STEVENS

THE IMPACTS OF GLEN CANYON DAM ON RIPARIAN VEGETATION AND SOIL STABILITY IN THE COLORADO RIVER CORRIDOR, GRAND CANYON, ARIZONA: 1991 DRAFT ANNUAL REPORT

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31 DECEMBER, 1991

SPONSORED BY:

THE NATIONAL PARK SERVICE
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ABSTRACT

The effects of Glen Canyon Dam operations are under study by the National Park Service and Northern Arizona University to ascertain whether daily fluctuating discharge patterns affect riparian vegetation. Several topics are discusssed in this preliminary report.

Reduced flooding frequency after completion of Glen Canyon Dam in 1963 allowed fluvial marshes to form in low velocity channel margin environments in wide reaches. Marshes were scoured by spillover flooding in 1983 and have begun to redevelope since 1987. Approximately 146 wet and 954 dry fluvial marshes occur in the Colorado River corridor downstream from Lees Ferry, Arizona. Total marsh area was conservatively estimated at 25.8ha, with 30% as wet marsh, dominated by Typha domingenisi, Juncus spp. and Scirpus spp. Dry marsh dominants included Phragmites australis and Equisetum laevigatum. Riverside marshes in this system were generally small, typically less than 0.5 ha, with wet marshes significantly larger than dry marshes. Mean standing crop and estimated productivity of fluvial marshes in this system was 0.74 kg/m^2 and 147.8 g $C/m^2/yr$, respectively, values about 6% reported for marshes. Low productivity may be due to reduced duff accumulation and damage to vegetation (flattening and silt-coated) by high daily flows. Marsh assemblage composition and succession was related to sediment distribution and discharge, with wet marshes requiring a frequency of daily inundation between 0.4 and 0.9. More than 95% of the wet marsh vegetation in this system lies between the 283 m^3/sec (10,000 cfs) and 566 m^3/sec (20,000 cfs) stages. While fluvial marshes redevelop rather quickly after flooding events (e.g. 1983-1986), obligate marsh animal populations may not be as resilient. Willowflycatcher, which depend on marsh habitats, are believed to be nearly extirpated from this system.

Riparian seedling establishment was greatest in the New High Water Zone and was dominated by herbaceous species there. Seedling density varied as a function of particle size, and differed between plant groups (xerophytes and phreatophytes) in wide versus narrow channels. Tamarix ramosissima seedling density was low in 1991, but limited establishment suggests that this species may be capable of continuing to colonize the river corridor under fluctuating flow regimes.

River stage was demonstrated to affect plant water potential for pre-dawn Salix exigua, a ubiquitous riparian phreatophyte in the Colorado River corridor. Further studies will determine whether similar patterns apply to Tamarix ramosissima and growth of both species.

In addition, studies of long-term vegetation quadrats, Old High Water Zone phreatophyte growth, and the status of listed, endemic and non-native species are underway. Thus far, no plants species appear to be at risk from dam operations; however, several previously unrecorded non-native species are colonizing the river corridor, including Erianthus ravennae, a large Eurasian bunchgrass.

CHAPTER I: THE RIPARIAN VEGETATION PROJECT

INTRODUCTION

Problem Statement

Riparian vegetation is a highly zoned assemblage comprised of emergent, phreatophyte and upland plant species which respond to and interact with fluvial geomorphic and hydrologic processes (Johnson and Jones 1977; Hupp 1985; Reichenbacher 1984; Stevens 1989). Streamside vegetation is a focal point for biodiversity in arid lands, providing essential food and habitat resources for fish and terrestrial fauna. For example, riparian habitat comprises only about 0.05% of Arizona's portion of the Colorado River drainage, but supports more than 50% of the plant and animal species in that landscape (Simcox and Zube 1985; Stevens in prep.). More than 90% of pre-settlement riparian vegetation in the Southwest has been eliminated through deforestation, development and uninformed land management practices (Johnson et al. 1985). These issues make riparian vegetation an important field of study.

Riparian vegetation serves as an intermediary between abiotic components and higher trophic levels. It plays a significant role in both aquatic and terrestrial ecosystem dynamics, and provides erosion control and shade for recreationists. Management of riparian habitat requires an efficient ability to assess changes in resource attributes through time, criteria which are best met by using field survey techniques and Geographic Information Systems (GIS) approaches.

Colorado River corridor riparian vegetation links aquatic and terrestrial components of the dam-controlled fluvial ecosystem. Riparian vegetation affects lotic processes by providing protected riverbank and backwater habitats needed by larval fish, by contributing organic matter and terrestrial invertebrate life, and by providing resting habitat for adult aquatic invertebrates (e.g. Chironomidae; Blinn et al. 1992). Streamside vegetation in this system provides food and habitat for more than 1,100 plant species; several thousand invertebrate species; 25 amphibian and reptile species; obligate songbird species, such as willow flycatcher Bell's vireo and yellowthroat, as well as a rapidly increasing nesting waterfowl population and hundreds of migratory avian species; and more than 32 mammal species, including several obligate taxa such as beaver (Brown et al. 1987; Stevens and Waring 1988; Brown and Carothers 1990; Stevens and Kline 1991; Water Science and Technology Board 1991). Colorado River riparian vegetation also enhances recreational use of the river corridor (Carothers and Johnson 1982; Water Science and Technology Board 1987, 1991).

The pre-dam Colorado River corridor supported a limited growth of largely annual vegetation between the low water line and the 3,000 m^3/sec stage (Clover and Jotter 1944; Turner and Karpiscak 1980). Completion of Glen Canyon Dam on the Colorado River in 1963 reduced flooding and unintentionally fostered development of a profuse stand of riverside vegetation through lower Glen Canyon and Grand Canyon (Carothers and Aitchison 1976; Johnson 1991). Establishment of riparian vegetation began soon after closure of Glen Canyon Dam (Martin 1970 unpublished; Phillips et al. 1977). Carothers et al. (1979) described zonation of river corridor vegetation, noting a xerophyte-dominated talus community (Zone 1) dominated by a perched, pre-dam "old high water zone" (OHWZ; Zone 2) community dominated by <u>Prosopis glandulosa</u> and <u>Acacia greggii</u> lying above the approximate 3500 m^3/sec stage; a "back beach zone" (our quotes) with little vegetation (Zone 3) between the approximate 1150 m^3/sec and 3500 m^3/sec stages; and a new high water zone (NHWZ; Zone 4) below the approximate 1150 m^3/sec stage at the post-dam river edge and dominated by exotic <u>Tamarix ramosissima</u>. Several authors reported rapid successional development of riparian vegetation in this system, with initial colonization by <u>Tamarix ramosissima</u> and subsequent succession of native species (Martin 1970 unpublished; Brian 1982; Stevens 1985, 1989; Phillips et al. 1987). Glen Canyon Dam operations affect NHWZ and OHWZ plant germination and growth through flooding, erosion and soil moisture availability (Anderson and Ruffner 1988; Brian 1988; Pucherelli 1988; Stevens and Waring 1988; Waring and Stevens 1988; Stevens 1989).

Growing concern over the impacts of river regulation on environmental resources in the Colorado River corridor below Glen Canyon Dam prompted the Bureau of Reclamation to initiate the Glen Canyon Environmental Studies program (GCES). Phase I GCES studies and Stevens (1989) concluded that normal dam operations affected processes such as bank erosion, soil nutrient availability, and soil moisture status that influences riparian vegetation; however, Phase I was conducted during spillover flooding in 1983-1986. GCES Phase II was initiated to evaluate the effects of low and fluctuating flows on this system, and to provide information for a Department of Interior Environmental Impact Statement (EIS).

This report is designed to provide EIS team members with preliminary information on potential discharge impacts to riparian vegetation based on studies in the Colorado River corridor (Table 1.1; Fig. 1.1). Readers are advised that the data and analyses presented here are provisional, and these conclusions may be revised when analyses are completed.

The riparian vegetation zones and related processes directly affected by dam operations are discussed in several sections in this preliminary study: (1) the structure, distribution, development and maintenance requirements of post-dam marshes; (2) effects of dam operations on plant water stress; and (3) germination and establishment patterns in Zones 2, 3, and 4.

Objectives

1. Compile historical information on riparian and desert vegetation in the Colorado River corridor.

2. Facilitate mapping of riverine soils and vegetation in the Bureau of Reclamation's Geographic Information System (GIS).

3. Evaluate the status of plant community development by establishment and censusing of detailed study plots in characteristic habitats in the Colorado River corridor between Glen Canyon Dam and Lake Mead, Arizona, to serve as easily censused monitoring sites for system-wide evaluation of long-term vegetation changes.

4. Determine the interactions between discharge from Glen Canyon Dam operations, riparian vegetation characteristics and beach/bank stability.

5. Determine whether dam operations are influencing listed, endemic, exotic or critical species.

6. Refine the NPS vegetation monitoring program to guarantee that it will provide adequate information for effective long-term management.

Hypotheses Tested

This study addresses several of the GCES Phase II Research Questions (RQ; Bureau of Reclamation 1990). This project will assist in preparation of the GCES Geographic Information Systems base map. We are evaluating the role of riparian vegetation in retarding bank erosion in RQ 1: "How significant are the discharge fluctuation, minimum discharges, and ramping in the degradation or aggradation of beaches?"). We are also examining the effects of dam operations on soil water dynamics and plant growth in RQ 2: "Do discharge fluctuations, differences in minimum discharges, or different rates of change in daily discharges (ramping rates) interact with other uses and components of the Canyon to affect rates of sediment degradation?" RQ 2.2 addresses the role of riparian vegetation in sandbar stabilization, and RQ2.2b involves the effects of dam operations on invasion rates of exotic plant species. The effects of recreational use on rare or endemic plants is under study through plant demographic and distribution studies in RQ 12 ("How does rafting/camping affect other Canyon resources?").

Table 1.1: Long-term vegetation study plots established and censused in 1991. Vegetation plots were 5m x 10m: RS - riparian strip, GB - general beach, M - marsh, DF - debris fan, OHW - old high water, X - xeric (desert). Data on density, species richness, basal area and site characteristics are being compiled.

VEGETATIONPLOTS CENSUSED

CR MILE	RS	GB	M	DF	OHW	X
-6.5R	x	x		x	x	x
0.0R	Survey of vegetation at Lees Ferry cableway					
1.0R		x			x	x
Paria River	x				x*	x
2.6L	x	x		x	x	x
21.8R	x	x		x	x	x
31.5R	x			x		x
41.0L	x	x		x		
43.1L	x	x	x	x	x	x
51.5L	x	x	x	x	x	x
55.5R			x			
61.0	Survey of vegetation at Little Colorado R. cableway					
68.1R	x	x	x	x	x	x
71.5L	x	x	x	x	x	x
Clear Creek	x				x*	x
88.0	Survey of vegetation at Grand Canyon cableway					
94.0L	x	x		x	x	x
Crystal Creek					x*	x
103.9R	x	x		x	x	x
Shinumo Creek	x					x
119.1R	x	x			x	
122.1L	x	x		x	x	x
122.8L	x	x	x	x	x	x
Tapeats Creek		x				x
137.0L	x	x			x	
143.5R	x	x		x	x	
Kanab Creek	x					x
145.0L	x	x		x	x	
Matkatamiba	x				x*	x
Havasu Creek	24 RS and OHW* study plots					
166.0	Survey of vegetation at National Canyon cableway					
172.1L	x	x	x	x	x	x
194.1L	x	x	x	x	x	x
213.0R	x	x	x	x	x	x
219.9R	x	x	x	x	x	x
225.0	Survey of vegetation near Diamond Creek cableway					

* tributary equivalent

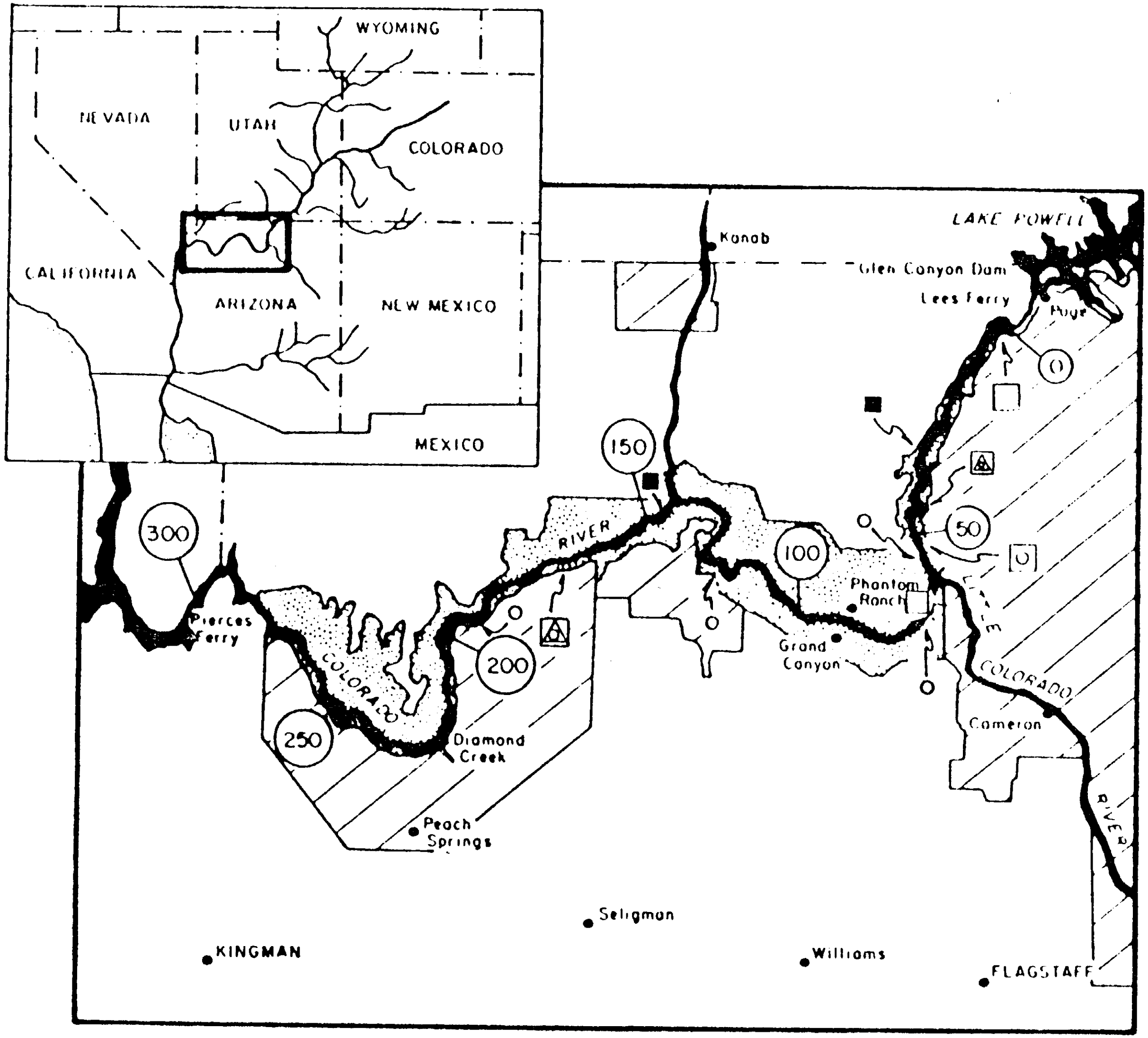

Figure 1.1: Map of study sites in Glen and Grand Canyons, Arizona. Open circles (○) are marsh study sites; open triangles (△) are plant water potential study sites; Open squares (□) are shoot-root density study sites; and filled squares (■) are long-term seedling growth sites.

CHAPTER II: FLUVIAL MARSH STUDIES IN GRAND CANYON

INTRODUCTION

Problem Statement

Fluvial marshes in the Colorado River corridor in Grand Canyon are biologically productive patches of emergent and herbaceous vegetation that develop in periodically inundated areas. Marshes develop as a result of interaction between geomorphic/hydrologic factors and the life history strategies of potential constituent plant species. Fluvial marshes in the Colorado River corridor in Glen Canyon and Grand Canyon lie at the edge of, or wholly within, the zone that is inundated by normal dam operations, and are therefore directly influenced by the discharge regimes of Glen Canyon Dam.

This chapter addresses fluvial marsh distribution at several spatial and temporal scales in the Colorado River corrridor in Grand Canyon National Park, including: marsh development rates under dam operations; present distribution, size; species composition, community structure and productivity; maintenance requirements as related to discharge; and succession.

Objectives

1. Determine the historical development of fluvial marshes in the post-dam Colorado River corridor in Grand Canyon.

2. Determine the contemporary distribution of fluvial marshes in the river corridor.

3. Determine the structure, composition, and productivity of fluvial marshes.

4. Determine the influence of Glen Canyon Dam operations on marsh distribution, composition and successional change.

Hypotheses Tested

The hypotheses tested in this study involve whether regulated discharges influence the development, distribution, productivity and/or successional status of marshes in the Colorado River downstream from Glen Canyon Dam.

METHODS AND SCOPE

Marsh Definition

Marshes were defined according to Cowardin et al. (1979) as patches of emergent annual or perennial vegetation occupying low-lying, periodically inundated habitats. Marsh plant species in this system occurred across a moisture gradient (Phillips et al. 1977; Stevens 1989). "Dry marsh" (drought tolerant) plant species included emergent Equisetum spp. and Phragmites australis and various grass and herbaceous species.

"Wet marsh" (inundation tolerant) species included Carex spp., Scirpus spp. and other sedges, Juncus spp., Typha spp. and emergent, herbaceous vegetation.

Study Sites

Six "wet" marshes were selected along the Colorado River for study in this preliminary report, including Colorado River miles (RMs) 43L, 55.5R, 71L, 122L, 172L and 194L (Fig. 1.1). These marshes were selected on the basis of historical and topographic information, and distribution through the river corridor. All sites except CRM 55.5R were used by Beus and Avery (1991) to monitor sandbar stability during the GCES test flows of 1990-1991. The marshes at CRM's 43L and 55.5R have been under study for the past decade.

Historical Studies

The history of marsh development under dam operations was examined from several sets of aerial photography of the river corridor from 1965 to 1990, as well as incorporation of data by Phillips et al. (1977) and observations made by B.T. Brown (pers. comm.) and L.E. Stevens during the past two decades. Data were compiled on a reach-by-reach basis to evaluate geomorphologic controlling factors (Schmidt and Graf 1990). Aerial photographs from 1984 and 1990 were compared to determine recolonization rates of marshes after cessation of spillover flooding from 1983 to 1986. Detailed studies and/or oblique photographs of RM 43L and 55.5R marshes from 1965 and 1980-1991 were used to compare changes related to dam operations.

Present marsh distribution in the Colorado River corridor in Grand Canyon was determined during river trips in August, September, and October, 1991. Each patch of emergent vegetation observed along the river was recorded, along with information on species composition, size and fluvial deposit type. Marsh density and area were compiled for each of Schmidt and Graf's (1990) 11 geomorphic reaches.

Habitat Structure

Stratigraphy and marsh species composition were studied at six sites. Surficial sediments were described at 43L, 71L and 194L, and trenches and soil pits were excavated along surveyed transects across the return channel marshes at 43L and 194L. Stratigraphy was measured and samples were collected for grain-size analyses. Species composition and basal diameters (emergent species only) were recorded on 1.0 m-wide belt transects running perpendicularly across return channels at 10 m intervals. These transects were surveyed at 1.0 m intervals using electronic total station surveying equipment. Soil and vegetation maps were prepared for these three sites. In six marshes, live and organic matter was collected on four to six 0.5 m^2 plots selected in an unbiased fashion.

Hypsometric Analyses

Inundation tolerance of individual riparian plant species was evaluated in the vicinity of the U.S. Geological Survey stream gauging stations. Of the six cableways on the Colorado River in this reach, the Lees Ferry gauge is best suited for plant inundation tolerance studies because most of the common riparian species grow near the cableway, and the channel margins are composed of fine sediments so there are few substrate-related distributional constraints (i.e. there is little bedrock that may limit the distribution of some phreatophyte species). Elevational ranges of all major riparian plant species within 50 m of this cableway were surveyed using total station technology, with three or more low elevation and three or more high elevation readings/species. Those data were compared with the maximum daily flow duration curve for this cableway from 1 October, 1987 to 1 October, 1991 to derive a relationship between inundation tolerance and frequency of inundation.

Hypsometric analyses of wet and dry marsh cover were conducted using the Map Image Processing System (MIPS). Stage-discharge relationships for each marsh site were developed using data from ongoing erosion studies by Beus et al. (1991) at these sites. Comparison of marsh cover data at several stage elevations and maximum daily flow duration data for the 1987-1991 water years from Glen Canyon Dam (Bureau of Reclamation, Flagstaff, AZ) and the U.S. Geological Survey cableways at Lees Ferry and Grand Canyon (U.S. Geological Survey, Flagstaff, AZ) permitted analysis of inundation frequencies for marsh plant assemblages.

RESULTS

A Caveat Regarding Preliminary Analyses

The data and analyses presented here are provisional and readers are advised that conclusions may change as additional analyses are completed.

Post-Dam Marsh Development

Few fluvial marshes existed in the Colorado River corridor in Grand Canyon prior to 1965, and the completion of Glen Canyon Dam allowed many new fluvial marshes to develop (Clover and Jotter 1944; Turner and Karpiscak 1980; Table 2.1: Fig. 2.1A). A set of 1965 aerial photographs revealed fewer than 25 significant patches of riparian vegetation in the river corridor between Lees Ferry and Diamond Creek, and fewer than 10 of these appeared to include emergent vegetation. Inspection of vegetation patches at RMs 7.8R, 69R and 72L in 1991 revealed mixed stands of Phragmites australis and/or woody vegetation. No vegetation occurred on the RM 43L sandbar, and only woody or herbaceous vegetation occurred on the RM 55.5R bar in 1965. In 1976 Phillips et al. (1977) documented 37 small marshes in the river corridor. By 1980 profuse marsh vegetation had developed on the RM 43L and 55.5R sites. At RM 43L, a deeper water stand of Scirpus sp. in deeper water was surrounded by shallow-water Typha domingensis and peripheral woody Salix exigua, Tamarix ramosissima and limited Baccharis spp. By 1982 at least 40 patches of emergent vegetation occurred between Lees Ferry and Diamond Creek, excluding woody species and Equisetum laevigatum (Stevens and Waring 1985). Analysis of 1980 and 1982 aerial photography is underway and will probably reveal greater overall marsh density during this period.
Among its many impacts, the 1983-1986 spillover flooding eliminated 23 of 40 (58%) of the marshes in this system (Stevens and Waring 1985). Examination of sites where marshes existed prior to 1983 (e.g. RM 43L and 55.5R) revealed that marsh vegetation had been scoured out or killed by burial under newly-deposited sediments. In 1987, Brown (pers. comm.) counted 25 marshes between Lees Ferry and Diamond Creek, and Stevens observed initial colonization by Juncus spp., Typha domingensis and woody species in return channels (43L) and on bar platforms (55.5R). Subsequent recolonization of low-lying habitats with silt or finer substrata was rapid. Detailed analysis of 1984 and 1990 aerial photographs revealed that riparian vegetation recolonization was rapid on reattachment and channel margin deposits and slower on separation deposits (Fig. 2.1B). In 1991 at least 146 patches of wet marsh vegetation were counted in the Grand Canyon reach, a 6-fold gain in marsh density in five years.

Patterns of Fluvial Marsh Distribution

Fluvial marsh distribution in the Colorado River corridor varied on system-wide, reach-wide, local and micro-site scales. Approximately 1,100 patches of marsh vegetation were identified in the new high water zone of the river corridor betweeen Lees Ferry and Diamond Creek, of which at least 146 were "wet marshes" and 954 are "dry marshes". Total marsh area was conservatively estimated at 25.8ha, of which 30% (7.8 ha) was wet marsh (Typha domingensis, Juncus spp. and Scirpus spp.) and 70% (18 ha) was dry marsh (Equisetum laevigatum and Phragmites australis). Although fewer in number, wet marshes were significantly larger (0.051 ha, sd = .1444) than dry marshes (0.019 ha, sd = .0408; $F = 31.392$, $p < 0.001$, df = 1,1095).

At the system-wide scale, marsh density and size changed with distance downstream and reach width. Wet and dry marshes were restricted to wide reaches in the upper canyon. In the lower Canyon marshes were smaller, more common and found in all reaches in the lower Canyon. Fluvial marsh density/km was positively correlated with distance ($R^2 = 0.847$, $F = 22.221$, $p = 0.001$, df = 1,9; Fig. 2.2A). In particular, the density of Equisetum laevigatum patches increased dramatically with distance downstream from Lees Ferry. Mean marsh area decreased with distance downstream (Fig. 2.3A), but total area/km increased significantly with distance downstream ($F = 12.522$, $p = .008$, df = 1,8; Fig. 2.3B). This effect was due to the fact that fluvial marsh density and mean were significantly greater in wide reaches ($X^2 = 3596.8$, $v = 10$, $p < 0.001$) and several wide reaches are located in the lower Canyon.

Fluvial marshes occurred in five low-lying, fine-grained geomorphic settings: return channels associated with reattachment bars, reattachment bar platforms, channel margins, riverside seeps/tributary mouths, and (rarely) berm swales; however, these marshes are disproportionately distributed with respect to deposit types. Marsh species colonization of these deposit types significantly differs from their availability in the river corridor, with more marshes than expected on channel margins and separation deposits, and less frequently than expected on reattachment and upper pool deposits ($X^2 = 48.341$, $p < 0.001$, df = 3; Fig. 2.2B).

Marsh Habitat Structure

Vegetation and soil stratigraphic cross sections were prepared for the marshes at RM 43L, 71L and 194L (Figs. 2.5-2.9, respectively). Mapping revealed a strong relationship between marsh vegetation and soil texture. Wet marsh species occupied low-lying silt and clay substrata. Dry marsh species occupied slightly elevated silty fine sand substrata, and woody vegetation (e.g. Tamarix ramosissima and Salix exigua) in sand and at higher elevations. Wet marsh cover was significantly greater on clay/fine silt deposits ($F = 6.009$, $p = .016$, df = 1,126; Fig. 2.12). Marsh plant species collected at two sites are listed in Table 2.2.

Soil profile analyses in return channel marshes revealed a pattern of increasing stratigraphic complexity with proximity to the river. The rear, protected sections of the 43L and 194L return channels (cross sections A-A' in Figs. 2.6 and 2.9, respectively) were relatively simple, with few horizons of silts and interbedded fine sand. At 43L on cross section A the 1983 marsh surface was located at 0.5m depth, still containing Scirpus sp. stumps and mudcracks. Near the return channel mouths numerous clay/silt, silt and fine sand horizons were exposed (cross section C-C' in Figs. 2.6 and 2.9). Stratigraphic complexity suggested a more highly disturbed environment, one more conducive to herbaceous colonization rather than wet marsh colonization (e.g. Fig. 2.8, with herbaceous vegetation at the return channel mouth).

Hypsometric Analyses

Maximum daily discharge duration curves were plotted for the U.S. Geological Survey discharge gauges at Lees Ferry and Grand Canyon to interpret elevation-discharge relationships of riparian plant species (Fig. 2.10). Elevational analyses cableway revealed wide differences between plant species at the Lees Ferry cableway. (Figs. 2.11A and B). Xeric species, such as Gutierrezia sarothrae and Chrysothamnus nauseosus occur at elevations which have not been inundated in the past five years. Woody phreatophytes lie at and above the new high water line, between stages of 625 m^3/sec to more than 5000 m^3/sec and sustaining daily inundation from 0-30% of the time. Marsh macrophytes occupy low-lying areas between stage elevations of 280 (Juncus spp.) to 1800 m^3/sec (Phragmites australis and Equisetum spp.), which were inundated daily from 0-90% of the time. Typha domingensis at this site consisted of a two-ramet clone and suggest that this stand was relictual and therefore not a good indicator of the true moisture tolerance for this wet marsh species. Data from viable stands of Typha domingensis in the 43L, 71L and 194L marshes revealed that this species occupied the 425 and 566 m^3/sec stage elevations, sustaining daily inundation 45-90% of the time.

Marsh Succession

A preliminary model of riparian plant assemblage distribution with respect to primary abiotic factors (hydrology and sediment characteristics) suggests that the hydrologic regime strongly influences subsequent marsh development. Again, marshes occur almost exclusively on silty substrata deposited in low velocity environments (Fig. 2.12 A, B). No terrestrial vegetation exists in areas that are continuously inundated, but several grass and herbaceous species occupy areas that are wetted on a daily basis, including Agrostis stolonifera, Aster subulatus, Gnaphalium chilensis, Plantago spp., and Polypogon monspeliensis. If a marsh is wetted on a 1.1 to 2.5 day schedule, but not continuously, the assemblage will tend to be dominated by "wet marsh" taxa, such as Typha domingensis, Scirpus spp. and Juncus spp., with sandier patches dominated by Phragmites australis, Equisetum spp. and/or woody Salix exigua and Tamarix ramosissima. If the patch is wetted, on average, once every three or more days, it will tend to be dominated by "dry marsh" (Phragmites australis and Equisetum spp.), herbaceous dicot (Conyza canadensis), and/or woody phreatophyte species.

Analyses of standing crop and species richness data for six marshes revealed several patterns. Mean standing crop was 0.74 kg/m^2, with most of the organic matter as living material (Table 2.4; Fig. 2.13A). Comparison of these standing crop values with mean standing crop values (15 kg/m^2, Rickleffs 1979: 773) indicated that Colorado River marshes contained approximately 5% as much standing crop as is normal for marshes. This low standing crop value may be attributable to the observation that little duff accumulation occurred in marsh understory in this system and marsh vegetation was flattened and coated with silt. These observations suggest that fluctuating flows may negatively affect growing conditions, and litter may be transported out of the marshes, thereby slowing organic matter accumulation.

The sand bars under study here were scoured clean by spillover flooding that ended in the summer of 1986, thus standing crop collections made in August, 1991 represented five years of accumulation of organic matter, excluding that which may have decomposed during that period. Standing crop data constituted an estimate of mean productivity since August, 1986 of 147.8 g C/m^2/yr (Table 2.4), a value about 6% of the normal productivity for marshes (2,500 g C/m^2/yr, Rickleffs 1979: 773). The low productivity of Colorado River marshes may be attributable to the young age of these marshes, and/or to removal of organic matter by fluctuating discharges.

In all, 45 species of plants occurred on productivity collection plots in Colorado River marshes and mean species richness was 6.5 species/m^2 (Table 2.4). Species richness was significantly negatively correlated with standing crop ($R^2 = 0.271$, $F_{1,26} = 9.666$, $p = 0.005$; Fig. 2.13B). This latter relationship is attributable to the observation that fluvial marsh succession is initated by colonization of herbaceous species, which are shaded/crowded out by dominant wet marsh taxa, such as Typha domingenisi , Juncus spp. and Scirpus .

DISCUSSION

Riparian habitat management is a major concern throughout the United States. Wetlands, including riparian habitats, are among the most biologically productive and recreationally valuable terrestrial lands. This study focused on the effects of Glen Canyon Dam operations on fluvial marsh distribution, physical and biological characteristics, and development rates. The rate of development and maintenance of marshes is closely related to dam operations. Marshes provide a good example of linkage between structured geomorphology and fluvial ecosystem development (Hupp 1985).

Fluvial marshes developed as a result of completion of Glen Canyon Dam in 1963. Fluvial marshes were virtually non-existent in the pre-dam Colorado river corridor in the Grand Canyon between Lees Ferry and Diamond Creek except at spring sources (Clover and Jotter 1944; Turner and Karpiscak 1980). Photographic evidence does show increased riparian vegetation cover in wider reaches and with distance downstream in post-dam time, suggesting geomorphologic and elevational controls on riparian plant species. Analysis of 1965 photographs of the river corridor show small patches of marsh vegetation only at lower Tanner (RM 69R), Cardenas Creek (RM 71L), and at a very few spring sources along the river (e.g. Lava Falls (RM 179L). These photographs do not do permit identification of marsh plant species. Reduced flooding frequency after completion of Glen Canyon Dam in 1963 allowed fluvial marshes to form in eddies in wide reaches. Between 1965 and 1983 marshes formed on bars that were inundated peridoically. Marshes were scoured by spillover flooding in 1983 when discharge reached pre-dam annual flow levels. Following cessation of spillover flooding in 1986, marshes began to redevelop and are today rather common in the river corridor.

Approximately 1,100 patches of marsh vegetation were identified in the new high water zone of the Colorado River corridor betweeen Lees Ferry and Diamond Creek, of which at least 146 were "wet marshes" and 954 are "dry marshes". Total marsh area was conservatively estimated at 25.8ha, of which 30% (7.8 ha) was wet marsh and 70% (18 ha) was dry marsh dominated by Equisetum laevigatum). Riverside marshes in this system were generally small, typically less than 0.5 ha, with wet marshes significantly larger than dry marshes.

Fluvial marsh plant assemblages along the Colorado River developed in response to geomorphologic structural control and discharge parameters, and were non-randomly distributed. Marsh density was positively correlated with distance downstream from Lees Ferry, while marsh size was negatively correlated with distance. Low-lying sand bars (e.g. reattachment bars) are more abundant in the lower river corridor because of increased tributary sediment input. Additionally, reduced magnitude of fluctuation caused by peak flow attenuation over distance decreases the amount of bar area wetted by daily fluctuations. This phenomenon should reduce marsh size because of decreased availability of wetted area. Marsh size and density was also positively correlated with mean channel width per reach.

Marshes cannot form in settings where velocities are elevated because the clay/silt sediments required for germination cannot settle out there. Clay/silt substrates are essential for germination of marsh species and also suggest site stability (Stevens 1989a). In general, if a recirculation zone does not contain a low/no velocity setting such as a return channel that is protected by a high bar platform, it will not support wet marsh vegetation. For these reasons, large eddies like those at Jackass Canyon, Saddle Canyon, RM 122R and National Canyon do not support wet marsh vegetation.

Silt and clay sediments on which fluvial marshes form have significantly greater nutrient levels and greater moisture holding capacity than do the coarser sediments associated with current reattachment bars (Stevens 1989), and marsh sediments are more often subjected to reduction and water-logging. Macrophyte plant species (e.g. cattails, bulrushes and other emergent species) that dominate marshes in this system occur between the approximate 300 m^3/sec and 500 m^3/sec stages on deposits with silt+clay:sand ratios of approximately 1:1. Vascular aquatic species colonized rapidly, displacing early successional herbaceous flora. Woody riparian phreatophytes (exotic saltcedar, native sandbar willow and other species) grow only above the 500m^3/sec stage and tolerate coarser-grained substrata and higher velocity environments.

Analyses of standing crop and species richness data for six marshes revealed several patterns. Mean standing crop was 0.74 kg/m^2, with most of the organic matter as living material (Table 2.4; Fig. 2.13A). Comparison of these standing crop values with mean standing crop values for marshes (15 kg/m^2, Rickleffs 1979: 773) indicated that Colorado River marshes contain only 5% as much standing crop as is normal for marshes. This low standing crop value may be attributable to the observation that little duff accumulation occurred in marsh understory in this system and marsh vegetation was flattened and coated with silt. These observations suggest that fluctuating flows may negatively affect growing conditions, and litter may be transported out of the marshes, thereby slowing organic matter accumulation.

The sand bars under study here were scoured clean by spillover flooding that ended in the summer of 1986, thus standing crop collections made in August, 1991 represented five years of accumulation of organic matter, excluding that which may have decomposed during that period. Standing crop data constituted an estimate of mean productivity since August, 1986 of 147.8 g C/m^2/yr (Table 2.4), a value about 6% of the normal productivity for marshes (2,500 g C/m^2/yr, Rickleffs 1979: 773). The low productivity of Colorado River marshes may be attributable to the young age of these marshes, and/or to removal of organic matter by fluctuating discharges.

The composition and successional trajectories of fluvial marshes was largely a function of geomorphology, hydrology and particle size distribution in patches. Species richness was significantly negatively correlated with standing crop. Distribution of marsh and riparian assemblages was a function of sediment particle size and inundation frequency. Wet marsh assemblages colonized low-lying silt deposits that were inundated daily between 40% and 90% of the time. Dry marshes required a less frequent daily inundation regime.

A conceptual successional model of marsh succession was developed based on observations in Grand Canyon from 1986-1991 (Fig. 2.14B). Once silt deposition occurred, initial colonization by herbaceous and grass species took place along moisture and particle size gradients. Lower/wetter/siltier habitats were colonized by grass and herbaceous species, including Agrostis stolonifera, Aster subulatus, Gnaphalium chilensis, Plantago spp., Polygonum spp. and Polypogon monspeliensis. Higher/drier/sandier habitats were occupied by hèrbaceous Conyza canadensis, Melilotus spp. and Sonchus asper. In subsequent years seedling establishment by clonal deciduous macrophytes (wet and dry marsh assemblages) and woody species (Tamarix ramosissima and limited Salix exigua) took place. Herbaceous species persisted in the daily inundation zone at low stages (down to the approximate 300 m^3/sec stage), in disturbed settings, or until shaded by marsh or woody species. Marsh succession was initated by colonization of herbaceous species, which persist in disturbed habitats or are subsequently shaded/crowded out by dominant wet marsh taxa, such as Typha domingenisis, Juncus spp. and Scirpus spp. in relatively undisturbed marshes. Invasion from the patch edges by clonal woody phreatophytes, especially Aster spinosus, Salix exigua and Tessaria sericea, also occurred and continued through time.

Glen Canyon Dam operations affect almost all aspects of marsh ecology, including development, distribution, diversity and standing crop and successional trajectories. Reduction of the inundation frequency during the growing season will affect the area of marsh cover and species composition. Marshes observed during interim flows of October and November, 1991 (low flow months) were not inundated, and if low flow regimes are prolonged during growing season months, particularly the hot, dry months of May - August, wet (cattail/bulrush) marsh cover willbe reduced. Precisely how much cover willbe lost is a matter of speculation and monitoring. Marshes can redevelop within a matter of a few years time following a flooding event; however, obligate marsh vertebrate populations, such as willow flycatcher, yellowthroat and rails, may not be as resilient. Loss of marsh cover may well be attributable for the near extirpation of willow flycatcher from the Colorado River corridor in Grand Canyon (B.T.Brown, pers. comm.).

Marshes constitute a unique linkage between geomorphological, hydrological and biological characteristics in this dam-controlled system. An understanding of geochemistry, sediment distribution, return current channel development and aggradation, erosion, and plant life history characteristics are required if fluvial marshes are to be maintained in this system.

CONCLUSIONS

1. Reduced flooding frequency after completion of Glen Canyon Dam in 1963 allowed fluvial marshes to form in low velocity channel marging environments in the Colorado River corridor. Marshes were scoured by spillover flooding in 1983 when discharge reached pre-dam annual flow levels. Following cessation of spillover flooding in 1986, marshes began to redevelop and are today rather common in the river corridor.

2. Approximately 146 wet and 954 dry fluvial marshes occur in the Colorado River corridor downstream from Lees Ferry, Arizona. Total marsh area was conservatively estimated at 25.8ha, with 30% as wet marsh, dominated by <u>Typha domingenisi</u>, <u>Juncus</u> spp. and <u>Scirpus</u> spp. Dry marsh dominants included <u>Phragmites australis</u> and <u>Equisetum laevigatum</u>. Riverside marshes in this system were generally small, typically less than 0.5 ha, with wet marshes significantly larger than dry marshes.

3. Mean standing crop and estimated productivity of fluvial marshes in this system was 0.74 kg/m^2 and 147.8 g $C/m^2/yr$, respectively, values about 6% of the reported means for marshes. Low productivity may be due to reduced duff accumulation and damage to vegetation (flattening and silt-coated) by high daily flows.

4. Marsh assemblage composition and succession was related to sediment distribution and discharge, with wet marshes requiring a frequency of daily inundation between 0.4 and 0.9. More than 95% of the wet marsh vegetation in this system lies between the 283 m^3/sec (10,000 cfs) and 566 m^3/sec (20,000 cfs) stages. Species richness was negatively correlated with standing crop.

5. Fluvial marshes undergo succession within the first few years from an herbaceous assemblate to a wet marsh macrophytic assemblage in lower/silty habitats or a dry marsh and woody assemblage in higher/drier/sandier habitats.

6. Although fluvial marshes may redevelop rather quickly after a flooding event (e.g. 1983-1986), marsh animal populations may not be as resilient. Willow flycatcher, which depend on marsh habitats, are believed to be nearly extirpated in this system.

Table 2.1: Fluvial marsh distribution in the Colorado River corridor, Grand Canyon, Arizona, 1965-1991. Reaches after Schmidt and Graf (1990).

	NUMBER OF MARSHES/KM					
REACH	1965	1977	1982*	1984*	1987	1991
1	1	0			4	2
2	0	0			0	0
3	0	2			0	1
4	1	12			2	44
5	3	8			4	10
6	0	2			1	1
7	0	0			0	0
8	1	0			0	0
9	0	0			0	9
10	1	11			14	72
11	1	2			0	9
TOTAL	8	37	40	17	26	146

* Data from Stevens and Waring (1985)

Table 2.2: Plant species collected from marshes at Colorado River Mile 43L and 194L, Grand Canyon, Arizona, 1988-1991.

FAMILY: GENUS SPECIES	43L COLLECTION DATE	194L COLLECTION DATE
BORAGINACEAE:		
Cryptantha nevandensis	8905	
Heliotropium curassavicum		8908
CHENOPODIACEAE:		
Kochia sp. (?)		8908
COMPOSITAE:		
Ambrosia confertiflora		8908
Artemisia dracunculus		8910
Artemisia ludoviciana		9108
Aster subulatis		8908, 9108
Bebbia juncea		8910
Conyza canadensis		9108
Eclipta alba		9107
Erigeron sp.		9107, 9108
Gnaphalium chilense	8910	
Melilotus officionale	8910	
Sonchus asper	8910	8908
CRUCIFERAE:		
Lepidium latifolium		9108
Lepidium lasiocarpium (?)	8805	
Lepidium sp.		
CYPERACEAE:		
Carex hystericina		9107
Eleocharis parishii	9106	
Scirpus acutus	9106	
Scirpus maritimus	8910	8910, 9107, 9108
Scirpus validus		9107
EQUISETACEAE:		
Equisetum hiemale		9108
Equisetum laevigatum		9108
EUPHORBIACEAE:		
Euphorbia sp.		8908
GRAMINEAE:		
Agropyron sp.	9109	
Agrostis sp.		9108
Agrostis semiverticillata	8910	8908
Agrostis stolonifera	9104	9107, 9108
Andropogon glomeratus		9107

FAMILY: GENUS SPECIES	43L COLLECTION DATE	194L COLLECTION DATE
GRAMINEAE:(cont.)		
Bothriochloa barbinodis	8910, 9109	9009, 9107
Bromus rubens	9104	
Bromus wildenowii	9008, 9108	
Echinochloa crusgalli	8910, 9008, 9108	9009, 9107,9108
Elymus canadensis	8910, 9106	
Eragrostis pectinacea	9109	
Hordeum jubatum	8910, 9106	
Muhlenbergia asperfolia	9008, 9104	9009
Muhlenbergia porteri	9104	
Oryzopsis miliacea		8910, 9107
Oryzopsis hymenoides	9109	
Panicum capilare	8910, 9109	9108
Paspalum dilatatum		8910, 9107,9108
Phragmites australis	9109	
Poa bigelovii	9104	
Poa compressa (?)	9104	
Poa fendleriana	9104	
Polypogon monspeliensis		9108
Puccinellia nutralliana (?)		9107
Schizachyrium scoparium	9104	
Sporobolus airoides		8908, 9111
Sporobolus contractus		9108
Sporobolus cryptandrus	9104	9108
Sporobolus flexuosus	8910	8910, 9108
JUNCACEAE		
Juncus articulatus		8908
Juncus ensifolius	8910	8908
Juncus tenuis	8910	
Juncus torreyi	9106	8908, 9108
LEGUMINOSAE:		
Alhagii camelorum		
PLANTAGINACEAE:		
Plantago major	8910, 9008	8908, 9108
POLYGONACEAE:		
Polygonum aviculare		9107
Polygonum persicaria		8908, 9107
SOLANACEAE:		
Solanum sp.		8908
TYPHACEAE:		
Typha domingensis	9106	9108
VERBENACEAE:		
Verbena sp.		8908

Table 2.3: Mean standing crop (g/m^2), estimated productivity ($g\ C/m^2/yr$) between August, 1986 and August, 1991, and mean plant species richness/m^2 at six fluvial marshes in the Colorado River corridor, Grand Canyon, Arizona (data from Westover et al. 1991).

MILE (SIDE)	n	MEAN STANDING CROP (g/M^2) (SD)	ESTIMATED PRODUCTIVITY 1986-1991 ($g\ C/M^2/yr$)	MEAN SPECIES RICHNESS/ $0.5m^2$
43.1L	5	917.2 (400.042)	183.4	7.0 (1.871)
55.5R	5	379.0 (277.666)	75.8	11.4 (2.966)
71.1L	5	609.6 (629.916)	121.9	6.8 (4.207)
122.8L	4	329.0 (280.608)	65.8	9.8 (4.500)
172.1L	4	1062.8 (830.408)	212.6	2.8 (0.957)
194.1L	6	1055.0 (916.406)	211.0	2.3 (1.633)
MEAN OR TOTAL		738.8 (644.230)	147.8	6.5 (4.314)

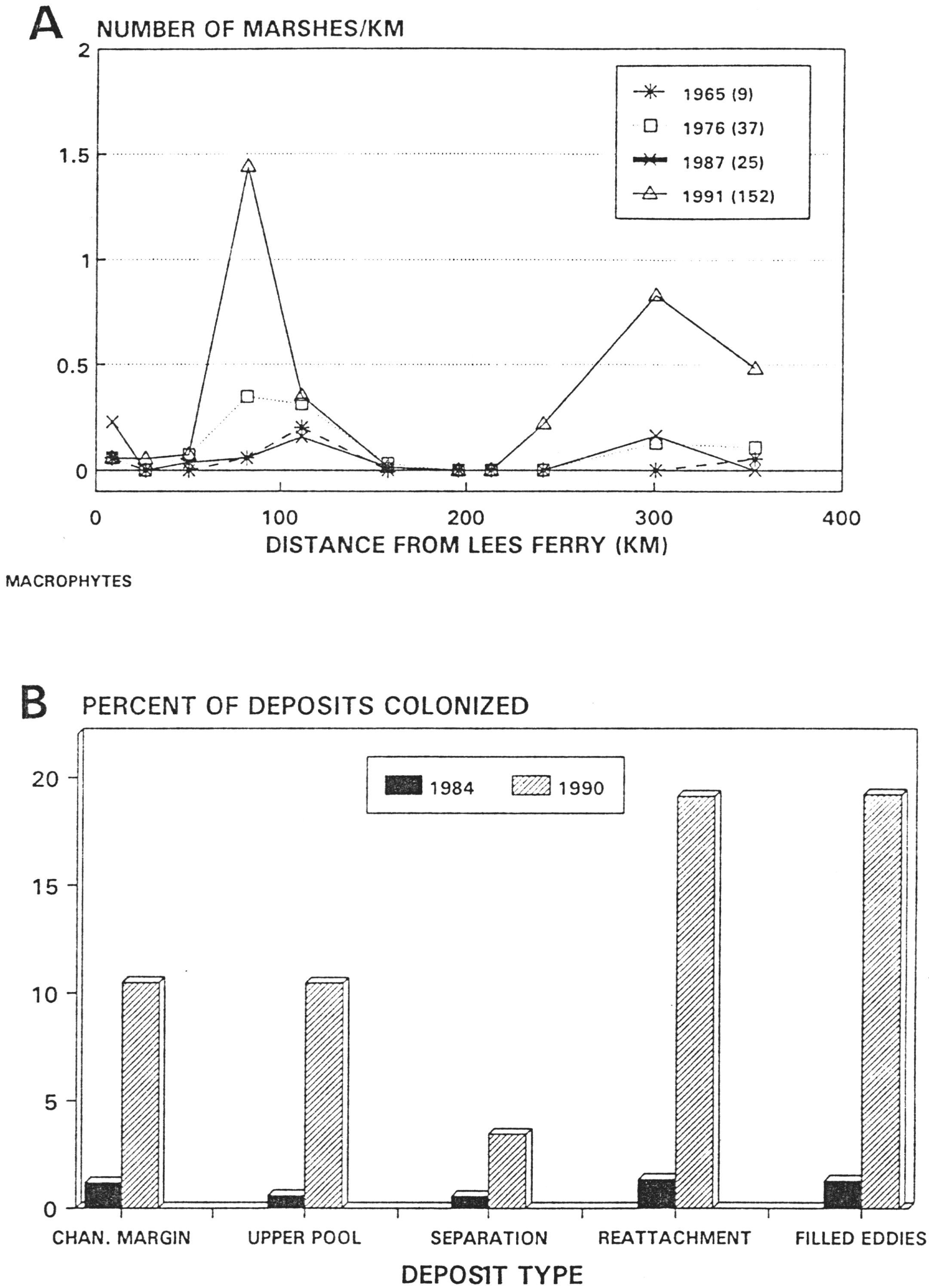

Figure 2.1: Historical changes in marsh distribution in the Grand Canyon, Arizona, 1991. (A) Changes in marsh density by reach, 1965-1990. (B) Change in number of sandbars colonized by vegetation, 1984-1990 (from aerial photo analyses).

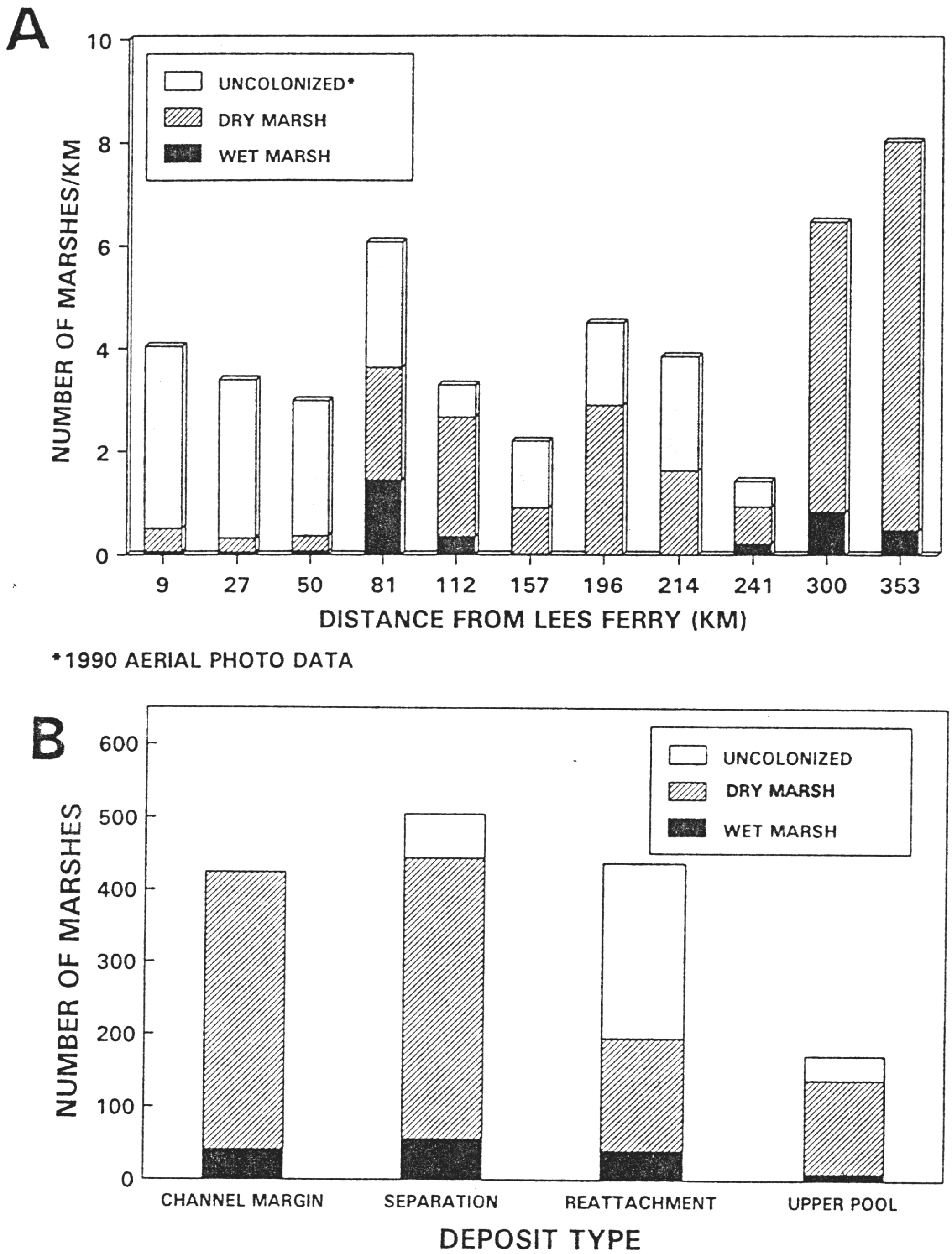

Figure 2.2: Marsh density in relation to geomorphology in the Colorado River corridor in 1991, Grand Canyon, Arizona. (A) Wet and dry marsh and uncolonized sandbar density/km in the Schmidt and Graf's (1990) 11 geomorphic reaches. (B) Total number of wet and dry marshes and uncolonized sandbars in four different deposit types.

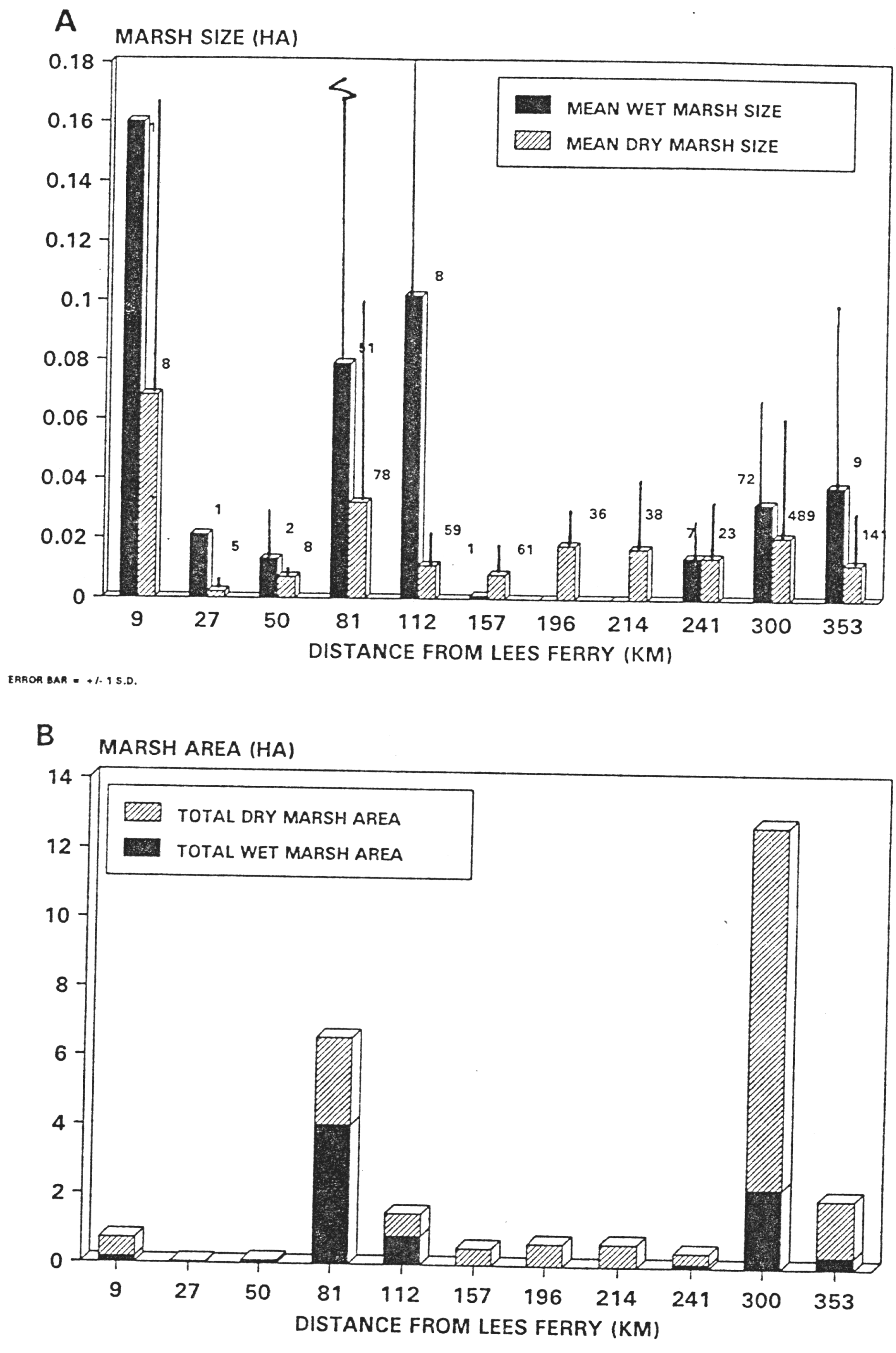

Figure 2.3: Areal extent of marshes in the geomorphologic reaches of the Colorado River in 1991, Grand Canyon National Park, Arizona. (A) Mean marsh size (ha) by reach. (B) Total marsh area (ha) by reach.

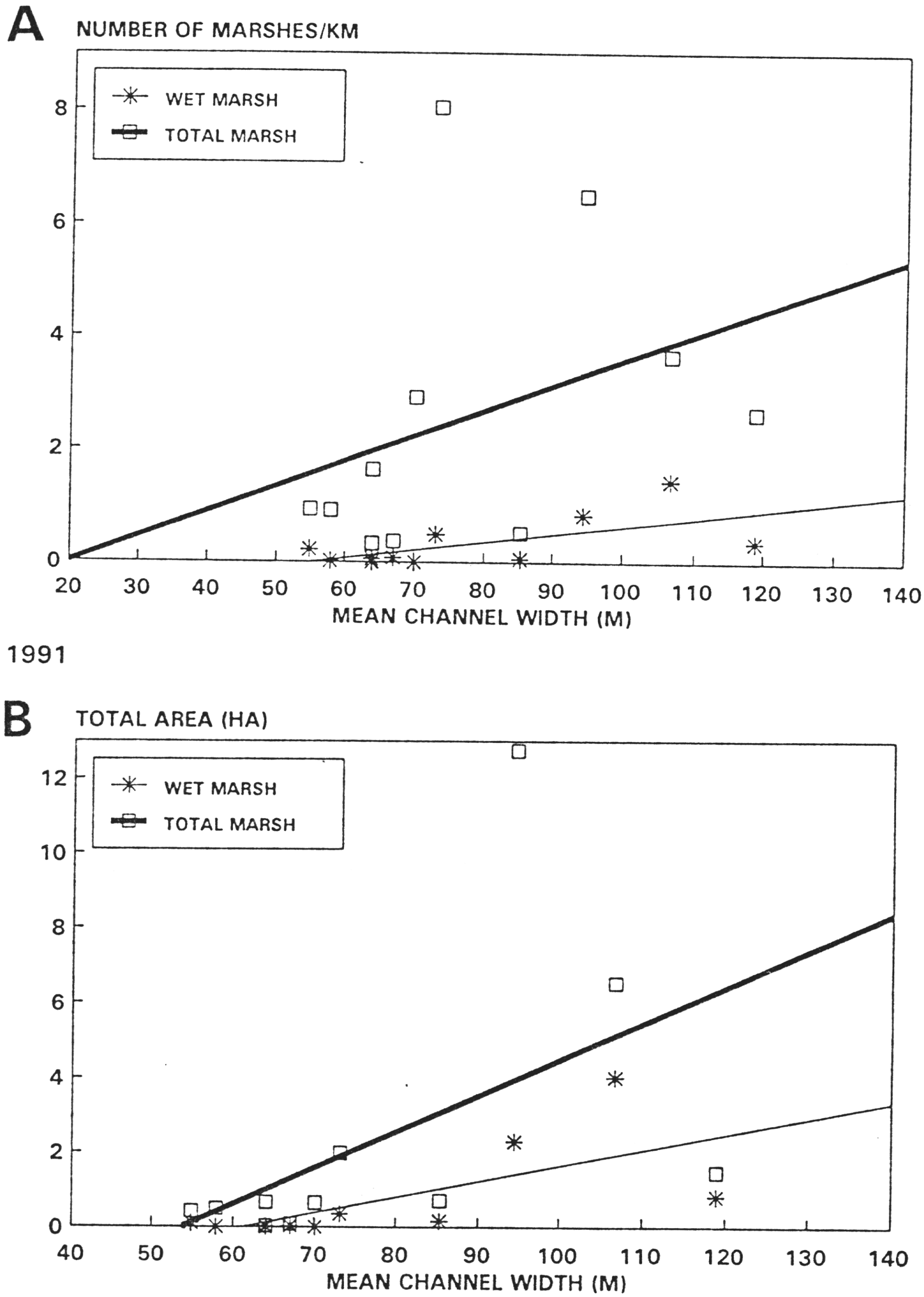

Figure 2.4: Marsh distribution in relation to channel width. (A) Marsh density/km as a function of channel width (m). (B) Marsh area (ha) as a function of channel width (m).

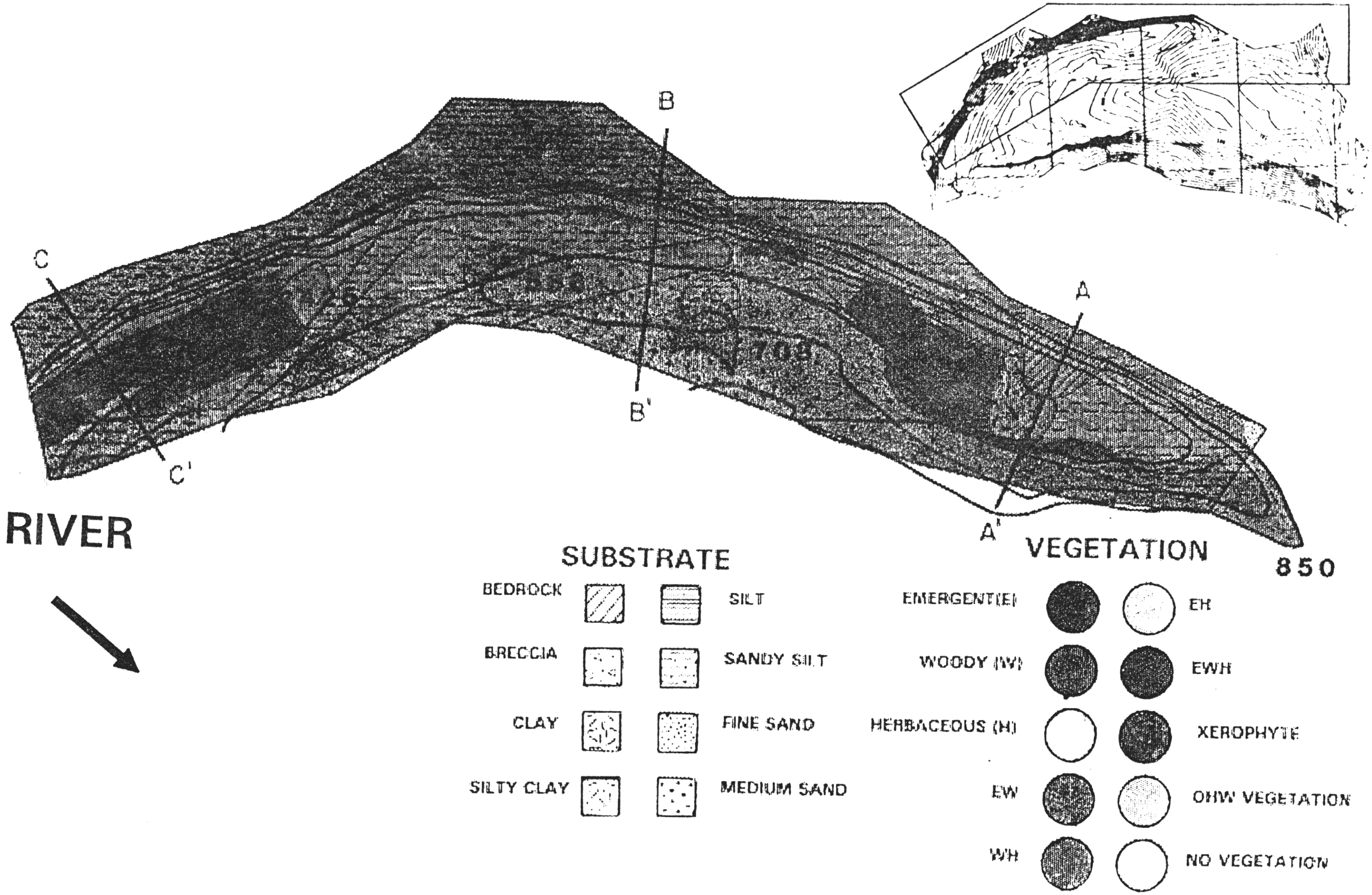

Figure 2.5: Topographic map and vegetation and soils map of 43L marsh, a return channel marsh, October, 1991, Grand Canyon, Arizona.

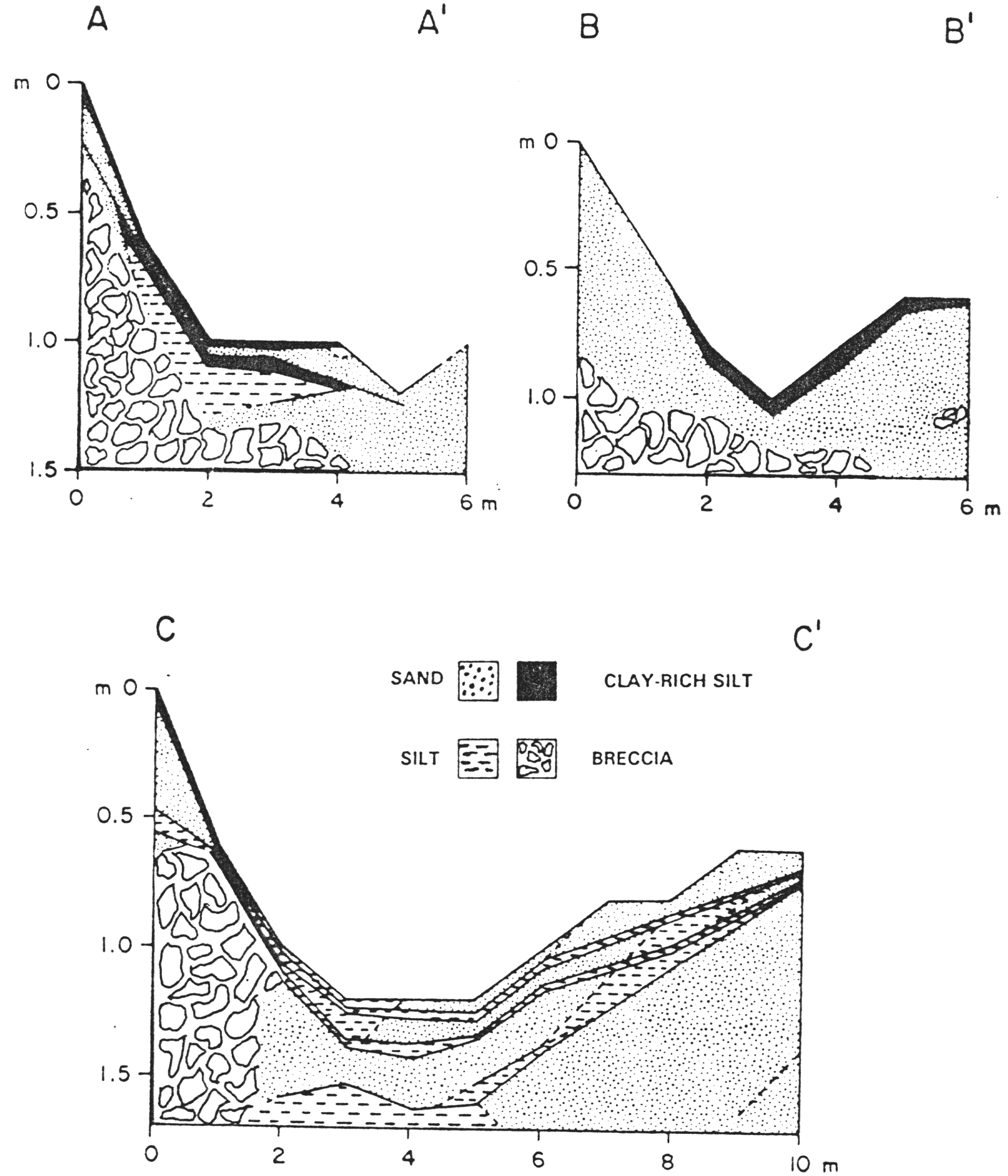

Figure 2.6: Stratigraphic cross sections through the 43L return channel marsh in October, 1991, Grand Canyon, Arizona.

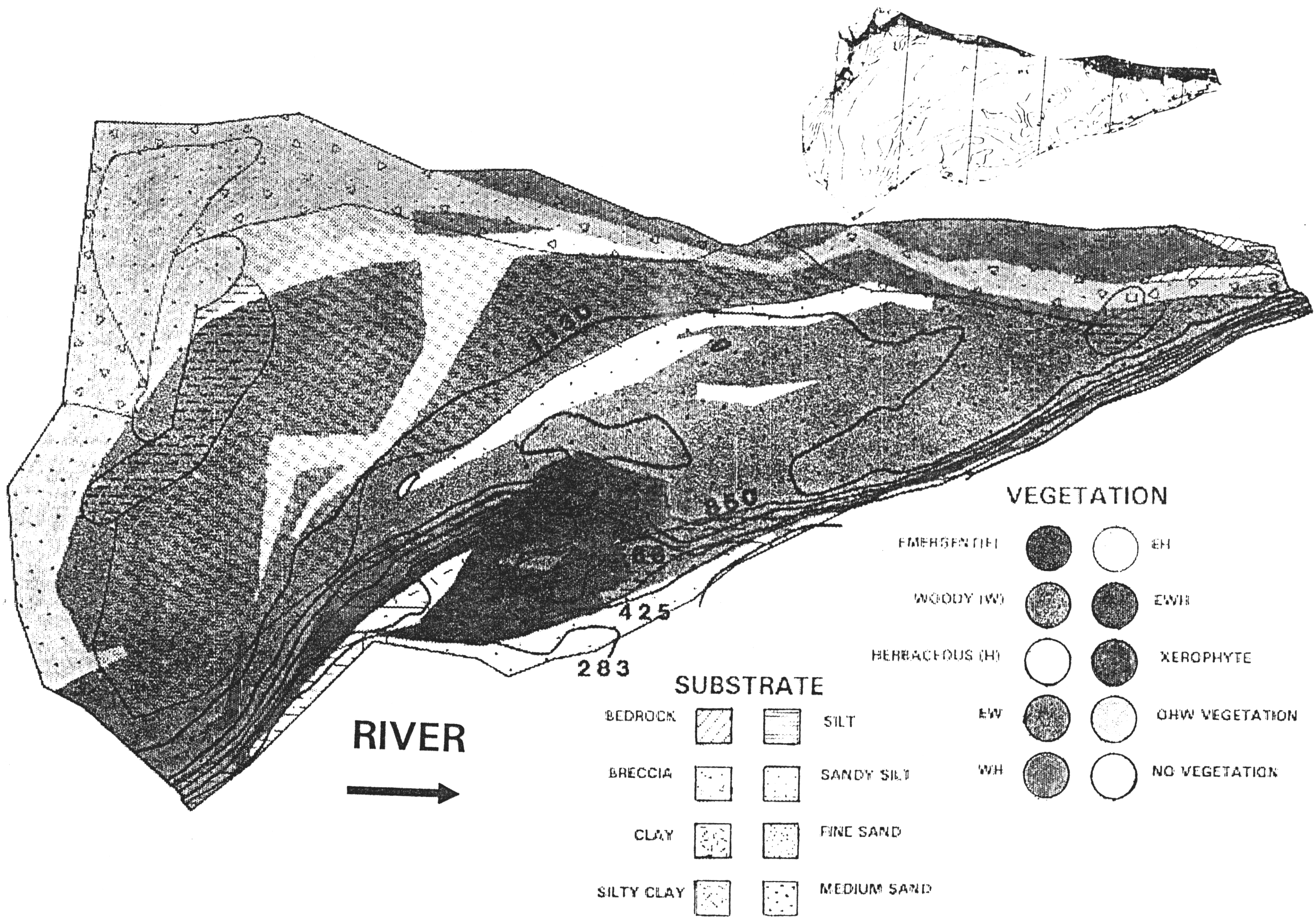

Figure 2.7: Topographic map and vegetation and soils map of the 71L marsh, a return channel/platform marsh, October, 1991, Grand Canyon, Arizona.

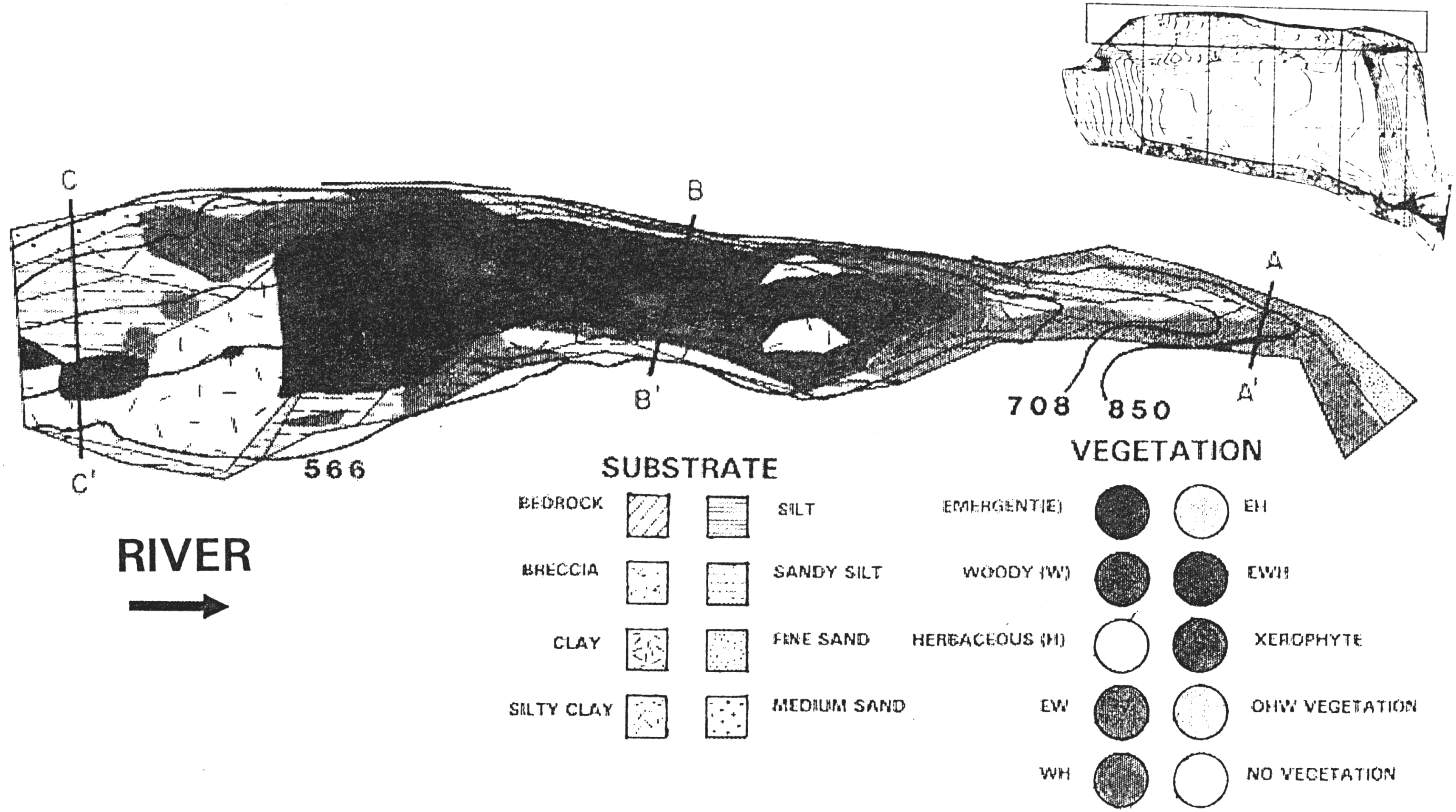

Figure 2.8: Topographic map and vegetation and soils map of 194L marsh, a return channel marsh, October, 1991, Grand Canyon, Arizona.

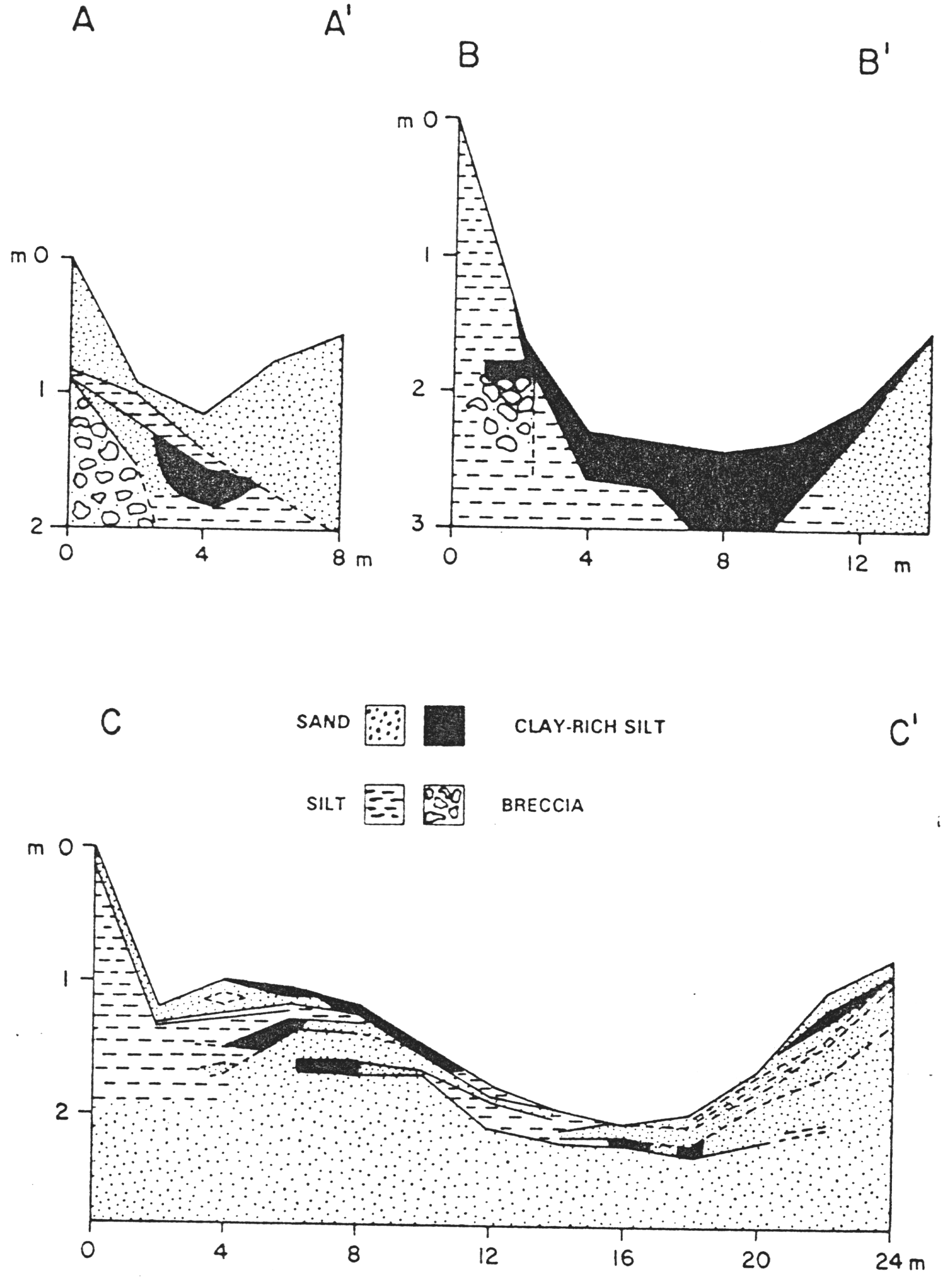

Figure 2.9: Stratigraphic cross sections through the 194L return channel marsh in October, 1991, Grand Canyon, Arizona.

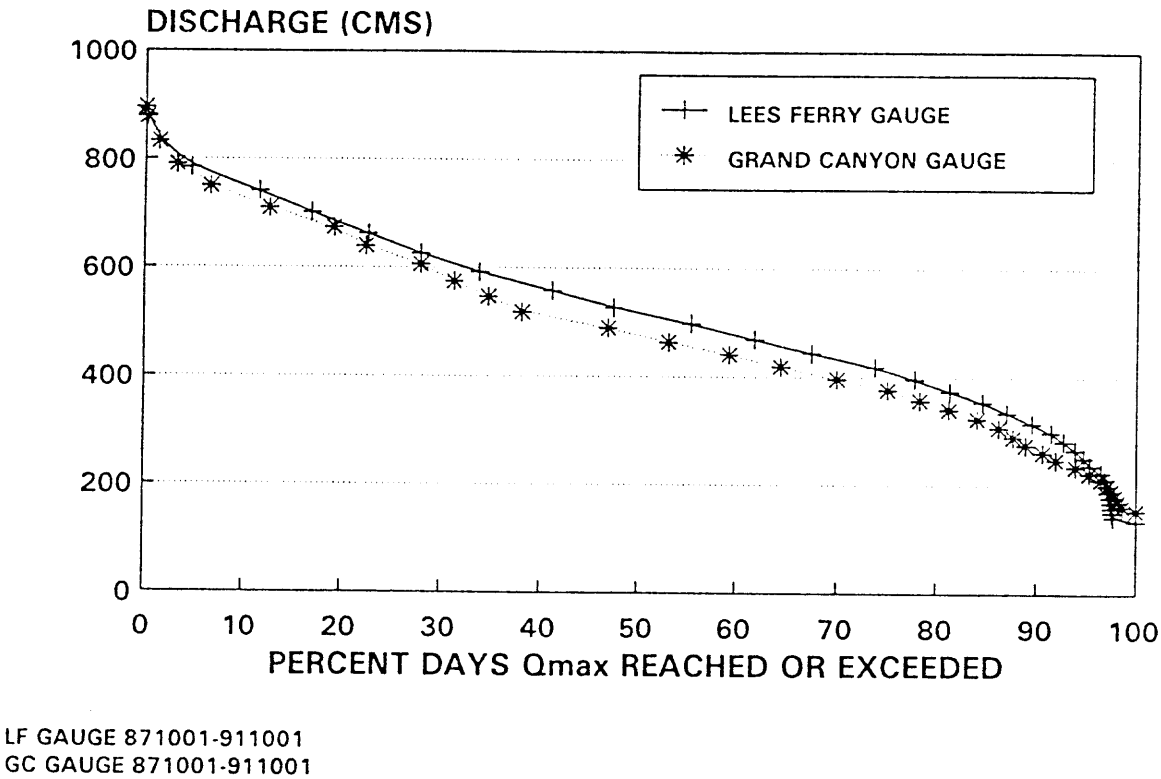

Figure 2.10: Maximum daily flow duration curves from the U.S.Geological Survey discharge gauges at Lees Ferry and Grand Canyon during Water Years 1987-1991.

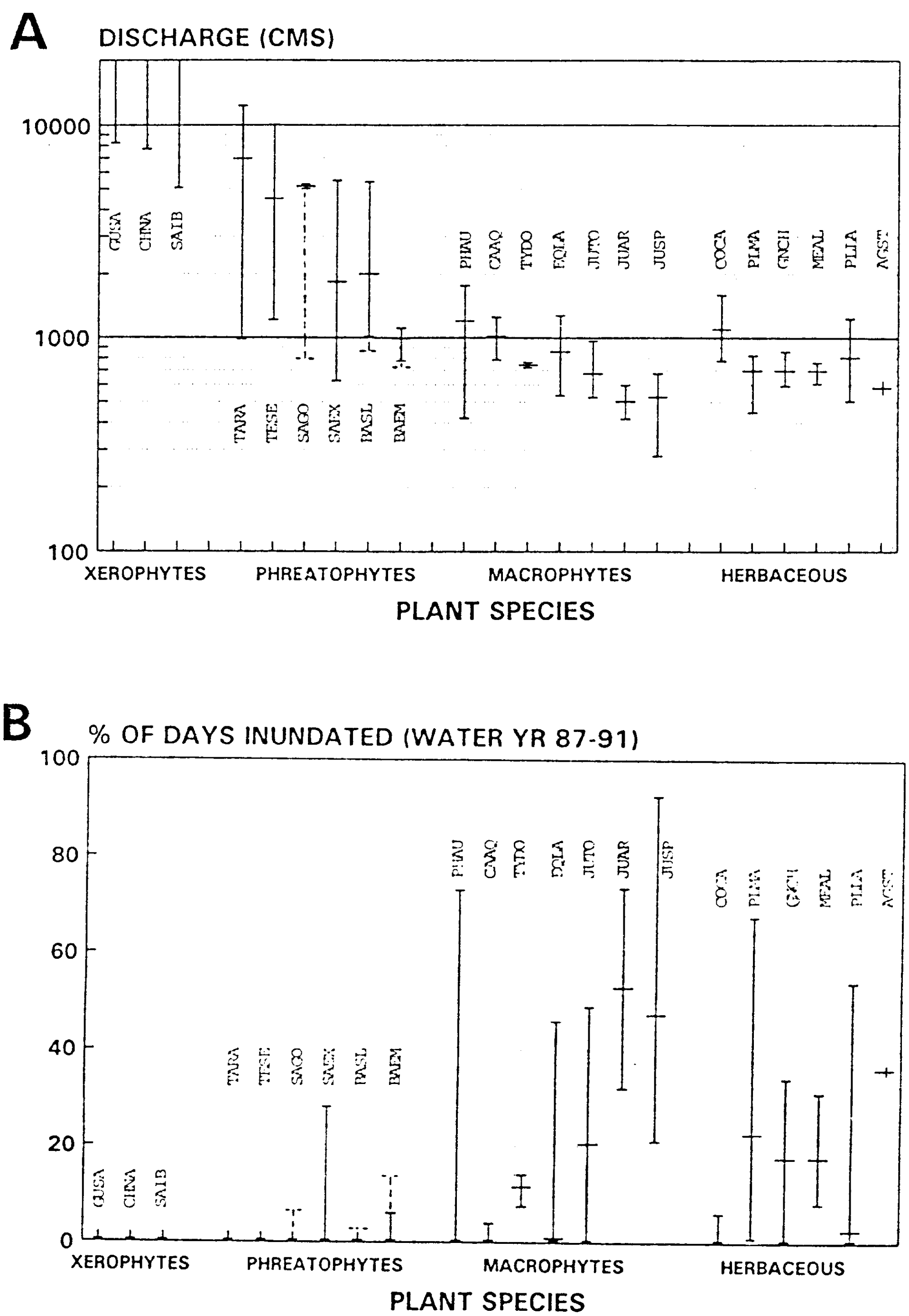

Figure 2.11: Inundation tolerance of four groups of riparian plant species in the vicinity of the U.S. Geological Survey discharge gauge. (A) Stage elevations of riparian plant species. (B) Inundation frequency of riparian plant species during Water Years 1987-1991.

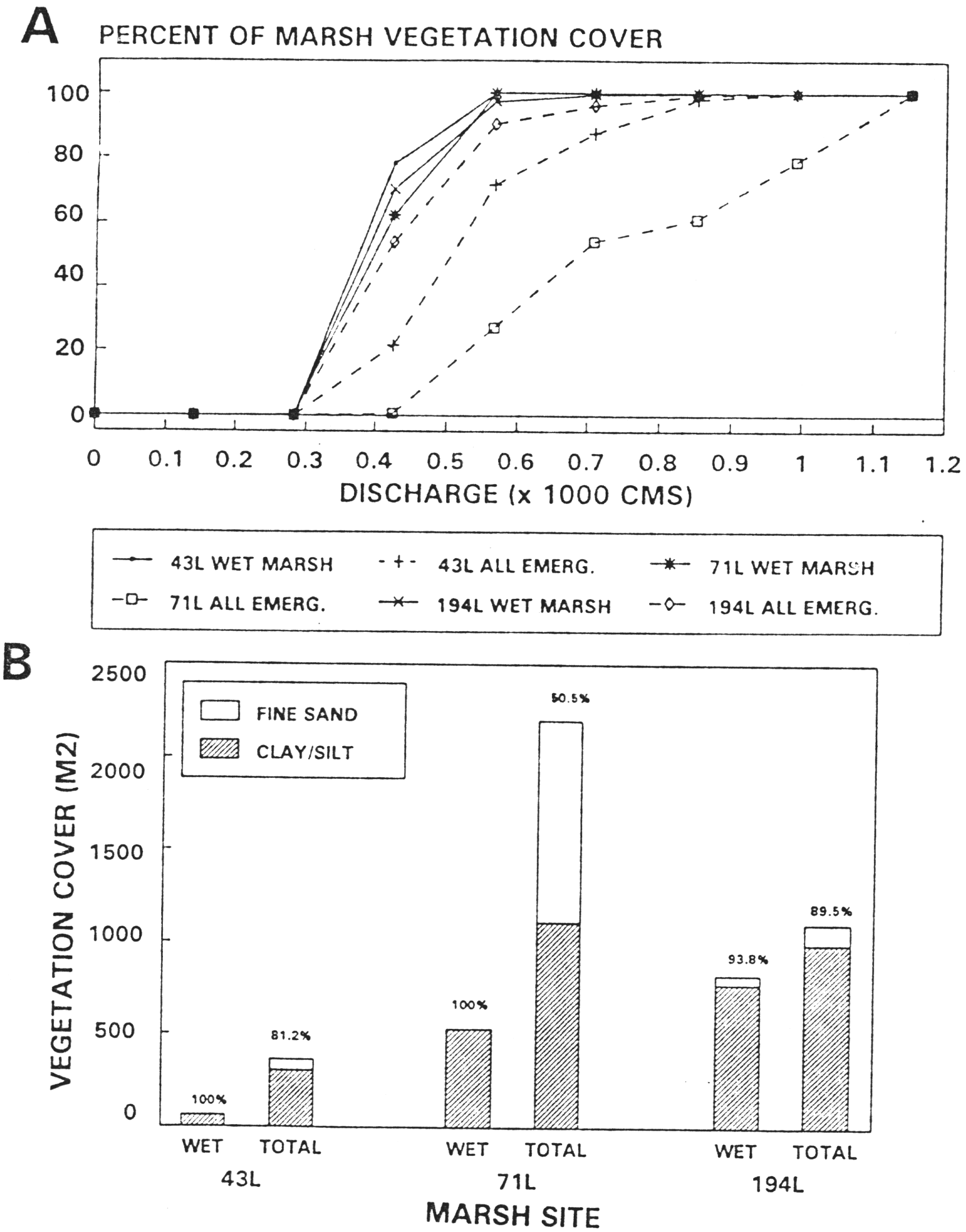

Figure 2.12: Relationship between wet and total marsh vegetation cover, inundation regime and sediment grain size in three fluvial marshes (43L, 71L and 194L), Grand Canyon, Arizona. (A) Hypsometric inundation frequency of wet and total marsh cover at 43L, 71L and 194L marshes during Water Years 1987-1991, Grand Canyon, Arizona. (B) Distribution of wet and total marsh cover as a function of grain size at 43L, 71L and 194L marshes.

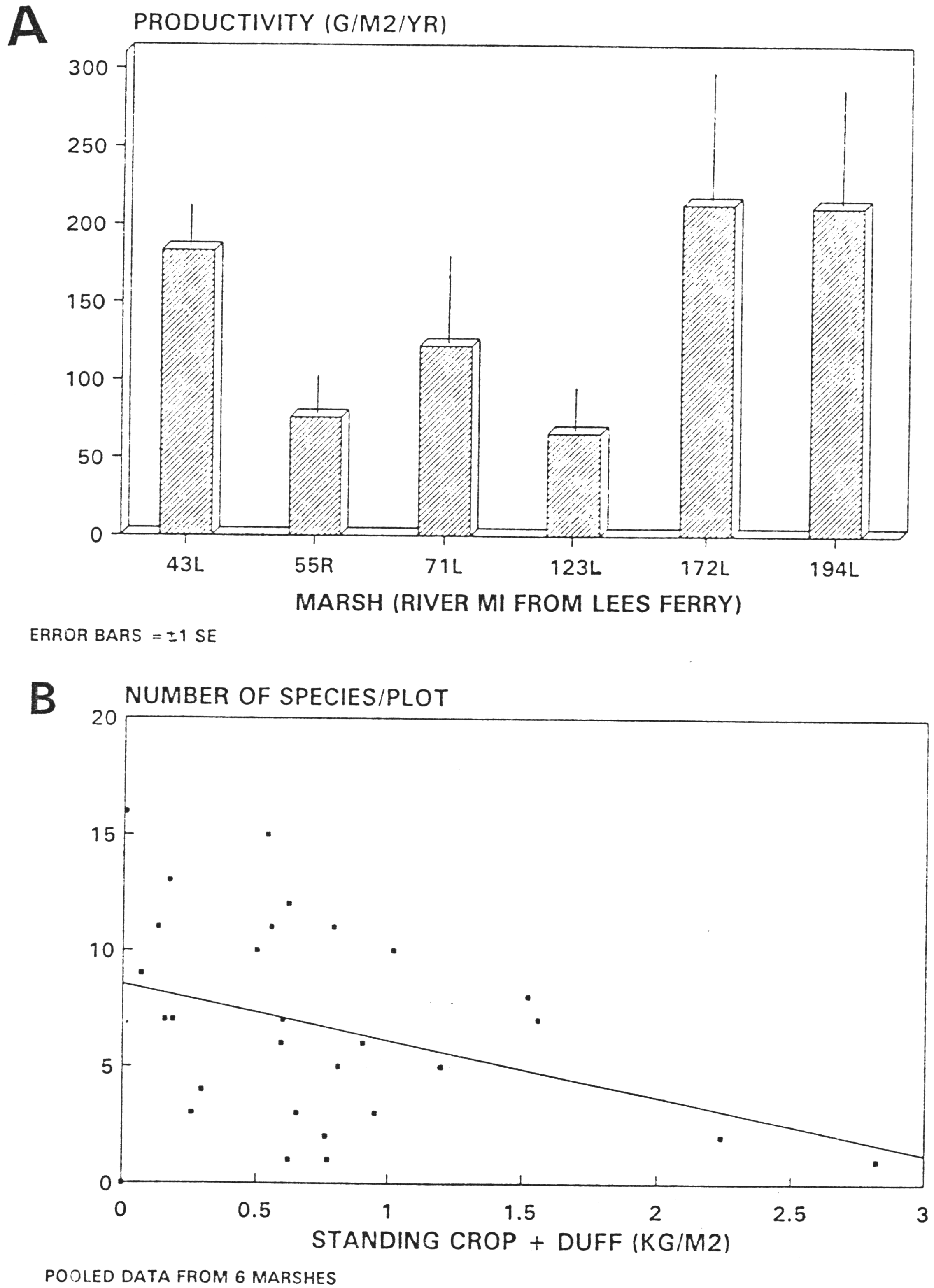

Figure 2.13: Productivity and diversity of fluvial marshes in the Colorado River corridor, Grand Canyon National Park. (A) Estimated mean productivity (g $C/m^2/yr$) of six fluvial marshes. (B) Linear regression of species richness/$0.5m^2$ as a function of standing crop (kg/m^2). See text for statistics.

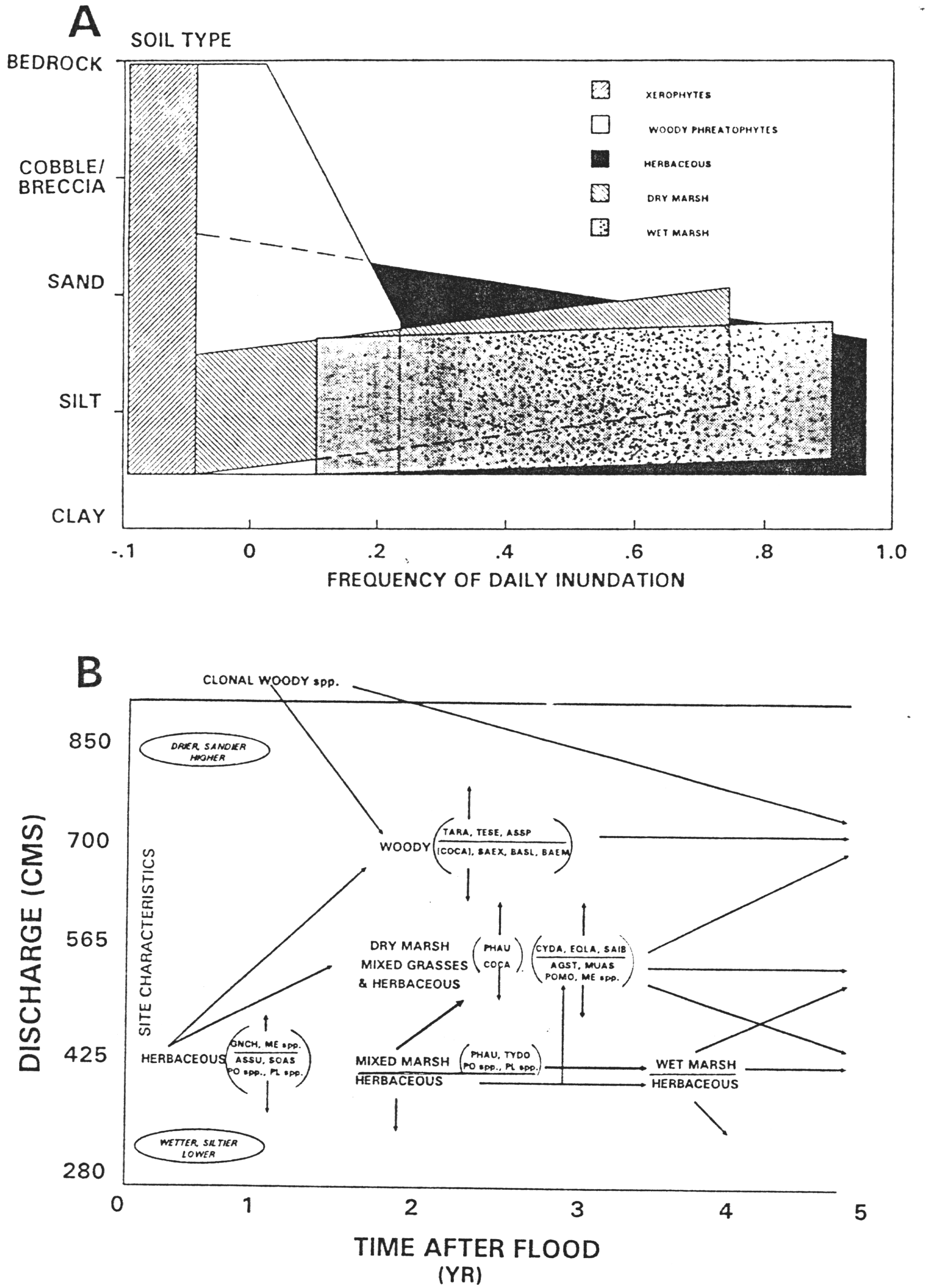

Figure 2.14: Riparian vegetation assemblage structure and succession. (A) Structure of riparian vegetation assemblages in relation to frequency of daily inundation and soil texture. (B) Successional trajectory of fluvial marshes in Grand Canyon. Data compiled from observations on marsh development from 1986-1991.

CHAPTER III: PHREATOPHYTE ESTABLISHMENT STUDIES

ABSTRACT

Questions regarding ecesis (germination and establishment) of native versus non-native riparian plant species were addressed by examining seedling distribution patterns in 68 5m x 50m belt transects in the NHW, "back beach" and OHW zones between Lees Ferry and Diamond Creek. Allindividual plants in each belt transect were identified, counted and assigned to an age class (seedling, sapling or adult), and soil conditions were recorded. Data was also compile dooo Data are being compiled to distinguish differences between geomorphic reaches and soil types, in relation to disharge regimes, and compared with results of a similar study by Stevens and Waring in 1988. Plant demography patterns from 1988-1988 were compared with those observed in the present study.

INTRODUCTION

Problem Statement

The potential for stabilization of sand bar by riparian vegetation has stimulated interest in studies of phreatophyte germination and establishment in the Colorado River corridor downstream from Glen Canyon Dam since 1970 (Martin 1970, unpublished; Turner and Karpiscak 1980; Stevens and Waring 1988; Stevens and Waring 1989; Stevens 1989a). Vegetation colonization patterns on sand bars were undertaken in Glen Canyon Environmental Studies flow program and will continue through the 1992 growing season. This portion of the Riparian Vegetation Project willincorporate data from long-term study plots; however, analyses of those data are not yet complete. Thus, this chapter presents preliminary analyses on several patterns of riparian seedling distribution from data collected throughout the river corridor in October, 1991, and in relation to discharge parameters from Glen Canyon Dam.

Phreatophyte colonization patterns along the Colorado River in the Grand Canyon have been under study since 1980 (Stevens 1985; Stevens and Waring 1985; Stevens and Waring 1988; Waring and Stevens 1988; Stevens 1989). These authors documented a pattern of flood-induced germination and establishment. Limited establishment of woody phreatophytes was observed between 1980 and 1982, except immediately following flooding in 1980. A burst of establishment immediately following the spillover flooding of 1983-1986, and subsequent decline in germination throughout the river corridor. Survivorship of saplings left perched at higher stage elevations declined as normal operations resumed in 1987, and local bursts of germination have only occurred following tributary flooding events. Some woody species are capable of clonal expansion through running roots (e.g. Salix exigua and Tessaria sericea), and have been able to increase in this system over species that reproduce solely by seed (e.g. Tamarix ramosissima and Baccharis spp.; Stevens 1989).

Objectives

1. To assess patterns of phreatphyte seedling establishment in the Colorado River corridor in Grand Canyon.

2. To determine whether colonization of Tamarix ramosissima or other non-native speices is increasing in proportion to native species.

Hypotheses. Tested

This component of the riparian vegetation project addresses Glen Canyon Environmental Studies research question 2: "Do discharge fluctuations, differences in minimum discharges, or different rates of change in daily discharges (ramping rates) interact with other uses and components of the Canyon to affect rates of sediment degradation (Bureau of Reclamation 1990: 4)." Specifically, this component project relates to Research Hypothesis 2.2 questioning the relationship betweeen the role of vegetation as a beach stabilizer and the magnitude of daily discharge fluctuation (p. 5). Fluctuating discharge may influence establishment patterns and thereby influence sand bar stability. We examined the hypothesis that germination of riparian phreatophytes is affected by dam operations. In addition, we examined the hypothesis that Tamarix ramosissima is still actively colonizing the river corridor.

METHODS AND SCOPE

To assess patterns of phreatophyte seedling establishment in the Colorado River corridor, we censused randomly selected 5m x 50m belt transects running parallel to the river in three flood zones These zones included the Old High Water zone (Zone 2 of Carothers et al. 1979), lying above the 3,500 m^3/sec stage; the "back beach" zone (Zone 3) between the 1,400 m^3/sec and the 3,000 m^3/sec stages; and the new high water zone, lying between the 700 m^3/sec and the 1,100 m^3/sec stages. More than 20 replicate transects were censused in each flood zone. Plant species were grouped by moisture requirements into xeric or desert species (Gutierrezia spp., Agave utahensis, Ephedra spp., cacti, and others); nonclonal phreatophytes (Tamarix ramosissima, Baccharis spp., Haplopappus acredenius, Prosopis glandulosa, Acacia greggii and others); and clonal phreatophytes, including Salix exigua, Tessaria sericea and Aster spinosus). Allplants were identified, categorized by age class, and counted on each transect. These data were compared with results of previous studies to determine whether changes in establishment patterns had occurred.

RESULTS

Seedling density/m^2 varied as a function of floodzone, substrate particle size, and channel width between reaches. Seedling density increased from the old high water zone (Zone 2) to the new high water zone (Zone 4; Fig. 3.1). Seedling density in the Zone 2 (Old High Water Zone) was co-dominated by Lepidium montanum, Gutierrezia sarothrae and Acacia greggii (Fig. 3.2A). The Zone 3 seedling population was dominated by herbaceous Oenothera pallida and low densities of Acacia, Brickellia longifolia, Haplopappus acredenius and Baccharis sarothroides (Fig. 3.2B). Zone 4 (the new high water zone) contained nearly five-fold more seedlings than Zone 3, with strong dominance by herbaceous Gnaphalium chilense, Veronica spp. and occasional woody phreatophytes (Fig. 3.2C). The limited but consistent occurrence of Tamarix ramosissima seedlings in these samples suggests that it is still becomings established under the present dam operations. While the probability of survivorship of any Tamarix seedlings encountered in 1991 is extremely low, fluctuating flow regimes do permit Tamarix germination at the water's edge.

Seedling density varied by plant growth form and substratum particle size (Fig. 3.3A). Woody clonal phreatophyte shoots were excluded from boulder fields and bedrock habitats overall, and were more abundant in sand/rock and sand deposits. Nonclonal species such as Baccharis spp. and Tamarix were most abundant in sand and boulder fields. Xerophytes were most common in sandy habitats and least common in bedrock.

Proximity to the water's edge influenced woody seedling density more than channel width (Fig. 3.3B). Non-clonal phreatophytes, such as Brickellia longifolia and Baccharis spp., dominated the seedling population

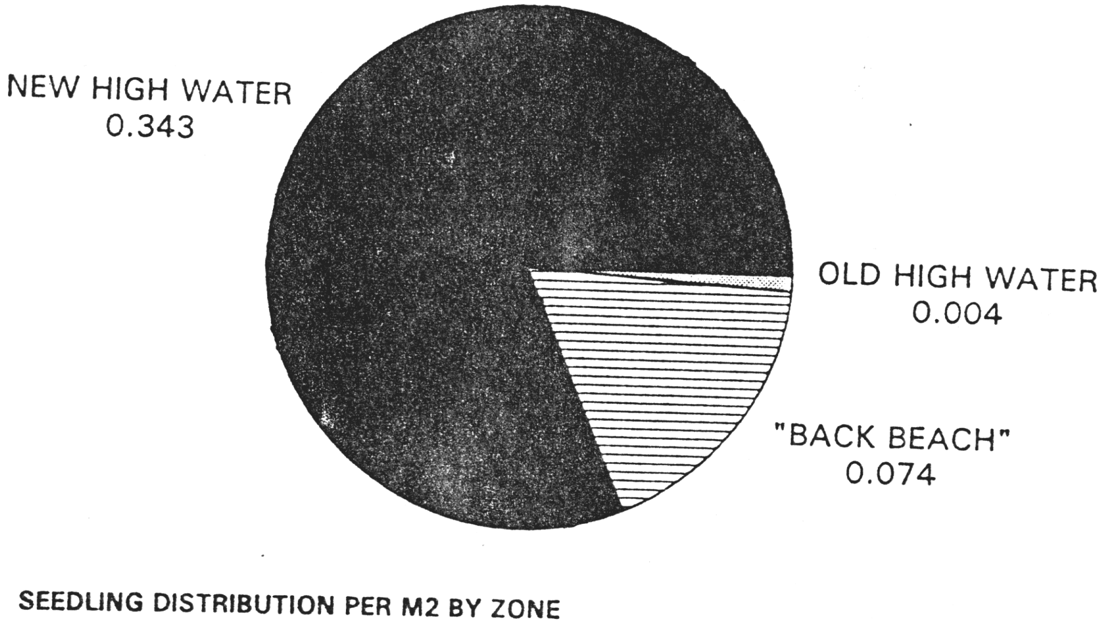

Figure 3.1: Colorado River riparian plant seedling density/m^2 in Zones 2 (Old High water Zone) to 4 (New High Water Zone), Grand Canyon, Arizona.

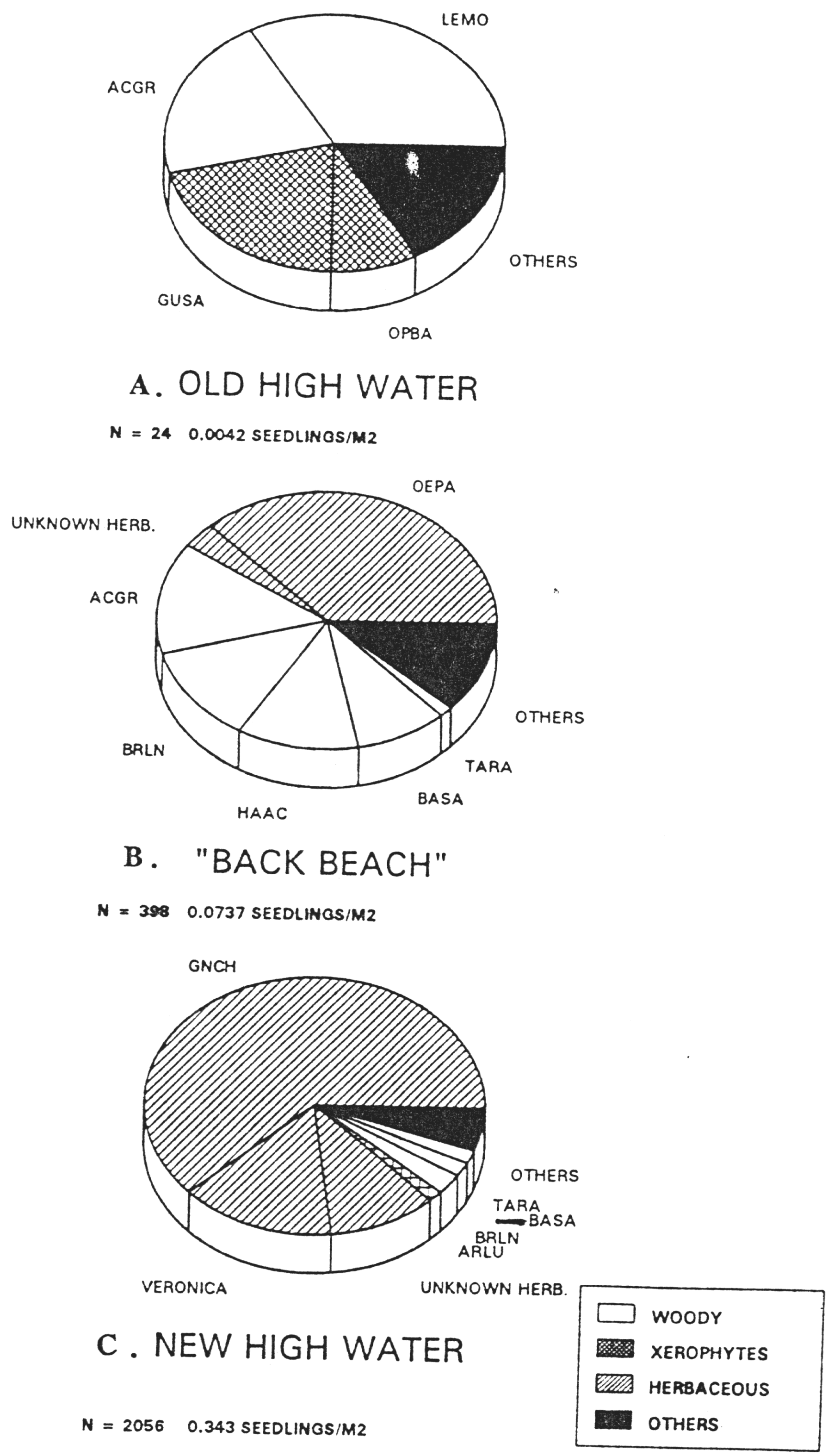

Figure 3.2: Seedling density as a function of stage elevation along the Colorado River in Grand Canyon. (A) Zone 2 (Old High Water Zone), (B) Zone 3 (the "Back Beach" Zone), and (C) Zone 4 (the New High Water Zone).

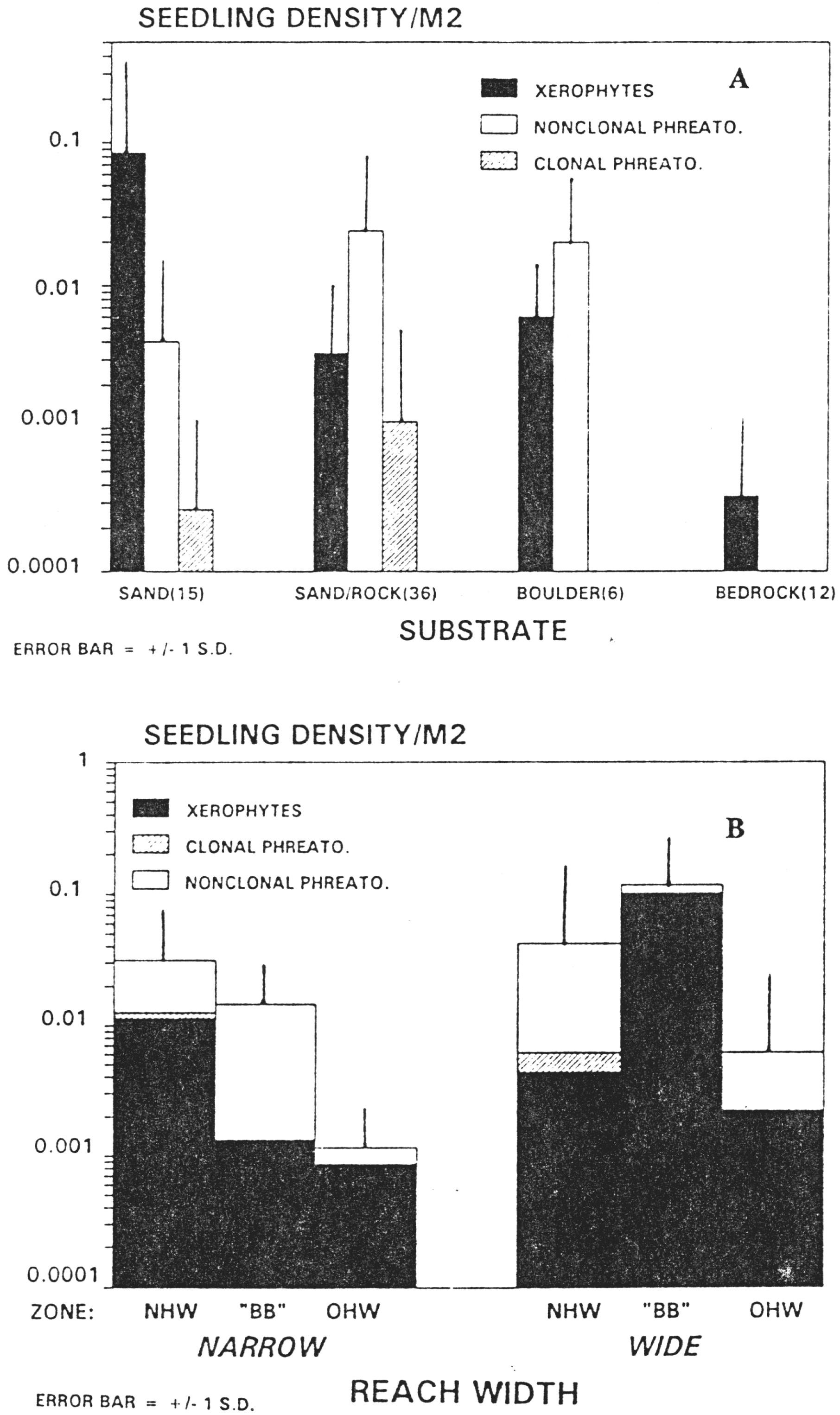

Figure 3.3: (A) Seedling density/m ^{2} as a function of plant growth form and substratum particle size. (B) Woody seedling density/m ^{2} as a function of channel width and proximity to the river's edge.

across the elevation gradient both narrow and wide reaches. Seedling density generally decreased across the elevational gradient, but Zone 3 in wide reaches had a greater density of xerophyte seedlings.

DISCUSSION

These preliminary results will be augmented by additional data and analyses in the near future; however, several patterns are suggested. The results presented here generally support earlier findings by Stevens and Waring (1989) that germination of woody phreatophytes is limited during periods without flooding. Tamarix ramosissima densities were far lower in 1991 than they were during the flood years of 1983-1986; however, this species's limited success in establishment at the top of the zone of fluctuation suggests that it may continue to invade under higher ranges of fluctuations. This species is capable of reproducing during it's third year, or earlier, so occupation of a highly disturbed zone may still permit successful reproduction.

Tamarix ramosissima is the dominant woody plant species along the Colorado River and is opportunistic and can tolerate prolonged inundation and desiccation (Stevens and Waring 1988; Stevens 1989a). This non-native species is therefore well adapted to a river system with erratic discharge patterns, such as the Colorado River in Grand Canyon. Tamarix quickly colonizes moist, freshly disturbed habitats, such as perennial stream channels after flooding events, via eolian transport of its tiny, numerous seeds. The two dozen perennial tributaries of the Colorado River are subject to floods of various magnitudes that expose patches of disturbed soil (Webb et al. 1987). If dam operations enhance Tamarix population expansion along the river, seed dispersal into tributaries means that Tamarix populations may increase in these pristine stream channels. Each of the 11 quadrats established in Havasu Creek by Stevens (pers. comm.) after the 80-year flood in September, 1990, contained Tamarix seedlings. Prior to that flood, Tamarix had been a rare element of the Havasu Creek riparian plant assemblage. Survivorship of those seedlings is being monitored to determine how Tamarix fares in this tributary.

CONCLUSIONS

1. Riparian seedling establishment was greatest in the New High Water Zone, at the top of present dam operations, and was dominated there by herbaceous species.

2. Seedling density varied as a function of particle size, and differed between plant groups (xerophytes and phreatophytes) in wide versus narrow channels.

3. Tamarix ramosissima seedling density was low in 1991, but limited establishment suggests that this species may be capable of continuing to colonize the river corridor under fluctuating flow regimes.

CHAPTER IV: PLANT WATER POTENTIAL STUDIES

INTRODUCTION

Problem Statement

The potential for stabilization of sand bar by riparian vegetation stimulated interest in several related studies in the Colorado River corridor downstream from Glen Canyon Dam. Vegetation colonization, growth and stabilizing effects on sand bars were undertaken beginning during the Glen Canyon Environmental Studies test flow program, and will continue through the 1992 growing season. In this chapter we present preliminary analyses on studies of plant water potential studies of riparian vegetation as it relates to discharge parameters from Glen Canyon Dam.

Riparian phreatophyte plant species require direct contact the groundwater table or capillary fringe for photosynthesis, growth and reproduction. In a regulated river system, such as the Colorado River downstream from Glen Canyon Dam, the elevation of the bankstored groundwater table responds quickly to changes in river stage (Carpenter and Carruth 1992). Changes in groundwater depth may therefore affect streamside plant performance in regulated river systems through impacts to soil moisture availability.

Maintenance of water balance is a prerequisite for plant survival and growth, particularly for arid lands riparian phreatophytes. These species rely on shallow groundwater in stream channels and are often poorly adapted to surrounding xeric conditions. Plants vary in their moisture requirements, but all terrestrial species maintain a negative plant water potential (PWP) by transpiring moisture to the atmosphere at the leaf or stem surface. If insufficient soil water is available to maintain the water balance, the plant may become stressed, and may wilt or die. Each terrestrial plant species functions within its own PWP range, which varies across moisture gradients and between species. Desert-adapted plant species typically are well adapted to drought stress and demonstrate extremely low values of PWP. For example, creosotebush (Larrea tridentata) can continue to photosynthesize at PWP values lower than -600 KPa. In contrast, Grand Canyon riparian plant species are much less tolerant of drought, and commonly operate in the range of -20 to -300 KPa (Thompson and Thompson 1990).

Measurement of PWP was pioneered by P.F. Schollander and associates (1965) with the development of a pressure bomb method. By placing the cut stem of a plant into a chamber and pressurizing it with N_2 gas, xylem fluid is forced out of the cut stem. The pressure (measured in KPa) required to drive fluid out of the stem is a measure of PWP. PWP is a negative value, so a high pressure reading means PWP is low and the plant is operating under low water availability. As is to be expected, PWP changes dramatically over the course of a day, with moderate values in the pre-dawn hours and much lower values during the day when transpiration is maximized. Predawn PWP measurements are most conservative and are most often used to evaluate plant moisture stress; however, mid-day values may also provide information on plant responses to moisture availability. Thompson and Thompson (1990) reported significant changes in PWP between pre-dawn and mid-day among 10 riparian plant species in the Colorado River corridor, but found little variation within individual plants at any one time.

Objectives

1. Determine whether riparian vegetation colonization of the Colorado River corridor is affected by Glen Canyon Dam operations.

2. Determine whether dam operations affect plant water potential and growth (PWP) of native Salix exigua and non-native Tamarix ramosissima .

Hypotheses Tested

This component of the riparian vegetation project tests the hypothesis that dam operations affect the moisture stress and growth of riparian vegetation. This relates to Glen Canyon Environmental Studies research question 2: "Do discharge fluctuations, differences in minimum discharges, or different rates of change in daily discharges (ramping rates) interact with other uses and components of the Canyon to affect rates of sediment degradation (Bureau of Reclamation 1990: 4)." Specifically, Research Hypothesis 2.2 questions the relationship betweeen the role of vegetation as a beach stabilizer and the magnitude of daily discharge fluctuation (p. 5). Fluctuating discharge may influence plant survivorship and growth patterns and thereby affect sand bar stability.

METHODS AND SCOPE

Plant water potential was measured on Salix exigua and Tamarix ramosissima plants at RM 43L and RM 172 during the GCES flow tests period in the spring and summer of 1991. These sites were used because groundwater fluctuation data are available there. These two plant species were selected for study because they co-dominate sand bars in this system and Salix is successionally replacing Tamarix (Stevens 1989a). Only data on pre-dawn Salix PWP at 43L and 172L are presented here. Data on mid-day PWP for both species and pre-dawn PWP for Tamarix are still being analyzed.

Sampling was conducted between midnight and 5:00 a.m. and from 1:00 p.m. to 4:30 p.m. on 15 tagged and surveyed plants. Temperature and relative humidity were recorded approximately every half hour. Pre-dawn Salix exigua plant moisture stress data from the 43L site were sorted into two groups: low plants (occurring below the 850 m^3/sec stage) and high plants (>850 m^3/sec stage). Growth data are being analyzed for these plants to determine whether PWP levels affect growth rates.

RESULTS

Separate stepwise multiple regressions were run for each set of plants and coefficients for temperature and humidity were calculated (Table 4.1). Analysis of low plants at RM 43L revealed significant negative correlations between PWP for both relative humidity (and stage, and a significant positive correlation between PWP and temperature (Table 4.1). In the high plant population at RM 43L, temperature and relative humidity effects were significant, but stage was not (Table 4.1). Salix exigua occurred only in the low (<850 m^3/sec) zone at RM 172L.

Data from the nearby (RM 40) R-200 stage recorder were used to estimate stage at the RM 43L site (U.S. Geoogical Survey provisional data). Stage discharge relationships were correlated between the R-200 site and the RM 43L site using 141.5 m^3/sec and 424.8 m^3/sec constant flow elevations derived from the topographic data of Beus and Avery (1991). PWP data were then segregated according to discharge and flucutation levels based on distribution of data points. Discharge levels were: low (141.5 m^3/sec to 311.5 m^3/sec) and high (311.5 to 481.4 m^3/sec). Analysis of variance of two discharge levels indicated that PWP was significantly higher (less stressful) under high discharge ($F_{2,496} = 5.619, p = 0.004$). A similar analysis was performed for the RM 172L Salix data, with similar results ($F_{1,426} = 26.096$, $p < 0.001$). A similar approach will be used to determine differences between fluctuating discharges.

Data were adjusted to remove the effects of temperature and relative humidity and modeled to illustrate the effects of discharge on PWP independent of atmospheric stress (Fig. 4.1). The model was run for low and high elevation plants separateiy under conditions of low (temperature - 2sd, relative humidity + 2sd), mean (temperature = mean, relative humidity = mean) and high (temperature = mean + 2sd, relative humidity = mean - 2sd) levels of atmospheric stress. Model results demonstrate the significant effects of stage with atmospheric stress removed for RM 43L low Salix and RM 172L Salix, but not high Salix at RM 43L.

DISCUSSION AND CONCLUSIONS

The role of riverside vegetation in sand bar stabilization is unknown at present; however, riparian vegetation plays a significant role in riparian ecosystem dynamics. Therefore, knowledge of flow conditions that improve habitat conditions for vegetation are important. The results presented here suggest that stage influences PWP levels in Salix exigua, a ubiquitous riparian phreatophyte in the Colorado River corridor. Stage was negatively correlated with PWP levels in Salix in the New High Water Zone. "Back Beach" Salix sustain lower (potentially more stressful) PWP levels. These results are conservative because they are pre-dawn values. Additional analyses presently underway will determine whether similar patterns apply to mid-day Salix and both pre-dawn and midday Tamarix at these sites.

Sand Bar Stability Studies

In addition to determining whether dam operations influence plant stress and growth, we are also investigating the interaction between sand bar stability and vegetation density is being evaluated at three spatial scales. Lengths of different root size classes, and shoot density is being evaluated on the Beus et al. (1991) survey beaches. These data, combined with grain size information, will be used to evalate the stability of repeated survyed points above and below the $850m^3$/sec stage. Scour wires placed in beach faces in different vegetation densities are being remeasured to determine change in soil surface depth. Historical vegetation mapping on the GCES-II Geographic Information System willused to determine riparian vegetation played any role in sand bar protection during the 1983 flooding event. This analysis is just beginning.

Table 4.1: Stepwise multiple linear regression analyses and summary of *Salix exigua* plant water potential (PWP in MPa) as a function of temperature (T in °C), relative humidity (RH in %) and discharge (Q in m^3/sec) for low (<850 m^3/sec) and high (>850 m^3/sec) at RM 43L and low plants at RM 172L, Grand Canyon National Park, Arizona.

SITE	ELEVATION	MULTIPLE LINEAR REGRESSION EQUATION	R^2	F	p	DF
43L	Low	PWP=0.4611+0.0120(T)-0.0029(RH)-0.3177(Q)+e	0.1583	33.81	<0.001	3,500
43L	High	PWP=0.5335+0.0073(T)-0.0021(RH)+e	0.0798	18.26	<0.001	2,421
172L	Low	PWP=0.8615+0.0038(T)-0.0062(RH)-0.2321(Q)+e	0.144	17.99	<0.001	4,427

SUMMARY OF STEPWISE MULTIPLE REGRESSION PROCEDURE FOR PWP:

		PREDICTOR VARIABLE · MODEL R^2 (F_{df}; p)		
SITE	ELEVATION	TEMPERATURE	RELATIVE HUMIDITY	DISCHARGE STAGE
43L	Low	0.137 ($11.734^{3,500}$;0.0007)	0.159 ($12.778^{3,500}$;0.0004)	0.169 ($6.227^{3,500}$;0.0129)
43L	High	0.072 ($6.639^{2,421}$;0.0444)	0.080 ($3.640^{2,421}$;0.0571)	Not Significant
172L	Low	0.144 ($3.324^{4,427}$;0.0690)	0.106 ($50.844^{4,427}$;0.0001)	0.138 ($3.987^{4,427}$;0.0465)

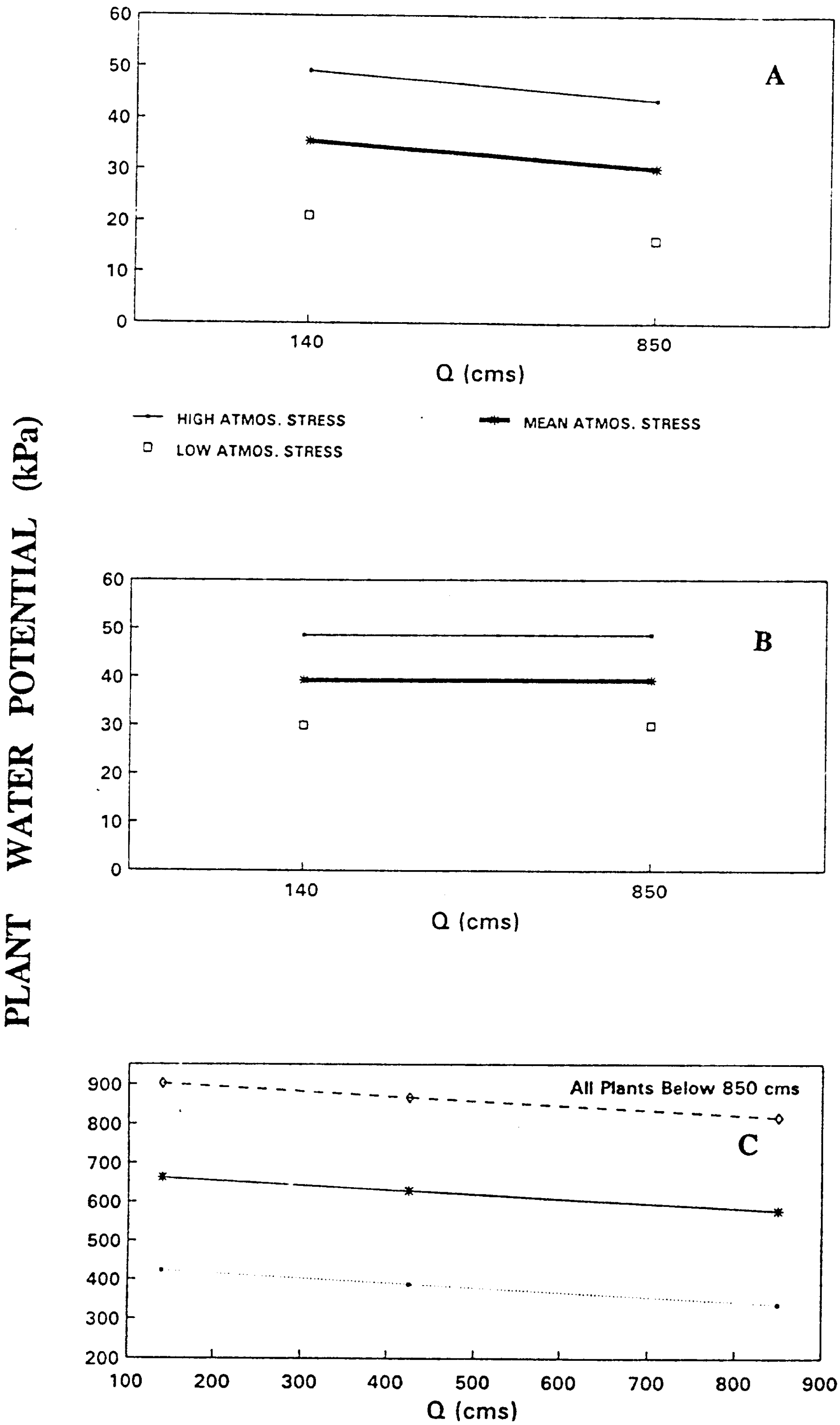

Figure 4.1: Adjusted pre-dawn plant water potential of Salix exigua under low, moderate and high atmospheric stress, in the Colorado River corridor, Grand Canyon National Park, Arizona. (A) Salix below the 850 m^3/sec discharge elevation at RM 43L. (B) Salix above the 850 m^3/sec discharge elevation at RM 43L. (C) Salix below the 850 m^3/sec discharge elevation at RM 172L.

CHAPTER V: OTHER RIPARIAN VEGETATION STUDIES UNDERWAY

INTRODUCTION

Several other components of this Colorado River riparian vegetation project are underway. In addition to the components presented here, we are evaluating the status of listed and endemic plant species in the Colorado River corridor, examining growth patterns of Old High Water Zone vegetation, and gathering data on long-term study quadrats. These additional studies willprovide the National Park Service with additional information on which to base management decisions. These studies are briefly mentioned here, and further information will available as the project components are completed.

Listed, Endemic and Non-Native Species

The status of listed, endemic and exotic species is being evaluated through the literature, through herbarium specimens and through censuses of long term plots.

Listed Species : Thus far, Flaveria mcdougallii is the only listed species encountered in the river corridor. It inhabits springs and seeps from RM 148 to about RM 179, but all populations appear to lie at or above the Old High Water Zone, and are thus buffered from direct dam operational effects.

Endemic Species : Euphorbia aaron-rossii , a recently discovered endemic taxon, is found in the 1200-2500 m^3/sec zone in upper Marble Canyon. This species is rather widely distributed in upper Grand Canyon, and populations occur up numerous tributaries, including Jackass Canyon, Salt Water Wash, Eminence Break, and elsewhere. This species does not appear to be at risk from dam operations.

Non-Native Species : Several new non-native species are invading the Colorado River corridor in Grand Canyon National Park (Table 5.1). The most conspicuous of these is plume grass (Erianthus ravennae). This species was first observed at Lees Ferry by Phillips (Phillips et al., 1987) and is a tall Eurasian bunchgrass. During the marsh inventories in 1991, several hundred individuals were counted throughout the river corridor. Densities are low enough that elimination of individuals may work as a management program, but such a program should be undertaken immediately if the advance of this species is to be halted.

A new non-native Lepidium (mustard) species has extensively colonized marshes throughout Marble Canyon in 1990-1991. The specimens have been sent to taxonomists for identification, but it appears to be a new species for the Grand Canyon.

New Records for Grand Canyon: Thus far, seven new records of vascular plants have been collected from the Colorado River in Grand Canyon National Park (Table 5.1). Because much emphasis has been on fluvial marshes, most of the new records are wetland species. Most identified to date have been monocots; however, we anticipate additional dicot records as identification proceeds.

Old High Water Zone Studies

We are beginning to analyze Celtis reticulata and other Old High Water Zone phreatophytes growth patterns under regulated discharge regimes. This latter study is being conducted to ascertain whether dam operations have affected growth of the tree species that comprise this unique habitat within Grand Canyon. Thus, approximately more than 120 cores of Celtis reticulata have been collected and prepared, and analyses are underway by the University of Arizona Tree Ring Laboratory, Tucson, Arizona. We also plan to monitor Prosopis and Acacia growth using plants from the GCES-I study by Anderson and Ruffner (1988).

Long-term Study Plots

Long-term study sites are under investigation in this project, with randomly selected quadrats placed in six geomorphologic settings examined at each site. Geomorphologic settings include marsh, riparian strip, general beach, debris fan, old high water zone and xeric (control) sites in the surrounding desert. Quadrats are being established in tributaries to serve as additional controls. Efforts to locate populations of listed species are also underway. Study sites and status of censusing efforts are listed in Table 1.1. Information from these sites and other studies will be used to: (1) describe patterns of riparian plant density and diversity, (2) document baseline vegetation conditions for monitoring, and (3) determine the status of listed exotic whether exotic species are continuing to invade the river corridor.

Table 5.1: New records of plant species and rapidly invading exotic species of the Grand Canyon, Arizona, 1991.

CRUCIFERAE:
Lepidium sp.*
CYPERACEAE:
Scirpus acutus
GRAMINEAE:
Eragrostis curvula / chloromelas (?)
Erianthus ravennae **
Paspalum dilatatum
Setaria lutescens
JUNCACEAE:
Juncus filiformis
Juncus nevadensis

*New exotic species, actively invading beaches in Marble Canyon
**Previously reported exotic species, now rapidly invading the river corridor

DRAFT

Chapter VI:

PATTERNS OF RIPARIAN VEGETATION ESTABLISHMENT BETWEEN 1983 - 1988 ALONG THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK, ARIZONA

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Chapter VI:

PATTERNS OF RIPARIAN VEGETATION ESTABLISHMENT BETWEEN 1983 - 1988 ALONG THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK, ARIZONA

ABSTRACT

Development of riparian vegetation is commonplace downstream from impoundments, yet information on establishment and maintenance of that vegetation is sparse. We monitored 20 sites along the Colorado River in Grand Canyon National Park between 1984 and 1989. This period encompassed 3 years of spillover flooding (1984-1986) and three years of "normal dam operations" (low and fluctuating discharge) from Glen Canyon Dam.

1) Phreatophyte ecesis (germination and establishment) varied little between years in the "tidal" zone, but was strictly flood-induced on higher terraces.

2) Vegetation established in the tidal zone may contribute to bank stability, but is at risk to normal, fluctuating dam operations.

3) Significant interactions between dam operations, flooding regimes, stage, substrate types, and interspecific differences affected the distribution and growth of phreatophyte saplings.

a) Years with normal dam operations, coupled with tributary contributions of fine sediments, provided suitable germination habitats for some riparian species (e.g. 1987-1988); however, years with little tributary sediment input and extreme fluctuations (e.g. 1989) resulted in little germination of riparian phreatophytes.

b) Saplings grew faster and maintained higher densities in silty sand in the tidal zone, as compared to other substrates or Zone 3.

c) Selectively advantaged by its fecundity and stress tolerance, <u>Tamarix ramosissima</u> sapling density increased under normal dam operations.

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Chapter VI: Patterns of Riparian Vegetation Establishment Between 1983 - 1988 Along the Colorado River in Grand Canyon, Arizona

DRAFT

INTRODUCTION

Regulated discharge below large impoundments may facilitate the development of riparian vegetation; however, the mechanisms of establishment and maintenance of riparian vegetation along regulated streams have received little study (Carothers et al. 1979; Turner and Karpicscak 1980; Nilsson 1985; Stevens 1989a, b). Riparian vegetation develops in response to inter-related factors, including: 1) the flooding disturbance regime, which influences mature plant density and composition, and exposes patches of substrates suitable for colonization; 2) the species pool; 3) propagule abundance; and 4) germination and establishment requirements of constituent species (Koslowski 1984; Reichenbacher 1984; Stevens and Waring 1985; Stevens 1989; Stromberg and Patten 1990). Ecesis (germination and establishment) of riparian vegetation is strongly influenced by flooding (Stevens and Waring 1988; Waring and Stevens 1988; Stevens 1989). Floods are "killing events" (sensu Sousa 1984) that decrease biological organization (i.e. diversity and complexity of trophic structure) and lower the "trajectory of ecological succession" by direct reduction of biomass and diversity, thereby returning the ecosystem to an earlier stage of development (Odum 1981). Flooding is the most ubiquitous form of disturbance in riparian ecosystems, and in regulated rivers, flooding mechanically reduces riparian plant community development, resulting in a "perpetual succession" (Campbell and Green 1968). Post-impoundment flooding in regulated river corridors provides insight into the processes that structure phreatophyte communities (Stevens 1989a). Alteration of the disturbance regime in regulated rivers may change the course of riparian succession by affecting recruitment and biotic interactions (Stevens 1989).

Construction of Glen Canyon Dam accidentally enhanced riparian vegetation growth along more than 475km of the Colorado River in Grand Canyon National Park (Carothers and Aitchison 1976; Turner and Karpiscak 1980; Water Science and Technology Board 1987). Although the presence of this new riparian vegetation has been documented, the suite of factors regulating community growth and compositional change has only begun to be explored.

In this study we monitored ecesis and stand development of perennial riparian vegetation along the Colorado River in Grand Canyon National Park following a post-dam flood-of-record ($3400m^3$/sec) in 1983. Study began in 1984 during the spillover flooding event that ended in 1986, and we followed three years of "normal" dam operations (daily fluctuating flows from a minimum of $30m^3$/sec to a maximum of approximately $1,000m^3$/sec). We evaluated the effects of dam operations through time, stage, substrate, distance from Glen Canyon Dam, and interspecific life history differences, on riparian plant ecesis, sapling growth, and recruitment.

METHODS AND SCOPE

Study Sites

Twenty study sites were selected from the 55 sites examined by Stevens and Waring (1988; Table 1, Figure 1). Sites were selected on the basis of: 1) comparability of slope, geomorphology, and substrate (all occurred on low-gradient, debris fans dominated by cobble and sand substrates); 2) distribution throughout the river corridor; 3) availability of historical vegetation data; and 4) low to minimum level of recreational and/or tributary impacts. No effort was made to standardize azimuth because the wide, low-gradient debris fans on which quadrats were located obscured subtle exposural effects.

Quadrats were 30m in length (parallel to the river) and encompassed two zones: the "intertidal" new high water zone (NHWZ), below the approximate $1150m^3/sec$ stage (Zone 4 of Carothers et al. 1979), and the superlittoral or "back beach" zone (Zone 3 of Carothers et al. 1979) from $1200m^3/sec$ to $2500m^3/sec$ stage. These two zones received different flooding impacts. The lower portions of the NHWZ was inundated on a daily and seasonal basis during the entire period of study, whereas the Zone 3, was inundated only during 1984-1986. Thus these two zones appeared suitable to examine trends in recruitment related to flooding. Further details on these quadrats are discussed in Stevens and Waring (1988).

Riparian Vegetation

The vegetation studied here included all perennial plant life occurring on the two flood zone terraces along the Colorado River. Four groups of species were identified: clonal phreatophytes (e.g. Salix exigua and Tessaria sericea); 2) exotic tamarisk (Tamarix ramosissima), with density patterns analyzed separately from 3) the other non-clonal phreatophytes (e.g. Baccharis spp., Prosopis glandulosa, Brickellia longifolia, and other species); and 4) xerophytes (e.g. Cactaceae, Larrea tridentata, Encelia farinosa). Acacia greggii, Baccharis sarothroides, and Haplopappus acredenius were considered as non-clonal, strongly facultative phreatophyte species. We followed the taxonomy of Phillips et al. (1987). The dominant riparian species occurring in this system are listed in Table 2.

Data Collection

Quadrats were censused between 1984 and 1989 (Table 1). All perennial species were recorded, along with measurements of seedling, sapling and mature plant densities, and species richness. Seedlings were defined as plants less than six months in age, having a single, non-woody stem, and/or other seedling characteristics. Saplings were defined as plants which were not seedlings, were less than one meter in height (e.g. Tamarix ramosissima, Tessaria sericea, Salix exigua), and/or were between 0.5 and 3 years in age. Reproductively mature plants were greater than 1m in height, greater than 3 years in age, or showed evidence of reproduction.

Seedling Density: Seedling density provided a measure of germination success in different substrates, on different flood terraces, and between years. Seedling density/m2 was evaluated on the quadrats from 1984-1989. A corridor-wide evaluation of seedling density and species richness in different fluvial substrate types was accomplished by censusing randomly selected 2m x 50m transects in the NHWZ. Additional data were compiled and analyzed from surveys in 1987.

Sapling Density: Sapling density was monitored on quadrats. Sapling distribution was further evaluated throughout the river corridor by stopping at randomly selected Colorado River miles (Stevens 1983) and censusing 2m x 50m belt transects in the NHWZ and the Zone 3. Data collected included sapling species, and distance to the canopy edge of the nearest mature plant.

The effect of substrate on sapling growth rate was assessed by marking more than 1100 sapling Tamarix ramosissima, Salix exigua and Baccharis salicifolia in May, 1988, and remeasuring those plants in September/October, 1988. These three species were selected because they represented three different phreatophyte architectural types identified by Stevens and Waring (1988) as responding differentially to flooding disturbance.

The effect of stage on sapling Tamarix ramosissima growth was evaluated on the South Canyon quadrat (CR Mile 31R) and at Mohawk Canyon (CR Mile 171L). Fifty saplings were marked in May, 1988 in the NHWZ and 50 were marked in the Zone 3 at each site. Data were analyzed separately for these two sites because the South Canyon quadrat was dominated by cobble, whereas the Mohawk Canyon site had higher dominance of silty sand.

Mature Plant Density: Data on 1984 mature plant population dynamics were compiled from Stevens and Waring (1988) and compared with quadrat data gathered in this study. Recovery of riparian plant community from the 1983 flooding event was confounded by a lack of 1982 data. Comparison of the present mature-plant data with 1982 (pre-flooding) riparian plant densities was approximated using Stevens and Waring's (1988: 236) estimates of system-wide mortality by species, including several members of each of the four guilds under study here. These estimates were used to generate expected 1982 population densities of the four guilds. This approach is flawed by not having information on all members of each guild, and by using system-wide data to estimate 1982 densities on 20 quadrats. Results are therefore presented to solely to demonstrate trends in vegetation recovery and development in this system.

Data were analyzed using parametric univariate and multivariate analyses of variance from SPSS and SYSTAT software packages (Hull and Nie 1981; Wilkinson 1989).

RESULTS

Analyses of factors affecting riparian perennial plant seedling density are discussed below, followed by analyses of sapling distribution, abundance, survivorship, growth and species richness. Analyses of changes in the density and composition of mature riparian plants concludes this section. Data from the National Canyon quadrat were not included in the analyses because of persistent, severe impacts from tributary flooding.

Seedling Distribution

Temporal Patterns: Total seedling density decreased significantly through time as discharge returned to normal operations (Table 3; Figures 2, 3). Phreatophyte seedling density declined significantly from the 1984-1986 flooding period to the 1987-1988 normal operations period. Xerophyte seedling density did not change on quadrats over the period of study (Table 3).

Stage Effects: Mean phreatophyte seedling density decreased significantly in the Zone 3 following subsidence of 1983-1986 floodwaters. Zone 3 seedling densities were highest during and immediately following flooding events, and were significantly lower during non-flooding periods of "normal dam operations" (Table 3; figures 2, 3). Little if any germination of facultative or obligate phreatophyte species was observed during years of normal operations (after 1986) in the Zone 3. These patterns gave rise to a marginally significant zone x year interaction effect for phreatophytes (Table 3).

Mean phreatophyte seedling density decreased only slightly and non-significantly in the NHWZ following subsidence of post-dam flooding in 1986 (Figure 2). Phreatophyte seedling density remained elevated in the $< 950 m^3/sec$ zone (lower NHWZ), with conspicuous Tamarix ramosissima establishment observed in the littoral (fluctuating) zone between the $650 m^3/sec$ and $950 m^3/sec$ stage, particularly in the lower Grand

Canyon in 1987-1988. In 1989 comparatively little establishment took place below the $950 m^3/sec$ stage. We attributed this pattern to a low volume of tributary-derived sediments (1989 was a drought year), coupled with extreme fluctuations.

The continuity of seedling density between spillover (1984-1986) versus normal operations years (1987-1989) in the NHWZ was also attributed to tributary flooding influences. Although upstream sites, such as the South Canyon quadrat (CR Mile 31R; Figure 4), had little phreatophyte seedling establishment during the summer of 1988, a large tributary flood deposited a silt bed on the lower Kanab Creek quadrat (CR Mile 144R) and initiated extensive germination of Tamarix ramosissima (Figure 5). Seedling density in the NHWZ reached 21.44 T. ramosissima seedlings/m^2, a value 3.5 times greater than any other recorded during the period of study. This outlier was excluded from analyses.

A non-significant trend of increased xerophyte seedling density was observed in the Zone 3 (Table 3, figures 2, 3), suggesting that xerophyte germination strategies do not generally depend on flooding. Similarly, facultative phreatophyte species, such as Baccharis sarothroides and Haplopappus acredenius were observed to germinate during the winter months, apparently requiring only winter precipitation, and not flooding, for ecesis.

Distance Effects: Distance from Glen Canyon Dam was used as a covariate in the above analyses, but did not statistically influence seedling density on debris fans (Table 3).

Recruitment Environments: Ecesis of Tamarix ramosissima and other woody and herbaceous species occurred during 1987 and 1988 in tributary-derived, silt-rich sediments deposited in backwater return channels throughout the river corridor and below the $950 m^3/sec$ stage. This pattern was not observed on the quadrats (except the Kanab Creek quadrat noted above) because quadrat census data reflected changes occurring on debris fan deposits (cobble and sand), rather than beach and return channel deposits. An observed, but unverified, positive correlation between sapling density and distance from Glen Canyon Dam in NHWZ fine sediments may be attributed to the combined effects of increased propagule abundance (most phreatophyte seeds are water-dispersed), increased volume of aggraded sediments with distance from the dam, and perhaps decreased erosion of those sediments.

Of particular significance was the rapid proliferation of marsh vegetation in backwaters where post-1986 aggraded sediments accumulated. Between 1987 and 1989, marsh plant species richness rose from 0 to nearly 50 species in backwaters at the Anasazi Bridge (43L), Upper Kwagunt Marsh (CR Mile 56R), and 194.1L. Rapid recolonization of these marshes was noted for Typha spp., Phragmites australis, Carex spp., Scirpus americana, and numerous herbaceous species. Low densities of Salix exigua seedlings were found at the Anasazi Bridge and upper Kwagunt sites in 1987, the first coyote willow seedlings found in the river corridor since 1980. Widespread erosion of these aggraded sediment deposits was observed in 1989, a drought year with little tributary flooding and large variance in daily discharge.

Sapling Distribution and Growth

Stage Effects: Sapling density, species composition, and growth rates varied significantly with respect to stage. Mean phreatophyte seedling density was ten-fold greater in the NHWZ as compared to the old high water zone ($p < 0.001$, df = 5,190; Table 4; Figure 6). Tamarix ramosissima saplings dominated the riverside, with dominance shifting to Haplopappus acredenius and, in the old high water zone, Brickellia longifolia saplings. These differences between species gave rise to a significant interaction effect between species and stage (Table 4).

The differential distribution of Tamarix ramosissima saplings by stage was attributable, in part, to decreased survivorship and growth rates on upper terraces. Survivorship was examined by measuring nearest neighbor distances within T. ramosissima sapling stands on NHWZ and Zone 3 terraces at Mohawk Canyon (CR Mile

171L; Figure 7). Mean nearest neighbor distance between 2 year-old T. ramosissima saplings decreased 4.5cm/yr in the Zone 3, but only 1.62cm/yr in the NHWZ from 1988 to 1989 (Figure 7A). This indicated that sapling survivorship was greater on the Zone 3 terrace as compared to the NHWZ terrace.

Tamarix ramosissima sapling growth was assessed at the South Canyon site (CR Mile31R) and the Mohawk Canyon site (171L). Marked saplings in the NHWZ at South Canyon grew, on average, more than 16cm during the 1988 growing season, while Zone 3 saplings grew less than 6.5cm during the same time period (analysis of variance $F = 6.497$, $p = 0.013$, df = 1,85; Figure 8). The stunted, desiccated appearance of Zone 3 seedlings suggested that stage-related growth differences were attributable to reduced soil moisture availability. Sapling starting height in May, 1988 proved to be a significant covariate overall ($F = 4.354$, $p = 0.040$, df = 1,85), with regression effects not significantly different within terraces ($F = 1.039$, $p > 0.50$, df = 1,40 for NHWZ; and $F = 3.025$, $p > 0.10$, df = 1,44 for the Zone 3).

Data from the Mohawk Canyon site also demonstrated stage-related differences in Tamarix ramosissima sapling growth. There, the mean height of two year-old T. ramosissima saplings was significantly greater in the NHWZ (mean = 86.2cm) than in the Zone 3 (mean = 27.6cm; Welch's approximate $t = 33.158$, $p < 0.001$, $v = 145.657$; Figure 7B).

Substrate Texture Effects: Sapling density and diversity were strongly influenced by substrate texture, as demonstrated by analysis of 49 50m2 transects below the $1150m^3$/sec stage in 1988 (Table 5). Sapling densities were significantly greater in silt-rich substrates than in cobble or talus deposits, and were lowest in sand and bedrock substrates. In contrast, sapling species richness was lowest in sand, intermediate in silt, bedrock and talus deposits, and highest in cobble substrates.

Analyses of marked Tamarix ramosissima and Baccharis salicifolia saplings, and young Salix exigua ramets in silty sand substrates in the NHWZ revealed the following growth pattern during 1988 (Table 6; Figure 9):

Baccharis salicifolia > Salix exigua > Tamarix ramosissima

This same pattern of differential growth rate between species was maintained on cobble bars, but was overall significantly reduced in the coarser substrate. Although the order of growth remained similar between the two substrate types, B. salicifolia growth was disproportionately reduced on cobble bars, creating a significant interaction between species and substrate (Table 6).

Canopy Effects: Recruitment of all major phreatophyte species except Prosopis glandulosa, occurred in unshaded sites, with only 7.8% of 412 seedlings (10 species) found beneath the canopies of mature plants. The mean distance from a phreatophyte sapling to the nearest mature-plant canopy edge was 2.80m (n = 412, se = 0.196m). Furthermore, the distance between saplings and canopy edges differed significantly between phreatophyte species (Figure 10). Tessaria sericea, Acacia greggii and Salix exigua occurred significantly closer to canopy edges, while all four Baccharis species, Tamarix ramosissima, and Prosopis glandulosa were intermediate in distance from canopy edges, and Brickellia longifolia occurred farthest from canopy edges (analysis of variance $F = 4.483$, $p = 0.000$, df = 9, 404). Subsequent observations suggested that the proximity of T. sericea and S. exigua to canopy edges was attributed to clonal architectural strategies rather than seedling habitat requirements.

Effects of Distance Downstream from Glen Canyon Dam: Quadrat data demonstrated a non-significant positive correlation between sapling density and distance downstream from Glen Canyon Dam (MANOVA Wilk's $F = 1.616$, $p = 0.204$, df = 2,93). A larger data set (Stevens 1989b) revealed that this pattern was significant ($p < 0.01$). Analysis of covariance of sapling growth rates in 1988 also revealed a non-significant trend of increased growth with distance downstream ($F = 2.862$, $p = 0.091$, df = 1,800). Both trends may have been attributed to a positive correlation between silt concentration in NHWZ riparian sediments and distance from the dam.

Riparian Plant Community Development

Comparison of 1984 to 1988 Data: Quadrat monitoring data between 1984 and 1988 revealed significant changes in riparian plant species composition through time, with differential net increases in density among several plant guilds, including Tamarix ramosissima, other non-clonal phreatophytes (i.e. Baccharis spp., Prosopis glandulosa, Brickellia longifolia, etc.), and clonal phreatophytes (i.e. Salix exigua, Tessaria sericea and Aster spinosus), and xerophytes (i.e. Cactaceae, Encelia farinosa, Larrea tridentata), depending on zone (Table 7; Figure 11).

Changes in community composition through time were not uniformly linear between guilds (Figure 12). In the NHWZ xerophyte density remained low while phreatophyte densities increased. Declines in T. ramosissima and clonal phreatophyte densities in 1988 reflect increased mortality of these guilds, probably in response to drought stress. Xerophyte density increased strongly in the Zone 3, while phreatophyte densities (especially clonal phreatophytes) peaked in 1985 and declined under normal dam operations.

Net 1984-1988 increase in the density of woody riparian plants varied significantly between zones ($p = 0.000$; Table 7, Figure 13). Univariate analyses suggested that stem density of Tamarix, other-non-clonal phreatophytes, and probably clonal phreatophytes increased significantly in the NHWZ during the interval of study, but not in the Zone 3. Evidence of recruitment was apparent from analyses of Tamarix ramosissima demography in this system. A cohort "wave" passed through the T. ramosissima size class distributions in the NHWZ during the period of data collection (e.g. figures 4, 5). In contrast to phreatophyte groups, xerophyte density remained low and unchanged in the NHWZ but increased significantly in the Zone 3 (Figure 11).

Comparison of Estimated 1982 and 1988 Data: Comparison of estimates of 1982 mature plant group densities with mature plant group densities in 1984 and 1988 were based on Stevens and Waring's (1988: 236) system-wide estimates of plant mortality data (Table 8). These results should be regarded as tentative because of the many assumptions involved in the calculations. Given that caveat, these data suggested that 1988 riparian plant density recovered to approximately 75% of its 1982 density below the 1700m^3/sec stage. Population recovery from the 1983-1986 flooding varied between species groups. For example, Tamarix ramosissima density increased by 223% from 1982 to 1988. T. ramosissima comprised approximately 8% of the total stem density in 1982, and comprised 20% of the total woody stem density in 1988. Other non-clonal phreatophytes achieved 95% of their pre-flood densities, while clonal phreatophytes achieved only 50% of their former density by 1988. Estimates of xerophyte densities were based on too few species to be reliable. These tentative estimates suggested that recovery is underway and that, as saplings mature, dominance of T. ramosissima in the system will increase. Validity of these patterns was supported by field data and observations.

DISCUSSION

This study of riparian plant community development along the Colorado River revealed significant interactions between dam operations and riparian plant community development and dam operations, including: abiotic and biotic constraints on germination, seedling and sapling distribution, growth, and survivorship; and the direction of riparian vegetation development in this system. In the following discussion we address the effects of dam operations on ecesis, recruitment, and the riparian plant community, with particular emphasis on the changing status of exotic Tamarix ramosissima. Management issues and future monitoring recommendations are then discussed.

Ecesis

Considerable ecesis occurred in the "tidal" portion of the NHWZ (below approximately 800m^3/sec) during "normal dam operations" in 1987 and 1988. Earlier GCES studies suggested that dam operations had little direct effect on NHWZ vegetation, but these conclusions were based on evidence gathered during the spillover flooding period. "Normal dam operations" directly affected ecesis and growth in the NHWZ (U.S. Dept. of Interior 1988). Although experimental studies of Waring and Stevens (1988) demonstrated that daily inundation reduced seedling survivorship and sapling growth, some species (notably Tamarix ramosissima and marsh species) have colonized the littoral zone since 1986. Littoral ecesis apparently depended on deposition of tributary-derived sediments along the channel margins because ecesis was prevalent in 1987-1988 (years with spring and summer tributary flooding), but was insignificant in 1989, a drought year. These findings complement the results of Stevens and Waring (1988) who found that flooding and suitable substrates were required for phreatophyte germination. Littoral vegetation may be of considerable value for riverbank stability, but the numerous cutbanks observed in 1989 suggest that this vegetation is at risk because of erosion under "normal operations" (extreme fluctuating discharges).

Most, but not all, riparian phreatophyte species depended on flooding events for germination and establishment, with virtually no ecesis of most phreatophyte species during non-flooding years in the Back Beach Zone. However, this study demonstrated that germination of riparian plants was not solely flood-induced. In addition to flooding, seedling density was influenced by stage, and substrate type, with a non-significant trend of increased density correlated with distance from Glen Canyon Dam. Several species of facultative phreatophytes were found to germinate during the winter months, including Baccharis sarothroides and Haplopappus acredenius. In general, the phreatophyte guild appeared to require flooding for germination, while xerophytes and facultative phreatophytes relied on winter precipitation. Thus in wet winters, all guilds were likely to germinate, while in dry years phreatophyte seedlings predominate. These germination events influenced subsequent riparian plant community composition.

Recruitment

Changes in riparian plant community composition were the result of differential flood-induced recruitment, and to the drought-induced differential mortality. Evidence of recruitment was apparent from analyses of Tamarix ramosissima demography in this system. A cohort "wave" passed through the T. ramosissima size class distributions in the NHWZ during the period of data collection (e.g. South Canyon and Kanab Creek quadrats). Saplings established in the upper terrace zones were apparently dewatered as operations returned to normal in mid-1986. These saplings grew more slowly (Figure 8), and generally appeared drought-stressed, as compared to those growing at the water's edge.

Sapling density, growth, survivorship, diversity, and species composition were influenced by interactions between substrate texture, stage (zone), and soil water holding capacity. Other studies have shown that substrate texture influenced soil moisture (Stevens 1989a, and unpublished data). Silt substrates supported the highest densities of saplings, while cobble bars supported the most diverse communities. Sand deposits were extensively colonized by clonally-expanding phreatophytes, but sand and bedrock substrates hosted the lowest densities and lowest diversity of riparian plants. Sapling growth rates were significantly higher in the NHWZ and in fine-grained sediments. Substrate influence over plant community structure has also been described in the developing shoreline plant communities around Lake Powell (G. Waring, pers. obs.).

Interspecific differences in sapling growth, distribution and tolerance of shading were found between the dominant riparian species studied. For example, Baccharis salicifolia saplings consistently grew faster than Salix exigua and Tamarix ramosissima saplings. The proportions of T. ramosissima and Brickellia longifolia in the community were negatively correlated with respect to stage. Lastly, clonal phreatophyte ramets maintained the closest proximity to canopy edges, while species such T. ramosissima and Brickellia longifolia were consistently found only in fully exposed sites.

Riparian Plant Community Dynamics

Dam operations interact with natural characteristics of various species to shape the structure and composition of riparian vegetation. The ramifications of 1983-1986 flooding will require at least a decade and probably longer to become manifest; however, some patterns based on recruitment data can be suggested. Present levels of increasing phreatophyte sapling density in the NHWZ assures that, under normal operations, riparian vegetation will become increasingly dense, particularly in wider reaches. However, dam operations and drought apparently result in coarsening substrate texture, and are likely to reduce the potential for establishment of phreatophyte species. The low sapling density in narrow reaches of the river suggest that a much longer period of time (decades) will be required to achieve pre-1983 densities and cover. Lastly, marsh development, which depends on discharge, tributary sediment contributions and channel width/depth ratio, will proceed rapidly provided that erratic high discharges are minimized (Schmidt et al. in prep.).

The recovery of riparian vegetation from 1983-1986 flooding varied between plant groups. A conservative estimate of 75% recovery was based on 1983-1984 mortality estimates (Stevens and Waring 1988: 236). Vegetation recovery has been curvilinear for some plant groups, such as Tamarix ramosissima and clonal phreatophytes, which proliferated rapidly at the end of the 1983-1986 flooding episode and which declined under normal operations, probably because the Zone 3 was dewatered and saplings became water-stressed. Non-clonal phreatophyte density in the NHWZ, and xerophyte density in the Zone 3, increased relatively uniformly during this five year study.

Tamarisk Population Dynamics: Establishment and maintenance of Tamarix ramosissima was strongly influenced by dam operations and ecesis always occurred in association with mainstream or tributary flooding and silt deposition. Tamarisk ecesis occurred under spillover flooding from 1984-1986 in the Zone 3, and in the NHWZ during normal dam operations. The Zone 3 was colonized, albeit briefly, by T. ramosissima as a result of 1984-1986 flooding, but T. ramosissima colonization in the NHWZ has continued under normal operations. Although most colonization failed in the Zone 3, T. ramosissima will in all likelihood continue to increase in the NHWZ, particularly below the 950m^3/sec stage. Suitable germination sites are made available through any flooding action or other rapid change in discharge . As such, germination site availability increased not only following subsidence of extreme discharges, but also under the fluctuating discharge regime of normal dam operations. Present, extreme fluctuations appear to facilitate the continued spread of this exotic. Also, although as yet undocumented, increasing tamarisk density along the river may serve to increase propagule abundance, and therefore increase the rate and extent of tamarisk colonization in tributaries. In this manner, dam operations may indirectly influence plant community dynamics in unregulated tributary riparian habitats.

Tamarix ramosissima dominance along the river is likely to increase with the maturation of saplings established during 1983-1986, and under subsequent normal operations. The success of T. ramosissima in this system has been attributed to its phenomenal fecundity and its ability to withstand inundation and desiccation stress, as compared to native species (Stevens 1989a and in press). Under optimal conditions, a tamarisk sapling requires about 10 years to reach the stature of a small tree, and sites with high T. ramosissima sapling densities (e.g. the South Canyon quadrat at CR Mile 31R, and the Kanab Creek quadrat, CR Mile 144R) will be visually dominated by tamarisk by about 1995 if left undisturbed. Once established, T. ramosissima is extremely difficult to eradicate (Kunzman et al. 1989). Because no phreatophyte species establish beneath the canopies of mature plants, subsequent establishment of other, non-clonal phreatophytes will be slow or unlikely until the habitat is once again disturbed. Because the sites studies here are cobble-dominated debris fans, and because rhizomatous phreatophytes have difficulty invading cobble substrates, debris fans near the river's edge will remain dominated by tamarisk, not by clonal species. Erratic flooding regimes are believed to favor tamarisk persistence as well as establishment over native species. Stevens and Waring (1988) recommended using winter and early spring flooding discharges to facilitate the establishment of native phreatophytes.

Management of riparian habitat is a major concern throughout the United States. Wetlands, including riparian habitats, are among the most biologically productive and recreationally valuable of terrestrial lands. Unfortunately, riparian habitats are poorly managed because of a lack of concern, conflicting management priorities, and inadequate information (Johnson et al. 1985). Despite the fact that riparian habitat often comprises less than 3% of the landscape in the Southwest, it often supports more than 70% of the species occurring in that landscape. Riparian vegetation serves as an intermediary state variable between abiotic components and higher trophic levels, and plays a significant role in both aquatic and terrestrial ecosystem dynamics, as well as providing erosion control and shade for recreationists.

Management of the biologically productive riparian habitat along the Colorado River in the Grand Canyon is the responsibility of the National Park Service, the Bureau of Reclamation, and the U.S. Fish and Wildlife Service. Any decision regarding dam operating criteria will influence the future development of the riparian plant community, its associated faunae, other ecological processes, and river recreation. Maximizing biological potential is one of several options that deserves consideration in this system because riparian habitat is biologically productive and is seriously threatened throughout in the region.

In order to understand how to achieve that biological potential, more detailed understanding of natural plant community dynamics in unregulated tributaries will be required. Ecological stability afforded by discharge regulation probably favors native vegetation in this system, particularly clonal phreatophytes and macrophytes. Erratic, highly fluctuating flows favor recruitment and differential survival of exotic Tamarix ramosissima. Riparian plant succession is probably proceeding in this system in the NHWZ because of the comparative stability afforded by regulated discharge, and is probably slowed or reversed by erratic discharge regimes which limit silt deposition and the availability of germination sites under normal dam operations (Stevens 1989a).

The Zone 3 is somewhat removed from the vagaries of normal dam operations, lying above the maximum powerplant discharge stage. Only bypass flooding can affect vegetation development in that zone. Because germination is facilitated by flooding, recruitment of deep-rooted phreatophyte species such as Populus fremontii, Prosopis glandulosa, or Fraxinus pennsylvanica is unlikely in the Zone 3 without an intentional establishment program. Such a management policy could be used to prevent or retard erosion of pre-dam sediments which lie above the Zone 3 and sometimes protect cultural resource sites.

The relationship between riparian vegetation and sediment deposit stability is an important management question which can only be resolved with detailed field experimental effort. The silt deposits that are required for ecesis of most phreatophyte tend to be more resistant to erosion than do sand deposits in which germination is rarely successful (Stevens 1989a). Future studies should consider the effects of plant cover, stem density, survivorship, longevity, and growth and duff accumulation rates between species used for stabilization. Slope and soil moisture play significant roles in riparian plant growth and substrate stability.

CONCLUSIONS

1. Phreatophyte ecesis (germination and establishment) was strongly influenced by dam operations, with more-or-less continuous germination in the NHWZ and episodic (flood-related) ecesis in the Zone 3. In contrast, xerophyte ecesis was affected by flooding regimes prior to 1987, but not by normal dam operations.

2. Considerable ecesis took place in the "tidal" zone below the approximate $800 m^3/sec$ stage under "normal operations" during 1987-1988. Such vegetation may be of considerable value for riverbank stability, but is apparently at risk under "normal operations" (extreme fluctuating discharges).

3. Significant interactions between dam operations, flooding regimes, stage, substrate types, and interspecific differences affected the distribution and growth of phreatophyte saplings.

a. Years with normal dam operations, coupled with tributary contributions of fine sediments, provided suitable germination habitats for some riparian species (e.g. 1987-1988); however, years with little tributary sediment input and extreme fluctuations (e.g. 1989) resulted in little germination of riparian phreatophytes.

b. Saplings grew faster and maintained higher densities in silty sand in the NHWZ, as compared to other substrates or the Zone 3.

c. Interspecific differences in desiccation and inundation tolerance favor different species in different settings. Selectively advantaged by its fecundity and stress tolerance, Tamarix ramosissima sapling density is increasing in the NHWZ under normal operations.

4. By 1988, riparian vegetation had recovered to approximately 75% of its pre-1983 density on debris fans; however, dominance by Tamarix ramosissima will probably increase as saplings established since 1983 mature and begin to dominate this system.

Table 1: Twenty quadrats in the Colorado River corridor in Grand Canyon National Park, Arizona, and dates quadrats were censused, 1984-1988.

QUADRAT	COLORADO RIVER MILE/SIDE	DATES CENSUSED (MONTH/YR)
South Canyon	31.0R	06/84,08/84,06/85,04/86, 09/86,10/87,05/88,09/88
Lower 34 Mile	34.0R	06/84,04/86,05/88
Buck Farm	41.0R	06/84,04/86,09/86,05/88, 09/88
Lower Anasazi Bridge _Tamarix_	43.5L	10/80,10/82,09/83,06/84, 04/86,09/86,05/88
48-Mile Quadrat	48.4R	10/80,10/82,06/84,05/88
Upper Little Nankoweap	51.5R	06/84,04/86,09/86,10/87, 05/88,09/88
Lower Little Nankoweap	52.0R	06/84,08/84,06/85,04/86, 09/86,10/87,05/88,09/88
Tanner Canyon	68.0R	06/84,05/88,09/88
104-Mile Canyon	104.0R	06/84,06/85,04/86,09/86, 05/88,09/88
119-Mile Rapid	119.0L	07/84,08/84,06/85,04/86, 09/86,05/88,10/88
122-Mile Canyon	122.1R	07/84,06/85,04/86,05/88
Upper Galloway Canyon	131.5R	07/84,06/85,04/86,09/86, 10/87,05/88,10/88
Upper Deubendorff Rapid	131.7R	07/84,04/86,09/96,05/88, 10/88
Doris Rapid	138.0L	07/84,06/85,05/88,10/88
Fishtail Rapid	139.0R	08/84,06/85,05/88,10/88
Kanab Creek	144.0R	07/84,08/84,06/85,04/86, 09/86,05/88,10/88

	Stevens and Waring, Riparian Vegetation	
Mohawk Canyon	171.0R	07/84,08/84,06/85,04/86, 09/86,10/87,05/88,10/88
Lower Lava	180.0R	07/84,04/86,09/86,05/88, 10/88
Parashant Canyon	198.5R	07/84,06/85,04/86,09/86, 05/88,10/88
Upper Granite Park	208.0R	07/84,08/84,04/86,09/86, 05/88,10/88

Table 2: Common riparian dominant species discussed in this report, in alphabetical order (taxonomy of Phillips et al. 1987).

GENUS	SPECIES	FAMILY	GROUP*
Acacia	greggii	Fabaceae	X
Alhagi	camelorum	Fabaceae	P
Aster	spinosus	Asteraceae	P
Baccharis	brachyophylla	Asteraceae	P
Baccharis	emoryi		P
Baccharis	salicifolia		P
Baccharis	sarothroides		P
Brickellia	longifolia	Asteraceae	P
Celtis	reticulata	Ulmaceae	P
Cercis	occidentalis	Fabaceae	P
Encelia	farinosa	Asteraceae	X
Haplopappus	acredenius	Asteraceae	P
Larrea	tridentata	Xygophyllaceae	X
Phragmites	australis	Poaceae	M/P
Prosopis	glandulosa	Fabaceae	P
Salix	exigua	Salicaceae	P
Salix	gooddingii		P
Tamarix	ramosissima	Tamaricaceae	P
Typha	dominica	Typhaceae	M
Typha	latifolia		M
Tessaria	sericea	Asteraceae	P

* M - Macrophytes, P - Phreatophytes, X - Xerophytes

Table 3: Multiple analysis of variance of perennial riparian seedling and mature plant densities on 20 quadrats encompassing two floodzones in the Colorado River corridor in Grand Canyon National Park, Arizona. Response variables included natural log-transformed total seedling density (SD) and mature plant density (AD). Predictor variables included discharge year (flood-year or non-flood-year) and stage (< 40,000cfs or 40,000-60,000cfs terraces), with distance from Glen Canyon Dam as a covariate.

SOURCE	WILK'S LAMBDA APPROX. F	p	df	SIGNIFICANCE OF RESPONSE VARIABLES
Year	21.934	0.000	2,93	SD**, AD***
Stage	3.803	0.026	2,93	AD*, SD t
Year x Stage	4.094	0.020	2,93	AD*
Covariate (Distance)	1.616	0.204	2,93	SD t

t p < 0.01, * p < 0.05, ** p < 0.010, *** p < 0.001y

Table 4: Analysis of variance table of log-transformed sapling density of 6 perennial riparian plant species in 6 floodzones (overbank terraces) in the Colorado River corridor in Grand Canyon National Park, Arizona. Data from 114 2m-wide belt transects (Stevens 1989b).

SOURCE	F	p	df
Zone	2.765	0.000	5, 190
Species	6.991	0.000	6, 190
Zone x Species	1.730	0.032	20, 190

Table 5: Sapling density and species richness of dominant woody riparian plant species in 5 substrate types in the Colorado River corridor, Grand Canyon National Park, Arizona. Response variables were log-transformed seedling density and untransformed species richness, and predictor variable was substrate texture (Wilk's lambda approximate $F = 13.555$, $p < 0.001$, $df = 4,48$). Lower case letters signify results of univariate oneway AOV range test groupings on log-transformed seedling density and untransformed species richness.

SUBSTRATE TYPE	NO. QUADRATS SAMPLED	MEAN SAPLING DENSITY/m2 (SD)	MEAN SAPLING SPECIES RICHNESS
Silt	7	3314.4 (4364.9)a	1.86 (1.464)xy
Sand	11	9.9 (12.973)b	1.18 (1.168)x
Cobble	13	35.6 (26.691)c	4.92 (2.326)z
Talus	9	45.1 (40.968)c	3.89 (2.369)yz
Bedrock	9	11.8 (8.715)bc	3.11 (1.167)xyz

Table 6: Analysis of covariance table of sapling growth of three woody phreatophyte species in sandy silt versus cobble substrates in the Colorado River riparian corridor in Grand Canyon National Park, Arizona (pooled data from 50 transects).

SOURCE	F	p	df
Species	27.252	0.000	2,800
Substrate Type	188.964	0.000	1,800
Covariates:			
Distance from Dam	2.862	0.091	1,800
Initial Height	43.893	0.000	1,800

Table 7: Multiple analysis of covariance table of net change in mature riparian woody perennial plant densities between 1984 and 1988 on 20 quadrats along the Colorado River in Grand Canyon National Park. Response variables were plant density/m^2 of four groups, including *Tamarix ramosissima* (Tara), other non-clonal phreatophytes (ONCP), clonal phreatophytes (CP), and xerophytes (X). Predictor variables were zone (New High Water Zone versus the 1200-2500 m^3/sec zone), with a covariate of distance from Glen Canyon Dam.

UNIVARIATE F TESTS:

SOURCE	WILK'S APPROX. F	p	DF	SIGNIFICANCE OF RESPONSE VARS.
Zone	7.268	0.000	4,26	Tara**, ONCP t, CP nsd, X**
Mile (Covar.)	0.684	0.609	4,26	All nsd

nsd = no statistical difference; t(rend) = $p < 0.10$; ** $p < 0.01$

Table 8: Mean riparian plant densities from 1982 (estimated from Stevens and Waring, 1988: 236 mortality estimates), 1984 and 1988 below the $1700 m^3/sec$ stage in the Colorado River corridor, Grand Canyon National Park, Arizona.

PLANT GROUP	ESTIMATED MEAN 1982 DENSITY/m^2	MEAN 1984 DENSITY/m^2	MEAN 1988 DENSITY/m^2
Tamarix ramosissima	0.107[a]	0.062	0.240
Other Non-Clonal Phreatophytes	0.296[b]	0.100	0.280
Clonal Phreatophytes	0.955[c]	0.198	0.492

a - mean total mortality estimate for *T. ramosissima* = 41.9%
b - mean total mortality estimate for other non-clonal phreatophytes = 66.3% based on mortality estimates for 7 species
c - mean total mortality estimate for clonal phreatophytes = 79.22% based on mortality estimates for 5 species

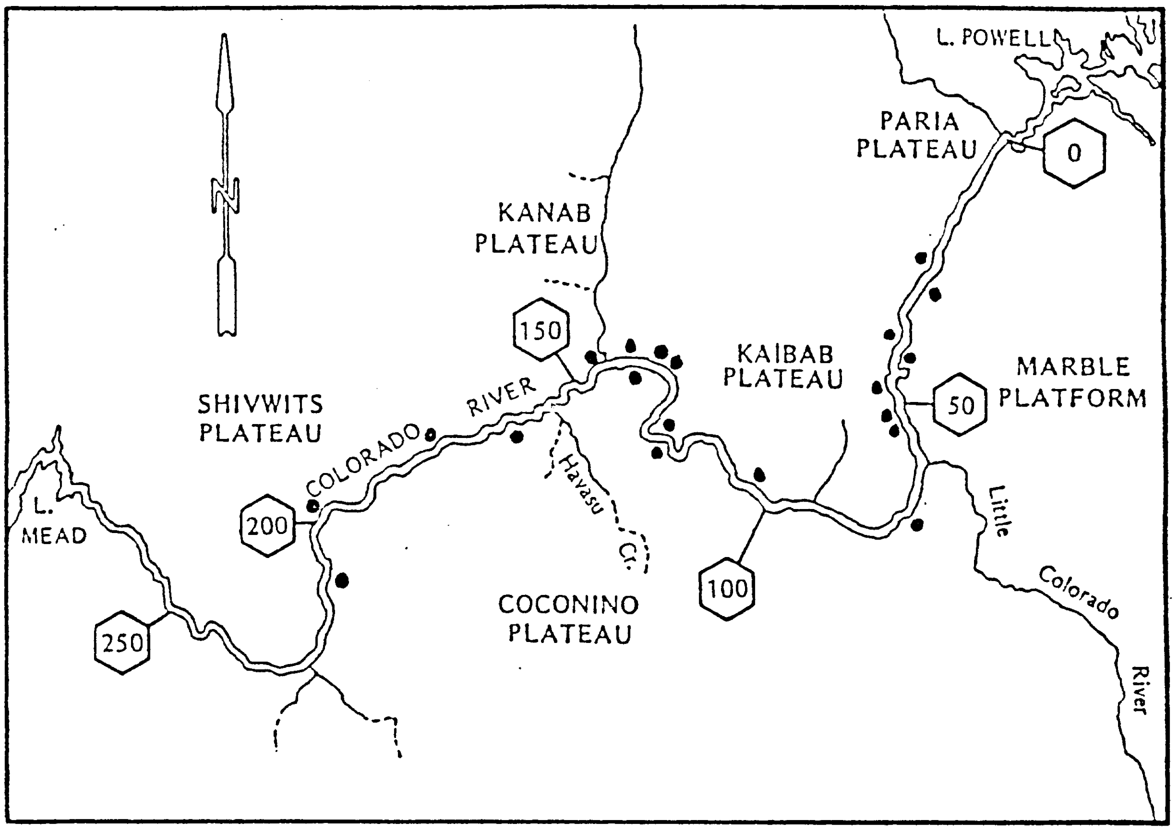

Figure 1: Map of quadrats along the Colorado River in Grand Canyon National Park, Arizona censused in this study.

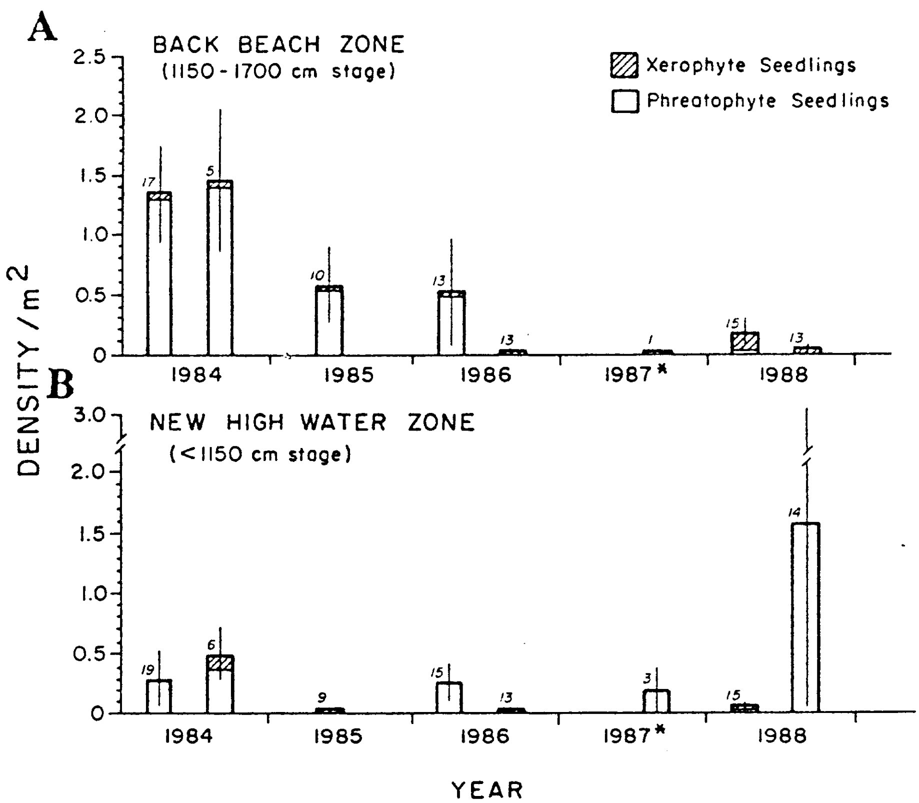

Figure 2: Mean phreatophyte and xerophyte seedling densities/m^2 in the New High Water Zone <1150cms stage) and the "Back Beach" Zone (1150-1700cms stage) on quadrats censused from 1984 through 1988 in the Colorado River in Grand Canyon National Park, Arizona. Error bars are +- 1 se.

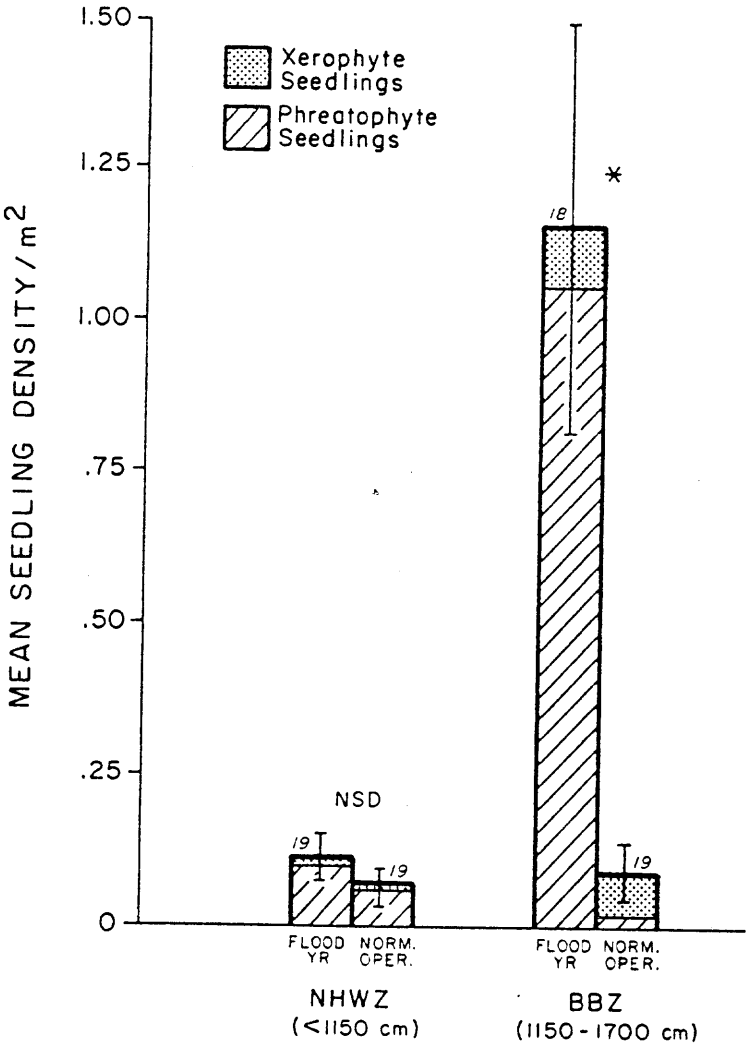

Figure 3: Mean phreatophyte and xerophyte seedling densities/m^2 during flood versus non-flood years from 1984 through 1988 in the Colorado River in Grand Canyon National Park, Arizona. Error bars are +- 1 se; nsd = not statistically different; * = $p < 0.05$.

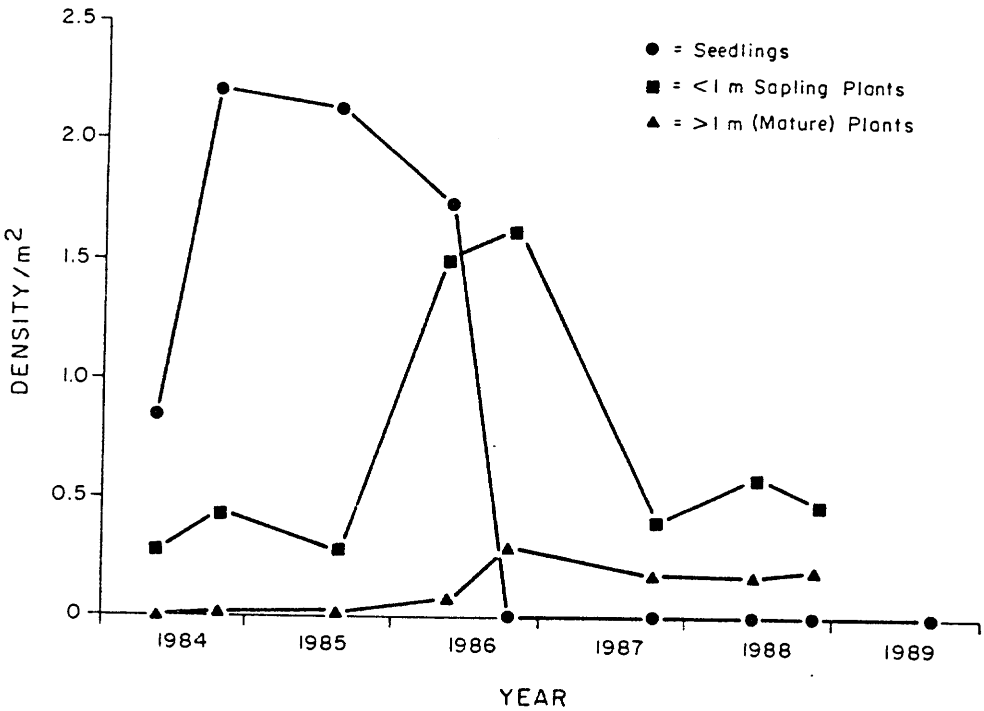

Figure 4: <u>Tamarix</u> <u>ramosissima</u> seedling, sapling, and mature plant density/m^2 on the South Canyon quadrat (CR Mile 31R) in Grand Canyon National Park, Arizona, 1984-1989.

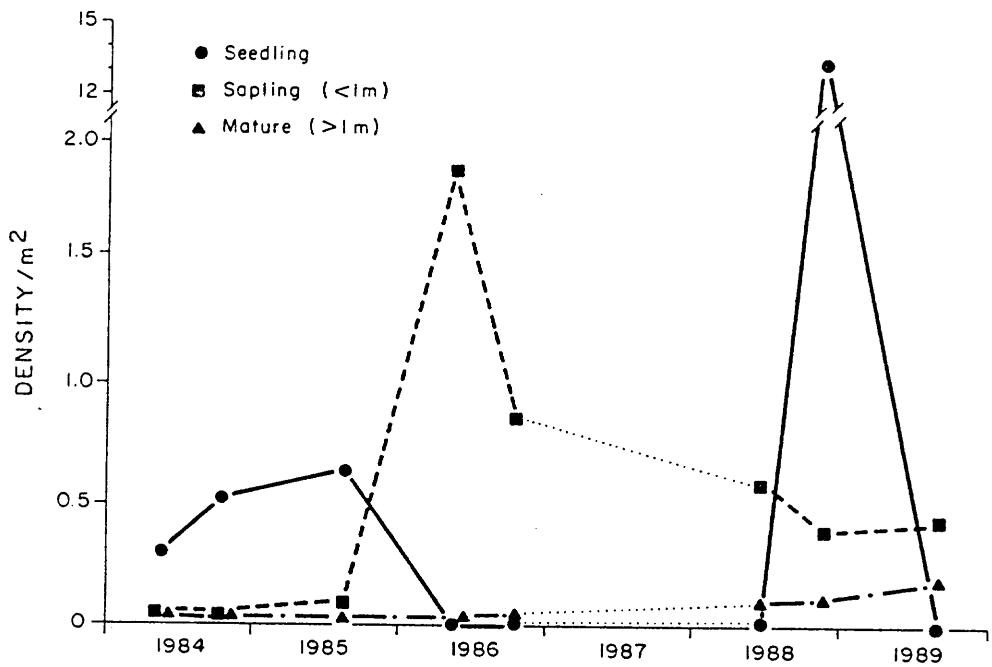

Figure 5: _Tamarix_ _ramosissima_ seedling, sapling, and mature plant density/m^2 on the Kanab Creek quadrat (CR Mile 144R) in Grand Canyon National Park, Arizona, 1984-1989.

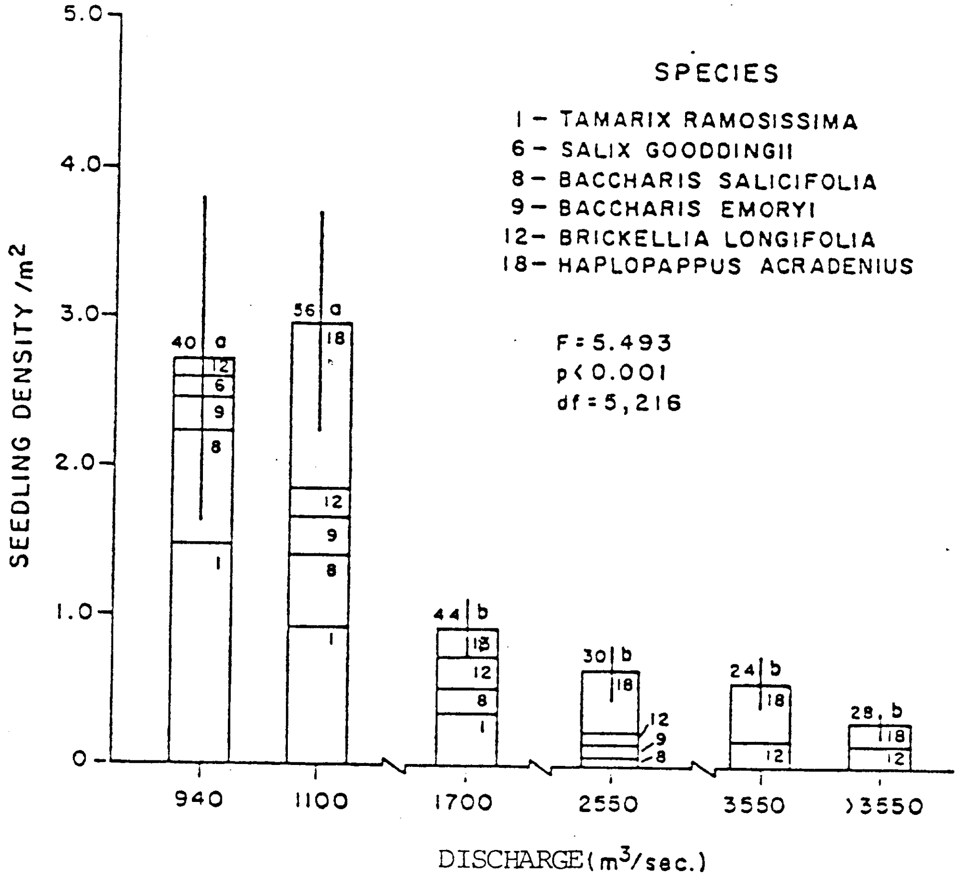

Figure 6: Common riparian phreatophyte densities/m^2 on channel margin deposits in 1987 along the Colorado River in Grand Canyon National Park, Arizona. Lower case letter signify univariate range test comparisons. Error bars are +- 1 se.

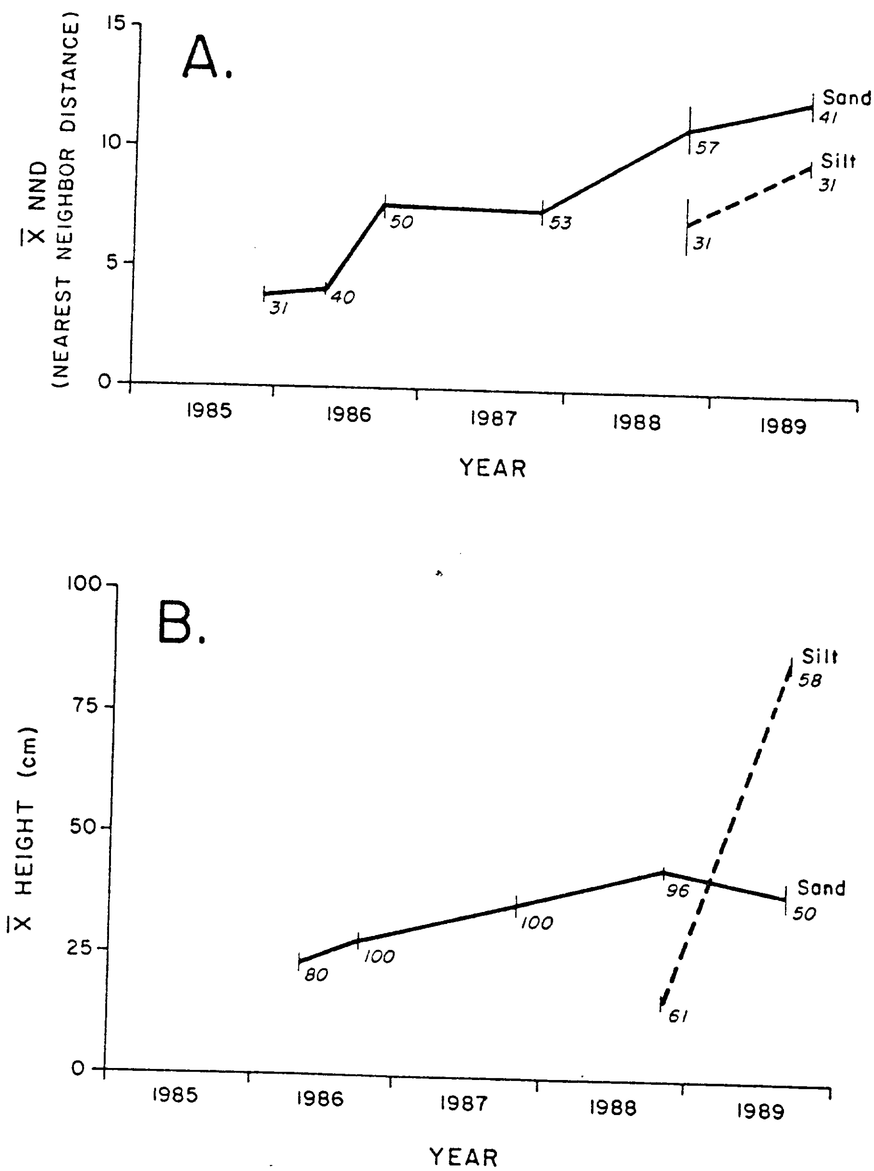

Figure 7: A. Mean <u>Tamarix ramosissima</u> sapling nearest neighbor distances and B. mean <u>Tamarix ramosissima</u> sapling height from 1985 through 1989 at the mouth of Mohawk Canyon (CR MIle 171L) in Grand Canyon National Park, Arizona. Error bars are +- 1 se.

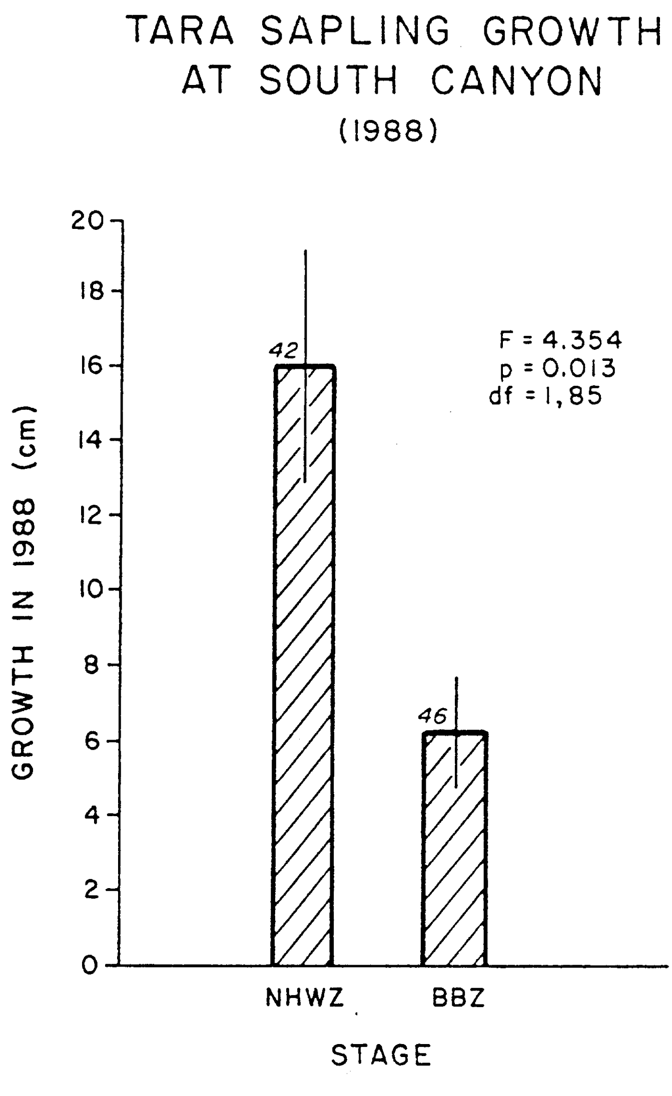

Figure 8: Mean Tamarix ramosissima sapling growth in the New High Water Zone (< 1150cms = NHWZ) versus the "Back Beach Zone (1150-1700cms = BBZ) during the 1988 growing season at South Canyon (CR Mile 31R) in Grand Canyon National Park, Arizona. Error bars are +- 1 se.

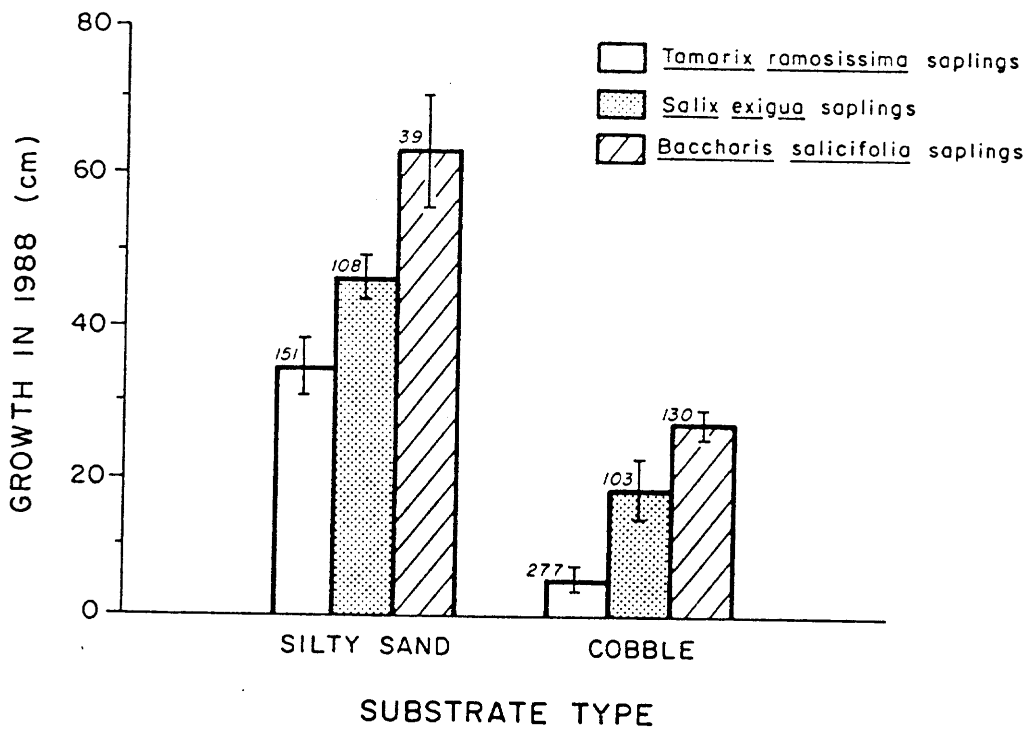

Figure 9: Mean sapling height gain of three species of common phreatophytes in silty sand versus cobble substrates in 1988 in the Colorado River corridor, Grand Canyon National Park, Arizona. Error bars are +-1 se.

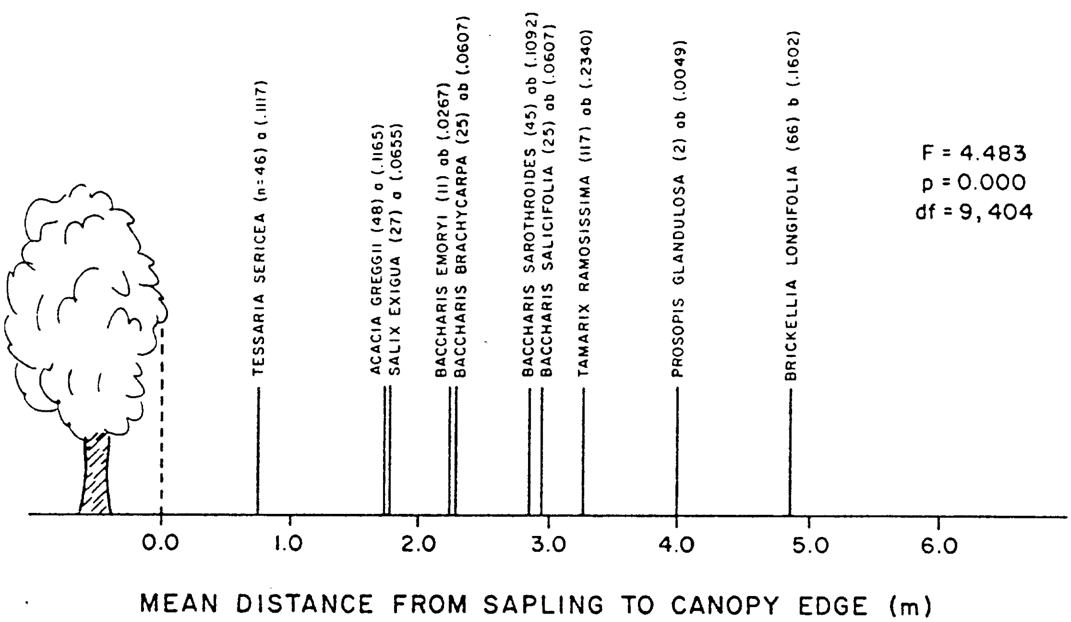

Figure 10: Mean distance of common phreatophyte species saplings to the nearest mature-plant canopy edge. Numbers in parentheses are sample size, and lower case letters signify results of univariate range tests.

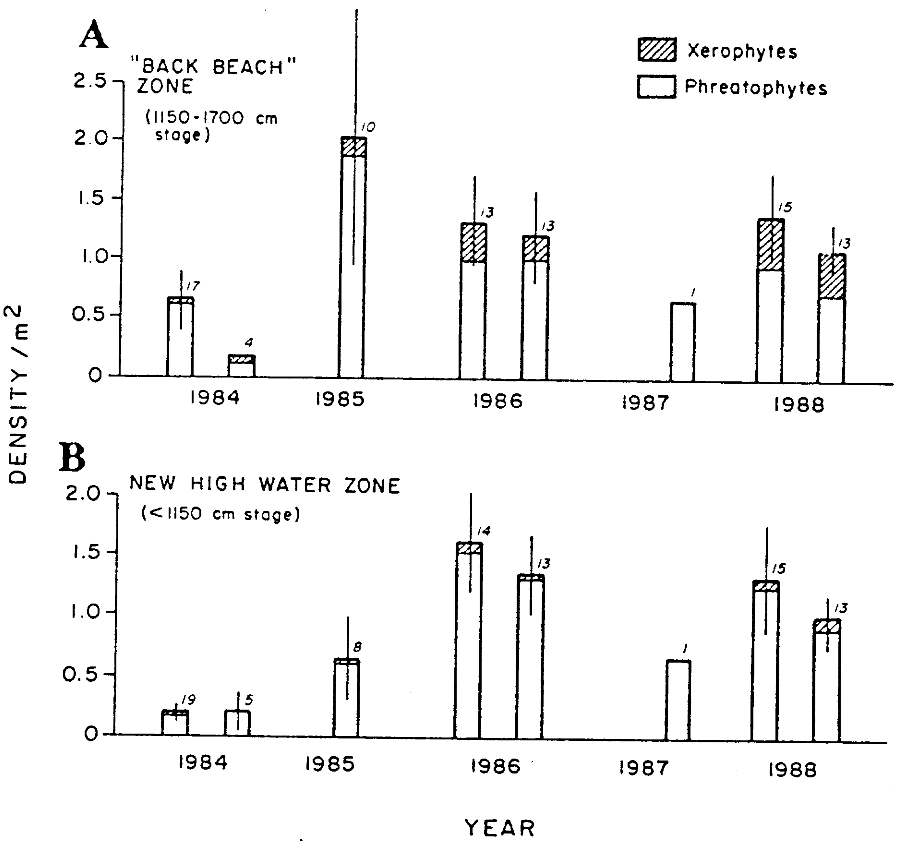

Figure 11: Mean densities/m^2 mature phreatophytes and xerophytes in the New High Water Zone <1150cms stage) and the "Back Beach" Zone (1150-1700cms stage) on quadrats censused from 1984 through 1988 in the Colorado River in Grand Canyon National Park, Arizona. Error bars are +- 1 se.

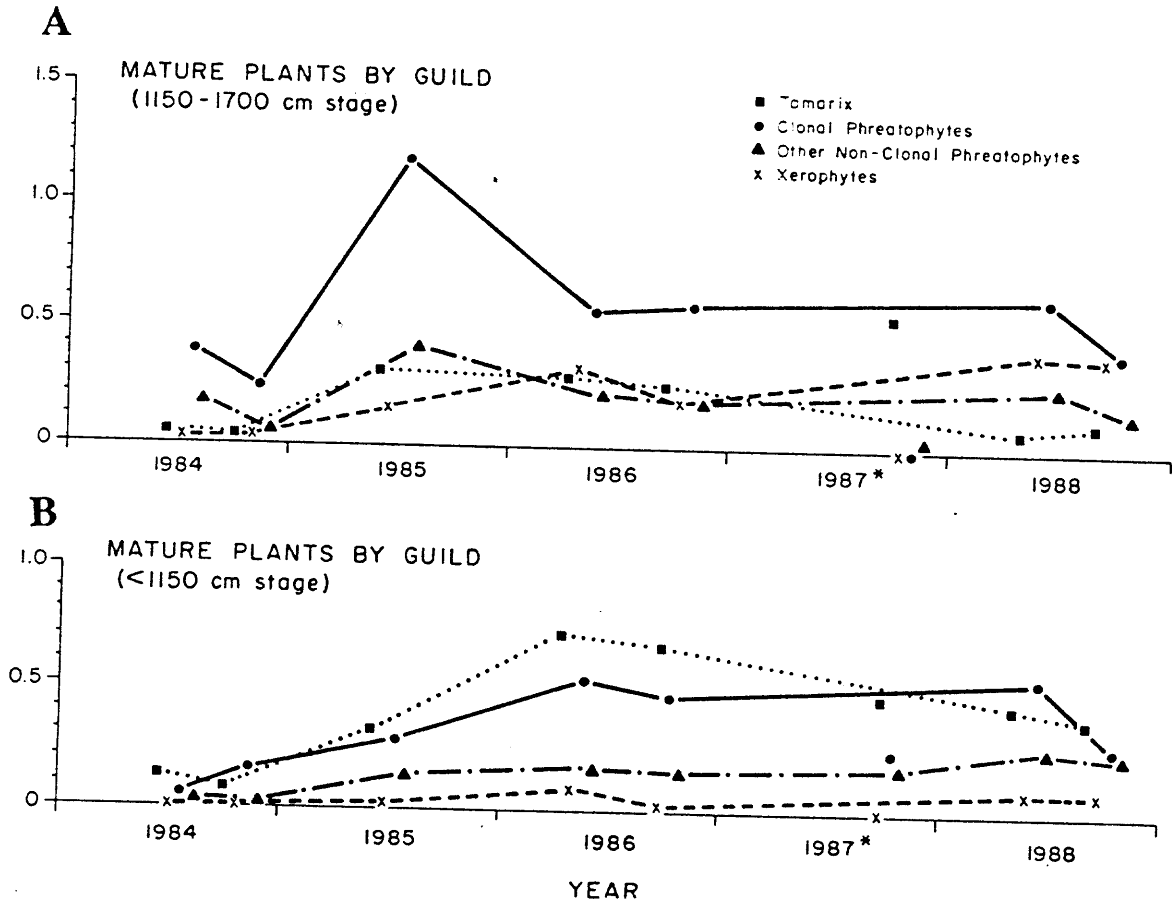

Figure 12: Mean mature-plant densities/m^2 of four groups of woody perennial riparian plants, including Tamarix ramosissima, other non-clonal phreatophytes, clonal phreatophytes, and xerophytes, in the New High Water Zone <1150cms stage) and the "Back Beach" Zone (1150-1700cms stage) on quadrats censused from 1984 through 1988 in the Colorado River in Grand Canyon National Park, Arizona.

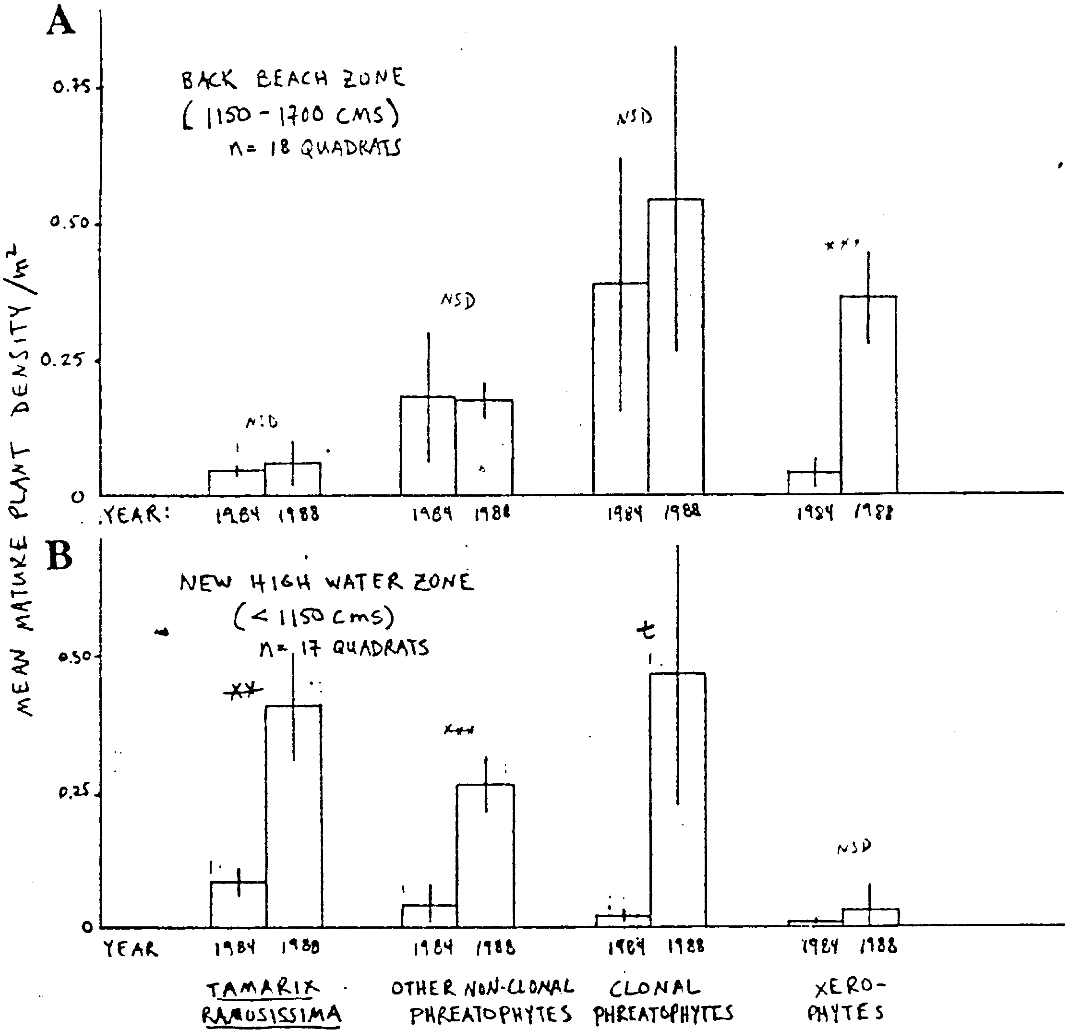

Figure 13: Mean mature-plant densities/m^2 of four groups of woody perennial riparian plants, including <u>Tamarix ramosissima</u>, other non-clonal phreatophytes, clonal phreatophytes, and xerophytes, in the New High Water Zone <1150cms stage) and the "Back Beach" Zone (1150-1700cms stage) in 1984 and 1988 on quadrats in the Colorado River in Grand Canyon National Park, Arizona. Bars are +- 1 se.

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CHAPTER VII: MANAGEMENTCONSIDERATIONS

The effects of Glen Canyon Dam operations are under study by the National Park Service and Northern Arizona University to ascertain whether daily fluctuating discharge patterns affect riparian vegetation. Several topics are discusssed in this preliminary report. The following conclusions are drawn from these preliminary results:

1. Reduced flooding frequency after completion of Glen Canyon Dam in 1963 allowed fluvial marshes to form in low velocity channel margin environments in wide reaches. Marshes were scoured by spillover flooding in 1983 and have begun to redevelope since 1987. Approximately 146 wet and 954 dry fluvial marshes occur in the Colorado River corridor downstream from Lees Ferry, Arizona. Total marsh area was conservatively estimated at 25.8ha, with 30% as wet marsh, dominated by Typha domingenisi, Juncus spp. and Scirpus spp. Dry marsh dominants included Phragmites australis and Equisetum laevigatum. Riverside marshes in this system were generally small, typically less than 0.5 ha, with wet marshes significantly larger than dry marshes. Mean standing crop and estimated productivity of fluvial marshes in this system was 0.74 kg/m^2 and 147.8 g $C/m^2/yr$, respectively, values about 6% reported for marshes. Low productivity may be due to reduced duff accumulation and damage to vegetation (flattening and silt-coated) by high daily flows. Marsh assemblage composition and succession was related to sediment distribution and discharge, with wet marshes requiring a frequency of daily inundation between 0.4 and 0.9. More than 95% of the wet marsh vegetation in this system lies between the 283 m^3/sec (10,000 cfs) and 566 m^3/sec (20,000 cfs) stages. While fluvialmarshes redevelop rather quickly after flooding events (e.g. 1983-1986), obligate marsh animal populations may not be as resilient. Willowflycatcher, which depend on marsh habitats, are believed to be nearly extirpated from this system.

2. Riparian seedling establishment was greatest in the New High Water Zone and was dominated by herbaceous species there. Seedling density varied as a function of particle size, and differed between plant groups (xerophytes and phreatophytes) in wide versus narrow channels. Tamarix ramosissima seedling density was low in 1991, but limited establishment suggests that this species may be capable of continuing to colonize the river corridor under fluctuating flow regimes.

3. River stage was demonstrated to affect plant water potential for pre-dawn Salix exigua, a ubiquitous riparian phreatophyte in the Colorado River corridor. Further studies willdetermine whether similar patterns apply to Tamarix ramosissima and growth of both species.

4. In addition, studies of long-term vegetation quadrats, Old High Water Zone phreatophyte growth, and the status of listed, endemic and non-native species are underway. Thus far, no plants species appear to be at risk from dam operations; however, several previously unrecorded non-native species are colonizing the river corridor, including Erianthus ravennae, a large Eurasian bunchgrass. Prompt action may prevent this species from successfully invading the river corridor.

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