

## SALIX EXIGUA CLONAL GROWTH AND POPULATION DYNAMICS IN RELATION TO DISTURBANCE REGIME VARIATION

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**Abstract.** Willows are important riparian colonizers. However, the predominant models of early riparian colonization, which emphasize seedling recruitment, are inadequate to explain the success of these species in light of the extremely low rates of seedling survival observed. We used molecular fingerprinting markers (AFLPs) to identify and characterize *Salix exigua* clones on six sites, ranging in size from 850 to 1150 m<sup>2</sup>, located on two rivers. Clones as large as 325 m<sup>2</sup> were detected, and an average of six clones per site occupied 75% of the vegetated area. Building on Mahoney and Rood's recruitment box model, we propose a model whereby prolific clonal growth allows for long-term colonization of riparian zones, and the balance between the relative importance of seedling regeneration and clonal growth varies based upon disturbance regime. A reduction in disturbance regime resulted in greater clonal growth and reduced genotypic variation. It is probable that, with an extended reduction in disturbance, the *Salix exigua* component would be represented by fewer, larger clones and would eventually decline significantly when these clones are replaced by taller and more shade tolerant species.

**Key words:** clonal growth; colonization; disturbance; genet; molecular marker; ramet; riparian woodland; *Salix exigua*; willow.

### INTRODUCTION

Across the northern hemisphere, cottonwoods and willows are ecologically important colonizers in riparian communities. The "recruitment box model" (Mahoney and Rood 1998, similar model proposed by Auble and Scott 1998) describes the necessary stream stage patterns for successful cottonwood (*Populus* sp.) seedling establishment, and is the predominant model for understanding riparian site colonization. While this model focuses on the dynamics of seedling establishment, several authors have found that seedling survival of riparian colonizers, including both cottonwoods and willows, is extremely rare (Barnes 1985, Bradley and Smith 1986, Sacchi and Price 1992, Stromberg et al. 1993, Mahoney and Rood 1998, Johnson 2000). Despite this, sandbar willow (*Salix exigua*) is known to form dense thickets and is a major component in early successional riparian zones. We propose that clonal growth, through the formation of ramets, may be an important mode of local colonization and a useful addition to riparian colonization models.

Watkinson and Powell (1993) modeled clonal growth in *Ranunculus repens* and found that in the absence of recurring disturbance, populations initiated from a limited number of seedlings with high mortality are eventually dominated by a few large clones. Here, we explore the impact of a significant moderation in the flood disturbance regime on *Salix exigua* clones. We com-

pared two rivers that are very similar in size and location in California, but as a result of dam construction one of the river systems has a much more moderate disturbance regime. Based upon Watkinson and Powell's predictions one would expect the influence of clones to be greater under the conditions of lower disturbance found on the dammed river.

With the introduction of molecular genetic fingerprinting techniques, it is possible to identify woody plant clones and their ramets under natural conditions (Douhovnikoff et al. 2004). In this study we use these techniques to: (1) determine the identity, size, and characteristics of willow clones, (2) evaluate the role clonal growth may play in riparian zone colonization and productivity in order to build upon the recruitment box model, and (3) assess the effects of disturbance regime change on clonal growth.

### METHODS

#### Site selection

Six sites dominated by *Salix exigua* stands within riparian corridors consisting of at least 750-m<sup>2</sup> of contiguous vegetated area were selected for this study. Three sites were located on the undammed (high disturbance) Cosumnes River and three located on the dammed (low disturbance) Mokelumne River. Both rivers are comparable in watershed size (Cosumnes, 1388 km<sup>2</sup>; Mokelumne, 1712 km<sup>2</sup>), have similar mean annual runoff (Cosumnes, 443 × 10<sup>6</sup> m<sup>3</sup>; Mokelumne, 486 × 10<sup>6</sup> m<sup>3</sup>), flow parallel to each other out of the western Sierra Nevada into the Sacramento Valley, and occur

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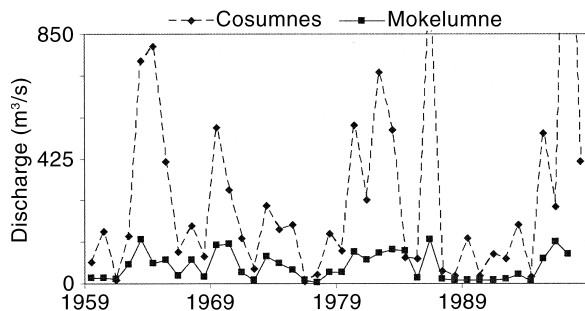


FIG. 1. Annual maximum instantaneous peak streamflow hydrograph for Cosumnes and Mokelumne Rivers (1959–1998).

at similar latitudes (Cosumnes, 38°30' N; Mokelumne, 38°09' N). Sites were located on both rivers at similar altitudes on the alluvial fan downstream of the confined canyon of the Sierra Foothills and upstream of the depositional plain of the Sacramento Valley bottom. The similarity in size, but the differences in disturbance characteristics make these rivers ideal choices for comparative studies.

**Relative disturbance levels.**—For the comparison of disturbance regimes and selection of rivers for this study, the relative disturbance index (RDI) developed by Douhovnikoff (*unpublished manuscript*) was used:

$$\text{RDI} = \frac{1}{n} \sum_1^n \left( \frac{F_n}{\frac{1}{n} \sum_1^n f_n} \right)$$

where  $F$  is the annual peak flow and  $f$  is the annual mean flow. This simple index is a measure of the magnitude difference between a river's peak flows and its mean flow. The mean flow is a rough estimate of the lower boundary of the "recruitment band" proposed by Mahoney and Rood (1998). The RDI quantifies the magnitude of peak flow disturbances above this assumed lower boundary for willow recruitment.

Based on RDI values the relative disturbance on the Cosumnes River (RDI = 19.6, SD = 3.6) is more than four times greater than on the Mokelumne River (RDI = 4.0, SD = 0.5). The coefficient of variation was also greater on the Cosumnes indicating that in addition to being a higher disturbance river, flows are also more variable from year to year (Fig. 1). The Mokelumne, on the other hand, is a low disturbance river with little flow variability from year to year. When compared to each other and 18 other Sacramento Valley rivers, we found that the Cosumnes was the fourth most disturbed river, while the Mokelumne River ranked 16th.

#### Sampling methods

A 5-m grid layout was used for sampling each site. At the intersections of this grid, 1 × 1 m<sup>2</sup> plots were established. The number of plots per site was dependent on willow stand size. The elevation of each plot from the river thalweg was measured using a surveyor's tran-

sit. Within each plot, all willow stems taller than 0.5 m were counted and measured for diameter at a height of 5 cm. In order to assess canopy structure the tallest stem within the square plot was then measured for height and canopy dimensions. Finally a visual estimate was made of canopy cover.

**Clone identification.**—Leaves were collected from the stem closest to the center of each plot (DNA stem) to provide the DNA fingerprint or genetic identity of the plot. This DNA fingerprint was then compared to that of every other plot within the site. Based upon similarity thresholds and selection criteria described in *Methods: DNA fingerprinting*, plots with genetic similarities greater than the threshold for clones were identified as members of the same clone.

**DNA fingerprinting and extraction.**—Amplified fragment length polymorphisms (AFLPs) were used to generate genetic fingerprints. Due to the very large numbers of loci that can be detected, the AFLP molecular method can be a sensitive fingerprinting technique that offers potential for assignment of individuals to clones. However, choice of loci is critical; too few or low levels of polymorphism may result in lack of resolution of genetically distinct, but closely related individuals, and too many or high levels of polymorphism may reveal confusing within-genet differences. In order to minimize these risks, we selected highly polymorphic loci and developed a statistical method for clone identification (Douhovnikoff and Dodd 2003). This methodology also offers the potential to identify genets that are closely related to each other (i.e., probable siblings).

DNA was extracted according to methods developed by Cullings (1992). DNA concentrations were established by electrophoresis on agarose gels and comparisons with lambda standards.

**AFLP analysis.**—The AFLP method developed by Vos et al. (1995) was performed with the following modifications: restriction digestion and ligation were performed simultaneously in a 50-μL solution containing 250 ng of genomic DNA, 5 units (1 unit = 10<sup>-7</sup> L) of *EcoRI*, 5 units of *MseI*, 5 μL 10× restriction-ligation buffer (100 mmol/L Tris-Acetate, 100 mmol/L MgAc, 500 mmol/L KAc, 50 mmol/L DTT), 1 unit T4 DNA ligase, 0.2 mmol/L ATP, 1.0 μmol/L *MseI* adapter, and 0.1 μmol/L *EcoRI* adapter. The restriction-ligation reaction was incubated for 4 h at 37°C, then diluted to 200 μL with 1XTE. Pre-amplification was performed in a 25-μL solution containing 2.5 μL of diluted restriction-ligation product, 0.2 mmol/L dNTP's, 0.3 μM of each primary amplification primer, 2.5 μL PCR buffer (100 mmol/L Tris-HCl, 500 mmol/L KCl, 20 mmol/L MgCl<sub>2</sub>, 13 mg/mL BSA), and 0.5 unit *Taq* polymerase. For the primary amplification primers, *EcoRI* primer was identical to the adapter sequence, whereas the *MseI* primer had an extra "C" as a selective nucleotide. The PCR reaction was performed on a Techne Genius thermocycler (Techne, Burlington, New Jersey,

TABLE 1. Site characteristics.

| Site       | Area sampled (m <sup>2</sup> ) | Open area (%) | Vegetated area occupied by clones (%) | No. clones | No. genotypes | Proportion distinguishable (PD) values | No. sibling families (% area occupied by largest family) |
|------------|--------------------------------|---------------|---------------------------------------|------------|---------------|--|--|
| Cosumnes   |                                |               |                                       |            |               |  |  |
| Site C1    | 875                            | 44            | 81                                    | 4          | 11            | 0.31                                   | 1 (100)  |
| Site C2    | 875                            | 23            | 77                                    | 9          | 18            | 0.51                                   | 1 (100)  |
| Site C3    | 850                            | 30            | 36                                    | 3          | 24            | 0.70                                   | 6 (82)   |
| Mean       |                                | 32            | 65                                    | 5          | 18            | 0.51                                   |  |
| Mokelumne  |                                |               |                                       |            |               |  |  |
| Site M1    | 875                            | 3             | 76                                    | 5          | 14            | 0.40                                   | 1 (100)  |
| Site M2    | 875                            | 7             | 80                                    | 6          | 13            | 0.37                                   | 2 (97)   |
| Site M3    | 1150                           | 2             | 70                                    | 7          | 22            | 0.47                                   | 2 (98)   |
| Mean       |                                | 4             | 74                                    | 6          | 16            | 0.41                                   |  |
| Grand mean |                                | 18            | 75                                    | 6          | 17            | 0.46                                   |  |

USA) for 28 cycles using the following cycling parameters: 30 s at 94°C, 60 s at 60°C, and 60 s at 72°C. The primary amplification product was then diluted to 250  $\mu$ L with 1XTE. Selective amplification was performed in a 25- $\mu$ L solution containing 6.25- $\mu$ L diluted primary amplification product, 0.2 mmol/L dNTP's, 0.06  $\mu$ mol/L *EcoRI* fluoresced selective primer, 0.3  $\mu$ mol/L *MseI* selective primer, 2.5  $\mu$ L 10 $\times$  buffer, and 0.5 unit *Taq* polymerase. We prescreened 32 selective primer pairs and chose three pairs that were reliable and highly polymorphic for this study (*MseI*-CCAA/*EcoRI*-GTA, *MseI*-CTC/*EcoRI*-TAC, and *MseI*-CGTG/*EcoRI*-GTA). The selective PCR reaction had two cycle sets: 13 cycles of 30 s at 94°C, 30 s at 65°C (annealing temperature was lowered 0.7°C at each cycle), and 60 s at 72°C, followed by 18 cycles of 30 s at 94°C, 30 s at 56°C, and 60 s at 72°C. Fingerprint data were obtained by running the amplified samples on an ABI Prism 3100 DNA Sequencing System (PE Applied Biosystems, Foster City, California, USA) using PE Applied Biosystems protocols. Band scoring was completed with the Genescan and Genotyper software (PE Applied Biosystems, Foster City, California, USA).

#### Data groups

Plots were grouped into three categories. (1) "Open plots" had no stems and no canopy. (2) "Small genet plots" had unique DNA fingerprints that were not matched to the fingerprint of any other plot. The "DNA stem" sampled from these plots, while not part of larger clones detected on the 5-m grid, may have been anything from a single stem genet to part of a smaller clone. All stems located in these squares were identified as small genets. (3) "Clone plots" had two or more plots with genetically matching DNA stems. All other stems located in these plots were considered part of the same clone. It is possible that some of the stems counted and measured within the plot were not part of the larger clone. However, results from Douhovnikoff and Dodd (2003) suggest that *Salix exigua* clones have a phalanx

clonal structure whereby clone plots are contiguous with limited mixing of stems between clones.

#### Clone size and diversity

For each clone, clone size was estimated. Total values were calculated as the mean of all plot values (i.e., number of stems, basal area) within each clone, multiplied by the total area occupied by the same clone. (On the 5  $\times$  5 m grid each 1-m<sup>2</sup> plot was a representative sample of the surrounding 25 m<sup>2</sup>.)

In order to assess the relative importance of clonal growth on each site, sample proportion distinguishable (PD) values were calculated as the number of genets divided by the total number of stems genetically sampled (Ellstrand and Roose 1987). This metric of clonal diversity measures the percentage of stems sampled that were genetically distinct.

#### Data analysis

Data were structured and analyzed at three spatial scales (plot, clone, and site). In each case, *t* tests were used to investigate significant differences between the Mokelumne and Cosumnes Rivers, and when relevant, clone vs. small genet plots within them.

## RESULTS

### Clone identification

A total of 102 genotypes were identified of which 34 were clones, 16 on the Cosumnes and 18 on the Mokelumne River (Table 1). Within each river system, all sites sampled were made up of multiple clones. An average of six clones was detected per site, and clones occupied ~75% of the vegetated area.

The largest clone was detected on site M1 in 13 sample squares and covered an area of ~325 m<sup>2</sup> (Fig. 2). This clone was so large it occupied almost 40% of the entire field site sampled. We identified seven additional clones each of which included eight or more square plots, covered an area >200 m<sup>2</sup>, and occupied >20% of the entire sample grid.

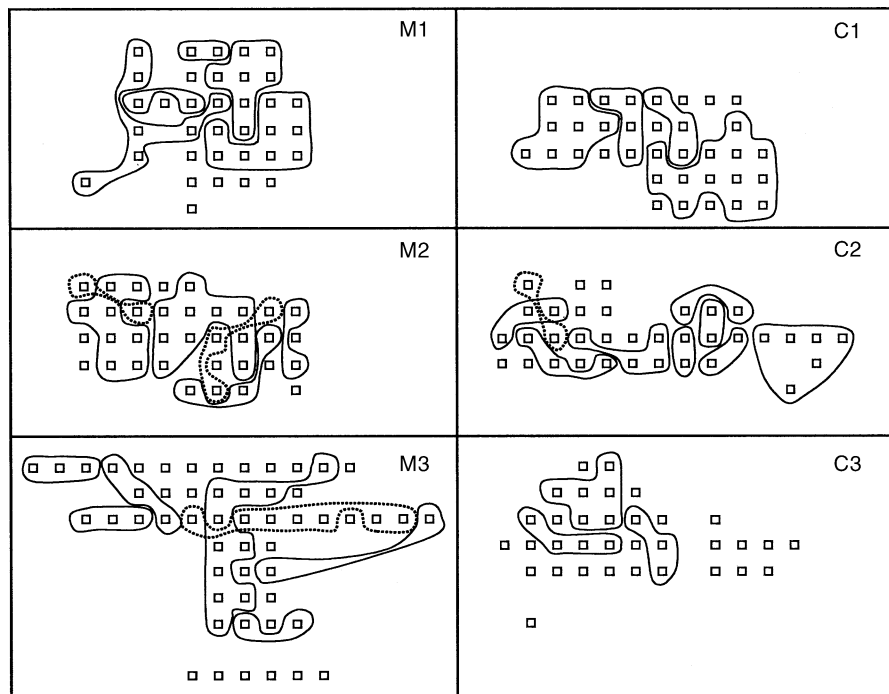


FIG. 2. Site maps. Data collection sample plots are spaced on a 5-m grid. All plots identified as members of same clone are outlined. Dashed lines are used to clarify overlapping genets. Remaining plots are small genets.

For all sites, the PD values ranged from 0.31 to 0.70, with an overall mean of 0.46. (As the importance of clone representation increases, PD value decreases.) Comparisons to other studies are difficult because PD values are sensitive to sampling structure, but at this large sampling scale these values indicate that clonal growth is significant. PD values for the Mokelumne sites (0.37–0.47) varied little around the mean of 0.41. However, PD values on the Cosumnes sites ranged from 0.31 to 0.70 and were inversely related to mean site elevation from the thalweg ( $R^2 = 0.98$ ,  $P = <0.05$ ).

A limited amount of genet intermingling was detected and clones were largely contiguous. A few cases of probable flood training (Gom and Rood 1999) were found with elongated clones  $>20$  m long, and one case of probable branch propagation was detected where a clonal sample plot was separated by  $>30$  m from the rest of the clone.

Sites appear to be dominated by a single family. On three sites, all genotypes were identified as being closely related (putative siblings). On two sites, all but one genotype, and on one site, all but five genotypes were siblings.

#### *Clone characteristics*

Clones were larger on the Mokelumne River in terms of total number of stems per clone and total basal area per clone (Fig. 3a). Significant differences were also found in the characteristics of stems within clones. Clone size, as measured by mean basal area per stem,

mean maximum height, and mean canopy cover were all significantly greater on the Mokelumne River.

A partition of the data by rivers revealed that clones on the Mokelumne had significantly greater maximum heights, greater maximum diameters, and greater canopy cover than small genets (Fig. 3b). However, on the Cosumnes River, there were no significant differences between clones and small genets except for number of stems per square meter, with clones having fewer stems than small genets.

Sites on the Cosumnes River had an average of  $>30\%$  open space compared to the 5% open space found on the Mokelumne River sites. This is area not occupied by stems or covered by canopy and is an estimate of area available for colonization.

## DISCUSSION

### *Importance of clonal growth*

Our data show that clonal growth is an important component in the life history of *Salix exigua*. Large clones were detected on all sites sampled and covered areas as great as 325 m<sup>2</sup>. In addition to being very large, clone size is not evenly distributed among genotypes. Averaged across all sites, as few as six clones out of 17 genotypes detected occupied 75% of the vegetative area. The average PD value of 0.46, measured on the wide 5-m spacing used in this study, indicates low levels of genet variability and high levels of clonal growth.

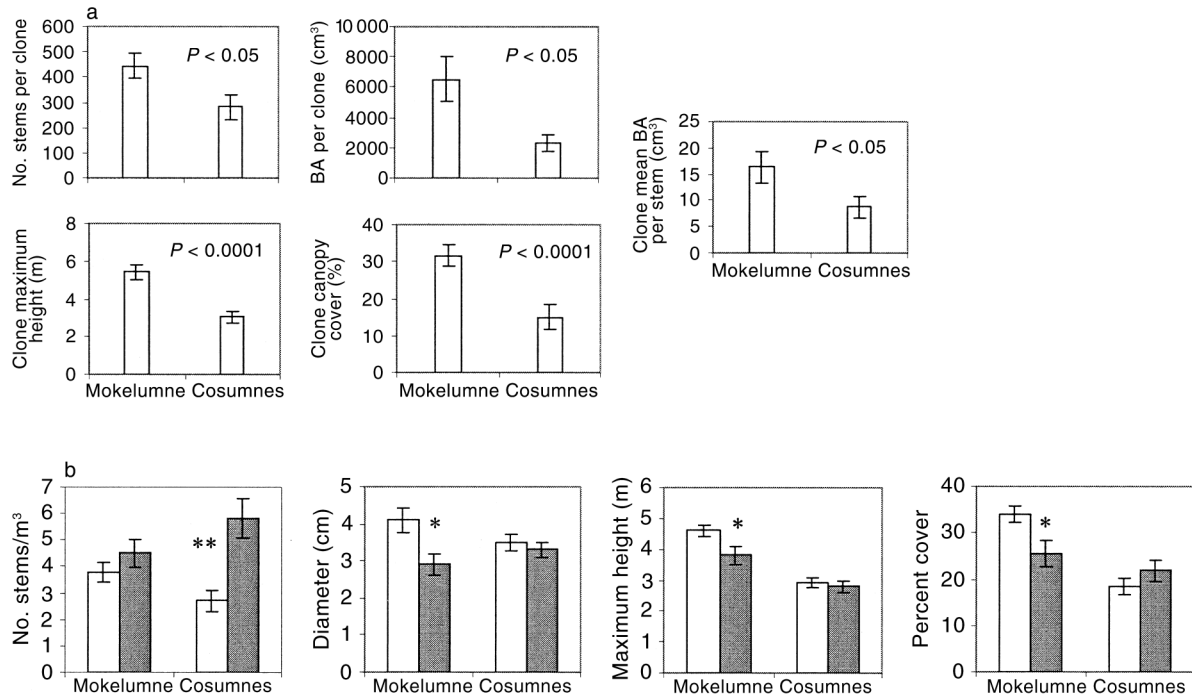


FIG. 3. (a) The clone size values (mean  $\pm$  1 SE) for the Mokelumne ( $n = 18$ ) and Cosumnes ( $n = 17$ ) Rivers. (b) The sample square values (mean  $\pm$  1 SE) for clones (open bars) and small genets (gray bars) by river. Significant differences within rivers are marked above relevant bars ( $*P < 0.05$ ;  $**P < 0.0005$ ). "BA" denotes basal area.

At three of our six sites, all genotypes were identified as closely related (siblings), at two sites only a single genotype was identified as non-sibling, and at one site five genotypes were identified as non-siblings. Therefore, it appears that on each site there is a single family contributing almost all of the seedlings recruited into the populations. *Salix exigua* genets stagger their dispersal timing (V. Douhovnikoff, *personal observation*). The parent releasing seeds onto the newly exposed substrate after a stand-clearing flood at the ideal time for germination and survival will likely have the greatest chance of reproductive success.

Seedlings from other parents may establish themselves at other times, but as Eriksson (1993) points out, there is an advantage to being "first at site" such as a greater success in the capture of space and resources (Kays and Harper 1974, *Lolium perenne*), and those few seedlings contributed later by other parents are more likely to be lost from the population (Hartnett and Bazzaz 1985, *Solidago canadensis*; Dorken and Eckert 2001, *Decodon verticillatus*). At all sites, non-sibling genets were from small genet plots, but every clone identified was a sibling of all other clones on its site. Thus, the familial cohort (same family and age class) is dominating the site. This evidence of a single contributing family and dominance by the initial cohort suggests a recruitment pattern of initial seedling recruitment (ISR; Eriksson 1993).

It is unlikely that seedling recruitment into the mature willow population is very common. For the best

chance of survival past the first year, seedlings must germinate in those rare areas that are both close enough to the stream for adequate water (Niiyama 1990, *Salix* sp.), and yet somehow protected from intense scouring in periods of high flows (Mahoney and Rood 1998). In addition to drought stress and scouring other common sources of seedling mortality include herbivory, competition, and pathogens. In this study, first year seedling mortality was 100% on all six study sites for two consecutive years. These observations were consistent with several other studies that also found first year mortality of willow and cottonwood seedlings at or near 100% (McBride and Strahan 1984, Barnes 1985, Bradley and Smith 1986, Sacchi and Price 1992, Stromberg et al. 1993, Mahoney and Rood 1998, Johnson 2000). As a result, seedling recruitment alone appears to be insufficient to explain willow success. It is difficult to study the demographics of this species. There is no practical means to age clones due to, among other reasons, difficulty in identifying the original ramet, and seedling mortality is so high that it is rare to observe recruitment. However, these data suggest an ability to grow clonally makes it possible for a limited number of successful seedlings to eventually colonize a relatively large area. Thousands of seeds might result in hundreds of seedlings, which would then result in progressively fewer mature genets made up of more and more ramets. Building on Mahoney and Rood's recruitment box model, we propose a model for future testing whereby prolific clonal growth allows for the



PLATE 1. Mature stand of *Salix exigua* located on dammed river with moderated disturbance regime. Photo credit: V. Douhovnikoff.

longer-term colonization of riparian zones, and the balance between the relative importance of seedling regeneration and clonal growth varies based upon disturbance regime.

#### *Effects of reduced disturbance*

Reduced flooding tends to reduce the availability of moist seedbeds necessary for cottonwood seedling establishment (Rood and Mahoney 1990). Sacchi and Price (1992) add that hydrologic changes such as those resulting from dam construction and streamflow regulation can eliminate the predictability of spring floods, which are important for the success of species lacking seed dormancy, and seed dispersal can become out of sync with the receding flood limb essential for willow seedling establishment. They also found that arroyo willow (*Salix lasiolepis*) seedlings only became established in open areas and not on vegetated banks. Therefore, seedling recruitment, which is already limited under conditions of natural disturbance, becomes even less likely under conditions of significantly reduced disturbance.

For clonal plants with limited seedling recruitment and reduced disturbance, Watkinson and Powell (1993) predict that eventually the number of genets in a population declines due to density-dependent mortality. Kays and Harper (1974) observed that under conditions of self-thinning smaller genets tend to be the first elim-

inated. This is probably due to the observation that as clone size increases efficiencies of scale may also increase (Stueffer et al. 1998) and the risk of genet death may decrease (Cook 1983). Thus, as our results suggest, in the absence of regular disturbance the relative importance of clonal growth increases and larger genets tend to occupy a site.

In general, greater elevation riparian sites are disturbed less by floods, and as we have noted less disturbance results in increased importance of clonal growth as opposed to establishment from seed. Accordingly, a negative correlation was found between PD values and mean elevation of the three Cosumnes sites ( $R^2 = 0.98$ ,  $P = 0.04$ ), and all three sites from the Mokelumne had PD values comparable to the higher elevation sites on the Cosumnes. Similarly, Wilson (1970) found higher levels of vegetative propagation of *Populus deltoids* on higher terraces.

#### *Conservation implications*

As is the case on the Mokelumne River, reduced disturbance and resulting greater canopy cover, height, and productivity permits greater maximum diameter growth. The more time stems have to grow the greater the disturbance necessary to significantly damage or remove them. Stems are also able to get taller, placing their canopies above most flows and out of harm's way (see Plate 1). As a result, a positive feedback cycle is

initiated resulting in larger stems with denser canopies released from the constraints of regular disturbances. It is likely, that in order to reestablish an equilibrium whereby willows are constrained and maintained by regular disturbances, more than just a return to historical flood intervals will be necessary, such as an extremely large stand replacing flood. In the absence of this, we predict the increase in site dominance by large clones, a reduction in genotypic diversity and site heterogeneity, and that over time willow clones will be replaced by taller stemmed and more shade tolerant species (Strahan 1981, Boggs and Weaver 1994, McLeod et al. 2001, Spencer et al. 2001). Therefore, in the short term willow densities and clone size may increase, but in the long term the willow component of these riparian zones will be significantly diminished.

Traditionally riparian restoration has focused on planting and creating conditions for seedling and cutting survival (Friedman et al. 1995). However, an understanding of how to maximize potential clonal growth may lead to greater restoration success rates.

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#### LITERATURE CITED

- Auble, G. T., and M. L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. *Wetlands* **18**:546–556.
- Barnes, W. J. 1985. Population dynamics of woody plants on a river island. *Canadian Journal of Botany* **63**:647–655.
- Boggs, K., and T. Weaver. 1994. Changes in vegetation and nutrient pools during riparian succession. *Wetlands* **14**:98–109.
- Bradley, C. E., and D. G. Smith. 1986. Plains cottonwood [*Populus deltoides* var. *occidentalis*] recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta [Canada] and northern Montana [USA]. *Canadian Journal of Botany* **64**:1433–1442.
- Cook, R. E. 1983. Clonal plant populations. *American Scientist* **71**:244–253.
- Cullings, K. 1992. Design and testing of a plant-specific PCR primer for ecological and evolutionary studies. *Molecular Ecology* **1**:233–240.
- Dorken, M. E., and C. G. Eckert. 2001. Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *Journal of Ecology* **89**:339–350.
- Douhovnikoff, V., A. M. Cheng, and R. S. Dodd. 2004. Incidence, size, and spatial structure of clones in second-growth stands of coast redwood, *Sequoia sempervirens* (Cupressaceae). *American Journal of Botany*, **91**:1140–1146.
- Douhovnikoff, V., and R. S. Dodd. 2003. Intra-clonal variation and a similarity threshold for identification of clones: application to *Salix exigua*. *Theoretical and Applied Genetics* **106**:1307–1315.
- Ellstrand, N. C., and M. L. Roose. 1987. Patterns of genotypic diversity in clonal plant species. *American Journal of Botany* **74**:123–131.
- Eriksson, O. 1993. Dynamics of genets in clonal plants. *Trends in Ecology and Evolution* **8**:313–316.
- Friedman, J. M., M. L. Scott, and W. M. Lewis. 1995. Restoration of riparian forest using irrigation, artificial disturbance, and natural seedfall. *Environmental Management* **19**:547–558.
- Gom, L. A., and S. B. Rood. 1999. Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. *Canadian Journal of Botany* **77**:1095–1105.
- Hartnett, D. C., and F. A. Bazzaz. 1985. The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *Journal of Ecology* **73**:407–414.
- Johnson, W. C. 2000. Tree recruitment and survival in rivers: influence of hydrological processes. *Hydrological Processes* **14**:3051–3074.
- Kays, S., and J. L. Harper. 1974. The regulation of plant and tiller density in a grassland sward. *Journal of Ecology* **62**:97–105.
- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment: an integrative model. *Wetlands* **18**:634–645.
- McBride, J. R., and J. Strahan. 1984. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. *American Midland Naturalist* **112**:235–245.
- McLeod, K. W., M. R. Reed, and E. A. Nelson. 2001. Influence of a willow canopy on tree seedling establishment for wetland restoration. *Wetlands* **21**:395–402.
- Niiyama, K. 1990. The role of seed dispersal and seedling traits in colonization and coexistence of *Salix* spp. in a seasonally flooded habitat. *Ecological Research* **5**:317–332.
- Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management* **14**:451–464.
- Sacchi, C. F., and P. W. Price. 1992. The relative roles of abiotic and biotic factors in seedling demography of arroyo willow (*Salix lasiolepis*: Salicaceae). *American Journal of Botany* **79**:395–405.
- Spencer, D. R., J. E. Perry, and G. M. Silberhorn. 2001. Early secondary succession in bottomland hardwood forests of southeastern Virginia. *Environmental Management* **27**:559–570.
- Strahan, J. 1981. Regeneration of riparian forests of the Central Valley. Pages 58–67 in R. E. Warner and K. M. Hendrix, editors. *California riparian systems*. University of California Press, Berkeley, California, USA.
- Stromberg, J. C., B. D. Richter, D. T. Patten, and L. G. Wolden. 1993. Response of a Sonoran riparian forest to a 10-year return flood. *Great Basin Naturalist* **53**:118–130.
- Stueffer, J. F., H. J. Daring, and F. Schieving. 1998. A model on optimal root–shoot allocation and water transport in clonal plants. *Ecological Modeling* **111**:171–186.
- Vos, P., R. Hogers, M. Bleeker, M. Reijans, T. van de Lee, M. Hornes, A. Frijters, J. Pot, J. Peleman, M. Kuiper, and M. Zabeau. 1995. AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research* **23**:4407–4414.
- Watkinson, A. R., and J. C. Powell. 1993. Seedling recruitment and the maintenance of clonal diversity in plant populations: a computer simulation of *Ranunculus repens*. *Journal of Ecology* **81**:707–717.
- Wilson, R. E. 1970. Succession in stands of *Populus deltoides* along the Missouri River in southeastern South Dakota. *American Midland Naturalist* **83**:330–342.