RESEARCH

Establishment of Native and Invasive Plants along a Rangeland Riparian Gradient

by Roger L. Sheley, Paul B. Hook, and Ronald R. LeCain

ABSTRACT

Environmental resource gradients affect plant establishment during invasive weed management and ecological restoration. We investigated how hydrology and nitrogen (N) availability influence establishment of native and invasive species along a dry-wet gradient. We hypothesized that 1) emergence and growth would be higher in subirrigated environments than in saturated or dry environments; 2) annuals and invasive exotics would respond more to N availability than late-successional perennials; and 3) N effects would be greatest in subirrigated environments. In the greenhouse, seedling emergence was uniform across dry to subirrigated pots for upland species, and across subirrigated to saturated, but not flooded pots for riparian species. Seedling biomass was greatest in subirrigated environments. Seedling emergence in the field was at or near zero for most species in subirrigated sites. In the greenhouse, biomass increased with N availability, and responses to N were greatest in subirrigated pots. In both experiments, the upland invasive, spotted knapweed (*Centaurea maculosa*), responded more to N availability than bluebunch wheatgrass (*Agropyron spicatum*). However, such differences were not found for the riparian species, possibly due to low emergence. Possible explanations for low emergence in subirrigated field sites include predation by small rodents, which were more active in the transition than upland or wetland areas. Establishment of spotted knapweed and Canada thistle (*Cirsium arvense*) in riparian sites was limited by poor germination and seedling survival. Once established, growth was good in subirrigated environments, indicating that weeds may invade riparian sites in spite of poor initial establishment, which suggests caution towards ecological restoration practices that increase N availability.

Keywords: environmental gradient, seedling establishment, weeds, ecological restoration, *Agropyron spicatum*, *Beckmannia syzigachne*, *Centaurea maculosa*, *Cirsium arvense*, *Deschampsia cespitosa*, *Helianthus annuus*

Management areas typically contain uplands and wetlands that differ greatly in terms of their environmental resource gradients (Chambers and others 1999, Castelli and others 2000). Information about the relationships between environmental resource gradients and plant establishment could help ecologists and land managers identify sites at risk for exotic plant invasion. It could also aid ecological restorationists by helping them match desirable species to appropriate sites and in designing the correct manipulations of topography, soils, and nutrients. For instance, with water limited in uplands, riparian areas might be expected to grade from transitional sites where abundant water enhances plant survival and growth to wetter sites where flooding limits germination and anoxia reduces survival and growth (Megonigal and others 1997). Thus, plant establishment would be expected to be favored at transitions between the upland range and perennially saturated wetlands.

Research suggests that low resource levels may be better tolerated by plant species that have slower growth rates, slower nutrient uptake, low nutrient concentrations, and long life spans (Grime 1979). This set of characteristics is typical of many desirable native species. Scientists have also found that plants capable of rapid growth are favored in resource-rich environments (Menges and Waller 1983, McLendon and Redente 1991, Redente and others 1992). Such plants are characterized by rapid nutrient uptake, high tissue nutrient concentrations, and short life spans, and include many invasive plants (McLendon and Redente 1991, Redente and others 1992). Riparian sites with high availability of water and nutrients may face particularly high risks for weed invasion (Planty-Tabacchi and others 1996, Kotanen and others 1998, Stohlgren and others 1998).

In revegetation efforts, fertilizer application or high, pre-existing nutrient levels potentially favor weedy species over late-successional species. Various strategies to reduce site fertility, such as carbon amendments, have been proposed to foster dominance by desirable native species and increase biodiversity in restoration projects (McLendon and Redente 1991, Redente and others 1992, Reever Morghan and Seastedt 1999, Herron and others 2001).

There are few studies about the effects of resource gradients on the establishment of native and exotic herbaceous species in northern Rocky Mountains and Great Plains rangeland riparian communities. In the study reported in this article, we evaluated influences of resource gradients on seedling emergence and early growth in a rangeland riparian ecosystem. We hypothesized that 1) for all species, seedling emergence and growth is greater in transitional, subirrigated environments than in dry, water-limited environments or in saturated environments; 2) early successional

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and invasive exotic species respond more strongly to increased and decreased nitrogen availability than late-successional species; and 3) nitrogen (N) effects on early growth vary with water level.

Materials and Methods

In the study, we conducted parallel field and greenhouse experiments. We randomly assigned species and N treatments to replicate plots in the field or containers in the greenhouse. Due to our inability to control water levels or soil types in the field, these factors could not be randomized there. We were able to randomly assign water levels in the greenhouse, however.

Field Site

We established the field experiments along a 200-m, upland-to-wetland transect perpendicular to Warm Springs Creek, near Norris, in southwestern Montana. The site, which is located 4,789 ft (1460 m) above sea level, receives 16 inches (40 cm) mean annual precipitation and has a mean annual temperature of 43.7°F (6.5°C).

In May 1998, we selected four study areas based on their water table levels and vegetation. The four areas represented a groundwater-controlled, toe-slope gradient of soil water availability, flooding stress, vegetation, and soil development (Table 1). The upland area had a water table well below the root zone; a typical, relatively infertile semiarid rangeland soil; and was dominated by sparse native grasses and a club moss. The wetland area was predominantly saturated or shallowly flooded, had a deep peat soil, and was dominated by beaked sedge (*Carex utriculata*). The two transition areas featured a gradient from deeper to shallower subirrigation and from dominance by native grasses to sedges with a 65.6-ft- (20-m-) wide zone of Canada thistle (Cirsium arvense). Near-surface conditions shifted from aerobic in the upper transitional area to weakly anaerobic in the lower transitional area and strongly anaerobic in the wetland (C. Kelling and P. Hook unpublished data). Two indices of nitrogen availability showed lower N in the upland than the other three areas.

Table 1. Physical and ecological characteristics of four rangeland study sites.

	Upland	Upper transition	Lower transition	Wetland
Relative elevation (m)	6.11	2.04	1.71	0.01
Percent slope	4.7	5.5	3.0	0.8
Mean depth to water (m)	>2.5	0.30-0.60	0.15-0.30	0.00-0.14
Maximum depth to water (m)	>2.65	0.68-1.06	0.61-0.68	0.08-0.52
Minimum depth to water (m)	2.26	0.04-0.38	-0.07-0.04	-0.05- 0.08
Festuca idahoensis cover (%)	37	62	3	0
Selaginella densa cover (%)	58	0	0	0
Cirsium arvense cover (%)	0	31	35	0
Carex spp. cover (%)	0	7	66	98
Plant biomass (g/m^2)	230	910	910	990
Soil type	Aridic Agriborol	Pachic Haploboroll	Oxyaquic Haploboroll	Fluvaquentic Cryofibrist
Sand/silt/clay content (%)	56/20/	24 48/	24/28	51/27/22
18/43/39				
Soil bulk density (g/cm^3)	1.17	0.80	0.46	0.09
Organic matter (%)	5	13	24	52
Extractable soil N (g/m^2)	0.9	2.0	3.1	4.3
Ion-exchange resin N (mg/L)	2.5	10.7	10.5	11.2

Field Experiment

In each study area, we delineated seventy-two 1-m^2 plots, leaving a 1-m buffer separating the plots. Vegetation was eliminated and removed from the plots, but not buffers. In October 1998, each plot was seeded with one of six, randomly assigned, experimental species. Seeds were hand broadcasted and covered with 0.08 inches (2 mm) of sand to protect them from predation. One of four nutrient treatments was randomly assigned to each plot: control, low nitrogen (10 kg N/ha), high nitrogen (100 kg N/ha), or sucrose (1,000 kg C/ha). The addition of sucrose was intended to deplete nutrients by increasing microbial immobilization (McLendon and Redente 1991, Reever Morghan and Seastedt 1999). Granular 46-0-0 ammonium nitrate and sucrose were applied monthly in April, May, June, and July 1999.

We assessed seedling establishment in the central 0.25 m^2 of each plot in August 1999 and May 2000. Using a 0.25-m^2 frame divided into one hundred 5-cm x 5-cm cells, we counted seedlings in a sub-sample of ten cells. Aboveground biomass was harvested in August 1999 from the central 0.25 m^2 of all plots, then oven-dried, and weighed. Water levels were monitored weekly from May through October 1998 and from April through August 1999, using a network of 40 observation wells (5-cm diameter, 0.3-2.7 m deep) extending from the downhill side of the upland study area to the streamside edge of the wetland study area. Surface elevations were surveyed at all wells and experimental plots. They were used to interpolate average water levels for individual plots. We observed extensive rodent activity in 1999. In May 2000, we surveyed all experimental plots for rodent signs such as tracks, digging or other soil disturbances and assigned a rating of zero, low, medium, or high rodent activity.

Data were analyzed using ANOVA at a significance level of 0.10. Low emergence largely negated statistical analysis of seedling counts; where adequate, emergence data were analyzed as described below for biomass. To evaluate spatial variation along the transect, biomass trends were analyzed for species that emerged in all study areas using linear and quadratic contrasts in two-way ANOVAs (study area x nutrient treatment). We analyzed nutrient responses for each study area and species separately by one-way ANOVA because study areas were not randomized or replicated, and because low emergence resulted in many combinations of study area and species for which most data were zeroes. We used linear contrasts to test the hypothesis that biomass increased with N availability, with treatments ranked in the

Table 2. Characteristics of six species used in greenhouse and field experiments.

Species	Common name	Origin, life cycle & form	Characteristic successional stage	Riparian revegetation potential	Invasive & noxious weed status	Wetland indicator status	Riparian occurrence (Montana)
Agropyron spicatum (Pursh) Scribn. & Smith (*Pseudoregneria spicata*)	Bluebunch wheatgrass	Native, Perennial grass	Late			Facultative upland -	13%
Helianthus annuus L.	Common sunflower	Native, Annual forb	Early		Invasive; listed in Iowa & Minnesota	Facultative upland +	1%
Centaurea maculosa Lam. (*Centaurea biebersteinii*)	Spotted knapweed	Exotic, Perennial forb	Early to late		Invasive; listed in 14 U.S. states	Obligate upland	22%
Deschampsia caespitosa (L.) Beauv.	Tufted hairgrass	Native, Perennial grass	Late	Low short-term Medium long-term		Facultative wetland	39%
Beckmannia syzigachne (Steud.) Fern.	American sloughgrass	Native, Annual grass	Early	Medium short-term Medium long-term		Obligate wetland	13%
Cirsium arvense (L.) Scop.	Canada thistle	Exotic, Perennial forb	Early to mid-seral	Low short-term Medium long-term	Invasive; listed in 29 U.S. states	Facultative upland +	60%

order sucrose, control, low N, and high N. To evaluate the persistence and delayed recruitment of weeds, we counted Canada thistle and spotted knapweed (*Centaurea maculosa*) in plots on June 19, 2001. Unfortunately, the vegetative spread of Canada thistle from the buffers prevented identification of plants originating from seed in the transition zone.

Greenhouse Experiment

In the greenhouse, we created a water-level gradient approximately parallel to field hydrologic conditions, but with a uniform soil. We established seven water levels and three nutrient levels in a completely randomized factorial design with two replications. The experiment was repeated twice: from March-July 1999 (Trial 1) and from September 1999-January 2000 (Trial 2).

Each of 42 plastic tubs (50 cm x 40 cm wide x 40 cm deep) contained six pots (10 cm x 10 cm wide x 36 cm deep) filled with sandy-clay loam soil, each seeded with one of the six plant species. Seed was broadcast on the soil surface at a rate of 3,000 seeds/m^2 in Trial 1 and, because some species had poor germination in Trial 1, at 6,000 seeds/m^2 in Trial 2. Germination of Canada thistle seed remained poor in Trial 2. In order to provide an adequate sample to evaluate growth response in Trial 2, we transplanted Canada thistle seedlings from pots with successful germination to empty pots after emergence was quantified.

We created the depth-to-water-table gradient by maintaining free water in each tub at one of six levels: 0 or 0.8 inches (2 cm) above the soil surface or 2, 4, 8 or 12 inches (5, 10, 20 or 30 cm, respectively) below the soil surface. Pots were open at the bottom to allow water exchange. For the "dry" treatment, tubs contained no free water to subirrigate the pots.

We randomly assigned one of three nutrient treatments to each tub. Treatments were applied as 16 weekly increments by watering each pot with 4.7 fluid ounces (155 ml) of deionized water, an ammonium chloride solution (39 mg N/L or the equivalent to 100 kg N/ha), or a sucrose solution (400 mg carbon/L or 1,000 kg of carbon/ha). This watering regime was equivalent to 0.6 inches (1.6 cm) of rain per week and was based on historical data for the field site.

Seedlings were counted 70 days after planting, then thinned to one plant per pot. Aboveground biomass was harvested 130 days after planting, oven-dried, and weighed. Data were analyzed by ANOVA using a significance level of 0.10. To meet statistical assumptions and to focus analysis on patterns of water level and nutrient response, we ranked the values for each trial and species, and then analyzed the rank-transformed data.

We tested water level responses related to Hypothesis 1 with planned contrasts that compared the two deepest levels of subirrigation to other water level categories: 1) "subirrigated" (-8 and -12 inches) compared to "dry", 2) subirrigated compared to "nearly-saturated" (-2 and -4 inches), and 3) subirrigated compared to "flooded" (0 and +0.8 inches). We tested responses to nutrient treatments (Hypothesis 2) using a linear contrast with treatments ordered from sucrose addition (lowest nutrient level) to control to nitrogen addition. To address Hypothesis 3, we analyzed the data from each of the four water level categories separately, again using a linear contrast to test nutrient responses.

Experimental Species

We investigated six species—bluebunch wheatgrass (*Agropyron spicatum*), American sloughgrass (*Beckmannia syzigachne*), tufted hairgrass (*Deschampsia cespitosa*), common sunflower (*Helianthus annuus*), spotted knapweed, Canada thistle—each of which is common to the northern Rocky Mountains and Great Plains. These species also have contrasting life history characteristics (Table 2). Common sunflower and bluebunch wheatgrass are upland, native species with annual and perennial life cycles, respectively. Spotted knapweed is an exotic, perennial, noxious weed that reproduces mainly by seed (Sheley and others 1999). Common sunflower and bluebunch wheatgrass represent early and late-successional species, while spotted knapweed has both early and late- successional traits (Sheley and others 1999). Since the successional status of many riparian species is unclear, we also used life cycle and short-term and long-term revegetation potential as criteria to select wetland species (Hansen and others 1995). American sloughgrass and tufted hairgrass are native wetland species with annual and perennial life cycles and intermediate and low short-term revegetation potential, respectively (Hansen and others 1995). Canada thistle is an exotic, perennial, clonal noxious weed common in diverse upland habitats in humid regions of North America (Morishita 1999) and in wetlands and riparian areas in the northern Great Plains and intermountain west (Hansen and others 1995).

Results

Field Experiment-Emergence

Emergence was extremely poor in the upper and lower transitional areas with no seedlings of five of the six species and low emergence rates for tufted hairgrass (Figures 1a, 1b). In the upper transitional area, about half the tufted hairgrass seedlings survived into 2000. In the lower transitional area, tufted hairgrass seedling numbers nearly tripled, increasing to more than 100 seedlings/m^2 in 2000. However, this was the only case of an increase in seedling numbers for any species in this area from 1999 to 2000.

In upland plots, emergence averaged 240 seedlings/m^2 for spotted knapweed and 47 seedlings/m^2 for bluebunch wheatgrass in 1999. Nearly 80 percent of the spotted knapweed seedlings persisted into the second growing season, but fewer than half of the bluebunch wheatgrass seedlings survived. Emergence of tufted hairgrass averaged 93 seedlings/m^2 in upland plots in 1999, but virtually no seedlings survived into the second year.

In wetland plots, emergence averaged 130 spotted knapweed and 20 bluebunch wheatgrass seedlings/m^2 in 1999, although these were concentrated exclusively on higher elevation microsites and no seedlings of either species survived into 2000. Emergence averaged 300 seedlings/m^2 for tufted hairgrass and 580 seedlings/m^2 for American sloughgrass in the wetland area in 1999, and more than one-third of seedlings of both species survived into 2000. Annual sunflower seedlings were found only in the wetland, where they averaged 17 seedlings/m^2, although they were confined to the four highest elevation wetland plots, and none survived into 2000.

Canada thistle did not emerge at any of the four study areas. Nutrient treatments significantly affected emergence of only one species, American sloughgrass, which had lower emergence with sucrose addition than other treatments in both years.

Using a brief opportunity to observe our sites in June 2001, we were able to assess weed establishment at that time. Following a year of drought, we found Canada thistle and spotted knapweed plants in riparian sites where they had not been detected previously. Seven Canada thistle plants averaging 4 inches (10 cm) tall were present in three wetland plots with elevated microsites. We could not evaluate Canada thistle establishment from seedlings in the transition because the area was so heavily covered with thistles to begin with. We found no Canada thistle plants in the upland area. Spotted knapweed was absent from the wetland and we found only one plant in the highest part of the lower transition zone. A total of 68 spotted knapweed individuals (6/m^2 in plots seeded with spotted knapweed) occurred in the upper transition area, strongly concentrated in the highest elevation plots. Spotted knapweed remained abundant in all upland plots where it had been seeded (average density 60 plants/m^2).

Field Experiment—Biomass Patterns

The August 1999 biomass patterns were broadly similar to those for emergence, with most species absent from the transitional areas, spotted knapweed and bluebunch wheatgrass growing better in upland than wetland plots, and tufted hairgrass and American sloughgrass growing better in wetland than upland plots (Figure 1c). Only tufted hairgrass grew in all study areas and in all nutrient treatments, and linear trend analysis showed that its biomass increased significantly from upland to wetland plots. Regression analyses for transition zone and wetland plots in which tufted hairgrass emerged indicated that depth to water accounted for a modest but significant proportion of variation in biomass ($r^2 = 0.37$). Foliage and flowering shoots remaining from 2000 were about four times larger in upper transition than in upland plots.

Biomass showed more nutrient effects than emergence, but nutrient effects on biomass were not found consistently. Linear trend analyses indicated that biomass increased significantly with increasing nitrogen for spotted knapweed in upland plots and American sloughgrass in wetland plots (Figure 2). In contrast, linear trend analysis did not show a significant biomass trend with increasing nitrogen for bluebunch wheatgrass in the upland. In the upper transitional area only, tufted hairgrass had significantly higher biomass in high-N plots than other treatments.

Field Experiment—Rodent Activity

Both frequency and intensity of rodent activity were greatest in the upper transitional area, where 89 percent of plots showed signs of rodent activity with plot excavation and burial nearly total in extreme cases (Figure 3). Rodent activity was intermediate in the lower transitional area (46 percent of plots), low in the upland area (11 percent), and absent in the wetland.

Greenhouse Experiment—Emergence

Though seedling emergence and biomass values differed significantly between Trials 1 and 2, average patterns of water level response (Figure 4a) were generally similar between both trials in our greenhouse experiment. When species with substantial emergence (bluebunch wheatgrass, spotted knapweed, tufted hairgrass, and American sloughgrass) were analyzed together, emergence was higher in subirrigated pots than each of the other water level categories. However, emergence patterns varied among species, with upland species showing greater sensitivity to excessive wetness and wetland species suffering with inadequate moisture. For example, emergence of the two upland perennials—bluebunch wheatgrass and spotted knapweed—

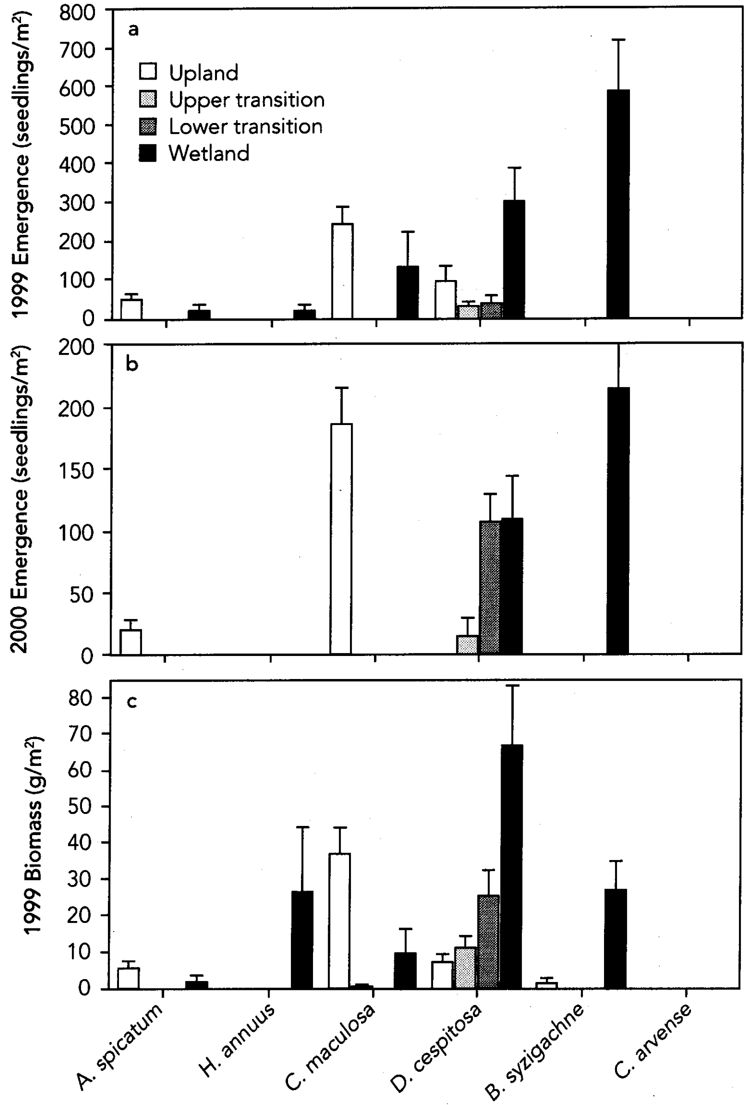

Figure 1. Seedling emergence and aboveground biomass of seeded species-bluebunch wheatgrass (*Agropyron spicatum*), annual sunflower (*Helianthus annuus*), spotted knapweed (*Centaurea maculosa*), tufted hairgrass (*Deschampsia cespitosa*), American sloughgrass (*Beckmannia syzigachne*), Canada thistle (*Cirsium arvense*)—in four study areas on an upland-to-wetland gradient at Red Bluff Research Ranch, Montana. Each bar represents the average, across all three nitrogen treatments, of 12 plots per species at each study area. Error bars are one standard error.

declined with increasing wetness; emergence was significantly lower in nearly saturated or flooded pots than in the subirrigated pots. Emergence of bluebunch wheatgrass and spotted knapweed was as great in dry pots as in the subirrigated pots. In contrast, tufted hairgrass and American sloughgrass had significantly lower emergence in dry pots as compared to the subirrigated pots. Emergence of tufted hairgrass was significantly lower in flooded pots than the subirrigated pots. Emergence of American sloughgrass did not differ among subirrigated, nearly-saturated, and flooded pots. Emergence of annual sunflower and Canada thistle was very poor and did not show any consistent trends.

Greenhouse Experiment—Biomass

When analyzed across species (bluebunch wheatgrass, spotted knapweed, tufted hairgrass, and American sloughgrass), biomass was significantly higher in the subirrigated pots than each of the other water level categories (Figure 4b, Figure 5a). Unlike emergence patterns, however, significant interactions between depth and species reflected only subtle differences among species, not basic differences in response patterns. Biomass of each of these four species, as well as Canada thistle transplants in Trial 2, was significantly higher in the subirrigated pots than at other water levels. Excessive wetness generally reduced biomass, but effects were greater for upland than wetland species. In flooded and nearly-saturated pots, biomass was higher for tufted hairgrass and American sloughgrass than for bluebunch wheatgrass and spotted knapweed, for example. In subirrigated pots, biomass was higher for tufted hairgrass and spotted knapweed than bluebunch wheatgrass. In dry pots, biomass did not differ significantly among species and was uniformly low. With low emergence in both trials, annual sunflower biomass showed no clear statistical trends.

Greenhouse Experiment—Nutrient Treatments

Nutrient treatments affected biomass more than emergence. Averaged across depths, nutrient treatments affected emergence of tufted hairgrass and American sloughgrass but not bluebunch wheatgrass and spotted knapweed. For tufted hairgrass and American sloughgrass, emergence was significantly lower with sucrose addition than in controls, but nitrogen addition did not increase emergence. Averaged across depths and species, biomass differed significantly among all three nutrient treatments, increasing from sucrose to control to nitrogen. Nitrogen addition enhanced production of tufted hairgrass, bluebunch wheatgrass, and spotted knapweed compared to control and sucrose treatments (Figure 5b). Nitrogen enhanced production of American sloughgrass compared to controls but not the sucrose treatment.

Nutrient effects varied significantly with water level. Nitrogen enhanced emergence in the dry pots, depressed emergence in the subirrigated pots, and had no effect

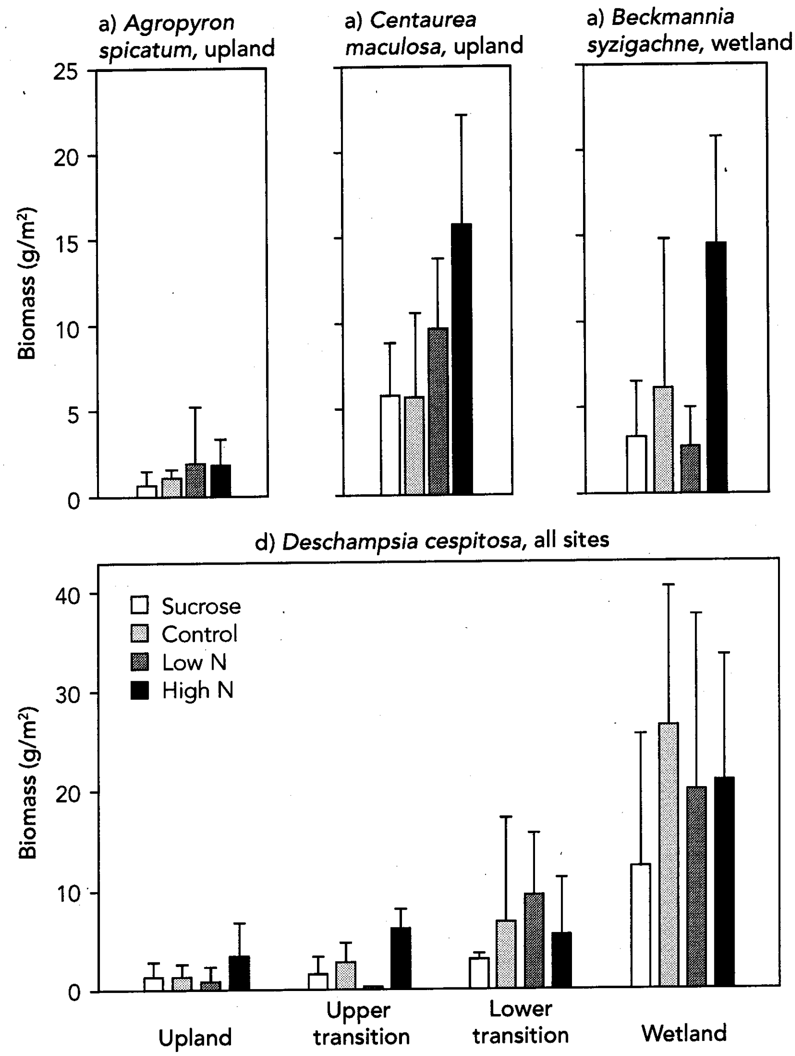

Figure 2. The biomass response of four species to various treatments in the field experiment at Red Bluff Research Ranch, Montana. Only combinations of species and study area with adequate emergence and survival to analyze N response are shown. Each bar represents the mean of three plots. Error bars are one standard error.

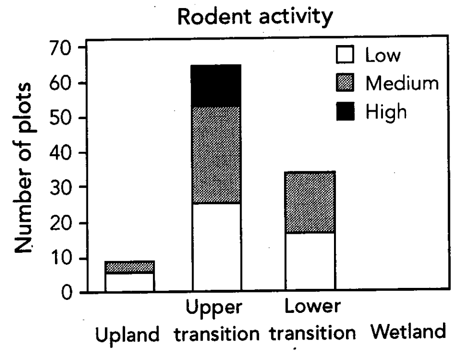

Figure 3. Patterns of rodent activity at four study areas on an upland-to-wetland gradient at Red Bluff Research Ranch, Montana. Rodent activity in each of 72 experimental plots per study area was rated in four categories from none to high according to visual indicators including tracks, digging, and other soil disturbances.

under wetter conditions. Nutrient treatments did not affect biomass in the dry pots, but in the other three water level categories biomass was significantly greater in N than in the sucrose and control treatments (Figure 5c). Biomass increases associated with N addition were three to five times higher in the subirrigated pots than in the nearly saturated or flooded pots, but relative increases were similar (60-80 percent greater than controls). For all species, except Canada thistle, the greatest response to N was seen in the subirrigated pots. When analyzed separately within each water level category, nutrient treatment effects on emergence and biomass did not vary significantly among species. However, we observed some apparent differences in response in the subirrigated and nearly saturated pots, which included the highest average biomass and the highest biomass response to N. In these water level categories, average biomass responses to N addition were twice as high for spotted knapweed as bluebunch wheatgrass whether measured as actual increases in mass (3.3 g/pot for spotted knapweed compared to 1.1 g/pot for bluebunch wheatgrass) or percentage increase (195 percent for spotted knapweed compared to 85 percent for bluebunch wheatgrass). Responses of spotted knapweed to N also tended to be greater than those for wetland species. Under flooded conditions, American sloughgrass had the most positive biomass response to N, although it was relatively small (1.2 g/pot).

Implications for Restoration and Management

We tested three hypotheses in this study: 1) seedling emergence and growth is greater in transitional, subirrigated environments than in dry, water-limited environments or in saturated environments; 2) early successional and invasive exotic species respond more strongly to increased and decreased nitrogen availability than late successional species; 3) nitrogen (N) effects on early growth vary with water level.

In terms of our first hypothesis, we found that patterns of plant response to water-level gradients differed for seedling emergence and plant biomass, and depended on the environmental setting (greenhouse or field). In our study, wetland plants grew better than upland plants under flooded or nearly saturated conditions, while all species showed restricted growth when simulated rainfall was the only source of water. Growth was more sensitive to water level than emergence, with subirrigation providing the most favorable environment.

Semiarid rangelands provide a great contrast between intermediate and upland environments, and we expected optimal growth in the transitional areas.

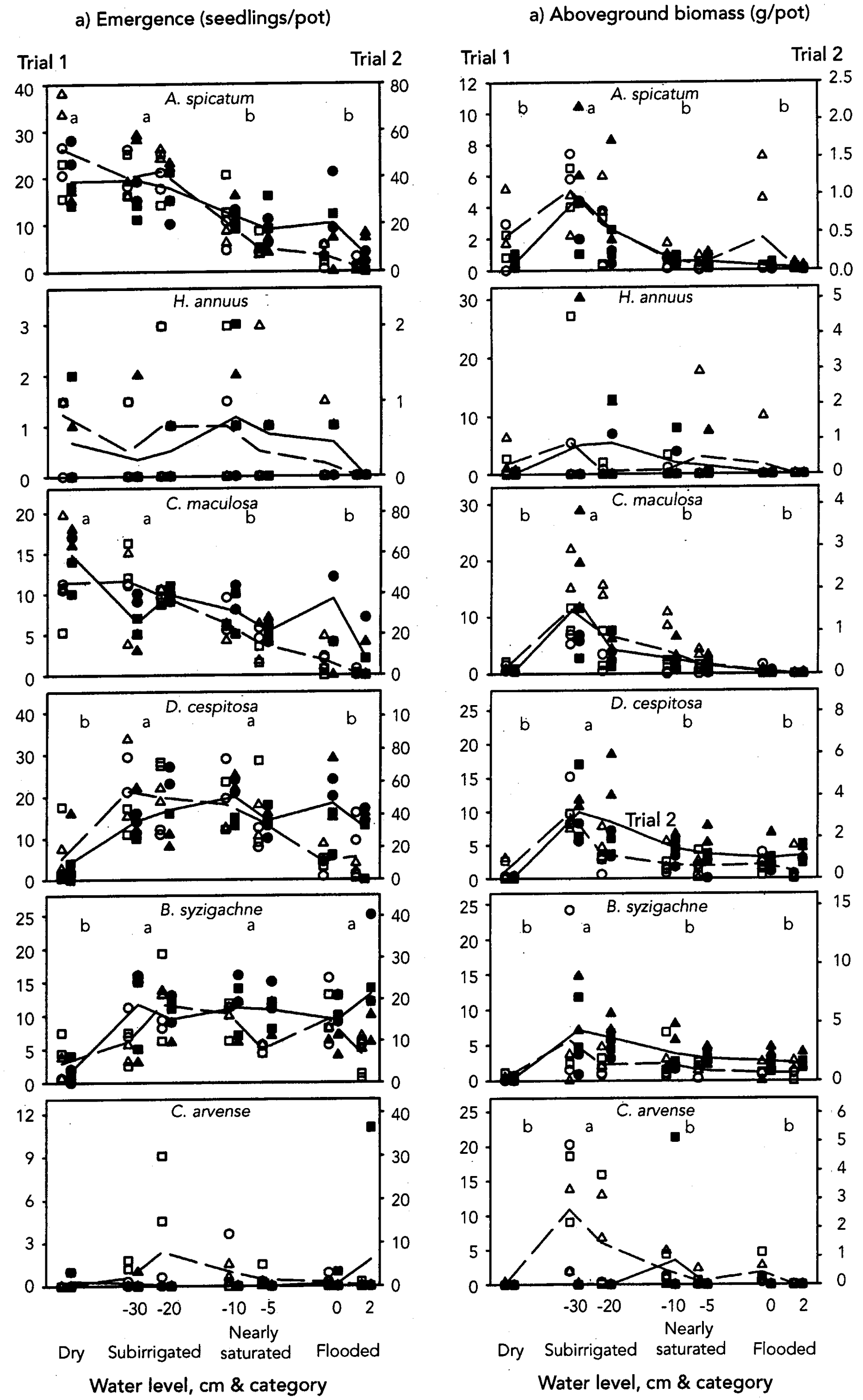

Figure 4. Seedling emergence (day 70) and biomass (day 130) response to water level and nitrogen treatments in greenhouse experiments. Water levels are depth of free water surface above (greater than 0) or below (less than 0) the soil surface. "Dry" pots received only simulated rainfall. Symbols represent values for individual pots (● = sucrose, ■ = control, ▲ = nitrogen treatment). To show patterns of water-level response, lines connect means for each water level, across nitrogen treatments. Results for Trial 1 are represented by the left axis on each panel and by filled symbols and continuous lines, and results for Trial 2 by the right axis, unfilled symbols, and dashed lines. Note differences in scale between Trials 1 and 2. Lower case letters represent results of planned contrasts between subirrigated pots and each of the other water level categories. A "b" above data for dry, nearly saturated, or flooded pots indicates that emergence or biomass values were significantly lower than in subirrigated pots (see Methods section for details).

That is not what we observed, however. Instead, tufted hairgrass, the only species with substantial emergence across the entire water-level gradient, increased in terms of biomass with increasing wetness. This pattern probably reflected the combined effects of low water availability in upland plots and low germination and survival in the transition zone. The limited establishment in the transition zone surprised us, considering the existing Canada thistle infestation, greenhouse results showing that subirrigation favored seedling emergence and growth, and published evidence that resource-rich riparian sites are favorable for seedling establishment (Planty-Tabacchi and others 1996, Kotanen and others 1998, Stohlgren and others 1998). A number of factors, including poor seed contact with the soil, phytotoxicity from nearby Canada thistles, and seed predation by rodents and birds, may have contributed to limited emergence of seedlings in the transition zone.

Regardless of its causes, failure of seedings in the subirrigated transition zone has potentially important implications for ecological restorationists and land managers. If factors other than site hydrology and livestock herbivory limit plant establishment, they need to be addressed in planning and implementing riparian restoration projects. For instance, had we been attempting an ecological restoration project at this site, it would have failed spectacularly, and we would not have known the reason or the remedy. Now, with the results of the study in mind, we could proceed in a more strategic and informed manner. It is important to remember that the strategies and costs for successful restoration differ greatly if the seedling establishment bottleneck is caused

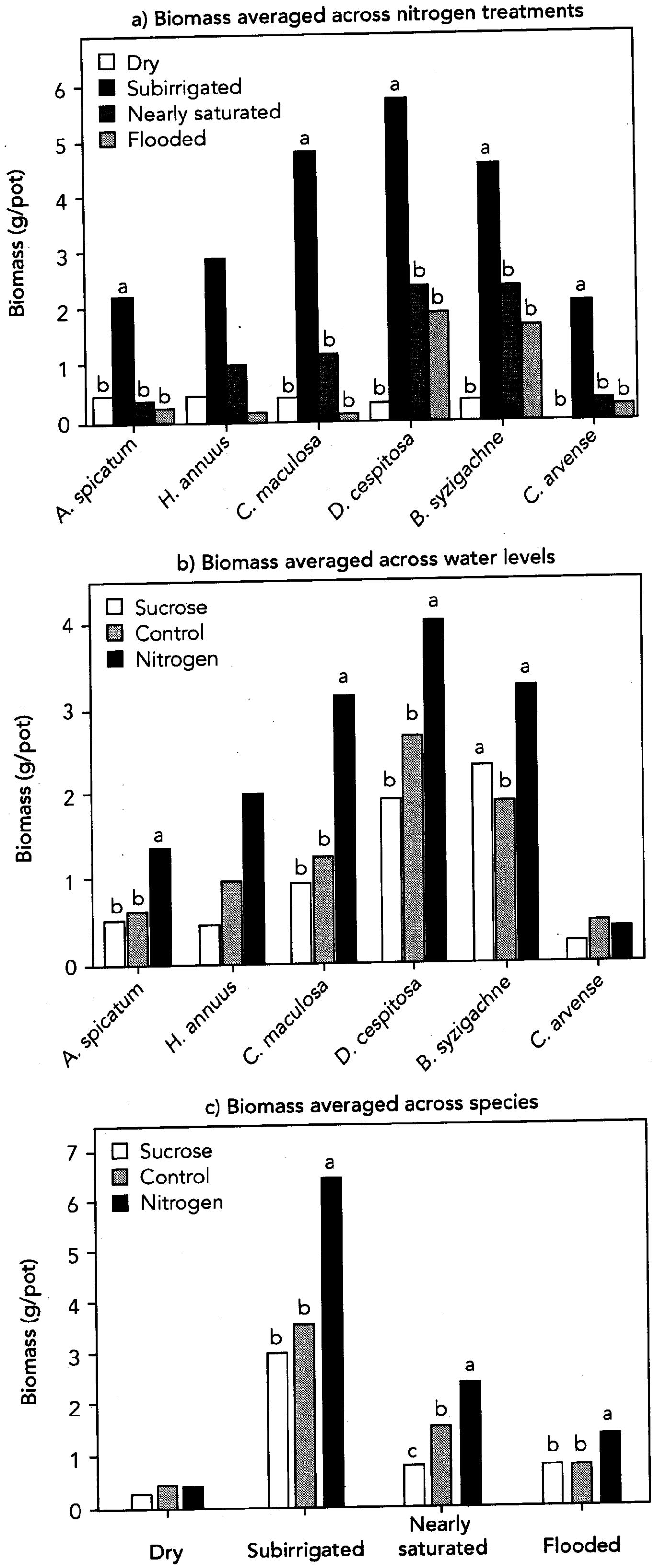

Figure 5. Biomass response to water level and nitrogen treatments in greenhouse experiments. Values are averaged across both Trials 1 and 2 and across a) nitrogen treatments, b) water levels, and c) species to show, respectively, interactions between species and water level, species and nitrogen treatment, and water level and nitrogen treatment. Graphs a and b represent averages across Trials 1 and 2, except for Canada thistle, which is for Trial 2 only due to very low emergence in Trial 1. Graph c represents average of the four species with relatively complete data across treatments and water levels, excluding annual sunflower and Canada thistle, which both had low emergence and many zero values. In graph a, lower case letters represent results of planned contrasts between subirrigated pots and each of the other water level categories; a letter "b" above data for dry, nearly saturated, or flooded pots indicates that emergence or biomass values were significantly lower than in subirrigated pots (see Methods section for details). In graphs b and c, biomass values that differed significantly within each species (graph b) or water level (graph c) are indicated by different lower case letters. Post hoc comparisons used Tukey's test.

by soil or surface conditions or by seed and seedling predation. The former situation requires surface manipulations, such as removing surface litter and soil and adding nutrients, whereas the latter requires fencing, trapping, or other types of animal control. Alternatively, vegetative plantings might be used to bypass the bottleneck.

The very limited and delayed establishment of Canada thistle and spotted knapweed from seed in wetland and transitional areas raises questions about how these weeds are able to invade riparian-upland transition zones so effectively. Since both Canada thistle and spotted knapweed occur in diverse Montana riparian sites (Table 1, Hansen and others 1995) and are common weeds in riparian restoration projects in the northern Rocky Mountain region, their lack of success in this study is surprising. Moreover, the existing population of Canada thistle in the subirrigated transition zone indicates that this zone was susceptible to invasion. Bakker (1960) documented that although invasion by Canada thistle became severe after several years, its initial establishment was very slow in spite of directly adjacent seed sources and was probably due to low production of viable seed, poor dispersal, and wet soil. Though Canada thistle emergence rates were low in our greenhouse study, they were high enough that a substantial number of seedlings should have emerged in field plots given the high seeding rate. We could not account for the lack of thistle emergence in the field.

Nutrient Effects and Management

In testing our second hypothesis, we discovered that the nutrient treatments generally did not affect seedling emergence but frequently affected plant growth, providing limited evidence that N management may affect early succession in riparian areas and adjacent uplands. Biomass responses in the greenhouse were consistent with the hypothesis that effects of N addition are greater in subirrigated than in saturated or rain-fed environments. Unfortunately, poor emergence in the field limited our ability to evaluate treatment effects on growth. Some results for upland species supported the hypothesis that an invasive weed would respond more to N availability than a late-successional native, however. In subirrigated and nearly saturated pots in the greenhouse, spotted knapweed responded more than bluebunch wheatgrass to N addition. In upland plots in the field, spotted knapweed responded significantly to nutrient treatments, while bluebunch wheatgrass did not.

We recommend that land managers and ecological restorationists take a cautious approach to fertilizing given the results of our study and evidence that resource-rich riparian and wetland ecosystems are particularly vulnerable to exotic plant invasions (Stohlgren and others 1998), that nutrient enrichment can promote dominance by species with traits common in weeds, effectively reversing succession (McLendon and Redente 1991, Redente and others 1992, Reever Morghan and Seastedt 1999), and that high N availability benefits Canada thistle more than native upland grasses (Lowe and others 2002). Although sugar had limited influence on seedling emergence in our study, long-term experiments may be necessary to determine the effects of carbon addition on vegetation dynamics after restoration.

Conclusions

We believe that our findings have implications for the ecological restoration of intermountain and Great Plains rangelands and riparian areas. It is often thought that restoring riparian areas has a higher probability of success than on adjacent uplands. The results of this study indicate that restoration of these areas is difficult even when carefully matching species traits with variable hydrologic conditions occurring along an environmental gradient. We also found that invasive weeds did not establish well, but tended to be large and robust in transition areas from wet to upland conditions. Furthermore, invasive weeds tended to grow best in areas with higher N availability, suggesting use of caution when fertilizing during ecological restoration.

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