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REGULATION LEADS TO INCREASES IN RIPARIAN VEGETATION, BUT NOT DIRECT ALLOCHTHONOUS INPUTS, ALONG THE COLORADO RIVER IN GRAND CANYON, ARIZONA[§]

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ABSTRACT

Dams and associated river regulation have led to the expansion of riparian vegetation, especially nonnative species, along downstream ecosystems. Nonnative saltcedar is one of the dominant riparian plants along virtually every major river system in the arid western United States, but allochthonous inputs have never been quantified along a segment of a large river that is dominated by saltcedar. We developed a novel method for estimating direct allochthonous inputs along the 387 km-long reach of the Colorado River downstream of Glen Canyon Dam that utilized a GIS vegetation map developed from aerial photographs, empirical and literature-derived litter production data for the dominant vegetation types, and virtual shorelines of annual peak discharge (566 $m^3 s^{-1}$ stage elevation). Using this method, we estimate that direct allochthonous inputs from riparian vegetation for the entire reach studied total 186 metric tons $year^{-1}$, which represents mean inputs of 470 gAFDM $m^{-1} year^{-1}$ of shoreline or 5.17 gAFDM $m^{-2} year^{-1}$ of river surface. These values are comparable to allochthonous inputs for other large rivers and systems that also have sparse riparian vegetation. Nonnative saltcedar represents a significant component of annual allochthonous inputs (36% of total direct inputs) in the Colorado River. We also estimated direct allochthonous inputs for 46.8 km of the Colorado River prior to closure of Glen Canyon Dam using a vegetation map that was developed from historical photographs. Regulation has led to significant increases in riparian vegetation (270–319% increase in cover, depending on stage elevation), but annual allochthonous inputs appear unaffected by regulation because of the lower flood peaks on the post-dam river. Published in 2010 by John Wiley & Sons, Ltd.

KEY WORDS: allochthonous, organic matter budget, river regulation, Glen Canyon Dam, Colorado River, Grand Canyon, remote sensing

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INTRODUCTION

The construction of dams and associated river regulation has had a dramatic impact on riparian vegetation throughout the world (Ligon *et al.*, 1995; Nilsson and Berggren, 2000). River regulation often reduces peak flood discharge, it alters geomorphic processes such as sediment transport and deposition, and it can reduce downstream discharge due to evaporative losses in reservoirs or because of upstream use, among other things (Ligon *et al.*, 1995). The effect that these changes in the physical template have on riparian vegetation varies depending on the geomorphic setting of the river (Scott *et al.*, 1996; Nilsson and Berggren, 2000). Riparian vegetation in narrow, canyon-bound systems, is restricted to high elevation terraces that are safe from disturbance (Scott *et al.*, 1996; DeWine and Cooper, 2007); regulation of canyon bound rivers, by reducing peak discharges, facilitates the expansion of riparian vegetation onto lower elevation fluvial surfaces (Turner and Karpiscak, 1980; DeWine and Cooper, 2007).

Nonnative species are often the dominant colonizers of riparian zones that have been altered by regulation (Planty-Tabacchi *et al.*, 1996; Nilsson and Berggren, 2000). Nonnative saltcedar (*Tamarix* spp.) dominates vast stretches of virtually every major river system in the western United States including the Colorado River and the Rio Grande (Friedman *et al.*, 2005) and river regulation appears to be a major factor contributing to its expansion (Stromberg *et al.*, 2007). Saltcedar is now the second most common woody species of riparian zones in the western United States based on normalized cover (Friedman *et al.*, 2005), occupying some 600 000 ha of habitat in the region (DiTomaso, 1998). A saltcedar habitat suitability map developed by Morisette *et al.* (2006) indicates there are still large areas of the United States that could potentially be colonized by saltcedar. Further, saltcedar appears to be frost-sensitive (Lesica and Miles, 2001) and its occurrence throughout the western United States is positively correlated with mean annual minimum temperatures (Friedman *et al.*, 2005); the distribution of saltcedar may expand northward and with altitude if winter temperatures warm due to global change (Friedman *et al.*, 2005).

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Nonliving organic carbon is an important energy input to most food webs, particularly streams and river (Allan and Castillo, 2007). In the study of streams and rivers, this detritus is referred to as organic matter and if it originates from outside the system (e.g. leaf litter falling into a river from riparian vegetation) it is termed allochthonous organic matter. In contrast, organic matter that originates from within the system is termed autochthonous (e.g. aquatic macrophytes or algae). Litter addition and exclusion experiments have shown that invertebrate biomass and production are tied to the quantity of allochthonous inputs (Richardson and Neill, 1991; Wallace *et al.*, 1997).

Allochthonous organic matter from riparian vegetation usually dominates the organic matter input budgets of small streams (Fisher and Likens, 1973; Benfield, 1997). Allochthonous organic matter can also dominate the input budget for large rivers (Meyer and Edwards, 1990; Howarth *et al.*, 1996; Benfield, 1997), but in large rivers it is typically derived from upstream reaches and tributaries, or extensive floodplains. The quantity of direct allochthonous inputs (those inputs that fall directly into the river, as opposed to lateral inputs, which can be wind-blown or enter the river during inundation of a large floodplain) for large rivers are usually minor relative to small streams because the channel is wider and the cover of riparian vegetation represents a small fraction of the river surface (Conners and Naiman, 1984). Nonetheless, no studies have quantified whether river regulation and subsequent vegetation expansion has altered allochthonous inputs from riparian vegetation. Further, allochthonous inputs from riparian vegetation have never been quantified for a large river system in the western United States that is dominated by saltcedar.

The Colorado River below Glen Canyon Dam is 6th order, confined by canyon walls and therefore lacks floodplains. Prior to regulation, the Colorado River was a highly turbid, sediment-rich river that was characterized by highly variable water temperatures (range ~0–30°C) and discharges (Topping *et al.*, 2003). Over the period 1921–1963, peak annual discharge was 2407 $m^3 s^{-1}$, and discharge decreased through late summer and fall to values as low as 28 $m^3 s^{-1}$ (Topping *et al.*, 2003). Annual sediment loads estimated to pass by the Lees Ferry gage (located 25 km downstream of Glen Canyon Dam) were 57 ± 3 million metric tons (Topping *et al.*, 2000) and allochthonous inputs of detritus from the upstream watershed were likely the dominant organic matter input of the pre-dam river (Woodbury, 1959). The invertebrate fauna was likely diverse and dominated by mayflies (Ephemeroptera), caddisflies (Trichoptera) and Diptera and included predatory stoneflies (Plecoptera) and Odonates (Haden *et al.*, 2003). The fish fauna was depauperate, but seven of the eight species that were native to the Colorado River mainstem were endemic (Minckley, 1991).

Pre-dam riparian vegetation was composed primarily of woody riparian species (Clover and Jotter, 1944; Turner and Karpiscak, 1980), including mesquite (*Prosopis glandulosa*), seepwillow (*Baccharis emoryi*), saltcedar (*Tamarix* spp.) and arrowweed (*Pluchea sericea*); these species were generally confined to terraces and habitats above the stage elevation of pre-dam floods. Wetland species such as coyote willow (*Salix exigua*), Goodings willow (*Salix goodingii*), cattail (*Tyhpa latifolia*) and common reed (*Phragmites australis*) were sparsely distributed along the river corridor in association with floodplain-type geomorphology that was relatively uncommon (Clover and Jotter, 1944; Webb *et al.*, 2002). Sparse vegetation below the stage elevation of average floods suggests that allochthonous inputs from riparian vegetation were probably low.

The closure of Glen Canyon Dam in 1963 dramatically altered the physical template of the Colorado River ecosystem (CRE) in the Grand Canyon. The hypolimnetic withdrawal from Lake Powell results in cold and relatively constant water temperatures (range 9–16°C; Voichick and Wright, 2007). From 1963 to 1991 annual peak discharge was typically 877 $m^3 s^{-1}$, which represents the power plant capacity of Glen Canyon Dam (Topping *et al.*, 2003); this is 36% of pre-dam average peak discharge and since 1992 peak annual discharge has averaged 566 $m^3 s^{-1}$. Annual sediment loads at Lees Ferry (Figure 1) are less than 1% of pre-dam values (0.24 ± 0.01 million metric tons) (Topping *et al.*, 2000). The invertebrate fauna is now dominated by nonnative taxa including the New Zealand mudsnail (*Potomopyrgus antipodarum*), amphipod crustaceans (*Gammarus lacustris*) and nearctic Dipterans (Blinn and Cole, 1991). Four of the eight species of fish native to the mainstem Colorado River are now locally extinct (Minckley, 1991).

Riparian vegetation expanded to lower stage elevations due to regulation (Turner and Karpiscak, 1980; Webb, 1996; Webb *et al.*, 2002); by 1973 the vegetated area below the annual pre-dam flood stage had increased by more than 50% (Waring, 1995) and saltcedar was the dominant colonizer (Figure 2; Turner and Karpiscak, 1980; Webb, 1996). The relatively stable post-dam hydrograph also promoted the expansion of fluvial wetlands throughout the river corridor (Stevens *et al.*, 1995). The riparian and wetland species that were previously restricted to uncommon floodplain habitats were able to colonize other types of low-velocity habitats including return channels and channel margins. Fine-grain sediment (silts and clays) accumulated in these areas and formed a lower plant habitat zone within the post-dam riparian community that was subject to daily inundation. The assemblage that established in this lower zone included native plants such as cattails and common reed, sedges (*Carex* sp.), rushes (*Juncus* sp.), bulrushes (*Schoenoplectus* sp.) and nonnative plants such as bentgrass (*Agrostis stolonifera*), rabbitfoot grass (*Polypogon monospeliensis*) and common plantain (*Plantago major*).

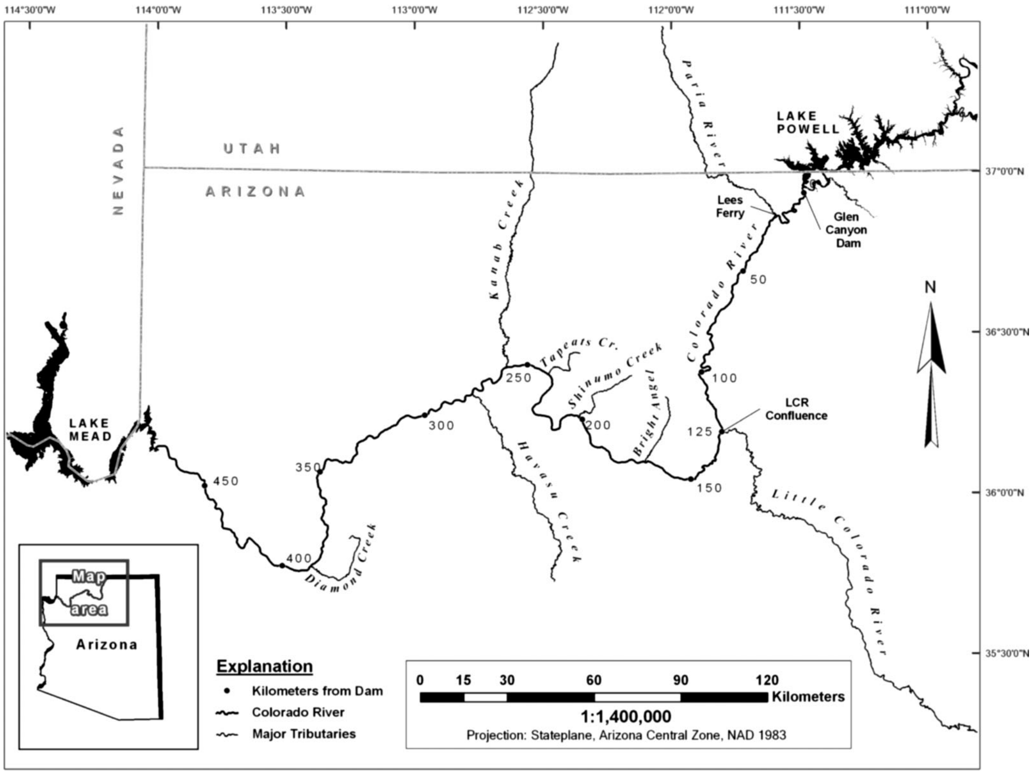

Figure 1. Geographic extent of study area showing major canyon tributaries. Our study reach was from just below Glen Canyon Dam to the confluence of the Colorado River and Diamond Creek, near river kilometre 400

River regulation and associated reduced flood frequency have resulted in the development of three well-defined vegetation zones: (1) an active riparian zone of shoreline habitats below the 877 $m^3 s^{-1}$ stage that includes plants occupying the annual flood zone; (2) post-dam riparian habitats below the 1416 $m^3 s^{-1}$ stage; (3) pre-dam riparian habitats above that (Figure 3; Carothers and Aitchison, 1976). Post-dam riparian zones are dominated by saltcedar while pre-dam riparian zones are dominated by mesquite, acacia and desert shrubs. Changes in riparian vegetation and flood magnitude and frequency may have altered allochthonous inputs to the CRE. The purpose of this study was to (1) quantify allochthonous inputs from riparian vegetation along a large regulated river system that is also dominated by saltcedar, a widespread nonnative plant along regulated rivers; (2) determine whether Glen Canyon Dam has affected the quantity of direct allochthonous inputs for the CRE through its effects on riparian vegetation or annual flood volumes.

METHODS

Study site

The segment of the Colorado River that we studied runs from just below Glen Canyon Dam to Diamond Creek, a distance of 387 river kilometres (Figure 1). Elevation decreases 521 m from Lees Ferry (elevation 947 m) to Diamond Creek (elevation 426 m), with an average gradient of 0.0013 $m\,m^{-1}$. Along this segment the river channel passes through 12 geomorphic reaches (Schmidt and Graf, 1990) that vary in width and depth because of differences in the underlying bedrock.

Vegetative area and biomass

The cover of riparian vegetation was determined using a GIS vegetation base map for the CRE (Ralston *et al.*, 2008) developed from colour-infrared digital imagery taken in May 2002, so our analysis of post-dam allochthonous inputs is for 2002 (Figure 4a and b). These images have a resolution of 22 cm. Six vegetation classes for the vegetation map were identified using two-way species indicator analysis (Hill, 1979): (1) wetland grasses and sedges (e.g. *Typha latifolia* and *Ph. australis*), (2) saltcedar (*Tamarix* spp.), (3) riparian shrubs (e.g. *Baccharis* spp. and *S. exigua*), (4) arrowweed (*Pl. sericea*), (5) sparse desert shrubs and grasses (e.g. *Gutierrezia sarothrae* and *Sporobolus contractus*) and (6) mesquite-acacia (*Pr. glandulosa* and *Acacia gregii*). Some vegetation classes were defined by a single dominant taxon (e.g. saltcedar), while others were defined by co-dominant taxa that had similar cover values (e.g. mesquite-acacia). Because automated mapping accuracies for these classes

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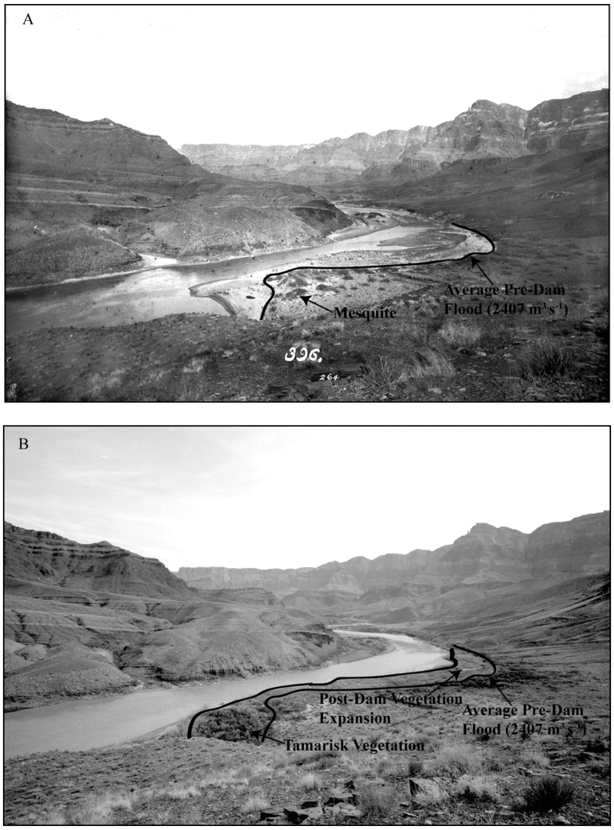

Figure 2. Repeat photographs of the Cardenas Creek area of the Colorado River, located 139 river kilometres below Glen Canyon Dam. Panel (A) was taken in 1890 (R. Stanton, #396, National Archives and Records Administration), with the stage elevation of the average pre-dam flood highlighted. Panel (B) shows the same location in 1993 (T. Wise, Stake 1440, USGS Desert Laboratory Repeat Photography Collection) and shoreward expansion of vegetation due to regulation is evident. Modified from Webb (1996)

were less than 70%, we used the relative cover of each vegetation class among geomorphic reaches, as determined by ground-truthing, to develop our estimates of allochthonous inputs (see below). Ground-truthing was completed for 10% of the study area and included portions of each geomorphic reach.

Using ArcMap (©ESRI 2005 v.9.1), the vegetation coverage was intersected with a virtual shoreline that represented a stage elevation of $566\,m^3\,s^{-1}$ (annual peak discharge at the time of this study) and $227\,m^3\,s^{-1}$ (stage elevation of river when aerial photographs were taken) to determine both the total area below the $566\,m^3\,s^{-1}$ stage elevation and total vegetative cover below $566\,m^3\,s^{-1}$ (Figure 4b). Virtual shorelines (227 and $566\,m^3\,s^{-1}$) were produced by coupling a stage-discharge model for the Colorado River to a digital elevation model for the entire river corridor (Magirl *et al.*, 2008). Although the accuracy of the virtual shorelines was not assessed, the stage-discharge model that was used to develop the virtual shorelines had an average error of 23% at a discharge of $227\,m^3\,s^{-1}$ and 11% at a discharge of $566\,m^3\,s^{-1}$ based on comparisons of predicted and measured stage at 45 sites distributed throughout the canyon (Magirl *et al.*, 2008).

Average channel widths, which was used as the denominator when determining the quantity of allochthonous inputs per square metre of river surface, were determined for the $566\,m^3\,s^{-1}$ stage elevation using ArcMap.

Allochthonous inputs

Direct allochthonous inputs to the CRE are from herbaceous vegetation growing below the $566\,m^3\,s^{-1}$ stage elevation and perennial vegetation growing below, or

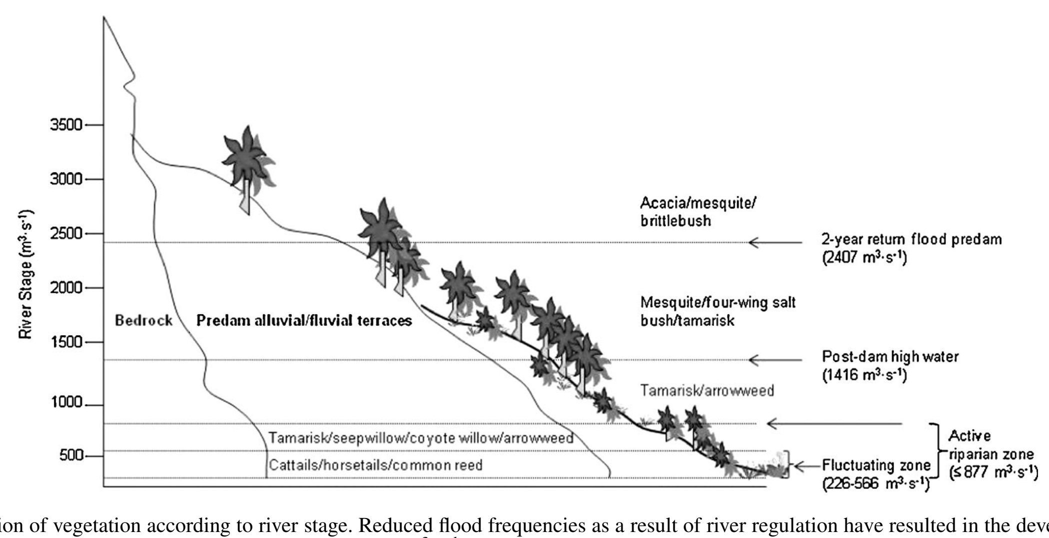

Figure 3. Zonation of vegetation according to river stage. Reduced flood frequencies as a result of river regulation have resulted in the development of three well-defined vegetation zones: Shoreline habitats below the $877\,m^3\,s^{-1}$ stage, post-dam riparian habitats ('new high water zone') below the $1416\,m^3\,s^{-1}$ stage, and pre-dam riparian habitats ('old high water zone') above that. After Carothers and Aitchison (1976). Post-dam habitat is dominated by tamarisk, while pre-dam habitat was dominated by mesquite, acacia and other desert shrubs

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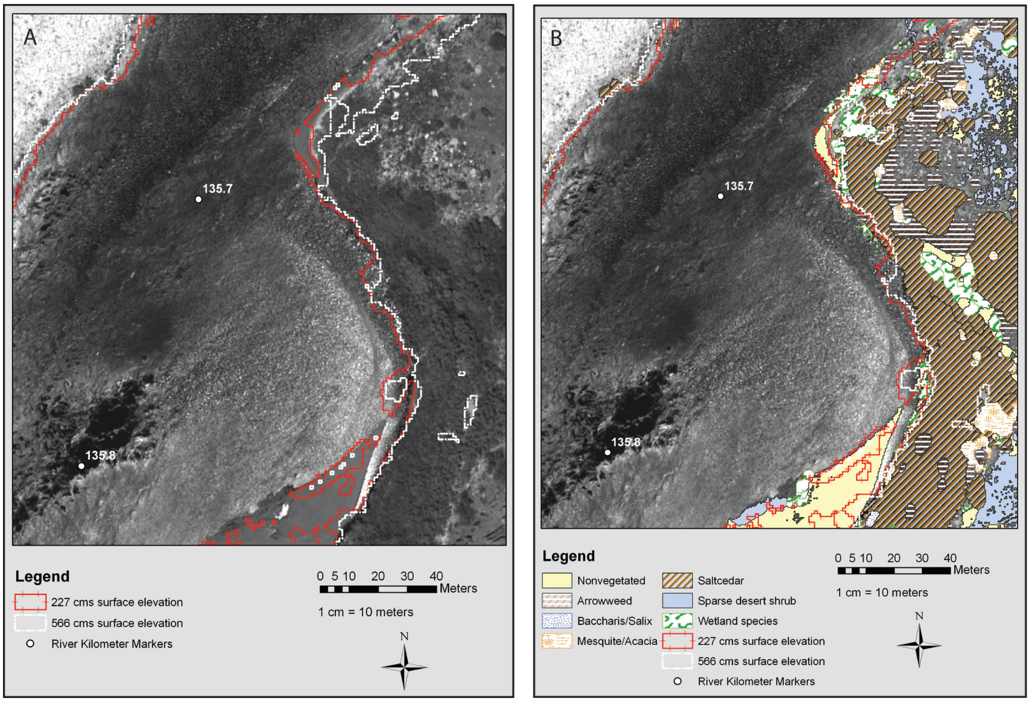

Figure 4. Aerial photographs of the Colorado River and its riparian vegetation around river kilometre 135.7 (A) and the corresponding GIS vegetation coverage (B). Direct allochthonous inputs along the Colorado River come from the vegetation that is between the 227 $m^3 s^{-1}$ (red line) and the 566 $m^3 s^{-1}$ (white line) virtual shorelines

overhanging, the 566 $m^3 s^{-1}$ stage elevation. To quantify allochthonous inputs from herbaceous vegetation (Wetland Grasses and Sedges vegetation type) we harvested above ground biomass at 44 sites throughout the study reach in October 2003, the time of annual peak biomass. At each site, vegetation was harvested from four 1 m^2 quadrats randomly placed below the 566 $m^3 s^{-1}$ stage elevation. Quadrats were located in areas selected for ground-truthing of the vegetation map. The wet-weight of harvested vegetation was measured in the field (Sartorius® Model EB6, Bradford, MA) and then a representative sub-sample of the harvested vegetation was taken and also weighed. Sub-samples were stored for the duration of the 2-week river trip in waterproof containers. At the conclusion of the river trip sub-samples were ashed for 2 h at 550°C and then reweighed. The wet-weight to ash-free dry mass (AFDM) relationship for the sub-sample was then used to determine the AFDM of the harvested vegetation samples.

Allochthonous inputs for the wetland vegetation type were estimated by multiplying the mean annual production estimate from our harvests with vegetation mapping data on the extent of this vegetation class below the 566 $m^3 s^{-1}$ surface elevation, assuming that 100% of this vegetation was captured by the river when daily peak discharge increased to 566 $m^3 s^{-1}$ in January–March 2004 (Figure 5). Stevens and others (1995) reported that marshes in the CRE contained minimal litter because daily fluctuating flows associated with hydropower production were effective at exporting it, which suggests that our above assumption is reasonable.

Litter production estimates for perennial vegetation were taken from published studies. Mean annual saltcedar litter production was taken from Kennedy and Hobbie (2004). We were unable to find published litter production estimates for the dominant species of the other vegetation classes, so we used the mean ‘Desert and Semi-Desert Scrub’ litter production value (90 g dry weight m^{-2} $year^{-1}$) in Whittaker

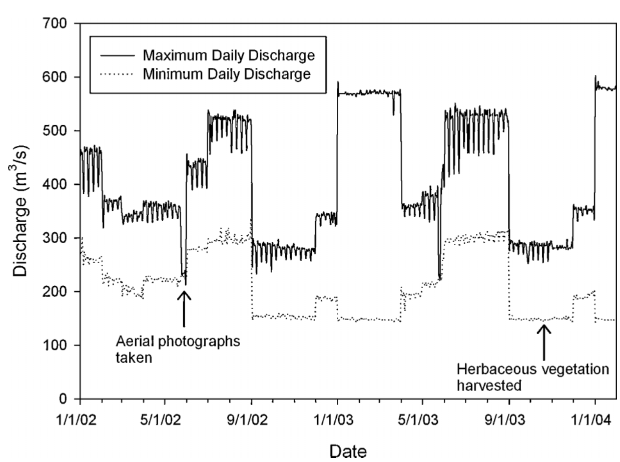

Figure 5. Maximum and minimum daily discharge at Lees Ferry, AZ (USGS gage number 09380000) from 1 January 2002 to 31 January 2004. Dates are reported as Day/Month/Year

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(1975). Kennedy and Hobbie (2004) report the percent ash of litter for three desert riparian plant species; we used the average of these values (AFDM is 85% of dry weight) to convert the Whittaker (1975) value to AFDM (i.e. 76.5 gAFDM m^{-2} $year^{-1}$). Allochthonous inputs from perennial vegetation were made in the same way as above for herbaceous vegetation – by intersecting the vegetation map with virtual shorelines and multiplying the resulting area estimate by annual production values. Ideally, we would have measured direct and lateral allochthonous litter inputs from deciduous vegetation by placing litter traps below the 566 $m^3 s^{-1}$ stage elevation. However, this was not possible because daily fluctuations in river stage associated with hydropower production that can exceed 2 m would have displaced the traps (see Figure 5). Litter traps also would have been an eyesore to the thousands of people that annually navigate the CRE on private and commercial rafting trips through Grand Canyon National Park.

There are several sources of uncertainty or error associated with our estimates of direct allochthonous inputs including: (1) the accuracy of virtual shorelines, (2) the accuracy of vegetative area measurements derived from aerial photographs, (3) the accuracy of relative cover of vegetation types as determined by ground truthing and (4) the accuracy of litter production values. Simultaneously accounting for all these sources of uncertainty would be extremely challenging. Regardless, we attempt to capture the effect that all these sources of uncertainty would have on the estimated allochthonous inputs by also computing allochthonous inputs using a broad range of litter production values: the 95% confidence interval of mean production for saltcedar (180–418 gAFDM m^{-2} $year^{-1}$) and wetland (190–323 gAFDM m^{-2} $year^{-1}$) vegetation classes and the full range of 'Desert and Semi-Desert Scrub' production values (9–213 gAFDM m^{-2} $year^{-1}$) presented in Whittaker (1975).

Pre-dam vegetation and allochthonous inputs

To determine whether regulation of the Colorado River has affected the cover of riparian vegetation we intersected a 1965 GIS vegetation coverage developed by Waring (1995) that encompasses portions of 5 geomorphic reaches and covers 46.8 km of river with the 566 and 2407 $m^3 s^{-1}$ virtual shorelines. We then repeated this procedure for the identical segments of the 2002 GIS coverage and compared the vegetated area estimates. The minimum plant size mapped by Waring (1995) was 4 m^2, so we present two values for vegetated cover in 2002 along these segments – one that includes all plants and one where plants <4 m^2 are excluded. To determine whether regulation has affected annual allochthonous inputs along the Colorado River, we multiplied the 1965 vegetated area estimates for the 2407 $m^3 s^{-1}$ stage elevation, which approximates the pre-dam annual return flood, by the mean and range of 'Desert and Semi-Desert Scrub' values from Whittaker (1975) – there is no quantitative information on cover by different species or vegetation types in the pre-dam river. We then compared these allochthonous input values with the 2002 estimates for these segments at a stage elevation of 566 $m^3 s^{-1}$, which represents annual peak discharge in the post-dam river. Although Glen Canyon Dam was completed in 1963, we feel 1965 can be used as a proxy for pre-dam conditions because it is unlikely vegetated area would have changed substantially in just 2 years and any new colonists would have probably been smaller than the minimum mapping unit of 4 m^2 after just 2 years of growth.

We also computed vegetated area and allochthonous inputs for this segment of the post-dam river during Controlled Floods that have occurred as part of the Glen Canyon Dam Adaptive Management Program (http://www.gcdamp.gov/, accessed April 7, 2010) by intersecting the 2002 vegetation map with the 1270 $m^3 s^{-1}$ virtual shoreline.

RESULTS

Allochthonous inputs

The production of the Wetland Grasses and Sedges vegetation type averaged 257 gAFDM m^{-2} $year^{-1}$ ($n = 174$, 95% CI = 190–324 gAFDM m^{-2} $year^{-1}$). Vegetation cover below the 566 $m^3 s^{-1}$ stage elevation averaged 17%. Wetland Grasses and Sedges was the most common vegetation type (mean relative cover of 55%), followed by saltcedar (mean relative cover of 36%; Table I). The four other vegetation types (riparian shrubs – 4.7%, arrowweed – 3.0%, sparse desert shrubs and grasses – 0.8% and mesquite-acacia – 0.1%) collectively represented 8.6% of the vegetated area below the 566 $m^3 s^{-1}$ stage elevation (Table I).

Total estimated litter inputs for the entire 387 km reach of river were 186 metric tons AFDM, 42% of which was saltcedar litter (Table I). Among all geomorphic reaches, allochthonous litter inputs averaged 470 gAFDM m^{-1} $year^{-1}$ of shoreline (range 320–653) or 5.17 gAFDM m^{-2} $year^{-1}$ of river surface (range 3.53–7.19; Table II).

Annual allochthonous inputs differed among geomorphic reaches with inputs per meter of shoreline being positively and significantly correlated with channel width (Spearman's $\rho = 0.7972$, $p = 0.0019$). Inputs for the three narrowest geomorphic reaches – Muav Gorge, Upper Granite Gorge and Supai – range from 145 to 240 gAFDM m^{-1} $year^{-1}$ of shoreline while the widest reaches – Glen Canyon, Lower Marble Canyon and the Lower Canyon – have inputs ranging from 527 to 1525 gAFDM m^{-1} $year^{-1}$ of shoreline (Table II).

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Table I. Vegetation types, mean relative cover (95% confidence interval), vegetated area, annual litter production and annual allochthonous inputs (range of potential inputs based on 95% CI or range for production values) for vegetation growing below the 566 $m^3 s^{-1}$ stage elevation along the 387 km-long segment of the Colorado River downstream of Glen Canyon Dam

Vegetation type	Relative cover (95% CI)	Vegetated area (m^2)	Mean annual litter production ($g m^{-2} year^{-1}$)	Mean annual allochthonous inputs (metric tons $year^{-1}$) (95% CI or range)
Wetland	55.4% (43.1–67.7)	4.00×10^5	257 (190–324)[a]	103 (76.0–130)
Saltcedar	36.0% (24.0–48.1)	2.61×10^5	299 (180–418)[b]	78.0 (47.0–109)
Other	8.58% (4.86–12.3)	6.19×10^4	76.5 (9–213)[c]	4.73 (0.557–13.2)
Total	100%	7.21×10^5		186 (124–253)

[a]Mean (95% CI), from this study.
[b]Mean (95% CI), from Kennedy and Hobbie (2004).
[c]Mean (range) of annual above-ground production for 'Desert and Semi-Desert Scrub', from Whittaker (1975).

Regulation of the Colorado River has led to substantial increases in riparian vegetation (Table III). For the 46.8 km of river that we have both pre- and post-dam vegetated area data, we found that vegetated area was 270% greater in 2002 relative to 1965 for a stage elevation of 566 $m^3 s^{-1}$ (79 223 m^2 vs. 29 408 m^2). For a stage elevation of 2407 $m^3 s^{-1}$, vegetated area in 2002 was 232% greater relative to 1965 (776 403 m^2 vs. 233 852 m^2).

The total vegetated area contributing to annual direct allochthonous inputs in 1965 (233 852 m^2 for 2407 $m^3 s^{-1}$ stage elevation) was considerably higher than 2002 (79 223 m^2 for 566 $m^3 s^{-1}$ stage elevation with plants <4 m^2 in size excluded). Multiplying the 1965 vegetated area estimate by the mean and range of production values from Whittaker (1975) yields mean inputs among the five geomorphic reaches of 382 gAFDM $m^{-1} year^{-1}$ (range 45–1064). Mean inputs among the same segments in 2002 were 434 gAFDM $m^{-1} year^{-1}$ (range 289–590) when plants <4 m^2 were excluded.

In 2002, mean relative cover below the 1270 $m^3 s^{-1}$ stage elevation was Saltcedar – 43.9%, Wetland Grasses and Sedges – 25.8% and the other four vegetation types (riparian shrubs – 6.4%, arrowweed – 13.7%, sparse desert shrubs and grasses – 8.0% and mesquite-acacia – 2.1%) collectively represented 30.2%. Using the mean and range of Desert and Semi-Desert Scrub production for all vegetation types except Saltcedar and Wetland yields estimated allochthonous inputs of 1437 gAFDM $m^{-1} year^{-1}$ (range 851–2158)

Table II. Reach length, channel width, total area, vegetated area, vegetation cover and annual allochthonous inputs for each geomorphic reach

Geomorphic reach	Reach length (km)	Channel width (m)	Total area (m^2)	Total veg. area (m^2)	Veg. cover (%)	Inputs	
						gAFDM $m^{-1} year^{-1}$	gAFDM $m^{-2} year^{-1}$
Glen Canyon	25.4	153.0	649 000	168 000	26	1700	11.1
Permian	16.7	111.2	170 000	29 400	17	452	4.07
Supai	18.2	70.8	119 000	21 400	18	301	4.26
Redwall	21.4	82.8	182 000	30 000	16	418	5.05
Lower Marble	41.2	111.6	428 000	147 000	34	918	8.23
Furnace Flats	25.6	122.5	531 000	44 500	8	446	3.64
Upper Granite Gorge	65.0	67.5	466 000	40 800	9	161	2.39
Aisles	12.4	85.2	118 000	11 900	10	247	2.90
Middle Granite Gorge	23.3	72.7	221 000	23 700	11	262	3.61
Muav Gorge	32.2	59.0	224 000	33 500	15	267	4.53
Lower Canyon	86.7	94.1	1 010 000	147 000	15	436	4.64
Lower Granite Gorge	19.4	84.1	159 000	23 100	15	306	3.64
Total	387.5		4.28×10^6	7.22×10^5			
Mean (range)		90.9			17	470 (320–653)	5.17 (3.53–7.19)

Mean allochthonous inputs per metre of shoreline and per square metre of river surface were calculated using mean litter production values (see Methods Section) and weighted by the length of reaches. We also present a range of mean allochthonous input values for the entire 387 km-long segment studied, in parentheses, that were calculated using the 95% confidence interval or range of litter production values for different vegetation types (see Methods Section).

Table III. Comparison of vegetated area and allochthonous inputs for the years 1965, which approximates pre-dam conditions, and 2002 for stage elevations 566 $m^3 s^{-1}$ (peak annual discharge during this study), 1270 $m^3 s^{-1}$ (approximate discharge of post-dam experimental floods) and 2407 $m^3 s^{-1}$ (average annual peak discharge during pre-dam period)

Geomorphic reach	Length of segment (km)	Vegetated area (m^2)				Allochthonous inputs (gAFDM m^{-1} $year^{-1}$)		
		Pre-dam (1965)		Post-dam (2002)		Pre-dam (1965)[a]	Post-dam (2002)[b]	
		566 $m^3 s^{-1}$	2407 $m^3 s^{-1}$	566 $m^3 s^{-1}$	2407 $m^3 s^{-1}$	2407 $m^3 s^{-1}$	566 $m^3 s^{-1}$	1270 $m^3 s^{-1}$
Glen Canyon	4.2	4790	29 400	23 900 (26 000)	85 000 (90 400)	534	1460	2520
Lower Marble Canyon	8.9	9540	79 200	15 500 (18 200)	165 000 (178 000)	681	447	1660
Furnace Flats	19.6	14 000	114 000	27 600 (36 200)	340 000 (379 000)	443	362	1630
Middle Granite Gorge	9.8	305	4260	7380 (12 000)	60 300 (76 200)	33	193	610
Lower Canyon	4.3	742	7320	4780 (6670)	47 300 (53 300)	130	285	911
Totals	46.8	29 400	234 000	79 200 (99 000)	698 000 (776 000)			
Mean (range)						382 (45–1060)	434 (289–590)	1440 (851–2160)

The minimum mapping unit for the 1965 coverage developed by Waring (1995) was 4 m^2. For 2002, we provide two estimates of vegetated area, one that only includes plants larger than 4 m^2, to facilitate comparison with pre-dam data, and one that includes all plants down to the minimum mapping unit of 0.5 m^2 (parentheses). Specific allochthonous input values calculated based on Desert and Semi-Desert Scrub production value. Range reported for among reach average comes from range of Desert and Semi-Desert Scrub production values.

[b]Allochthonous input values for 566 $m^3 s^{-1}$ stage elevation based on relative cover estimates reported in Table I and vegetation area estimates that exclude plants <4 m^2 to facilitate comparison with pre-dam data. Allochthonous input values for 1270 $m^3 s^{-1}$ stage elevation are based on area estimates that include plants of all sizes.

for years when peak annual discharge is 1270 $m^3 s^{-1}$; this value does not account for organic matter that would accumulate in this zone during years when no Controlled Floods occurred.

DISCUSSION

Annual allochthonous inputs

Direct allochthonous inputs to the CRE from riparian vegetation are comparable in magnitude to published values for other large river systems or systems where riparian vegetation is also sparse (Conners and Naiman, 1984; Benfield, 1997; Jones *et al.*, 1997). We estimate that direct allochthonous inputs for the CRE average 470 gAFDM m^{-1} $year^{-1}$ of shoreline or 5.17 gAFDM m^{-2} $year^{-1}$ of river surface. Benfield (1997) presents allochthonous inputs for 33 streams and rivers ranging from first to ninth order. Direct inputs were less than 100 gAFDM m^{-2} $year^{-1}$, or roughly the same order of magnitude as we estimated for the CRE, in 10 of these streams. Four of the eight rivers that were fifth order or greater fell into this category (Sycamore Creek, AZ; Muskrat River, Quebec; Matamek River, Quebec; Moise River, Quebec), and the other six systems with inputs less than 100 gAFDM m^{-2} $year^{-1}$ were from arid and/or polar regions where riparian vegetation is sparse (Caribou Creek 2 and 3, Alaska; Canada Stream, Antarctica; Deep Creek, Idaho; Monument Creek, Alaska; Kuparuk River, Alaska).

Our allochthonous input estimates are conservative because we did not include lateral inputs (i.e. wind-blown inputs). Direct and lateral allochthonous inputs are available for 18 of the 33 systems presented in Benfield (1997). Across all 18 of these systems, lateral inputs average 34% of total inputs and the range is 9% (Keppel Creek, Australia) to 100% (Kuparuk River, Alaska). Lateral inputs average 19% of total inputs for the systems that have direct inputs comparable to the CRE (only 6 of the 10 systems that have direct inputs <100 gAFDM m^{-2} $year^{-1}$ also have lateral input data available). Assuming that lateral inputs on the CRE are 19–34% of total inputs yields estimated total inputs of 6.38–7.84 gAFDM m^{-2} $year^{-1}$ and lateral inputs of 1.21–2.67 gAFDM m^{-2} $year^{-1}$.

Our results are also consistent with previous estimates of vegetation biomass for marshes along the Colorado River. Stevens *et al.* (1995) report average biomass of marsh vegetation associated with debris fan eddy complexes as 641 gAFDM m^{-2}. Our biomass estimates for the Wetland

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vegetation class was lower (257 gAFDM m^{-2}) than Stevens *et al.* (1995), but our value includes true marshes as well as sparser herbaceous vegetation.

Litter from nonnative saltcedar represents the second most common type of allochthonous input (36%), after Wetland vegetation, to the Colorado River. Saltcedar is the most common vegetation type at higher stage elevations, but this material is only captured by the Colorado River during years when Controlled Floods are conducted. Changes in the quality of allochthonous inputs to streams can affect invertebrate populations and assemblages (Smock and Macgregor, 1988), however the quality of saltcedar litter as a food source is comparable to native species based on in-stream decomposition studies (Pomeroy *et al.*, 2000; Bailey *et al.*, 2001; Kennedy and Hobbie, 2004) and invertebrate feeding experiments (Moline and Poff, 2008).

If flood peaks along the CRE were higher, our research indicates this would lead to large increases in allochthonous inputs. As part of the Glen Canyon Dam Adaptive Management Program, Controlled Floods with a discharge of $\sim$1270 $m^3 s^{-1}$ have been conducted in 1996, 2004 and 2008. Were Controlled Floods to be conducted annually, we estimate this would result in a roughly threefold increase in allochthonous inputs (Table III) relative to peak discharge during the time of this study, and even greater if Controlled Floods stimulate production of riparian vegetation. However, Controlled Floods may lead to increases in the distribution of saltcedar at higher stage elevations by providing the wetted soils that it requires for germination; although saltcedar is a dominant species along the CRE (42% relative cover below 1270 $m^3 s^{-1}$ stage elevation), there are still large areas of suitable habitat that have not been colonized by saltcedar (B. Ralston, personal observation, 2010). If Controlled Floods are conducted in late winter/early spring prior to saltcedar flowering and seed production, it seems unlikely that Controlled Floods will contribute to future expansion of saltcedar.

Effects of regulation on vegetation and allochthonous inputs

Our study indicates that regulation of the Colorado River in Grand Canyon has led to a roughly threefold increase in the cover of riparian vegetation for a given stage elevation, which is consistent with studies from other regulated rivers (Nilsson and Jansson, 1995; Merritt and Cooper, 2000; Nilsson and Berggren, 2000). However, because average annual flood peaks on the post-dam river are only one quarter of pre-dam values, the vegetated area contributing to annual allochthonous inputs has actually decreased considerably (i.e. 233 852 m^2 of vegetation for 1965 vs. 79 233 m^2 for 2002 along the 46.8 km of river corridor investigated). There are no published estimates of annual litter production for pre-dam vegetation so to estimate allochthonous inputs we used the average and range of production values for 'Desert and Semi-Desert Scrub' (Whittaker, 1975), which yields average inputs of 382 gAFDM m^{-1} $year^{-1}$ (range 45–1064). Anecdotal accounts suggest pre-dam vegetation was sparse and dominated by taxa that are considered Desert Shrubs (i.e. mesquite; Clover and Jotter, 1944; Turner and Karpiscak, 1980). Our coarse estimate of average pre-dam inputs lies within the range of post-dam estimates (289–590 gAFDM m^{-1} $year^{-1}$) but the upper estimate of pre-dam inputs (1064 gAFDM m^{-1} $year^{-1}$) might be more realistic. Sponseller and Fisher (2006) report the annual litter production of *Pr. velutina*, a congener of the *Pr. glandulosa* that is found in Grand Canyon, varied with position in a Sonoran desert landscape and increased along both upland – riparian and upstream – downstream gradients. Specifically, the lowest litter production (37.1 gAFDM m^{-2} $year^{-1}$) occurred in upland sites along a first order segment and the highest litter production (198.7 gAFDM m^{-2} $year^{-1}$) occurred on riparian terraces along fifth order Sycamore Creek (Sponseller and Fisher, 2006). The production of annual grasses growing beneath *Pr. velutina* was also substantial (40–70% of total above ground litter production) leading to total litter production for mesquite habitats of 136.6–446.4 gAFDM m^{-2} $year^{-1}$. Thus, regulation of the Colorado River has led to increases in riparian vegetation, but allochthonous inputs have not changed, and may have even decreased, because of lower flood peaks on the post-dam river.

It is possible that increases in riparian vegetation associated with regulation have strengthened terrestrial – aquatic linkages along the Colorado River in other ways. Drift-feeding fishes can rely heavily on fluxes of terrestrial invertebrates into streams (Baxter *et al.*, 2005). The total abundance of terrestrial invertebrates along the Colorado River likely increased due to regulation-mediated increases in riparian vegetation. Fluxes of terrestrial invertebrates may have increased with regulation even though direct allochthonous litter inputs have not because this flux can be dominated by 'lateral' (e.g. inputs derived from aerially or terrestrially dispersing invertebrates, wind-blown inputs) rather than direct inputs (Baxter *et al.*, 2005). Sub-adult humpback chub (*Gila cypha*), an endangered fish that is native to the Colorado River basin, preferentially occupy shoreline habitats that are vegetated (i.e. Wetland Grasses and Sedges; Converse *et al.*, 1998) relative to other shoreline habitats (i.e. cliff faces, talus slopes, sand bars). It is unclear whether humpback chub are preferentially occupying vegetated shorelines because of the cover they provide, the flux of terrestrial invertebrates from the shoreline vegetation, or some other factors, but it is clear that vegetated shorelines were virtually absent along the pre-dam river (Waring, 1995).

Allochthonous inputs may represent one of the only facets of the Colorado River organic matter budget that was not dramatically altered when Glen Canyon Dam and Lake Powell severed the connection between the Colorado River and its upstream watershed. This research indicates that regulation of the Colorado River has led to a nearly 300% increase in the cover of riparian vegetation. Saltcedar is a dominant component of riparian vegetation along the Colorado River, especially at higher stage elevations. Surprisingly, increases in riparian vegetation associated with regulation and the invasion of nonnative saltcedar do not appear to have led to higher allochthonous inputs because annual flood peaks are considerably lower now than historically.

DISCLAIMER

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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