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EFFECTS OF THE POST-GLEN CANYON DAM FLOW REGIME ON THE OLD HIGH WATER LINE PLANT COMMUNITY ALONG THE COLORADO RIVER IN GRAND CANYON

Terrestrial Biology of the
Glen Canyon Environmental Studies

By

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Growth and reproduction of native riparian trees were studied along the Colorado River in Grand Canyon. Populations of mesquite and acacia in the old high water zone were found to be growing and reproducing successfully. Shoot growth in adults is not significantly related to river flow levels. Adult mortality was highest near the river's edge and may reflect damage from the greater than 90,000 cfs flows in 1983. Under the post-dam river flow regime the frequency and height of the highest river flows continue to be the factors controlling the distribution of acacia and mesquite, as they were in the pre-dam era. Establishment of seedlings and survivorship of younger age classes now occurs in the new high water zone. This will lead to relocation of the old high water zone closer to the river's edge in the future. The fate of mesquite and acacia in the old high water zone is unknown. The trees are long lived and may need only a few seedling recruitment events to replace themselves. Acacia are more drought tolerant than mesquite and show greater seedling establishment in the old high water zone. Current river flow patterns have their greatest effect on germination and survivorship of seedlings and saplings. An analysis of the reproductive effort of adult mesquite showed mesquite seeds have high viability and low rates of abortion and predation, but establishment is low.

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ABSTRACT

Growth and reproduction of native riparian trees were studied along the Colorado River in Grand Canyon. Populations of mesquite and acacia in the old high water line riparian zone (OHWL) were found to be growing and reproducing successfully. Shoot growth in adults is not significantly related to river flow levels. However, adult mortality was highest near the river's edge and may reflect damage from > 90,000 cfs flows in 1983.

Under the post-dam river flow regime the frequency and height of the highest river flows continue to be the factors controlling the distribution of acacia and mesquite, as they were in the pre-dam era. Establishment of seedlings and survivorship of younger age classes now occurs in the new high water line riparian zone (NHWL). This will likely lead to a relocation of the OHWL community closer to the river's edge in the future. The fate of mesquite and acacia in the OHWL community farther from the river is unknown. Though there are few seedlings and saplings in the OHWL the trees are very long lived and may need only a few seedling recruitment events to replace themselves. Acacia are more drought tolerant than mesquite and show greater seedling establishment in the OHWL than mesquite. They are more likely to remain in both the OWHL and NHWL in the future while mesquite migrates to the NHWL.

Current river flow patterns have their greatest effect on germination and survivorship of seedlings and saplings. Younger age classes of acacia are much more common than younger age classes of mesquite, though survivorship for mesquite seedlings and saplings is higher. Seedlings have the lowest survivorship. Saplings 2-3 years old have greater survivorship than saplings 3-5 years old which germinated in 1983 when dam releases were abnormally high. These seedlings established far from the river's edge and have higher mortality from reduced soil moisture now that water levels have dropped.

An analysis of the reproductive effort of adult mesquite thoughout the flowering/fruiting cycle showed that mesquite seeds have high viability and relatively low rates of abortion and predation. However, rates of seedling establishment are low. Because seedlings typically establish at the water's edge they are more susceptible to changes in river flow patterns than adults. If dam releases are low during the period of establishment in July, August and September seedlings may be inundated at higher flows. If dam releases are abnormally high during seedling establishment seedlings have a greater chance of mortality from desiccation as dam releases return to normal and river flow levels decrease.

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Introduction

The Colorado River in Grand Canyon supports a unique riparian resource. Its 275 miles of protected riparian habitat represent the longest contiguous protected riparian corridor in the western United States. Riparian habitats are especially valuable in arid regions and have long been recognized as contributing to the biotic diversity of arid environments in disproportion to their area (Shreve 1951). The additional available water permits the growth of plant species not found in surrounding upland habitats and increases the productivity of riparian plant communities over upland communities (Campbell and Green 1968, Nilsen et al. 1984, Van Auken and Bush 1985, Warren and Anderson 1985). The increased diversity and productivity of the riparian vegetation in turn support animals that are rare or absent in strictly upland habitats (Lowe 1964).

Before the closure of Glen Canyon Dam, the riparian habitat along the Colorado River in the Grand Canyon was characterized by three vegetation belts running parallel to the river (Figure 1; Carothers et al. 1979). The zone closest to the river was subject to annual, scouring floods and consequently supported only ephemeral herbaceous species and short-lived mesophytic woody plants that invaded between floods. The zone farthest from the river was not influenced by river flows and was composed of desert vegetation. Between these two zones was a vegetation belt whose lower boundary was delineated by the high water line of major floods. This stable plant community is called the old high water line (OHWL) riparian zone. It is dominated by woody plants such as apache plume (*Fallugia paradoxa*), redbud (*Cercis occidentalis*), netleaf hackberry (*Celtis reticulata*), western honey mesquite (*Prosopis glandulosa*) and catclaw acacia (*Acacia greggii*). Apache plume dominates the OHWL community above river mile (RM) 40 and mesquite and acacia dominate below that point to Lake Mead (Carothers et al. 1979). Since the closure of Glen Canyon Dam river flow levels are less variable and scouring floods have become much less frequent, allowing the development of a new riparian zone in the old ephemeral zone. This newly formed community, termed the new high water line (NHWL), consists of fast growing trees and shrubs (Figure 1; Carothers et al. 1979).

The two dominant native tree species throughout the river corridor in the Grand Canyon are western honey mesquite and catclaw acacia. This study focused on these two species because of their importance in the pre-dam riparian community.

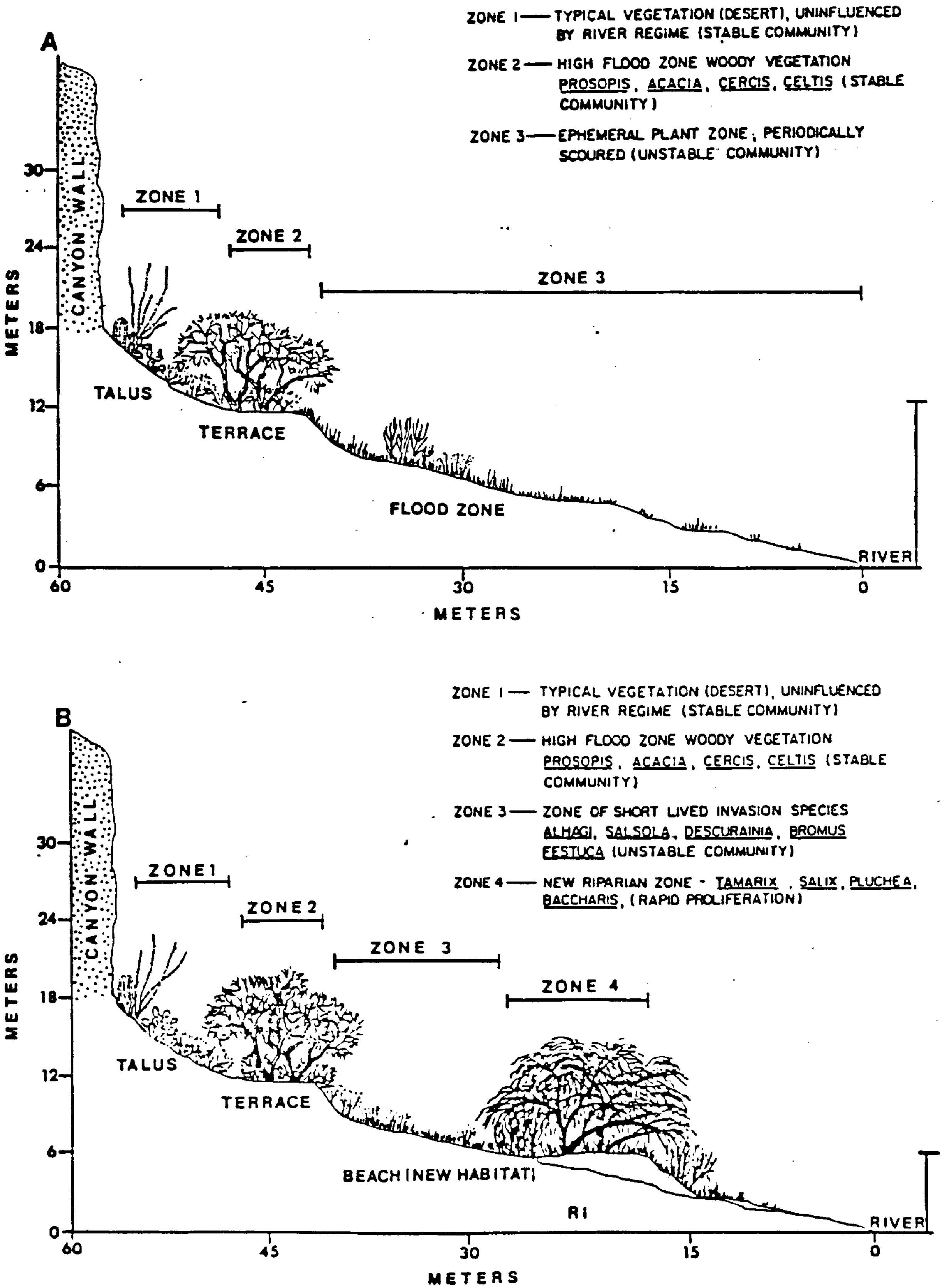

Figure 1. Vegetation zones along the Colorado River before and after construction of Glen Canyon Dam.

Western honey mesquite (Prosopis glandulosa var. torreyana Torr.) is widely distributed throughout southern California, Arizona, and New Mexico. Its northward distribution is limited by freezing temperatures (Meyer et al. 1973, Mooney et al. 1977) and it is generally not found above the Mogollon Rim. Its only occurrence north of the Mogollon Rim is the isolated population in the Grand Canyon. Though it is not restricted to riparian habitats throughout the Southwest (Campbell and Green 1968), mesquite is an obligate riparian species in the Grand Canyon. It is restricted mainly to alluvial terraces, and talus slopes along the river or a short distance up the tributaries. It is absent from adjacent non-riparian habitats (Warren et al. 1982). Mesquite has two disjunct areas of distribution in the Grand Canyon. It first appears below Glen Canyon Dam at RM 40 and extends to RM 77. It is rare in the inner gorge of the Grand Canyon from RM 77 to 165 where there are few alluvial terraces. Mesquite reappears again in large numbers at RM 165 and extends to Lake Mead.

Mesquite is a long-lived phreatophyte with large below ground biomass and long tap roots, often reaching considerable depths to the water table (Meyer et al. 1971, Mooney et al. 1977). The long lifespan of mesquite, often greater than 100 years, means that many of the adult individuals in Grand Canyon were present long before the dam was built over 20 years ago.

Mesquite studied in California and southern Arizona has two periods of leaf production and shoot elongation, in March/April, after the winter rains and again in July/August after the summer rains. Mesquite produces flowers after the leaves mature, with a large peak in May and a much smaller, often unpredictable effort in July. The fruits mature in July/August and the seeds germinate mainly in August/September after the summer rains (Sharifi et al. 1983, Solbrig and Cantino 1975) though some seeds may overwinter and germinate in April after winter rains and warming soil temperatures (Haas et al. 1983).

Catclaw acacia (Acacia greggi Gray) is a more drought tolerant species than mesquite and is not restricted to the riparian portions of the Grand Canyon (Warren et al. 1982); however, it reaches its greatest size and density in riparian situations along tributaries or within influence of the river. It is found on most substrates in the canyon including crevices in steep bedrock outcrops. Acacia has a continuous distribution from RM 40 to Lake Mead, but it often occurs in lower densities than mesquite.

Catclaw acacia is also a long-lived phreatophyte (Nilsen et al. 1984) and like mesquite spans both pre- and post-dam periods. However, acacia probably does not have as great a below ground biomass as mesquite. Like mesquite, acacia is leafless during the winter. Acacia flowers in early spring and produces leaves in mid spring (Nilsen et al. 1984).

The OHWL riparian zone is an extremely important component of the Grand Canyon ecosystem. It provides nesting sites and foraging substrate for birds (Brown and Johnson 1986), cover for reptiles and amphibians (Warren and Schwalbe 1985), and breeding sites and food sources for insects (Stevens and Waring 1986). In addition, mesquite and acacia pods provide an abundant food source rich in carbohydrates and protein that is an important item in the diet of many insects and mammals. For these reasons, any reduction in the extent or vigor of OHWL vegetation will have impacts on many other components of the Grand Canyon ecosystem.

Formation and dynamics of the OHWL riparian zone appear to be related to water availability and flood frequency. Historically, the lower boundary of perennial vegetation was determined by the scouring line of floods, below which establishment could not occur (Carothers et al. 1979, Turner and Karpiscak 1980). The upper boundary appears to be determined by two major factors. Most important is the level of soil saturation by annual floods which provided moisture for a sufficient duration to allow successful germination and establishment of seedlings. A second factor is the availability of suitable soil to support stands of perennial riparian plants.

Turner and Karpiscak (1980) have described many of the changes in Colorado River riparian vegetation since the closure of Glen Canyon Dam. Pre-dam flow levels changed with the seasons, varying from low water in the winter to very high water in the late spring/early summer due to snowmelt, and a second, smaller peak in July/August due to summer rains. Annual flow varied greatly depending upon patterns and amount of precipitation in the previous winter. Post-dam annual flows are much less variable from year to year and between seasons. However, daily flows are much more variable since dam completion due to fluctuation of water releases from Glen Canyon Dam in response to electrical generation demands.

Post-dam water temperature is more consistent and much colder than pre-dam flows. In addition, the post-dam sediment load of the river water is much less than pre-dam loads. This affects the extent and formation of beach areas suitable for plant colonization (Schmidt 1986) and possibly the nutrient levels in alluvial soils (Stevens and Waring 1986).

There are several potential impacts of post-dam flow release patterns on the OHWL riparian zone. Possibly the most important change is reduced available soil moisture in the late spring and summer which was provided by pre-dam seasonal floods. High late-spring floods from snowmelt had several important effects. They provided moisture to mesquite and catclaw located high on the shore above normal river levels during the flowering and fruiting season. High water also moistened the soil prior to seed germination in midsummer, leading to increased germination success. These early summer floods were extremely important because they occurred during the dry season when moisture was not available from precipitation.

Late summer floods from summer rains are much smaller under the influence of Glen Canyon Dam and consist of muddy flows from the tributaries below the dam. Summer floods carried high sediment loads that were possibly important in replenishing nutrient levels of shoreline soils. The low sediment load of post-dam flows could lead to a decrease in soil nutrient levels which would effect vigor of both adult and seedling trees. If post-dam flows result in erosion of beach and terrace areas in the NHWL due to increased sediment carrying capacity, this could reduce the area available for colonization by seedling mesquite and acacia.

This pattern of post-dam flows was drastically altered in 1983 with the filling of Lake Powell and the exceptionally high releases required to prevent overflow of the dam. For the first time since the completion of Glen Canyon Dam the Colorado River reached previous pre-dam flood stages in excess of 90,000 cubic feet/second (cfs). This was also the first time in 20 years that the OHWL riparian zone received overbank flows similar to pre-dam watering patterns. With the filling of Lake Powell, future periodic high releases of water similar to pre-dam levels are much more likely following winters with heavy snowfall.

Objectives

The overall objective of this study was to determine the effects of dam-controlled river flows in the Colorado River on the health of OHWL riparian vegetation in the Grand Canyon. This research was prompted by one major question: Are mesquite and acacia in the Old High Water Line community dying out? The extremely high flows in 1983 watered much of the perched OHWL community for the first time in over 20 years, therefore, one aspect of this study was designed to compare growth in 1983 with that in subsequent years. However, to determine whether or not a community is senescent all aspects of the life history of the dominant species should be examined. Therefore, this study was divided into 4 major parts:

1) Adult growth was measured to determine the general vigor of adults. Comparisons between river and adjacent tributary sites were made to distinguish between the effects of river flow regimes and local climatic effects such as precipitation and temperature. In particular, we wanted to know if adult growth varied between years with different flow regimes, especially under very high flows similar to pre-dam levels, and lower post-dam steady and fluctuating flows.

2) Age class distribution was censused to determine the age class structure of mesquite and acacia and to determine whether there were differences in the distribution of age classes across habitats and soil substrates. In particular, we want to determine where reproduction was successful and whether mesquite and acacia are replacing themselves in the OHWL community and/or moving into the NHWL zone.

3) Adult reproductive effort and success were measured in several ways. At the population level the proportion of trees flowering at each site and the phenology of flowering were surveyed to determine whether the number of trees flowering and successfully fruiting varied along the river corridor. At the individual level, the number of flowers, fruits and seeds produced were measured to determine the effort expended at each stage of flowering and how fruit production in Grand Canyon compares to that at other locations documented in the literature. In addition, seed predation, abortion, and viability were compared at different sites along the river corridor to assess fruiting success.

4) Tagged seedlings and saplings were followed to determine the effects of flooding, fluctuating flows and steady flows on survivorship of different age classes. Germination success in experimental plots at different distances from the river was measured to determine the effect of river flows on seedling germination and establishment and to establish populations for long-term monitoring as flows change.

Mesquite and acacia are long-lived trees and the effects of the post-Glen Canyon Dam flow regime may take a long time to be manifested. Therefore, the studies initiated as part of this project have been designed for long term monitoring as well as the short-term results presented here. In general, adults are likely to be affected by large or long-term changes in river flows but will probably not be affected by daily fluctuations in flows. Seedlings and saplings are likely to be affected by short-term changes in river flows such as daily fluctuations and flooding.

Methods

Each of the four major components of the study were replicated at a series of locations along the river corridor in Grand Canyon. This was done because it was thought that variation in geologic substrate, landform, and local climate in different river reaches might have significant effects on riparian tree growth and reproduction. This study was begun in June, 1984 and continued through September, 1986.

Study Areas: The Glen Canyon Environmental Studies team has divided the Colorado River into 5 reaches in the Grand Canyon that correspond to the location of USGS gaging stations:

1. Glen Canyon Dam to Lees Ferry (RM -15 - 0)
2. Lees Ferry to the Little Colorado River (RM 0 - 62)
3. Little Colorado River to Phantom Ranch (RM 62 - 88)
4. Phantom Ranch to National Canyon (RM 88 - 166)
5. National Canyon to Diamond Creek (RM 166 - 225)

One primary study site in each reach (except for Reach 1 which has no mesquite or acacia) was chosen at the beginning of the study to measure growth in adults and demography. Additional sites were sampled in each reach to increase the sample size for demography and reproductive studies in the OHWL and NHWL (Table 1).

Adult Growth: One site in each reach was chosen for monitoring adult growth. These sites were chosen on the basis of two criteria: 1) Presence of large, dense stands of mesquite and catclaw acacia in the OHWL riparian zone, and 2) Presence of stands of mesquite or acacia in tributaries adjacent to OHWL study sites. Tributary sites served as controls to compare growth of mesquite and acacia under the influence of ambient precipitation with OHWL trees under the influence of river flows. Three of the tributary sites, Unkar, National and Granite Park, had intermittent surface flow and one site, Nankoweap, had permanent water flowing.

Mesquite adults were selected for growth studies at all sites except in Reach 4 where mesquite is not present. We emphasized mesquite over catclaw acacia because, unlike acacia, it is restricted to riparian areas and therefore was expected to show a greater dependence on river flows.

Forty trees were selected for growth measurements at each site, 20 in the OHWL and 20 in the adjacent tributary. Tributary trees were measured to compare growth in trees under the same local precipitation and temperature regimes as OHWL trees but away from the influence of river flows.

Table 1. Summary of study sites and sampling activities at each site.

Study Site	RM*	Age Class Survey NHWL	OHWL	Tagged Plants	Flower Phenology	Inflores. Density	Seed Viability
Buckfarm	41 R	X	X		X	X	
Eminence	43 L	X	X	X			
Saddle	47 R	X	X	X	X	X	X
Little Nanko	52 R	X	X	X			
Nankoweap !	53 R	X	X	X	X	X	X
Awatubi	56 R	X	X	X			
Kwagunt	58 R	X	X	X			
Palisades	65 L	X	X	X			
Espejo	66 L	X	X	X	X		X
Tanner	68 L	X	X				
Cardenas	70 L	X	X	X	X	X	X
Unkar !	72 R	X	X	X	X	X	X
Fossil	125 L	X	X				
Fishtail	139 R	X	X				
National !	166 L	X	X	X			
Fern Glen	168 R	X	X	X	X	X	
Stairway	171 R	X	X	X	X		
Mowhawk	171 L	X	X	X	X		
Cove	174 R	X	X	X	X		
	176 R	X	X	X	X	X	
Lower Lava	179 R	X	X		X		
	183 L	X	X	X	X	X	
Whitmore	187 R	X	X	X	X		
	191 R	X			X	X	
	194 L	X		X	X	X	
Parashant	198 R	X	X	X	X	X	
Spring	204 R	X	X	X	X	X	
Granite Pk !	209 L	X	X	X	X	X	X
	214 R	X			X		
	217 L	X			X		
	220 R	X			X		

* River miles downstream from Lees Ferry, from Stevens 1984.

! These are the 4 primary study sites. In addition, to the sampling activities listed they are the sites for shoot growth measurements radial growth measurements and age class surveys in tributaries.

Individual trees were chosen on the basis of current year's shoot growth in 1984 and their position in the OHWL. Similar numbers of trees were selected in the lower and upper portions of the OHWL zone.

Trees were marked with a numbered aluminum band around the trunk. Where low level aerial photographs were available, each individual tree was marked on the photo for future relocation. Total height, maximum and minimum canopy diameter, and distance from the river were measured for each individual.

Mesquite shoot growth has been shown to be highly correlated with overall tree vigor and soil moisture conditions (Sharifi et al. 1983). Shoot growth was therefore chosen as the primary variable measured. Both current year's and previous year's shoots can be identified by leaf and bark characteristics on mesquite and catclaw. This allowed us to measure the effects of the 1983 flood on shoot growth, although our study began in 1984.

Mesquite produces two kinds of new growth each year, short shoots and long shoots (Burkhart 1976). Current year growth is recognized by a single bipinnate leaf per leaf node. In short shoots the leaf internodes are extremely small and difficult to measure. In addition short shoots show little variation in length between years. For these reasons long shoots were measured to compare growth. The first-year long shoot has smooth bark that is green or reddish in color and has leaf nodes that show little of the bud-scar buildup that results from succeeding seasons of leaf growth and dehiscence. Second year growth is similar to current year's growth but has more than one leaf per node. Again, the stem is generally smooth and green or reddish in color and the leaf nodes are not enlarged. Stems older than two years are usually dark gray or brown with roughened bark and have enlarged leaf nodes (Meyer et al. 1971).

One of the possible biases in estimating first-year growth from one year old shoots is that the shoot tip may die back a short distance during the winter. This bias was corrected by re-measuring 1984 shoot growth in 1985 to estimate die-back in the first year following growth.

Twenty current year's shoots and twenty previous year's shoots were measured per tree. Shoots were selected for measurement from all sides of each tree, with 5 shoots sampled on sides facing each of the 4 compass directions. Shoots were measured to the nearest cm and it was noted whether the shoot was still growing or whether growth for the season had ceased by examining the tip of the stem for leaf buds.

Radial stem growth was measured as a second index of overall tree vigor. Diameter of the root crown was measured for each individual selected for shoot measurements. A dendrometer similar to that described by Liming (1957) was placed on each individual to measure long term changes in radial growth. In cases where trees had multiple trunks, the largest healthy trunk was selected. The dendrometers were constructed of 2-inch wide strips of light weight aluminum wrapped around the trunk with a 2-inch overlap at the ends and held together with a light spring (#C-25, Century Spring Co., Los Angeles, CA). As radial growth increases, the spring stretches and the overlapping aluminum strip expands away from a point marked at the initial end position. Radial growth is calculated by measuring circumference changes indicated by the expansion of the strip end away from the initial point. Each time radial growth is measured, a line is scribed and dated at that point. The dendrometer does not interfere with growth and since it remains on the tree radial growth can be measured over long time periods.

Patterns of radial growth over longer periods of time were determined by measuring the width of annual growth rings on selected individuals. Narrow wedges were cut from healthy trunks of seven acacia and five mesquite without killing trees. Mesquite did not show identifiable growth rings and could not be dated or measured. However, catclaw did show recognisable annual growth rings. Trunk sections were dated by the late Dr. C. W. Ferguson, Tree Ring Laboratory, University of Arizona and annual growth increments measured by Dr. B. Kincaid, Department of Botany/Microbiology, Arizona State University.

Standard dendrochronological procedures to correct for aging (Fritts 1976) were not suitable as none discriminate between decrease in growth due to age and decrease due to long term environmental changes such as altered river hydrology. An alternate method to correct for the normal slowing in growth as trees age was proposed by Reily and Johnson (1982). This involves adjusting (increasing) postdam growth by multiplying it by the proportional change in growth that occurred during two equal pre-dam periods. The multiplier is calculated by dividing total growth for the first period by total growth in the later period. However, this method was suitable for only one of the trees measured in this study since most of the trees did not show a consistent slowdown in growth or were not old enough to give two equal 20 year periods of predam growth.

Variation in mean shoot growth between habitats (river and tributary) and years (1983, 1984, 1985, and 1986) was compared with two-way ANOVA and Tukey's aposteriori test of means (Sokal and Rohlf 1981). The effects of river flow levels on mean shoot growth were determined by regression analysis (Sokal and Rohlf 1981). Mean annual tree ring growth from before and after the closure of Glen Canyon Dam was compared using ANOVA and Tukey's test of means.

Age Class Distribution: Mesquite and acacia were divided into 4 age classes, seedlings, saplings < 5 years, saplings > 5 years, and adults. Adults were determined by the size at which trees began to flower. Seedlings less than one year old were recognized by having a single leaf per leaf node and no circular bud scars indicating new shoot initiation. Saplings < 5 years were determined by counting the circular bud scars from each years shoot growth. Saplings > 5 years were also identified by counting bud scars for more tnat 5 years, but they were not yet reproductive size.

Age class surveys were conducted by censusing belt transects that were oriented parallel to the shore line. The width of the transects varied from 10 to 30 meters depending upon the number of people walking the transect. Each person covered a width of approximately 3m. The length and width of the transects also varied with the size of the habitat patch to be sampled, with transect length ranging from 50 to 100 meters. Soil substrate, riparian zone (NHWL, OHWL, or tributary), river mile, reach and transect dimensions were recorded at each transect site. The NHWL was further subdivided into two zones, one below the 50,000 cfs line and one above the line, and age class surveys were done in each of the two subdivisions. All seedlings and some saplings were tagged to monitor survivorship. The density of each age class is expressed as individuals/1000m^2. Age classes of each species were summarized and compared across reach, zone, and soil substrate using Pearson's chi square test (Snedecor and Cochran 1967). 215 age class survey transects were censused in the NHWL and OHWL at 73 sites over the course of the study.

Seedling and Sapling Survivorship: Seedlings and saplings were tagged with aluminum tags during age class surveys. 424 mesquite and 317 acacia seedling and saplings were tagged. Location, river zone (NHWL, OHWL, and TRIB), soil substrate, age, and height were recorded for each individual. In 1986 river flows were steady at 50,000 cfs for one month leaving a silt line that allowed us to divide the NHWL into 2 zones, above and below the 50,000 cfs line. An attempt was made to relocate tagged individuals at least once each year, however approximately half the tagged individuals were not found again.

Adult Reproductive Effort and Success: Studies of reproductive effort concentrated on mesquite for two reasons. 1) Mesquite are obligate riparian trees and should be most sensitive to post-dam flow regimes. 2) Since many fewer mesquite seedlings were found than acacia seedlings and we were particularly interested in determining at what stage (flowering, fruiting, seed production, seed viability, or germination) the breakdown in mesquite reproductive success occurred. If these studies continue we hope to gather comparative data for acacia.

Flower phenology of mesquite populations was surveyed along belt transects similar to those described for age class distribution. All trees on the transects were recorded as being in bud, full bloom, past bloom (flowers had dried up or fallen from the rachis without producing fruit), fruit, or not flowering. Several sites had trees that went through a second flowering cycle later in the summer. These second flowering periods were recorded separately. The proportion of trees in each category was summarized and compared by reach and river mile using Pearson's chi square test. Thirty-six phenology surveys at 24 sites were done in the OHWL from May to August 1986 (Table 1).

The density of inflorescences in different flowering stages was measured for 135 trees at 13 sites. Inflorescences were counted and recorded as buds, full blooms, past blooms (flowers had dried up or fallen off the rachis) and fruits on eight branches per tree, all of which were marked with aluminum tags. In addition, the number of fruits/inflorescence and seeds/fruits were counted. The numbers and stages of inflorescences on marked trees were resampled several times throughout the blooming season from May to August, 1986. Trees were selected only if they were in bloom during the first sampling period in May or June. Since the purpose of the study was to determine the proportion of flowers that result in fruit and viable seed, the branches with the largest numbers of inflorescences were selected. Each branch was tagged at 1 cm diameter and its cumulative length was measured out to the tips of all forks of the branch. Inflorescence counts were standardized by branch length and are expressed as the number/meter of branch length. Inflorescence counts and the proportion of inflorescences resulting in fruit were summarized by site and reach and compared with ANOVA and Tukey's test of means.

Rates of seed predation and abortion were measured for 288 fruits from 29 trees at 7 sites. Seeds were removed from the pod and the number of predated, aborted and good seeds counted. The major seed predator was a bruchid beetle *Algarobius prosopis* (Le Conte) (Stevens pers. comm). Predated seeds were recognized by a hole bored in the seed coat and in several cases the presence of the larvae.

Aborted seeds were much smaller and darker than normal seeds and were either flattened or shriveled. The proportion of predated and aborted seeds was summarized by tree and site and compared with ANOVA and Tukey's test of means.

Fifty to 100 good seeds were tested from each tree to determine viability. Seeds were scarified by nicking the seed coat opposite the micropyle end. Mechanical scarification such as this has been shown to result in the highest germination rates (Khan et al. 1984). Seeds were soaked for 1 hour then placed in petri dishes on wet filter paper. Seeds were recorded as germinated once the root had broken through the micropyle end. 98% of the seeds which germinated did so in the first 24 hours, though seeds were followed for 48 hours.

Two experimental plots were established in 1986, one at Nankoweap (mile 53) in August, and one at Granite Park (mile 209) in July, to test germination and survivorship success of scarified seeds. At each site 3 parallel 100m seed transects were established; two in the NHWL at the flow line for 30,000 cfs and at the flow line for 50,000 cfs, and the third in the transition between the NHWL and OHWL at the flow line for 90,000 cfs. Seeds were soaked overnight, then planted in groups of three at one meter intervals along the transect for a total of 300 seeds/transect and 900 seeds/plot. The three seeds in each group were placed approximately 2 cm apart and planted at a depth of 1-2 cm, which corresponds to the most sucessful planting depth recorded by Glendening and Paulsen, 1955. Seeds were watered with one cup of river water at the time of planting. Germination success was determined by observing a subset of seeds that were germinated in petri dishes in the manner described above. The plots were resampled one month after planting to determine establishment.

Results

Shoot Growth: During the four years of the study river flow levels were higher and more stable than for most of the preceding 20 years since dam construction. Means calculated for the highest daily flows during the four growing seasons were not significantly different throughout the study, with the exception of 1983 which was extraordinarily high (Table 2). Following unusually high snowfall in the winter of 1982-83, Lake Powell filled and Glen Canyon Dam was forced to release daily flows of up to 93,000 cfs. Although flow levels of this extreme magnitude did not occur during subsequent years, the high level of the lake resulted in spring floods (defined by the Bureau of Reclamation as river flows in excess of 31,000 cfs) in each year of the study (Table 2).

Table 2. Highest river flow levels (in cfs): for the year, averaged over the month of highest flows, and averaged over the growing season (March-October).

Year	Highest Flow of the Year	Mean Highest Daily Flow/Month of Highest Flows	Mean Highest Daily Flow/ Growing Season
1983	93,200	60,006 (June)	39,006
1984	44,069	41,662 (June)	35,920
1985	55,195	40,418 (June)	29,791
1986	48,034	42,553 (May)	30,570

Mesquite shoot growth did not show a strong consistent relationship to river flow levels. The expected result, if high flows do benefit the vigor of the OHWL mesquite, was that growth during the 1983 season of high flows would be significantly greater than growth during the other 3 years. Mean shoot growth was regressed against three different river flow variables; the highest flow reached in each year, mean maximum daily high for the month of highest flows, and mean maximum daily high for the growing season from March to October (Table 2). Daily maximum flows were chosen rather than average daily flows for this analysis because it was expected that maximum flow levels would have the greatest effect on soil moisture in the OHWL zone. The regression analysis did not show any positive correlation (r) between shoot growth of riparian trees and maximum river flow levels. Although none of the regressions were significant, mesquite growth in river trees for all reaches did show a weak trend toward a general decline in growth from a high in 1983 to a low in 1986 (Table 3). The fact that no such consistent trend was observed in tributary trees serves to emphasize the declining trend in growth of river trees.

In general, there were no significant differences in summed mesquite shoot growth between river and adjacent tributary control sites (Table 3). At Nankoweap, there was no difference in shoot growth between years or between river and tributary sites, except for 1986 during which we observed low growth in both the river and tributary trees. There was no significant difference in growth between sites in any years at Unkar. River trees at Granite Park showed lower shoot growth than tributary trees except in 1983 when flows were at their highest.

Table 3. Mean total shoot growth/tree (cm) for all mesquites at each site compared across habitats (river vs. tributary sites). Means with the same subscript are not significantly different by one-way ANOVA and Tukey's test of means at p<.05.

Site	River				Tributary				F	P
	1983	1984	1985	1986	1983	1984	1985	1986	Value	
Nankoweap	442 *	472 *	476 *	283 !$	464 *	493 *	346 *!	160 $	11.1	<.001
Unkar	517	513	383	395	484	550	554	376	2.0	NS
Granite Park	504 *	363 !	386 !*	281 !	379 !*	450 *	500 *	410 *	6.0	<.001

National Canyon was the only major study site at which acacia was the dominant old zone tree and mesquite was absent. There was no significant difference in shoot growth of acacia at National Canyon between years or sites (Table 4). Individual trees showed significant variation in mean shoot growth over the four years sampled, however the variation showed no consistent pattern across years (Appendix A).

Table 4. Mean total shoot growth/tree (cm) for all acacia at the National Canyon site compared across habitats (river vs. tributary sites). Means are not significantly different by one-way ANOVA and Tukey's test of means at p<.05.

Site	River				Tributary				F	P
	1983	1984	1985	1986	1983	1984	1985	1986	Value	
National Canyon	363	267	256	325	344	278	351	295	1.8	NS

One possible source of bias in the shoot growth analysis was comparison of growth measurements which were made during the same season in which growth occurred, with measurements of 1983 growth which were made retrospectively in 1984. The potential biases introduced by this approach are underestimating the length of previous year's shoots because the tips died back, or underestimating the length of current year's shoot because they have not stopped growing. The accuracy of retrospective shoot growth measurements was evaluated by following individually marked shoots on six trees at Granite Park (Table 5). There was no significant difference observed in mean 1984 shoot growth measured in both 1984 and retrospectively in 1985, indicating that the retrospective measurements are suitable for comparison with current season measurements in this study.

Table 5. Growth (cm) of individually marked mesquite shoots (20/tree) at Granite Park measured in 1984 as current year's growth and measured again in 1985 as previous year's growth. There is no significant difference between means by one-way ANOVA and Tukey's HSD test of means.

Dendrometer Number	Mean 1984 Shoot Growth (cm) Measured in 1984	Measured in 1985
River		
33085-11	15.15	15.20
33085-12	17.85	18.50
33085-13	17.05	16.75
33085-14	23.90	32.50
Tributary		
33085-15	18.65	19.15
33085-26	17.40	17.80

Radial Stem Growth: Radial stem growth is a good measure of overall tree vigor, but it was not found to vary as much on a short-term basis as did shoot growth. The dendrometers placed on trees in 1983 were resampled in subsequent years. Few dendrometers showed any movement except those on a few trees located near a seep in the Unkar tributary. Dendrometer measurements will be important in long-term monitoring of study trees, but were not sensitive to variation in single-season growth rates.

An attempt was made to evaluate long-term growth patterns by measuring annual growth rings on narrow wedges from mesquite trunks. However, the Grand Canyon mesquite sections showed diffuse growth in which annual growth rings were not visible. Mesquite often fails to form recognizable annual rings, especially if the trees are under stress (C. Ferguson, per. comm.), therefore this effort was unsuccessful, though mesquite from other areas have been successfully aged.

Acacia do exibit well defined annual growth rings, making it possible to age trees and measure growth increments over specific periods. Analysis of acacia growth rings was used to determine the effect of post-dam flows over the long term. In a general sense the results from tree ring analysis of acacia sections should be applicable to mesquite.

Annual growth rings were counted for 5 acacia individuals, 4 along the river and 1 in a tributary site. Twenty years of post-dam growth (1964-1983) was compared with two equal periods of pre-dam growth (1923-1943 and 1944-1964) (Table 6). Post-dam growth was not adjusted for a normal decline in growth because most trees did not show a consistent decline in growth over the two pre-dam periods. In all the river trees post-dam growth was smaller than both of the twenty year pre-dam growth increments. Mean growth for these periods was significantly different in 2 of the 4 trees. The tributary tree, the oldest of all trees sampled, had greater growth after the dam than during either pre-dam period. This observation was surprising, since older trees usually grow more slowly than young trees, and serves to emphasize the significance of the reduction in post-dam growth of river trees sampled.

Table 6. Sixty years growth of 5 catclaw acacia along the Colorado River in the Grand Canyon determined by tree ring analysis. Growth increments are in mm. Means with the same symbol beside them are not significantly different by one-way ANOVA and Tukey's HSD Test at $p<.05$.

	Tree Location				
	Nankoweap Top OHWL	Nankoweap Lower OHWL	Unkar Lower OHWL	National Lower OHWL	National Tributary
1924-1943					
Total	-	12.01	19.48	23.08	8.00
Mean	-	0.60*	0.97*	1.15*	0.40*
1944-1963					
Total	18.24	12.38	21.61	15.43	7.91
Mean	0.91*	0.70*	1.08*	0.77*!	0.40*
1964-1983					
Total	16.86	10.95	8.33	14.98	9.24
Mean	0.80*	0.52*	0.40!	0.71!	0.44*
Age (yrs.)	45	65	65	81	100
F Value	6.16	NS	22.41	3.92	NS

Interpretation of patterns of acacia growth rings is less certain than for commercial tree species since very few tree ring laboratories have analyzed growth curves of acacia. One potential problem is that acacia may put on more than one growth ring per year. This is unlikely in the Grand Canyon since acacia tends to go dormant over the winter and maintains photosynthesis throughout the summer (Szarek and Woodhouse, 1978). This problem could be eliminated if enough samples were collected to cross date the acacia trunk sections.

Age Class Distribution: The density of acacia and mesquite, expressed as individuals/1000m^2, was found to vary significantly between different reaches of the river (Table 7). Adult mesquite were more common than adult acacia in all reaches except for reach 4 where mesquite were not present. However, younger age classes of acacia occurred in significantly higher densities than younger age classes of mesquite throughout the river corridor.

Table 7. Age class distribution of mesquite and acacia across river reach. Density is expressed as individuals-/1000m^2. Percentages in parentheses are summed across reaches and indicate how each individual age class is distributed among reaches. (X^2=272.2, DF=21, p<.001).

Age Class	Reach 2	Reach 3	Reach 4	Reach 5
No. Sites Surveyed	17	15	5	36
Acacia				
Seedling	0 (0)	6 (11)	3 (5)	47 (84)
Sapling <5	11 (3)	64 (18)	74 (20)	215 (59)
Sapling >5	11 (9)	9 (8)	27 (23)	70 (60)
Adult	12 (8)	5 (3)	79 (50)	61 (39)
Total Acacia	34 (5)	84 (12)	183 (26)	393 (57)
Mesquite				
Seedling	0 (0)	10 (83)	0 (0)	2 (17)
Sapling <5	2 (13)	8 (53)	0 (0)	5 (33)
Sapling >5	2 (50)	1 (25)	0 (0)	1 (25)
Adult	28 (27)	28 (27)	0 (0)	46 (45)
Total Mesquite	32 (24)	47 (35)	0 (0)	54 (41)
Total Density	66 (8)	131 (16)	183 (22)	447 (54)

The density of different age classes of both mesquite and acacia also varied significantly between the three major riparian habitats (Figure 2). Most of the adult mesquite and acacia are found in the OHWL while most of the younger age classes are found in the NHWL or tributaries (Table 8). Acacia accounted for the vast majority of all seedlings and saplings regardless of habitat, outnumbering mesquite seedlings and saplings by 17:1.

Table 8. Age class distribution of mesquite and acacia in three riparian habitats, New High Water Line (NHWL), Old High Water Line (OHWL) and tributary (TRIB). Density is expressed as individuals/1000m^2; percentages are in parentheses and indicate how each age class is distributed across the 3 habitats. (X^2=360.8, DF=14, p<.001)

	Habitat		
Age Class	NHWL	OHWL	TRIB
No. Sites Surveyed	39	27	7
Acacia			
Seedling	18 (32)	2 (4)	36 (64)
Sapling <5	235 (65)	44 (12)	85 (23)
Sapling >5	59 (50)	39 (33)	19 (16)
Adult	23 (15)	88 (56)	46 (29)
Total Acacia	335 (48)	173 (25)	186 (27)
Mesquite			
Seedling	4 (33)	2 (17)	6 (50)
Sapling <5	13 (87)	0 (0)	2 (13)
Sapling >5	4 (100)	0 (0)	0 (0)
Adult	4 (4)	88 (86)	10 (10)
Total Mesquite	25 (19)	90 (68)	18 (14)
Total Density	360 (44)	263 (32)	204 (25)

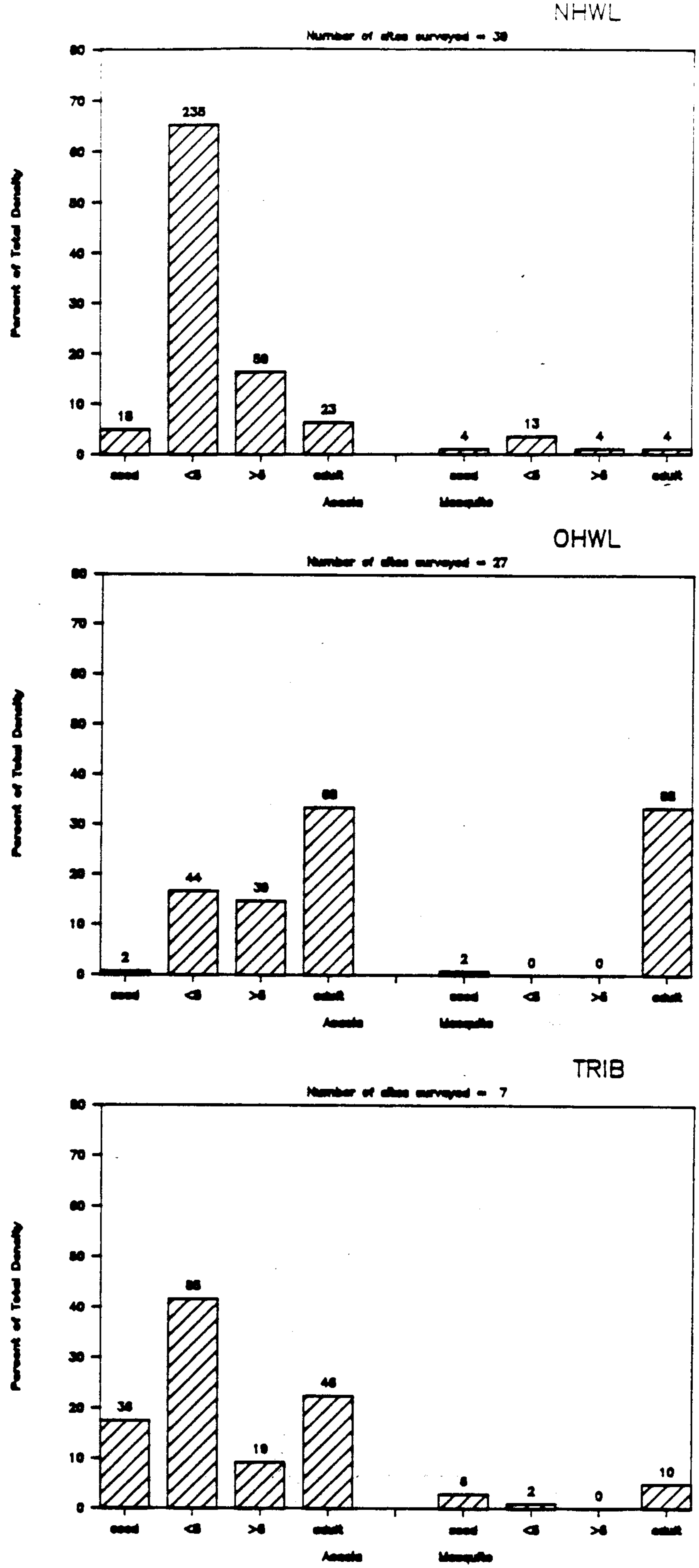

Figure 2. Age Class distribution of mesquite and acacia in three riparian habitats.

Species distribution and age classes also varied over soil substrate types (Figure 3). Adult mesquite were most abundant on deep fine grained substrates such as sand and silty alluvium (Table 9). Adult acacia, in contrast, were most abundant on talus but also were found on sand and silty alluvial terraces with mesquite. Younger age classes of both mesquite and acacia were most commonly found in rocky soils on talus and on cobble bars and alluvial tributary deltas characterized by sand/cobbles and streambed cobbles.

Table 9. Age class distribution of mesquite and acacia across soil substrates. Density is expressed as individuals/1000m^2; percentages are in parentheses and represent how each individual age class is distributed across substrates. (X^2=356.5 F=28, p<.001).

Age Class	Sand	Soil Substrate Sand/ Cobbles	Streambed Cobbles	Talus	Silty Alluvium
No. Sites Surveyed	14	27	4	10	18
Acacia					
Seedling	0 (0)	1 (2)	34 (61)	3 (5)	18 (32)
Sapling <5	17 (5)	30 (8)	84 (23)	75 (21)	158 (43)
Sapling >5	15 (13)	18 (15)	16 (14)	29 (25)	39 (33)
Adult	24 (15)	2 (1)	1 (1)	79 (50)	51 (32)
Total Acacia	56 (8)	51 (7)	135 (19)	186 (27)	266 (38)
Mesquite					
Seedling	2 (17)	0 (0)	8 (67)	2 (17)	0 (0)
Sapling <5	1 (7)	4 (27)	6 (40)	2 (13)	2 (13)
Sapling >5	1 (25)	3 (75)	0 (0)	0 (0)	0 (0)
Adult	40 (39)	1 (1)	0 (0)	12 (12)	49 (48)
Total Mesquite	44 (33)	8 (6)	14 (11)	16 (12)	51 (38)
Total	100 (12)	59 (7)	149 (18)	202 (24)	317 (38)

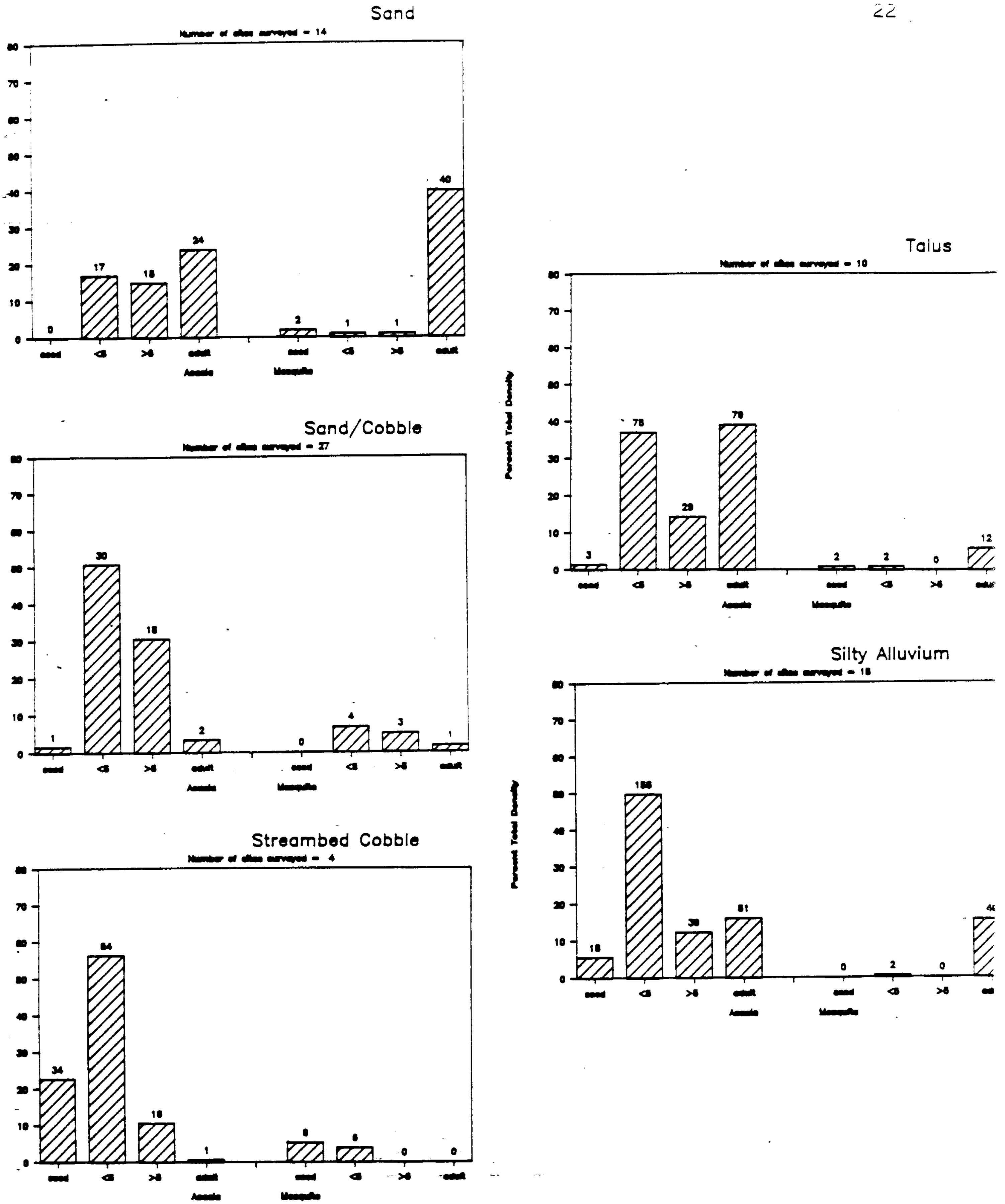

Figure 3. Age class distribution of mesquite and acacia across soil substrates.

Seedling, Sapling and Adult Mortality: Mesquite were found to have significantly higher survivorship than acacia in all age classes except adults. Not surprisingly, mortality was highest in the seedling age class for tagged individuals of both mesquite and acacia (Figure 4). Both species also were similar in lacking any mortality among those individuals in the greater than five year age class.

One unexpected observation was that for both species, 2-3 year old saplings had higher survivorship than 3-5 year-old saplings (Figure 4). We expected to find that mortality would decline steadily in the older age classes. The 3-5 year old age class includes the cohort of 1983 which became established during the high flows of that year. Many of them are now located higher on the shore than normal high flow levels and may be dying due to lack of adequate soil moisture.

Fifty percent of tagged mesquite and sixty-eight percent of tagged acacias were not relocated. There are several possible explanations for this: tags were removed by recreational visitors, tagged individuals were missed in subsequent surveys, especially in tributaries which were surveyed less intensively after the first year of the study, and, most importantly, some individuals died and the tags were buried or washed away. Greater than 60% of unrelocated individuals were seedlings (Table 10) suggesting that many seedlings were not relocated simply because they died. Seedlings of both species dry up within a few days after death, and within a week or two they are often completely unrecognizable. Plants that were not relocated were not included in the mortality analysis, however the high incidence of seedlings in this group indicates that mortality was probably underestimated in seedlings as compared with other age classes.

Table 10. Number and (percent) of different age classes of tagged mesquite and acacia that were not relocated in subsequent surveys.

Age Class	Mesquite	Acacia
Seedling	128 (61)	96 (42)
Sapling < 5	71 (34)	188 (50)
Sapling > 5	6 (3)	0
Total	211	214

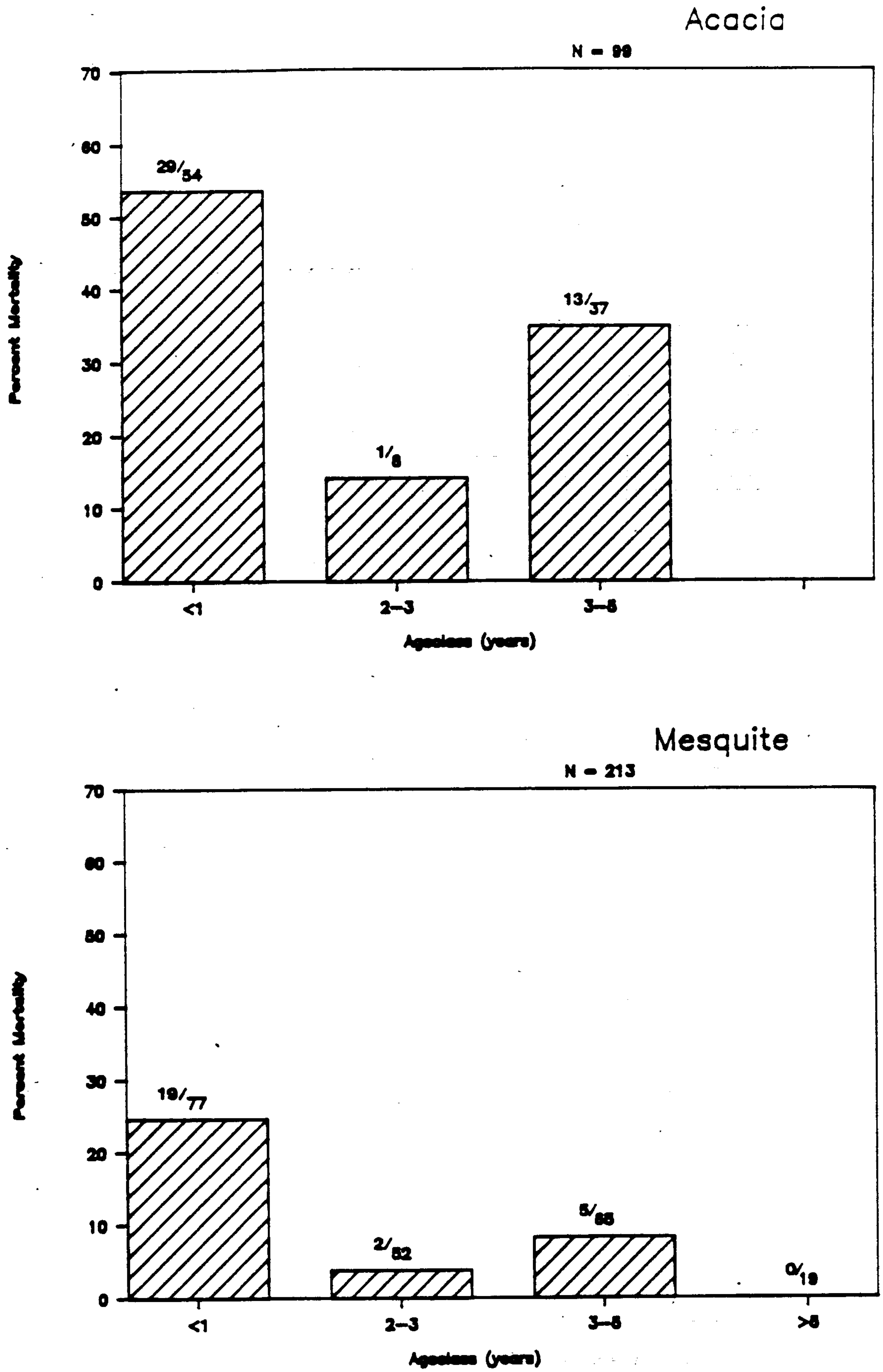

Figure 4. Percent mortality of different age classes of tagged mesquite and acacia.

An examination of subadult mortality patterns in the different riparian zones showed that lowest mortality for both mesquite and acacia was in the NHWL (Figure 5). Mesquite showed much lower mortality than acacia in the new zone, but higher mortality in the old zone.

During age class surveys in the different riparian zones we also censused dead adult trees. In most cases it was clear from the condition of the bark and wood that the trees had been dead for at least two to three years. The proportion of dead adults found during age class surveys was higher for mesquite than acacia (Table 11). Both mesquite and acacia were observed to have similar adult mortality in the OHWL. However, although acacia had similar mortality in both the old and new zones, adult mesquite mortality was observed to be much higher in the new zone, where the percent dead trees was about 29% than in the old, where the percent dead was approximately 7%. Adult mesquite closest to the river below the 50,000 cfs line had 5 times greater mortality than did adults farther from the river above the 50,000 cfs line. Virtually all adult mortality in the NHWL can be attributed to inundation during the flood of 1983.

Table 11. Mortality of adult mesquite and acacia in NHWL and OHWL habitats.

Zone	No. Sites Surveyed	Mesquite # Alive	Mesquite # Dead	Mesquite % Dead	Acacia # Alive	Acacia # Dead	Acacia % Dead
NHWL							
< 50K cfs	8	22	12	35.3	0	0	0
> 50K cfs	8	67	6	8.2	30	1	3.2
NHWL	20	109	45	29.2	67	8	10.7
TOTAL NHWL	37	198	63	24.1	97	9	8.5
OHWL	17	527	38	6.7	449	33	6.8

Mesquite Reproductive Effort and Success: Reproductive success of mesquite was studied to try to evaluate why, after twenty years with dam-controlled river flows, there are so few mesquite of younger age classes in the new riparian zone. A breakdown in the reproductive cycle could occur in several places: trees may fail to bloom, flowers may not be fertilized, fertile fruits may not mature, or germination may be low. Each of these factors was examined.

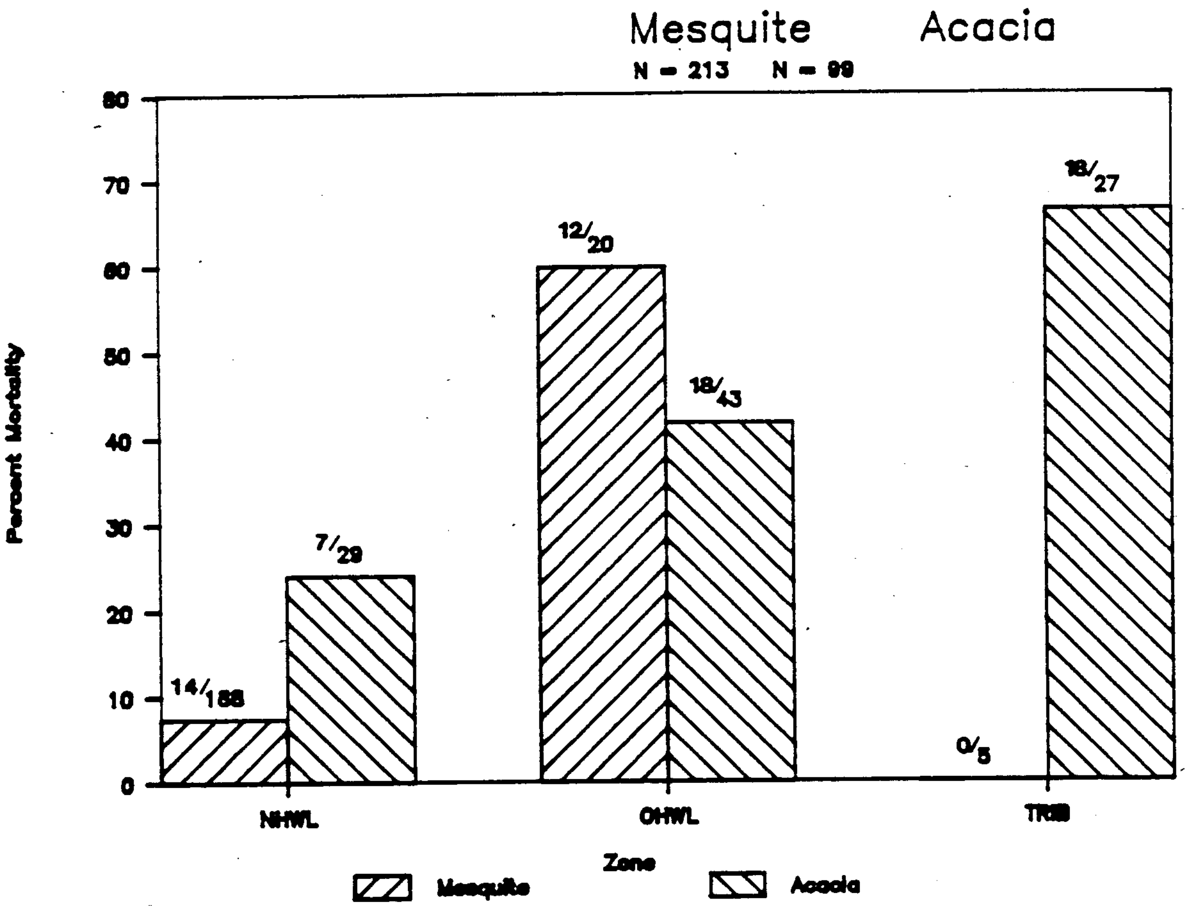

Figure 5. Percent mortality oi tagged seedlings and saplings in the NHWL and OHWL.

The logisitics of performing research on the river require boat trips lasting approximately three weeks plus turn-around time between trips. A minimum time between sampling of at least four weeks prevented adequate sampling throughout the entire flowering cycle. Phenology observations were therefore timed to coincide with fruiting periods to determine fruiting success of trees at the various sites along the river.

Flowering phenology was found to vary substantially between reaches along the river (Table 12). The lowest blooming frequency occured in Reach 5, where almost 3/4 of the population failed to bloom. The highest blooming frequency occurred in Reach 3 where less than a quarter of the population failed to bloom. In addition, the highest percentage of fruiting trees was found in Reach 3.

Table 12. Flowering phenology of mesquite. Percentage of the adult mesquite population by reach in different stages of blooming and fruiting.

Reach	Date	% Not Blooming	% Bud	% Full Bloom	% Past Bloom	% Fruit	% Blooming Twice
2	5/86	36.8	0	10.8	48.4	4.0	0
	8/86	54.4	2.2	23.9	19.6	0	0
3	5/86	23.9	0	2.8	60.6	12.7	0
	8/86	35.7	0.8	4.9	1.6	32.8	24.2
5	5/86	71.0	0.3	1.2	12.3	15.2	0
	8/86	70.2	1.2	5.1	3.2	19.4	0.9

For date X^2=250.6, df=5, p<.001

For Reach X^2=656.7, df=10, p<.001

Several trees experienced a second season of flowering in the late summer; 24% of the trees in reach three went through two cycles of flowering and a few in reach five. By following individual inflorescences we found that the second cycle of flowering produced fewer fruits/flower than the first flowering cycle. Two flowering cycles were also observed by Solbrig and Cantino (1975) and Turner (1963) in mesquite near Tucson, Arizona.

Phenology of individual inflorescences was also followed on marked branches (Table 13). The highest number of fruits/tree, mean fruits/inflorescence, and percent values for total infloresences producing fruit were found in reach five. However, the total number of seeds/tree did not vary significantly with reach. The proportion of flowers producing fruit was calculated from the total number of inflorescences using an estimate of 230 mean flowers/inflorescence counted by Solbrig and Cantino for Tucson trees in 1975. An average of 0.36% of flowers produced fruit in the Grand Canyon trees compared to an average of 0.06% of flowers producing fruit in the Tucson trees (Solbrig and Cantino, 1975).

Table 13. Mean number of mesquite inflorescences (infl) in each flowering stage/ tree across river reach. Inflorescences were counted on 8 branches/tree.

Reach	# Trees	Buds	Full Bloom	Past Bloom	Fruiting Infl.	$\overline{X}$ Fruit/ Infl.	$\overline{X}$ Seeds/ Fruit	% of Infl. Producing Fruit	# Fruits	# Seeds
2	20	70 *	49	61	14	2.0 *!	4.7 *!	29	28 *	154
3	9	16 !	21	76	27	1.9 *	5.4 *	29	46 *!	306
5	25	15 !	10	47	32	3.0 !	2.3 !	43	104 !	231
F values		4.2	2.3	0.6	2.9	3.9	3.5	0.8	6.4	0.7
p		<.05	NS	NS	NS	<.05	<.05	NS	<.01	NS

Rates of seed predation and abortion were determined for 288 fruits from seven sites (Table 14). Predation rates were generally below ten percent except in fruit from RM 53, 72 and 209, where seed predation ranged up to 28 percent. Seed abortion rates generally ranged from ten to twenty percent, but at RM 46 and 53 abortion rates were 33 and 48 percent.

Table 14. Mean number and percent of predated, aborted and good mesquite seeds per fruit. Means with the same symbol are not significantly different by a one-way ANOVA and Tukey's test of means at p<.05. Means are compared down colums.

Site (RM)	# Fruits Sampled	$\overline{X}$ Seeds Predated	$\overline{X}$ Seeds Aborted	$\overline{X}$ Seeds Good	% Seeds Predated	% Seeds Aborted	% Seeds Good
46	78	0.4 *	3.9 !	7.6 *	3.8 *!	32.7 !	63.5 !$
47	1	0.0 *	2.0 *	14.0 !	0 *	12.5 *	87.5 #
53	3	1.3 *	8.3 $	8.0 *	10.3 !	48.1 !	41.5 *
66	33	1.1 *	1.8 *	14.7 !	6.0 *!	10.0 *	84.0 #
70	17	1.0 *	2.8 *	11.2 $	6.9 *!	18.6 *	74.5 $#
72	37	4.2 !	1.8 *	8.8 *$	28.4 $	13.7 *	58.0 !
209	119	1.7 *	1.6 *	10.3 *$	12.7 !	12.5 *	74.7 $#
F Value		12.2	12.8	12.1	12.5	15.9	7.8
P		<.001	<.001	<.001	<.001	<.001	<.001

Seed viability was found to be quite high at all sites (Table 15). A total of 96 percent of all seeds tested germinated successfully. Most seeds that germinated did so within the first 24 to 48 hours. Usually the seeds swelled noticeably during the first twenty-four hours, after which the radical would begin emerging from the micropyle. Those seeds that were used for field survival trials were first placed in petri dishes and scored for germination. They were planted after germination was observed but before the root had extended to a length that would make it susceptible to damage during planting. Viability of the seeds planted at Nankoweap was 88% and viability of seed planted at Granite Park was 99%.

Table 15. Percent germination of scarified mesquite seeds.

RM	# Seeds Tested	# Germinated	% Germinated
46	64	56	87.5
66	398	378	95.0
70	187	185	98.9
72	242	228	94.2
209	378	375	99.2
Total	1269	1222	96.3

After one month, less than 4% of all seeds planted in the field trials survived as seedlings (Table 16). A dramatic decline in survival was observed among seeds planted along the 50,000 and 90,000 cfs lines as compared to those along the 30,000 line. This corresponds with results from studies of Prosopis velutina which showed increasing germination with increasing soil moisture levels up to 13% soil moisture content (Glendening and Paulsen 1955). Among the seeds planted nearest the river eight percent survived to one month as seedlings. However, only 0.3 percent of the seeds on the 50,000 cfs transect survived, and none survived along the 90,000 cfs line. Stems of dead seedlings were not found indicating that planted seedlings never broke the surface.

Table 16. Mesquite seedling survival after one month in experimental plantings at different distances from the river. Seeds were planted at the river flow lines for 30,000 cfs, 50,000 cfs and 90,000 cfs.

Site	Transect Location	# Seeds Planted	# Seedlings Surviving	# Dead Stems
Nankoweap (RM 53)	30,000 cfs	300	17	0
	50,000 cfs	300	0	0
	90,000 cfs	300	0	0
Granite Park (Rm 209)	30,000 cfs	300	31	2
	50,000 cfs	300	2	7
	90,000 cfs	300	0	0

Discussion

Adult Growth and Mortality: Mesquite and acacia show vigorous shoot growth in all years sampled and growth in river sites was not significantly different from growth in tributary sites which were not influenced by river flows. This indicates that adult growth is independent of river flows and ambient precipitation is adequate to maintain adult growth, or that the roots of these phreatophytes reach to the water table during most river flow levels.

However, river flows have been consistently above "normal" post-dam flows for the 4 years of the study. In fact, dam releases since Lake Powell filled in 1983 have been similar to pre-dam flow releases with high to moderate floods in the late spring tapering off through late summer and winter. Bank storage of soil moisture after high spring flows would serve to minimize between year differences in dam releases during years with high water in late spring. It is possible that differences in growth of river and tributary trees would be more apparent in a year without high spring river flows. A weak decline in shoot growth of river trees since 1983 may support this idea.

Individual trees showed significant differences in growth over four years, however, there was little consistency among the 20 trees at each site. The high between-year variation for individuals indicates that local factors and patterns of vigor in individuals may override the effects of river flows on trees, at least over the short-term.

Evidence from tree ring analysis of acacia indicates that there has been a long-term effect of Glen Canyon Dam on growth of acacia. Similarly, tree ring analysis has shown that along the Missouri River in North Dakota elm, ash and oak have experienced post-dam decreases in growth after the establishment of the Garrison Dam in 1953 (Reily and Johnson, 1982).

Though high spring dam releases may slightly improve shoot growth in river trees, high flows, especially the very high flows of 1983 do lead to increased mortality of mesquite adults in the NHWL. Mesquites closest to the river below the 50,000 cfs line have higher percent mortality than do mesquites away from the river's edge or in the OHWL.

Aerial photo analysis of the OHWL riparian zone indicated a reduction in the extent of mesquite and acacia from 1963 to 1985 (Pucherelli, 1986) and may reflect either reduced growth rates and/or increased mortality under the post-dam flow regime. The reduction in the aerial extent of OHWL species was greatest in the upper, cooler reaches of the river and may also be the result of severe freezes in 1978 and 1984, which lead to high mortality of mesquite in southern Arizona (Glinski and Brown 1982). Mesquite in this area responded to freezing with canopy die-back but later resprouted from the base.

Seedling Establishment and Survivorship: Establishment and survivorship of seedlings appears to be affected more by short- and long-term changes in river flow patterns than does growth in adults. The most striking change in the community is the establishment of acacia and mesquite in the NHWL since the completion of Glen Canyon Dam. In fact, most reproduction occurs in the NHWL. Subadult mesquite in the OHWL are rare indicating that ambient precipitation is too low to support seedlings away from the influence of river flows. Subadult acacia are found in much greater numbers than mesquite in all riparian habitats.

However, mortality of acacia is higher than mesquite across all age classes. For both mesquite and acacia, seedlings show highest mortality. Increased mortality of saplings 3-5 years old over younger saplings may be the result of seedlings that germinated at water's edge during high flows in 1983 and were later stranded far from normal flows.

Mortality for all age classes of mesquite and acacia is higher in the OHWL than in the NHWL. Mesquite shows proportionally a much greater increase in mortality from the NHWL to the OHWL perhaps reflecting lower drought tolerance for subadult mesquite than subadult acacia.

Reproductive Effort of Adult Mesquite: The study of mesquite reproductive effort was motivated by the question, why are there so few mesquite seedlings and saplings in both the old and new riparian zones. A breakdown in reproduction could come at any phase in the reproductive cycle: flowers may not become fruits; fruits may not mature; seeds may not be viable; seedlings may not become established.

Not only are adults growing vigorously in the OHWL but some members of each population are flowering and producing fruit. Flowering phenology at the population level showed that 30-65% of the mesquite bloomed at each site and 4-20% of the trees produced fruit. When individual inflorescences were followed, between 30-43% were found to produce fruit. Though only 30% of the trees surveyed in Reach 5 bloomed this year, Reach 5 had the highest mean fruits/inflorescence and the highest number of fruits/tree, which compensated somewhat for differences in blooming at the population level.

There is little comparative data on reproduction in mesquite. However, the percentage of flowers producing fruit in Grand Canyon is 5 times higher than a similar study from Tucson (Solbrig and Cantino 1975). However, this difference may not be important because the sample size of the Tucson study was small and flowering effort can vary considerably between years.

There is no comparative data available for rates of seed predation and abortion in mesquite. Based on rates of seed predation and abortion observed in other legume species, successful seed production in Grand Canyon mesquite appeared to be relatively high. At all but two sites greater than 60% of the seeds per fruit appeared healthy. At the two sites with high frequency of damaged seeds, Nankoweap had a high rate of abortion (48%) and Unkar had a high rate of predation (28%) which lowered the percent good seeds. Among those seeds that appeared healthy, the viability of seeds was uniformly high (96%) for scarified seeds. Unscarified seeds have lower viability (20%) and take much longer to germinate (Glendening and Paulsen 1955).

Results of experimental planting show that seedling establishment is low and is concentrated on the river's edge. No planted seedlings survived at sites away from the area of wetted soil near the shoreline. The breakdown in recruitment therefore appears to be a low level of germination and establishment of viable seeds. However, there are several factors that could affect the success of experimental plantings; seeds may have been planted to deep, soil temperature may have been too low, or the seasonal conditions may not have been adequate for germination in the local area.

Conclusions

Adverse effects of managed river flow regimes should have their greatest influence on seedlings. Seedlings rely on the wetted soil near the river's edge for germination and establishment. This has both short and long-term consequences. In the short-term, seedlings and saplings run a greater risk of mortality from dam releases than other age classes. If dam releases vary from week to week, seedlings that germinate near the river's edge when dam releases are low will be innundated and die as flows rise. Seedlings that germinate when dam releases are high may suffer dessication mortality when river flows drop. In the long-term the extent of mesquite and acacia in the NHWL will depend on patterns of seedling establishment and survival. As in the past, before the construction of Glen Canyon dam, survival will depend the height of spring floods. Mesquite and acacia will persist in the NHWL and in fact both already have reproducing adults in the new zone.

Short-term changes in dam releases, such as fluctuating flows probably will have little effect on adult mesquite and acacia in the OHWL. The long-term effects of post-dam flows on these adults is difficult to determine. Tree ring analysis of acacia implies a decrease in growth rates under post-dam flows. In addition, the lack of young age classes of mesquite in the OHWL may lead to the movement of that species into the NHWL. However, mesquite are very long lived and seedling recruitment may only need to occur once every 10-30 years for mesquite to persist in the OHWL. Acacia is likely to persist in the OHWL because it is more drought tolerant than mesquite and not restricted to riparian zones in the Grand Canyon. Under the post-dam flow regime, the OHWL is becoming more xeric and acacia may become the dominant tree in that zone.

Recommendations for Operating Criteria

Daily fluctuations in river levels are not likely to directly affect deep rooted trees. However, indirect effects such as leaching of nutrients from riparian soils (Stevens and Waring 1986) and erosion of alluvial deposits (Schmidt 1986) could have significant, deleterious, long-term effects on the vigor and extent of existing OHWL vegetation and establishment of OHWL species in the new high water line zone.

Seedling and sapling density in the new zone is high in tributaries and alluvial tributary deltas characterized by silt and streambed cobbles. This indicates that seedling establishment may be sensitive to nutrient levels. Selection of a flow regime that reduces the rates of nutrient leaching and beach erosion is particularly important because nutrient leaching appears to be an irreversible effect due to the reduced sediment load below Glen Canyon Dam. Management alternatives that minimize leaching of shoreline soils and erosion of beaches should be favored.

The Bureau of Reclamation flow regime alternatives proposed for Glen Canyon Dam (Wegner 1985) are discussed below. The advantages and disadvantages of each of the scenarios is discussed. If any of the proposed flow regimes result in lower rates of nutrient loss they are favored to maintain vegetation productivity.

Alternative 1: Monthly base flow releases

This alternative is favored by Stevens and Waring (1986) as the regime with the lowest rates of nutrient leaching. Nutrient levels may have a significant effect on seedling establishment and may be important in long-term vigor and persistence of the OHWL community. Alternative 1 would encourage seedling establishment at the 14,600 cfs line and above (the highest flow level under this regime) which could result in a downward expansion of the total area colonized by OHWL species. However, since seedlings tend to germinate near the river's edge floods greater than the base loaded maximum could result in increased mortality from inundation.

Alternative 2: Maximized power plant releases to 31,500 cfs

Alternative 2 may result in increased nutrient leaching (Stevens and Waring, 1986). If this is the case it would not be favored for long-term management of the OHWL community, especially OHWL species colonizing the new zone. Seedlings will not establish below the 31,500 cfs line and the potential extent of OHWL species will be less than under alternative 1 or 3. However, if flows greater than predicted occur frequently, mortality due to drowning or scouring may be less under alternative 2 because establishment of seedlings will occur higher on the river bank, and the period of inundation will be reduced.

Alternative 3: Maximized power plant releases from 8,000 to 25,000 cfs.

Alternative 3 may result in lower rates of nutrient leaching than alternatives 2, 4, and 5 (Steven and Waring, 1986) and would be favored over all but alternative 1 for long-term management of the OHWL community if this is the case. The area available for colonization by seedlings would be greater than under alternatives 2, 4, and 5. However, if greater than predicted flows occur frequently, mortality could be higher under this alternative than under alternatives with mean high water levels of 31,500. Alternative 3 may be the best compromise between reducing nutrient leaching rates and protecting seedlings and saplings from drowning and scouring as a result floods.

Alternative 4: Maximized power releases except during the recreation season

The costs and benefits of alternative 4 to the OHWL community are similar to alternative 2, except for one important factor. Seeds germinate mainly during the summer when flows would be steady at 25,000 cfs. Those seedlings germinating near the mean high water line would likely be drowned when the water rose again to 31,500 cfs.

Alternative 5: Maximized fishery flows

The costs and benefits of alternative 5 to the OHWL community are similar to alternative 2. Seedling mortality due to desiccation may be increased under alternative 5. Seedlings that germinate during the summer when flows reach 31,500 cfs may suffer desiccation during the winter when flows only reach 10,000 cfs. However, precipitation during the winter may ameliorate this effect.

Periodic high floods at 10-20 year intervals

Adult growth of acacia and mesquite in the OHWL did not increase markedly after the high water in 1983. This indicates that periodic high floods do not have a positive effect important enough to warrant including periodic high floods as a management alternative. In addition, high floods result in high mortality of individuals in the NHWL. Inundation mortality results primarily from drowning and secondarily from scouring erosion (Stevens and Waring, 1986). Short-term high floods may result in less mortality for adults than longer floods with greater inundation time. Though periodic floods may open areas for seedling colonization, the balance between sapling mortality and new establishment is unknown. The inundaton survival threshold for mesquite and acacia is also unknown. Given the evidence of increased mortality from floods and the lack of evidence for increased establishment we would recommend against periodic flooding as a management alternative.

LITERATURE CITED

Brown, B. T. and R. R. Johnson. 1986. Fluctuating flows from Glen Canyon Dam and their effect on breeding birds of the Colorado River. Final Report, Glen Canyon Environmental Studies, NPS, Grand Canyon National Park, Arizona.

Burkart, A. 1976. A Monograph of the genus Prosopis (Leguminosae subfam. Mimosoideae). J. Arnold Arboretum 57:220.

Campbell, C. J. and W. Green. 1968. Perpetual succession of stream channel vegetation in a semi-arid region. J. Az. Acad. Sci. 5:86-98.

Carothers, S. W., S. W. Aitchison, and R. R. Johnson. 1979. Natural resources, white water recreation and river management alternative on the Colorado River, Grand Canyon National Park, Arizona. In R. M. Linn, Ed. Proc. First Conference on Scientific Research in the National Parks, I:253-260.

Fritts, H. C. 1976. Tree rings and climate. Academic Press Inc., New York.

Glendening, G. E. and H. A. Paulsen Jr. 1955. Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. USDA Tech. Bull. No. 1127.

Glinski, R. L. and D. E. Brown. 1982. Mesquite (Prosopis juliflora) response to severe freezing in Southeastern Arizona. J. Az. Acad. Sci. 17:15-18.

Gnanadesikan, R. 1977. Methods for statistical analysis of multivariate observations. John Wiley & Sons, New York.

Haas, R. H., R. E. Meyer, C. J. Scifres and J. H. Brock. 1973. Growth and development of mesquite, p. 10-19 In Mesquite, Research Monograph 1, Texas Agric. Exp. Station, College Station.

Khan, D., S. S. Shaukat, and M. Faheemuddin. 1984. Germination studies of certain desert plants. Pakistan Jour. Bot. 16:231-254.

Liming F. G. 1957. Homemade dendrometers. Journal of Forestry 55:575-577.

Lowe, C. H. 1964. The vertebrates of Arizona. 270 pp. University of Arizona Press, Tucson.

Meyer, R. E., R. J. Haas and C. W. Wendt. 1973. Interaction of environmental variables on growth and development of honey mesquite. Bot. Gaz. 134:173-178.

Meyer, R. E., H. L. Morton, R. H. Haas, E. D. Robison, and T. E. Riley. 1971. Morphology and anatomy of honey mesquite. US Dept. Agric. Tech. Bull. 1423. 186 p.

Mooney, H. A., B. B. Simpson, and O. T. Solbrig. 1977. Phenology, morphology, physiology. Pages 26-43 in B. B. Simpson ed. Mesquite: its biology in two desert ecosystems. Dowden, Hutchinson, and Ross, Stroudsburg, Penn.

Nilsen, E. T., M. R. Sharifi, and P. W. Rundel. 1984. Comparative water relations of phreatophytes in the Sonoran Desert of California. Ecology 65:767-778.

Pucherelli, M. J. 1986. Evaluation of riparian vegetation trends in the Grand Canyon using multitemporal remote sensing techniques. Glen Canyon Environmental Studies, GCES Report No. A5.

Reily, P. W. and W. C. Johnson. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. Can. J. Bot. 60:2410-2423.

Schmidt, J. 1986. Bar/beach stability studies in Grand Canyon, Arizona. Glen Canyon Environmental Studies, GCES Report No. D4.

Sharifi, M. R., E. T. Nilsen, R. Virginia, P. W. Rundel, and W. M. Jarrell. 1983. Phenological patterns of current season shoots of Prosopis glandulosa var. torreyana in the Sonoran Desert of Southern California. Flora 173:265-277.

Shreve, F. 1951. Vegetation and flora of the Sonoran Desert. Volume I. Vegetation. Carnegie Institution of Washington Publication 591. 192 pp.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods. Iowa State Univ. Press, Ames Iowa. 593 pp.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd. Edition. W. H. Freeman and Co. 859 pp.

Solbrig, O. T. and P. D. Cantino. 1975. Reproductive adaptations in Prosopis (Leguminosae, Mimosoideae). J. Arnold Arboreteum 56:185-210.

Stevens, L. E. 1984. The Colorado River in Grand Canyon, 2nd. ed. Red Lake Books. Flagstaff, AZ. 107 pp.

Stevens L. E. and G. L. Waring. 1986. Effects of post-dam flooding on riparian substrates, vegetation and invertebrate populations in the Colorado River corridor in Grand Canyon, Arizona. Glen Canyon Environmental Studies, GCES Report No. A2.

Szarek, S. R. and Woodhouse R. M. 1978. Eco-physiological studies of Sonoran Desert plants, part 4: Seasonal photosynthetic capacities of Acacia greggii and Cercidium microphyllum. Oecologica 37:221-230.

Turner, R. M. 1963. Growth in four species of Sonoran Desert trees. Ecol. 44:760-765.

Turner, R. M. and M. M. Karpiscak. 1980. Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. USGS Prof. Paper 1132. US Govt. Printing Off. Washington D. C.

Van Auken, O. W. and J. K. Bush. 1985. Secondary succession on terraces of the San-Antonio River Texas, USA. Bull. Torrey Bot. Club 112:158-166.

Warren P. W. and L. S. Anderson. 1985. Gradient analysis of a Sonoran Desert wash. Pages 150-155 in Riparian Ecosystems and their Management: Reconciling Conflicting Uses. Gen. Tech. Rep. RM 120, Rocky Mtn. Forest and Range Sta., Fort Collins, CO.

Warren, P. W., K. L. Reichhardt, D. A. Mouat, B. T. Brown, and R. R. Johnson. 1982. Vegetation of Grand Canyon National Park. NPS Tech. Rep. No. 9, CPSU, University of Arizona, Tucson, AZ.

Warren, P. W. and C. H. Schwalbe. 1985. Herpetofauna in riparian habitats along the Colorado River in Grand Canyon. Pages 347-354 in Riparian Ecosystems and their Management: Reconciling Conflicting Uses. Gen. Tech. Rep. RM 120, Rocky Mtn. Forest and Range Sta., Fort Collins, CO.

Wegner, D. 1985. Glen Canyon Environmental Studies subteam meetings, March 25-27, 1985. Phoenix, AZ. 21 p.

APPENDIX A

MEAN SHOOT GROWTH, BASAL DIAMETER AND CANOPY VOLUME OF INDIVIDUAL MESQUITE AND ACACIA

Table 1. Mesquite shoot growth across years for each tree at the river site at Nankoweap Canyon. Means with similar symbols beside them are not significantly different from one another by one-way ANOVA and Tukey's test ($p<.05$, $n=20$). Basal diameter and shoot growth are measured in centimeters. Canopy volume is measured in sq. m.

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
80384-01	13.9	100.6	27.8 !	19.6 *	15.4 *	0.0 $	45.4	<.001
80384-02	10.9	—	26.7 !	21.4 *	21.4 *	0.0 $	84.2	<.001
80384-04	31.3	345.0	24.8 *!	24.9 *!	21.8 *	30.2 !	2.7	<.05
80384-05	2.8	4.5	20.2 *	16.6 *	17.4 *	0.0 !	57.2	<.001
80384-06	26.7	874.5	17.4 *	23.5 *	34.0 !	16.8 *	13.8	<.001
80384-08	1.3	14.8	21.2 *	19.6 *	9.2 !	0.0 $	32.9	<.001
80384-09	37.4	218.7	20.4 *!	25.2 *	17.3 !	16.6 !	5.3	<.01
80384-10	3.2	23.6	25.1 *	21.6 *	19.4 *	30.8 *	2.1	NS
80384-11	31.2	683.6	23.4 *	24.2 *	27.3 *	3.2 !	61.6	<.001
no dendro	—	96.5	30.7 *	24.2 !	15.4 $	0.0 #	81.2	<.001
32185-21	64.9	2034.1	19.0 *	26.1 !	21.1 *!	25.8 !	5.1	<.01
32185-22	41.6	806.3	24.2 *	31.0 !	22.8 *	22.4 *	5.2	<.01
32185-23	19.8	149.7	22.0 *	20.2 *$	11.2 !	15.3 !$	10.2	<.001
32185-24	56.6	1403.3	22.2 !	37.4 *	39.8 *	34.0 *	7.2	<.001
32185-25	39.6	427.2	16.9 *	19.7 *	24.0 *	35.5 !	15.5	<.001
32185-26	73.0	635.1	21.0*	29.4*	41.0 !	8.2 $	21.0	<.001
32185-27	28.5	490.4	19.0 *	23.4 *	27.0 *	25.6 *	0.8	NS
32185-29	21.5	200.7	18.1 *	23.0 *	51.4 !	18.2 *	27.0	<.001

Table 2. Mesqite shoot growth across years at the tributary site at Nankoweap Canyon. Means with similar symbols beside them are not significantly different from one another by one-way ANOVA and Tukey's test ($p<.05$, $n=20$).

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
80284-01	13.7	57.5	20.0 *!	22.6 *	15.8 !	0.0 $	70.0	<.00
80284-02	13.6	50.9	17.0 *	16.8 *	14.1 *	0.0 !	59.9	<.001
80284-03	—	77.0	24.5 *	23.7 *	11.4 !	0.0 $	36.2	<.001
80284-3a	54.1	306.8	26.6 *	28.4 *	15.0 !	0.0 $	68.1	<.001
no dendro	32.4	141.3	28.1 *	25.1 *	29.1 *	24.2 *	0.8	NS
80284-07	25.8	71.2	22.4 *	29.2 *	24.2 *	6.8 !	14.8	<.001
31285-01	40.3	296.5	24.3 *	24.2 *	21.0 *	0.0 !	62.7	<.001
32185-02	22.4	250.9	26.4 *!	29.6 *	18.8 !	0.0 $	42.3	<.001
32185-03	30.4	1155.4	25.4 *	24.4 *	14.0 !	20.8 *!	4.1	<.01
32185-04	57.0	1121.4	31.9 *	33.1 *	17.6 !	18.2 !	8.6	<.001
32185-05	26.7	294.2	20.1 *	21.0 *	17.8 *	28.0 !	8.1	<.001
32185-06	17.8	154.6	20.7 *	24.6 *!	29.6 !	3.8 $	38.4	<.001
32185-07	32.6	334.1	19.6 *	26.2 *!	21.6 *	29.8 !	6.1	<.01
32185-08	45.0	331.0	22.3 *	26.4 *	13.8 !	6.8 !	17.3	<.001
32285-09	33.2	429.9	20.7 *!	22.8 *	16.9 !	0.0 $	94.2	<.001
32285-10	30.5	325.8	23.9 *	28.6 *	17.2 !	0.0 $	84.9	<.001
32285-11	17.4	126.0	20.6 *	18.5 *	20.2 *	2.2 !	27.1	<.001
32285-13	18.5	113.9	25.2 *	18.8 !	14.6 !	19.6 *!	8.1	<.001

Table 3. Mesquite shoot growth across years at the river site at Unkar Canyon. Means with similar symbols beside them are not significantly different from one another by one-way ANOVA and Tukey's test ($p<.05$, $n=20$). Basal diameter and shoot growth are measured in centimeters. Canopy volume is measured in m^2.

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
80484-12	12.1	70.9	28.4 !	17.4 *	14.1 *	0.0 $	68.6	<.00
80485-13	107.0	118.2	35.2 *!	39.4 !	28.6 *	28.4 *	7.8	<.001
80484-14	14.7	44.2	30.0 !	17.1 *$	17.2 *	12.3 $	33.8	<.001
80484-15	18.5	320.3	26.2 *	17.4 !	23.2 *!	20.0 *!	3.3	<.05
80484-16	61.0	629.5	20.4 *	26.6 !	15.0 $	24.6 *!	15.9	<.001
32385-11	34.0	478.8	21.6 *	30.1 !	20.2 *	16.5 *	10.2	<.001
32385-12	44.2	475.9	24.3 *	36.8 !	16.0 $	8.0 #	36.8	<.001
32385-13	71.7	1165.6	28.2 *	27.4 *	17.6 !	23.8 *!	7.1	<.001
32385-14	29.0	659.8	20.6 *	18.9 *!	15.8 !$	13.8 $	5.6	<.01
32385-15	28.6	393.2	32.4 *	29.4 *	14.6 !	4.0 $	35.8	<.001
32385-16	26.2	532.1	18.2 *!	21.7 *	14.0 !	5.7 $	21.4	<.001
32385-17	21.8	458.2	20.0 *	24.6 *	24.7 *	18.8 *	3.1	<.05
32385-18	30.1	170.2	24.4 *!	26.4 *	17.4 !	20.7 *!	3.5	<.05
32385-19	15.5	55.8	22.0 *	19.3 *	19.3 *	0.5 !	66.3	<.001

Table 4. Mesquite shoot growth across years at the tributary site at Unkar Canyon. Means with similar symbols beside them are not significantly different from each other at $p < .05$.

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
80484-01	17.1	92.0	26.5 *!	31.7 *	31.8 *	21.8 !	5.3	<.01
80484-02	9.9	46.9	16.8 *!	19.8 *	11.2 $	15.3 !$	9.4	<.001
80484-03	34.3	70.7	22.4 *	21.9 *	25.2 *	23.0 *	0.6	NS
80484-04	34.7	676.0	29.3 *	30.2 *	19.6 !	22.7 !	6.3	<.01
80484-05	11.2	223.8	22.6 *$	24.0 *	18.4 !$	15.6 !	8.6	<.001
80484-06	4.5	215.5	35.1 *	31.0 *	20.3 !	0.0 $	93.3	<.001
32385-01	21.5	260.9	14.2 *	21.7 !$	26.6 !	18.9 *$	10.3	<.001
32385-02	21.5	344.7	22.4 *	30.8 !	36.5 !	20.6 *	11.4	<.001
32385-03	7.4	123.3	30.8 *!	29.9 *!	36.5 !	22.2 *	6.2	<.01
32385-04	36.5	656.9	30.0 *	42.4 !	47.4 !	28.6 *	17.4	<.001
32385-05	19.0	238.1	25.3 *!	29.6 *	25.3 *!	21.2 !	4.0	<.05
32385-06	6.7	58.2	24.8 *!	32.2 $	31.4 !$	22.8 *	6.3	<.01
32385-07	18.2	117.5	21.4 *	22.0 *	28.3 !	2.6 $	64.1	<.001
32385-08	21.7	158.3	23.0 *	26.2 *	30.6 *	25.1 *	2.2	NS
32385-09	48.6	1618.3	18.6 *	19.4 *	26.7 !	21.8 *!	4.2	<.01

Table 5. Mesquite shoot growth across years at the river site at Granite Park. Means with similar symbols beside them are not significantly different from one another one-way ANOVA by Tukey's test ($p<.05$, $n=20$). Basal diameter and shoot growth are measured in centimeters. Canopy volume is measured in m^2.

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
81184-01	18.8	114.7	25.2 *	20.0 *	12.8 !	0.0 $	53.6	<.001
81184-02	16.5	68.7	21.4 !	11.0 *	15.5 *	0.0 $	52.7	<.001
81184-03	13.6	139.5	29.4 !	18.9 *	18.0 *	13.6 *	16.5	<.001
81184-06	23.6	336.1	38.1 !	24.6 *	27.2 *	13.6 $	16.9	<.001
32985-01	17.3	112.7	20.8 *	13.6 *	31.0 !	19.7 *	9.8	<.001
32985-02	10.7	64.5	27.0 *!	19.4 *	27.7 !	24.2 *!	2.9	<.05
32985-03	10.9	38.7	22.8 *	25.0 *	19.4 *	19.4 *	2.0	NS
32985-04	27.6	71.8	17.6 *	15.3 *	34.3 !	19.6 *	23.6	<.001
32985-05	12.3	104.1	29.5 !	17.8 *	19.2 *	14.2 *	11.2	<.001
32985-06	31.3	218.4	18.6 *	14.7 *!	12.2 !	16.0 *!	3.5	<.05
32985-07	13.4	149.4	20.0 *	17.8 *	19.8 *	26.8 !	5.5	<.01
32985-08	14.0	54.3	16.8 *	14.1 *!	11.4 !$	8.0 $	9.5	<.001
32985-09	39.6	269.4	21.2 *	20.3 *!	18.3 *!	14.9 !	3.4	<.05
32985-10	22.2	201.5	21.1 *	17.0 *!	17.2 *!	13.6 !	5.4	<.01
33085-11	19.5	146.6	24.8 !	15.2 *	12.8 *	17.4 *	13.3	<.001
33085-12	16.3	418.2	27.6 !	17.8 *$	19.1 *	11.8 $	14.4	<.001
33085-13	15.6	161.4	25.2 !	17.0 *	16.9 *	18.0 *	8.2	<.001
33085-14	26.9	133.1	33.1 *	23.9 !	34.2 *	16.5 !	14.4	<.001

Table 6. Mesquite shoot growth across years at the tributary site at Granite Park. Means with similar symbols beside them are not significantly different from one another by one-way ANOVA and Tukey's test ($p < .05$, $n = 20$).

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
81184-01	16.0	484.1	19.3 *	28.4 !	20.8 *	30.8 !	15.9	<.001
81184-02	25.9	163.4	18.4 *	28.2 !	21.4 *	22.8 *	9.1	<.001
81184-03	29.2	190.6	16.9 *	17.2 *	16.0 *	16.0 *	0.2	NS
81184-04	6.1	42.1	22.4 *	19.8 *	20.2 *	19.9 *	0.9	NS
81184-05	25.7	398.2	28.8 *	44.4 !	32.3 *!	0.0 $	58.9	<.001
81184-06	34.0	1176.7	14.4 !	24.4 *	22.5 *	30.8 *	11.0	<.001
33085-15	17.7	193.2	20.3 *	18.6 *	19.7 *	8.2 !	10.9	<.001
33085-16	21.4	116.4	16.2 *	15.0 *	17.6 *	26.0 !	6.7	<.001
33085-17	17.0	110.4	17.0 *	18.8 *	24.9 !	25.2 !	8.7	<.001
33085-18	44.6	1591.4	18.6 *	20.6 *!	28.2 !	22.5 *!	3.8	<.05
33085-19	26.4	445.2	15.4 *	18.9 *	20.8 *	18.4 *	1.9	NS
33085-20	15.8	62.8	16.8 *	19.4 *	29.6 !	31.0 !	11.2	<.001
33085-21	18.5	489.4	32.8 *	27.8 *	29.4 *	27.6 *	1.0	NS
33085-22	33.1	565.3	19.8 *	19.8 *	23.2 *	19.7 *	1.3	NS
33085-23	17.6	113.0	18.8 *	17.2 *	37.5 !	28.2 $	16.5	<.001
33085-24	47.1	879.1	16.2 *	26.0 !	31.4 !	15.2 *	9.7	<.001
33085-25	21.7	111.5	18.2 *	18.2 *	33.4 !	21.8 *	9.0	<.001
33085-26	26.9	129.8	11.9 *	17.4 !	11.9 *	20.1 !	10.2	<.001
33085-27	20.4	450.7	13.8 *	20.5 *	28.8 !	25.4 !	7.6	<.001

Table 7. Acacia shoot growth across years at the river site at National Canyon. Means with similar symbols beside them are not significantly different from one another by ANOVA and Tukey's test ($p<.05$, $n=20$).

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
80984-01	6.3	100.0	24.6 *	15.8 *	16.1 *	21.2 *	1.5	NS
80984-02	2.0	4.8	6.0 *	4.4 *	4.6 *	11.5 !	9.4	<.001
80984-03	—	165.9	10.9 *	10.1 *	17.0 !	16.6 !	6.6	<.01
80984-04	6.5	48.0	35.4 *	25.7 *	20.0 *	29.1 *	2.1	NS
80984-05	14.4	176.7	19.0 *	19.6 *	11.4 !	14.2 *!	4.7	<.01
80984-06	87.0	87.0	24.4 *	22.4 *	18.2 *	25.0 *	1.2	NS
80984-07	13.0	540.7	24.1 !	11.8 *	11.4 *	11.8 *	11.2	<.001
80984-08	4.0	97.1	11.0 *!	12.4 *	6.2 !	9.8 *!	3.4	<.05
80984-09	6.7	77.9	16.8 *!	13.1 !	10.6 !	20.5 *	5.8	<.05
80984-10	7.9	191.2	15.8 !	10.1 *	8.6 *	10.4 *	11.1	<.001
80984-11	10.1	217.9	18.0 *	10.8 *	13.7 *	16.1 *	2.3	NS
80984-12	7.5	200.9	12.4 *	9.8 *	9.3 *	2.9 !	7.9	<.001
80984-13	11.2	158.7	15.3 *!	10.4 *	12.5 *	23.8 !	4.7	<.01
80984-14	9.8	142.2	20.1 *	13.8 *!	11.4 !	13.2 !	4.2	<.01
32785-789	8.1	220.8	13.8 *!	9.2 *	15.0 !	15.5 !	4.1	<.05
32785-790	11.9	140.3	22.7 !	13.8 *	10.4 *	7.2 *	11.0	<.001
32785-791	12.4	—	15.9 *	14.4 *	16.9 *	18.9 *	0.8	NS
32785-792	29.3	379.7	22.8 *	9.1 !	17.4 *!	18.4 *!	5.0	<.01
32785-793	5.8	79.8	17.1 *	13.2 *	11.6 *	17.7 *	0.9	NS
32785-794	8.6	206.3	17.6	17.3 *	13.0 *	21.2 *	1.8	NS

Table 8. Acacia shoot growth across years at the tributary site at National Canyon. Means with similar symbols beside them are not significantly different from one another ANOVA and Tukey's test (p<.05, n=20).

Dendrometer Number	Basal Diameter	Canopy Volume	Mean Shoot Growth 1983	1984	1985	1986	F Value	P
80984-01	15.7	315.4	23.4 *	12.0 *	28.0 *	16.6 *	2.4	NS
80984-04	14.5	210.6	11.6 *	10.5 *	9.8 *	8.0 *	0.9	NS
80984-06	28.1	757.6	16.9 *	14.9 *	26.7 !	11.6 *	8.8	<.001
80984-07	5.6	84.4	19.4 *	15.8 *	29.5 !	14.2 *	10.7	<.001
80984-09	16.1	604.2	18.5 *!	14.0 *	24.2 !$	29.5 $	6.8	<.001
80984-10	7.3	184.0	15.0 *	11.2 *	14.8 *	23.3 !	6.1	<.01
80984-11	7.7	206.3	14.2 *!	11.7 !	21.3 *	13.4 *!	3.3	<.05
80984-12	8.7	272.2	16.2 *	13.4 *	9.0 !	9.2 !	15.6	<.001
80984-13	18.8	340.8	17.2 *	17.6 *!	18.8 *!	35.6 !	5.7	<.01
80984-14	20.1	256.6	21.5 *	23.9 *	27.8 *	18.8 *	1.8	NS
32785-795	9.9	128.6	11.8 *	12.6 *	17.4 *	18.2 *	1.6	NS
32785-796	11.5	260.1	13.0 *	11.8 *	13.3 *	12.3 *	0.4	NS
32785-797	14.0	228.3	14.7 *	13.8 *	15.0 *	18.3 *	1.6	NS
32785-798	35.2	1255.3	15.7 *!	11.8 *	22.2 !	21.0 !	5.2	<.01
32785-800	17.8	399.0	13.6 *	11.5 *	18.1 *	45.0 !	21.9	<.001