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SOIL-PLANT RELATIONS ALONG A SOIL-WATER GRADIENT IN GREAT BASIN RIPARIAN MEADOWS

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Abstract: Throughout the western states, riparian ecosystems have been affected by water diversions or spring and seep developments that decrease the quantity of instream flows and result in lowered water-tables. Water extraction is especially damaging in arid and semi-arid regions where the presence of instream and ground-water flows are crucial to riparian vegetation. We examined the temporal and spatial relationships between hydrologic gradients, vegetation, and soils in two central Nevada riparian meadows in order to identify plant species and environmental variables that can serve as indicators of water-table status. Species frequency and aerial cover, ground-cover composition, depth to water-table, and soil morphological and physical properties were measured along hydrologic gradients within two riparian meadow complexes. TWINSPAN, cluster, and multivariate discriminant analyses classified the vegetation into four ecosystem types. These occurred along the hydrologic gradient and included, from wettest to driest, wet meadow, mesic meadow, dry meadow, and basin big sagebrush meadow types. Canonical correspondence analysis (CCA) indicated that the variables most strongly related to plant species frequency within both meadows were those associated with depth to water-table. Integrative variables, including the number of days that depth to water-table was less than 30 cm and less than 70 cm, and degree-days of anaerobiosis were most closely related to the wet and mesic meadow vegetation types. The range in depth to water-table, elevation, and aerial cover of gravel and litter were all related to the dry and sagebrush meadow vegetation types. Indicator species associated with particular water-table regimes were identified for each vegetation type based on two-way ordered tables. *Carex nebrascensis*, an obligate riparian species, occurred at water-tables of 0–30 cm below the surface and was the most reliable indicator of shallow water-tables. Large temporal and spatial variability in water-table depths for the mesic and dry meadow types suggests that species associated with these types could be used only to indicate broad ranges in water-table depth. Integrative environmental variables that incorporated the temporal variation in water-tables (i.e., days that depth to water-table was less than 30 and 70 cm; degree days of anaerobiosis; range in water-table depth during the growing season) demonstrated closer relationships to the vegetation types than water-table alone. They were also more sensitive to the spatial and temporal differences in water-tables than individual plant species or vegetation types. Environmental and integrative environmental variables may respond more quickly to changes in local hydrology than plant species and are possibly more sensitive indicators of both current water-table status and potential vegetation.

Key Words: riparian, water-table, degree day, redox potential, vegetation classification, indicator species

INTRODUCTION

Riparian vegetation plays a critical role in maintaining riparian ecosystem function by promoting stream bank stability and water quality, reducing the potential for erosion, increasing the storage of nutrients and water, and providing forage and habitat for wildlife (Knight and Bottorff 1984, Knopf et al. 1988, Rood et al. 1995, Gillian and Brown 1997). In riparian ecosystems in the western U.S., water supply is a function of both instream flows (Rood and Mahoney 1990, Stromberg et al. 1993) and ground-water available from springs and seeps (Allen-Diaz 1991). Stream diversion, development of springs and seeps, and ground-water pumping can result in both direct and indirect effects on riparian water tables. Water-table declines can cause shifts in plant composition from mesic to xeric species and decreases in the overall extent of riparian ecosystems. The loss of riparian vegetation can affect stream channel stability by increasing bank erosion and resulting in channel degradation or aggradation (Rosgen 1996).

To determine the hydrologic regime required to support riparian vegetation, it is necessary to understand the relationships between water availability, soil characteristics, and vegetation. A strong connection exists between water-table depth, soil-water content, and wetland riparian species (Merendino et al. 1990, Allen-Diaz 1991, Stromberg et al. 1996, Weixelman et al. 1996, Yabe and Onimaru 1997). In Sierra Nevada meadows, hydric vegetation occurs where the water-table is 0–40 cm below the surface, and mesic vegetation exists where the water-table is 20–80 cm below the surface (Allen-Diaz 1991). Along the San Pedro River in Arizona, obligate wetland herbaceous species are found where the water-table is 0–25 cm below the surface (Stromberg et al. 1996). Obligate and facultative wetland trees occur where the water-table is 140–380 cm, and facultative wetland shrubs are found where the water-table is 120–150 cm below the surface (Stromberg et al. 1996).

Soil morphological, physical, and chemical properties are closely related to both hydrologic regimes and plant species distributions. The thickness of organic horizons, soil particle sizes, and levels of available nutrients are all highly responsive to hydrologic regimes (Naiman et al. 1994, Chambers et al. 1999). Oxidation-reduction (redox) potentials indicate electron availability (Faulkner et al. 1989), the degree of anaerobiosis, and the level of biological activity (Pearcy et al. 1989). They are important in determining plant species distributions (Sanchez et al. 1998) and have been used to classify wetland ecosystems (Faulkner and Patrick 1992, Megonial et al. 1993). In addition, soil temperatures are influenced by the level and duration of saturation and can affect plant species distributions due to their effects on chemical reactions and biological processes (Ratliff and Harding 1993).

In arid and semi-arid systems where the variability in hydrologic regimes is high both among and within years (e.g., Martin 1999), integrative environmental variables can be used to incorporate the temporal dynamics of ecosystems. Integrative variables include soil moisture content during the growing season and number of degree-days (Naiman et al. 1994, Stohlgren and Baccard 1997). Degree-days have traditionally been used to examine the effects of temperature over a given time period in phenological studies (Wang 1960). However, temperature is seldom the only controlling variable and degree days can be used in conjunction with other environmental variables. For example, redox potentials and soil temperatures can be used to calculate the degree days of anaerobic soil conditions, providing an integrative measure of the stress to which riparian vegetation is exposed (Naiman et al. 1994).

Plants have often been used as indicators of environmental conditions in wetland riparian ecosystems, including pH and water level in peatlands (Jeglum 1971) and ground- or surface- water sources in wetlands (Goslee et al. 1997). Because many plant species or vegetation types show close associations with particular water-table regimes, they can serve as indicators of ground-water status in riparian ecosystems. Herbaceous species are often more closely associated with a particular level of soil moisture and may be more sensitive indicators of water-table conditions than woody or shrub species (Stromberg et al. 1996).

Few studies have identified both plant species and environmental variables that can be used as indicators of ground-water conditions in riparian ecosystems (but see Allen-Diaz 1991, Stromberg et al. 1996). In this study, we examined the relationships among shallow subsurface hydrology, plant species composition, and soil morphological and physical characteristics in two central Nevada riparian meadow complexes. The objectives were to (1) evaluate the temporal and spatial relationships among the hydrologic gradients, riparian vegetation, and soils; (2) determine the environmental variables that are closely associated with and that accurately classify the vegetation types; and (3) identify both plant species and environmental variables that can serve as indicators of ground-water conditions.

METHODS

Study Site Description

Two meadows complexes adjacent to perennial stream systems were selected in the summer of 1997 that represented typical Great Basin riparian ecosystems. The meadows were in the Big Creek drainage in the Toiyabe Mountain Range (elevation 2146 m, 39°19′28″N, 117°7′16″W) and in the Corral Canyon drainage in the Toquima Mountain Range (elevation 2377 m, 39°7′13.5″N, 116°48′38.6″W) in Nevada, USA. Both sites are within the Austin Ranger District of the Humboldt-Toiyabe National Forest. Basins in the Toiyabe and Toquima Mountain Ranges are semi-arid and receive precipitation primarily in the form of snow (Weixelman et al. 1996). The majority of streams in these ranges occur within narrow valleys, are characterized by low flows, and show signs of incision. During the two years of study, 1997 and 1998, Big

Table 1. Precipitation for 1997 and 1998 at the Big Creek and Corral Canyon study sites and Snotel stations. Overwinter is October–April, and growing season is May–September. Values are totals (cm).

Drainage	Site	Period	1997	1998	Long-term Average
Big Creek	Study site	Overwinter	34	56	
		Growing Season	16	22	
		Total	**50**	**78**	
	Snotel station	**Total**	**65**	**106**	**48**
Corral Canyon	Study site	Overwinter	6	32	
		Growing Season	10	11	
		Total	**16**	**43**	
	Snotel station	**Total**	**98**	**105**	**51**
Austin, NV		**Total**	*	*	**38**

* Not available.

Creek received 50 cm and 78 cm of precipitation, respectively, while Corral Canyon received 16+ cm and 43 cm of precipitation (Table 1). The long-term annual average precipitation obtained from NRCS Snotel Stations in Big Creek and Corral Canyon is 48 cm and 51 cm, respectively, while in nearby Austin, NV, it is 38 cm. The low overwinter precipitation values at the Corral Canyon site compared to the Snotel Stations in 1997 indicate a rain gage malfunction. The highest and lowest daily flows for Big Creek in 1997 were 0.19 m^3/s and 0.11 m^3/s, respectively. In 1998, the highest and lowest daily flows were 1.50 m^3/s and 0.38 m^3/s. Stream flow in Corral Canyon was low (<0.01 m^3/s low flow).

In central Nevada, geomorphology strongly influences the characteristics of stream reaches and, consequently, soils and vegetation. Alluvial fans or other geomorphic features, such as faults or bedrock, block down valley subsurface flows resulting in locally elevated water-tables and meadow ecosystems (Chambers et al. 1998). In areas with elevated water-tables, stream discharges increase due to incoming flows from adjacent water-tables. Within Big Creek and Corral Canyon, alluvial fans are present at the base of the study systems. In both cases, it appears that stream discharge increases in these reaches. Depositional areas occur immediately upstream from the fans that are characterized by low gradients and finer textured soils (Chambers et al. 1999). Meadow complexes exist in these regions along hydrologic gradients that have water-tables ranging from the soil surface at the lowest elevation upstream of the fans to depths of 400 cm or greater at the upper end of the meadow complexes.

The Big Creek and Corral Canyon meadow complexes are characterized by four primary ecosystem types: wet or *Carex nebrascensis* meadow, mesic meadow, dry meadow, and basin big sagebrush meadow (Weixelman et al. 1996). The dominant species within the wet meadow type are *C. nebrascensis, Juncus balticus,* and *Alopecurus aequalis* Sobol. This vegetation type occurs where depth to water-table is within 30 cm of the surface (Chambers et al. 1999). The mesic meadow type includes *Poa pratensis* ssp. *pratensis, J. balticus, Agrostis stolonifera,* and *Hordeum brachyantherum* or *Iris missouriensis.* This type occurs where depth to water-table ranges from 30 to 80 cm (Chambers et al. 1999). The dry meadow type consists of *Muhlenbergia richardsonis* ssp. *richardsonis, Poa secunda* ssp. *juncifolia, Elymus trachycaulus* ssp. *trachycaulus* (L.) Gould ex Shinn., and *Carex douglasii* and occurs where depth to water-table ranges from 120 to 160 cm (Linnerooth 1999). The basin big sagebrush vegetation type is comprised of *Artemisia tridentata* Nutt. ssp. *tridentata, Leymus cinereus Elymus elymoides,* and *P. secunda* ssp. *secunda* and is restricted to areas where depth to field capacity is greater than 100 cm (Weixelman et al. 1996).

Study Design

To characterize the individual vegetation types and the transition zones between them, transects (n~20) were located perpendicular to the stream at 15-m intervals throughout the meadow at each site. Depending on the width of the riparian corridor and the vegetation types encountered, two to four sample locations were selected along each transect. There were 52 sample locations at Big Creek and 66 sample locations at Corral Canyon. At each sample location, depth to water-table, individual species frequency and aerial cover, and total aerial cover of vegetation, litter, bare ground, rock and gravel were examined. At a subset of sample locations (29 in Big Creek and 20 in Corral Canyon), soil-water content, depth to saturation, temperature, and oxidation-reduction potential (redox) were measured. Also, soil types were determined and soil profiles characterized within each of the four vegetation

Vegetation

Species frequency and aerial cover were sampled in areas adjacent to all sample locations (within 50 cm) in three clustered, 0.1 m^2 quadrats. Frequency was determined from the nested, rooted frequency method using a nested plot frame (Weixelman et al. 1990). Specifically, species rooted within the smallest plot (0.01 m^2) were assigned a 4, those rooted in the 0.04 m^2 plot a 3, those in the 0.07 m^2 plot a 2, and those in the 0.1 m^2 plot a one. Percentage aerial cover of each species was ocularly estimated for entire 0.1 m^2 quadrats using the following codes: 1 = 0–2%; 2 = 2–5%; 3 = 5–15%; 4 = 15–25%; 5 = 25–35%; 6 = 35–45%; 7 = 45–55%; 8 = 55–65%; 9 = 65–75%; 10 = 75–85%; 11 = 85–95%; and 12 = 95–100% (Chambers 1983). At each sample location, ground-cover was characterized according to basal vegetation, litter, bare ground, gravel, rock, and dung using point frame techniques (Chambers 1983). In the sagebrush dominated areas, 1-m × 1-m plots were placed over the smaller plots and sagebrush presence or absence was recorded. Vegetation sampling occurred for two weeks in mid-July of 1998 when plants were in flower and could be readily identified.

Hydrologic Regime

At both sites, piezometers were installed at each sample location to monitor ground-water levels. In July 1997, piezometers slotted at the base were installed to 20 cm below the water-table or, if the water-table was not reached, until the piezometer could be driven no deeper due to rocky substrate (approximately 6 m). Nested piezometers spaced about 30 cm apart were installed at sample locations where impermeable soil layers or artesian conditions occurred to ensure that the actual water-table elevation was being measured (about 20 sites within each meadow). Depth to ground-water was measured using an electronic water-level meter at three- week intervals in fall 1997 (September and October) and throughout the 1998 growing season and fall (May–October). During the remainder of both years, measurements were taken monthly when sites were accessible. Elevations for each piezometer location were surveyed using a Topcon Total station.

Soil Characteristics

Soil profiles were characterized and soil types determined in summer 1998 from soil pits located in each vegetation type. Two additional soil cores in the vicinity of each soil pit were examined to ensure the accuracy of the soil descriptions. Soil pit characterization included determining soil taxa, horizon depths, matrix color, mottle color, and root size and abundance (Soil Survey Staff 1975, 1992).

Three replicate soil samples, one from the soil pit and one from each core, were collected from each horizon, and soil particle size and water retention were quantified in the lab. Samples were sieved to remove coarse fragments, and particle size distributions were determined by running samples through nested sieves to the <2-mm fraction. The d50 and d80 particles sizes were calculated for each replicate. Soil-water retention (−0.03 and −1.5 MPa) was determined for the O, A, and B horizons, when present, from the <2-mm fraction using methods described by Klute (1986). These pressures indicate the amount of water available at field capacity and permanent wilting point for the different soil types.

Redox potential, soil moisture content, depth to saturation, and soil temperature were sampled within a 50 cm radius of the piezometer locations at three-week intervals in June–October 1998. This period included spring high flows, summer low flows, and fall recharge. Redox potentials were measured following methods outlined by Faulkner et al. (1989), Mueller *et al.* (1985), and Veneman and Pickering (1983). Platinum electrodes and salt bridges were placed at a depth of 30 cm and measurements taken using a Ag/AgCl reference electrode and portable voltmeter. Equipment was tested for accuracy prior to installation and was given seven days to equilibrate *in situ* before the first measurements were taken (Light 1972). If redox potentials were less than 300 mV, soils were considered to be anaerobic (Faulkner and Patrick 1992). Soil temperatures were measured at 30 cm depths and within 30 cm of the redox potential apparatus using thermocouples. Thermocouple measurements were made using a type TC thermocouple thermometer. Redox potentials and soil temperatures were used to calculate the number of degree days of anaerobiosis for each location using the formula (Wang 1960): number of days since the beginning of anaerobiosis* (temperature in °C−4°C).

Gravimetric soil-water content was measured at three-week intervals in June–October 1998 by extracting 50-ml soil cores from the 0–10 cm, 25–35 cm, and 55–65 cm depth intervals using an auger. The cores were dried at 105°C for 24 hours (Faulkner et al. 1989), and soil-water content was determined. In the process of extracting the soil cores, depth to soil saturation as identified by a shiny, moist soil appearance was recorded. If depth to saturation was not reached by 65 cm, no value was recorded.

Statistical Analyses

Multivariate statistical analyses were used to examine relationships among the vegetation samples based on species frequency and aerial cover values, and among the vegetation results and environmental variables (depth to water-table, elevation, redox potential, soil temperature, degree-days of anaerobiosis, and soil moisture content). Integrative variables (number of days in the growing season that depth to water-table was less than 30 cm and 70 cm, range in depth to water-table, redox potential, temperature, and moisture content during the growing season, and number of degree days of anaerobiosis during the growing season), and ground-cover percentages were also included in the analysis. The number of days the water-table was less than a certain depth was extrapolated based on the water-level hydrographs. Variables with three samples per sample location were averaged to establish one set of values for each location. The results from the absolute values for depth to water-table, redox potential, temperature, and moisture content were not significant and were eliminated from subsequent analyses.

Two-way indicator species analysis (TWINSPAN, Hill 1979, McCune and Mefford 1995) and cluster analysis (Sneath and Sokal 1963, Romesburg 1984, McCune and Mefford 1995) were used to first classify the vegetation samples into plant community groups based on both species frequency and aerial cover values. Results were similar between classification methods for both data sets. Thus, TWINSPAN analysis based on species frequency was used for the remaining analyses. TWINSPAN is based on division of sequential reciprocal averaging ordinations and separated sample locations into groups according to the presence or absence of species. A multivariate discriminant analysis by backward selection followed as a verification of classification results by independent analyses based on the raw and integrated environmental variables (Grieg-Smith 1983, Ludwig and Reynolds 1988, SAS 1990). This helped to determine the relative importance of each environmental variable in explaining the TWINSPAN groups that were based on plant species composition. Following the discriminant analysis, one-way analysis of variance was run to determine which identified variables differed significantly for the groups of sites or vegetation types.

Canonical correspondence analysis (CCA) (ter Braak 1986, 1987, McCune and Mefford 1995), a direct gradient analysis, was used next to ordinate the vegetation based upon its nested frequency values while directly incorporating the influence of the environmental variables. CCA assumes that no correlation exists between environmental variables and that there is linearity in the relationships between the environmental variables and vegetation responses on the ordination axes (Grieg-Smith 1983, Palmer 1993). Default options were chosen so as not to weight rare species. In the multivariate discriminant analysis all data were used. Due to the limitations of CCA, vegetation and environmental data were restricted to those measurements with greater than zero variance. Results of the analyses were compared to each other to identify important environmental variables and those most significant in structuring the vegetation types. Because of potential entry order effects (Tausch et al. 1995), the data were re-ordered, and results were examined for inconsistencies.

In addition to the above analyses, a two-way repeated measures analysis of variance with repeated measures on date was used to examine differences between the vegetation types in depth to water-table, redox potential, and temperature (SAS 1990). A three-way repeated measures analysis of variance with repeated measures on date and depth was used to examine differences in soil moisture content between vegetation types. Mean comparisons used protected least squared denominators.

RESULTS

TWINSPAN Classification of Vegetation Types

TWINSPAN classification of the nested frequency data for each site yielded four vegetation types. The four vegetation types corresponded to the wet meadow type, mesic meadow type, dry meadow type, and basin big sagebrush meadow type classified by Weixelman et al. (1996). Two-way ordered tables for each site illustrated the relationships between species and sample locations (Table 2). At both sites, *C. nebrascensis* dominated the wet meadow type. At Big Creek, *J. balticus* was classified into the wet meadow type, while in Corral Canyon, *J. balticus* was classified into the mesic meadow type. Other species within either the wet or mesic meadow type included *A. stolonifera, Deschampsia caespitosa* and *Festuca rubra.* At both sites, *P. pratensis* ssp. *pratensis* was classified into the mesic meadow type. *Taraxacum officinale, Achillea millefolium, Medicago lupulina,* and *Equisetum laevigatum* also occurred within the mesic meadow type. The dry meadow and sagebrush vegetation types at Big Creek were dominated by *Agropyron intermedium* because the drainage had been aerially seeded with this and other introduced species following a fire in the 1960s. At Corral Canyon, the dry meadow type was dominated by *Carex praegracilis* and *A. intermedium* but also included *P. secunda* ssp. *juncifolia* and *M. richardsonis* ssp. *richardsonis. Carex douglasii* and *Arabis divaricarpa* were classified into the sagebrush

Table 2. Species associated with the different vegetation types for the Big Creek and Corral Canyon study sites. Groups are based upon divisions in the TWINSPAN classification two-way ordered tables.

Vegetation Type	Big Creek	Corral Canyon
Wet meadow	*Carex nebrascensis* Dewey	*Agrostis stolonifera* L.
	Eleocharis macrostachya Britt. ex Small	*Carex nebrascensis* Dewey
	Epilobium glaberrimum Barbey	*Carex simulata* Mack.
	Glyceria elata (Lam.) A. Hitchc.	*Deschampsia caespitosa* (L.) Beauv.
	Juncus balticus Willd.	*Epilobium glaberrimum* Barbey
	Mimulus guttatus DC.	*Festuca rubra* L.
	Potentilla anserina L.	*Stellaria media* (L.) Vill.
		Trifolium longipes Nutt. in T. & G.
		Trifolium wormskioldii Lehm.
Mesic meadow	*Achillea millefolium* L.	*Achillea millefolium* L.
	Agrostis stolonifera L.	*Aster occientalis* (Nutt.) T. & G.
	Aster occidentalis (Nutt.) T. & G.	*Cirsium drummondii* S. L. Welsh
	Carex praegracilis W. Boott	*Equisetum laevigatum* A. Br.
	Cicuta douglasii (DC.) J. Coulter & Rose	*Hordeum brachyantherum* Nevski
	Equisetum laevigatum A. Br.	*Iris missouriensis* Nutt.
	Medicago lupulina L.	*Juncus balticus* Willd.
	Poa pratensis ssp. *pratensis* L.	*Poa pratensis* ssp. *pratensis* L.
	Rumex crispus L.	*Potentilla gracilis* Dougl. ex Hook.
	Taraxicum officinale Weber ex Wiggers	*Rosa woodsii* Lindl.
	Urtica dioicia L.	*Stellaria longipes* Goldie
	Viola palustris L.	*Taraxicum offinale* Weber ex Wiggers
		Viola palustris L.
Dry meadow	*Agropyron intermedium* (Host) Beauv.	*Agoseris retrorsa* (Benth.) E. Greene
	Carex microptera Mack.	*Agryopyron intermedium* (Host) Beauv.
	Gayophytum diffusum T. & G.	*Carex praegracillis* W. Boott
	Lesquerella tenella A. Nels.	*Muhlenbergia richardsonis* (Trin.) Rydb.
		Poa secunda ssp. *juncifolia* (Scribner) R. Soreng
		Potentilla gracilis Dougl. ex Hook.
Sagebrush	*Arabis divaricarpa* A. Nels.	*Amsinckia tessellata* A. Gray
	Carex douglasii F. Boott in Hook.	*Arabis divaricarpa* A. Nels.
	Elymus glaucus Buckley	*Artemisia tridentata* ssp. *tridentata* Nutt.
		Carex douglasii F. Boott in Hook.
		Chrysothamnus nauseousus (Pallas) Britt.
		Chrysothamnus viscidiflorus (Hook.) Nutt.
		Collinsia parviflora Lindley
		Descurania sophia (L.) Webb
		Elymus elymoides (Raf.) Swezey
		Gayophytum diffusum T. & G.
		Leymus cinereus (Scribner & Merr.) A. Löve
		Poa secunda ssp. *secunda* Presl

type at both sites. In addition, *L. cinereus*, *P. secunda* ssp. *secunda*, *Descurania sophia*, *E. elymoides*, and *A. tridentata* ssp. *tridentata* were present in the sagebrush type at Corral Canyon.

Hydrologic Regime

Precipitation was lower in 1997 than 1998 (Table 1). Discharge in Big Creek reflected these differences, with high flows of 0.19 m^3/s in 1997 and 1.5 m^3/s in 1998. In 1998, depths to water-table differed significantly between vegetation types and dates at Big Creek (df = 3,114, F = 6.56, p = 0.0025 and df = 5,114, F = 4.94, p = 0.0004, respectively) and at Corral Canyon (df = 3,74, F = 11.28, p = 0.0004 and df = 5,74, F = 3.79, p = 0.0041, respectively) (Figure 1). Depth to water-table in the wet meadow vegetation type ranged from 0 to 21 cm in Big Creek and 0 to 30 cm in Corral Canyon. Within the mesic meadow type, depth to water-table ranged from 0 to 34 cm in Big Creek and 90 to 149 cm in Corral Canyon. Depth to water-table in the dry meadow type ranged from 30 to 55 cm in Big Creek and 133

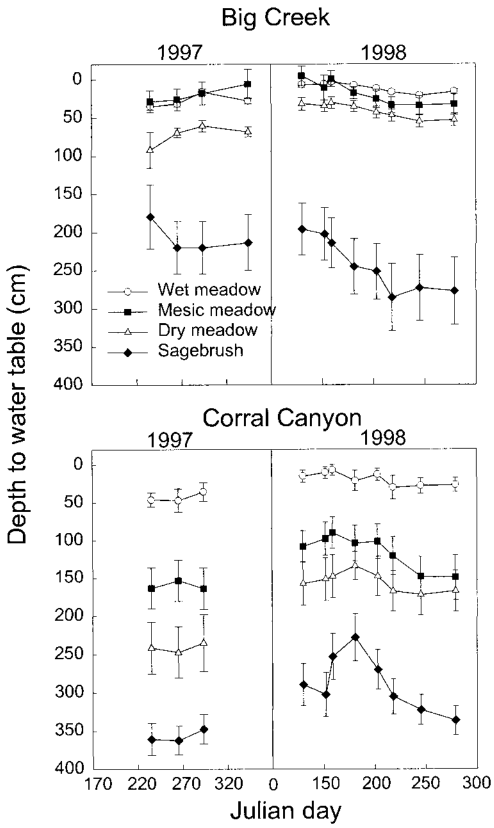

Figure 1. Depth to water-table for Big Creek and Corral Canyon in 1997 and 1998. Values are mean ± S.E.

to 172 cm in Corral Canyon. Within the sagebrush type, depth to water-table was consistently deep and ranged from 196 to 400 cm and greater in Big Creek and 228 to 400 cm and greater in Corral Canyon. Sample locations in the wet meadow had the shallowest depths to water-table and least variation at both sites, with the exception of December 1997 and May-early June 1998 at Big Creek. At both sites, the deepest depths to water-table and greatest variation were in the sagebrush type. There was less distinction in depth to water-table among vegetation types in Big Creek than in Corral Canyon. Also, within the two sites, variation in the depth to water-table increased as depth increased (Figure 1).

Maximum depth to water-table for the wet and mesic meadow types was reached in early September, while the dry meadow and sagebrush types reached maximum depths in early October at both the Big Creek and Corral Canyon sites (Figure 1).

Soil Characteristics

Morphology. Soils were classified as mollisols, specifically cryoborolls in Big Creek and haplocryolls in Corral Canyon (Table 3). The organic matter present in these soil types creates a soft soil of dark color and indicates a history of productive fluvial ecosystems. Soils of the wet meadow type had O_e and O_i horizons and no B horizons. Roots were most abundant in the O_e, O_i, and A horizons. Soils of the mesic meadow type had shallow A horizons at both sites and a buried A horizon in Corral Canyon. Redoximorphic features were present in the B and C horizons of these soils, and roots were most abundant in the A1 and A horizons. Soils of the dry meadow type differed between sites, with deep A horizons in Big Creek and a shallow A horizon in Corral Canyon. Like the mesic meadow soils, there was a buried A horizon in the dry meadow soils of Corral Canyon. Redoximorphic features were present in the C horizons of Big Creek and the buried A horizon of Corral Canyon dry meadow soils. Soils of the sagebrush type differed between sites. In Big Creek, there were no B or C horizons, while A, B, and C horizons existed in Corral Canyon. Soil particle size throughout the profile was more consistent in Big Creek soils than in Corral Canyon. In Big Creek, the d80 particle size diameter ranged from <2 mm to 13.2 mm, while the d50 particle size diameter ranged from <2 mm to 6.68 mm across the vegetation types (Table 3). Coarse material was prevalent in Big Creek soils for all four vegetation types, with the dry meadow and sagebrush types having the largest diameter material. In Corral Canyon, d80 particle size diameter was <2 mm in all but the sagebrush type, which ranged from 4.7 to 6.68 mm. The d50 particle size diameter in Corral Canyon was <2 mm across the vegetation types.

At both sites, root size decreased with increasing depths with the exception of coarse roots in lower soil horizons of the sagebrush type in Corral Canyon (Table 3). Likewise, root abundance was greatest at the soil surface and decreased with increasing depth. Soil moisture holding capacities varied between vegetation types (Table 3). Specifically, soil moisture holding capacities were greatest in soils of the wet meadow type and lowest in the sagebrush vegetation type at both sites. Soil moisture holding capacity of the mesic meadow soils were greater than those of the dry meadow in Big Creek, while in Corral Canyon mesic and dry meadow soils demonstrated the reverse trend.

Redox Potential and Temperature. Redox potentials differed significantly among vegetation types and dates in Big Creek ($df = 3{,}114$, $F = 12.64$, $p < 0.0001$ and $df = 5{,}114$, $F = 5.11$, $p = 0.0003$, respectively) and among vegetation types in Corral Canyon ($df = 3{,}74$, $F = 15.27$, $p < 0.0001$) (Figure 2). Although precipitation amounts differed between Big Creek and Corral Canyon, sample locations in the wet meadow vegetation type at both sites were consistently the most anaerobic (negative redox potential) throughout the 1998 sampling period. In Big Creek, sample locations in the

Table 3. Soil descriptions and characterizations for the Big Creek and Corral Canyon study sites. Root size (diameter) vf = very fine (<1 mm), f = fine (1–2 mm), m = medium (2–5 mm), and c = coarse (5–10 mm). Root abundance/decimeter² 3 = many (>100), 2 = common (10–100), and 1 = few (<10).

Site	Vegetation Type	Soil Taxa	Horizon	Depth (cm)	Matrix Color (moist)	Mottle Color	Root Size & Abundance	D80 (mm)	D50 (mm)	Moisture Content at −0.3 MPa	Moisture Content at −1.5 MPa	Moisture Holding Capacity (%)
Big Creek	Wet meadow	Aquic cryoboroll	Oe	0–19	10YR2/1		3vf 3f 2m	<2	<2	74.73	16.45	58.28
			A	19–32	10YR2/1		3vf 2f	4.7	<2	54.33	8.37	45.96
			2A	32–60	10YR2/1		1 vf 1f	6.68	<2	34.59	5.67	28.92
			3Cg	60–76	10GY5/1			6.68	<2			
			4Cg	76–104	10YR3/2			6.68	<2			
	Mesic meadow	Aquic cumulic cryoboroll	A1	0–8	10YR2/1		2vf 2f 1m	6.68	<2	47.08	11.11	35.97
			A2	8–30	10YR2/1		2vf 1m	6.68	<2	36.93	7.14	29.79
			2Bg1	30–48	10YR3/2	10YR4/6		9.42	2.00	32.70	5.19	27.51
			2Bg2	48–73	10YR3/2	7.5YR4/4		13.2	4.70			
			3Cg	73–84	5GY3/1	7.5YR4/6		13.2	2.00			
	Dry meadow	Aquic cryoboroll	A1	0–15	10YR2/2		2vf 1f	9.4	<2	13.04	4.74	8.3
			A2	15–30	10YR2/1		1vf	13.2	2.00	11.55	5.08	6.47
			A3	30–45	10YR2/2		1vf	11.2	<2	10.79	4.61	6.18
			Bw1	45–52	10YR3/1		1vf	6.68	<2			
			Bw2	52–67	10YR3/1		1vf	11.2	<2			
			C	67–91	10YR3/2	7.5YR5/6		13.2	2.00			
			Cg	91–107	10YR3/2	7.5YR5/6		13.2	2.00			
	Sagebrush	Pachic cryoboroll	A1	0–23	10YR2/1		2vf 1f	11.2	6.68	12.92	6.26	6.66
			A2	23–42	10YR2/2		1vf	11.2	2.00	11.49	4.81	6.68
			2A	42–55	10YR2/2		1vf	13.2	2.00	11.58	5.28	6.3
			3A	55–91	10YR3/1		1vf	11.2	2.00			
			3Ac	91–98	10YR3/1			11.2	2.00			
Corral Canyon	Wet meadow	Haplocryoll	A	0–14	10YR2/1		3vf 2f 2m	<2	<2	77.57	11.10	66.65
			2Oi	14–31	10YR2/2		2vf 1f	<2	<2	64.43	8.00	56.43
			3A	31–55	10YR2/2		1vf 1f	<2	<2	92.65	10.84	81.81
			4Oe	55–72	10YR2/2		1vf	<2	<2			
			5A	72–100	10YR3/1		1m	<2	<2			
			6Oi	100–118	10YR3/3		1f	<2	<2			
			7A	118–130	10YR3/1		1f	<2	<2			
	Mesic meadow	Aquic cumulic haplocryoll	A	0–14	10YR2/2		3vf 2f 1m	<2	<2	11.97	6.20	5.77
			2B	14–28	10YR2/1		1vf	<2	<2	10.20	4.66	5.54
			3Bg	28–52	10YR3/1	7.5YR4/6	1vf	<2	<2	11.46	4.98	6.48
			4A	52–80	10YR2/1		1vf	<2	<2			
			5C1	80–107	10YR3/1	10YR3/4	1vf	<2	<2			
			6C2g	107–128	10YR3/2		1vf	<2	<2			

Table 3. Continued.

Site	Vegetation Type	Soil Taxa	Hori-zon	Depth (cm)	Matrix Color (moist)	Mottle Color	Root Size & Abundance	D80 (mm)	D50 (mm)	Moisture Content at −0.3 MPa	Moisture Content at −1.5 MPa	Moisture Holding Capacity (%)
	Dry meadow	Pachic haplocryoll	A	0–11	10YR2/2		3vf 3f 1m	<2	<2	14.12	6.30	7.82
			Bw	11–25	10YR2/2		1vf	<2	<2	14.59	4.48	10.11
			2B	25–57	10YR2/1		1vf	<2	<2	11.27	5.58	5.69
			3A	57–85	10YR2/1	10YR3/3	1vf	<2	<2			
			3C	85–110	10YR3/1			<2	<2			
	Sagebrush	Pachic haplocryoll	A	0–12	10YR2/2		2vf 1f 1m	4.7	<2	8.39	3.93	4.46
			Bw	12–28	10YR2/1		1vf 1f 1c	6.68	<2	10.48	3.19	7.29
			2A	28–52	10YR3/1		1vf 1c	4.7	<2	13.09	3.82	9.27
			2C	52–68	10YR3/3			6.68	<2			

mesic meadow and sagebrush vegetation types became aerobic (positive redox potential) early in the growing season, while in Corral Canyon, the dry meadow and sagebrush type sample locations became aerobic early. Soil temperatures differed significantly among dates in Big Creek (df = 5,114, F = 264.31, $p < 0.0001$) and among vegetation types and dates in Corral Canyon (df = 3,74, F = 8.12, p = 0.0019 and df = 5,74, F = 465.48, $p < 0.0001$, respectively) (Figure 3). An interaction between vegetation type and date at both sites was probably due to the individual response of each vegetation type to changes in temperature over time. The sagebrush vegetation type at both sites had the largest range in temperature during the sampling period. In Big Creek, soils of the mesic meadow and sagebrush vegetation types reached peak temperatures earlier than those in the wet and dry meadow vegetation types. In Corral Canyon, soils of the wet meadow, mesic meadow, and sagebrush vegetation types reached peak temperatures prior to soils of the dry meadow type. At all dates, the dry meadow type demonstrated the warmest temperatures. Redox potential and temperature did not differ as much between vegetation types in Big Creek as in Corral Canyon.

Moisture Content. Differences in soil moisture content were significant among vegetation type, date, and depth at Big Creek (df = 3,161, F = 13.58, $p < 0.0001$; df = 4,161, F = 5.22, p = 0.0008; and df = 2,161, F = 6.39, p = 0.0037, respectively) and among vegetation types and dates for Corral Canyon (df = 3,127, F = 6.20, p = 0.0054 and df = 4,127, F = 2.76, p = 0.0352, respectively) (Figure 4). There were significant interactions between vegetation type and depth (df = 6,161, F = 6.48, $p < 0.0001$) and date and depth (df = 8,161, F = 2.23, p = 0.0280) in Big Creek, while in Corral Canyon, significant interactions occurred between vegetation type and depth (df = 6,127, F = 2.67, p = 0.0322) and vegetation type, depth, and date (df = 24,127, F = 1.67, p = 0.0371). Wet meadow soils had the greatest percent soil moisture at all three depths and decreased with depth at both sites, with the exception of one sampling point in Corral Canyon at the third depth (Figure 4). As observed in the redox results, there were smaller differences in soil moisture content between vegetation types in Big Creek than in Corral Canyon. In Big Creek, soil moisture content overlapped between the mesic and dry meadow types at all depths and dates, but there was little overlap in soil moisture content values between the four vegetation types in Corral Canyon. Soil moisture content was consistently less in dry meadow soils than those of the sagebrush type.

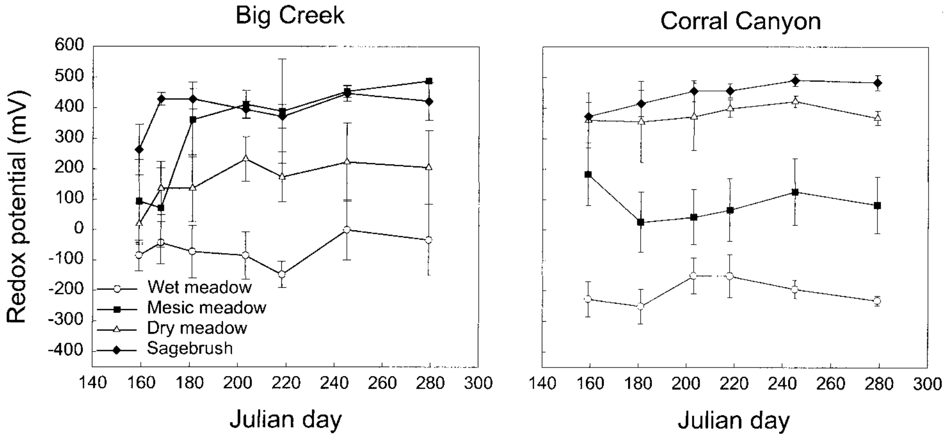

Figure 2. Oxidation-reduction (redox) potential at 30 cm for Big Creek and Corral Canyon in 1998. Values are mean ± S.E.

Relationships Among Vegetation Types and Environmental Variables

Discriminant Analysis. Multivariate discriminant analysis based on the environmental and vegetation variables correctly verified 100 percent of the sample locations in the wet meadow, mesic meadow, and sagebrush vegetation types in Big Creek from the TWINSPAN classification using plant species composition. For the dry meadow vegetation type, one of the five sample locations was included in the wet meadow vegetation type by discriminant analysis. The number of days that depth to water table was less than 30 cm, degree days of anaerobiosis, percent cover of litter, vegetation, bare ground, and gravel, and elevation all were significant variables ($p \leq 0.01$) in the discriminant analysis (Table 4). The number of days the depth to water table was less than 30 cm differed between the vegetation types (df = 3,22, $F = 6.77$, $p < 0.0021$). Sample locations in the wet meadow type had greater number of days where the depth to water table was less than 30 cm than those in the sagebrush vegetation type ($p \leq 0.05$). Vegetation types also differed in the percent cover of bare ground (df = 3,22, $F = 5.78$, $p < 0.0045$). Wet meadow vegetation type locations had greater percent cover of bare ground than those in the dry meadow and sagebrush vegetation types ($p \leq 0.05$). The elevation above the reference base differed between vegetation types (df = 3,21, $F = 17.51$, $p < 0.0001$). Sample locations in the wet meadow type were lower than those in the sagebrush type, and mesic meadow sample locations were lower than those in the dry meadow and sagebrush vegetation types ($p \leq 0.05$). The number of degree-days of anaerobiosis was not significant in the discriminant analysis; however, one-way ANOVA tests indicated that it differed significantly between the vegetation types (df = 3,22, $F = 17.91$, $p < 0.0001$). The wet meadow type sample locations were anaerobic longer than those of the three other vegetation types, and sample locations in the dry meadow type were more an-

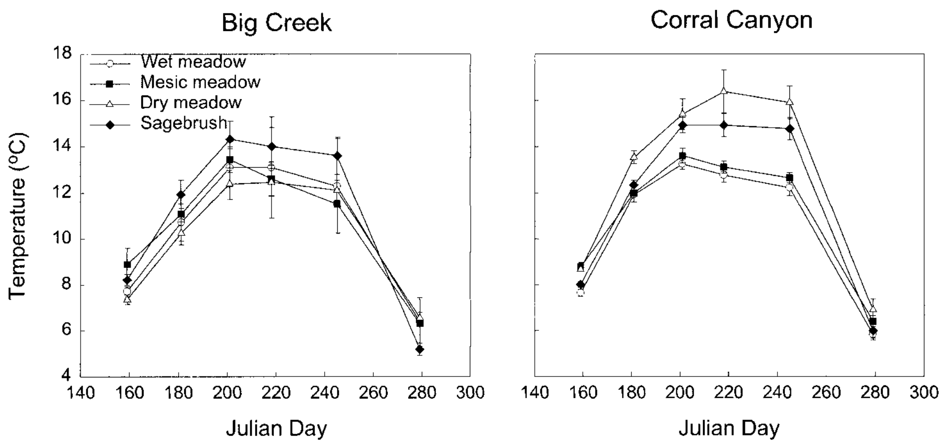

Figure 3. Soil temperature at 30 cm for Big Creek and Corral Canyon in 1998. Values are mean ± S.E.

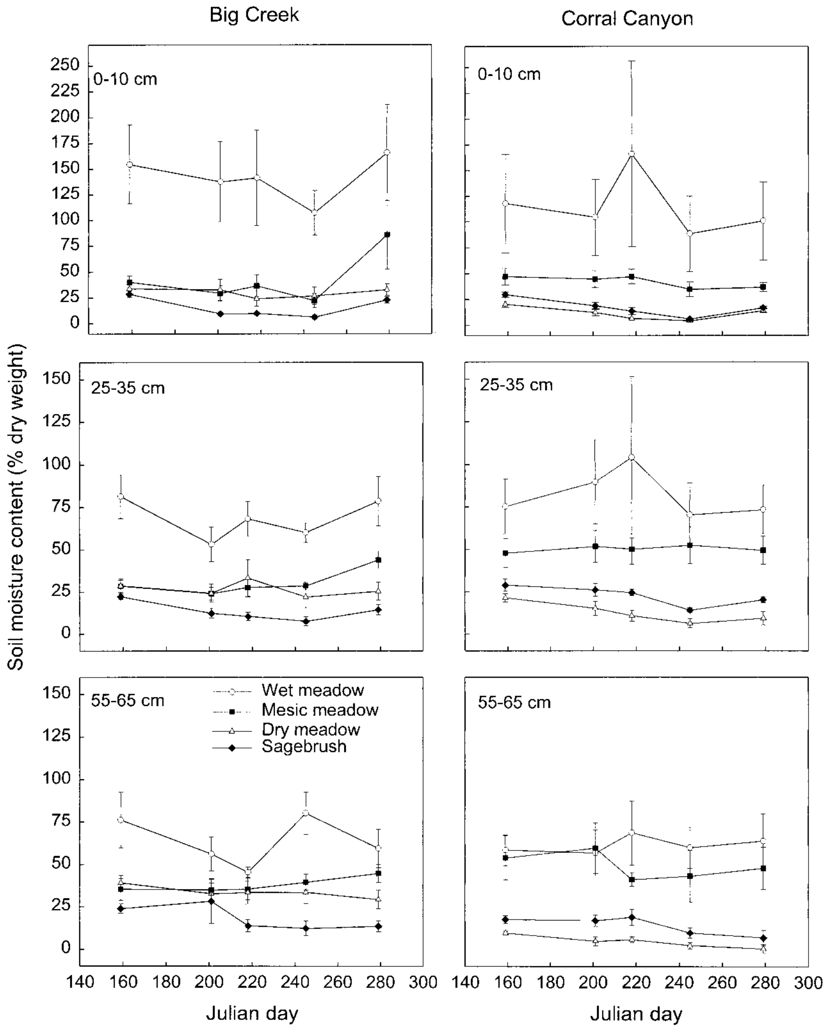

Figure 4. Soil moisture content (percentage dry weight) at 0–10 cm, 25–35 cm, and 55–65 cm for Big Creek and Corral Canyon in 1998. Values are mean ± S.E.

aerobic than those of the sagebrush type ($p \leq 0.05$). The percentage cover of vegetation, litter, and gravel did not differ between vegetation types.

In Corral Canyon, the multivariate discriminant analysis correctly verified 100 percent of the sample locations for all four vegetation types. Significant variables in the discriminant analysis included the percent cover of vegetation, litter, and gravel, the range in soil temperature, the range in soil moisture content at 25–35 cm and 55–65 cm, and the degree days of anaerobiosis ($p \leq 0.05$; Table 4). The vegetation types differed in the percent cover of vegetation (df = 3,16, F = 17.21, $p < 0.0001$) and litter (df = 3,16, F = 17.82, $p < 0.0001$). Sample locations in the wet and mesic meadow types had a higher percent cover of vegetation and lower percent cover of litter than those in the sagebrush type ($p < 0.05$). The range in soil temperature differed between vegetation types (df = 3,16, F = 11.06, $p < 0.0004$). Wet meadow sample locations were cooler than those in the dry meadow type, and mesic meadow sample locations were cooler than those in the dry meadow and sagebrush vegetation types ($p \leq 0.05$). The degree days of anaerobiosis also differed between vegetation types (df = 3,16, F = 8.64, $p < 0.0012$). Sample locations in the wet meadow type had greater number of degree days of anaerobiosis than those in the dry meadow and sagebrush types, and mesic meadow sample locations had greater number of degree days of anaerobiosis than those in the sagebrush type ($p \leq 0.05$). Although not significant in the discriminant analysis, a one-way ANOVA indicated that the number of days the depth to water table was less than 30 cm differed between vegetation types (df = 3,16, F = 17.59, $p < 0.0001$). Sample locations in the wet meadow and mesic meadow types had higher water tables than those in the dry meadow

Table 4. R-squared values for discriminant analysis and canonical correspondence analysis (CCA) axes 1 and 2 for the Big Creek and Corral Canyon study sites. Significance at $p \leq 0.05$ is indicated by *. Significance at $p \leq 0.01$ is indicated by **. The absence of a variable indicates that it was dropped during backward elimination (discriminant analysis) or due to high correlation with other variables (CCA).

Site	Variable	Discriminant Analysis	CCA Axis 1	CCA Axis 2
Big Creek	Range in depth to water table (DWT)	0.1357	0.356	0.208
	No. days DWT < 30 cm	0.7480**	0.806**	0.124
	No. days DWT < 70 cm	0.2224	0.600**	0.044
	% cover vegetation	0.6191**	0.192	0.010
	% cover litter	0.6179**	0.262	0.367
	% cover bare ground	0.6083**	0.671**	0.399
	% cover gravel	0.6179**	0.310	0.809**
	Range in soil moisture at 0–10 cm	0.0488	—	—
	Range in soil moisture at 25–35 cm	0.3695	—	—
	Range in soil moisture at 55–65 cm	0.2978	0.164	0.173
	Range in soil temperature	0.4475	—	—
	Range in soil redox potential	0.1612	—	—
	Degree-days of anaerobiosis	0.0420	0.838**	0.066
	Elevation	0.8639**	0.165	0.052
	CCA Eigenvalue	—	0.614	0.431
Corral Canyon	Range in depth to water table (DWT)	0.7005	0.835**	0.098
	No. days DWT < 30 cm	0.8222	0.786**	0.202
	No. days DWT < 70 cm	0.7706	0.807**	0.106
	% cover vegetation	0.9802**	0.907**	0.133
	% cover litter	0.9870**	0.921**	0.117
	% cover bare ground	—	—	—
	% cover gravel	0.9826**	—	—
	Range in soil moisture at 0–10 cm	—	—	—
	Range in soil moisture at 25–35 cm	0.8268*	0.017	0.204
	Range in soil moisture at 55–65 cm	0.9246*	0.098	0.180
	Range in soil temperature	0.9704**	0.620**	0.148
	Range in soil redox potential	0.6635	0.281	0.453*
	Degree-days of anaerobiosis	0.9813**	0.720**	0.441*
	Elevation	0.7895	0.795**	0.061
	CCA Eigenvalue	—	0.791	0.479

and sagebrush types ($p \leq 0.05$). The percent cover of gravel and ranges in soil moisture content at 25–35 cm and 55–65 cm did not differ between sample locations for the four vegetation types.

Canonical Correspondence Analysis (CCA). When constrained by the environmental data, CCA provides additional information on the relationships between sample locations and environmental variables through direct gradient analysis (Figure 5). Axes 1 and 2 cumulatively explained 31% of the variance in the Big Creek CCA and 27.5% of the variance in the Corral Canyon CCA. At Big Creek, Axis 1 was correlated with number of days depth to water table was less than 30 cm and 70 cm, percent cover of bare ground, and number of degree days of anaerobiosis ($p \leq 0.01$; Table 4). Axis 2 of the Big Creek CCA ordination was correlated with percent cover of gravel ($p \leq 0.01$). At Corral Canyon, Axis 1 was correlated with the range in depth to water table, number of days depth to water table was less than 30 cm and 70 cm, percentage cover of vegetation and litter, range in soil temperature, number of degree days of anaerobiosis, and elevation ($p \leq 0.01$; Table 4). Axis 2 of the Corral Canyon CCA ordination was significantly correlated with the range in redox potential and the degree days of anaerobiosis ($p \leq 0.05$). Axis 1 of the Big Creek and Corral Canyon CCA ordinations demonstrates hydrologic gradients by correlation with depth to water table-associated variables. In addition, Axis 1 reveals vegetational gradients by showing correlation with vegetation-associated cover variables. Finally, Axis 1 shows an elevational gradient for the Corral Canyon CCA ordination.

DISCUSSION

Gradients in depth to water-table, soil moisture holding capacity, and soil-moisture content existed

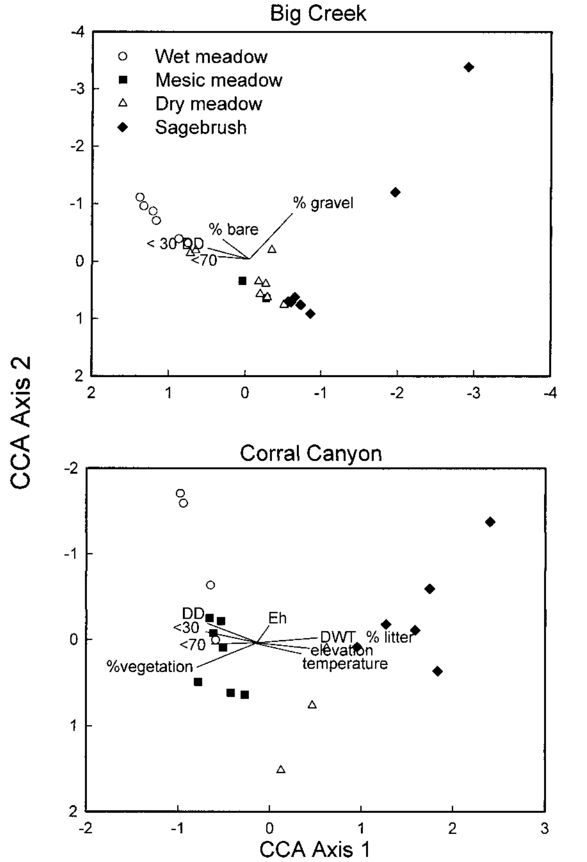

Figure 5. Canonical correspondence analysis (CCA) ordinations of sample plots in Big Creek and Corral Canyon. CCA ordination is based upon species composition but is constrained by the environmental and integrative variables. DWT = the range in depth to water-table; <30 = the number of days the depth to water-table was less than 30 cm; <70 = the number of days the depth to water-table was less than 70 cm; Eh = the range in soil redox potential; DD = the number of degree days of anaerobiosis; % bare, gravel, litter, and vegetation = percentage aerial cover of each category.

within the Big Creek and Corral Canyon meadow systems. Hydrology is often the primary factor influencing vegetation patterns in riparian ecosystems (Allen-Diaz 1991, Stromberg et al. 1996, Yabe and Onimaru 1997), and in this study, the four vegetation types were distinctly arrayed along the water-table and soil-moisture gradients at both sites. Species composition of the vegetation types was similar to that reported in studies of other western riparian meadows (Allen-Diaz 1991, Weixelman et al. 1996), but water-table depths differed in some cases (Table 5). Similar to other studies, the wet meadow type was dominated by *C. nebrascensis*, consistently had the shallowest depth to water-table (0 to 30 cm), and demonstrated the most saturated conditions of all four vegetation types (Chambers et al. 1999, Green unpub.). The mesic meadow type was

Table 5. Indicator plant species and the range in the depth to water table of each vegetation type in the Big Creek and Corral Canyon study sites.

Vegetation Type	Indicator Species	Depth to Water Table (cm)			
		Big Creek	Corral Canyon	Literature	
Wet meadow	*Carex nebraskensis*	0–21	0–30	0–30	Chambers et al. 1999
				0–30	Green unpubl.
Mesic meadow	*Poa pratensis, Juncus balticus*	0–34	90–149	30–80	Chambers et al. 1999
				Depth to field capacity < 1 m	Weixelman et al. 1996
Dry meadow	*Carex praegracillis, Agropyron intermedium*	30–55	133–172	120–160	Linnerooth 1999
				Depth to field capacity 70 to >100 cm	Weixelman et al. 1996
Sagebrush meadow	*Carex douglassii, Elymus elymoides*	196–400+	228–400+		

dominated by *P. pratensis* ssp. *pratensis* and *J. balticus* and spanned slightly wider ranges in depth to water-table than those reported in previous central Nevada riparian research (Weixelman et al. 1996, Chambers et al. 1999). Plant species composition of the dry meadow type consisted mainly of *C. praegracilis* and *A. intermedium.* In Big Creek, the depth to water-table for the dry meadow type was shallow compared to ranges reported elsewhere, while the range in Corral Canyon was more consistent with previous findings (Weixelman et al. 1996). Plant species classified into the sagebrush type were *C. douglasii, P. secunda* ssp. *secunda, L. cinereus, Elymus glaucus,* and *A. tridentata* ssp. *tridentata.* The sagebrush vegetation type had the greatest depth to water-table at both sites. At Big Creek, the depths to water-table in the mesic and dry meadow types at Big Creek were probably shallower than those reported previously because of higher than average precipitation in 1997 and 1998 (Table 1). In 1998, side valley ground-water seeps that were not observed in 1997 actively flowed, resulting in more shallow water-tables at both the mesic and dry meadow sampling locations. In central Nevada, these meadow types have large seasonal and yearly differences in water-table depths (Linnerooth 1999, Martin 1999). Changes in species phenology, photosynthetic rates, water relations, rooting activity, biomass, and reproductive effort can result from annual differences in precipitation and water-tables (Linnerooth 1999, Martin 1999). Individual species abundances may show slight increases or decreases during one or more wet or dry years (Martin 1999), but overall species composition seems to reflect longer-term averages in water-table depths (Chambers and Tausch, unpublished data).

The soil characteristics of the four vegetation types were similar to those found for other central Nevada meadow ecosystems (Weixelman et al. 1996, Chambers et al. 1999), and differences among types could be explained by water-table depth. The vegetation types within shallower water-table depths, i.e., the wet and mesic meadows, tended to have higher organic matter, finer soil particle sizes, and higher soil moisture holding capacities than the types with deeper water tables. Redoximorphic features, in particular mottling, occurred where the depth to water-table fluctuated between soil wetting and drying, such as in the mesic and dry meadow type soils.

Patterns in soil moisture content followed those of depth to water-table with the exception of the mesic meadow type in Big Creek and the dry meadow type in Corral Canyon. In Big Creek, moisture content in the mesic meadow soils was often less than that of the dry meadow. This unexpected pattern is probably due to the side valley seeps in Big Creek in 1998. In Corral Canyon, the dry meadow soils had the lowest moisture content. This is probably because many dry meadow sampling locations were located on the edges of the riparian corridor and at higher elevations than those of the other vegetation types.

The depth to water-table over the growing season affects the extent and length of soil inundation and oxygen diffusion. Thus, redox potentials and water-table depths are inversely related (Pickering and Veneman 1984, Zobeck and Ritchie 1984, Megonigal et al. 1993). Soils in the *C. nebrascensis* type had negative redox potentials throughout the study period at both sites, indicating reducing conditions. Such prolonged reduced conditions have been observed in *Carex* spp. communities in northeastern Oregon riparian ecosystems (Green unpub.). Redox potentials were only slightly reducing in the dry meadow type in Big Creek and the mesic meadow type in Corral Canyon. Mean redox potentials were greater than 350 mV in soils of the mesic meadow and sagebrush vegetation types in Big Creek and in the dry meadow and sagebrush vegetation types in Corral Canyon, demonstrating aerobic conditions and oxidized inorganic ions. Differences in redox potentials of wet and moist meadow soils depend on the time of year and are influenced by precipitation patterns (Naiman et al. 1994). We found that the side valley ground-water seeps and greater precipitation in Big Creek led to wetter, more reduced soils than in Corral Canyon. Seasonal patterns in redox potential paralleled those of depth to water-table and soil moisture content. Throughout the growing season, depth to water-table increased and soil moisture decreased causing redox potentials to become more positive in all vegetation types. Fall ground-water recharge led to decreased depths to water-table and increased soil moisture, causing redox potentials to become more negative in all vegetation types.

Soil temperatures were influenced by the hydrology of the individual sites and the sampling locations with respect to the stream and overstory vegetation. The lack of a clear pattern in soil temperatures in Big Creek is probably due to the influence of the side valley ground-water seeps. In Big Creek, dry meadow sample locations had cold soil temperatures because of their close proximity to the stream and the existence of overstory vegetation. In Corral Canyon, there was a clear distinction between vegetation types in soil temperatures. Surprisingly, the dry meadow type demonstrated warmer temperatures than the sagebrush type. This is because dry meadow sampling locations were farther from the stream than the sagebrush sampling locations. Also, overstory vegetation in the sagebrush type provided greater shade than in the dry meadow type.

Table 6. Values of the integrative environmental variables (mean ± SE) most closely related to the vegetation types in the Big Creek and Corral Canyon study sites. Depth to water table is abbreviated as DWT.

Site	Vegetation type	Range in DWT	# of days DWT is 0–30 cm	# days DWT is 0–70 cm	Degree days of anaerobiosis
Big Creek	Wet meadow	10 ± 2	59 ± 0	59 ± 0	537 ± 38
	Mesic meadow	29 ± 2	5 ± 5	59 ± 0	2 ± 29
	Dry meadow	20 ± 3	32 ± 9	53 ± 5	308 ± 92
	Sagebrush	25 ± 9	0 ± 0	12 ± 8	1 ± 1
Corral Canyon	Wet meadow	3 ± 3	59 ± 0	59 ± 0	544 ± 20
	Mesic meadow	33 ± 10	41 ± 9	49 ± 8	393 ± 88
	Dry meadow	30 ± 10	0 ± 0	0 ± 0	148 ± 148
	Sagebrush	90 ± 10	0 ± 0	0 ± 0	32 ± 31

SYNTHESIS

Knowledge of both indicator species and environmental variables may be necessary to predict the response of riparian ecosystems to changes in water-table levels. Plant species can be used to represent local environmental conditions and have been used previously as indicators of ground-water status (Allen-Diaz 1991, Stromberg 1996). The multivariate analyses allowed us to identify indicator plant species and the ranges in water-table depths over which they occurred (Table 5). The uniform results observed in the wet meadow types suggest that *C. nebrascensis*, a dominant, riparian obligate, is a dependable indicator of shallow water-table conditions. A small increase in depth to ground-water could effectively eliminate this vegetation type. In contrast, large temporal and spatial variability existed in water-table depths for the mesic and dry meadow types. This suggests that species that dominate these types could be used only to indicate broad ranges in water-table depths, especially when measured over short time intervals.

The CCA ordinations clearly showed a close relationship between plant species composition and those variables associated with depth to water-table. Certain integrated variables that incorporated temporal variation demonstrated closer relationships to the different vegetation types than water-table depth alone (Table 6). The number of days the depth to water-table was less than 30 cm and 70 cm and the number of degree days of anaerobiosis during the growing season were related to the wet and mesic meadow types. The range in depth to water-table during the growing season, as well as relative elevation, presence of shrubs, and percentage aerial cover of gravel and litter, was related to the dry meadow and sagebrush vegetation types. Other studies have identified elevation and hydrologic variables as those most closely related to plant distributions (Allen-Diaz 1991, Stromberg et al. 1996, Yabe and Onimaru 1997). The integrated variables were more sensitive to the spatial and temporal differences in water-tables that existed within the meadows than individual species or vegetation types. They would be expected to respond more rapidly to changes in local hydrology than plant species and are probably more reliable indicators of both current water-table status and potential vegetation. Our study reinforces the importance of measuring integrative environmental variables that incorporate the temporal aspects of water-tables and soil-water content when evaluating ground-water status in arid and semiarid riparian ecosystems.

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