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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Ronald Roy LeCain

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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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 propugules (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. Decompostion 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. <u>To determine the influence of a hydrologic gradient on the seedling establishment of early successional, late successional and invasive weedy species.</u> 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. <u>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.</u> 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 Methods

Experimental 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/ m^2 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/ m^2 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	Succesional Stage	Short-Term Reveg. Potential*	Long-Term Reveg. Potential*
Agropyron spicatum	Native Perennial Grass	Late	NA	NA
Helianthus annuus	Native Annual Forb	Early	NA	NA
Centaurea maculosa	Exotic Perennial Forb	Early to late (Invasive weed)	NA	NA
Deschampsia cespitosa	Native Perennial Grass	NA	Low	High
Beckmannia syzigachne	Native Annual Grass	NA	Moderate	Low
Cirsium arvense	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 cm^2 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-tranformed 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
A. spicatum	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
C. maculosa	Sucrose	12.51	-1.11	0.33	0.05
	Control	11.45	-1.29	0.51	0.01
	High N	NS	NS	NS	NS
H. annuus	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
D. cespitosa	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
C. arvense	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
B. syzigachne	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS

* NS signifies the model is not significant at $\alpha=0.10$
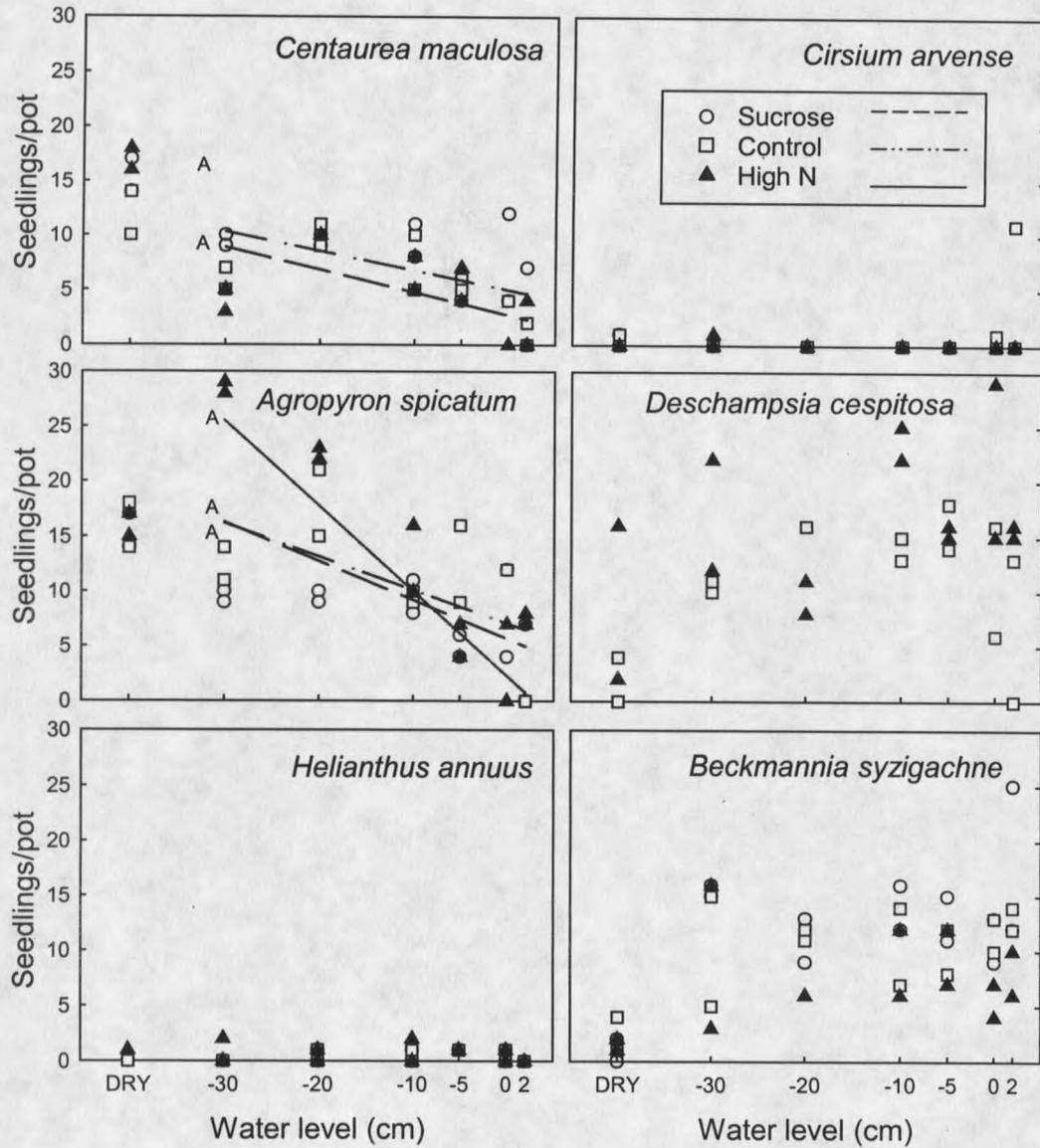
Figure 1. Seedling emergence in response to depth of water table, and sucrose and N additions in the first greenhouse experiment. Significant regressions are shown by lines and reported in Table 2. Regression models with the same letter are not significantly different. Regression analyses exclude dry 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
A. spicatum	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
C. maculosa	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
H. annuus	Sucrose	1.25	-0.19	0.25	0.10
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
D. cespitosa	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
C. arvense	Sucrose	NS	NS	NS	NS
	Control	16.5	-2.5	0.25	0.10
	High N	NS	NS	NS	NS
B. syzigachne	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS

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

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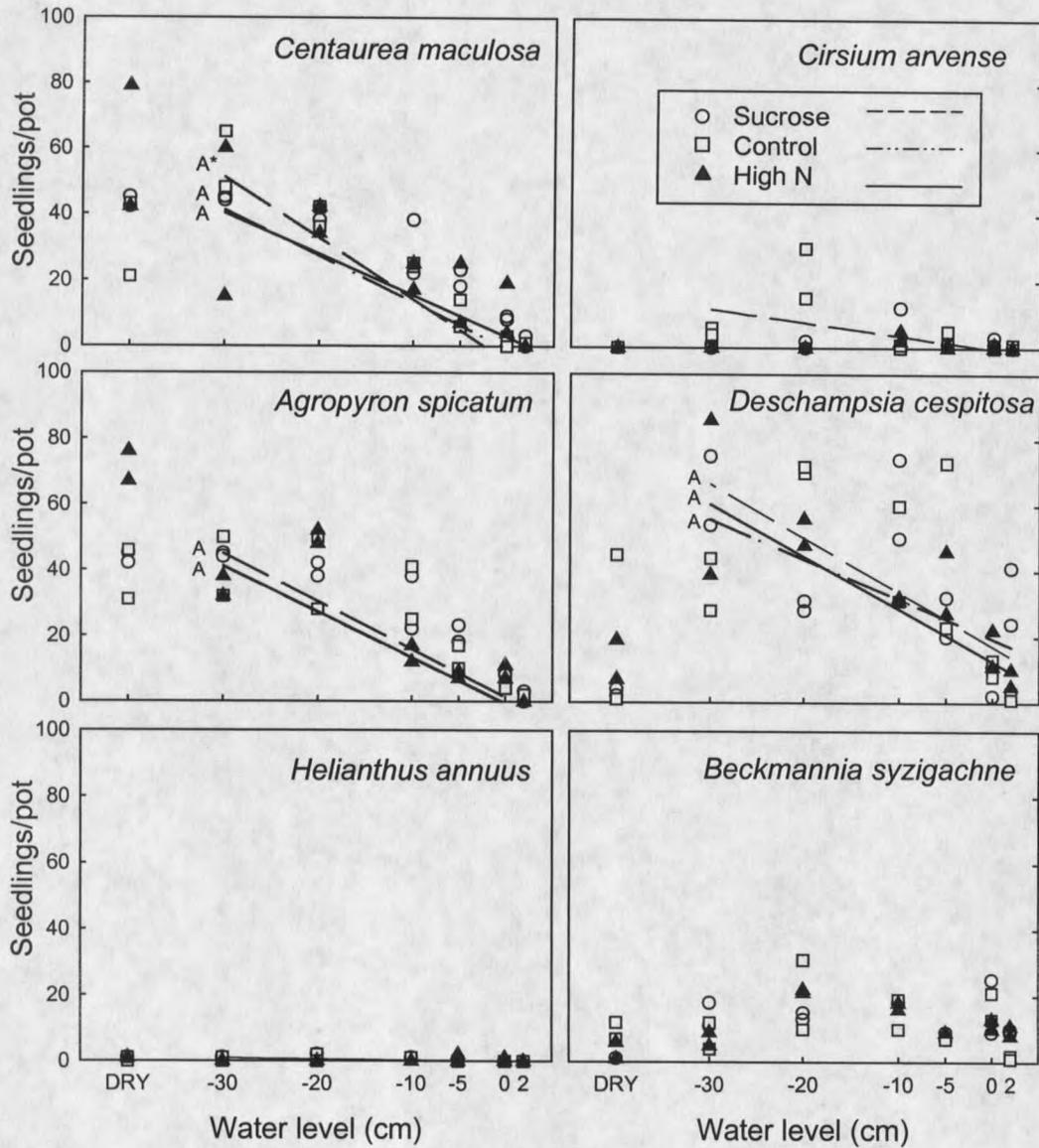
Figure 2. Seedling emergence in response to depth of water table, and sucrose and N additions in the second greenhouse experiment. Significant regressions are shown by lines and reported in Table 3. Regression models with the same letter are not significantly different. Regressions exclude dry treatment.

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
A. spicatum	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
C. maculosa	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
H. annuus	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	15.80	-2.58	0.26	0.09
D. cespitosa	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
C. arvense	Sucrose	NS	NS	NS	NS
	Control	NS	NS	NS	NS
	High N	NS	NS	NS	NS
B. syzigachne	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 $\alpha = 0.10$.