

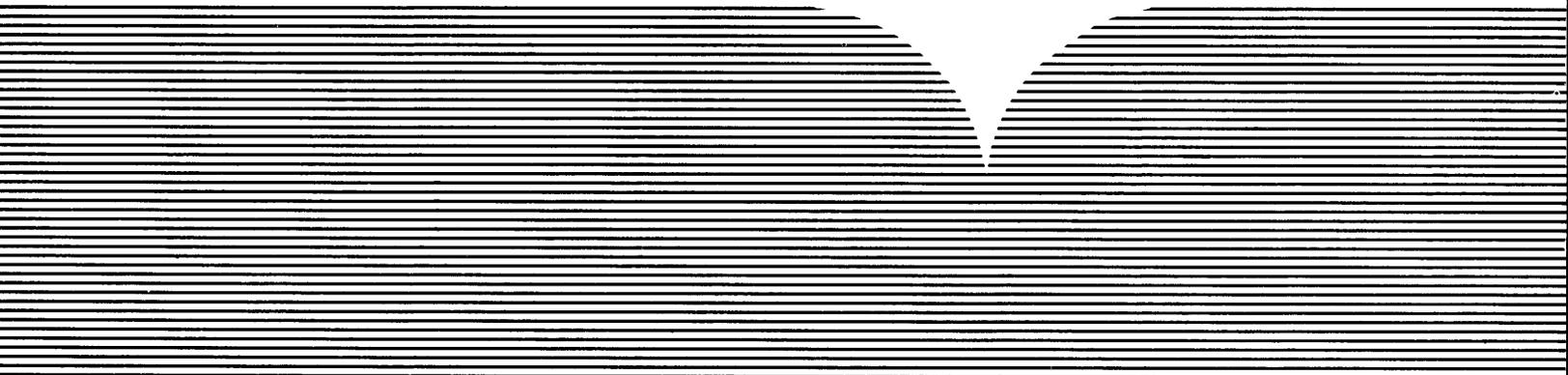
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EFFECTS OF RECENT FLOODING ON RIPARIAN
PLANT ESTABLISHMENT IN GRAND CANYON

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THE EFFECTS OF RECENT FLOODING ON RIPARIAN PLANT ESTABLISHMENT

IN GRAND CANYON

Terrestrial Biology of the
Glen Canyon Environmental Studies

By

Gwendolyn L. Waring

and

Lawrence E. Stevens

Glen Canyon Environmental Studies

11 November, 1986

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ABSTRACT

Censusing populations of 4 riparian perennial woody plant species following the flood of 1983 in Grand Canyon has revealed that replacement of individuals lost in that flood is occurring at relatively few sites. This means that there has been an overall loss of plants due to this flood or that large scale replacement of individuals lost is a much longer process. Based on experiments and observations, we suggest that continued flooding since 1983 is the single most important factor accounting for lack of replacement. Flood-related changes in substrate may also be contributing to this pattern, as the coarser, larger grained sands now comprising beaches are relatively infertile, desiccate quickly and result in reduced plant growth in experiments. In experiments, survivorship was lowest in full inundation versus fluctuating treatments for 6 month old seedlings, while the reverse was true for 1 month seedlings, with the latter being due to removal disturbance due to fluctuating flows. All species were found to be highly vulnerable to desiccation, with all dying within 3-5 days without water. Most plots found to be colonized by seed dispersing tamarisk and Baccharis spp. were cobble bars, with cobble bars appearing to offer seedlings protection from desiccation and from removal due to flooding. This represents a major habitat shift for tamarisk which previously colonized silt bars and the quality of cobble bars as a substrate for older plants remains to be seen. Most plots colonized by vegetatively or rhizomally reproducing coyote willow and arrowweed were sand beaches, which these clonal species reinvade with runners from the backs of beaches following flooding. While small seedlings of most species were found in the 20,000 to 40,000 cfs zone, establishment of older seedlings appeared to be occurring at about the 40,000 cfs zone, indicating that the belt of vegetation nearest the river is shifting to higher ground, probably in direct response to flooding. Tamarisk, coyote willow and seepwillow all produce seeds throughout the growing season, while arrowweed, desert broom, acacia, mesquite and others have more restricted reproductive periods each year.

ACKNOWLEDGEMENTS

Many people assisted us with various phases of this study. We thank Steve Hodapp, Martha Hahn-O'Neill, John Thomas, Barbara Rice, Mark Westoby and Peter Price for helping to focus the questions addressed in this study. The NPS rangers at Lee's Ferry, John Dick, Pat Mott, Tom Workman and Chester and Kathy helped immeasurably with logistics to make the study a successful one. Thanks to Larry Belli for granting us permission to conduct experiments at Lee's Ferry. Many friends helped with censusing along the river, Joanne Itami, Tim Craig, Diana Kimmerling, Mike Kearsely, Ruth Cashman, Nancy Moran, Mary Moran, and many more. Thanks to Graydon Bell for keeping us on track statistically. Thanks to Jan Reimer at Grand Canyon for being so helpful with the business end of the study. We especially thank Dave Wegner for serving as such an inspiration and for supporting our efforts to study this system.

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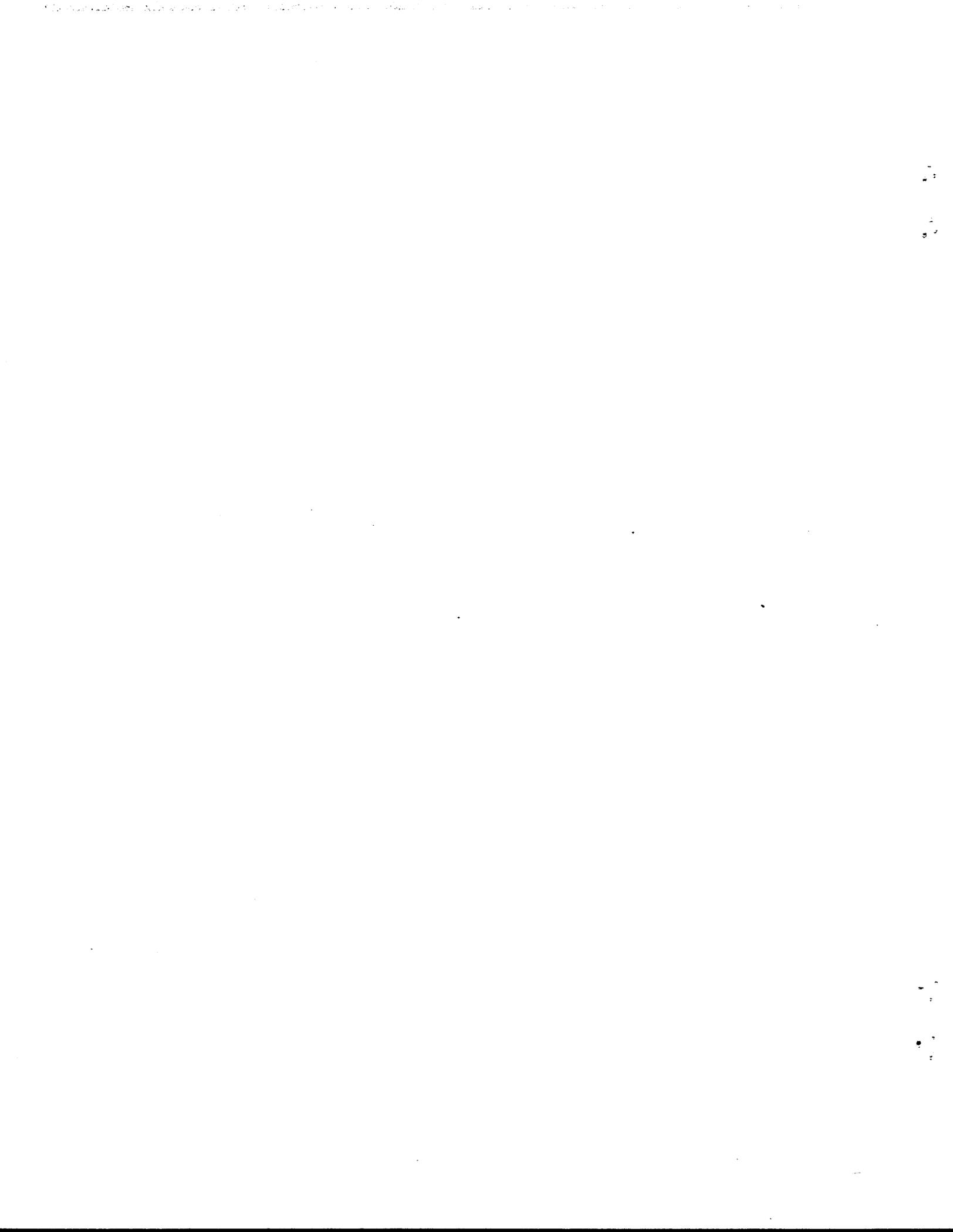
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INTRODUCTION

Flooding in 1983 in the Colorado River in Grand Canyon caused many dramatic changes through the corridor. From census studies Stevens and Waring (1985) estimated that 50% of riparian or riverside plants were lost during the 1983 flood, due to drowning or removal. Later, as floodwaters receded, beaches were colonized by large numbers of seedlings of many plant species. And on some beaches, significant amounts of fine particled sediments and organic and inorganic nutrients were lost by leaching and scouring during flooding, with mostly coarse grained and relatively infertile sand being redeposited.

We regard these as the most pronounced and perhaps most influential consequences of the 1983 flood in the riparian plant community in Grand Canyon. One could hypothesize that the tight coupling of major mortality and germination events in these riparian species enables populations to persist in the midst of flooding. This possibility prompted us to ask the essential question of whether or not 1986 populations are reaching pre-flood densities, implying replacement and perhaps equilibrium; or are they declining or perhaps even increasing in response to major flooding. We also examined the proximate factors, germination success, inundation or constant flooding or fluctuating flooding, desiccation and substrate as potential mechanisms behind the patterns.

The effects of flooding on riparian plant populations are well documented. Perhaps most importantly, periodically flooded plant systems are generally very dynamic and unstable. For example, floodplains and deltaic communities are often characterized by high levels of primary biological production from early successional stage species, while later seral species cannot get established (Petts 1984). In a longterm study, Lindsey et al. (1961) demonstrated that flooding can totally redefine and regulate certain features of riparian plant communities and their success. On the Wabash River, plants never successfully colonized zones of beaches which underwent periodic large floods. Each year newly colonizing seedlings would be swept away. According to Lindsey et al. (1961), flood-intolerant species tend to be excluded from flooded regions. Black willow (Salix nigra) and sand bar willow (S. interior) stands are very common plants along the banks of the periodically flooded Wabash River, while they are joined by many less flood tolerant species on the more stable beaches of its dammed and sister tributary, the Tippecanoe River. Plant diversity is often greater in nonflooded or mildly flooded systems because fewer species can tolerate flooding (Lindsey et al. 1961). Severe flooding can limit the distribution of even the most flood tolerant species. In Grand Canyon, prior to the construction of Glen Canyon Dam, populations of tamarisk, willow, seepwillow and arrowweed were small and restricted to reaches protected from flooding (Turner and Karpiscak 1980). Since construction of the dam, reduced flooding has permitted all of these species to expand their ranges significantly throughout the river corridor. Elsewhere, truly prolonged and consistent flooding (18 years) has eliminated several species, and prevented replacement of existing

populations along Lake Chicot, because of lack of appropriate germination conditions (Eggler and Moore 1961). While species and populations vary in their tolerance of flooding conditions, Keeley (1979) found that even the most flood-adapted populations of Nyssa sylvatica (tupelo) were negatively affected by severe flooding. So that while populations and communities of plants may persist in flooded systems, they cannot thrive there if flooding is excessive.

Effects of flooding tend to be harshest on seeds, seedlings and smaller plants (Demaree 1932, Harms et al. 1980, Hosner 1958, Kozlowski 1984), thereby reducing the number of potential recruits. Although the seeds of many riparian plant species germinate in response to flooding, or at least in receding floodwaters, many cannot germinate and establish under prolonged flood conditions (DeBell and Naylor 1972, Demaree 1932, Eggler and Moore 1961). Horton et al. (1960) proposed that populations of Tamarix chinensis could actually be limited by removing standing seed crops with well-timed flooding. Young shallow-rooted seedlings are very susceptible to uprooting and are carried away by floodwaters (Lindsey 1961). Seedlings that become established in flood zones often grow less than nonflooded individuals, or become structurally deformed (Lindsey et al. 1961, Kozlowski 1984). Many species have a better chance of surviving flooding when some of the canopy is not under water, perhaps because they can continue to photosynthesize and exchange gases with the atmosphere (Demaree 1932, Harms et al. 1980). According to Kozlowski (1984), duration of flooding can make a tremendous difference in seedling survivorship. Flooding during winter months, when plants are physiologically dormant, may be less harmful to plants (Lindsey et al. 1961). Adults of some plant species are highly flood-tolerant while their seedlings are flood-intolerant (Kozlowski 1984). According to Bannaster (1964), Keeley (1979) and others, flood-tolerant species are often particularly intolerant of water shortages. Accordingly, while flooding can stimulate germination in the seeds of many riparian plant species, too quick a drop of floodwaters during warm periods can cause rapid soil drying and kill shallow-rooted colonizing seedlings (Horton et al. 1960, Lindsey et al. 1961).

Flooding has seemingly opposing effects on plants in different life history stages, by, at once, causing substantial mortality to established plants and serving as a prerequisite for establishment for seedlings. This invariably leads to dynamism in a plant population. A fundamental question would be whether flood-related germination of seedlings can make up for flood caused mortality and thus indicate that this life history strategy is effective. This has not been specifically addressed in the literature.

Impounded or dammed rivers can be particularly erosive environments (Lindsey et al. 1961, Petts 1984, Taylor 1978, Kozlowski 1984) and there is evidence that plants do not perform as well in poorer, sandier soils which are often left behind (Barko and Smart 1986). Fine particle silts are more easily picked up and transported than are sand particles and sand particles are more easily redeposited than are finer particles in the water column. Loss of organic and inorganic nutrients is also

accelerated by flooding (Stevens and Waring, 1985 BOR1). Several studies on plant performance have shown that plants grow more slowly in sandy than in silty substrates (Barko and Smart 1986, Sand-Jensen and Sondergaard 1979) This relationship is regarded as a nutritional one, with sandy soils being more sterile than others. In an impounded river system, this factor may increasingly limit the ability of plants to become established over time.

OBJECTIVES

To address these issues we devised the following questions and predictions about plant establishment in Grand Canyon following the 1983 flood and have attempted to answer them in this study.

1. Have densities of perennial riparian plants increased to or exceeded those of 1983? Or, put another way, is the plant community recovering from the 1983 flooding event? If yes, then this plant system is tolerant of severe flooding, based on 3 years of post-flood information. If no, then flooding has disturbed the system so severely that recovery, if possible, is a longer process.

2. With respect to factors affecting plant establishment, A. Do different durations and intensities of flooding such as fluctuating flows and constant inundations affect plants, especially younger plants in a predictable manner? For instance, is survivorship lower among plants which are fully inundated for longer periods of time? If so, as we would predict, then concrete recommendations can be made about the flow regime which will allow the most seedlings to become established in the future.

2. B. What is the role of changing substrate texture in the post-dam environment? We predict that changing substrate type in Grand Canyon will negatively affect plant performance and consider what this will mean to future seedling establishment.

3. When are seeds of riparian plants available in the environment to be recruited into populations and does this vary between species? Can vegetative reproduction, specifically of stem tissue removed during flooding, occur when branches get buried in beaches, and thus represent a viable form of reproduction for species. The latter is particularly relevant to clonal, rhizomally spreading species such as coyote willow and arrowweed, which may depend more on vegetative than sexual or seed reproduction.

The System: While many perennial and annual plants occur along the river in Grand Canyon, we chose 6 of the most abundant species to concentrate our questions on: the exotic tamarisk (Tamarix chinensis), and native clonal coyote willow (Salix exigua) and arrowweed (Jessaria sericea); and the composite, Baccharis spp. including B. alicifolia, B. emoryi and B. sarothroides.

Tamarisk is a native of the Middle East and since its introduction into

the U. S. in the late 1800's, it has spread and become the dominant species of riparian plant along many drainages in the Southwest (Graf 1978). It has a deep tap root and is highly fecund (Stevens 1985) and large numbers survived the 1983 flood.

Coyote willow and arrowweed are shallow-rooted clonal species, with individual plants sometimes covering entire beaches. Large portions of coyote willow and arrowweed clones were removed during the 1983 flood, although few clones were entirely lost due to the flood (Stevens and Waring 1985-BOR1). This suggests that these plants are tolerant of some aspects of flooding, such as inundation (see Hosner 1958), and intolerant of others, i.e. increased velocity of water in floods leading to removal. Some portions of these clones remained in place on most beaches and are recolonizing beaches by sending out their underground stems (Stevens and Waring 1985).

The seepwillows are shallow-rooted plants which occupy stream banks and riparian settings throughout the Southwest. Baccharis salicifolia and B. emoryi occur throughout the Colorado River corridor in Grand Canyon, while B. sarothroides occurs only at lower elevations in the corridor. The first 2 species are obligate riparian species, while B. sarothroides is a facultatively riparian plant. All of these species produce large numbers of relatively long-lived seeds.

METHODS

Seedling Establishment in Grand Canyon: 1. Census information comparing 1984 and 1986 plant densities: To measure seedling establishment in Grand Canyon following the 1983 flooding event, we censused Tamarix chinensis, Salix exigua, Baccharis spp. and Tessaria sericea at 15 quadrats throughout the canyon from 1984 to 1986 (see Appendix 1, Fig. 1). These sites were distributed throughout the 4 sections of the canyon and were located on beaches which were relatively free of tributary and human influence. Each quadrat was 30 meters (m) long and extended approximately to the 60,000 cfs line. These 15 quadrats were colonized by seedlings following the 1983 flood and we censused each quadrat 3 times to measure recruitment or establishment, defined here as a plant's surviving beyond the very small seedling stage (>20 cm). Sampling dates were 21 June-7 July, 1984, 1-17 June, 1985, and 15-30 Sept., 1986. At each quadrat the densities of Tamarix, Salix, Baccharis and Tessaria were determined in the following manner: all individuals of each species were counted into one of 4 size classes: Size class 1 (SC1) = 1-20 cm (seedlings), SC2 = > 20 cm - < 1 m, SC3 = > 1 m - < 2 m, SC4 = > 2 m. With this information, we calculated plant densities/size class/species/quadrat/year (density = # live stems/area of quadrat in m²).

We used size class information to measure seedling establishment. With a 2-way ANOVA we tested for differences in density per size class between 1984 and 1986, with year and quadrat as main effects. With this we could detect any changes in SC1 and SC2 size class densities between

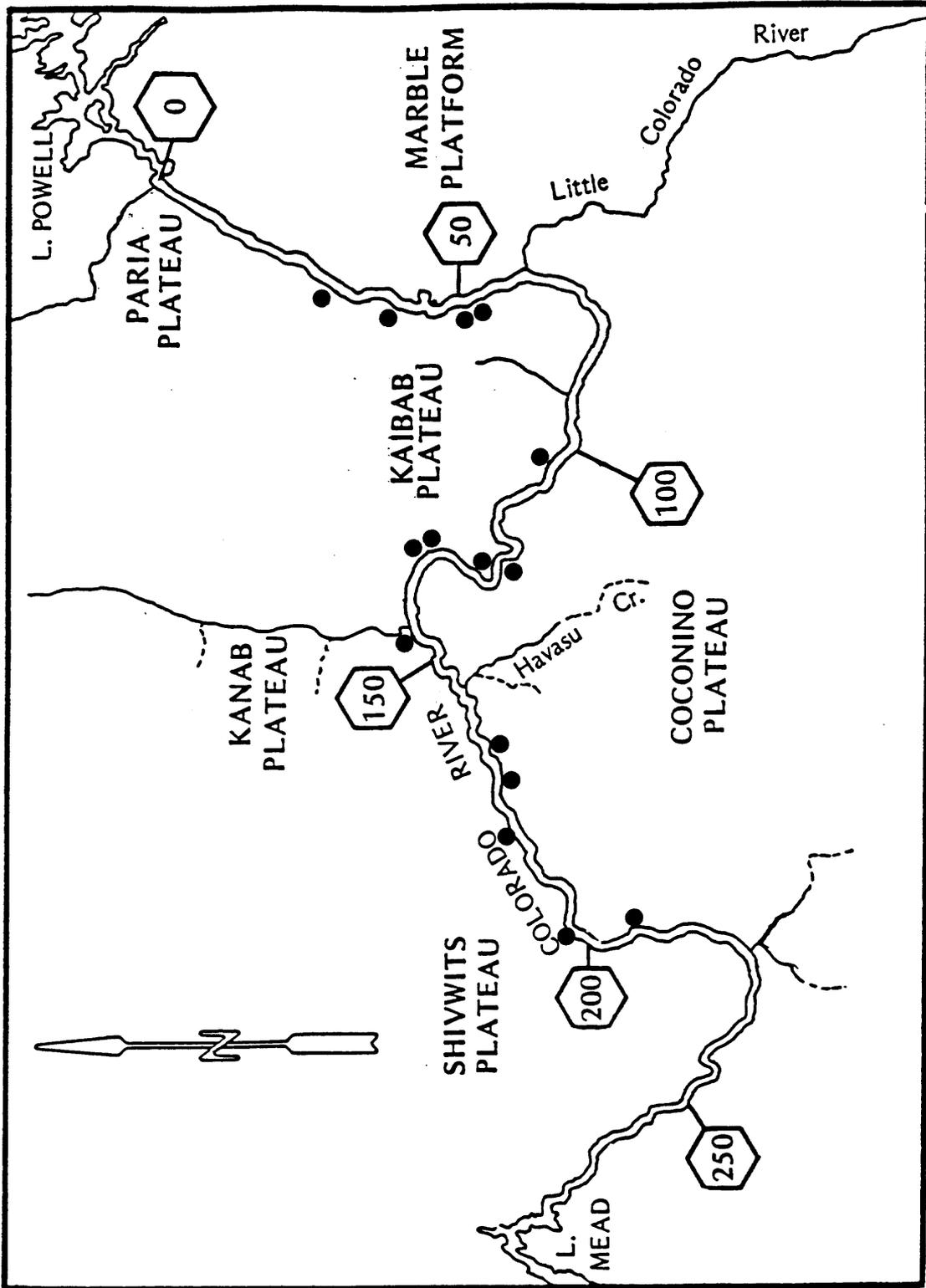


Figure 1. Dots indicate location of quadrats censused from 1984 to 1986 to measure densities of Tamarix, Salix, Baccharis and Tessaria.

years, which would indicate whether these groups, which we regard as having been established in 1984, have persisted through to 1986. This information we used to determine if flood-induced germination events of 1983-1984 have produced seedlings capable of replacing adult plants lost in the 1983 flooding event.

Measuring replacement of plants lost in 1983 flood: To determine if recruitment since the 1983 flooding event was sufficient to replace adult plants lost in that flood, we compared the density of dead individuals > SC2 in height in 1984 with the number of live individuals > SC2 in September, 1986 on the 15 quadrats censused. Paired t-test statistics were calculated for each of the four target species on every plot in which that species occurred. This measure of flood-related mortality substantially underestimated the density of dead individuals in 1984 because it did not account for removal due to scouring. To make this comparison more accurate we adjusted the density of dead individuals/m² in 1984 using our estimates of removal rates for each species (Stevens and Waring, 1985-BOR1).

To understand changes which might occur in population structure within a year, we censused the same 15 quadrats in April 1986, and compared size class densities per species between April and September 1986. A 2-way ANOVA, with season (Apr., Sept.) and quadrat as main effects, was used.

Predicting adult plant densities from seedling densities: We analyzed the relationship between seedling densities and densities of larger size classes the following year on the quadrats that provided evidence of colonization and recruitment, to determine if the relationship was a predictable one (i.e., do large seedling germination events give rise to larger numbers of juvenile plants?). Because older, larger seedlings have a greater probability of surviving to adulthood and are often capable of sexual reproduction, an understanding of this relationship is important. Tamarisk, seepwillow and arrowweed plants over 1 m in height are capable of sexual reproduction. To accomplish this analysis, we used a lagged regression model with density data from quadrats censused from 1984 through 1986. We attempted to correlate the density of 1984 seedlings with the density of 1985 SC2 plants, and the densities of 1985 SC2 plants with those of 1986 SC3 plants using linear regression for each of the species of interest.

To verify that SC1 and SC2 size classes were established in 1984, we collected 75 tamarisk stems and 53 coyote willow stems of various sizes, measured the height (cm) and age of each, and regressed age with height.

2. Factors Affecting Seedling Establishment: We used experiments and empirical information to determine the effects of inundation, fluctuating flows, desiccation and substrate on plant growth and survivorship. A. Inundation, fluctuating flow and desiccation experiments: Percent survivorship of 1 month old and 6 month old seedlings of Tamarix, Salix and Baccharis salicifolia under a variety of flow and desiccation regimes was examined experimentally. Seeds of

tamarisk, coyote willow and seepwillow were collected from at least 10 plants at Lee's Ferry in the fall of 1985 and kept refrigerated at 4° C until January 1986. B. salicifolia seeds were germinated in January, 1986. We had little success with germinating tamarisk or coyote willow seeds and instead, collected 2 month tamarisk seedlings in December from Lee's Ferry (they were 8 months old when we experimented with them) and used 6 month old plants provided by L. Stevens' experimental plant population at Lees Ferry. Seedlings or seeds were planted in 8"x8"x8" pots (tamarisk) or 5"x7"x3" pots (willow, seepwillow) filled with an equal mix of coarse (post-dam) and fine grained silty sand (pre-dam) from the Lee's Ferry area. Plants (6-10 per pot) were grown in the Terrestrial Ecology Laboratory at Bilby Research Center at NAU, in Flagstaff, AZ, from 15 January until 15 June, 1986. The plants were grown with 16 hours of light/day, with lighting involving a 1:1 ratio of cool white:growlux lights. Plants were watered daily and fertilized monthly with Miracle Gro® according to instructions until 20 May, 1986. No fertilizer was applied after this time. For one month plants, seeds of all species were successfully germinated 15 May, 1986, and grown in the Bilby laboratory until 15 June, 1986. They were otherwise treated identically to 6 month plants. On the evening of 16 June, 1986, all potted plants were transported in a Ryder® truck to Lee's Ferry, AZ, where experiments were conducted. All plants received 50% shade under a slat-roofed 'ramada' near the river and were allowed to acclimate until 20 June when treatments commenced.

Seven treatments were run with 10 replicates (pots) per treatment for 6 month old plants and 9 replicates for 1 month old plants: 1. 1 month of inundation (I4 for 4 weeks) in which pots were completely submerged in the Colorado River for 1 full month, 2. 2 weeks full inundation (I2), 3. 1 month fluctuating flows (F4 for fluctuations for 4 weeks) in which pots were completely submerged in the Colorado River for 12 hours during the day and removed for 12 hours at night every day for 1 month, 4. 2 weeks fluctuating flows (F2), 5. 2 weeks desiccation (D2) in which plants on shore were not watered for 2 weeks, 6. 1 week desiccation (D1), 7. controls (grown on shore in partial shade, watered daily). One month treatments were conducted from 20 June to 20 July and 2 week treatments ran from 20 June to 4 July. Plants were allowed a one week recovery period following treatments, to definitively survive or die. Because all of our I4 plants were washed downstream by a tributary flood on 18 July, we re-ran this treatment from 20 July to 20 August, using extra plants which had been growing with control plants at riverside. These I4 plants were, thus, 1 month older and perhaps more resilient than the 6 month old plants used in other treatments. At the end of this period the percent of seedlings surviving per pot was calculated (# alive at end of experiment/# alive at beginning). The data were square root and then arcsin transformed and analyzed with ANOVA, with treatment as the main effect. We also studied effects of treatments on plant growth by measuring the height of 4 plants/pot before and after the experiment. These data were analyzed with ANOVA, again with treatment as the main effect.

2. B. Effects of Substrate on Seedling Germination: To determine the

ability of seeds to germinate in different soil types, tamarisk and coyote willow seeds were added to 3" petri dishes containing silty soil ($n = 6$) and coarse sand ($n = 6$) on 27 June, 1986. The plates were then watered daily and the seedlings were allowed to germinate. At the end of 10 days, the # of germinated seedlings/ dish were counted and % germination/species/substrate type was determined and analyzed with ANOVA, with soil type as the main effect.

2. C. Effects of Substrate on Seedling Growth and Survivorship:
 Laboratory experiments: Root and shoot growth rates in fine (pre-dam) versus coarse (post-dam) riparian sediments were compared for Tamarix chinensis, Salix exigua and Baccharis salicifolia seedlings. Fine-grained and coarse-grained sediments were collected from the riparian zone at Lees Ferry, Arizona. Fresh seeds from 8 or more individual plants of each species were collected in the Grand Canyon from July through September, 1986. Sediments and seeds were transported to the laboratory in Flagstaff and seeds were germinated in petri dishes. Two- to four-day old seedlings of these species were transferred to 3.5 cm x 30 cm glass tubes containing one or the other sediment type. Seedlings were grown for 29 to 34 days at approximately 25 C with daily watering. Seedlings were grown under a 1:1 combination of growlights and regular fluorescent lights at an intensity of 1,120 footcandles (the equivalent of weak shade), with 16 hours of light/day. After one month of growth seedlings were gently flushed from the tubes, and root length and shoot height were measured. Each treatment was replicated at least 6 times, and data were analyzed using a 2-way ANOVA with soil texture (2 levels) and species (3 species) as main effects of root and shoot growth rates (mm/day).

2 C. Field Observations on Substrates Colonized by Tamarisk: Tamarisk densities were censused in sandy and cobble substrates to verify an earlier observation that tamarisk and other species seedlings were found more consistently in cobble substrates than in sand substrates. We censused three sites in the 40,000 - 60,000cfs zone in reach 5, in September, 1986. At each site, tamarisk seedling densities were measured in 30-50 randomly selected 1.0 m² plots in sand and in an equal number of randomly selected 1.0 m² plots in uniform cobble substrate. Results were analysed with a 2-way ANOVA, treating substrate type and site as main effects on tamarisk seedling density.

To study more precisely Tamarix survivorship and growth with proximity to the river and exposure to flooding in the wild we examined the fate of individual plants in exposed and less exposed settings. Thirty or more young tamarisks at each of 5 sites were tagged with parakeet bird bands and their heights were measured in April, 1986 and again in September, 1986. Three stands of 2 year old plants were studied at 52R, 131R and 171L; these stands occurred at about the 40,000 cfs zone, with 52R being a protected and sandy site, 131R being a moderately protected cobble bar and 171L being a sandy and exposed site. At Mile 43.5L (President Harding) and 172R, populations of 6 month old seedlings were measured for growth and survivorship. Mortality between seasons in 1986 was analyzed with chi square analysis and changes in height were

compared with ANOVA. Densities were measured at 171R by measuring randomly selected nearest neighbor distances between April and September of 1986.

3. Timing or Phenology of Plant Reproduction in Grand Canyon:

Information on when the seeds of different species are produced was compiled from several sources. Timing information on tamarisk, coyote willow, seepwillow, desert broom and arrowweed were gathered during three research river expeditions, three commercial river trips, several hiking expeditions throughout the Grand Canyon, as well as twelve trips to the Lees Ferry area, between November, 1985 and October, 1986. Phenological status was classified in the following ten categories:

<u>PHENOLOGICAL CATEGORY</u>	<u>DESCRIPTION</u>
0	No leaves or flowers.
1	Young leaves.
2	Fully leafed out.
3	Developing flower buds.
4	Fully developed flower buds.
5	Flower buds beginning to open.
6	Full bloom.
7	Flowers dead, seeds immature.
8	Seeds mature and dispersing.
9	Seeds dispersal completed.
10	Chlorosis

We also compared patterns in plant phenology between the different species and between the different sections of the river corridor. We examined the large collection of Colorado River corridor plants housed at the Museum of Northern Arizona in Flagstaff, AZ and compiled phenological data from these specimens.

We derived detailed information on reproductive phenology of Tamarix chinensis by tagging 13 plants at Lees Ferry and estimating the percentage of the canopy covered with flower heads at monthly intervals from April through October, 1986.

Other Forms of Reproduction: Vegetative Reproduction: To determine viability of vegetative reproduction of tamarisk, coyote willow, seepwillow and arrowweed in the Grand Canyon, the following methods were used: At Lee's Ferry, 15 willow and 15 arrowweed stems, all shorter than 1 m and bearing some root stock, were planted in wet sand along the river on 25 June, 1986. The cuttings were checked 2 weeks later on 9 July, and the # and % of plants surviving were calculated.

At 2 beach sites in Grand Canyon (43.5L and 66.0L), 3 rows of tamarisk, coyote willow, seepwillow and arrowweed cuttings were planted in April, 1986, with the 1st row 1 m from the river and each successive row 1 m

further from the river. Six sets of cuttings were planted in the 1st and 3rd rows with 8 in the middle row, with each of the 4 species occurring in the 1st set and tamarisk, willow and arrowweed occurring in the last 2 sets. Percent survivorship of the cuttings was measured in September, 1986. Survivorship of the cuttings meant that stems cut from live plants had successfully rooted and become established.

RESULTS

1. Establishment of Seedlings in Grand Canyon: Census information. In examining plant census information collected in 49 quadrats in 1984, we found high levels of seedling colonization by the species of interest at only 21 sites. This means that extensive plant establishment occurred on 43% of the sites examined. More cobble bar sites were extensively colonized than would be expected by chance alone, while fewer sand and talus sites were extensively colonized than would be predicted by chance alone ($\chi^2 = 5.0$, $p < .05$, $df = 1$). The cobble bar sites were colonized largely by sexually reproducing, seed dispersing tamarisk, and Baccharis spp. In most cases, the sand substrate sites that were heavily colonized were invaded from the periphery by clonal coyote willow and/or arrowweed. Little colonization occurred on talus sites. Because 1983 flood-induced adult plant mortality was extensive at most of the 49 quadrats, it is apparent that this plant system has not recovered densities of plants lost in 1983. Additional flooding has occurred since 1983 (Fig. 2) and we believe that this has contributed to this pattern.

At 15 of the sites on which substantial plant establishment occurred, we found that seedling densities for 3 of 4 species did not vary significantly between 1984 and 1986. All tamarisk densities did increase significantly between 1984 and 1986 and densities of other larger plants in 1986 were either no different than or, in the case of seepwillow, exceeded those of 1984 (Table 1, Figure 3). These patterns suggest that locally, large numbers of young recruits are entering the system on some beaches. This means that once established, plants are surviving in large numbers.

Clonal colonization by willow and arrowweed occurred mainly on quadrats comprised of sandy substrates, while tamarisk and seepwillow seedlings were most common on cobble bars. This reflects a major shift in substrate type colonized, particularly for tamarisk, for which most older stands occur on silt bars.

Densities of tamarisk seedlings (1-20 cm) were significantly lower in 1986 than in 1984 (Table 1, Fig. 3). Densities of SC2 and SC3 plants increased significantly between 1984 and 1986, implying that densities of juvenile tamarisks, which colonized beaches after the flood of 1983, were becoming established.

Densities of seepwillow seedlings did not vary significantly between

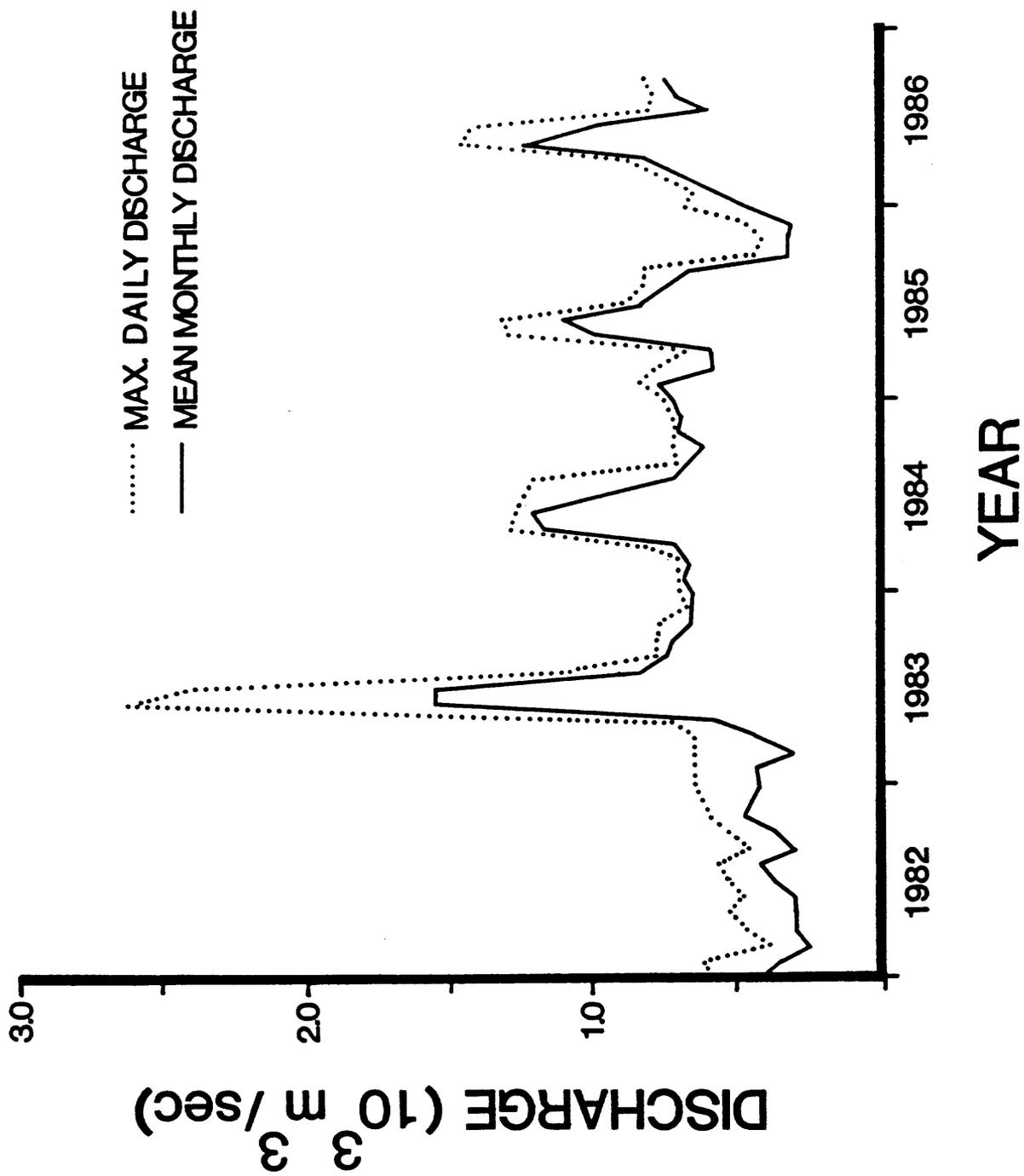


FIGURE 2 : MAXIMUM DAILY DISCHARGE AND MEAN MONTHLY DISCHARGE FROM GLEN CANYON DAM, 1982-1986, AS MEASURED AT THE U.S. GEOLOGICAL SURVEY GAUGING STATION AT LEES FERRY, ARIZONA.

TABLE 1 : RIPARIAN PLANT DENSITIES BY SIZE CLASS FROM QUADRATS, 1984 - 1986.

SPECIES	SIZE CLASS	1984		1985		1986		P	d.f.
		\bar{x}/m^2 (se)	\bar{x}/m^2 (se)	\bar{x}/m^2 (se)	\bar{x}/m^2 (se)	\bar{x}/m^2 (se)	\bar{x}/m^2 (se)		
Tach	S	0.428 (± 0.115)	0.433 ($\pm 0.1-7$)	0.235 (± 0.074)	0.000	1,14			
	1	0.023 (± 0.009)	0.092 (± 0.030)	0.165 (± 0.048)	0.050	1,14			
	2	0.184 (± 0.008)	0.592 (± 0.028)	0.063 (± 0.018)	0.040	1,14			
Saex	S	0.031 (± 0.025)	0.185 (± 0.118)	0.052 (± 0.023)	0.300	1, 5			
	1	0.089 (± 0.059)	0.168 (± 0.065)	0.333 (± 0.159)	0.575	1, 5			
	2	0.052 (± 0.027)	0.122 (± 0.086)	0.230 (± 0.153)	0.389	1, 5			
Basp	S	0.045 (± 0.033)	0.070 (± 0.043)	0.044 (± 0.014)	0.265	1,12			
	1	0.012 (± 0.004)	0.086 (± 0.046)	0.047 (± 0.015)	0.074	1,12			
	2	0.007 (± 0.003)	0.025 (± 0.016)	0.027 (± 0.010)	0.031	1,12			
Tese	S	0.013 (± 0.013)	0.104 (± 0.068)	0.056 (± 0.039)	0.221	1, 6			
	1	0.247 (± 0.226)	0.325 (± 0.213)	0.200 (± 0.119)	0.500	1, 6			
	2	0.048 (± 0.038)	0.218 (± 0.177)	0.356 (± 0.234)	0.340	1, 6			

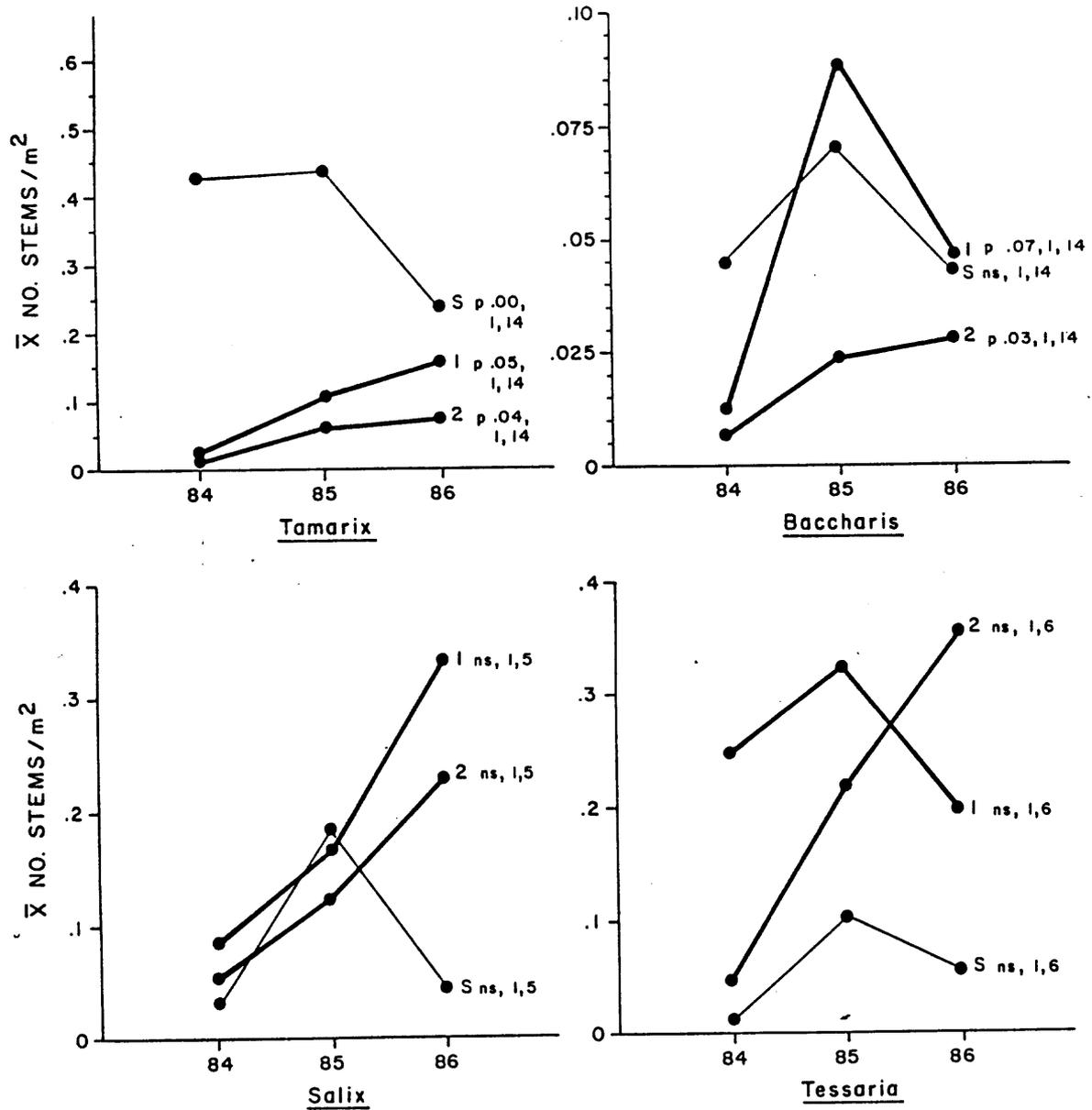


Figure 3. Mean densities of Tamarix, Baccharis, Salix and Tessaria by size class between 1984 and 1986 (S = seedling, 1-20cm; 1 = 20cm - 1m; 2 = 1 - 2m).

1984 and 1986 (Table 1, Fig. 3). SC2 plants increased nonsignificantly between 1984 and 1986, while densities of SC3 plants increased significantly between 1984 and 1986. As with tamarisk, the numbers of young plants becoming established on some beaches since 1983 are increasing slightly.

Densities of coyote willow sprouts did not vary significantly between 1984 and 1986 (Table 1, Fig. 3). Densities of SC2 and SC3 plants increased, though not significantly, between 1984 and 1986 (Table 1, Fig. 3). Overall, there was no noticeable change in willow stem densities between 1984 and 1986. Over the course of 6 years extensive study, we have only found 4 coyote willow seedlings in this system.

Densities of arrowweed sprouts did not vary significantly between 1984 and 1986, although there was a trend of slight increase between the 2 periods (Table 1, Fig. 3). Neither SC1 or SC2 plant densities varied significantly between 1984 and 1986, although densities of SC3 plants increased slightly between the 2 periods (Table 1, Fig. 3). Overall, there appears to have been little change in densities of young arrowweed stems between 1984 and 1986. Like coyote willow, arrowweed seedlings are extremely rare in this system, with only 8 seedlings found in 6 years.

On examining population changes between April and September, 1986, for these species, we found that seedling densities declined nonsignificantly in all species by September and densities of SC2 tamarisk and arrowweed, and SC2 and 3 coyote willow increased significantly, while Baccharis spp. densities did not change significantly (Table 2, Fig. 4).

Replacement of plants lost in the 1983 flood: Our comparison of densities of live stems in 1986 to densities of dead stems (both adjusted and unadjusted for removal mortality) in 1984 revealed no significant differences between the groups for any species (Fig. 5), implying that plant populations may be replacing themselves on these beaches. Paired t-test values were nonsignificant ($p > 0.05$) for the densities of dead 1984 (adjusted and unadjusted) versus live 1986 densities of adult tamarisks ($df = 14$ quadrats), seepwillow and desert broom ($df = 13$), coyote willow ($df = 5$) or arrowweed ($df = 4$). Despite the apparent differences in dead 1984 versus live 1986 stem densities of each species illustrated in Fig. 4, the standard deviations approached or exceeded the means in all cases. A non-significant trend of increasing densities of tamarisk and coyote willow and decreasing densities of seepwillow and arrowweed, respectively, reflects the greater efficacy of recolonization by the first two species and the high levels of mortality suffered by the latter two taxa levels as a result of flooding.

Predicting adult plant densities from seedling densities: Densities of tamarisk seedlings were correlated with densities of plants in the next size class (SC1) in 1985, but not in 1986 (Table 3). In 1985 and 1986, SC1 densities were strongly correlated with densities of the next size

TABLE 2: RIPARIAN PLANT DENSITIES BY SIZE CLASS FROM QUADRATS, APRIL TO SEPTEMBER, 1986.

SPECIES	SIZE CLASS	APRIL		SEPTEMBER		P	df
		\bar{x}/m^2 (se)	\bar{x}/m^2 (se)	\bar{x}/m^2 (se)	\bar{x}/m^2 (se)		
Tach	S	0.433 (± 0.164)	0.185 (± 0.051)	0.186	1, 25		
	1	0.056 (± 0.014)	0.058 (± 0.011)	0.848	1, 81		
	2	0.006 (± 0.001)	0.010 (± 0.002)	0.000	1, 108		
Saex	S	0.035 (± 0.016)	0.016 (± 0.008)	0.342	1, 25		
	1	0.043 (± 0.006)	0.029 (± 0.008)	0.016	1, 81		
	2	0.006 (± 0.002)	0.020 (± 0.008)	0.002	1, 108		
Basp	S	0.309 (± 0.201)	0.030 (± 0.012)	0.194	1, 25		
	1	0.016 (± 0.003)	0.015 (± 0.003)	0.601	1, 81		
	2	0.004 (± 0.002)	0.005 (± 0.001)	0.676	1, 108		
Tese	S	0.028 (± 0.017)	0.017 (± 0.012)	0.605	1, 25		
	1	0.046 (± 0.015)	0.030 (± 0.010)	0.000	1, 81		
	2	0.029 (± 0.010)	0.038 (± 0.012)	0.267	1, 108		

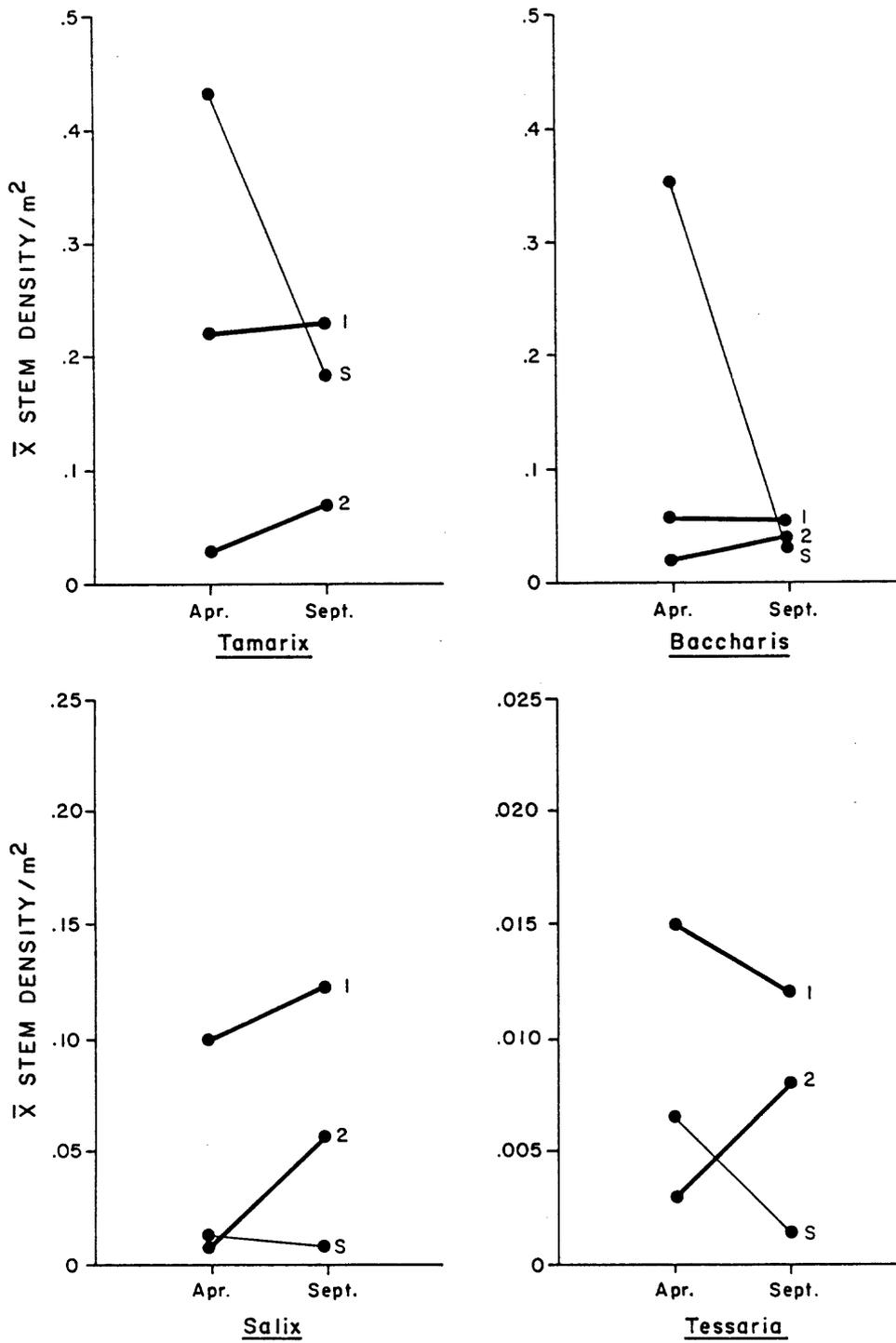


Figure 4. Mean densities of Tamarix, Baccharis, Salix and Tessaria by size class between April and September, 1986 (S = seedling, 1-20 cm; 1 = 20 cm - 1 m; 2 = 1 m - 2 m).

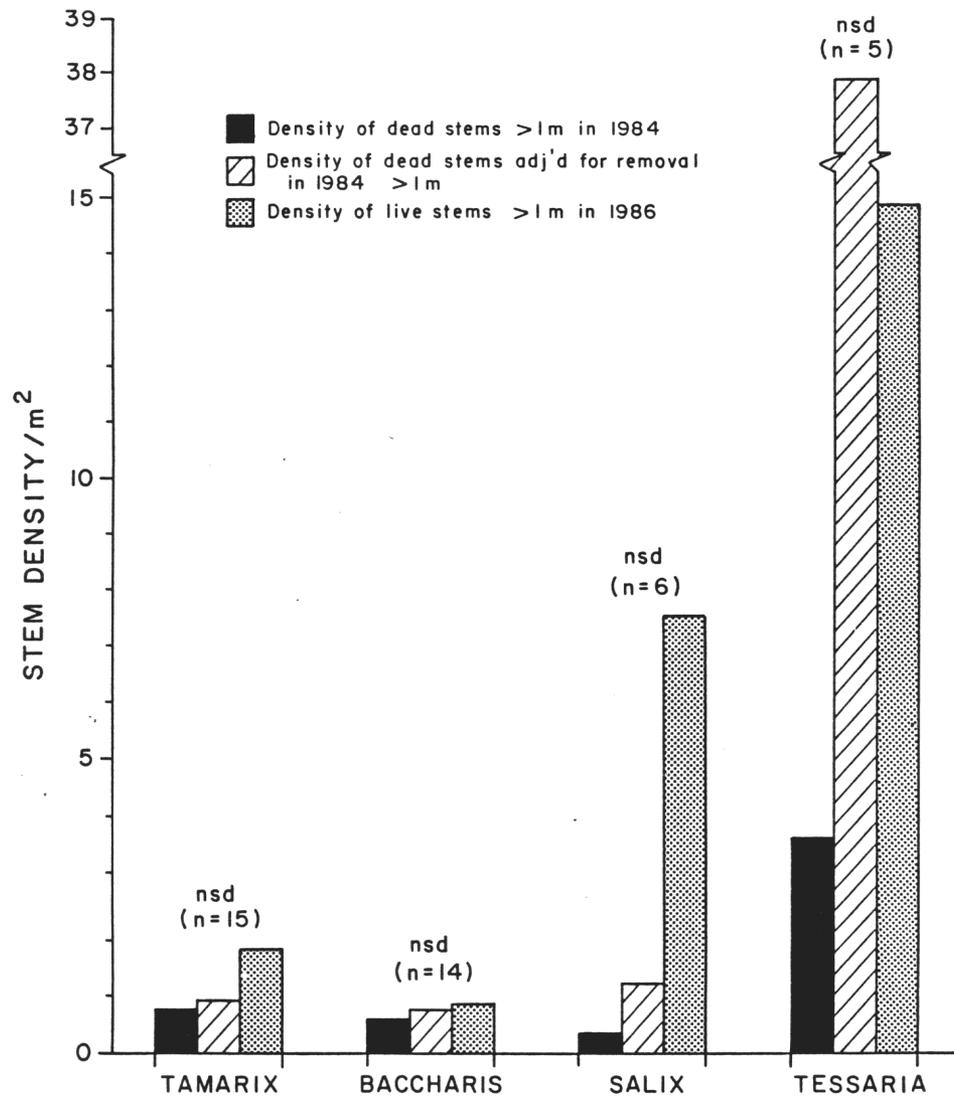


FIGURE 5 : A COMPARISON OF THE DENSITY OF DEAD STEMS (UNADJUSTED AND ADJUSTED FOR REMOVAL) OF TAMARIX, BACCHARIS, SALIX EXIGUA, AND TESSARIA IN 1984 AS COMPARED TO LIVE STEM DENSITIES OF THESE SPECIES IN 1986 ON SELECTED QUADRATS ALONG THE COLORADO RIVER IN THE GRAND CANYON.

TABLE 3 : CORRELATION OF RECRUITMENT SUCCESS BETWEEN THREE SIZE CLASSES AND THREE YEARS FOR FOUR RIPARIAN PLANT SPECIES IN THE COLORADO RIVER CORRIDOR IN THE GRAND CANYON.

SPECIES	SIZE CLASS	\bar{X} (STAN.DEV.)	R^2 (p df)	SIZE CLASS	\bar{X} (STAN.DEV.)	R^2 (p df)
Tach	Seed ₈₄	11.294 (9.552)	0.553 (0.025 1,6)	SC1 ₈₄	0.890 (1.329)	0.802 (0.005 1,6)
	SC1 ₈₅ -SC1 ₈₄	1.759 (2.808)		SC2 ₈₅ -SC2 ₈₄	1.669 (4.502)	
	Seed ₈₅	14.546 (18.325)	0.127 (nsd 1,6)	SC1 ₈₅	2.649 (2.915)	0.558 (0.025 1,6)
	SC1 ₈₆ -SC1 ₈₅	1.879 (3.506)		SC2 ₈₆ -SC2 ₈₅	1.373 (1.633)	
Saex	Seed ₈₄	1.879 (2.424)	0.174 (nsd 1,4)	SC1 ₈₄	4.652 (5.567)	0.106 (nsd 1,3)
	SC1 ₈₅ -SC1 ₈₄	3.472 (6.769)		SC2 ₈₅ -SC2 ₈₄	4.852 (9.285)	
	Seed ₈₅	10.443 (8.320)	0.000 (nsd 1,4)	SC1 ₈₅	8.123 (1.862)	0.000 (nsd 1,3)
	SC1 ₈₆ -SC1 ₈₅	11.456 (6.466)		SC2 ₈₆ -SC2 ₈₅	3.213 (13.220)	
Basp	Seed ₈₄	2.030 (4.839)	0.779 (0.025 1,4)	SC1 ₈₄	0.335 (0.374)	0.000 (nsd 1,5)
	SC1 ₈₅ -SC1 ₈₄	2.370 (3.787)		SC2 ₈₅ -SC2 ₈₄	0.588 (1.273)	
	Seed ₈₅	2.106 (3.395)	0.000 (nsd 1,4)	SC1 ₈₅	2.572 (3.692)	0.859 (0.005 1,5)
	SC1 ₈₆ -SC1 ₈₅	-0.898 (2.214)		SC2 ₈₆ -SC2 ₈₅	0.636 (0.874)	
Tese	Seed ₈₄	0.559 (1.235)	0.444 (nsd 1,3)	SC1 ₈₄	10.034 (4.292)	0.991 (0.005 1,3)
	SC1 ₈₅ -SC1 ₈₄	-0.294 (10.872)		SC2 ₈₅ -SC2 ₈₄	6.360 (12.392)	
	Seed ₈₅	3.125 (4.569)	0.000 (nsd 1,3)	SC1 ₈₅	9.740 (14.295)	0.540 (nsd 1,3)
	SC1 ₈₆ -SC1 ₈₅	-1.775 (6.231)		SC2 ₈₆ -SC2 ₈₅	8.209 (20.367)	

class (SC2) in the next year. For tamarisk, the ratio of 1984 seedlings to 1985 SC1 was 6.5:1. Likewise, larger tamarisk size classes revealed recruitment success ratios that were closer to 2:1 in 1985 and 1986. These trends indicate that levels of seedling mortality are substantial, and that tamarisk seedlings are more likely to perish than are larger size classes, as expected. Correlations between different size classes in coyote willow were low and nonsignificant for both years, perhaps due to the small number of quadrats examined, die-back, and/or coyote willow's ability to grow more than 1.0 m/yr. Like tamarisk, Baccharis seedling densities were correlated with subsequent SC1 densities in 1985 but not in 1986. Correlation of Baccharis SC1 to SC2 densities were significantly correlated in 1986 (representing a continuation of the recruitment success initiated in 1984 among Baccharis seedlings). Correlation of arrowweed seedling densities to subsequent SC1 densities was non-significant; however, recruitment success of larger size classes was significant. Despite small sample sizes and variances that exceeded means, both size classes of coyote willow, seepwillow and arrowweed had ratios of Seedling:SC1 and SC1:SC2 of between 1 to 2.5:1, indicating potentially higher probability of survivorship among recruits of these species. Higher correlation of recruitment success was generally found for 1984-1985 comparisons than for 1985-1986 comparisons for all species. This trend may be a response to several factors including 1) abnormally dry spring conditions in 1986, 2) flooding in excess of 50,000 cfs in May and June, 1986, or 3) unrecognized factors; however, more data are needed to resolve recruitment success using these analytical techniques.

Tamarisk height and age were strongly correlated, although variation did exist in the relationship, based on a sample of field plants ($R^2 = 51\%$, $p < .0000$, $df = 1,75$). The relationship between age and height in coyote willow was stronger ($R^2 = 67.0\%$, $p < .0000$, $df = 1,51$).

2. Factors affecting seedling establishment: A. Effects of flooding, fluctuating flows and desiccation on 2 age classes of plants. In experimental tests of seedling survivorship at Lee's Ferry, all treatments produced significant reductions in seedling survivorship and growth relative to control plants in both age classes and in all species (Table 4, Fig. 6). Our prediction that increasing levels of submergence in water (i.e., fluctuating flows as compared to complete inundation) should result in reduced survivorship and growth in all 3 plant species, was generally proven out by the results of this experiment.

All 6 month old tamarisk subjected to inundation or fluctuating flows exhibited significantly lower levels of survivorship and growth, except for seedlings receiving the 4 week inundation (I4) treatment. This apparent discrepancy is probably due to the fact that this group was treated one month later so that the plants were larger and resistant than younger plants (see Methods). All plants in the desiccation treatments died within 5 days after water was withheld.

Six month seepwillow in the I4 and I2 treatments had significantly lower levels of survivorship than did F4 and F2 plants or controls (Table 4,

TABLE 4 : PERCENT SURVIVORSHIP AND GROWTH OF SIX MONTH OLD RIPARIAN PLANT SPECIES EXPOSED TO SEVEN TREATMENTS OF INUNDATION AND DESICCATION (TRANSFORMED DATA).

SPECIES	PERCENT SURVIVORSHIP							GROWTH (cm)							
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	
Tach	\bar{X}	0.70	0.33	0.36	0.92	0.00	0.00	1.27	-1.52	-2.29	-0.09	-0.36	0.00	0.00	6.04
	$\pm se$	0.13	0.07	0.08	0.12	--	--	0.04	0.64	0.72	0.28	0.54	--	--	0.92
	n	10	10	9	10	10	10	10	10	10	9	10	10	10	10
	p	p = 0.000							p = 0.000						
Saex	\bar{X}	0.89	0.87	0.87	0.99	0.00	0.00	1.07	-4.67	-0.15	0.21	0.90	0.00	0.00	4.37
	$\pm se$	0.08	0.09	0.09	0.06	--	--	0.04	2.21	0.25	1.46	0.60	--	--	1.30
	n	9	9	9	9	9	9	9	6	6	7	9	9	9	9
	p	p = 0.250							p = 0.0008						
Basp	\bar{X}	0.73	0.98	1.26	1.21	0.00	0.00	1.21	-0.31	-2.31	-0.16	0.75	0.00	0.00	5.18
	$\pm se$	0.10	0.11	0.06	0.06	--	--	0.01	0.30	0.67	0.27	0.32	--	--	0.44
	n	10	10	10	10	10	10	10	10	10	10	10	10	10	10
	p	p = 0.000							p = 0.000						

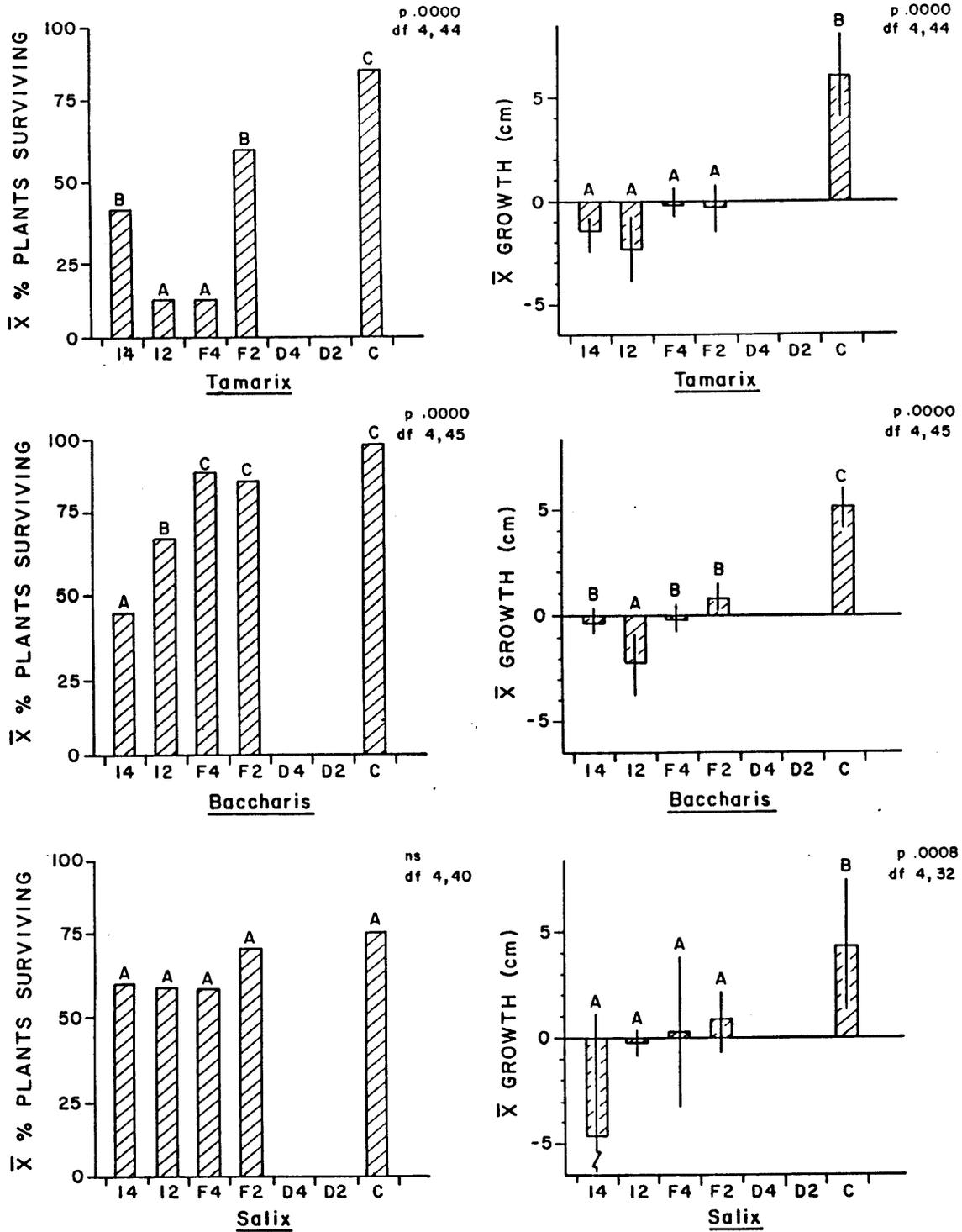


Figure 6. Mean percent survivorship and growth of 6 month old *Tamarix*, *Baccharis* and *Salix* in flooding and desiccation experiments (I4 = 4 weeks inundation, I2 = 2 weeks inundation, F4 = 4 weeks fluctuating flows, F2 = 2 weeks fluctuating flows, D4 = 4 weeks desiccation, D2 = 2 weeks desiccation, C = controls).

Fig. 6). All water treated plants (I4-F2) either died back or grew significantly less than controls. I2 plants died back significantly more than did plants in any other water treatment, even I4 plants. Again, we suggest that this has resulted from I4 plants being one month older and perhaps more resilient. All desiccated plants died within 5 days of the beginning of the treatments.

There was no significant difference in survivorship of 6 month willows among all treatments, although survivorship in the harshest treatments (I4, I2 and F4) was slightly lower than that of F2 or control plants (Table 4, Fig. 6). Growth responses of all water treated plants were significantly lower than that of controls. Although the groups were not significantly different from one another, there was a trend of less growth with consecutively harsher treatments. Willows in the desiccation treatments died within 3 days of the beginning of the treatment.

Survivorship of 1 month seedlings was generally lower than that of 6 month seedlings in all treatments (Table 5, Fig. 7). Some of this was due to generally lower levels of survivorship in younger plants and is indicated by the fact that survivorship is lower in the 1 month old than in the 6 month old control plants. Interestingly, lower levels of survivorship generally occurred in plants which underwent fluctuating (F4 or F2) treatments. We interpret this to mean that fluctuating flow disturbance is removing these small, shallow-rooted seedlings. While levels of survivorship were often very low for these plants, it is impressive and noteworthy that some plants did survive such harsh and protracted conditions.

Among 1 month old tamarisk, lowest levels of survivorship occurred in pots in the fluctuating flow treatments (Table 5, Fig. 7). We attribute this to the changing water levels removing a greater proportion of plants because their shallow roots didn't anchor them in the soil. More plants survived in the F2 treatment than the F4 treatment, although this pattern was not significant. All desiccated plants died within 3 days of the beginning of the treatments.

Among 1 month old seepwillow seedlings, only I2 plants survived and there was no significant difference in survivorship of I2 or control plants. Again, removal due to fluctuating flows seemed to account for most mortality. Desiccated plants died within 3 days of treatment commencement.

One month old coyote willows in I4, F2 and F4 treatments had significantly lower levels of survivorship than did I2 or control plants, while there was no difference in level of survivorship between I2 or control plants (Table 5, Fig. 7). This again suggested that fluctuating flows removed large numbers of plants. Additionally, the I4 treatment apparently exceeded the levels of tolerance of most 1 month old coyote willow seedlings to inundation.

Effects of Substrate on Plant Germination: In experiments, survivorship

TABLE 5: PERCENT SURVIVORSHIP OF ONE MONTH OLD RIPARIAN PLANT SPECIES EXPOSED TO SEVEN TREATMENTS OF INUNDATION AND DESICCATION (TRANSFORMED PROPORTIONS).

SPECIES	TREATMENTS							
	1	2	3	4	5	6	7	
Tach	\bar{X}	0.48	0.51	0.19	0.37	0.00	0.00	1.06
	$\pm se$	0.17	0.06	0.03	0.08	--	--	0.07
	n	7	9	9	9	9	9	9
	p =	0.000						
Saex	\bar{X}	0.32	0.79	0.30	0.33	0.00	0.00	0.93
	$\pm se$	0.06	0.08	0.07	0.10	--	--	0.08
	n	9	9	9	8	9	9	9
	p =	0.000						
Bas1	\bar{X}	0.00	0.58	0.00	0.00	0.00	0.00	0.59
	$\pm se$	--	0.07	--	--	--	--	0.09
	n	9	9	9	8	9	9	9
	p =	nsd						

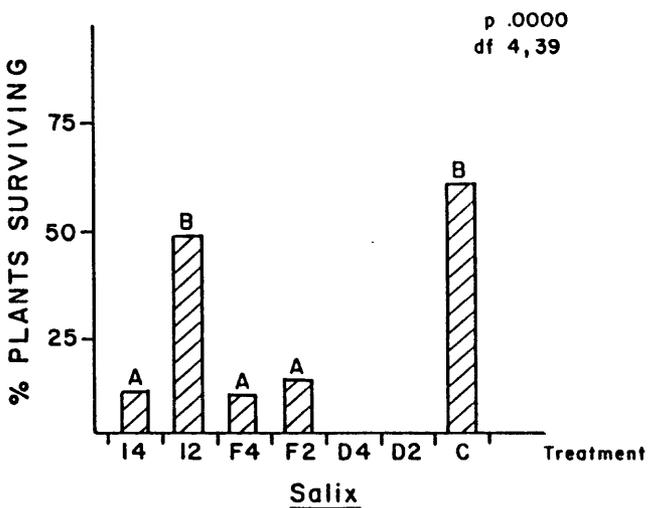
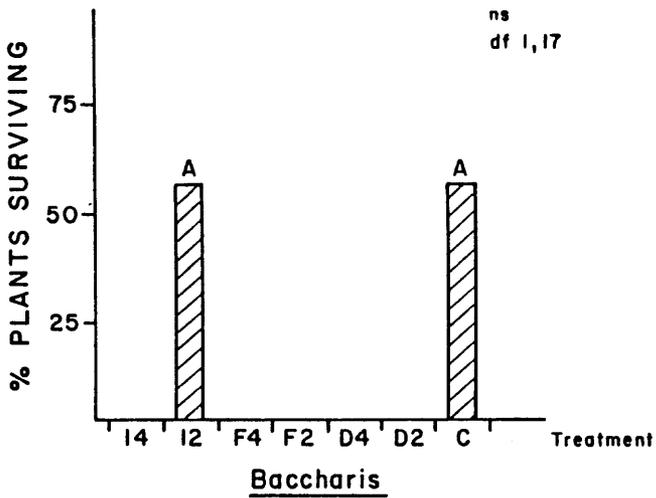
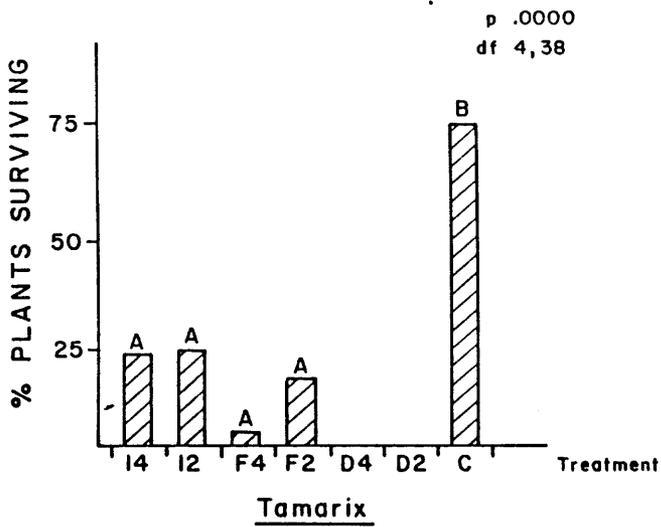


Figure 7. Mean percent survivorship of 1 month old Tamarix, Baccharis and Salix in flooding and desiccation experiments (I4 = 4 weeks inundation, I2 = 2 weeks inundation, F4 = 4 weeks fluctuating flows, F2 = 2 weeks flows, D4 = 4 weeks desiccation, D2 = 2 weeks desicc., C = controls).

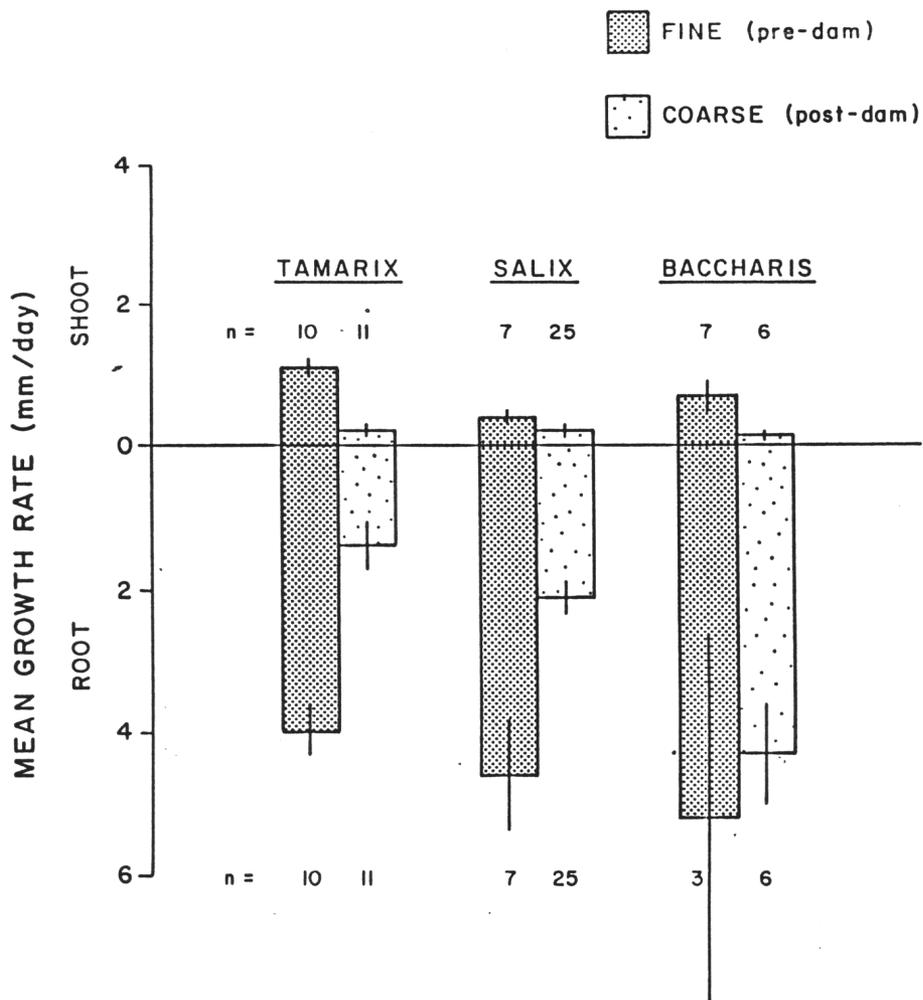


FIGURE 8: MEAN ROOT AND SHOOT GROWTH RATES OF *TAMARIX CHINENSIS*, *SALIX EXIGUA*, AND *BACCHARIS SALICIFOLIA* IN SILTY (PRE-DAM) VERSUS SANDY (POST-DAM) SUBSTRATES. SEE TEXT FOR STATISTICS.

TABLE 6: A COMPARISON OF TAMARISK SEEDLING DENSITIES ON SAND VERSUS COBBLE SUBSTRATES AT THREE SITES IN THE LOWER GRAND CANYON IN SEPTEMBER, 1986.

		SITE:			Mean
		1	2	3	Plants/ M ²
<u>SUBSTRATE TYPE</u>	SAND	0.96	0.00	0.22	0.42
	n	(51)	(40)	(51)	(142)
	COBBLE	2.03	0.35	1.55	1.20
	n	(29)	(40)	(29)	(98)

of newly germinated tamarisk and willow seedlings for 2 weeks was high (tamarisk, mean = 96% on silt and 98% on sand, $F_{1,10} = 1.84$, ns; coyote willow, mean = 80% on silt, 95% on sand, $F_{1,10} = 0.14$, ns) and were not significantly different on silt versus sand substrates. This indicates that at least initially, with water availability held constant, substrate type does not affect seedling colonization.

Effects of Substrate of Plant Growth: In experiments, the shoots and roots of seedlings (pooled across species) grew twice as much in fine (pre-dam) versus coarse (post-dam) soil ($p = .000$, $df = 1,61$ for roots, and $p = .000$, $df = 1,66$ for shoots). Analysis of seedling root growth data showed significantly greater root and shoot growth rates for all species in fine (pre-dam) soils as compared to coarse (post-dam) sediments (Fig. 8). Mean root growth rate for all plant species pooled was 4.4 mm/day in pre-dam soils and 2.2 mm/day in coarse, post-dam sediments. And the growth rate of Baccharis salicifolia seedlings was significantly greater than that of Tamarix or Salix. Shoot growth rates demonstrated a similar trend, but Tamarix (1.1 mm/day) grew more than twice as fast than the other two species' seedlings (0.5 mm/day for Baccharis and 0.4 mm/day for Salix exigua).

Field observations on substrate and survivorship: Analysis of Tamarix chinensis seedling density on sand versus cobble substrate types at three sites revealed significantly more tamarisk establishment in cobble substrates than in sand substrates (Table 6). Mean tamarisk seedling density was 0.42 plants/m² on the sand sites and 1.20 plants/m² in cobble substrates ($p = 0.009$, $df = 1,234$). Differences between sites were also significant ($p = 0.007$, $df = 2,234$), but there was no interaction between substrate and site ($p > 0.05$, $df = 3,234$). This pattern suggests that some aspect of substrate quality in cobble areas, such as enhanced moisture retention or microsite stability, now favors Tamarix establishment in cobble versus open sand. In marked contrast, virtually all of the dense stands of mature tamarisk in this system occur in relict pre-dam fine sediment deposits.

At miles 43.5L and 172L, densities of 6 month old tamarisk seedlings declined precipitously between April and September, 1986. The density of seedlings at mile 43.5L dropped from 450 seedlings/m² in April to 0.15 seedlings/m² in September, presumably as a direct result of flooding in May and June, 1986. This seedling bed lay beneath a mature Tamarix canopy and was somewhat protected from scouring by reduced current velocity among the mature trees. Seedling density at Mile 172L was reduced from a density of 979 Tamarix seedlings/m² in April to 0/m² by mid-summer, 1986. This site was inspected during commercial river trips by Stevens in late May, 1986 at which time it was inundated, and again on 1 July, 1986, at which time no seedlings remained.

Mortality of tagged 2 year old tamarisk plants was lowest in plants protected from flooding: 6.5% ($n = 31$) in a protected mesic site at 52R, intermediate (32%, $n = 25$) in a moderately exposed rock bar at 131R and highest (50%, $n = 42$) on a riverside sand bar at 171.5R ($\chi^2 = 15.64$, $p = 0.005$ at $d.f. = 2$). These plants were all subjected to approximately

one month of inundation in 1986 and the results reflect a trend of higher mortality with increasing exposure to flooding and perhaps decreasing elevation (increasing heat stress). A non-significant trend of decreasing growth with increased exposure (proximity to the river) and decreasing elevation, was also observed in these marked Tamarix plants. Growth at the protected site averaged 12.67 cm (n = 25), growth at the 131R site averaged 8.21 cm (n = 17), and growth at the 171L site averaged 0.02cm (n = 21). It appears that exposure and perhaps elevationally imposed stress, have severe effects on growth and survivorship of seedlings.

A closer inspection of the 171L site using nearest neighbor distance (NND) estimates of density (Southwood, 1979) revealed that density decreased significantly in the 2-year old Tamarix stand between April and September, 1986. In April the mean nearest neighbor distance between 40 tamarisk plants was 3.9cm (corresponding to a mean density of 167.8 plants/m² for n = 42 NND measurements), while the September mean NND had declined to 7.75cm (a density of 41.6 plants/m², n = 88) (p < 0.001, df = 1,128). Although density decreased significantly at this site in 1986, mean plant height did not change significantly. The April mean plant height at this site was 70.2 cm and the September mean height was 71.0 cm (p = 0.93, df = 38).

Timing of Seed Production in Grand Canyon: The seven species of perennial shrubs and small trees we studied separated out into two groups on the basis of seed production phenology, into those producing seeds throughout the growing season (Tamarix chinensis, Salix exigua and Baccharis salicifolia) and those producing seeds only during a short interval in mid-summer (Tessaria sericea) or only in fall (Baccharis emoryi and B. sarothroides).

Tamarix chinensis: This dominant exotic riparian species is widely known for its impressive reproductive capacity (Graf 1977; Horton et al. 1960; Warren and Turner 1975; Stevens 1985). Tamarisk is capable of producing enormous numbers of minute, wind dispersed seeds which are relatively short-lived and germinate rapidly (<24 hours, Warren and Turner 1975). In the Colorado River corridor T. chinensis produced seeds from late April through October, with seed production in the lower Canyon several weeks ahead of plants at Lees Ferry (Fig. 9). Although T. chinensis produced seed throughout the growing season, its reproductive output was not constant. At Lees Ferry, 13 marked plants on pre-dam terraces reached a peak of raceme production between mid-May and early June, and thereafter the mean level of reproductive output declined to nominal levels (Fig.10). Thus T. chinensis seed production was greatest in early summer and was nominal from mid-summer through fall in 1986 in this system.

Salix exigua: This abundant species occupies the river and stream banks in the Grand Canyon down to approximately mile 210, forming dense clones of wand-like stems on beaches. Its seeds are minute, short-lived, wind-dispersed and germinate even faster than tamarisk seeds (Stevens, pers. comm.). Like tamarisk, coyote willow produced seed throughout the

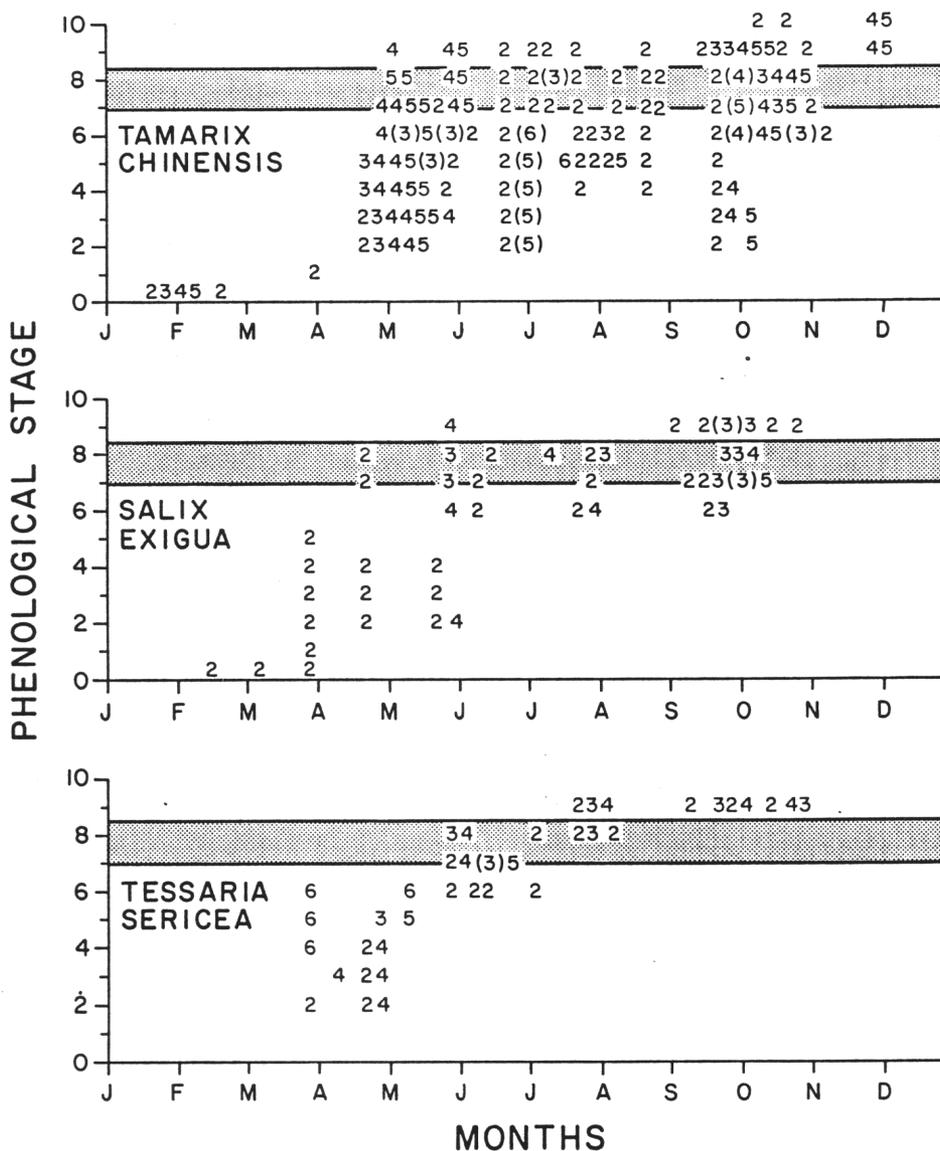


FIGURE 9 : PHENOLOGICAL BEHAVIOR OF TAMARISK, COYOTE WILLOW AND ARROWWEED THROUGH THE GROWING SEASON IN THE COLORADO RIVER CORRIDOR IN THE GRAND CANYON. GREY AREA INDICATES WHEN SEEDS ARE BEING RELEASED BY THESE SPECIES; NUMBERS REFER TO SECTIONS OF THE RIVER WHERE OBSERVATIONS WERE MADE.

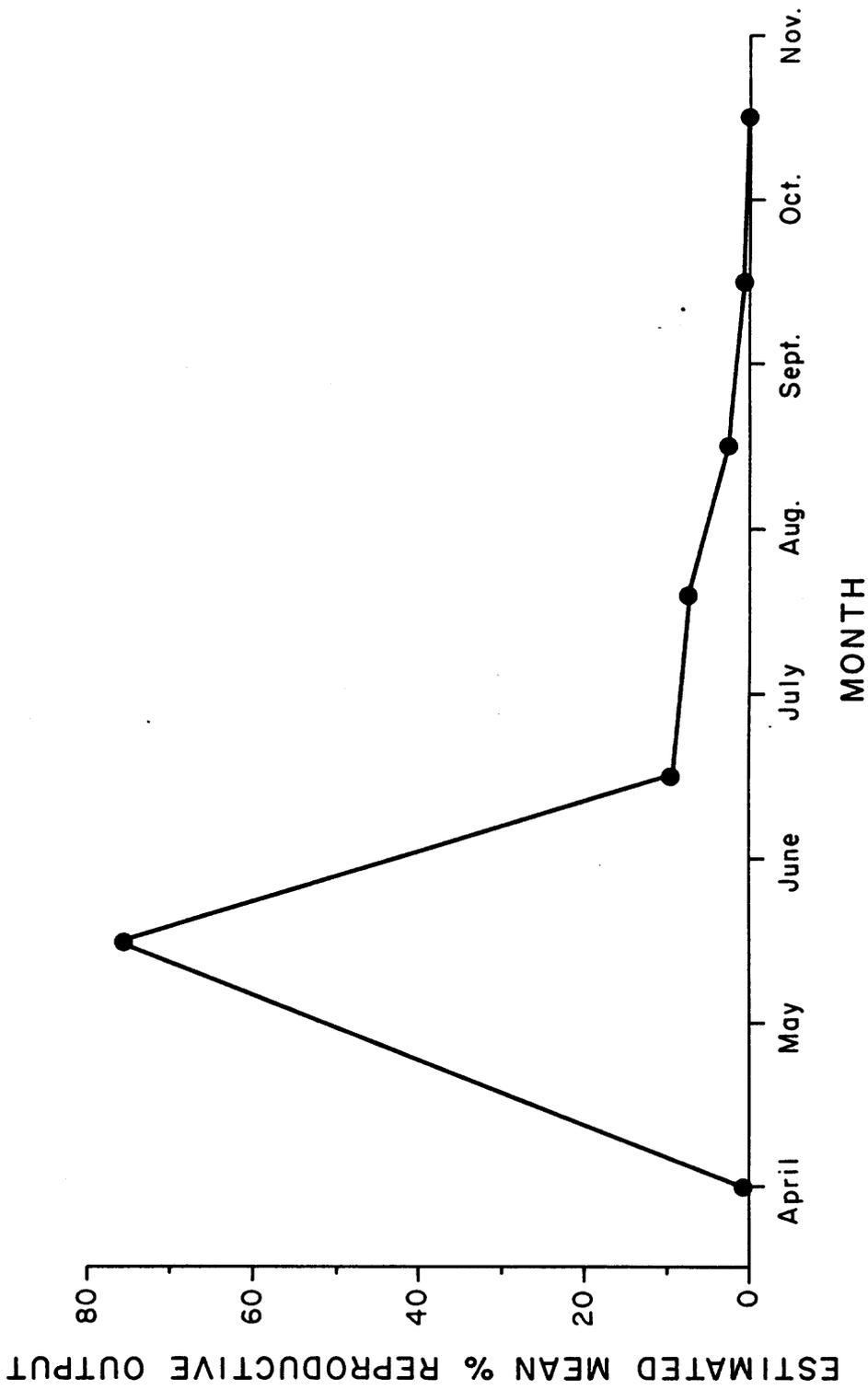


FIGURE 10: ESTIMATED MEAN PERCENT REPRODUCTIVE OUTPUT OF THIRTEEN ADULT TAMARISK TREES THROUGH THE 1986 GROWING SEASON AT LEES FERRY, ARIZONA.

growing season in 1986 (Fig. 9), although seed production appeared to be more constant. We believe willow seedlings are rarities in Grand Canyon, with only 3 seedlings found in this study.

Tessaria sericea: Arrowweed is a native, clonal composite which occupies silt and sand substrates throughout the Colorado River corridor in Grand Canyon. It produces large numbers of moderate-sized, wind dispersed seeds which are relatively long-lived and slow to germinate (Stevens, pers. comm.). Unlike tamarisk, coyote willow and Baccharis salicifolia, arrowweed produced seed only during a relatively discrete period between early June and early August (Fig.9).

Baccharis salicifolia: Seepwillow is a native composite shrub which can reach nearly 4.0m in height and occurs widely throughout the river corridor. It produces moderate quantities of intermediate-sized, wind-dispersed seeds which are relatively long-lived (Stevens, pers. comm.). Seepwillow produced seeds from mid-July through mid-September in Section 2 (at Lees Ferry) and from early April through December below Mile 88 (Fig. 11). Whether this divergent blooming pattern is genetic or environmentally induced remains to be determined.

Baccharis emoryi and B. sarothroides: Emory's seepwillow and desert broom are native shrub-forming composite and they share a similar seed production phenology. The former species occurs in the upper 4 sections, while desert broom only occurs downstairs from lower section 3. Both species produce moderate numbers of intermediate-sized, wind-dispersed seeds once a year, with the peak of seed production from mid-September through mid-November for B. emoryi, and the peak of seed production for B. sarothroides from mid-October through late November (Fig. 11). Only desert broom seeds germinated along the river without flood-related disturbances.

Other Species: We observed seed production among the other common perennial or semi-riparian species in the river corridor, including common reed (Phragmites australis), honey mesquite (Prosopis glandulosa), catclaw (Acacia greggii), camelthorn (Alhagi camelorum), Goodding's willow (Salix gooddingii), Fremont's cottonwood (Populus fremontii), Aster spinosus, Baccharis sergiloides, Brickellia longifolia, and Haplopappus acradenius. Common reed produces seed in October and November. Mesquite and catclaw produce seed in mid- to late summer and mesquite occasionally has two periods of bloom. Camelthorn is a noxious exotic and blooms in mid-summer and produces seeds throughout the summer and fall. Goodding's willow blooms in April and May, producing seeds in late spring. Fremont's cottonwood produces seed in late March or April. Aster blooms and produces seed from mid-summer through fall, while the other Compositae species (Baccharis, Brickellia, and Haplopappus) produce seed in the fall months. Except for Goodding's willow and cottonwood, viable seeds of all of these species are present in the environment in late summer and fall.

Vegetative Reproduction: In experiments vegetative reproduction of tamarisk, coyote willow, and seepwillow was highly successful, while

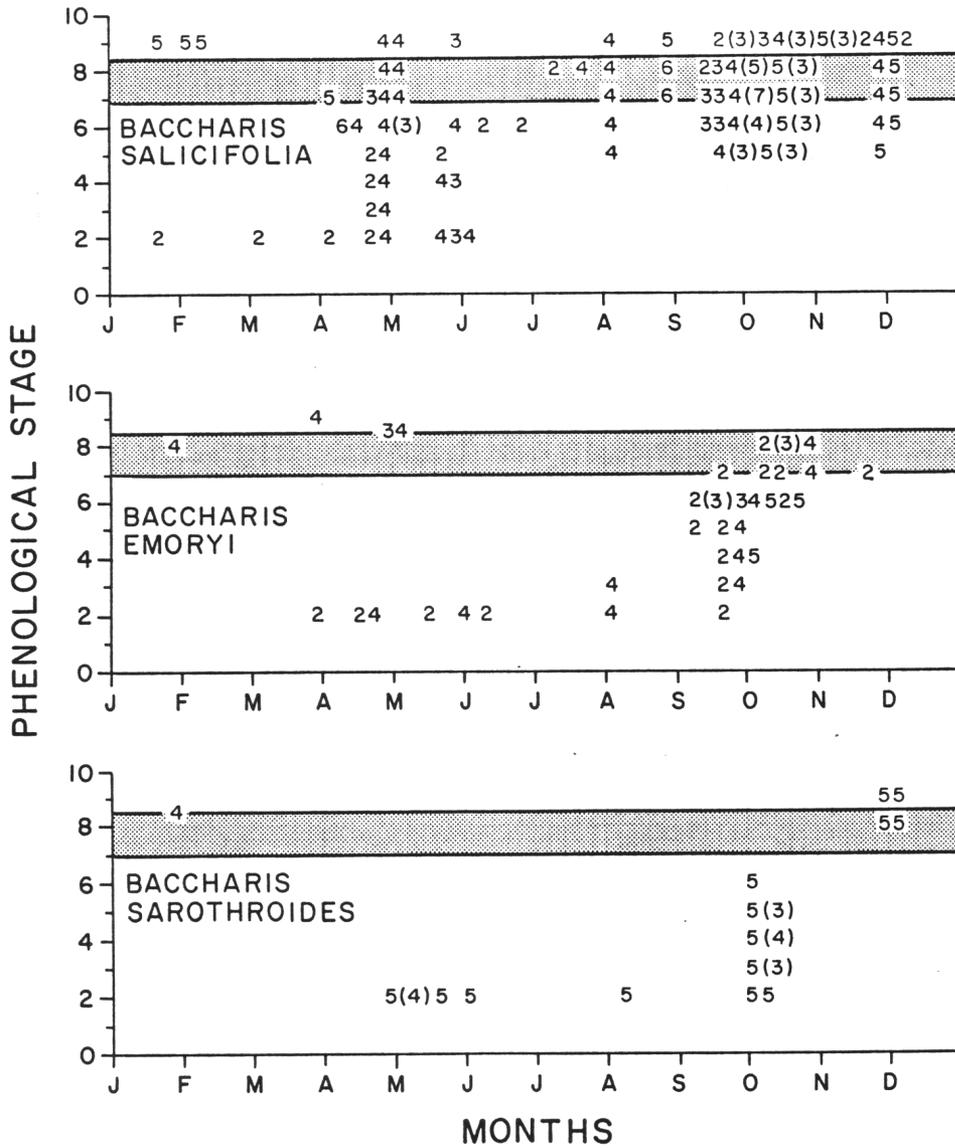


FIGURE 11: PHENOLOGICAL BEHAVIOR OF THREE BACCHARIS SPECIES THROUGH THE GROWING SEASON IN THE COLORADO RIVER CORRIDOR IN THE GRAND CANYON. GREY AREA INDICATES WHEN SEEDS ARE BEING RELEASED BY THESE SPECIES, AND NUMBERS REFER TO SECTIONS OF THE RIVER IN WHICH OBSERVATIONS WERE MADE.

arrowweed was less successful in becoming established from planted stems. At Lee's Ferry, 100% (n = 15) of willow stems planted in wet sand became established, while 87% (n=13) of the 15 arrowweed stems planted became established.

At the 43.5L mile site, none of the planted stems survived. We attribute this to the site's being several meters over the water and the planted stems dried out and died. At the 66.0L site, 44% (n = 29) of 66 stems planted survived, with higher levels of survivorship occurring closer to the river (Fig. 12). Tamarisk, coyote willow and seepwillow were successfully established, while only 1 arrowweed stem rooted and grew. In all cases, the foliage died back and plants were producing new lateral shoots. This is a stressful experience for plants, and although it has been successful in an experimental setting, the likelihood of it occurring with great frequency in nature is low. Plant cuttings as a means of establishing plants might be considered, however.

DISCUSSION

This study has determined that replacement of plants lost in the 1983 flood in Grand Canyon has been a slow and localized process. For all species we studied, there was an overall decline in numbers, due largely to a severe decline in numbers during the 1983 flood and a lack of reestablishment to date, 3 years later. Because the negative effects of flooding on plants are well established (see Introduction), this result is not surprising. Our results point to two primary mechanisms which appear to be restricting plant recolonization to very specific sites or habitats within the riparian zone in Grand Canyon: 1.) continued flooding since 1983 and 2.) a decline in substrate quality. By understanding the role of these mechanisms, Glen Canyon Dam managers may be able to reverse this trend of plant loss in the Grand Canyon.

Most colonization in Grand Canyon is now occurring on cobble bars and to a lesser extent, on sandy substrates. Considering that most large old stands of tamarisk in the Canyon occur in silty pre-dam sediments, this represents a dramatic shift in this species' pattern of establishment. We believe that this change is due, in part, to a loss of finer substrates (silts) and accumulation of coarse sand, and perhaps more importantly to continued flooding which has effectively prevented colonization of most beaches by seedlings. Our seedling growth experiments demonstrate that seedlings of all species grow more slowly in post-dam sand substrates than in pre-dam silts. In on-going experiments, Stevens (pers. comm.) corroborated the pattern of reduced growth rates for two-year old tamarisk and coyote willow in coarse post-dam substrates, as compared to pre-dam silts. In his experiments, both tamarisk and coyote willow cuttings grew significantly more in silt than sand over a period of 90 days. The longterm effects of silt versus sand substrates on plant survivorship, growth and reproductive potential are not presently understood.

Establishment of plants on cobble bar sites has been impressive.

Densities of the species we studied, especially tamarisk and Baccharis spp. are approaching pre-flood densities, or, in the case of tamarisk, are actually exceeding previous numbers at some sites. At present, we hypothesize that two factors account for this level of recruitment success. The cobble bar substrate may offer unique microsite features that facilitate increased germination and increased establishment of seedlings. Cobbly or rocky substrates may slow soil desiccation, which would allow colonizing seedlings to sink roots to an adequate depth before the soil dries; and cobble bars probably protect larger seedlings from being uprooted and removed by floodwaters. In contrast, sand beaches lack such barriers against seedling desiccation and removal. The success of plants on cobble bars deserves further attention, because the behavior (i.e. long-term survivorship, growth and reproductive potential) of plants in this substrate as compared to others is poorly understood.

Sand beaches that are being colonized, are being invaded primarily by clonal species. Both coyote willow and arrowweed were found most commonly on sandy beaches reinvading beaches from nonexposed peripheries, via rhizomes or underground running shoots. The ability of these vegetatively reproductive populations to expand on sandy beaches is one which sexual, seed dispersing species do not have, probably because of flooding disturbance and/or rapid soil desiccation. Stevens and Waring (1985-BOR1) showed that plants on sand substrates experienced the highest levels of scouring removal. Even clonal plants occasionally fail to successfully colonize some sandy beaches: coyote willow runners were noted invading the beach at 118.5L mile in June, 1984, and by late August, 1984, they were wilting and dying back in the summer heat. Clonal coyote willow and arrowweed have not been very successful in colonizing cobble substrates, perhaps because their underground running roots cannot move between rocks.

Another distinctive pattern involves a shift in establishment from about the 30,000 cfs zone to about the 40,000 cfs zone along Grand Canyon beaches. While small seedlings were seen below the 40,000 cfs zone, most more mature recruits were encountered at the 40,000 cfs zone. This suggests that the beach area located below the 40,000 line is flooded too frequently to permit plant colonization, and represents an upslope migration for the Colorado River new high water zone plant community. This 40,000 to 60,000 cfs zone was, prior to 1983, largely devoid of riparian vegetation, presumably because of insufficient water. Plants that colonized this zone after 1983 may face severe desiccation if discharge levels remain below 30,000 cfs during hot spring months.

Because most of the recruits we counted were still young plants in 1986, it is unlikely that all will survive. While we do not fully understand age-related mortality in these species, we do know from our experiments that younger plants are more vulnerable to 'natural' mortality and to flood-related mortality than are older plants. Because of this we doubt that all of the juvenile plants we saw in 1986, most of which probably established in 1984, are likely to survive alive in another 3 years. However, under benign conditions, some of them probably will.

In this chapter we review and discuss the Bureau of Reclamation's five flow regime alternatives proposed for Glen Canyon Dam (Wegner 1985).

Alternative 1: Monthly base-loaded power plant releases.

A base-loaded or relatively constant flow regime is preferred for this riparian plant community because recruitment and recovery occur faster in a disturbance-free environments. Such a flow regime would minimize leaching and loss of nutrients and fine particle substrates, minimize scouring removal and drowning of riparian vegetation, and promote survival of established seedlings.

Alternative 2: Status quo with maximized power releases.

This alternative would continue to negatively affect riparian plant community development by damaging existing plants and by retarding recruitment in the floodzone nearest the river where riparian vegetation could be the most profuse. Because flooding events are particularly erosive in impounded rivers, maximized power releases would promote additional leaching of nutrients and fine particled sediments from the system.

Alternative 3. Maximized power plant releases between 8,000cfs and 25,000cfs.

This flow regime would be more likely than Alternative 2 to support a healthy riparian plant community along the Colorado River. The proliferation of riparian vegetation from 1965 to 1982 occurred, for the most part, under such a flow regime. If erosion could be minimized by slowing the rate of change in discharge, the negative impacts of this flow regime on the riparian plant community could be mitigated.

Alternative 4: Seasonally base-loaded flows with maximized power releases in other seasons.

This alternative is not preferred because it would result in continued disturbance of existing riparian plant life, retarded recolonization and recovery of the streamside vegetation, and would probably promote continued high rates of substrate erosion and nutrient depletion in this system.

Alternative 5: Maximized fishery releases.

This alternative is not recommended for the reasons discussed under Alternative 2 (above).

The Timing of Spillovers

Although flooding disturbance promoted germination, our studies indicate that post-dam flooding from 1983 to the present have had a negative impact on overall riparian plant community development in the Colorado River corridor in the Grand Canyon. Because recovery may require a decade or more, erratic releases should be avoided in this system if at all possible. If spills are necessary in the future, we suggest that

they be restricted in amplitude and duration as much as possible. At present we predict that duration of flooding exerts a greater effect on survivorship than does amplitude, but this question deserves more study. Our examination of seed production phenology among the riparian plant species of interest clearly indicates that seeds of virtually all species are present in the environment in late summer and fall, when Tamarix seed production has declined. If a future spill is necessary in the Colorado River corridor, a late summer or fall flood could be used advantageously to disperse seeds of native riparian species instead of tamarisk, and thereby increase riparian plant diversity; however, to be an effective agent of germination and increased plant diversity, flooding disturbance should be a rare event, not a frequent event, in this system.

CONCLUSIONS

1. Twenty-one of 49 quadrats censused showed high levels of plant recolonization or replacement.
2. On 15 quadrats, 1986 densities of Tamarix chinensis, Salix exigua, Baccharis spp. and Tessaria sericea approached preflood densities.
3. While it is impossible to predict densities of older plants from seedling densities, large germination events are essential for replacement.
4. Mortality and damage of 6 month old plants was greatest in the harshest flooding (inundation) treatments, while fluctuating flow treatments caused highest levels of mortality in 1 month old plants, due to removal of these shallow-rooted seedlings.
5. In the wild, mortality of 2 year old plants increased from 6% to 50% with increased exposure to flooding.
6. All plants wilted and died rapidly (within 5 days) when desiccated.
7. Tamarisk and coyote willow can germinate and survive for at least 2 weeks in fine- or coarse-grained sediments (when adequate water is provided), but root and shoot growth rates of tamarisk, coyote willow and seepwillow seedlings and 2 year old plants are significantly higher in fine-grained sediments. The ability to rapidly outgrow the seedling stage should enhance a plant's ability to survive future harsh conditions of flooding or desiccation.
8. Most post-flood establishment of tamarisk and seepwillow seedlings occurred on cobble bar substrates, perhaps because such sites offer protection from desiccation and flooding.
9. Most post-flood establishment of clonal coyote willow and arrowweed occurred on sandy beaches, involving a reinvasion of runners from protected peripheries of beaches.
10. A pattern of seedling establishment at about the 40,000 cfs zone was observed along the Colorado River, representing a shift from previous establishment of plants below that zone prior to 1983.
11. Tamarisk, Baccharis salicifolia and coyote willow seeds are produced throughout the growing season, while seeds of arrowweed, B. emoryi, B. sarothroides, Brickellia sp., acacia, mesquite and cottonwood are produced during brief periods during the growing season.
12. Seepwillow and coyote willow seeds are produced continuously throughout the growing season, while most tamarisk seeds are produced early in the growing season.

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APPENDIX 1:
 DATA FROM FIFTEEN QUADRATS IN THE RIPARIAN ZONE OF THE COLORADO RIVER
 IN THE GRAND CANYON, JUNE, 1984 TO SEPTEMBER, 1986

KEY:

River Mile	Miles from Lees Ferry downstream to quadrat; L = left (south) side, R = right (north) side of river
Year	46 = June 1984, 56 = 1985, 69 = September 1986
Flood Zone	1 = 20,000 to 40,000, 2 = 40,000 to 60,000 cfs zone.
Quadrat Width	Quadrat width (m) from approximate 20,000 to 60,000 stage
Size Class	1 = seedlings, 2 = 0.3 - 1.0m, 3 = 1.0 - 2.0m, 3 = >2.0m
No. Tach	Number of <u>Tamarix chinensis</u> in given size class on quadrat
No. Saex	Number of <u>Salix exigua</u> in a given size class on quadrat
No. Baspp	Number of <u>Baccharis salicifolia</u> , <u>B. emoryi</u> , and/or <u>B. sarothroides</u> in a given size class on quadrat
No. Tese	Number of <u>Tessaria sericea</u> in given size class on quadrat
Plot No.	Quadrat number, 1-15
Section	2 = Lees Ferry - Mile 61, 3 = 61 - 88, 4 = 88 - 166.5, 5 = 166.5 - 226

APPENDIX 2:
 DATA FROM FIFTEEN QUADRATS IN THE RIPARIAN ZONE OF THE COLORADO RIVER
 IN THE GRAND CANYON, APRIL TO SEPTEMBER, 1986

KEY:

Quadrat No.	1 = 31R, 2 = 41R, 3 = 52R, 4 = 52.5R, 5 = 104R, 6 = 118.5L, 7 = 122.1R, 8 = 131.0R, 9 = 131.5R, 10 = 143R, 11 = 166.5L, 12 = 171.5L, 13 = 180.1R, 14 = 198.5R, 15 = 208.5R
Period	1 = April, 1986; 2 = September, 1986
Zone	1 = 20,000 to 40,000, 2 = 40,000 to 60,000 cfs zone.
Width	Quadrat width (m) from approximate 20,000 to 60,000 stage
Size Class	1 = seedlings, 2 = 0.3 - 1.0m, 3 = 1.0 - 2.0m, 3 = >2.0m
No. Tach	Number of <u>Tamarix chinensis</u> in given size class on quadrat
No. Saex	Number of <u>Salix exigua</u> in a given size class on quadrat
No. Baspp	Number of <u>Baccharis salicifolia</u> , <u>B. emoryi</u> , and/or <u>B. sarothroides</u> in a given size class on quadrat
No. Tese	Number of <u>Tessaria sericea</u> in given size class on quadrat

APPENDIX 3:
 DATA FROM SEVEN EXPERIMENTAL TREATMENTS WITH
 SIX MONTH OLD RIPARIAN SEEDLINGS

KEY:

Species	1 = Tamarisk, 2 = coyote willow, 3 = seepwillow
Treatment	1 = 1 month of complete inundation, 2 = 2 weeks of complete inundation, 3 = one month of fluctuating flow, 4 = 2 weeks of fluctuating flow, 5 = two weeks of desiccation, 6 = 1 week of desiccation, 7 = controls
Pot No.	Number of replicates (pots)
Survivorship	Percent surviving at end of experiment
Sqrt Survshp	Square root of survivorship
Asin(survshp) ^{1/2}	Arcsine transformation of the square root of survivorship

APPENDIX 4:
 DATA FROM SEVEN EXPERIMENTAL TREATMENTS WITH
 ONE MONTH OLD RIPARIAN SEEDLINGS

KEY:

Species	1 = Tamarisk, 2 = coyote willow, 3 = seepwillow
Treatment	1 = 1 month of complete inundation, 2 = 2 weeks of complete inundation, 3 = one month of fluctuating flow, 4 = 2 weeks of fluctuating flow, 5 = two weeks of desiccation, 6 = 1 week of desiccation, 7 = controls
Pot No.	Number of replicates (pots)
Survivorship	Percent surviving at end of experiment
Sqrt Survshp	Square root of survivorship
Asin(survshp) ^{1/2}	Arcsine transformation of the square root of survivorship

APPENDIX 5:

A COMPARISON OF THE DENSITY OF DEAD STEMS ON QUADRATS IN 1984
 (UNADJUSTED AND ADJUSTED FOR REMOVAL) WITH THE DENSITY OF
 1986 LIVE STEMS OF TAMARISK, COYOTE WILLOW, SEEPWILLOWS, AND ARROWWEED

KEY:

Plot No.	1 = 31R, 2 = 41R, 3 = 52R, 4 = 52.5R, 5 = 104R, 6 = 118.5L, 7 = 122.1R, 8 = 131R, 9 = 131.5R, 10 = 143R, 11 = 166.5L, 12 = 171.5L, 13 = 180.2R, 14 = 198.5R, 15 = 208.5L
Plot Width	Quadrat width (m)
Species	1 = <u>Tamarix chinensis</u> , 2 = <u>Salix exigua</u> , 3 = <u>Baccharis spp.</u> , 4 = <u>Tessaria sericea</u>
No. Live in 1984	Number of living plants on the quadrat in 1986
No. Dead in 1984	Number of dead plants on the quadrat following the 1983 flood
Est'd % Removal	Estimate of percent removal by scouring in 1983 (estimates from Stevens and Waring, 1985)

PLOT NO.	PLOT WIDTH (m)	SPECIES	NO. LIVE IN 1986	NO. DEAD IN 1984	ESTIMATED % REMOVED IN 1983
111	60	1	26	33	19
111	60	2	26	0	72
111	60	3	0	0	74
111	60	4	0	0	90
111	60	5	0	0	19
111	60	6	0	0	72
111	60	7	0	0	74
111	60	8	0	0	90
111	60	9	0	0	19
111	60	10	0	0	72
111	60	11	0	0	74
111	60	12	0	0	90
111	60	13	0	0	19
111	60	14	0	0	72
111	60	15	0	0	74
111	60	16	0	0	90
111	60	17	0	0	19
111	60	18	0	0	72
111	60	19	0	0	74
111	60	20	0	0	90
111	60	21	0	0	19
111	60	22	0	0	72
111	60	23	0	0	74
111	60	24	0	0	90
111	60	25	0	0	19
111	60	26	0	0	72
111	60	27	0	0	74
111	60	28	0	0	90
111	60	29	0	0	19
111	60	30	0	0	72
111	60	31	0	0	74
111	60	32	0	0	90
111	60	33	0	0	19
111	60	34	0	0	72
111	60	35	0	0	74
111	60	36	0	0	90
111	60	37	0	0	19
111	60	38	0	0	72
111	60	39	0	0	74
111	60	40	0	0	90
111	60	41	0	0	19
111	60	42	0	0	72
111	60	43	0	0	74
111	60	44	0	0	90
111	60	45	0	0	19
111	60	46	0	0	72
111	60	47	0	0	74
111	60	48	0	0	90
111	60	49	0	0	19
111	60	50	0	0	72
111	60	51	0	0	74
111	60	52	0	0	90
111	60	53	0	0	19
111	60	54	0	0	72
111	60	55	0	0	74
111	60	56	0	0	90
111	60	57	0	0	19
111	60	58	0	0	72
111	60	59	0	0	74
111	60	60	0	0	90
111	60	61	0	0	19
111	60	62	0	0	72
111	60	63	0	0	74
111	60	64	0	0	90
111	60	65	0	0	19
111	60	66	0	0	72
111	60	67	0	0	74
111	60	68	0	0	90
111	60	69	0	0	19
111	60	70	0	0	72
111	60	71	0	0	74
111	60	72	0	0	90
111	60	73	0	0	19
111	60	74	0	0	72
111	60	75	0	0	74
111	60	76	0	0	90
111	60	77	0	0	19
111	60	78	0	0	72
111	60	79	0	0	74
111	60	80	0	0	90
111	60	81	0	0	19
111	60	82	0	0	72
111	60	83	0	0	74
111	60	84	0	0	90
111	60	85	0	0	19
111	60	86	0	0	72
111	60	87	0	0	74
111	60	88	0	0	90
111	60	89	0	0	19
111	60	90	0	0	72
111	60	91	0	0	74
111	60	92	0	0	90
111	60	93	0	0	19
111	60	94	0	0	72
111	60	95	0	0	74
111	60	96	0	0	90
111	60	97	0	0	19
111	60	98	0	0	72
111	60	99	0	0	74
111	60	100	0	0	90

APPENDIX 6:
 CHANGES IN DENSITY OF DIFFERENT SIZE CLASSES OF RIPARIAN PLANT SPECIES
 FROM 1984 TO 1986 ON FIFTEEN QUADRATS

KEY:

Species	1 = <u>Tamarix chinensis</u> , 2 = <u>Salix exigua</u> , 3 = <u>Baccharis spp.</u> , 4 = <u>Tessaria sericea</u>
Plot No.	Quadrat No., 1 - 15.
SC1 ₈₅	Density of 0.3 to 1.0 m plants in 1985
SC2 ₈₅	Density of plants GT 1.0 m in 1985
S ₈₄	Density of seedlings in 1984
SC2 ₈₆	Density of plants GT 1.0 m in 1986
SC1 ₈₄	Density of 0.3 to 1.0 m plants in 1984
SC2 ₈₄	Density of plants GT 1.0 m in 1984
SC1 ₈₆ -SC1 ₈₅	Change in density of plants 0.3 to 1.0 m from 1985 to 1986
S ₈₅	Density of seedlings in 1985

APPENDIX 7:
OCCURRENCE OF TAMARIX SEEDLINGS IN DIFFERENT SUBSTRATE TYPES
AT THREE LOCATIONS IN THE LOWER GRAND CANYON IN SEPTEMBER, 1986

KEY:

Site No.	1 = Mile 171.5L, 2 = Mile 180.2R, 3 = Mile 198.5R
Substrate Type	1 = sand, 2 = cobble
No. Tach/m ²	Density of tamarisk seedlings on randomly selected 1.0 m ² plots

APPENDIX 8:
GROWTH AND ORIGINAL HEIGHT OF TWO YEAR OLD TAMARISK AT THREE SITES
IN THE COLORADO RIVER CORRIDOR IN 1986

KEY:

Site	1 = Mile 52R, 2 = Mile 131.5R, 3 = Mile 171.5L
Growth	Change in height (cm) of an individual between April and September, 1986
Original Ht	Initial height of an individual tamarisk in April, 1986

SITE	GROWTH (cm)	ORIGINAL HT (cm)
N	20	121
N	13	35
N	10	66
N	5	47
N	5	74
N	5	40
N	5	33
N	-12	28
N	1	9
N	1	24
N	2	18
N	21	50
N	3	77
N	11	64
N	20	92
N	7	81
N	4	106
N	46	43
N	16	18
N	17	52
N	7	88
N	-0	48
N	-28	88
N	-28	42
N	7	18
N	24	38
N	3	43
N	35	12
N	24	9
N	15	24
N	19	44
N	28	60
N	41	86
N	1	55
N	2	55
N	19	33
N	34	98
N	11	68
N	11	21
N	0	25
N	-0	62
N	5	38
N	9	33
N	4	11
N	4	88
N	11	56
N	3	55
N	-0	60
N	-1	46
N	-1	11
N	1	61
N	4	39
N	5	79
N	1	99
N	2	56
N	-7	28
N	-15	21
N	-15	87
N	0	59
N	0	55
N	-2	84
N	-2	14
N	6	80
N	21	96
N	19	84

APPENDIX 9:
NEAREST NEIGHBOR DISTANCES AND HEIGHTS OF NEIGHBORS
IN A TWO YEAR OLD STAND OF TAMARISK IN APRIL AND SEPTEMBER, 1986
AT COLORADO RIVER MILE 171.5L

KEY:

Sample Period	1 = 28 April, 1986, 2 = 28 September, 1986
NND	Nearest neighbor distance (cm) of a randomly selected individual
Ht Neighbor 1	Height of a randomly selected plant (cm)
Ht Neighbor 2	Height of the nearest neighbor to the randomly selected individual (cm)

APPENDIX 10:
OBSERVATIONS ON THE PHENOLOGY OF FOUR RIPARIAN PLANT SPECIES IN THE
COLORADO RIVER CORRIDOR IN THE GRAND CANYON

KEY:

Species	Tach = tamarisk, Saex = coyote willow, Tese = arrow- weed, Basl = seep willow, Baem = Emory's seepwillow, Basr = desert broom
Date	Day, Month, Year
River Mile	Observation point, in miles downstream from Lees Ferry; L = left (south), R = right (north) side of river
Phenology Stage	0 = no leaves, 1 = young leaves, 2 = mature leaves, 3 = developing flower buds, 4 = mature flower buds, 5 = beginning bloom, 6 = full bloom, 7 = post bloom, 8 = seed production, 9 = post seed production, 10 = chlorosis
No. of Plants Observed	Number of plants in census

* = data taken from Museum of Northern Arizona herbarium

SPECIES	DATE (DAY, MO, YR)	RIVER MILE	PHENOLOGICAL STAGE	NO. OF PLANTS OBSERVED
BASR	20 05 66	174.0	2	1
BASR	22 05 66	165.0	2	2
BASR	25 05 66	166.0	2	3
BASR	27 05 66	200.0	2	1

APPENDIX 11:
REPRODUCTIVE PHENOLOGY OF THIRTEEN MARKED TAMARISK
AT LEES FERRY, ARIZONA

KEY:

Plant No.	Plant number (1 to 13)
Period	1 = 15 April, 2 = 15 May, 3 = 15 June, 4 = 15 July, 5 = 15 August, 6 = 15 September, 7 = 15 October, 1986
% Bloom	Percent of an individual's canopy covered with inflorescences
Arcsine % Bloom	Arcsine transformation of percent bloom data

