Prepared in cooperation with the Bureau of Reclamation Glen Canyon Adaptive Management Program

Assessment of Riparian Vegetation Patterns and Change Downstream from Glen Canyon Dam from 2014 to 2019

Open-File Report 2023–1026

U.S. Department of the Interior
U.S. Geological Survey

Cover: Riparian plant community in Grand Canyon downstream from the confluence of National Canyon and the Colorado River. Photograph by Emily Palmquist, U.S. Geological Survey, September 2022.

Assessment of Riparian Vegetation Patterns and Change Downstream from Glen Canyon Dam from 2014 to 2019

By Emily C. Palmquist, Bradley J. Butterfield, and Barbara E. Ralston

Prepared in cooperation with the Bureau of Reclamation Glen Canyon Adaptive
Management Program

Open-File Report 2023–1026

U.S. Department of the Interior
U.S. Geological Survey

U.S. Geological Survey, Reston, Virginia: 2023

Suggested citation:
Palmquist, E.C., Butterfield, B.J., and Ralston, B.E., 2023, Assessment of riparian vegetation patterns and change downstream from Glen Canyon Dam from 2014 to 2019: U.S. Geological Survey Open-File Report 2023–1026, 55 p., https://doi.org/10.3133/ofr20231026.

Associated data for this publication:
Palmquist, E.C., Butterfield, B.J., and Ralston, B.E., 2022, Riparian vegetation data downstream of Glen Canyon Dam in Glen Canyon National Recreation Area and Grand Canyon National Park, AZ from 2014 to 2019: U.S. Geological Survey data release, https://doi.org/10.5066/P9KEHY2S.

ISSN 2331-1258 (online)

Acknowledgments

The data in this report were collected in cooperation with Dustin Perkins, Amy Washuta, and Luke Gommerman from the Northern Colorado Plateau Network Inventory & Monitoring program and with Joseph Hazel and Matthew Kaplinski at Northern Arizona University. More than 100 volunteers, boat operators, and collaborators assisted with data collection during this study period.

Data collection and management were conducted in cooperation with Paul Grams, Thomas Gushue, James Hensleigh, Anna Knight, Sarah Sterner, Andrea Hazelton, Erica Fraley, Laura Durning, and Joel Sankey. Joshua Caster assisted with climate data and summaries.

Contents

Figures

Tables

Conversion Factors

U.S. customary units to International System of Units

Multiply	By	To obtain
foot (ft)	0.3048	meter (m)
mile (mi)	1.609	kilometer (km)
yard (yd)	0.9144	meter (m)
acre-foot per day (acre-ft/d)	0.01427	cubic meter per second (m^3)
cubic foot per second (ft^3)	0.02832	cubic meter per second (m^3)
million gallons per day (Mgal/d)	0.04381	cubic meter per second (m^3)

International System of Units to U.S. customary units

Multiply	By	To obtain
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
meter (m)	1.094	yard (yd)
cubic meter per second (m^3)	70.07	acre-foot per day (acre-ft/d)
cubic meter per second (m^3)	35.31	cubic foot per second (ft^3)
cubic meter per second (m^3)	22.83	million gallons per day (Mgal/d)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$°F = (1.8 \times °C) + 32.$$

Datum

Vertical coordinate information is referenced to the National Geodetic Vertical Datum of 1929 (NGVD1929).

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD83).

Altitude, as used in this report, refers to distance above the vertical datum.

Abbreviations

DCA	Detrended correspondence analysis
GCMRC	Grand Canyon Monitoring and Research Center
HFE	high-flow experiment
Rkm	River kilometer

Assessment of Riparian Vegetation Patterns and Change Downstream from Glen Canyon Dam from 2014 to 2019

By Emily C. Palmquist,[1] Bradley J. Butterfield,[2] and Barbara E. Ralston[1]

Abstract

Changes in riparian vegetation cover and composition occur in relation to flow regime, geomorphic template, and climate, and can have cascading effects on aquatic and terrestrial ecosystems. Tracking such changes over time is therefore an important part of monitoring the condition and trajectory of riparian ecosystems. Maintaining diverse, self-sustaining riparian vegetation comprised of mostly native species is identified in the Glen Canyon Dam Long-Term Experimental and Management Plan as a key resource objective for the section of the Colorado River between Glen Canyon Dam and Lake Mead. The U.S. Geological Survey Grand Canyon Monitoring and Research Center implemented an annual monitoring program in 2014 to assess the status and trends of riparian vegetation along this section of river, particularly as they relate to flow regime. In this report, we summarize plant species composition and cover data collected under the annual monitoring program from 2014 to 2019, with special consideration given to the hydrologic position, associated geomorphic feature class, local climate patterns, native and nonnative species, and floristic region for key vegetation metrics and species. We divided the study area into four river segments (referred to as Glen Canyon, Marble Canyon, eastern Grand Canyon, and western Grand Canyon) on the basis of geography and floristic composition and calculated each recorded plant species' relative frequency and foliar cover by river segment. These data were then used to evaluate species composition relationships among river segments, hydrologic zones, geomorphic features, and sampling years through ordination analysis. Temporal trends in our focal resource objectives—species richness, total foliar cover, proportion of native to nonnative species richness, proportion of native to nonnative species cover, *Tamarix* cover, *Pluchea sericea* cover, and *Baccharis* species cover—were assessed using mixed-effects models. Four patterns related to species composition emerged: (1) species composition of fixed-site sandbars differed from that of randomly selected sites (including randomly selected sandbars), (2) species composition of Glen Canyon sites differed from that of other previously identified floristic regions, (3) species composition differed across hydrologic zones related to dam operations, and (4) species composition within river segments did not change across years. For temporal patterns, four main findings emerged: (1) trends differed between fixed-sites and randomly selected sites; (2) although few directional changes were observed from 2014 to 2019, *Baccharis* species cover increased at randomly selected sites in areas influenced by daily water fluctuations; (3) native species cover and richness were greater than nonnative species cover and richness across all hydrologic zones; and (4) the temporal trend metrics used here can be used across floristic groups, enabling assessment of the Colorado River ecosystem as a whole. In addition to these findings, lists of recorded plant species are included as appendixes. The variations and patterns in vegetation status and trends presented in this report can be used as a baseline against which future monitoring can be compared.

Introduction

Riparian ecosystems are dynamic, disturbance-driven habitats (Poff and others, 1997), and temporal changes to riparian vegetation are integral to riparian functioning (Naiman and Decamps, 1997; Tabacchi and others, 1998). Disturbance events, particularly floods, periodically reshape riparian areas by eroding and depositing sediment, distributing seeds and propagules, redistributing nutrients, and damaging or removing vegetation (Stevens and Waring, 1986; Gregory and others, 1991; Tabacchi and others, 1998; Dong and others, 2016). Between large disturbance events, succession occurs, leading to changes in vegetation structure, composition, and aerial extent (Webb and Leake, 2006; Stromberg and others, 2010; Sarr and others, 2011; Sankey and others, 2015). Changes in riparian vegetation composition and cover over time are therefore expected consequences of natural ecosystem processes.

Flow regime is a primary controlling factor for riparian vegetation composition and change (Poff and others, 1997; Stromberg and others, 2007). The timing, magnitude, duration, and frequency of flooding establishes the rate of succession and development of riparian vegetation (Tabacchi and others, 1998). Natural flow regimes can be highly dynamic within a year but are fairly predictable across years, such that high and low flows exhibit a consistent seasonality (Poff and others, 1997; Topping and others, 2003). High volume or long

---

[1] U.S. Geological Survey

[2] Northern Arizona University

duration floods can remove vegetation, clearing the riparian area for new colonization (Stevens and Waring, 1985; Dean and Schmidt, 2011). Many *Populus* (cottonwood) and *Salix* (willow) species require vegetation-clearing floods during species-specific times of the year in order to germinate (González and others, 2018); without such floods, their populations decline (Rood and others, 2005; Merritt and Poff, 2010; Mortenson and Weisberg, 2010). Reduced flood peaks—whether due to climate shifts or river regulation—can create an opportunity for riparian vegetation to expand and stabilize the floodplain (Sankey and others, 2015; Scott and others, 2018). Increasing year-round baseflows (in other words, creating a constant water supply) in concert with flood-peak reduction provides the context for woody riparian species to proliferate (Stromberg and others, 2007; Mortenson and Weisberg, 2010; Sankey and others, 2015) and can promote clonal growth (Douhovnikoff and others, 2005; Ralston, 2011)—an example of how alterations to flow regime can change the composition, cover, and diversity of riparian vegetation. The parameters of the new flow regime and the available species pool determine the resulting riparian vegetation community.

The influence of flow regime on trends in riparian vegetation change is constrained by a hierarchy of environmental variables. At a broad scale, riparian vegetation communities shift along longitudinal gradients related to climate (McShane and others, 2015; Palmquist and others, 2018a). As changes in climate occur over time (manifested as temperature, precipitation, and subsequent flow dynamics), riparian species composition is also likely to change (Perry and others, 2015; Reynolds and others, 2015). Within landscape-scale patterns of climate, channel form, geology, geomorphology, and alternating constrained and floodplain river reaches affect species occurrence (Tabacchi and others, 1998; McShane and others, 2015). Flow interactions with geomorphology maintain a mosaic of vegetation patches with differing species compositions based on differences in soil water holding capacity and topography (Lytle and Poff, 2004; Lite and others, 2005; Stromberg and others, 2007). Channel form controls the velocity and depth of flows, such that narrow reaches have different flood dynamics than wide reaches. At a local scale, species turnover occurs along lateral gradients related to water and oxygen availability (Bendix, 1994b; Lite and others, 2005), with more flood tolerant species growing closer to base flows (McCoy-Sulentic and others, 2017a).

River regulation via large dams affects riparian vegetation composition and cover through many of the same mechanisms listed above. Large dams dramatically change flow regime and reduce sediment inputs (Webb and others, 1999; Gloss and others, 2005; Magilligan and Nislow, 2005). They can alter the geomorphic template of a river by changing the grain size distribution of sediment deposits, eroding potential habitat for vegetation, and changing feedback loops between vegetation and sediment (Rubin and others, 2002; Hazel and others, 2006; Butterfield and others, 2020). Depending on pre- and post-dam flow characteristics, riparian vegetation can increase or decrease in cover and richness, shift in species composition, maintain or lose functional groups, and change in genetic structure (Jansson and others, 2000; Douhovnikoff and others, 2005; Beauchamp and Stromberg, 2008; Merritt and Poff, 2010; Bejarano and others, 2012; Werth and others, 2014; Sankey and others, 2015; Bejarano and others, 2018). Vegetation changes related to dam operations can occur on different time and spatial scales depending on the natural processes affected and species longevity. Long after dam operations are implemented, riparian vegetation composition and cover can continue to shift as a result of ecosystem change, flow regime management, invasive plant species management, and the occurrence of other disturbances such as fire, restoration efforts, and insect herbivory (Stevens and others, 1995; Kearsley and Ayers, 1996; Sankey and others, 2015).

Tracking riparian vegetation change is a primary method for assessing riparian ecosystem condition because riparian vegetation exists at the intersection between aquatic and terrestrial systems and provides habitat and other key resources for both (Merritt and others, 2017; Palmquist and others, 2018b; Perkins and others, 2018). Consistent monitoring of vegetation and periodic assessment of the data collected to identify changes to riparian species diversity, distributions, and cover provide information about the trajectory of riparian vegetation change relative to hydrology and other abiotic or management manipulations (for example, invasive plant management). In this report, we examine plant species composition and trends in plant cover from 2014 to 2019 along the segment of the Colorado River between Glen Canyon Dam and Lake Mead. These patterns are analyzed in the context of hydrologic, geomorphological, and climate parameters and discussed relative to other sources of vegetation change (for example, vegetation management actions and biological control of invasive species).

The segment of the Colorado River between Glen Canyon Dam and Lake Mead supports a culturally and ecologically important riparian ecosystem that fulfills a variety of societal and ecological functions. Located in northwestern Arizona, this section of the Colorado River (hereafter referred to as the “study area” or “study reach”) flows through the lower part of Glen Canyon, Marble Canyon, and Grand Canyon within Glen Canyon National Recreation Area (GLCA) and Grand Canyon National Park (GRCA). The study area supports a suite of animal life including birds, mammals, amphibians, reptiles, and invertebrates (Carothers and others, 1976; Schmidt and others, 1998; Stevens and others, 2001; Holmes and others, 2005). Riparian vegetation in Grand Canyon is traditionally important to many regional tribes, in part for its role in supporting the overall health of Grand Canyon ecosystems and for the usefulness of particular species (Mayes and Lacy, 1989; Fairley, 2005; Jackson-Kelly and Hubbs, 2007). Some plant species are important to river recreationists for the shade and protection from wind they provide in a hot, dry climate (Stewart and others, 2003). In the southwestern United States, where riparian areas are often impaired and degraded (Stromberg and others, 2012; Stromberg and others, 2013), this riparian area supports some functions lost in other dryland areas (Spence, 2006).

Riparian vegetation expansion in the study area has a positive effect on bird communities. The diversity and abundance of bird species increased with the establishment of perennial riparian vegetation near the river's edge (Brown and Johnson, 1985) and are predicted to increase further as habitat patches grow larger and become more contiguous (Holmes and others, 2005). The volume and location of woody plant species are identified as key qualities for predicting the abundance of breeding birds (Sogge and others, 1998; Spence, 2006). Plant species composition is also important to breeding birds; for example, *Prosopis glandulosa* (honey mesquite) and *Senegalia greggii* (catclaw acacia) densities promote bird density (Kearsley and others, 2004). Changes to the extent, amount, and species composition of riparian vegetation in the study area will affect bird diversity and abundance (Holmes and others, 2005).

In the study area, increases in shrubby riparian plant cover are considered detrimental to campsites and archeological sites, which are identified as key resources in the Glen Canyon Dam Long-Term Experimental and Management Plan (U.S. Department of the Interior, 2016; Durning and others, 2021). Increased shrub cover on historically large, bare sandbars is the primary cause of a 37-percent reduction from 2002 to 2016 in the limited camping area available for the more than 25,000 boaters and hikers that recreate in the area annually (National Park Service, 2006; Hadley and others, 2018). The study area provides a unique wilderness experience for recreationists that is supported in part by access to a sufficient number of suitable campsites and day use areas (Kearsley and others, 1994; Kaplinski and others, 2005). Vegetation expansion on large sandbars in the study area also reduces aeolian transport of sand, which has historically facilitated the burial and protection of archeological sites (East and others, 2017; Hadley and others, 2018; Kasprak and others, 2018); thus, vegetation expansion decreases the stability of the unique cultural legacy found along the Colorado River (Sankey and Draut, 2014). Vegetation expansion near the river edge is predicted to continue (Sankey and others, 2015; Kasprak and others, 2018), potentially exacerbating the negative effects of riparian vegetation expansion on these Colorado River resources.

As identified in the record of decision for the Glen Canyon Dam Long-Term Experimental and Management Plan final environmental impact statement (U.S. Department of the Interior, 2016), the goal for riparian vegetation in the study area is to "maintain native vegetation and wildlife habitat, in various stages of maturity, such that they are diverse, healthy, productive, self-sustaining, and ecologically appropriate." The long-term monitoring data presented herein can be used to address questions related to the diversity, productivity, and relative dominance of native and nonnative species in terms of areal cover and species composition. Assessing the quality of wildlife habitat would require additional sampling of vegetation structure, and assessing the maturity, health, and sustainability of vegetation would require plant growth and demography monitoring that is beyond the scope of this program. However, the long-term monitoring data herein can provide indirect insights into such objectives. The objective of ecological appropriateness can be judged by stakeholders on the basis of the results presented in this report.

To reliably and consistently track changes to riparian vegetation within the study area, a long-term monitoring protocol was developed and implemented by the Grand Canyon Monitoring and Research Center (GCMRC; Palmquist and others, 2018b; Palmquist and others, 2019). Given the influence of geomorphology, climate, and flow regime in determining riparian vegetation composition and cover, the protocol incorporates geomorphic feature classes, flow parameters, and river segments related to floristic groups and climate into vegetation sampling. The primary objectives of the GCMRC riparian monitoring program are as follows:

- Annually measure and summarize the status (that is, composition and cover) of native and nonnative vascular plant species within the riparian zone of the Colorado River between Glen Canyon Dam and Lake Mead.
- At 5-year intervals, assess change in the vegetation composition and cover within the riparian zone, as related to geomorphic setting and dam operations (particularly flow regime).
- Collect data in such a manner that it can be used by multiple stakeholders and is compatible with the basin-wide monitoring program overseen by the National Park Service's Northern Colorado Plateau Network Inventory and Monitoring program (Perkins and others, 2018).

This status and trends report summarizes species composition and cover data collected from 2014 to 2019, with special consideration given to floristic region, hydrologic position, associated geomorphic feature, and native and nonnative species.

Methods

Study Area

Physical Setting

The section of the Colorado River between Glen Canyon Dam and the high-water inflow of Lake Mead is an approximately 415-kilometer (km; 260-mile [mi]) reach that passes through Glen Canyon National Recreation Area and Grand Canyon National Park (fig. 1). Locations along the river are denoted using river kilometers (Rkm; Gushue, 2019)—that is, by their distance downstream (positive numbers) or upstream (negative numbers) from Lees Ferry as measured in kilometers along the channel centerline. For the purposes of the GCMRC riparian monitoring program, the river corridor is divided into four segments that relate to geography and floristic composition (Palmquist and others, 2018a): the Glen Canyon river segment, spanning from Rkm −25 to Rkm 0 (hereafter referred to as "Glen Canyon"); the Marble Canyon

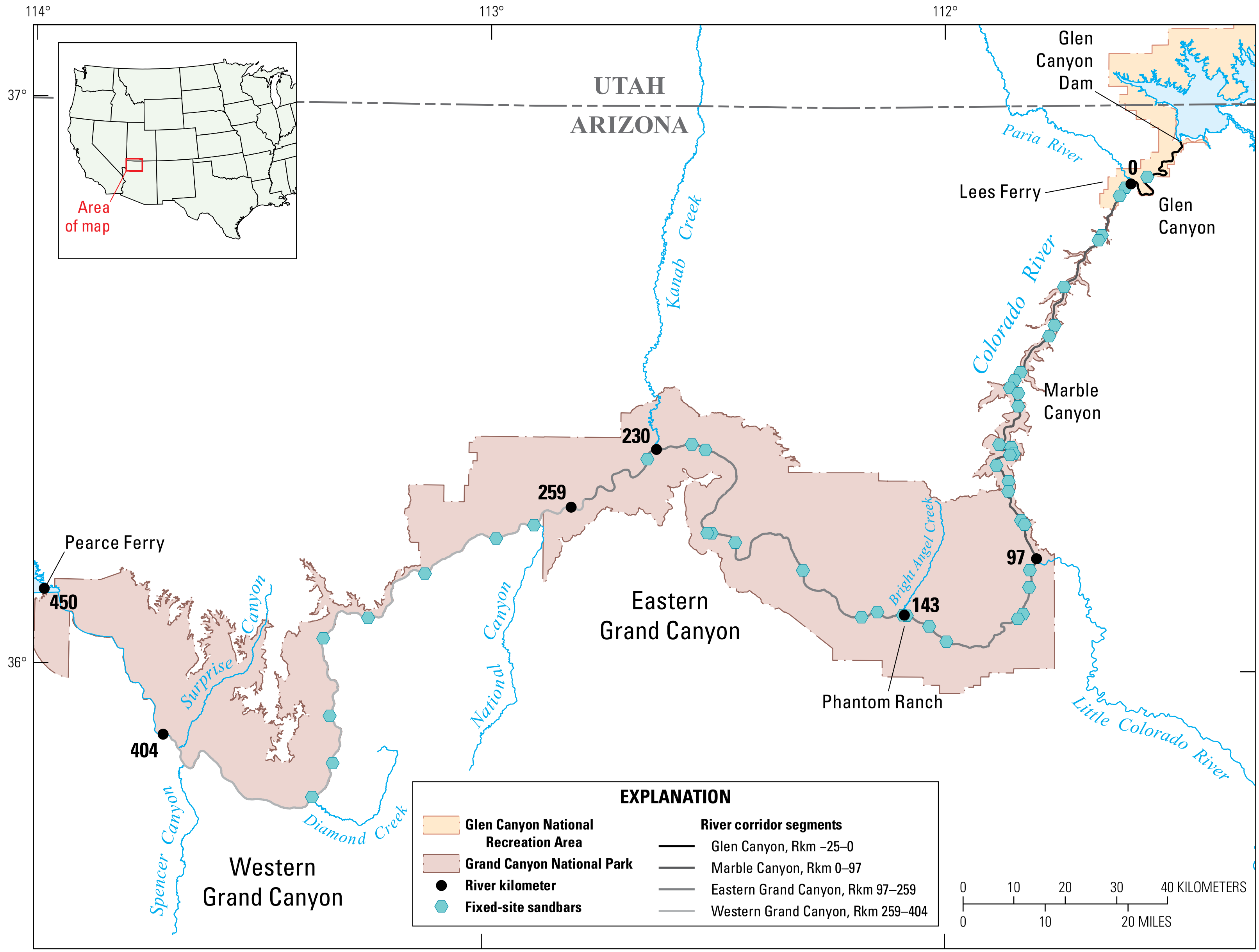

Figure 1. Map of the Colorado River between Glen Canyon Dam and the high-water inflow of Lake Mead, with eight tributaries identified. The river corridor is divided into four segments (shown in different shades of gray) that relate to geography and floristic patterns: the Glen Canyon segment, spanning from Glen Canyon Dam to Lees Ferry (river kilometers [Rkm] −25–0); the Marble Canyon segment, spanning from Lees Ferry to the Little Colorado River (Rkm 0–97); the eastern Grand Canyon segment, spanning from the Little Colorado River to National Canyon (Rkm 97–259); and the western Grand Canyon segment, spanning from National Canyon to the high-water inflow of Lake Mead (Rkm 259–404). Fixed-site sandbar locations are indicated by blue hexagons.

segment, spanning from Rkm 0 to Rkm 97 (hereafter “Marble Canyon”); the eastern Grand Canyon segment, spanning from Rkm 97 to Rkm 259 (hereafter “eastern Grand Canyon”); and the western Grand Canyon segment, spanning from Rkm 259 to Rkm 404 (hereafter “western Grand Canyon”; fig. 1). At Rkm 404, the high-water line of Lake Mead is apparent on the shorelines of the Colorado River as deltaic sediments that were deposited when the reservoir was full; these deposits are not included in the GCMRC riparian monitoring protocol.

The geologic rock layers at river level include limestones, sandstones, and Precambrian metamorphic rocks, with each layer affecting the channel width and associated habitable area for plants. Throughout the study area, the Colorado River is a canyon-bound river with a pool-drop rapid system in which rapids are associated with tributary debris fans (Schmidt and Graf, 1990). Approximately 740 tributaries (most of them ephemeral) join the Colorado River’s mainstem between Glen Canyon Dam and Lake Mead (Griffiths and others, 2004). Debris fans originating from these tributaries form channel constrictions that create rapids and affect the direction and velocity of the river current and associated sediment deposition (Rubin and others, 1990). Upstream from a channel constriction, water pools and the current is slower, and sediment can accumulate along the upstream shoreline. Downstream from a constriction, part of the current recirculates upstream and slows, creating an eddy wherein sediment deposition can also occur. Shorelines both upstream and downstream from channel constrictions are areas where sediment accumulates and forms sandbars (fig. 2; Schmidt and Graf, 1990; Mueller and others, 2018). Within this geomorphic

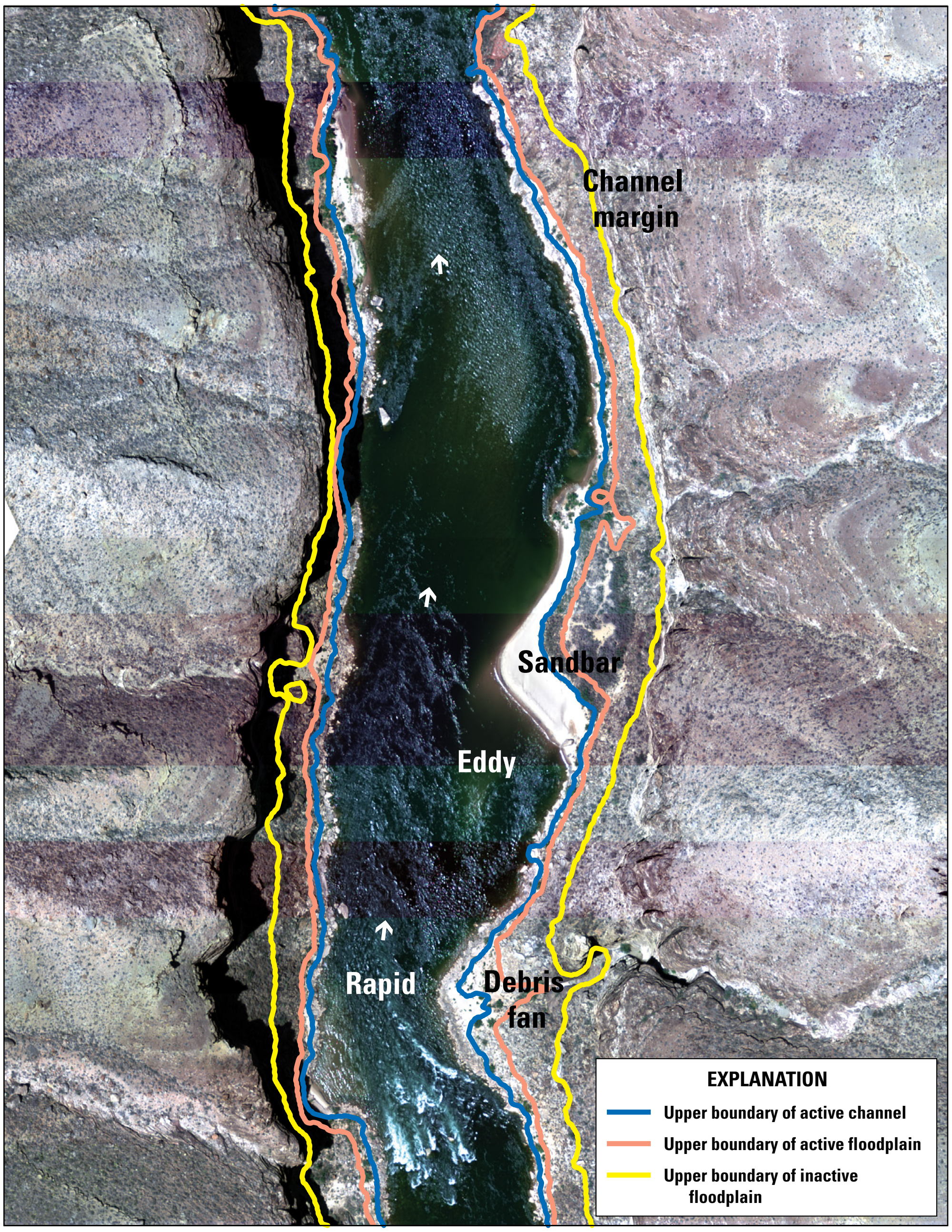

Figure 2. Aerial photograph showing examples of the generalized feature classes (debris fan, sandbar, and channel margin) that form the geomorphic template of the Colorado River within the study area. Debris fans are cone-shaped, coarse-grained sediment deposits emanating from tributaries, and sandbars are fine-grained deposits that form upstream and downstream from debris fans; the channel margin feature class encompasses all other shorelines. Hydrologic zones related to Glen Canyon Dam operations (active channel, active floodplain, and inactive floodplain) are also depicted. The active channel is the area inundated by daily flow fluctuations (discharges of 707 cubic meters per second [m^3/s] or less); the active floodplain is the area flooded by high flow experiments (discharges between 707 and 1,274 m^3/s); and the inactive floodplain, which is rarely flooded under current dam operations, is the area inundated by discharges of more than 1,274 m^3/s. White arrows indicate the direction of flow. Base image from Durning and others (2016).

template, there are three generalized feature classes on which riparian vegetation can grow: debris fans, sandbars, and channel margins. Debris fans are triangular or cone-shaped deposits of boulders, cobbles, gravel, and sand that typically emanate from tributaries; and sandbars are fine-grained deposits located upstream and downstream from debris fans. Channel margins encompass all other shorelines and can consist of bedrock and (or) deposited boulders, cobbles, gravel, and sand (fig. 2).

Hydrology

The hydrology of the study reach is controlled by Glen Canyon Dam (fig. 1). Before dam operations began in 1963, the Colorado River had a seasonal snowmelt-dominated hydrograph with large seasonal flow volume variation and little daily variation; in the post-dam era, however, discharge fluctuates daily but is relatively similar across seasons (figs. 3, 4). Except for large, unplanned floods in the 1980s, post-dam floods peak at less than half the magnitude of pre-dam floods, are relatively infrequent, and occur primarily in the fall rather than late spring and summer (as was typical before the dam; Topping and others, 2003). Within the post-dam era, the magnitude of daily fluctuations from 1963 to the mid-1990s was greater (sometimes exceeding 790 m^3/s) than it is under current conditions (in which it does not exceed 226 m^3/s) owing to the implementation of the Modified Low Fluctuating Flow operation pattern (U.S. Department of the Interior, 2016). The potential for releases exceeding 707 m^3/s over several days has increased relative to that from 1963 to 2011 owing to implementation of the Experimental Management Plan for Glen Canyon Dam. This plan incorporates short-duration (that is, dayslong) high-flow experiment (HFE) releases in spring or fall if resource criteria for water, sediment, and fish are met (U.S. Department of the Interior, 2016). The pre-dam high-water line, the experimental high flows, and the daily fluctuating flows create a gradient of inundation frequency ranging from a more frequently flooded area close to the river to an infrequently flooded area far away from the shoreline (fig. 2). Three hydrologic zones are delineated based on these effects of dam operations (fig. 4). The active channel is the area that can be inundated by daily fluctuating flows (that is, by flows of 708 m^3/s or less) and is the most frequently flooded zone. The active floodplain is the area inundated by HFE releases (that is, by discharges between 708 and 1,274 m^3/s) and is less frequently flooded than the active channel. The inactive floodplain is the area within the historical high-water line that is no longer inundated by planned dam releases. The inactive floodplain zone was last flooded in the 1980s and is currently more influenced by local precipitation than river flows (Sankey and others, 2015).

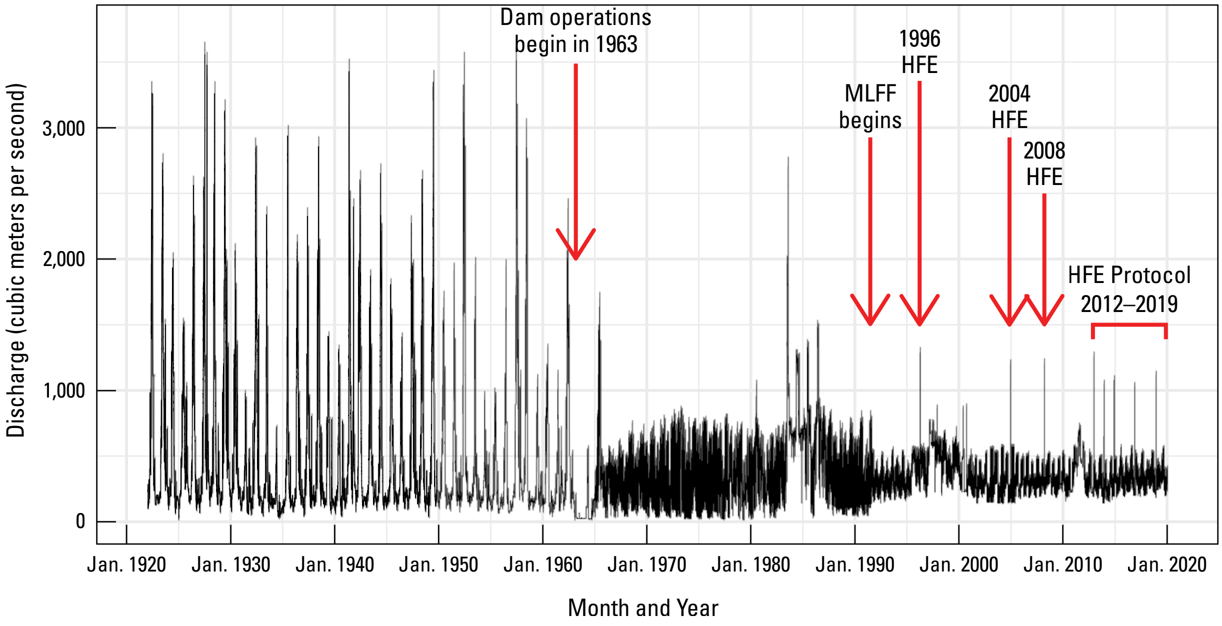

Figure 3. Hydrograph of the Colorado River from 1921 to present, as recorded at Lees Ferry, Arizona. Notable changes in dam operations are indicated. MLFF, Modified Low Fluctuating Flow; HFE, high flow experiment; m^3/s, cubic meters per second.

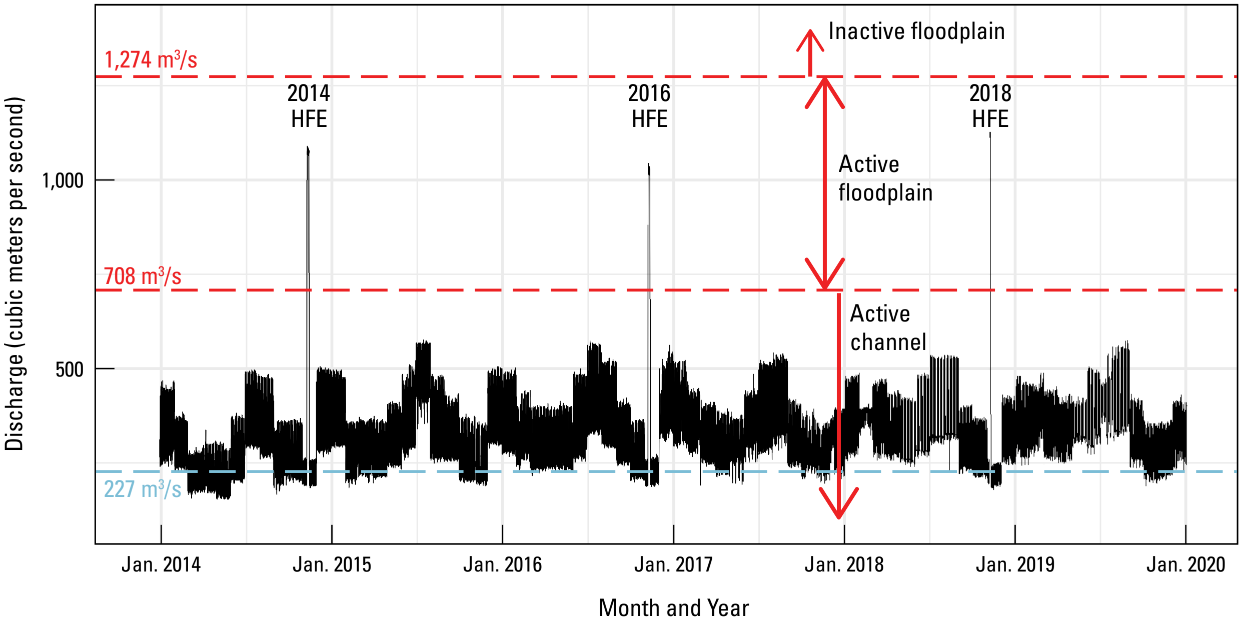

Figure 4. Hydrograph showing hourly discharge data for the Colorado River at Lees Ferry, Arizona, from January 1, 2014, to December 31, 2019. High flow experiment (HFE) releases are labeled (for example, "2014 HFE"). Red dashed lines indicate discharge levels from Glen Canyon Dam that are used by this study to delineate three hydrologic zones (active channel, active floodplain, and inactive floodplain) on the basis of inundation frequency. Red arrows indicate the range of discharge levels associated with each hydrologic zone. Active channel is defined as the area inundated by daily fluctuating flows that range up to 708 cubic meters per second [m^3/s]. Active floodplain is defined as the area inundated by HFE releases (that is, by discharges between 708 and 1,274 m^3/s). Inactive floodplain is defined as the area within the historical high-water line that is no longer inundated by planned dam releases. Light blue dashed line represents the minimum daytime flow (227 m^3/s) from Glen Canyon Dam under the Long-Term Experimental and Management Plan record of decision (U.S. Department of the Interior, 2016).

Riparian Vegetation History and Floristic Distributions

Vegetation growing along the study reach varies greatly in structure, functional strategies, wetland indicator status, and floristic affinities (McCoy-Sulentic and others, 2017a; McCoy-Sulentic and others, 2017b; Palmquist and others, 2017; Palmquist and others, 2018a). Species range from less than 1 centimeter tall to over 8 meters (m) tall and include annual, biennial, and perennial forbs, sedges, rushes, grasses, shrubs, and trees (Palmquist and others, 2017). Vegetation is densely layered in some parts of the canyon, consisting of a short-statured herbaceous layer (for example, *Schedonorus arundinaceus*, *Cynodon dactylon*, *Equisetum* x *ferrissii*, *Euthamia occidentalis*, *Bromus diandrus*), a midstory to overstory layer of woody shrubs (for example, *Baccharis emoryi*, *Baccharis salicifolia*, *Pluchea sericea*), and sometimes an overstory of trees (*Prosopis glandulosa*, *Tamarix*). Individuals of *Tamarix* (saltcedar) in this study area (hereafter "*Tamarix*") conform to the morphology of *T. ramosissima* and *T. chinensis* and are likely hybrids of the two species given their widespread introgression in the western United States (Gaskin and Schaal, 2002). In other areas, such as less vegetated sandbars or newer debris fans, vegetation is sparse and short, comprised mostly of smaller shrubs and grasses.

Plant species in the study area are associated primarily with desert and semiarid regions of the western United States, particularly the Mojave and Sonoran deserts but also the Colorado Plateau, Great Basin, and the Rocky Mountains (Palmquist and others, 2018a). Floristic patterns along the river follow an increasing temperature gradient with distance from Glen Canyon Dam, and three distinct floristic regions can be delineated that correspond with different river segments (Butterfield and others, 2018; Palmquist and others, 2018a). Of these floristic regions, Marble Canyon (Rkm 0–97) contains the highest proportion of species with affinities to higher elevation regions, particularly the Colorado Plateau and Rocky Mountains. Eastern Grand Canyon (Rkm 97–259) features an intermediate floristic group comprising a mixture of plants from Marble Canyon and western Grand Canyon. Western Grand Canyon (Rkm 259–404) is dominated by species with affinities to the Mojave and Sonoran deserts. Glen Canyon (Rkm −25–0) was not included in Palmquist and others (2018a), but we address it in the present study to determine if the unique species found there differentiate Glen Canyon floristically from Marble Canyon. Species composition also shifts laterally away from the river's edge with decreasing flood tolerance and increasing drought tolerance (McCoy-Sulentic and others, 2017a; Butterfield and others, 2018). These shifts in species composition result in a corresponding shift in functional trait values (McCoy-Sulentic and others, 2017a).

Prior to dam operations, the shoreline of the Colorado River through Marble and Grand Canyons was characterized much more by rock and sand than by riparian vegetation (Webb, 1996; Webb and others, 2011; Scott and others, 2018). The species recorded in the pre-dam era by Clover and Jotter (1944) are many of the dominant species recorded in current surveys, including nonnative species such as *Cynodon dactylon* (Bermuda grass) and *Tamarix*. Native riparian trees such as *Populus fremontii* (Fremont cottonwood) and *Salix gooddingii* (Gooding's willow) were largely absent in the pre-dam era except at the mouths of tributaries and more protected areas (Clover and Jotter, 1944; Turner and Karpiscak, 1980; Scott and others, 2018), though *S. gooddingii* appears to have been more common than *P. fremontii* (Clover and Jotter, 1944; Turner and Karpiscak, 1980). Naturally occurring *P. fremontii* and *S. gooddingii* stands are still uncommon in the study area.

Regulated flows from Glen Canyon Dam have allowed the areal cover of riparian vegetation to increase since dam operations began in 1963 (Sankey and others, 2015; Mueller and others, 2018), though growth rates vary in space and time. Variable flow patterns, including large floods in the 1980s and increased base flows, have alternately removed some vegetation (Stevens and Waring, 1986), supported fluvial marshes (Stevens and others, 1995), supported woody plant expansion into fluvial marshes (Kearsley and Ayers, 1996), promoted germination of and then eroded nonnative *Tamarix* seedlings (Porter and Kearsley, 2001), and created conditions favorable to clonal species (Ralston, 2010; Durning and others, 2021). Particularly since the beginning of Modified Low Fluctuating Flow in the early 1990s, vegetated area has increased in the active channel and active floodplain from approximately 5–9 percent to 25–40 percent depending on hydrological position (Sankey and others, 2015). Vegetation expansion is projected to continue under current dam operations and could increase 12 percent over the next 15 years (Kasprak and others, 2018).

Climate Variability

The climate of the study area is warm and dry with most precipitation falling in the winter and late summer (fig. 5; Caster and Sankey, 2016). Late summer precipitation

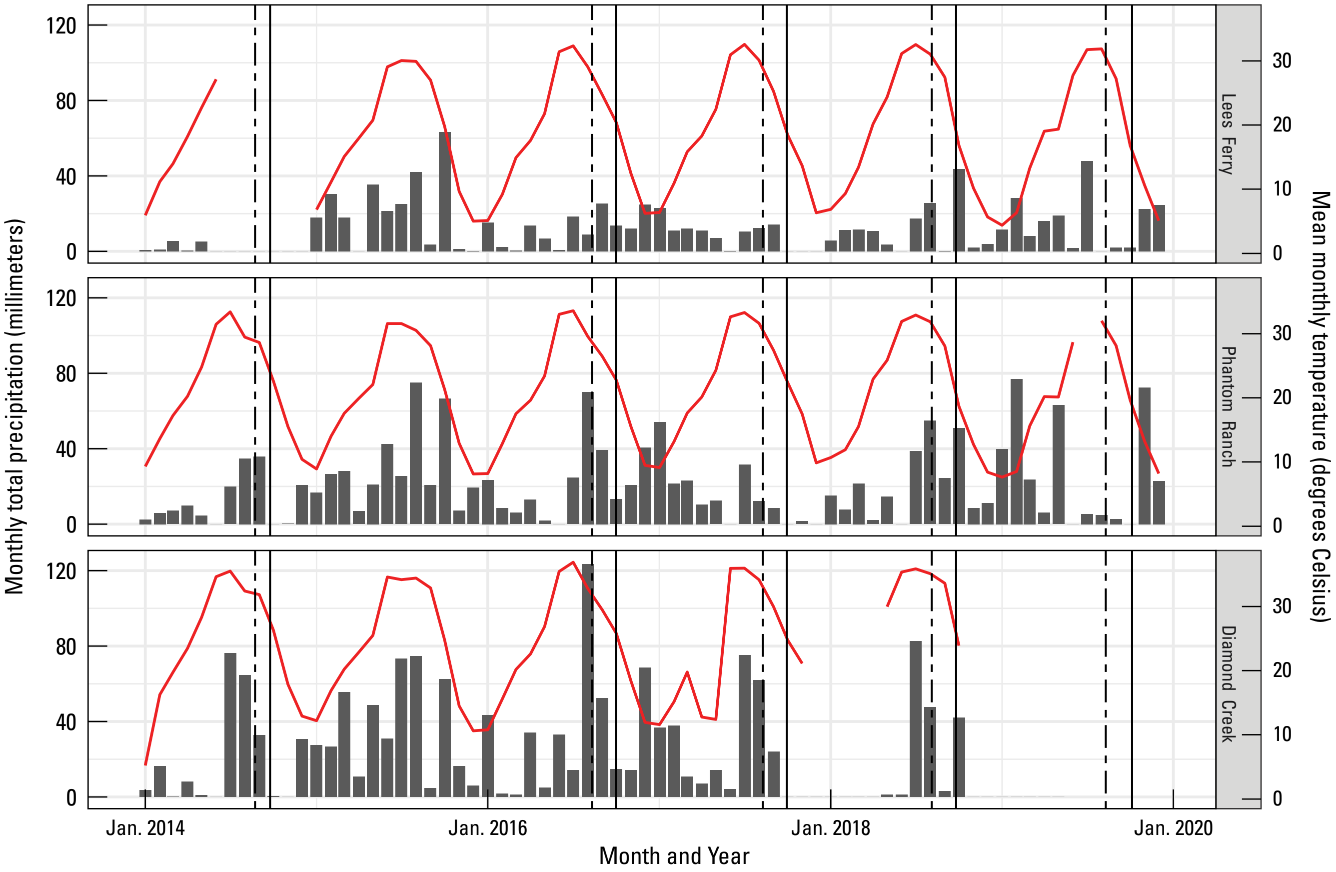

Figure 5. Mean monthly temperature (shown as red line) and monthly total precipitation (shown as gray bars) during the study period, as measured at meteorological stations at Lees Ferry, Phantom Ranch, and near the confluence of the Colorado River and Diamond Creek (labeled as "Diamond Creek" in figure), Arizona. Dash-dot and solid vertical lines indicate sampling events for randomly selected sites and fixed-site sandbars, respectively.

is associated with the North American monsoon and characterized by intense, localized thunderstorms between July and October. March through June and October through December are typically dry periods.

Climate data were acquired for the study period from three weather stations along the Colorado River: PGEA3, located at Lees Ferry (Rkm 0); USC00026471, located at Phantom Ranch (Rkm 143); and AZ G:03:0072, located near the confluence of Diamond Creek and the Colorado River (Rkm 359). Data for PGEA3 were downloaded from MesoWest (https://mesowest.utah.edu/) and for USC00026471 from the National Climate Data Center (https://www.ncdc.noaa.gov/cdo-web/). Data from AZ G:03:0072 were sourced from Caster and others (2018). Temperatures associated with the weather station at Lees Ferry were coolest, with a mean average temperature of 18.2 °C during the study period. Phantom Ranch temperatures were warmer at 20.4 °C, and Diamond Creek temperatures were warmest at 24.3 °C. The weather station at Lees Ferry received less average annual precipitation (164 millimeters [mm]) than the Phantom Ranch (250 mm) and Diamond Creek (337 mm) stations. In general, 2015 and 2016 were the wettest years. The driest years were 2014 and 2017, and 2019 had an exceptionally dry summer season (fig. 5).

Data Collection and Preparation

Data collection follows the methods described in detail in Palmquist and others (2018b) with a few exceptions. Data are collected at two different types of sites once per year: randomly selected sites that encompass multiple geomorphic features and are in different locations each year; and fixed-site eddy sandbars that are resampled each year. Pilot studies were conducted in 2012 and 2013 at a subset of locations for both fixed-site and random site datasets (table 1). Generally consistent sampling methods started in 2014 but were slightly modified for 2016 through 2019. Modifications from 2014 consist of adding an estimate of total living foliar cover, adding a separate estimation of overhanging plant species, and changing from estimating multiple grain-size categories to grouping all grain sizes greater than 2 mm into one category.

In August and early September, randomly selected debris fans, channel margins, and eddy sandbars were sampled. The random sampling protocol aimed to sample approximately equal numbers of these geomorphic features within each floristic segment each year (table 2). Each year, a new set of sites were randomly selected in ArcGIS (Palmquist and others, 2018b). Sites that are sampled are removed from the pool of potential sampling sites for a five-year period.

Table 1. Number of sites sampled for randomly selected sites and fixed-site sandbars by year.

[Dataset definitions are as follows: “Glen Canyon random,” randomly selected sites sampled in Glen Canyon (river kilometers [Rkm] −25–0); “Marble Canyon random,” randomly selected sites sampled in Marble Canyon (Rkm 0–97); “Eastern GRCA random,” randomly selected sites sampled in eastern Grand Canyon (Rkm 97 to 259); “Western GRCA random,” randomly selected sites sampled in western Grand Canyon (Rkm 259 to 404); Fixed-site sandbars, sandbars that are sampled annually across all river segments. “Pilot” indicates a smaller test subset of sites were sampled.]

Dataset	2012	2013	2014	2015	2016	2017	2018	2019
Glen Canyon random	0	0	0	6	7	6	6	7
Marble Canyon random	0	Pilot	25	0	21	25	25	25
Eastern GRCA random	0	Pilot	32	0	29	25	36	36
Western GRCA random	0	Pilot	39	0	32	32	31	34
Fixed-site sandbars	Pilot	42	42	43	43	43	43	42

Table 2. Number of randomly selected channel margin (CM), debris fan (DF), and sandbar (SB) sites and fixed-site sandbars for each river segment, with randomly selected sites further divided into years.

[Number of fixed-site sandbars (“Fixed-site SB”) within each river segment are not separated by year or geomorphic feature class because these sites are sampled annually and are all sandbars. River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Dataset	Glen Canyon			Marble Canyon			Eastern GRCA			Western GRCA		
	CM	DF	SB	CM	DF	SB	CM	DF	SB	CM	DF	SB
2014	0	0	0	11	7	7	16	10	6	17	11	11
2016	2	3	2	7	6	8	8	9	12	13	14	5
2017	2	2	2	9	7	9	10	10	5	11	11	10
2018	2	2	2	7	9	9	13	10	13	9	10	12
2019	2	2	3	7	9	9	12	12	12	10	13	11
Total	**8**	**9**	**9**	**41**	**38**	**42**	**59**	**51**	**48**	**60**	**59**	**49**
Fixed-site SB	--	--	1	--	--	20	--	--	14	--	--	8

In late September and October, fixed-site eddy sandbars were sampled. These sites are locations previously identified for long-term geomorphic change monitoring (Kaplinski and others, 2014) and only include sandbars. They are a mix of commonly used campsites and rarely visited locations that are mostly located in Marble Canyon and eastern Grand Canyon. Two of these sites (−6 Mile in Glen Canyon and Granite Camp in eastern Grand Canyon) have undergone previous revegetation activities consisting of *Tamarix* removal and subsequent planting of native species (Ralston and Sarr, 2017). These sites were retained in analyses in order to fully evaluate riparian vegetation of the study area.

Sampling was separated by river segments related to geography and floristic composition: Glen Canyon (Rkm −25–0), Marble Canyon (Rkm 0–97), eastern Grand Canyon (Rkm 97–259), and western Grand Canyon (Rkm 259–404). The number of sites sampled per river segment is based on segment length, such that the maximum sampling rate is one sample collected per 2.5 river miles (4.1 Rkm). For the purpose of analysis, data from randomly selected sites and fixed-site sandbars were compiled for 2014 and from 2016 to 2019. Data from 2012 and 2013 were excluded from analyses because of inconsistencies with data collection. As few randomly selected sites were sampled in 2015, all data from that year were also excluded from analyses to make comparisons across time similar.

Individual species cover and total living foliar cover values are estimated within 1-square-meter (m^2) quadrats arranged along transects and stratified by flooding frequency. At randomly selected sites, three transects are placed perpendicular to the river's current, each with nine sample quadrats (for a total of 27 quadrats per site; fig. 6). At fixed-site sandbars, the site layout consists of a predetermined number of transects and quadrats based on sandbar size and shape. These sites can have three or four transects with six or nine quadrats each.

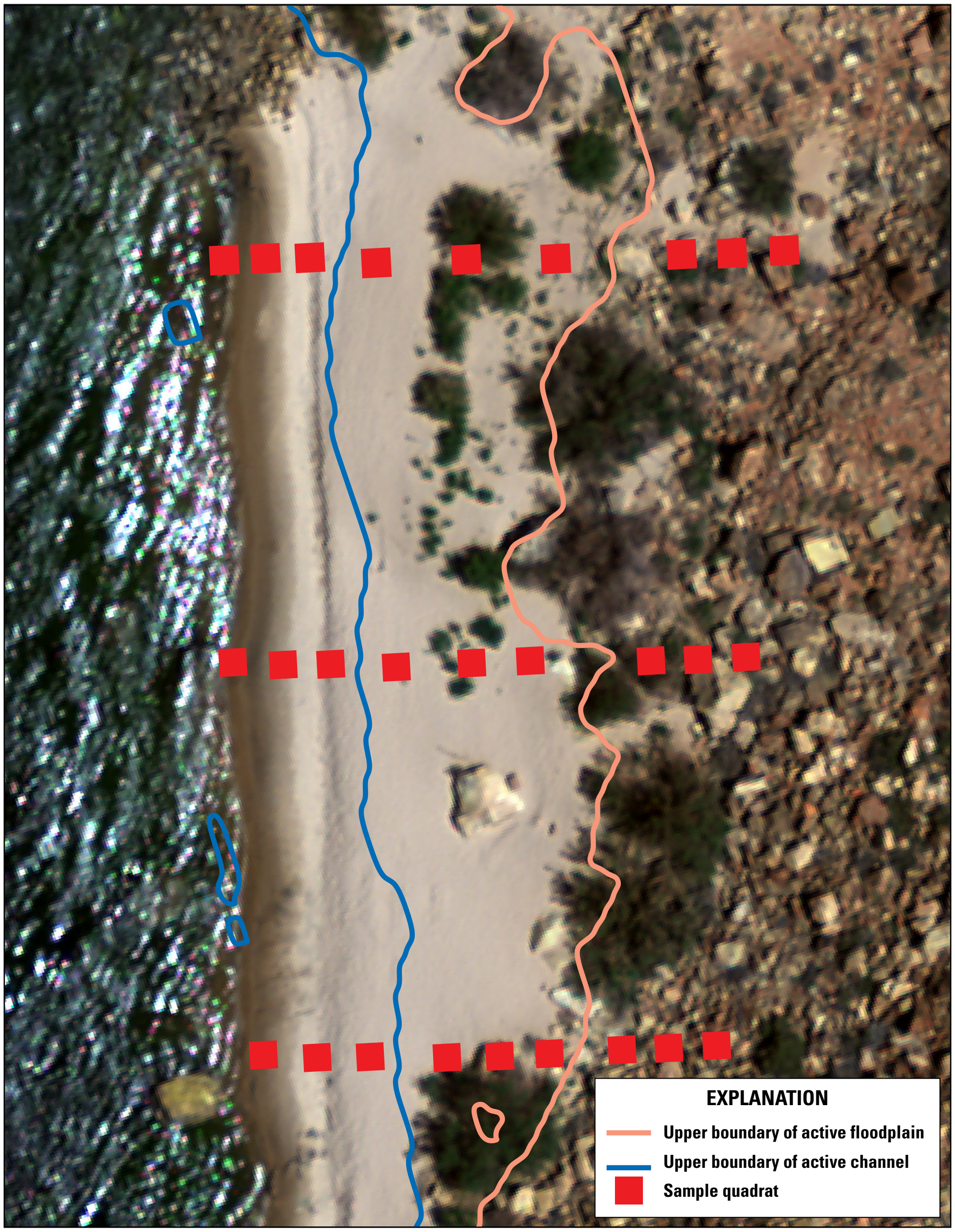

Figure 6. Diagram illustrating the sampling layout for randomly selected sites. Three transects are placed perpendicular to the river channel, and nine 1-square-meter (m^2) sample quadrats (illustrated as red squares, not shown to scale) are placed on each transect. Quadrats are stratified by hydrologic zone (active channel, active floodplain, and inactive floodplain). Base image from Durning and others (2016).

Quadrats are stratified across the three hydrologic zones defined by dam operation parameters: the active channel, the active floodplain, and the inactive floodplain (fig. 6). Equal numbers of quadrats are placed in each zone.

At each quadrat, visual cover estimates of each plant species rooted inside the frame, each species hanging over the frame but rooted outside of it, and total living foliar cover rooted inside the frame are recorded. The latter two estimates were not conducted in 2014. To standardize total living foliar cover across all years for analyses, the variable was estimated by summing all cover values for recorded species.

For additional details on sample site layout and data collection, see Palmquist and others (2018b). Data used for analyses are available from the U.S. Geological Survey ScienceBase catalog (Palmquist and others, 2022).

Descriptive Summaries

Species Lists

Lists of recorded species were compiled for the randomly selected sites dataset (app. 1) and for the fixed-site sandbars dataset (app. 2) using the R software environment (R Core Team, 2021). Each list includes the number of sites at which each species was recorded for the study area and by river segment (app. 1, 2).

Community Composition

Differences in community composition (that is, differences in recorded species and their relative abundances) between geomorphic feature classes in the random sampling dataset and the fixed-site sandbars were assessed through ordination. To reduce the effect of zero-inflated data on the ordination results, relative abundance was quantified as the average cover of a species across all plots within a site and hydrologic zone for each year. This resulted in a total of 1,925 site-zone-year sample points. A detrended correspondence analysis (DCA) was first performed using the “decorana” function in the R vegan package (Oksanen and others, 2015) to determine if the primary compositional gradient was unimodal or linear. The first DCA axis had a length of 7.4 standard deviations, indicating a unimodal gradient and supporting the continued use of DCA as an appropriate ordination technique. Statistical differences in community composition between geomorphic feature types, river segments, hydrologic zones, and years were highly significant based on both the analysis of variance and permutational analysis of variance of DCA scores (all pairwise p-values < 0.001). Thus, DCA results were further used for visualization and descriptive purposes. Differences between categories of each factor (for example, between the active channel and active floodplain in the hydrologic zone analysis) were visualized in the DCA with error bars reflecting two standard errors of the mean.

Species Frequency

For both randomly selected sites and fixed-site sandbars, the relative frequency of each species was calculated as the number of sites at which the species was recorded divided by the total number of sites (total number of randomly selected sites = 472; total number of fixed-site sandbars = 43). Relative frequency was calculated for the entire study area for both randomly selected and fixed sites, and for each floristic segment for the randomly selected sites. Relative frequency was not calculated by floristic segment for the fixed-site sandbars dataset because of the small sample sizes for some segments.

Foliar Cover

Average cover and standard deviation were calculated for each species by floristic segment and geomorphic feature (fixed-site sandbars were treated as a fourth geomorphic feature). Average site-level cover values for individual species were calculated in R by adding overhanging cover values to rooted cover values for each quadrat, then calculating the mean cover for each site. For fixed-site sandbars, average cover values were calculated for each year (as opposed to across years). Glen Canyon and Marble Canyon were combined because of the small sample sizes in Glen Canyon. The five species with the highest cover values for the randomly selected sites and fixed-site sandbars were graphed (see “Results” section).

To visualize differences in total cover across the study area, total foliar cover estimates for 2016 through 2019 were averaged by site for the randomly selected sites and plotted against the corresponding river kilometer. The mean, maximum, minimum, and standard deviation of total foliar cover values were calculated for each river segment.

Temporal Trends by Hydrologic Zone

In accordance with the riparian vegetation resource goals outlined in the Glen Canyon Dam Long-Term Experimental and Management Plan, the species richness (total number of species), standardized proportion of native species richness versus nonnative species richness (number of native species divided by total number of species), total foliar cover (as percentage of quadrat), and proportion of native species cover versus nonnative species cover per quadrat were analyzed for temporal trends. *Tamarix*, *Pluchea sericea* (arrowweed), and *Baccharis* spp. were also analyzed for temporal trends, as these are species of management interest (U.S. Department of the Interior, 2016; U.S. Department of the Interior, 2020). For *Baccharis* spp. analyses, *Baccharis emoryi* (Emory’s baccharis), *Baccharis salicifolia* (mule fat), and *Baccharis sarothroides* (desertbroom) were grouped and analyzed together. These three species have similar hydrologic niches (Butterfield and others, 2018) and are frequent in different segments of the study area (Palmquist and others, 2018a). Data were analyzed separately for the randomly selected sites and fixed-site sandbar sites using mixed-effects models with site as a random effect. This approach was used to accommodate the statistical non-independence of plots within the same site. Initial models were conducted with hydrologic zone (active channel, active floodplain, and inactive floodplain), floristic region (Glen Canyon-Marble Canyon river segment, eastern Grand Canyon river segment, and western Grand Canyon river segment), geomorphic feature type (sandbar, debris fan, and channel margin), and year (2014, 2016, 2017, 2018, and

2019) as fixed effects, including all possible interactions, for the random sampling sites. The geomorphic feature type fixed effect was absent from analyses of the fixed-site sandbars. Year, as a fixed effect, was treated as a categorical variable to account for potentially strong nonlinearities in vegetation status among years and because of the absence of complete data in 2015.

Hydrologic zone consistently presented in initial analyses as the strongest predictor variable of most aspects of vegetation status. The inclusion of geomorphic feature and floristic region, even when significant, often did not result in significant differences among factor levels based on post-hoc analyses, and not all variables had sufficient data density to include all factors in a single model. For the sake of clarity and consistency, all models presented in this report are based on the interaction between hydrologic zone and year. Year was included in all models because of the explicit interest in identifying temporal trends in vegetation status. Mixed-effects models were conducted with the "lmer" function in the lme4 package in R (Bates and others, 2015) and Tukey's post-hoc comparisons were conducted with the "emmeans" function in the emmeans package in R (Lenth and others, 2018).

Results

Descriptive Summaries

Lists of recorded species for the randomly selected sites and the fixed-site sandbars are available in appendix 1 and appendix 2, respectively. The number of species recorded at randomly selected sites was 296; at the fixed-site sandbars, 218 species were recorded.

Community Composition

Geomorphic feature, river segment, and hydrologic zone exhibited differences in community composition (fig. 7). There was little difference across years. Community

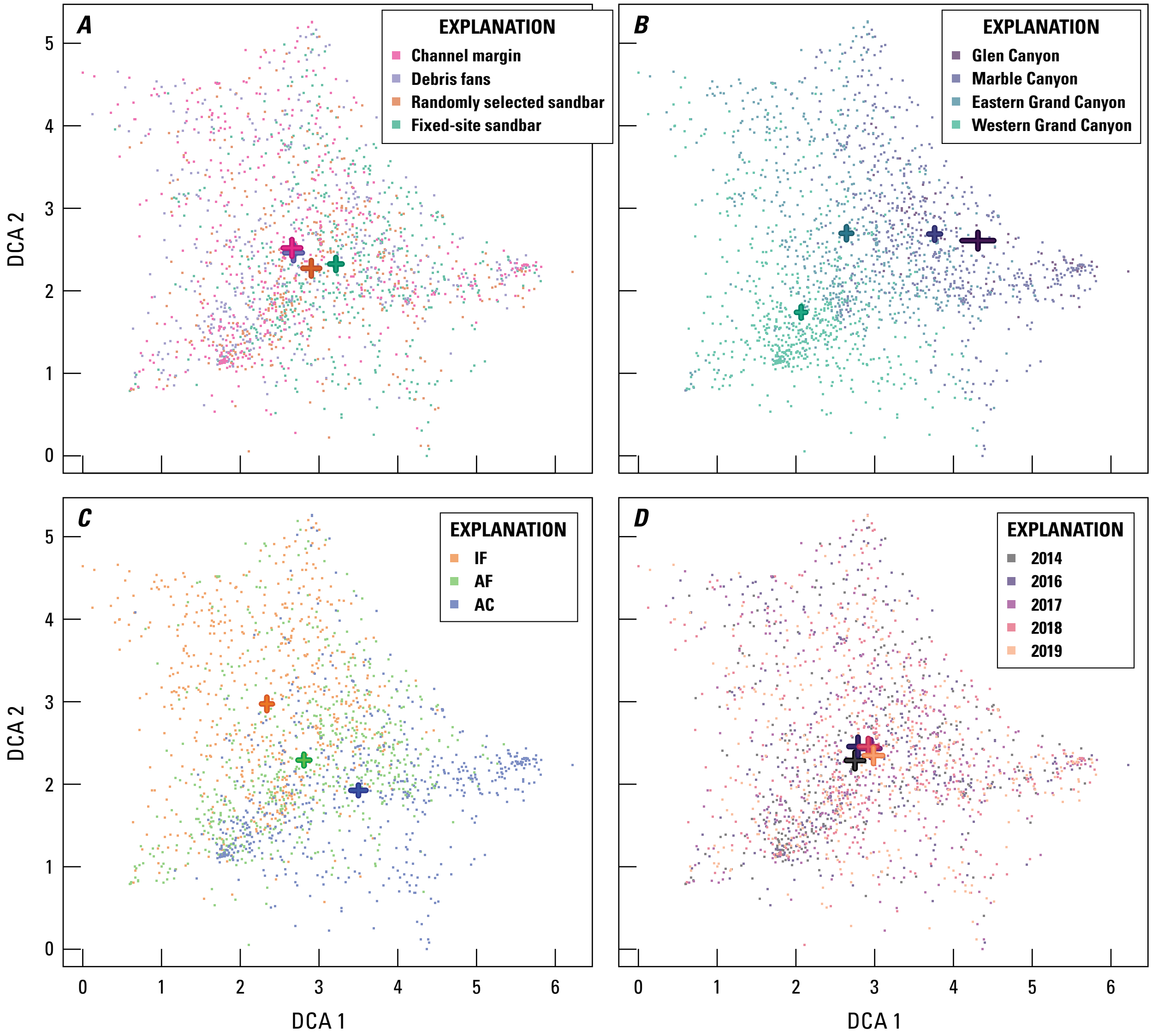

Figure 7. Detrended correspondence analysis scores for all monitoring sites during the study period, grouped by geomorphic feature class (*A*), river segment (*B*), hydrologic zone (*C*), and sampling year (*D*) data classes. Crosses indicate mean scores ±2 standard errors for each data class. Symbols in explanation are enlarged by four times their size in the graph. DCA 1, detrended correspondence analysis 1; DCA 2, detrended correspondence analysis 2; AC, active channel; AF, active floodplain; IF, inactive floodplain.

composition differed substantially between the fixed-site sandbar and the randomly selected debris fan and channel margin sites, with random sampling sandbars intermediate (fig. 7). Debris fan and channel margin sites did not differ in composition. These differences were most strongly expressed along the first DCA axis. Glen Canyon, Marble Canyon, eastern Grand Canyon, and western Grand Canyon also differed in community composition. Glen Canyon and Marble Canyon were most similar in community composition. The community composition of sites in eastern Grand Canyon was intermediate between the community composition of sites in western Grand Canyon and that of Glen Canyon and Marble Canyon sites. Hydrologic zones also showed differences in plant species composition, with the active channel and the inactive floodplain exhibiting the greatest difference.

Species Frequency

The three most frequent native species were the same for randomly selected sites and fixed-site sandbars: *Baccharis emoryi*, *Sporobolus flexuosus* (mesa dropseed), and *Equisetum* x *ferrissii* (horsetail; tables 3, 4). *Bromus* species and *Tamarix* were the most frequent nonnative groups for both types of sites (tables 5, 6). *Cynodon dactylon* was frequent at both randomly selected sites and fixed-site sandbars but more so at the former. When frequency was calculated for each floristic segment, both native and nonnative species frequencies changed with respect to study-wide frequency. Some species were frequent throughout the corridor (*B. emoryi*, *Tamarix*, *Bromus rubens*), whereas many were only frequent in certain segments (for example, *Artemisia ludoviciana*, *Euthamia occidentalis*, *Salix exigua*, *Pluchea sericea*, *Isocoma acradenia*, *Alhagi maurorum*, *Cynodon dactylon*, *Schedonorus arundinaceus*).

Table 3. The 10 most frequently recorded native plant species at randomly selected sites for the entire study area and for each river segment.

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon, river kilometers 97 to 259; western Grand Canyon, river kilometers 259 to 404.]

Scientific name	Common name	Growth form	Relative frequency
	Entire study area		
Baccharis emoryi	Emory's baccharis	Shrub	0.64
Equisetum x *ferrissii*	horsetail	Forb	0.54
Sporobolus flexuosus	mesa dropseed	Graminoid	0.45
Aristida purpurea	purple threeawn	Graminoid	0.42
Euthamia occidentalis	western goldentop	Forb	0.37
Bothriochloa barbinodis	cane bluestem	Graminoid	0.33
Brickellia longifolia	longleaf brickellbush	Shrub	0.32
Artemisia ludoviciana	white sagebrush	Forb	0.32
Baccharis sarothroides	desertbroom	Shrub	0.31
Pluchea sericea	arrowweed	Shrub	0.30
	Glen Canyon		
Artemisia ludoviciana	white sagebrush	Forb	0.92
Baccharis emoryi	Emory's baccharis	Shrub	0.88
Euthamia occidentalis	western goldentop	Forb	0.88
Equisetum x *ferrissii*	horsetail	Forb	0.77
Salix exigua	Coyote willow	Shrub	0.77
Carex emoryi	Emory's sedge	Sedge	0.58
Chloracantha spinosa	spiny chloracantha	Forb	0.58
Muhlenbergia asperifolia	scratchgrass	Graminoid	0.58
Mentha arvensis	wild mint	Forb	0.46
Sporobolus flexuosus	mesa dropseed	Graminoid	0.46
	Marble Canyon		
Baccharis emoryi	Emory's baccharis	Shrub	0.93
Equisetum x *ferrissii*	horsetail	Forb	0.80
Artemisia ludoviciana	white sagebrush	Forb	0.73
Euthamia occidentalis	western goldentop	Forb	0.65
Brickellia longifolia	longleaf brickellbush	Shrub	0.56

Table 3. The 10 most frequently recorded native plant species at randomly selected sites for the entire study area and for each river segment.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon, river kilometers 97 to 259; western Grand Canyon, river kilometers 259 to 404.]

Scientific name	Common name	Growth form	Relative frequency
Marble Canyon—Continued			
Sporobolus flexuosus	mesa dropseed	Graminoid	0.52
Salix exigua	coyote willow	Shrub	0.47
Muhlenbergia asperifolia	scratchgrass	Graminoid	0.46
Chloracantha spinosa	spiny chloracantha	Forb	0.42
Aristida purpurea	purple threeawn	Graminoid	0.38
Eastern Grand Canyon			
Baccharis emoryi	Emory's baccharis	Shrub	0.52
Aristida purpurea	purple threeawn	Graminoid	0.51
Sporobolus flexuosus	mesa dropseed	Graminoid	0.47
Baccharis salicifolia	mule-fat	Shrub	0.42
Bothriochloa barbinodis	cane bluestem	Graminoid	0.42
Brickellia longifolia	longleaf brickellbush	Shrub	0.39
Aristida arizonica	Arizona threeawn	Graminoid	0.38
Isocoma acradenia	alkali goldenbush	Shrub	0.37
Sporobolus spp.	dropseed	Graminoid	0.35
Senegalia greggii	catclaw acacia	Tree	0.34
Western Grand Canyon			
Baccharis sarothroides	desertbroom	Shrub	0.74
Equisetum x *ferrissii*	horsetail	Forb	0.55
Baccharis emoryi	Emory's baccharis	Shrub	0.50
Isocoma acradenia	alkali goldenbush	Shrub	0.43
Aristida purpurea	purple threeawn	Graminoid	0.41
Pluchea sericea	arrowweed	Shrub	0.41
Senegalia greggii	catclaw acacia	Tree	0.39
Bothriochloa barbinodis	cane bluestem	Graminoid	0.38
Sporobolus flexuosus	mesa dropseed	Graminoid	0.38
Baccharis salicifolia	mule-fat	Shrub	0.34

Table 4. The 10 most frequently recorded native plant species at fixed-site sandbars for the entire study area.

Scientific name	Common name	Growth form	Relative frequency
Baccharis emoryi	Emory's baccharis	Shrub	0.93
Sporobolus flexuosus	mesa dropseed	Graminoid	0.91
Equisetum x *ferrissii*	horsetail	Forb	0.70
Sporobolus cryptandrus	sand dropseed	Graminoid	0.70
Euthamia occidentalis	western goldentop	Forb	0.65
Salix exigua	coyote willow	Shrub	0.63
Sporobolus spp.	dropseed	Graminoid	0.63
Sporobolus contractus	spike dropseed	Shrub	0.60
Muhlenbergia asperifolia	scratchgrass	Graminoid	0.58
Pluchea sericea	arrowweed	Shrub	0.58

Table 5. The 10 most frequently recorded nonnative plant species at randomly selected sites for the entire study area and for each river segment.

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon, river kilometers 97 to 259; western Grand Canyon, river kilometers 259 to 404.]

Scientific name	Common name	Growth form	Relative frequency
	Entire study area		
Bromus rubens	red brome	Graminoid	0.74
Tamarix	salt cedar	Tree	0.62
Cynodon dactylon	Bermudagrass	Graminoid	0.51
Bromus diandrus	ripgut brome	Graminoid	0.45
Schedonorus arundinaceus	tall fescue	Graminoid	0.33
Alhagi maurorum	camelthorn	Forb	0.27
Conyza canadensis	Canadian horseweed	Forb	0.23
Agrostis stolonifera	creeping bentgrass	Graminoid	0.23
Melilotus officinalis	sweetclover	Forb	0.22
Polypogon viridis	beardless rabbitsfoot grass	Graminoid	0.17
	Glen Canyon		
Schedonorus arundinaceus	tall fescue	Graminoid	1.00
Bromus rubens	red brome	Graminoid	0.92
Tamarix	salt cedar	Tree	0.85
Agrostis gigantea	redtop	Graminoid	0.81
Bromus diandrus	ripgut brome	Graminoid	0.81
Plantago lanceolata	narrowleaf plantain	Forb	0.81
Melilotus officinalis	sweetclover	Forb	0.46
Agrostis stolonifera	creeping bentgrass	Graminoid	0.38
Taraxacum officinale	common dandelion	Forb	0.23
Bromus tectorum	cheatgrass	Graminoid	0.19
	Marble Canyon		
Bromus rubens	red brome	Graminoid	0.79
Schedonorus arundinaceus	tall fescue	Graminoid	0.78
Tamarix	salt cedar	Tree	0.73
Agrostis stolonifera	creeping bentgrass	Graminoid	0.60
Bromus diandrus	ripgut brome	Graminoid	0.59
Polypogon viridis	beardless rabbitsfoot grass	Graminoid	0.37
Conyza canadensis	Canadian horseweed	Forb	0.26
Salsola tragus	prickly Russian thistle	Forb	0.24
Melilotus officinalis	sweetclover	Forb	0.21
Poa pratensis	Kentucky bluegrass	Graminoid	0.18
	Eastern Grand Canyon		
Bromus rubens	red brome	Graminoid	0.75
Tamarix	salt cedar	Tree	0.58
Cynodon dactylon	Bermudagrass	Graminoid	0.46
Alhagi maurorum	camelthorn	Forb	0.39
Bromus diandrus	ripgut brome	Graminoid	0.28
Conyza canadensis	Canadian horseweed	Forb	0.20
Salsola tragus	prickly Russian thistle	Forb	0.18

Scientific name	Common name	Growth form	Relative frequency
Bromus rubens	red brome	Graminoid	1.00
Tamarix	saltcedar	Tree	0.98
Bromus diandrus	ripgut brome	Graminoid	0.84
Bromus spp.	brome	Graminoid	0.72
Polypogon viridis	beardless rabbitsfoot grass	Graminoid	0.56
Salsola tragus	prickly Russian thistle	Forb	0.56
Conyza canadensis	Canadian horseweed	Forb	0.53
Schedonorus arundinaceus	tall fescue	Graminoid	0.47
Schismus arabicus	Arabian schismus	Graminoid	0.44
Cynodon dactylon	Bermudagrass	Graminoid	0.37

Foliar Cover

The five species with the highest average foliar cover in each river segment differ for randomly selected sites and fixed-site sandbars (figs. 8, 9, 10). In Glen and Marble Canyons, the species at randomly selected sites with the highest average cover are *Baccharis emoryi*, *Tamarix*, *Schedonorus arundinaceus* (tall fescue), *Bromus diandrus* (ripgut brome), and *Equisetum* x *ferrissii*; for fixed-site sandbars, *Tamarix*, *B. emoryi*, *Pluchea sericea*, *Phragmites australis* (common reed), and *S. arundinaceus* have the highest average cover. In eastern Grand Canyon, the highest average cover species are *Tamarix*, *B. emoryi*, *P. sericea*, *Baccharis salicifolia*, and *Cynodon dactylon* for the randomly selected sites and *P. sericea*, *Tamarix*, *B. emoryi*, *Salix exigua* (coyote willow), and *B. salicifolia* for the fixed-site sandbars. In western Grand Canyon, the highest average cover species are *C. dactylon*, *Baccharis sarothroides*, *B. emoryi*, *Tamarix*, and *Prosopis glandulosa* for the randomly selected sites, and *C. dactylon*, *P. sericea*, *B. emoryi*, *P. australis*, and *Tamarix* for the fixed-site sandbars.

The four nonnative species occurring in the five highest cover value species also show different distributions. *Tamarix* has high living cover across all river segments and geomorphic features as compared to all the other species (table 7, figs. 8, 9, 10). *Cynodon dactylon* cover is close to zero in Glen and Marble Canyons, greater in eastern Grand Canyon, and high in western Grand Canyon, with little variation among geomorphic features in any segment (table 7). *Schedonorus arundinaceus* and *Bromus diandrus*

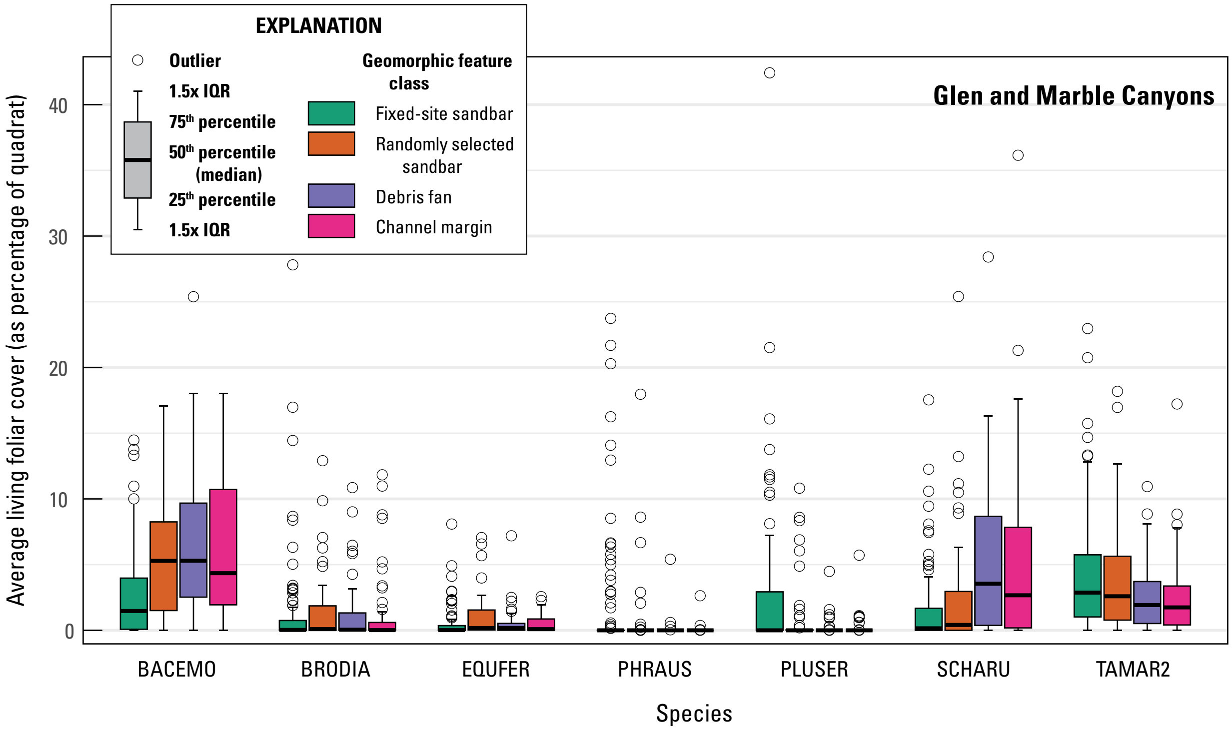

Figure 8. Average living foliar cover for the dominant species in Glen Canyon and Marble Canyon (river kilometers −25–97), separated by geomorphic feature class. Species shown consist of the five species with the highest average cover on the randomly selected sites and the five species with the highest average cover on the fixed-site sandbars (note that some species are dominant at both types of sites). Species names abbreviated as follows: BACEMO, *Baccharis emoryi*; BRODIA, *Bromus diandrus*; EQUFER, *Equisetum* x *ferrissii*; PHRAUS, *Phragmites australis*; PLUSER, *Pluchea sericea*; SCHARU, *Schedonorus arundinaceus*; TAMAR2, *Tamarix*. Whiskers extend to the most extreme data point that is not more than 1.5 times the interquartile range (IQR).

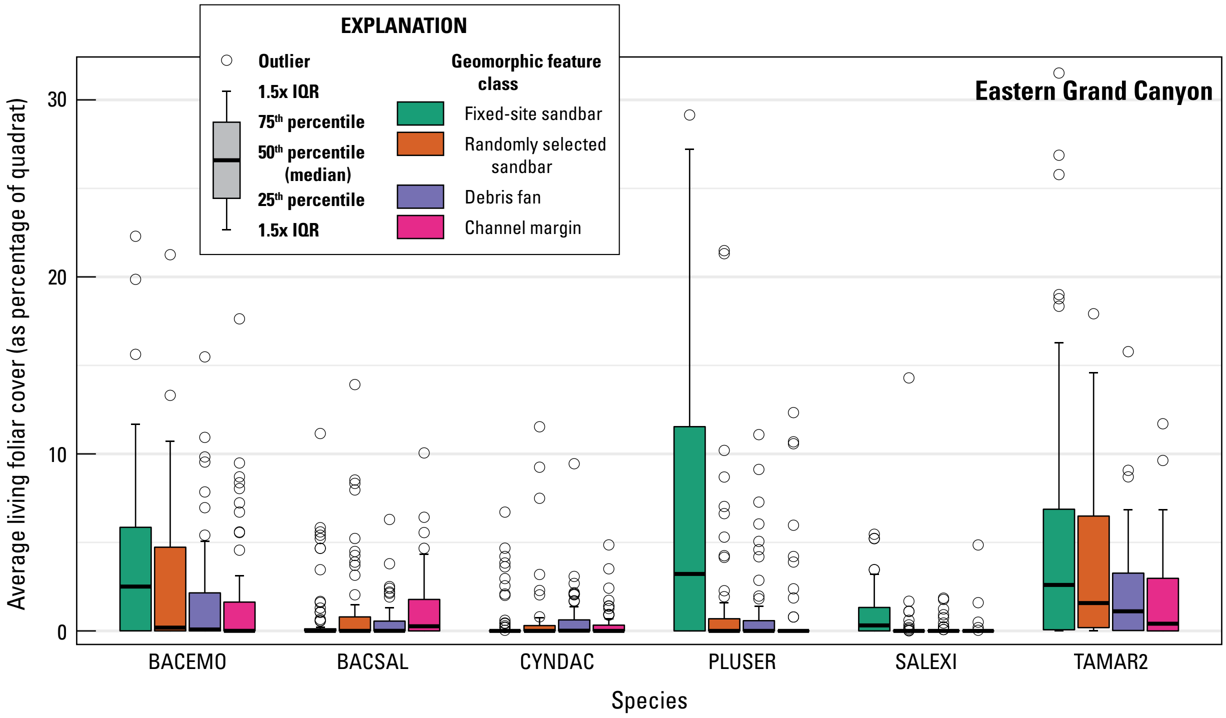

Figure 9. Average living foliar cover for the dominant species in eastern Grand Canyon (river kilometers 97–259), separated by geomorphic feature class. Species shown consist of the five species with the highest average cover on the randomly selected sites and the five species with the highest average cover on the fixed-site sandbars (note that some species are dominant at both types of sites). Species names abbreviated as follows: BACEMO, *Baccharis emoryi*; BACSAL, *Baccharis salicifolia*; CYNDAC, *Cynodon dactylon*; PLUSER, *Pluchea sericea*; SALEXI, *Salix exigua*; TAMAR2, *Tamarix*. Whiskers extend to the most extreme data point that is not more than 1.5 times the interquartile range (IQR).

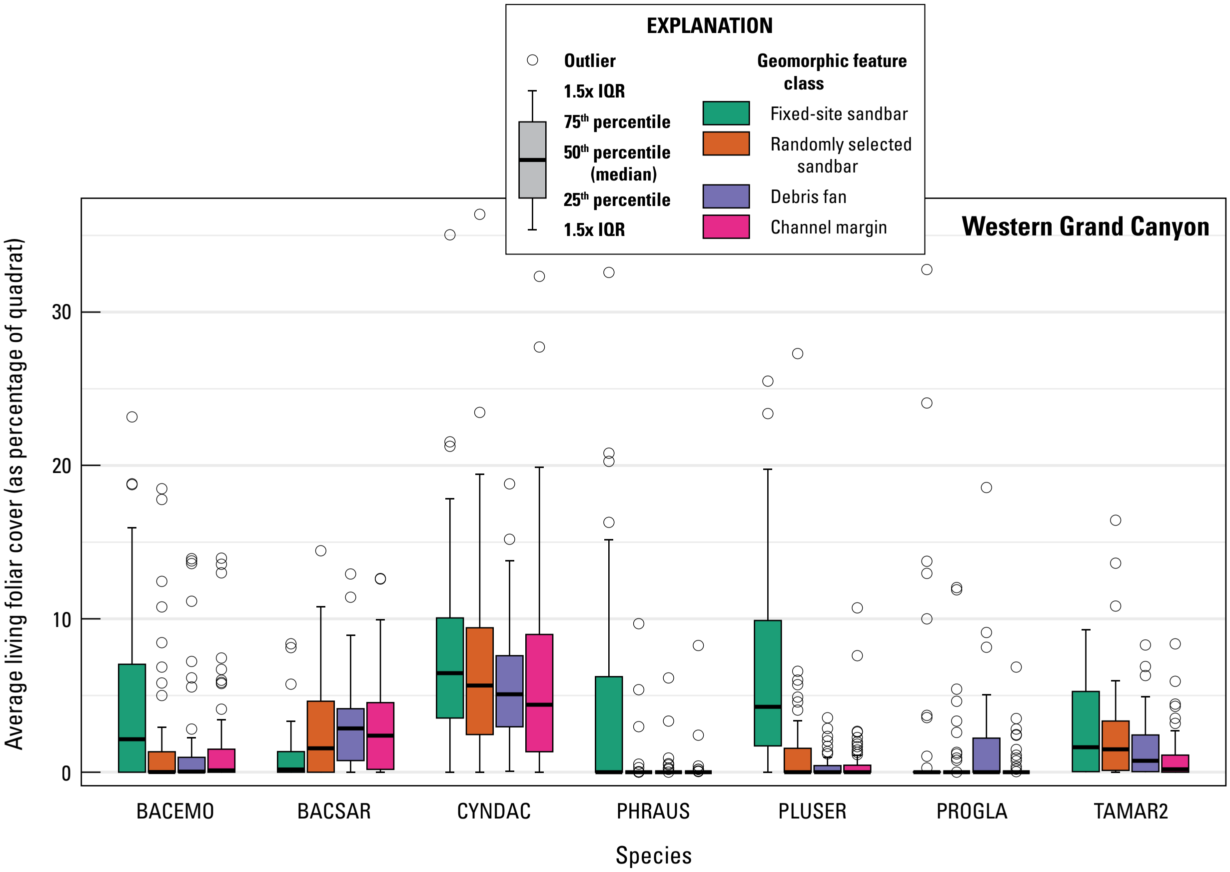

Figure 10. Average living foliar cover for the dominant species in western Grand Canyon (river kilometers 259–404), separated by geomorphic feature class. Species shown consist of the five species with the highest average cover on the randomly selected sites and the five species with the highest average cover on the fixed-site sandbars (note that some species are dominant at both types of sites). Species names abbreviated as follows: BACEMO, *Baccharis emoryi*; BACSAR, *Baccharis sarothroides*; CYNDAC, *Cynodon dactylon*; PHRAUS, *Phragmites australis*; PLUSER, *Pluchea sericea*; PROGLA, *Prosopis glandulosa*; TAMAR2, *Tamarix*. Whiskers extend to the most extreme data point that is not more than 1.5 times the interquartile range (IQR).

Table 7. Mean living foliar cover (as percentage of quadrat) and standard deviations (in parentheses) by river segment and geomorphic feature.

[Species listed are one of the top five highest average foliar cover species in at least one river segment of the study area. River segments are delineated by river kilometers as follows: Glen Canyon and Marble Canyon (“Glen/Marble Canyon”), river kilometers −25 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

River segment	Fixed-site sandbars	Randomly selected sites		
		Sandbars	Debris fans	Channel margins
		Baccharis emoryi		
Glen/Marble Canyon	2.7 (3.4)	5.4 (4.5)	6.8 (5.5)	6.1 (5.3)
Eastern GRCA	3.7 (4.7)	2.8 (4.4)	2.0 (3.4)	1.7 (3.4)
Western GRCA	4.5 (6.1)	2.1 (4.4)	1.5 (3.5)	1.7 (3.3)
		Baccharis salicifolia		
Glen/Marble Canyon	0.2 (0.8)	0.3 (1.3)	0.2 (0.8)	0.1 (0.5)
Eastern GRCA	0.8 (2.0)	1.4 (3.0)	0.6 (1.2)	1.2 (1.9)
Western GRCA	0.6 (1.3)	0.7 (1.7)	0.7 (2.0)	0.5 (1.2)

Table 7. Mean living foliar cover (as percentage of quadrat) and standard deviations (in parentheses) by river segment and geomorphic feature.—Continued

[Species listed are one of the top five highest average foliar cover species in at least one river segment of the study area. River segments are delineated by river kilometers as follows: Glen Canyon and Marble Canyon (“Glen/Marble Canyon”), river kilometers −25 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

River segment	Fixed-site sandbars	Randomly selected sites		
		Sandbars	Debris fans	Channel margins
		Baccharis sarothroides		
Glen/Marble Canyon	0.0 (0.2)	0.0 (0.1)	0.0 (0.0)	0.0 (0.0)
Eastern GRCA	0.3 (1.3)	0.3 (1.0)	0.3 (0.7)	0.3 (0.8)
Western GRCA	1.2 (2.1)	2.9 (3.4)	3.2 (2.9)	3.1 (3.2)
		Bromus diandrus		
Glen/Marble Canyon	1.3 (3.7)	1.5 (2.6)	1.3 (2.5)	1.3 (2.9)
Eastern GRCA	0.2 (0.5)	0.1 (0.2)	0.0 (0.1)	0.0 (0.1)
Western GRCA	0.5 (1.7)	0.3 (0.7)	0.2 (0.5)	0.1 (0.5)
		Cynodon dactylon		
Glen/Marble Canyon	0.0 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Eastern GRCA	0.5 (1.3)	0.8 (2.4)	0.7 (1.5)	0.4 (0.9)
Western GRCA	8.0 (7.0)	7.1 (7.1)	5.8 (4.0)	6.3 (6.8)
		Equisetum x *ferrissii*		
Glen/Marble Canyon	0.5 (1.2)	1.1 (1.7)	0.6 (1.2)	0.5 (0.7)
Eastern GRCA	0.5 (1.9)	0.4 (1.0)	0.1 (0.4)	0.0 (0.2)
Western GRCA	1.8 (4.7)	0.7 (1.6)	0.6 (1.7)	0.9 (2.3)
		Phragmites australis		
Glen/Marble Canyon	1.7 (4.6)	0.8 (2.9)	0.1 (0.8)	0.1 (0.4)
Eastern GRCA	0.7 (2.1)	0.4 (2.5)	0.1 (0.6)	0.2 (1.7)
Western GRCA	3.9 (7.5)	0.4 (1.6)	0.2 (0.9)	0.2 (1.1)
		Pluchea sericea		
Glen/Marble Canyon	2.5 (5.7)	1.0 (2.5)	0.2 (0.7)	0.2 (0.9)
Eastern GRCA	6.4 (7.8)	2.0 (4.8)	1.2 (2.5)	0.9 (2.7)
Western GRCA	6.9 (6.8)	1.6 (4.2)	0.4 (0.7)	0.7 (1.8)
		Prosopis glandulosa		
Glen/Marble Canyon	0.2 (0.9)	0.1 (0.6)	0.2 (0.7)	0.0 (0.2)
Eastern GRCA	0.3 (1.1)	0.3 (1.4)	0.3 (0.9)	0.3 (1.0)
Western GRCA	2.6 (6.9)	0.9 (2.6)	1.5 (3.1)	0.4 (1.1)
		Salix exigua		
Glen/Marble Canyon	1.3 (1.9)	0.5 (1.1)	0.7 (1.5)	0.4 (0.7)
Eastern GRCA	0.9 (1.3)	0.4 (2.1)	0.2 (0.4)	0.1 (0.7)
Western GRCA	0.2 (0.7)	0.0 (0.1)	0.0 (0.0)	0.0 (0.2)
		Schedonorus arundinaceus		
Glen/Marble Canyon	1.5 (2.9)	2.6 (4.6)	5.3 (6.0)	5.6 (7.2)
Eastern GRCA	0.1 (0.3)	0.1 (0.2)	0.1 (0.3)	0.0 (0.2)
Western GRCA	0.0 (0.0)	0.0 (0.1)	0.1 (0.2)	0.0 (0.1)
		Tamarix		
Glen/Marble Canyon	4.2 (4.5)	4.3 (4.5)	2.6 (2.7)	2.6 (3.2)
Eastern GRCA	5.1 (6.9)	3.8 (4.4)	2.1 (3.0)	1.8 (2.7)
Western GRCA	2.8 (3.2)	2.4 (3.4)	1.6 (2.0)	1.0 (1.6)

are only in the top five cover estimates for randomly selected features in Glen and Marble Canyons (table 7). *Schedonorus arundinaceus* has particularly high cover on debris fans and channel margins in Glen and Marble Canyons (fig. 8) and low cover elsewhere. *Bromus diandrus* shows little cover variation among geomorphic features in Glen and Marble Canyons (fig. 8); its cover is close to zero elsewhere.

Three native *Baccharis* species have different distributions within the study area. *Baccharis emoryi* has high cover across all geomorphic feature classes in Glen and Marble Canyons and at fixed-site sandbars in eastern Grand Canyon and western Grand Canyon, but less cover at randomly selected sites in western Grand Canyon (table 7). *Baccharis salicifolia* is one of the five highest cover species in only eastern Grand Canyon (fig. 9); it has less cover in Glen and Marble Canyons and western Grand Canyon. *Baccharis sarothroides* is one of the five highest cover species in western Grand Canyon (fig. 10), where it has similar cover across all geomorphic feature classes at randomly selected sites but slightly less cover at fixed-site sandbars. In Glen and Marble Canyons, however, *Baccharis sarothroides* has almost no cover and little more in eastern Grand Canyon (table 7).

Of the other native species, *Pluchea sericea* and *Phragmites australis* both have higher cover on fixed-site sandbars than randomly selected sandbars, debris fans, and channel margins (table 7). *Pluchea sericea* cover is higher in eastern and western Grand Canyon than in Glen and Marble Canyons (table 7). *Phragmites australis* also has higher cover in western Grand Canyon than elsewhere (table 7). *Salix exigua* is one of the five highest cover species on fixed-site sandbars in only eastern Grand Canyon (fig. 9), despite having higher average cover on fixed-site sandbars in Glen and Marble Canyons (table 7). Cover values for *S. exigua* in western Grand Canyon are close to zero. *Prosopis glandulosa* cover is greatest in western Grand Canyon.

As shown in figure 11, Glen Canyon has the highest average total foliar cover (29.0±12.2 percent) of all river segments. Marble Canyon and western Grand Canyon have the next highest average total foliar cover values at 14.0±9.4 percent and 13.8±9.1 percent, respectively, and eastern Grand Canyon has the lowest average total percentage of foliar cover (8.7±6.5 percent) of the four river segments. Site average total foliar cover is variable within river segments, ranging from 9.3 to 58.1 percent in Glen Canyon, 0.1 to 37.8 percent in Marble Canyon, 0.5 to 36.5 percent in eastern Grand Canyon, and 0.4 to 42.5 percent in western Grand Canyon.

Temporal Trends by Hydrologic Zone

Statistical results of the mixed-effects models are presented in table 8. Results for each of the response variables are discussed in the following sections.

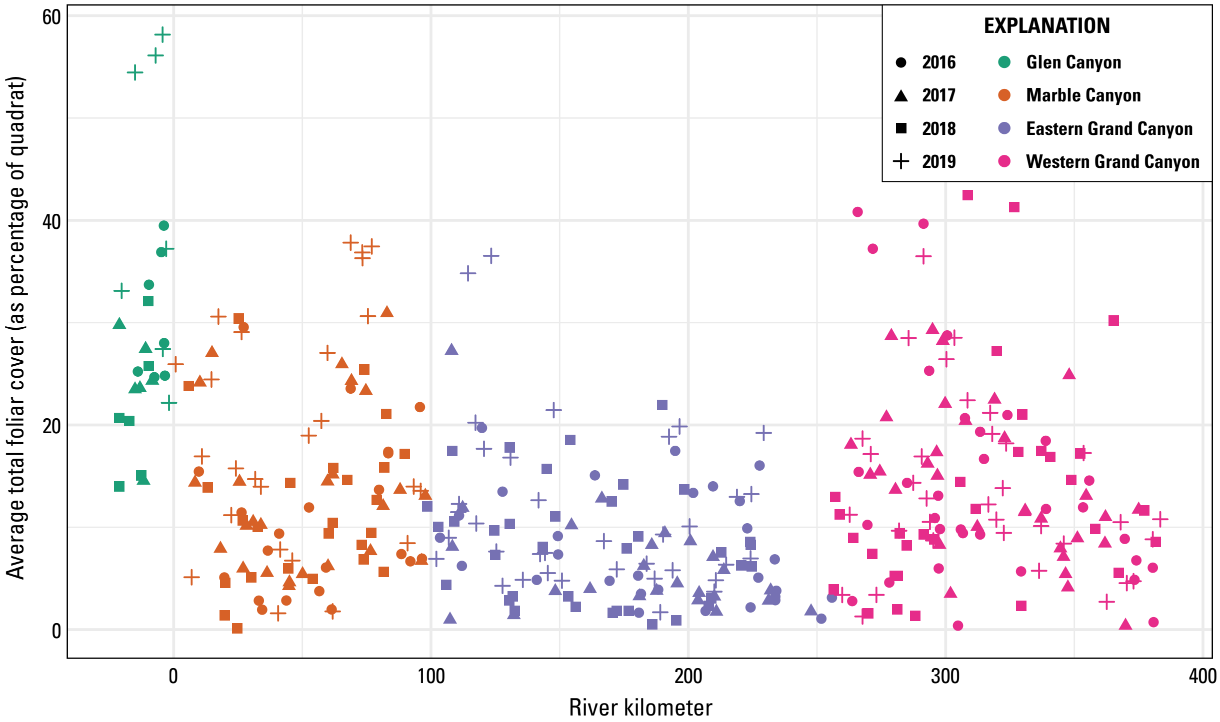

Figure 11. Average total foliar cover (as percentage of quadrat) for randomly selected sites by river kilometer. Sample year is indicated by point shape. River segments (indicated by color) are defined as follows: Glen Canyon, river kilometers (Rkm) –25 to 0; Marble Canyon, Rkm 0 to 97; eastern Grand Canyon, Rkm 97 to 259; western Grand Canyon, Rkm 259 to 404.

Species Richness

Total species richness (average number of species per square meter) exhibited significant interaction effects between hydrologic zone and year (table 8). The main effect of hydrologic zone was not significant across the randomly selected sites, but for fixed-site sandbars, hydrologic zone had a much greater effect than year (see difference in F-values in table 8). This difference is largely due to a substantial drop in species richness in the active channel relative to the other hydrologic zones that is observed at fixed-site sandbars but not at randomly selected sites (fig. 12). Species richness in the inactive floodplain and active floodplain was generally lower in 2014 and 2017 than in other years, with the exception of comparably low species richness in the active floodplain of fixed-site sandbars in 2019. Species richness at randomly selected sites was lowest in 2014; at the fixed-site sandbars, species richness was lowest in 2019.

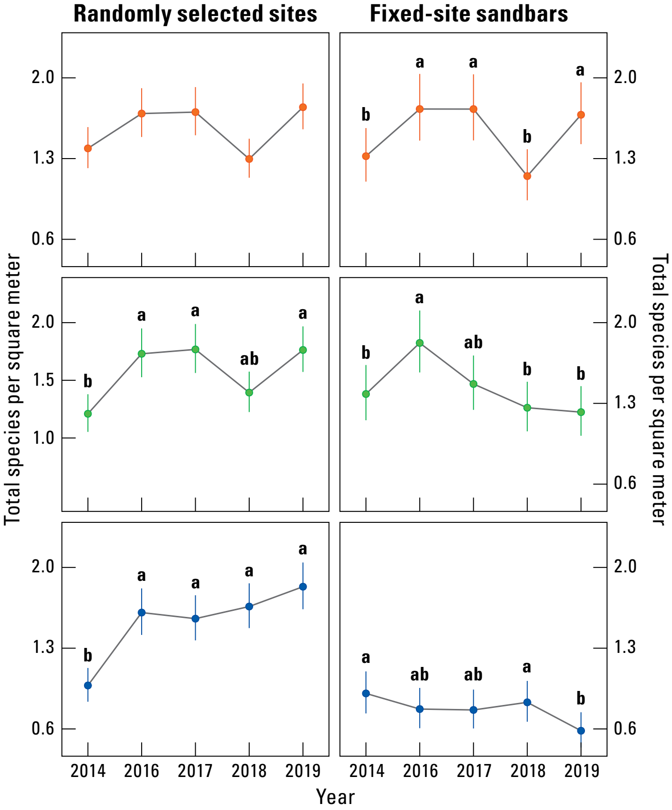

Figure 12. Fitted-model estimates for total species richness across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

Table 8. Generalized linear mixed-effects model results for each of the response variables on randomly selected sites and fixed-site sandbars.

[P-values <0.001 are notated as 0. Zone refers to hydrologic zone (active channel, active floodplain, inactive floodplain). **Abbreviations**: SS, sum of squares; df, degrees of freedom; F, F-statistics; P, p-value.]

Dependent variable	Fixed effect	Randomly selected sites				Fixed-site sandbars			
		SS	df	F	P	SS	df	F	P
Total species richness	Zone	0.2	2, 11890	2.2	0.109	27.3	2, 5960	240.2	0
	Year	1.5	4, 460	7.7	0	2.8	4, 5949	12.5	0
	Zone:year	5.2	8, 11889	13.5	0	4.6	8, 5951	10.1	0
Proportion of native versus nonnative species richness	Zone	35.8	2, 9293	46.8	0	14.9	2, 4032	20.5	0
	Year	10.7	4, 446	7.0	0	29.0	4, 4017	19.9	0
	Zone:year	31.6	8, 9292	10.3	0	11.2	8, 4021	3.8	0
Total cover	Zone	48.7	2, 11891	83.5	0	396.0	2, 5959	123.1	0
	Year	10.2	4, 461	8.7	0	104.2	4, 5948	25.9	0
	Zone:year	39.5	8, 11891	17.0	0	22.3	8, 5951	13.4	0
Proportion of native versus nonnative cover	Zone	144.5	2, 9309	131.0	0	6.6	2, 4035	6.4	0.002
	Year	9.6	4, 450	4.4	0.002	26.9	4, 4018	12.9	0
	Zone:year	29.9	8, 9308	6.8	0	5.6	8, 4023	1.3	0.220
Tamarix cover	Zone	6.8	2, 11983	51.8	0	17.4	2, 5987	77.2	0
	Year	0.1	4, 455	0.4	0.784	13.4	4, 5959	29.7	0
	Zone:year	2.0	8, 11982	3.9	0	8.5	8, 5971	9.5	0
Pluchea sericea cover	Zone	6.3	2, 11888	90.4	0	58.4	2, 5956	191.6	0
	Year	0.2	4, 461	1.2	0.311	3.0	4, 5948	4.9	0.001
	Zone:year	0.5	8, 11888	1.7	0.090	2.2	8, 5950	1.8	0.071
Baccharis spp. cover	Zone	31.4	2, 11965	99.4	0	17.5	2, 5987	62.7	0
	Year	0.9	4, 462	1.4	0.232	6.4	4, 5958	11.6	0
	Zone:year	13.7	8, 11965	10.8	0	5.7	8, 5969	5.1	0

Native species richness exceeded nonnative species richness, on average, across hydrologic zones and years except within the active floodplain and active channel at randomly selected sites in 2014 (fig. 13). The interactive effect of hydrologic zone and year was significant in both datasets, but the main effect of hydrologic zone was stronger in the randomly selected sites dataset. The year 2014 generally showed a decrease in native species dominance in the randomly selected sites dataset, whereas the fixed-site sandbars dataset was less dominated by native species in 2017 and 2019. In general, native species dominance was more pronounced at fixed-site sandbars (where it became increasingly pronounced in the active floodplain and active channel) than across randomly selected sites, though the proportion of native species in the active channel did increase through time for the randomly selected sites dataset.

Foliar Cover

The interactive effect of hydrologic zone and year on total foliar cover was significant in both datasets, where the main effect of hydrologic zone was greater than that of year (table 8). Cover was lowest in 2014 in the active floodplain and active channel of the randomly selected sites dataset, and lowest in 2019 in the fixed-site sandbars dataset (fig. 14). From 2014 through 2018, cover in the inactive and active floodplains was greater at the fixed-site sandbar sites than at the randomly selected sites, though the reduction in cover on the fixed-site sandbars in 2019 nullified that difference.

Native species cover exceeded that of nonnative species, on average, across hydrologic zones and years except within the active floodplain in 2014 and the active channel in 2014 and 2016 for the randomly selected sites dataset (fig. 15). The

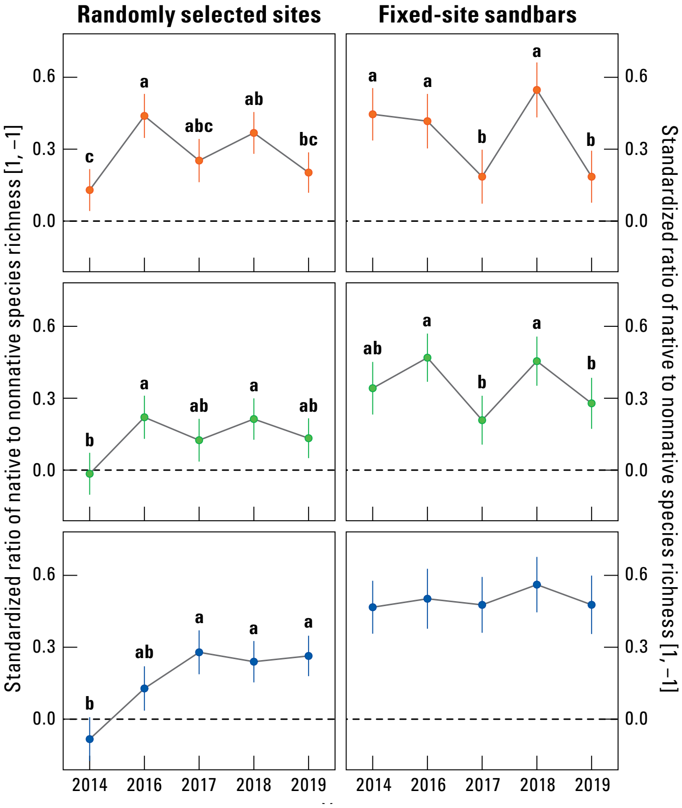

Figure 13. Fitted-model estimates for the proportion of native versus nonnative species richness across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

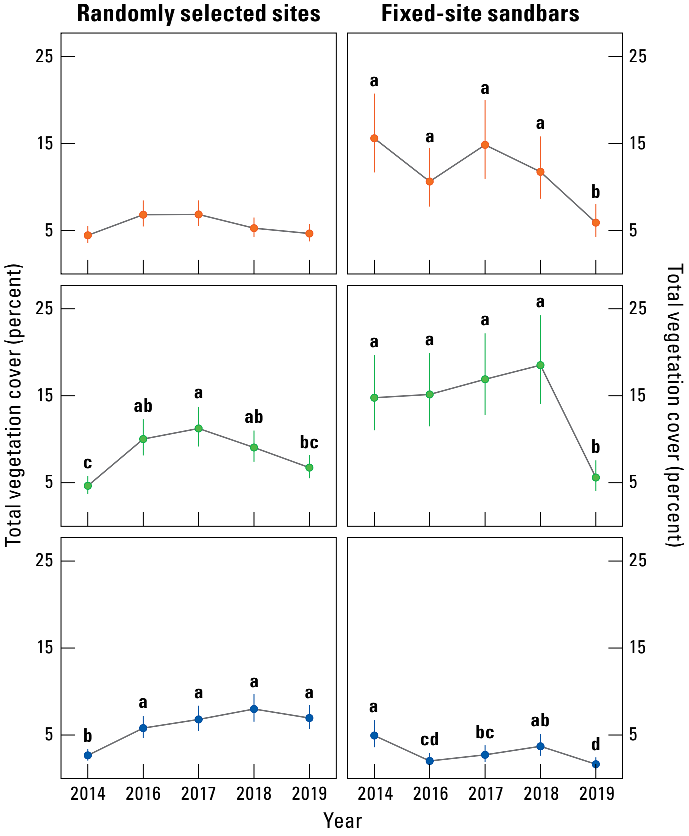

Figure 14. Fitted-model estimates for total vegetation cover across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

interactive effect of hydrologic zone and year was significant for the randomly selected sites but not the fixed-site sandbars. Hydrologic zone had the predominant main effect in the randomly selected sites dataset, whereas year had a stronger main effect in the fixed-site sandbars (table 8). This difference is attributable to the decline in native species dominance from the inactive floodplain to the active channel in the randomly selected sites—a pattern not observed on the fixed-site sandbars. The fixed-site sandbars exhibited a significant drop in native species dominance in the upper two hydrologic zones in 2017.

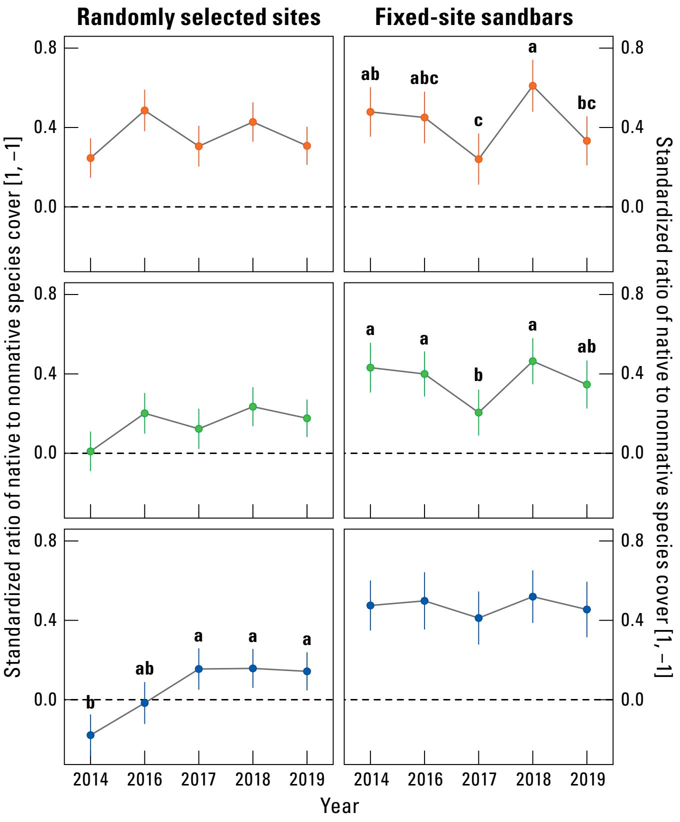

Figure 15. Fitted-model estimates for the proportion of native versus nonnative species cover across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

Species of Interest

Tamarix cover showed interactive effects of hydrologic zone and year, though the main effect of year was not significant at the randomly selected sites and was weaker than that of hydrologic zone in the fixed-site sandbars (table 8). *Tamarix* cover generally decreased from higher to lower elevation hydrologic zones (fig. 16); a significant increase in *Tamarix* cover at the fixed-site sandbars between 2014 and 2016 was nullified in subsequent years by a decline in cover back to 2014 levels.

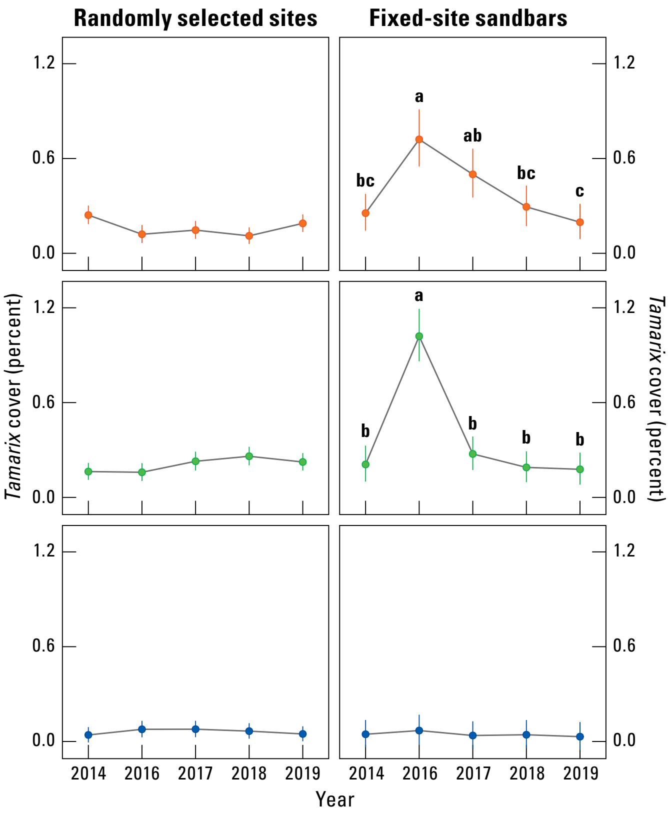

Figure 16. Fitted-model estimates for *Tamarix* species cover across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

Pluchea sericea cover was consistently greater on the fixed-site sandbars at elevations above the channel (that is, within the inactive floodplain and active floodplain hydrologic zones) than at the randomly selected sites (fig. 17). The interaction between hydrologic zone and year was not significant in either dataset. The main effect of year was weak in the fixed-site sandbar dataset, driven by a decline in cover in the active channel over time.

Hydrologic zone and year had a significant interactive effect in both datasets on the cover of *Baccharis* species, with hydrologic zone having the stronger main effect (table 8). *Baccharis* species cover was generally higher in the active floodplain for both datasets, although consistent cover increase in the active channel of the randomly selected sites resulted in comparable cover between the active floodplain and active channel in that dataset by the end of the study period (fig. 18). *Baccharis* species cover peaked in 2016 in the active floodplain of the fixed-site sandbars but showed no other temporal trends in that dataset.

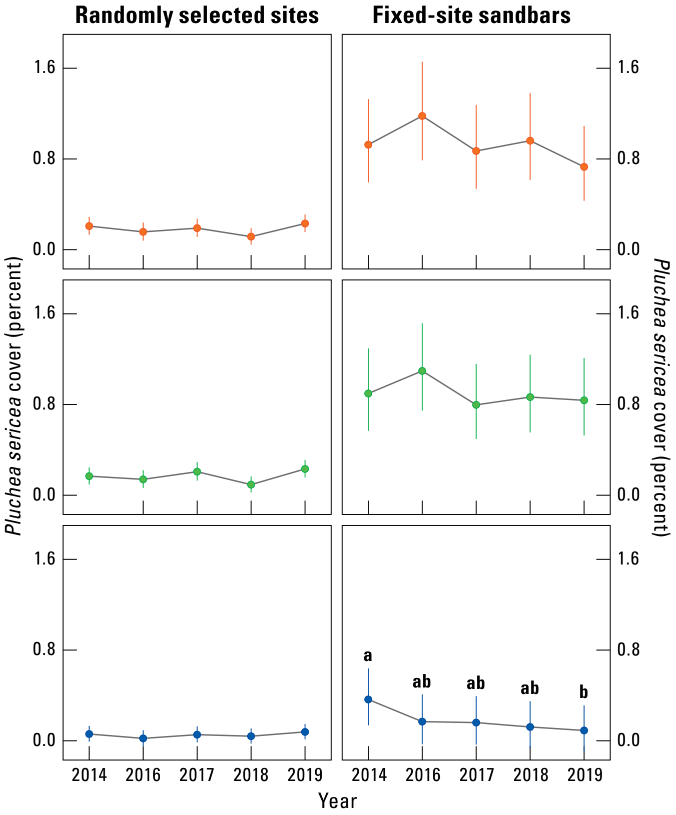

Figure 17. Fitted-model estimates for *Pluchea sericea* (arrowweed) cover across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

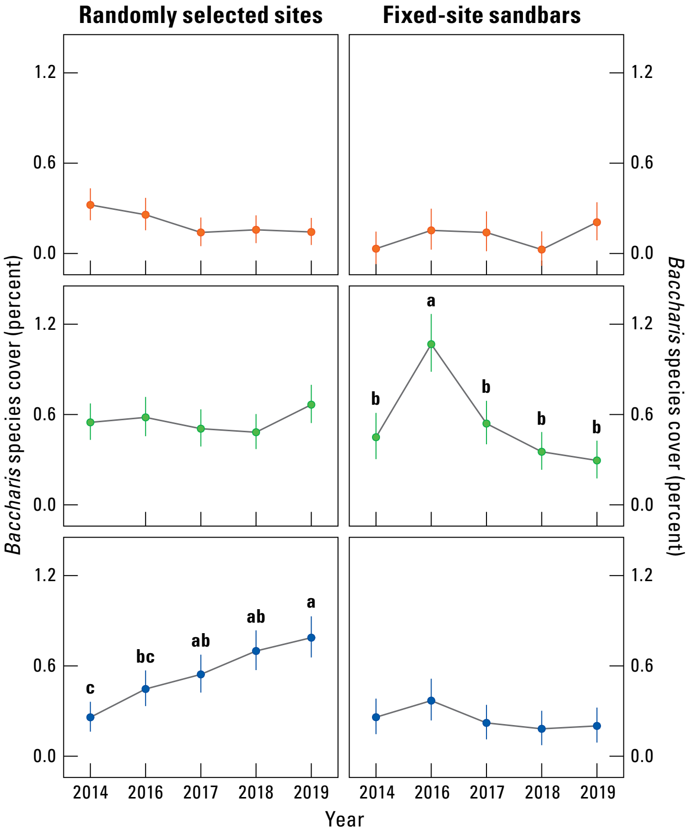

Figure 18. Fitted-model estimates for *Baccharis* species cover across hydrologic zones (active channel shown in blue; active floodplain shown in green; inactive floodplain shown in orange). Different lowercase letters indicate significant differences at α = 0.05 based on Tukey's post-hoc comparisons.

Discussion

Differences Among Sample Sites

The community composition and temporal dynamics of fixed-site sandbars differ throughout the study area from those of randomly selected sites, including randomly selected sandbars. The differences in composition between fixed-site sandbars and randomly selected sandbars may reflect differences in disturbance resulting from visitor use, differential effects of HFE releases, historical or current vegetation management (Ralston and Sarr, 2017; U.S. Department of the Interior, 2020), and (or) fundamental differences in grain size or geomorphic settings (Mueller and others, 2018). The results of this study support analyzing data from randomly selected sites (including randomly selected sandbars) and fixed-site sandbars separately for status and trends assessments, as well as maintaining separate monitoring activities for the two types of sites. Data from randomly selected sites represent the breadth and variability of riparian vegetation across multiple geomorphic features, whereas data from the fixed-site sandbars provide an in-depth look at campsites and eddy sandbars identified as key resources in the Glen Canyon Dam Long-Term Experimental and Management Plan.

One of the differences between fixed-site sandbars and randomly selected sites is the prevalence of *Pluchea sericea* (arrowweed). This species is notably higher in cover and frequency on fixed-site sandbars and is especially prevalent in Grand Canyon. Because of its affinity for growing at popular campsites, *P. sericea* has been implicated in the reduction of available campsite area within the study area (Hadley and others, 2018) and is now being targeted for removal from a few fixed-site sandbars and other campsites as part of the Glen Canyon Dam Adaptive Management Program triennial budget and work plan (U.S. Department of the Interior, 2020). Grand Canyon National Park staff are coordinating with GCMRC and Northern Arizona University scientists to implement non-flow-related experimental vegetation treatments to assess if and how vegetation removal at key sandbars can increase usable campsite area and facilitate aeolian transport of sand to upland dunes. The fixed-site sandbars included in these efforts in 2019 were Basalt Camp and 122 Mile Camp (Palmquist and others, 2018b).

The clonal habit, high salinity tolerance (Vandersande and others, 2001), and rapid resprouting capabilities (Busch and Smith, 1993) of *P. sericea* make the species well suited for growing on highly disturbed sand deposits as well as in conjunction with—or following mortality of—*Tamarix* stands. HFE releases are designed to deposit sand on eddy sandbars with the goal of creating large, open sand deposits, and fixed-site sandbars are known to change rapidly in volume depending on flow patterns (Mueller and others, 2014). At the same time, *Tamarix* stands in the study area are being defoliated as a result of the tamarisk beetle (*Diorhabda carinulata*; Bedford and others, 2018), and *P. sericea* commonly grows with living and dying *Tamarix* (Busch and Smith, 1995; Hadley and others, 2018; González and others, 2020). Conditions in the study area appear to be conducive to *P. sericea* occupancy, particularly on sandbars. It is anticipated, then, that this species will continue to do well in the study area.

Geographic Patterns

Floristic patterns documented in 2014 in randomly selected sites (Palmquist and others, 2018a) remained clearly delineated across years and with more intensive sampling. Sampling in the Glen Canyon river segment has now shown that randomly selected sites in Glen Canyon are floristically similar to randomly selected sites in Marble Canyon, although they are compositionally different. Glen Canyon has higher frequencies of plant species that are either absent or rare in other parts of the study area, such as *Sisyrinchium demissum* (blue-eyed grass), *Juncus torreyi* (desert olive), *Juncus arcticus* (arctic rush), *Mentha arvensis* (wild mint), *Epipactis gigantea* (stream orchid), *Plantago lanceolata* (narrowleaf plantain), and *Epilobium ciliatum* (fringed willowherb; see app. 1). These (and similar) species reflect a greater presence of flood-tolerant fluvial marsh species in Glen Canyon relative to the rest of the study area. Glen Canyon also has higher overall foliar cover values than the rest of the study area. These qualities (greater presence of fluvial marsh species and high foliar cover) may be the result of daily hydropower waves and a lack of suspended sediment within the river segment, factors which together produce daily inundations of very clear water that provide light and water to flood-tolerant species (Blindow and others, 1993). Because of its short length, the Glen Canyon river segment has a small annual sample size (consisting of approximately six randomly selected sites and one fixed-site sandbar), and data from this segment must therefore be grouped with data from the neighboring Marble Canyon river segment for some status and trend analyses.

The floristic associations that currently exist are not necessarily static through time. As climate, dam operations, and tributary flow patterns change, it is likely that species distributions along the Colorado River will also change (Capon and others, 2013; McShane and others, 2015; Perry and others, 2015). The current floristic groups may remain similar but shift geographically. For example, the desert riparian community in Grand Canyon may become more prevalent in Marble Canyon over time. Alternatively, novel floristic groups may emerge as individual species respond independently to environmental changes on the basis of their specific physiological traits and niche preferences (Hobbs and others, 2006; Catford and others, 2013). Because different vegetation types differentially influence sediment deposition (Butterfield and others, 2020), drive community level functional traits (McCoy-Sulentic and others, 2017a), and respond to hydrologic and climatic variables (Butterfield and others, 2018), it is important to track shifts in riparian vegetation communities over time.

Total riparian vegetation cover is variable across and within segments. Narrow sections of Grand Canyon tend to have lower total vegetated area, as illustrated by Sankey and others (2015), but a lack of habitable area should not be reflected in the total cover estimates provided in this report. The sampled area (comprising no more than twenty-seven 1-m^2 quadrats) is similar for all randomly selected sites, and quadrats are arranged based on the width of the hydrologic zones; therefore, a site that is 50-m wide can have a similar total foliar cover estimate as a site that is 10-m wide. The reduced total foliar cover exhibited in eastern Grand Canyon, then, is likely due to other contributing factors such as increased shading from canyon walls, increased flow velocity due to a narrower channel, coarser soil components (in other words, soil containing more gravels and rock), and so on. These same factors may be related to the high variability in total vegetation cover throughout the canyon, indicating strong interactions between river flows and other environmental variables (Bendix, 1994a; Butterfield and others, 2018; Butterfield and others, 2020). To predict vegetation response to flows and increase vegetation restoration success, it is important to better understand how river flows and other environmental variables jointly influence plant species in the study area.

Temporal Dynamics

The indicators used to assess management goals within Grand Canyon have demonstrated few directional changes from 2014 to 2019, with observed trends primarily occurring within the area influenced by daily dam operations (that is, within the active channel). Some fluctuations in vegetation status can be attributed to interannual climatic variation (discussed below), but for some temporal variations in species of interest (for example, the 2016 *Baccharis* and *Tamarix* peak in the active floodplain of sandbars), the drivers are less evident. The status and trends herein provide a baseline of interannual variation against which future monitoring can be compared. The annual timesteps of the monitoring data illustrate that collecting data less frequently (for example, every other year) would make it more difficult to detect trends or be confident that observed patterns indicate trends in vegetation change. Additionally, less frequent sampling could miss nonlinear responses to unique changes in dam operations (such as flows designed for trout management and HFE releases).

In general, vegetation status and dynamics at randomly selected sites differed from those at fixed-site sandbars, indicating that different processes regulate vegetation in these different geomorphic settings. For example, species richness is lower in the active channel of fixed-site sandbars than in the active channel of randomly selected sites. Another example is that *Baccharis* species are increasing in the active channel of randomly selected sites but not in the active channel of fixed-site sandbars. These results imply that different management strategies may be necessary to obtain vegetation and recreation resource goals in these different settings.

Species diversity and total foliar cover showed temporal patterns in the active channel that were consistent with the overriding influence of river flows (rather than climate variability) on vegetation affected by daily fluctuations. Species richness, cover, and native species dominance increased over time in the active channel across randomly selected sites; whereas in the active channel of fixed-site sandbars, species richness and cover both decreased slightly over time, and native species dominance did not change. The increase in native species dominance across randomly selected sites reflects a shift from nonnative species dominance in 2014, and native species dominance at randomly selected sites has begun to converge on the higher level of native species dominance that has been consistently observed in the active channel of the fixed-site sandbars. This increase in native species dominance, as well as the overall increase in species richness and cover across randomly selected sites, likely reflects the consistent flow regime and low intensity of disturbance over the study period, which has allowed establishment and expansion of more native species in the active channel. The increased prevalence of large native shrubs in the genus *Baccharis* is emblematic of this change.

The opposite pattern of declining species richness and cover in the fixed-site sandbars may reflect the combined impacts of hydrological and climatic factors. The lower species richness and cover of 2019 largely drove this trend, which is consistent with the combination of a HFE in the fall of 2018 and virtually no monsoon precipitation in 2019. The reduction in species richness is unlikely to be related to vegetation removals conducted by the National Park Service at the Basalt Camp and 122 Mile Camp fixed-site sandbars in 2019 (U.S. Department of the Interior, 2017). Encroaching *Pluchea sericea* was removed to increase usable camping area and facilitate increased transport of windblown sand to upland areas. Because of the limited number of sites affected, the relatively small extent of areas cleared, the few species removed, and the notable lack of change in cover of the targeted species (*P. sericea*), it is most probable that the fall 2018 HFE and the dry 2019 monsoon season are jointly related to the lower species richness and cover observed in 2019.

The active floodplain and inactive floodplain exhibited greater sensitivity to interannual climate variability, though species richness and vegetation cover appeared to be responsive to different aspects of precipitation. Species richness was generally lowest in 2014 and 2018, the years with the lowest total annual precipitation. Vegetation cover was lowest in 2014 and 2019; the latter year, though not particularly dry in terms of total annual precipitation, had one of the driest monsoon seasons in decades. In contrast, although 2018 was dry in terms of total annual precipitation, that year's monsoon season was close to average. These differing patterns are consistent with the influence of herbaceous, often annual species that make up a large proportion of the species pool but contribute less than woody vegetation to total ecosystem productivity. The apparent effect of a relatively dry 2019 monsoon suggests that vegetation productivity is constrained by warm-season precipitation. The fixed-site sandbars, which in normal years had generally higher vegetation cover than the randomly selected sites, seem to have been particularly sensitive to the dry monsoon season in 2019. This apparent sensitivity could reflect the higher initial vegetative cover of fixed-site sandbars, which could have resulted in more intense competition in 2019, or it could reflect that the fixed-site sandbars experience more severe water deficits under dry conditions because of their typically coarse substrates.

Some species of interest appeared to exhibit sensitivity to monsoon precipitation, though the evidence is weak and may be conflated with effects of HFE frequency. *Baccharis* and *Tamarix* had peak cover in 2016 in the active floodplain (and *Tamarix* in the inactive floodplain) of fixed-site sandbars. *Pluchea sericea* had a minor increase in cover that year, as well, though it was not significantly different than other years. Precipitation during the 2016 monsoon was high following an average precipitation winter and spring, which may account for these increases in cover but does not account for these anomalies not being observable across the randomly selected sites. Another possibility is that the lack of a HFE in 2015 allowed these woody plants to expand on the less stable sandbar surfaces, though a similar response was not seen in 2018 after the lack of a HFE in 2017. Regardless, the fact that this anomaly was only observed on the fixed-site sandbars suggests an influence of either substrate type, sandbar reconfiguration, or both. The amount and quality of active floodplain and inactive floodplain habitat could have been quite different in 2016 because of HFE releases in the three consecutive years from 2012 to 2014. Further investigation of the effects of HFE releases on species of interest in terms of habitat quality and lag effects are warranted.

Riparian vegetation in the study area is expected to increase over time because habitat is still available and base flows are anticipated to remain stable (Sankey and others, 2015; Kasprak and others, 2018; Kasprak and others, 2021). In an evaluation of riparian vegetation expansion between 2002 and 2013, Durning and others (2021) showed that most encroachment occurred between 2002 and 2009 and that the years from 2009 to 2013 were characterized by less encroachment by a smaller set of species. During the timeframe analyzed here (2014–2019), foliar cover does not appear to be increasing, suggesting that the slower rate of encroachment that Durning and others (2021) noted from 2009 to 2013 is continuing. The exception to this trend is the increasing *Baccharis* spp. cover in the active channel. Durning and others (2021) also found that *Baccharis* species were one of the primary contributors to recent vegetation encroachment, so this pattern of growth is also continuing. It is likely that *Baccharis* species are driving the greater proportion of native species in the active channel. *Baccharis emoryi* is high in cover across all geomorphic features and is the only native species with cover estimates approaching those of nonnative *Tamarix* and *Cynodon dactylon*. *Baccharis sarothroides* is also a large contributor to vegetation cover in western Grand Canyon. Although *P. sericea* is a major contributor to vegetation cover on fixed-site sandbars, its cover did not increase from 2014 to 2019. Vegetation increases in the past have not proceeded consistently across years, space, or species in the study area and are related to river flows, geomorphology, and climate (Carothers and others, 1976; Brian, 1982; Sankey and others, 2015; Butterfield and others, 2018; Mueller and others, 2018; Butterfield and others, 2020; Durning and others, 2021). Determining the flow patterns that lead to one species increasing in cover and (or) frequency while the cover and frequency of others remain the same would improve our abilities to predict the trajectory of riparian vegetation change and help define useful management actions.

The riparian area of the Colorado River between Glen Canyon Dam and Lake Mead is currently undergoing a visible change in its native to nonnative species ratio. *Diorhabda carinulata* (tamarisk beetle) has been present in the ecosystem since at least 2009 and, as of 2013, affected approximately 15 percent of *Tamarix* (Bedford and others, 2018). Over the timeframe covered here, monitoring efforts have not recorded significant decreases in living *Tamarix* cover, despite observable defoliation events. In this study, defoliated and fully healthy *Tamarix* are recorded similarly, so only tree mortality would be observable. Repeated defoliation events weaken *Tamarix* and can eventually result in tree mortality, but limb loss and resource depletion occur first (Bean and Dudley, 2018). Thus, considering 85 percent of *Tamarix* had not been affected by the tamarisk beetle in 2013, it is likely that *Tamarix* mortality is not yet recordable. The efforts of this monitoring protocol (which records dead *Tamarix*; Palmquist and others, 2018b) and periodic overflights (which can successfully track *Tamarix* defoliation and mortality; Bedford and others, 2018) are together expected to be able to track the effects of the tamarisk beetle on *Tamarix* cover over time.

The metrics used to track key riparian vegetation qualities (species richness, native to nonnative species ratio, total foliar cover) are promising for tracking management goals in the face of changing climate and flow conditions. These metrics are not dependent upon specific species and compositions; rather, they are simply related to the total number of species, the number of native species, and areal cover. The apparent lack of importance of both geomorphic feature and floristic region in the mixed-effects models of vegetation metrics (species richness, native to nonnative species ratio, total foliar cover) means that they can be evaluated across the entire study area (and thus do not require that the study area be divided into multiple river segments). Any future species distribution shifts will not necessarily change the outcome of these metrics, so values will be comparable over time. Shifts in species richness, native to nonnative species ratios, and total foliar cover can indicate if species are being lost over time, if nonnative species are predominating, or if total vegetation cover is declining or increasing. Although species composition is important because of the ecosystem services provided by specific species, measures of species richness, native to nonnative species ratios, and total foliar cover can provide a simple assessment of vegetation status that is useful for assessing the state of riparian vegetation along the Colorado River between Glen Canyon Dam and Lake Mead over time.

References Cited

Bates, D., Mächler, M., Bolker, B., and Walker, S., 2015, Fitting linear mixed-effects models using Ime4: Journal of Statistical Software, v. 67, no. 1, p. 1–48, https://doi.org/10.18637/jss.v067.i01.

Bean, D., and Dudley, T., 2018, A synoptic review of *Tamarix* biocontrol in North America—Tracking success in the midst of controversy: BioControl, v. 63, no. 3, p. 361–376, https://doi.org/10.1007/s10526-018-9880-x.

Beauchamp, V.B., and Stromberg, J.C., 2008, Changes to herbaceous plant communities on a regulated desert river: River Research and Applications, v. 24, no. 6, p. 754–770, https://doi.org/10.1002/rra.1078.

Bedford, A., Sankey, T.T., Sankey, J.B., Durning, L.E., and Ralston, B.E., 2018, Remote sensing of tamarisk beetle (*Diorhabda carinulata*) impacts along 412 km of the Colorado River in the Grand Canyon, Arizona, USA: Ecological Indicators, v. 89, p. 365–375, https://doi.org/10.1016/j.ecolind.2018.02.026.

Bejarano, M.D., González del Tánago, M., de Jalón, D.G., Marchamalo, M., Sordo-Ward, Á., and Solana-Gutiérrez, J., 2012, Responses of riparian guilds to flow alterations in a Mediterranean stream: Journal of Vegetation Science, v. 23, no. 3, p. 443–458, https://doi.org/10.1111/j.1654-1103.2011.01360.x.

Bejarano, M.D., Nilsson, C., and Aguiar, F.C., 2018, Riparian plant guilds become simpler and most likely fewer following flow regulation: Journal of Applied Ecology, v. 55, no. 1, p. 365–376, https://doi.org/10.1111/1365-2664.12949.

Bendix, J., 1994a, Among-site variation in riparian vegetation of the southern California Transverse Ranges: American Midland Naturalist, v. 132, no. 1, p. 136–151, https://doi.org/10.2307/2426208.

Bendix, J., 1994b, Scale, direction, and pattern in riparian vegetation-environment relationships: Annals of the Association of American Geographers, v. 84, no. 4, p. 652–665, https://doi.org/10.1111/j.1467-8306.1994.tb01881.x.

Blindow, I., Andersson, G., Hargeby, A., and Johansson, S., 1993, Long□term pattern of alternative stable states in two shallow eutrophic lakes: Freshwater Biology, v. 30, no. 1, p. 159–167, https://doi.org/10.1111/j.1365-2427.1993.tb00796.x.

Brian, N.J., 1982, A preliminary study of the riparian coyote willow communities along the Colorado River in Grand Canyon National Park, Arizona: Flagstaff, Northern Arizona University, M.S. thesis, 84 p.

Brown, B.T., and Johnson, R.R., 1985, Glen Canyon Dam, fluctuating water levels, and riparian breeding birds—The need for management compromise on the Colorado River in Grand Canyon, *in* Riparian ecosystems and their management—Reconciling conflicting uses [Proceedings for the First North American Riparian Conference, Tucson, Ariz., April 16–18, 1985]: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-120, 523 p., https://doi.org/10.2737/RM-GTR-120.

Busch, D.E., and Smith, S.D., 1993, Effects of fire on water and salinity relations of riparian woody taxa: Oecologia, v. 94, no. 2, p. 186–194, https://doi.org/10.1007/BF00341316.

Busch, D.E., and Smith, S.D., 1995, Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S: Ecological Monographs, v. 65, no. 3, p. 347–370, https://doi.org/10.2307/2937064.

Butterfield, B.J., Grams, P.E., Durning, L.E., Hazel, J.E., Palmquist, E.C., Ralston, B.E., and Sankey, J.B., 2020, Associations between riparian plant morphological guilds and fluvial sediment dynamics along the regulated Colorado River in Grand Canyon: River Research and Applications, v. 36, no. 3, p. 410–421, https://doi.org/10.1002/rra.3589.

Butterfield, B.J., Palmquist, E.C., and Ralston, B.E., 2018, Hydrological regime and climate interactively shape riparian vegetation composition along the Colorado River, Grand Canyon: Applied Vegetation Science, v. 21, no. 4, p. 572–583, https://doi.org/10.1111/avsc.12390.

Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D.S., Stewardson, M., Roberts, J., Parsons, M., and Williams, S.E., 2013, Riparian ecosystems in the 21st century—Hotspots for climate change adaptation?: Ecosystems, v. 16, no. 3, p. 359–381, https://doi.org/10.1007/s10021-013-9656-1.

Carothers, S.W., Aitchison, S.W., Karpiscak, M.M., Rufner, G.A., Sharber, N.J., Shoemaker, P.L., Stevens, L.E., Theroux, M.E., and Tomko, D.S., 1976, An ecological survey of the riparian zone of the Colorado River and its tributaries between Lees Ferry and the Grand Wash Cliffs—Final research report: U.S. Department of the Interior, National Park Service, Grand Canyon National Park, Colorado River Research Series Contribution no. 38, Technical Report no. 10, prepared by Museum of Northern Arizona, Flagstaff, Ariz., under contract no. CX821500007, 251 p. [Available at http://www.riversimulator.org/Resources/NPS/GCresearch/1976no10riparian.pdf.]

Caster, J.J., and Sankey, J.B., 2016, Variability in rainfall at monitoring stations and derivation of a long-term rainfall intensity record in the Grand Canyon Region, Arizona, USA: U.S. Geological Survey Scientific Investigations Report 2016–5012, 38 p., https://doi.org/10.3133/sir20165012.

Caster, J.J., Sankey, J.B., and Fairley, H., 2018, Meteorological data for selected sites along the Colorado River corridor, Arizona, 2014–2015: U.S. Geological Survey data release, https://doi.org/10.5066/F7DZ0771.

Catford, J.A., Naiman, R.J., Chambers, L.E., Roberts, J., Douglas, M., and Davies, P., 2013, Predicting novel riparian ecosystems in a changing climate: Ecosystems, v. 16, no. 3, p. 382–400, https://doi.org/10.1007/s10021-012-9566-7.

Clover, E.U., and Jotter, L., 1944, Floristic studies in the canyon of the Colorado and tributaries: American Midland Naturalist, v. 32, no. 3, p. 591–642, https://doi.org/10.2307/2421241.

Dean, D.J., and Schmidt, J.C., 2011, The role of feedback mechanisms in historic channel changes of the lower Rio Grande in the Big Bend region: Geomorphology, v. 126, no. 3–4, p. 333–349, https://doi.org/10.1016/j.geomorph.2010.03.009.

Dong, X., Grimm, N.B., Ogle, K., and Franklin, J., 2016, Temporal variability in hydrology modifies the influence of geomorphology on wetland distribution along a desert stream: Journal of Ecology, v. 104, no. 1, p. 18–30, https://doi.org/10.1111/1365-2745.12450.

Douhovnikoff, V., McBride, J.R., and Dodd, R.S., 2005, *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation: Ecology, v. 86, no. 2, p. 446–452, https://doi.org/10.1890/04-0257.

Durning, L.E., Sankey, J.B., Davis, P.A., and Sankey, T.T., 2016, Four-band image mosaic of the Colorado River corridor downstream of Glen Canyon Dam in Arizona, derived from the May 2013 airborne image acquisition: U.S. Geological Survey Data Series 1027, https://doi.org/10.3133/ds1027.

Durning, L.E., Sankey, J.B., Yackulic, C.B., Grams, P.E., Butterfield, B.J., and Sankey, T.T., 2021, Hydrologic and geomorphic effects on riparian plant species occurrence and encroachment—Remote sensing of 360 km of the Colorado River in Grand Canyon: Ecohydrology, v. 14, no. 8, https://doi.org/10.1002/eco.2344.

East, A.E., Sankey, J.B., Fairley, H.C., Caster, J.J., and Kasprak, A., 2017, Modern landscape processes affecting archaeological sites along the Colorado River corridor downstream of Glen Canyon Dam, Glen Canyon National Recreation Area, Arizona: U.S. Geological Survey Scientific Investigations Report 2017–5082, 22 p., https://doi.org/10.3133/sir20175082.

Fairley, H.C., 2005, Cultural resources in the Colorado River corridor, *in* Gloss, S.P., Lovich, J.E., and Melis, T.S., eds., The state of the Colorado River ecosystem in Grand Canyon—A report of the Grand Canyon Monitoring and Research Center 1991–2004: U.S. Geological Survey Circular 1282, p. 177–192., https://doi.org/10.3133/cir1282.

Gaskin, J.F., and Schaal, B.A., 2002, Hybrid *Tamarix* widespread in the U.S. invasion and undetected in native Asian range: Proceedings of the National Academy of Sciences of the United States of America, v. 99, no. 17, p. 11256–11259, https://doi.org/10.1073/pnas.132403299.

Gloss, S., Lovich, J.E., and Melis, T.S., eds., 2005, The state of the Colorado River ecosystem in Grand Canyon—A report of the Grand Canyon Monitoring and Research Center 1991–2004: U.S. Geological Survey Circular 1282, 220 p., https://doi.org/10.3133/cir1282.

González, E., Martínez-Fernández, V., Shafroth, P.B., Sher, A.A., Henry, A.L., Garófano-Gómez, V., and Corenblit, D., 2018, Regeneration of *Salicaceae* riparian forests in the Northern Hemisphere—A new framework and management tool: Journal of Environmental Management, v. 218, p. 374–387, https://doi.org/10.1016/j.jenvman.2018.04.069.

González, E., Shafroth, P.B., Lee, S.R., Ostoja, S.M., and Brooks, M.L., 2020, Combined effects of biological control of an invasive shrub and fluvial processes on riparian vegetation dynamics: Biological Invasions, v. 22, no. 7, p. 2339–2356, https://doi.org/10.1007/s10530-020-02259-9.

Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W., 1991, An ecosystem perspective of riparian zones: Bioscience, v. 41, no. 8, p. 540–551, https://doi.org/10.2307/1311607.

Griffiths, P.G., Webb, R.H., and Melis, T.S., 2004, Frequency and initiation of debris flows in Grand Canyon, Arizona: Journal of Geophysical Research, v. 109, no. F4, article F04002, 14 p., https://doi.org/10.1029/2003JF000077.

Gushue, T.M., 2019, Colorado River mile system, Grand Canyon, Arizona: U.S. Geological Survey data release, https://doi.org/10.5066/P9IRL3GV.

Hadley, D.R., Grams, P.E., and Kaplinski, M.A., 2018, Quantifying geomorphic and vegetation change at sandbar campsites in response to flow regulation and controlled floods, Grand Canyon National Park, Arizona: River Research and Applications, v. 34, no. 9, p. 1208–1218, https://doi.org/10.1002/rra.3349.

Hazel, J.E., Jr., Topping, D.J., Schmidt, J.C., and Kaplinski, M., 2006, Influence of a dam on fine-sediment storage in a canyon river: Journal of Geophysical Research, v. 111, no. F1, article F01025, 16 p., https://doi.org/10.1029/2004JF000193.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R., and Zobel, M., 2006, Novel ecosystems—Theoretical and management aspects of the new ecological world order: Global Ecology and Biogeography, v. 15, no. 1, p. 1–7, https://doi.org/10.1111/j.1466-822X.2006.00212.x.

Holmes, J.A., Spence, J.R., and Sogge, M.K., 2005, Birds of the Colorado River in Grand Canyon—A synthesis of status, trends and dam operations effects, *in* Gloss, S.P., Lovich, J.E., and Melis, T.S., eds., The state of the Colorado River ecosystem in Grand Canyon—A report of the Grand Canyon Monitoring and Research Center 1991–2004: U.S. Geological Survey Circular 1282, p. 123–138., https://doi.org/10.3133/cir1282.

Jackson-Kelly, L., and Hubbs, D., 2007, Traditional Hualapai ecological monitoring knowledge monitoring protocols—Adaptive Management Program Technical Working Group meeting: Phoenix, Ariz., April 2–3, 2007, Hualapai Tribe, Department of Cultural Resources, 27-slide presentation. [Available at https://www.usbr.gov/uc/progact/amp/twg/2007-04-02-twg-meeting/Attach_13c.pdf.]

Jansson, R., Nilsson, C., Dynesius, M., and Andersson, E., 2000, Effects of river regulation on river-margin vegetation—A comparison of eight boreal rivers: Ecological Applications, v. 10, no. 1, p. 203–224, https://doi.org/10.1890/1051-0761(2000)010[0203:EORROR]2.0.CO;2.

Kaplinski, M., Behan, J., Hazel, J.E., Parnell, R.A., and Fairley, H.C., 2005, Recreational values and campsites in the Colorado River ecosystem, *in* Gloss, S.P., Lovich, J.E., and Melis, T.S., eds., The state of the Colorado River ecosystem in Grand Canyon—A report of the Grand Canyon Monitoring and Research Center 1991–2004: U.S. Geological Survey Circular 1282, p. 193–205., https://doi.org/10.3133/cir1282.

Kaplinski, M.A., Hazel, J.E., Parnell, R., Hadley, D.R., and Grams, P.E., 2014, Colorado River campsite monitoring, 1998–2012, Grand Canyon National Park, Arizona: U.S. Geological Survey Open-File Report 2014–1161, 24 p., https://doi.org/10.3133/ofr20141161.

Kasprak, A., Sankey, J.B., Buscombe, D., Caster, J., East, A.E., and Grams, P.E., 2018, Quantifying and forecasting changes in the areal extent of river valley sediment in response to altered hydrology and land cover: Progress in Physical Geography, v. 42, no. 6, p. 739–764, https://doi.org/10.1177/0309133318795846.

Kasprak, A., Sankey, J.B., and Butterfield, B.J., 2021, Discharge records and sand extents along the Colorado River between Glen Canyon Dam and Phantom Ranch, Arizona: U.S. Geological Survey data release, https://doi.org/10.5066/P918E2P3.

Kearsley, L.H., Schmidt, J.C., and Warren, K.D., 1994, Effects of Glen Canyon Dam on Colorado River sand deposits used as campsites in Grand Canyon National Park, USA: Regulated Rivers, v. 9, no. 3, p. 137–149, https://doi.org/10.1002/rrr.3450090302.

Kearsley, M.J.C., and Ayers, T.J., 1996, The effects of interim flows from Glen Canyon Dam on riparian vegetation in the Colorado River corridor, Grand Canyon National Park, Arizona—Final report: Grand Canyon, Ariz., Grand Canyon National Park, Grand Canyon Science Center, prepared by Northern Arizona University, Flagstaff, Ariz., under cooperative agreement work order no. 8041-8-0002, 702 p. [Available at http://www.riversimulator.org/Resources/GCMRC/Terrestrial/Kearsley1996b.pdf.]

Kearsley, M.J.C., Cobb, N., Yard, H., Lightfoot, D., Brantley, S., Carpenter, G., and Frey, J., 2004, Inventory and monitoring of terrestrial riparian resources in the Colorado River corridor of Grand Canyon—An integrative approach [Draft final report]: Flagstaff, Ariz., U.S. Geological Survey, Grand Canyon Monitoring and Research Center, prepared by authors under cooperative agreement and assistance awards nos. 01-WRAG-0044 (NAU) and 01-WRAG-0034 (HYC), 218 p.

Lenth, R., Singmann, H., Love, J., Buerkner, P., and Herve, M., 2018, Emmeans: Estimated marginal means, aka least-squares means: R package version, v. 1, no. 1, p. 3.

Lite, S.J., Bagstad, K.J., and Stromberg, J.C., 2005, Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA: Journal of Arid Environments, v. 63, no. 4, p. 785–813, https://doi.org/10.1016/j.jaridenv.2005.03.026.

Lytle, D.A., and Poff, N.L., 2004, Adaptation to natural flow regimes: Trends in Ecology & Evolution, v. 19, no. 2, p. 94–100, https://doi.org/10.1016/j.tree.2003.10.002.

Magilligan, F.J., and Nislow, K.H., 2005, Changes in hydrologic regime by dams: Geomorphology, v. 71, no. 1-2, p. 61–78, https://doi.org/10.1016/j.geomorph.2004.08.017.

Mayes, V.O., and Lacy, B.B., 1989, Nanise'—A Navajo herbal—One hundred plants from the Navajo Reservation: Tsaile, Ariz., Navajo Community College Press, 153 p.

McCoy-Sulentic, M.E., Kolb, T.E., Merritt, D.M., Palmquist, E., Ralston, B.E., Sarr, D.A., and Shafroth, P.B., 2017a, Changes in community-level riparian plant traits over inundation gradients, Colorado River, Grand Canyon: Wetlands, v. 37, no. 4, p. 635–646, https://doi.org/10.1007/s13157-017-0895-3.

McCoy-Sulentic, M.E., Kolb, T.E., Merritt, D.M., Palmquist, E.C., Ralston, B.E., and Sarr, D.A., 2017b, Variation in species-level plant functional traits over wetland indicator status categories: Ecology and Evolution, v. 7, no. 11, p. 3732–3744, https://doi.org/10.1002/ece3.2975.

McShane, R., Auerbach, D., Friedman, J.M., Auble, G.T., Shafroth, P.B., Merigliano, M.F., Scott, J.M., and Poff, N.L., 2015, Distribution of invasive and native riparian woody plants across the western USA in relation to climate, river flow, floodplain geometry and patterns of introduction: Ecography, v. 38, no. 12, p. 1254–1265, https://doi.org/10.1111/ecog.01285.

Merritt, D.M., Manning, M.E., and Hough-Snee, N., eds., 2017, The National Riparian Core Protocol—A riparian vegetation monitoring protocol for wadeable streams of the conterminous United States: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, National Riparian Technical Team, General Technical Report RMRS-GTR-367, 35 p., https://doi.org/10.2737/RMRS-GTR-367.

Merritt, D.M., and Poff, N.L., 2010, Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American Rivers: Ecological Applications, v. 20, no. 1, p. 135–152, https://doi.org/10.1890/08-2251.1.

Mortenson, S.G., and Weisberg, P.J., 2010, Does river regulation increase the dominance of invasive woody species in riparian landscapes?: Global Ecology and Biogeography, v. 19, no. 4, p. 562–574, https://doi.org/10.1111/j.1466-8238.2010.00533.x.

Mueller, E.R., Grams, P.E., Hazel, J.E., Jr., and Schmidt, J.C., 2018, Variability in eddy sandbar dynamics during two decades of controlled flooding of the Colorado River in the Grand Canyon: Sedimentary Geology, v. 363, p. 181–199, https://doi.org/10.1016/j.sedgeo.2017.11.007.

Mueller, E.R., Grams, P.E., Schmidt, J.C., Hazel, J.E., Jr., Alexander, J.S., and Kaplinski, M., 2014, The influence of controlled floods on fine sediment storage in debris fan-affected canyons of the Colorado River Basin: Geomorphology, v. 226, p. 65–75, https://doi.org/10.1016/j.geomorph.2014.07.029.

Naiman, R.J., and Decamps, H., 1997, The ecology of interfaces—Riparian zones: Annual Review of Ecology and Systematics, v. 28, no. 1, p. 621–658, https://doi.org/10.1146/annurev.ecolsys.28.1.621.

National Park Service, 2006, Colorado River management plan: U.S. Department of the Interior, National Park Service, Grand Canyon National Park, 35 p. [Available at https://www.nps.gov/grca/learn/management/upload/CRMPIF_s.pdf.]

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H.S., Szoecs, E., and Wagner, H., 2015, vegan—Community ecology package, version 2.3-2: R Foundation for Statistical Computing software release. [Additional information is available at https://CRAN.R-project.org/package=vegan.]

Palmquist, E.C., Butterfield, B.J., and Ralston, B.E., 2022, Riparian vegetation data downstream of Glen Canyon Dam in Glen Canyon National Recreation Area and Grand Canyon National Park, AZ from 2014 to 2019: U.S. Geological Survey data release, https://doi.org/10.5066/P9KEHY2S.

Palmquist, E.C., Ralston, B.E., Merritt, D.M., and Shafroth, P.B., 2018a, Landscape-scale processes influence riparian plant composition along a regulated river: Journal of Arid Environments, v. 148, p. 54–64, https://doi.org/10.1016/j.jaridenv.2017.10.001.

Palmquist, E.C., Ralston, B.E., Sarr, D.A., and Johnson, T.C., 2018b, Monitoring riparian-vegetation composition and cover along the Colorado River downstream of Glen Canyon Dam, Arizona: U.S. Geological Survey Techniques and Methods, book 2, chap. A14, 65 p., https://doi.org/10.3133/tm2A14.

Palmquist, E., Ralston, B.E., Sarr, D.A., Merritt, D.M., Shafroth, P.B., and Scott, J.A., 2017, Functional traits and ecological affinities of riparian plants along the Colorado River in Grand Canyon: Western North American Naturalist, v. 77, no. 1, p. 22–30, https://doi.org/10.3398/064.077.0104.

Palmquist, E.C., Sterner, S.A., and Ralston, B.E., 2019, A comparison of riparian vegetation sampling methods along a large, regulated river: River Research and Applications, v. 35, no. 6, p. 759–767, https://doi.org/10.1002/rra.3440.

Perkins, D.W., Scott, M., Auble, G., Wondzell, M., Holmquist-Johnson, C., Wahlig, E., Thomas, H., and Wight, A., 2018, Big rivers monitoring protocol for park units in the Northern Colorado Plateau Network—Version 1.01: Fort Collins, Colo., Department of the Interior, National Park Service, Natural Resource Report NPS/NCPN/NRR-2018/1707, 46 p. [Available at https://irma.nps.gov/DataStore/Reference/Profile/2254720.]

Perry, L.G., Reynolds, L.V., Beechie, T.J., Collins, M.J., and Shafroth, P.B., 2015, Incorporating climate change projections into riparian restoration planning and design: Ecohydrology, v. 8, no. 5, p. 863–879, https://doi.org/10.1002/eco.1645.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C., 1997, The natural flow regime—A paradigm for river conservation and restoration: Bioscience, v. 47, no. 11, p. 769–784, https://doi.org/10.2307/1313099.

Porter, M.E., and Kearsley, M.J.C., 2001, The response of salt cedar, Tamarix chinensis, to experimental flows in Grand Canyon: Hydrology and Water Resources in Arizona and the Southwest, v. 31, p. 45–50, https://doi.org/10150/296583.

R Core Team, 2021, R—A language and environment for statistical computing, version 4.1.2 (Bird Hippie): R Foundation for Statistical Computing software release. [Additional information is available at https://www.r-project.org/.]

Ralston, B.E., 2010, Riparian vegetation response to the March 2008 short-duration, high-flow experiment—Implications of timing and frequency of flood disturbance on nonnative plant establishment along the Colorado River below Glen Canyon Dam: U.S. Geological Survey Open-File Report 2010–1022, 30 p., https://doi.org/10.3133/ofr20101022.

Ralston, B.E., 2011, Summary report of responses of key resources to the 2000 low steady summer flow experiment, along the Colorado River downstream from Glen Canyon Dam, Arizona: U.S. Geological Survey Open-File Report 2011–1220, 129 p., https://doi.org/10.3133/ofr20111220.

Ralston, B.E., and Sarr, D.A., 2017, Case studies of riparian and watershed restoration in the southwestern United States—Principles, challenges, and successes: U.S. Geological Survey Open-File Report 2017–1091, 116 p., https://doi.org/10.3133/ofr20171091.

Reynolds, L.V., Shafroth, P.B., and Poff, N.L., 2015, Modeled intermittency risk for small streams in the Upper Colorado River Basin under climate change: Journal of Hydrology, v. 523, p. 768–780, https://doi.org/10.1016/j.jhydrol.2015.02.025.

Rood, S.B., Samuelson, G.M., Braatne, J.H., Gourley, C.R., Hughes, F.M.R., and Mahoney, J.M., 2005, Managing river flows to restore floodplain forests: Frontiers in Ecology and the Environment, v. 3, no. 4, p. 193–201, https://doi.org/10.1890/1540-9295(2005)003[0193:MRFTRF]2.0.CO;2.

Rubin, D.M., Schmidt, J.C., and Moore, J.N., 1990, Origin, structure, and evolution of a reattachment bar, Colorado River, Grand Canyon, Arizona: Journal of Sedimentary Research, v. 60, no. 6, p. 982–991, https://doi.org/10.1306/D426765E-2B26-11D7-8648000102C1865D.

Rubin, D.M., Topping, D.J., Schmidt, J.C., Hazel, J., Kaplinski, M., and Melis, T.S., 2002, Recent sediment studies refute Glen Canyon Dam hypothesis: Eos, v. 83, no. 25, p. 273, 277–278, https://doi.org/10.1029/2002EO000191.

Sankey, J.B., and Draut, A.E., 2014, Gully annealing by aeolian sediment—Field and remote-sensing investigation of aeolian-hillslope-fluvial interactions, Colorado River corridor, Arizona, USA: Geomorphology, v. 220, p. 68–80, https://doi.org/10.1016/j.geomorph.2014.05.028.

Sankey, J.B., Ralston, B.E., Grams, P.E., Schmidt, J.C., and Cagney, L.E., 2015, Riparian vegetation, Colorado River, and climate—Five decades of spatiotemporal dynamics in the Grand Canyon with river regulation: Journal of Geophysical Research—Biogeosciences, v. 120, no. 8, p. 1532–1547, https://doi.org/10.1002/2015JG002991.

Sarr, D.A., Hibbs, D.E., Shatford, J.P.A., and Momsen, R., 2011, Influences of life history, environmental gradients, and disturbance on riparian tree regeneration in western Oregon: Forest Ecology and Management, v. 261, no. 7, p. 1241–1253, https://doi.org/10.1016/j.foreco.2011.01.002.

Schmidt, J.C., and Graf, J.B., 1990, Aggradation and degradation of alluvial sand deposits, 1965–1986, Colorado River, Grand Canyon National Park, Arizona: U.S. Geological Survey Professional Paper 1493, 74 p., https://doi.org/10.3133/pp1493.

Schmidt, J.C., Webb, R.H., Valdez, R.A., Marzolf, G.R., and Stevens, L.E., 1998, Science and values in river restoration in the Grand Canyon: Bioscience, v. 48, no. 9, p. 735–747, https://doi.org/10.2307/1313336.

Scott, M.L., Webb, R.H., Johnson, R.R., Turner, R.M., Friedman, J.M., and Fairley, H.C., 2018, Evaluating riparian vegetation change in canyon-bound reaches of the Colorado River using spatially extensive matched photo sets, chap. 9 *of* Johnson, R.R., Carothers, S.W., Finch, D.M., and Kingsley, K.J., eds., Riparian ecology—Past, present, future: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-377, 226 p., https://doi.org/10.2737/RMRS-GTR-377.

Sogge, M.K., Felley, D., and Wotawa, M., 1998, Riparian bird community ecology in the Grand Canyon—Final report: U.S. Department of the Interior, Bureau of Reclamation, prepared by U.S. Geological Survey, Colorado Plateau Field Station, Flagstaff, Ariz., under cooperative agreement no. 8031-8-0002, 276 p., 3 app. [Also available at http://www.riversimulator.org/Resources/GCMRC/Terrestrial/Sogge1998a.pdf.]

Spence, J.R., 2006, The riparian and aquatic bird communities along the Colorado River from Glen Canyon Dam to Lake Mead, 1996–2000—Final report: Flagstaff, Ariz., U.S. Geological Survey, Grand Canyon Monitoring and Research Center, prepared by National Park Service, Resource Management Division, Glen Canyon National Recreation Area, Page, Ariz., under interagency acquisition no. 1425-98-AA-40-22680, 283 p.

Stevens, L.E., Ayers, T.J., Bennett, J.B., Christensen, K., Kearsley, M.J.C., Meretsky, V.J., Phillips, A.M., III, Parnell, R.A., Spence, J.R., Sogge, M.K., Springer, A.E., and Wegner, D.L., 2001, Planned flooding and Colorado River riparian trade-offs downstream from Glen Canyon Dam, Arizona: Ecological Applications, v. 11, no. 3, p. 701–710, https://doi.org/10.1890/1051-0761(2001)011[0701:PFACRR]2.0.CO;2.

Stevens, L.E., Schmidt, J.C., Ayers, T.J., and Brown, B.T., 1995, Flow regulation, geomorphology, and Colorado River marsh development in the Grand Canyon, Arizona: Ecological Applications, v. 5, no. 4, p. 1025–1039, https://doi.org/10.2307/2269352.

Stevens, L.E., and Waring, G.L., 1985, Effects of prolonged flooding on riparian vegetation in Grand Canyon, *in* Riparian ecosystems and their management— Reconciling conflicting uses [Proceedings for the First North American Riparian Conference, Tucson, Ariz., April 16–18, 1985]: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-120, 523 p., https://doi.org/10.2737/RM-GTR-120.

Stevens, L.E., and Waring, G.L., 1986, Effects of post-dam flooding on riparian substrates, vegetation, and invertebrate populations in the Colorado River corridor in Grand Canyon, Arizona—Terrestrial biology of the Glen Canyon Environmental Studies: Salt Lake City, Utah, Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies report GCES 19/87, 175 p.

Stewart, W., Larkin, K., Orland, B., and Anderson, D., 2003, Boater preferences for beach characteristics downstream from Glen Canyon Dam, Arizona: Journal of Environmental Management, v. 69, no. 2, p. 201–211, https://doi.org/10.1016/j.jenvman.2003.08.001.

Stromberg, J.C., Andersen, D.C., and Scott, M.L., 2012, Riparian floodplain wetlands of the arid and semiarid southwest, *in* Batzer, D.P., and Baldwin, A.H., eds., Wetland habitats of North America—Ecology and conservation concerns: Berkeley, University of California Press, p. 343–356.

Stromberg, J.C., Beauchamp, V.C., Dixon, M.D., Lite, S.J., and Paradzick, C., 2007, Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States: Freshwater Biology, v. 52, no. 4, p. 651–679, https://doi.org/10.1111/j.1365-2427.2006.01713.x.

Stromberg, J.C., McCluney, K.E., Dixon, M.D., and Meixner, T., 2013, Dryland riparian ecosystems in the American southwest—Sensitivity and resilience to climatic extremes: Ecosystems, v. 16, no. 3, p. 411–415, https://doi.org/10.1007/s10021-012-9606-3.

Stromberg, J.C., Tluczek, M.G., Hazelton, A.F., and Ajami, H., 2010, A century of riparian forest expansion following extreme disturbance—Spatio-temporal change in Populus/Salix/Tamarix forests along the Upper San Pedro River, Arizona, USA: Forest Ecology and Management, v. 259, no. 6, p. 1181–1189, https://doi.org/10.1016/j.foreco.2010.01.005.

Tabacchi, E., Correll, D.L., Hauer, R., Pinay, G., Planty-Tabacchi, A.-M., and Wissmar, R.C., 1998, Development, maintenance and role of riparian vegetation in the river landscape: Freshwater Biology, v. 40, no. 3, p. 497–516, https://doi.org/10.1046/j.1365-2427.1998.00381.x.

Topping, D.J., Schmidt, J.C., and Vierra, L.E., 2003, Computation and analysis of the instantaneous-discharge record for the Colorado River at Lees Ferry, Arizona—May 8, 1921, through September 30, 2000: U.S. Geological Survey Professional Paper 1677, 118 p., https://doi.org/10.3133/pp1677.

Turner, R.M., and Karpiscak, M.M., 1980, Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona: U.S. Geological Survey Professional Paper 1132, 125 p., https://doi.org/10.3133/pp1132.

U.S. Department of the Interior, 2016, Record of decision for the Glen Canyon Dam Long-Term Experimental and Management Plan Final Environmental Impact Statement: Salt Lake City, Utah, U.S. Bureau of Reclamation, Upper Colorado Region, and Lakewood, Colo., National Park Service, Intermountain Region, 196 p. [Available at https://ltempeis.anl.gov/documents/docs/LTEMP_ROD.pdf.]

U.S. Department of the Interior, 2017, Glen Canyon Dam Adaptive Management Program triennial budget and work plan—Fiscal years 2018–2020 [September 11, 2017, final draft]: Salt Lake City, Utah, Bureau of Reclamation, Upper Colorado Regional Office, and Flagstaff, Ariz., U.S. Geological Survey, Grand Canyon Monitoring and Research Center, 316 p. [Available at https://www.usbr.gov/uc/progact/amp/amwg/2017-09-20-amwg-meeting/Attach_04a.pdf.]

U.S. Department of the Interior, 2020, Glen Canyon Dam Adaptive Management Program triennial budget and work plan—Fiscal years 2021–2023 [September 4, 2020, final draft]: Salt Lake City, Utah, Bureau of Reclamation, Upper Colorado Regional Office, and Flagstaff, Ariz., U.S. Geological Survey, Grand Canyon Monitoring and Research Center, 418 p. [Available at http://gcdamp.com/images_gcdamp_com/5/53/1-GCMRC_TWP2021-23_SEPT-FINAL-v3.pdf.]

Vandersande, M.W., Glenn, E.P., and Walworth, J.L., 2001, Tolerance of five riparian plants from the lower Colorado River to salinity drought and inundation: Journal of Arid Environments, v. 49, no. 1, p. 147–159, https://doi.org/10.1006/jare.2001.0839.

Webb, R.H., 1996, Grand Canyon—A century of change—Rephotography of the 1889–1890 Stanton expedition: Tucson, University of Arizona Press, 290 p.

Webb, R.H., Belnap, J., Scott, M.L., and Esque, T.C., 2011, Long-term change in perennial vegetation along the Colorado River in Grand Canyon National Park (1889–2010): Park Science, v. 28, no. 2, p. 83–87.

Webb, R.H., and Leake, S.A., 2006, Ground-water surface-water interactions and long-term change in riverine riparian vegetation in the southwestern United States: Journal of Hydrology, v. 320, no. 3–4, p. 302–323, https://doi.org/10.1016/j.jhydrol.2005.07.022.

Webb, R.H., Wegner, D.L., Andrews, E.D., Valdez, R.A., and Patten, D.T., 1999, Downstream effects of Glen Canyon Dam in Grand Canyon—A review, *in* Webb, R.H., Schmidt, J.C., Marzolf, G.R., and Valdez, R.A., eds., The controlled flood in Grand Canyon: Geophysical Monograph Series 110: Washington, D.C., American Geophysical Union, p. 1–21, https://doi.org/10.1029/GM110p0001.

Werth, S., Schödl, M., and Scheidegger, C., 2014, Dams and canyons disrupt gene flow among populations of a threatened riparian plant: Freshwater Biology, v. 59, no. 12, p. 2502–2515, https://doi.org/10.1111/fwb.12449.

Appendix 1. Species List for Randomly Selected Sites

Table 1.1 provides a list of all recorded species in the randomly selected sites dataset.

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Nyctaginaceae	*Abronia elliptica*	fragrant white sand verbena	Forb	Native	1	0	0	1	0
Aceraceae	*Acer negundo*	boxelder	Tree	Native	1	0	1	0	0
Poaceae	*Achnatherum aridum*	Mormon needle grass	Graminoid	Native	1	1	0	0	0
Poaceae	*Achnatherum hymenoides*	Indian ricegrass	Graminoid	Native	36	3	20	10	3
Poaceae	*Achnatherum speciosum*	desert needlegrass	Graminoid	Native	30	0	20	8	2
Asteraceae	*Acourtia wrightii*	brownfoot	Forb	Native	1	0	1	0	0
Asteraceae	*Adenophyllum porophylloides*	San Filipe dogweed	Shrub	Native	1	0	0	1	0
Asparagaceae	*Agave utahensis*	Utah agave	Shrub	Native	8	0	4	4	0
Poaceae	*Agrostis exarata*	spike bentgrass	Graminoid	Native	1	0	1	0	0
Poaceae	*Agrostis gigantea*	redtop	Graminoid	Nonnative	45	21	19	2	3
Poaceae	*Agrostis* spp.	bentgrass	Graminoid		1	0	1	0	0
Poaceae	*Agrostis stolonifera*	creeping bentgrass	Graminoid	Nonnative	108	10	72	17	9
Fabaceae	*Alhagi maurorum*	camelthorn	Shrub	Nonnative	127	0	0	62	65
Nyctaginaceae	*Allionia incarnata*	trailing windmills	Forb	Native	5	0	1	2	2
Verbanaceae	*Aloysia wrightii*	Wright's beebrush	Shrub	Native	6	0	3	3	0
Amaranthaceae	*Amaranthus* spp.	pigweed	Forb		1	0	0	1	0
Asteraceae	*Ambrosia acanthicarpa*	flatspine bur ragweed	Forb	Native	13	1	4	5	3
Asteraceae	*Ambrosia psilostachya*	perennial ragweed	Forb	Native	1	0	0	1	0
Asteraceae	*Ambrosia tomentosa*	skeletonleaf bur ragweed	Forb	Native	3	0	2	0	1
Apocynaceae	*Amsonia tomentosa*	wooly bluestar	Forb	Native	1	0	1	0	0
Poaceae	*Andropogon gerardii*	big bluestem	Graminoid	Native	1	0	0	0	1
Poaceae	*Andropogon glomeratus*	bushy bluestem	Graminoid	Native	34	0	1	4	29
Apocynaceae	*Apocynum cannabinum*	Indianhemp	Forb	Native	23	4	18	1	0
Euphorbiaceae	*Argythamnia neomexicana*	New Mexico silverbush	Forb	Native	2	0	0	0	2
Poaceae	*Aristida adscensionis*	six weeks threeawn	Graminoid	Native	1	0	0	0	1
Poaceae	*Aristida arizonica*	Arizona threeawn	Graminoid	Native	109	0	8	60	41
Poaceae	*Aristida purpurea*	purple threeawn	Graminoid	Native	197	3	46	80	68
Poaceae	*Aristida* spp.	threeawn	Graminoid	Native	6	0	4	2	0
Poaceae	*Aristida ternipes*	spidergrass	Graminoid	Native	8	0	0	3	5

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Aristolochiaceae	*Aristolochia watsonii*	Watson's dutchman's pipe	Forb	Native	1	0	0	1	0
Asteraceae	*Artemisia dracunculus*	tarragon	Forb	Native	4	0	2	2	0
Asteraceae	*Artemisia frigida*	prairie sagewort	Shrub	Native	1	1	0	0	0
Asteraceae	*Artemisia ludoviciana*	white sagebrush	Forb	Native	150	24	88	29	9
Asteraceae	*Artemisia tridentata*	big sagebrush	Shrub	Native	2	0	2	0	0
Asclepiadaceae	*Asclepias latifolia*	broad leaf milkweed	Forb	Native	1	0	1	0	0
Asteraceae	*Aster* spp.				2	0	0	0	2
Fabaceae	*Astragalus amphioxys*	aladdin's slippers	Forb	Native	1	0	0	1	0
Fabaceae	*Astragalus* spp.	milkvetch	Forb	Native	5	0	3	2	0
Pteridaceae	*Astrolepsis cochisensis*	Cochise scaly cloakfern	Forb	Native	1	0	0	0	1
Chenopodiaceae	*Atriplex canescens*	fourwing saltbush	Shrub	Native	6	2	3	1	0
Chenopodiaceae	*Atriplex garrettii*	Garrett's saltbush	Shrub	Native	1	0	1	0	0
Chenopodiaceae	*Atriplex obovata*	mound saltbush	Shrub	Native	1	0	1	0	0
Asteraceae	*Baccharis brachyphylla*	shortleaf baccharis	Shrub	Native	5	0	2	3	0
Asteraceae	*Baccharis emoryi*	Emory's baccharis	Shrub	Native	302	23	113	82	84
Asteraceae	*Baccharis salicifolia*	mule-fat	Shrub	Native	138	0	15	67	56
Asteraceae	*Baccharis sarothroides*	desertbroom	Shrub	Native	148	0	0	24	124
Asteraceae	*Baccharis sergiloides*	desert baccharis	Shrub	Native	21	0	1	16	4
Asteraceae	*Baccharis* spp.		Shrub	Native	5	0	0	3	2
Asteraceae	*Bebbia juncea*	sweetbush	Shrub	Native	65	0	2	32	31
Euphorbiaceae	*Bernardia incana*	hoary myrtlecroton	Shrub	Native	1	0	0	1	0
Apiales	*Berula erecta*	cutleaf waterparsnip	Forb	Native	1	1	0	0	0
Brassicaceae	*Boechera perennans*	perennial rockcress	Forb	Native	4	0	3	0	1
Nyctaginaceae	*Boerhavia intermedia*	fivewing spiderling	Forb	Native	3	0	0	2	1
Nyctaginaceae	*Boerhavia* spp.	spiderling	Forb	Native	4	2	1	1	0
Nyctaginaceae	*Boerhavia spicata*	creeping spiderling	Forb	Native	1	0	0	0	1
Nyctaginaceae	*Boerhavia torreyana*	creeping spiderling	Forb	Native	2	0	2	0	0
Nyctaginaceae	*Boerhavia wrightii*	largebract spiderling	Forb	Native	5	0	0	1	4
Poaceae	*Bothriochloa barbinodis*	cane bluestem	Graminoid	Native	155	2	24	66	63
Poaceae	*Bothriochloa laguroides*	silver beardgrass	Graminoid	Native	72	0	35	20	17

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon ("Eastern GRCA"), river kilometers 97 to 259; western Grand Canyon ("Western GRCA"), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Poaceae	*Bothriochloa saccharoides*	plumed beardgrass	Graminoid	Native	9	0	1	5	3
Poaceae	*Bouteloua aristidoides*	needle grama	Graminoid	Native	11	0	2	1	8
Poaceae	*Bouteloua barbata*	sixweeks grama	Graminoid	Native	23	0	3	14	6
Poaceae	*Bouteloua curtipendula*	sideoats grama	Graminoid	Native	9	0	4	5	0
Poaceae	*Bouteloua trifida*	red gramma	Graminoid	Native	1	0	0	0	1
Brassicaceae	*Brassicaceae* unknown				9	1	2	2	4
Asteraceae	*Brickellia atractyloides*	spearleaf brickellbush	Shrub	Native	4	0	1	3	0
Asteraceae	*Brickellia californica*	California brickellbush	Shrub	Native	1	0	0	0	1
Asteraceae	*Brickellia coulteri*	Coulter's brickellbush	Shrub	Native	4	0	0	1	3
Asteraceae	*Brickellia longifolia*	longleaf brickellbush	Shrub	Native	150	7	68	62	13
Asteraceae	*Brickellia microphylla*	littleleaf brickellbush	Shrub	Native	1	1	0	0	0
Poaceae	*Bromus catharticus*	rescuegrass	Graminoid	Nonnative	19	3	15	1	0
Poaceae	*Bromus diandrus*	ripgut brome	Graminoid	Nonnative	211	21	71	45	74
Poaceae	*Bromus japonicus*	field brome	Graminoid	Nonnative	1	0	0	1	0
Poaceae	*Bromus rubens*	red brome	Graminoid	Nonnative	350	24	96	119	111
Poaceae	*Bromus* spp.	brome	Graminoid	Nonnative	20	0	10	6	4
Poaceae	*Bromus tectorum*	cheatgrass	Graminoid	Nonnative	14	5	4	3	2
Celastraceae	*Canotia holocantha*	crucifixition thorn	Shrub	Native	1	0	0	0	1
Cyperaceae	*Carex emoryi*	Emory's sedge	Graminoid	Native	50	15	29	2	4
Cyperaceae	*Carex* spp.		Graminoid	Native	2	0	2	0	0
Scrophulariaceae	*Castilleja linariifolia*	Wyoming Indian paint-brush	Forb	Native	1	1	0	0	0
Ulmaceae	*Celtis reticulata*	netleaf hackberry	Tree	Native	6	4	2	0	0
Euphorbiaceae	*Chamaesyce albomarginata*	white margin sandmat	Forb	Native	2	0	0	1	1
Euphorbiaceae	*Chamaesyce arizonica*	Arizona sandmat	Forb	Native	11	0	3	7	1
Euphorbiaceae	*Chamaesyce glyptosperma*	ribseed sandmat	Forb	Native	2	1	0	1	0
Euphorbiaceae	*Chamaesyce micrersperma*	Sonoran sandmat	Forb	Native	5	0	2	3	0
Euphorbiaceae	*Chamaesyce revoluta*	thread stem sandmat	Forb	Native	1	0	0	0	1
Euphorbiaceae	*Chamaesyce serpillifolia*	thyme leaf sandmat	Forb	Native	1	0	0	0	1
Euphorbiaceae	*Chamaesyce* spp.	sandmat	Forb		19	0	4	13	2

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Algae	*Chara* spp.		Algae	Native	2	2	0	0	0
Pteridaceae	*Cheilanthes parryi*	Parry's lipfern	Fern	Native	9	0	0	8	1
Asteraceae	*Chloracantha spinosa*	spiny chloracantha	Forb	Native	123	15	51	25	32
Asteraceae	*Chrysothamnus linifolius*	spearleaf rabbitbrush	Shrub	Native	3	0	3	0	0
Cyperaceae	*Cladium californicum*	California sawgrass	Graminoid	Native	1	0	1	0	0
Asteraceae	*Conyza canadensis*	Canadian horseweed	Forb	Nonnative	110	2	31	32	45
Amaranthaceae	*Corispermum americanum*	American bugseed	Forb	Native	1	0	1	0	0
Boraginaceae	*Cryptantha gracilis*	narrow stem cat's eye	Forb	Native	4	0	4	0	0
Boraginaceae	*Cryptantha racemosa*	bushy cryptantha	Forb	Native	6	0	3	3	0
Boraginaceae	*Cryptantha* spp.		Forb		15	0	1	4	10
Poaceae	*Cynodon dactylon*	Bermudagrass	Graminoid	Nonnative	243	3	5	72	163
Cyperaceae	*Cyperus squarrosus*	bearded flatsedge	Graminoid	Native	1	1	0	0	0
Poaceae	*Dasyochloa pulchella*	low woollygrass	Graminoid	Native	11	0	2	6	3
Solanaceae	*Datura wrightii*	sacred thorn-apple	Forb	Native	35	1	19	10	5
Brassicaceae	*Descurainia pinnata*	western tansymustard	Forb	Native	5	0	1	4	0
Brassicaceae	*Descurainia* spp.	tansymustard			16	0	3	7	6
Poaceae	*Dicanthelium acuminatum*	tapered rosette grass	Graminoid	Native	1	0	0	0	1
Asteraceae	*Dicoria canescens*	desert twinbugs	Forb	Native	28	0	4	19	5
Poaceae	*Digitaria californica*	Arizona cottoncup	Graminoid	Native	3	0	0	2	1
Poaceae	*Digitaria sanguinalis*	hairy crabgrass	Graminoid	Nonnative	1	1	0	0	0
Poaceae	*Distichlis spicata*	saltgrass	Graminoid	Native	30	5	19	6	0
Brassicaceae	*Draba* spp.		Forb		6	0	0	3	3
Cactaceae	*Echinocactus polycephalus*	cottontop cactus	Shrub	Native	1	0	0	1	0
Cactaceae	*Echinocereus coccineus*	scarlet hedgehog cactus	Shrub	Native	1	0	0	0	1
Cactaceae	*Echinocereus engelmanii*	Engelmann's hedgehog cactus	Shrub	Native	3	0	2	1	0
Poaceae	*Echinochloa crus-galli*	barnyardgrass	Graminoid	Nonnative	3	0	2	0	1
Elaeagnaceae	*Elaeagnus angustifolia*	Russian olive	Tree	Nonnative	2	0	1	1	0
Cyperaceae	*Eleocharis palustris*	common spikerush	Graminoid	Native	4	1	2	0	1
Poaceae	*Elymus canadensis*	Canada wildrye	Graminoid	Native	36	4	15	10	7

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon ("Eastern GRCA"), river kilometers 97 to 259; western Grand Canyon ("Western GRCA"), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Poaceae	*Elymus elymoides*	squirreltail	Graminoid	Native	6	0	6	0	0
Poaceae	*Elymus* spp.	wildrye	Graminoid		1	0	1	0	0
Poaceae	*Elymus trachycaulus*	slender wheatgrass	Graminoid	Native	20	3	17	0	0
Asteraceae	*Encelia farinosa*	brittlebush	Shrub	Native	111	0	9	51	51
Asteraceae	*Encelia frutescens*	button brittlebush	Shrub	Native	2	0	1	1	0
Asteraceae	*Encelia resinifera*	sticky brittlebush	Shrub	Native	1	0	0	0	1
Asteraceae	*Encelia virginensis*	virgin river brittlebush	Shrub	Native	2	0	0	0	2
Poaceae	*Enneapogon desvauxii*	nineawn pappusgrass	Graminoid	Native	3	0	1	2	0
Ephedraceae	*Ephedra fasiculata*	Arizona jointfir	Shrub	Native	9	0	0	5	4
Ephedraceae	*Ephedra nevadensis*	Nevada jointfir	Shrub	Native	2	0	1	1	0
Ephedraceae	*Ephedra torreyi*	Torrey's jointfir	Shrub	Native	35	6	23	6	0
Ephedraceae	*Ephedra viridis*	Mormon tea	Shrub	Native	10	0	0	7	3
Onagraceae	*Epilobium ciliatum*	fringed willowherb	Forb	Native	5	3	2	0	0
Orchidaceae	*Epipactis gigantea*	stream orchid	Forb	Native	15	7	1	2	5
Equisetaceae	*Equisetum arvense*	field horsetail	Forb	Native	24	0	22	1	1
Equisetaceae	*Equisetum* x *ferrissii*	horsetail	Forb	Native	254	20	97	45	92
Poaceae	*Eragrostis cilianensis*	stinkgrass	Graminoid	Nonnative	1	0	1	0	0
Poaceae	*Eragrostis curvula*	weeping lovegrass	Graminoid	Nonnative	10	0	9	1	0
Poaceae	*Eragrotsis pectinacea*	tufted lovegrass	Graminoid	Native	1	1	0	0	0
Asteraceae	*Ericameria nauseosa*	rubber rabbitbrush	Shrub	Native	1	0	1	0	0
Asteraceae	*Erigeron divergens*	spreading fleabane	Forb	Native	22	2	4	8	8
Asteraceae	*Erigeron flagellaris*	trailing fleabane	Forb	Native	3	0	0	3	0
Asteraceae	*Erigeron lobatus*	lobed fleabane	Forb	Native	32	0	6	19	7
Asteraceae	*Erigeron* spp.	fleabane		Native	3	0	1	0	2
Polygonaceae	*Eriogonum deflexum*	flatcrown buckwheat	Forb	Native	2	0	0	2	0
Polygonaceae	*Eriogonum fasciculatum*	Eastern Mojave buckwheat	Shrub	Native	3	0	0	0	3
Polygonaceae	*Eriogonum heermannii*	Heermann's buckwheat	Shrub	Native	1	0	1	0	0
Polygonaceae	*Eriogonum inflatum*	desert trumpet	Forb	Native	2	1	0	1	0
Polygonaceae	*Eriogonum* spp.	buckwheat			4	0	0	2	2

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Polygonaceae	*Eriogonum wrightii*	bastardsage	Shrub	Native	10	0	0	0	10
Cactaceae	*Escobaria vivipara*	spinystar	Shrub	Native	1	0	0	1	0
Loasaceae	*Eucnide urens*	desert stingbush	Shrub	Native	2	0	0	2	0
Euphorbiaceae	*Euphorbia aaron-rossii*	Marble Canyon spurge	Forb	Native	2	0	2	0	0
Asteraceae	*Euthamia occidentalis*	western goldentop	Forb	Native	174	23	79	25	47
Rosaceae	*Fallugia paradoxa*	Apache plume	Shrub	Native	6	0	6	0	0
Cactaceae	*Ferocactus cylindraceus*	California barrel cactus	Shrub	Native	2	0	0	1	1
Bryophyte	*Fontinalis* spp.				1	1	0	0	0
Asclepiadaceae	*Funastrum cynanchoides*	fringed twinevine	Forb	Native	42	4	14	3	21
Rubiaceae	*Galium* spp.	bedstraw			1	0	0	1	0
Rubiaceae	*Galium stellatum*	starry bedstraw	Forb	Native	29	0	4	21	4
Fabaceae	*Glycyrrhiza lepidota*	American licorice	Forb	Native	1	0	1	0	0
Asteraceae	*Gutierrezia microcephala*	threadleaf snakeweed	Shrub	Native	81	3	39	33	6
Asteraceae	*Gutierrezia sarothrae*	broom snakeweed	Shrub	Native	85	0	13	38	34
Asteraceae	*Gutierrezia* spp.	snakeweed	Shrub	Native	71	2	10	35	24
Lamiaceae	*Hedeoma nana*	dwarf false pennyroyal	Forb	Native	10	0	1	5	4
Lamiaceae	*Hedeoma* spp.	false pennyroyal	Forb	Native	1	0	0	1	0
Asteraceae	*Helianthus annus*	common sunflower	Forb	Native	1	0	1	0	0
Poaceae	*Hesperostipa comata*	needle and thread	Graminoid	Native	3	0	3	0	0
Poaceae	*Heteropogon contortus*	tanglehead	Graminoid	Native	1	0	0	1	0
Asteraceae	*Heterotheca villosa*	hairy false goldenaster	Forb	Native	2	0	1	0	1
Poaceae	*Hilaria jamesii*	James' galleta	Graminoid	Native	3	0	0	3	0
Poaceae	*Hilaria rigida*	big galleta	Graminoid	Native	12	0	0	10	2
Asteraceae	*Hofmeisteria pluriseta*	bush arrowleaf	Forb	Native	3	0	0	2	1
Poaceae	*Hopia obtusa*	vine mesquite	Graminoid	Native	39	4	14	11	10
Poaceae	*Hordeum jubatum*	foxtail barley	Graminoid	Native	3	0	3	0	0
Poaceae	*Imperata brevifolia*	California satintail	Graminoid	Native	12	0	0	4	8
Asteraceae	*Isocoma acradenia*	alkali goldenbush	Shrub	Native	132	2	0	58	72
Juncaceae	*Juncus acutus*	spiny rush	Graminoid	Native	1	0	0	0	1
Juncaceae	*Juncus arcticus*	arctic rush	Graminoid	Native	37	16	14	7	0

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Juncaceae	*Juncus articulatus*	jointleaf rush	Graminoid	Native	70	15	29	11	15
Juncaceae	*Juncus* spp.	rush	Graminoid	Native	2	0	1	1	0
Juncaceae	*Juncus torreyi*	Torrey's rush	Graminoid	Native	8	5	1	1	1
Zygophyllaceae	*Kallstroemia californica*	California caltrop	Forb	Native	2	0	2	0	0
Asteraceae	*Lactuca serriola*	prickly lettuce	Forb	Nonnative	1	0	0	0	1
Boraginaceae	*Lappula occidentalis*	flatspine stickseed	Forb	Native	1	0	0	0	1
Brassicaceae	*Lepidium densiflorum*	common pepperweed	Forb	Nonnative	16	0	2	2	12
Brassicaceae	*Lepidium fremontii*	desert pepperweed	Shrub	Native	15	3	12	0	0
Brassicaceae	*Lepidium latifolium*	broadleaved pepperweed	Forb	Nonnative	9	1	6	1	1
Brassicaceae	*Lepidium montanum*	mountain pepperweed	Forb	Native	28	12	14	2	0
Solanaceae	*Lycium pallida*	pale desert-thorn	Shrub	Native	1	0	0	0	1
Asteraceae	*Machaeranthera canescens*	hoary tansyaster	Forb	Native	2	0	2	0	0
Malvaceae	*Malvella leprosa*	alkali mallow	Forb	Native	7	0	7	0	0
Cactaceae	*Mammillaria grahamii*	Graham's nipple cactus	Shrub	Native	47	0	3	22	22
Scrophulariaceae	*Maurandella antirrhiniflora*	roving sailor	Forb	Native	7	0	2	3	2
Fabaceae	*Melilotus officinalis*	sweetclover	Forb	Nonnative	103	12	26	19	46
Lamiaceae	*Mentha arvensis*	wild mint	Forb	Native	15	14	1	0	0
Loasaceae	*Mentzelia multiflora*	adonis blazingstar	Forb	Native	1	0	0	1	0
Nyctaginaceae	*Mirabilis laevis* var. *villosa*	wishbone-bush	Forb	Native	4	0	0	2	2
Nyctaginaceae	*Mirabilis multiflora*	Colorado four o' clock	Forb	Native	5	0	0	2	3
Nyctaginaceae	*Mirabilis* spp.	four o' clock		Native	1	0	0	0	1
Poaceae	*Muhlenbergia appressa*	Devils Canyon muhly	Graminoid	Native	6	0	0	5	1
Poaceae	*Muhlenbergia asperifolia*	scratchgrass	Graminoid	Native	98	15	56	26	1
Poaceae	*Muhlenbergia porteri*	bush muhly	Graminoid	Native	19	0	14	3	2
Pteridaceae	*Myriopteris gracilis*	slender lip fern	Forb	Native	2	0	0	2	0
Brassicaceae	*Nasturtium officinale*	watercress	Forb	Nonnative	5	5	0	0	0
Solanaceae	*Nicotiana glauca*	tree tobacco	Shrub	Nonnative	1	0	1	0	0
Solanaceae	*Nicotiana obtusifolia*	desert tobacco	Forb	Native	2	0	1	1	0
Solanaceae	*Nicotiana trigonophylla*	desert tobacco	Forb	Native	1	1	0	0	0
Nyctaginaceae	*Nyctaginaceae*				2	0	0	2	0

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Onagraceae	*Oenothera curtiflora*	velvetweed	Forb	Native	2	2	0	0	0
Onagraceae	*Oenothera elata*	Hooker's evening primrose	Forb	Native	17	5	1	4	7
Onagraceae	*Oenothera pallida*	pale evening primrose	Forb	Native	29	2	13	8	6
Onagraceae	*Oenothera* spp.	primrose	Forb	Native	4	1	2	1	0
Cactaceae	*Opuntia basilaris*	beavertail pricklypear	Shrub	Native	12	1	7	2	2
Cactaceae	*Opuntia phaeacantha*	tulip pricklypear	Shrub	Native	1	1	0	0	0
Cactaceae	*Opuntia* spp.	pricklypear	Shrub	Native	25	2	4	6	13
Orobanchaceae	*Orobanche* spp.		Forb	Native	2	0	0	1	1
Poaceae	*Panicum capillare*	witchgrass	Graminoid	Native	1	1	0	0	0
Vitaceae	*Parthenocissus vitaceae*	woodbine	Forb	Native	1	1	0	0	0
Poaceae	*Paspalum dilatatum*	dallisgrass	Graminoid	Nonnative	3	0	0	0	3
Asteraceae	*Pectis papposa*	manybristle chinchweed	Forb	Native	1	0	0	0	1
Viscaceae	*Phoradendron californicum*	mesquite mistletoe	Shrub	Native	1	0	0	0	1
Poaceae	*Phragmites australis*	common reed	Graminoid	Native	57	4	17	13	23
Solanaceae	*Physalis crassifolia*	ground cheery	Forb	Native	4	0	0	0	4
Poaceae	*Piptatherum miliaceum*	smilograss	Graminoid	Nonnative	64	0	0	0	64
Plantaginaceae	*Plantago lanceolata*	narrowleaf plantain	Forb	Nonnative	41	21	18	1	1
Plantaginaceae	*Plantago major*	common plantain	Forb	Nonnative	16	4	4	2	6
Plantaginaceae	*Plantago ovata*	desert Indianwheat	Forb	Native	5	0	0	1	4
Plantaginaceae	*Plantago patagonica*	wooly plantain	Forb	Native	12	1	1	7	3
Asteraceae	*Pluchea sericea*	arrowweed	Shrub	Native	142	8	26	40	68
Poaceae	*Poa annua*	annual bluegrass	Graminoid	Nonnative	2	0	1	1	0
Poaceae	*Poa fendleriana*	mutton grass	Graminoid	Native	2	0	2	0	0
Poaceae	*Poa longiligula*	longtongue muttongrass	Graminoid	Native	4	0	4	0	0
Poaceae	*Poa pratensis*	Kentucky bluegrass	Graminoid	Nonnative	27	3	22	1	1
Poaceae	*Poa* spp.	bluegrass	Graminoid		2	0	2	0	0
Poaceae	*Polypogon interruptus*	ditch rabbitsfoot grass	Graminoid	Native	3	0	1	2	0
Poaceae	*Polypogon monspeliensis*	annual rabbitsfoot grass	Graminoid	Nonnative	36	1	7	12	16
Poaceae	*Polypogon viridis*	beardless rabbitsfoot grass	Graminoid	Nonnative	81	5	45	20	11
Asteraceae	*Porophyllum gracile*	slender poreleaf	Shrub	Native	85	0	0	46	39

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Portulacaceae	*Portulaca halimoides*	silkcotton purslane	Forb	Native	2	1	0	0	1
Portulacaceae	*Portulaca oleracea*	little hogweed	Forb	Nonnative	7	1	1	4	1
Fabaceae	*Prosopis glandulosa*	honey mesquite	Tree	Native	34	0	4	7	23
Asteraceae	*Pseudognaphalium canescens*	Wright's cudweed	Forb	Nonnative	1	0	1	0	0
Asteraceae	*Pseudognaphalium luteoalbum*	Jersey cudweed	Forb	Native	9	1	5	1	2
Asteraceae	*Pseudognaphalium* spp.	cudweed	Forb	Native	6	1	4	1	0
Asteraceae	*Pseudognaphalium stramineum*	cottonbatting plant	Forb	Native	6	0	4	2	0
Fabaceae	*Psorothamnus fremontii*	Fremont's dalea	Shrub	Native	1	0	0	0	1
Fagaceae	*Quercus turbinella*	Sonoran scrub oak	Tree	Native	1	1	0	0	0
Ranunculaceae	*Ranunculus cymbalaria*	alkali buttercup	Forb	Native	2	1	1	0	0
Anacardiaceae	*Rhus trilobata*	skunkbush sumac	Shrub	Native	2	0	1	1	0
Polygonaceae	*Rumex crispus*	curly dock	Forb	Nonnative	1	0	1	0	0
Salicaceae	*Salix exigua*	narrowleaf willow, coyote willow	Shrub	Native	114	20	57	26	11
Amaranthaceae	*Salsola tragus*	prickly Russian thistle	Forb	Nonnative	72	2	29	28	13
Poaceae	*Schedonorus arundinaceus*	tall fescue	Graminoid	Nonnative	157	26	94	20	17
Poaceae	*Schismus arabicus*	Arabian schismus	Graminoid	Nonnative	44	4	10	16	14
Poaceae	*Schizachyrium scoparium*	little bluestem	Graminoid	Native	9	0	4	1	4
Cyperaceae	*Schoenoplectus acutus*	hardstem bulrush	Graminoid	Native	3	1	1	1	0
Cyperaceae	*Schoenoplectus americanus*	chairmaker's bulrush	Graminoid	Native	4	0	3	1	0
Cyperaceae	*Schoenoplectus pungens*	common threesquare	Graminoid	Native	12	4	2	2	4
Fabaceae	*Senegalia greggii*	catclaw acacia	Tree	Native	136	0	17	54	65
Fabaceae	*Senna covesii*	Coues' cassia	Forb	Native	5	0	0	1	4
Poaceae	*Setaria leucopila*	streambed bristlegrass	Graminoid	Native	2	0	0	0	2
Iridaceae	*Sisyrinchium demissum*	stiff blue-eyed grass	Forb	Native	3	3	0	0	0
Asteraceae	*Solidago missouriensis*	Missouri goldenrod	Forb	Native	1	0	0	1	0
Asteraceae	*Solidago velutina*	three-nerve goldenrod	Forb	Native	1	0	0	1	0
Asteraceae	*Sonchus arvensis*	field sowthistle	Forb	Nonnative	1	0	0	1	0
Asteraceae	*Sonchus asper*	spiny sowthistle	Forb	Nonnative	5	0	3	0	2
Asteraceae	*Sonchus oleraceus*	common sowthistle	Forb	Nonnative	10	0	7	1	2

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Asteraceae	*Sonchus* spp.	sowthistle	Forb	Nonnative	37	2	16	8	11
Malvaceae	*Sphaeralcea ambigua*	desert globemallow	Forb	Native	3	0	1	0	2
Malvaceae	*Sphaeralcea grossulariifolia*	gooseberryleaf globemallow	Forb	Native	5	2	1	0	2
Malvaceae	*Sphaeralcea parvifolia*	small-leaf globemallow	Forb	Native	2	0	0	0	2
Malvaceae	*Sphaeralcea* spp.	globemallow	Forb	Native	1	0	0	1	0
Poaceae	*Sphenopholis obtusata*	prairie wedgescale	Graminoid	Native	1	0	0	0	1
Poaceae	*Sporobolus airoides*	alkali sacaton	Graminoid	Native	5	0	1	3	1
Poaceae	*Sporobolus contractus*	spike dropseed	Graminoid	Native	43	1	11	26	5
Poaceae	*Sporobolus cryptandrus*	sand dropseed	Graminoid	Native	91	3	23	44	21
Poaceae	*Sporobolus flexuosus*	mesa dropseed	Graminoid	Native	212	12	63	74	63
Poaceae	*Sporobolus gigantea*	giant dropseed	Graminoid	Native	15	0	2	6	7
Poaceae	*Sprorobolus* spp.	dropseed	Graminoid	Native	109	7	25	55	22
Brassicaceae	*Stanleya pinnata*	desert princesplume	Shrub	Native	20	8	10	1	1
Asteraceae	*Stephanomeria pauciflora*	brownplume wirelettuce	Shrub	Native	103	6	40	42	15
Poaceae	*Stipa* spp.		Graminoid	Native	1	0	0	1	0
Asteraceae	*Symphyotrichum subulatum*	southern annual saltmarsh aster	Forb	Native	18	0	0	0	18
Tamaricaceae	*Tamarix ramosissima* x *T. chinensis*	saltcedar	Tree	Nonnative	291	22	88	91	90
Asteraceae	*Taraxacum officinale*	common dandelion	Forb	Nonnative	8	6	2	0	0
Asteraceae	*Thymophylla pentachaeta*	fiveneedle pricklyleaf	Forb	Native	47	0	24	18	5
Boraginaceae	*Tiquilia latior*	matted crinklemat	Forb	Native	9	1	4	2	2
Poaceae	*Tridens muticus*	slim tridens	Graminoid	Native	25	0	6	10	9
Asteraceae	*Trixis californica*	American threefold	Shrub	Native	4	0	0	1	3
	Unknown graminoid		Graminoid		19	0	7	9	3
Scrophulariaceae	*Veronica anagallis-aquatica*	water speedwell	Forb	Native	3	1	2	0	0
Poaceae	*Vulpia octoflora*	sixweeks fescue	Graminoid	Native	32	1	2	15	14
Asteraceae	*Xanthisma spinulosum*	lacy tansyaster	Forb	Native	41	0	12	19	10
Asteraceae	*Xanthium strumarium*	rough cocklebur	Forb	Native	17	2	2	3	10

Table 1.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Asparagaceae	*Yucca angustissima*	narrowleaf yucca	Shrub	Native	2	0	2	0	0
Gentianaceae	*Zeltnera arizonica*	Arizona centaury	Forb	Native	9	0	0	2	7
Gentianaceae	*Zeltnera calycosa*	Arizona centaury	Forb	Native	2	0	0	1	1
Gentianaceae	*Zeltnera exaltata*	desert centaury	Forb	Native	18	1	0	0	17

Appendix 2. Species List for Fixed-Site Sandbars

Table 2.1 provides a list of all recorded species in the fixed-site sandbars dataset.

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Nyctaginaceae	*Abronia elliptica*	fragrant white sand verbena	Forb	Native	2	0	0	1	1
Poaceae	*Achnatherum hymenoides*	Indian ricegrass	Graminoid	Native	13	0	9	4	0
Poaceae	*Achnatherum speciosum*	desert needlegrass	Graminoid	Native	7	0	7	0	0
Asteraceae	*Acroptilon repens*	hardheads	Forb	Nonnative	1	0	1	0	0
Asparagaceae	*Agave utahensis*	Utah agave	Shrub	Native	1	0	1	0	0
Poaceae	*Agrostis exarata*	spike bentgrass	Graminoid	Native	1	0	1	0	0
Poaceae	*Agrostis gigantea*	redtop	Graminoid	Nonnative	5	1	4	0	0
Poaceae	*Agrostis* spp.	bentgrass	Graminoid		1	0	0	0	1
Poaceae	*Agrostis stolonifera*	creeping bentgrass	Graminoid	Nonnative	15	1	11	3	0
Fabaceae	*Alhagi maurorum*	camelthorn	Shrub	Nonnative	11	0	0	5	6
Nyctaginaceae	*Allionia incarnata*	trailing windmills	Forb	Native	4	1	1	0	2
Verbanaceae	*Aloysia wrightii*	Wright's beebrush	Shrub	Native	1	0	1	0	0
Amaranthaceae	*Amaranthus albus*	prostrate pigweed	Forb	Nonnative	1	0	1	0	0
Asteraceae	*Ambrosia acanthicarpa*	flatspine bur ragweed	Forb	Native	3	0	2	1	0
Poaceae	*Andropogon glomeratus*	bushy bluestem	Graminoid	Native	3	0	0	2	1
	Aquatic plant				1	1	0	0	0
Poaceae	*Aristida arizonica*	Arizona threeawn	Graminoid	Native	10	0	3	6	1
Poaceae	*Aristida purpurea*	purple threeawn	Graminoid	Native	24	0	10	12	2
Poaceae	*Aristida* spp.		Graminoid	Native	3	0	2	1	0
Asteraceae	*Artemisia dracunculus*	tarragon	Forb	Native	3	0	1	2	0
Asteraceae	*Artemisia ludoviciana*	white sagebrush	Forb	Native	23	1	14	6	2
Asteraceae	*Aster* spp.				1	0	0	1	0
Fabaceae	*Astragalus amphioxys*	aladdin's slippers	Forb	Native	1	0	1	0	0
Chenopodiaceae	*Atriplex canescens*	fourwing saltbush	Shrub	Native	2	1	1	0	0
Chenopodiaceae	*Atriplex garrettii*	Garrett's saltbush	Shrub	Native	1	0	1	0	0
Asteraceae	*Baccharis emoryi*	Emory's baccharis	Shrub	Native	40	1	19	12	8
Asteraceae	*Baccharis salicifolia*	mule-fat	Shrub	Native	18	0	4	8	6
Asteraceae	*Baccharis sarothroides*	desertbroom	Shrub	Native	12	0	2	3	7
Asteraceae	*Baccharis sergiloides*	desert baccharis	Shrub	Native	4	0	1	2	1
Asteraceae	*Bebbia juncea*	sweetbush	Shrub	Native	6	0	2	4	0

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon ("Eastern GRCA"), river kilometers 97 to 259; western Grand Canyon ("Western GRCA"), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Brassicaceae	*Boechera perennans*	perennial rockcress	Forb	Native	1	0	1	0	0
Nyctaginaceae	*Boerhavia coulteri*	Coulter's spiderling	Forb	Native	1	0	1	0	0
Nyctaginaceae	*Boerhavia torreyana*	creeping spiderling	Forb	Native	1	1	0	0	0
Poaceae	*Bothriochloa barbinodis*	cane bluestem	Graminoid	Native	17	0	6	9	2
Poaceae	*Bothriochloa laguroides*	silver beardgrass	Graminoid	Native	5	0	3	2	0
Poaceae	*Bouteloua aristidoides*	needle grama	Graminoid	Native	8	1	4	2	1
Poaceae	*Bouteloua barbata*	sixweeks grama	Graminoid	Native	19	1	8	7	3
Brassicaceae	*Brassicaceae* unknown				1	0	0	1	0
Asteraceae	*Brickellia californica*	California brickellbush	Shrub	Native	2	0	1	0	1
Asteraceae	*Brickellia longifolia*	longleaf brickellbush	Shrub	Native	22	1	14	6	1
Poaceae	*Bromus catharticus*	rescuegrass	Graminoid	Nonnative	7	0	7	0	0
Poaceae	*Bromus diandrus*	ripgut brome	Graminoid	Nonnative	36	1	17	11	7
Poaceae	*Bromus rubens*	red brome	Graminoid	Nonnative	43	1	20	14	8
Poaceae	*Bromus* spp.	brome	Graminoid	Nonnative	31	1	14	10	6
Poaceae	*Bromus tectorum*	cheatgrass	Graminoid	Nonnative	16	1	9	4	2
Onagraceae	*Camissonia* spp.	suncup			1	0	1	0	0
Onagraceae	*Camissonia walkeri*	Walker's suncup	Forb	Native	1	0	0	0	1
Cyperaceae	*Carex emoryi*	Emory's sedge	Graminoid	Native	13	1	9	3	0
Cyperaceae	*Carex* spp.		Graminoid	Native	5	0	5	0	0
Euphorbiaceae	*Chamaesyce arizonica*	Arizona sandmat	Forb	Native	1	0	1	0	0
Euphorbiaceae	*Chamaesyce fendleri*	Fendler's sandmat	Forb	Native	4	0	1	2	1
Euphorbiaceae	*Chamaesyce glyptosperma*	ribseed sandmat	Forb	Native	1	0	0	1	0
Euphorbiaceae	*Chamaesyce microsperma*	Sonoran sandmat	Forb	Native	2	1	0	1	0
Euphorbiaceae	*Chamaesyce serpillifolia*	thyme leaf sandmat	Forb	Native	2	0	0	2	0
Euphorbiaceae	*Chamaesyce* spp.	sandmat	Forb		3	0	2	1	0
Algae	*Chara* spp.		Algae	Native	1	0	1	0	0
Pteridaceae	*Cheilanthes parryi*	Parry's lipfern	Fern	Native	1	0	0	1	0
Asteraceae	*Chloracantha spinosa*	spiny chloracantha	Forb	Native	19	1	10	5	3
Asteraceae	*Chrysothamnus* spp.	rabbittbrush	Shrub	Native	1	0	1	0	0
Asteraceae	*Conyza canadensis*	Canadian horseweed	Forb	Nonnative	23	0	12	6	5

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Amaranthaceae	*Corispermum americanum*	American bugseed	Forb	Native	3	0	3	0	0
Boraginaceae	*Cryptantha racemosa*	bushy cryptantha	Forb	Native	2	0	2	0	0
Boraginaceae	*Cryptantha* spp.		Forb		5	0	1	4	0
Cactaceae	*Cylindropuntia whipplei*	Whipple cholla	Shrub	Native	1	0	1	0	0
Poaceae	*Cynodon dactylon*	Bermudagrass	Graminoid	Nonnative	16	0	2	6	8
Cyperaceae	*Cyperus esculentus*	yellow nutsedge	Graminoid	Native	1	0	0	0	1
Poaceae	*Dasyochloa pulchella*	low woollygrass	Graminoid	Native	2	0	1	0	1
Solanaceae	*Datura wrightii*	sacred thorn-apple	Forb	Native	20	1	14	3	2
Brassicaceae	*Descurainia pinnata*	western tansymustard	Forb	Native	1	0	0	1	0
Brassicaceae	*Descurainia* spp.	tansymustard			13	0	7	5	1
Asteraceae	*Dicoria canescens*	desert twinbugs	Forb	Native	18	0	7	6	5
Poaceae	*Digitaria californica*	Arizona cottoncup	Graminoid	Native	1	0	0	1	0
Poaceae	*Distichlis spicata*	saltgrass	Graminoid	Native	5	0	3	2	0
Cactaceae	*Echinocereus* spp.	Hedgehog cactus	Shrub	Native	1	0	1	0	0
Poaceae	*Echinochloa colona*	jungle rice	Graminoid	Nonnative	1	0	1	0	0
Cyperaceae	*Eleocharis palustris*	common spikerush	Graminoid	Native	2	1	0	1	0
Poaceae	*Elymus canadensis*	Canada wildrye	Graminoid	Native	9	0	6	3	0
Poaceae	*Elymus elymoides*	squirreltail	Graminoid	Native	1	0	1	0	0
Poaceae	*Elymus trachycaulus*	slender wheatgrass	Graminoid	Native	3	0	2	1	0
Asteraceae	*Encelia farinosa*	brittlebush	Shrub	Native	8	0	2	4	2
Poaceae	*Enneapogon desvauxii*	nineawn pappusgrass	Graminoid	Native	4	0	3	1	0
Ephedraceae	*Ephedra fasiculata*	Arizona jointfir	Shrub	Native	1	0	0	1	0
Ephedraceae	*Ephedra torreyi*	Torrey's jointfir	Shrub	Native	3	0	3	0	0
Ephedraceae	*Ephedra viridis*	Mormon tea	Shrub	Native	1	0	0	1	0
Onagraceae	*Epilobium ciliatum*	fringed willowherb	Forb	Native	1	1	0	0	0
Orchidaceae	*Epipactis gigantea*	stream orchid	Forb	Native	1	1	0	0	0
Equisetaceae	*Equisetum arvense*	field horsetail	Forb	Native	6	0	6	0	0
Equisetaceae	*Equisetum* x *ferrissii*	horsetail	Forb	Native	30	1	15	8	6
Equisetaceae	*Equisetum* spp.	horsetail	Forb	Native	2	0	2	0	0
Poaceae	*Eragrostis cilianensis*	stinkgrass	Graminoid	Nonnative	3	0	3	0	0

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Poaceae	*Eragrostis curvula*	weeping lovegrass	Graminoid	Nonnative	6	0	6	0	0
Poaceae	*Eragrostis lehmanniana*	Lehmann lovegrass	Graminoid	Nonnative	1	0	1	0	0
Asteraceae	*Ericameria nauseosa*	rubber rabbitbrush	Shrub	Native	1	0	0	1	0
Asteraceae	*Erigeron divergens*	spreading fleabane	Forb	Native	5	0	3	2	0
Asteraceae	*Erigeron flagellaris*	trailing fleabane	Forb	Native	1	0	0	1	0
Asteraceae	*Erigeron lobatus*	lobed fleabane	Forb	Native	3	0	1	2	0
Geraniaceae	*Erodium cicutarium*	redstem stork's bill	Forb	Nonnative	1	0	1	0	0
Asteraceae	*Euthamia occidentalis*	western goldentop	Forb	Native	28	1	13	9	5
Rosaceae	*Fallugia paradoxa*	Apache plume	Shrub	Native	2	0	2	0	0
Oleaceae	*Fraxinus anomala*	singleleaf ash	Tree	Native	1	1	0	0	0
Asclepiadaceae	*Funastrum cynanchoides*	fringed twinevine	Forb	Native	16	1	8	3	4
Rubiaceae	*Galium stellatum*	starry bedstraw	Forb	Native	2	0	0	2	0
Asteraceae	*Gutierrezia microcephala*	threadleaf snakeweed	Shrub	Native	5	0	4	1	0
Asteraceae	*Gutierrezia sarothrae*	broom snakeweed	Shrub	Native	19	0	12	5	2
Asteraceae	*Gutierrezia* spp.	snakeweed	Shrub	Native	5	0	4	1	0
Lamiaceae	*Hedeoma* spp.	false pennyroyal	Forb	Native	2	1	0	1	0
Asteraceae	*Heterotheca villosa*	hairy false goldenaster	Forb	Native	1	0	1	0	0
Poaceae	*Hilaria rigida*	big galleta	Graminoid	Native	4	0	0	4	0
Asteraceae	*Hofmeisteria pluriseta*	bush arrowleaf	Forb	Native	1	0	0	1	0
Poaceae	*Hopia obtusa*	vine mesquite	Graminoid	Native	4	0	4	0	0
Poaceae	*Hordeum jubatum*	foxtail barley	Graminoid	Native	1	1	0	0	0
Poaceae	*Imperata brevifolia*	California satintail	Graminoid	Native	4	0	1	3	0
Asteraceae	*Isocoma acradenia*	alkali goldenbush	Shrub	Native	12	0	0	6	6
Juncaceae	*Juncus arcticus*	arctic rush	Graminoid	Native	8	1	5	2	0
Juncaceae	*Juncus articulatus*	jointleaf rush	Graminoid	Native	18	1	9	6	2
Juncaceae	*Juncus bufonius*	toad rush	Graminoid	Native	1	0	1	0	0
Juncaceae	*Juncus ensifolius*	dagger leaf rush	Graminoid	Native	1	0	1	0	0
Juncaceae	*Juncus* spp.	rush	Graminoid	Native	2	0	2	0	0
Juncaceae	*Juncus torreyi*	Torrey's rush	Graminoid	Native	7	1	4	2	0
Juncaceae	*Juncus xiphioides*	irisleaf rush	Graminoid	Native	1	0	1	0	0

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Krameriaceae	*Krameria erecta*	little leaf ratany	Shrub	Native	1	0	0	0	1
Zygophyllaceae	*Larrea tridentata*	creosote bush	Shrub	Native	1	0	0	0	1
Brassicaceae	*Lepidium fremontii*	desert pepperweed	Shrub	Native	7	1	6	0	0
Brassicaceae	*Lepidium lasiocarpum*	hairy pod pepperwort	Forb	Native	2	0	2	0	0
Brassicaceae	*Lepidium latifolium*	broadleaved pepperweed	Forb	Nonnative	3	1	2	0	0
Brassicaceae	*Lepidium montanum*	mountain pepperweed	Forb	Native	9	1	8	0	0
Brassicaceae	*Lepidium* spp.	pepperweed			4	0	3	1	0
Brassicaceae	*Lesquerella purpurea*	rose bladderpod	Forb	Native	1	0	0	1	0
Polemoniaceae	*Linanthus bigelovii*	Bigelow’s linanthus	Forb	Native	1	0	1	0	0
Asteraceae	*Machaeranthera canescens*	hoary tansyaster	Forb	Native	4	0	4	0	0
Cactaceae	*Mammillaria grahamii*	Graham's nipple cactus	Shrub	Native	2	0	0	1	1
Scrophulariaceae	*Maurandella antirrhiniflora*	roving sailor	Forb	Native	1	0	0	1	0
Fabaceae	*Melilotus officinalis*	sweetclover	Forb	Nonnative	15	1	6	7	1
Lamiaceae	*Mentha arvensis*	wild mint	Forb	Native	1	1	0	0	0
Nyctaginaceae	*Mirabilis laevis* var. *villosa*	wishbone-bush	Forb	Native	1	0	0	1	0
Poaceae	*Muhlenbergia appressa*	Devils Canyon muhly	Graminoid	Native	2	0	0	2	0
Poaceae	*Muhlenbergia asperifolia*	scratchgrass	Graminoid	Native	25	1	13	7	4
Poaceae	*Muhlenbergia microsperma*	littleseed muhly	Graminoid	Native	6	1	1	3	1
Poaceae	*Muhlenbergia porteri*	bush muhly	Graminoid	Native	5	0	5	0	0
Brassicaceae	*Nasturtium officinale*	watercress	Forb	Nonnative	1	1	0	0	0
Solanaceae	*Nicotiana obtusifolia*	desert tobacco	Forb	Native	1	0	1	0	0
Onagraceae	*Oenothera elata*	Hooker's evening primrose	Forb	Native	4	0	1	2	1
Onagraceae	*Oenothera pallida*	pale evening primrose	Forb	Native	7	1	4	2	0
Onagraceae	*Oenothera* spp.	primrose	Forb	Native	1	0	1	0	0
Cactaceae	*Opuntia basilaris*	beavertail pricklypear	Shrub	Native	1	0	1	0	0
Cactaceae	*Opuntia* spp.	pricklypear	Shrub	Native	6	0	3	2	1
Poaceae	*Panicum capillare*	witchgrass	Graminoid	Native	2	0	1	0	1
Urticaceae	*Parietaria pensylvanica*	Pennsylvania pellitory	Forb	Native	1	0	0	1	0
Poaceae	*Phragmites australis*	common reed	Graminoid	Native	16	0	8	4	4
Solanaceae	*Physalis crassifolia*	ground cheery	Forb	Native	1	0	0	0	1

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Poaceae	*Piptatherum miliaceum*	smilograss	Graminoid	Nonnative	7	0	0	0	7
Plantaginaceae	*Plantago lanceolata*	narrowleaf plantain	Forb	Nonnative	7	1	6	0	0
Plantaginaceae	*Plantago major*	common plantain	Forb	Nonnative	6	1	4	1	0
Plantaginaceae	*Plantago ovata*	desert Indianwheat	Forb	Native	2	0	0	0	2
Plantaginaceae	*Plantago patagonica*	wooly plantain	Forb	Native	5	0	1	3	1
Asteraceae	*Pluchea sericea*	arrowweed	Shrub	Native	25	0	8	9	8
Poaceae	*Poa longiligula*	longtongue muttongrass	Graminoid	Native	2	0	1	1	0
Poaceae	*Poa pratensis*	Kentucky bluegrass	Graminoid	Nonnative	4	1	3	0	0
Poaceae	*Poa* spp.	bluegrass	Graminoid		1	0	1	0	0
Poaceae	*Polypogon interruptus*	ditch rabbitsfoot grass	Graminoid	Native	8	0	6	2	0
Poaceae	*Polypogon monspeliensis*	annual rabbitsfoot grass	Graminoid	Nonnative	13	1	4	4	4
Poaceae	*Polypogon viridis*	beardless rabbitsfoot grass	Graminoid	Nonnative	24	0	12	10	2
Salicaceae	*Populus fremontii*	Fremont cottonwood	Tree	Native	1	0	0	1	0
Asteraceae	*Porophyllum gracile*	slender poreleaf	Shrub	Native	6	0	0	6	0
Fabaceae	*Prosopis glandulosa*	honey mesquite	Tree	Native	15	0	3	8	4
Asteraceae	*Pseudognaphalium luteoalbum*	Jersey cudweed	Forb	Native	4	0	3	1	0
Asteraceae	*Pseudognaphalium stramineum*	cottonbatting plant	Forb	Native	7	0	4	3	0
Poaceae	*Saccharum ravennae*	ravenna grass	Graminoid	Nonnative	1	0	0	0	1
Salicaceae	*Salix exigua*	narrowleaf willow, coyote willow	Shrub	Native	27	1	15	10	1
Salicaceae	*Salix gooddingii*	Goodding's willow	Tree	Native	2	1	0	1	0
Amaranthaceae	*Salsola tragus*	prickly Russian thistle	Forb	Nonnative	24	1	15	5	3
Poaceae	*Schedonorus arundinaceus*	tall fescue	Graminoid	Nonnative	20	1	15	4	0
Poaceae	*Schismus arabicus*	Arabian schismus	Graminoid	Nonnative	19	0	11	4	4
Cyperaceae	*Schoenoplectus acutus*	hardstem bulrush	Graminoid	Native	3	0	2	0	1
Cyperaceae	*Schoenoplectus americanus*	chairmaker's bulrush	Graminoid	Native	2	0	2	0	0
Cyperaceae	*Schoenoplectus pungens*	common threesquare	Graminoid	Native	9	0	5	4	0
Fabaceae	*Senegalia greggii*	catclaw acacia	Tree	Native	21	0	6	12	3
Poaceae	*Setaria grisebachii*	Grisebach's bristlegrass	Graminoid	Native	1	0	0	1	0
Poaceae	*Setaria leucopila*	streambed bristlegrass	Graminoid	Native	2	0	0	1	1

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Elaeagnaceae	*Shepherdia rotundifolia*	roundleaf buffaloberry	Shrub	Native	1	0	1	0	0
Brassicaeae	*Sisymbrium* spp.	hedgemustard	Forb	Nonnative	4	0	2	2	0
Brassicaceae	*Sisymbrium altissimum*	Tall tumblemustard	Forb	Nonnative	1	0	1	0	0
Brassicaceae	*Sisymbrium irio*	London rocket	Forb	Nonnative	1	0	1	0	0
Asteraceae	*Sonchus asper*	spiny sowthistle	Forb	Nonnative	2	0	2	0	0
Asteraceae	*Sonchus* spp.	sowthistle	Forb	Nonnative	15	0	8	4	3
Malvaceae	*Sphaeralcea ambigua*	desert globemallow	Forb	Native	4	1	2	1	0
Malvaceae	*Sphaeralcea grossulariifolia*	gooseberryleaf globemallow	Forb	Native	4	0	1	1	2
Malvaceae	*Sphaeralcea* spp.		Forb	Native	1	0	1	0	0
Poaceae	*Sporobolus contractus*	spike dropseed	Graminoid	Native	26	0	12	10	4
Poaceae	*Sporobolus cryptandrus*	sand dropseed	Graminoid	Native	30	1	12	11	6
Poaceae	*Sporobolus flexuosus*	mesa dropseed	Graminoid	Native	39	1	19	14	5
Poaceae	*Sporobolus gigantea*	giant dropseed	Graminoid	Native	12	0	4	5	3
Poaceae	*Sprorobolus* spp.	dropseed	Graminoid	Native	27	1	13	11	2
Brassicaceae	*Stanleya pinnata*	desert princesplume	Shrub	Native	4	1	3	0	0
Asteraceae	*Stephanomeria pauciflora*	brownplume wirelettuce	Shrub	Native	22	0	16	4	2
Brassicaceae	*Streptanthella longirostris*	longbeak streptanthella	Forb	Native	2	0	2	0	0
Poaceae	*Stipa* spp.		Graminoid	Native	1	0	1	0	0
Asteraceae	*Stylocline micropoides*	Woollyhead neststraw	Forb	Native	1	0	0	1	0
Asteraceae	*Symphyotrichum divaricatum*	southern annual saltmarsh aster	Forb	Native	2	0	1	1	0
Asteraceae	*Symphyotrichum subulatum*	southern annual saltmarsh aster	Forb	Native	8	0	3	3	2
Tamaricaceae	*Tamarix ramosissima* x *T. chinensis*	salt cedar	Tree	Nonnative	37	1	18	11	7
Asteraceae	*Taraxacum officinale*	common dandelion	Forb	Nonnative	1	0	1	0	0
Asteraceae	*Thymophylla pentachaeta*	fiveneedle pricklyleaf	Forb	Native	11	0	7	3	1
Boraginaceae	*Tiquilia latior*	matted crinklemat	Forb	Native	1	0	0	0	1
Zygophyllaceae	*Tribulus terrestris*	puncturevine	Forb	Nonnative	1	1	0	0	0
Poaceae	*Tridens muticus*	slim tridens	Graminoid	Native	1	0	1	0	0

Table 2.1. Family, scientific name, common name, growth form, native status, and number of sites at which each species has been recorded in the study area and within floristic segments.—Continued

[River segments are delineated by river kilometers as follows: Glen Canyon, river kilometers −25 to 0; Marble Canyon, river kilometers 0 to 97; eastern Grand Canyon (“Eastern GRCA”), river kilometers 97 to 259; western Grand Canyon (“Western GRCA”), river kilometers 259 to 404.]

Family	Scientific name	Common name	Growth form	Native status	Total	Glen Canyon	Marble Canyon	Eastern GRCA	Western GRCA
Asteraceae	*Trixis californica*	American threefold	Shrub	Native	1	0	0	1	0
Typhaceae	*Typha* spp.	cattail	Graminoid		1	0	0	1	0
Typhaceae	*Typha domingensis*	Southern cattail	Graminoid	Native	1	0	0	1	0
Scrophulariaceae	*Veronica americana*	American speedwell	Forb	Native	1	0	1	0	0
Scrophulariaceae	*Veronica anagallis-aquatica*	water speedwell	Forb	Native	2	0	2	0	0
Poaceae	*Vulpia octoflora*	sixweeks fescue	Graminoid	Native	18	0	10	6	2
Asteraceae	*Xanthium strumarium*	rough cocklebur	Forb	Native	1	0	0	1	0
Asteraceae	*Xylorhiza tortifolia*	Mojave woodyaster	Forb	Native	2	0	2	0	0
Asparagaceae	*Yucca elata*	soaptree yucca	Shrub	Native	1	0	0	1	0
Zannichelliaceae	*Zannichellia palustris*	Horned pondweed	Forb	Native	1	0	1	0	0
Gentianaceae	*Zeltnera arizonica*	Arizona centaury	Forb	Native	1	0	0	1	0

Moffett Field Publishing Service Center
Manuscript approved March 16, 2023
Edited by Timothy Herold
Illustrative support by Katie Sullivan
Layout by Kimber Petersen

Palmquist and others—**Assessment of Riparian Vegetation Patterns and Change Downstream from Glen Canyon Dam, 2014–2019**—OFR 2023–1026

ISSN 2331-1258 (online)
https://doi.org/10.3133/ofr20231026