

The Influence of Restored Flooding on
Floodplain Plant Distributions

By

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ABSTRACT

Recent work in riparian restoration has focused on the importance of restoration of physical processes. The assumption behind this is that if rivers are reconnected to their natural floodplain desired vegetation will quickly colonize. This dissertation consists of three studies conducted to test this assumption. The study site is series of former agricultural fields that were separated from the Cosumnes River by high levees until 1985, 1995, and 1998 when the levees were breached and the fields were allowed to flood at moderately high flows (Figure 2.1).

The first two studies result from the observation that natural recruitment of *Quercus lobata*, the dominant late successional riparian tree species, is almost completely limited to the oldest sand splay that was created when water flowed through the 1985 breach and dropped its sediment load. First, an experiment was conducted to determine the impact of inundation timing and duration on acorn germination. The results showed that the lower elevation areas, without new sand deposition, maybe be unsuitable for *Quercus lobata* establishment in all but the driest years. The second study tested the idea that existing forest may facilitate *Quercus lobata* growth or survivorship and looked at the impact of flooding on growth. We found that oaks actually grow faster on the open floodplain than they did in either an early successional cottonwood willow forest or an existing oak forest. On the open floodplain there was a significant negative relationship between inundation and growth rate, but we did not observe any mortality in the three years of the study.

The final study looked at community assembly in the herbaceous wetland communities on the open floodplain. 260 permanent plots were installed along

elevational gradients and monitored for three years. Even the seven year old plots (resulting from the 1995 breach) do not show strong community relationships, show persistent evidence of dispersal limitation, and do not resemble reference communities. They are all, however, dominated by native wetland species and the species in the reference community are all also found in the restored community. Taken together these results suggest that although flooding has been restored and native species have been restored, plant communities are slower to reform.

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CHAPTER 1

INFLUENCE OF FLOOD DURATION AND TIMING ON QUERCUS LOBATA GERMINATION

ABSTRACT

The impact of seasonal flood inundation on riparian tree establishment has been extensively investigated in the southeastern United States, but similar research has not been undertaken in the West where the timing of flooding is different. This study investigates the impact of inundation duration and timing on germination of a major late successional dominant in Californian riparian forests, *Quercus lobata*. Mature oak forests can withstand long periods of winter flooding while they are dormant, but it is not clear what impact such flooding has on acorns, which do not experience winter dormancy. Preliminary observations on a restored floodplain on the Cosumnes River suggest that prolonged flooding limits oak establishment. This observation was tested using greenhouse experiments that measured the impact of inundation patterns, soil texture, and maternal family on acorn germination. Flooding tolerance of *Quercus lobata* appears to be similar to southeastern riparian oaks. Sustained flooding substantially reduces acorn germination rates, but short flooding periods and flooding that ended early in the spring did not have a significant impact on subsequent germination. Maternal groups exhibit significant differences in emergence time, weight and overall survival, but the pattern of response is broadly similar. Soil texture also affects seedling emergence. Acorns planted in sandy soils are more likely to germinate after flooding than those in clay. These results have important implications for restoration of floodplain forests. The presence of healthy adult trees does not necessarily predict the success of natural regeneration, since the trees may have been established under a historic flooding regime. Rather, timing and duration of seasonal inundation is likely to be a more important indicator of potential restoration success.

INTRODUCTION

Regional differences in the timing of peak discharges have resulted in different assumptions about riparian tree establishment in different parts of the United States. In the Southeast where flooding occurs throughout the spring and early summer, inundation during the growing season is clearly a substantial cause of mortality. As a result, researchers have concentrated on the physiological and morphological adaptations that allow survival in the anaerobic conditions created by flooding (Anderson and Pezeshki 1999, Bledsoe and Shear 2000, Sharitz and Mitsch 1993, McLeod et al. 2000, Wall 1999). They have found substantial evidence that both growth and establishment of floodplain trees are impacted by flood duration, intensity, and timing (Siebel and Blom 1998 on the Rhine, Gardiner and Hodges 1996).

By contrast in California and other regions of the country where flooding occurs in the winter and early spring, when mature trees are dormant, floodplain research has focused principally on the role of geomorphology in limiting tree distributions (Harris 1987, McBride and Strahan 1986, Scott et al. 1997). Lower limits of plant distributions are assumed to be caused by scour rather than inundation patterns (Mahoney and Rood 1998, Harris 1987). Researchers have devoted little attention to role inundation may play in limiting the invasion of the secondary successional species. Where the relationship between soil moisture and successional establishment has been studied, it has been from the perspective of low soil moisture as an upper, elevational limit to plant distributions (Callaway 1990, Danner and Knapp 2001, Meyer 2000, Stromberg and Patten 1996).

Although western floodplain trees are deciduous and thus dormant during the winter floods many secondary successional species release their seeds in the fall and undergo no dormancy. Valley oaks, *Quercus lobata*, are the dominant climax species on the floodplains

of California's Central Valley. They are members of the white oaks subgenus, *Quercus*, and thus undergo no winter seed dormancy. The roots of valley oak seedlings begin growing in the fall, sometimes while they are still on the mother tree, and shoots begin to grow in early spring (Jepson 1910). As a result recruitment of valley oaks may be determined by their ability to withstand inundation during their first year. Observations of patterns of recruitment on a restored floodplain on the Cosumnes River in California seem to confirm this. Recruitment is common on high elevation sandy sites, but is comparatively rare on adjacent low elevation sites with heavy clay soils.

There have been numerous studies of seedling growth in a variety of California oaks species (Griffin 1971, McCreary 1991, Matsuda and McBride 1986, Matsuda and McBride 1989, Hobbs and Young 2001). The primary focus of this work is on the factors affecting oak recruitment in upland oak savannahs. The two studies (Matsuda and McBride 1986, Griffin 1971) that kept track of groups of acorns from the same maternal tree found that valley oaks showed much higher between group variation in germination timing than the other more upland species tested. It is possible that this variation may be maintained in the population by yearly variation in the timing of flooding.

Studies of *Quercus* germination and establishment in the southeastern US suggest that both duration and timing of inundation are important, but none of them looked at inundation periods of longer than 8 weeks. In a wet year in California it is not uncommon for sections of the floodplain to be inundated for 20 weeks or more (Figure 1.1). The specific objective of this inundation experiment is to address three questions. (1) Are the flood tolerances of western acorns similar to those of acorns in the south? If inundation is not an important selection pressure on western oaks then western acorns should show reduced flood tolerance. (2) What are the upper limits of inundation that valley oak acorns

can survive and what impact do timing and soil texture have on this upper limit? (3) Are there differences in flood tolerance between maternal groups?

METHODS

Acorn inundation experiments were conducted at the experimental greenhouses on the University of California, Davis campus. This work is part of a larger field research effort on the Cosumnes River investigating the role of seasonal inundation in determining plant distributions. Observations of patterns of natural oak regeneration and planting success on a restored floodplain suggested that inundation may limit the establishment of *Quercus lobata* (Trowbridge, unpublished data, Tu 2000).

These field observations served as the basis for the design of this experiment. Seeds were collected from trees along the Cosumnes River. Soils used for plantings were extracted from the Cosumnes River Floodplain. Finally, inundation times were based on gage data from the United States Geological Survey's Michigan Bar gage upstream from the project. Floodwaters flow onto the experimental floodplain when the Michigan bar gage exceeds 20 m³/s (USGS gaging station 11335000). Historical inundation of the floodplain typically ends by April or May and lasts up to 155 days (Figure 1.1). Experimental flood timing and duration were chosen based on the 94 year record (1908-2002) at the Michigan Bar gage and an assumed threshold of 20 m³/s.(Figure 1.1).

Mature acorns without cracks or insect exit holes were collected from five trees at two different sites along the Cosumnes River. One site is across the river from the restored floodplain and another is 6.5 km upstream. Approximately 300 acorns were collected from each tree October 19, 1999 (tree A), October 30 (trees B and C), and November 3 (trees E and F) and then stored in a refrigerator. Acorns were soaked briefly in water to detect inviable seeds; acorns that floated were discarded. Samples of 20 acorns from each mother

tree were weighed on November 5 and all the acorns from the mother trees with the heaviest and lightest acorns (C and E) were weighed before planting. 1274 cone shape pots (3.8 by 21 cm) were filled with either sand or clay collected from the floodplain restoration site. The acorns were planted, point down, approximately 2 cm below the soil surface to replicate burial by birds or mammals and prevent desiccation, between November 16 and November 20. Some acorns had developed exit holes while in storage. These were not eliminated because previous studies have shown that weevil damage does not lead to reduction in germination (Hobbs and Young 2001, Steele et al. 1993).

The pots were randomly assigned to positions in 18 different trays that were immersed in two large tanks (125 gallons) at assigned times. Over the course of the experiment the pots were re-randomized 4 times to minimize block effects and to facilitate the inundation treatments. The experiment included a total of 130 treatments: 2 soil types by 5 mother trees by 13 different combinations of duration and timing of inundation (figure 1.2). One of these 13 combinations was a control treatment that was never inundated. There were 10 replicate acorns in each treatment except for the treatments involving maternal group “A”, where fewer acorns limited the treatment to 9 replicates; resulting in a total of 1274 pots.

The experiment was conducted outside at the UC Davis experimental greenhouses. Throughout the rainy season (January –April) the pots that were not in the tanks were watered once a week in weeks where there was no natural precipitation. From May to the end of the experiment all pots were watered twice a week.

Previous experiments have suggested that anoxic conditions and high temperatures in the tanks might impact germination (Guo 1998, Briscoe 1961). The water on the floodplain is not naturally anoxic in the spring (Keith Whitener personal communication November, 2000) so an aquarium bubbler was used to maintain dissolved oxygen and

eliminate the growth of algae. The temperature in the tanks was also measured once a week. In order to keep the temperature within the range found on the restored floodplain warm water was drained and replaced with cool tap water. This was difficult to maintain when the air temperatures exceeded 40°C.

From April –July, emergence day (± 3 days) was recorded for each shoot. The experiment was ended in July after no additional sprouts were observed for one month. At that time the above ground shoots were clipped and watering was stopped. In late summer (August, September) the acorns were harvested and the number of roots and shoots were recorded.

Data Analysis

Statistical analyses were carried out primarily using Statistica (StatSoft, Inc. 2001). Germination and survivorship were analyzed with the Julian date the plants were put into the tanks, date they were taken out of the tanks, duration of inundation, soil texture, and mother tree as covariates (Hosmer and Lemeshow 1989). Acorn germination was analyzed by developmental stage (Figure 1.3). The DUD stage compares the traits of acorns that did not germinate at all to those that did. The ROOT analysis compares the traits of acorns that germinated, grew one root and then did not continue to grow after they were removed from the tanks to those that did continue to grow (either by putting out more roots or a shoot). The STEM analysis compares acorn that only grew additional roots after removal from the tanks to ones that grew stems. The final stage analyzed EMERGENCE by comparing stems that emerged from the soil surface to stems that did not. At each stage the maximum likelihood ratio test was used to determine the best model by comparing the likelihood ratio of the model with all the covariates to the models with all the possible combinations of covariates. The best model was assumed to be the model that included the fewest covariates and yet did

not differ significantly ($p < 0.05$) from the saturated model. In order to satisfy the assumption of a linear relationship between the logit and the covariate and to improve model fit (analyzed using Stat View and Pearson χ^2 statistic) the covariate duration of inundation was transformed using either natural log or a quadratic transformation.

Since only the weights of the acorns from two of the five maternal groups were measured, a separate analysis was performed on a subset of the data to determine the relative importance of weight and mother tree. These two covariates were highly collinear, but the trees that had largest acorns also produced some small ones so it was possible to separate the impact of the two predictors. Genetic differences in emergence dates were also analyzed separately using ANOVA. Control data and flooded data were analyzed separately to determine the impact of flooding on the pattern of genetic differences in emergence dates. Post hoc tests for comparison of means were done using Fisher's Least Significant Difference.

Flooded and control data were compared using a G test (a likelihood ratio test for goodness of fit). For this comparison the duration of inundation or day out in question was lumped together with all the shorter inundation durations or earlier dates of removal from the tanks. For example the null hypothesis for the comparison between 9 weeks of inundation and the control is that 9 weeks or less of flooding has no significant impact on overall chance of survival to the EMERGENCE stage.

RESULTS

Sustained flooding substantially reduced acorn germination rates (Figure 1.4). Short flooding periods and flooding that ended early in the season, however, did not have a significant negative impact on subsequent germination. There were significant differences in

emergence date, weight and overall survival of the maternal groups. Soil texture also substantially mitigated the impact of flooding on seedling emergence.

Impact of covariates by developmental stage

The relative importance of the covariates changed throughout the course of seedling development (Figure 1.4 and Table 1.1). Duration of inundation was part of the best model for all developmental stages. Duration of inundation, day in, and day out are obviously closely related. Day in was a significant univariate predictor in the first developmental stage (DUD), but when combined with duration of inundation it did not add to the overall likelihood ratio. The importance of day in at the DUD stage may have been related to the timing of root emergence, relative to date of inundation. If the acorns were inundated before they grew their first root they were more likely to never grow a root and thus be a DUD. Day out was by far the most important predictor at the ROOT stage, the stage that separated the seedlings that died in the tanks from those that continued to grow after removal. Thus, the later in the season the seedling remained in the tanks, regardless of overall duration of inundation the more likely they were to drown.

Maternal genetics was significant at all stages of seedling development, but was most important at the DUD and STEM stages. This variation may have been the result of genetic differences in the flooding tolerance or difference in maternal allocation of resources. Soil texture did not play a significant role until the final stage of development when the stem was growing toward the soil surface.

Soil Texture

Soil texture had an important mitigating impact on duration and timing of inundation (Figure 1.5). 80% of the unflooded (control) acorns in sand germinated while only 63% of the unflooded (control) acorns in clay did (G test p value = 0.064). Acorns that were flooded for 3 weeks showed no significant reduction in germination (9% in sand and 8% in clay, p =

0.25 and 0.26). After 6 weeks of inundation, however, only 6% of the acorns in clay germinated while 55% of those in sand did. This represents a significant decline in germination in sand ($p = 0.03$) and a highly significant decline in clay ($p = 9 \times 10^{-5}$). Seedling stems were able to emerge more quickly through the sandy soil than clay allowing increased overall survival. Sandy soils allowed the acorns to survive longer periods of flooding. Germination rates for acorns in clay showed survivorship similar to acorns in sand that had been flooded for an additional 3 weeks.

Maternal Genetics and emergence date

The maternal groups differed significantly in emergence dates for both the control and flooded treatments (flooded $p = 0.0078$ and control $p = 0.0036$). In the control treatment there was an early emerging cluster including maternal groups A, B, and C and a late emerging cluster that included maternal groups E and F. This pattern in the control treatment does not predict either emergence date with flooding or the pattern of overall survival (figure 1.6, I & II). Maternal groups B and F had the highest survival in the control and flooded groups, but in the absence of flooding group B was in the early emergence cluster and F was in the late cluster. Regardless of their average emergence date in the control, these two successful maternal groups were able to switch their emergence date later than the other, less successful groups, under flooded conditions. This plasticity and their late emergence date may have contributed to increased survival under flooding.

The impact of the duration of inundation on germination also varied across maternal group (figure 1.6, III). Group A was the least impacted by flooding. Seedlings of group A that were flooded for up to 9 weeks did not have significantly different survival rates from the control. This effect was due in large part to the low survival rate of group A acorns in the control group. Although survival of group A seedlings in the control was substantially lower

than the other groups the survival of seedlings of group A that were flooded was no different than groups C and E and only slightly less than groups B and F.

Maternal Genetics and Weight

The covariates maternal family and acorn weight were highly collinear making it difficult to separate their relative impacts. The weights of the maternal groups with the heaviest (group C) and lightest acorns (group E) were measured. Neither of these groups, however, turned out to have the highest overall survival rate. The impact of weight for this subset of the data varied considerably by developmental stage. Neither weight nor maternal family was a significant univariate predictor of survival at the STEM or EMERGENCE stage for this subset of the data. At the DUD stage it was impossible to separate the impact of family from the impact of weight. When weight was corrected for maternal genetics (by dividing the weight by the average maternal group weight) there was no significant effect of corrected weight on survival beyond the DUD stage. Corrected weight was, however, a significant predictor of survival at the ROOT stage. This suggests that maternal genetics determines whether an acorn is a DUD but weight determines whether it can survive long periods of inundation.

DISCUSSION

The results of this study demonstrate the importance of timing and duration of flooding to germination of oaks in a California lowland floodplain. Maternal group, soil type, and weight were all important mitigating factors. Heavy acorns in sandy soil from maternal group B survived long periods or late season flooding the best.

These results are consistent with studies conducted on germination of southern oaks. Guo et al. 1998 found that germination of southern bottomland oaks was not affected by

flooding for up to 30 days whereas the germination of acorns from upland oaks was substantially reduced after only 10 days of flooding, particularly by spring flooding. Briscoe (1961) found that one of the bottomland oaks that Guo et al. tested showed reduced germination after 34 days and another species show no reduction after 34 days. Larsen (1963), however, found only small differences between upland and bottomland oaks. One of his bottomland oaks however actually experienced higher germination after 8 weeks of inundation than in the control, but there was not a strong relationship between duration of inundation and survival for any of the species that he used. The results of this study suggest that *Quercus lobata* has similar flood tolerance to those of southern bottomland oaks and substantially better than upland oaks from that region. This suggests that despite the differences in timing of flooding between the two regions, the flooding selection pressures on germination are similar.

Previous studies of the impact of flooding on acorn germination have suggested that temperature (Guo 1998) and dissolved oxygen (Briscoe 1961) may be significant causes of mortality for inundated acorns. Guo (1998) attributes the lack of survival of his spring flooding treatment (between March 17 and April 16) to increased water temperature and resulting increased anaerobic metabolism. Temperature was allowed to vary in this study as well (from an average weekly high of 13.8°C to 20.4°C and a max water temperature of 33.8°C). Since the temperature also increases on the restored floodplain in the spring no effort was made to distinguish between the impact of temperature and timing on acorn germination. As mentioned earlier a bubbler was used to keep the dissolved oxygen in the tanks at saturation.

The variation in emergence date with maternal group observed in this experiment is consistent with observations of previous experiments (Matsuda and McBride 1986, Griffin

1971). Although emergence date in the absence of flooding did not predict ability to survive flooding, plasticity of emergence dates did improve survival. In particular maternal group B acorns emerged early in the control and late in the flooded treatments and experienced high survival whereas the other groups that emerged early in the control were unable to shift their emergence date later in the flooding treatment and had low survival.

Since this was primarily a germination experiment a pot size much smaller than the trees would need to actually survive was chosen so that a large number of treatments could be easily manipulated. This choice, however, likely impacted survival at the later developmental stages and may have affected the relationship between soil texture and emergence date. Some stems that would have been able to grow to the surface in a larger pot may have been constrained by the pots especially in clay soils.

This experiment was intended to reproduce conditions on the restored floodplain at the Cosumnes River Preserve. This floodplain consists of several former agricultural fields where levees have been breached allowing sediment and water to flow onto the floodplain during the rainy season. The sediment is deposited near the breaches as the velocity of the water decreases, forming sand splays (Florshiem and Mount 2002). These splays are colonized by pioneer tree species (*Populus fremontii* and *Salix sp.*). The oldest sand splay at the site was created in 1985 and now supports a mature primary successional forest with numerous oak saplings in the understory. Natural oak regeneration on the rest of the floodplain is limited and efforts at planting acorns have met with limited success. The former agricultural fields have heavy clay soil and are at considerably lower elevation than the sand splays. This experiment suggests a possible explanation for these observations.

Since the sand splays are at higher elevation they drain earlier than the rest of the floodplain. The oldest sand splay is an average of 0.4 meters above the rest of the floodplain so it takes approximately an additional 200 cfs to flood. Flows of this magnitude are less

common in the spring when runoff is often snowmelt dominated. This experiment has shown that late season flooding can substantially reduce germination and heavy clay soils reduce stem emergence. The sandy soils of the splays also drain more quickly and, while it was impossible to duplicate these conditions in pots used for this experiment, this quicker drainage should also improve survival.

This experiment shows that flooding well within the natural range of floodplain inundation can limit acorn germination and in some cases lower the survival probability to zero. There is substantial genetic variation in emergence date and flood tolerance between maternal groups. This variation, combined with variation in flooding and masting cycles, suggests that valley oak recruitment on the floodplain is highly episodic. The distributions of other late successional species that disperse their seeds in the fall (such as *Acer negundo* and *Fraxinus latifolia*) may also be limited by the ability of their seeds to withstand inundation. Drezner et. al (2001) found that cover of plants with animal dispersed seeds (which commonly ripen in the fall) increased with elevation on the Hassayampa River in Arizona, while *Salix sp.* and *Populus sp.* whose seeds are wind dispersed in the spring, are not limited by elevation. It may be possible for restoration projects such as the one described here to increase recruitment of late successional species by manipulating flood frequency and timing through careful site selection, the use of weirs or shallower levee breaches, but more information is needed.

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Table 1.1. Likelihood ratio test and goodness of fit statistic for the best models for each developmental stage. See Figure 1.4 caption for an explanation of R^2_L

| | Best model | intercept likelihood | model likelihood | chi square | p value | pearson | p value | R^2 | R^2_L |
|-----------|----------------------------|-------------------------|---------------------|------------|-----------------------|---------|---------|-------|---------|
| DUD | duration ² +mom | -574.074 | -407.286 | 333.58 | 6.0×10^{-70} | 21.170 | 0.4486 | 29.1% | 99.3% |
| ROOT | out+mom | -503.893 | -366.488 | 274.81 | 2.6×10^{-57} | 14.175 | 0.4368 | 27.3% | 97.8% |
| STEM | ln(duration)+out+mom | -389.191 | -304.400 | 169.58 | 5.5×10^{-34} | 26.688 | 0.3192 | 21.8% | 100.0% |
| EMERGENCE | saturated model | -326.684 | -228.157 | 197.05 | 4.8×10^{-39} | 96.798 | 0.2933 | 30.2% | 100.0% |

Figure 1.1. The number of times between 1908 and 2002 that the restored floodplain would have flooded. These bar charts are based on gage data from the Michigan Bar gage and the threshold for flooding the restored floodplain at the Cosumnes River Preserve. The black bars are the values represented by the experimental treatments.

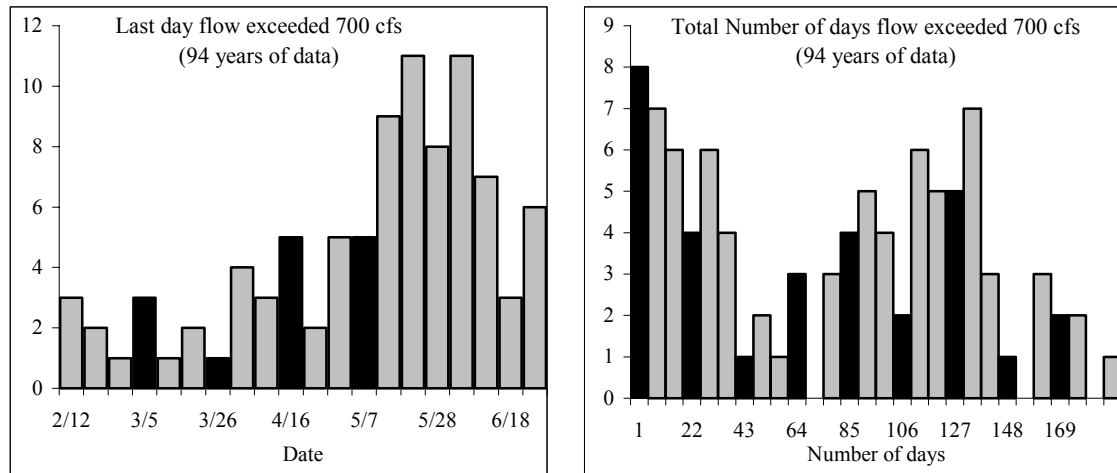


Figure 1.2. The bars represent the time that the various treatments were in the tanks. There is no bar for the top treatment because it is the control and thus never went into the tanks.

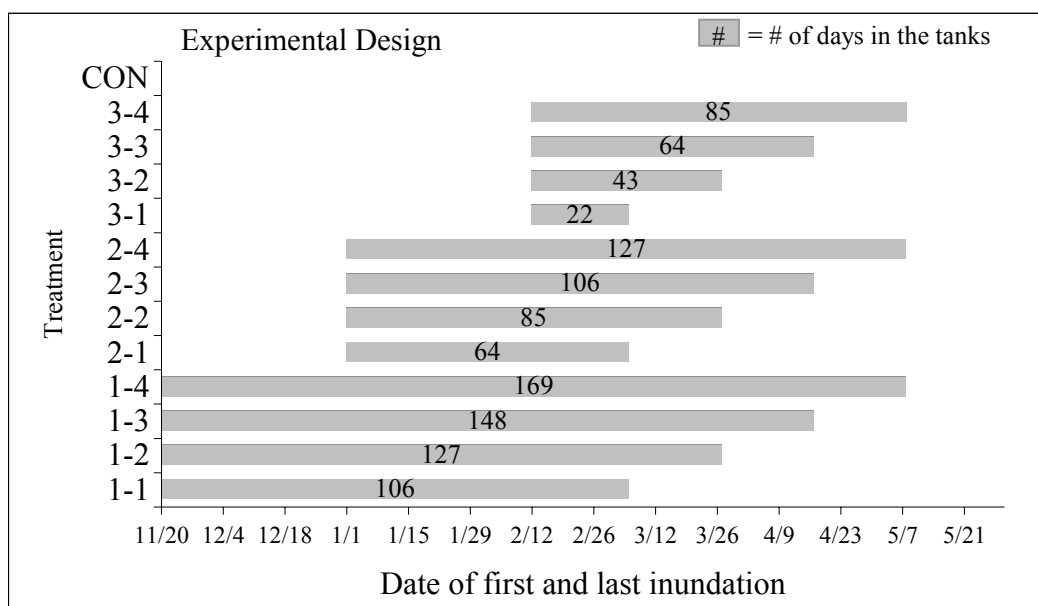


Figure 1.3. The words in capital letters are the names of the developmental stages and the percentage are the percent of the acorns that made it to that stage that either died or went on to the next stage. Dead acorns are shaded.

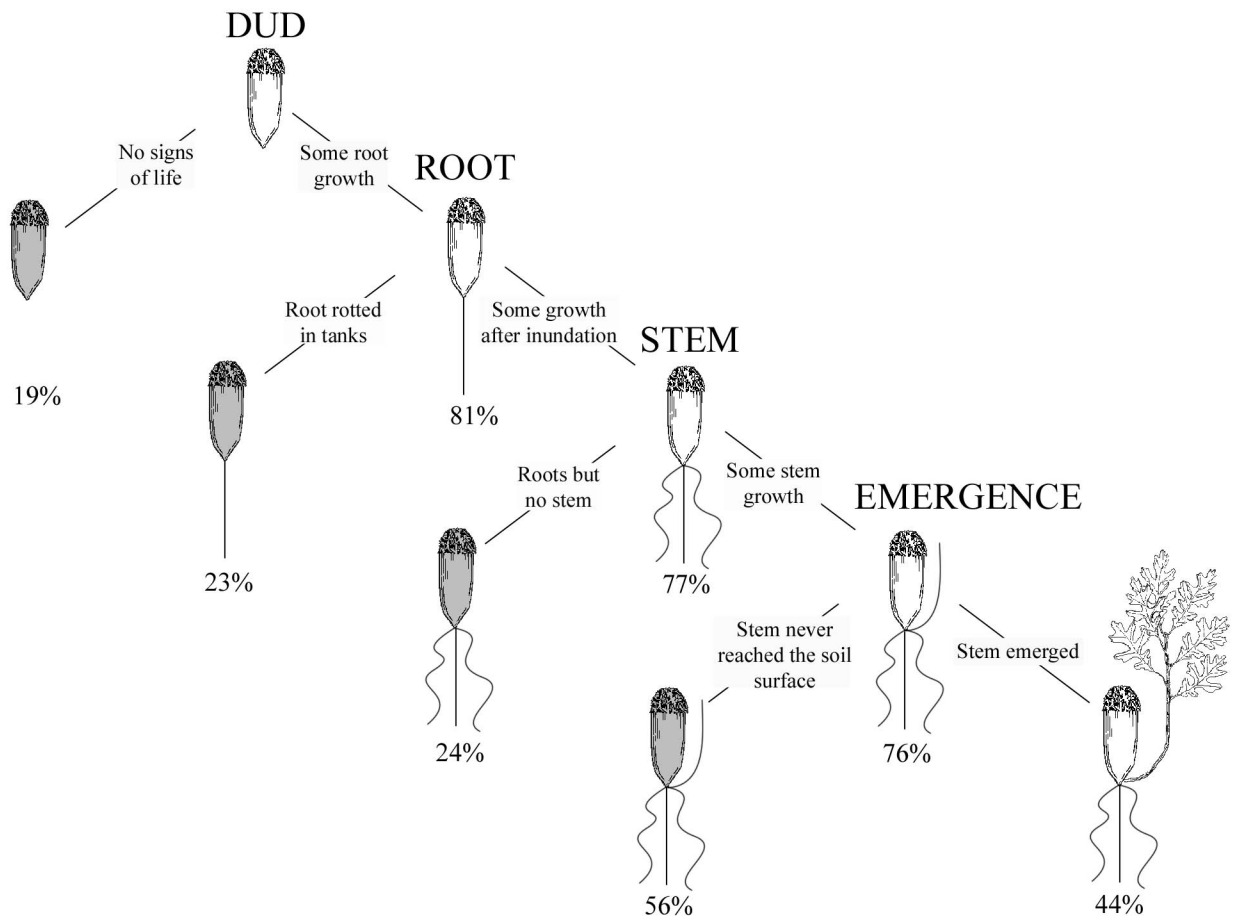


Figure 1.4. R^2_L is a measure of the likelihood ratio comparing the univariate likelihood with the likelihood of the model without any covariates rescaled as a proportion of the likelihood for the saturated model. The stars indicate covariates that were used in the best model.

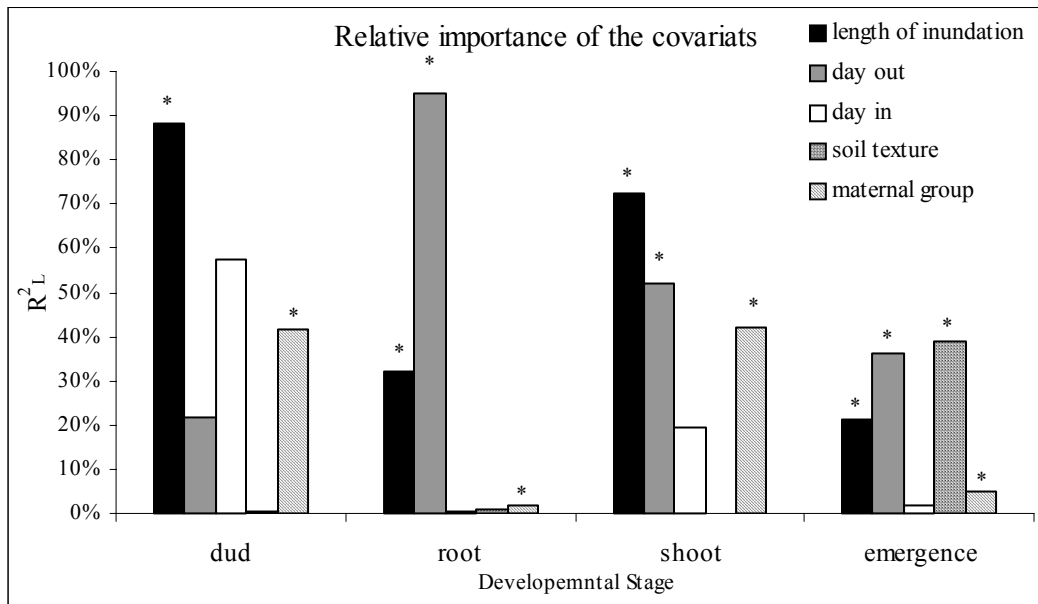


Figure 1.5. The impact of inundation and timing on overall percent survival for both sand and clay treatments. The circles are the p values for a G test comparing the control and flooded treatments (right axis). The horizontal line is at $p = 0.05$. The bars are the total percent survival in clay (black bars) and sand (white bars) under different durations of inundation (A) and timing of inundation (B).

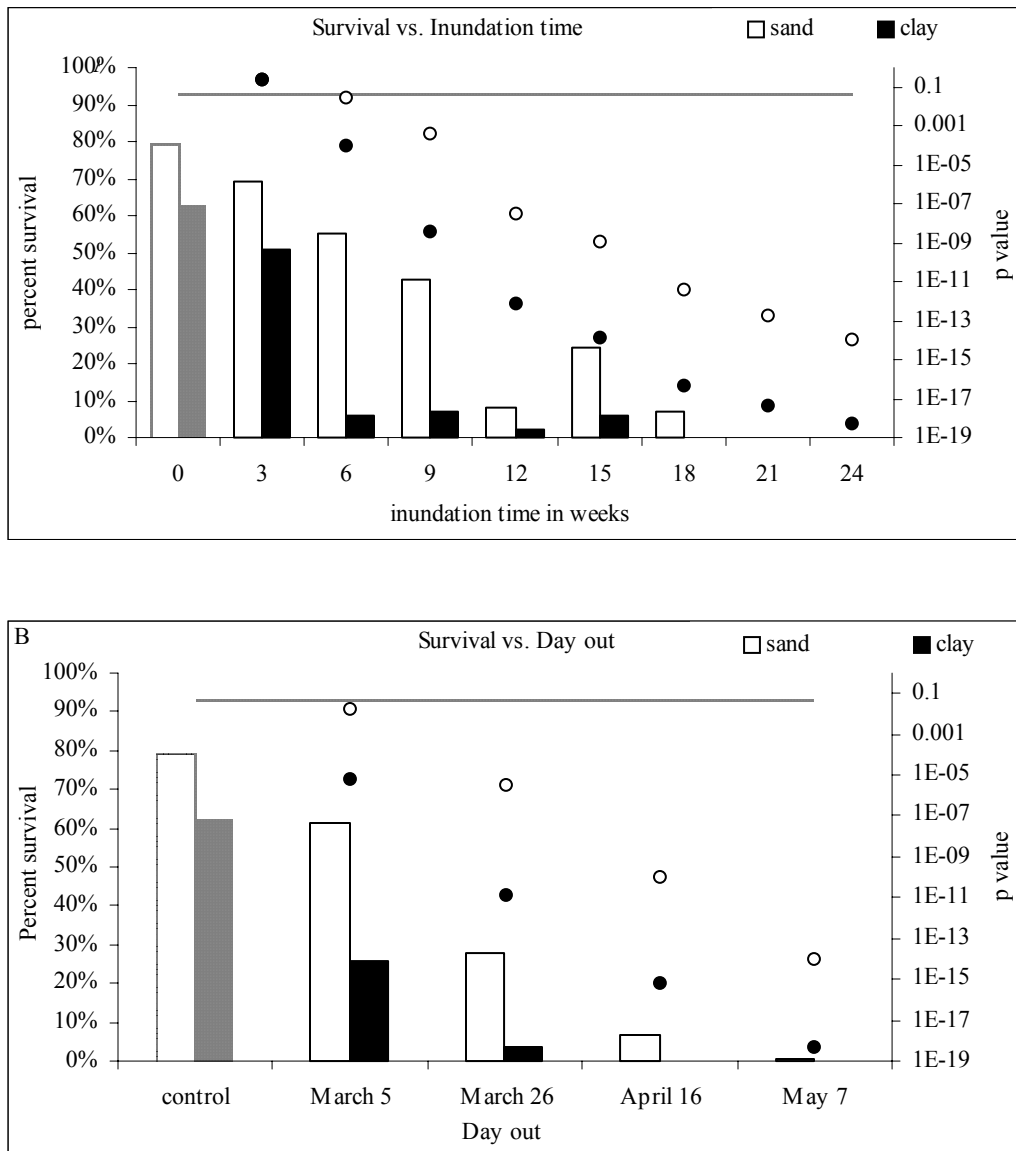
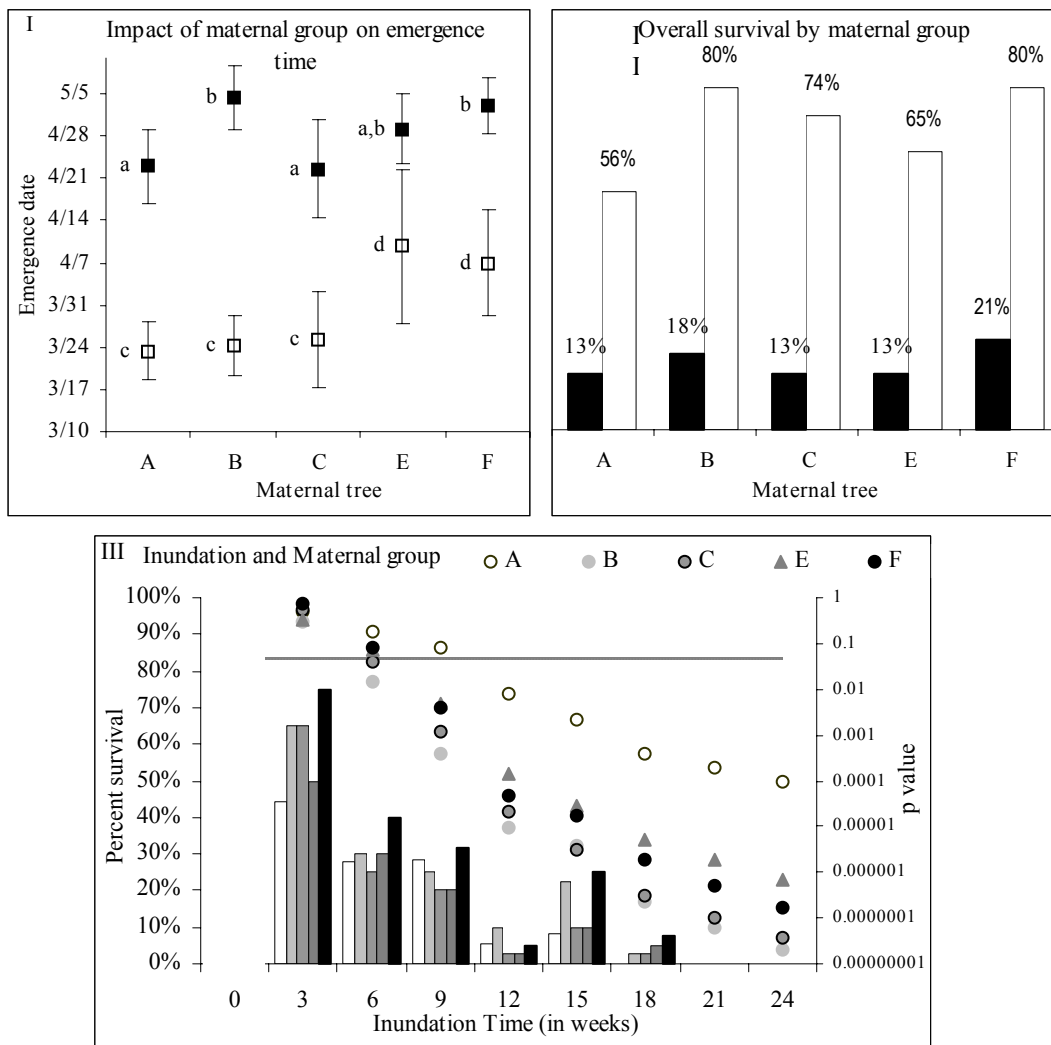


Figure 1.6. **I** shows the differences in average emergence date for the five different maternal trees clear squares represent the control and black squares represent the flooded treatments. **II** shows that maternal group B and F had the highest overall survival both in the control and flooded treatments. **III** illustrates the interaction between inundation and mother tree. The p values on the right and the symbols are the result of a G test comparing the flooded treatments to the control. The bars are percent survival for the different maternal groups at different inundation times.



CHAPTER 2

COMPARING GROWTH PERFORMANCE OF FLOODPLAIN OAKS

ABSTRACT

Concerns about the loss of riparian habitat and lack of oak regeneration in California have led to a proliferation of restoration projects. Adequate understanding of the physical and successional processes that control natural regeneration, however, has lagged behind public desire for restoration. Although there have been numerous studies of upland oak regeneration and growth there has been no research investigating oak sapling growth in riparian environments. This study looks at the performance of valley oak (*Quercus lobata* Nee), a dominant late successional riparian species in California. Growth was measured over the course of three years at four different sites. The sites were chosen to represent the range of successional stages and surface age. Growth was significantly higher on younger, unforested sites. There was no difference in growth rate in the two, forested sites (early successional cottonwood willow forest and late successional mature oak forest). Herbivory was highest in the cottonwood willow forest, where density of young oaks was also highest. The impact of flooding was measured on the youngest floodplain surface, an open floodplain restoration site where acorns were planted the year our study began. There was a significant negative impact of flooding on sapling growth in all but the first year of growth. Taken together these results suggest that existing forest trees and flooding both inhibit the growth of valley oaks on the floodplain, and that restoration in open sites may be more successful than restoration under an existing canopy.

INTRODUCTION

Riparian forests play a disproportionately large role in the regional landscape. They are important natural corridors and provide essential habitat for a wide range of vertebrate species including many threatened and endangered species (Brinson et al. 1981, Dynesius and Nilsson 1994). The position of riparian forests at the interface between aquatic and terrestrial systems allows them to mediate fluxes of water, dissolved and particulate matter, and organisms (Gregory et al. 1991). By the late 1980's less than 5% of the Sacramento Valley's original riparian forest remained and most of the remaining fragments were along the upper Sacramento River (Hunter et al. 1999). With so little remaining, preservation of existing riparian habitats in the lower Sacramento Valley will be insufficient to maintain these vital ecosystem functions. Restoration efforts will be necessary and are being implemented throughout the valley with varying degrees of success (Kondolf and Micheli 1995, Stromberg 2001). An understanding of the relationship between physical processes and the vegetation dynamics of floodplain species is needed for this effort to be successful. We are particularly interested in whether simply restoring physical floodplain processes to the floodplain will be sufficient to allow native forests to reestablish without additional planting of early successional species.

The successional sequence in riparian forests has been described in a wide variety of systems (Strahan 1984, Walker et al. 1986, Streng et al. 1989, Tu 2000). These authors have described a classic successional series. Disturbance-adapted tree species with small seeds (e.g., cottonwoods and willows) are initially dominant. Trees with intermediate sized seeds that disperse more slowly (e.g., maple and ash) slowly invade these relatively open, early successional forests and finally, large seeded shade tolerant species (e.g.,

oaks) dominate the site until disturbance restarts the successional sequence. This conceptual model assumes that disturbed riparian habitat will progress through an orderly sequence of dominance, but there are several possible mechanisms that could produce this observed pattern. These different mechanisms have different implications for restoration.

First, traditional succession theories suggest that early successional species alter their environment, making it more suitable for later successional species (Clements 1928). On the floodplain there are several ways that cottonwood/willow forests might facilitate the growth of valley oak trees. The shade in the forest may ameliorate summer drought conditions, or cause the young oaks to allocate more energy to vertical growth (Holmes 1995, Burger et al. 1996). Herbivory rates in the forest may be less than on the floodplain savanna. Litter accumulation in the forest may provide important nutrients that could increase either growth rate or survival. Finally, cottonwood willow forests may change the physical environment by trapping sediments and protecting small oaks from scour. These mechanisms suggest that successful restoration of valley oaks will require initial restoration of cottonwood / willow forests.

Alternatively, the successional mechanism may be allogenic. Valley oaks may grow equally well wherever the physical conditions are suitable for their establishment. Callaway (1992) suggests that valley oaks are not shade tolerant and experience lower growth rates and higher mortality in the shade. Environments that are unsuitable for cottonwood and willow establishment may also be unsuitable for oak establishment.

On the restored floodplain where this research is conducted, there are currently four environments: 1) highly disturbed areas near the levee breaches; 2) low-lying ponds

and channels that remain inundated too long for trees to become established; 3) floodplain forest dominated by either valley oaks or cottonwoods; 4) open floodplain dominated by herbaceous wetland species, agricultural weeds and some tree seedlings. This classification is similar to that described from the few remaining natural floodplains (Lewis 2000, Junk 1997). The first two environments are not suitable for oak establishment because of high disturbance and prolonged inundation. The goal of our study is to predict vegetation trajectories in the latter two environments by focusing on differences in oak density and performance.

Young valley oaks (*Quercus lobata*) have established naturally in both the forested and open floodplain environments. Density, however, is dramatically higher in cottonwood / willow forests than in either the open floodplain or the mature oak forest. This suggests that either the early successional forest may be facilitating growth and survival of young oaks or that local dispersal vectors favor these forests. An oak planting project on one of the open floodplain sites allowed us to observe the impact of the early successional forest on growth separate from the issue of establishment. To determine the effect of successional stage on oak performance, we measured growth rate and survival of young oaks at four sites of different successional stages, from open floodplain through mature valley oak forest. We also tested two potential mechanisms by which forests may facilitate oak growth: 1) herbivory of young oaks at the different aged sites, and 2) the impact of flooding within an early successional site.

STUDY SITE

Our study site is a 130 ha floodplain located on the Nature Conservancy's Cosumnes River Preserve in the lower Cosumnes River basin approximately 5.5 km upstream from the confluence with the Mokelumne River (Figure 2.1), just east of the Sacramento/San Joaquin River Delta. The Cosumnes River is tidally influenced in the study reach. Although there is water in the channel throughout the year, there is often no connection with the upper Cosumnes basin in the summer. The Cosumnes River originates at low elevation in the Sierra Nevada, so the impact of snow melt on the floodplain is limited. There are numerous small dams and diversions on the tributaries and main stem of the Cosumnes but none are large enough to alter peak flows (Florsheim and Mount 2002).

There are several levee breaches along the study reach that allow water and sediment to flow out onto abandoned agricultural fields where setback levees partially contain the floodwaters (Figure 2.1). The first of these breaches occurred accidentally during the winter of 1985 and was closed the following spring. A large sand deposit from this flood was not removed and a cottonwood and willow forest quickly established. The Nature Conservancy stopped farming and intentionally breached the levee downstream of the original breach in the fall of 1995. Several more accidental breaches were created upstream of this area during the floods of January 1997. In the fall of 1997 the Army Corps of Engineers widened the breach furthest upstream and regraded the sand deposition area, clearing the sand and newly established cottonwood and willow trees and creating an artificial pond. Another sand deposit was established at this breach in spring of 1998, resulting in cottonwood and willow establishment.

In the fall of 1998 six thousand acorns were planted on this, youngest, floodplain and a section of the older floodplain. A group of convicts from a local jail planted the acorns by pushing them into the ground with their boots. These acorns were in no way protected from competition, herbivory or flooding.

METHODS

We surveyed four habitat patches to examine tree performance. These sites are: (A) a restoration site on the 1998 floodplain restoration where the oaks were planted; (B) a 1996 floodplain restoration site where some of the oaks were planted and some established naturally; (C) 1985 floodplain site in the cottonwood willow forest with natural establishment; and (D) a mature floodplain oak forest also with natural establishment (Figure 2.1). At the newer open floodplain sites (A and B) we measured all the oaks that we could find within the area indicated in figure 2.1. The sites C and D were sub-sampled because oak densities were much higher in these two locations. A minimum of thirty-six trees were located and measured in each sub-sampled location.

In order to gauge performance of oak trees we measured the stem length (cm, base to highest tip) and stem basal diameter (mm) for each stem that emerged separately from the ground in the fall of 1999. For each stem we counted the total number of branchlets per tree and the number of branchlets chewed off by herbivores during the 1999 growing season. We remeasured height at the end of the 2000 growing season (winter 2000). For a sub-sample (~30 trees) of trees in each site we also categorized the morphology, and assigned trees to a morphology class.

Finally, we looked at the within site relationship between flooding and growth rate. To do this we measured tree height again at site A at the end of the 2001 growing season and surveyed the location and elevation of each stem using a Lieca TC800 total station. We used ANCOVA to test the between year differences in growth with elevation as a covariate and to test whether the differences in late season flooding in 2000 and 2001 caused a change in the relationship between elevation and growth. Since there was more flooding in 2000 we hypothesized that there might be a larger impact of elevation on growth, which would result in a steeper slope in the regression line.

Trees were selected in the forested sites to span the range of sizes observed on the floodplain restoration sites. All the trees measured were less than or equal to 125cm. Mean tree size among populations was not the same at the four sites ($F = 22.122$, $p < 0.0000$). However, within the sites trees did not exhibit a relationship between height and growth (site A, $p = 0.560$; site B, $p = 0.115$; site C, $p = 0.079$; site D, $p = 0.806$). As a result, all subsequent analyses are presented simply by population and not as a function of tree height. No trees died in any population during the course of this study, so we do not analyze mortality.

RESULTS

Growth

Trees in the forests grew significantly less than trees on the open floodplain ($F = 22.88$, $p < 0.001$, Figure 2.2). Some trees in both environments experienced negative height growth, which may have been a result of herbivory. Trees that declined in total stem height were included in the analyses. The exclusion of these trees changes the effect

size of the difference in height growth across populations, but not the significance of the comparison.

Growth by Elevation

Growth of established trees in the 2000 and 2001 growing seasons was greater at higher elevations (Figure 2.3). Although the elevation range is only 16 cm this translates to a substantial difference in length of inundation. These trees remain inundated after the floodplain and river disconnect and rates of evaporation and seepage to the groundwater are between 1 and 2 cm a day. Snowmelt pulses and late spring rain frequently reflood the lower elevation trees. There was a significant positive relationship between growth and elevation in both the 2000 and 2001 growing seasons. In the first year of growth (1999) there was a slightly negative, though not significant, relationship. In all three years of the study there were substantial outliers (observations more than two standard deviations from the prediction). In 2001 two of the low outliers had negative growth and thus seem to be the clear result of herbivory. Each year one or two of the trees undergo a period of rapid growth that is 30 to 60 cm more than can be explained by elevation. These were different trees each year. There was less late season flooding in 2001 than in 2000 (4 days of flooding after March 1 vs. 38 days in spring of 2000). Despite these differences the results of the ANCOVA of growth by year with elevation as a covariate showed that there was not a significant difference between growth in 2000 and 2001 ($p = 0.12$) and that although the slope of the regression line in 2000 is steeper there is not a significant difference in slopes either ($p = 0.61$).

Herbivory

Most (80%) oak trees surveyed were impacted by herbivory of branch tips and herbivory was significantly higher in the two forest sites than on the open floodplain sites (Figure 2.4). Only 34% and 65% of the trees on the two open floodplain sites (A, B) had one or more damaged branchlets while 97% and 83% of the trees in the forested sites (C, D) were damaged. Branchlet damage measurements provide a more detailed picture of both the amount of herbivory per tree and the variation between trees. The mean proportion of branchlets per tree damaged was 53% in the cottonwood forest (C) compared to 6% and 14% on open floodplain sites (A, B). Herbivory in the mature oak forest (D) was 17%, intermediate between the open floodplain and the cottonwood forest.

On the open floodplain the elevation gradient affected the surrounding herbaceous vegetation. At higher elevations the vegetation surrounding our observed oaks was higher than the young trees and while at low elevations it was more open and less than 10 cm in height. This difference, however, had no systematic impact on herbivory. At the youngest floodplain site (A) the trees surrounded by low vegetation were damaged more than those surrounded by high vegetation (8% vs 0%), but the height of the surrounding vegetation didn't affect the herbivory rate at site B. Growth rate was higher where the surrounding vegetation was higher but flooding clearly confounded this relationship.

Diameter by Population and Height

The ratio of height to basal diameter provides a quantitative description of morphology. Trees with a large height to diameter ratio are taller and thinner than trees with a low height to diameter ratio. Trees in the forest understory were thinner for a given height than trees on the open floodplain (Figure 2.5). Among the floodplain sites, trees at

site B were shorter and thicker than site A. Trees with taller surrounding vegetation had larger height to diameter ratios than tree surrounded by low vegetation, but the difference was not significant.

Morphology by Population

We analyzed morphological variation among populations using a contingency table analysis. Populations significantly vary ($X^2 = 94.5$, and a $p < 0.001$) with forested sites having a larger proportion (80% and 62%) of individuals demonstrating a tree-like morphology, while fewer than 15% exhibited tree-like morphology at either floodplain site. Floodplain populations varied with 70% of trees on the older floodplain exhibiting shrub-like morphologies, while 85% of trees on the younger floodplain restoration exhibiting intermediate morphologies (Figure 2.6).

DISCUSSION

Although we observed a significant impact of successional stage on oak performance it was not the facilitation relationship that we hypothesized. Existing forests may facilitate oak establishment but they do not increase growth or provide protection from herbivory. Open floodplain trees clearly outperformed trees growing within either an early successional (cottonwood) or late-successional (oak) forest canopy. Growth rates are higher, stem diameters are larger for a given height, and herbivory rates are lower in both floodplain sites than in either of the forest sites. Although elevation also has a significant positive impact on growth within the youngest site, the increased elevation in the existing forests does not counteract the other negative impacts of the forest on growth of young oaks.

Tree morphology results are more ambiguous. If we assume that a tree-like morphology indicates healthy growth, then we would surmise that floodplain trees are performing poorly, given the low rates of tree-like morphology in these populations. This pattern would be expected if herbivory on branches is the primary cause of shrub-like growth form by breaking off buds and initiating new lateral bud formation. In contrast, if we assume that shrub-like morphology is a function of increased light levels allowing increased growth rates of lateral branches, then we once again conclude that floodplain trees are performing better than trees within the forested sites.

Since herbivory rates on the floodplain were generally low, we conclude that high light levels is stimulating lateral branch development and that shrub-like morphology is a not an indicator of poor performance or branching stimulated by herbivory, but increased biomass and high growth rate. Within the open floodplain sites, lower elevation trees that tend to be surrounded by lower herbaceous vegetation tend to show a more shrub like growth form. This further supports the hypothesis that this growth form is a response to increased light levels.

These data suggest that oak trees that establish on open floodplain survive as well and grow faster than trees under a canopy. Despite the short time period, the lack of any mortality suggests that many of these floodplain oak recruits may mature into mature adult trees. As a result, one might expect that these trees would be able to mature directly into an oak canopy floodplain forest. Natural establishment on the open floodplain, however, may not be adequate to create a closed canopy oak forest. Tu (2000) observed densities in mature oak forest along the Cosumnes River of from 100 to 400 trees per hectare. There are less than two trees per hectare on the section of floodplain B where no

additional oaks were planted. However, since oak establishment is known to be episodic it is unclear whether it is appropriate to extrapolate densities in this way.

At site C, the cottonwood and willow forest, the density of young oaks far exceed 400 trees per ha. Despite their slow growth rates this abundant establishment suggest that these trees are more likely to become a dense mature forest. In 30 or 40 years there will be gaps created by senescence and death of the current over story trees and the surviving young oaks will experience reduced competition. It is not clear why there is more oak establishment at site C than any of the other sites. It may be because the elevation of the sand splay is higher than the surrounding floodplain or because birds or mammals prefer to bury acorns in the forest or in loose sand. It is clear from this research that the processes controlling establishment are different from the processes controlling growth.

Recent studies have shown a propensity for oaks to be recruitment limited and declining in a variety of ecosystems (e.g., McCreary 1989, Rice et al. 1993, Sork 1993). We can conclude that reconnecting the river with its floodplain is sufficient to create the conditions necessary for oak growth and survival but it is not clear that this kind of passive restoration will create conditions for adequate establishment throughout floodplain. Most of the naturally established trees on the floodplains appear to be a uniform age, suggesting that the combination of conditions that allows for successful oak establishment may be comparatively rare. The years since the levees were breached have been unusually wet. The prolonged late season flooding may have prevented establishment. Guo et al. (1998) found that even oaks that are adapted to flooding could not germinate after long periods of late season flooding. The success of some of the oaks planted in 1998, however, suggests that seed source limitations or dispersal limitations

may also play an important role. As riparian oak forests become smaller and more fragmented due to habitat destruction, dispersal limitation may become an important barrier.

In order to facilitate restoration, ecologists are moving toward a model of restoring natural river processes and allowing communities to reestablish naturally. Although this may be effective for many species such as willows, it is not likely to be true for species that cannot disperse in order to colonize these newly restored sites. Within this context, it is critical to understand the limiting factors for riparian oak forest establishment. From this study we learn that the performance of young trees is not likely to be a limiting constraint. We still do not know the extent to which recruitment is limited by factors such as seed production and dispersal, or the extent to which particular flood conditions conducive to seed germination and early establishment may limit recruitment.

ACKNOWLEDGEMENTS

We would like to thank Ramona Swenson and Jeff Mount for their comments on various drafts and the Nature Conservancy for generously allowing us work on their preserve. This research was funded by the David and Lucile Packard Foundation (grant number 98-3584).

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Figure 2.1. Chronology of restoration activities at the study site. Dashed lines show the location of levees and breaches. The white polygons are sand splays created by the levee breaches. The location of study sites (A-D) are shown on the most recent map.

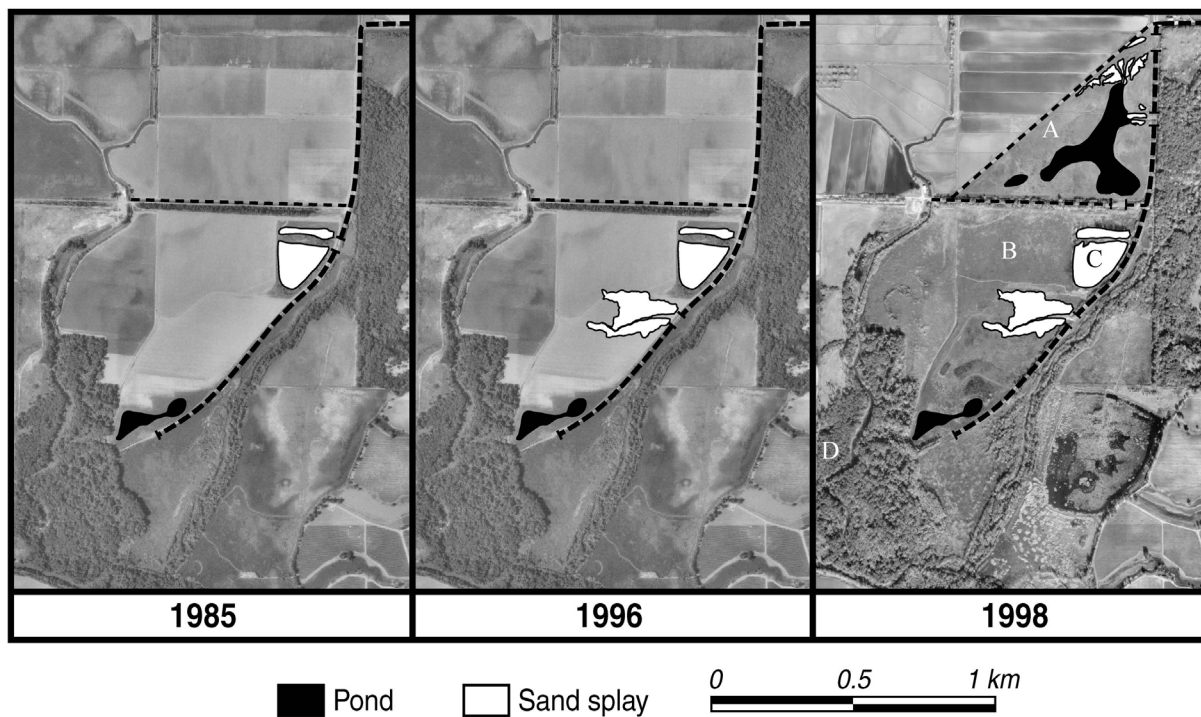


Figure 2.2. Results of ANOVA and post hoc tests comparing growth between 1999 and 2000

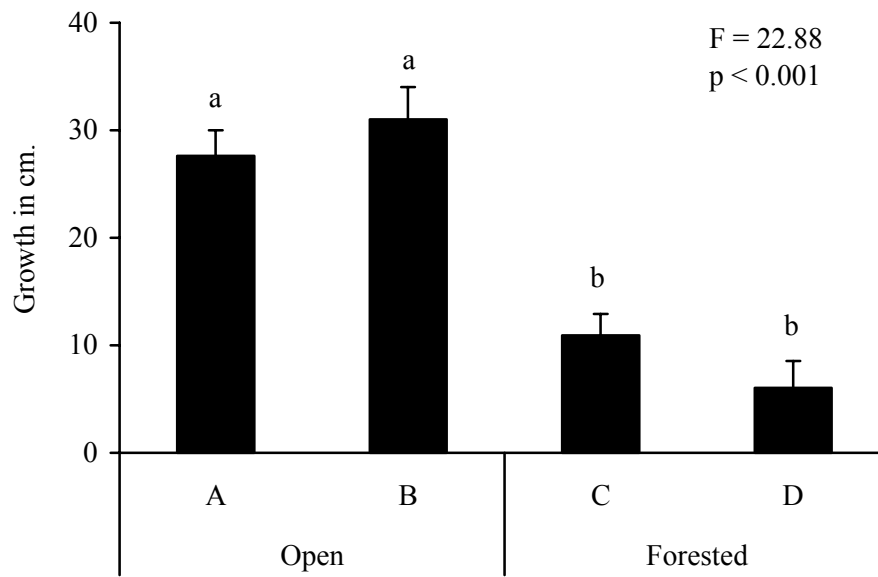
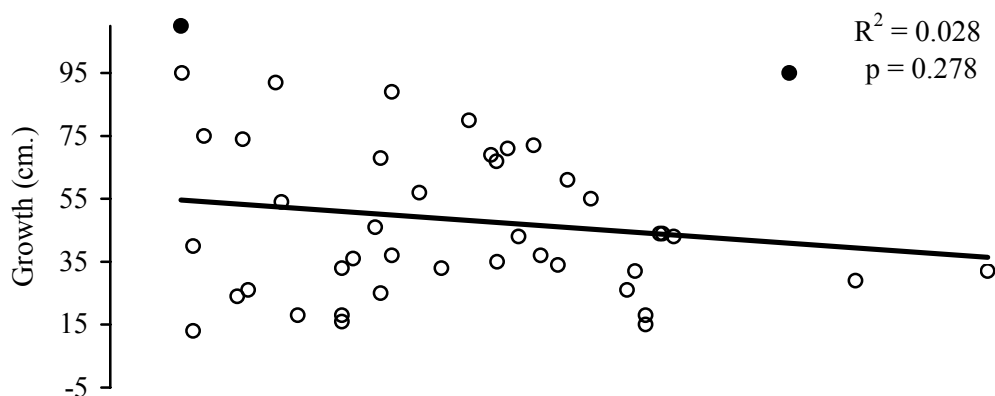
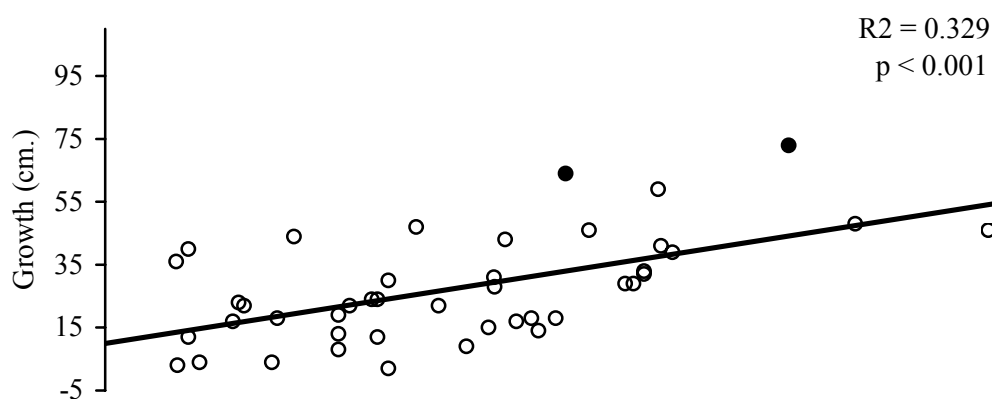


Figure 2.3. Regression results of growth (in cm.) vs. elevation (in meters), which is a surrogate for length of inundation. The filled dots are outliers. Statistics were calculated with the outliers in. A) First year of growth after 130 days of flooding, B) there were 70 days of flooding before the 2000 growing season, C) there were 12 days of flooding before the 2001 growing season.

A) 1999



B) 2000



C) 2001

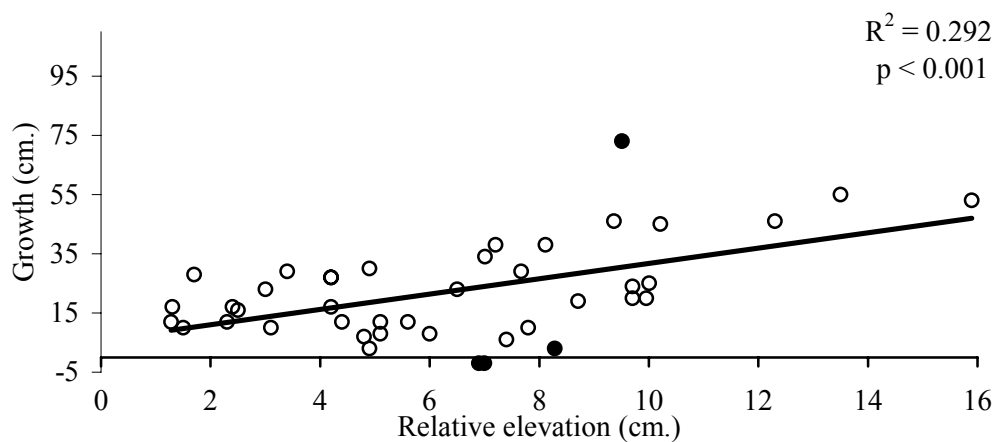


Figure 2.4. Three separate measures of herbivory. The striped bars show the mean percent of branchlets damaged per tree in 1999. The solids show the percent of trees damaged and the white bars show the percent of trees with negative growth in 1999. This is a measure of herbivory in the 2000 growing season. There were no trees with negative growth at the open floodplain sites.

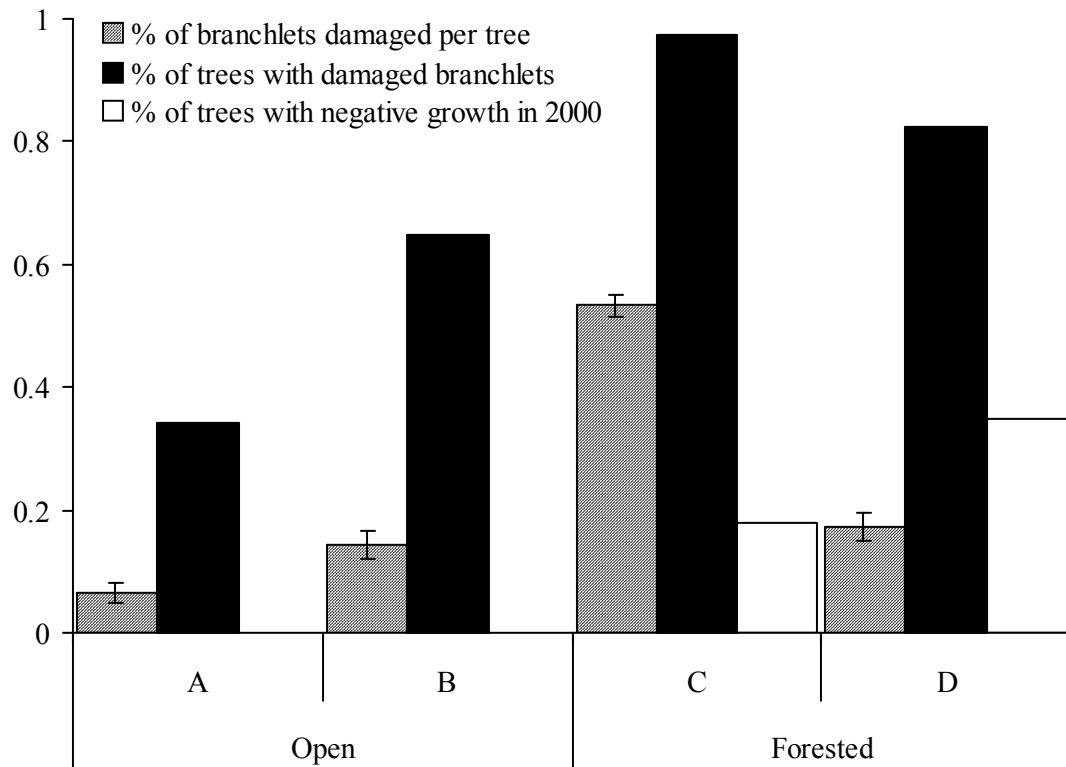


Figure 2.5. The ratio of height to basal diameter is a measure of morphology. Shrub like saplings have a lower ratio than tall like saplings

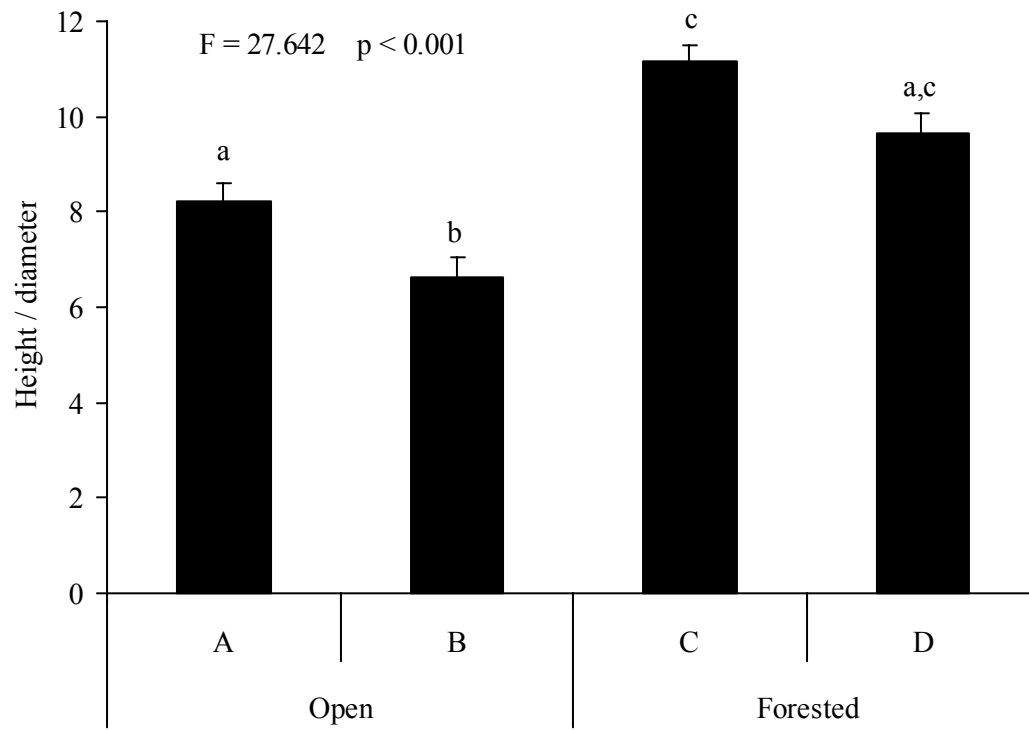
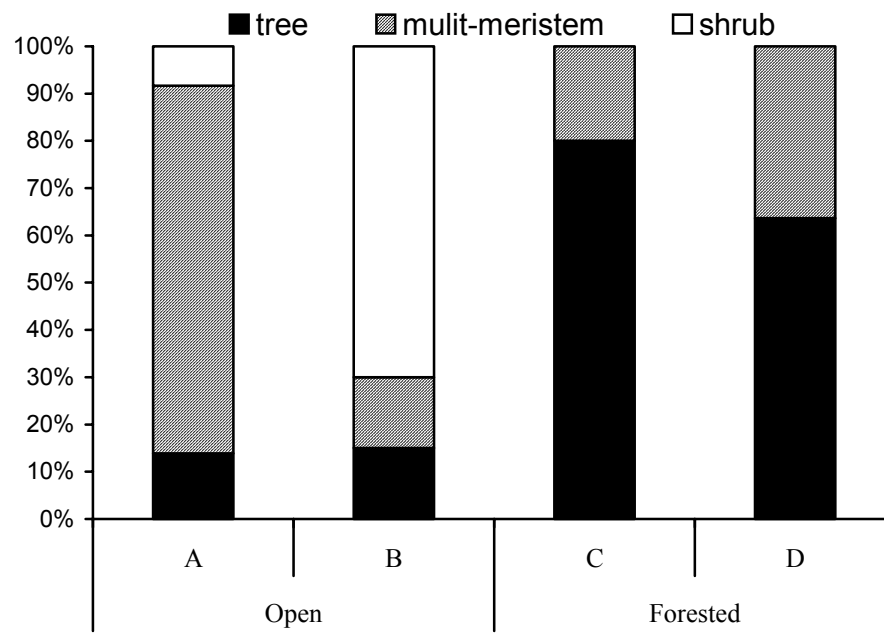


Figure 2.6. Saplings in the forest tend to be more tree-like, having one clear apical meristem and main stem. Saplings on the open floodplain tend to be more shrub-like with multiple main stems and a spherical appearance



CHAPTER 3

THE IMPORTANCE OF STOCHASTICITY ON A RESTORED FLOODPLAIN

ABSTRACT

There has been a recent interest in more process-based approaches to riparian restoration. Underlying this interest is the assumption that we understand the relevant processes and can reproduce them. This study tests the idea that deterministic assembly rules can be found that will predict which species will be found at a given site based on the tolerances of the local species to the environmental conditions. If this is true then: 1) places with similar environmental conditions should have similar species compositions; 2) plots that are near each other but with different environmental conditions should not be similar; and 3) species and community distributions should shift with changes in environmental conditions.

To investigate these hypotheses 260 herbaceous vegetation plots were sampled for three years on two large restored floodplains in California's central valley. The plots were classified into communities using TWINSpan and these communities differed significantly with respect to the main environmental gradient (inundation). The average similarity of the plots in these communities, however, was weak (36%). Bray-Curtis similarities were calculated for each pair of plots and patterns in similarity were used to test the strength of communities and the relative importance of proximity and inundation. On the younger floodplain there was a trend of increasing similarity for plots with similar environmental conditions over the time of the study, but there was also a significant effect of proximity on plot similarity. In addition the shifts in species and community distributions did not closely track the changes in environmental conditions. Taken together, this evidence suggests that assembly of communities is more stochastic than

deterministic and if restoration of specific communities is desired some species may need to be planted.

INTRODUCTION

Large-scale restoration projects provide a unique opportunity to test predictions made by ecological theory and improve our understanding of the processes governing plant distributions. At the same time the success of future restoration and conservation projects depends on a solid understanding of the processes that govern ecological systems. In floodplain wetland systems, external factors such as hydrology and soil fertility clearly play an important role in determining community composition, but it is unclear whether the restoration of the physical system alone will be adequate to allow the regrowth of native wetland plant communities. Invasive species have changed the regional species pool and, while disturbance is part of all floodplain systems, the scale and nature of recent human disturbance is unprecedented. In light of these changes, stochastic processes such as dispersal limitation may play a larger role than has been assumed by wetland ecologists.

Recent theoretical and experimental work on community assembly in wetlands has focused on predicting community composition based on knowledge of the autecological tolerances of the species in the regional pool. Once these tolerances are known then a community of plants can be constructed to match the physical conditions of any given site. Physical conditions and biological factors such as competition and herbivory filter out species whose traits do not match the environment (Keddy 2000, Tofts and Silvertown 2002, Weinhold and van der Valk). As a result restoration should be

a matter of creating the necessary physical conditions to support the species of interest. Restoration practitioners have, in contrast, spent considerable time and money constructing communities by reintroducing desired species.

Mesocosm and seedbank experiments (Casanova and Brock 2000, van der Valk 1981, Stokey and Hunt 1994) have shown that different flooding regimes and soil fertility (Weiher and Keddy 1995) do filter out different species and yield different plant communities. These assembly models are, however, equilibrium models in the sense that they assume that all the species in the general regional pool are represented in the seed bank or can quickly disperse to available sites with appropriate environmental conditions. In wetlands such as lake shores, prairie potholes or salt marshes where disturbance is limited in intensity or extent this is likely to be true. In restored wetlands or floodplains where disturbance can be intense and cover large areas, community assembly may be more contingent and less deterministic (Galatowitsch and van der Valk 1996).

Other assembly models (Drake et al. 1996, Robinson and Edgemon 1988) have found that historical contingencies such as invasion order are important determinants of community composition in experimental communities. In environments where disturbances are frequent and intense, priority effects may play a large role in community dynamics. From a theoretical perspective it is important to explore the limitations of deterministic assembly rules in order to demonstrate the conditions under which they are important (Belyea and Lancaster 1999). From an applied perspective, knowledge of the species and habitats that are likely to be impacted by dispersal limitation could save time and resources currently expended on intensive plantings.

There are two main purposes of this study. First, to test the success of this process-based restoration approach, in terms of the establishment and persistence of native wetland species. Second, to test whether community assembly on a large restored floodplain proceeds in a deterministic fashion with species quickly sorting themselves into communities based on their tolerances of environmental conditions. The alternative condition is that these plant communities are essentially either stochastic or chaotic (Samuels and Drake 1997). Floodplain herbaceous plant communities are inherently short lived. At high elevations they are invaded by trees and converted to forest, while at low elevation they are repeatedly scoured. If communities are going to form at all in this environment, it would presumably have to happen quickly. Two hypotheses were proposed in order to investigate this question. 1) If community assembly is deterministic, then species should sort themselves into strong communities along the controlling environmental gradient, and the cover and extent of individual species and the communities themselves should fluctuate with environmental conditions. 2) If instead historical contingencies govern community assembly, then species distributions should be patchy with neighboring plots having more species in common than distant plots with similar environmental conditions. In addition some species, which are limited by dispersal, should be increasing without regard to environmental conditions.

SITE DESCRIPTION

The study site is a 130 ha floodplain located on the Nature Conservancy's Cosumnes River Preserve in California's Central Valley east of the Sacramento/San Joaquin River Delta. The Cosumnes River is tidally influenced in the study reach. There

is water in the channel throughout the year although the river is disconnected from the upper basin in the summer. The Cosumnes originates in the Sierra Nevada but most of the watershed is at low elevation so snow melt plays only a minor role on the floodplain. The majority of storm pulses occur in the winter. There are numerous small dams and diversions on the tributaries and main stem of the Cosumnes but none are large enough to alter the peak flows (Florsheim and Mount 2002).

Several levee breaches along the study reach allow water and sediment to flow out onto two interconnected abandoned agricultural fields. Low set back levees partially contain the floodwaters within the floodplains. The first of these breaches occurred in early 1986 and was closed the following spring. The resulting large sand deposit was not removed and a cottonwood willow forest quickly established. Farming continued around the forest until fall of 1995, when the Nature Conservancy intentionally breached the levee downstream of the original breach. This older, downstream floodplain is referred to as the southern floodplain. The levee upstream of this area accidentally breached during the floods of 1997. In the fall of 1997 the Army Corps of Engineers widened the furthest upstream of these breaches, built setback levees to contain the flow, and regraded the floodplain, creating an artificial pond. As a result plant establishment did not occur on this northern floodplain until spring of 1998 (Figure 3.1). In their current configurations water flows onto the floodplains in the winter and spring in a series of storm pulses and then slowly drains throughout the late spring and summer. The three years of the study were different both in terms of length of inundation and the last day of flooding (Figure 3.2).

METHODS

This study was initiated in the summer of 2000, when the northern floodplain had been fallow and seasonally flooded for three years and the southern for five. 260 permanent plot markers were installed along 16 transects (140 on the northern floodplain and 120 on the southern). The transects were located in areas with clear elevational gradients and in such a way as to be representative of the range of elevations on the floodplain. Areas close to the breaches where sediment deposition and high flow conditions alter plant communities were eliminated. Within the selected areas the beginning of each transect was located randomly by throwing a Frisbee backwards. The transects were then laid out perpendicular to the gradient. Some are 100 meters long and some are 50 depending on the length of the local gradient. Either 20 or 10 plots were then located along the transect using a random number generator and distance from the beginning of the transect. The random numbers were rounded to the nearest whole number and numbers resulting in plot placement closer than 2 meters were eliminated. The plots were surveyed using a Lieca TC800 total station and mapped onto an arbitrary coordinate system. All pairwise distances between the plots were calculated using the Pythagorean theorem. 40 additional plots were surveyed in 2002 to better represent the range on elevations on the floodplain.

In the first week of August in 2000, 2001, and 2002 the plots were visited. A plastic hula-hoop with an area of $1/3 \text{ m}^2$ and cross strings attached to indicate the middle of the plot was placed over each plot marker. Cover was estimated within each plot using modified Daubenmire cover classes (<1, 1-5, 5-25, 25-50, 50-75, 75-95, >95)(Mueller-Dombois and Ellenberg 1974). Plants were identified using The Jepson Manual

(Hickman 1993) and a plant list provided by the Cosumnes River Preserve. Dr. Ellen Dean at the University of California, Davis herbarium confirmed the identification of all problematic species (primarily Poaceae).

Community Analyses

In order to detect community structure on the floodplain, plots were classified into communities based on their species cover using TWINSAN (a classification method that uses reciprocal averaging and species indicator values to classify plots by hierarchical division, Hill 1979). The two floodplains were classified separately because there are some species that are more common on one floodplain than the other. All three years of data were classified together so that cross year comparisons could be made. Only the most common species on each floodplain were used in this analysis (22 on the southern and 23 on the northern floodplain). Species whose total cover was less than 10% of the area sampled were not used because such rare species may not have been in all plots where they could be community members. Four communities were identified that had roughly similar species compositions on both floodplains. They were labeled Group 1 – 4 based on the average elevation of the plots classified in each group with Group 1 being the lowest.

Inundation was hypothesized to be the main gradient controlling plant distributions within the floodplains. Multinomial logistic regression was used to test whether elevation was a significant predictor of community. Plot number, transect and year were also used as predictor variables since they were not independent. Analyses were performed using StatView (SAS 1998).

The strength of these communities was assessed by comparing the similarity of plots within each community to the similarity of plots in different communities using MEANSIM6, a program developed by John Van Sickle (Van Sickle 1997). If the communities are ecologically significant then plots within the community should have similar species cover, which should be clearly different from the species composition and cover of plots in other communities. In addition, if species are in some way in the process of sorting themselves into communities, then the similarities of plots within a community should increase through time. For each pair of plots percent similarity was calculated using Bray-Curtis similarity, a similarity measure based on the ratio of the minimum cover value divided by the total cover value, of the two pairs, for each species. Values range from 0, when there are no species in common to 1, when the cover of all the species is the same. (Legendre and Legendre 1998). The average of all the similarities within each community was calculated. In order to calculate overall mean within community similarity for each year, the community means were weighted according to the number of plots per community. Mean between community similarity was then divided by weighted mean within plot similarity to create the ratio $M_{(obs)}$. The smaller this ratio is the stronger the community classification.

Dispersal limitation

The importance of dispersal limitation was tested in two ways. First, the trends in species cover, presence, and range were identified. Change in presence was a change in the number of plots where the species was found. Change in cover was the change in total cover of the species on the floodplain, and change in range was a change in the difference in elevation of the highest and lowest plots where it was found. Range was not

calculated if a species occurred in fewer than three plots. Cover and presence were standardized so that their sum was 100% and then combined and divided by 2 to create an importance value, which also sums to 100%. Species that were increasing over the three years of the study in both range and importance value on both floodplains were considered to be overcoming dispersal limitation. Species that increased and decreased with changes in inundation were assumed not to be limited by dispersal. Finally, species that uniformly decreased through the study period were assumed to be disturbance adapted species or agricultural weeds that occupied the site before restoration.

Second, it was assumed that dispersal limited species would arrive in a limited number of locations and then slowly spread to suitable locations throughout the floodplain. If this is the case then after the initial disturbance plots should be most similar in composition and cover to their neighbors, but through time they should be more similar to plots that are at similar elevations throughout the floodplain. Distance, elevational difference, and year were used in a multiple regression to predict the Bray-Curtis similarities of pairs of plots. Plot number and transect number were included as dummy variables. Year by elevation and year by distance interaction terms were used to detect changes in the importance of the two explanatory variables through time. Analyses were performed using Statistica 6.0 (StatSoft 2001).

RESULTS

Autecological trends

The first two years after the breach on the northern floodplain was created *Xanthium strumarium*, a disturbance adapted annual, was the dominant plant on the

floodplain with patches of *Euthamia occidentalis* and *Polygonum amphibium*. Though *Xanthium strumarium* is native, it is a common agricultural weed and is considered invasive by some managers (Wright and Schweers 1984, Holm 1991, Whitson et al. 2001). Throughout the course of the study *X. strumarium* has remained common but other species have become established and it is no longer the only dominant species. No one species or group of species dominated the floodplains throughout the study. The species that covered the largest percentage of the northern floodplain (37%) in 2000, *Eleocharis acicularis*, only covered 2% of the plot area in 2002. *Crypsis schoenoides* and *Echinochloa crus galli* (invasive annual grasses) show the same decreasing pattern while *Bidens frondosa* and *Aster subulatus* (native, annual composites) increased dramatically on both floodplains. *Cyperus eragrostis* (native perennial sedge) is now the most common species on the northern floodplain and *Bidens frondosa* is the most common on the southern floodplain. In general invasive agricultural weeds have decreased in abundance while native wetland forbs have increased. Young trees make up a small proportion of the cover.

Most of the non-native species seem to be decreasing in abundance but there are two species that may create problems. *Lepidium latifolium* is only currently in one plot on the northern floodplain but there are small patches spread throughout both floodplains, especially in disturbed, slightly higher elevation sites like the levees and sand splays. Prolonged spring flooding is known to kill this species (Bossard et al. 2000) but with remnant populations on the levees it may be a continual problem. *Mentha pulegium* is also considered invasive, particularly in vernal pools (Bossard et al. 2000), and has increased substantially, especially on the northern floodplain. In 2000 it was isolated to

one high elevation patch, but now it has spread to the middle elevation communities as well on both floodplains.

There was no clear overall pattern in the change in the species distributions over time. There were individual species that showed each of the expected patterns and other species that showed no pattern at all (Table 3.1). Eight species clearly increased their distributions by most measures on both floodplains and four species decreased. There were a few species that seemed to track the differences in flooding, but the majority of species showed no clear patterns.

There were some natural history and family level trends (Figure 3.3 and 3.4). Perennial species increased and native species increased in cover on the southern floodplain and remained the same on the northern floodplain. Species in the Asteraceae and Cyperaceae families mostly increased while Poaceae and Polygonaceae decreased. Species were also grouped by wetland indicator status to investigate trends. Obligate wetland species decreased throughout the study but the difference was made up almost completely by an increase in species classified as facultative wetland species with almost no change in the frequency of upland, facultative upland, and facultative species (for an explanation of the wetland indicator system see Reed 1988).

Community Analyses

Since the communities on the two floodplains were classified separately, community compositions were different on the two floodplains (Table 3.2). The lowest elevation communities were fairly similar. They have similar species in similar abundances. The two middle elevation communities were less similar. They had more or

less the same species composition, but the abundances were different. The highest elevation plots, which were also more isolated, had few species in common.

Although elevation is clearly an important gradient controlling plant distribution, the communities identified by TWINSpan were fairly weak. The average within community similarity was 36%. Although this is twice the average between community similarity of 18%, it does not suggest a strong ecological relationship between the species. Although the within community similarity on the southern, older, floodplain is higher, there also does not seem to be a yearly trend in the community strength on either floodplain (Table 3.3).

Elevation was a significant predictor of community grouping ($p = 1.7 \times 10^{-61}$ north and $p = 7.2 \times 10^{-31}$ south). The best model included both transect and year ($p = 5.5 \times 10^{-128}$ north and $p = 2.7 \times 10^{-87}$ south). Plot was a better predictor of community grouping, but there was no significant difference between the plot only and elevation only models ($p = 0.998$ north and $p = 0.17$ south). Although elevation clearly plays an important role in community and species distributions, elevational shifts in their distributions do not exactly track inundation. The mean elevation of all the communities and most of the species decreased dramatically from 2000 to 2001 when the number of days of flow onto the floodplain decreased from 107 to 26. In 2002, however when conditions got wetter, with 64 days of flow, distributions of communities and species continued to move down slope or stayed the same instead of moving back up.

Dispersal limitations

Elevation difference and physical distance were significant predictors of plot similarity on both floodplains (Table 3.4). Similarity decreased linearly with elevation

change, but the relationship between distance and similarity was logarithmic; similarity decreased quickly up to about 100 meters, but beyond that point distance was not as important a determinant of similarity (Figure 3.5). There was also a significant elevation by distance effect suggesting that plots that are near each other and at the same elevation are more similar than distant plots at the same elevation. On the northern, younger, floodplain there was a significant year by distance and year by elevation effect but the coefficients were of opposite signs suggesting that elevation is becoming more important and distance less so. There was no significant year by distance or year by elevation effect on the southern floodplain (Table 3).

DISCUSSION

Historical contingency clearly plays an important role on this restored floodplain even seven years after the cessation of farming and restoration of flooding. Although elevation is an important control of species distribution, only weak “communities” of interacting species have formed. These results suggest that although restoration of floodplain wetlands could be delayed by dispersal limitation, especially for perennial species, invasive species have not fundamentally changed the community assembly process. Agricultural weeds from the surrounding farmland completely dominate the levees and sand splays but have been out-competed on the less disturbed, lower elevation portions of the floodplain.

The topography of the floodplains plays an important role in dispersal limitation. Low elevation communities are fairly contiguous throughout the two floodplains. Wind and water flow through these habitats, dispersing seeds across and between the

floodplains. In contrast the higher elevation plots are much more isolated. The three patches of high elevation habitat that were sampled are hundreds of meters apart and though they share a common inundation regime have almost no species in common. The northern floodplain had an artificial pond in the center that split areas of mid and high elevation habitat while the southern floodplain slopes from north to south creating more contiguous habitat. This may have contributed to the observed differences in the dispersal limitation on the two floodplains.

The fertility and agricultural history of the two floodplains may also contribute to observed differences. The southern floodplain was planted in row crops while the northern field was in rice. In 2001 much of the middle elevation habitat on the southern floodplain was covered in *Lotus purshianus*, a nitrogen fixer, while the same species was rare on the northern floodplain. *Cyperus eragrostis* is the most common mid-elevation species on the northern floodplain while it is less common on the southern floodplain. *Polygonum amphibium* is also much more common on the southern floodplain. These differences may be explained by differences in fertility or by differences in flooding history. The two years before the northern floodplain was created were very wet. In contrast 2001 and 2002 have both been relatively dry. Thus, we would expect that plants that can only establish in wet conditions would be more common on the southern floodplain. *Polygonum amphibium* in particular seems to follow this pattern. It grows in all communities on the southern floodplain, but only the lowest elevation communities on the northern floodplain.

The community results are more ambiguous. Clearly there is a statistically significant difference between the similarities of species within communities and between

communities, but the ecological significance is not as convincing. If a community is a group of plants that co-occur, not just because of their mutual tolerance for the physical conditions, but also because of their biological interactions, then an average of 36% similarity seems low. How can species interactions be structuring communities when the biological landscape is so variable? This would seem to support Gleason's individualist hypothesis (Gleason 1939) over Clements' community unity hypothesis (Clements 1916). However, the importance of competition is likely to increase as dispersal limitation decreases. The overall decrease in observed species' ranges suggests that competition may be starting to limit the distribution of some species.

The movement of the community boundaries through time, in response to yearly changes in inundation, may make the formation of tight communities of plants based on biological interactions unlikely. 75% (77% on the northern floodplain and 72% on the southern) of the plots changed community classification at least once in the three years of the study. Only the highest and the lowest elevation plots had stable species compositions. This could have extended the effect of dispersal limitation because in order for annual species to closely track the yearly changes in inundation they have to disperse to areas where they can't currently grow but where they may be able to grow in future years.

The communities that were identified do not correspond well to any of the communities defined by Sawyer and Keeler-Wolf (1995). The broad physical conditions on the floodplain are similar to those described for the Bulrush and Bulrush-cattail, Cattail and Spikerush series, but the species compositions do not match. South of the restored floodplains, and slightly lower in elevation, there is a reference community that

was not farmed or leveed. This area is dominated by *Scirpus fluviatilis* with patches of *Polygonum amphibium*, *Paspalum distichum*, and *Euthamia occidentalis*. *Typha latifolia* is also a common dominant in areas of the preserve that are permanently flooded. Through time, with the formation of organic rich soils, these same communities may dominate the lower elevation sections of the restored floodplain. *Quercus lobata* seedlings in the higher elevation communities suggest that these areas will eventually become valley oak riparian forest.

Autecological trends may also have been impacted by the prevalence of plot transitions. In 2000 75% of the plots were classified into Group 1 (the lowest elevation community), while in 2002 only 16% were. The opposite is true of Group 3. In 2000 only 3% of plots were classified into Group 3 but by 2002 44% were. Species with strong associations with communities that were increasing tended also to increase in presence, cover, and range while species associated with low elevation areas of the floodplain decreased.

The decoupling of the changes in inundation and average community and species elevation suggests that species have a limited ability to respond to environmental changes. There seem to be two reasonable explanations for the low 2002 average community elevations. First, since up-slope boundaries in wetlands are often caused by competition and down-slope boundaries are caused by tolerance to inundation (Keddy 2000) superior competitors should have moved down slope in 2001. Some of them may have been limited by their ability to disperse and so in 2002 when conditions were wetter their tolerance for inundation was not exceeded. Another possible explanation is that establishment limits plant distributions. Van der Valk (1981) showed that only a small

number of species could establish in saturated condition. In 2001 perennial species may have become established further down slope than they could have in the past. In 2002 these perennials may have been able to persist in wetter environments where they could not have become established. In future years, if perennial species continue to increase, the large elevation shifts observed in this study may be dampened.

In summary, this research suggests that although native species readily established after the restoration of flooding, plant establishment is stochastic. As a result communities dominated by native perennials are slow to form and, if managers have specific species targets, some plantings may be necessary. Communities that are not structured by competition but by stochastic processes may be more vulnerable to invasion.

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