A STUDY OF DEVELOPING RIPARIAN COMMUNITIES ALONG THE SHORELINE OF LAKE POWELL, ARIZONA AND UTAH

FINAL REPORT

GWENDOLYN L. WARING
MUSEUM OF NORTHERN ARIZONA
FLAGSTAFF, ARIZONA

CONTRACT NO. CA-1463-5-0001

FEBRUARY 1, 1992

1988 TO 1991

DRAFT

TABLE OF CONTENTS

ABSTRACT

The riparian plant community along Lake Powell's shoreline is dominated by the nonnative *Tamarisk ramosissima*, with rarer occurrences of native riparian species including *Baccharis salicifolia*, *Baccharis emoryi*, *Salix gooddingii*, *Populus fremontii*, *Brickellia longifolia* and *Tessaria sericea*. This young community was established in the early 1980's when Lake Powell reached full pool. As the lake elevation has subsequently dropped, these plant communities have continued to persist despite decreased water availability. Although plant growth rates are limited by drought conditions, mortality has been remarkably low. These patterns suggest that the extensive shoreline of Lake Powell can support a riparian ecosystem.

Field experiments revealed that native riparian plant species can persist in the presence of the nonnative tamarisk, which suggests that management efforts to enhance the diversity of these communities will be possible.

A census of animal species (amphibians, reptiles, mammals, birds and insects) revealed that more than 70 associated vertebrate and invertebrate taxa are associated with shoreline tamarisk . The diversity of animals associated with these plants is substantial, although lower than that found with native riparian plants or with tamarisk along the Colorado River in Grand Canyon. This lower level of faunal diversity may be influenced by the fact that this is a young, developing ecosystem and severely water-limited.

This represents one of the few studies to detail all major animal taxa associated with an exotic plant species.

The results of this study lead to the prediction that biotic diversity along the shoreline of Lake Powell will increase with time, while also varying inversely with lake elevation, due to the important effects of water availability on productivity.

ACKNOWLEDGEMENTS

Many people volunteered their time and assistance in this project. Special thanks are extended to David Siemens, Larry Stevens, Wendy Stevens, Carol Sue Vann, Rusty Tweed, Dave Duckett, Kim Claypool, Rick Harris, Clive Pennack, Lenore, Neil Cobb and Chuck Wood for assistance in the field and with logistics. Thanks to National Park Service Resource Management for considerable assistance and support, and to Larry Stevens for reviewing the manuscript.

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

Although most major rivers in North America have impoundments and large reservoirs in place, the ecology of the shoreline ecosystems that develop along these reservoirs is poorly understood. There is a pressing need to improve our understanding of these systems because they have the potential to support large communities of riparian plants and animals. Riparian habitat, especially in the Southwest, can support rich floras and faunas, and yet most of this habitat is being lost or altered at a rapid rate. Although large reservoirs with their extensive shorelines, such as Lake Powell in Arizona and Utah, have unique dynamics, such as large fluctuations in lake elevations, they may be able to provide habitat for riparian ecosystems.

This report documents one of the few efforts to describe the shoreline ecosystem associated with a western reservoir--Lake Powell. The objectives of this study were comprehensive: (1) to describe the plant communities along the shoreline, including their species composition, distribution and responses to fluctuating lake levels; (2) evaluate the potential for enhancing the diversity of these plant communities which are currently dominated by the nonnative <u>Tamarix</u> <u>ramosissima</u>; this was accomplished with a series of field experiments designed to determine interactions between native riparian plants and this nonnative; and (3) to describe the fauna associated with these plants.

These results were also compared with those of a biotic survey conducted in Glen Canyon in the 1950's, prior to the completion of Glen Canyon Dam, and revealed the effects of impoundment on a riparian ecosystem. This study laid the groundwork for long-term monitoring and improving our understanding of how young lacustrine ecosystems develop.

CHAPTER 2

RIPARIAN PLANT COMMUNITIES ALONG THE SHORELINE OF LAKE POWELL: DIVERSITY, PRODUCTIVITY AND FUTURE PROSPECTS

INTRODUCTION

Enormous reservoirs of water have developed behind dams along the Colorado River and the shorelines of these lakes have the potential to support extensive, riparian habitat. The productivity of these lacustrine habitats is especially important in the southwestern United States, because riparian habitats support large numbers of plant and animal species (Johnson and Carothers 1982, Knopf et al. 1988). There is also a premium on this habitat in the Southwest, due to its limited occurrence and extensive destruction (Knopf et al. 1988). In this study I describe the riparian plant community along the shoreline of Lake Powell, a reservoir on the Colorado River, and plant responses to factors most likely to threaten the persistence of this habitat.

Factors such as fluctuations in lake levels stand to influence the success of riparian communities along southwestern reservoirs. The dams along the Colorado River generate hydroelectricity and provide water storage, and power demands and the vagaries of weather guarantee that shoreline levels will never be stable. An understanding of the influence of such factors on plant establishment and performance will reveal what potential southwestern reservoirs have to support riparian communities of plants and animals.

The shoreline along Lake Powell measures 2,961 kilometers (1,823 miles), longer than the coastline of the western United States. This reservoir reached its full pool level of 1,138 m (3,700 feet), in 1980 and again in 1983 (Fig. 2-1), and the shoreline was rapidly colonized by riparian plants. Between 1986 and 1991 the elevation of Lake Powell dropped more than 25 m (75 feet) below full pool due to power demands and drought conditions, leaving these riparian plant populations perched far above the water.

Here I describe the relatively young riparian plant community that has become established along Lake Powell's shoreline during the 1980's and its response to declining lake levels. This study included a census of these plant communities to determine species composition and distributions, and the establishment of permanent plots within which demographic information, including growth rates, recruitment and mortality were measured. I also discuss the ability of native plant species to become established in communities that are dominated largely by the exotic plant, tamarisk or saltcedar (<u>Tamarix</u> <u>ramosissima</u>) and the responses of plants to different substrate types that are characteristic of the shoreline.

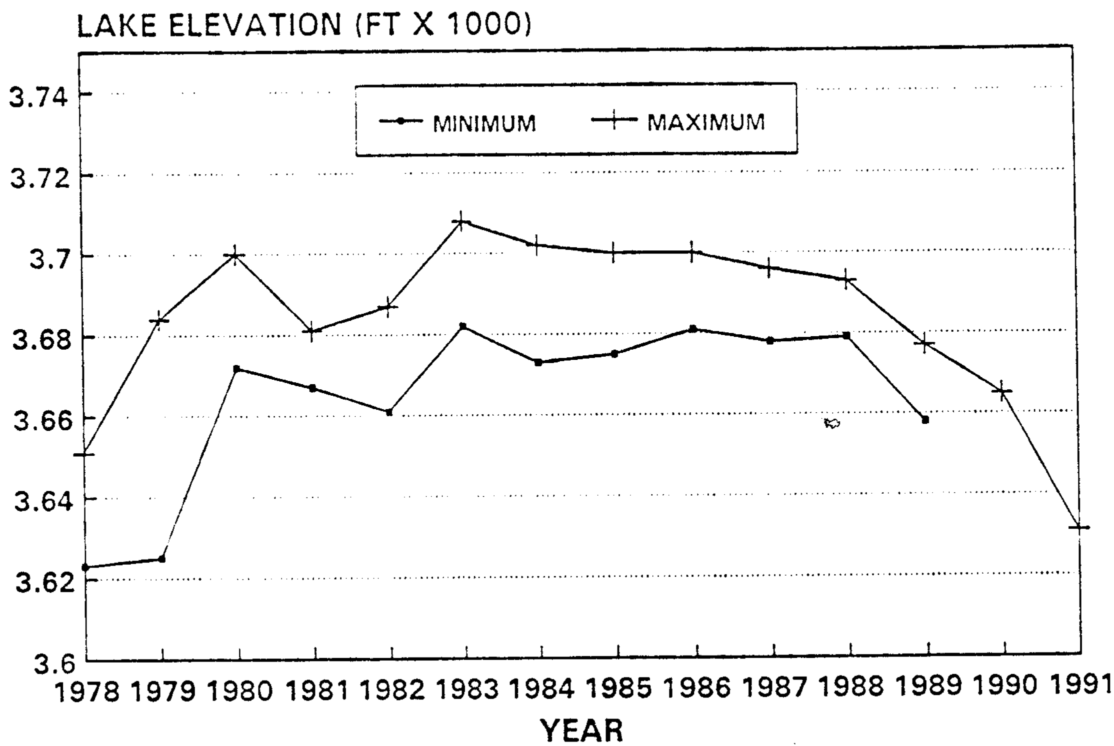


Figure 2-1. Maximum and minimum lake level elevations of Lake Powell between 1978 and 1991.

STUDY SITE

Lake Powell reservoir occupies Glen Canyon through northern Arizona and southern Utah along the Colorado River, in Glen Canyon National Recreation Area. Most of this basin is comprised of Navajo, Kayenta and Wingate sandstones and Chinle shales of the Glen Canyon Group (Potter and Drake 1989). The maximum lake elevation is 1,138 m (3,700′) at full pool, although the surrounding cliffs extend up to 1,230-1,540 m (4,000-5,000′). The habitat surrounding the lake is described as Upper Sonoran, and precipitation averages 15 cm (6") annually (Potter and Drake 1989).

The most conspicuous plant colonists of the shoreline are exotic species, including tamarisk (*Tamarix ramosissima*) and Russian thistle or tumbleweed (*Salsola iberica*). Both species produce copious numbers of seeds that have rapid germination rates and good dispersal abilities. The annual Russian thistle germinates only in wet sand and consequently its populations closely follow the changing shoreline levels. Native riparian species such as seep-willow (*Baccharis salicifolia*), Emory's baccharis (*B. emoryi*), cottonwood (*Populus fremontii*), brickellbush (*Brickellia longifolia*), Goodding's willow (*Salix gooddingii*), arrowweed (*Tessaria sericea*) have reported from the tributaries (Potter and Drake 1989).

METHODS

Census of Shoreline Riparian Plants and Soils

In November, 1988 and 1990, shoreline plant communities of Lake Powell were selected at random and censused (n = 173 and n = 119, respectively) to provide a basic description of these communities. Densities of riparian plants occurring on major substrate types along the lake were determined by recording the presence of plant species and their densities. Substrate type (sand, cobble, talus, bedrock; after Potter and Pattison 1976), location on lake (lakefront or cove or side canyon) and area of each census site (typically 25 by 50 m), and species and numbers of plants present were recorded. The presence of other perennial and annual species was noted. The occurrence of plants establishing below the 3700 ft lake level was recorded.

Conspicuous plant species of wet tributaries and springs that feed into Lake Powell were also recorded; these sites included the San Juan River, Ticaboo Creek, Reflection Canyon, and Slickrock Canyon, and springs in Rock Creek, Oak Bay, Good Hope Bay (two sites), east of the Escalante River confluence and south of Lewellyn Canyon, .

Samples of soils were collected from some sand beaches to describe the particle size of these sediments. Soils were dried, and 100 grams (g) were analyzed. Samples were sieved through 2 screens with mesh sizes designated by the USGS designations fine and coarse particles (Black 1965): a 1 millimeter (mm) mesh designed to sort fine and coarse sand, and a 0.0625 mm mesh designed to sort silt and clay from sand. Proportions of sediment in each grain size class were determined. According to Bodman and Mahmud (1932), sand-silt substrates comprised of less than 20% silt are classified as sand.

Establishment, Growth and Mortality of Riparian Plants

In 1988 permanent plots were established along Lake Powell to obtain demographic information on these populations including plant growth rates, and rates of recruitment and mortality in different substrates over two full growing seasons. Densities, growth and mortality of woody riparian plant species in these plots were measured in November, 1988, and again November 1990. Fifteen plots in sand, 11 in cobble and talus, and 8 in bedrock. The plots were located on 30 by 60 minute quadrat maps of Lake Powell, and corners of plots were marked with paint and metal stakes. Photographs of each plot were taken.

The following measurements were taken per plot: 1) densities per plant species; 2) a minimum of 10 riparian plants (including tamarisk, *Baccharis salicifolia*, *B. emoryi*, and *Brickellia longifolia*) per plot were tagged and height and circumference and mortality in these plants were measured in November, 1988 and November, 1990. Plant size measurements made in 1988 provided an estimate of plant growth rates on different substrates up to that date. Growth measurements between 1988 and 1990 revealed current patterns of plant growth in response to declining lake elevation, in addition to substrate. The presence of additional perennial and annual plant species was noted.

In 1988, more than 50 complete cross sections of tamarisk trunks were collected in various permanent plots to determine dates of tamarisk establishment, and to determine age and size relations in this species. Cross sections were polished to assure accurate counts of annual rings, and trunk circumference was measured.

Recruitment and mortality were estimated for tamarisk, B. salicifolia, B. emoryi and Brickellia longifolia in the permanent plots. All permanent plots were considered in estimating gain or loss of B. salicifolia, B. emoryi and Brickellia longifolia, because their densities were consistently low. However, estimates of gain or loss in tamarisk populations were based on counts in plots with relatively low plant densities, where change in plant numbers could be measured accurately. Number of plots with dead plants and proportions of dead plants were estimated. Frequency of mortality in different size (circumference) classes and on different substrates was estimated for tamarisk, B. salicifolia and B. emoryi.

The relationship between plant size, growth and substrate in tamarisk and B. salicifolia were analyzed with Multivariate Analysis of Variance (MANOVA; SYSTAT 1989). Site was not used in the analysis, because none of these response parameters were significantly different among sites for tamarisk or *B. salicifolia* (tamarisk size and growth by site: $P_{1,312} = 0.143$; *B. salicifolia* size and growth by site: $P_{1,52} = 0.191$). The Tukey range test (SYSTAT 1989) was used to detect significant differences among means. The occurrence of tamarisk and *B. salicifolia* on different substrates, and frequency of mortality were compared with Chi square analysis (SYSTAT 1989). Densities of tamarisk on different substrates were compared using ANOVA (SYSTAT 1989).

RESULTS

More than 50 plant species were encountered along the lake shoreline and/or in side canyons and springs during this study (Table 2-1).

Census of Shoreline Riparian Plants

Shoreline Riparian Communities: Species Composition, Densities and Substrate Relations: The plant communities along Lake Powell are simple, typically comprised of tamarisk and very low densities of native riparian species including *B. salicifolia*, *B. emoryi*, *Brickellia longifolia* and *P. fremontii*.

In a random census, woody riparian plants were found at 66% (n = 77) of the random census sites, indicating that considerable colonization of the Lake Powell shoreline has occurred (Table 2-2). Tamarisk was encountered more commonly than any other species along the lake shoreline and

Table 2-1 Plant species found in the riparian zone along the shoreline of Lake Powe and its tributaries, and on different substrates.

	LAKE	TRIBUTARIES or SPRINGS	SAND	COBBLE	TALUS	BEDROCK
Woody Perennials:						
Tamarix ramosissima	x	x	x	x	x	x
Baccharis salicifoia	x	-	x	x	x	x
B. emoryi	x	x	x	x	x	x
Populus fremontii	x	x	x			?
Brickellia longifolia	x	x	x	x	x	x
B. scabra	x					
Tessaria sericea	x	x	x	x	x	x
Rhus trilobatum	x	x	x		x	x
Chrysothamnus nauseousus	x	x	x			x
Atriplex spp.	x	x	x	x	x	
Coleogne ramosissima	x	-			x	x
Yucca angustissima	x	-	x		x	x
Ephedra spp.	x	-	x		x	x
Opuntia sp.	x	x				x
Cercis occidentalis	-	x			x	
Salix exigua	-	x	x	x	-	-
S. gooddingii	x	x	x			?
S. sp.	-	x	x	-	-	-
Berberis sp.	-	x				
Shepherdia rotundifolia	-	x				
Rhamnus sp.	-	x				
Fraxinus anomala	-	x				
Fraxinus velutina?	-	x				
Acer negundo	-	x	x			
Herbaceous Perennials:						
Dyssodia acerosa				x	x	x
Phragmites australis	-	x	x			
Imperatra brevifolia						
Gutierrezia microcephala	x	x	x	x	x	x
Encelia frutescens	x	x	x			x
Malva sp.	x	x	x		x	
Stephanomaria exigua	x			x	x	x
Stephanomaria tenuifolia	x			x	x	x
Tiquilia latior		x				x
Mentzelia sp.		x	x			
Artemesia sp.	x	x	x		x	
Artemesia sp.	x	x	x		x	

Table 2-1 (cont.)

	LAKE	TRIBUTARIES or SPRINGS	SAND	COBBLE	TALUS	BEDROCK
<u>Herbaceous Perennials</u>:						
Oenothera hookeri	x	x	x		x	
Oenothera sp.	x	x	x		x	
Astragalus sp.	x		x		x	x
Eriogonum sp.	x	x	x		x	
Eriogonum sp.	x	x	x		x	
Typha domingensis	-	x	x			
Ipomopsis sp.		x	x			
Scirpus sp.	-	x	x	x	-	-
Juncus sp.	-	x	x	x	-	-
Nicotiana trigonophylla	x	-	?	?	?	x
Adiantum capillua-veneris	-	x	x		x	
Petrophytum caespitosum	x	x	-		-	x
Equisitem sp.	-	x	x			
<u>Annuals</u>:						
Physaria sp.	x		x			
Salsola iberica	x	x	x			
Conyza canadensis	x	x	x	x	x	
Gnaphalium wrightii	x	x	x	x		
Gnaphalium sp.	x	x	x	x		
Datura metaloides	x	x	x		x	
Miribalis multiflora	x		x			x
Helianthus sp.		x	x			
Dicoria brandegei	x	-	x			

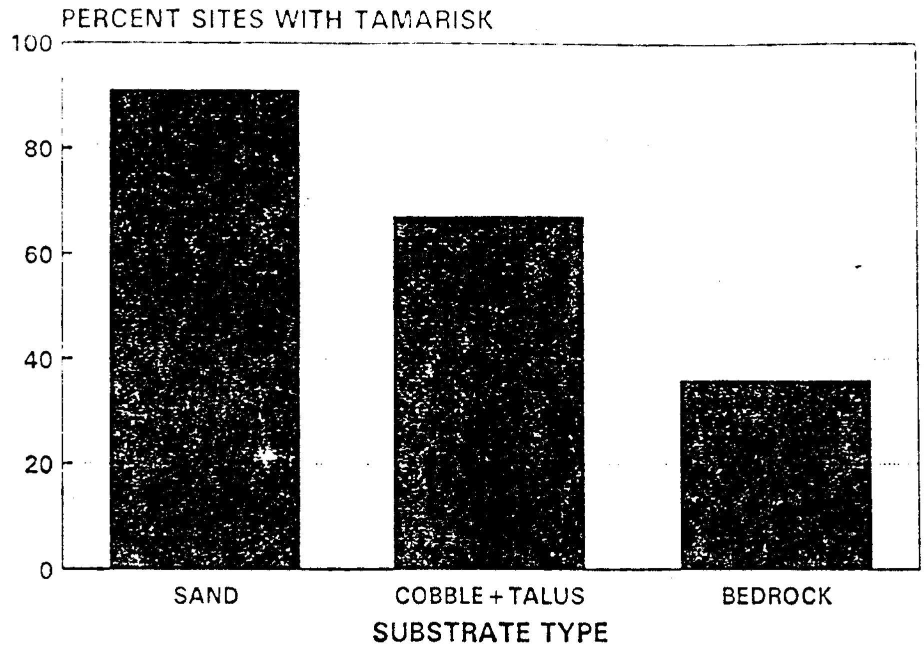
Table 2-2. Perennial riparian plants encountered in census plots along the shoreline of Lake Powell, based on a random survey in 1988 (n = 173 sites).

SPECIES:	# SITES PRESENT:	% SITES PRESENT:	# PLANTS ENCOUNTERED:
Tamarix ramosissima	115	66.0	5,017
Baccharis salicifolia	13	7.0	44
Baccharis emoryi	5	3	7
Populus fremontii	2	1.0	2
Tessaria sericea	7	4.0	47
Brickellia longifolia	19	11.0	28

was found at 66% of the random census sites in 1988 (Table 2). Native woody riparian species, including B. salicifolia, B. emoryi, Tessaria sericea, P. fremontii, and Brickellia longifolia, were found at 13% of the sites (Table 2). B. salicifolia and Brickellia longifolia were the most commonly encountered native species along the lake shoreline. B. salicifolia occurred in large numbers in some reaches of the lake, although it was absent in perennial tributaries. B. salicifolia is apparently new to the main channel environment of the Colorado River through Lake Powell; it was not found by the botanical expeditions of Woodbury et al. (1959) or Clover and Jotter (1944) through Glen Canyon.

Herbaceous perennials, such as wire lettuce (Stephanomeria spp.), wild tobacco (Nicotiana trigonophylla), snakeweed (Gutierrezia microcephala), horseweed (Conyza canadensis), pussy toes (Gnaphalium spp.) and brickellbush (Brickellia scabra) also occur, though rarely, in these communities. Xeric plants such as Yucca angustissima, Coleogne ramosissima, and Atriplex spp. occasionally extend their ranges down into these shoreline communities from the desert above the 1,138 m lake level (Table 2-1).

Plant Distributions on Substrates: Riparian plants were not uniformly distributed among the different substrate types (sand, cobble, talus, bedrock) along Lake Powell (Fig. 2-2). Distributional patterns are complicated by the



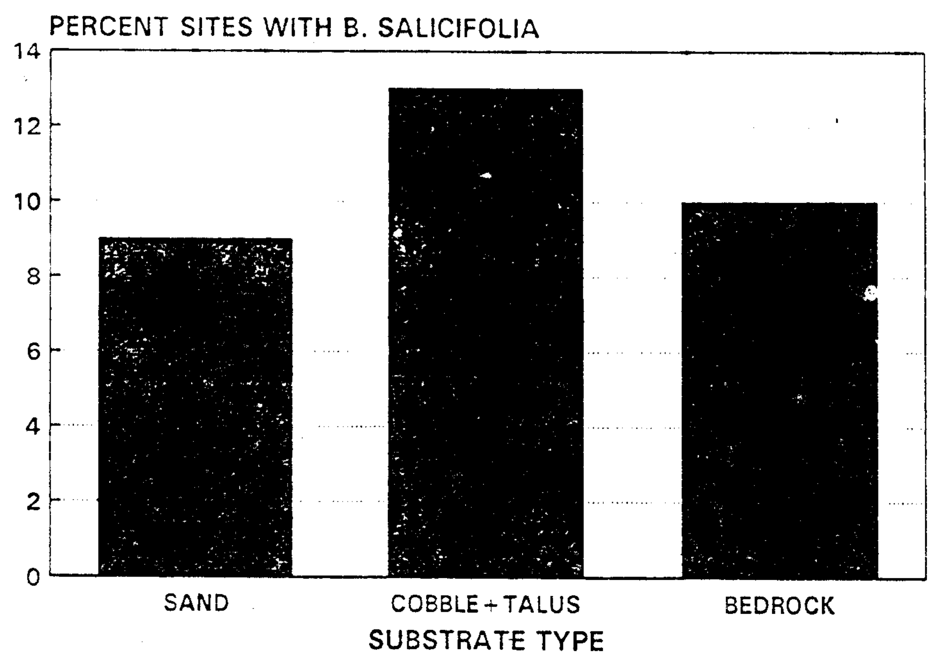


Figure 2-2. Frequency of Tamarix ramosissima and Baccharis salicifolia occurrence at sites on different substrates on Lake Powell, based on a random census, 1990.

idiosyncratic responses of different species to substrates. Tamarisk was most commonly encountered on sand beaches, occurring on 91% of all sandy sites, with intermediate levels of colonization on cobble and talus sites (X^2 = 27.38, df = 2, P < .005; Fig. 2-2). It occurred least frequently on bedrock (36% of bedrock sites). B. emoryi was found only on sand and talus, while Tessaria sericea and B. salicifolia were encountered with comparable frequency on all substrates. B. salicifolia occurred on different substrates ranged between 8 to 11% on census sites (Fig. 2-2). Brickellia longifolia was encountered most frequently on talus (74%; X^2 = 18.29, df = 3, P < 0.005). Populus fremontii was found at 2 sand sites. These results indicate that substrate exerts a strong influence on the distributions of some plant species along Lake Powell.

Plant densities, as well as frequency of occurrence, were influenced by substrates (Fig. 2-3). Tamarisk densities were significantly lower on bedrock than sand or cobble sites and highest on sand (Fig. 2-3; $P_{3,159}$ = 0.02). B. salicifolia densities were significantly higher on cobble than any other substrate (Fig. 2-3; $P_{3,159}$ = 0.000). Densities of Brickellia longifolia were comparable on different substrates; typically one plant per site was found. Plants were also distributed differently on the different substrates, with plants growing in bedrock being concentrated along fracture lines, while plants in sandy sites were more dispersed.

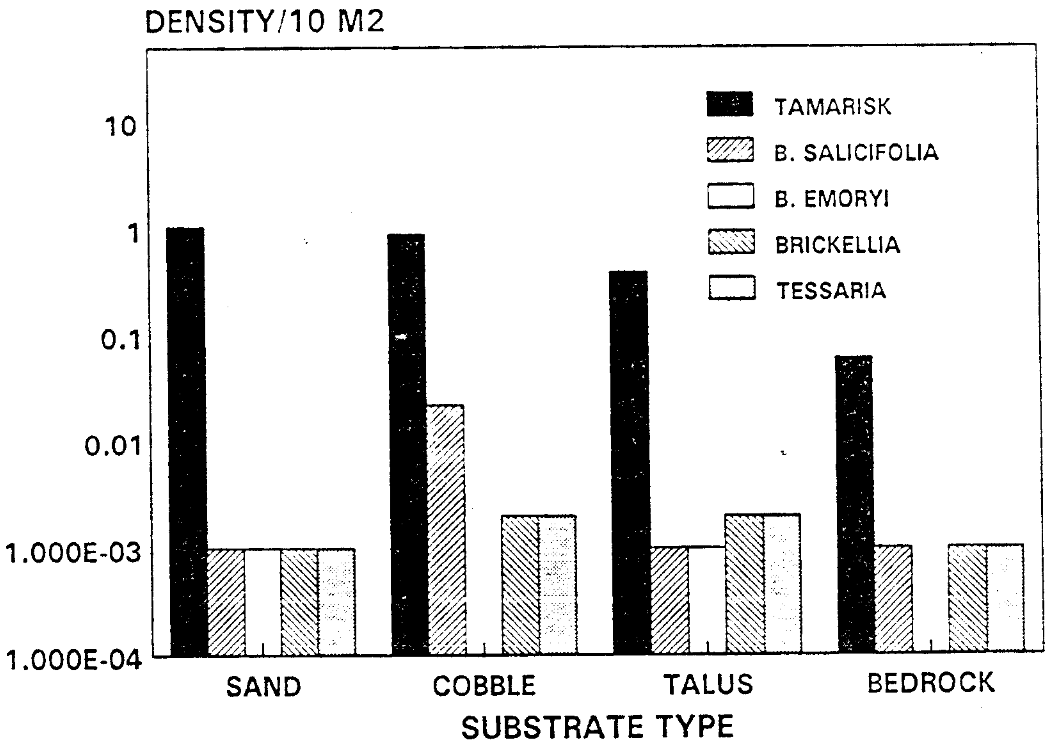


Figure 2-3. Densities of riparian plants per 10 m^2 on different substrates based on a random census in 1988.

Perennial shrubs, including _Stephanomeria_ spp., _Encelia frutescens_, _Dyssodia acerosa_, and _Gutierrezia microcephala_, occurred most frequently on talus (46% of talus sites) than any other substrate (X^2 = 7.93, df = 3, $P < .05$; Fig. 2-4). Talus may have better water holding capacity than sand, while offering more colonizable habitat than bedrock. There was no relationship between the occurrence of annual plants, such as _Datura metaloides_, twin-pod (_Physaria_ sp.) and horseweed (_Conyza canadensis_), and substrate type.

Woody riparian plants were encountered with comparable frequency along exposed lake shoreline and in protected side canyons (X^2 = 1.22, df = 1, $P > 0.05$). By contrast, annual plants were encountered significantly more often in coves or side canyons (36%) than along lake shoreline (22%; X^2 = 4.46, df = 1, $P < .05$). The restricted distributions of annual species may be due to the harsher conditions found along the lake shoreline or to limited dispersal out of tributaries onto the lake.

Extensive plant communities were found below the full pool lake elevation. Stands of tamarisk and native species such as _B_. _salicifolia_ and _B_. _emoryi_ were found below the high water line at nearly 30% of the random census sites.

Silt-sized particles never exceeded 6.5% of the soil sampled from sand sites (s.d. 3.0, range = 0 to 12% silt per 100 g sample) (Appendix 1), indicating that sand beaches are comprised largely of coarse-grained particles, which are regarded as poor substrates for plants (Stevens 1988). This

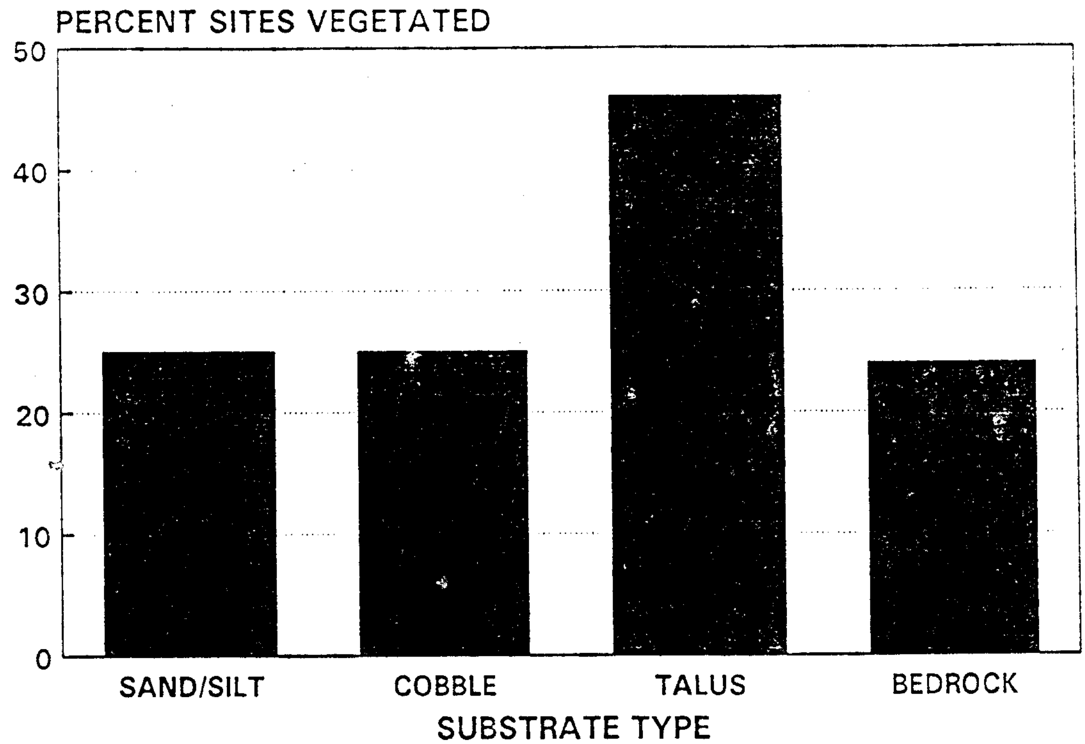


Fig. 2-4. Distributions of perennial shrubs according to substrate type along Lake Powell. Species include _Encelia frutscens_, _Coleogyne ramosissima_, _Ephedra_ sp., _Dyssodia_ sp., _Artemesia_ sp., _Chrysothamnus_ sp., _Atriplex_ sp., _Yucca_ sp., _Gutierrezia_ sp.

helps to account for the low productivity of these communities.

By combining Potter and Pattison's (1976) estimates of the proportion of each substrate type along Lake Powell's shoreline with this study's estimates of colonization of each substrate type, it was possible to estimate the total amount of Lake Powell's 2,961 kilometers (1823 miles) of shoreline that are colonized by riparian plants (Table 2-3). According to this analysis, a considerable amount of lake shoreline (approximately 40%) is colonized by plants. However, most of this area is comprised of bedrock, where mean densities of tamarisk are very low (Fig. 2-3).

Plant Species of Tributaries and Springs

Species richness and productivity in plant communities in 9 perennial tributaries and springs along Lake Powell appeared to be much greater than in shoreline habitat. These sites were comprised of dense stands of riparian species including *Salix gooddingii*, *Salix exigua*, *P. fremontii*, *B. emoryi*, *Acer negundo*, *Typha* sp., sedges, rushes and others (Table 1). These canyon communities bear a strong resemblance to those described by Woodbury et al. in the 1950's (1959). *P. fremontii* was more abundant in perennial tributaries than in the main channel in the 1950's, as is true today (Woodbury et al. 1959). Today tamarisk is the dominant woody riparian species along the lake shoreline, and it is rare in most wet tributaries and

Table 2-3. Estimated length of Lake Powell shoreline colonized by riparian plants at the 3700' elevation in 1990. Plants include all woody riparian species. Percentage and description of different substrates are based on Potter and Pattison (1971).

SUBSTRATE	% OF SUBSTRATE/ KM, MI OF SUBSTRATE	% COLONIZATION	LENGTH OF COLONIZED SUBSTRATE, KM/ MI
SAND	2.19 (64.86) (39.92)	91.43	59.30 36.50
COBBLE	0.93 (27.54) (16.95)	100.00	27.54 16.95
TALUS	18.98 (562.12) (345.09)	67.00	376.62 231.21
BEDROCK	77.24 (2,287.59) (1,408.08)	36.00	823.50 506.91
ROCK SLIDES (NOT STUDIED)	0.66	---	---
		TOTAL LENGTH OF SHORELINE COLONIZED BY RIPARIAN PLANTS:	1,286.96 KM 791.57 MI

springs, presumably due to high densities of native species and a lack of disturbed habitat. Its distribution is similar to that prior to the inundation of Glen Canyon; that is, tamarisk densities were higher along the main channel than in the tributaries of the Colorado River. These canyons and springs serve as important refugia for native plants as well as important sources for current and potential colonization of Lake Powell shorelines.

By visiting several of the wet tributaries in 1988 and again in 1990, I observed rapid migration of riparian plants through these drainages as they became exposed by declining lake levels. A section of Reflection Canyon that was submerged under lake water in 1988, subsequently became exposed as the lake level dropped and by 1990 it was colonized by high densities of S. gooddingii and P. fremontii that measured up to 5 m in height, and by S. exigua and Typha sp. In Slickrock Canyon, which is a low gradient drainage, 1,830 m (over 1 mile) of tributary drainage became exposed between 1988 and 1990. By 1990, nearly all of this distance was colonized with high densities of tamarisk, P. fremontii, S. gooddingii, S. exigua, B. emoryi and Phragmites sp. In the upper portion of this exposed drainage the average height of most species was between 1.5 and 2.0 m, while S. gooddingii near the new lake shoreline were less than 0.5 m. The establishment of high densities of these plants that have attained large size in less than 2 years verifies how productive riparian habitat can be, and demonstrates that native species, as well as tamarisk, can disperse rapidly over large distances when conditions are suitable.

Demography of Shoreline Plant Communities: Establishment, Growth and Mortality

Establishment of Tamarisk: The majority (35%) of the 55 tamarisk collected for age measurements became established in 1983 when the elevation of Lake Powell exceeded the full pool line (Fig. 2-5). The lake level also reached full pool during the next 2 years (Fig. 2-1). The shoreline sediments were probably wet for the better part of three years, providing colonizing seedlings with optimal establishment habitat. This appears to be the ideal environment for establishment of tamarisk and native riparian species along Lake Powell.

The circumferences of plants that established in 1983 were highly variable, ranging from 2.2 to 27.0 cm; while the circumference of plants across all cohorts ranged from 2.2 to 35.8 cm. Most of this variation in size was due to substrate (see Growth section).

The oldest tamarisk found were 10 and 20 years (in 1988), and both were found in side canyons. The 20 year old plant occurred up Ticaboo Creek, and exhibited small growth rings (< 1 mm/year) until 1980, after which time over half of the plant's radius was amassed, as evidenced by larger diameter growth rings (@ 5 mm/year). Lake Powell reached

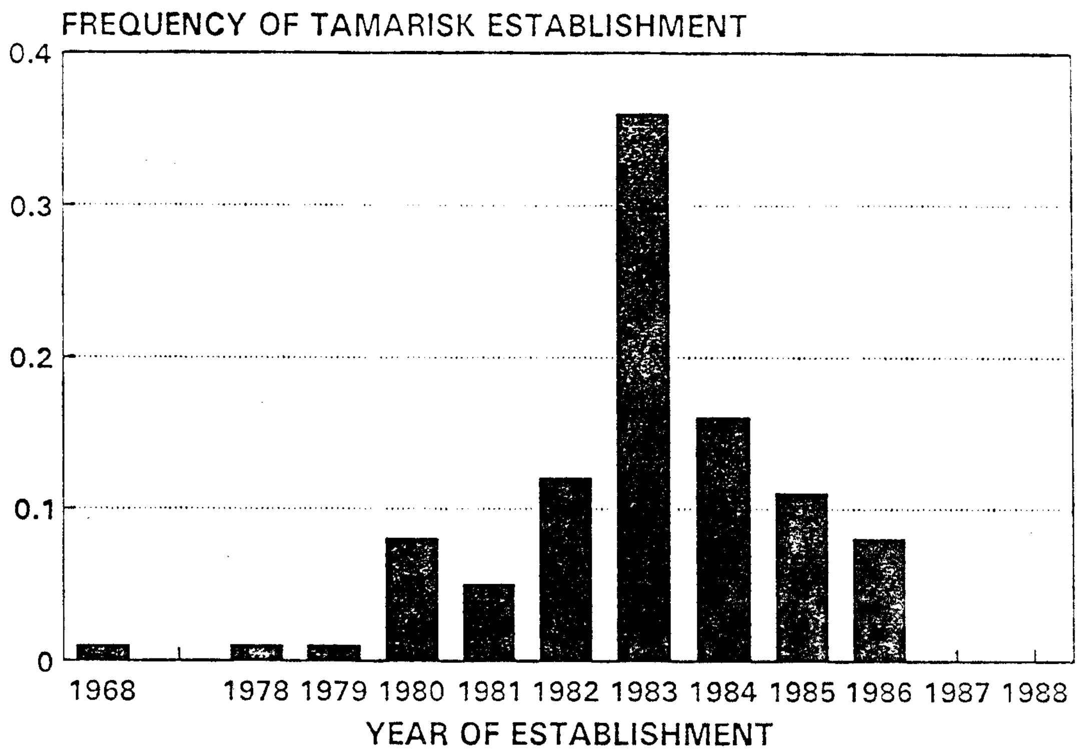


Fig. 2-5. Percentage of Lake Powell Tamarix ramosissima established in different years between 1968 and 1990 at the full pool line (1,138 m), based on a sample of 55 plants.

full pool for the first time in 1980. This indicates that the lake affected growth of pre-existing plants as well as colonization patterns.

Plant Growth Patterns Up to 1988: Plant growth varied significantly among substrate types and each species exhibited a unique response to the different substrates (Table 2-4). Circumferences measured in 1988 were considered to reflect plant growth rates. Tamarisk and B. salicifolia circumference were both largest on talus, while bedrock was the poorest substrate for tamarisk and Brickellia longifolia and sand was the poorest substrate for B. salicifolia. Tamarisk height and circumference were significantly greater on sand and talus than on cobble or bedrock (Table 2-4, 2-5). Mean circumference in B. salicifolia was significantly greater on talus than any other substrate (Table 2-4, 2-5). B. salicifolia height did not vary significantly among substrates, although it was also greatest on talus. B. emoryi size was comparable on sand, cobble and talus, and lowest on bedrock, although data for cobble and bedrock were limited (Table 4). Brickellia longifolia height was comparable on cobble and bedrock (Table 2-4).

Plant Growth Between 1988 and 1990: Tamarisk and B. salicifolia growth rates did not vary on different substrate types between 1988 and 1990, contrary to patterns prior to 1988 (Table 2-4, 2-5). Drought conditions resulting from low lake levels have eliminated substrate influences on

Table 2-4. A: Mean plant height (m), circumference (cm), according to species and substrate in 1990. B: Estimate of plant growth as measured by changes in plant height (m), and circumference (cm) between 1990. Letters indicate statistically significant differences among mean .05.

SPECIES/ SUBSTRATE	A: HEIGHT (M)	CIRCUMFERENCE (CM)	B: INCREASED HEIGHT (M)	INCREASED CIRC. (CM)
Tamarix ramosissima				
Sand	2.19^{A}	7.95^{AB}	0.16	0.76
	(1.26)	(6.12)	(0.24)	(1.44)
	(160)	(159)	(154)	(153)
Cobble	1.72^{AB}	4.64^{C}	0.10	0.52
	(2.27)	(3.23)	(0.16)	(0.58)
	(37)	(37)	(37	(37)
Talus	2.15^{A}	9.17^{A}	0.25	0.97
	(0.87)	(8.67)	(0.31)	(1.45)
	(56)	(56)	(56)	(54)
Bedrock	1.36^{B}	5.87^{BC}	0.10	0.70
	(0.60)	(3.72)	(0.15)	(0.96)
	(73)	(73)	(71)	(70)
Chinle	2.17	8.07	0.06	0.99
	(1.14)	(6.23)	(0.10)	(0.90)
	(7)	(7)	(7)	(7)
Baccharis salicifolia				
Sand	1.48	4.72^{A}	0.05	0.39
	(0.85)	(2.39)	(0.06)	(0.48)
	(18)	(17)	(18)	(17)
Cobble	2.17	5.92^{A}	0.35	0.64
	(1.35)	(2.31)	(1.15)	(0.82)
	(24)	(24)	(24)	(24)
Talus	3.00	12.95^{B}	0.06	0.45
	(0.28)	(6.58)	(0.08)	(0.49)
	(2)	(2)	(2)	(2)
Bedrock	1.88	7.27^{A}	0.11	0.83
	(0.65)	(2.93)	(0.13)	(0.89)
	(12)	(12)	(12)	(11)

Table 2-4 (cont.)

SPECIES/ SUBSTRATE	A: HEIGHT (M)	CIRCUMFERENCE (CM)	B: INCREASED HEIGHT (M)	INCREASED CIRC. (CM)
Baccharis emoryi				
Sand	1.25 (0.59) (15)	6.45 (4.75) (14)	0.07 (0.11) (15)	1.29 (1.37) (15)
Cobble	1.60 (1)	6.00 (1)	--	1.70 (1)
Talus	1.03 (0.37) (8)	6.34 (3.19) (8)	0.09 (0.10) (8)	1.61 (1.07) (8)
Bedrock	1.01 (1)	4.60 (1)	0.03 (1)	1.10 (1)
Brickellia longifolia				
Cobble	0.63 (0.22) (3)	--	0.19 (0.01) (3)	--
Bedrock	0.67 (0.25) (2)	--	0.01 (1)	--
Populus fremontii				
Chinle	1.92 (1)	6.50 (1)	0.00 (1)	0.30 (1)
Salix gooddingii				
Sand	2.72 (0.68) (2)	11.35 (2.19) (2)	0.05 (0.07) (2)	1.10 (0.99) (2)

Table 2-5. Statistical comparison of height (HT), circumference (CIRC in 1988, and growth (GR-HT, GR-CIRC) in _Tamarix ramosissima_ and _B. salicifolia_ between 1988 and 1990, using MANOVA; * = P < .05, ** = P < .001.

FACTOR	WILK'S F	DF	P	SIGNIF. OF FACTOR			
				HT.	CIRC	GR-HT.	GR-CIRC.
SUBSTRATE	3.516	12,952	0.000	**	**	NS	NS
SPECIES	0.265	4,360	0.900	NS	NS	NS	NS
INTERACTION	1.500	12,944	0.118	*	NS	*	NS

plant growth patterns, causing all substrates to be equally poor.

Population Change: Mortality and Recruitment: Levels of plant mortality were strongly affected by substrate type and plant size. Tamarisk mortality was low (17%), despite a low lake elevation during the last 3 years. Mortality was significantly more common among smaller plants. Significantly more tamarisk in the 0-2 cm circumference class died between 1988 and 1990 ($X^2 = 135.31$, df = 6, $P < .005$; Fig. 2-6). This was the only size class that was susceptible to mortality and indicates that plants with a circumference of greater than 2 cm have a high probability of surviving the very protracted drought conditions that have resulted from low lake levels.

Significantly more tamarisk died on cobble (35%) than on any other substrate ($X^2 = 45.01$, df = 4, $P < .005$; Fig. 2-6). This result agrees with the growth patterns of tamarisk on cobble, where plants were smallest and slowest growing.

Percent mortality was higher in _B_. _salicifolia_ (32%, n = 43) than in tamarisk, suggesting that _B_. _salicifolia_ is less tolerant of drought conditions. This level of mortality is still relatively low, considering that these plants have been severely water limited for 3 years. Nearly all of this mortality occurred in smaller plants with circumferences less than 6 cm (93%, n = 40), with circumference ranging up to 18 cm (Fig. 2-7). Thirty-eight

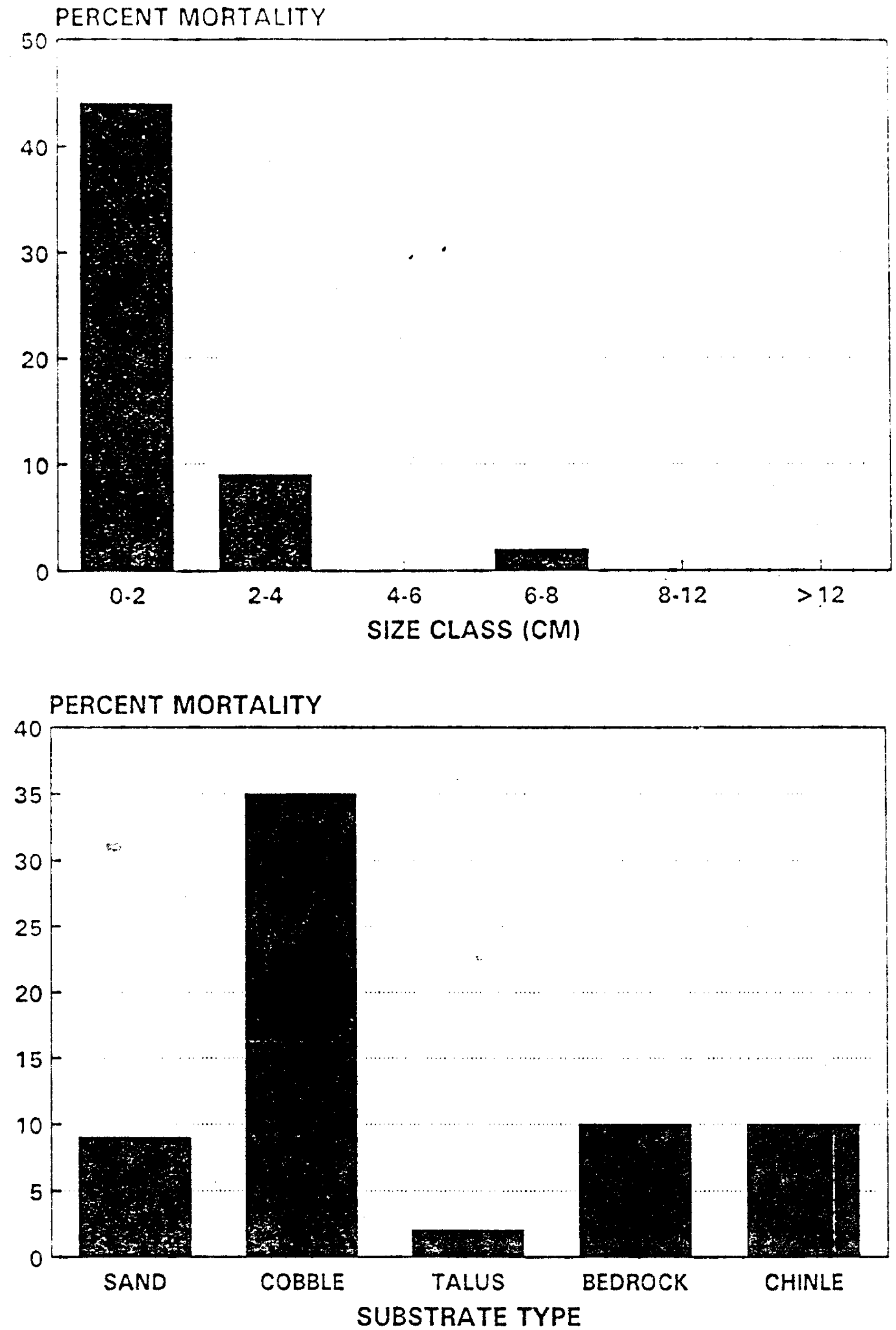


Fig. 2-6. Percent Tamarix ramosissima mortality by size class (circumference in cm), and by substrate type, on permanent plots between 1988 and 1990.

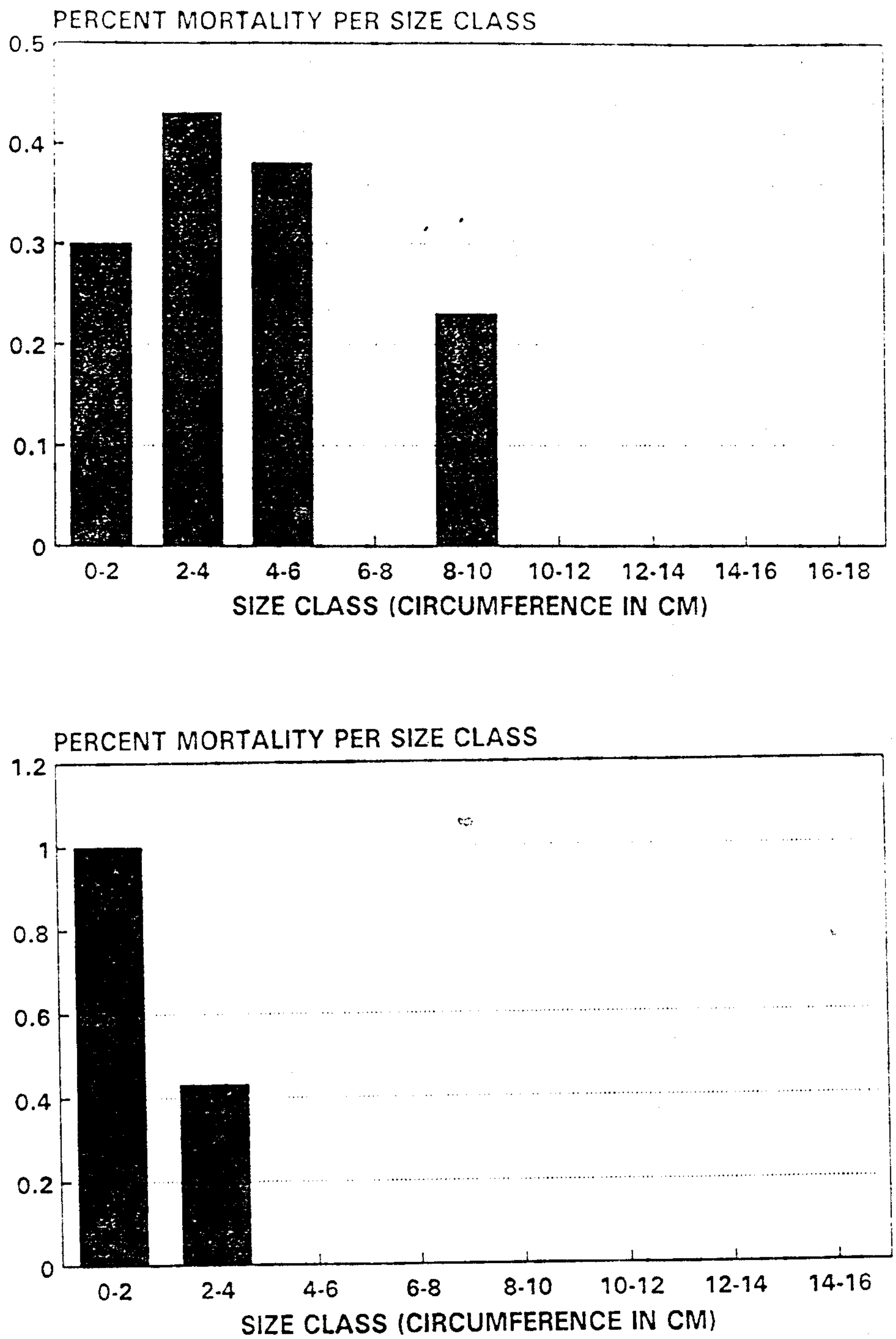


Fig. 2-7. Percent Baccharis salicifolia (above) and B. emoryi (below) mortality by plant size class (circumference in cm) on permanent plots between 1988 and 1990.

percent of the plants in these smaller size classes (0 to 6 cm) died between 1988 and 1990. Mortality was greatest on sand beaches (58%, n = 7) and lowest on talus (n = 0) and bedrock (22%, n = 2) substrates. These patterns agree with B. salicifolia growth measurements (Table 2-4).

Mortality was lower in B. emoryi than in B. salicifolia, suggesting a greater tolerance of drought conditions. Only 22% of the 37 B. emoryi encountered died between 1988 and 1990. All mortality occurred in plants with a circumference less than 4 cm, while plant circumference exceeded 14 cm (Fig. 2-7). Although B. emoryi was most common and largest on sandy beaches, mortality was highest (27%) on this substrate between 1988-1990. These results suggest that sand changes from a good to a poor substrate for B. emoryi during drought conditions and this species may have a greater chance of surviving such conditions in other substrates.

Brickellia longifolia occurred at 8 permanent cobble, talus and bedrock sites and no mortality was observed. Clumps of Tessaria sericea at a sand site numbered 125 in 1988 and dropped to 26 in 1990, reflecting an intolerance of water stress.

There was no evidence of recruitment of seedlings in tamarisk, B. salicifolia or B. emoryi populations in the permanent plots between 1988 and 1990, indicating that the current environment for riparian plants along Lake Powell is too dry for population growth. There was no tamarisk recruitment (0 of 22 sites) although there was a loss of plants in 50% of these same sites. Similarly, there was no evidence of recruitment in plots containing B. salicifolia (0 of 16) or B. emoryi (0 of 10), although loss of individuals in these plots was found.

Comparison of Different Plant Trait Responses

This study revealed that the fate of riparian plants in this system is dependent on a complex interaction between life history parameters and environmental factors, including substrate and water availability. While a particular substrate may be suitable for initial establishment, it may not provide conditions necessary for survival, growth and reproduction, especially due to lake fluctuations. Patterns of frequency of occurrence and densities of tamarisk, for instance, were similar among the different substrates, while performance parameters, including growth and mortality, also tended to agree with one another (Table 2-6). However, these two groups of plant characteristics often did not agree (Table 2-6). For instance, tamarisk occurrence and densities were higher on sand and cobble than on talus or bedrock; however, tamarisk performance (growth and survivorship) was best on talus and poorest on cobble (Table 2-6). Inconsistencies also occurred in patterns of B. salicifolia establishment and performance. Drought conditions have probably contributed to these discrepancies.

These relationships must be taken into account when devising programs to manage these species.

DISCUSSION

The riparian plant communities that have developed along the shoreline of Lake Powell are proving to be highly resilient during four years of low lake levels. This is true for native species as well as the nonnative tamarisk. While this study found no evidence of recruitment and little growth or productivity in these populations, mortality was low. In light of these findings, it appears that this large reservoir system does have the potential to support a riparian ecosystem, including a diverse fauna, (see Chapter 4), as well as flora.

While shoreline plant communities are dominated by the nonnative tamarisk (98%), native riparian species continue to dominate wet tributaries and springs near the lake, almost to the exclusion of tamarisk. The latter was also true in the 1950's (Woodbury et al. 1959). The wet tributaries and springs of Lake Powell serve as refugia for diverse and highly productive communities of plants, and they are an important source for future colonization, both natural and managed, of the lake shoreline. They need protection and further study.

Native riparian species are rare along the lake, although this study found that they are persisting in tamarisk-dominated stands, indicating that not only can Lake

Powell support a riparian ecosystem, but it can support a diverse flora. The most common native riparian species encountered along the lake in this census was Baccharis salicifolia (Asteraceae), that occurs only along the lake and appears to be a relative newcomer to this system; it was not seen in the main channel of Glen Canyon during earlier botanical surveys in the 1940's and 1950's (Woodbury et al. 1959, Clover and Jotter 1944).

Additional native riparian woody species, Baccharis emoryi, Populus fremontii, and Tessaria sericea were only rarely encountered in the census. According to Woodbury et al. (1959), P. fremontii was relatively rare along the main channel prior to the inundation of Glen Canyon, and more common in side canyons, as is true today. Baccharis emoryi was more common on along the main channel of Glen Canyon than in tributaries during the 1950's (Woodbury et al. 1959). Its drought tolerance may enable it to become abundant along the lake shoreline (see Chapter 3). This species is a slow disperser; the pappus associated with each of its seeds falls off shortly after seed dispersal, guaranteeing that it will not disperse far (L.E. Stevens, pers. comm).

Fluctuating lake levels, variable substrates and idiosyncratic ecological needs of the different plant species in these communities will make managing this system for diversity a challenging proposition. This study found that good colonization substrates can cease to be good sites for later growth and survival if water becomes limiting. Sand, especially, tends to become a poor substrate as lake levels drop, although most species readily colonize wet sand. It is clear, however, that plant size can mitigate this effect to a certain extent, so planting programs should strive to have plants well-established before the elevation of Lake Powell drops again in the future.

This study of the plant communities along the shoreline of Lake Powell has revealed an important ecosystem in the making and many of the details that need to be considered to manage it wisely.

CHAPTER 3

SURVIVORSHIP AND GROWTH OF NATIVE RIPARIAN PLANTS IN TAMARISK STANDS: AN EXPERIMENTAL ANALYSIS

INTRODUCTION

While the rapid invasion of the nonnative tamarisk (*Tamarix ramosissima*) in southwestern riparian ecosystems is well-documented, and aspects of its natural history are now understood (Clover and Jotter 1944, Robinson 1965, Christensen 1962, Horton 1962, 1964, Potter and Pattison 1976, Pattison and Drake 1989), questions remain about the role of tamarisk's interactions with native plant species in this process. The large numbers of seeds that tamarisk produces and their ability to disperse great distances have facilitated its spread through the Southwest and enabled it to colonize disturbed habitats at a faster rate than native species (Stevens 1989, Warren and Turner 1975). Very often, however, tamarisk occurs in close proximity to native species, and its effects on natives and ability to coexist with them are not well understood.

Tamarisk's success in riparian ecosystems might suggest that it is a highly competitive species, however, the one competition study known suggests the opposite. Growth in young tamarisk was strongly suppressed in the presence of the native coyote willow (*Salix exigua*), while there is no competitive interaction between older plants of the two species (Stevens 1989). Coyote willow, with its clonal growth habit, is also thought to be replacing tamarisk on some beaches in the Grand Canyon (Stevens 1989). These findings suggest that the rapid spread of tamarisk through riparian habitat in the Southwest is not due to competitiveness and that its presence in these communities may be only temporary or successional. Ultimately, more research is needed on tamarisk interactions with native species and in different environmental settings to improve our understanding of the ecological significance of tamarisk in southwestern riparian ecosystems and to enhance our ability to manage it.

Here I present the results of a series of field experiments designed to evaluate interactions between tamarisk and four southwestern native plant species that are commonly found in riparian ecosystems, including those of the Lake Powell region: *Baccharis salicifolia*, *B. emoryi*, *Populus fremontii* and *Salix gooddingii*. These experiments evaluated species interactions when native plants were introduced into shoreline tamarisk stands with supplemental water and without water, and interactions between species when grown in the close confines of pots, where competitive interactions are most likely to appear. A major objective of this study was to determine the feasibility of introducing these species into existing tamarisk stands that dominate the shoreline of Lake Powell in Glen Canyon National Recreation Area, Arizona and Utah. The National Park Service is interested in enhancing the overall biotic diversity of Lake Powell's extensive shoreline by increasing the diversity of its plants communities.

STUDY SITE

Lake Powell occurs behind Glen Canyon Dam in northern Arizona and southern Utah, along the Colorado River. Competition experiments were conducted at Wahweap beach, at the southern end of Lake Powell and at the Lees Ferry nursery, which is approximately 16 km (10 mi.) southwest of Wahweap. Wahweap beach is at 1,138 m (3700') above sea level on top of Navajo sandstone. The vegetation there is dominated by tamarisk, with low densities native riparian plants including Goodding's willow (_Salix gooddingii_), Emoryi's baccharis (_Baccharis emoryi_), and arrowweed (_Tessaria sericea_). The riparian vegetation is backed by high desert vegetation including narrow-leaf yucca (_Yucca angustissima_), Mormon tea (_Ephedra viridis_), and black brush (_Coleogne ramosissima_). The Lees Ferry nursery site occurs at 1,010 m (3,330') above level. It is surrounded by a dense stand of mature tamarisk and sparse Goodding's willow.

METHODS

Plant Acquisition and Propagation: Plant material for the interaction experiments was collected during March, 1989. Cuttings of _Populus fremontii_, and _Baccharis emoryi_, and _Tamarix ramosissima_ saplings, were collected in Reflection Canyon and Cottonwood Canyon, two perennial tributaries of Lake Powell. Cuttings of Baccharis salicifolia were collected at Oak Canyon. Cuttings of Salix gooddingii were collected from the Lees Ferry area. Upon return to the laboratory at Museum of Northern Arizona (MNA), cuttings were placed in water with aeration pumps for several days. The water in buckets was changed every other day. Cuttings were clipped to a length of less than 0.5 m. Cuttings were potted in a medium of peat moss and vermiculite in individual Rootrainer (Tm) pots measuring 5 cm x 5 cm x 20 cm. In the greenhouse, pots were watered daily and misted every two hours throughout the day for two weeks. Plants were watered at biweekly intervals with Miracle Gro (Tm) fertilizer, according to specifications. Plants were grown in the MNA greenhouse from March until June 1989, and were then transferred into the field for experimental work.

Wahweap Experiments: The experiments as Wahweap evaluated the consequences of (1) introducing rooted native plants into a tamarisk stand receiving supplemental water, and (2) introducing rooted native plants and unrooted cuttings of native plants into an unwatered tamarisk stand. A field plot with an automated watering system was established near Wahweap Marina along the shoreline of Lake Powell at the high water level (1,138 m or 3700') in August, 1989. This site occurred in a large extensive stand of young tamarisk plants with a mean density of 2.13 plants/m^2. These plants averaged 1.30 m (s.d = 0.707) in height. A 200

m^2 plot was established and fenced to prevent trampling and herbivory. Greenhouse plants less than 0.5 m in height were planted directly in the sand. *Tamarix ramosissima*, *Baccharis salicifolia*, *B. emoryi*, *Populus fremontii* and *Salix gooddingii* were used. Plants were planted in two types of microsites: in small open patches or in close proximity (within 0.5 m) to tamarisks, to determine the effect of tamarisk on plant growth and survivorship. The 'open patch' treatment was replicated 6 times per species, and the 'adjacent to tamarisk' treatment was replicated 12 times per species. Each plant was fertilized initially with Miracle Gro (Tm). Each plant received water three times per day for ten minutes, at 8am, 12pm, and 4pm, throughout the growing season, and once per day for ten minutes at 8am during winter months. Plant height was measured at the beginning of the experiment and at 4 later intervals, over the course of 2 full growing seasons between 1989 and 1991. Plant reproduction was also noted.

Plant growth rates were determined from these measurements and were analyzed with Analysis of Variance (ANOVA; SYSTAT 1989), to determine the influence of proximity to tamarisk, and species on plant performance.

The same plant species were planted in the same design in an unwatered plot next to the watered plot in August, 1989, to determine whether native plants could survive without supplemented water. Plants were fertilized and watered initially. Plant height was measured at the beginning, middle and end of this 2 year experiment. The lake level of Lake Powell remained low throughout 1989 and 1990, providing the opportunity to determine the effect of severe water deficits on native plant establishment along the lake shoreline.

In September, 1990, larger rooted and unrooted plants were introduced into the unwatered plot at Wahweap beach. Larger plants were used to determine if increased plant size would increase plant survivorship. *Baccharis salicifolia*, *B. emoryi*, *Populus fremontii* and *Salix gooddingii* were planted. Rooted cuttings ranging between 1 and 2 m in height were planted in a grid, with plants 2 m apart. Ten to 20 plants per species were used. Unrooted cuttings of plants ranging in height between 1.5 and 4 m were planted in a grid, with plants 2 m apart. The unrooted cuttings were collected in the Lees Ferry area. All plants were fertilized and watered at the beginning of the experiment.

Lee's Ferry Nursery Experiments: Combinations of the same native plants and tamarisk were established in pots to study interactions in a more controlled and restricted setting, where competitive interactions between species were most likely to be found. The experiment was conducted in the nursery at Lees Ferry, Arizona, starting in June, 1989. Plants were planted in pots containing sand from Lake Powell's shoreline. Two plants were placed into each 10 liter pot (23 cm tall, 26 cm wide). Plants were arranged in such a way that native species occurred alone (2 plants) or with tamarisk (one native plant, one tamarisk) in pots, to measure the response of native species to this exotic species. Plants were watered three times per day, for four minutes at 8am, 12pm and 4pm. Each treatment was replicated 20 times. Plant height was measured at the beginning of the experiment and at the end of one full growing season. At the end of the experiment, plants were harvested from the pots, dried and root and stem material were weighed to determine level of biomass increase and allocation patterns to roots and stems.

Growth and biomass data were log transformed (log(data+1)) and analyzed with ANOVA to test for differences according to presence or absence of tamarisk (SYSTAT 1989, Zar 1984).

RESULTS

Survivorship and Growth of Native Riparian Plants in a Tamarisk Stand Along Lake Powell at Wahweap

The Watered Plot: Over 2 full growing seasons, four native riparian plant species, *Baccharis salicifolia*, *B. emoryi*, *Populus fremontii*, and *Salix gooddingii*, survived and exhibited considerable growth in the tamarisk stand at Wahweap, indicating that native species can thrive in the presence of this nonnative species. Native plant growth was comparable regardless of whether individuals occurred in close proximity to tamarisk or in open patches (Table 3-1, 3-2). Both *Baccharis salicifolia* and *Salix gooddingii*

Table 3-1. Plant growth (m) in Wahweap watered plot. A. Growth of native plants and tamarisk introduced into plot. B. Growth of *Tamarix ramosissima* adjacent to transplanted native plants and tamarisk. * = *Baccharis salicifolia* growth prior to December 1990 subzero temperatures.

A. PLANTS INTRODUCED INTO PLOT:	ALONE Mean (s.d.)	WITH Mean (s.d.)
Baccharis salicifolia	-0.067 (.632) 0.595 (.297)*	0.195 (.451) 0.713 (.284)*
B. emoryi	0.580 (.169)	0.560 (.247)
Populus fremontii	0.908 (.402)	0.941 (.405)
Salix gooddingii	0.260 (.161)	0.433 (.216)
Tamarix ramosissima	0.547 (.181)	0.538 (.261)

B. ADJACENT T. RAMOSISSIMA OCCURRING WITH:	MEAN (s.d.)
Tamarisx ramosissima	0.045 (.540)
Baccharis salicifolia	0.188 (.182)
B. emoryi	0.156 (.279)
Populus fremontii	0.183 (.262)
Salix gooddingii	0.124 (.255)

Table 3-2. Analysis of plant growth patterns according to proximity to _Tamarix_ _ramosissima_ in the watered plot at Wahweap.

Variable	Coefficent	T	P (2 Tail)
Constant	0.272	0.707	0.482
Treatment	0.054	0.242	0.809
Species	0.030	0.259	0.796
Treatment * Species	0.010	0.154	0.878

SOURCE	S.S.	DF	MEAN SQUARE	F	P
Regression	0.560	3	0.187	1.043	0.378
Error	15.585	87	0.179		

exhibited a nonsignificant trend of increased growth when in close proximity to tamarisk.

There were no significant differences in growth rates among species or significant interactions between species and proximity to tamarisk (Table 3-2). Populus fremontii tended to grow most, with some individuals growing more than a meter in height during the 2 growing seasons (range = 0.33 to 1.60 m). Salix gooddingii grew the least on average, with individuals growing between 0.06 and 0.7 m. Of all plants transplanted into the tamarisk stand, only 2 Baccharis salicifolia died, and this appeared to be the result of frost damage rather than from biotic interactions (see below).

Although Baccharis salicifolia grew vigorously during most of the experiment, plants died back extensively following a heavy freeze during December, 1990 (Table 3-1). As a result the final growth measurements for this species do not reflect the extent to which it grew during the 2 year experiment (Table 3-1). This was the only species found to be negatively affected by this freezing event.

Baccharis salicifolia, B. emoryi and Salix gooddingii flowered in the plot during the experiment. More than 50% of the Baccharis species (B. salicifolia = 55%; B. emoryi = 67%) produced inflorescences, while 11% of Salix gooddingii (n = 2) bloomed during this time. The reproduction of these species, along with their vegetative growth, further indicates that native plants can thrive in the presence of tamarisk.

The growth rates of the naturally-established tamarisk within the stand ('adjacent tamarisk') did not differ significantly regardless of which plant species was planted nearby ($F_{1, 59}$ = 0.286, P = 0.595; Table 3-1), indicating that native species have a comparable effect, or lack of effect, on tamarisk growth. The lower average growth of tamarisk in the presence of transplanted tamarisk (Table 3-1) was attributable to one plant that died back more than a meter during the experiment. Without this individual, average tamarisk growth in the presence of transplanted tamarisk was comparable to tamarisk growth in the presence of the other species (mean = 0.186 m).

These results indicate that native plants can be successfully introduced into dense tamarisk stands along Lake Powell when water is available. Native plants as small as 0.5 M in height can become established in the presence of plants that are 3 to 4 times taller.

The Unwatered Plot: Both Baccharis salicifolia and B. emoryi survived without supplemental water for over 2 growing seasons in the unwatered plot at Wahweap. More B. emoryi (60%) survived than B. salicifolia (20%). These results suggest that B. emoryi, in particular, is a good candidate for increasing species diversity in the shoreline plant communities of Lake Powell. Proximity to tamarisk did not negatively influence Baccharis survivorship, as 77% of surviving B. emoryi and all B. salicifolia occurred in close proximity to tamarisk. No P. fremontii or S. gooddingii survived the 'no water' treatment.

Plant growth in the surviving Baccharis species was nominal during the 2 years (Table 3-3); however more plants exhibited an increase in height during the second growing season than during the first. While more than 70% of B. emoryi exhibited negative growth or dieback during 1990, 66% showed positive growth or increased height in 1991. This suggests that plant establishment is a protracted process, and perhaps especially when water availability is low.

Four (44%) of the surviving B. emoryi and 1 B. salicifolia flowered during the late summer of 1991 (Table 3-3). This further indicates that these native riparian species can successfully establish without supplemental water.

Survival of larger rooted cuttings was high for B. emoryi (100%) during the 1991 growing season. No B. salicifolia, P. fremontii or S. gooddingii survived, suggesting that larger plant size does not improve the ability of these species to tolerate water stress.

Of the unrooted poles planted in the unwatered plot, only one B. salicifolia survived. Live branch material in this individual had died back to the ground. This result suggests that rooted plants are more likely than unrooted plants to become established without supplemental water.

Table 3-3. Survivorship and growth in native plants introduced into the unwatered *Tamarix ramosissima* plot at Wahweap.

SPECIES	% SURVIVORSHIP	MEAN GROWTH (M)		% SURVIVING PLANTS FLOWERING
		8/89-5/90	5/90-10/91	
Bacccharis salicifolia	20%	-0.192 (s.d.)	-0.03 (s.d.)	33%
B. emoryi	60%	-0.170 (s.d.)	0.06 (s.d.)	44%
Populus fremontii	0%	--	--	
Salix gooddingii	0%	--	--	

Naturally-Established Native Plants at Wahweap: Survivorship was high and growth was detected in a small population of Baccharis emoryi (n = 5) and Salix gooddingii (n = 4) found at the Wahweap site. Only 1 of 4 Salix gooddingii died in 1991, indicating a surprising tolerance of drought in this riparian species. While plant growth was lower than in nearby watered plants, positive growth was detected in both species (mean growth between 1990 and 1991: B. emoryi = 0.186 m, s.d = 0.291; S. gooddingii = 0.182 m, s.d. = .195). The survival of S. gooddingii, especially, suggests that native species will be able to persist along the shoreline if they are established when the lake elevation is high.

Lees Ferry Experiments: Growth of Native Riparian Plants in Pots with Tamarisk

The Lees Ferry interaction experiments in pots revealed a significant negative effect of tamarisk on several native species that was not realized in the Wahweap field experiment, even though the latter ran for a longer period of time. Baccharis emoryi and P. fremontii grew significantly less in pots with tamarisk than in pots with conspecifics (Table 3-4, 3-5). Both species grew only half as much in the presence of tamarisk, with P. fremontii growing less than any other species when in the presence of tamarisk. While these two native species appear to avoid negative interactions with tamarisk in the field, they

Table 3-4. Growth (m) of <u>Tamarix ramosissima</u> and native species in monospecific and bispecific plantings in he experimental garden at Lee's Ferry, Arizona, based on six months. * = $p < 0.01$.

SPECIES	INTERACTION	GROWTH (s.d.)
Baccharis salicifolia	with B. salicifolia	.488 (.190)
	with T. ramosissima	.473 (.237)
Baccharis emoryi*	with B. emoryi	.288 (.149)^{A}
	with T. ramosissima	.194 (.119)^{B}
Populus fremontii*	with P. fremontii	.357 (.207)^{A}
	with T. ramosissima	.171 (.097)^{B}
Tamarix ramosissima*	with T. ramosissima	.523 (.245)^{A}
	with B. salicifolia	.654 (.229)^{AB}
	with B. emoryi	.788 (.219)^{B}
	with P. fremontii	.718 (.279)^{AB}

Table 3-5. Analysis of native species interactions with *Tamarix ramosissima* and plant growth patterns in pot experiments at Lees Ferry, Arizona. Treatment = presence of tamarisk or a conspecific in pots; species = *Baccharis salicifolia*, *B. emoryi*, *Populus fremontii* and *Tamarix ramosissima*.

Variable	**Coefficent**	**T**	**P (2 Tail)**
Constant	4.722	27.209	0.000
Treatment	-0.002	-0.039	0.969
Species	-0.753	-8.252	0.000
Treatment * Species	0.057	3.070	0.002

SOURCE	**S.S.**	**DF**	**MEAN SQUARE**	**F**	**P**
Regression	57.104	3	19.0350	51.147	0.000
Error	101.970	274	0.372		

apparently cannot avoid them in the close confines of pots. Growth rates of B. salicifoli. were not influenced by the presence of tamarisk in the same pot (Table 4, 5).

The growth of tamarisk itself was also suppressed in the presence of tamarisk (Table 3-4). Tamarisk tended to grow more in pots containing native species than with tamarisk, and this pattern was significant in the presence of Baccharis emoryi (Table 3-4, 3-5).

Growth rates in all species were significantly different except for B. emoryi and P. fremontii (Table 3-4, 3-5). Tamarisk grew the most on average and B. emoryi grew the least.

Patterns in the amount of biomass that plants acquired generally agreed with growth patterns, although biomass accumulation was not significantly different whether plants were in the tamarisk presence or absence on (Table 3-6). Relative allocation to root versus shoot growth did not differ significantly between treatments, although there was a consistent trend of lower % root mass when plants were grown in pots with tamarisk (Table 3-6).

DISCUSSION

Four species of native plants were able to persist, grow and reproduce in close proximity to tamarisk in field experiments along the shoreline of Lake Powell. Tamarisk did not exert a negative, competitive effect on native plants over a two-year period. These results discount the notion that tamarisk is a highly competitive species, while supporting the contention that tamarisk's success in the Southwest results from other aspects of its natural history, such as abundant seed production, extensive dispersal abilities and drought tolerance (Stevens 1989). While establishment of native plants in tamarisk stands was especially successful with supplemental water, at least one Baccharis species became established in large numbers in an unwatered tamarisk stand. The persistence of naturally-established riparian species nearby, such as Baccharis emoryi and Salix gooddingii, further supports the conclusion that Lake Powell's shoreline plant communities can support a greater diversity of plant species. While tamarisk will probably never be eradicated from the Southwest, these findings suggest that biotic diversity in some of the riparian areas that it currently dominates, such as the shoreline of Lake Powell, can be successfully enhanced through proper management.

Experiments at Lees Ferry revealed that tamarisk can exert a strong competitive edge in interactions with some, though not all, native plants when they co-occur in pots. Rather than reflecting a discrepancy of results, the Lees Ferry findings represent an extreme outcome along a gradient of potential interactions between native plants and tamarisk. These results suggest that in an environment that is more saturated and productive than the Lake Powell shoreline, competitive interactions are more likely to occur.

Most of the native plant species studied have potential to thrive in the Lake Powell shoreline communities. *Baccharis emoryi*, seems like a particularly viable candidate to introduce into young tamarisk stands. It grows and reproduces with or without supplemented water, and the genus *Baccharis* is known to support a great array of insect species (Boldt and Robbins 1990). The success of *B. emoryi* in the experiments mirrors its success in other populations along Lake Powell, where it has persisted through several years of low lake elevations (see Chapter 3).

Introductions of other native species, including *Baccharis salicifolia*, *Populus fremontii* and *Salix gooddingii*, could be made when the elevation of Lake Powell reaches full pool again, and the results of this study indicate that such a program has a high probability of succeeding.

CHAPTER 4

THE FAUNA ASSOCIATED WITH TAMARISK STANDS ALONG LAKE POWELL, ARIZONA AND UTAH

INTRODUCTION

As nonnative plants such as tamarisk (Tamaricaceae: *Tamarix ramosissima* Deneb.) become established in riparian habitats, it is important to understand their capacity to support native animal species. This is especially important because southwestern riparian ecosystems can support high levels of faunal diversity (Knopf et al. 1988). While it is predicted that exotic plant species will have a negative influence on animal diversity, some studies indicate the opposite trend. Tamarisk-dominated riparian communities in Grand Canyon can support very high densities of many animal taxa, including reptiles (Warren and Schwalbe 1988), birds (Brown and Trosset 1989) and insects (Stevens 1976, 1985). These patterns suggest that invasions by this species into some riparian communities have no effect or a positive effect on riparian animal species.

The fauna associated with the tamarisk-dominated community along Lake Powell faces especially harsh conditions due to fluctuating lake levels that have left plants perched far above available water (see Chapter 2). The ability of such a community to support animal life is not known. However, the extensive shoreline of Lake Powell--longer than the west coast of the United States--has the potential to support a diverse riparian fauna, and thus stands to be a productive biological resource.

The emerging shoreline communities along the lake today are of recent origin and this study is the first report of their development. Here I present the results of a preliminary survey of the major animal taxa associated with tamarisk-dominated communities along Lake Powell. In this study, the tamarisk-associated fauna are also compared with those in other native and tamarisk-dominated systems today, and prior to the construction of Glen Canyon Dam.

STUDY SITES

Extensive colonization of Lake Powell's shoreline by tamarisk and other plant species occurred in the early 1980's as the lake filled to capacity (1,138 m or 3,700 ft) for the first time. These plant communities are now strongly dominated by tamarisk, with low densities of native riparian species also occurring (see Chapter 2). The basin and surrounding shoreline are comprised of sandstones, especially Navajo sandstone. The shoreline plant communities are backed by upper Sonoran flora including narrow leaf yucca (Yucca angustissima), Mormon tea (Ephedra viridis), black brush (Coleogne ramosissima), grasses and cacti (Clover and Jotter 1944).

METHODS

In June 1990, animal censuses were conducted in tamarisk stands at 14 shoreline sites. These included sites along open lake (n = 8), on Antelope Island (n = 2), and in side canyons (n = 4) (Table 4-1).

Vegetation: At each site a 100 m transect was established in the vegetation stand and vegetation was censused in 1.0 m^2 plots at 3 m intervals. The side of the transect and distance from the line for establishing the plots were randomly determined. A minimum of 33 m^2 of vegetation was measured for plant density and size (ht in meters) at each site.

Reptiles: Belt transects were censused for reptiles using a modified Emlen (1971) technique. This method involved walking a 5 m-wide belt transect 100 to 300 m long and recording all individuals observed. Multiple parallel transect belts were censused at each site, depending on plot size. Densities are reported as abundance per hectare (ha). Reptiles observed outside the census plot or time period were also recorded.

Birds: A modified Emlen (1971) belt transect technique was used to measure absolute densities of birds. This involved walking slowly through the transect, stopping at 20 m intervals, looking and listening and recording all individuals encountered. Belt width was 20 m. Bird censuses were conducted between 4 and 6 am. Time of census start and close and general weather conditions were noted.

Table 4-1. *Tamarix ramosissima* study sites along Lake Powell.

SITE NO.	LOCATION	HABITAT TYPE
1.	Wahweap Bay	Open lake
2.	Lone Rock Beach	Open lake
3.	Antelope Island	Island
4.	Antelope Island	Island
5.	Romana Bench	Open lake
6.	Romana Bench	Open lake
7.	E. of Gregory Butte	Open lake
8.	Dominguez Butte	Open lake
9.	Rock Creek	Canyon
10.	W. of Rock Creek	Canyon
11.	N. of San Juan confluence-West	Open lake
12.	N. of San Juan confluence-East	Open lake
13.	Llewellyn Gulch	Canyon
14.	Cottonwood Canyon	Canyon

Densities are reported as abundance/ha. Individuals occurring outside the census plot or time period were also noted. Occurrence of nests in tamarisk was also noted.

Mammals: Each site was sampled with 100 Sherman live traps for one night (= 100 trapnights/site), using the standard methods outlined in Brower and Zar (1984). One hundred traps were set out at 5 m intervals after 5 pm and each trap was baited with oatmeal and peanut butter. Traps were checked between 4 and 6 am. Mammal densities are reported as numbers trapped per 100 trapnights. The weight and sex of captured individuals were measured.

Arthropods: Arthropods including insects and spiders were sampled on tamarisk by vigorously sweepnetting plants 100 times (100 sweeps, Brower and Zar 1984). Samples were killed with ethyl acetate and stored in vials containing 70% ethanol. In the laboratory, individuals were categorized according to taxonomic order and in some cases family, and counted. Numbers of morphological types or taxa per sample were also determined, although specimens were not identified to specifies level. Densities are reported as numbers per 100 sweeps. Time of day and general weather conditions were recorded.

Analyses: Species richness (= number of species), densities and species diversity (H') were calculated for each taxon (reptiles, birds, etc.) from each site. The Shannon diversity index or H' is derived from $H' = -\sum p_i \log p_i$, where $p_i = n_i/N_i$ (Brower and Zar 1984). This index of species diversity takes both numbers of species and densities into account. The relationships among numbers of species and densities within and between taxa (e.g. reptile densities and arthropod densities) were determined with Pearson's correlation analysis, using the Bonferroni probability adjustment to control for Type I errors (SYSTAT 1989). Multiple analysis of variance (MANOVA) was used to test for differences in species richness, densities and H' among the taxa between sites on open lake shoreline, islands and in tributary canyons (SYSTAT 1989).

RESULTS

Faunal diversity and distributions

More than 40 species of reptiles, birds, mammals and 30 species of arthropods were found in tamarisk stands along Lake Powell's shoreline in this survey (Table 2,3). An additional 16 vertebrate species were observed outside the survey (Table 4-2,4-3).

Species richness and densities were greater among arthropods than any other taxa found in tamarisk stands, while reptile species numbers and densities were lowest (Table 4). The diversity of birds was higher than that of any other vertebrate taxon, as measured by H' (Table 4-4).

There were no significant patterns in the distributions of the different taxa relative to one another, based on a Pearson's correlation analysis and Bonferroni adjusted probabilities. That is, numbers of species and densities of

II. BIRDS (cont.)

Alaudidae:
- Eremophila alpestris (Horned lark)
- Tachycineta thalassina (Violet-green swallow)
- Stelgidopteryx serripennis (Rough-winged swallow)
- Hirundo pyrrhonota (Cliff swallow)
- Hirundo rustica (Barn swallow)

Corvidae:
- Corvus corax (Common raven)

Troglodytidae:
- Catherpes mexicanus (Canyon wren)*
- Salpinctes obsoletus (Rock wren)

Muscicaipidae:
- Polioptila caerulea (Blue gray gnatcatcher)

Emberizidae:
- Dendroica petechia (Yellow warbler)
- Unknown parulid*
- Amphispiza bilineata (Black-throated sparrow)
- Passer domesticus (English sparrow)*

Icteridae:
- Sturnella neglecta (Western meadowlark)
- Xanthocephalus xanthocephalus (Yellow-headed blackbird)
- Icterus galbula (Northern oriole)*

Fringillidae:
- Carpodacus mexicanus (House finch)

III. MAMMALS:

Heteromyiidae:
- Perognathus longimembris (Little pocket mouse)
- Perognathus amplus (Arizona pocket mouse)
- Perognathus formosus (Long-tailed pocket mouse)
- Dipodomys ordii (Ord kangaroo rat)

Cricetidae:
- Reithrodontomys megalotis (Western harvest mouse)
- Peromyscus crinitus (Canyon mouse)
- Peromyscus maniculatus (Deer mouse)
- Peromyscus boylei (Brush mouse)
- Peromyscus truei (Pinyon mouse)
- Onychomys leucogaster (Northern grasshopper mouse)
- Neotoma lepida (Desert woodrat)

Table 4-2. Animal taxa found in _Tamarix_ _ramosissima_ stands along Lake Powell, June, 1990. * = collected outside of census.

I. REPTILES AND AMPHIBIANS:

Lizards:

Iguanidae:
- Sceloporus magister (Desert spiny lizard)
- Uta stansburiana (Side-blotched lizard)
- Phrynosoma platyrhinos (Desert horned lizard)
- Iguanid sp. ?

Teiidae:
- Cnemidophorus tigris (Western whiptail)

Snakes:

Crotalidae:
- Crotalus viridis (Western rattlesnake)

Outside of census:

- Bufo punctatus (Red-spotted toad)*
- Crotaphytus wislizenii (Leopard lizard)*

II. BIRDS:

Cathartidae:
- Cathartes aura (Turkey vulture)*

Phasianidae:
- Callipepla gambelii (Quail)

Columbidae:
- Zenaida macroura (Mourning dove)

Caprimulgiidae:
- Chordeiles acutipennis (Lesser nighthawk)*

Apodidae:
- Aeronautes saxatalis (White-throated swift)

Trochilidae:
- Archilochus alexandri (Black-chinned hummingbird)

Tyrannidae:
- Tyrannus vociferans (Cassin's kingbird)*
- Myiarchus tyrannulus (Ash-throated flycatcher)
- Empidonax sp. ? (flycatcher)*
- Sayornis saya (Say's phoebe)

the different taxa did not covary significantly with one another across the 14 sites (Table 4-5). There was, however, a strong positive correlation between number of reptile species and densities ($r = .809$, $P = .07$); and between bird species richness and densities ($r = .785$, $P = .12$; Table 4-5). Such patterns reflect the similar ecological needs exhibited within these taxonomic groups. This information should be useful in efforts to manage for biodiversity in Lake Powell's shoreline communities. By contrast, arthropod communities on tamarisk were typically dominated by a phloem-sucking leafhopper or by pollinating flies, leading to a poor correlation between species richness and densities (see Arthropod section below).

Densities of arthropods were significantly higher on tamarisks in tributary canyons than on the lake shoreline or on islands (Table 4-6, 4-7). Arthropod densities were nearly four times higher on tamarisk in canyons than in the other habitats. Diversity and abundance also tended to be greater in populations of reptiles, birds and mammals in canyons, although these patterns were not significant. These environments may be more productive than open lake habitat, due to more water availability in perennial streams and/or closer proximity to populations of native plants and animals. Canyon sites are also better protected than the open lake sites, leading to a more stable environment. There were strong, though nonsignificant, differences in plant densities between the three types of sites, with

Table 4-4. Average number of species (# SP), density, and diversity (H') in <u>Tamarix</u> <u>ramosissima</u> stands along Lake Powell.

REPTILES			BIRDS			MAMMALS			INSECTS		
# SP	DENSITY/ HECTARE	H'	# SP	DENSITY/ HECTARE	H'	# SP	DENSITY/ 100 TRAPS	H'	# SP	DENSITY/ 100 SWEEPS	H'
1.21	.399	.106	3.57	0.96	.442	2.64	8.71	.298	7.91	391.27	.39[illegible]
(1.05)	(.59)	(.16)	(2.50)	(1.01)	(.28)	(1.50)	(6.70)	(.22)	(3.11)	(339.85)	(.2[illegible]

Table 4-3 (cont.)

SPECIES	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	TOTAL
ARTHROPODS:															
ARACHNIDA:	1		1	2	3		5	2	13	8	3	4			42
INSECTA:															
Ephemeroptera	1														1
Orthoptera	1		2												3
Thysanoptera	12			12			6	15	10	19					74
Hemiptera															
Reduviidae	1											1			2
Other	5									1		3			9
Homoptera															
Cicadellidae	17		19	399	36		625	114	818	798	141	169			3136
Other			1	62		48		88	34	1		17			251
Neuroptera									1	2		2			5
Coleoptera			1		2		1	1	7	1		14			27
Lepidoptera										2	3	1			6
Diptera	15		18	29	221		18	9	47	23	59	69			508
Hymenoptera															
Formicidae	3		8	2			4	8	36	3	4	3			71
Wasps and bees			2	13	2		33	29	38	35	4	6			162
Unknown	1						3	1	1			1			7
Number	54		52	519	264	48	695	267	1005	893	217	290			4304

Table 4-3 (cont.)

SPECIES	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	TOTAL
MAMMALS:															
Perognathus longimembrus					1				13	9					23
P. amplus														1	1
P. formosus									1				3		4
Dipodomys ordii	1	6	3	3	3	3		2	3					2	26
Reithrodontomys megalotis		1			1								2	1	5
Peromyscus crintius											6	1	1		8
P. maniculatus			10	5	2	19	3	1	2	3			2		47
P. boylei													1		1
P. truei	1														1
Onychomys leucogaster	1					1									2
Neotoma lepida									2				2		4
Lepus californicus		1*		3*					1*						
Sylvilagus nuttall i	1*		1*	1*		1*									
Ammospermophilus sp.					1*							1*			
Canis latrans					1*										
Fox or ringtail					1*										
Number	3	7	13	8	7	23	3	3	21	12	6	1	11	4	122
No. of species	3	2	2	2	4	3	1	2	5	2	1	1	6	3	11

Table 4-3 (cont.)

SPECIES	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	TOTAL
BIRDS:															
Archilochus alexandri									1						1
Chordeiles acutipennis			1*												-
Tyrannus vociferans			1*												-
Cathartes aura											1*			1*	-
Callipepla gambelii									1						1
Zenaida macroura	4		2*					1					1		6
Aeronautes saxatalis													1		1
Myiarchus tyrannulus				2*	1*				1,1*			1*	2*	1	2
Empidonax sp. ?													1*		-
Sayrunis saya									many*	1					1
Eremophila alpestris				3*	2,2*		14,1*								16
Tachycineta thalassina			4*	4*			@						1,3*	2*	2
Stelgidopteryx serripennis	2				1*		@							1	4
Hirundo pyrrhonota		1													1
Hirundo rustica					1	1	@								3
Unknown swallow						1	1								2
Corvus corax	7	2			2		5				1*		1,1*	1*	17
Catherpes mexicanus											2*	1*	1*	1*	-
Salpinctes obsoletus								1	1*				1,1*		2
Polioptila caerulea														2	2
Dendroica petechia	2						2*								2
Unknown Parulid									1*						-
Amphispiza bilineata			1*	2*	2	2,2*	3	5,2*	1,2*					1,1*	14
Passer domesticus	1*														-
Xanthocephalus anthocephalus	1					1,1*									2
Icterus galbula									1*						-
Carpodacus mexicanus	8	1	1*				1*	4	2*	3	2,3*	1*	1	4	23
Unknown						2	3,1*		1		1				7
Number	24	4	-	-	7	7	29	11	5	4	3	-	6	9	109
No. of Species	6	3	0	0	4	5	8	4	5	2	2	0	6	4	19+

Table 4-3. Number of animals encountered during 1990 census of shoreline *Tamarix ramosissima* stands. * = observation near site boundaries or not during census period; @ = numbers not established.

SPECIES	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	TO
AMPHIBIANS:															
Bufo punctatus											1*				
REPTILES:															
Sceloperus magister		1*							1*	1			3*		1
Uta stansburiana	2	1	1	3			1*	1	4,1*	5	2	7	1*	1*	26
Phrynosoma platyrhinos					1										1
Iguanid sp. ?		1													1
Cnemidophorus tigris		2		1*					1	8	1*	1	4*	1*	12
Crotalus viridis											1				1
Crotaphytus wislizenii				1*											-
Number	2	4	1	3	1	0	0	1	5	14	3	8	0	0	41
No. Species	1	3	1	1	1	0	0	1	2	3	2	2	0	0	6

Table 4-5. Pearson correlation matrix of species numbers and densities of reptiles, birds, mammals and arthropods in _Tamarix ramosissima_ communities along Lake Powell. Bartlett's Chi square = 36.85, df = 28, P = .122.

	REPTILE SP	REPTILE NO	BIRD SP	BIRD NO	MAMMAL SP	MAMMAL NO	INSECT SP	INSECT NO
REPTILE SP	--							
REPTILE NO	.809	--						
BIRD SP	-.486	-.399	--					
BIRD NO	-.273	-.210	.785	--				
MAMMAL SP	-.008	-.151	.316	.162	--			
MAMMAL NO	-.019	-.087	.054	-.200	.593	--		
INSECT SP	-.613	.671	-.188	.179	-.166	-.441	--	
INSECT NO	-.448	.438	.155	-.002	.202	.202	.430	--

Table 4-6. Average number of species (# SP), density, and diversity (H′) in *Tamarix ramosissima* stands along open lake, on Antelope Island and in side canyons of Lake Powell. Standard deviation in parentheses below means. * = P < .05.

HABITAT TYPE:	REPTILES # SP	REPTILES DENSITY/ HECTARE	REPTILES H′	BIRDS # SP	BIRDS DENSITY/ HECTARE	BIRDS H′	MAMMALS # SP	MAMMALS DENSITY/ 100 TRAPS	MAMMALS H′	INSECTS # SP	INSECTS DENSITY/ 100 SWEEPS	INSECTS H′
OPEN LAKE	1.25	.353	.111	4.00	1.16	.482	2.12	6.62	.215	7.27	262.14	.395
(N = 8)	(1.03)	(.54)	(.17)	(2.45)	(1.26)	(.24)	(1.13)	(6.96)	(.22)	(3.64)	(215.42)	(.26)
ISLAND	1.00	.161	.000	0.00	0.00	.000	2.00	10.50	.261	7.50	285.50	.510
(N = 2)	(0.0)	(.12)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(3.54)	(.04)	(.71)	(330.22)	(.21)
CANYON	1.25	.609	.150	4.50	1.06	.584	4.00	12.00	.483	10.50	949.00*	.295
(N = 4)	(1.50)	(.83)	(.24)	(1.73)	(.21)	(.24)	(1.83)	(6.98)	(.20)	(.71)	(79.20)	(.09)

Table 4-7. Numbers of species, densities and diversity of animals in *T. ramosissima* stands according to habitat, including open lake, islands and canyons of Lake Powell.

	FACTOR/ P =			
1. NUMBER OF SPECIES:	**REPTILES**	**BIRDS**	**MAMMALS**	**ARTHROPOD**
Wilk's Lambda = .494 F = 1.537, df = 4,6, P = .303	.057	.448	.274	.257
2. DENSITIES:	**REPTILES**	**BIRDS**	**MAMMALS**	**ARTHROPOD**
Wilk's Lambda = .265 F = 4.159, df = 4,6, P = .060	.172	.541	.091	.012
3. DIVERSITY:	**REPTILES**	**BIRDS**	**MAMMALS**	**ARTHROPOD**
Wilk's Lambda = .415 F = 2.112, df = 4,6, P = .197	.078	.558	.386	.770

canyon sites tending to have the highest densities and island sites the lowest, densities of tamarisk (mean # tamarisk/m^2, lake = 4.38, s.d. 1.98; island = 1.78, s.d. = 1.10; canyon = 15.87, s.d. = 13.68; df = 2, 10; P = .07). Plant densities may also have contributed to these trends in animal distributions, as well as reflecting more productive environments. The distributions of animals in these three types of habitats deserve further study.

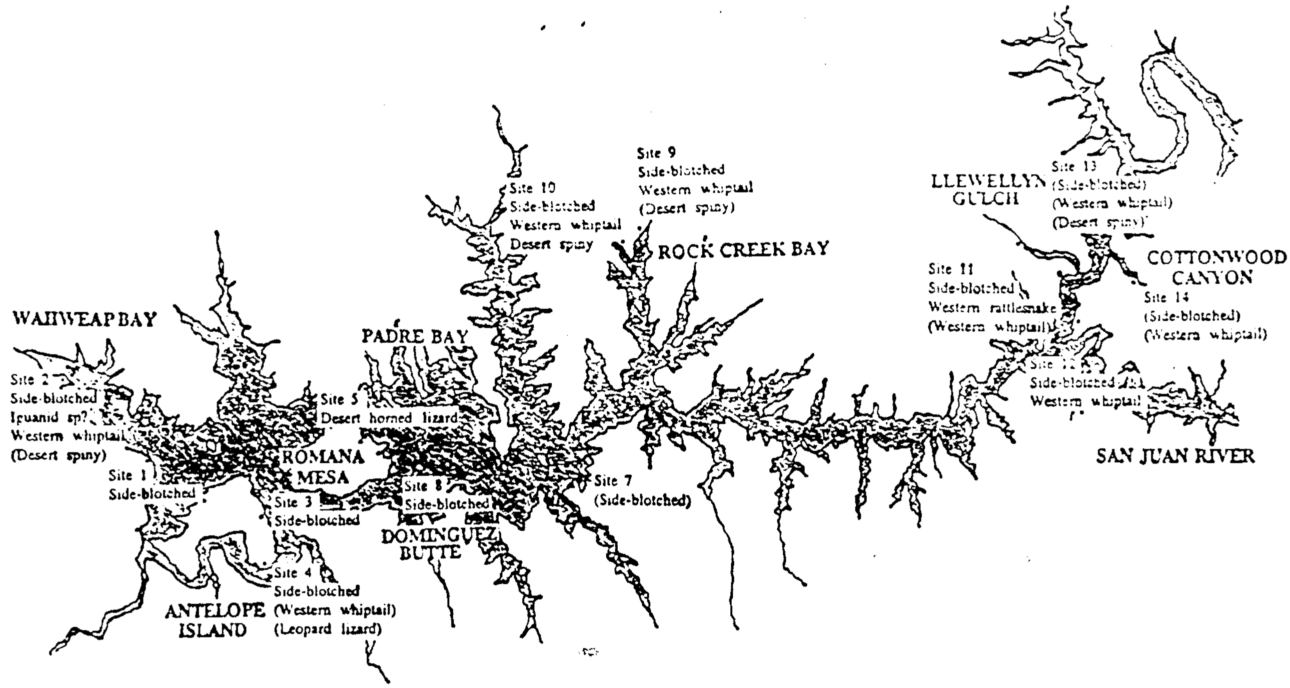
There was no significant relationship between species numbers, densities and H′ and tamarisk height.

Taxa

Amphibians: No amphibians were seen in tamarisk stands during the survey, probably due to the extremely dry conditions existing there. However, the red-spotted toad (Bufo punctatus) was seen at a small spring adjacent to site # 11, approximately 800 m south of Llewellyn Gulch. Amphibians in this system are probably restricted to wet and productive environments such as springs and tributary canyons with perennial streams. The red-spotted toad is widely-distributed through the Grand Canyon to the southwest, and feeds on small arthropods, while serving as a resource for predators including birds, skunks and ringtail cats (Miller et al. 1982). Woodbury (1959) found this species to be common in Glen Canyon in the 1950′s, and located populations with several kilometers of this site.

Reptiles: Six reptile species were encountered during the survey and an additional species, the leopard lizard (Crotaphytus wislizeni), was seen outside the survey (Table 4-3, Fig. 4-1). The side-blotched lizard, Uta stansburiana, was more commonly encountered than any other reptile species in the survey (Table 4-3), representing an important insect predator in this system. Next most common was the western whiptail (Cnemidophorus tigris). The desert spiny lizard (Sceloporus magister) was seen at only one site during the survey, although it was found at several other locations outside the survey (Table 4-3). The desert horned lizard (Phrynosoma platyrhinos), western rattlesnake (Crotalus viridis) and an unknown iguanid were each seen once during the survey (Table 4-3).

Uta stansburiana, Cnemidophorus tigris and Sceloporus magister were also found to be most abundant in a lizard survey in the riparian zone in Grand Canyon (Warren and Schwalbe 1988); and the pattern of their abundance relative to one another was also the same as in this study: side-blotched lizards > western whiptails > desert spiny lizards. Woodbury (1959) also found these species to be common in Glen Canyon prior to the completion of Glen Canyon Dam. The highest number of lizards was found at Site # 10 (western tributary of Rock Creek). The high level of human refuse evident at this site and high arthropod densities may have contributed to high lizard densities.



LAKE POWELL
GLEN CANYON NATIONAL RECREATION AREA
UTAH AND ARIZONA

Figure 4-1. Distributions of reptile species encountered in a survey of Tamarix ramosissima stands along Lake Powell.

Densities of reptiles were 30 times lower in tamarisk stands along Lake Powell than along the Colorado River in Grand Canyon. Warren and Schwalbe (1988) found an average of 141 lizards/ha in open tamarisk stands along the Colorado river in Grand Canyon in 1986, while this survey found approximately 4 lizards/ha in open tamarisk stands. It is probably significant that Warren and Schwalbe sampled tamarisk stands within close proximity to the Colorado River, while the tamarisk stands sampled in this study were more than 20 m (65 ft) above the water line, resulting in a less productive environment. It seems likely that productivity in Lake Powell's shoreline communities is greater during periods when the lake level is higher, and perhaps densities of reptiles also increase during these periods. However, Beus et al. (1991) reported that more than half of the riparian lizards collected in a Grand Canyon survey had fed on aquatic derived invertebrates such as chironomid midges and buffalo gnats, which suggests that low biotic productivity in Lake Powell may also limit lizard densities.

Despite lower lizard densities in tamarisk stands along Lake Powell than in Grand Canyon, the structure of lizard communities in these two regions are strikingly similar with regards to the species that dominant them and their relative abundances.

Birds: Nineteen species of birds and several unknown species were counted in a census of the 14 tamarisk stands

(Table 4-3, Fig. 4-2). An additional 8 species were observed outside the census period or the boundaries of the plots (Table 4-3). The mean number of bird species per site was 3.64 (s.d. = 2.50; range = 0 to 8). Low numbers of bird species have also been reported in tamarisk stands on the lower Colorado River, although the lower elevation and latitude of those study areas may have influenced the findings (Ohmart et al. 1988).

Most bird species observed were facultative or obligate insectivores, as has been found in other riparian ecosystems (e.g., Stevens et al. 1977). More than 75% of the species in this census were insectivorous, as were more than 50% of species observed outside the census, and presumably the arthropod community associated with tamarisk is an important resource for these species.

At least 8 of the 19 (42%) species in the census are thought to breed only in riparian habitat (Table 4-3). This number of breeding species is lower than that reported for other southwestern riparian habitats that are comprised of native vegetation and receive more water (e.g. Stevens et al. 1977, Carothers et al. 1974). It is, however, in accord with the results of a study in Grand Canyon, in which 11 obligate riparian bird species were found to nest in tamarisk as well as in native riparian vegetation (Brown and Trosset 1989). Black-throated sparrow nests were found in tamarisk at two Lake Powell sites (Antelope Island and Dominguez Butte), and may represent a new nesting record for

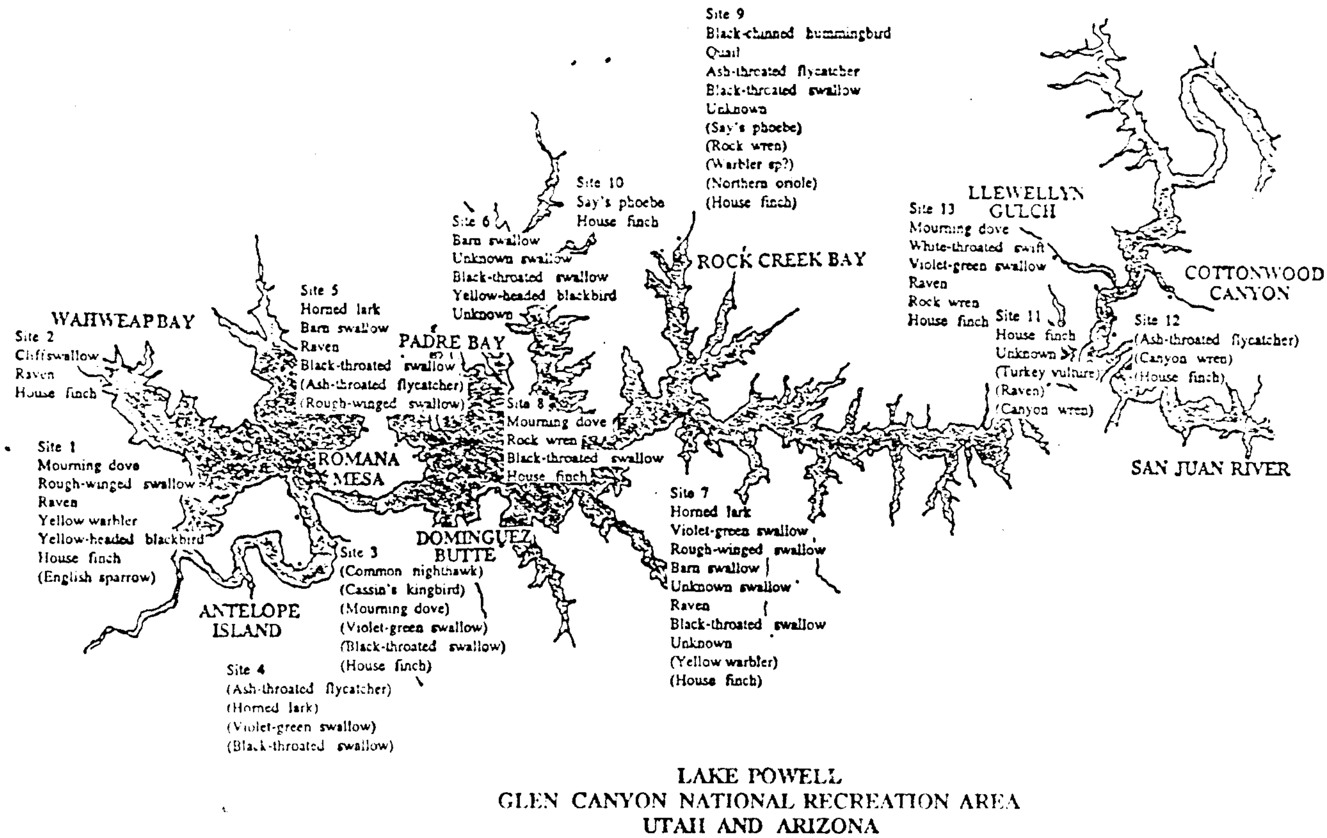


Figure 4-2. Distributions of bird species encountered in a survey of Tamarix ramosissima stands along Lake Powell.

this desert species. Black-throated sparrows also exhibited foraging behavior among the tamarisk at these sites.

Mean density of birds was 9.01/ha (s.d. = 9.27; range = 0 to 34.37/ha). Unfortunately, there is no quantitative description of pre-dam bird densities in Glen Canyon with which to compare these patterns. However, the mean number of species and densities of birds in this census were 2 to 4 times lower than those found in stands of native riparian vegetation in Arizona (mean # species, range = 2.3 to 7.3/ha; mean densities, range = 8.5 to 47.8/ha; Stevens et al. 1977). House finches were seen more than any other species (21%, n = 23), followed by horned larks (15%, n = 16), ravens (16%, n = 17) and black-throated sparrows (12%, n = 13). These four species were also found to be common in the 1950's (Behle and Higgins 1959). No other species comprised more than 5% of the total number of birds seen in the current census. One large flock of violet-green swallows, rough-winged swallows and barn swallows was seen during the census at site # 7.

We briefly observed either a willow flycatcher or western flycatcher at site # 13 (Lewellyn Gulch) during this study. The willow flycatcher, <u>Empidonax</u> <u>traillii</u> <u>eximus</u>, was described as a common summer resident in Glen Canyon during the 1950's (Behle and Higgins 1959), although it is on the brink of extinction today (Brown et al. 1987). The largest population, consisting of two pairs, occurs downstream in Marble Canyon (L. Stevens, personal communication). The western flycatcher was considered rare in the 1950's (Behle and Higgins 1959). Empidonax populations in Glen Canyon should be monitored.

The highest numbers of bird species and densities were found at the Wahweap site (# 1) and at site # 7 due east of Gregory Butte (Fig. 4-2). The vegetation at the Wahweap site included native species such as Salix gooddingii and Baccharis emoryi, several Russian olives, and an experimental garden containing numerous native plants and supplemental water (see Chapter 2). Carothers et al. (1974) also found that augmented water availability increased the abundance of birds at riparian sites in the Verde Valley. The Gregory Butte site was located along a wide bench with high densities of tamarisk seedlings and Russian thistle, which represents attractive habitat to the horned larks and swallows that were abundant there. Horned larks are predominantly granivores, feeding on seeds of annual plants.

Mammals: Eleven species of rodents were collected in the live trap survey at the 14 sites (Table 4-3, Fig. 4-3). Three species comprised more than 75% of all individuals encountered: the deer mouse (Peromyscus maniculatus) was the most commonly encountered (38% of all individuals), followed by Ord's kangaroo rat (Dipodomys ordii)(21%), and the little pocket mouse (Perognathus longimembrus)(18%). Outside the survey we also found evidence of antelope ground squirrels, coyote and fox or ringtail (Table 4-3).

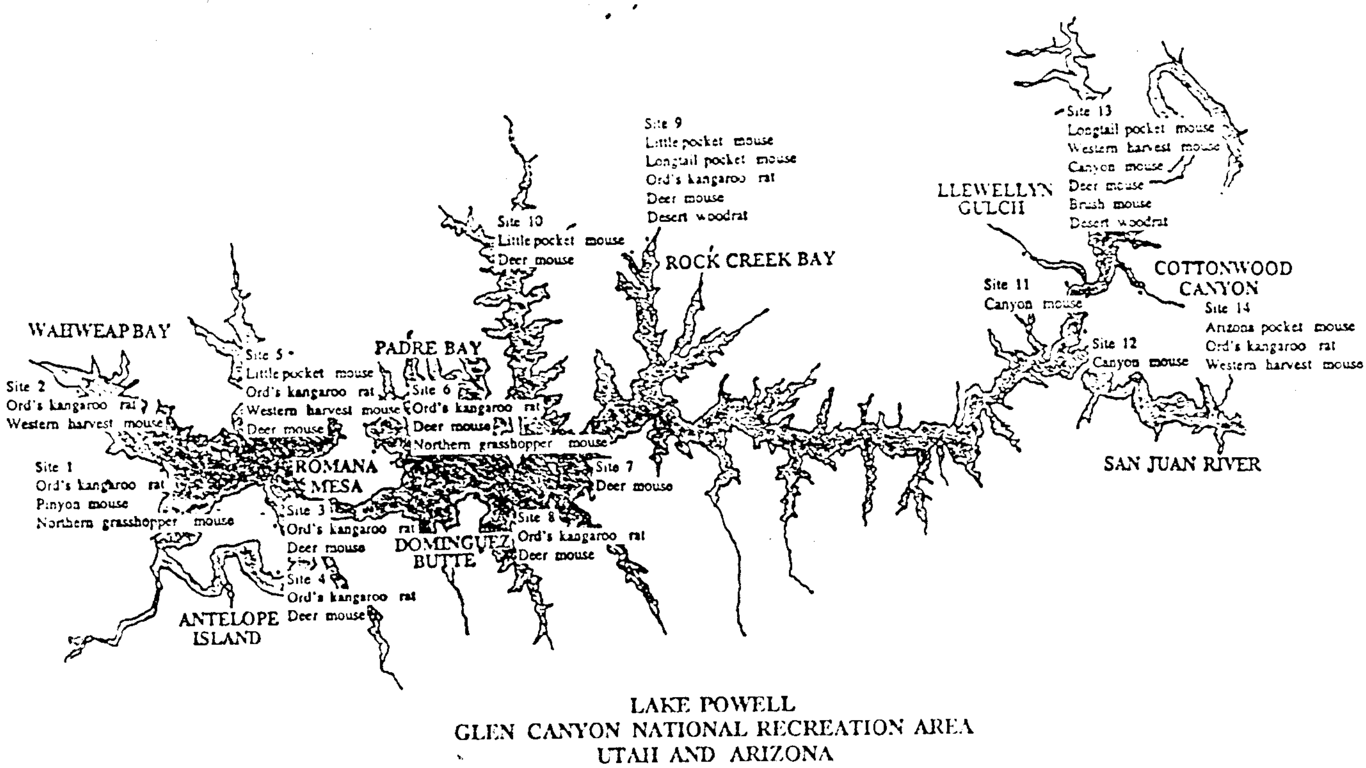


Figure 4-3. Distributions of mammal species encountered in a survey of Tamarix ramosissima stands along Lake Powell.

In 1958, Durrant and Dean (1959) collected 20 small mammal species in a survey of 14 sites on river terraces and banks in Glen Canyon. Durrant and Dean (1959) also found _P. maniculatus_ to be more common than other species along the pre-dam Colorado River in Glen Canyon (33% of all individuals encountered). However, the other common species in their survey differed from this study; they included the brush mouse (_Peromyscus boylii_)(17%) and the canyon mouse (_P. crinitus_)(17%). These species have also been reported from Grand Canyon downstream (Carothers and Aitchison 1976). No other species comprised more than 10% of the individuals collected in the traps.

The mean number of species encountered per site was 2.64 (s.d. = 1.44; range = 1 to 6 species per 100 trapnights) (Table 4-4). Average trapping success per night was 8.36% (s.d. = 6.30; range = 1 to 23 individuals per 100 trapnights). Durrant and Dean (1959) reported a higher trap success of species (mean per site = 4.64, s.d. = 1.10; range = 1 to 33), and individuals (mean per site = 15.43%, s.d. = 7.30; range = 6 to 33) on river terraces and banks, based on 100 trapnight sampling.

The findings of the Durrant and Dean (1959) survey and the current survey differ markedly, indicating that there has been a substantial loss of species and densities of mammals during the shift in habitat from riverine to lacustrine in the last 30 years. Durrant and Dean (1959) found additional species of ground squirrels, chipmunks, woodrats (Neotoma albigula, N. mexicana, N. cinerea), and pocket mice (Perognathus parvus). The lower productivity of the tamarisk community along Lake Powell explains some of these discrepancies; however, substantial habitat alteration must account for some of the faunal change. For instance the canyon mouse was one of the more commonly encountered rodent species in Glen Canyon during the 1950's (Durrant and Dean 1959); however, canyon habitat has been lost in the main channel with the development of Lake Powell and as a consequence this species was found only in canyon tributaries of the lake in this survey. Some differences may be also attributable to Durrant and Dean's use of snap traps as opposed to the live traps used in this study.

Sex ratios of several rodent species deviated considerably from 1:1 (Table 4-8). Nine times as many female as male Perognathus longimembrus were found, while twice as many male Peromyscus maniculatus were found. Weights of individuals generally corresponded to published weight ranges for these species (Burt and Grossenheider 1976) (Table 4-8).

Arthropods: Eleven classes of arthropods were found in Lake Powell's tamarisk stands (Table 4-3). The most abundantly represented taxa included plant sucking bugs (Homoptera) and flies (Diptera) (Table 4-3). Although most arthropods were not identified below class or occasionally family level, up to 32 different arthropod morphs were found in some samples from some sites, reflecting a high level of

Table 4-8. Sex and weight of small mammal species collected during the Lake Powell animal survey.

SPECIES	SEX F/M	WEIGHT (g)/(s.d.) FEMALE	MALE
Perognathus longimembrus	18/2	8.35 (1.156)	7.90 (1.64)
Perognathus amplus	1/0	11.00 (--)	
Perognathus formosus	2/2	13.50 (7.07)	15.75 (1.06)
Dipodomys ordii	12/12	52.77 (4.17)	58.00 (8.88)
Reithrodontomys megalotis	1/3	10.50 (--)	11.75 (1.77)
Peromyscus crinitus	6/2	15.00 (4.43)	22.00 (6.34)
Peromyscus maniculatus	14/32	16.84 (6.14)	15.54 (4.13)
Peromyscus boylei	0/1	17.50 (--)	
Peromyscus truei	0/1	--	30.00 (--)
Onychomys leucogaster	1/2	33.00 (--)	34.00 (--)
Neotoma lepida	1/3	-- --	-- --

a is
s[redacted] in
n[redacted]
h[redacted]
h[redacted]t
well
e[redacted]a),
a),
[redacted]a)

e[redacted]-4).
eps of
d[redacted]

eber,
l[redacted]cted
ost
s[redacted]in
v[redacted]al
3[redacted].
a[redacted]
ed
s[redacted]that
s that
9[redacted]5,
l[redacted]tatus

promote the buildup of
es (Stevens 1985). This
food source for many
d reptiles) encountered in

ON

e Powell support a diverse
ater. Tamarisk is more
gested of nonnative
more productive than open
oductive than island
useful in future
nt of diversity in
ing ecosystem is young and
n may reveal that
It seems likely that
jected to fluctuating
ity of fauna and flora
ondence to lake
unity being most
ds of high lake levels.

CHAPTER 5

CONCLUSIONS AND RECOMMENDATIONS

The shoreline communities of Lake Powell are resilient, diverse and complicated. Despite four years of severe water stress, these communities are persisting, with relatively little mortality and supporting a fauna containing more than 70 species of animals. When the biotic diversity of this system is compared with other, more productive systems, it is lower, and it is clear that there has been a considerable loss of species since the formation of the lake. However, this system is young, dynamic and unique, making such comparisons not entirely valid. Lake Powell's shoreline biota represents an ongoing experiment. Long-term monitoring based on the methods of this study, including the use of the permanent study plots, will be necessary to follow the health of this system that exists at the mercy of power demands and a variable climate.

Experiments and observations revealed that native plant species can persist, grow and reproduce in the presence of tamarisk. This suggests that it will be possible to manage for increased diversity in the shoreline plant communities, which in turn will lead to a more diverse fauna. The survival of naturally established, as well as experimentally established, native plants suggests that they may be able to persist under the highly variable conditions that are an integral part of this system.

The results of this study provide many details of how to maximize the success of a planting program, including what species to use, and when and where to introduce them. The optimal time to introduce most species will be when the lake again reaches full pool. However, it may be prudent to reassess the health of the existing community at that time, to guarantee that such a program is feasible.

The perennial tributaries of Lake Powell represent refugia for highly diverse and productive riparian communities. These areas are worthy and in need of further understanding and better protection. Their increasing insularity makes them all the more fragile, and may jeopardize the future of their populations and species. Species that are currently threatened were found in many of these side canyons during the 1950's, necessitating a survey of these areas. Grazing, which occurs in many of them, should be stopped or regulated. These habitats are also important sources for future colonization of Lake Powell's shoreline.

Although animal diversity is lower in the lake shoreline communities than in native communities or tamarisk stands in Grand Canyon, a surprising number of species are represented. Many features of the existing communities, including key species and dominant species occupied similar positions in communities that existed in Glen Canyon prior to the lake. The greatest diversity of animals seems to be in the wet tributaries, providing one more reason for their protection and monitoring. Several species, including possibly the willow flycatcher, are at risk throughout their ranges, and surveys of the appropriate habitat should be conducted to assess their presence in the recreation area.

These results lead to the prediction that shoreline biotic diversity will increase with time, while also fluctuating inversely with lake elevations. These predictions should be tested in the years to come.

LITERATURE CITED

Behle, W.H. and H.G. Higgins. 1959. Birds of Glen Canyon. In Dibble, C.E., ed., Ecological studies of the flora and fauna in Glen Canyon. Univ. Utah, Anthropological Papers No. 40, Salt Lake City.

Beus, S.S., L.E. Stevens and F.Lojko. 1991. Colorado River studies: 1991 Annual Report. Grand Canyon National Park, Grand Canyon.

Black, C.A. 1965. Methods of soil analysis. Part One: Physical and mineralogical properties, including statistics of measurement and sampling. American Society of Agronomy, Inc. Madison, WI.

Bodman, G.B. and Mahmud, A.J. 1932. The use of the moisture equivalent in the textural classification of soils. Soil Sci. 33:363-374.

Boldt, P. and T.O.Robbins. 1990. Phytophagous and flower-visiting insect fauna of Baccharis salicifolia (Asteraceae) in the southwestern United States and northern Mexico. Environ. Entomol. 19:515-523.

Brower, J.E. and J.H. Zar. 1984. Field and laboratory methods for general ecology. William Brown Publ., Dubuque, Iowa.

Brown, B.T., S.W. Carothers and R.R. Johnson. 1987. Grand Canyon birds. University of Arizona Press, Tucson.

Brown, B.T. and R.R. Johnson. 1988. Fluctuating flows from Glen Canyon Dam and their effect of breeding birds of the Colorado River. Glen Canyon Environmental Studies, Executive Summaries of Technical Reports. Bureau of Reclamation. Nat. Tech. Inform. Serv. Rept. No. PB88-183512/AS, Springfield, VA.

Brown, B.T. and M.W. Trosset. 1989. Nesting-habitat relationships of riparian birds along the Colorado River in Grand Canyon, Arizona. Southwestern Naturalist 34:260-270.

Burt, W.H. and R.P Grossenheider. 1976. A field guide to the mammals. Houghton Mifflin Company Boston.

Carothers, S.W. and S.W. Aitchison, eds. 1976. An ecological survey of the riparian zone of the Colorado River between Lees Ferry and the Grand Wash Cliffs, Arizona. National Park Service Report, Contract No. CX821500007, Grand Canyon, Arizona.

Carothers, S.W., R.R. Johnson and S.W. Aitchison. 1974. Population structure and social organization of southwestern riparian birds. Amer. Zool. 14:97-108.

Christensen, E.M. 1962. The rate of naturalization of Tamarix in Utah. Am. Midl. Natl. 68:51-57.

Clover, E.U. and L. Jotter. 1944. Floristic studies in the canyon of the Colorado and tributaries. Amer. Midl. Nat. 32:591-642.

Dibble, C.E., ed., 1959. Ecological studies of the flora and fauna in Glen Canyon. Univ. Utah, Anthropological Papers No. 40, Salt Lake City.

Durrant, S.D. and N.K. Dean 1959. Mammals of Glen Canon. In Dibble, C.E., ed., 1959. Ecological studies of the flora and fauna in Glen Canyon. Univ. Utah, Anthropological Papers No. 40, Salt Lake City.

Emlen, J.T. 1971. Population densities of birds derived from transect counts, Auk 88:323-342.

Graf, W.L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geol. Soc. Am. Bull. 89:1491-1501.

Horton, J.S. 1962. Taxonomic notes on Tamarix pentandra in Arizona. Southwest Natur. 7:22-28.

Horton, J.S. 1964. Notes on the introduction of deciduous tamarisk. U.S. Dept. Agric. For. Serv.. Res. Note RM-16. 14 pp.

Johnson, R.R. and S.W. Carothers. 1982. Riparian habitats and recreation: interrelationships and impacts in the Southwest and Rocky Mountain region. U.S.D.A. For. Serv. Eisenhower Consort. Bull. No. 12.

Knopf, F.L., R.R. Johnson, T.Rich, F.B. Samson and R.C. Szaro. 1988. Conservation of riparian ecosystems on the United States. Wilson Bull. 100:272-284.

Miller, D.M., R.A. Young, T.W. Gatlin and J.A. Richardson. 1982. Amphibians and reptiles of the Grand Canyon. GCNHA, Grand Canyon, Arizona.

Potter, L.D. and C.L Drake. 1989. Lake Powell: Virgin flow to dynamo. University of New Mexico Press, Albuquerque, N.M.

Potter, L.D. and N.B. Pattison. 1976. Shoreline ecology of Lake Powell. Lake Powell Res. Proj. Bull. No. 29. 235 pp.

Robinson, T.W. 1965. Introduction, spread and areal extent of saltcedar (Tamarix) in the western states. USGS Prof. Pap. 11 pp.

Stevens 1976. Insect production of native and introduced dominant plant species, In Carothers, S.W. and S.W. Aitchison, eds. An ecological survey of the riparian zone of the Colorado River between Lees Ferry and the Grand Wash Cliffs, Arizona. National Park Service Report, Contract No. CX821500007, Grand Canyon, Arizona.

Stevens, L.E., B.T. Brown, J.M. Simpson and R.R. Johnson. 1977. The importance of riparian habitat to migrating birds. In R.R. Johnson and D.A. Jones, Tech. coord., Importance, preservation and management of riparian habitat. USDA For. Serv. Gen. Tech. Rept. RM-43.

Stevens, L.E. 1985. Invertebrate herbivore community dynamics on Tamarix chinensis Loueiro and Salix exigus Nuttal in the Grand Canyon, Arizona. M.S. Thesis, Northern Arizona Uiversity, Flagstaff, AZ.

Stevens, L.E. 1989. Mechanisms of riparian plant community organization and succession in the Grand Canyon, Arizona. Ph.D. Dissertation, Northern Arizona University, Flagstaff, Arizona.

SYSTAT. 1989. The system for statistics for the pc. SYSTAT, inc., Evanston, Ill.

Warren, D.K. and R.M. Turner. 1975. Saltcedar (Tamarix chinensis) seed production, seedling establishment and response to inundation. J. Ariz. Acad. Sci. 10:135-144.

Warren, P.L. and C.R. Schwalbe. 1988. Lizards along the Colorado River in Grand Canyon National Park: possible effects of fluctuating river flows. Glen Canyon Environmental Studies, Executive Summaries of Technical Reports. Bureau of Reclamation. Nat. Tech. Inform. Serv. Rept. No. PB88-183538/AS, Springfield, VA.

Woodbury, A. M. 1959. Amphibians and reptiles of Glen Canyon. In Dibble, C.E., ed., Ecological studies of the flora and fauna in Glen Canyon. Univ. Utah, Anthropological Papers No. 40, Salt Lake City.

Woodbury, A.M., S.D. Durrant and S.Flowers. 1959. Survey of vegetation in the Glen Canyon Reservoir Basin. Univ. Utah Anthropological Papers No. 36, Salt Lake City.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, N.J.

Appendix 1. Proportions of sand and silt particles in samples from sand and silt beaches.

	Mean % sand (s.d.)	Mean % silt (s.d.)
'Sand' sites (n = 13 samples):	91.08 (10.05)	2.0 (1.0)
'Silt' sites (n = 4 samples)	91.37 (3.30)	6.5 (3.0)