



Establishment of native and invasive species along a riparian resource gradient
by Ronald Roy LeCain

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Land Rehabilitation

Montana State University

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Abstract:

I investigated influences of hydrology and nutrient availability on establishment of indigenous plants and non-indigenous weeds. I hypothesized that subirrigated and moist (but not saturated) locations along hydrologic gradients favor emergence and early growth for all studied species, and that high levels of inorganic N favor annuals and weeds more strongly than desirable perennials. In a field study, I established four areas along a hydrologic gradient spanning water table depths from two meters in the upland to saturation in the wetland. Six species (*Centaurea maculosa* (Lam.), *Agropyron spicatum* (Scribn. & Smith), *Helianthus annuus* (L.), *Cirsium arvense* (L.), *Deschampsia cespitosa* (L.) and *Bechnannia syzigachne* (Steud.) were planted as monocultures in cleared plots in October 1998. One of two N treatments (10 kg N/ha/yr, 100 kg N/ha/yr), a carbon treatment (1000 kg C/ha/yr) or a control was randomly applied to each plot. Seedling emergence and growth data were collected during August 1999, and seedling emergence data was collected in May 2000. In the greenhouse the six species were planted in pots maintained at: 0 or 2 cm above the soil surface, 5, 10, 20 and 30 cm below the soil surface, or "dry" with no sub-irrigation. In the greenhouse, intermediate water levels had high emergence and growth for most species. In the field emergence, was low in equivalent hydrologic settings; high rodent activity in transitional areas may have contributed to poor establishment. In both experiments, hydrologic gradients influenced early growth more than emergence, particularly with facultative wetland species. In addition, *C. maculosa* and *A. spicatum* (upland species) emerged in the wetland, but did not survive. Results suggest that early emergence is a poor indicator of successful riparian plant establishment. *C. arvense* emerged poorly in both experiments and appeared to be germination limited. Responses to N treatments were similar in both experiments, although results were commonly non-significant. In most cases increasing N increased growth of *C. maculosa*, but not *A. spicatum*. These results provide some evidence that N may be managed to affect early succession in riparian areas and adjacent uplands.

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ALONG A RIPARIAN RESOURCE GRADIENT

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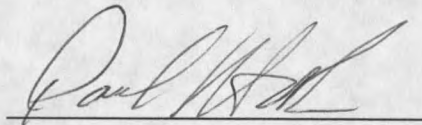
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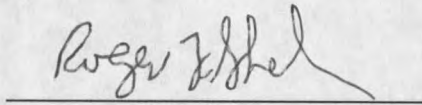
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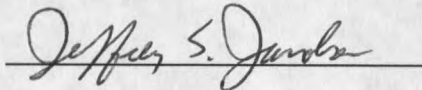


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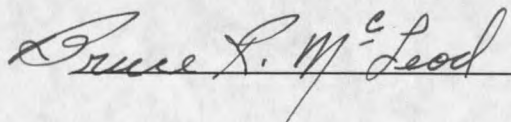


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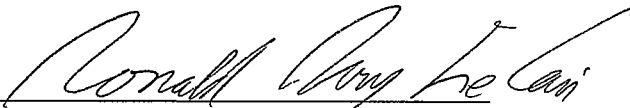
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ABSTRACT

I investigated influences of hydrology and nutrient availability on establishment of indigenous plants and non-indigenous weeds. I hypothesized that subirrigated and moist (but not saturated) locations along hydrologic gradients favor emergence and early growth for all studied species, and that high levels of inorganic N favor annuals and weeds more strongly than desirable perennials. In a field study, I established four areas along a hydrologic gradient spanning water table depths from two meters in the upland to saturation in the wetland. Six species (*Centaurea maculosa* (Lam.), *Agropyron spicatum* (Scribn. & Smith), *Helianthus annuus* (L.), *Cirsium arvense* (L.), *Deschampsia cespitosa* (L.) and *Beckmannia syzigachne* (Steud.) were planted as monocultures in cleared plots in October 1998. One of two N treatments (10 kg N/ha/yr, 100 kg N/ha/yr), a carbon treatment (1000 kg C/ha/yr) or a control was randomly applied to each plot. Seedling emergence and growth data were collected during August 1999, and seedling emergence data was collected in May 2000. In the greenhouse the six species were planted in pots maintained at: 0 or 2 cm above the soil surface, 5, 10, 20 and 30 cm below the soil surface, or "dry" with no sub-irrigation. In the greenhouse, intermediate water levels had high emergence and growth for most species. In the field emergence, was low in equivalent hydrologic settings; high rodent activity in transitional areas may have contributed to poor establishment. In both experiments, hydrologic gradients influenced early growth more than emergence, particularly with facultative wetland species. In addition, *C. maculosa* and *A. spicatum* (upland species) emerged in the wetland, but did not survive. Results suggest that early emergence is a poor indicator of successful riparian plant establishment. *C. arvense* emerged poorly in both experiments and appeared to be germination limited. Responses to N treatments were similar in both experiments, although results were commonly non-significant. In most cases increasing N increased growth of *C. maculosa*, but not *A. spicatum*. These results provide some evidence that N may be managed to affect early succession in riparian areas and adjacent uplands.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Riparian areas represent only 1-3 percent of the land area in the northern Great Plains and northern Rocky Mountains (Naiman and Decamps 1997), but they play a highly significant role in general ecosystem and watershed health. Their role is particularly important in the semi-arid west where water is often the resource that limits plant production. Riparian ecosystems benefit from water "subsidies", and their enhanced production and structure provide many ecological and physical benefits. Unfortunately, some of the factors responsible for these benefits also expose riparian areas to weed invasions and complicate restoration of disturbed sites.

Healthy riparian vegetation can protect water quality, mitigate flooding, stabilize banks, and improve fish and wildlife habitat (Satterlund and Adams 1992, Osborne and Kovacic 1993, Mitsch and Gosselink, 1993). Riparian buffers can reduce inputs of nitrate and sediment to streams (Synder et al. 1998, Reddy et al. 1989, Yates and Sheridan 1983, Lowrance et al. 1995). Floodplain water storage and dense stands of riparian vegetation can reduce downstream flooding thereby protecting valuable lands (Patten 1998).

In western, semi-arid, rangeland settings riparian areas offer exceptional habitat with high structural diversity and biomass production far in excess of surrounding uplands (Windell 1992). These narrow bands of habitat are vital to the maintenance of biodiversity in the more extensive, surrounding uplands (Naiman and Decamps 1997).

The high production is due, in part, to high soil moisture provided by flooding and sub-irrigation. The frequent disturbances that occur along waterways as a result of floods, ice and shifts in stream courses also rejuvenate riparian areas, creating disturbed sites devoid of vegetation and ideal for establishment of rapidly growing, early seral species such as cottonwoods or willows (Patten 1998).

Naturally, occurring disturbances play an integral role in establishing healthy stands of desirable riparian vegetation but riparian areas are also frequently subject to disturbance and degradation by human activities (Patten 1998, Faber et al. 1989).

Riparian cover in the Missouri River flood plain of northeast Montana declined by an average of 2482 acres a year between 1938 and 1982, primarily because of agricultural development (Hoar and Erwin 1985). Other anthropogenic disturbances occur as a result of improper grazing, resource extraction, urban development, dam construction and recreation (Patten 1998).

The combination of human and naturally occurring disturbances put riparian areas at risk for invasion by non-indigenous, weedy plants. Compounding this risk, waterways provide efficient seed transport for spread of non-indigenous, plant propagules (Pysek and Prach 1993). Human transportation corridors often follow waterways and accelerate propagule movement. Once stands of weeds establish in riparian areas they may serve as beachheads for invasions of the surrounding landscape (Pysek and Prach 1993). Weed invasions are a particular concern in restoration projects. Weeds can prevent successful establishment of desirable vegetation, reduce species diversity, degrade ecosystem function (Smith et al. 1998), and cause costly project failures. Invasions of riparian areas and wetlands by selected exotic plants such as *Lythrum salicaria* (purple loosestrife)

(Thompson et al. 1987, Balogh 1986) are well studied, but the biotic and abiotic processes driving invasions are not well researched for most exotic species in the northern Great Plains and northern Rocky Mountains.

Gradients in soil and water resources generally have a major influence on spatial patterns of plants in riparian areas (Lockaby and Conner 1999, Bedford et al. 1996). The highly variable levels of soil and water resources found in riparian areas complicate efforts to restore desirable vegetation (Lowrance et al. 1995, Cooper and Andrus, 1994). Because plant species respond differently to environmental conditions, information on the influences of soils and hydrology on seedling establishment is necessary for successful riparian restoration. In spite of the importance of this information, there has been relatively little research on the influences of hydrology and nutrient availability on establishment and growth of non-woody plants in western riparian areas. Improved understanding of environmental gradients and their effects on plant establishment should aid efforts to protect and restore western riparian areas by helping to match desirable species to appropriate sites and to recognize sites at high risk for weed invasion.

Strong gradients in soil and water resources exist in riparian areas because they serve as the interface between terrestrial and aquatic ecosystems. Riparian areas in semiarid regions typically extend from sites that are seasonally submerged to upland sites where significant water deficits occur. Areas of standing water or groundwater discharge may be saturated throughout the year. The most direct consequences for plants are strong gradients in availability of soil water and oxygen, but hydrology drives many soil forming and nutrient cycling processes as well. Gradients of hydrology, soils, and ecology have been extensively investigated along transitions between ombrotrophic and

minerotrophic bogs (Bridgham et al 1998) in eastern U.S. floodplain wetland forests (Lockaby et al. 1996, Lockaby and Conner 1999) and coastal wetlands (Adams 1993), but investigation of soil and water gradients in western riparian areas has been limited (Patten 1998).

Hydrology can influence vegetation by inducing anoxic conditions in wetter locations, thereby shifting dominance to plants species able to cope with oxygen stress. In New England salt marshes such physical stresses, including flooding and salinity, control distribution of vegetation (Bertness and Ellison 1987). The influence of physical factors is most pronounced along physical resource/stress gradients where physical stress is highest. Conversely, biotic interactions have the most influence in locations where stress is low (Bertness et al. 1992, Bertness and Ellison 1987). Highly competitive species tend to dominate in these low-stress areas, relegating less competitive, more stress tolerant species to physically stressful habitats (Keddy 1984).

A similar shift from abiotic to biotic controls of plant distribution may be encountered in western U.S. riparian areas. Physical stresses in this environment include probable oxygen deprivation in areas saturated for substantial portions of the growing season, and drought stress in areas with no water subsidy from surface or shallow ground water (Patten 1998, Satterlund and Adams 1992). Hence, it is reasonable to expect that, within rangeland riparian plant communities, highly competitive species will dominate at intermediate locations along upland-to-wetland resource gradients, where both water and oxygen availability are high. Less competitive, more stress tolerant species are expected to dominate at the wet and dry extremes.

Hydrology can also affect vegetation patterns indirectly through effects on nutrient cycling. Inorganic nitrogen (N) is the primary limiting resource for plant production in riverine and depressional wetland forests (Lockaby, 1999) and in North American marshes (Boyer and Zedler 1998). Nitrogen dynamics vary strongly with hydrologic conditions. Decomposition of organic matter and associated nitrogen mineralization, for example, are influenced by surface elevations and water levels (Lockaby et al. 1995, Lockaby et al. 1996). Flooding generally promotes decomposition with highest rates in microsites that are aerobic but moist (Mitch and Gosselink, 1993). Variation in N turnover rates in peatlands studied by Bridgham et al. (1993) were explained primarily by aeration status and community type, with highest mineralization rates in aerobic sites (Bridgham et al. 1998). Consequently, N availability on rangeland riparian gradients may be expected, like plant growth, to be greatest at intermediate locations with moist but not saturated soils.

The combined effects of hydrology and nutrient concentration on plant competition were investigated by Newman et al. (1996) who found these factors interacted to create specific advantages for different species in different environments in the Everglades ecosystem. They suggested that the responses of these species are associated with species growth rates, tissue concentrations of P, and responses to contrasting environmental conditions.

General ecological theories have been developed to predict relationships between plant traits, community dynamics and soil nutrients (Tilman and Wedin 1991, McLendon and Redente 1991). In upland ecosystems species with early successional characteristics (rapid growth rates, high tissue nutrient concentrations, annual life cycles and rapid

nutrient uptake rates) are favored by high levels of soil nitrogen (Tilman and Wedin 1991, McLendon and Redente 1991, Redente et al. 1992). Conversely low levels of available N are tolerated better by species with late successional traits (slow growth rates, low tissue nutrient concentrations, perennial life cycles, slow nutrient uptake rates). The applicability of these concepts to weed management was investigated by Herron et al. (2000), who found that reduction of soil N, through the planting of a cover crop of annual rye, shifted the successional trajectory away from a weedy species (*Centaurea maculosa*) and towards desirable, perennial bunchgrasses. The relationship between N and the relative success of plants with different characteristics apparently has not been investigated in rangeland riparian areas, where the spatial variation in hydrology may modify effects of N. Because riparian areas are at high risk for weed invasion, it is important to know if nutrient management can either increase or decrease the risk.

Establishment of sustainable stands of desirable vegetation in disturbed riparian areas, and in areas degraded by non-indigenous plant invasions, is thought to be vital to restoring the varied beneficial functions of riparian ecosystems. Damage to riparian lands can diminish ecosystem services, affecting ecological integrity far beyond the site of the disturbance. Restoration and maintenance of healthy stands of desirable, riparian vegetation seeks to enhance these services and may also play an important role in limiting the spread of invasive, non-indigenous species. The seedling establishment phase is a bottleneck that restoration ecologists struggle with in the development of healthy, native plant communities (Sheley and Petroff 1999). Thus, information on the abiotic and biotic controls of establishment of desirable species, and invasive, non-indigenous species, may contribute to our ability to maintain healthy, functioning riparian ecosystems.

The purpose of this study was to determine the influences of hydrologic setting and nutrient availability on seedling emergence and early growth in a rangeland, riparian ecosystem. The study had two specific objectives:

- I. To determine the influence of a hydrologic gradient on the seedling establishment of early successional, late successional and invasive weedy species. Highest seedling emergence and growth for all species were hypothesized to occur in unflooded conditions with high soil water availability. Such environments are present at intermediate locations along riparian gradients where soil water is high because of sub-irrigation but is not high enough to induce prolonged, waterlogged, anaerobic conditions.
- II. To investigate the influences of plant available nitrogen on the seedling establishment of early successional, late successional and invasive weedy species along a hydrologic gradient. Following the research summarized above, early successional and weedy species were hypothesized to respond strongly to nitrogen availability with greatly enhanced seedling emergence and growth in a high nitrogen environment and inhibited emergence and growth in low nitrogen environments. By comparison, late successional species would have smaller positive responses to high nitrogen and smaller negative responses to low N.

Hypotheses were investigated with parallel greenhouse experiments (Chapter 2) and field experiments (Chapter 3).

CHAPTER 2

EFFECTS OF AN EXPERIMENTAL WATER TABLE GRADIENT AND NITROGEN ADDITIONS ON THE ESTABLISHMENT OF NATIVE AND INVASIVE SPECIES

Introduction

Naturally occurring hydrologic gradients are characterized by strong variation in many factors other than depth to water, including soil properties, nutrient cycling, and herbivory. A greenhouse study was used to investigate the effects of nitrogen and depth to water on plant establishment under controlled conditions using a uniform soil. Water levels in this experiment were designed to parallel the hydrologic gradient in the field study (Chapter 3), and greenhouse nitrogen treatments included three of the four nitrogen treatments used in the field study.

Materials and MethodsExperimental Design

This experiment was conducted twice in a greenhouse at Montana State University's Plant Growth Center. Both experiment one and experiment two used completely randomized three factor, factorial designs with two replications. Factors consisted of six plant species, seven water levels, and three nitrogen levels.

Species Selection and Seeding

Six species common to the Northern Rocky Mountains were investigated (Table 1). These species represented contrasting life history characteristics. *Helianthus annuus*

and *Agropyron spicatum* are upland, native species representing early and late successional communities (Stubbendieck et al. 1991) (Table 1). *Centaurea maculosa* is an upland, perennial noxious weed (Sheley and Petroff 1999). Because successional status of many wetland species is unclear, life cycle and short-term versus long-term revegetation potential were used to select wetland species (Hansen et al. 1997). These characteristics may correlate with successional status or with the ability to exploit resource rich sites versus the ability to survive and compete in resource poor, highly stressful environments. *Beckmannia syzigachne* and *Deschampsia cespitosa* are wetland species representing species with high short-term revegetation potential and high long-term revegetation potential, (Hansen et al. 1997) and annual and perennial life cycles respectively (Cooper and Meirings 1989). *Cirsium arvense* is a perennial, invasive weed common in riparian areas (Sheley and Petroff 1999).

In the first experiment each species was broadcast seeded on the soil surface at a rate of 3000 seeds/ m² in 10 cm by 10 cm by 36 cm tapered tree pots packed with a sandy, clay loam soil. In the second experiment, species were seeded at a rate of 6000 seeds/ m² to provide higher establishment for species that demonstrated poor germination in the first experiment. Germination was still poor with *C. arvense* in the second experiment. To compensate for this in evaluating growth response, we transplanted *C. arvense* from pots with successful germination to empty pots for the growth portion of the study.

Table 1. Life history characteristics of experimental upland and wetland species

Species	Life Cycle & Growth Form	Successional Stage	Short-Term Reveg. Potential*	Long-Term Reveg. Potential*
<i>Agropyron spicatum</i>	Native Perennial Grass	Late	NA	NA
<i>Helianthus annuus</i>	Native Annual Forb	Early	NA	NA
<i>Centaurea maculosa</i>	Exotic Perennial Forb	Early to late (Invasive weed)	NA	NA
<i>Deschampsia cespitosa</i>	Native Perennial Grass	NA	Low	High
<i>Beckmannia syzigachne</i>	Native Annual Grass	NA	Moderate	Low
<i>Cirsium arvense</i>	Exotic Perennial Forb	NA	NA	NA

*Revegetation potential based on Hansen et al. (1997).

Greenhouse Water Treatment

Six pots were placed in each of 42 plastic tubs (40 cm deep by 40 cm wide by 50 cm long) and each pot was seeded with one of the six species. A depth-to-water-table gradient was created by maintaining each tub at one of seven, randomly assigned,

constant water levels: 0 and 2 cm above the soil surface, 5, 10, 20 and 30 cm below the soil surface, and "dry" with no water from sub-irrigation. Pots were left open at the bottom to allow water flow into and out of the soil column. All pots were also watered from above weekly with 155 ml of deionized water, N solution or sucrose solution. This watering regime was designed to simulate spring rainfall in a southwest Montana, semi-arid, rangeland environment (data for Norris, MT, Western Regional Climate Center, Reno, NV).

Nitrogen Treatments

One of three nutrient treatments was randomly assigned to each tub: a control with no additions, high nitrogen addition (equivalent to 100 Kg N/ha applied to 100 cm² soil surface) and nutrient depletion through the addition of sucrose (1000 Kg C/ha). Sucrose provides a carbon source for microbes leading to increased immobilization of nitrogen and other nutrients. These treatments were applied in weekly increments for 16 weeks through additions to each pot of either 155 ml of deionized water, 155 ml of deionized water with 0.024 g of ammonium chloride in solution (0.006 g of N), or 155 ml of deionized water with 0.149 g of sucrose in solution (0.062g of C).

Sampling and Data Analysis

In both experiments, seedlings were counted 70 days after planting. At this time plants were thinned to a single individual per pot. Aboveground biomass was harvested 130 days after planting then dried to a constant mass and weighed. Biomass and emergence results from the first and second experiments were compared using analysis of variance at the 0.10 significance level. This revealed that results of the two experiments

were significantly different. Therefore, data from the two experiments were analyzed separately.

Multiple, linear regression analysis was used to assess the effects of treatments on seedling establishment and biomass. The initial models tested included depth to water table, nitrogen treatment, and location in the greenhouse as independent variables and either seedling emergence or biomass of individual species as the dependent variables. Significance of independent variables was tested at the 0.10 level. The final models presented were constructed by stepwise elimination of nonsignificant, independent variables. Better fits for some species were obtained using natural log transformations of emergence or biomass data. For consistency, predicted values were then un-transformed for graphical presentation; as a result, these models are shown as exponentially decreasing curves. Residual sums of squares were analyzed to test for significant differences between regression models for each N treatment within a species (Ratkowski 1983). Regression analyses used data only for flooded to sub-irrigated pots (water table elevation ranging from +2 cm to -30 cm). The "dry" (non-subirrigated) treatment was not included in the regression because it did not represent a quantitative continuation of the independent variable (depth to water table). Data from the dry pots were analyzed separately using one way analysis of variance to assess the effects of N treatments on emergence and growth with no sub-irrigation.

Results

Seedling Emergence

Analysis of variance for pots with no sub-irrigation ("dry") showed no significant effect of N treatments on number of seedlings for any species in either experiment. Regression analysis of seedling emergence of upland species from the first experiment showed significant relationships between depth to water table and emergence for *A. spicatum* and *C. maculosa* (Table 2 and Figure 1). Analysis of *A. spicatum* yielded significant, linear regression models for the sucrose, control and high N treatments. These models showed a negative relationship between rising water table and emergence with a 10 cm rise in water table predicting a decrease of approximately two seeds per pot with the sucrose and control treatments. As reflected by reported r^2 values (Tables 2-5) there is substantial uncertainty in predicted relationships. This trend was more pronounced with the high N treatment showing a decrease of about five seedlings per pot with a 10 cm rise in water table. Analysis of *C. maculosa* yielded significant regression models for the sucrose and control treatments with a 10 cm rise in water table predicting a decrease of approximately one seedling per pot (Table 2 and Figure 1). There was no significant difference between these regressions. No significant relationships were found between water depth and seedling emergence for *H. annuus*; however, because germination of *H. annuus* was very low, evidence of any relationship could not be determined. Emergence of the wetland species was not affected significantly by depth to water.

Table 2. Regression models for seedling emergence response to depth of water table, and sucrose and N additions for the first greenhouse experiment.

Species	Treatment	Intercept	slope	r ²	P value
<i>A. spicatum</i>	Sucrose	20.00	-1.90	0.29	0.04
	Control	20.70	-2.21	0.43	<0.01
	High N	35.20	-4.84	0.77	<0.01
<i>C. maculosa</i>	Sucrose	12.51	-1.11	0.33	0.05
	Control	11.45	-1.29	0.51	0.01
	High N	NS	NS	NS	NS
<i>H. annuus</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
<i>D. cespitosa</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
<i>C. arvense</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
<i>B. syzigachne</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS

* NS signifies the model is not significant at $\alpha=0.10$

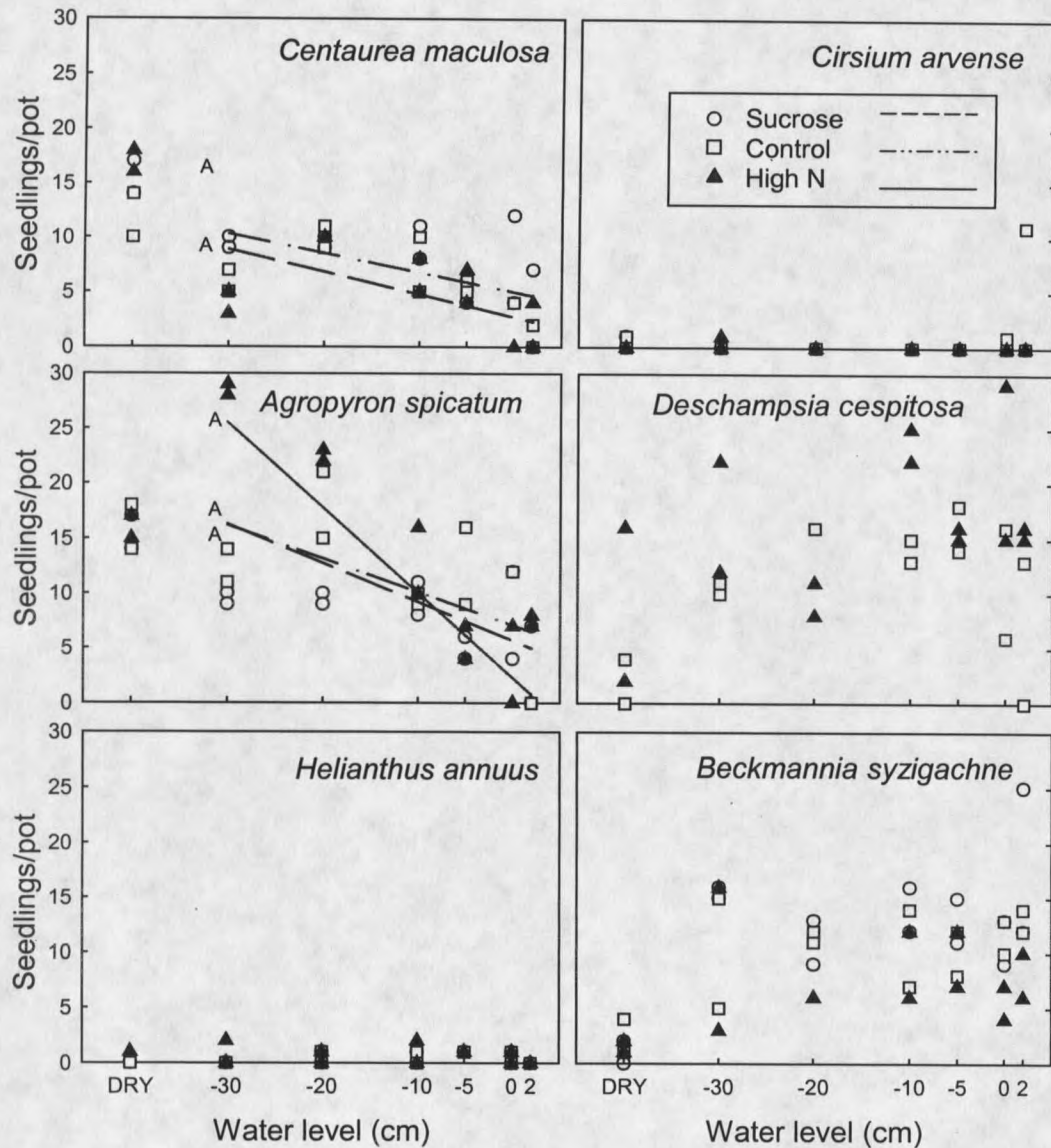


Figure 1. Seedling emergence in response to depth of water table, and sucrose and N additions in the first greenhouse experiment. Significant regressions are shown by lines and reported in Table 2. Regression models with the same letter are not significantly different. Regression analyses exclude dry treatment.

Regression analyses for the second experiment showed results similar to the first experiment indicating a significant relationship between seedling emergence and depth to water table for *A. spicatum* and *C. maculosa* (Table 3 and Figure 2). Models for both species showed a negative relationship between rising water table and emergence. A 10-cm rise in water table predicted a reduction of approximately 8 seedlings per pot at all N levels. For both species linear regression models were significant for sucrose, control and high N treatment levels, but there were no significant differences among the models. These models explained a higher percentage of the variability in seedling emergence with water depth than those from the first experiment (Tables 2 and 3).

Analysis of wetland species seedling emergence for the second experiment showed significant responses of *D. cespitosa* to water depth in the sucrose, control and high N treatments (Table 3 and Figure 2). Models at all three N levels indicated a negative relationship between rising water table seedling emergence. A 10-cm rise in water table predicted a decrease of approximately 10 seedlings per pot. There were no significant differences between the regression models. *C. arvense* seedling emergence responded to water significantly only in the control treatment (Table 3 and Figure 2). This model predicted a decrease of approximately two seedlings per pot with a 10-cm rise in water table. Analysis of effects of water level and N on *C. arvense* was hampered by poor germination in both experiments. This did not reflect low *C. arvense* seed viability; tests indicated 30-40% germination on moist filter paper. *B. syzigachne* seedling emergence did not vary significantly with water level.

Table 3. Regression models for seedling emergence response to depth of water table, and sucrose and N additions for the second greenhouse experiment.

Species	Treatment	Intercept	slope	r ²	P value
<i>A. spicatum</i>	Sucrose	58.40	-8.70	0.79	<0.10
	Control	63.18	-9.11	0.79	<0.10
	High N	58.57	-8.70	0.72	<0.10
<i>C. maculosa</i>	Sucrose	65.18	-9.11	0.94	<0.10
	Control	74.09	-11.56	0.90	<0.10
	High N	55.64	-7.77	0.59	<0.10
<i>H. annuus</i>	Sucrose	1.25	-0.19	0.25	0.10
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
<i>D. cespitosa</i>	Sucrose	70.9	-7.57	0.35	0.04
	Control	80.37	-9.97	0.42	0.02
	High N	82.82	-10.76	0.71	<0.10
<i>C. arvense</i>	Sucrose	NS	NS	NS	NS
	Control	16.5	-2.5	0.25	0.10
	High N	NS	NS	NS	NS
<i>B. syzigachne</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS

* NS signifies the model is not significant at $\alpha = 0.10$.

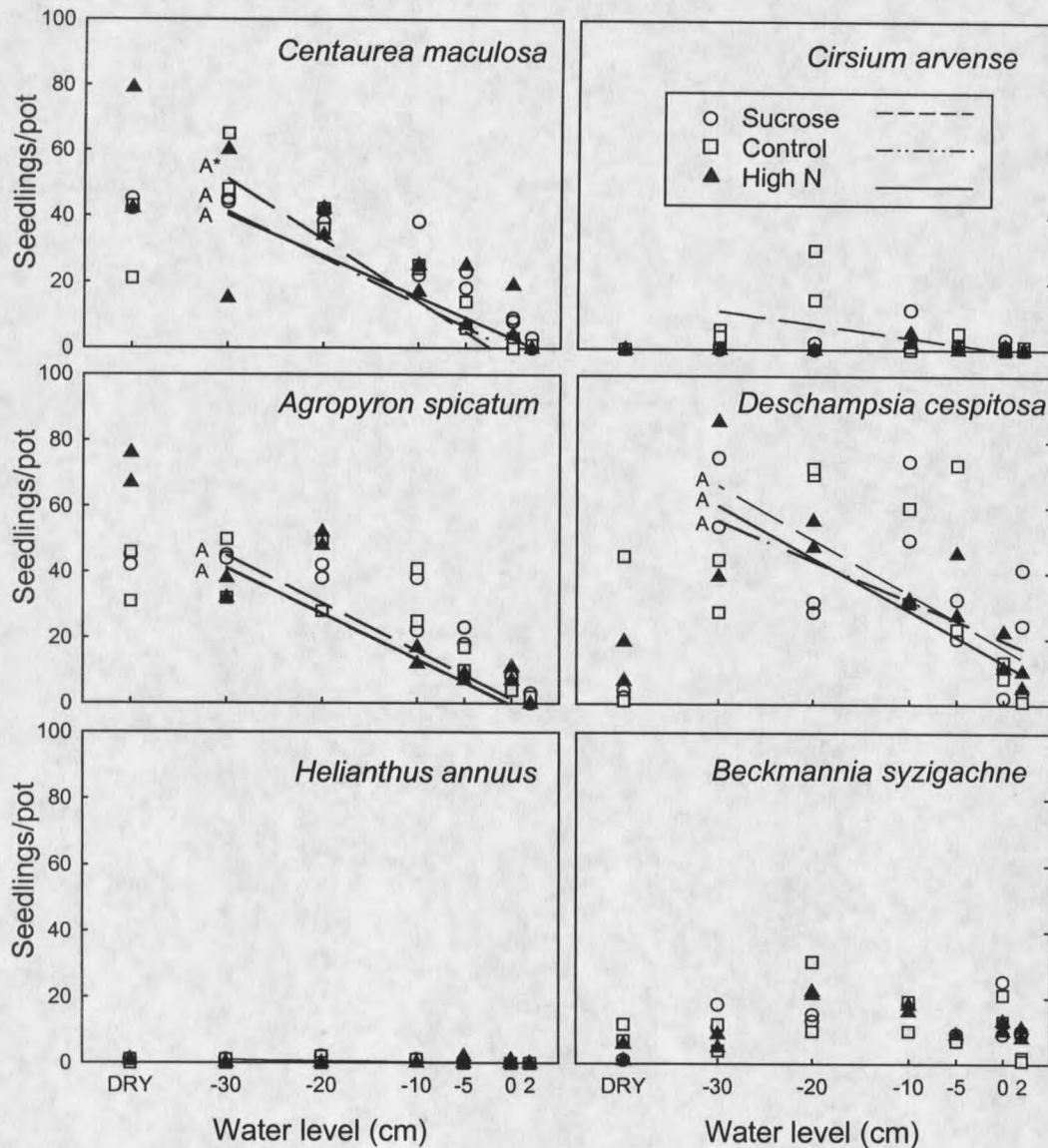


Figure 2. Seedling emergence in response to depth of water table, and sucrose and N additions in the second greenhouse experiment. Significant regressions are shown by lines and reported in Table 3. Regression models with the same letter are not significantly different. Regressions exclude dry treatment.

Biomass

Analysis of variance for pots with no sub-irrigation showed no significant effect of N treatments on biomass for any species in either experiment. In the first experiment biomass for all three upland species decreased significantly as water level rose (Table 4 and Figure 3). A 10 cm rise in water table predicted a decrease of approximately one g of *A. spicatum* biomass for the sucrose and control treatments, and two g at the high N treatments. The high N model was significantly different. Nitrogen addition resulted in higher biomass, particularly at -20 and -30 cm water levels. The sucrose and control models were not significantly different. Results for *C. maculosa* were similar to *A. spicatum* with biomass significantly higher for the high N treatment than the control or sucrose models, and no significant difference between the control and sucrose treatments. *H. annuus* biomass responded significantly to water depth in the high N treatment only. Biomass of the wetland species *D. cespitosa* and *B. syzigachne* in the first experiment decreased significantly with rising water table (Table 4 and Figure 3). Both species showed a decrease of approximately 3-g of biomass at all N levels with a 10-cm rise in water table. Because emergence and growth of *C. arvense* were consistently low, no significant relationships with water level and N were found. For *D. cespitosa* the regression models predicted higher biomass for the high N treatment than the sucrose. The control did not differ significantly from the other treatments. These models predicted a decrease of approximately 3-g of biomass with a 10-cm rise in water table. Significant regression models for *B. syzigachne* were found for the control and the high N treatments, and the model for the high N treatment predicted higher biomass than the control treatment. The *C. maculosa* model predicted approximately a 0.5-g reduction in

Table 4. Regression models for above ground biomass response to depth of water table, and sucrose and N additions for the first greenhouse experiment.

Species	Treatment	Intercept	slope	r ²	P value
<i>A. spicatum</i>	Sucrose	3.07	-0.51	0.51	0.01
	Control	3.30	-0.51	0.54	0.01
	High N	9.43	-1.54	0.58	0.01
<i>C. maculosa</i>	Sucrose	2.47	-0.39	0.83	<0.10
	Control	2.67	-0.40	0.73	<0.10
	High N	4.12	-0.61	0.88	<0.10
<i>H. annuus</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	15.80	-2.58	0.26	0.09
<i>D. cespitosa</i>	Sucrose	7.55	-0.93	0.46	0.01
	Control	11.30	-1.36	0.37	0.04
	High N	16.80	-1.97	0.58	<0.10
<i>C. arvense</i>	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
<i>B. syzigachne</i>	Sucrose	NS	NS	NS	NS
	Control	2.44	-0.21	0.64	<0.10
	High N	2.86	-0.22	0.67	<0.10

* NS signifies the model is not significant at $\alpha = 0.10$.

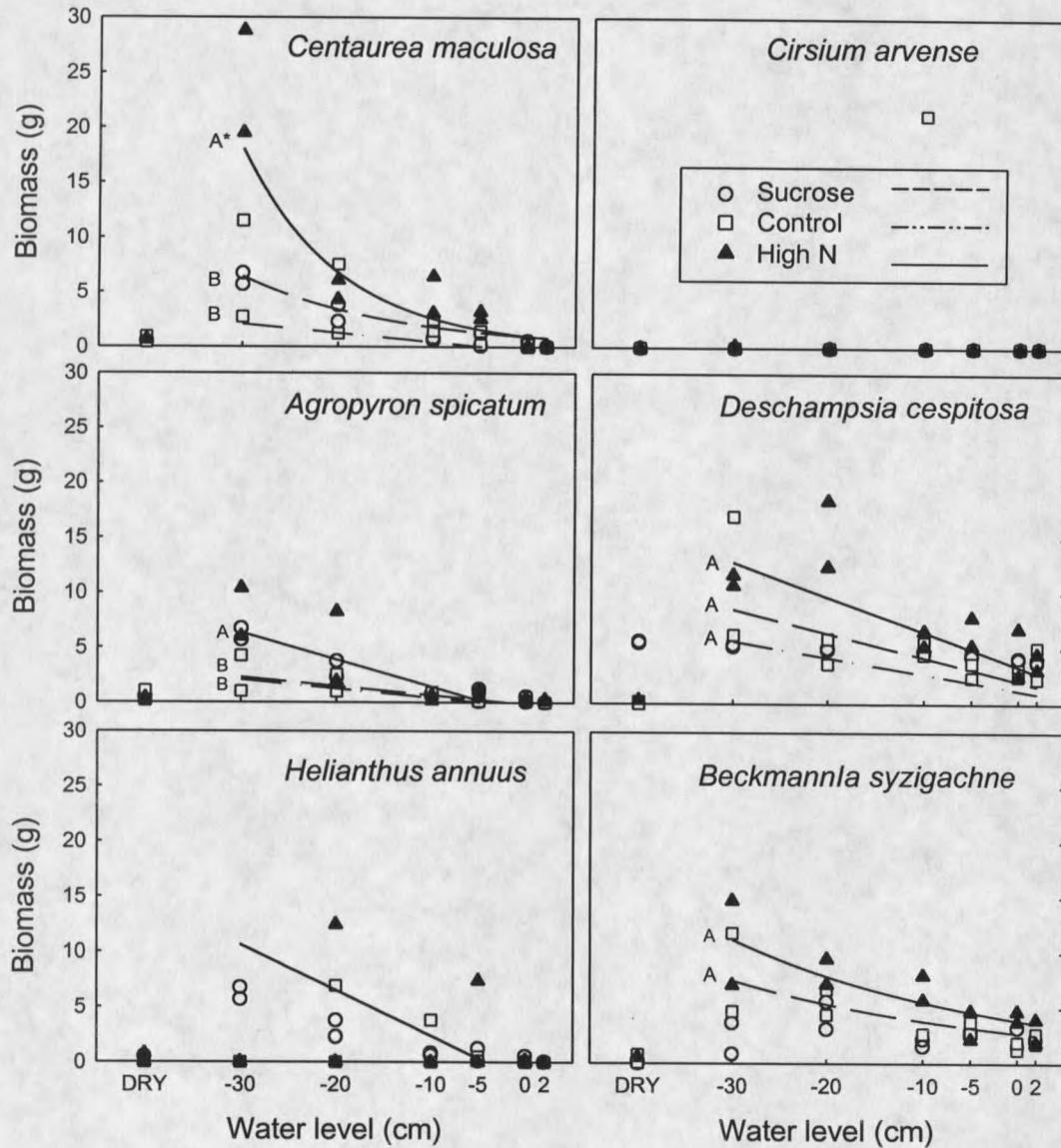


Figure 3. Above ground biomass response to depth of water table, and sucrose and N additions in the first greenhouse experiment. Significant regressions are shown by lines and reported in Table 4. Regression models with the same letter are not significantly different. Regression analyses exclude dry treatment

biomass with 10-cm rise in water table in sucrose and control treatments (Table 5 and Figure 4). The response to water level was more pronounced at the high N level, particularly at the -30 and -20 levels. A 10-cm rise in water table predicted a decrease in

Table 5. Regression models for above ground biomass response to depth of water table, and sucrose and N additions for the second greenhouse experiment.

Species	Treatment	Intercept	slope	r ²	P value
<i>A. spicatum</i>	Sucrose	1.34	-0.23	0.56	0.01
	Control	1.11	-0.18	0.56	0.00
	High N	NS	NS	NS	NS
<i>C. maculosa</i>	Sucrose	0.58	-0.09	0.53	0.01
	Control	0.97	-0.16	0.75	0.00
	High N	1.84	-0.27	0.95	0.00
<i>H. annuus</i>	Sucrose	0.43	-0.07	0.25	0.09
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
<i>D. cespitosa</i>	Sucrose	3.33	-0.50	0.38	0.03
	Control	3.01	-0.46	0.67	0.00
	High N	3.00	-0.39	0.52	0.01
<i>C. arvense</i>	Sucrose	0.93	-0.15	0.30	0.06
	Control	1.63	-0.24	0.46	0.02
	High N	1.44	-0.21	0.47	0.01
<i>B. syzigachne</i>	Sucrose	NS	NS	NS	NS
	Control	2.67	-0.31	0.26	0.09
	High N	NS	NS	NS	NS

* NS signifies the model is not significant at $\alpha=0.10$.

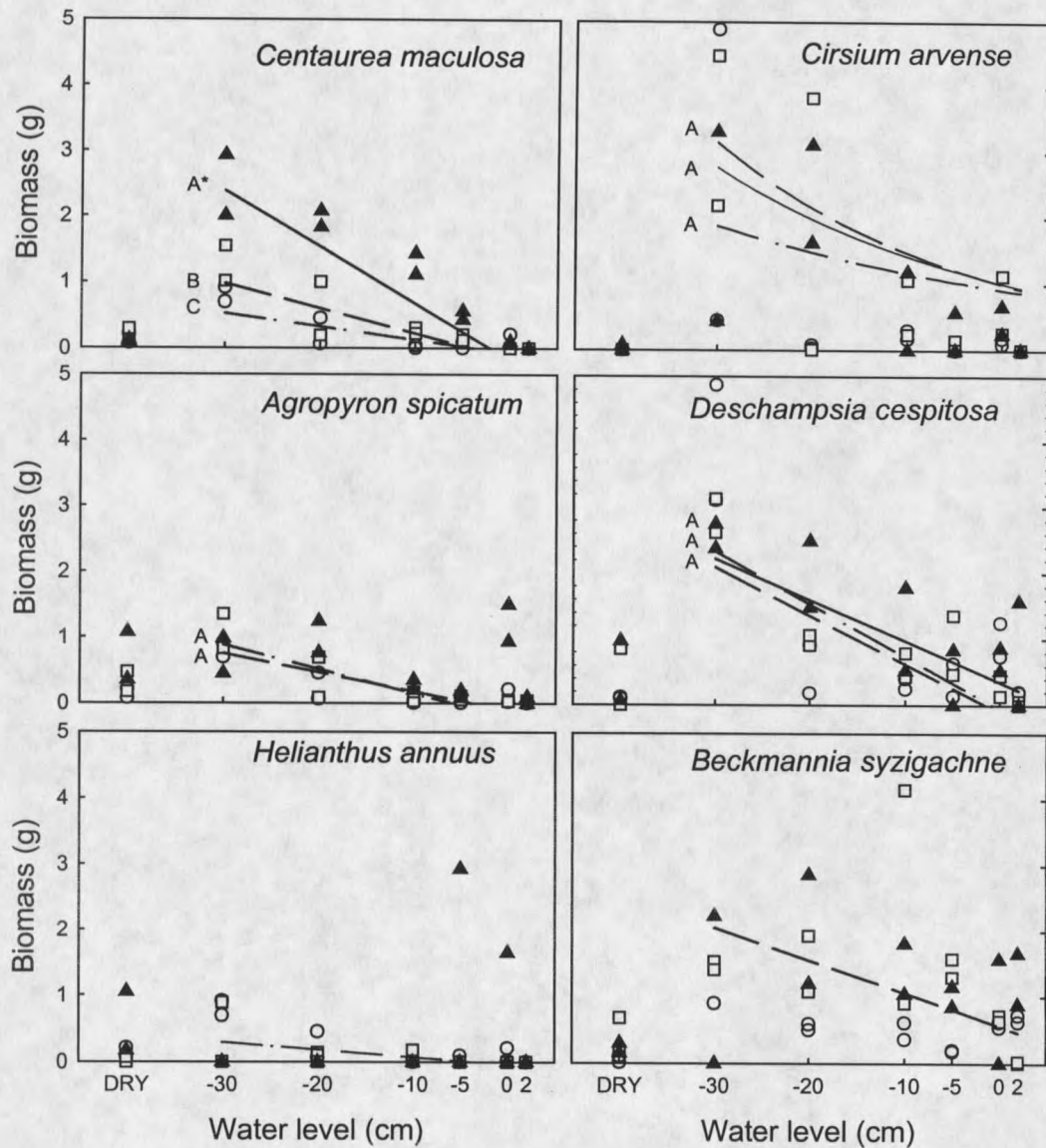


Figure 4. Above ground biomass response to depth of water table, and sucrose and N additions in the second greenhouse experiment. Significant regressions are shown by lines and reported in Table 5. Regression models with the same letter are not significantly different. Regression analyses exclude dry treatment.

biomass ranging from approximately 1.0 g to 0.25 g. Models for *C. maculosa* at all N treatments were significantly different and biomass was highest in high N treatment. *H. annuus* biomass decreased by approximately 0.10 g with a 10-cm rise in water table in the sucrose treatment, but the fit of this model was poor explaining only 25% of the variability in biomass with water depth. Models for the other treatments were not significant.

Biomass of the wetland species *D. cespitosa*, *C. arvense*, and *B. syzigachne* showed a weak, negative relationship between rising water-table elevation and biomass with a 10 cm rise in water table predicting a decrease of approximately 0.01 g of plant biomass (Table 5 and Figure 4). Models were significant in all N treatments for *D. cespitosa* and *C. arvense*, but none of the models were significantly different. The *B. syzigachne* model was significant only in control treatment, and this model only explained 26% of the variability in biomass with water depth.

Discussion

Emergence responses to water depth were varied and species specific, but upland species' responses were generally more pronounced. Nitrogen did not affect any species emergence. In the early stages of emergence it is likely that little development of roots had occurred, perhaps limiting the influence of nutrients on seedling emergence and growth. Seedling emergence results in both experiments showed the upland perennial grass (*A. spicatum*) and the perennial weed (*C. maculosa*) to be relatively intolerant of wet conditions. The linear trend of increasing emergence from flooded to sub-irrigated pots shows highest establishment for both of these species at the -20 to -30-cm water

levels. Recall that the "dry" (non-subirrigated) treatment was not included in the regression. Scatter plots, however, reveal relatively high emergence of upland species in dry tubs, similar to that seen at the -30 cm level. It is possible that the optimal depth to water table for these upland species was not contained in this experiment (e.g. a depth to water of -40 cm, -50 cm, etc.). Results suggest, though, that highest emergence for the upland plants studied occurs in sub-irrigated to dry environments, and that emergence is inhibited as the water table rises above 20 to 30 cm below the soil surface. Similarly, van der Valk et al. (1992) found an inverse relationship between soil moisture and upland plant recruitment in prairie pothole wetlands.

In contrast to the upland species, seedling emergence of the facultative wetland species studied was only slightly affected by water depth. In the first experiment, emergence was not related to water level, and in the second experiment, significant regression models for *D. cespitosa* and *C. arvensis* explained only a small fraction of variation in emergence (Table 4). For *D. cespitosa*, emergence appeared to be approximately uniform for water levels from -5 to -30 cm and lower for saturated flooded and dry treatments. A pot study on *Populus deltoides* (Aiton) (plains cottonwood) had similar emergence at all sub-irrigated water levels except the driest (water table 50 and 60 cm below soil surface) (Shafroth et al. 1994). Conversely, emergence of *Sabal palmetto* (Walt.) (cabbage palm) was inversely related to increasing water table elevation, but the relationship occurred only on sites with highly saline water (Perry and Williams 1996). This suggests that in freshwater wetlands, depths ranging from flooded to sub-irrigated conditions may all be favorable for wetland species establishment. Depth to water may

not significantly influence emergence until it is deeper than those levels investigated in this experiment.

C. arvense was an exception to the observed emergence pattern. In both experiments, this weedy species germinated poorly, in contrast to *C. maculosa*. *C. arvense* is a dioecious species that ordinarily grows in patches. Therefore sterile heads of female flowers are common if pollen producing flowers are not near (Moore 1975). Germination may limit establishment of this species, suggesting management should focus on control of vegetative spread from existing infestations (Sheley and Petroff 1999).

Results suggest that while emergence of upland species is inhibited by sub-irrigation when the water table rises higher than 20 to 30 cm below the surface, wetland species emerge relatively successfully in these environments at all sub-irrigated water levels studied, and in some cases with flooding. Supporting this, research on lake shore zonation found exposure to waves, not depth to water table, to be most influential on vegetative patterns (Wilson and Keddy 1986, Wilson 1986). In addition, soil particle size is highly influential on germination of shoreline plants, though this effect is most pronounced in drier locations (Keddy and Constabel 1986). Facultative wetland species may be ideal for re-vegetation of subirrigated areas with spatial and temporal variations in water table. Furthermore, it may be possible to use seed mixes composed of facultative wetland species without fine tuning them for narrow, micro-environments in riparian areas, because they may emerge successfully across the sub-irrigated and flooded zone of the hydrologic gradient. Subsequently survival and growth will restrict a species' distribution to appropriate environments.

Biomass response to depth of water table did not show a distinction between upland and wetland species. In both experiments, most species' growth was enhanced significantly by lower water levels, within the sub-irrigated tubs, in at least one treatment (sucrose, control or high N). Similarly, oat yields were highest in W. Montana wet meadows with a water table 12" (30.5 cm) below the soil surface (Klages and Asleson 1959). This growth response is similar to the seedling emergence response for the upland species, but contrasts with the lack of a water level effect on seedling emergence of the facultative wetlands species. This suggests that while some wetland plants' germination may not be limited by flooding, once their roots extend down through the soil they are subjected to flooding stress that can limit growth. *Scirpus maritimus* (an obligate wetland plant) showed an opposite response yielding greater biomass in flooded soils (Liefers and Shay 1980). In contrast, Shipley et al. (1990) found no differences in productivity of facultative wetland species along a lake-shore, depth to water table gradient. They focused on the adult stage of growth using transplanted plants, not early establishment and growth. For the first experiment little biomass data was available for *C. arvense* because germination was very low. During the second experiment, though, many *C. arvense* transplants performed well, suggesting that once this weed is established it can thrive in riparian areas. Individual *C. arvense* seedlings, once established, can rapidly form dense patches (Donald 1994).

N treatments influenced plant growth, but not seedling emergence. Generally, nitrogen addition encouraged plant growth, but this trend was somewhat inconsistent between the two experiments and among species. No wetland species' growth was influenced by nitrogen additions, suggesting N management may not be important for

revegetation of the facultative wetland species studied. In the stressful environment of a flooded or saturated soil, N may not be the limiting factor for growth. In contrast, N additions to *Spartina foliosa* (cordgrass) communities increased stem length and canopy cover (Boyer and Zedler 1998). Cordgrass, an obligate wetland plant, may be more tolerant of flooding stress than the facultative wetland species in this experiment, perhaps allowing it to take advantage of N supplements. In addition, N application to saturated or flooded soils may be negated by denitrification (Reddy et al. 1989).

The upland species *C. maculosa* and *A. spicatum* responded to N additions. In the first experiment, *C. maculosa* and *A. spicatum* showed similar responses with regression models predicting highest biomass with the high N treatment. This suggests that growth of the perennial grass and weed species studied is equally affected by N in the early stages of establishment. In the second experiment, though, *C. maculosa* growth was fostered by N addition and inhibited by sucrose. In contrast, no difference between sucrose and control treatments for *A. spicatum* occurred. This suggests that N may favor weeds, as argued by a growing body of research on the potential of directing succession by altering nutrient availability (Tilman and Wedin 1991, McLendon and Redente 1991, Redente et al. 1992, Herron et al. 1999). The inconsistent results of the two greenhouse experiments suggest that predictability of plant responses to hydrology and nutrients may be limited, particularly in a field setting. However, if results of the second experiment are confirmed by further research, they may have important implications for the promotion of *C. maculosa* over native grasses by N addition. In light of published research and some of the results presented here, caution in use of N in riparian revegetation is recommended.

CHAPTER 3

EFFECTS OF A NATURAL RIPARIAN RESOURCE GRADIENT ON THE
ESTABLISHMENT OF NATIVE AND INVASIVE SPECIESIntroduction

The greenhouse study reported in Chapter 2 investigated effects of water level and nitrogen on plant establishment under relatively controlled conditions. The field study investigated the influences of hydrology and nitrogen on plant establishment under more realistic conditions applicable to riparian restoration and weed management. A nitrogen manipulation experiment was conducted at four locations along an upland-to-wetland gradient with strong variation in depth to water, soils, and animal activity.

Materials and MethodsSite Characterization

The experiment was performed along a 200 m upland/riparian gradient found on Warm Spring Creek at Red Bluff Research Ranch, approximately 2 km. east of Norris, MT (45° 35' N, 111° 39' W). Dominant grasses in upland areas include *Festuca idahoensis* (Elmer) and *Bouteloua gracilis* (Lag.) with occasional occurrences of *Agropyron smithii* (Rydb.) and *Agropyron spicatum*, (Scribn. and Smith). Upland shrubs and forbs include *Artemesia frigida* (Willd.), *Gutierrezia sarothrae* (Britt. and Rusby), *Achillea millefolium* (L.), *Iva axillaris* (Pursh) and *Grindelia squarrosa* (Dunal). Upland basal cover is dominated by *Selaginella densa* (Rydb.). Subirrigated locations along the

gradient are almost exclusively dominated by *Carex* spp., except for a pronounced band of *Cirsium arvense* (L.), approximately 3 meters wide, at the transition from wetland to upland, and some *Typha latifolia* L.). Mapped soil types include the Varney cobbly clay loam in the uplands and fluvaquentic haplaquolls in the subirrigated areas (Boast and Shelito 1989). Mean annual precipitation is 39.7 cm (15.0 inches) and mean annual temperature is C°(F°). Elevation is approximately 1460 m (4800 feet).

Four study areas were established along the gradient. Locations were based on survey of water table levels May of 1998. The upland study area was placed at a location with a May 1998 water table greater than 1.5 m below ground surface. Two transitional study sites were placed where the May 1998 water table was 49 cm to 28 cm and 15 cm to 3 cm below the surface. The wetland study site was placed in a saturated site where water was at or above the level of the soil surface. Transitional areas were adjacent to each other and approximately 60 m from upland and wetland areas. A spring creek originated 33 m below the lower transitional area and flowed within 4 m of the wetland. Sites were fenced to exclude livestock.

Groundwater levels were characterized with a series of shallow wells. Seventeen wells were placed at the two transitional areas, and another 17 at the wetland area. In each area eight wells were placed along two sides of the experimental areas, running downslope, and one well in the center. Wells were made of perforated PVC pipe and inserted to a depth of 30-200 cm using a bucket auger in May of 1998. Six additional wells were placed between the upland and transitional areas in June of 1999. These were inserted to a depth of 1.3-2.7 m with a truck-mounted, hydraulic auger. Water levels were measured weekly from May to October in 1998 and from April to August in 1999,

and once in May of 2000. Soil surface elevations at all wells and experimental plots were determined using a laser level and used to estimate water table depths relative to the soil surface in individual plots and to describe water table and soil surface elevation. Water table depths for study plots were estimated by linear interpolation between wells.

Elevations are reported relative to the water surface in the spring creek at the base of the wetland study area.

To characterize soil texture, five 15 cm. deep by 4.9 cm. diameter soil cores were collected from each of the four study areas. Four samples were collected from the corners of each enclosure and one sample was collected from the center. Sand, silt and clay content of soils were measured using the hydrometer method (Bouyoucos 1962).

To characterize bulk density, five soil samples of known volume were collected from each area. In the upland areas, 15 X 4.9 cm cores were used. In transitional and wetland areas, coring resulted in compacted samples, so, five, rectangular samples were cut with a soil knife and measured to calculate volume. All samples were oven dried at 105 °C for 48 hours, and weighed. Sample masses were divided by sample volumes to calculate bulk density.

To characterize background levels of inorganic N, five samples located in the undisturbed buffer zones between plots were collected in each study area. Two 15 X 4.9 cm. soil cores were collected at each point, composited, and sieved through a 2mm screen. Ten gram soil subsamples were placed in 100-ml containers with 50 ml of 2M KCL, and shaken for one hour on a reciprocal shaker. Extracts were filtered through Whatman #42 filters and frozen at -20 ° C for later analysis. Ammonium and nitrate

concentrations were estimated colormetrically (Yang et al. 1998) using a Spectronic 601 spectrophotometer

Experimental Design

The experiment was a completely randomized, two factor, factorial design with three replications. Factors consisted of six plant species: [*Centaurea maculosa* (Lam.), *Agropyron spicatum* (Scribn. and smith), *Helianthus annuus* (L.), *Cirsium arvense* (L.), *Deschampsia cespitosa* (L.) and *Beckmannia syzigachne* (Steud)] and four N treatments: [control, 10 kg N/ha/yr, 100 kg N/ha/yr, and nutrient depletion through the addition of sucrose at 1000 kg C/ha/yr]. The design was repeated at four different areas along the hydrologic gradient.

Species Selection

Six species common to the northern Rocky Mountains were investigated (Table 1, Chapter 2). These species represented contrasting, life history characteristics.

Helianthus annuus and *Agropyron spicatum* are upland, native species representing early and late successional communities (Stubbenieck, Hatch and Butterfield 1991).

Centaurea maculosa is an upland, perennial non-indigenous weed (Sheley and Petroff, 1999). Because successional status of many wetland species is unclear, life cycle and short-term versus long-term revegetation potential were used to select wetland species (Hansen et al. 1997). These characteristics may correlate with successional status or with the ability to exploit resource rich sites versus the ability to survive and compete in resource poor, highly stressful environments. *Beckmannia syzigachne* and *Deschampsia cespitosa* are wetland species representing species with either high short-term

revegetation potential high long-term revegetation potential, (Hansen et al. 1997) and annual and perennial life cycles, respectively (Cooper and Meirings 1989). *Cirsium arvense* is a perennial, non-indigenous invasive weed common in riparian areas (Sheley and Petroff 1999).

Nitrogen Treatment

One of four nutrient treatments was randomly assigned to each plot: control, low nitrogen addition (10 kg N/ha/yr), high nitrogen addition (100 kg N/ha/yr) or nutrient depletion through the addition of sucrose (1000 kg C/ha/yr). Sucrose provides a carbon source for microbes leading to increased immobilization of nitrogen. Granular 46-0-0 ammonium nitrate and sucrose were applied to the experimental plots on April 11, May 11, June 8, and July 7, 1999. On each of these dates 0.98 g of ammonium nitrate was applied to each 1 m² plot for the low N treatment, 9.8 grams of NH₄NO₃ for the high N treatment, and 83.3 grams of sucrose for the N depletion treatment.

Inorganic N was monitored by placing ion exchange resin bags (Yang et al. 1991) in subset of plots. Bags were randomly placed in three plots randomly selected from each of the four N treatments, resulting in twelve bags at each area. Bags were placed approximately five cm below the soil surface on April 11, May 11, June 8, July 7, and August 3, 1999, removed after 28 days, and stored at 4° C for a maximum of 48 hours. Inorganic N was extracted and analyzed using the procedures described for soils.

Experimental Procedure

Livestock exclosures were constructed of field fencing for all four study sites during May and June of 1998. The two transitional sites were included in a single

exclosure of 39 by 19 meters. Upland and wetland sites were placed in individual exclosures of 21 by 19 meters. Seventy-two, 1-m square plots were delineated in each of the four exclosures with a one-meter buffer separating plots. Vegetation was eliminated from plots by applying a 1% solution of glyphosate (Rodeo®) herbicide using a backpack sprayer. Plots were sprayed on June 12, June 22 and July 17, 1998. A spray shield was used to restrict herbicide application to the experimental plots. When all above ground vegetation was dead, a gas powered weed eater and leaf rake were used to remove standing dead plants and litter. To minimize soil disturbance, seedbeds were left with 2-cm high stubble of dead vegetation.

Experimental species were seeded on randomly assigned, cleared, 1 m² plots. Plots were seeded on October 22 and 24, 1998. Seeds were hand broadcasted and covered with a thin (less than 2 mm) layer of inert sand to protect them from predation.

Sampling and Data Analysis

Seedling establishment was assessed by counting seedlings on August 4, 1999 and May 25, 2000. Counts were performed using a 0.25 m² frame divided into 100, 5 x 5-cm cells. The frames was placed on the inside 0.25 m² of each plot and seedlings were counted in a sub-sample of ten cells. Above ground biomass was harvested on August 9, 1999 from the inside 0.25 m² of all plots, oven dried and weighed.

Significance of N treatment effects on emergence and biomass for each location and species was assessed using one way analysis of variance (SAS version 7, SAS institute, Cary, NC). Species that emerged in all areas were analyzed for biomass trends across the gradient using linear and quadratic contrasts. Trend analysis was also

performed for N effects within sites for to test the hypothesis that biomass increases with N availability, with treatments ranked in the order sucrose, control, low N, and high N.

During 1999, extensive rodent activity was observed within the two transitional areas. Predation of seeded species by meadow voles (*Microtus* spp.) or other rodents may affect establishment. I attempted to quantify this rodent activity in with a visual estimate of rodent activity during May 2000. Plots were surveyed for rodent sign such as tracks, digging or other soil disturbances and assigned an index from 0 to 4 (0=no activity and 4=high activity).

Results

Site Characterization

Extrapolation from wells below the upland site indicated that depth to water table in upland plots was greater than two meters during the growing season (Figure 5).

Upland surface elevation ranged from 5.6 to 6.6 m above the spring creek. Median depths to water in the two transitional areas ranged from 55 cm below the surface in the highest wells to 15 cm below the soil surface in the lowest wells. Transition zone surface elevation ranged from 162 to 222 cm above the spring creek. Median depths to water in the wetland ranged from 15 cm below to 3 cm above the soil surface and increased with distance from the spring creek. Wetland surface elevations ranged from a few cm below to 10 cm above the spring creek, with up to 15 cm micro-relief within 1 m. During the study period, water levels fluctuated by 40 to 55 cm throughout the transition zone. Soils were saturated at or near the surface at least part of the time in the lower transition area but became increasingly dry in the upper transition area. High water levels were slightly

above the surface at the lower edge of the transition zone, 5 cm below the surface between the lower and upper transition areas, and 40 cm below the surface at the upper edge. Maximum depth to water increased from 35 cm below the surface at the lower edge to 94 cm at the upper edge.

Water levels fluctuated less in the wetland area than the transition area, and fluctuations increased with distance from the spring creek. Wells farthest from the creek showed water levels substantially below the creek in June and July, 1998, and from mid-July through early August, 1999. Water levels in wells near the creek remained near the surface during these periods, resulting in a water table that sloped strongly away from the creek (up to 65 cm difference over 17 m).

Soil textures varied along the gradient. The upland, upper transitional and lower transitional soils are sandy loams, while the wetland soils are silty clay loams. Bulk density declined from the upland area (1.14 g/cm^3) to the upper and lower transitional areas (0.81 g/cm^3 and 0.55 g/cm^3) and the wetland area (0.47 g/cm^3).

Inorganic soil nitrogen increased downslope (Figure 6). Highest levels of inorganic N were found in the lower transitional and wetland areas and these were not statistically different ($p < 0.10$). Resin bag N was lower in the upland area, and did not differ among other sites (Figure 7). Resin bag N showed no clear pattern in response to N treatments in any of the areas.

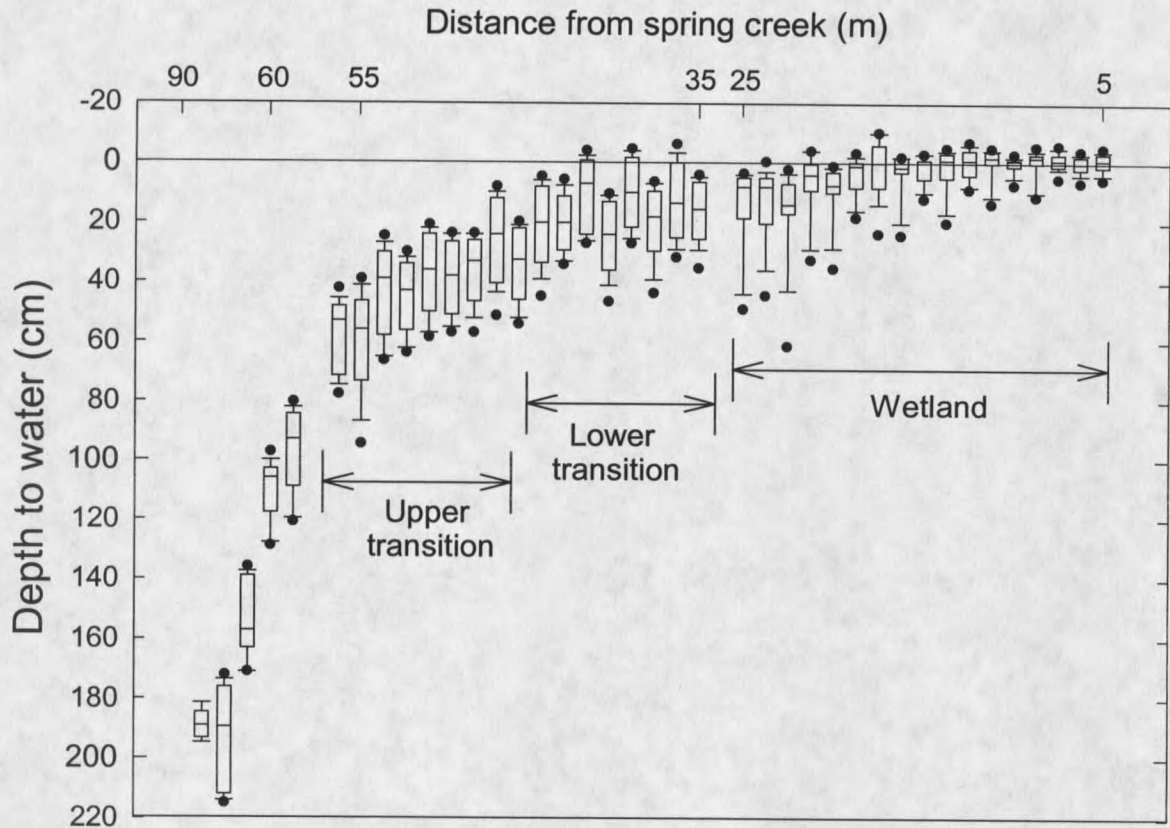


Figure 5. Depth to water in wells along the riparian gradient for May 1998 to May 2000. Boxes represent 25th and 75th percentiles, bars represent 10th and 90th percentiles, and dots are maximum and minimum depths. The solid lines within each box represent median depth to water for that well.

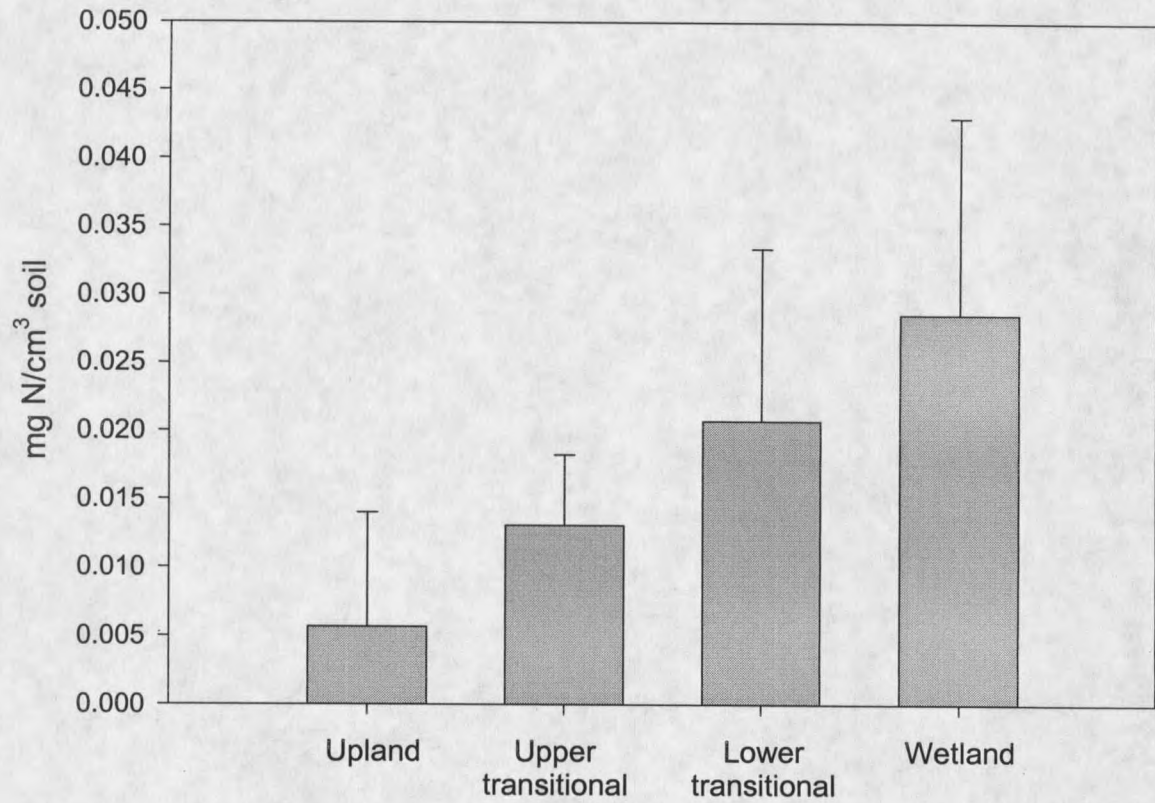


Figure 6. Average inorganic N extracted from 0-15 cm depth soil samples prior to application of N treatments. Error bars represent one standard deviation.

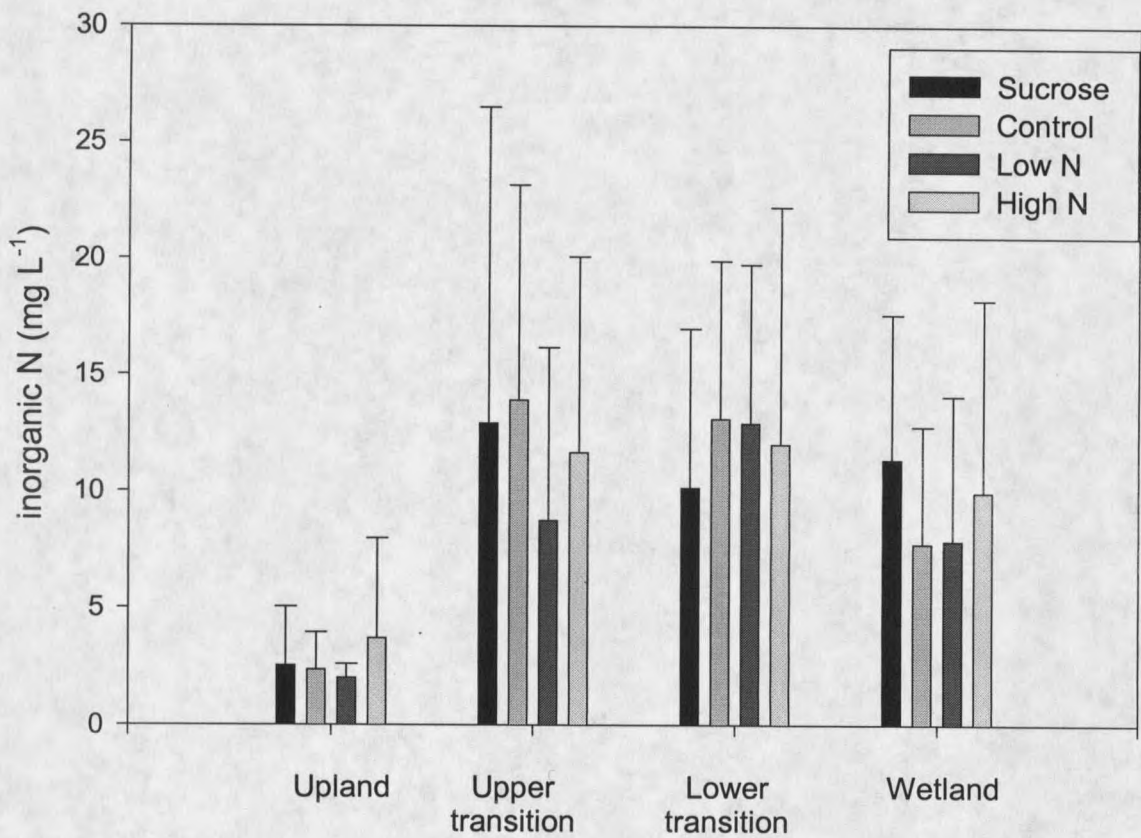


Figure 7. Season long mean inorganic N extracted from resin bags placed at 3 cm depth monthly throughout the 1999 growing season. Error bars represent one standard deviation.

Highest rodent activity was observed in the upper transitional site (Figure 8). The lower transitional site had moderate rodent activity in its upper portions and almost no activity in lower portions. The upland site showed low rodent activity, and the wetland had no observable activity.

Seedling emergence

Seedling counts were similar in 1999 and 2000. Emergence was very poor in both the lower and upper transitional areas. On average, about 200 *C. maculosa* and 40 *A. spicatum* seedlings emerged in the 0.25 m² upland plots (Figure 9) and persisted into the second growing season (Figure 10). About 100 *C. maculosa* and 20 *A. spicatum* seedlings emerged in the higher elevation 0.25 m² wetland plots in 1999, but neither species persisted there (Figure 9 and 10). Emergence of *H. annuus* was very low in all areas, although about 20 seedlings emerged in 1999 in the four highest wetland plots. About 300 *D. cespitosa* and 600 *B. syzigachne* seedlings emerged in wetland plots. In addition, *D. cespitosa* emerged across the gradient, but did not persist in the upland area and had low persistence in the upper transitional areas (Figures 9 and 10). This species was the only one to emerge in the two transitional areas with about 40 seedling in upper transitional plots and 50 seedlings in lower transitional plots. *C. arvense* did not emerge at any site. Most species showed no significant response to N treatments ($p < 0.10$). The exception to this was *B. syzigachne*. Emergence of this species was depressed by sucrose treatments in both the 1999 and 2000 counts.

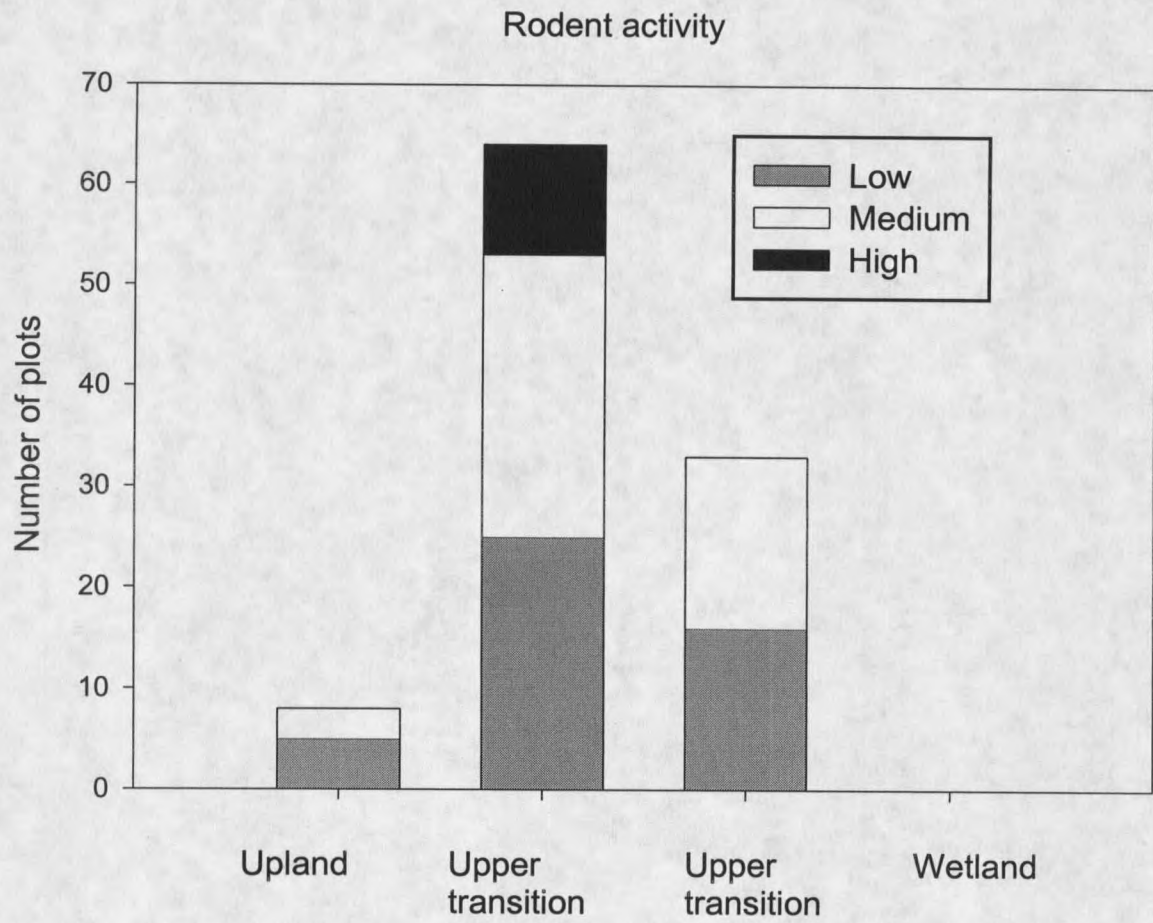


Figure 8. Frequency of rodent activity observed in the field in May of 2000.

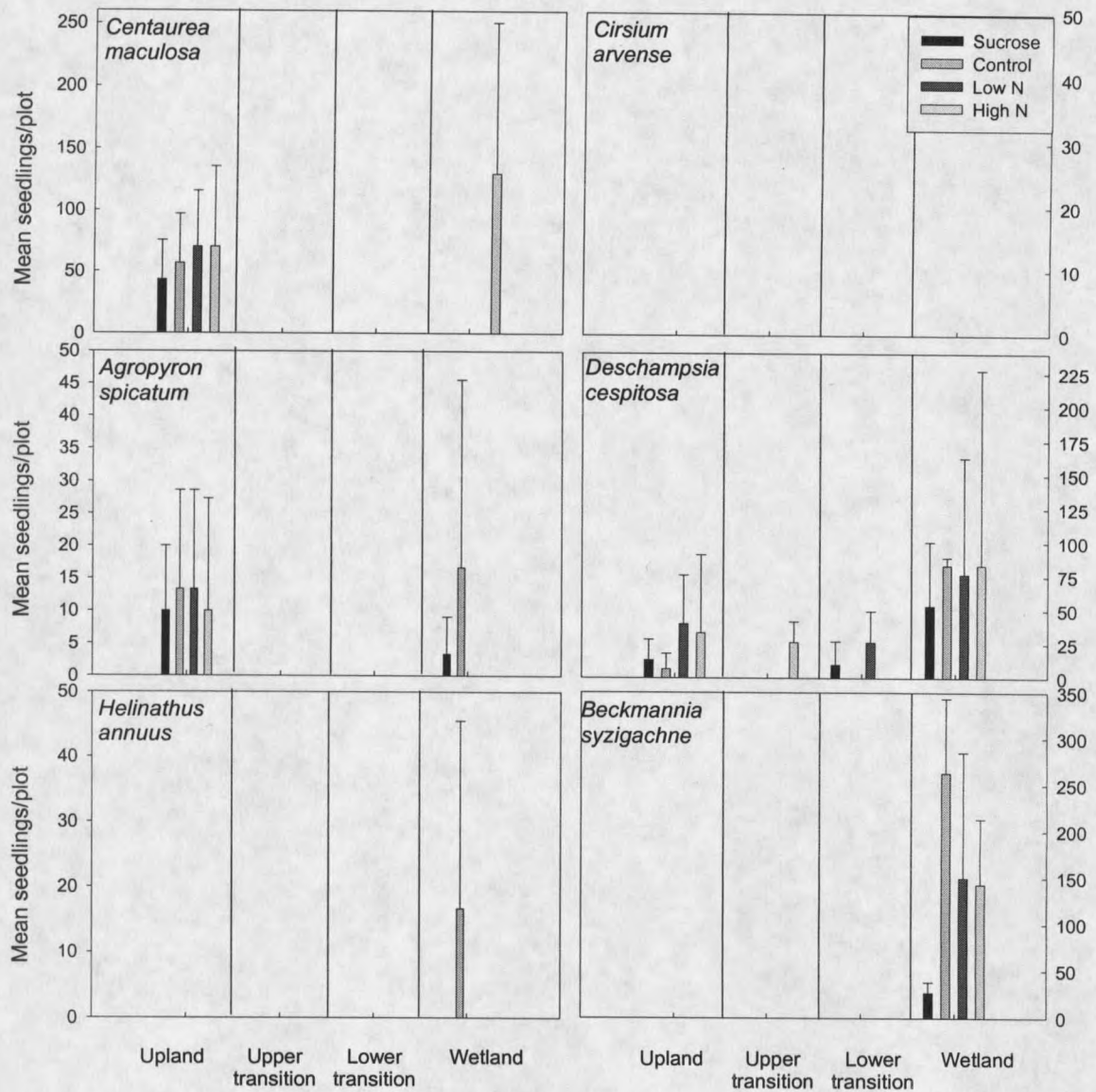


Figure 9. Seedling emergence response to N treatments at four areas along an upland to wetland gradient in 1999. Error bars represent one standard deviation.

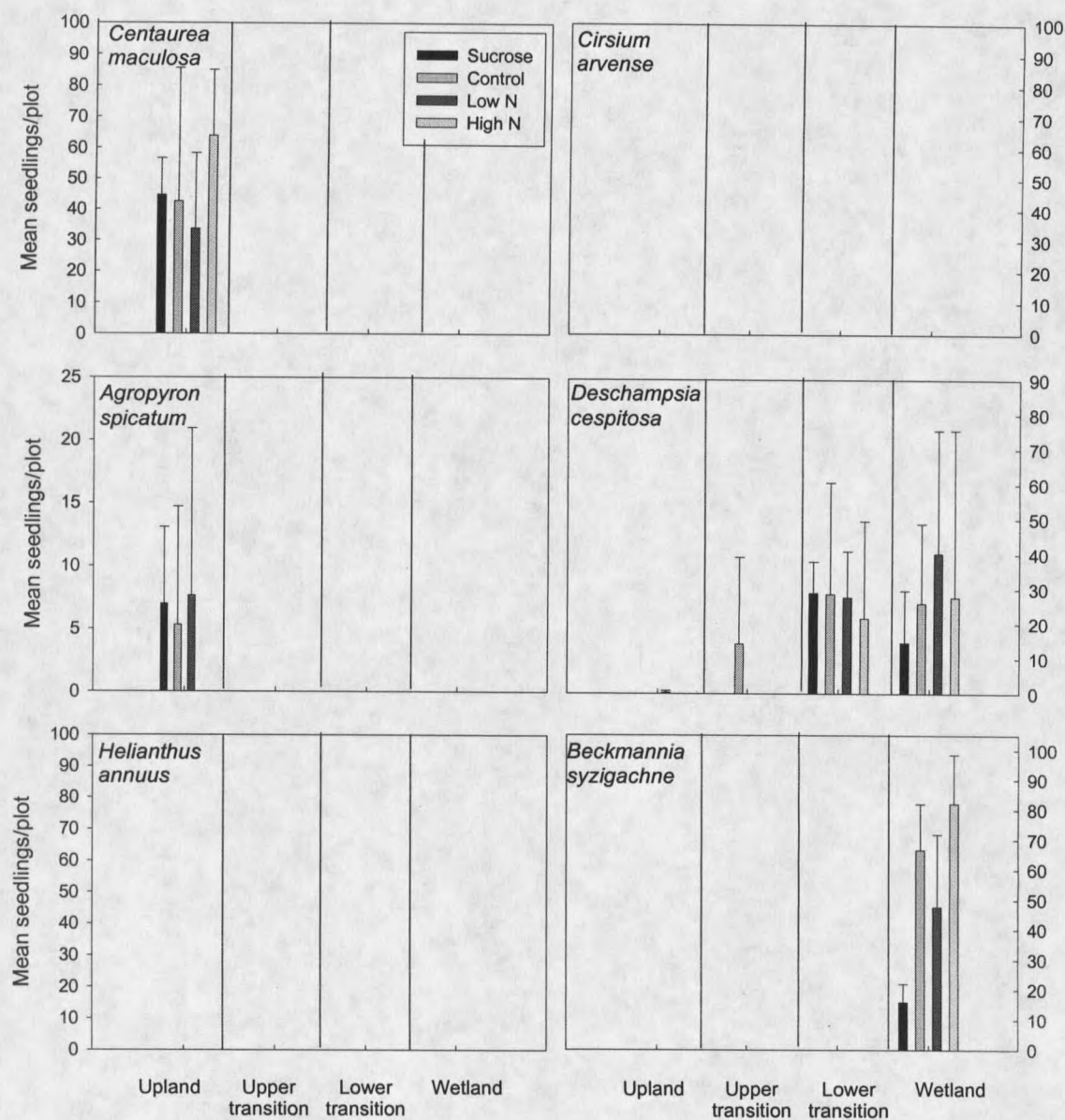


Figure 10. Seedling emergence response to N treatments at four areas along an upland to wetland gradient in June 2000. Error bars represent one standard deviation.

Biomass

Growth patterns were similar to emergence, but showed more N effects (Figure 11). *Deschampsia cespitosa* grew in all areas at all N treatments, and linear trend analysis showed that biomass increased down gradient ($p < 0.10$). Regression analyses for plots in which *D. cespitosa* emerged indicated that depth to water accounted for 37% of variation in biomass (Biomass, $g = 23.7 - 0.57 \text{ depth}$, $r^2 = 0.37$). The only species that yielded a significant overall F-test for response to N treatments in ANOVA ($p < 0.10$) was *D. cespitosa* in the upper transitional site, which showed highest growth with the high N treatment. However, trend analyses indicated that *C. maculosa* and *B. syzigachne* grew better with increasing nitrogen. While both overall F-tests were marginally non-significant ($p = 0.12$ and 0.11 respectively), linear trend analyses revealed significant trends of increasing biomass with increasing N for *C. maculosa* biomass in the upland ($p = 0.03$) and *B. syzigachne* in the wetland ($p = 0.07$). In contrast, linear trend analysis of *A. spicatum* in the upland ($p = 0.40$) revealed no significant biomass trend with increasing N.

Discussion

I hypothesized that highest emergence and growth would occur in the transitional sites, where soil water was high due to sub-irrigation, but was not so high as to induce flooding stress. Results contradicted this hypothesis. Only *D. cespitosa* showed any emergence in the two transitional areas, and growth increased from the upland to the wetland site with low to intermediate biomass in the transition. The failure of

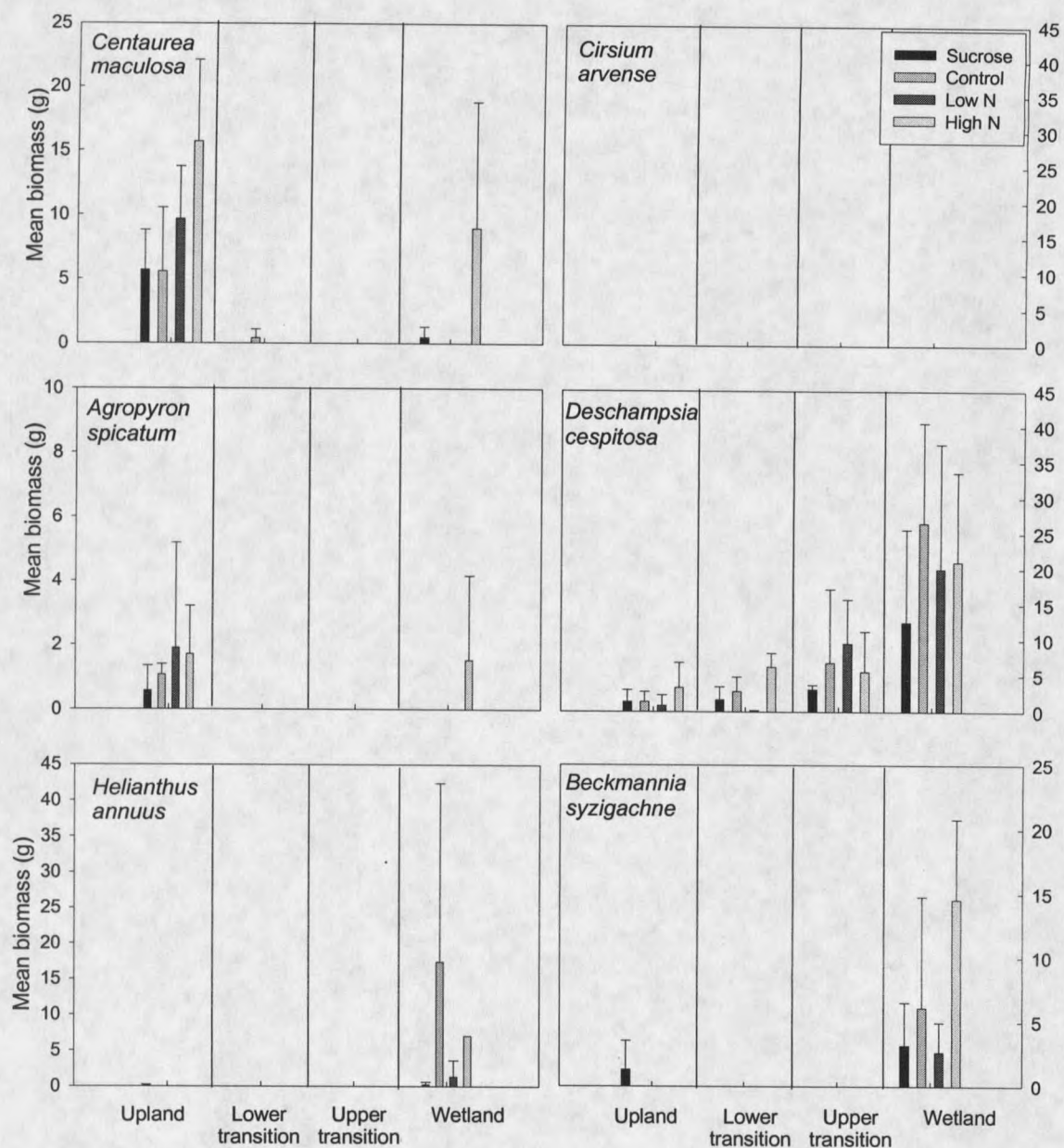


Figure 11. Plant biomass in response to N treatments at four sites along an upland wetland gradient in 1999. Error bars represent one standard deviation.

other species to emerge in the transitional areas is probably due to environmental factors not investigated in this experiment. The relatively high level of rodent activity observed in the transitional areas, for example, may partially or fully account for lack seedlings. In a coastal dune environment, rodents removed 86% of *Lupinus arboreus* (bush lupine) seedlings, substantially reducing establishment (Marron and Simms 1983). Rodent grazing and seedling disturbance in semi-arid grasslands research (Clement and Young 1996) significantly reduced *Purshia tridentata* (Prush) (antelope bitterbrush) recruitment. Similarly, rodent seed predation was highly influential on establishment of *Pseudotsuga menziesii* (Douglas fir) in N. California with clipping by rodents being the primary cause of mortality (Maguire 1989). In research on plant neighbor interactions in a coastal marsh environment, small mammal herbivory overrode other biotic interactions such as competition and mutualism (Taylor et al. 1997). Although not evaluated experimentally in this study, seed predation appeared to be the most likely explanation for poor establishment in transitional plots. Further investigation of seed predation in riparian areas may help prevent costly failures of revegetation projects.

Cirsium arvense failed to germinate in any area, including the wetland where other facultative wetland species thrived. *C. arvense* is a dioecious species that ordinarily grows in patches. Sterile heads of female flowers are common if pollen producing flowers are not near (Moore 1975), but Individual *C. arvense* seedlings, once established, can rapidly form dense patches (Donald 1994). Aggressive vegetative spread of this invasive weed into the upper transitional area from out side the plots was observed during both growing seasons. Together, my results and published research suggest that establishment of this invasive weed is limited by the seedling emergence phase, but once

established it can rapidly spread and thrive in intermediate locations along an upland-wetland gradient.

H. annuus, an annual, upland forb, emerged only in the wetland, primarily on hummocks that were elevated above the water table. The emergence of this species on relatively dry hummocks suggests that microtopography may have a significant role in seedling establishment. Gabrielle(1997) found that small-scale variability in surface elevation of 1-3 cm yielded significant differences in wetland plant communities. The failure of this species to emerge in the upland or upper transitional sites, hydrologic settings that seem more suitable for this species, bolsters the argument that predation, or other environmental factors not investigated in this experiment, influenced emergence.

In 1999 *D. cespitosa* emerged in the upland, and *C. maculosa* and *A. spicatum* emerged in the wetland, but none of these three species were present in these areas in the 2000 season. This suggest that hydrologic setting influences early growth more than emergence. Shafroth et al. (1994). investigated response of *Populus deltoides* (Aiton) (plains cottonwood) to water table elevation. They found that *Populus deltoides* research *P. deltoides* seedlings emerged similarly at all hydrologic settings except the driest (water table 50 and 60 cm below soil surface). Results for *D. cespitosa* provided the best comparison between emergence and biomass and showed that biomass differed more than emergence between wet and dry sites. *D. cespitosa* seedlings were present in all areas in 1999, but growth was very low in the upland and upper transitional sites where moisture was more limited and ws clearly superior in the wetland area. Wetland plants frequently are sensitive to soil moisture. For example, Lieffers and Shay (1980) found *Scirpus maritimus* (an obligate wetland plant) grew best in flooded soils.

Like depth to water, N treatments affected growth more than emergence. The most consistent trend of emergence response to N treatments was shown by *B. syzigachne*. Emergence of this annual species was inhibited by sucrose additions. In contrast, the perennial *D. cespitosa* showed no response to N treatments. However, the lack of consistent emergence responses to N limits interpretations.

Biomass results provide some indications that high levels of inorganic N favor annuals and invasive weeds. Emergence was poor and variability of the data was too great to allow statistical detection of N effects for most species at most sites. However, the two species effected by N were a non-indigenous weed and a native annual (*C. maculosa* and *B. syzigachne* respectively). Trend analysis for these species revealed biomass to increase with increasing N. In contrast, the native, upland perennial (*A. spicatum*) did not respond significantly to increasing N. This is consistent with the hypothesis that plants with traits associated with early successional species (annual life cycles, rapid growth rates etc.) and weedy species are favored by environments with higher inorganic N levels (Tilman and Wedin 1991, McLendon and Redente 1991, Redente et al. 1992).

Inconsistent emergence and lack of statistical power limits the interpretation of N effects and their implications for riparian zone restoration and management. Previous research in upland settings supports the hypothesis that desirable plant communities may be fostered by N reduction (Herron 1998, McLendon and Redente 1991, Redente et al. 1992). This study provides some evidence that N management may effect early succession in riparian areas and adjacent uplands, but further research is necessary to evaluate the efficacy of N management in riparian restoration. In particular, research on

N management should be performed at more realistic scales in the context of riparian restoration projects.

In addition, research on riparian plant establishment should investigate the host of other factors not investigated here that may have affected establishment, such as seed predation and microtopography. The extremely poor plant establishment, in spite of the apparently ideal environment provided by transitional areas along a riparian resource gradient, is noteworthy. While further research is needed, land managers and restoration ecologists should view these results as a cautionary reminder for riparian area restoration projects. Consideration of rodent activity, and use of planting methods other than seeding, may help avoid costly project failures. In addition, N additions should be applied with caution, because they may encourage the growth of non-indigenous weeds.

CHAPTER 4

SUMMARY AND MANAGEMENT IMPLICATIONS

This study investigated the influences of hydrology and nutrient availability on the establishment of desirable native plants and invasive weeds. I hypothesized that intermediate locations along a hydrologic gradient would favor early growth and emergence for all studied species. I further hypothesized, following published research (Tilman & Wedin 1991, McLendon & Redente 1991, Redente et al. 1992) that high levels of inorganic N would favor annuals and weedy species more strongly than desirable perennials.

Results provided some support for both these hypotheses, but plant emergence results of the greenhouse and field experiment were contradictory, particularly in response to hydrologic gradients. In the greenhouse, intermediate hydrologic settings, with a depth to water table 20 to 30 cm below the soil surface, resulted in high emergence and growth for most studied species. In the field, though, emergence was very low in a similar transitional hydrologic setting. These disparate results suggest that naturally occurring, hydrologic gradients are complex and include environmental factors other than N and depth to water that may influence seedling establishment. Some of these factors may override apparently favorable environmental conditions. One factor observed, but not investigated experimentally, in the field experiment was high rodent activity in the transitional study areas. Previous research has demonstrated significant negative impacts of seed and seedling predation on establishment (Maron & Simms 1983, Clement and

Young 1996, Maguire 1989). Consideration of seed predation by rodents, along with other environmental factors that vary along riparian gradients, may help restoration ecologists avoid costly project failures.

In both the greenhouse and field experiment, the hydrologic gradient influenced early growth more than emergence, particularly with facultative wetland species. In the greenhouse, significant regression models explained relatively high percentages of the variability in growth with depth to water table. In contrast, emergence results yielded few significant regression models, and these explained little of the variability in emergence of facultative wetland species with depth to water table. The field experiment had similar trends. One of the facultative wetland species, *D. cespitosa*, emerged in all areas in 1999, but growth was very low in the upland and upper transitional sites where moisture was more limited. *D. cespitosa* was not found in the upland the next year. In addition, *C. maculosa* and *A. spicatum* (upland species) emerged in elevated microsites in the wetland, but did not survive into the 2000 season. These results suggest that early emergence is a poor indicator of successful riparian plant establishment.

Cirsium arvense emerged poorly in both the field and greenhouse. This common riparian weed appeared to be limited at the germination stage. In the greenhouse, though, *C. arvense* transplants performed well, suggesting that once this weed establishes it can thrive in riparian areas. Similarly, I observed aggressive vegetative spread of *C. arvense* into field experimental plots from adjacent infestations. These results suggest management of *C. arvense* should focus on prevention of establishment in non-infested areas and control of vegetative spread from existing infestations.

Similar responses to N treatments occurred in the greenhouse and field, although significant results were limited in both experiments. Greenhouse results were contradictory between the two repetitions of the experiment. In the first repetition both *C. maculosa* and *A. spicatum* grew best with high N, but in the second repetition only *C. maculosa* growth was enhanced by N additions. Field results were similar to the second greenhouse repetition. Linear trend analysis revealed that *C. maculosa* growth increased with increasing N, but showed no significant influence of N on *A. spicatum*. These results provide some evidence that N management may affect early succession in riparian areas and adjacent uplands, but further research is necessary to evaluate the efficacy of N management to aid riparian restoration.

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