Pattern of Woody Species Establishment on Point Bars on the Middle Sacramento River, California

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Introduction

Riparian forest is a dynamic vegetation type that is shaped by a complex interaction between fluvial and ecological processes (Thompson 1961, Leopold et al. 1964, McBride and Strahan 1984, Strahan 1984, Harris 1987, Cepello 1991, Gregory et al. 1991, Griggs and Small 2001). Channel movement and sediment deposition initiate a succession sequence that begins with pioneer species on bare surfaces, typically point bars (McBride and Strahan 1984, Strahan 1984, Cepello 1991). In western North America, this woody pioneer community is dominated by cottonwoods and willows (Braatne et al. 1996). Establishment of these species is controlled by a combination of factors: creation of appropriate substrate for germination, timing of seed dispersal, adequate subsurface moisture, and site stablility (Braatne et al. 1996, Mahoney and Rood 1998). Where channel movement occurs frequently, riparian forest vegetation tends to be dominated by mature cottonwoods and willows. Farther from the channel, or on landforms that have not experienced an active channel for many decades, riparian forest tends to develop into one dominated by valley oak and elderberry (Strahan 1984, Chapin et al. 2002). The process from point bar seedlings to mature cottonwoods and willows on a stable floodplain can take as little as 50 years in the Central Valley of California (Griggs and Small 2001). However, early establishment does not necessarily ensure that succession will proceed to a mature forest. Scouring flows or river avulsion can eliminate all young vegetation from a developing point bar and reset the succession clock.

In the past two decades much attention has been devoted to the ecological requirements of woody riparian pioneers in western North America, for two main reasons: their value to wildlife (Gaines 1977, Griggs and Small 2001) and because the extent and regeneration of riparian forests have declined along with the increasing regulation of many western rivers. Dams and other diversions alter the natural hydrograph, which can have several negative impacts on riparian vegetation such as lack of appropriate conditions for seedling establishment, lack of subsurface water to support root growth and maturation of saplings, or even death of adult trees (Rood and Heinze-Milne 1989, Stromberg 1993, Rood and Mahoney 1996, Busch and Smith 1995, Mahoney and Rood 1998). Examining the causes of recruitment failure or stand death has led in turn to a good understanding of the requirements for successful establishment, summarized in the recruitment box concept of Mahoney and Rood (1998).

Much of our current knowledge of the ecology of pioneer riparian species comes from studies outside California, primarily in desert rivers (Stromberg et al. 1991, Shafroth et al. 1998) and northern temperate rivers (Rood and Mahoney 1995, Rood et al. 1995, Auble et al. 1997, Rood et al. 1998). Although several studies and reviews of California riparian vegetation communities have been published (Thompson 1961, Holstein 1984, Katibah 1984, Strahan 1984, Cepello 1991, Griggs and Small 2001), quantitative studies of cottonwood and willow colonization and establishment in California in general, and along the Sacramento River in particular, are generally lacking (exceptions include Strahan 1984, and Roberts et al. 2002). This lack of published work is especially curious given the major ecological importance of the Sacramento River in northern California (Sacramento River Conservation Area Handbook 2002). The extent to which studies from elsewhere can be extrapolated to California is not documented. California has a Mediterranean climate typified by hot, dry summers and cool wet winters that in North America occurs only in California and small portions of southern Oregon and northern Baja California. Climate and watershed position strongly influence alluvial water table characteristics (Braatne et al. 1996). The Sacramento River is a regulated river, and is thus subject to the negative impacts discussed above. Further, differences in species composition of riparian vegetation exist among locations in western North America. The term riparian cottonwood can refer to five different species of *Populus*. For example, the cottonwood of California's Central Valley, *Populus fremontii* (Fremont cottonwood), occurs outside of California only in Arizona, Nevada, New Mexico and southern Utah, and one of the dominant pioneering willows, *Salix gooddingii* (Goodding's black willow) is common only in California, Arizona and parts of western Nevada. Caution must be used when extrapolating ecological information across climates, wide geographic regions, and species within a genus or section.

The goals of this study are to: (1) document the pattern and extent of woody riparian species establishment on point bars along the middle Sacramento River between Colusa and Red Bluff; (2) relate pattern of establishment to physical parameters such as substrate type and elevation above river base flow; (3) determine whether our current ecological understanding of pioneer riparian species recruitment applies to the Sacramento River in northern California; and (4)initiate a long-term permanent-plot study of riparian pioneer species to evaluate the effects of flooding and deposition on recruitment, growth, and survival.

Methods

Six point bars along the middle Sacramento River between river miles 163-245 were chosen for sampling of woody riparian colonists from June 12, 2002 to July 1, 2002. Sites were chosen based on criteria of accessibility, size, and to achieve a wide geographic range. Locations and specifics of these six sites are given in Table 1. At each point bar, permanent belt transects were established at upstream, midstream, and downstream locations. Transects were 1m wide, perpendicular to the river channel and of variable length, extending from the water's edge to the beginning of fully established riparian forest (defined as nearly100% canopy cover, with stems at least 2.5m high). Rebar was used to mark the 25m mark (25m from the water's edge on the sample date; Table 1) and the endpoint of each transect. In late November, precise spatial locations and elevations of transect endpoints and river levels were determined (Table 1; Adam Henderson, California Department of Water Resources, pers.comm.). The permanent markers and GPS coordinates ensure that future sampling of these transects will occur in precisely the same location as the original sampling regardless of erosion or deposition. Table 2 gives stage and discharge data for three gages along the study reach on the dates of sampling and GIS measurement. Because study sites were at different locations than these gages, gage data will be used for comparative purposes only. Relative elevation above water level on the day of sampling was determined along the entire transect using a rod and level and the river height as a zero point. Ideally, river height on the day of sampling should be at mean low water so as to mesh with studies such as Mahoney and Rood (1998). This study did not take place exactly at mean low water. However, inspection of 2002 river stage data for the three gages in Table 2 showed that the sample period was close to the summer low point; in fact the river fluctuated less than one foot over the summer. For example, the Hamilton City gage had a low point of 129.77 in early May 2002, then increased to 130.00 on May 15, to 131.00 on June 22 and stayed in the low 131's or high 130's throughout the summer (www.cdec.water.ca.gov/selectQuery.html). Thus, our river baseline metrics approximated mean low water for that year.

Along each transect stem density and heights of all woody species were recorded in contiguous 1m^2 quadrats. Presence or absence of herbaceous species was also noted, but no attempt was made to identify individual herbaceous species. Stem density of woody species was recorded as follows: all stems were counted if <20; if >20 then the number of stems was visually estimated as belonging to one of the following categories: 21-50, 51-100, 100+. No quantitative attempt was made to differentiate seed-origin stems (genets) from sprout-origin stems (ramets), although it was noted where one or the other reproductive mode was strongly suggested. The midpoint of a category was used in density calculations. One height value for each species in the quadrat was obtained using a meter stick and visually averaging over all stems in the quadrat. This technique was used because a pilot study showed that stems of a species rarely varied in height more than a few cm within the quadrat. Surface substrate type was also recorded for each quadrat as silt, sand, gravel, cobble, or their combination (not more than two combinations per quadrat). Substrate was identified using the texture-by-feel method feel for silt and sand, and visually estimated for gravel (>sand but <1 cm diam.) and cobble (>1 cm). Subsurface composition was not measured. Species nomenclature follows the Jepson Manual (Hickman 1993).

Results

A total of 3,412 quadrats were sampled along 18 transects at the six sites. Of those quadrats, 492 (14.4%) contained woody species, primarily *P. fremontii* and three willow species, *Salix exigua* (narrow-leaved willow), *S. gooddingii*, and *S. lasiolepis* (arroyo willow). Two *Acer negundo* (box elder) stems and five unknown willow seedlings (probably *S. laevigata*) were also recorded but are omitted from the analyses below due to insufficient sample size.

Pattern of colonization differed among sites, species, and position on the point bar (Tables 3 and 4). In the site effect, Chico Landing (RM 194) had the highest percentage of quadrats colonized (32%), followed by RM 172 (23%), Pine Creek (RM 196; 13%), Haleakala (RM 233; 8%), Rio Vista (RM 215; 7%), and Deadman's Reach (RM 186; <1%) (Table 3). The most common species encountered overall as measured by frequency of occurrence in quadrats was *S. exigua*, followed by *S. gooddingii*, then *P. fremontii*, and *S. lasiolepis* (Table 3). Although species composition differed somewhat across sites, analysis of this effect will be postponed until demographic data become available later in 2003.

There were substantial differences in colonization pattern according to position on the point bar. Downstream quadrats had a higher percentage of colonization as compared to midstream or upstream quadrats (23%, 14.2%, and 8.4%, respectively; Table 4). *S. gooddingii* was the most frequent species in upstream transects (55%) whereas *S. exigua* was the most frequent in midstream (38%) and downstream (59%) quadrats (Table 4). *P. fremontii* was most frequent in midstream quadrats (14.2%). Stem density data according to position on the point bar are presented in Table 5 and show the same general pattern as does Table 4. Over all 18 transects the mean density per quadrat was 4.7 stems, but the median was only 1. Thus, the density data are heavily skewed by a few quadrats containing hundreds of small stems, and so should be interpreted with caution. The analyses below use the quadrat, not individual stems, as the relevant ecological unit. Should a scouring or depositional flood occur, it is likely that the entire quadrat as a unit would be affected regardless of density. Further, should a high-density quadrat survive scouring floods, it is likely that self-thinning will eventually reduce stem numbers to a very small number, making the original high-density number unimportant. Either way, quadrat fate (or fate of that spatial location) is more relevant to forest establishment than is individual seedling or stem fate.

Stem heights are presented in Table 6 as a function of both site and position on the point bar. *Salix* spp. and *P. fremontii* both averaged 100cm in height across sites and spatial position, but there is high variability in stem height among sites (Table 6). Stems at site RM 172 averaged 2.6m in height, whereas the few stems at site RM 233 averaged 0.3m. Such a difference may reflect age, growth rate, or recent scouring at RM 233. As stated above in the Methods section, no attempt was made to accurately differentiate seed-origin stems genets from sprout-origin stems (ramets) through excavation in the belt transect. However, observations from off-transect excavations showed that sprout-origin stems have a more robust appearance at ground level than do seed-origin stems. Very little sprout-origin morphology was observed, thus it is likely that the vast majority of the stems in this study were of seed origin. If one assumes a mean growth rate of 1m/year (Braatne et al. 1996), this suggests an approximate mean age for stems in this study of one year (i.e. germinated in 2001). Future studies (summer 2003) will document height changes in quadrats as well as begin to determine stem ages through ring-counting of selected individuals.

Colonization occurred primarily in narrow elevation bands on point bars (Fig. 1). Although there were some differences among upstream, midstream and downstream locations, the mean elevation of colonization for *P. fremontii* and *Salix spp*. was always 0 to 1.75m above the waterline (in June on the sample date). Only *P. fremontii* in upstream locations had a mean elevation of colonization < 1.0m (*S. lasiolepis* was not included in this analysis due to low sample size). For downstream quadrats, where most colonization occurred the pattern is even more dramatic with the mean elevation of colonization for all three species 1.2 to 1.6m above low water (Fig. 1). Topography of point bars differed according to river position and may affect colonization rate. Figure 2 shows the elevation profile of all 18 transects. Downstream transects had more area and lower slope angles within the 1.0 to 1.75m colonization zone than did upstream and midstream transects.

Surface substrate analysis (silt, sand, gravel, or cobble) reveals that cobble is by far the most common substrate type at all three point bar positions, followed by sand, silt, and combinations of sand, silt, and cobble (Table 7, Fig. 3). No significant difference in substrate type was detected across spatial position on point bars (Fig 3), but some differences do occur among sites (Table 7). Chico Landing, Deadman's Reach, and RM 172 were the lowest in cobble. Species in this study strongly preferred sand or silt as a substrate type as opposed to cobble (Figure 4; Chi-square test, $p<0.001$). Sand and silt together comprised 31% of the total substrate over all quadrats but accounted for 64% of the colonized quadrats.

Discussion

This study documents the pattern of early establishment of woody riparian pioneer species on point bars along the middle Sacramento River in California between river miles 172 and 233. Overall, 14.4% of the land area sampled contained colonists. In descending order of importance, *Salix exigua, S. gooddingii, P. fremontii,* and *S. lasiolepis* comprised nearly all of the species encountered. These species are all highly adapted for their pioneering niche (Holstein 1984). All species are in the family Salicaceae, arguably the most important riparian family in the world (Holstein 1984). All four species are dioecious and have very light, wind-dispersed comose seeds (Holstein 1984). *S. exigua*, also known locally as sandbar willow, commonly forms large thickets on point or sand bars (Katibah 1984) but drops in abundance in more mature forests, although it can achieve tree form and size. *P. fremontii* is the dominant tree of riparian forests <50 years old along the middle and lower Sacramento River, along with *S. gooddingii*. Holstein (1984) reports that *S. gooddingii* is a better pioneer than *P. fremontii*, because it tolerates stress better as long as abundant water is available. *S. gooddingii* and *P. fremontii* also dominate riparian forests in other river systems where they co-occur (Stromberg et al. 1991).

Colonization on point bars occurred within a narrow elevation band above low water. *P. fremontii*, *S. gooddingii*, and *S. exigua* all had a mean overall elevation of establishment above low water of 0.2 to 1.75m, and a narrower range of 1.2 to 1.6m on downstream transects. The existence of this narrow band has been reported widely elsewhere in the literature for cottonwood species (summaries in Braatne et al. 1996, Mahoney and Rood 1998) and for *S. gooddingii* in Arizona (Shafroth et al. 1998). However, the precise elevation interval depends on the river system (Mahoney and Rood 1998). Mahoney and Rood report a general value of 2 to 5 feet (0.6 to 1.7m). This range reported here of approximately 4-5 feet above low water thus fits within the recruitment box of (Mahoney and Rood 1998) but at the top end.. However, in this dynamic fluvial system colonization does not necessarily lead to establishment or maturation. Determining the elevation above low water at which mature trees originally colonized ensures that that elevation was successful at that location in that year. In this way, Roberts et al. (2002), using elevation of initial establishment of mature *P. fremontii*, obtained a range of establishment for the Sacramento River of 5.5 to 9 feet (1.7 to 2.7m) above mean low water. It is important to note that some colonizing elevations reported in this study fall into this range of (Roberts et al. 2002). From the boxplots in Figure 1, all species have some occurrences at relative elevations above 3m, especially in upstream and midstream transects. It is certainly plausible that lower elevation recruits could be removed by future scouring floods, leaving only the higher elevation recruits to survive and become mature forest trees. As this study is extended into the future, precise information on survivorship as a function of elevation should become available.

Results from this study demonstrated that not all point bars are equivalent with respect to probability of colonization. Some bars are full of colonists (Chico Landing, RM 172) and others are nearly devoid (Deadman's Reach). Point bar topography (Figure 2) is important because the slope controls the rate of water recession following high water flows. As is well documented (Braatne et al. 1996) for cottonwoods (and likely for willows as well), successful recruitment depends on a delicate coincidence of timing of seed dispersal with appropriately wetted substrate. If a bar is too steep, little surface area will fit into the recruitment zone. In addition to slope, the large point bars of the Sacramento River sometimes contain small river channels many meters away from the main channel; these may act to keep surface soil moisture levels high during the crucial few days of seed germination in interior portions of the bar before roots can penetrate to the water table. Such small channels are apparent in Fig. 2 at RM 172 and Chico Landing, especially.

Substrate type also affects probability of colonization (Braatne et al. 1996, Steiger and Gurnell 2003). Cottonwoods and willows germinate best on bare, moist surfaces that contain particle sizes conducive to water retention and root penetration (McBride and Strahan 1984). In this study, with >50% of the point bar substrate as cobble, there was a significant positive association between cottonwood and willows occurrence and silt or sand substrates (Fig. 4). Again, the sites with the highest colonization, RM 172 and Chico Landing, have relatively high amounts of silt or sand (Table 5). It is important to again note that only surface substrate was measured in this study. Subsurface stratigraphy could also be an important influence on colonization. For example, the presence of a thick gravel layer beneath an apparently favorable surface could kill developing roots due to the poor moisture-holding capacity of the gravel. Other factors not considered in this study could be equally important in explaining differences in pattern of colonization. These include the extent and location of bank protection (riprap) upstream and across from a site, which can alter hydrological forces acting on a point bar (Larsen et al. 2002); and flood flow velocity across the bar (a function of discharge and channel configuration), which affects erosive ability and particle size deposition (Leopold et al. 1964). Future studies are planned to address some of these other variables.

In summary, this study documents the occurrence and some of the physical conditions under which woody riparian species colonize point bars along the middle Sacramento River. An elevational zone of establishment was calculated for *P. fremontii, S. gooddingii* and *S. exigua*. In downstream point bar locations, where most colonization occurred, the recruitment zone was calculated to be 1.2 to 1.6m above low water. Information from published studies on other river systems on the ecological and hydrological requirements of riparian colonists appears generally applicable to the Sacramento River. Factors that affect probability of success include a low slope angle on the point bar, which places more area into the recruitment zone than would a high slope angle; and sand or silt as a substrate type. However, for small-statured individuals growing in exposed sites on an active floodplain, the future is uncertain and end is always near. The next scouring flood may wipe away many or even most individuals; conversely, a period of several years without scouring flows may allow these individuals to resist scouring effects, trap sediment, and build the floodplain. The fate of these colonists will be ascertained in future studies of these permanently marked transects to better understand the relationship between colonization and mature forest.

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Table 1. Spatial locations, elevations and lengths of transects. GPS data (UTM Zone 10, NAD 83, NAVD 88) are courtesy of Adam Henderson @ DWR, Red Bluff. Equivalent inland endpoint values for a site indicate a common endpoint for all transects at that site. The 25m stake was 25m from the river's edge on the day of vegetation sampling. Stake Elevation is elevation in feet at ground level. River Elevation (in feet) is the water level where the transect line intersected the river on 11/25/02 or 11/26/02. Transect Length is in meters.

				25m Stake			Inland Endpoint		
Site Name	**River Mile**	**Veg Sample Date**	**GPS Data (11/25/02 and 11/26/02)**	**Upstream**	**Midstream**	**Downstream**	**Upstream**	**Midstream**	**Downstream**
RM 233	233	6/19/02	Northing	4437512.83	4437372.07	4437185.16	4437457.87	4437358.85	4437214.81
			Easting	575133.87	575265.98	575190.25	575105.32	575220.17	575187.33
			Stake Elevation (ft)	227.95	222.29	221.91	227.8	225.08	222.81
			River Elevation (ft)	214.79	213.22	213.05			
			Transect Length (m)	87	72	79			
Rio Vista	215	6/12/02	Northing	4414791.03	4414415.84	4414310.88	4414660	4414660	4414660
			Easting	579974.9	579780.42	580096.21	580123.88	580123.88	580123.88
			Stake Elevation (ft)	167.12	165.56	164.77	173.34	173.34	173.34
			River Elevation (ft)	160.01	159.22	159.11			
			Transect Length (m)	247	450	376			
Pine Creek	196	6/26/02	Northing	4398863.61	4398888.95	4398748.34	4398721.16	4398721.16	4398721.16
			Easting	588989.81	589176.27	589262.85	589107.39	589107.39	589107.39
			Stake Elevation (ft)	124.88	129.35	132.13	134.99	134.99	134.99
			River Elevation (ft)	missing	121.98	122.02			
			Transect Length (m)	121	201	169			
Chico Landing	194	6/20/02	Northing	4397428.93	4397207.42	4398748.34	4397331.57	4397236.35	4397124.4
			Easting	589671.48	589774.83	589262.85	589831.45	589827.7	589886.51
			Stake Elevation (ft)	123.86	129.68	132.13	122.04	128.47	125.64
			River Elevation (ft)	118.53	118.5	117.98			
			Transect Length (m)	214	110	200			

Table 1 continued.

				25m Stake			Inland Endpoint		
Site Name	**River Mile**	**Veg Sample Date**	**GPS Data (11/25/02 and 11/26/02)**	**Upstream**	**Midstream**	**Downstream**	**Upstream**	**Midstream**	**Downstream**
Deadman's Reach	186	7/1/02	Northing	4389155.25	4389076.68	4388853.58	4388946.28	4388946.28	4388946.28
			Easting	587047.83	586788.91	586735.99	586967.77	586967.77	586967.77
			Stake Elevation (ft)	106.65	107.45	108.54	112.77	112.77	112.77
			River Elevation (ft)	99.71	99.71	99.67			
			Transect Length (m)	251	246	225			
RM 172	172	6/18/02	Northing	4373665.17	4373229.25	4372827.82	4372862.67	4372862.67	4372862.67
			Easting	586778.22	587016.69	586880.04	586853.47	586853.47	586853.47
			Stake Elevation (ft)	78.08	79.38	79.43	81.45	81.45	81.45
			River Elevation (ft)	74.26	73.42	73.05			
			Transect Length (m)	250	200	111			

Table 2. River stage and discharge data on days of vegetation measurement for three gages along the study reach (source: DWR at www.cdec.water.ca.gov.selectQuery.html). All times were 1200 hours on the date specified. Height values are in feet, discharge values in cubic feet/second (cfs). Bend Bridge is a USGS gage; all others are DWR gages.

	Sample Date	Vina/Woodson Bridge (RM 218)		Hamilton City (RM 199)		Ord Ferry (RM 184)	
		Stage	Discharge	Stage	Discharge	Stage	Discharge
Sample Site							
Rio Vista	6/12/02	167.64	10,941	130.26	7,503	96.84	8,349
RM 172	6/18/02	168.07	12,890	130.75	9,482	97.45	9,840
RM 233	6/19/02	168.12	13,130	130.83	9,836	97.53	10,054
Chico Landing	6/20/02	168.14	13,227	130.80	9,702	97.45	9,840
Pine Creek	6/26/02	168.34	14,222	131.09	11,050	97.87	10,982
Deadman's Reach	7/01/02	168.21	13,570	131.03	10,761	97.87	10,954
GPS Data	11/25/02	166.11	5,695	129.09	4,412	95.23	3,970
	11/26/02	166.13	5,752	129.11	4,463	95.24	3,990

Table 3. Colonization frequency and occurrence of species across the six study sites. Only quadrats containing at least one species are counted; stem density within quadrats is not considered here. Number of quadrats per site is an estimate of site seedling abundance.

Site	# Quadrats with Seedlings	Percent of Point Bar Colonized	Species Relative Frequency (%)			
			Populus fremontii	*Salix gooddingii*	*Salix exigua*	*Salix lasiolepis*
RM 233	19	8.2%	21%	11%	68%	0
Rio Vista (215)	78	7.2%	23%	49%	22%	6%
Pine Creek (196)	72	12.7%	15%	47%	31%	7%
Chico Landing (194)	166	31.6%	21%	38%	48%	0%
Deadman's Reach (186)	4	<1%	0%	75%	25%	0%
RM 172	114	22.6%	4%	39%	48%	9%

Table 4. Species occurrence on point bars in relation to spatial position on point bars, all study sites combined. Only quadrats containing at least one species are counted; stem density within quadrats is not considered.

			Species Relative Frequency			
	# Quadrats Sampled	Quadrats with Seedlings	*Populus fremontii*	*Salix gooddingii*	*Salix exigua*	*Salix lasiolepis*
Upstream	1230	8.4%	12%	55%	27%	6%
Midstream	1282	14.2%	24%	35%	38%	3%
Downstream	900	23%	11%	27%	59%	4%

Table 5. Species relative stem density (number of stems of a species divided by the total stems of all species X 100) in relation to spatial position on point bars, all sites combined.

		Species Relative Density			
	# Stems	*Populus fremontii*	*Salix gooddingii*	*Salix exigua*	*Salix lasiolepis*
Upstream	507	8%	63%	26%	3%
Midstream	775	29%	32%	37%	2%
Downstream	1045*	5%	13%	43%	39%*

*These values are heavily influenced by four quadrats at RM 172, each containing over 100 *S. lasiolepis* seedlings.

Table 6. Mean stem heights (cm) by taxa, site, and position on point bars. For each quadrat, an average height was estimated for each species. Values are means of all estimated heights in quadrats, with sample size (number of quadrats) in parentheses. *Salix* spp. are combined totals for *S. gooddingii*, *S. exigua*, and *S. lasiolepis*.

	Upstream		Midstream		Downstream		Site Mean	Site Mean
Site	*Salix* spp.	*Populus fremontii*	*Salix* spp.	*Populus fremontii*	*Salix* spp.	*Populus fremontii*	*Salix* spp..	*Populus fremontii*
RM 233	65 (2)	0 (0)	101.7 (3)	35 (1)	75.5 (11)	33.3 (3)	80.7	34.2
Rio Vista (215)	82.7 (15)	133.3 (3)	92.3 (38)	42.9 (17)	216 (5)	0 (0)	130.3	88.1
Pine Creek WCB (196)	110 (22)	17.8 (6)	172 (23)	101 (5)	176.3 (8)	400 (1)	152.7	172.9
Chico Landing (194)	92 (3)	66.7 (17)	27.1 (26)	26.3 (14)	81.2 (93)	65.8 (18)	66.8	52.9
Deadman's Reach (185)	65 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	65.0	0.0
RM 172	126.1 (22)	0 (0)	137.6 (27)	255 (4)	74.5 (62)	0 (0)	112.7	255.0
Overall Mean (cm)	90.1	72.6	88.4	92.0	103.9	166.4		

Table 7. Point bar substrate composition, all three transects combined. All quadrats were included, with and without colonists. Values are in percent.

Substrate Type	RM 233	RV	PC WCB	CL	DM	RM 172
Silt	5	6	4	13	16	17
Sand	29	3	2	32	18	47
Gravel	0	1	1	0	5	8
Cobble	57	66	79	46	44	26
Sand/Cobble	7	13	6	0	11	2
Silt/Cobble	2	11	7	9	6	1
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Total	100	100	100	100	100	100

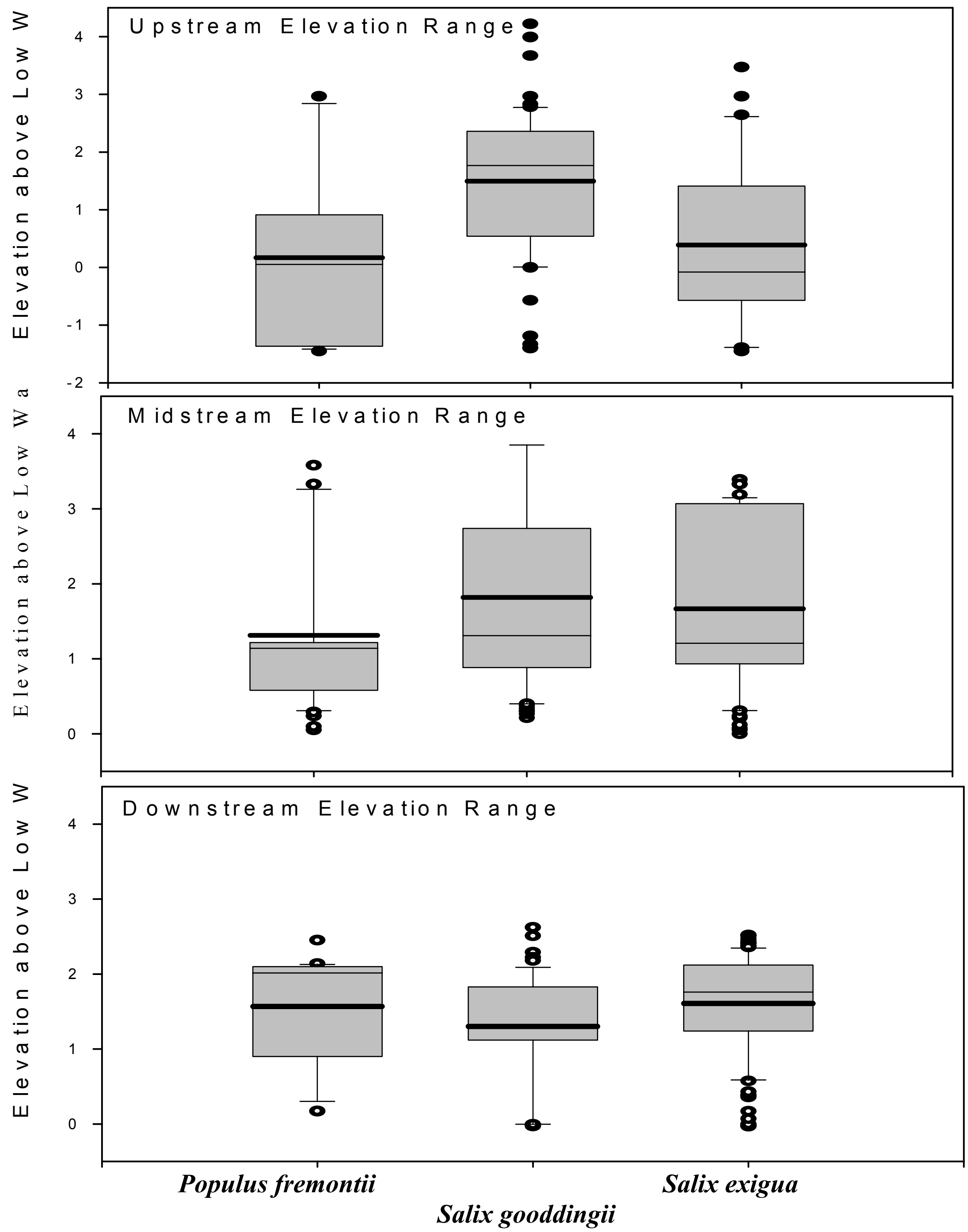

Figure 1. Boxplots showing elevation range of quadrats containing seedlings. The thick black horizontal line is the mean (i.e. mean of all quadrats containing that species), the thin black horizontal line is the median, the shaded box represents the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and outliers are shown as black circles.

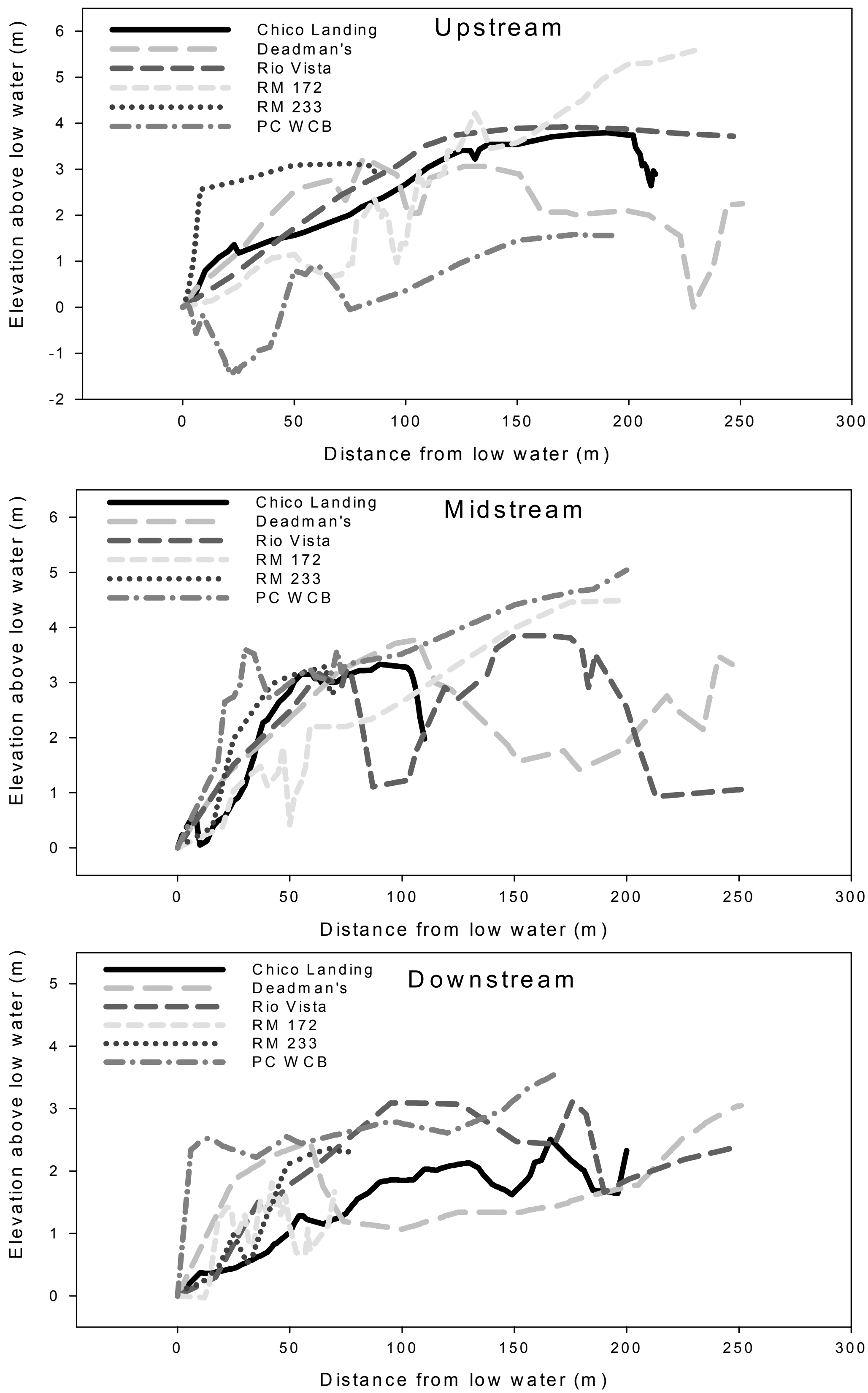

Figure 2. Topographic profiles of upstream, midstream, and downstream transects on point bars. Note that downstream transects generally have a lower slope than do upstream or midstream transects.

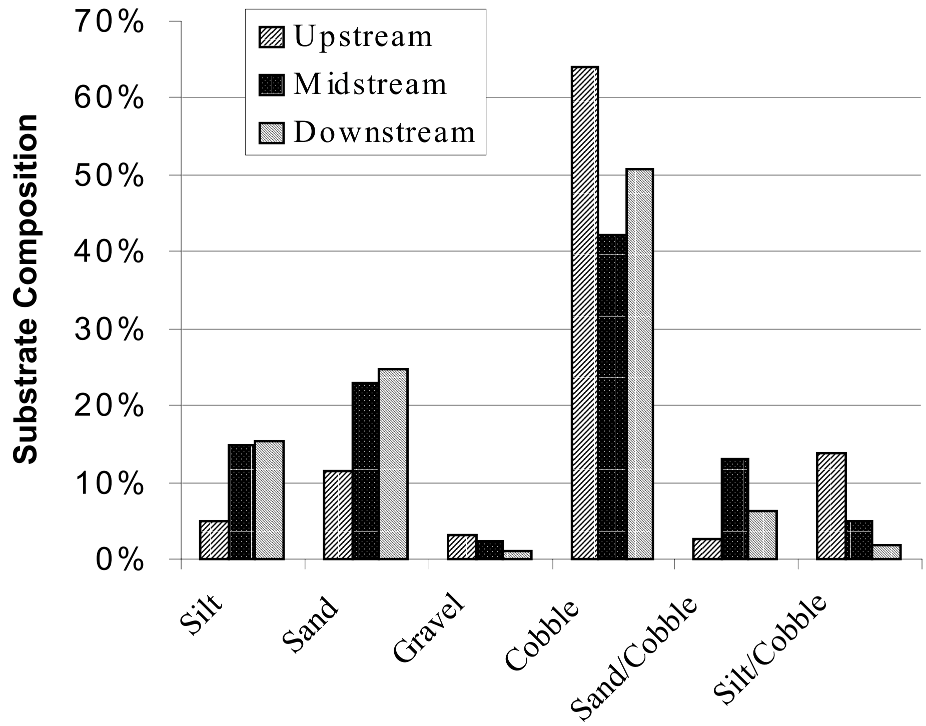

Figure 3. Substrate composition as a function of spatial location on point bars.

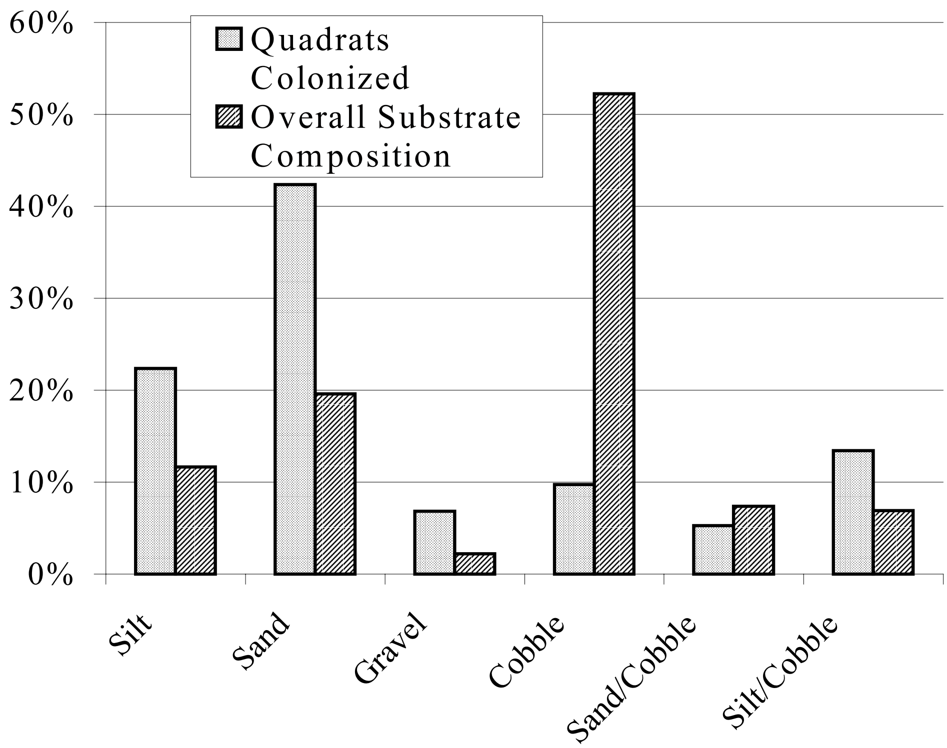

Figure 4. Occurrence of colonists in different substrate types on point bars. Colonists are *P. fremontii*, *alix gooddingii*, *S. exigua*, and *S. lasiolepis*.

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