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**SEASONAL FLOODING  
AND RIPARIAN FOREST RESTORATION  
IN THE MIDDLE RIO GRANDE VALLEY**

**Final Report**

Cooperative Agreement 14-16-0002-91-228

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## ABSTRACT

Water management and flow regulation along the Middle Rio Grande during this century has decoupled the linkage between the floodplain and the river and resulted in extensive changes in the riparian forest ecosystem. The elimination of flooding has disrupted the functional integrity of these **disconnected** forests and contributed to the decline of the Rio Grande Valley cottonwood. This study suggests that re-establishing a regime of seasonal flooding in the cottonwood forest lining the river, known locally as the *bosque*, will initiate a **re-organization** phase of restoration characterized by distinct changes in biological populations and ecological processes. Three years of experimental, seasonal flooding at the Bosque del Apache National Wildlife Refuge in central New Mexico has increased leaf and wood decomposition, growth of mature cottonwood trees, and populations of soil bacteria and fungi, and has also initiated a restructuring of surface-active arthropod populations. Groundwater chemistry changes suggest that overland flooding has begun to decrease the accumulation of carbon on the forest floor by saturating organic litter; concurrently, ammonium rich water has been made available for soil microflora and sorptive processes in this previously nitrogen-limited system. Comparisons with a naturally-flooded bosque provide estimates of **steady-state** conditions within the riparian forest. Data from this site suggest that long-term annual flooding significantly decreases the accumulation of wood and leaf litter on the forest floor.

Based on these results, we propose the following four-step approach to **partial restoration** of the Middle Rio Grande bosque, with an emphasis on re-establishing basic riverine-riparian functioning and selected restoration of vegetation: (1) establish an extensive ecosystem monitoring program along the Rio Grande; (2) initiate carefully regulated seasonal overbank flooding or its equivalent at sites selected both for the maintenance of mature forests and the establishment of new ones; (3) manage riparian forest sites to improve habitat diversity; and (4) re-create diverse wetland sites both inside and outside of the present levee system.

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## INTRODUCTION

Overbank flooding was once an integral component of riparian forest ecosystems along rivers in the arid Southwest, influencing a variety of abiotic and biotic processes (Stromberg et al. 1991). The hydrology of the Rio Grande was historically characterized by seasonal flooding, primarily in response to spring snow melt from high mountain catchments or from intense summer thunderstorms (Corps of Engineers 1958, Crawford et al. 1993). This relatively sinuous and braided river meandered through the valley, bordered by a mosaic of vegetation types including cottonwood (*Populus deltoides* ssp. *wislizenii* (Wats.) Eckenwalder) forests in various successional stages, wet meadows, marshes, and ponds. However, water management during this century has greatly altered various aspects of the floodplain ecosystem (Crawford et al. 1993). Dam construction in the upper basins and river channelization have prevented annual flooding in recent decades (Bullard and Wells 1992), and groundwater drainage, initiated to decrease waterlogging and salinization in heavily irrigated floodplain soils, has lowered watertables (Scurlock 1993). Structural changes in the riparian vegetation were rapid and easily detected. For example, the valley lost over half its wetlands in just 50 years (Crawford et al. 1993). Similarly, cottonwood germination, which requires scoured sandbars and moisture provided by high river flows (Stromberg et al. 1991, Scott et al. 1993) has decreased, resulting in limited establishment of new trees and a predicted decline in the regional population (Howe and Knopf 1991). Meanwhile, invasion by exotic plants such as tamarisk (*Tamarix ramosissima* Ledeb.) and Russian olive (*Elaeagnus angustifolia* L.) has altered the species composition in the valley; without changes in the current water management, these exotics may dominate riparian forests within the next 50 to 100 years (Howe and Knopf 1991).

How water regulation has affected ecosystem functioning within the Rio Grande riparian forest, known locally as the *bosque*, is less obvious and not well documented. For example, the buildup of wood and leaf litter on the forest floor may prove to be a key regulator of ecosystem dynamics. This undecomposed organic matter immobilizes essential nutrients, particularly carbon and nitrogen, effectively eliminating them from the nutrient cycle. Water from low intensity spring floods may increase the rate of decomposition of this stored litter, thereby freeing nutrients essential to plant growth. This primary production in turn supports consumers, from fungi to birds and mammals, thus affecting the health of the entire ecosystem. An additional consequence of litter buildup in the absence of flooding and decreased decomposition may be an increased potential for fire. Fires in the *bosque* have increased in recent years, which may in part reflect this buildup of fuel (Stuever et al. in review). Annual floods should indirectly decrease the risk of fires by increasing decomposition rates and thus reducing the standing fuel supply; floods also may directly decrease fire risk by clearing out woody debris and wetting materials retained during the hot summer months.

This study began in 1991 to investigate the effects of flooding on both structural and functional components of the Rio Grande riparian ecosystem. Here we present the results of five years of study in riparian forest sites at the Bosque del Apache National Wildlife Refuge in central New Mexico. These sites are separated from the river by a levee and have been isolated from flooding for at least 50 years. Included are data reflecting three seasons of experimental flooding at one mixed-cottonwood site and two experimental floods at a tamarisk-dominated site. Data for these flood sites are compared with data collected at similar non-flooded control sites, as well as with data collected within each site during two or three years of sampling prior to experimental flooding. In addition, a pair of sites in mixed-cottonwood forest within the levee and immediately adjacent to the river was added during the fourth year of the study; one of these floods directly from the Rio Grande when run-off is high, while the other remains unflooded. This riverside flood site provides a reference against which to compare the experimental flood site and thus serves as an estimate of the eventual goal for restoration efforts.

This document concludes with our recommendations for partial restoration of the Rio Grande riparian forest using manipulated flooding. Our goal is to provide sound, ecologically based recommendations for restoration that are possible to implement within the current social and political conditions along the Valley. This will require a long-term commitment from all interested in the continuance of the Rio Grande bosque, including an interagency structure dedicated to long-term monitoring of the bosque ecosystem throughout the valley. Here we highlight key ecosystem components, based on five years of research, that we believe are essential to monitor in forest sites situated throughout the length of the Middle Rio Grande Valley in order to determine the ecosystem health of these sites and to identify potential locations for restoration efforts.

## METHODS

### SITE DESCRIPTION

Four study sites were established during the summer of 1991 at Bosque del Apache National Wildlife Refuge, elevation approximately 1400 m, located about 5 km south of San Antonio, Socorro County, New Mexico (Figure 1). The Refuge covers approximately 14.5 km of the Rio Grande and its associated riparian vegetation, including both mixed cottonwood forests and extensive tracts of tamarisk. Two study sites were selected in mixed cottonwood forests ("cottonwood" sites) and two in nearly pure tamarisk stands ("tamarisk" sites). All four sites lie outside the river levee and have been isolated from flooding for more than 50 years. For each forest type, one site was designated as the "control" site, to remain unflooded, and one as the "flood" site. Throughout this report, these four sites are referred to as "Cottonwood Control", "Cottonwood Flood", "Tamarisk Control", and "Tamarisk Flood".

Both cottonwood sites and Tamarisk Flood were in a strip of continuous forest, 200 - 300 m wide, immediately west of the continuously filled Low Flow Conveyance Channel that parallels the river levee, approximately 0.5 km west of the Rio Grande (Figure 1). The strip varies from areas dominated by cottonwood to nearly pure stands of tamarisk. Cottonwood Flood was 3.7 km south of Cottonwood Control, while Tamarisk Flood was 3.5 km south of Cottonwood Flood. In August 1994, two additional sites were added that lie within the levee, in a second strip of riparian forest, 100 - 200 m wide, and approximately 200 m east of the cottonwood sites and Tamarisk Flood (Figure 1). This strip of forest also contains sections dominated by cottonwood interspersed with stands of tamarisk and is bounded on its east side by the Rio Grande. One site, "River Flood", is inundated directly from the river during high flows. The second, "River Control", is isolated from flooding by a groin dike that extends perpendicular to the river. West of these linear forests are agricultural fields and intermittently flooded wetland areas, with scattered cottonwood and tamarisk but without large continuous stretches of cottonwood forest. Chihuahuan upland vegetation lies west of the fields, approximately 2 km west of the study sites.

Tamarisk Control was approximately 5.8 km south of Tamarisk Flood, 1.5 km west of the river, and 0.5 km east of Chihuahuan upland vegetation (Figure 1). The site was within an extensive stand of tamarisk with no continuous cottonwood forests within at least one km of it. A large, continuously flowing water conveyance channel ran between the stand of tamarisk containing the study site and the upland vegetation.

The intensive study areas at Cottonwood Control and Cottonwood Flood include approximately 3.1 ha, centered on a 200-m diameter circle, with 12, 100-m transect lines radiating out from the center (Figure 2). This "web" design was established for small mammal trapping; for convenience, other sampling procedures were distributed within the structure of this web. The canopy of these is dominated by Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*), ranging from 8 m to 15 m in height; the

subcanopy consists of Goodding willow (*Salix gooddingii* Ball.) and tamarisk (*Tamarix ramosissima*). Understory shrubs include seepwillow (*Baccharis glutinosa* Pers.) and New Mexico olive (*Forestiera neomexicana* Gray) in varied proportions, as well as scattered Russian olive (*Elaeagnus angustifolia*), screwbean mesquite (*Prosopis pubescens* Benth.), wolfberry (*Lycium torreyi* Gray) and desert indigobush (*Amorpha fruticosa* L.). A variety of herbaceous understory species also occur at the sites (Appendix C - 1).

At each tamarisk site, we established a grid of 10 parallel transects, each 60-65 m long and 50 m apart (Figure 3). All sampling procedures were conducted within these grids, resulting in an intensive study area of approximately 2.7 ha at each tamarisk site. These two sites consist nearly exclusively of tamarisk, with heights ranging from 3 m to 7 m. A few scattered seepwillows are present, along with a patchy herbaceous understory under openings in the tamarisk canopy. Tamarisk Control includes a small area with scattered cottonwoods.

The river sites were too narrow for the web design used at the established cottonwood sites, so transects were used as at tamarisk sites. Each river site has ten 60 m transects, with adjacent transects separated by 20 m. These study sites cover approximately 1.1 ha. The orientation of sampling procedures at these sites corresponds to that used at the tamarisk sites (Figure 3). These sites have a primarily cottonwood canopy, with understory vegetation including tamarisk, seepwillow, New Mexico olive and Russian olive. Understory vegetation is sparse, particularly at River Flood where the overstory is more complete.

## EXPERIMENTAL FLOODING

After two years of collecting baseline data, Cottonwood Flood was experimentally flooded for approximately one month during each of three years, with the assistance of Refuge personnel. Floods occurred 17 May - 12 June 1993, 19 May - 19 June 1994, and 17 May - 17 June 1995, and were timed to match the historical timing of peak flow for the Rio Grande, based on the mean annual hydrograph for the period 1889 - 1990 recorded at the USGS Gaging Station at Embudo, New Mexico (Slack et al. 1993). Water diversion structures installed by Refuge personnel allowed water to be provided from a riverside canal; this included a combination of water diverted directly off the Rio Grande, irrigation return flows from agricultural fields and ground water recharge accumulated in the nearby Low Flow Channel (Taylor et al. 1994). Floods covered approximately 10 ha of the surrounding riparian forest. Cottonwood Control remained unflooded throughout the study. Surface water depth during inundation varied across the Cottonwood Flood site due to topographic variation; depth at peak flood ranged from nearly 20 cm to 200 cm, with an average of about 50 cm. Daily surface water heights measured in a depression near the north end of the site are presented in Figure 4.

River Flood was flooded directly from the Rio Grande. We did not monitor the duration of the early summer flood at this site in 1994. A second flood occurred in August of that year and lasted for a few days. During 1995, flooding lasted for approximately 2.5 months from mid-May through late July; surface water height measured on the first transect averaged about 20 cm throughout the flood (Figure 4). Most of River Control was isolated from flooding by a groin dike, although the peripheral area was partially inundated.

## ABIOTIC FACTORS

### Meteorological conditions

Meteorological variables at each site were monitored with a Campbell Scientific CR10 data logger housed in a water-proof casing. A meteorological station was installed at each cottonwood site in October 1991 and located at each tamarisk site from October 1991 through late December 1994. Stations at tamarisk sites were then moved to the river sites, where they remain. Data loggers continuously monitor air temperature (2 m above ground, sheltered from direct sunlight), ground temperature (at 4 cm and 15 cm below the surface), soil moisture (at 15 cm below the surface), and wind speed (at 2 m above the ground). Data were downloaded approximately once a month and transferred to a mainframe computer system for archiving and analysis. Annual data summaries include daily maximum and minimum air temperature, daily maximum and minimum soil temperature at two depths, soil moisture potential and daily mean wind speeds. These summaries provide estimates of weather conditions at each site throughout the year. Rainfall data were provided by the U.S. Fish and Wildlife Service (recorded at Refuge headquarters) and by the UNM Long Term Ecological Research (LTER) project (recorded in cottonwood forest near the north Refuge boundary, on the east bank of the Rio Grande).

### Hydrology and water chemistry

Hydrological studies were done in collaboration with Dr. H. Maurice Valett and colleagues at the University of New Mexico, with funding from the National Science Foundation. In February and March 1993, five groundwater monitoring wells were installed at each cottonwood site and four wells were installed at each tamarisk site. Twelve additional wells were installed at each cottonwood site in April 1994, making a total of 17 wells at each of those sites. Seven wells were installed at each river site in March 1995. Wells were distributed throughout each site and each consisted of 5-cm diameter PVC pipe screened for 1-2 m beneath the water table. A single well at each cottonwood site was equipped with an automated pressure transducer in 1994 to electronically record changes in water table elevation. In remaining wells, water table elevation and groundwater samples were obtained every 3-4 days for two weeks before flooding, throughout the duration of the flood, and for 10 days following the end of the flood. Depth to water table was measured at the five original wells at each cottonwood site, as well as at tamarisk and river sites, once every other month during the non-flood periods in 1994 and 1995. During flooding, dikes and input and output flumes allowed for gauging of the surface water flow. Surface water samples were taken at flumes and from interior regions near groundwater wells. All samples were analyzed for dissolved organic carbon (DOC), ammonium-nitrogen ( $\text{NH}_4\text{-N}$ ), nitrate-nitrogen ( $\text{NO}_3\text{-N}$ ), soluble reactive phosphorus (SRP), dissolved oxygen (DO), and temperature. Methods for chemical analyses follow Keith (1990).

Rates of forest floor metabolism at cottonwood sites in 1994 and 1995 and at River Flood in 1995 were analyzed in metabolic chambers constructed of 30-cm diameter PVC pipe inserted 10 cm beneath the litter layer, and equipped with sampling ports. At Cottonwood Control, five chambers measuring "dry" metabolism quantified  $\text{CO}_2$  liberation during 4-hour incubations. At Cottonwood Flood, five chambers incubated and circulated ambient flood water. Water, DO, and  $\text{CO}_2$  samples were obtained throughout the incubations to assess rates of respiration and changes in nutrient concentrations. At each site, chambers were placed in close proximity to each other on relatively uniform surfaces of undisturbed cottonwood leaf litter. Before the onset of flooding, "dry respiration" rates at both sites were determined in the chambers.

## Soils

Dr. Carleton White at the University of New Mexico and Dr. Thomas Kieft at New Mexico Institute of Mining and Technology provided soil analyses. Ten soil samples were collected from stratified locations within each site. Samples were collected from cottonwood sites on 22 September 1992, 2 September 1993, 26 September 1994, and 20 October 1995, and from river sites on 26 September 1994 and 20 October 1995. Tamarisk sites were sampled on 22 September 1992. Samples were collected by driving a 7.8-cm diameter corer to a depth of 10 cm. Samples were sieved through a 2-mm sieve and the larger fragments discarded. Soils were analyzed for the following properties: field water content; organic matter content; water holding capacity (WHC); mineralizable  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-H}$ , and their sum; extractable cations (Na, K, Ca, Mg); cation exchange capacity (CEC); sodium absorption ratio (SAR); texture (% sand, silt, and clay); pH; conductivity; percent moisture; total organic carbon, biomass carbon and their ratio; basal respiration; metabolic quotient; total nitrogen; and total phosphorus. Methods for these procedures follow Richards (1969), Anderson and Domsch (1978), and Page (1982).

## Silt deposition

We quantified silt deposited at Cottonwood Flood and River Flood in 1995 by placing ceramic tiles in various locations within each site and measuring the silt collected on each during inundation. Prior to the floods at both sites, ten 20 x 20 cm ceramic tiles were placed in each of four types of locations within each site. Ten tiles were placed on the upstream side of an obstruction (such as a fallen log or pile of sticks) and these were paired with ten tiles placed on the downstream side of the same obstruction. Ten tiles were placed within the main channel area observed at River Flood and within low areas of Cottonwood Flood known to remain submerged. These were paired with tiles placed upslope from the channel, but still in areas that were inundated during the flood. After flood waters had receded at each site, we collected the sediment-laden tiles, placed separately in plastic bags and brought them to the lab. There, all sediment was scraped off the upper surface of each tile into a weigh boat, oven-dried at 60°C until constant weight (up to several weeks for samples from River Flood) and weighed. The sediment included some leaves and other organic debris deposited during the flood.

The dry-weight of silt deposited per  $\text{m}^2$  of forest floor per day was estimated assuming 30 days of inundation at Cottonwood Flood and 45 days of inundation at River Flood. Averages were calculated for each location within each forest (before obstruction, after obstruction, in channel, and upslope). Differences in the weight of silt deposited in each of the four locations were compared within each site using a Kruskal-Wallis test, and the overall amount of silt deposited was compared between sites using Wilcoxon Rank Sum tests (NPAR1WAY procedure, SAS Institute, Inc. 1989).

## FOREST FLOOR LITTER: PRODUCTION, DECOMPOSITION AND STORAGE

### Litter production: litterfall traps

Litter production was monitored at all sites using litter traps consisting of 50-cm diameter by 10-cm deep rubber tubs left in place for continuous collection of litterfall between September and March each year beginning in 1991. Twelve traps were present at each site and contents were collected monthly. At River Flood, the late August 1994 flood inundated traps, thus the September collection at that site may

have missed some leaf fall. To alleviate this problem in the future, litterfall traps at River Flood were placed approximately 3 feet above ground on PVC pipe stands to keep samplers above water level.

Samples from all sites were oven-dried at 60°C for 48 hours and weighed. The cumulative dry-weight (gms / m<sup>2</sup>) for the entire litter sample (leaves of all plant species, twigs, reproductive parts) was plotted against time for cottonwood and tamarisk sites during five litterfall seasons. Since we observed annual variation in total litter production, this was compared between sites within each year using paired t-tests (TTEST procedure, SAS Institute, Inc. 1989).

To better understand differences between sites in litter production, samples from the cottonwood and river sites were sorted during 1994-95 and 1995-96 seasons to separate cottonwood leaves from other materials in the litter. Whole cottonwood leaves ( $\geq 2/3$  of the leaf present) were counted and weighed for each sample. The monthly cumulative dry-weights numbers of cottonwood leaves were plotted against time to determine annual litter production at cottonwood and river sites during the last two seasons. Cumulative litter measurements at cottonwood and river sites during 1994-95 accurately predicted the cumulative weight of cottonwood leaves (CC,  $r^2 = 0.94$ ,  $P = 0.0001$ ; CF,  $r^2 = 0.89$ ,  $P = 0.0001$ ; RC,  $r^2 = 0.91$ ,  $P = 0.0001$ ; RF,  $r^2 = 0.99$ ,  $P = 0.0001$ ; CORR procedure, SAS Institute, Inc. 1989); therefore, we estimated the total biomass of cottonwood leaves produced during the first three seasons at cottonwood sites based on total litterfall each year using the regression equations:

$$\text{CC, cumulative weight of leaves} = (0.707) \times (\text{cumulative weight of litter}) - 1.052$$

$$\text{CF, cumulative weight of leaves} = (0.690) \times (\text{cumulative weight of litter}) - 1.134$$

Then, to better illustrate relative differences between cottonwood control and flood sites before and after experimental flooding, we calculated intersite differences in the estimated total cottonwood leaves per m<sup>2</sup> collected at flood and control sites (total biomass of leaves at Cottonwood Flood - total biomass of leaves at Cottonwood Control) each year. Similar differences in leaf production between river sites during 1994-95 and 1995-96 were calculated for comparisons. These values were plotted across years to illustrate relative changes in leaf production between sites due to flooding.

In addition, variation in the size of individual leaves at cottonwood and river sites was estimated in 1994-95 and 1995-96 by measuring the width and mass in a subsample of 10 whole cottonwood leaves from each tub (or as many as present if fewer than 10) each month at each site, giving up to 120 leaves measured per site. Leaf width was strongly correlated with the area measured by a leaf area meter (model CI-201; CID, Inc.) for leaves collected at the two cottonwood sites in October 1994 ( $r^2 = 0.96$ ,  $P = 0.006$  after Bonferroni adjustment); therefore, we used the width measurements as estimates of leaf area, based on the regression,  $\text{area} = (\text{width} \times 0.55) - 14.25$ . We calculated specific mass as mass per unit area (gms / cm<sup>2</sup>).

### Leaf decomposition

Leaf decomposition bags were placed at all sites each fall beginning in 1991 and were collected periodically throughout the following year to measure rates of leaf decomposition. Bags were made of 15 x 15 cm fiberglass screening and contained 5 grams of either cottonwood or tamarisk leaves to be used in each forest type, respectively. Leaves were collected in mid-October each year, prior to abscission, from at least 10 individual trees of each species at a site near the study areas, and were air dried to constant weight (usually several days) before being placed in the mesh bags. In late October or early November each year, 20 cottonwood bags were placed at each cottonwood site and 20 tamarisk bags were placed at each tamarisk site. The first sets of bags were installed at the river sites in November 1994. Bags were arranged in a five by four bag grid at each site, and all were covered with a hardware cloth cage to deter



animal interference. Five bags were collected from each site on each of four dates each year (see Appendix B - 5 for dates). The first collections were made the same day the bags were placed at the sites, to correct for handling loss to bag contents during the installation. Additional collections were made the following April (prior to flooding), June (immediately after flooding) and November. The post-flooding "June" collections at the river sites in 1994 were actually made in early August, since River Flood remained inundated until late July. In the lab, the contents were removed from collected bags, dried at 60°C for 48 hours, weighed, ground using a Wiley Mill, and subsamples were ashed in a 500°C muffle furnace for two hours to determine ash-free dry-weight.

Ash-free dry-weights of leaves in each forest type for each collection date each year were compared using Wilcoxon Rank Sum tests (NPAR1WAY procedure, SAS Institute, Inc. 1989). Significance values were Bonferroni-adjusted for multiple tests within each year. To assess site differences in the rates of decomposition between each pair of collection dates (inter-sample periods), we calculated the slope of each line between collections. The rate of change in leaf weight was considered to be the difference between the ash-free dry-weight of each bag and the mean ash-free dry-weight for the previous collection; these were averaged to give a mean rate for each site during each inter-sample period. These calculated rates were compared between sites for each inter-sample period and among years within each site for each inter-sample period using Wilcoxon Rank Sum tests and Kruskal-Wallis tests, respectively (NPAR1WAY procedure, SAS Institute, Inc. 1989).

To estimate the direct influence of leaching on decomposition, we measured weight changes of leaves placed in water for 24 and 48 hours in the laboratory. Nine samples, each containing 5 grams of air-dried cottonwood leaves, were made as for leaf decomposition bags, except that these were not placed within mesh bags as described above. Instead, three samples were immediately oven-dried at 60°C for 48 hours to determine the original moisture content. The remaining six samples were placed in separate beakers, each with 1000 ml of distilled water, and covered with parafilm. Beakers were placed on a Fisher Scientific Electronic Stirrer (model 2008) set at 500 rpms to simulate water movement during flooding and to prevent formation of a boundary layer of air around the leaves. Three samples were removed after 24 hours and the remaining three after 48 hours. The water was first decanted off each sample, then remaining water was removed using a vacuum funnel. Leachate was collected and analyzed for dissolved organic carbon. Leaves were placed in a 60°C oven for 48 hours, and re-weighed. Initial weights were corrected for moisture content and the percent loss of initial dry-weight was calculated for each sample. These were averaged across the three samples for each time to give the mean percent of initial dry-weight lost over 24 and 48 hours.

### Log decomposition

A series of *Populus* logs was placed at cottonwood control and flood sites on 20 June 1991 to estimate the rates of wood decomposition in flooded and non-flooded forests. Logs were cut into 1-m sections from fallen trees located within an area several km south of the study sites. These dead trees were supported above the ground by the branches of other trees that had fallen previously. Initial diameters averaged  $13.04 \pm 0.26$  cm at Cottonwood Control and  $12.74 \pm 0.29$  cm at Cottonwood Flood. Single disks approximately 3 cm thick were removed from both ends of each log as they were cut, then analyzed in the lab for initial moisture and organic content. Logs were initially very dry and without bark, but of sound wood. Each was weighed in the field, and 20 were placed in a row at each of the cottonwood sites; logs at Cottonwood Flood were anchored using rebars to prevent movement during flooding. Four logs were collected from each site in April 1993, prior to experimental flooding. Additional sets of four logs, representing two and three years of annual flooding at Cottonwood Flood, respectively, were collected from each site in November 1994 and 1995. Another series of logs was

installed at river sites on 19 April 1994. Diameters of these logs averaged  $13.22 \pm 0.49$  cm at River Control and  $15.42 \pm 1.70$  cm at River Flood. A single collection was made at these two sites in November 1995, reflecting a single, 2.5 month flood at River Flood. Logs were initially processed as at cottonwood sites.

Logs collected from all sites were oven-dried at 60°C until they reached constant weight (2 - 3 weeks) and re-weighed. Three disks were cut from each log, one at each end and one at a random location along the log. Several ground samples were taken from each disk using a power drill. All ground samples for each log were combined and ashed in a 500°C muffle furnace for two hours to determine the ash-free dry-weight of each log. For logs collected in 1993, 1994, and 1995, the percent of the initial ash-free dry-weight remaining was recorded and used to calculate an average for each site. The mean percent of the initial weight remaining was then compared between sites for 1993 (prior to flooding), 1994 (after two floods) and 1995 (after three floods) using Wilcoxon Rank Sum tests (NPAR1WAY procedure, SAS Institute, Inc. 1989). Decay rates were calculated based on the single exponential model discussed by Olson (1963):

$$y_t = y_0 e^{-kt}$$

where  $y_0$  is the initial mass of material,  $y_t$  is the mass left at time  $t$ , and  $k$  is the decay rate constant. This model assumes uniform density in the logs.

### Forest floor litter and wood storage

**Forest floor litter:** Samples of the standing stock of organic matter were collected from the forest floor at cottonwood and tamarisk sites each spring and fall, beginning in September 1991. Sampling at river sites was begun in September 1994. Collection dates are given in Appendix B - 7. During each collection, ten 10 x 10 cm samples, each including litter taken down to the mineral soil layer, were collected from randomly chosen locations distributed throughout each site. Samples were returned to the lab, dried in a 60°C oven to constant weight, and weighed. Subsamples were ground using a Wiley Mill and ashed at 500°C in a muffle furnace for two hours to determine the ash-free dry-weight of organic matter in each original sample. Depositional layering of sediment during flooding at River Flood resulted in clay and mineral soil mixed with litter in samples collected in September 1994; due to difficulties in differentiating the lower limit of litter for these samples, they were excluded from analyses. The average ash-free dry-weight of organic litter was calculated for each collection at each site. Intersite differences in mean litter storage between flood and control sites were calculated for cottonwood and tamarisk sites for each collection, and these were plotted across time to determine relative changes in litter storage in response to flooding. Ash-free dry-weight was compared among cottonwood and river sites for 1995 using a Kruskal-Wallis test for each collection (NPAR1WAY procedure, SAS Institute, Inc. 1989).

**Biomass of woody debris:** Woody biomass was estimated at cottonwood and river sites following the linear and planar intersect methods of Van Wagner (1968) and Brown (1971, 1974). Wood on the ground was measured along 20 sample transects distributed throughout each of the four study sites; each transect extended 2 m above the ground. Snags were not counted. Each piece of wood intersecting the transect was defined as either fine woody debris (FWD,  $\leq 2$  cm diameter) or coarse woody debris (CWD,  $> 2$  cm diameter). FWD was classified by diameter size (0 - 0.5 cm, 0.51 - 1.0 cm, 1.01 - 2.0 cm) and the number of intersections of each class was summed over transects 2-m in length for each of the smallest two classes and 5 m in length for the largest class. CWD was counted along 15-m long transects. Each piece of CWD was classified by origin as *Populus*, *Tamarix*, *Baccharis*, and "other", and decomposition

class as I (slight/none) = slight or no bark slippage, wood sound, and little or no decay throughout if split; II (moderate) = partial or complete bark slippage, decay extending to core, split wood with center decay but sound outer layers, and III (advanced) = partial or complete bark slippage, decayed throughout, and also all rotten wood. For each piece of CWD, the diameter at the point of intersection was measured.

Density was estimated for FWD based on measurements of diameter and mass using preliminary samples oven-dried at 60°C to constant weight; all species were combined in each size class and extent of decomposition was not considered. These values were 0.485 g / cm<sup>3</sup> (0.0 - 0.5 cm diameter), 0.532 g / cm<sup>3</sup> (0.51 - 1.0 cm diameter) and 0.506 g / cm<sup>3</sup> (1.01 - 2.0 cm diameter). Densities for CWD were estimated based on measurements of oven-dried samples for each of the three species and three decomposition classes, with mean values of these used for pieces not identifiable to species (Appendix B - 8).

Woody biomass was estimated following formulas of Van Wagner (1968) and Brown and Roussopoulos (1974):

For FWD, 0-2.00 cm diameter:

$$mass(kg/ha) = \frac{1.2337 \times 10^5 S d_q^2 n}{L}$$

where S = mean density (g / cm<sup>3</sup>), d<sub>q</sub><sup>2</sup> = quadratic mean diameter (cm), n = number of intersections per sample plane, and L = length of sample plane (cm). Quadratic mean diameters (average squared diameters) were calculated from preliminary sample measurements throughout the bosque sites.

For CWD, > 2.00 cm diameter:

$$mass(kg/ha) = \frac{1.2337 \times 10^5 S_x \sum d_q^2}{L}$$

where S<sub>x</sub> = mean density for each species based on decomposition stage, Σd<sub>q</sub><sup>2</sup> = sum of individual squared diameters, and L = length of sample plane.

Biomass of FWD, CWD and total woody debris (FWD + CWD) was averaged within each of the four sites and compared among sites using analysis of variance; square-root transformed data were used for CWD and total biomass (ANOVA procedure, SAS Institute, Inc. 1989). Total woody debris was summarized by decomposition class and species.

## PRIMARY PRODUCTION

### Understory species richness and abundance

Abundance and species richness estimates of woody and herbaceous understory vegetation were made to characterize cottonwood and river sites, and to estimate the effects of flooding on this structural aspect of the forest. Measurements were made at cottonwood sites beginning in spring 1993, prior to flooding; however, the first fall measurements were made after flooding began that year. Measurements were taken at the cottonwood sites 5-6 May and 15-16 September 1993, 3 May and 4 October 1994, and

1 May and 2-3 October 1995. Measurements at the river sites were taken on 17 October 1994, 28 April and 9-10 October 1995. Understory measurements were recorded along 12 (cottonwood) or 10 (river), 30-m transects at each site. Transects were located between the main web or grid transects and thus were stratified throughout each site. Along each transect, the identity, location and intercept length of all understory species were recorded. *Populus*, *Salix*, and *Tamarix* were excluded. From these data, we estimated the total number of understory species present as well as the average numbers of species per transect at each site. The number of individuals and intercept lengths for each species were summed along each transect, and averaged across the 10 or 12 transects for each site. Species were combined into three plant-type classes (shrubs, forbs, grasses) and average intercept lengths for these were estimated at each site for each date.

Since sampling was begun in May immediately prior to the first flood, we do not have a pre-flood fall measurements for Cottonwood Flood. Thus, we do not know if vegetation at that site changed after flooding began, nor do we know initial differences between the control and flood site prior to flooding. Therefore, rather than comparing sites, we made comparisons across time within each site to determine whether vegetation changed at Cottonwood Flood after three years of flooding. We compared the average number of species per transect and the average intercept length for each of shrubs, forbs and grasses across six sample periods at cottonwood sites and three sample periods at river sites using a Kruskal-Wallis test (NPAR1WAY procedure, SAS Institute, Inc. 1989) within each site.

### Herbaceous biomass

Net above ground production of herbaceous understory vegetation was estimated by clipping and measuring annual growth at all sites. Samples were collected at cottonwood and tamarisk sites on 26 September 1991, 23 September 1992, and 22 September 1993, and at all six sites on 28-29 September 1994 and 26-27 September 1995. In 1991, ten sample locations were stratified throughout each cottonwood and tamarisk site. Due to the high variance in herbaceous growth among sampling locations at cottonwood sites during 1991, in subsequent years paired samples were taken from locations stratified throughout each site. For each location, one sample was collected under full canopy and a nearby sample was collected with no canopy (100% sky visible overhead). The dense nature of tamarisk sites and the full overstory at the river flood site prevented open sample locations, therefore samples were randomly located at tamarisk and river sites each year. For each sample, all above ground herbaceous growth was collected within a 0.5 m<sup>2</sup> plot. Samples were oven-dried at 60°C for 48 h and weighed; beginning in 1992, samples were separated into grass and non-grass components. Variation in the dry weight of forb and grass biomass per m<sup>2</sup> was compared across years within each site using Kruskal-Wallis tests, and between flood and control sites within each year and forest type using Wilcoxon Rank Sum tests (NPAR1WAY procedure, SAS Institute, Inc. 1989). Since 1991 samples were collected with a different method at cottonwood sites, these were excluded from analyses; all years were used for tamarisk sites. Statistical comparisons were not made for river sites since herbaceous growth was essentially absent there in 1994.

### Foliage density and diversity

Foliage measurements were collected at the two cottonwood sites on 3-4 July 1991, 7 July 1994 and 7 July 1995 following the methodology of Anderson and Ohmart (1986). These data were used to calculate the mean foliage density, foliage height diversity (vertical diversity) and patchiness (horizontal diversity). The sampling transect followed the north-south transects of the mammal webs (lines 1 and 7). At each site, measurements were taken every 10 m, alternating one meter east or west of the transect,

giving 18 sample points within each site; these were pooled into 6 plots each including 3 points. At each sample point, the distance to the nearest foliage at each of six heights (0.15 m, 0.5 m, 1.0 m, 2.0 m, 3.0 m, 5.0 m) was measured. Heights above 5 m were not used due to the difficulty of consistently measuring heights and estimating distances at 10 m and higher; thus, these measurements effectively describe only the subcanopy layers.

### Growth of major tree species

Canopy trees were selected at cottonwood and tamarisk sites in June 1991 and tagged for recognition to monitor the effect of flooding on growth of mature woody species. Diameter at breast height (DBH; 1.5 m above the ground) was initially measured for 141 cottonwood trees at Cottonwood Control, 138 cottonwood trees at Cottonwood Flood and 120 tamarisk trees at each tamarisk site (24-25 June 1991 for cottonwood sites and Tamarisk Flood, 3 July 1991 for Tamarisk Control). Due to various complicating factors including mortality, these sample sizes were reduced to 127 (CC), 132 (CF), 109 (TC) and 79 (TF) for final analyses. DBH was re-measured 6-8 April 1993, 6-8 April 1994, 5-6 April 1995 and 1-4 April 1996. In addition, 50 trees were selected at each river site and initial DBH measurements were taken 11-12 April 1995; these trees were re-measured 5 April 1996. Tree survival at cottonwood sites was determined in September 1994, April 1995, and April 1996 by visually checking trees for the presence of green leaves.

Mean growth rates were greater at Cottonwood Flood than at Cottonwood Control prior to experimental flooding, thus the total change in DBH between the beginning and end of the study was not a useful measure. Instead, for cottonwood sites we compared the acceleration or change between pre-flood growth rates (change in DBH between 1991 and 1993) and post-flood growth rates (change in DBH between 1993 and 1996). Thus the acceleration,  $a$ , of growth after the initiation of flooding (before and after 1993) was defined as

$$a = \frac{\left(\frac{\Delta D}{\Delta t}\right)_{96-93} - \left(\frac{\Delta D}{\Delta t}\right)_{93-91}}{\Delta t}$$

where

$$\left(\frac{\Delta D}{\Delta t}\right)$$

is the change in DBH for the given time interval. For tamarisk sites, acceleration was determined as the change in growth rates between 1991 - 1994 (pre-flood) and 1994 - 1996 (post-flood). Although Tamarisk Flood was not fully inundated across the surface in 1994, the rise in ground water likely affected most trees at the site. Mean change of growth after initiation of flooding was compared between sites within the cottonwood and tamarisk forests using Wilcoxon Rank Sum tests (NPAR1WAY procedure, SAS Institute, Inc. 1989). The frequency distributions of DBH measurements in 1991 and 1996 were compared within each site using Kolmogorov-Smirnov Goodness of Fit tests (Zar 1974).

To account for the high variance in acceleration within each site, we plotted the initial (1991) DBH for each tree against the change of growth rates and calculated linear regressions (REG procedure, SAS Institute, Inc. 1989).

### **Cottonwood recruitment**

We searched twelve 10 x 30 m plots at each site for the presence of seedlings in May and October each of 1993, 1994 and 1995.

### **Tree and shrub density**

The density of woody plant species was estimated for cottonwood sites on 5-6 May 1993, prior to the first flood, and again on 2-3 October 1995, after three experimental floods. Similar measurements were made at the river sites on 9-10 October 1995. All trees and shrubs were counted within twelve 10 x 30 m plots at each cottonwood site and ten 10 x 30 m plots at each river site. The plots fall along the transects used for understory species richness estimates, located between the main site transects. In each plot, we recorded the number of individuals of all woody species, classified by height as < 0.5 m, > 0.5 m, or dead. Stems obviously joined at the base, or clumps of stems as in the case of *Tamarix* or *Forestiera*, were counted as a single individual. Also with *Tamarix*, clumps were counted as living if at least one living stem or shoot was present. This occurred frequently at River Flood, where clumps often included predominantly dead stems but were counted as living if any living shoot was present. The mean density (number of individuals per hectare) for each species in each class was calculated for each site and provides information for characterizing sites. We compared tree and shrub densities in 1993 and 1995 at cottonwood sites to estimate recruitment and mortality of woody species. Densities for 1995 were compared among cottonwood and river sites.

## **CONSUMERS**

### **Soil bacteria and fungi**

Soil samples were analyzed for mycorrhizae, other fungi, and various other microbial parameters by Dr. Shivcham Dhillion at the Agricultural University of Norway and the Centre National de la Recherche Scientifique and Centre d' Ecologie Fonctionnelle et Evolutive, France. Soil samples were collected at both cottonwood sites before and after each experimental flood: 13 May and 7 July 1993, 27 April and 5 July 1994, and 19 April and 14 July 1995. Samples at tamarisk sites were collected on 13 May 1993, 27 April and 7 July 1994, and 19 April and 14 July 1995. River sites were sampled on 19 April and 1 September 1995. For each collection, ten soil cores (3 cm diameter by 10 cm length) were taken from locations distributed throughout each site. Cores were homogenized within each site and a sub-sample was used to estimate fungal and microbial parameters.

### **Surface-active and aerial arthropods**

Surface-active and aerial macroarthropods were sampled at cottonwood and tamarisk sites beginning in July 1991; these sites were also sampled in August, October and December 1991. Cottonwood sites were then sampled in February, April, June, August, October and December during each of 1992, 1993, 1994, and 1995, with additional samples collected during May of 1993, 1994, and 1995, immediately prior to flooding. No collections were made in December 1992 due to heavy snowfall. Tamarisk sites were sampled on the same schedule through June 1994. At that time our effort was shifted to the river sites, which were sampled in August, October, and December 1994 and during 1995; the river sites were not sampled in June 1995 because they were underwater.

Surface-active arthropods were collected in pitfall traps opened for 48 h during each trapping period. There were 30 pitfall traps at each site, distributed throughout the mammal trapping web (cottonwood sites, Figure 2) or grid (tamarisk and river sites, Figure 3). All arthropods captured were collected and frozen, then later identified and counted to give an estimate of taxonomic richness and abundance. Aerial insects were captured on 10 x 15 cm yellow sticky traps (Chroma line card traps, Phero Tech Inc.), hung from trees at the ends of transects for 48 h concurrently with pitfall trapping. Ten sticky traps were stratified throughout at each site during each trapping session. Sticky trap captures were later identified to order, suborder, or family, and counted.

The six sites were compared for total taxonomic richness during the entire study period, as well as richness of all insects combined, and of ants, carabid beetles and spiders. Abundance of isopods (*Armadillidium vulgare* sow bugs and *Porcellio laevis* wood lice), ants (all species), beetles (the three most common families: Carabidae, Staphylinidae, and Tenebrionidae), crickets (*Gryllus alogus*), and spiders (one family, Lycosidae) were summarized by month within each site for 1991 through 1995. We then used random intervention analysis (RIA, Carpenter et al. 1989) to compare intersite differences in the total number of individuals of each of these taxa between Cottonwood Control and Cottonwood Flood before and after the initiation of flooding. In addition, we compared taxonomic richness of ants and of carabid beetles at cottonwood control and flood sites before and after flooding, and between river sites, using the Morisita-Horn quantitative similarity index ( $C_{mH}$ ; Magurran 1988),

$$C_{mH} = \frac{2\sum(an_i bn_i)}{(da+db)aNbN}$$

where  $aN$  = total number of individuals in site A and  $an_i$  = number of individuals in the  $i$ th species in A.

$$da = \frac{\sum an_i^2}{aN^2}$$

Abundance of aerial insects within each of ten taxonomic groups were summarized by month for each site. We used RIA to compare pre- and post-flood differences between Cottonwood Control and Cottonwood Flood for four of these groups: leafhoppers, chalcidoid wasps, nemotoceran flies and all other flies.

### Mammals

Rodents were monitored through live-trapping and mark-recapture studies. Traps were set at cottonwood and tamarisk sites in June, August, and October, 1991 and April, June, August, and October (cottonwood only) 1992. In 1993 and 1995, rodents were trapped at cottonwood sites immediately prior to flooding the flood site in May, immediately after the flood dried out in June, and again in August. Rodents at tamarisk sites were trapped at the same times in 1993, but we did not set traps at tamarisk sites in 1995. We did not trap rodents at any site in 1994 due to the hantavirus outbreak in the region (Mills et al. 1995). To provide a comparison between cottonwood sites and a naturally flooding forest, we set traps for a single, three-night period at the two river sites in late August 1995, two weeks after the August trapping at cottonwood sites. Since we do not have data reflecting the influence of flooding on rodents in tamarisk, those sites have been excluded from this discussion. However, rodent abundance at these sites

was high and several species were present that were not captured at cottonwood sites; a comparison of rodent populations in tamarisk and cottonwood vegetation is presented in Ellis et al. (in press).

A trapping web was established at each cottonwood site, consisting of a 200-m diameter circle, with twelve 100-m transects radiating out from a center point (Figure 2; Anderson et al. 1983). Twelve standard Sherman live traps (model LFATDG) were placed along each transect, every 5 m for the first 20 m, then at 10 m intervals thereafter; four additional traps were placed at the center of the web, for a total of 148 traps per web. River sites were too small for trapping webs. Instead, we established a grid of ten 60-m transects at each site (Figure 3). Transects were separated by 20 m and six traps were placed along each at 10-m intervals, for a total of 60 traps at each site.

Trapping periods consisted of three consecutive nights of trapping at the two cottonwood sites. Traps were baited with raw oatmeal. Captured rodents were given ear tags for individual identification. Species, sex, age, and reproductive condition were recorded before each was released. Rodents trapped during the single trapping period at river sites were marked on their chests with colored marking pens to determine recaptures within the trapping period; species, age, sex and reproductive condition were recorded before each release.

We compared rodent species composition and richness at the cottonwood sites. Densities were calculated using the DISTANCE program (Buckland et al. 1993, Laake et al. 1993). We used the uniform model with four possible adjustments (no adjustment, cosine, simple polynomial, hermite polynomial) and used the minimum Akaike information criteria and Chi-squared Goodness of Fit tests to select the best fit model for each site for each sample period. The two outermost traps on each line were deleted to eliminate an edge effect, and occasional pooling was used to accommodate uneven distributions (Buckland et al. 1993). For three cases at Cottonwood Flood when truncated sample sizes were less than ten individuals (June 1991, May 1995, June 1995), density was calculated as the number of individuals captured per unit area; no variance estimates were possible for these. Adult sex ratios and percentage of adult males and females in reproductive condition were calculated for each site during each trapping period. Sex ratios within each site were compared using Chi-square Goodness of Fit tests for each sample period with an expected equal ratio of males to females (Zar 1974). The percentage of adults in reproductive condition at the two sites were compared using Chi-square Goodness of Fit tests for each sample period. Percentages of mice captured in May of 1993 and 1995 (immediately prior to the experimental floods) and recaptured in June (immediately following flooding) and August (two months after flooding) of the same year, were calculated for each site, as was the number of "new" mice (not captured in May) for each month. Similar values were calculated for captures in 1992 (when both sites were kept dry), except that initial values were based on April captures, with recaptures calculated for June and August. For river sites, the total number of mice captured over three nights, and the percent trap success, were compared between flood and control sites. Although differences in design preclude a statistical comparison of densities with the cottonwood sites, the values obtained provide an estimate of relative differences between the river flood site and its control.

To determine whether mice used trees, which provide potential refugia during flooding, we placed traps in trees at cottonwood sites. We attached 20 aluminum platforms approximately 2 m above the ground on trees chosen at random but stratified throughout the web area; their diameters at 1.5 m above the base ranged from 88 to 1257 mm. A single Sherman trap baited with raw oatmeal was placed on each platform with the open door facing the trunk. Tree traps were set simultaneously at both sites for three consecutive nights immediately following ground trapping in June, August and October 1991, June and August 1992, and May, June and August 1993. In addition, tree traps were set at both sites for 2 consecutive nights during peak flood in 1993. All mice captured in tree traps were processed as described above. Trapping success for tree traps was calculated for each site during each trapping period.



## RESULTS AND DISCUSSION

### ABIOTIC FACTORS

#### Meteorological conditions

Although both intra- and inter-annual variations in weather conditions were observed throughout the five years of study, some general patterns in meteorological variables emerged. Here we present figures for only one year for each variable at each site, but overall patterns were consistent among years. Air and soil temperatures showed considerable daily variation, but reached highest peaks during mid-June to August at all sites (Figures 5, 6, 7). Flooding substantially depressed summer soil temperatures at cottonwood and tamarisk flood sites (Figures 5, 7); this decrease was especially dramatic for soil temperatures at 4 cm at Tamarisk Flood in 1994, when soil temperatures at Tamarisk Control remained extremely high (Figure 7). Although the soil temperatures at 15 cm depth at River Flood were not decreased relative to River Control during the summer of 1995 (Figure 6), this may reflect a malfunctioning probe at River Control, which produced intermittently erroneous readings which in turn may have led to lower average temperatures there. At River Flood there was a greater reduction in soil temperature at 4 cm than at 15 cm relative to River Control, while at cottonwood and tamarisk sites soil temperatures at both depths were depressed at flood sites relative to their controls. Air temperatures were also depressed at flood sites during flooding, which corresponds to the period with hottest air temperatures. Thus flooding, by depressing air and soil temperatures, may be an important regulator of the activity of various soil and surface-active organisms.

Rainfall varied considerably among years (Figure 8). Many semi-arid regions, including the southwestern United States, experience variable rainfall as a result of the El Niño/Southern Oscillation phenomenon (Nicholls 1988). Locally, warm-phase (El Niño) events result in increased winter and spring rainfall. Both 1991-92 and 1992-93 were considered El Niño years locally (Dahm and Moore 1994), although the latter was a much weaker event with less spring precipitation (Figure 8). In addition, 1994-95 began as an El Niño event, with relatively high winter precipitation, but this was aborted with lower than normal spring precipitation (D. Moore, personal communication). In contrast, both 1990-91 and 1993-94 experienced relatively low (though normal) winter precipitation, with more of the annual precipitation arriving during the summer monsoon season. Such variation in the timing of precipitation may significantly influence growth and activity of both primary producers and various consumers. However, overbank flooding may moderate the effects of spring and summer drought by wetting the forest during such dry periods.

Flooding also influenced the wettability of the soil. As expected, soils at all flood sites were saturated during the period of flooding, while soils at controls remained dry until the period of later summer rains (Figures 9, 10, 11). More important, however, may be the increased frequency at which flood site soils were re-wetted after the period of flooding. Saturating the soils during flooding may allow subsequent precipitation to enter more easily, while soils that remain dry throughout the winter and spring tend to be hydrophobic and do not allow water to percolate through easily. This conclusion is supported by observations at Cottonwood Control. Soil at that site was frequently wet throughout the summer of 1992, but this followed the winter of high precipitation during which soils were saturated, thus decreasing hydrophobicity.

Wind was the most variable of the meteorological conditions measured. However, there was a consistent pattern for more wind during the winter and especially the spring, with little or no wind present during the hot summer months (Figures 12, 13, 14). Wind is not directly affected by flooding, and differences observed between control and flood sites were present prior to flooding, at least at cottonwood

and tamarisk sites. However, flooding may have an indirect effect via its influence on the structure of the forest. Recorded wind speeds were actually greater at River Flood than at River Control or Cottonwood Flood, which may reflect the lower density of understory shrubs at River Flood and thus the potential for greater air movement within the forest.

### Hydrology and water chemistry

Distinct biogeochemical patterns during three years of experimental flooding suggest that the forest is quickly reorganizing in response to reestablished site hydrology. During each month-long flood, groundwater levels increased by slightly more than 2 meters (Figure 15); average temperatures of this groundwater increased at Cottonwood Flood during inundation and gradually became equal to those of surface water, indicating a strong surface water-groundwater connection (Figure 16). The combined waters saturated the rooting zone and surface litter layer, resulting in a biological oxygen demand that generated anoxia in groundwater wells and in surface water near the forest floor. Although dissolved oxygen (DO) in the groundwater at Cottonwood Flood increased relative to Cottonwood Control (Figure 17), it remained below levels of the well-oxygenated surface water (ca. 8 mg/L DO). In these anoxic environments, groundwater nitrate-nitrogen ( $\text{NO}_3\text{-N}$ ) concentrations were below detection levels at both sites. Groundwater concentrations of ammonium-nitrogen ( $\text{NH}_4\text{-N}$ ) were higher (200-600 ppb) and the water was rich in soluble reactive phosphorus (SRP, 30-100 ppb). In contrast, the oxygenated water entering Cottonwood Flood contained 100-200 ppb  $\text{NO}_3\text{-N}$  and 40-60 ppb SRP. Material budgets calculated from solute loads showed that the forest retained the vast majority of  $\text{NO}_3\text{-N}$  and SRP, probably associated with biological and physical processes or solute immobilization.

Dissolved organic carbon (DOC) concentrations consistently increased in groundwater at Cottonwood Flood during experimental flooding. During each of the three floods, surface water DOC concentrations increased from input levels of 3-5 ppm (concentrations characteristic of groundwater at the Cottonwood Control) to late flood concentrations of 20-30 ppm; groundwater DOC concentrations at Cottonwood Flood showed similar increases (Figure 18). Material budgets indicate that more carbon was lost from the site than entered it in flood water, although the extent of carbon liberation decreased across the three experimental floods. Plateau concentrations of DOC in groundwater at Cottonwood Flood decreased sequentially from over 25 ppm in 1993 to near 20 ppm in 1994 and finally to near 15 ppm in 1995 (Figure 18), suggesting that flooding is beginning to exhaust the supply of water soluble carbon generated by saturation of forest floor materials.

In contrast, repeated flooding appears to be increasing the post-flood concentrations of  $\text{NH}_4\text{-N}$  (Figure 19). During each flood, concentrations of  $\text{NH}_4\text{-N}$  have decreased greatly from pre-flood values of approximately 0.25 to 0.5 ppm to peak flood minimal values of approximately 0.04-0.06 ppm. Preliminary analyses suggest that  $\text{NH}_4\text{-N}$  may be immobilized in the shallow aquifer sediments (i.e. 10-50 cm depth) by microbial demand and by sorptive processes. Following recession of the water table,  $\text{NH}_4\text{-N}$  levels rebound to concentrations greater than pre-flood values. Perhaps as a result, pre-flood  $\text{NH}_4\text{-N}$  concentrations have increased steadily across the three experimental floods.

Respiration data are only available for 1994 at this time. During initial respiration assays under flooded conditions, DO was present on the submerged litter layer (ca. 1 mg/L). Biological oxygen demand calculated from metabolic chambers ( $1.13 \pm 0.56 \text{ mg L}^{-1} \text{ hr}^{-1}$ ) was nearly an order of magnitude higher than in the water column and approached rates comparable for untreated sewage. Our data suggest, however, that litter decomposition during flooding occurs primarily because of anaerobic processes in the anoxic layer of saturated leaf litter. Lack of significant  $\text{NO}_3\text{-N}$  in the flood water and the strong aroma of "sulfurous" gases suggests that sulfate reduction may be the dominant terminal electron accepting process. Incubations on the forest floor one day after draining flood water showed that respiration at

Cottonwood Flood was more than 200 times that measured for Cottonwood Control ( $1.4 \pm 0.05 \text{ g OM m}^{-1} \text{ d}^{-1}$  vs  $0.006 \pm 0.001 \text{ g OM m}^{-1} \text{ d}^{-1}$ ). If metabolic demand of surface water is added, areal respiration at Cottonwood Flood may be more than 600 times higher than at Cottonwood Control.

Overall, these data suggest that surface flooding at Cottonwood Flood mobilizes carbon in dissolved form and exports it down into the saturated rooting zone. In contrast, the rising water table transports ammonium-rich water upward where it may be utilized by soil microflora, immobilized through sorptive processes or possibly taken up by riparian vegetation.

Inundation at River Flood presented a very different picture. It lasted for about 2.5 months in 1996, with a measured depth averaging near 20 cm throughout the flood. Well head elevation increased early during inundation, but then decreased slightly to remain at a fairly constant level throughout the remainder of the flood (Figure 20a). Unlike at cottonwood sites, the temperature of groundwater continued to increase at both river flood and control sites during the period of flooding (Figures 16, 20b); however, there was a greater increase in temperature at River Flood during the period of increased groundwater elevation at that site. Dissolved oxygen in the groundwater at River Flood also increased to levels above that of River Control during the rise in groundwater elevation, but these levels dropped mid-way through the flood and remained similar between the two sites (Figure 20c). Data for water chemistry at river sites are not yet available.

Tamarisk sites were monitored for groundwater elevation only. Well head elevation rose appreciably during inundation each year at Tamarisk Flood while groundwater levels dropped at Tamarisk Control (Figure 21). This rise in groundwater at Tamarisk Flood in 1994 occurred in spite of incomplete inundation at the surface of that site, again suggesting a strong surface water - groundwater connection.

### Soils

Both experimental and "natural" (i.e., river) flooding appeared to generate a number of trends in soil structure and composition (see Appendix A - 1 through A - 4 for summary). The percent of silt in soils at Cottonwood Control remained relatively high and constant between 1992 and 1995, while the varying percentages of sand and clay reflected the small scale heterogeneity of those textural elements at that site (Figure 22). Less silt was present at Cottonwood Flood where, after three years of flooding, the percent of clay increased slightly. Silt tended to dominate at both river sites, especially at River Flood after the long period of inundation in 1995. This finding is consistent with results of our silt deposition measurements (see below, **Silt Deposition**). An increase in soil crumb structure by the third year of flooding was noted at Cottonwood Flood, and well developed crumb structure was even more obvious at the regularly flooded River Flood site. Much of the change at Cottonwood Flood can be attributed to the high soil/litter activity of earthworms recorded immediately following exposure of the flood-wetted soil. Far fewer earthworms were seen at the River Flood. Soil development in the experimentally flooded bosque may therefore be enhanced by a combination of decaying leaves, some silt deposition and brief but intense earthworm activity.

Extractable cations were significantly reduced at both Cottonwood Control and Cottonwood Flood between 1992 and 1993, most likely because of heavy rains shortly before sampling in 1993 (Figure 23 and Figure 8). However, while the monovalent cations sodium and potassium increased again at Cottonwood Control during the next two years, concentrations of these remained low at Cottonwood Flood. Thus, although possible flushing effects of the first flood may have been compounded by the high August 1993 rainfall, apparent effects of the following two floods were observed. This was also supported by sodium and potassium concentrations at river sites, which were lower at River Flood than River Control. In contrast, the divalent cations calcium and magnesium appeared unaffected by flooding at Cottonwood Flood compared with those at Cottonwood Control (Figure 23). However, both were more

concentrated at River Flood than at River Control, especially in 1995 following prolonged inundation at the former site. Just how these calcium and magnesium concentrations might have been influenced by heavy late spring / early summer runoff is not clear. Sodium absorption ratios also showed the presumed depression effect of heavy August 1993 precipitation, followed by a greater increase at Cottonwood Control compared to Cottonwood Flood (Figure 24a). Conductivity values on the other hand were always higher at Cottonwood Control than at the flooded sites (Figure 24b), but this difference increased after flooding. The lowering of sodium by floodwaters may be important to bosque soils and vegetation since sodium ions disperse soil colloids, which then form a relatively impervious soil structure (Buckham and Brady 1969, p 407).

Soil nutrients apparently were also affected by flooding. Total phosphorous declined slightly at Cottonwood Flood compared with Cottonwood Control following each experimental flood (Figure 25a) while River Flood had a significantly lower mean level of phosphorus than River Control in 1995, but not in 1994. Reduced phosphorous levels in bosque soils following the floods, and extremely low levels in cottonwood leaves in some areas of the bosque (D. Rowland in prep.), suggest that phosphorous may be a limited resource in parts of the forest and imply a valuable absorptive role for mycorrhizal fungi in such places (D. Rowland pers. comm.). Total carbon was consistently more abundant at Cottonwood Control than at Cottonwood Flood, where it showed a declining trend (Figure 25b); the inverse was observed at river sites, with increasing carbon levels recorded River Flood. Heavy deposition of silt by the flooding river, which buried plant litter, may have been responsible for this high total carbon value at River Flood; there was less surface litter at River Flood than at the other sites (see below, **Litter Storage**). The steady increase in total nitrogen (Figure 25c) is difficult to explain. Similar values at River Control and River Flood imply no obvious effect of Rio Grande flooding on forest soil total nitrogen in the superficial soil layers.

Biomass carbon and basal respiration, while significantly higher in River Flood soil in 1994 than in soils at all other sites that year (Figure 26), were not significantly higher in 1995, when constant inundation by the river probably lasted longer. Prolonged exposure to anaerobic conditions may have been responsible for the difference. An immediate response of basal respiration to the first experimental flood at Cottonwood Flood was clear. That year (1993) marked the first prolonged exposure to water by the site in over 50 years, and may have depressed basal respiration because of the anaerobic "shock effect" of that first flood.

Soils at the two tamarisk sites differed from each other in a number of ways (Appendix A - 4). Samples were collected from these sites only in 1992, and do not reflect an influence of flooding. However, concentrations of all extractable cations, as well as the cation exchange capacity and sodium absorption ratio were significantly higher at Tamarisk Flood than at Tamarisk Control. Soil texture differed between the sites, with more sand in soil at Tamarisk Control while more clay was present in soils at Tamarisk Flood. Other differences included a greater field water content and water holding capacity at the flood site (reflecting the higher clay content) as well as more organic matter at that site. We do not know the history for soils at these sites, therefore we are unable to account for these differences.

### Silt deposition

More silt was deposited during natural flooding by the Rio Grande than by artificial flooding (Figure 27). Silt deposited at River Flood averaged  $155.06 \text{ g / m}^2 / \text{day}$  while silt at Cottonwood Flood averaged  $8.03 \text{ g / m}^2 / \text{day}$  (Wilcoxon Rank Sum test,  $Z = -7.56$ ,  $P = 0.0001$ ). There were no differences in the amount of silt deposited at different locations within River Flood (Kruskal-Wallis test,  $P > 0.05$ ; Figure 27), while at Cottonwood Flood more silt was deposited in channel locations ( $\chi^2 = 18.934$ ,  $P = 0.003$ ). This may reflect differences in site topography. At Cottonwood Flood, locations before and after obstructions were also upslope, with less standing water, while at River Flood locations before and after obstructions were in the main channel within the site. Clearly, water coming from the Rio Grande is heavily laden with silt and much of this is deposited within the forest. This serves both as an input of

nutrients to the forest as well as a means to "clean" water flowing back into the river. That less sediment was deposited at Cottonwood Flood reflects the origin of the water; water for the manipulated flood was diverted from the riverside canal and had more time to deposit silt before entering the study area.

## FOREST FLOOR LITTER: PRODUCTION, DECOMPOSITION AND STORAGE

### Litter production: litterfall traps

Experimental flooding significantly affected litter production. While total litter production did not differ between cottonwood control and flood sites during the first two litterfall seasons, prior to flooding (t-test,  $P > 0.05$ ; Figure 28), litterfall was significantly lower at Cottonwood Flood after the first experimental flood ( $T = 2.463$ ,  $P = 0.022$ ). There was a trend for slightly lower litterfall at Cottonwood Flood after the second flood, but the difference in total litterfall was not significant (Figure 28). Following three seasons of flooding, there was a shift toward greater litter production at Cottonwood Flood early in the season, but again final differences in total litterfall were not significant. Annual intersite differences in total cottonwood leaffall clearly illustrate the temporal pattern of the flooding effect (Figure 29). Intersite differences in total leaffall were small during the two seasons prior to flooding. However, a large negative value followed the first experimental flood, indicating much lower leaffall at Cottonwood Flood compared to Cottonwood Control. The magnitude of this difference was less following the second flood, and had shifted to a positive value following the third flood, signifying greater leaffall at Cottonwood Flood. Positive intersite differences for River Flood and River Control during 1994-95 and 1995-96 suggest that flooded forests consistently produce more leaves than do unflooded sites (Figure 29). Thus, although reinstating flooding may initially depress litter production, repeated flooding appears to favor this ecosystem component. Further, this transition appears to occur very rapidly, with positive effects detectable within a few years. Initial suppression of leaf production may indicate a physiological shock due to anoxic conditions in the rooting zone.

This conclusion is supported by comparing the weight of total cottonwood leaffall among cottonwood and river sites during the final two seasons (Figure 30). Total leaffall was significantly greater at River Flood than at the other three sites during both seasons (ANOVA, 1994-95,  $F = 8.30$ ,  $P = 0.0001$ ; 1995-96,  $F = 5.34$ ,  $P = 0.013$ ). Although differences among the other three sites were not significant, leaffall at Cottonwood Flood was the lowest of the three in 1994-95 and the heaviest of the three in 1995-96. Thus there was a slight shift in the relative standing of leaffall at Cottonwood Flood compared to the two control sites. In contrast, the number of leaves produced did not follow this same pattern. Analysis of variance for the total number of cottonwood leaves produced among the four sites was marginally significant for 1994-95 ( $F = 2.60$ ,  $P = 0.052$ ). Multiple t-tests indicated that river and cottonwood flood sites did not differ from each other in the number of leaves produced, but River Flood produced more leaves than the two control sites, while Cottonwood Flood did not differ from the controls. However, ANOVA for the total number of leaves produced among sites during 1995-96 was not significant ( $P = 0.113$ ); neither flood site differed from its control. Combined with the above data on total weight, this suggests that the size or weight of individual leaves may vary among sites.

Mean leaf width, which correlates with leaf area, did differ significantly among sites during both 1994-95 (Kruskal-Wallis test,  $\chi^2 = 114.53$ ,  $P = 0.0001$ ) and 1995-96 ( $\chi^2 = 21.04$ ,  $P = 0.0001$ ). Leaves were larger at River Flood compared to the other three sites during 1994-95, while they were smaller at Cottonwood Flood (Figure 31a). In 1995-96, leaves were again larger at River Flood compared to the other three sites, but the size of leaves at Cottonwood Flood did not differ from that at the two control sites. Monthly variation in the size of leaves collected was also observed within each season and among sites (Figure 31b, c). Larger leaves were dropped from trees early in the season at River Flood during both years and at Cottonwood Flood during 1994-95. In contrast, leaves dropped at Cottonwood Flood

during 1995-96, and at both control sites during both years, tended to be larger later in the season. Overall, leaves were slightly larger in 1994-95 than in 1995-96 (Figure 31a).

In contrast to leaf width, leaf specific mass was greater during 1995-96 (Figure 32a). Thus, these leaves were smaller but thicker than those produced the year before. Variation in specific mass within each year was less than variation in width, suggesting intraseasonal changes in thickness. Leaves at both flood sites were generally similar during 1994-95, except in February 1995 when leaves at Cottonwood Flood had greater specific mass (Figure 32b). In contrast, during 1995-96 leaves at Cottonwood Flood had greater specific mass in September, while specific mass of leaves at River Flood were greater in December and February (Figure 32c).

This variation in the size and thickness of leaves reflects conditions experienced by the tree when the leaves are formed. The first 3-4 leaves to emerge on a branch, which occurs in May in this region, are those pre-formed the previous winter (D. Rowland, personal communication), and the size of these leaves may therefore reflect the precipitation experienced at the time of formation. A second set of leaves typically emerges throughout the summer, beginning in mid-June; formation of these may be more affected by summer moisture conditions. It is unknown whether these two sets of leaves drop from the tree at different times, but it is reasonable to assume that the earlier formed leaves senesce first. Precipitation during the winter of 1993-94 was much lower than that during the winter of 1994-95 (Figure 8), suggesting that leaves formed during the dry winter were larger and thinner than leaves produced during the wet winter, although this relationship is not known for certain. Summer flooding may affect the size of the second set of leaves formed, suggesting that leaves dropped later in the season may reflect these conditions. During 1994-95 these leaves were smaller but thicker at Cottonwood Flood compared to Cottonwood Control, but this relationship did not hold during 1995-96. Thus although these data suggest that trees produce smaller and thicker leaves during periods of greater moisture availability, additional studies are needed to confirm this conclusion. The leaves at River Flood were consistently larger earlier in the season. This suggests beneficial conditions at that site during each winter, which may reflect the general health of the trees as compared to other sites.

Litterfall at tamarisk sites showed no effects of flooding. Total litterfall did not differ between control and flood sites for any year (t-tests, all  $P > 0.05$ ; Figure 33). Some variation in total litterfall among years was observed, but this was not consistent with that seen at cottonwood sites. Lowest total litterfall at both tamarisk sites was recorded in 1991-92, while lowest total litterfall at both cottonwood sites was in 1994-95 (Figure 33, 28). Highest totals at both flood sites were recorded in 1995-96, while the highest at Tamarisk Control was in 1992-93 and at Cottonwood Control in 1993-94. Litterfall values are summarized in Appendix B - 1 and B - 2.

### Leaf decomposition

Flooding accelerated leaf decomposition in all three forest types (Figure 34, 35), and this acceleration was detected during the first period of inundation at each flood site. In all flood sites, ash-free dry-weights of leaves in decomposition bags decreased markedly between the April and June collections during the periods of inundation. Pair-wise comparisons between Cottonwood Control and Cottonwood Flood indicate no significant differences between sites for each collection in 1991-92 (no flooding; Figure 34) or for the first two collections in 1992-93, 1993-94 and 1994-95 (prior to flooding each year; Wilcoxon Rank Sum tests, all  $P > 0.05$ ). In contrast, the average ash-free dry-weight of leaves was significantly lower at Cottonwood Flood for the last two collections each year following flooding (June and November collections each year:  $Z = 2.51$ ,  $P = 0.0122$ ). Similarly, the mean weight of leaves in decomposition bags at River Control and River Flood did not differ in the first November or April collections, prior to flooding, but mean weights were significantly lower at River Flood in both post-flooding collections (June and November,  $Z = 2.51$ ,  $P = 0.0122$ ). In addition, patterns of leaf mass loss were virtually identical at river and cottonwood control sites and at river and cottonwood flood sites in 1994-95 (Figure 34). A summary of decomposition bag data is presented in Appendix B - 3 and B - 4.

Following Bonferroni adjustments, the average ash-free dry-weights of leaves in decomposition bags at tamarisk sites did not differ significantly 1991-92. However, final ash-free dry-weights were significantly lower at Tamarisk Control in 1992-93 ( $Z = -2.51$ ,  $P = 0.012$ ; Figure 35), prior to flooding at Tamarisk Flood. After Tamarisk Flood was partially inundated in 1994, there was a significant shift in the relative mean weights at the two sites, with decomposing leaves being lighter at Tamarisk Flood in both June and November ( $Z = 2.51$ ,  $P = 0.0122$ ). In 1994-95, tamarisk sites again did not differ for the first two collections, while the mean weight of leaves in bags at Tamarisk Flood was significantly lower immediately after flooding (June,  $Z = 2.51$ ,  $P = 0.0122$ ). Final differences in November 1995, however, were not significant after Bonferroni adjustment ( $P = 0.04$ ), reflecting continued decomposition at Tamarisk Control between June and November (Figure 35).

Rates of mass loss between collection dates provide further support for the positive influence of flooding on leaf decomposition. In all years in both cottonwood and tamarisk forests, leaves at control and flood sites lost similar amounts of mass between the first and second collection dates (Figures 34, 35), although these rates changed significantly among years at all sites (Kruskal-Wallis tests, CC,  $\chi^2 = 13.54$ ,  $P = 0.0036$ ; CF,  $\chi^2 = 14.15$ ,  $P = 0.0027$ ; TC,  $\chi^2 = 16.71$ ,  $P = 0.0008$ ; TF,  $\chi^2 = 15.65$ ,  $P = 0.0013$ ). In both cottonwood and tamarisk forests, leaves lost more mass during the winter of 1991-92 than during other years, probably reflecting increased precipitation that winter. While the rates of mass loss between April and June did not differ among years at Cottonwood Control, rates of mass loss were greater between April and June at Cottonwood Flood during the flood years of 1993, 1994 and 1995 ( $\chi^2 = 12.50$ ,  $P = 0.0019$ ). At both sites there was a significant difference among years in weight lost between June and November collections (CC,  $\chi^2 = 10.27$ ,  $P = 0.0164$ ; CF,  $\chi^2 = 9.62$ ,  $P = 0.0081$ ). At Cottonwood Flood, this significant year effect for the final period reflects slightly greater loss during 1992, while weight loss after June was nearly negligible in years of flooding.

Considerable inter-annual variation in rates of weight loss of leaves was observed at tamarisk sites. Both control and flood sites differed among years in the rate of change between the first two collections (TC,  $\chi^2 = 16.71$ ,  $P = 0.0008$ , TF  $\chi^2 = 15.65$ ,  $P = 0.0013$ ) and between April and June (TC,  $\chi^2 = 12.19$ ,  $P = 0.0068$ ; TF,  $\chi^2 = 16.25$ ,  $P = 0.0010$ ). However, only Tamarisk Flood differed among years in the rate of change in weight between June and November ( $\chi^2 = 13.04$ ,  $P = 0.0046$ ). This reflected in part a negligible change in the weight of leaves during the final year, following flooding. The striking change in the rate of decomposition between April and June at Tamarisk Flood after inundation compared to years without flooding strongly supports the conclusion that flooding accelerates decomposition (Figure 35).

A comparison of leaf decomposition at River Flood and Cottonwood Flood yields an unexpected result. Weight lost by leaves at River Flood, during 2.5 months of flooding, did not differ from that lost by leaves exposed to only one month of flooding at Cottonwood Flood (Figure 34). This suggests that this weight change may primarily reflect leaching from the leaves. Leaching increases rates of leaf decomposition (Peterson and Rolfe 1982, Shure et al. 1986) and previous studies suggest that most leaching occurs within 24 hours of inundation (Webster and Benfield 1986). In laboratory tests, leaves placed in water lost an average of  $32.4 \pm 2.4$  % of their initial dry mass during the first 24 hours, with samples ranging from 29.2 to 37.1 %, while leaves left in water for 48 hours lost an average of  $35.2 \pm 0.9$  % of initial mass (Figure 36). Thus, approximately one-third of the initial weight was lost during the first 24 hours with only an additional 2.8 % lost during the second 24 hours. This suggests that leaves exposed to flooding in the field may also lose weight rapidly due to leaching. Additional weight lost beyond 30-35 % probably reflects other mechanisms, particularly fungal and microbial respiration. Most mass loss during leaching was due to the loss of soluble organic compounds. Dissolved organic carbon averaged  $456.37 \pm 58.35$  mg C L<sup>-1</sup> (range 366.44 to 565.75 mg C L<sup>-1</sup>) for leachate from leaves inundated for 24 hours and  $620.28 \pm 96.17$  mg C L<sup>-1</sup> (range 445.46 to 777.15 mg C L<sup>-1</sup>) for leaves inundated for 48 hours (Figure 36). Thus approximately 9.4 % of the initial dry mass was lost as DOC during the first 24 h, with an additional 3.4 % of the initial mass lost as DOC during the second 24 h.

To compare these experimentally determined leaching rates to our field-collected data, we calculated the average percent of initial dry-weight lost by leaves in decomposition bags between

collection dates (Table 1). These values were calculated from the mean ash-free dry-weights presented in Appendix B - 3. The results illustrate four main points. First, as discussed above, there was considerable inter-annual variation in the percent of initial mass lost during the November to April winter period (Table 1). Values for this period were generally similar between sites but varied greatly among years, which probably reflects winter precipitation. Over-winter loss was greatest in 1991-92 (22.4 - 31.7 %), reflecting the moist El Niño conditions that winter, and lowest in 1993-94 (5.9 - 6.4 %), which was a relatively dry winter. Second, flooding did result in rapid weight-loss during the April to June period (Table 1). During flooding, leaves at Cottonwood Flood lost 30 - 50 % of their initial weight and leaves at River Flood lost about 40 % of their initial weight, while weight loss of leaves at the control sites ranged from 0 to 5 % during the same period. Third, in years when leaves lost more weight during the winter, additional loss during flooding was lower, with the final amount lost similar among years (Table 1). As stated above, weight loss beyond about 35 % probably reflects fungal and microbial respiration. Thus, the relative importance of these different mechanisms of decomposition may vary temporally within different years.

Finally, the percent of the initial weight lost over the entire year was greater at the flood sites compared to their controls, and this difference was relatively greater in dry years when initial over-winter weight changes were low (Table 1). Thus flooding may play an important role in regulating the timing of nutrient cycling. Early summer flooding greatly increases the breakdown of leaves and thus presumably increases the release of nutrients at a time critical for plant growth. In sites that remain dry throughout the early growing season, and especially during years with low winter precipitation, nutrients contained in dead leaf tissue are functionally removed from the system at that time. Therefore, flooding appears both to increase the rate of leaf decomposition, thereby stimulating the cycling of essential nutrients within the ecosystem, as well as to influence the timing of such nutrient release, thus directly affecting other components of the system.

### Log decomposition

Compared to Cottonwood Control, logs decomposed faster after three seasons of flooding at Cottonwood Flood (Figure 37). Logs at both cottonwood sites lost very little mass between 1991 and 1993, prior to flooding Cottonwood Flood. Decay rates during this period were  $0.004 \text{ y}^{-1}$  and  $0.003 \text{ y}^{-1}$  for logs at Cottonwood Control and Cottonwood Flood, respectively. A rate of  $0.003 \text{ y}^{-1}$  predicts a half-life of 231.0 years based on the single exponential decay model. These decay rates are comparable to those of large conifers in the Pacific Northwest (Harmon et al. 1986). Although differences between sites were not significant due to small sample sizes, logs at Cottonwood Flood had lost 8.24% of their initial mass by 1994, after two seasonal floods, compared to 3.94% lost by logs at Cottonwood Control (Wilcoxon Rank Sum test,  $P = 0.112$ ; Figure 37). After three floods, logs at Cottonwood Flood had lost 15.21% of their initial mass, while logs at Cottonwood Control lost only 4.22% of their initial mass during that period; again, differences were not significant due to small sample sizes ( $P = 0.061$ ). The average decay rate for logs at Cottonwood Flood between 1993 and 1995, reflecting three seasonal floods, was  $0.065 \text{ y}^{-1}$ , which predicts a half-life of 10.6 years. During the same period, the decay rate for logs at Cottonwood Control was  $0.015 \text{ y}^{-1}$ . This includes a slightly accelerated decay rate between 1993 and 1994 (Figure 37), which reflects the influence of moister conditions associated with the El Niño episode experienced during that period, and thus illustrates the annual variation in climatic influences typical of this region. The rate returned to  $0.003 \text{ y}^{-1}$  during the drier 1994 to 1995 period; an overall decay rate for logs at Cottonwood Control for the entire 1991-1995 was  $0.010 \text{ y}^{-1}$ , which predicts a half-life of 69.3 years. Although no decay rates are available in the literature for *Populus deltoides*, rates for *P. tremuloides* range from  $0.049 \text{ y}^{-1}$  in northern Minnesota (Miller 1983) to  $0.070 \text{ y}^{-1}$  in northern New Mexico (Gosz 1980), with predicted half-lives of 14.0 and 9.8 years, respectively. These decomposition rates in much moister climatic conditions are similar to the rate of  $0.065 \text{ y}^{-1}$  and half-life of 10.6 years for logs at the flooded site. These results suggest that flooding may accelerate decomposition of woody debris in



the arid southwestern riparian forest. Average weights for logs collected at each site are presented in Appendix B - 6.

Initial weights and sizes of logs did not differ between river sites (all Wilcoxon Rank Sum comparisons,  $P > 0.05$ ). Initial ashfree dry-weight for logs at River Control averaged  $6.39 \pm 0.49$  kg while that for River Flood averaged  $5.69 \pm 0.41$  kg. The mean percent of the initial mass remaining for logs collected in November 1995 was  $102 \pm 1$  % for River Control and  $100 \pm 0.5$  % for River Flood. Thus logs did not lose weight during the April to November period, in spite of 2.5 months of inundation at River Flood. The apparent increase in mass observed for several logs at each site resulting in mean values greater than 100 % may reflect increased nitrogen contents in logs due to colonization by fungi.

A more thorough discussion of wood decomposition is presented in Ellis et al., in review.

### Forest floor litter and wood storage

**Forest floor litter:** Three seasonal floods did not substantially reduce litter storage in the cottonwood forest, although flooding appeared to reduce the standing stock of litter in tamarisk. This result may in part reflect the high variance in litter storage at cottonwood sites (Figure 38). Litter within the cottonwood forest is very patchily distributed and appears to reflect local microtopography, with leaves accumulating in swales while being blown clear of high points. Similar variation in litter accumulation was quantified in the cottonwood forest at the Rio Grande Nature Center in Albuquerque (C. Finance, personal communication). In contrast, litter is more uniformly distributed within tamarisk sites (personal observations, Figure 39). These sites contained less topographic variation, and the distribution of tamarisk leaves appears less influenced by wind. Further, tamarisk trees are more uniformly and densely distributed, resulting in a more complete cover of litter beneath. Intersite differences between the flood and control sites across time within each forest illustrated this difference and suggests a positive effect of flooding within the tamarisk forest (Figure 40a). The difference between mean litter storage at flood and control sites within the cottonwood forest varied considerably, with no clear shift in the relationship between sites before and after flooding. At tamarisk sites, in contrast, there was detectable increase in litter storage at Tamarisk Flood relative to Tamarisk Control prior to flooding, indicating greater litter buildup at Tamarisk Flood, followed by a sharp decrease in the quantity of litter at Tamarisk Flood immediately following each flood in 1994 and 1995 (Figure 40b).

Preliminary measurements of litter at river sites suggests that long-term flooding does decrease litter storage. Although litter storage at River Control did not differ from that at cottonwood sites in 1995, values for River Flood were significantly lower in both April and September (Kruskal-Wallis tests, April:  $\chi^2 = 17.238$ ,  $P = 0.0006$ , September:  $\chi^2 = 15.993$ ,  $P = 0.0011$ ; Figure 41). Thus, although three floods were not enough to significantly reduce litter storage after 50 years of accumulation within non-flooded forests, repeated annual flooding does appear to affect this component of the riparian ecosystem. Mean litter storage values for all dates are presented in Appendix B - 7.

**Biomass of woody debris:** Although three years of seasonal flooding did not significantly reduce total woody debris at Cottonwood Flood compared to Cottonwood Control, lower biomass at River Flood compared to its control and the two other sites suggest that repeated flooding reduces woody biomass on the forest floor. Biomass of total woody debris was significantly lower at River Flood than at the other three sites, which were not significantly different from each other (ANOVA,  $F_{3,76} = 9.36$ ,  $P = 0.0001$ ; Figure 42). Similarly, biomass of coarse woody debris (CWD) was significantly lower at River Control than at the other sites (ANOVA,  $F_{3,76} = 6.27$ ,  $P = 0.0007$ ; Figure 42), which again did not differ from each other. In contrast, a significant ANOVA for biomass of fine woody debris (FWD) ( $F_{3,76} = 18.25$ ,  $P = 0.0001$ ), followed by multiple t-tests, indicated more FWD at Cottonwood Control than at the other three sites (Figure 42). Further, although FWD at Cottonwood Flood was greater than at River Flood, FWD did not differ significantly between Cottonwood Flood and River Control or between River Control and River Flood. Woody biomass estimates are presented in Appendix B - 9.

The distribution of woody biomass among transects within each site further illustrates the effects of flooding on forest floor wood (Figure 43). Most transects at River Flood contained less than 30 Mg / ha of woody debris, with a range of only 3.8 to 22.5 Mg / ha. In contrast, biomass estimates measured along individual transects at River Control ranged from 4.9 to 106.9 Mg / ha, with a much more patchy distribution of debris at that site. However, the biomass of woody debris measured among transects at the cottonwood sites was distributed similarly, with most transects at both sites containing 30 - 40 Mg / ha total biomass (Figure 43). This suggests that these distributions were roughly equal before experimental flooding and that three seasons of flooding were not enough to reduce it significantly.

We have found no estimates for woody biomass in riparian forests in arid regions; however, values for this study are comparable to the range recorded for temperate deciduous forests (Harmon et al. 1986). CWD estimates for our non-flooded sites were greater than those calculated for a *Populus tremuloides* forest in northern New Mexico that experienced over three times the annual precipitation as measured at Bosque del Apache (Gosz 1980, Dahm and Molles 1992). In contrast, the biomass of CWD at our River Flood site was much lower than that measured in the *P. tremuloides* forest.

Most of the identifiable wood found on the forest floor during this study was from *Populus* (Figure 44a). Although we have not measured the living biomass for all woody species at the sites, visual estimates suggest that *Populus* predominates living biomass as well. Each site contained a minor component of *Tamarix*, but more *Baccharis* sticks were present at Cottonwood Control than at other sites. Most of the wood greater than 2 cm diameter was in the advanced decomposition class at all sites (Figure 44b). In contrast, in many ecosystems the largest fraction of CWD falls in the intermediate or youngest decay classes (Harmon et al. 1986). *Populus* wood is very soft and begins to decay while still in the tree, as dead branches begin to shed bark rapidly (personal observations). However, although decay begins quickly, complete decomposition apparently progresses more slowly, as suggested by the slow rates of decay calculated for logs in the absence of flooding (see above, **Log Decomposition**). More wood at Cottonwood Control was in the slight to moderate decay classes than at Cottonwood Flood, suggesting that flooding may promote initial decomposition. River Flood had essentially no wood in the slight to moderate decomposition class.

A more thorough discussion of the biomass of woody debris is presented in Ellis et al., in review.

## PRIMARY PRODUCTION

### Understory species richness and abundance

There was no detectable effect of flooding on understory vegetation. The average number of understory species present per transect did not change across 3 years at either cottonwood site, or across 1.5 years at river sites (Kruskal-Wallis test,  $P > 0.05$ ; Figure 45). However, there was some variation in the total number of understory species present (Figure 46). Although shrub species richness did not change, with 3 to 4 species present at cottonwood sites, 2 species at River Control and 3 species at River Flood (Figure 46a, Appendix C - 2 through C - 6), forb species richness was more variable (Figure 46b, Appendix C - 2 through C - 6). Forb richness at Cottonwood Flood varied annually, but tended to be similar between spring and fall samples, while Cottonwood Flood had more forb species in the fall of each year than in the spring. River Control had high forb richness each year, while no forbs were recorded at River Flood. Grasses were essentially absent at Cottonwood Control and at River Flood, while 3 to 4 species were recorded at River Control (Figure 46c). In contrast, Cottonwood Flood had 3 to 9 grass species.

There was no significant change in the average intercept length (cover) of shrubs, forbs or grasses across 3 years at cottonwood sites or across 1.5 years at river sites (all  $P > 0.05$ ; Figure 47). There was a tendency for cover of each class to increase slightly between spring and fall, but considerable variation was present and increases were not significant. Most notable was the increase in grass cover between

spring and fall 1993. Although this increase was significant in a pair-wise test within that year, there was no difference when the entire 3 year sample period was considered, with grass cover in subsequent years intermediate to the 1993 measurements. We did not measure understory vegetation in 1991 or 1992; however, our observations suggest that grass abundance at Cottonwood Flood increased considerably after the first flood, which may reflect the addition of nitrogen as well as the input of water. Grasses were very localized and present primarily at the north end of the site. Since abundance estimates reflect averaging in southern transects that contained no grass, these estimates are low relative to the localized abundance at the north end of the site. The fact that no grasses were recorded at River Flood suggests that flooding per se does not promote their growth. Instead, we suggest that sunlight availability may be the primary factor influencing understory abundance in general. River Flood has a complete cottonwood canopy, with little light passing through to ground level. Where sunlight is available, as in the more open Cottonwood Flood, flooding and perhaps the input of nitrogen may promote grasses in particular. Historically, the patchiness of the multi-aged stands of forest may have provided spatial variation in forest cover, with understory plants more abundant in both young sites with low canopies and old sites with lower tree densities, while mature stands with complete cover, such as River Flood, probably lacked this structural component.

### Herbaceous biomass

Herbaceous growth varied considerably among years (Figures 48, 49, 50). Although these data suggest that flooding may reduce forb growth while promoting grasses, again an overriding factor appears to be the availability of sunlight. Herbaceous growth at cottonwood sites was generally greater in open areas with no canopy than at locations with a full canopy overhead (Figure 48). Cottonwood control and flood sites differed in measured herbaceous biomass only in 1994, when the greater mass of forbs collected in open locations at Cottonwood Control was marginally significant (Wilcoxon Rank Sum test,  $Z = -1.9446$ ,  $P = 0.052$ ) and the mass of grass was greater at Cottonwood Flood ( $Z = 2.6077$ ,  $P = 0.009$ ). However, although neither forb weight nor grass weight differed significantly among years in open locations or under full canopy at Cottonwood Control (Kruskal-Wallis tests, all  $P > 0.05$ ), there were significant differences among years at Cottonwood Flood for both forbs ( $\chi^2 = 15.561$ ,  $P = 0.001$ ) and grasses ( $\chi^2 = 17.294$ ,  $P = 0.0006$ ) in open locations (Figure 48). Forb weight was greatest at that site in 1992 and lower in each of the three seasons following flooding, while grass weight generally increased over this period. The increase in grasses at the north end of the site was striking over the three years of study, particularly in open areas. As described for understory species richness and abundance measurements above, much of this increase was not detected in the sampling procedure, since only one sample was collected along each of ten randomly selected transects; thus, the area with most of the grass growth was not fully sampled, and those values were averaged in with areas that had no grass. Forb weight for samples collected under full canopy at Cottonwood Flood also differed among years ( $\chi^2 = 10.431$ ,  $P = 0.015$ ), with a greater value in 1992 compared to other years. Again, the biomass of grasses clipped under full canopy locations did not differ significantly among years, there was a noticeable trend towards increasing mass at those locations as well (Figure 48). Herbaceous biomass data are summarized in Appendix C - 7 through C - 9.

Annual variation was also evident for herbaceous growth at tamarisk sites (Figure 49). Forb weight was greater at Tamarisk Control in 1991 ( $Z = 2.4859$ ,  $P = 0.013$ ) and in 1995 ( $Z = 2.7058$ ,  $P = 0.007$ ), while it was marginally greater at Tamarisk Flood in 1993 ( $Z = 1.9525$ ,  $P = 0.051$ ); differences in other years were not significant. Growth at both sites was greatest in 1992 (Figure 49). Some of this annual variation may reflect moisture availability. In July of 1991, the Tamarisk Control site was accidentally partially flooded for a period of a few days, and we observed an increase of herbaceous growth following that event. Similarly, the winter and spring of 1992 were exceptionally wet compared to other years of the study (Figure 8), and herbaceous growth at both sites was higher then compared to the three years following. However, the decrease at Tamarisk Flood compared to Tamarisk Control in

1995 suggests that water standing on the site for a month may inhibit growth. Grasses were essentially absent in all years except 1995 at Tamarisk Flood. This increase does reflect flooding, as we observed an increase of saltgrass following flooding in the open ditch running along the west side of that site. This spread into the edge of the site and was collected primarily near the end of one transect. Although the abundance of this grass was increasing and it was spreading into the edge of the tamarisk vegetation, very little was within the forest under the full canopy. This further supports our contention that sunlight is an overriding factor contributing to herbaceous growth.

Very little herbaceous growth was present at river sites (Figure 50). While biomass values for both forbs and grasses were essentially zero at both sites in 1994, both forbs and grasses were present in low abundance in 1995 at River Control. As observed at the other sites, herbaceous growth at these sites occurred primarily in open areas with no canopy. Observations at River Flood again support our conclusions about light availability, in suggesting that flooding may act indirectly on herbaceous growth through its effect on the canopy. Cottonwood density was higher at River Flood and they formed a nearly closed canopy which excluded sunlight from the forest floor during the growing season. Trees at cottonwood sites and at River Control were more patchily distributed, thus allowing sunlight to reach patches of the forest floor; these locations supported herbaceous growth. Where grass was present in open areas at Cottonwood Flood, it spread rapidly following flooding, although forb growth was suppressed. Therefore flooding may have its greatest influence on herbaceous growth via its effect on the health and growth of canopy trees.

#### **Foliage density and diversity**

Foliage height diversity (FHD), a measure of the complexity of structure within the forest, was consistently 0.47 at Cottonwood Control during all years, and changed only slightly at Cottonwood Flood from 0.46 in 1991 to 0.47 in 1994 and 0.48 in 1995. Thus sites did not differ in the amount of structural complexity, nor did this change among years. However, foliage density values indicate that the amount of vegetation in each height class decreased at both sites between 1991 and 1994 (Figure 51). Values then remained similar in 1995 at Cottonwood Flood, while foliage density increased slightly at Cottonwood Control. Changes at Cottonwood Control primarily reflect increases at the lower size classes. Estimates of horizontal diversity, or patchiness, indicates the distribution of vegetation within each height class. Patchiness dropped substantially at both sites between 1991 and 1994 (Figure 52), suggesting increased uniformity in the distribution of vegetation. Patchiness then increased at Cottonwood Control in 1995 while continuing to decrease at Cottonwood Flood. Foliage density measurements used to calculate foliage diversity and patchiness are presented in Appendix C - 10 and C - 11.

Foliage density and patchiness data suggest that different factors may be influencing vegetation at the two sites. The initial drop in foliage density and patchiness at both sites may reflect local climatic conditions. However, opposite responses in 1995 suggest that suppressive effects of the flood may override these factors at Cottonwood Flood. Flooding appears to decrease both the density of vegetation and the patchiness of its distribution.

#### **Growth of major tree species**

Flooding promoted the growth of established cottonwood trees. The size-class distribution of trees at Cottonwood Flood changed significantly between 1991 and 1996 (Figure 53; Kolmogorov-Smirnov Goodness of Fit test,  $D = 0.1364$ ,  $P < 0.02$ ), which reflected a shift of individuals from the 0 to 10 cm and 10 to 20 cm size classes to the 20 to 30 cm and 30 to 40 cm size classes. In contrast, the size-class distribution of trees at Cottonwood Control did not change during this period. However, since the mean DBH of trees at Cottonwood Flood increased more during the 1991 to 1993 pre-flood period than did the mean DBH of trees at Cottonwood Control (Figure 54), this change in size class distribution alone does not indicate a positive effect of flooding.

The change in growth rates before and after flooding is more conclusive. A positive acceleration, or change in growth rates, would indicate that growth rates between 1993 to 1996 were greater than rates between 1991 to 1993, while a negative change in growth rates would indicate that growth rates decreased during the 1993 to 1996 period. Trees at Cottonwood Flood increased growth rates after the initiation of flooding, with an average change of  $0.33 \pm 0.15 \text{ mm y}^{-2}$ , while trees at Cottonwood Control on average decreased growth rates ( $-0.19 \pm 0.10 \text{ mm y}^{-2}$ ; Figure 55). Differences in these average changes in growth rates at the two sites were significant (Wilcoxon Rank Sum test;  $Z = -2.713$ ,  $P = 0.007$ ). Further, trees at the upper and lower ends of the size-class distributions reacted differently to flooding. On average, growth rates of trees at Cottonwood Flood with initial diameter less than 40 cm did not change before and after flooding, while the small trees at Cottonwood Control decreased growth rates (Figure 55). The difference in growth rates for small trees at the two sites was significant (Wilcoxon Rank Sum test,  $Z = -2.156$ ,  $P = 0.031$ ). In contrast, trees at both sites with initial diameter greater than 40 cm had, on average, positive increases in growth rates (Figures 55); although these values did not differ significantly between sites, they tended to be greater at Cottonwood Flood.

Relatively high variance in acceleration or change in growth rates indicates considerable variation among individuals at both sites. We assessed this individual variation by plotting initial size of individuals (DBH in 1991) against the individual change in growth rates after flooding (Figure 56). Trees at Cottonwood Flood with initial diameters greater than 40 cm showed a significant positive increase in growth after flooding (linear regression,  $F = 20.20$ ,  $P = 0.0001$ ), with larger trees showing a greater response. No relationship existed among larger trees at Cottonwood Control, with little overall change in growth rates. In contrast, we observed more variation in the changes in growth rates at Cottonwood Flood with initial diameters less than 40 cm (Figure 56). Although the average change in growth rates for small individuals at Cottonwood Flood did not differ from zero ( $0.07 \pm 0.13 \text{ mm y}^{-2}$ ), some individuals showed substantial increases in growth while others decreased growth rates after flooding. Growth rates for small trees at Cottonwood Control were more tightly clustered near the zero line, with slightly more individuals exhibiting negative changes. The decrease in growth rates by small trees at Cottonwood Control may reflect the change in annual precipitation patterns. Increased precipitation during 1992 and 1993 may have increased the growth rates of these smaller trees, while the drier conditions of 1994 to 1996 may have decreased their growth rates. Larger trees with deeper taproots may be able to draw upon shallow ground water and so are less influenced by year to year variation in precipitation. These data suggest that flooding may select against some small individuals and thin mature stands, allowing the remaining trees to grow larger.

Trees at the river sites were significantly larger than trees at the cottonwood control and flood sites (Kruskal-Wallis test,  $\chi^2 = 33.345$ ,  $P = 0.0001$ ). While the mean DBH at Cottonwood Control and Cottonwood Flood in 1996 were 24.3 cm ( $\pm 1.2$ ) and 27.0 cm ( $\pm 1.5$ ), respectively, diameters averaged 33.2 cm ( $\pm 2.4$ ) at River Control and 33.6 cm ( $\pm 1.6$ ) at River Flood. The distribution of individuals at the river sites indicates more trees in larger size classes (Figure 57) compared to those at the cottonwood sites (Figure 53).

What is the source of variation among individuals? To answer this question, we considered the sex of individual trees relative to changes in growth rates. Although we have recorded sexes for fewer individuals at the river sites, preliminary sex ratio data indicate that both cottonwood sites and River Control were male biased, while River Flood may have more females (Table 2). Many individuals were non-reproductive at the cottonwood sites, with fewer so at river sites, so the sexes of these trees are unknown. These tended to be smaller, and thus presumably younger, individuals (Figure 58), although the relationship between size and age is not known. Most individuals greater than 40 cm DBH at Cottonwood Flood were males. Combined with the greater number of females at River Flood, this suggests that female survival may be greater under moist conditions while males may survive better under drier conditions, as would have been the case at Cottonwood Flood prior to our experimental flooding. These data do not indicate the timing of selection for males or females, that is, whether differential survival occurs among seedlings, saplings, or among older trees. However, the high variance in growth

responses to flooding by established trees less than 40 cm suggests that some differential response is present among those trees, although we do not know whether such selection might have occurred at younger ages under regular flooding conditions. Regular flooding along the river, providing greater water availability during establishment phases, may influence cottonwood sex ratios over a larger spatial scale in the valley, and thus may strongly influence reproductive output and population dynamics.

Our data suggest further that physiological responses to flooding by individual cottonwoods may differ at sites where floods are restored versus sites that have a long history of flooding. Litter production results suggest that trees at Cottonwood Flood may suffer from initial root stress under anoxic conditions when flooding is first restored (see above, **Litter production: litterfall traps**). These growth responses support this idea, suggesting that larger, more established trees with better developed root systems are better able to withstand the stress of the anoxic conditions during experimental flooding.

Although we did not assess mortality of cottonwood trees in 1993, prior to flooding, three of the trees monitored at each cottonwood site had died by September 1994. Two more trees died at Cottonwood Flood between September 1994 and April 1996, while nine trees died at Cottonwood Control during the last year alone. Thus approximately 2% of the trees died at each site between 1991 and 1994. However, only 1.5 % more trees died at Cottonwood Flood between 1994 and 1996, while 6.5 % died at Cottonwood Control. This difference in mortality suggests that flooding may benefit long-term survival of cottonwood trees. This may be particularly important during periods of drought, as experienced by the region during the winter of 1995-1996. Trees at Cottonwood Flood may be more able to withstand a dry winter period when preceded by a substantial summer flood. Continued monitoring of these trees will reveal more long-term effects of flooding.

Size-class distributions of tamarisk trees changed significantly between 1991 and 1996 at both tamarisk sites (Figure 59; Kolmogorov-Smirnov Goodness of Fit tests, Tamarisk Control,  $D = 0.395$ ,  $P < 0.001$ , Tamarisk Flood,  $D = 0.241$ ,  $P < 0.001$ ). Growth rates decreased at both sites between the 1991-94 and 1994-96 periods (Figure 54). However, the decrease at Tamarisk Control was significantly greater (Wilcoxon Rank Sum test,  $\chi^2 = 3.466$ ,  $P = 0.0005$ ). Whether the relatively lower decrease in growth rates at Tamarisk Flood reflects the influence of flooding is unknown.

### Cottonwood recruitment

There was no successful cottonwood establishment within the main study area. Establishment did occur at Cottonwood Flood near the edge of the study area, where the ground was cleared by a bulldozer to install a water control structure. There was no overstory at this location and an adjoining ditch contained water for most of the study. Seedlings were established there from natural seed fall during the first flood and persisted, supporting earlier reports that cottonwoods require a scoured sandbar, full sunlight and a high water table for successful germination (Scott et al. 1993).

### Tree and shrub density

Three years of flooding did not affect tree and shrub densities; densities for all woody species were similar between years within both Cottonwood Flood and Cottonwood Control (Figure 60, 61). There was a slight increase in the number of dead *Salix* at both flood and control sites (Figure 60). Although there was a trend for increased size of *Amorpha* at Cottonwood Flood, suggesting a positive effect of flooding, high variance gives insignificant results (Figure 61). The greater density of *Amorpha* at River Flood compared to River Control suggests that flooding benefits this species (Figure 63). Tree and shrub densities are summarized in Appendix C - 12 through C - 14.

*Populus* density was higher at Cottonwood Flood compared to River Flood and Cottonwood Control. *Populus* density was lowest at River Control (Figure 62). However, although *Populus* density was lower at River Flood, trees were larger at that site (see *Growth of major tree species*). This resulted in a more complete canopy cover at River Flood, while patchy canopies typified the other sites.

*Tamarix* densities were higher at both river sites compared to cottonwood sites (Figure 62), and the number of dead *Tamarix* clumps at River Flood were much higher than at the other three sites. The high density of "living" clumps at River Flood reflects the sampling technique used. Since a clump was counted as living even if only a tiny living sprout was present, many clumps were counted that included over 95% dead stems. Thus an actual count of individual stems within each clump would reveal a much lower density of living stems at this site. *Tamarix* clumps at other sites included primarily living stems. These data strongly suggest that flooding decreases *Tamarix* survivorship, although they do not differentiate between the direct effects of standing water and indirect effects of decreased sunlight due to a more complete overstory. *Tamarix* at River Flood were mostly concentrated along the eastern edge of the study area, on relatively high ground that did not experience complete surface submergence throughout the entire flood. This may reflect a negative effect of the water on adult trees, or may indicate that *Tamarix* establishment was more successful on the higher sandbar, while young plants that germinated in the channel were scoured away. Observations of vegetation south of River Flood reveal healthy stands of very large *Tamarix* that are discolored at their bases from exposure to floodwater, indicating that flooding *per se* is not detrimental to *Tamarix*. As discussed for herbaceous vegetation, sunlight availability is likely more important to *Tamarix* survival. If *Populus* are established prior to or simultaneously with *Tamarix* under the beneficial conditions of flooding, the latter may gradually die as the *Populus* overstory becomes more complete and shades the plants below. Thus annual flooding, especially on open sites with new seedling establishment, may help to limit *Tamarix* by improving *Populus* establishment and growth.

*Amorpha* was the most common understory shrub at River Flood, but was very patchy in distribution (Figure 63). In contrast, *Forestiera* was the most common understory shrub at Cottonwood Flood while *Baccharis* was most common at Cottonwood Control. River Control contained a minor component of *Baccharis*. These shrubs also appear affected by light availability, as they are more abundant under gaps in the canopy.

## CONSUMERS

### Soil bacteria and fungi

Soil bacteria and fungi showed rapid responses to flooding. Although cottonwood sites differed for some parameters prior to flooding, values for most parameters increased relatively more at Cottonwood Flood (Appendix D - 1). Microbial biomass carbon levels increased at Cottonwood Flood after the first flood, and increased at that site after each subsequent flood (Figure 64). Although total bacteria, aerobic heterotrophic bacteria, and cellulose decomposers did not increase after one annual flood, these parameters increased at Cottonwood Flood by 1994 and remained elevated (Figure 64). Similar increases were seen at River Flood relative to River Control after flooding in 1995 (Figure 64; Appendix D - 2).

Dehydrogenase activity, which indicates biological activity in the soil, increased dramatically at Cottonwood Flood after inundation in both 1994 and 1995, and at River Flood in 1995, while pre-flood levels were similar between control and flood sites (Figure 65). Levels of this enzyme were not measured in 1993. Although total fungi showed an unexplained increase at Cottonwood Control in 1993, levels increased at Cottonwood Flood in both 1994 and 1995, as well as at River Flood (Figure 65). Mycorrhizal inoculum potential also increased at cottonwood and river flood sites after inundation each year.

Levels of both bacterial and fungal parameters tended to be higher at cottonwood sites than at river sites. This probably reflects the greater abundance of potential substrate present at cottonwood sites. These values may eventually decrease after several years of repeated flooding as bacterial and fungal activity decrease the standing stock of organic matter on the forest floor.

*Tamarix* control and flood sites differed in total bacteria, aerobic heterotrophic bacteria, chitin decomposers and mycorrhizal inoculum potential prior to flooding (Appendix D - 3). As was the case

at cottonwood sites, tamarisk sites differed in most bacterial and fungal parameters after flooding, with increases in values at Tamarisk Flood. Thus soil organisms located below this exotic vegetation show responses similar to those in soils in native forests. However, values for most of these parameters were lower at tamarisk sites compared to cottonwood sites (Appendix D - 1 and D - 3).

Microbial and fungal activity influences rates of wood and leaf decomposition (Harmon et al. 1986). In an old growth forest in the Pacific Northwest, microbial respiration decreased during the late-summer drought, indicating an effect of temperature and moisture on seasonal decay rates of coarse woody debris (Marra and Edmonds 1994). Both moisture content and aeration influence the growth of wood decay fungi (Rayner and Todd 1979). In general, optimal fungal growth in wood occurs at about 40 % moisture, with 26 - 32 % of wet weight needed for the initiation of decay, as well as a pore space containing approximately 20 % air (Rayner and Todd 1979). As moisture increases above 40 %, conditions become increasingly anaerobic and growth of most fungi in wood declines. An inverse relationship between decay rate and annual precipitation for *Abies* and *Tsuga* (Harmon et al. 1987) illustrates how excessive moisture may decrease aeration essential to obligate aerobic fungi (Harmon and Chen 1991). These studies suggest that fungi may be inactive during periods of inundation in the riparian forest, but that residual moisture retained in wetted logs may provide conditions favoring bacterial and fungal growth. Thus, intermittent wetting of riparian soils combined with water draw-downs to increase aeration may optimize potential decomposition within these forests.

### Surface-active and aerial arthropods

**Surface-active arthropods:** Pitfall captures suggest that annual flooding leads to a restructuring of the surface-active arthropod community, with increases or decreases in various groups. Although total taxonomic richness of arthropods over the entire study period did not differ between control and flood sites within each forest type (Figure 66, Appendix E - 1), differences in richness were detected within certain groups. More species of ants were captured at control sites compared to flood sites, while carabid beetles were more common at flood sites (Figure 66). Cottonwood sites had greater richness overall than the other two forest types, while taxonomic richness was generally greater at tamarisk than at river sites (Figure 66). This may in part reflect sampling effort, with the greatest number of collections made at cottonwood (30), followed by tamarisk (20) and river (9) sites. Spider richness was particularly high at tamarisk sites (Figure 66, Appendix E - 1). Since all spiders are predators, this suggests a significant arthropod food base present in these sites; this is supported by our abundance data which indicate that tamarisk supports a fairly diverse and abundant arthropod community (Appendix E - 1). We will present abundance data for surface-active arthropods at tamarisk sites, but our data are insufficient to discuss how flooding affects these populations.

Two species of exotic isopods, *Armadillidium vulgare* sow bugs and *Porcellio laevis* wood lice, which are both macrodetritivores, were the most common arthropods captured at all study sites. Abundance varied over time at both cottonwood and tamarisk sites (Figures 67, 68). Randomized intervention analysis (RIA) showed a significant decrease in the relative abundance of *Armadillidium* at Cottonwood Flood after the initiation of flooding ( $P < 0.009$ ; Figure 69). However, this may be a temporary effect, as the decrease was strongest after the first flood and *Armadillidium* abundance appears to be recovering (Figure 69). *Armadillidium* was also more common at River Control than at River Flood, but numbers at those sites were lower than at cottonwood sites (Figure 67). Although population activity of *Porcelio* was less clearly related to flooding since captures of this species were lower at Cottonwood Flood relative to Cottonwood Control during the pre-flood period, *Porcelio* has been virtually absent from Cottonwood Flood since flooding was begun. However, this species was more common at River Flood than at Cottonwood Flood.

While *Armadillidium* captures declined following flooding, cricket (*Gryllus alogus*) populations increased significantly (RIA,  $P < 0.02$ ; Figures 70, 71). Cricket captures were very low throughout 1991 and 1992, with slightly more captured at Cottonwood Control than at Cottonwood Flood during that time



(Figure 70). Cricket abundance was quite low at tamarisk sites throughout the study (Figure 70). There was a slight increase in the number of crickets at Cottonwood Flood after the 1993 flood, followed by a dramatic increase in cricket captures following the 1994 flood. Cricket captures were only slightly higher at Cottonwood Flood than at Cottonwood Control in 1995, but captures at River Flood were high in both 1994 and 1995. We (CSC, MCM) have also observed high cricket densities in naturally flooding bosque on the east side of the Rio Grande near the north end of Bosque del Apache. Crickets may have been the primary macrodetritivore in the unaltered river system, prior to the removal of flooding and introduction of exotic isopods. While isopods can consume relatively dry, intact leaf litter, crickets prefer moist, partially decayed leaves (CSC, personal observation), as created by periods of annual inundation. Thus a shift in abundance from isopods to crickets may reflect a difference in resource availability. Alternately, the shift may reflect a difference in direct tolerance to standing water. We observed large numbers of crickets fleeing in advance of the incoming floodwaters at the initiation of the 1994 flood; therefore, high post-flood numbers may partly reflect rapid recolonization after water receded. However, since large numbers of post-flood crickets were early instars, flooding may have promoted laying and/or hatching of their eggs. In contrast, isopods were regularly observed clinging to floating wood or tree trunks during the flood, suggesting they are unable to vacate a flooded patch of forest. Observations following additional floods will indicate whether this apparent change in the dominant macrodetritivores remains consistent with flooding, or whether *Armadillidium* populations will continue to recover after the initial suppression.

Ant abundance (all species combined) was high in the summer of 1991 at both cottonwood sites and Tamarisk Flood (Figure 72), and then variable in other years. Although the decrease in ant abundance after flooding was not significant in the RIA ( $P < 0.22$ ; Figure 73), this reflects the high number of ants captured in a single trap at Cottonwood Control in August 1991, which suggests an ant nest was located next to the trap at that time. Without this point, the data suggest that ant abundance decreased at Cottonwood Flood after flooding (Figure 73). A summary of ant taxonomic richness indicate 12 taxa present at Cottonwood Control during the pre-flood period and 15 taxa present during the post-flood period, while at Cottonwood Flood there were 7 taxa prior to flooding and 6 taxa recorded after flooding (Table 3). Total abundance of ants during all pre-flood samples at Cottonwood Control was 506 individuals while during the period after flooding this increased to 780 individuals (Table 3). In contrast, total pre-flood abundance at Cottonwood Flood was 369 individuals, with captures dropping to 87 individuals after flooding. Twelve ant taxa were recorded at River Control, with a total of 255 individuals, while only 7 taxa and 124 individuals were captured at River Flood (Table 3). The Morisita-Horn quantitative similarity index for ant taxa between Cottonwood Control and Cottonwood Flood prior to flooding was 0.81, which dropped to 0.71 for the period after flooding was begun. This value was 0.12 for the two river sites. Thus cottonwood sites show greater similarity in the taxonomic richness of ants than do river sites, but this similarity may be decreasing.

Four of the six ant species present at Cottonwood Flood after flooding were present in very low numbers ( $\leq 4$  individuals captured; Table 3). Although 52 *Monomorium minimum* were captured at Cottonwood Flood after flooding, that was a decrease from 332 individuals prior to flooding; meanwhile, 255 and 205 individuals of that species were captured at Cottonwood Control during pre- and post-flood collections, respectively. *Monomorium minimum* is a ground-dwelling species adapted to forest clearings (Hölldobler and Wilson 1990) and was the dominant species at Cottonwood Control, as well as at Cottonwood Flood prior to flooding. It was absent from both river sites. In contrast, the number of *Crematogaster cerasi*, a largely arboreal species, increased at Cottonwood Flood after flooding and was by far the most common ant at River Flood. Hölldobler and Wilson (1990) suggest that, when present, *Crematogaster* is a dominant species and may form the core of the local ant community, while affecting the composition and abundance of not only other ant species but other arthropods and plants as well. Two species of *Pogonomyrmex*, large ground-dwelling harvester ants, were also present at control sites but absent from flood sites, although this difference was observed prior to flooding at cottonwood sites.

Beetle population responses to flooding varied. Carabid beetles, consisting mainly of predatory species, increased after flooding, although this increase was not significant with the RIA ( $P < 0.23$ ; Figures 74a, 75). This lack of significance was most likely driven by the initial suppression of carabids immediately following the 1993 flood (Figure 75); without the August 1993 value, there is a clear increase in the number of carabid beetles. This is summarized more clearly by the total number of individuals captured before and after flood: captures increased from 14 to 126 individuals at Cottonwood Flood, while at Cottonwood Control captures increased from 3 to 36 individuals (Table 4). Carabid abundance was also quite high at River Flood (Figure 74a). Taxonomic richness of carabids also increased with flooding. Thirteen taxa within this family were present at Cottonwood Flood during post-flood collections, compared to five taxa at that site prior to flooding (Table 4). Meanwhile, six taxa were captured at Cottonwood Control during the post-flood period, with two taxa present there during the initial period. River Flood was also more taxonomically rich than River Control, with 9 and 4 taxa, respectively. The similarity index between cottonwood sites decreased from 0.85 prior to flooding to 0.46 after flooding, while the similarity index at river sites was 0.21. Thus, flooding appears to favor both abundance and diversity of carabid beetles. In contrast, both staphylinid and tenebrionid beetles appeared to decrease slightly after flooding (Figure 74b, c), although tenebrionid abundance increased slightly in June of both 1993 and 1995. Very few individuals of either of these families were captured at River Flood. Staphylinids and tenebrionids were generally more common at tamarisk sites than were carabids (Figure 76).

Abundance of the most common family of spiders, Lycosidae, was quite variable at all sites (Figure 77) and appeared unaffected by flooding (RIA,  $P < 0.81$ ; Figure 78), although increases in captures were observed during both 1993 and 1994. Recolonization after flooding may be rapid, and high numbers may reflect abundant prey availability. Lycosid abundance at Cottonwood Flood may also be affected by the flooding procedure. Cottonwood Flood was bordered by a borrow ditch that held water year-round since the first flood. Lycosid spiders are attracted to moist areas, and their high mobility would allow them to move readily across Cottonwood Flood while responding to water in the adjacent ditch. Slightly more lycosids were captured at River Flood than at River Control during 1994, but abundance at both sites was fairly low during 1995. Overall, these results suggest that lycosid abundance may be more influenced by some factor other than flooding.

**Aerial insects:** We classified captures on sticky traps into nine groups of insects: aphids (Homoptera, Aphididae), leafhoppers (Homoptera, Cicadellidae), nematoceran flies (Diptera, suborder Nematocera), other flies (Diptera), ichneumonid wasps (Hymenoptera, Ichneumonidae), chalcidoid wasps (Hymenoptera, Chalcidoidea), other bees and wasps (Hymenoptera), beetles (Coleoptera) and thrips (Thysanoptera) (Appendix E - 2 through E - 4). Populations of aerial insects were generally quite variable over time, and flooding appeared to significantly affect only leafhopper abundance.

Leafhopper populations varied over time (Figure 79a), with a significant decrease in abundance after the initiation of flooding (RIA,  $P < 0.007$ ; Figure 80a). Aphids were typically fairly low in number and were unaffected by flooding (Figure 79b). An interesting and unexplained peak in aphid abundance was observed in October 1995 at Cottonwood Flood and both river sites. Populations of both nematoceran flies, as well as other flies combined, were also variable over time (Figure 81), but neither were affected significantly by flooding ( $P > 0.05$ ; Figure 82). Similarly, populations of both ichneumonid and chalcidoid wasps varied over time, while other wasps were generally low in number except during the spring and summer of 1995 (Figure 83). However, there were no differences in abundance of chalcidoid wasps before and after flooding (Figure 80b). Beetles captured on sticky traps showed mid-summer peaks (Figure 84a), but these were not affected by flooding. Thrips generally showed peaks in abundance in May or June, with especially high numbers in 1995 (Figure 84b), but no flooding effects were detected.

Aerial insects were also fairly abundant at tamarisk sites, and showed considerable variation over time as at cottonwood sites (Appendix E - 3). Since our trapping data in tamarisk do not cover the period of flooding, these data are not presented graphically. However, it is significant to note that the abundance of aerial insects at tamarisk sites was often equal or greater than at cottonwood sites, indicating use of this

habitat by these consumers. In addition, aerial insects may provide significant food resources for other consumers, including birds. We have observed numerous warblers in these sites (Ellis 1995), which suggests that these birds are successfully using this resource.

### Mammals

**Species composition and abundance:** Three years of experimental flooding did not appear to affect the rodent community. Species composition at Cottonwood Flood, although variable among years, did not change relative to Cottonwood Control in response to flooding. *Peromyscus leucopus* was the dominant species in all years at both sites, while *Reithrodontomys megalotis* and *Neotoma albigula* occurred irregularly and in low numbers (Figure 85 and Appendix F - 1 through F - 4). *P. leucopus* was the only species caught at river sites. The following results focus on *P. leucopus*. A more detailed discussion of these results is presented in Ellis et al. (in review).

Experimental flooding had no detectable effect on the abundance of *P. leucopus*; annual variation in abundance was high at both cottonwood sites, both before and after flooding (Figure 85). Densities at the sites after month-long floods in 1993 through 1995 were not consistently different from those observed prior to flooding. Further, densities at Cottonwood Flood were within the normal range of those detected at that site in 1991 and 1992, suggesting that they were within the normal range of annual variation. However, although rodent abundance did not change significantly after three experimental floods, *P. leucopus* was more abundant at River Flood than at River Control during the single trapping effort there in 1995. A total of 47 *P. leucopus* was captured at River Flood over 180 trap-nights, with nightly trap success ranging from 50 - 65 %. Meanwhile, only 22 individuals were captured at River Control, with nightly trap success ranging from 17 - 35%. Although these data are limited, they suggest that *P. leucopus* are not adversely affected by long-term (2.5 months) flooding and that populations may actually benefit from it.

*Peromyscus leucopus* is common in floodplain woodlands in other regions of the United States, especially where flooding occurs (Layne 1958, Wetzel 1958, Ruffer 1961, Blem and Blem 1975, Mumford and Whittaker 1982), although other studies have shown negative effects of flooding (Blair 1939, McCarley 1959, Turner 1966).

**Reproductive activity:** Reproductive activity of *P. leucopus* did not appear to be affected by experimental flooding; all adults at Cottonwood Flood were in reproductive condition immediately after flooding and the control and flood sites did not differ in the percentage of adults in reproductive condition for any sample period (Figure 86a). Although slightly more adults were reproductively active at River Control (89.5%) than at River Flood (69.2 %) in late August 1995, three juveniles and seven subadults were captured at River Flood while no juveniles and only three subadults were captured at River Control. This suggests that reproduction had occurred at River Flood and that reproductive activity at the two river sites was not synchronized.

Adult sex ratios of *P. leucopus* varied within each cottonwood site prior to flooding (Figure 86b). With the exception of Cottonwood Flood in June 1991, both sites tended to have nearly even or slightly male-biased sex ratios during the first two years of the study. There was a greater male-bias at Cottonwood Flood following the initiation of flooding in 1993, although a male-bias was also detected at Cottonwood Control during some of those periods. Adult sex ratio was male-biased at Cottonwood Flood in August of both years following flooding, but was even in August of the two years preceding flooding. The population at River Flood had an even sex ratio (51.4 % males) in August 1995, while there was a significant male bias at River Control (63.2 %;  $P < 0.01$ ). Many populations of *P. leucopus* show male-biased sex ratios (e.g., Terman and Sassaman 1967, Myton 1974, Barry and Francq 1980), while other studies report even sex ratios (Nicholson 1941, Blem and Blem 1975). Although a male-biased sex ratio may suggest that males are wandering more or have larger home ranges, it is not clear

whether this reflects an influence of flooding or whether these shifts may reflect random variations in sex ratio.

**Activity during flooding:** With the decrease in vegetation lining the Rio Grande it is important to ask whether mice can remain in the inundated forest during flooding, or must disperse to adjacent areas, which in many reaches along the valley may no longer contain suitable habitat. Our data from traps placed in trees during the flood indicate that some mice do remain within the flooded forest. Mice were captured in trees at both cottonwood sites in all trapping periods (Figure 87 and Appendix F - 5). Trapping success in trees tended to be slightly greater at Cottonwood Control prior to flooding, while during the flood trapping success in trees was slightly greater at Cottonwood Flood. Trapping success was similar at the two sites following the flood. The climbing ability of *P. leucopus* is well documented (e.g., Horner 1954, Kaufman et al. 1985, Smith and Speller 1970) and many studies document the use of trees as day refuges (Wolff and Hurlbutt 1982) and nesting sites (Nicholson 1941, Ruffer 1961, Tadlock and Klein 1979). Several studies suggest that this species may use trees as refugia during flooding (Wetzel 1958, McCarley 1959, Mumford and Whittaker 1982). Further, *P. leucopus* is known to be a capable swimmer (Teeters 1945, Ruffer 1961, Sheppe 1965) and easily travels through flooded areas both by swimming (LME, personal observation) and by travelling across fallen logs (Ruffer 1961, LME, personal observation). Thus, the presence of standing water does not appear to inhibit *P. leucopus* activity. The gradual rise of water in this type of flooding likely provides adequate time for mice to move in response to inundation. At Cottonwood Flood, large quantities of fallen branches, toppled trees and various shrubs, in addition to standing large trees, provide ample refugia during a flood. We have also captured *R. megalotis* and *N. albigula* in trees during this study, indicating that these species likewise have the potential to escape flood water.

Figure 88a indicates that in 1992, with no flooding, more of the mice captured in April were recaptured in June and August at Cottonwood Control than at Cottonwood Flood. Site differences were slightly greater in 1993, when proportionately fewer of the mice at the flood site were recaptured immediately following the flood, compared to the percent recaptured at the control site at that time. Differences between sites in August recapture rates were small in 1993. In 1995, June recaptures were again slightly greater at Cottonwood Control, while proportionately more mice were recaptured in August at Cottonwood Flood. Figure 88b shows that sites were similar in the proportion of new individuals (mice not caught in April or May) caught in August 1992 and in June and August in 1993, but slightly more new individuals were caught at the flood site in August 1992 and in June and August 1995.

These data suggest that during the first experimental flood, some mice did leave the site, but they returned to the site within two months of flooding. By the third year of flooding, proportionately more mice were recaptured, although the actual number was lower for both sites compared to previous years. Proportionately higher August recaptures at Cottonwood Flood, as well as an increase in new individuals captured there, suggest that conditions at the flood site may have been favorable after flooding. This was observed in a bottomland site in Illinois, where although some floodplain *P. leucopus* disappeared for a month or more after flooding, they eventually returned and post-flooding site tenacity was high (Blem and Blem 1975). Further, there was no evidence in that study that mice moved to the uplands from the floodplain after flooding; rather, all post-flood movement was from the uplands into the floodplain. In Ohio, *P. leucopus* increased use of peripheral portions of their home range in response to small-scale spring flooding, even though these areas were also partially inundated (Ruffer 1961).

## SUMMARY

- 1. Meteorological conditions:** Soil and air temperatures at all three forests were reduced during flooding, which occurred in late spring - early summer, the warmest time of the year. Precipitation varied greatly among years; increased winter precipitation was recorded during 1991-92, 1992-93, and 1994-95, in response to the influence of El Niño conditions. Soils at flood sites were saturated during flooding and re-wetted frequently following flooding. In contrast, soils at control sites typically remained dry until the late-summer thunderstorms. Thus flooding may decrease hydrophobicity of soils and thereby increase infiltration of late summer precipitation.
- 2. Hydrology and water chemistry:** Water table elevation at Cottonwood Flood increased by slightly over 2 m during flooding, completely saturating the rooting zone. Although dissolved oxygen in groundwater at Cottonwood Flood increased during flooding relative to that at Cottonwood Control, it remained well below levels of the oxygenated flood water. Dissolved organic carbon levels increased in groundwater at Cottonwood Flood during flooding, but plateau concentrations decreased each year, suggesting a decrease in the supply of water soluble carbon in the forest floor. Repeated flooding increased post-flood levels of ammonium-nitrogen; however, levels decreased during peak flood, perhaps due to immobilization in the shallow aquifer sediments by microbial demand and sorptive processes.
- 3. Soils:** Experimental flooding increased the crumb structure of soil at Cottonwood Flood; a well-developed crumb structure was also evident in soil at River Flood. Soils at Cottonwood Control and the river sites contained relatively high fractions of silt; this was especially true for the latter in 1995, while the fraction of clay increased the last year at Cottonwood Flood. Flooding appeared to decrease concentrations of the monovalent cations sodium and potassium, while the divalent cations calcium and magnesium appeared unaffected by three seasons of experimental flooding; however, the divalent cations were higher at River Flood than at River Control. Flooding may have also depressed sodium absorption ratios. Total phosphorus and carbon may have decreased slightly at Cottonwood Flood relative to Cottonwood Control, while total carbon was higher at River Flood than River Control. Total nitrogen increased appreciably at both cottonwood sites throughout the study, but not at the river sites. Basal respiration decreased at Cottonwood Flood only after the first flood, apparently in response to anoxic conditions. It increased significantly at River Flood in 1994, but not in 1995 following 2.5 months of inundation.
- 4. Silt deposition:** Considerably more silt was deposited during the natural flood than during the experimental flood. At River Flood, an average of  $155.06 \text{ g / m}^2 / \text{day}$  was deposited by flood water, while silt deposited at Cottonwood Flood averaged only  $8.03 \text{ g / m}^2 / \text{day}$ . Flooding from the Rio Grande contributes a significant amount of nutrient-laden sediments to the forest while the water is in turned "cleaned" during this passage through the bosque.
- 5. Litter production:** There was a temporal shift in the effect of flooding on litter production. Litter production was depressed at Cottonwood Flood relative to Cottonwood Control after the first flood, but this effect decreased after the second flood and was reversed after the third flood. More cottonwood leaves were produced at River Flood than at the other three sites during the last two study seasons, and leaves were also generally larger there. Overall, cottonwood leaves at all sites were larger and thinner in 1994-95 than in 1995-96. Litterfall at tamarisk sites was unaffected by flooding.
- 6. Leaf decomposition and leaching:** Flooding increased rates of leaf decomposition in all three forests and appears to help regulate the timing of nutrient release and cycling. Additional annual variation in leaf decomposition may reflect amounts of precipitation, because increased overwinter decomposition occurred during years with high winter precipitation. Approximately 30-35 % of leaf mass loss appears mediated

by leaching during the first 24-48 hours of inundation, with additional loss probably reflecting microbial and fungal respiration.

7. **Log decomposition:** Flooding increased wood decomposition. The decay rate of *Populus* logs at Cottonwood Flood during 1993 through 1995 was  $0.065 \text{ y}^{-1}$ , which predicts a half-life of 10.6 years, while the overall decay rate for logs at Cottonwood Control during 1991 through 1995 was  $0.010 \text{ y}^{-1}$ , which predicts a half-life of 69.3 years. Thus, flooding should significantly reduce the residence time of woody debris and thereby promote nutrient cycling within the forest.

8. **Forest floor litter:** There was no significant effect of flooding on litter storage at cottonwood sites, while flooding reduced forest floor litter at tamarisk sites. This difference may in part reflect the greater spatial variation in litter distribution at cottonwood sites. However, preliminary estimates of litter storage at river sites suggests that long-term flooding reduces forest floor litter. Thus, three experimental floods may not be enough to reduce the long-term accumulation of litter.

9. **Biomass of woody debris:** Biomass of woody debris was lower at River Flood than at the other three sites, suggesting that repeated annual flooding decreases the storage of wood build-up on the forest floor. However, three seasons of experimental flooding were not enough to significantly reduce wood biomass at Cottonwood Flood.

10. **Understory species richness and abundance:** Flooding did not affect species richness or abundance of understory vegetation overall, although the abundance of grasses may have increased at Cottonwood Flood. Sunlight availability is likely the primary factor influencing the distribution and abundance of understory vegetation.

11. **Herbaceous biomass:** There was a significant decrease in forb biomass over time at Cottonwood Flood, while the biomass of grasses increased. Meanwhile, neither of these changed significantly among years at Cottonwood Control. Thus, flooding may inhibit forb growth while promoting grasses. However, herbaceous growth appears more directly influenced by sunlight availability; flooding may thus affect herbaceous growth more via its effect on the growth of the cottonwood overstory, which shades out herbaceous growth when canopy cover is high. Data from River Flood support this conclusion.

12. **Foliage density and diversity:** Flooding appears to decrease both the density and patchiness of vegetation, particularly at lower size classes. Annual variation in climatic conditions may also affect these structural components of the forest ecosystem.

13. **Growth of major tree species:** Flooding appears to promote the growth of mature cottonwoods. There was a positive increase in growth rates after flooding among trees at Cottonwood Flood with initial diameters greater than 40 cm, with greater increases in growth among larger trees. In contrast, trees with diameters less than 40 cm diameter showed considerable variation in their responses. Flooding may select against certain individuals in smaller size classes. Trees at river sites were larger than those at cottonwood sites. Limited sex ratio data suggest that more females were present at River Flood, while the other three sites were male-biased. Mortality of mature cottonwood trees was lower at Cottonwood Flood than at Cottonwood Control during the period after annual flooding was begun.

14. **Cottonwood recruitment:** There was no successful cottonwood establishment within the main study area of any site.

15. **Tree and shrub density:** Experimental flooding did not affect tree and shrub densities, although data suggest that *Amorpha* may benefit from flooding. River Flood contained more dead *Tamarix* than did other sites; this may have been caused by reduced light availability under the full canopy of River Flood.

16. **Soil microbes and fungi:** Flooding significantly increased a variety of aspects of the microbial community, including total abundance of bacteria and fungi. Most parameters responded rapidly to flooding, with significant increases seen after only 1-2 floods. Increased bacterial and fungal activity indicates increased decomposition; intermittent flooding combined with aeration may provide optimal conditions for this functional response.

17. **Surface-active arthropods:** Flooding appears to alter the structure of the surface-active arthropod community. Abundance of the macrodetritivore *Armadillidium vulgare*, an exotic isopod, decreased while that of *Gryllus alogus*, a native cricket, increased. Abundance and taxonomic richness of ants decreased after flooding. Numbers of *Monomorium minimum*, a ground-dwelling ant common at Cottonwood Flood prior to flooding, decreased while numbers of *Crematogaster cerasi*, an arboreal species, increased. Carabid beetle abundance and richness increased after flooding; both were high at River Flood. Lycosid spiders were unaffected overall by flooding.

18. **Aerial insects:** Leafhopper abundance decreased after flooding at Cottonwood Flood. Populations of other aerial insects captured on sticky traps appeared unaffected by flooding.

19. **Mammals:** Mammals were not immediately affected by experimental flooding. Species composition did not change at the flooded site, and abundance and reproductive activity of *Peromyscus leucopus*, the most common rodent at all sites, did not change at Cottonwood Flood relative to Cottonwood Control. At least some individuals climbed trees during flooding and although some individuals may have left the site, these returned within two months after flooding. While there were no apparent short-term effects of re-introducing flooding, flooding may eventually affect species composition or abundance by altering habitat characteristics.

## GENERAL DISCUSSION

Flood control on the Rio Grande, and other large rivers, has severed the historic connection between the river and its riparian forest (Benke 1990, Lieurance et al. 1994, Molles et al. 1995). By eliminating the annual flood pulse on the Rio Grande, flood control has substantially changed the structure and function of the riparian forest ecosystem. Based on results of this study, we predict that flooding previously isolated riparian forest will initiate reorganization of the ecosystem and that this process of reorganization will eventually return the riparian forest to a position similar to its historic state. We propose that restoration of flooding will involve three phases: 1) the initial **disconnected phase**, represented in the present study by the Cottonwood and River Control sites, 2) a **reorganization phase** initiated with the first of a series of floods and represented in this study by the Cottonwood Flood site and 3) a **steady-state phase** that will approximate conditions prior to flood control, represented in the present study by the River Flood site.

The structure and function of the riparian forest should differ substantially during the disconnected, reorganization and steady-state phases. Figure 89 shows our predictions for differences in forest floor respiration during these phases. During the disconnected phase, because of moisture limitation, forest floor respiration will be orders of magnitude lower than during the other phases. During the initial stages of the reorganization phase, when organic matter pools are at their maximum and the pool of relatively labile organic matter is still large, forest floor respiration will be maximum. As reorganization proceeds, annual flooding will continue to produce pulses of intense forest floor respiration but the height of the respiratory

peak will be progressively damped as accelerated decomposition reduces the quantity and quality of organic matter on the forest floor. Eventually, at the point where the pool of organic matter consists principally of the past season's litter fall, the respiratory peaks will level off and the system will enter the steady-state phase. Respiration data collected during this study supports these predictions (Figure 89).

Other ecosystem variables should respond differently during reorganization. For example, because of potential physiological stress induced by flooding the rooting zone of the riparian forest, we predicted that leaf fall would be temporarily depressed at Cottonwood Flood (Figure 90). However, we also predicted that leaf fall would increase with subsequent flooding as trees adjusted physiologically to the changed environmental conditions. Eventually, leaf fall should increase at Cottonwood Flood compared to Cottonwood Control as flooding increases nutrient availability. These predictions have been supported by the patterns in leaf fall observed across the study sites over the course of this five year study. Leaf production was depressed in response to the first flood but recovered substantially following the second and third floods. Because the relative leaf fall remained greater at River Flood even after the third flood, the reorganization of leaf litter production appears to still be in progress at Cottonwood Flood. We conclude that reorganization of leaf litter production may take up to five annual floods.

Many other aspects of ecosystem structure and function should also vary predictably across the above phases of restoration but they should differ in the amount of time required for restoration (Table 5). The results of the three experimental floods indicate that the time required for restoration of ecosystem components will range from less than one year to decades. For instance, small mammal populations showed little or no response to the three experimental floods, indicating that restoration of flooding may not lead to a reorganization of these populations within the length of time studied, if at all.

In contrast, populations of decomposer fungi, mycorrhizal fungi, and surface-active arthropods all showed highly significant responses to the experimental floods. Both groups of fungi doubled their activity during the course of each flood at Cottonwood Flood but returned to levels comparable to those at Cottonwood Control within months. Thus, reorganization of fungal populations appears to take less than a year. Surface active arthropods showed a greater response to flooding than fungi but the response appears to have built up over the course of the three floods. Consequently, we suggest that reorganization of surface active arthropod populations will take a few years.

The effects of flooding on rate of leaf decomposition appeared to change over the course of the first two experimental floods, again suggesting a distinctive reorganization period. Leaf mass loss was greater in response to the second flood than in response to the first. By the third experimental flood, leaf decomposition was virtually identical at the cottonwood and river flood sites, indicating that reorganization of this process might be complete by the third flood.

The orders of magnitude increase in forest floor respiration in response to experimental flooding indicates a dramatic response by the forest floor community. However, even with this high rate of respiration during flooding, it will probably take a decade or more for forest floor decomposers to consume the large quantities of woody debris that have accumulated at Cottonwood Flood. The predicted half-life of approximately 10.6 years for logs at Cottonwood Flood is consistent with a prediction of reorganization of the forest floor litter pool lasting one or more decades. One of the reasons that so much time will be required is that high levels of forest floor respiration occur in short-term pulses associated with the flooding.

As predicted at the outset of this study, the three experimental floods studied during the course of this project have begun a process of reorganization of the Cottonwood Flood site. These floods appear to have begun a process of change that, with continued experimental flooding, will cause Cottonwood Flood to become progressively more like the River Flood site. Long term study and continued flooding of the study sites should demonstrate the time required to substantially restore isolated riparian forests to historic condition.



## RECOMMENDATIONS FOR RESTORATION OF THE MIDDLE RIO GRANDE RIPARIAN ECOSYSTEM

Intensive water management combined with other human-induced changes, such as the introduction of exotic woody plant species, have resulted in a much-altered riparian ecosystem along the Middle Rio Grande Valley. Given the extent of these changes, efforts to restore completely the valley to its pre-settlement condition are clearly impractical, both logistically and politically. From a practical perspective, structural changes such as the establishment of tamarisk as a major component of the forest ecosystem are irreversible. Under these conditions, we therefore advocate the re-establishment of basic riverine-riparian **functioning** and selected restoration of vegetation, rather than attempting to preserve a bosque that is itself an artifact of civilization. We propose that sustaining ecosystem integrity, in the form of carefully planned and executed **partial restoration**, is the only reasonable alternative to substantial ecosystem change. Such change, we predict, will be the eventual outcome of "status quo management" occurring with the unlimited growth of the basin's human population and its continued high rates of water consumption.

Based on results of this study and in keeping with the more inclusive recommendations of the "Middle Rio Grande Ecosystem: Bosque Biological Management Plan" (Crawford et al. 1993), we propose the following four components for a Valley-wide restoration program: (1) establishment of an extensive ecosystem monitoring program along the Rio Grande; (2) carefully regulated seasonal overbank flooding or its equivalent, including sites selected both for the maintenance of mature forests and for the establishment of new ones; (3) riparian forest management leading to improved habitat diversity; and (4) creation of diverse wetlands inside and outside of the present levee system (Crawford et al. 1994). The final two components, while critical for a comprehensive partial restoration program in the Valley, are beyond the scope of our study and will not be discussed here.

### Ecosystem monitoring in the Middle Rio Grande Valley

During this research we established practical methods for monitoring seasonal and yearly changes in populations and ecological processes that occur in the bosque. Our monitoring protocol, in addition to its value for measuring the effects of flooding, allows us to chart baseline ecosystem changes over time. In our opinion, long-term records of ecosystem change should provide the foundation for planning management strategies. Accordingly, we recommend that a network for monitoring key variables be established, with selected sites along the Middle Rio Grande. For reasons of expense and complexity, not all variables that we measure at the Refuge are appropriate for general monitoring. However, many can be handled easily by teams of volunteers, which would make the entire monitoring program economically feasible (Crawford et al. 1996).

We believe that participation by the citizens of the Valley is critical to the success of a restoration program. A commitment to long-term monitoring requires both an interagency structure to provide funding and logistical support, as well as a dependable source of personnel. We suggest that the latter may be provided by citizen volunteers, based on our awareness of an extensive pool of citizens interested in the well-being of the bosque. Educating people about the project should take place at many levels, from young school children through top executives and politicians. The value of ecosystem restoration needs to be understood and accepted by the public as non-threatening and essential to our own well-being.

The actual monitoring procedure (see Table 6) would involve systematic collection and recording of groundwater depth changes (using shallow wells), litterfall and litter decomposition, and aspects of primary production (e.g., woody plant distribution and growth) and animal activity (e.g., pitfall trapping for "indicator" arthropods). The volunteer teams collecting the data would function synchronously, at predetermined intervals, and would be coordinated by from a central source (possibly UNM) by

appropriate personnel, including a salaried program coordinator. Data management and analysis would be performed at that source, and the products of analyses would be made available to managing agencies and other institutions, as well as to individuals with an interest in the management of the riparian ecosystem.

### Overbank flooding as a tool for partial restoration

Our reorganization model for restoration (see **GENERAL DISCUSSION** above) illustrates two important concepts to be considered during partial restoration efforts. First, restoration cannot proceed directly from the disconnected phase to the steady-state phase, but rather the system must proceed through a period of reorganization. Thus, restoration efforts likely will not produce the desired results immediately, which must be considered when evaluating the success of such a program. Second, the rate at which different ecosystem components pass through this reorganization phase will vary, and the duration of restoration projects must be designed to account for this variance. For example, restoring the biomass of woody debris and forest floor litter to steady-state levels will require a commitment of at least a decade or longer of continued restoration efforts. With these considerations in mind, we propose two types of sites to be used for partial restoration (Figure 91). In selecting all sites, various attributes should be considered for successful flooding. These include distance from flowing water, depths to groundwater, permeability of soil, and topographic features, in addition to legal considerations of water availability.

*Restoration and maintenance of established forest sites:* This is typified by the isolated cottonwood sites studied in our research at Bosque del Apache. We predict that an applied flooding regime at this type of site will lead to a steady state within two to three decades. To achieve this goal, water usually will have to be supplied annually during the runoff season either from the river or from ditches. Another alternative may be groundwater pumping for the hard-to-flood northern reaches. While flooding of this type of site will enhance the ecological integrity of the established forest, recruitment of new cottonwood seedlings should not be expected, since the shade of older trees inhibits the growth and survival of newly germinated seedlings (Howe and Knopf 1991). Maintenance of forests in the steady-state phase will also require this procedure.

Although we have maintained a flooding regime utilizing month-long periods of inundation each year, our data, combined with other sources (e.g., Junk et al. 1989, Bayley 1995), suggest that a less water-intensive pulsing of short duration floods would likely produce the desired results. Therefore, we suggest that to re-establish and maintain the ecological integrity of mature forests, these sites be inundated for a period of three to four days during the high runoff season. Ideally, two to three such pulses, with water drawn off in between and separated by several days to a week or more, could be applied during this period. The combination of wetting and aeration obtained by removing the water appear to favor the most rapid functional responses. This regime consumes far less water than a continuous inundation, thus increasing its economic feasibility, and is also less labor-intensive. Such a regime should be repeated annually for the duration of the program. Flooding could be eliminated entirely during years of extreme drought and water shortage, particularly for sites in the steady-state phase, but the re-establishment of steady-state conditions will be reached more rapidly with annual inundation.

*Creation of new forest sites:* This type of site is typified by silt bars and treeless riverbanks, which can be used to create new riparian forests via the germination of flood-planted cottonwood and willow seedlings (e.g. Stromberg et al. 1993). These sites should have porous soils and little plant cover, conditions that can be generated naturally by previous flood scouring or by mechanical removal of existing vegetation, as successfully accomplished by personnel at the Bosque del Apache refuge (J. Taylor, personal communication). A single flood, either directly from the river or via water maintenance canals,

can lead to successful establishment of native woody plant species when timed to correspond with the release of wind-blown seeds from nearby source trees (e.g. during peak runoff). Mechanical removal combined with complete wetting during this period of seed release also allows floodplain sites distant from the river to be restored in this manner. Although simultaneous germination of tamarisk seeds can be a problem in these cases, if cottonwood seedlings get a rapid start they can compete well (A. Sher, personal communication). Post-germination drawdown of water must proceed at a rate commensurate with the ability of seedlings to send roots downward. Desirable rates of soil drying are discussed in Mahoney and Rood (1991) and Scott et al. (1993). Also, young seedlings must be protected from additional scouring floods until well established. Knowing soil salinity is critical for these establishment sites, since cottonwood seeds do not germinate in very saline soils (Sheets et al. 1994).

The goal of such partial restoration should be to establish and maintain a mosaic of riparian forest stands including a range of ages that can be accessed and flooded with relative ease (Crawford et al. 1996). Ideally, restoration sites should be strung along all reaches of the river. However, political reality dictates otherwise in central New Mexico. Due to land ownership control along the Rio Grande, and because the degraded northern riverbed generally precludes overbank flooding, initial restoration efforts should focus on areas south of Belen. One area with potential for restoration is the San Marcial region, just south of the Refuge border, and the floodplain between it and the river's delta at Elephant Butte Reservoir. The Bureau of Reclamation owns much of this land, while private landowners control the rest, especially in the northern part. The entire region has high water tables and in places supports shallow marshes containing drowned tamarisk. The riverbed is highly aggraded and tends to be perched due to sediment deposition. The area includes stands of native cottonwood, tree willow, and coyote willow, while monotypic stands of tamarisk also occur throughout the region. Nevertheless, this is probably the best candidate landscape in the Middle Rio Grande Valley for restoring native bosque and a variety of wetlands. Other sites could be considered for partial restoration in lands controlled by the Middle Rio Grande Conservancy District to the north of the Refuge, and by the Pueblos along the river, if supported by these agencies.

Partial restoration of the Middle Rio Grande riparian ecosystem will require a comprehensive program incorporating revegetation of native species and alterations of existing habitats to restore the ecological diversity of the Valley at a landscape scale, as well as substantial changes in current water management practices. Continued water use at current rates in the Valley almost certainly ensure failure. The persistence of a cottonwood bosque will depend upon the cooperation of those controlling access to lands along the river, as well as a significant commitment by residents of the Valley. Long-range planning for how the Middle Rio Grande is to be managed should be one of New Mexico's highest resource priorities.

## COLLABORATORS

- Dr. Shivcharn Dhillon, Agricultural University of Norway - NLH, Norway, and Centre National de la Recherche Scientifique and Centre d' Ecologie Fonctionnelle et Evolutive, France - soil bacteria, mycorrhizae and other soil fungi
- Dr. H. Maurice Valett, Michelle Baker, Francelia Lieurance, and John Morrice, University of New Mexico - hydrology and water chemistry
- Dr. Carleton White, University of New Mexico and Dr. Thomas Kieft, New Mexico Institute of Mining and Technology - soil structure, chemistry and metabolism

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Table 1. Average percent loss of initial dry-weight of leaves in decomposition bags between sampling periods. Values are the percent change between sampling periods calculated from the average ash-free dry-weight of leaves for each collection; cumulative percent loss is given in parentheses. Negative values are an artifact of statistical averaging; these essentially indicate no change.

	November - April	April - June	June - November
1991-92			
Cottonwood Control	22.4 %	6.4 % (28.8 %)	3.9 % (32.7 %)
Cottonwood Flood	31.7 %	-5.2 % (26.4 %)	15.0 % (41.4 %)
1992-93			
Cottonwood Control	16.1 %	5.1 % (21.2 %)	10.8 % (32.0 %)
Cottonwood Flood	17.7 %	30.0 % (47.7 %)	-1.2 % (46.4 %)
1993-94			
Cottonwood Control	5.9 %	4.0 % (9.9 %)	14.7 % (24.6 %)
Cottonwood Flood	6.4 %	50.3 % (56.7 %)	-0.3 % (56.4 %)
1994-95			
Cottonwood Control	19.6 %	0.9 % (20.5 %)	2.4 % (22.9 %)
Cottonwood Flood	21.5 %	34.6 % (56.1 %)	-2.3 % (53.8 %)
River Control	22.5 %	0.0 % (22.5 %)	2.8 % (25.3 %)
River Flood	19.5 %	39.8 % (59.3 %)	-0.5 % (58.8 %)

Table 2. Sexes of monitored canopy trees at cottonwood and river sites. Ratio is the number of males to females, including only those trees for which sex is known. Sex identifications were made in April 1995.

	males	females	non-reproductive	unknown	ratio
Cottonwood Control	61	52	20	7	1.17
Cottonwood Flood	61	37	29	8	1.65
River Control	24	9	2	16	2.67
River Flood	12	18	6	14	0.67



Table 3. Abundance and diversity of ants before and after flooding at cottonwood and river sites. "Pre" includes collections prior to the initiation of flooding (1991 through May 1993); "post" includes all collections after flooding was initiated (June 1993 through 1995). Value is the total number of individuals captured at each site during each pre- or post-flood collection (all months combined). River sites include collections beginning August 1994 through 1995.

	Cottonwood Control		Cottonwood Flood		River Control	River Flood
	pre	post	pre	post		
<b>Dolichoderinae</b>						
<i>Dorymyrmex insana</i>	16	16		1		
<i>Tapinoma sessile</i>				1		8
<b>Ecitoninae</b>						
<i>Neivamyrmex nigrescens</i>		60	8	4		4
<i>Neivamyrmex</i> sp.	7					
<b>Formicinae</b>						
<i>Camponotus sansabeanus</i>					1	
<i>Camponotus vicinus</i>	2	1		3	1	
<i>Formica hewitti</i>					49	
<i>Formica neogagates</i>					84	
<i>Lasius fallax</i>		5			2	
<i>Lasius niger</i>					33	2
<b>Myrmicinae</b>						
	2					
<i>Crematogaster cerasi</i>	98	138	18	26	15	105
<i>Leptothorax andrei</i>		8			43	2
<i>Leptothorax nitens</i>		41			1	
<i>Leptothorax obliquicanthus</i>		10				
<i>Leptothorax pergrandei</i>	3		2			
<i>Leptothorax t. texanus</i>						2
<i>Leptothorax</i> sp. 1	2	1	2			
<i>Monomorium minimum</i>	255	205	332	52		
<i>Pheidole pilifera</i>		17				
<i>Pheidole</i> sp.	1				1	

Table 3, continued.

	Cottonwood Control		Cottonwood Flood		River Control	River Flood
	pre	post	pre	post		
<i>Pogonomyrmex barbatus</i>		26			11	
<i>Pogonomyrmex occidentalis</i>	48	27			14	
<i>Solenopsis molesta</i>		100				
<i>Solenopsis</i> sp.	71	125	5			
<b>Ponerinae</b>						
<i>Hypoponera opaciceps</i>						1
<i>Hypoponera</i> sp.	1		2			
<b>Total number of taxa</b>	12	15	7	6	12	7
<b>Total number of individuals</b>	506	780	369	87	255	124

Table 4. Abundance of carabid beetles before and after flooding at cottonwood and river sites. "Pre" includes collections prior to the initiation of experimental flooding (1991 through May 1993); "post" includes all collections after flooding was initiated (June 1993 through 1995). Value is the total number of individuals captured during each pre- or post-flood period (all months combined).

	Cottonwood Control		Cottonwood Flood		River Control	River Flood
	pre	post	pre	post		
To family only (includes larvae)	2	4	1	12	2	
<i>Agonum decorum</i>				10		115
<i>Agonum</i> sp.		1		1		
<i>Amara</i> sp.		2	2	1	2	
<i>Badister</i> sp.						2
<i>Bemidion timidum</i>				1		
<i>Bradycellus</i> sp.				3		
<i>Calathus opaculus</i>	1	27	9	30	11	24
<i>Chlaenius sericeus</i>				1		8
<i>Chlaenius tricolor</i>						1
<i>Chlaenius</i> sp.			1			15
<i>Evarthrus</i> sp.		1		1		
<i>Harpalus pennsylvanicus</i>			1			
Perigonini						2
<i>Pterostichus chalcites</i>		1		60	1	64
<i>Pterostichus</i> sp. # 2				1		
<i>Scarites lissopterus</i>				3		
<i>Tachys</i> sp.				2		3
Total number of taxa	2	6	5	13	4	9
Total number of individuals	3	36	14	126	16	234

Table 5. Expected magnitude and timing of responses to ecosystem reorganization.

State Variable \ Subsystem	Magnitude of Response during Reorganization	Timing of Response during Reorganization
1) small mammals	no response	no reorganization
2) decomposer fungi	increase of 2 X	one month \ very rapid
3) mycorrhizal fungi	increase of 2 X	one month \ very rapid
4) surface-active arthropods	orders of magnitude	years \ rapid
5) leaf decomposition	rate increase of 50 %	5 years \ intermediate
6) leaf production	rate change of 2-3 X	5 years \ intermediate
7) forest floor respiration	orders of magnitude increase	decades \ slower
8) decomposition of woody debris	orders of magnitude increase mass reduced to 1 / 3 X	decades \ slower

Table 6. Recommended variables for a Middle Rio Grande Valley monitoring program.

Variable	Method	Frequency
Groundwater depth	Groundwater wells	monthly
Litter production	Litterfall tubs	monthly
Litter decomposition	Decomposition bags	seasonal (4 X / year)
Litter storage	Transect estimates	at least once per 5 years
Woody biomass	Transect estimates	at least once per 5 years
Woody plant density and distribution	Mapping and plot counts	at least once per 5 years
Size and growth of cottonwood trees	DBH measurements	annually
Arthropod populations (isopods, crickets, ants, carabid and tenebrionid beetles)	Pitfall trapping	warm season (May, June, August, October)

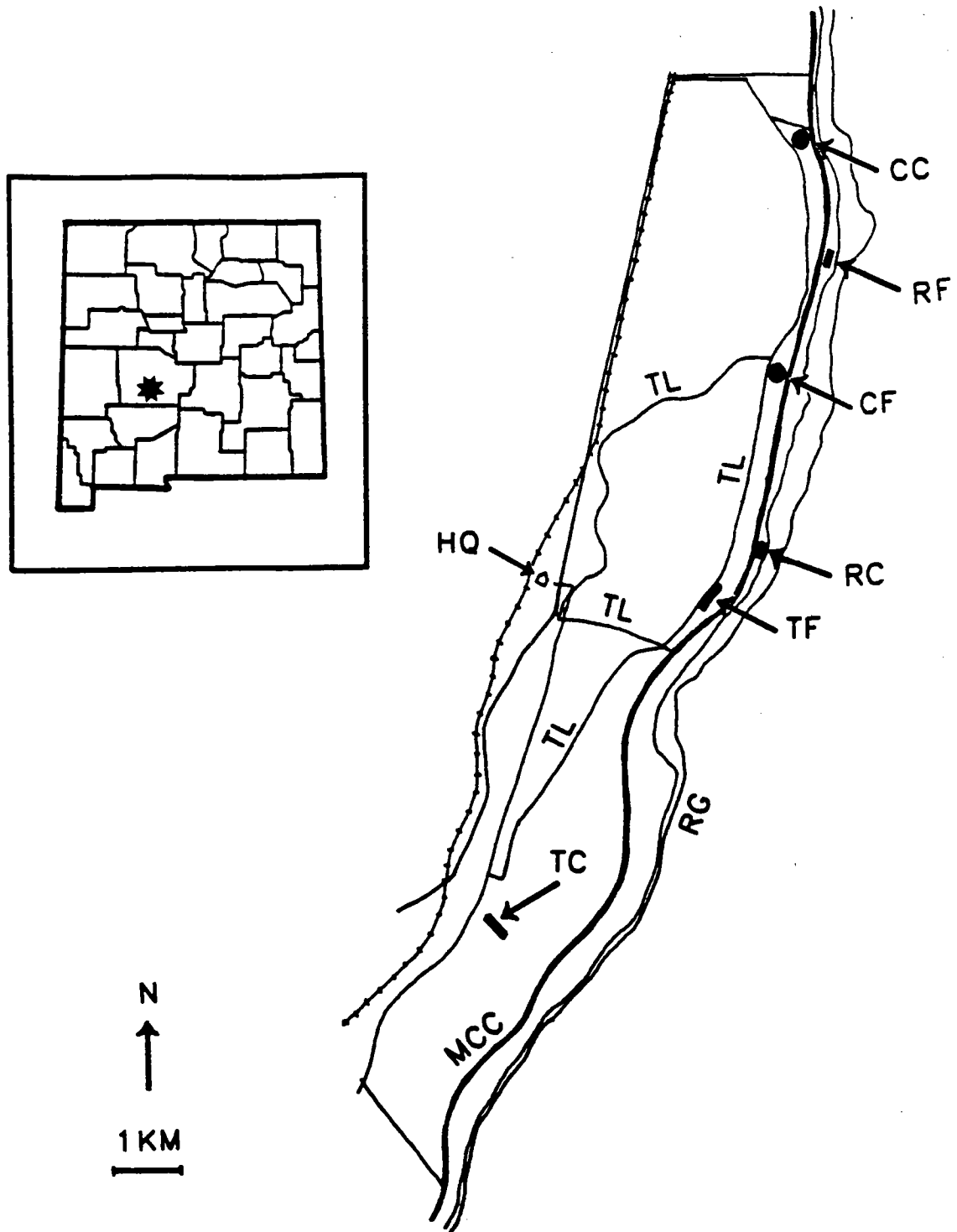


Figure 1. Location of study sites within Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico. The six study sites are Cottonwood Control (CC), Cottonwood Flood (CF), River Control (RC), River Flood (RF), Tamarisk Control (TC), and Tamarisk Flood (TF). The Refuge headquarters (HQ) and tour loop (TL) are indicated. MCC is the main conveyance channel and RG is the Rio Grande. The approximate location of the refuge is indicated on the inset map of New Mexico.

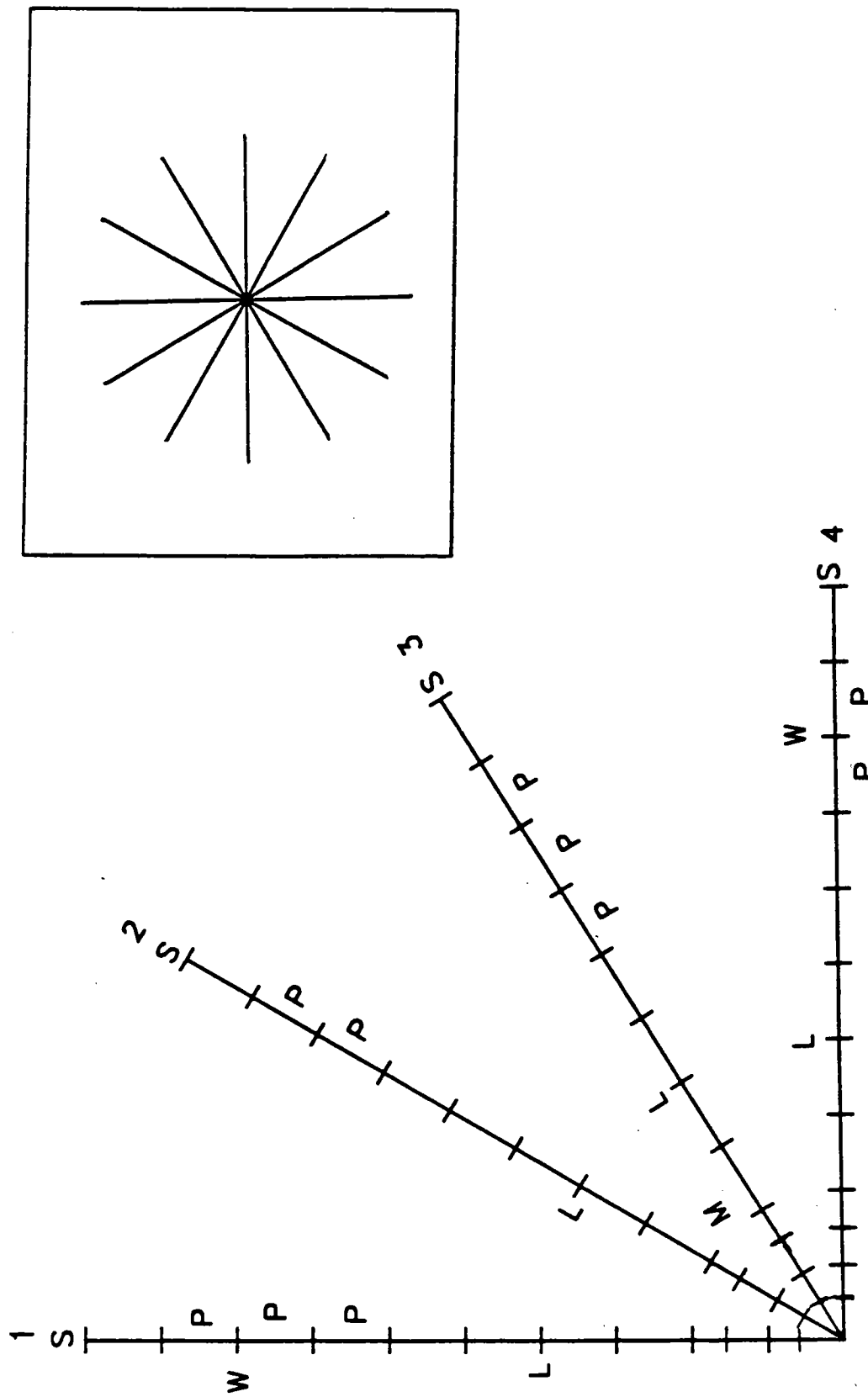


Figure 2. Schematic diagram of cottonwood site design. Inset is diagram of mammal web, with twelve 100-m transects. Transects 1 - 4 are enlarged to show mammal trapping stations (short bars), pitfall trap locations (P), sticky trap locations (S), and litterfall tubs (L). The meteorological station is indicated by M and W represents water sampling wells. Mammal traps are 10 m apart, except the inner four on each transect which are 5 m apart. Four mammal traps are placed at the center of the web. Other sampling is scattered throughout the web.

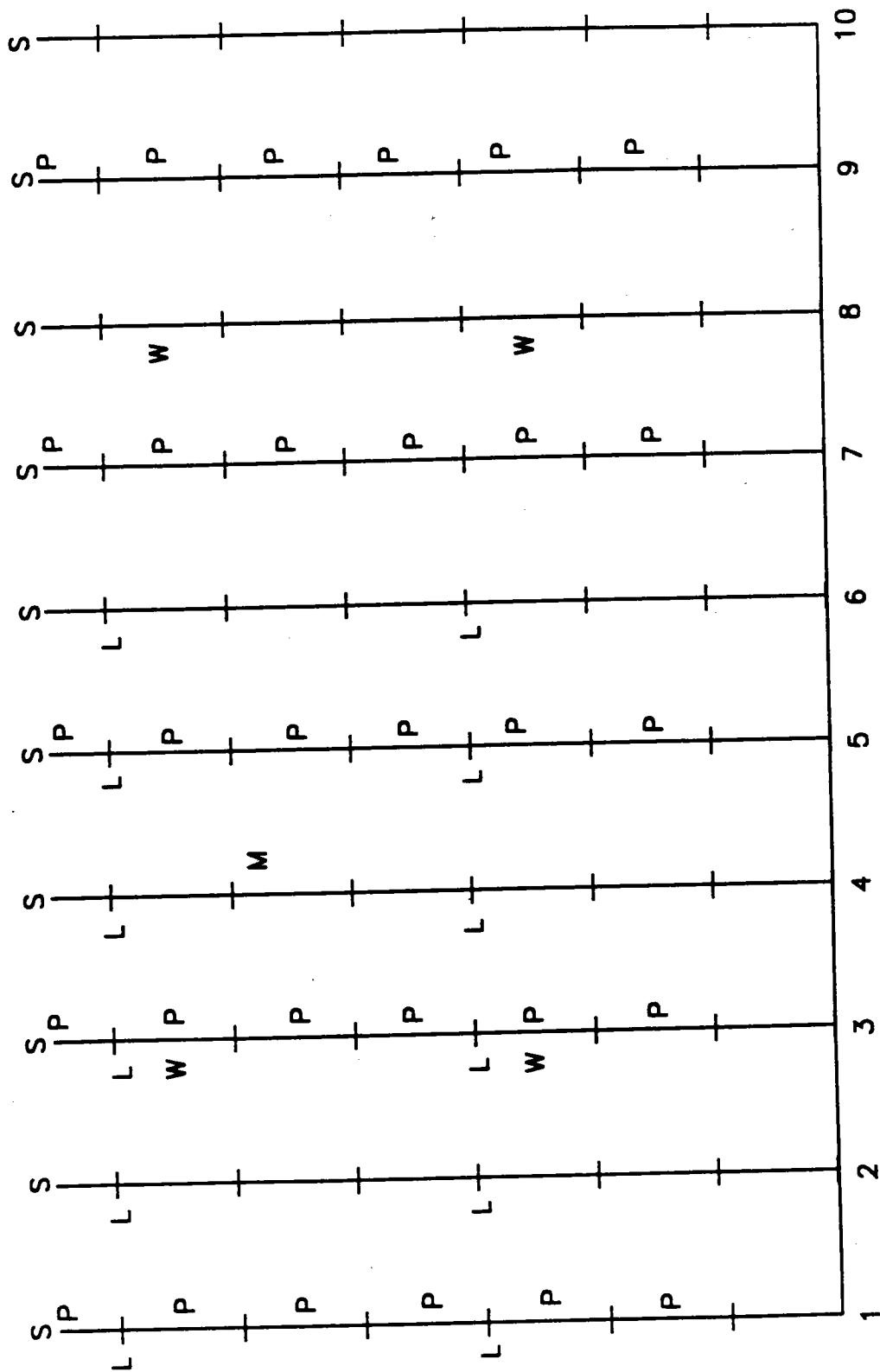


Figure 3. Schematic diagram of tamarisk site design. Short horizontal bars are locations of mammal trapping stations, P indicates pitfall trap locations, S indicates sticky trap locations, and L indicates location of litterfall tubes. M is the location of the meteorological station and W indicates water sampling wells. Diagram is not to scale: transects 1 - 10 are each 50 m apart; mammal trap locations are 10 m apart. Other sampling is scattered throughout the grid. River sites have a similar design, except that transects are 20 m apart and water sampling wells are located on line 1 (two wells), line 6 (three wells) and line 10 (two wells).



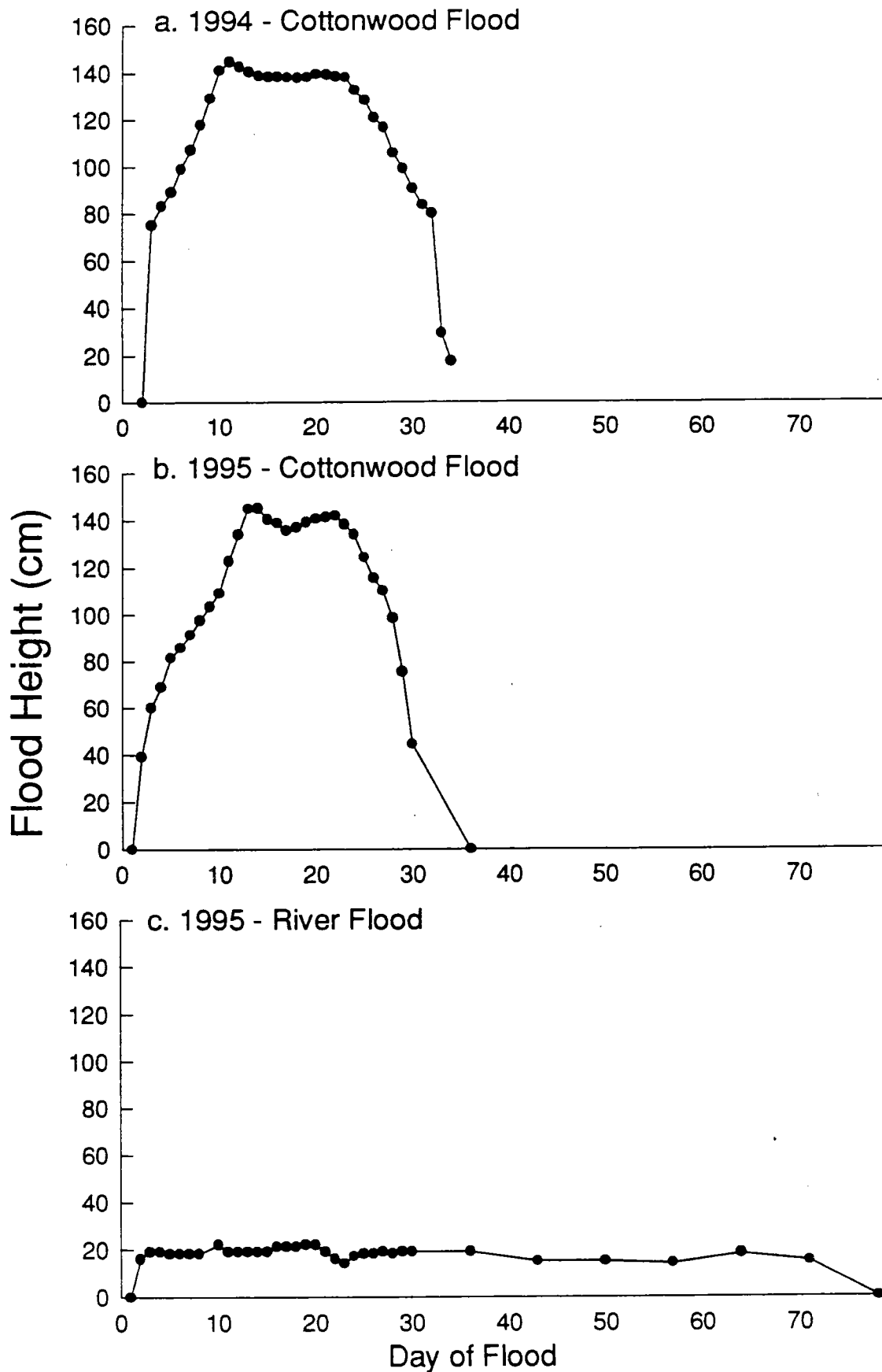


Figure 4. Surface water height at Cottonwood Flood in a) 1994 and b) 1995, and c) at River Flood in 1995. Height at Cottonwood Flood was measured in the depression at the north end of the site; majority of flooded areas was lower than this value. Height at River Flood was measured at the first well on transect #1.

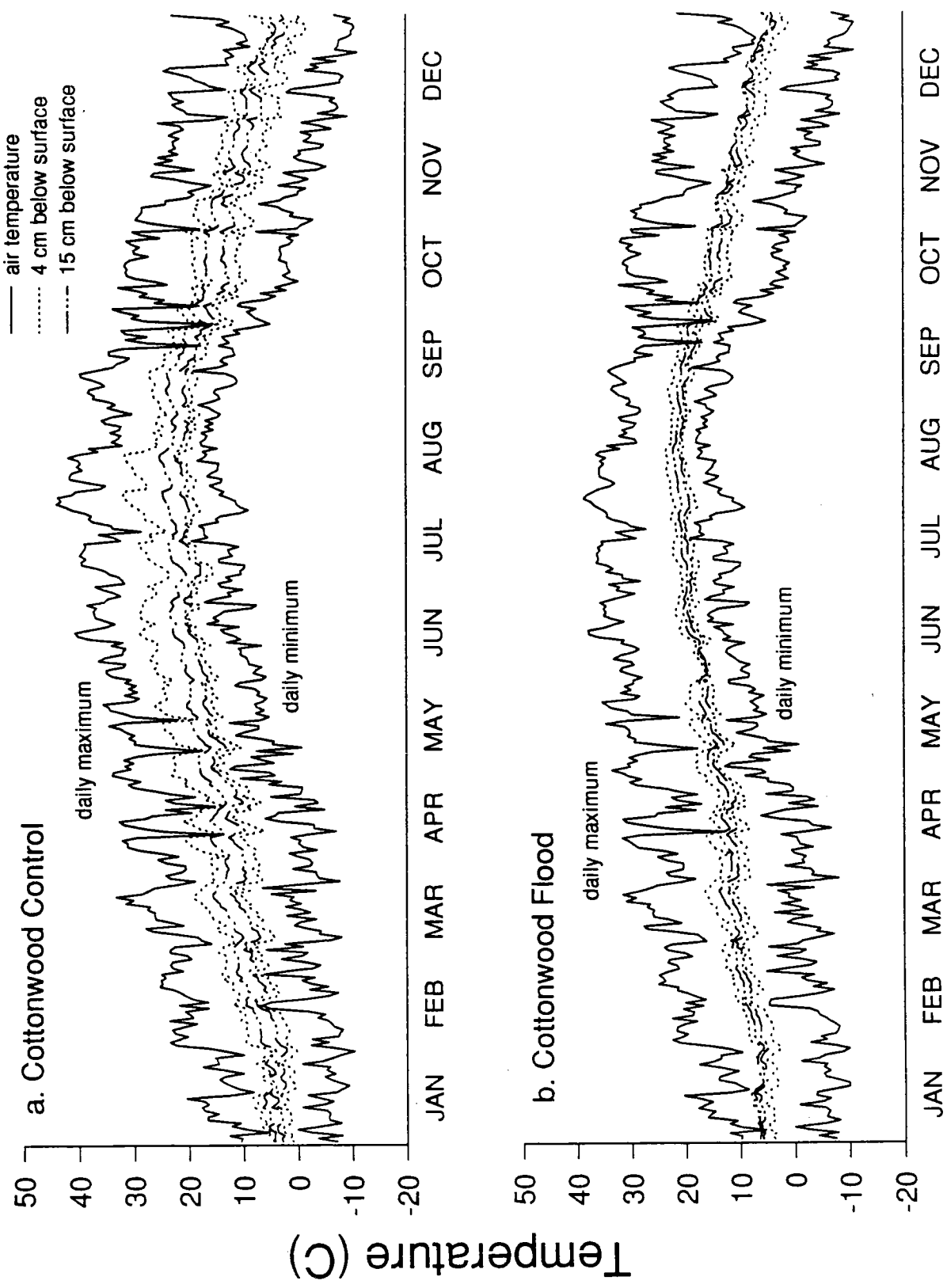


Figure 5. Air and soil temperatures at cottonwood sites in 1995.

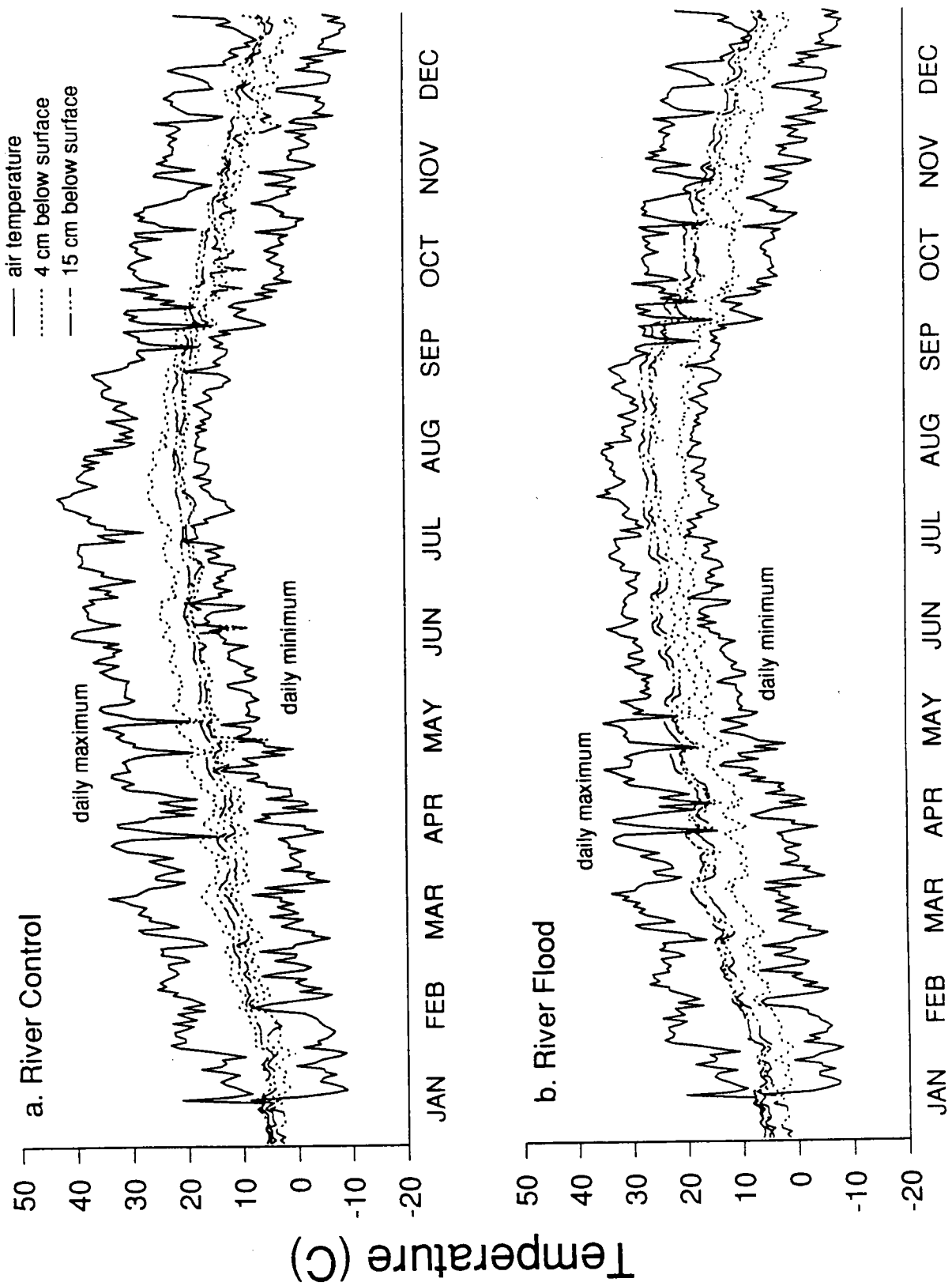


Figure 6. Air and soil temperatures at river sites in 1995.

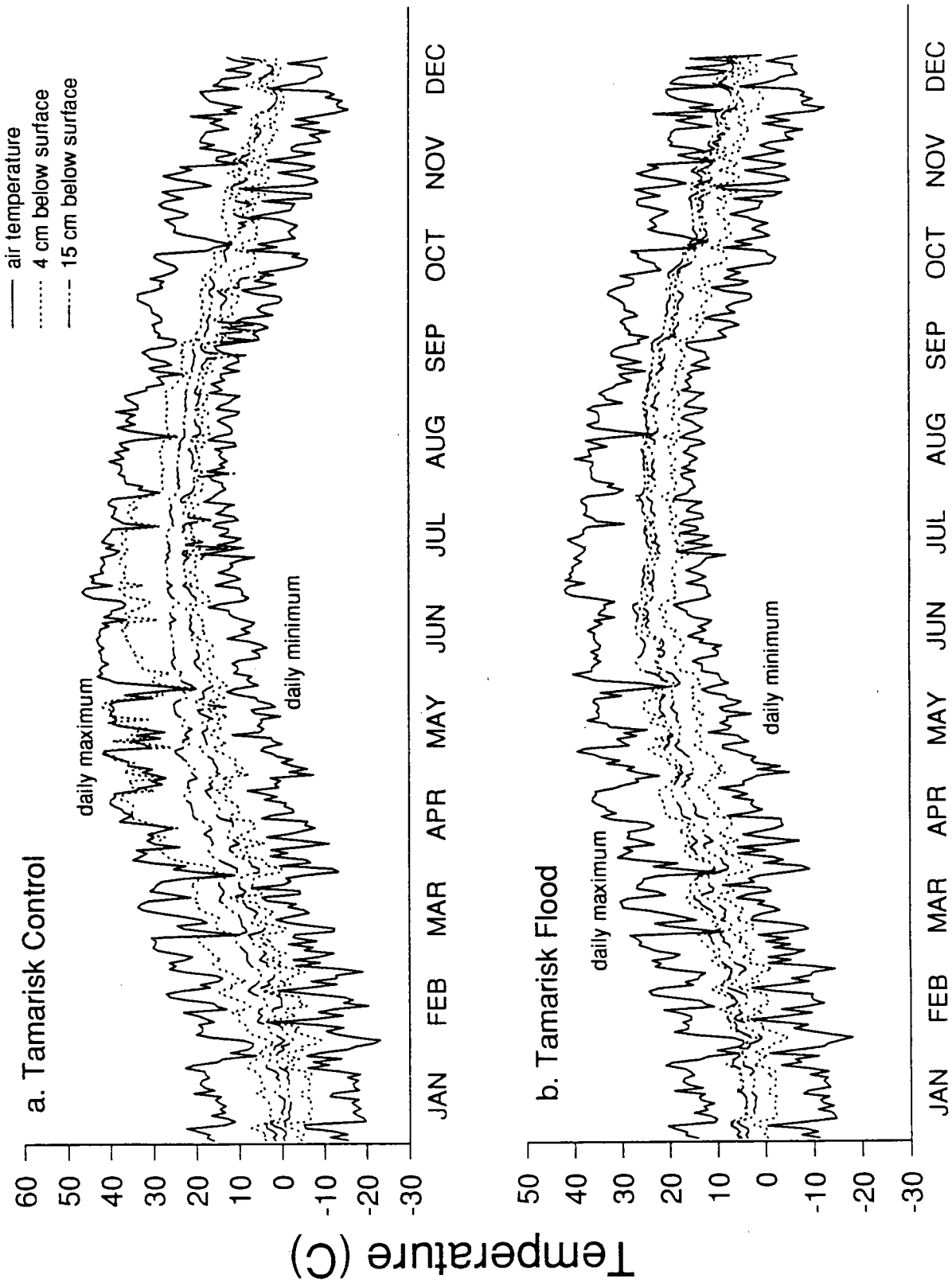


Figure 7. Air and soil temperatures at tamarisk sites in 1994.

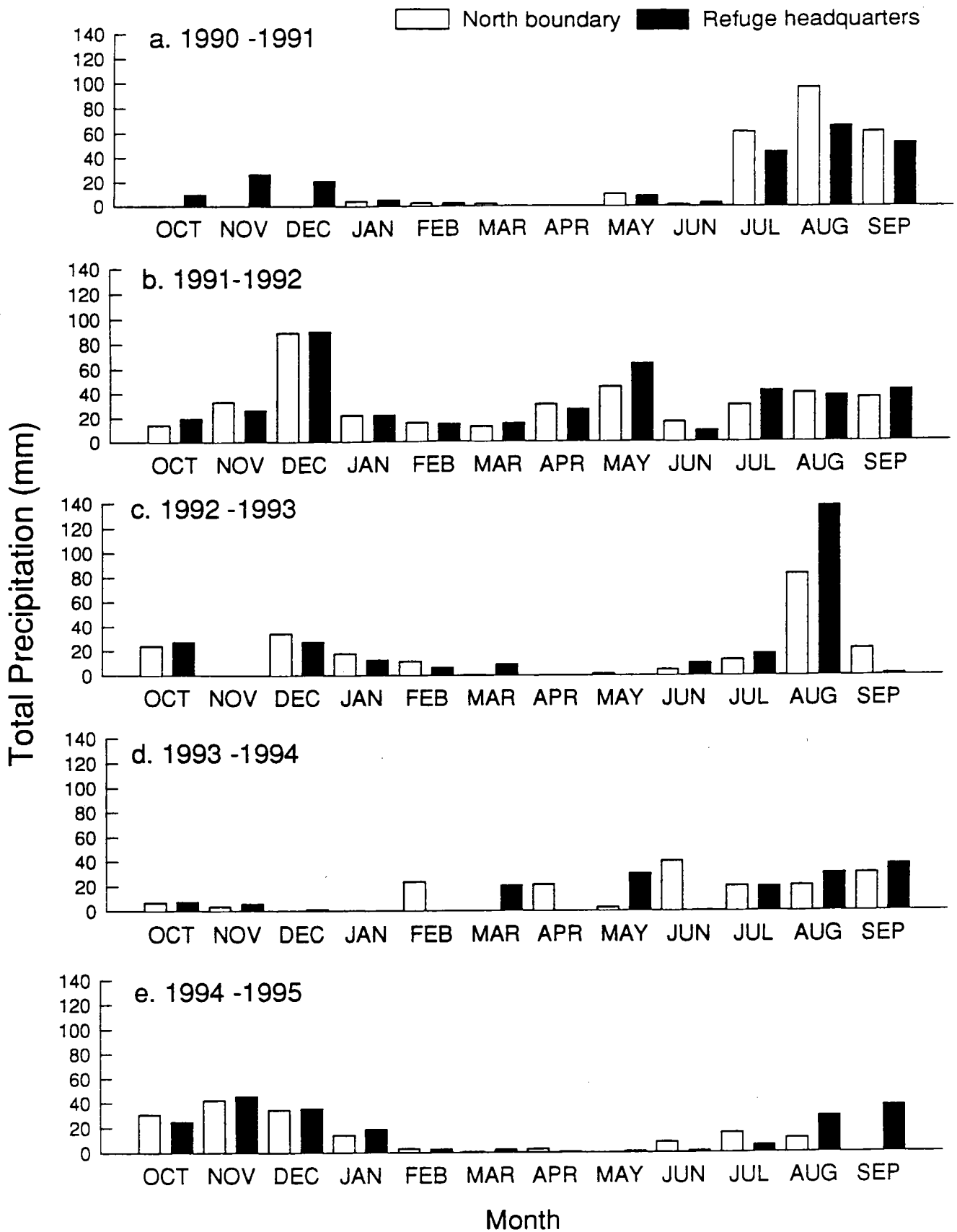


Figure 8. Precipitation at Bosque del Apache during 1991 through 1995, recorded at the Refuge headquarters and near the north Refuge boundary. Data are presented by water-year.

..... Cottonwood Control — Cottonwood Flood

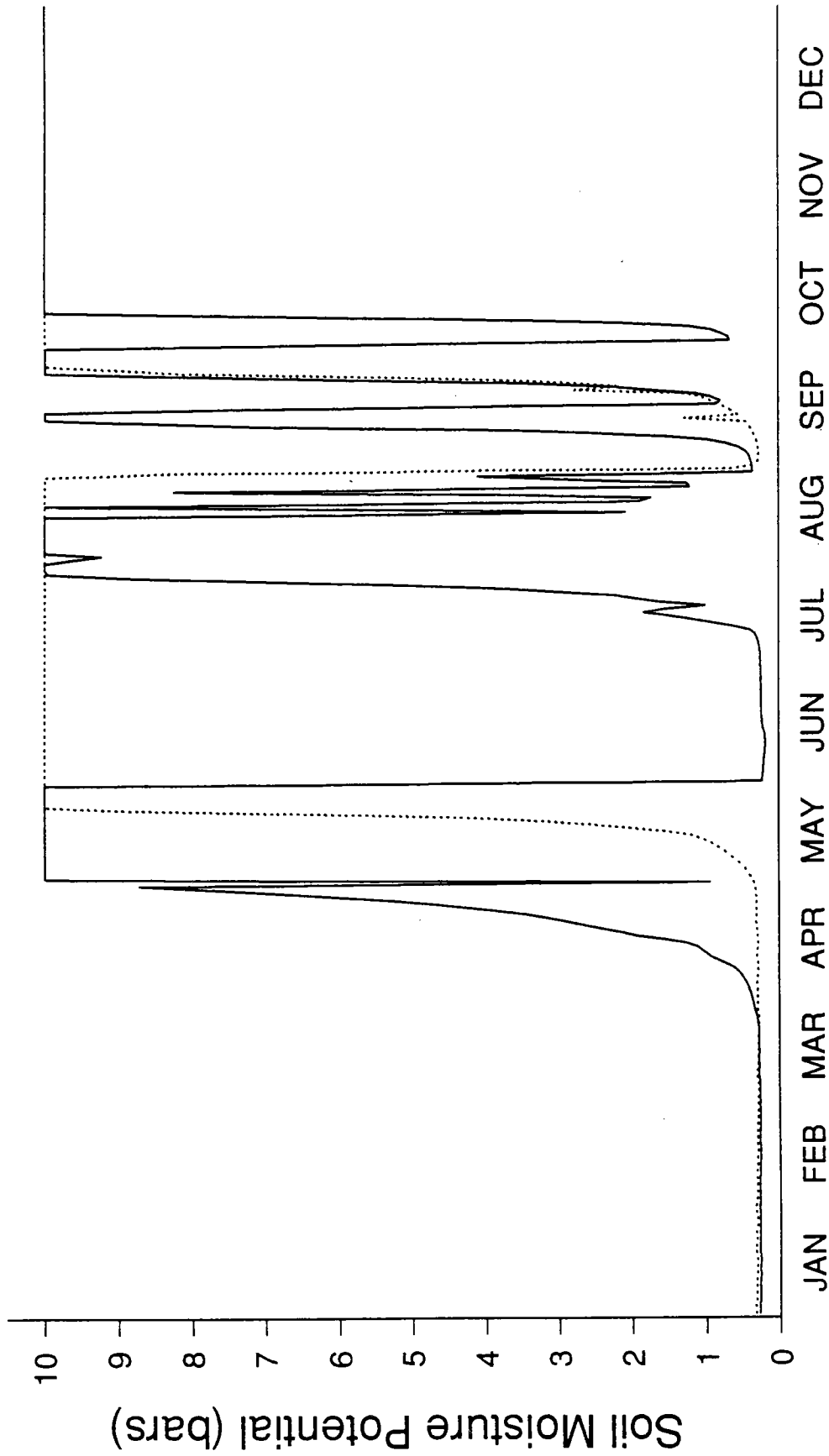


Figure 9. Soil moisture potentials at cottonwood sites in 1995. Soil moisture potential of 10 indicates dry soil, while values of 0.2 indicate saturated soil.

..... River Control — River Flood

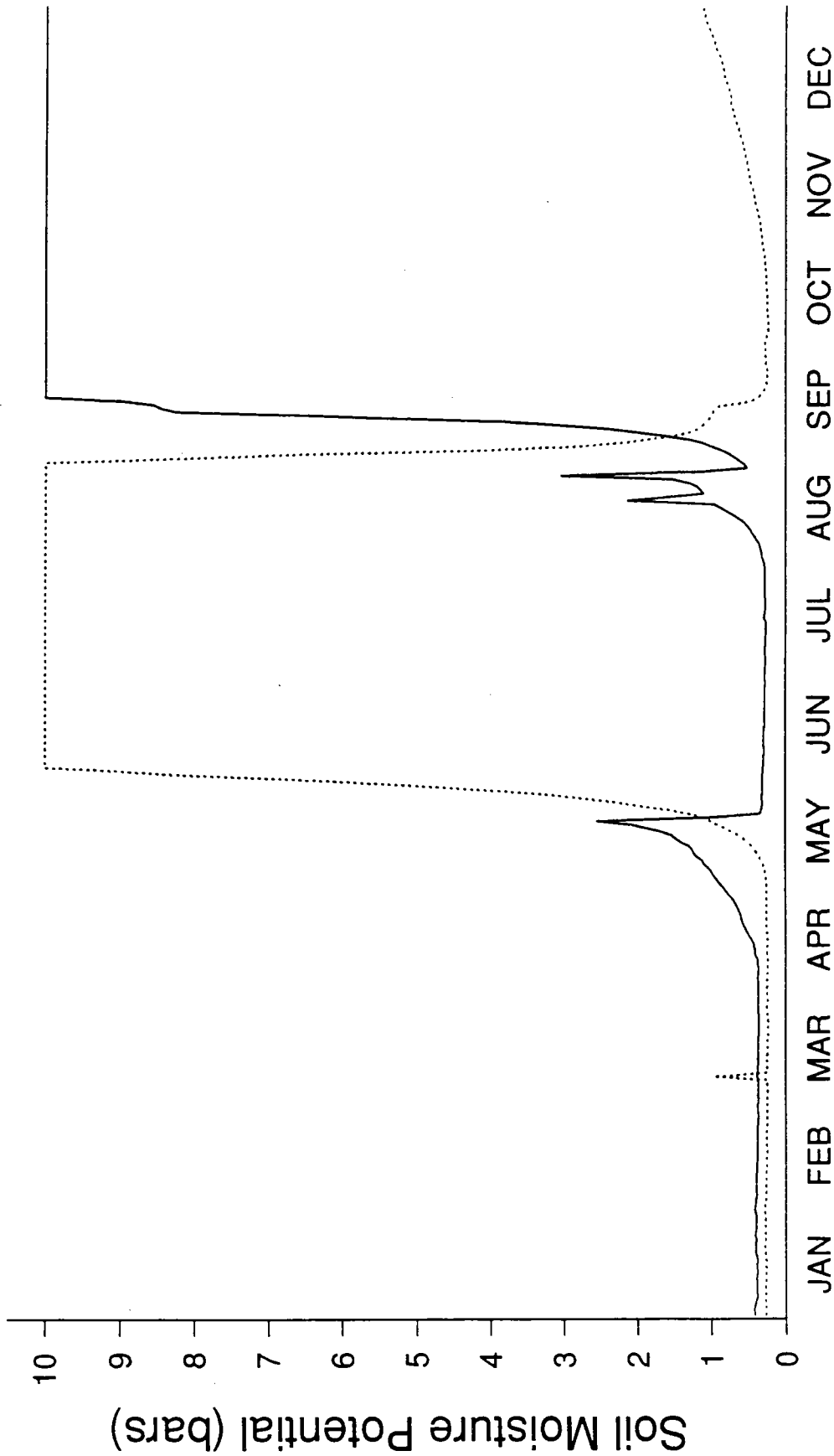


Figure 10. Soil moisture potentials at river sites in 1995. Soil moisture potential of 10 indicates dry soil, while values of 0.2 indicate saturated soil.

..... Tamarisk Control      —— Tamarisk Flood

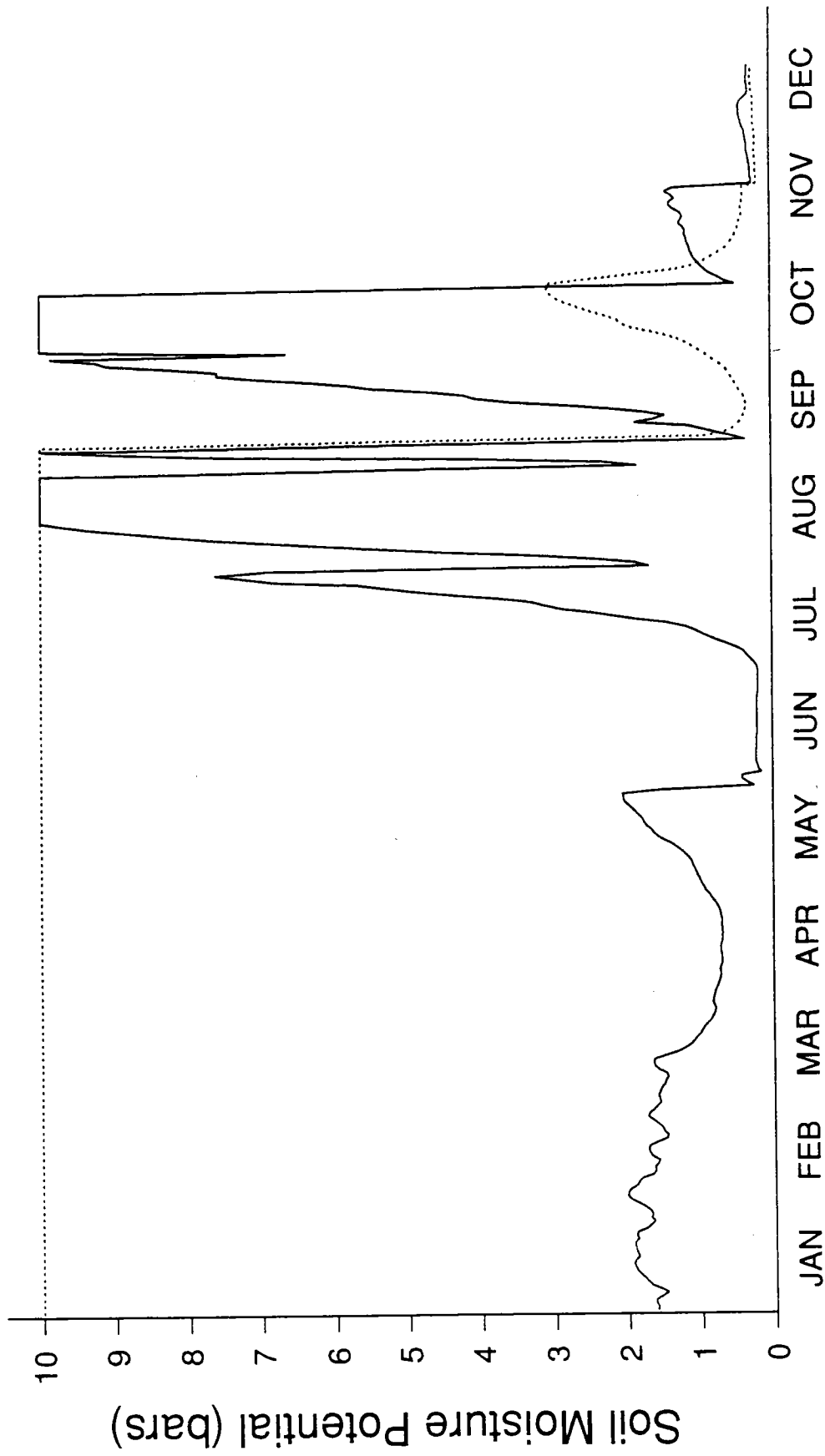


Figure 11. Soil moisture potentials at tamarisk sites in 1994. Soil moisture potential of 10 indicates dry soil, while values of 0.2 indicate saturated soil.



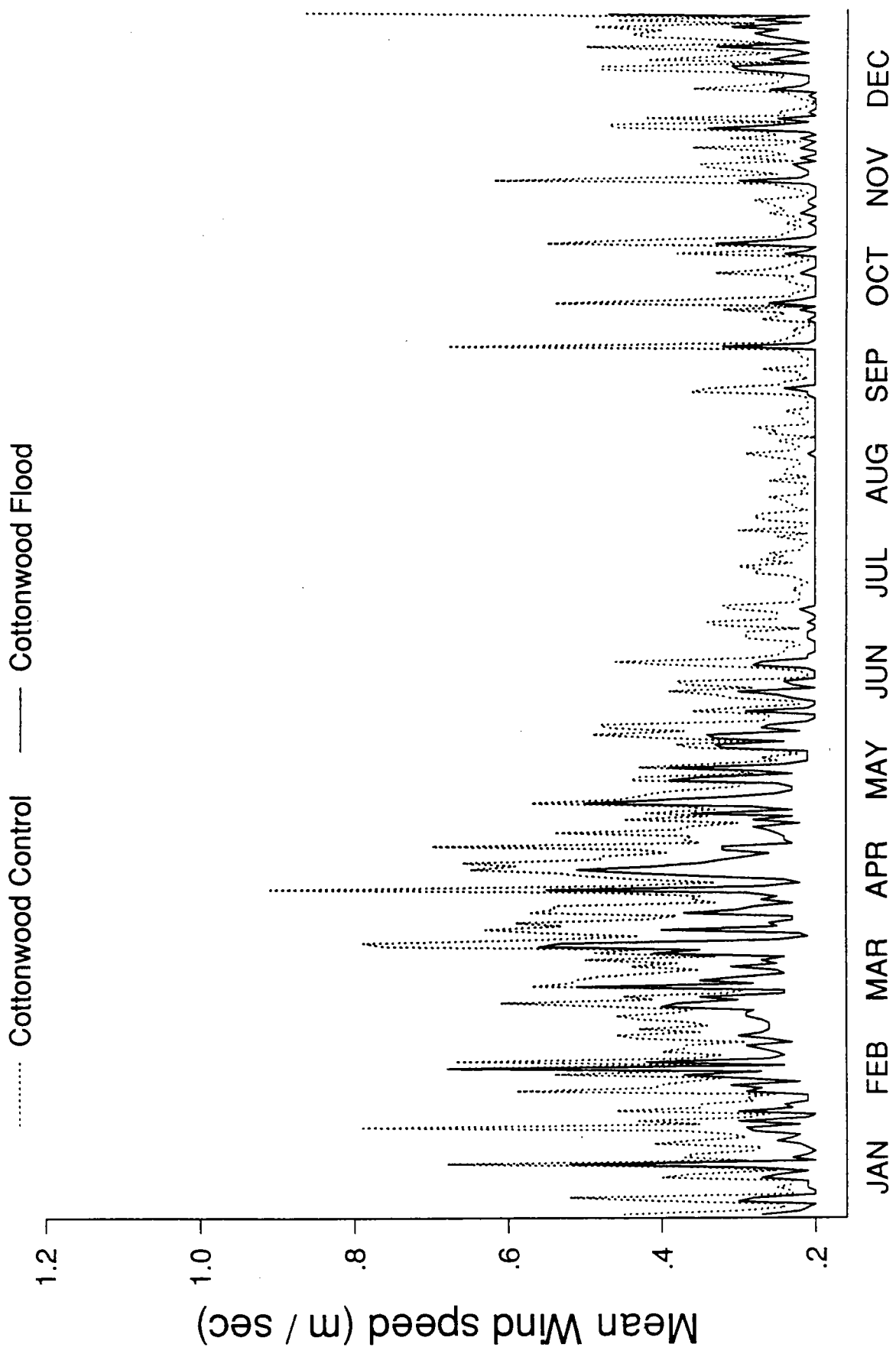


Figure 12. Daily mean wind speed at cottonwood sites in 1995.

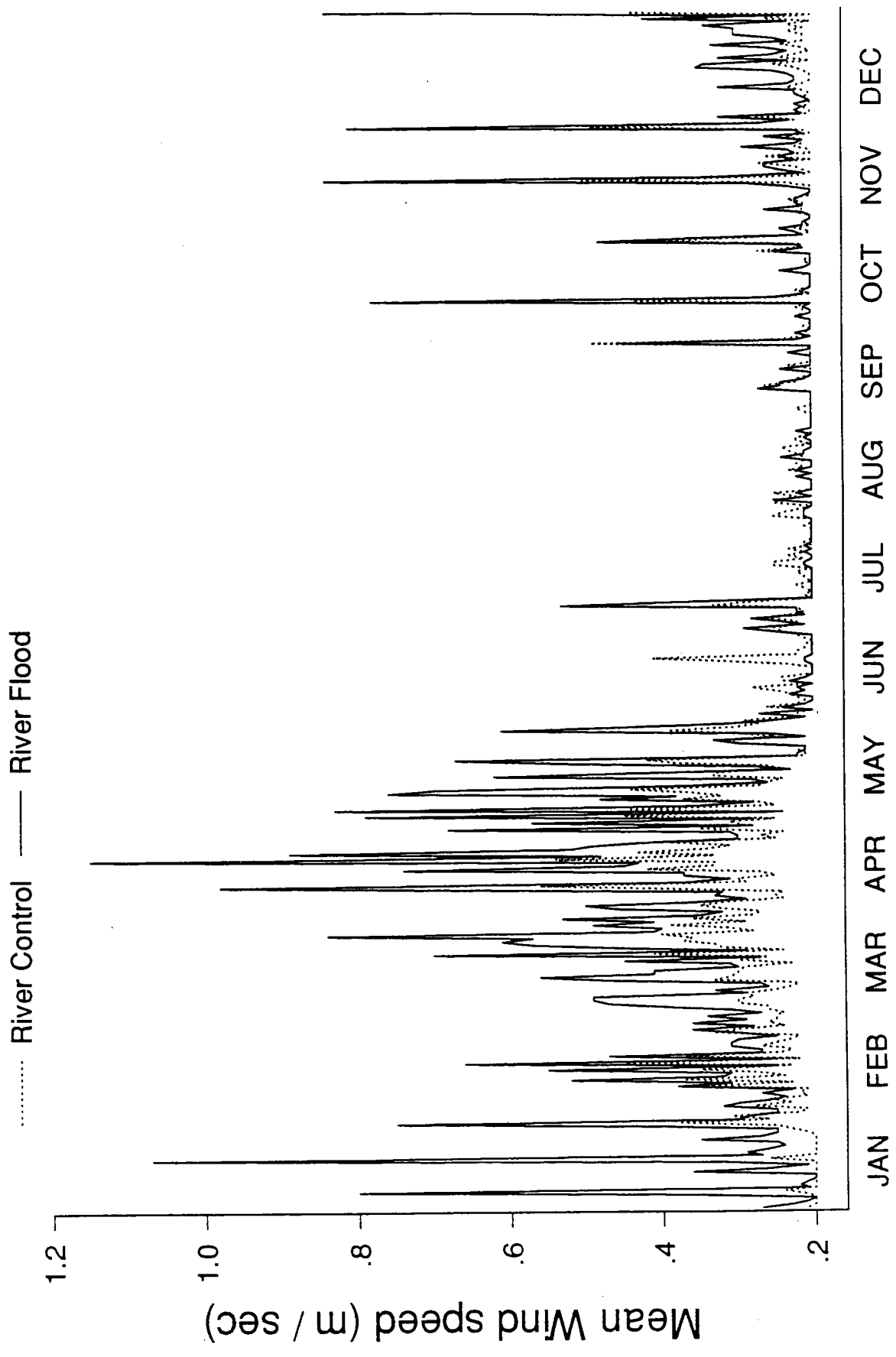


Figure 13. Daily mean wind speed at river sites in 1995.

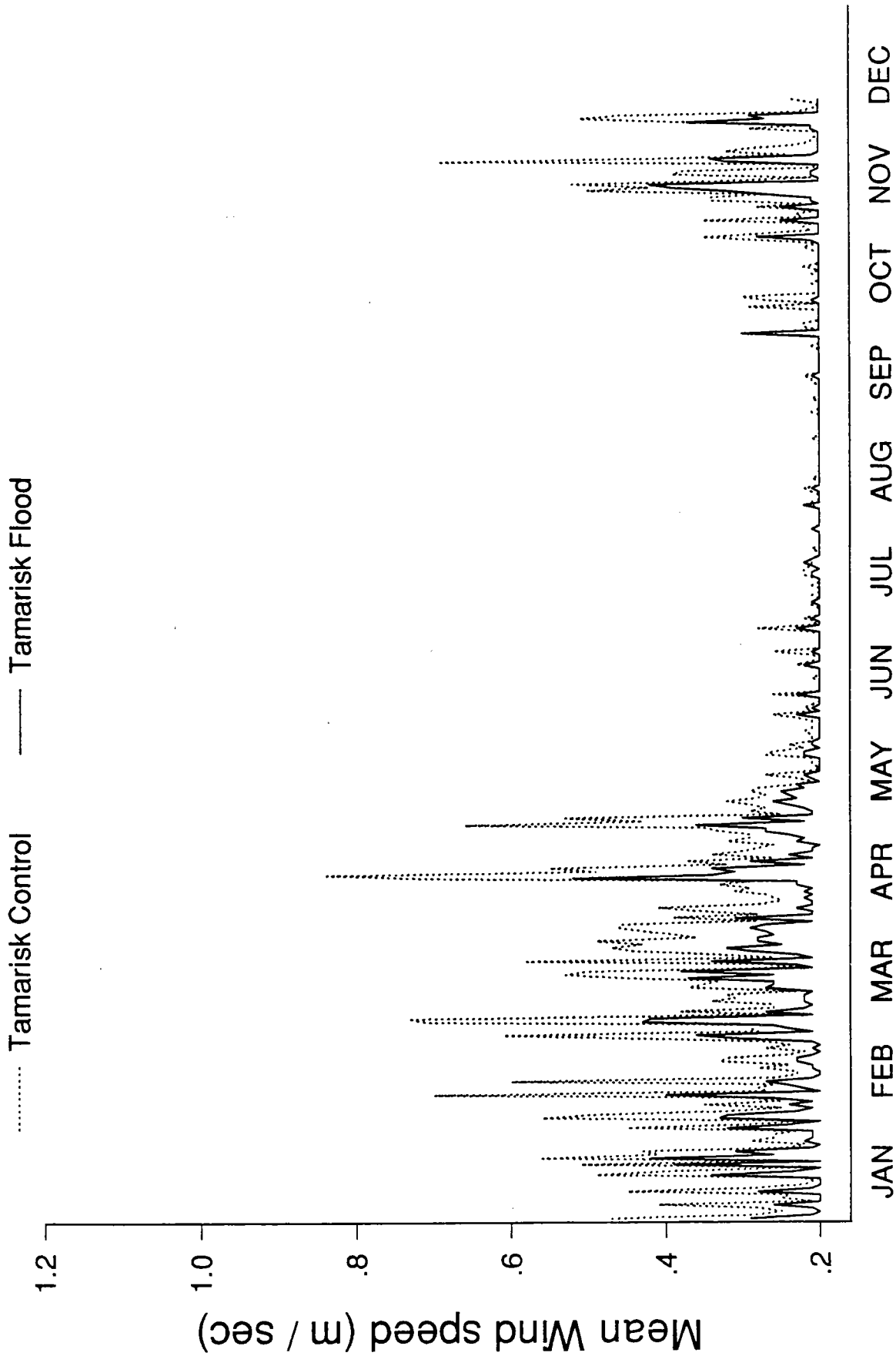


Figure 14. Daily mean wind speed at tamarisk sites in 1994.

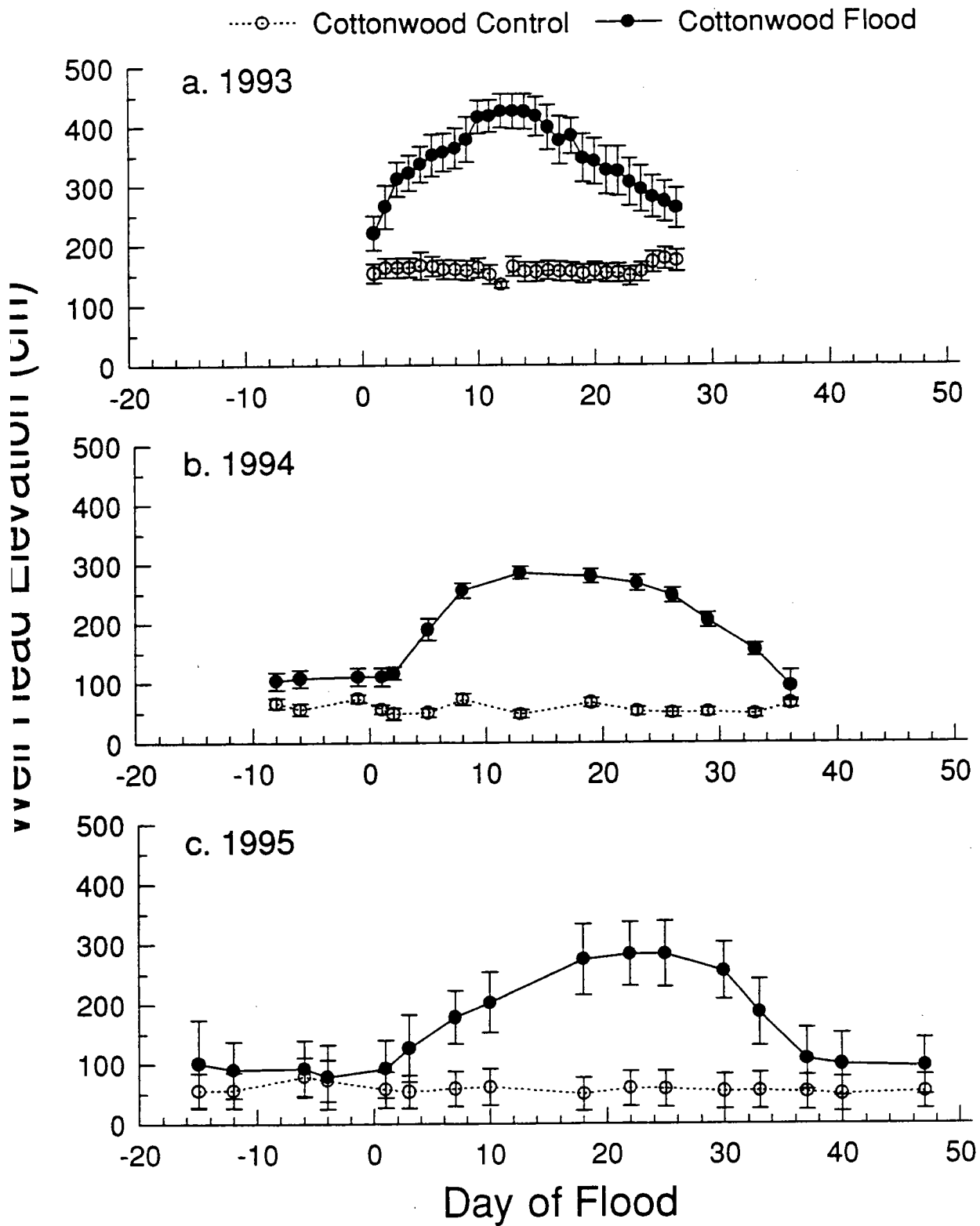


Figure 15. Average well head elevation of groundwater at cottonwood sites during a) 1993, b) 1994, and c) 1995 flood periods. Day of flood indicates number of days from the initiation of flooding (Day 0 = start of flood) each year.

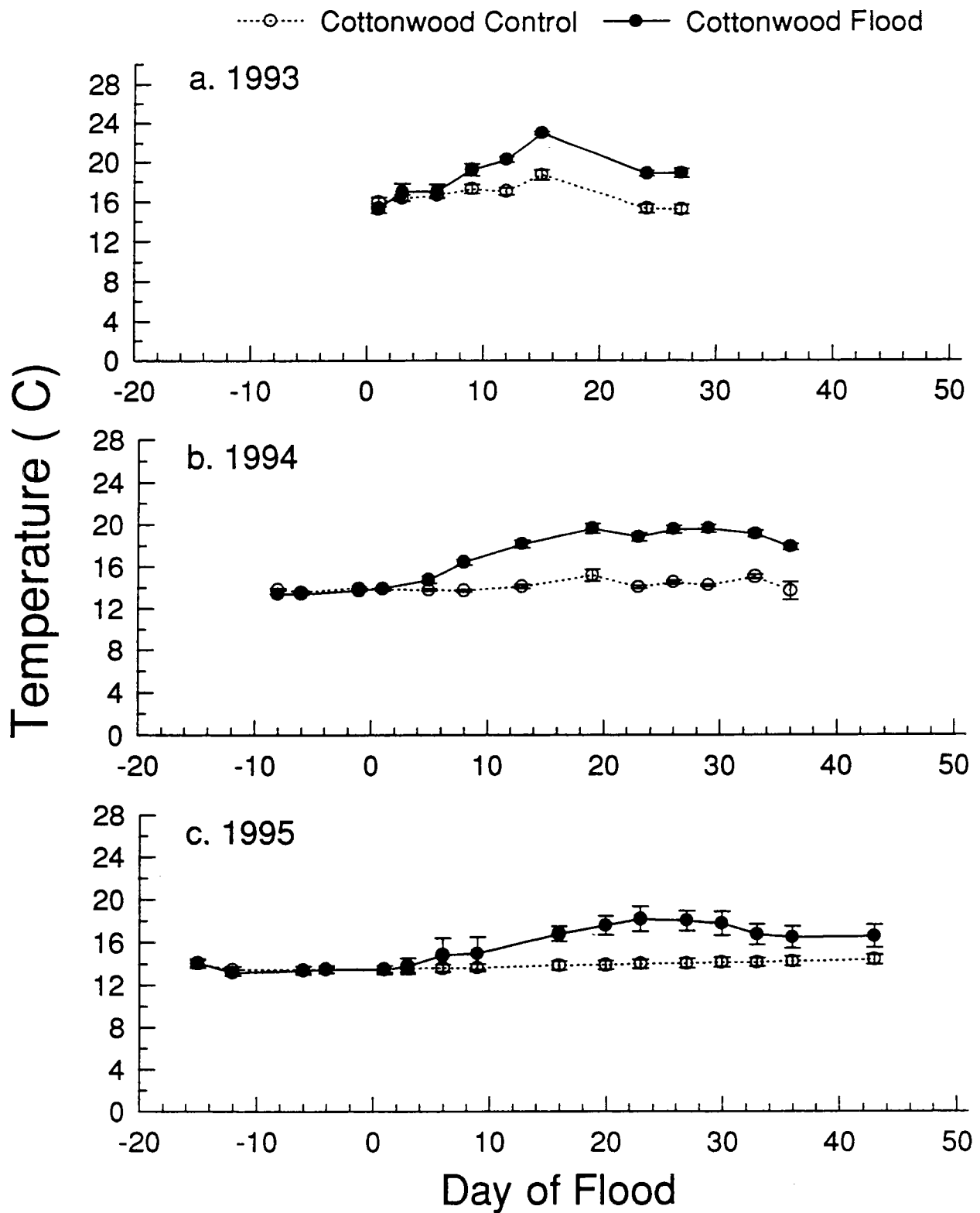


Figure 16. Average temperature of groundwater at cottonwood sites during a) 1993, b) 1994, and c) 1995 flood periods. Day of flood indicates number of days from the initiation of flooding (Day 0 = start of flood) each year.

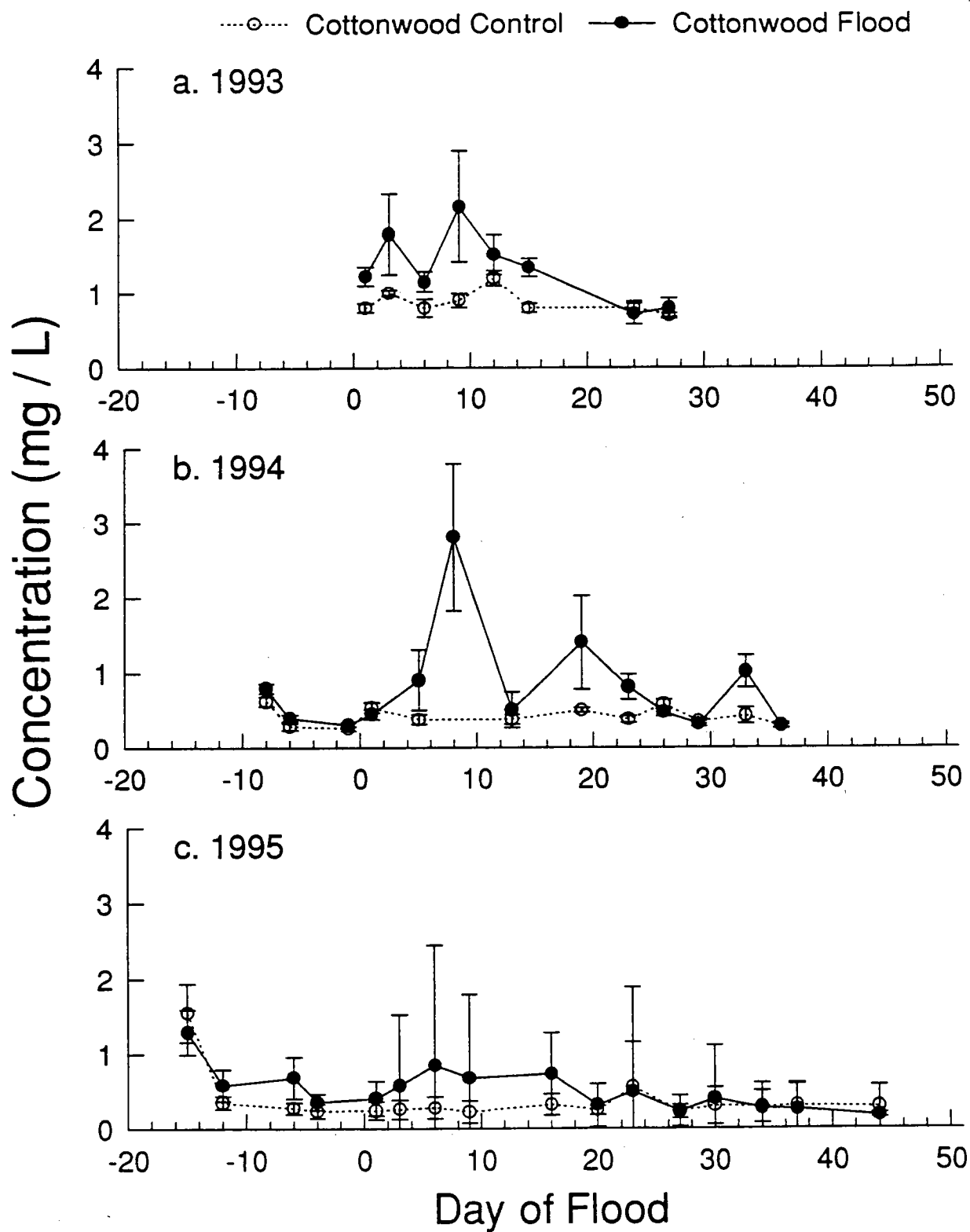


Figure 17. Average dissolved oxygen (DO) concentrations in groundwater at cottonwood sites during a) 1993, b) 1994, and c) 1995 flood periods. Day of flood indicates number of days from the initiation of flooding (Day 0 = start of flood) each year.

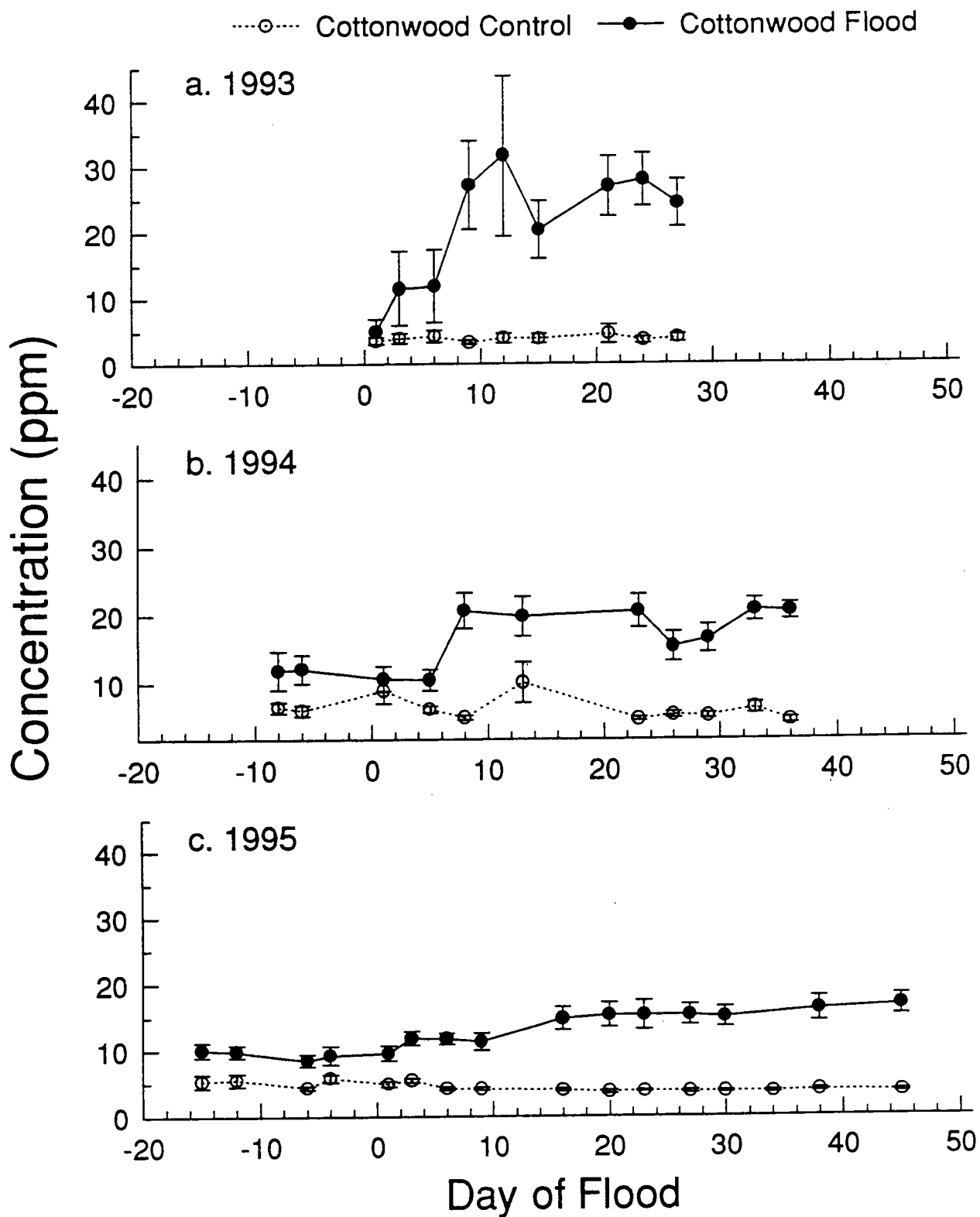


Figure 18. Average dissolved organic carbon (DOC) concentrations in groundwater at cottonwood sites during a) 1993, b) 1994, and c) 1995 flood periods. Day of flood indicates number of days from the initiation of flooding (Day 0 = start of flood) each year.

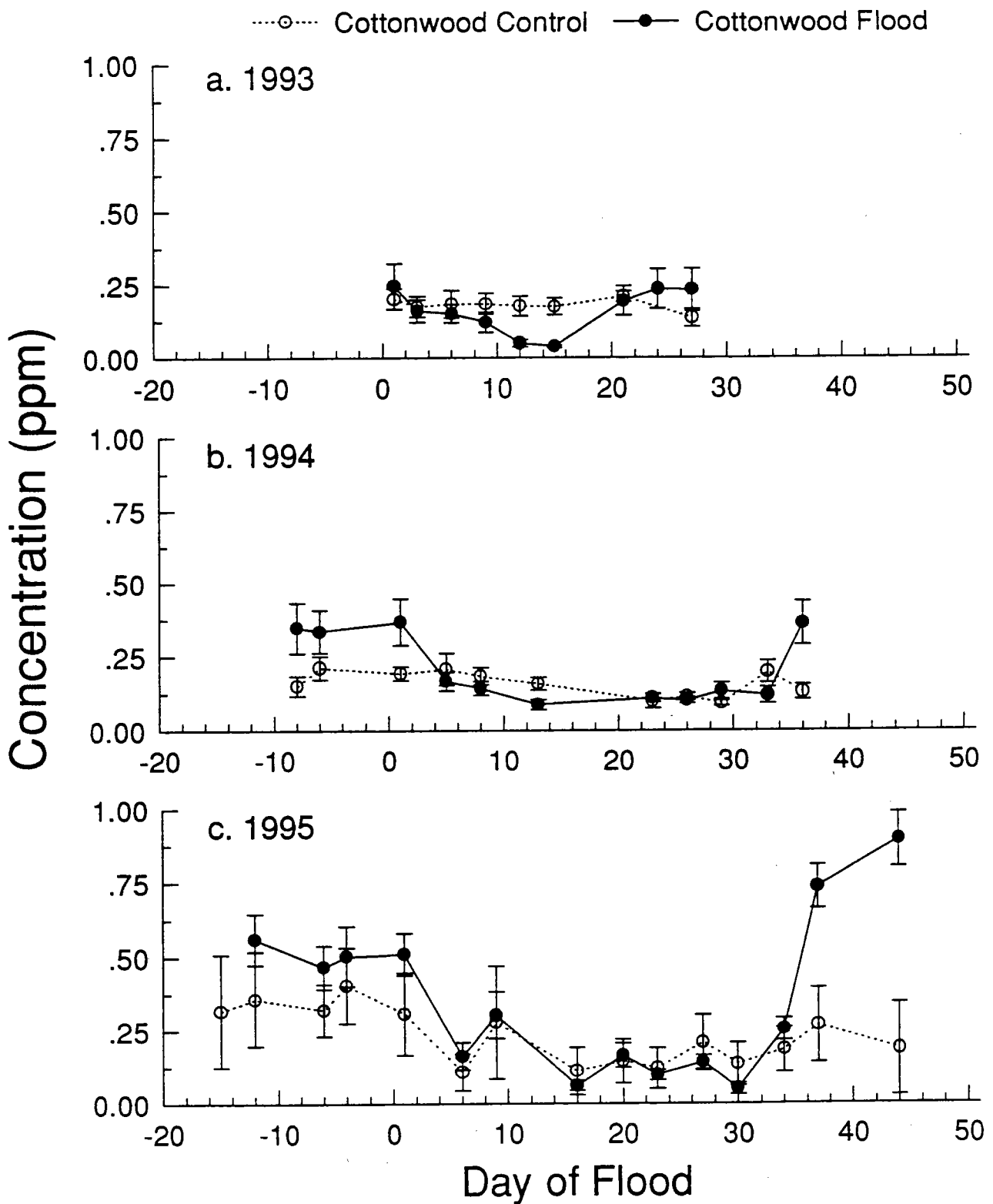


Figure 19. Average ammonium-nitrogen ( $\text{NH}_4\text{-N}$ ) concentrations in groundwater at cottonwood sites during a) 1993, b) 1994, and c) 1995 flood periods. Day of flood indicates number of days from the initiation of flooding (Day 0 = start of flood) each year.



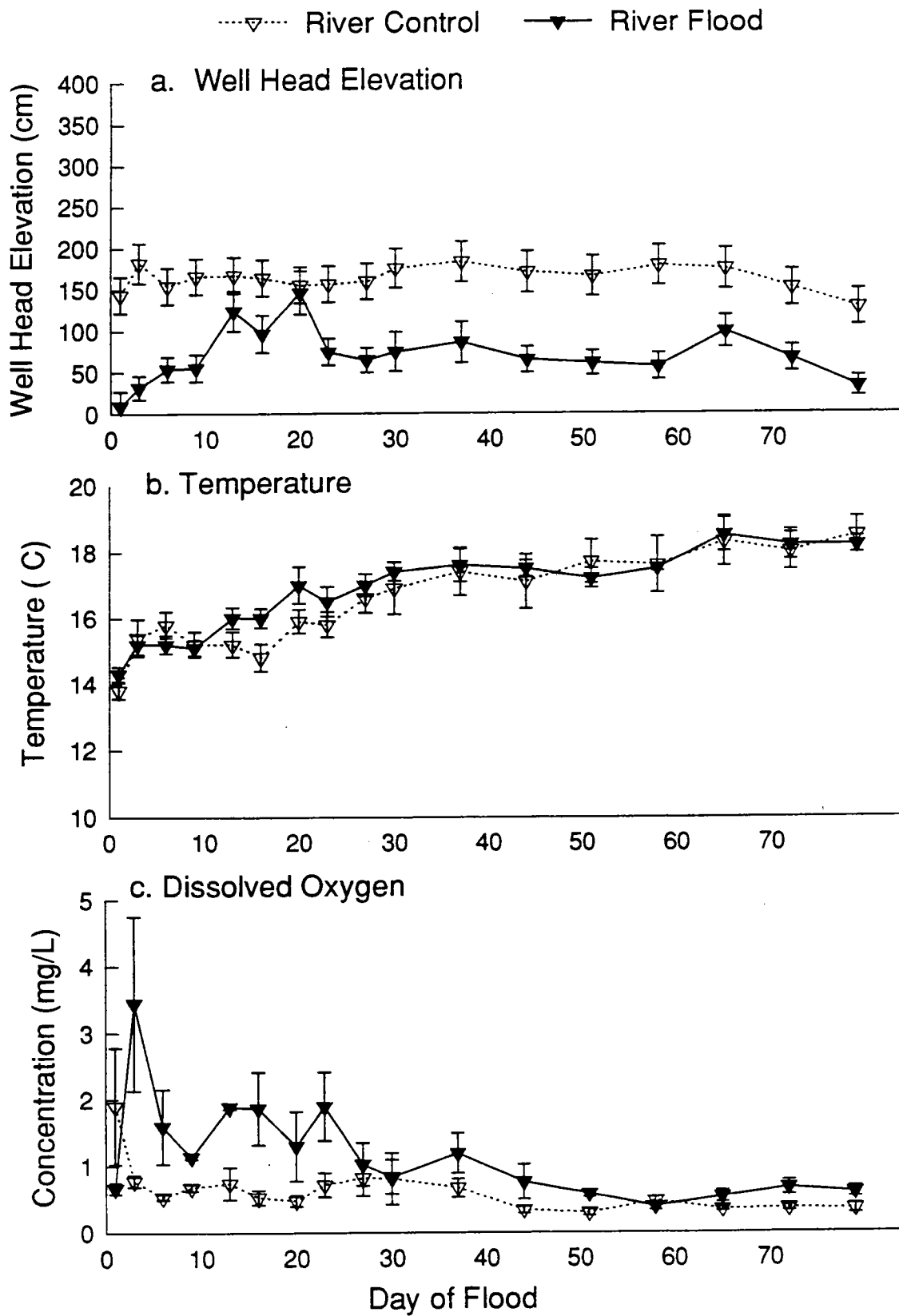


Figure 20. Groundwater elevation (a), temperature (b), and dissolved oxygen (c) at river sites during the 1995 flood. River Flood was inundated for approximately 2.5 months during mid-May through July. Values are the mean for seven wells at each site; vertical bars indicate standard error.

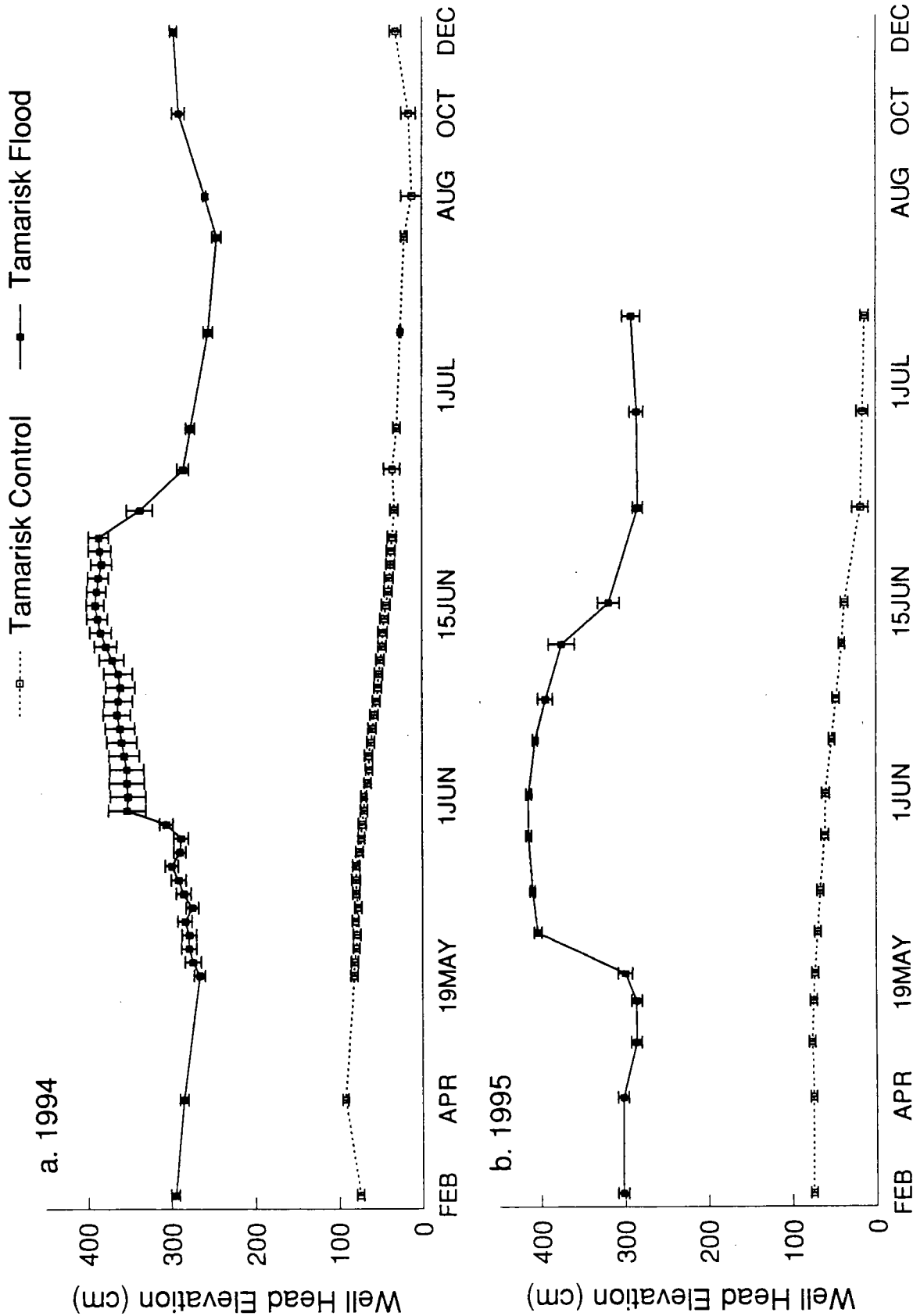


Figure 21. Well head elevation at tamarisk sites during a) 1994 and b) 1995 floods. Tamarisk Flood was inundated for approximately one month during May to June each year. Values are the mean for three (control) or four (flood) wells; vertical bars are standard error.

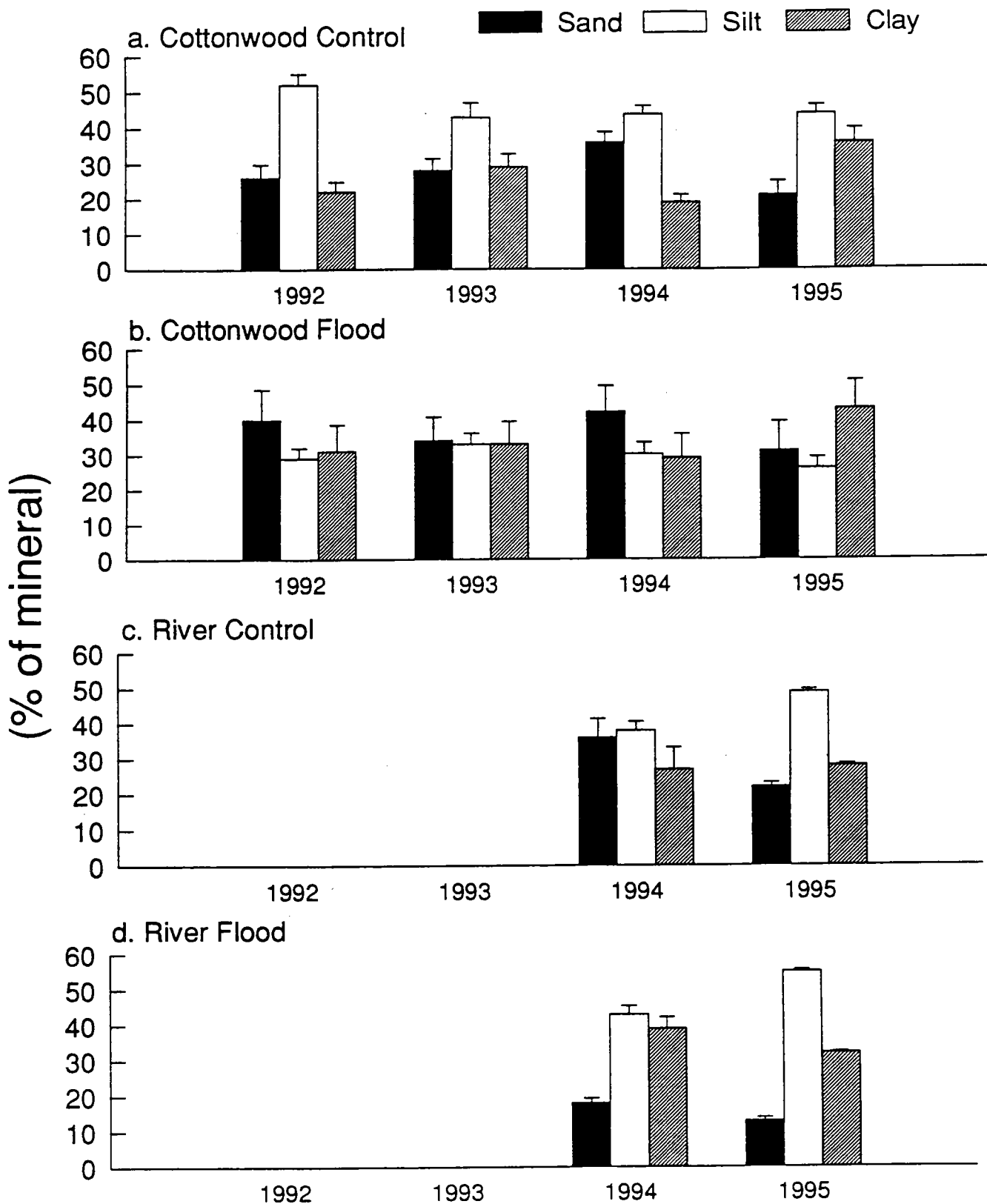


Figure 22. Soil texture at cottonwood and river sites during 1992 through 1995.

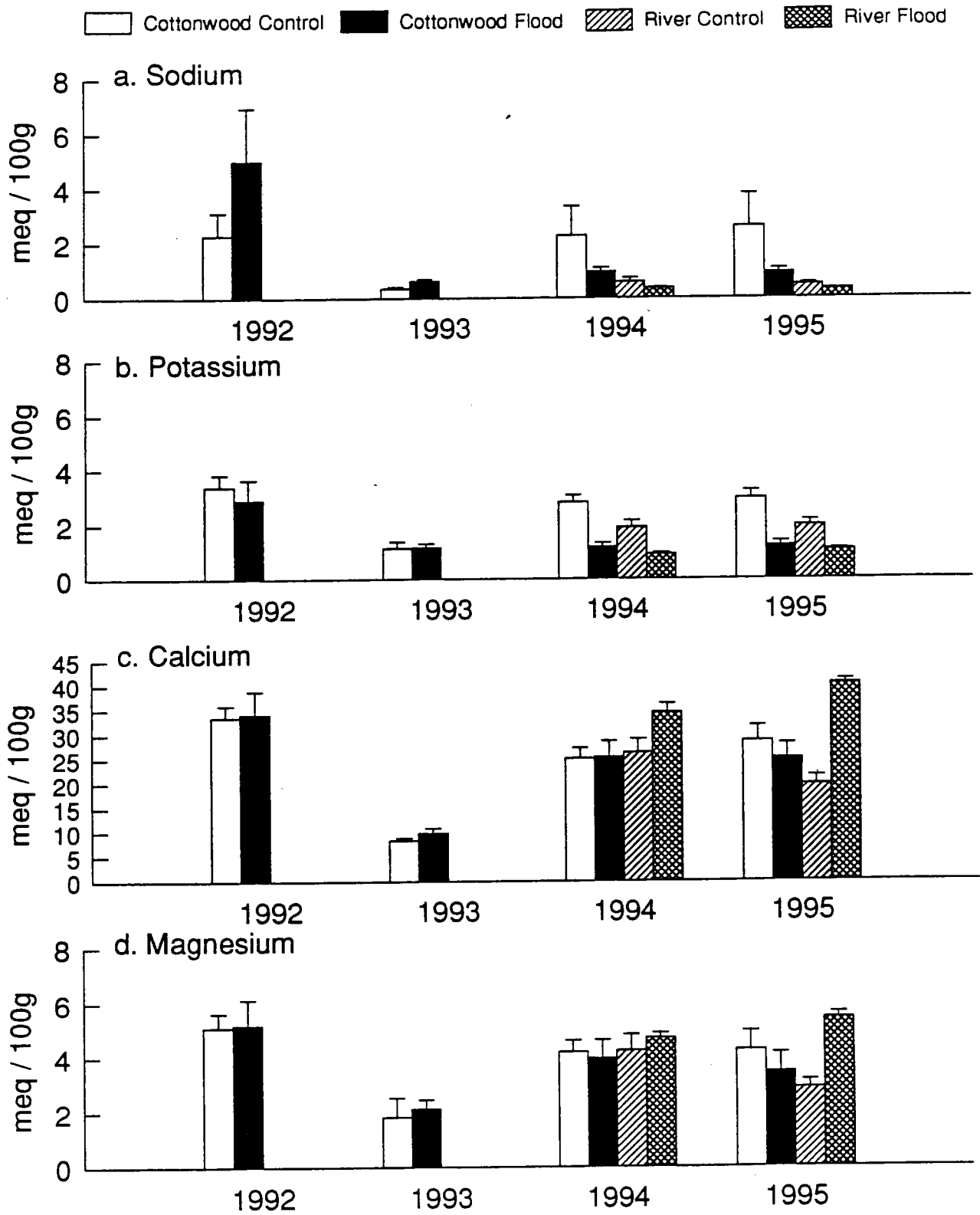


Figure 23. Extractable cations present in soils at cottonwood and river sites during 1992 through 1995.

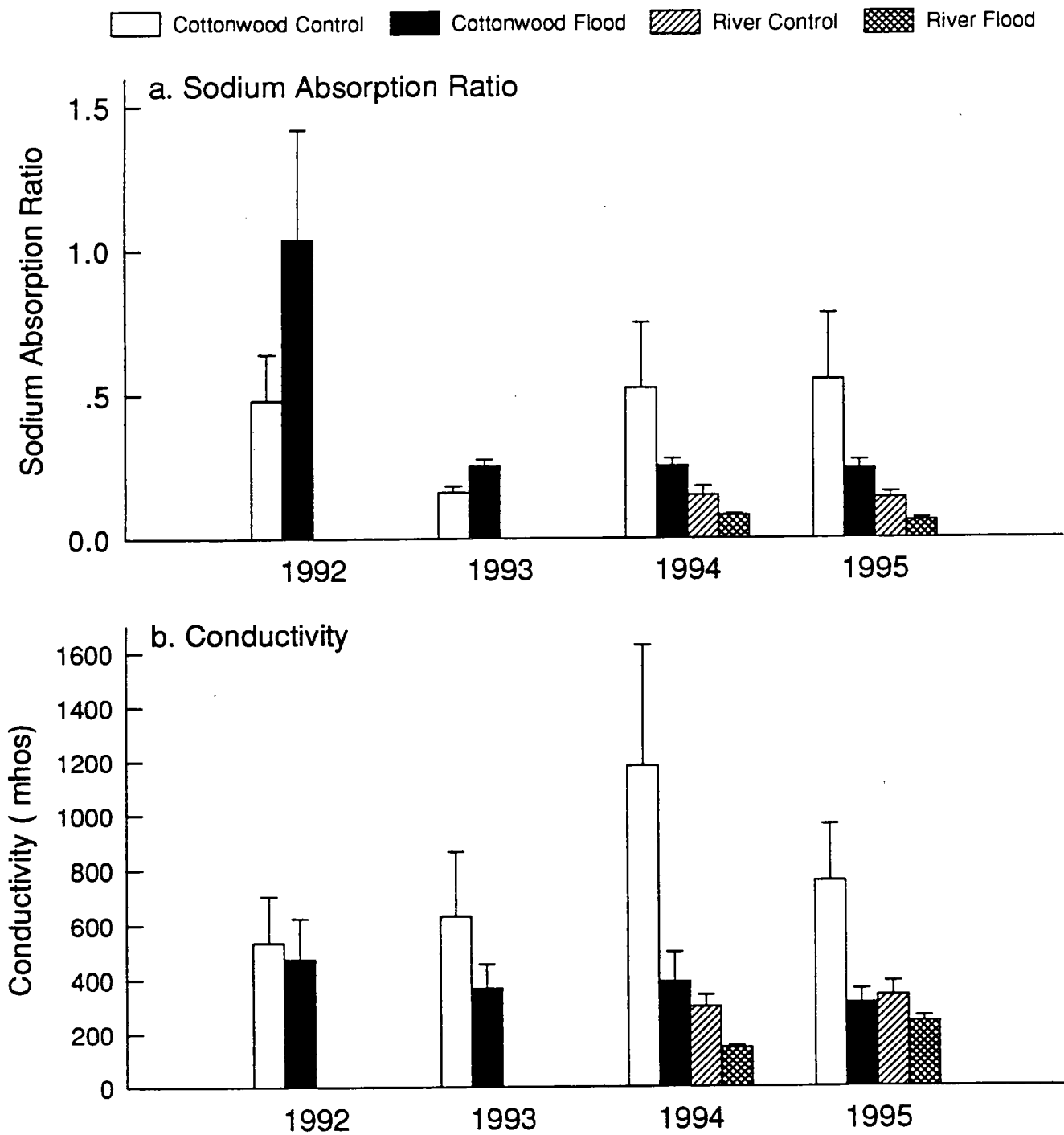


Figure 24. a) Sodium absorption ratio and b) conductivity at cottonwood and river sites during 1992 through 1995.

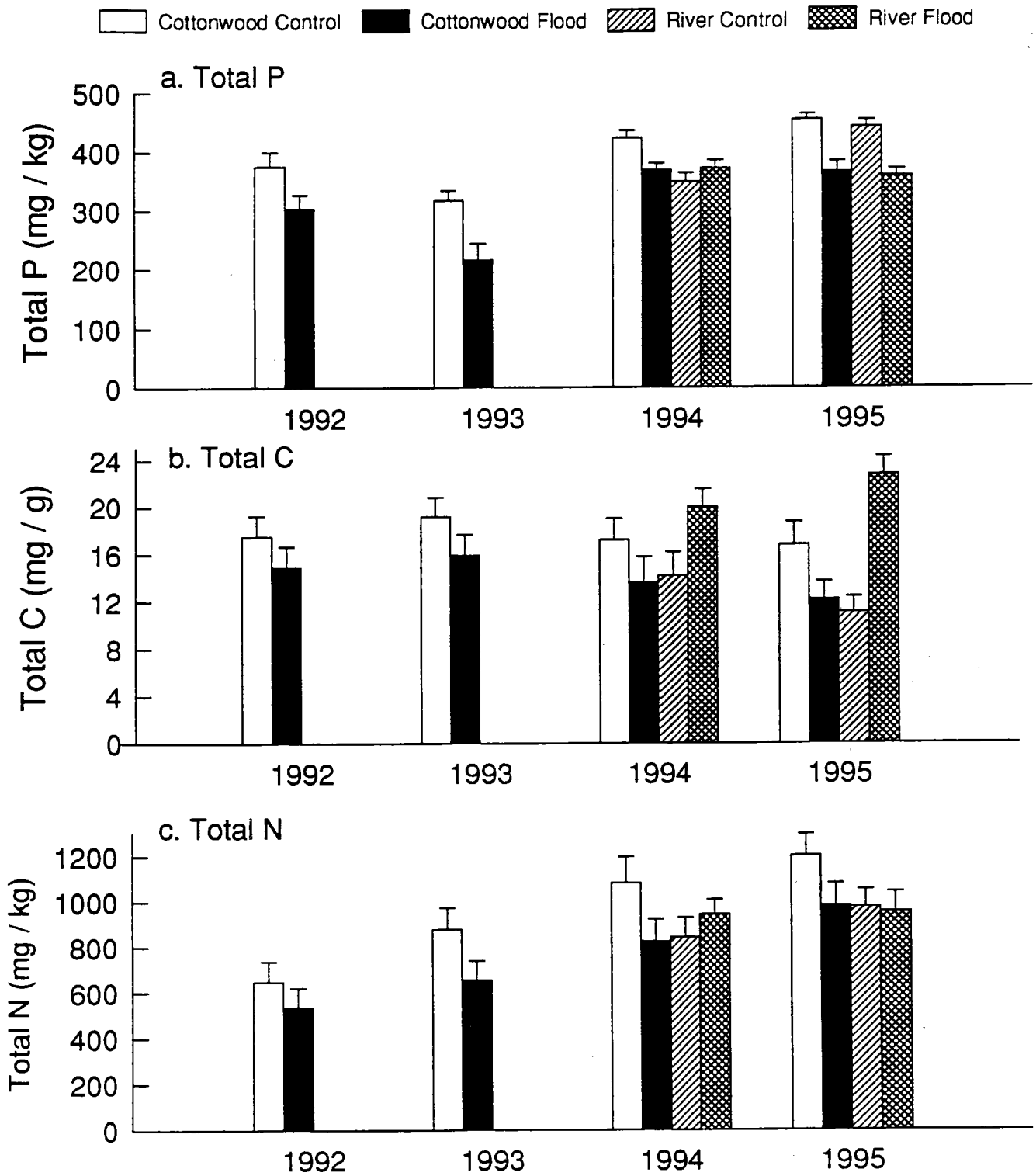


Figure 25. Total a) phosphorus, b) carbon, and c) nitrogen in soils at cottonwood and river sites during 1992 through 1995.

Cottonwood Control
  Cottonwood Flood
  River Control
  River Flood

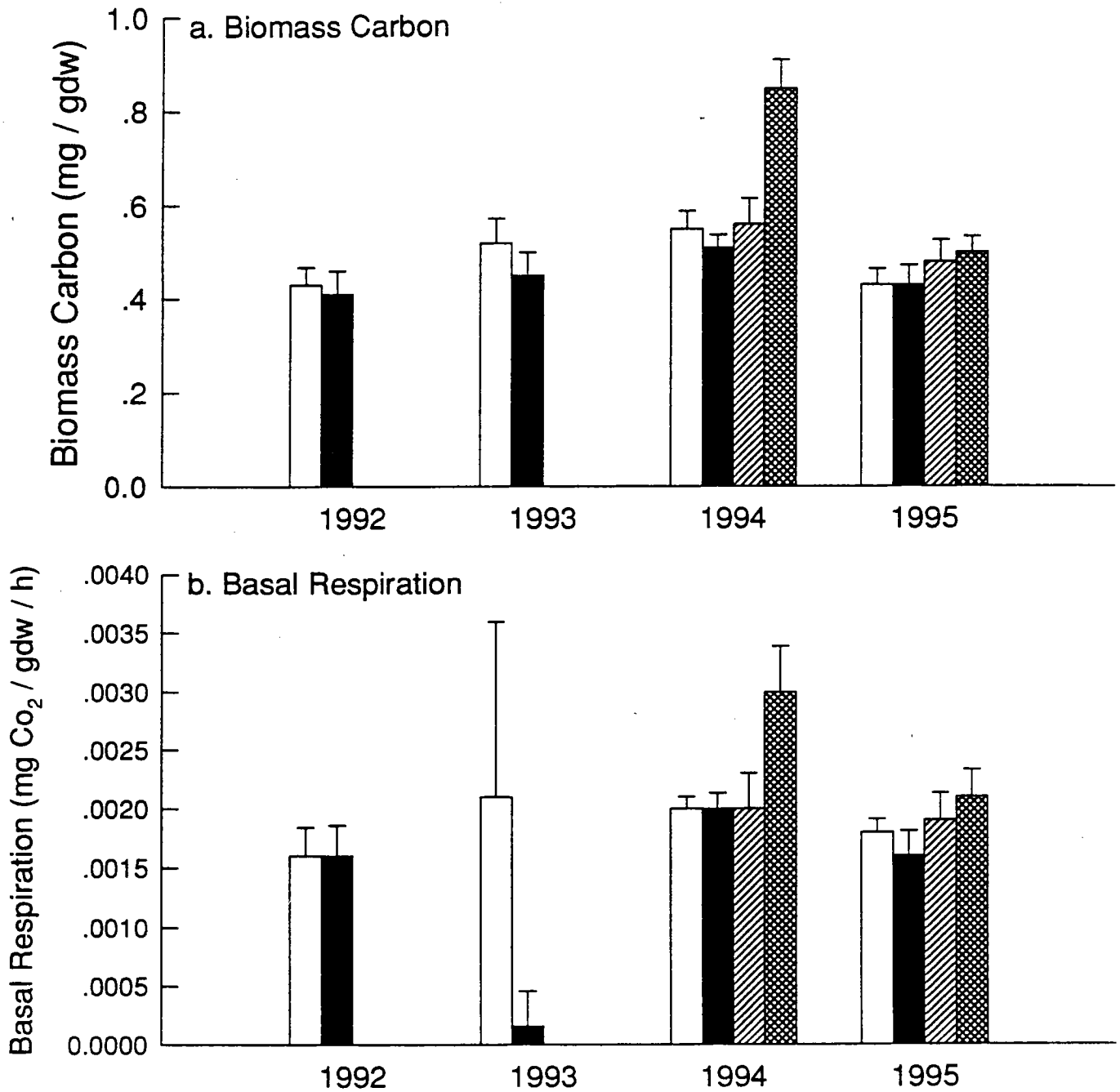


Figure 26. a) Biomass carbon and b) basal respiration in soils at cottonwood and river sites during 1992 through 1995.

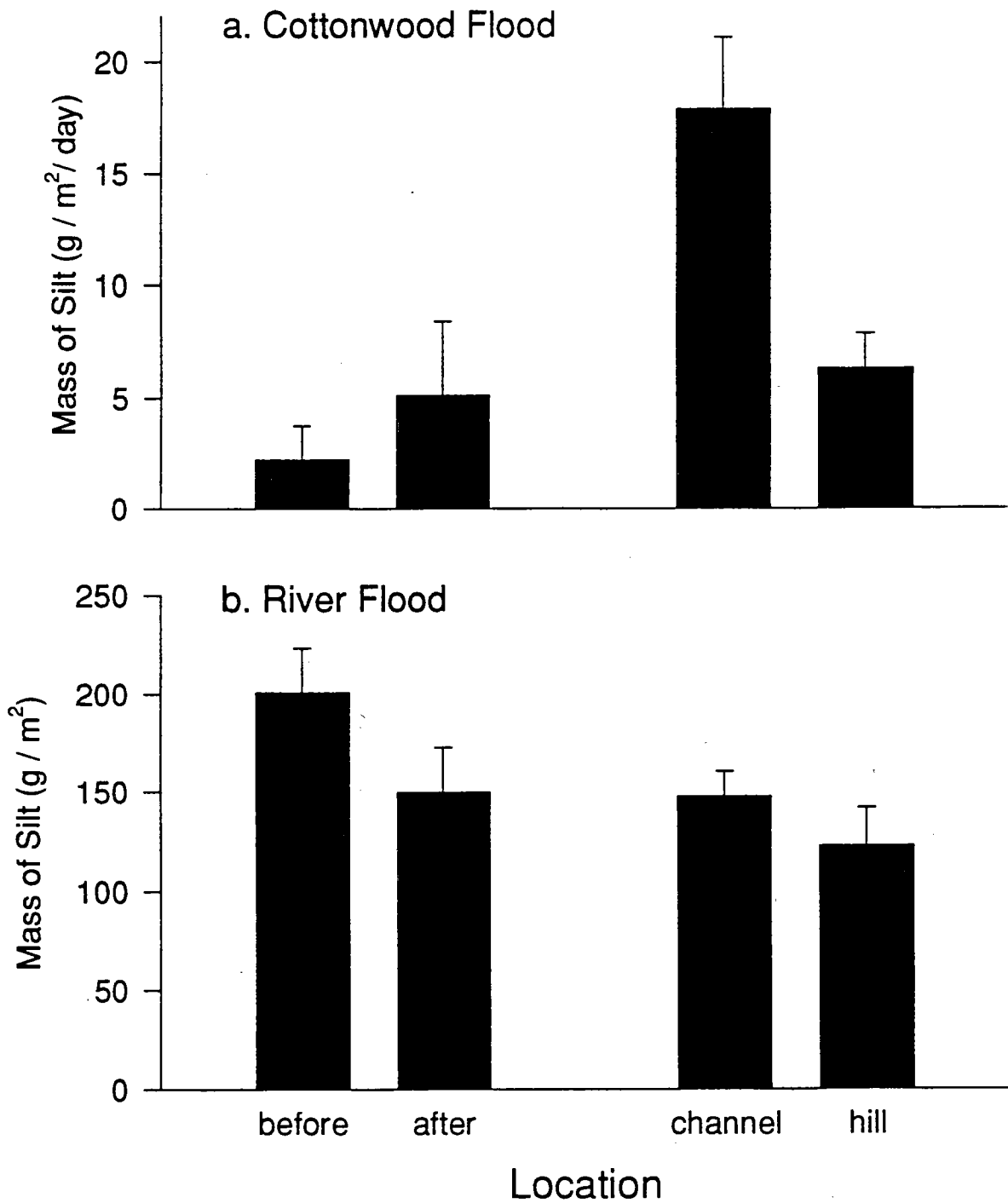


Figure 27. Total organic and inorganic sediment deposited per day on ceramic tiles during the 1995 floods at a) Cottonwood Flood and b) River Flood. Values are the average total oven dry mass of sediment for 10 tiles at each site within each collection location; vertical bars indicate standard errors. Locations are: "before" = before obstruction, "after" = after obstruction, "channel" = in channel, "hill" = upslope from channel but still underwater.



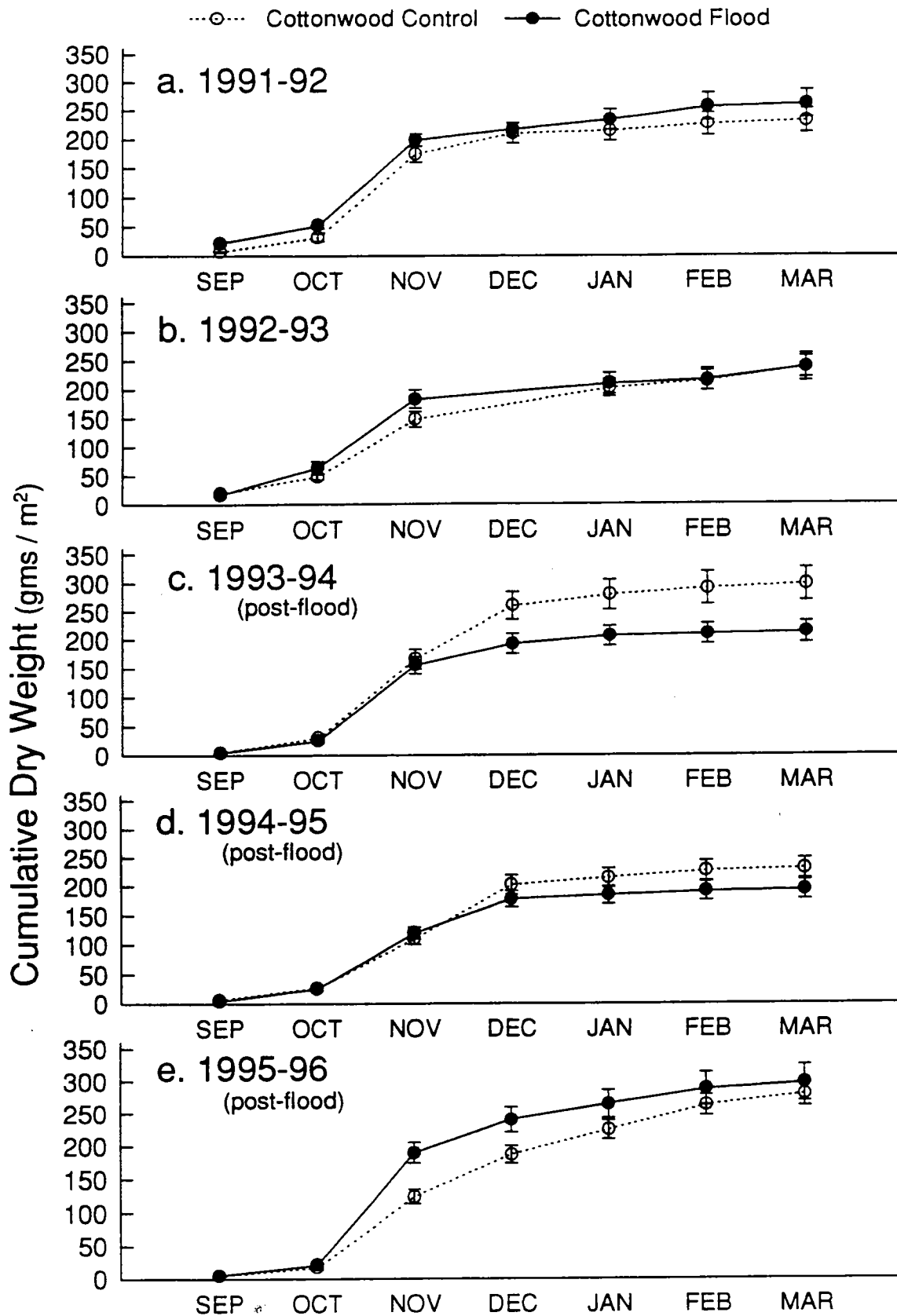


Figure 28. Cumulative litterfall at cottonwood sites during five litterfall seasons. Values are the average for 12 litter tubs at each site; vertical bars are standard errors. Litter includes leaves of all species, sticks, and other plant parts. Cottonwood flood was inundated during May to June 1993, 1994, and 1995.

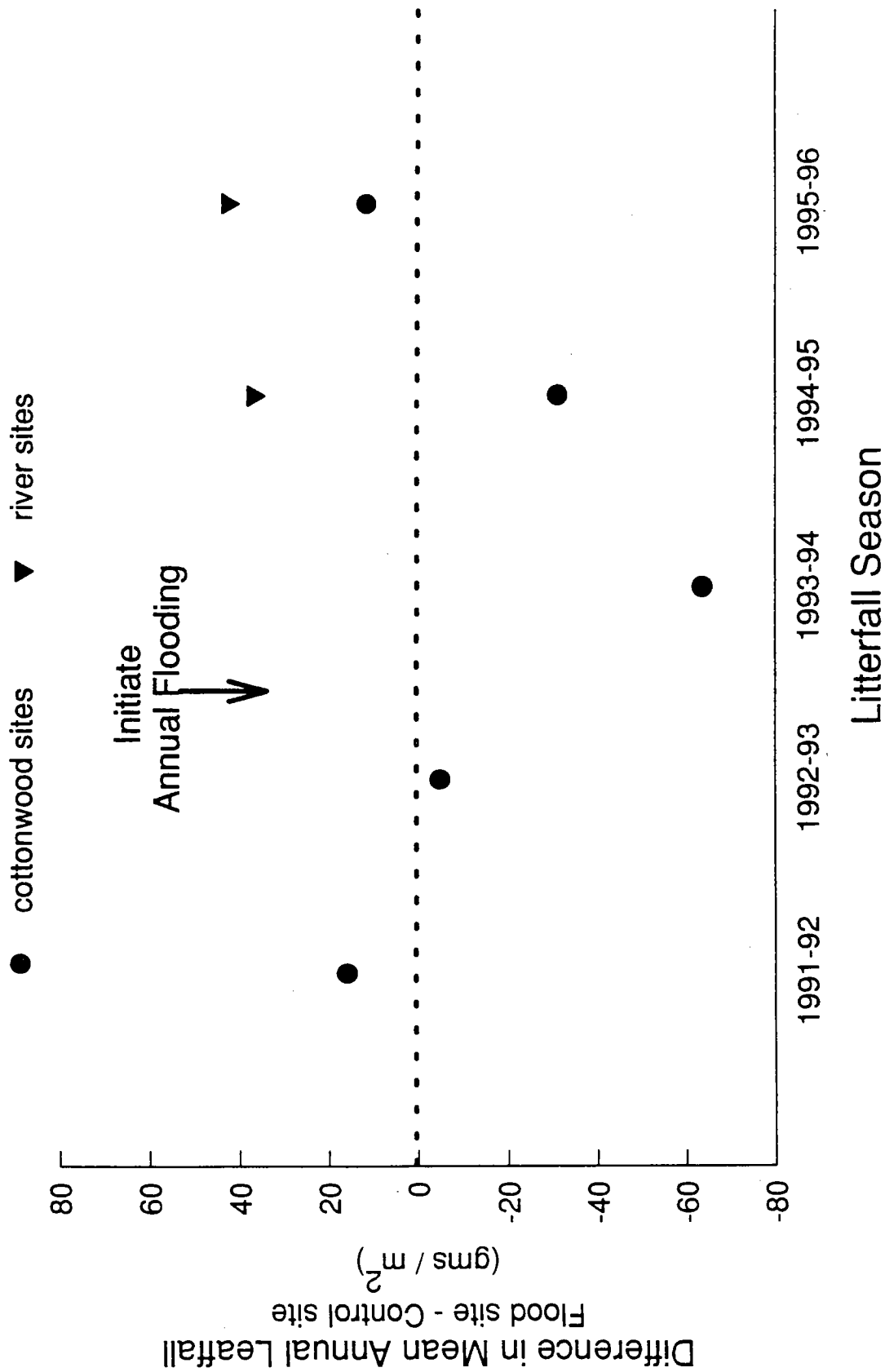


Figure 29. Intersite differences in total leaffall at cottonwood sites during 1991-92 through 1995-96 and at river sites in 1994-95 and 1995-96. Values are the difference in the total weight of cottonwood leaves between each flood and control site.

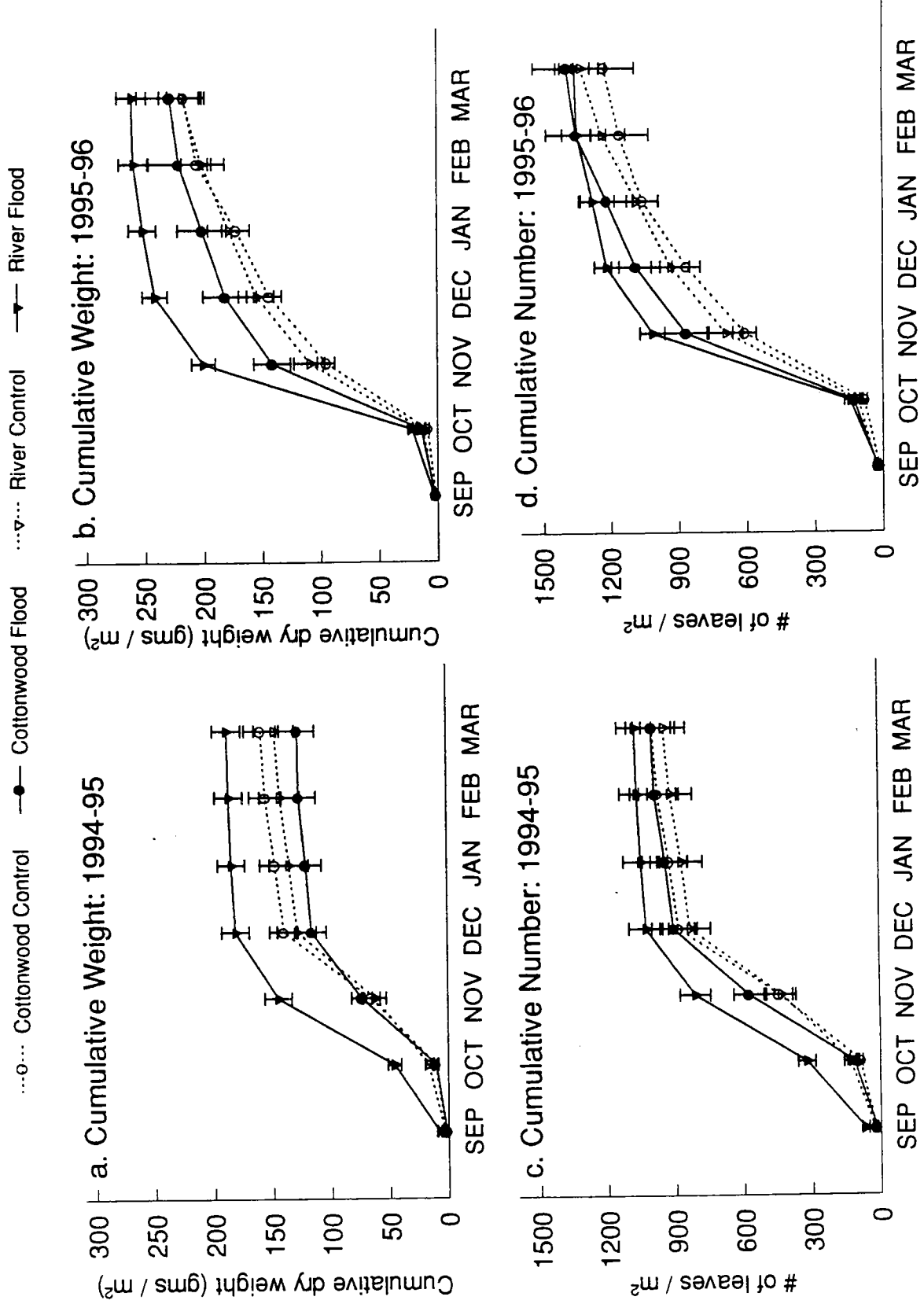
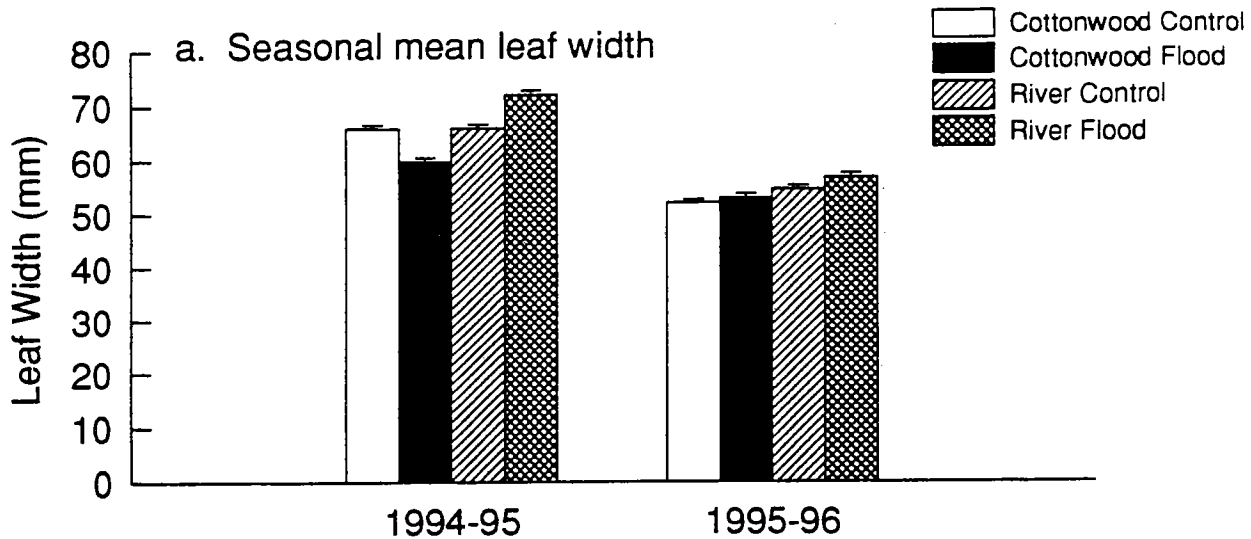


Figure 30. Cumulative weight of cottonwood leaves at cottonwood and river sites in a) 1994-95 and b) 1995-96, and cumulative number of cottonwood leaves at those sites in c) 1994-95 and d) 1995-96. Values are the mean for twelve litter tubs at each site; vertical bars are standard error.



○ Cottonwood Control   ● Cottonwood Flood   ▽ River Control   ▼ River Flood

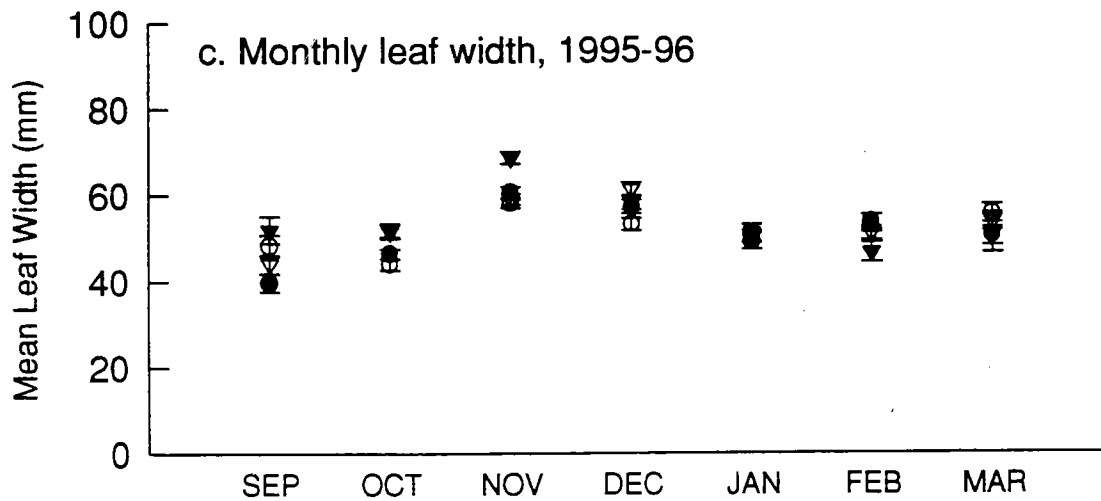
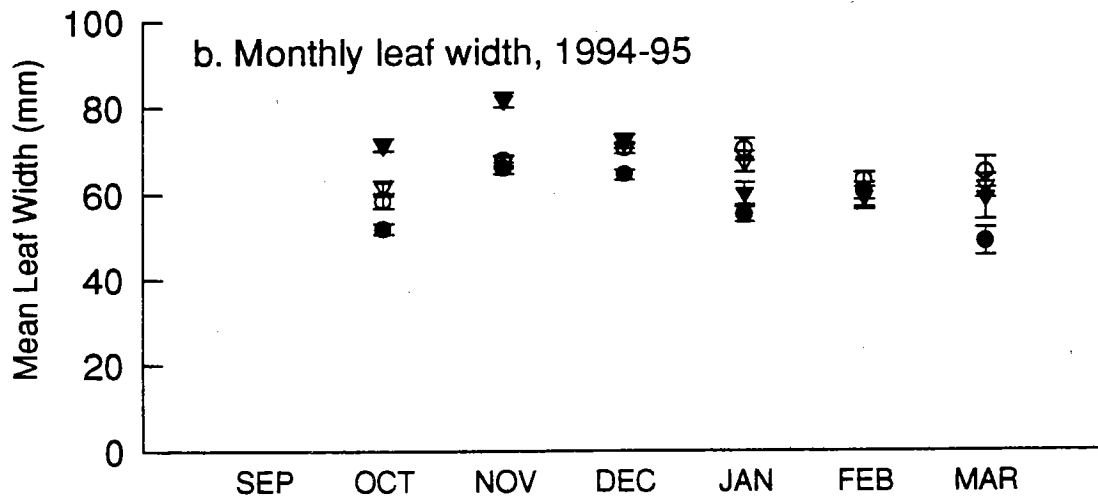


Figure 31. a) Seasonal mean leaf width for 1994-95 and 1995-96, and monthly mean leaf width for b) 1994-95 and c) 1995-96. Sample size varies among collections.

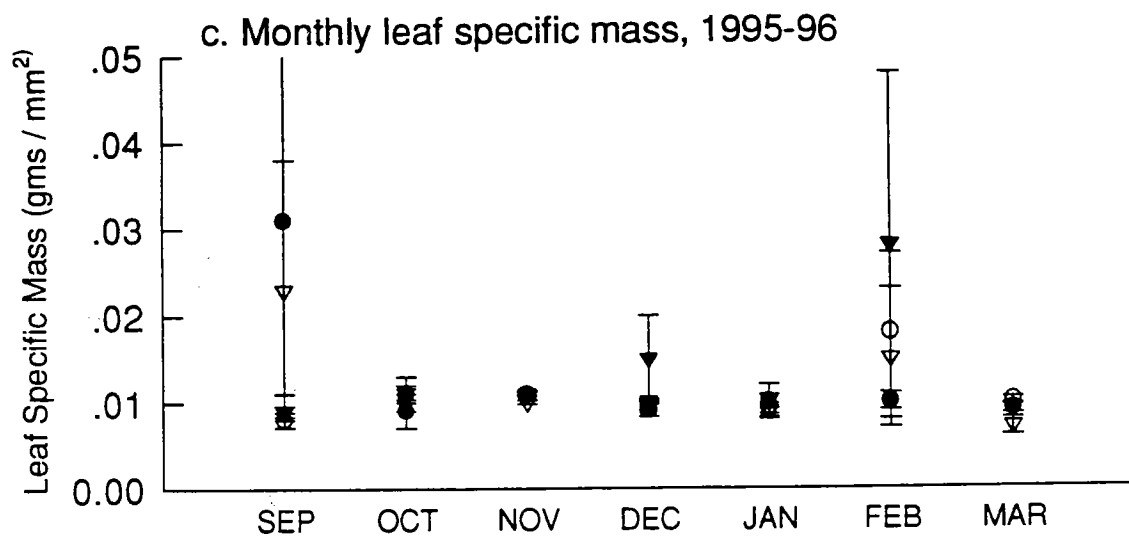
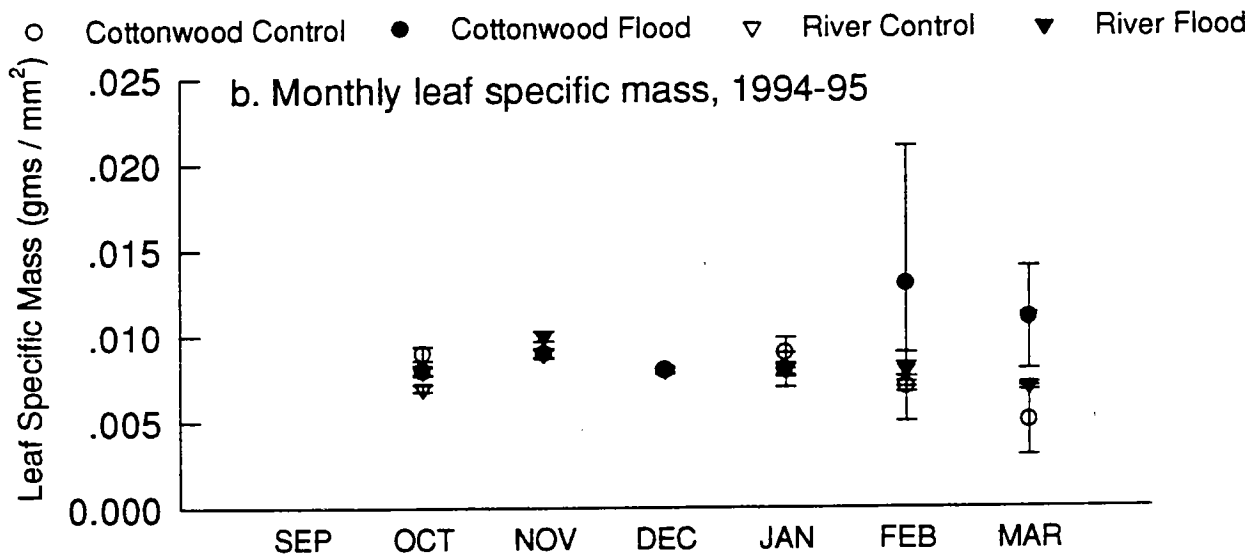
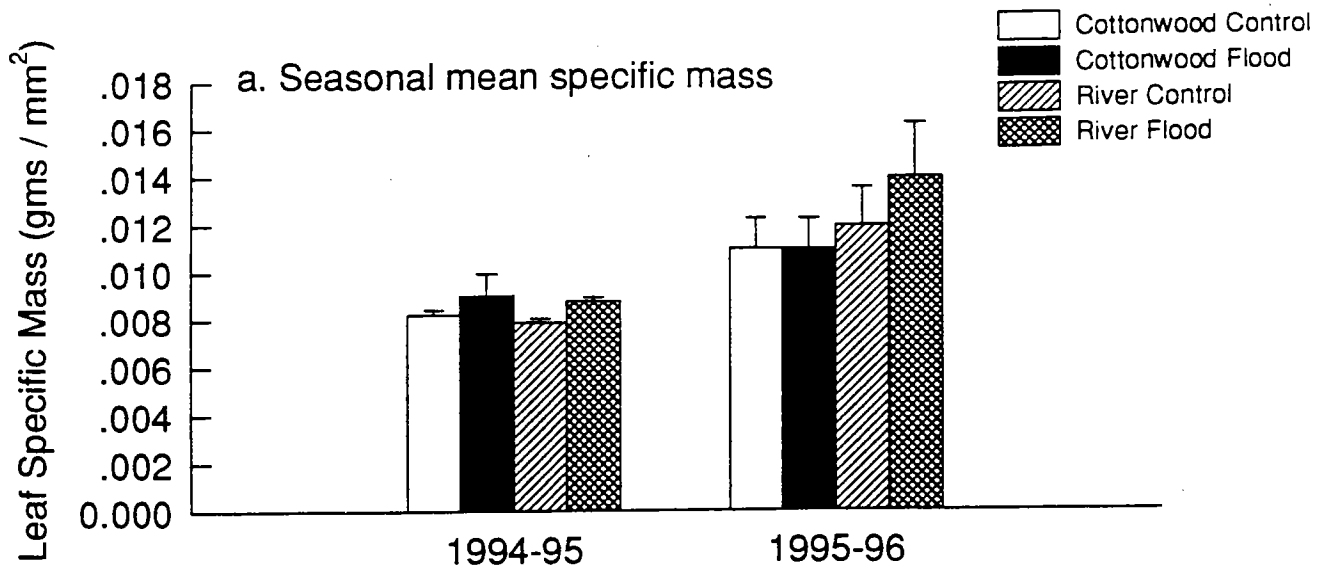


Figure 32. a) Seasonal mean specific mass for leaves during 1994-95 and 1995-96, and monthly mean specific mass for leaves during b) 1994-95 and c) 1995-96. Note differences in scale on b and c. Sample size varies among collections.

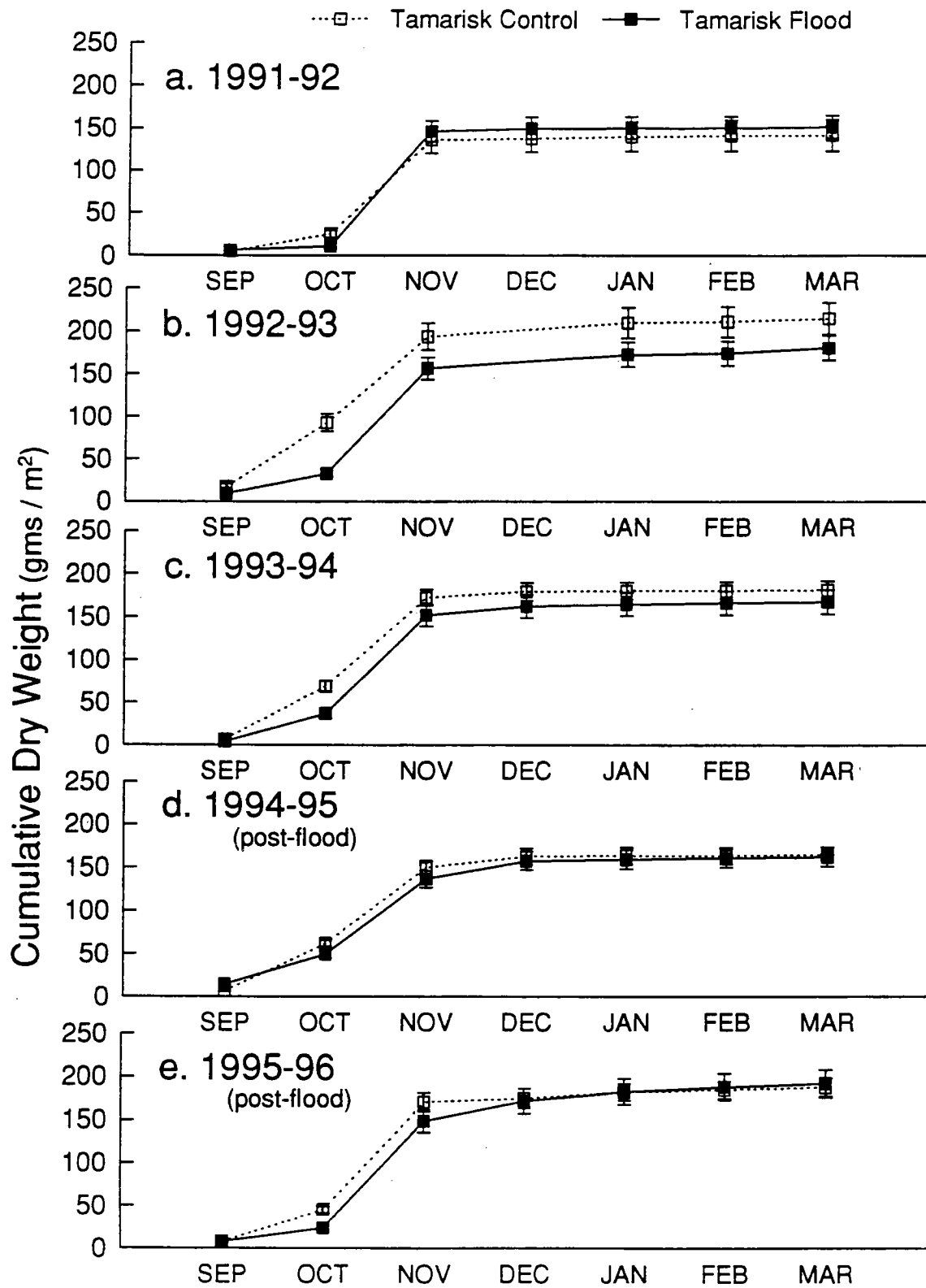


Figure 33. Cumulative litterfall at tamarisk sites during five litterfall seasons. Values are the means for 12 litter tubs at each site; vertical bars are standard errors. Tamarisk Flood was partially inundated during June 1994 and fully inundated during June 1995.

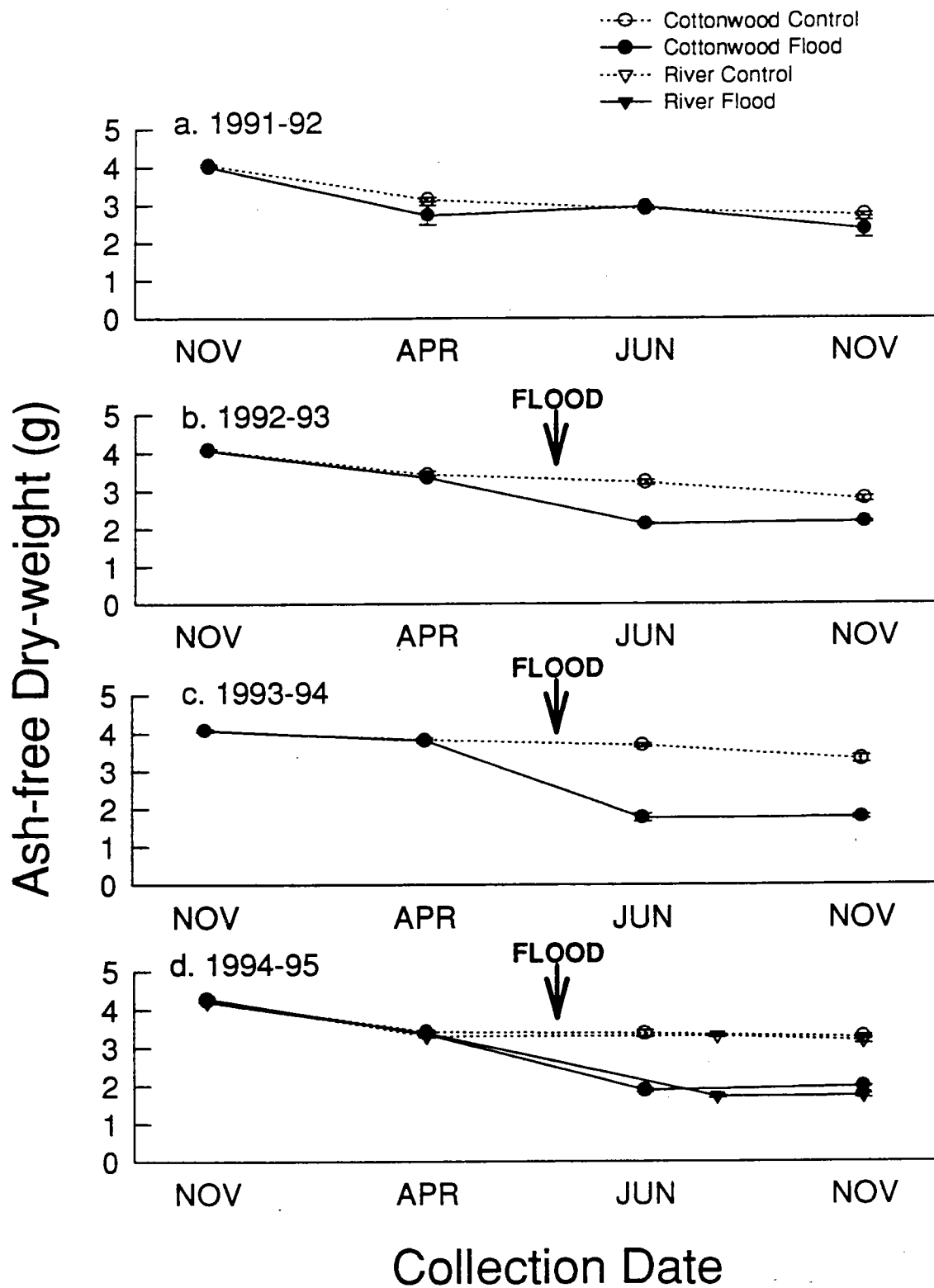


Figure 34. Changes in the mass of leaves in decomposition bags at cottonwood and river sites during a) 1991 - 92, b) 1992 - 93, c) 1993 - 94, and d) 1994 - 95. Cottonwood Flood was inundated for approximately one month between May and June in 1993, 1994, and 1995. River Flood was added in fall 1994 and was inundated for approximately 2.5 months in 1995. The third collection at River Flood was made in early August. Values are the mean ash-free dry-weight of leaves in five bags for each site; vertical bars are standard error.

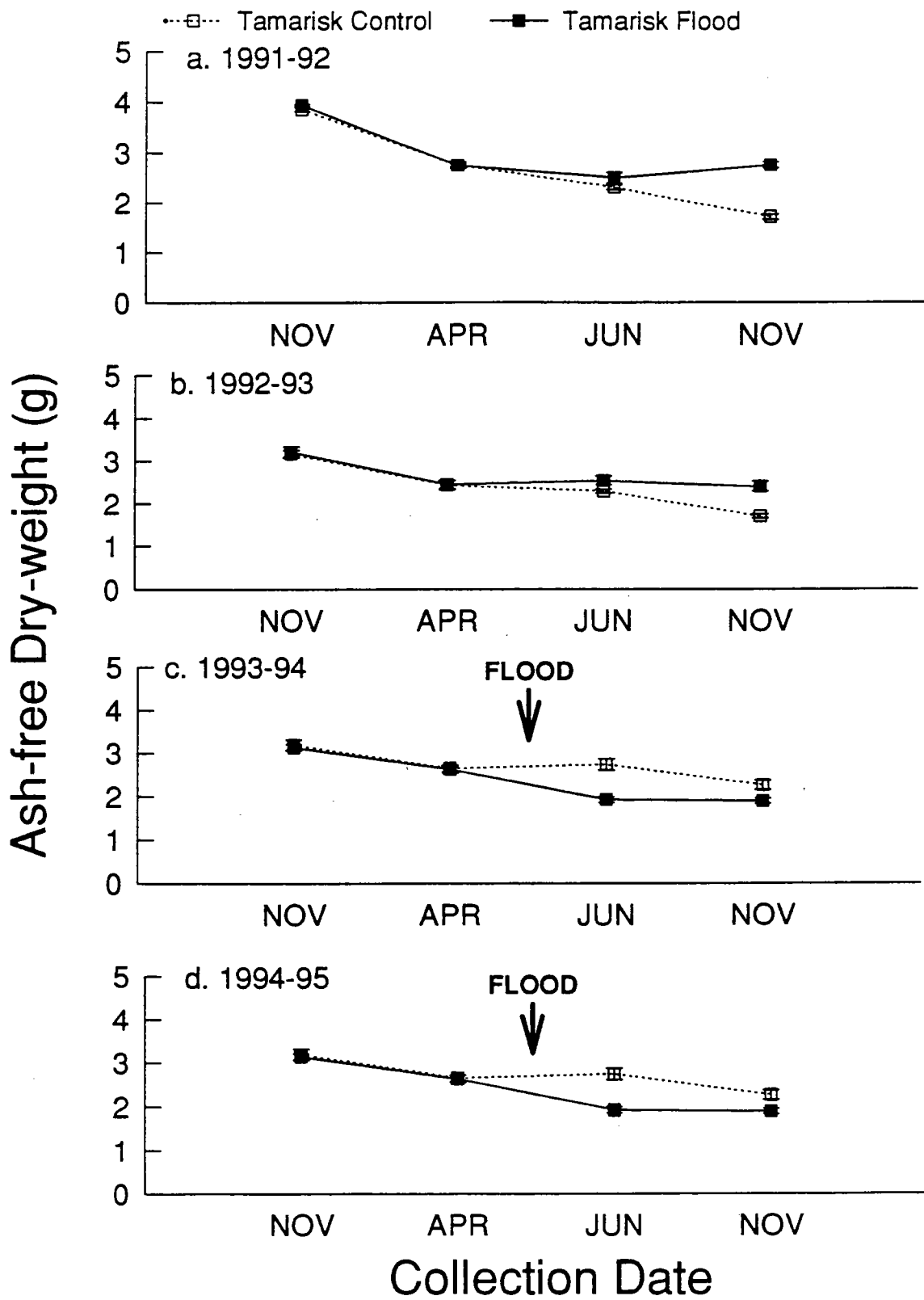


Figure 35. Changes in the mass of leaves in decomposition bags at tamarisk sites during a) 1991 - 92, b) 1992 - 93, c) 1993 - 94 and d) 1994 - 95. Tamarisk Flood was partially inundated during May to June 1994 and fully inundated during June 1995. Values are the mean ash-free dry-weight of leaves in five bags for each site; vertical bars are standard error.



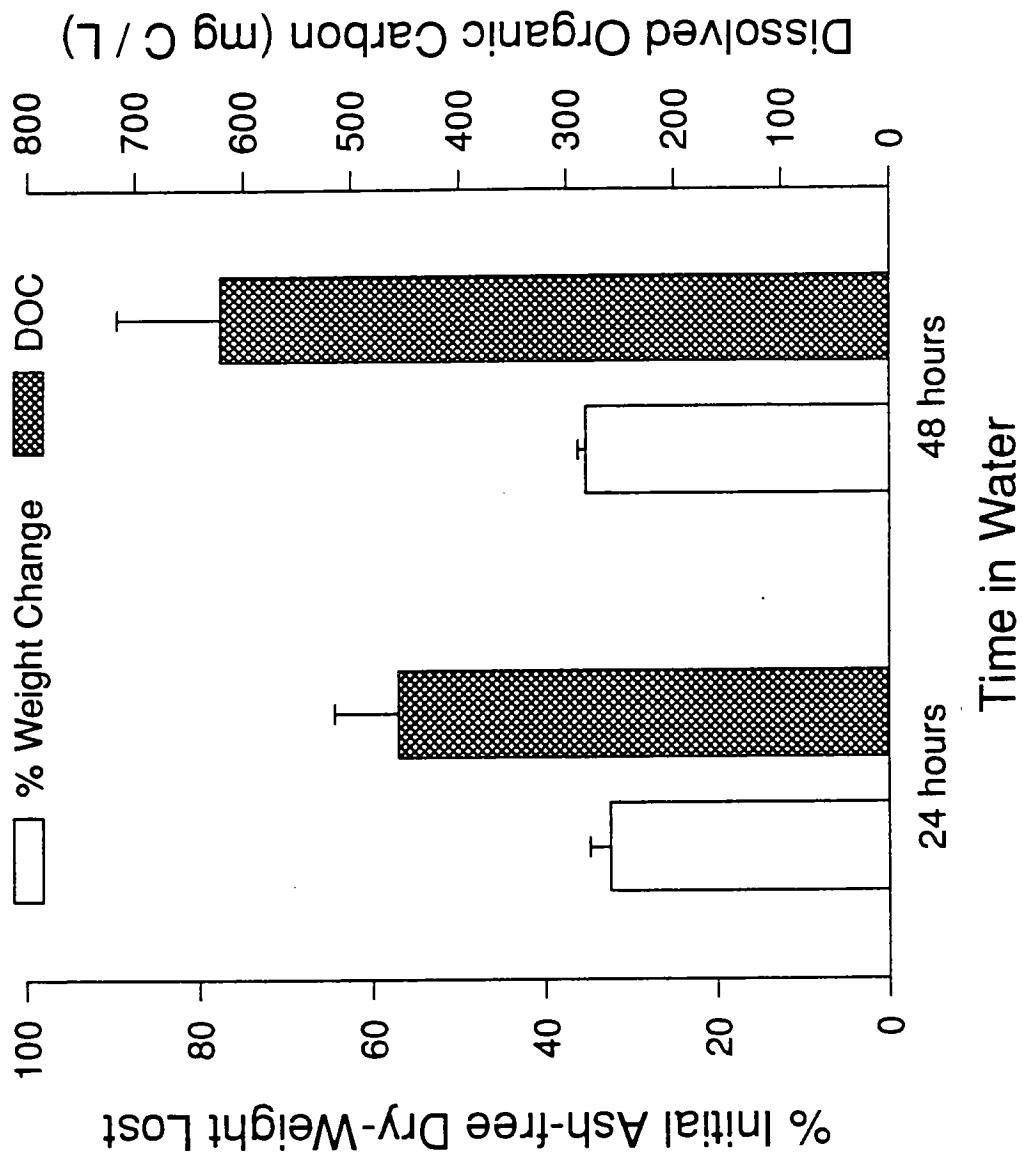


Figure 36. Weight change and dissolved organic carbon liberated during leaching of cottonwood leaves placed in water for 24 and 48 hours. Values are means of three samples for each time; vertical bar is standard error.

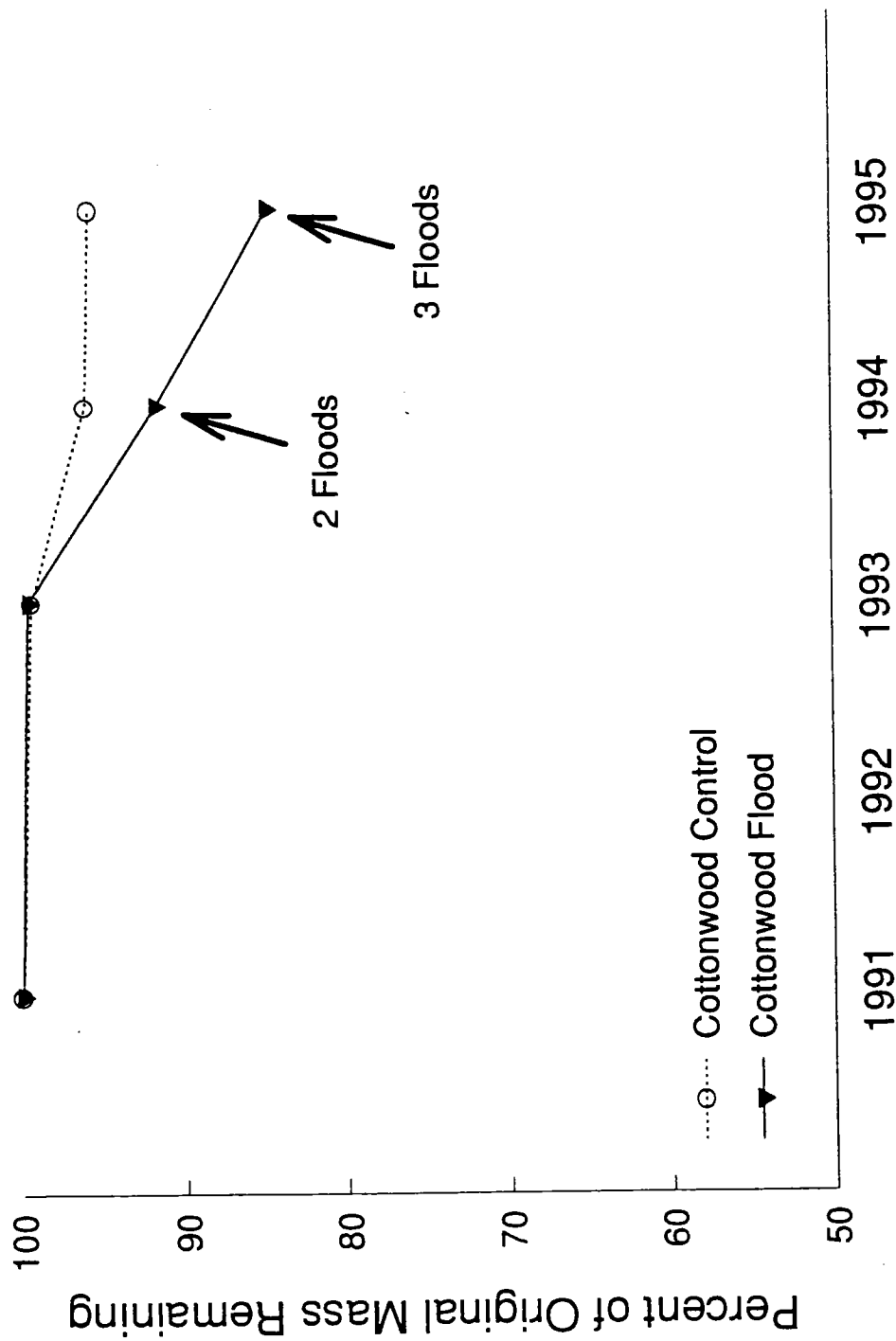


Figure 37. Decomposition of cottonwood logs at cottonwood sites. Logs were placed at sites in June 1991; 1993 collection was made prior to flooding, while 1994 and 1995 collections reflect 2 and 3 seasons of flooding, respectively.

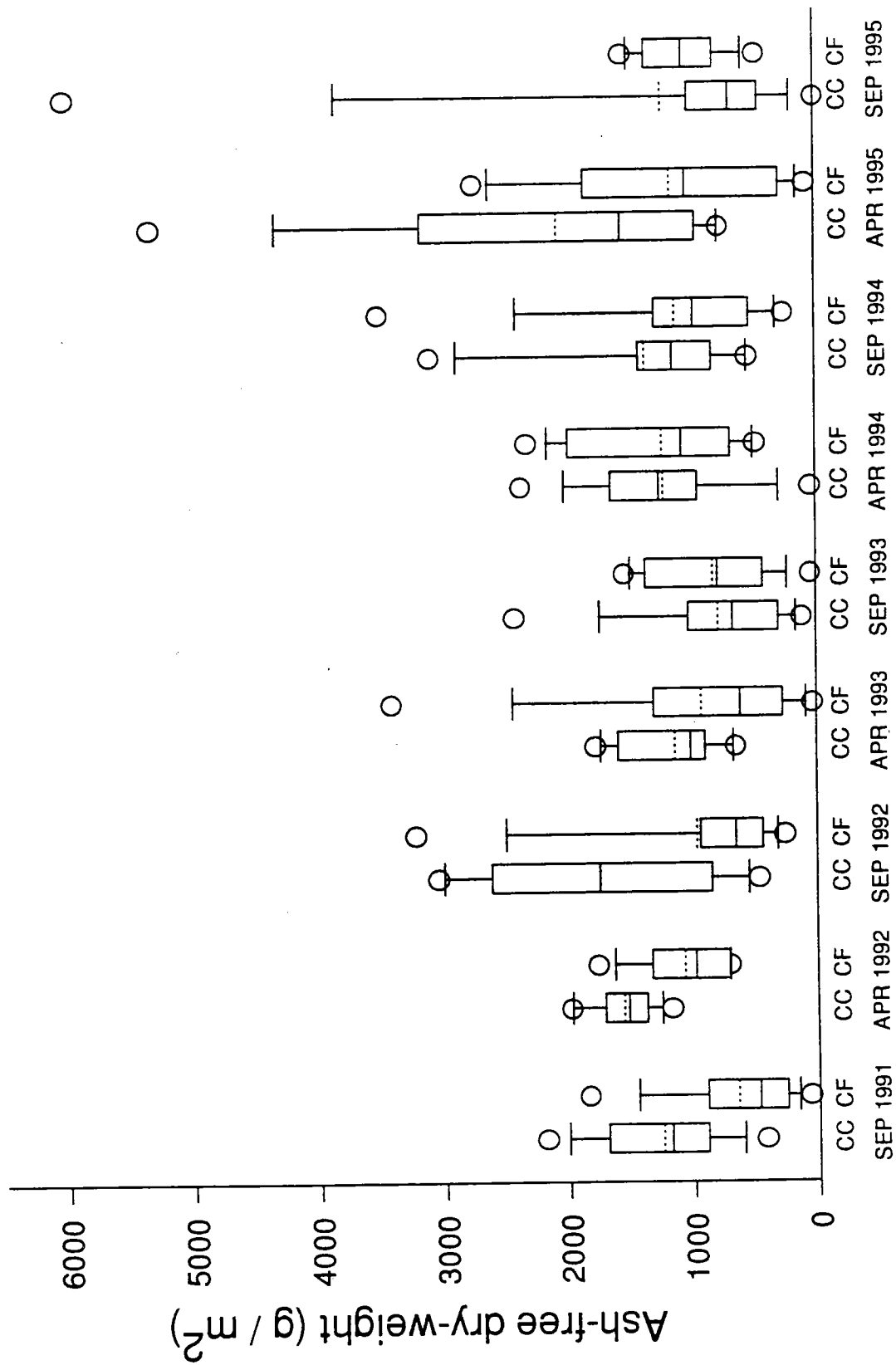


Figure 38. Litter storage values for cottonwood sites, 1991 through 1995. Values are the ash-free dry-weight of forest floor litter collected from ten 10 x 10 cm plots at each site on each date, corrected to per m<sup>2</sup> values. Box includes 50% of the data, solid horizontal line is median, dashed line is mean, vertical bars indicate 90th and 10th percentiles, and circles indicate outlying points.

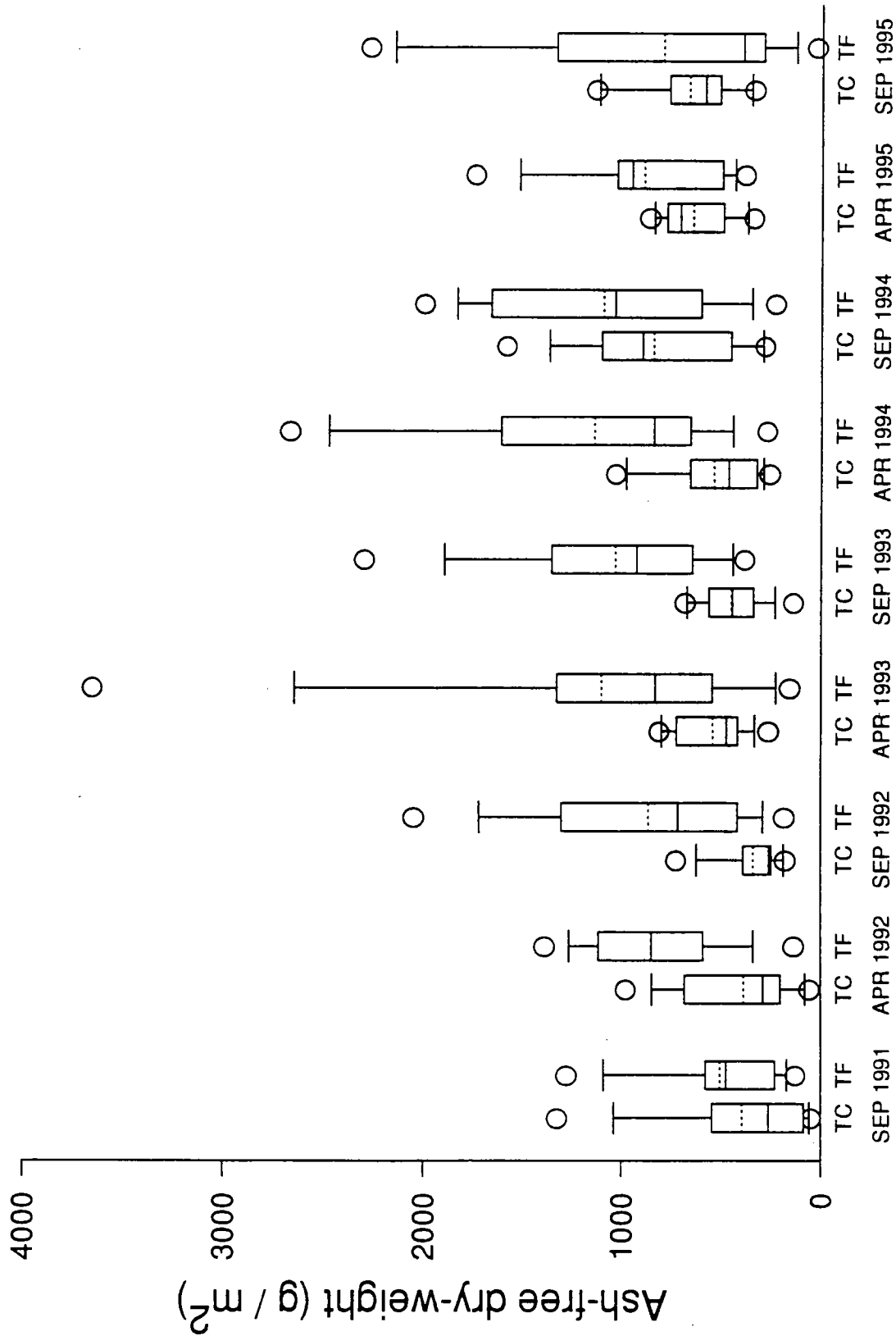


Figure 39. Litter storage values for tamarisk sites, 1991 through 1995. Values are the ash-free dry-weight of forest floor litter collected from ten 10 x 10 cm plots at each site on each date, corrected to per m<sup>2</sup> values. Box includes 50 % of the data, solid horizontal line is median, dashed line is mean, vertical bars indicate 90th and 10th percentiles, and circles indicate outlying points.

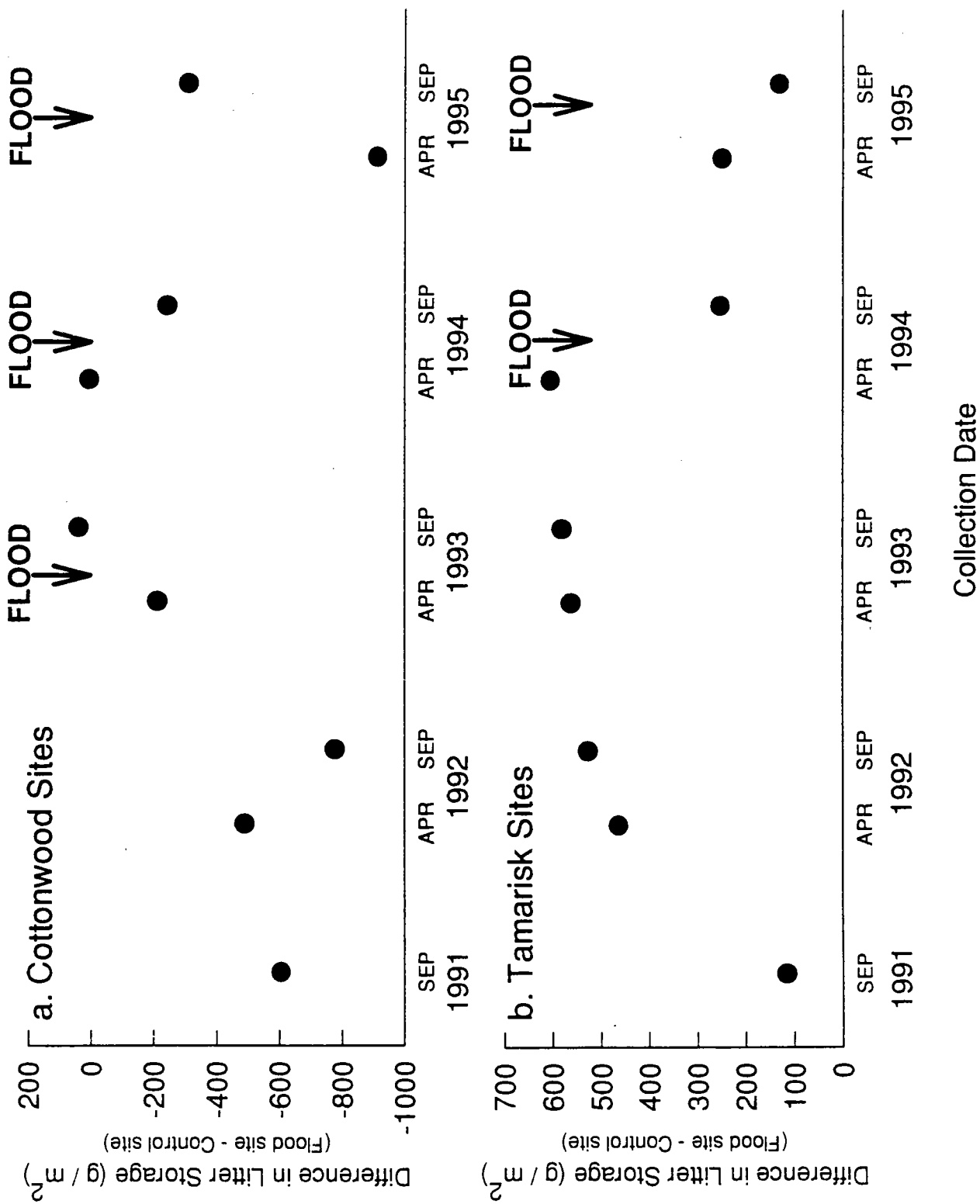


Figure 40. Difference in litter storage between control and flood sites in a) cottonwood and b) tamarisk forests. Values are the mean litter storage at the flood site - the mean litter storage at the control site (ash-free dry-weight, g / m<sup>2</sup>) for each date.

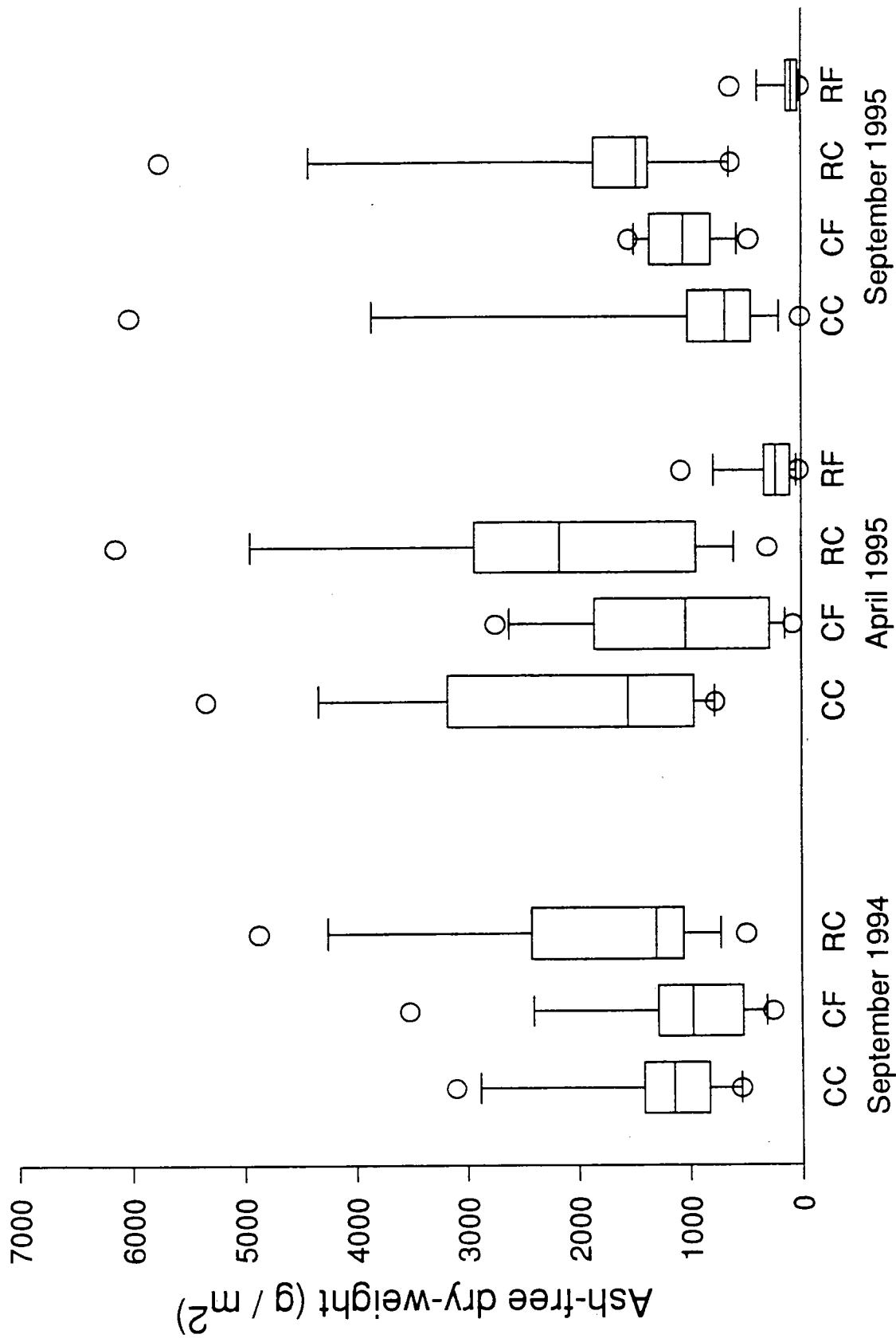


Figure 41. Litter storage values for cottonwood and river sites in 1994 and 1995. Values are the ash-free dry-weight of forest floor litter collected from ten 10 x 10 cm plots at each site on each date, corrected to per m<sup>2</sup> values. Box includes 50% of the data, solid horizontal line is median, dashed line is mean, vertical bars indicate 90th and 10th percentiles, and circles indicate outlying points. Samples were not collected at River Flood in September 1994.

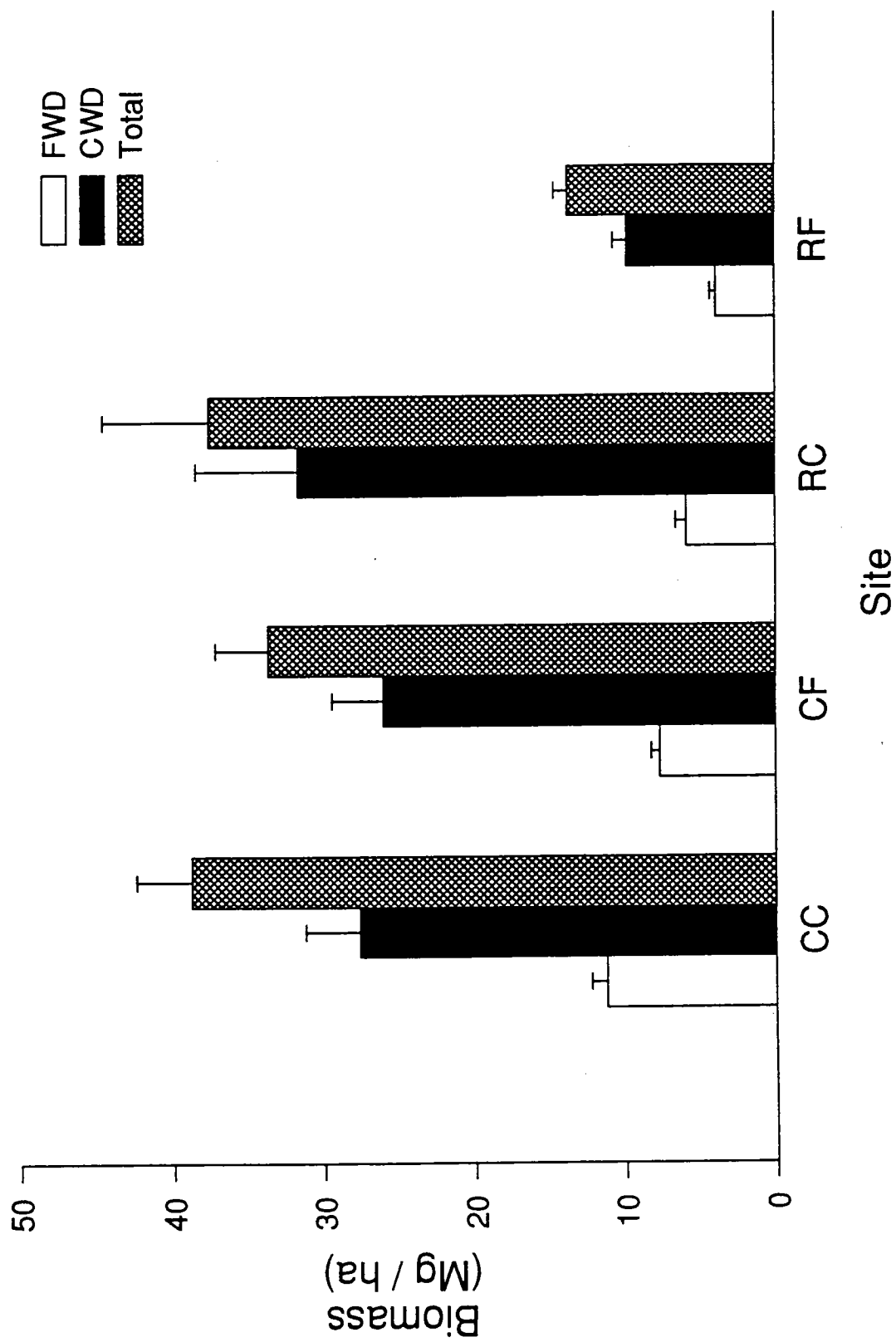


Figure 42. Biomass estimates (Mg / ha) of fine woody debris (FWD, < 2 cm diameter), coarse woody debris (CWD, > 2 cm diameter), and total woody debris (FWD + CWD) at cottonwood and river sites.

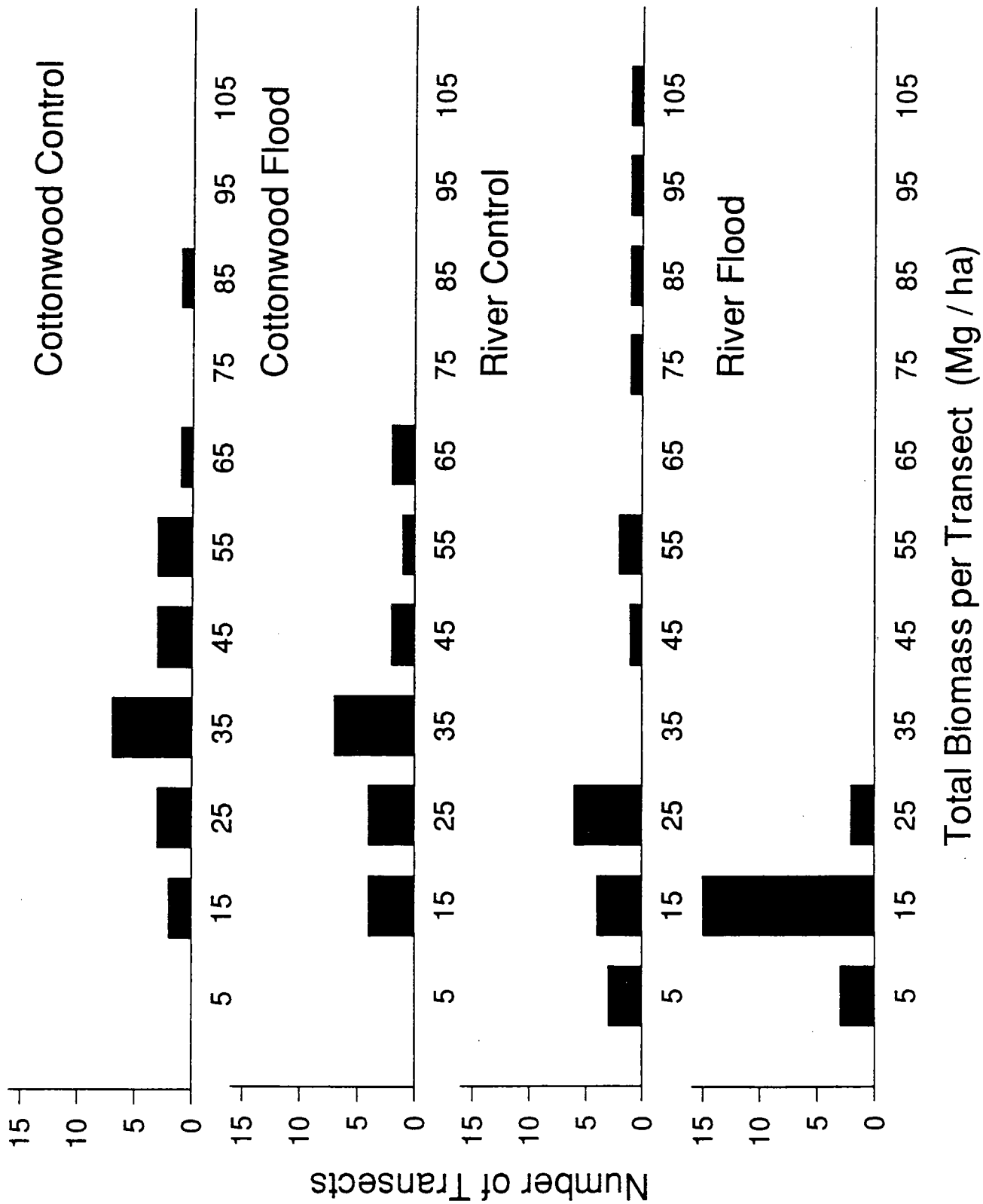


Figure 43. Frequency distribution among transects of biomass of total woody debris estimated at each cottonwood and river site. Biomass was estimated along 20 transects at each site. Values along horizontal axis represent midpoints of biomass size classes.



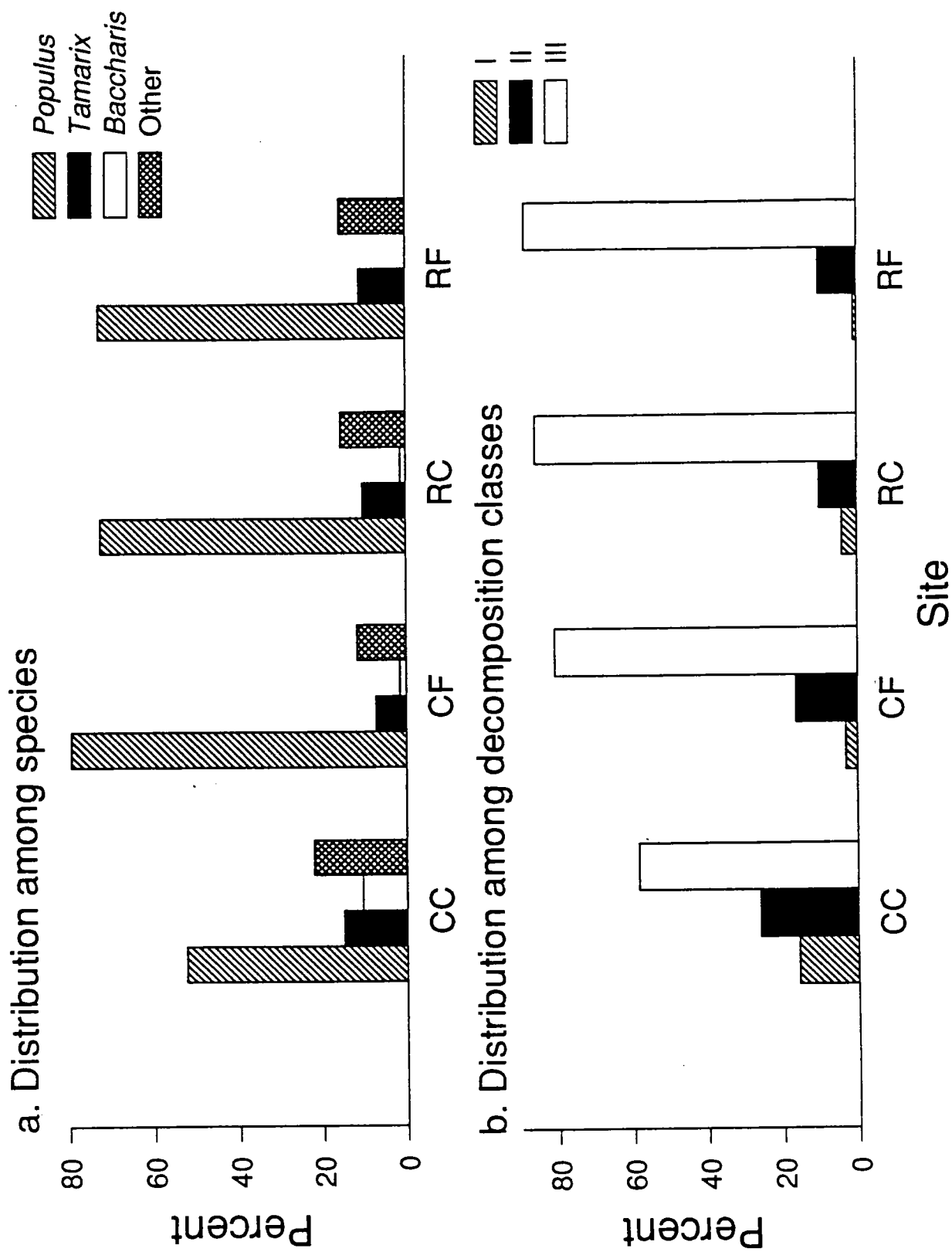


Figure 44. Distribution of coarse woody debris a) among woody plant species and b) among decomposition classes: I = slight or no decay, II = moderate decay, III = advanced decay.

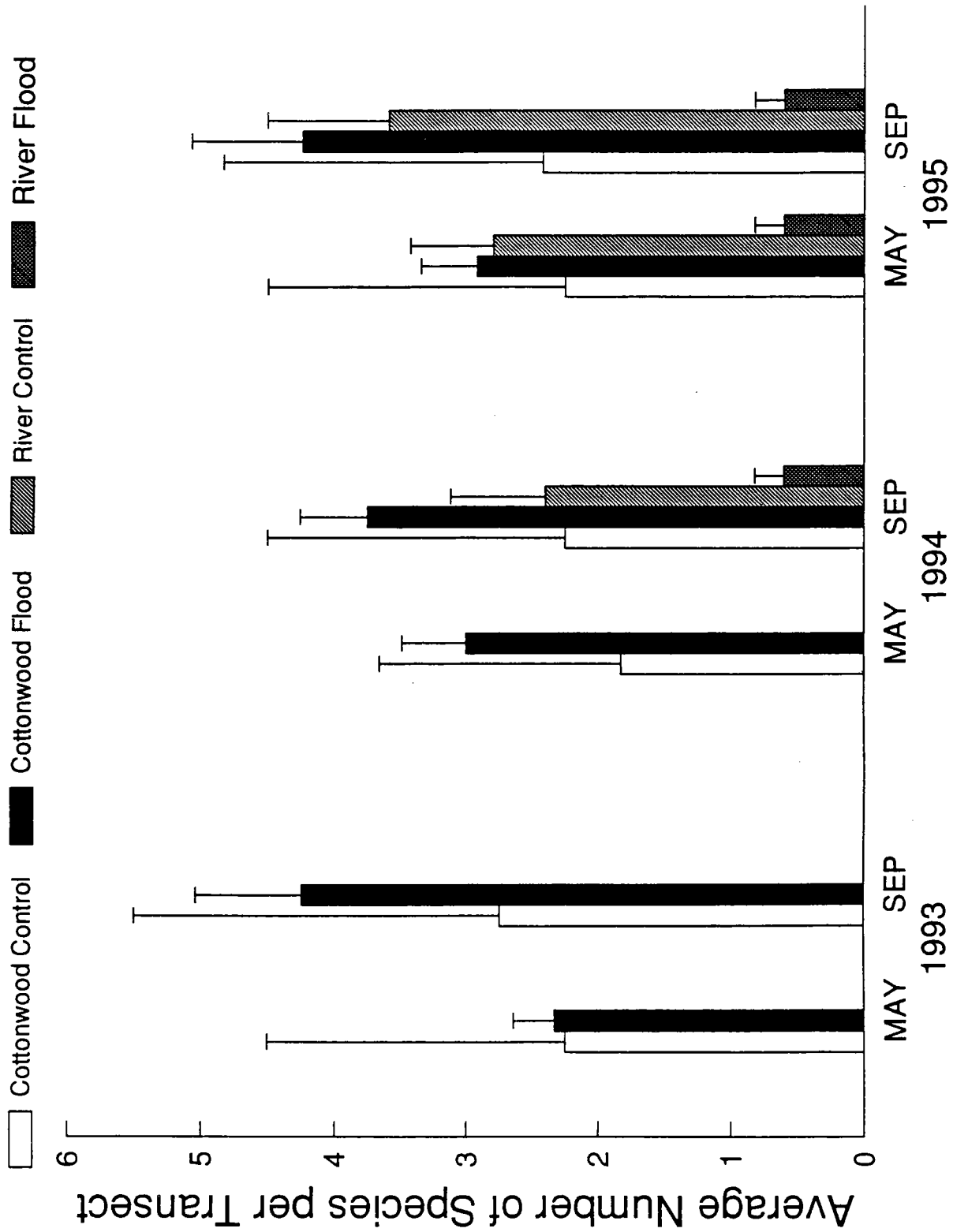


Figure 45. Average number of understory species at cottonwood and river sites. Values are the average number of species along 12 transects at cottonwood sites and 10 transects at river sites; vertical bars are standard error.

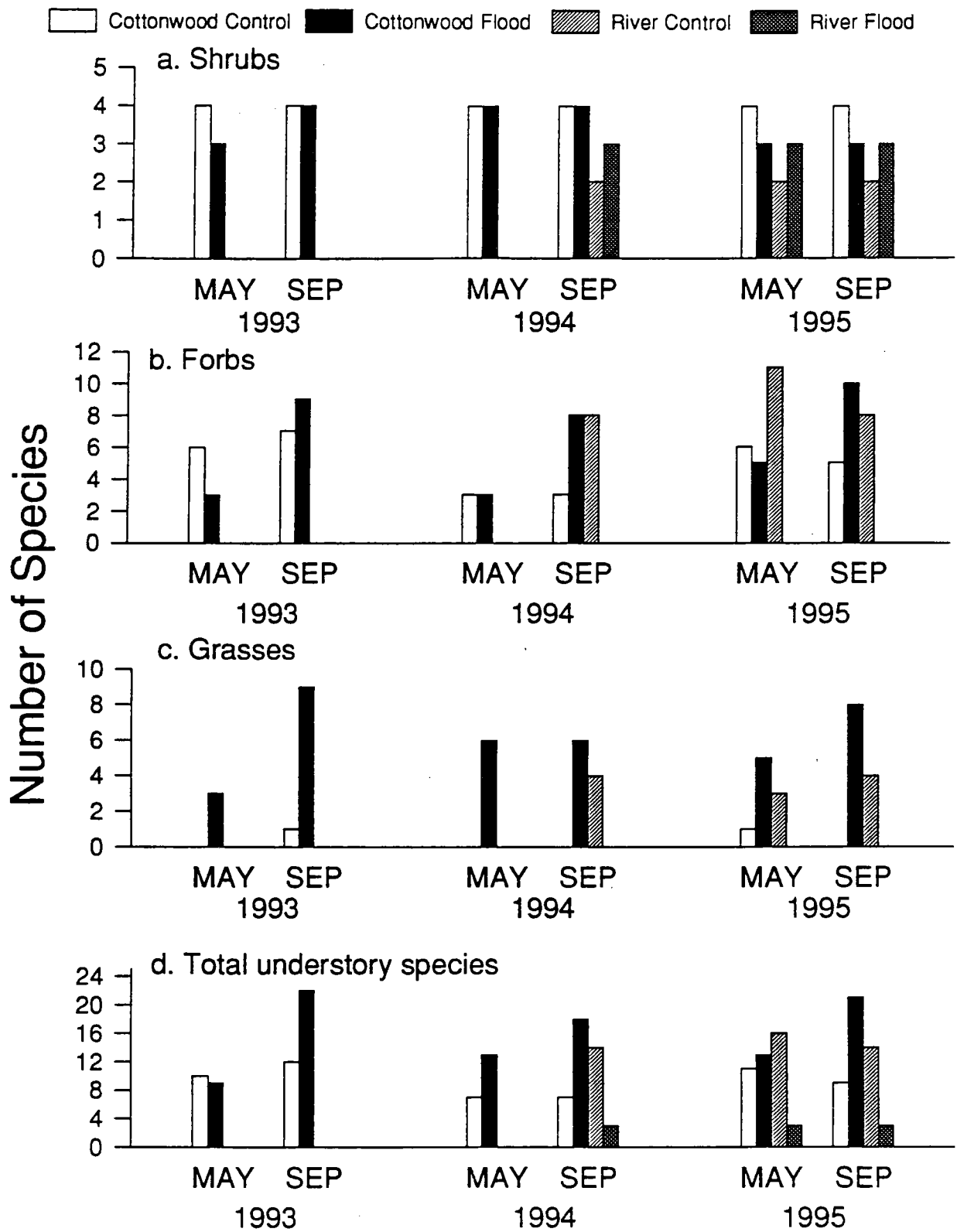


Figure 46. Numbers of understory vegetation species along transects at cottonwood and river sites. Total number of species of a) shrubs, b) forbs, c) grasses and d) all understory plants, counted along 12 transects at cottonwood sites and 10 transects at river sites.

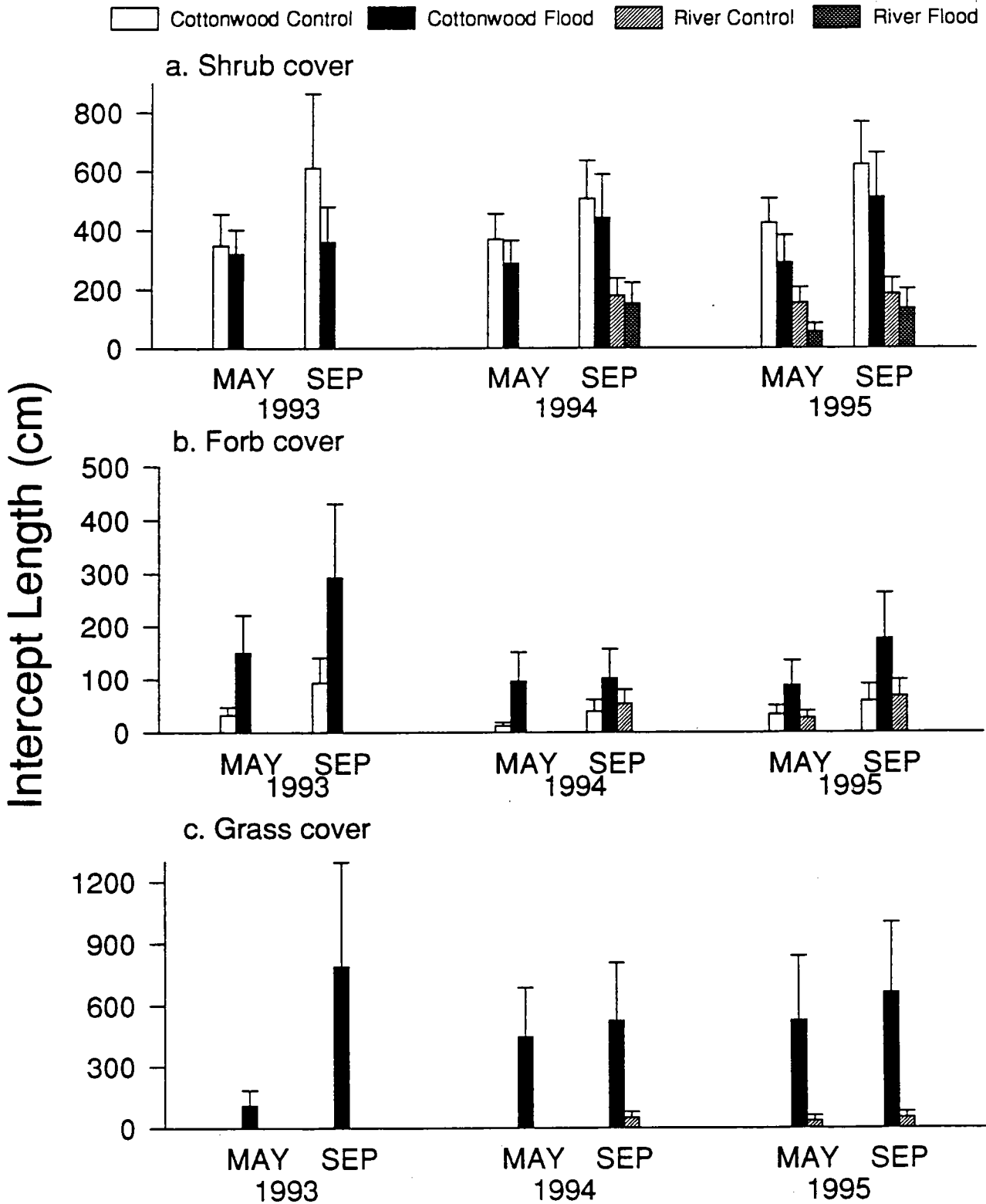


Figure 47. Estimates of understory species cover, based on line intercept measurements. Cover estimates for a) shrubs, b) forbs, and c) grasses. Values are the mean intercept length (cm), averaged along 12 transects at each cottonwood site and 10 transects at each river site; vertical bars are standard error. Cottonwood Flood was inundated each year between spring and fall measurements.

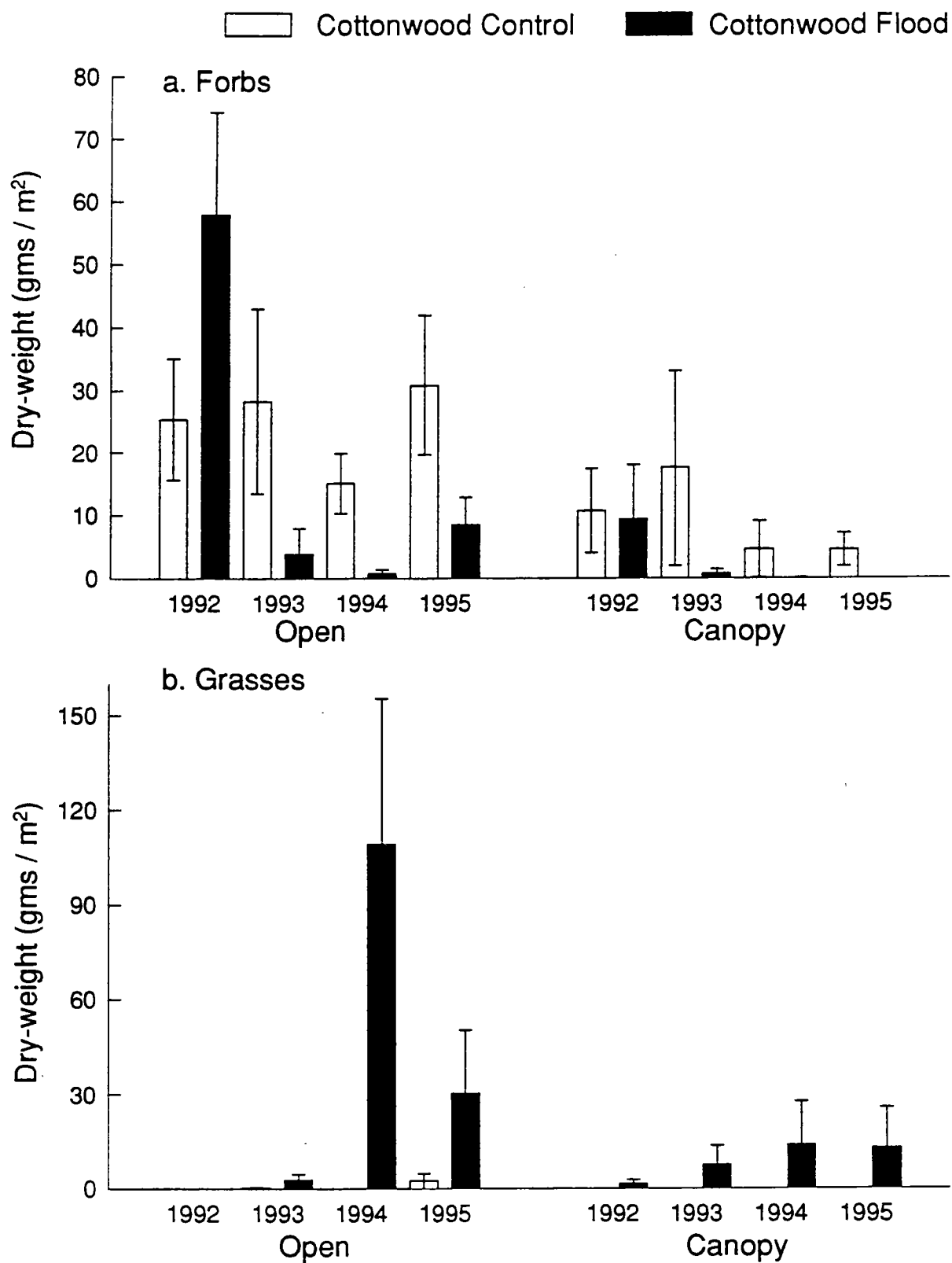


Figure 48. Understory biomass production at cottonwood sites in 1992 through 1995. Values represent the average oven-dry weight (grams / m<sup>2</sup>) for a) forbs and b) grasses clipped from 0.5 m<sup>2</sup> plots from each site in open (no canopy cover) and canopy (full canopy cover) locations. Vertical bars are standard error. Averages are for ten plots for all canopy estimates, as well as open measurements in 1992 and 1993. Values for open locations in 1994 represent 3 plots and for 1995 represent 6 plots.

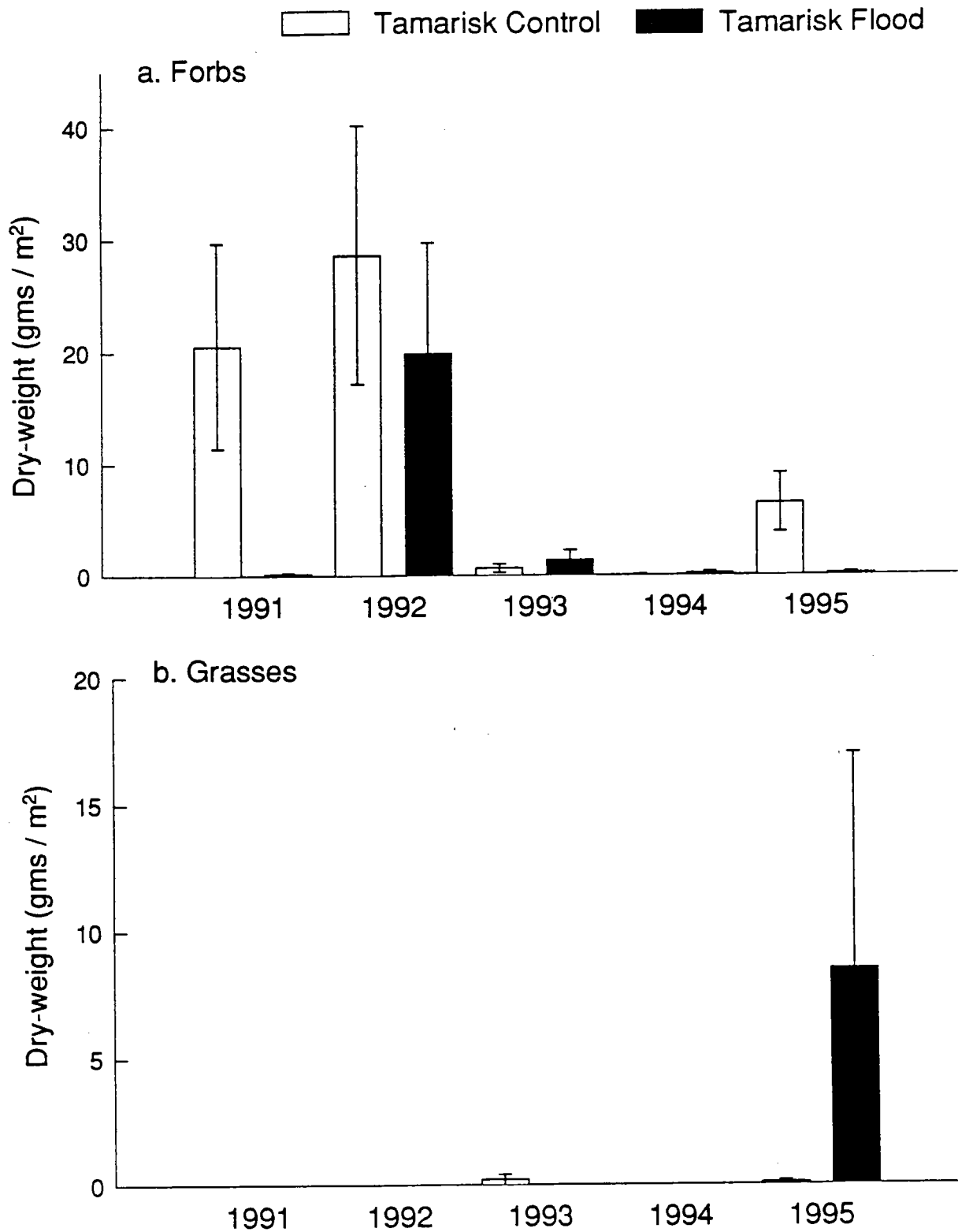


Figure 49. Understory biomass production at tamarisk sites in 1991 through 1995. Values represent the average oven-dry weight (grams / m<sup>2</sup>) of a) forbs and b) grasses clipped from ten 0.5 m<sup>2</sup> plots at each site. Vertical bars are standard error.

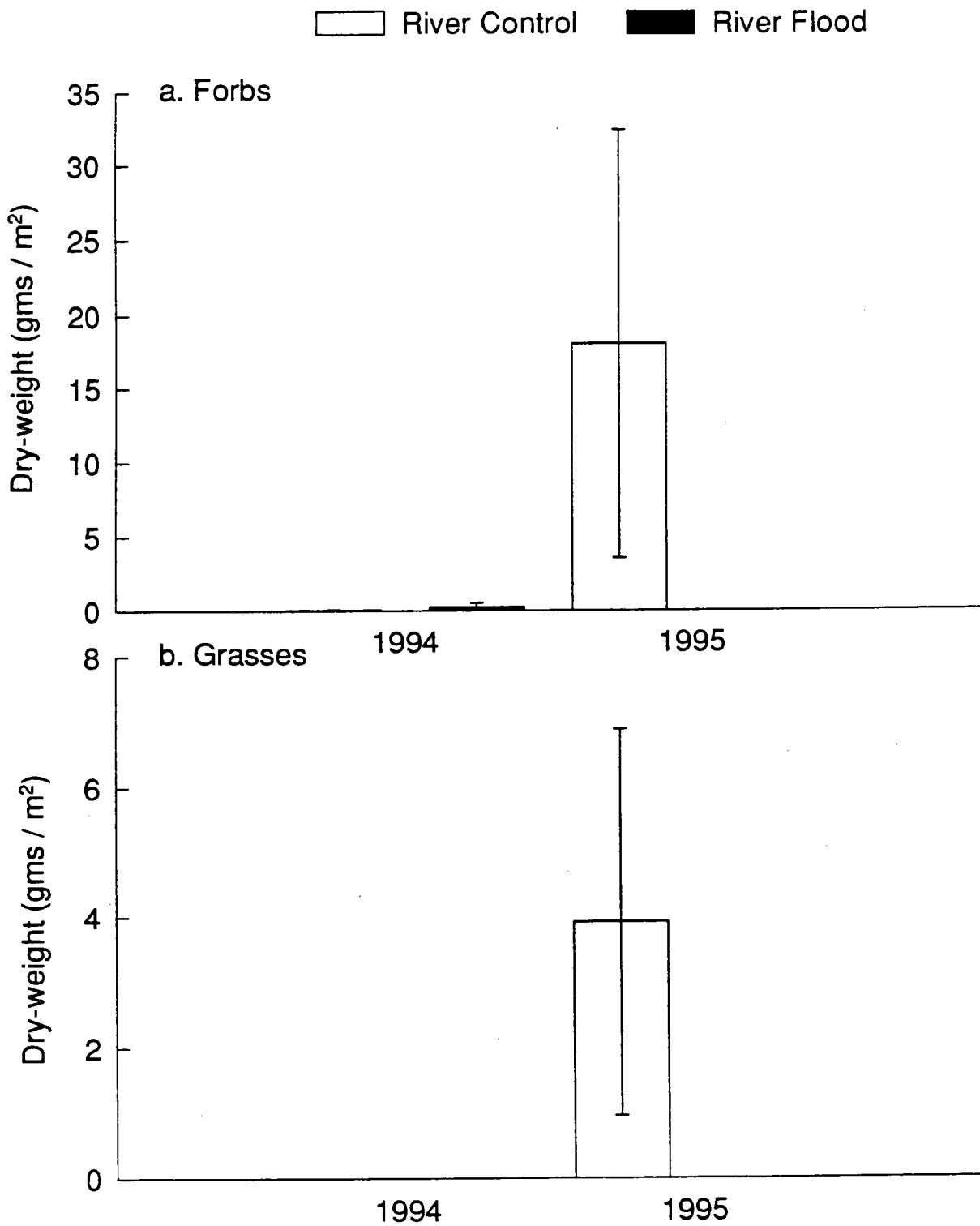


Figure 50. Understory biomass production at river sites in 1994 and 1995. Values represent the average oven-dry weight of a) forbs and b) grasses clipped from ten 0.5 m<sup>2</sup> plots at each site. Vertical bars are standard error.

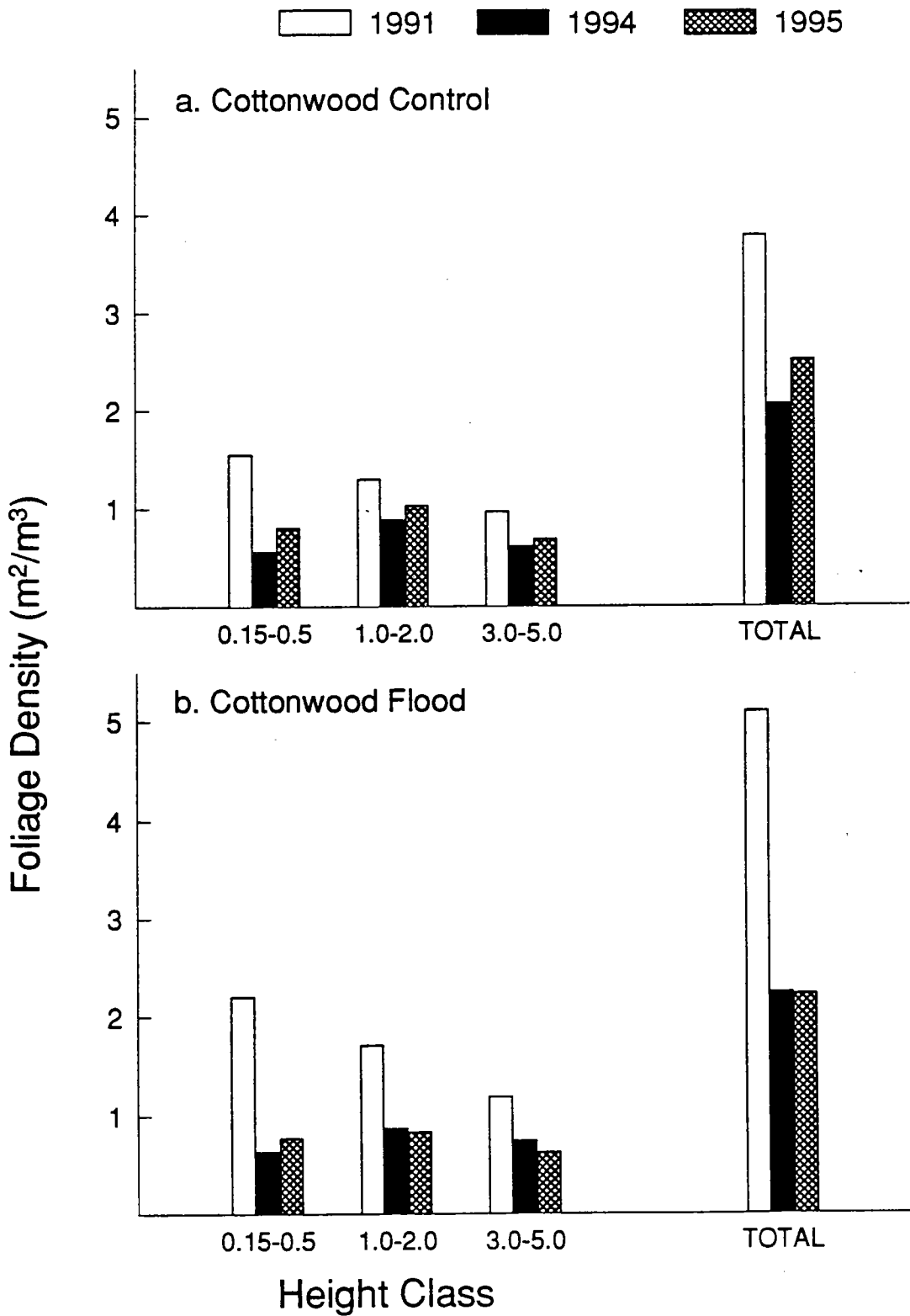


Figure 51. Mean total foliage density of vegetation at cottonwood sites, measured in July 1991, 1994, and 1995. Values are a measure of the density of vegetation in each height class. Total combines height classes.



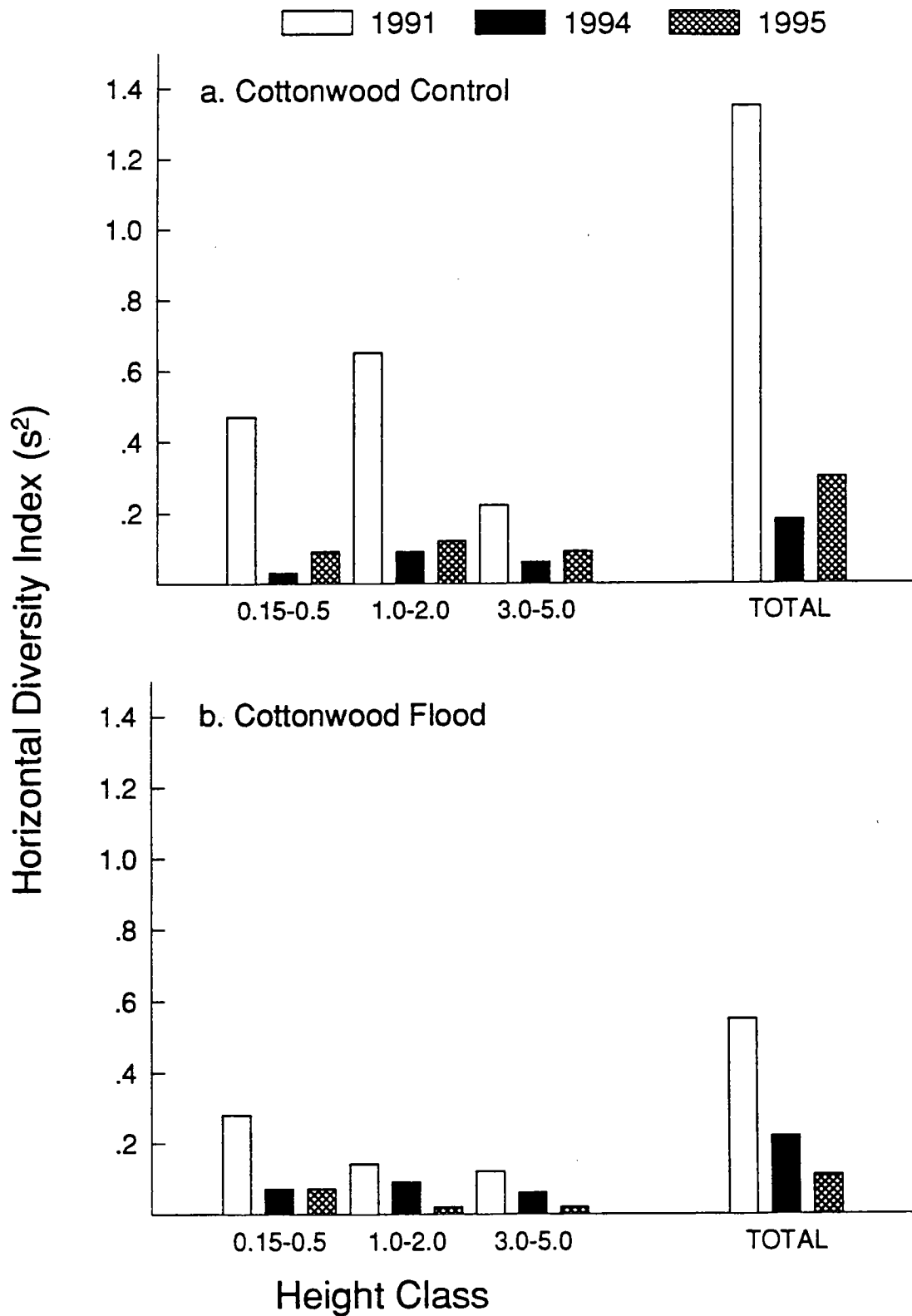


Figure 52. Horizontal diversity (patchiness) estimates for vegetation at cottonwood sites, measured in July 1991, 1994, and 1995. Horizontal diversity is the variance associated with the mean total foliage density.

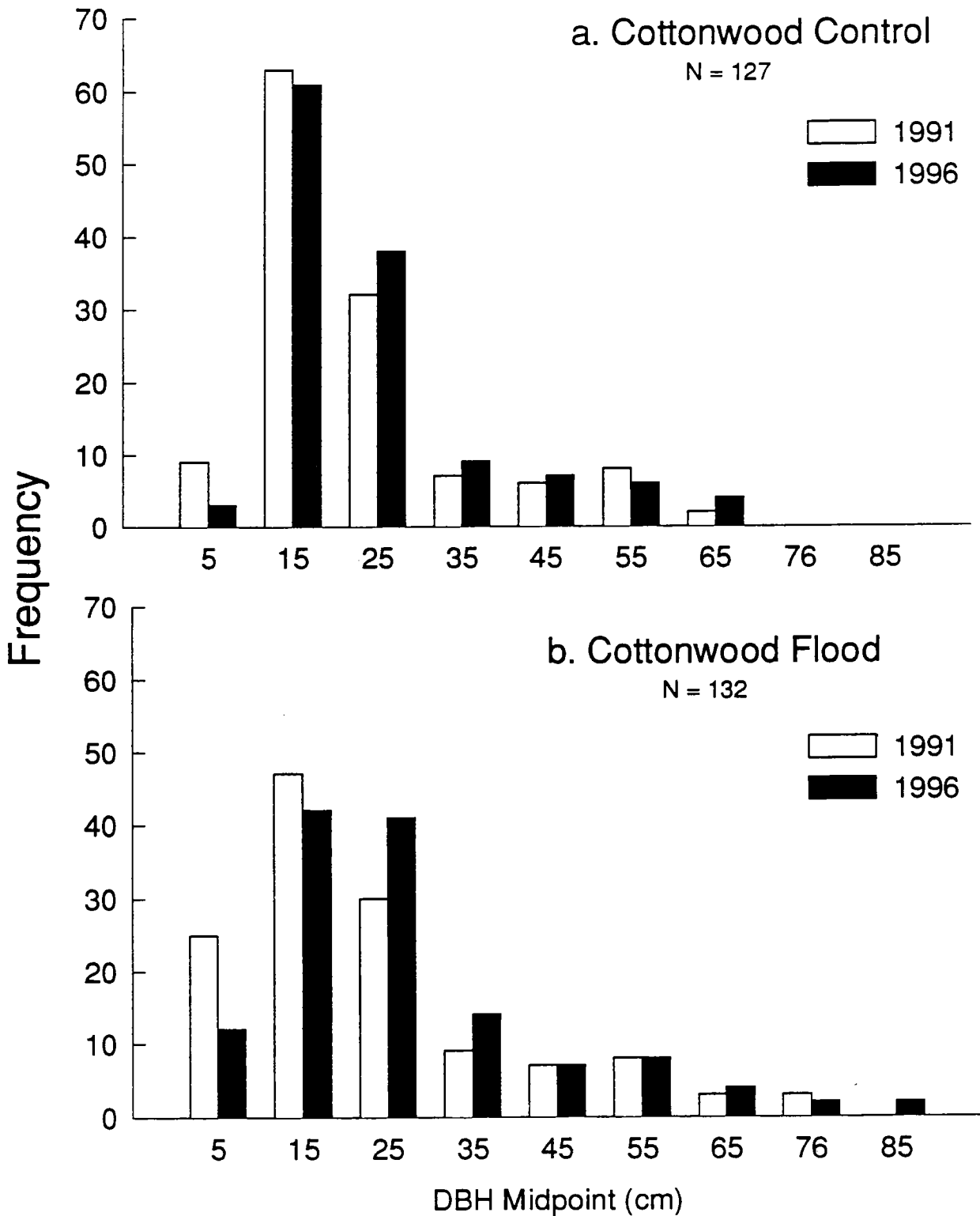


Figure 53. Frequency distributions of diameter at breast height (DBH) measurements for cottonwood trees at cottonwood sites, measured in July 1991 and April 1996. Differences in distributions between years were significant for Cottonwood Flood but not for Cottonwood Control.

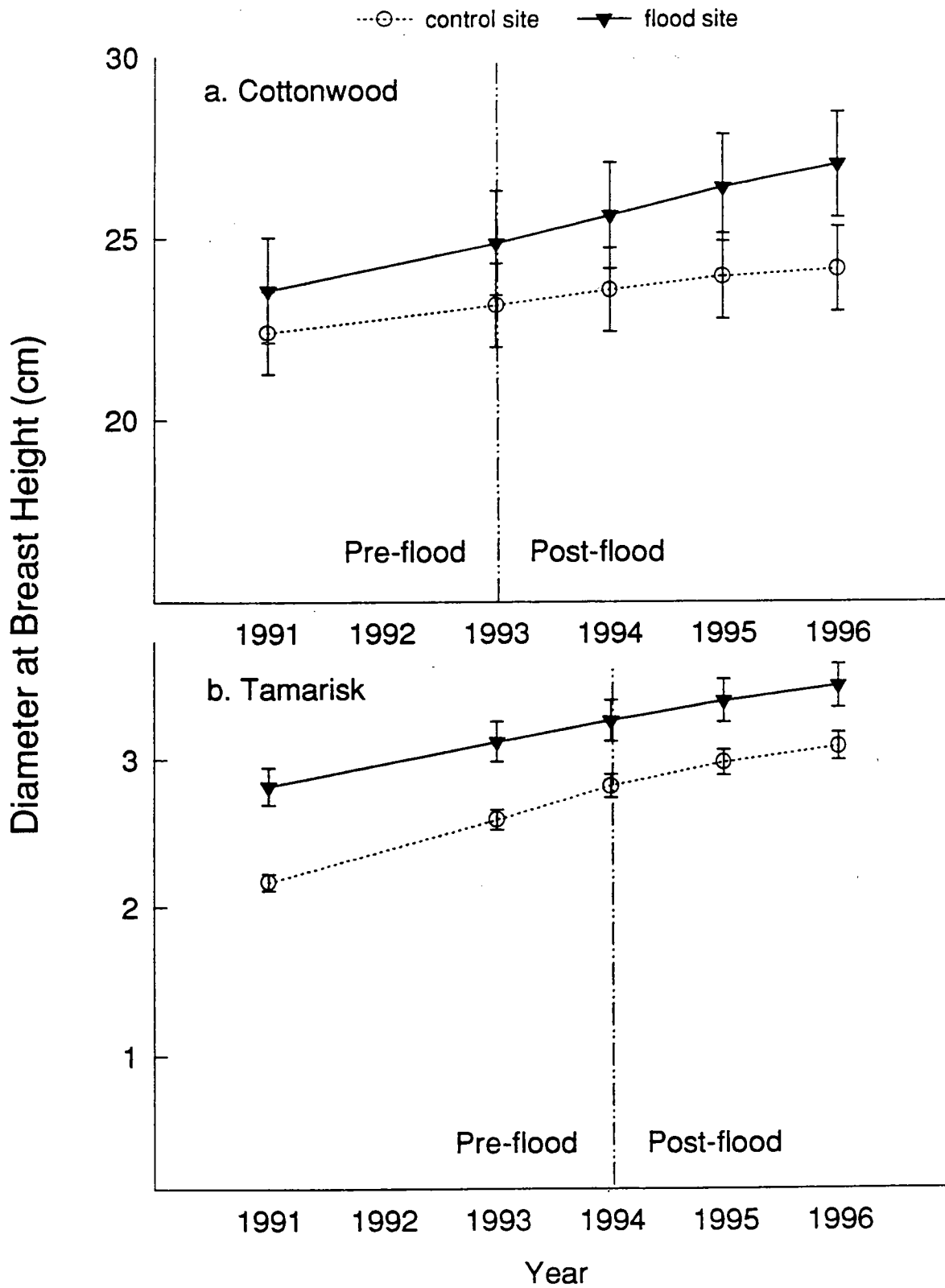


Figure 54. Mean diameter at breast height (DBH) measurements for cottonwood and tamarisk sites. Vertical bars are standard errors. Cottonwood Flood was inundated during May - June 1993, 1994, and 1995. Tamarisk Flood was partially inundated during 1994 and fully inundated during May - June 1995.

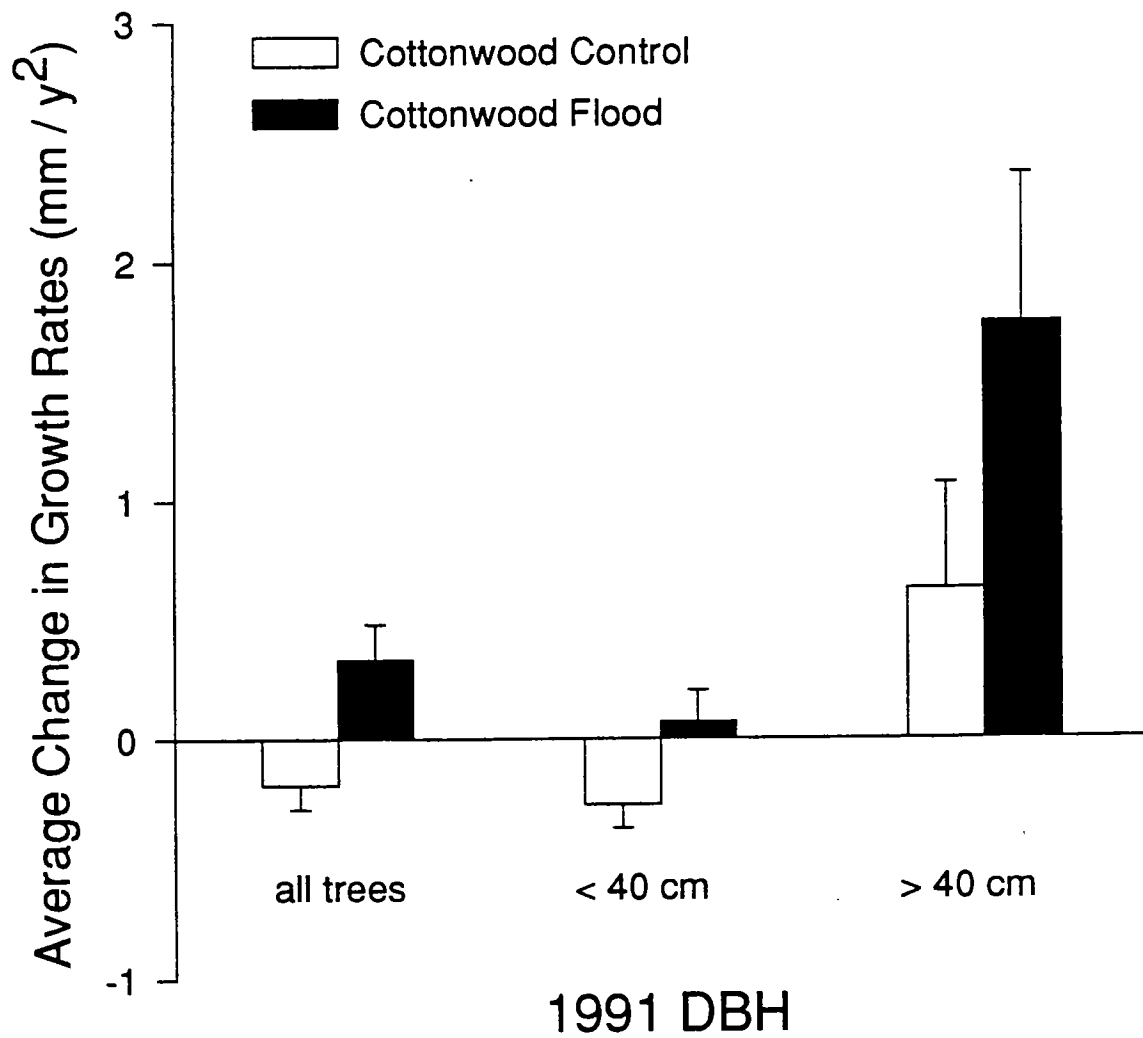


Figure 55. Average change in growth rates at Cottonwood Control and Cottonwood Flood for all trees, and for trees with initial diameter less than or greater than 40 cm. A value of zero change indicates no difference between growth rates during 1991 to 1993 and 1993 to 1996.

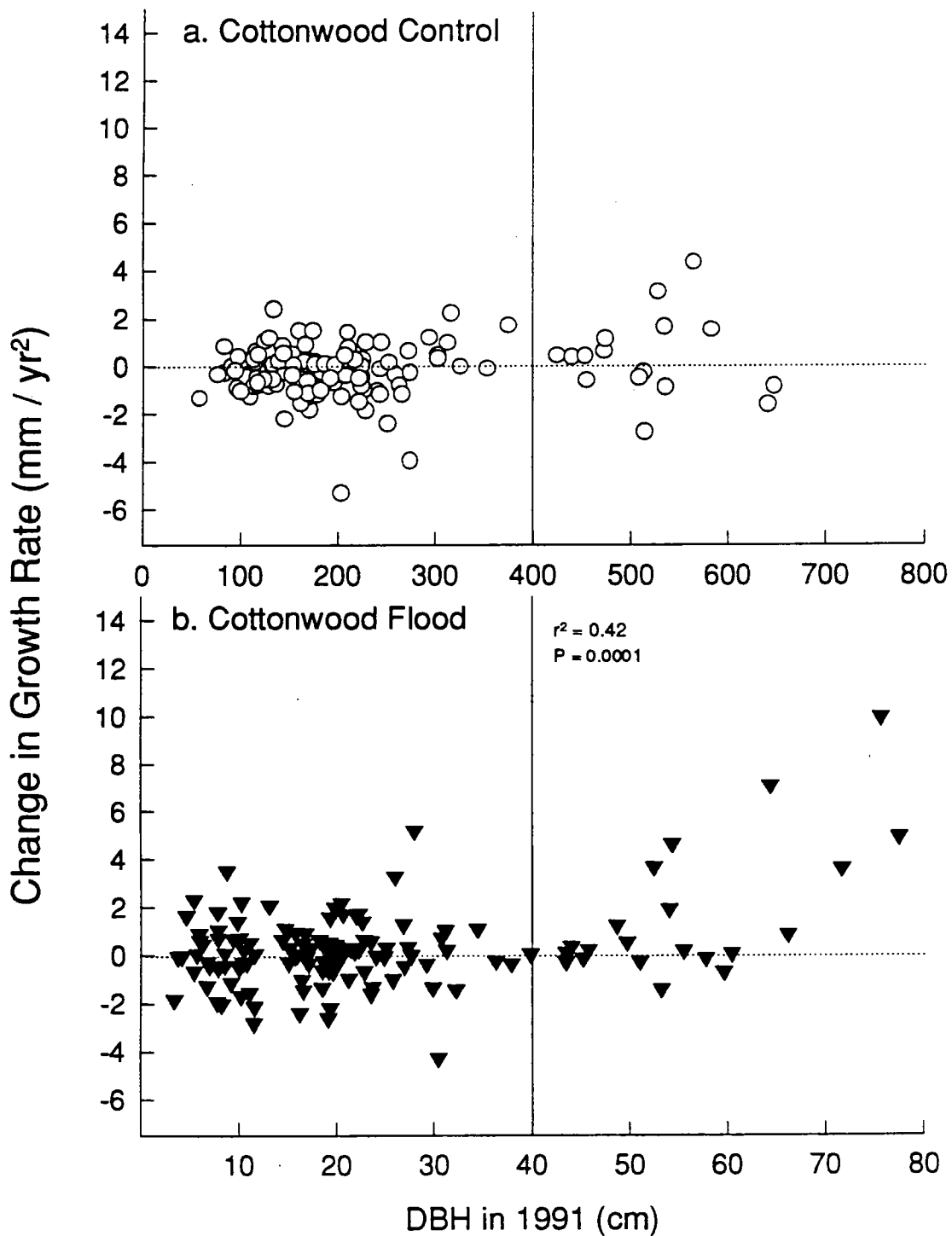


Figure 56. Change in growth rates between 1991 to 1993 and 1993 to 1996 for individual cottonwood trees at cottonwood sites. Values are the change in growth rates for individual trees before and after the initiation of flooding at Cottonwood Flood, plotted against the initial DBH for each tree. Dotted line indicates no change in growth rate; values above this line indicate increased growth rates after 1993 while values below this line indicate decreased growth rates. The positive regression for trees greater than 40 cm DBH is significant for Cottonwood Flood; no relationship exists for Cottonwood Control.

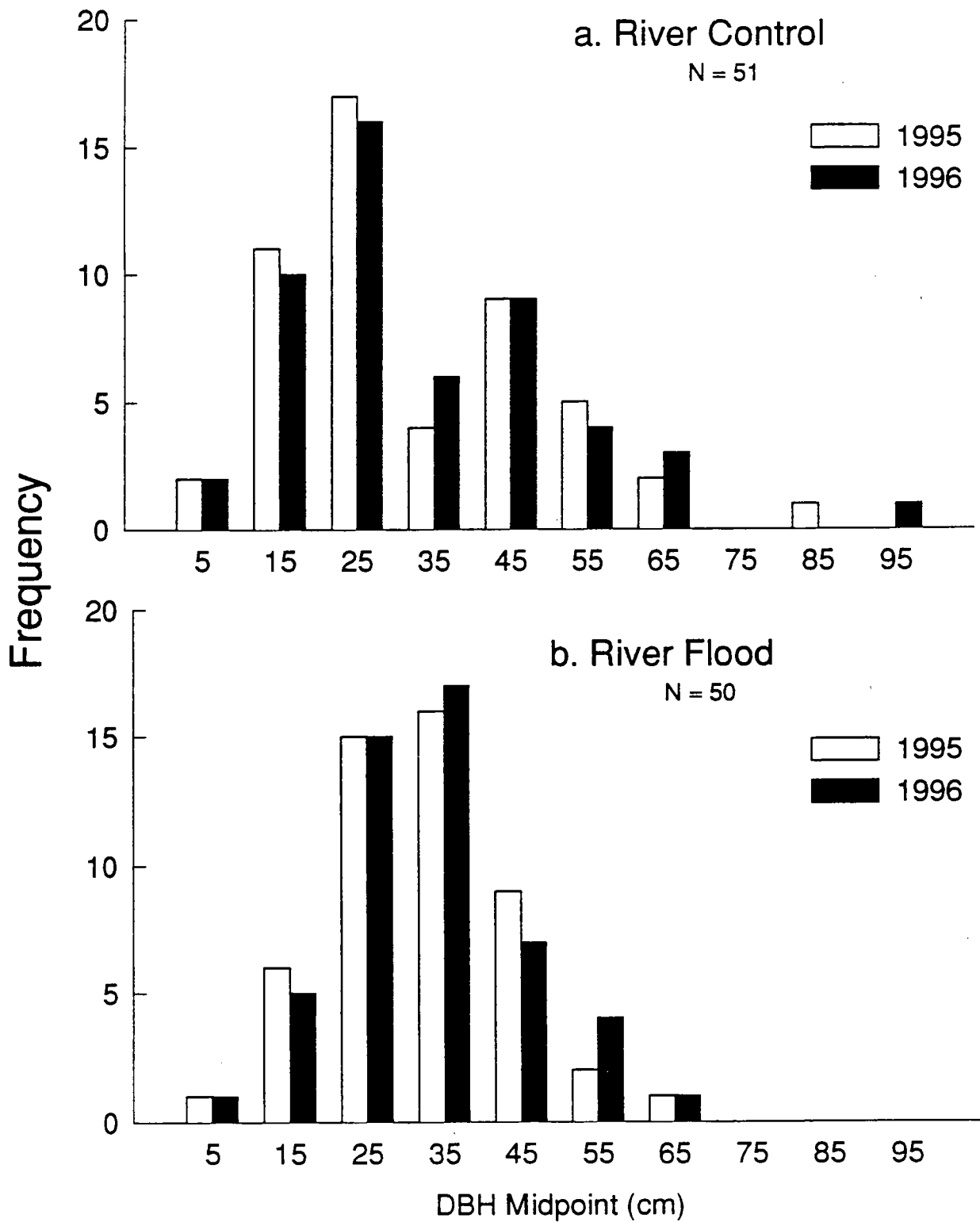


Figure 57. Frequency distributions of diameter at breast height (DBH) measurements for cottonwood trees at river sites, measured in April 1995 and April 1996. Differences in distributions between years were not significant for either site.

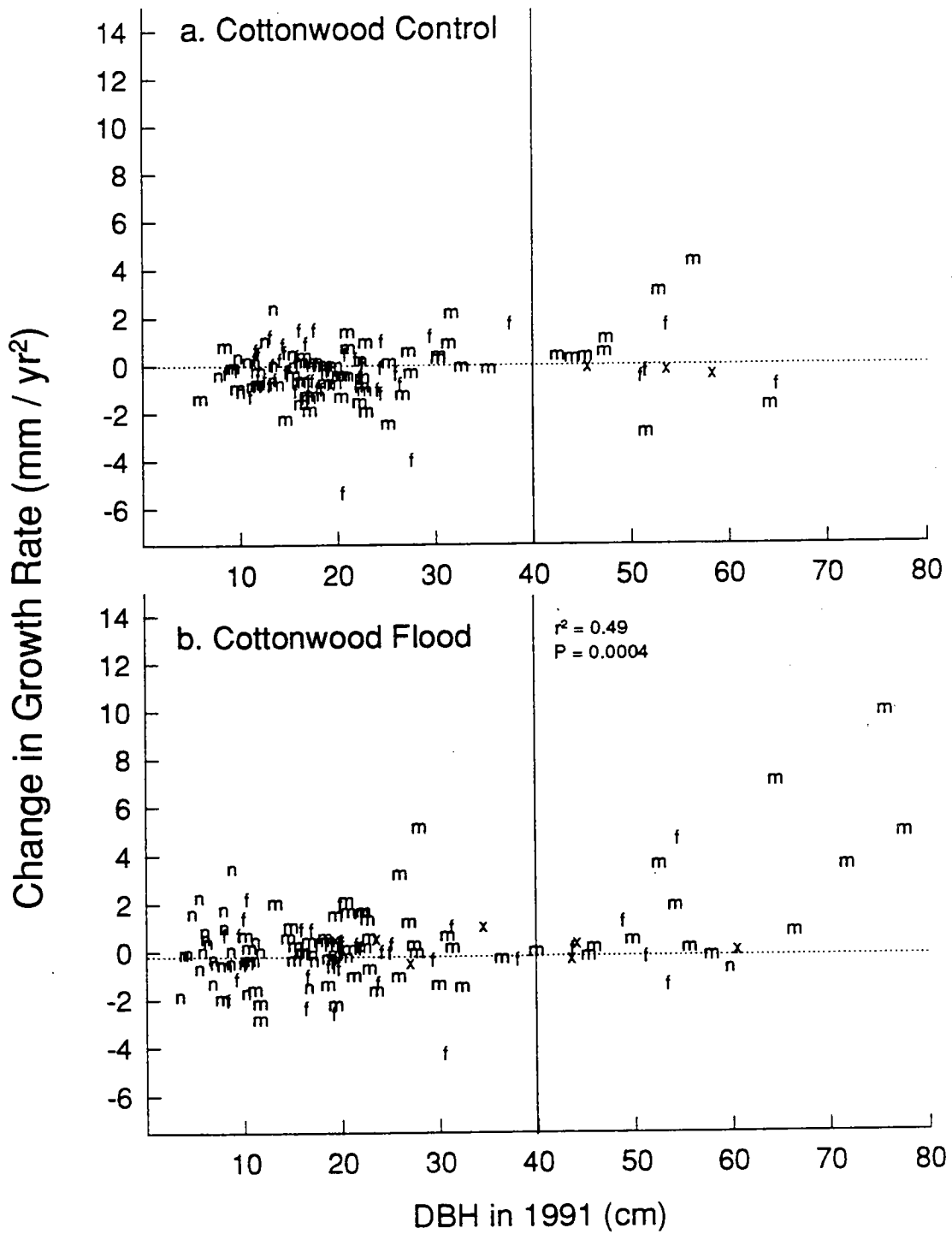


Figure 58. Change in growth rates of individual cottonwood trees at cottonwood sites, identified by sex. m = male, f = female, n = non-reproductive (sex unknown), x = sex not checked.

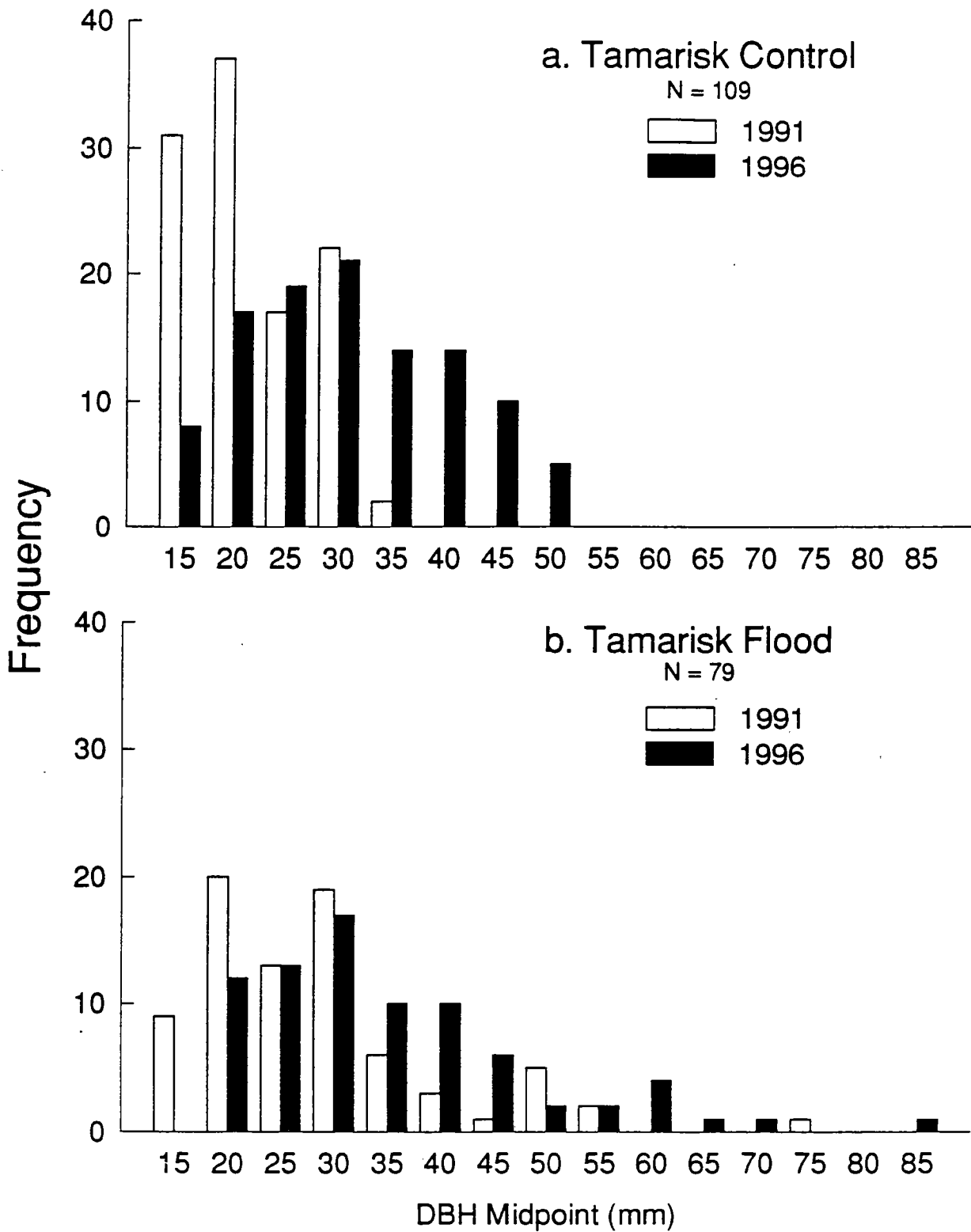


Figure 59. Frequency distributions of diameter at breast height (DBH) measurements for tamarisk trees at tamarisk sites measured July 1991 and April 1996. Differences in distributions between years were significant for both sites.



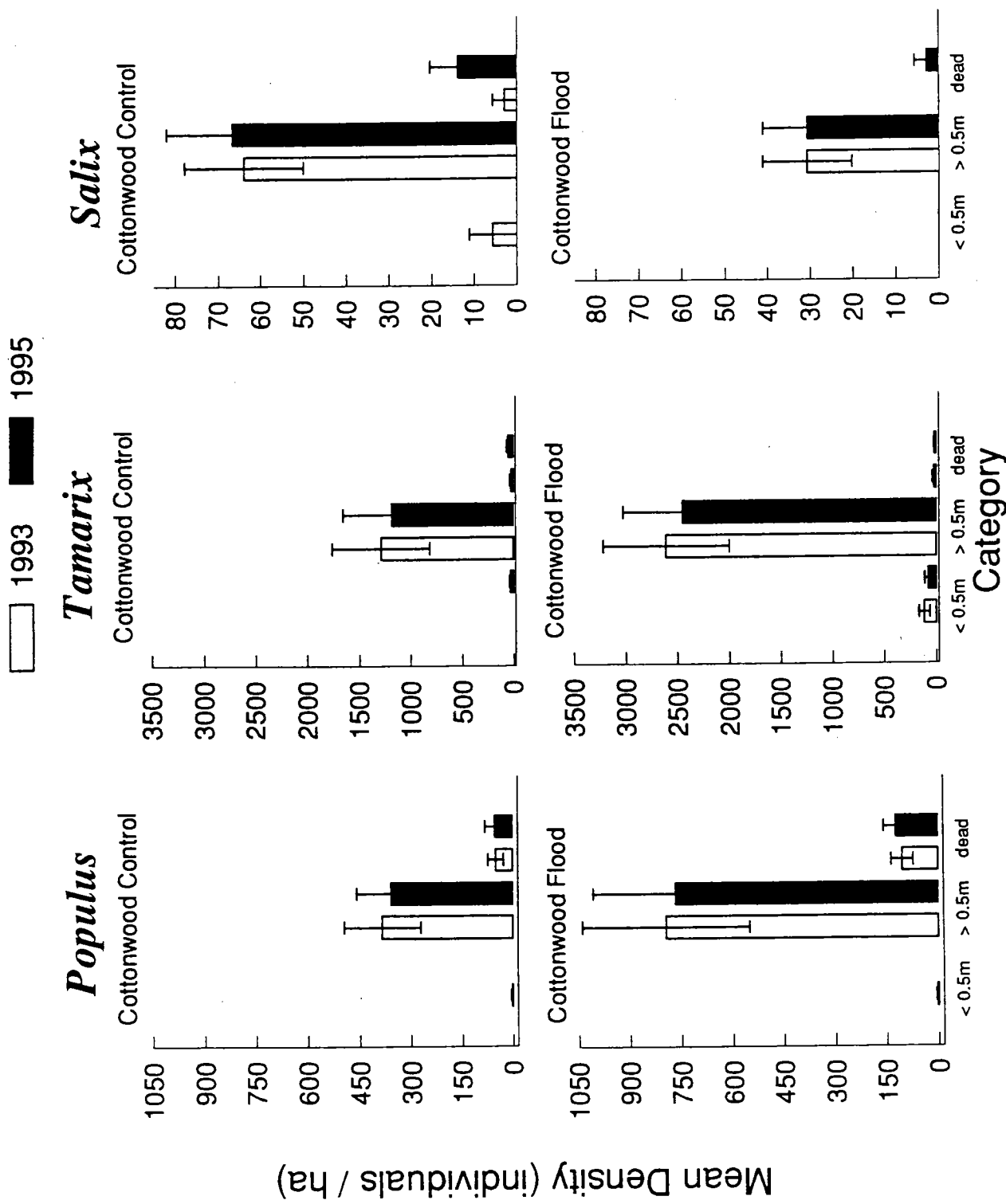


Figure 60. Mean densities of tree species at cottonwood sites in 1993 and 1995. Values are the average number of individuals per hectare, based on twelve, 10 x 30 m plots per site.

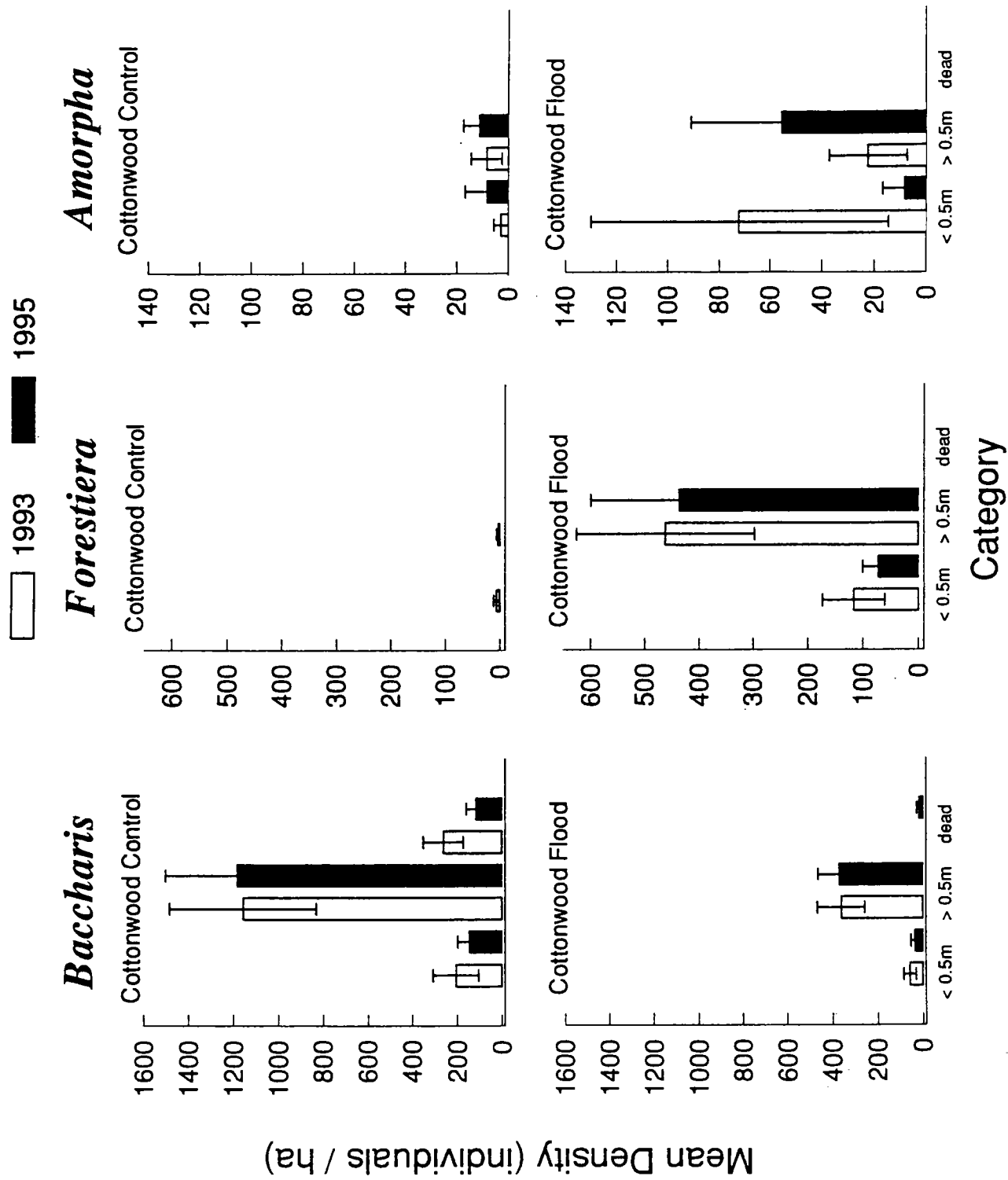


Figure 61. Mean densities of shrub species at cottonwood sites in 1993 and 1995. Values are the average number of individuals per hectare, based on twelve, 10 x 30 m plots per site.

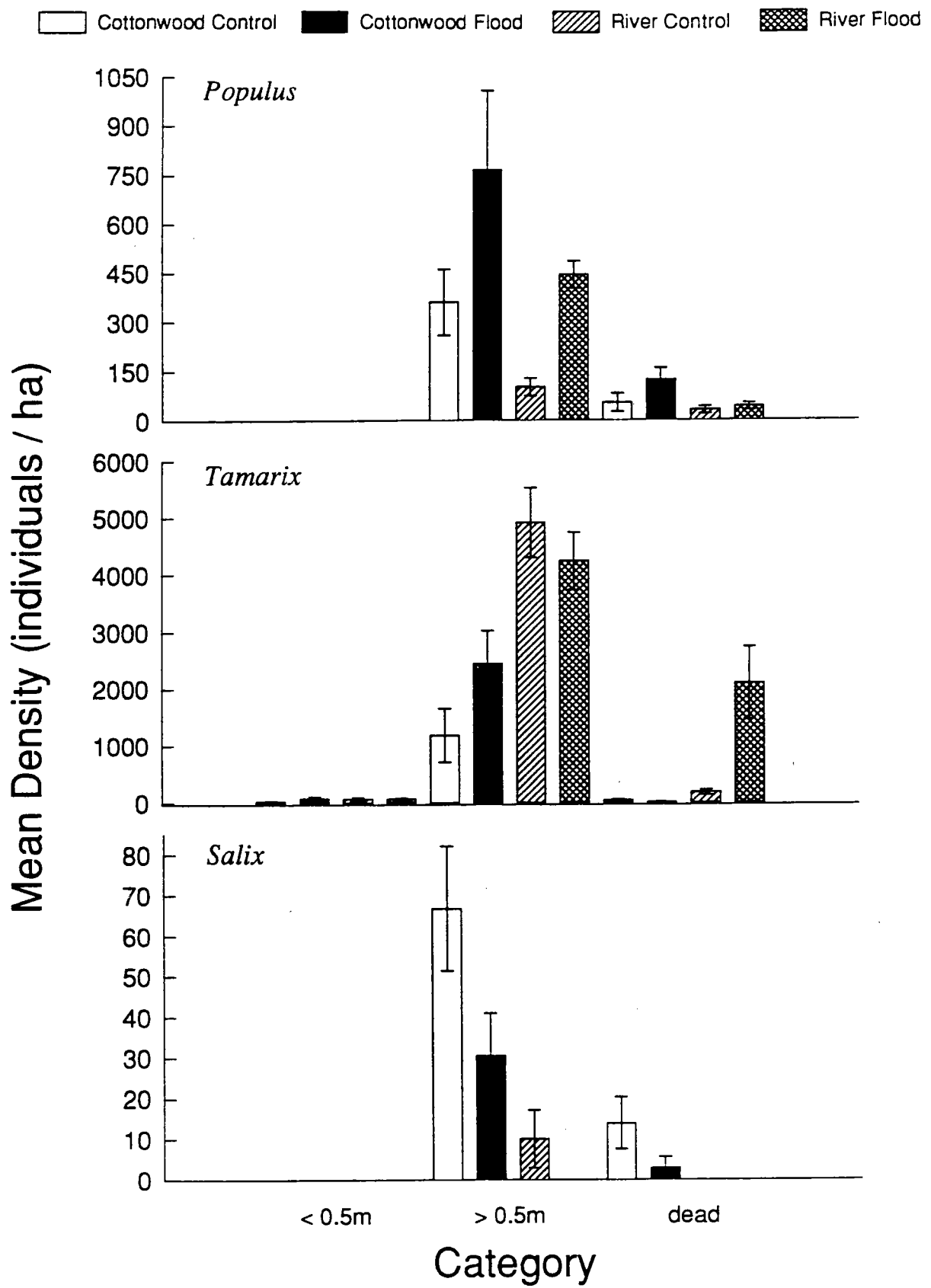


Figure 62. Mean density of tree species at cottonwood and river sites in 1995. Values are the mean number of individuals per ha counted in 12 (cottonwood) or 10 (river) 10 x 30 m plots at each site.

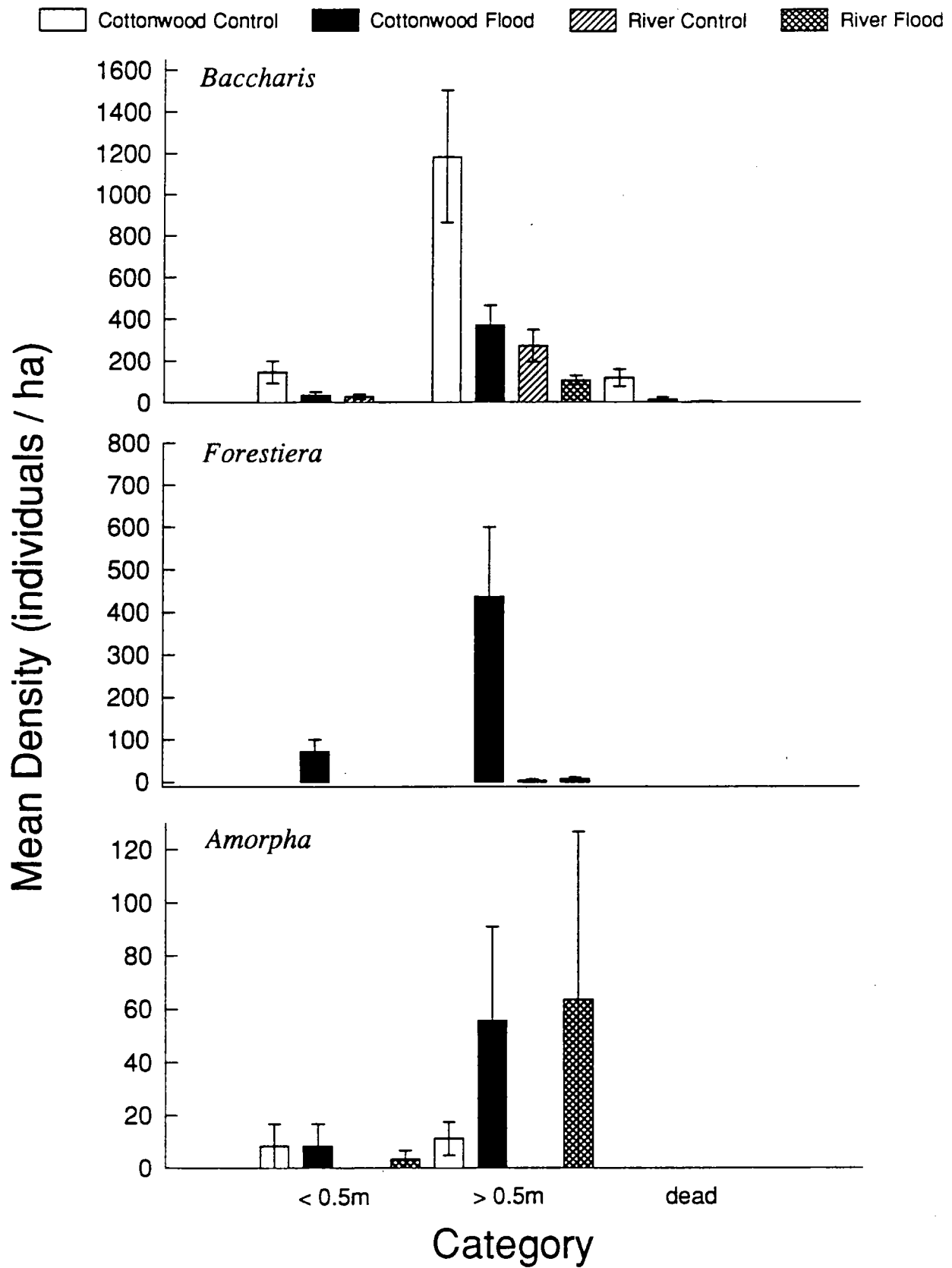


Figure 63. Mean density of shrub species at cottonwood and river sites in 1995. Values are the mean number of individuals per ha counted in 12 (cottonwood) or 10 (river) 10 x 30 m plots at each site.

# Abundance

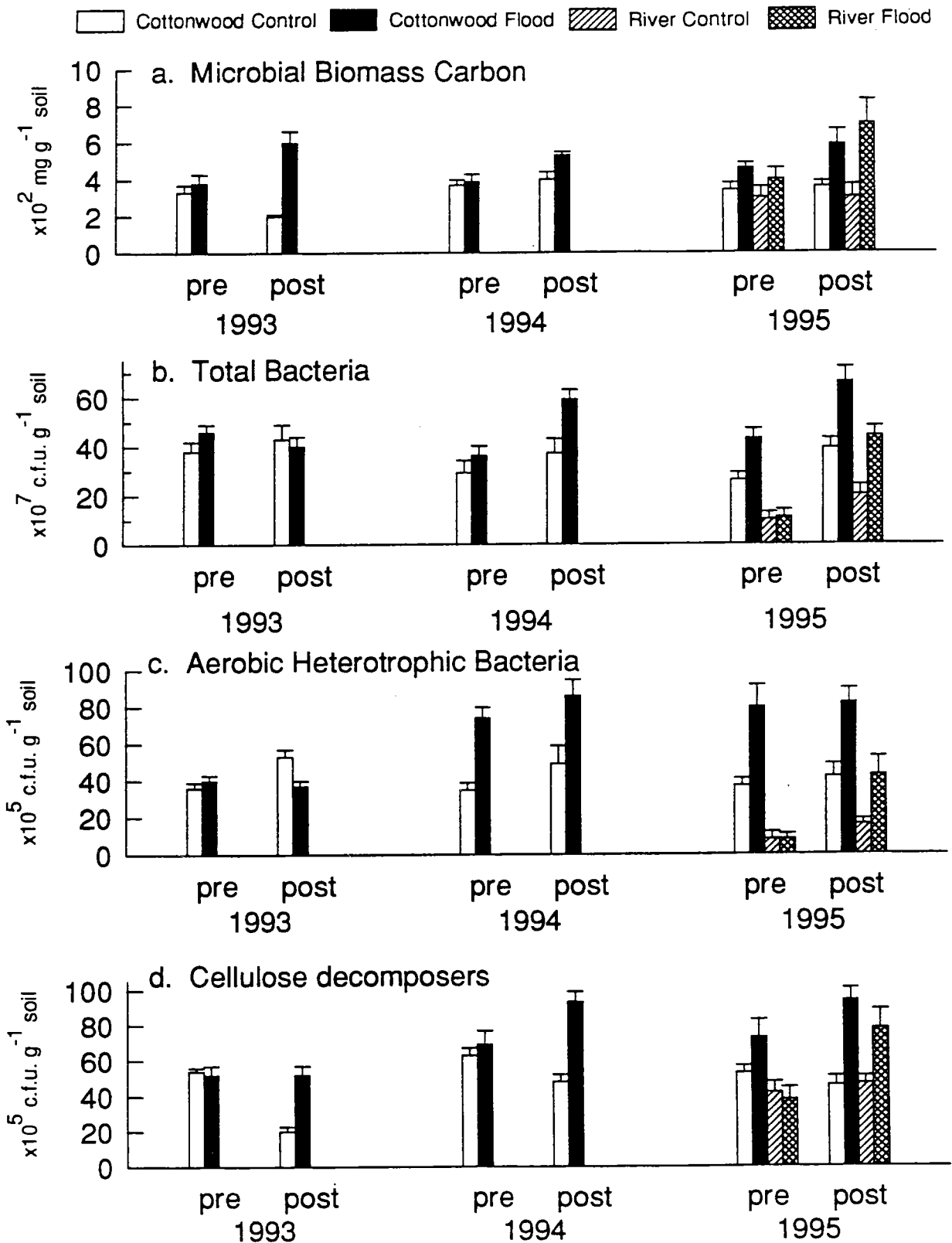


Figure 64. Comparison of soil bacteria characteristics at cottonwood and river sites before and after flooding in 1993, 1994, and 1995. Values are the mean for ten samples at each site; vertical bars indicate standard errors.

Abundance

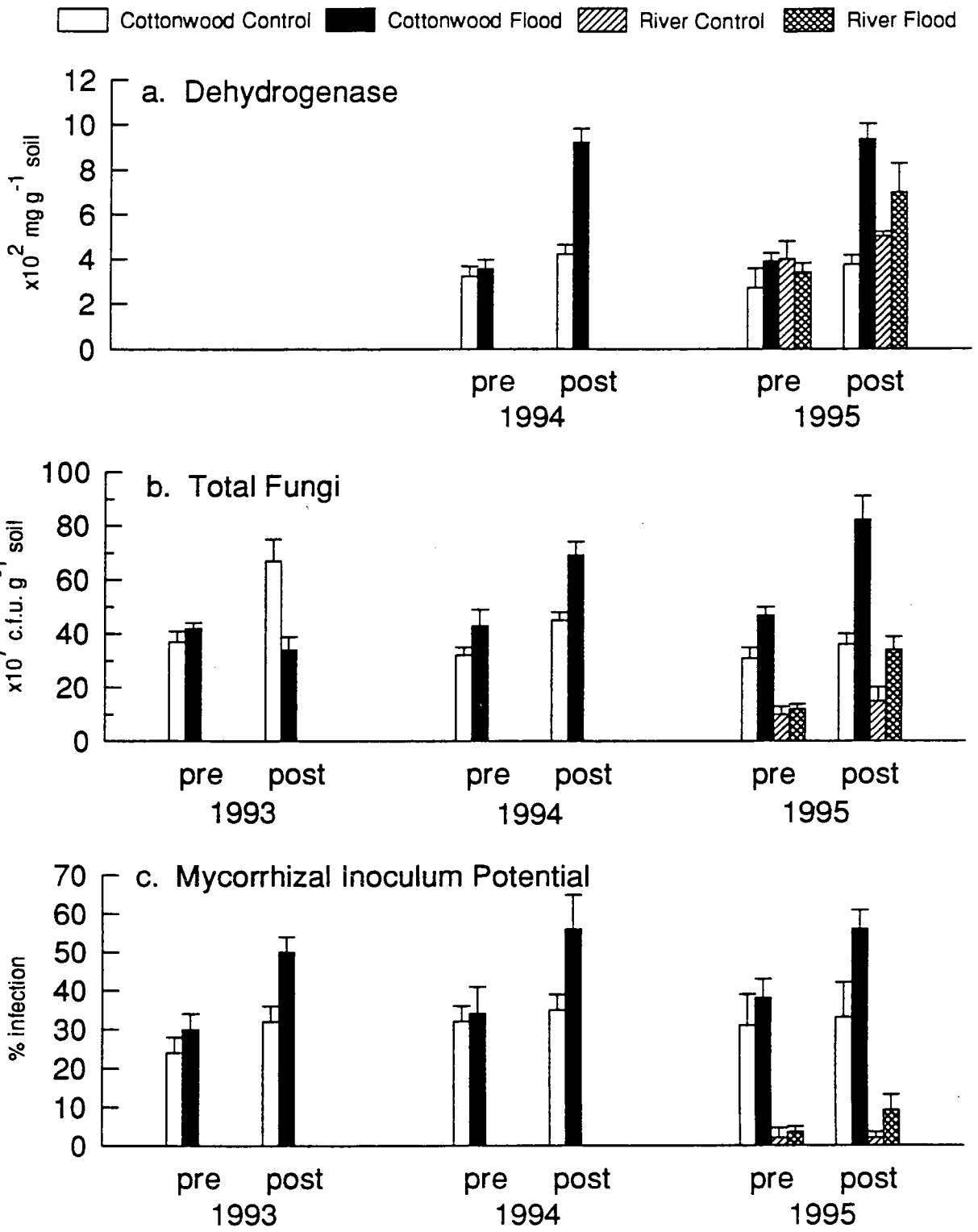


Figure 65. Comparison of soil fungi characteristics at cottonwood and river sites before and after flooding in 1993, 1994, and 1995. Values are the mean for ten samples at each site; vertical bars indicate standard errors.

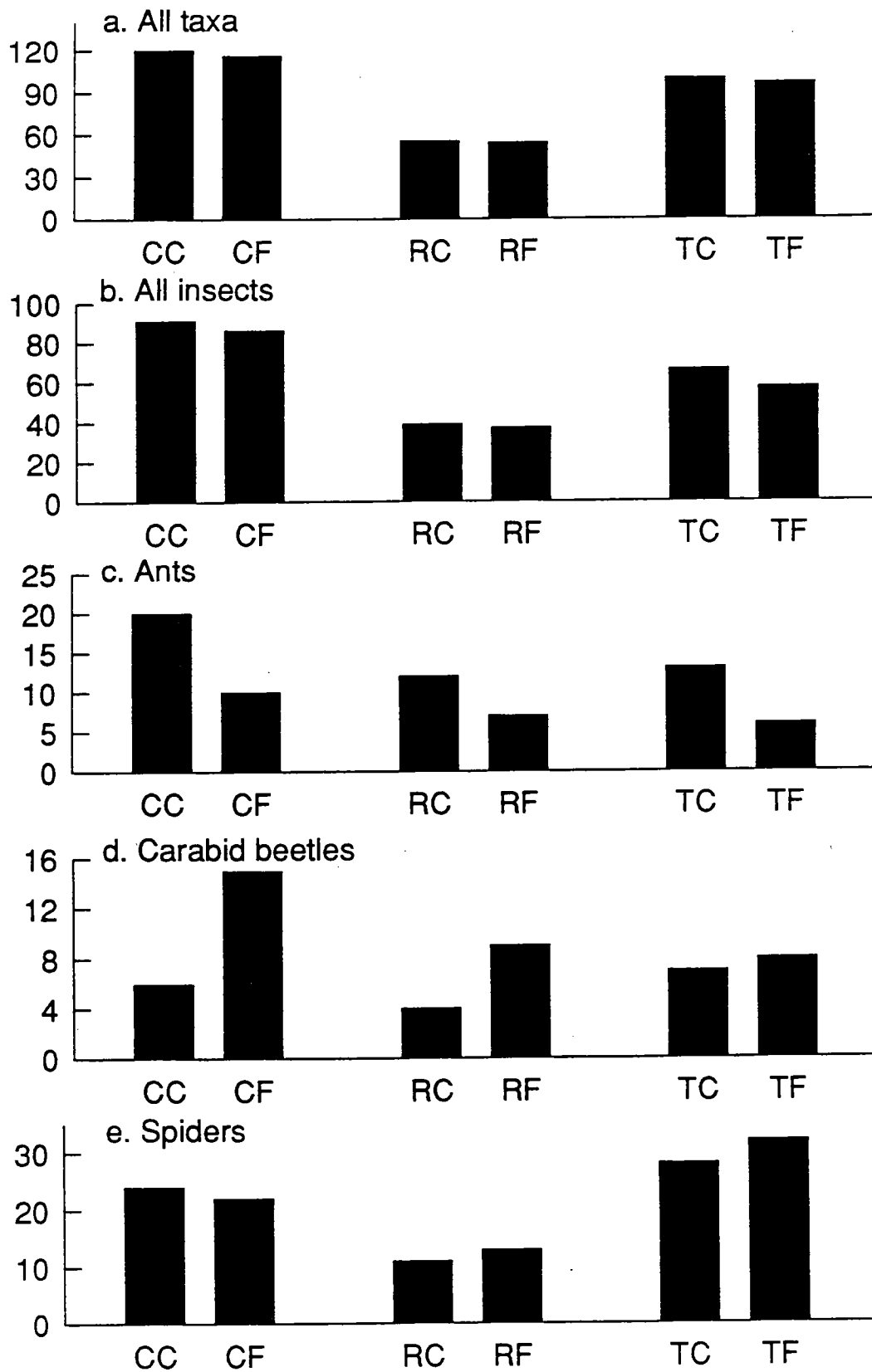


Figure 66. Taxonomic richness of various arthropod groups at all study sites over the entire study. Richness is combined from all collections within each site.

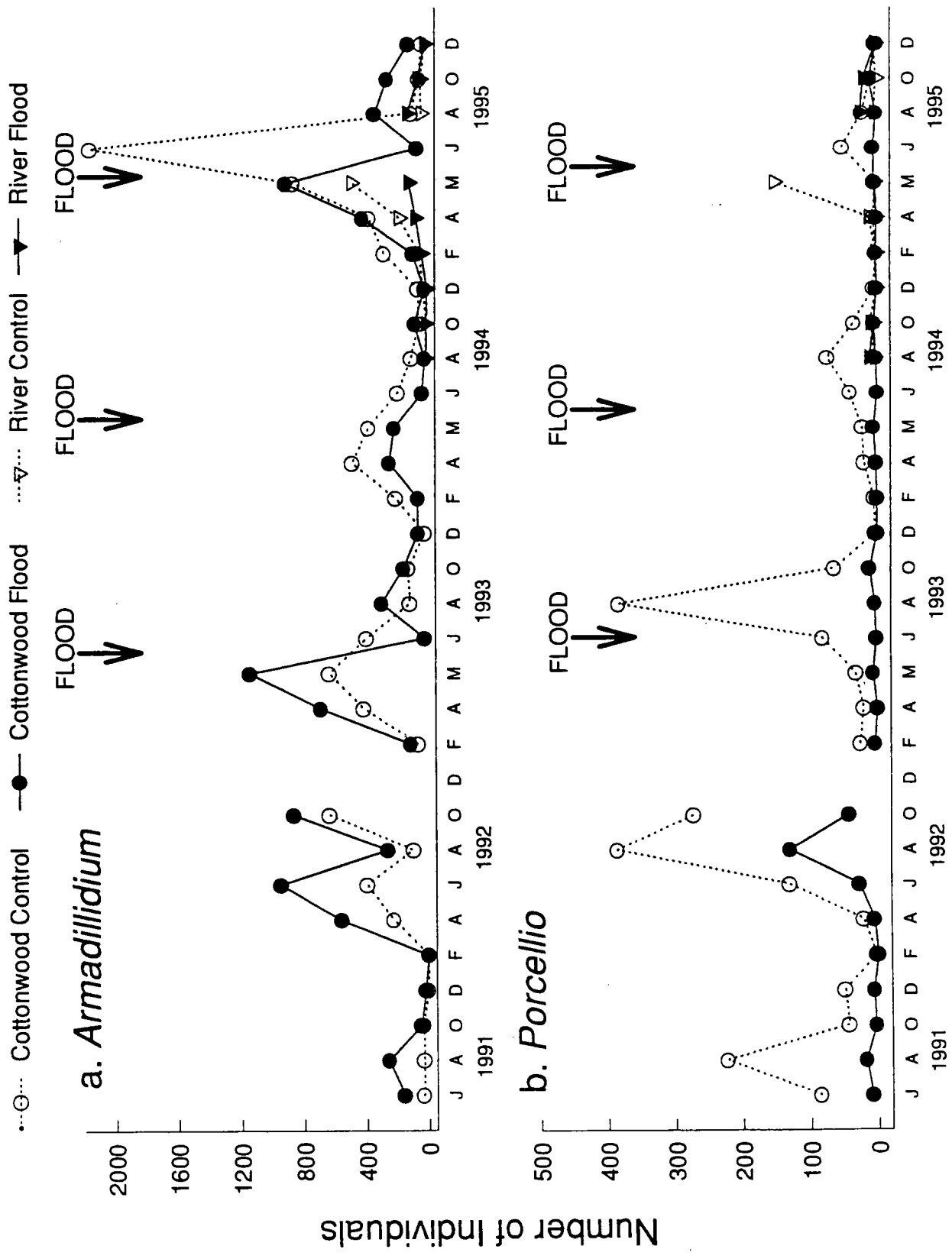


Figure 67. Abundance of a) *Armadillidium vulgare* and b) *Porcellio laevis* captured in pitfall traps at cottonwood and river sites during 1991 through 1995. Values are the total number of individuals captured in 30 pitfall traps at each site during each 48 h trapping period. Cottonwood Flood was inundated between the May and June collections during 1993, 1994, and 1995.



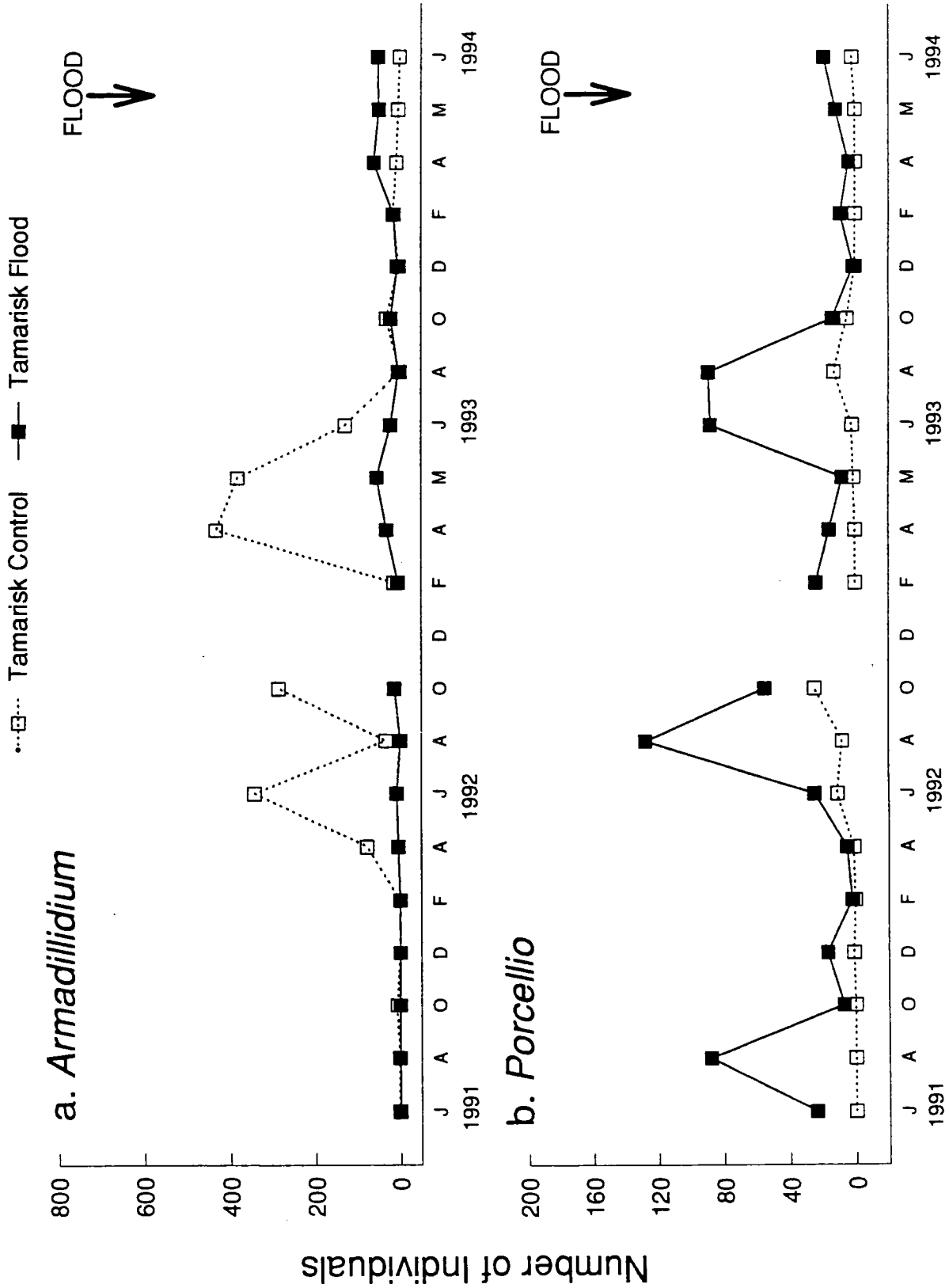


Figure 68. Abundance of a) *Armadillidium vulgare* and b) *Porcellio laevis* captured in pitfall traps at tamarisk sites during 1991 through 1994. Values are the total number of individuals captured in 30 pitfall traps at each site during each 48 h trapping period. Tamarisk Flood was partially inundated between the May and June collections during 1994. Traps were removed after June 1994.

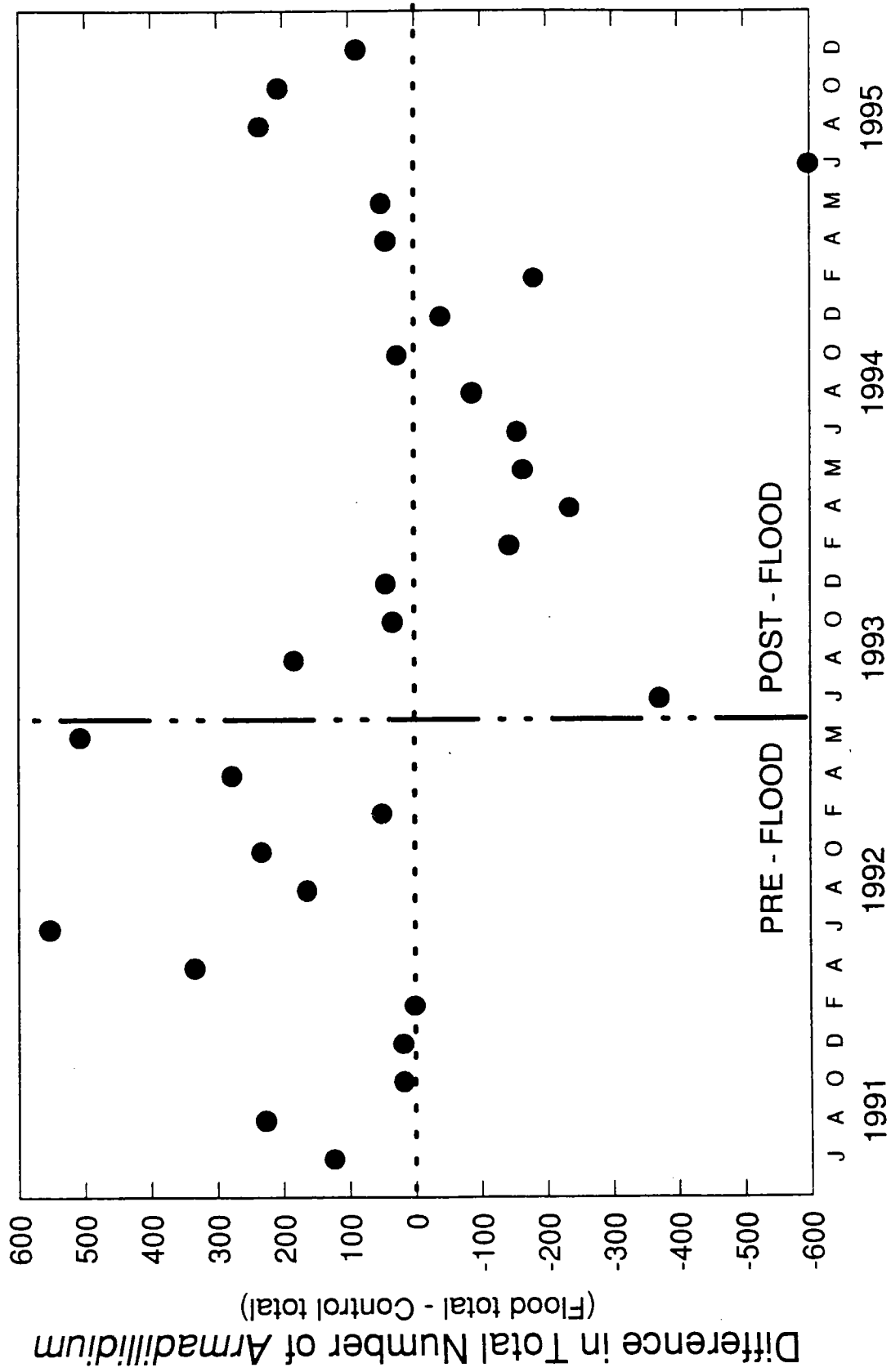


Figure 69. Intersite differences in *Armadillidium vulgare* abundance at cottonwood sites. Vertical line indicates timing of first annual flood.

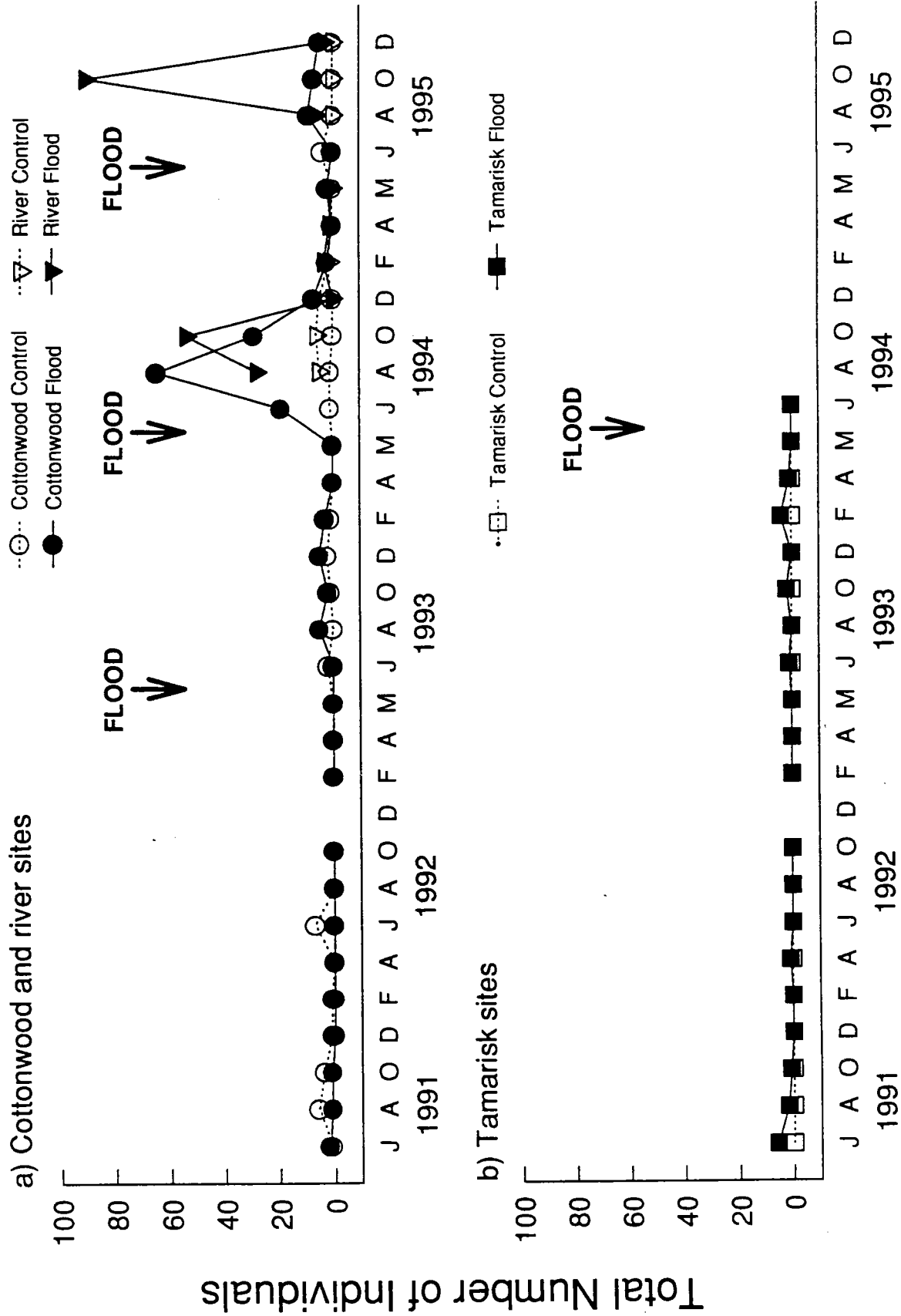


Figure 70. Abundance of *Gryllus alogus* captured in pitfall traps at a) cottonwood and river and b) tamarisk sites from 1991 through 1995. Values are the total number of individuals captured in 30 pitfall traps at each site during 48 h trapping periods each month. Cottonwood Flood was inundated between May and June collections in 1993, 1994, and 1995. Trapping at river sites began in August 1994. Tamarisk Flood was partially inundated in 1994, but arthropods were not collected at those sites after June 1994.

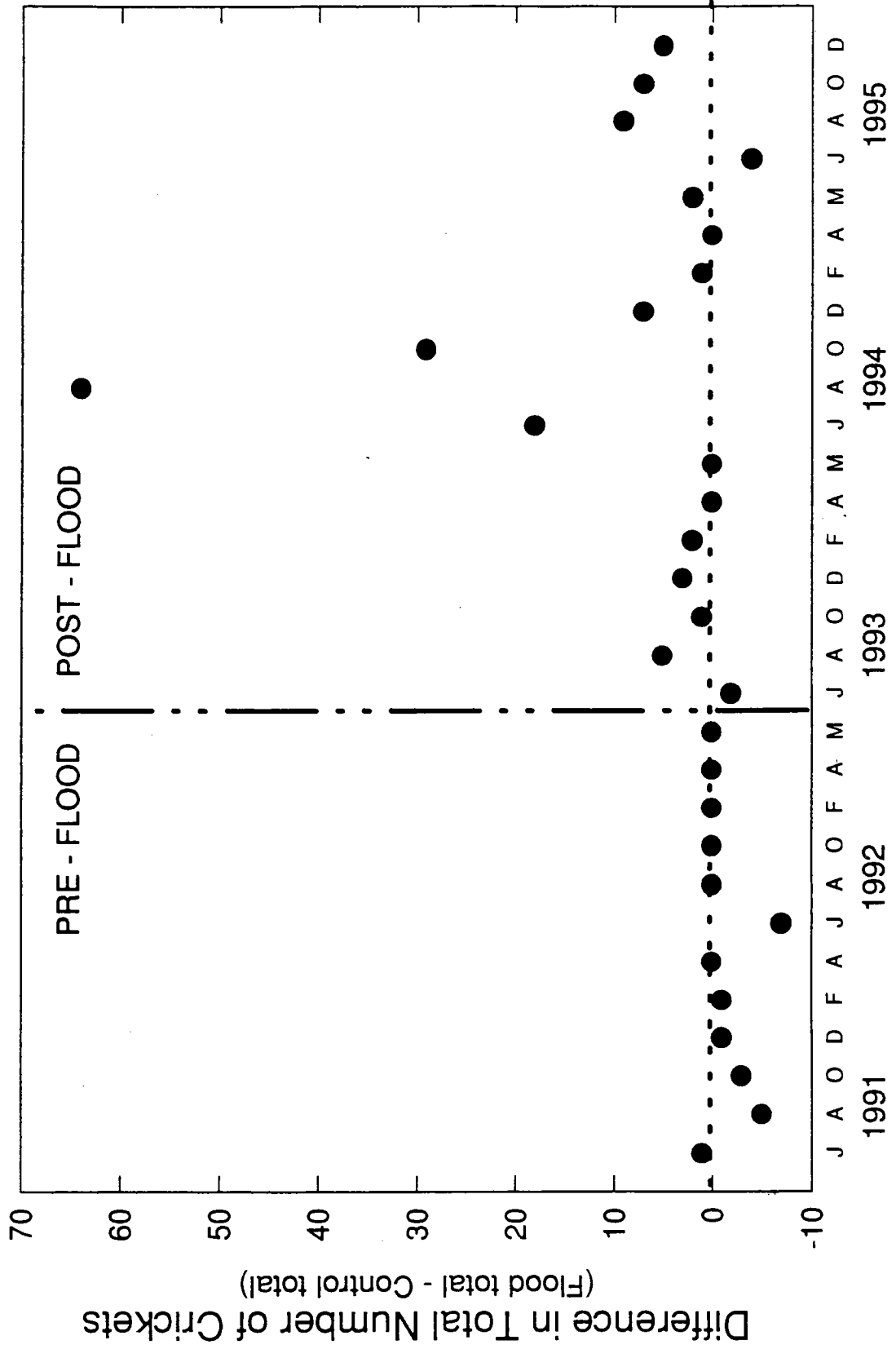


Figure 71. Intersite differences in *Gryllus atlogus* abundance at cottonwood sites. Vertical line indicates timing of first annual flood.



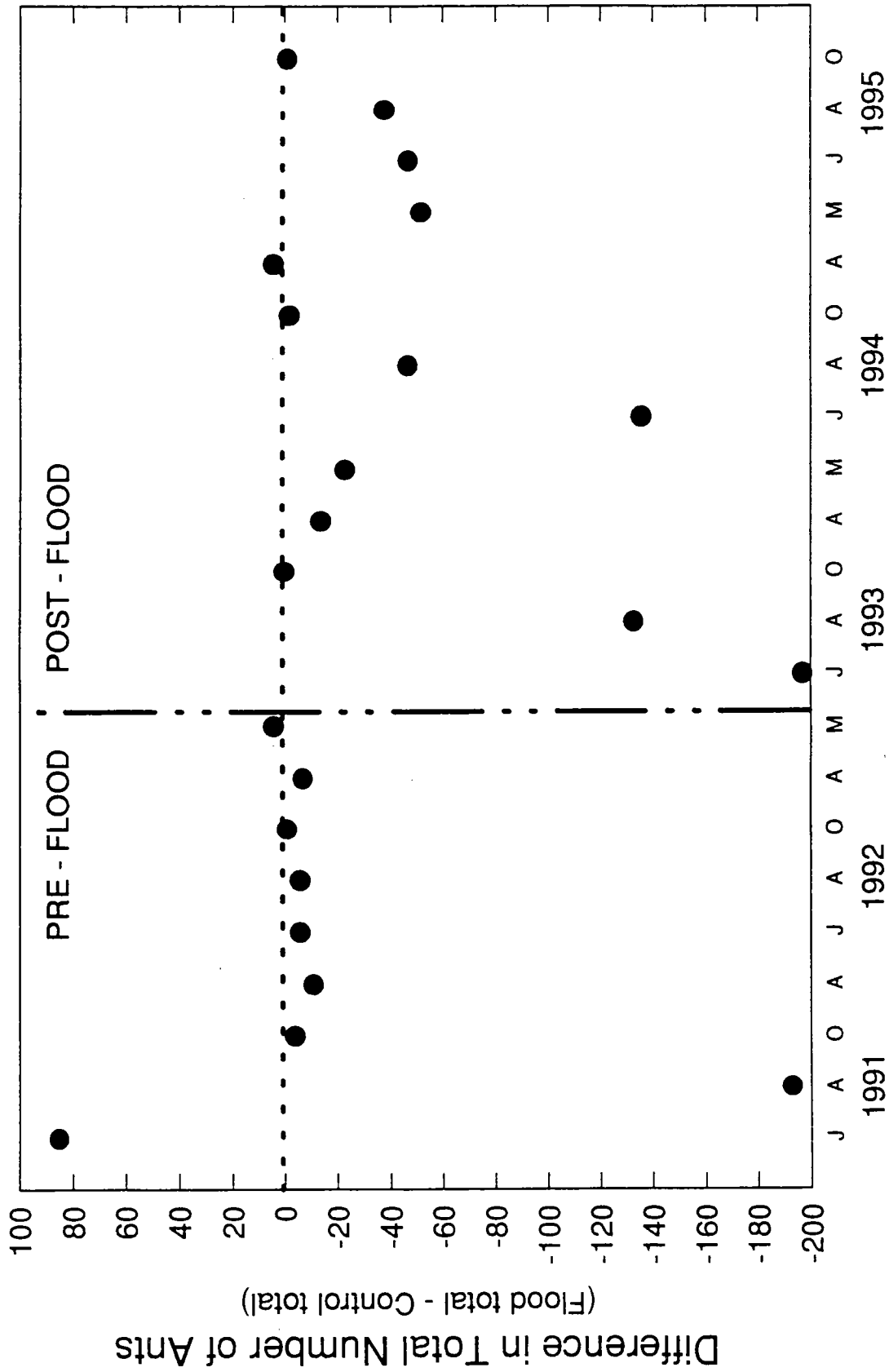


Figure 73. Intersite differences in ant abundance (all species combined) at cottonwood sites. Vertical bar indicates timing of first annual flooding. Included are data for April, May, June, August and October; winter periods of inactivity are excluded.

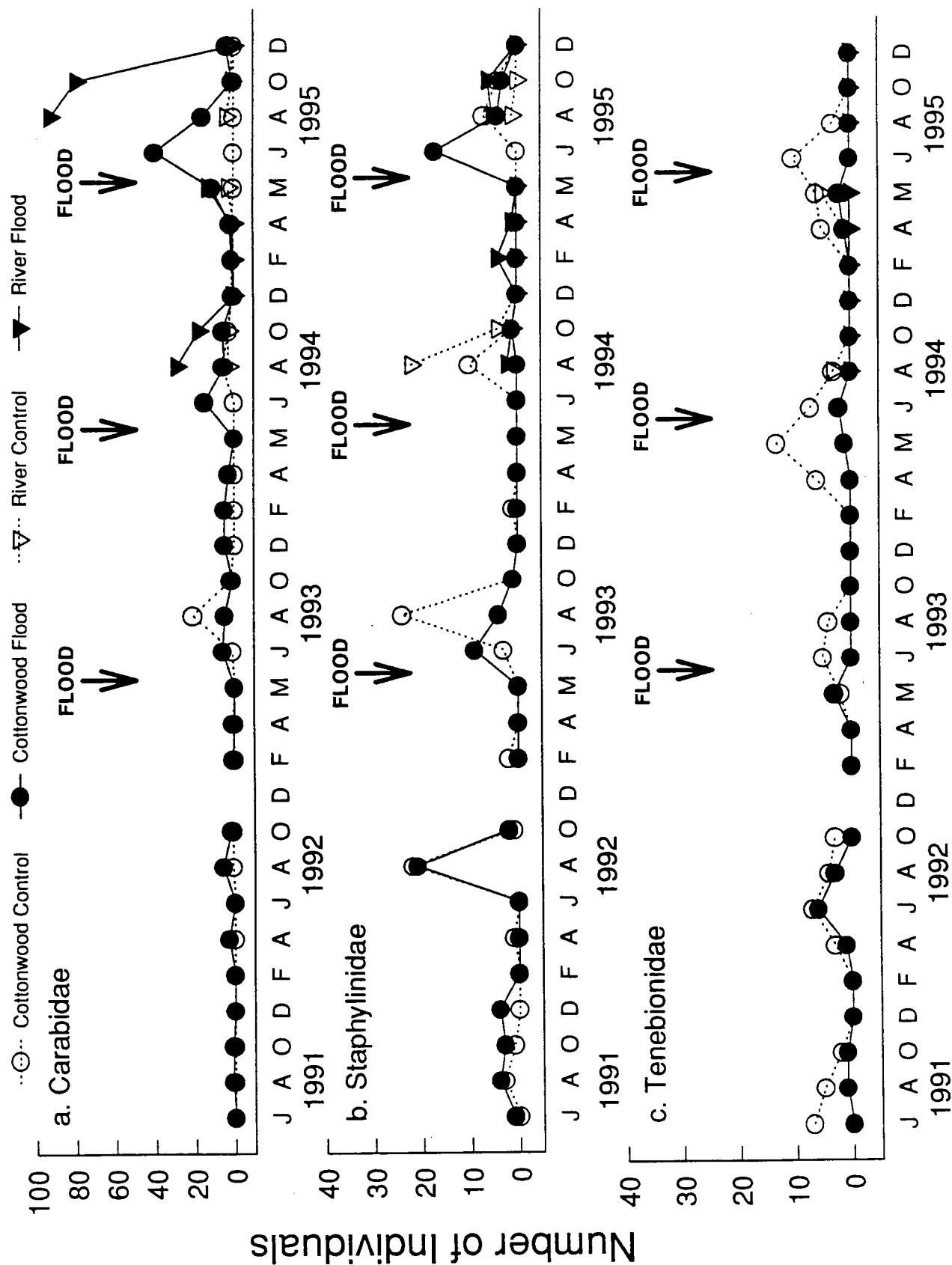


Figure 74. Abundance of a) carabid, b) staphylinid, and c) tenebrionid beetles captured in pitfall traps at cottonwood and river sites during 1991 through 1995. Values are the total number of individuals captured in 30 traps at each site during each trapping period. Cottonwood Flood was inundated between the May and June collections in 1993, 1994, and 1995. Trapping at river sites began in August 1994; these sites were not trapped in June 1995, since River Flood was still inundated at that time.

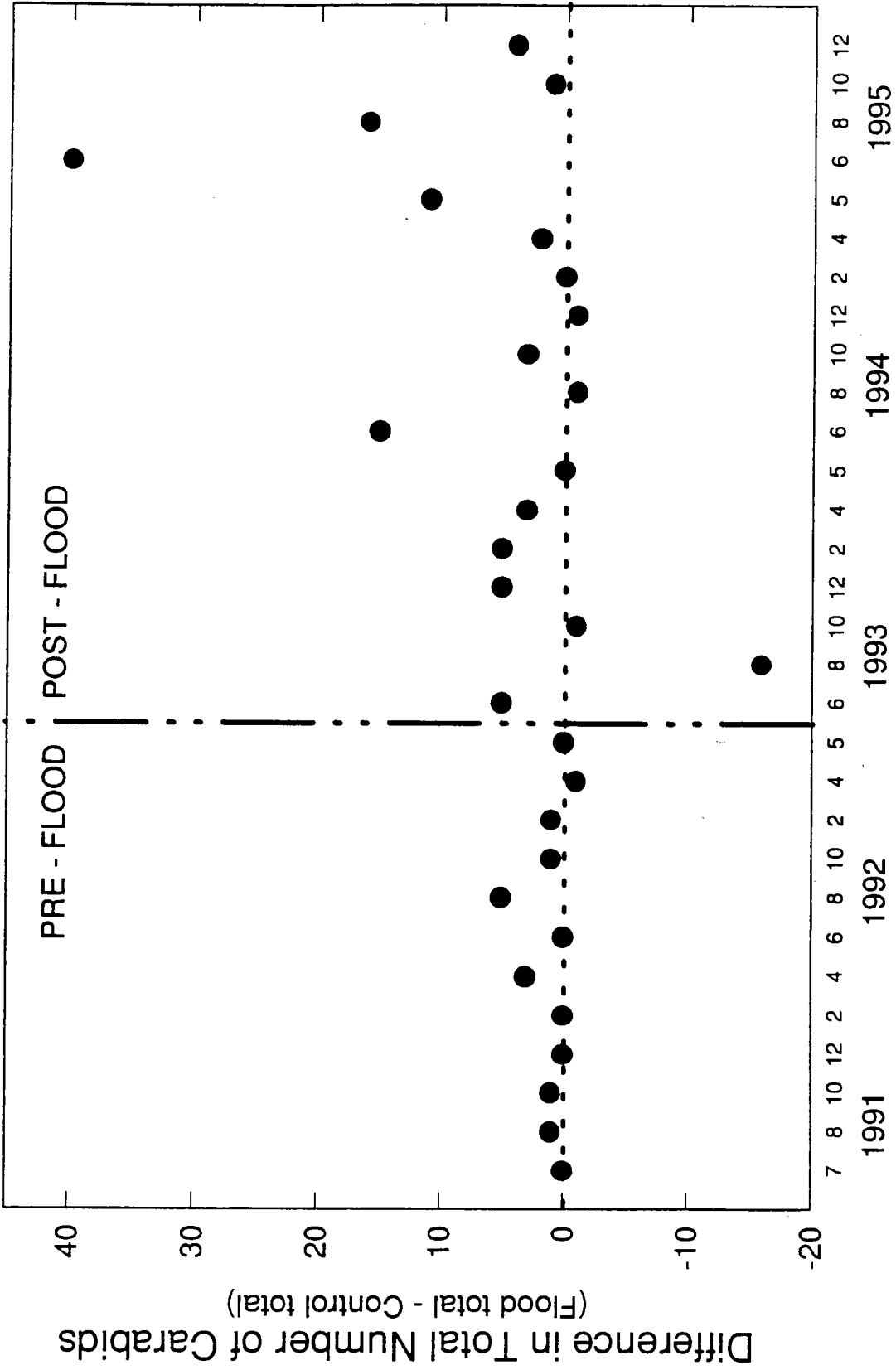


Figure 75. Intersite differences in carabid beetle abundance at cottonwood sites. Vertical line indicates timing of first annual flood.



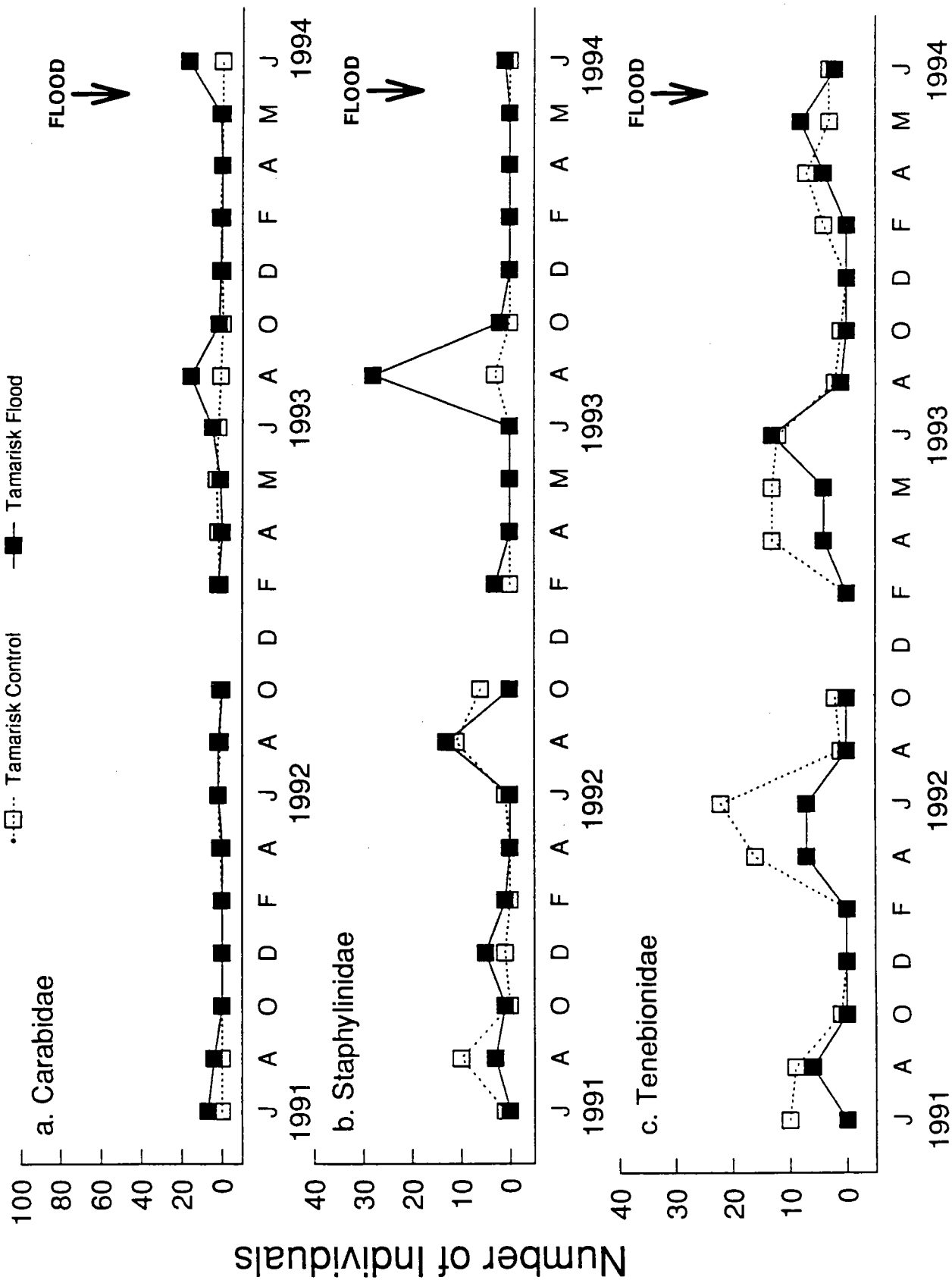


Figure 76. Abundance of a) carabid, b) staphylinid, and c) tenebrionid beetles captured in pitfall traps at tamarisk sites during 1991 through 1994. Values are the total number of individuals captured in 30 traps at each site during each 48 h trapping period. Tamarisk Flood was partially inundated between the May and June collections in 1994. Traps were removed after June 1994.

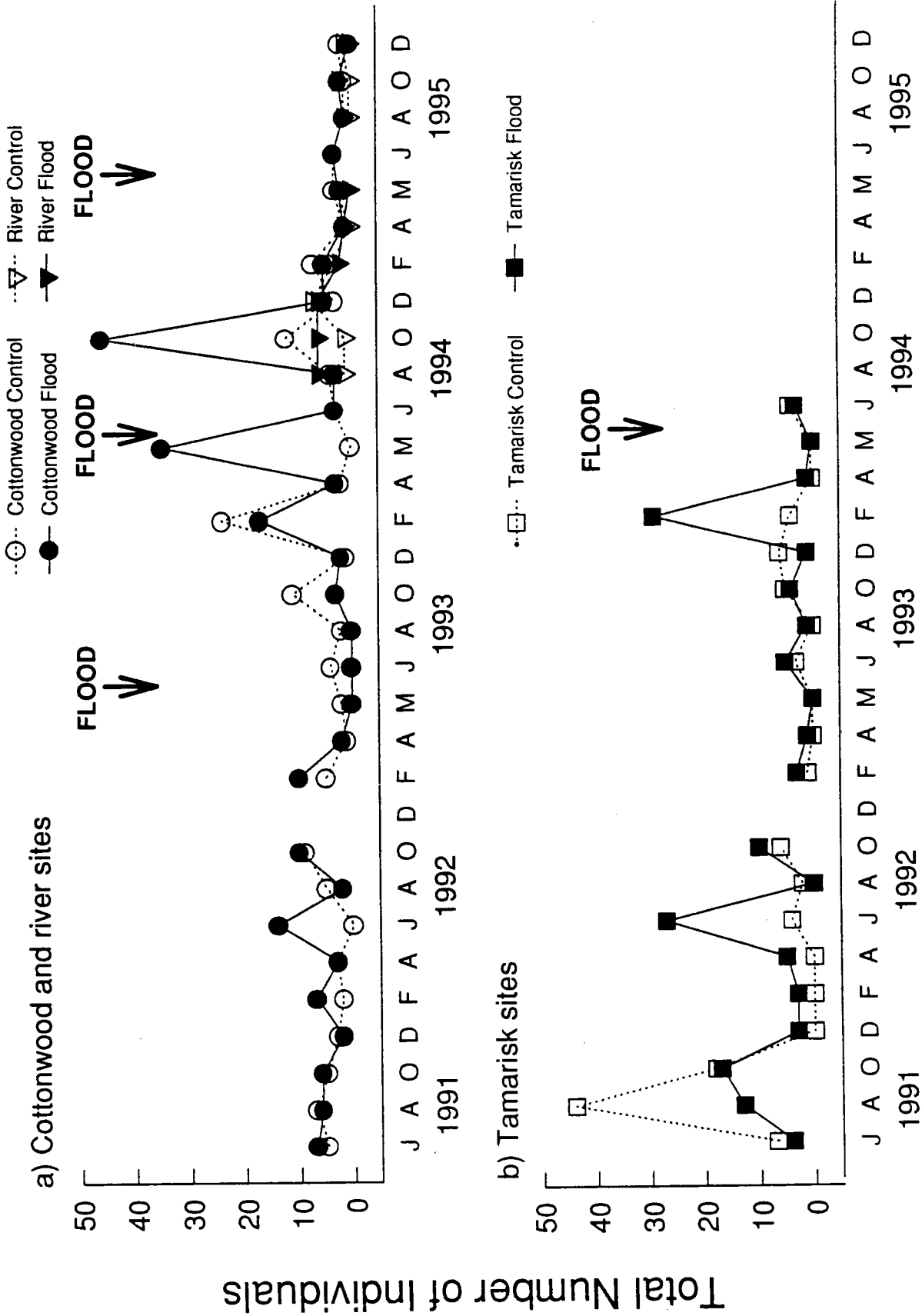


Figure 77. Abundance of lycosid spiders captured in pitfall traps at a) cottonwood and river and b) tamarisk sites from 1991 through 1995. Values are the total number of individuals captured in 30 pitfall traps at each site during 48 h trapping periods each month. Cottonwood Flood was inundated between May and June collections in 1993, 1994, and 1995. Trapping at river sites began in August 1994. Tamarisk Flood was partially inundated in 1994, but arthropods were not collected at those sites after June 1994.

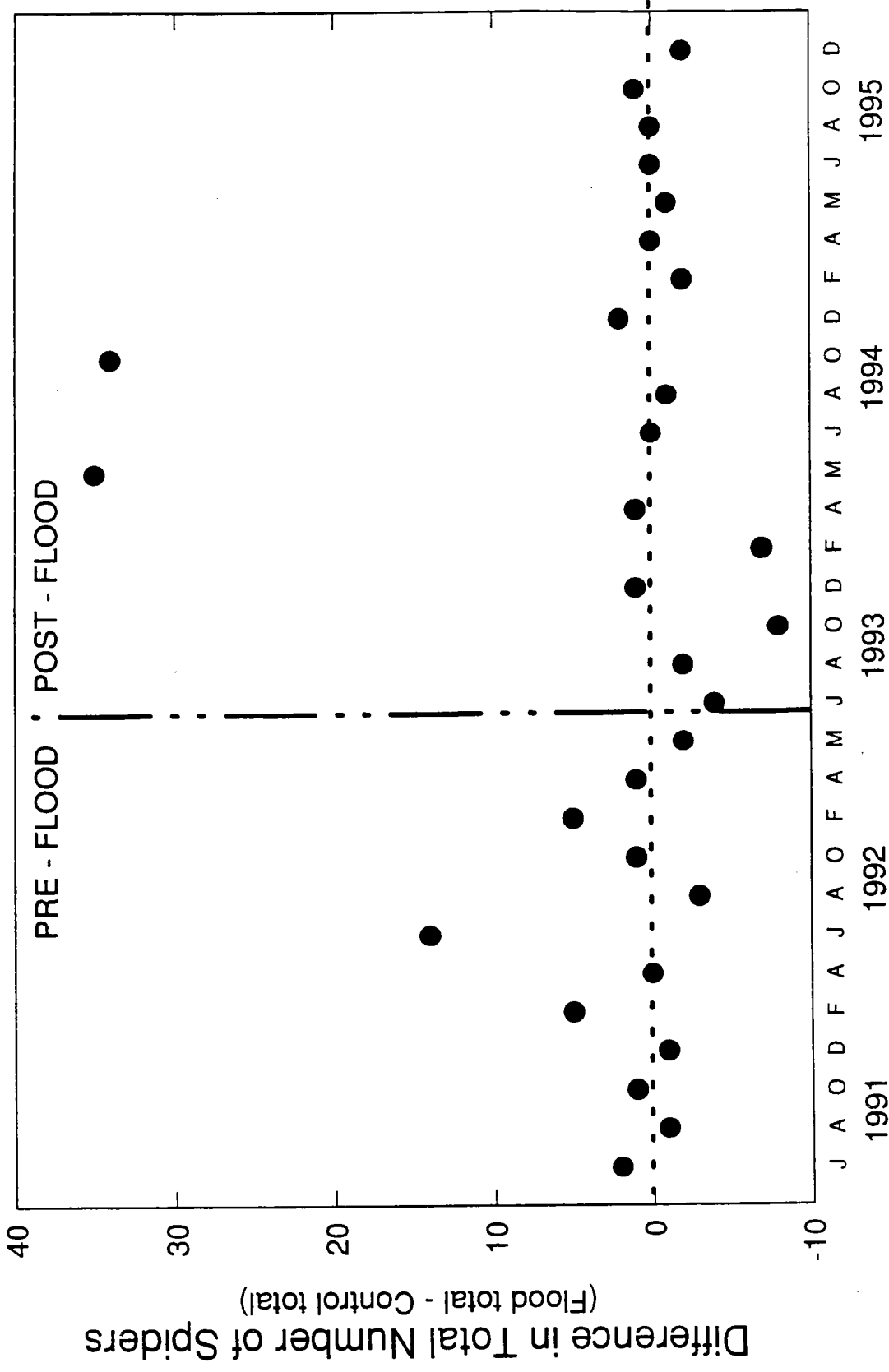


Figure 78. Intersite differences in lycosid spider abundance at cottonwood sites. Vertical line indicates timing of first annual flood.

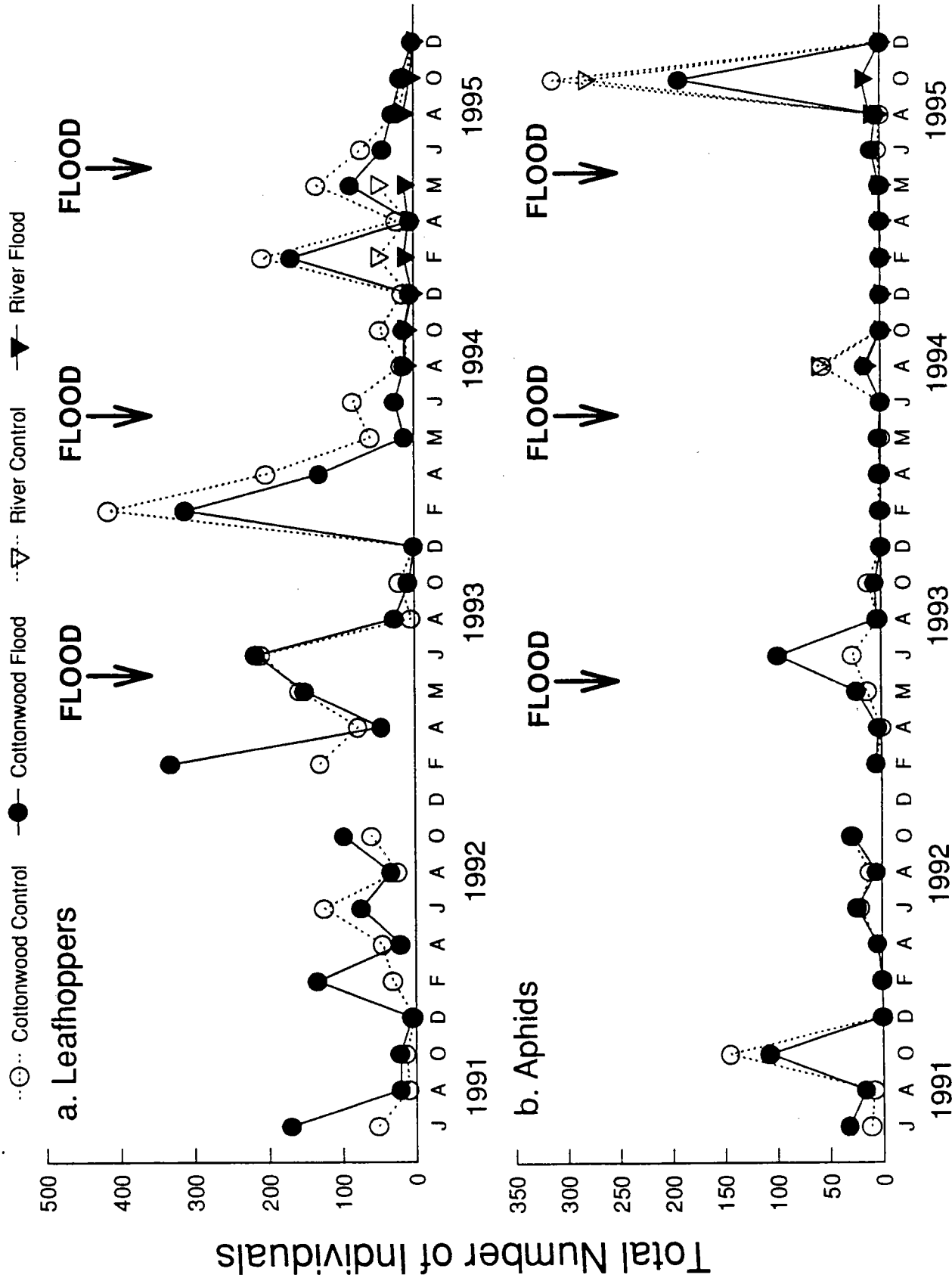


Figure 79. Abundance of a) leafhoppers and b) aphids at cottonwood and river sites during 1991 through 1995. Values are the total number of individuals captured on ten sticky traps during 48 h trapping periods at each site for each date.

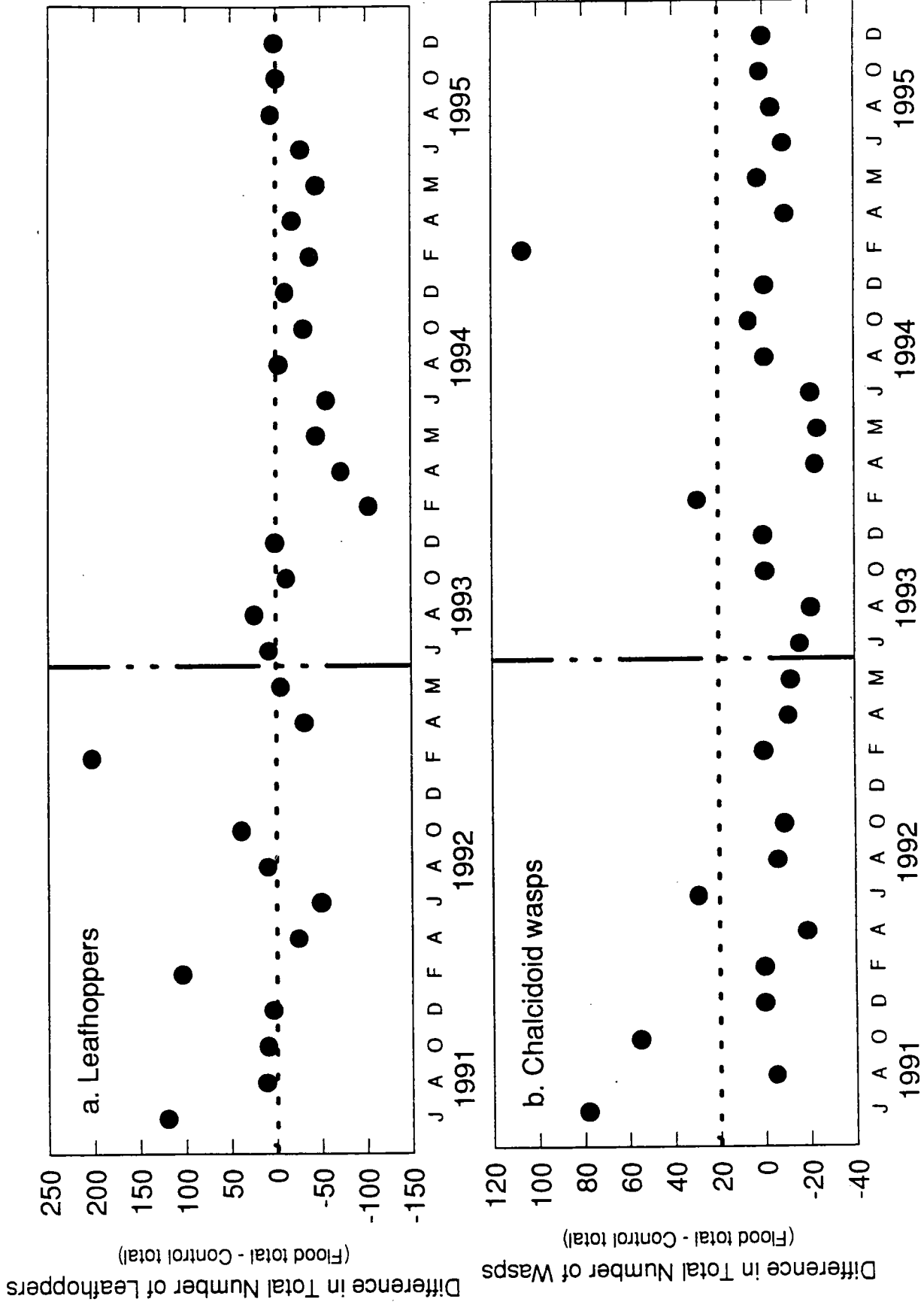


Figure 80. Intersite differences in a) leafhopper and b) chalcidoid wasp abundance at cottonwood sites. Vertical lines indicate timing of the first annual flood.

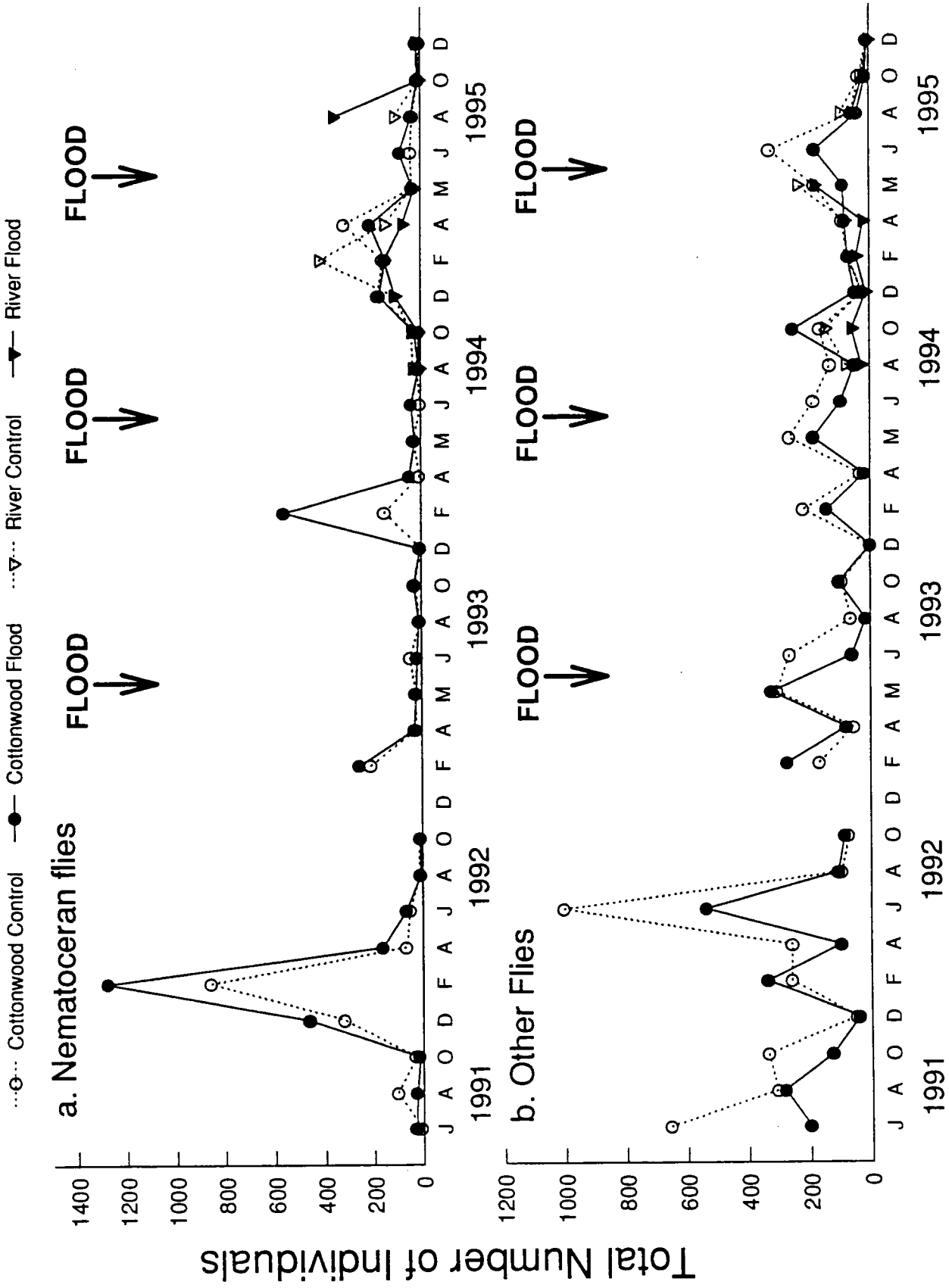


Figure 81. Abundance of a) nematoceran flies and b) other flies at cottonwood and river sites during 1991 through 1995. Values are the total number of individuals captured on ten sticky traps during 48 h trapping periods at each site for each date.

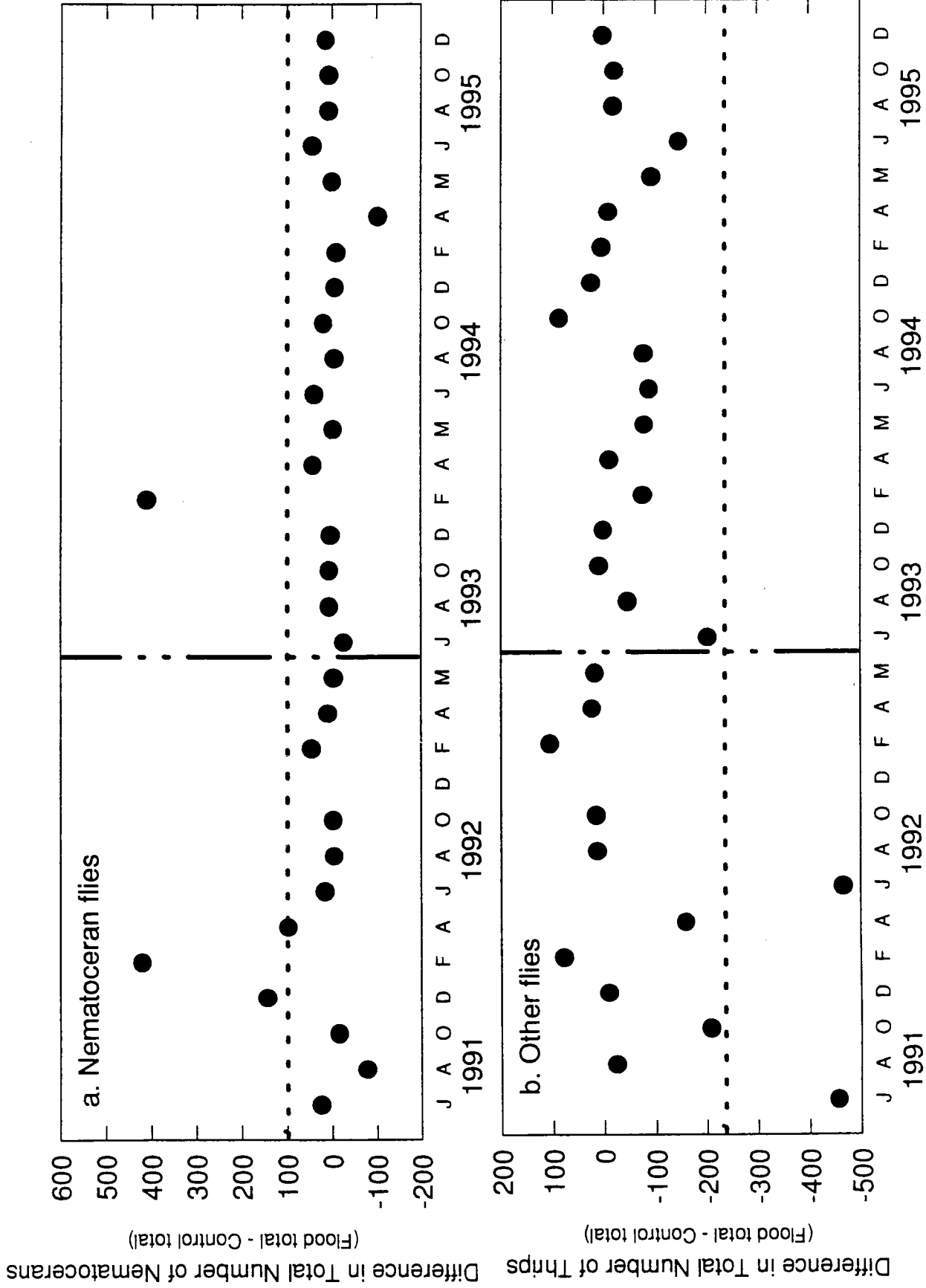


Figure 82. Intersite differences in abundance of a) nematoceran flies and b) other flies at cottonwood sites. Vertical lines indicate timing of first annual flood.

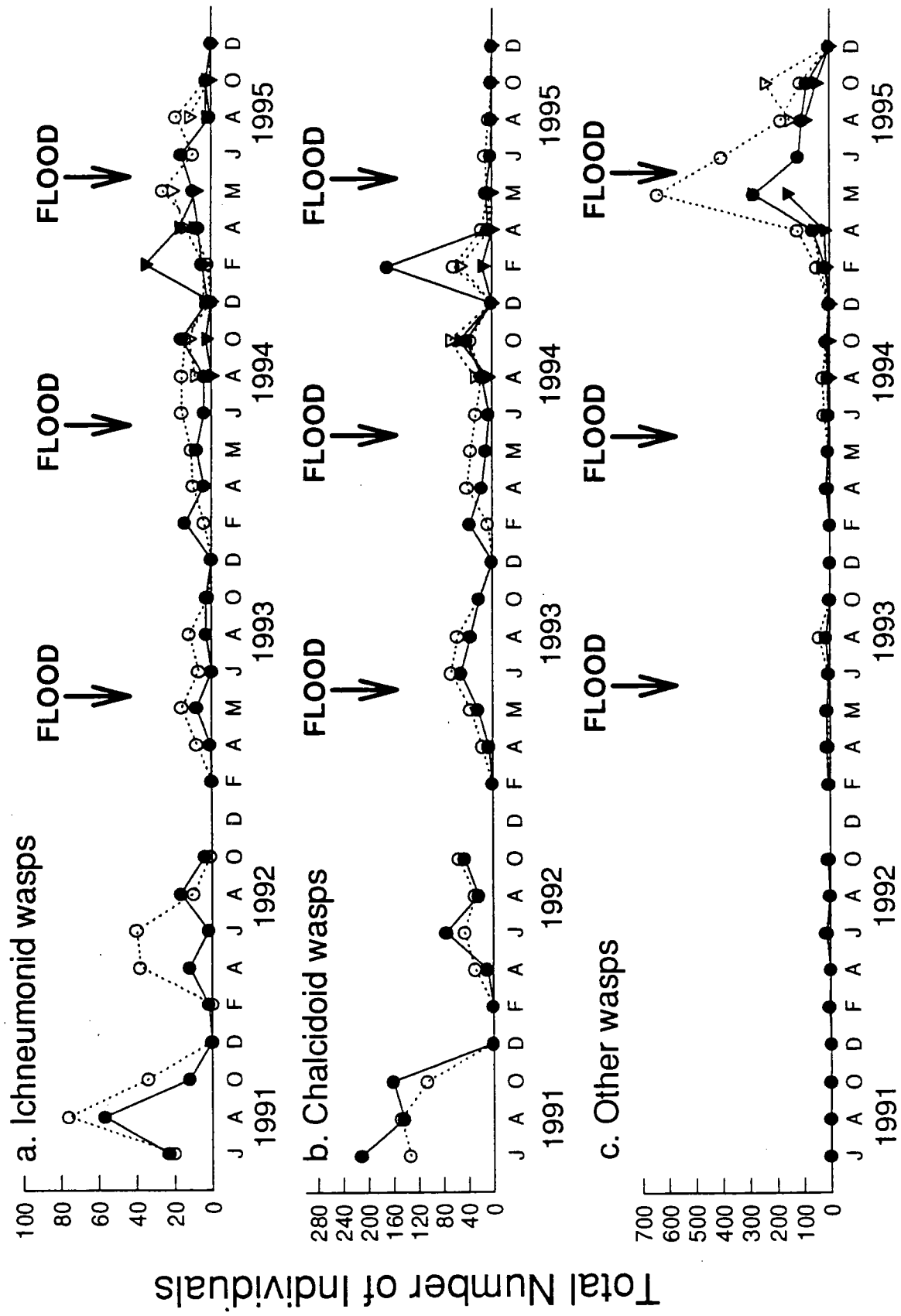


Figure 83. Abundance of a) ichneumonid, b) chalcidoid, and c) other wasps at cottonwood and river sites during 1991 through 1995. Values are the total number of individuals captured on ten sticky traps during 48 h trapping periods at each site for each date.



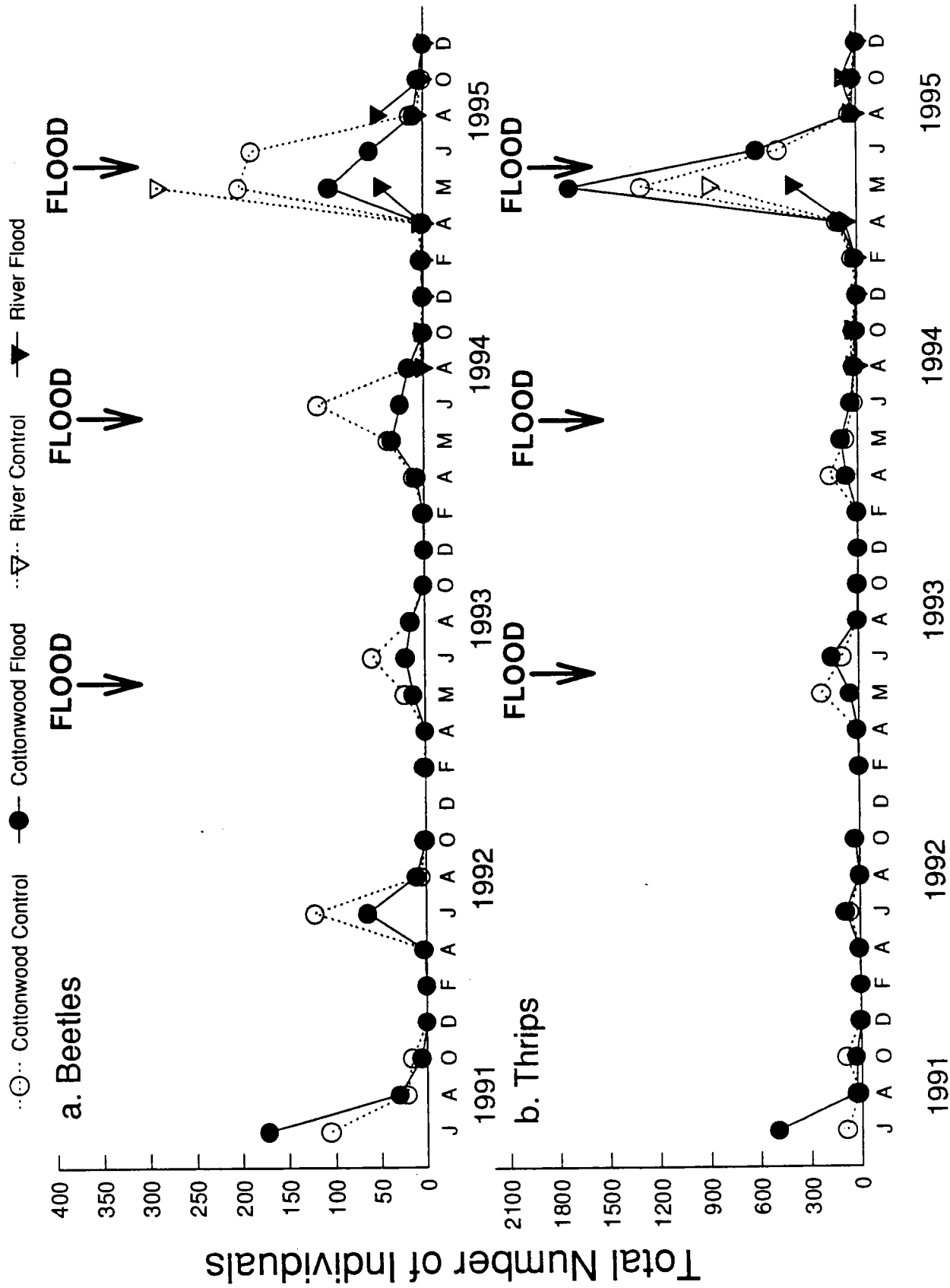


Figure 84. Abundance of a) beetles and b) thrips at cottonwood and river sites during 1991 through 1995. Values are the total number of individuals captured on ten sticky traps during 48 h trapping periods at each site for each date.

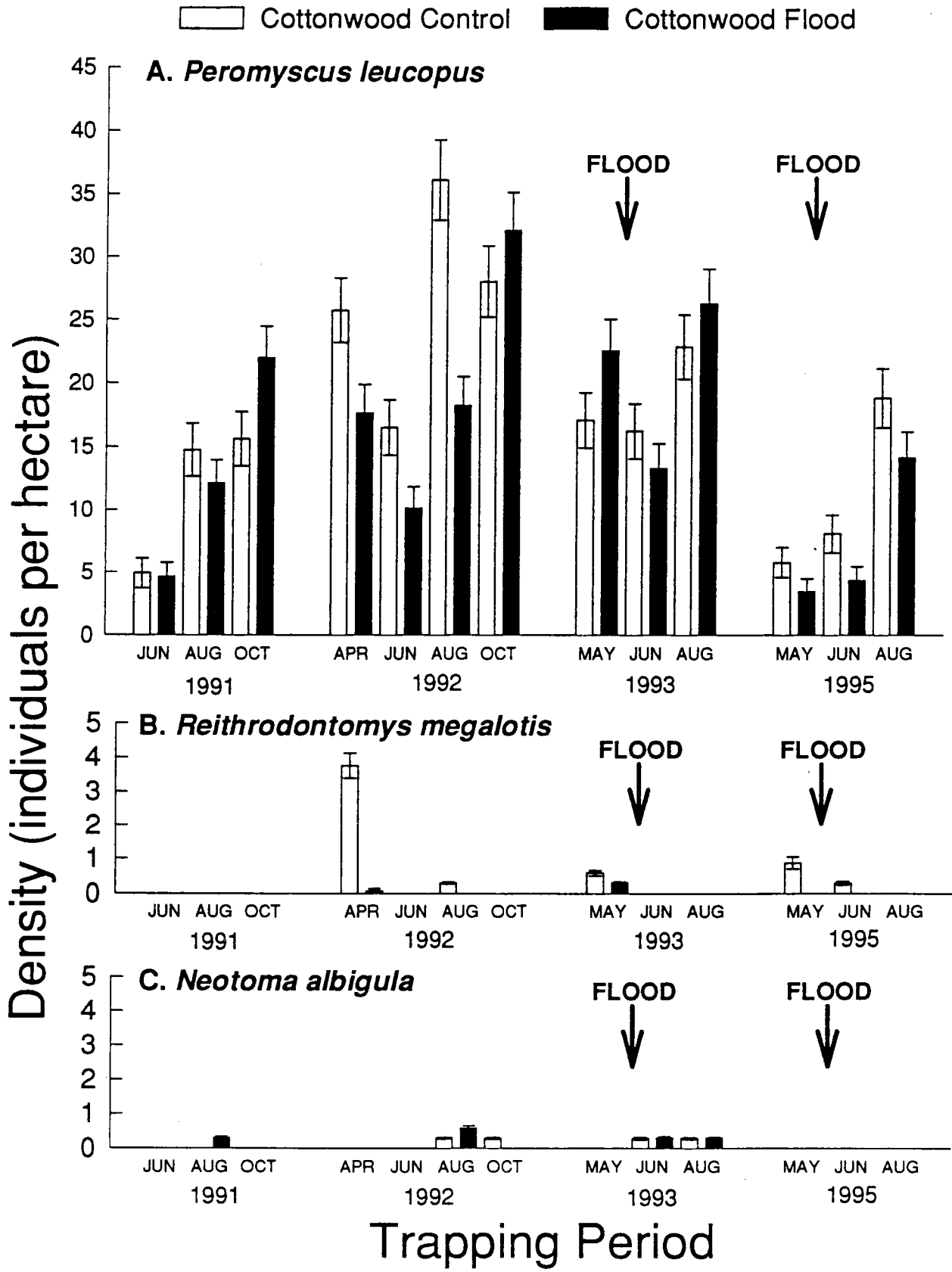


Figure 85. Densities of a) *Peromyscus leucopus*, b) *Reithrodontomys megalotis*, and c) *Neotoma albigula* captured in ground traps at cottonwood sites during 1991, 1992, 1993, and 1995.

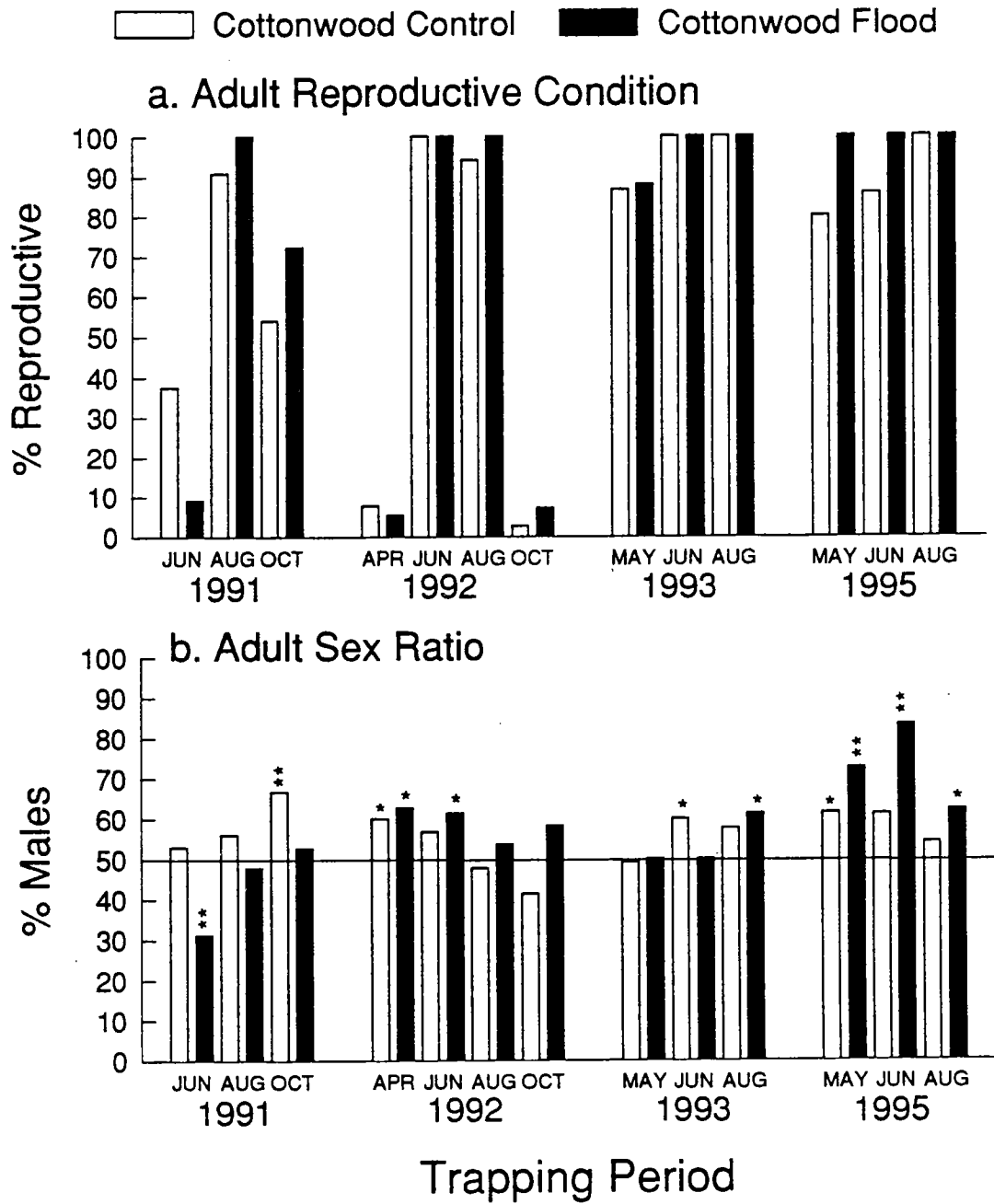


Figure 86. a) Percent of adult *Peromyscus leucopus* in reproductive condition and b) adult sex ratio for *P. leucopus* captured during each year. Asterisks indicate sex ratios significantly different from 50:50.

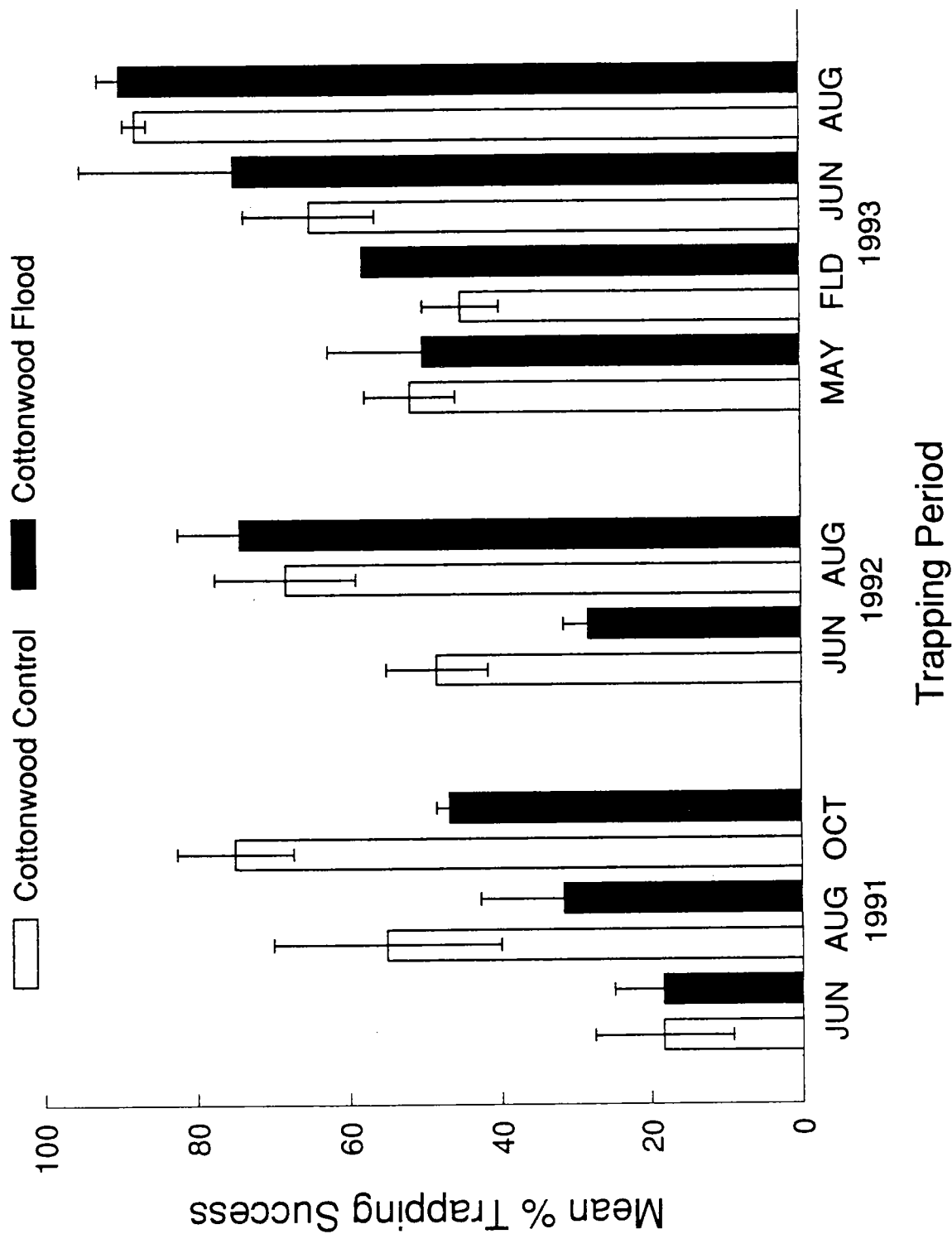


Figure 87. Mean trapping success in traps placed in cottonwood trees during 1991, 1992, and 1993. FLD indicates trapping during peak flood.

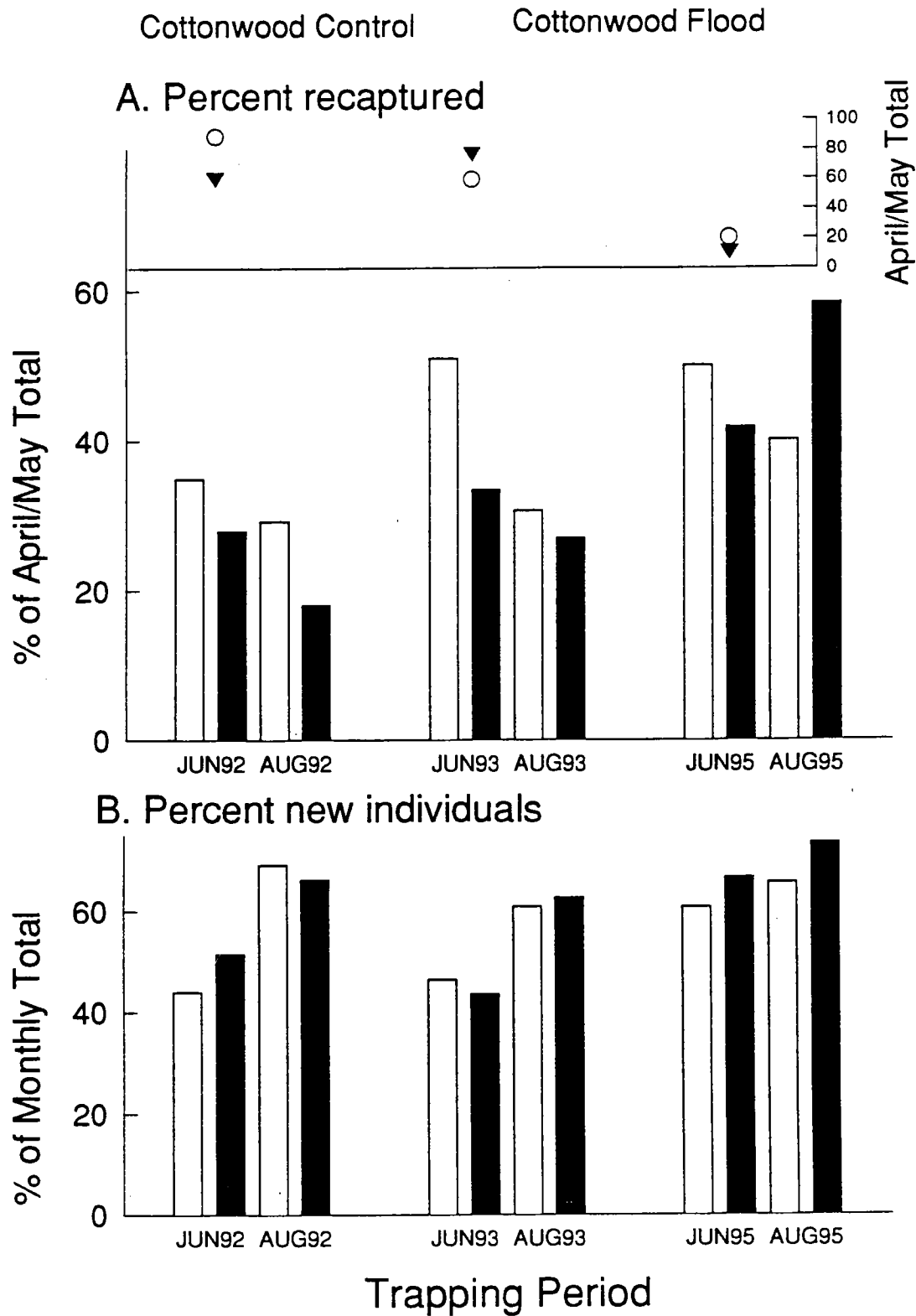


Figure 88. a) Percent of *Peromyscus leucopus* captured in April or May that were recaptured in June and August. Upper graph indicates the total number of *P. leucopus* captured in April or May at each site. b) Percent of new individuals (those not captured in April or May) trapped during June and August each year.

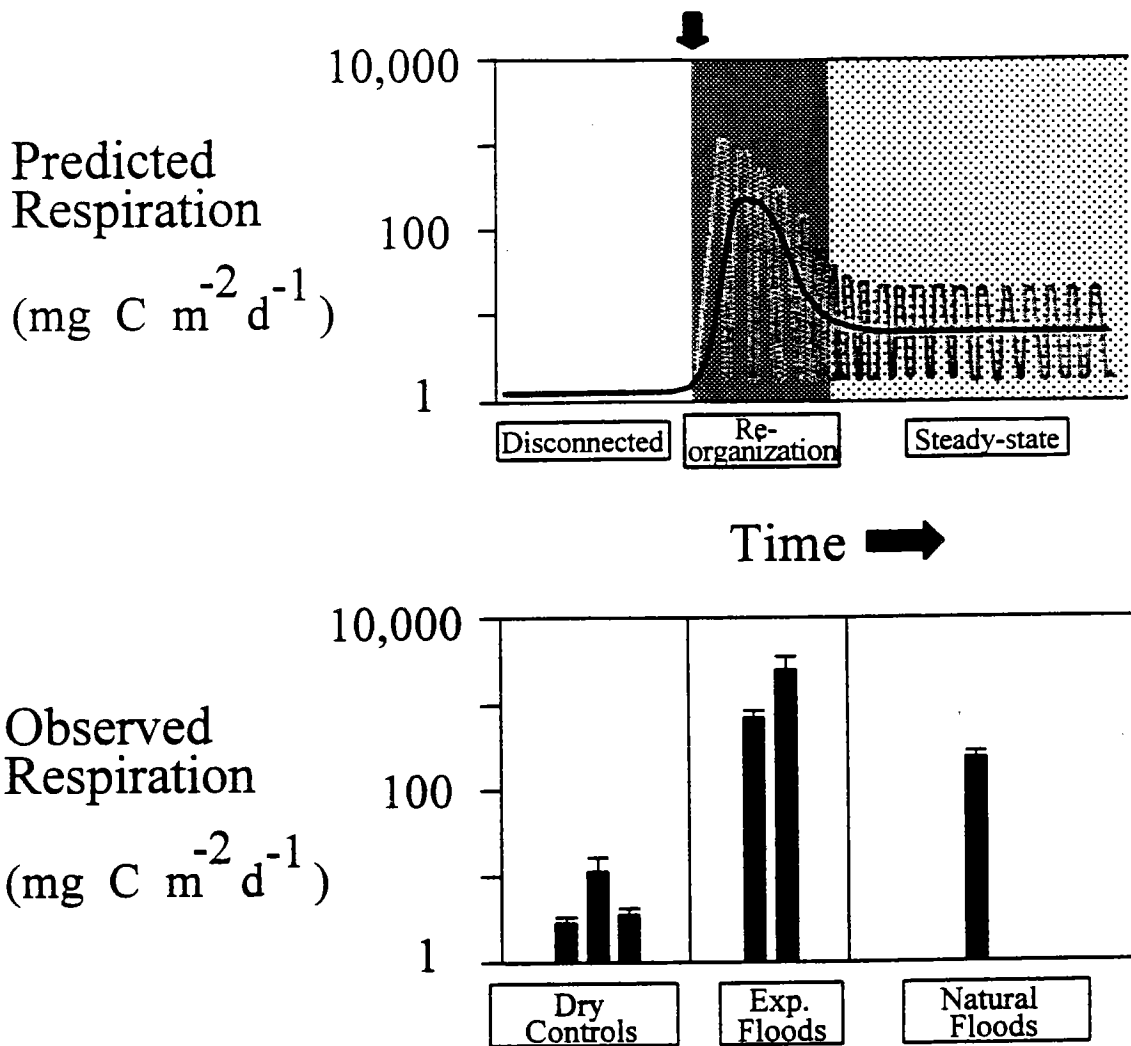


Figure 89. Predicted and observed response of forest floor respiration to functional restoration. Upper graph shows predicted respiration values for the disconnected, re-organization, and steady-state phases of restoration. Bottom graph shows actual respiration values measured at the dry control sites (Cottonwood Control, River Control), during two years of experimental flooding (Cottonwood Flood) and at the naturally flooded site (River Flood).

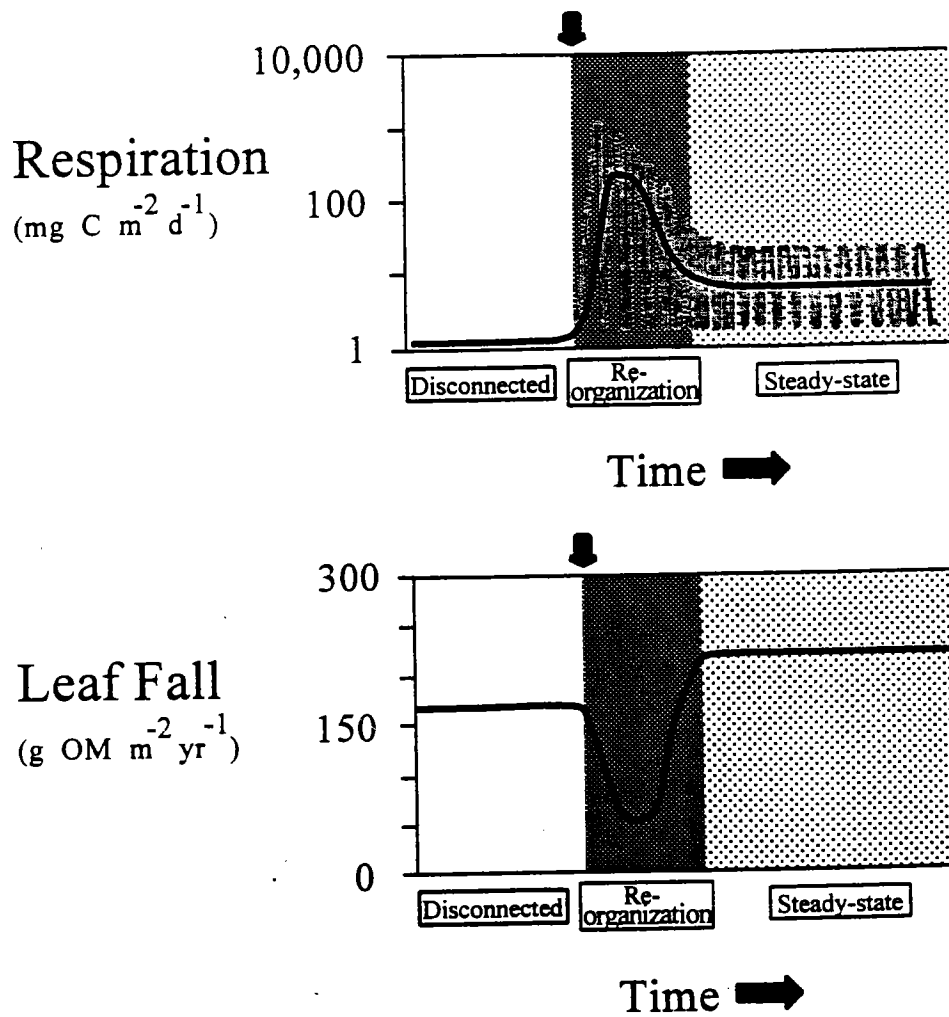


Figure 90. Comparison between predicted phase responses to restoration of seasonal flooding for forest floor respiration and cottonwood leaf fall.

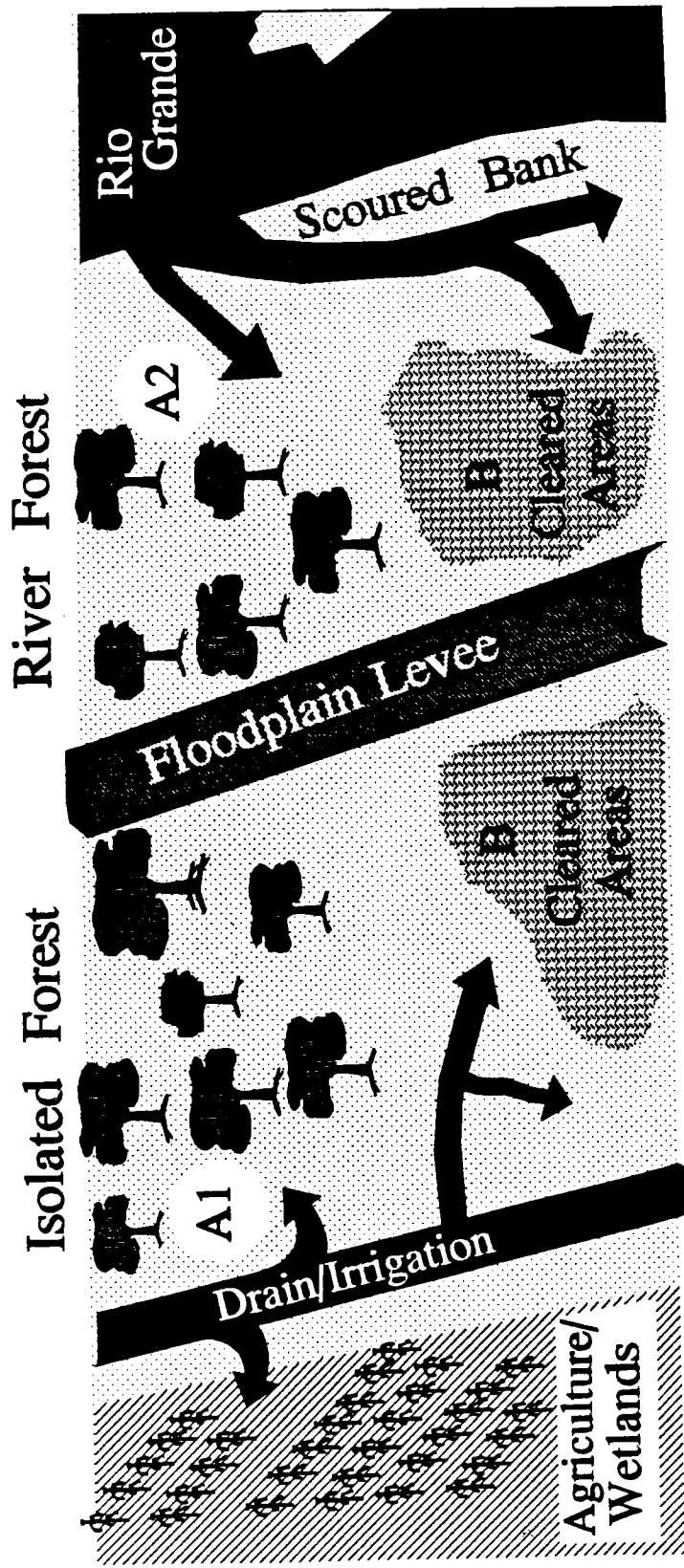


Figure 91. Proposed alternatives for bosque restoration. Pictured are examples of potential sites for restoration efforts: A1 = disconnected forest restoration, A2 = maintenance of mature forests, and B = creation of new forests.



**APPENDIX A - SUMMARY OF SOIL CHEMISTRY  
DATA, 1992 - 1995**

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APPENDIX A - 1. Summary of soil analyses for cottonwood sites, prior to flooding (September 1992) and after the first experimental flood (September 1993). Values are means for 10 samples at each site; standard errors are given in parentheses.

	1992		1993	
	Cottonwood Control	Cottonwood Flood	Cottonwood Control	Cottonwood Flood
Extractable Cations (all expressed as meq/100g)				
Sodium	2.3 (0.83)	5.0 (1.94)	0.36 (0.05)	0.62 (0.08)
Potassium	3.4 (0.43)	2.9 (0.75)	1.15 (0.22)	1.16 (0.14)
Calcium	33.5 (2.44)	34.1 (4.8)	8.33 (0.53)	9.79 (1.1)
Magnesium	5.1 (0.53)	5.2 (0.94)	1.84 (0.7)	2.14 (0.33)
Sum Cations	44.3 (3.8)	47.3 (7.3)	11.7 (0.74)	13.7 (1.5)
Cation Exchange Capacity (meq/100g)	23.4 (1.7)	23.0 (3.7)	16.5 (1.2)	24.9 (2.9)
Sodium Absorption Ratio	0.48 (0.16)	1.04 (0.38)	0.16 (0.021)	0.25 (0.024)
Texture (% of mineral)				
Sand	26 (3.7)	40 (8.6)	28 (3.3)	34 (6.7)
Silt	52 (3.0)	29 (3.0)	43 (4.1)	33 (3.0)
Clay	22 (2.8)	31 (7.6)	29 (3.8)	33 (6.4)
Mineralizable N (88 days)				
NH <sub>4</sub> (mg/kg)	1.6 (0.17)	1.3 (0.15)	1.6 (0.2)	1.04 (0.15)
NO <sub>3</sub> + NH <sub>4</sub> (mg/kg)	24.9 (5.7)	18.5 (6.2)	9.6 (1.8)	6.2 (1.4)
Field Water Content (ml/g)	0.17 (1.012)	0.17 (0.015)	0.19 (0.01)	0.19 (0.025)
50% of Water Holding Capacity (ml/g)	0.28 (0.012)	0.27 (0.017)	0.305 (0.016)	0.29 (0.041)
Organic Matter Content (%)	5.3 (0.4)	5.0 (0.5)	5.4 (0.5)	4.7 (0.4)
Conductivity (µmhos)	536 (170)	475 (150)	632 (234)	368 (88)
Total N (mg/kg)	647 (92)	537 (85)	880 (94)	656 (85)
Total P (mg/kg)	376 (25)	304 (24)	318 (16)	216 (28)
Total N / Total P	1.71 (0.22)	1.7 (0.21)	2.76 (0.27)	3.29 (0.38)
Total Organic Carbon (mg/gdw)	17.5 (1.73)	14.9 (1.75)	19.16 (1.64)	15.87 (1.76)
Biomass Carbon (mg/gdw)	0.43 (0.0378)	0.41 (0.0503)	0.52 (0.0531)	0.45 (0.0499)
Basal Respiration (mg CO <sub>2</sub> /gdw/h)	0.0016 (0.00024)	0.0016 (0.00026)	0.0021 (0.0015)	0.00016 (0.00030)
Biomass C / Total Organic C (mg/mg)	25.46 (5.062)	27.75 (5.573)	27.69 (6.526)	29.55 (8.190)
Metabolic Quotient (mg CO <sub>2</sub> /h/mg biomass C)	0.0038 (0.00083)	0.0043 (0.0020)	0.0043 (0.00082)	0.0034 (0.0017)
Total C / Total N	29.4 (2.8)	36.1 (7.9)	22.4 (1.2)	27.3 (4.3)
Total C / Total P	48.1 (5.6)	51.3 (7.1)	61.1 (5.7)	93.1 (23.7)

APPENDIX A - 2. Summary of soil analyses for cottonwood and river sites for September 1994. Values are means for 10 samples at each site; standard errors are given in parentheses.

	Cottonwood Control	Cottonwood Flood	River Control	River Flood
Extractable Cations (all expressed as meq/100g)				
Sodium	2.27 (1.07)	0.96 (0.14)	0.59 (0.14)	0.35 (0.03)
Potassium	2.81 (0.25)	1.18 (0.15)	1.89 (0.25)	0.92 (0.05)
Calcium	25.2 (2.0)	25.4 (3.2)	26.3 (2.7)	34.4 (1.8)
Magnesium	4.19 (0.43)	3.96 (0.69)	4.25 (0.58)	4.71 (0.18)
Sum Cations	34.6 (3.4)	31.5 (4.1)	33.1 (3.5)	40.4 (1.9)
Cation Exchange Capacity (meq/100g)	20.5 (1.4)	19.8 (2.4)	21.1 (2.3)	28.7 (1.6)
Sodium Absorption Ratio	0.52 (0.228)	0.25 (0.025)	0.15 (0.029)	0.08 (0.006)
Texture (% of mineral)				
Sand	36 (2.9)	42 (7.4)	36 (5.3)	18 (1.4)
Silt	44 (2.3)	30 (3.4)	38 (2.5)	43 (2.3)
Clay	19 (2.1)	29 (6.8)	27 (6.2)	39 (3.1)
Field Water Content (ml/g)	0.075 (0.009)	0.155 (0.053)	0.13 (0.022)	0.146 (0.009)
50% of Water Holding Capacity (ml/g)	0.21 (0.006)	0.23 (0.012)	0.22 (0.009)	0.27 (0.006)
Organic Matter Content (%)	5.1 (0.4)	4.6 (0.7)	4.8 (0.5)	6.3 (0.3)
Conductivity ( $\mu$ mhos)	1183 (443)	390 (109)	298 (43)	144 (8)
Total C (mg/g)	17.2 (1.8)	13.6 (2.2)	14.2 (2.0)	20.0 (1.5)
Total N (mg/kg)	1082 (115)	827 (97)	845 (85)	944 (66)
Total P (mg/kg)	424 (13)	369 (12)	349 (15)	373 (14)
Total N / Total P	2.51 (0.22)	2.29 (0.30)	2.42 (0.20)	2.55 (0.19)
Biomass Carbon (mg/gdw)	0.546 (0.039)	0.505 (0.028)	0.560 (0.055)	0.852 (0.062)
Basal Respiration (mg CO <sub>2</sub> /gdw/h)	0.002 (0.00010)	0.002 (0.00013)	0.002 (0.00030)	0.003 (0.00039)
Biomass C / Total Organic C (mg/mg)	0.034 (0.003)	0.038 (0.005)	0.042 (0.003)	0.043 (0.002)
Metabolic Quotient (mg CO <sub>2</sub> /h/mg biomass C)	0.004 (0.00031)	0.004 (0.00032)	0.004 (0.00044)	0.004 (0.00029)
Total C / Total N	16.1 (0.82)	19.2 (2.5)	16.3 (0.96)	21.4 (1.2)
Total C / Total P	40.1 (3.5)	40.0 (4.6)	41.0 (5.0)	54.4 (5.0)

APPENDIX A - 3. Summary of soil analyses for cottonwood and river sites for October 1995. Values are means for 10 samples at each site; standard errors are given in parentheses.

	Cottonwood Control	Cottonwood Flood	River Control	River Flood
Extractable Cations (all expressed as meq/100g)				
Sodium	2.6 (1.2)	0.93 (0.14)	0.47 (0.07)	0.31 (0.02)
Potassium	2.96 (0.28)	1.21 (0.17)	1.97 (0.18)	1.08 (0.03)
Calcium	28.6 (3.1)	25.1 (3.0)	19.8 (1.8)	40.4 (0.8)
Magnesium	4.27 (0.7)	3.47 (0.7)	2.87 (0.3)	5.43 (0.2)
Cation Exchange Capacity (meq/100g)	21.9 (1.7)	23.3 (3.4)	17.9 (2.1)	37.6 (1.3)
Sodium Absorption Ratio	0.55 (0.23)	0.24 (0.03)	0.14 (0.02)	0.06 (0.01)
Texture (% of mineral)				
Sand	20.5 (4.0)	31.2 (8.3)	22.4 (1.2)	13.1 (0.9)
Silt	43.8 (2.4)	25.7 (3.1)	49.4 (0.7)	55.4 (0.5)
Clay	35.6 (3.9)	43.1 (7.8)	28.1 (0.5)	31.7 (0.3)
Mineralizable N (84 days)				
NH <sub>4</sub> (mg/kg)	1.56 (0.16)	1.43 (0.13)	1.69 (0.22)	1.76 (0.07)
NO <sub>3</sub> -N (mg/kg)	20.7 (2.4)	17.3 (2.9)	23.7 (3.7)	13.4 (1.7)
NH <sub>4</sub> -N + NO <sub>3</sub> -N	22.3 (2.5)	18.7 (2.8)	25.4 (3.8)	15.3 (1.7)
Field Water Content (ml/g)	0.11 (0.013)	0.13 (0.019)	0.13 (0.015)	0.23 (0.009)
50% of Water Holding Capacity (ml/g)	0.28 (0.011)	0.30 (0.021)	0.26 (0.01)	0.38 (0.022)
Conductivity (µmhos)	759 (205)	310 (54)	339 (52)	240 (21)
Total C (mg/g)	16.8 (1.9)	12.2 (1.5)	11.1 (1.3)	22.7 (1.6)
Total N (mg/kg)	1202 (94)	984 (97)	977 (75)	955 (86)
Total P (mg/kg)	455 (9.6)	366 (18)	443 (11)	359 (12)
Total N / Total P	2.65 (0.2)	2.69 (0.2)	2.18 (0.1)	2.64 (0.2)
Biomass Carbon (mg/gdw)	0.432 (0.0337)	0.428 (0.0421)	0.477 (0.0462)	0.501 (0.0335)
Basal Respiration (mg CO <sub>2</sub> /gdw/h)	0.0018 (0.00011)	0.0016 (0.00021)	0.0019 (0.00023)	0.0021 (0.00023)

APPENDIX A - 4. Summary of soil analyses for tamarisk sites for September 1992. Values are means for 10 samples at each site; standard errors are given in parentheses.

	Tamarisk Control	Tamarisk Flood
Extractable Cations (all expressed as meq/100g)		
Sodium	1.9 (0.45)	5.7 (0.59)
Potassium	2.2 (0.38)	3.9 (0.29)
Calcium	31.3 (3.5)	44.5 (0.83)
Magnesium	4.3 (1.09)	6.7 (0.19)
Sum Cations	39.8 (5.0)	60.9 (0.71)
Cation Exchange Capacity (meq/100g)	23.0 (3.6)	31.3 (1.4)
Sodium Absorption Ratio	0.44 (0.09)	1.13 (0.12)
Texture (% of mineral)		
Sand	35 (8.4)	10 (1.2)
Silt	45 (6.0)	42 (3.5)
Clay	21 (4.7)	48 (4.1)
Mineralizable N (88 days)		
NH <sub>4</sub> (mg/kg)	1.4 (0.06)	1.1 (0.07)
NO <sub>3</sub> + NH <sub>4</sub> (mg/kg)	24.0 (4.7)	18.8 (4.1)
Field Water Content (ml/g)	0.18 (0.018)	0.24 (0.039)
50% of Water Holding Capacity (ml/g)	0.24 (0.018)	0.35 (0.014)
Organic Matter Content (%)	4.3 (0.6)	6.4 (0.4)
Conductivity (µmhos)	288 (58)	476 (87)
Total Organic Carbon (mg/gdw)	18.0 (2.35)	21.3 (1.44)
Biomass Carbon (mg/gdw)	0.664 (0.079)	0.538 (0.070)
Basal Respiration (mg CO <sub>2</sub> /gdw/h)	0.309 (0.024)	0.25 (0.079)
Biomass C / Total Organic C (mg/mg)	0.0458 (0.018)	0.0305 (0.010)
Metabolic Quotient (mg CO <sub>2</sub> /h/mg biomass C)	0.0226 (0.009)	0.0141 (0.004)

## APPENDIX B - SUMMARY OF DECOMPOSITION DATA, 1991 - 1995

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APPENDIX B - 1. Biomass of total annual litterfall (Total) and total annual cottonwood leaffall (Leaves) for cottonwood and river sites during 1991 through 1996. Values are the average total biomass per m<sup>2</sup> of all litter and of cottonwood leaves collected in 12 tubs at each site between September and the following March each year; standard error is given in parentheses. For the 1994-95 and 1995-96 litterfall seasons, values for the biomass of cottonwood leaves were measured directly; for 1992-92, 1992-93 and 1993-94, these were estimated using regression equations (see methods). Collections at river sites were begun in fall 1994.

Season	Cottonwood Control		Cottonwood Flood		River Control		River Flood	
	Total	Leaves	Total	Leaves	Total	Leaves	Total	Leaves
1991-92	234.21 (20.21)	164.53 (14.29)	263.58 (23.90)	180.74 (16.49)				
1992-93	238.19 (19.05)	167.35 (13.46)	237.43 (23.61)	162.69 (16.29)				
1993-94	297.42 (28.90)	209.22 (20.43)	212.85 (18.55)	145.73 (21.80)				
1994-95	230.55 (17.73)	159.18 (13.61)	193.57 (16.21)	127.98 (15.02)	227.19 (20.70)	147.48 (17.03)	217.45 (13.88)	188.11 (12.10)
1995-96	279.33 (18.52)	217.11 (13.51)	296.31 (27.50)	228.73 (27.50)	312.84 (29.58)	218.10 (19.52)	307.43 (17.09)	260.98 (12.42)

APPENDIX B - 2. Summary of total annual litterfall for tamarisk sites during 1991 through 1996. Values are the average total biomass per m<sup>2</sup> of litter collected in 12 tubs at each site between September and the following March each year; standard error is given in parentheses.

Season	Tamarisk Control	Tamarisk Flood
1991-92	141.77 (18.13)	151.80 (13.32)
1992-93	214.51 (18.31)	180.33 (14.38)
1993-94	181.56 (10.55)	167.46 (13.93)
1994-95	164.80 (9.70)	162.47 (11.05)
1995-96	187.31 (10.47)	191.78 (16.15)

APPENDIX B - 3. Summary of decomposition bag data for cottonwood and river sites in 1991 - 1995. Values are the mean ash-free dry-weight for leaves in five bags at each site for each collection; standard error is given in parentheses. See APPENDIX B - 5 for collection dates.

site	Collection			
	1	2	3	4
1991-92				
Cottonwood Control	4.06 (0.02)	3.15 (0.06)	2.89 (0.04)	2.73 (0.05)
Cottonwood Flood	4.01 (0.01)	2.74 (0.26)	2.95 (0.04)	2.35 (0.23)
1992-93				
Cottonwood Control	4.09 (0.02)	3.43 (0.08)	3.22 (0.06)	2.78 (0.07)
Cottonwood Flood	4.07 (0.03)	3.35 (0.05)	2.13 (0.03)	2.18 (0.03)
1993-94				
Cottonwood Control	4.08 (0.04)	3.84 (0.03)	3.68 (0.05)	3.32 (0.10)
Cottonwood Flood	4.08 (0.03)	3.82 (0.07)	1.77 (0.11)	1.78 (0.06)
1994-95				
Cottonwood Control	4.24 (0.02)	3.41 (0.04)	3.37 (0.08)	3.27 (0.06)
Cottonwood Flood	4.28 (0.03)	3.36 (0.07)	1.88 (0.05)	1.98 (0.02)
River Control	4.26 (0.03)	3.30 (0.03)	3.30 (0.03)	3.18 (0.07)
River Flood	4.20 (0.01)	3.38 (0.05)	1.71 (0.04)	1.73 (0.05)



APPENDIX B - 4. Summary of decomposition bag data for tamarisk sites in 1991 - 1995. Values are the mean ash-free dry-weight for leaves in five bags at each site for each collection; standard error is given in parentheses. See APPENDIX B - 5 for collection dates.

site	Collection			
	1	2	3	4
1991-92				
Tamarisk Control	3.86 (0.04)	2.76 (0.03)	2.31 (0.05)	1.72 (0.05)
Tamarisk Flood	3.94 (0.02)	2.76 (0.07)	2.50 (0.11)	2.76 (0.06)
1992-93				
Tamarisk Control	3.17 (0.09)	2.43 (0.11)	2.29 (0.05)	1.70 (0.05)
Tamarisk Flood	3.22 (0.12)	2.45 (0.10)	2.54 (0.10)	2.40 (0.12)
1993-94				
Tamarisk Control	3.47 (0.14)	3.35 (0.06)	2.98 (0.05)	2.50 (0.08)
Tamarisk Flood	3.59 (0.11)	3.36 (0.04)	2.35 (0.04)	1.94 (0.10)
1994-95				
Tamarisk Control	3.19 (0.13)	2.65 (0.08)	2.74 (0.13)	2.26 (0.11)
Tamarisk Flood	3.14 (0.07)	2.63 (0.08)	1.92 (0.07)	1.89 (0.06)

APPENDIX B - 5. Collection dates for decomposition bags at cottonwood, tamarisk, and river sites. Five bags were collected from each site on each date. Collection 1 was made the same day sets of bags were placed at the sites.

Season	Collection			
	1	2	3	4
1991-92	5 November 1991	21 April 1992	26 June 1992	27 October 1992
1992-93	27 October 1992	15 April 1993	25 June 1993	3 November 1993
1993-94	3 November 1993	20 April 1994	30 June 1994	7 November 1994
1994-95	7 November 1994	20 April 1995	27 June 1995 <sup>1</sup> 10 August 1995 <sup>2</sup>	7 November 1995

<sup>1</sup> cottonwood and tamarisk sites

<sup>2</sup> river sites

APPENDIX B - 6. Summary of data for decomposition log analyses for 1991 - 1995. Values are the mean ash-free dry-weight (kg) for each collection; standard error is given in parentheses. Logs were placed at cottonwood sites in June 1991 and at river sites in April 1995. N=20 for cottonwood sites in 1991, N = 16 for river sites in April 1995, N = 4 for each site in other years. Comparisons reported in the text were based on the percent of original log weight remaining at the time of collection.

Collection Date	Cottonwood Control	Cottonwood Flood	River Control	River Flood
20 June 1991 (installation, cottonwood sites)	6.435 (0.26)	6.003 (0.26)		
15 April 1993 (pre-flood)	5.676 (0.32)	5.503 (0.63)		
7 November 1994 (two floods)	6.872 (0.72)	5.768 (0.45)		
19 April 1995 (installation, river sites)			6.390 (0.49)	5.693 (0.41)
7 November 1995 (three floods, cottonwood; one flood, river)	6.334 (0.65)	4.469 (0.54)	7.380 (1.09)	6.052 (0.54)

APPENDIX B - 7. Summary of forest floor litter storage at all sites, 1991-1995. Means are for ten randomly collected 10 x 10 cm plot samples at each site for each collection date; standard error is in parentheses. River sites were added to the study in August 1994.

	Cottonwood		Cottonwood		River		Tamarisk	
	Control	Flood	Control	Flood	Control	Flood	Control	Flood
1991								
21 September	1252.63 (165.33)	646.44 (163.77)					394.22 (128.30)	508.04 (111.17)
1992								
22 April	1558.21 (82.04)	1068.46 (121.91)					388.14 (95.09)	851.84 (114.36)
23 September	1744.38 (316.74)	967.87 (285.52)					340.37 (54.04)	867.03 (179.58)
1993								
5 April	1139.49 (128.25)	928.55 (315.25)					542.52 (58.42)	1103.91 (318.48)
8 September	786.21 (212.19)	829.19 (156.93)					451.99 (53.83)	1032.58 (180.22)
1994								
5 April	1219.55 (202.19)	1229.20 (206.67)					537.48 (83.30)	1142.01 (247.65)
7-8 September	1360.52 (271.56)	1119.96 (291.23)			1858.91 (437.69)		843.91 (130.96)	1096.14 (187.00)
1995								
4-5 April	2067.59 (461.05)	1154.67 (296.60)			2276.37 (545.02)		646.08 (57.32)	894.06 (133.23)
6-7 September	1362.15 (596.96)	1055.98 (108.71)			1957.93 (474.93)		668.81 (87.03)	798.15 (269.80)

APPENDIX B - 8. Average densities ( $g / cm^3$ ) of coarse woody debris of *Populus*, *Tamarix*, and *Baccharis* used to estimate biomass in three decomposition classes. Mean values were used for samples for which species could not be determined.

Species	Decomposition Class		
	I	II	III
<u>Populus</u>	0.522	0.515	0.306
<u>Tamarix</u>	0.604	0.557	0.423
<u>Baccharis</u>	0.529	0.519	0.455
mean	0.557	0.529	0.386

APPENDIX B - 9. Average biomass values for fine woody debris, coarse woody debris, and total woody debris at cottonwood and river sites, measured in 1995. Values are mean biomass along twenty transects at each site; standard error is given in parentheses.

	Cottonwood Control	Cottonwood Flood	River Control	River Flood
Fine Woody Debris ( $\leq$ cm diameter)	11.19 (1.06)	7.66 (0.59)	5.91 (0.69)	3.90 (0.38)
Coarse Woody Debris ( $>$ 2 cm diameter)	27.60 (3.60)	26.03 (3.37)	31.17 (6.78)	9.82 (0.90)
Total Woody Debris	38.79 (3.64)	33.68 (3.51)	37.63 (6.95)	13.72 (0.94)

## APPENDIX C - SUMMARY OF VEGETATION DATA, 1991 - 1995

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APPENDIX C - 1. Plant species list for cottonwood and river sites. Some species included here were not recorded along understory vegetation transects. Nomenclature follows Kartez (1994).

Species	CC	CF	RC	RF
<b>Apocynaceae</b>				
<i>Apocynum cannabinum</i> L. Indianhemp		x		
<b>Asclepiadaceae</b>				
<i>Asclepias subverticillata</i> (Gray) Vail whorled milkweed		x		
<b>Boraginaceae</b>				
species 1			x	
<b>Chenopodiaceae</b>				
<i>Atriplex canescens</i> (Pursh) Nutt. fourwing saltbush	x			
<i>Chenopodium album</i> L. lambsquarters	x			
<b>Compositae</b>				
<i>Ambrosia psilostachya</i> DC. western ragweed	x	x		
<i>Baccharis salicifolia</i> (Ruiz & Pavón) Pers. SY = <i>Baccharis glutinosa</i> Pers. seepwillow	x	x	x	x
<i>Bahia dessecta</i> (Gray) Britt. ragleaf bahia			x	
<i>Chloracantha spinosa</i> (Benth.) Nesom spiny aster		x	x	
<i>Conyza canadensis</i> (L.) Cronq. Canadian horseweed	x	x	x	
<i>Erigeron flagellaris</i> Gray trailing fleabane	x		x	
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby broom snakeweed	x	x		
<i>Helianthus</i> sp. sunflower		x		
<i>Ratibida tagetes</i> (James) Barnh. green prairie coneflower	x	x	x	
<i>Senecio multicapitatus</i> Greenm. ex Rydb. ragwort groundsel			x	
<i>Sonchus</i> sp. 1			x	
<i>Sonchus</i> sp. 2			x	

## APPENDIX C - 1, continued.

Species	CC	CF	RC	RF
<i>Sonchus</i> sp. 3		x	x	
<i>Xanthium strumarium</i> L. rough cocklebur		x		
Cruciferae				
<i>Descurainia pinnata</i> (Walt.) Britt. white tansymustard	x	x		
<i>Descurainia sophia</i> (L.) Webb ex Prantl herb sophia	x			
Elaeagnaceae				
<i>Elaeagnus angustifolia</i> L. Russian olive		x	x	x
Euphorbiaceae				
<i>Chamaesyce serpyllifolia</i> (Pers.) Small thymeleaf sandmat		x		
Fabaceae				
<i>Amorpha fruticosa</i> L. desert indigobush	x	x		x
<i>Medicago sativa</i> L. alfalfa			x	
<i>Melilotus officinalis</i> (L.) Lam. yellow sweet clover	x	x	x	
<i>Sphaerophysa salsula</i> (Pallas) DC. red bladderpod		x	x	
<i>Prosopis pubescens</i> Benth. screwbean mesquite	x	x		
Gramineae				
<i>Aristida ternipes</i> var. <i>hamulosa</i> (Henr.) Trent poverty threeawn		x	x	
<i>Aristida purpurea</i> Nutt. purple threeawn			x	
<i>Cenchrus carolinianus</i> Walt. coastal sandbur		x		
<i>Distichlis spicata</i> (L.) Greene inland saltgrass		x		
<i>Muhlenbergia asperifolia</i> (Nees & Meyen ex Trin.) Parodi alkali muhly		x		
<i>Muhlenbergia porteri</i> Scribn. ex Beal bush muhly			x	

APPENDIX C - 1, continued.

Species	CC	CF	RC	RF
<i>Panicum obtusum</i> Kunth obtuse panicgrass		x		
<i>Setaria leucopila</i> (Scribn. & Merr.) K. Schum. streambed bristlegrass		x		
<i>Setaria glauca</i> (L.) Beauv. yellow bristlegrass		x		
<i>Sorghum halepense</i> (L.) Pers. Johnsongrass		x	x	
<i>Sporobolus airoides</i> (Torr.) Torr. alkali sacaton		x	x	
<i>Sporobolus cryptandrus</i> (Torr.) Gray sand dropseed		x	x	
<i>Sporobolus wrightii</i> Munro ex Scribn. giant sacaton			x	
<b>Juncaceae</b>				
<i>Juncus mexicanus</i> Willd. ex J.A. & J. H. Schultes Mexican rush		x		
<b>Malvaceae</b>				
<i>Sphaeralcea angustifolia</i> ssp. <i>lobata</i> (Woot.) Kearney copper globemallow	x	x		
<b>Oleaceae</b>				
<i>Forestiera pubescens</i> Nutt. var. <i>pubescens</i> <i>SY = Forestiera neomexicana</i> Gray New Mexico olive	x	x		
<b>Onagraceae</b>				
<i>Gaura parviflora</i> Dougl. ex Lehm velvetweed		x		
<b>Ranunculaceae</b>				
<i>Clematis ligusticifolia</i> Nutt. western white clematis		x	x	
<b>Salicaceae</b>				
<i>Salix gooddingii</i> Ball Goodding's willow	x	x	x	
<i>Salix exigua</i> Nutt. sandbar willow	x			
<i>Populus deltoides</i> ssp. <i>wislizenii</i> (Wats.) Eckenwalder Rio Grande cottonwood	x	x	x	x



## APPENDIX C - 1, continued.

Species	CC	CF	RC	RF
<b>Scrophulariaceae</b>				
<i>Verbascum thapsus</i> L. common mullein			x	
<b>Solanaceae</b>				
<i>Chamaesaracha sordida</i> (Dunal) Gray hairy five eyes		x		
<i>Datura wrightii</i> Regel jimsonweed	x			
<i>Lycium torreyi</i> Gray squawhorn	x	x		
<i>Physalis virginiana</i> P. Mill. Virginia groundcherry	x	x	x	
<i>Solanum elaeagnifolium</i> Cav. silverleaf nightshade	x	x	x	
<b>Tamaricaceae</b>				
<i>Tamarix ramosissima</i> Ledeb. tamarisk / saltcedar	x	x	x	x

APPENDIX C - 2. Mean understory vegetation measurements for individual species at cottonwood sites in 1993, averaged across 12 transects per site. Standard errors are in parentheses.

Species	May				September			
	Cottonwood Control		Cottonwood Flood		Cottonwood Control		Cottonwood Flood	
	mean no. inds <sup>1</sup>	mean intercept <sup>2</sup>	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Shrubs</b>								
<i>Amorpha fruticosa</i>	0.083 (0.083)	14.17 (14.17)	0.083 (0.083)	49.17 (49.17)	0.25 (0.25)	14.58 (14.58)	0.083 (0.083)	51.17 (51.17)
<i>Baccharis glutinosa</i>	2.75 (0.93)	233.58 (87.25)	0.92 (0.50)	117.08 (48.05)	4.50 (1.41)	533.00 (240.11)	1.17 (0.58)	159.25 (91.59)
<i>Forestiera neomexicana</i>	0.083 (0.083)	35.00 (35.00)	1.17 (0.44)	152.92 (56.64)	0.17 (0.11)	40.58 (28.63)	1.83 (0.55)	148.25 (59.29)
<i>Lycium torreyi</i>	0.75 (0.66)	64.50 (62.26)			0.083 (0.083)	23.42 (23.42)		
<i>Prosopis pubescens</i>							0.17 (0.17)	0.17 (0.17)
<b>Forbs</b>								
<i>Ambrosia psilostachya</i>	0.67 (0.67)	1.00 (1.00)			0.42 (0.42)	2.58 (2.58)		
<i>Apocynum cannabinum</i>							0.83 (0.75)	14.08 (13.64)
<i>Asclepias subverticillata</i>							0.083 (0.083)	1.58 (1.58)
<i>Chamaesyce serpyllifolia</i>							7.83 (7.21)	87.83 (76.91)
<i>Chenopodium album</i>	0.083 (0.083)	0.33 (0.33)			0.083 (0.083)	3.67 (3.67)		
<i>Clematis ligusticifolia</i>			0.92 (0.58)	149.92 (70.92)			1.08 (0.47)	177.67 (97.02)
<i>Conyza canadensis</i>	0.58 (0.42)	1.75 (0.95)	0.17 (0.17)	0.25 (0.25)	0.17 (0.11)	2.33 (1.74)	0.83 (0.53)	3.83 (2.21)
<i>Melilotus officinalis</i>					0.083 (0.083)	0.083 (0.083)		
<i>Physalis virginiana</i>							0.58 (0.58)	2.50 (2.50)
<i>Ratibida tagetes</i>	3.83 (1.90)	20.83 (9.88)			5.50 (2.98)	22.25 (12.06)		
<i>Solanum elaeagnifolium</i>	0.17 (0.17)	0.42 (0.42)			2.75 (1.51)	20.67 (12.20)	0.083 (0.083)	0.92 (0.92)
<i>Sphaeralcea angustifolia</i>	2.08 (1.22)	7.92 (4.46)			5.75 (3.34)	42.50 (22.43)		
<i>Sphaerophysa salsola</i>			0.083 (0.083)	0.17 (0.17)			0.42 (0.42)	4.50 (4.50)
unidentified species 1							0.083 (0.083)	0.33 (0.33)

## APPENDIX C - 2, continued.

Species	May				September			
	Cottonwood Control		Cottonwood Flood		Cottonwood Control		Cottonwood Flood	
	mean no. inds <sup>1</sup>	mean intercept <sup>2</sup>	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Grasses</b>								
<i>Aristida terniped</i> var. <i>hamulosa</i>							0.083 (0.083)	2.25 (2.25)
<i>Cenchrus pauciflorus</i>							0.17 (0.17)	0.33 (0.33)
<i>Distichlis spicata</i>			4.08 (2.42)	96.83 (73.13)			1.67 (0.87)	446.00 (235.86)
<i>Muhlenbergia asperifolia</i>							3.50 (1.95)	427.25 (237.53)
<i>Panicum obtusum</i>							0.083 (0.083)	72.75 (72.75)
<i>Setaria leucopila</i>							0.17 (0.17)	1.33 (1.33)
<i>Sorghum halepense</i>							0.083 (0.083)	2.50 (2.50)
<i>Sporobolus airoides</i>			0.17 (0.11)	14.17 (10.03)			0.25 (0.13)	35.67 (19.65)
unidentified grass			1.08 (0.57)	117.83 (81.56)	0.33 (0.33)	0.67 (0.67)	1.00 (0.75)	18.00 (16.26)
<b>Number of Species</b>								
Shrubs	4		3		4		4	
Forbs	6		3		7		9	
Grasses	0		3		1		9	
Total	10		9		12		22	
Average Number of Species per Transect	2.25 (0.41)		2.33 (0.31)		2.75 (0.55)		4.25 (0.79)	
<b>Average Total Cover (cm)</b>								
Shrubs	347.25 (108.14)		319.17 (81.39)		611.58 (253.13)		359.83 (119.36)	
Forbs	32.25 (14.75)		150.33 (71.01)		94.08 (46.51)		293.25 (138.13)	
Grasses			111.00 (74.31)		0.67 (0.67)		788.75 (507.67)	

<sup>1</sup> Mean number of individuals, averaged across 12 30-m transects.<sup>2</sup> Mean intercept length, in cm, averaged across 12 30-m transects.

APPENDIX C - 3. Mean understory vegetation measurements for individual species at cottonwood sites in 1994, averaged across 12 transects per site. Standard errors are in parentheses.

Species	May				September			
	Cottonwood Control		Cottonwood Flood		Cottonwood Control		Cottonwood Flood	
	mean no. inds <sup>1</sup>	mean intercept <sup>2</sup>	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Shrubs</b>								
<i>Amorpha fruticosa</i>	0.083 (0.083)	5.83 (5.83)	0.083 (0.083)	33.08 (33.08)	0.25 (0.18)	20.33 (14.65)	0.17 (0.17)	32.33 (32.33)
<i>Baccharis glutinosa</i>	3.33 (0.86)	263.75 (64.99)	1.17 (0.47)	89.0 (47.26)	3.67 (0.98)	397.83 (123.59)	1.42 (0.51)	228.58 (111.29)
<i>Forestiera neomexicana</i>	0.083 (0.083)	24.42 (24.42)	1.50 (0.53)	163.8 (53.01)	0.083 (0.083)	29.17 (29.17)	1.83 (0.83)	177.83 (66.07)
<i>Lycium torreyi</i>	0.83 (0.75)	75.33 (70.65)			0.33 (0.22)	58.67 (56.26)	0.083 (0.083)	2.083 (2.083)
<i>Prosopis pubescens</i>			0.083 (0.083)	0.83 (0.83)				
<b>Forbs</b>								
<i>Apocynum cannabinum</i>			0.083 (0.083)	0.25 (0.25)			0.33 (0.26)	6.67 (5.25)
<i>Asclepias subverticillata</i>							0.083 (0.083)	1.00 (1.00)
<i>Chamaesyce serpyllifolia</i>							0.17 (0.11)	1.08 (0.74)
<i>Clematis ligusticifolia</i>			1.0 (0.46)	95.5 (54.56)			0.42 (0.26)	75.67 (52.52)
<i>Conyza canadensis</i>							2.00 (1.40)	11.42 (8.82)
<i>Physalis virginiana</i>							0.17 (0.17)	1.00 (1.00)
<i>Ratibida tagetes</i>	2.83 (1.58)	9.50 (5.42)			4.75 (2.50)	14.33 (8.57)		
<i>Solanum elaeagnifolium</i>	0.083 (0.083)	0.083 (0.083)			2.17 (1.40)	11.17 (7.46)	0.083 (0.083)	2.17 (2.17)
<i>Sphaeralcea angustifolia</i>	1.17 (0.91)	2.75 (1.83)			3.17 (1.56)	13.67 (6.92)		
<i>Sphaerophysa salsola</i>			0.083 (0.083)	0.83 (0.83)			0.33 (0.33)	3.00 (3.00)

APPENDIX C - 3, continued.

Species	May				September			
	Cottonwood Control		Cottonwood Flood		Cottonwood Control		Cottonwood Flood	
	mean no. inds <sup>1</sup>	mean intercept <sup>2</sup>	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Grasses</b>								
<i>Distichlis spicata</i>			0.67 (0.47)	37.92 (26.09)			0.58 (0.34)	79.83 (50.87)
<i>Muhlenbergia asperifolia</i>			1.92 (1.16)	311.83 (167.60)			2.58 (1.64)	324.92 (168.21)
<i>Panicum obtusum</i>			0.67 (0.43)	71.92 (57.44)			0.42 (0.34)	87.25 (84.47)
<i>Setaria leucopila</i>			0.17 (0.17)	2.17 (2.17)			0.17 (0.17)	7.50 (7.50)
<i>Sorghum halpense</i>							0.083 (0.083)	3.33 (3.33)
<i>Sporobolus airoides</i>			0.17 (0.11)	16.58 (11.96)			0.17 (0.11)	20.50 (15.23)
<i>Sporobolus cryptandrus</i>			0.083 (0.083)	4.00 (4.00)				
<b>Number of Species</b>								
Shrubs	4		4		4		4	
Forbs	3		3		3		8	
Grasses	0		6		0		6	
Total	7		13		7		18	
Average Number of Species per Transect	1.83 (0.30)		3.00 (0.49)		2.25 (0.35)		3.75 (0.51)	
<b>Average Total Cover (cm)</b>								
Shrubs	369.33 (86.11)		286.75 (76.85)		506.00 (129.92)		440.83 (148.05)	
Forbs	12.33 (6.73)		96.58 (54.43)		39.17 (22.16)		102.00 (54.67)	
Grasses			444.42 (241.55)				523.33 (282.21)	

<sup>1</sup> Mean number of individuals, averaged across 12 30-m transects.

<sup>2</sup> Mean intercept length, in cm, averaged across 12 30-m transects.

APPENDIX C - 4. Mean understory vegetation measurements for individual species at river sites in 1994, averaged across 10 transects per site. Standard errors are in parentheses.

Species	September			
	River Control		River Flood	
	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Shrubs</b>				
<i>Amorpha fruticosa</i>			0.50 (0.50)	54.00 (54.0)
<i>Baccharis glutinosa</i>	1.30 (0.45)	128.30 (46.24)	0.50 (0.22)	49.20 (32.48)
<i>Elaeagnus angustifolia</i>	0.10 (0.10)	49.0 (49.0)	0.10 (0.10)	48.00 (48.00)
<b>Forbs</b>				
<i>Chloracantha spinosa</i>	0.30 (0.30)	11.60 (11.60)		
<i>Clematis ligusticifolia</i>	0.10 (0.10)	0.20 (0.20)		
<i>Melilotus officinalis</i>	0.20 (0.20)	1.40 (1.40)		
<i>Ratibida tagetes</i>	5.90 (3.85)	29.50 (18.61)		
<i>Senecio multicapitatus</i>	0.10 (0.10)	0.90 (0.90)		
<i>Bahia dissecta</i>	0.10 (0.10)	0.20 (0.20)		
<i>Solanum elaeagnifolium</i>	0.60 (0.43)	4.50 (4.07)		
<i>Sphaerophysa salsola</i>	0.20 (0.20)	6.00 (6.00)		
<b>Grasses</b>				
<i>Aristida ternipes</i> var. <i>hamulosa</i>	0.20 (0.20)	4.20 (4.20)		
<i>Sorghum halpense</i>	0.20 (0.20)	1.80 (1.80)		
<i>Sporobolus airoides</i>	0.20 (0.13)	41.50 (29.19)		
<i>Sporobolus cryptandrus</i>	0.20 (0.13)	2.50 (2.39)		
<b>Number of Species</b>				
Shrubs		2		3
Forbs		8		0
Grasses		4		0
Total		14		3

APPENDIX C - 4, continued

Species	September			
	River Control		River Flood	
	mean no. inds	mean intercept	mean no. inds	mean intercept
Average Number of Species per Transect	2.40 (0.72)		0.60 (0.22)	
Average Total Cover (cm)				
Shrubs	177.30 (58.43)		151.20 (69.88)	
Forbs	54.30 (26.66)			
Grasses	50.00 (29.85)			

<sup>1</sup> Mean number of individuals, averaged across 10 30-m transects.

<sup>2</sup> Mean intercept length, in cm, averaged across 10 30-m transects.

APPENDIX C - 5. Mean understory vegetation measurements for individual species at cottonwood sites in 1995, averaged across 12 transects per site. Standard errors are in parentheses.

Species	May				September			
	Cottonwood Control		Cottonwood Flood		Cottonwood Control		Cottonwood Flood	
	mean no. inds <sup>1</sup>	mean intercept <sup>2</sup>	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Shrubs</b>								
<i>Amorpha fruticosa</i>	0.083 (0.083)	8.33 (8.33)	0.083 (0.083)	26.67 (26.67)	0.17 (0.17)	9.58 (9.58)	0.083 (0.083)	47.92 (47.92)
<i>Baccharis glutinosa</i>	3.67 (0.85)	318.83 (74.98)	1.25 (0.66)	87.08 (44.66)	5.00 (1.70)	484.17 (134.03)	1.25 (0.64)	205.92 (99.54)
<i>Forestiera neomexicana</i>	0.083 (0.083)	36.67 (36.67)	2.00 (0.83)	173.25 (65.36)	0.083 (0.083)	37.50 (37.50)	2.08 (0.73)	256.42 (108.41)
<i>Lycium torreyi</i>	0.33 (0.22)	58.67 (58.12)			1.50 (1.25)	90.08 (80.20)		
<b>Forbs</b>								
<i>Apocynum cannabinum</i>							0.42 (0.26)	12.67 (7.20)
<i>Asclepias subverticillata</i>			0.17 (0.17)	1.67 (1.67)			0.25 (0.25)	4.67 (4.67)
<i>Chamaesyce serpyllifolia</i>							1.67 (1.18)	59.33 (56.23)
<i>Chenopodium album</i>	0.25 (0.25)	0.58 (0.58)			0.33 (0.33)	1.50 (1.50)		
<i>Clematis ligusticifolia</i>			0.42 (0.34)	60.83 (41.31)			0.42 (0.29)	22.25 (16.43)
<i>Conyza canadensis</i>			4.33 (3.63)	25.33 (19.18)	0.25 (0.18)	4.25 (3.58)	1.42 (0.68)	71.83 (58.03)
<i>Descurainia pinnata</i>	0.67 (0.67)	3.08 (3.08)	0.25 (0.25)	0.67 (0.67)				
<i>Descurainia sophia</i>	0.83 (0.83)	1.67 (1.67)						
<i>Helianthus sp.</i>							0.083 (0.083)	1.17 (1.17)
<i>Melilotus officinalis</i>			0.083 (0.083)	0.33 (0.33)				
<i>Physalis virginiana</i>							0.50 (0.50)	3.33 (3.33)
<i>Ratibida tagetes</i>	3.08 (1.75)	15.42 (8.23)			3.92 (2.09)	19.08 (12.15)		
<i>Solanum elaeagnifolium</i>	0.083 (0.083)	0.083 (0.083)			2.00 (1.29)	12.33 (7.38)	0.083 (0.083)	0.083 (0.083)
<i>Sonchus sp. 3</i>							0.25 (0.18)	0.33 (0.26)
<i>Sphaeralcea angustifolia</i>	3.42 (1.96)	12.25 (6.10)			4.25 (2.19)	21.58 (11.41)		
<i>Sphaerophysa salsola</i>							0.083 (0.083)	0.83 (0.83)



APPENDIX C - 5, continued.

Species	May				September			
	Cottonwood Control		Cottonwood Flood		Cottonwood Control		Cottonwood Flood	
	mean no. inds <sup>1</sup>	mean intercept <sup>2</sup>	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Grasses</b>								
<i>Cenchrus pauciflorus</i>							0.083 (0.083)	0.083 (0.083)
<i>Distichlis spicata</i>			0.83 (0.53)	44.50 (29.43)			0.33 (0.19)	76.25 (45.38)
<i>Muhlenbergia asperifolia</i>			1.67 (0.96)	397.42 (232.42)			3.08 (1.69)	428.17 (229.95)
<i>Panicum obtusum</i>			0.17 (0.11)	70.75 (70.21)			1.08 (0.76)	105.67 (86.01)
<i>Setaria leucopila</i>			0.083 (0.083)	1.33 (1.33)			0.17 (0.17)	12.92 (12.92)
<i>Setaria glauca</i>							0.083 (0.083)	2.08 (2.08)
<i>Sorghum halpense</i>							0.083 (0.083)	6.67 (6.67)
<i>Sporobolus airoides</i>			0.17 (0.11)	9.08 (6.16)			0.33 (0.22)	26.75 (18.29)
unidentified grass	0.083 (0.083)	0.083 (0.083)						
<b>Number of Species</b>								
Shrubs		4		3		4		3
Forbs		6		5		5		10
Grasses		1		5		0		8
Total		11		13		9		21
Average Number of Species per Transect		2.25 (0.43)		2.92 (0.43)		2.42 (0.50)		4.25 (0.83)
<b>Average Total Cover (cm)</b>								
Shrubs		422.50 (83.55)		287.00 (94.13)		621.33 (144.75)		510.25 (151.57)
Forbs		33.08 (17.33)		88.83 (47.05)		58.75 (31.89)		176.50 (87.06)
Grasses				523.08 (313.93)				658.50 (343.06)

<sup>1</sup> Mean number of individuals, averaged across 12 30-m transects.

<sup>2</sup> Mean intercept length, in cm, averaged across 12 30-m transects.

APPENDIX C - 6. Mean understory vegetation measurements for individual species at river sites in 1995, averaged across 10 transects per site. Standard errors are in parentheses.

Species	May				September			
	River Control		River Flood		River Control		River Flood	
	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Shrubs</b>								
<i>Amorpha fruticosa</i>			0.20 (0.20)	8.50 (8.50)			0.50 (0.50)	47.70 (47.70)
<i>Baccharis glutinosa</i>	0.80 (0.33)	67.70 (27.69)	0.50 (0.22)	45.00 (28.94)	1.60 (0.52)	137.60 (47.11)	0.70 (0.40)	34.90 (15.38)
<i>Elaeagnus angustifolia</i>	0.30 (0.21)	84.50 (56.34)	0.10 (0.10)	0.45 (0.45)	0.30 (0.21)	45.30 (44.42)	0.10 (0.10)	50.00 (50.00)
<b>Forbs</b>								
Boraginaceae sp.	0.20 (0.20)	0.20 (0.20)						
<i>Chloracantha spinosa</i>					0.10 (0.10)	2.10 (2.10)		
<i>Coryza canadensis</i>	6.10 (4.19)	9.10 (5.94)			1.90 (1.46)	10.20 (7.04)		
<i>Descurainia pinnata</i>	0.40 (0.40)	0.31 (0.31)						
<i>Erigeron flagellaris</i>	0.20 (0.20)	0.20 (0.20)						
<i>Medicago sativa</i>	0.20 (0.20)	1.20 (1.20)						
<i>Melilotus officinalis</i>					0.90 (0.80)	23.80 (18.36)		
<i>Ratibida tagetes</i>	3.20 (2.24)	13.30 (9.37)			7.10 (4.41)	19.10 (11.79)		
<i>Senecio multicapitatus</i>					0.10 (0.10)	1.00 (1.00)		
<i>Solanum elaeagnifolium</i>	0.10 (0.10)	0.20 (0.20)			0.70 (0.30)	3.70 (1.58)		
<i>Sonchus</i> sp. 1	0.10 (0.10)	0.10 (0.10)						
<i>Sonchus</i> sp. 2	0.30 (0.30)	0.60 (0.60)			0.30 (0.21)	3.80 (2.80)		
<i>Sonchus</i> sp. 3	0.20 (0.13)	0.40 (0.27)						
<i>Sphaerophysa salsola</i>	0.10 (0.10)	1.50 (1.50)			0.60 (0.60)	3.90 (3.90)		

APPENDIX C - 6, continued

Species	May				September			
	River Control		River Flood		River Control		River Flood	
	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept	mean no. inds	mean intercept
<b>Grasses</b>								
<i>Aristida turnipes</i> var. <i>hamulosa</i>					0.10 (0.10)	4.50 (4.50)		
<i>Aristida purpurea</i>	0.10 (0.10)	2.80 (2.80)						
<i>Muhlenbergia asperifolia</i>					0.10 (0.10)	0.60 (0.60)		
<i>Muhlenbergia porteri</i>	0.10 (0.10)	1.70 (1.70)						
<i>Panicum obtusum</i>					0.40 (0.22)	4.10 (2.88)		
<i>Sporobolus airoides</i>					0.40 (0.22)	41.30 (25.81)		
<i>Sporobolus wrightii</i>	0.10 (0.10)	27.50 (27.50)						
<b>Number of Species</b>								
Shrubs		2		3		2		3
Forbs		11		0		8		0
Grasses		3		0		4		0
Total		16		3		14		3
Average Number of Species per Transect		2.80 (0.63)		0.60 (0.22)		3.60 (0.91)		0.60 (0.22)
<b>Average Total Cover (cm)</b>								
Shrubs		152.20 (51.67)		53.95 (28.73)		182.90 (53.08)		132.60 (66.19)
Forbs		27.20 (12.75)				67.60 (31.29)		
Grasses		32.00 (27.37)				50.50 (27.36)		

<sup>1</sup> Mean number of individuals, averaged across 10 30-m transects.

<sup>2</sup> Mean intercept length, in cm, averaged across 10 30-m transects.

APPENDIX C - 7. Herbaceous understory biomass production (clipped plot samples) at cottonwood sites in 1992 through 1995. Values are the mean biomass (grams per m<sup>2</sup>) for ten (or fewer<sup>1</sup>) plots; standard error is given in parentheses. Open collections were made in locations with 100% sky visible overhead. Canopy collections were made at locations with 100% canopy cover overhead.

	Cottonwood Control			Cottonwood Flood		
	N <sup>1</sup>	open	canopy	N <sup>1</sup>	open	canopy
1992	9					
forbs		25.30 (9.75)	10.58 (6.66)		57.76 (16.60)	9.18 (8.61)
grasses		-	-		-	1.38 (1.38)
1993						
forbs		28.17 (14.81)	17.45 (15.56)		3.83 (4.05)	0.69 (0.69)
grasses		0.18 (0.14)	-		2.73 (1.94)	7.49 (6.24)
1994	6			3		
forbs		15.00 (4.82)	4.50 (4.46)		0.65 (0.65)	0.03 (0.03)
grasses		-	-		109.22 (46.23)	13.84 (13.77)
1995	6			6		
forbs		30.70 (11.14)	4.42 (2.65)		8.43 (4.27)	-
grasses		2.41 (2.41)	-		30.26 (20.10)	12.86 (12.86)

<sup>1</sup> Only sample sizes less than 10 are indicated; these are for open locations only and represent places where no open location could be found. Sample size is 10 for all other collections.

APPENDIX C - 8. Herbaceous understory biomass production (clipped plot samples) at river sites in 1994 through 1995. Values are the mean biomass (grams per m<sup>2</sup>) for ten plots; standard error is given in parentheses.

	River Control	River Flood
1994		
forbs	0.03 (0.03)	0.26 (0.26)
1995		
forbs	17.98 (14.42)	-
grass	3.92 (2.96)	-

APPENDIX C - 9. Herbaceous understory biomass production (clipped plot samples) at tamarisk sites in 1991 through 1995. Values are the mean biomass (grams per m<sup>2</sup>) for ten plots; standard error is given in parentheses.

	Tamarisk Control	Tamarisk Flood
1991		
forbs <sup>1</sup>	20.53 (9.17)	0.14 (0.09)
1992		
forbs	28.63 (11.54)	19.84 (9.89)
grass	-	-
1993		
forbs	0.61 (0.36)	1.35 (0.91)
grass	0.20 (0.20)	-
1994		
forbs	0.02 (0.01)	0.16 (0.16)
grass	-	-
1995		
forbs	6.47 (2.64)	0.11 (0.10)
grass	0.07 (0.07)	8.51 (8.51)

<sup>1</sup> Samples in 1991 were not separated into forbs and grasses

APPENDIX C - 10. Vegetation structure estimates for cottonwood sites, calculated from foliage density measurements taken 3 - 4 July 1991, 7 July 1994, and 7 July 1995.

	Height Class			Total
	0.15-0.5m	1.0-2.0m	3.0-5.0m	
<b>Mean Total Density</b> (m <sup>2</sup> /m <sup>3</sup> )				
Control Site - 1991	1.54	1.29	0.96	3.78
1994	0.56	0.88	0.61	2.05
1995	0.80	1.02	0.68	2.50
Flood Site - 1991	2.20	1.71	1.19	5.10
1994	0.63	0.87	0.74	2.24
1995	0.77	0.83	0.62	2.22
<b>Patchiness Index</b> (s <sup>2</sup> )				
Control Site - 1991	0.47	0.65	0.22	1.35
1994	0.03	0.09	0.06	0.18
1995	0.09	0.12	0.09	0.30
Flood Site - 1991	0.28	0.14	0.12	0.55
1994	0.07	0.09	0.06	0.22
1995	0.07	0.02	0.02	0.11
<b>Foliage Height Diversity</b>				
Control Site - 1991				0.47
1994				0.47
1995				0.47
Flood Site - 1991				0.46
1994				0.47
1995				0.48

APPENDIX C-11. Foliage density estimates used for calculating patchiness and foliage height diversity at cottonwood sites. Values at each height for each plot reflect measurements taken at three points along the transect. Measurements taken 3 - 4 July 1991, 7 July 1994 and 7 July 1995.

Site	Plot	Foliage density (m <sup>2</sup> /m <sup>3</sup> )					
		0.15m	0.50m	1.0m	2.0m	3.0m	5.0m
1991							
Control	1	0.84	0.64	0.77	0.50	0.47	0.34
	2	0.19	2.51	0.15	0.19	0.16	0.13
	3	1.33	1.35	0.89	0.16	0.20	1.27
	4	0.23	0.52	0.83	3.06	1.65	0.37
	5	0.81	0.13	0.20	0.25	0.20	0.26
	6	0.30	0.37	0.37	0.34	0.43	0.27
Flood	1	0.55	0.83	0.49	0.50	0.36	0.26
	2	2.21	0.69	0.68	0.78	0.71	0.51
	3	1.63	1.25	1.32	1.14	0.64	0.34
	4	0.40	0.43	0.54	0.48	0.42	0.35
	5	0.82	1.03	1.12	0.56	0.78	0.39
	6	1.21	0.72	1.07	1.58	1.54	0.83
1994							
Control	1	0.25	0.54	0.70	0.47	0.26	0.20
	2	0.19	0.26	0.42	0.17	0.15	0.12
	3	0.13	0.28	0.87	0.58	0.18	0.68
	4	0.29	0.28	0.43	0.54	0.39	0.40
	5	0.46	0.16	0.23	0.26	0.21	0.21
	6	0.27	0.24	0.31	0.31	0.46	0.34
Flood	1	0.15	0.19	0.17	0.31	0.22	0.24
	2	0.38	0.42	0.35	0.43	0.19	0.31
	3	0.22	0.28	0.32	0.69	0.75	0.19
	4	0.12	0.31	0.34	0.41	0.31	0.28
	5	0.17	0.40	0.44	1.04	0.50	0.51
	6	0.79	0.34	0.35	0.35	0.50	0.45



APPENDIX C - 11, continued.

Site	Plot	Foliage density (m <sup>2</sup> /m <sup>3</sup> )					
		0.15m	0.50m	1.0m	2.0m	3.0m	5.0m
1995							
Control	1	0.30	0.60	0.52	0.37	0.22	0.49
	2	0.24	0.27	0.33	0.22	0.13	0.19
	3	0.29	0.79	1.00	0.69	0.20	0.87
	4	0.42	0.59	0.68	0.75	0.53	0.42
	5	0.67	0.15	0.34	0.25	0.21	0.26
	6	0.16	0.31	0.39	0.59	0.35	0.23
Flood	1	0.16	0.18	0.31	0.31	0.24	0.35
	2	0.73	0.33	0.41	0.34	0.20	0.29
	3	0.22	0.36	0.37	0.35	0.24	0.24
	4	0.53	0.37	0.35	0.41	0.33	0.29
	5	0.24	0.48	0.47	0.67	0.56	0.20
	6	0.57	0.46	0.48	0.51	0.36	0.41

APPENDIX C - 12. Density estimates for tree and shrub species at cottonwood sites in May 1993, prior to flooding. Estimates are the mean number of individuals per hectare, averaged across twelve transects per site; standard error is given in parentheses.

	< 1 meter		> 1 meter		dead	
	control site	flood site	control site	flood site	control site	flood site
<i>Amorpha fruticosa</i>	2.78 (2.78)	72.22 (57.85)	8.33 (5.98)	22.22 (14.98)		
<i>Atriplex canescens</i>			2.78 (2.78)			
<i>Baccharis glutinosa</i>	205.54 (101.65)	55.55 (27.01)	1158.22 (327.73)	361.08 (105.39)	261.09 (89.12)	
<i>Forestiera neomexicana</i>	5.56 (5.56)	116.66 (56.18)	2.78 (2.78)	461.07 (164.30)		
<i>Gutierrezia sarothrae</i>	2.78 (2.78)	25.00 (25.00)				
<i>Lycium torreyi</i>	38.89 (35.96)		119.43 (116.44)			
<i>Populus deltoides</i>	2.78 (2.78)	2.78 (2.78)	383.30 (111.94)	794.37 (243.92)	50.00 (22.66)	102.77 (32.68)
<i>Prosopis pubescens</i>			2.78 (2.78)	11.11 (7.49)		
<i>Salix gooddingii</i>	5.56 (5.56)		63.88 (13.89)	30.55 (10.43)	2.78 (2.78)	
<i>Tamarix ramosissima</i>		111.10 (51.79)	1285.98 (474.30)	2610.85 (609.64)	16.67 (13.91)	19.44 (13.27)

APPENDIX C - 13. Density estimates for tree and shrub species at cottonwood sites in October 1995, reflecting three seasons of flooding at Cottonwood Flood. Estimates are the mean number of individuals per hectare, averaged across twelve transects per site; standard error is given in parentheses.

	< 1 meter		> 1 meter		dead	
	control site	flood site	control site	flood site	control site	flood site
<i>Amorpha fruticosa</i>	8.33 (8.33)	8.33 (8.33)	11.11 (6.27)	55.55 (35.37)		
<i>Atriplex canescens</i>			2.78 (2.78)			
<i>Baccharis glutinosa</i>	144.43 (53.07)	33.33 (17.41)	1183.22 (319.68)	369.41 (94.93)	116.66 (41.33)	13.89 (11.20)
<i>Forestiera neomexicana</i>		72.22 (28.37)		436.07 (162.89)		
<i>Gutierrezia sarothrae</i>		5.56 (5.56)				5.56 (5.56)
<i>Lycium torreyi</i>	366.63 (345.96)		133.32 (127.38)			
<i>Populus deltoides</i>			358.30 (100.84)	766.59 (240.66)	52.77 (28.26)	122.21 (35.37)
<i>Prosopis pubescens</i>			2.78 (2.78)	2.78 (2.78)		
<i>Salix gooddingii</i>			66.66 (15.35)	30.55 (10.43)	13.89 (6.43)	2.78 (2.78)
<i>Salix exigua</i>			2.78 (2.78)			
<i>Tamarix ramosissima</i>	25.00 (13.05)	74.99 (34.84)	1183.22 (471.40)	2452.53 (570.97)	47.22 (17.14)	13.89 (6.43)

APPENDIX C - 14. Density estimates for tree and shrub species at river sites in October 1995. Estimates are the mean number of individuals per hectare, averaged across twelve transects per site; standard error is given in parentheses.

	< 1 meter		> 1 meter		dead	
	control site	flood site	control site	flood site	control site	flood site
<i>Amorpha fruticosa</i>		3.33 (3.33)		63.33 (63.33)		
<i>Baccharis glutinosa</i>	26.66 (11.97)		269.97 (77.20)	106.66 (22.66)	3.33 (3.33)	
<i>Elaeagnus angustifolia</i>			30.00 (16.06)			
<i>Forestiera neomexicana</i>			3.33 (3.33)	6.67 (4.44)		
<i>Populus deltoides</i>			99.99 (26.29)	443.29 (41.58)	30.00 (10.48)	40.00 (10.89)
<i>Salix gooddingii</i>			10.00 (7.11)			
<i>Tamarix ramosissima</i>	66.66 (27.66)	73.33 (15.55)	4909.51 (612.18)	4239.58 (502.78)	186.65 (46.40)	2099.79 (637.76)

## APPENDIX D - SUMMARY OF SOIL BACTERIA AND FUNGI DATA, 1993 - 1995

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APPENDIX D - 1. Summary of microbial parameters from soils collected at cottonwood sites before and after flooding in 1993, 1994, and 1995. Values are means of 10 samples collected from each site; standard errors are given in parentheses. Statistical comparisons were made for both sites across all collection dates; within each row, means with different letters are significantly different at  $P < 0.01$ .

	1993				1994				1995			
	pre-flood		post-flood		pre-flood		post-flood		pre-flood		post-flood	
	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF
Microbial Biomass Carbon (x 10 <sup>2</sup> µg g <sup>-1</sup> soil)	3.3 (0.4) b	3.8 (0.5) b	2.0 (0.1) a	6.0 (0.6) d	3.7 (0.3) b	3.9 (0.4) b	4.0 (0.4) b	5.3 (0.2) d	3.4 (0.4) b	4.6 (0.3) c	3.6 (0.3) b	5.9 (0.8) d
Total Bacteria (x 10 <sup>7</sup> c.f.u. g <sup>-1</sup> soil)*	38 (4) b	46 (3) b	43 (6) b	40 (4) b	29 (5) a	36 (4) b	37 (6) b	59 (4) c	26 (3) a	43 (4) b	39 (4) b	66 (6) c
Aerobic Heterotrophic Bacteria (x 10 <sup>5</sup> c.f.u. g <sup>-1</sup> soil)*	36 (3) a	40 (3) a	53 (4) b	37 (3) a	35 (4) a	74 (6) c	49 (10) ab	86 (9) c	37 (4) a	80 (12) c	42 (7) ab	82 (8) c
Streptomyces spp. (x 10 <sup>5</sup> c.f.u. g <sup>-1</sup> soil)*	24 (2) b	29 (1) c	16 (4) a	21 (1) ab	21 (5) ab	30 (5) bc	24 (6) ab	29 (8) b	27 (9) ab	33 (10) b	23 (5) ab	27 (6) b
Chitin decomposers (x 10 <sup>5</sup> c.f.u. g <sup>-1</sup> soil)*	64 (2) a	65 (1) a	75 (6) b	62 (2) a	58 (12) ab	70 (8) b	62 (8) ab	76 (5) b	69 (10) ab	75 (5) ab	70 (4) ab	56 (12) a
Cellulose decomposers (x 10 <sup>5</sup> c.f.u. g <sup>-1</sup> soil)*	54 (2) b	52 (5) b	20 (3) a	52 (5) b	63 (4) c	69 (8) c	48 (4) b	93 (6) d	53 (4) b	73 (10) c	46 (5) b	94 (7) d
Total Fungi (x 10 <sup>3</sup> g <sup>-1</sup> soil)	37 (4) ab	42 (2) a	67 (8) c	34 (5) a	32 (3) a	43 (6) b	45 (3) b	69 (5) c	31 (4) a	47 (3) b	36 (4) ab	82 (9) c
Total Hyphal Lengths (cm g <sup>-1</sup> soil)	8 (1) a	10 (1) ab	10 (0.5) a	16 (0.8) c	9 (3) a	13 (3) a	14 (5) bc	23 (2) d	8 (2) ab	11 (2) ab	12 (3) ab	20 (4) d
Basidiomycete Hyphal Lengths (cm g <sup>-1</sup> soil)	3 (0.4) b	3 (0.7) b	1 (0.1) a	2 (0.5) b	3 (1) b	5 (3) bc	2 (0) ab	7 (2) c	3 (2) b	5 (2) b	2 (1) ab	8 (2) c
VAM spore numbers (per 100 g soil)	27 (4) c	42 (10) d	14 (5) b	5 (1) a	26 (5) c	30 (3) d	17 (7) bc	22 (4) c	30 (7) d	34 (3) d	16 (3) b	19 (3) bc
Mycorrhizal Inoculum Potential (% infection)	24 (4) a	30 (4) a	32 (4) a	50 (4) b	32 (4) a	34 (7) a	35 (4) a	56 (9) b	31 (8) a	38 (5) a	33 (9) a	56 (5) b
Root Length Colonized (%)	23 (3) b	29 (4) b	11 (4) a	26 (2) b	45 (4) d	33 (6) c	48 (4) cd	49 (7) de	38 (3) c	39 (4) cd	40 (6) cd	56 (5) e

Appendix D - 1, continued.

	1993				1994				1995			
	pre-flood		post-flood		pre-flood		post-flood		pre-flood		post-flood	
	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF
No. of VAM <sup>†</sup> species	6 (0)	6 (0)	4 (1)	4(0.5)	6 (2)	6 (0)	6 (0)	6 (0)	6(0)	6 (0)	6 (0)	6 (0)
No. of ECM <sup>‡</sup> species	4 (1)	4 (2)	4(0.5)	6 (1)	5(1)	5 (0)	4 (3)	4(0)	5 (1)	4 (0)	4 (0)	4 (0)
Dehydrogenase <sup>¶</sup> µg g <sup>-1</sup> h <sup>-1</sup>					3.21 (0.47)	3.56 (0.41)	4.19 (0.45)	9.26 (0.62)	2.72 (0.86)	3.90 (0.37)	3.75 (0.40)	9.4 (0.66)
					a	ab	b	c	a	b	ab	c

\* c.f.u. = colony forming units per gram of dry-weight soil

† = Mean number of VAM (vesicular-arbuscular mycorrhizal fungi)

‡ = Mean number of ECM (ectomycorrhizal fungi)

¶ = denitrification enzyme activity not measured in 1993

APPENDIX D - 2. Summary of microbial parameters from soils collected at river sites before and after flooding in 1995. Values are means of 10 samples collected from each site; standard errors are given in parentheses. Statistical comparisons were made between sites across both collections; within each row, means with different letters are significantly different at  $P < 0.01$ .

	1995			
	pre-flood		post-flood	
	RC	RF	RC	RF
Microbial Biomass Carbon ( $\times 10^2 \mu\text{g g}^{-1}$ soil)	3 (0.6) a	4 (0.6) a	3 (0.7) a	7 (1.3) b
Total Bacteria ( $\times 10^7$ c.f.u. $\text{g}^{-1}$ soil)*	10 (3) a	11 (3) a	20 (4) b	44 (4) c
Aerobic Heterotrophic Bacteria ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	8 (4) a	8 (3) a	16 (3) b	43 (10) c
Streptomyces spp. ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	9 (4)	11 (2)	13 (3)	21 (11)
Chitin decomposers ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	18 (5) a	20 (5) a	21 (4) a	31 (5) b
Cellulose decomposers ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	42 (6) a	38 (7) a	47 (4) a	78 (11) b
Total Fungi ( $\times 10^3$ $\text{g}^{-1}$ soil)	10 (3) a	12 (2) a	15 (5) a	34 (5) a
Total Hyphal Lengths ( $\text{cm g}^{-1}$ soil)	8 (0.7) b	10 (1.8) bc	7 (1) a	13 (18) c
Basidiomycete Hyphal Lengths ( $\text{cm g}^{-1}$ soil)	1 (0.3)	1 (0.5)	1 (0.4)	1 (0.4)
VAM spore numbers (per 100 g soil)	3 (1)	4 (2)	3 (2)	8 (5)
Mycorrhizal Inoculum Potential (% infection)	2 (2.5) a	3.5 (1.5) a	2 (1.5) a	9.1(4) b
Root Length Colonized (%)	5 (4)	7(4)	5 (6)	6 (3)
No. of VAM <sup>†</sup> species	1 (1)	1(1)	1(0)	2 (1)
No. of ECM <sup>‡</sup> species	0.5 (1)	0.6 (0.8)	0	1 (0.7)
Dehydrogenase	4 (0.8) a	3.4 (0.4) a	5 (0.2) a	7 (1.3) b

\* c.f.u. = colony forming units per gram of dry-weight soil

<sup>†</sup> = Mean number of VAM (vesicular-arbuscular mycorrhizal fungi)

<sup>‡</sup> = Mean number of ECM (ectomycorrhizal fungi)



APPENDIX D - 3. Summary of microbial parameters from soils collected at tamarisk sites in May 1993, and before and after flooding in 1994 and 1995. Values are means of 10 samples collected from each site in 1993 and 1994 and from Tamarisk Flood in 1995, and of 8 samples from Tamarisk Control in 1995; standard errors are given in parentheses. Statistical comparisons were made between sites in 1993, and for both sites across all collection dates in 1994 and 1995; within each row, means with different letters are significantly different at  $P < 0.01$  for 1993, and for 1994 and 1995.

	1993			1994			1995							
	pre-flood			post-flood			pre-flood			post-flood				
	TC	TF		TC	TF		TC	TF		TC	TF			
Microbial Biomass Carbon ( $\times 10^2 \mu\text{g g}^{-1}$ soil)	3.1 (0.1)	2.4 (0.1)		3.4 (0.4) a	2.9 (0.4) a		3.4 (0.1) a	4.3 (0.4) bc		3.6 (0.3) ab	2.9 (0.6) a		3.3 (0.3) a	4.6 (0.3) c
Total Bacteria ( $\times 10^7$ c.f.u. $\text{g}^{-1}$ soil)*	9 (3) a	18 (1) b		10 (3) a	15 (4) ab		17 (3) b	24 (3) c		10 (2) a	17 (3) b		13 (4) ab	27 (2) c
Aerobic Heterotrophic Bacteria ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	12 (3) a	24 (2) b		12 (2) a	27 (2) b		15 (5) a	36 (5) c		14 (4) a	33 (4) c		14 (3) a	39 (3) c
Streptomyces spp. ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	15 (1)	13 (2)		12 (6) a	15 (2) a		16 (3) ab	22 (4) b		15 (4) ab	18 (3) ab		17 (2) ab	25 (8) b
Chitin decomposers ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	26 (1) a	34 (3) b		30 (4) a	38 (2) bc		28 (2) a	40 (3) c		35 (3) abc	38 (4) bc		37 (4) bc	37 (5) bc
Cellulose decomposers ( $\times 10^5$ c.f.u. $\text{g}^{-1}$ soil)*	33 (3)	38 (3)		42 (2) a	55 (3) c		35 (4) b	67 (3) d		42 (3) a	52 (2) c		35 (5) b	72 (7) d
Total Fungi ( $\times 10^3$ $\text{g}^{-1}$ soil)	4 (2)	8 (2)		6 (2) a	19 (4) c		9 (3) ab	36 (6) d		6 (1) a	20 (3) c		11 (2) b	39 (3) d
Total Hyphal Lengths ( $\text{cm g}^{-1}$ soil)	8.6 (0.3)	8.5 (0.6)		7 (3) ab	8 (3) ab		7 (2) a	12 (2) b		8 (2) ab	10 (0.5) ab		9 (2) ab	14 (3) bc
Basidiomycete Hyphal Lengths ( $\text{cm g}^{-1}$ soil)	1.3 (0.2)	1.9 (0.2)		2 (1)	4 (2)		2 (0.5)	4 (1)		2 (2)	3 (2)		2 (0.5)	4 (1)
VAM spore numbers (per 100 g soil)	5 (2)	7 (2)		4 (2) a	8 (4) ab		10 (3) b	7 (4) ab		4 (1) a	6 (2) ab		12 (3) b	5 (3) a

Appendix D - 3, continued.

	1993			1994			1995			
	pre-flood			pre-flood			pre-flood			
	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF
Mycorrhizal Inoculum Potential (% infection)	8 (2) a	14 (3) b	8 (2) a	17 (5) b	12 (3) ab	25 (6) c	7 (3) a	16 (2) b	9 (2) a	26 (2) c
Root Length Colonized (%)	5 (8)	10 (2)	4 (2)	7 (2) a	7 (5) ab	7 (2) a	6 (2) a	8 (2) ab	8 (4) ab	9 (2) ab
No. of VAM <sup>†</sup> species	3 (2)	4 (2)	3 (2)	4 (0)	3 (0)	4 (0)	3 (1)	4 (0)	3 (1)	4 (0)
No. of ECM <sup>†</sup> species	0	0	0	0	0	0	0	0	0	0
Dehydrogenase <sup>‡</sup> µg g <sup>-1</sup> h <sup>-1</sup>	3.76 (0.3) a	4.13 (0.14) a	3.76 (0.3) a	4.13 (0.14) a	4.27 (0.82) ab	8.15 (0.37) c	3.7 (0.40) a	5.0 (0.23) b	3.53 (0.73) a	7.5 (0.59) c

\* c.f.u. = colony forming units per gram of dry-weight soil  
<sup>†</sup> = Mean number of VAM (vesicular-arbuscular mycorrhizal fungi)  
<sup>‡</sup> = Mean number of ECM (ectomycorrhizal fungi)  
<sup>‡</sup> denitrification enzyme activity not measured in 1993

**APPENDIX E - SUMMARY OF SURFACE-ACTIVE AND AERIAL  
ARTHROPOD DATA, 1991 - 1995**

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APPENDIX E - 1. Arthropod species checklist for all study sites. "x" indicates that species was present in at least one 48 h collection during the five year study; abundance is not indicated. Sites: CC = Cottonwood Control, CF = Cottonwood Flood, RC = River Control, RF = River Flood, TC = Tamarisk Control, TF = Tamarisk Flood. Sample effort: cottonwood sites = 30 collections, tamarisk sites = 20 collections, river sites = 9 collections.

	CC	CF	RC	RF	TC	TF
<b>ARACHNIDA</b>						
<b>Pseudoscorpionida</b>						
unidentified family	x	x	x	x	x	x
<b>Araneae</b>						
unidentified family					x	
Agelenidae					x	
Araneidae				x		x
<i>Araneus trifolium</i>					x	
Clubionidae						x
Dictynidae	x				x	x
<i>Dictyna subulata</i>					x	
<i>Dictyna</i> sp.					x	
<i>Mallos</i> sp.	x	x	x			x
<b>Dysderidae</b>						
<i>Dysdera crocata</i>	x	x			x	x
<b>Gnaphosidae</b>						
<i>Drassyllus</i> sp.	x	x		x	x	x
<i>Gnaphosa</i> sp.					x	
<i>Haplodrassus</i> sp.	x	x	x		x	x
<i>Herpyllus ecclesiasticus</i>	x					
<i>Herpyllus</i> sp.	x	x				
<i>Poecilochroa</i> sp.					x	
<i>Zelotes anglo</i>		x				
<i>Zelotes fratris</i>					x	
<i>Zelotes lasalanus</i>					x	x
<i>Zelotes tuobus</i>						x
<i>Zelotes</i> sp.	x	x	x	x	x	x

APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
Hahniidae						
<i>Neoantistea</i> sp.				X		
Homalonychidae						X
Linyphiidae	X	X	X	X	X	X
Lycosidae	X	X		X	X	X
<i>Allocosa</i> sp.						X
<i>Alopecosa</i> sp.	X	X				X
<i>Lycosa</i> sp. # 1	X	X	X	X	X	X
<i>Lycosa</i> sp. # 2		X				
<i>Pardosa</i> sp.		X		X		X
<i>Pirata</i> sp.	X	X	X	X	X	X
Micryphantidae	X	X			X	X
Pholcidae					X	
<i>Physocyclus</i> sp.					X	
<i>Psilochorus</i> sp.	X				X	X
Salticidae					X	X
<i>Habrocestum</i> sp.		X	X			
<i>Habronattus</i> sp.	X	X	X	X	X	X
<i>Phidippus audax</i>				X		
<i>Sitticus</i> sp.	X	X			X	X
Tetragnathidae						
<i>Pachygnatha</i> sp.		X				
<i>Tetragnatha</i> sp.						X
Theridiidae	X		X		X	X
<i>Crustulina</i> sp.	X					X
<i>Euryopis</i> sp.			X			X
<i>Latrodectus hesperus</i>						X
<i>Latrodectus</i> sp.						X
<i>Steatoda borealis</i>		X				X
<i>Steatoda</i> sp.	X	X				

## APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
Thomisidae	x					
<i>Misumenops</i> sp.	x	x	x	x	x	
<i>Xysticus</i> sp.	x					x
<b>Acarina</b>						
unidentified family	x	x	x		x	x
<b>MALACOSTRACA</b>						
<b>Isopoda</b>						
Armadillidae						
<i>Armadillidium vulgare</i>	x	x	x	x	x	x
Porcellionidae						
<i>Porcellio laevis</i>	x	x	x	x	x	x
<b>CHILOPODA</b>						
<b>Scolopendromorpha</b>						
Scolopendridae						
		x	x		x	x
<b>Lithobiomorpha</b>						
unidentified family						
		x			x	x
Henicopidae						
		x		x		
Lithobiidae						
	x	x				x
<b>INSECTA</b>						
<b>Thysanura</b>						
Lepismatidae						
	x	x				
Nicoletiidae						
	x					
<b>Orthoptera</b>						
Gryllacrididae						
	x	x				
Gryllidae						
<i>Gryllus alogus</i>	x	x	x	x		x

APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
Raphidophoridae		x	x		x	
<i>Ceuthophilus gertschi</i>	x	x	x			
<i>Ceuthophilus pallidus</i>	x	x				
<b>Blattaria</b>						
unidentified family				x		
<b>Isoptera</b>						
Rhinotermitidae						
<i>Reticulitermes</i> sp.		x				
Termitidae		x				
<b>Psocoptera</b>						
unidentified family		x			x	x
Ectopsocidae						x
<b>Thysanoptera</b>						
unidentified family					x	
<b>Hemiptera</b>						
unidentified family		x				x
Gerridae						
<i>Gerris</i> sp.		x	x			
Lygaeidae		x			x	
<i>Cymodema</i> sp.			x			
<i>Cymus coriacipennis</i>						x
<i>Ochrimnus</i> sp.	x					
<i>Ozophorus</i> sp.	x	x		x		
<i>Peritrechus</i> sp.		x				
<i>Sisamnes</i> sp.					x	
Miridae						
<i>Oncerometopus</i> sp.		x				
Reduviidae	x	x			x	x
<i>Barce</i> sp.					x	
<i>Empicoris</i> sp.	x					
<i>Gardena</i> sp.	x					

## APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
<i>Ghinallelia</i> sp.						x
<i>Pseudometapterus</i> sp.						x
<b>Homoptera</b>						
unidentified family	x				x	
Aphididae						x
Cicadellidae	x	x		x	x	
Cicadidae	x					
Delphacidae	x					
Kinnaridae						x
<b>Coleoptera</b>						
Family unknown	x	x	x	x	x	x
Anthicidae						
<i>Baulius tenuis</i>		x		x		
<i>Baulius</i> sp.				x		
<i>Ischyropalpus</i> sp.		x				
Carabidae	x	x	x		x	x
<i>Agonum decorum</i>		x		x		
<i>Agonum</i> sp.	x	x				
<i>Amara carinata</i>					x	
<i>Amara littoralis</i>					x	
<i>Amara</i> sp.	x	x	x		x	
<i>Badister</i> sp.				x		
<i>Bemidion timidum</i>		x				
<i>Bradycellus</i> sp.		x				
<i>Calathus opaculus</i>	x	x	x	x	x	x
<i>Chlaenius sericeus</i>		x		x		x
<i>Chlaenius tricolor</i>				x		
<i>Chlaenius</i> sp.		x		x		
<i>Evarthrus</i> sp.	x	x			x	
<i>Harpalus pennsylvanicus</i>		x				
Perigonini				x		



APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
<i>Pterostichus chalcites</i>	x	x	x	x		x
<i>Pterostichus</i> sp. #2		x				
<i>Scarites lissopterus</i>		x			x	x
<i>Scarites</i> sp.						x
<i>Selenophorus planipennis</i>						x
<i>Stenolophus</i> sp.						x
<i>Tachys</i> sp.		x		x		
Cerambycidae						
<i>Prionus</i> sp.	x				x	
Chrysomelidae						
<i>Allicta</i> sp.					x	
<i>Chrysomela scripta</i>		x				
Eumolpinae	x	x				
<i>Graphops</i> sp.	x					
Coccinellidae						
Coccidulini			x			
Corylophidae					x	
Cryptophagidae						
<i>Cryptophagus</i> sp.	x	x	x	x		x
Cucujidae						
<i>Cathartus</i> sp.					x	
Curculionidae						
<i>Hypera postica</i>	x					
<i>Otiorhynchus cercopeus</i>			x			
<i>Otiorhynchus ovatus</i>	x		x			
<i>Rhypodillus brevicollis</i>	x					
<i>Sphenophorus</i> sp.		x				
<i>Stenichnus</i> sp.						x
Dermestidae	x	x			x	x
Dytiscidae						
<i>Laccophilus</i> sp.		x				

## APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
Elateridae						
<i>Aeolus mellillus</i>	x	x				
<i>Athos</i> sp.	x					
<i>Conoderus sordidus</i>	x			x		
<i>Melanotus</i> sp.					x	
Eucnemidae						
		x				
Histeridae						
<i>Aphelosternus</i> sp.		x				
<i>Euspilotus assimilis</i>		x				
<i>Geomysaprinus</i> sp.		x				
<i>Hypocaccus</i> sp.	x	x				
Lathridiidae						
<i>Corticaria</i> sp.		x				
<i>Enicmus</i> sp.					x	
<i>Melanophthalma</i> sp.						x
Limulodidae						
<i>Limulodes</i> sp.					x	
Melandryidae						
<i>Anaspis</i> sp.	x					x
Pselaphidae						
<i>Reichenbachia</i> sp.	x	x		x	x	
Ptilidae						
					x	
Ptinidae						
<i>Ptinus fur</i>		x				x
Scarabaeidae						
<i>Aphodius</i> sp.					x	
<i>Ataenius</i> sp.		x			x	
<i>Hoplia</i> sp.	x	x	x			
<i>Ochodaeus</i> sp.		x				
<i>Omorgus punctatus</i>	x	x	x		x	x
<i>Onthophagus</i> sp.		x				

APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
<i>Pseudataenius</i> sp.	x					
<i>Serica alternata</i>	x					
<i>Serica</i> sp.	x					
<i>Trox monahus</i>	x					x
Silphidae						
<i>Nicrophorus</i> sp.						x
Staphylinidae						
Aleocharinae	x	x		x	x	x
<i>Astenus longiusculus</i>		x				
Paederinae	x			x	x	x
Paederini		x				
<i>Platydracus pennsylvanicus</i>		x				
<i>Platydracus sepulchralis</i>	x	x	x	x	x	x
<i>Platydracus</i> sp.	x	x			x	x
<i>Olisthaerus</i> sp.					x	
<i>Quedius</i> sp.						x
<i>Staphylinus ater</i>	x	x	x	x		x
<i>Staphylinus</i> sp.	x	x				x
<i>Tachyporus</i> sp.				x		
Trichophyini					x	
Tenebrionidae						
<i>Agroporis rufipes</i>		x				
<i>Areoschizus decipiens</i>	x					
<i>Asidopsis opacus</i>	x					
<i>Blapstinus fortis</i>	x	x	x		x	x
<i>Blapstinus pimalis</i>			x			x
<i>Blapstinus</i> sp.	x				x	x
<i>Embaphion confusum</i>	x					
<i>Embaphion</i> sp.		x				
<i>Eleodes extricatus</i>	x				x	x
<i>Eleodes fusiformis</i>		x			x	x

## APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
<i>Eleodes gracilis</i>					x	
<i>Eleodes longicollis</i>	x		x		x	
<i>Eleodes obsoletus</i>	x					
<i>Eleodes sponsus</i>	x					
<i>Eleodes suturalis</i>	x	x	x		x	x
<i>Eleodes</i> sp.					x	
<i>Metoponium</i> sp.	x				x	
<b>Neuroptera</b>						
Myrmeleontidae	x					
<b>Lepidoptera</b>						
unidentified family	x	x	x	x	x	x
Noctuidae	x	x			x	
Acanthopteroctetidae					x	x
<b>Diptera</b>						
unidentified family	x	x	x	x	x	x
Cecidomyiidae	x	x	x	x	x	
Chironomidae	x					
Culicidae						x
Sciaridae	x					
Sphaeroceridae		x				
<b>Siphonaptera</b>						
Pulicidae	x					
<b>Hymenoptera</b>						
Andrenidae	x				x	
Ceraphronidae						x
Chalcidoidea			x		x	
Diapriidae	x	x				
Formicidae					x	x
Dolichoderinae						
<i>Dorymyrmex insana</i>	x	x			x	
<i>Tapinoma sessile</i>		x		x	x	x

APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
Ecitoninae						
<i>Neivamyrmex nigrescens</i>	x	x		x	x	
<i>Neivamyrmex</i> sp.	x					
Formicinae						
<i>Camponotus sansabeanus</i>			x			
<i>Camponotus vicinus</i>	x	x	x			
<i>Formica hewitti</i>			x		x	
<i>Formica neogagates</i>			x		x	
<i>Formica</i> sp.					x	
<i>Lasius fallax</i>	x		x			
<i>Lasius niger</i>			x	x	x	
<i>Lasius</i> sp.					x	
Myrmicinae						
<i>Crematogaster cerasi</i>	x	x	x	x		x
<i>Leptothorax andrei</i>	x		x	x		
<i>Leptothorax nitens</i>	x		x			x
<i>Leptothorax obliquicanthus</i>	x					
<i>Leptothorax pergrandei</i>	x	x			x	
<i>Leptothorax t. texanus</i>				x		
<i>Leptothorax</i> sp. 1	x	x				
<i>Monomorium cyaneum</i>						x
<i>Monomorium minimum</i>	x	x			x	x
<i>Pheidole pilifera</i>	x					
<i>Pheidole</i> sp.	x		x			
<i>Pogonomyrmex barbatus</i>	x		x			
<i>Pogonomyrmex occidentalis</i>	x		x		x	
<i>Solenopsis molesta</i>	x					
<i>Solenopsis</i> sp.	x	x			x	
Ponerinae						
<i>Hypoponera opaciceps</i>				x		
<i>Hypoponera</i> sp.		x				

APPENDIX E - 1, continued.

	CC	CF	RC	RF	TC	TF
Halictidae						
<i>Sphcodes</i> sp.						x
Mutillidae						
<i>Dasymutilla</i> sp.	x	x	x		x	
Pompillidae						x
Scelionidae				x		
Total insect taxa	91	86	39	37	66	57
Total spider taxa	24	22	11	13	28	32
Total taxa - all classes	120	116	55	54	100	96

APPENDIX E - 2. Summary of monthly sticky trap data for cottonwood sites, 1991 through 1995. Values are the total number of individuals captured on ten sticky traps at each site within each collection.

	Aphids		Leafhoppers		Nematoceran flies		Other Flies		Ichneumonid wasps		Chalcidoid wasps		Other hymenoptera		Beetles		Thrips		Other taxa		Total (all taxa)		
	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	
1991																							
July	11	32	51	170	8	31	656	199	20	23	133	211	1	2	105	172	85	493	5	9	1075	1342	
August	8	16	10	21	106	27	307	282	76	57	148	143	0	1	22	30	14	28	11	8	702	613	
October	145	107	13	22	31	15	336	126	34	12	106	161	0	1	16	6	90	30	7	1	778	481	
December	0	0	3	6	320	463	48	38	0	0	0	0	0	0	0	0	3	0	0	0	374	507	
1992																							
February	0	0	31	134	862	1281	259	337	0	2	0	0	3	5	0	0	0	0	2	1	1157	1760	
April	4	4	45	20	68	165	257	97	38	12	29	10	0	0	3	3	5	3	1	2	450	316	
June	20	23	124	74	54	69	1004	537	40	2	46	75	16	12	122	64	60	86	1	2	1487	944	
August	11	5	24	33	14	9	95	107	10	17	29	23	1	1	6	11	0	2	2	5	191	213	
October	29	27	59	97	14	11	72	86	1	4	55	46	5	10	2	0	28	28	12	21	277	330	
1993																							
February	5	5	129	331	210	255	166	271	0	0	1	1	5	7	2	0	1	0	0	1	519	871	
April	0	3	77	45	24	32	55	78	8	1	17	6	7	14	0	0	9	8	4	2	201	189	
May	13	23	156	150	28	24	305	322	16	8	35	23	10	13	22	13	222	152	14	5	817	733	
June	27	98	209	216	49	22	263	59	7	0	66	50	7	5	58	21	99	159	7	16	792	646	
August	2	4	4	27	8	13	62	15	12	3	56	35	42	15	16	15	3	4	4	9	199	140	
October	12	6	20	8	29	34	93	102	2	3	22	21	1	1	1	1	1	3	2	2	183	183	
December	0	0	0	0	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	6	

Appendix E - 2, continued.

	Aphids		Leafhoppers		Nematoceran flies		Other Flies		Ichneumonid wasps		Chalcidoid wasps		Other hymenoptera		Beetles		Thrips		Other taxa		Total (all taxa)		
	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	CC	CF	
1994																							
February	1	0	415	311	151	561	216	139	4	14	7	36	0	0	0	2	1	4	2	0	0	797	1067
April	2	0	202	129	8	49	31	19	10	4	40	17	8	15	12	8	165	68	8	3	3	486	312
May	0	2	59	13	30	27	263	183	11	8	34	10	6	7	39	35	73	99	15	5	5	530	389
June	0	0	83	26	3	41	183	94	16	4	26	5	20	5	116	26	22	40	5	3	3	474	244
August	55	15	17	13	17	11	129	50	16	4	17	16	8	17	17	17	24	15	8	2	2	326	151
October	0	0	46	14	9	27	162	248	14	16	35	41	13	13	0	1	22	4	12	31	313	395	
December	0	0	15	4	178	170	23	47	0	2	1	0	3	1	0	1	0	1	0	1	0	220	227
1995																							
February	0	0	206	167	155	144	68	71	2	5	61	167	48	16	2	3	31	8	4	3	3	577	584
April	0	1	23	4	313	208	90	80	9	7	16	6	118	61	1	0	117	99	0	11	688	477	
May	0	1	132	86	35	34	179	85	26	10	8	10	638	279	202	103	1289	1721	2	8	2491	2337	
June	2	8	71	42	43	86	324	177	10	16	11	2	400	114	188	59	468	598	15	32	1532	1134	
August	0	4	24	29	35	41	58	39	19	1	5	1	179	102	15	11	42	24	34	25	411	277	
October	312	191	18	17	10	16	33	12	3	3	1	2	106	84	1	6	22	18	6	5	512	354	
December	0	0	1	2	5	19	7	8	0	0	0	0	2	2	0	0	0	0	2	0	0	17	31



Appendix E - 3. Summary of monthly sticky trap data for tamarisk sites, 1991 through 1994. Values are the total number of individuals captured on ten sticky traps at each site within each collection.

	Aphids		Leafhoppers		Nematoceran flies		Other Flies		Ichneumonid wasps		Chalcidoid wasps		Other hymenoptera		Beetles		Thrips		Other taxa		Total (all taxa)		
	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	
1991																							
July	10	16	80	32	10	12	78	128	4	40	54	99	2	0	33	17	89	77	6	5	366	426	
August	7	12	13	3	27	58	94	158	33	22	47	117	0	0	1	20	18	27	6	2	246	419	
October	13	135	4	2	8	12	155	172	122	2	83	43	0	0	0	0	19	10	4	0	408	381	
December	0	0	0	1	22	393	10	25	0	0	0	0	0	0	2	0	273	0	0	0	307	419	
1992																							
February	0	0	10	0	179	543	127	81	2	0	3	2	1	0	0	0	3	0	0	0	325	626	
April	4	2	0	2	541	171	189	250	23	33	15	16	30	1	6	4	20	4	0	1	828	484	
June	23	29	35	12	43	98	231	445	2	11	45	132	12	2	33	23	74	67	2	3	508	823	
August	13	21	16	36	34	112	85	106	18	1	19	28	5	2	6	3	12	2	0	2	208	313	
October	6	7	102	45	2	9	11	35	4	1	52	13	0	1	2	2	9	1	2	0	190	112	
1993																							
February	0	1	6	1	61	160	60	47	1	0	0	0	0	1	1	2	3	1	2	1	134	214	
April	1	0	4	2	10	157	56	33	2	7	12	12	25	5	1	0	9	7	2	4	122	227	
May	8	8	4	8	16	73	89	365	7	5	7	7	11	2	21	61	175	88	2	1	340	607	
June	0	21	337	478	16	176	34	95	3	2	105	191	5	7	28	19	91	117	6	13	625	1119	
August	9	3	47	21	7	35	25	140	10	5	30	129	46	42	3	5	0	4	16	8	193	392	
October	2	2	1	2	13	160	84	128	1	1	36	28	4	2	0	2	2	0	5	2	148	327	
December	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	

Appendix E - 3, continued.

	Aphids		Leafhoppers		Nematoceran flies		Other Flies		Ichneumonid wasps		Chalcidoid wasps		Other hymenoptera		Beetles		Thrips		Other taxa		Total (all taxa)		
	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	TC	TF	
1994																							
February	0	0	38	5	26	118	27	33	14	1	2	0	0	0	0	4	0	0	7	0	1	107	169
April	0	0	11	10	27	240	27	50	7	12	88	24	29	11	5	10	22	12	21	7	7	237	376
May	0	0	1	17	79	40	137	342	3	1	17	9	7	3	18	53	37	74	10	4	4	309	543
June	0	0	3	1	5	67	41	96	7	9	15	6	5	4	27	11	42	72	1	1	1	146	267

Appendix E - 4. Summary of monthly sticky trap data for river sites, 1994 through 1995. Values are the total number of individuals captured on ten sticky traps at each site within each collection.

	Aphids		Leafhoppers		Nematoceran flies		Other Flies		Ichneumonid wasps		Chalcidoid wasps		Other hymenoptera		Beetles		Thrips		Other taxa		Total (all taxa)		
	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	RC	RF	
1994																							
August	59	14	11	11	33	7	77	27	9	0	28	6	7	1	3	2	30	1	1	0	258	69	
October	0	0	10	13	40	11	143	58	12	3	67	52	3	7	4	2	36	23	9	6	324	175	
December	0	0	7	2	110	105	24	12	4	0	0	0	2	0	0	0	0	0	0	0	147	119	
1995																							
February	0	0	49	13	415	149	70	43	4	35	51	16	33	12	1	1	15	6	3	1	641	276	
April	0	0	6	7	147	74	79	21	14	17	3	0	61	18	6	0	104	69	3	3	425	210	
May	0	2	49	13	35	26	233	177	21	8	5	1	285	156	291	47	885	385	4	4	1809	819	
August	3	9	20	14	108	357	93	55	12	3	1	2	147	90	8	51	43	12	19	8	454	601	
October	281	17	10	5	10	6	29	20	1	3	0	0	238	48	2	2	30	89	2	3	603	193	
December	0	0	1	0	11	22	3	4	0	0	0	0	0	0	0	0	0	0	0	0	15	26	

**APPENDIX F - SUMMARY OF SMALL MAMMAL DATA,  
1991-1995**

APPENDIX F - 1.	Pre-flood summary of rodent capture data for cottonwood ground trapping webs in 1991 .....	210
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APPENDIX F - 1. Pre-flood summary of rodent capture data for cottonwood ground trapping webs in 1991. Values represent the estimated density of individuals (number of individuals per hectare) for each site; standard error is shown in parentheses (where no standard error is given, values were calculated as the number of individuals per unit area, due to small sample sizes). Trapping effort: 148 traps per web x 3 trap nights = 444 trap-nights per site.

Species	April		June		August		October	
	control	flood	control	flood	control	flood	control	flood
<i>Peromyscus leucopus</i>			4.85 (1.46)	4.48	13.66 (2.45)	9.68 (2.02)	14.54 (2.53)	36.96 (9.75)
<i>Neotoma albigula</i>						0.45 (0.09)		

APPENDIX F - 2. Pre-flood summary of rodent capture data for cottonwood ground trapping webs in 1992. Values represent the estimated density of individuals (number of individuals per hectare) for each site; standard error is shown in parentheses. Trapping effort: 148 traps per web x 3 trap nights = 444 trap-nights per site.

Species	April		June		August		October	
	control	flood	control	flood	control	flood	control	flood
<i>Reithrodontomys megalotis</i>	6.88 (1.53)	0.88 (0.14)			1.41 (0.42)			
<i>Peromyscus leucopus</i>	44.87 (9.94)	16.30 (2.61)	77.52 (37.31)	29.38 (10.26)	125.25 (37.44)	14.97 (2.49)	87.52 (22.43)	69.98 (12.86)
<i>Neotoma albigula</i>					1.41 (0.42)	0.89 (0.15)	1.24 (0.32)	

APPENDIX F - 3. Summary of rodent capture data for cottonwood ground trapping webs in 1993. Values represent the estimated density of individuals (number of individuals per hectare) for each site; standard error is shown in parentheses. Trapping effort: 148 traps per web x 3 trap nights = 444 trap-nights per site. Flood site was inundated for approximately 27 days between the May and June trapping periods.

Species	May		June		August	
	control	flood	control	flood	control	flood
<i>Reithrodontomys megalotis</i>	5.98 (1.56)	2.10 (0.56)				
<i>Peromyscus leucopus</i>	65.80 (17.14)	86.09 (22.96)	16.29 (2.65)	12.35 (2.29)	22.02 (3.09)	25.98 (3.35)
<i>Neotoma albigula</i>			0.45 (0.07)	0.43 (0.08)	0.45 (0.06)	0.45 (0.06)

APPENDIX F - 4. Summary of rodent capture data for cottonwood ground trapping webs in 1995. Values represent the estimated density of individuals (number of individuals per hectare) for each site; standard error is shown in parentheses (where no standard error is given, values were calculated as the number of individuals per unit are, due to low sample size). Trapping effort: 148 traps per web x 3 trap nights = 444 trap-nights per site. Flood site was inundated for approximately 30 days between the May and June trapping periods.

Species	May		June		August	
	control	flood	control	flood	control	flood
<i>Reithrodontomys megalotis</i>	0.88 (0.24)		0.44 (0.10)			
<i>Peromyscus leucopus</i>	5.29 (1.41)	1.49	7.93 (1.82)	3.48	16.74 (2.72)	13.66 (2.45)

APPENDIX F - 5. Summary of rodent captures in tree traps at cottonwood sites during 1991 - 1993. Values represent the total number of *Peromyscus leucopus* captured in twenty tree traps at each site each night, except where other species is indicated; values in parentheses are the percentage capture success. Total is the total number of individuals captured in tree traps over the three nights for each trapping session, except where indicated.

Species	Control Site				Flood Site			
	Night				Night			
	1	2	3	total	1	2	3	total
1991								
June	0	5 (25)	6 (30)	10	1 (5)	5 (25)	5 (25)	10
August	8 (40)	17 (85)	8 (40)	24	9 (45)	2 (10)	8 (40)	15
October	16 (80)	12 (60)	17 (85)	30	9 (40)	9 (40)	10 (50)	24
1992								
April <sup>1</sup>	13 (65)			13	8 (40)			8
June	11 (55)	11 (55)	7 (35)	20	5 (25)	5 (25)	7 (35)	13
August								
<i>Peromyscus leucopus</i>	16 (80)	10 (50)	15 (75)	32	18 (90)	14 (70)	12 (60)	35
<i>Neotoma albigula</i>							1 (5)	1
1993								
May	12 (60)	11 (55)	8 (40)	21	12 (60)	13 (65)	5 (25)	19
May - peak flood <sup>2</sup>	8 (40)	10 (50)		16	11 (58)	11 (58)		19
June	10 (50)	13 (65)	16 (80)	25	7 (35)	18 (90)	20 (100)	38
August								
<i>Peromyscus leucopus</i>	18 (90)	17 (85)	17 (85)	40	18 (90)	17 (85)	19 (95)	37
<i>Neotoma albigula</i>		1 (05)		1				

<sup>1</sup> Sites were trapped for only one night in April 1992.

<sup>2</sup> Sites were trapped for two nights during peak flood; flood site had 19 tree traps.