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EFFECTS OF WATER TABLE, CLIPPING, AND SPECIES INTERACTIONS ON *CAREX NEBRASCENSIS* AND *POA PRATENSIS* IN RIPARIAN MEADOWS

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Abstract: In this study, we hypothesized that the primary variable determining species responses and interactions within wet/mesic riparian meadows in central Nevada, USA was the water table but that the direct and indirect effects of livestock grazing modified both species responses and interactions. We tested this hypothesis for two widespread riparian species, *Carex nebrascensis* and *Poa pratensis* ssp. *pratensis,* that co-occur but have maximum expression at different water tables. *Carex nebrascensis* has widely spread tillers typical of 'guerilla' plant architecture, while *P. pratensis* has closely spaced and compact tillers typical of 'phalanx' plant architecture. Individuals of both species were grown at mid- and low water tables with or without neighbors and were either clipped or not clipped at the end of the first growing season. For the study site with the most complete record, mean water-table depth during the growing season (May through August) on the mid sites was −32 cm in year 1 and −7cm in year 2. Water-table depth on the low sites was −69 cm in year 1 and −31 cm in year 2. Plant survival, tillering, biomass, and seed production over a 2-yr period were used to quantify the species responses. Water table had no effect on tillering or biomass of *C. nebrascensis,* indicating that it is adapted for growth and persistence over the range of water tables examined. In contrast, growth and tillering of *P. pratensis* was severely restricted at more shallow water tables. *Poa pratensis* had about 50% fewer tillers and lower biomass (9.0 vs 46.5 g) for neighbor-removed plots on mid- than low-water-table sites at one of the study meadows. Further, tiller numbers of *P. pratensis* increased over time on the low-water-table plots, but decreased on the mid-water-table plots. Clipping had no effect on the survival, tillering, or growth of either species. The clipping treatment may not have removed sufficient leaf mass or may have been applied too near the end of the growing season to elicit a response. Neighborhood removal resulted in a 3- to 10-fold increase in tillering and higher plant mass (1.3 vs. 9.5 g) for *C. nebrascensis. Poa pratensis* showed an even greater response to neighbor removal. Tillering was 6- to 100-fold greater and mass was 15 to 50 times greater on neighbor removed than neighbor-intact plots. Comparisons between single species and mixed species plots indicated that there was an interaction between the species that limited tiller production in *C. nebrascensis.* These results indicate that *P. pratensis,* the 'phalanx' species, is capable of more rapidly responding to disturbances that remove neighbors and increase available space than *C. nebrascensis,* the 'guerilla' species. Contrary to previous studies, the interactions between the two species do not seem to be related to plant architecture and can be best attributed to generally greater growth rates and increased competitive ability for *P. pratensis* at lower water tables. Grazing may further alter the relative competitive ability of the two species in favor of *P. pratensis.*

Key Words: environmental gradient, neighborhood, competition, clipping, tillering, biomass

INTRODUCTION

The vegetation structure of riparian meadows in semi-arid ecosystems is dependent upon a complex set of interacting abiotic and biotic factors. As in other types of wetlands, the driving abiotic factor in riparian meadows is the hydrologic regime. The hydrologic regime influences soil water contents (Castelli et al. 2000, Martin and Chambers in press), soil redox potentials (Castelli et al. 2000), and soil nutrients (Chambers et al. 1999), and consequently, species composi-

tion (Allen-Diaz 1991, Stromberg et al. 1996, Castelli et al. 2000, Martin and Chambers 2001). In semi-arid ecosystems, the hydrologic regime, as reflected by water-table depth, is often highly spatially and temporally variable, and this variability influences rooting depth and activity (Martin and Chambers in press), water relations and gas exchange (Seeger 1993, Sala and Nowak 1997, Svejcar and Reigel 1998), and vegetative and sexual reproductive effort (Martin 1999) of individual species across riparian meadows on a seasonal as well as yearly basis.

Herbivory is one of the primary biotic factors influencing species responses and interactions and community dynamics in these semi-arid ecosystems. Because of their proximity to perennial water sources and high productivity, riparian meadows have been extensively used by both native herbivores and livestock for forage (Kauffman and Krueger 1984, Belsky et al. 1999). Herbivore activities directly impact vegetation through consumption of plant materials and indirectly through effects on nutrient cycles and soil disturbance (Crawley 1983). Grazing can alter competitive relations through increased light intensity to the soil surface and remaining vegetation, increased water or nutrient availability to remaining vegetation, and activation of dormant meristems (Owen 1981, Dyer et al. 1993, McNaughton 1993, Noy-Meir 1993, Painter and Belsky 1993). Grazing animals that congregate in riparian areas can significantly reduce vegetation cover and severely disturb the soil surface (Kauffman and Kruegar 1984, Belsky et al. 1999), creating open patches that facilitate seedling establishment and the vegetative spread of nearby plants via tillering.

The majority of studies conducted within these systems have focused on species or community response to either water table or herbivory and have largely ignored interacting effects. Past research in Great Basin riparian meadows led us to hypothesize that the primary variable determining species responses and interactions within these meadows was water-table depth but that the direct and indirect effects of livestock grazing modified both species responses and interactions. In this study, we tested this hypothesis for two widespread riparian species, *Carex nebrascensis* Dewey and *Poa pratensis* L., that co-occur but that have maximum expression at different water-table depths.

Carex nebrascensis, a sedge, is the dominant species in meadows that have been classified as the Nebraska sedge type and that have relatively high water tables during the active growing season (May through August) (0 to −20 cm), while *P. pratensis,* a grass, is the dominant species in meadows that have been classified as the mesic graminoid ecosystem type and that have low water tables (−60 to −80 cm) (Weixelman et al. 1996). Meadows with intermediate water tables (−30 to −50 cm) are co-dominated by both species (Weixelman et al. 1996, Chambers et al. 1999). Existing studies indicate that *C. nebrascensis* is less tolerant of grazing than *P. pratensis.* Grazing had no effect on vegetative reproduction of *C. nebrascensis* but slowed shoot growth in Sierra Nevada meadows (Ratliff and Westfall 1987). In contrast, *P. pratensis* has been described as an increaser species in heavily grazed riparian meadows in the western United States (Weixelman et al. 1996). The abundance of *P. pratensis* significantly increases in grazed riparian meadows, while no increases and even decreases occur in sites excluded from grazing (Schultz and Leininger 1990, Green and Kauffman 1995). Some agronomic studies indicate that growth of *P. pratensis* is stimulated by frequent clipping (Mortimer and Ahlgren 1936, Ahlgren 1938). However, other agronomic studies indicate that close clipping (2.5 cm) has no effect on tiller production and may reduce vegetative production and seed yields (Thompson and Clark 1993).

The two species have clonal growth but differ in terms of tiller dynamics. *Poa pratensis* has tillers (ramets) that are closely spaced and compact, while *C. nebrascensis* has tillers that are more loosely arranged and widely spread (termed 'phalanx' and 'guerilla' plant architecture, respectively, by Lovett Doust 1981). In addition to grazing, the proximity, composition, and abundance of neighboring plants affect both the rate of tiller formation and tiller spacing (Price and Marshall 1999). In turn, the production and spatial spread of individual tillers directly influences the interactions of clonal plants with other plants and their spatial environment (Humphrey and Pyke 1998).

In this study, we examined the effects of water-table depth, neighborhood species interactions, and herbivory on the survival, tillering, biomass, and seed production of *C. nebrascensis* and *P. pratensis* in two central Nevada riparian meadows. We addressed three questions: 1) How does water table influence species responses and interactions? 2) How do neighbor removal and clipping affect species responses and interactions? 3) What are the combined effects of water table, neighbor removal, and clipping on species responses and interactions?

METHODS

The two study meadows are located on the Humboldt-Toiyabe National Forest in Corral Canyon, Toquima Mountain Range (elev. 2358 m; 39°07′13.5″N, 116°48′39″W) and in Kingston Canyon, Toiyabe Mountain Range (elev. 2218 m; 39°15′30′N, 117°09′30″W). Both meadows occur in broad valley bottoms adjacent to perennial streams. In this semi-arid region, most precipitation arrives during the win-

ter as snow, and peak runoff is during snowmelt in early June. Convective summer storms occasionally result in significant precipitation and runoff. The only long-term weather station in the area, Austin, Nevada, USA (1950 m), has mean annual precipitation of 310 mm.

In June 1996, low- and mid-water-table sites were located within each of the two study meadows based on the proximity of ground water to the soil surface and on species composition. Wells established at the time of selection indicated that the water table was between −50 and −60 cm for the low-water-table sites and between −30 and −40 cm at the mid-water-table sites. The low-water-table sites were characterized by approximately 55% *P. pratensis* and 5% *C. nebrascensis,* and the mid-water-table sites had approximately 35% of each species. Soils on the low-water-table sites were aquic Cryoborolls, while those on the mid-water-table sites were cumulic Cryaquolls (Weixelman et al. 1996, Chambers et al. 1999). Both of the meadows are currently part of U.S. Forest Service grazing allotments. The season of use alternates between mid-summer (June/July) and late summer (Aug/Sept), and the level of forage removal is 50% by weight.

At each low- and mid-water-table site, study plots were located in areas with homogeneous vegetation, soils, and depth to water table. For each low- and mid-water-table site, twelve 180-cm-diameter plots were established and one of four possible scenarios was randomly assigned to each plot: neighbors intact no clipping (NINC), neighbors removed no clipping (NRNC), neighbors intact with clipping (NICL), and neighbors removed with clipping (NRCL) (Figure 1). This resulted in a factorial design with three replications of each treatment. Considerable spatial and temporal variability exists in depth to water table across these meadows (Castelli et al. 2000, Martin and Chambers 2001), and plots were located 50 cm apart to minimize the area required and ensure that depth to water table remained fairly uniform across the site. Water table was monitored monthly throughout the growing season from 4 wells established around the perimeter of each set of treatment plots. Precipitation data were collected at both sites with a standard 30 cm diameter rain gauge.

All vegetation within the neighbor-removal treatment plots was killed with an application of a contact herbicide (Round-up®). The plots were then hand-spaded, and all plant material was removed. Metal flashing was buried around the perimeter of each plot to a depth of 30 cm to prevent encroachment of tillers of plants from outside the plots. We assumed this would have no effect on the target plants, as there was 60 cm between target plants and the exclosure.

Individuals of the two species were transplanted into

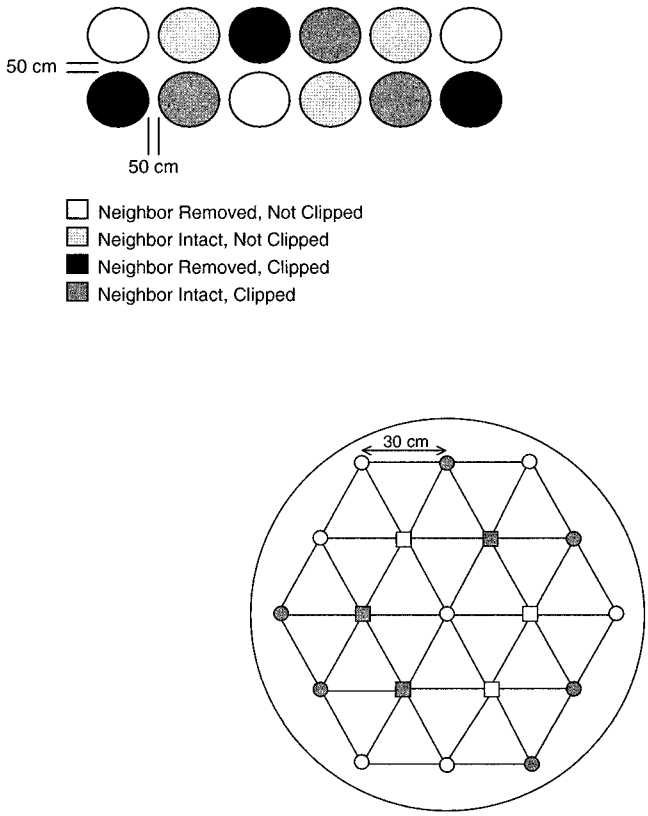

Figure 1. The layout of the twelve plots at one water-table level (upper left) and a detail of one of the circular plots (lower right). The hexagonal design provides uniform spacing in all directions. The target plants are the squares. Plants of one species are shown as closed squares or circles, while those of the second species are shown as open squares or circles.

both neighbors-intact and neighbors-removed plots using a hexagonal planting grid with a 30 cm spacing (Figure 1). The hexagon pattern was used as it provides a uniform exposure to neighbors (Chambers 1991, Humphrey and Pyke 1998), and it was assumed that the 30-cm spacing would prevent competition between individuals on hexagonal points. One of the two species was randomly assigned to each point on the hexagon. Target plants consisted of three individuals of each species located in the inner grid positions (excluding the center) (3 individuals × 3 replicates = 9 individuals for each treatment per water table at each site) (Figure 1). Intraspecific competition effects were evaluated with a set of six neighbor-removal plots established at the Corral Canyon mid-water-table site. Within these plots, all of the transplants were either *C. nebrascensis* or *P. pratensis* (3 plots/species, 6 target individuals/plot). Species were randomly assigned to individual plots.

Individuals of approximately the same size and mass were transplanted into the plots in late May 1997.

The average number of tillers of *C. nebrascensis* transplants was two, while for *P. pratensis*, the average was six. Plants were grown in the greenhouse from seeds collected from the study sites at the end of the 1996 growing season. After germination, seedlings were transferred to individual containers. Containerized seedlings were placed outside in Austin, Nevada to acclimate to local conditions for 1 wk prior to transplanting. Any transplants that died during the first four weeks were replaced.

The clipping treatment consisted of removing approximately 50% of the aboveground biomass of all transplants with scissors. Clipping was conducted in mid-September 1997, after the first tiller census, and all clippings were removed from the plots. The clipping treatment approximated the level of grazing use recommended for these meadows by the U.S. Forest Service. Insect herbivory was negligible and appeared uniform for both species.

In mid-September 1997 and both mid-May and mid-August 1998, tillers at or beyond the first leaf stage were counted for each of the target plants. In September 1998, inflorescences and seeds (if any) were collected from the plants. The aboveground portion of all surviving tillers of each transplant was then harvested. Oven dried (72 hr @ 60°C) mass of both leaves and inflorescences was determined in the lab. Seeds were separated from inflorescences, and the total number of filled seeds per plant were counted under a dissecting microscope.

Analysis

Differences in transplant survival among water tables and treatments were analyzed by site and species with logistic regression in PROC LIFEREG (Weibull distribution, likelihood ratio test) (SAS Institute 1995), a procedure that uses estimated lifespans of individuals rather than survival probabilities (Fox 1993). The output is interpreted in terms of the intercept for its specific model. Variables for the intercept were selected based on consistent survival for the two-year study period. Tiller production data were analyzed using 4-way (water table, neighborhood, clipping, and time) repeated measures analysis of variance with repeated measures on time. A 3-way (water table, neighborhood, and clipping) analysis of variance with a completely randomized design was used to analyze biomass and seed production data. Mean comparisons were performed for factors that were significant in the analysis of variance using the least significant means procedure (SAS 1990).

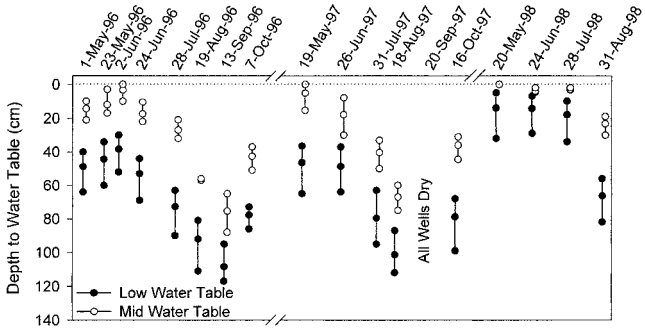

Figure 2. Depth to water table (max, mean, min) for the Corral Canyon study site from 1 May 96 through 31 Aug 98 (n = 4).

RESULTS

Precipitation differed between years and sites. In 1997, growing season and total precipitation on the Kingston site were only 14 and 29 cm, respectively, but in 1998, growing season and total precipitation were 21 and 70 cm. In 1997, the Corral site received growing precipitation (14 cm) that was similar to the Kingston site. However, Corral had lower growing season (11 cm) and total precipitation (39 cm) than Kingston in 1998.

The water tables on these sites reflected the yearly differences in precipitation and showed strong seasonal declines. The most complete record is for Corral Canyon where data were collected the year prior to the study (Figure 2). In 1997, the first year of the study, mean water-table depths during the growing season (May through August) were within the expected ranges on both the mid- (−32 cm) and low sites (−69 cm). In contrast, water-table depths during the growing season were higher than expected in 1998, averaging −7 cm on the mid-site and −31 cm on the low site. Water tables in Kingston Canyon were generally 10 to 20 cm lower but showed similar trends.

Transplant survival and lifespans of *C. nebrascensis* had greater differences than survival and lifespans of *P. pratensis* for both sites and treatments (Figure 3). In general, for *C. nebrascensis*, the lifespan estimate was shorter at Corral than Kingston Canyon (0.38 for Corral vs. 1.0 for Kingston; $P < 0.0001$). At Corral Canyon, the mid-water-table plot had a longer lifespan estimate than the low-water-table plot (1.74 for mid vs. 1.0 for low; $P = 0.0199$). Also, the neighbor-intact plots had a shorter lifespan estimate on the Corral site (0.34 vs. 1.0; $P < 0.0001$). This difference did not exist at the Kingston site. Clipping had no significant effects in the lifespan analysis.

For *P. pratensis*, there were no significant differences among sites or water tables in the lifespan analysis. The only significant treatment effect was on the

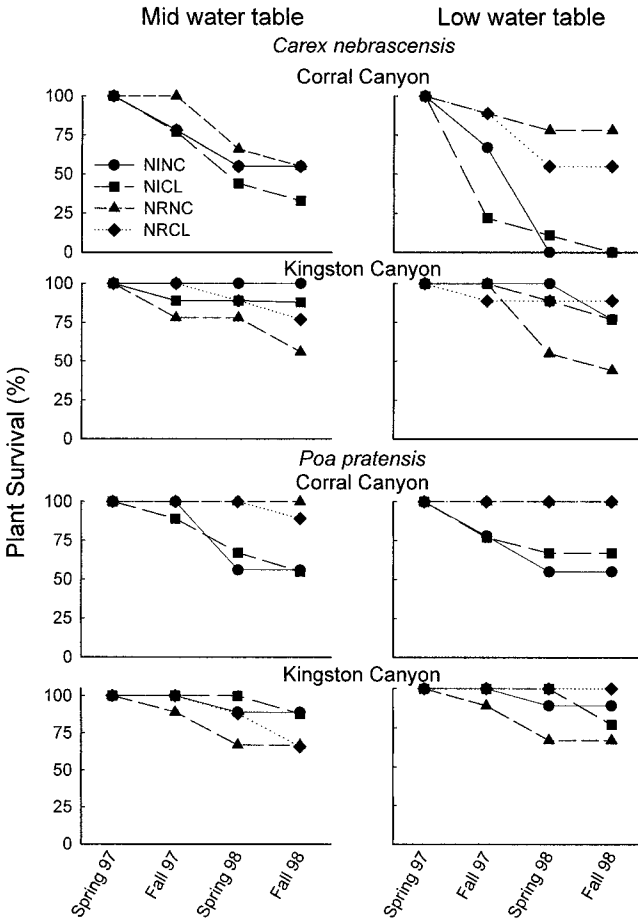

Figure 3. Percentage survival of transplants of *Carex nebrascensis* and *Poa pratensis* at both study sites for all sampling periods. Values are means; n = 9. NINC = neighbors intact, not clipped; NICL = neighbors intact, clipped; NRNC = neighbors removed, not clipped; NRCL = neighbors removed, clipped.

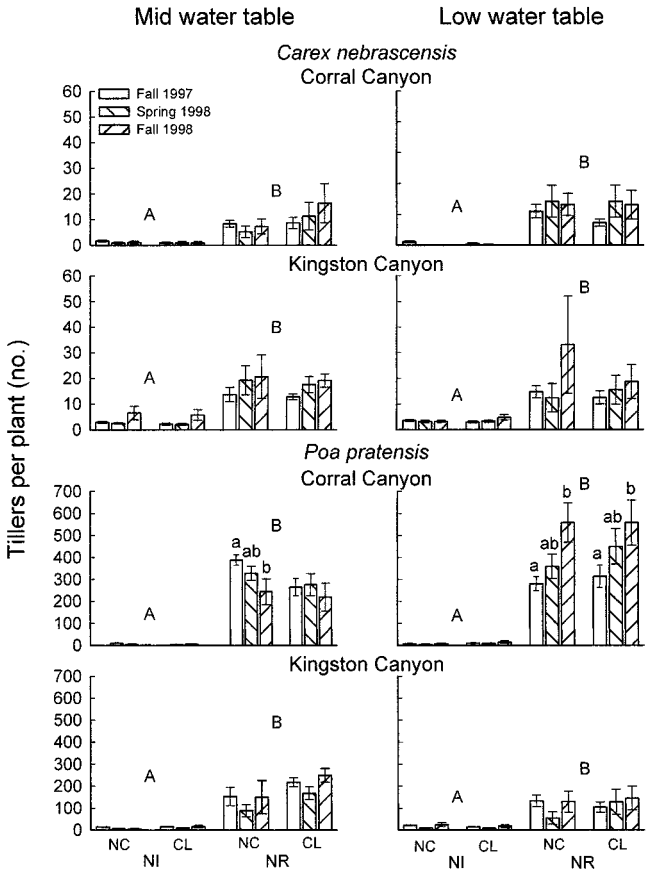

Figure 4. Number of tillers per plant for *C. nebrascensis* and *P. pratensis* for each treatment at the two study sites in fall 1997, spring 1998, and fall 1998. Upper case letters indicate significant differences ($P \leq 0.05$) between neighborhood treatments within water tables. Lower case letters indicate significant differences ($P \leq 0.05$) among dates within neighborhood and clipping treatments. Values are mean ± S.E.; n = 9. NINC = neighbors intact, not clipped; NICL = neighbors intact, clipped; NRNC = neighbors removed, not clipped; NRCL = neighbors removed, clipped.

Corral site, where the neighbor intact plot had significantly lower life span estimates than the neighbor removed treatment (0.10 vs. 1.0; P = 0.0021).

The tillering response of the two species was similar at both sites. For *C. nebrascensis,* neither water-table depth nor clipping had a significant effect on tiller number. However, tiller number was significantly larger in neighbor-removed than neighbor-intact plots at both Corral Canyon ($F_{1,16}$ = 22.9, P = 0.0001) and Kingston Canyon ($F_{1,16}$ = 15.8, P = 0.0001) (Figure 4). At Corral Canyon, neighbor-removed plots had more than ten times the number of tillers of neighbor-intact plots, while at Kingston Canyon, neighbor-removed plots had 3 to 7 times more tillers. Also, there were significant increases in overall tiller number over time at Kingston Canyon ($F_{2,32}$ = 3.5, P = 0.0429).

For *P. pratensis,* water table had a minimal effect on tillering, while clipping had no effect. Neighbor-removed plots had significantly larger tiller numbers than neighbor intact plots at both Corral Canyon ($F_{1,16}$ = 96.6, P = 0.0001) and Kingston Canyon ($F_{1,16}$ = 25.6, P = 0.0001) (Figure 4). At Corral Canyon, there were significant decreases in tiller number over time on the mid-water-table plot for the not clipped, neighbor-removed plots and increases in the tiller number on the low water table for both the clipped and not clipped, neighbor-removed plots (time × water table × neighborhood; $F_{2,32}$ = 8.0, P = 0.0015).

Analysis of the plant biomass data for *C. nebrascensis* indicated that the neighborhood treatment alone was the only significant factor for both Corral Canyon ($F_{1,16}$ = 21.0, P = 0.0003) and Kingston Canyon ($F_{1,16}$ = 7.5, P = 0.0151). Average biomass in the neighbor-removed plots at Corral was 9.2 g and only 0.4 g in the neighbor intact plots (Figure 5). At Kingston, average biomass in the neighbor-removed plots was 9.8

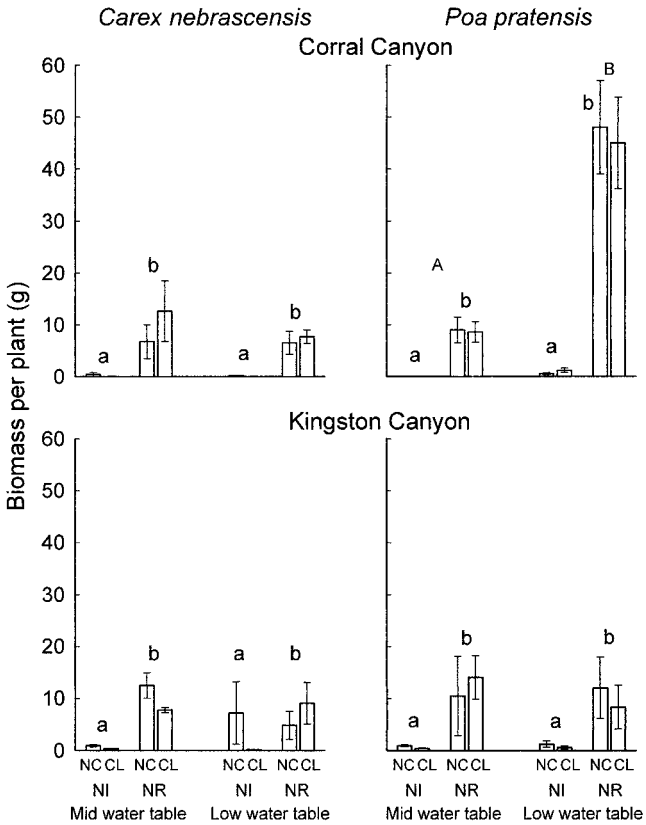

Figure 5. Biomass per plant for *C. nebrascensis* and *P. pratensis* for each treatment at the two study sites in fall 1998. Upper case letters indicate significant differences ($P \leq 0.05$) between water tables within sites. Lower case letters indicate significant differences ($P \leq 0.05$) between neighborhood treatments within water table. Values are mean ± S.E.; n = 9. NINC = neighbors intact, not clipped; NICL = neighbors intact, clipped; NRNC = neighbors removed, not clipped; NRCL = neighbors removed, clipped.

g compared to 2.2 g in the neighbor-intact plots. Neither clipping nor water table had a significant effect on plant biomass for *C. nebrascensis.*

For *P. pratensis,* the neighborhhood treatment was again the only significant factor at Kingston Canyon ($F_{1,16}$ = 14.7 P = 0.0013). Average biomass in the neighbor-removed plots was 11.9 g compared to 0.8 g for the neighbor-intact plots (Figure 4). There was a significant water table by neighborhood interaction at Corral Canyon ($F_{1,16}$ = 14.7, P = 0.0013). Average biomass in the neighbor-removed plots was 8.8 g and only 0.1 g in the neighbor-intact plots for the mid-water-table site. The average was 46.5 g in the neighbor-removed and 0.8 g in the neighbor-intact plots for the low-water-table sites.

Sexual reproductive effort was mostly limited to *P. pratensis* at Kingston Canyon. Only one *C. nebrascensis* in all of the plots produced seed. *Poa pratensis* only produced seeds in the neighbor-removed, low-water-table site at Corral Canyon, and there was no difference between clipping treatments. For *P. pratensis* at Kingston (Table 1), there were significantly more seeds per plant in the neighbor-removed compared to the neighbor-intact plots ($F_{1,16}$ = 14.7, P = 0.0014). Neither water table nor clipping had a significant effect.

Table 1. The number of filled seeds per plant for *Poa pratensis* at Kingston Canyon. Values are mean ± S.E.; n is variable.

Water Table	Neighbors Intact		Neighbors removed	
	Not clipped	Clipped	Not clipped	Clipped
Mid	18 ± 18	57 ± 40	481 ± 48	891 ± 104
Low	46 ± 18	15 ± 14	615 ± 56	294 ± 241

The comparison between the single species plots and the mixed species plots for the mid-water table at Corral indicated that there was no difference in either tiller number ($F_{1,4}$ = 2.5, P = 0.0701) or biomass ($F_{1,4}$ = 2.1, P = 0.1409) for *P. pratensis.* Also, there were no differences in plant mass for *C. nebrascensis* in the single species plots compared to the mixed species plots ($F_{1,4}$ = 0.96, P = 0.3902). However, there were significantly fewer tillers in the mixed species plots compared to the single species plots for all three sampling periods ($F_{1,4}$ = 5.7, P = 0.0048). In the fall of 1997, the mixed species plots had 27 fewer tillers, and the difference was 7 tillers for both 1998 sampling periods.

DISCUSSION

As hypothesized, the two species showed significant differences in their responses to the different water-table regimes. *Poa pratensis* had larger tiller numbers and, for neighbor-removed plots, greater biomass at mid- than low water tables at Corral Canyon. Further, tiller numbers of *P. pratensis* increased over time on the low-water-table plots but decreased on the mid-water-table plots. In contrast, water table had no effect on tillering or biomass of *C. nebrascensis.* Soil saturation due to high water tables results in more negative redox potentials and, thus, less available oxygen within the rooting zone (Castelli et al. 2000). *Carex nebrascensis* is an obligate riparian species that dominates in these meadow systems where water tables remain 0 to −20 cm from the soil surface throughout much of the growing season (Weixelman et al. 1996, Chambers et al. 1999). It has root characteristics typical of wetland species, including aerenchymous tissues. In contrast, *P. pratensis* is a facultative riparian species that has its greatest abundance in these meadow systems where water tables during the growing season generally average 60 to 80 cm below the soil

surface (Weixelman et al. 1996, Chambers et al. 1999). It has no root adaptations for growth in wetland soils. The response of the two species indicates that while *C. nebrascensis* is adapted for growth and persistence over the range of water tables examined, growth and tillering of *P. pratensis* is severely restricted at more shallow water tables.

Relatively high spatial variability and strong seasonal declines in water tables are typical of these semi-arid ecosystems (Castelli et al. 2000, Martin and Chambers 2001). Water-table depths were within expected ranges during the 1997 growing season but were higher than expected during much of the 1998 growing season due to above average precipitation. Prolonged soil saturation on the mid-water-table sites in 1998 may have contributed to low growth rates and tiller numbers for *P. pratensis.* Relatively high water tables on the low sites also may have resulted in more growth and tillering on the Corral Canyon sites. In general, the low abundance of *P. pratensis* on mid-water-table sites coupled with its response to the 1998 hydrologic regime, indicates that while this species does not tolerate saturated soil conditions, it can take advantage of relatively high soil-water availability.

Clipping had no effect on plant survival, tillering, or growth in either species. The results of previous studies conducted on the two species indicate that clipping height influences tillering response. An agronomic study of *P. pratensis* indicated that tiller number did not differ for plants clipped to 2.5 cm or 7.5 cm but that close clipping resulted in lower leaf lengths (Thompson and Clark 1993). Similarly, a field study of *C. nebrascensis* indicated that while there was no difference in shoot frequency following livestock grazing, there was a decrease in shoot mass (Ratliff and Westfall 1987). In the current study, the clipping treatment may not have removed sufficient leaf mass to elicit a response. Also, the clipping treatment was applied near the end of the growing season when plants were already beginning to senesce, and this may have further minimized effects. The season of use in many of these systems alternates among years between mid- and late summer, and herbage removal earlier in the growing season may have greater effects.

Neighborhood removal resulted in a highly significant response, increasing tillering and growth in *C. nebrascensis* and survival, tillering, and growth in *P. pratensis.* These increases were undoubtedly the result of increased space and resource availability. More interesting was that the difference in tillering and growth between the neighbor-removed and neighbor-intact plots was much greater for *P. pratensis* than *C. nebrascensis,* especially on the low-water-table plots. This suggests that *P. pratensis* is capable of more rapid response to disturbances that remove neighbors and increase available space than *C. nebrascensis* in areas with water tables favorable to both species. Further, comparisons between the single species and mixed species plots indicated that there was an interaction between the species that limited tiller production in *C. nebrascensis.* Despite its spreading, 'guerilla' architecture, *Carex nebrascensis* seems to show relatively low growth rates. In contrast, *P. pratensis* has high growth rates and a compact, 'phalanx' plant architecture. Previous studies have indicated that species of the 'guerrilla' type were better competitors than species of the 'phalanx' type until sites became more fully occupied (Cheplick 1997, Humphrey and Pyke 1998). In the current study, *P. pratensis,* the 'phalanx' species, had more rapid tillering and vegetative spread on neighbor-removed plots than *C. nebrascensis,* the 'guerrilla' species. The interactions between the two species do not seem to be related to plant architecture and can be best attributed to generally higher growth rates leading to increased competitive ability for *P. pratensis* at lower water tables.

The effects of neighbor removal on seed production paralleled those for plant survival, tillering, and growth. Seed production was limited to relatively large tillers of *P. pratensis* at Corral Canyon in the neighbor removed plots and occurred primarily on low-water-table plots. The tillers of both species must overwinter prior to flowering (Ratliff and Westfall 1987, Thompson and Clark 1993) and thus, only 2-year-old tillers were capable of producing seed. The fact that seed production was limited to neighbor removal plots was probably related to greater resource availability and the greater plant mass on the neighbor-removed plots than on the neighbor-intact plots. Clonal species typically invest more in seed production under favorable site conditions with low plant density and competition, and switch to primarily vegetative growth as density increases (Loehle 1987, Eriksson 1989, Humphrey and Pyke 1998). Also, seed production is dependent on plant size, and plants must achieve a certain size before they are large enough to acquire sufficient resources for reproduction (Chambers 1991). Seed production by *P. pratensis* but not *C. nebrascensis* is again indicative of higher growth rates and a greater ability to more rapidly acquire resources following surface disturbances that remove neighbors.

The interactions between the two species may depend upon the direct and indirect effects of grazing in non-manipulated field situations. *Poa pratensis* is used in agronomic situations for pastures, meadow hay production, and lawns (Thompson and Clark 1993) and has become widely naturalized in native ecosystems. While there is some evidence that the *P. pratensis* that occurs in these meadows is a native subspecies (Robert Soreng, pers. comm.), it generally has been assumed

that the species was introduced into riparian ecosystems throughout the Intermountain Region at the time of European settlement (Cronquist et al. 1994). Existing research for riparian meadows indicates that *P. pratensis* shows significant increases in cover in response to both grazing and clipping but shows decreases or remains unchanged in the absence of grazing (Schultz and Leininger 1990, Green and Kauffman 1995, Martin and Chambers 2001). In these same meadows, *C. nebrascensis* shoot growth or cover increases in response to release from grazing and either remains unchanged or decreases under grazing (Ratliff and Westfall 1987, Martin and Chambers 2001). This indicates that grazing may alter the competitive interactions of the two species, effectively increasing the competitive ability of *P. pratensis* and decreasing that of *C. nebrascensis.*

The results of this study increase our understanding of the interacting abiotic and biotic factors that structure riparian meadow communities. Water table had a differential effect on the two species. *Carex nebrascensis* responded similarly to the two water-table regimes, indicating that it is adapted for survival and growth over the range of water-table depths studied. In contrast, *P. pratensis* had significantly lower growth and tillering rates on shallow water-table plots, reflecting its lack of tolerance of saturated soil conditions and status as a facultative upland species. Spatial and temporal variability in precipitation and water-table regimes is large in these ecosystems (Castelli et al. 2000, Martin and Chambers 2001). The distribution and abundance of these species are undoubtedly a function of both the timing and duration of soil saturation and soil-water availability during the growing season. Disturbances resulting from livestock grazing or other animal activities that increase both space and resources within the community allow both species to expand locally. Under environmental conditions that are favorable to both species, *P. pratensis* has higher rates of growth and expansion and is able to limit the growth and tillering of *C. nebrascensis.* Grazing may alter the relative competitive ability of the two species in favor of *P. pratensis.*

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