RESEARCH ARTICLE

Key Points:
- Riparian vegetation is still responding to flow regulation after five decades
- Vegetation response varies with inundation frequency, base flow, and precipitation
- Inundation frequency >5% may limit expansion on bare surfaces and sandbars

Riparian vegetation, Colorado River, and climate: Five decades of spatiotemporal dynamics in the Grand Canyon with river regulation

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Abstract Documentation of the interacting effects of river regulation and climate on riparian vegetation has typically been limited to small segments of rivers or focused on individual plant species. We examine spatiotemporal variability in riparian vegetation for the Colorado River in Grand Canyon relative to river regulation and climate, over the five decades since completion of the upstream Glen Canyon Dam in 1963. Long-term changes along this highly modified, large segment of the river provide insights for management of similar riparian ecosystems around the world. We analyze vegetation extent based on maps and imagery from eight dates between 1965 and 2009, coupled with the instantaneous hydrograph for the entire period. Analysis confirms a net increase in vegetated area since completion of the dam. Magnitude and timing of such vegetation changes are river stage-dependent. Vegetation expansion is coincident with inundation frequency changes and is unlikely to occur for time periods when inundation frequency exceeds approximately 5%. Vegetation expansion at lower zones of the riparian area is greater during the periods with lower peak and higher base flows, while vegetation at higher zones couples with precipitation patterns and decreases during drought. Short pulses of high flow, such as the controlled floods of the Colorado River in 1996, 2004, and 2008, do not keep vegetation from expanding onto bare sand habitat. Management intended to promote resilience of riparian vegetation must contend with communities that are sensitive to the interacting effects of altered flood regimes and water availability from river and precipitation.

1. Introduction

River regulation affects the diversity and function of riparian ecosystems throughout the world [*Nilsson and Berggren*, 2000; *Nilsson et al.*, 2005]. Most of the downstream effects of large dams on riparian ecosystems are directly or indirectly related to changes in flow regime and sediment transport capacity caused by operational schedules for water storage or hydropower production and to decreased sediment supply caused by trapping of sediment in the upstream reservoir [*Schmidt and Wilcock*, 2008]. If flood control and hydroelectricity are the primary objectives of a reservoir, then the magnitude of floods is typically reduced, the level of base flows is typically increased, and daily fluctuations in discharge (hydro-peaking) can be large [*Jones*, 2013].

A common effect of river regulation is channel narrowing [*Williams and Wolman*, 1984; *Grams and Schmidt*, 2002], which is caused by flood control [*Schmidt and Wilcock*, 2008]. Narrowing is often associated with riverward expansion of riparian vegetation into the predam active channel [*Auble et al.*, 2005; *Grams et al.*, 2007; *Stromberg et al.*, 2007]. Narrowing has been observed in systems where the postdam sediment mass balance is perturbed into surplus, perturbed into deficit, or is relatively unaltered [*Schmidt and Wilcock*, 2008]. In conditions of sediment surplus, channel narrowing is typically associated with the deposition of postdam floodplains that are inset within the predam channel [*Allred and Schmidt*, 1999; *Grams and Schmidt*, 2002], and these new deposits can be colonized by riparian vegetation. In conditions of sediment deficit and bed incision, riparian vegetation may encroach downward into the new postdam channel [*Grams et al.*, 2007]. *Manners et al.* [2014] demonstrated that narrowing also occurs where the channel is invaded by nonnative species, even though the flood regime and sediment supply are little perturbed.

The primary driver of channel narrowing is reduction of flood magnitude, which alters disturbance regimes that control the establishment and succession of riparian vegetation and potentially reduces the availability of water to vegetation due to decreased alluvial groundwater recharge [*Webb and Leake*, 2006]. If the predam

floodplain is no longer inundated, drought tolerant species typically replace riparian species. However, changes in base flow also affect the availability of groundwater to riparian vegetation, and hydro-peaking can create a daily disturbance regime.

Reduction in runoff volume caused by climate change may exacerbate the effects of flood control for riparian vegetation, because water managers may need to further alter flow regimes in order to meet water supply needs [*Perry et al.*, 2012, 2013]. Anticipated effects of these climate and management factors include contraction of riparian zones and reduction in the likelihood of plant recruitment in upslope areas farther from the channel [*Perry et al.*, 2012, 2013]. Detailed assessments of the response of vegetation to changes in dam operations during long time periods are therefore essential to understand and predict the long-term effects of altered flow regimes on riparian ecosystems [*Johnson*, 1994; *Christensen et al.*, 2004; *Grantz et al.*, 2007; *Dixon et al.*, 2012].

Riparian vegetation typically responds to streamflow along a continuum from low-elevation zones that are inundated frequently to zones higher in elevation that are inundated less frequently (we use "elevation" to describe the position of a riparian zone relative to the base flow water surface). In all zones, floods create disturbance and inundate surfaces, but floods can also increase water availability to vegetation even in the absence of direct inundation by temporarily increasing the level of the alluvial groundwater table [*Stromberg et al.*, 2007]. In low-elevation zones, base flows control water availability and the area of habitable space for vegetation, while in high-elevation zones, base flows can control the availability of groundwater to phreatophytic vegetation [*Stromberg et al.*, 2007].

In this study, we use high-resolution imagery to assess riparian vegetation response over nearly five decades for a 362 km segment of the Colorado River downstream from Glen Canyon Dam. Our first objective is to describe the long-term (1965–2009) temporal stability and changes in total vegetation along a continuum of low- to high-elevation zones. Due to flood control and sediment deficit conditions in this segment of the river, we predict that observed changes will indicate a long-term lowering of the riparian area in which riparian vegetation expands downward to fill in lower zones. Our second objective is to evaluate whether, and how, total vegetation varies as a function of streamflow variables of floods (magnitude of peak flows), base flow (magnitude of low flows), and flow duration (duration of inundation or elevated base flow), as well as precipitation (drought), from 1965 to 2009 along the continuum of zones.
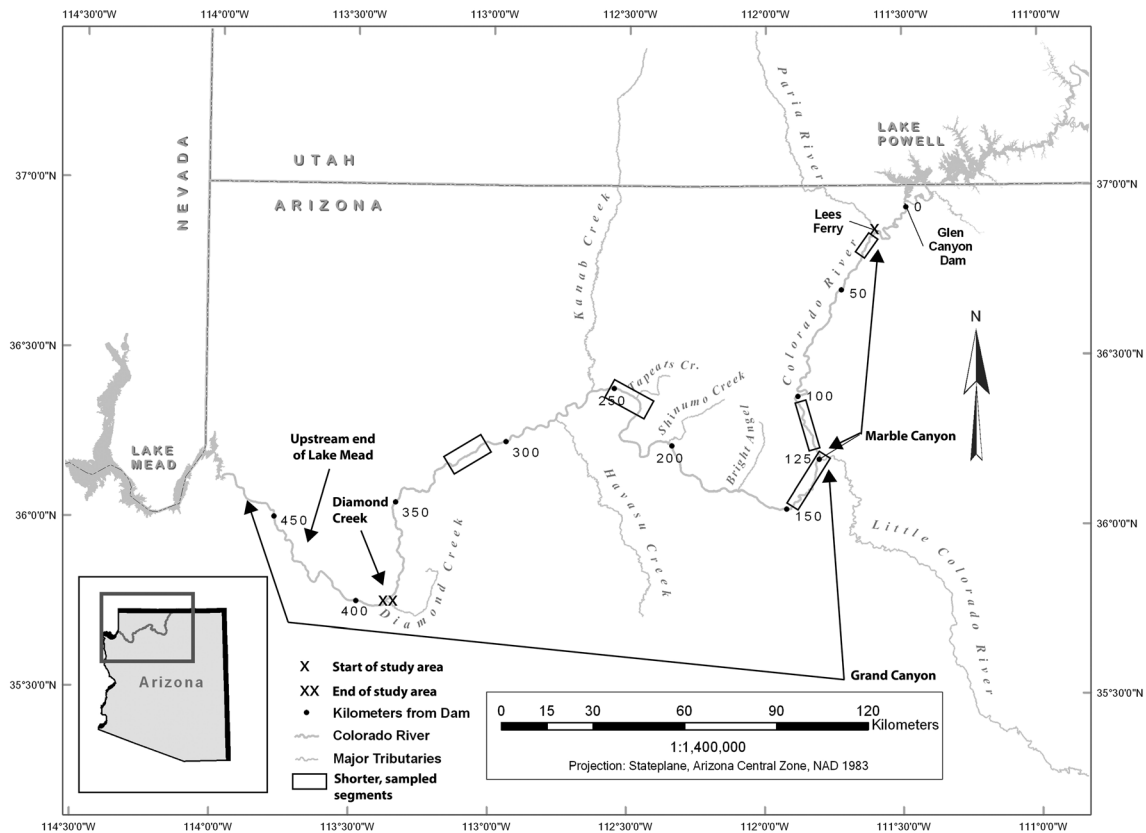
2. Study Area

Our study area is the Colorado River between Lees Ferry, AZ, and Diamond Creek, AZ, 362 km downstream (Figure 1). The study area includes all of Marble Canyon and 262 km of Grand Canyon (Figure 1). The study area is one of the most studied segments of the Colorado River for riparian vegetation, geomorphology, native and sport fisheries, and aquatic food webs, as well as other resources as cited in compendium volumes [*Webb et al.*, 1999; *Gloss et al.*, 2005; *Melis*, 2011].

2.1. Hydrology

Glen Canyon Dam was completed in March 1963, and Lake Powell reservoir filled for the first time in 1980. The most notable effect of flow regulation was the dramatic change in disturbance regimes: from seasonal disturbance of spring floods due to snowmelt in the large-scale Colorado River basin to daily disturbance of hydro-peaking [*Topping et al.*, 2000; *White et al.*, 2005]. The postdam period may be divided into two distinct periods of different reservoir release patterns (Figure 2): (1) the period between 1963 and 1992 when power-plant operations involved unrestricted hydro-peaking and when long-duration floods occurred between 1983 and 1986 and (2) the period after 1992 when the range of daily hydro-peaking was restricted and when short-duration controlled floods occurred in 1996, 2004, and 2008 [*U.S. Department of the Interior*, 1996; *Schmidt and Grams*, 2011b].

Local rainfall mostly occurs in winter and during the summer/fall period of the North American monsoon; this rainfall supplements the amount of water available to riparian vegetation from streamflow. Two droughts when there was little rainfall occurred during this five-decade period (Figure 3) [*Woodhouse et al.*, 2010; *Cook et al.*, 2009; *Hereford et al.*, 2014]. The mid-20th century drought started in the early 1940s and ended in the late 1970s. The early 21st century drought started in the late 1990s and is currently ongoing. A wet episode intervened between the late 1970s and mid-1990s.

Figure 1. Map of the study area which is the Colorado River corridor between Lees Ferry and Diamond Creek, Arizona, USA. Lees Ferry is 25 km downstream from Glen Canyon Dam and is at the upstream end of Marble Canyon. Marble Canyon is defined as that part of the Colorado River between the Paria and Little Colorado Rivers and is approximately 100 km long. Grand Canyon is downstream from the Little Colorado River and is approximately 350 km long. Diamond Creek is 362 km downstream from Lees Ferry and approximately 50 km from the upstream end of Lake Mead reservoir. The study area is therefore all of Marble Canyon and 262 km of Grand Canyon to Diamond Creek, below which some of the remaining portion of Grand Canyon is inundated by Lake Mead.

2.2. Geomorphology

The Colorado River flows through a debris fan-affected canyon throughout the entire study area. The debris fans occur at tributary confluences, and control channel gradient, and create large areas of recirculating flow (eddies) in the lee of each fan (Figure 4) [*Howard and Dolan*, 1981; *Schmidt and Graf*, 1990]. Vegetation grows on alluvial and colluvial deposits, including the fine-grained channel-margin deposits along the banks of pools upstream from debris fans, the coarse boulder debris fans themselves, and eddy sandbars immediately downstream [*Schmidt and Rubin*, 1995]. Elsewhere, vegetation grows on channel-margin deposits that occur where the river is unobstructed. The areal extent of fine sediment deposits along the river channel is dependent on valley width. Narrow parts of the river, where the valley is only slightly wider than the active river channel, occur in the upstream half of Marble Canyon (Figure 1) and in some gorges of Grand Canyon and have a smaller capacity to store sediment above the river's base flow.

Trapping of fine sediment in Lake Powell coupled with dam operations capable of transporting large volumes of fine sediment have resulted in sediment deficit downstream from Glen Canyon Dam [*Laursen and Silverston*, 1976; *Topping et al.*, 2003]. Conditions of fine sediment export resulted in a general decline in sandbar area from the predam period to the postdam period [*Schmidt et al.*, 2004; *Wright et al.*, 2008].

2.3. Predam Vegetation

The predam riparian plant community was characterized by episodic recruitment and periodic disturbance, resulting in an ephemeral presence of most species. Extensively developed gallery forests, or dense stands of riparian shrubs, were rare. Surveys conducted prior to dam construction, and comparisons of predam and postdam photographs, identify a sparse plant assemblage [*Clover and Jotter*, 1944; *Turner and Karpiscak*, 1980; *Stephens and Shoemaker*, 1987]. The assemblage was composed of early successional riparian species
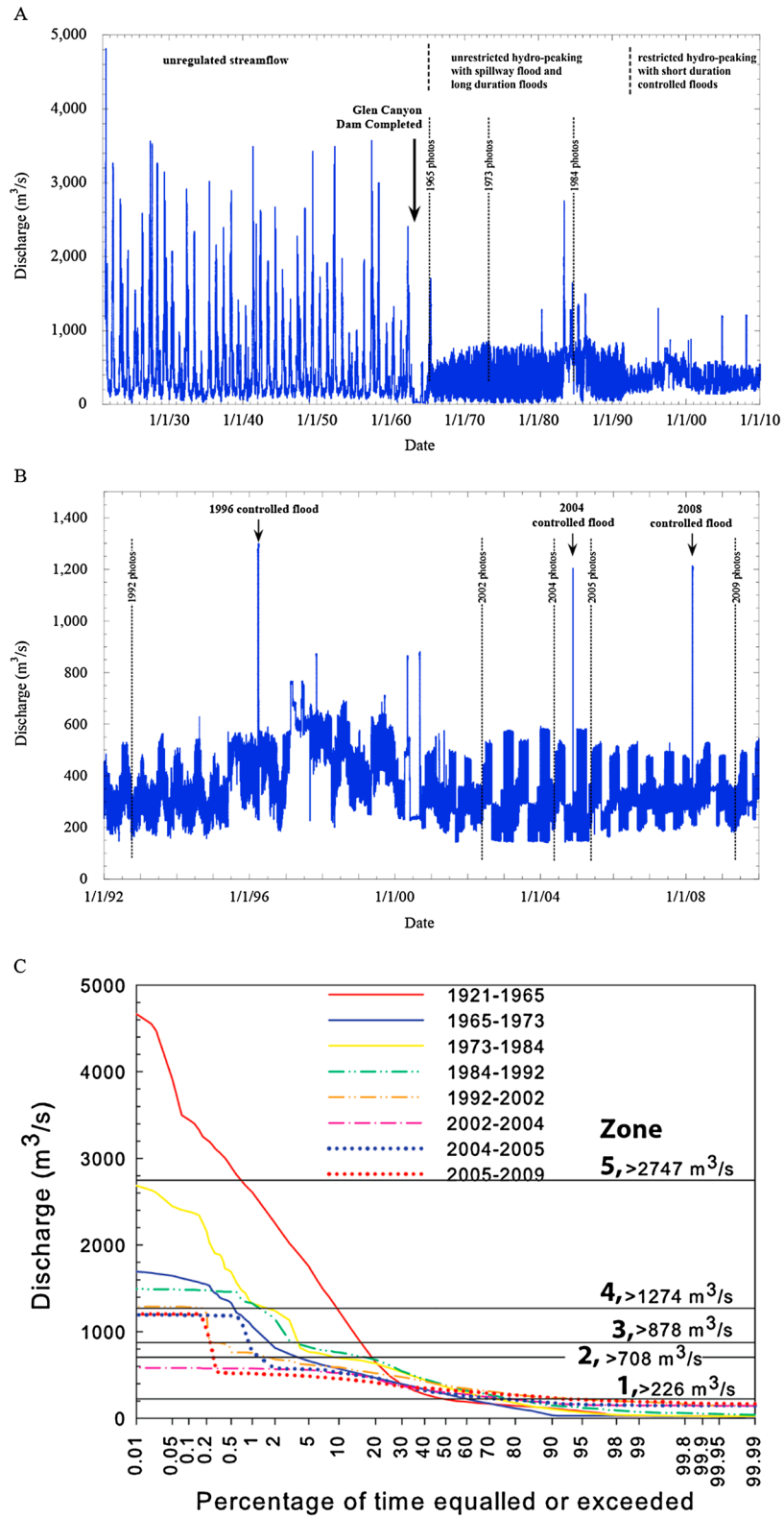
Figure 2. (a) Hydrograph of the Colorado River at Lees Ferry (U.S. Geological Survey station 09380000) from 1921 to 2010 and (b) from 1992 to 2010. The acquisition dates of each set of imagery used in the study are shown (1965, 1973, 1984, 1992, 2002, 2004, 2005, and 2009), as are major flood and operational events related to Glen Canyon Dam. (c) Flow duration curves (inundation frequency) for the time intervals analyzed between image dates. Please refer to Table 1 for definitions of zones.
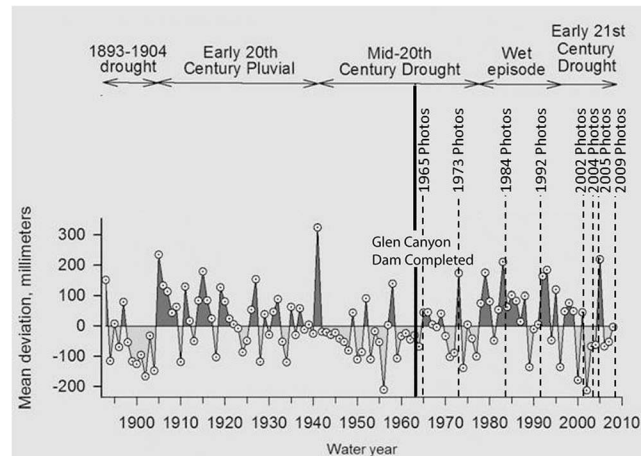
Figure 3. Long-term temporal patterns of precipitation and key droughts and wet periods for the Grand Canyon region modified with permission from *Hereford et al.* [2014] and http://esp.cr.usgs.gov/projects/sw/historical/precip_sw.html. *Y* axis is precipitation expressed as mean deviation from individual weather station averages. The acquisition dates of imagery used in the study are shown (1965, 1973, 1984, 1992, 2002, 2004, 2005, and 2009), as is the completion of Glen Canyon Dam in 1963.

that occupied areas subject to periodic inundation by common floods, facultative riparian species, and small xeric shrubs. Recruitment of woody riparian vegetation (e.g., cottonwood, *Populus* spp., and tamarisk, *Tamarix* spp.) was coincident—or, in the case of tamarisk, recruitment lagged by 1 year—with years of large-magnitude runoff [*Mortenson et al.*, 2012].

The duration, magnitude, and timing of flooding affected patterns of scour and fill [*Schmidt and Rubin*, 1995] as well as the probability of seed germination. Predam photographs show that much of the nearshore habitat was bare sand and mud [*Stephens and Shoemaker*, 1987; *Webb*, 1996]. Riparian vegetation usually occurred on the banks adjacent to the ponded flow upstream from debris fans and along the banks of the flow expansions downstream (Figure 4). Vegetation was generally located one to several meters above the stage of base flow [*Clover and Jotter*, 1944; *Grams et al.*, 2007]. Facultative riparian species such as mesquite (*Prosopis glandulosa*), acacia (*Acacia greggii*), desert olive (*Forestiera neomexicana*), tamarisk, and cliffrose (*Purshia* sp.) formed a band of vegetation near the stage of mean annual peak flood. Other desert and upland shrubs such as saltbush (*Atriplex canescens*) and snakeweed (*Gutierrezia sarothrae*) were also found along these banks [*Clover and Jotter*, 1944]. Pioneer riparian species such as coyote willow (*Salix exigua*), seepwillow (*Baccharis salicifolia*), and tamarisk occurred in a zone that *Clover and Jotter* [1944] described as the wet sand zone, that was closer to the water's edge. Cottonwoods and Goodding's Willows (*Salix gooddingii*) also occurred in the wet sand zone and were associated with reaches where the valley widened and a larger floodplain existed [*Turner and Karpiscak*, 1980; *Mast and Waring*, 1997].

2.4. Postdam Vegetation

The postdam reduction in flooding allowed plant colonization onto channel-margin deposits and eddy sandbars. Thus, riparian vegetation expanded into the predam active channel. *Turner and Karpiscak* [1980] were the first to qualitatively record changes in vegetation along the river corridor and noted the expansion of tamarisk throughout Marble and Grand Canyons. *Waring* [1995] followed *Turner and Karpiscak* [1980] and quantified temporal vegetation change between 1965 and 1992 in five river segments that varied in length from 4 to 27 km. *Stevens et al.* [1995] documented the development of fluvial marsh communities following dam completion. *Mortenson et al.* [2012] showed how changes in the flow regime resulted in successive recruitment of tamarisk to lower river stages. Collectively, these studies showed expansion of vegetation in Marble and Grand Canyons in response to river regulation.
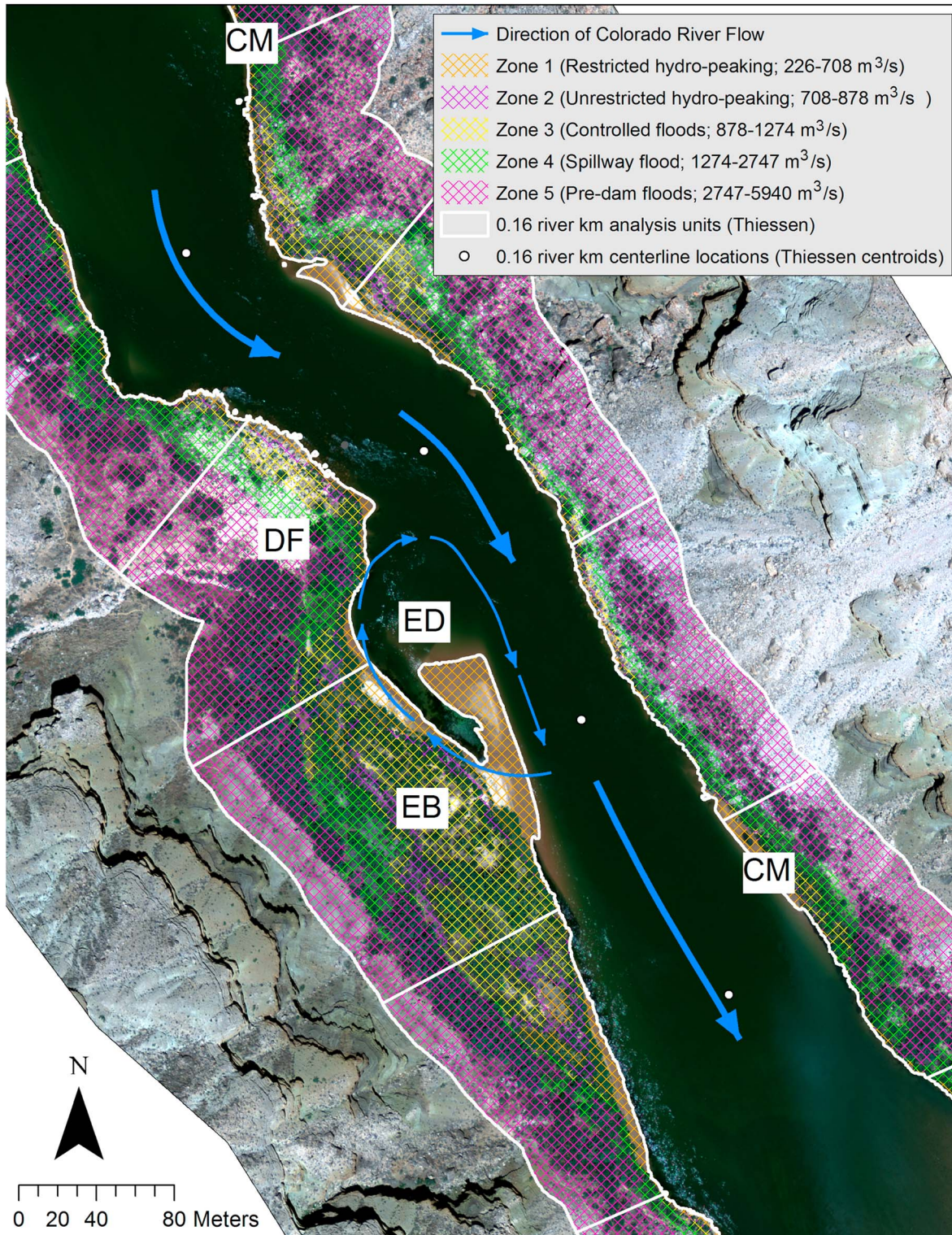
3. Methods

We analyze vegetation changes from 1965 to 2009 in five distinct zones that have different frequencies of inundation during different parts of the postdam era (Table 1 and Figure 2c). We use image-based classifications of total vegetation from 1965, 1973, 1984, 1992, 2002, 2004, 2005, and 2009, as well as streamflow, and topographic data coupled with one-dimensional flow model predictions of the stage of streamflow (Table 2).

3.1. Terrestrial Area

Vegetation changes are quantified by zone in 0.16 km units, measured by points along the channel centerline from Lees Ferry to Diamond Creek (Figure 4). These units are defined by constructing a Thiessen polygon

Figure 4. Aerial image taken May 2009 showing a debris fan and eddy 115 km downstream from Glen Canyon Dam (see time series in Figure 8a as well). The extent of each riparian zone (inundated by the specified flow) is shown. Please refer to Table 1 for definitions of zones. Vegetated area was quantified from the imagery for each riparian zone in Thiessen units. The Thiessen units were centered on the channel centerline in 0.16 km increments from Lees Ferry to Diamond Creek. The large arrows indicate the direction of flow in the main current of the river, and smaller arrows show recirculating flow at high discharge. The large eddy sandbar on the south side of the river was deposited in an eddy of recirculating current that forms downstream from the channel constriction created by the debris fan at high discharge. Channel margin sandbars occur as narrow deposits along the banks outside the influence of debris fan-created eddies. Each sandbar consists of an unvegetated portion that is more regularly inundated and a much larger vegetated portion that is infrequently inundated.

Table 1. Descriptions of the Five Riparian Zones in Which Vegetation Changes Are Analyzed[a]

Zone	Flow Regime Attribute	Description	Discharge Range
1	Postdam restricted hydro-peaking	Restricted hydro-peaking was instituted in the early 1990s and limits maximum power-plant releases to 708 m^3/s. Zone 1 is the area inundated by this flow regime attribute that is also above the elevation of common postdam base flows of 226 m^3/s.	226–708 m^3/s
2	Postdam unrestricted hydro-peaking	Unrestricted hydro-peaking occurred between 1965 and the early 1990s when maximum power-plant releases sometimes reached 878 m^3/s. Zone 2 is the area inundated by this flow regime attribute that is also above zone 1.	708–878 m^3/s
3	Postdam controlled floods	Controlled floods[b] of approximately 1274 m^3/s and between 3 and 7 days duration occurred in 1996, 2004, and 2008 during the period of modern environmental management. Similar magnitude floods of between 39 and 76 days duration occurred between 1984 and 1986. Zone 3 is the area inundated by these floods that is also above zone 2.	878–1274 m^3/s
4	Postdam spillway flood	The Glen Canyon Dam spillway was used in 1983 when peak discharge reached 2747 m^3/s. Zone 4 is the area inundated by this flow that is also above zone 3.	1274–2747 m^3/s
5	Predam floods	Predam floods reached elevations higher than 2747 m^3/s. The magnitude of the maximum historic, predam flood[c] that occurred in 1884 was 5940 m^3/s. Zone 5 is the area inundated by these predam flows that is also above zone 4.	2747–5940 m^3/s

[a]Each zone is defined by the stage of the highest discharge of the respective flow regime attribute.
[b]*Schmidt and Grams* [2011a, 2011b].
[c]*Topping et al.* [2003].

around each point along the centerline. For each Thiessen polygon, we define the terrestrial area available for vegetation establishment as the entire area between the elevation of common postdam base flows (~226 m^3/s) and the elevation reached by the maximum recorded flood in the predam period (5940 m^3/s in 1884) [*Topping et al.*, 2003]. The channel below the lower bound is nearly always inundated and bare of vegetation. The upper bound has not been inundated in more than 100 years and therefore is used to define the maximum extent of predam riparian vegetation. We then further subdivide the terrestrial area within each Thiessen polygon into five zones based on elevation above base flow stage (Table 1).

Because we define the zones and the terrestrial area therein based on discharge required for inundation (Table 1), the boundaries are sensitive to changes in topography. However, accurate maps of shoreline topography are not available for the images acquired prior to 2002. We therefore define the upper extent of the riparian area

Table 2. Description of Data Used for Analyses of Multidecadal Vegetation Change

| Author	Type of Data[a]	Years	River Segment Covered (km Downstream of Glen Canyon Dam)	Discharge During Data Acquisition[b]
Waring [1995]	Total vegetation maps[c]	1965, 1973, 1984, 1992	25–29; 107–116.5; 121.5–142.5; 239–249.5; 313–318	variable
Ralston et al. [2008]	Vegetation map[d]; observed shoreline at 226 m^3/s	2002	0–442	~226 m^3/s
USGS [unpublished]	Total vegetation map[c]; observed shoreline at 226 m^3/s	2004, 2005	25–29; 107–116.5; 121.5–142.5; 239–249.5; 313–318	~226 m^3/s
Davis [2012, 2013]	Total vegetation map[c]; observed shoreline at 226 m^3/s	2009	0–467	~226 m^3/s
Kearsley et al. [2015]	Vegetation map[d]	2012	25–387	N/A
USGS [unpublished]	Geomorphic features (debris fans, eddies, and channel margins)	2002	25–387	N/A
USGS [unpublished]	River centerline	2000	0–476	N/A
Magirl et al. [2008]	Modeled stage-elevation shorelines	2002	25–387	N/A
USGS[e]	Streamflow record for Colorado River at Lees Ferry[e]	1921 to present	Gauge located 25 km downstream from dam	N/A
Hereford et al. [2014]	Precipitation record for Grand Canyon	1950–2010	0–467	N/A

[a]Each data set is available from the U.S. Geological Survey Grand Canyon Monitoring and Research Center (doi:10.5066/F7J67F0P; http://sbsc.wr.usgs.gov/geospatial/Data/USGS_2015_JSankey_Riparian_Vegetation_And_Colorado_River.zip; https://www.sciencebase.gov/catalog/item/5575b3c1e4b08f9309d4bafc; http://www.gcmrc.gov/), with the exception of *Hereford et al.* [2014], *Kearsley et al.* [2015], and the USGS streamflow record.
[b]Discharge references the gauge at Lees Ferry and potentially varies downstream as a function of tributary flows into the Colorado River.
[c]"Total vegetation map" refers to maps with units that are not defined by species composition.
[d]"Vegetation map" refers to maps with units that are defined by species composition.
[e]http://www.gcmrc.gov/discharge_qw_sediment/station/GCDAMP/09380000.
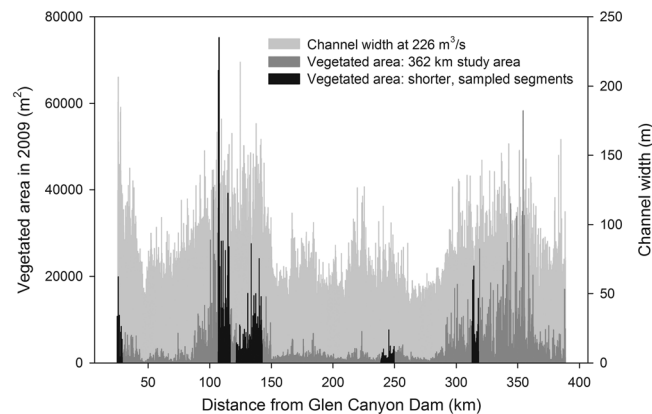
Figure 5. Total vegetated area in 2009 (m^2) versus river kilometer for the entire 2009 data set and the shorter, sampled segments used in the long-term analysis. Note that vegetated area varies by relative width of the river channel. Areas of low vegetation tend to be located where the river channel and the canyon are narrower, such as Marble Canyon and the gorges of Grand Canyon.

and the boundaries between each zone based on topography observed in 2002. The imagery from 2002, 2004, 2005, and 2009 were acquired at an approximate steady discharge of $226 \, m^3/s$, and we use the delineation of the observed shoreline in the image to define the lower extent of the terrestrial area for each of these dates [*Davis*, 2012]. Thus, for the lowest zone (zone 1), the terrestrial area varies between 2002 and 2009 based on shoreline topography. We use the 2002 shoreline to define the lower extent of the terrestrial area for the 1965–1992 data.

Because observations of water-surface elevations for discharges above $226 \, m^3/s$ are not available throughout the entire study area, the best practical method to define boundaries between the five zones and the upper extent of the terrestrial area is the flow model developed by *Magirl et al.* [2008]. This one-dimensional flow model for the entire 362 km of the river channel between Lees Ferry and Diamond Creek was calibrated to the water-surface elevation at $226 \, m^3/s$ and consists of 2682 cross sections at approximately 130 m intervals [*Magirl et al.*, 2008]. Model-predicted water-surface elevations were estimated to be accurate to within 0.4 m for discharges less than $1300 \, m^3/s$, within 1.0 m for discharges up to $2500 \, m^3/s$, and within 1.5 m for discharges up to $5900 \, m^3/s$ [*Magirl et al.*, 2008]. The model-predicted water-surface elevations for the discharge defining the upper extent of the terrestrial area and the discharges defining the boundaries between each riparian zone were projected onto a digital elevation model derived from the 2002 images, interpolating water-surface elevation between each of the cross sections [*Magirl et al.*, 2008]. The result is a continuous map of each of the five zones (Figure 4).

The assumption that the boundaries between the zones are constant introduces some uncertainty into the analysis of changes in vegetation in the zones, although it does not affect the analysis of changes in the total extent of riparian vegetation. For example, the mean change in terrestrial area for zone 1 in sequential years of imagery for 2002, 2004, 2005, and 2009 varies from −9% (decreased area) to +17% (increased area) per 0.16 km unit. We are not able to similarly quantify changes in the shoreline topography and terrestrial area for zone 1 between 1965 and 1992. For zones 2–5, however, the areas are constant throughout all images analyzed (1965–2009).

3.2. Vegetated Area

The image-based classifications of total vegetation in each year (Table 2) are used to determine the proportion of terrestrial area that is vegetated ("vegetated area" %) within each zone for each 0.16 river kilometer unit. We analyze long-term change for five shorter, sampled segments of the study area, because, with the exception of 2002 and 2009, the vegetation classifications were completed only in these segments (Figure 1 and Table 2) [*Waring*, 1995]. These sampled segments together cover approximately 14% of the study area, while the 2002 and 2009 data sets include the entire study area.

The long-term (1965–2009) rate of change in vegetated area (%/yr) is determined by the slope coefficient of linear regression of mean vegetated area versus year for the five zones. Spatial and temporal variability in vegetated area are further analyzed in several ways. Long-lived, stable, dense vegetation patches with greater than 60% canopy cover are identified by spatially intersecting the vegetated area data sets for all years to identify vegetation patches that persist from 1965 to 2009. The vegetated area attributed to these persistent (stable) patches is determined for each zone. The composition of the persistent patches within each of the five zones is determined from the vegetation type that each patch was most recently mapped [*Kearsley et al.*, 2015].
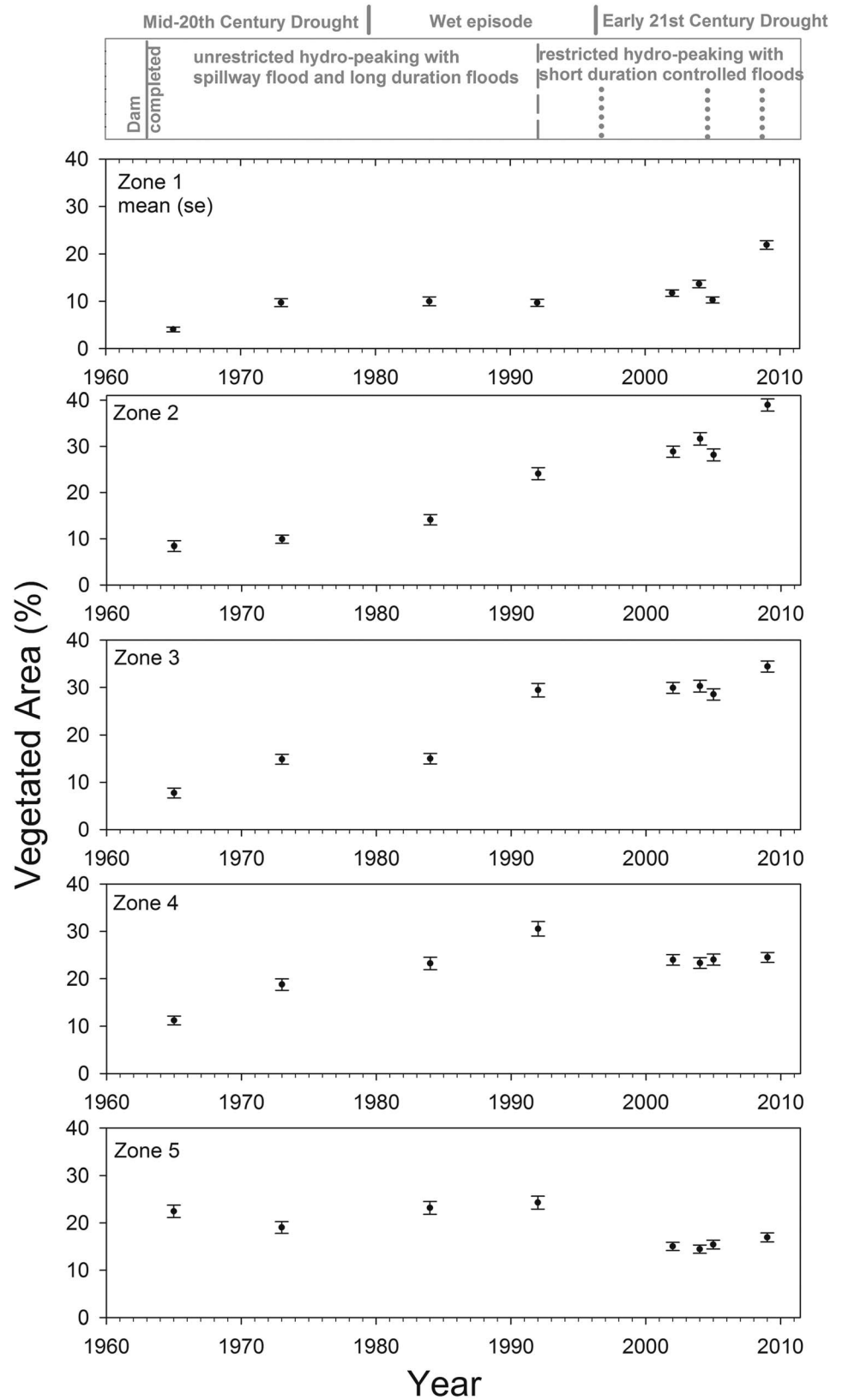
Figure 6. Mean (standard error)-vegetated area measured from aerial imagery in eight, postdam acquisition dates in each of the five riparian zones. Different patterns in the long-term trends of vegetated area are evident for the zones. The different patterns can be in part explained by effects and interactions of river hydrology and precipitation (drought).
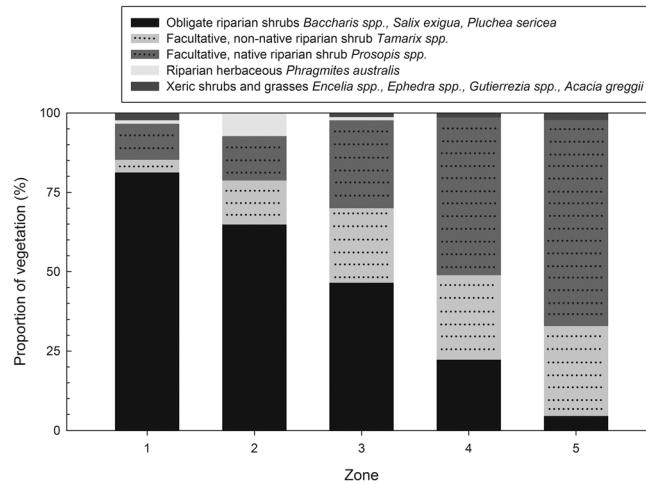
Figure 7. Vegetation composition of zones for locations persistently vegetated from 1965 to 2009. Composition is summarized by dominant lifeform and species.

The shorter sampled segments introduce some uncertainty for making inference to the entire study area. Prior to this study, we compared the shorter sampled segments to the entire 362 km of river in the 2009 data (Figure 5). We found that the sampled segments include a diverse range of biogeomorphic conditions along the river and provide a reasonable subset for making inference to the entire study area. The sampled segments include locations where the river is both wide and narrow (Figure 5). However, the proportion of terrestrial area that is vegetated in the sampled segments is 5.7% larger than in the entire corridor. The sampled segments include a comparable area of eddies, but more debris fans, and fewer channel margin deposits.

The classifications of total vegetation also introduce some uncertainty into the analysis of changes in vegetation among the zones. The maps of total vegetation from all dates were produced with methods that included image interpretation to exhaustively identify total vegetation [*Waring*, 1995; *Ralston et al.*, 2008; *Davis*, 2012]. Image interpretation of high spatial resolution imagery has been shown to produce very high classification accuracies and excellent correlation (e.g., >90%) between maps of total vegetation produced by independent analysts and ground truth [*Booth et al.*, 2005; *Duniway et al.*, 2012]. The total classification accuracy of vegetation presence and absence in the maps of total vegetation from each date of imagery that we use is estimated to be greater than 95% [*Ralston et al.*, 2008].

Table 3. Relative Ability of Five Metrics to Predict Vegetated Area Within and Among Zones[a]

Zone	Metric	x	x SE	y_o	y_o SE	AICc	ΔAICc
1	Peak flow	−0.006	0.002	17.903	2.431	51.97	0.00
	Duration of elevated base flow	0.252	0.087	−7.353	6.582	52.55	0.59
	Low flow	0.050	0.020	6.140	2.468	53.75	1.78
	Constant	not applicable (NA)	NA	11.385	1.787	53.96	2.00
2	Low flow	0.141	0.022	8.105	2.788	55.69	0.00
	Peak flow	−0.013	0.004	37.177	5.362	64.62	8.93
	Constant	NA	NA	22.999	3.909	66.48	10.79
3	Low flow	0.116	0.026	11.459	3.304	58.41	0.00
	Peak flow	−0.012	0.003	36.911	4.303	61.10	2.69
	Duration of elevated base flow	−1.431	0.507	28.321	2.923	63.28	4.87
	Duration of inundation	−2.150	0.843	27.334	2.931	64.17	5.75
	Constant	NA	NA	23.760	3.442	64.45	6.03
4	Constant	NA	NA	22.433	1.961	55.45	0.00
5	Precipitation drought	−6.518	2.287	23.727	1.980	48.88	0.00
	Constant	NA	NA	18.839	1.407	50.13	1.29
All	Duration of inundation	−1.034	0.238	22.241	1.246	274.85	0.00
	Duration of elevated base flow	−0.144	0.040	22.352	1.367	279.19	4.34
	Low flow	0.059	0.018	13.603	2.211	280.44	5.59
	Peak flow	−0.006	0.002	26.925	2.447	280.84	5.99
	Constant	NA	NA	19.883	1.354	288.63	13.79

[a]Predictors are peak flow (1% exceedance), low flow (99% exceedance), duration of inundation (i.e., percent of time flows inundate entire zone), duration of elevated base flow (i.e., percent of time flows reach but do not completely inundate entire zone), and precipitation drought (indicator variable signifying whether vegetated area was measured from imagery acquired during a regionally significant drought). Models are ranked by their respective delta AICc from univariate GLM analysis. AICc is the Akaike information criterion for small sample size. Delta AICc shows the difference between the model AICc and the lowest AICc for the zone. Only models with delta AICc smaller than the constant model are shown.
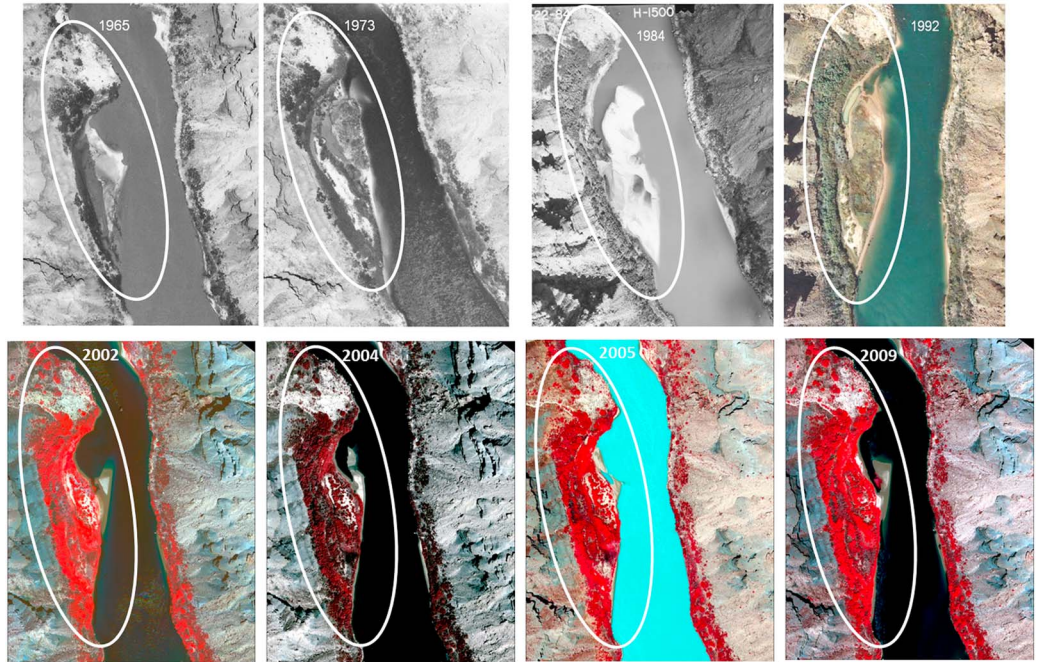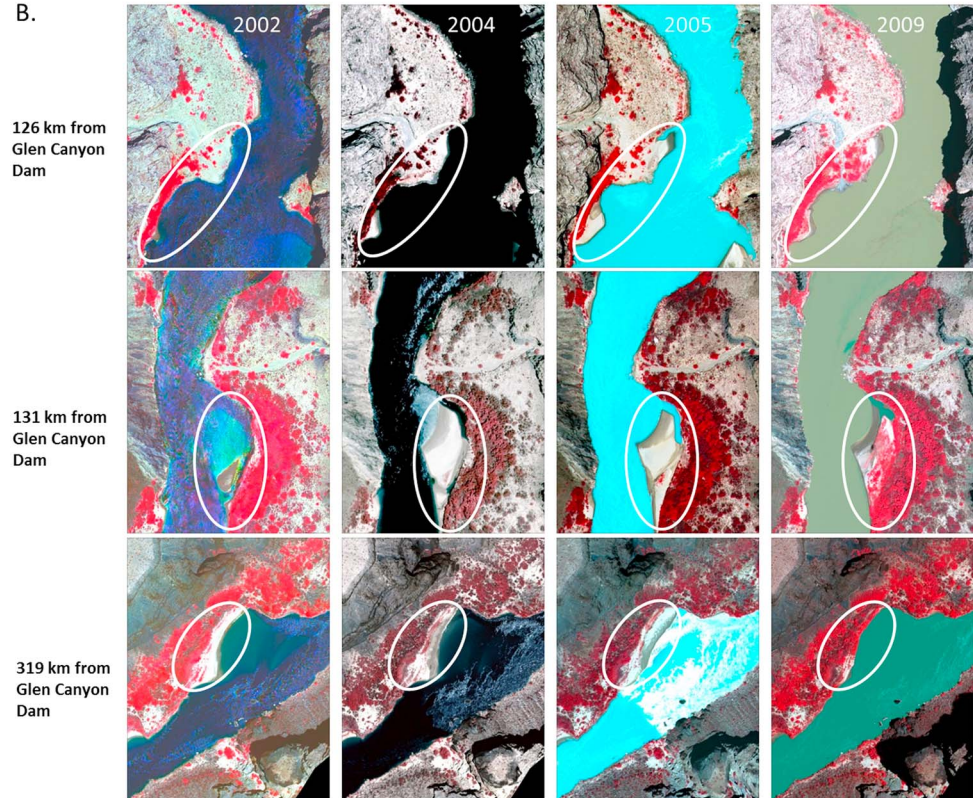
Figure 8. Time series of imagery from several locations throughout the study area. The images from 2002 to 2009 are displayed as false-color composites. (a) Riparian vegetation was suppressed at low elevations during periods of greater flow duration of the 1970s and 1980s, and had reached, and potentially plateaued at high levels of vegetated area in intermediate zones by the 1990s and 2000s. (b) Riparian vegetation expansion was subsequently confined to narrow zones of shoreline (e.g., eddy bars in circled eddy areas) that exhibited dramatic rates of expansion in response to subtle changes in area of exposed sand during the 2000s.

3.3. Streamflow

To characterize the flow regime for each epoch between analyzed imagery, we compute the duration of flows using the instantaneous discharge record for the Colorado River at Lees Ferry, Arizona (U.S. Geological Survey station 09380000). The instantaneous flow record is obtained from discharge computed from the digitized trace of the instantaneous stage record [*Topping et al.*, 2003]. This record containing values at unequal intervals (http://www.gcmrc.gov/discharge_qw_sediment/station/GCDAMP/09380000) is resampled by linear interpolation to create a record with fixed 1 h intervals. This record is used to compute the proportion of time discharge equaled or exceeded a given magnitude for each interval between dates of image acquisition and for the entire period of record preceding the 1965 imagery (1921–1965). These results are used to determine the proportion of time each of the five zones is completely inundated for each interval between aerial imagery used to map vegetation.

3.4. Drought

An indicator variable is created to describe whether a particular vegetated area value (imagery data set) was acquired during a drought, or not, based on *Hereford et al.*'s [2014] definitions of the durations of regional droughts (Figure 3). Henceforth, we refer to this variable as "precipitation drought." The precipitation data used by *Hereford et al.* [2014] to define the time span of each drought were from inner canyon, canyon rim, and regional weather stations.

3.5. Analysis of Vegetation, Streamflow, and Drought

We evaluate the relative ability of five metrics to predict vegetated area within and among zones: peak flow (1% exceedance), low flow (99% exceedance), duration of inundation (i.e., percent of time flows inundate the entire zone), duration of elevated base flow (i.e., percent of time flows reach but do not completely inundate the zone), and and precipitation drought. For each zone, we predict vegetated area as a function of each metric, and as a function of a constant (1), using univariate generalized linear model (GLM) analysis. We evaluate the relative predictive ability of each metric within each zone by comparing models by AICc (Akaike information criterion for small sample size) [*Akaike*, 1974]. Within each zone, we consider the metric in the model with the lowest AICc to be the best predictor of vegetated area. Within each zone, we consider models with delta AICc less than 2.0 to not differ significantly from the model with the best predictor (where delta AICc is the difference between the model AIC and the lowest AICc for the zone).

4. Results

4.1. Vegetation Change

From 1965 to 2009 there is a net increase in vegetation in zones 1–4 (Figure 6). The rate of increase is greatest for zones 2 and 3 (mean = 0.6%/yr, and standard error = 0.1%/yr, in each zone) and somewhat less for zones 1 and 4 (mean = 0.2%/yr, standard error = 0.1%/yr, in each zone). Vegetation decreases in zone 5 at a mean rate of 0.2%/yr (standard error = 0.1) from 1965 to 2009. While the rates are useful for summarizing long-term changes over the entire study period, they imply that the changes are constant with time. The long-term changes in vegetation are noticeably different in the five zones and for some intervals of image dates, however (Figure 6). In zones 1–4 mean-vegetated area is lowest in 1965 and increases from 1965 to 1973. From 1973 to 1992, vegetation does not increase in zone 1 but does in zones 2–4 when hydro-peaking was unconstrained, one long-duration spillway flood occurred, and three other long-duration floods occurred [*Schmidt and Grams*, 2011b]. The 1983 spillway flood and other long-duration floods that occurred between 1984 and 1986 are known to have removed areas of vegetation within zones 1–4 [*Stevens and Waring*, 1986]. Therefore, more vegetation probably existed prior to these events than is shown in the 1973 or 1984 imagery (Figure 6). Vegetated area peaks in 1992 in zone 4 (Figure 6). Vegetation decreases slightly (~2%) in zones 1–3 between 2004 and 2005 during which time the 2004 controlled flood occurred (Figure 6). Vegetation dramatically increases (~6–12%) from 2005 to 2009 in zones 1–3; the 2008 controlled flood occurred during this time (Figure 6). Throughout the five decades, changes in zone 5 are very different compared to most of the lower zones (Figure 6). In zone 5, vegetated area peaks in 1992 and then declines in the next two decades, which is similar to changes from 1992 to 2009 in zone 4.

4.2. Vegetation Composition and Persistence

There is a larger proportion of persistently vegetated area during the five decades in the higher zones. The proportion of the zone that is persistently vegetated in zone 5 (mean = 7.4%, standard error = 0.6%) is 2 times greater than zone 4 (mean = 3.2%, standard error = 0.44%) and an order of magnitude greater than zones 1–3 (mean = 0.3%, 0.9%, and 1.7%, standard error = 0.1%, 0.4%, and 0.7%, respectively). These persistent vegetation patches are overwhelmingly composed of woody plants in all zones (Figure 7). The proportion of obligate riparian shrubs *Baccharis* spp., *Salix exigua*, *Pluchea sericea*, and the fluvial marsh species *Phragmites australis* decreases from low to high zones. The proportion of the facultative, native riparian shrub *Prosopis* spp. with deep-root system increases along the same elevation gradient. The facultative, nonnative riparian shrub *Tamarix* spp. increases along the gradient as well, though to a lesser extent at higher zones.

4.3. Relationships of Vegetation to Streamflow and Drought

The best predictors of vegetated area differ among zones (Table 3). In zone 1, the best predictor of vegetated area is peak flow, although duration of elevated base flow and low flow are also significant. Relationships indicate that vegetation decreases with larger peak flows and that vegetation increases with larger low flows and longer duration of elevated base flow. The peak flow relationship suggests that disturbance by large floods controls the amount of vegetated area in this zone. The relationship for elevated base flow suggests that flows that do not inundate the entire zone for long duration may provide water for pulses of vegetation expansion (for example, the increases in vegetation in zone 1 from 2002 to 2004 and 2005 to 2009 that are depicted in Figure 6 are periods of elevated base flow).

In zones 2 and 3, low flow is the best predictor of vegetated area. Relationships indicate that in these zones vegetation increases with larger low flows. This suggests that shallow groundwater might make more water available to deep-rooted plants when low flows are larger. In zone 4, none of the metrics is a significant predictor of vegetated area. In zone 5, precipitation drought is the best predictor of vegetated area, though does not differ significantly from the constant model; the relationship indicates that vegetation decreases during drought.

In the entire riparian area (i.e., when data are analyzed among all zones), the duration of inundation is the best predictor of vegetated area. Vegetated area decreases with longer duration of inundation. We use the model coefficients for duration of inundation for all zones (Table 3) to estimate inundation duration that can keep riparian vegetation from expanding. At the beginning of our study in 1965, vegetated area is less than 12% in zones 1–4 (Figure 6). The model indicates that vegetated area does not exceed 12% when a zone is inundated for more than 10% of time. Conversely, in our data, vegetated area does not exceed 12% (Figure 6) for any zones inundated ≥5% of time (Figure 2c). Therefore, a useful estimate of inundation that can control the expansion of riparian vegetation is at least 10% duration and possibly as low as 5%. The flow duration curves for each of the time steps (Figure 2c) suggest that 5% duration of inundation is never exceeded in zone 5, is exceeded only prior to 1965 for zones 2–4, and is exceeded prior to 1965 and from 1973 to 1992 in zone 1.

The statistical relationships between vegetation and hydrology are consistent with changes depicted in the aerial images. For example, there is more unvegetated, bare sand visible in the images from 1965 to 1992, which is the period of unrestricted hydro-peaking that is characterized by greater duration of inundation and larger peak flows (Figure 8a). Many areas of bare sand in the 1965 image are more vegetated in the 1973 image but then less vegetated in the 1984 image due to scour of vegetation caused by high peak flows during the spillway flood of 1983 [*Rubin et al.*, 1990]. In the images after 1992, bare sand is mostly confined to narrow areas of shorelines (e.g., eddy bars in circled eddy areas in Figures 8a and 8b) that exhibit dramatic vegetation expansion during the 2000s. From 2002 to 2009 the bare eddy bars were inundated infrequently, but elevated base flows at specific time intervals might have promoted pulses of riparian vegetation expansion. Further upslope, vegetation appears to reach and plateau at high cover during the 2000s.

5. Discussion

Analyses of classified remotely sensed imagery for locations along 362 km of the Colorado River in Marble and Grand Canyons confirm that there has been a progressive increase in riparian vegetation during the five decades since the completion of Glen Canyon Dam. The magnitude and timing of vegetation changes differ along five zones of the riparian area that are defined by stage above common postdam base flows. Much of

the long-term increases in vegetation occurred in the lowest zones that are inundated by hydro-peaking and were once part of the predam active channel. This finding indicates a downward expansion of vegetation that filled in parts of the predam active channel, resulting in a long-term lowering of the riparian area [*Auble et al.*, 2005; *Stromberg et al.*, 2007].

Vegetation in lower zones is substantially shorter-lived than vegetation in higher zones. This is attributable to a greater susceptibility of vegetation at lower elevations to flooding, scouring, and burial [*Stevens et al.*, 1995]. This is also attributable to the composition of long-lived, facultative riparian and phreatophytic vegetation that can access deeper water at higher elevations [*Clover and Jotter*, 1944; *Turner and Karpiscak*, 1980]. In all zones, the long-term composition of vegetation is overwhelmingly woody. Thus, results indicate a long-term expansion of woody vegetation over the five decades; spatiotemporal trends exhibited in regulated rivers throughout the western U.S. and elsewhere [*Friedman et al.*, 2005; *Webb and Leake*, 2006; *Mortenson and Weisberg*, 2010]. The nonnative woody species tamarisk is ubiquitous across zones but is a codominant species with other riparian shrubs. This contrasts with the upper basin of the Colorado River in Utah and Colorado where tamarisk often dominates the landscape [*Merritt and Cooper*, 2000; *Cooper et al.*, 2003] and suggests that tamarisk and other riparian shrubs may respond similarly to altered flow regimes and climate in our study area.

The hydrology of the past five decades on the regulated Colorado River is characterized by net decreases in flood magnitude, increases in the magnitude of base flows, and recent drought [*Topping et al.*, 2003; *Mortenson et al.*, 2012; *Hereford et al.*, 2014]. Our results suggest that for riparian vegetation in zone 1 these changes in hydrology increase habitable space, decrease disturbance, and potentially increase water availability. Collectively, these changes promote colonization of low-elevation bare surfaces and sandbars. In contrast, the long-term expansion of riparian vegetation in zones 2 and 3 is most influenced by elevated base flows that make groundwater more available to plants. In zone 4, effects of streamflow and precipitation on vegetated area are not resolved. In zone 5, vegetation varies as a function of precipitation. The effects observed in the lower zones are supported by previous research specific to shorter time intervals and/or species [*Cooper et al.*, 2003; *Stevens et al.*, 1995; *Turner and Karpiscak*, 1980; *Waring*, 1995; *Mortenson et al.*, 2012]. The effects in the highest zone indicate a decoupling of climate and hydrology that can be characteristic of regulated rivers [*Johnson*, 2002; *Mortenson et al.*, 2012; *Perry et al.*, 2012, 2013]. It is particularly interesting that in zone 4, vegetation increases during the first three decades of the study in similar fashion to zones 1–3 in which vegetation responds to streamflow but then decreases from 1992 to 2009 which is consistent with drought-related changes in zone 5. It is possible that the relative influence of streamflow versus precipitation shifted for zone 4 during the past five decades and might explain why neither type of environmental variable predicts vegetation changes in this zone.

In the future, river managers might consider changing dam operations in order to optimize a regulated flood regime that can rehabilitate or increase the resilience of riparian ecosystems. However, under anticipated future aridity [*U.S. Department of the Interior*, 2012], managers will contend with the compound effects of riparian vegetation communities that continue to expand at lower zones of the riparian area, yet that are subjected to drought and have become increasingly disconnected from river hydrology at higher zones.

6. Summary and Conclusions

Large dams decouple predam riparian vegetation from the streamflow regime for those zones of the riparian area that are never again inundated. At those zones, vegetated area varies with precipitation and drought. For zones that are rarely inundated by the postdam flow regime, there may be a decadal period of expansion of riparian vegetation into parts of the active channel that are abandoned due to flood control, but eventually, that response wanes. At even lower zones, however, riparian vegetation proliferates. Five decades since completion of the Glen Canyon Dam, riparian vegetation communities of the downstream Colorado River are subjected to drought and disconnected from river hydrology at higher zones, yet continue to expand at lower zones. Flow regimes downstream from Glen Canyon Dam that decrease the magnitude and frequency of peak floods but that also increase base flows result in riparian vegetation expansion and lowering of the riparian area. Short pulses of high flow, such as the controlled floods of the Colorado River in 1996, 2004, and 2008, do not keep vegetation from expanding onto bare sand habitat. Vegetation expansion is coincident with inundation frequency; vegetated area apparently does not expand, in our study,

if the surface is inundated for as little as 5% of the time (e.g., 18 d/yr), which might be a useful estimate of inundation that can keep riparian vegetation expansion at bay.

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