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Restoration of riparian meadows degraded by livestock grazing: above- and belowground responses

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Abstract

Riparian meadows in the western US are highly productive areas within the riparian corridor that have been extensively utilized for livestock grazing and that are often degraded. This study aimed to increase our understanding of both the functional responses and restoration potential of mesic meadow systems in central Nevada, USA. Nitrogen addition and clipping treatments were used to examine grazing effects, while aeration and revegetation were included to evaluate potential restoration treatments. Belowground response was determined by examining gravimetric soil water content and rooting depth and activity. Aboveground response was determined for two key mesic meadow species, *Carex nebrascensis* and *Poa pratensis*, by quantifying gas exchange and water relations. Large yearly and seasonal differences among water tables largely determined the rooting activity and depth in these mesic meadows and influenced treatment responses. Little rooting activity occurred within or at the surface of the water table and rooting depth increased as water table level lowered during the growing season. In general, nitrogen addition decreased rooting activity and depth relative to controls. It resulted in less negative water potentials and photosynthetic rates that were higher early in the growing season, but lower later in the growing season. The effects of nitrogen addition could be attributed to accelerated phenology and earlier senescence. Clipping resulted in less negative plant water potentials in *Carex* and *Poa*, and *Poa* had higher photosynthetic rates immediately after clipping but only for certain dates and comparisons. Aeration increased rooting activity and depth where there was no confounding effect of water table. Also, predawn and midday water potentials were generally less negative for *Carex* and *Poa* in aerated plots. Establishment on the revegetation plots was dominated by annual and early seral species and, consequently, these plots exhibited reduced rooting depth and activity early in the growing season and high root turnover. Results indicate that water table depth and its effects on soil water are dominant factors in determining the functional processes and recovery potentials of these riparian meadows. Clipping had minimal effects on above- and belowground responses, perhaps because clipping was performed late in the growing season after plants had begun to senescence. Nitrogen addition decreased rooting activity and altered phenology, indicating deleterious effects. Aeration was effective at overcoming some of the negative affects of overgrazing and may be an effective restoration treatment. However, revegetation may have limited potential due to establishment constraints of the dominant species.

Introduction

In recent years, considerable attention has been focused on riparian areas because of the role they play within the landscape (Goodwin et al. 1997). As the interface between terrestrial and aquatic environments, riparian areas support critically important ecological functions and a diversity of animal species

(Knopf et al. 1988; Goodwin et al. 1997). Within watersheds of the semiarid Great Basin, meadows are among the most productive components within the riparian corridor and represent a valuable resource (Kauffman and Krueger 1984; Knopf et al. 1988). They are frequently associated with seeps or springs (Jensen and Platts 1990), and are characterized by water tables that vary both spatially and temporally (Castelli et al. 2000).

Because of their productivity, meadows have been exploited for livestock grazing, often leading to extensive degradation (Kauffman and Krueger 1984; Clary and Webster 1989; Kauffman et al. 1997). Trampling by grazing livestock decreases soil macropore spaces, resulting in soil compaction. Soil compaction decreases infiltration and leads to reduced root growth and lower plant production (Orr 1960; Laycock and Conrad 1967; Bohn and Buckhouse 1985). Livestock grazing also alters nutrient dynamics. While nitrogen is deposited in the excreta of the grazing animals, much of this is likely lost due to volatilization and leaching (Watson and Lapins 1969; Floate 1970; Woodmansee 1978). Moreover, removal of vegetation through grazing probably results in a net export of nitrogen from grazed systems, which can lead to changes in both species composition and production (Berendse et al. 1992).

Land managers are attempting to improve the conditions of disturbed riparian areas because of their importance (Richter 1992; Van Haveren et al. 1997). Little is known about the effects of various land uses or land management activities on meadow functioning. Linkages between severity of degradation and changes in hydrologic regime, soil properties, and vegetation are largely unknown, and need to be investigated so that sound management practices can be implemented.

The primary objectives of this study were to (1) increase our understanding of how Great Basin riparian meadow ecosystems function, (2) examine the recovery processes within degraded mesic meadow ecosystems, and (3) evaluate specific restoration techniques for these ecosystems. Within riparian areas of the Great Basin, meadow ecosystem types occur along a continuum from high to low water tables. *Carex nebrascensis* [hereafter referred to as *Carex*] dominates sites that have high water tables (0–30 cm from the surface) and *Poa pratensis* [hereafter referred to as *Poa*] dominates sites with low water tables (60–80 cm). Sites with intermediate water tables (40–50 cm) are co-dominated by *Carex* and *Poa* (Chambers et al. 1999). This study focused on the low to intermediate ends of the moisture gradient because these meadow ecosystems are among the most heavily utilized by livestock. It examined both above and belowground responses of riparian meadow systems to treatments designed to increase our understanding of the restoration potential of these meadows. Nitrogen and herbage removal treatments were included to examine grazing effects, while aeration and revegetation were included to assess potential restoration treatments. The questions addressed were: (1) how do nitrogen addition, herbage removal, aeration, and revegetation affect soil moisture, rooting activity and rooting depth within these meadows, and (2) how do these treatments affect the gas exchange and water relations characteristics of *Carex* and *Poa*?

Methods

Study sites

During the summer of 1995, three suitable meadow sites were identified in the Austin Ranger District of the Humbolt-Toiyabe National Forest, Nevada (Figure 1). Selection was based on species composition (approximately 10% *Carex* and approximately 40% *Poa*) and proximity of the groundwater to the soil surface. Wells established at each site indicated that the water table levels were located at depths between 40 and 60 cm deep at the three sites. The selected sites included Corral Canyon (39°7′13.5″ N, 116°48′38.6″ W, 2368 m elevation) in the Toquima Mountain Range, and Cahill Canyon (39°27′57.6″ N, 117°2′0.4″ W, 2325 m elevation) and Emigrant Canyon (39°30′35.4″ N, 117°1′5.9″ W, 2174 m elevation) in the Toiyabe Mountain Range (Figure 1). All three sites are located in trough drainageways. Cahill Canyon and Emigrant Canyon have soils that are aquic cryoborolls. Corral Canyon has soils that range from aquic cryoborrols to cryaquols. The nearby town of Austin, NV, with the only long-term weather data in the region, has mean annual precipitation of 31 cm. Approximately 60% arrives as winter snow. Convective thunderstorms during summer months can contribute significant precipitation.

Study design

The study design was a completely randomized block with a control and four main treatments: nitrogen ad-

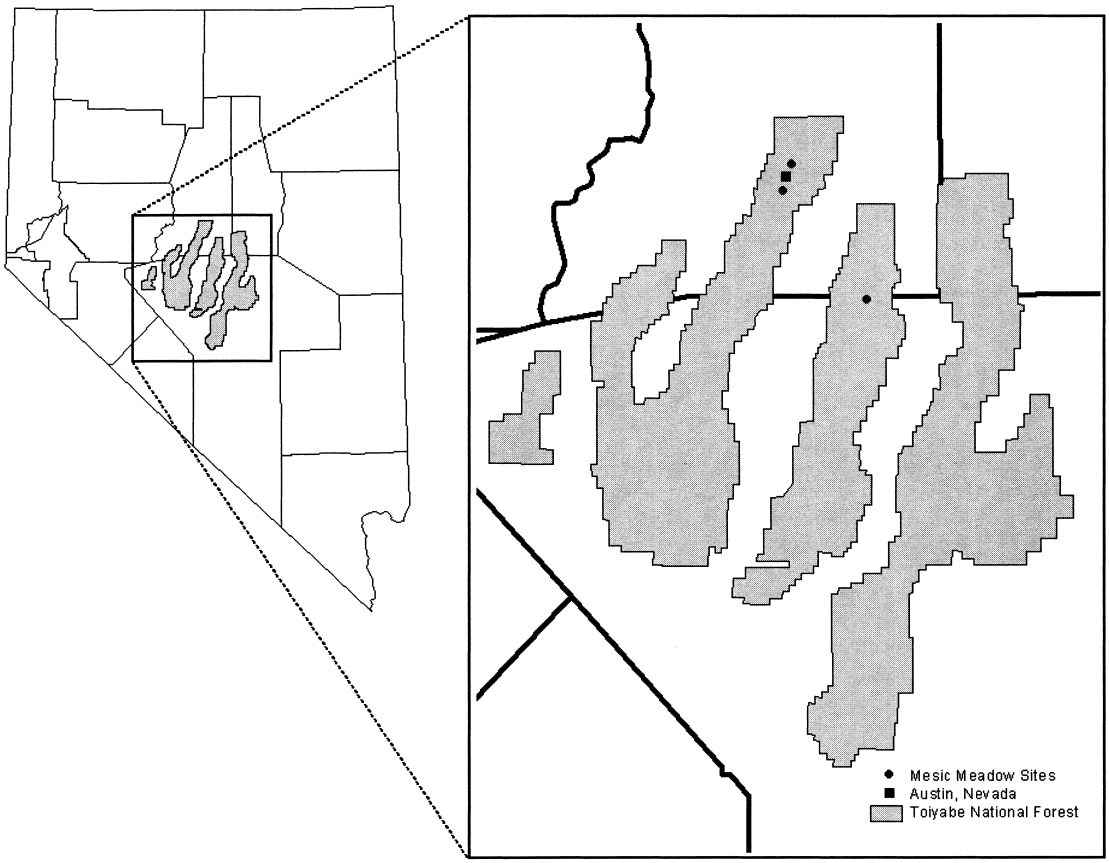

Figure 1. Map of Nevada indicating the boundaries of the Humboldt-Toiyabe National Forest and the locations of the study sites.

dition, clipping, aeration, and revegetation. Four additional treatments included clipping in combination with the nitrogen addition, aeration, and revegetation treatments, bringing the total number of treatments to eight. One block (replicate) was located within each of the three study sites (Corral, Emigrant, and Cahill) to examine treatment differences across sites. Three additional blocks (replicates) were placed at 1 site (Corral) to evaluate differences within a single site. At each site, study plots (blocks) were located in areas that appeared homogeneous in terms of vegetation, soils, and depth to water table. Plot sizes were not uniform due to the small size of these meadows, and ranged from 16 m^2 to 25 m^2. Fences designed to exclude livestock were constructed around the study plots at each site. A standard 30 cm diameter rain gage was placed near the plots within the exclosure at each study site.

The edaphic characteristics of each site were evaluated at the time of plot establishment. Soils were classified as described in Chambers et al. (1999). Bulk density samples (n = 6) were taken at depths of 0–15, 15–30, and 30–45 cm at each study site, and infiltration rates were determined by double ring infiltrometry (n = 3) for each site. A series of wells (7–9) that extended into the water table were established using perforated PVC pipe (10 cm diameter) around the perimeter of each study plot.

Treatments

Aeration consisted of using an electric drill equipped with a 2 cm diameter, power ship auger to drill into the soil. Holes were uniformly spaced at 20 cm intervals to a depth of 30 cm. Aeration has been shown to overcome the effects of subsurface compaction and improve plant water relations in forested systems (Nambiar and Sands 1992). The compacted layer within these meadows occurs 15 to 30 cm below the surface (Weixelman et al. 1996), and aeration should have penetrated this layer, allowing water to infiltrate

and, through natural freeze / thaw processes, break up the compacted soil layer.

Nitrogen addition consisted of a hand application of sulfur-coated urea (36-0-0), a slow release nitrogen fertilizer, at a rate of 100 kg ha^{-1} repeated in fall 1995, 1996, and 1997. This type of fertilizer and application rate have been shown to increase both above- and belowground production and disease resistance in both *Carex* and *Poa* (Davis and Dernoeden 1991; Thompson and Clark 1993; Reece et al. 1994). Composite plant tissue samples were collected (n = 5) during the 1998 growing season at all sites from randomly selected locations within both nitrogen treatment plots and control plots. These were analyzed for nitrogen content using a CHN autoanalyzer.

The revegetation treatment consisted of killing all existing vegetation with a short-lived herbicide application (Round-up®). The soil was then tilled with a commercial grade roto-tiller to break up the sod, create a suitable seedbed, and allow for removal of dead plant material. Six species (*Carex athrostachya*, *C. nebrascensis*, *C. praegracilis*, *Deschampsia caespitosa*, *Trifolium monanthum*, *and T. wormskjoldii*) were selected for seeding based on their abundance in similar, less degraded meadows. Seeds were collected adjacent to the study areas and returned to the laboratory for cleaning and viability tests. Seeding rate was 150 viable seeds m^{-2} for all species except *Trifolium wormskjoldii*, which was seeded at a rate of 125 seeds m^{-2} due to the limited number of seeds collected. Straw mulch blankets (5 cm thick, Granite Seed Co.) were placed over the seeded areas to aid seedling establishment by improving soil moisture retention and insuring that the seeds and top soil were not blown away.

The clipping treatment, applied alone as a treatment and in combination with each of the other treatments, consisted of mowing the aboveground vegetation with a power mower to a stubble height of between 8 and 10 cm. This removed approximately 50% of the aboveground biomass of both *Carex* and *Poa*. Clipping was conducted once a year in late July, and the clipped material was removed from the plot. This timing and level were used to simulate the level of grazing recommended for these sites.

Belowground responses

The root periscope/minirhizotron technique was used to assess belowground response (Richards 1984; Karl and Doescher 1991; Svejcar and Trent 1995). Three minirhizotron tubes were installed in nondestructive sampling areas within each treatment plot. Minirhizotrons consisted of 105 cm long Tenite Buterate tubing (U.S. Plastics Corp.), with 38 mm o.d., and 2 mm wall thickness. The entire lengths of the minirhizotrons were marked with 2 cm bands at intervals of 10 cm with a waterproof marker and installed so that the center of the bands was at 5, 15, 25, 35, 45, 55, and 65 cm from the soil surface. A gas powered soil auger, 45 mm o.d. was used to excavate the soil to allow insertion of the minirhizotron tube. Minirhizotrons were inserted 30 degrees from horizontal to help keep roots from growing down along the tubes (Svejcar and Trent 1995). A 5 cm length of each minirhizotron was left aboveground to allow for the attachment of the root periscope (Edmunds Scientific Corp.). Rubber stoppers were glued into the bottom of each tube to keep ground water and debris from entering the tubes from below and caps were placed over the upper end. All aboveground portions of the minirhizotrons were covered with metal cans to prevent sunlight from entering, as roots exposed to light may suberize more rapidly and growth may be inhibited (Lake 1987). The total number of root intersections in the 2 cm bands were counted and presented as number of roots cm^{-2}.

Physiological responses

Plant physiological responses for *Carex* and *Poa* were determined for plots that received aeration, nutrient addition, clipping only and the control. Treatments were selected so that the independent effects of each treatment could be determined and because time constraints did not allow for the determination of responses to all treatments.

Within each treatment plot, individual plants or ramets (n = 6) of each species were selected randomly. Photosynthesis, transpiration, and stomatal conductance were measured with an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA.). Measurements were conducted between 1000 and 1400 hrs on cloudless days using upper canopy leaves that were approximately the same size and exposed to full sunlight. Water use efficiency (WUE) was calculated as the ratio of photosynthesis to transpiration. At the conclusion of each field measurement, light-sensitive diazopaper was inserted into the sample cuvette under the leaf and exposed to the sun. This created a shadow of the portion of the leaf that was within the chamber. Leaf images were fixed us-

Table 1. Soil bulk density and infiltration characteristics for each of the study sites. Values are mean (±SE).

Site	Bulk density (g cm^{-3})			Infiltration (mm min^{-1})
	0–5 cm	5–15 cm	15–30 cm	
Corral No. 1	1.06 (0.05)	1.14 (0.18)	1.27 (0.09)	23.3 (11.0)
Corral No. 3	0.76 (0.02)	1.16 (0.03)	1.29 (0.14)	16.2 (1.6)
Corral No. 4	0.77 (0.06)	1.29 (0.04)	1.47 (0.07)	15.2 (6.6)
Cahill	0.93 (0.07)	1.09 (0.04)	1.34 (0.07)	53.5 (7.0)
Emigrant	0.96 (0.03)	1.01 (0.08)	1.26 (0.07)	17.1 (2.3)

ing ammonium hydroxide. These images were returned to the laboratory and the area of the portion of the leaf that was within the chamber was measured with an LI-3000 area meter (LI-COR, Inc., Lincoln, NE, USA.).

Predawn and midday xylem water potential were determined for randomly selected individuals (n = 6) of both *Carex* and *Poa* within each treatment plot using a Sholander pressure chamber (3000 series, Soil-Moisture Equip. Corp., Santa Barbara, CA, USA). Predawn measurements were conducted between 0300 and 0600 hours. Midday measurements were conducted between 1000 and 1400 hrs. For all physiological parameters, one set of replicates were measured each day, with 5 days passing between the first and last set of measurements. Measurements were conducted once monthly from May through August. There were few significant differences in stomatal conductance or WUE between any of the treatment plots and control plots for either *Carex* or *Poa* and these data are not presented.

Statistical analysis

Rooting activity data were analyzed by year using a four factor (block, treatment, depth, and time) analysis of variance (ANOVA) with repeated measures on depth and time. Soil moisture data were analyzed by year using 4 factor (block, treatment, depth, and time) ANOVA with repeated measures on depth and time. A three factor (block, treatment, and time) ANOVA with repeated measures on time was used to analyze both the water relations and gas exchange data for each species individually by year. Blocks served as the replicates to examine treatment differences both for the across site (Emigrant, Cahill, and Corral) and within site (Corral #1, Corral #3, and Corral #4) comparisons. Comparisons were only made between each treatment and the control or between the main effect and main effect plus clipping. Mean comparisons were performed using least square means (SAS Institute Inc. 1990).

Results

Edaphic characteristics

Bulk densities were relatively high and increased progressively with depth at all three sites (Table 1). The bulk density for Corral #1, the driest block at Corral Canyon, was significantly greater than for Corral #3 and Corral #4 at the 0–5 cm depth ($P \leqslant 0.05$). Bulk density values did not differ between sites for either the 5–15 cm or 15–30 cm depths. Infiltration rates on the Cahill site were relatively high, 53.5 mm min^{-1} (Table 1). For the Corral and Emigrant sites, infiltration rates were similar to one another and were significantly lower than for the Cahill site.

Environmental variables

As expected for Great Basin ecosystems, most precipitation fell during the winter months. Precipitation amounts varied between sites and years (Table 2). The Corral Canyon site received the least total precipitation, but the highest growing season precipitation. The Emigrant site received the most precipitation. Precipitation amounts were slightly higher in 1997 than in 1996, and 1998 had higher precipitation than the 2 previous years.

Depth to water table was highly variable both temporally and spatially during the course of the study (Figure 2). Seasonal declines in water table depth occurred at all sites, with the degree of spring recharge depending on the amount of overwinter precipitation. In 1998, the year with the most overwinter precipitation, spring recharge was greater than in either 1996 or 1997, with water table levels at or near the surface of all sites for a large portion of the growing season.

Table 2. Precipitation amounts at each study location for the three years of the study. Overwinter is from October to May and Growing Season is from June to September.

Site	Period	Precipitation (cm) 1996	1997	1998
Corral				
	Overwinter	19.5	–	28
	Growing Season	11.0	13.5	11
	Total	30.5	–	39
Cahill				
	Overwinter	29	–	46
	Growing Season	6	–	2
	Total	35	–	48
Emigrant				
	Overwinter	26	18	59
	Growing Season	8	24	5
	Total	32	42	64

Seasonal differences varied among sites. For example, during the 1996 growing season, the water table decline at both Cahill and Emigrant Canyon was greater than 1 m. By the end of the 1997 growing season, the water table depth at Emigrant Canyon was > 2 m. However, at the beginning of the 1998 growing season there was running water at depths up to 10 cm over most of the Emigrant site, and there was still standing water on the plots in Oct. In contrast, at the Corral #3 site there was only a 24 cm difference in average water table elevation during the entire growing season in 1996 – a trend that persisted through 1997 and 1998.

The factor that likely had the greatest impact on the study was the range in water table depths across each study site for a particular sampling period (Figure 2). The greatest range in water table depth was observed at the Cahill Canyon site with a difference of over 1 m being common across the 16 m^2 study site. Corral #1 also exhibited high levels of spatial variability with differences as great as 60 cm found between wells only 10 m apart. The least variable sites were Corral #3, Corral #4 and Emigrant. This high level of spatial variability was not apparent at the time of site selection in August of 1995; however, the 3 years of data suggest that it is typical of these riparian meadows.

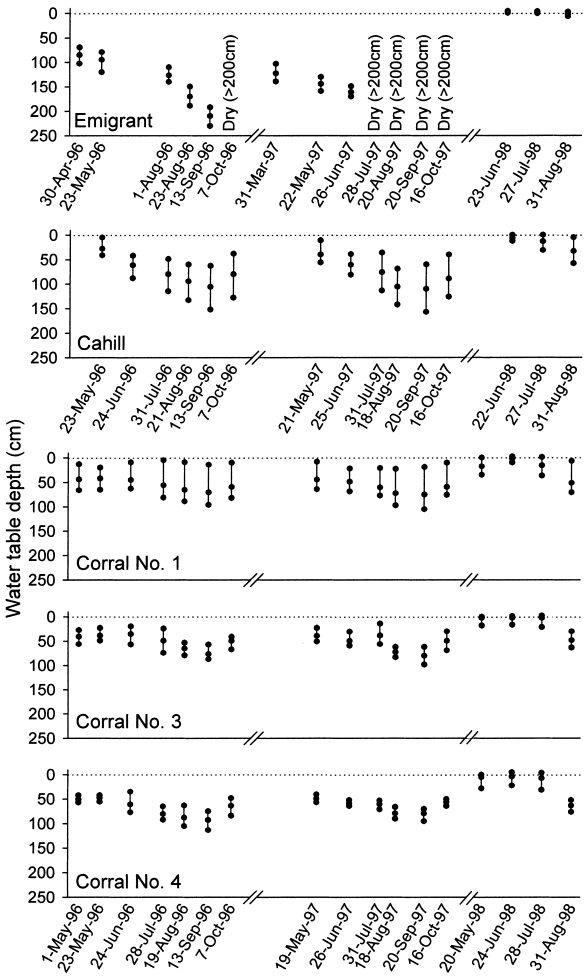

Figure 2. Water table depths for the study plots in 1996, 1997, and 1998. Mean water table depth for each sampling period is indicated by the circle at the center of the line. The top of each line indicates the minimum depth to the water table within a study plot at a particular sampling time; the bottom indicates the maximum depth.

Belowground responses

Soil moisture content was significantly lower in 1996 than in 1997 both across sites and within sites (Figure 3, Table 3). Within years, soil moisture patterns varied among both dates and depths for both comparisons. During the spring sampling, all sites were either saturated or at field capacity in both years. In 1996, soil moisture contents in May and June were 50% higher than in July and August. By the end of the growing season, soil moisture tended to be higher at the 30–45 cm depth than near the surface (Figure 3). In 1997, a year with higher growing season precipitation, soil moisture was again higher in May and June than July and, especially August. The 0–5

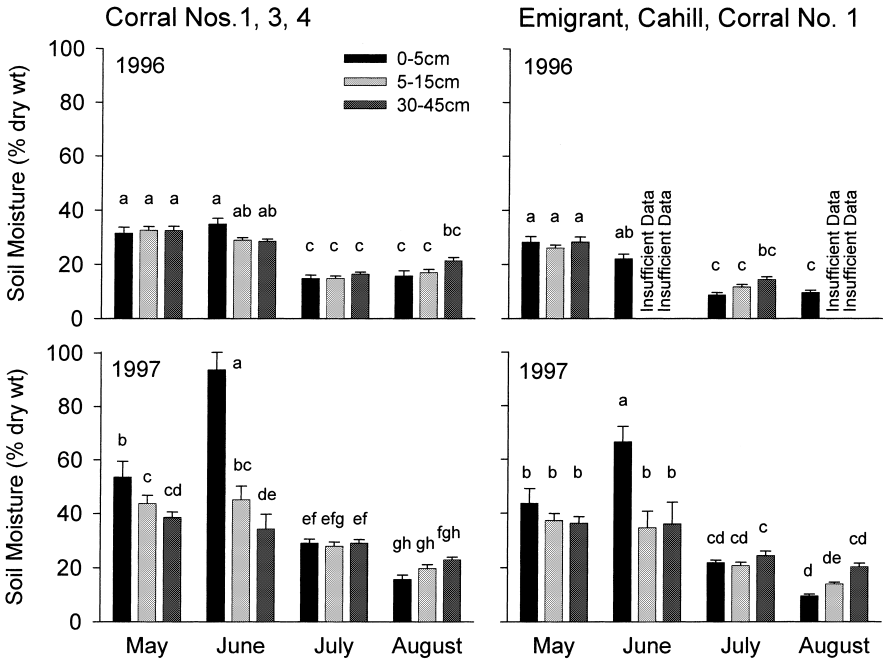

Figure 3. Soil moisture contents for the within site (Corral Nos. 1, 3 and 4) and across site (Emigrant, Cahill and Corral No. 1) comparisons for 1996 and 1997. Values are mean ± SE. Unlike letters indicate significant differences among dates and depths within years ($P \leqslant 0.05$).

cm depth had the highest values in May and June, but by August, the 30–45 cm depth often had the highest values (Figure 3). Importantly, treatment had no effect on soil moisture contents for either the within or across site comparison.

Significant increases in the maximum depth of new roots and root density (activity) occurred as water tables declined over the growing season (Figure 4, Table 4). While the highest rooting activity was always at near surface depths early in the growing season, the highest activity was often at intermediate or lower depths late in the growing season. The zone of maximum rooting activity varied among years depending on the depth to water table. During 1997, the year with the lowest water tables, overall rooting activities were as high at lower depths as at near surface depths. In contrast, during 1998, the wettest year, rooting activities were highest at intermediate and near surface depths ($P < 0.05$).

Treatment effects on rooting activity varied both among dates and depths (Figure 4, Table 4). Aeration alone had few significant effects on rooting activity. However, aerated plots that were clipped often had higher rooting activity than all other treatments in 1997 for both the across and within site comparisons (Figure 4). In all 3 years and for both comparisons, rooting activity of aerated plots, and especially aerated plots that had been clipped, was higher at deeper sampling depths than at near surface depths ($P < 0.05$).

Nitrogen addition and nitrogen addition plus clipping resulted in significantly lower rooting activity than for controls in 1997 for the across site comparison, and in 1998 for the within site comparison at several depths (Figure 4). Although not significant, this trend existed for several of the other comparisons. In all 3 years and for both comparisons, rooting activity in nitrogen addition plots and nitrogen addition plots that were clipped tended to be higher at near surface depths than at deeper depths relative to controls ($P < 0.05$).

The revegetation plots exhibited distinct patterns in rooting activity. In May of 1996, the revegetation treatment had significantly lower rooting activity than the control for both across and within site comparisons (Figure 4; $P < 0.05$). These differences persisted through the summer. During 1997 and 1998, the establishment of annuals and early seral species (e.g., *Bromus tectorum*, *Hordeum brachyantherum*) minimized differences in rooting activity between the revegetation treatment and control plots, especially for near surface depths (Figure 4).

The primary effect of clipping alone was on the zone of rooting activity. Similar to nitrogen addition

Table 3. Results of the ANOVAs for gravimetric soil moisture content.

Factor	df	Corral Nos. 1, 3 & 4 F	Emigrant, Cahill, & Corral No. 1 F
Trt	4	0.33	2.38
Block	2	10.57**	20.69***
Trt (Block) (err A)	8		
Depth	2	4.24*	1.26
Depth*Trt	8	0.22	0.85
Depth*Trt (Block) (error B)	20		
Date	3	72.36***	39.90***
Date*Trt	12	0.79	1.25
Date*Depth	6	12.99***	3.97**
Date*Trt*Depth	24	0.76	0.51
Date*Trt*Depth (Block) (error C)	90		
Yr	1	119.55***	62.75***
Yr*Trt	4	0.59	1.42
Yr*Depth	2	17.26***	6.57**
Yr*Date	3	17.39***	10.53***
Yr*Trt*Date	8	0.98	0.71
Yr*Date*Trt	12	1.26	1.10
Yr*Date*Depth	6	9.61***	3.25**
Yr*Date*Trt*Depth	24	0.87	0.44
Yr*Date*Trt*Depth (Block) (error D)	120		

and nitrogen addition plus clipping, clipping alone resulted in higher rooting activity for near surface depths than deeper depths for most years and dates when compared to the controls ($P < 0.05$).

Aboveground responses

For both *Carex* and *Poa*, there were seasonal declines in predawn water potentials (Figure 5, Table 5). These declines were much less evident in 1997, probably due to greater summer thunderstorm activity and higher soil water contents. In general, few significant treatment effects were evident from our conservative analysis. However, apparent differences did exist in August of 1996 when soil moisture contents were the lowest. In 1996, *Carex* consistently had the least negative predawn water potentials on aerated plots for both the across and within site comparisons (Figure 5). Similarly, *Poa* had less negative water potentials on aerated plots than on controls in 1996 for both comparisons. Also, predawn water potentials for *Carex* and *Poa* on nitrogen addition and clipped plots were higher than on controls in 1996, but only for the within site comparison.

As expected, results for the midday water potentials paralleled those for the predawn water potentials (Figure 6, Table 5). Few significant differences existed, but for August of 1996, *Carex* had the least negative midday water potentials on aerated plots. *Poa* again had less negative water potentials on aerated plots than controls. For both *Carex* and *Poa*, midday water potentials were less negative on nitrogen addition and clipped plots than on controls for the within site comparison.

Like water potential, photosynthesis decreased as the growing season progressed (Figure 7, Table 5). photosynthetic rates for both *Carex* and *Poa* tended to be higher in May on nitrogen addition plots than on controls in 1996 for the across site comparison. Although not shown, photosynthetic rates also were higher for *Poa* in the nitrogen addition plots for the within site comparison in May 1996. The photosynthetic rates in the nitrogen addition plots were nearly equal to the control by June 1996, and by August 1996, the nitrogen plots tended to have lower photosynthetic rates than the controls (Figure 7). The phenology of *Poa* was altered by nitrogen addition, potentially explaining the differences in photosynthetic rates. Flowering began in late May for plants in the nitrogen addition plots at Corral Canyon. By late June, seed heads had completely developed and seeds were nearly ripe by the July sampling period. In con-

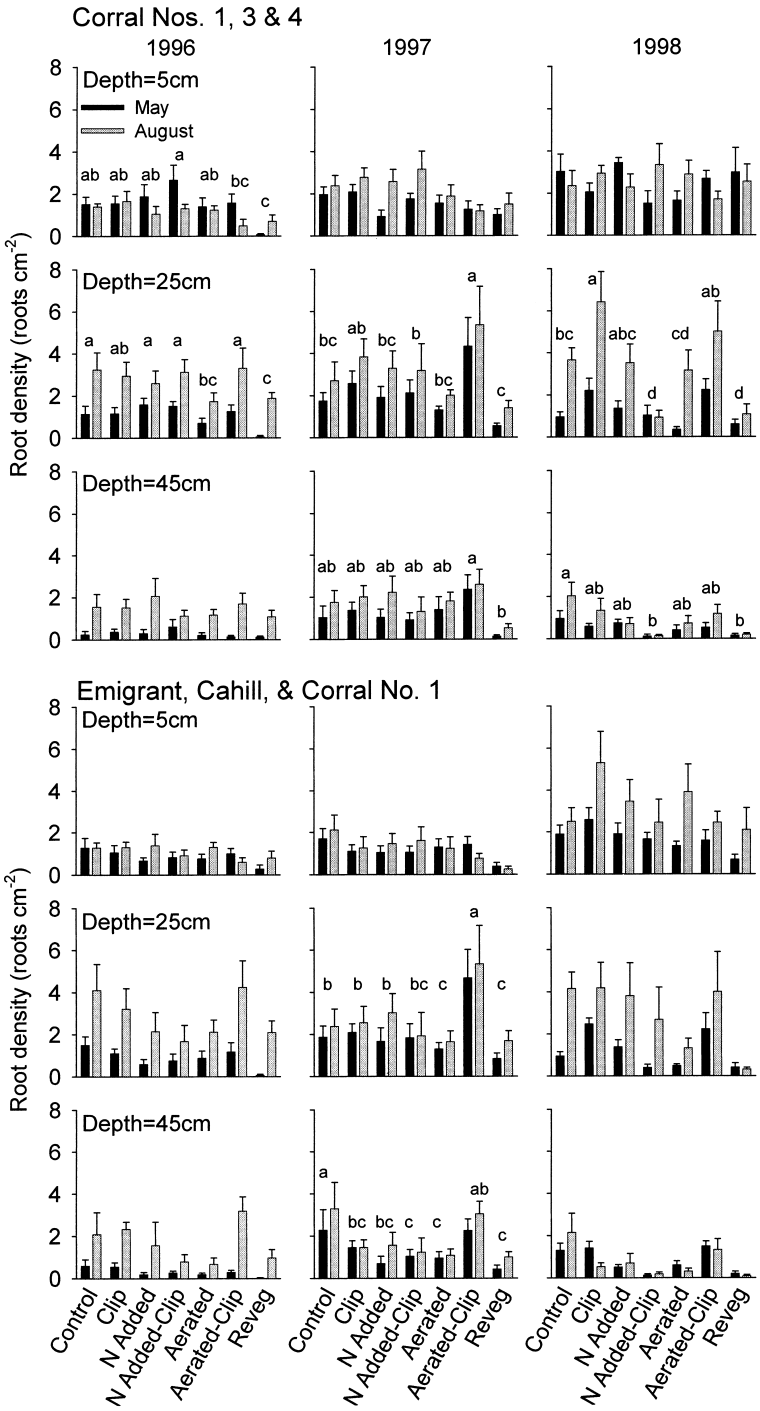

Figure 4. Rooting activity for the within site (Corral Nos. 1, 3 and 4) and across site (Emigrant, Cahill and Corral No. 1) comparisons for 1996 and 1997. Values are mean ± SE. Unlike letters indicate significant differences among treatments within years and depths ($P \leq 0.05$).

trast, flowering did not begin until late June in the control plots, and seed ripening did not occur until mid- to late August.

While not species specific, the 1998 analysis of tissue nitrogen content indicated that there was a significant difference between plants in the nitrogen treatment plots and the control plots. Nitrogen treat-

Table 4. Results of the ANOVAs for rooting activity.

Factor	df	1996 F	1997 F	1998 F
Corral Nos. 1, 3 and 4				
Trt	7	6.15**	1.82	2.93*
Block	2	4.70	3.88*	0.27
Trt (Block) (error A)	14			
Depth	7	47.52***	19.26***	44.44***
Depth × Trt	49	1.66*	1.36+	1.54*
Depth × Trt (Block) (error B)	112			
Date	1	67.58***	124.85***	32.16***
Date × Trt	7	0.74	1.23	6.39***
Date × Depth	7	6.49***	3.41**	10.13***
Date × Depth × Trt	49	0.44	0.61	1.57*
Date × Depth × Trt (Block) (error C)	128			
Emigrant, Cahill, and Corral No. 1				
Trt	7	4.17*	2.10	4.22*
Block	2	8.97**	5.83	0.44
Trt (Block) (error A)	14			
Depth	7	32.81***	8.84***	25.39***
Depth × Trt	49	1.25	0.67	0.71
Depth × Trt (Block) (error B)	112			
Date	1	142.54***	32.72***	16.52***
Date × Trt	7	2.86*	0.68	2.06+
Date × Depth	7	8.16***	1.39	5.98***
Date × Depth × Trt	49	0.88	0.44	0.57
Date × Depth × Trt (Block) (error C)	128			

ment plots had approximately 23% greater tissue nitrogen content than the control plots. There were no statistical differences in tissue nitrogen contents (g N kg^{-1} dry wt) for the nitrogen addition plots across the five study blocks. Values ranged from 16.0 to 17.7 g kg^{-1} with an average across the sites of 16.8 g kg^{-1}. Significant differences in tissue nitrogen content did exist across the sites for the control plots ($P < 0.05$). Values ranged from 10.8 to 16.9 g kg^{-1}, with an average across the sites of 13.7 g kg^{-1}.

Aeration had a limited effect on the photosynthetic rates of *Carex*. For *Poa*, aeration appeared to resulted in higher potosynthetic rates in May 1996 for the across site comparison, but this difference was not significant (Figure 7).

Carex did not exhibit consistent responses to the clipping treatment. For *Poa*, clipped plots had higher photosynthetic rates following the August clipping treatment in 1997 for the within and across site comparison and tended to have the same response in 1997 for the within site comparison (Figure 7).

Discussion

This study illustrates the complexities of riparian meadow systems in the Great Basin. It also indicates that longer-term studies are necessary to capture the high levels of spatial and temporal variability that exist in these systems. Results, while not always consistent, provide insights into the functional processes of mesic graminoid ecosystems. They also indicate that some treatments may be effective in restoring riparian meadow systems.

The lack of consistent treatment effects between years and among blocks within this study is likely an artifact of the confounding effects of water table depth on plant responses. High spatial and temporal variability existed in water tables and soil water contents. It was common to have 30 cm differences in depth to water table between treatment plots on our field sites (Figure 2). For *Carex* in mesic meadows in the Sierra Nevada, differences in plant water relations and photosynthetic rates existed between sites that

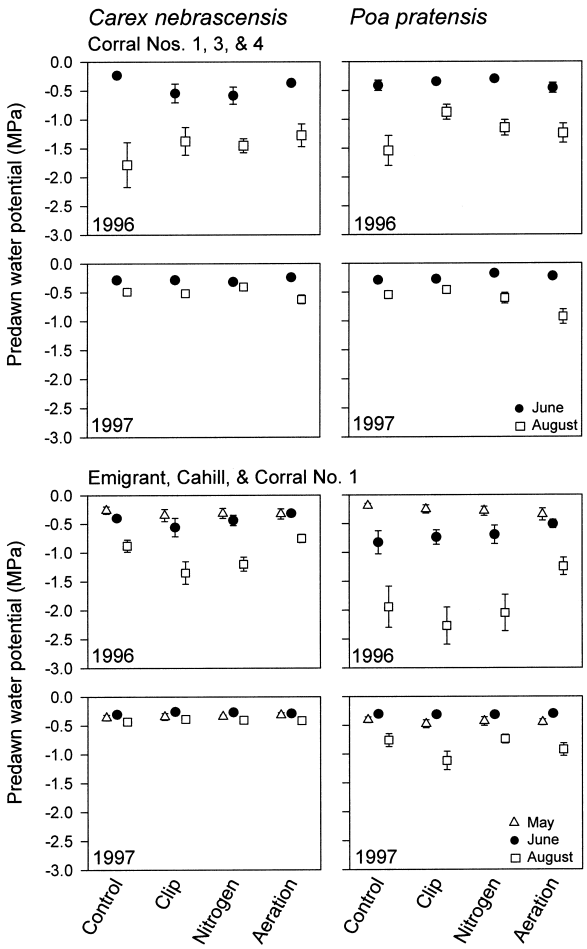

Figure 5. Predawn xylem pressure potentials of *Carex*, and *Poa* in June and August of 1996 and May, June, and August for 1997 for the within site (Corral Nos. 1, 3 and 4) and across site (Emigrant, Cahill and Corral No. 1) comparisons. Values are mean ± SE.

had 30 to 60 cm differences in depth to water table (Svejcar and Riegel 1998), and depth to water table was significantly correlated with gas exchange characteristics and stomatal conductivity along a water table gradient (Seeger 1993). In contrast, in a 15-week glasshouse study with *Carex*, no differences in plant water relations or gas exchange were found in response to lowering the water table from 15 to 75 cm (Sala and Nowak 1997).

Rooting depth and activity, plant and soil water relations, and photosynthesis were all highly related to spatial and temporal differences in water table depth. The seasonal declines and yearly differences among water table depths largely determined rooting activity and depth in these mesic meadow systems. Rooting activity and root biomass are concentrated in the upper 40 cm of the soil for *Carex*, but some roots may be able to reach groundwater at depths to 130 cm (Svejcar and Trent 1995; Sala and Nowak 1997). In the Sierra Nevada, minimal rooting activity was observed within the water table, and active rooting in the upper 40 cm did not occur until the water table dropped below that point (Svejcar and Trent 1995). In this study, rooting depth and activity increased over the growing season as water table depth and soil moisture content decreased (Figure 4). Differences among years are illustrated by the Cahill Canyon data. During 1997, there was generally a decrease in rooting activity at 5 cm between the May and August sample dates, but an increase at the 45 cm depth. Average water table depth declined from 40 cm to 106 cm during that time (Figure 1). In contrast, during 1998 when water tables declined only from 9 to 32 cm, rooting activity at 5 cm greatly increased between May and August, but decreased at 45 cm (Figure 4). Decreased rooting activity at 45 cm during the wet year was likely due to senescence caused by anaerobic or hypoxic soil conditions within the water table (Castelli et al. 2000).

Since these study sites were no longer grazed, we were able to examine the effects of each treatment compared to a control naturally recovering from grazing. The release of nutrients tied up in biomass has been proposed as a benefit of grazing, however grazing usually results in a net loss of nitrogen (Frank et al. 1995). In irrigated agronomic studies, fertilization with the type of nitrogen fertilizer used here has been shown to increase below- as well as aboveground biomass and tiller size of *Poa*. (Mortimer and Ahlgren 1936; Davis and Dernoeden 1991). Other studies indicate that nitrogen addition results in increased shoot:root ratios (Shaver and Melillo 1983). Increasing belowground biomass or tiller diameter may be an effective means of reducing soil compaction (Warren et al. 1986). Thus, nitrogen addition could potentially ameliorate nitrogen loss and reduce soil compaction if root growth is increased. In our nitrogen treatment plots, overall rooting activity and the depth of maximum rooting activity was usually decreased relative to the controls. Also, plant water relations for both *Carex* and *Poa* were generally less negative. Both species exhibited greater photosynthetic rates early in the growing season, but by July, there was either no difference or photosynthetic rates were reduced. These responses were likely due to the accelerated phenology that was observed in *Poa* and more rapid growth when water tables and soil water con-

Table 5. Results of the ANOVAs for the predawn ($Y_{predawn}$) and midday (Y_{midday}) water potentials and for photosynthesis for both *Carex* and *Poa*.

		Carex			*Poa*		
Factor	df	$Y_{predawn}$	Y_{midday}	PSN	$Y_{predawn}$	Y_{midday}	PSN
Corral Nos. 1, 3 and 4							
1996							
Trt	3	0.15	1.84	3.82+	1.52	2.09	7.03*
Block	2	1.67	4.24+	15.96**	3.04	0.30	11.11**
Block*Trt (error A)	6						
Date	1	13.79**	0.14	3.01	20.85**	0.16	2.53
Date*Trt	3	0.38	1.76	1.59	0.47	0.99	1.04
Block*Date*Trt (error B)	8						
1997							
Trt	3	0.76	6.24*	2.82	2.60	1.16	1.96
Block	2	5.23*	0.50	0.68	5.95*	2.58	1.09
Block*Trt (error A)	6						
Date	1	6.60*	9.19*	13.57**	10.73*	30.68***	0.11
Date*Trt	3	0.47	2.38	0.22	0.91	0.44	1.98
Block*Date*Trt (error B)	8						
Emigrant, Cahill, and Corral No. 1							
1996							
Trt	3	1.31	0.04	2.05	1.16	2.43	0.42
Block	2	3.17	1.50	2.09	18.18**	20.37**	3.84+
Trt (Block) (error A)	6						
Date	2	9.22**	3.89*	31.99***	21.66***	4.39*	12.07**
Date*Trt	6	0.32	0.81	1.04	0.59	0.23	0.63
Date*Trt (Block) (error B)	12						
1997							
Trt	3	1.14	2.32	1.67	0.91	0.74	2.96
Block	2	11.67**	0.21	0.73	15.69**	26.78***	2.11
Trt (Block) (error A)	6						
Date	2	9.20**	25.14***	16.94***	12.47**	14.70**	7.43**
Date*Trt	6	0.11	1.07	0.37	0.31	0.14	0.59
Date*Trt (Block) (error B)	12						

tents were higher. The decreased rooting depth and activity and the accelerated development may alter species competitive relationships. Thus, results from both the above and belowground portion of the study indicate that nitrogen addition may retard recovery processes within these meadows.

In this study, clipping was used to simulate herbivory and was included as a treatment because it is likely that these meadows will continue to be used as pastures for domestic livestock. Plant responses to herbivory include decreased carbon allocation to roots resulting in decreased root growth, or increased photosynthetic rates due to compensatory photosynthesis or a change in leaf age composition (Caldwell et al. 1981; Caldwell and Nowak 1984; Holland and Detling 1990). Clipping had limited effects on the above and belowground variables in this study. Clipping alone resulted in relatively higher rooting activ-

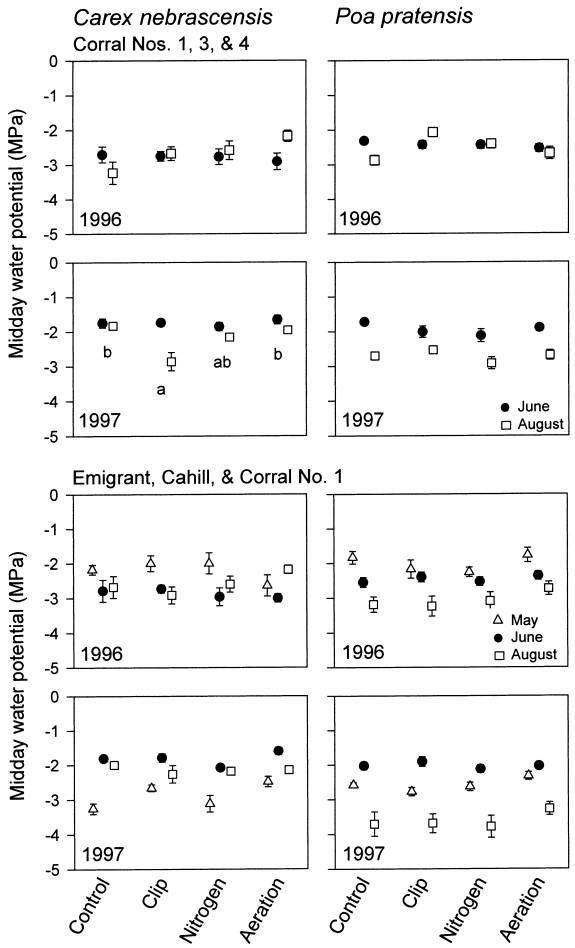

Figure 6. Midday xylem pressure potentials of *Carex* and *Poa* in June and August of 1996 and May, June, and August for 1997 for the within site (Corral Nos. 1, 3, and 4) and across site (Emigrant, Cahill and Corral No. 1) comparisons. Values are mean ± SE.

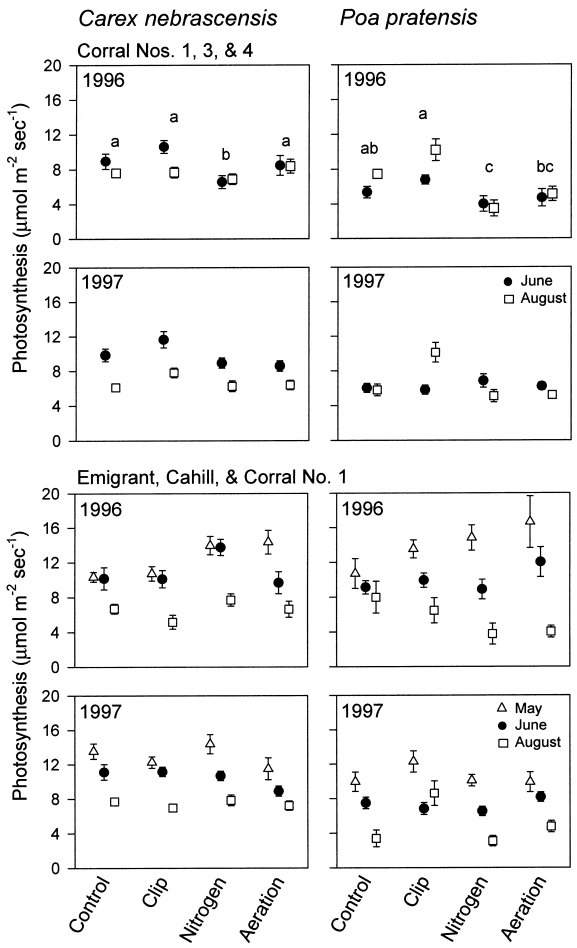

Figure 7. Photosynthetic responses of *Carex* and *Poa* in June and August of 1996 and May, June, and August for 1997 for the within site (Corral Nos. 1, 3 and 4) and across site (Emigrant, Cahill and Corral No. 1) comparisons. Values are mean ± SE. Unlike letters indicate significant differences among treatments.

ity for near surface depths and, in combination with aeration, resulted in higher rooting activity and depth in 1997. Less negative plant water relations were observed in *Carex* and *Poa*, and *Poa* had greater photosynthetic rates immediately following clipping but only for certain dates and comparisons. The lack of clear results may be due to the level and timing of the clipping treatment. A similar study indicated that defoliation to a 10 cm stubble height did not significantly affect biomass production (Clary 1995). Also, clipping did not occur until late in the growing season after plants had already begun to senesce.

In our mesic meadows, bulk density values were similar to those of heavily grazed sites with loam or silty loam soils (Orr 1960), while infiltration values were like those reported for moderately grazed sites with loamy fine sand soils (Rhoades et al. 1964). In general, there was a positive response to the aeration treatment. Soil compaction has been shown to decrease root growth, rooting depth and root weights of *Poa* and to have negative effects on plant water relations (Agnew and Carrow 1985a, 1985b). Aeration eliminated the effects of soil compaction in a forested ecosystem (Nambiar and Sands 1992), and increased rooting depth and activity at our sites when the treatment was not confounded by water table. Aeration also resulted in increases, although not significant, in predawn and midday water potential for both *Poa* and *Carex*. A more consistent response might have been observed had the treatment been applied more than once.

Results from the revegetation treatment can be explained largely by the establishment of annual and

early seral species. Both 1996 and 1997 were comparatively dry years and there was no establishment of seeded species in 1996, and only limited establishment in 1997 and 1998. While there were differences in rooting activity and depth early in all three years, there were no differences by the end of the growing seasons. Also, there were no differences in soil moisture content.

Water table depths in Great Basin riparian areas are spatially and temporally variable and have major effects on the functional processes and recovery potentials of meadow ecosystems (Castelli et al. 2000; Martin and Chambers 2001). Because plant rooting activities and depths track water table depth and soil water content, the effects of grazing and restoration treatments can be confounded by yearly and seasonal differences in water tables. This indicates that in studies designed to evaluate structural and functional processes in similar types of meadows, water table depth should be measured in individual treatment plots and treated as a covariate when evaluating treatment effects on plant response variables (Martin and Chambers 2001).

Results of the grazing treatments indicate that late season herbage removal at moderate levels may have few effects because many of the species have already begun to senesce. Other aspects of grazing such as nitrogen deposition can decrease rooting activity, alter plant phenology, and may retard recovery of these meadow ecosystems. Recovery processes may be accelerated by aeration treatments, especially for meadows that occur at the dry end of the continuum. However, the potential of revegetation as a treatment may be limited due to establishment constraints on the dominant species.

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