River Flow and Riparian Vegetation Dynamics – Implications for Management of the Yampa River through Dinosaur National Monument

Final Report Submitted to the National Park Service

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Executive Summary

This report addresses the relation between flow of the Yampa River and occurrence of herbaceous and woody riparian vegetation in Dinosaur National Monument (DINO) with the goal of informing management decisions related to potential future water development. The Yampa River in DINO flows through diverse valley settings, from the relatively broad restricted meanders of Deerlodge Park to narrower canyons, including debris fan-affected reaches in the upper Yampa Canyon and entrenched meanders in Harding Hole and Laddie Park. Analysis of occurrence of all plant species measured in 1470 quadrats by multiple authors over the last 24 years shows that riparian vegetation along the Yampa River is strongly related to valley setting and geomorphic surfaces, defined here as active channel, active floodplain, inactive floodplain, and upland. Principal Coordinates Ordination arrayed quadrats and species along gradients of overall cover and moisture availability, from upland and inactive floodplain quadrats and associated xeric species like western wheat grass (*Pascopyrum smithii*), cheatgrass (*Bromus tectorum*), and saltgrass (*Distichlis spicata*) to active channel and active floodplain quadrats supporting more mesic species including sandbar willow (*Salix exigua*), wild licorice (*Glycyrrhiza lepidota*), and cordgrass (*Spartina* spp.). Indicator species analysis identified plants strongly correlated with geomorphic surfaces. These species indicate state changes in geomorphic surfaces, such as the conversion of active channel to floodplain during channel narrowing.

The dominant woody riparian species along the Yampa River are invasive tamarisk (*Tamarix ramosissima*), and native Fremont cottonwood (*Populus deltoides* ssp. *wislizenii*), box elder (*Acer negundo* L. var. *interius*), and sandbar willow (*Salix exigua*). These species differ in tolerance of drought, salinity, inundation, flood disturbance and shade, and in seed size, timing of seed dispersal and ability to form root sprouts. These physiological and ecological differences interact with flow variation and geomorphic setting, resulting in differential patterns of occurrence. For example, in park settings cottonwood is far more abundant than box elder, while the reverse is true in canyons.

Synthesis of existing knowledge from the Yampa and Green rivers and elsewhere suggests that the following flow-vegetation relations can be used to assess effects of future flow alterations in the Yampa River.

- High variability in flow within and between years removes vegetation through erosion, extended inundation and desiccation, creating the broad, open surfaces in and near the channel that are characteristic of lightly regulated rivers in western North America. This flow variability provides opportunities for establishment of disturbance-dependent riparian species.

- Flow regulation that results in lower peak flows and higher low flows allows proliferation of woody riparian vegetation, mostly tamarisk in canyon reaches, but both tamarisk and cottonwood in parks. Denser near-channel vegetation promotes sediment deposition leading to channel narrowing. Decreasing flow variability also increases area of species associated with extremely high and low inundation durations relative to species associated with moderate inundation duration. In addition, such flow regulation decreases occurrence of species tolerant of fluvial disturbance, while increasing occurrence of species tolerant of extended inundation.

- Over the long term, establishment of cottonwood and tamarisk requires disturbance by large floods, which provides openings for new individuals. At the annual time scale, establishment can occur in any year or location that provides a moist, open surface free from frequent future disturbance. In canyons, where channel movement is limited, low surfaces are too frequently disturbed for long-term survival of cottonwood, and establishment requirements are generally met only in years of moderate to high peak flows. In park settings cottonwood establishment may also occur in years of low peak flows where survival is promoted by movement of the channel away from the seedling.

- Peak flows early in the growing season promote establishment of cottonwood and sandbar willow seedlings relative to those of tamarisk. This is because cottonwood and willow seed release occurs early in the summer, while that of tamarisk occurs later. Late season seed release of tamarisk allows it to establish lower on the floodplain than cottonwood.

- Because of its shade tolerance and the energy stored in its large seeds, box elder can become established beneath existing vegetation, an ability not shared by cottonwood, tamarisk or willow. Although box elder does not require flood disturbance, it does take advantage of soil moisture from floods, which allow this species to become established high above the channel.

- Decreases in flow peaks, volumes or base flows decrease growth and survival of cottonwood relative to drought-tolerant tamarisk. Storing water from the spring peak in a reservoir for release after the April-July cottonwood growth window may also decrease growth and survival of cottonwood relative to tamarisk. Decreases in peak flows decrease floodplain inundation, which can reduce growth of floodplain species by preventing recharge of the floodplain aquifer.

- Two or more years in a row with similar flows promote establishment of woody vegetation. Subsequent sediment deposition around this vegetation, especially if the vegetation is tamarisk, results in channel narrowing and simplification.

- Rapid declines in the descending limb of the hydrograph kill riparian woody seedlings by desiccation. Fluctuations in the descending limb can kill seedlings by desiccation and inundation. Thus rapid declines and fluctuations would be counterproductive following early-season peaks prescribed to promote cottonwood, but would be consistent with the goal of preventing tamarisk establishment following a late-season peak.

- The tendency of regulated flows to keep returning to a small number of fixed discharge values (such as power plant capacity or a fixed minimum flow) can cause unnaturally sharp banding of geomorphic surfaces, topography and vegetation that is not necessarily erased by large flood peaks.

- Changes in sediment load relative to transport capacity may promote channel change especially in alluvial settings. For example, decreases in sediment input from the Little Snake River Basin since 1960 (or earlier) could be associated with channel narrowing and temporary increases in establishment of both cottonwood and tamarisk along the Yampa River.

- Increases in salinity of water or soil promote tamarisk over the native woody species. Even if water salinity does not increase, floodplain soil salinity can be increased by decreasing the flushing caused by overbank flooding.

Acknowledgments

Introduction

Dinosaur National Monument protects long sections of the Yampa River (Figure 1), the last lightly regulated large river in the Colorado River Basin. The National Park Service (NPS) is charged with maintaining natural riverine resources and processes in DINO for future generations. The purpose of this document is to describe the relations between streamflow and riparian vegetation in order to inform considerations of possible changes in flow (Poff and Zimmerman 2010) and to guide management decisions in the context of potential future water development. Because of the important interactions among flow, riparian vegetation and sediment transport, this report also addresses the role of vegetation in channel change resulting from flow regulation. The Introduction describes general flow-vegetation relationships and is followed by a chapter presenting recent research relating flow to occurrence patterns of all riparian plant species along the Green and Yampa rivers. This is followed by a chapter focusing on hydrologic controls on establishment and survival of four dominant woody species. Effects of flow regulation are explored by comparing vegetation dynamics along the lightly regulated Yampa River to those along more heavily regulated systems, especially the Green River (Figure 1).

General Flow-Vegetation Relationships

The riparian zone is a transitional area between aquatic ecosystems associated with a river and the surrounding terrestrial ecosystems
The ecological distinctiveness of riparian zones is a central tenet in riparian ecology. Vegetation in the riparian zone is influenced by streamflow, alluvial groundwater and flow-driven land-forming processes and is structurally and compositionally distinctive from vegetation in both aquatic and upland terrestrial ecosystems (Brinson et al. 1981, Naiman et al. 2005, Sabo et al. 2005).   The capacity of moving water to erode, transport and deposit sediment, along with the ability of vegetation to influence erosion and deposition patterns, is responsible for the creation and maintenance of riparian ecosystems (Brinson et al. 1981, Manners et al. 2011). Free-flowing rivers in arid and semi-arid regions of the western US experience relatively frequent large floods of variable magnitude that are responsible for maintaining relatively wide active channels and a mosaic of unvegetated patches of alluvial material across the floodplain and within stands of riparian forest (Bagstad et al. 2006).

Flow variability removes some plants, and provides opportunities for establishment of others
Although plants require water for survival, high flows kill plants by erosion and extended inundation (Sigafoos 1964, Gill 1970, Auble and Scott 1998), and low flows kill plants through desiccation (Auble and Scott 1998). As a result the zone near the channel is often sparsely vegetated, especially if flow variability is high. Removal of some plants, however, provides opportunities for establishment of others. Seedlings of many riparian species require moist sunny surfaces created by fluvial disturbance (Friedman et al. 1996). Lightly regulated rivers of western North America often have large inter- and intra-annual flow variability, resulting in rapid channel movement, sparse vegetation near the channel and abundant opportunities for establishment of disturbance-dependent species. Where geology or flow regulation reduces flow variability, the result is a narrow channel

bordered by dense vegetation with little opportunity for establishment of disturbance-dependent species (O'Connor and Grant 2003).
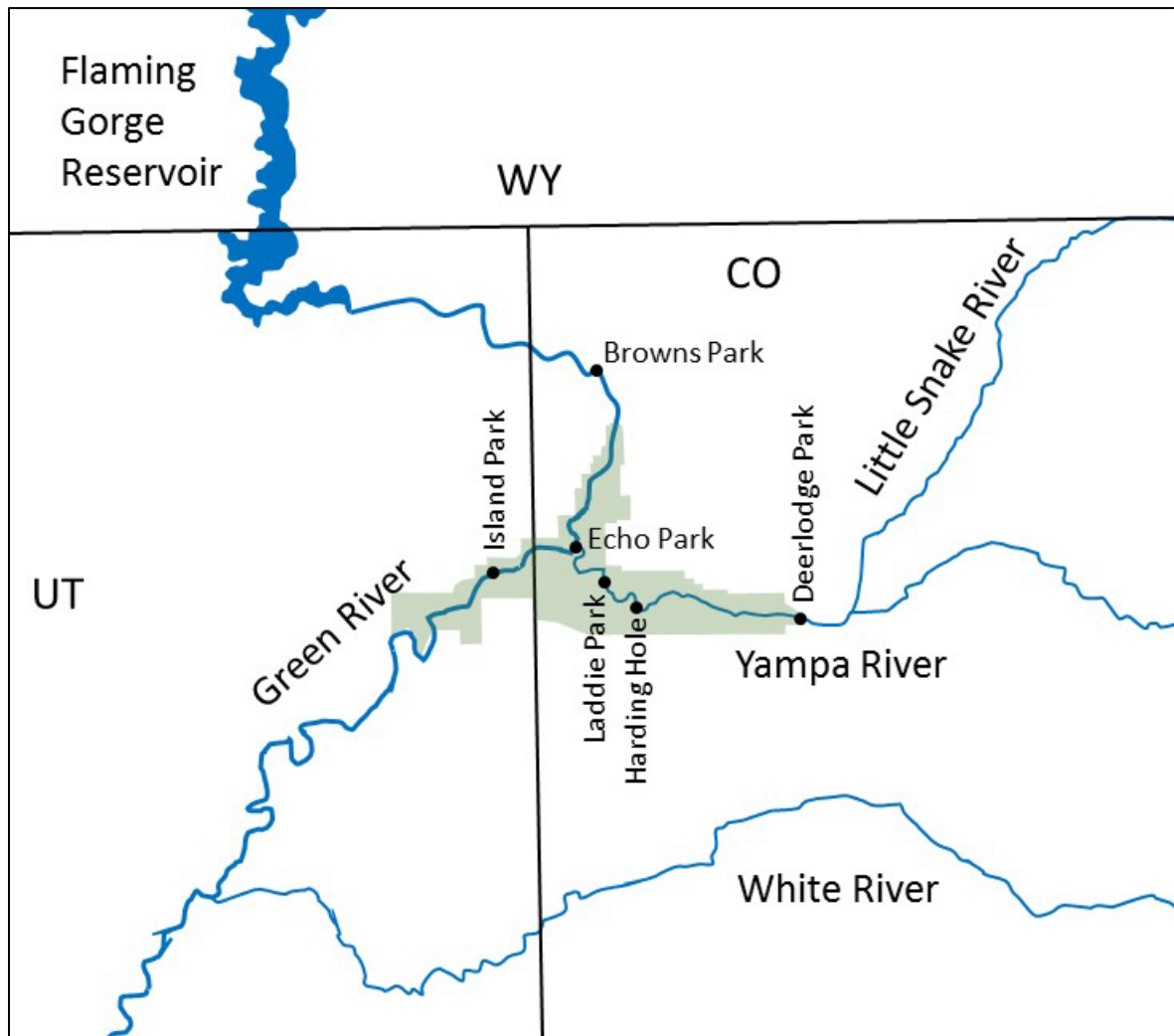
Figure 1. Location of Dinosaur National Monument (shaded green) and the Yampa River within the Green River watershed.

Reductions in streamflow magnitude and variability result in a correspondingly narrower active river channel, as perennial terrestrial vegetation establishes and survives on formerly active portions of the channel. Thus flow regulation of rivers in western North America has generally caused channel narrowing and encroachment of riparian woody and herbaceous vegetation (Nadler and Schumm 1981, Williams and Wolman 1984, Everitt 1993, Friedman et al. 1998, Johnson 1994, Allred and Schmidt 1999, Mortenson and Weisberg 2010, Webb et al. 2011).

Disturbance-dependent vegetation may be promoted by channel change initiated by a shift in the balance between the flows of water and sediment. An increase in sediment concentration, caused for example by decreasing flow without changing sediment supply, can cause local sediment deposition,

which may promote channel movement, increasing establishment opportunities for disturbance dependent vegetation (Everitt 1993, 1998). In contrast, a decrease in sediment supply may allow channel stabilization, temporarily increasing establishment opportunities for disturbance dependent species as the channel narrows.

Pattern in riparian vegetation perpendicular to the river is primarily attributed to physical gradients of moisture availability and fluvial disturbance created by variations in stream surface flow, fluvial landforms, and valley setting

The description, analysis and interpretation of the patterning in riparian vegetation perpendicular to the channel has been an important research focus for riparian ecologists. Systematic variation in the structure and composition of riparian vegetation away from the channel is a visually striking expression of environmental gradients associated with streams (Malanson 1993, Bendix 1994, Friedman et al. 2006). The abundance of water and the frequency and intensity of physical disturbance decrease with distance from and height above the channel. The effects of decreasing water abundance are increasing drought stress in arid environments like DINO (Zimmerman 1969) and decreasing anoxia stress in humid environments such as those found in the southeastern United States (Bedinger 1979). The disturbance gradient influences shade (Menges and Waller 1983), litter cover (Friedman et al. 1996), sediment particle size (Robertson et al. 1978) and soil development (Boggs and Weaver 1994), and controls plant longevity and life form (Hupp and Osterkamp 1985). Because the depth of inundation produced by a given flow varies from one cross section to the next, the hydrologic gradient is often quantified in terms of inundation frequency (Hupp and Osterkamp 1985) or inundation duration (the fraction of the year a site is inundated; Bedinger 1979, Auble et al. 1994, 2005). Riparian environments are typically composed of a mosaic of fluvial surfaces. To the extent that these surfaces are distinct in inundation frequency and duration, they also tend to have distinct vegetation (Hupp and Osterkamp 1985). Similarly, fluvial surfaces of different ages have different histories of riverine disturbance and inundation, producing distinct vegetation (Friedman et al. 1996).

Tributary inputs and downstream variation in geologic setting influence fluvial processes and riparian vegetation by controlling delivery of water and sediment (Gregory et al. 1991). In canyon environments, steep lateral gradients limit channel migration and produce landslides and debris fans that alter sediment particle size and disturbance patterns. Steep channel gradients result in high boundary shear stresses that sweep fine particles downstream, leaving coarse particles in the channel boundary. In contrast, where rivers flow through broad alluvial valleys, gradient is lower, particle size is smaller, landslides and debris fans influence less of the floodplain, and lateral migration is more extensive. These differences between canyons and alluvial valleys lead to strong differences in vegetation (Chambers et al. 2004, Friedman et al. 2006). For example, species requiring fine sediments and intolerant of physical disturbance are more abundant in wide valley settings (Cowles 1901, Hupp 1986).

Vegetation patterns perpendicular to the river can be used to predict changes in vegetation resulting from flow alteration

Relationships between vegetation and flow can be used to predict changes in vegetation resulting from flow alteration (Franz and Bazzaz 1977, Auble et al. 1994, 2005, Primack 2000). For example,

Auble et al. (1994, 2005) combined plot sampling of vegetation with hydraulic models in short (<1 km) reaches of the Gunnison and Fremont rivers to relate plant species and community occurrence to inundation duration. Assuming that these flow-vegetation relationships are invariant, the authors assessed how changes in the flow-duration curve would redistribute plants among the sampled plots. This approach assumes that vegetation, flow and channel form are in quasi-equilibrium, and therefore cannot predict transient responses to large changes in flow.

Patterns of Overall Plant Species Occurrence along the Yampa River

This section begins with a new analysis of species occurrence data collected by M.L. Scott and others at DINO. The goal of this analysis is to characterize vegetation patterns in relation to fluvial surfaces, channel type and gradients of moisture availability and shade. These results are then considered along with previously published studies to relate overall patterns of species occurrence to flow in the Yampa River.

Analysis of Species Occurrence Data

This section combines data on species occurrence in plots collected by multiple authors (Appendix A). Between 1993 and 2002 riparian vegetation was sampled throughout the study reach using 37 10x10 m quadrats (Merritt and Cooper 2000) and 208 dimensionless releves (Cooper et al. 1999, 2003). From 2009 to 2012, 887 1x1m quadrats (Scott et al. in preparation) were located systematically along transects throughout the Yampa River bottomland within DINO. In 2010 and 2013, 196 and 248 quadrats (1x1 m; Scott et al. in preparation) were located randomly across the bottomland. Finally, in 2014, Scott and Merritt sampled 15 randomly located 1x1 m quadrats (Scott et al. in preparation). We combined field observations and aerial imagery to map geomorphic surfaces: *active channel* (AC); *active floodplain* (AF); *inactive floodplain* (IF); and *upland* (U) (O'Connor and Grant 2003, Gendaszek et al. 2012, Scott et al., in preparation), and were able to use the map to assign a geomorphic surface to 1470 of the 1591 quadrats and releves. We applied Principal Coordinates Ordination (PCO) in PRIMER (Clarke and Gorley 2015) to these 1470 samples to explore patterns of species variability among quadrats and species. In a data set of species occurring in plots, each species is a variable, and examining all of these variables at once is overwhelmingly complex. PCO reduces that complexity to a small number (in this case 2) of dominant gradients. For this analysis, we retained quadrats without plants by defining the absence of plants as a pseudospecies.

Next, bare quadrats (464 total) and rare species were dropped from the dataset and a Permutational Multivariate Analysis of Variance (PerMANOVA) was run in PRIMER in order to quantify the influence of geomorphic surface and channel type on vegetation. Other criteria for inclusion in these analyses were: species must occur in at least three quadrats; quadrats must contain at least three species; or, quadrats with less than 3 species must have a total vegetation cover value of ≥30%. This resulted in elimination of 807 quadrats and inclusion of 663 vegetated quadrats in these analyses. Percent cover data were square-root transformed. Bray Curtis dissimilarity matrices were constructed for use in PerMANOVA. Due to unequal sample sizes (unbalanced design) between the factors in the design, Type III sums of squares were used. With the edited vegetation dataset we examined broad-scale differences in vegetation across the three channel types as well as the contribution of geomorphic surfaces across and within channel types.

Abundance of riparian plant species shows strong fidelity to fluvial surfaces and strong influence of the hydraulic gradient and geologic setting

Vegetation along the Yampa River within DINO exhibits strong and predictable patterns along and across the river valley. Along the river, vegetation varies strongly among channel types. Across the valley, vegetation varies from the largely unvegetated active stream channel deposits, to frequently flooded active floodplains, rarely inundated inactive floodplains, and then to upland vegetation of alluvial terraces in parks or on colluvial deposits in steep-walled canyons (Fischer et al. 1983, Scott et al. in preparation).

Scott et al. (in preparation) describe three channel types along the Yampa River in DINO with distinct channel planforms based on previous work by FLO Engineering (1998), Grams and Schmidt (1999) and Larson (2004). These channel types are: restricted meanders in the alluvial valley of Deerlodge Park (Figure 1); debris fan-affected sections in the bedrock controlled reach of upper Yampa Canyon; and entrenched meanders seen in Harding Hole and Laddie Park (Figure 1). The elevation and extent of mapped geomorphic features along the Yampa River reflect localized erosional and depositional processes that differ from bedrock to alluvial reaches (Grams and Schmidt 1999) and include a range of different bed and bank morphologies as well as floodplain forms and processes (Brierley and Fryirs 2005).

Ordination can reveal structure in large, complex data sets by projecting results in two or more dimensions such that species and samples that are most similar will appear close together and those most different will appear far apart. Results of the PCO demonstrate clear gradients (Figure 2) separating largely bare active channel and active floodplain quadrats from those on inactive floodplain and upland. The ordination distributes plots along a cover gradient on the horizontal axis from bare plots on the right to densely vegetated plots on the left. The vertical axis is a moisture gradient reflecting the combined influence of inundation frequency, depth to groundwater and differences among fluvial surfaces. High on the vertical axis are upland and inactive floodplain quadrats and associated xeric species like western wheat grass (*Pascopyrum smithii*), cheatgrass (*Bromus tectorum*), and saltgrass (*Distichlis spicata*). Low on the axis are active channel and active floodplain quadrats supporting more mesic species, including sandbar willow (*Salix exigua*), wild licorice (*Glycyrrhiza lepidota*), and cordgrass (*Spartina* spp.).
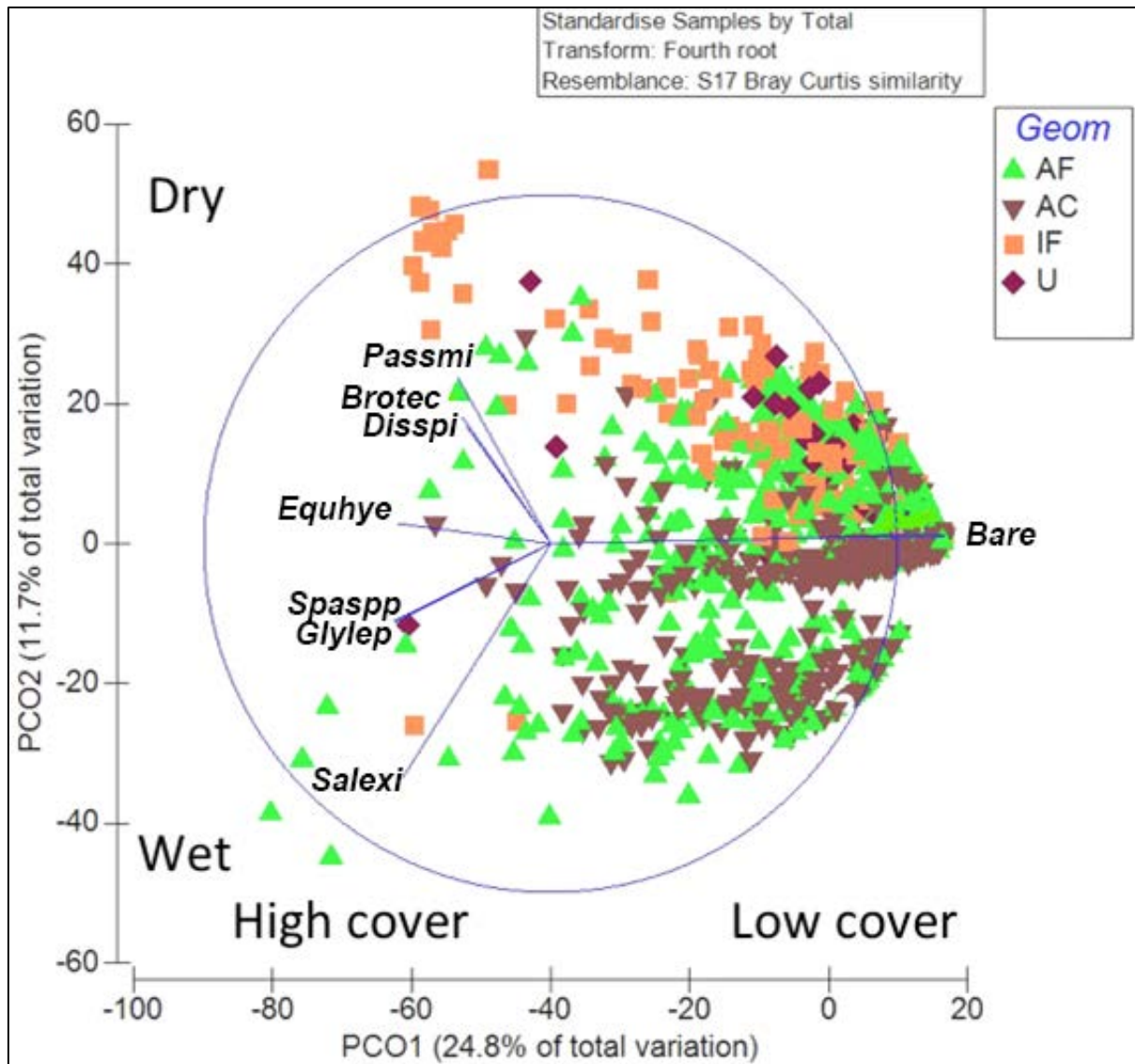
Figure 2. Principal Coordinates Ordination (PCO) of species and samples from 1470 quadrats and releves sampled along the Yampa River in DINO. The ordination shows clear gradients structuring plant species composition on four geomorphic surfaces: active channel (AC), active floodplain (AF), inactive floodplain (IF) and upland (U). The cover gradient along the first axis is likely a combination of frequency and intensity of fluvial disturbance for active channel and active floodplain plots and moisture limitations for inactive floodplain and upland plots. Passmi is *Pascopyrum smithii* (western wheatgrass), Brotec is *Bromus tectorum* (cheatgrass), Disspi is *Distichlis spicata* (saltgrass), Equhye is *Equisetum hyemale* (scouring rush horsetail), Spaspp is *Spartina* spp. (cordgrass), Glylep is *Glycyrrhiza lepidota* (wild licorice), Salexi is *Salix exigua* (sandbar willow), and Bare is a pseudospecies indicating vegetation was absent.

Lightly regulated rivers, like the Yampa, often exhibit largely bare active-channel bars, which are reflected in the ordination (Figure 2). Further, the broad overlap of active floodplain quadrats with both active channel quadrats on the one hand and inactive floodplain and upland quadrats on the other, reflects a continuum of change in vegetation across these surfaces, maintained by the history of

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flow variability on the Yampa. Such broad vegetation transitions are typically not seen along regulated rivers, where differences between predominantly wetland and upland vegetation occur relatively abruptly over short distances (Merritt and Cooper 2000).

PerMANOVA analyses indicated that there are significant, broad scale differences in species composition across the three channel types (Pseudo-F = 6.90, p = 0.001), geomorphic surfaces (Pseudo-F = 9.77, p = 0.001), and the interaction between these factors (Pseudo-F = 4.69, p=0.001). At a finer scale, PerMANOVA t-test results of pairwise surface comparisons within channel types revealed significant differences in almost all cases (Table 1).

Table 1. Results of perMANOVA pair-wise t-test comparisons of floristic differences between geomorphic surface types within three different channel types along the Yampa River in DINO.

Geomorphic Surfaces[A]	DFA[B]		ENM[B]		REM[B]	
	t statistic	p	t statistic	p	t statistic	p
AC, AF	1.67	0.003[C]	4.21	0.001[C]	1.14	0.201
AC, IF	2.59	0.001[C]	5.84	0.001[C]	1.39	0.068
AC, U	2.51	0.001[C]	3.72	0.001[C]	3.41	0.002[C]
AF, IF	2.12	0.001[C]	4.13	0.001[C]	2.43	0.001[C]
AF, U	2.30	0.001[C]	3.01	0.001[C]	4.81	0.001[C]
IF, U	1.10	0.27	1.88	0.001[C]	4.68	0.001[C]

[A] Geomorphic surface abbreviations are: AC=Active channel; AF=Active floodplain; IF=Inactive floodplain; and U=Upland.

[B] Channel type abbreviations are: (DFA)=debris fan affected; (ENM)=entrenched meanders and (REM)=restricted meanders.

[C] Significant probabilities (<0.05) are italicized.

Using the edited dataset described above, we also performed an indicator species analysis using the *Indval* package in R, and employed the functions *multipatt* and *pruneindicators* (Dufrene and Legendre 1997) to identify a select group of species or species combinations with high positive predictive value and sensitivity for specific geomorphic surfaces within each channel type. Indicator species are a small set of species that reflect the physical or biotic conditions of specific environments and provide evidence for the effects of environmental change (De Caceres et al. 2012). The results of our indicator species analyses are presented in Table 2, which represents a succinct list of species and species combinations that indicate state changes in geomorphic surfaces, such as the conversion of active channel surfaces to floodplain during channel narrowing. Two values are used to assess the indicator species or species combinations: the positive predictive value (*A*) and the sensitivity or fidelity (*B*). In our case, *A* is the conditional probability that a sampled location belongs to a specific geomorphic surface within a channel type, given the presence of the indicator species.

The second conditional probability, *B*, represents the probability of finding the indicator species on that type of geomorphic surface within the channel type (De Caceres et al. 2012).

We identified important indicator species or species combinations for each geomorphic surface within channel types. Indicator species results are consistent with the ordination results and provide a list of species that generally show high affinity and relatively frequent occurrence on one or a combination of geomorphic surfaces. These species broadly differed among geomorphic surfaces and between reaches. A notable exception was *Equisetum* spp., or horsetail (*E. hyemale* and *E. laevigatum*), which was an indicator species in both debris-fan-affected reaches (on active channel and active floodplain) and restricted-meander reaches (on active floodplain, Table 2).

Table 2. Conditional probabilities from Indicator Species Analysis. The *A* statistic is the positive predictive value of the indicator for the geomorphic surface within a channel type, ranging from 0=no predictive value to 1=perfect prediction. The *B* statistic is the sensitivity or fidelity of the indicator to the specific surface, ranging from 0=no fidelity to 1=perfect fidelity. Channel type abbreviations are: DFA=Debris fan affected; ENM=Entrenched meanders; REM=Restricted meanders. Geomorphic surface abbreviations are: AC=Active Channel; AF=Active Floodplain; IF=Inactive Floodplain; U=Upland.

Channel Type	Geomorphic Surface	Indicator Species and Species Combinations	*A*	*B*
DFA	AC	*Equisetum* spp. (horsetail)	0.726	0.632
DFA	AC	*Polygonum amphibium* (water knotweed)	0.969	0.387
DFA	AC	*Salix exigua* (sandbar willow)	0.701	0.489
DFA	AF	*Glycyrrhiza lepidota* (wild licorice)	0.534	0.607
DFA	AF	*Equisetum* spp. + *G. lepidota*	0.695	0.428
DFA	AF	*Apocynum cannabinum* (Indianhemp) + *G. lepidota*	0.801	0.230
DFA	IF	*Bromus tectorum* (cheatgrass)	0.450	0.538
DFA	IF	*Rhus trilobata* (skunkbrush)	0.593	0.384
DFA	IF	*Tamarix ramosissima* (tamarisk)	0.710	0.307
DFA	U	*Heterotheca villosa* (hairy false goldenaster)	0.969	0.571
DFA	U	*Alyssum desertorum* (desert madwort) + *B. tectorum*	0.750	0.428
DFA	U	*Ericameria nauseosa* (rubber rabbitbrush)	1.000	0.285
ENM	AC	*Eleocharis palustris* (spike rush)	0.715	0.424
ENM	AC	*Argentina anserine* (silverweed cinquefoil)	0.831	0.337
ENM	AC	*Equisetum arvense* (field horsetail)	0.924	0.279
ENM	AF	*Salix exigua* (sandbar willow)	0.702	0.405
ENM	AF	*Tamarix ramosissima* (tamarisk)	0.648	0.272

Table 2 (continued). Conditional probabilities from Indicator Species Analysis. The *A* statistic is the positive predictive value of the indicator for the geomorphic surface within a channel type, ranging from 0=no predictive value to 1=perfect prediction. The *B* statistic is the sensitivity or fidelity of the indicator to the specific surface, ranging from 0=no fidelity to 1=perfect fidelity. Channel type abbreviations are: DFA=Debris fan affected; ENM=Entrenched meanders; REM=Restricted meanders. Geomorphic surface abbreviations are: AC=Active Channel; AF=Active Floodplain; IF=Inactive Floodplain; U=Upland.

Channel Type	Geomorphic Surface	Indicator Species and Species Combinations	*A*	*B*
ENM	AF	*Glycyrrhiza lepidota* (wild licorice)	0.561	0.288
ENM	IF	*Bromus tectorum* (cheatgrass)	0.902	0.688
ENM	IF	*Bromus tectorum* + *Pascopyrum smithii*	0.966	0.311
ENM	IF	*Pascopyrum smithii* (western wheatgrass)	0.885	0.311
ENM	U	*Alyssum desertorum* + *Bromus tectorum* + *Sporobolus cryptandrus* (sand dropseed)	0.636	0.583
ENM	U	*Alyssum desertorum* + *Sporobolus cryptandrus*	0.533	0.666
ENM	U	*Alyssum desertorum* + *Bromus tectorum*	0.583	0.583
REM	AC	*Chamaesyce glyptosperma* (ribseed sandmat)+ *Echinochloa crus-galli* (barnyard grass)+ *Juncus bufonius* (toad rush) + *Plantago major* (common plantain)	0.333	0.577
REM	AC	*Chamaesyce glyptosperma* + *Echinochloa crus-galli* + *Juncus bufonius* + *Plantago major* + *Polygonum lapathifolium* (curlytop knotweed)	0.333	0.577
REM	AC	*Chamaesyce glyptosperma* + *Echinochloa crus-galli* + *Juncus bufonius* + *Plantago major* + *Populus fremontii* (Fremont cottonwood)	0.333	0.577
REM	AF	*Equisetum* spp. (horsetail)	0.827	0.707
REM	AF	*Equisetum* spp. + *Pascopyrum smithii* (western wheatgrass)	0.685	0.555
REM	AF	*Distichlis spicata* (saltgrass) + *Equisetum* spp.	0.868	0.292
REM	IF	*Poa* spp. *(pratensis and compressa*; bluegrass*)*	0.793	0.653
REM	IF	*Poa* spp. + *Populus fremontii* (Fremont cottonwood)	0.951	0.500
REM	IF	*Pascopyrum smithii* (western wheatgrass) + *Poa* spp.	0.812	0.576
REM	U	*Bromus tectorum* (cheatgrass)	0.949	1.000
REM	U	*Bromus tectorum* + *Descurainia sophia* (herb sophia)	1.000	0.857
REM	U	*Bromus tectorum* + *Sarcobatus vermiculatus* (greasewood)	1.000	0.857

Active channel indicators typically occur with relatively low cover and frequency. For example, ribseed sandmat (*Chamaesyce glyptosperma*) and cocklebur (*Xanthium strumarium*) are weedy annuals found sparingly on sandy, active channel bars in the alluvial, restricted meander reach of the

Yampa. Common spike rush (*Eleocharis palustris*) and silverweed cinquefoil (*Argentina anserina*), perennial wetland species, are active channel indicators in the entrenched meander reach where vegetation cover on coarser textured bars is typically higher than in the alluvial reach. Water knotweed (*Polygonum amphibium*) is an active channel indicator in the debris fan affected reach where it begins growth as an aquatic plant during high, spring river stages and concludes growth as a terrestrial plant following stage declines. Water knotweed, sandbar willow (*Salix exigua*) and field horsetails are active channel indicators in the debris fan affected reach. Whereas active channel indicators have high affinity for active channel surfaces, their densities would be hypothesized to increase, at least initially, if the channel feature on which they were growing, began converting to floodplain. Similarly, increases in active floodplain indicators on active channel features are hypothesized to be evidence of floodplain construction and a directional channel narrowing process, at least locally.

Common and easily identifiable active floodplain indicators in the restricted meander reach included field horsetails and saltgrass (*Distichlis spicata*). Important and easily identifiable active floodplain indicators in the debris fan affected reach included wild licorice (*Glycyrrhiza lepidota*), often accompanied by Indianhemp (*Apocynum cannabinum*), and field horsetails. In restricted meander reaches, sandbar willow, tamarisk (*Tamarix ramosissima*) and wild licorice are notable active floodplain indicators (Table 2).

Some species, including field horsetails, tamarisk and sandbar willow are significant indicators of two geomorphic surfaces such as active channel and active floodplain or active and inactive floodplains. Work by Manners et al. (2014) in two entrenched meander reaches of the Yampa, documented the active participation of tamarisk and sandbar willow in the channel narrowing that has taken place in these settings over the past 50 years. Their involvement in vertical accretion of floodplain surfaces is suggested by their identified fidelity to multiple surfaces. Tamarisk is also frequently encountered on AC surfaces in debris fan affected and entrenched meander reaches, but did not appear as significant in the indicator analyses. Although tamarisk and sandbar willow may be the main participants in floodplain construction, the other rhizomatous perennials associated with multiple surfaces may play a role in the channel narrowing process, or would at least be expected to appear and persist through different stages of narrowing.

These results are consistent with other studies showing high fidelity of riparian species to fluvial surfaces (Hupp and Osterkamp 1985, Harris 1987). The strong ordering of plots on axis 2 of the PCO (Figure 2) from wet to dry—from active channel to active floodplain to inactive floodplain to upland—and from high to low cover along axis 1, demonstrates the strong influence of the underlying gradients of moisture availability and disturbance frequency and intensity (Auble et al. 1994, 1997, 2005, Friedman et al. 1996, Chapin et al. 2002, Merritt and Cooper 2000). The relation of individual species to fluvial surfaces and the positions of species on the hydraulic gradient represented by PCO axis 1 are consistent with similar studies from elsewhere in the Colorado Plateau. For example, two of the Indicator Species for the driest (Upland and Inactive Floodplain) surfaces at DINO, sand dropseed (*Sporobolus cryptandrus*) and cheatgrass *(Bromus tectorum)*, were also strongly associated with the driest of three surface types identified along the Gunnison River in

Black Canyon of the Gunnison National Park (Auble et al. 1994). One of the indicator species for the active channel and floodplain at DINO, scouring rush horsetail (*Equisetum hyemale*), also dominated the middle of the three Gunnison River community types, and one commonly occurring species for the DINO channel, common spikerush (*Eleocharis palustris*), was also a dominant of the wettest of the three Gunnison River types (Auble et al. 1994). The fluvial surfaces occupied by the Indicator Species identified at DINO and the positions of those surfaces on the hydraulic gradient implied by the PCO axes are strongly consistent with mean inundation durations for the same species at the Black Canyon of the Gunnison and the Fremont River (Table 2, Auble et al. 2005 and unpublished data).

Influence of Flow on Overall Species Occurrence Patterns

Flow regulation decreases flow variability, steepening the inundation-duration gradient and decreasing the area occupied by species associated with moderate inundation durations

Reservoir construction typically decreases magnitude and frequency of peak flows, and increases base flows (Magilligan and Nislow 2005). This decreases inundation duration on high surfaces, while increasing it on low surfaces. Along the Gunnison and Fremont rivers, Auble et al. (1994, 2005) combined a hydraulic model with randomly selected vegetation plots to determine the position of species and communities on the inundation-duration gradient, and then modelled how changes in the flow regime would redistribute plants among plots. A decrease in flow variability designed to mimic stronger effects of reservoir management reduced the area occupied by species and communities found in the middle of the hydraulic gradient, and increased the area occupied by species and communities characteristic of very wet or dry sites (Auble et al. 1994, 2005). This effect was then observed by Merritt and Cooper (2000) along the Green River downstream of Flaming Gorge Reservoir in Browns Park, Colorado, where riparian plant communities fell into two distinct groups: (1) rarely inundated high surfaces occupied by old cottonwood forest, desert shrubland and tamarisk shrubland, and (2) low surfaces inundated more than 150 days per year and occupied by fluvial marsh vegetation dominated by willow, rush (*Juncus)* and spikerush (*Eleocharis*). Along the less regulated Yampa River at Deerlodge Park the more gradual gradient in inundation duration is associated with a more gradual gradient in riparian vegetation (Merritt and Cooper 2000, Figure 2, Table 1).

The streamward extent of riparian vegetation is controlled by scour and extended inundation by the Yampa River

Removal of riparian vegetation is accomplished by the combined effects of flow magnitude and duration. High flows can instantaneously remove riparian plants by mobilizing the underlying sediment. Extended inundation kills plants by denying oxygen to the roots. At Black Canyon of the Gunnison National Park in Colorado, Friedman and Auble (1999) related survival of riparian box elder (*Acer negundo*) to tree age, hydraulic position, and flow history, finding these plants were killed by local boundary shear stress instantaneously exceeding the critical value for mobilizing the underlying sediment or by continuous inundation of the sediment surface for more than 85 days during the growing season. These hydraulic processes control removal of all plants, but threshold values vary with sediment particle size and plant species, size and abundance. For example, fluid drag on plant stems can reduce local flow velocity and shear stress, and tensile strength of roots can

increase the shear stress necessary for sediment mobilization (Griffin et al. 2005, 2014, Vincent et al. 2009). This increase in erosion resistance due to vegetation is greatest when stems and roots are close together. Plants prolong survival of extended inundation using hollow stems that transport oxygen to roots, and chemical processes that reduce toxicity of compounds produced in anaerobic soils. This resistance to extended inundation increases with plant height and root development (Gill 1970). Because resistance to erosion and extended inundation increases with plant age, increasing the time between flow events reduces the area cleared of riparian vegetation (Friedman and Auble 1999).

The influence of flow in limiting streamward extent of riparian vegetation is evident along the Yampa River in DINO (Figure 2). Plots in the Active Channel had lower total vegetation cover (9%), compared with Active Floodplain (23%), Inactive Floodplain (40%) and adjacent Upland surfaces (25%). The effects of flood disturbance were obvious throughout the Yampa River corridor in DINO following the flood of 2011, including the direct removal of vegetation by high localized sheer stresses and mortality resulting from long-duration inundation (Figure 3).

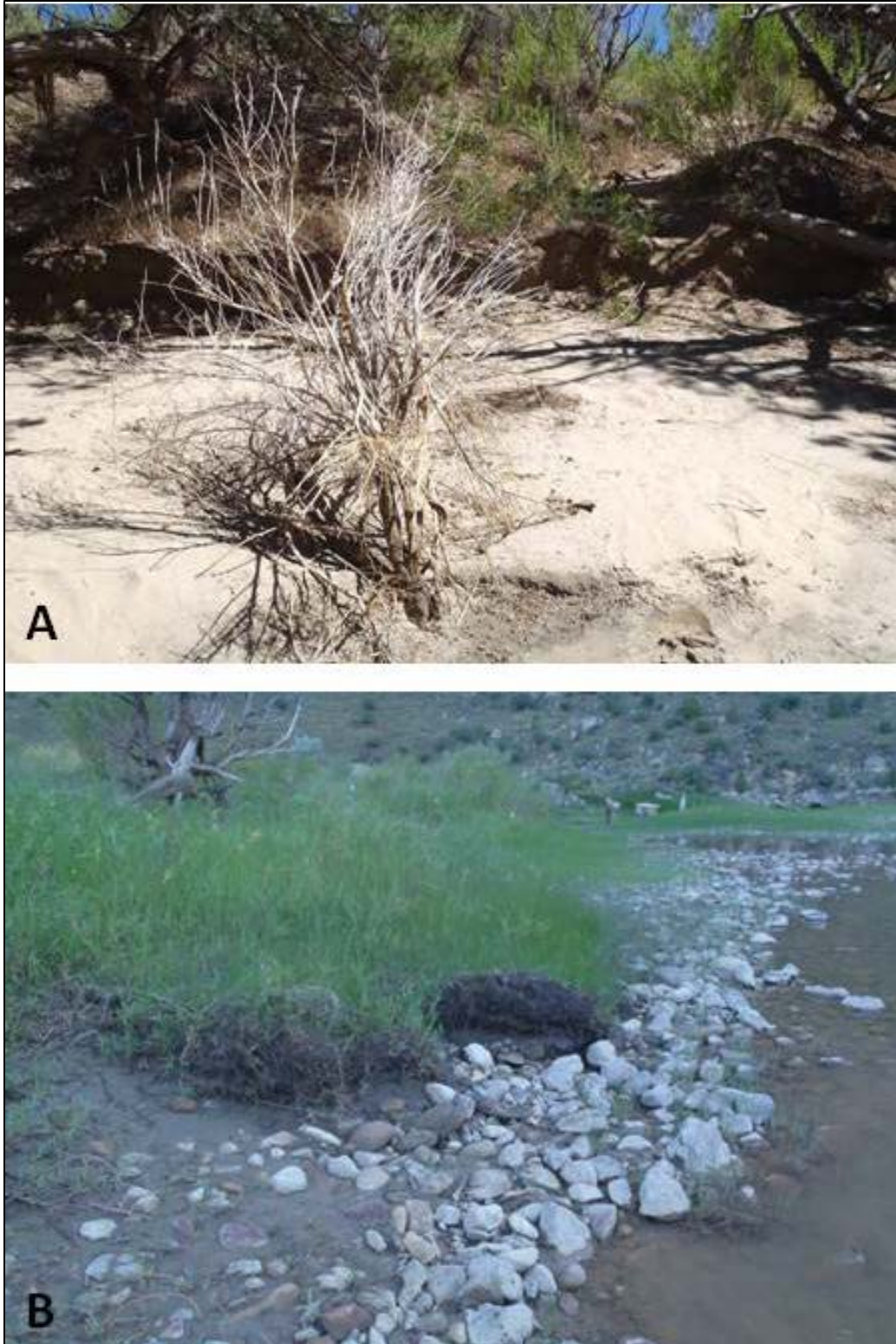**Figure 3.** Illustration of the effects of the 2011 flood on vegetation along the Yampa River in DINO. A) A rabbitbrush (*Ericameria nauseosa*) established on the upper edge of an eddy bar at Anderson Hole, killed by prolonged inundation and partial erosion of the root system. B) The leading edge of a dense root mat of common spikerush (*Eleocharis palustris*) peeled away from underlying cobbles in lower Harding Hole.

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Channel clearing by the Yampa River strongly influences species composition of riparian vegetation near the channel

In addition to limiting total vegetation cover near the channel, scour and extended inundation affect species composition. Most plants able to survive near the channels of the Green and Yampa rivers are annuals completing their life cycle between disturbances (Merritt and Cooper 2000), or perennials capable of vegetative reproduction from belowground roots or rhizomes. In a study of vegetation along the Green and Yampa rivers in DINO, Fischer et al. (1983) placed the following species in this group of perennials: scouring rush horsetail *(Equisetum hyemale)*, smooth horsetail (*E. laevigatum*), sedge (*Carex aquatilis* [sic], likely *emoryi*), spikerush (*Eleocharis* sp. likely *palustris*), wild licorice (*Glycyrrhiza lepidota*), Indianhemp (*Apocynum cannabinum*), milkweed (*Asclepias* sp. likely *speciosa*), water knotweed (*Polygonum amphibium*), povertyweed (*Iva axillaris*) and skeletonleaf bur ragweed (*Franseria discolor* [sic] now *Ambrosia tomentosa*). Many of these species have hollow stems and produce large numbers of seeds widely dispersed by water or wind. Two of these species, Indianhemp and spikerush, were significant indicators for active channel in our analysis (Table 2). We found all of these species in our current study, and all had high frequencies (>9%) except skeletonleaf bur ragweed, milkweed, sedge and water knotweed. There are two important reasons why more of these species were not significant indicators: 1) these species are naturally sparse in the active channel, and 2) many of these species are associated with small, discontinuous patches of active floodplain, which Fischer et al. (1983) included in their floodzone. Thus, scouring rush horsetail was actually an active floodplain indicator in our analysis (Table 2). Fischer et al. (1983) note that horsetail (presumably *Equisetum hyemale* and *E. laevigatum*) has invaded formerly active channel deposits in the post-dam period along the Green River in Lodore Canyon, DINO.

Flood-maintained physical heterogeneity has profound influence on riparian plant diversity and distribution. As existing areas of vegetation are removed by flood disturbance, new opportunities for establishment are created, producing a mosaic of patches differing in age and species composition and influenced by hydrogeomorphic position (Naiman et al. 1993, Sarr et al. 2005). Higher above and farther away from the river, fluvial disturbance is less intense and frequent, reducing opportunities for establishment of species that are good dispersers, but poor competitors, resulting in decreased species diversity (Friedman et al. 1996). Along the Yampa and Green rivers mean plant species richness in cottonwood forest was more than 50% lower on high, old (>250 years) sites than on low young (<20 years) sites (Uowolo et al. 2005).

Flow regulation shifts vegetation from species dependent upon physical disturbance to species tolerant of extended inundation

Flow stabilization changes the relative importance of erosion and extended inundation in clearing riparian vegetation. A decrease in peak flows reduces the clearing effects of erosion, while an increase in lower flows increases the clearing effects of extended inundation, at least on species susceptible to anoxia. For example, prior to construction of the Aspinall Unit Dams on the Gunnison River from 1966-1976, erosion cleared larger areas of the riparian zone than extended inundation at Warner Point along the Gunnison River in Black Canyon of the Gunnison National Park (Friedman and Auble 1999). After reservoir construction, however, the total area cleared of riparian vegetation decreased, and extended inundation became the dominant mechanism for vegetation removal

(Friedman and Auble 1999). Mean species richness in floodplain cottonwood forest was 40% higher along the lightly regulated Yampa River at Deerlodge Park than along the heavily regulated Green River at Browns Park (Uowolo et al. 2005). This reduction in species diversity was attributable in part to a lack of overbank flooding in Browns Park and a resulting transition in floodplain vegetation composition from a riparian community to a less diverse upland community (Merritt and Cooper 2000). A similar loss in floodplain species diversity was observed when comparing a flow-regulated reach of the Bill Williams River, Arizona, with its upstream and unregulated tributary (Stromberg et al. 2012). In this case, reduced fluvial disturbance: 1) reduced open space available for colonization by annual herbaceous vegetation; and 2) contributed to increases in forest biomass, which in turn depressed the diversity and abundance of understory species.

Along the Green River in Browns Park, increased low flows have resulted in inundation duration of 148 days per year on low-lying depositional bars and islands, compared to 43 days for comparable surfaces on the relatively unregulated Yampa River at Deerlodge Park (Merritt and Cooper 2000). On these low-lying surfaces at Browns Park, reduction in peak flows and increase in low flows have promoted development of anoxic soils and proliferation of dense marsh vegetation consisting of species tolerant of anoxia, such as common spikerush (*Eleocharis palustris*), knotted rush (*Juncus nodosus*), common threesquare (*Schoenoplectus pungens*) and sandbar willow (*Salix exigua*) (Merritt and Cooper 2000). Surfaces of comparable elevation along the less regulated Yampa River at Deerlodge Park have lower inundation duration, are subject to shear stresses of higher frequency and magnitude, and are more sparsely vegetated. Dominant plants include annual and short-lived perennial species able to colonize new sites rapidly after disturbance, such as ribseed sandmat (*Chamaesyce glyptosperma*), marsh cudweed (*Gnaphalium uliginosum*), water mudwort (*Limosella aquatica*), curlytop knotweed (*Persicaria lapathifolia*), rough cocklebur (*Xanthium strumarium*), and foxtail barley (*Critesion jubatum*) (Merritt and Cooper 2000). Fischer et al. (1983) predicted that increased flow regulation on the Yampa could allow establishment of species of non-flowing wetland habitats that were found at that time on the more regulated Green River, but not on the less regulated Yampa; these species included redtop (*Agrostis alba)*, alkali buttercup (*Ranunculus cymbalaria*), cinquefoil (*Potentilla* sp.), and cattail (*Typha* sp.). Increases in wetland species following flow regulation have also been documented in Grand Canyon (Stevens et al. 1995).

Flow regulation can increase occurrence of invasive species
In a study of twelve invasive species in 1316 stream reaches in 12 western states, Ringold et al. (2008) found that the invasive species were much more likely to occur on streams with large upstream dams than on streams without them. Similarly, along the River Murray, Australia, a decrease in high flows increased the cover of invasive species by inhibiting native species adapted to the pre-dam flow regime (Catford et al. 2014). Perkins et al. (2016) compared occurrence of invasive species along 171 km of river in canyons of the relatively unregulated Yampa River in DINO, the moderately regulated Green River downstream of the confluence with the Yampa River, and the heavily regulated Green River between Flaming Gorge Dam and the confluence with the Yampa River. The three rivers had invasive patch density of 3.3, 4.4 and 10.1 patches/ha, and 0.04, 0.22 and 0.28 invasive species/m^2, supporting the hypothesis that flow regulation increases occurrence of invasive species along the Yampa-Green system. In addition to tamarisk, important invasive species

along the Yampa and Green rivers include Russian olive (*Elaeagnus angustifolia*), common reed (*Phragmites australis*), Canada thistle (*Cirsium arvense*) and broadleaf pepperwort (*Lepidium latifolium*; Perkins et al. 2016). Worldwide, and along the Yampa and Green rivers, riparian invasive species tend to have high seed availability and dispersal potential and are tolerant of flooding and drought (Catford and Jansson 2014, Perkins et al. 2016). Therefore, whereas native riparian species adapted to the pre-disturbance flow regime can be inhibited by flow regulation, invasive riparian species tend to have the ability to colonize regulated or unregulated systems. For example, even in the absence of heavy flow regulation, invasive species are gradually increasing along the relatively unregulated Yampa River (Perkins et al. 2016). This means that maintaining flow variability helps to maintain native riparian vegetation, but does not completely prevent the spread of invasive species.

Factors Controlling Abundance of Dominant Woody Species along the Yampa River

The dominant woody riparian species along the Yampa River are tamarisk (*Tamarix ramosissima*), Fremont cottonwood (*Populus fremontii*), box elder (*Acer negundo*) and sandbar willow (*Salix exigua*). These species differ in tolerance of drought, salinity, inundation, flood disturbance and shade and in seed size, timing of seed dispersal and ability to form root sprouts. These physiological and ecological differences interact with flow variation and geomorphic setting, resulting in differential patterns of occurrence. In the following sections these differences are defined on the basis of literature from the Yampa River and elsewhere with the goal of assessing how changes in Yampa River flow would affect woody species abundance.

Physiological and ecological differences among the four dominant woody species

Tamarisk is the most tolerant of drought and high salinity, but the least competitive under conditions of abundant moisture and low salinity

Tamarisk is more tolerant of drought and high salinity than the other three woody dominant species. Tamarisk has higher water use efficiency than cottonwood (Busch and Smith 1995) and can persist at lower leaf water potentials than sandbar willow (Cleverly et al. 1997). Sandbar willow and cottonwood, but not tamarisk, generally depend upon root contact with a shallow water table (Busch et al. 1992, but see Zimmerman 1969). Cottonwood is also susceptible to cavitation of xylem vessels at low water potentials, which requires it to close stomata, reducing photosynthesis, to avoid cavitation under drought (Tyree et al. 1994). Cottonwood, willow and box elder exclude salt at the roots, a strategy that increases the osmotic gradient against water uptake in saline soil. In contrast, tamarisk takes up and tolerates the salt, excreting it from the leaves (Busch and Smith 1995), a strategy that increases survival and allows more rapid growth at high salinity (Glenn and Nagler 2005). As a result tamarisk grows faster than cottonwood and willow under high salinity (Vandersande et al. 2001) and drought (Perry et al. 2012, Garssen et al. 2014). In contrast, willow, cottonwood and box elder grow faster and are competitively dominant over tamarisk where salinity is low and the water table is close to the surface (Vandersande et al. 2001, Sher et al. 2002, Glenn and Nagler 2005, DeWine and Cooper 2008, Lite and Stromberg 2005, Garssen et al. 2014). Seedling drought tolerances of cottonwood and sandbar willow are similar. In one controlled study, sandbar willow seedlings did not survive water-table declines faster than 1 cm/d, while eastern cottonwood (*Populus deltoides*) seedlings survived declines of up to 4 cm/d (Amlin and Rood 2002). In another study Fremont cottonwood and sandbar willow had similar mortality rates across different rates of water-table decline (Stella et al. 2010). Other studies suggest 2.5 cm/d is the maximum tolerable water-table decline rate for cottonwood seedlings (Mahoney and Rood 1998). The northern tamarisk beetle (*Diorhabda carinulata*) was introduced to DINO in 2006 and 2007 to control tamarisk. The beetle caused widespread tamarisk defoliation and dieback in DINO in 2012 and 2013, but had smaller effects in 2014-2016 (Williams 2016). Herbivory by this beetle should further reduce competitiveness of tamarisk relative to the other dominant species. Decline in tamarisk could allow increase in the native competitors described here or invasive competitors like the large-seeded shrub Russian olive (*Elaeagnus angustifolia*).

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Mortality from inundation and flood disturbance

Mortality from prolonged inundation is associated with oxygen depletion in the root zone or exhaustion of energy reserves. Therefore, flooding causes higher mortality during the growing season than during the dormant season. The duration of flooding a tree can survive depends upon water depth and upon plant species, age, size and gender (Friedman and Auble 1999). Warm water can cause more rapid mortality than cold water because oxygen solubility in water decreases with increasing temperature, and because oxygen consumption by plants and soil biota increases with increasing temperature. Flood tolerance of mature tamarisk is less than that of mature cottonwood, box elder or willow. Mature tamarisk can survive complete submergence during the growing-season for up to 70 days and partial submergence for up to 98 days (Warren and Turner 1975). In a Kansas Lake less than 4% (40 out of thousands) of tamarisk survived inundation for one year (Tomanek and Ziegler 1962). In contrast, mature box elder, cottonwood and willow can generally survive inundation for at least an entire growing season (Whitlow and Harris 1979). Saplings can be killed by shorter flow durations than trees. For example, along the Gunnison River in Black Canyon of the Gunnison National Park, CO, box elder saplings are killed by inundation for 85 days (Friedman and Auble 1999). Seedlings can be killed by even shorter flood durations, but species differences and survival times vary. For example, in a Colorado study, fall flooding for 25 days resulted in 0.8% survival for tamarisk and 20.8% survival for plains cottonwood (*Populus deltoides* subsp. *monilifera*; Gladwin and Roelle 1998). In contrast, in a New Mexico study, seedling survival after 30 days of fall flooding was 43.5% for 6-8-week-old tamarisk seedlings, 2% for 4-week-old tamarisks, and 0% for 6-8-week old Rio Grande cottonwoods (*Populus deltoides* subsp. *wislizenii*; Sprenger et al. 2001). Flooding may favor cottonwood seedlings over those of tamarisk when the tamarisk seedlings are younger (established later in the season) or when the flow overtops the tamarisk, but not the taller cottonwood (Sprenger et al. 2001). Sandbar willow may be more flood tolerant than cottonwood. In a controlled study, roots of sandbar willow penetrated the water table, while roots of cottonwood remained within the capillary fringe (Amlin and Rood 2002). Finally, recently germinated seedlings may not be able to survive any inundation. For example, young tamarisk seedlings 5 and 10 days old can be removed instantly by flooding because the roots are not strong enough to prevent uprooting due to the buoyancy of the seedlings (Horton et al. 1960).

All the woody dominants are subject to removal by mobilization of underlying sediment (Friedman and Auble 1999) or by damage from rapidly flowing water, sediment and woody debris. Each tamarisk and sandbar willow plant produces abundant small stems, allowing quick recovery following flood damage. Unlike tamarisk, sandbar willow has flexible stems that can lie down without breaking in a flood, and the ability to form root sprouts, enabling lateral movement in response to channel change. In contrast, box elder and cottonwood produce fewer, larger stems, resulting in slower recovery. In both Yampa and Lodore Canyons within DINO, the elevational range occupied by tamarisk extends closer to the river than that of box elder (DeWine and Cooper 2010). Because there is no evidence that tamarisk tolerates longer inundation than box elder (see above), this difference in distribution appears to result from a superior ability in tamarisk to recover from frequent disturbance as well as the dispersal of abundant tamarisk seeds during gradual summer drawdown, promoting tamarisk establishment at low elevations.

Whereas cottonwood, willow and tamarisk are all intolerant of shade, box elder is moderately shade tolerant

Box elder is more tolerant of shade than the other dominant woody species. On a scale from 1 (very intolerant of shade) to 5 (very tolerant of shade) Fremont Cottonwood is rated 1.35, tamarisk 1.35, and box elder 3.47 (Niinemets and Valladares 2006). Sandbar willow, like cottonwood and tamarisk, is classified as shade intolerant (Anderson 2006). DeWine and Cooper (2008) studied competition between box elder and tamarisk along the Green and Yampa rivers in DINO. Shade treatments had a stronger negative effect on growth and survival for tamarisk than for box elder. The presence of canopy box elders within 1 and 2 m was significantly related to tamarisk mortality, but the presence of canopy tamarisk was not related to box elder mortality. They observed sites where tamarisk had established first, but later died, apparently through shading from box elder. Therefore, box elder is able to become established on flood-moistened sites beneath a tamarisk canopy, and then to overtop and kill the tamarisk. This successional sequence is limited along the Green River by flow regulation, which has reduced the high flows necessary to provide surface moisture for box elder establishment within tamarisk stands (DeWine and Cooper 2008).

Box elder has the largest seeds, while tamarisk and sandbar willow have the smallest

Of the four dominant woody species box elder has the largest seed size (22-55 mg, Zasada and Strong 2008), followed by Fremont cottonwood (0.9 mg, Schweitzer et al. 2002) and then tamarisk and sandbar willow (both around 0.1 mg, Perry et al. 2013). Larger seeds contain more stored energy, allowing plants to live temporarily in a relatively dark environment or to grow rapidly upon germination. The large seeds and shade tolerance of box elder allow this species to germinate in crevices on the talus slopes common in canyons or to germinate beneath leaf litter or within competing vegetation. In contrast, the other 3 species require a bare substrate for successful establishment. The relatively large seeds of cottonwood compared to tamarisk and willow may help to give cottonwood seedlings a short-term competitive advantage where sufficient moisture is present and salinity is not too high (Sher et al. 2002, Amlin and Rood 2002).

Tamarisk has a longer and later season of seed release than cottonwood and sandbar willow

Fremont cottonwood, tamarisk and sandbar willow produce many small seeds dispersed by wind and water to become established on bare, moist surfaces such as recently deposited sediment (Glenn and Nagler 2005). Because these seeds lack dormancy and have short longevity, they must find a suitable environment for germination within weeks of dispersal. Fremont cottonwood and sandbar willow seeds are released for a short period in spring or early summer, often coinciding with the declining limb of flow peaks in unregulated rivers (Stella et al. 2006). In contrast the season of tamarisk seed release tends to start later than that of cottonwood and willow and extends through most of the growing season (Warren and Turner 1975, Stromberg 1997). Box elder seeds ripen in the fall and are released gradually until spring. Because they have dormancy, box elder seeds do not need to fall on a site that is immediately suitable for germination (Maeglin and Ohmann 1973).

Along the Yampa River, Fremont cottonwood seed dispersal occurs over a 4-6 week period coinciding with declining river stage following the annual peak. At Deerlodge Park, cottonwood seed dispersal occurred from early June to mid-July in 1994 and from late June to late July in 1995

(Cooper et al. 1999). In 1995, tamarisk seed dispersal at Deerlodge Park began later than that of cottonwood, in early to mid-July, and continued until mid-September (Cooper et al. 1999).

Sandbar willow spreads laterally most rapidly by root sprouting

All four woody dominants are able to re-sprout from the root crown or buried stems, allowing them to recover when stems are damaged or buried by floods. Unlike the other three species, however, sandbar willow forms abundant root sprouts allowing it to spread laterally in wet environments even when there are no seedling establishment opportunities (Schweitzer et al. 2002). When Glen Canyon Dam decreased flows in 1963, formerly bare surfaces along the channel of the Colorado River downstream of the dam were colonized by seedlings of tamarisk. After this burst of establishment, some of the tamarisk was gradually replaced by sandbar willow because of the latter's capability of vegetative lateral spread (Stevens 1989). At Browns Park along the Green River downstream of Flaming Gorge Dam, stabilization of river flows decreased erosive peaks, while increasing inundation duration on low surfaces to 259 days per year. These low surfaces became dominated by rhizomatous perennial species capable of surviving extended inundation and spreading vegetatively, including sandbar willow (Merritt and Cooper 2000). Because of sandbar willow's shallow roots and lack of drought tolerance, its ability to spread vegetatively comes into play only on wet surfaces protected from extreme disturbance by flow regulation or some other factor.

Zonation of the four dominant woody species perpendicular to and along the river

Zonation perpendicular to the river

Because it does not rely on flood disturbance for establishment, box elder occurs higher on the floodplain than any of the other dominants (DeWine and Cooper 2010). For example, box elder occurs on talus slopes where moisture is sufficient, above the zone of flood inundation. Where drought is limiting, tamarisk can occur higher on cross sections than sandbar willow (Table 2). Similarly, adult eastern cottonwoods (*Populus deltoides*) generally persist at higher elevations on the floodplain than sandbar willow (Cordes et al. 1997), perhaps because cottonwood is more deeply rooted. Along the Rio Puerco, New Mexico, sandbar willow roots tend to be shallow (Friedman et al. 2015), thin, porous, and quickly consumed by insect larvae (J. Friedman personal observation, 2000). In canyons, the shrubs tamarisk and sandbar willow occur closer to the channel than the trees box elder and cottonwood (Cooper et al. 2003, DeWine and Cooper 2010) because formation of a large number of small stems allows more rapid recovery after frequent physical disturbance in this high energy environment and because tamarisk's extended season of seed release allows establishment late in the season on low surfaces. Because of its rhizomatous habit and strong tolerance of inundation, sandbar willow can extend downward past the other dominants in low-energy environments with long periods of inundation and limited seedling establishment opportunities (Merritt and Cooper 2000).

Zonation along the river. Cottonwood is more common in parks than canyons, while box elder is more common in canyons than in parks

In the upper Colorado River Basin, including DINO, box elder is more common in canyons than in parks, and cottonwood is more common in parks than in canyons, a pattern that predates flow regulation (Stephens and Shoemaker 1987, DeWine and Cooper 2010). The causes of this spatial

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segregation are not completely understood, but may be related to the high shade tolerance and large seed size of box elder relative to cottonwood (Johnson et al. 1976), which allow box elder to become established on talus slopes, providing a seed source for the floodplain in canyons. Cottonwood may be uncommon in canyons because of shade intolerance, lack of an upland seed source, short seed dispersal season, large aboveground biomass and small number of stem sprouts (relative to tamarisk), and lateral confinement of the floodplain, which limits area of bare, moist surfaces necessary for seedling establishment. Tamarisk is abundant in both park and canyon settings. Sandbar willow is also common and increasing in both settings, but less abundant than tamarisk (Manners et al. 2014). Box elder occupies more area than tamarisk in both Yampa and Lodore canyons (DeWine and Cooper 2010).

Establishment and survival of the four woody dominants in relation to flow and channel change

Seedling establishment of tamarisk, cottonwood and willow occurs on sites moistened and disturbed by the river in both high and low-flow years

Tamarisk, cottonwood and willow all produce seeds that must germinate within weeks after dispersal, forming seedlings that require abundant light and moisture. Therefore, in any year, seedling establishment is limited to the zone irrigated and disturbed by the river at the time of seed release (Scott et al. 1996). On a floodplain cross section the high limit of this zone is the stage of the peak discharge, as long as the discharge did not occur more than a few weeks before the period of seed release (Auble and Scott 1998, Manners et al. 2014). Seedling establishment near the high limit is further constrained by desiccation caused by flows declining more rapidly than about 2.5 cm/d in the year of establishment especially on coarse substrates (Mahoney and Rood 1998). The low limit of the establishment zone is roughly the stage at the end of the period of seed dispersal (Manners et al. 2014). Because small seedlings have very limited ability to survive desiccation or flooding, plants may be killed by flow fluctuations in the first few years of life, reducing the size of the observed zone of establishment (Auble and Scott 1998), but susceptibility to such flow fluctuations decreases with age. One way to prevent establishment of unwanted riparian vegetation during drawdown is to use dam releases to superimpose fluctuations in flow on the drawdown. This technique has been used to control vegetation supporting malaria mosquitoes on reservoir margins in the southeastern United States (Hall et al. 1946). Because a zone of successful seedling establishment may occur in a high-flow or low-flow year, establishment of tamarisk, cottonwood and willow can occur at a wide range of elevations (Manners et al. 2014). Seedlings established at low elevations are more likely to survive future high flows if protected by sediment deposition, which decreases inundation depth, and channel migration away from the site of establishment. Such geomorphic changes occur along meandering or narrowing channels, and are spatially limited by lateral confinement within canyons (Scott et al. 1996, 1997).

Spatially extensive cottonwood recruitment in alluvial park settings has occurred in years of low, moderate and high peak flows. Spatially limited cottonwood recruitment in canyon-bound reaches occurs in years of moderate and high peaks

Along an unconfined, alluvial reach of the Yampa River in Deerlodge Park, where cottonwood is dominant, some level of cottonwood recruitment occurred almost every year during the 1970s and

throughout the 1980s, including years in which peak flood flows were large (1974 and 1984; 597 and 940 m^3/s; 21,100 and 33,200 ft^3/s), moderate (1980 and 1988; 467 and 411 m^3/s; 16,500 and 14,500 ft^3/s), and small (1981; 239 m^3/s; 8,400 ft^3/s) (Cooper et al. 2003; Grams and Schmidt 2002). Peak flows at Deerlodge Park are calculated following Schmidt and Manners (in review). Along the Green River in Canyonlands National Park cottonwood became established following a similarly wide range of flows (Scott and Miller 2017). In canyons, where cottonwood is much less abundant, cottonwood establishment may be limited to years of higher flow. For example, in Yampa Canyon, cottonwood established and survived at relatively high elevations on fine-grained eddy bars in years featuring moderate to high peak flows (1970, 1974, 1984, 1986, 1988 and 1993; 511, 597, 940, 479, 411 and 464 m^3/s; 18,000, 21,100, 33,200, 16,900, 14,500, and 16,400 ft^3/s; Cooper et al. 2003). Failure of cottonwood recruitment in canyons in lower flow years may be related to the short period of cottonwood seed dispersal and floodplain confinement, which lead to a narrow zone of establishment in low flow years, and damage to young cottonwoods by frequent flood disturbance on low-lying surfaces.

Tamarisk establishment along the Yampa River occurs in association with a wide range of peak flows

Tamarisk becomes established in association with a wide range of peak flows in both alluvial reaches and canyons. At Deerlodge Park relatively large numbers of tamarisk established in 1949, 1957, 1965, 1968, 1981, 1984, 1988, 1989, and 1993, when peak discharges were 353, 565, 434, 442, 239, 940, 411, 174, and 464 m^3/s (12,500, 20,000, 15,300, 15,600, 8,400, 33,200, 14,500, 6,100, and 16,400 ft^3/s; Cooper et al. 2003). In Yampa Canyon, relatively large numbers of tamarisk established in 1960, 1984, 1986, 1988, 1990 and 1991, with peak discharges of 309, 940, 479, 411, 282 and 281 m^3/s (10,900, 33,200, 16,900, 14,500, 10,000 and 9,900 ft^3/s; Cooper et al. 2003).

As a result of the offset in seed dispersal timing between cottonwood and tamarisk, early flow peaks promote cottonwood establishment, while later peaks promote tamarisk

Because of the difference in seed dispersal timing, early summer flow peaks promote cottonwood establishment, while mid- to late-summer peaks promote tamarisk (Everitt 1995, Cooper et al. 2003). Therefore, regulation that delays flow peaks favors tamarisk over cottonwood and willow (Merritt and Poff 2010, Stromberg et al. 2007, McShane et al. 2015). For example, construction of Flaming Gorge Reservoir on the Green River resulted in seasonal delay of peak flows downstream in 1975 and 1983 (July 7, 1975 and July 8, 1983 at Greendale Utah, Gage 9234500). In these two years tamarisk but not cottonwood became established at Browns Park. In contrast, peak flows in 1984 and 1986 were earlier (May 7, 1984 and May 20, 1986) and led to recruitment of cottonwood (Cooper et al. 2003).

Because tamarisk seed release continues much later in the season than that of cottonwood and willow, the tamarisk zone of establishment extends down closer to the river

In Deerlodge Park both cottonwood and tamarisk establishment elevations range from about 75 to 300 cm above the elevation of base flow. In Yampa Canyon, cottonwood establishment occurred at a similar range of elevations, but tamarisk establishment extended down to around 25 cm above the elevation of base flow (Cooper et al. 2003). Tamarisk became established at low elevations in Yampa Canyon during a multi-year drought. Dispersal of seeds in late summer enabled tamarisk seeds to

germinate on surfaces covered by water during the period of cottonwood seed release (Manners et al. 2014).

Tamarisk most strongly promotes floodplain construction by sediment deposition
Fluid drag on woody stems of all four species decreases local velocity, reducing erosion and promoting deposition of fine-grained sediment (Manners et al. 2013, 2014). Fluid drag is proportional to stem diameter not stem cross-sectional area. For example, two stems each 3 cm in diameter have a similar effect on flow to that of one stem 6 cm in diameter, even though the latter stem contains twice as much wood. Although trees like box elder and cottonwood have thicker stems, their effect on the flow field is smaller than that of shrubs like sandbar willow and young tamarisk (Graf 1978), because shrubs have far more stems (Griffin et al. 2014). Relative to those of tamarisk, sandbar willow stems are more flexible, lying down along the ground surface during floods. This tendency enhances survival of sandbar willow stems and reduces erosion of underlying sediment, but also reduces the effect of sandbar willow stems on flow velocities and sediment deposition when velocities are high (Griffin and Smith 2004). Therefore, of the four dominant woody species, tamarisk most strongly promotes floodplain construction by fine sediment deposition (Manners et al. 2014). Increase in tamarisk in Yampa Canyon in the 1980s led to channel narrowing by sediment deposition in the 1990s (Manners et al. 2014).

Tamarisk has a suite of characteristics that promote channel narrowing
The ability of tamarisk to disperse seeds throughout the summer allows it to become established at low elevations adjacent to the channel. Tolerance of inundation and scouring enable the tamarisk to persist adjacent to the channel. The high density of relatively stiff stems create a large fluid drag, promoting sediment deposition, reducing damage to the tamarisk by flood inundation and disturbance. Drought tolerance of adults allows the tamarisk to survive even after sediment deposition has raised the surface elevation. In trenches at Laddie Park in Yampa Canyon, 84% of excavated tamarisks germinated below the stage of the 2-year flood (Manners et al. 2014).

Decreases in peak flows may cause a short-term narrowing that provides temporary opportunities for establishment of riparian pioneer species, and a long-term decrease in formation of new surfaces suitable for establishment of riparian pioneer species
Cottonwood, tamarisk and willow seeds germinate on open, moist surfaces prepared by flooding. If high flows are reduced, then there is a long-term decrease in the area disturbed by the river and available for these pioneer seedlings (Johnson et al. 1976). Over the short term, however, reduced peak flows can result in transient geomorphic changes including channel narrowing, as channel dimensions adjust to the reduced ability of the river to erode and transport sediment. The area of new floodplain formed through channel narrowing is affected by initial channel width. In other words, wide braided channels may narrow more than channels that were narrow to begin with, such as channels within canyons or meandering channels. The process of channel narrowing includes establishment of pioneer riparian vegetation on the former channel bed (Friedman et al. 1998). For example, construction of Flaming Gorge Reservoir for power production on the Green River eliminated the flood peak in most years, greatly reducing the opportunity for cottonwood establishment. Almost all cottonwood reproduction since dam construction at Browns Park, downstream of Flaming Gorge Dam, occurred in 1984 and 1986, when large reservoir inflows

necessitated large flow releases at the time of cottonwood seed dispersal (Cooper et al. 2003). In addition, the decreases in peak flows along the Green River have allowed establishment of pioneer riparian species, primarily tamarisk, on the channel bed, resulting in channel narrowing and development of a tamarisk forest. Between Flaming Gorge Dam and the Yampa River confluence this process has decreased channel width by 10-30% (Grams and Schmidt 2005).

Decreases in early summer flows can reduce growth and survival of cottonwood forest

In arid and semi-arid regions riparian cottonwood growth is limited by water availability, which is often driven by flow during the growth period in spring and early summer (Meko et al. 2015). Along the Green and Yampa rivers, annual ring width of Fremont cottonwood is strongly correlated with flow (Schook et al. 2016a), and survival is decreased during periods of low flow (Andersen 2015). By decreasing early summer flows, flow regulation may decrease growth and kill trees. For example, construction of Flaming Gorge Reservoir on the Green River killed hundreds of cottonwoods at Browns Park and caused a reduction in growth of surviving trees that continued at least through 2011 (Andersen 2016, Schook et al. 2016a). Decrease in survival and growth appears to have resulted from the acute decrease in peak and mean annual flows during reservoir filling in the early 1960s (Schook et al. 2016a), the reduction in surface moisture caused by reduced overbank flooding since dam construction (Reily and Johnson 1982) and the reduction of flow during the growing season (Meko et al. 2015, Schook et al. 2016b). Since 1992, changes in reservoir operation to mimic a natural flow regime have resulted in increased cottonwood growth at Browns Park, but growth rates continue to be lower than those at Deerlodge Park (Andersen 2016). In Island Park, downstream of the confluence with the Yampa River, the change to the annual hydrograph has been less severe than at Browns Park, and dam effects on cottonwood growth were not detected (Schook et al. 2016a).

Bed degradation can reduce growth and survival of cottonwood forest

Variation in sediment load in relation to sediment transport capacity can lead to changes in river bed elevation in alluvial reaches, resulting in changes in floodplain water-table depth. For example, along the Mojave River, California, flooding in 1993 caused channel incision, lowering the water table, and causing mortality of riparian cottonwood trees (Scott et al. 2000). Water-table declines of 1.5 m or more killed 58-93% of trees. Where the water-table decline was less than 1 m, stand mortality was 7-13%. In a study with plains cottonwood in eastern Colorado water-table declines of more than 1 m caused 88% mortality, while declines of about 0.5 m reduced branch growth, but had no measurable effect on survival, stem growth or live crown volume (Scott et al. 1999). Such changes in bed elevation are more likely in alluvial reaches, where channel bed elevation is not controlled by bedrock. The susceptibility of riparian trees to desiccation by bed degradation is greater if the water-table depth was formerly shallow and stable, a situation that deters formation of deep roots (Scott et al. 1999).

Successful and widespread recruitment of box elder along the Yampa River in DINO is dependent on relatively infrequent high peak flows

Because of the energy stored in its large seeds, and because of the shade tolerance of saplings and adults, box elder can become established in the presence of leaf litter and pre-existing vegetation (DeWine and Cooper 2008, 2010). Therefore, unlike the other three dominant species, box elder is not dependent upon flood disturbance for establishment. In fact, box elder commonly germinates and

survives when a flood irrigates but does not physically disturb an older surface where seeds may have accumulated over multiple years. Although box elder does not require flood disturbance, its establishment high on the floodplain is limited by moisture from flooding. This limitation is demonstrated by the strong temporal relation between box elder establishment and flood years on the Green and Yampa rivers (DeWine and Cooper 2007), the reduction in box elder forest area and height above base flow following flow regulation on the Green River but not on the less regulated Yampa River (DeWine and Cooper 2007), and the fact that irrigation strongly promotes survival of box elder seedlings (DeWine and Cooper 2010).

Large floods are strongly associated with recruitment of box-elder forest in Yampa Canyon and in Whirlpool and Lodore canyons along the Green River, and dam-related decreases in flood peaks on the Green River have reduced box-elder recruitment (DeWine and Cooper 2007). In Yampa Canyon, all of 41 juvenile to young adult box elder stems dating to between 1964 and 2004 became established in years with peak annual flows higher than the 1964-2004 mean of 394 m^3/s (13,900 ft^3/s), and 71% of these stems were established during the year of the peak flow of record, 915 m^3/s (32,300 ft^3/s) in 1984 (DeWine and Cooper 2007). In Lodore Canyon on the Green River 89% of 37 sampled stems dated to 1983, 1984, 1986 and 1997, 4 of the 5 highest annual peaks between 1963 and 2000. Failure of box elder recruitment in the second-highest flow year (1999) may have been caused by desiccation related to rapid flow decline following the peak (DeWine and Cooper 2007). In Whirlpool Canyon all of 24 stems were established in years of peak flow higher than the post-dam (1964-2004) mean of 495 m^3/s (17,500 ft^3/s) and 75% were established in years with peak flows above 600 m^3/s (21,200 ft^3/s). Decreases in peak flows caused by construction of Flaming Gorge Reservoir on the Green River are associated with decreased regeneration of box elder forest at Whirlpool and Lodore canyons. The ratio of post-dam/pre-dam box elder forest areas was 0.51 in the lightly regulated Yampa Canyon, 0.41 in the moderately regulated Whirlpool Canyon, and 0.09 in the heavily regulated Lodore Canyon (DeWine and Cooper 2007). The lower values at Whirlpool and especially Lodore Canyons suggest that flow regulation has decreased box elder establishment at these two sites relative to Yampa Canyon. Box elder establishment elevations relative to the base flow water surface did not differ between sites for trees established before flow regulation (Yampa= 3.9 m, Whirlpool = 3.9 m, Lodore = 3.8 m) but differed strongly for trees established after flow regulation on the Green River (Yampa = 3.1 m, Whirlpool = 2.5 m, Lodore = 1.8 m; DeWine and Cooper 2007). The relatively low recent values for Whirlpool and Lodore Canyons indicate that flow regulation has decreased flood stages and box elder establishment heights at these sites relative to Yampa Canyon. In summary, the decrease in peak flows caused by Flaming Gorge Reservoir has caused reduced establishment of box elder at higher elevations on the floodplain and increased box elder establishment closer to the channel. Because the area of new habitat near the channel is limited, the overall effect is a decrease in establishment. Flow regulation has also promoted channelward encroachment of box elder on the floodplain of the Gunnison River in Black Canyon of the Gunnison National Park (Friedman and Auble 1999).

Two or more years in a row with similar flows promote establishment of woody vegetation, and subsequent sediment deposition around this vegetation can lead to channel narrowing

Seedlings of tamarisk and cottonwood are susceptible to removal in subsequent years by desiccation due to low flows or inundation and disturbance due to high flows. Establishment elevation in the first year determines the susceptibility to desiccation or inundation in the second year. Seedlings established high on the bank in a high-flow year will die from desiccation if flow is much lower in year two. Conversely, seedlings established low on the bank in a low-flow year will die from inundation or disturbance if the peak is larger in year two. Thus flow variability between years helps to maintain a wide channel and sparsely vegetated floodplain. In contrast, sequences of years with similar flows promote establishment of woody plants, mostly tamarisk in canyons (Manners et al. 2014) and both tamarisk and cottonwood in parks (Cooper et al. 2003). Once established the vegetation promotes sediment deposition and channel narrowing. Defining wet and dry years as years with total runoff greater than the 75th percentile or less than the 25th percentile, Manners et al. (2014) found a strong increase since 1976 in the tendency for wet years to follow wet years and dry years to follow dry years in the Yampa River. They argue that this increase in interannual flow autocorrelation is responsible for the expansion of tamarisk in wide sections of Yampa Canyon since the mid-1980s and subsequent channel narrowing. A similar sequence of events has occurred at Deerlodge Park, except that the new vegetation is dominated by both cottonwood and tamarisk (Merritt and Cooper 2000, Cooper et al. 2003). These changes in vegetation and channel width have occurred in the absence of changes in mean annual flow peak or volume (Manners et al. 2014).

Discretization of flows can produce shelving of geomorphic surfaces and enhanced banding of riparian vegetation

Discretization occurs when the sequence of stream flows has a dramatically greater than natural tendency to take on a relatively small number of fixed or discrete values such as a power plant capacity or a fixed minimum flow. A multi-year tendency to return to exactly the same flow values can be expected to have unnatural effects on channel geomorphology and thus riparian vegetation. There are multiple causes of stream flow discretization including fixed capacities of engineering structures and the operational advantages of working with fixed values of volume and discharge – even when trying to incorporate understanding of environmental effects of streamflow in a framework of specific flow prescriptions. The direction of expected effects of discretization is towards a more discrete banding of geomorphic surfaces and topography (e.g., a more pronounced "shelving" of the bank at specific flow lines) and more discrete distribution and density of riparian vegetation (Rood et al 2010). Some of these effects may persist through sequences of higher flow that are not competent to completely rework the topography and vegetation of the bottomland.

Variation in sediment load in relation to sediment transport capacity can affect channel migration rate, influencing establishment of riparian woody vegetation

Especially in alluvial reaches, imbalance between sediment supply and transport capacity can affect channel change rates. Such imbalances may be especially strong when water and sediment come from different parts of the watershed. For example, about 69 percent of the sediment in the Yampa River at Deerlodge Park comes from the Little Snake River, while 73 percent of the water at Deerlodge Park comes from the Yampa River watershed upstream of the confluence with the Little

Snake River (Andrews 1980, Schmidt and Manners in review). A large change in sediment input from the Little Snake River or flow from the Yampa River can lead to channel changes, especially in alluvial reaches like Deerlodge Park, where bed elevation is not controlled by bedrock and lateral migration is relatively unconstrained. Sediment delivery from the Little Snake River is episodic and controlled by floods in low-elevation tributaries, especially Sand Creek (Topping et al. in review). Sand yield from the Little Snake Basin has decreased since the last major tributary floods in the 1960s (Topping et al. in review). This decrease in sand supply could be causing local bed degradation, contributing to observed narrowing of the Yampa River since the 1980s (Manners et al. 2014, Merritt and Cooper 2000). The occurrence of such bed degradation has not been documented, however. At a longer time scale, there is evidence that the arroyo cycle that affected dryland streams throughout the Southwest (Cooke and Reeves 1976), including the nearby White River Watershed (Womack and Schumm 1977), caused increased sediment delivery from the low-elevation part of the Little Snake Watershed from about 1880 through the 1960s (Andrews 1978, Parker et al. 1985). Increased delivery of sand to Deerlodge Park could have partially filled the channel at times, leading to increased channel migration and cottonwood establishment, a hypothesis that is supported by the observation by Andersen (2015) that much of the floodplain at Deerlodge Park is occupied by cottonwood cohorts established in 1929, 1947 and 1952.

Reduction in peak flows related to climate change could allow encroachment of tamarisk and other vegetation and associated channel narrowing

Higher temperatures in the Colorado River Basin associated with climate change are increasing evaporation, causing lower annual flood peaks and flow volumes (Udall and Overpeck 2017). This trend may be exacerbated in the future by increased water withdrawals caused by increased drought and increasing human population. Decreased flood peaks should promote encroachment of vegetation, especially tamarisk and associated sediment deposition and channel narrowing. Higher temperatures would increase desiccation stress on the floodplain, which would promote tamarisk. Increases in temperature are also causing earlier snowmelt and are expected to cause earlier seed release as well (Perry et al. 2012). Because seed release is controlled by both temperature (which shifts with global change) and photoperiod (which does not shift), the change in timing of seed release may not be as strong as that in flow timing (Perry et al. 2012). The result could be earlier timing of peak flows relative to seed release, which would be expected to benefit cottonwood relative to tamarisk.

Conclusions

The Yampa River is the last remaining large river in the Colorado River system that still exhibits the hallmarks of a natural system: large flow variability within and between years resulting in rapid channel movement, sparse vegetation near the channel and abundant opportunities for establishment of disturbance-dependent species. Channel and vegetation changes along the nearby Green River since construction of Flaming Gorge Dam illustrate the potential effects of future flow regulation on the Yampa River. Storage of snowmelt in reservoirs would decrease peak flows, decreasing channel migration and the establishment of flood dependent species like box elder and cottonwood. Decreased flood disturbance would promote channel-ward encroachment of vegetation including invasive tamarisk, leading to sediment deposition around vegetation and channel narrowing. Delays in peak flows related to reservoir storage would favor late-flowering tamarisk. Increases in base flows would decrease desiccation stress on the floodplain, further increasing floodplain vegetation density, leading to replacement of disturbance-dependent species by competitors. Adjacent to the channel, similar stable base flows year after year would promote development of marsh vegetation tolerant of extended inundation, including native sandbar willow. Because most of the water in the Yampa River below Deerlodge Park comes from the upper Yampa, while most of the sediment comes from the lower Little Snake Basin, changes in water management in either Basin could influence the balance between water and sediment downstream of the confluence of the Yampa and Little Snake Rivers. An ongoing multi-decadal decrease in sediment output of the Little Snake Basin (Topping et al. in review) may be contributing to modest tamarisk encroachment and channel narrowing along the Yampa River. Finally, decreases in peak flows resulting from climate change could also contribute to vegetation encroachment and channel narrowing.

Research Needs

Two research directions could improve flow management of floodplain vegetation along the Yampa River.

First, improve quantification of the relation between flow and change in vegetation and channel geometry in order to facilitate inclusion of vegetation considerations in water management decisions.

1) Establish permanent vegetation plots with known inundating discharge, so that observed changes in vegetation can be precisely tied to the inundation gradient. Annual sampling of these plots would allow attribution of vegetation changes at the selected locations to specific flow events. Number, size and location of plots must be adequate to quantify changes in species of special interest, including not only tamarisk, but also native *Salix exigua* and invasive *Phragmites australis*, which appear to be expanding rapidly in recent decades (Tamara Naumann, personal communication).

2) Annually collect high resolution satellite imagery of the Yampa River from Maybell to the confluence with the Green River to enable attribution of landscape-level vegetation and channel change to specific flow events.

Second, improve understanding of the effect of time lags in sediment transport on vegetation dynamics and channel geometry in the Yampa River System. Ongoing detailed sediment measurements within the Yampa River system suggest that present sand load and channel geometry of the Yampa River are strongly influenced by floods that supplied sediment from tributaries to the Little Snake River many decades ago (Topping et al. in review). To be able to predict how future changes in flow and sediment supply will affect channel geometry and vegetation, we need to understand the ongoing influence of past events and associated time lags.

3) Use aerial photography, satellite imagery and the first detailed map of the site (U.S. Geological Survey 1922) to reconstruct the history of channel change at Deerlodge Park. Then test the hypothesis that the rate of channel movement was high from 1922 to 1938, the date of the first aerial photography, in response to sediment delivered as a result of arroyo cutting in the Little Snake Basin. Collect current and historic channel elevation data from the Little Snake Basin to test the hypothesis that arroyo cutting and filling has occurred there.

4) Core 100 randomly selected trees at Deerlodge Park to determine approximate ages. Then calculate the distribution of forest area as a function of age. Use these data to test the hypothesis that most of the forest dates to the early 1900s, when sediment from the Little Snake River may have caused rapid channel migration in Deerlodge Park.

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Appendix A

Species Occurrence Data

This appendix provides a clickable link in IRMA to the species occurrence data analyzed in Section "Patterns of Overall Plant Species Occurrence along the Yampa River" beginning on page 5 of this report.

Plant Species Occurrence by Plot

Natural Resource Stewardship and Science

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