PLANT SPECIES DISTRIBUTION IN RELATION TO WATER-TABLE DEPTH AND SOIL REDOX POTENTIAL IN MONTANE RIPARIAN MEADOWS

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Abstract: The distribution of riparian plant species is largely driven by hydrologic and soil variables, and riparian plant communities frequently occur in relatively distinct zones along streamside elevational and soil textural gradients. In two montane meadows in northeast Oregon, USA, we examined plant species distribution in three riparian plant communities—defined as wet, moist, and dry meadow—along short topographic gradients. We established transects from streamside wet meadow communities to the dry meadow communities located on the floodplain terrace. Within each of the three communities, we sampled plant species composition and cover and monitored water-table depth and soil redox potential (E_h) at 10- and 25-cm depths through three growing seasons (1997, 1998, and 1999). The study objectives were (1) to characterize and compare seasonal patterns of water-table depth and soil redox potential in portions of the floodplain dominated by the three different plant communities; (2) to compare plant species composition, distribution, and diversity among the three communities; and (3) to relate plant species diversity and distribution to water-table depth and redox potential. Strong environmental gradients existed along the transects. Water-table depth followed the seasonal patterns of stream stage and discharge and was consistently highest in the wet meadow communities (ranging from +26 cm above the soil surface to −37 cm below the surface), lowest in the dry meadow communities (−8 cm to − 115 cm), and intermediate in the moist meadow communities (+17 cm to −73 cm). Dynamics of redox potential were associated with the seasonal fluctuations in water-table depth and differed among the plant communities. In the wet meadow communities, anaerobic soil conditions (E_h ≤ 300 mV) occurred from March through July at 10-cm depth and throughout the year at 25-cm depth. In the moist meadow communities, soils were anaerobic during spring high flows and aerobic in summer and fall during low flows. In the dry meadow communities, soil conditions were predominantly aerobic throughout the year at both depths. Wet meadow communities were dominated by sedges (*Carex* spp.) and had the lowest species richness and diversity, whereas dry meadow communities were composed of a mixture of grasses and forbs and had the greatest number of species. Species richness and total plant cover were negatively correlated with mean water-table depth and positively correlated with mean redox potential at 10-cm and 25-cm depths ($P < 0.01$). Distribution of the 18 most abundant plant species in relation to water-table depth and soil redox potential showed that certain species, such as the obligate wetland sedges, occurred within a fairly restricted range of water-table depth, whereas other graminoids occurred over wide ranges. These results suggest that the biological diversity often observed in montane riparian meadows is strongly related to steep environmental gradients in hydrology and soil redox status.

Key Words: wetland indicators, plant species richness, plant species diversity, water-table depth, montane riparian meadows, oxidation-reduction potential, Blue Mountains, Oregon

INTRODUCTION

Hydrologic flow regime is the major factor governing physical and biotic processes and aquatic and riparian biota in stream-riparian corridors (Poff et al. 1997, Tabacchi et al. 1998). The composition and distribution of riparian vegetation are primarily determined by features of the hydrologic regime, including infrequent large floods (Stromberg et al. 1997, Rood et al. 1998), seasonal flooding (Auble and Scott 1998), duration of inundation (Roberts and Ludwig 1991, Auble et al. 1994), instream flows (Nilsson 1987, Stromberg and Patten 1990, Stromberg 1993, Rood et al. 1995), and levels of shallow ground water (Allen-Diaz 1991, Stromberg et al. 1996, Castelli et al. 2000). The hydrologic regime, particularly water-table dynamics associated with seasonal flooding, also influences riparian soils by controlling the areal extent and duration of saturation. In saturated soils, oxidation-reduction potential, or redox potential, indicates the occurrence and intensity of anaerobic conditions and provides an integrative measure of physical and biological conditions in subsurface environments (Cogger et al. 1992, Mitsch and Gosselink 1993). Spatial and temporal gradients in redox potential commonly occur within the near stream portions of riparian areas (Dahm et al. 1998, Hedin et al. 1998, McClain et al. 2003). Knowledge of soil redox potential assists in understanding the soil environment occupied by different plant species and provides insights into functional characteristics of saturated riparian environments. This may be especially important in riparian meadows, where fine-textured soils are common and longitudinal gradients are less steep than elsewhere along the stream-riparian corridor.

The influence of hydrologic variables and soil redox potential on plant characteristics has been investigated most frequently under controlled experimental conditions (Moog and Janiesch 1990, Brix and Sorrell 1996, Kludze and DeLaune 1996, Yetka and Galatowitsch 1999). Distinctive features of riparian plant communities that reflect responses to steep environmental gradients include species richness, diversity and types of growth forms, and species composition and distribution (Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997, Tabacchi et al. 1998). Although controlled experimental work has identified hydrologic requirements for a few species under specified conditions, results may have limited utility in predicting species presence or abundance in natural settings. Most field investigations of interactions among hydrologic variables, redox potential, and plant species distribution have been conducted in salt marshes with low species diversity and have focused on obligate wetland species (Howes et al. 1981, DeLaune et al. 1983,

Woerner and Hackney 1997). Fewer studies on relationships among hydrology, soil redox potential, and plant species distribution have been conducted in riparian areas (Cooper 1990, Green 1992, Castelli et al. 2000), and little is known about the spatial and temporal extent, duration, or intensity of soil redox conditions associated with most riparian plant communities (Dwire et al. 2000). Moreover, limited data are available on the tolerances and responses of common riparian plant species to flooding and low soil redox potentials in natural environments (Keddy 1999).

In two riparian meadows in northeast Oregon, USA, we examined relations among water-table depth, redox potential, and plant species distribution in three riparian plant communities along streamside gradients. The three communities—*a priori* defined as wet, moist, and dry meadow—occurred along a short topographic gradient and occupied different geomorphic positions on the floodplain. The study objectives were (1) to characterize and compare seasonal patterns of water-table depth and soil redox potential in portions of the floodplain dominated by the three different plant communities; (2) to compare plant species composition and diversity among the three communities; and (3) to relate plant species diversity and distribution to water-table depth and redox potential. Special attention was given to the occurrence of dominant herbaceous species in relation to water-table depth and soil redox potential.

METHODS

Study Site Descriptions

The study sites are located along valley segments of West Chicken Creek (45°06′15″ N, 118°19′41″W) and Limber Jim Creek (45°3′17″N, 118°24′11″ W), two second-order tributaries to the upper Grande Ronde River, northeast Oregon (Figure 1), and are administered by the Wallowa-Whitman National Forest. Although livestock have historically grazed both sites, these meadows are among the least disturbed montane meadows of the region. The West Chicken Creek study site was fenced to exclude livestock in 1993, and the Limber Jim Creek study site has not been managed for livestock grazing since 1978; however, native ungulates and occasional trespass cattle graze both sites. The study sites have similar histories of upslope logging. The two streams are similar in elevation ($\approx$ 1320 m) and gradient (2 to 2.5%). However, Limber Jim Creek is a wider, larger stream with considerably greater discharge in spring and a larger drainage area than West Chicken Creek (Table 1). Mean annual precipitation is approximately 65 cm, with > 80% falling between November and May, primarily as snow
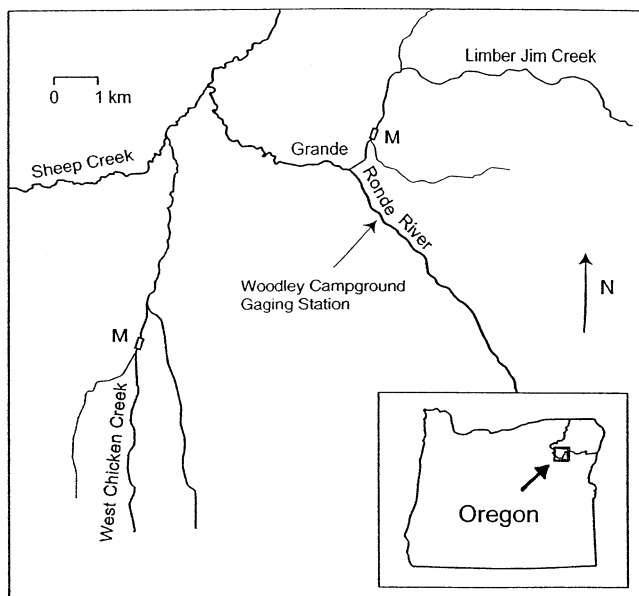
Figure 1. Study area showing locations of meadow (M) study sites along West Chicken Creek and Limber Jim Creek and stream gaging station at Woodley Campground on the Grande Ronde River, northeast Oregon.

Table 1. Watershed and stream physical characteristics of West Chicken Creek and Limber Jim Creek along the meadow study sites, northeast Oregon.

Variable	West Chicken Creek	Limber Jim Creek
Catchment Area (km²)[1]	21.8	34.4
Aspect (stream flow direction)	southwest	north
Wetted Width : Thalweg Depth[2]	5.3	10.1
Sinuosity[3]	3.8	2.1
Discharge (m³/sec)[4]	0.01–1.0	0.01–2.5

[1] from Bohle 1994.
[2] Average ratio of wetted width to thalweg depth based on paired measurements of stream width and depth collected along ≈ 200 m of stream.
[3] Sinuosity calculated as ratio of stream length to valley length.
[4] Discharge data collected by the USDA Forest Service, Wallowa-Whitman National Forest, La Grande Ranger District. Values indicate the range of discharge from April through October 1998.

(1961–1990; USDA Natural Resource Conservation Service). The stream hydrographs are dominated by spring snowmelt, which typically begins in March or April, with peak flows in May (Figure 2; Clarke et al. 1997). During the period of our study, the snowpack varied among years: the basin-wide snowpack for the Grande Ronde River was 143% of average in May 1997, 69% of average in May 1998, and 128% of average in May 1999 (USDA Natural Resource Conservation Service).

The study sites were approximately 250 m in length and 80 m in width. The meadow vegetation was composed of three plant communities, which are distributed along a topographic moisture gradient across the narrow floodplain (Figure 3, Otting 1998, Dwire 2001). We refer to the three communities as wet, moist, and dry meadow. Streamside wet meadow communities are typically flooded for several weeks each spring, whereas moist meadow communities, which occur at somewhat higher relative elevation, may only
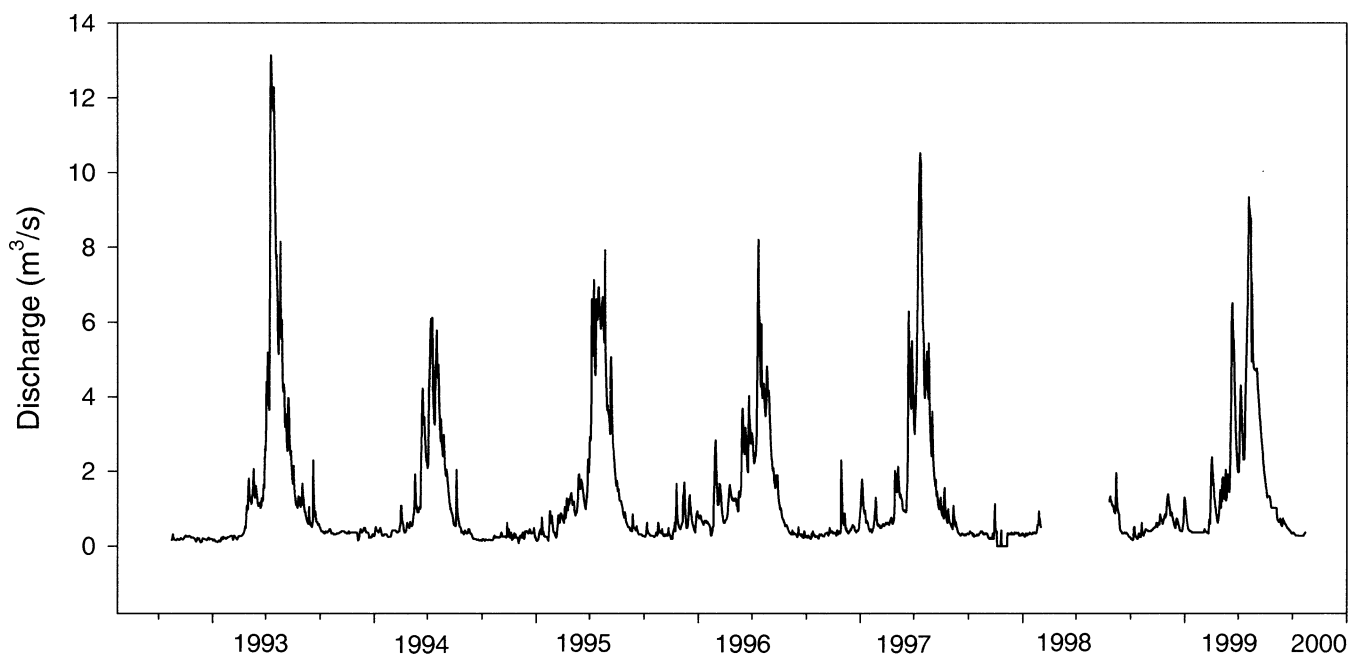

Figure 2. Daily discharge data for the water years 1993–1999 obtained from the Oregon Water Resources Department gaging station at Woodley Campground, upper Grande Ronde River, Oregon. Data for 1998 were lost due to vandalism.
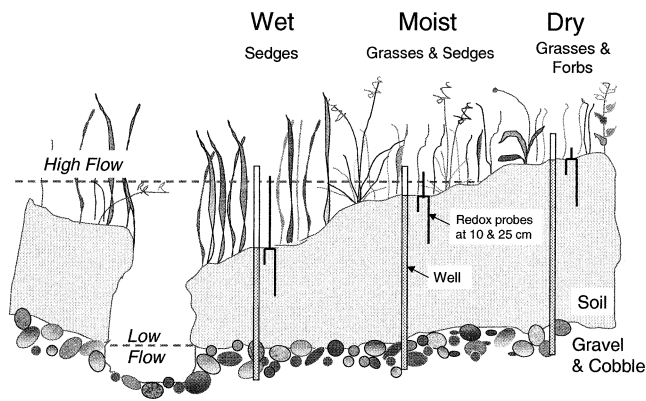
Figure 3. Cross section of a well transect, showing installation of wells and probes for measurement of soil redox potential in the wet, moist, and dry meadow plant communities.
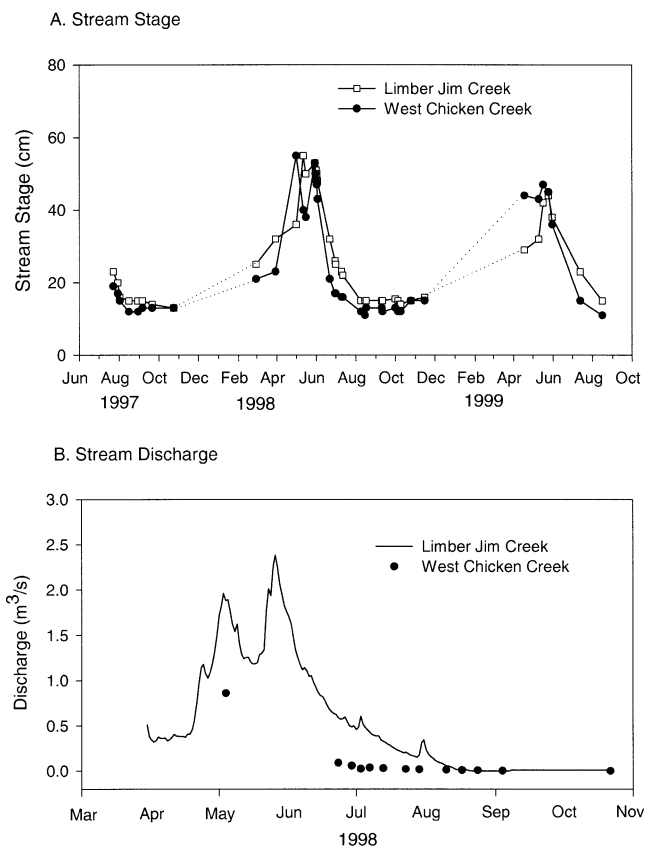

Figure 4. (A) Stream stage for Limber Jim Creek and West Chicken Creek from July 1997 through August 1999. Dashed line indicates periods when data were not collected. (B) Discharge at the downstream end of the meadow study sites for April through October 1998. Data are continuous for Limber Jim Creek and discrete for West Chicken Creek.

be inundated for short periods during snowmelt runoff. At both sites, the wet and moist meadow communities are restricted to the near stream zone and along relict channels. Dry meadow communities generally occur on floodplain terraces (Figure 3) and rarely experience any overland flooding.

The upstream forest reaches and valley uplands were dominated by several conifer species, principally Engelmann spruce (*Picea engelmannii* Parry), Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), and lodgepole pine (*Pinus contorta* Dougl.) (Case 1995, Brookshire and Dwire 2003). Geology of the floodplain meadows consists of Holocene alluvium, which has been deposited over Grande Ronde Basalt (Ferns and Taubeneck 1994, Ferns 1998). The shallow alluvial soils (~ 40 cm to 120 cm deep) are ash-influenced Mollisols and Entisols, underlain by coarse gravels (Robert Ottersberg, Cordilleran Connection, personal communication).

Physical Variables

Daily discharge data for the upper Grande Ronde River were calculated from water-level records collected at the Woodley Campground gaging station, located upstream from the study sites, 1993 through 1999 by the Oregon Water Resources Department (Figure 1, Figure 2). Unfortunately, water-level data for 1998 were lost due to vandalism. At West Chicken Creek and Limber Jim Creek, discharge data were collected at gaging stations established near the downstream boundaries of the meadow study sites by the USDA Forest Service, Wallowa-Whitman National Forest, La Grande Ranger District. Water-level recorders were installed in spring and removed in fall. A staff gauge was installed at each gaging station, and stream stage was recorded during each site visit from July

1997 through September 1999. In 1998, continuous water-level measurements allowed estimation of discharge for Limber Jim Creek from April through October (Figure 4); unfortunately, continuous water-level records for West Chicken Creek were lost due to disturbance of the monitoring equipment by trespass cattle in July 1998. Instantaneous discharge was measured periodically at West Chicken Creek using a flow meter (Figure 4).

To characterize the stream channels, paired measurements of wetted width and thalweg depth were collected along approximately 200 m of stream at each site (Robert Beschta, Oregon State University, unpublished data), and the average ratio of wetted width to thalweg depth was calculated for each site (Table 1). Sinuosity was calculated as the ratio of stream length to valley length; stream length measurements were obtained during site surveys, which included characterizing longitudinal profiles of the stream thalweg within each 250 m meadow study site (Table 1).

Water-Table Depth and Soil Redox Potential

To determine the seasonal hydrologic and soil conditions of the three meadow communities, water-table depth and soil redox potential were monitored along five transects established at each site. Prior to transect establishment (May 1997), plant communities were mapped, and locations for installation of wells were randomly selected within five streamside wet meadow communities. Transects extended from each of the wet meadow well locations to the floodplain terrace through the moist and dry meadow communities (Figure 3). Along each transect, well locations were randomly selected within the moist and dry communities, for a total of five wells within each community at each site. At West Chicken Creek, transect length averaged 18 m (range 14 m to 22 m); at Limber Jim Creek, transect length averaged 11 m (range 9 m to 14 m).

To measure water-table depth, holes were driven with a steel rod and sledge hammer through the shallow soils and into the underlying gravels, and wells were installed approximately 20 cm into the gravel layer (Figure 3). Depths of the wells ranged from 64 cm to 121 cm below the surface. Well casings were made from 2.54-cm-diameter PVC pipe, drilled with 0.32-cm-diameter holes. Water-table depth was measured with a metered copper wire connected to an ohmmeter by lowering the wire into each well and recording the depth of contact with water. To measure soil redox potential, platinum electrodes were installed within 0.5 m of each well at 10-and 25-cm depths (n = 3 probes per depth). Platinum electrodes were constructed by soldering a 15-mm length of 18-gauge Pt wire to varying lengths of insulated 18-gauge Cu wire, and sealing the Pt-Cu junction with a waterproof epoxy (similar to construction described by Mueller et al. 1985, Faulkner et al. 1989, Cogger et al. 1992). Following installation, probes were allowed to equilibrate for 7 to 10 days before measurements were taken. 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). To correct the voltmeter measurements, 214 mV was added to each value (Bohn 1971, Bates 1973). Soils were considered to be anaerobic if redox potential was less than + 300 mV (Gambrell and Patrick 1978, Faulkner and Patrick 1992). Water-table depth and soil redox potential were measured from July 1997 through August 1999, approximately every two-to-three weeks during the spring, fall, and summer seasons, for a total of 28 sampling dates at West Chicken Creek and 26 sampling dates at Limber Jim Creek.

Plant Species Distribution

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, for a total of 20 plots for each community type (four plots × five well locations per community type) at each site. Vegetation data were collected from 14 to 29 July 1997. Percent cover of all vascular plant species, mixed bryophytes, and ground surface features (bare ground, litter, and water) was recorded for each plot. Cover was ocularly estimated using the following intervals: 1% units up to 5%, 5% units from 5–100% (after Daubenmire 1959, Gauch 1982). Multiple layers of plant cover occurred in some plots, resulting in total cover that exceeded 100%. Nomenclature and native or introduced status followed Hitchcock and Cronquist (1973), except for the family Cyperaceae (Hickman 1993). Each species was assigned to a USFWS growth habit and Wetland Indicator Category (Reed 1988, 1996).

Data Analyses

Mean redox potential (n = 3) was calculated for each well location, depth, and date of sampling; resulting means were used in all analyses. For each site, repeated-measures analysis of variance was used to test for plant community differences in water-table depth, redox potential at 10-cm depth, and redox potential at 25-cm depth (Ramsey and Schafer 1997). Plant community was treated as a fixed factor, water-table depth and redox potential were treated as the repeated variables, and an interaction term was included in each model to examine the relationship between plant community and sampling date. During each season, 2–3 wells per site, located in the moist and dry meadow communities, went 'dry' in late summer and fall. For these sampling dates, the depth of the well was used as the value for water-table depth. Normality and homogeneity of variance for water-table depth, redox, and vegetation data were examined through summary statistics, examination of residuals, and conducting Levene's tests (Ramsey and Schafer, 1997). Analyses of variance were conducted using Statistical Analysis System (SAS 1990).

To calculate species diversity measures and evaluate plant cover, data from the four 0.5 m × 0.5 m plots surrounding each well were combined. Species diversity was summarized for the communities using the following measures: average species richness per well location, species heterogeneity, total number of species, and Shannon-Weiner diversity index, indicated by *H'* (Magurran 1988, Krebs 1989). To calculate average species richness per well location, the number

of species occurring in the four 0.5 m × 0.5 m plots surrounding each well were first combined and averaged, and then data from the five well locations for each community at each site were averaged. Community differences in average species richness per well location were tested using analysis of variance and Tukey's honest significant difference (HSD), a multiple comparison test conducted in SAS (SAS 1990). Species heterogeneity was calculated as the ratio of the total number of species in each community to the average number of species per well location (Whittaker 1972, Wilson and Mohler 1983). Shannon-Weiner diversity indices were calculated for each site individually, as well as both sites combined. Similarity in species occurrence among the communities was evaluated by calculating Sörensens coefficients (Magurran 1988).

To calculate cover for individual species, data from the four 0.5 m × 0.5 m plots surrounding each well were first combined and averaged, and then data from the five well locations for each community at each site were averaged. A weighted average index, or wetland prevalence index, was calculated to determine predominance of hydrophytic vegetation (Wentworth et al. 1988) for each community at each site. The wetland prevalence index, also referred to as a wetland score (National Research Council 1995), was computed by weighting the abundance (cover) of each species with the following index values for each Wetland Indicator Category: obligate wetland (OBL) = 1, facultative wetland (FACW) = 2, facultative (FAC) = 3, facultative upland (FACU) = 4, upland (UP) = 5. Wetland prevalence indices were calculated as follows:

$$\text{Prevalence Index} = \frac{\sum A_i W_i}{\sum W_i}$$

Where:

A_i = the abundance (cover) of species i
W_i = Wetland Indicator Category index value for species i
 i = species

Vegetation has been defined as hydrophytic if the wetland prevalence index was less than 3.0 (Wentworth et al. 1988, US Army Corps of Engineers 1989).

Spearman rank correlations among species richness (total number of species occurring in four 0.5 m² plots at each well location), mean plant cover, soil depth, and hydrologic and redox variables were conducted for each site (n = 15 well locations per site). The following variables were used in correlation analyses for water-table depth, redox potential at 10 cm depth, and redox potential at 25 cm depth: mean, median, and interquartile range. These means, medians, and inter-

quartile ranges were calculated from the combined data collected during 1997, 1998, and 1999, and we considered them to be representative of growing season conditions. The interquartile range (i.e., the range of the middle 50% of the data), is an estimate of the degree of fluctuation in water-table depth or redox potential. Correlations were conducted using SAS (SAS 1990).

The streamside habitats of the 18 most abundant plant species (Table 2) were characterized by summarizing water-table depth and soil redox potential data for all well locations (both sites) where the species of interest occupied ≥ 5% cover. These common species were selected because each species accounted for ≥ 5% mean cover in one or more plant communities at West Chicken Creek or Limber Jim Creek. Medians and quartile ranges of water-table depth and redox potential were calculated (Ramsey and Shafer 1997) and plotted for each of the 18 species.

RESULTS

Seasonal Dynamics of Water-Table Depth and Soil Redox Potential

Water-Table Depth.   Strong spatial and temporal gradients in water-table depth existed along the near stream transects (Figure 5). Water-table depth differed among the plant communities at both West Chicken Creek ($F_{2, 12}$ = 37.5, $P < 0.01$) and Limber Jim Creek ($F_{2, 12}$ = 24.4, $P < 0.01$). Interactions between plant community and sampling date were not significant at either site, and the water-table was consistently highest in the wet meadow communities, lowest in the dry meadow communities, and intermediate in the moist meadow communities (Figure 5).

Peak water-tables occurred during high flows in late May in 1998 and 1999. During high flows, the wet meadow communities were flooded for four to six weeks, with water remaining well above the soil surface for much of the period. The moist meadow communities were inundated intermittently during high flows, with depth to water-table ranging from +17 (above the soil surface) to −23 cm at West Chicken Creek and from +3 to −30 cm at Limber Jim Creek. During spring high flows, considerably more overland flooding occurred at West Chicken Creek than at Limber Jim Creek, possibly reflecting the channel characteristics of the two streams. In the dry meadow communities, the depth to water-table ranged from −17 to −52 cm at West Chicken Creek and from −7 to −53 cm at Limber Jim Creek during spring high flows.

Maximum depths to water-table occurred in mid-to-late September at all sampling locations, during seasonal low-flows, and prior to fall rains each year. Dur-

Table 2. Percent cover (mean ± 1SE, n = 5), USFWS growth habit and Wetland Indicator Category of dominant species (≥ 5% cover) for the wet, moist, and dry meadow plant communities at West Chicken Creek and Limber Jim Creek.

Species	West Chicken Creek	Limber Jim Creek	Growth Habit[1]	Wetland Indicator Category[2]
Wet Meadow				
Carex utriculata Boott.	64 ± 17	3 ± 2	PNEGL	OBL
Carex aquatilis Wahl.	28 ± 13	88 ± 4	PNEGL	OBL
Moist Meadow				
Deschampsia cespitosa (L.) Beauv.	35 ± 11	6 ± 3	PNG	FACW
Poa pratensis L.	20 ± 3	9 ± 2	PIG	FACU
Calamogrostis canadensis (Michx.) Beauv	3 ± 2	25 ± 7	PNG	FACW
Juncus balticus Willd.	5 ± 5	8 ± 3	PNGL	OBL
Carex aquatilis Wahl.	7 ± 3	6 ± 3	PNGL	OBL
Carex microptera Mack.	6 ± 3	1 ± 1	PNGL	FAC
Carex lanuginosa Michx.	4 ± 1	15 ± 8	PNGL	OBL
Polemonium occidentale Greene	10 ± 7	5 ± 7	PNF	FACW
Senecio pseudoareus Rydb.	7 ± 4	3 ± 2	PNF	FACW
Fragaria virginiana Duchesne	0.2 ± 0.1	5 ± 5	PNF	FACU
Arnica chamisonis Less.	5 ± 2	6 ± 2	PNF	FACW
Dry Meadow				
Poa pratensis L.	50 ± 8	19 ± 2	PIG	FACU
Deschampsia cespitosa (L.) Beauv	11 ± 5	2 ± 1	PNG	FACW
Danthonia californica Boland.	10 ± 4	0	PNG	FACU
Juncus balticus Willd.	2 ± 1	16 ± 7	PNGL	OBL
Trifolium repens L.	9 ± 3	16 ± 1	PIF	FACU
Trifolium longipes Nutt.	8 ± 5	5 ± 1	PNF	FAC
Fragaria virginiana Duchesne	4 ± 3	20 ± 5	PNF	FACU
Potentilla gracilis Dougl.	7 ± 2	15 ± 6	PNF	FAC
Achillea millefolium L.	8 ± 4	5 ± 1	PNF	FACU
Aster occidentalis (Nutt.) T&G	6 ± 1	5 ± 1	PNF	FAC
Mixed bryophytes	9 ± 1	5 ± 1	moss	

[1] Growth habit includes P = perennial, E = emergent, F = forb, G = grass, GL = grasslike; N = native, and I = introduced.

[2] USFWS Wetland Indicator Categories are OBL = obligate wetland; FACW = facultative wetland; FAC = facultative; FACU = facultative upland (Reed 1988).

ing late summer in the wet meadow communities, water-table depth ranged from −21 to −36 cm at West Chicken Creek and from −25 to −37 cm at Limber Jim Creek. In the moist meadow communities, water-table depth ranged from ≈ −38 to −73 cm at both West Chicken Creek and Limber Jim Creek in late summer. In the dry meadow communities, maximum depths to the water-table ranged from −75 to −115 cm at West Chicken Creek and from −58 to −84 cm at Limber Jim Creek. Differences in the water-table depth between the plant communities were greater at West Chicken Creek than Limber Jim Creek for most sampling dates.

Soil Redox Potential. Seasonal patterns in soil redox potential were distinctive for each plant community, showing that different soil environments existed along the near stream transects (Figure 6). At West Chicken Creek, interactions between plant community and sampling date for soil redox potential were significant at both depths (10 cm depth: $F_{2, 12} = 10.4$, $P < 0.01$; 25 cm depth: $F_{2, 12} = 16.3$, $P < 0.01$); however, at Limber Jim Creek, interactions were not significant at either depth. Redox measurements were highly variable on most sampling dates, particularly in the wet and moist communities (Figure 6). Throughout the sampling period, redox potential measurements were least variable in the dry communities at 10 cm (CV = 14% for both sites) and most variable in the wet communities at 25 cm (CV = 442% at West Chicken Creek, CV = 194% at Limber Jim Creek).

There were significant differences in soil redox potential at both 10-cm and 25-cm depth among plant communities at both West Chicken Creek (10-cm depth: $F_{2, 12} = 11.4$, $P < 0.01$; 25-cm depth: $F_{2, 12} = 22.7$, $P < 0.01$) and Limber Jim Creek (10-cm depth: $F_{2, 12} = 9.5$, $P < 0.01$; 25-cm depth: $F_{2, 12} = 6.2$, $P = 0.01$). In the wet meadow communities, redox potentials at 10-cm depth indicated mostly anaerobic con-

A. West Chicken Creek
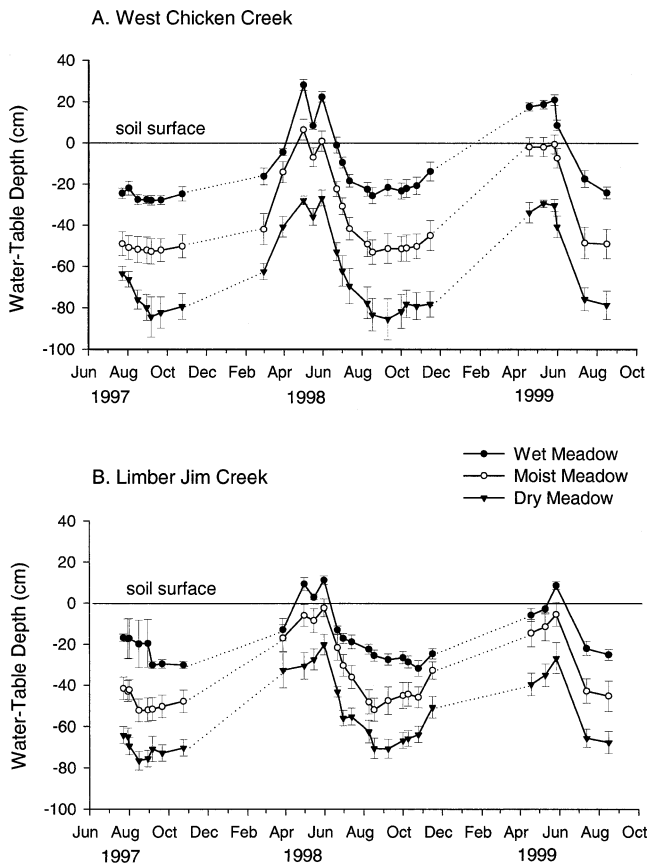
West Chicken Creek
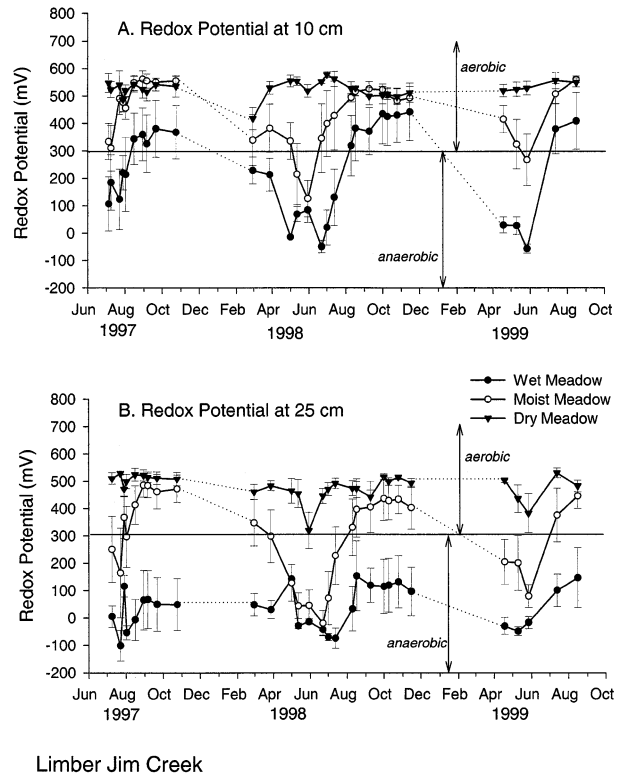

Figure 5. Water-table depth (mean ± 1 SE) in wet, moist, and dry meadow communities at (A) West Chicken Creek (B) and Limber Jim Creek from July 1997 through August 1999. Dashed line indicates periods when data were not collected.

ditions from spring through mid-summer; redox values ranged from −113 to 436 mV at West Chicken Creek and from −136 to 361 mV at Limber Jim Creek during the period from 13 May 1998 through 9 August 1998. In late summer and fall, redox potentials at 10-cm depth in the wet meadows were mostly aerobic, particularly at West Chicken Creek (Figure 6A and B). At 25 cm, however, redox potentials in the wet meadow communities remained anaerobic at most sampling locations throughout the sampling period. Although measurements indicated that soil conditions were consistently anaerobic, soil redox potential at 25 cm in the wet meadows still displayed seasonal patterns. Lowest redox potentials, indicating highly reducing conditions (Gambrell et al. 1991) occurred from mid-May to mid-July in both 1998 and 1999 (range: −126 to 73 mV at West Chicken Creek and from −136 to 155 mV at Limber Jim Creek). Higher redox potentials, indicating moderately reducing to oxidized conditions, occurred from mid-September to mid-October (range: from −40 to 394 mV at West Chicken Creek and from −15 to 558 mV at Limber Jim Creek).

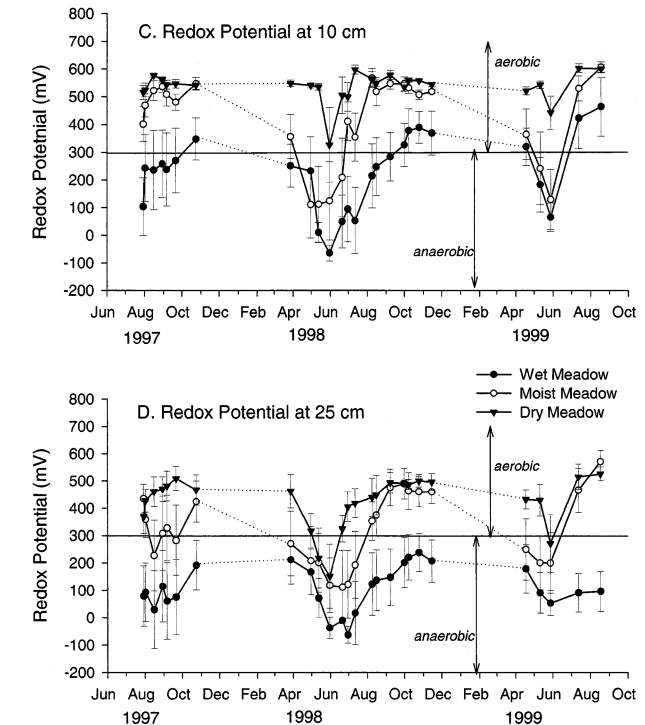Figure 6. Mean soil redox potential (mean ± 1 SE) at (A) 10-cm depth and (B) 25-cm depth in wet, moist, and dry meadow communities at West Chicken Creek and mean soil redox potential at (C) 10-cm depth and (D) 25-cm depth in wet, moist, and dry meadow communities at Limber Jim Creek. Dashed line indicates periods when data were not collected.

Table 3. Diversity measures and wetland prevalence indices for the wet, moist, and dry meadow plant communities at West Chicken Creek and Limber Jim Creek, northeast Oregon. For each site, different letters denote a significant difference between community means (Tukey's honest significant difference, α = 0.05).

	n	No. species per well location (mean ± SD)	Species Heterogeneity	Total No. Species	Shannon-Weiner H′	Wetland Prevalence Index (mean ± SD)
West Chicken Creek						
Wet Meadow	5	7 ± 5[a]	2.00	14	1.89	1.07 ± 0.06
Moist Meadow	5	14 ± 4[b]	2.39	33	2.06	2.39 ± 0.27
Dry Meadow	5	19 ± 5[c]	1.96	37	2.50	3.50 ± 0.10
All	15	13 ± 7	4.01	53	4.20	2.32 ± 1.04
Limber Jim Creek						
Wet Meadow	5	4 ± 1[a]	2.50	9	1.95	1.04 ± 0.04
Moist Meadow	5	15 ± 4[b]	1.97	30	2.05	2.13 ± 0.48
Dry Meadow	5	20 ± 4[c]	1.81	37	2.50	3.14 ± 0.40
All	15	13 ± 8	3.60	47	3.66	2.10 ± 0.95
Both Sites						
Wet Meadow	10	5 ± 4[a]	3.40	18	2.75	1.05 ± 0.05
Moist Meadow	10	14 ± 4[b]	2.97	43	3.01	2.26 ± 0.39
Dry Meadow	10	20 ± 5[c]	2.60	51	3.46	3.32 ± 0.33
All	30	13 ± 7	4.80	63	4.96	2.21 ± 0.99

In the moist meadows communities, soils underwent marked seasonal shifts from reduced to oxidized conditions. The seasonal range in redox potential was considerably greater in the moist communities than in either the wet or dry communities at both depths (Figure 6). From spring to mid-July, redox potentials in the moist meadow communities were intermediate between the wet and dry communities. From mid-July through mid-October, redox potentials at 10 cm in the moist communities were very similar to the dry communities, averaging 513 ± 7 (mean ± 1SE) for both sites. For the same time period, average redox potential at 25 cm for the moist communities was 394 ± 20 at West Chicken Creek and 385 ± 22 at Limber Jim Creek.

In the dry meadow communities at West Chicken Creek, redox potential at 10 cm remained above 300 mV throughout the sampling period, indicating that soil conditions were continuously aerobic (Figure 6A). At Limber Jim Creek, average redox potential in the dry meadow community at 10 cm remained aerobic with the exception of a short period in May 1998, when soils at two dry meadow well locations became anaerobic, averaging 22 mV on 31 May 1998 (Figure 6C). In the dry meadow communities at both sites, redox potentials at 25 cm decreased during spring flooding in both 1998 and 1999 (Figure 6B and 6D).

Plant Species Distribution

The wet meadow communities were dominated by *Carex utriculata* and *Carex aquatilis* at West Chicken

Creek and by *Carex aquatilis* at Limber Jim Creek (Table 2). In the moist meadow communities, the grasses *Deschampsia cespitosa* and *Poa pratensis* comprised ≈ 55% cover at West Chicken Creek, whereas the grass *Calamagrostis canadensis* and sedge *Carex lanuginosa* comprised ≈ 40% combined cover at Limber Jim Creek. In the dry meadows at West Chicken Creek, forbs and graminoids were about equal in cover, with *Poa pratensis* being the most abundant graminoid. In the dry meadow communities at Limber Jim Creek, forb species comprised ≈ 65% of the plant cover, with *Fragaria virginiana* being the most abundant species. Abundant graminoids were *Poa pratensis* and *Juncus balticus*. Bryophytes, dominated by the moss *Philonotis fontana* (Hedw.) Brid., were most common in the dry meadows, particularly at West Chicken Creek (Table 2).

For both sites combined, 63 vascular taxa were sampled in the 10 transects and 30 well locations (Table 3). Perennial forbs accounted for the largest number of species (34 taxa), followed by sedges (*Carex* spp., 10 taxa), and perennial grasses (9 taxa). Less common taxa included annual grasses and forbs (5 taxa), rushes (*Juncus* and *Luzula* spp., 3 taxa), and horsetails (*Equisetum* spp., 2 taxa). Floristically, the sites were similar, sharing approximately 70% of the vascular taxa. Sörensen's similarity coefficients indicated that there was considerable overlap of species between the two sites, particularly in the dry meadow (0.61) and moist meadow communities (0.63), whereas the wet meadow communities shared fewer species (0.43). The number

of species per well location differed among communities at West Chicken Creek ($F_{2, 12}$ = 9.4, P < 0.01), Limber Jim Creek ($F_{2, 12}$ = 11.6, P < 0.01), and both sites combined ($F_{2, 27}$ = 10.4, P < 0.01). At both sites, the wet meadow communities had the fewest number of species (2 to 13 species per well location), and the dry meadow communities had the largest number of species (12 to 26 species per well location) (Table 3). H' values were lowest in the wet meadow communities, intermediate in the moist meadow communities, and highest in the dry meadow communities at both sites (Table 3). Within each community, the total number of species was similar at both sites (Table 3).

Within each site, Sörensen's coefficients indicated that the dry and moist meadow communities were similar in species composition (0.60 and 0.72, West Chicken Creek and Limber Jim Creek, respectively), whereas moist and wet communities shared fewer species (0.43 and 0.26), and wet and dry meadow communities were the least similar in species composition (0.12 and 0.17). At West Chicken Creek, ≈ 24% of the species occurred in both the wet and moist communities, whereas 40% were present in both the moist and dry. At Limber Jim Creek, approximately 14% of the species occurred in both the wet and moist communities, whereas 60% were present in both the moist and dry. At each site, only 11% of the species occurred in both the wet and dry communities.

Nine non-native species, which occurred at both sites, were sampled. The most abundant non-native species were the grass *Poa pratensis* and the forb *Trifolium repens* (Growth habits PIG and PIF in Table 2). At both sites, *Poa pratensis* occurred at all of the moist and dry well locations and accounted for ≈ 23% mean total cover at West Chicken Creek and ≈ 9% at Limber Jim Creek. Whereas *Trifolium repens* occurred at all the dry well locations at both sites, this species was also present at three of the five moist well locations at Limber Jim Creek. The remaining seven non-native species—*Agrostis alba var. stolinifera* L., *Rumex crispus* L., *Veronica serpyllifolia* L., *Plantago major* L., *Taraxacum officianale* Weber, *Phleum pratense* L., *Ceratium nutans* Raf.—occurred mostly at the dry well locations and generally averaged less than 1% cover at each site.

The distribution of species partitioned within Wetland Indicator Categories reflected compositional differences among the three communities (Figure 7). In the wet meadow communities, ≈ 28 % of the species were obligate wetland (OBL) and ≈ 44 % were facultative wetland (FACW) (Figure 7A); OBL species composed over 97% of the plant cover. In the moist meadow communities, 30% of the species were categorized as FACW and accounted for ≈ 59% of the plant cover (Figure 7B). Although the dry meadow
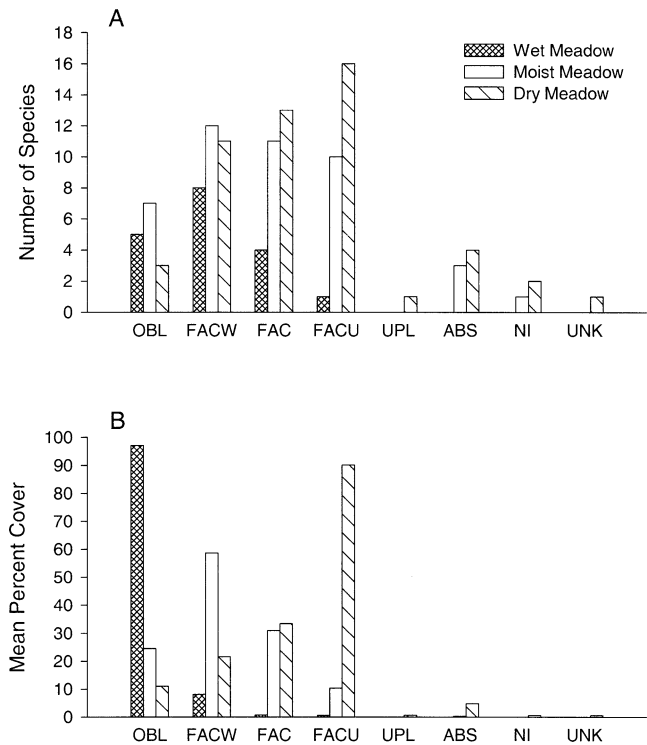

Figure 7. Number of species (A) and proportion of species cover (B) in USFWS Indicator Categories for the wet, moist, and dry meadow communities at West Chicken Creek and Limber Jim Creek (data from both sites are combined).

communities included species from all categories, facultative upland (FACU) species comprised 90% of the plant cover. These results are reflected in the wetland prevalence indices for the communities (Table 3), which show that the wet and moist communities were dominated by hydrophytic vegetation (index values < 3.0), whereas the dry meadows were composed largely of mesophytic and 'drier end' species (index values > 3.0).

Relationships Among Water-Table Depth, Soil Redox Potential, and Plant Species Distribution

Species richness and plant cover were strongly correlated to mean water-table depth (P < 0.01 and P < 0.05, respectively; Table 4). In addition, species richness and plant cover were positively correlated to mean redox potential at both 10 and 25 cm depths, indicating that more species occurred where soils were better aerated. The correlations between species richness and plant cover with the interquartile range of water-table depth were different for each site. At West Chicken Creek, species richness was not significantly correlated to the interquartile range of water-table depth, although plant cover was positively correlated. At Limber Jim Creek, species richness was highly cor-

Table 4. Spearman rank correlation coefficients for correlations among species richness, plant cover, water-table depth, and soil variables for (A) West Chicken Creek and (B) Limber Jim Creek. Correlations are based on 15 well locations per site.

	WTD Ave	WTD IQR	E_h 10cm Ave	E_h 10cm IQR	E_h 25cm Ave	E_h 25 cm IQR
A) West Chicken Creek						
Sp Richness	−0.75*	0.44[NS]	0.55*	−0.36[NS]	0.58*	−0.10[NS]
P1 Cover	−0.90**	0.60*	0.72*	−0.62*	0.69*	−0.26[NS]
Soil Depth	0.69*	−0.39[NS]	−0.50[NS]	0.57*	−0.51*	0.21[NS]
WTD Med	0.99**	−0.64*	−0.84**	0.73*	−0.88**	0.31[NS]
E_h 10cm Med	−0.70*	0.13[NS]	0.90**	−0.65*	0.81**	−0.34[NS]
E_h 25cm Med	−0.87**	0.34[NS]	0.86**	−0.71*	0.93**	−0.32[NS]
B) Limber Jim Creek						
Sp Richness	−0.75*	0.76**	0.68*	−0.42[NS]	0.65*	−0.08[NS]
P1 Cover	−0.77**	0.46	0.71*	−0.74*	0.73*	−0.21[NS]
Soil Depth	−0.53*	−0.43[NS]	−0.36[NS]	0.39[NS]	−0.39[NS]	0.41[NS]
WTD Med	0.99**	−0.74*	−0.90**	0.74*	−0.87**	0.29[NS]
E_h 10cm Med	−0.76**	0.39[NS]	0.87**	−0.67*	0.77**	−0.30[NS]
E_h 25cm Med	−0.73*	0.44[NS]	0.68*	−0.58*	0.94**	−0.14[NS]

** $P \leq 0.01$, * $P \leq 0.05$, [NS] $P > 0.10$.
Variables are defined as follows: Sp Richness = Species richness, number of species per well location; P1 Cover = average total plant cover; Soil Depth = depth of soil to gravel layer; WTD Ave = average water-table depth; WTD Med = median water-table depth; WTD IQR = interquartile range of water-table depth; E_h 10 cm Ave = average redox potential at 10-cm depth; E_h 10 cm IQR = interquartile range of redox potential at 10-cm depth; E_h 10 cm Med = median redox potential at 10-cm depth; E_h 25 cm Ave = average redox potential at 25-cm depth; E_h 25 cm IQR = interquartile range of redox potential at 25-cm depth; E_h 25cm Med = median redox potential at 25-cm depth.
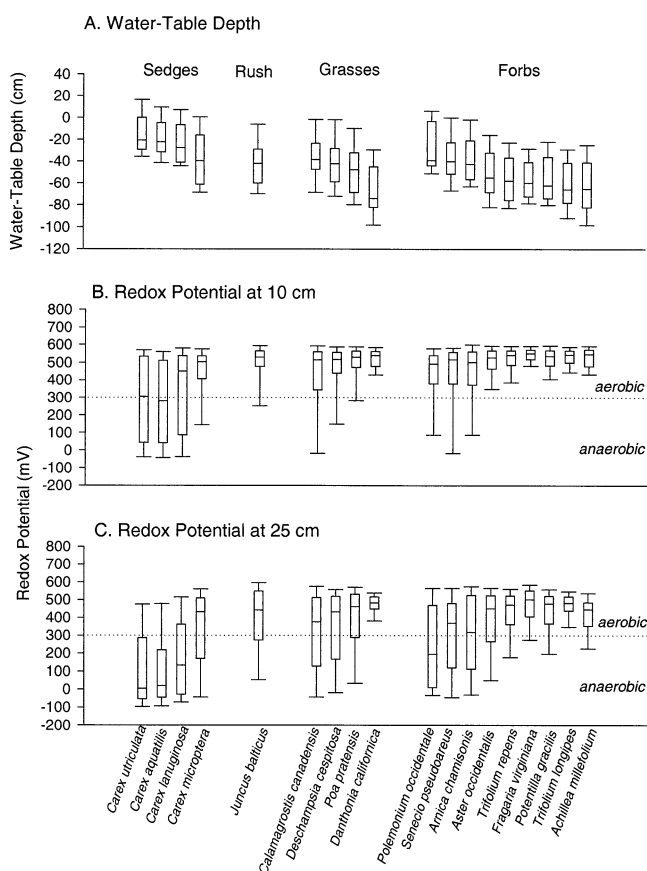

Figure 8. Distribution of the 18 most abundant species for (A) median water-table depth (B) median redox potential at 10-cm depth, and (C) median redox potential at 25-cm depth.

related with water-table depth interquartile range ($P < 0.01$, Table 4), whereas plant cover was weakly correlated ($r_s = 0.46$, $P = 0.08$). The interquartile range (i.e., the range of data between the 25th and 75th quartiles (Ramsey and Schafer 1997)) is an expression of the extent of fluctuation in water-table depth or redox potential. The mean interquartile range of water-table depth was greater at West Chicken Creek (36 cm; range = 18–61 cm) than at Limber Jim Creek (26 cm; range 9–50 cm). Species richness was not significantly correlated to interquartile range of redox potential (both depths) at either site; however, plant cover was negatively correlated to the interquartile range of redox potential at 10 cm depth ($P < 0.05$; Table 4). All soil redox potential variables, except interquartile range of redox potential at 25-cm depth, were strongly correlated with mean and median water-table depth (Table 4).

The eighteen most abundant species displayed a range of distributions in relation to water-table depth and redox potential at 10 and 25 cm depth (Figure 8). The ranges show a large degree of overlap among species and growth forms (i.e., sedges, rush, grasses, forbs) for each variable (i.e., water-table depth, soil redox potential at 10 and 25 cm). However, consideration of the medians and ranges of the three variables together reveal certain distinctions. For example, the range in water-table depth for obligate wetland sedges, *Carex utriculata*, *Carex aquatilis*, and *Carex lanuginosa*, show considerable overlap; however, median redox potential at both 10 and 25 cm depths indicate

that *Carex utriculata* and *Carex aquatilis* occupied locations where the soil conditions were, on average, more reducing than those where *Carex lanuginosa* occurred.

DISCUSSION

Water-Table Depth and Soil Redox Potential

Strong gradients in water-table depth and soil redox potential existed along the near-stream transects at each site. Seasonal dynamics in water-table depth paralleled those of stream stage, with peak flows associated with spring snowmelt resulting in maximum water-table depths in each plant community. During the study period, the seasonal patterns of water-table depth were similar at both sites and consistent from year-to-year (Figure 5). The differences in mean water-table depth between the wet and moist communities and between the moist and dry communities ranged from 16 to 28 cm. Whereas the influence of summer and fall rain storms was detected as a brief increase in water-table depth at a few wells (personal observation; Otting 1998), growing season water-table depth appeared to be largely governed by spring snowmelt, followed by the gradual draining of stored retention water of the basins. Given the limitations of our well-sampling design, we were not able to determine whether the seasonal rise in water-table depth is driven by overbank stream flows or subsurface saturation and seepage during snow melt run-off. However, soil moisture content at different depths in the three plant communities suggests that a combination of these processes influences water-table depth (Dwire 2001).

During low flows, water-table depth was slightly higher in the moist and dry communities at Limber Jim Creek than at West Chicken Creek. Although discharge was over two times as great at Limber Jim Creek during spring high flows (Table 1), much less overland flooding occurred at this site, and high flow water-table depth was slightly lower in the wet and moist communities (Brookshire and Dwire 2003). These differences may be partly explained by characteristics of the two channels. Limber Jim Creek has a higher width-to-depth ratio and is less sinuous than West Chicken Creek (Table 1). At Limber Jim Creek, the streamside wet and moist communities were less extensive. Consequently, mean transect lengths were shorter, and most wells in the moist and dry communities were located closer to the stream than at West Chicken Creek.

Dynamics of soil redox potential followed the seasonal fluctuations in stream stage and water-table depth, particularly in the wet and moist communities. This strong interaction is reflected in significant cor-

relations among water-table depth and redox potential variables (Table 4). When soils in these communities were saturated as a consequence of high flows, soil conditions became anaerobic. In the wet meadow community, soil conditions at 25 cm remained anaerobic throughout the sampling period. Persistent anaerobic conditions were also observed in *Carex nebrascensis* Dewey communities at 30-cm depth in central Nevada (Castelli et al. 2000) and *Carex nebrascensis* and *Carex utriculata* communities at 10- and 30-cm depths in northeast Oregon (Green 1992). Redox potentials increased in the moist meadow community—indicating that the soils became increasingly aerobic—as the water-table declined during the summer months. In the dry meadow communities, which were briefly or never saturated within 30 cm of the surface, redox potentials indicated well-oxidized conditions, with relatively little change through the seasons. These seasonal patterns in water-table depth and associated redox potential measured at Limber Jim Creek and West Chicken Creek are likely representative of montane riparian meadows that occur throughout the western U.S. Similar relationships among seasonal water-table depth, redox potential, and meadow plant communities have been observed in wetland prairies in western Oregon (Finley 1995), riparian meadows in northeast Oregon (Green 1992) and central Nevada (Castelli et al. 2000), and a Colorado fen (Cooper 1990, Cooper et al. 1998).

Plant Species Distribution

Each of the three communities at both sites had similar floristic composition (Table 2), and measures of diversity and wetland prevalence indices (Table 3). For example, the wet communities had the lowest number of species per well location, lowest total number of species, and lowest wetland prevalence index of the three communities. The moist and dry meadow communities at each site also shared similar characteristics. Mean total plant cover was lowest in the wet communities, intermediate in the moist communities, and highest in the dry meadow communities. Despite these similarities, the respective communities were dominated by different species at each site, thus differing in composition and illustrating the diversity of plant assemblages that can occur in riparian meadows (Crowe and Clausnitzer 1997). Differences in composition could be partially explained by the channel characteristics and extent of overland flow in spring at the two study sites, as well as the attributes of the plant species. The occurrence of widespread non-native species, particularly *Poa pratensis* and *Trifolium repens*, likely reflects the grazing history of both sites (Crowe and Clausnitzer 1997), as well as the invasive capacity and persistence of these species. In grazed meadows,

Poa pratensis appears to have a competitive advantage over native species, particularly at lower water-table depths (Martin and Chambers 2001). This non-native species is nearly ubiquitous throughout the western U.S. and may persist for decades in moist and dry meadow sites following the cessation of livestock grazing (Allen-Diaz 1991).

Relations Among Water-Table Depth, Redox Potential, and Plant Species Distribution

The strong correlations of species richness and plant cover with mean water-table depth reinforce the importance of growing season variables in explaining the distribution of meadow vegetation. In most studies of montane riparian ecosystems, water-table depth is measured during a growing season of approximately four months (Halpern 1986, Otting 1998, Law et al. 2000). Although multi-year, seasonal characterization of water-table depth (Figure 5, this study; Allen-Diaz 1991, Stringham et al. 2001) assists in understanding the hydrology of riparian meadows, growing season hydrologic variables are effective explanatory variables for plant species composition (Castelli et al. 2000). Correlations between species richness and mean redox potential were not as strong as those for water-table-depth variables (Table 4), which may be due to the strong correlations between water-levels and redox potential, as well as the high temporal variability in redox potential within each community type.

The zonation and composition of plant communities in riparian meadows reflects the competitive abilities, moisture and nutrient requirements, and stress tolerance of anoxic conditions of individual plant species (Sculthorpe 1967, Blom et al. 1994, Blom and Voesenek 1996, French and Chambers 1996). The temporal variability of water-table depth and reduced soil conditions, as well as the duration of saturation, strongly influences the distribution of meadow species (Castelli et al. 2001). Ranges in water-table depth and redox potential for 18 common species demonstrate large overlap but also a consistent distribution along the hydrologic gradient. In two floodplain meadows in England, Silvertown et al. (1999) found that fine-scale differences in soil moisture and aeration status structured the plant communities and assisted in defining niche separation among species and assemblages. At West Chicken Creek and Limber Jim Creek, the segregation of plant species along the near-stream transects suggests that physiological constraints in response to soil saturation may be largely regulating species distribution. At well locations in the wet meadow communities where mean redox potential was below 300 mV at 10-cm depth, nearly the entire soil profile is anaerobic throughout the year. The distribution of

species in relation to redox potential at 10-cm depth implies that fewer species can tolerate sustained anaerobic soil conditions, whereas the distribution of species in relation to redox potential at 25-cm depth suggests that a greater number of species tolerate anaerobic conditions that occur deeper in the soil profile (Figure 8).

The ranges in water-table depth observed for common species (Figure 8) are similar to those reported in other studies (Halpern 1986, Manning et al. 1989, Allen-Diaz 1991, Cooper 1990, Castelli et al. 2000, Law et al. 2000, Stringham et al. 2001). In this study, the obligate wetland sedges, *Carex utriculata* and *Carex aquatilis*, only occurred in locations where water levels ranged from 20 cm above the surface to -40 cm, which are very similar to the results reported for these species in meadows of south-central Oregon (Padgett 1982). In a meadow in the southern Sierra Nevada, California, water levels associated with *Carex rostrata* Stokes (= *C. utriculata* Boott) remained above the soil surface for the entire season (6 July to 8 November, 1983), although data were collected in a particularly wet year (Halpern 1986). In meadows of western Montana dominated by *Carex utriculata*, Law et al. (2000) reported water levels that ranged from approximately -10 cm to -30 cm. In communities dominated by *Calamagrostis canadensis* in a Colorado fen, water-table depths ranged from 0 to -90 cm during one year and from 0 to -140 cm during the second year (Cooper 1990). In this study, *Calamagrostis canadensis* occurred in locations with water levels ranging from $+5$ to -70 cm, with a median of -38 cm. In meadows of the northern Sierra Nevada, California, Allen-Diaz (1991) reported similar ranges for *Deschampsia cespitosa* (-10 to -80 cm; this study = $+5$ to -80 cm), *Carex lanuginosa* (-15 to -54 cm; this study = $+20$ to -55cm), *Poa pratensis* (-20 to -60 cm; this study = 0 to -85 cm), and *Potentilla gracilis* (-25 to -62 cm; this study = -25 to -85 cm).

The rush, *Juncus balticus*, occurs among numerous habitats in riparian meadows, and published ranges in water-table depth reflect its widespread distribution. Manning et al. (1989) reported water-table depths ranging from 0 to -15 cm depth for a *Juncus balticus* community type in northern Nevada. For 'mesic meadows' in central Nevada that were dominated by *Poa pratensis* -*Juncus balticus*, Castelli et al. (2000) reported water-table depths ranging from 0 to -34 cm at one site and from -90 to -149 cm at another site. In this study, *Juncus balticus* occurred in locations where water levels ranged from the soil surface to approximately -70 cm, with a median water-table depth of -45 cm. These disparate ranges likely reflect the plasticity of *Juncus balticus*, which is widespread throughout the western U.S. These results further sug-

gest that *Juncus balticus* may be misclassified as an obligate wetland species (Reed 1988, 1996) throughout portions of the western U.S. and may be more accurately classified as a facultative wetland species in some regions.

The strong relations between common riparian plant species and water-table depth underscore the potential impact of changes in water-table for riparian plant diversity (Naiman et al. 1993, Naiman and Decamps 1997, Patten 1998). Although alternative state and transition concepts have been invoked to describe potential shifts in riparian meadow plant communities (Stringham et al. 2001), our results show that the distribution of meadow plant species reflect strong short-scale environmental gradients, driven by seasonal water-table depths and resulting soil conditions. Certain species, such as the obligate wetland sedges, occurred within a fairly restricted range of water-table depth, whereas the graminoids *Deschampsia cespitosa*, *Juncus balticus*, and *Poa pratensis* occurred over wide ranges. The overlap in ranges of water-table depth (Figure 8) for individual species suggests that small changes in this hydrologic property could potentially result in shifts in dominance by different species and ultimately replacement or loss of certain species. Because water-table depth in meadow environments is largely determined by seasonal streamflow and stage, stream-channel incision and increased width-to-depth ratios could potentially lead to the disconnection of floodplains from natural hydrologic regimes. Declines in the water table have been cited as a primary cause for degradation of riparian plant communities in incised floodplain reaches (Platts 1983, Platts and Nelson 1989, Crowe and Clausnitzer 1997, Martin and Chambers 2001, Chambers et al. 2004), whereas increases in the water table have contributed to the restoration of meadows (Cooper et al. 1998). The distribution of above- and below-ground biomass is largely determined by species composition in these montane meadows (Toledo and Kauffman 2001, Dwire et al. 2004) and influences riparian functions, such as provision of organic matter to streams and increased stability of stream banks (Dwire 2001, Brookshire and Dwire 2003). Results presented here describe hydrologic conditions that support a composition of native and non-native species, thus increasing our ability to predict plant community changes associated with potential shifts in water-table depth. This knowledge can be used to provide direction for assessment of altered riparian condition due to water or land use, as well as restoration of riparian meadows.

ACKNOWLEDGMENTS

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