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Relationships among hydrogeomorphic processes and the distribution, age and stand characteristics of woody species in Great Basin upland riparian areas

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ABSTRACT

Riparian ecosystems often constitute less than one percent of the central Great Basin landscape but provide critical ecosystem services. Shrubs and trees are fundamental components of these riparian ecosystems that can provide stabilization of sediment and resistance to stream down-cutting. This can promotes ground-water recharge and maintenance of elevated water tables. Fluvial processes shape landforms and riparian woody species distribution across those fluvial landforms. In the arid to semi-arid west, riparian woody species are distributed along vertical elevation gradients within stream reaches (i.e., height above and distance from the channel) and along longitudinal elevation gradients within watersheds (i.e., contributing area and local bedrock) according to their life history and ecophysiological traits. Thus, knowledge of the hydrogeomorphic context at both watershed and stream reach scales is essential for understanding woody species establishment and persistence in riparian ecosystems.

This study was located in the central Great Basin across four study watersheds characterized by small watershed size, low relief, and narrow valley floors. Streams were relatively high stream gradient, channel bed material was coarse to fine-grained and bedrock geology varied among watersheds. The study examined the influences of hydrogeomorphic setting and flood disturbance on the distribution, age and stand characteristics of four "key" woody riparian species (*Betula occidentalis*, *Salix exigua*, *Salix lutea*, and *Populus tremuloides*) with different ecological amplitudes and life history characteristics. Three questions were addressed: (1) How do hydrogeomorphic factors affect the spatial patterning of riparian woody species with different ecological amplitudes and life history traits ? (2) How do the hydrogeomorphic setting and flood events affect establishment of woody species with different ecological amplitudes and life history traits ? (3) How does the hydrogeomorphic setting affect the stand structure of woody species with different ecological amplitudes and life history traits ? Geomorphic data were sampled along stream cross-sections and included all inset terraces and

surfaces from the channel thalweg to the valley floor (upland) surface. Woody vegetation data were sampled along the same cross-sections for size and abundance. Watershed data pertaining to each cross-section were obtained following field data collection (e.g. contributing area, local bedrock). The strongest influences on spatial patterning of the woody species were longitudinal gradients in the watershed and vertical gradients perpendicular to the stream within stream reaches. Ecological amplitudes and life history traits often aligned directly with those gradients.

P. tremuloides dominated the upper watersheds where cooler temperatures were coincident with species requirements. *Salix* spp. dominated moderate elevations and active channel zones in all of the study watersheds demonstrating its tolerance of flood disturbance and inundation. *B. occidentalis* was most abundant at intermediate to low elevations with constricted valleys and high stream power. *B. occidentalis* often occurred in reaches exhibiting channel incision and lowering water tables, as indicated by steep bank angles and high entrenchment ratios, and had low recruitment.

Tree age structures showed a pulse of seedling establishment following regional flooding in 1983/1985. Seedling establishment following the 1983 and 1985 floods was watershed-specific and highly predictable (72.6 %) according to environmental context. Seedling establishment was positively associated with the incised alluvial process zone, small clasts in the channel bed, low stream gradients, and a high number of inset stream terraces. As in other riparian areas of the semi-arid west woody species seedling establishment depended on bare, moist alluvial substrates with constant soil moisture provided by fine-grained bed material.

Woody species stand characteristics were sensitive to geomorphic process zone type and specific watershed characteristics. Young, low density stands and new establishment due to flooding were strongly related to the incised alluvial process zone and specific watershed characteristics. Riparian succession and stand structure were only slightly related to geomorphic variables in these watersheds. The study watersheds differ in relative sensitivity to disturbance,

but all are in an incisional phase. The 1983/1985 flood resulted in widespread stream incision and reinitiated successional processes. Flood effects were most pronounced in the alluvial process zone which is characterized by active deposition and erosion and in San Juan Canyon which has volcanic lithology, flashy flows and compounding perturbations (roads in valley bottom, beaver dams). Abundance of newly established stands was low for *B. occidentalis*. Because of the location of *B.occidentalis* in areas prone to flood disturbance and incision, this species has generally low recruitment and is of management concern.

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INTRODUCTION

In arid and semiarid regions of the United States, riparian ecosystems often constitute less than one percent of the landscape but provide critical ecosystem services including a sustained supply of high quality water and habitat for a diversity of aquatic and terrestrial plants and animals (National Research Council 2001). Shrubs and trees are fundamental components of these riparian ecosystems that can provide stabilization of sediment that compose streambanks and floodplains (Hupp and Osterkamp 1996; Patten 1998). They also tend to prevent the river from down-cutting, and thus promote ground-water recharge and maintenance of elevated water tables (Patten 1998). Trees and shrubs provide shade that regulates light and water temperature regimes and contribute organic matter that provides food for aquatic and terrestrial biota (Naiman *et al.* 1993; Wallace *et al.* 1996). They supply forage for livestock and, on a scenic level, provide highly desirable fall colors. Loss of native riparian shrub and tree species (Busch and Smith 1995; Cooper *et al.* 2006) due to widespread riparian ecosystem degradation (National Research Council 2001) is placing many of these ecosystem services at risk. A better understanding of the interaction among riparian woody species, geomorphic controls, and hydrologic regimes in riparian ecosystems is critical for their preservation in arid and semi-arid regions.

Fluvial processes are a major determinant of plant community composition adjacent to streams. Floods are, perhaps, the most important extrinsic factor in riparian systems (Kondolf and Piegay 2003). The effects of floods on riparian community organization have both hydrologic and geomorphic components (Bendix and Hupp 2000). Riparian plant distribution is controlled by fluvial geomorphic settings and processes- cycles of aggradation and degradation (Hupp and Ostercamp 1996). Floods influence the geomorphic setting by creating new features such as point bars (Hupp and Ostercamp 1996); slumps, debris flows, tributary alluvial fans (Scott *et al.* 1996); floodplains, terraces, and inset terraces formed by channel narrowing and/or channel incision (Baker and Walford 1995; Friedman *et al.* 1996). Fluvial processes interact with existing

geomorphic settings (local bedrock, geologic history, and tributary influences; Scott *et al.* 1996). Flood generated surfaces devoid of vegetation facilitate riparian species establishment and partially explain the spatial and temporal patchiness of riparian community organization.

Riparian vegetation patterns are related to the geomorphic setting but differentiate along water table gradients (Bendix and Hupp 2000; Merritt and Cooper 2000). Water availability, as indicated by stream channel elevation, is often the primary control on riparian species distributions (Bendix and Hupp 2000; Chambers *et al.* 2004b; Hupp and Ostercamp 1996; Merritt and Cooper 2000; Stromberg *et al.* 1996). The likelihood of a given species germinating and persisting on a particular landform is a function of (1) the suitability of the site for germination and establishment, and (2) the ambient environmental conditions at the site that permit persistence at least until reproductive age (Hupp and Osterkamp 1996; Kondolf and Piegay 2003). The occurrence of suitable sites for germination must coincide with seed dispersal of riparian plants. Mahoney and Rood (1998) described a "recruitment box model" for cottonwoods that integrates the annual hydrograph, stream stage patterns, and the timed release of woody seeds. This model is important for understanding seedling recruitment, but asexual pathways for woody species establishment following floods must also be considered (lateral root sprouting, root crown resprouting).

Riparian shrubs and trees are typically disturbance adapted species that are subjected frequently to flooding, abrasion, drought, and freezing (Naiman and Decamps 1997). Community dynamics are partly controlled by the life history traits of the plants. Riparian woody species tend to share ecophysiological traits that allow them to resist, endure, or avoid disturbance such as (1) flexible stems and roots to withstand high levels of shear stress accompanying floods (Salicaceae, Karrenberg *et al.* 2002; Naiman and Decamps 1997); (2) air space (aerenchyma) in roots and stems to avoid anoxia during inundation (Naiman and Decamps 1997); (3) sexual reproduction via large crops of small, wind- and water-dispersed seeds (*B. occidentalis*, Uchytil 1989a;

Williams and Arnold 2001;Salicaceae, Karrenberg *et al.* 2002; Gage and Cooper 2004); and, most importantly; (4) the ability to reproduce asexually (suckering from lateral roots [*P. tremuloides*, Sheppard *et al.* 2001; *S. exigua*, Douhovnikoff *et al.* 2005], resprouts from the root crown or stem base [Bellingham and Sparrow 2000], vegetative propagules [Salicaceae, Karrenberg *et al.* 2002; Naiman and Decamps 1997; USDA 2008]). Bellingham and Sparrow (2000) suggested that the amount of resprouting vs. seeding establishment depended upon on the severity of disturbance. Where disturbance intensity was high or extremely low, reproduction of seed should be favored, while intermediate disturbance intensity should promote resprouting.

Though similar in some biological features, woody riparian species occur in different hydrologic and geomorphic settings. In arid regions of the northern hemisphere, members of the Salicaceae (e.g. *Salix* spp., *Populus* spp.) play an important role in colonizing active floodplains (Karrenberg *et al.* 2002; Scott *et al.* 1996); stream point bars, drained beaver ponds, and abandoned channels (Rocky Mountains of North America; Cooper *et al.* 2006). *Salix* species are capable of occupying banks of streams subject to long-term inundation from flooding or ponding (up to 5 years, Amlin and Rood 2001; USDA 2008), while aspen (*Populus tremuloides*) occurs on mid- and upper- terraces (the transition zone) because it cannot tolerate inundation (Perala 1990). Water birch (*Betula occidentalis*), a western North American woody riparian species occupies moist locations adjacent to streams where flood risk is high (USDA 2008). Friedman *et al.* (2006) found that *B. occidentalis* populations along Plum Creek, in the plains of eastern Colorado, reached their peak abundance on sites with recurrence intervals of inundation between 2.2 and 4.6 years. Disturbance adapted shrubs and trees dominate riparian areas because they are able to survive and regenerate under unpredictable disturbance regimes.

Longitudinal elevation gradients along the length of the valley floor and vertical gradients perpendicular to the stream are interrelated and exert strong influences on riparian vegetation patterns (Amlin and Rood 2001; Bendix and Hupp 2000; Cooper *et al*. 2003; Engelhardt 2009;

Friedman *et al*. 1996, 2006; Hupp and Ostercamp 1996; Karrenberg *et al*. 2003; Mahoney and Rood 1998). Vertical gradients perpendicular to the stream, such as height above and distance from the stream channel, determine soil water availability and susceptibility to flood disturbance. Small differences in elevations above the channel (cm) can lead to pronounced differences in inundation (Kondolf and Piegay 2003) and thereby determine species patterns based on inundation-tolerance and drought-tolerance (Amlin and Rood 2001). In the arid to semiarid west, longitudinal elevation gradients are generally characterized in the downstream direction as having increasing evapotranspiration demands, increasing temperature, decreasing precipitation, decreasing stream gradient, increasing depth to bedrock, increasing watershed size (Patten 1998); and increasing watershed contributing area, thus, higher unit steam power (Bendix 1997). Rate of groundwater drawdown following high flows is also important and related to elevation. Several studies have examined how species differentiate along these elevational gradients, especially *Populus* spp. and *Salix* spp. (Amlin and Rood 2001, 2002; Karrenberg *et al*. 2002; Mahoney and Rood 1998); or how woody species establishment relates to flow and local and watershed elevations (Friedman *et al*. 1996; Mortenson and Weisberg 2010; Scott *et al*. 1996, 1997). Measurable temporal gradients of stream-to-upland vegetation are obtainable from relatively stable streams with low flood frequencies (Patten 1998). Few riparian studies have examined relationships among hydrogeomorphic processes and the distribution, age, and stand structure of riparian woody species along longitudinal and vertical gradients.

Streams in the humid eastern U.S. differ from streams in the arid west, where riparian vegetation depends on groundwater or river water to meet species water requirements (Hupp and Ostercamp 1996). The arid west of North America extends west from the 100th meridian to the crest of the Cascades and Sierra Nevada, south from southern Canada to northern Mexico. This geographic region, often recognized as the Basin and Range Province described by Fenneman (1931), contains a variety of environmental and geographic gradients to which riparian plants

must adapt (Patten 1998). The one standard description for riparian ecosystems in the arid west is that the riparian zone essentially encompasses alluvial sediment deposits where the river and alluvial ground water supplement limited local precipitation (Gregory *et al*. 1991). The moisture/elevation gradients determine the distribution of riparian vegetation. However, there also are marked differences among western streams including channel patterns (e.g. braided, meandering, straight), fluvial and geomorphic processes.

Fluvial geomorphologists have designed classification schemes for river segments (e.g. Brierley and Fryirs 2000; Frissel *et al.* 1986; Montgomery and Buffington 1997; Rosgen 1996; Schumm 1985) and use them as a tool to assess stream condition, predict disturbance response, and interpret history of channel change (Montgomery and Buffington 1997). Process zones, defined as designated river sections, generally have uniform hydrologic and geomorphic characteristics and behaviors. Montgomery and Buffington (1997) linked channel process to channel form and offered a process-based mountain drainage basin classification based on channel-reach morphology. Schumm (1985)'s classification was also "process-based" but it was based on channel pattern, channel type, and relative stability. The boundary conditions for process zones include channel: (1) geomorphology (e.g. pool, riffle, run, terrace, fill); (2) geometry; (3) planform; (4) geology; (5) particle size; and (6) landform position. Disturbance patterns are inherently patchy between process zones (local-scale) resulting in diverse conditions under which woody plants assemble (Cooper *et al*. 2003).

Each characteristic (above) that delineates a process zone is highly influential on a site-to-site basis. Landform position is critical in aridlands because it affects access to moisture as well as flood regime (Hupp and Ostercamp 1996). Particle size (i.e. sediment vs. cobble) affects infiltration and surface conditions for plant establishment (Baker and Walford 1995; Renofalt *et al.* 2007). Local and basin geology have a significant influence on sensitivity to channel incision and geochemistry of surface and groundwaters (Chambers and Miller 2004). The configuration of

a river in plan view influences the path of water during high-flows; as does the channel's cross sectional profile or geometry. The geomorphic units are important biophysical attributes because they represent specific associations between landscape morphology and the set of processes that produce that form (Brierley and Fryirs 2000). Examples include pool, riffle, run, terrace, fill, and bench. Determining the role of process zone characteristics in episodes of woody species establishment and persistence yields a more complete understanding of the spatial and temporal patterns of riparian woodlands.

Dendrochronology can provide botanical evidence of hydro-geomorphic events, such as high flows (Kondolf and Piegay 2003). Dendrochronology techniques have been widely used to yield information on episodes of woody riparian species establishment in the semi-arid west (e.g. Baker and Walford 1995; Charron and Johnson 2006; Cooper *et al.* 2003, 2006; Friedman *et al.* 1996; Karrenberg *et al*. 2003; Scott *et al.* 1997). The age of the oldest woody species on a surface (e.g. terrace, bank) can be used as a surrogate for the year the underlying surface formed (e.g. Chambers *et al*. 1998; Friedman *et al.* 1996). Tree-ring dating for the interpretation of geomorphic processes is called dendrogeomorphology and is becoming an increasingly common technique (Kondolf and Piegay 2003). Two studies using a tree age approach have been conducted in the Great Basin along mountain streams. Henderson (2001) used a hydroclimatic approach (study was conducted adjacent to stream gages) and found that near-stream establishment of *Betula occidentalis*, *Salix* spp., and *Populus* spp. date primarily to significant high flow events that occurred during the last 50 years in central Nevada. Chambers *et al.* (1998) dated *Salix* spp. occupying near-stream surfaces and found that similar maximum ages occurred at similar surface heights above the stream channel. The maximum age within a stand appeared to be highly correlated with time since the last major flood event. Both studies cited the need for further investigation of large scale geomorphic effects and the influence of stream reach characteristics. A long-term study on the Hassayampa River, a small unregulated river west of

Phoenix, Arizona, showed how the hydrologic and geomorphic processes that result in stream-to-upland riparian vegetation gradient can represent temporal gradients, as well as temporal stages of succession (Patten 1998).

Several studies have documented the relationships of geomorphology and fluvial landforms with woody species distribution and establishment including cottonwoods (e.g. Friedman *et al*. 1996; Kranjcec *et al.* 1998, Rood *et al.* 1994); cottonwoods interaction with invasive woody riparian species (e.g. Cooper et. 2003; Scott *et al.* 1996, 1997; Shafroth *et al.* 1995, 1998); and certain species of *Salix* (e.g. Amlin and Rood 2002; Auble *et al.* 1994; Douhovnikoff *et al.* 2005; Friedman *et al*. 2006; Gage and Cooper 2004; Karrenberg *et al.* 2002). However, we still lack sufficient information on the processes that control the establishment of *Betula occidentalis* (Friedman *et al.* 2006), *Salix* spp. (Cooper *et al.* 2006) and *P. tremuloides* to facilitate effective restoration of riparian areas. Further, population declines of *Salix* spp. (Cooper *et al*. 2006) and *P. tremuloides* (Worrall *et al*. 2008) are of great concern in the western U.S. The highly dynamic rivers that characterize the semi-arid mountain rivers of the west offer an exceptional opportunity to investigate, in detail, woody species response across a wide range of hydro-eco-geomorphic conditions (Kondolf and Piegay 2003).

The focus of this research is on streams in upland drainage basins of the central Great Basin. Many of the stream systems are currently functioning as non-equilibrium systems which results from the disequilibrium between the controlling factors (e.g. a change in the rates of sediment or water delivery to the system) and channel form over time ranging from decades to centuries (Germanoski and Miller 2004). Channel morphology in this region is still responding to a major drought that occurred from 2500 to 1900 YBP (Miller *et al.* 2001, 2004). During this dry period much of the fine-grained sediment was eroded from adjacent hillslopes. Consequently, the streams are sediment limited and exhibit a natural tendency to incise during high flow (flood) events. Recent anthropogenic (grazing, road construction, road captures, dams, mining, campsite

construction) and natural (beaver activity, wildfire, landslide, flood) disturbance have increased the rate and magnitude of incision (Lahde 2003, Chambers *et al*. 2004b). Floods that are capable of entraining channel bed sediment also are controlling incision and riparian ecosystem dynamics (Chambers *et al*. 1998). Stream incision has led to a decrease in aerial extent of stream associated riparian ecosystems as well as significant changes in species composition (Chambers *et al*. 1998). Geomorphic responses to disturbance are variable both among basins (Germanoski and Miller 2004) and among process zones within basins, and have significant effects on riparian vegetation (Chambers *et al*. 2004a). Little is currently known about the importance of episodic high flow events and stream incision on the age and stand dynamics of woody species within these systems or the implications for management. The present research examines the relationships among basin (large scale) and process-zone (small scale) geomorphic characteristics, woody vegetation distribution, age, stand structure, and species-specific response to flood.

This study focuses on four upland watersheds in the Toiyabe Mountain Range of central Nevada. The process zones within each watershed are delineated and the geomorphic characteristics of each process zone determined. The age and stand characteristics of four "key" woody riparian species (*Betula occidentalis*, *Salix exigua*, *Salix lutea*, and *Populus tremuloides*) were examined in relation to different fluvial surfaces that occur within each process zone (e.g. Chambers *et al.* 1998; Friedman *et al.* 1996). The specific objective of this study was to gain an understanding of the relationship between hydrogeomorphic variables and riparian woody species spatial patterning and stand dynamics, especially in response to natural flood disturbance in the central Great Basin. Three questions were addressed: (1) How do hydrogeomorphic factors affect the spatial patterning of riparian woody species with different ecological amplitudes and life history traits? (2) How do the hydrogeomorphic setting and floods affect establishment of woody species with different ecological amplitudes and life history traits? (3) How does the

hydrogeomorphic setting affect the stand structure of woody species with different ecological amplitudes and life history traits?

In general, I hypothesized that species occurrence and stand structure were related to the geomorphic characteristics of the different process zones or hydro-geomorphic characteristics that define the process zones. I also predicted that woody species life history traits were related to the hydro-geomorphic characteristics of the process zones. Finally, I predicted that the present age structure of riparian woody species in central Great Basin mountain ranges was related to a temporal sequence of fluvial surfaces formed during recent floods.

Study Species

Betula occidentalis Hook.

Water birch (*B. occidentalis*) is a small tree or large shrub with multiple trunks that form crowded dense thickets (USDA 2008). It is found commonly in all the western states along rivers, streams, and in moist locations at elevations from 4,500 to 10,000 ft (USDA 2008; Hickman 1993). In central Nevada riparian areas, it is common along stream terraces at canyon mouth constrictions and on sandy trough-shaped floodplains (Weixelman *et al.* 1996). It is shallow-rooted and occurs only where water table is just beneath the surface (Uchytil 1989a; Weixelman *et al.* 1996). Although its roots can help to stabilize stream banks, *B. occidentalis* are frequently uprooted by wind, water, or heavy snow (Weixelman *et al.* 1996). Soils vary from gravelly, cobbly to medium textured (USDA 2008) and its nutrient requirement is high (i.e. high magnesium and calcium) (Uchytil 1989a). Weixelman *et al.* (1996) found that it occurs on soils with extremely high infiltration rates. Depth to field capacity was generally within a meter. It favors alluvial terraces, steep sideslopes, or sediment adjacent to streams where flood risk is high (Uchytil 1989a). A close relative to *B. occidentalis* (family: Betulaceae), alder (*Alnus*), is also found adjacent to streams.

B. occidentalis' primary method of reproduction is by wind throw or water dispersed seed (Uchytil 1989a; Williams and Arnold 2001). Its seed is dispersed in the fall and can germinate then or the following spring (Uchytil 1989a). The seeds are lightweight and extremely small causing them to be at a great risk for mortality particularly where light is limited (Walters and Reich 1996). The lightweight *B. occidentalis* seeds are often seen blowing over snow (Lanner 1983). Seed longevity is not known but its seeds outlive those of the other study species (Salicaceae, 4 weeks maximum). Another mode of regeneration commonly employed is sprouting from the root crown. As the tree/shrub grows, dormant buds hidden beneath the bark at the base of the trunk begin to sprout sending up small new trunks alongside the original one (Uchytil 1989a). Resprouting is a response to intermediate disturbance such as flood (Bellingham and Sparrow 2000). Often times, a massive clump of up to a hundred or more stems of all sizes is formed, resulting in a "crowded dense thicket" (USDA 2008). It provides shaded galleries and cool water important for wildlife, birds and fish (Weixelman *et al.* 1996).

Populus tremuloides Michaux

Quaking aspen (*P. tremuloides*) is a clonal tree found in dense stands, usually consisting of one clone or aggregates of clones that are often broadly even-aged (Howard 1996). It is widespread throughout North America growing on a wide spectrum of landforms including waterways, canyons and mountainsides from 1,200 m to 3,000 m (Howard 1996). In central Nevada riparian areas, it is found from 1,800 m to 2,400 m in trough floodplains, and on stream terraces and toeslopes (Weixelman *et al.* 1996). Its elevational range indicates tolerance to severe cold but not high temperatures or low soil water availability concurrent with low elevations (Jones *et al.* 1985; Worrall *et al.* 2008). *P. tremuloides* occupies a drier ecotone, farthest from the stream, above the zone of cottonwoods and facultative riparian *Salix* (Amlin and Rood 2001). In stream environments it generally occurs on mid- and upper- terraces (the transition zone) because it does not tolerate long-term inundation (Perala 1990). Prolonged flooding usually results in a

fungal infection that reduces stem life (Peterson *et al.* 1992). *P. tremuloides* prefers a substrate that is well-drained, loamy, high in organic matter and nutrients (Perala 1990). It provides important breeding, foraging, and wildlife habitat for a variety of birds and mammals (Howard 1996; Sheppard *et al.* 2001).

P. tremuloides primarily regenerates vegetatively via root suckering (formation of adventitious shoots) after mature stems die from fire, disease, snow damage (avalanche) or other perturbances that initiate a suckering event (Sheppard *et al.* 2001). In central Nevada riparian areas, it reproduces clonally at the cue of disturbance to the canopy (fire, beaver; Weixelman *et al.* 1996). Lateral roots may extend, shallowly, more than 30 m into open areas (Buell and Buell 1959; Sheppard 2006). "Sinker roots" may descend from points often below ramets reaching depths of more than 2.7 m (Johnston 1970, Johnston *et al.* 1969). *P. tremuloides* cannot reproduce beneath its own canopy because it is highly shade intolerant (Karrenberg 2002). Windblown or water transported seed is another, but less effective, method of *P. tremuloides* reproduction (Howard 1996). Seed viability lasts for 2-4 weeks strictly under favorable conditions of low temperature and low humidity (Howard 1996). Optimum conditions for germination include moist alluvium, adequate drainage and freedom from disturbance and competition (Howard 1996).

Salix exigua Nutt.

Coyote willow (*Salix exigua*) is a clonal, “creeping-type” willow with numerous slender stems (USDA 2008). It is widespread in the western United States up to 2,700 m. At high elevations it is confined to streamside communities adjacent to flowing water (Stromberg 1996). In central Nevada riparian areas, it favors trough floodplains, streambanks, ditches and gravel bars (Weixelman *et al.* 1996). *S. exigua* spreads primarily by way of underground rhizomes that have the ability to adventitiously root (e.g. Krasny *et al.* 1988). This reproduction strategy allows it to survive and spread in heavily disturbed zones near the channel. *Salix* exigua is the only *Salix*

in Nevada that forms large clones by sprouting from root runners and is highly adapted for colonizing disturbed areas (Goodrick 1992). Its fitness has been well-documented in the west. Though less utilized as a regeneration strategy (Douhovnickoff *et al.* 2005), *S. exigua* also can regenerate from broken roots or stems, which are transported downstream and deposited by floodwaters and later sprout (Karrenberg 2002). Unlike most other *Salix*, *S. exigua* cannot resprout from its root crown and relies primarily on rhizomes (Anderson 2006). *S. exigua* is a poor competitor for light and moisture; it does not persist on older, drier, shaded sites (Auble *et al.* 1994; Friedman *et al.* 1996). It can withstand flood periods during two or more growing seasons and is also highly drought resistant (Anderson 2006). *S. exigua* prefers coarse soil but will grow on moist soil, from gravel to silt and at extremely low nutrient levels (Anderson 2006).

It is known for its dense clonal thickets that develop from shoot buds on lateral roots (Douhovnickoff *et al.* 2005). Seedling mortality is high so it relies primarily on asexual reproduction; Douhovnickoff *et al.* (2005) found seedling mortality to be 100% within six different disturbance regimes over two years. However, episodic establishment by seed can be quite extensive when conditions are right (Chambers *et al*. 1998). Its seeds are only viable for a short period of time (Young and Clements 2003). Fire and flood periodically wipe out the vegetation, leaving a blank seedbed for new *Salix* establishment (Weixelman *et al*. 2006). In the absence of disturbance, stands can become decadent (Douhovnickoff *et al.* 2005). Over time *Salix* clones can be replaced by taller stemmed, more shade tolerant species (Douhovnickoff *et al.* 2005). Their stems typically live to age 10 and only sometimes older to 20 years old (Anderson 2006); although they have been routinely aged up to 50 years old in central Great Basin riparian systems (pers. comm. J. Chambers January 2009). They are highly palatable to livestock, big game, and beavers (Kovalchick *et al*. 1998).

Salix lutea Nutt.

Yellow willow (*Salix lutea*) is a riparian shrub with a rounded shape, occasionally becoming a multi-stemmed tree (USDA 2008). It is found at low to moderate elevations, very commonly from 1,200 to 2,300 m (USDA 2008). It grows along the banks of streams in coarse cobble and on moist terraces with deep, fine textured soils (USDA 2008). In central Nevada riparian areas it is found from 1,500 to 2,600 m, usually below 2,300 m (Weixelman *et al*. 1996); at low stream gradients within trough floodplains (Weixelman *et al*. 1996). It is a pioneer species that grows along streambanks subjected to periodic flooding but it also can be long-lived on moist terraces away from the channel (Youngblood *et al*. 1985). If conditions become permanently drier on these upper terraces, *S. lutea* stands can be replaced by grass-dominated communities (Hansen *et al*. 1988) or *P. tremuloides* (Weixelman *et al*. 1996). *S. lutea* often shares regeneration niches with *S. exigua*. It occupies the vertical gradient above *S. exigua* (Amlin and Rood 2001; Chambers *et al*. 2004b) and withstands more rapid water decline rates than *S. exigua* (Amlin and Rood 2000).

Regeneration primarily occurs vegetatively from broken roots or stems, which are transported downstream and deposited by floodwaters and later sprout (Karrenberg 2002). *S. lutea* resprouts vigorously from its root crown or stem base following disturbance but it cannot produce lateral shoots (*S. exigua* and *P. tremuloides* can produce lateral shoots) (Karrenberg 2002; Uchytil 1989b). As with *S. exigua*, fire and flood are its agents for regeneration (Weixelman *et al*. 2006). Windblown or water transported seed is one method of reproduction but the seeds are viable for only a few days and must germinate within 12-24 hours on a moist alluvial surface (Uchytil 1989b).

METHODS

Study Area

The study was located within the Great Basin of central Nevada in four watersheds of the Toiyabe Mountain Range: Kingston, San Juan, Cottonwood and Birch (Figure 1). Birch and

Kingston have east-facing aspects, whereas San Juan and Cottonwood have west-facing aspects. Watershed elevations range from 1,850 to 3,200 m with precipitation averages ranging from about 25 cm at the basin mouths to 55 cm at upper elevations (Chambers and Miller 2004). Precipitation falls largely as snow during winter months (60 %; Chambers and Miller 2004). There is a pronounced annual runoff of snowmelt in late May or early June. Localized convective summer storms result in flash floods, augmenting stream flow (Chambers and Miller 2004).

This research focused on the main channels of perennial streams. The stream systems are defined as narrow, high stream gradient, and coarse-grained, with a natural tendency to incise (USDA Forest Service 1996). The watersheds are small (mean = 4475 ha, range = 2200 to 7292) with high relief (mean = 1332 m, range = 1078 to 1574 m) (Engelhardt 2009). Maximum regional peak flows range from 0.214 to 0.683 m^3/s (7.56 to 23.12 cfs); typical low flows for the region tend to be between 0.015 to 0.063m^3/s (0.53 to 2.22 cfs) (Hess and Bohman 1996; Weixelman *et al.* 1996). Geology influences the hydrograph of individual watersheds, and watersheds underlain by volcanic rock (e.g. San Juan Creek) can have flashier hydrographs than those of watersheds underlain by sedimentary rock (e.g. Kingston Canyon) due to longer retention times in sedimentary watersheds (Chambers and Miller 2001). Lithology and watershed size and shape influence flow regimes and sediment characteristics and, thus, the propensity for incision (Chambers and Miller 2004; Germanoski and Miller 2004). Lithologies underlying the watersheds are igneous in San Juan Canyon (mostly volcanics with some carbonates and intrusives) characterized by smoothed longitudinal profiles and deep incision; sedimentary in Kingston Canyon (carbonates, siliciclastics and phyllite) characterized by coarse channel bed material and moderate incision; a mix of igneous and sedimentary bedrock in Birch Canyon (intrusives, siliciclastastics, carbonates, volcanics and alluvium) characterized by discontinuous and localized incision and mostly quartzite with some volcanic and intrusive bedrock in

Cottonwood Canyon characterized by steep stream gradients with moderate incision (Germanoski and Miller 2004).

Upland watersheds within the Toiyabe, Toquima, and Monitor Ranges of central Nevada have similar valley floor morphologies that are characterized by stream systems incised into low relief, narrow (< 150 m wide) valley floors (Miller *et al.* 2001). Valley widths are sometimes restricted by bedrock to as little as 20 m (e.g. Birch Canyon). These central Nevada mountain ranges are north-south fault blocked characterized by complex structural geology (Kleinhample and Ziony 1985). Side-valley alluvial fans often traverse the entire width of the valley floor confining the axial channel between alluvial fan deposits and hillslope colluvium or bedrock (Miller *et al.* 2001). All of the channels are prone to incision to varying degrees based on watershed sensitivity (Germanoski and Miller 2004). Watershed sensitivity is defined as the propensity of a system to respond to an external disturbance and is based on characteristics including geology (e.g. volcanic, sedimentary), relief (e.g. ruggedness, stream power, hysometric integral), watershed shape (e.g. elongated, equant), fan influence, longitudinal profile (e.g. stepped, smoothed), incision (e.g. deep, localized), and terraces (e.g. discontinuous, continuous) (Germanoski and Miller 2004). Channel incision can alter the physical and hydrologic systems, resulting in changes to the distribution and composition of vegetation in the riparian zone (Germanoski and Miller 2004).

Riparian vegetation consists of stringers of quaking aspen (*Populus tremuloides*), narrowleaf cottonwood (*P. angustifolia*), willows (*Salix* spp.), water birch (*Betula occidentalis*), and meadow complexes (USDA Forest Service 1996). Within these riparian areas, stream incision and water table declines have allowed encroachment of basin big sagebrush (*Artemesia tridentata* ssp. *tridentata*) (Linnerooth *et al.* 1998). At low to middle elevations, Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis*) communities are interspersed with singleleaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) woodlands. At higher

elevations, mountain big sagebrush (*Artemesia tridentata* ssp. *vaseyana*) and limber pine (*Pinus flexilis*) dominate.

The study area falls within the Austin-Tonopah Ranger District of the Humboldt-Toiyabe National Forest and is managed by the USDA Forest Service. Small inholdings of private property exist within the study area. Prior and continuing land-use activity include mining, domestic livestock grazing, dams, road construction, water diversions to private ranchers, and recreational activity such as fishing, hunting, camping, and hiking (e.g. Toiyabe Crest Trail and Arc Dome Wilderness). A graded secondary road exists along or partly along the valley bottoms of most watersheds, often intertwined with the stream (Lahde 2003).

Data Collection

Geomorphic data

Prior to field sampling, process zones and vegetation types were mapped along the main channel of each watershed. Classification and identification of process zones were based on the predominant geomorphic process (erosion, deposition, or transport) and valley fill material (Table 1 from Engelhardt 2009). Process zones were delineated on color photocopies of 1:15,000 - 1:19,000 scale aerial photographs (Humboldt-Toiyabe National Forest 1993). Vegetation was field mapped according to ecological types defined by Weixelman et al. (1996) and delineated on color photocopies of 1:3,000 scale aerial photographs (Humboldt-Toiyabe National Forest, 2003) or on color prints of 1:3,000 scale National Agriculture Inventory Program (NAIP) images. Process zones and vegetation types were digitized from paper maps to raster NAIP imagery in a Geographic Information System (GIS). Several ecological types were aggregated resulting in seven final vegetation types (aspen, birch, cottonwood, *C. utriculata* meadow, mesic meadow, narrow mesic and willow) and a stratified design was used to locate three to five field sampling sites in all process zone/vegetation type combinations within each watershed for a total of 184 sites. Sampling sites were systematically located to characterize representative conditions based

on field inspections. Geomorphic and vegetation data were collected simultaneously at all sampling sites.

At each sampling site transects were located perpendicular to the stream channel to include all inset terraces and surfaces from the channel thalweg to the valley floor (upland) surface. Terraces were identified as discrete, level surfaces adjacent to the stream that had transferable heights above the stream channel from the nearest to farthest point on the terrace. Cross-sectional profiles were measured with a leveled meter tape and stadia rod. Field measurements included active channel width, depth, and width:depth ratio, entrenchment width, depth, and width:depth ratio, as well as surface width, height above the channel, and distance from the channel. Stream gradient was calculated by measuring horizontal distance with a meter tape and vertical distance with a clinometer and stadia rod. Other geomorphic data collected included stream bank angles, riparian zone width, valley width, and descriptive geomorphic units (e.g. riffle, run). Channel particle size distribution and lithology were collected using the Wolman Pebble Count method (Wolman 1954). Channel bed D_{50}, D_{84}, as well as percent content of seven rock types (carbonate, intrusive, metasediment, quartzite, sandstone, siliciclastic, volcanic) were derived. Soil samples were taken from the active channel bank, air dried and analyzed for percentage of fine fragments by passing them through a 2 mm sieve. The entrenchment depth was the vertical height from the valley floor surface to the channel thalweg, and the entrenchment width was the corresponding horizontal distance between valley floor surfaces. Elevation, valley slope, contributing area and main channel length above each site were calculated from a 10-m Digital Elevation Model. Bedrock geology of each site was obtained from the USGS Geologic Map of Nevada (1: 250,000; Crafford 2007)

Woody species data

Riparian woody species were sampled at the same time and location as the geomorphic data. To sample shrubs, paired plots were located along the cross sectional transect at the mid-

point of each definable terrace or slope. *S. lutea* was treated as a shrub in this study although it can occur in tree life form. Plot frames (1.0 m^2) were placed on each side of the tape at a distance of one meter from the tape. Shrubs were identified to species and sampled by maturity class. Maturity classes included seedling, juvenile, mature (reproductive), decadent, and dead. Aerial cover was estimated using the following codes: **1=**<1%, **2**=1-5%, **3**=6-15%, **4**=16-25%, **5**=26-35%, **6**=36-45%, **7**=46-55%, **8**=56-65%, **9**=66-75%, **10**=76-85%, **11**=86-95%, **12**=96-100% (Castelli *et al*. 2000). *Salix* species were evaluated for mean and maximum height, mean and maximum stem diameter, # of individuals (when discernable), # of total stems, # of total dead stems, and diameter of largest dead stem. Total live stem density, stem density of dead, stem density of individual clusters, and stem density of the seedling and juvenile class for each surface were later derived. For the analyses, shrub data and aerial cover from the paired plots were averaged to produce one value per transect.

At sites with trees (*Populus* spp. and *B. occidentalis*), a 2-m belt transect was located parallel to and on the upstream side of the geomorphic transect. *B. occidentalis* was treated as a tree in this study although it often occurs as a shrub life form. Aerial cover of each tree species by maturity class was ocularly estimated by surface and recorded using the same codes as for shrubs. For each individual tree occurring within the belt transect, the species, maturity class (same as shrubs), tree height (live individuals only), and tree basal diameter (live and dead individuals) were recorded by stream surface. For *B. occidentalis*, if there were fewer than two individual trees per surface pair (left and right side of channel) the belt transect was expanded to a 5-m width. We measured the root crown maximum diameter and the diameter perpendicular to the maximum diameter in place of a single measurement of tree basal diameter for *B. occidentalis*. Basal diameters of the single largest live and dead *B. occidentalis* stems on each tree were also measured. We counted the number of stems > 5 cm in diameter, and recorded a code for the total number of stems (1=1-10, 2=11-25, 3=26-50, 4=51=100, 5=101-150, 6=151). Total live stem

density, stem density of stems > 5 cm, stem density of dead, stem density of individual clusters, stem density of the seedling and juvenile class, and basal area of clusters for each surface were later derived. For the analyses, tree data and aerial cover were averaged across surfaces to produce one value per transect.

Cores or stem cross-sections of *S. lutea*, *Salix exigua* and *Betula occidentalis* were collected adjacent to the cross-sectional profile on the dominant terraces identified at the site. If discrete terraces were not present, trees or shrubs were *not* sampled. Accurate height above water table was obtainable on discrete terraces but not on sloping surfaces. Individuals with the largest diameters were selected on each discrete terrace with the goal of aging the oldest individuals. The age of the oldest individuals on a discrete terrace can be used as a surrogate for both date of terrace origin and riparian woody species establishment date (Chambers *et al*. 1998). Largest diameter stems were often found as root wads (e.g. *B. occidentalis*) overhanging the incised channel. Four samples from separate individuals on each discrete terrace at each site were obtained when possible. Across the 184 sites we sampled 374 individuals. If the oldest stem was dead, as often occurred, the oldest living stem was sampled. Sample height and diameter were recorded along with a comprehensive description of the sample site.

If the stem was less than 10 cm in diameter, the root crown was excavated from below the ground surface with hand trowels and the individual was extracted below the root crown (e.g. Sigafoos 1964; Scott *et al.* 1997). In cases where digging was obstructed the stem was removed at the lowest possible point in an effort to sample the oldest possible age. When stems were greater than 10 cm in diameter (e.g. *B. occidentalis*), we cored at the lowest possible point, nearest to the root crown (Asherin and Mata 2001; Phipps 1985). Accurate determination of tree age cannot be obtained without excavating the original root flare (Scott *et al.* 1996). However, early successional species aged above the root collar are less severely underestimated than mid- to late-successional species because they have fewer missing growth rings (Gutsell and Johnson 2002).

A slightly different sampling design was used for *P. tremuloides*. This species is less likely to occur on surfaces adjacent to the channel, but may respond to large flood events or the climatic conditions (higher available moisture) that often occur coincidentally with floods. *P. tremuloides* suckering events are triggered by a range of disturbances such as fire (Sheppard *et al*. 2006; Weixelman *et al*. 1996). However, *P. tremuloides* cannot withstand long-term inundation (Perala 1990). Thus, for *P. tremuloides* a range of diameters were sampled to determine the most recent establishment event. *P. tremuloides* stands in the study area were uneven-aged but usually had 2-3 different age classes or "cohorts." Four individuals from 2 size classes (excluding the oldest class which usually consisted of few decadent individuals) were sampled; 2 with diameters ranging from 2.0 cm - 6.0 cm and 2 ranging from 6.0 cm -10.0 cm. Older individuals were excluded because we were interested in suckering events caused by recent disturbance.

Following standard dendrochronology and stem ageing procedures, cores were dried, mounted, sanded with a belt sander, and then sanded by hand with progressively finer-grained sandpaper to distinguish annual growth rings (Asherin and Mata 2001; Phipps 1985). Cross-sections were sliced into "cookies" with a band saw until the point of origin (where root tissue transitions to pith) became clear (Sigafoos 1964). To date, we assumed that one ring was added for each growing season; i.e. the annual ring (Stokes and Smiley 1968). Growth rings were counted by two different people using a microscope. A third person counted a random subset of the samples. If the core did not capture the pith, missing years were calculated using a pith locator. Distance to the pith was estimated by lining up concentric circles on transparent templates to actual tree rings. This distance was then divided by the average width of the three oldest samples by species. If *P. tremuloides* samples were difficult to count, they were stained with Fehling's solution which distinguishes sapwood from heartwood (Asherin and Mata 2001).

Formal cross-dating of tree ring chronologies was attempted but proved unsuccessful. There were no developed tree ring chronologies or marker years (e.g. consecutive narrow rings

that indicate drought) available for these species in central Nevada riparian areas (WDC for Paleoclimatology 2009). Cross-dating of specimens for better determination of age was attempted on half the samples. First, I tracked marker years using the skeleton plot method. Second, I used a statistical program COFECHA (Grissino-Mayer 2001) to assess the quality of the tree ring chronology. Samples failed to be eligible for creating a chronology because they were too altered by their riparian environment (i.e. proximity to water; Schweingruber 1988; Stokes and Smiley 1968) resulting in complacent growth rings. In addition, I often failed to sample the root flare including pith. Counting difficulties such as faint rings, false rings and obstruction by fungal pathogens or rot were problems. Stems were not aged to annual precision. All of the ages used in the analyses had a dating accuracy of 4.0 to 5.0 where 5.0 indicates the highest accuracy rating.

Statistical Analyses

Geomorphic characteristics and process zones

Forty-four geomorphic variables were measured or derived from each transect and surface for use in the analysis (Table 2). The term 'geomorphic' is used throughout to represent both geomorphic and channel characteristics. Overall correlations among geomorphic variables were investigated with Pearson Product Moment Correlation and were used to select variables for further analysis. Abundance of process zones (Table 1) in each study watershed and proportion of process zones across the study watersheds (Figure 1) were calculated.

Woody species distributions

Species distributions within process zones were calculated using dominant cover of most abundant species per surface as the measure of abundance. Spatial patterning of the woody species along the main channels of the study watersheds was described by mapping. ArcGIS 9.2 software was used for all mapping. The dominant woody species for each transect was plotted. Woody species dominance was determined by summing total cover per surface for each transect and assigning dominance to the species with the most cover.

Principal Component Analysis (PCA) was used to explore the correlation structure of the geomorphic variables and to identify underlying gradients defining spatial patterning of the woody species. The geomorphic variables used in the PCA included area above the transect, bank angle, entrenchment ratio, height above thalweg, number of knickpoints, riparian width and distance to water's edge (Table 2). Representative variables were chosen based on within-group correlations from Pearson Product Moment Correlation. Prior to analyses, normality of the geomorphic variables was assessed with quantile-quantile plots that compared the data to a normal distribution function. Square-root or natural log transformations were performed if needed and skewness was assessed. Almost all of the variables obtained an absolute value of skewness < 1 (a few fell within an absolute value of 2) meeting the PCA requirement of multivariate normality (McCune and Grace 2002). Each surface was assigned a dominant species based on dominant cover.

The PCA ordination used a varimax rotation which maximizes the loadings of individual variables and improves interpretability (McCune and Grace 2002). Results were presented as a principle component biplot with PC score centroids and 95 % confidence intervals, and used to compare key woody species distributions according to fluvial geomorphology. One-way analysis of variance (ANOVA) examined differences among the four key woody species for each of the geomorphic variables. Additional explanatory geomorphic variables were included in the ANOVAs for enhanced interpretation of distribution. Normal alpha level (α=0.05) was adjusted to fit the Bonferroni correction for multiple tests (α/number of individual tests). Multiple comparison tests for significant differences among woody species were performed using the Bonferroni method. These tests and PCA were performed in S-PLUS 8.0 (version 8.0, TIBCO Software Inc., Palo Alto, CA, US).

Age structure of the woody species

Factors important for riparian woody species establishment include high flow events and local geomorphic characteristics. High flow events occurred in central Nevada during the mid and late 1960s (1965 and 1969), 1970s (1973, 1975, and 1978) and early 1980s (1983 and 1985). These events triggered formation of inset terraces within the stream channels and subsequent establishment of riparian woody species (Chambers *et al*. 1998, Henderson 2001). Thus, the age of the oldest individuals on a discrete terrace can be used as a surrogate for both date of terrace origin and riparian woody species establishment date (Chambers *et al*. 1998). In these analyses, maximum age of trees and shrubs were determined for each discrete terrace, given an accuracy of ± 3 years and assigned to known high flow events.

Multivariate analyses were used to evaluate the geomorphic characteristics of sites and discrete terraces with establishment during the high flow events with the greatest overall establishment of riparian woody species (1983/1985). Logistic regression was used because the response variable (establishment vs. no-establishment) was binary. The geomorphic variables used in the analyses included watershed, process zone, bedrock, largest lithology, largest clast size, number of discrete terraces, entrenchment width, area above, stream gradient, and valley width (Table 2). Prior to analyses, normality of the geomorphic variables was assessed with quantile-quantile plots that compared the data to a normal distribution function and skewness was compared across different transformations (e.g. log natural). All of the variables obtained an absolute value of skewness < 1 indicating no transformation was necessary. Stepwise regression was used to select the multivariate model with the best fit based on the lowest Akaike's Information Criterion (AIC) statistic (Hastie and Pregibon 1993).

To measure how well the best-fit model predicted establishment, classification accuracy (total % of observations the model predicted correctly), model sensitivity (% predicted establishment correctly classified), and model specificity (predicted no-establishment correctly classified) values were calculated. The cutoff threshold for establishment was adjusted to fit the

observed proportion of presences. Nagelkerke pseudo- R^2 value also was calculated to see how well the model captured variation in the data (Nagelkerke 1991). Confidence intervals for the beta coefficients were calculated to describe the odds of establishment associated with varying levels of each geomorphic variable, after accounting for the effects of the other variables. Model fit was further assessed by fitting a receiver operating characteristic (ROC) curve and calculating the area under the curve (Fielding and Bell 1997). One-way ANOVAs examined differences in geomorphic characteristics between discrete terraces with establishment vs. no-establishment. All statistical analyses were performed in the statistical package S-PLUS 8.0 (version 8.0, TIBCO Software Inc., Palo Alto, CA, US) and R (version 2.10.1, The R Foundation for Statistical Computing, Vienna, Austria).

The quantity and quality of local precipitation and stream gauging data were inadequate for detecting establishment of riparian woody species in response to high flow events at the scale of individual basins. However, hydro-climatic chronologies of overall riparian woody species establishment were developed for annual precipitation and annual discharge. Precipitation data were obtained from the Austin, Nevada weather station which was monitored by the Western Regional Climate Center from 1960 to 2000 (Desert Research Institute, Nevada). Annual cumulative water-year (October-September) discharge was calculated for Kingston Canyon from the US Geological Survey discharge records from 1967 to 1998. Kingston Canyon was the only study watershed with gauging data, and the gauge was discontinued in 1998.

Precipitation and discharge were graphically compared to maximum age per discrete terrace for each species, except for the 2 *Salix* spp. which were combined. Only tree ages with high dating accuracy (4.0 to 5.0) were used. This approach allowed for comparison of episodes of establishment, or lack thereof, to hydro-climatic factors as well as an examination of the response across and within species.

Distribution of sites that recorded establishment in response to the 1983/1985 flood events were mapped along the main channels to show spatial patterning. Distributions of maximum age for each species in the study watersheds were also mapped and paired with age distribution histograms. The 2 *Salix* spp. were combined because there were only 13 discrete terraces with *S. exigua*. Ages in these maps were all high accuracy ages (4.0 to 5.0).

Stand structure of the woody species

Stand structure variables were used to assess population dynamics and sustainability for each species. Pearson Product Moment Correlation and ecological interpretation were used to select the descriptor variables (Table 3). Descriptor variables represented other variables from within-group correlations and unique aspects of stand structure. Outlier variables were eliminated from analyses.

Cluster analysis was used to group each species into stand structural types based on the 5-7 descriptor variables using Euclidean (Pythagorean) distance measures and Ward's group linkage methods. Descriptive variables were relativized prior to analyses for comparability (McCune and Grace 2002). Surfaces that exceeded three standard deviations or formed their own group at the 5 group level or below were considered outliers and removed from the analyses. Cluster analysis yielded 2-5 possible groupings of descriptor variables into stand structural types.

Final decision on number of groups indicating stand structural types within species were evaluated using bar graphs and results from non-parametric Multi-Response Permutation Procedures (MRPP). Bar graphs were used to compare the means of descriptor variables for each stand structural group. MRPP evaluated significant differences across groups using Euclidean (Pythagorean) distance measures. Chance-corrected within group agreement was measured by the A-statistic where A=1 means all items within a group are identical (>0.3 is fairly high; McCune and Grace 2002) and the likelihood of an observed difference due to chance was measured with a probability value (p). T described the separation between groups where a greater negative value

meant a stronger separation. Finally, group differences were examined with Kruskal-Wallis rank sum tests performed in the statistical package S-PLUS 8.0 (version 8.0, TIBCO Software Inc., Palo Alto, CA, US).

Relationships among stand structural types and geomorphic characteristics were examined using Non-Metric Multidimensional Scaling (NMS) ordination and Euclidean distance measures. NMS was chosen for its capacity to deal with non-normal data and to find the strongest structure of the data in ordination space (McCune and Grace 2002). Ordinations for each species were performed separately and the data were relativized prior to analyses. Varimax rotation was used to maximize the loadings of individual variables and improve interpretability (McCune and Grace 2002). Fifty runs of real data for 1-D to 6-D solutions with 500 iterations were performed. Fifty runs of randomized data and Monte Carlo tests were run to find the probability that a similar final stress could have been obtained by chance. Preliminary runs delivered an optimal starting number seed and preferred dimension that were used in subsequent runs. Strength of the final ordination was evaluated based on final stress and instability of the solution, total amount of variation explained by the axes and the orthogonality (un-correlated nature) of the axes. Surfaces in ordination space were coded by stand structural types for interpretation of woody species pattern. Geomorphic variables were aggregated to the surface level then overlaid as vectors in the ordination biplot to identify geomorphic characteristics underlying spatial patterning of stand structure. Cluster analysis, MRPP, and NMS were performed in PC-ORD 5.31 (version 5.31, MjM Software, Gleneden Beach, OR, US).

The geomorphic characteristics that provided the highest correlation coefficients with the NMS ordination axes (mostly $0.2 \leq r \leq -0.2$) were examined for significant differences among stand structural types. This approach identified important geomorphic characteristics along which stand types for each species were defined. Important geomorphic variables were normalized with log natural or square root transformations where necessary and subject to one-way ANOVAs. Alpha

level was adjusted to fit the Bonferroni correction for multiple tests. These tests were performed in the statistical package S-PLUS 8.0 (version 8.0, TIBCO Software Inc., Palo Alto, CA, US).

Histograms of species abundance per surface were generated to show abundance of stand structure types within the 4 study watersheds. The sample unit was per species per surface and showed abundance across and within species and watersheds. Stand structural type abundance for each species within process zones was calculated. Assignment of stand structural type per surface was used as the measure of abundance.

RESULTS

Geomorphic characteristics and process zones

Geomorphic variables exhibited significant correlations within and across characteristics for site, transect, surface, channel, and channel lithologies (Table 4). For site, elevation decreased with increasing contributing area and stream length above the site (Table 4). Wide surfaces had greater heights above the channel and distances from the water's edge. Number of knickpoints were more frequent with higher stream gradients. Lower in the watersheds, channel thalwegs and channel water widths increased, and stream gradients decreased (Table 4). Higher in the watersheds, percent quartz in the channel increased and metasediments decreased. Riparian width increased where stream gradients and channel clast size decreased. Number of discrete terraces increased with wider entrenchment. Knickpoint frequency increased with increasing size of woody debris in the channel (Table 4).

Process zones across the study watersheds consisted primarily of incised alluvial (54.1 %) and incised colluvial (39.2 %) valley. Bedrock valley (1.6 %) was rare and occurred only in Birch Canyon. Aggrading alluvial valley (5.0 %) occurred only in Kingston Canyon. Abundance of incised alluvial (54.1 %) and incised colluvial (45.9 %) valley were evenly distributed in San Juan Canyon. Cottonwood Canyon was comprised primarily of incised alluvial (68.1 %) valley

with the rest incised colluvial (31.9 %) valley. Kingston Canyon was comprised of incised colluvial (40.6 %), incised alluvial (35.6 %), and aggrading alluvial (23.8 %) valley. Birch Canyon was comprised of incised alluvial (58.9 %), incised colluvial (33.9 %) and bedrock (7.1 %) valley. Engelhardt (2009) found that incised alluvial and incised colluvial valleys are evenly distributed across elevational gradients throughout the study watersheds.

Distributions of woody species

The four woody species occurred in the study watersheds along a total of 207 transects and on a total of 482 surfaces. Abundance of each species in the study watersheds was fairly evenly distributed in incised alluvial and incised colluvial valleys. These process zones exhibited highly similar channel characteristics but the incised colluvial process zone had narrower valley widths and higher stream gradients than the incised alluvial process zone (Engelhardt 2009). Incised alluvial valleys were characterized by *S. lutea* (48.5 %), *P. tremuloides* (22.8 %), *S. exigua* (15.8 %), and *B. occidentalis* (12.9 %). Incised colluvial valleys were characterized by *S. lutea* (37.4 %), *P. tremuloides* (34.5 %), *S. exigua* (14.6 %), and *B. occidentalis* (13.5 %). Bedrock valley was a mix of *B. occidentalis* (71.4 %) and *S. lutea* (28.6 %). Aggrading alluvial valley was dominated by *S. exigua* (43.5 %) and *S. lutea* (56.5 %).

The dominant woody species in the watersheds occurred over the elevational gradient with *B. occidentalis* at low to intermediate elevations, *S. exigua* and *S. lutea* primarily at intermediate elevations, and *P. tremuloides* in the upper watersheds (Figure 2). *P. tremuloides* was absent from Kingston Canyon, sparse in Birch Canyon, and abundant in San Juan and Cottonwood Canyons.

The first two principal components of the PCA were sufficient for interpreting the relationship of the geomorphic data to the woody species (cumulative variance =45%). Principal Component (PC) 1 represented surface position relative to the stream (Table 5) and separated the

trees (*B. occidentalis* and *P. tremuloides*) from the *Salix* spp. (Figure 3). *B. occidentalis* and *P. tremuloides* were associated with greater heights above the channel defined by significantly greater distances from the water's edge (4.83 m and6.87 m, respectively), heights above the water surface (1.45 m and 1.34 m, respectively), and surface widths (4.20 m and 5.38 m, respectively) than the *Salix* spp. (Table 6). The *Salix* spp. were associated with closer proximities to the water's edge (2.61 m and 1.40 m, respectively), lower heights above the thalweg (0.59 m and 0.48 m, respectively) and narrower surfaces widths (3.13 m and 2.74 m, respectively) (Table 6). *S. exigua* had consistently greater means for surface related variables than *S. lutea* which caused it to plot separately from *S. lutea* (Table 6, Figure 3).

PC 2 represented watershed position (contributing area above) and bank angle (Table 5) which primarily distinguished *B. occidentalis* from *P. tremuloides* (Figure 3). *B.occidentalis* had a significantly greater contributing area and bank angle ($5.59x10^7$m and 56.4%, respectively) than *P. tremuloides* ($1.76x10^7$m and 43.1%, respectively) (Table 6). *S. lutea* had a significantly lower bank angle (40.7%) than *B. occidentalis*. The bank angle of *S. exigua* did not differ significantly from the other species (Table 6). The biplot also showed *S. lutea* occurring above *B. occidentalis* and *S. exigua* in the watersheds (Figure 3). The distribution of species according to contributing area above the site was corroborated by the woody species distribution map (Figure 2).

Several other geomorphic variables further differentiate species distributions. S. *exigua* was associated with wider and more shallow entrenchment than *P. tremuloides* (Table 4). *P. tremuloides* had significantly higher quartz content in the channel (57.4 %) than the other species and also occurred higher in the watersheds (Table 6). Generally, increasing quartz was associated with upper watershed positions (Table 4). Volcanics in the channel were significantly more abundant with *P. tremuloides* (34.9 %) and *S. lutea* (31.9 %) than *B. occidentalis* (16.4 %) and *S. exigua* (23.5 %) (Table 6). This result was only relevant for San Juan Canyon. San Juan Canyon had a mean of 66.4 % volcanics in the channel while the other study watersheds had means of

less than 15.2 % (Kingston Canyon had 0.0 %). Knickpoints occurred at 43.5 % of *P. tremuloides* sites (mean number of knickpoints = 0.88) and 23.0 % of *S. lutea* sites (mean number of knickpoints = 0.36) (Table 6). Riparian width was narrowest at *B. occidentalis* sites (20.19 m) and widest at *Salix* spp. sites (~36 m) (Table 6).

Age structure of woody species

The early 1980s floods (1983 and 1985) resulted in the highest tree and shrub establishment, accounting for 30 % of establishment for all species combined (Table 7). Likewise, of the discrete terraces aged, 30 % originated in response to the high flows of 1983 and 1985. In Kingston Canyon annual water-year runoff averaged 40 cubic feet per second (cfs) for the period of record. In 1983 and 1985, annual water-year runoff was 385 cfs and 221 cfs, consecutively.

The best-fit model from stepwise regression indicated that establishment in response to the 1983 and 1985 flood was best explained as a function of process zone, watershed, height above thalweg, number of discrete terraces, largest clast in the channel and stream gradient. The model had an overall classification accuracy of 72.6 %, model sensitivity of 82.5 % and model specificity of 68.4 % indicating reasonable predictive power. The AUC value from the ROC curve indicated a well-fit model (0.82). A random model would have an AUC value of 0.5. Nagelkerke's pseudo R^2 value (0.33) was sufficient to explain the variation in the data.

Establishment in response to the 1983 and 1985 high flows was highest (75 %) within the incised alluvial process zone and San Juan watershed. The odds of establishment were 83 % less in the incised colluvial process zone (Table 8). Fifty-eight percent of establishment events occurred in San Juan Canyon, more than all of the other canyons combined (χ^2=11.24, p=0.011). Total number of discrete terraces and stream gradient showed weak effects (Table 8); however, their combined effect in the model was important and their means were significantly different.

The number of discrete terraces was significantly higher at sites with establishment ($F_{1,133}$=5.83, p=0.017; establishment: 3.00±0.12, no-establishment: 2.60±0.01). Stream gradient was significantly less steep at sites with establishment ($F_{1,133}$ =6.68, p=0.011; establishment: 3.2 %±0.39, no-establishment: 4.4 %±0.25). The odds of establishment decreased by 93 % for each 1 centimeter increase in largest clast size in the channel (Table 8). Size of the largest clast was significantly smaller at sites with establishment ($F_{1,133}$ =12.61, p=0.001; establishment: 25.11 cm±1.87, no-establishment: 35.22 cm±1.67). Overall, the flood was effective within alluvial-based process zones that had the propensity to create multiple discrete terraces.

Salix spp. showed a pulse of new establishment during the flood years of 1983 and 1985 but *B. occidentalis* only showed a slight increase (Figure 4). Only 9 out of 47 discrete terraces with *B. occidentalis* had individuals less than 30 years old. *Salix* spp. showed continued but reduced recruitment after the 1983 and 1985 flood. However, after the 1975 flood there was a lack of establishment potentially as a result of relatively low spring runoff or the 1983/1985 flood removed them (Figure 4). Like the *Salix*, *P. tremuloides* also exhibited a pulse of establishment in response to the 1983/1985 high flow event. However, establishment of *P. tremuloides* from 1985 through about 1994 was relatively continuous. The lack of recent establishment reflects the fact that stems < 2cm in diameter were not aged.

Age structure differed among the study watersheds. San Juan Canyon accounted for 58 % of establishment resulting from the 1983 and 1985 floods. The dominant process zone supporting establishment was incised alluvial valleys corroborating the results of the multiple regression (Figure 5). *B. occidentalis* establishment occurred primarily at the mouth of the canyon, while *P. tremuloides* establishment dominated the upper canyon. *S. lutea* establishment was scattered throughout the canyon while there was only one occurrence of *S. exigua* establishment. There were many new discrete terraces at the confluence of the south and east fork occupied by *P. tremuloides* and *Salix* spp.

There was a general pattern of mixed-age distribution across and within the study watersheds (Figure 6). In both San Juan and Cottonwood Canyons, *Salix* spp. had evenly distributed ages with highest frequencies in the 20s and 30s. *P. tremuloides* also had high frequencies of trees in the 20s and 30s with an extremely old individual in upper Cottonwood (116 years old) (Figure 6c). In upper San Juan there was a small cluster of old *B. occidentalis* dating back to 1929. However, *B. occidentalis* in the westside canyons, San Juan and Cottonwood, had an age distribution that was generally younger than the eastside canyons, Kingston and Birch (Figure 6c).

In Birch Canyon, *P. tremuloides* had high frequencies of trees in their 30s and 50s mostly occurring in the upper watershed along the south fork (Figure 6a). *Salix* spp. were concentrated in the mid to upper canyon with age ranges that connected them to both the 1990s and 1980s floods (Figure 6a). In lower Birch Canyon, *B.occidentalis* had a wide range of ages with high frequencies of trees in their 50s and 80s. *B. occidentalis* was older in lower Kingston Canyon than in all the other canyons with 14 discrete terraces between 30 and 140 years old and 3 discrete terraces below the age of 30. Likewise, *Salix* spp. were older in lower Kingston Canyon with a high frequency of trees in their 40s (Figure 6b).

Stand structure of woody species

The cluster analysis grouped stand structure into three primary types across the woody species (1) young, low density, (YLD; n=282); (2) mature, regenerating, stable (MRS; n=158); and (3) mature, dense, decadent (MDD; n=100) (Table 9). Stand structure types differed significantly based on MRPP ($A=0.418$, $p<0.000$, $T=-34.4$) and showed significant differences in stand descriptor variables (Table 9).

YLD stands generally were characterized by low dead stem densities, low cover, and young individuals (Table 9). Also, total stem densities were low and stems were short (excluding

P. tremuloides) indicating a sparse, small-statured stand. YLD stands had a wide range of seedling and juvenile densities but, except for birch, were generally low (Table 9).

MRS stands were characterized by total stem densities in the mid range for *S. exigua* and *S. lutea*, intermediate densities of dead stems across species, and seedling and juvenile densities in the mid to high range (Table 9). These characteristics indicate a stable mature stand with active regeneration. MRS stands for *B. occidentalis* and *S. lutea* were characterized by active asexual reproduction via resprouting from the root crown (SD/Indiv). Canopy cover was high for the 2 trees and in the intermediate range for *Salix* spp. Heights were in the intermediate range for all species except *P. tremuloides* which had exceptionally tall trees in the MRS group (Table 9).

MDD stands were characterized by high densities of dead stems (Table 9) indicating decadence. Total stem densities also were high except for *B. occidentalis* reflecting the dense growth habit of these species. In the case of *B. occidentalis*, decadent trees and lack of disturbance results in an inability to resprout from the root crown. In addition, *B. occidentalis* MDD type had the oldest trees. The MDD type had the tallest stems except for *P. tremuloides*. Sheppard *et al*. (2006) described *P. tremuloides* as short and stunted when found in the upper portions of watersheds due to a short growing season and harsh winter conditions. Canopy cover was high for the *Salix* spp. and in the intermediate range for the 2 trees. *S. exigua* only had 6 surfaces in the MDD type, but total stem densities and dead stem densities exceeded the MRS stands 3-fold (Table 9).

The NMS ordinations revealed differences in geomorphic affinities for the different stand structural types of the woody species. The ordinations had 2-Dimensional solutions except for *P. tremuloides* which had a 3-D solution (Table 10). The strength of the ordination was verified by the proportion of variance represented by each axis (Table 10), cumulative R^2 and the orthogonality of the axes (Table 10). Pearson's correlation (r) of each geomorphic characteristic

with the axes (Table 11) helped to identify the top 5-7 important geomorphic controls for each species.

Betula occidentalis. The NMS ordination biplot had 3 geomorphic vectors that were correlated with ordination axes (R^2>0.1) and that distinguished *B. occidentalis* stand structural types (Figure 7a). Axis 1 defined the stand types along a gradient of entrenchment width (r=-0.48), intrusives in the channel (r=0.38), and stream gradient (r=0.31) (Figure 7a). YLD and MDD stands were associated with wider entrenchment widths (10.53 m and 9.57 m, respectively), less intrusives in the channel (3.4 % and 3.0 % respectively) and lower stream gradients (3.4 % and 3.3 % respectively) (Appendix 1). MRS stands were associated with narrower entrenchment widths (6.03 m), intrusives in the channel (21.8 %), and steeper stream gradients (4.2 %). High intrusives in the channel indicate that it is 60 % more likely to have igneous bedrock than any other bedrock type (F_{484}=109.87, p=0.000). Also, increasing stream gradients were associated with greater contributing areas (Table 4).

YLD stands occupied surfaces with high entrenchment width to depth ratios and low bank angles (5.45 and 36.4 %, respectively) whereas both MRS and MDD were limited to sites with low entrenchment width to depth ratios (3.39 and 3.21, respectively) and steep bank angles (55.2 % and 62.8 %, respectively). The latter scenario indicated a more incised channel that would have limited access to overland flows. The width of riparian zone vegetation was greatest for YLD stands (25.05 m) and narrowest for MRS stands (16.36 m), while MDD stands were inbetween (21.81 m) (Appendix 1).

Populus tremuloides. The NMS ordination biplot had 1 geomorphic vector that was correlated to the axes (R^2>0.05) and that distinguished *P. tremuloides* stand structural types (Figure 7b). Axis 3 defined the stand types along a gradient of surface width (r=-0.22) (Figure 7b). YLD and MRS stands were associated with wider surface widths (6.47 m, 5.12 m respectively) (Appendix 1). MDD stands were associated with narrower surface widths (3.96 m).

Channel constituents (e.g. fines) were important for distinguishing stand structural types. Percent sandstone in the channel (r=0.23) was increasing where volcanics were decreasing (r=-0.33; Table 4). Percent fines and volcanics in the channel were most abundant for MRS stands (51.5 % and 44.6 %, respectively) and least abundant in the MDD stands (41.9 % and 29.0 %, respectively). Quartz in the channel was most abundant in the MDD stands (63.2 %) which were found at sites with the least stream length above (7,164.52 m), 2,000 m above the other types (Appendix 1).

Salix exigua. The NMS ordination biplot had 3 geomorphic vectors that were correlated to the axes (R^2>0.1) and that distinguished *S. exigua* stand structural types (Figure 7c). Axis 2 defines the stand types along a gradient of entrenchment width (r=0.21) and bank angle (r=-0.21) (Figure 7c). YLD stands were associated with wider entrenchment widths and low bank angles (8.75 m and 40.2 %) whereas MRS and MDD stands were associated with narrower entrenchment widths (7.41 m, 5.29m respectively) and steeper bank angles (44.9 %, 47.5 % respectively) (Appendix 1).

Stand structural types were not strongly distinguished by geomorphic characteristics. MDD had the highest number of discrete terraces (mean number of discrete terraces = 2.88) followed by MRS (mean number of discrete terraces = 2.70) and YLD stands had the lowest (mean number of discrete terraces = 2.17) (Appendix 1). Woody debris in the channel was greatest for MRS and MDD stand types (7.0% and 7.3% respectively) and least for YLD stands (2.3 %). Surface height above the channel was greatest for the MDD type (0.39m), in the mid-range for MRS stands (0.21 m) and lowest for YLD stands (0.15 m) (Appendix 1). Likewise, increasing heights above the water surface were associated with increasing surface widths and distance from water's edge (Table 4).

Salix lutea. The NMS ordination biplot had 4 geomorphic vectors that were correlated to the axes (R^2>0.1) and that distinguished *S. lutea* stand structural types (Figure 7d). Axis 1

defines the stand types along a gradient of thalweg depth (r=-0.11), woody debris diameter in the channel (r=-0.15), and percent quartz in the channel (r=0.14) (Figure 7d). Thalweg depth was slightly deeper for YLD stands (0.17 m) and shallowest for MDD stands (0.12 m) (Appendix 1). YLD and MRS stands had larger woody debris in then channel (0.02 m for both) than MDD stands (0.01 m). Quartz in the channel was most abundant in the MDD stands (58.4 %) and less abundant in the YLD and MRS stands (44.0 %, 48.4 % respectively).

Stand structural types were not strongly distinguished by geomorphic characteristics. Water width in the channel was widest for the YLD stands (1.86 m) and less wide for MRS and MDD stands (1.62 m, 1.61 m respectively) (Appendix 1). Increasing thalweg depth was associated with increasing water widths in the channel (Table 4). Number of discrete terraces was greatest for the MRS and MDD stands (mean number of discrete terraces = 3.00, 2.92 respectively) and lowest for the YLD stands (mean number of discrete terraces = 2.73) (Appendix 1).

The abundance of the stand structure types varied within the watersheds. *B. occidentalis* was most abundant in Kingston Canyon and had the highest frequencies of MDD stands there (n=15) (Figure 8). The other canyons had few surfaces with *B. occidentalis* MDD stands and many surfaces with YLD and MRS stands. There were no *P. tremuloides* surfaces sampled in Kingston and only 10 in Birch Canyon which consisted of YLD and MDD stands (Figure 8). *P. tremuloides* had high frequencies in Cottonwood and San Juan Canyons with the YLD and MDD stand types dominating in both canyons. *S. exigua* was present in every watershed but was least abundant in Cottonwood Canyon (Figure 8). The *S. exigua* YLD stand type was overall the most frequent with the MDD type only occurring on 6 surfaces. Birch and San Juan Canyon had high frequencies of MRS and MDD *S. lutea* stands but they were less frequent in Cottonwood and Kingston Canyon (Figure 8). YLD *S. lutea* stands had low abundance across all the watersheds.

The abundance of the stand structure types also varied within process zones. YLD stands were found in more abundance in incised alluvial than incised colluvial valleys across species (Table 12). Bedrock valley was primarily comprised of MRS *B. occidentalis* stands with some YLD and MRS *Salix* spp. stands. The remaining *B. occidentalis* stands were evenly distributed between incised alluvial and incised colluvial valleys. *P. tremuloides* stand types were fairly evenly distributed between incised alluvial and incised colluvial valleys (Table 12). Aggrading alluvial valley consisted of mixed *S. exigua* and *S. lutea* stand types (Table 12). *S. exigua* and *S. lutea* stand types dominated incised alluvial valleys (Table 12).

DISCUSSION

The strongest influences on spatial patterning of the key woody species were longitudinal gradients in the watershed (e.g. contributing area and bedrock of a site) and vertical gradients perpendicular to the stream (e.g. height above and distance from the channel). Other studies of riparian woody species in the semi arid to arid west yielded similar results (Auble *et al.* 1994; Engelhardt 2009; Friedman *et al.* 1996, 2006; Hupp and Osterkamp 1996; Mahoney and Rood 1998; Scott *et al*. 1996, 1997). Geology and morphology of individual watersheds were closely related to basin sensitivity to disturbance (floods), partially explaining woody species patterns. This is consistent with other research in the study watersheds (Chambers *et al*. 2004b; Engelhardt 2009).

The following discussion will focus on factors that I found to be important for establishment and persistence of woody vegetation both within and among the four study watersheds. This includes an in-depth investigation of our key riparian woody species, the interplay between their ecological amplitudes and life history traits and the fluvial geomorphic setting.

Differences in species distributions

Populus tremuloides was dominant in the upper watersheds above *B. occidentalis* and *Salix* dominated sites, but often co-occurred with *Salix* spp. Other studies of riparian ecosystems in the semi arid to arid west found *P. tremuloides* at higher elevations (460 to 3,660 m; Engelhardt 2009; Flerchinger *et al*. 1996; Jones *et al*. 1985; Sheppard *et al*. 2006). Its elevational range indicates tolerance to severe cold but not high temperatures or low soil water availability concurrent with low elevations (Jones *et al*. 1985; Worrall *et al*. 2008). *P. tremuloides* needs relatively high water availability to satisfy its heavy evapotranspirational (ET) demands (Jones and DeByle 1985). Plant species at high elevations have an advantage because the colder temperature decrease ET demands meeting species water requirements sooner (Patten 1998). *P. tremuloides* was associated most frequently with watersheds dominated by volcanics and quartz in the channel (San Juan and Cottonwood, respectively). Previous research has shown that these watersheds have rugged terrain, incision-dominated responses, high stream power, and high hypsometric integrals, indicating greater land area at high elevation (Engelhardt 2009; Germanoski and Miller 2004). Such watersheds can effectively capture and retain snow, producing extended water availability above and adjacent to the riparian area from snowmelt. In the western U.S. in general, the parent rock type on which *P. tremuloides* occurs is extremely varied and it grows on almost the full spectrum on landforms (Jones and DeByle 1985).

Cross-sectional analyses showed that *P. tremuloides* was found on wide surfaces at greater heights above and distances from the stream than the other riparian woody species. *P. tremuloides* communities can be large in riparian areas with sufficiently high water tables or on side-slopes with adequate soil water (Sheppard *et al*. 2006). Lateral roots may extend more than 100 feet (30 m) into adjacent open areas (Buell and Buell 1959). I observed *P. tremuloides* spreading clonally on wide floodplains and slopes leading down to the valley bottoms. For proper root function it requires unsaturated soils at least seasonally and it cannot tolerate inundation

(Perala 1990). At higher elevations, soil water needs are likely met by snow melt during the winter and spring months. As the soil becomes drier *P. tremuloides* uses its deep root system to maintain water requirements (Johnston 1970, Johnston *et al*. 1969). Studies of soil water depletion indicate rooting depths of at least 9 feet on deep, well-drained soils (Johnston 1970, Johnston *et al*. 1969). Its deep roots likely allow it to persist on sites high above the channel, and its tall stems allow it to compete with streamside *Salix* spp. for light (as with *P. angustifolia*, Friedman *et al*. 2006).

Populus, as a genus, is less tolerant of flood disturbance and inundation than other riparian species explaining its occurrence at greater distances and heights above the stream (Amlin and Rood 2002; Friedman *et al*. 1996; Merritt and Cooper 2000; Scott *et al*. 1996, 1997). Amlin and Rood (2001) showed *P. tremuloides* in a drier ecotone, farthest from the stream, above the zone of cottonwoods (non-clonal *Populus* spp.) and facultative riparian *Salix*. Riparian *P. tremuloides* typically rely on fire, and sometimes beaver disturbance, for stand rejuvenation and maintenance (Sheppard *et al* 2006; Weixelman *et al*. 1996). Sites where *P. tremuloides* occurred also were characterized by low bank angles and higher numbers of knickpoints. Upper watersheds, where *P. tremuloides* was most frequent, were highly correlated with low bank angles and steep stream gradients. Low bank angles were highly correlated to high entrenchment ratios which indicates less stream incision and higher water tables. A knickpoint is a short, over-steepened segment of the longitudinal profile of the channel (Chambers *et al*. 2004b). Presence of knickpoints may not be reflective of a geomorphic response but rather local flow restrictions caused by woody debris from either the high litter substrate of *P. tremuloides* or beaver activity in the upper watershed.

Salix spp. were dominant in all of the study watersheds at low stream gradients and intermediate elevations as has been found previously (Weixelman *et al*. 1996). Both species occurred across a broad range of geologic types: metasediments in Kingston, siliciclastics in

Birch and volcanics in San Juan and Cottonwood Canyons (Chambers *et al*. 2004b; Engelhardt 2009). *Salix* spp. were the only species that occurred in the aggrading alluvial process zone which is characterized by active sediment deposition and high water tables. This is likely attributable to its ability to reproduce vegetatively (*S. exigua* and *S. lutea*; Karrenberg 2002) and form large clones by sprouting from root runners (*S. exigua*) once establishment has occurred. *S. exigua* can persist on sites with short return intervals of inundation (< 2.2 years, Friedman *et al*. 2006) such as in the aggrading alluvial process zone.

Both *Salix* species are notably successful at colonizing riparian areas in the arid west (Amlin and Rood 2001; Karrenberg *et al*. 2002; Patten 1998; Mortenson and Weisberg 2010), and often dominate the riparian zone. Along a gradient perpendicular to the stream, *Salix* spp. were found on narrow surfaces at low heights above and short distances from the stream channel. These results parallel other studies in the western U.S. of *Salix* spp. (Amlin and Rood 2002; Auble *et al*. 1994; Douhovnikoff *et al.* 2005; Friedman *et al*. 2006; Gage and Cooper 2004; Karrenberg *et al.* 2002). Close proximities to the stream are characterized by higher water tables and greater susceptibility to flood disturbance (Chambers *et al.* 2004b; Merritt and Cooper 2000). *Salix* share ecophysiological traits, such as flexible stems and air space in their stems and roots that allow them to endure and resist high flow events, high water tables and inundation (Naiman and Decamps 1997). Because of these characteristics, *Salix* spp. have a competitive advantage over *Populus* spp. at low heights above the channel in streamside zones (Amlin and Rood 2001, 2002; Karrenberg *et al*. 2002; Mahoney and Rood 1998). I found that *S. exigua* and *S. lutea* occupied similar heights above the stream. In contrast, Amlin and Rood (2002) found that *S.exigua* occupied the vertical elevation closer to the stream than *S. lutea*.

Salix spp. occurred in significantly wider riparian zones than *B. occidentalis*. Wider riparian zones were highly correlated with greater valley widths and low stream gradients. Low stream gradients facilitate deposition and subsequent erosion of sediments (Kondolf and Piegay

2003). In central Nevada, wider valley floors often are associated with side-valley alluvial fans or bedrock constrictions that occur down-valley and, consequently, with elevated water tables (Jewett *et al*. 2004).

B. occidentalis dominated the lower elevations of the study watersheds below *Salix* spp. and *P. tremuloides* where most canyons were constricted (at the mouth). *B. occidentalis* was associated with higher stream power than *Salix* spp. due to its occurrence lower in the watersheds or in the bedrock valley process zone. *B. occidentalis* also dominated the uncommon bedrock valley process zone, where channel form was created by valley form. These process zones tend to have large particle sizes and steep stream gradients (Engelhardt 2009). In western North America, *B. occidentalis* is restricted to streams in mountainous regions (USDA 2008). I found it along streams above 1,959 meters. The only other study that included *B. occidentalis* in western North America that I located (Friedman *et al*. 2006) was along rivers above 1,530 meters. *B. occidentalis* was most abundant at lower elevations in Kingston Canyon which was dominated by sedimentary and metasedimentary geology. The reaches of Kingston Canyon where *B. occidentalis* occurred were characterized by a narrow valley with relatively high stream power and several episodes of past incision (Chambers *et al*. 2004b). The occurrence of *B. occidentalis* in constricted valleys with high stream power indicate a capacity to withstand significant high flows.

Cross-sectional analyses showed that mature *B. occidentalis* occurred on wide surfaces at greater heights above and distances from the stream. Similarly, Friedman *et al*. (2006) found *B. occidentalis* on greater heights above the stream than other woody species, particularly *S. exigua*. These authors also found that *B. occidentalis* persisted on sites with longer recurrence intervals of inundation (2.2-4.6 years). The few immature *B. occidentalis* that occurred in our watersheds (n = 8) occurred at low heights (n=3) adjacent to the stream. These surfaces consisted of inset stream terraces and of fluvial deposition areas behind debris dams. Similar to other riparian woody

species, *B. occidentalis* undoubtedly requires high soil water availability for seedling establishment. *B. occidentalis* reproduces primarily by seed (Utchyl 1989) and has longer seed viability than most riparian woody species (Salicaceae, maximum 4 weeks). It disseminates seed in the fall and can germinate then or the following spring (Uchytil 1989a) at the time of peak annual runoff of snowmelt.

The occurrence of mature *B. occidentalis* on surfaces with greater heights above the channel, and the lack of younger trees, likely was due to their location in flood or incision prone areas in our stream systems. Stream bank angle was significantly steeper than for the other woody riparian species. Lower watersheds were highly correlated with high stream power, high stream gradients, steep bank angle, narrow valley widths and narrow extent of riparian vegetation in this study. Lower watersheds also were highly correlated with finer grains in the channel bed which when combined with higher stream power may facilitate incision and steepening of the bank angle. Based on its position in the watersheds and along the streams it appears that *B. occidentalis* has the capacity to tolerate flood disturbance and, in the absence of significant stream incision, may even benefit from mechanical damage from floods for stand rejuvenation (resprouting) and maintenance. More research is needed to understand the relationships among hydrologic and geomorphic processes and the establishment and persistence of *B. occidentalis*.

It is of conservation concern that *B. occidentalis* is largely found on upper surfaces with steep bank angles and low entrenchment ratios, which indicate abandoned surfaces with lowering water tables. It is a shallowly rooted species that requires relatively high water tables (Uchytil 1989a; Weixelman *et al*. 1996). Consequently, *B. occidentalis* is frequently uprooted by wind, water, or heavy snow (Weixelman *et al*. 1996). In the watersheds, large mature individuals frequently occur on undercut stream banks above incising channels. Progressive lowering of the water table may lead to population declines.

Climate change in the Great Basin foreshadows an increase in both drought and flood frequency (Chambers and Pellent 2008). Increased temperatures and precipitation would likely lead to earlier spring runoff, decreased snowpack and decreased soil water availability (Smith and Wagner 2006). Specific effects of climate change on our woody riparian species are not exactly known. I suspect climate change will increase incision processes in the study watersheds and place *B. occidentalis* populations (and other species) at greater risk. Cooper *et al*. (2006) predicted climate change in the Rocky Mountains would likely lesson opportunities for establishment of *Salix* spp. Landhausser *et al*. (2010) predicted expansion of *P. tremuloides* into higher altitudes under warmer climate conditions in the central Rocky Mountains. However, because *P. tremuloides* already occupies the uppermost altitudes of the central Great Basin, its distribution could potentially be narrowed.

Effects of flood disturbance

The 1983 and 1985 high flow disturbance event triggered a significant episode of woody species establishment, generating a "cohort" (Oliver and Larson 1996) of similar aged trees and shrubs. Similar to an earlier study in central Nevada watersheds, *S. exigua* and *S. lutea* dated primarily to the high water years of 1983 and 1985 (Chambers *et al*. 1998). In addition, our results yielded a set of geomorphic parameters, that when combined as recommended by Scott *et al*. (1996, 1997), described surfaces ideal for cohort establishment. At the watershed scale, establishment was highest within San Juan watershed and the incised alluvial process zone. At reach scales, flood induced establishment was related to small clasts in the channel bed, low stream gradients, and a high number of inset stream terraces.

Other studies of riparian woody species establishment in the arid west found that sites suitable for establishment after extreme flooding are bare, moist surfaces protected from disturbance (Friedman *et al*. 1996; Mortenson and Weisberg 2010; Scott *et al*. 1996, 1997; Young

and Clements 2003). In our study system these were relatively low stream gradient sites that were repeatedly disturbed as indicated by a high number of inset terraces and that were characterized by relatively small clasts on the lowest terraces. At large scales, the necessary geomorphic conditions were a function of specific watershed characteristics as in San Juan or more general process zone characteristics. The high level of establishment in San Juan watershed can be related to its geomorphic characteristics and incision history. San Juan has high peak flows and has exhibited several episodes of incision in recent history (Germanoski and Miller 2004). Its basin morphometry and size does not particularly promote high peak flows. However, the channel bed is unusually erodible because of fine-grained bed material derived from welded-tuff (volcanics) that underlies most of the watershed (Germanoski and Miller 2004). Factors such as road capture and beaver dam failure also have exacerbated recent channel incision in this watershed (Lahde 2003). The net effect of the watershed's geomorphic characteristics and other factors has been repeated recent incision and formation of inset terraces with the necessary conditions for woody species establishment. The incised alluvial process zone is comprised of deep alluvial deposits in flat, broad valleys and its functional processes are deposition and erosion during high flows (Engelhardt 2009). Lower stream gradients with fine-grained bed material can erode and deposit fresh sediments during high flow events. Erosional processes during high flows have the capacity to create new, inset terraces with exposed surfaces (Miller *et al*. 2004).

The 1983 and 1985 cohorts were located largely on inset stream terraces. Different species are typically distributed along a vertical gradient to the stream based on inundation tolerance (Amlin and Rood 2001) and soil moisture and water-table requirements for establishment and growth (Bendix and Hupp 2000; Merritt and Cooper 2000). The mode of establishment of riparian woody species following floods often differs among species (lateral spread vs. seed) and within species (vegetative propagules vs. seed). However, in arid regions, seed dissemination must be concomitant with moisture provided by high flows for establishment

to occur (Mahoney and Rood 1998; Scott *et al*. 1996). *Salix* species and *B. occidentalis* were frequently found with complete taproots and root crowns indicating reproduction by seed rather than vegetative propagules (e.g. stem segments).

The stem dating analyses revealed that known historic floods elicited a species-specific response. *Salix* exhibited the strongest response to the known floods across all the study watersheds corroborating its designation as a well-adapted streamside species (Amlin and Rood 2001, 2002; Johnson *et al*. 2000; Karrenberg *et al*. 2002; Mahoney and Rood 1998). *Salix* can reproduce vegetatively and, therefore, may not have been as tightly restricted to bare, moist surfaces for establishment (Scott *et al*. 1997). *P. tremuloides* had a continuous response demonstrating its reliance on disturbances other than flood to trigger lateral sprouting (Sheppard *et al* 2006; Weixelman *et al*. 1996). However, *P. tremuloides* may have responded to the mechanical damage of flood within highly sensitive watersheds (San Juan Canyon). Birch were generally older (>30 years old) and responded to flood disturbance primarily by way of resprouting from existing clusters. Establishment by seed for *B. occidentalis* was apparently a very rare occurrence and required low moist surfaces.

Stand and age structure

The cluster and ordination results suggest that riparian forest stand structure was influenced by fluvial geomorphology. However, the ANOVAs showed that stand structural types were not strongly distinguished by geomorphic characteristics except for *B. occidentalis*. Riparian forest structure was often explained by watershed specific characteristics such as watershed lithology and morphology. The YLD stand type was most abundant in the incised alluvial process zone across all woody species. YLD stands required the higher water availability provided by wide entrenchment and high entrenchment ratios (low incision) allowing high water tables, deposition of fine sediment, and slow water table drawdown post flood meeting the requirements

for establishment from seed (Amlin and Rood 2001). Other studies have used stand descriptor variables to characterize stand structural type (Garbarino *et al*. 2009; Poage and Tappeiner 2005), but relatively few have used them in relation to fluvial geomorphic or environmental gradients (Garbarino *et al*. 2009; Lamotte 1990; Meitzen 2009; Villarin *et al*. 2009). Mechanisms such as water table decline and channel migration can influence the course of riparian succession, present stand structure, and future successional trajectories (Meitzen 2009).

B. occidentalis was most abundant in lower Kingston Canyon where it had higher frequencies of MDD stand types than in the other watersheds. Also, *Salix* spp. were oldest in lower Kingston canyon where both entrenchment width and bank angles were high. Progressive stream incision during high flows likely increased mortality of established *Salix* and *B. occidentalis* cohorts due to water table drawdown. *B. occidentalis* MRS stands occurred at slightly, but significantly, steeper stream gradients and had more intrusives in the channel bed than MDD and YLD stands. MRS stands were abundant in Birch Canyon and were characterized by steep stream gradients and intrusive bedrock. However, intrusive bedrock in Birch Canyon was higher than all the other study watersheds (Germinoski and Miller 2004), and likely weighted the results.

Cottonwood Canyon had high quartz in the channel in the upper watershed which supported *P.tremuloides* and *S. lutea* MDD stands. Cottonwood Canyon likely experiences heavy snowpack in the winter leading to higher risk of winter storm damage and longer periods of available moisture that can facilitate fungus and blight and increase mortality of *P. tremuloides* (Peterson 1992). Inundation lasting more than two growing seasons can cause branch and crown dieback of *Populus* (*P. balsamifera,* Amlin and Rood 2001). The *S. lutea* YLD stands were generally not abundant possibly because either incision was causing progressive water table declines or the most recent floods (1995 and 1998) were not adequate to trigger new

establishment. In general, *Salix* ages ranged between 20 and 40 years old likely sustaining high mortality from recent floods.

Conclusions

Riparian woody species distribution reflected longitudinal gradients in the watershed and vertical gradients perpendicular to the stream within stream reaches. Ecological amplitudes and life history traits often aligned directly with those gradients. Watershed morphology and geology were also strong predictors of species occurrence. *P. tremuloides* dominated the upper watersheds, particularly watersheds with greater land area at high elevations (San Juan and Cottonwood Canyons), and was found at greater distances and heights above the active channel on wide surfaces. These finding are in concert with species requirements for cooler temperatures found at higher elevations, seasonally unsaturated soils found at greater distances from the channel; as well as species traits such as intolerance for inundation and lateral root spread colonizing wide surfaces. *Salix* spp. were dominant in all of the study watersheds at low stream gradients and intermediate elevations, and were found at close-proximities to the active channel. These findings demonstrate that *Salix* spp. are broadly adapted to the active channel zone. Shared ecophysiological traits allow them to endure and resist high flows and inundation. *B. occidentalis* was most abundant at lower elevations and was found at greater distances and heights above the active channel on wide surfaces with steep stream bank angle. These findings indicate an adaptation to the higher unit stream powers found lower in the watersheds. However, steep bank angle and greater heights above the channel are related to incision and lowering water tablesand little active recruitment was occurring.

These watersheds are predisposed to incise but the forces driving present ecosystem degradation (e.g. grading of roads, road captures, mining, grazing) should be mitigated, where necessary, to prevent accelerated incision rates and possible declines in *B. occidentalis*

populations. Cottonwood (*P. angustifolia*) populations were present in these watersheds prior to recent incision, but residual populations are declining. Cottonwood is recognized as a keystone species in riparian ecosystems across the west and the fate of these ecosystems often follow the fate of cottonwood populations (Mahoney and Rood 1998).

Salix exhibited the highest frequencies of establishment resulting from historic floods likely because of their ability to reproduce by seed, resprout (*S. lutea*) and spread laterally (*S. exigua*). *P. tremuloides* had a continuous response demonstrating its reliance on asexual reproduction from lateral root sprouts. Birch responded to flood disturbance primarily by way of resprouting from existing clusters. Establishment by seed for *B. occidentalis* was apparently a very rare occurrence. Standard dendrochronology approaches and the historic flood record showed a pulse of seedling establishment following regional flooding in 1983/1985. Seedling establishment following the 1983 and 1985 floods was watershed-specific and highly predictable (72.6 %) according to environmental context. Geomorphic characteristics important for determining establishment included: incised alluvial process zone, small clasts in the channel bed, low stream gradients, and a high number of inset stream terraces. As in other riparian areas of the semi-arid west woody species establishment depended on: bare, moist alluvial substrates with constant soil moisture provided by fine-grained bed material.

Woody species distribution was sensitive to geomorphic process zone type. Young, low density stands and new establishment due to flooding were strongly related to the incised alluvial process zone. Riparian forest stand structure was related to fluvial geomorphic characteristics especially for *B. occidentalis*. The other woody species had stand structural/geomorphic affinities that were weakly correlated. The woody species all reflected watershed-specific responses. For example, quartz as a channel bed material was associated with degenerating, decadent stands of *P. tremuloides*. However, quartz was also highly correlated to the upper watershed of Cottonwood Canyon where winter storm damage could be the culprit. Another example is

demonstrated by *B. occidentalis*. Mature, regenerating stable (MRS) stands were associated with intrusives in the channel bed. However, Birch Canyon has the highest abundance of intrusive of all the watersheds and likely weighted the results. This portion of the analyses may have been more useful for diagnosing species stand structure at the level of individual watersheds if more sampling sites were available.

The study watersheds differ in relative sensitivity to disturbance, but all are in an incisional phase. The 1983/1985 flood resulted in widespread stream incision and reinitiated successional processes. Flood effects were most pronounced in the alluvial process zone which is characterized by active deposition and erosion and in San Juan Canyon which has volcanic lithology, flashy flows and compounding perturbations (roads in valley bottom, beaver dams). Abundance of newly established stands were low for *B. occidentalis*. Because of the location of *B.occidentalis* in areas prone to flood disturbance and incision, this species has generally low recruitment and is of management concern. However, its longevity and ability to survive floods suggest that only infrequent establishment events may be sufficient for persistence.

Naturally flowing streams in the semi-arid west are rare and due to ongoing natural and anthropogenic perturbations restoration can be challenging. An improved understanding of woody species establishment and persistence is essential for sustaining the integrity of these valuable ecosystems.

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TABLES & FIGURES

Table 1. Characteristics and descriptions of main channel process zones occurring in the study watersheds (from Engelhardt 2009).

Process Zone	Frequency	Valley Fill Composition	Dominant Processes	Description
Aggrading Alluvial (AA)	rare	alluvium	deposition, channel avulsion	aggrading generally localized and often associated with avulsion processes, defined by deposition along margins of channel or on valley floor
Bedrock Valley (BV)	uncommon	bedrock	sediment transport	distinct channels with significant bedrock exposure in channel bed and along channel margins, channel form created by valley form, minimal sediment along banks
Incised Alluvial (IA)	very common	alluvium	erosion, sediment transport, sediment storage	flat and broad valley underlain by alluvial deposits, channel generally incised into alluvium, major long-term and minor short-term storage
Incised Colluvial (IC)	common	colluvium and fan material	erosion, sediment generation, sediment transport	channel incised into colluvial and fan deposits, steep channel banks and well-defined erodible channel form, significant long-term and limited short-term storage

Table 2. Geomorphic variables used in the study and their descriptions.

Geomorphic Variables	Description
Site Characteristics	
Watershed	map name of watershed
Vegetation Type	vegetation type of the site
Process Zone	geomorphic process zone of the site
Bedrock	bedrock of site as indicated by geologic map
Area Above (m)	contributing area above the site
Stream Length Above (m)	stream length of main channel above the site
Elevation (m)	elevation of the site
Riparian Zone Width (m)	width of riparian vegetation
Valley Width (m)	measured width of valley
Valley Slope (%)	valley slope, parallel to stream
Transect Characteristics	
Transect	transect #
Entrenchment Depth (m)	difference in ht between valley floor and thalweg
Entrenchment W:D Ratio	incised width divided by incised depth
Entrenchment Width (m)	horizontal distance between valley floor surfaces
Surface Characteristics	
Distance to Water's Edge (m)	distance from water edge
Height Above Channel Thalweg (m)	height of surface above channel thalweg
Height Above Water Surface (m)	height of surface above water surface in channel
Number of Terraces	# terraces observed on both sides of the channel
Surface Width (m)	width of surface
Terrace/Slope	surface type, terrace vs. slope (in-field)
Terrace/Slope GIS	surface type, terrace vs. slope (digital profile)

Table 2 (cont.).

Geomorphic Variables	Description
Channel Characteristics	
Bank Angle (%)	bank angle
Knickpoints (#)	# of Knickpoints
Stream Gradient (%)	stream gradient
Thalweg Depth (m)	thalweg depth, water surface to thalweg
Water Width (m)	water width, in channel at time of sampling
Channel D_{50} (mm)	channel bed D_{50} from Wolman pebble count
Channel D_{84} (mm)	channel bed D_{84} from Wolman pebble count
Fines (%)	% sediments in bank soil sample <2mm in di.
Largest Clast Size (cm)	diameter of largest clast
Woody Debris (%)	% woody debris cover in channel
WD Mean Diam. (m)	mean diameter of woody debris in channel
Channel Lithology	
Carbonate (%)	% clasts that were carbonate
Intrusive (%)	% clasts that were intrusives
Metasedimentary (%)	% clasts that were metasedimentary
Quartzite (%)	% clasts that were quartzites
Sandstone (%)	% clasts that were sandstone
Siliciclastic (%)	% clasts that were siliciclastics
Silt (%)	% channel bed with silt
Volcanic (%)	% clasts that were volcanics
Dominant Lithology	most abundant lithology- Wolman pebble count
Largest Clasts Dom. Lith. (%)	% dominant lith. of 10 largest clasts in the channel
Largest Clasts Dom. Lithology	dominant lith. of 10 largest clasts in the channel
Largest Clast Lithology	lithology of the largest clast in the channel

Table 3. Total number of transects and total number of surfaces occupied by riparian woody species in the four study watersheds. Selected descriptor variables are included for each species. SD is stem density, Ht is height, SJ is seedlings and juveniles.

Woody Species	Tran	Surf	Variables Used in Analysis
B. occidentalis	39	137	Basal Area, Ht, Largest Dead Stem Diameter, SD of Individual Clusters, SD of SJ, SD of Stems >5cm, SD Total
P. tremuloides	37	65	Cover, Ht, SD of Dead, SD of SJ, SD total
S. exigua	48	113	Cover, Ht, SD of Dead, SD of SJ, SD Total
S. lutea	83	225	Cover, Ht, SD of Dead, SD of Individual Clusters, SD of SJ, SD Total

Table 4. Pearson Product Moment Correlations between surface and transect geomorphic variables (n=184). Correlations in bold are significant at 0.30≥r≥0.3.

	AREA.A	BNK.ANG	CARB%	D_{50}	D_{84}	ELEV	ENT.DEP	ENT.RAT	ENT.WD	FINES%	GRADNT	HT.THAL	HT.WTR	INTRU%	KNICK	LG.PDOM	LRG.CST	METASED%	NM.TERR	PCT.DOM	QUARTZ%	RIP.WID	S.LNGTH	SANDST%	SF.WID	SILICIC%	SILT%	THAL	V.SLP	VAL.WID	VOLCAN%	W.DIST	WOO.Di	WOOD%	WTR.WD
AREA.A	1.00																																		
BNK.ANG	0.14	1.00																																	
CARB%	**0.52**	0.09	1.00																																
D_{50}	0.10	0.01	**0.33**	1.00																															
D_{84}	0.28	0.14	**0.50**	**0.86**	1.00																														
ELEV	**-0.74**	-0.19	**-0.37**	-0.09	-0.20	1.00																													
ENT.DEP	-0.03	0.14	0.11	0.15	0.16	-0.19	1.00																												
ENT.RAT	0.22	**-0.38**	0.01	-0.06	-0.06	0.02	**-0.46**	1.00																											
ENT.WD	0.15	-0.12	0.08	0.11	0.15	-0.21	**0.52**	0.27	1.00																										
FINES%	0.25	0.09	0.07	-0.10	-0.07	-0.30	-0.02	-0.06	-0.02	1.00																									
GRADNT	-0.26	0.09	-0.01	0.18	0.21	**0.43**	0.04	-0.17	-0.11	-0.27	1.00																								
HT.THAL	0.14	0.22	0.15	0.17	0.24	-0.06	0.28	-0.24	0.12	-0.09	0.19	1.00																							
HT.WTR	0.07	0.20	0.11	0.10	0.17	-0.02	0.28	-0.24	0.11	-0.12	0.22	**0.99**	1.00																						
INTRU%	0.14	0.07	-0.09	0.04	0.05	-0.17	0.05	-0.18	-0.13	0.12	0.08	0.08	0.08	1.00																					
KNICK	-0.11	0.08	-0.02	0.15	0.14	0.20	0.12	-0.12	0.02	-0.19	**0.31**	0.12	0.13	0.27	1.00																				
LG.PDOM	-0.20	0.17	-0.10	0.00	-0.04	0.06	0.12	-0.11	0.07	-0.09	-0.04	0.08	0.11	0.16	0.08	1.00																			
LRG.CST	0.23	0.23	0.28	**0.45**	**0.57**	-0.21	0.26	-0.21	0.15	-0.08	0.28	0.26	0.25	0.16	0.12	0.15	1.00																		
METASED%	**0.61**	0.01	**0.35**	-0.07	0.08	-0.15	**-0.32**	**0.37**	-0.14	-0.01	-0.18	-0.04	-0.09	-0.16	-0.15	-0.14	-0.05	1.00																	
NM.TERR	-0.18	-0.12	-0.10	0.03	0.00	-0.11	**0.42**	-0.16	**0.36**	0.05	-0.02	0.04	0.06	0.02	-0.08	0.08	0.03	**-0.38**	1.00																
PCT.DOM	**-0.33**	0.00	-0.18	-0.02	-0.07	0.21	-0.06	-0.06	0.02	0.10	-0.12	-0.02	-0.01	-0.14	0.15	0.28	-0.13	-0.25	0.03	1.00															
QUARTZ%	**-0.53**	-0.14	**-0.34**	-0.03	-0.18	**0.30**	-0.01	-0.20	-0.25	-0.17	0.06	-0.10	-0.03	0.02	0.14	0.04	-0.14	**-0.41**	0.03	-0.01	1.00														
RIP.WID	-0.04	0.00	-0.06	-0.22	-0.26	0.07	**-0.31**	0.10	-0.29	0.17	**-0.34**	-0.14	-0.17	-0.05	-0.15	-0.11	**-0.39**	0.15	-0.15	0.16	-0.06	1.00													
S.LNGTH	**0.85**	0.18	**0.33**	0.06	0.18	**-0.79**	0.16	0.12	**0.35**	0.29	**-0.33**	0.16	0.10	0.12	-0.12	-0.06	0.19	0.29	0.02	-0.16	**-0.64**	-0.05	1.00												
SANDST%	0.03	0.00	0.13	-0.09	-0.07	-0.07	-0.05	-0.03	-0.11	-0.09	-0.07	0.04	0.04	0.00	-0.17	-0.03	-0.09	0.05	0.00	-0.20	0.19	0.12	-0.07	1.00											
SF.WID	0.01	-0.02	0.04	-0.01	0.04	0.03	0.01	0.05	0.05	-0.04	0.03	**0.53**	**0.53**	0.00	0.03	0.05	0.04	-0.04	-0.06	0.12	-0.03	0.08	0.03	0.03	1.00										
SILICIC%	0.06	-0.14	0.00	-0.11	-0.13	-0.16	0.22	-0.05	0.11	-0.08	-0.06	0.05	0.04	0.04	-0.02	-0.06	-0.07	-0.10	0.09	-0.18	-0.01	-0.09	0.18	0.23	0.05	1.00									
SILT%	-0.02	-0.19	-0.06	-0.21	-0.20	0.09	-0.19	0.02	-0.19	0.24	-0.19	-0.07	-0.12	0.01	-0.10	**-0.38**	-0.24	-0.02	-0.12	0.22	-0.16	**0.34**	-0.03	-0.05	0.05	-0.02	1.00								
THAL	**0.54**	0.09	0.27	-0.05	0.10	-0.30	-0.08	0.03	0.00	0.20	-0.19	0.05	-0.07	0.03	-0.05	**-0.33**	0.01	**0.47**	-0.18	-0.04	**-0.54**	0.21	**0.46**	-0.02	0.02	0.02	**0.49**	1.00							
V.SLP	-0.05	0.02	0.02	**0.69**	**0.60**	0.05	0.09	-0.03	0.08	-0.06	0.08	0.11	0.00	0.01	0.07	0.05	0.10	-0.08	0.06	0.00	-0.01	-0.11	-0.01	-0.04	-0.03	-0.02	-0.07	-0.09	1.00						
VAL.WID	-0.13	-0.10	-0.09	-0.26	**-0.32**	0.08	-0.14	0.16	-0.16	0.03	**-0.38**	-0.27	-0.27	-0.13	-0.14	-0.21	**-0.47**	0.10	0.00	-0.09	0.22	**0.55**	-0.23	0.21	-0.05	-0.07	0.20	0.07	-0.12	1.00					
VOLCAN%	-0.23	0.14	-0.23	0.03	-0.01	0.00	**0.31**	-0.09	**0.42**	0.02	0.12	0.06	0.07	-0.18	-0.05	0.21	0.11	**-0.49**	**0.35**	0.24	**-0.43**	-0.14	0.21	**-0.33**	0.02	0.05	-0.16	-0.17	0.08	-0.27	1.00				
W.DIST	0.00	0.10	0.09	0.07	0.09	0.02	0.16	-0.03	0.20	-0.04	0.14	**0.47**	**0.48**	-0.01	0.08	0.11	0.13	-0.12	0.12	0.13	-0.10	-0.03	0.09	-0.02	**0.39**	0.02	-0.07	-0.05	0.00	-0.17	0.17	1.00			
WOO.Di	-0.18	0.03	-0.01	0.24	0.25	**0.31**	0.15	-0.15	-0.01	-0.20	**0.36**	0.19	0.21	-0.04	**0.37**	0.11	0.29	-0.12	0.02	0.12	0.13	-0.06	-0.21	-0.14	0.10	-0.04	-0.09	-0.19	0.05	-0.17	0.03	0.11	1.00		
WOOD%	0.26	0.25	0.21	0.08	0.15	-0.16	0.06	-0.16	-0.07	0.02	0.20	0.15	0.14	0.09	0.12	0.05	0.09	0.06	-0.26	0.02	-0.22	-0.10	0.28	-0.07	0.04	0.03	-0.08	0.10	0.00	-0.23	0.09	0.06	0.18	1.00	
WTR.WD	**0.65**	0.02	**0.40**	0.20	0.26	**-0.32**	-0.05	**0.34**	0.17	0.02	-0.10	0.11	0.06	-0.01	0.17	-0.11	0.17	**0.46**	**-0.37**	-0.13	**-0.32**	-0.02	**0.52**	-0.03	0.07	0.04	0.02	**0.38**	-0.01	-0.14	-0.24	0.05	0.08	0.19	1.00

Table 5. Principal component loadings for the first 2 principal components (PCs) of the woody species distribution analysis. PC loading score cut-off was set at 0.10.

Axis	**PC 1**	**PC 2**
% Variance Explained	27%	18%
Geomorphic Characteristics		
Area Above	-	-0.78
Height Above Thalweg	-0.69	-
Bank Angle	-	-0.60
Distance to Channel	-0.72	-

Table 6. Results of one-way ANOVA tests (F values and p-values) comparing differences in geomorphic characteristics across woody species. Geomorphic variables not used in the PCA are in italics. Values are mean ± standard deviations. F values in bold are significant at $\alpha<0.013$ based on the Bonferroni correction for multiple tests. Significant differences among species are indicated by unshared letters using the Bonferroni multiple comparisons method.

Primary Geomorphic Characteristics	**F**	**p**	***B. occidentalis***	***P.tremuloides***	***S. exigua***	***S. lutea***
			(n=59)	**(n=114)**	**(n=73)**	**(n=196)**
Channel Lithology						
Quartz (%)	***17.85***	*0.000*	*0.27±0.03 a*	*0.57±0.03 b*	*0.44±0.03 c*	*0.47±0.02 c*
Volcanics (%)	***9.05***	*0.000*	*0.16±0.03 a*	*0.34±0.03 b*	*0.24±0.03 ac*	*0.32±0.02 bc*
Site						
Area Above	**85.58**	*0.000*	$5.59x10^{7}±1.64x10^{6}$ a	$1.76x10^{7}±1.18x10^{6}$ b	$3.12x10^{7}±1.77x10^{6}$ c	$2.39x10^{7}±1.07x10^{6}$ d
Bank Angle (%)	**5.38**	*0.001*	0.56±0.04 a	0.43±0.02 b	0.46±0.03 abc	0.41±0.02 bc
Entrenchment W:D Ratio	**3.79**	*0.011*	4.74±0.27 ab	4.21±0.19 a	5.42±0.34 b	5.09±0.21 ab
Entrenchment Depth	***5.11***	*0.002*	*1.98±0.09 c*	*1.98±0.06 ac*	*1.75±0.12 c*	*1.72±0.07 bc*
Knickpoints	**6.39**	*0.000*	0.68±0.14 ab	0.88±0.12 a	0.47±0.09 ab	0.36±0.06 b
Riparian Width	**4.29**	*0.005*	20.19±1.28 a	26.31±1.08 ab	36.36±3.97 b	36.68±2.36 b
Stream Length Above	***45.11***	*0.000*	*16060.10±306.39 a*	*8252.68±536.57 b*	*10815.63±473.60 c*	*9018.06±310.91 b*
Terrace						
Height Above Thalweg	**68.47**	0.000	1.45±0.10 a	1.34±0.07 a	0.59±0.08 b	0.48±0.04 b
Surface Width	***24.10***	*0.000*	*4.20±0.36 a*	*5.38±0.37 a*	*3.13±0.39 b*	*02.74±0.22 b*
Water's Edge Distance	**76.71**	0.000	4.83±0.73 a	6.87±0.46 a	2.61±0.70 b	1.40±0.15 b

Table 7. Percentage of trees and shrubs aged that established in response to known high flow events. An accuracy of ± 3 years was applied to each age.

High Flow Events	S. lutea n=43	S. exigua n=12	Salix spp. n=52	P. tremuloides n=40	B. occidentalis n=44	All Species Combined
1995/1998	28%	50%	32%	20%	0%	18%
1983/1985	44%	25%	42%	28%	18%	30%
1973/1975/1978	28%	8%	28%	27%	14%	23%
1965/1969	7%	0%	8%	15%	14%	12%

Table 8. Results from the odds ratio analysis examining the 4 key woody species establishment response to the 1983 and 1985 flood as a function of geomorphic variables. Variables in the best-fit model from stepwise regression, direction of effect (positive or negative), beta coefficients of the best predictors, their 95 % confidence intervals, and odds ratios are given. Reference factor level effects are relative to IA for process zone and Birch for watershed.

Model Variables	**Direction of Effect**	**Beta Coefficient**	**Odds Ratio**	**Confidence Interval**
Process Zone				
Incised alluvial (IA)				
Incised colluvial (IC)	-	0.18	0.83	0.72 to 0.96
Watershed				
Birch				
Cottonwood	+	0.01	1.01	0.81 to 1.26
Kingston	+	0.00	1.00	0.80 to1.24
San Juan	+	0.21	1.23	1.01 to 1.49
Number of Terraces	+	0.06	1.06	0.98 to 1.16
Stream Gradient	-	0.02	0.98	0.95 to 1.01
Largest Clast	-	0.07	0.93	0.89 to 0.98

Table 9. Results of Kruskal-Wallis rank tests (χ^2 and p-values) comparing differences in primary stand characteristics for 3 stand structural types across the 4 key woody species. Stand characteristics are mean ± standard error. χ^2 values in bold are significant at $p<0.05$. SD is stem density, SJ is seedlings and juveniles. *The measurement used for *B. occidentalis* dead is diameter of largest dead stem within individual clusters.

				Young Low Density	Mature Regenerating Stable	Mature Dense Decadent
		χ^2	p	(n=282)	(n=158)	(n=100)
B. occidentalis		$F_{1,63}$=		n=14	n=19	n=32
	SD SJ	2.68	0.262	0.26±0.24	0.02±0.01	0.00±0.00
	Dead*(m)	4.98	0.083	0.01±0.01	0.12±0.08	0.15±0.09
	SD Total	**49.36**	0.000	0.30±0.15	9.39±0.77	2.24±0.27
	SD/Indiv	**16.80**	0.000	0.35±0.24	0.22±0.02	0.10±0.01
	% Cover	**18.68**	0.000	0.08±0.03	0.29±0.04	0.27±0.03
	Height (m)	**16.24**	0.000	3.15±0.41	6.06±0.41	7.85±0.57
	Age	na	na	30.00±0.00	44.00±8.83	58.00±0.00
P. tremuloides		$F_{1,135}$=		n=73	n=17	n=47
	SD SJ	**13.32**	0.000	0.30±0.05	0.83±0.24	0.78±0.14
	SD Dead	4.98	0.083	0.04±0.01	0.04±0.03	0.08±0.03
	SD Total	0.21	0.900	0.56±0.05	0.46±0.08	1.39±0.15
	% Cover	5.70	0.060	0.20±0.02	0.26±0.05	0.16±0.03
	Height (m)	**102.18**	0.000	4.30±0.12	7.77±0.36	1.88±0.12
	Age	3.94	0.140	26.00±2.80	36.00±15.75	34.00±4.12
S. exigua		$F_{1,111}$=		n=67	n=40	n=6
	SD SJ	1.56	0.460	1.21± 0.17	2.48± 0.53	1.58± 0.74
	SD Dead	**33.99**	0.000	0.77± 0.15	3.23± 0.53	11.83± 1.05
	SD Total	**77.34**	0.000	1.68± 0.18	7.45± 0.47	14.25± 1.33
	% Cover	**28.70**	0.000	13.62± 1.95	27.33± 3.67	55.58± 5.37
	Height (m)	**14.59**	0.001	1.53± 0.16	2.40± 0.19	2.63± 0.51
	Age	na	na	na	na	28.00± 7.82
S. lutea		$F_{1,223}$=		n=121	n=80	n=24
	SD SJ	**8.69**	0.013	0.17±0.04	0.94±0.22	1.02±0.61
	SD Dead	0.71	0.700	0.11±0.04	2.00±0.24	7.46±1.21
	SD Total	1.15	0.564	0.33±0.06	5.34±0.33	14.33±1.11
	SD/Indiv	3.24	0.198	0.36±0.06	4.35±0.23	11.48±1.58
	% Cover	3.12	0.210	0.23±0.02	0.46±0.04	0.60±0.09
	Height (m)	1.92	0.383	2.44±0.25	1.93±0.16	2.01±0.28
	Age	0.81	0.667	20.00±2.08	21.00±2.32	29.00±12.38

Table 10. NMS ordination outputs for woody riparian species and their final solutions.

	Dimension	Axes	Orthogonality	Final Stress	Final Instability	Cumulative R^2
B. occidentalis	2	1 vs 2	97.0%	7.36	0.057	98.0%
P. tremuloides	3	1 vs 2	100.0%	0.88	0.062	59.0%
		1 vs 3	92.8%			
		2 vs 3	99.9%			
S. exigua	2	1 vs 2	91.0%	7.55	0.053	98.0%
S. lutea	2	1 vs 2	68.3%	7.02	0.038	97.0%

Table 11. Pearson's correlation coefficients (r) for geomorphic characteristics with strong correlations to at least one axis for the 4 woody species. Proportion of variance represented by each NMS axis (R^2) is given. Correlations $0.2 \leq r \leq -0.2$ are in bold.

	B. occidentalis		***P. tremuloides***			***S. exigua***		***S. lutea***	
	Axis 1	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Geomorphic Characteristics	R^2=67%	R^2=31%	R^2=5%	R^2=7%	R^2=47%	R^2=33%	R^2=65%	R^2=82%	R^2=15%
Surface Width	-	-	**-0.32**	-0.10	**-0.22**	-	-	-	-
Fines in Channel (%)	-	-	-0.17	-0.05	-0.19	-	-	-	-
Sandstone (%)	-	-	0.13	-0.06	**0.23**	-	-	-	-
Volcanics (%)	-	-	**-0.20**	-0.03	-0.16	-	-	-	-
Entrenchment Width	**-0.48**	0.02	**-0.26**	-0.04	-0.11	-0.10	**0.21**	-	-
Entrenchment W:D Ratio	**-0.27**	-0.01	-	-	-	-	-	-	-
Riparian Width	**-0.25**	-0.05	-	-	-	-	-	-	-
Bank Angle	**0.21**	**0.28**	-	-	-	0.02	**-0.21**	-	-
Knickpoints	**0.26**	0.12	-	-	-	-	-	-	-
Gradient	**0.31**	0.18	-	-	-	-	-	-	-
Intrusive (%)	**0.38**	-0.02	-	-	-	-	-	-	-
Elevation	-	-	-	-	-	0.07	-0.14	-	-
Height Above Thalweg	-	-	-	-	-	0.03	0.16	-	-
Number of Terraces	-	-	-	-	-	0.11	0.16	-	-
Woody Debris Diameter	-	-	-	-	-	-	-	-0.15	0.09
Woody Debris in Channel (%)	-	-	-	-	-	-	-	-0.15	0.05
Water Width	-	-	-	-	-	-	-	-0.13	0.08
Thalweg Depth	-	-	-	-	-	-	-	-0.11	0.09
Quartz (%)	-	-	-	-	-	-	-	0.14	-0.01

Table 12. Percentage abundance of process zone for each stand type by woody species. Abundance measure was number of surfaces.

	Aggrading Alluvial	Bedrock Valley	Incised Alluvial	Incised Colluvial
B. occidentalis				
YLD	0.0%	0.0%	78.6%	21.4%
MRS	0.0%	26.3%	36.8%	36.8%
MDD	0.0%	0.0%	50.0%	50.0%
P. tremuloides				
YLD	0.0%	0.0%	56.2%	43.8%
MRS	0.0%	0.0%	47.1%	52.9%
MDD	0.0%	0.0%	42.6%	57.4%
S. exigua				
YLD	14.9%	1.5%	47.8%	35.8%
MRS	10.0%	0.0%	57.5%	32.5%
MDD	16.7%	0.0%	66.7%	16.7%
S. lutea				
YLD	9.9%	0.8%	60.3%	28.9%
MRS	3.8%	1.3%	65.0%	30.0%
MDD	0.0%	0.0%	58.3%	41.7%

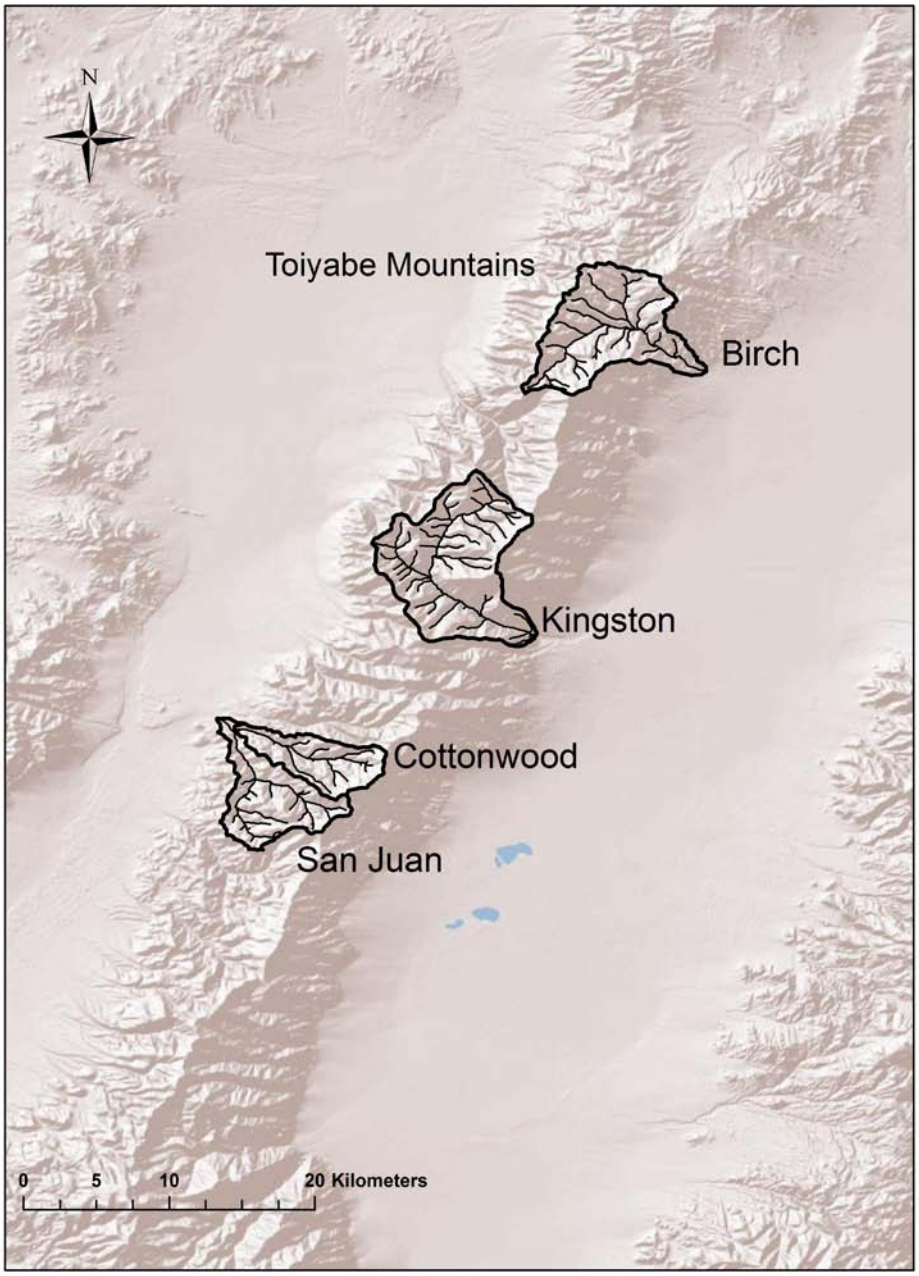


Figure 1. Locations of the four study watersheds in the Toiyabe mountain range, central Nevada, USA. Birch and Kingston Canyons are on the east side of the range and Cottonwood and San Juan Canyons are on the west.

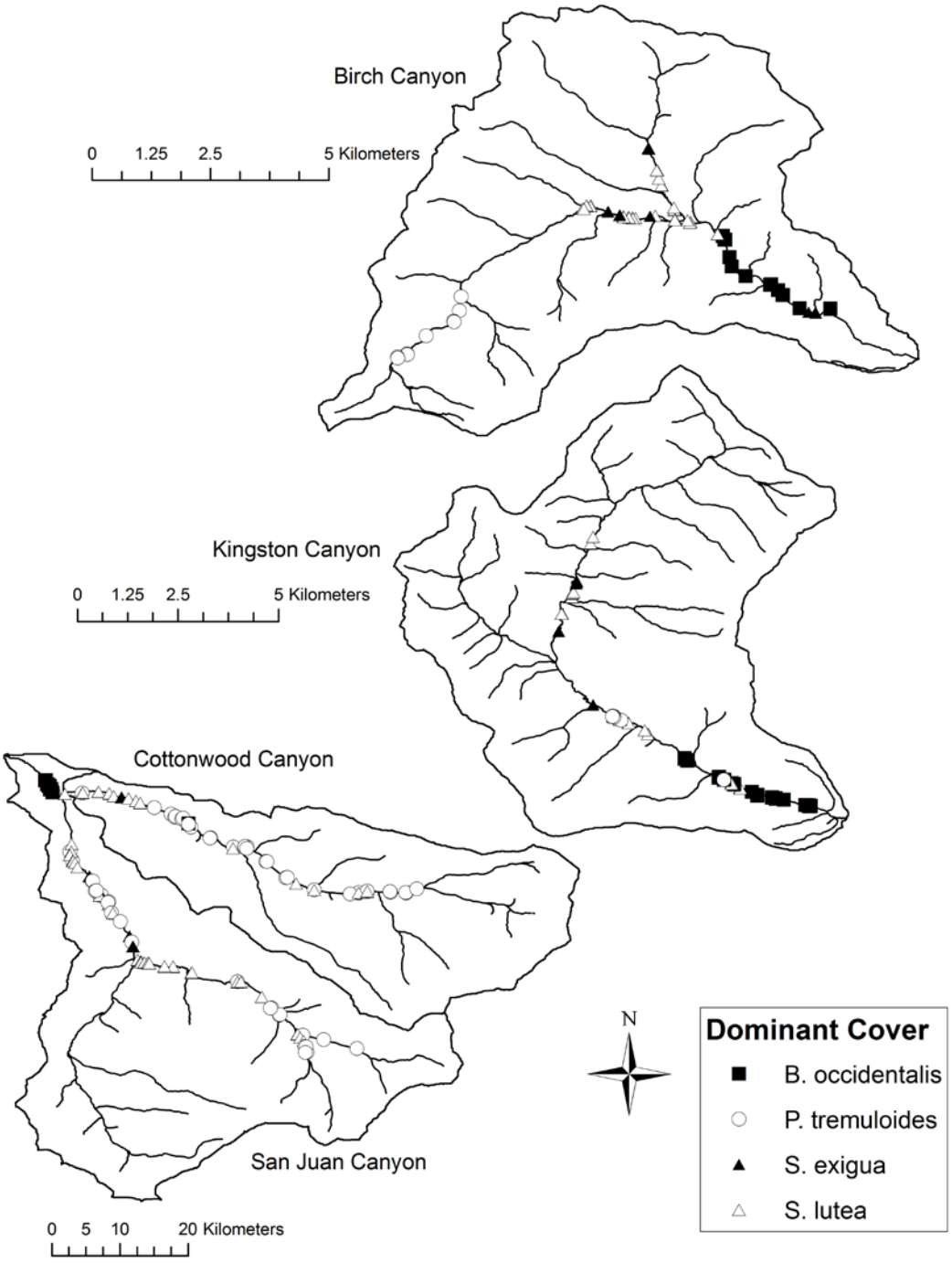


Figure 2. Woody species distribution in the Toiyabe mountain range, central Nevada, USA showing dominant species per transect (n=265). Birch and Kingston Canyons are on the east side of the range and Cottonwood and San Juan Canyons are on the west.

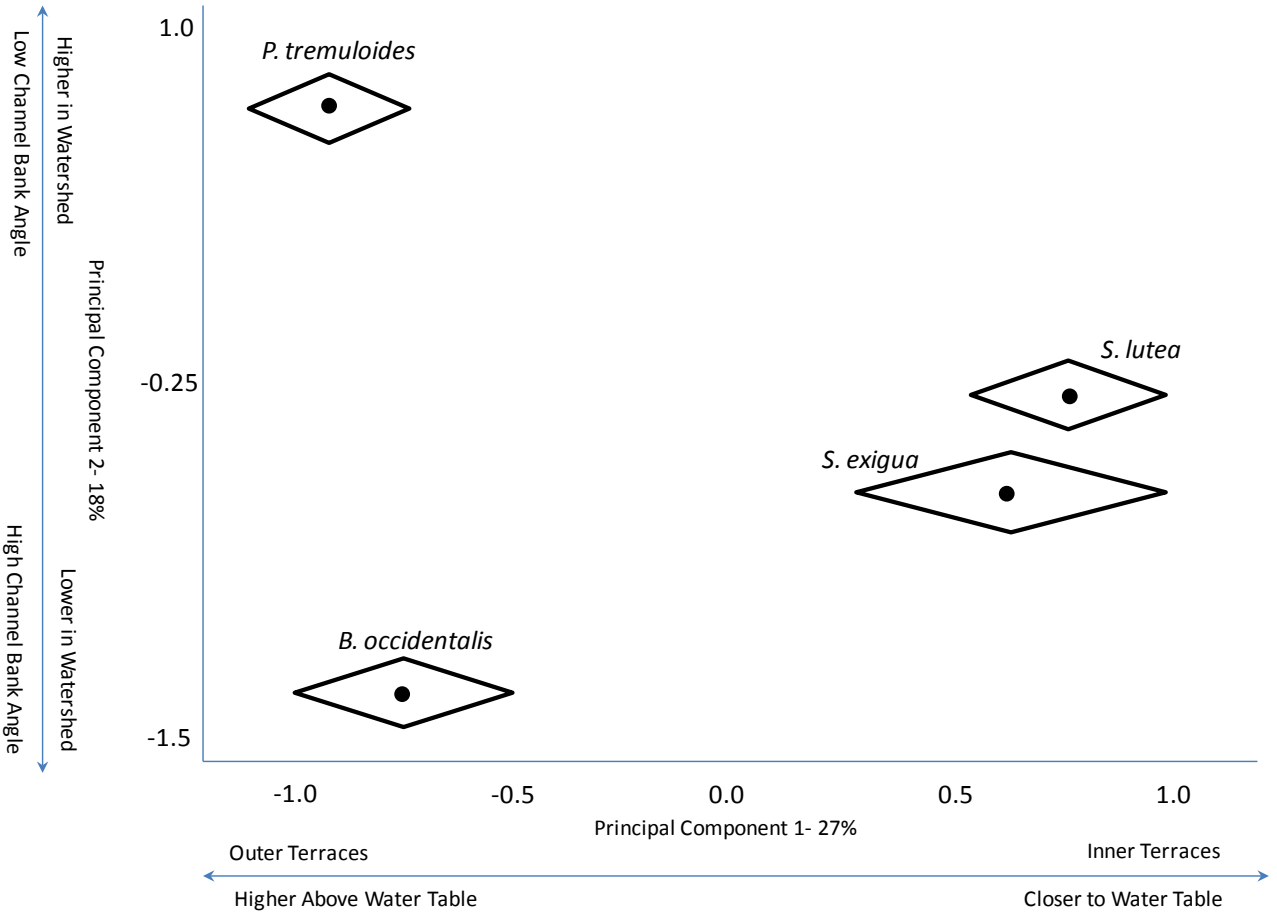


Figure 3. Biplot of principal component (PC) 1 vs. PC 2 with varimax rotation from principal component analysis on geomorphic variables. Mean PC scores for woody species dominating surfaces (n=482) were plotted with 95% confidence intervals as diamonds.

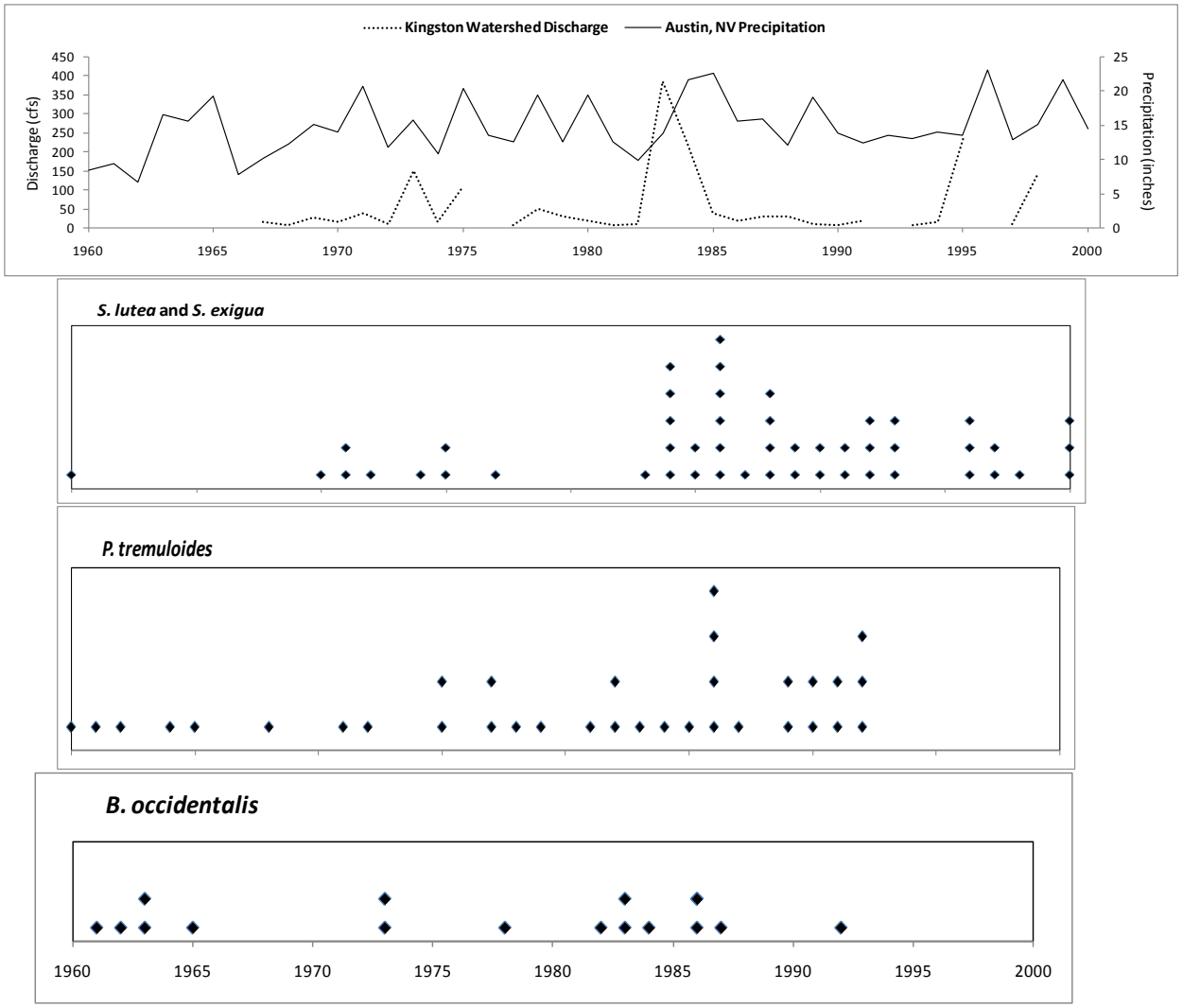


Figure 4. Comparison of annual precipitation data from Austin, Nevada and water-year discharge from Kinston Canyon to episodes of riparian woody species establishment. Data for the different species are high accuracy age data from the surfaces on which they occurred. Missing years of discharge data: 1960-1968, 1976, 1992, 1996, 1998-2000.

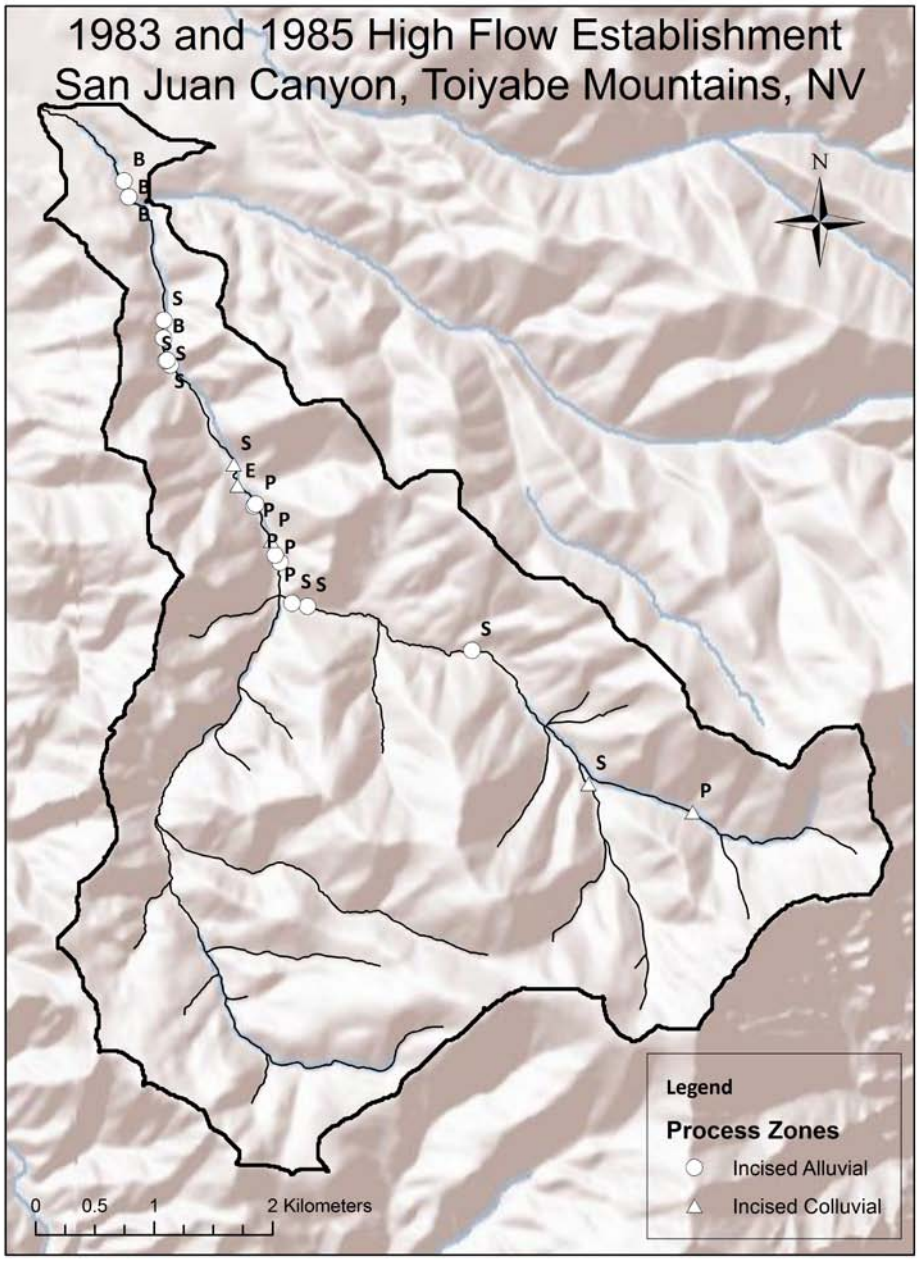
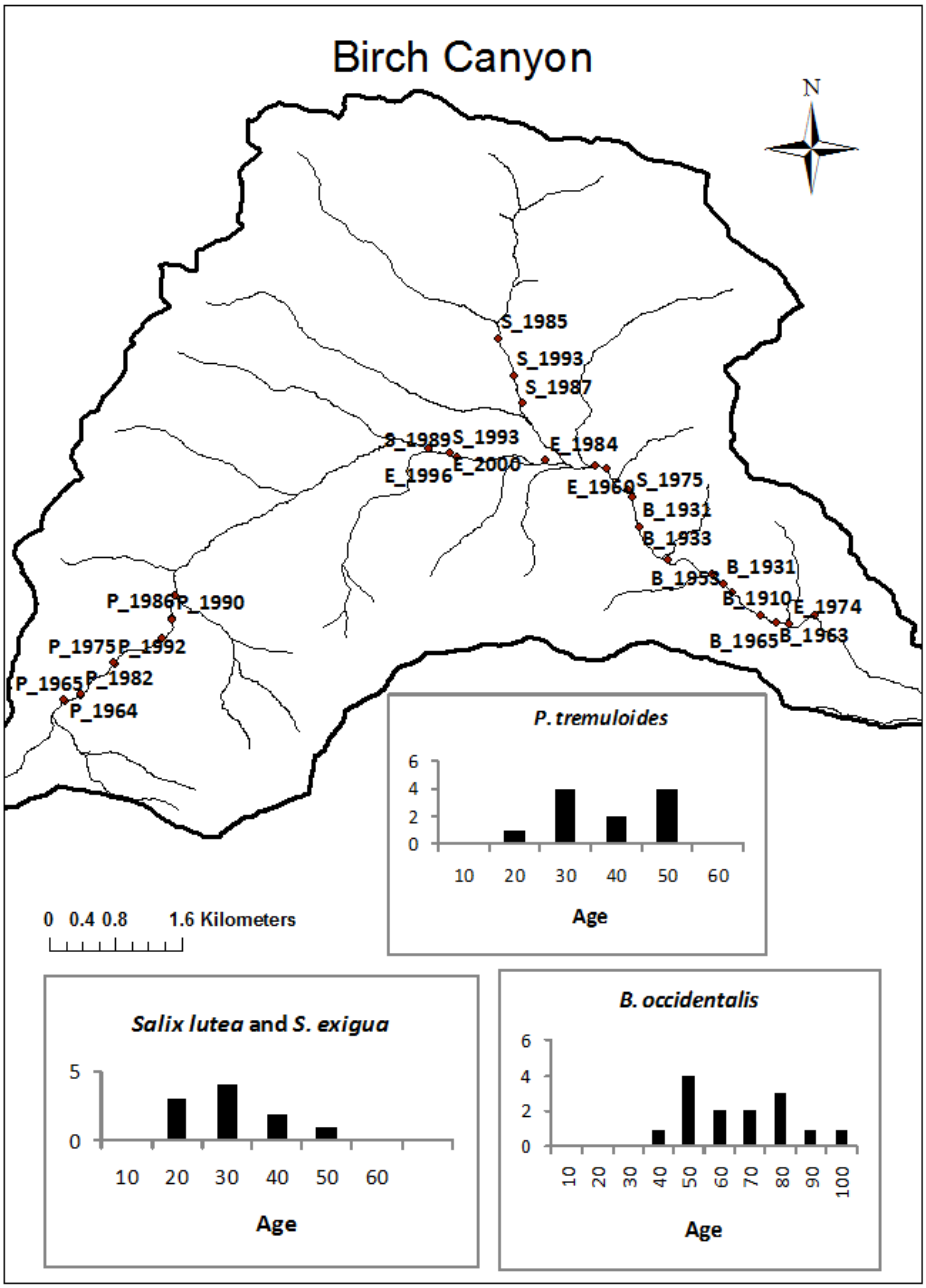
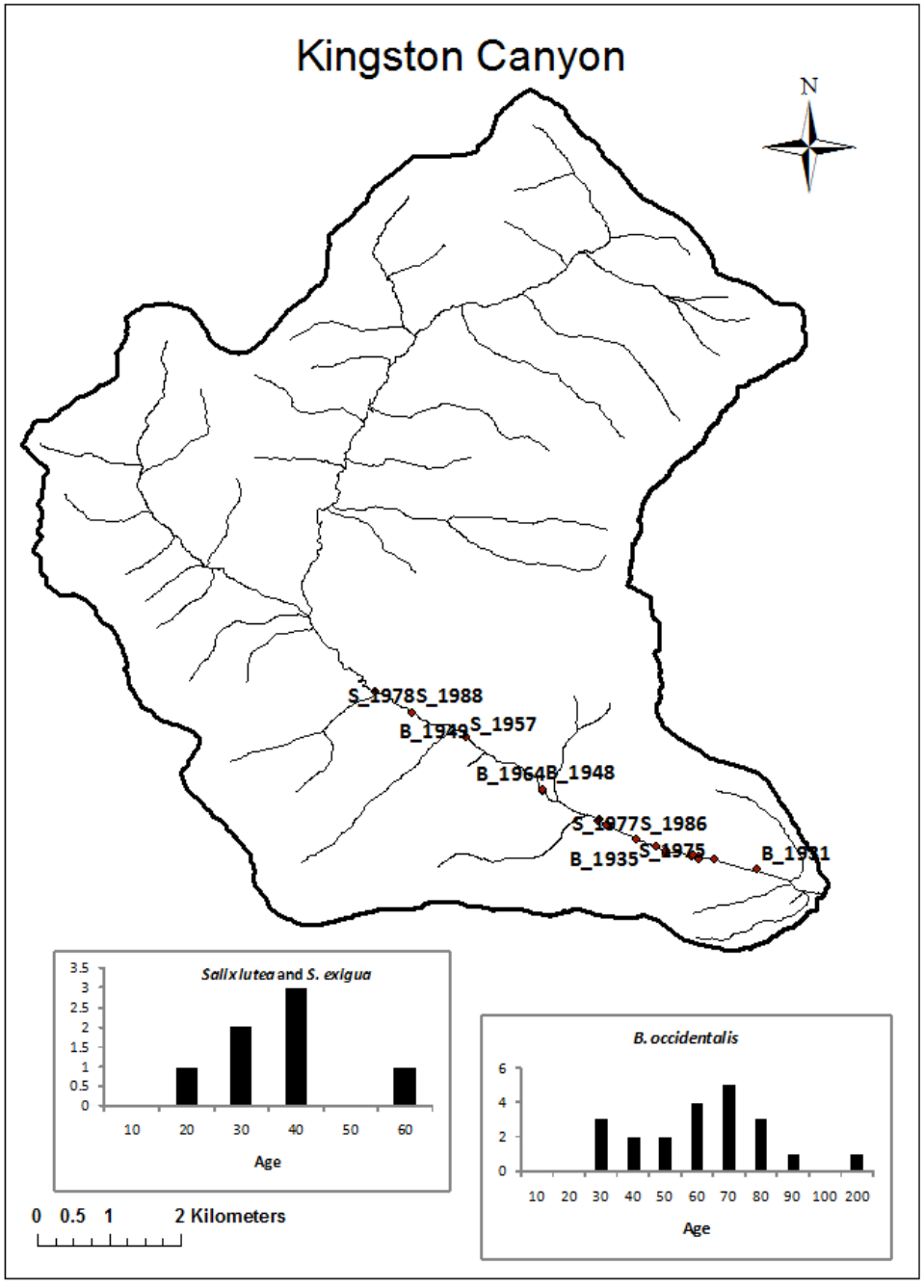


Figure 5. Establishment in response to the 1983 and 1985 high flow events in San Juan Canyon. Most establishment occurred within incised alluvial valleys. Species are indicated by letters: B, *Betula occidentalis*; E: *Salix exigua*; P: *Populus tremuloides*; S: *Salix lutea*.

a)


Birch Canyon
N
S_1985
S_1993
S_1987
S_1989
S_1993
E_1984
E_1996
E_2000
E_1960
S_1975
B_1931
B_1933
B_1955
B_1931
B_1910
E_1974
B_1965
B_1963
P_1986
P_1990
P_1975
P_1992
P_1965
P_1982
P_1964
0 0.4 0.8 1.6 Kilometers
P. tremuloides
6
4
2
0
10 20 30 40 50 60
Age
Salix lutea and S. exigua
5
0
10 20 30 40 50 60
Age
B. occidentalis
6
4
2
0
10 20 30 40 50 60 70 80 90 100
Age

b)


Kingston Canyon
N
S_1978
S_1988
B_1949
S_1957
B_1964
B_1948
S_1977
S_1986
S_1975
B_1935
B_1931
Salix lutea and S. exigua
3.5
3
2.5
2
1.5
1
0.5
0
10
20
30
40
50
60
Age
B. occidentalis
6
4
2
0
10
20
30
40
50
60
70
80
90
100
200
Age
0 0.5 1 2 Kilometers

c)

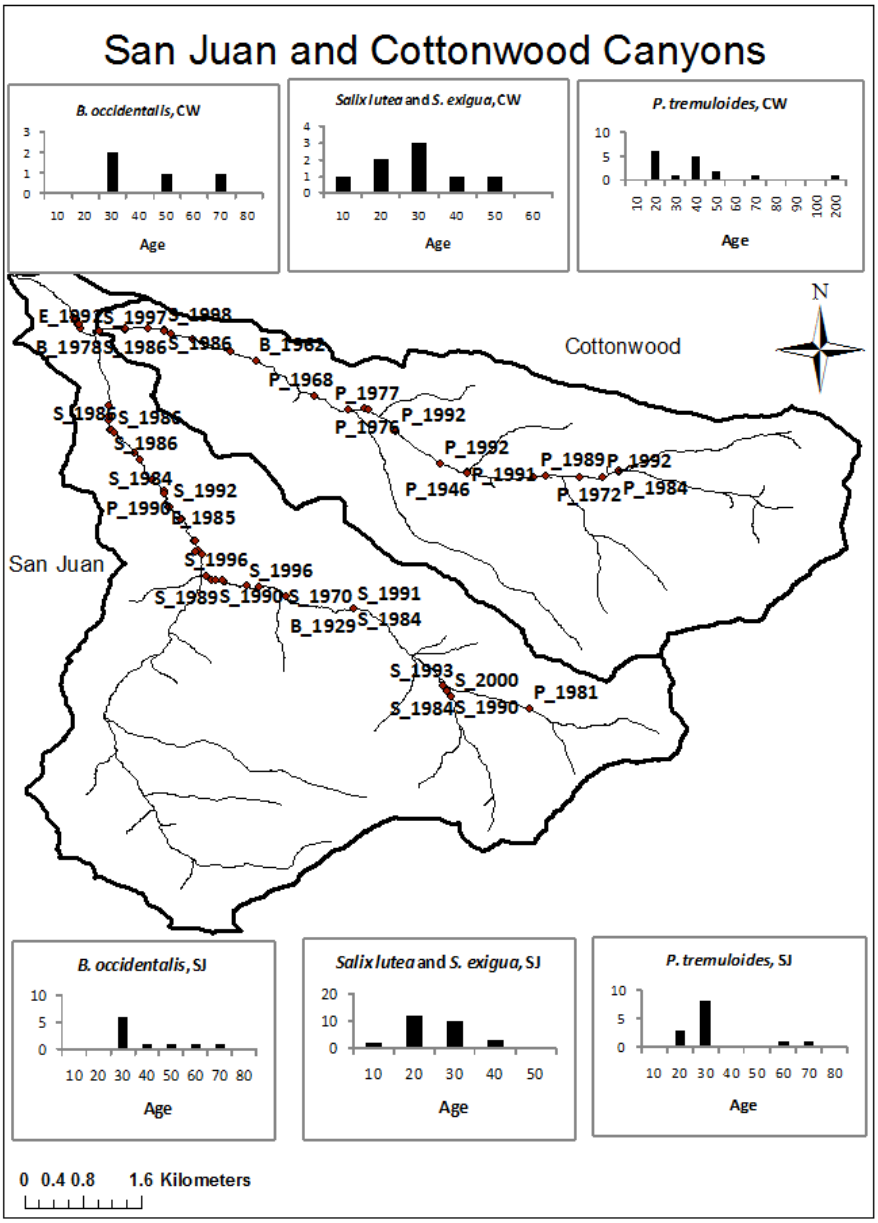


Figure 6. Age distributions and frequency histograms (# of discrete terraces) of the woody species in the study watersheds a) Birch, b) Kingston, c) San Juan and Cottonwood Canyons located in the Toiyabe Mountain Range, central Nevada. Year of establishment is shown by species. Species are indicated by letters B: *Betula occidentalis*, E: *Salix exigua*, P: *Populus tremuloides*, S: *Salix lutea*.

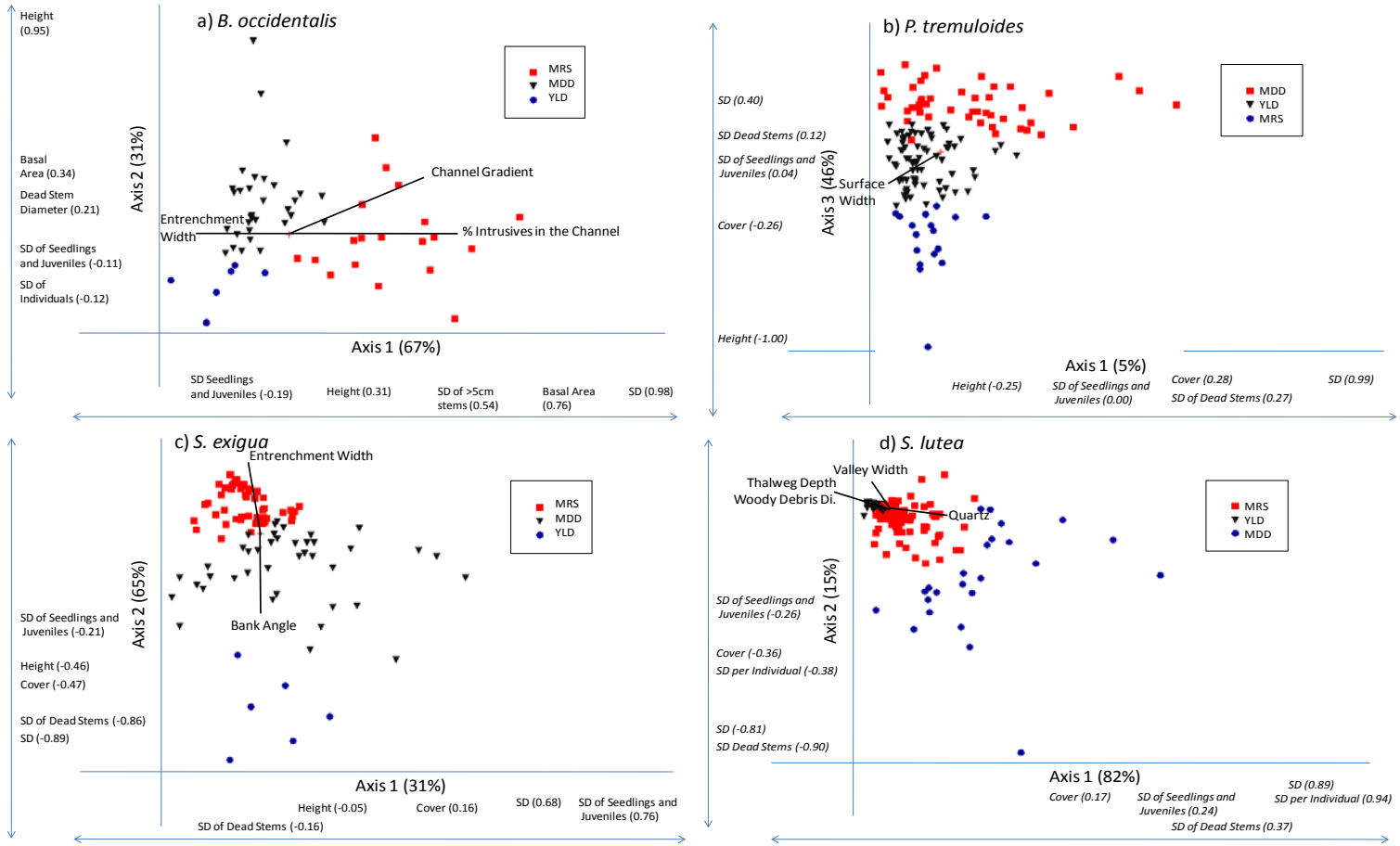


Figure 7. Biplots from Non-Metric Multidimensional Scaling (NMS) ordination of stand structure characteristics and groups with an overlay of associated geomorphic characteristics. Woody species are a) *B. occidentalis*; b) *P. tremuloides*; c) *S. exigua*; and d) *S. lutea*. Stand structural types are (1) young, low density, (YLD; n=282); (2) mature, regenerating, stable (MRS; n=158); and (3) mature, dense, decadent (MDD; n=100).

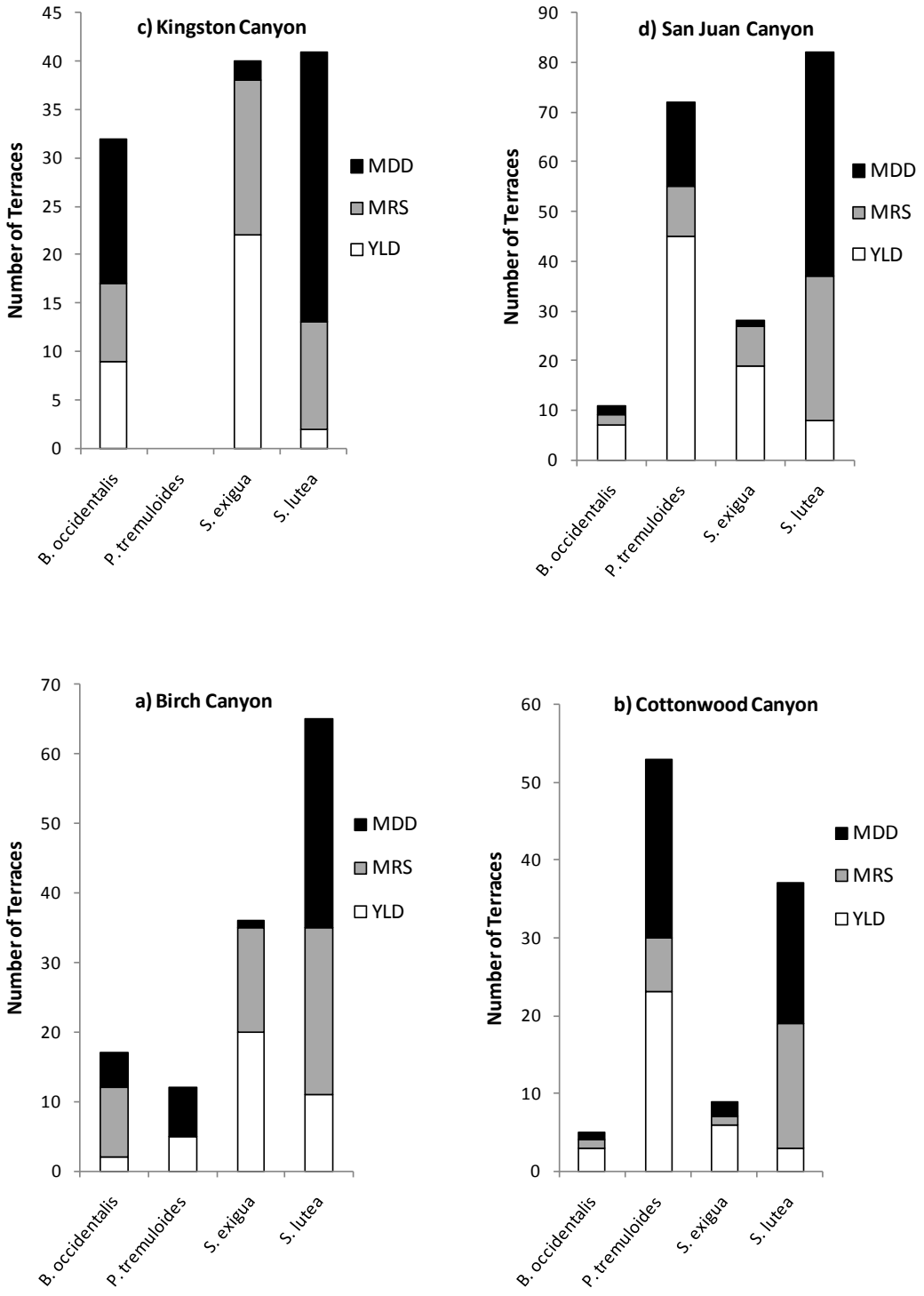


Figure 8. Number of surfaces characterized by stand structural type by species. Stand structural types are (1) young, low density, (YLD; n=282); (2) mature, regenerating, stable (MRS; n=158); and (3) mature, dense, decadent (MDD; n=100). Study watersheds are a) Birch Canyon; b) Cottonwood Canyon; c) Kingston Canyon; and d) San Juan Canyon.

APPENDIX

Appendix 1. Results of one-way ANOVA tests (F values and p-values) comparing differences in geomorphic characteristics by key woody species. Geomorphic characteristics are raw data means ± standard errors. F values in bold are significant at $\alpha \leq 0.017$ based on the Bonferroni correction.

Primary Geomorphic Characteristics by Species	F	p	Young Low Density	Mature Regenerating Stable	Mature Dense Decadent
			(n=282)	(n=158)	(n=100)
B. occidentalis	$F_{1,63}$=		n=14	n=19	n=32
Bank Angle (%)	5.82	0.019	0.36±0.06	0.55±0.06	0.63±0.05
Entrenchment Width	**10.35**	0.000	10.53±0.90	6.03±0.49	9.57± 0.74
Entrenchment W:D	**10.63**	0.002	5.45±0.39	3.69±0.45	5.21± 0.39
Gradient(%)	**12.07**	0.001	0.03±0.00	0.04±0.00	0.03± 0.00
Intrusives(%)	**5.03**	0.009	0.03±0.01	0.22±0.06	0.03± 0.01
Riparian Width	**8.11**	0.006	25.05±3.33	16.36±1.36	21.81± 2.37
P. tremuloides	$F_{1,135}$=		n=73	n=17	n=47
Fines in Channel (%)	3.09	0.081	0.49±0.17	0.52±0.03	0.42±0.02
Quartz (%)	0.58	0.449	0.51±0.04	0.52±0.00	0.63±0.04
Sandstone (%)	5.66	0.019	0.01±0.00	0.00±0.00	0.02±0.01
Stream Length Above	0.62	0.434	9385.18±	9335.61±	7164.52±
Surface Width	0.00	0.979	6.47±0.50	5.12±0.78	3.96±0.50
Volcanics (%)	1.05	0.308	0.44±0.04	0.45±0.08	0.29±0.05
S. exigua	$F_{1,111}$=		n=67	n=40	n=6
Bank Angle (%)	0.57	0.569	0.40±0.03	0.45±0.04	0.48±0.13
Entrenchment Width	2.77	0.067	8.75±0.05	7.41±0.69	5.29±0.87
Number of Terraces	2.84	0.095	2.17±0.40	2.70±0.12	2.88±0.12
Surface Height Above Water	1.22	0.272	0.15±0.07	0.21±0.05	0.39±0.07
Surface Width	0.32	0.573	3.78±1.66	2.40±0.39	2.99±0.34
Woody Debris (%)	1.99	0.161	0.02±0.01	0.07±0.01	0.07±0.01
S. lutea	$F_{1,223}$=		n=121	n=80	n=24
Number of Terraces (#)	0.59	0.445	2.73± 0.08	3.00±0.09	2.92±0.19
Quartz (%)	1.36	0.245	0.44± 0.03	0.48±0.03	0.58±0.05
Thalweg Depth	0.71	0.401	0.17± 0.01	0.15±0.01	0.12±0.01
Water Width	0.17	0.678	1.86± 0.07	1.62±0.07	1.61±0.19
Woody Debris Di. In Channel	0.83	0.362	0.02± 0.00	0.02±0.00	0.01±0.00