Rangeland Ecol Manage 65:394–400 | July 2012 | DOI: 10.2111/REM-D-11-00159.1

Biomass Production and Net Ecosystem Exchange Following Defoliation in a Wet Sedge Community

Chad S. Boyd[1] *and Tony J. Svejcar*[2]

Authors are [1]*Research Scientist and* [2]*Research Leader, USDA-ARS Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA.*

Abstract

Riparian ecosystems provide many ecosystem services, including serving as an important forage resource for livestock grazing operations. We evaluated defoliation impacts on above- and belowground production, and net ecosystem exchange of CO_2 (NEE), in a wet sedge (*Carex nebrascensis* Dewey)-dominated plant community. In June or July of 2004–2005, experimental plots were clipped to 10 cm stubble height and paired control plots left unclipped. All plots were clipped to 2.5 cm in mid-September, and end-of-season and season-long aboveground production calculated. Root ingrowth cores were used to estimate annual root production and root length density (RLD). A portable gas exchange system and plexiglass chamber were used to measure NEE in 2005. An elevated water table in 2005 vs. 2004 was associated with higher ($P < 0.001$) season-long aboveground production (about double), but lower ($P \leq 0.05$) belowground production (about half). Total productivity did not differ between years, but below-:aboveground ratios were 3× higher in 2004 vs. 2005. RLD was not different between years ($P > 0.05$). Clipping reduced ($P \leq 0.05$) end-of-season aboveground standing crop by 33% to 73% depending on clipping month and year. Effects of clipping month on season-long aboveground production were inconsistent between years; June clipping decreased ($P \leq 0.05$) production (–10%) in 2005 and July clipping decreased ($P \leq 0.05$) production (–25%) in 2004. NEE for June-clipped plots recovered within 1 mo of clipping, whereas NEE for plots clipped in July remained below unclipped levels at the end of the growing season. Water table levels strongly influenced below-:aboveground ratios, although total production was relatively stable between years. Year effects overwhelmed clipping effects on season-long aboveground production. Defoliation after mid-summer did not allow recovery of photosynthetic capacity by the end of the growing season, suggesting the potential for long-term impact with regular late-season defoliation.

Resumen

Los ecosistemas rivereños proveen muchos servicios, incluyendo ser una fuente importante de forraje para operaciones de pastoreo. Evaluamos los impactos de la defoliación en la producción aérea y subterránea, y el intercambio neto de CO_2 (NEE), en una comunidad de humedales dominada por juncos (*Carex nebrascensis* Dewey). En junio o julio de 2004–2005, las parcelas experimentales fueron cortadas 10 cm por encima del suelo y parcelas control en pares se dejaron sin cortar. Todas las parcelas fueron cortadas a 2.5 cm a mediados de septiembre, y al final de la temporada y la producción aérea de toda la temporada la fue calculada. Los núcleos de crecimiento interno de la raíz se usaron para estimar la producción anual de raíz y la densidad de la longitud radicular (RDL). Un sistema portable de intercambio de gases y una cámara plexiglass se utilizaron para medir NEE en 2005. Un alto nivel de agua en 2005 vs. 2004 asociado con una alta ($P < 0.001$) producción aérea de toda la temporada (cerca del doble), pero menor ($P \leq 0.05$) que la producción subterránea (cerca de la mitad). La productividad total no fue diferente entre años, pero la tasa subterránea:aérea fue 3× superior en 2004 vs. 2005. RDL no fue diferente entre años ($P > 0.05$). El corte redujo ($P \leq 0.05$) la producción aérea al final de la temporada de 33% a 73% dependiendo del año y el mes de corte. Los efectos de corte en cada mes sobre producción aérea fueron inconsistentes entre años, los cortes durante junio redujeron ($P \leq 0.05$) la producción (–10%) en 2005 y los cortes durante julio redujeron ($P \leq 0.05$) la producción (–25%) en 2004. NEE en las parcelas cortadas en Junio se recuperaron dentro del mes después del corte. Además NEE para las parcelas cortadas en julio permanecieron por debajo de los niveles de las no-cortadas al final de la etapa de crecimiento. Los niveles de la tabla de agua influenciaron fuertemente la tasa subterránea:aérea, aunque la producción total fue relativamente estable entre años. Los efectos de los cortes anuales afectaron la producción anual aérea durante toda la temporada. La defoliación después de la mitad del verano no permitió la recuperación de la capacidad fotosintética al final de la época de crecimiento, sugiriendo el potencial impacto a largo plazo con defoliaciones regulares al final de la temporada.

Key Words: herbivory, livestock grazing, photosynthesis, riparian area, root production, water table

INTRODUCTION

Riparian areas provide a variety of important ecosystem services, including habitat for a broad diversity of plant and animal species, an abundant water supply, carbon sequestration, and flood attenuation (George et al. 2011). Maintenance of riparian obligate plant species is critical to both the short-

---

Correspondence: Chad Boyd, USDA-ARS EOARC, 67826-A Hwy 205, Burns, OR 97720, USA. Email: chad.boyd@oregonstate.edu

Manuscript received 2 September 2011; manuscript accepted 31 March 2012.

and long-term integrity of riparian ecosystems (George et al. 2011). In meadow stream systems, roots of sedges and other phreatophytic graminoids serve to stabilize banks during high water events and aboveground vegetation traps water-borne sediments, helping to maintain channel structure and the associated high water table needed by riparian plant species (Clary and Leininger 2000). The high root biomass and root length density of sedges (*Carex* sp., Manning et al. 1989), in particular, is critical to bank integrity (Kleinfelder et al. 1992; Toledo and Kauffman 2001). Transition to other, less densely-rooted facultative riparian species such as Kentucky bluegrass (*Poa pratensis* L.) can ultimately lead to bank degradation, loss of channel structure, decreased water availability for plant growth, and transition to upland plant communities (Winward 1994). Even in the absence of species change, livestock grazing or defoliation can reduce aboveground production of riparian plants (Boyd and Svejcar 2004), sediment filtration (Kauffman et al. 1983), and modify soil properties (Marlow et al. 2006).

Within-season maintenance of above- and belowground production depends, in part, on the recovery of photosynthetic capacity following defoliation (Welker et al. 2004). Net ecosystem exchange (NEE) represents the balance of carbon entering and leaving a defined area via CO_2 exchange and can be used as an index to plant recovery from herbivory. From a functional standpoint, the importance of belowground production in riparian communities is at least equal to that of aboveground production. At present, only a few studies (e.g., Martin and Chambers 2002; Blank et al. 2006) have addressed the effects of defoliation on belowground production in wet sedge communities. Knowledge of riparian root production dynamics, either with or without defoliation, is limited due to both a lack of published information, as well as inadequacies in existing literature. Much of the published riparian grazing literature is plagued with experimental deficiencies, often stemming from a reliance on long-term exclosures that were set up in the absence of specific experimental designs (Sarr 2002). Additionally, limited work (Kiley and Schneider 2005) indicates a high degree of spatial variability in root production and biomass, further complicating research on belowground productivity.

Our objectives were to evaluate impacts of defoliation and defoliation timing on above- and belowground growth patterns and NEE of CO_2 in a wet sedge community. Based on earlier work (Boyd and Svejcar 2004), we hypothesized that early season (June) defoliation would not affect above- or belowground production, but production and recovery of photosynthetic capacity would decrease with late-season (July) defoliation in association with reduced late-season water availability and more limited time for recovery prior to the end of the growing season.

METHODS

Experimental Design and Site Layout

We used a randomized complete block design with four, 6 × 12 m sites (blocks) located along Nicoll Creek, Harney County, Oregon (43.48N, 119.72W). Nicoll Creek is a small (< 2-m width) C-channel (Rosgen 1994) stream with perennial flow. Sites were approximately 1 400 m elevation, and livestock were excluded with electric fences. Our study area was located within a larger management unit that has been historically grazed by cattle during portions of most growing seasons. Riparian plant communities were dominated by Nebraska sedge (*Carex nebrascensis* Dewey) with lesser amounts of wooly sedge (*C. lanuginosa* Michx.) and Baltic rush (*Juncus balticus* Willd.). Grasses included Kentucky bluegrass and redtop (*Agrostis* spp.). Data for above- and belowground production variables and depth to groundwater were collected in the 2004 and 2005 growing seasons and NEE measurements were taken in 2005. Precipitation data were collected at a nearby automated weather station on the Northern Great Basin Experimental Range.

At each site, we located four 250 × 50 cm macroplots with the long axis of the macroplot oriented parallel to the stream and within the zone of hydrophytic influence; the distal edge of macroplots was within 1 m of the stream under base flow conditions. Within site, two macroplots were randomly assigned to June clipping and two were assigned to July clipping. Macroplots were then split into 125 × 50 cm paired microplots. One microplot within each pair was randomly chosen to be clipped and the remaining microplot was not clipped; clipping was extended out 10 cm along both long axes of microplots. We chose a paired-plot design due to high potential variability in belowground production (Kiley and Schneider 2005). We located a PVC well (Law et al. 2000) for groundwater measurements in the center of each site. Wells were within 50 cm of the stream edge at base flow and were installed to a depth of 75 cm belowground. Three of the four macroplots at site two and two of the four microplots at site one were grazed by cattle in early August of 2004, and were omitted from all analyses for 2004.

Each year, clipped microplots were hand-defoliated to 10 cm stubble height in either the third week of June or the third week of July. All microplots were clipped to 2.5 cm at the end of the growing season (mid-September) and plant material from two 40 × 50 cm quadrats retained. Quadrats were placed no closer than 5 cm to a microplot boundary. Retained clippings were dried and weighed, and season-long production was estimated as end-of-season standing crop for control plots and end-of-season standing crop plus the weight of previously clipped material (in June or July) for experimental plots.

We used the root ingrowth technique of Boyd and Svejcar (2009) to measure belowground plant production. Two 7.6-cm-diameter cores were installed to 30 cm in each microplot and filled with sand in the fall of 2003 and 2004. Cores were harvested in September of 2004 and 2005 by driving a 35-cm length of 5.1-cm-diameter PVC casing into the center of the core. The edge of the PVC in contact with the soil was camphored so that it would cut roots as the casing was driven into the ground. A 4.5-horsepower shop vac with an in-line collection reservoir was then used to evacuate the sand and root material from the PVC casing (Boyd and Svejcar 2009). The two cores from each microplot were combined for analysis. All material was bagged, drained of excess water, and frozen until analysis. Frozen root materials were thawed and washed in a root washer (Gillison's Variety Fabrications Inc., Benzonia, MI) over a 0.5-mm-mesh screen. Roots were arranged on a scanner bed (Epson Expression 10,000XL; Epson America, Inc., Long Beach, CA), scanned to digital form, and total root length density was estimated using the WinRhizo program (RHIZO-Regent instruments, Quebec City, Quebec, Canada; Kumar et al. 2010). Root materials were then oven-dried and weighed. Total production was calculated as the within-microplot sum of root production and season-long aboveground production.

Within each site we randomly selected one June and one July macroplot for measurement of NEE. All NEE measurements were taken in full sun between 1 000 and 1 400 hours using a LICOR-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) programmed to take three readings at 15-s intervals. These three readings were averaged to determine change in chamber CO_2 concentration over time within a 40 × 50 × 80 cm open-topped Plexiglass chamber. A Plexiglass frame with Lexan sheeting was used to cover the top during measurements and two fans located in upper corners of the chamber promoted air mixing. The chamber was placed on a 40 × 50 cm metal frame that was pushed into the ground in each microplot until about 1 cm protruded above the soil surface. Measurements were initiated the day after clipping and continued at 2-wk intervals through mid-September.

Data Analysis

Data were examined for skewness and kurtosis (PROC UNIVARIATE, SAS 1999). When normality or homogeneity of variance assumptions was violated, data were weighted by the inverse of the treatment variance (Neter et al. 1990; James and Drenovsky 2007). Daily precipitation values were summed within month and cumulative water-year precipitation was calculated by month for 2004 (1 October 2003 to 30 September 2004) and 2005 (1 October 2004 to 30 September 2005). Long-term average precipitation was calculated by averaging across values from 1937 to 2002. The influence of treatment and year on above- and belowground production was modeled using mixed model analysis of variance (SAS 1999). Covariance structure was determined using the Akaike's Information Criterion (Littell et al. 1996). Block and the block × treatment interaction were considered random effects in the model. Because of the paired-plot design, we considered treatments as: 1) June clipped; 2) June unclipped (i.e., paired control); 3) July clipped; and 4) July unclipped. We used repeated measures analysis of variance (PROC MIXED, SAS 1999; Littell et al. 1996) with repeated date within year to model the influence of clipping on gas exchange measurements within a month of clipping. When significant main or interactive effects were found, we assessed differences in treatment means using the LS MEANS (SAS 1999) procedure ($\alpha=0.05$). All mean values are reported with their associated standard error.

RESULTS

Water-year precipitation was 229.1 mm in 2004 and 256.0 mm in 2005, and both years were drier than the long-term average (288.2 mm). Depth-to-groundwater readings reflect standing water until early to mid-July in both years (Fig. 1); standing water was present approximately 2 wk longer in 2005 than in 2004. Groundwater was at maximum depth in early to mid-August (approx 8 to 10 cm below the ground surface). Between years, 2005 had higher groundwater elevation through the early to mid-growing season but was drier in late August and September.

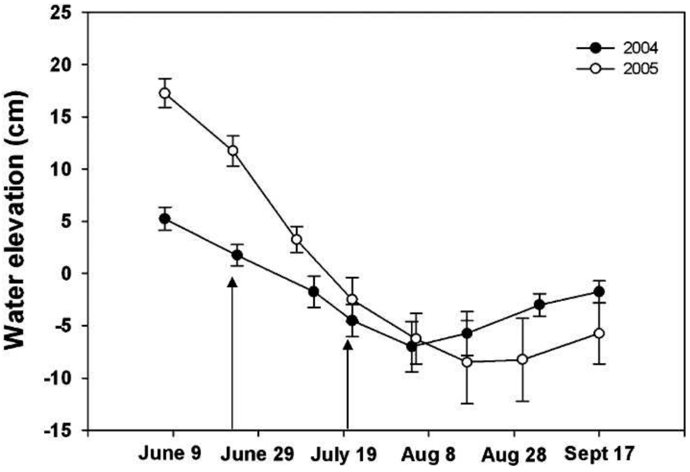

Figure 1. Growing season groundwater elevations for wet sedge plots in southeast Oregon. Positive values indicate standing water and negative values reflect belowground distance to water table. Arrows indicate defoliation dates.

End-of-season aboveground standing crop values varied by year ($P < 0.001$), treatment ($P < 0.001$), and the interaction ($P=0.043$). Values ranged from 945.19 $g \cdot m^{-2}$ (± 60.42) for unclipped July plots in 2005 to 140.0 $g \cdot m^{-2}$ (± 13.2) for clipped July plots in 2004 (Fig. 2a). Clipped treatments were lower than paired unclipped in all cases (Fig. 2a). Season-long aboveground production for unclipped plots averaged 449.6 $g \cdot m^{-2}$ (± 29.5) in 2004 and 892 $g \cdot m^{-2}$ (± 32.5) in 2005. Our clipping treatments removed 56.9% (± 2.5) and 33.8% (± 2.5) of season-long production in 2004 and 2005, respectively. Season-long aboveground production was influenced by year ($P < 0.001$), treatment ($P=0.010$), and the interaction ($P=0.020$); both clipped and unclipped treatments were highest in 2005, but clipping did not have a consistent effect on season-long production between years (Fig. 2b). July clipping decreased season-long production by 25% in 2004, whereas June clipping reduced season-long production by 10% in 2005 but had no effect in 2004.

Root production was not influenced by treatment ($P=0.266$) but varied by year ($P=0.015$) and was highest for 2004 (553.5 $g \cdot m^{-2}$ ± 84.8); production decreased by 44% to 307.8 $g \cdot m^{-2}$ (± 20.7) in 2005. Root length density (RLD) was not influenced by treatment ($P=0.660$) or year ($P=0.246$), and values ranged from 5.65 $cm \cdot cm^{-3}$ (± 1.71) for June-clipped plots in 2005 to 9.37 $cm \cdot cm^{-3}$ (± 4.34) for unclipped July plots in 2005. Total production varied by treatment ($P=0.011$), but not year ($P=0.152$). Values ranged from 962.8 $g \cdot m^{-2}$ (± 40.7) for June-clipped plots to 1 216.9 $g \cdot m^{-2}$ (± 80.8) for July-unclipped plots (Fig. 3). Within a treatment month, clipped and unclipped plots (June or July) were not different ($P > 0.05$). Below-:aboveground production ratios decreased from 1.33 (± 0.20) to 0.37 (± 0.03) between years ($P=0.002$), were unaffected by treatment ($P=0.641$), and reflected increased allocation to root biomass in 2004 and increased aboveground allocation in 2005 (Fig. 3).

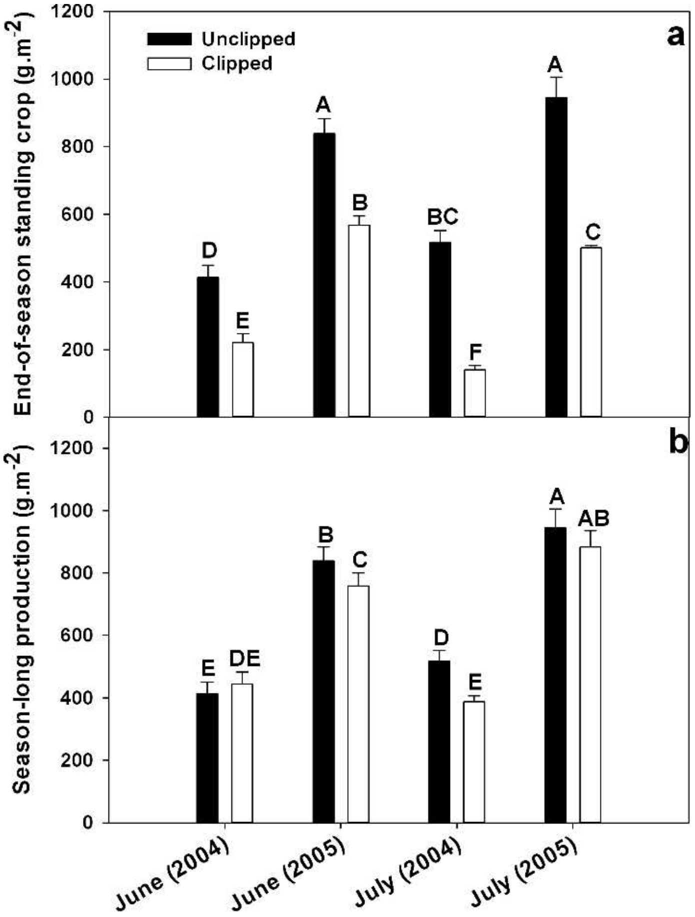

Figure 2. (**a**) End-of-season aboveground standing crop and (**b**) season-long aboveground production for wet sedge plots in eastern Oregon. Clipped plots were hand clipped to 10 cm stubble height in June or July of the corresponding year. Different letters indicate differences within a graph (α=0.05).

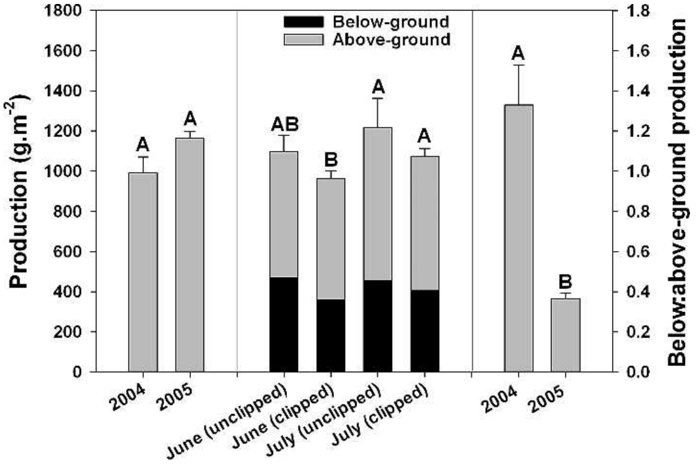

Figure 3. (**Left panel**) Total production (sum of above- and belowground) by year and (**middle panel**) clipping treatment and (**right panel**) below: aboveground production ratios for wet sedge plots in eastern Oregon. Clipped plots were hand clipped to 10 cm stubble height in June or July of the corresponding year. Different letters indicate differences within a graph and panel (α=0.05).

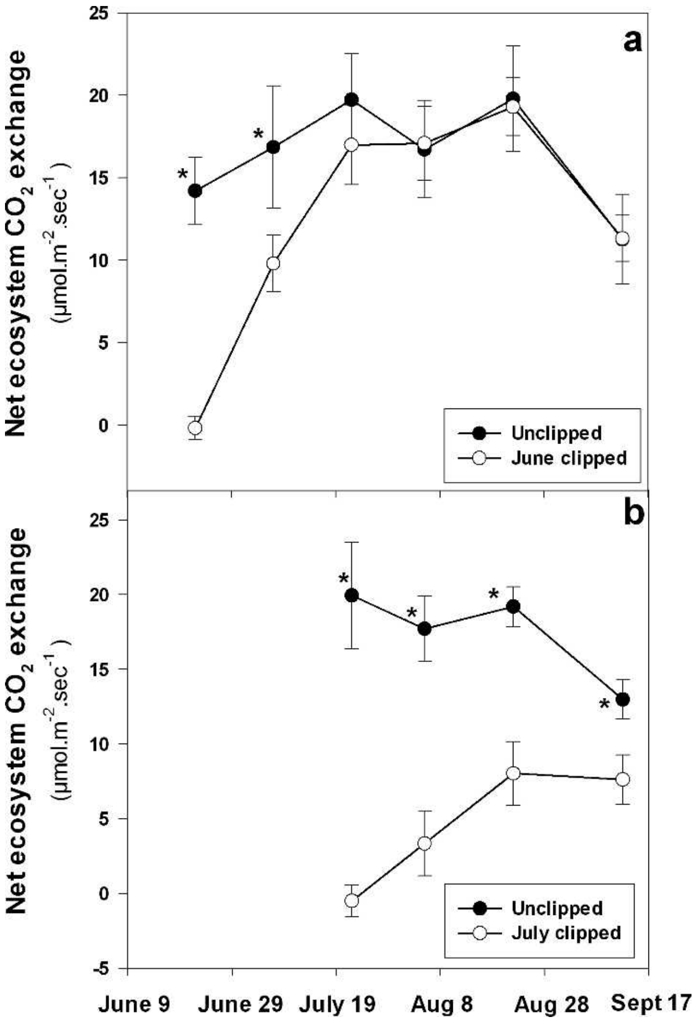

Figure 4. Net ecosystem exchange of CO$_2$ for wet-sedge swards clipped to 10-cm stubble height in (**a**) June or (**b**) July in 2005. Asterisks denote significant differences within a graph and day (α=0.05). Initial readings within a month of clipping were taken on the day subsequent to clipping treatment.

Net ecosystem exchange for June plots varied by clipping (P=0.008), date ($P < 0.001$), and the interaction ($P < 0.001$, Fig. 4a). Values for unclipped June plots ranged from a maximum of 19.8 μmol · m^{-2} · s^{-1} (± 3.2) on August 22 to a low of 11.3 μmol · m^{-2} · s^{-1} (± 2.7) on September 12. Values for clipped plots were initially less than unclipped ($P < 0.05$), but reached and maintained parity by July 22. Unclipped July plots had maximal values of 20.0 μmol · m^{-2} · s^{-1} (± 3.6) on July 22 and were lowest on September 12 (13.0 μmol · m^{-2} · s^{-1} ± 1.3). NEE for July plots varied by clipping ($P < 0.001$), date ($P < 0.001$), and the interaction ($P < 0.001$). July clipped plots were less than unclipped ($P < 0.05$) for all dates and reached a maximum of 58.8% (± 5.7) of unclipped values by the end of data collection in mid-September (Fig. 4b). For both clipping months, initial values following clipping were < 3% of unclipped plots.

DISCUSSION

Although roots generally comprise a large proportion of total plant biomass, there have been few attempts to quantify annual root production in either rangeland or riparian systems. In our work, including root production provides a different conclusion about annual growth patterns than would aboveground production alone. We found that aboveground production, and the relationship between root and shoot production, differed greatly between years, despite the fact that study communities were located near a stream and apparently were not subject to severe water stress. Between-year differences in responses were linked to small differences in the level of the water table. Effects of varying the timing of clipping differed between years and were relatively minor compared to year effects. Overall, our results suggest that plant production in riparian systems is highly sensitive to relatively small changes in the water table which, in turn, affects the sensitivity of aboveground production to clipping. Total plant production was stable with respect to both between-year variability and clipping effects due to differential allocation to below- and aboveground growth. High water table favored aboveground growth but may restrict belowground growth (Svejcar and Trent 1995).

Root Growth and Year Effects

Our results could reflect resource allocation strategies that are timed to cope with seasonally flooded conditions (Blanch et al. 1999; Burke and Chambers 2003); resource allocation to aboveground growth increases with high water tables, and low water tables promote belowground allocation. When belowground biomass is flooded, gas exchange can decrease (Steed et al. 2002), and anoxic conditions result in an increased reliance on anaerobic respiration, which in turn decreases energy availability (Pradet and Raymond 1983). Other authors have reported that spatial patterns of sedge root production followed declining water levels (Martin and Chambers 2002) and that aboveground production is favored with higher water tables (Sala and Nowak 1997).

High year-to-year variation makes it difficult to compare our annual root production values to estimates of total belowground biomass. If we average root production over the 2-yr period ($=450\ \mathrm{g \cdot m^{-2}}$), the value would be 18% of the total root biomass values measured for a similar plant community by Manning et al. (1989). To arrive at this figure, we added large and fine root biomass at the 0–30-cm depth (sum$=2\,486\ \mathrm{g \cdot m^{-2}}$) from Manning et al. (1989, table 2). Ratio of annual root production to total root biomass (18%) suggests on average a 5-yr turnover of roots in this plant community. This estimate is in line with turnover rates calculated for other graminoid communities (e.g., Dahlman and Kucera 1965). The high degree of annual variation in root production indicates that turnover rates might depend on environmental conditions, or that total root biomass also might fluctuate over time. RLD exhibited much less variation over years than did root production. Compared to literature values of total RLD for similar wet sedge communities, there was a slower rate of turnover for length than for mass. The average RLD for 0–30 cm in a wet sedge community was about 120 $\mathrm{cm \cdot cm^{-3}}$ reported by Manning et al. (1989), and for 0–25 cm was about 110 $\mathrm{cm \cdot cm^{-3}}$ as reported by Blank et al. (2006). Our values of annual RLD production were in the range of 6 to 9 $\mathrm{cm \cdot cm^{-3}}$ for unclipped treatments. These data suggest that increased root production in 2004 was more a function of enhanced individual root biomass than an increase in density of roots.

The years of the study were not as different from a weather standpoint as we might have assumed from the plant growth data. Despite below-average precipitation, groundwater levels observed in the current study were well within the range reported for wet sedge communities, and water availability was probably not a limiting factor for sedge growth, maintenance or reproduction (Allen-Diaz 1991; Castelli et al. 2000; Law et al. 2000). That said, the clipping treatments we applied had relatively less effect than year-to-year weather variation on any of the measured parameters. We measured no influence of clipping on root production or RLD in this wet sedge community. Other researchers also found root biomass (Smith et al. 1993; Clary and Kinney 2002), root activity (Martin and Chambers 2002), and RLD (Blank et al. 2006) to be relatively unaffected by moderate grazing or clipping in riparian systems.

Greater aboveground production in 2005 was associated with increased groundwater during the June–July period. In contrast, we found an inverse relationship between above- and belowground productivity, and decreased belowground production with increased groundwater. For example, below:aboveground production ratios were at least three times higher in 2004 as compared to 2005 (Fig. 3). Yearly shifts in root:shoot allocation of this magnitude were not found in the literature, but most of the existing work has centered on upland species. Interestingly, these tradeoffs in allocation took place within a relatively constant level of total (above- and belowground) production between years (Fig. 3). This between-year stability in total production probably is associated with sufficient water availability and might not be representative of water-limited years or sites. Also, extreme between-year variability in below-:aboveground production ratios should be considered in light of the fact that annual root production might comprise only a small portion of total root standing crop as described above.

Defoliation Effects

Aboveground end-of-season standing crop decreased with clipping in June or July, but the effect of clipping on aboveground season-long production was less clear. Inconsistent with our initial hypothesis, the present data do not suggest that late-season defoliation (i.e., July) has a more negative impact on aboveground season-long production compared to early season defoliation (i.e., June; Fig. 2a). In fact, relative to year effects, clipping in either month produced only a small decrease (10–25%) or no decrease (depending on year) in aboveground production. Similarly, the current data do not support our hypothesis that root production would be reduced with July, but not June clipping; root production was not influenced by clipping treatment but had strong interannual variation.

Grazing or clipping to stubble heights lower than 8–10 cm might decrease the resilience of both above- and belowground production (Clary and Kinney 2002), particularly if defoliation occurs late in the growing season when water availability is declining (Sheeter and Svejcar 1997; Boyd and Svejcar 2004).

That said, the level of defoliation in our study is consistent with current allowable use levels on federally-controlled grazing allotments in the western United States and thus has widespread applicability. In the present study, clipping to 10-cm stubble height removed approximately 23% more of season-long aboveground production in 2004 as compared to 2005. The increased severity of clipping treatments did not hamper aboveground recovery of June-clipped plots in 2004; nor did aboveground recovery from defoliation come at the expense of belowground production. In fact, season-long aboveground production for June clipping was numerically (though not statistically) higher than unclipped in 2004 but less than unclipped in 2005 (Fig. 2b). In contrast, season-long production of July-clipped plots was lower than unclipped in 2004 but not 2005, suggesting that the importance of defoliation date varies (depending on water availability) with later season defoliation having a more negative impact in a drier year (Fig. 2b).

Previous gas exchange work with *C. nebrascensis* and other riparian and meadow species has focused on flux per unit of leaf area (e.g., Svejcar and Trent 1995; Svejcar and Riegel 1998; Martin and Chambers 2002). The present work represents the first reporting of sward-level CO_2 exchange (i.e., NEE) in relation to defoliation in sedge-dominated plant communities. Measuring gas exchange at the sward level integrates defoliation-induced changes in leaf area, as well as any changes in soil respiration due to defoliation. Our results indicate negative NEE immediately following clipping to 10 cm (Fig. 4) in either June or July (i.e., CO_2 production from respiration exceeds uptake in photosynthesis). Consistent with our hypothesis, we measured rapid recovery (within 1 mo) of photosynthetic capacity following June but not July defoliation. Lack of NEE recovery for July-clipped plots (Fig. 4) suggests that either leaf area remained lower than unclipped plots, or that photosynthesis rate had leveled off by our last measurement date in mid-September (by which time CO_2 exchange rates were dropping for unclipped plots). The inability of July-clipped plots to recover photosynthetic capacity prior to the end of the growing season is reflected in lower end-of-season aboveground standing crop values as compared to June-clipped plots (Fig. 2a). Recovery of photosynthetic capacity (or NEE) might be important in maintaining the productivity of grazed plant communities. Our data suggest that the relationship between defoliation timing and NEE recovery (as shown in Fig. 4) is an important consideration in the sustainable management of riparian sedge plant communities, at least during years of low water availability. The influence of defoliation on gas exchange in subarctic North American sedges has received little attention. One study (Martin and Chambers 2002) found that clipping to 8–10 cm in late July had no impact on leaf photosynthesis rate.

MANAGEMENT IMPLICATIONS

From a management standpoint, our results indicate that clipping to 10 cm in June or July can decrease aboveground end-of-season standing crop by 33 to 73% (depending on year and clipping month). However, season-long production of aboveground biomass was more strongly influenced by year as opposed to clipping treatment. Similarly, annual root production and below-:aboveground production ratios varied strongly between years, but were not influenced by clipping. Both above- and belowground biomass production in wet sedge communities appear resilient to the effects of moderate levels of defoliation in June or July with adequate moisture. Patterns of photosynthesis (or NEE) recovery over time in this study, combined with information from extant literature, suggest that potential for in-season recovery of biomass lost to defoliation will drop sharply with later season defoliation (e.g., August). Timing of defoliation relative to resource availability and thus NEE recovery, appears to be an important consideration in sustainable management of these plant communities. Our results using hand-clipping to defoliate plants might differ in some respects relative to impacts of grazing livestock. Specifically, hoof impacts can suppress plant growth, and changes in channel morphology and thus streamside hydrology with hoof action (particularly when soils are wet during the early growing season) could decrease the ability of plants to recover from defoliation impacts by reducing water availability (Clary 1995, 1999; Clary and Leininger 2000).

ACKNOWLEDGMENTS

The authors wish to thank Mark and Susan Doverspike for allowing use of their property for this study. We are also grateful for the field assistance of Karl Hopkins and Ray Angel. We thank Kirk Davies and Jeremy James for providing critical reviews of an earlier draft of this manuscript.

LITERATURE CITED

Allen-Diaz, B. H. 1991. Water table and plant species relationships in Sierra Nevada Meadows. *American Midland Naturalist* 126:30–43.

Blanch, S. J., G. G. Ganf, and K. F. Walker. 1999. Growth and resource allocation in response to flooding in the emergent sedge *Bolboschoenus medianus*. *Aquatic Botany* 63:145–160.

Blank, R. R., T. Svejcar, and G. Riegel. 2006. Soil attributes in a Sierra Nevada riparian meadow as influenced by grazing. *Rangeland Ecology & Management* 59:321–329.

Boyd, C. S., and T. J. Svejcar. 2004. Regrowth and production of herbaceous riparian vegetation following defoliation. *Journal of Range Management* 57:448–454.

Boyd, C. S., and T. J. Svejcar. 2009. A technique for estimating riparian root production. *Rangeland Ecology & Management* 62:198–202.

Burke, M. K., and J. L. Chambers. 2003. Root dynamics in bottomland hardwood forests of the southeastern United States Coastal Plain. *Plant and Soil* 250:141–153.

Castelli, R. M., J. C. Chambers, and R. J. Tausch. 2000. Soil–plant relations along a soil–water gradient in Great Basin riparian meadows. *Wetlands* 20:251–266.

Clary, W. P. 1995. Vegetation and soil responses to grazing simulation on riparian meadows. *Journal of Range Management* 48:18–25.

Clary, W. P. 1999. Stream channel and vegetation responses to late spring cattle grazing. *Journal of Range Management* 52:218–227.

Clary, W. P., and J. W. Kinney. 2002. Streambank and vegetation response to simulated cattle grazing. *Wetlands* 22:139–148.

Clary, W. P., and W. C. Leininger. 2000. Stubble height as a tool for management of riparian areas. *Journal of Range Management* 53:562–573.

Dahlman, R. C., and C. L. Kucera. 1965. Root productivity and turnover in native prairie. *Ecology* 46:84–89.

George, M. R., R. D. Jackson, C. S. Boyd, and K. W. Tate. 2011. A scientific assessment of the effectiveness of riparian management practices *In:* D. D. Briske [ed.]. Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Lawrence, KS, USA: USDA-NRCS. p. 213–252.

James, J. J., and R. E. Drenovsky. 2007. A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology & Management* 60:395–400.

Kauffman, J. B., W. C. Krueger, and M. Vavra. 1983. Effects of late season cattle grazing on riparian plant communities. *Journal of Range Management* 36:685–691.

Kiley, D. K., and R. L. Schneider. 2005. Riparian roots through time, space and disturbance. *Plant and Soil* 269:259–272.

Kleinfelder, D., S. Swanson, G. Norris, and W. Clary. 1992. Unconfined compressive strength of some streambank soils with herbaceous roots. *Journal of the Soil Science Society of America* 56:920–924.

Kumar, S., R. P. Udawatta, and S. H. Anderson. 2010. Root length density and carbon content of agroforestry and grass buffers under grazed pasture systems in Hapludalf. *Agroforest Systems* 80:85–96.

Law, D. J., C. B. Marlow, J. C. Mosley, S. Custer, P. Hook, and B. Leinard. 2000. Water table dynamics and soil texture of three riparian plant communities. *Northwest Science* 74:234–241.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. Cary, NC, USA: SAS Institute, Inc. 656 p.

Manning, M. E., S. R. Swanson, T. Svejcar, and J. Trent. 1989. Rooting characteristics of four intermountain meadow community types. *Journal of Range Management* 42:309–312.

Marlow, C. B., R. Fink, and H. Sherwood. 2006. Grazed stubble height as a criterion for controlling sediment production from grazing lands. *Journal of the American Water Resources Association* 42:891–900.

Martin, D., and J. Chambers. 2002. Restoration of riparian meadows degraded by livestock grazing: above- and below-ground responses. *Plant Ecology* 163:77–91.

Pradet, A., and P. Raymond. 1983. Adenine nucleotide ratios and adenylate energy charge in energy metabolism. *Annual Review of Plant Physiology* 34:199–224.

Rosgen, D. L. 1994. A classification of natural rivers. *Catena* 22:169–199.

Sala, A., and R. S. Nowak. 1997. Biomass trends in a Nebraska sedge meadow, Sierra National Forest, California. *Aquatic Botany* 30:109–124.

Sarr, D. A. 2002. Riparian livestock exclosure research in the western United States: a critique and some recommendations. *Environmental Management* 30:516–526.

[SAS] SAS Institute, Inc. 1999. SAS procedures guide, release 8.0. Cary, NC, USA: SAS Institute, Inc. 441 p.

Sheeter, G., and T. Svejcar. 1997. Streamside vegetation regrowth after clipping. *Rangelands* 19:30–31.

Smith, M. A., J. L. Dodd, Q. D. Skinner, and J. D. Rodgers. 1993. Dynamics of vegetation along and adjacent to an ephemeral channel. *Journal of Range Management* 46:56–64.

Steed, J. E., L. E. DeWald, and T. E. Kolb. 2002. Physiological and growth responses of riparian sedge transplants to groundwater depth. *International Journal of Plant Science* 163:925–936.

Svejcar, T. J., and G. M. Riegel. 1998. Spatial pattern of gas exchange for montane meadow species. *Journal of Vegetation Science* 9:85–94.

Svejcar, T. J., and J. D. Trent. 1995. Gas exchange and water relations of Lemmon's willow and Nebraska sedge. *Journal of Range Management* 48:121–125.

Toledo, Z. O., and J. B. Kauffman. 2001. Root biomass in relation to channel morphology of headwater streams. *Journal of the American Water Resources Association* 37:1653–1663.

Welker, J. M., J. T. Fahnestock, K. L. Povirk, C. J. Bilbrough, and R. E. Piper. 2004. Alpine grassland CO_2 exchange and nitrogen cycling: grazing history effects, Medicine Bow Range, Wyoming, U.S.A. *Arctic, Antarctic and Alpine Research* 36:11–20.

Winward, A. H. 1994. Management of livestock in riparian areas. *In:* G. A. Rasmussen and J. P. Dobrowolski [eds.]. Riparian resources: a symposium on the disturbances, management, economics, and conflicts associated with riparian ecosystems. Logan, UT, USA: College of Natural Resources, Utah State University. p. 49–52.