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The Role of Abandoned Channels as Refugia for Sustaining Pioneer Riparian Forest Ecosystems

John C. Stella,[1]* Maya K. Hayden,[2] John J. Battles,[2] Hervé Piégay,[3] Simon Dufour,[4] and Alexander K. Fremier[5]

[1]Department of Forest and Natural Resources Management, State University of New York College of Environmental Science and Forestry, One Forestry Drive, Syracuse, New York 13210, USA; [2]Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720, USA; [3]CNRS UMR 5600 EVS/Site ENS Lyon, University of Lyon, 15 Parvis René Descartes, BP 7000, 69342 Lyon Cedex 07, France; [4]COSTEL-CNRS LETG UMR 6554, Département de Géographie, Université Rennes 2, Place du Recteur Henri Le Moal, 35043 Rennes Cedex, France; [5]Department of Fish and Wildlife Resources, University of Idaho, Box 441136, Moscow, Idaho 83844-1136, USA

Abstract

In disturbance-prone ecosystems, organisms often persist in spatial refugia during stressful periods. A clear example is the colonization of abandoned river channels by pioneer riparian trees. Here, we examine the prominence of this establishment pathway for a foundation tree species (Fremont cottonwood, *Populus fremontii*) within the riparian corridor of a large river, the Sacramento River in central California. We quantified the total proportion of forest that initiated as a result of channel abandonment for a 160-km reach, analyzed concurrent patterns of tree establishment with floodplain accretion and sedimentation history, and developed a conceptual model of biogeomorphic evolution of abandoned channels. Historical air photo analysis indicated that stands associated with abandoned channels comprised more than 50% of the total extant cottonwood forest area. Tree-ring evidence showed that cottonwood stands commonly developed immediately following abandonment, and the recruitment window ranged from 4 to 40 years, but was less than 10 years at most sites. Rates of floodplain rise and fine sediment accumulation were high in young sites and decreased logarithmically over time. Together, these results suggest that abandoned channels are an important refuge for cottonwood recruitment, that the greatest opportunity for colonization occurs within a short period after the cutoff event, and that sedimentation processes influence the duration of the colonization window. On rivers where tree recruitment along the active channel is severely limited by hydrologic regulation and/or land management, abandoned channel refugia may play an even more important role in sustaining an ecologically functional riparian corridor. Preserving bank erosion, active meander corridors and forest regeneration zones created by cutoff events are therefore key conservation measures on shifting rivers.

Key words: abandoned channel; cottonwood; Salicaceae; floodplain; recruitment refugia; riparian; Sacramento River; dendrochronology; oxbow; persistence strategy.

Introduction

Pioneer or early colonizing plant species typically have more than one life history strategy for persistence (Bond and Midgley 2001). Species that rely

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*Corresponding author; e-mail: stella@esf.edu

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on disturbance events for regeneration opportunities must find ways to maintain their populations during periods of relative stability. For pioneer trees, traits contributing to persistence include: long life (for example, *Sequoiadendron giganteum*; York and others 2009), seed burial (for example, *Prunus pensylvanica*; Marks 1974), cone serotiny (many *Pinus* species; Ne'eman and others 2004), and vegetative propagation (for example, *Salix exigua*; Douhovnikoff and others 2005). Another persistence strategy in disturbance-prone or spatially heterogeneous systems is the use of spatial refugia. Marks (1983) hypothesized that native herbaceous plants of the northeastern United States were able to colonize forest gaps created by fine-scale disturbances, and persist by moving from one temporary gap to another. For instream aquatic organisms, hydraulic refugia during high flows and pockets of standing water during droughts are critical to population recovery, and the loss of this habitat heterogeneity in altered river systems has been the focus of many restoration efforts (Sedell and others 1990; Lake and others 2007). However, the importance of spatial refugia for riparian plant species or more generally for trees is less appreciated (but see Cooper and others 2003).

Riparian corridors are complex, spatially heterogeneous ecosystems where hydrogeomorphic processes largely dictate both the disturbance regime and resource supply rate (Naiman and Décamps 1997; Stromberg and others 2007). Abiotic heterogeneity produces diverse and dynamic biological communities. Decades of river regulation in conjunction with other human modifications (for example, channelization and floodplain land use change) have altered the structure and function of these riparian ecosystems (Friedman and others 1998; Nilsson and Berggren 2000). Stabilization of the natural flood regime and channelization of previously free-flowing rivers have had particularly detrimental effects on pioneer tree populations (Fenner and others 1985; Jansson and others 2000; Johnson 1994; Graf 2006; Braatne and others 2007), which in the temperate zone are often composed of fast-growing, disturbance-adapted cottonwood (*Populus*) and willow (*Salix*) species. *Populus*, typically the dominant tree, is a foundation species (sensu Ellison and others 2005) in the riparian ecosystem. As such, it defines much of the structure of a community by creating locally stable conditions for other species, and by modulating fundamental ecosystem processes (nomenclature from Dayton 1972, as cited in Ellison and others 2005). *Populus* productivity and growth is critical to the rapid stabilization of substrate, nutrient cycling, soil development, and food web networks that link terrestrial and aquatic systems (Braatne and others 1996; Patten 1998; Whitham and others 1999).

Although pioneer species are common even in altered river systems, clear empirical evidence shows declines both in the extent of mature forest as a result of land conversion, and in the frequency of new cohort recruitment downstream of dams along many rivers in the Western U.S. (Buer and others 1989; Cooper and others 1999; Dykaar and Wigington 2000; Braatne and others 2007). If aging stands are not replaced with sufficient frequency or spatial distribution, long-term persistence of these species and the vital ecosystem processes they mediate are threatened.

One largely unexplored avenue for persistence of these species in alluvial river ecosystems is within abandoned channels in the adjacent floodplain. Abandoned channels are recognized as large, structurally diverse features in floodplains (Bornette and others 1998; Ward 1998), and associations between abandoned channels and pioneer tree species have been emphasized in previous studies (Kalliola and others 1991; Shankman 1991, 1993; Cordes and others 1997; Dykaar and Wigington 2000; Polzin and Rood 2006). However, to date neither their potential as refugia in functioning river systems, nor their added value as rare habitats in impaired systems, have been quantified or described mechanistically. Their role in sustaining riparian forests hinges on their size, unique physical environment, spatial distribution, and longevity in the landscape (Shankman 1991; Cordes and others 1997).

Though they are common features in many lowland and piedmont alluvial rivers, abandoned channels have been considered thus far a relatively minor pathway in the recruitment of pioneer riparian trees (Naiman and others 2010). In actively meandering river systems, the primary pathway for recruitment occurs along the margins of the active channel (Mahoney and Rood 1998; Dixon and others 2002; Braatne and others 2007), in which progressive migration of the river channel drives parallel processes of landform evolution and pioneer vegetation dynamics (Figure 1A–C) (Everitt 1968). However, flow regulation, bank armoring and floodplain constriction reduce channel migration and cutoff events (Larsen and others 2007; Michalková and others 2010), which alter the conditions required for successful cottonwood recruitment (Mahoney and Rood 1998) and over time shift pioneer forests to fewer, older, and more spatially isolated stands. Because these modifications are widespread on many rivers and encompass the full

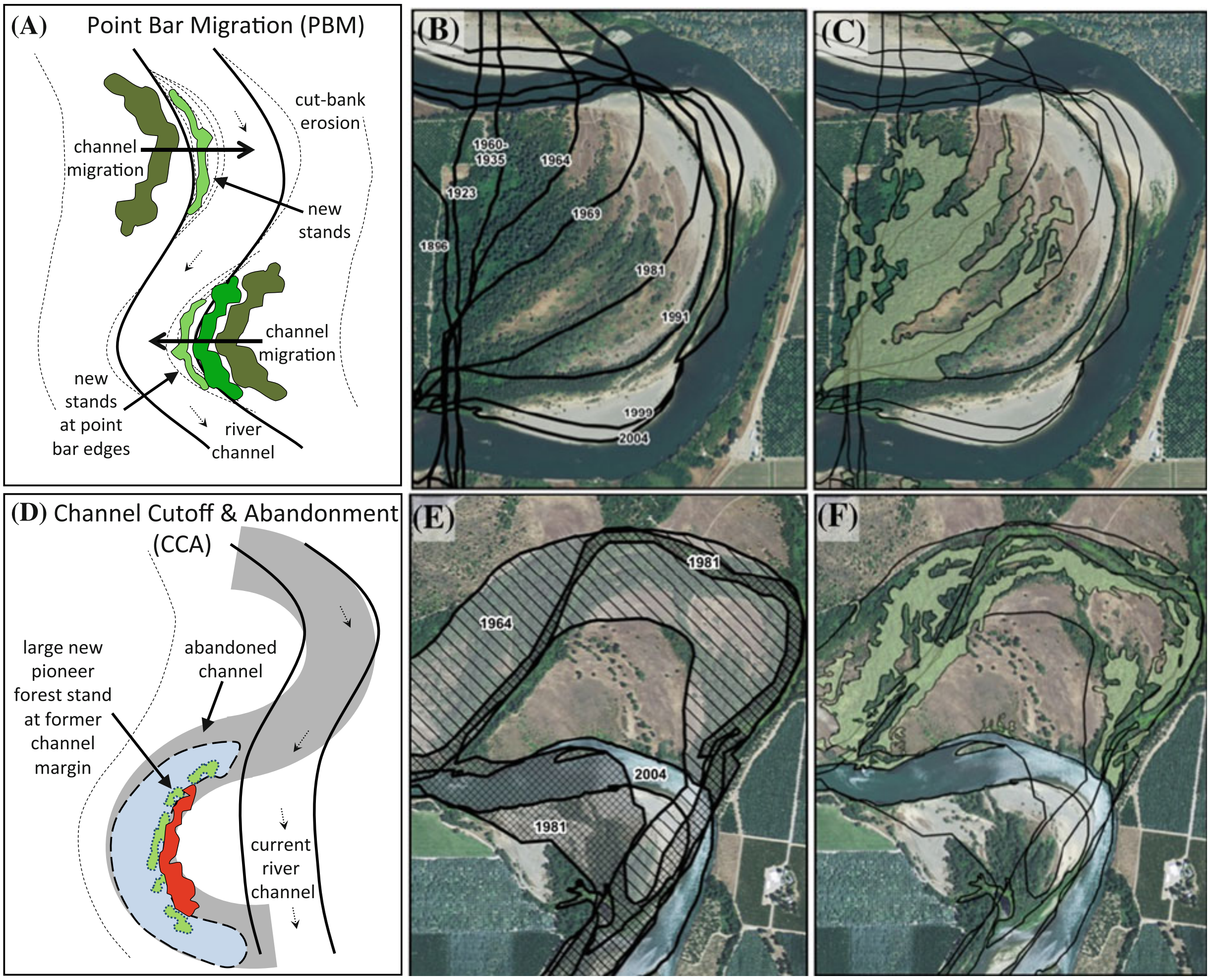

Figure 1. Planform pattern of pioneer forest stand development following point bar migration (**A**–**C**), and channel cutoff and abandonment (**D**–**F**). **A**, **D** The general forest development patterns; successive forest stands (*light green*) may be patchy or continuous. **B**, **E** Historical channel migration and cutoff events at representative areas of the Sacramento River. *Lines* in **B** correspond to the leading edge of the migrating point bar in different years. Polygons in **E** represent the area of the wetted channel in 1964 (*single hatching*), 1981 (*double hatching*), and 2004 (*no hatching*). **C**, **F** Cottonwood forest stands (*shaded green* polygons) mapped from 2007 aerial photographs.

floodplain (that is, not just active channel), we argue that restoration or mitigation plans must consider the role of abandoned channel processes on population-level forest stand dynamics.

Pioneer Tree Recruitment in Abandoned Channels: A Complementary Pathway

We propose that pioneer tree recruitment in abandoned channels (Figure 1D–F) occurs as a result of two interacting processes: (1) the geomorphic evolution of abandoned channels from aquatic to terrestrial environments (that is, channel dewatering from sediment accretion and fining following channel cutoff), and (2) vegetation colonization and subsequent community dynamics. At a coarse scale, both processes are dependent on the physical disturbance regime, particularly the frequency and magnitude of flooding. The early geomorphic evolution and terrestrialization of abandoned channels in river/floodplain ecosystems is driven by sedimentation processes that proceed in two main phases, bedload infilling and blockage, and long-term fine sedimentation (Gagliano and Howard 1984; Constantine and others 2010). The first phase encompasses the time period after the cutoff event when the abandoned channel remains hydrologically connected to the main channel, transporting coarse bedload material into the abandoned channel until a plug of sediment forms at the upstream (and sometimes downstream) end of the abandoned channel. Within oxbows (former channel meanders), the bedload infilling stage is also characterized by a dewatering of the inner bank of the abandoned channel, the width being reduced by more than 50% at the apex of the meander bend. The fine sedimentation stage then follows, when the abandoned channel functions as a floodplain lake that fills typically in a backwater fashion from downstream, depositing fine suspended sediment when flood flows recede. Thus, over time there is both a filling and a fining of substrate within the abandoned channel, which has implications for soil water availability for plants. The controls on the initial bedload processes are not well understood, and depend on site-specific factors such as the inner geometry of the abandoned channel and its connection angle with the main channel (Constantine and others 2010). Once a channel is abandoned, the deposition rate of coarse and fine sediment is influenced at the reach scale by sediment supply and the frequency of flooding (Shields and Abt 1989; Constantine and others 2010). The spatial distribution of grain sizes and length of time an abandoned channel remains in its aquatic phase is better understood, and depends on factors affecting the rate of sedimentation into the channel (Piégay and others 2008).

Similar to point bars, newly abandoned channels fulfill the necessary requirements for pioneer tree germination and survival, namely bare mineral substrate, abundant water, and lack of competition (Mahoney and Rood 1998; Braatne and others 1996). Unlike point bar habitats, abandoned channels do not experience the same frequency or magnitude of scour as active channel bars at a given flow regime (Constantine and others 2010). Thus, seedlings that initiate close to low-flow stage in abandoned channels are more likely to survive subsequent floods and recruit to the overall population. In addition, the increased proportion of fine sediment deposited in abandoned channels relative to point bars (Fisk 1947; Constantine and others 2010) potentially mitigates desiccation mortality associated with sudden water table recession during critical summer growth periods (Amlin and Rood 2002; Stella and others 2010). Therefore, although they do not form with the same consistency as point bars, abandoned channels constitute a type of 'safe site' for pioneer tree seedlings (Enright and Lamont 1989; Polzin and Rood 2006).

In this paper, we examine the abandoned channel pathway to pioneer stand initiation and assess its potential to contribute to the conservation of foundation riparian species. To illustrate this idea, we discuss results from a study of *Populus fremontii* (Fremont cottonwood) recruitment along the middle reach of the Sacramento River in the Central Valley of California and present a conceptual model of pioneer tree recruitment and stand dynamics that is linked to the biophysical evolution of abandoned channels. Our first objective was to determine if the proportion of extant riparian forest originating within abandoned channels represented an important fraction of our study system (Objective 1). Secondly, we measured tree ages to test a prediction that the timing of forest initiation should be strongly correlated with channel cutoff events, with at least one cohort developing, and the oldest trees within an abandoned channel establishing within the first year(s) following channel cutoff (Objective 2). We then documented the fine sedimentation rate in these abandoned channels with field evidence and remotely sensed data to compare the timing of recruitment to terrestrialization (Objective 3). Finally, we developed a conceptual model that describes how the vegetation patterns observed result from a variable 'recruitment window' that is constrained by the timing and pace of sediment deposition in abandoned channels (Objective 4). Our ultimate goal is to provide a process-based perspective that captures the ecosystem dynamics of these abandoned channels and that guides management, conservation and restoration efforts (sensu Naiman and others 2010).

Methods

Site Description

The Sacramento River catchment is the largest in California, draining 68,000 km^2 from the Sierra Nevada and Klamath Mountains, Coast Ranges, and the southern end of the Cascades and Modoc Plateau, through the northern half of the Great Central Valley to the San Francisco Bay-Delta (Figure 2). We selected this river because its hydrology is regulated by an upstream dam, it is an actively shifting piedmont river with many abandoned channels, and new knowledge on linked geomorphological and ecological processes was needed to inform river conservation strategies. The middle reach of the river extends for 160 river kilometers, from a major diversion dam in Red Bluff (Tehama County) downstream to the overflow weir in Colusa (Colusa County). This reach is a gravel-bed, meandering section of stream set within a fine-grained floodplain alluvium. The mainstem is regulated at Shasta Dam that was built to capture peak flows for irrigation supply and hydropower generation during the summer dry

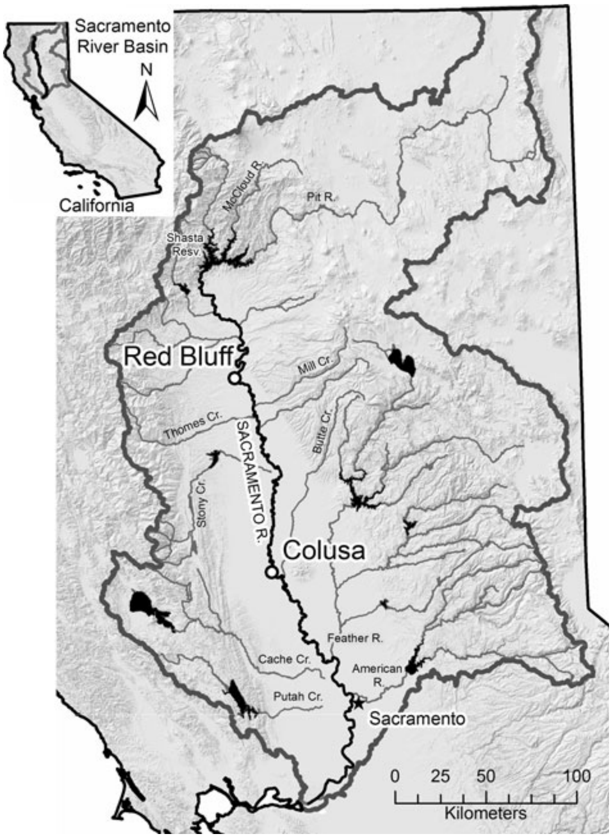

Figure 2. Sacramento River study area. The middle reach extends between Red Bluff and Colusa.

season. Levees are set back from the main channel with isolated areas of rock revetment (Buer and others 1989). All major tributaries are regulated by either storage or overflow dams. Despite significant flow regulation with truncated peak flows, reduced sediment supply, and elevated base flows, geomorphically significant events still occur and result in active, although protracted, channel migration, and cutoffs (Larsen and others 2007; Micheli and Larsen 2010). Despite an estimated loss of 90% of riparian forest area throughout the Central Valley since European settlement, the middle Sacramento River corridor has the largest network of cottonwood-dominated forest stands remaining in California (Buer and others 1989).

Landscape Analysis of Pioneer Forest Association with Abandoned Channels

Considering the unique hydro-geomorphic and biotic conditions, we hypothesize that pioneer stand initiation within abandoned channels is a recruitment and establishment pathway complementary to that occurring on point bars. This pathway would only be compelling if it resulted in a non-negligible amount of forest area created relative to the primary point bar migration pathway (Objective 1). To validate this hypothesis, we quantified the amount of existing pioneer riparian forest in the middle reach of the Sacramento River associated with channel cutoff and abandonment versus progressive lateral migration of point bars. We performed a GIS-based analysis on the reach using an existing (1999) riparian vegetation map developed by California State University, Chico, a channel centerline digitized by the California Department of Water Resources from 1999 aerial photography (1:7,200 scale), and abandoned channel features mapped by Michalková and others (2010). Our analysis focused on the Cottonwood Forest cover class ($N = 500$ polygons), one of 12 mapped cover classes. We developed a statistical model to classify forest patch origin from either point bar migration (PBM) or channel cutoff and abandonment (CCA), using landscape metrics and a classification and regression tree (CART) analysis (De'ath and Fabricius 2000; Venables and Ripley 2003). The CART analysis is a non-parametric approach to classification commonly used in ecology to parse plant communities along environmental and/or management gradients. More recently its value in addressing landscape-level questions has been noted (Urban and others 2002) but we are unaware of a previous application of CART to link ecological and geomorphic data in riparian systems.

First, we selected a random sample of 10% of the cottonwood patches to use as a training data set, stratified by polygon area to ensure representation of larger patches. We determined patch origin process, CCA or PBM, using time-series historical aerial photographs from 1942, 1962, 1985, and 1999 (Spatial scale from 1:7,200 to 1:24,000 (Greco and others 2007). Photos were digitized and rectified (see Michalková and others 2010). In cases where the initiation of forest vegetation within a training polygon pre-dated the earliest photography (1942), a new polygon was randomly selected to replace it from the remaining 450 polygons of the full data set.

The training data set was extracted and used to develop a classification and regression tree (CART) based on spatial metrics calculated in ArcGIS (Version 9.2, ESRI), which included patch area, distance from patch centroid to the 1999 main channel centerline and to the nearest abandoned channel feature, and the difference between these distances. The CART analyses were performed in Splus (v8.1, Insightful Corp.), and resulted in a classification that was then used to assign an origin (CCA or PBM) to the remaining data set of polygons ($N = 450$). This classification model was validated using a random 7% sample of polygons ($N = 33$) that were not included in the training data set and involved the same visual assessment and classification used on the training data set.

Timing of Cottonwood Stand Initiation Relative to Channel Cutoff

We examined the age structure of existing forest stands via tree-ring analysis in abandoned channels distributed across our study area to understand the pattern and frequency of tree establishment within this geomorphic setting (Objective 2). Age of the channel since cutoff was estimated independently from time-series historical aerial photographs. Nine sites were selected, spanning a range of 15–100 years since cutoff, from an existing list of 30 abandoned channel sites that were analyzed previously for geomorphic characteristics (Michalková and others 2010). One site contained two abandoned channels that developed in separate cutoff events; therefore the total number of abandoned channel ages was 10 from the nine sites. The existing cottonwood forest stand at each site was stratified into an upstream, middle, and downstream segment, and a 10-m wide belt transect was located randomly within each segment. Each transect was established perpendicular to the inside bend of each abandoned channel and extended 45 m into the associated forest patch. This distance was a conservative estimate of floodplain area that developed within the wetted width of the original channel; aerial photographs confirmed that all transects were located on areas that experienced bedload and fine sediment infilling and not on point bars colonized prior to channel cutoff.

The occurrence of all cottonwood trees (seedlings, saplings, and adults) was recorded within each transect. Approximately 5–13 cottonwood trees were selected at each site, cored using a 5.15 mm increment borer, and aged via tree-ring analysis. Trees were selected to sample the largest and smallest individuals at the site. The largest tree visible from the transect (but not necessarily contained within the 10-m width of the belt transect) was also included to ensure that the oldest trees present at the site were captured. Due to accretion of sediment since the time of establishment, coring heights were in some cases substantially higher than the original root crown and tree ages thus represent minimum values. However, sectioning of saplings indicates that due to the rapid growth rate of this species, fewer than five rings may be missing above the root crown (Hayden, unpublished data). We quantified the correspondence of tree age with site age using ordinary least squares (OLS) regression with site age as the lone predictor of tree age. We developed separate relationships for the oldest and youngest trees at each site.

Patterns of Floodplain Accretion Following Cutoff

We analyzed the geomorphic evolution of abandoned channels during forest development (Objective 3) by quantifying floodplain elevation change since time of cutoff using a combination of field measurements and analysis of remotely-sensed topographic data. At the nine abandoned channel sites used for dendrochronological analysis, we surveyed the elevation of the floodplain along each 45-m transect relative to early summer baseflow elevation in the river using an autolevel (Model AT-G4, Topcon Corp., Tokyo). In addition to topography, we measured accumulation of fine sediment above the former gravel bar surface since time of cutoff. At two locations along each transect (meters four and 44 on the 45-m transects) we used a soil auger to penetrate the fine substrate to the depth of the coarse gravel layer, which was assumed to be the gravel surface following initial bedload filling in the years following cutoff (Piégay and others 2008). When the corer touches the gravel, a clear sound occurs so that the fine sediment depth is estimated with low error (±5 cm, consistent among samples). Six fine sediment depth measurements were made per site. We related the long-term fine sediment accumulation rate (cm y^{-1}) to site age using OLS regression with both predictor and response variables log-transformed to satisfy residual assumptions. This represents a minimum accumulation rate, because it measures solely the fine sediment fraction deposited, which generally begins after the coarse bedload filling stage ends, approximately 1–5 years after cutoff.

We estimated floodplain accretion using a 2007 LiDAR (light detection and ranging) digital elevation surface and GIS dataset of historical channel positions (Greco and others 2007) at 12 additional channel cutoff sites. For areas of known channel abandonment, we extracted the LiDAR surface elevation relative to the river channel water surface. This difference approximates the height of floodplain, or depth of fine grain sediment, above water surface during the LiDAR data collection period. We used mean daily flow stage from the US Geological Survey gauge at Bend Bridge (gauge # 11377100) to compare daily mean discharge and gauge height between the two periods to ensure that the base topographic datum (that is, water surface elevation) was comparable between field and LiDAR datasets. The average flow during the single-day LiDAR flight (22 February 2006) was 256 and 285 $m^3 s^{-1}$ during the field surveys (29 April–8 May 2007). At the gauge, this represented a 0.17 m difference in flow stage, with resulting potential higher relative elevation values calculated for the LiDAR sites. Because the channel cross-section is narrower at the gauge location and the stage-discharge relationship typically steeper than at our sites, we did not adjust the original estimates of relative elevation.

The long-term sediment accretion rate within the former channels was estimated by dividing the relative elevation surface in 2007 by the time since cutoff, which was determined from historical aerial photos. The result is a rough estimate of floodplain accretion rate due to cumulative sedimentation events. Because this method does not include sediment accumulation in the lowest part of the former channel (that is, below the current water surface), these estimates represent lower rates than if averaged over the entire former channel. Furthermore, any error associated with long-term trends in the elevation of the water surface (for example, due to progressive channel bed incision or aggradation) in the active channel since abandonment of the adjacent channel is not accounted for by this methodology.

We analyzed the floodplain accretion data using analysis of covariance (ANCOVA), with site age as a continuous predictor and method (field versus LiDAR) as a categorical factor to determine how well site age predicts the accretion rate of the floodplain surface and whether there were consistent prediction differences (model bias) depending on the method of estimation, field survey versus LiDAR. Site age was log-transformed to satisfy residual assumptions. Following this analysis, we specified the best functional form of the floodplain accretion rate by comparing three simple models of elevation change as a function of site age: linear, exponential association, and saturating. Functions were fitted using CurveExpert 1.4 (D. Hyams, http://www.curveexpert.net), and compared using residual least squares.

Results

Pioneer Forest Association with Abandoned Channels

The CART analyses resulted in a classification accuracy of 84% for the training data set (Table 1). This accuracy estimate excludes five of the 50 polygons that could not be classified using the historical aerial photos because forests either developed on mid-channel bars (not clearly associated with one of our two processes) or were heavily altered (for example, cleared for agriculture) at some point during forest development. Validation with the random 7% sample of polygons that were not included in the training data set yielded a total accuracy of 73%. However, the model more accurately predicted forest patches originating from point bar migration (user accuracy = 92%) than those associated with channel cut-off (user accuracy = 60%, Table 2). The best predictors of channel abandonment origin were proximity to an abandoned channel relative to the active one (difference in distance ≥265 m), and patch area at least 1.2 ha. When the CART model was applied to the full data set of Cottonwood Forest (500 polygons), 54% of total forest area was associated with channel abandonment (Table 2). This area was represented by 148 patches, which comprised 29.6% of the total number of patches,

Table 1. Classification Error Matrices for Training and Validation Data Sets for the Analysis of Extant Cottonwood Forest Patch Origin

	Training data set					Validation data set			
	Actual			User's accuracy		Actual			User's accuracy
Predicted	CCA	PBM	Total		Predicted	CCA	PBM	Total	
CCA	15	3	18	83%	CCA	12	8	20	60%
PBM	4	23	27	85%	PBM	1	12	13	92%
Total	19	26	45[1]		Total	13	20	33	
Producer's accuracy	79%	88%		84%	Producer's accuracy	92%	60%		73%

Abbreviations for the process of origin are CCA for 'channel cutoff and abandonment' and PBM for 'point bar migration'. Actual data are based on visual assessment of patch origin from time-series aerial photographs. Predictions were based on results using the classification and regression tree (CART).
[1]Note: 5 out of the 50 sites in the original training data set could not be classified using the aerial photographs because forests either developed on mid-channel bars (not clearly associated with one of our two processes of interest) or were heavily altered (for example, cleared for agriculture) at some point during forest development.

Table 2. Predicted Process of Origin of Cottonwood Forest Stands on the Sacramento River

Process of origin	Number of patches		Forest area		Patch area (ha)		
	Total	Percent	Total (ha)	Percent of all forest	Median	Mean	SE
Channel cut-off and abandonment (CCA)	148	29.6	849	53.8	2.1	5.7	±0.7
Point bar migration (PBM)	352	70.4	730	46.2	0.3	2.1	±0.3

Totals reflect the application of a classification and regression tree model on the full set of extant stands (N = 500).

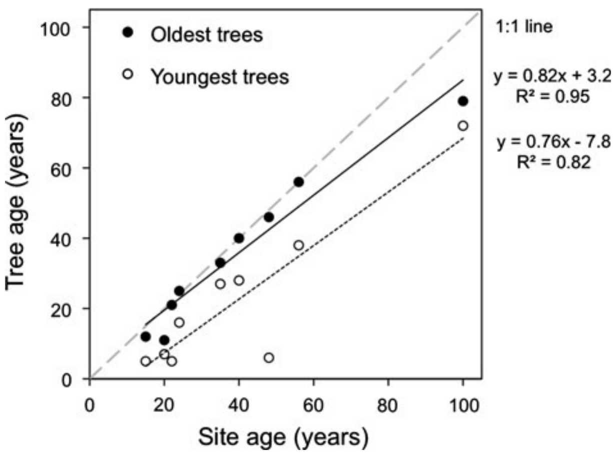

Figure 3. Age of oldest (*solid circles*) and youngest (*open circles*) cottonwood trees compared to site age in nine abandoned channel stands from the study area. Tree ages were determined from dendrochronological analysis and represent a minimum value. Site age was estimated from time-series historical aerial photographs. At all but two stands, the oldest tree cored dated to within 3 years of the estimated cutoff year.

with a median patch area of 2.1 ha. Forest patches associated with point bar migration were more numerous (352 of 500 patches), but were smaller, with a median area of 0.3 ha.

Timing of Cottonwood Stand Initiation Relative to Channel Cutoff

The combined dendrochronological and aerial photo analysis indicates that cottonwood forest patches developed at all sites following cutoff (Figure 3). In all but the oldest abandoned channel, the first cohort established at or near the time of the cutoff event. Estimates of time since cutoff from the aerial photographs ranged from 15 to 100 years, and the maximum tree age for the same sites ranged from 11 to 79 years. OLS regression of the oldest trees as a function of site age ($F_{1,7} = 117$, $P < 0.001$) yielded $r^2 = 0.95$ and the relationship:

$$\text{tree age} = 0.82 * \text{site age} + 3.2 \quad (1)$$

OLS regression of the youngest trees at each site as a function of site age ($F_{1,7} = 33$, $P < 0.001$) yielded $r^2 = 0.82$ and the relationship:

$$\text{tree age} = 0.76 * \text{site age} - 7.8 \quad (2)$$

Evidence of young trees at each site indicates that successive recruitment events occurred within a window ranging from 4 to 40 years (Figure 3). In other words, following channel abandonment, the time frame when abiotic and biotic conditions were suitable for cottonwood recruitment ranged tenfold, with no correlation between site age and the recruitment window length.

Floodplain Accretion Following Cutoff

Analysis of floodplain accretion using both the field and LiDAR datasets revealed that site age was a significant predictor of relative elevation ($F_{1,18} = 47.5$, $P < 0.001$), and that there were no differences between the method of estimation (field vs. LiDAR; $F_{1,18} = 1.9$, $P = 0.18$), nor interactions between site age and method of estimation. The best-fitting model with site age as the sole predictor was an exponential association function with the formula:

$$\text{relative elevation} = 3.08\left(1 - e^{-0.037\text{site age}}\right) \quad (3)$$

with relative elevation in meters and site age in years (Figure 4A). The fit from this model is adjusted $r^2 = 0.69$. Sediment coring from the abandoned channel sites indicates that average fine sediment depth ±1SE across all sites is 306 ± 31 cm, with a range of 116–443 cm across all sites. When divided by site age, this corresponds to an average sedimentation rate ranging from 4 to 18 cm y^{-1} (Figure 4B). This rate was significantly and negatively related to site age in a log–log relationship ($F_{1,8} = 11.5$, $P = 0.009$, adjusted $r^2 = 0.54$):

$$\text{sedimentation rate} = 86.4 * \text{site age}^{-0.65} \quad (4)$$

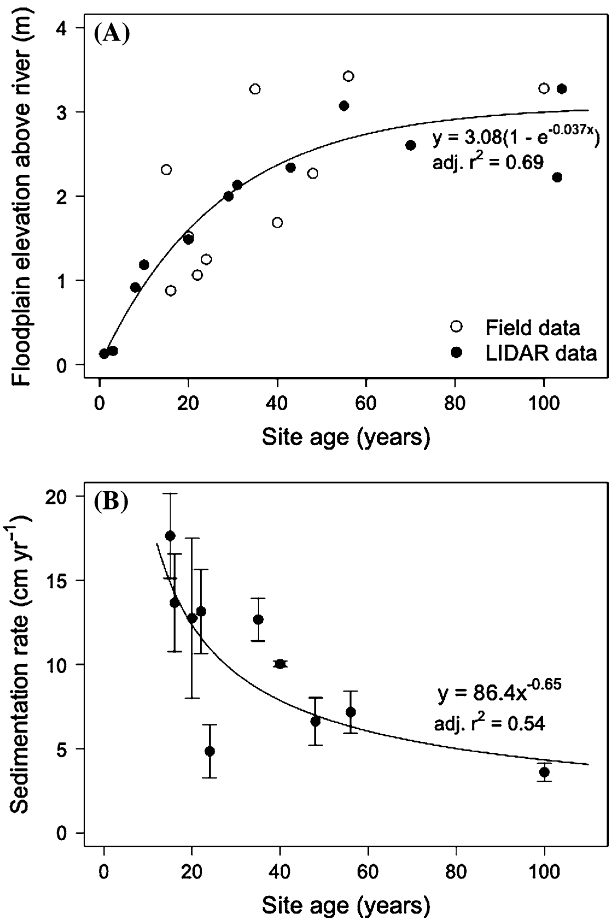

Figure 4. Patterns of floodplain accretion and fine sediment accumulation in abandoned channels on the Sacramento River (**A**) relative floodplain elevation measured at 22 sites as the mean ground height above the low-flow water surface in the adjacent channel. The *fitted line* is an exponential association function where *y* is relative elevation in meters and *x* is site age in years. **B** Long-term fine sediment accumulation data (site means ± 1SE) with site age from 10 abandoned channel sites; the *fitted line* is a power function.

Discussion

These results support the patterns outlined in our conceptual model (Figure 1) describing how pioneer forest stands develop directly from channel abandonment and terrestrialization. First, a large proportion of pioneer forest area was associated with abandoned channels (Objective 1, Table 2), despite the fact that the majority of cottonwood patches (70%) within our study reach established as a result of point bar migration. Cottonwood patches that developed in abandoned channels were on average more than twice as large in area. Even though channel cutoff events occur sporadically compared to point bar migration and fewer than a third of forest patches were associated with abandoned channels, the latter comprised more than half of the total extant cottonwood forest area. We do acknowledge that the classification tree tended to over-estimate the number of stands originating in abandoned channels (Table 1). Nevertheless our results support the contention that abandoned channels represent important recruitment opportunities in dynamic alluvial river systems. More general studies of vegetation development on meandering rivers demonstrate this pattern and support this process (Shankman 1991, 1993; Kalliola and others 1991; Cordes and others 1997; Dykaar and Wigington 2000; Cooper and others 2003; Polzin and Rood 2006). However, in streams where channel meandering and abandonment is less common, further analysis is needed to establish the generality of this finding.

Secondly, abandoned channel sites were colonized immediately upon or shortly after cutoff, and conditions were sufficiently favorable to allow these trees to survive to maturity at all sites (Objective 2, Figure 3). These success rates are in contrast to point bar environments where recruitment opportunities occur every year but long-term establishment is infrequent (Johnson 1994; Scott and others 1997; Shafroth and others 2002). Though they provide the same transient resource pulses and competition-free environment as point bars, abandoned channels experience a dramatic decline in disturbance intensity following cutoff. We propose that this difference in disturbance intensity is the crucial factor that allows these areas to serve as safe sites for forest regeneration. Because cottonwood trees produce a seed crop every year and these seeds are widely dispersed via wind and water (Braatne and others 1996), we expect that a viable cohort would be available whenever a cutoff event occurs. This expectation was borne out at all but our oldest site (Figure 3).

Third, the establishment opportunity following cutoff was often relatively brief, as would be expected for a pioneer species (Objective 3). We observed a narrow age range exhibited by trees at most of the sites, with a median span of 9 years between oldest and youngest trees (Figure 3). This period also corresponds to the greatest changes in the physical environment, when bedload supply is still active and high rates of fine sedimentation (Figure 4B) lead to rapid accretion of the floodplain surface (Figure 4A). During this period when frequent flooding deposits successive sediment lenses into the abandoned channels, pioneer species adaptations such as adventitious roots and sprouting would favor them over other species more sensitive to burial and substrate disturbance (Lytle and Poff 2004). In time, a negative feedback is imposed as the elevation of the floodplain increases and the long-term sedimentation rate attenuates dramatically (Figure 4B), because lower frequency floods of higher magnitude are required to impose continued geomorphic change. These more benign local conditions as former channels evolve will likely favor plant species less tolerant of stress but with greater ability to compete for light and other resources (Pacala and Rees 1998; Grime 2001; Corenblit and others 2007). We suggest that this shift in geomorphic conditions and local disturbance frequency closes the window of opportunity for recruitment by woody pioneers. We discuss the probable ecological mechanisms for this shift in the next section.

Though multiple lines of evidence strongly support this model of riparian ecosystem development, we acknowledge that our study comprises one river, and the most intensive investigations were conducted at fewer than a dozen sites. Importantly, the landscape-level analyses that complemented the intensive site-based work confirm that the timing of establishment evident in tree-rings and sediment cores matches the overall pattern of forest development from the CART analysis of air photos (Tables 1, 2) and floodplain accretion estimated from LiDAR (Figure 4A). Furthermore, the sites where tree and sediment cores were extracted are representative of a group of greater than 30 extant abandoned channels (and >90 historical ones) identified on the Sacramento River that were formed under both natural and regulated flow regimes (Michalková and others 2010).

Other studies support the broader applicability of these processes, with similar patterns of complementary forest establishment pathways in a variety of alluvial river ecosystems. These include observations from a very similar Mediterranean system in Oregon (Dykaar and Wigington 2000), as well as tropical (Kalliola and others 1991), humid temperate (Shankman 1991, 1993), semi-humid continental (Cordes and others 1997; Polzin and Rood 2006), semi-arid lowland (Cooper and others 2003), arid (Asplund and Gooch 1988), and montane ecosystems (Cooper and others 2006). For example, Kalliola and others (1991) noted the greater habitat size and increased persistence of pioneer woody seedlings in abandoned channels compared to channel margins on 16 rivers in the Peruvian Amazon. Shankman (1991, 1993) observed distinct patterns of association of *Salix* spp. and *Taxodium* spp. trees with abandoned channels and their absence along the active margin of the Hatchie River (Tennessee, USA). Abiotic conditions within abandoned channels, in this case extended annual flooding, precluded colonization by herbaceous species and allowed recruitment of woody seedlings. Where channel migration and cutoffs were prevented by channel straightening and levees, seedling establishment was curtailed and led to vegetation communities dominated by later-successional species. In studies that expressly investigated riparian *Populus* species associations with various geomorphic landforms, mature cottonwoods were at least as common in abandoned channels as along point and island bars (Cordes and others 1997; Dykaar and Wigington 2000; Cooper and others 2003), and sometimes more so (Asplund and Gooch 1988).

Ecological Mechanisms that Drive Forest Generation Patterns

Despite the consistency in the pattern of cottonwood recruitment in abandoned channels along the middle reach of the Sacramento River, the opportunity for recruitment and establishment of pioneer forest stands was not equal at all sites. The window for tree establishment ranged from 4 to 40 years and the differences were not explained by age since cutoff (Figure 3). Understanding the environmental conditions that foster a multi-aged forest structure, one similar to point bar forests (Figure 1A–C), is important not only for determining the population age structure of the current forest but also for predicting future trends under conditions that may shift the hydrogeomorphic regime (Harper and others, in press). Herein, we propose ecological mechanisms based on plant life history characteristics and resource competition dynamics that likely influence these patterns (Bornette and others 2008) (Objective 4).

After channel abandonment, changes in physical conditions associated with the infilling of the abandoned channel by fines and in biotic conditions associated with vegetation development produce an environment that becomes increasingly challenging for early colonizing plants (Figure 5A, B). Most pioneer species, including cottonwood, have a ''colonizer'' strategy where effective dispersal and rapid growth is ''traded-off'' for weaker competitive ability (Pacala and Rees 1998). The greatly reduced intensity of disturbance in abandoned channels along with high resource availability (that is, light and soil moisture) that allows pioneer seedlings to thrive also fosters the subsequent establishment of competitors. Therefore, the development of vegetation communities in

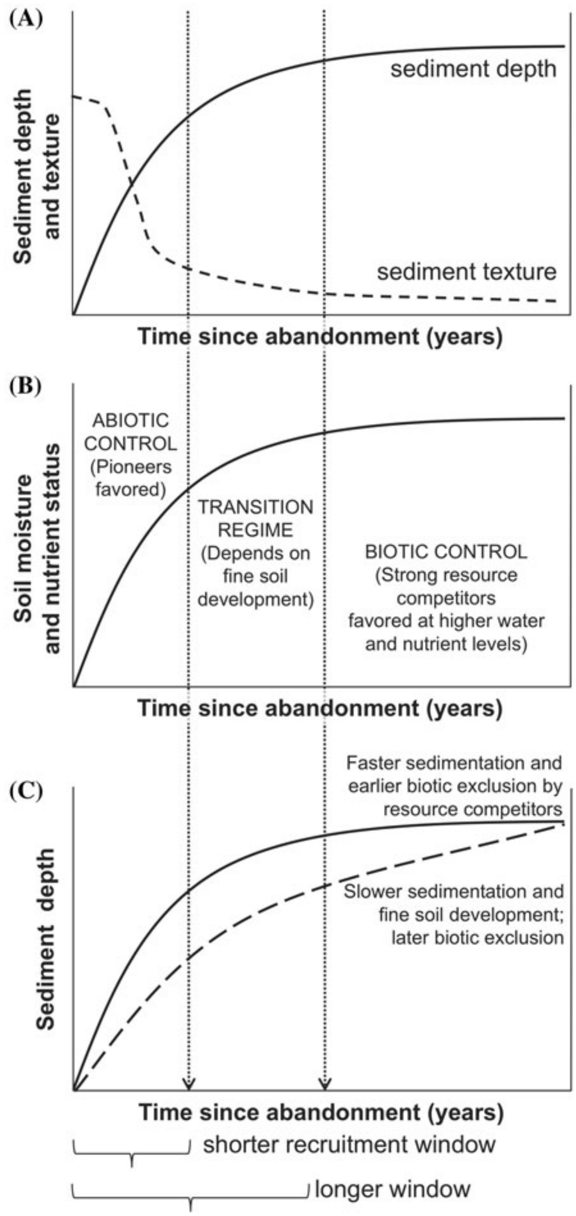

Figure 5. Conceptual model of geomorphic factors driving vegetation colonization and dynamics following channel abandonment. **A** Changes in sediment depth and texture in abandoned channels with time since abandonment; **B** corresponding changes in soil moisture and nutrient status, and the transition period between abiotic and biotic control; **C** relationship between sediment accretion rate and the duration of the riparian tree recruitment window in abandoned channels. A faster sedimentation rate results in a shorter recruitment window and faster transition to biotic control over community dynamics.

abandoned channels depends on the balance of physical conditions that favors pioneer woody plants (Lytle and Poff 2004) versus species that may be better competitors in less-dynamic habitats (Figure 5A; Toner and Keddy 1997). For example, differences in the disturbance regime generated significant changes in herbaceous species composition, tree recruitment, and forest succession between current and formerly active areas of the floodplain (Cordes and others 1997; Dufour and Piégay 2008, 2010).

We propose that the transition in sediment texture from gravel to sand is a key driver of plant community dynamics in abandoned channels, with increased fining initiating a suite of biophysical changes that support greater interspecific competition (Figure 5). Sediment texture acts upon several aspects of plant life history in riparian zones, most importantly soil moisture availability. Drought stress is an important factor limiting plant success in dynamic riparian zones (Stella and others 2010; Stella and Battles 2010). Finer sediment allows for higher capillary rise within the vadose zone and a lag in water table decline in the abandoned channel relative to the main channel, dampening the effect that river stage fluctuations have on water availability. The sediment fining is also a clear indicator of changes in hydraulic conditions (less frequent flood, lower magnitude of flows) that in effect reduce the risk of plant mortality. These abiotic conditions foster the rapid development and high productivity of the vegetation that in turn improve soil water-holding capacity and nutrient supply (Figure 5B). These changes have the cumulative effect of decreasing abiotic stress and making the riparian environment more benign to plants that are good resource competitors.

We expect that competition becomes an important driver of vegetation patterns faster and to a greater degree in abandoned channels because of the great attenuation of the disturbance regime compared to point bar environments. Over time as both woody plants and herbaceous vegetation establish, resource demand outstrips supply, and the channel transitions from a period in which abiotic factors are the primary drivers of woody vegetation dynamics, to conditions where biotic interactions, particularly competition for light and moisture, become more dominant (Figure 5B; Corenblit and others 2007). It is possible that the ecological transition occurs around the time the channel shifts from the blockage phase (that is, a more physically dynamic environment) to infilling with fines (that is, a more benign one). Given the life history traits of pioneer woody species, we propose that these changes impose a recruitment threshold whereby pioneer woody species are excluded by competition with plant species better able to exploit resources in a more stable physical environment (for example, Shankman 1991).

If these are the dominant drivers of vegetation dynamics in abandoned channels, temporal aspects of the sediment transport regime control the length of the pioneer tree recruitment window by mediating the swiftness with which a competitive environment develops within the former channel (Figure 5C; Citterio and Piégay 2009). We propose that abandoned channels that fill quickly (that is, with a short blockage phase) develop a competitive environment earlier, and therefore present a very brief opportunity for recruitment of pioneer plants. Conversely, channels experiencing slower accretion of fine sediment, either as a result of antecedent channel and floodplain morphology (Constantine and Dunne 2008, Constantine and others 2010) or else limited sediment supply, reach this threshold more slowly and maintain longer recruitment opportunities for woody pioneers. This transition period could be slow and gradual or it could be a threshold event, perhaps as a result of a large, episodic deposition event that leads to sudden plug formation. If this transition period or threshold exists, it should be reflected in the structure of existing forest stands, with age distributions weighted more heavily to the period immediately after cutoff. Thus, we would expect to see multiple-cohort stands develop at sites with a long initial phase of bedload infill or that remain in the blockage phase for longer, and potentially only a single cohort at sites that have disconnected rapidly since channel abandonment.

Considerations for Pioneer Tree Populations and Management

The strong association of pioneer forest initiation with channel abandonment has implications for corridor-wide populations of riparian trees as well as their associated ecosystem. Evidence from field studies (for example, Mahoney and Rood 1998; Shafroth and others 2002), population modeling (for example, Lytle and Merritt 2004; Harper and others in press), and successful restoration projects (for example, Rood and others 2003, 2005a) all indicate that opportunities for successful recruitment are the limiting demographic step for pioneer riparian trees. Most critically, researchers and land managers need to value abandoned channels as critical safe sites for pioneer forest generation (Shankman 1991; Dykaar and Wigington 2000) and to integrate them fully into conservation planning (sensu Piégay and Hicks 2005), which thus far has focused primarily on point bar and active channel environments. Secondly, in contrast to point bars, where tree establishment does not occur every year because of desiccation in summer or subsequent floods that eradicate recent seedling cohorts (Johnson 1994; Shafroth and others 2002; Dixon and others 2002), we expect channel abandonment to result in at least one viable cohort for every cutoff event as we observed on the Sacramento River (Figure 3), even in years with low spring discharge.

Channel abandonment is expected to most strongly influence forest dynamics in river systems subject to flow regulation and/or climate change, where the primary recruitment pathway on point bars may be inhibited due to decoupling of the natural flow regime from the life history requirements of pioneer trees (Mahoney and Rood 1998). Significant modifications to flow magnitude and timing from dams and diversions are generally detrimental to long-term recruitment for pioneer species (Stella and others 2006; Braatne and others 2007). Moreover, depending on the degree of impoundment, alluvial channels in piedmont and lowland areas become entrenched which severely limits lateral movement and cutoff events. However, in some river systems channel cutoff-forming floods still occur with some frequency (Hooke 2008; Micheli and Larsen 2010), and the abandoned channel recruitment pathway may be critical to the long-term persistence of pioneer riparian tree populations in the larger ecosystem. Therefore, it is important to maintain the ability of river channels to shift laterally via some mechanism, whether it may be by progressive meandering or punctuated cutoff events (Piégay and others 2005; Florsheim and others 2008). By creating recruitment refugia in years with low spring flows, abandoned channels will eventually support large forest stands, which can serve as propagule sources to complement restoration strategies that re-establish natural flow regimes during wet years (for example, Rood and others 2005b).

Climate change represents another driver that may make the role of abandoned channel forest stands more important in the future. In a broad range study of hydrologic changes in the Rocky Mountains, Rood and others (2005b) found that streamflow volume declined, spring run-off and peak flows occurred earlier, and that summer and early autumn flows were considerably reduced over the course of the 20th century. The ecological implications of these trends are poorer conditions for seedling establishment along active river channels because of increased asynchrony between peak flows and cottonwood seed release timing (Stella and others 2006) and increased duration and severity of summer droughts that would stress seedlings (Rood and others 2008). Currently throughout the Western U.S., a greater proportion of annual precipitation falls as rain versus snow than historically (Knowles and others 2006), with serious implications for the frequency, timing and magnitude of high-discharge events and the dependent ecological communities (Yarnell and others 2010). In California, greater climate variability is expected to occur within the next century, with warmer winter storms providing more and earlier runoff than currently, and less snowmelt runoff occurring in spring (Maurer and others 2007; Cayan and others 2008). These developments will pose increased challenges for water management on regulated rivers such as the Sacramento River, and potentially alter rates of channel bank erosion, meandering, and cutoff events on both regulated and unimpaired systems. As a result, these conditions may increase the importance of abandoned channel forest stands if recruitment along active channels continues to decline with diminished snowmelt floods and increased summer drought (Rood and others 2008; Yarnell and others 2010), but channel avulsion rates remain similar and the more benign abiotic conditions in abandoned channels continue to provide safe sites for seedlings. Factoring in these likely changes to the physical drivers in linked river-floodplain systems will be necessary for developing effective management and conservation plans for floodplain forests and the critical ecosystem they support.

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