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Terrestrial Vegetation Work for 1997 Steady Low and High Flows

Draft Final Report

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PREFACE

Although the United States is officially on a course towards joining the rest of the world in embracing the metric (SI) system of measurement, old habits and ways of thinking change slowly in a place where 100,000 years is considered an eye blink. Because most references to places, and indeed many of the place names, in the Colorado River corridor of Grand Canyon are based on river mileage downstream of Lees Ferry, we use miles for designation of distance along the river corridor (river miles, or RM in this report). Similarly, because dam managers and those who have worked in the river corridor have historically referred to discharge from Glen Canyon Dam in terms of thousands of cubic feet per second (kcfs), we will do so in this report. Conversions to SI equivalents are straightforward: cubic meters per second (CMS) = kcfs * 0.0283 and river kilometers (rKm)= river mile * 1.61. All other measurements of plants and habitats are in SI units.

There are many sources for determining plant identities in the southwestern United States. Often, these give conflicting names, depending on differences of opinions of the authors of the floras, taxonomic revisions more recent than the source, and so on. We follow the naming conventions in Kartesz et al. (1990) in this report. We commonly use acronyms for plant names to speed up our data collection. Abbreviations used in the data files are as per previous reports, and a glossary of these abbreviations can be found as Appendix A in both the Kearsley and Ayers (1996) experimental flood report and the Kearsley et al (1996) vegetation monitoring report.

Finally, this is a draft of the final report to be produced for this project. The numbers and conclusions drawn from them are subject to change and revision on review. Consequently, it would be inappropriate to cite either until they are part of an approved final report.

ABSTRACT

We measured the impacts of an experimental flood in 1996 and season-long high, near-constant flows on the seed banks of nine monitoring sites. Four exotic, potentially invasive plant species disappeared from the seed bank over the study period. However, they were present in such low numbers to begin with that any normal inter-annual fluctuations may have prevented us from detecting these species in the 1997 censuses. In addition, the number of individuals and diversity of species present in the seed bank dropped as a result of the experimental flood in 1996. On average, 60% of the individuals were lost from vegetation polygons in our sites, and the species diversity dropped by an average of 45%. These figures represent approximately 20 to 35% less loss than was reported on in previous reports made from preliminary data. Samples collected later in the season in both years indicate that both the diversity and numbers are in the process of recovering. Censuses in June 1997 showed numbers of seeds were a third higher and the number of species was two-thirds higher than in phenologically matched 1996 samples.

Because the soil seed bank is such an important part of plant community dynamics, we have recommended a series of actions to continue the process of recovery. First, daily fluctuations should be kept to a minimum, and flow levels should be kept as high as possible. This will ensure a high water table for annuals and herbaceous perennials which were so affected by the experimental flood. And second, seasonal variation in flow levels (e.g. high summer, low winter) should allow for increased biodiversity in the plant community. Because species differ in the tolerance of their seeds and seedlings for flooding, competitively inferior species which can tolerate flooding of their seeds may find a refuge in the lower elevation areas where competitively superior, but flood intolerant, species are excluded for some portion of the year.

INTRODUCTION

One of the most fundamentally important aspects of vegetation dynamics is the interactions among soil seed banks, vegetation, and disturbance. Seedbanks represent the potential for regeneration after disturbances (Grubb 1977, Grime 1989, Fenner 1992). The timing, intensity, predictability, and type of disturbance are usually integrated into the seeds and germination aspects of the life history characters of species (Thompson and Grime 1979, Grime 1989). In areas with large frequent disturbances, soil seed and propagule banks are often the only mode of regeneration (Ohtsuka and Ohsawa 1994).

In freshwater marshes where daily tides are present, the seed bank tends to act as a conservative force in community dynamics. The composition of the soil seed banks tends to reflect the surface vegetation (Leck and Graveline 1979), and annual losses from it and additions to it are an integral part of the maintenance of species composition within sites (Leck and Graveline 1979, Leck and Simpson 1987, Leck 1989).

In contrast, in wetland habitats without daily tidal fluctuations and in other types of riparian habitats, disturbance events and the soil seed bank are creative forces, driving successional patterns. Seed banks can have representatives of species which do not occur anywhere near at the present time, but represent remnants of earlier stages, or rudiments of later seral stages (Oosting and Humphreys 1940, Grubb 1977, Harmon and Franklin 1995). Alternatively, a species may not be present in the vegetation until a sequence of environmental conditions allow seeds to break dormancy, often in a temporally predictable pattern (van der Valk 1981, Smith and Kadlec 1983).

An important consequence of this latter pattern is that seed banks create the opportunity for high levels of biodiversity in riparian areas where favorable conditions might otherwise lead to competitive exclusion by one or a few species (Grubb 1977). For example, flora associated with the Atlantic coastal

plain if eastern Canada is maintained in low elevation portions of lake shores in Ontario because flooding during periods of high water drowns the otherwise competitively superior local shrub community (Keddy and Reznicek 1982). During periods of low water, the flood tolerant seeds germinate, occupying newly available substrate. Similarly, diversity in flood tolerance of seeds and a locally varying hydrograph has led to the maintenance of high levels of diversity in the near-shore plant communities of upstate New York ponds (Schneider 1994). As the local climate shifts between wetter and dryer conditions on a decadal scale, these communities come and go with the rise and fall of the shoreline.

Despite the large amount of literature on the effects of river regulation on riparian vegetation (Johnson and Carothers 1982, Nilsson and Jansson 1995, Frissell and Bayles 1996, Nilsson et al. 1997), the interaction between river regulation and seed banks has been studied only in a few other systems. A thorough review of the literature over the past two decades revealed only two other systems in with the effects of river regulation on seed banks was investigated. First, seed banks in cypress-tupelo bottomland forests in the Savannah River drainage in South Carolina, U.S.A., have not fared well as a result of river management. High flows during peak germination and establishment periods, together with the floating away of the seed rain to inappropriate habitats have led to a degeneration of the seed banks in these habitats (Sharitz and Lee 1985, Huenneke and Sharitz 1986). Second, on the Dalaelvan River in Sweden, seeds of woody species are drowned by periods of high dam discharges, preventing regeneration within riparian woodland habitats (Skoglund and Verwijst 1989).

The purpose of this study was to assess how the dynamics of riparian seed banks were affected by a controlled flood in 1996 and two years of near-constant high flows during the growing seasons in 1996 and 1997. We have reported on seed bank responses to the high flows before using preliminary data (Kearsley and Ayers 1996), but the extremely seasonal nature of seed banks (Thompson and Grime

1979) and the fact that we had only data from early and late in the same year, limited the usefulness of the conclusions drawn in that study (Leck and Simpson 1987, Grime 1989, Harmon and Franklin 1995). Here we address four questions about the seed banks of nine monitoring sites. First, what impact did the flood and subsequent high flows have on four exotic and potentially invasive plant species? We were concerned about the spread of camelthorn (*Alhagi camelorum*), spreading lovegrass (*Eragrostis curvula*), ravenna grass (*Erianthus ravennae*), and perennial pepperweed (*Lepidium latifolium*). These species are either listed as noxious weeds or known to have been invasive in other systems (Whitson et al. 1992). Second, what effect was there on the size of the riparian seed bank in general? We had reported on losses averaging 80% of the individuals in our monitoring sites, but those were comparisons of early- and late-season samples. Third, what was the impact on measures of diversity in the seed bank? We had reported losses on the same scale as for individuals, but some species simply do not germinate without some kind of chilling cues (Fenner 1992). Finally, were there individual species which demonstrated unusual responses to the flow regime, either positive or negative? Many riparian species are either disturbance and / or flood specialists, and others are intolerant of those conditions (van der Valk 1981, Murdoch and Ellis 1992, Edwards et al. 1994).

METHODS

The field collections described in this report were performed during two downstream river trips. Early season collections were done during a February 1997 river trip run in conjunction with National Park Service Archaeology personnel, Hopi Tribe Archaeology personnel, and G.C.M.R.C. survey personnel. Late season collections were made during a June 1997 trip with the same group.

Study Sites

The work in this report was conducted in eleven monitoring sites which have been part of vegetation monitoring for the past three to seven years. The sites are distributed among geomorphic

Table 1. The location of soil seed bank sampling sites in the Colorado River corridor and integration with other studies. The studies do not include many which were conducted during the 1996 controlled flood.

River Mile	Site Name	Geomorphic Reach (Character [+])	Special GIS Site	Other Studies[++]
-6.5 L	Hidden Slough	2 (N)	14	M, V, G, S
43.1 L	Anasazi Bridge Camp	6 (W)	3	M, V, G, S, F
51.2 L	Unnamed Camp	6 (W)	4	M, V, S, A, F
55.5 R	Kwagunt Marsh	6 (W)	4	M, V, G, C, F
68.2 R	Tanner Beach	7 (W)	5	M, V, S, F
71.4 L	Cardenas Marsh	7 (W)	5	M, V, A, F
93.9 L	Granite Camp	8 (N)	6	M, V, S, F
122.8 L	Forster Camp	9 (N)	7	M, V, S, F
194.1 L	Hualapai Acres	12 (W)	10	M, V, G, S, F
209.0 L	Granite Park	12 (W)	11	M, V, F
249.5 L	Below Lost Creek	14 (N)	12	M, V, A

[+] Geomorphic character per Schmidt and Graf (1990): W = Wide reach, N = Narrow reach
[++]Other studies: M = NAU vegetation mapping, V = Interim Flows vegetation quadrats, G = NAU groundwater studies, S = NAU sandbar studies, C = ASU climatology studies, A = N.P.S. Avifauna Studies, F = 1996 experimental flood seed bank studies

reaches of the Grand Canyon portion of the Colorado River, and have are being studied as part of several other projects (Table 1). The sites were chosen on the basis of many criteria, several of which are relevant to the present study. The first was large size and relative areal stability over the previous 7 years so that we would not be faced with the losses of sites. Second, we looked for sites with multiple other studies being conducted there so that results could be integrated with related areas such as groundwater studies and sediment erosion studies. Third, sites were chosen to reflect the geomorphic diversity of the river corridor Schmidt and Graf 1990), with wide reaches being emphasized simply because that is where most of the riparian vegetation develops (Stevens et al. 1996). Finally, sites had

to have a great deal of within-site geomorphic diversity, so that all sites would contain variants of riparian woodland and shrubland vegetation, herbaceous wetland vegetation, channel margin vegetation, and typical bar-top open sandy sites.

Vegetation Maps and Polygons

We sampled seed banks in eleven vegetation monitoring sites, nine of which had been sampled in 1996 as part of the Experimental Beach / Habitat Building Flows (Table 1). Each of these sites has had detailed vegetation maps created, ground-truthed and censussed each year since 1995. The maps are divided into patches of internally consistent patches of vegetation, or polygons, which are distinct from the patches which surround them. Our sampling used these vegetation polygons as the experimental unit.

Random Point Selection

Our sampling was based on selecting three randomly located points per polygon. Because polygons varied widely in size and shape, not all could be sampled in identical manners. In this section we describe the several methods we used for locating a random point using a table of six-digit random numbers.

In large polygons (5 to 20 m diameter), we used the six digit numbers in a pace-turn pattern. The collector would walk through the polygon until directed by the recorder to stop. From that point the recorder would direct the collector to the random point using the six-digit number. The first digit was used as the number of paces forward, the second as a direction (even = right, odd = left), the third as a number of paces, the fourth as a direction, and the fifth as a number of paces. In the cases of sampling vertical structure and soil texture transects, the sixth digit was used as a direction as above.

In the cases where a polygon was long but narrow (< 3 m wide), we used a series of two-digit numbers for sampling during a transit of the polygon. The collector would walk along the long axis of

the polygon until directed to stop by the recorder. The recorder would then direct the collector by using the first digit was the number of paces forward, and the second was whether to sample to the left (digits = 0 to 2), straight ahead (digits 3 to 6), or to the right (digits 7 to 9).

To sample small (< 3 m diameter) and / or narrow polygons in which through transit would have caused damage or posed a danger (e.g., steep slopes or heavy vegetation), or take an unnecessary amount of time (e.g. extremely thick Tamarisk stands) we often used an around-and-in approach using two-digit random numbers. In this method, the collector would walk around the periphery of the polygon until the recorder told them to stop. The first digit of the pair was then used as the number of paces along the perimeter, the second was the number of paces to be walked into the polygon.

The fact that we were working in irregularly shaped and often small patches of habitat required that we be flexible when applying these methods. There were times when these methods needed to be slightly modified to meet unique situations. If pacing would cause the collector to exit the polygon, the collector could pace to the margin, turn 180° and continue pacing back into the polygon. Alternatively, the collector could convert the number of paces to a percentage of the distance to the margin and use that number.

In some situations, time constraints made it impossible to use the pace and turn methods. In these cases, the collector would walk through the polygon until ordered to stop by the recorder, at which point the collector would throw the trowel over their shoulder to land at a haphazard location. Because these methods tend to under-sample some parts of a polygon (Greig-Smith 1983 page 23), this was not the preferred method.

Seed Bank Samples

We examined the effects of the high flows on the distribution of weedy species by comparing the seed banks of polygons early and late in the season. Each sample contained approximately 100 to

200 g fresh weight of soil. The sample, which included surface duff, was collected from the top 10 cm of the soil.

We potted approximately 100 g of each sample in 7 cm square pots. We placed a small amount of sterile potting mix on the bottom of each pot (approximately 1 cm deep) to prevent soil loss during watering but allow drainage of excess water. We then placed the pots on a misting bench at the Northern Arizona University Research Greenhouse and kept them moist as seeds germinated. The watering schedule included 32 seconds of mist every eight minutes plus a daily thorough wetting with a watering can. After six weeks, the misting schedule was adjusted to 16 seconds every 16 minutes, and two of the daily waterings per week were replaced with half strength 10-10-10 soluble fertilizer.

As seedlings became identifiable, we recorded their numbers and identity, and discarded them. We identified many common species based on vegetative characters before flowering took place. For example, our experience in the field made it easy to identify small individuals of *Typha domingensis, Gnaphalium chilense, Baccharis emoryi B. glutinosa,* and *Isocoma acradenia*, among others. Others which were less distinctive, such as species of *Erigeron* and *Centaurium* could not be identified until flowers were present.

Data Analysis

We analyzed the effects of the high flows, and the subsequent flows in a number of ways. First, we focused on four exotic species of concern: camelthorn (*Alhagi camelorum*), lovegrass (*Eragrostis curvula*), Ravenna grass (*Erianthus ravennae*), and perennial pepperweed (*Lepidium latifolium*). These species are all either considered noxious weeds in Grand Canyon, or have been declared noxious weeds by authorities in other areas (e.g. Whitson et al. 1992). For each site, we counted the number of seedlings of these species which germinated in both early and late collections in each year. Because the numbers were so low in both cases, we did not subject them to statistical analyses.

We also compared a number of attributes of seed bank samples in the two collections. Because seed bank contents are highly seasonal in nature (Thompson and Grime 1979, van der Valk 1981, Thompson 1992), we separated the analyses of early and late samples. By doing so we could control for the effects of losses due to germination, germination cues, and the seasonality of the seed rain.

For each site, we compared the total number of seedlings in early and late samples from 1997 with similar samples from 1996 using a Wilcoxon T. All three soil samples from each polygon were pooled before running the analysis. We also compared the total number of species in each polygon using the non-parametric paired Wilcoxon T on polygon data from each site. We compared both measures of seedbank health across all sites using another Wilcoxon T test, with site as the pairing factor. Finally, we examined the early (February) sample data for species which showed unusual amounts of change between the two years, such as rare species becoming abundant and more common species disappearing. We did not use the June data simply because both samples had so few individuals and species to begin with, it would be difficult, or perhaps misleading, to base conclusions about changes in a species' seed bank based on such small numbers. In the cases of species whose abundance did not change radically from one year to the next, the number of seeds of the species in question was converted to a proportion of the total seed bank at each site, and these proportions were compared between years using the paired, non-parametric Wilcoxon T.

RESULTS

Weedy species

Although the numbers of individuals were very low in all sites, the data indicate the high flows of summer 1996 and 1997 did not favor the four species of concern (Table 2). Despite anecdotal evidence of the spread of camelthorn, our data indicate that the species has been lost from the seed banks of the nine monitoring sites. Seeds of *A. camelorum* were found in three sites in 1996 but in

none in 1997. Similarly, seeds of lovegrass and perennial pepperweed were found in only one site each in 1996, but in none in 1997. The efforts of the National Park Service aimed at controlling Ravenna grass are obviously paying off; no samples in 1996 or 1997 contained seeds of the species.

February and June censuses in 1996 and 1997. n.a. = sampling was not conducted at this site in 1996.

Site	*Alhagi camelorum*		*Eragrostis curvula*		*Erianthus ravennae*		*Lepidium latifolium*	
	1996	1997	1996	1997	1996	1997	1996	1997
- 6 R	n.a.	0	n.a.	0	n.a.	0	n.a.	0
43 L	0	0	1	0	0	0	0	0
51 L	0	0	1	0	0	0	0	0
55 R	0	0	0	0	0	0	0	0
68 R	0	0	0	0	0	0	0	0
72 L	4	0	0	0	0	0	0	0
94 L	2	0	0	0	0	0	0	0
123 L	0	0	0	0	0	0	0	0
194 L	0	0	0	0	0	0	0	0
209 L	7	0	0	0	0	0	1	0
249 L	n.a.	0	n.a.	0	n.a.	0	n.a.	0

February community data

The data show a significant reduction in the numbers of germinating seedlings between February 1996 and February 1997 (Figure 1, Table 3). Sites lost, on average, between 2 and twenty seedlings per polygon, averaging a loss of 10.6 per polygon across all sites. These losses represented between 44% and 81% of the 1996 seedling numbers, with an average percentage loss of 64%. In all sites except the two with the smallest seed banks in 1996 (68 R and 209 L), the losses of germinable

Table 3. Changes in the number of individuals, species diversity, and Shannon-Weiner diversity indices of seed bank soil samples between February 1996 and February 1997.

Site	Number of Individuals			Number of Species (S)			Diversity (H')		
	1996	1997	% Change	1996	1997	% Change	1996	1997	% Change
43 L	16.5	5.3	- 68%	3.65	1.26	- 66 %	0.842	0.317	- 62 %
51 R	24.1	4.6	- 81 %	3.18	1.45	- 54 %	0.636	0.345	- 46 %
55 R	46.1	8.9	-81 %	5.49	1.56	- 72 %	0.972	0.247	- 75 %
68 R	3.7	1.9	-50 %	1.00	1.12	+ 12 %	0.216	0.208	- 4 %
72 L	12.4	6.1	- 51 %	3.04	2.19	- 56 %	0.718	0.583	- 19 %
94 L	9.5	2.0	- 79 %	1.50	0.39	- 82 %	0.299	0.039	- 87 %
123 L	5.5	2.1	- 63 %	2.41	1.47	- 39 %	0.569	0.201	- 65 %
194 L	12.9	5.8	- 55 %	3.53	1.84	- 48 %	0.935	0.407	- 57 %
209 L	4.1	2.3	- 44 %	1.91	1.26	- 34 %	0.511	0.323	- 37 %
Mean % Change			- 64 %			- 43 %			- 46 %

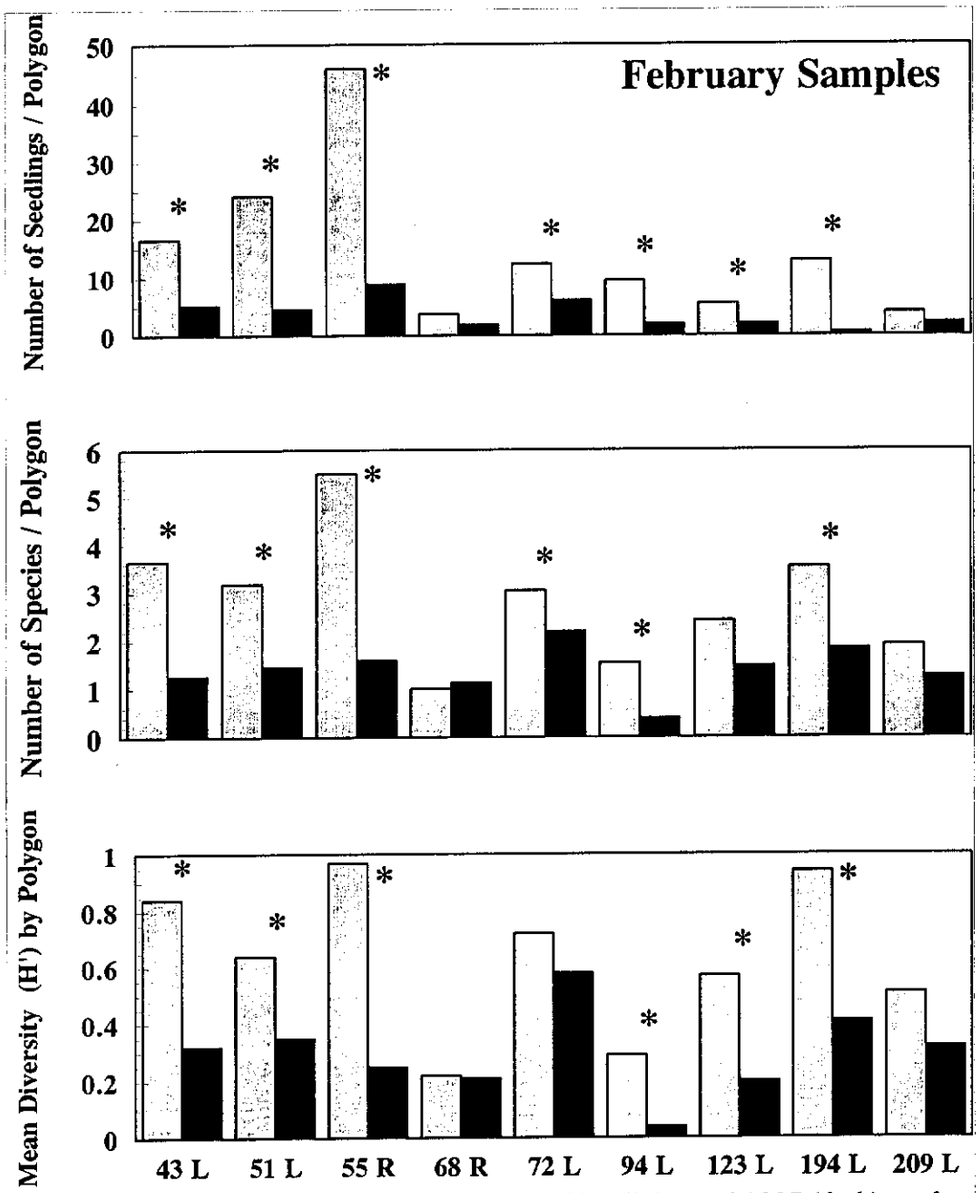

Figure 1. Comparison of the Feburary 1996 (light) and 1997 (dark) seed bank samples in terms of their mean numbers (top), species diversity (middle) and Shannon-Weiner diversity H' (bottom) per polygon. Asterisks indicate significant differences.

seeds was statistically significant (Figure X). An overall test across all sites also showed that the difference between the mean number of seedlings in 1996 and 1997 February samples was statistically significant ($n = 9$, $T = -22.5$, $p < 0.002$).

Similarly, six of the nine sites showed statistically significant decreases in the number of species germinating in each polygon between February 1996 and February 1997 (Figure 1, Table 3). On average, the changes in species diversity ranged from a + 0.1 species per polygon to -3.9 species per polygon, with an overall average of -1.5 species. These changes represented between a 12% gain and an 82% loss of species diversity, averaging a loss of 43% over the course of the year. An overall test for the significance of these changes showed a significant loss of diversity between 1996 and 1997 ($n = 9$, $T = -21.5$, $p < 0.004$).

The Shannon-Weiner diversity index (H') for polygons declined in all sites, significantly so in six of the nine sites (Figure 1, Table 3). The site mean measures of H' dropped between 0.008 and 0.725 in the February samples from 1996 and 1997. This represented a loss of between 4% and 87% of the 1996 values. The overall test of this pattern showed an loss of 0.335 across all sites, which represented a statistically significant decrease ($n = 9$, $T = 22.5$, $p < 0.002$).

June community data

The patterns in the June samples of 1996 and 1997 are very different from, and in some cases the opposite of, the results from the February samples (Figure 2, Table 4). Only three of the nine sites showed significant changes in the number of germinable seeds, and those were all increases between 1996 and 1997. Within sites, changes in the number of germinable seeds ranged from a loss of 1.5 to a gain of 4.8 individuals per polygon, with an average gain of 0.8 individuals. These represented percentages ranges from a loss of 41% to a gain of 152% of the June 1996 seedling numbers. An overall test for changes across all sites showed no significant difference between 1996 and 1997 ($n = 9$, $T = 8.5$, n.s.).

Only two of the nine sites showed significant changes in species diversity (S) in the June samples between 1996 and 1997, and those were both increases (Figure 2, Table 4). Changes in mean

Table 4. Changes in the mean number of individuals, species diversity, and Shannon-Weiner diversity indices of polygon seed bank soil samples between June 1996 and June 1997.

Site	Number of Individuals			Number of Species (S)			Diversity (H')		
	1996	1997	% Change	1996	1997	% Change	1996	1997	% Change
43 L	2.6	2.3	- 13 %	0.94	0.74	- 21 %	0.226	0.220	- 3 %
51 R	3.1	7.9	+ 152 %	0.34	1.29	+ 272 %	0.023	0.236	+ 909 %
55 R	4.8	6.3	+ 31 %	0.73	1.91	+ 160 %	0.112	0.506	+ 352 %
68 R	1.2	0.9	- 26 %	0.59	0.40	- 32 %	0.129	0.053	- 59 %
72 L	3.6	6.2	+ 75 %	1.35	1.12	- 17 %	0.344	0.208	- 40 %
94 L	0.2	0.5	+ 108 %	0.24	0.42	+ 77 %	0.081	0.058	- 28 %
123 L	0.6	1.1	+ 71 %	0.40	0.71	+ 75 %	0.035	0.035	+ 2 %
194 L	3.6	2.1	- 41 %	0.70	0.92	+ 32 %	0.132	0.181	+ 37 %
209 L	1.6	1.3	- 37 %	0.54	0.81	+ 49 %	0.036	0.147	+ 308 %
Mean % Change			+ 36 %			+ 66 %			+ 164 %

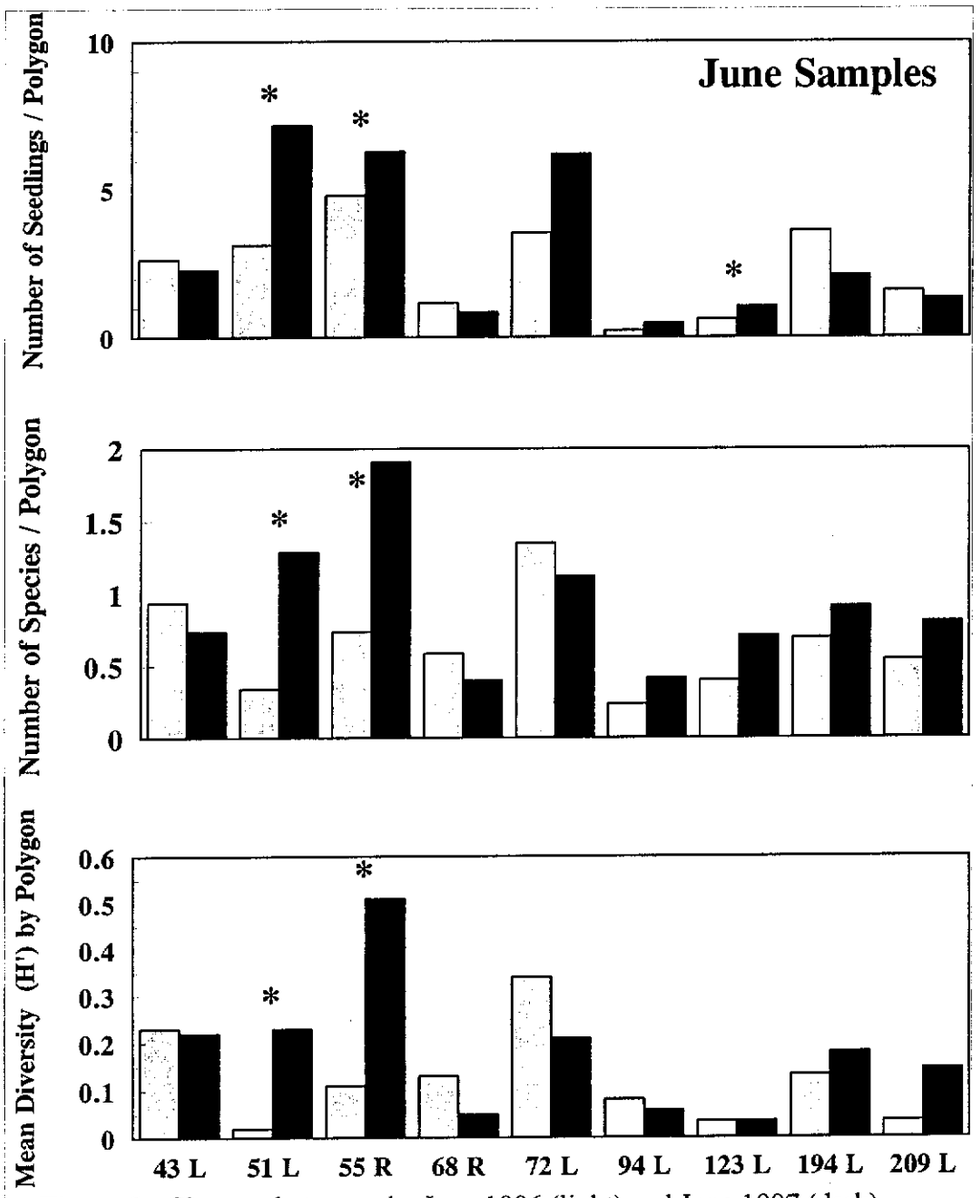

Figure 2. Changes between the June 1996 (light) and June 1997 (dark) censuses in the mean number of seeds (top), number of species (middle), and Shannon-Weiner diversity H' (bottom) per polygon. Asterisks indicate significant differences between years.

polygon S within sites ranged from a loss of 0.23 species to a gain of almost 1.2 species, averaging a gain of 0.3 species. These changes represented a range of percentage changes of between a loss of 32% to a gain of 160%, with an overall average of a 66% gain. An overall test for change across all sites

showed a non-significant increase in S (n = 9, T = 12.5, n.s.).

Similarly, only two sites showed significant changes in the Shannon-Weiner diversity index (H') between 1996 and 1997, both of which were increases (Figure 2, Table 4). Within sites, changes in the information-theoretic index of diversity ranged from a loss of 0.136 to a gain of 0.394, with an average of a gain of 0.058. These changes represented percentage changes ranging from a loss of 59% to a gain of 909%, with an average of a gain of 164%. An overall test across all sites showed a non-significant increase in H' (n = 9, T = 5.5, n.s.)

Individual Species

Because June samples in both years contained so few species and individuals, we have concentrated on the results from the February 1996 and 1997 samples in our consideration of changes in the abundance of individual species. Several species stood out as having changed in ways which differed significantly from the overall pattern of change. Some showed far greater losses than the overall 64% losses across all species, others showed increases, or at least no significant losses of germinable seed bank size as a result of the 1996 high flows and the intervening high, near-constant flows. We selected four of these species, two which showed massive losses and two which did not change significantly, for further examination. To select the former, we looked for species which were consistently present in all sites in relatively large amounts, ranked near the top of most sites in their 1996 abundances, and which were either absent or present at only low levels at all sites in 1997. The latter species were selected on the basis of an opposite pattern.

Two native species stood out as having lost far more individuals than the average species between 1996 and 1997 (Figure 3). First, waterbent grass, *Agrostis semiverticillata*, all but disappeared from seed banks as determined by our methods. In 1996, the seed banks of the nine sites averaged between one and fifty *A. semiverticillata* germinations per polygon. In 1997, only two sites, Cardenas

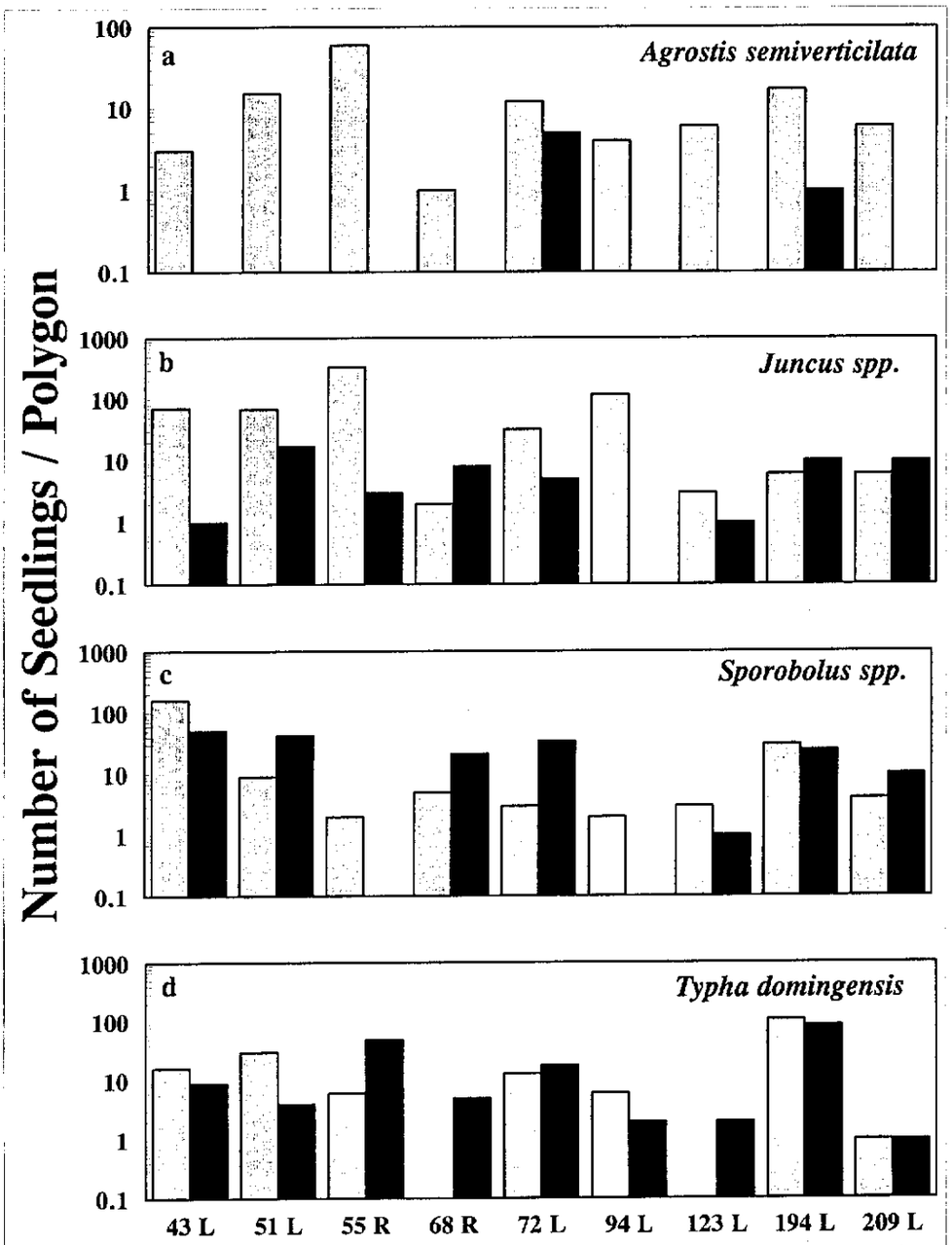

Figure 3. Species whose numbers changed unusually as a result of the 1996 experimental flood. a) *Agrostis semiverticillata* and b) *Juncus* spp. all but disappeared from the seed bank while c) *Sporobolus* spp. and d) *Typha domingensis* were mostly unaffected.

and Hualapai Acres, had any individuals at all. The difference was highly statistically significant, even with the low sample size of 9 sites ($n = 9$, $T = -22.5$, $p < 0.005$). Similarly but less dramatically, the

number of individuals of *Juncus* spp. dropped between 1996 and 1997. In 1996, polygons in the nine sites averages between 2 and 333 individuals per polygon, averaging 71 germinations (median = 32). In 1997, the nine sites averaged between 0 and 17 germinations, averaging approximately 6 per polygon (median = 5).

In contrast, cattails (*Typha domingensis*) showed no changes between the two censuses. Soil samples from the nine sites in 1996 averaged between 0 and 116 germinations per polygon, averaging 19.8 across all sites. In 1997, polygons averaged between 1 and 85 individuals, averaging 19.4 across all sites, a non-significant difference ($n = 9$, $T = -2$, n.s.). Similarly, species of dropseed grasses (*Sporobolus* spp.), principally *S. cryptandrus* and *S. flexuosus*, were more or less unaffected by the experimental flood and intervening high flows. In 1996, sites averaged between 2 and 160 germinations per polygon, with an overall average of 24.2 individuals across all sites. In 1997, polygons contained between 0 and 50 individuals, with an overall average of 21.0 per polygon. The differences were not significant statistically ($n = 9$, $T = 3$, n.s.).

Because seed banks shrank by 64% overall between February 1996 and February 1997, our finding of no change between 1996 and 1997 for cattails and dropseeds represented an increase in the proportion of these species in the site seed banks. In 1996, cattail seeds accounted for an average of 4% of site seed banks, while in 1997 they represented more than 13%, a significant increase ($n = 9$, $t = 21.5$, $p < 0.005$). Dropseed seeds comprised an average of approximately 5% of site seed banks in 1996 compared with an average of nearly 18% in 1997, a significant increase also ($n = 9$, $T = 19.5$, $p < 0.001$).

DISCUSSION

Here we have demonstrated that the experimental flood of 1996 had a negative effect on the soil seed banks of riparian habitats in the Colorado River corridor of Grand Canyon. Up to 80% of the

individuals, species diversity, and Shannon-Weiner diversity accounted for in the February 1996 samples is missing in the February 1997 samples. Although we had reported similar findings based on comparisons of the February and June 1996 data (Kearsley and Ayers 1996), the highly seasonal nature of seed bank composition and its determinants made these results questionable (e.g. Thompson and Grime 1979, Leck and Simpson 1987). The results of the 1996 / 1997 comparisons show less loss of the seed bank measures than did the February / June 1996 comparisons (64% vs. 81% of individuals, 45% vs. 80% of species diversity).

We have also documented that the seed banks of the nine monitoring sites may be recovering rapidly. Comparisons of mid-summer samples in 1996 and 1997 show significant and non-significant increases in numbers and diversity of germinable seeds. In some sites there was more than a 150% and 270% increase in individuals and species diversity over the 1996 samples. Although none of the overall tests across all sites showed significant differences, the data show a man increase of 36% of individuals, 66% in the number of species, and 164% in the average Shannon-Weiner diversity index for polygons. Thus, at least for species with readily germinable seeds in mid-summer, the negative aspects of the experimental flood have been reversed by the high, near-constant flows of the past two years.

Further, we have shown that the effects on individual species varied enormously. Some species all but disappeared from the seed bank between 1996 and 1997, while others either increased in abundance or showed no change over the same time period. The life histories of species at either extreme do not allow for easy generalizations. The species we described in the previous section as having unusually large losses and those which showed no impact both included clonal herbs (cattails and rushes) and perennial bunch grasses (waterbent grass and dropseeds). Habitat likewise gives no real clue as to the generality of patterns, since both cattails and rushes are obligate wetland species (Reed 1988). Dropseeds tend to be facultative upland species, and waterbent grass is a facultative

wetland species, but the lack of pattern in wetland species prevents us from drawing any general conclusions from these facts.

Finally, weedy species of concern did disappear as a function of the high flows, according to our methods. However, they were present in such low numbers to begin with that even moderate amounts of spatial and inter-annual variation might have led to our inability to detect their seeds in 1997. We found no seeds of these four species in most of our sites in 1996, and the largest aggregation of any species was seven individuals per site in 1996 (Table 2).

Sources of seed bank patterns

We attribute the observed changes in the February seed bank size and species composition to the 1996 experimental flood. Field observations and data from our studies and others (Kearsley and Ayers 1996, R. Parnell and A. Springer, Northern Arizona University personal communications) indicate that the flood affected the soil surface, either through burial by channel bottom sands or, in a few places, erosion of the surface soils. We believe that the new sand was relatively sterile and did not bring in seeds.

We therefore attribute changes to our measurements of the mid-summer seed banks to the effects of the high, near-constant discharges from Glen Canyon Dam in the rest of 1996 and early 1997. Under conditions of near-constant flows, groundwater elevation tends to equilibrate with river surface elevations (A. Springer, Northern Arizona University, personal communication), so that the high flows of the past two growing seasons would have resulted in readily available groundwater for many species at low and intermediate elevations. The readily available ground water should have made reaching reproductive maturity (for annuals) and large seed crops (for all species) more likely (Harper 1977 Chapter 2, Fenner 1992 Chapter 1, Bonis et al. 1995). Thus the loss of seeds from the seed bank should have been at least partially offset by the higher flows' causing inputs to the site's seed banks.

Alternatively the flood could simply have reworked the sediments and churned the seeds into the soil at similar densities to pre-flood conditions, at which several other factors could have affected seed bank numbers, but we do not believe these to be more than minor factors in this case. First, our estimates of dramatic changes in seed bank numbers could be simply the result of normal spatial and inter-annual variation. Soil seed banks are notoriously variable in desert settings, both spatially and temporally (Reichman 1984, Kemp 1989, Cornelius et al. 1991). However, the fact that we detected the February samples' pattern of loss across all sites indicates that the patter came from a source other than random variation. Second, seed predation could have increased after the flood and then dropped of in late 1996 and early 1997. However, one effect of the experimental flood was the removal of most colonies of harvester ants, the most common seed predator in Grand Canyon (personal observations), so that one would have predicted an increase in seeds available, based solely on predation considerations. Third, seeds could have been drowned by the flood flows so that the February 1997 samples would have shown a dramatic decrease in seed numbers. However, many riparian species, and most wetland species, including rushes, tolerate or require saturated soil during dormancy for periods far longer than the two weeks of high flows in 1996 (Keddy and Reznicek 1982, Smith and Kadlec 1983, Schneider 1994). Thus the impact of the flood waters directly on seeds would have been minimal.

Finally, precipitation patterns could have produced changes in seed numbers we have reported on here through reductions in seed production. Figure 4 shows monthly and total annual precipitation in 1995 and 1996, the years preceding the current study when seeds would have been added to the seed bank. The data (unpublished numbers provided by the National Climatic Data Center and K. Shinkle of Grand Canyon National Park) show that 1995 precipitation was approximately 1 standard deviation above average and 1996 was an exceptionally dry year at more than 7 standard deviations below average. Further, the deviations were in a pattern consistent with the losses and gains in numbers and

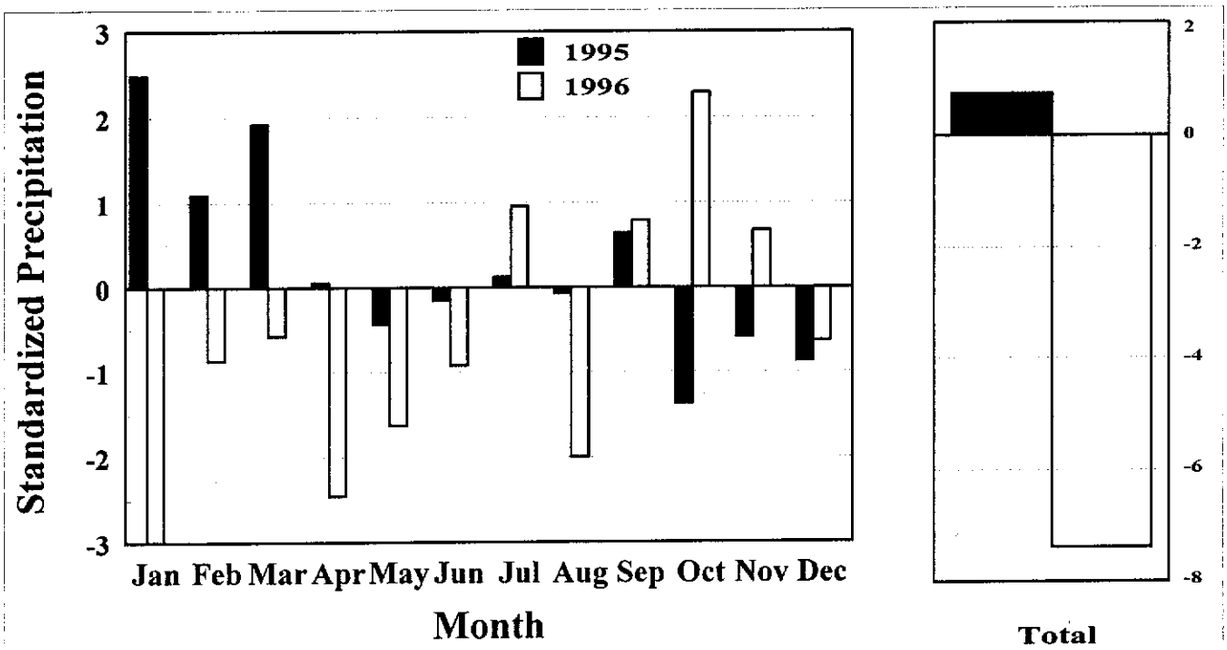

Figure 4. Monthly and annual precipitation at Phantom Ranch, relative to means and standard deviations from the previous 20 years of record. For each data point, the monthly or annual mean was subtracted from the value and the resulting deviation was divided by the standard deviation for that month or for the year.

species richness. Specifically, in 1995, which was the most recent year during which species would have added individuals to the seed bank, rainfall was far above average for the first four months (Figure 4), when many of the annuals would be growing and dropping seeds. By contrast, the late season precipitation was mostly below average, so that seeds germinating at that time would have had reduced growth and reproduction. Combined with the early-season pattern, this may have resulted in high seed numbers for the early 1996 seed bank estimates and lower in the later ones.

During the 1996 growing season, in which some 1997 seeds were produced, the pattern was reversed. Early season rainfall was far below average, and late season monthly total precipitation was generally above average. Thus, this would have resulted in low numbers of 1997 early season seed bank numbers, and an increase in the late season numbers.

We believe that the effects if these precipitation patterns were of secondary importance to the

effects of the flood and high flows for two reasons. First, data from the beach surveys and observations on particle size changes in the sites showed that much of the riparian habitat was buried under medium-fine coarse sand from the channel bottom and that most of the herbaceous species were buried and / or flattened (Kearsley and Ayers 1996, Kearsley et al. 1996). Any effects of rainfall in 1995 and 1996 would have been only a modification of the effects of this burial, perhaps a reinforcement by the dry conditions of the burial under more or less sterile sand. And second, some of the species which seem to have recovered in 1997 were perennials, like cattails, whose root systems were well below the soil surface and likely unaffected by additional rain in 1996. Thus it is far more likely that the recovery of species in the seed bank resulted from greater access to elevated groundwater than increased surface water from rainfall.

Importance of seed bank patterns

We feel that the patterns we have documented in the seed banks of the nine monitoring sites are important for a number of reasons. First, seedbanks represent the potential for regeneration of vegetation patches within sites. In tidal freshwater wetlands, such as those in Grand Canyon, seethe seed bank acts as a conservative force. Seeds and propagules of species present in the extant vegetation allow recolonization of these species after disturbances or the mortality of adults (Leck and Graveline 1979, Leck and Simpson 1987). In other riparian habitat types, the seed bank acts as a creative force, in part driving successional patterns (van der Valk 1981, Keddy and Reznicek 1982, Smith and Kadlec 1983). Therefore, the recovery of seed banks after their burial and scour in the monitoring sites represents the recovery of both the ability of wetland patches to recover and the successional trajectory of other riparian patches.

Second, in many habitat types, the seed bank allows the storage of biodiversity in local plant assemblages. Seeds of many species remain in the soil until whatever germination inhibition has been

enforcing dormancy (Fenner 1985 chapter 5, Keddy and Constabel 1986). This release, whether due to reservoir drawdown, erosion of overlying soil layers, or disturbance of the soil surface, often produces a flora which has not been present since the last such event (Keddy and Reznicek 1982, Smith and Kadlec 1983, Schneider 1994). Thus, a recovering seed bank is important in the creation of temporally distinct assemblages by which an increase in diversity can be maintained.

Third, a recovering seed bank will lead to the recovery of the herb layer which was lost in the experimental flood of 1996. Most of these species were annuals which, by definition, must be regenerated each year. The perennial grasses, which represented most of the rest of this layer, were also lost from most parts of the riparian habitats, and their recovery depends on their dispersal by seed into these habitats and the subsequent establishment.

Finally, the loss of dormant seeds on or near the soil surface during the experimental flood likely has had impacts on seed predators and higher trophic levels. Riparian habitats are far more productive than other areas of Grand Canyon (references in Stevens et al. 1996). We have conservatively estimated that the top 5 cm of soil averaged approximately 5,000 seeds / m^2 in riparian patches, and as many as 25,000 / m^2 in some patches. Further, because most of the seeds were from annual species, whose seeds tend to be rather large (Fenner 1985, Keddy and Constabel 1986, Baker 1990), this represented a large resource for seed-eating insects, birds and rodents. The loss of this resource may have had serious implications for these species and higher trophic levels.

MANAGEMENT RECOMMENDATIONS

Seed banks are an important component of plant communities. In high-disturbance areas, such as the river corridor of Grand Canyon, they determine much of the community trajectory in patches after disturbances. Monitoring of this resource should continue in order to document the changes to the seed bank in this dynamic system.

We believe that the further recovery of the seed banks in riparian patches will depend on two aspects of dam operations. First, much of the recovery of seed banks we documented was a function of near-constant discharges from Glen Canyon Dam. We would therefore recommend that flows during the growing season (March through September) fluctuate very little around some high level, perhaps the 21 to 24 kcfs of this past year. Wetland plants and other with their root systems in the groundwater will grow more vigorously and produce more seed with the consistently available groundwater. Ground water levels under fluctuating flows do not reach levels as high as those attained during steady, or near-steady, flows (A. Springer, N.A.U. Geology, personal communication).

Second, annual variation in the mean water level will likely allow for increased plant species diversity. As seen during both reservoir drawdowns and natural fluctuations in water levels, species which are less competitive but which have seeds that are more tolerant of saturated soil conditions may find refuges in a near-shore area that is only exposed for part of the year (Baker 1990, Bonis et al. 1995). Thus, a seasonal change in the average water level should create a mosaic of habitats in time which allows greater species diversity to develop, so long as the flows are more or less steady.

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Appendix A

Germination Data from February 1997 Soil
Seed Bank Samples

The data are organized by site and arranged in a series of columns whose identities are as follows:

POLYGON: The number which identifies that polygon in that site. These are of the form: MMMPPP where "MMM" is a three-digit site location by river mile and "PPP" is a three digit polygon number which corresponds to numbers assigned during vegetation mapping during the past three years. For example, data from polygon number 17 in the monitoring site at river mile 51.2 L would be listed as 051017.

SPECIES: An acronym for species, usually four to six letters long. These acronyms are, together with the species they identify, are listed in Appendix A of both the Kearsley and Ayers (1996) flood report and the Kearsley et al. (1996) vegetation monitoring report. Taxonomy is according to Kartesz et al. (1990).

NUMBER: The number of seedlings of that species which germinated in soil samples from that polygon. Numbers are pooled across samples within the polygon.

NOTE: In the interests of saving paper and costs in the production of this draft report, we have included the data from one site only in this appendix.

Site: 43.1 Left

POLYGON	SPECIES	NUMBER
043002	BRRU	3
043008	ENFA	1
043010	BAEM	1
043010	BOSA	2
043010	MUAS	4
043011	GNCH	1
043011	PLMA	1
043011	SPCR	18
043011	SPCR	7
043011	TYDO	4
043011	VEAM	17
043015	BOSA	2
043015	GNCH	1
043016	JUBA	1
043018	CAMU	15
043018	GNCH	5
043018	TYDO	3
043019	BAEM	1
043019	GNCH	1
043024	COCA	1
043027	SPCR	9
043028	BRRU	2
043028	SPCR	2
043032	CHNI	1
043032	SPCR	1
043032	VEAM	1
043041	BAEM	3
043044	SPCR	1
043048	GNCH	2
043059	GNCH	7
043059	SPCR	1
043060	BAEM	1
043060	BRRU	1
043060	SPCR	5
043064	BAEM	1
043064	GNCH	1
043064	SPCR	4
043064	TYDO	2
043091	SPCR	1
043092	DYPE	5
043092	SPCR	1

Appendix B

Germination Data from June 1997 Soil
Seed Bank Samples

The data are organized by site and arranged in a series of columns whose identities are as follows:

POLYGON: The number which identifies that polygon in that site. These are of the form: MMMPPP where "MMM" is a three-digit site location by river mile and "PPP" is a three digit polygon number which corresponds to numbers assigned during vegetation mapping during the past three years. For example, data from polygon number 17 in the monitoring site at river mile 51.2 L would be listed as 051017.

SPECIES: An acronym for species, usually four to six letters long. These acronyms are, together with the species they identify, are listed in Appendix A of both the Kearsley and Ayers (1996) flood report and the Kearsley et al. (1996) vegetation monitoring report. Taxonomy is according to Kartesz et al. (1990).

NUMBER: The number of seedlings of that species which germinated in soil samples from that polygon. Numbers are pooled across samples within the polygon.

NOTE: In the interests of saving paper and costs in the production of this draft report, we have included the data from one site only in this appendix.

Site: 43.1 L

POLYGON	SPECIES	NUMBER
043003	BRRU	10
043003	GNCH	4
043003	TYDO	5
043008	BRRU	3
043008	GNCH	1
043008	JUBA	2
043011	BRRU	1
043012	GNCH	2
043012	JUTO	1
043012	TYDO	1
043015	JUAR	1
043015	TARA	1
043016	PACA	1
043026	SPCR	2
043028	GNCH	3
043028	TYDO	3
043028	VEAM	1
043031	BRRU	1
043031	MUAS	1
043032	GNCH	15
043063	BRRU	1
043063	VEAM	1
043091	TYDO	1