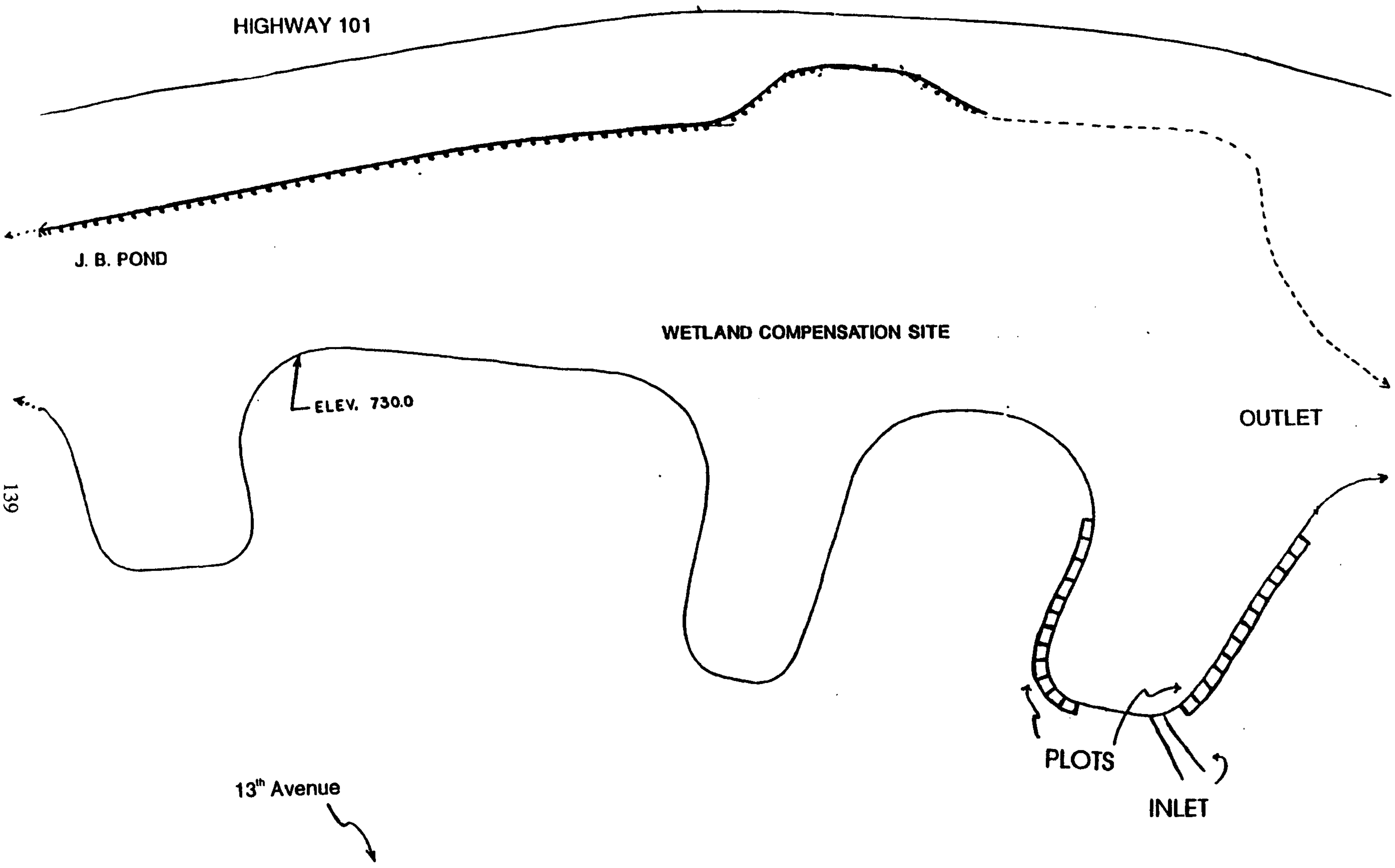

Figure 5.1. East end of Shakopee compensation wetland (J.B.Pond) showing location of research plots.

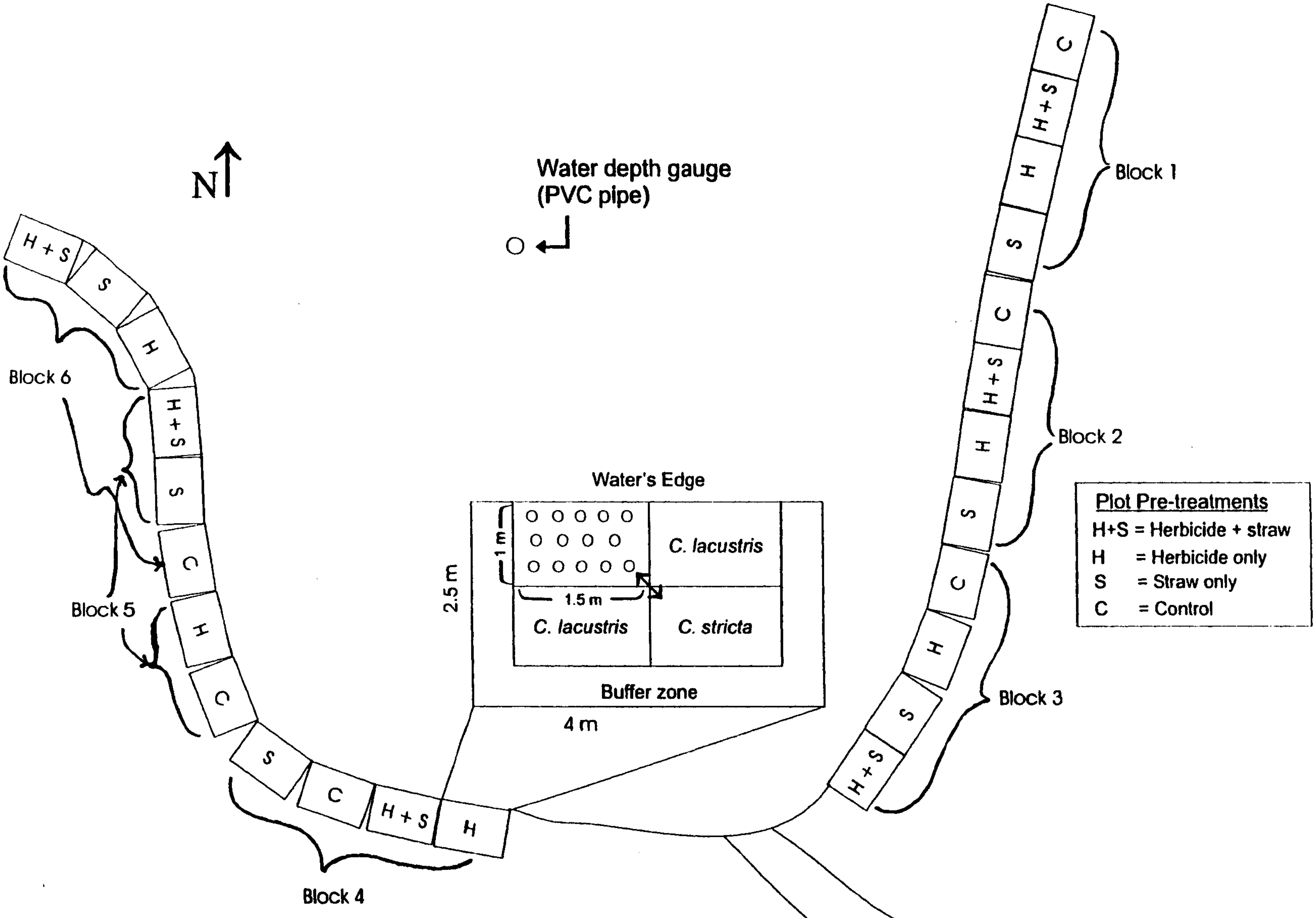

Figure 5.2. Planting Design for Shakopee Bypass Wetland Revegetation Project - 1997

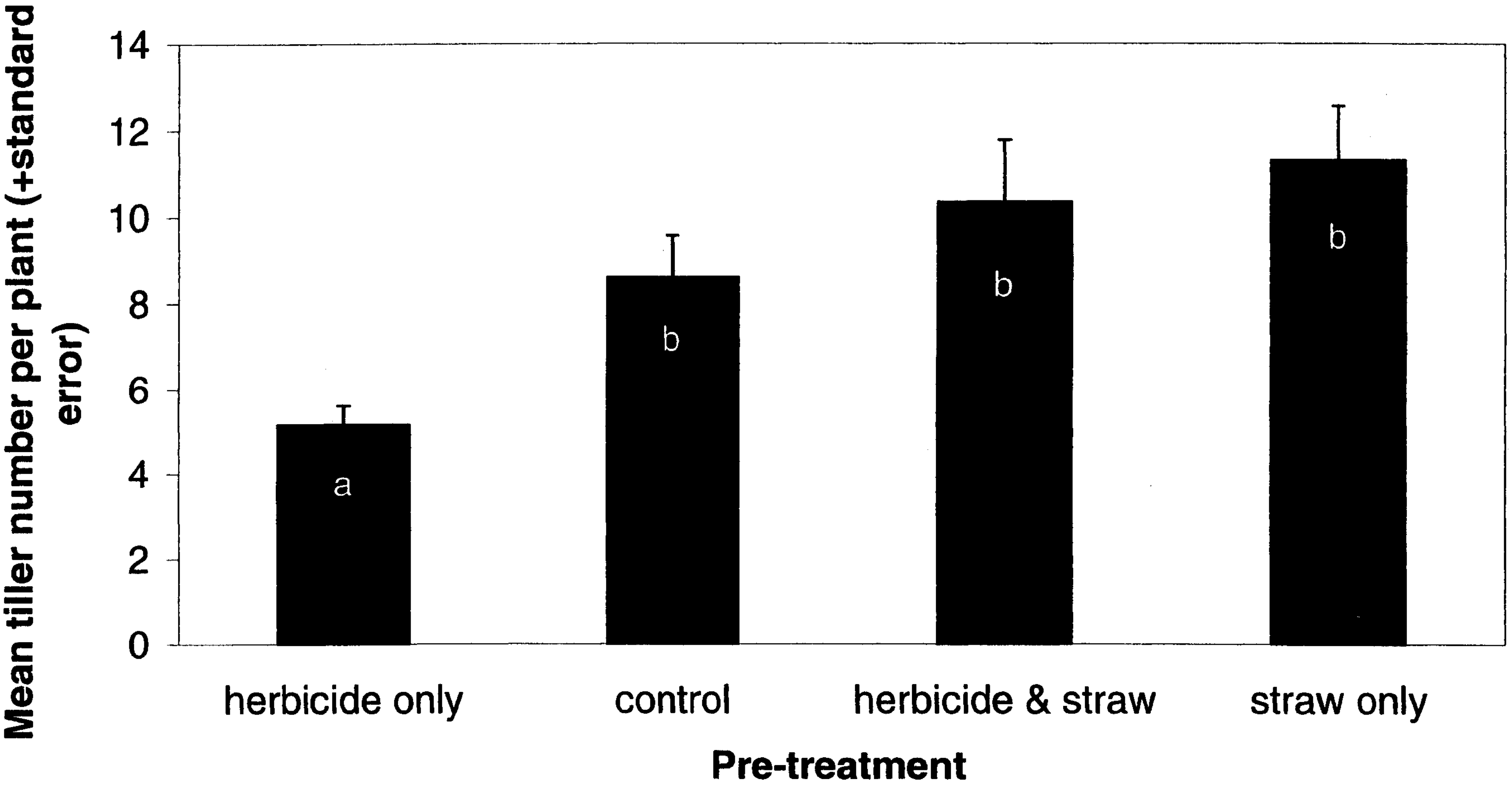

Figure 5.3. Mean tiller number per plant for *C. stricta* averaged by plot pre-treatment across both high and low elevations from the 1997 Shakopee wetland revegetation experiment. Means with the same letter are not significantly different (alpha = 0.01)

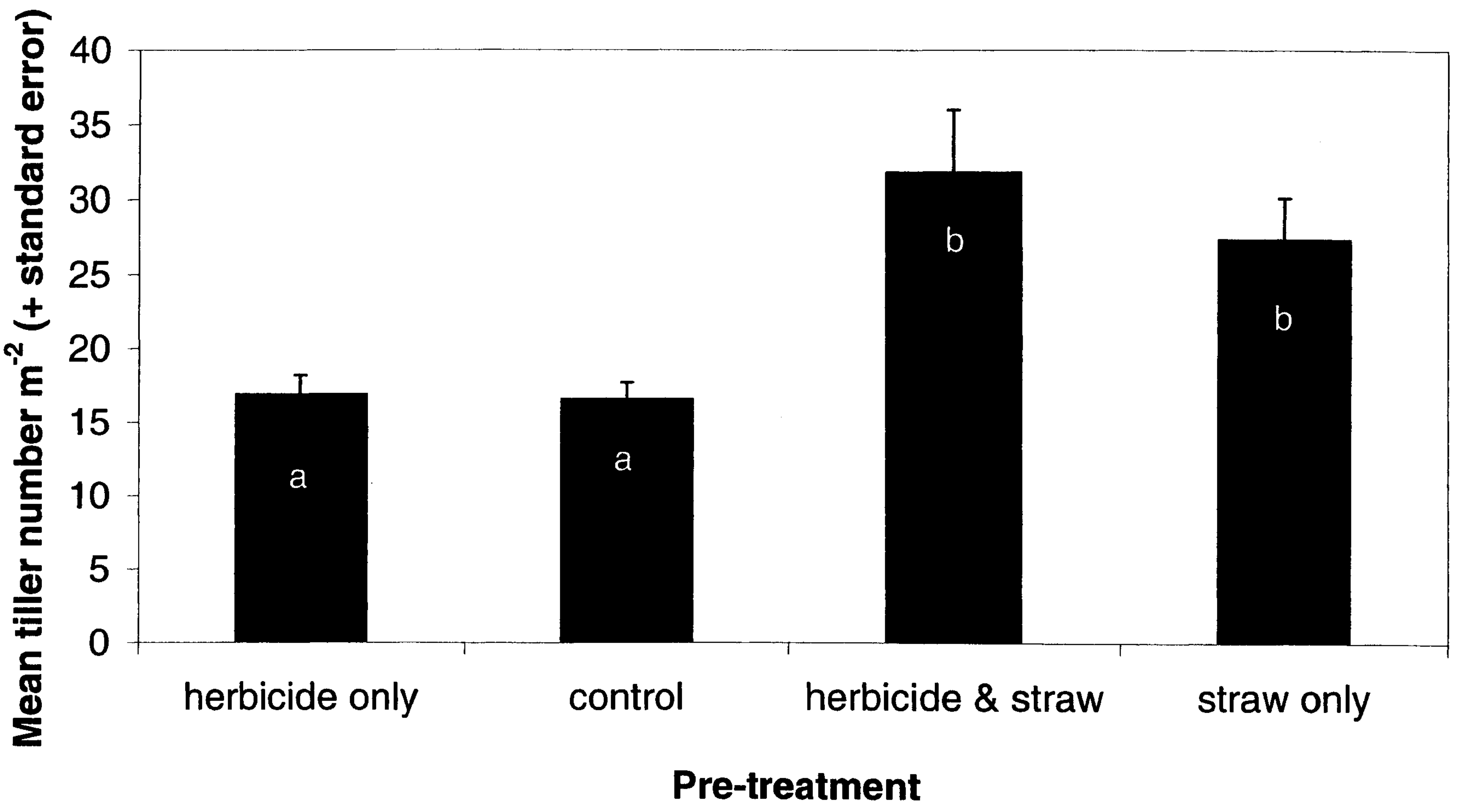

Figure 5.4. Mean tiller number m^{-2} for *C. lacustris* averaged by plot pre-treatment across both high and low elevations from the 1997 Shakopee wetland revegetation experiment. Means with the same letter are not significantly different (alpha = 0.01).

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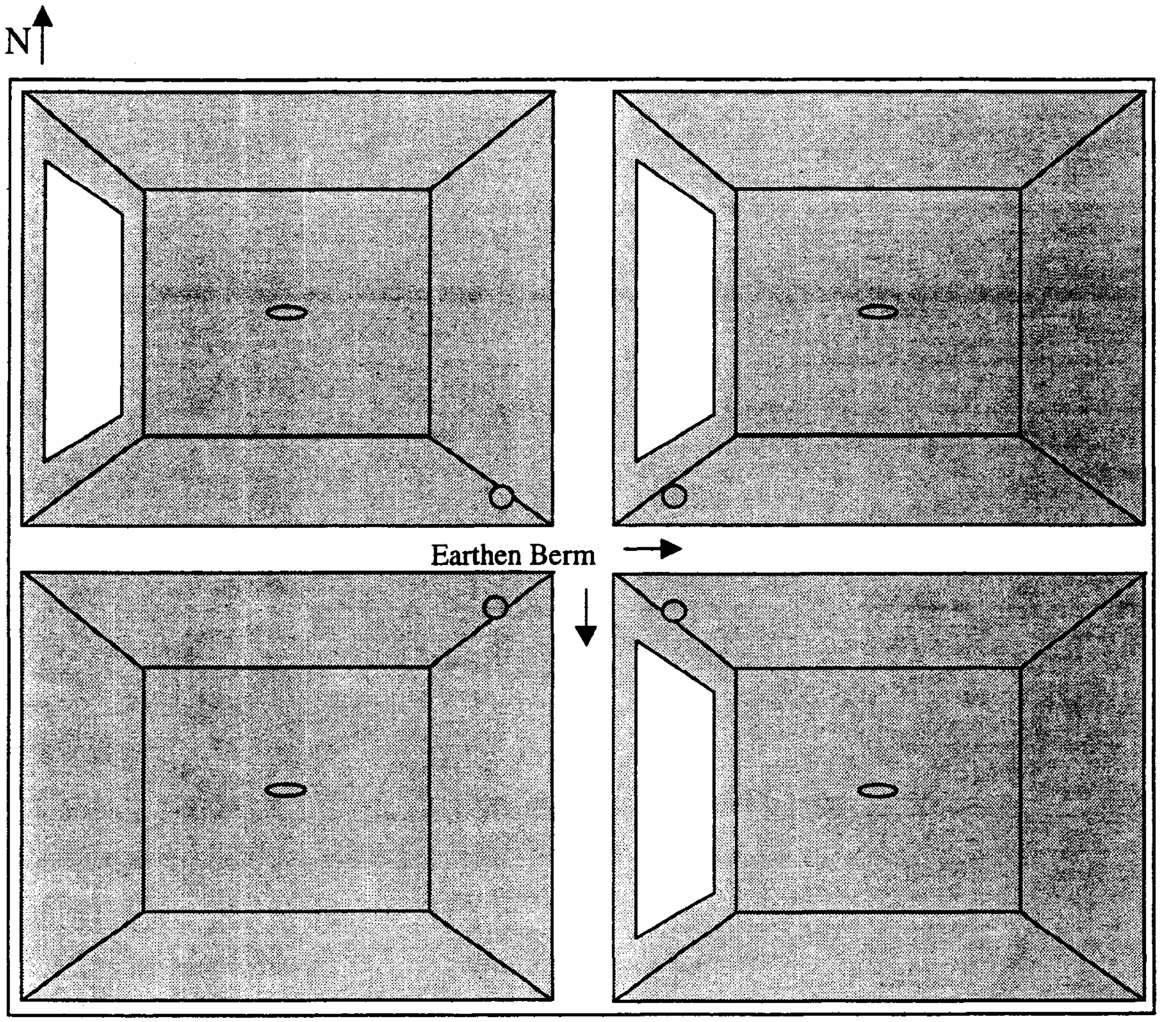
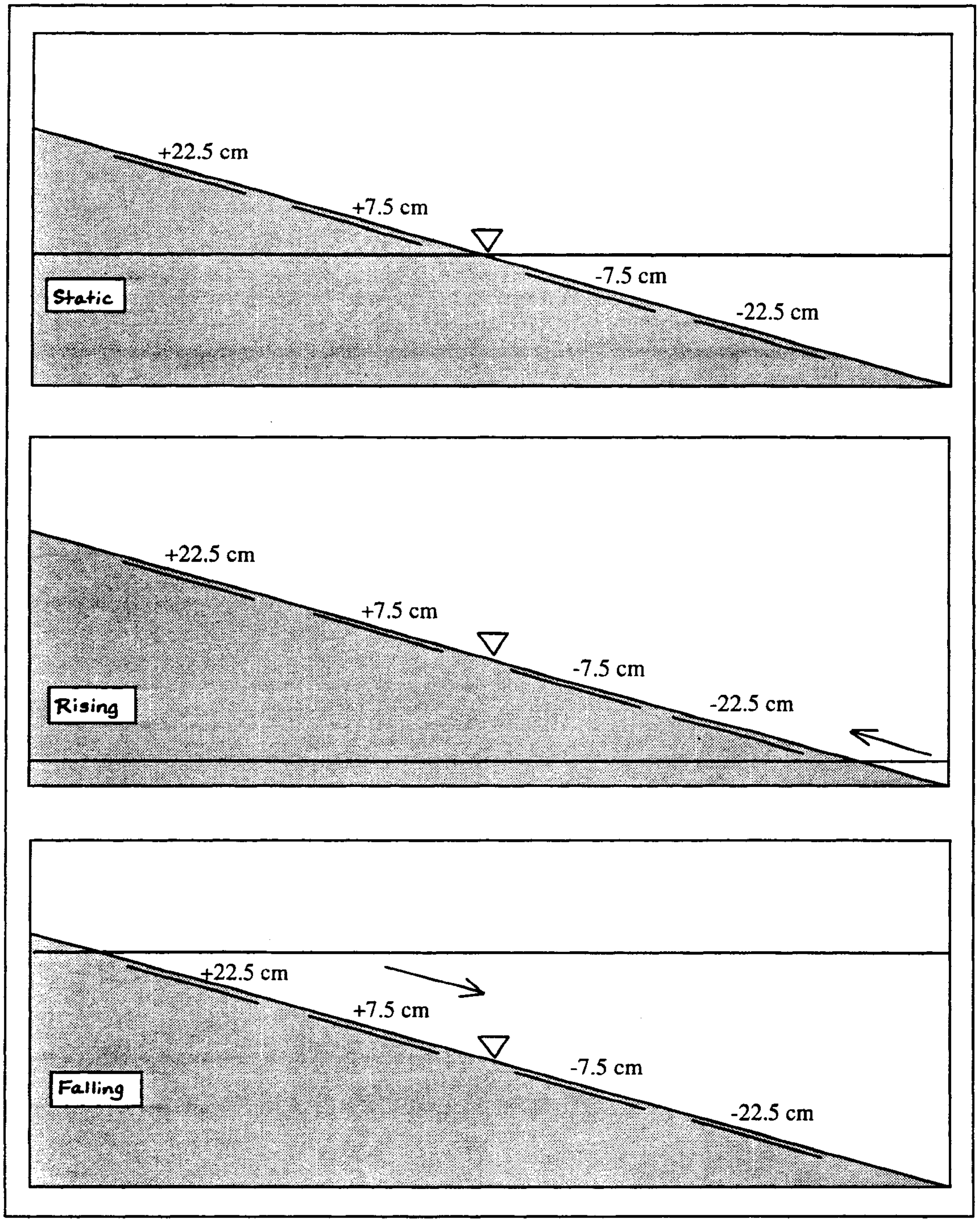
APPENDIX A

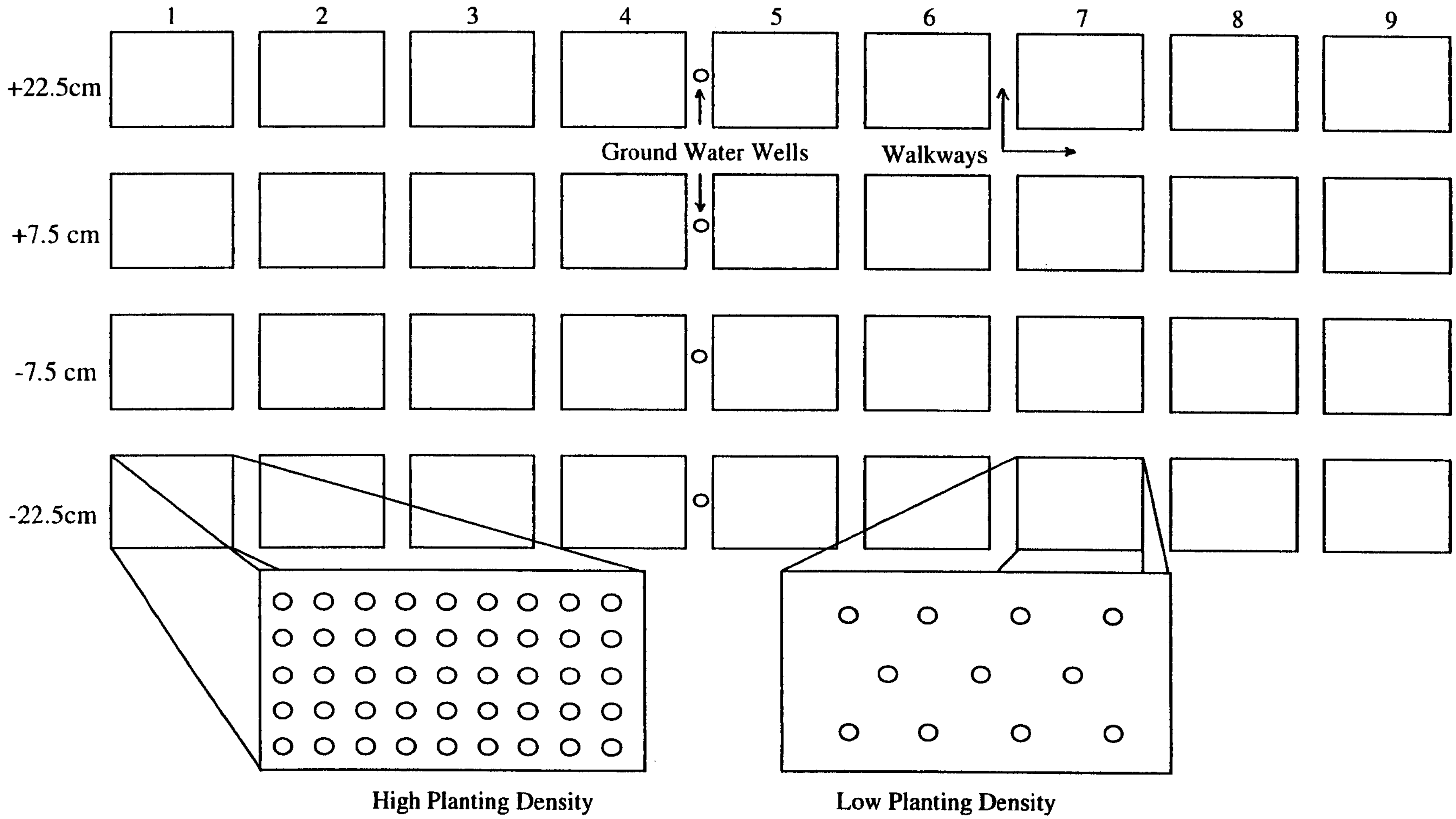
EXPERIMENTAL DESIGN FOR FIELD STUDY AT THE UNIVERSITY OF MINNESOTA LANDSCAPE ARBORETUM



Top view of diked experimental wetland located at the University of Minnesota Landscape Arboretum, Chanhassen, MN. Each basin is approximately one tenth of an acre with a flat bottom and sides graded to a 20:1 slope. Water inlet valves, indicated with small circles, are located in the inner corner of each basin. Outlet tiles, indicated with ellipses, are located in the center of each basin. Experiments were established on the east-facing slope of the NW, NE, and SE basins (unshaded polygons).



Static, rising, and falling water regimes shown in cross-section. Water level at the beginning of the growing season is indicated with a horizontal line. The inverted triangle represents the mean seasonal water level. The numbers refer to the height above or below mean water level of the four elevational treatments (rows). Water level in the static water regime was maintained at the mean seasonal water level for the entire growing season. Water level in the rising water regime started at the bottom of the -22.5 cm row and was raised at a rate of five vertical centimeters every two weeks until the +22.5 cm row was inundated at the end of the growing season. Water level in the falling water regime started at the upper edge of the +22.5 cm row and fell over the growing season until the -22.5 cm row was exposed.



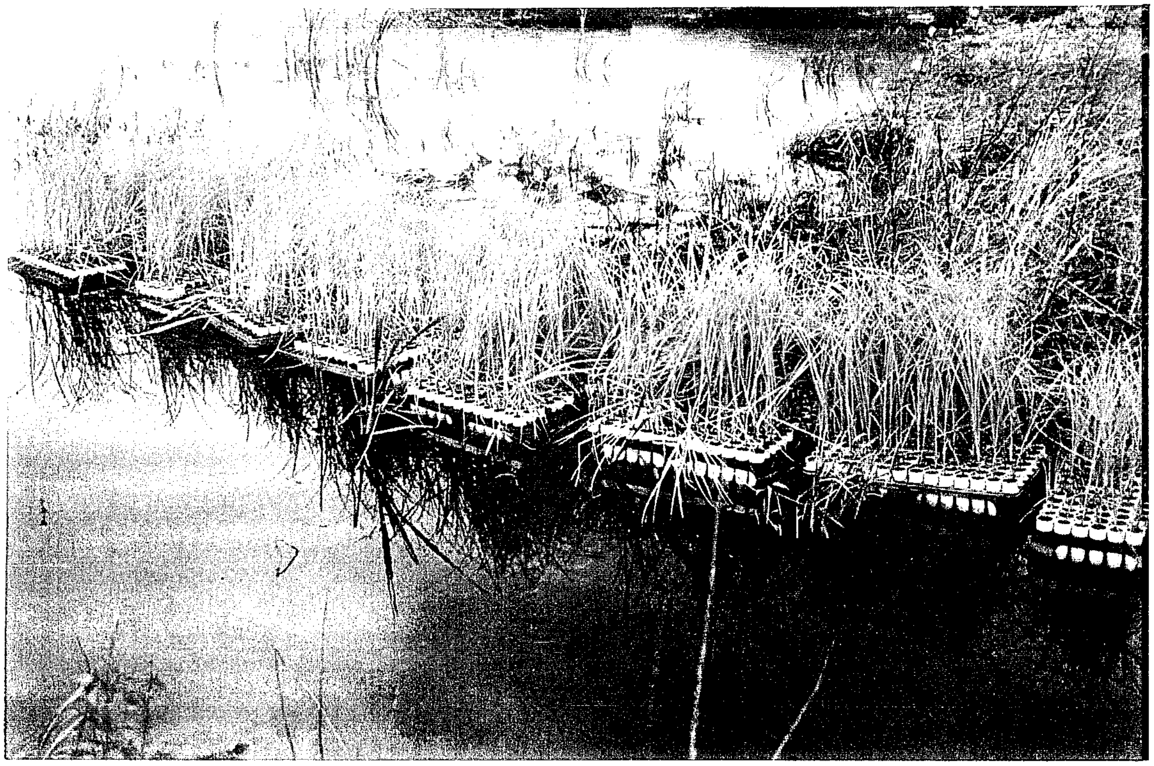
Experimental design for east slope of basins. Plots were arranged along an elevational gradient from upland (+22.5 cm) to bottom of basin (-22.5 cm). Elevation of soil surface above or below the mean water level is indicated alongside each elevational treatment (row). Each 2.5 m x 2 m plot was planted with either 45 (high density), 10 (low density) or no (control) seedlings of *Carex lacustris* or *Carex stricta*. Sedges were planted in monotypic stands.

APPENDIX B

PHOTOGRAPHS OF SHAKOPEE PLANTING

MN/DOT volunteer planting crew in plots with (foreground) and without (background) organic top-dressing (hay)

Bob Jacobson (Mn/DOT) applying herbicide pre-treatment to plots at the J.B. Pond



Carex seedlings in 'conetainer' racks before planting

John Mulhouse (U of MN) preparing tray of seedlings for planting team

Mn/DOT volunteers planting through hay top-dressing (top) and in control plot (below)

Dave Biesboer (U of MN) planting sedge seedling through hay top-dressing