

## Growth of Valley Oak (*Quercus Lobata* Nee) in Four Floodplain Environments in the Central Valley of California

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Received 26 March 2003; accepted in revised form 25 February 2004

*Key words:* Community assembly, levees, *Quercus lobata*, restoration, succession

### Abstract

Although there have been numerous studies of California upland oak regeneration and growth there has been no research investigating oak sapling growth in riparian environments. This study looks at the growth response of young valley oak (*Quercus lobata* Nee), a dominant late successional riparian species in California, across environmental variation on a floodplain. 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 these efforts 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. In this case the late arrival of the oaks would simply be a result of dispersal limitation.

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 are inadequate to facilitate open floodplain establishment. 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 3.5 miles upstream from the confluence with the Mokelumne River (Figure 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 in the Sierra Nevada, but the majority of the watershed is at low elevation such that it is primarily a rain driven watershed. 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 1). The first of these breaches occurred accidentally during the floods of February 1985 and was closed the follow-

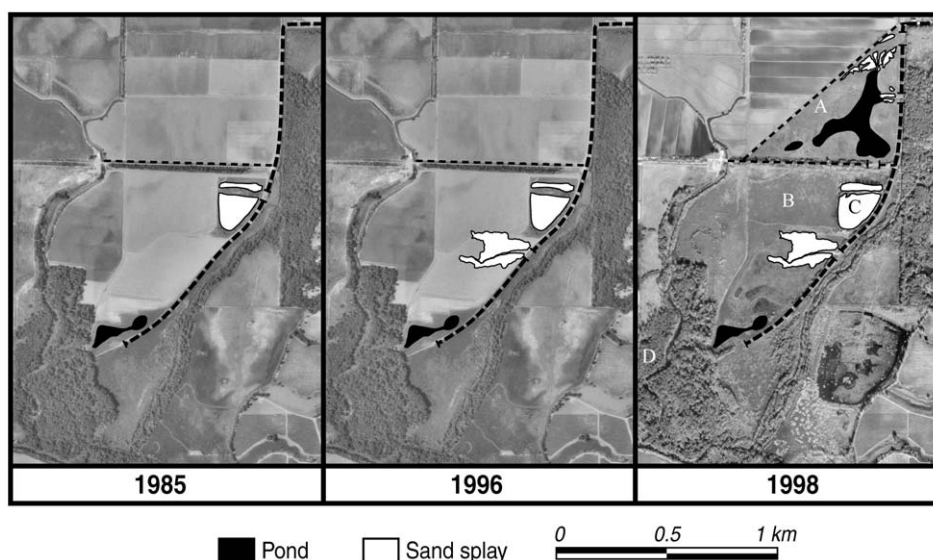


Figure 1. Chronology of restoration activities at the study site. Dashed lines show the location of levees and breaches. The white polygons are sand splays created by the levee breaches. The location of study sites (A-D) are shown on the most recent map.

ing 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 splay was deposited 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 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 1). At the newer open floodplain sites (A and B) we measured all the oaks that we could find within the area outlined in Figure 1. The sites C and D were sub-sampled for trees as oak densities were much higher in these two locations. A minimum of thirty-six trees were located and measured in each sub-sampled location. Despite the replication of trees within these four sites, sites are not replicated with respect to times since restoration began nor canopy cover. As a consequence, our statistical inferences are limited to these particular floodplain sites, although we have no reason to believe these sites to be unique in any way.

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 previous growing season. We remeasured height at the end of the 2000 growing season (winter 2000). Canopy cover, and hence light conditions, as well as levels and types of herbivory can alter tree morphology and influence potential recruitment success. We measured tree morphology using two metrics. First, a ratio of stem basal diameter to height is an indication of resources allocated to height growth. Second, a scale from shrub-

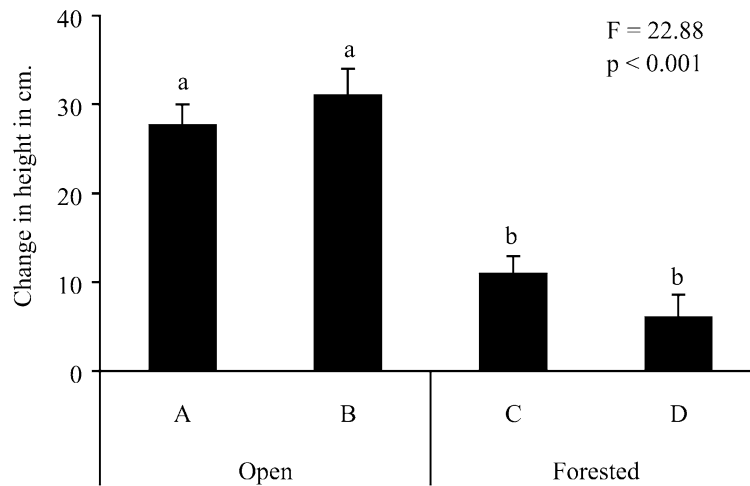


Figure 2. Results of ANOVA and post hoc tests comparing the change in height ('growth') between 1999 and 2000.

like (multiple apical meristems) to tree-like (a single dominant apical meristem) was used to subjectively classify the gross morphology of trees.

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. 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). 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 because herbivory may also have reduced apparent growth in other trees. 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 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 becomes disconnected from the river 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

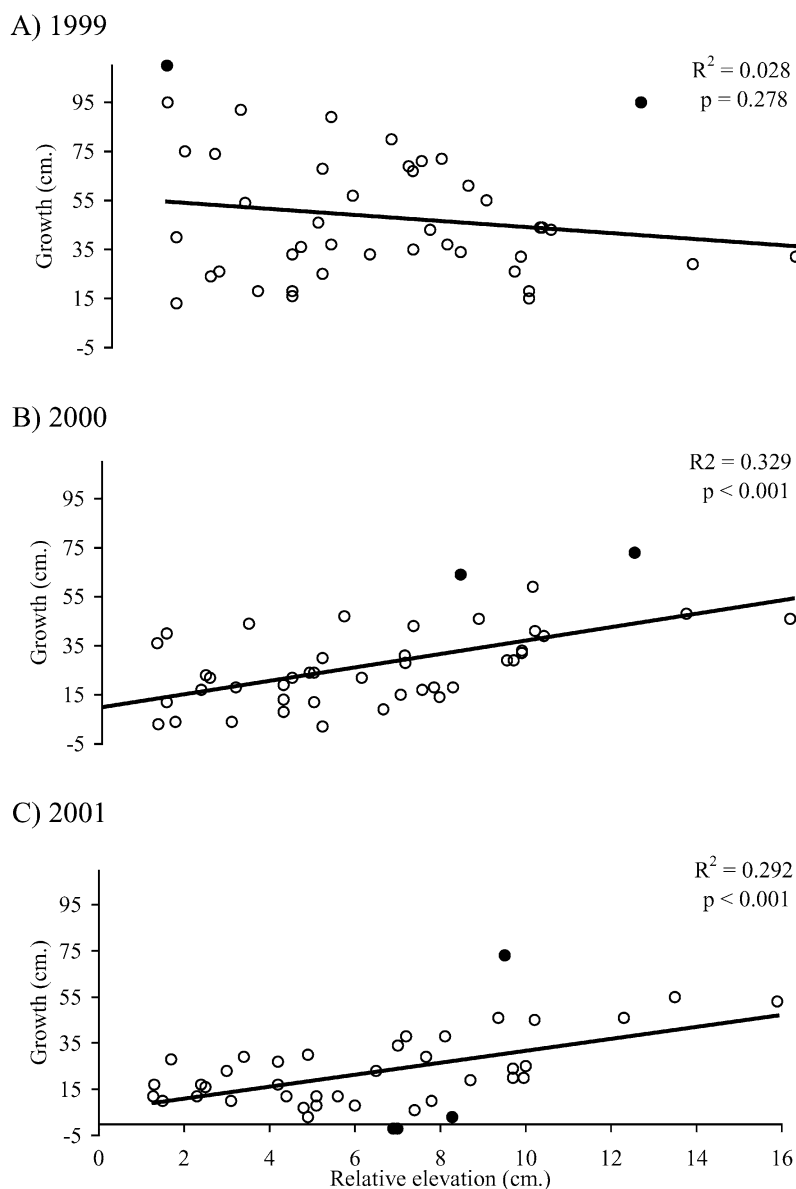


Figure 3. Regression results of growth (in cm.) vs. elevation (in cm), which is a surrogate for length of inundation. The filled dots are outliers. Statistics were calculated with the outliers in. A) First year of growth after 135 days of flooding, B) there were 107 days of flooding before the 2000 growing season, C) there were 26 days of flooding before the 2001 growing season.

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 (22 days of flooding after March 15 vs. 69 days in 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 ( $p = 0.61$ ).

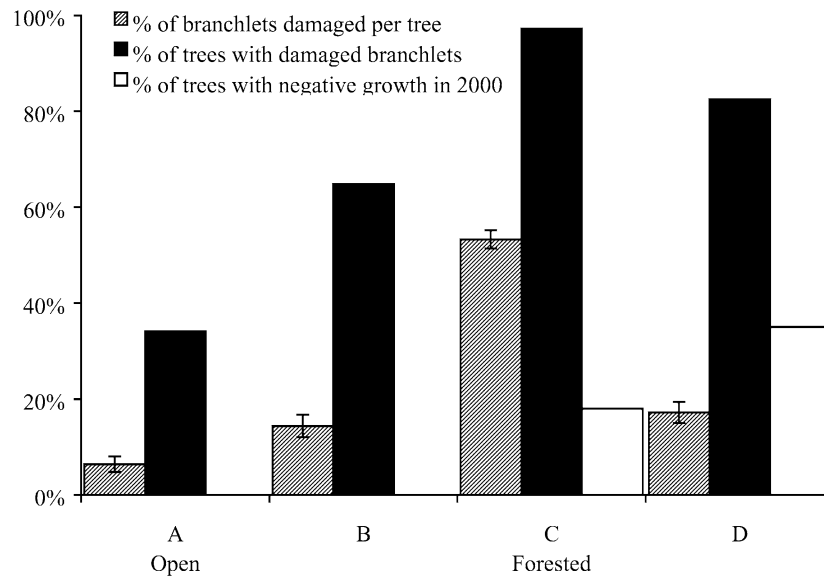


Figure 4. Three separate measures of herbivory. The striped bars show the mean percent of branchlets damaged per tree in 1999. The solids show the percent of trees damaged and the white bars show the percent of trees with negative growth in 1999. This is a measure of herbivory in the 2000 growing season. There were no trees with negative growth at the open floodplain sites.

### 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 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 average proportion of branchlets per tree damaged was 53% in the cottonwood forest (C) were damaged compared to 6% and 14% on open floodplain sites (A, B). Average per tree 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 confounded this relationship.

Possibly as a consequence of low light, increased herbivory, or both, trees within the two forested sites were tall and thin, relative to those on the floodplain. 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 significantly thinner for a given height than trees on the open floodplain ( $F = 27.6$ ,  $p < 0.001$ ). In fact, the height to diameter ratio was 30% higher in the two forested sites ( $C = 111.6$ ;  $D = 96.5$ ) than the open sites ( $A = 82.1$ ;  $B = 66.3$ ). Trees with taller surrounding vegetation had larger height to diameter ratios than tree surrounded by low vegetation, but the difference was not significant. On average, 73% of the trees in forested sites C and D were single meristem and tree-like in growth form compared to just 14% of individuals on the floodplain sites (A and B).

### 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. Perhaps the most telling result we found was one that we could not analyze: not a single tree died during the study in any of our four locations. This survivorship, along with good performance on the floodplain, suggest that all of these sites may be likely to mature into an oak forest once trees are established.

The height by diameter ratio data is more ambiguous. If we assume that high rates of growth, relative to diameter, indicates healthy growth, then we would surmise that floodplain trees are performing poorly, given their height to diameter ratios. This pattern would be expected if herbivory on branches is the primary cause of this low growth form by breaking off buds and initiating new lateral bud formation. In contrast, if we assume that low height to diameter ratios are 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 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 have lower height to diameter ratios. 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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