University of Idaho
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SHIFTS IN SPECIES COMPOSITION AS INTERPRETED THROUGH FLOODPLAIN AGE ON THE SACRAMENTO RIVER

ERP 0620021 PROJECT REPORT

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1.0 Purpose

The purpose of this report is to provide a detailed analysis of species composition, relative cover, and frequency as a function of floodplain age (FPA) and relative elevation on the Sacramento River, CA.

2.0 Introduction

Riparian plant communities are associated with a variety of abiotic and biotic factors that drive propagule dispersal, recruitment and establishment in river systems (Naiman and Decamps 1997, Sarr and Hibbs 2007). These factors are primarily driven by hydro-geomorphic processes acting over a gradient of floodplain types. Over multiple time scales, floodplain surfaces are created, destroyed, and modified by channel migration and overbank flooding (Steiger et al. 2005, Greco et al. 2007, Sarr and Hibbs 2007). As sediment is deposited on the floodplain and new surfaces emerge, upper floodplain areas stabilize and riparian plant communities develop (Naiman and Decamps 1997). Variability in species composition is caused by the timing of such events relative to each other, the character of the series of events and host of biotic process, not limited to dispersal and competition.

Riparian areas generally follow a successional model of vegetation dynamics with a progression of species assemblages from new to old floodplains. However, the assemblage of species on newly created surfaces can be highly variable. Potentially, assembly rules are a more appropriate model to apply to the initial colonization of these surfaces that in turn impact the trajectory of vegetation dynamics. Assembly rules posit that the initial physical and biotic conditions on newly created surfaces should have a strong impact on determining the species composition through time. Here, we begin to examine the variability in vegetation composition using both assembly rules and a successional model of vegetation dynamics.

With these principles in mind, we utilized the most recent floodplain age surface map dataset (Fremier and Girvetz *in prep*) to analyze the relationship between floodplain age and species composition, relative cover, and frequency. In addition, we use two topographic surfaces of relative elevation to correlate vegetation with the presumed hydrological gradient. Floodplains of similar age and relative elevation were used to extract forest patches with varying dominance of cottonwood to compare entire species communities in the presence and absence of cottonwood.

The overall objective of this report is to analyze vegetation development on the Sacramento River floodplain in relation to two landscape variables – floodplain age and relative elevation. Specifically, we consider two questions: 1) what are the patterns of species composition over these gradients? 2) With the loss of cottonwood, what is the character of the replacement community? We feel that both a descriptive and more question-driven approach to the landscape analysis of riparian vegetation on the Sacramento River will give managers and restoration practitioners more detailed information to make informed decisions.

3.0 Methods

Floodplain age is defined as the time elapsed since a specific area changed from aquatic to terrestrial (e.g. river channel to point bar). A floodplain age map is a composite map detailing the history of channel movement through a floodplain. During the course of this project, a newer version of our floodplain age mapping algorithm was developed to capture the spatial extent of channel abandonment and it now also interpolates between channel years to produce a continuous surface of channel movement. The floodplain age composite map was created for the Sacramento River from Red Bluff to Colusa, CA for all available years (Fremier and Girvetz *in prep; Figure 1*). The detailed component maps of channel position were on average 10-15 years apart, however the earliest channel maps had the largest time steps (1904 to 1920). To create a continuous surface of floodplain age, channel positions between sequential channels were interpolated using a geographic information system (GIS). The interpolation methods use the straight line distance between river edges to delineate the progressive movement of the channel. Areas of channel abandonment were not interpolated. The map contains (1) an estimated continuous surface of floodplain age and (2) a floodplain type over the mapped area, progressive channel migration versus abandoned channel (*Figure 1*). For the vegetation classification analysis we *regrouped* the floodplain age gradient into five distinct groups: 1: 2007 to 1984, 2: 1983 to 1969, 3: 1970 to 1954, 4: 1953 to 1921, and 5: 1920 to 1903. These groups are roughly 20 year brackets of time to average floodplain composition and natural heterogeneity in the system. Without these sequential breaks, the breaks would reflect available aerial photography dates thereby having larger time gaps between the earliest photos.

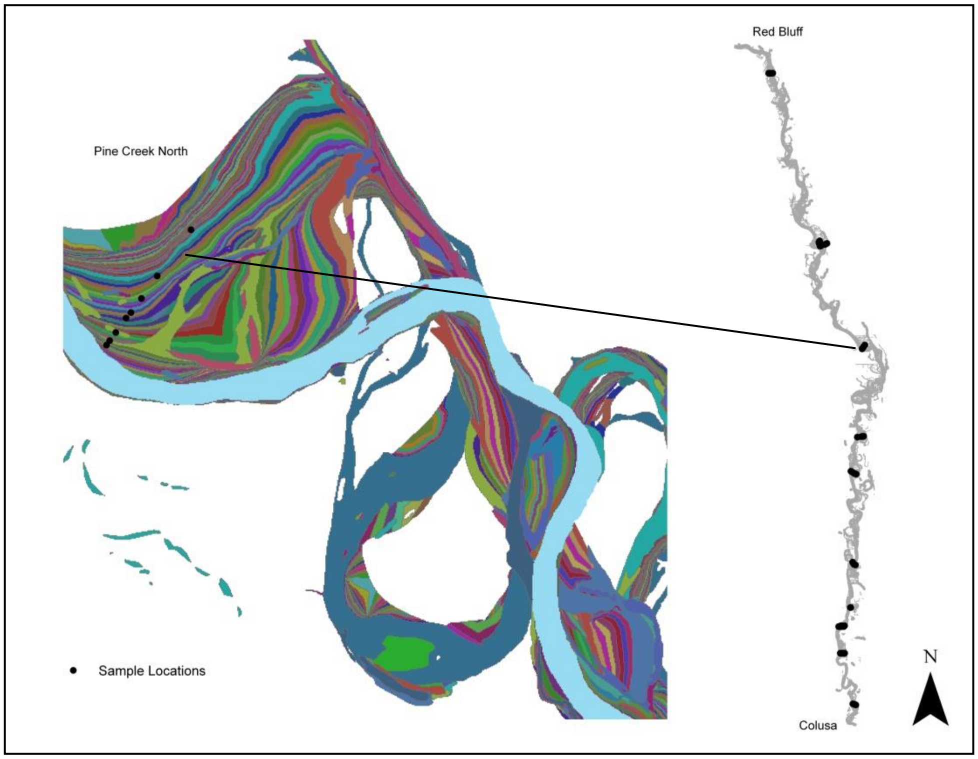

Figure 1. Plot placement within the study reach and across the floodplain age gradient at Pine Creek North.

3.1. Species Composition, relative cover, and frequency

The relationship between species occurrence and floodplain age has been described on the Sacramento River by Greco (1999), Fremier (2003), Vaghti (2003) and again by Greco *et al.(*2007*)*. Greco linked vegetation patterns to yellow-bill cuckoo habitat. Fremier (2003) described the relationship between woody species and FPA while Vaghti (2003) designed a vegetation classification using Department of Fish and Game (DFG) and California Native Plant Society (CNPS) protocols. Greco et al. used a geospatial layer of vegetation interpreted from aerial photography to compare classes of riparian vegetation across the floodplain and relative elevation variables (Greco et al. 2007, Greco et al. 2008). However, a description of the full complement of species in relation to floodplain age and relative elevation remains understudied with respect to two processes – channel abandonment and the replacement of cottonwood.

Vegetation Survey and Analysis: We measured understory and overstory composition using intensive modified Whittaker plots (Barnett and Stohlgren 2003). In addition, smaller 2m x 5m plots were sampled along transects in remnant forest tracts to collect species composition, diversity, and substrate type across different floodplain ages (Fremier and Girvetz *in prep*). Transect location was initially dependent on river bend formation (point bar) and property access, while individual transect placement was concentrated in areas that encompassed both a variety of floodplain ages (FPA) and vegetation communities beginning at rivers edge and ending in the interior forest. Transects were digitized in ArcMap® 9.2, imported into Microsoft ® Pathfinder Office ® (v 4.0), and exported into a Trimble® Geo XT ™ unit equipped with a Hurricane™ antenna. Plot position was based on field assessed changes in FPA, vegetation type, or substrate change (Figure 1). Changes in FPA and vegetation category was determined by referencing a floodplain age map and the 2007 vegetation map loaded into ArcPad® 7.1 on a Trimble® GeoXT ™ or Trimble® GeoXM ™ GPS unit.

We calculated species composition, relative cover, and frequency within each floodplain age group to investigate the distribution of species across the floodplain age surface. Composition was measured as species richness (absolute and Simpson's Diversity Index), Jaccard Dissimilarity, and indicator species analysis with a Monte Carlo test of significance. Percent cover and species richness data was log transformed for analyses. In some cases, floodplain age category "1903" was excluded from analyses as it remains one of the least descriptive floodplain age classes due to the restraints of aerial photography. All plots and species were checked for outliers and deleted if they were greater than three standard deviations from the mean (McCune and Grace 2002). No plots or species exceeded this cutoff. Individual species frequencies for all 102 species are contained in the species frequency table in the appendix.

To make this dataset more applicable to a 2007 vegetation map, the Manual of California Vegetation II (2009) and Vaghti (2003) vegetation associations, we assigned vegetation community values based on overstory dominance and understory (low tree, shrub and herbaceous layers) composition (Sawyer et al. 2009). Plots that did not contain overstory species (gravel bar and grassland vegetation) or that did not fit into one of these categories were excluded or assigned a preliminary vegetation classification based on overstory dominance and understory composition. Preliminary vegetation associations were only assigned to plots that contained an overstory and that had three or more replicates; all other plots were excluded from this analysis. To link floodplain age (FPA) with forested vegetation community we intersected the Vaghti (2003) plots with the floodplain age map (Greco et al. 2007) in GIS and applied contingency analysis using floodplain age ranges for both datasets. We then compared the FPA distribution of vegetation communities between the Vaghti (2003) vegetation classification and our dataset. To establish a range of floodplain ages for a specific vegetation community, we used an ANOVA and Tukey-Kramer HSD test in JMP IN 8 (SAS Institute2008) to test the mean FPA value for each vegetation community and for each dataset by floodplain age.

3.2. Cottonwood Replacement

On the Sacramento River, where the hydrograph is modified and floodplain geomorphology is altered, researchers have observed changes in recruitment patterns of Fremont cottonwood (*Populus fremontii ssp. fremontii*) changes (Roberts et al. 2002). This observation is common in river systems in western North America (Fenner et al. 1985, Johnson 2002), but a detailed analysis of stand replacement dynamics following the selective loss of cottonwood is understudied and an important factor to consider in restoration and planning. Therefore, we investigated the encroachment and potential stand replacement of Fremont's cottonwood by Northern California walnut (*Juglans hindsii*) and California box elder (*Acer negundo var. californicum*) on the Sacramento River, which are hypothesized to have expanded as a result of hydrological modifications and agricultural practices throughout the 20th century (Fremier 2003). To do this, we first summarized historical descriptions of Sacramento River riparian vegetation;

second, we located floodplain surfaces with similar floodplain ages and relative elevations. We then queried the field data do compare species composition on these surfaces and highlighted forest stands with and without cottonwood. And finally, we examined total species composition to evaluate the overall effects of stand replacement.

We established vegetation community floodplain position using NMS ordination measured by Sorensens similarity in PCORD 5.21 (McCune and Mefford 2006) using a random starting configuration with 200 iterations with a 0.00001 stability criterion, 50 runs with real data and the Monte Carlo probability test. This was completed using species abundance, vegetation class, relative elevation, floodplain age, and distance from channel.

To measure the species composition of Fremont cottonwood, Northern California walnut and California box elder forests, a threshold of 10% cover for of either of these three species was set; all plots that did not fall within these criteria were excluded from the forest composition analyses. Species cover data was converted to CNPS cover classes to reduce variations in sampling (1:<1; 2:1-5; 3:5-15; 4:15-25; 5:25-50; 6:50-75; 7:>75). We ran Cluster Analysis on the remaining plots (n=44) using Euclidean distance and Ward's method(McCune and Mefford 2006). We initially established 11 groups, where by adding additional groups clusters would result in multiple single plot clusters. Next, we cut this dendogram based on the lowest mean p-value and highest number of significant indicator species from the indicator species analysis of the 11 original clusters (Vaghti 2003). The best solution occurred at five clusters, however we chose four clusters as indicator species because results were similar and the goal is to look for broad trends in forest composition, at the alliance versus the association level of vegetation community composition (data not shown). To test overall compositional agreement within each group, we ran Multi-Response Permutation Procedure (MRPP) using a Sorensen (Bray-Curtis) measure of similarity, where all data were rank transformed and pairwise comparisons made. To measure species diversity within and between groups we also measured alpha diversity and beta diversity using average Jaccard similarity of a oneway ANOVA and Tukey-Kramer HSD to determine significance between groups; species nativity was used to look at the ratio of native to nonnative species richness within and between communities. To identify the floodplain niche of these forests, we ran NMS ordination (methods as above) and included variables of species abundance, relative elevation, floodplain age, distance from channel, vegetation map class, and overstory dominance.

4.0 Results and Discussion

4.1. Species Composition

Plots were sampled on 43 distinct floodplain age surfaces that fell between the years 1903 and 2007. A total of 102 plant species were recorded in 95 plots, 52 were native and 50 were non-native. Species richness was not higher in any of the five floodplain age groups. Species richness is often limited by factors such as light, water availability and non-native species prevalence, and further investigation of species richness, including jackknife estimations, may provide more insight to this relationship (McCune and Grace 2002). Additionally, species richness might have been limited by late summer sampling and small plot size. Jaccard dissimilarity results indicate that plots on the lowest floodplains, gravel bar, grassland, and sandbar willow communities, were most dissimilar to all other floodplain age groups ($F_{(14,4450)}=18.609$; $p<0.0001$; Table 1). Additionally, plots that were most similar to each other were on higher floodplain ages, indicating increased heterogeneity on low to mid floodplain surfaces where disturbance is more frequent.

Table 1.Mean Jaccard dissimilarity between plots and grouped by floodplain age group.

	FPA 1	FPA 2	FPA 3	FPA 4	FPA 5
FPA 1	0.96402				
FPA 2	0.961048	0.946356			
FPA 3	0.978059	0.950904	0.947818		
FPA 4	0.972796	0.940153	0.923113	0.893702	
FPA 5	0.979856	0.952338	0.940244	0.923122	0.938975

Species that were indicators of each floodplain age group were identified using indicator species analysis. Identified species generally followed the expected successional sequence, with early successional species occurring on young floodplains and later successional species occurring on older floodplains. Species on young (>1983) surfaces were generally flood tolerant species, such as *S. exigua*, *L. peploides*, and *P. lapathifolium* (Table 2). FPA group 5, the oldest surface, was indicated by *Q. lobata*. Mid-aged forests reflected the importance of understory native species such as *E. glaucus* and *A. californica* that grow in dense stands in the understories of later successional riparian forests. In general, floodplain age groups older than 1970 (older than FPA group 3) contain understory and overstory species that are considered mid to late successional riparian forests (Vaghti 2003). To some extent, these species assemblages are reflected in the Vaghti (2003) riparian forest vegetation communities which were also quantified by floodplain age.

Table 2. The results of indicator species analysis for floodplain age groups one through five.

Taxa	Common Name	FPA Group	Indicator Value	Mean (± SD)	p-value
Crypsis schoenoides	swamp picklegrass	1	12.5	4.9 ± 2.81	0.048
Juncus oxymeris	pointed rush	1	12.5	4.8 ± 2.77	0.0506
Ludwigia peploides	primrose	1	12.5	5 ± 2.72	0.0472
Melilotus alba	yellow sweetclover	1	12.5	6 ± 2.49	0.048
Chenopodium ambrosioides	Mexican tea	1	18.7	4.9 ± 3.26	0.0062
Salix exigua	sandbar willow	1	24.9	8.5 ± 4	0.004
Polygonum lapathifolium	curlytop knotweed	1	25	5.7 ± 3.37	0.0006
Sorghum halepense	Johnson grass	1	36.5	8.6 ± 4.4	0.0002
Conyza canadensis	Canadian horseweed	2	16.2	5.7 ± 3.27	0.0156

Leymus triticoides	creeping wild rye	3	15.3	7.8 ± 4	0.0552
Aristolochia californica	California pipevine	3	23.4	9.9 ± 4.42	0.015
Rumex salicifolius	willow dock	4	15.5	5.5 ± 3.32	0.0176
Juglans hindsii	black walnut	4	29.1	15.7 ± 4.32	0.012
Quercus lobata	valley oak	5	29.2	8.3 ± 3.9	0.0006

To further link our plot data with established vegetation associations, we identified 19 forested vegetation communities within our dataset, of which 18 correlated directly with alliances or associations described in the MCVII (2009) and 14 to the associations developed by Vaghti (2003) (Table 3). Excluded forest assemblages included communities were *Alnus rhombifolia* was the dominant overstory species - a recognized vegetation alliance by the MCVII but a relatively uncommon species on the Sacramento River. Communities that were added as preliminary vegetation associations that were not included in the Vaghti (2003) classification included *Juglans hindsii/Acer negundo* and a *Juglans hindsii/Salix gooddingii* preliminary vegetation communities; these preliminary *Juglans* communities are very similar to their Vaghti (2003) cottonwood counterparts. Additionally, we identified a *Populus fremontii/Juglans hindsii* preliminary community, and an *Acer negundo* preliminary community. The majority of these communities were described in the MCVII (2009).

We were able to describe the association of vegetation communities with floodplain age through a combination of contingency analysis and ANOVAs. The vegetation communities described by Vaghti (2003) and the data presented here are distributed within a similar range of floodplain ages (Figure 2) Only one vegetation community, *Populus fremontii/Artemisia douglasiana*, is distributed on different FPA surfaces ($F_{(1,5)}=26$; $p=0.004$). Vegetation communities are dispersed across floodplain ages that correspond to what one would expect, based on the dominant overstory species' ($F_{(18,123)}=5.03$; $p<0.0001$; Table 3) (Vaghti 2003). For example, stands of Fremont cottonwood and Goodding's willow occur on younger floodplains that range in age from 17 to 25 years old (Figure 2). The restrictions of this vegetation community have been widely studied in other systems where its occurrence is linked to a groundwater depth of less than four meters (Lite and Stromberg 2005).

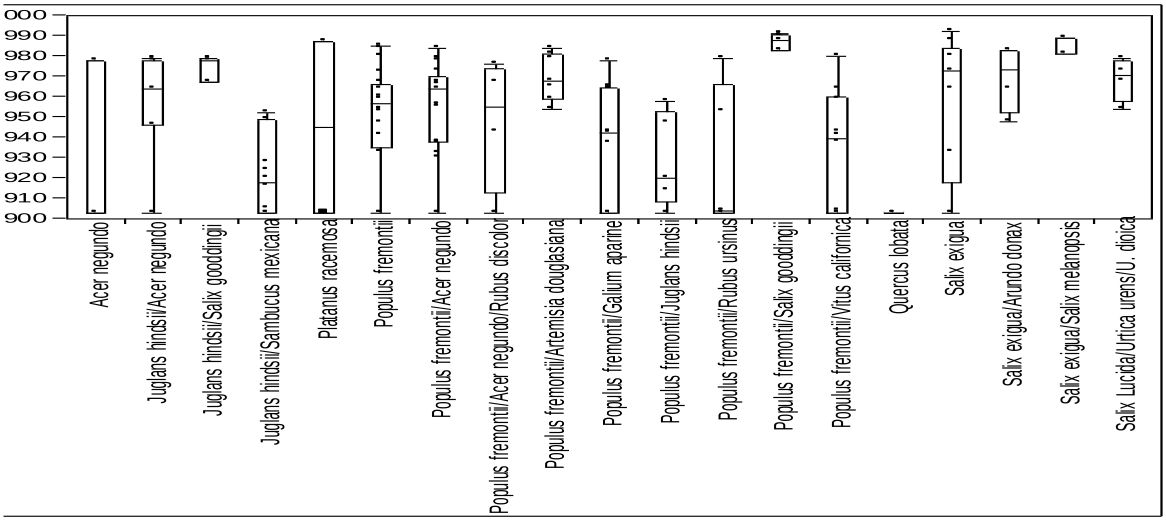

Figure 2. The floodplain age distribution of forested vegetation communities on the Sacramento River.

Table 3. Vaghti (2003) classification, Manual of California Vegetation II (2009) alliance or association, and preliminary vegetation communities and their floodplain age range, mean, and standard deviation.

Vegetation Community	**Floodplain Age Range**	**Mean Floodplain Age (±standard deviation)**	**Vaghti (2003)**	**MCV II (2009)**
Acer negundo	1903-1978	1928±43.3	-	X
Juglans hindsii/Acer negundo	1903-1979	1954±26.2	-	X
Juglans hindsii/Salix gooddingii	1967-1979	1974.67±6.65	-	X
Juglans hindsii/Sambucus mexicana	1903-1952	1922.14±20.4	X	X
Platanus racemosa	1903-1987	1945±48.5	-	X
Populus fremontii	1903-1985	1948.8±27.16	X	X
Populus fremontii/Acer negundo	1903-1984	1956.12±21.37	X	X
Populus fremontii/Acer negundo/Rubus discolor	1903-1976	1947.25±32.62	X	X
Populus fremontii/Artemisia douglasiana	1954-1984	1970±11.6	X	X
Populus fremontii/Galium	1903-1978	1937.56±28.9	X	-

aparine				
Populus fremontii/Juglans hindsii	1903-1958	1928.4±23.16	-	X
Populus fremontii/Rubus ursinus	1903-1979	1928.4±35.5	X	X
Populus fremontii/Salix gooddingii	1983-1991	1987±3.8	X	X
Populus fremontii/Vitis californica	1903-1980	1933.8±29.0	X	X
Quercus lobata	1903	1903±0	X	X
Salix exigua	1903-1992	1957.3±35.28	X	X
Salix exigua/Arundo donax	1948-1983	1969.5±16.9	X	X
Salix exigua/Salix melanopsis	1981-1989	1983.67± 4.62	X	X
Salix lucida/Urtica sp.	1954-1979	1968.5± 10.66	X	X

4.2. Species Relative Cover and Frequency

4.2.1. Total Cover

The natural log (ln) of total cover (calculated as the ln of total overstory + understory cover) was highest on mid to high level floodplains (39 to 86 years; Figure 3). Cover was lowest in the youngest floodplain surfaces; where floodplain ages ranging from 0 to 38 years (FPA group 1 and 2) had the lowest average cover of all the classes ($F_{(4,87)}=3.59$; $p=0.0092$). Cover then decreases after around 86 years (1922), indicating that the most dense forests are in the mid-aged medium disturbance zone on the floodplain.

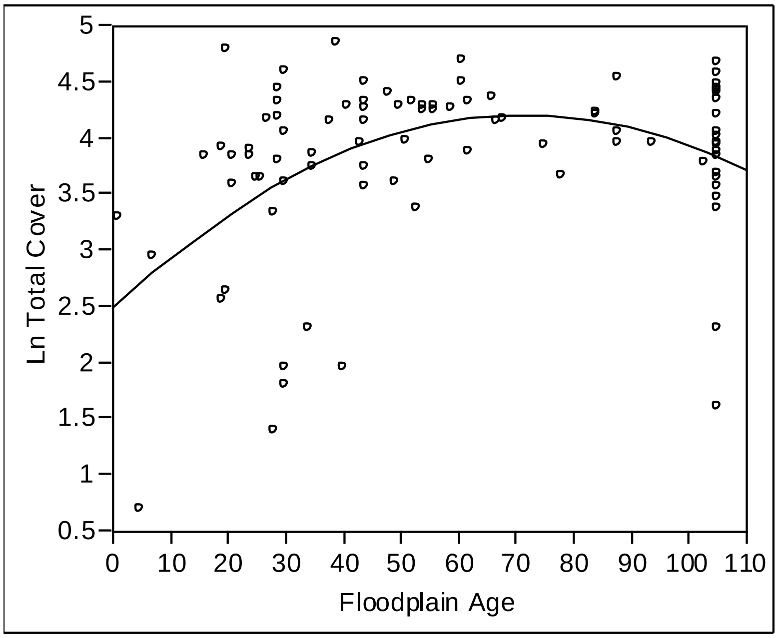

Figure 3. Ln total plot cover by floodplain age on the Sacramento River. Plots on mid to old floodplains have higher cover values than those on younger, less developed floodplains.

4.2.2. Overstory Cover and Frequency

Sixteen species, or about 16% of the total species encountered, contributed to the overstory cover in samples along the Sacramento River. Of those 16, nine are trees and the remainder vines or large shrubs. Total overstory cover was not significantly correlated to floodplain age (data not shown). The oscillations between high and low overstory cover may be indicative of vegetation transitions as large riparian tree species shift from their active growth stage to senescence and eventually transition to the next seral stage (Williams 2006). On a species basis, overstory cover was highly variable and there is evidence of a transition from Fremont's cottonwood/black walnut forest to valley oak forest around 1950 as black walnut and Fremont's cottonwood become less dense and valley oak begins to occur in denser stands (Figure 4). *Populus* species live between 80 to 150 years and recruitment is generally limited to near channel surfaces which limits its longevity on an accreting floodplain, making space for species adapted to dryer conditions (Fenner et al. 1985, Merritt and Cooper 2000, Lytle and Merritt 2004). Additionally, the persistence of box elder forests across the floodplain, a species that was not mentioned as dominant in historical accounts, could be increasing its distribution due to peak flow modifications (DeWine and Cooper 2007).

Species including *Juglans hindsii, Populus fremontii ssp. fremontii,* and *Acer negundo var. californicum* were very frequent in each floodplain age group. The frequency of *J. hindsii* and *A. negundo var. californicum* provides evidence that these species have colonized large areas along the Sacramento River in recent years (See Appendix I). In particular, the prevalence of *J. hindsii* is believed to be increasing due to a mixture of orchard abandonment and hybridization with the cultivated *J. regia* (Hickman 1993). Box elder recruitment in water regulated systems may be affected by changes in peak flow hydrology compared to pre-regulation conditions (DeWine and Cooper 2007). *Quercus lobata* was only present in plots older than 1955 and occurred in and was only present on floodplain ages between 1903 and 1945 in transects.

Generally, shrubs that occur on young floodplains do not extend onto older surfaces, likely due to water restrictions. *Salix exigua* is the only species that occurs on young surfaces to reoccur on older floodplains. A shift in composition appears at around 1970 (FPA 3) where species that are more common in a traditional riparian forest understory begin to be more frequent. *Rubus ursinus* was the most frequent shrub species in all floodplain age groups. It shared frequency, but not necessarily overlap, with *Salix exigua* in FPA 1 and *Toxicodendron diversilobum* in FPA 4. *Rosa californica* and *Baccharis pilularis* were the most infrequent shrub species in our samples.

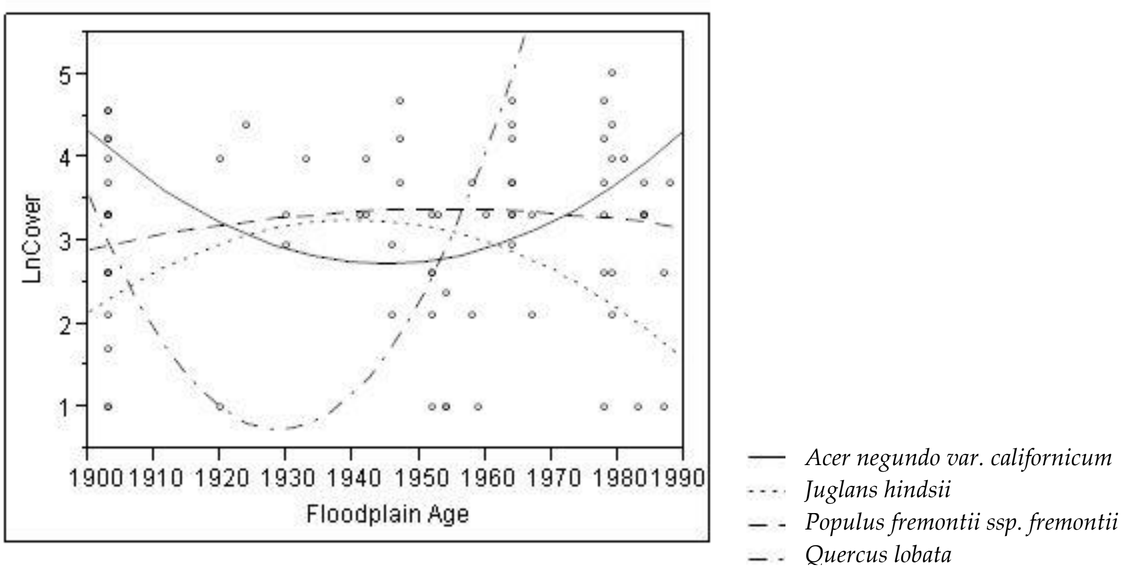

Figure 4. Ln average cover across floodplain age for *Acer negundo* var. *californicum*, *Juglans hindsii, Populus fremontii ssp. fremontii, and Quercus lobata*.

4.2.3. Understory Cover and Frequency

The understory on newer surfaces (younger than 1970) appears to be plagued by non-native species *Sorghum halepense* and *Piptatherum miliaceum.* The understories of these young surfaces also support *Artemisia douglasiana*, which creates dense stands in open forests and forest edges. As the floodplain ages, *Bromus diandrus, Brassica nigra, Carex barbarae, Elymus glaucus*, and *Vitis californica* all play significant roles in the understory of older floodplain age surfaces. This transition has been observed in many instances and is linked to individual species preference for high light or low light environments (Holl and Crone 2004).

4.2.4. Herbaceous Species and Vines

Artemisia californica was the most frequent herbaceous species overall and occurred most frequently on FPA 2 and FPA 4. However, *A. caucalis* and *G. aparine* were very frequent in mid-aged floodplains and created dense mats of dried vegetation in many areas of the floodplain, especially those with more open canopies. The prevalence of *G. aparine* was noted by Holl and Crone (2004) and again by (McClain et al. 2009) in both restoration and remnant forests.

4.2.5. Graminoid

Native graminoid or monocot species along the Sacramento River are important to the development of both forest understory and remnant channel or oxbows created during successive hydrologic events. Restoration forests along the Sacramento River can resist invasion by maintaining high densities of on *C. barbarae* and *E. glaucus* (Holl and Crone 2004). These species contribute heavily to the understory cover in forested areas as they grow in virtual monocultures and can be rhizomatous. *C. barbarae*, *E. glaucus*, and *L. triticoides* all occur frequently on older floodplain surfaces (>1970) but are much less common on newly formed surfaces (<1970), likely due to disturbance regime and canopy cover.

4.2.6. Non-Native Species

Riparian vegetation dynamics is threatened by the encroachment of non-native overstory and understory species. Tree or shrub species, including unnatural stands of black walnut, quickly spreading stands of tree of heaven (*Ailanthus altissima*), tamarisk (*Tamarisk sp.*), fig (*Ficus carica*), and giant reed (*Arundo donax*) can transform environmental variables from well beyond those of native communities. There is some evidence that invasive overstory species will exclude native species due to high levels of shade and possible soil chemistry alteration (Reinhart et al. 2006). The understory can also inhibit overstory species recruitment by outcompeting tree and shrub seedlings. *B. diandrus* and *R. discolor*, both extremely pervasive along the Sacramento River, are documented as inhibiting the recruitment of *Quercus* species in California (Gordon and Rice 2000, Tyler et al. 2006, Williams et al. 2006). Understory development is likely impeded by competition from *B. diandrus* on surfaces that are older than 1970 and *R. discolor* in stands older than 1955. Other non-native species such as *Lepidium latifolium* and *Centaurea solstitialis* may thwart understory and overstory species development by competition for resources. Stands of non-native species were not specifically targeted in this study, and their impacts to both overstory and understory recruitment are under-studied in this system.

The prevalence of *Ludwigia peploides* along the river channel and on young floodplain surfaces (younger than 1983) on the Sacramento River was made increasingly evident by the 2007 vegetation map (Appendix 1) (Nelson et al. 2008). *Ludwigia* invasions have serious impacts to aquatic communities as well as communities reliant on the interface between the channel and the floodplain. Additionally, its invasion on more inland surfaces, specifically remnant channels and oxbow lakes, will heavily impact plant species diversity by reducing opportunities for native species colonization and wildlife usage by reducing wildlife access to water in the summer months.

4.2.7. Historical Description

In the riparian forests of the Sacramento Valley, Fremont cottonwood is a common and persistent species through time (Sargent 1919, Jepson 1925, Thompson 1961, Conard et al. 1980, Greco 1999). The pre-Euro-american vegetation found in the Central Valley, according to Thompson's (1961) historical review of explorers and scientists during the 19th and early 20th century, consisted of three major plant associations: 1) prairies with scattered valley oak (*Quercus lobata*), 2) marsh grass community on lower floodplains, and 3) riparian forests. The dominant riparian species were: sycamore (*Platanus racemosa*), Oregon ash (*Fraxinus latifolia*), cottonwood, alder (*Alnus rhombifolia*), button willow (*Cephalanthus occidentalis*), and several true willows, Goodding's black (*Salix gooddingii*), narrow-leaved (*S. exigua*), red (*S. laevigata*), shining (*S. lucida*) and arroyo (*S. lasiolepis*). Jepson (1925), pg 6) gives riparian stands only a cursory overview, "the narrow curtain of trees along the stream is composed of *Platanus racemosa*, *Populus fremontii*, Sa*lix nigra var. vallicol*a, *laevigata* and *lasiandra* [*lucida*] – though the willows are not confined to the valley floors." Separate from oak woodlands, California sycamore (*Platanus* *racemosa*) forest was emphasized in many descriptions by early explorers. The sycamore forests were more distant from river bank than the cottonwood-willow stands and were described as extending miles from the river channel (Thompson 1961). On drier sites these forests were noted for the large trunks (> 6ft (1.8m) dbh) and open canopy of valley oak (Thompson 1961). Knapp (1965) referred to riparian forests as 'California sycamore bottomland woods.' According to the Society of American Foresters (1954) the valley stands were described as a sycamore-walnut-ash variant of the western United States 'cottonwood-willow' forest type (Barbour and Major 1988). And finally, under Klyver's (1931) classification three groups existed: a 'willow-poplar association' and 'sycamore consociation' and 'valley oak'.

In addition to these three associations, it is important to understand the historical distributions of the other key tree species in the riparian forest of the Sacramento River. In the descriptions by Captain Sir Edward Belcher (Bentham et al. 1844), he noted other woody species such as oak, ash, plane (*Platanus racemosa*), laurel, sumac (sic) [Thompson noted that Belcher probably most likely meant poison oak (*Toxicodendron diversiloba*) rather than sumac], hickory [He also noted that buckeye (*Aesculus californica*) was misnamed hickory since hickory does not exist in California], walnut, roses, wild grapes, *Arbutus* and other small shrubs in the vicinity of the river ((Thompson 1961)on Belcher, 1843). In addition, as early as 1837 the northern California black walnut was discovered along the Sacramento River by Richard Brinsley Hinds. In early work by Jepson (1925) made the observation that the central walnut trees are found adjacent to Native American encampments and predominately at the confluence of rivers. At that time the northern California black walnut (*Juglans californica var. hindsii*) was considered a subspecies of the southern walnut that was transferred to the northern reach by aboriginal American trade. However, as soon as the 1923 version of his manual, Jepson argues to change the northern subspecies to species (*J. hindsii)* status and that its distribution is not dependent on Native American trade. In a report regarding distribution of the northern California walnut, H. H. Thomsen (1963) concludes that northern walnut's narrow distribution in northern central California and the Bay Area region is not dependent on the past Native American trade, but is probably the migration southward of walnut over geologic time. The understanding of walnut distribution is further complicated because walnuts hybridize readily with other introduced stock, such as *J. regia* (*J. hindsii* is commonly used as root stock for commercial propagation). Most likely, the walnut trees growing within the Sacramento River corridor constitute a swarm of natural and introduced walnut stock. This concept is further fortified in light of the contracted distribution of the natural walnut distribution Jepson initially described (Sawyer 2003). Therefore, this report uses the term 'walnut' to describe the genus level plant. This is possible because stems within the genera can be considered ecologically similar (Sawyer 2003).

Continuing the discussion of modern walnut distributions, regardless of its 'native' status, from the earliest accounts to Conard et al.'s work (1980), black walnut was present throughout the human record in the Sacramento Valley but typically did not form large pure stands. Additionally, Oregon ash (*Fraxinus latifolia*) persists through the early to present record; however, it remained in relative low abundance. It is unclear if ash covered much area in the middle section of the river. In Conard et al.'s work, both species are associated with higher floodplains that replace cottonwood stands over time. In fact, Roberts, et al. (1980) list both species (walnut and ash) as 'uncommon'. However, Conard et al. listed walnut as present in oak woodland stands but not present in riparian; yet, ash was the main sub-dominant species in both community classifications.

Often associated with walnut and ash is box elder (*Acer negundo subs. californicum*). Although box elder is not mentioned in early transcriptions, it is thought to pre-date human settlement in riparian areas of California (Jepson 1925) here are neither direct references in the literature questioning its native status nor changes to its specific distribution in California. In general, box elder tends to replace stands of cottonwood through time on higher and older floodplains across North America (Weaver 1960, Johnson et al. 1976). This trend remains true in California riparian areas (Conard et al. 1980, Warner and Hendrix 1984, Greco 1999) In addition, it is repeatedly considered a pioneer species because it is hardy, fast growing and tolerant of slope instability and heavy sediment deposition (Hupp 1992). It should be noted that Conard et al. (1980) associate walnut more with valley oak forests and box elder with riparian forests.

In general, vegetation patches along point bars on the Sacramento River are dominated by narrow-leaved willow. Many reports mention Goodding's black willow and button willow with varying and isolated canopy coverage. With time, cottonwoods eventually out-compete the mixed willow stand for resources, notably light. Tu (2000) concludes this transition to occur at 11-14 years. She separates a cottonwood state from the mixed riparian forest state as described by Conard et al. (1980). In both reports the authors describe species composition trending toward box elder and ash dominance before a late seral forest stage of sycamore and valley oak. Caution is advised when applying Conard et al.'s and Tu's reports to successional sequences on the middle section of the Sacramento River since both studies are predominately in the lower reaches of the Sacramento and San Joaquin valleys; however, the general trend toward valley oak starting from mixed willow, to cottonwood and mixed riparian remains persistent in the literature (including Holland 1986, Greco 1999).

In terms of patch and environmental characteristics on newly deposited floodplains (e.g. point bars), stands typically form in striated patterns parallel to the river flow. With continued channel migration over time, patches often become more distant from the channel and therefore receive less flood water inundation. This distance has been shown to correlate with vegetation patterns (Sigafoos 1961, Everitt 1968, Osterkamp and Hupp 1984, Strahan 1984, Cepello 1991). In addition, scientific literature has focused on soil texture and depth to groundwater as important variables controlling species establishment and distribution patterns (Bryan 1928, Sigafoos 1961, Frye and Quinn 1979, McBride and Strahan 1984, Stromberg 1993). The distribution of sediment is important to the colonization location of seed dispersed cottonwoods. The depth to groundwater at a site helps explain the transition of phreatophytic to non-phreatophytic species.

4.2.8. Stand Replacement of Cottonwood

The 2007 vegetation map of the Sacramento River delineates 23% of the landscape as Fremont's cottonwood while black walnut and box elder vegetation types extend over almost 8% and 3% of the landscape, respectively (Nelson et al. 2008, Viers et al. 2009). The results of a floodplain-wide ordination indicated a poor relationship to physical variables and vegetation types particularly with respect to non-forest community types; however, Figure 5 visually depicts the expected successional sequence of forest species, where plant communities are distributed from gravel bar to mixed riparian forests to valley oak stands (3D solution, final stress = 20.76).

Plots in forested stands were clustered into four groups with very low divisive chaining (1.48%; Figure 6). The resulting groups are separated predominately by herbaceous species, where overstory species have lower overall importance values (Table 4). All but two of the *P. fremontii ssp. fremontii* dominated plots were separated out from the *A. negundo var. californicum* and *J. hindsii* plots in the first cluster (Figure 6). The other three clusters are implicated by a mix of overstory dominance that is defined by understory composition (Table 4). For example, Santa Barbara sedge (*Carex barbarae*) is the only significant indicator of Group 3. Its prevalence is supported by all three overstory species in Group 3, with a split between black walnut and Fremont's cottonwood, with a single plot of box elder. Mean dissimilarity between plots (beta diversity) was greatest between Groups 20 - 1, and 6 - 1, respectively ($F_{(9,936)}$=43.99; p<0.0001; Table 5), however, there was no difference in alpha diversity (i.e., richness) between clusters (p>0.05). Non-native richness was higher in group 6, Fremont's cottonwood overstory group, than in any other group ($F_{(3,34)}$=4.26;p<0.01). Comparatively, native richness was higher in groups 1, 3, and 20 than non-native richness (p<0.01) while there was no observable difference between the two in Group 6 (p>0.05). Additionally, we found that each of the groups had high within-group species agreement and were well separated in species space (MRPP: T: -14.13; A=0.41; p<0.00001).

Our NMS ordination of forested plots resulted in a better relationship to the physical variables than the floodplain-wide ordination (3D solution: 17.72 stress). We observed a relationship between floodplain age, relative elevation and overstory dominance, where Fremont's cottonwood differentiates itself from box elder and walnut forests (Figure 7). The second axis is correlated with floodplain age (R^2=0.268) and relative elevation (R^2=0.202), as calculated by the Pearson's correlation coefficient. These data show strong separation between the Group 1 group and the Group 20 along the FPA-RE gradient with Group 20 generally on lower relative elevation and younger surfaces. This suggests a transition from *Populus* stands to *Acer-Juglans* stands as floodplains become older and more elevated from the channel. The understory of the *Populus* group is generally composed of densely growing forbs and grasses such as *Artemisia douglasiana*, *Piptatherum miliaceum*, and *Galium aparine*. The understory of the *Acer-Juglans* group is characterized by vine and shrub species such as *Vitis californica* and both native and non-native blackberry species. However, in the absence of cottonwood, our data does not present a clear trajectory to indicate which type of community the floodplain transitions into. It is possible that without cottonwood recruitment, the system becomes more dominated by non-native grassland communities.

Table 4. Indicator Species Analysis of Cluster Analysis results and corresponding forest type.

Species	Cluster	IV	Mean±SD	p-value
Acer negundo var. californicum	1	46.6	24.1±6.09	0.0048
Juglans hindsii	1	43.3	25.5±5.14	0.0038
Vitis californica	1	36.5	18.2±6.94	0.0186
Carex barbarae	3	80.8	15.8±7.12	0.0002
Bromus diandrus	6	50.3	19.5±6.77	0.0014
Anthriscus caucalis	6	35.8	21.5±6.42	0.0402
Marah fabaceus	6	33.3	10±5	0.0144
Avena fatua	6	33.3	10±5	0.0144
Bromus hordeaceus	6	33.3	10.1±5.2	0.0172
Leymus triticoides	6	26.7	10.4±6.09	0.0482
Brassica nigra	6	23.2	10.6±6.13	0.0596
Artemisia douglasiana	20	47.7	21.2±6.54	0.0034
Populus fremontii ssp. fremontii	20	37.4	24.5±5.35	0.0314

Table 5. Mean Jaccard Dissimilarity results from the four clusters.

Cluster	Name	1	3	6	20
1	*Acer/Juglans*	0.82092			
3	*Carex barbarae*	0.880499	0.74985		
6	Annual grassland	0.934586	0.921897	0.762238	
20	*Populus fremontii*	0.949642	0.906626	0.865721	0.803918

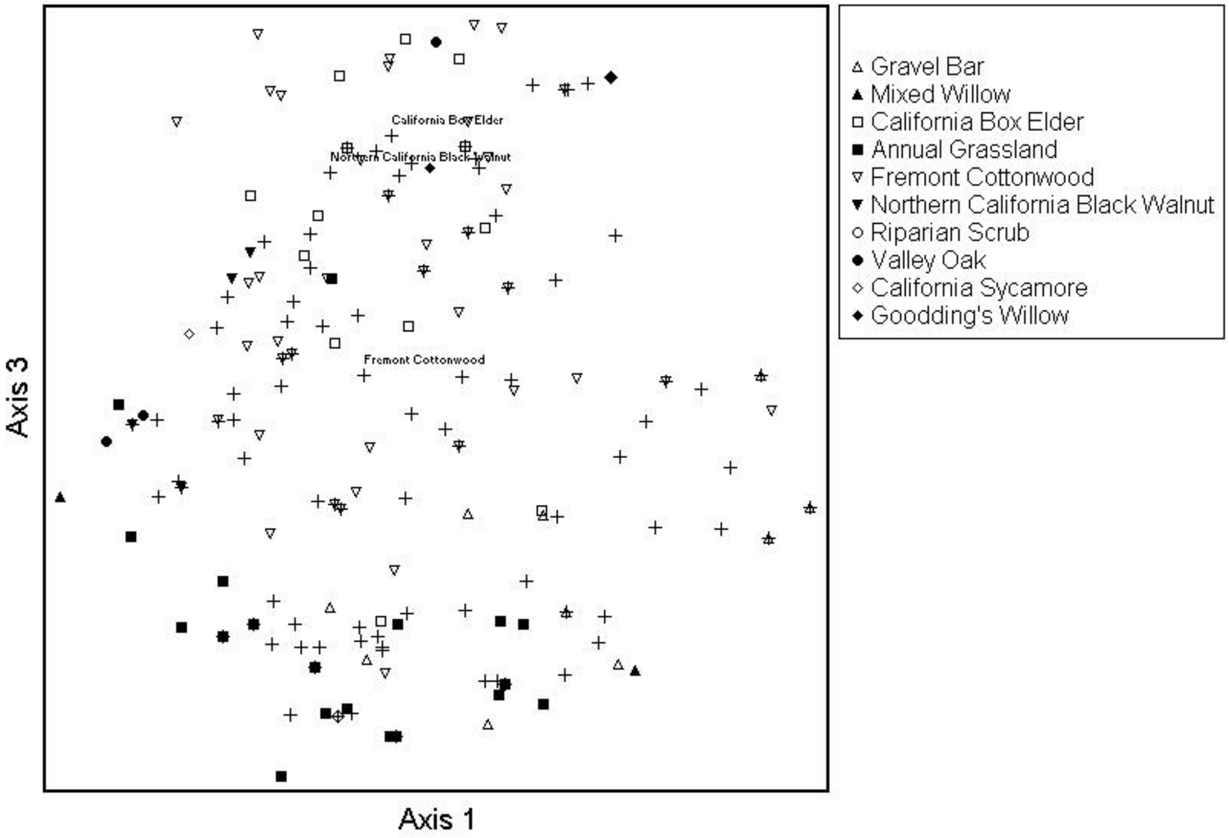

Figure 5. Nonmetric Multidimensional Scaling for all vegetation map classes on the Sacramento River (variance measured as r2 of axes 1 through 3: 0.112, 0.104, 0.228). The plus signs (+) are species positions along axes scores. Generally the gravel bar and grassland groups separated well. Cottonwood, walnut and box elder show overlap is species composition when compared to dissimilar groups.

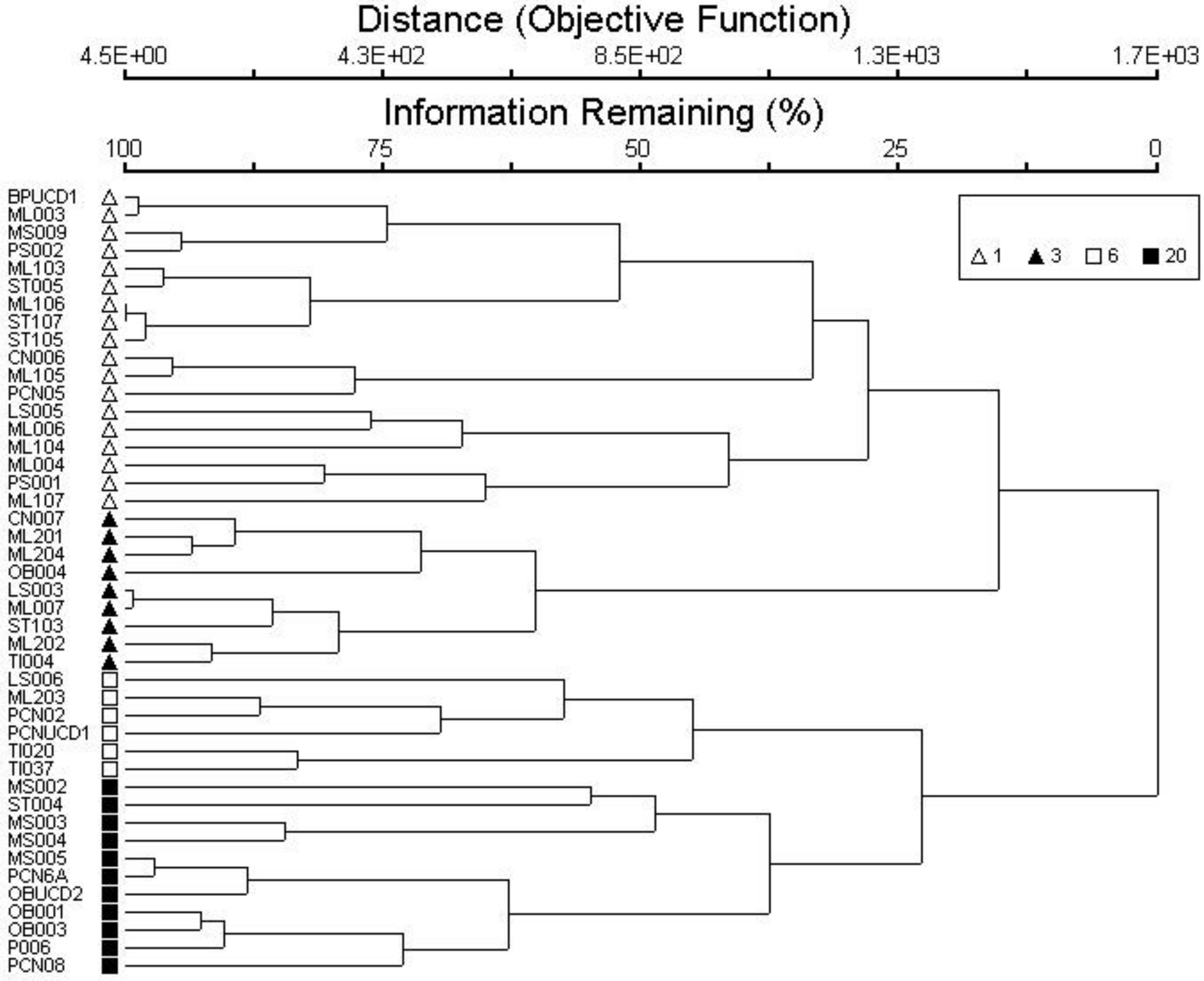

Figure 6. Cluster diagram showing the high degree of separation between defined groups.

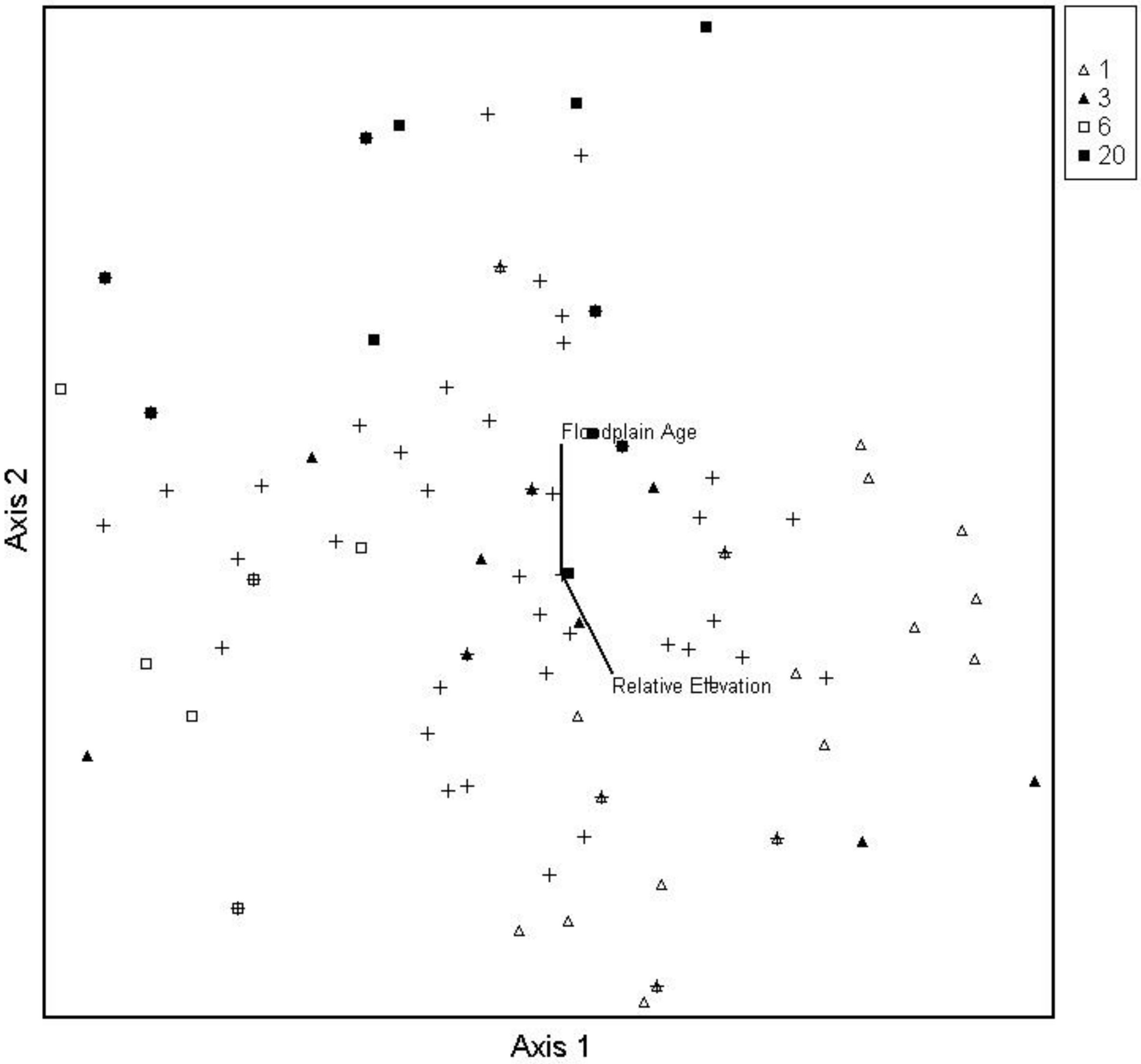

Figure 7. NMS ordination showing the relationship between the environmental variables and the species groups. FPA and RE are inversely correlated due to the fact the FPA is the calendar year, not years since deposition (high RE values equals lower years, e.g. 1904, 1938, etc).

5.0 Conclusion

The relationship between floodplain age and plant species composition is linked to the fluctuation of successional processes driven by river channel migration and channel abandonment. The relationship between riparian species composition and the construction of floodplain age generally conforms well to a successional sequence in forest types (Baker and Walford 1995). However, in analysis of the entire floodplain, the successional model lacks the structure to explain non-forested community types and invasive species. In the case of abandoned channels and the loss of pioneer species, the assembly rules model can be a useful framework to understand changes in riparian vegetation.

We observed repeatable transitions in forest stand development of species dominance between each five of the floodplain age groups. The transition of species composition that occurs between about year 38 and year 70 provides us with a detailed description of what species play a role in the advancement of valley oak forest and the disappearance of Fremont's cottonwood. By delineating the floodplain into distinct temporal units, we are able to piece together a history of specific vegetation communities while making assumptions about its future trajectories. These observations can be directly applied to restoration management and confirm many of the observations about the relationship between restoration and remnant riparian sites (Holl and Crone 2004, McClain et al. 2009)

With continued poor recruitment of cottonwood, it is clear that California box elder and Northern California walnut communities will become more prevalent on the floodplain. California box elder and Northern California walnut communities have already increased in their abundance when comparing current and historical observations. These communities have already become dominant on the landscape and appear to follow cottonwood in the forest successional sequence. This departure from historical conditions will only increase with the continued senescence of pre- and post dam cottonwoods. Although these newly emerging communities might be replacing cottonwoods due to lack of recruitment, it is probably not the only community transition. The historical descriptions of Central Valley riparian vegetation indicate gallery forests dominated by sycamore. Currently sycamore is not found in abundance on the river, it is rarely found in pure stands, and it is considered by many as a hybrid with the London plane tree (*Platanus x acerifolia*). Is the increased abundance in box elder and walnut due to decreased competition and indirectly caused by lack of sycamore recruitment? Currently, we lack a basic understanding of sycamore recruitment, genetic hybridization, and sycamore importance in the riparian community to help answer this and other important questions about the future of the Sacramento River riparian ecosystem.

With the failure of cottonwood to recruit over large areas and on a regular basis, it is likely that California box elder, Northern California walnut, and annual grasslands will become more ubiquitous on the floodplain as an alternative to pioneering cottonwood successional sequences. Box elder and walnut are not pioneer species but can recruit under willow communities. Thus, with the continued recruitment and development of willow stands, box elder and walnut will most likely follow in progression, essentially eliminating the cottonwood forest type from a typical successional sequence. However, in locations on the floodplain where neither cottonwood nor willow recruit, we have observed a potential increase in annual grasslands. A comparison of pre-dam and post-dam landscapes will help to understand the extent of grassland encroachment on the floodplain, and if this is caused by past land uses, reduced competition facilitated by the lack of woody species recruitment, or because post-dam river flows are high enough to scour seedling sized plants. In other words, it is unclear if there is a woody recruitment problem on the Sacramento River like other impounded rivers in semi-arid regions.

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7.0 Appendix

Please see associated file, SpeciesFrequency.pdf