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RESPONSES OF OBLIGATE VERSUS FACULTATIVE RIPARIAN SHRUBS FOLLOWING RIVER DAMMING

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ABSTRACT

Riparian or streamside woodlands include obligate riparian trees and shrubs (obligates) that are restricted to streamside zones, and facultative riparian species that are abundant in, but not restricted to the riparian areas. Due to their distinctive life history requirements, it may be predicted that the ecological specialist obligates would be more vulnerable than the facultative generalists to impacts from river damming and flow regulation. We tested this along the Snake River through Hells Canyon, USA, where two native riparian shrubs dominate: the obligate sandbar willow (*Salix exigua*), and the facultative, netleaf hackberry (*Celtis reticulata*). We assessed riparian conditions over the past century by comparing ground-level and aerial photographs taken after 1907 and in the 1950s in advance of three dams, versus recent conditions. These comparisons revealed three changes downstream from the dams: (1) the depletion of surface sands and sandbars and (2) reductions in sandbar willow versus (3) the proliferation of hackberry in dense bands above the typical high-water line. The willow decline probably resulted from the depletion of sand following sediment trapping by the reservoirs, combined with changes in the seasonal water flow pattern. The increase in hackberry may have resulted from a beneficial 'irrigation effect' of daily water releases for power generation during the summer. The opposing responses reflect the plants' differing life histories and may partially resolve impacts of river regulation on alluvial sediments versus the instream flow pattern. We consider other riparian studies that suggest that obligates such as cottonwoods (*Populus angustifolia*, *P. deltoides* and *P. fremontii*) are highly vulnerable to river regulation, while facultative trees and shrubs such as trembling aspen (*Populus tremuloides*), wolf-willow (*Elaeagnus commutata*) and velvet mesquite (*Prosopis velutina*) are more resilient. These results suggest that conservation of riparian woodlands should emphasize the ecological specialist obligates, while facultative species may be less vulnerable to river regulation. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: *Celtis reticulata*; hackberry; riparian ecology; instream flow needs; river damming; *Salix exigua*; Snake River; willow

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INTRODUCTION

Riparian or streamside woodlands represent biologically rich interfaces between rivers and terrestrial ecosystems (Naiman *et al.*, 2005). Riparian woodlands such as floodplain forests are generally vulnerable to river regulation but there are considerable differences in sensitivities of different trees and shrubs (Auble *et al.*, 1994; Johnson *et al.*, 1995; Jansson *et al.*, 2000). Ecological studies of riparian plant species have been undertaken in an attempt to recognize patterns of vulnerability and this understanding could assist in managing river flows for environmental conservation (Shafroth *et al.*, 1998; Dixon and Johnson, 1999; Nilsson and Svedmark, 2002; Shafroth *et al.*, 2002; Auble *et al.*, 2005).

A primary categorization of riparian plants considers their distribution, and obligate riparian plants or 'obligates' are ecological specialists that are restricted to the streamside zones. Ecological specialists typically display distinctive adaptations which provide a high degree of benefit but over a narrow range of conditions (Feinsinger *et al.*, 1981; Futuyma and Moreno, 1988; Wilson and Yoshimura, 1994), and riparian obligates may have traits such as restricted intervals of seed release and viability, narrow substrate requirements for successful colonization, and particular flood and drought tolerances (Krasny *et al.*, 1988; Karrenberg *et al.*, 2002; Rood *et al.*, 2003a). In

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contrast, ecological generalists display less specific adaptations that are beneficial over a broader niche range. Facultative riparian plants are ecological generalists that are often abundant in riparian areas, but are also typically sparsely distributed in adjacent upland zones and can thus grow and reproduce in either riparian or upland environments.

Of the riparian plants, the woody shrubs and trees are especially important with respect to ecological services including sediment and bank stabilization, the assimilation of nutrients and other pollutants and the provision of wildlife habitats (Naiman *et al*., 2005). Woody plants are consequently of high priority for riparian conservation (Richter and Richter, 2000; Rood *et al*., 2005a). Both obligate and facultative species occur in most areas and this provides an opportunity to compare consequences of ecological specialization. In comparing patterns across diverse taxa, McKinney and Lockwood (1999) conclude that many ecological generalists, such as some invasive weeds, are often more resilient than specialists and may even thrive following human alteration. From this pattern it would be predicted that riparian obligates would be more vulnerable to river damming and flow regulation than facultative plants.

We recognized an ideal study opportunity with the Snake River through Hells Canyon (Schmidt *et al*., 1995; Braatne *et al*., 2008). This is a physically dramatic riverscape in a narrow, deep V-valley cut through basalt bedrock (Vallier, 1998). With very hot and dry summers (hence, 'Hells Canyon'), relatively few plant species occur and this simplifies ecological comparison. Within the narrow riparian bands, two native woody plants predominate: the obligate shrub, sandbar willow (*Salix exigua*), and the facultative shrub or small tree, netleaf hackberry (*Celtis reticulata*).

Since native riverine organisms are generally adapted to the natural flow and disturbance regimes (Poff *et al*., 1997; Shafroth *et al*., 2002; Rood *et al*., 2007), we predicted that there would be negative impacts of river regulation on most native woody riparian plants in Hells Canyon. We further anticipated that the specialist, sandbar willow, would be particularly vulnerable to human alteration, possibly due to more specific hydrogeomorphic requirements, the demands for particular patterns of water and sediment substrate (Karrenberg *et al*., 2002; Rood *et al*., 2003a; Dixon and Turner, 2006). In contrast, due to a broader niche range, we predicted that the generalist, netleaf hackberry, would be more robust relative to the environmental alteration.

We further sought to understand the underlying basis for the responses of these two shrubs and analysed river hydrology and considered alluvial sediments (Kondolf, 1997). We thus considered a general prediction relative to the ecological specialization and vulnerability of riparian shrubs to river regulation, and then considered possible explanations for differing responses of the two shrubs.

METHODS

Study system

The Snake River through Hells Canyon defines the border between Oregon and Washington, and Idaho, USA (Figure 1, Braatne *et al*., 2008). Here, the Snake River has a fairly steep gradient and was developed for hydroelectric power generation with the implementation of three large dams, Brownlee, Oxbow and Hells Canyon, in 1958, 1961 and 1967, respectively. These are collectively managed as the Hells Canyon Complex (HCC). Below the HCC, Hells Canyon provides a relatively inaccessible landscape and this has limited other human impacts. Instream flows are almost entirely determined by water release from the HCC since contributions from local streams are minor above the Imnaha and Salmon River inflows (Figure 1).

Through Hells Canyon, riparian vegetation is limited to narrow bands flanking the river and the two native woody plants that predominate are very different with respect to ecological specialization. The obligate sandbar willow, *S. exigua* Nuttall (also ' coyote' or 'narrowleaf' willow; syn. *S. interior* Rowlee), is common along streams throughout western North America and is restricted to low elevation streamside zones (Krasny *et al*., 1988; Ottenbreit and Staniforth, 1992; Friedman *et al*., 2006; Dixon and Turner, 2006). In contrast, the generalist netleaf hackberry (*C. reticulata* Torr.; syn. *Celtis laevigata* Willd.) is abundant in higher riparian zones and also occurs extensively but sparsely in the upland (Debolt and McCune, 1995; Salzer *et al*., 1996). The designations of sandbar willow as an obligate and of hackberry as a facultative species are consistent with regional designations relative to wetland occurrence (US-FWS, 1996).

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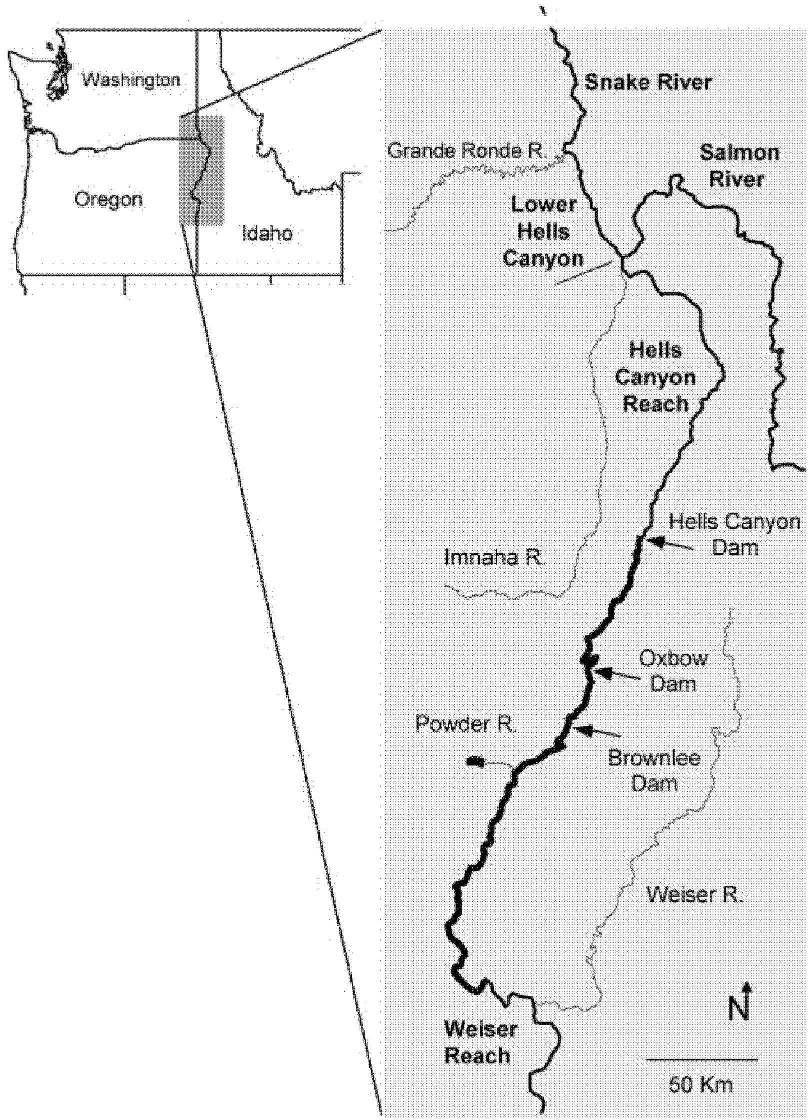

Figure 1. Map of the reaches and dams along the Snake River through Hells Canyon. Modified from Braatne *et al.* 2008.

Photograph comparisons

To investigate changes in these shrubs following damming, we obtained the General Land Office (GLO) survey records from the 1870s to 1935 for the Idaho portion through Hells Canyon. We also searched regional archives for ground-level photographs taken in Hells Canyon prior to the HCC. Photographs were sought that had sharp clarity, and we avoided locations with apparent human impacts such near homes or ranches. Suitable photographs provided comparison points that were relocated and re-photographed during river floats in the summers of 1998 through 2000. This provided comparative photograph pairs with the original photograph representing the pre-HCC conditions and the contemporary photograph revealing conditions after four decades of operation of the HCC. This research strategy was similar to that undertaken for the Colorado River through Grand Canyon by Webb (1996) and represents a temporal comparison of pre- versus post-project conditions (Underwood, 1994, Braatne *et al.*, 2008).

The black and white photographs were digitally scanned at 300 dots per inch to provide resolutions similar to those of the contemporary digital photographs, which were viewed as grey-scale images for consistency. The pairs

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were viewed on computer monitors, allowing adjustment of image brightness, contrast and size. After initial qualitative comparison, we rated the changes in the extents of: (1) exposed surface sands that occurred as sand bars and as interstitial sands between cobbles, (2) sandbar willow and (3) netleaf hackberry. For each photograph pair where each feature existed, we three authors independently rated the apparent post-dam change as decrease (−) or increase (+). If our initial interpretations were not unanimous, we reassessed the pair, until unanimous assessments were reached. This provided the response for each photograph pair, and the probabilities of patterns across the multiple pairs were investigated with binomial probabilities (i.e. the probability of 5 of 5 comparisons showing a decrease $= (\frac{1}{2})^5$).

For each photograph point, we obtained aerial photograph pairs from the United States Department of Agriculture Aerial Photographic Records office, Salt Lake, UT, with one in the pre-dam period (typically August 1955, black and white) and a contemporary match (typically August 1997, true colour). Aerial photograph scales ranged from 1:6000 to 1:20 000.

Hydrology

River discharges (Q, flow rate) from Snake River hydrometric gauges were obtained from the United States Geological Survey (USGS) water website (http://water.usgs.gov/) and from Idaho Power Company for flow releases from the Hells Canyon Dam, the final dam in the HCC. We analysed mean annual (Q_a), annual maximum mean daily (Q_{max}), monthly (Q_{Month}) and mean daily (Q_d) values and annual hydrographs for the periods of verified record, generally from 1911 to 2005. Q_d values were averaged over three, 11-year intervals to compare flow regimes from 1911 to 1921 ('natural' = prior to the major dams upstream of the HCC), 1946 to 1956 ('pre-HCC' = after upstream damming but prior to the HCC) and 1990 to 2000 ('post-HCC', after implementation of the HCC). To reveal the summer diurnal pattern, 15-min interval Q data ($Q_i = Q$ 'instantaneous') were accessed from the USGS 'near real-time' data for 2006. Statistical analyses with Microsoft Excel (Redmond, WA) and JMP (SAS, Cary, NC) investigated historic trends through regression (Rood *et al*., 2005b).

RESULTS

Comparative photograph pairs

We located 240 photographs that displayed the Snake River above and through Hells Canyon, prior to the HCC. Photographs were particularly located at the Washington State University, the Idaho Historical Society, Lewis and Clark State College, the Nez Perce County Historical Society and Idaho Power Company (Blair *et al*., 2002). Many photographs focussed on people and some were situated at home-sites or other altered locations, and riparian zones were visible in the backgrounds, providing supplemental information about the pre-HCC conditions. Thirty-one historic photographs provided views that were suitable for the photograph comparison points, with sufficient focus and contrast to reveal the riparian substrate and shrubs, and limited human impact.

Twelve of the 31 photograph points occurred along the unimpounded Hells Canyon reach of the Snake River, between the Hells Canyon Dam and the Salmon River inflow (Figure 1). Three of these photograph pairs are presented in Figure 2 and interpretations for all 12 pairs are provided in Table I, along with information from the land survey records. For reference, all 31 photographs and pairs are presented in Blair *et al*. (2002).

Six, five and six of the photograph points showed sites that were inundated or impacted by Brownlee, Oxbow and Hells Canyon dams and reservoirs, respectively. One pre-dam photograph is provided for each reservoir in Figure 3 and information for all reservoir sites is provided in Table II. The river valley becomes progressively more confined downstream and the landscape inundated by the Oxbow and Hells Canyon reservoirs closely resembled the reach downstream from the HCC (Figure 3).

Three photograph points represented sites between Weiser and Brownlee Reservoir, the upper HCC reservoir. These revealed an alluvial reach with a broad valley and physical landscape that was very different from that through Hells Canyon (Braatne *et al*., 2008). The archival photographs were from 1902 and 1908 and displayed sand-covered banks and abundant sandbar willow and hackberry. In contrast, by 1999, these sites were dominated

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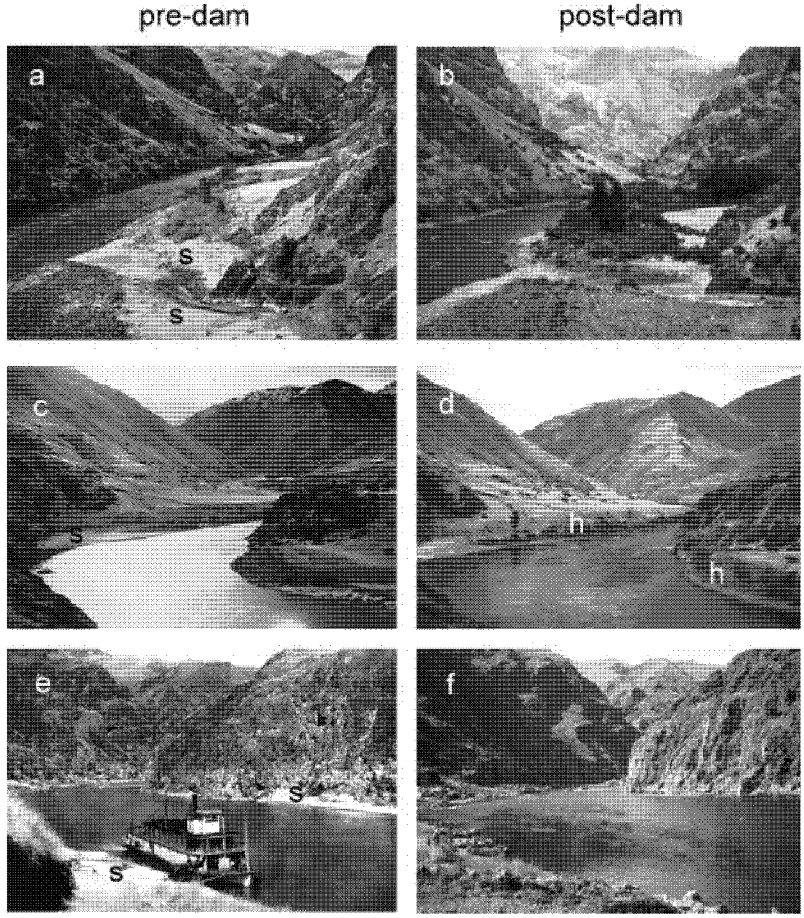

Figure 2. Three ground-level photograph comparisons for sites SR-3 (top, a and b, sites described in Table I), SR-4 (middle, c and d) and SR-11 (bottom, e and f) along the Hells Canyon reach of the Snake River, showing pre-dam versus post-dam conditions. The 's' indicates sand and the 'h' indicates hackberry. Photos a and c—1955 by F.R. McCormick; b, d and f—1999, J. Braatne; e—1903, John Miller Collections, Nez Perce Historical Society.

by exotic woody plants including salt-cedar (*Tamarix* spp.), Russian olive (*Elaeagnus angustifolia*) and European willows (*Salix alba* and other species).

Physical conditions

The photograph pairs consistently indicated minimal change in the physical landscape (Figure 2). Channel and bank positions and conditions were apparently constant, reflecting the dominant erosion-resistant bedrock. Large boulders were often conspicuous and some recognizable boulders were relocated.

In the pre-HCC photographs for sites along the downstream reach and between the reservoirs, surface sands were abundant (Tables I and II, Figures 2 and 3). In contrast, these same positions were often covered by cobbles in 1999 through 2003 (Figure 2). In the pre-dam condition, surface sands were conspicuous in bars such as along the inside of meanders and in protected sites, and also in relatively exposed sites (such as in Figure 2E, right-side).

The depletion of surface sands along the downstream Hells Canyon reach provided the most conspicuous difference between the historic ground-level photographs and recent conditions (Table I). This depletion was also apparent in the comparisons of pre- versus post-HCC aerial photographs (Figure 4) that reinforced the prior analyses by Schmidt *et al.* (1995) and thus is not further presented here.

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Table I. Descriptions of sites along the Hells Canyon reach of Snake River (SR) from General Land Office (GLO) Surveys and comparisons of historic and recent photographs

Photo point	Location (year of historic photo)	GLO Records	Surface features		Vegetation		Change		
			Historic photo	Current photo	Historic photo	Current photo	Sand	Willow	Hackberry
SR-1	Deep Ck RM247 (1951)[1]	Willow, buckbrush scattered pine/fir (1935)	Fines, bedrock, sandbars	Cobble and bedrock[2]	Scattered pine and hackberry	Scattered pine and hackberry	o	o	o
SR-2	Saddle creek RM 236 (1934)	Willow, maple[3] with scattered pine/fir (1910)	Alluvial fan with fine to cobble	Alluvial fan with fine to cobble	Hackberry with sparse cover along Saddle Ck	Hackberry with diverse riparian vegetation along Saddle Ck	−	o	+
SR-3	Johnson bar RM230 (1953)		Fines to bedrock	Cobble to bedrock	Scattered pine and hackberry	Extension of hackberry with increased foliage	−	−	+
SR-4	Sheep creek RM229.5 (1953)		Rocky rapids with sands to cobble	Rocky rapids with cobble	Scattered pine and hackberry	Expansion and growth of hackberry	−	−	+
SR-5	Pine bar RM 227.5 (1930s)		Large sandbar deposit	Highly-eroded sandbar	Scattered pine with extensive willow	Scattered pine, some hackberry, no willow	−	−	o
SR-6	Pittsburg landing RM 215 (1928)	Willow, maple[2] with scattered pine/fir (1901-04)	Bedrock to cobble	Bedrock to cobble	Scattered hackberry	Scattered hackberry	−	o	+
SR-7	Pittsburg landing RM 214.5 (1953)		Fines to cobble banks	Cobble banks	Fringe of hackberry	Expanded fringe of hackberry	−	−	+
SR-8	Getty creek RM 206 (1928)	Bedrock to cobble slopes	Bedrock to cobble slopes	Sparse upland vegetation	Sparse upland vegetation	o	o	+	
SR-9	Ragtown bar RM 205 (1928)		Cobble slopes	cobble slopes	Scattered hackberry	scattered hackberry	−	o	+
SR-10	Dug bar RM 196.5 (1928)	Cliffs, ravines, basalt ledges, no timber (1906)	Basalt cliffs/talus slopes	Basalt cliffs/talus slopes	Scattered hackberry	Scattered hackberry	−	o	+
SR-11	Eureka bar RM 191.5 (1903)	No timber/ no other notes	Rocky slopes with large and small sandbars	Remnant sandbar	Willow along sandbar fringe	Altered willow patch	−	−	o
SR-12	Above Salmon R. RM188.5 (1928)		Steep rocky slopes	Steep rocky slopes	Minimal riparian vegetation	Minimal riparian vegetation	o	o	o
	Total (binomial p)						9/9–($p = 0.002$)	5/5–($P = 0.039$)	8/8 + ($p = 0.004$)

Three photograph pairs are presented in Figure 2 and all pairs are displayed in Blair *et al.* (2002). Apparent changes in surface sand, sandbar willow and netleaf hackberry were assessed in photograph pairs as decrease (−) or increase (+). These features were absent or insufficient for assessment (o) at some sites.

[1]RM = river mile.

[2]There was some construction alteration at this site.

[3]Maple' in the GLO record very probably refers to hackberry, which has a similar leaf shape.

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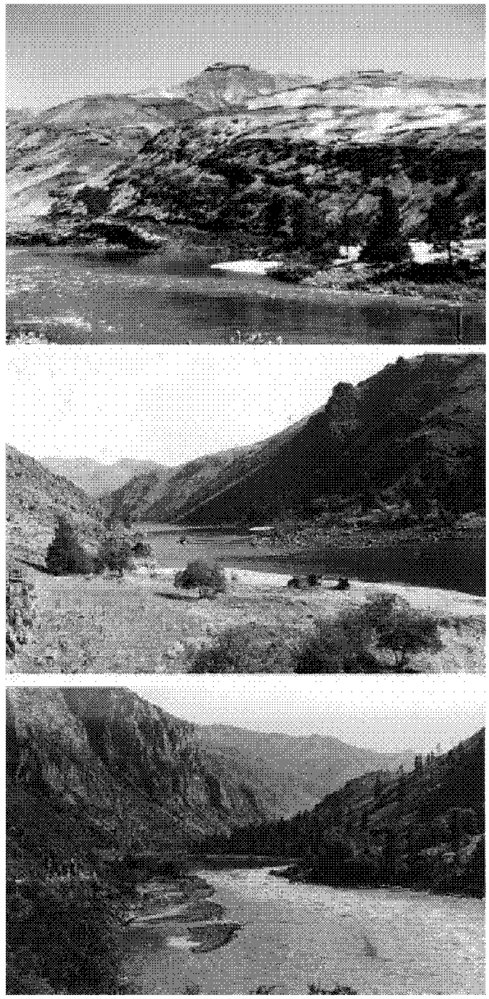

Figure 3. Historic photographs of zones inundated by the Hells Canyon Complex of dams and reservoirs showing typical conditions with common sandbars and sandbar willow: (a) Brownlee Dam site, 1953 (BR-6, Table II); (b) Oxbow Dam site, 1953 (OX-1); (c) Kinney Creek Rapids, 1953 (HC-5) (a and b by F.R. McCormick, c by P. Basche).

Willow versus hackberry

Two changes in woody vegetation were consistently indicated in the comparative pairs and in comparisons of the survey records and observations of the 240 total historic photographs, versus field observations and photographs along the river valley in 1999 through 2003 (Table I and Figure 2). Sandbar willow was consistently the first-listed plant in the GLO surveys, indicating prominent occurrence from 1901 through 1935 (Table I). Due to its light, pubescent, narrow leaves, the shrub was less conspicuous in some of the pre-dam photographs but in photographs with sharper resolution and closer views, the prevalence of sandbar willow prior to damming was confirmed (Tables I and II and Figures 2 and 3). In each of the five cases in which formal comparison was possible, there was a considerable reduction in sandbar willow in the post-HCC photograph (Table I). Confirming the early abundance of sandbar willow through Hells Canyon, it was present in 15 of the 16 photographs of the riparian zones upstream of, or inundated by the HCC reservoirs (Table II).

The comparisons also indicated a second change in woody riparian vegetation after damming, an apparent increase of netleaf hackberry (Table I and Figure 2). In both the pre- and post-dam photographs, hackberry occurred sparsely in the upland zones (Figures 2 and 3). Hackberry was consistently more abundant in the riparian zones, and

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Table II. Riparian conditions in historic photographs of sites along the Snake River upstream from Hells Canyon (Weiser, WR) and through Hells Canyon in sites that were inundated by Brownlee (BR), Oxbow (OX) or Hells Canyon (HC) reservoir

Site	Location	Year	Sand	Willow	Hackberry
WR-1	Weiser bridge	1908	+	+	+
WR-2	Westlake island ferry	1908	+	+	+
WR-3	Farewell bend	1902	+	+	+
BR-1	Burnt river bridge	1899	++	+	—
BR-2	Morgan creek	1952	+	++	+
BR-3	Hibbard creek	1950's	—	+	—
BR-4	Soda creek	1952	+	+	—
BR-5	Powder river	1956	+++	+	+
BR-6	Brownlee dam	1953	++	++	—
OX-1	Oxbow dam	1953	++	+	+
OX-2a	Scorpion creek	1953	++	?	?
OX-2b	Scorpion creek	1953	++	-	+
OX-3a	Oxbow tip	1953	+	?	+
OX-3b	Oxbow tip	1953	+	?	+
HC-1	Hells Canyon park	1950	—	+	—
HC-2	Ballard bridge	1953	—	++	-
HC-3	McGraw creek	1953	+	+	+
HC-4	Spring creek	1953	—	+	+
HC-5	Kinney creek rapids	1953	+	+	+
HC-6	Eagle bar landing	1953	—	?	?
Total			14/19+	15/16+	12/18+

Three photographs are presented in Figure 3 and all photographs are displayed in Blair *et al.* (2002). From the photographs, surface sand, sandbar willow and netleaf hackberry were assessed as absent (—), present (+), abundant (++) or profuse (+++). A few photographs were taken from points high above the river producing ambiguity relative to shrub occurrence (?) and these were excluded from Totals.

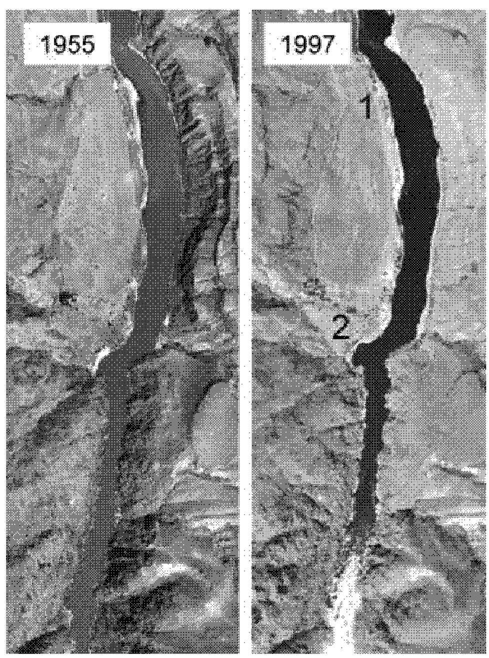

Figure 4. Pairs of aerial photographs from 1955 (left) versus 1997 (right) for the Snake River through Hells Canyon along Dug Bar (SR-10) showing the depletion of sand bars along a gradual meander lobe (1) and in a protected cove (2).

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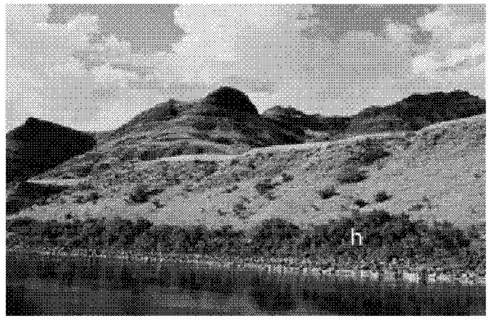

Figure 5. The typical, dense band of hackberry (h) above the mean annual high water line along the Snake River in Hells Canyon (September 1999, near SR-6, S.B. Rood).

following damming the shrub occurred in dense and relatively continuous bands near the typical high water line (Figures 2 and 5). Bands were often particularly dense on steep banks such as along those sloping down from the extensive terraces formed by the massive Bonneville floods (Vallier, 1998, Figure 5). During the 1999–2003 field observations, the dense hackberry bands were conspicuous along the length of the Snake River through the Hells Canyon reach and the increase was even apparent in some of the aerial photographs.

Historic hydrology

Despite the considerable upstream water diversions for agricultural irrigation (Parkinson *et al.*, 2003), total annual discharge of the Snake River through Hells Canyon did not dramatically decline through the past century ($r = 0.058$, ns; Figure 6). After about 1960 the annual discharge has been highly variable, and there was an increase in the frequency of low-flow years in recent decades ($Q_a < 350\ m^3\ s^{-1}$ (the low flow in the pre-dam interval); 4 years from 1911 to 1960 vs. 12 years from 1961 to 2005, $\chi^2 = 4.9$, $p < 0.05$).

The spring peak is important for seedling recruitment of riparian *Salicaceae* (Scott *et al.*, 1996, Mahoney and Rood, 1998; Karrenberg *et al.*, 2002; Dixon and Turner, 2006) and while daily maximum flows did not change consistently over the past century (Figure 7), the broad spring peak was progressively attenuated (Figure 8). Major

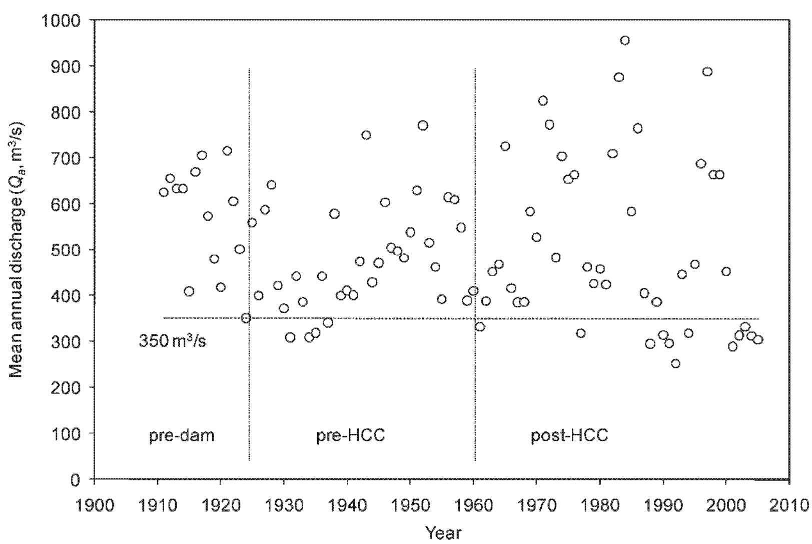

Figure 6. Mean annual discharge (Q_a) of the Snake River at Weiser, Idaho (1910–2004) before (pre-HCC) and after (post-HCC) the implementation of the Hells Canyon Complex (HCC) of three hydroelectric dams. To simplify comparison, a dashed line represents $350\ m^3\ s^{-1}$, the approximate pre-dam low flow.

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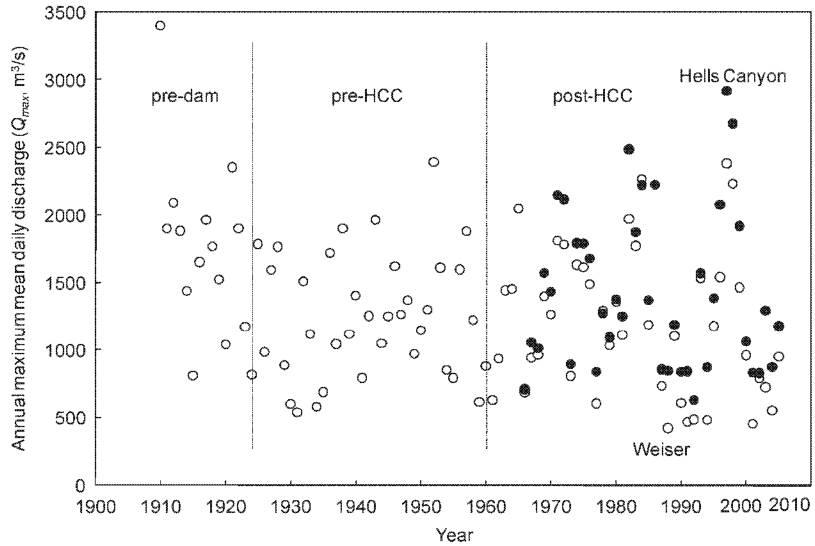

Figure 7. Annual maximum mean daily discharges (Q_{max}) of the Snake River at Weiser (o), Idaho and in Hells Canyon (●).

changes occurred after the upstream dams were implemented (Figure 8B) and further attenuation has followed (Figure 8C). The attenuation was largely due to increased regulation upstream since the daily and spring peaks were generally similar upstream and downstream of the HCC (Figures 7 and 8).

While the spring peak has been attenuated, the subsequent post-peak recession has persisted (prior to Julian Day 200, Figure 8). Low flows continued to occur in late summer, and flows often increased with autumn rains. The combination of rain and snowmelt increased flows through the winter to the next spring peak, and the HCC has slightly altered this seasonal component (Figure 8).

In contrast to the reduction of spring flows, late summer flows were elevated following the early damming of the Snake River (Figure 9). Prior to the implementation of the major Snake River dams, August discharge averaged about 200 $m^3 s^{-1}$ (Figure 9). From 1925 to 1960, during the period of damming and increasing regulation upstream of the HCC, the August discharge progressively increased to about 350 $m^3 s^{-1}$ (Figure 9). After 1960, the hydrologic record reflects extensive variation in the late summer flows (Figures 8 and 9).

Although river flow data are often represented and archived as daily mean discharges, hydroelectric dams are generally operated with diurnal flow pulsing as has occurred for the HCC (Figure 10). The pulsing shown for August 2006 was typical for the low flow period of mid- to late summer (Figure 8). As shown, the daily flow varied 2.2-fold, from about 250–550 $m^3 s^{-1}$ (Figure 10). This daily flow pulsing would elevate the river stage for a few hours in most days.

DISCUSSION

This study provided a pre- versus post-damming temporal comparison, one of the most obvious approaches to assess ecological impacts from river damming (Braatne *et al.*, 2008). This study approach is often hindered by the lack of pre-dam data and the comparison of photograph pairs is somewhat qualitative and may thus reveal the direction of change, but not detailed aspects relating to the magnitude or timing.

Our observation of the depletion of surface sands is consistent with the well-established sediment-trapping by large reservoirs (Schmidt *et al.*, 1995, Kondolf, 1997). The depletion of sand bars through Hells Canyon was previously described by Schmidt *et al.*, (1995), following analyses of aerial photographs. With respect to this depletion of alluvial sediments, 48 upstream dams along the Snake River and its tributaries would have severed the

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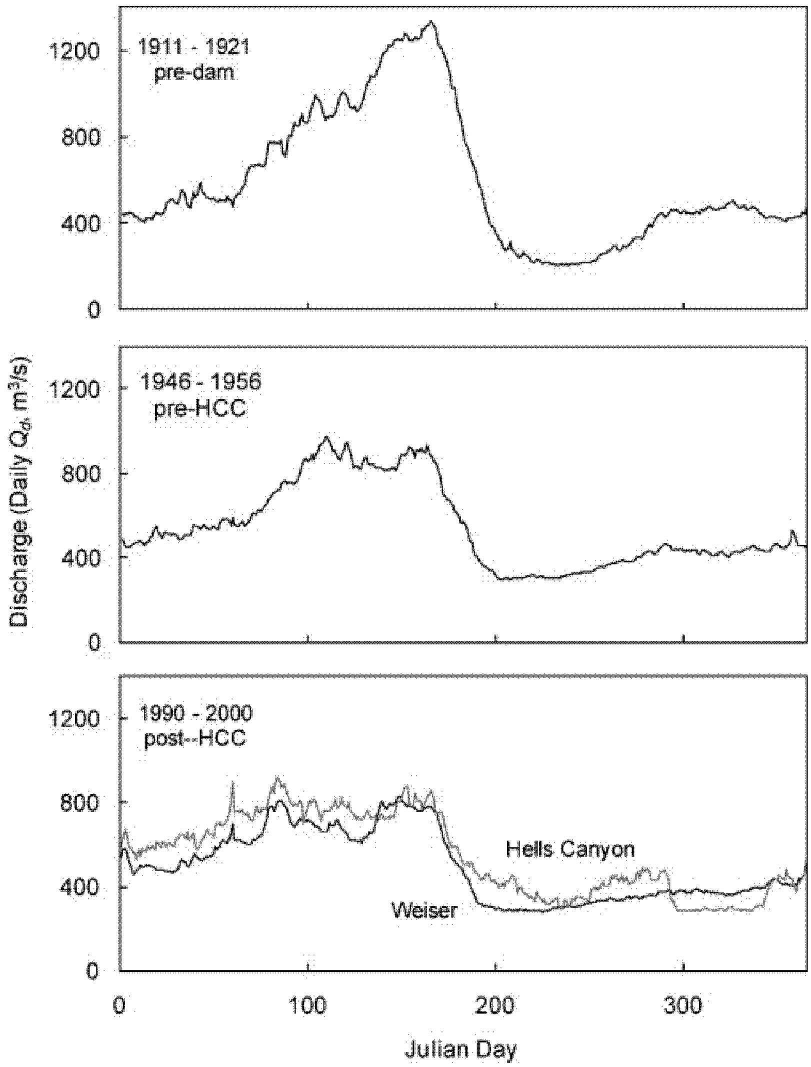

Figure 8. Seasonal daily mean discharge (Q_d) for Snake River at Weiser, Idaho, for intervals prior to major dams ('natural', 1911–1921), and before and after the implementation of the Hells Canyon Complex (HCC). Flows through Hells Canyon are also indicated in the post-HCC interval.

supply of sands from those upstream watersheds and contributed to the depletion, in addition to the local impacts from the HCC (Parkinson *et al.*, 2003).

The second apparent change was the depletion of sandbar willow and prior studies have revealed reductions in this obligate riparian shrub following damming of other rivers (Lesica and Miles, 1999; Rood *et al.*, 2003b). This shrub is often associated with sandbars and is commonly very abundant around the sandbar margins, while the central portions of sandbars are generally barren of vegetation. This distribution may reflect the additional stability around the margins due to cobbles and boulders that provide a secure substrate and prevent uprooting of the willow with flood flows that suspend sands.

The decline of sandbar willow through Hells Canyon probably results at least partly from the depletion of sands. The loss of sands would reduce the moisture-retention capacity and capillarity of the riparian substrate (Mahoney and Rood, 1998; Amlin and Rood, 2002). Subsequent drought stress would have been increased during the more frequent, low-flow years (Figure 6). Changes in the seasonal streamflow pattern could degrade conditions relative to

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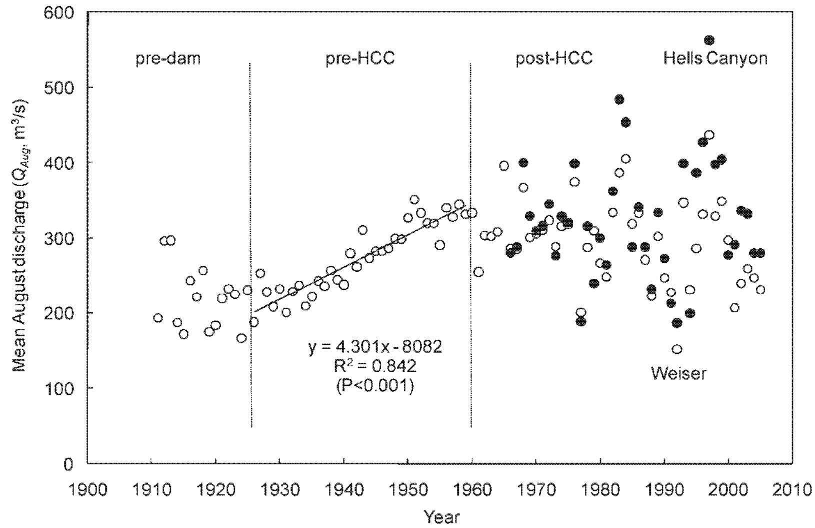

Figure 9. Mean discharge in August of the Snake River at Weiser, Idaho and in Hells Canyon after the implementation of the Hells Canyon Complex (HCC) of three hydroelectric dams. A linear regression is fit to the intermediate interval since these data appeared to display a linear trend.

seedling recruitment while consequences on clonal expansion could be different, and even beneficial (Krasny *et al.*, 1988; Ottenbreit and Staniforth, 1992; Shafroth *et al.*, 1998; Amlin and Rood, 2002; Dixon and Turner, 2006). Sandbar willow is probably tolerant of, and dependent upon, the natural flow and disturbance regimes (Ottenbreit and Staniforth, 1992; Karrenberg *et al.*, 2002; Dixon and Turner, 2006; Rood *et al.*, 2007) and changes due to river regulation would degrade conditions for this riparian obligate.

Our third observation was unexpected and most novel, the apparent proliferation of hackberry in dense bands above the typical high-water line. Like sandbar willow, hackberry can establish through seedlings or expand through clonal root suckers but it is adapted to a broader environmental range than sandbar willow (Debolt and

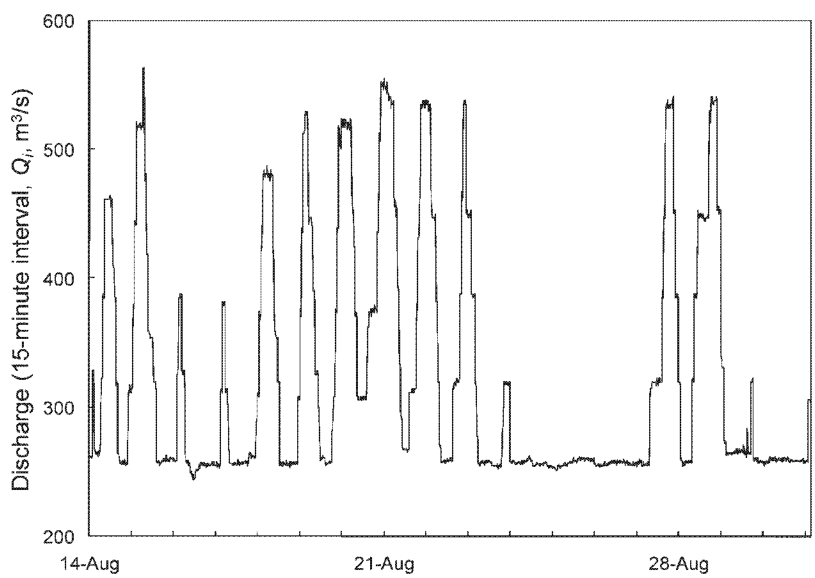

Figure 10. Discharge averaged over 15-min intervals of the Snake River in Hells Canyon, from 14 August to 1 September 2006, showing diurnal variation associated with hydroelectric power generation.

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McCune, 1995; Salzer *et al.*, 1996). As a facultative riparian plant, hackberry is more drought-tolerant and less dependent upon the natural instream flow and fluvial disturbance regimes. We had anticipated that due to alteration away from the natural conditions, both the obligate and facultative riparian shrubs would be diminished following river regulation. In contrast, hackberry apparently increased following damming.

The increase in hackberry may result partly from reduced competition due to the decline of sandbar willow and also possibly as a result of release from prior sheep grazing pressure (Wissmar *et al.*, 1994; Parkinson *et al.*, 2003). We also believe that a substantial benefit originated from the supplemental moisture provided by the diurnal flow pulsing associated with hydroelectric power generation. Due to this diurnal pulsing, the adjacent riparian fringe would be saturated and following some groundwater infiltration, the root zone would remain moist for some interval thereafter. We thus believe that the daily peak of $550\,m^3\,s^{-1}$ rather the daily mean discharge would probably be more relevant for hackberry growth (Figure 8, Stromberg *et al.*, 1993; Springer *et al.*, 1999; Rood *et al.*, 2003a).

With diurnal flow pulsing, the root-zone below the hackberry band would receive supplemental moisture through the stressful, hot and dry summer interval. This could act somewhat like the periodic sub-irrigation in a hydroponic greenhouse operation, in which a coarse substrate is saturated by elevating the water level for a daily interval. We characterize this as a beneficial 'irrigation effect' that probably contributes to the proliferation of hackberry. Consistent with this interpretation, there were generally dense but narrow bands of hackberry above the typical high-water line (Figure 5), a distribution that differed somewhat from the more dispersed natural pattern (Figure 2, for example 2C vs. 2D).

It might be expected that the irrigation effect would also benefit sandbar willow but we observed that the dense bands were consistently dominated by hackberry (Figure 5). Sandbar willow is an ecological pioneer that requires barren sites for colonization and expansion, and is probably a poor competitor with established vegetation (Krasny *et al.*, 1988; Ottenbreit and Staniforth, 1992; Dixon and Turner, 2006).

The proliferation of hackberry is notable as an increase in the abundance of a native, woody riparian plant, following river regulation. There are prior reports of increases in riparian trees and shrubs following damming and these cases have often reflected expansion into zones in which natural flooding would have previously excluded colonization (Johnson, 1994; Friedman *et al.*, 1998; Shafroth *et al.*, 2002). With the increase in hackberry through Hells Canyon there would be a corresponding increase in wildlife habitat. We observed that spiders and webs were very abundant in the hackberry band, and this might suggest an abundant invertebrate community. In Hells Canyon, hackberry also provides dense nesting habitat for many birds and especially neotropical migrants, and these and other wildlife species are likely to benefit from the hackberry band (Blair *et al.*, 2002).

Our results from the photograph comparisons also provide direction for further field study. We would thus encourage quantitative assessments of riparian surface sediments and vegetation, and particularly sandbar willow and hackberry, above, through and below Hells Canyon. We would also recommend similar analyses along the adjacent lower gorge of the free-flowing Salmon River, to provide a complementary spatial comparison (Braatne *et al.*, 2008).

Ecological specialization and vulnerability of other riparian plants

Following the opposing responses of sandbar willow versus hackberry, a further question follows, 'Is the association between ecological specialization and vulnerability typical for other riparian shrubs and trees?' Possibly the most extensively studied riparian plants are cottonwoods, *Populus* species that often comprise dominant trees in riparian woodlands around the Northern Hemisphere (Scott *et al.*, 1996; Shafroth *et al.*, 1998; Rood *et al.*, 2003b; Braatne *et al.*, 2007). The section *Aigeiros* prairie cottonwood, *Populus deltoides*, and Fremont cottonwood, *Populus fremontii*, occur as riparian obligates in the drier ecoregions of western North America, and are particularly sensitive to river damming. In contrast, the section *Tacamahaca*, 'balsam poplars', balsam poplar, *Populus balsamifera*, and black cottonwood, *Populus trichocarpa*, are facultative riparian trees that may be less vulnerable (Krasny *et al.*, 1988; Polzin and Rood, 2006). The narrowleaf cottonwood (*Populus angustifolia*) is somewhat intermediate between those two groups, with respect to ecological specialization and environmental vulnerability (Rood *et al.*, 2003a). Further extending the pattern, the trembling aspen, *Populus tremuloides*, is

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primarily an upland tree but is also a facultative riparian species and appears to be less responsive to river damming than cottonwoods.

The comparisons can also be made across genera. In many semi-arid regions of western North America, the facultative riparian shrub, wolf-willow, *Elaeagnus commutata*, displays distributions similar to hackberry, occurring sparsely in upland areas and more densely in the moister riparian zones. We have observed abundant wolf-willow in riparian zones downstream from dams, in areas where cottonwoods have declined, and quantitative analyses of this shrub would be worthwhile. Wolf-willow is related to Russian olive, *E. angustifolia*, an invasive, exotic tree that thrives along some regulated river reaches (Lesica and Miles, 1999; Pearce and Smith, 2000; Katz and Shafroth, 2003). Wolf-willow and Russian olive are facultative riparian species and their apparent abundance downstream of dams supports the pattern of reduced vulnerability of ecological generalists.

South of Hells Canyon, mesquites (*Prosopis* sp.) are abundant facultative riparian shrubs and trees. Different species occur, with velvet mesquite (*Prosopis velutina*) being well studied in riparian zones (Stromberg *et al.*, 1993). The velvet mesquite life history is partly coordinated with the natural flow regime, but it is probably less sensitive to flow alteration than the obligate riparian Fremont cottonwood that overlaps in distribution. This provides another comparison that supports the greater vulnerability of obligates.

With this association between ecological specialization and vulnerability to river regulation, we recommend that obligate riparian trees and shrubs would provide the appropriate focus for analyses of the ecological health of riparian woodlands. Due to their higher sensitivity, these species should be more diagnostic for scientific studies and for monitoring management practices intended for the conservation and restoration of floodplain forests (Richter and Richter, 2000; Rood *et al.*, 2005a). We further recommend that the niche breadth and degree of ecological specialization should be characterized across other riparian shrubs and trees, to identify candidate species for monitoring and conservation efforts in other ecoregions worldwide. For such characterization, hydrogeomorphic requirements would be defined, along with life history characteristics relative to seed and seedling development, and aspects of environmental adaptation such as flood and drought tolerance and nutrient requirements and adaptations.

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