



Influences of watershed geomorphology on extent and composition of riparian vegetation

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Keywords

Basin morphometry; Flood regime; Forest; Great Basin; Lithology; Meadow; Nevada; Ordination; Scale; Small watersheds.

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Abstract

Question: How strongly do watershed morphometry and geology influence the extent and composition of vegetation along riparian corridors?

Location: Eighteen upland watersheds in central Nevada, USA.

Methods: Watershed (drainage basin) morphometry and geology were derived from digital data sets (DEMs and geologic maps). Riparian corridors were classified into five vegetation types (riparian forest, riparian shrub, wet/mesic meadow, dry meadow and shrub dry meadow) using high-resolution aerial photography. Regression and multivariate analyses were used to relate geomorphic characteristics to riparian vegetation extent and composition.

Results: Riparian extent ranged from 0.4% to 3.6% of watershed area, was positively related to percentage intrusive bedrock and drainage density, and was negatively related to percentage carbonate bedrock and relative stream power. Riparian forest and shrub types occupied more than 75% of the riparian corridor in 12 of 18 watersheds; meadow types comprised a smaller proportion. Watershed size, topography and geology were important in predicting riparian composition. Riparian forest and shrub types were more abundant in small, rugged watersheds of high relief. Meadow types were more abundant in large, low gradient and less rugged watersheds. The importance of woody vegetation increased with more volcanic and intrusive bedrock, whereas meadow vegetation increased with increasing alluvium, carbonate and metasedimentary rock types.

Conclusions: Watershed geomorphology significantly constrains extent and abundance of woody versus herbaceous vegetation within the riparian corridor. Watershed variables related to riparian vegetation are likely indicators of run-off regimes or water and sediment transport. Consideration of relationships between watershed-scale geomorphology and riparian vegetation can improve prediction and inform restoration efforts.

Introduction

Riparian areas are critical landscape components that supply numerous ecosystem services and sustain biodiversity (Naiman & Décamps 1997). In arid to semi-arid regions, riparian areas are often highly degraded (National Research Council 2002). Anthropogenic disturbances, including water diversions, roads in valley bottoms and overgrazing by livestock, have increased the effects of natural disturbances like flooding and resulted in channel aggradation or incision, altered water table levels and adverse changes in riparian ecosystem structure and function (Stromberg et al. 1996; Scott et al. 2000; Chambers

et al. 2004b; Loheide & Gorelick 2007). A key limitation in the management and restoration of degraded riparian ecosystems is knowledge of the watershed-scale controls on hydrogeomorphic regimes, which in turn influence the extent and composition of riparian vegetation communities (Williams et al. 1997; Wohl et al. 2005; Shaw & Cooper 2008). In the upland watersheds of topographically diverse regions, individual watersheds can differ in geology and morphometry (size and shape) and, consequently, in hydrogeomorphic regimes and vegetation patterns. An improved understanding of the effects of watershed-scale properties on the extent and composition of riparian vegetation is needed to accurately predict responses to climate

change and anthropogenic disturbances, and to develop appropriate strategies for restoration and management.

Most research on the environmental controls on riparian vegetation in arid and semi-arid ecosystems has focused on local or reach scales and within large river systems (e.g. Stromberg et al. 1996; Merritt & Cooper 2000). A smaller body of work has related the species composition and pattern of riparian vegetation communities to the watershed-scale properties of small upland watersheds (Baker 1989; Bendix 1994; Shaw & Cooper 2008). Research at local or reach scales has shown repeatedly that the composition of riparian vegetation can be predicted based on land form type and position, substrate characteristics, water availability and tolerance to flooding (see reviews in Hupp & Osterkamp 1996; Hughes 1997; Bendix & Hupp 2000). It also has shown that hydrogeomorphic regimes can be altered significantly by anthropogenic modifications, such as groundwater pumping and river regulation, that plant communities are highly sensitive to these changes (Stromberg et al. 1996; Cooper et al. 2003), and that these relationships can be effectively modelled at reach scale (e.g. Hupp & Rinaldi 2007).

Studies that also included watershed variables indicate that several watershed properties, including area, length, relief and ruggedness, are important predictors of vegetation types (Baker 1989). Baker (1989) concluded that more locally determined environmental variables such as channel characteristics were generally less important predictors of vegetation types than drainage basin variables. Regardless of scale or approach, measures of stream gradient or stream power are often strong predictors of riparian vegetation (Baker 1989; Bendix 1994, 1997). Many watershed-scale properties are related to vegetation types because of their influence on both flood characteristics and the timing and duration of water availability. Collectively, watershed morphology and geology regulate the movement of water and sediment from hillslopes to the channel and through the channel network. Watershed size, relief and shape are related to flood discharge and time-to-peak flow (Costa 1987; Patton 1988; Howard 1990). Bedrock geology is related to infiltration and run-off rates via the hydraulic conductivity of surface and subsurface materials and influences the grain size and erodibility of materials on the hillslopes and in the channel (Kelson & Wells 1989; Sable & Wohl 2006). Because of the strength of these relationships, watershed-scale properties often can serve as surrogates for hydrograph properties in small upland watersheds that are not gauged (Germanoski & Miller 2004).

The likelihood that a particular riparian vegetation type will occur in a given watershed depends on the ecological tolerances of the component plant species and their preferences for specific hydrogeomorphic conditions, including

water availability, anaerobic soils, surface characteristics and flood disturbance regimes (Harris 1988; Hupp & Osterkamp 1996; Steiger et al. 2005). In riparian areas of the western USA, vegetation types dominated by native woody species such as *Populus* and *Salix* spp. often depend on flooding and other disturbances because their reproduction requires bare surfaces for seedling establishment or physical damage to mature individuals to initiate resprouting and suckering (Rood et al. 1994; Scott et al. 1996; Sheppard et al. 2001; Karrenberg et al. 2002). In contrast, riparian meadows and wetlands depend on reliable groundwater sources (Allen-Diaz 1991; Castelli et al. 2000; Loheide & Gorelick 2007). Research in upland watersheds of the central Great Basin indicates that watershed-scale properties including geology, relief characteristics and shape parameters, influence not only hydrologic regimes and geomorphic settings but also the response of individual watersheds to floods and other disturbances (Germanoski & Miller 2004). Reach-scale studies of the hydrogeomorphic and vegetation characteristics in a subset of these same watersheds indicate that these watershed-scale properties are strong predictors of disturbance regimes and vegetation types along the riparian corridor (Chambers et al. 2004a,b). However, no studies in these or other watersheds have directly examined the relationships of watershed-scale properties to the extent and composition of the riparian vegetation within the riparian corridor.

In this study, we quantified the relationships among watershed (drainage basin) lithology and geomorphology and watershed-scale riparian vegetation, as measured by riparian extent (the relative abundance of riparian vegetation within a watershed) and composition (the relative abundance of different vegetation types within the riparian corridor). To critically evaluate these relationships, we selected small, upland watersheds within the same region that had similar climates and upland vegetation but that spanned a range of conditions for lithology and geomorphology. Our analysis was similar to that of Shoutis et al. (2010) who used digitally-derived terrain variables to predict riparian vegetation extent and composition for different sites within a single mountain watershed in the northern Rocky Mountains.

We determined the watershed-scale properties of 18 small, upland watersheds in the central Great Basin and mapped the riparian vegetation types (riparian forest, riparian shrub, wet/mesic meadow, dry meadow and shrub dry meadow) within each watershed. We hypothesized that watershed-scale properties would be strongly related to the extent and composition of riparian vegetation, and used generalized linear regression and multivariate ordination analyses to evaluate these relationships. We made two predictions:

1. Extent of riparian vegetation is related to watershed characteristics that influence the availability of water adjacent to the main channel, including watershed geology, size and gradient. Larger, lower gradient watersheds with more metasedimentary and carbonate rocks will have a higher abundance of riparian vegetation.

2. Riparian composition is strongly related to watershed characteristics that influence flood regimes, sediment transport and water retention, including hypsometric integral, relative stream power and topographic relief. Woody vegetation types will dominate small, steep watersheds with resistant rock types that promote flash run-off regimes and transport of coarse sediments. Meadow vegetation types will occur in higher proportions in lower gradient watersheds with more erodible rock types that supply abundant fine sediments and promote longer water retention times.

We discuss the use of this approach and the implications of our results for the management and restoration of riparian areas in small, upland watersheds.

Methods

Site description

The Great Basin section of the Basin and Range physiographic province is a semi-arid, internally-drained basin in the western United States, encompassing approximately 650 000 km² of land, including most of Nevada and portions of neighbouring states. The Great Basin is characterized by a series of isolated north–south trending mountain ranges and intervening valleys. We studied 18 upland watersheds in the Toiyabe, Toquima, Monitor and White

Pine mountain ranges of central Nevada (Fig. 1), which are characterized by similar climate, upland vegetation and land-use history, but vary with respect to geomorphology and geology. Watersheds range in area from 531 to 15 215 ha. Elevations range from approximately 2000 m to over 3500 m. Mean annual precipitation ranges from 20 cm at the watershed mouth to 45 cm at the highest elevation, and falls primarily as winter snow, with peak run-off occurring in late May to early June. Occasional thunderstorms augment stream flow during the summer months. The watersheds are underlain by a variety of lithologies including volcanic, granitic and carbonate rocks and are characterized by relatively narrow valleys occupied by streams with generally high gradient and coarse, gravel-bed channels. All watersheds are either third- or fourth-order drainages according to the Strahler method of stream ordering (Strahler 1957).

Along perennial stream reaches, woody vegetation consists of narrow bands of water birch (*Betula occidentalis*), coyote willow (*Salix exigua*), yellow willow (*Salix lutea*), wild rose (*Rosa woodsii*), narrowleaf cottonwood (*Populus angustifolia*) and quaking aspen (*Populus tremuloides*). Meadows occur in areas with elevated water tables and are characterized by wetland obligate and facultative graminoids and forbs (e.g. *Carex nebrascensis*, *Deschampsia cespitosa*, *Juncus arcticus* and *Symphyotrichum spathulatum*). Basin and mountain big sagebrush (*Artemisia tridentata* ssp. *tridentata* and *vaseyana*) occur in dry meadows and along ephemeral stream reaches. A detailed ecological type classification exists for central Nevada riparian areas based on soil, water, climate and plant species composition (Weixelman et al. 1996).

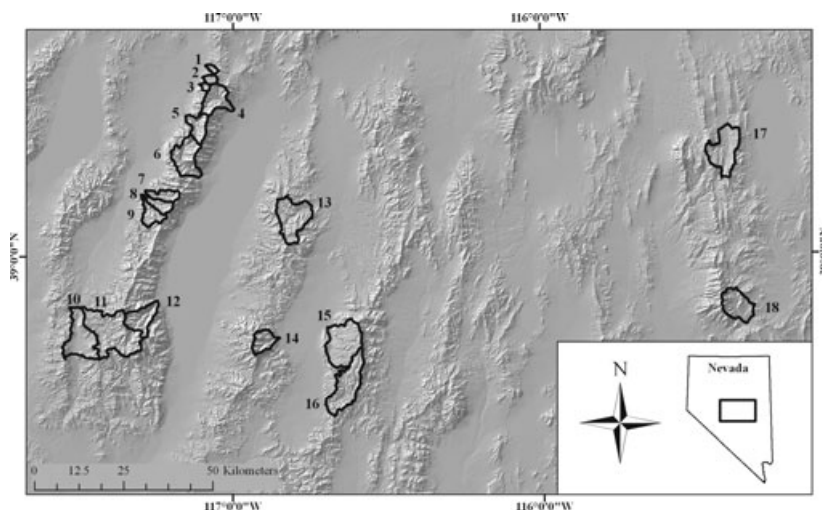


Fig. 1. The locations of the 18 study watersheds in the Toiyabe, Toquima, Monitor and White Pine Mountain ranges of central Nevada, USA: (1) Marshall, (2) Veetch, (3) Johnson, (4) Birch, (5) Big, (6) Kingston, (7) Washington, (8) Cottonwood, (9) San Juan, (10) Indian, (11) Upper Reese, (12) South Twin, (13) Stoneberger, (14) Pine, (15) Mosquito, (16) Barley, (17) Illipa and (18) Little Currant.

The study watersheds are managed by the Austin Ranger District of the Humboldt-Toiyabe National Forest, with the exception of several small private inholdings. Historic and current human uses include grazing, mining, water diversions and recreation. A graded secondary road is present along all or part of the valley bottom in most watersheds.

Geomorphic variables

Watershed morphometrics (Table 1) were derived from 10-m resolution digital elevation models (DEMs) using ArcHydro tools (version 1.2; ESRI, Redlands, CA, USA) in ArcGIS 9.2 software. While ArcHydro cannot distinguish between channelized and unchannelized valley segments, potentially resulting in measurement error for channel lengths, the ArcHydro approach is consistent and more objective compared to a manual approach. Cells of internal drainage or “sinks” in the DEMs were identified and filled in order to properly determine water flow direction and accumulation. The bottom of the watershed or “pour point” was defined as the location where the main stream channel exited the constrained portion of the canyon and flowed onto a broad alluvial fan. Watershed boundaries were derived by delineating all DEM cells that flowed into the pour point.

Stream networks in each watershed were derived based on the cumulative number of upstream cells draining to each cell (O’Callaghan & Mark 1984). The critical threshold for stream definition represents the minimum upstream drainage area necessary to initiate a stream. We used a critical threshold of 0.08% or 8% of the total watershed area because this value produced stream networks that closely resembled those identified in the field and on 1:24 000 topographic maps.

Watershed area was calculated from the derived watershed polygons, and watershed length was calculated

by summing the length of the main stream channel and the distance from the top of the main channel to the watershed boundary. Total stream length was calculated by summing the lengths of all stream segments in each watershed. Because planimetric and surface area measurements can differ significantly in mountainous settings, all watershed area and length measurements were slope-corrected to account for the additional area of curved surfaces. Slope-corrected values for the remaining morphometric variables were derived from slope-corrected area, length and total stream length. Hypsometric integral (HI) was not slope-corrected because it is defined as horizontal, cross-sectional area relative to elevation above the watershed outlet (Strahler 1952). HI is used as a measure of the erosional state of the watershed; larger values indicate less eroded landscapes with a greater proportion of land area at high elevation. A hydrogeomorphic study of these same watersheds identified HI as one of the most critical attributes for watershed sensitivity to flood disturbance and channel incision (Germanoski & Miller 2004). Thus, we expected this variable to be strongly related to riparian vegetation extent and composition. HI was calculated by reclassifying the DEM into 10-m elevation bands and calculating the planimetric area of each band. Relativized planimetric area above each band, normalized by watershed area, was plotted against relativized elevation, and HI was set equal to the area under the curve.

Explanations of additional morphometric variables are given in Table 1. Larger values of drainage density (Horton 1945), ruggedness (Melton 1957) and relief ratio (Schumm 1956) indicate more rapid, higher magnitude transport and delivery of water and sediment. Stream power, the product of channel discharge and slope (Bull 1979), could not be directly calculated because the majority of the study watersheds are ungauged. Instead, relative stream power was calculated as the product of watershed

Table 1. Morphometric parameters derived for each of the study watersheds.

Morphometric	Abbreviation	Unit	Explanation or Equation of Definition
Watershed Area	AREA	ha	Surface area of the watershed
Watershed Length	LNGTH_W	km	Length of the watershed along the main channel
Total Stream Length	TLNGTH_S	km	Sum of the length of all channels in the drainage network
Drainage Density	DRNDN	km km ⁻²	TLNGTH_S/AREA
Shreve Magnitude	SHREVE	#	Number of first-order streams in the watershed
Relief	RELIEF	m	Elevation difference between highest and lowest points in the watershed
Ruggedness	RUGGED	—	RELIEF * DRNDN
Relief Ratio	RLFRATIO	—	RELIEF/LNGTH_W
Relative Stream Power	STRMPOW	km ²	AREA * RLFRATIO
Watershed Shape	SHAPE	—	(LNGTH_W) ² /AREA
Hypsometric Integral	HI	%	Percentage area under a dimensionless curve produced as the ratio of h/H and a/A, where h = elevation, H = watershed relief, a = planimetric area above h, and A = planimetric watershed area

area and relief ratio. Watershed area is used as a proxy for discharge (Bendix 1997). The two variables are expected to be proportional within the set of study watersheds, although the relationship between them can vary due to differences in hydrologic connectivity and evapotranspiration. Relief ratio provides a reasonable estimate of average channel gradient or slope (Strahler 1957). Large values of relative stream power indicate higher amounts of energy available to transport water and sediment. Larger values of watershed shape (Strahler 1964) indicate more elongated watersheds with a slower but more sustained response to precipitation events due to a greater variety of flow path lengths and range of travel times.

Bedrock geology of each watershed was obtained from the USGS Geologic Map of Nevada (1:250 000; Crafford 2007). The geologic map was clipped to watershed boundaries and the relative proportion of seven bedrock lithologies (alluvium, carbonate, intrusive igneous, metasedimentary, quartzite, siliclastics, volcanic) within each watershed was calculated as a percentage of total watershed area. Carbonate rocks include limestone and dolomite; intrusive igneous rocks are primarily granite and some quartz monzonite; volcanic rocks are comprised of welded tuff and rhyolitic tuff; metasedimentary rocks are phyllite, schist and slate; and siliclastics include shale and siltstone.

Vegetation classification

Riparian vegetation was classified from USDA National Agricultural Imagery Program (NAIP) images of the study area taken during the 2006 agricultural growing season. The images are true-colour, digital orthophotographs with 1-m resolution. Riparian vegetation in the 18 study watersheds, encompassing a total mapped area of 17.2 km², was assigned to one of five types: riparian forest, riparian shrub, wet/mesic meadow, dry meadow and shrub dry meadow (Table 2). These aggregated vegetation types encompassed

the full range of plant communities found in central Nevada riparian areas and could be reliably differentiated on the NAIP imagery.

The NAIP images were clipped to the boundaries of each watershed and segmented into polygons of maximum spectral and textural homogeneity using eCognition image processing software (version 4.0; Definiens Imaging, München, Germany). The software segments images into self-similar polygons based on user-defined scale, colour and shape parameters. The size of the polygons increases as the scale parameter increases. Colour and shape parameters are expressed as decimal values ranging between 0 and 1, and constrained to sum to 1. A higher colour parameter maximizes the contribution of colour and minimizes the contribution of shape to the segmentation process. Similarly, the shape parameter is also expressed as a sum of two proportional values describing the relative weights assigned to smoothness and compactness. A higher smoothness value allows for long and irregular patches, as are typically observed in a riparian environment. Upon testing many possible combinations of parameters, the combination that maximized classification accuracy included the following parameter values: scale = 30, colour = 0.9, shape = 0.1, smoothness = 0.7 and compactness = 0.3.

The resulting polygons that bounded riparian vegetation were manually photo-interpreted into one of the five vegetation types. Riparian vegetation included the linear patches of vegetation along both axial and secondary channels. Large circular patches of hillslope vegetation that were likely spring-fed or snowmelt-dependent were not classified as riparian vegetation. Riparian polygons were extracted in a GIS and the relative extent of riparian vegetation was calculated by summing the areas of all riparian polygons in each watershed and dividing by total watershed area. Riparian composition was determined by calculating the relative proportions of the five vegetation types within each of the study watersheds. All areas of vegetation polygons were slope-corrected in order to measure surface area.

Table 2. Riparian vegetation types identified on NAIP imagery for the 18 study watersheds.

Vegetation Type	Abbreviation	Description	Important Species
Shrub Dry Meadow	SHRB MDW	Sagebrush overstorey with riparian facultative	<i>Artemisia tridentata</i> , <i>Chrysothamnus viscidiflorus</i> , <i>Leymus cinereus</i> , <i>Leymus triticoides</i> , <i>Pascopyrum smithii</i>
Dry Meadow	DRY MDW	Riparian facultative and upland graminoid species with fewer forb species	<i>Poa secunda</i> ssp. <i>juncifolia</i> , <i>Muhlenbergia richardsonis</i> , <i>Leymus triticoides</i>
Wet/Mesic Meadow	WM MDW	Riparian obligate and facultative graminoid and forb species	<i>Carex</i> spp., <i>Deschampsia cespitosa</i> , <i>Juncus balticus</i> , <i>Poa pratensis</i>
Riparian Shrub	SHRUB	Overstorey of riparian obligate shrubs	<i>Betula occidentalis</i> , <i>Salix</i> spp., <i>Rosa woodsii</i> , <i>Prunus virginiana</i>
Riparian Forest	FOREST	Overstorey of riparian obligate and facultative trees	<i>Populus angustifolia</i> , <i>Populus tremuloides</i>

Statistical analysis

To determine the relationship between watershed morphometrics and relative riparian extent, an information theoretic approach utilizing the Akaike's information criterion (AIC) statistic was used to compare models (Burnham & Anderson 2002). Multiple linear regression models were developed to relate the relative extent of riparian vegetation to ecologically significant watershed environmental variables, and AIC weights (w_i) for each model were calculated according to the formula:

$$w_i = \frac{\exp(-1/2\Delta_i)}{\sum_{r=1}^R \exp(-1/2\Delta_r)}$$

where Δ_i is the difference in the minimum AIC value and the AIC value of model i , and Δ_r is the difference in the minimum AIC value and the AIC value of each model in the set of R models. The relative importance of the best predictor variables was determined by calculating variable weights (w_+), the sum of the AIC weights of all models containing the variable of interest. The larger the value of w , the more important the model or variable is relative to the other models or variables. Regression residuals were examined for spatial autocorrelation using Moran's I global autocorrelation statistic, and by plotting omnidirectional correlograms (Legendre & Fortin 1989).

To assess vegetation classification accuracy, we used independent data collected by field-mapping each of the five vegetation types along the entire length of the riparian corridor in four of the 18 watersheds. We randomly selected 3450 points that occurred within the extent of the vegetation classification and field mapping. Agreement between the classification and field-mapped vegetation was summarized in an error matrix and compared to chance agreement using the kappa statistic K_{HAT} (Congalton & Green 1999). Values of $K_{\text{HAT}} > 0.80$ represent strong agreement, values between 0.80 and 0.40 represent moderate agreement, and values of $K_{\text{HAT}} < 0.40$ represent poor agreement.

The relationships between composition of vegetation types and watershed morphometrics and geology were examined with multivariate statistical methods. Non-metric multidimensional scaling (NMS) was used to produce an ordination of the study watersheds based on the relative proportions of riparian vegetation types. We used the Sørensen (i.e. Bray-Curtis) distance measure, with random starting configurations and 250 permutations, each with real and randomized data, providing the basis for a Monte Carlo significance test for each of six dimensions initially tested. The final NMS solution included the number of dimensions that minimized final

stress values (McCune & Grace 2002). Vegetation proportions were arc-sine square-root transformed prior to analysis. Important environmental gradients of watershed morphometry were identified by examining Pearson's correlation coefficients (r) of environmental variables with axis scores and graphical interpretation of species distributions along the ordination axes.

Ordination analyses were conducted using PC-ORD (version 5.10; MjM Software, Gleneden Beach, OR, USA). All other statistical analyses were completed with S-PLUS (version 8.1; TIBCO Software Inc., Palo Alto, CA, USA).

Results

Riparian extent

'Riparian vegetation extent ranged from 0.4% to 3.6% of the total watershed areas. AIC-weighted model comparisons and AIC weights of individual variables indicated that riparian vegetation extent was best explained as a function of both geologic and morphometric variables (Table 3a). Together, the percentage of intrusive and carbonate bedrock and the relative stream power of the watershed explained 64% of the variation in riparian vegetation extent. Riparian vegetation extent increased with more

Table 3. AIC analysis of linear regression models of the influence of watershed geomorphology on riparian vegetation extent. (a) Hypothesized regression models, R^2 values, AIC and Δ_i scores, and model weights (w_i). (b) Variable weight (w_+) and direction of effect for the best predictor variables. %Carb = carbonate (%); DrnDn = drainage density (km km^{-2}); %Intrsv = intrusive igneous (%); StrmPow = relative stream power (km^2).

(a)				
Model	Multiple			
	R^2	AIC	Δ_i	w_i
%Intrsv + %Carb + StrmPow	0.64	-124.910	0.000	0.465
%Intrsv + %Carb + StrmPow + DrnDn	0.64	-122.997	1.913	0.179
%Intrsv + %Carb + DrnDn	0.59	-122.638	2.272	0.149
%Intrsv + %Carb	0.53	-122.143	2.767	0.116
%Intrsv + StrmPow	0.45	-119.337	5.573	0.029
%Intrsv	0.39	-119.205	5.705	0.027
StrmPow	0.33	-117.768	7.142	0.013
DrnDn	0.31	-117.084	7.826	0.009
DrnDn + StrmPow	0.36	-116.461	8.450	0.007
%Carb	0.28	-116.391	8.519	0.007
(b)				
Variable	w_+	Direction of Effect		
%Intrsv	0.964	+		
%Carb	0.915	-		
StrmPow	0.692	-		
DrnDn	0.344	+		

intrusive bedrock and decreased with more carbonate bedrock and higher relative stream power (Table 3b). Residuals from the most parsimonious regression model (Table 3b) were not spatially autocorrelated at $P \leq 0.05$ over any lag distance (global Moran's $I = 0.134$, $P = 0.502$).

Riparian composition

Classification accuracy of vegetation types was 82% overall ($K_{\text{HAT}} = 0.74$, $P < 0.001$), suggesting strong agreement between the classification and field-identified vegetation. Most misclassifications resulted from confusion of the wet/mesic and shrub dry meadow types for dry meadow, and riparian forest for riparian shrub (Engelhardt 2009).

All five vegetation types occurred in all 18 watersheds, except for the shrub dry meadow type, which was absent from two watersheds. Twelve of the 18 watersheds had a woody component (riparian forest and riparian shrub) that occupied more than 75% of the riparian zone (Fig. 2). The proportion of riparian forest showed high variation among the watersheds (median = 0.260, range = 0.010–0.721), but the proportion of riparian shrub was generally larger and more consistent (median = 0.414, range = 0.032–0.729). Meadow types typically occupied smaller proportions of the riparian corridor, with several exceptions. Illipah and Indian had larger dry and shrub dry meadow components and several watersheds (e.g. Illipah, Johnson) had considerable wet/mesic meadow cover (median = 0.056, range = 0.002–0.506).

The NMS ordination of watershed vegetation composition resulted in a three-dimensional solution with Final Stress = 2.81 and cumulative $R^2 = 0.84$. All five vegeta-

tion types separated clearly on Axis 3 (Fig. 3a), which explained the majority (56%) of the variance in vegetation composition and described a gradient of watershed size and topography (Table 4). Riparian forest and shrub occurred in greater proportions in small, high relief and rugged watersheds. In contrast, the three meadow types were more abundant in large, low gradient and less rugged watersheds. Axis 1 and 2 explained similar, but smaller, proportions of the variance (15% and 14%, respectively).

Axis 1, which was strongly associated with geology as well as relief (Table 4), separated wet/mesic meadow from shrub dry meadow, and wet/mesic meadow and shrub dry meadow from a cluster of the remaining three types (Fig. 3). The meadow types differed primarily in their association with watershed relief and geology. Wet/mesic meadow was most abundant in low-relief watersheds, dry meadow was most abundant in high-relief watersheds, and shrub dry meadow was intermediate. Also, wet/mesic meadow was positively associated with the percentage of metasedimentary and carbonate rock, dry meadow was positively associated with the percentage of volcanic rock, and shrub dry meadow was intermediate. On Axis 2, which represents a gradient of erosion (HI), stream power and geology (Table 4), riparian forest was clearly separated from the rest of the vegetation types and was associated with watersheds of large HI and more intrusive igneous bedrock (Fig. 3b).

Subtle differences in the relationships of vegetation proportion and watershed geomorphology were found by identifying the best predictor variable for each of the vegetation types. Although the proportions of riparian forest and riparian shrub increased in watersheds of similar geomorphology, riparian shrub was correlated with higher stream power but lower HI than riparian forest (Fig. 3b). The best univariate predictor of riparian forest proportion was HI (Fig. 4a); riparian shrub proportion was best predicted by relative stream power (Fig. 4b). The three meadow types were generally more abundant in similar kinds of watersheds, but the proportion of wet/mesic meadow was best predicted by watershed relief (Fig. 4c) whereas the proportions of dry meadow and shrub dry meadow were best predicted by watershed ruggedness (Fig. 4d, e).

Bedrock lithology of the watersheds was also important in distinguishing riparian vegetation composition (Fig. 3, Table 4). Higher proportions of riparian forest occurred in watersheds dominated by volcanic and intrusive rocks. Riparian shrub proportion was higher in watersheds with more volcanic bedrock. Higher proportions of the wet/mesic meadow and shrub dry meadow types were correlated with larger percentages of alluvium, carbonate rocks and metasedimentary rocks within a watershed.

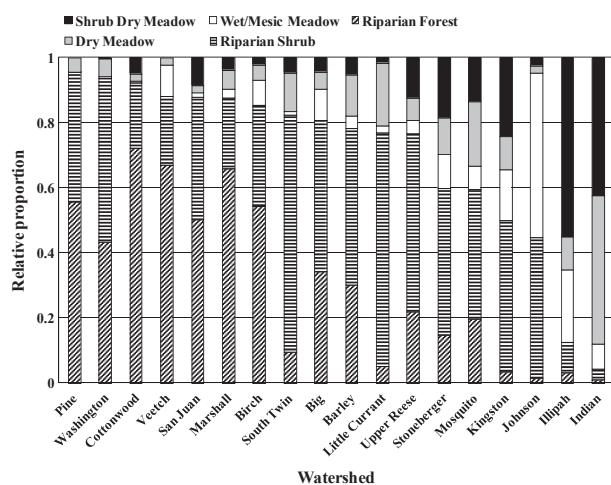


Fig. 2. Relative proportions of five riparian vegetation types occurring in 18 upland watersheds of the central Great Basin, with watersheds ordered according to decreasing proportion of woody vegetation.

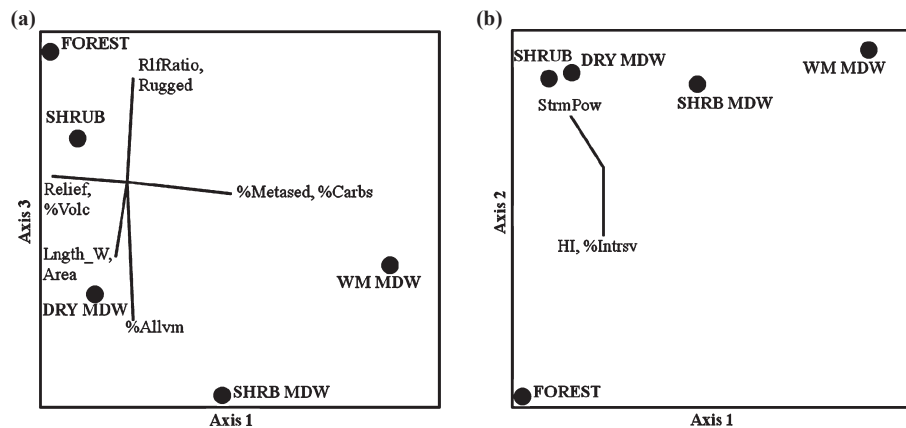


Fig. 3. Non-metric multidimensional scaling ordination biplots of riparian vegetation types with watershed morphometrics and lithology. FOREST, Riparian Forest; SHRUB, Riparian Shrub; WM MDW, Wet/Mesic Meadow; DRY MDW, Dry Meadow; SHRB MDW, Shrub Dry Meadow.

Table 4. Proportion of variance (R^2) represented by each NMS axis and Pearson correlations (r) of watershed morphometry and geology with each NMS axis. Geologic variables abbreviated as: % Allvm = percentage alluvium, %Carb = percentage carbonate, %Intrsv = percentage intrusive, %Metased = percentage metasedimentary, %Qrtzt = percentage quartzite, %Silclt = percentage siliclastics, %Volc = percentage volcanic. Pearson correlations exceeding |0.5| are shown in bold font. Abbreviations for morphometric variables are listed in Table 2.

	Axis		
	3	1	2
	$R^2 = 0.56$	$R^2 = 0.15$	$R^2 = 0.14$
%Allvm	-0.756	0.179	0.110
Shreve	-0.667	-0.057	0.426
Rugged	0.660	-0.039	-0.146
RlfRatio	0.645	0.215	-0.125
TLngth_S	-0.635	-0.175	0.406
Area_W	-0.555	-0.191	0.401
Lngth_W	-0.541	-0.279	0.354
HI	0.417	0.007	-0.501
%Qrtzt	0.408	0.031	-0.324
DrnDn	0.391	0.362	-0.369
%Carb	-0.327	0.656	0.526
%Intrsv	0.318	0.064	-0.533
Relief	0.216	-0.558	0.368
Shape_W	-0.194	-0.370	-0.038
StrmPow	-0.186	-0.426	0.522
%Silclt	-0.139	0.369	0.047
%Volc	-0.091	-0.574	0.232
%Metased	-0.024	0.633	0.137

Discussion

Our research helps to fill an information gap concerning how watershed-scale geomorphology influences the extent and character of riparian vegetation for small upland basins, complementing a much larger body of literature addressing influences of geomorphology at the scale

of the river reach (e.g. Wasklewicz 2001; Dixon et al. 2002). We found strong relationships among watershed-scale geomorphology and riparian vegetation extent and composition. The extent of the riparian zone was closely related to bedrock lithology in the watersheds, but in a direction counter to our hypothesis – riparian extent increased with percentage intrusives and decreased with percentage carbonates. Carbonate rocks can be more resistant than intrusive rocks to weathering in arid climates (Cooke et al. 1993) but greater fracturing results in more water diversion to the subsurface. In this study, watersheds with more carbonate bedrock and greater subsurface flow supported seep and spring systems and extensive meadow complexes along the main stream channels in areas with bedrock constrictions and low-permeability substrates. However, along ephemeral tributary drainages, riparian vegetation was confined to narrow corridors of shrub or herbaceous vegetation, thereby reducing the overall riparian extent. Watersheds underlain by more intrusive rocks were characterized by higher drainage density with continuous riparian zones comprised of riparian forests on multiple terraces, resulting in high overall riparian extent.

Riparian vegetation extent decreased with greater relative stream power. Large values of stream power indicate higher amounts of energy available to transport water and sediment (Bull 1979). Stream power was greatest in watersheds characterized by large size, high relief, low drainage densities and volcanic lithologies. In the central Great Basin, the response of these types of watershed to large flood flows has been localized to continuous channel incision (Germanoski & Miller 2004). Incision can contribute to lowering of the local water table and result in a transition from riparian to upland species (Belsky et al. 1999; Chambers et al. 2004b; Loheide & Gorelick 2007).

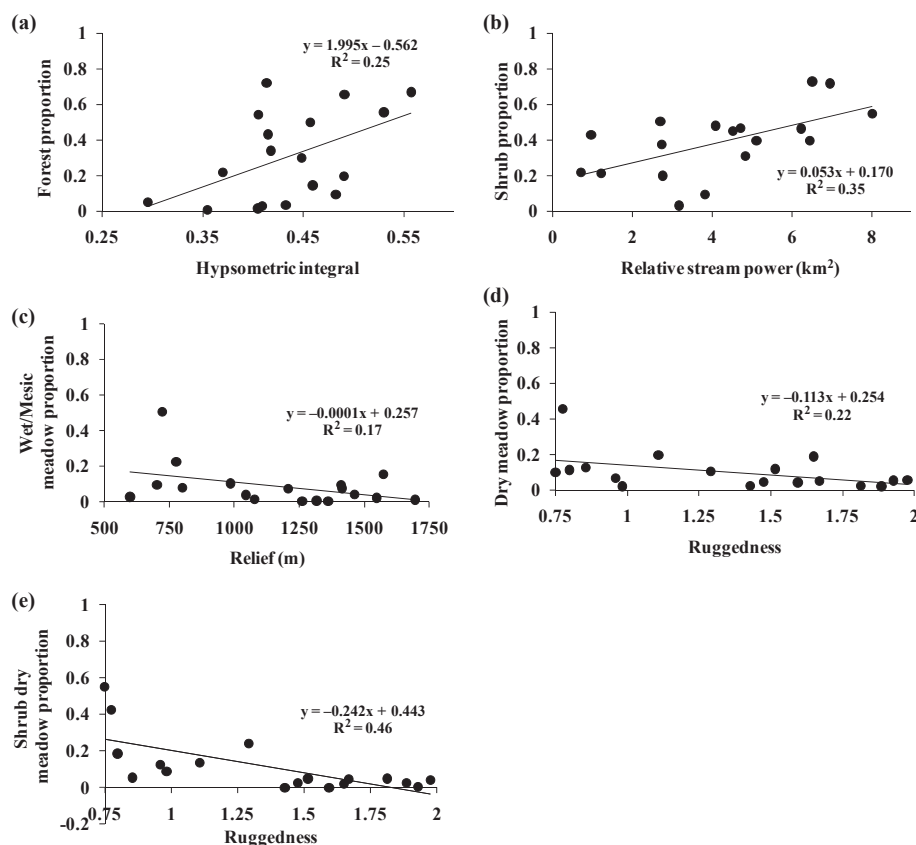


Fig. 4. Relationships between relative proportions of riparian vegetation types and watershed morphometric variables with the best explanatory power.

Although all five vegetation types were identified in the majority of the watersheds, the relative proportion of riparian vegetation types was strongly related to watershed morphometry and geology. As predicted, woody vegetation types were best explained by watershed variables related to the hydrograph and the potential for flood disturbances. Small, steep and rugged watersheds promote rapid run-off (Howard 1990; Germanoski & Miller 2004) and riparian forest and shrub types were generally more abundant in these kinds of watershed.

Watersheds with larger HI, indicating greater landmass above the base elevation of the watershed, were characterized by large proportions of riparian forest (*Populus* spp.). Such watersheds can most effectively capture and retain snow, producing higher snowmelt discharge in spring and early summer. Spring floods are especially important for the regeneration of *Populus* species such as *P. angustifolia* (Scott et al. 1996). *P. tremuloides*, a facultative riparian species with primarily clonal reproduction, is frequently associated with greater water availability and cooler temperatures (Weixelman et al. 1996). Watersheds with high relative stream power were most positively associated with the riparian shrub type. The species comprising this vegeta-

tion type (*Betula* and *Salix* spp.) share traits that allow them to thrive where scouring floods are likely, including high bending stability of shoots and roots, and the ability to re-sprout when uprooted or damaged by flood water (Karrenberg et al. 2002; Naiman et al. 2005).

The geology of watersheds with large proportions of riparian forest and shrub primarily consisted of volcanic and intrusive rocks. Watersheds underlain primarily by coarse-grained intrusive rocks are potentially more hydrologically responsive to precipitation events (higher discharge) than those underlain by sedimentary rocks (Kelson & Wells 1989). Due to high fracturing rates, intrusive igneous rocks are sources of non-cohesive pebble-sized sediments, known as grus, that promote infiltration but that are also readily eroded. Previous research in central Nevada indicates that watersheds underlain by volcanic rocks funnel precipitation directly to the stream channels, resulting in shorter lag times, higher peak flows and shorter-duration high flows compared to watersheds underlain by other rock types (Amacher et al. 2004; Germanoski & Miller 2004). These results support our findings because disturbance-tolerant woody vegetation types were most abundant in watersheds underlain by more volcanic and intrusive rocks.

Riparian meadows are dependent on groundwater and reach their greatest extent where geomorphic conditions promote fine sediment deposition and elevated water tables (Allen-Diaz 1991; Miller et al. 2001; Jewett et al. 2004). In this study, larger but more gently sloping watersheds contained higher proportions of meadow types. Larger watersheds with slower water release times likely are conducive to the persistent high water tables necessary to support meadow ecosystems. These watersheds had the highest percentage of alluvial deposits, indicating sediment supply in excess of transport capacity (Montgomery & Buffington 1997). The wet/mesic meadow type was strongly associated with a higher percentage of carbonate and metasedimentary rocks within the watershed. These rock types promote infiltration and maintenance of high groundwater levels, and weather to produce smaller sediment particle sizes compared to intrusive igneous rocks (Kelson & Wells 1989; Sable & Wohl 2006). Fine-grained meadow sediments of lower hydraulic conductivity favour higher water tables and hence provide suitable conditions for persistence of wet/mesic meadow vegetation (Loheide et al. 2009; Lowry & Loheide 2010). These watersheds were also characterized by less topographic relief, which facilitates longer water and sediment retention times. Finally, side-valley alluvial fans are common and important geomorphic features that can constrain flow and result in sediment deposition upstream (Miller et al. 2001). In those cases where elevated water tables occur above the alluvial fans, meadow ecosystems are common (Chambers et al. 2004b; Jewett et al. 2004). Our results suggest that watershed characteristics related to water and sediment residence times are important for predicting the abundance of meadow vegetation types.

Our results were obtained from a series of watersheds with similar climate but different geomorphic architecture and bedrock types and demonstrate that watershed-scale lithology and geomorphology are strongly related to the extent and composition of riparian vegetation. Geology and watershed morphometry, attributes that influence run-off regimes as well as water and sediment retention, successfully explained the majority of the variation in patterns of vegetation in the riparian corridor. These results parallel those of other recent studies that indicate watershed-scale properties influence riparian communities directly and independently as well as through constraints on reach-scale environments (e.g. Chambers et al. 2004b; Sarr & Hibbs 2007; Baker & Wiley 2009; Mortenson & Weisberg 2010). Although prediction of the vegetation type at any specific position in the watershed depends on local site factors, watershed-scale properties constrain the extent of the riparian corridor within the watershed as well as the abundance of a given vegetation

type within that corridor. Multi-scale, hierarchical modeling of riparian vegetation typically considers finer scales of geomorphic units (e.g. sandbars), transverse variation along river cross-sections, and longitudinal variation along the elevational gradient within a single watershed (e.g. Dixon et al. 2002; Yang et al. 2011). Our work suggests that predictive models of riparian vegetation may not be generalizable among watersheds unless watershed-level lithologic and geomorphologic characteristics are incorporated.

Knowledge of the relationships among watershed lithology, geomorphology and riparian vegetation types can be used to develop management and restoration strategies for small, upland watersheds. The findings of this study are consistent with our previous research that related the hydrogeomorphic and vegetation characteristics of individual stream reaches to the watershed-scale properties of a subset of the study watersheds (Chambers et al. 2004b). These findings also confirm that digitally-derived terrain models can be used to characterize watershed and riparian vegetation and assist in watershed-scale planning efforts over large landscapes. We illustrate the use of information from this study for management and restoration planning, with an example from watersheds with volcanic lithologies. As indicated in this study, watersheds underlain primarily by volcanic rocks are typically characterized by high relief basins, shorter lag times and higher peak flows, and disturbance-tolerant woody vegetation. Additional geomorphic interpretation indicates that watersheds also characterized by narrow valley bottoms and bedrock controls are typically flood-dominated and can exhibit significant channel change during high flows (Germanoski & Miller 2004). Consequently, these watersheds are highly sensitive to both natural and anthropogenic disturbance and require proactive management of land uses like livestock grazing, roads and recreation. Management and restoration in these types of watershed should focus on maintaining natural channel configurations and re-establishing the woody riparian vegetation that characterizes the riparian corridors (Chambers et al. 2004a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Watershed morphometry and bedrock lithology of eighteen upland watersheds in the central Great Basin.

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