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Plant biomass and species composition along an environmental gradient in montane riparian meadows

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Abstract In riparian meadows, narrow zonation of the dominant vegetation frequently occurs along the elevational gradient from the stream edge to the floodplain terrace. We measured plant species composition and above- and belowground biomass in three riparian plant communities—a priori defined as wet, moist, and dry meadow—along short streamside topographic gradients in two montane meadows in northeast Oregon. The objectives were to: (1) compare above- and belowground biomass in the three meadow communities; (2) examine relations among plant species richness, biomass distribution, water table depth, and soil redox potential along the streamside elevational gradients. We installed wells and platinum electrodes along transects (perpendicular to the stream; $n=5$ per site) through the three plant communities,

and monitored water table depth and soil redox potential (10 and 25 cm depth) from July 1997 to August 1999. Mean water table depth and soil redox potential differed significantly along the transects, and characterized a strong environmental gradient. Community differences in plant species composition were reflected in biomass distribution. Highest total biomass (live+dead) occurred in the sedge-dominated wet meadows ($4,311\pm 289$ g/m²), intermediate biomass ($2,236\pm 221$ g/m²) was seen in the moist meadow communities, dominated by grasses and sedges, and lowest biomass ($1,403\pm 113$ g/m²) was observed in the more diverse dry meadows, dominated by grasses and forbs. In the wet and moist communities, belowground biomass (live+dead) comprised 68–81% of the totals. Rhizome-to-root ratios and distinctive vertical profiles of belowground biomass reflected characteristics of the dominant graminoid species within each community. Total biomass was positively correlated with mean water table depth, and negatively correlated with mean redox potential (10 cm and 25 cm depths; $P < 0.01$) and species richness ($P < 0.05$), indicating that the distribution of biomass coincided with the streamside edaphic gradient in these riparian meadows.

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Introduction

Characteristics of streamside vegetation are strongly correlated to the hydrologic regime and related edaphic gradients in soil moisture and substrate characteristics along riparian corridors (Auble et al. 1994; Naiman and Decamps 1997; Stromberg et al. 1996; Tabacchi et al. 1998). The composition and distribution of riparian plant communities are influenced by seasonal flooding (Auble and Scott 1998), duration of inundation (Roberts and Ludwig 1991; Auble et al. 1994), and levels of shallow groundwater (Allen-Diaz 1991; Stromberg et al. 1996;

Castelli et al. 2000; Shafroth et al. 2000). Seasonal flooding and changes in water table depth also influence riparian soils by controlling the extent and duration of saturation, resulting in spatial and temporal gradients in soil aeration status, as indicated by variation in oxidation-reduction (redox) potentials (Gambrell et al. 1991; Cogger et al. 1992; Castelli et al. 2000). In riparian meadows, zonation of dominant vegetation frequently occurs along streamside elevational gradients. Narrow bands of *Carex*-dominated communities occur on the lowest end of the gradient near the stream edge, are completely flooded for weeks during spring, and are exposed to shallow water table depths throughout the growing season. Mixed herbaceous communities are arrayed along the remainder of the elevational gradient to the floodplain terrace, the highest end of the gradient. Although near-stream environmental gradients occur commonly in riparian meadows throughout the western USA (Allen-Diaz 1991; Crowe and Clausnitzer 1997), limited empirical data are available on spatial and temporal differences in hydrologic and edaphic conditions along the gradients and how these relate to vegetation characteristics (Castelli et al. 2000).

Distinctive features of plant communities that reflect responses to strong environmental gradients include species composition, species richness, the types of different growth forms, and plant biomass structure (i.e., the distribution of biomass among the above and below-ground components; van der Maarel and Tityanova 1989). Previous studies on biomass totals for the common streamside sedge species (*Carex aquatilis* and *Carex utriculata*) have focused on carbon sequestration, and have been conducted in wetlands, primarily marshes and fens, where these species occur in extensive, nearly monospecific stands, and have been shown to be highly productive (Brinson et al. 1981). Throughout the western USA, these same sedge species occur along riparian corridors, where they are frequently confined to narrow bands along the stream. The distribution of biomass in streamside plant communities affects multiple ecological functions. Aboveground biomass provides habitat and forage for wildlife (Kauffman et al. 1997, 2001), furnishes shade and organic matter inputs to streams (Gregory et al. 1991; Naiman and Decamps 1997), and increases roughness of stream banks and floodplains, thus dissipating hydraulic energy and potentially trapping sediment (Bennett et al. 2002). Belowground biomass affects subsurface biogeochemical processes (Schipper et al. 1993) and floodplain soil development, and provides habitat for aquatic organisms. In addition, the amount and vertical distribution of belowground biomass components may greatly contribute to stabilization of stream banks (Simon and Collison 2002). Despite the importance of these functions for stream-riparian ecosystems, few studies have investigated the biomass structure of dominant riparian plant communities, particularly in relation to hydrologic and edaphic gradients (Manning et al. 1989; Otting 1998).

In two montane meadows in northeastern Oregon, USA, we investigated relationships among plant species rich-

ness, above- and belowground biomass, water table depth, and soil redox potential in three riparian plant communities. The three communities—referred to as wet, moist, and dry meadow—occurred along an elevational gradient from the stream edge to the floodplain terrace. The objectives of the study were to: (1) compare amounts and distribution of above- and belowground biomass in the three meadow plant communities; (2) examine relations among plant species richness, biomass, water table depths, and soil redox potential along the streamside elevational gradients. Special attention was given to community differences in biomass components and the vertical distribution of belowground biomass.

Materials and methods

Study sites

The study sites were located along unconstrained reaches of West Chicken Creek (45°06'15"N, 118°19'41"W) and Limber Jim Creek (45°03'17"N, 118°24'11"W), two second-order tributaries to the upper Grande Ronde River, northeast Oregon, USA. The two streams are located ≈13 km from each other and are similar in elevation (≈1,320 m) and gradient (2.0–2.5%). However, Limber Jim Creek drains a larger area than West Chicken Creek (34.4 km² and 21.8 km², respectively), and is a wider, larger stream. During the period of study, stream discharge ranged from 0.01 to 2.5 m³/s at Limber Jim Creek, and 0.01–1.0 m³/s at West Chicken Creek. Mean annual precipitation is approximately 55 cm, with >80% falling between November and June. The hydrologic regime is dominated by spring snowmelt, which typically begins in March or April, with peak flows in May (Clarke et al. 1997). Although the meadows were historically grazed by sheep and cattle, the West Chicken Creek study site was fenced to exclude livestock in 1993, and the Limber Jim Creek study site has not been grazed by livestock since 1978, with the exception of occasional trespass cattle.

The study sites were approximately 250 m in length and 80 m in width. The meadow vegetation was composed of three dominant plant communities—defined as wet, moist, and dry meadow—which occurred along an elevational moisture gradient from the stream edge to the floodplain terrace (Otting 1998; Dwire 2001). The streamside wet meadow communities were lowest in elevation (relative to the moist and dry communities) and flooded each spring for several weeks. Moist meadow communities were intermediate in relative elevation and were partially inundated during spring flooding. Dry meadow communities occurred on floodplain terraces (highest in relative elevation), which were infrequently flooded, and occupied approximately 70% of the area at each study site. Geology of the floodplain meadows consists of shallow fine-textured Holocene alluvium, which was deposited over Grande Ronde Basalt (Ferns and Taubeneck 1994; Ferns 1998). The alluvial soils (~40 cm to 120 cm deep) are ash-influenced Mollisols and Entisols, with high silt and clay content, underlain by coarse gravels.

Water table depth and soil redox potential

To characterize streamside hydrologic and soil conditions, water table depth and soil redox potential were measured along transects located perpendicular to the streams. In June 1997, five transects were established through the three dominant meadow plant communities at each site. Along the transects, well locations were randomly selected within each plant community, resulting in a total of five well locations per community at each site. At West Chicken Creek, the average transect length, perpendicular to the stream's edge, was 18 m (range 14–22 m), and the distance between well

locations within the three plant communities ranged from 2 to 6 m. At Limber Jim Creek, the average transect length was 11 m (range 9–14 m), and the distance between well locations within the three plant communities ranged from 2 to 4 m. Wells were installed approximately 20 cm into the gravel layer underlying the soil; well depths ranged from 64 cm to 112 cm below the soil surface. Well casings were made from 2.54-cm-diameter PVC pipe, drilled with 0.32-cm-diameter holes along the entire buried length.

Water table depth was measured with a metered copper wire connected to an Ohmmeter. The wire was lowered into each well, and depth of contact with water was recorded. To measure soil redox potential, platinum electrodes were installed in the soil within 0.5 m of each well at 10 cm and 25 cm depths ($n=3$ probes per depth; Mueller et al. 1985). Redox potential was measured using a voltmeter in conjunction with a saturated single-junction Ag/AgCl reference electrode (similar to method described by Faulkner et al. 1989). The voltmeter measurements were corrected by adding 214 mV to each value (Bohn 1971). Soils were considered to be anaerobic if redox potential was less than +300 mV (Gambrell et al. 1991; Faulkner and Patrick 1992). Water table depth and redox potential were measured from July 1997 to August 1999 inclusive, approximately every 2–3 weeks during the spring, fall, and summer seasons.

Plant composition and biomass

Plant species composition and cover were sampled in four 0.5 m×0.5-m plots that were located ≈0.25 m directly to the north, south, east, and west of each well. Data were collected from 14 to 29 July 1997. Cover of all vascular plant species, mixed bryophytes, and ground surface features (bare ground, litter, and water) was recorded for each plot. Cover was estimated using the following intervals: 1% units up to 5%, 5% units from 5–100% (after Daubenmire 1959). Because multiple layers of plant cover occurred in some plots, total cover sometimes exceeded 100%. Nomenclature followed Hitchcock and Cronquist (1973), except for the family *Cyperaceae* (Hickman 1993).

Aboveground biomass was sampled from three 0.25 m×0.25-m plots that were randomly located within 1.5 m of each well. Between 23–27 September 1997, all litter and vegetation rooted within the plots was clipped to the ground surface. No woody vegetation was rooted in the plots; however, any transported wood and woody debris that occurred in the plots was sampled. Aboveground biomass samples were air-dried, then sorted into five categories—forbs, graminoids, moss, litter, and wood—oven dried for 72 h at 65°C, and weighed. Subsamples from each category and plant community were ashed at 550°C for 12 h, and all aboveground biomass values are reported on an ash-free dry mass basis (AFDM; g/m²).

Belowground biomass samples were collected at two of the three plots ($n=2$ replicates per well location) clipped for aboveground biomass to a depth of 40 cm, using a Gidding soil coring and

sampling tube (8 cm diameter). Belowground biomass samples were collected from 25 to 27 October 1997. After extraction, each core was sliced into 10-cm segments, yielding samples from the following depths: 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm. Samples were stored at 4°C until processed (maximum storage time was 6 weeks). Belowground biomass samples were washed using a hydropneumatic elutriation system with 0.5-mm-mesh screens (Gillison's, Benzonia, Mich.), and dried at 65°C for at least 24 h. Dried samples were sorted into rhizomes and roots, but not separated into live and dead categories. Roots were fine to very fine (Böhn 1979); all roots encountered were ≤1.3 mm diameter, with over 80% being ≤0.8 mm diameter. Sorted samples were dried at 65°C for at least 48 h, weighed, then ashed at 550°C for 12 h to obtain AFDM g/m².

Data analysis

Mean redox potential ($n=3$ replicates) was calculated for each well location, depth, and date of sampling. Biomass values were averaged for each well location ($n=3$ for aboveground components, $n=2$ for belowground components). For each site, one-way ANOVA was used to test for community differences in mean water table depth, total plant cover, and total biomass. For each site, belowground biomass data were analyzed using a split-plot ANOVA with depth nested within plant community. Data for redox potential, species richness, and forb, moss, and woody litter biomass did not meet ANOVA assumptions regarding distribution and variance, and were analyzed using Kruskal-Wallis tests. Comparisons between communities for these variables, and for ratios of belowground-to-aboveground biomass and rhizome-to-root biomass, were made using Dunn's tests (with TK-type modification; Hochberg and Tamhane 1987). For each site, community differences in components of above- and belowground biomass were tested using Hochberg's tests (Hochberg and Tamhane 1987). Community differences in total belowground biomass were tested using Tukey's honest significant difference (HSD); differences in belowground biomass between depths were tested using adjusted Tukey's HSD (Bonferroni adjustment). Statistical analyses were performed in SAS version 6.12 (SAS 1990).

Species richness was the total number of vascular plant species occurring within the four plots per well location. Mean plant cover ($n=4$ plots) was calculated for each well location. Spearman rank correlations among mean total biomass, species richness, mean plant cover, soil depth, and hydrological and redox variables were conducted for each site ($n=15$ per site). Physical variables used in correlation analyses were mean, median, and interquartile range of water table depth, and redox potential at 10 cm and 25 cm depths. The interquartile range, i.e., the range of data between the 25th and 75th quartiles, was used as an expression of the degree of fluctuation in water table depth or redox potential.

Table 1 Mean (± 1 SD) water table depth and soil redox potential for the wet, moist, and dry meadow plant communities at West Chicken Creek and Limber Jim Creek. For each site, *different letters* denote a significant difference between community means [Tukey's

honest significant difference (HSD) for water table depth; Dunn's test for redox potential, $\alpha=0.05$, number of observations ranged from 121 to 142]

Location	Water table depth (cm)	Soil redox potential at 10 cm depth (mV)	Soil redox potential at 25 cm depth (mV)
West Chicken Creek			
Wet meadow	-11±23 a	248±231 a	37±168 a
Moist meadow	-35±24 b	441±167 b	309±226 b
Dry meadow	-63±24 c	528±60 c	482±83 c
Limber Jim Creek			
Wet meadow	-18±12 a	231±231 a	113±200 a
Moist meadow	-35±23 b	414±210 b	320±237 b
Dry meadow	-56±23 c	537±88 c	425±148 c

Results

Water table depth and soil redox potential

Mean water table depth and soil redox potential differed significantly among the three meadow communities (Table 1). Variation in water table depth and soil redox potential along the streamside gradients reflected seasonal patterns of stream stage and discharge (Dwire et al. 2000; Dwire 2001). Soil redox potentials were highly variable, particularly at 25 cm depth in the wet (range -195 to 627 mV) and moist (range -144 to 647 mV) meadow communities, and indicated shifts from anaerobic (≤ 300 mV) to aerobic (> 300 mV) conditions in response to a seasonal lowering of water table depth. In the dry meadow communities, soil conditions (0–25 cm depth) remained mostly aerobic throughout the year, particularly at the 10 cm depth (282–659 mV), resulting in less variation in soil redox potential (Table 1).

Plant species composition and aboveground biomass

Total aboveground biomass did not differ significantly among the three meadow communities (Table 2); however, the relative contribution of individual biomass components was indicative of community differences in species composition (Fig. 1). Wet meadow communities were dominated by *Carex aquatilis* and *Carex utriculata* and were lowest in species richness and cover (Table 2; $\alpha=0.05$). Moist meadow communities, intermediate in species richness and cover, were dominated by *Deschampsia cespitosa* and *Poa pratensis* at West Chicken Creek, and by *Calamagrostis canadensis* and *Carex lanuginosa* at Limber Jim Creek. The dry meadow communities, highest in species richness and cover, were composed of a mixture of forbs and graminoids, with the dominant graminoids being *P. pratensis* and *Juncus balticus*. In the wet meadow communities, aboveground biomass was composed almost entirely of plant material from the dominant sedge species (≈ 90 – 98% of total; graminoid+litter biomass). In the moist and dry meadow communities, graminoid biomass (≈ 46 – 66% of the total aboveground biomass) was composed of a mixture of grass, sedge, and rush species. Forbs

comprised $< 1\%$ of the total aboveground biomass in the wet meadow communities and 6–12% of the aboveground totals for the moist and dry communities (Fig. 1). Herbaceous litter was a large component in each community (18–34% of total aboveground biomass). Moss biomass, a minor component in the wet communities, comprised $\approx 23\%$ of the aboveground total for the dry meadow at West Chicken Creek, and 11–17% in the moist and dry communities at Limber Jim Creek. Woody debris (noted as wood in Fig. 1), which was likely deposited during high flows (Brookshire and Dwire 2003), was highest in the wet meadow communities.

At Limber Jim Creek, aboveground biomass was negatively correlated to species richness ($r_s = -0.62$, $P=0.03$). At West Chicken Creek, however, aboveground biomass was not significantly correlated to either species richness or plant cover (Electronic Supplementary Material, Table 1). Correlations of aboveground biomass with mean and interquartile ranges of water table depth and soil redox potential were weak or not significant (Electronic Supplementary Material, Table 1).

Belowground biomass

Total belowground biomass (roots+rhizomes, combined for all depths) was notably greater than total aboveground biomass in each plant community (Fig. 1, Table 2), and differed among the communities at both West Chicken Creek ($F_{2,12}=36.1$, $P < 0.01$) and Limber Jim Creek ($F_{2,12}=24.7$, $P < 0.01$). In the wet and moist meadow communities, belowground biomass comprised ≈ 68 – 81% of the total biomass (Table 2), and belowground-to-aboveground ratios were approximately two- to threefold higher than those for the dry meadow communities (Table 2, Fig. 1). At both sites, root biomass comprised 50–69% of the total belowground biomass, while rhizome biomass comprised 30–50% (Fig. 1). Rhizome-to-root ratios were lowest in the dry meadow communities, and did not differ significantly between the wet and moist communities (Table 2).

The vertical distribution of belowground biomass was distinctive for each community (Fig. 2), and significant differences in root, rhizome, and total belowground

Table 2 Plant cover, species richness, and biomass totals and ratios (ash-free dry mass g/m^2 ; mean ± 1 SE, $n=5$) for West Chicken Creek and Limber Jim Creek. Within each site, *different letters* denote a significant difference between community means (Tukey's HSD for plant cover and biomass totals; Dunn's tests for species richness and biomass ratios, $\alpha=0.05$)

	West Chicken Creek			Limber Jim Creek		
	Wet	Moist	Dry	Wet	Moist	Dry
Plant cover (%)	109 \pm 1 a	126 \pm 1 b	147 \pm 1 c	96 \pm 1 a	111 \pm 1 b	152 \pm 1 c
Species richness	7 \pm 5 a	14 \pm 4 a, b	19 \pm 5 b	4 \pm 1 a	15 \pm 4 b	20 \pm 4 b
Biomass totals						
Aboveground (AG)	809 \pm 78 a	711 \pm 25 a	654 \pm 88 a	627 \pm 36 a	603 \pm 23 a	513 \pm 34 a
Belowground (BG)	3,502 \pm 344 a	1,525 \pm 206 b	749 \pm 82 c	2,712 \pm 285 a	2,412 \pm 147 a	939 \pm 82 b
AG and BG	4,311 \pm 289 a	2,236 \pm 221 b	1,403 \pm 113 c	3,338 \pm 284 a	3,015 \pm 155 a	1451 \pm 103 b
Biomass ratios						
Rhizomes/roots	0.72 \pm 0.16 a	0.94 \pm 0.24 a	0.43 \pm 0.09 a	1.04 \pm 0.15 a	1.00 \pm 0.12 a	0.57 \pm 0.06 b
BG total/AG total	4.60 \pm 0.76 a	2.13 \pm 0.25 b	1.23 \pm 0.22 b	4.38 \pm 0.56 a	4.01 \pm 0.24 a	1.84 \pm 0.14 b

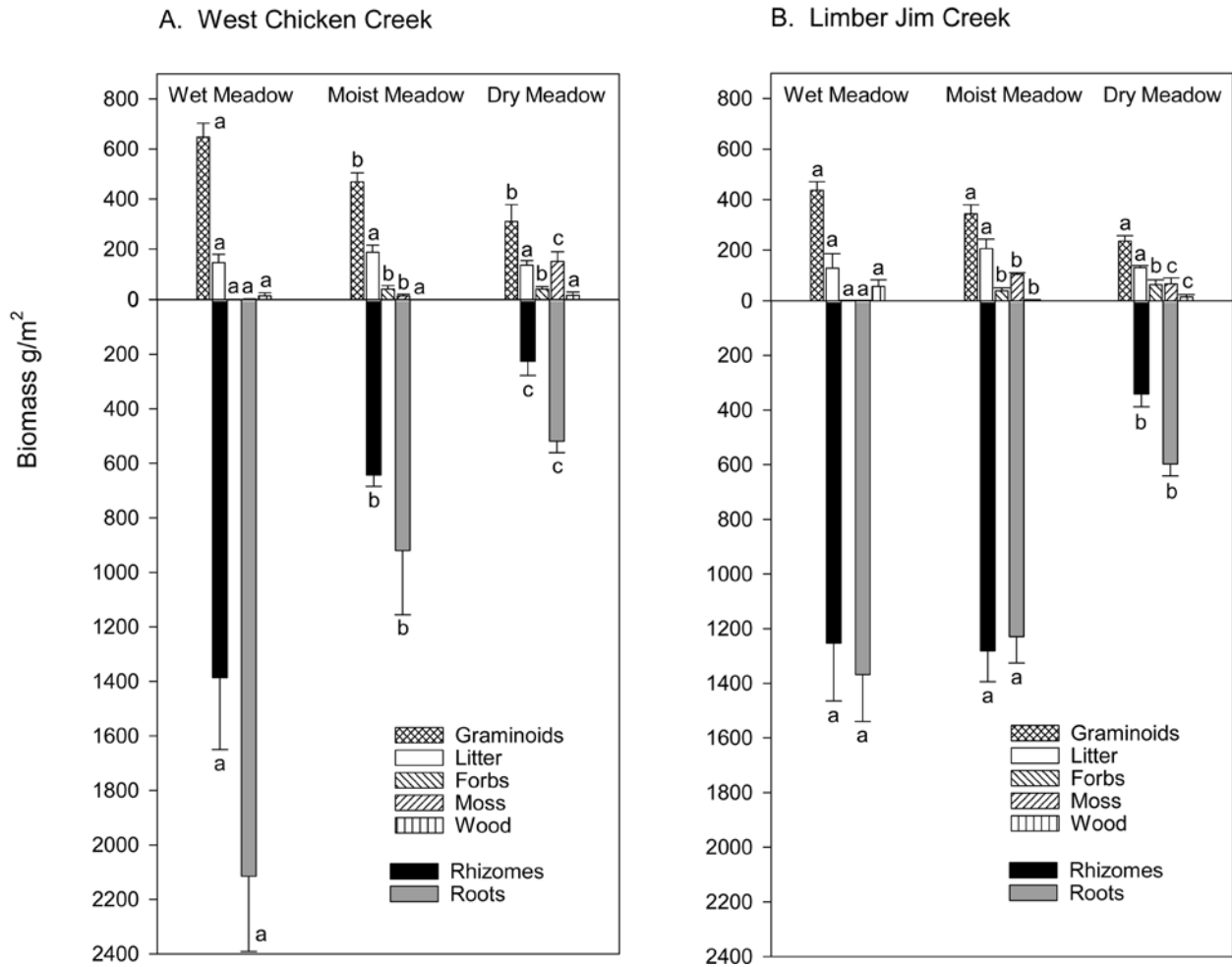


Fig. 1 Distribution of biomass (ash-free dry mass basis, mean ± 1 SE, $n=5$, g/m^2) in the wet, moist, and dry meadow communities at West Chicken Creek (A) and Limber Jim Creek (B). Components of aboveground biomass are shown above the x-axis, belowground components are shown below the x-axis. Within each biomass

component for each site, different letters denote a significant difference between means [Dunn's tests for forb, moss, and wood; Tukey's honest significant difference (HSD) with Bonferroni adjustment for all other components, $\alpha/3=0.15$]

biomass with depth were observed for both sites ($P<0.0001$; Electronic Supplementary Material, Table 1). In the wet meadow communities, 33–37% of the total belowground biomass occurred in the top 0–10 cm and 23–28% occurred in the 10–20 cm and 20–30 cm depth increments (Fig. 2). In the moist meadow communities, $\approx 56\%$ of the belowground biomass occurred within the top 10 cm of the soil profile. In contrast, $\approx 60\text{--}76\%$ of the total belowground biomass occurred in the top 10 cm in the dry communities, and no significant differences in total biomass were observed between the lower two depths (20–40 cm) at either site (Fig. 2).

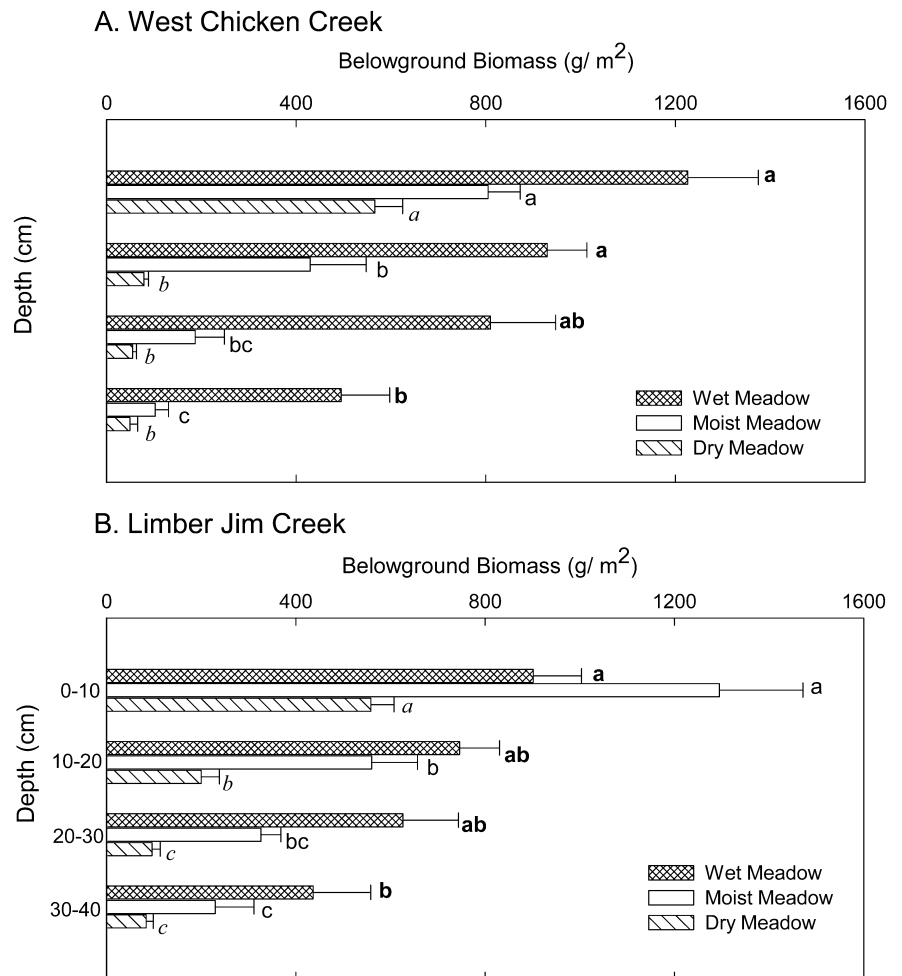
Belowground and total biomass were negatively correlated with plant species richness and cover (Electronic Supplementary Material, Table 2). At West Chicken Creek and Limber Jim Creek, belowground biomass was positively correlated with mean water table depth ($r_s=0.89$ and $r_s=0.74$, $P<0.01$, respectively) and negatively correlated with mean soil redox potential at 10 cm depth ($r_s=-0.85$ and $r_s=-0.74$, $P<0.01$) and 25 cm depth ($r_s=-0.92$ and $r_s=-0.73$, $P<0.01$). The interquartile range (range of

data between the 25th and 75th quartiles) was used as an indicator of the degree of fluctuation in water table depth or redox potential. Belowground biomass was positively correlated to interquartile range of redox potential at 10 cm depth at both West Chicken Creek ($r_s=0.82$, $P<0.01$) and Limber Jim Creek ($r_s=0.69$, $P<0.01$). However, correlations among belowground biomass and interquartile range of water table depth and redox potential at 25 cm depth were weak or not significant.

Discussion

The distribution of plant biomass differed markedly among the three plant communities in these riparian meadows, particularly belowground (Fig. 1). Significant differences in mean water table depth and soil redox potential (10 and 25 cm depths) among the communities indicated the environmental gradient that occurred along the sampled transects. Strong correlations among total biomass, mean water table depth, and mean soil redox

Fig. 2 Vertical distribution of total belowground biomass for the wet, moist, and dry meadow plant communities at West Chicken Creek (A) and Limber Jim Creek (B) (mean \pm 1 SE, $n=5$). Within each community, different letters denote a significant difference in total biomass between depths (Tukey's HSD with Bonferroni adjustment, $\alpha/3=0.15$)



potential revealed that the distribution of biomass corresponded to the environmental gradient (Electronic Supplementary Material, Table 2). Highest total biomass occurred in the sedge-dominated, wet meadow communities and lowest biomass was observed in the more diverse dry meadow communities, dominated by a mixture of grasses and forbs. The ratios of belowground-to-aboveground biomass, which were 2–4 times higher in the wet meadow communities than in the dry meadows, were also indicative of community differences in plant species composition. Moreover, the distinctive vertical profiles of belowground biomass within each community (Fig. 2), as well as the rhizome-to-root ratios (Table 1), reflected the characteristics and distribution of the common graminoid species.

The dominant sedges of the wet meadow communities (*Carex aquatilis* and *Carex utriculata*) are clonal species that form extensive horizontal and vertical networks of long, stout rhizomes (Hultgren 1989; Bernard 1990), interspersed with expansive meshes of fine roots (Saarinen 1996). Although anaerobic soil conditions can strongly influence the energy status and survival of roots (Drew 1992; Brix and Sorrell 1996), these sedge species form well-developed aerenchyma and are capable of extensive belowground production in low oxygen and anoxic

environments (Fagerstedt 1992; Perata and Alpi 1993), as indicated by the occurrence of considerable biomass throughout the 40-cm profile sampled in this study (Fig. 2). Physiological benefits of allocation to belowground tissue may include exposure to microsites with differing aeration and nutrient status. The dominant graminoids in the moist meadow communities at Limber Jim Creek (*Carex lanuginosa* and *Calamagrostis canadensis*) are also strongly rhizomatous (Crowe and Clausnitzer 1997), which likely explains the similar rhizome-to-root ratios, total amounts, and vertical distribution of belowground biomass between the wet and moist communities at this site (Table 2, Fig. 2). Extensive belowground growth of rhizomes likely serves as a regenerative mechanism for spatial expansion of these graminoid species. In contrast, belowground biomass in the dry meadow communities was concentrated within 10 cm of the soil surface (Fig. 2), and rhizome-to-root ratios were approximately half those observed in the wet and moist communities (Table 2). These distribution characteristics may be due to the growth attributes of *P. pratensis*, the dominant grass in the dry meadows, which is shallow rooted and produces short rhizomes that extend horizontally near the soil surface (Tilman and Wedin 1991). In addition, the forb species occurring in the dry

meadow communities do not have extensive belowground structures (Crowe and Clausnitzer 1997; Dwire 2001).

Surprisingly, total aboveground biomass was similar among communities (Table 1). However, community differences in species composition and growth forms were evident in the various components of aboveground biomass (Fig. 1). At West Chicken Creek, for example, graminoid aboveground biomass in the wet community ($648 \pm 55 \text{ g/m}^2$) was more than twice that in the dry community ($310 \pm 68 \text{ g/m}^2$), but the amount of moss biomass in the dry community ($152 \pm 38 \text{ g/m}^2$) was large enough to result in comparable community totals. Moss also accounted for $\approx 17\%$ of the aboveground biomass in the moist community at Limber Jim Creek ($105 \pm 6 \text{ g/m}^2$), underscoring the contribution of non-vascular plants to community composition in these riparian meadows (Crowe and Clausnitzer 1997). The relationship between plant species richness and biomass, a topic of considerable study and discussion (Mittelbach et al. 2001), has been shown to differ depending on the scale of observation (Moore and Keddy 1989), community type (Gough et al. 1994), and the role of environmental variables (Grace 1999). In these meadows, the highest number of species was associated with the lowest community biomass, which is consistent with patterns observed in other herbaceous plant communities occurring along strong environmental gradients (Garcia et al. 1993; Gough et al. 1994). The higher species richness in the moist and dry meadow communities was primarily due to the occurrence of diverse forbs. While forbs add to species richness and canopy cover in riparian herbaceous communities, they typically do not contribute significantly to biomass, either above or belowground. These results highlight the importance of including belowground biomass estimates in the evaluation of species diversity-biomass relationships for herbaceous plant communities.

In each community, a portion of the belowground biomass was composed of necromass. Since we did not separate belowground biomass into live and dead material, we are unable to assess the proportion of dead tissue in our belowground biomass samples. Amounts of necromass may have been greater in samples from the wet and moist meadow communities, where decomposition was mediated by seasonal shifts in saturation and aeration status. As soils become waterlogged and increasingly anoxic, biomass decay rates, composition and metabolism of microbial communities, and biogeochemical reactions change dramatically (Baker et al. 2000). In the wet and moist meadow communities, soil redox potential underwent large fluctuations at both 10 and 25 cm depths (Dwire et al. 2000). Significant correlations of belowground biomass with the interquartile range of soil redox potential (at 10 cm depth) suggested that fluctuations in redox values near the soil surface influenced biomass distribution, which may be partly explained by variation in the decomposition environment. However, belowground production may also have been greater in these sedge-dominated communities. In arctic (Henry et al. 1990) and alpine (Fisk et al. 1998) meadows dominated by sedge

species, approximately 65–75% of the net production was belowground. In a 1-year experimental study, Aerts et al. (1992) found that 60–70% of the biomass for *Carex rostrata* (currently *Carex utriculata*) was allocated to belowground tissues, with $\approx 16\%$ allocated to rhizomes. The proportion of belowground necromass also depends on root longevity, which can vary from a few weeks to over a year (Aerts et al. 1989; Eissenstat and Yanai 1997), depending on species, soil nutrient status (Van der Krift and Berendse 2002), and environmental conditions. In a boreal fen, turnover time for roots and rhizomes of *C. rostrata* (currently *C. utriculata*) was found to be about 7 months (Saarinen 1996); little is known, however, about the longevity and turnover of belowground components for other dominant meadow graminoids. In a long-term study of ten Siberian grasslands (meadows and steppes), $\approx 34\text{--}43\%$ of the belowground phytomass was composed of dead material, and the highest proportion of living biomass ($\approx 66\%$) occurred in mesophytic meadows, which were similar in species composition to our dry meadow communities (Titlyanova et al. 1999). In Nevada, Manning et al. (1989) measured live belowground biomass in four meadow plant communities, defined by the dominant graminoid. Live belowground biomass for their *Carex nebrascensis* community ($3,382 \text{ g/m}^2$, 0–40 cm depth) was comparable to our wet meadow belowground totals (Table 2); however, their live belowground biomass total for *Poa nevadensis* communities (555 g/m^2 , 0–40 cm depth) was lower than our dry meadow belowground values (Table 2). We recognize that the proportion of belowground necromass may be high in these meadows and likely varies along the streamside gradients. However, due to high belowground production in sedge-dominated meadows, we speculate that the community patterns of belowground biomass distribution reported here may not have differed substantially if we had separated live from dead material, and presented data for living belowground biomass.

Given the limitation of one harvest, we assumed that fall was the optimal time for the collection of maximum graminoid biomass, both above- and belowground (Bernard and Hankinson 1979; Aerts et al. 1992). Aboveground biomass values for the wet and moist meadows (Table 2) are similar to values reported for other meadows (Manning et al. 1989; Bernard 1990; Jakrlová 1993) and within the range ($500\text{--}1,050 \text{ g/m}^2$) presented in a review of biomass distribution in temperate sedge-dominated wetlands (Bernard et al. 1988). Although our values for belowground biomass (Table 2) greatly exceeded the range ($150\text{--}900 \text{ g/m}^2$) given by Bernard et al. (1988), they are comparable to those presented for other riparian meadows dominated by similar graminoid species (Manning et al. 1989; Fiala 1993; Otting 1998; Toledo and Kauffman 2001). Discrepancies among biomass values presented here and data reported in the literature may be largely due to ecological differences in study sites (e.g., differences in light and nutrient limitation), but they may also be influenced by differences in sampling and processing methods, annual variation (Jakrlová 1993; Thormann and

Bailey 1997), seasonal variation (Aerts et al. 1992), and presentation of results as air-dry mass, dry mass, and AFDM.

This study provides empirical data that characterized the hydrologic and edaphic conditions and related characteristics of the dominant plant communities that occurred along streamside elevational gradients in montane riparian meadows. The zonation of the dominant meadow plant communities appeared to be regulated by varying water table depths and associated soil redox conditions. In the wet meadow communities, dominant *Carex* species were tolerant of seasonal flooding, shallow water table depths, and anaerobic soil conditions that likely restricted the distribution of other meadow species. The moist and dry meadow communities were composed of a greater diversity of species and life forms, which were generally less tolerant of waterlogged conditions; in these communities, competition and other biotic interactions likely play a greater role in determining species composition and vegetation structure (Grime 1979; Keddy 1992).

The distribution of above- and belowground biomass, which is largely determined by the plant species and growth forms occurring within the streamside plant communities, coincided with spatial gradients in water table depth and redox potential. The plant biomass structure in these communities influence ecological functions at the stream-riparian interface by dissipating hydraulic energy, trapping sediment, stabilizing banks, and contributing inputs of organic matter to the stream and floodplain.

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