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Abandoned Channels as Refugia for Sustaining Pioneer Riparian Forests

By

Maya Kumari Hayden

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

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Summer 2015

Abandoned Channels as Refugia for Sustaining Pioneer Riparian Forests

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Abstract

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Doctor of Philosophy in Environmental Science, Policy and Management

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In North America, cottonwood (*Populus*) and other members of the family Salicaceae are considered to exhibit the classic colonization-competition trade-off. Adaptations that make them highly successful colonists in disturbance-prone floodplain environments appear to reduce their ability to compete for resources in more benign environments. Because cottonwood recruitment dynamics are so tightly coupled to the natural disturbance regime, river regulation has led to widespread decline in seedling establishment along the active channel. However, pioneer trees that require disturbance events for regeneration use a variety of strategies for persisting during periods of relative stability. The use of spatial refugia, while critical for population recovery of many mobile organisms, is generally not considered an important strategy for trees. Episodic channel abandonment in meandering river systems, and the subsequent infill and terrestrialization of the abandoned channel, has been recently highlighted as critical for maintaining the population of a key pioneer riparian tree species, Fremont cottonwood (*Populus fremontii*). While controls on seedling establishment along the active channel are predominantly abiotic, temporal changes in abandoned channels result in a shift toward a more physically stable and more competitive environment. How a species with such strong colonization traits can establish in abandoned channels, and for how long, are the main questions addressed in my dissertation.

In a controlled community mesocosm experiment (Chapter 1), I used field-informed gradients of substrate texture and herbaceous cover to test interacting effects of soil moisture and interspecific competition on first year cottonwood seedling survival. I found that primary controls on cottonwood seedling establishment switched from abiotic to biotic drivers as a result of the biogeomorphic development of abandoned channels. Like on the active channel, seedlings were strongly moisture limited in conditions immediately following channel abandonment, but competition became a more important determinant of survival in conditions representative of an older abandoned channel. However, I also found that cottonwood seedlings were better competitors than anticipated, and were able to survive in the more physically benign and competitive conditions as well as the more physically stressful conditions to which they are classically adapted. This suggests that abandoned channels provide conditions favorable for cottonwood establishment for a broad window of time. While my focus was on understanding mechanisms controlling seedling establishment within abandoned channels, my results clarify interactions between abiotic and biotic controls that are more broadly applicable within a

meandering river corridor. My results also add to evidence that species lie along a competition-colonization continuum, and have implications for incorporating secondary recruitment locations into management and restoration of pioneer riparian forests.

The well-known interspecific trade-off of high-light growth in early colonizing species, versus low-light survival in species that are better resource competitors, leads to the logical conclusion that pioneer trees such as cottonwood are shade intolerant. Empirical evidence also finds seedlings rarely establish in vegetated areas. So how are cottonwoods able to establish in the more densely vegetated (i.e., shadier) environment of abandoned channels? I examined this question using a shade-cloth mesocosm experiment (Chapter 2), in which I considered interactive gradients of moisture and light. In dry ecosystems, sunlight can be considered both a resource and a stress, with shading reducing evaporative demand by maintaining a cooler understory microclimate. I found that shading resulted in reduced vapor pressure deficits and higher soil moistures, and a strong positive effect on first year cottonwood seedling survival in the Mediterranean climate of California. However, seedlings that survived to the end of the experiment showed decreased final biomass and root growth in shade. These results suggest that cottonwoods are much more plastic in their shade tolerance than has been previously assumed. The positive effect of shade on survival was observed regardless of soil moisture availability, whereas the positive effect of sun on growth was much stronger in wetter conditions, suggesting that soil moisture is the dominant limiting resource for seedling growth. I conclude that their high moisture requirement, along with their plasticity in shade tolerance, is what allows cottonwoods to successfully establish in abandoned channels. I suggest that lack of understory recruitment along the active channel may have more to do with the fact that vegetated areas are typically higher and drier as a result of biogeomorphic feedbacks.

Based on current theory and previous empirical evidence, it was considered likely that cottonwood establishment would be limited to the period immediately following channel abandonment, when the abandoned channel retains elements of physical dynamism to which the species is well adapted. However, my experimental evidence of better competitive ability and more plastic shade-tolerance, particularly under conditions of high soil moisture, suggested that cottonwood establishment in abandoned channels may be supported for a much longer window of time. On the Sacramento River, California, I used a chronosequence (space-for-time) approach to understand patterns of cottonwood establishment as a function of time since abandonment and biogeomorphic stage (Chapter 3). I examined patterns in overstory community composition and cottonwood diameter size distribution as indicators of past establishment dynamics. I used tree ring analysis to sample the age structure and determine establishment timing. I addressed the main sources of error in the use of tree ring analysis for determining establishment age by cross-dating tree cores, and developing and applying correction-factors for cores potentially missing the earliest years of growth. I also quantified the uncertainty around my correction-factors using a Monte Carlo simulation approach, and propagated the uncertainty through my analyses. My results support a recruitment window that begins at channel abandonment, and consistently lasts ~ 20 years, regardless of site age. Thus, while channel abandonment is episodic, a cohort of trees always successfully establishes, and cohorts can continue to successfully establish for a period of approximately two decades. The duration of the recruitment window extends in time the spatial refuge provided by abandoned channels, and thus helps ensure continued persistence of the cottonwood population.

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CHAPTER 1 | Tradeoffs between abiotic and biotic controls on early seedling establishment of *Populus fremontii* in abandoned channels

ABSTRACT

In North America, cottonwood (*Populus*) and other members of the family Salicaceae are considered to exhibit the classic colonization-competition trade-off, where adaptations that make them highly successful colonists in disturbance-prone floodplain environments reduce their ability to compete for resources in more benign environments. Because cottonwood recruitment dynamics are so tightly coupled to the natural disturbance regime, anthropogenic changes from river regulation have led to widespread declines in seedling establishment along the active channel. Recent work has demonstrated the importance of secondary recruitment into abandoned channels in the population dynamics of *P. fremontii*. While controls on seedling establishment along the active channel are predominantly abiotic, temporal changes in abandoned channels result in a shift toward a more physically stable and more competitive environment, which we hypothesized would limit cottonwood seedling establishment. In a controlled community mesocosm experiment, we used field-informed gradients of substrate texture and herbaceous cover to test interacting effects of soil moisture and interspecific competition on first year cottonwood seedling survival. We found that primary controls on cottonwood seedling establishment switched from abiotic to biotic drivers as a result of the biogeomorphic development of abandoned channels. Like on the active channel, seedlings were strongly moisture limited in conditions immediately following channel abandonment, but competition became a more important determinant of survival in conditions representative of an older abandoned channel. However, we also found that cottonwood seedlings were better competitors than anticipated, and were able to survive in the more physically benign and competitive conditions as well as the more physically stressful conditions typical of success for a species with such strong colonization traits. This means abandoned channels provide conditions favorable for cottonwood establishment for a much broader window of time. While our focus was on understanding mechanisms controlling seedling establishment within abandoned channels, our results clarify interactions between abiotic and biotic controls that are more broadly applicable within a meandering river corridor. Our results also add to evidence that species lie along a competition-colonization continuum, and have implications for incorporating secondary recruitment locations into management and restoration of pioneer riparian forests.

INTRODUCTION

Pioneer species typically have traits that tightly couple their recruitment dynamics to the disturbance regime. For plants, traits that increase the probability of recruitment in disturbance-prone environments include profuse propagule production, long-range dispersal, seed dormancy

and germination cued to disturbance, and fast juvenile growth rates (Bazzaz, 1979; Howe and Smallwood, 1982; Sousa, 1984). However, traits that improve colonization success in disturbance-prone environments often come at the cost of reduced competitiveness for resources in more benign environments, where other strategies (e.g., shade tolerance, high nutrient use efficiency, chemical defenses) are often required for success (Connell and Slatyer, 1977; Hastings, 1980; Huston and Smith, 1987; Tilman, 1994). This competition-colonization trade-off is based on physiological and energetic constraints that prevent any one species from maximizing competitive ability across all environmental conditions (Huston and Smith, 1987).

Riparian plant communities provide a good example of this competition-colonization dynamic. Along rivers in North America, channel margins and young floodplains are dominated by woody pioneer plants in the family Salicaceae. These cottonwood (*Populus*) and willow (*Salix*) species exhibit traits that enhance recruitment in disturbance-prone floodplain systems, including abundant seed production, extensive dispersal via wind and water, fast seedling growth rates, and vegetative reproduction from fragments of both roots and shoots (Catford and Jansson, 2014; Corenblit et al., 2014; Karrenberg et al., 2002; Lytle and Poff, 2004). These characteristics allow propagules to quickly colonize bare substrates that are created or exposed by seasonal flooding. The presumption under the competition-colonization trade-off hypothesis is that these pioneer species would fare poorly in a more competitive environment. Indeed, the common reference to shade-intolerance and poor interspecific competitive ability of cottonwood (summarized in Braatne et al., 1996; Burns and Honkala, 1990; Karrenberg et al., 2002) supports this presumption.

Another consequence of disturbance-dependence for these pioneer riparian trees is that recruitment success is sensitive to anthropogenic changes in the disturbance regime (Rood and Mahoney, 1990; Stella et al., 2010). Seedling establishment tends to be the largest demographic bottleneck in cottonwood population dynamics (Lytle and Merritt, 2004). The impacts of river management on the hydrogeomorphic disturbance regime (i.e., the frequency, timing, duration, and magnitude of floods, as well as changes to sediment supply), have had profound negative consequences on establishment success of riparian pioneer tree seedlings (Braatne et al., 2007; Fenner et al., 1985; Friedman et al., 1998; Jansson et al., 2000; Johnson, 1994; Rood and Mahoney, 1990). For example, first year seedling establishment in snowmelt-driven systems is dependent on timing with seasonal hydrology (Mahoney and Rood, 1998), a synchrony that is commonly disrupted by flow regulation (Stella et al., 2006). Changes to the moisture regime, as well as reduced channel migration from flow regulation and channel confinement, have led to well documented declines in the establishment of cottonwood and willow seedlings along active channel bars downstream of dams (Braatne et al., 2007; Buer et al., 1989; Cooper et al., 1999; Dykaar and Wigington, 2000; Johnson et al., 1976).

While seedling establishment along the active channel is considered the dominant pathway for regeneration of cottonwoods and willows in many unconfined river systems (Braatne et al., 1996; Naiman et al., 2010; Van Pelt et al., 2006), recruitment in secondary locations such as meander scroll swales, high elevation floodplain surfaces, and abandoned channels has also been documented (Asplund and Gooch, 1988; Cooper et al., 2003; Cordes et al., 1997; Dykaar and Wigington, 2000; Kalliola et al., 1991; Polzin and Rood, 2006; Shankman, 1993, 1991; Stella et al., 2011; Van Pelt et al., 2006). Our previous work along the middle reach of the Sacramento

River, California, USA (Stella et al., 2011) quantified the importance of abandoned channels for regeneration of disturbance-dependent pioneer forest dominated by Fremont cottonwood (*Populus fremontii*). More than half the area of current cottonwood-dominated forest within the 160-km study reach originally established in abandoned channels, rather than on an active channel bar or bank. This finding has important implications for long-term persistence of this species in a river system where management practices have negatively affected recruitment along the main channel (DWR, 2015, 2005). It is clear that pioneer riparian trees recruit into abandoned channels, and that these locations contribute significantly to population dynamics, particularly in managed river systems. However, despite a general understanding of seedling recruitment drivers in dryland regions (Stella et al., 2013), the mechanisms controlling establishment in abandoned channels are not well understood.

While abiotic factors overwhelmingly drive woody seedling establishment on active channel bars (Mahoney and Rood, 1998; Stella et al., 2010, 2006), dynamics within abandoned channels are complicated by interacting geomorphic and vegetation changes through time. Based on our field observations of abandoned channels along the middle Sacramento River, California, we proposed a conceptual model that links pioneer tree establishment to the biogeomorphic development of abandoned channels (Stella et al., 2011). The geomorphic evolution of abandoned channels (Constantine et al., 2009; Gagliano and Howard, 1984; Piégay et al., 2000; Shields and Abt, 1989) results in a temporal gradient of resource supply rates and environmental stresses. Newly abandoned channels retain many of the characteristics of active channel bars that provide for successful establishment of pioneer tree seedlings, including bare mineral substrate, access to water, and lack of competition (Braatne et al., 1996; Mahoney and Rood, 1998). Additionally, the immediate reduction in flow volume and momentum (i.e., the majority of the flow is now routing through the cutoff channel rather than the abandoned meander bend, and water velocity slows as it moves through the abandoned channel) is likely to improve seedling survival relative to the main channel because of reduced frequency and magnitude of physical disturbance (e.g., scour) (Polzin and Rood, 2006). Reduced flow momentum also leads to increased deposition. Sediment deposition creates a positive feedback of aggradation and fining (Citterio and Piégay, 2009; Constantine et al., 2009; Piégay et al., 2008), resulting in a general temporal pattern of channels infilling with progressively finer sediment. Physical environmental stresses are further reduced as the abandoned channels becomes increasingly hydrologically disconnected from the main channel. Soil water holding capacity increases as the texture of sediment shifts from coarse to fine and organic matter accumulates. Nutrients become more abundant in the soil, and over time more plants (especially herbaceous wetland species) have had the opportunity to colonize (Dufour et al., 2014; Shankman, 1991; Stella et al., 2011). As vegetation becomes more dense and physical stresses more benign, we predicted that conditions in the abandoned channel change from those favoring colonizing species, to those favoring better resource competitors (*sensu* Pacala and Rees 1998).

The goal of our present study was to test our conceptual understanding of establishment dynamics in abandoned channels using a controlled community mesocosm experiment along environmental gradients informed by field conditions. We focused on Fremont cottonwood (*P. fremontii*), because it is the dominant overstory tree in riparian forests of the western United States. We hypothesized that (1) the temporal change in biogeomorphic conditions within abandoned channels would result in a shift from abiotic to biotic constraints on establishment of

cottonwood seedlings, and (2) conditions immediately following channel abandonment would be more favorable for cottonwood seedling establishment than the more competitive environment that develops during fine sediment infilling, leading to a window of time available for pioneer tree recruitment. Substrate texture and the rate of water table drawdown coincident with river flow recession are well established abiotic constraints on cottonwood and willow seedling establishment along the active channel (Amlin and Rood, 2002; González et al., 2010; Horton and Clark, 2001; Hughes et al., 1997; Mahoney and Rood, 1992, 1991; Segelquist et al., 1993; Stella et al., 2010). Fewer studies have looked at biotic constraints on cottonwood; direct experimental evidence of seedling interspecific competitive abilities comes from a few field-based vegetation removal studies or experiments using shade cloth (Cooper and Andersen, 2012; Cooper et al., 1999; González-Muñoz et al., 2013; Taylor et al., 1999), or two-species interactions with other woody seedlings such as the invasive *Tamarix* spp. (Bhattacharjee et al., 2008a; Sher et al., 2000; Sher and Marshall, 2003). To our knowledge, no studies have experimentally examined the interactions of both abiotic and community-level biotic constraints on cottonwood seedling establishment. The interplay of these constraints directly determines the demography of cottonwood populations in abandoned channels, and by extension their persistence in the broader floodplain, and also informs our understanding of the expected trade-off between competitors and colonizers (*sensu* Pacala and Rees 1998).

METHODS

Background and field study area

Our mesocosm experiment was tied to field studies within abandoned channels (Dufour et al., 2014; Stella et al., 2011; Hayden, unpublished data) conducted along a 160 river-km reach of the mainstem Sacramento River, Tehama and Colusa counties, California (Appendix Figure A-1). This middle reach is a single-thread, gravel-bed, meandering section set within a wide agricultural valley in fine-grained floodplain alluvium. Average annual discharge at the upstream end of the reach is $350 \text{ m}^3 \text{ sec}^{-1}$ (US Geological Survey gauge 11377100). Bankfull channel width averages 300 m. Main channel slope ranges from 0.0002–0.0007 m m^{-1} , and median grain size of the channel bed ranges from 15 to 35mm (Constantine, 2006; Micheli et al., 2004), with much finer sand and silt deposits in the abandoned channels (Constantine et al., 2009; Dufour et al., 2014). Despite significant flow regulation with truncated peak flows, reduced sediment supply and elevated base flows, geomorphically significant events still occur and result in channel migration and cutoff (Micheli and Larsen, 2010; Singer, 2007). New abandoned channels are created with similar frequency as in pre-dam conditions, though they are typically smaller in length and surface area (Michalková et al., 2011). Despite an estimated loss of 90% of riparian forest area throughout the Central Valley since European settlement, the middle Sacramento River corridor supports the largest riparian forest area remaining in California (Buer et al., 1989). More than half of these extant pioneer forest stands initiated within abandoned channels (Stella et al., 2011).

We focused on two key variables that were most likely to limit first year seedling establishment within abandoned channels: (1) soil water availability, controlled by abiotic factors including river stage and substrate texture, and (2) interspecific competition with herbaceous wetland species, which would limit both above-ground (light) and below-ground (water) resource

availability. We quantified the range of environmental conditions present across a temporal gradient of abandoned channels along the middle Sacramento River using a chronosequence (space-for-time substitution) approach (Appendix A). We focused on the portion of the abandoned channel where woody seedlings were establishing—the area between the edge of surface water and where mature woody vegetation began. River stage and the rate of stage decline strongly affect the soil water table in floodplains (Busch et al., 1992; Stanford and Ward, 1988), but soil moisture retention and the amount of plant-available soil water is mediated by soil hydraulic properties that are largely a function of substrate texture (Brady and Weil, 1999; Sperry et al., 2002). Thus, we focused on grain size as a metric to quantify the ecologically-relevant abiotic changes that occur as an abandoned channel fills with sediment through time. To quantify the gradient of biotic resource demand, we identified and measured the percent cover of interspecific competitors within this seedling establishment zone at a subset of sites. Additional details of the field study are included in Appendix A.

We then used a mesocosm approach informed by field data. The benefits of this approach were to have the control to test and measure mechanism, but with careful replication of realistic field conditions at a spatiotemporal scale relevant to the processes governing seedling establishment, which is often a criticism of micro/meso-scale experiments (Carpenter 1996, Schindler 1998, but see Cadotte et al. 2005, Benton et al. 2007 for opposing views). We created fully crossed gradients of soil water availability (mediated by substrate textures and water table decline), and biotic resource demand (mediated by interspecific competitor cover of herbaceous wetland plants) in large rhizopod-style mesocosms (*sensu* Mahoney and Rood 1991). We then tracked survival of *P. fremontii* seedlings over the course of one growing season.

Mesocosm study site description and design

The mesocosm experiment was located outdoors in full sun at the University of California's Russell Research Station in Lafayette, CA (37°55'3.18"N, 122° 9'25.88"W). There were 58 days of water table drawdown, from mid-August to mid-October 2010. The region experiences a Mediterranean-type climate, with warm, dry summers, and cool, wet winters. Temperature during the drawdown period averaged 17.8°C (range 6.75–40.85°C). Mean daytime temperature and vapor pressure deficit were 21.8 °C and 1.65 kPa (range 0.85–6.69 kPa), respectively. Mean afternoon (12–4 pm) vapor pressure deficit was 2.63 kPa. The area averages 62.5 cm annual rainfall occurring primarily from late October through April. No precipitation occurred during the study.

Mesocosm pots were similar to the “rhizopod” design of Mahoney and Rood (1991), and consisted of 25.4 cm diameter X 120 cm tall opaque PVC pipe, capped and connected to a water table control reservoir (Appendix Figure B-1). Mesocosm pots were distributed among eight platforms. Each platform measured 2.4 m X 1.2 m in area, was leveled to ensure water table consistency among pots ($\pm < 1$ cm), and held 12-13 pots connected to the platform's water control reservoir. The apparatus in the control reservoir (float switch and overflow tube) allowed for precise changes to and maintenance of the water table. Stratifying by platform, we randomly assigned combinations of substrate (Coarse or Fine) and interspecific competitive cover to each pot. Each platform thus had a balance of both substrate types and a similar gradient of cover of interspecific competitors across substrate types.

Substrate

We chose two substrates that approximated the end members of the grain size distribution observed in our field sampling of the middle Sacramento River (Figure 1, Appendix A). The Coarse substrate had a median grain size (D_{50}) of 16.8 mm, composed of 70% gravel (D_{20} = 8.84 mm, D_{50} = 11.85 mm, D_{max} = 19.00 mm) and 30% sand (D_{20} = 0.31 mm, D_{50} = 0.53 mm, D_{80} = 1.05 mm) by weight. The sand filled the interstitial spaces in the gravel. This was similar to the grain size distribution we found on point bars in the Sacramento River (Appendix A), and is representative of a newly abandoned channel. Our Fine substrate was a fine sand (D_{20} = 0.16 mm, D_{50} = 0.23 mm, D_{80} = 0.49 mm) similar to the grain size distribution found in our abandoned channel field sites (≥ 15 years since abandonment) and at the downstream (depositional) end of our point bar field site (Figure 1). We obtained all substrates from a local aggregate supplier (American Soil and Stone, Richmond, CA). We placed a few centimeters of gravel rock (0.00275 m^3) at the bottom of all mesocosm pots to help with drainage, and then filled them with substrate (0.062 m^3). We compacted the substrate by flooding and draining the pots twice over 3 days, topping them off, and then repeating this process.

Soil fertility of both our experimental substrates—in terms of salinity, cation exchange capacity, organic matter, and major nutrients—was similar, and was typically at or below levels found on our Sacramento River point bar site (Appendix Table B-1). We originally included a third, intermediate substrate texture in our experimental design, but omitted it for analysis due to salinity levels that strongly affected cottonwood germination, even though the salinity was well below thresholds reported in the literature to affect cottonwood seedling physiology, growth or survival (Merritt and Shafroth, 2012).

Seed collection, germination, and establishment

Within our abandoned channel field study sites, germination and/or new growth of herbaceous species typically begins in late winter/early spring (~March), while cottonwoods do not begin releasing seed until late spring/early summer (~May; Hayden, pers. obs.). To simulate phenology and establishment timing observed at our field sites, we germinated the interspecific competitors in March 2010, and transplanted them into the mesocosms two weeks prior to cottonwood planting (July). We seeded the cottonwoods into this matrix, allowed them to germinate and grow for an additional two weeks, then began the water table drawdown (August).

Based on our field observations (Appendix A) and a pilot experiment to determine collection and propagation feasibility (Hayden, unpublished data), we selected three widespread and abundant herbaceous species to grow in competition with cottonwood seedlings (further details in Appendix A). These represented the three main growth forms present in our field plots— forb (*Lycopus americanus*), sedge (*Cyperus eragrostis*), and grass (*Echinochloa crus-galli*). We collected seeds of interspecific competitors from field sites in the Fall of 2009, and stored them in paper bags at room temperature. We germinated them in early March 2010 in $25.4 \text{ cm}^2 \times 2.5 \text{ cm}$ deep greenhouse flats. We used the sand substrate from the Coarse texture, so all plants would germinate on a uniform substrate. We used three different seeding densities to get a range of competitor cover similar to the range observed in the field (Figure 2). Flats were kept outdoors at the mesocosm facility under a translucent plastic sheeting to protect from direct sun and heavy rain, and were watered daily (or every other day during cooler periods) for four months. To

improve growth, we made three weekly applications in May of 30:10:10 NPK Miracle Grow fertilizer, applied at the manufacturer's recommended concentration.

One week prior to transplanting, overhead digital photos were used to measure foliar cover (see Data Collection and Processing for methods details), and we made adjustments to flat densities to ensure balanced cover distributions would be represented across each substrate type. The competitors were then transplanted into the mesocosms in mid-July by sliding the intact flat contents directly on top of the filled column and allowed to establish for two weeks prior to cottonwood addition.

In May 2010 we collected partially opened cottonwood catkins from three different restoration sites within our field study area near Hamilton City, CA (Appendix Figure A-1). Collections were made from the lower 8 m of a total of 15 source trees. We stored catkins in paper bags and allowed them to air dry at room temperature for 4–5 days until any unopened catkins had burst. Seeds were then separated from cotton, sealed dry with desiccant, and placed into cold storage at 5°C (E. Tozzi, UC Davis, pers. comm). Prior to planting, we confirmed seed viability was >90%.

Two weeks prior to the start of water table drawdown, we homogenized equal weight of seed from the 15 source trees and placed approximately 100 seeds in direct contact with the substrate surface, and evenly spread across each pot. To ensure the germination surface across all pots was the same, we sifted out any remaining roots from unused greenhouse flats of herbaceous competitors, and placed this sandy substrate on the surface of the cottonwood-only control pots. After one week, pots were thinned (66% of pots) or transplants added (12% of pots) to ensure 25–40 seedlings/pot (493–789 seedlings/m², or 1 seedling per 20.3–12.7 cm²). All seedlings were individually tagged with small, flexible plastic bands placed around (but not touching) the base of the stem. There were 2,082 seedlings alive at the start of the water table drawdown, with an average of 37 (±4.4 SD) seedlings per pot (730 seedlings/m², or 1 seedling per 13.7 cm²). Initial seedling densities were well balanced across treatment gradients.

Water table drawdown

The water table was kept at 5 cm below the substrate surface during the interspecific competitor establishment period (2 weeks), then raised to 3 cm below during *P. fremontii* germination and establishment (additional 2 weeks) to ensure adequate surface moisture. Just before the start of the experiment, we raised the water table to 1-cm depth, and then manually lowered the water in the reservoir 2 cm each day for the duration of the active drawdown period (58 days). We chose this rate based on prior work by Stella et al. (2010) in order to create a recession rate that was steep enough to induce differences in soil moisture between our two substrates, but not so severe as to cause complete cohort mortality. After lowering the water table in the control reservoir, the networked pots typically equilibrated gradually within 1-2 hours. We monitored the water table of each pot via a clear vinyl tube connected at the bottom and attached to the outside. Any drainage problems (typically air bubbles in the water lines that blocked equilibrating flows) were fixed on a daily basis.

Data collection and processing

We monitored survival of each individually tagged cottonwood seedling every three days over the experimental drawdown period. Seedlings were considered dead when both the leaves and the stem were brown and withered.

We measured growth of interspecific competitors by taking weekly overhead digital photographs of each pot, and measuring live foliar cover using pixel-based image classification. Our approach was similar to those of Johnson et al. (2003) and Richardson et al. (2001), and can be related to biomass and leaf area index (Chen et al., 2009, 2010). We used a 4-megapixel Canon PowerShot S45 camera, fixed with a mount over the center of each pot and 50 cm above the substrate surface. The camera was set to autofocus, with no flash, f-stop 3.5, and at a 10 mm focal length. Median exposure time was 1/60 sec (range: 1/20 – 1/200, though 90% of photos were between 1/40–1/125). The resulting images had a size of 2272 x 1704 pixels, with the pot encompassing approximately 45% of the image area (pot diameter ~1500 pixels). Images had a resolution of 180 dpi, and were saved as JPEGs. Photos were taken at the same time of day (afternoon, full sun) and with a tarp over the frame of the mesocosm platform to maintain similar light conditions from week to week. Two sequential photos were taken of each pot using the same camera settings in case of any autofocus problems.

All image processing was done in MATLAB (The MathWorks Inc., Massachusetts). The images were first processed to extract the pot area, masking the pixels in the remainder of the image frame. Next, the pixels containing live plant were determined using a thresholding algorithm based on RGB pixel values: Green - Blue > 50. We tested more complex algorithms and threshold values. Our selected algorithm was the most robust at differentiating plant from sand substrate, while picking up both green and red hues of live plant without the brown of litter or dead leaves. We had no issues with photos being out of focus, so we averaged the cover estimate from the two sequential photos taken of each pot to account for any differences in exposure time.

As a quality assurance check, we compared the automated pixel-based image processing method against a manual, grid-point intercept estimate from the photos, similar to the Digital Grid Overlay method of Booth et al. (2006, 2005). Details are provided in Appendix C. Manual grid-based point estimates tended to overestimate fraction live cover relative to automated pixel-based image processing, though there was good agreement at very low (<0.01) and high (>0.6) fraction cover (Appendix Figure C-1). Results from the two methods were highly correlated ($r^2 = 0.94$), with reasonable root mean square error (RMSE = 0.08). Good agreement between the two methods, and the fact that overestimation of cover is a common issue with point frequency techniques (Booth et al., 2006; Chen et al., 2010; Vanha-Majamaa et al., 2000), indicated that the automated image-processing method was consistent and robust.

We measured above and below ground biomass of interspecific competitors by harvesting at the end of the experiment. We clipped all above ground biomass, and separated it into live (green) and dead/litter (brown, withered) components for all pots that held interspecific competitors (n=24 per substrate). In a subsample of these pots (Coarse substrate n=8, Fine substrate n=12), we also collected root biomass by separating roots from substrate via wet sieving down to 1mm mesh. Samples were oven dried to constant weight at 65 °C.

Lastly, we accounted for potential block effects on light availability due to platform location through use of hemispherical photographs, following the high precision methods described by Eschtruth and Battles (2008). We took photos in the center of each platform at 1.2 m height to correspond to the soil surface of each mesocosm, and used Gap Light Analyzer software to compute the fraction of total transmitted radiation reaching each photo point (Frazer et al., 1999). Although our site was in an open area, this analysis quantified any differences in shading from neighboring buildings, trees, and topography related to platform location within our study site.

Soil moisture data collection and processing

Soil moisture was tracked in a subset of 10 pots (17% of total) using time-domain reflectometry (TDR100-based system with CS630 probes and CR800 data logger, Campbell Scientific Inc., Logan, Utah), which measures the apparent dielectric constant (K_a) of the medium (Ledieu et al., 1986). Because our substrates were much coarser than those in typical applications, we calibrated our sensors using standard gravimetric methods for each substrate (see Appendix D for calibration details).

Probes were installed horizontally through the wall of the pot at 10-cm, 30-cm, and 70-cm depths. We instrumented five pots of each substrate texture that spanned the foliar cover gradient. The treatment combinations that were instrumented included one pot of each substrate texture with the following competitive environment: controls with no plants grown, intraspecific controls with cottonwood-only, interspecific competitors-only (low and high cover), and high cover of interspecific competitors grown with cottonwood seedlings. The latter had four probes installed at 10-, 30-, 60-, and 90-cm depths. Dielectric constant readings were logged every 15 minutes for the duration of the experiment.

We calculated pot-averaged soil moisture through time by vertically integrating the data from the different probe depths using a root-weighted averaging approach (Baldocchi et al. 2004, Chen et al. 2008) for every logged time interval. This is a more biologically meaningful measure of plant available soil moisture compared to simple arithmetic averaging, because it weights the soil moisture at various depths by the distribution of roots. The vertically averaged index ($\langle \theta \rangle$) was determined by:

$$\langle \theta \rangle = \frac{\int_0^z \theta(z) dP(z)}{\int_0^z dP(z)}, \quad (1)$$

where $\theta(z)$ was a quadratic fit to the measured volumetric water content as a function of depth in cm (z). Because of the design of the water table drawdown, we knew that the bottom of the pot (120cm depth) was always saturated, and assigned this value as the maximum θ from the deepest probe.

$P(z)$ is the cumulative distribution of root mass from the surface to depth z . $P(z)$ follows the asymptotic model $P(z) = 1 - \beta^z$ (Gale and Grigal, 1987). β was determined from rooting depths of herbaceous competitors collected from a subset of pots (Fine $n=10/29$; Coarse $n=6/29$) at the end of the experiment. Because rooting depths were markedly different in each substrate, we calculated a β value for each. As a conservative estimate, we added one standard deviation to the average of the maximum rooting depth and assumed that 99% of the root mass was above this

depth. For Fine sand $\beta = 0.962$ (99% of root mass above 119.8 cm), and for Coarse $\beta = 0.949$ (99% root of mass above 88.2 cm). These values are within the range reported for root distributions of temperate deciduous forest and temperate grassland (Jackson et al., 1996). Lastly, the cumulative probability density sums to 1, thus the denominator is equal to 1.

Indices of predictor variables

From our time series data of interspecific competition (measured via overhead photography) and water availability (measured via soil moisture probes), we developed a suite of integrative indices within these two main “driver” categories (competition and soil moisture) to use as predictor variables in subsequent analyses of cottonwood seedling survival (Table 1).

Because interspecific competitors also grew and senesced over the course of the experiment, we chose three indices as integrative measures to estimate the magnitude and timing of resource competition: cumulative cover (C_{cum}), maximum cover (C_{max}), and time to maximum cover ($days C_{max}$) (Table 1). We calculated an index of cumulative cover by fitting a 3rd order polynomial function to the cover through time data derived from overhead photography for each pot, and integrated to get the area under the curve. We then calculated maximum cover and time to maximum cover by optimizing this same function to find its largest value and date.

As integrative measures of water resource availability through time, we calculated cumulative soil moisture (θ_{cum}) and two timing variables: number of days at saturation ($days \theta_{sat}$), and time to a water stress threshold ($days \theta_{0.1}$) (Table 1). We used cumulative soil moisture to estimate the magnitude of resource availability over the course of the entire experiment. Using the vertically integrated, pot-averaged soil moisture through time from our instrumented pots, we calculated the cumulative soil moisture by summing volumetric water content measured at each 15 minute logging interval. We compared these to numerical integrations from piece-wise linear interpolation and smooth spline functions. The difference in integration methods was <0.02%, so we chose the simpler summation method.

We used number of days at saturation ($days \theta_{sat}$) both as an index of water holding capacity of the substrate (coarser substrate drained faster, remaining saturated for a shorter period of time), and as a measure of the amount of time cottonwood seedlings spent in the condition of maximum water resource availability. We note that saturation as measured using our vertically integrated, pot-averaged approach does not mean the substrate surface remained flooded, which might lead to potentially stressful anoxic conditions for developing roots. We calculated our index as the number of days until a sustained negative slope in soil moisture through time was observed.

We used number of days to soil volumetric water content of 0.1 ($days \theta_{0.1}$) as a measure of the amount of time cottonwood seedlings spent above a water stress threshold. Soil volumetric water content and texture, as measured in our experiment, are directly related to water potential (Dane and Hopmans, 2002; Kosugi et al., 2002; van Genuchten, 1980), which is the more biologically relevant measure of plant available water. We used a conservative stress threshold guided by xylem pressures reported in the literature, below which cottonwoods begin to quickly lose hydraulic conductivity due to cavitation (< -1 MPa; see Appendix D for references). We converted our measured soil volumetric water content to soil water potential using the van Genuchten pedotransfer function (PTF) (van Genuchten 1980), with methods described in more

detail in Appendix D. Based on the PTF, we selected $\theta_{0.1}$ as a conservative threshold where the negative pressure or suction required to remove an additional increment of volumetric water content from the soil goes from linear to exponential (Appendix Figure D-3), greatly increasing the risk of cavitation and loss of hydraulic conductance. We calculated the number of days spent above this threshold as an index of time to water stress.

We calculated these three soil moisture indices for our 10 instrumented pots, and then extrapolated to predict soil moisture indices for non-instrumented pots. Our extrapolation was based on the assumption that because the experimental drawdown rate was the same in both substrates, pot to pot differences in index values were attributable to differences in substrate type (e.g., physiochemical properties that determine hydraulics) and biomass of plants grown in each pot (e.g., biotic differences in water uptake). Thus, we used C_{cum} as a robust measure of biomass, and fit a linear model to the instrumented pot data for each substrate and soil moisture index. We then used the linear model to predict pot-level soil moisture indices for the remaining pots, given their known C_{cum} .

Data Analysis

First, we modeled survival of *P. fremontii* seedlings through time using nonparametric Kaplan-Meier estimations to account for censored observations, using the “survival” package (Therneau, 2014) in R statistical software (version 3.1.0, R Core Team, 2014). To visualize temporal patterns, we lumped soil moisture into “high” and “low” moisture regimes based on substrate texture, and competition into binary categories of presence or absence of interspecific competitors.

Next, we modeled probability of survival to the end of the experiment as an estimate of over-summer survival using the logistic function:

$$\pi(x) = \frac{e^{g(x)}}{1 + e^{g(x)}} \quad (2)$$

where $\pi(x)$ is the survival probability and $g(x)$ is a linear function of predictor variables. All models included the covariate of initial seedling height (i.e., height just prior to start of drawdown), to account for individual differences in growth that developed during the stable establishment period. There were no differences in initial seedling height between substrates prior to start of drawdown ($p = 0.18$). There was a small but significant ($r^2 = 0.03$, $p < 0.001$) positive trend in initial cottonwood seedling height with increasing competitive cover, as measured by maximum cover, and this was more pronounced in the Coarse texture. However, these differences were within the range of measurement error (± 1 mm). Platform differences in percent total transmitted light (i.e., block effects due to positioning of each platform, as measured by hemispherical photography) did not explain any significant deviance in seedling survival when included in the logistic models, so we omitted it for purposes of parsimony.

Our full logistic models contained all possible combinations of a single competition and single moisture variable (main effects), as well as their interaction term. The full models all take the form $g(x) = \beta_0 + \beta_1 \times \text{initial seedling height} + \beta_2 \times \text{competition} + \beta_3 \times \text{moisture} + \beta_4 \times \text{competition} \times \text{moisture}$, where β_0 is the intercept, and β_{1-4} are fitted parameters. We also included reduced forms down to the base model of $g(x) = \beta_0 + \beta_1 \times \text{initial seedling height}$. There

were 9 full models (Table 2) and 16 reduced forms, for a total of 26 candidate models. Full models included only a single metric from each driver category (competition or moisture) because metrics within a driver category were correlated as expected. The two cover magnitude metrics were highly correlated (Pearson's $r = 0.93$), and the cover timing metric was strongly negatively correlated with both magnitude metrics ($r > 0.62$). All three soil moisture metrics were highly correlated ($r > 0.90$).

We ran logistic regressions of the suite of candidate models using a generalized linear model with a logit transformation, and compared them using an information theoretic approach (Burnham and Anderson 2002). For each model, we calculated Akaike's information criterion (AIC), differences in AIC values relative to the model with the lowest AIC (ΔAIC), and AIC weights (w_i). AIC provides a means of balancing goodness of fit with principles of parsimony. ΔAIC and the AIC weight are measures of the relative difference in the strength of evidence for each model. The model with the lowest AIC value is considered the best Kullback–Leibler estimated model for the data given the candidate set of models, and models $< 2 \Delta\text{AIC}$ have substantial empirical support (Burnham and Anderson 2013). Akaike weights (w_i) were calculated to normalize the strength of evidence for a given model and can be interpreted as the probability that a given model i is the best Kullback–Leibler model for the data given the candidate set of models (Burnham and Anderson, 2013). We also calculated area under the receiver operating characteristic curve (ROC) as a threshold-independent measure of model discrimination (i.e., the ability to distinguish live and dead seedlings), where 0.5 indicates no discrimination, 0.7 – 0.8 acceptable discrimination, and >0.8 excellent discrimination (Hosmer et al., 2013). Lastly, we calculated the variance inflation factor (VIF) to check for evidence of problematic multicollinearity, using a $\text{VIF} > 10$ threshold (Neter et al., 1996). All analyses were performed in R (version 3.1.0, R Core Team, 2014).

RESULTS

Temporal patterns of experimental biogeomorphic gradients

The Fine texture pots retained higher soil moisture for longer than the Coarse texture pots, despite the same rate of water table drawdown (Figure 3a). Soil moisture in the Coarse texture showed an abrupt and rapid decline that closely tracked the water table drawdown, such that pots remained saturated only for an average of 3.4 days (± 0.6 SD), reached the $\theta_{0.1}$ water stress threshold within 15.2 days (± 1.3 SD), and had cumulative soil moisture of $4.3 \text{ m}^3/\text{m}^3 \cdot \text{days}$ (± 0.3 SD). In contrast, Fine texture pots remained saturated almost 3 times longer (9.7 days ± 1.4 SD), and lost soil moisture at a much slower rate. Fine texture pots didn't reach the $\theta_{0.1}$ water stress threshold until 51.8 days (± 3.5 SD), and had cumulative soil moisture of $12.8 \text{ m}^3/\text{m}^3 \cdot \text{days}$ (± 0.8 SD). The maximum instantaneous rate of decline was on average an order of magnitude faster in the Coarse texture ($0.27 \text{ m}^3/\text{m}^3$ per day ± 0.06 SD) relative to Fine ($0.028 \text{ m}^3/\text{m}^3$ per day ± 0.006).

Interspecific competitor cover, as measured via overhead photography, typically peaked within the first week of the start of the experiment, and declined as foliage died (Figure 3b). The initial range of the cover gradient was 34 to 78% (with one outlier at 18%), declining to 2 to 49%. The

rate of decline was more pronounced in the Coarse texture, ending with fraction live foliar cover significantly lower than in the Fine substrate (mean \pm SE: $14 \pm 2\%$ in Coarse vs. $26 \pm 2\%$ in Fine; ANOVA $p < 0.0001$). However, there was no significant difference in total above- or below-ground biomass of interspecific competitors across substrates at the end of the experiment (Appendix Figure B-2), indicating that the same total biomass was produced, but died back more quickly in the Coarse substrate. Cover in the cottonwood-only control pots ranged from <0.5 to 7% .

Temporal patterns of cottonwood seedling survival

Based on Kaplan-Meier estimated survival probability curves, in the absence of interspecific competitors, cottonwood seedling survival probability was significantly higher (95% confidence intervals did not overlap) throughout the experiment in the higher soil moisture (Fine texture) environment, than in the lower soil moisture (Coarse texture) environment (Figure 3c). Median survival time (i.e., time to 0.5 survival probability) was 24 days in higher soil moisture compared to 9 days in lower soil moisture in the absence of interspecific competitors, and estimated survival probability at the end of the experiment was 0.39 compared to only 0.06 (Table 3). The highest mortality rates occurred within the first 3 weeks of drawdown.

The presence of herbaceous competitors had a negative effect on cottonwood seedling survival probability, but only after 30-40 days of water table drawdown. In the higher soil moisture environment, median survival time was similar: 24 days in the absence of competitors vs. 21 days with competitors (with overlapping 95% confidence intervals), but probability of surviving to the end of the experiment was only 0.16 when grown with competitors vs. 0.39 in absence. In the lower soil moisture environment in the absence of competitors, cottonwood seedling survival probability declined sharply within the first three weeks of the experiment (median survival time was 9 days), and then leveled off for the next four weeks. Seedling survival probability in the presence of competitors showed a steadier rate of decline (median survival time was 21 days, the same as that found in the higher soil moisture treatments), but ended with the lowest probability of survival, at 0.005.

End season survival probability

Logistic models that included maximum cover (C_{max}), either cumulative soil moisture (θ_{cum}) or days to a water stress threshold ($days \theta_{0.1}$), plus the interaction between the cover and soil moisture variables had the strongest support ($\Delta AIC < 2$, $w_i \geq 0.48$), with excellent discrimination (AUC = 0.91) and no problematic multicollinearity (VIF < 6) (Table 4). These ranked considerably higher than models lacking the interaction between cover and soil moisture ($\Delta AIC > 22$), or those with only a single-factor main effect ($\Delta AIC > 118$). In terms of model rankings, the parameter C_{max} was a better predictor of cottonwood survival than C_{cum} or days to C_{max} . For soil moisture metrics, θ_{cum} and $days \theta_{0.1}$ were indistinguishable, but both were better predictors than $days \theta_{sat}$. Models containing the $days \theta_{0.1}$ variable (Models 7-9) had poor support ($\Delta AIC > 19$) as well as VIFs > 10 , indicating multicollinearity that might lead to problematic parameter estimates.

In the two best models, the odds of cottonwood seedling survival were higher with lower magnitude of interspecific competition (C_{max}) and better soil moisture conditions, as measured

either by higher θ_{cum} or longer time to $\theta_{0.1}$ water stress threshold (Figure 4). When comparing centered and standardized variables (i.e., units are equivalent), the odds of the soil moisture effect were 1.9 times stronger than the competition effect. For example, holding all other variables at their mean value, a one standard deviation decrease in maximum competitive cover (27%) increased the odds of survival 4.9 times. A one standard deviation increase in θ_{cum} ($4.48 \text{ m}^3/\text{m}^3 \cdot \text{days}$) increased the odds of survival 9.2 times. The interaction term indicated that the effect of decreasing competition in a low soil moisture environment led to a larger relative increase in probability of survival than it did in a high soil moisture environment (Figure 4). In other words, the negative effect of competition was much stronger in low soil moisture conditions.

DISCUSSION

Our results support our first hypothesis that as a result of the biogeomorphic evolution of abandoned channels, primary controls on early seedling establishment switch from abiotic to biotic drivers. Water stress is the dominant control on survival in conditions representative of a recently abandoned channel (coarse alluvial substrate and barren of vegetation). Competition becomes a more important determinant of survival in conditions representative of an older abandoned channel undergoing infilling (finer substrate, and higher interspecific resource competition) and the consequent increase in soil moisture availability. We confirmed that processes governed by abiotic controls on soil moisture availability had a stronger relative effect on cottonwood seedling survival, but the significant secondary role of interspecific competitive interactions within abandoned channels is a key difference from dynamics controlling establishment on active channel bars. While our focus was on understanding mechanisms controlling seedling establishment within abandoned channels, our results clarify interactions between abiotic and biotic controls that are more broadly applicable within a meandering river corridor.

In regard to our second hypothesis, we found that survival probability at the end of the first growing season was similar between conditions representative of young and old abandoned channels. Contrary to expectations, conditions across all biogeomorphic phases of abandoned channels can support establishment of cottonwood seedlings. We illustrate this with the red line in Figure 4, which traces the combination of soil moisture and competitive conditions that occur during the evolution of an idealized abandoned channel. This assumes a linear relationship between sediment fining, which improves moisture conditions, and vegetation colonization. Our results suggest that the window of opportunity for cottonwood seedling establishment remains "open" throughout the biogeomorphic development of the channel. In fact, cottonwood seedlings were better competitors than anticipated given the prediction of the colonization-competition trade-off hypothesis and the prevailing view in the literature (summarized in Braatne et al., 1996; Burns and Honkala, 1990; Karrenberg et al., 2002). Our findings support the contention of Cooper et al. that cottonwood seedlings are not as shade-intolerant as originally thought. While it is well-established that cottonwoods have many traits that confer successful colonization in the face of disturbance (Braatne et al., 1996; Catford and Jansson, 2014; Corenblit et al., 2014; Karrenberg et al., 2002; Lytle and Poff, 2004), seedlings were not completely excluded by better competitors in the more benign environment. Our results support Seifan et al.'s (2013) contention

that the colonization-competition trade-off should be thought of as a continuum, rather than mutually exclusive categories that assume very strong competitive asymmetry (Muller-Landau, 2010).

Effects of substrate texture on soil moisture and cottonwood seedling survival

Our soil moisture measurements documented a clear water resource availability gradient associated with substrate textures and water table decline, as predicted from soil physics (Brady and Weil, 1999; Dane and Hopmans, 2002). Kaplan-Meier and logistic models indicated that higher soil moisture conditions had a strong, positive effect on end-season cottonwood seedling survival probability, regardless of the presence of interspecific competitors. The coarser substrate, consisting of a gravel-sand mix similar to that found on a newly abandoned former point bar (Figure 1), experienced a steeper rate of moisture loss coincident with water table drawdown. This trend resulted in lower soil moisture available either instantaneously or cumulatively as quantified by our various metrics. In contrast, the hydraulic properties of the fine texture substrate, representative of an older abandoned channel filling with fine sediment, buffered plants from the effects of the declining water table by retaining higher soil moisture for longer. Our results are as expected and in line with previous field (Bhattacharjee et al., 2008b; Johnson, 1994; others reviewed by Karrenberg et al., 2002; McBride and Strahan, 1984) and experimental (González et al., 2010; Mahoney and Rood, 1992) studies indicating that lower moisture conditions in coarser substrate led to high rates of water stress-induced mortality of cottonwood seedlings.

We had two metrics of soil moisture that performed equally well as predictors of seedling survival. One related to hydraulic stress (*days to* $\theta_{0.1}$), and the other was a measure of cumulative resource availability over the growing season (θ_{cum}). Current hypotheses regarding mechanisms of drought-induced mortality include direct effects of hydraulic failure resulting from cavitation, and indirect effects of prolonged stomatal closure—namely, carbon-starvation or increased susceptibility to cellular damage resulting from light- (photoinhibitory damage) and heat-stress (due to reduced evaporative cooling) (McDowell et al., 2008, 2013; Tozzi et al., 2013; Walters et al., 2002). For cottonwood seedlings, root growth rates that cannot keep up with the receding water table are implicated as a failure in resource acquisition, triggering the onset of these mechanisms of mortality (González et al., 2010; Mahoney and Rood, 1992; Stella and Battles, 2010). Additionally, as a low-elevation species adapted to living in wet environments, *P. fremontii* is known to be particularly vulnerable to cavitation, and tends to maintain xylem water potentials very close to their catastrophic threshold (Leffler et al., 2000; Pockman and Sperry, 2000; Pockman et al., 1995; Tozzi et al., 2013). Our water stress threshold of $\theta_{0.1}$ was a conservative estimate related to water potential below which there would likely be a rapid loss of xylem hydraulic conductivity (see Methods and Appendix D). There was a 3.5-fold difference in number of days spent above this water stress threshold in the fine relative to coarse substrate, and an almost 3-fold increase in median seedling survival time. However, Tozzie et al. (2013) also noted that shifts in leaf orientation from horizontal to vertical, which decrease light and heat stress, do not occur until seedlings are older (>90 days), suggesting indirect stresses are relatively stronger on younger seedlings. The more gradual mortality rate of cottonwood seedlings growing in the lower soil moisture environment in the presence of herbaceous competitors suggests there may have been a facilitative shading effect that supports the light/heat stress hypothesis.

Other factors that may have contributed to increased mortality in gravel substrate include decreased root penetration from mechanical resistance (Donald et al., 1987; Wiersum, 1957), and less available physical space for root growth in gravelly substrate, particularly when grown with densely rooted interspecific competitors. However, Gonzalez et al. (2010) found no substrate-driven differences in survival or growth in *P. alba* seedlings grown in saturated conditions. The coarse substrate used in our experiments did have small, but significantly lower levels of potassium and phosphorus, and higher pH compared to the fine substrate (Appendix Table B-1), though these were within the range of variability found in the field (NRCS, 2014; Hayden, unpublished data; Morken and Kondolf, unpublished data). If they were ecologically significant we expected to see differences in plant growth (Marler et al., 2001). However, there was no measurable effect on germination or early growth of cottonwood seedlings (i.e., when soil moisture levels were equivalent across substrates), nor did it affect the total shoot or root biomass of interspecific competitors. Thus, we conclude the effect of substrate texture on seedling survival was primarily driven by strong differences in soil moisture.

Effect of interspecific competition on cottonwood seedling survival and interactions with soil moisture

While the effect of soil moisture was the dominant factor driving seedling survival, increasing cover of interspecific competitors had a significant negative effect on end-of-season cottonwood seedling survival, and the effect was much stronger in lower soil moisture conditions. We held intraspecific competition purposely constant and on par with germination densities found in the field (Shafroth et al., 2002; Sher et al., 2002), such that differences are attributable to interspecific competition. There is common reference to shade-intolerance and poor interspecific competitive ability of cottonwood seedlings in the literature (Braatne et al., 1996; summarized in Burns and Honkala, 1990; Karrenberg et al., 2002). Much of this has been inferred from patterns of occurrence based on field observations of seedling recruitment locations, which are typically limited to bare, newly formed substrate, with little to no recruitment under existing stands or in the presence of heavy herbaceous cover (Hosner and Minckler, 1963, 1960; Johnson et al., 1976; Peterson, 2000). However, this pattern likely has more to do with abiotic processes that shape the formation of seedbeds rather than a direct effect of poor competitive ability of seedlings.

Surfaces that maintain appropriate summer seasonal soil moisture requirements necessary for cottonwood seedling survival are also often the ones subjected to previous scour or deposition that typically keeps competing vegetation cover low prior to arrival of cottonwood seeds (Mahoney and Rood, 1998; Scott et al., 1996). The point is not that competitive interactions are completely absent or affect cottonwood seedling recruitment in some areas, but that the processes governing vegetation dynamics on the active channel are so overwhelmingly driven by abiotic processes related to physical disturbance and resource supply (i.e., flooding, scour, deposition, and summer stage decline) that biotic interactions are typically less relevant to broad-scale seedling demographic patterns. In abandoned channels, however, this physical disturbance regime is muted, and the more stable physical conditions allow for development of a much more competitive environment (Dufour et al., 2014; Stella et al., 2011), which our results clearly indicate negatively affect cottonwood seedling survival. Cooper and Andersen (2012) propose a similar rationale for lack of recruitment along the active channel of the regulated Green River (Colorado, USA) following environmental flow releases—less dynamic, regulated flows have

allowed for the establishment of novel plant communities (e.g., dense vegetation on bars) such that occasional flow releases alone may not be enough to re-establish cottonwood seedlings in high numbers.

Results from field-based vegetation removal studies typically show positive or neutral effects of removal of interspecific competitors on seedling survival, though it remains unclear whether this is driven by above-ground (light availability/capture) vs. below-ground (water availability/demand) resource interactions (Cooper and Andersen, 2012; Stella, 2005; Taylor et al., 1999). Braatne et al. (1996) noted that because cottonwood seeds lack an endosperm, seedlings are highly dependent on photosynthate, and thus access to full sunlight is critical for sustained growth. However, direct evidence of competitive effects, including this study, suggests that cottonwoods may not be as shade intolerant as originally thought, and that competition for soil resources (particularly water) may be the stronger driver. Cooper et al. (1999) found that when seedlings were irrigated, there was no effect of a reduction in photosynthetically active radiation from shade cloth (down to 17% PAR) on survival of seedlings over the first summer growing season, and a decline in survival post-irrigation was similar among control and all shade levels. Further, they found soil moisture levels were higher under naturally established seedlings (in open sites) than they were under existing stands of saplings at similar relative elevations, suggesting lack of adequate surface soil moisture rather than light availability may be a reason why seedlings do not establish under existing stands. González-Muñoz et al. (2013) found negative effects of shading from shade cloth on *P. alba* seedling biomass, but only at heavy levels of shading ($\leq 35\%$ of full sun).

Our logistic modeling results showed a significant interaction effect between soil moisture and competition, with a stronger negative effect of competition on end-season seedling survival in low soil moisture conditions. Thus, in terms of resource scarcity, it suggests that cottonwood seedlings are not necessarily light limited at these levels of shading, but rather are constrained by below-ground competition for water. This is further supported by our finding that cottonwood seedlings grown in the presence of competitors in the lower soil moisture, coarse substrate survived at comparable rates as on higher soil moisture, fine substrate for approximately the first 40 days (Figure 3c), suggesting a facilitative effect. In the early weeks, the shading effect of interspecific competitors may have reduced soil surface temperatures and evaporative water loss from both the soil (Becker et al., 1988) and seedling leaf surface, which is perhaps particularly critical during the first few weeks of growth when seedlings are very small and more vulnerable to heat and water stress (Tozzi et al., 2013). However, understanding whether plants are competing for light or water is complicated by (1) the physiological interaction between water stress and reduced photosynthetic capacity resulting from stomatal closure (Valladares and Niinemets, 2008; Valladares, 2003), (2) the fact that light can be both a resource and a stress (photo-oxidation and heat) in water-limited situations (Walters et al., 2002), and (3) study design limitations—vegetation removal experiments such as those described above remove both above- and below-ground competition, and shade cloth experiments on cottonwoods have typically not accounted for co-occurring changes in soil moisture. Our experiment is no exception—we cannot clearly distinguish above- vs. below-ground competition because both were in play simultaneously.

Applicability of experimental results to field conditions

Our results suggest that cottonwood seedling establishment is not limited to recently abandoned channels, and that there is a broader window of recruitment opportunity for woody pioneer species. However, our study assumed that seed rain was constant regardless of biogeomorphic stage (i.e., we started with the same number of germinants in all treatment gradients). Two factors may reduce seed rain in more densely vegetated abandoned channels undergoing terrestrialization and colonization by plants: (1) dense vegetation can provide a physical barrier blocking cottony seed from coming into direct contact with the substrate, a condition necessary for germination (Fenner et al., 1984), and (2) loss of hydrochory in abandoned channels that become progressively more disconnected from the main channel may reduce seed dispersal (Leyer, 2006). Dependence solely on wind dispersal may be particularly problematic in river systems where the riparian corridor has been severely fragmented and reproductively mature stands are patchy (Battaglia et al., 2008; D. Merritt et al., 2010). Thus, while environmental conditions within older abandoned channels may be adequate to support continued establishment of cottonwood seedlings, the combined effect of reduced seed rain and decreased establishment success due to competitive dynamics predicted from our study may preclude any meaningful level of recruitment from a population or restoration perspective.

We also recognize that biogeomorphic evolution of an abandoned channel is not typically a steady, linear process (i.e., a constant rate of infilling and vegetation colonization), but may proceed in punctuated events resulting from (1) episodic sediment deposition related to frequency and magnitude of sediment supply and transport from flood flows, (2) changes in deposition that occur as the main channel continues to migrate, potentially moving further away from the abandoned channel, (3) the morphology of the abandoned channel itself (more arcuate vs. straight) that affects rates of deposition (Citterio and Piégay, 2009; Constantine et al., 2009; Piégay et al., 2002), and (4) nonlinear colonization and development of herbaceous vegetation. Thus, discrete deposition events may lead to periods when establishment conditions are better (i.e., above our idealized red line in Figure 4) and a large cohort develops in even-age patches similar to those that develop on point bars. Furthermore, depending on patterns of channel migration, an abandoned channel may get reoccupied by the main flow path and become the active channel again. Finally, while our focus was on conditions typical of abandoned channels, the conditions tested in our experiment (i.e., the entire response surface shown in Figure 4) are applicable to patches throughout the river corridor—e.g., on active channel bars, banks, and floodplains. While establishment conditions along the active channel are largely driven by abiotic controls, stabilization of the flow regime in some regulated rivers may have altered the balance between abiotic and biotic controls by facilitating more abundant and widespread establishment of interspecific competitors (Cooper and Andersen, 2012). Our experimental results are highly relevant to this situation as well.

Incorporating secondary recruitment locations into riparian forest management

Better understanding of the functional importance of riparian forests has resulted in substantial restoration efforts in recent decades in an attempt to reverse their significant declines (Bernhardt et al., 2005). Restoration strategies have focused on active revegetation (e.g., Alpert et al., 1999), or, more recently, on passive, process-based techniques using environmental flow releases to reconnect channel and floodplain processes (Acreman and Ferguson, 2010; Richter and Richter,

2000; Richter et al., 2003; Vaughan et al., 2009). The focus of these experimental flow releases has been to alleviate the effects of river regulation on recruitment of pioneer riparian forest based on our knowledge of recruitment processes along the active channel (Cooper and Andersen, 2012; Hall et al., 2009; D. M. Merritt et al., 2010; Rood et al., 2005, 2003; Wilcox and Shafroth, 2013). Understanding the early seedling establishment requirements within abandoned channels thus adds another strategy for restoration of pioneer forests in meandering alluvial river systems, and complements existing strategies of maintaining or re-establishing the processes (e.g., natural flows, sediment supply) and the physical space (i.e., unconstrained reaches) necessary for channel meandering.

The importance of abandoned channels as hydraulic refugia necessary for population recovery of mobile aquatic organisms has received much more attention in the restoration literature (Amoros and Bornette, 2002; Lake et al., 2007; Sedell et al., 1990; Tabacchi et al., 2009). These efforts have been primarily focused on the needs of aquatic organisms and typically employ a site-scale engineering approach. In contrast, the importance of abandoned channels for riparian plant species, particularly in regulated river systems, has only recently been quantified (Dufour et al., 2014; Stella et al., 2011)—though it clearly occurs in a variety of river systems (Asplund and Gooch, 1988; Cooper et al., 2003; Cordes et al., 1997; Dykaar and Wigington, 2000; Kalliola et al., 1991; Polzin and Rood, 2006; Shankman, 1993, 1991; Stella et al., 2011; Van Pelt et al., 2006). Channel abandonment, though episodic in nature, appears to guarantee establishment of at least one cohort of pioneer trees at or near the time of abandonment, regardless of flow conditions after abandonment (Stella et al., 2011). Our current experimental results suggest that environmental conditions throughout the biogeomorphic evolution of an abandoned channel can support additional cohorts of trees (i.e., a more open recruitment window). Thus, at minimum it provides a secondary pathway for seedling establishment in unregulated rivers, and is much more important in the population dynamics of pioneer trees within regulated river systems (Stella et al., 2011) where changes to the flow regime have curtailed recruitment along the active channel (Braatne et al., 2007). This is because in some regulated rivers, high flows (even if reduced) are still geomorphically active enough to produce episodic channel abandonment (Micheli and Larsen, 2010). As a longer-term approach to incorporating secondary recruitment locations for pioneer forest restoration, we recommend more explicit merging of broad-scale, passive restoration via environmental flows with site-scale, engineering efforts aimed at restoring floodplain habitat heterogeneity for aquatic taxa.

TABLES

Table 1. Summary of predictor variables used for model building. Cumulative metrics were integrated over the 58 day experiment period.

Driver Category	Measured Variable	Metric Type	Metric Abbrev.	Description	Units
Competition	Fraction live foliar cover	Magnitude	C_{cum}	Cumulative Cover	fraction cover · days
			C_{max}	Maximum Cover	fraction cover
		Timing	$days.C_{max}$	Number of days to maximum cover	days
Soil Moisture	Soil volumetric water content (θ)	Magnitude	θ_{cum}	Cumulative volumetric water content	$m^3 m^{-3} \cdot days$
			Timing	$days.\theta_{0.1}$	Number of days to stress threshold ($\theta=0.1$)
		$days.\theta_{sat}$		Number of days at saturation	days

Table 2. Suite of full models $g(x)$. All models include the base model of $\beta_0 + \beta_1 \times$ initial seedling height.

Full Model #	Cover (β_2)		Soil Moisture (β_3)		Interaction (β_4)
	Magnitude	Timing	Magnitude	Timing	
1	C_{cum}		θ_{cum}		$C_{cum} \times \theta_{cum}$
2	C_{cum}			$days.\theta_{0.1}$	$C_{cum} \times days.\theta_{0.1}$
3	C_{cum}			$days.\theta_{sat}$	$C_{cum} \times days.\theta_{sat}$
4	C_{max}		θ_{cum}		$C_{max} \times \theta_{cum}$
5	C_{max}			$days.\theta_{0.1}$	$C_{max} \times days.\theta_{0.1}$
6	C_{max}			$days.\theta_{sat}$	$C_{max} \times days.\theta_{sat}$
7		$days.C_{max}$	θ_{cum}		$days.C_{max} \times \theta_{cum}$
8		$days.C_{max}$		$days.\theta_{0.1}$	$days.C_{max} \times days.\theta_{0.1}$
9		$days.C_{max}$		$days.\theta_{sat}$	$days.C_{max} \times days.\theta_{sat}$

Table 3. Summary statistics of Kaplan-Meier estimated survival curves by categories of (1) substrate texture/soil water availability, and (2) presence/absence of interspecific competitors.

	Median Survival Time in Days (95% CI)	End-season Survival Probability (95% CI)
<i>Fine/High soil moisture</i>		
Controls	24 (21-36)	0.39 (0.33-0.45)
Competitors Present	21 (21-24)	0.16 (0.13-0.18)
<i>Coarse/Low soil moisture</i>		
Controls	9 (6-9)	0.06 (0.035-0.097)
Competitors Present	21 (21-24)	0.005 (0.0017-0.012)

Table 4. Top five ranked logistic regression models of end-of-season cottonwood seedling survival, as well as the best main-effects-only (no interaction term) and single factor models. All models included the base model of initial seedling height as a covariate. Models/variables defined in Tables 1 and 2.

Model Set	K*	Variables	AUC [†]	ΔAIC [‡]	w _i [§]
4 (Full)	5	$C_{max} + \theta_{cum} + C_{max} \times \theta_{cum}$	0.91	0.00	0.52
5 (Full)	5	$C_{max} + days.\theta_{0.1} + C_{max} \times days.\theta_{0.1}$	0.91	0.18	0.48
6 (Full)	5	$C_{max} + days.\theta_{sat} + C_{max} \times days.\theta_{sat}$	0.90	8.95	0.0059
9 (Full)	5	$days.C_{max} + days.\theta_{sat} + days.C_{max} \times days.\theta_{sat}$	0.90	19.34	0.000033
1 (Full)	5	$C_{cum} + \theta_{cum} + C_{cum} \times \theta_{cum}$	0.90	19.73	0.000027
4 (Reduced)	4	$C_{max} + \theta_{cum}$	0.90	22.26	0.000008
Single factor					
Soil	3	$days.\theta_{sat}$	0.87	118.62	9.0×10^{-27}
Moisture					
Single factor					
Competition	3	$days.C_{max}$	0.83	221.82	3.5×10^{-49}
Base model	2	<i>(Intercept + initial seedling height)</i>	0.76	384.16	9.2×10^{-122}

*K = total number of model parameters, including intercept and covariate of initial seedling height

[†]AUC = area under the receiver operating characteristic (ROC) curve

[‡]ΔAIC = relative difference in Akaike Information Criterion value from the model with the lowest AIC ($\Delta_i = AIC_i - AIC_{min}$).

[§]w_i = AIC weight, which represents the relative strength of evidence for each model given the data and the set of candidate models. $\sum w_i = 1$.

FIGURES

Figure 1. Grain size distributions for experimental substrates (Fine and Coarse) in comparison to field conditions. Field sites were from the middle Sacramento River study reach, including 10 abandoned channel sites ≥ 15 years old (Dufour et al. 2014), and one point bar site used as a proxy for a recently abandoned channel (see Appendix A for details). The gray polygon encloses the range of grain size distributions found within the establishment zone of abandoned channel sites that ranged from 15 to approximately 100 years since abandonment, with fine gray lines indicating individual sample results ($n=60$).

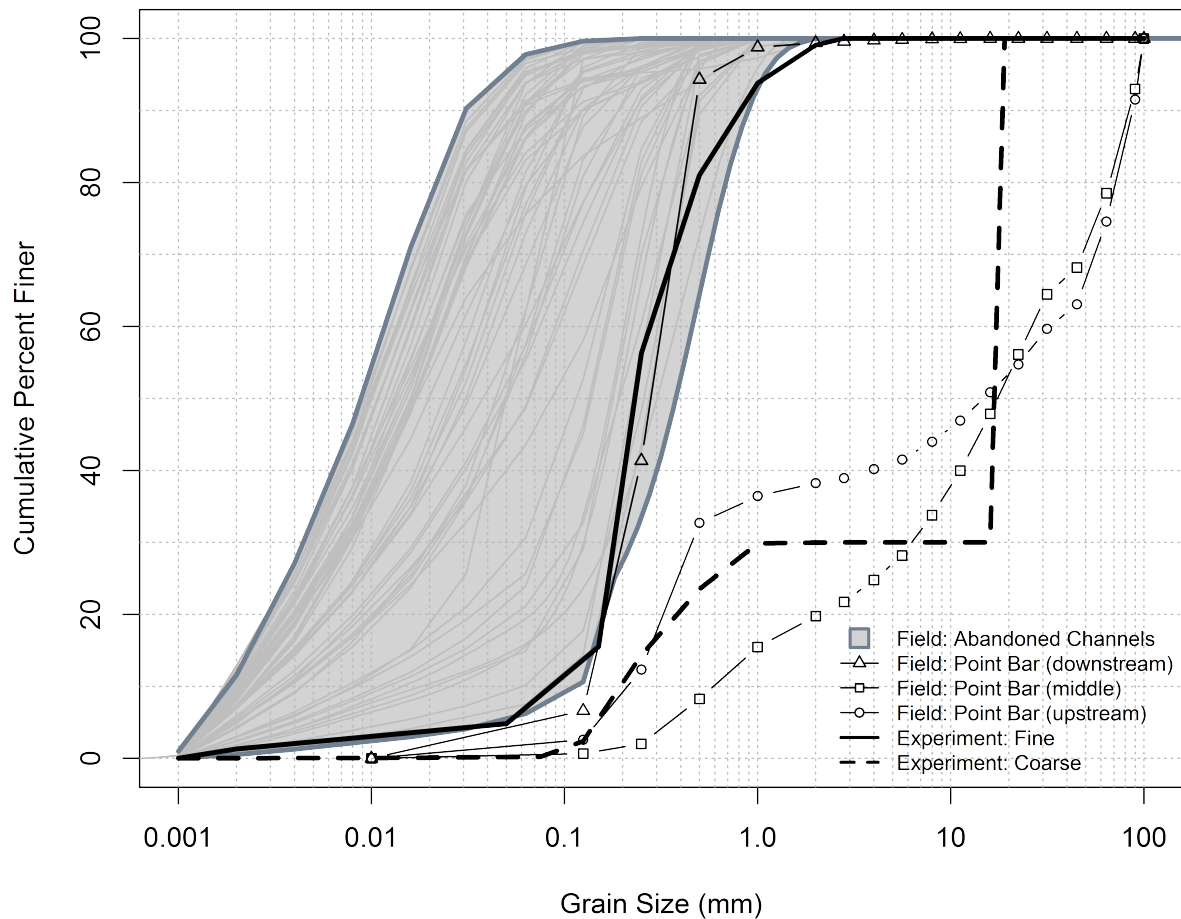


Figure 2. Gradient of cover used in the experiment in comparison to field conditions, by median grain size diameter (D_{50}). This shows the biogeomorphic trend observed in the field of increasing cover fraction with finer sediment texture. Means \pm 95% confidence intervals are shown. Field fraction cover was based on LAI-2000 measurements taken at 75 plots biweekly for a total of 5 surveys between June and August 2008 (Appendix A). Cover fraction for the experiment is based on maximum cover measured via overhead photography and pixel-based image processing. Median grain size was calculated from grain size distributions shown in Figure 3.

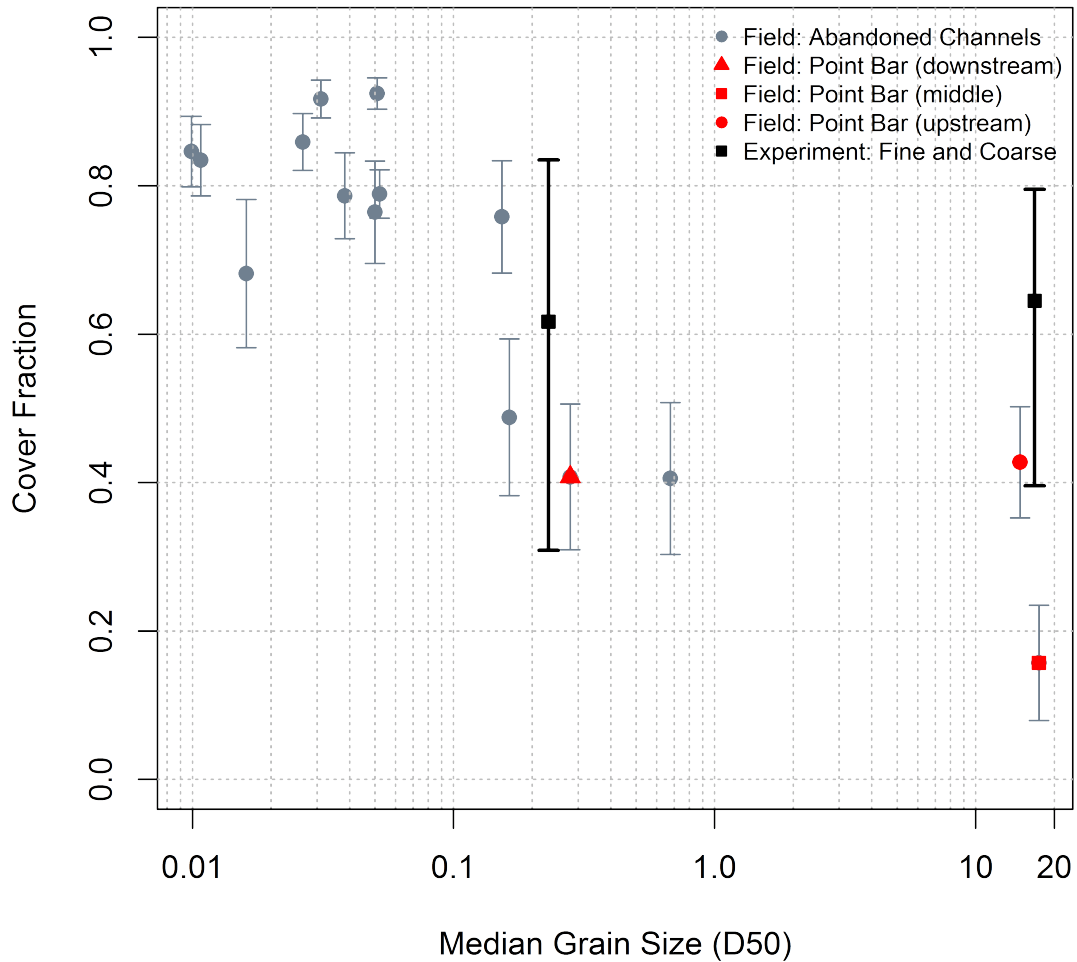


Figure 3. Experimental gradients and cottonwood seedling survival results over the course of the experimental drawdown period. Panel (A) shows the soil moisture gradient, as measured by volumetric water content (θ), from two representative pots of Fine and Coarse texture substrate (no plant controls). Panel (B) is fraction live foliar cover of all pots in the experiment, with controls of both textures (cottonwoods only) in black (n=14) and pots that included interspecific competitors in color by texture (n=48). The colored lines thus show the complete range of the competitive cover gradient imposed, as well as how cover changed through time. Panel (C) shows Kaplan-Meier estimated survival probability curves with 95% confidence intervals, grouped by high/low soil moisture (fine vs. coarse substrate = blue vs. brown) and presence/absence of interspecific competitors (light vs. dark colors) on cottonwood seedling survival. Cottonwood survival was censused every three days.

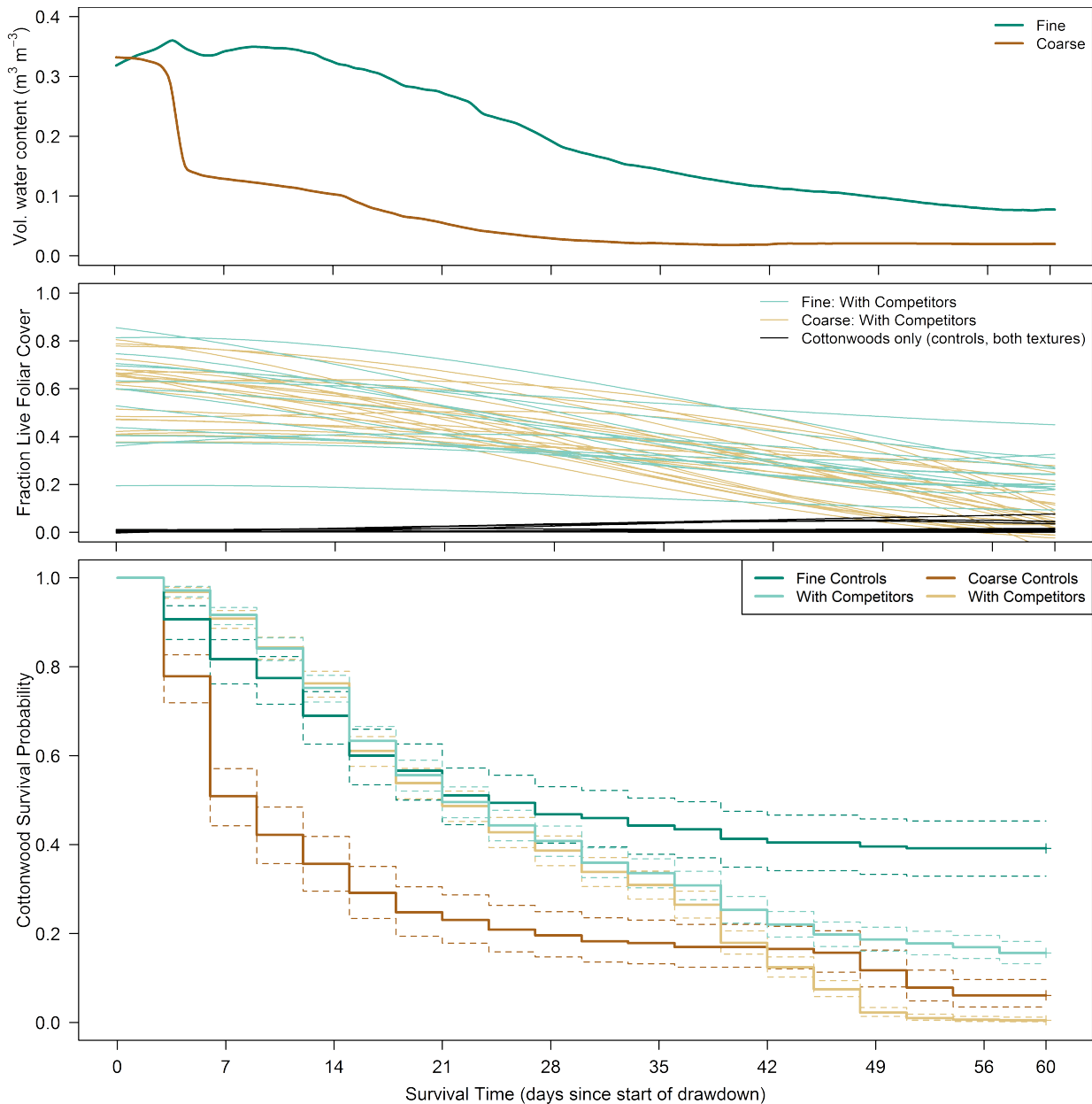
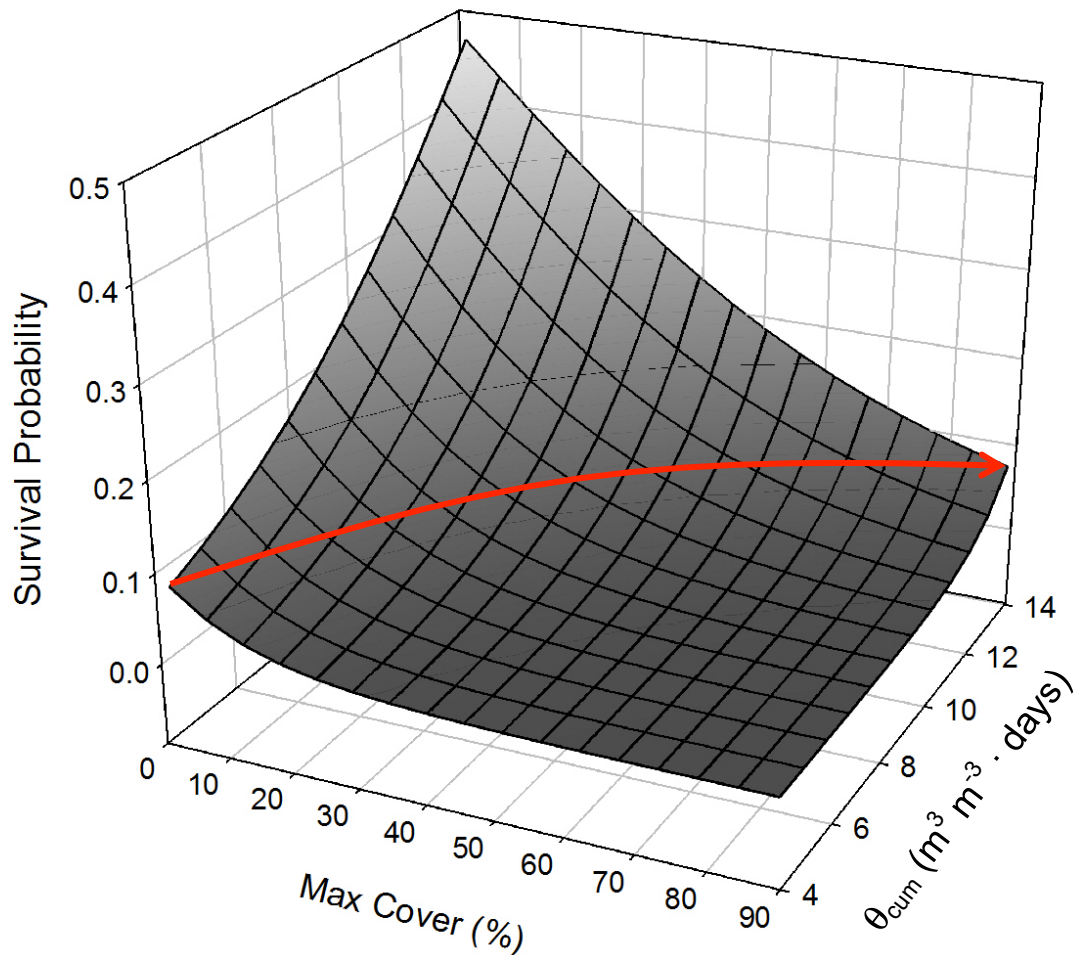


Figure 4. End-season cottonwood seedling survival probability predicted from the best logistic regression model. Probability of end-season cottonwood seedling survival as a function of soil moisture (measured by cumulative volumetric water content, θ_{cum}), and interspecific competition (measured by maximum cover, C_{max}), assuming mean initial seedling height (0.6 mm). The gray surface represents survival probability across all possible combinations of soil moisture and competitive cover conditions. The red arrow represents an idealized trajectory of conditions within abandoned channels through time that we observed in the field (see Figure 2), where newly abandoned channels begin with relatively bare (low competition), coarse substrate (low soil moisture) and over time develop more cover (higher competition) as the abandoned channel fills with finer substrate (higher soil moisture). Conditions above and below this line do occur, but in a more patchy configuration. All of these conditions would also be expected to occur in patches outside of abandoned channels (i.e., active channel bars and floodplains).



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APPENDIX A

Field study to determine range of field conditions used in mesocosm experiment

STUDY DESIGN OVERVIEW

To create realistic field conditions within our mesocosm study, we supplemented data from previous field studies (Dufour et al., 2014; Stella et al., 2011) with more detailed sampling at a subset of field sites along the middle Sacramento River (Figure A-1). The main goal of this effort was to parameterize the mesocosm environmental gradients (soil moisture and interspecific competition) by quantifying the depth to water table, substrate texture, species composition and abundance observed across a wide range of abandoned channel biogeomorphic stages.

As discussed in Dufour et al. (2014), we used time since abandonment and hydrogeomorphic considerations (e.g., main channel connectivity, grain size, channel planform) as proxies for biogeomorphic stage. From the original 10 abandoned channel sites, we selected a subset of four that ranged in age from approximately 15 to 50 years since cutoff, and added an active channel point bar as a reference for a newly abandoned channel. One of the 15 year-old sites remained hydrologically connected to the main channel at both upstream and downstream ends for most of the summer growing season. We refer to this as “active” in subsequent tables/figures. The other three abandoned channel sites were disconnected from main channel surface flow at one or both ends, meaning there was no active flow through the site. We refer to this condition as “blocked”.

At these five sites we sampled the physical and competitive environment within the area that presently might support cottonwood germination and establishment. We defined the “establishment zone” as the space between the waters edge and the start of established woody vegetation (typically saplings). Depending on the stage of the abandoned channel, the establishment zone was bare or vegetated with both herbaceous wetland species and woody seedlings.

We stratified each site longitudinally into upstream, middle, and downstream thirds, and installed five 1×1-m permanently monumented plots within each third, for a total of 15 plots per site (n=75 total plots). Within each third, we further stratified by elevation to sample the range of topography occurring within the establishment zone. Plots were then randomly placed at least 10 meters from any neighboring plot to minimize spatial autocorrelation. To capture vegetation phenology across the growing season, we surveyed the plots 5 times each, approximately biweekly between June and August 2008. When we discuss “seasonally averaged” values, we are referring to data averaged over the 5 survey periods.

SAMPLING METHODS

Substrate grain size

To capture the range of grain sizes found in abandoned channels across a gradient of biogeomorphic stage, we supplemented surface grain size data taken from previous field studies (Dufour et al., 2014), with bulk sampling from the point bar site. Grain size data from the 10 abandoned channels sites were collected along 3 transects per site that were oriented perpendicular to the channel centerline. Samples were collected using a 10 cm diameter × 20 cm

deep soil auger and analyzed with a laser granulometer (Malvern Mastersizer 2000, United Kingdom). We used data from the two lowest elevation transect positions (aquatic zone and 4m) to characterize the grain size of the cottonwood seedling establishment zone (n=60).

The point bar data was sieved from bulk samples of the upper 30 cm of substrate in the upstream, middle, and downstream portion of the point bar within ~10 m of the waters edge. Minimum sample volumes on the point bar were determined following recommendations from Church et al. (1987), as adapted for volume by Marshall and Sklar (2012), where the largest particle (D_{max}) contributed no more than 1% of the total sample volume for $32 \text{ mm} < D_{max} < 128 \text{ mm}$, assuming particle density of 2650 kg/m^3 and porosity of 0.35. Following Bunte and Abt (2001), particles $> 45 \text{ mm}$ were sorted and weighed in the field, and a subsample of the remainder was retained and sieved in the lab using a high capacity sieve shaker, as were the two experimental substrates.

Topography/Depth to water table

Plots were permanently marked with rebar, georeferenced with a high precision Trimble GPS unit during installation, and tied in to a local topographic benchmark with an auto level to connect to real world elevation. We estimated depth to water table at each survey by measuring elevation of each plot above nearest surface water using a line level.

Competitive environment

To quantify the competitive environment found in abandoned channels across the gradient of biogeomorphic stage, we measured canopy cover, species composition and abundance, and structure of vegetation within each plot. Canopy cover was measured with an LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, Nebraska), from three different positions around each plot (paired above/below canopy readings). Canopy cover was computed as $1 - \text{the diffuse non-interceptance (fraction of sky visible from below the canopy)}$ (LI-COR Biosciences, 1992; Rautiainen et al., 2005). Species composition and abundance was measured at each plot with visual estimates of percent cover by species. Nomenclature follows the second edition Jepson Flora (Baldwin et al., 2012). Observer bias was minimized by averaging cover estimates from two people. We also resampled one plot per site during each survey to quantify error. We also measured percent bare ground, litter, and woody debris ($>5\text{cm}$ diameter) present in each plot. Due to phenology of some species (i.e., certain grasses that didn't flower/set seed until late in season) identification could only be done to genus.

Species selection for mesocosm experiment

We calculated the Importance Value for each species found during each of the five survey periods by summing relative cover and relative frequency, then divided by two to rescale the value between 0 and 1. Thus, an Importance Value close to 1 indicates that the species was found at high cover in almost all plots. For the mesocosm experiment, our goal was to select a species representative of each of the three main herbaceous growth forms found in the field (forb, sedge, and grass). We selected the species in each growth form category with the highest Importance Value that could also be propagated from seed and grew quickly, based on propagation testing (Hayden, unpublished data).

RESULTS AND DISCUSSION

Figure A-2 shows the grain size distribution results from the two field data sets. We found a trend of increasing fraction canopy cover (as measured by LAI-2000) with finer sediment texture (i.e., smaller median grain size diameter (D_{50})) (Figure A-3). This was expected based on our understanding of the biogeomorphic evolution of abandoned channels. They begin as a bend along the coarser active channel. Following channel cutoff and abandonment, they fill with finer and finer sediment and become increasingly colonized by vegetation as physical conditions stabilize.

As expected, the point bar site had the lowest mean canopy cover overall (seasonally averaged fraction cover 0.33 ± 0.028 SE; Figures A-3 and A-4), indicative of the more physically dynamic and stressful conditions experienced along the coarse active channel. The youngest abandoned channel site that still remained hydrologically connected to the main channel (“active”) had the highest total species richness of all sites (Table A-1), but the lowest mean cover of the 4 abandoned channel sites (0.55 ± 0.033 ; Figure A-4). The three “blocked” abandoned channel sites had the highest fraction canopy cover (0.77–0.89), indicative of this later biogeomorphic stage. Based on these field data, we created a gradient of interspecific competitive cover for the mesocosm experiment that ranged between approximately 0.30–0.80 fraction cover (see main text Figure 2).

Based on Importance Value, the dominant species was the aquatic perennial forb *Ludwigia peploides* (Table A-2). This species was found at high cover and high frequency in the four abandoned channel sites, but was much less abundant on the point bar site. Other abundant species included perennial forbs (e.g., *Lycopus americanus*, *Xanthium strumarium*, *Equisetum arvense*) grasses (e.g., *Leersia oryzoides*, *Cynodon dactylon*), sedges (e.g., *Cyperus eragrostis*), and woody seedlings (*Salix exigua*, *Populus fremontii*, *Acer negundo*), which are typical of disturbed wetland areas.

Despite the abundance of *Ludwigia peploides*, it either spreads mostly vegetatively at our sites or sets seed very late, because we were unable to find enough seed in the Fall of 2009 to propagate it for our mesocosm experiment. We instead selected *Lycopus americanus* as the next most abundant forb. *Cyperus eragrostis*, the most abundant sedge, was easily collected and propagated from seed. The most abundant grass at our field sites was *Leersia oryzoides*; however as a perennial it did not produce enough seed in time for mesocosm propagation. Instead we selected the annual grass, *Echinochloa crus-galli*, which has a similar robust size and erect form as *L. oryzoides*. The final three species selected for use in the mesocosm experiment are highlighted in grey in Table A-2.

Table A-1. Species richness by site. Total site richness indicates total unique species found at the site level (i.e., in any plot during any survey at each site).

Years since abandonment	Main channel connectivity	Total Site Richness	Mean	Std.
			Plot Richness	Error
0 (Point Bar)	Active	53	12.1	2.1
15	Active	76	26.3	2.2
15	Blocked	42	11.5	1.6
20	Blocked	40	11.7	0.7
48	Blocked	27	10.4	1.1

Table A-2. Top 25 of a total of 97 species found during field surveys, ranked by seasonally averaged Importance Value (mean \pm SE of 5 survey periods). Species highlighted in grey were those selected as herbaceous competitors for the mesocosm experiment.

Species	Family	Growth Form	Non-native	Importance Value
<i>Ludwigia peploides</i>	Onagraceae	Perennial forb		0.502 (+0.017)
<i>Lycopus americanus</i>	Lamiaceae	Perennial forb		0.309 (+0.011)
<i>Leersia oryzoides</i>	Poaceae	Perennial grass		0.305 (+0.007)
<i>Salix exigua</i>	Salicaceae	Woody seedling		0.299 (+0.002)
<i>Populus fremontii</i>	Salicaceae	Woody seedling		0.235 (+0.001)
<i>Xanthium strumarium</i>	Asteraceae	Annual forb		0.227 (+0.004)
<i>Equisetum arvense</i>	Equisetaceae	Perennial forb		0.147 (+0.002)
<i>Cynodon dactylon</i>	Poaceae	Perennial grass	Yes	0.133 (+0.002)
<i>Cyperus eragrostis</i>	Cyperaceae	Perennial sedge/rush		0.132 (+0.001)
<i>Acer negundo</i>	Aceraceae	Woody seedling		0.132 (+0.004)
<i>Persicaria</i> spp.	Polygonaceae	Perennial forb		0.126 (+0.003)
<i>Cyperus strigosus</i>	Cyperaceae	Perennial sedge/rush		0.126 (+0.003)
<i>Juncus effusus</i>	Juncaceae	Perennial sedge/rush		0.125 (+0.001)
<i>Salix lasiandra</i>	Salicaceae	Woody seedling	Yes	0.12 (+0.003)
<i>Hypericum mutilum</i>	Clusiaceae	Annual/perennial forb	Yes	0.116 (+0.005)
<i>Salix lasiolepis</i>	Salicaceae	Woody seedling		0.108 (+0.002)
<i>Salix gooddingii</i>	Salicaceae	Woody seedling		0.105 (+0.002)
<i>Typha latifolia</i>	Typhaceae	Perennial forb		0.091 (+0.002)
<i>Salix melanopsis</i>	Salicaceae	Woody seedling		0.083 (+0.003)
<i>Equisetum laevigatum</i>	Equisetaceae	Annual forb		0.071 (+0.002)
<i>Echinochloa crus-galli</i>	Poaceae	Annual grass	Yes	0.064 (+0.002)
<i>Polypogon maritimus</i>	Poaceae	Annual grass	Yes	0.064 (+0.002)
<i>Melilotus albus</i>	Fabaceae	Annual/biennial forb	Yes	0.064 (+0.001)
<i>Polypogon monspeliensis</i>	Poaceae	Annual grass	Yes	0.054 (+0.001)
<i>Veronica anagallis-aquatica</i>	Scrophulariaceae	Perennial forb	Yes	0.054 (+0.002)

Figure A-1. Field study area map (middle reach Sacramento River).

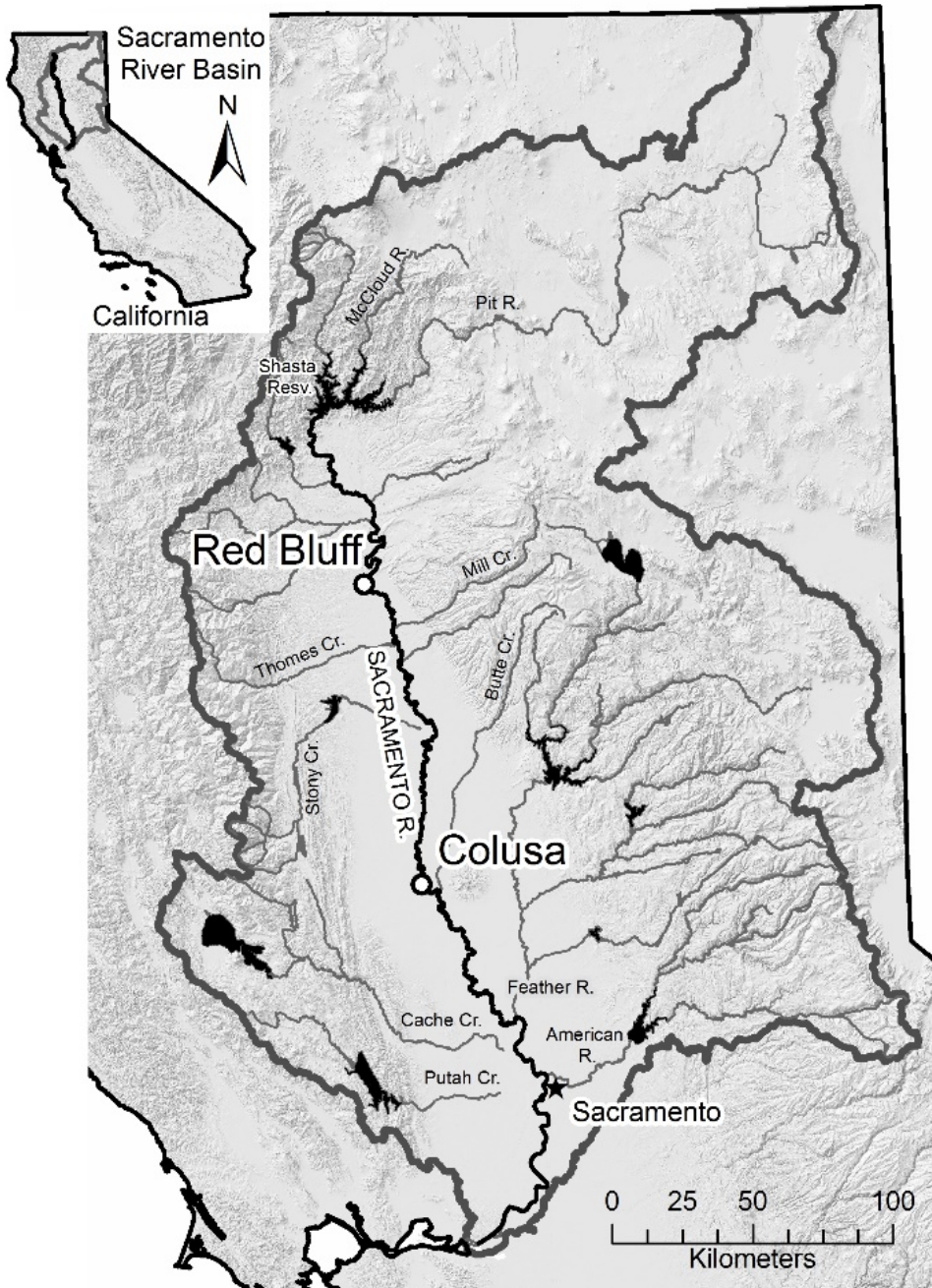


Figure A-2. Grain size distributions of field sites. Other abandoned channel sites indicate additional sites surveyed as part of Dufour et al. (2014).

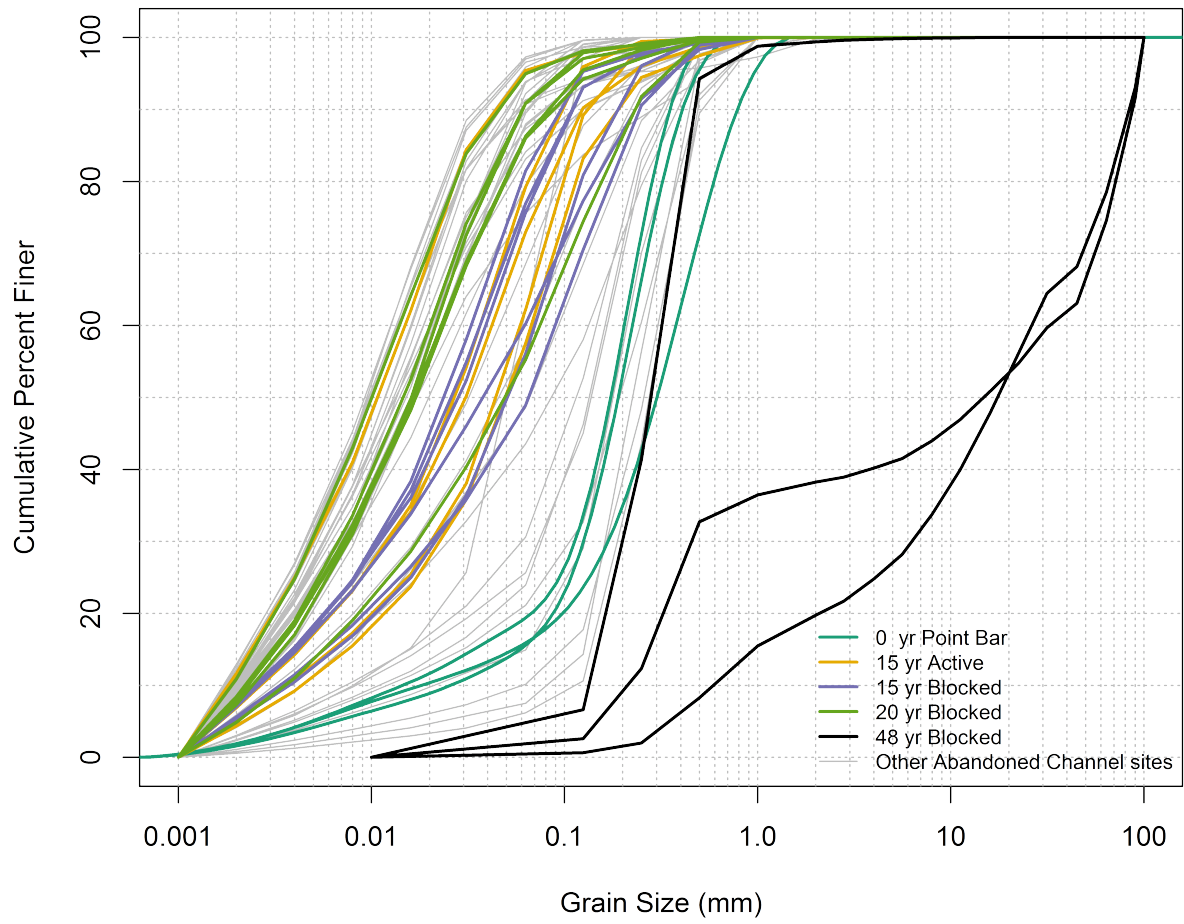


Figure A-3. Fraction canopy cover measured by LAI-2000 Plant Canopy Analyzer as a function of median grain size. Seasonally averaged mean of 5 plots \pm 95% CI from the upstream, middle, and downstream area of each site. Coarser grain size is indicative of a more active hydrogeomorphic disturbance regime.

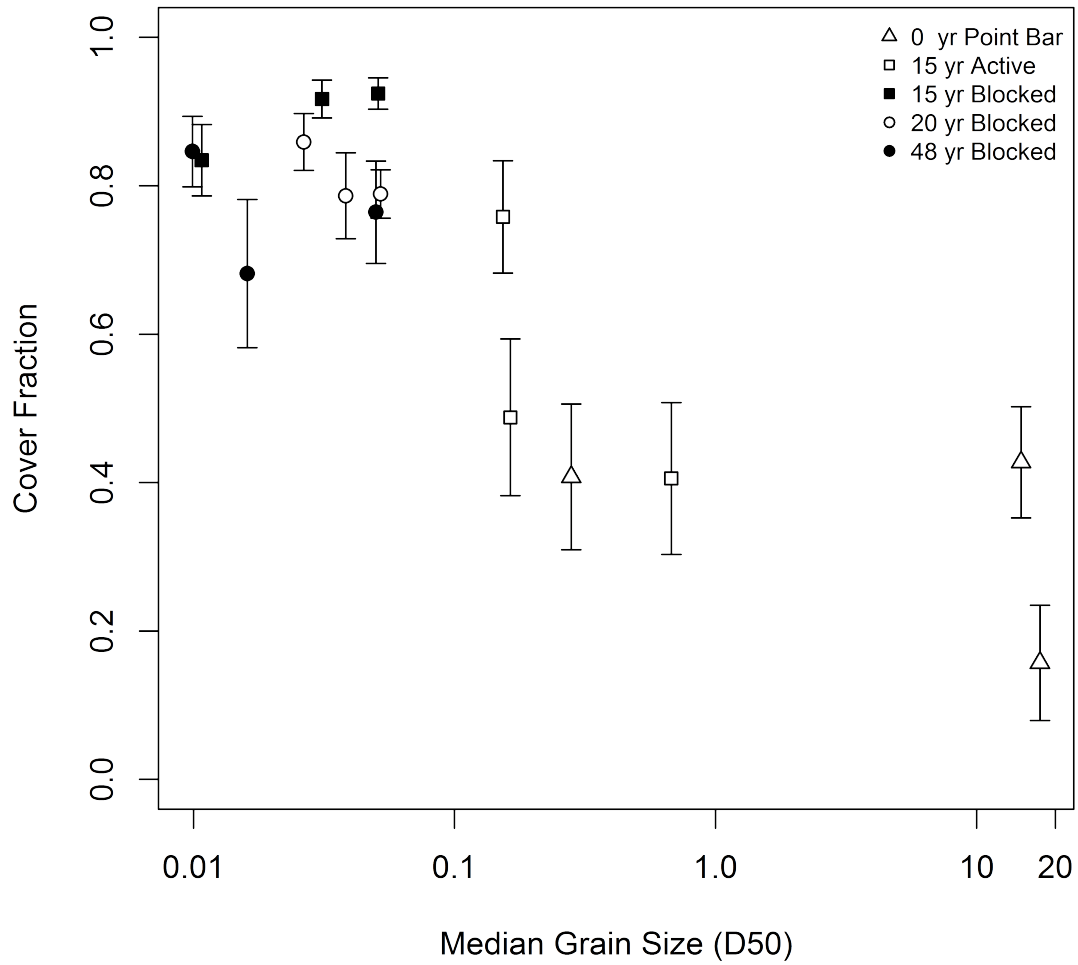
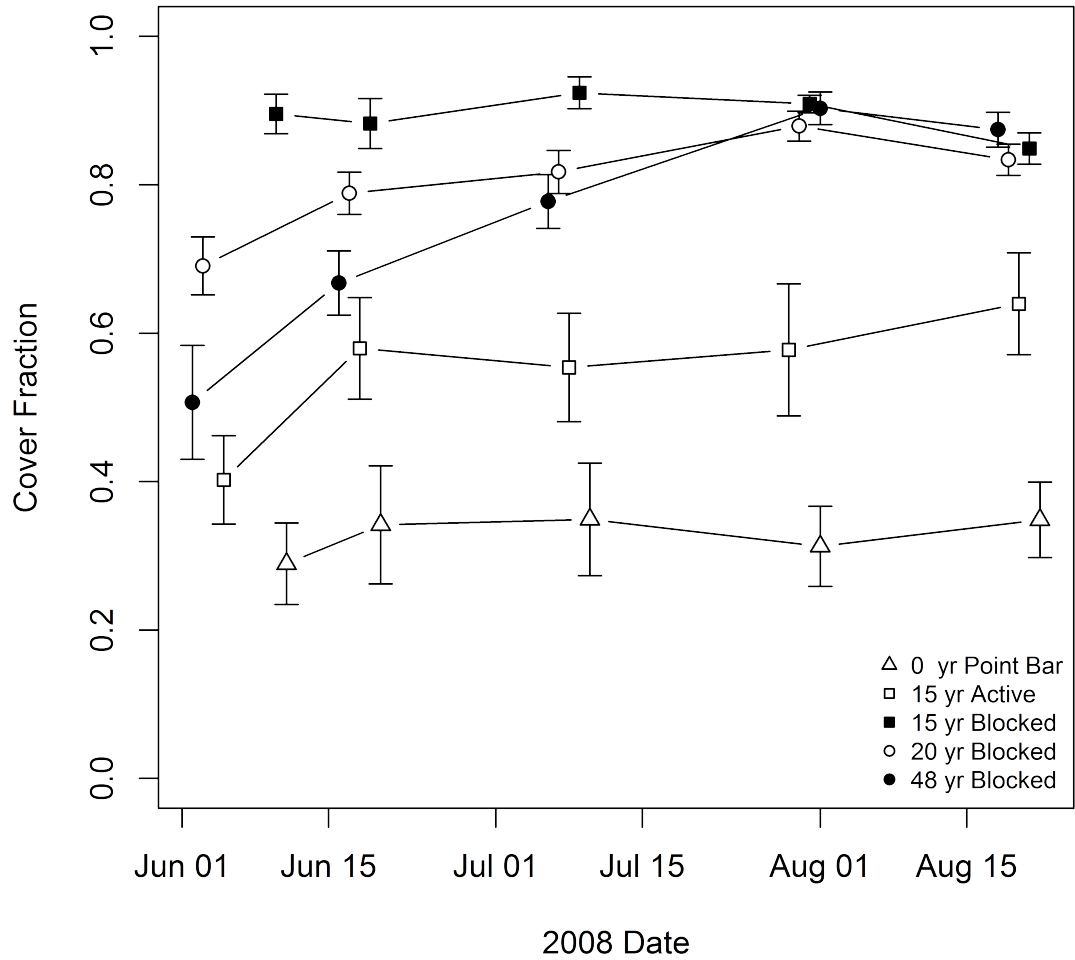


Figure A-4. Canopy cover fraction by site over the summer 2008 growing season, measured by LAI-2000 Plant Canopy Analyzer. Means of 15 plots per site \pm standard errors are shown.



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APPENDIX B

Supplemental mesocosm information

Table B-1. Soil fertility of mesocosm substrates in relation to field conditions from bulk samples of point bar site on the Sacramento River. Mean of 3 samples \pm SE. Significant differences were determined using Tukey multiple comparisons of means, with $\alpha = 0.05$.

	Fine (Mesocosm)	Coarse (Mesocosm)	Point Bar (Field)	Differences
EC (ds)	0.44 (± 0.175)	0.36 (± 0.090)	0.38 (± 0.067)	
NO ₃ -N (ppm)	0.16 (± 0.073)	0.72 (± 0.257)	2.57 (± 2.236)	
Olsen-P (ppm)	6.53 (± 0.088)	0.99 (± 0.000)	1.67 (± 0.406)	a, b, b
X.K (ppm)	20.00 (± 1.000)	5.67 (± 0.333)	33.33 (± 4.410)	a, b, c
X.K (meq100g)	0.05 (± 0.003)	0.01 (± 0.003)	0.08 (± 0.012)	a, b, c
X.Na (ppm)	24.00 (± 4.359)	15.00 (± 2.000)	14.67 (± 2.186)	
X.Na (meq100g)	0.10 (± 0.018)	0.07 (± 0.007)	0.06 (± 0.009)	
X.Ca (meq100g)	1.14 (± 0.025)	1.21 (± 0.090)	2.95 (± 0.337)	a, a, b
X.Mg (meq100g)	0.23 (± 0.015)	0.33 (± 0.003)	1.42 (± 0.189)	a, a, b
CEC (meq100g)	1.52 (± 0.027)	1.62 (± 0.100)	4.52 (± 0.527)	a, a, b
OM.LOI (percent)	0.21 (± 0.012)	0.16 (± 0.003)	0.55 (± 0.046)	a, a, b
pH	6.99 (± 0.193)	8.30 (± 0.053)	7.19 (± 0.325)	a, b, a

EC = Electrical Conductivity

X indicates "Exchangeable"

CEC = Cation Exchange Capacity

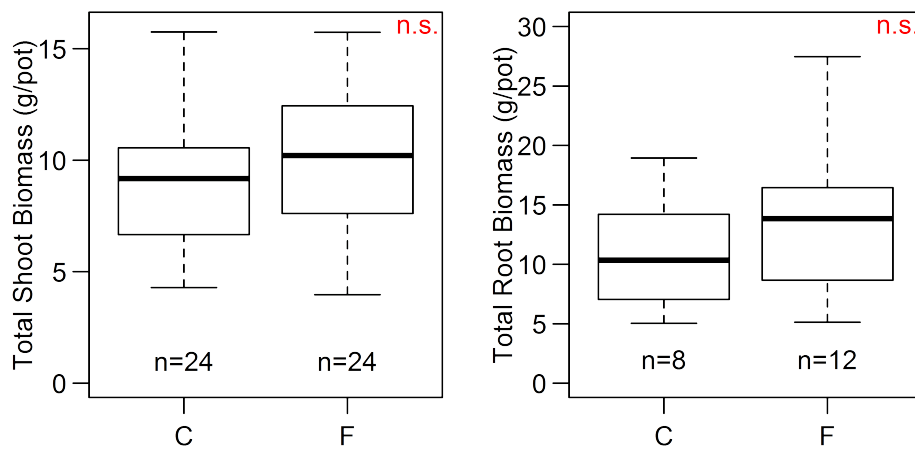
OM.LOI = Organic Matter – Loss on Ignition Method

Substrate was analyzed at the University of California, Davis Analytical Lab using standard methods (references available: <http://anlab.ucdavis.edu/methods-of-analysis>).

Figure B-1. Mesocosm design and set up.



Figure B-2. Total end-season above- and below-ground biomass of interspecific competitors, sampled by pot. Differences were not significant.



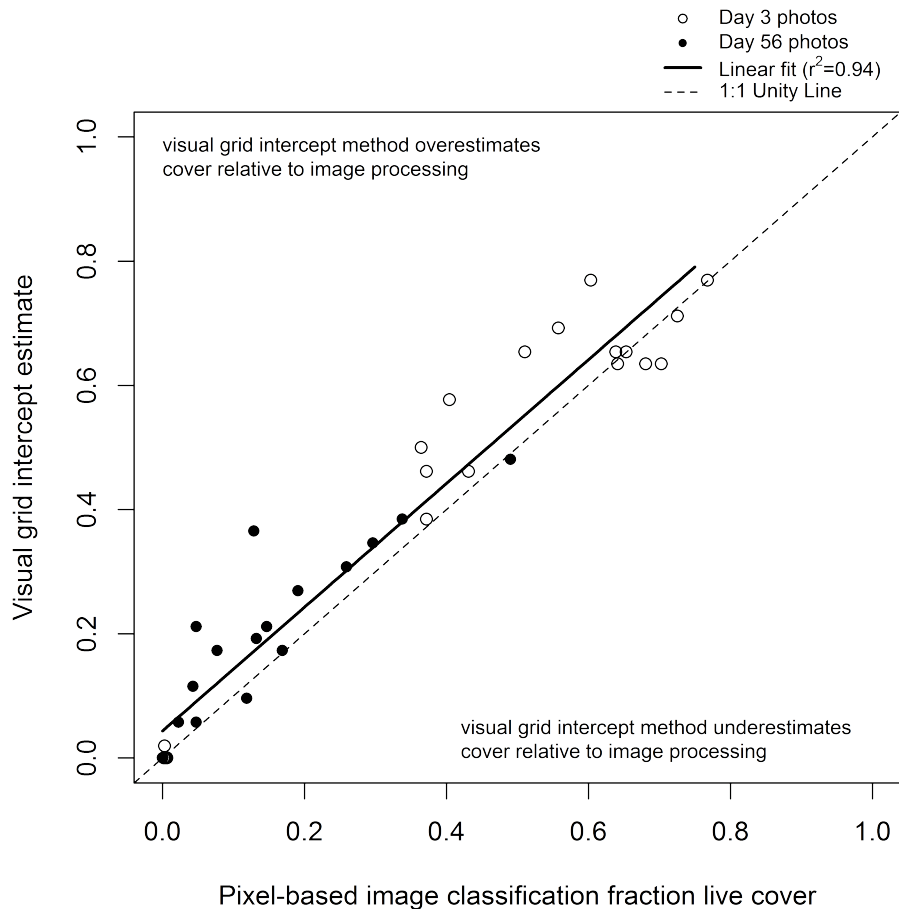
APPENDIX C

Image processing validation

METHODS

We digitally overlaid a 3 cm² grid on a stratified random subset of 40 photos. To capture the range in plant color, we stratified to include 20 photos each from the beginning (Day 3) and end (Day 56) of our experiment. For each day we randomly selected 5 photos from each quartile of cover (as estimated from pixel-based image-processing). We measured cover as the number of grid intersections that hit live plant, divided by the total number of grid intersections (52 total, density = 0.08 intersections/cm²). Grid intersections were 1 pixel wide. We performed the grid-based estimates onscreen, zoomed to the actual pot dimensions to better approximate a field-based estimate.

Figure C-1. Comparison of image-processed (pixel-based) estimate of fraction live cover with visual grid-based estimate. Points that lie on the 1:1 unity line indicate complete agreement between the two methods. Points above the unity line indicate that the visual grid-based method overestimated cover relative to image processing, and points below the unity line indicate an underestimate. Fraction live foliar cover measured from the two methods was highly correlated ($r^2 = 0.94$). Root mean squared error (RMSE) was 0.08; $n = 40$.



APPENDIX D

TDR soil moisture probe calibration and additional data analysis methods

CALIBRATION

Introduction

We used time domain reflectometry (TDR 100 with CS630 probes; Campbell Scientific, Logan, Utah) to measure soil moisture in our mesocosms. This method measures the apparent dielectric constant (K_a)¹ of the material surrounding the probes, based on the travel time for a pulsed electromagnetic signal (Campbell Scientific 2010). Because water has a high dielectric constant relative to other soil material, the change in water content can be directly related to changes in the dielectric (Campbell Scientific 2010). The method is non-destructive and has several benefits, including (1) ease of obtaining continuous measurements, (2) high accuracy ($\pm 0.02 \text{ m}^3/\text{m}^3$) that can be further improved with soil-specific calibration, (3) fine spatial and temporal resolution, and (4) no hazards such as those associated with neutron probe or gamma-attenuation techniques (Jones et al., 2002; Vaz et al., 2013; J. Ritter, Campbell Scientific, pers. comm. 2013). Calibration relationships between K_a and volumetric water content (θ) have been described both by empirical model fitting (e.g., Ledieu et al., 1986; Topp et al., 1980), and by physically based, dielectric mixing approaches that use dielectric constants and volume fractions for each soil constituent (see Jones et al., 2002 for a review).

The factory-recommended calibration equations for our TDR probes were based on either a linear fit to the square root of the dielectric constant (Ledieu et al. 1986), or a third order polynomial fit to the dielectric constant (e.g., Topp et al. 1980). The equations give very similar results in the range of θ less than approximately $0.5 \text{ m}^3/\text{m}^3$. The Topp equation is considered fairly robust for applications in soils with $\theta < 0.5 \text{ m}^3/\text{m}^3$, with textures ranging from clay to sand (Jones et al., 2002; Noborio, 2001; Vaz et al., 2013). While this captures the range of θ in our experiments, our substrate textures were much coarser than standard application conditions. In addition to soil type, factors such as salinity and temperature affect the relationship between dielectric and volumetric water content (Saito et al., 2013; Schwank and Green, 2007; Wraith and Or, 1999), and are not accounted for in the factory-recommended calibration equations. Lastly, because we installed the probes through the ~ 1 cm thick PVC sidewall of our mesocosms, rather than directly into soil, a portion of the probe rods was not directly in contact with the substrate. Since the resulting TDR reading is an average of the soil moisture from along the entire length of the probe rods, use of the standard calibration equation would have underestimated the volumetric water content. To ensure the accuracy of our sensors, we performed our own substrate-specific calibrations.

We calibrated our TDR sensors across the soil moisture gradient, from saturated to dry, using standard gravimetric methods and an empirical model fitting approach. For Fine textured substrate, we calibrated the sensors in-situ at the end of the experiments by taking soil cores from

¹ Technically the probes measure the **real relative apparent bulk dielectric permittivity**, often denoted ϵ . This is a measure of the “real” or energy storage component of permittivity “relative” to the permittivity of free space, calculated from the “apparent” length of the probe rods, and measuring the “bulk” or total permittivity of the air-water-soil system (Campbell Scientific, pers. comm.).

around a subset of probes. The higher hydraulic conductivity and larger grain size of Coarse textured substrate prohibited sampling via soil coring. Therefore, we performed these calibrations in the lab with a probe installed in a shortened pot set on top of a mass balance and filled to a known volume. We also used this lab setup to obtain a gravimetric measure of θ at saturation for the Fine substrate, since liquefaction prohibited obtaining accurate core samples in-situ.

Our calibration resolves accuracy issues related to effects of rod length due to installation, soil type, and salinity; however we did not directly calibrate for temperature effects. We did observe diurnal patterns in TDR measurements that corresponded with measured air temperature. However, we deemed it unnecessary to deal with additional complexities of temperature-related calibration (see Saito et al. 2013 for a recent simplification procedure) because (1) the fluctuations were very small and similar across substrate textures relative to the broader drying trend of interest, typically $\sqrt{K_a} \pm 0.05$ during saturated period, to < 0.02 at drier water content; (2) we maintained steady experimental drying so there were no additions of water for which we needed to compensate; and (3) our analyses involved only relative comparisons and all mesocosms experienced the same diurnal temperature fluctuations. Instead we used a seasonal-trend decomposition procedure described in more detail in the Soil Moisture Data Processing section below.

In-situ sampling of fine texture substrate

In-situ probes were located at 10 cm, 30 cm, and 70 cm depths within three “No Plant” Control pots, two from the 2011 experiment, and one from the 2010 experiment. We pooled data from the 9 probes to develop our calibration curve. We calibrated at 5 moisture levels across the soil moisture gradient. We laid the pots on their sides and cut them open longitudinally on one side to access the entire soil column (i.e., to obtain soil cores at the same time and location along the soil column as the probe measurements). Due to logistical constraints, the driest condition was represented from soil cores taken from the tops of the pots and calibrated to the shallowest probes (10 cm depth). Similarly, sampling for the wettest condition was limited to the two deepest probes (6 total). The intermediate soil moistures were calibrated from sampling at all 9 probes. Because the sand liquefies at saturation, we could not use the soil coring method to calibrate the saturated condition in-situ. Instead, we obtained a gravimetric measure of saturated water content in the lab using the set up described for Coarse substrate, and assigned this to the mean of dielectric constant readings logged from the in-situ probes at saturation.

Cores were 2.25 cm diameter X 10 cm long for a total volume of 39.76 cm^3 . Cores were taken near each probe, concurrent in time with a TDR reading. We were careful to avoid disturbing the soil immediately surrounding the probe so that subsequent readings would be unaffected. The sampling radius (i.e., radius of electromagnetic field surrounding the probe rods) is relatively small (measured as 2.2 cm for a similar probe; Vaz et al. 2013). Three cores were taken for the drier ($\sqrt{K_a} < 2.2$) moisture levels, and four cores for wetter ($\sqrt{K_a} = 3-3.5$) moisture levels. In order to sample the complete pot cross-section (pots were 25.4 cm diameter) and to account for any moisture differences due to the horizontal positioning of the pots, we typically took at least 2 cores from the same hole (0-10 cm, 10-20 cm). These cores were then immediately placed into a

Ziploc baggie and sealed. Samples were weighed, oven dried to constant weight at 100°C, and then re-weighed.

Volumetric water content (θ) was calculated as:

$$\theta = \frac{m_{wet} - m_{dry}}{\rho_w \times V_{core}},$$

the difference in mass between the wet and dry sample, divided by the density of water (1g/cm³) times the volume of the sampled core (38.76 cm³). This yields a dimensionless ratio, typically reported as m³/m³.

Lab calibration of coarse texture substrate

The higher hydraulic conductivity and larger grain size of the Coarse (gravel/sand) texture substrate meant it could not be sampled by soil coring. Therefore, we performed the calibration in the lab with a probe installed in a shortened pot that we set on top of a mass balance. We packed the calibration pot with oven dried substrate, using the same gravel:sand ratio (70:30 by weight) and the same method of packing as was used to fill the mesocosms (e.g., tapping with rubber mallet, repeated flooding/draining). The pot was the same diameter as the mesocosm pots (25.34 cm). We filled it to a depth of 8 cm, and installed the probe in the center (i.e., with 4 cm of substrate above and below), for a total volume of ~ 4 Liters. This was a little less than recommended by Benson and Wang (2006), but similar to that used for cross-calibration of several electromagnetic soil moisture sensing systems in a recent review (2.3 L; Vaz et al. 2013), and 14 times more than the estimated sampling volume of the probe (approximately 0.287 L; Vaz et al. 2013).

Just as in the mesocosms, the calibration pot was flooded from the bottom up. We recorded the weight of water coincident in time with a TDR reading, and repeated the flooding/draining process twice, for a total of 34 moisture levels from saturated to dry.

We then repeated the calibration using gravel-only, in order to account for settling of sand that occurred in the upper portion of some of the mesocosm pots during the experiment. This resulted in several of the 10 cm depth probes in Coarse substrate registering very high dielectric constants when saturated, and we wanted to ensure that the relationship between dielectric and volumetric water content accurately represented these high values. Because the gravel-only medium was so porous, the soil moisture was either saturated or dry, thus we included only three additional points (2 dry, 1 saturated) to our overall calibration function. The effect of adding these data to our gravel:sand calibration was minimal.

Model fitting of substrate-specific calibration curves

We fit several functional forms to our substrate-specific calibration data, and chose the model that gave both the best fit (as measured by adjusted r², to account for differences in number of parameters) and maintained a positive slope throughout the range of dielectric constants measured (i.e., no local maxima, so volumetric water content always increased with increasing dielectric constant).

For the fine texture substrate, the best fit was a linear fit to the square root of the dielectric constant (adjusted $r^2=0.84$), similar to the Ledieu equation (Figure D-1). The calibration curve overestimates θ at saturation, compared to actual saturated water content measured in the lab. However, for the purposes of the metrics extracted for the analyses described in the main body of this paper, the absolute value of θ at saturation has no effect. Thus we used the calibration function:

$$\theta = 0.1293\sqrt{K_a} - 0.156,$$

where θ is the volumetric water content, and K_a is the apparent dielectric constant measured by the sensor.

For the coarse texture substrate, the best fit given our criteria was a quadratic fit to K_a (adjusted $r^2=0.99$) (Figure D-2). Thus, the conversion used to relate measured dielectric constant to volumetric water content for the coarse substrate was:

$$\theta = (-1.459 * 10^{-4})K_a^2 + (1.767 * 10^{-2})K_a - (3.047 * 10^{-2})$$

The factory standard calibration equations would have underestimated the volumetric water content of the Fine substrate (Figure D-1), and overestimated it for the Coarse substrate (Figure D-2).

Soil moisture data processing

We removed obvious outliers from logged data that were well outside the range typically recorded ($1 < \sqrt{K_a} < 5$). Next we removed outliers from the diurnal temperature-driven fluctuation in dielectric constant measurements. We first quantified a threshold value as the maximum deviation from a one-hour moving mean during a time period when soil moisture was not changing rapidly, and where the probe was not obviously malfunctioning. This stable time period was different for each probe, but was at least 1 month long, and typically 2 months from mid-August to mid-October when the pots were slowly drying. We then removed outliers that were > 2 times this threshold value (typically $\sqrt{K_a} \pm 0.03$ to 0.05) from a one-hour moving mean over the entire time series.

We then used linear interpolation to fill any missing values, and a seasonal-trend decomposition procedure based on loess smoothing (Cleveland et al. 1990) to remove the high frequency variation driven by diurnal temperature fluctuations (stl function in “stats” package of R). The trend data were converted to volumetric water content using our substrate-specific calibration curves and used to generate all subsequent indices of soil moisture.

Additional rationale and methods details for water stress threshold index ($\theta_{0.1}$)

As a low-elevation species adapted to living in wet environments, *Populus fremontii* is known to be particularly vulnerable to cavitation, showing a steep loss of hydraulic conductivity beginning at xylem pressures below approximately -1.0 MPa, 50% loss at approximately -1.5 MPa, and catastrophic blockage at xylem pressures ranging from -2 to -2.25 MPa (Leffler et al., 2000; Pockman and Sperry, 2000; Pockman et al., 1995). Cottonwoods also tend to maintain xylem water potentials very close to their catastrophic cavitation threshold, suggesting that even a

small, sudden drop in soil moisture can result in catastrophic loss of xylem function (Leffler et al., 2000; Pockman et al., 1995; Tozzi et al., 2013). Lacking published comparisons of soil water potential at given xylem potentials for *P. fremontii* as a guide, we opted for a conservative approach in developing a water stress threshold based on soil water potential.

We converted our measured soil volumetric water content to soil water potential using the van Genuchten pedotransfer function (PTF) (van Genuchten, 1980) and estimating the necessary water retention parameters for our specific soils using the Rosetta model (Schaap et al., 2001) with percent sand, silt, clay, and bulk density as predictors (Figure D-3). We compared these substrate-specific PTFs to those of the general “sand” texture class provided by ROSETTA, using both the van Genuchten and Campbell (1974) PTF equations. We converted from van Genuchten to Campbell hydraulic parameters following Sommer and Stockle (2010). Given the coarse textures and negligible clay content of our two substrates compared to more typical soils, there was very little difference in the results of our substrate-specific PTFs at low soil volumetric water content. The Campbell equation did yield a different absolute difference in the relationship between volumetric water content and water potential at low soil moisture, but the form was similar, with a steep decline at pressures < -0.01 MPa. Based on these PTFs, we selected $\theta_{0.1}$ as a conservative threshold where the negative pressure or suction required to remove an additional increment of volumetric water content from the soil goes from linear to exponential, greatly increasing the risk of cavitation and loss of hydraulic conductance. We calculated the number of days spent above this threshold as an index of time to water stress, and used it as a predictor variable in our logistic regression modeling (see main text).

TDR PRECISION

We tested the precision of the TDR by taking 5 readings in succession (within a few minutes) from 12 randomly selected probes, under dry, stable moisture conditions. These probes were installed in-situ, at 10cm, 30cm, and 70cm depths in four different pots (3 fine, 1 medium texture). The range of differences in readings from any given probe was 0.008 to 0.036 La/L, with an average range of 0.02175. Using the calibration curve, this is equivalent to an average of 0.0025 m³/m³. Mean standard deviation was 0.009 La/L, equivalent to 0.0013 m³/m³ volumetric water content. Mean precision (SE) was 0.004 La/L, equivalent to 0.00057 m³/m³ volumetric water content.

Figure D-1. TDR soil moisture calibration curve for Fine texture substrate. Open circles are gravimetric data from soil core sampling. Solid black square indicates our estimate of saturation, based on lab measurement of θ at saturation and mean $\sqrt{K_a}$ for all 9 calibration probes at saturation. The black line includes all points, and is the final calibration curve used. The dashed lines show the standard Topp and Ledieu calibration equations for reference. All of our data to which we applied this calibration curve were $< 22 K_a$.

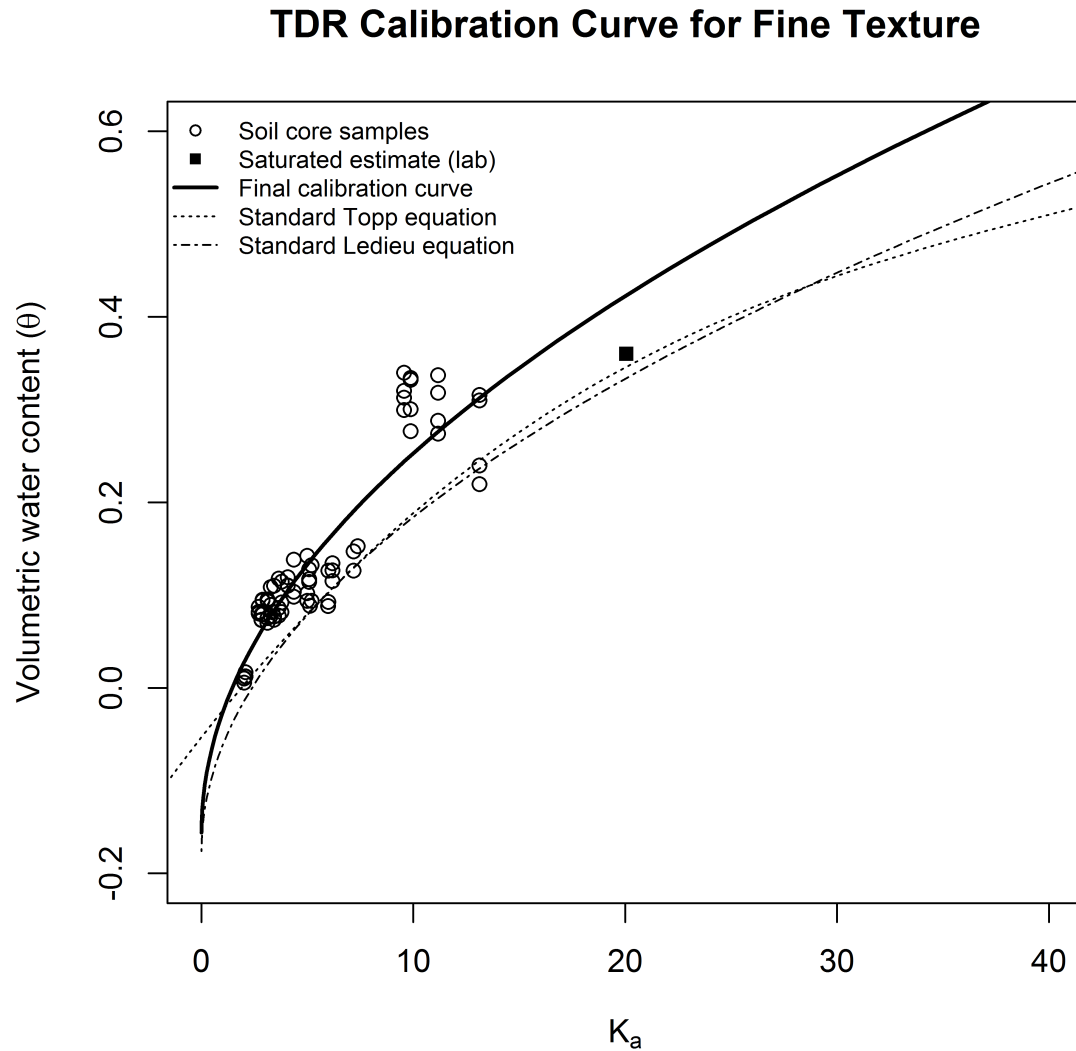


Figure D-2. TDR soil moisture calibration curve for Coarse texture substrate. We included gravel-only calibration points to account for settling that occurred at the top of some pots, which resulted in very high dielectric constant readings at saturation. See text for more details. The dashed lines show the standard Topp and Ledieu calibration equations for reference.

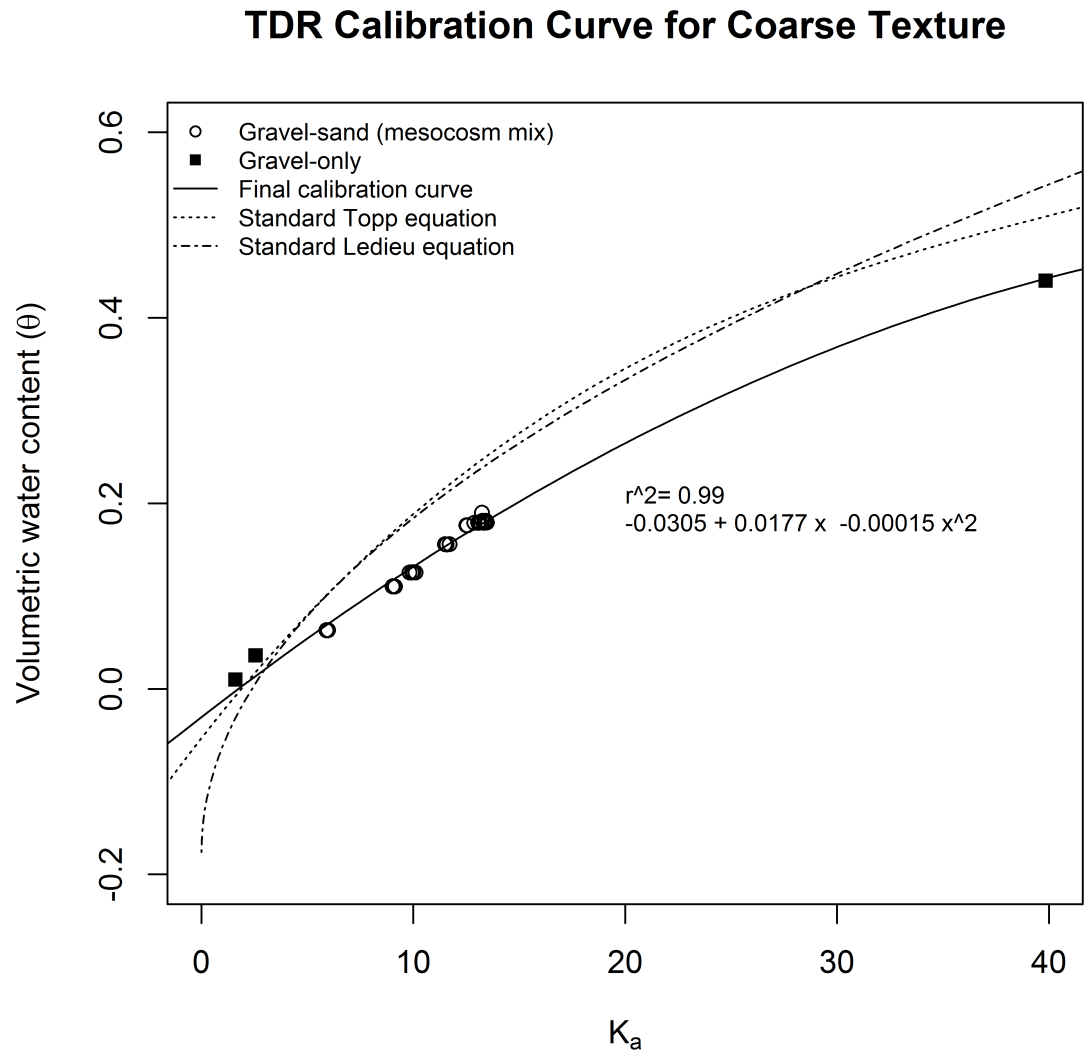
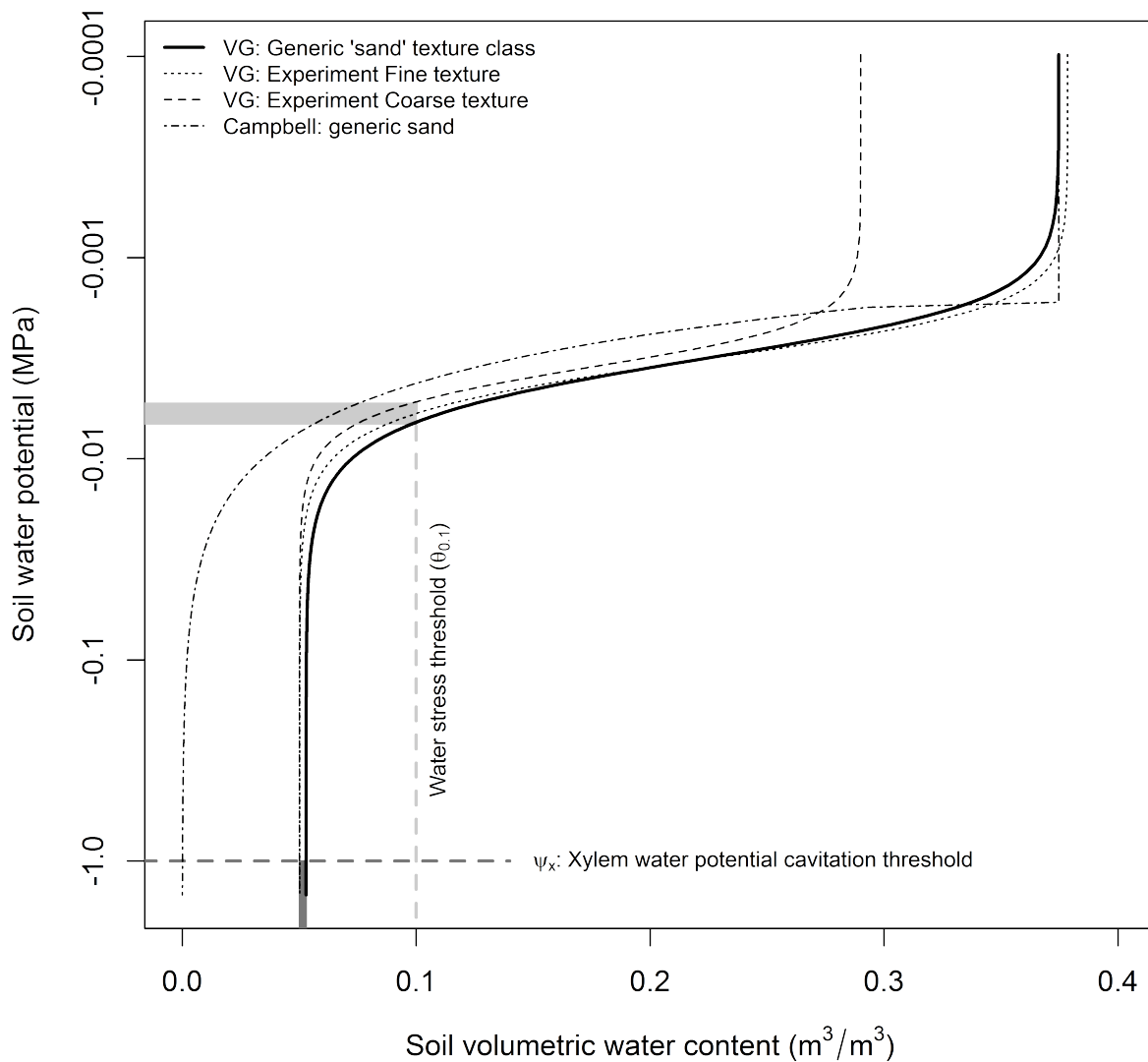


Figure D-3. Pedotransfer functions (PTF) used to convert volumetric water content to water potential, for the purposes of determining a water stress threshold. We show van Genuchten (VG) functions for the generic sand texture class, as well as those developed specifically for our Fine and Coarse textures, estimated with parameters from the ROSETTA model (Schaap et al. 2001) with percent sand, silt, clay, and bulk density as inputs. Campbell (1985) PTF for the generic sand texture class is shown for reference, in which we converted from van Genuchten to Campbell hydraulic parameters following Sommer and Stockle (2010). Xylem water potentials (Ψ_x) reported from the literature show steep loss of hydraulic function beginning at < -1 MPa (see text).



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CHAPTER 2 | Effect of light availability on survival and growth of *Populus fremontii* along a moisture gradient

ABSTRACT

Trade-off hypotheses are used to explain species coexistence, succession, or species-specific adaptation to a particular niche. Plant species are often categorized as having either a colonizer or competitor strategy, based on the assumption that physiological and energetic trade-offs limit the ability of a single species to dominate under all environmental stresses and resource conditions. The prevailing view of cottonwoods (*Populus* spp.) is that they are excellent pioneers. Traits that confer rapid and successful colonization of newly exposed surfaces, including small seeds and fast juvenile growth rates, represent a trade-off in resource use efficiency that limits success under resource-poor conditions. The well-known interspecific trade-off of high-light growth/ low-light survival leads to the common assumption that pioneer trees are shade intolerant. Yet how is it that a species with such strong colonizer traits can recruit so successfully into abandoned channels, which provide seedbed conditions of combined shade and moisture that support species with much stronger competitive traits? I examined this question using a shade-cloth mesocosm experiment, in which I considered interactive gradients of moisture and light. In dry ecosystems, sunlight can be considered both a resource and a stress, with shading reducing evaporative demand by maintaining a cooler understory microclimate. I found that shading resulted in reduced vapor pressure deficits and higher soil moistures, and a strong positive effect on first year cottonwood seedling survival. However, seedlings that survived to the end of the experiment showed decreased final biomass and root growth in shade. High survival, but low growth in shade, and low survival with high growth in sun suggests cottonwoods are much more plastic in their shade tolerance than has been previously assumed. The positive effect of shade on survival was observed regardless of soil moisture availability, whereas the negative effect of shade on growth was much stronger in wetter conditions, suggesting that soil moisture is the dominant limiting resource for seedling growth. I conclude that their high moisture requirement, along with their plasticity in shade tolerance, is what allows cottonwoods to successfully establish in abandoned channels. I suggest that lack of understory recruitment along the active channel has more to do with the fact that vegetated areas are typically higher and drier as a result of biogeomorphic feedbacks.

INTRODUCTION

The observed pattern of vegetation change following disturbance is typically that of widely-dispersing, fast-growing colonizer species being replaced by longer-lived, slower growing, more tolerant, or better resource-competitors (Connell and Slatyer, 1977; Grime, 1977; McCook, 1994; Tilman, 1990, 1985). Thus, plant species are often categorized as having either a colonizer

or competitor strategy based on the assumption that physiological and energetic trade-offs limit the ability of a single species to dominate under all environmental stresses and resource conditions (Bazzaz, 1979; Christensen, 2014; Connell and Slatyer, 1977; Huston and Smith, 1987; Tilman, 1990). However, the reality is often not so cleanly dichotomous (e.g., Muller-Landau, 2010; Seifan et al., 2013). As I described in Chapter 1, an interesting example are the cottonwood trees (*Populus* spp.) that dominate near-stream habitat along rivers in North America.

The prevailing view of cottonwoods is that they are disturbance-dependent pioneers, with traits that confer rapid and successful colonization of newly exposed surfaces (Catford and Jansson, 2014; Corenblit et al., 2014; Karrenberg et al., 2002; Lytle and Poff, 2004). However, because they are small-seeded, with seedlings rarely found in mature forest understory or intermixed with herbaceous vegetation (Hosner and Minckler, 1963, 1960; Johnson et al., 1976; Peterson, 2000), they are considered shade-intolerant and, more generally, poor resource competitors (summarized in Braatne et al., 1996; Burns and Honkala, 1990; Karrenberg et al., 2002). Much of our understanding of cottonwood establishment dynamics is based on research focused on the active river channel, where the flood regime is the primary driver of vegetation dynamics (Mahoney and Rood, 1998; Merritt et al., 2010; Scott et al., 1996; Stella et al., 2006; Stromberg et al., 2007). However, cottonwoods also recruit into abandoned channels, which experience greatly moderated disturbance regimes. Temporal changes in abandoned channels result in a shift toward a more physically stable environment (e.g., reduced frequency and intensity of flooding, lowered shear stresses, increased fine-sediment deposition) (Constantine et al., 2009; Gagliano and Howard, 1984; Piégay et al., 2000; Shields and Abt, 1989). As a consequence, abandoned channels support a more competitive environment for plant establishment than typically found along similar relative elevations of the active channel (Stella et al., 2011; Chapter 1). On regulated river systems where altered hydrology has significantly affected the processes necessary to support successful establishment along the active channel, abandoned channels can represent an important alternative location for establishment of pioneer trees (Stella et al., 2011). But the documented success of cottonwoods in abandoned channels raises an interesting question: How is a stereotypical colonizer species able to establish so successfully in the more competitive environment of abandoned channels?

The colonization-competition hypothesis suggests that pioneer species are usually not shade-tolerant (Rees et al., 2001). The trajectory in upland forests is strongly influenced by light availability, particularly in tropical and temperate systems (Canham et al., 1994; Kobe et al., 1995; Valladares and Niinemets, 2008; Valladares, 2003). In these ecosystems, species shade-tolerance can be the single-best predictor of the spatial pattern of seedling distributions and of species replacement through time (e.g., Canham et al., 1994; Pacala et al., 1994). Braatne et al. (1996) noted that because cottonwood seeds lack an endosperm, seedlings are highly dependent on photosynthate, and thus access to full sunlight is critical for sustained growth. At the same time, cottonwood recruitment in semi-arid environments is known to be limited by water availability (Amlin and Rood, 2002; González et al., 2010; Mahoney and Rood, 1992; Segelquist et al., 1993; Stella et al., 2010). For example, in my initial experiment (Chapter 1), soil moisture availability was the primary determinant of cottonwood seedling survival. In situations with multiple limiting resources, life history strategies can be more complicated than a suite of binary trade-offs in traits (Craine, 2009). Gradients of light and moisture availability are intrinsically

linked, resulting in interacting effects on plants (Niinemets and Valladares, 2006; Valladares, 2003). For example, in dry ecosystems, there is often a positive effect of shade, attributed to its ameliorating effect on understory microclimate (reduced thermal stress and evapotranspiration) (Holmgren et al., 1997). The value of shading is predicted to increase with increasing levels of moisture stress (Brooker and Callaghan, 1998; Callaway and Walker, 1997).

For cottonwoods in the arid West, Cooper et al. (1999) acknowledged the lack of clarity in the interactions between water availability and shading, and recommended further study. As I discussed in Chapter 1, the difficulty in identifying whether plants are light- or moisture-limited is due to (1) the physiological interaction between water stress and reduced photosynthetic capacity resulting from stomatal closure (Valladares and Niinemets, 2008; Valladares, 2003), (2) the fact that light can be both a resource and a stress (photo-oxidation and heat) in water-limited situations (Walters et al., 2002), and (3) study design limitations—vegetation removal experiments remove both above- and below-ground competition, and shade cloth experiments on cottonwoods have generally not accounted for co-occurring changes in soil moisture.

My present study seeks to quantify the competitive ability of cottonwood seedlings by examining the direct (light-limiting) and indirect (microclimatic) effects of shade under varying moisture conditions on cottonwood seedling survival and growth. My initial study established the capacity of cottonwoods to tolerate the presence of interspecific herbaceous competitors (Chapter 1) that dominate abandoned channels. However the design of the study could not distinguish whether this tolerance was due to the positive effect of shade on the plant water balance or the ability of cottonwood seedlings to compete for scarce resources. In order to understand whether interspecific competitors were affecting cottonwood survival by limiting above- or below-ground resources, I needed to examine the effect of shading on cottonwood seedlings in the absence of interspecific competition for below-ground resources.

I tested first year seedling survival and growth because juvenile survivorship is a major demographic bottleneck for trees in general (Clark and Clark, 1992; Connell, 1989; Kobe et al., 1995), and first-year growth and survival is particularly critical for riparian trees (Lytle and Merritt, 2004). I focused the study at the higher end of the moisture gradient because (1) I already know that low soil moisture is a strong driver of first-year cottonwood seedling mortality (Chapter 1; Mahoney and Rood, 1998; Stella and Battles, 2010; Stella et al., 2013), and (2) I wanted to recreate the moister field conditions observed in our gradient of abandoned channel field sites (Chapter 1). I also recognized the trade-off between light as a resource and as a contributor to moisture stress, and directly measured the influence of light on microclimate and soil moisture. Because I were interested in the implications for population dynamics, and seedlings germinate in variable densities in the field (Braatne et al., 1996; Shafroth et al., 2002; Sher et al., 2002), I tested the density-dependence of the shading response. I examined these interactions again using a mesocosm experiment (described in Chapter 1) tracking seedling survival and growth over a summer growing season.

I tested the following predictions: (1) shading results in higher soil moisture conditions by reducing air temperature, which lowers vapor pressure deficits and evapotranspiration, (2) when soil moisture is limiting, the effect of shading should be positive, resulting in higher survival in shade than in sun, (3) when soil moisture is abundant, sun becomes the limiting resource, so

survival should be higher in sun than in shade, and (4) the density-dependence of these responses should be a similar direction of response, but with higher magnitude differences at higher density (more intense intraspecific competition). My hypotheses focused on seedling survival, and the growth pattern of survivors was used to interpret how seedlings survive (e.g., allocation trade-offs), and as a predictor of subsequent survival (bigger seedlings have more reserves so tend to do better in following years).

METHODS

Experimental design

I conducted the mesocosm experiment in the same facility as described in Chapter 1. The experiment ran from early July through September 2011. The region experiences a Mediterranean-type climate, with warm, dry summers, and cool, wet winters. Air temperature during the experiment averaged 17.8°C (range 7.0–36.9°C). Mean daytime temperature and vapor pressure deficit were 21.3 °C and 1.38 kPa (range 0.01–5.45 kPa), respectively. Mean afternoon (12–4 pm) vapor pressure deficit was 2.36 kPa. The area averages 62.5 cm annual rainfall occurring primarily from late October through April. There was one day during the last week of the study with measurable precipitation (0.8 mm); I covered the platforms with clear plastic during this event.

Mesocosm pots were as described in detail in Chapter 1—25.4 cm diameter × 120 cm tall opaque PVC pipe, capped and connected to a water table control reservoir. A total of 100 pots were distributed among eight platforms. Each platform measured 2.4 m X 1.2 m in area, was leveled to ensure water table consistency among pots ($\pm < 1$ cm), and held 12-13 pots connected to the platform's water control reservoir. For logistical reasons, drawdown × sun treatments were blocked by platform, and were randomly assigned. Four platforms received water table drawdown rates of 2 cm/day, and 4 had a drawdown rate of 3cm/day. Because cottonwood seedlings are known to be very sensitive to seasonal drought (Chapter 1; Stella et al., 2010), I selected two milder recession rates that would be steep enough to induce measurable differences in soil moisture, but would keep moisture stress relatively low overall. Within each drawdown rate, one platform remained at full sun, and the others were covered (top and sides) with standard horticultural shade cloth of 30, 50, and 70 percent shade. This range corresponds to light conditions measured in abandoned channels in the field across a range of time since abandonment (Chapter 1: Figures 2, A-3, and A-4). Within each platform, pots were planted with alternating high (1578 seedlings/m²) and low (789 seedlings/m²) density of cottonwood seedlings, corresponding to densities observed in the field (Shafroth et al., 2002; Sher et al., 2002), and planted in my initial experiment (Chapter 1).

I used the same fine sand substrate ($D_{20} = 0.16$ mm, $D_{50} = 0.23$ mm, $D_{80} = 0.49$ mm) used in the first year experiment described in Chapter 1, which was similar to the grain size distribution found in our abandoned channel field sites (≥ 15 years since abandonment) and at the downstream (depositional) end of our point bar field site (Figure 1-1). Source material, pot filling and compaction were the same as described in Chapter 1.

Cottonwood seed collection and establishment

In June 2011 I collected partially opened cottonwood catkins from three different restoration sites within our field study area near Hamilton City, California. Collections were made from the lower 8 m of a total of 12 source trees. I stored catkins in paper bags and allowed them to air dry at room temperature for 4–5 days until any unopened catkins had burst. Seeds were then separated from cotton, homogenized with equal weight from all source trees, and planted within 2 weeks of collection. Average germination after one week was >90%.

Beginning one week after planting, pots were thinned so that half the pots on each platform began the experiment at a low density of 40 seedlings/pot (789 seedlings/m², or 1 seedling per 12.7 cm²), and the other half at high density of 80 seedlings/pot (1578 seedlings/m², or 1 seedling per 6.3 cm²). All seedlings were individually tagged with small, flexible plastic bands placed around (but not touching) the base of the stem. There were 720 seedlings in each drawdown × sun combination (platform), for a total of 5,760 seedlings alive at the start of the water table drawdown.

The water table was kept at 3 cm below the substrate surface during germination and establishment of cottonwood seedlings to ensure adequate surface moisture. Just before the start of the experiment, I raised the water table to 1-cm depth, and then manually lowered the water in the reservoir at the appropriate rate each day for the duration of the active drawdown period (39 days at 3cm/day; 58 days at 2cm/day). Monitoring and maintenance of the water table was the same as described in Chapter 1.

Data collection

To account for microclimatic effects of shading, I tracked air temperature on each platform, as well as relative humidity at the site using continuously logging HOBO sensors (15-minute logging intervals). Soil moisture was tracked in a subset of 12 pots (12% of total) using time-domain reflectometry (TDR100-based system with CS630 probes and CR800 data logger, Campbell Scientific Inc., Logan, Utah), as was described in Chapter 1 (also see Chapter 1, Appendix D for calibration details). Probes were installed horizontally through the wall of the pot at 10-cm, 30-cm, and 70-cm depths. I instrumented one high and one low density pot in each of the following treatment combinations: 2cm/day drawdown × full sun and 50% shade cloth; 3cm/day drawdown × full sun, 30%, and 70% shade cloth. In addition, I instrumented a negative control (substrate but no seedlings) for each drawdown and full sun condition.

I monitored survival of each individually tagged cottonwood seedling every three days for a total of 84 days. Seedlings were considered dead when both the leaves and the stem were brown and withered. I measured shoot height of seedlings every 6 days for the duration of the experiment, from soil surface to the base of the apical bud.

I harvested final above- and below-ground biomass of a subsample of seedlings that survived to the end of the experiment. I clipped individual stems and leaves for 64% of the surviving population, by harvesting 8 pots on each platform (3 high density, and 5 low density pots). In a subsample of the low density pots (2 pots/platform), I also collected individual seedling root biomass and measured root length. I laid pots horizontally on top of a large 1-mm mesh sieve,

cut them open longitudinally, and carefully separated roots with water. I was unable to separate individual seedlings in the higher density pots because roots had become intertwined. All biomass samples were oven dried to constant weight at 65 °C.

Quantifying environmental gradients

To understand the effect of the light and moisture gradients on cottonwood growth and survival, I calculated metrics of soil moisture, light availability, and vapor pressure deficit (to account for the shade-cooling effect).

Soil moisture

Soil moisture data from TDR probes were processed following similar methods of Chapter 1. First, I calculated pot-averaged soil moisture through time by vertically integrating over the 3 instrumented depths using a root-weighted averaging approach (Baldocchi et al., 2004; Chen et al., 2008). The vertically averaged index ($\langle \theta \rangle$) was determined by:

$$\langle \theta \rangle = \frac{\int_0^z \theta(z) dP(z)}{\int_0^z dP(z)}, \quad (1)$$

where $\theta(z)$ is a quadratic fit to the measured volumetric water content as a function of depth in cm (z). $P(z)$ is the cumulative distribution of root mass from the surface to depth z , and follows the asymptotic model $P(z) = 1 - \beta^z$ (Gale and Grigal, 1987). β values were determined from final root lengths of a subset of cottonwood seedlings grown at low density for each of the light/drawdown treatment combinations ($n= 60-79$). I assumed that 95% of the roots were within 2 standard deviations of the mean root length (Table 1). β values ranged from 0.968 to 0.945, which were similar to those used in the first experiment (Chapter 1) and those reported for temperate deciduous forest and grassland (Jackson et al., 1996). Lastly, the cumulative probability density sums to 1, thus the denominator is equal to 1.

Using this depth-averaged soil moisture time series, I then calculated the two best soil moisture metrics determined from Chapter 1 for each of the 12 instrumented pots: (1) cumulative soil moisture, numerically integrated over the 84 day experimental period (θ_{cum}), and (2) days to a water stress threshold of $\theta_{0.1}$. For details on the rationale and calculation of these metrics, see Chapter 1. I then extrapolated soil moisture metrics from the 12 instrumented pots to all pots by fitting a linear model for each of the two metrics that included drawdown rate, percent available sunlight (Table 2), and initial pot density as predictors ($R^2 > 0.90$).

Light availability

To calculate percent available sunlight for each platform, I multiplied percent light from the shade cloth treatment times the fraction total transmitted light from hemispherical photos taken on each platform (described in Chapter 1) (Table 2). This method estimates light availability due to platform location within the site (e.g., any differences in shading from neighboring buildings, trees, and topography), as well as the direct shade cloth treatment. Percent available sunlight was used as our metric for all subsequent analyses.

Vapor pressure deficit

Vapor pressure deficit was calculated for each platform (drawdown × shade cloth treatment) assuming well mixed air. For site-level relative humidity, any missing data was filled with linear interpolation. There were no gaps in platform-level temperature data. Following recommendations from Campbell and Norman (1998), I used the Tetens formula (Buck, 1981) with constants for environmental biophysics applications to calculate saturation vapor pressure at a given air temperature ($e_s(T_a)$), with temperature in degrees Celsius.

$$e_s(T_a) = 0.611 e^{\frac{17.502T_a}{T_a+240.97}} \quad (2)$$

I then used relative humidity (h_r), expressed as a fraction, to calculate vapor pressure deficit (vpd) for each logged time point. Saturation vapor pressure and vapor pressure deficit are in units of kilo pascals (kPa).

$$vpd = e_s(T_a)(1 - h_r) \quad (3)$$

I then calculated metrics for average daily minimum, mean, and maximum vapor pressure deficit, as well as average daily afternoon (12-4pm) minimum, mean, and maximum vapor pressure deficit to capture dynamics during the warmest, driest portion of the day.

Data Analysis

To quantify the effect of sun on microclimate, I regressed platform-level metrics of average daily maximum and minimum air temperatures and vapor pressure deficits measured across the sun gradient for the 84 day duration of the experiment. I used linear regression to determine if the slope was significantly different from zero. To quantify the effects of drawdown rate and sunlight on soil moisture, I regressed the cumulative volumetric water content metric (θ_{cum}) measured at 10cm depth against percent available sun and drawdown rate for all pots instrumented with soil moisture probes.

I modeled temporal patterns of *P. fremontii* seedling survival using nonparametric Kaplan-Meier estimations to account for censored observations, using the “survival” package (Therneau, 2014) in R statistical software (version 3.1.2, R Core Team, 2014). To visualize temporal patterns, I used the eight environmental treatment combinations of drawdown × sun. I lumped low and high initial seedling density because Kaplan-Meier confidence intervals were largely overlapping, indicating no significant density-dependent differences through time.

I quantified temporal trends in seedling height growth with linear mixed effects models (Pinheiro and Bates, 2000) The response variable was the mean height of live seedlings in each pot at the time of measurement. Explanatory variables included: day of experiment (linear and quadratic fits), initial seedling density, percent available sun, cumulative volumetric water content (θ_{cum}), and the interaction between sun and soil moisture, as well as reduced forms of the model down to the base model of day + random pot effect. Because of differences in the units of explanatory variables, I centered and standardized all variables prior to model fitting to simplify

interpretation of effect sizes. Model selection was based on Akaike's information criterion (AIC), as described in detail below. .

Next, I modeled probability of survival to the end of the experiment as an estimate of over-summer survival using the logistic function:

$$\pi(x) = \frac{e^{g(x)}}{1 + e^{g(x)}} \quad (4)$$

where $\pi(x)$ is the survival probability and $g(x)$ is a linear function of predictor variables (Hosmer et al., 2013). All models included the base model of intercept + covariate of initial seedling height (i.e., height just prior to start of drawdown), to account for individual differences in growth that developed during the stable establishment period. All explanatory variables were again centered and standardized prior to model fitting, and included initial seedling density, a single metric for soil moisture, percent available sun or vapor pressure deficit (but never both in the same model, as sun and vapor pressure deficit metrics were highly correlated), and the interaction between soil moisture and sun/vapor pressure deficit. I tested two different soil moisture metrics, one metric of percent available sun, and six different vapor pressure deficit metrics (see Quantifying Environmental Variables for details), for a total of 14 full models. Including reduced forms down to the base model, there were 99 models in the candidate set. Interactions between soil moisture and sun/vapor pressure deficit were only included if the main effect was in the model (i.e., adhering to the principal of marginality; Venables and Ripley, 2003). I also ran the logistic models on survival in the subset of pots that were harvested for final below-ground biomass. The density term was omitted (only low density pots were harvested for roots), so there were only 37 models in the candidate set.

For each model, I calculated Akaike's information criterion (AIC), differences in AIC values relative to the model with the lowest AIC (Δ AIC), and AIC weights (w_i). Δ AIC and the AIC weight are measures of the relative difference in the strength of evidence for each model. The model with the lowest AIC value is considered the best Kullback–Leibler estimated model for the data given the candidate set of models, and models $< 2 \Delta$ AIC have substantial empirical support (Burnham and Anderson 2013). Akaike weights (w_i) were calculated to normalize the strength of evidence for a given model and can be interpreted as the probability that a given model i is the best Kullback–Leibler model for the data given the candidate set of models (Burnham and Anderson, 2013). I also calculated area under the receiver operating characteristic curve (ROC) as a threshold-independent measure of model discrimination (i.e., the ability to distinguish live and dead seedlings), where 0.5 indicates no discrimination, 0.7 – 0.8 acceptable discrimination, and >0.8 excellent discrimination (Hosmer et al., 2013). Lastly, I calculated the variance inflation factor (VIF) to check for evidence of problematic multicollinearity, using a VIF > 10 threshold (Neter et al., 1996).

Using linear regression, I modeled final growth metrics from the subset of harvested pots as a function of the same suite of centered and standardized explanatory variables used for the end-season survival models. I included surviving seedling density as a measure of density-dependence, as harvested pots were all from low initial seedling density. The final (end-season) growth response variables included total biomass, shoot biomass, root biomass, shoot:root ratio,

shoot height, and root length. All biomass metrics were for dry biomass. Similar to the logistic regression models, I calculated AIC, Δ AIC, and AIC weights (w_i) for the purposes of model comparison. I also calculated adjusted R^2 as a measure of goodness of fit. All analyses were performed in R (version 3.1.2, R Core Team, 2014).

RESULTS

Effect of drawdown rate on soil moisture

As was my goal, the rate of drawdown had a measurable effect on soil moisture. The slower, 2cm/day drawdown rate maintained higher soil moistures for longer than the faster, 3cm/day drawdown rate (Figure 1). For example, it took almost twice as long for soil moisture to reach the water stress threshold of $\theta_{0.1}$ in the 2cm/day drawdown (41 ± 0.4 days) relative to the 3cm/day drawdown (22 ± 0.3 days).

Effect of shading on microclimate and soil moisture

With increasing shade, air temperatures measured on the platforms were cooler during the day, and slightly warmer at night. Maximum daily temperatures increased with increasing sun (slope = 0.09, $p \ll 0.0001$), with over a 4 degree difference in average daily maximum temperatures between the shadiest and sunniest treatments (Figure 2). The difference between daily maximum and minimum temperatures also increased with percent available sun (slope=0.1, $p \ll 0.0001$), ranging from 16 degrees in the heaviest shade to 21 degrees in full sun. Vapor pressure deficits were thus similarly correlated (Figure 2), with higher daily maximum deficits under increasing sun (slope=0.016 kPa/percent sun, $p \ll 0.0001$). There was up to a 1 kPa difference between average daily maximum deficit in the shadiest vs. sunniest treatments.

Soil moisture was positively affected by increasing shade, and the effect dissipated with depth. Cumulative volumetric water content (θ_{cum}) measured at 10cm depth was significantly lower (i.e., drier) with increasing percent sun (slope=-0.03, $p=0.03$) (Figure 3). The effect was more pronounced in the slower (2cm/day) drawdown rate. At 10cm depth, soil moisture in the 2cm/day drawdown treatment was lower in 33% percent sun compared to full sun (66%) beginning approximately 2.5 weeks after the start of drawdown, with a peak difference of approximately $0.03 \text{ m}^3/\text{m}^3$ in week 4. There was a similar pattern, though much weaker magnitude effect, in the 3cm/day drawdown, with a peak difference in week 3 of $0.016 \text{ m}^3/\text{m}^3$ between the shadiest (22%) and sunniest (56%) treatment. There was no significant difference in soil moisture with shading at 70cm depth for either drawdown rate.

Temporal patterns of cottonwood seedling survival and shoot growth

Cottonwood seedling survival probability was higher in the faster drawdown rate. Although survival probability took approximately 10 days longer to begin declining in the 2cm/day drawdown rate, declines were much steeper relative to the 3cm/day drawdown across all levels of shading (Figure 4). Survival was significantly lower (i.e., Kaplan-Meier confidence intervals did not overlap) in the slower compared to faster drawdown rate by day 33 in full sun and day 42 in the shadiest treatment. Survival probability in the highest level of shading (~20% available

sun) was significantly higher in both drawdown treatments, and declined with increasing sun. In the 2cm/day treatment, survival probability in the two intermediate levels of shading was similar, but there was a stronger trend of decreasing survival probability through time with increasing levels of percent available sun. In the 3cm/day drawdown, there were no clear differences among the intermediate shading and full sun treatments, but all three were significantly lower than the shadiest (19% sun) treatment.

Regardless of drawdown rate, shoot height of seedlings was higher in the shadiest treatment (~20% sun) within two weeks of the start of drawdown (Figure 5). Seedlings growing in the two intermediate levels of shading were consistently the shortest, with no measurable difference in height as a result of soil moisture. In the sunniest treatment, seedling shoot height was higher in the wetter (2cm/day drawdown) treatment by day 30, whereas in the 3cm/day rate seedling height remained similar to the two intermediate levels of shade. The seedlings in the faster drawdown under heaviest shade were approximately 0.5cm taller at the start of drawdown than any other treatments (reflecting more height growth during the stable water level establishment period that preceded drawdown), and maintained the steepest rate of growth for longest. However, my mixed effects modeling accounts for this by inclusion of pot as a random effect. In terms of height growth through time, the best (in terms of AIC) mixed effects model was a quadratic fit to height growth through time, and included percent sun, cumulative volumetric water content (θ_{cum}), and their interaction as explanatory variables (Table 3). The modeling predictions (Figure 6) support observations that (1) height growth was rapid in the first 2-3 weeks and then began to taper, (2) there was a strong positive effect of shading on height growth, and (3) the shade effect was stronger under drier conditions (i.e., significant interaction between sun and soil moisture).

End-season seedling survival and growth

Based on AIC, the best models for end-season survival and growth typically included parameters for density, soil moisture, sun, and either an interaction between soil moisture and sun, or between soil moisture and density (Table 4 and Table 5). In most survival and growth models, days to the water stress threshold of $\theta_{0.1}$ was a better soil moisture predictor than cumulative volumetric water content (θ_{cum}). Percent sun was a better predictor of most survival and growth variables than any of the correlated vapor pressure deficit metrics.

End-season survival probability decreased with increasing sun, but the effect of soil moisture was density-dependent (Figure 7). The soil moisture gradient had no effect on end-season survival in low density pots, but increasing soil moisture had a negative effect on survival probability in high density pots across all levels of shading.

In the subset of lower density (40 initial seedlings/pot) pots where I could extract below ground biomass of individual seedlings (16 pots for total $n=539$), I observed a similar decline in end-season survival with increasing percent sun (data not shown), along with a significant increase in most cumulative growth response metrics (end-season shoot and root biomass, root length) of survivors (Figure 8). While both above and below-ground biomass increased across the sun gradient, there was an allocation response dependent on surviving seedling density. With increasing vapor pressure deficit (which was strongly correlated with increasing sun; Figure 2),

there was proportionately more biomass put into shoots (increasing shoot:root ratio) of seedlings growing in pots with lower density of survivors, and more into roots in pots with higher density of survivors. There were also significant interactions between sun and soil moisture availability. Typically, the effect of increasing sun (lower survival, higher cumulative growth of survivors) as much stronger in higher soil moisture conditions than in lower soil moisture conditions. The lowest moisture stress environment (wetter, shadier conditions that resulted in reduced vapor pressure deficits) yielded the highest survival but lowest total biomass of individual survivors. Surviving seedlings in this condition were tall and skinny (high shoot height but lowest shoot biomass) with the smallest root length. At highest resource availability (wetter, sunny), survival was lowest but those that survived were the largest in terms of total biomass and root length. In the drier environment, survival still decreased with increasing sun, but total biomass remained intermediate across the sun gradient.

DISCUSSION

My experiment was focused on examining the shade-tolerance of cottonwood seedlings, in order to understand how a species with such strong colonization traits is able to recruit successfully into the more physically benign, but more crowded environment of abandoned channels. To be applicable to field conditions, I needed to explore the question of shade-tolerance within an environmentally realistic context. This goal required addressing the interacting resource limitations of light and soil moisture, which are inextricably linked (i.e., sun acts as both a resource and a stress). Results from field-based vegetation removal studies usually show positive or neutral effects of removal of interspecific competitors on cottonwood seedling survival, but these studies never clearly separated whether this was due to above- or below-ground competitive release (Cooper and Andersen, 2012; Stella, 2005; Taylor et al., 1999).

My results support that shading indirectly improves soil moisture conditions by ameliorating the microclimate (Becker et al., 1988), as observed in other woody Mediterranean systems (Bruno et al., 2014; Granda et al., 2014; Sánchez-Gómez et al., 2006). Shading resulted in significantly higher soil moisture conditions by lowering vapor pressure deficits. In the fine substrate of my first experiment (Chapter 1), I observed a similar pattern of increasing soil moisture (particularly at shallow depths) with increasing cover of herbaceous competitors. I also observed smaller diurnal temperature fluctuations in shadier conditions, meaning seedlings were exposed to a less variable microclimate in the shade.

I observed a strong positive effect of shading on seedling survival. The pattern was consistent throughout the growing season beginning 30-40 days after the start of water table drawdown (Figure 4), meaning timing of mortality was similar but the rate was steeper in sunnier conditions. This resulted in end-season survival probability that was strongly negatively affected by increasing sun (Figure 7). Contrary to my expectations, the effect was the same regardless of water table drawdown-induced soil moisture conditions. In other words, even when soil moisture was relatively high, shading still had a positive effect on cottonwood seedling survival. By design, my experiment tested conditions at the wetter end of the moisture gradient observed in riparian corridors (Stella et al., 2010), and the mesocosm site experienced a relatively mild summer during the experiment, so overall moisture stress conditions for seedlings were relatively

low. Thus, the indirect, positive effect of shading on survival is much stronger for this species than the direct, negative effect of reduced light availability. My intent with this experiment was to recreate conditions observed within abandoned channels (Chapter 1, Appendix A), so I did not include extremely low light levels. I recognize, however, that there is a threshold light level necessary for survival, and had I reduced light availability to extremely low levels I may not have observed such a purely positive effect. I also note that germination can be affected by light levels (Smith, 1982), which I accounted for by installing shade cloth after seeds had germinated.

The differences in survival can largely be explained by trade-offs in growth. While end-season survival was strongly negatively affected by increasing sun, sun had a positive effect on final dry biomass of survivors, particularly when soil moisture was higher (Figure 8a). This growth effect was similar to that observed from experiments with *Populus alba* (González-Muñoz et al., 2013). Thus, the condition of highest resource abundance (wetter, sunnier) yielded lowest survival, but those that survived were the largest in terms of final biomass, shoot height and root length. In contrast, the condition of lowest resource abundance (drier, shadier) yielded high survival, but those surviving to the end of the growing season were smaller, with low final biomass and root growth. The interspecific high-light growth/ low-light survival trade-off is based on a species that either grows slowly but has higher survival under low resource conditions (competitor/tolerator strategy), or grows quickly but has lower survival in higher resource abundance (colonizer strategy) (Kobe et al., 1995; Walters and Reich, 1996). My results indicate that cottonwood seedlings are employing both strategies. Trade-off hypotheses are often used to explain species coexistence, succession, or species-specific adaptation to a narrow regeneration niche (Bloor and Grubb, 2003; Gravel et al., 2010; Kobe et al., 1995; Sack, 2004; Schnitzer and Carson, 2001). My results suggest that cottonwood seedlings are much more plastic in their shade-tolerance, allowing them to recruit into a broader range of environments than one would typically assume based on the strong colonization traits of the species. While uncommon, this has been observed for other woody species (Negreiros et al., 2014; Seiwa, 2007), including a species of *Baccharis* that has similar colonizer traits (Negreiros et al., 2014). This plasticity lends support for a mechanism by which cottonwoods are able to dominate both on newly exposed bars of the active channel (poor survival but extremely high growth under combined high light/moisture resource conditions), and successfully recruit into the more physically benign, but more competitive (shadier) environment found within abandoned channels.

While soil moisture had very little effect on cottonwood survival within the ranges supplied in my experiment, I did see a strong interaction between soil moisture and sun in terms of final biomass and root length (Figure 8a and b). The positive effect of sun on final growth was much stronger in the higher soil moisture condition. Seedlings growing in higher soil moisture conditions were significantly larger (final biomass) and with much longer roots when grown at high vs. low sun. However, sun had only a slight positive effect on growth of seedlings in the lower soil moisture condition. This indicates that soil moisture, rather than sunlight, is the more limiting resource for cottonwood seedling growth. The effects of intraspecific competition (i.e., seedling density) on allocation patterns also support the hypothesis that competition for moisture is stronger. In pots that had low density of survivors, the survivors allocated more to shoots with increasing sun (Figure 8c). In pots that had high density of survivors, the survivors had allocated more to roots with increasing sun. These results complement the findings from my first experiment with interspecific competitors (Chapter 1). There was a strong interactive effect

between soil moisture and level of interspecific competition on cottonwood seedling survival (lowest survival in dry condition with high levels of interspecific competitors). Based on the current experiment, I cannot attribute this to light limitation because shading had a positive effect on survival even at high soil moisture. This lends further support that below-ground interactions and limitations on water availability are primarily driving first-year cottonwood establishment success when growing with other species (Cooper et al., 1999), at least at these light levels.

Seedlings growing in the shade had higher survival, but lower overall growth, particularly in higher moisture conditions. Lower net growth due to light-limitation means fewer reserves and structural support necessary to survive beyond the first year, particularly for seedlings subjected to high physical stresses characteristic of active channel bars and banks (Polzin and Rood, 2006). However, I suggest that the more physically benign conditions found in abandoned channels (lower frequency and intensity of disturbance, higher soil moisture retention in finer substrates), mean that growing conditions are less stressful and seedlings are less reliant on reserves from previous year's growth. Additionally, sites within abandoned channels that maintain adequate soil moisture for seedlings tend to be dominated by low-stature herbaceous competitors (Chapter 1 Appendix A; Dufour et al., 2014; Stella et al., 2011), which cottonwood seedlings are likely to eventually overtop. This means conditions of light-limitation on growth may be transient. Finally, in my previous experiment (Chapter 1), I noted an early facilitative effect of the presence of interspecific competitors on cottonwood seedlings growing in the lower soil moisture, coarse substrate. Seedlings in this condition survived at comparable rates as on higher soil moisture, fine substrate for the first ~40 days (Chapter 1, Figure 3c). This suggests that interspecific competitors that emerge and senesce early may be more facilitative (reducing evaporative water loss when seedlings are very small and more vulnerable to heat and water stress; Tozzi et al., 2013) than those that emerge or remain actively growing later in the summer when soil moisture becomes more limiting.

Whereas soil moisture and shade are correlated in many upland forests (i.e., shady sites are typically moist) (Ninemets and Valladares, 2006), the reverse is often true in semi-arid riparian forests. There is both a temporal and spatial aspect to the distribution of soil moisture in Mediterranean rivers. First, the annual summer drought of Mediterranean systems is coincident with the growing season, meaning soil moisture availability for plant growth is largely controlled by depth to the groundwater table (mediated by surface-water-ground-water interactions and the hydraulic properties of the substrate). Thus, resource gradients and plant community composition tend to stratify along a cross-section with distance from and elevation above the water surface (Bendix and Stella, 2013; Gregory et al., 1991; Naiman and Decamps, 1997; Naiman et al., 2005; Poff et al., 1997; Stella et al., 2013). Low elevation surfaces near the channel have higher moisture availability, and higher light availability due to overwinter flood-scouring of vegetation. Disturbance-adapted pioneers like cottonwood generally dominate on these surfaces. As a result, they have been assumed to be shade-intolerant and poor competitors. My results suggest that, at least for the seedling stage, their tolerance to shade is plastic. Combined with my observations from Chapter 1 and the significant regeneration observed within abandoned channels in the field (Stella et al., 2011), the implications are that cottonwoods seedlings are not limited in vegetated areas because of a lack of light availability, but because vegetated areas are typically higher and drier as a result of biogeomorphic feedbacks (Corenblit et al., 2014; Stella et al., 2013).

TABLES

Table 1. Parameters for pot-averaged (vertically integrated) soil moisture calculations.

Instrumented Treatment	95% of roots above depth (cm) (Mean root length + 2 SD)	β
2cm/day + full sun	90.7	0.968
2cm/day + 50% shade cloth	58.8	0.950
3cm/day + full sun	53.0	0.945
3cm/day + 30% shade cloth	53.0	0.945
3cm/day + 70% shade cloth	57.8	0.949

Table 2. Light treatments and calculation of percent available sunlight.

Drawdown rate	Platform	Hemi photos Fraction Total Transmitted Light	% Light from shade cloth	Percent Available Sunlight
2cm/day	H	0.662	100	66.2
	A	0.676	70	47.3
	F	0.655	50	32.8
	B	0.685	30	20.5
3cm/day	D	0.559	100	55.9
	E	0.623	70	43.6
	C	0.700	50	35.0
	G	0.638	30	19.1

Table 3. Parameters and model selection results of linear mixed effects modeling of cottonwood seedling shoot growth through time. Day is day of experiment, sun is percent available sunlight, cum.vwc is cumulative soil volumetric water content (θ_{cum}), and ϵ_{pot} is the random pot effect.

Model Parameters	ΔAIC^\ddagger	w_i^\S
day + day ² + sun × cum.vwc + ϵ_{pot}	0	0.97
day + day ² + init.density × sun × cum.vwc + ϵ_{pot}	7.01	2.9×10^{-02}
day + day ² + sun + cum.vwc + ϵ_{pot}	34.40	3.3×10^{-08}
day + day ² + sun + ϵ_{pot}	35.73	1.7×10^{-08}
day + day ² + init.density + sun + cum.vwc + ϵ_{pot}	36.36	1.2×10^{-08}
day + day ² + ϵ_{pot}	62.91	2.1×10^{-14}
day + init.density × sun × cum.vwc + ϵ_{pot}	71.39	3.1×10^{-16}
day + sun + cum.vwc + ϵ_{pot}	98.75	3.5×10^{-22}
day + sun + ϵ_{pot}	100.08	1.8×10^{-22}
day + init.density + sun + cum.vwc + ϵ_{pot}	100.71	1.3×10^{-22}
day + ϵ_{pot}	127.25	2.3×10^{-28}

[‡] ΔAIC = relative difference in Akaike Information Criterion value from the model with the lowest AIC ($\Delta_i = AIC_i - AIC_{min}$).

[§] w_i = AIC weight, which represents the relative strength of evidence for each model given the data and the set of candidate models. $\sum w_i = 1$.

Table 4. Top ranked logistic regression models of end-season survival probability.

Daysto.0.1vwc = days to the water stress threshold of $\theta_{0.1}$, cum.vwc = cumulative soil volumetric water content (θ_{cum}), sun = percent available sunlight, init.density = initial planting density, init.height is initial seedling height at the start of the experiment, vpd.d.max = daily maximum vapor pressure deficit (vpd), vpd.d.pm.mean/max = daily afternoon (12-4pm) mean/max vpd.

K*	Model Parameters (all models include init.height)	AUC [†]	Δ AIC [‡]	w _i [§]
<i>Survival models – full data set (99 candidate models)</i>				
6	daysto.0.1vwc + sun + init.density + init.density × daysto.0.1vwc	0.69	0	0.40
6	cum.vwc + sun + init.density + init.density × cum.vwc	0.69	2.38	0.12
5	daysto.0.1vwc + sun + sun:daysto.0.1vwc + init.height	0.69	3.26	0.08
<i>Survival models – root harvest data set (37 candidate models; no density term)</i>				
5	cum.vwc + vpd.d.pm.max + vpd.d.pm.max × cum.vwc	0.72	0	0.13
5	cum.vwc + vpd.d.max + vpd.d.max × cum.vwc	0.72	0.017	0.13
5	cum.vwc + vpd.pm.mean + vpd.d.pm.mean × cum.vwc	0.72	0.15	0.12
5	cum.vwc + sun + sun × cum.vwc	0.72	0.75	0.09

*K = total number of model parameters, including intercept and covariate of initial seedling height

†AUC = area under the receiver operating characteristic (ROC) curve

‡ Δ AIC = relative difference in Akaike Information Criterion value from the model with the lowest AIC ($\Delta_i = AIC_i - AIC_{min}$).

§w_i = AIC weight, which represents the relative strength of evidence for each model given the data and the set of candidate models. $\sum w_i = 1$.

Table 5. Top ranked linear regression models for end-season growth metrics (77 total candidate models). Daysto.0.1vwc = days to the water stress threshold of $\theta_{0.1}$, cum.vwc = cumulative soil volumetric water content (θ_{cum}), sun = percent available sunlight, final.density = density of seedlings that survived to end of experiment, init.height is initial seedling height at the start of the experiment, vpd.d.max = daily maximum vapor pressure deficit (vpd), vpd.d.pm.min = daily afternoon (12-4pm) minimum vpd.

K*	Model Parameters (all models include init.height)	Adj R ²	Δ AIC [‡]	w _i [§]
<i>Total biomass</i>				
7	daysto.0.1vwc + sun + final.density + sun:daysto.0.1vwc	0.25	0	0.59
7	cum.vwc + sun + final.density + sun:cum.vwc	0.24	0.76	0.41
7	cum.vwc + sun + final.density + final.density:cum.vwc	0.23	12.9	0.0009
<i>Shoot:root ratio</i>				
6	vpd.d.pm.min + final.density + final.density:vpd.d.pm.min	0.06	0	0.98
7	cum.vwc + sun + final.density + final.density:sun	0.05	10.92	0.0042
7	daysto.0.1vwc + sun + final.density + final.density:sun	0.05	11.56	0.0030
<i>Shoot height</i>				
6	daysto.0.1vwc + final.density + final.density:daysto.0.1vwc	0.27	0	0.41

K[*]	Model Parameters (all models include init.height)	Adj R²	ΔAIC[‡]	w_i[§]
7	daysto.0.1vwc + sun + final.density + final.n.p:daysto.0.1vwc	0.27	0.67	0.29
6	cum.vwc + final.density + final.density:cum.vwc	0.27	1.40	0.20
<i>Root length</i>				
7	cum.vwc + sun + final.density + sun:cum.vwc	0.28	0	0.78
7	daysto.0.1vwc + sun + final.density + sun:daysto.0.1vwc	0.28	3.22	0.16
7	cum.vwc + sun + final.density + final.density:cum.vwc	0.27	5.13	0.0060

* K = total number of model parameters, including intercept and covariate of initial seedling height

‡ ΔAIC = relative difference in Akaike Information Criterion value from the model with the lowest AIC ($\Delta_i = AIC_i - AIC_{min}$).

§ w_i = AIC weight, which represents the relative strength of evidence for each model given the data and the set of candidate models. $\sum w_i = 1$.

FIGURES

Figure 1. Effect of drawdown rate on soil moisture through time. Volumetric water content shown for each drawdown rate is depth-averaged (see Methods) for three different pots (negative control, low density, high density) in full sun. The experimental period was from July 9 to October 1.

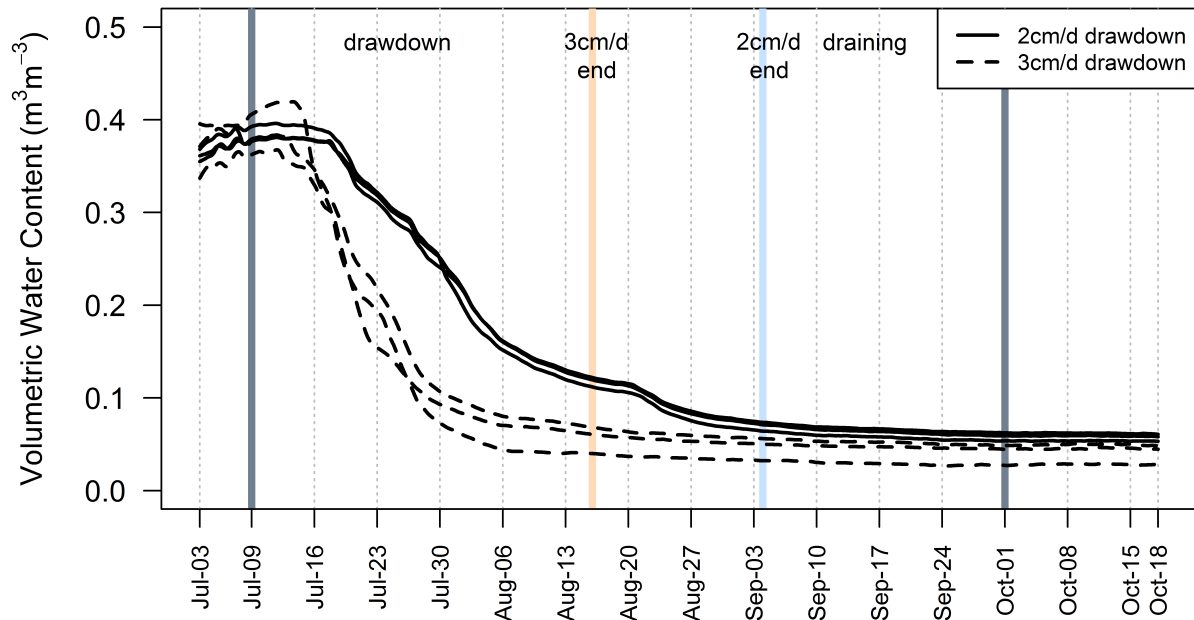


Figure 2. The effect of sunlight availability on temperature and vapor pressure deficit metrics during the experimental period (mean \pm standard error for n=85 days).

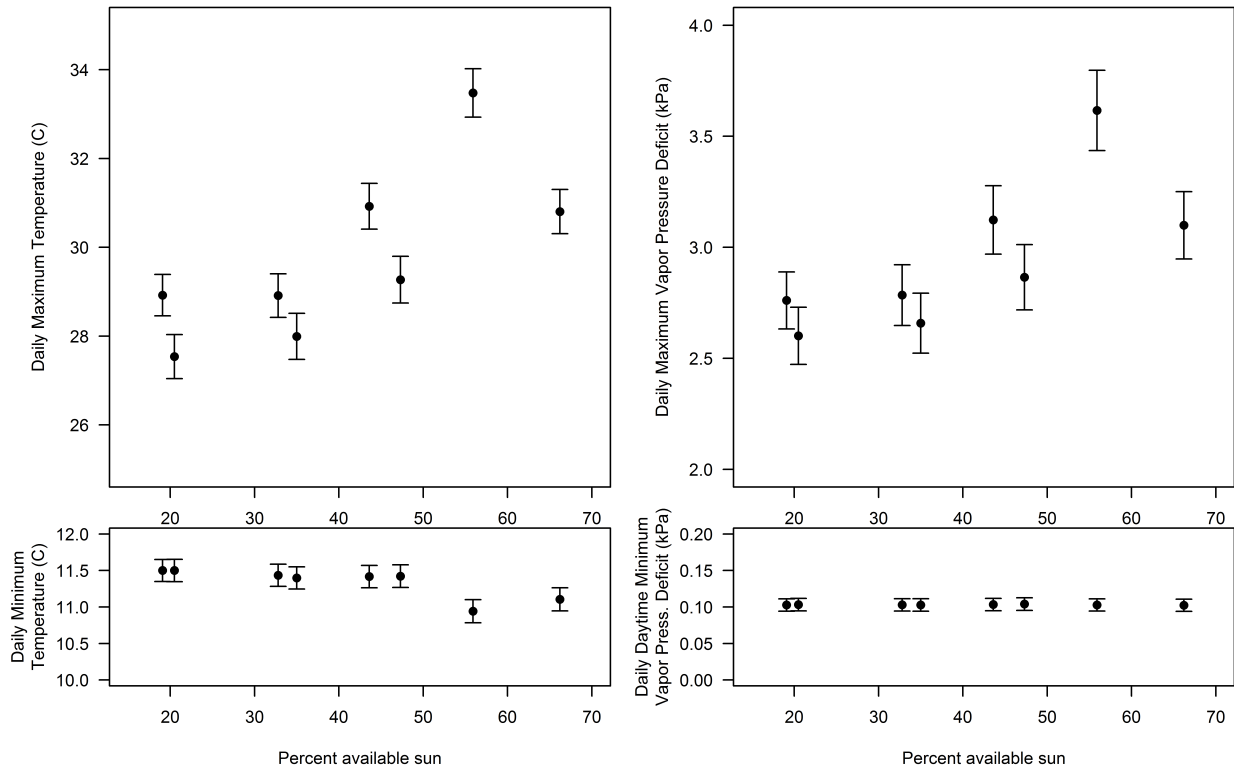


Figure 3. The effect of drawdown rate and sunlight availability on (a) cumulative soil volumetric water content (θ_{cum}) measured at 10cm-depth (means \pm SE). Not all treatment combinations were instrumented. Examples of soil volumetric water content (θ) through time at different levels of percent available sun in low density pots at (b) 2cm/day drawdown and (c) 3cm/day drawdown. Vertical bars indicate timing as shown in Figure 1.

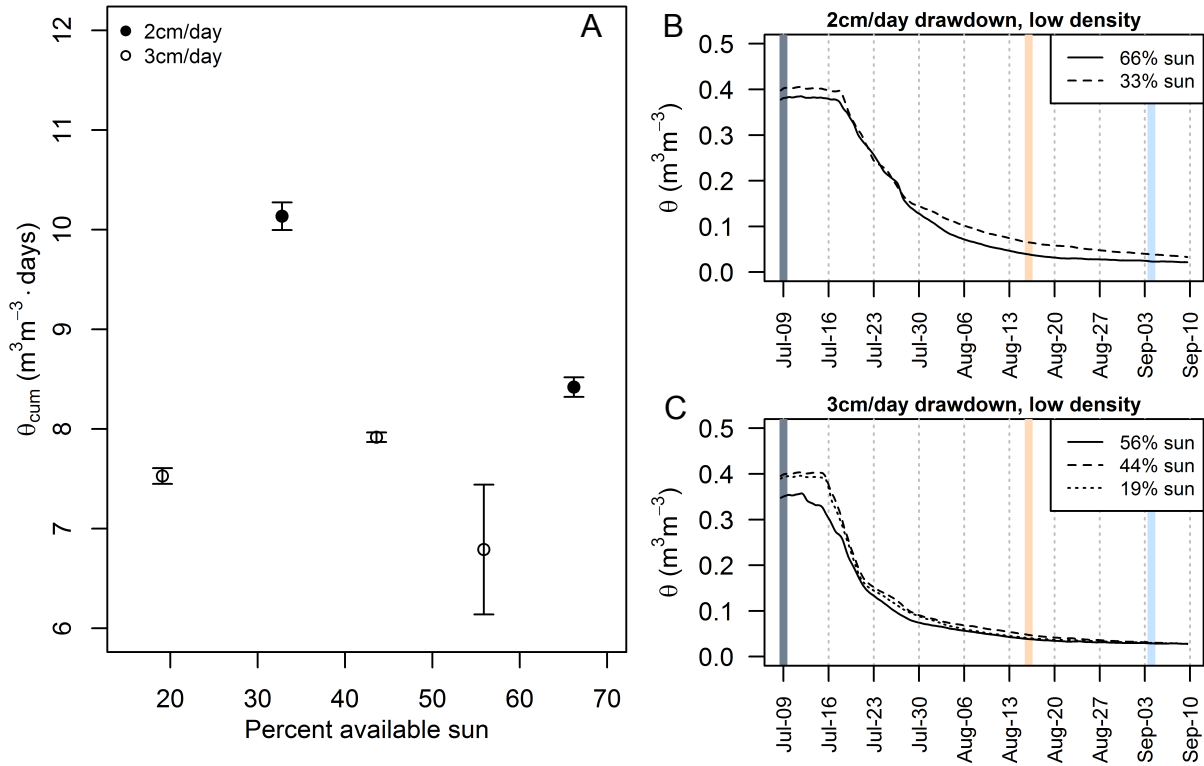


Figure 4. Cottonwood seedling survival probability through time under two different drawdown rates and four levels of shading. Solid lines are Kaplan-Meier survival curves, and dashed lines are $\pm 95\%$ CI. Note that sun is percent available sunlight (see Table 2), where the full sun treatment corresponds to 56-66%.

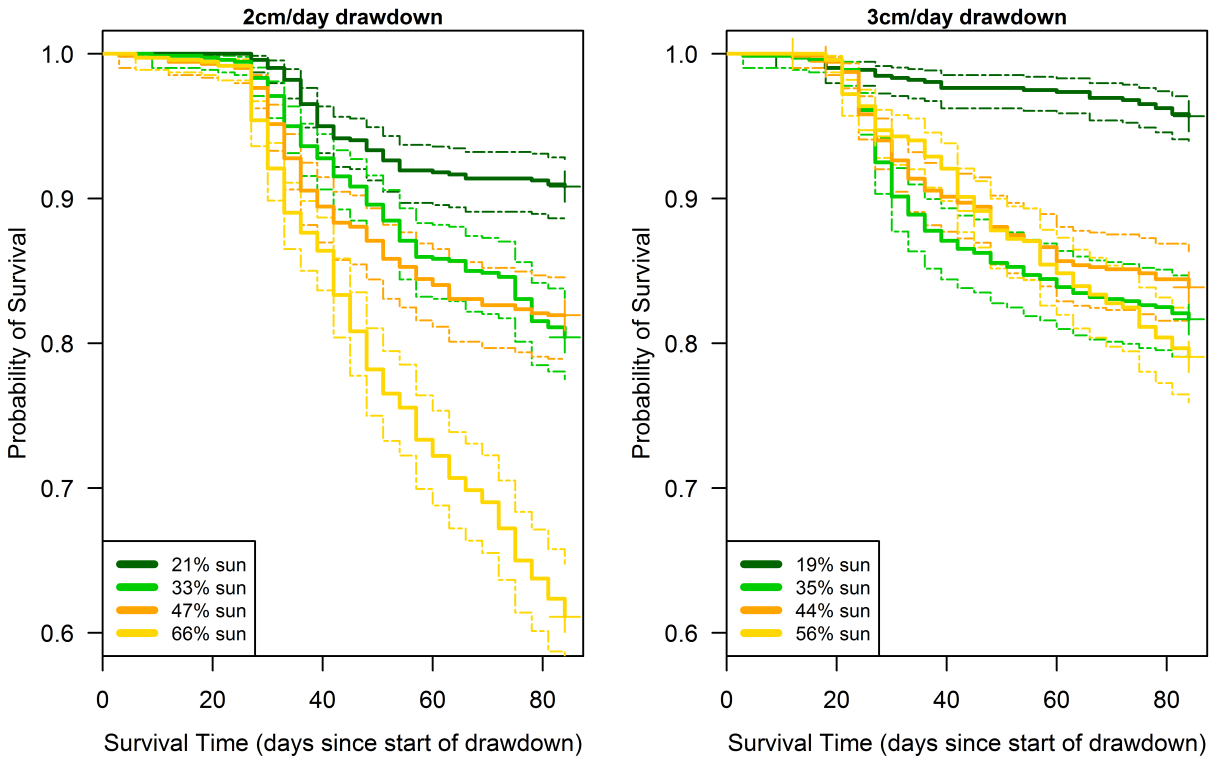


Figure 5. Temporal patterns of cottonwood seedling shoot height under different drawdown rates and percent available sun. Values shown are pot-level (n=12) mean height (\pm SE) of survivors at each timestep.

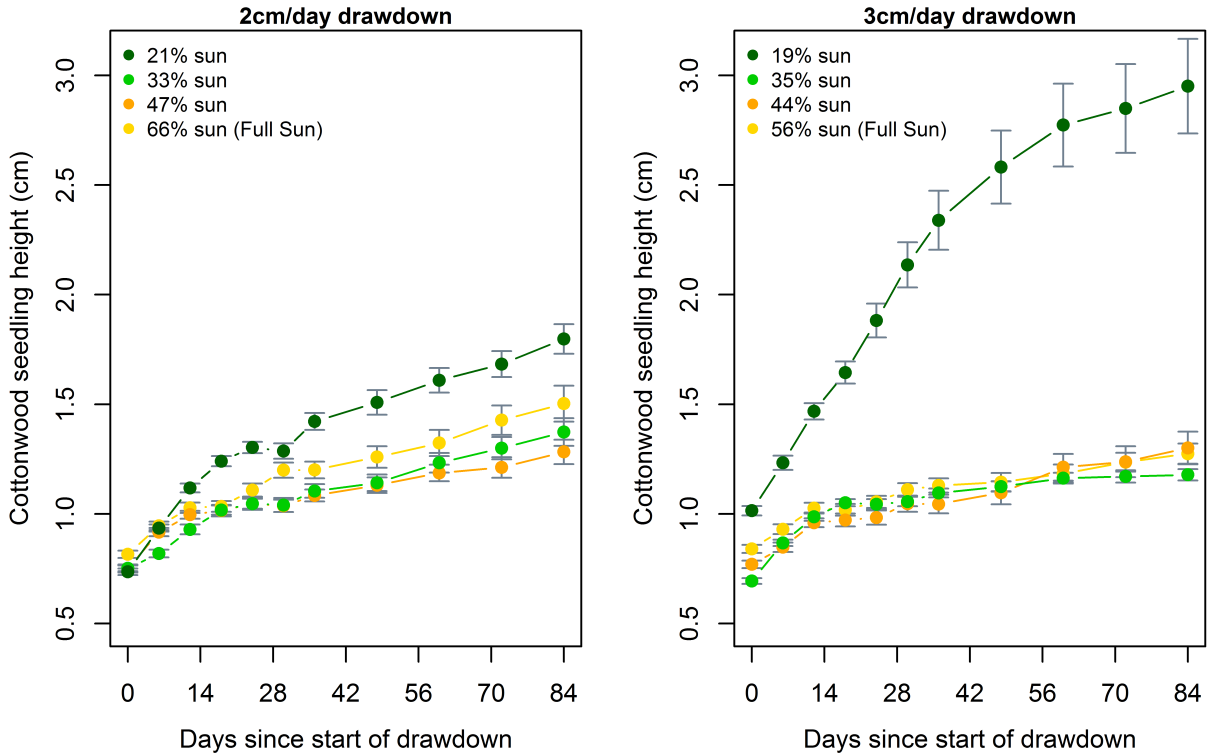


Figure 6. Predicted seedling shoot growth through time from top ranked linear mixed effects model. Values used for soil moisture and sun were based on the first (low) and third (high) quantiles for these gradients, which correspond to 20.5% and 47.3% sun, and 9.4 and 13.2 $\text{m}^3/\text{m}^3 \times \text{days}$ of soil moisture.

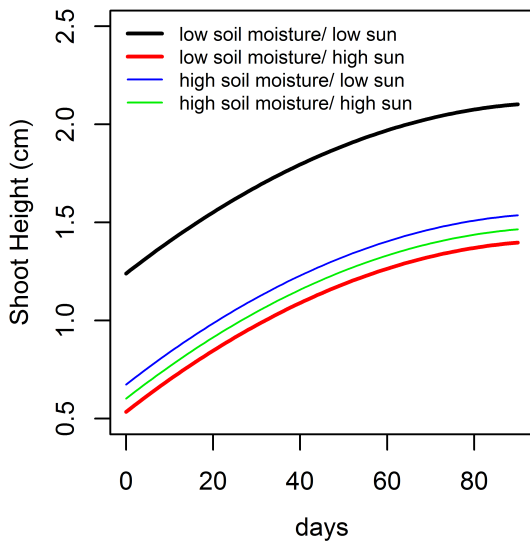


Figure 7. End-season survival response surfaces for the best logistic regression model (Table 4), showing the negative effect of sun and the interaction between initial density and soil moisture (expressed as days to the water stress threshold of $0.1 \text{ m}^3/\text{m}^3$). Survival probability is expressed as log odds of survival.

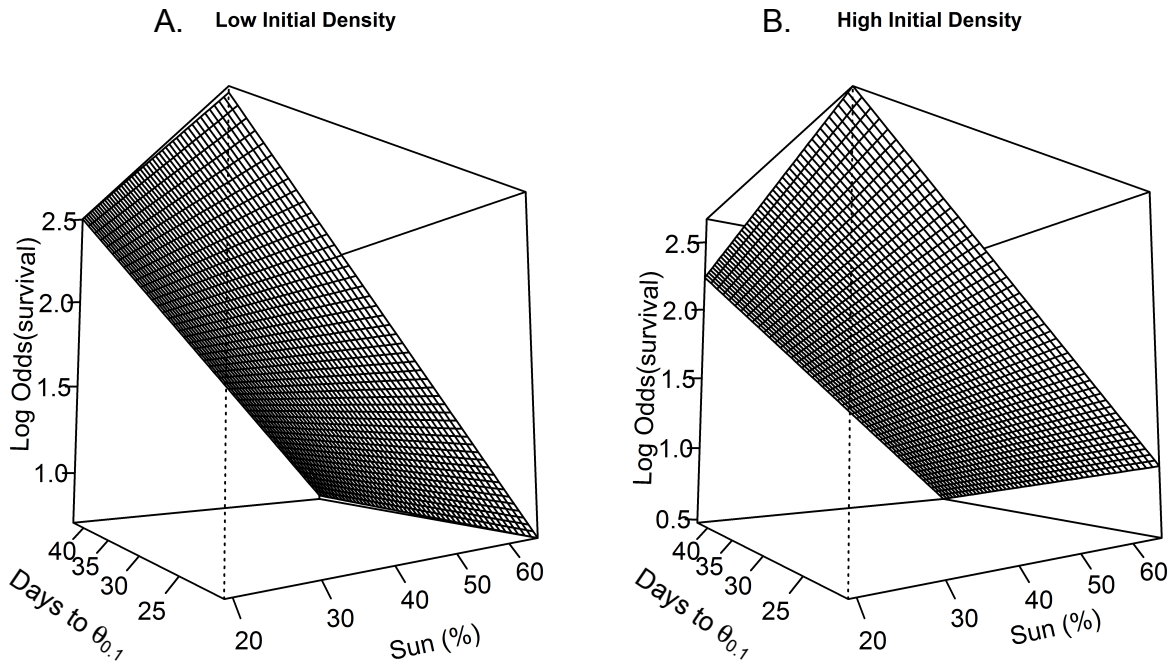
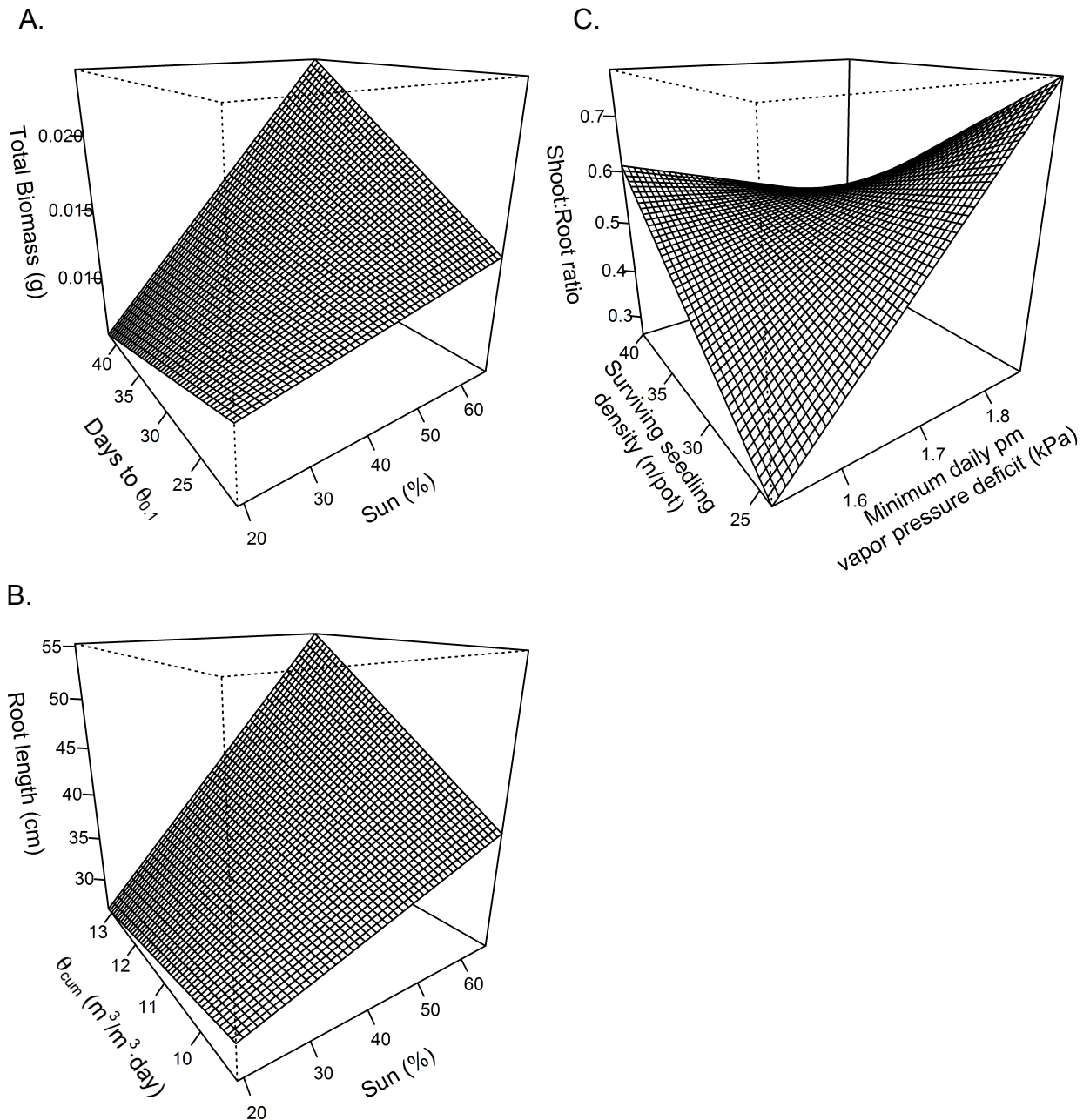


Figure 8. Response surfaces of cumulative growth metrics with respect to treatment gradients. The best models (Table 5) for (a) total biomass and (b) root length included interactions between metrics for soil moisture and sun (surviving seedling density held at mean value for figures shown). Shoot:root ratio (c) showed a density dependent response along the sun/vapor pressure deficit gradient.



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CHAPTER 3 | How long do abandoned channels support cottonwood establishment?

ABSTRACT

Pioneer trees that require disturbance events for regeneration use a variety of strategies for persisting during periods of relative stability. The use of spatial refugia, while critical for population recovery of many mobile organisms, is generally not considered an important strategy for trees. Episodic channel abandonment in meandering river systems, and the subsequent infill and terrestrialization of the abandoned channel, has been recently highlighted as critical for maintaining the population of a key pioneer riparian tree species, Fremont cottonwood (*Populus fremontii*). The species has disturbance-adapted reproductive strategies that confer strong colonization success, but is considered shade-intolerant and a poor competitor. Thus, it was considered likely that cottonwood establishment would be limited to the period immediately following channel abandonment, when the abandoned channel retains elements of physical dynamism to which the species is well adapted. However, new experimental evidence of better competitive ability and more plastic shade-tolerance, particularly under conditions of high soil moisture, suggests that cottonwood establishment in abandoned channels may be supported for a much longer window of time. On the Sacramento River, California, I used a chronosequence (space-for-time) approach to understand patterns of cottonwood establishment as a function of time since abandonment and biogeomorphic stage. I examined patterns in overstory community composition and cottonwood diameter size distribution as indicators of past establishment dynamics. I used tree ring analysis to sample the age structure. I addressed the main sources of error in the use of tree ring analysis for determining establishment age by cross-dating tree cores, and developing and applying correction-factors for cores potentially missing the earliest years of growth. I also quantified the uncertainty around my correction-factors using a Monte Carlo simulation approach, and propagated the uncertainty through my analyses. Overstory community composition, size-class distributions, and tree ages all support a recruitment window that begins at channel abandonment, and consistently lasts ~ 20 years, regardless of site age. Thus, while channel abandonment is episodic, a cohort of trees always successfully establishes, and cohorts can continue to successfully establish for a period of approximately two decades. The length of the recruitment window extends in time the spatial refuge provided by abandoned channels and thus helps ensure continued persistence of the cottonwood population.

INTRODUCTION

A fundamental question in ecology asks: How are populations buffered against extinction during adverse periods (Connell and Sousa, 1983; Whittaker and Klomp, 1975). For pioneer species that rely on disturbance for regeneration, a reduction in the intensity, frequency, and/or extent of disturbance qualifies as adversity and the challenge is for populations to persist during these periods of relatively stability (Marks, 1983). In theoretical terms, the goal is to ensure

overlapping populations (i.e., the storage effect, Warner and Chesson, 1985). Several strategies of persistence have been documented for pioneer tree species including long life (e.g., *Sequoiadendron giganteum*; York et al., 2009), seed burial (e.g., *Prunus pensylvanica*; Marks, 1974), cone serotiny (many *Pinus* species; Ne'eman et al., 2004), and vegetative propagation (e.g., *Salix exigua*; Douhovnikoff et al., 2005). A common persistence strategy critical for population recovery of mobile organisms in disturbance-prone or spatially heterogeneous systems is the use of spatial refugia (Sedell et al. 1990, Lake et al. 2007, Tabacchi et al. 2009). For trees, the concept of refugia has most often been applied in paleoecology to describe species retreat during periods of glaciation (Bennett et al., 1991; Willis and Van Andel, 2004). It is a concept less commonly applied to contemporary tree population dynamics (though see Marks, 1974).

Recently, Stella et al. (2011) presented a conceptual model of persistence for a riparian pioneer tree species, Fremont cottonwood (*Populus fremontii*). Along the rivers in the Central Valley of California, Fremont cottonwood is a foundational species (sensu Ellison et al., 2005). It is the dominant tree in the riparian ecosystem whose productivity and growth are critical to the rapid stabilization of substrate, nutrient cycling, soil development, and food web networks that link terrestrial and aquatic systems (Braatne et al., 1996; Patten, 1998). Contrary to expectations, Stella et al. (2011) determined that >50% of the extant cottonwood stands within the middle reach of the Sacramento River (California, USA) had established as seedlings within abandoned channels, rather than along active channel bars or banks. Prior to this study, channel abandonment had been considered a minor contributor to establishment of pioneer riparian forest (Naiman et al., 2010; Van Pelt et al., 2006). Instead, recruitment along the bars and banks of the active channel has been the focus of most research (Cooper et al., 1999; Mahoney and Rood, 1998; Stella et al., 2006). One important conclusion of this body of research was that anthropogenic changes to seasonal flow patterns and lateral channel migration (e.g., from water regulation, channel confinement, and land use change) have severely restricted conditions necessary for pioneer seedling establishment (Andersen et al., 2007; Braatne et al., 2007; Rood et al., 2005). The findings of Stella et al. (2011) suggested that, even in regulated rivers like the middle Sacramento, episodic channel abandonment, and its subsequent infill and terrestrialization, provides critical refugia for disturbance-dependent tree species.

Stella et al. (2011) hypothesized a cottonwood recruitment “time” window that is driven by temporal changes in sedimentation and vegetation colonization within abandoned channels. The geomorphic evolution of abandoned channels in meandering rivers results from sedimentation processes that proceed in two main phases: blockage and infilling (Gagliano and Howard 1984, Shields and Abt 1989, Constantine 2008, Constantine et al. 2009). The blockage phase encompasses the time period after the cutoff event when the abandoned channel remains hydrologically connected to the main channel. Coarse bedload material continues to be transported into the abandoned channel until a plug of sediment forms at the upstream-end of the channel (blockage). The infilling stage then follows, when the abandoned channel functions as a floodplain lake that fills only when overbank flows deposit fine suspended sediment.

As an abandoned channel fills over time there is both a reduction in the flood disturbance regime (frequency and intensity), and a fining of substrate, which combine to create more benign environmental conditions favorable for establishment of plant species that are less disturbance-

adapted, but better resource competitors (Chapter 1). As a result, there is an increase in cover of interspecific competitors through time (Chapter 1, Appendix A; Stella et al., 2011). Based on the current understanding of cottonwoods as a strong colonizer but weak competitor (Chapter 2; Catford and Jansson, 2014; Corenblit et al., 2014; Karrenberg et al., 2002; Lytle and Poff, 2004), we hypothesized that the “blockage” phase (right after abandonment when the abandoned channel retains some physical dynamism) would support cottonwood seedling establishment (Stella et al., 2011). However, once channels were blocked and the abandoned channel entered the “infilling” stage (fine sediment and dense vegetation colonization), the competition-colonization trade-off (Bazzaz, 1979; Connell and Slatyer, 1977; Huston and Smith, 1987; Tilman, 1990) suggests that cottonwood seedling establishment would be restricted by their poor competitive ability.

However, my mesocosm experiments suggest that cottonwoods are better competitors than current theory and empirical information suggest (Chapter 1), that they are more plastic in their shade-tolerance (Chapter 2), and that soil moisture is the dominant driver of successful establishment of first year seedlings (Chapters 1 and 2). My findings suggest that seedlings can, in fact, continue to establish (though perhaps at lower frequencies) at later biogeomorphic stages despite dense herbaceous cover or shade, because soil moisture conditions remain high in the finer substrate deposited during infilling. Thus, from my experiments I would predict a longer “window” of recruitment into abandoned channels that would not restrict cottonwood establishment to the earlier, more physically dynamic blockage phase. If true, the longer recruitment window would improve the value of abandoned channels as refugia for cottonwoods and by extension provide a means to ensure overlapping generations under adverse conditions (i.e. lack of disturbance due to river regulation). In other words, a longer recruitment window increases the probability of cottonwood persistence. However, while I found that cottonwood seedlings can tolerate more competitive conditions in a controlled setting, the mesocosm experiments by design did not capture the full spectrum of ecological processes that can strongly affect vegetation dynamics in the field, such as seed dispersal, herbivory, or climatic extremes. The goal of my final chapter was to reconstruct cottonwood establishment patterns from field data in order to test the predictions from my experiments regarding the size of the recruitment window. Thus, using a chronosequence (space-for-time) approach, I examined patterns in overstory community composition, cottonwood size, and age structure within abandoned channels of the Sacramento River, California, as an indicator of past establishment dynamics.

Because my primary interest was in understanding the timing and patterns of tree establishment following channel abandonment, I needed to make inferences from the ages of existing cottonwood trees. There are challenges in inferring timing of tree establishment using dendroecological techniques (Speer, 2010; Villalba and Veblen, 1997; Wong and Lertzman, 2001), particularly in riparian systems (Meko and Woodhouse, 2005; Stella et al., 2013) or more generally for dating of geomorphic surfaces (Koch, 2009; Shroder, 1980; Wiles et al., 1996). Three factors can reduce the accuracy of establishment ages obtained via increment coring (Koch, 2009). First, simple ring counts that are not cross-dated with other trees can result in over- or under-estimates because of individual tree growth anomalies that result in false or missing rings (e.g., Waring and O’Hara, 2006). Visual (i.e., skeleton-plotting) or statistically-based (e.g., COFECHA software) methods of comparing ring-width patterns are the standard for identifying growth anomalies (Fritts and Swetnam, 1989; Grissino-Mayer, 2001). Next,

increment cores that miss the pith (tree center), and coring of the tree above the root crown both result in underestimates of establishment date because they miss the earliest years of growth. Because of conical growth patterns in woody stems, the true age of a tree can only be determined if the annual tree rings can be counted at the root-shoot boundary (i.e., root crown). In riparian systems, burial of the root crown is common due to sedimentation and the interactions between vegetation and fluvial processes (Bendix and Stella, 2013; Corenblit et al., 2007). Even if root crowns can be excavated, deformation of the stem from adventitious roots can mean that no single cross-section along the trunk contains a record of all growth rings (DesRochers and Gagnon, 1997). There are a variety of techniques available to correct for errors due to missing pith (e.g., Norton et al., 1987; Rozas, 2003) and coring height (e.g., Fraver et al., 2011; Gutsell and Johnson, 2002; Palik and Pregitzer, 1995). However, even when they are applied, the uncertainty introduced by these corrections is not considered in the analysis (Wong and Lertzman, 2001). In contrast, quantifying this uncertainty is essential to providing realistic estimates of the recruitment window. Thus,

I addressed each of the three potential sources of error, calculated the uncertainty around my correction-factors using a Monte Carlo simulation approach, and propagated the uncertainty through my analyses (a novel application of this approach). Thus, uncertainty in my aging estimates is directly accounted for in subsequent analyses and in interpretation of results. In concert with data on overstory community composition and cottonwood population size structure, the robust analysis of cottonwood establishment age allowed me to more clearly infer the window of time that an abandoned channel provides refugia for cottonwoods.

METHODS

Study area

The Sacramento River catchment is the largest in California, draining 68,000 km² 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. 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, Figure 1). The area experiences a Mediterranean climate, with hot, dry summers and cool, wet winters. Average annual precipitation in the valley is 56 cm, over 80% of which typically falls between December and February (DWR, 1994). The average annual temperature is approximately 17 °C, reaching highs of 32–47 °C in summer, and lows around freezing in winter (DWR, 2006). Land use in the floodplain of the study reach is predominantly agricultural, dominated by fruit and nut orchards.

The middle reach of the Sacramento River is primarily a single-thread, gravel-bed, meandering section set within a fine-grained floodplain alluvium. Average annual discharge at the upstream end of the reach is 350 m³ sec⁻¹ (US Geological Survey gauge 11377100), and was historically a snow-melt driven system. Bankfull channel width averages 300 m, and channel slope ranges from 0.0007 m/m at the upstream end to 0.0002 m/m at the downstream end (Constantine, 2006; Micheli et al., 2004). The study reach is underlain by tertiary and quaternary sedimentary deposits (DWR, 1994), with banks that range from very hard, cemented material to coarse, non-

cohesive alluvium (Constantine, 2006). Alluvial deposits over the last century typically include a silty upper layer of overbank material on top of non-cohesive gravel and sand channel deposits (Constantine, 2006). The median grain size of the main channel bed ranges from 15 to 35 mm (Micheli et al., 2004), with much finer sand and silt deposits in the abandoned channels.

The mainstem of the Sacramento River is regulated at Shasta Dam, built in 1942 to capture peak flows for irrigation supply and hydropower generation. All major tributaries are also 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 channel migration and cutoffs (Greco et al., 2007; Micheli and Larsen, 2010; Singer, 2007). New abandoned channels appear to be created with similar frequency as in pre-dam conditions, but they are typically smaller in length and surface area, reflecting an increase in chute vs. neck cutoffs that has resulted from the complex interplay of land-use changes, historical timing of large floods, and effects of dams and bank revetment on channel migration (Michalková et al., 2011). 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 pioneer and mature forest stands remaining in California (Buer et al., 1989). A significant fraction (54%) of these extant pioneer forest stands initiated within abandoned channels (Stella et al., 2011).

Abandoned channel site selection and descriptions

As part of a comprehensive field campaign (Dufour et al., 2014; Stella et al., 2011), I collected vegetation data at 10 abandoned channel sites selected to represent the gradient from a pool of 30 present within the study reach (Michalková et al., 2011). All sites had a remnant wetland feature, as well as pioneer riparian forest present at some life-history stage. I confirmed vegetation conditions from aerial photographs and field-based reconnaissance. Because I was interested in understanding vegetation dynamics as channels fill and terrestrialize, I selected sites with a low angle of divergence from the main channel ($\sim \leq 50^\circ$) to avoid very sinuous oxbows that remain as large, long-lived oxbow lakes (Constantine et al., 2009). These highly sinuous abandoned channels also typically form from neck cutoffs, which occur with much less frequency than they did historically. As noted above, post-dam channel abandonment occurs predominantly via chute cutoff (Constantine and Dunne, 2008a; Michalková et al., 2011).

There are two aspects to the evolution of abandoned channels following channel cutoff and abandonment. First, there is a time component—older abandoned channels have had more time to accumulate both sediment and plant propagules (longer colonization time). Second, this time component is modified by biogeomorphic interactions (Bendix and Stella, 2013; Corenblit et al., 2010) that result from channel morphology (straight vs. sinuous channel planform), channel meander (e.g., whether the active channel meanders further away from the abandoned channel), sediment supply and transport, and dispersal and colonization (Citterio and Piégay, 2009; Constantine et al., 2009; Dufour et al., 2014; Stella et al., 2011). Stella et al. (2011) developed the conceptual model for cottonwood establishment based on biogeomorphic considerations, but supporting analyses considered primarily the time component. Subsequent analyses by Dufour et al. (2014) on the contribution of abandoned channels to understory diversity directly incorporated biogeomorphic stage into their analyses, by grouping sites based on geomorphic

characteristics. Recognizing the importance of both time and biogeomorphic stage as an indicator of processes controlling cottonwood establishment dynamics, I used time since abandonment and hydrogeomorphic considerations (e.g., main channel connectivity, grain size, channel planform) as proxies to stratify my sites according to biogeomorphic stage.

The ten sites were selected to span a range of time (15–100 years) since cut off, and represented a range of biogeomorphic stages in terms of geomorphic (notably sedimentation) and historical (i.e., plant colonization) conditions. Field observations and aerial photo analyses by Kondolf et al. (2006), Constantine (2008b; 2009), and Michalková et al. (2011) indicated that four of the sites were <25 years old and retained hydraulic connectivity to the main channel. Median upstream overbank discharge was 198 m³/s (C. Gomez, unpublished data; Figure 2). Most of these sites maintained surface water connections at the downstream end even into early summer, during cottonwood seed release. Following the nomenclature of Dufour et al. (2014), I refer to these sites as “young active”. Three of the six older (i.e., > 35 yrs) abandoned channels also retained hydraulic connectivity to the main channel, largely driven by channel planform and orientation. These three older sites shared a straighter channel morphology, resulting in a more active disturbance regime, with more frequent connection to upstream flows (median overbank discharge = 395 m³/s; Figure 2) and significantly coarser sediments deposited in the aquatic zone (Constantine et al., 2009). I refer to these as “old active”. The other three older channels were completely plugged at both upstream and downstream ends, and connected upstream only at high discharge (median overbank discharge = 1086 m³/s; Figure 2), resulting in a lower disturbance frequency (Dufour et al., 2014). I refer to these as “old backwater”. There were no young, disconnected channels along this reach of the Sacramento River. Thus, my analyses across sites compared three biogeomorphic stages that represent different time and disturbance regime conditions: four young active sites (hereafter named ‘YA’, all <25 years old); three old active sites (‘OA’; >35 years old) and three old backwater sites (‘OB’, >25 years old).

For each site selected, its assigned site age (years since abandonment) corresponded to the mid-point year between a sequential set of historical aerial photographs that showed the site before and after abandonment, as described in Constantine et al. (2009) and Stella et al. (2011). The uncertainty in aerial-photo derived site age was ± 2-3 years for 9 of 10 sites, and ± 4 years for the oldest site.

Sampling design

In late April and early May 2007, I surveyed the vegetation within the boundaries of the former wetted channel that had filled with sediment and were currently vegetated (*sensu* Citterio and Piégay, 2009). I did this to ensure I only sampled vegetation that colonized after abandonment. Each site was stratified into upstream, middle, and downstream thirds, and randomly placed one transect on the inner (convex) bend of each channel within each third, for a total of 3 transects per site. All transects were oriented perpendicular to the abandoned channel centerline, began at the transition between aquatic and terrestrial vegetation, and extended upslope away from the aquatic zone for 45 m. 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 (Michalková et al., 2011).

Coincident with the vegetation survey, collaborators (Dufour et al., 2014; Stella et al., 2011) assessed current hydrogeomorphic conditions by surveying topography along each transect relative to the summer baseflow surface water elevation in the river. The surveys were completed during a 10-day period when the mean flow was 266 m³/s at Vina-Woodson Bridge (DWR gage ID: VIN), 220 m³/s at Hamilton City (HMC) and 221 m³/s at Ord Ferry (ORD). Mean sedimentation conditions were characterized using long-term average net sedimentation derived by Stella et al. (2011). These were based on measuring the accumulation of fine sediment above the former gravel bar surface since time of cutoff (Piégay et al., 2008). This depth to gravel was also used as a conservative estimate of depth to root crown in the quantification of tree age uncertainty (detailed below).

Canopy community composition and cottonwood population size structure

To understand differences in woody species composition and dominance among the different sites and biogeomorphic stages, I sampled the overstory canopy composition along each transect by the line intercept method (Krebs, 1999). I quantified the frequency of each species along a transect by counting the presence or absence of the species at each 1-m point. I then calculated relative cover as a metric of abundance to account for overlapping strata of overstory vegetation (i.e., total canopy cover sums to one).

A 10-m belt transect (5 m on either side of the topographic transect line) was surveyed, and all cottonwood stems were mapped and inventoried (total area surveyed: 450m² X 3 transects = 1350m² per site). Trees were mapped via position along the transect (distance and elevation), and their diameter at breast height (DBH) was recorded. Stems shorter than breast-height were inventoried as “seedlings/saplings”. These small stems were counted but diameters were not recorded. If they were very dense (>1/m²) they were surveyed in 1-m wide bands perpendicular to the transect, and each stem within the band was assigned the location of the mid-point station position (e.g., band between 1m and 2m on the transect was recorded at station = 1.5m).

Tree establishment age

To examine age structure and establishment timing, I took increment cores from a sample of trees within our belt transect, stratified by diameter class. I collected cores from 5-18 trees per site using a 5.15 mm increment borer. At one site with much younger saplings, I also collected complete cross-sections (i.e., stem discs or “cookies”) from 12 small-diameter saplings (typically < 5 cm), for a total sample size of 91 trees. I collected cores at breast-height above the ground to avoid basal swell and areas of physical damage (e.g., from flood debris or beavers). I accounted for aging error due to height above root crown as part of my quantification of tree age uncertainty (below). Because growth anomalies are often asymmetric (e.g., a ring can appear “missing” in one part of the cross-section, but identifiable in another; Waring and O’Hara, 2006), I took two to three cores from each tree to minimize error in age estimates due to growth anomalies. I took one increment core from the side of a leaning tree, and one perpendicular to direction of lean (on the upper side of the inclined trunk, where greatest growth is in tension wood; Shroder, 1980).

Cores were air dried, mounted on single mounts (grooved wooden strips), and shaved with a razor blade to improve visibility of vessels and ring boundaries (Morino, 2008). Ring counts on all cores were checked by two people. For cross-dating purposes, annual radial growth increments were measured to 0.01 mm resolution using a dissecting microscope and a sliding-stage micrometer (Velmex Measuring System). For growth anomalies such as identifying missing or false rings, I used standard statistical cross-dating techniques (Grissino-Mayer, 2001; Holmes, 1983). A master chronology from 27 trees was constructed with the aid of the software program COFECHA (Grissino-Mayer, 2001). All cores were cross-dated against the master chronology, using COFECHA to help identify possible missing or false rings (Holmes, 1983). I selected one core per tree for analysis and use in cross-dating, based on the most physically intact core closest to the pith (i.e., oldest).

The efficacy of standard cross-dating techniques to detect false or missing rings in cottonwood is challenging. First, cottonwoods have diffuse porous wood anatomy, with ring boundaries that are difficult to interpret from a single core. However, with multiple cores, razor-blade surfacing (rather than the standard sanding technique) and careful attention to vessel patterns and ring boundary coloration, Morino (2008) was able to identify a false ring signature in the summer monsoon-influenced Fremont cottonwood of the desert southwest. We employed her techniques, even though a similar false-ring response was unlikely on a large, perennial river like the Sacramento. Additionally, cottonwoods are phreatophytic and thus tapped into the groundwater, so are considered less climate-sensitive. Sensitivity to climate is what produces the consistent pattern of narrow and wide rings that are the basis for accurate cross-dating techniques (Speer, 2010). However, Stella et al. (2013), showed that riparian trees in Mediterranean systems “experience stress that varies annually with hydroclimatic water supply, similar to sympatric upland species (e.g., pines and oaks) that are adapted to drier habitats and that are more typically used for dendrochronological studies.” We similarly found enough synchronous variation in ring widths to develop a master chronology. Finally, cottonwoods are a relatively short-lived tree (our oldest trees cored were ~80 years old), and defining the recruitment window required aging not just the oldest, but also the youngest trees at a site. Thus, 75% of the trees that I aged had <30 years of measurable growth rings. This limits the length of time-series overlap that can be used for statistically comparing ring width synchrony among trees, and means most young trees (<10 years old) did not cross-date well with the master chronology. However, fast growth rates of young cottonwood trees means rings of young trees were typically very large, with clear ring boundaries, which greatly reduced chances for missing or false rings. Despite these limitations, I was able to generate a master chronology with an interseries correlation of 0.492. My chronology also correlated well with a chronology of cottonwood sampled on Sacramento River main channel floodplain sites (A. Irons, SUNY ESF Master’s Thesis, in prep). Finally, even if some growth anomalies remained undetected, the likelihood of ring shifts producing differences in tree age of more than a few years is very low. The uncertainty is likely well within the bounds of error estimates generated in my corrections for missing pith and height to core, and therefore unlikely to change the interpretation of my results.

Estimating error and quantifying uncertainty in tree age

In collaboration with A. Irons and J. Stella from the SUNY College of Environmental Science and Forestry, I developed methods for estimating the number of rings missing from two possible sources of error: (1) cores that did not hit pith, and (2) core height above the root crown, which

results from burial of the original germination surface (i.e., from sediment deposition) and sampling height above the current ground surface. Both of these errors lead to underestimates of age by missing the earliest years of growth. I modified methods for estimating error due to missing pith. Since field realities prohibited us from sampling tree age at the root crown/germination surface, I developed an age-height correction factor using sectioned saplings, and measured sediment depth at abandoned channel field sites along the Sacramento River, California. Finally, for these last two potential sources of error, I went one step further and quantified the uncertainty in tree ages using a Monte Carlo simulation approach.

Following recommendations of A. Irons (pers. comm.), I measured the length of missing radius from cores that did not hit pith using the graphical method of Rozas (2003), which is based on the anatomical convergence of xylem rays at the pith. I then estimated the number of years of growth missing from this unaccounted radius by fitting a linear mixed effects model to radius data from the subset of increment cores that did hit pith ($n = 26$), similar to the approach taken by Fraver et al. (2011). I modeled the log-transformed relative growth year (i.e., first year of growth is closest to pith) as a function of log-transformed cumulative diameter growth to that year from pith-containing cores (fixed effect), and accounted for the random effect of individual tree growth (within-tree data dependence) by allowing slope and intercept to vary based on variation due to a specific pithed core. The linear mixed modeling approach allowed me to parse the variation due to individual tree from the residual error in the fixed effects (Pinheiro and Bates, 2006). This method is a more accurate reflection of the uncertainty in projecting age because it captures tree-to-tree variation in growth.

I used this model to predict the years of growth missing from cores that did not hit pith ($n=50$), and included a Monte Carlo approach to simulate the error distribution around these predictions:

$$\ln Y_{i,j} = (\beta_0 + b_{j,k}) + (\beta_1 + m_{j,k}) \ln r_i + \varepsilon_j \quad (1)$$

where $Y_{i,j}$ is the predicted number of years of growth missing from the i th tree on the j th iteration, r is the measured estimate of missing radius to pith for the i th tree, β_0 is the intercept for the fixed effect, b is the intercept from the randomly selected k th pithed core on the j th iteration, β_1 is the slope of the fixed effect, m is the slope from the randomly selected k th pithed core on the j th iteration, and ε is the error of the fixed effect selected for the j th iteration, which follows a normal distribution with mean 0 and standard deviation of the residuals of the fixed effect of cumulative growth.

For height above root crown, I used a conservative approach (i.e., yielding largest potential error) by assuming that the majority of cottonwoods germinated on coarser grain-size substrate that is typically found in recently abandoned channels (former point bars) (Chapter 1, Appendix A). I estimated depth of fine sediment accumulated above the former gravel surface via soil augering at the beginning and end of each of my transects (Stella et al., 2011), following methods of Piégay et al. (2008).

To estimate cottonwood height growth rates, I sectioned a total of 25 saplings from five locations within my study area. This included 12 saplings from two different abandoned channel sites, and 13 saplings from three point bar sites. I included the point bar sites because saplings were

abundant only at a limited number of the abandoned channel sites. Saplings ranged in height from 1.5–6.5 m (mean 3.28 m \pm 1.3 SD) with basal diameters of 1.9–6 cm (mean 3.6 cm \pm 1.2 SD). I sectioned each sapling every 0.5m, starting at the base of the stem. Average growth rates were calculated as the difference in height from basal to upper-most stem section, divided by the difference in number of annual growth rings. Thus, a two-meter tall sapling that had 5 annual growth rings at the base, and 1 annual growth ring at the top, grew two meters in 4 years for an average growth rate of 0.5m/year. To predict the number of years of growth missing as a function of stem height, I fit a linear model with years as the response variable, and predictor variables of height and location (point bar vs. abandoned channel) to account for differences in growing conditions.

Following methods of Yanai et al. (2010), I used the standard error of the regression as my measure of uncertainty (i.e., variation around the fitted equation), calculated as:

$$s_{y.x} = \sqrt{\frac{\sum(y_i - \hat{y}_i)^2}{n-q}} \quad (2)$$

where y is the dependent variable of years missing; y_i is the observed and \hat{y}_i is the predicted value of the i th observation, n is the number of observations, and q is the number of fitted parameters (3 in my case). I then used Monte Carlo simulation to estimate the error in tree age that resulted from estimates of coring height above root crown as:

$$Y_{i,j} = \beta_0 + \beta_1 H_i + \beta_2 L_i + \varepsilon_j \quad (3)$$

$$H_i = \binom{d_{1i} d_{2i}}{1} + 1.3 \quad (4)$$

where Y is the predicted number of years of growth missing from the i th tree on the j th Monte Carlo iteration, β_0 , β_1 , and β_2 are the fitted regression parameters (intercept and slope), H_i is the height to core in meters, L_i is the binary factor indicating location group (0 for point bar, 1 for abandoned channel) of the i th tree, and ε_j is the regression error sampled for the j th iteration. I assumed the regression error was normally distributed, with a mean of zero and standard deviation of $s_{y.x}$. For each transect, I had two measures of sediment depth (d_1 , d_2), taken at the beginning (4-m) and end (44-m). I accounted for uncertainty in tree-specific measurement of sediment depth by incorporating it into the Monte Carlo simulation. For the i th tree on the j th iteration, I randomly selected one of the two sedimentation depths measured along each transect, added 1.3 m to account for coring at breast height, and applied this value as the estimated height above root crown (H_i). For all my Monte Carlo simulations, the number of iterations (j) was 1000.

Data analysis

I examined the role of cottonwood within the context of the broader overstory plant community as a function of time and biogeomorphic stage. I calculated the relative proportion of each species along each line-intercept transect, and averaged these by site to get relative percent canopy cover by site. I calculated well-established species diversity metrics (Magurran, 2004) of richness (S), Shannon's diversity index (H') (Shannon and Weaver, 1949), and Pielou's index of

evenness (J) (Pielou, 1969) in order to describe general patterns in overstory species richness and abundance as a function of site age and biogeomorphic type. In order to document the distribution of size classes present at each site, I then quantified the cottonwood population size structure by calculating relative stem density by diameter class (5cm DBH bins) from the belt-transect data.

To quantify tree age distributions across the gradient of site age and biogeomorphic stage, I calculated metrics of mean, median, 97.5th and 2.5th quantiles, along with the estimated error due to missing pith and height to core in these metrics determined from Monte Carlo simulation. For estimates of mean tree age aggregated by site age, I also included sampling error to account for sample size. Estimates of the 97.5th and 2.5th percentile of tree ages were used as a metric to capture 95% of the tree age distribution at each site. This metric captures the vast majority of the range in tree ages, without undue influence from outliers. I used the difference between these two quantiles to define the recruitment time window, summarized both by site age and by biogeomorphic stage (young active, old active, old backwater).

As a check for potential sampling bias in our age data set, I compared the diameter size of trees sampled by increment coring with the complete size distribution data from the belt transects. This revealed that while sampling had successfully captured the largest size class present at all sites, in several cases I did not have representative age samples from the smallest diameter size class. This sampling error potentially results in an underestimate of the recruitment window. To address this, I developed a regression relationship between tree age and diameter from the cored trees. Because increment cores and diameters were taken at breast height, I used only the pith-corrected tree age in the regression model. Ideally, I would have applied this regression model to predict ages of trees from the complete size distribution data set. However, due to high variability in growth of larger trees, model predictions for trees > 40cm DBH were unreliable. Thus, I used the regression to show a general trend between tree size and age, but only generated predictions from the model for small-diameter trees where the model variance was low. . In cases where I did not have tree age data representative of the smallest diameter stems found within the belt transects, I used the pith-corrected age-dbh relationship and the height correction equation to generate a predicted age for the smallest size class stem. I used the mid-point of the smallest diameter class for prediction (i.e., predicting a 2.5cm DBH stem to represent the 0-5cm size class). The predicted age of the smallest diameter size class present at each site was used to provide an indication of the most recent cottonwood tree establishment, and thus how much the recruitment window may have been underestimated.

RESULTS

Overstory community composition and cottonwood population size structure as a function of site age and biogeomorphic stage

The overstory vegetation in the abandoned channels followed a common successional trajectory, dominated first by riparian scrub and transitioning to mixed riparian forest (Conard et al., 1980; Vaghti and Greco, 2007) with increasing time since abandonment. The lowest species diversity, in terms of richness, Shannon's diversity index, and Pielou's evenness index, was at the youngest and oldest site, and diversity peaked in the middle-aged sites (Table 1). Cottonwood was present

in the canopy along our transects at all but one site, and at ~20% of the relative canopy cover in all but the youngest and oldest sites. Young active abandoned channels were dominated by pioneer species of *Salix* (predominantly *S. exigua*, *S. lucida*, and *S. goodingii*) (Table 2), representative of a riparian scrub vegetation type (Vaghti and Greco, 2007). The two youngest sites had >90% relative canopy cover of *Salix* spp. (dominated by *S. exigua*), with proportionately more cottonwood in the two older young active sites. A more diverse canopy assemblage, in terms of both richness and evenness, was found in older sites. *Acer negundo*, a mid-successional species, appeared in increasing abundance with site age ≥ 20 yrs. Another typical mid-successional species, *Fraxinus latifolia*, was notably rare both in frequency and abundance, occurring in only the oldest site at low relative cover. *Juglans hindsii*, a mid- to late-successional species, appeared only in sites ≥ 48 years, but the species was abundant where present, averaging 24% of the canopy. Other mid-successional species typically associated with mixed riparian forest included (1) *Platanus racemosa*, which was present sporadically across the age range of sites, with 5-12% relative canopy cover where present, and (2) *Alnus rhombifolia*, which occurred in only two sites. Lastly, the invasive *Arundo donax* occurred as an overstory species at two older sites.

The size class distribution of cottonwoods within the $45 \times 10\text{m}$ belt transects also supports a typical progression of stand development through time, from many small to a few large trees. The young active sites supported high densities of small-diameter (<10cm) stems (Figure 3), with the two 20-22 year-old sites showing a traditional reverse-J shape distribution indicative of a multi-aged stand (Oliver and Larson, 1996). The largest diameter class in the young active sites was 35-40 cm DBH. In contrast, tree size-distribution at the older sites had gaps among the size classes (Figure 4). The older sites had lower densities of cottonwoods present overall, and the trees that were present were larger (>20cm, and included trees in the largest diameter size class (100-105 cm DBH). Despite the shift in size structure, cottonwood was maintained in the canopy at a fairly consistent proportion (~20%) for all but the youngest and oldest sites (Table 2).

Tree aging error estimates

The length of radius to pith was a significant predictor of age ($p < 0.001$ for the slope of the fixed effects). Based on the sample of tree cores that hit pith, the fitted parameters for the linear mixed effects model were as follows:

$$\ln Y_{pith} = (-1.50 + b_k) + (0.82 + m_k) \ln r + \varepsilon \quad (5)$$

$$b_k \sim N(\mu = 0, \sigma = 0.84)$$

$$m_k \sim N(\mu = 0, \sigma = 0.15)$$

$$\varepsilon \sim N(\mu = 0, \sigma = 0.52)$$

where Y_{pith} is the predicted number of years missing, r is the length of missing radius to pith, b_k and m_k are the errors in slope and intercept due to the random effect of the k th pithed core, and ε is the error of the fixed effect of radius length (standard deviation of fixed effect residuals).

Based on sectioning of saplings, the equation for predicting height to core was as follows:

$$Y_{ht} = 1.58 + 0.26H + 1.87L + \varepsilon_{reg} \quad (6)$$

$$\varepsilon_{reg} \sim N(\mu = 0, \sigma = 0.234)$$

where Y_{ht} is the number of predicted years missing as a function of coring height, H is height to core (sediment depth in meters plus height from current ground surface to core), L is a binary location group variable of 0 for point bar and 1 for abandoned channel, and ε_{reg} is the error of the regression. The model had an adjusted $r^2 = 0.80$, and $p < 0.0001$. The average growth rate for saplings growing in abandoned channels was 0.9 m/yr (± 0.29 SD), and 1.2 m/yr (± 0.31 SD) on point bars.

The estimated error in tree ages due to missing pith was smaller than for the error due to coring height when the missing radius to pith was less than approximately 20 mm (Figure 5). Half of the cores missing the pith fell into this category. The median number of years predicted to be missing due to missing pith was 1.1, and 3.4 for the 75th percentile. Otherwise, error due to missing pith was much larger than from coring height above root crown. Given the fast height growth of cottonwoods, even a height above the estimated establishment surface of 6 meters was predicted to only be missing ~5 years of early growth.

Timing of cottonwood establishment and the length of the recruitment window

Mean and median tree age of cored trees corresponded to the age of the site as estimated from aerial photographs (Figure 6). Thus, younger sites (i.e., those more recently abandoned) had correspondingly younger trees. With the exception of one outlier (the old backwater site), the young active sites had significantly younger trees (95% confidence intervals did not overlap), but site age was a better predictor than biogeomorphic stage. For all but 2 sites, estimates of the oldest trees at each site (97.5th quantile) overlap with aerial-photo-derived site age (Figure 7), indicating that a cohort of trees established at or very near the time of channel abandonment. At one site the 97.5th age quantile predates channel abandonment (40-year old backwater site), indicating the tail of the age distribution may have captured trees that established prior to channel abandonment. However, there were other trees sampled at this site whose age did correspond to the time of cutoff, as evident from mean and median age metrics (Figure 6). At the 100-year old active site, the 97.5 age quantile (i.e., the oldest trees) fell significantly below the maximum estimate in aerial-photo-derived site age (+4 years). In other words, the oldest surviving trees at this site recruited 10 to 20 years *after* channel abandonment.

Regardless of site age or biogeomorphic stage, the recruitment window for all but one site was < 18 years (Figure 7). Together with the correspondence between oldest trees and time of channel abandonment, this result indicates that cottonwood establishment occurs within the first two decades following channel abandonment, and then ceases. The oldest backwater site was an outlier, with a wide recruitment window of 39.2 yrs (95% CI: 37.9 – 43.5). Apparently, cottonwoods at this site have successfully established for a much longer period of time following channel abandonment. At the other extreme, one of the young active sites had a more narrow recruitment window of only 3.3 years (95% CI: 2.7-4.8). Recruitment windows averaged by biogeomorphic stage yielded differences only between young active (11.1 yrs, 10.0 – 16.7 95% CI), and old backwater stage (18.7 yrs, 17.4-23.4 95% CI). However, this difference is strongly influenced by the broad window of the outlier (old backwater) site mentioned above (Figure 7c). The old active stage overlapped with the other two stages (13.8 yrs, 10.9 – 22.2 95% CI).

Tree diameters and pith-corrected ages of cored trees were positively correlated ($R^2=0.88$), with small error in the relationship for trees < 20 cm DBH (Figure 8). However, there was an abrupt increase in variability with size at approximately 40 cm DHB. For example, while trees between 20-40 cm DBH showed very little difference in age, a tree with a diameter of 75 cm could be anywhere from ~ 20 to 70 years old (Figure 8).

I identified potential sampling bias in our age data due to lack of representation from the smallest diameter class at six sites (Figure 9 and Figure 10). However, in only three of these sites would this bias result in an adjusted recruitment window > 20 years (Table 3).

DISCUSSION

The conceptual model presented by Stella et al. (2011) suggesting controls on cottonwood establishment within abandoned channels is largely based on assumptions of a colonization-competition trade-off (Chapters 1 and 2). Cottonwoods are a pioneer species, with traits that confer strong colonization success in the disturbance-prone river environment (Catford and Jansson, 2014; Corenblit et al., 2014; Karrenberg et al., 2002; Lytle and Poff, 2004). Traits that confer colonization fitness often result in poor competitive ability in resource-poor environments (Connell and Slatyer, 1977; Hastings, 1980; Huston and Smith, 1987; Tilman, 1994), and this has been the typical explanation for why cottonwood establishment is limited to bare sites (i.e., no interspecific competitors). My collaborators and I extended this logic to abandoned channel dynamics (Stella et al., 2011), and hypothesized that the more competitive environment that develops during the infilling stage of an abandoned channel would limit cottonwood establishment. As a consequence, cottonwoods were predicted to establish within a narrow window following channel abandonment, when the abandoned channel retains a more physically dynamic regime for which cottonwoods are well adapted. However, my mesocosm experiments suggest cottonwoods are not as poor competitors as is the predominant view in the literature (Chapter 1), that soil moisture is the dominant determinant of seedling establishment (Chapter 1), and that they are more plastic in their tolerance to shade (Chapter 2). From the experiments, I predicted cottonwood seedlings should be able to establish (though perhaps at lower frequency) in the later stages of abandoned channel terrestrialization. Survival was significantly higher on fine sand substrate characteristic of later biogeomorphic stage, because finer substrate retained higher soil moisture for longer than coarser, gravel-sand substrate. Seedlings were also able to survive when competing with up to 80% herbaceous wetland vegetation cover (Chapter 1), and in shady conditions down to 20% of available sunlight (Chapter 2). Thus, my current study sought to examine cottonwood establishment timing in the field, and identify the window of recruitment opportunity provided by channel abandonment.

My results strongly support the observations of Stella et al. (2011) that channel abandonment provides an immediate colonization opportunity for cottonwood. The oldest trees at almost all sites corresponded to the time period of channel abandonment, as independently estimated via time-series aerial photographs. However, in the 100-year-old site, the oldest trees established much later than the time of initial channel abandonment. This result suggests no successful establishment for approximately a decade following channel abandonment. This site has the

straightest channel planform of all our sites, which means initial abandonment may not have reduced the frequency or intensity of the disturbance regime as much as it did in more curved sites. Thus, it is possible that the straighter abandoned channel did not provide safe-sites for seedlings (sensu Polzin and Rood, 2006) until enough aggradation had occurred to reduce flood frequency. It is also possible that the oldest trees at the 100-year-old site had already senesced (though we saw no evidence of large downed trees, they may have been transported away during a large historical flood), or were so rare that they were missed in our sampling.

Next, my results suggest that the recruitment window (i.e., length of time available for successful cottonwood establishment) lasts for almost two decades following channel abandonment. First, the tree age data show remarkable consistency in the length of time between the oldest and youngest trees, regardless of site age or biogeomorphic stage. This includes robust estimates of uncertainty that account for potential sources of error due to missing pith or depth of sediment deposited above the root crown. Second, the overstory vegetation in abandoned channels followed a common riparian forest successional trajectory with increasing time since abandonment (Table 2). The most recently abandoned sites (15 years old) were still dominated by *Salix* spp., an indicator that sites of this age still support conditions preferable for pioneer tree species. Third, the size class distribution of cottonwood stems showed small-diameter stems (<5cm DBH) in all sites ≤ 22 years old (Figure 3), but notably absent in sites older than 28 years (Figure 4). The older sites had transitioned to a more diverse mixed riparian forest, with fewer, larger-diameter cottonwood trees in addition to species such as *Acer negundo* and *Juglans hindsii*, which are characteristic of mid- to late-successional stages (Conard et al., 1980; Vaghti and Greco, 2007). At several sites I did not have cottonwood tree core samples from trees representative of the smallest diameter class present, which would result in an underestimate of the length of the recruitment window. Predictions based on the age-size relationship of cored trees (Figure 8) suggest that this could extend the window even further, up to 40 years at one site.

Reconstructing tree establishment age via tree cores is beset by uncertainties that make it difficult to distinguish even-aged cohorts that establish soon after the disturbance from multi-aged populations with multiple recruitment opportunities (Fahey and Lorimer, 2014). I applied state-of-the-art quality control and quality assurance techniques to minimize errors in the tree ring counts. My efforts included collecting multiple cores from each tree, obtaining two independent ring counts for each core, and using statistical cross-dating to correct for missing or false rings (Grissino-Mayer, 2001). In addition, I calculated robust estimates of error introduced by the correction for missing pith and buried stems. Finally errors in tree age were propagated via Monte Carlo simulation. The use of Monte Carlo simulations provide for the instances where errors cancel. Thus it not only returns a robust estimate of the tree age but also allows for a realistic approximation of the error distribution that directly inform our inferences regarding the size of the recruitment window.

My results support the contention of Stella et al. (2011) with regard to the importance of abandoned channels as spatial refugia for cottonwoods. Channel abandonment is episodic, but a cohort of trees always successfully establishes, and cohorts can continue to successfully establish for a window of approximately 20 years, and possibly up to 40 years at some sites. The length of the recruitment window extends in time the spatial refuge provided by abandoned channels and thus helps ensure continued persistence of the cottonwood population. In light of the significant

declines in seedling establishment along the active channel of regulated rivers (Braatne et al., 2007; Fenner et al., 1985; Friedman et al., 1998; Jansson et al., 2000; Johnson, 1994; Rood and Mahoney, 1990), conserving existing abandoned channels and maintaining active channel meander that leads to periodic channel abandonment is particularly critical for persistence of cottonwood populations faced with stabilized disturbance regimes.

TABLES

Table 1. Abandoned channel field site information and canopy diversity indices. YA = young, active; OA = old, active; OB = old, backwater, per Dufour et al. (2014). Estimated year of channel abandonment was derived from time-series historical aerial photographs. To maintain consistency with analyses of Stella et al. (2011) and Dufour et al. (2014), age of the site is age at time of sampling (2007). Location of the site refers to right or left bank (facing downstream), and river mile. S = species richness, H' = Shannon's Diversity Index, J=Pielou's Evenness Index. The evenness index yields a number between 0 and 1, with 1 indicating complete evenness (all species present at equal proportions).

Biogeomorphic Stage	Estimated Year of Cutoff	Site Age	Site #	Location	S	H'	J
YA	1992	15	10	L203	4	0.82	0.59
YA	1992	15	2	R174	5	1.28	0.80
YA	1987	20	8	R221E	8	1.85	0.89
YA	1985	22	3	R178	6	1.74	0.97
OB	1979	28	9	R237	7	1.80	0.92
OB	1967	40	5	R192	8	1.85	0.89
OB	1959	48	7	R221W	7	1.65	0.85
OA	1972	35	1	R168	6	1.59	0.89
OA	1951	56	4	R189	8	1.76	0.85
OA	1907	100	6	R193	4	1.04	0.75

Table 2. Mean site-level fraction relative cover of canopy vegetation from line intercept transects.

Dashed lines (--) indicate the species was not present along any transect at the site. Species codes are as follows:

POFR	<i>Populus fremontii</i>	ACNE	<i>Acer negundo</i>	JUHI	<i>Juglans hindsii</i>
PLRA	<i>Platanus racemosa</i>	ALRH	<i>Alnus rhombifolia</i>	FRLA	<i>Fraxinus latifolia</i>
ARDO	<i>Arundo donax</i>				

Type	Site Age	Site #	Location	Salix spp.*	POFR	ACNE	JUHI	PLRA	ALRH	FRLA	ARDO	Other†
YA	15	10	L203	0.96	0.04	--	--	--	--	--	--	--
YA	15	2	R174	0.91	0.09	--	--	--	--	--	--	--
YA	20	8	R221E	0.53	0.24	0.14	--	0.05	0.04	--	--	--
YA	22	3	R178	0.56	0.29	0.15	--	--	--	--	--	--
OB	28	9	R237	0.69	0.20	0.09	--	--	--	--	--	0.02
OB	40	5	R192	0.19	0.17	0.22	--	0.08	0.21	--	--	0.13
OB	48	7	R221W	0.24	--	0.37	0.12	--	--	--	0.19	0.08
OA	35	1	R168	0.33	0.24	0.25	0.18	--	--	--	--	--
OA	56	4	R189	0.06	0.20	0.14	0.34	0.12	--	--	0.12	0.03
OA	100	6	R193	--	0.06	0.55	0.33	--	--	0.07	--	--
Mean of All Sites				0.45	0.15	0.19	0.10	0.03	0.03	0.01	0.03	0.03

**Salix* spp. (in order of relative abundance) included: *S. exigua*, *S. goodingii*, *S. lucida*, *S. lasiolepis*, *S. laevigata*.

†Other species included: *Catalpa bignonioides*, *Ficus carica*, *Sambucus mexicana*, and *Vitis californica*.

Table 3. Estimates of the recruitment window for each site. $\Delta_{2.5}^{97.5}$ is the recruitment window estimated from the number of years between the oldest (97.5th percentile) and youngest (2.5th percentile) cottonwood trees sampled at each site, along with 95% confidence intervals (Figure 7). The oldest and youngest cored trees at each site are shown (mean age \pm SE of Monte Carlo simulations to address uncertainty from correction-factors), as well as the predicted age of the smallest size class tree found at each site. NA values indicate the smallest size class was sampled via increment coring. The adjusted window was calculated as:

$$\Delta_{2.5}^{97.5} + (Age_{youngest\ sampled} - Age_{youngest\ predicted})$$

Stage	Site Age (\pm 3 yrs)	Site #	Loc.	$\Delta_{2.5}^{97.5}$ (yrs)	Age _{youngest} Sampled	Age _{oldest} Sampled	Age _{youngest} Predicted	Adjusted Window
YA	15	10	L203	11.7 (10.7–13.9)	4.9 \pm 0.3	17.8 \pm 1.4	NA	11.7
YA	15	2	R174	15.5 (9.3–31.8)	9.2 \pm 0.2	26.1 \pm 6.4	6.4–7.0	18.1
YA	20	8	R221E	3.3 (2.7 – 4.8)	12.4 \pm 1.1	15.4 \pm 0.3	6.5–6.6	9.2
YA	22	3	R178	16.8 (14.9–23.3)	15.4 \pm 1.7	28.6 \pm 2.6	6.5–7.5	25.7
OB	28	9	R237	10.7 (8.4–15.7)	22.4 \pm 1.9	27.7 \pm 4.3	14.3–14.4	18.8
OA	35	1	R168	6.9 (5.2–15.6)	41.3 \pm 2.9	39.2 \pm 4.1	19.4–19.7	28.8
OB	40	5	R192	14.2 (12.3–21.7)	38.5 \pm 3.0	52.7 \pm 6.1	NA	14.2
OB	48	7	R221W	39.2 (37.9–43.5)	13.9 \pm 2.7	54.2 \pm 2.8	NA*	39.2
OA	56	4	R189	17.4 (15.2–23.3)	45.0 \pm 1.9	60.8 \pm 0.6	23.5	38.9
OA	100	6	R193	6.1 (5.3–11.1)	76.5 \pm 0.3	80.5 \pm 2.7	NA*	6.1

* These sites did not have cottonwood trees that fell within the belt transects.

FIGURES

Figure 1. Study area map and representative pictures of sites. Top = young 15 yr old site (L203), middle = young 20 yr old site, lower = older 48 yr old site, bottom panorama of young 15 yr old site (R174) showing young cottonwood and willow stand.

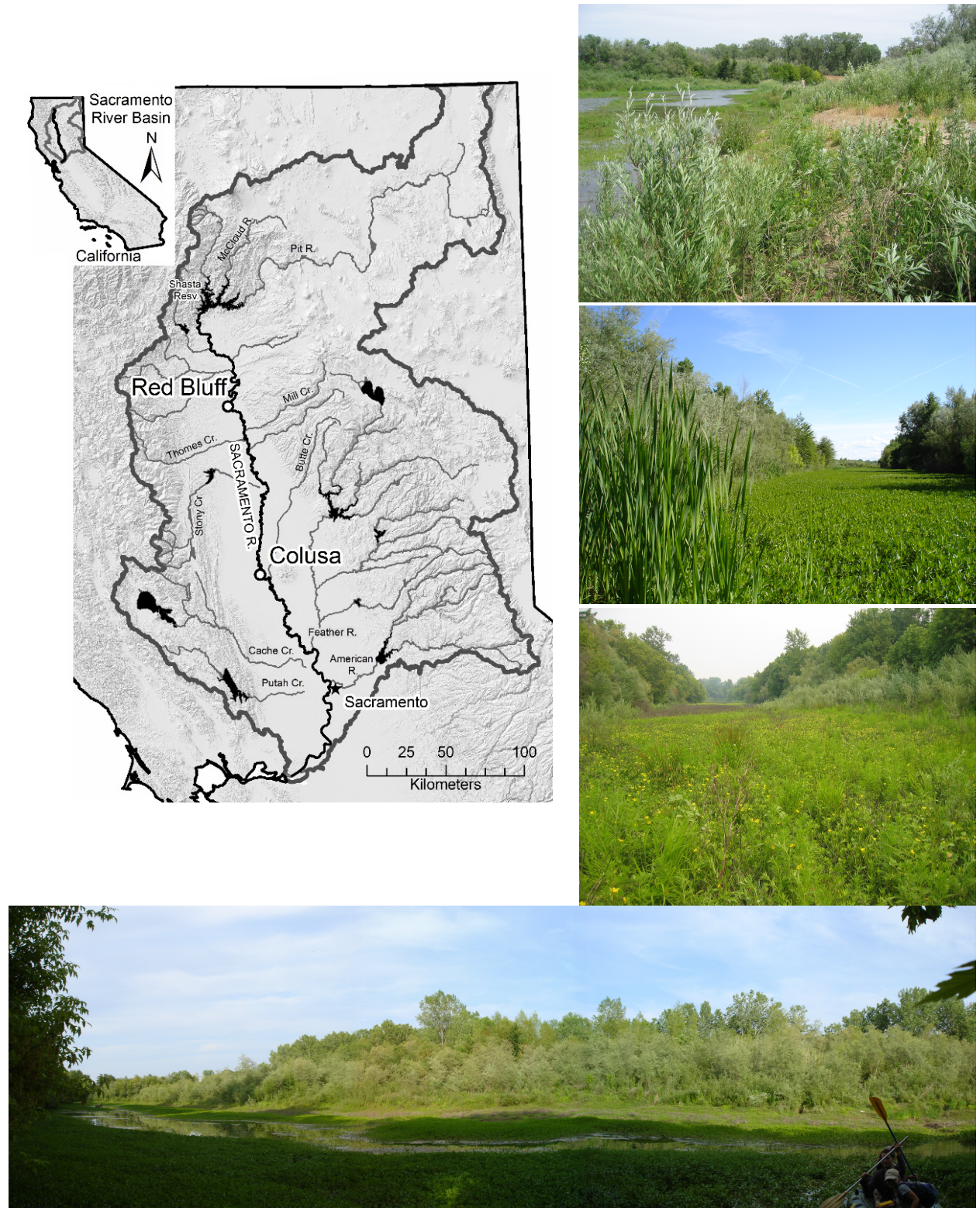
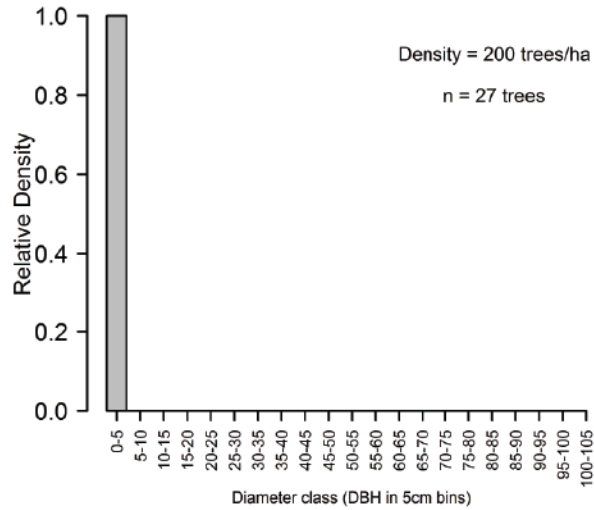


Figure 2. Median overbank discharge at the upstream end of abandoned channels of different biogeomorphic stage, from Dufour et al. 2014 (C. Gomez, unpublished data).

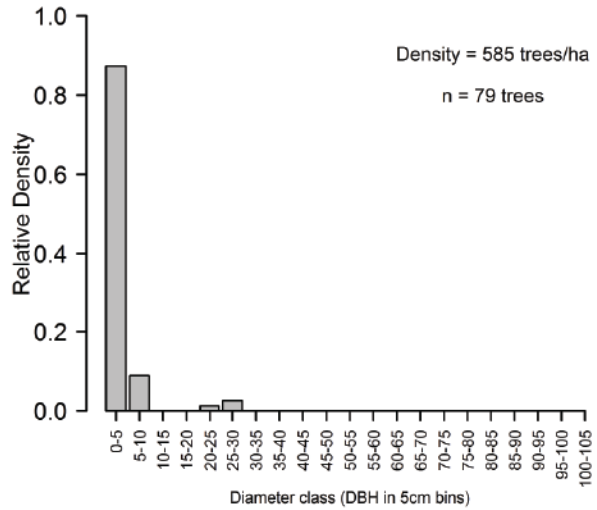


Figure 3. Relative density distributions by tree diameter class (5cm bins) that occurred along belt transects at each of the four young active (YA) sites.

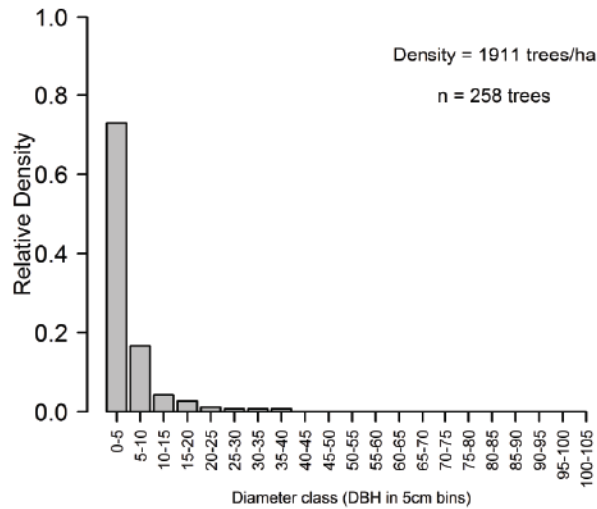
A. 15 yrs (L203)



B. 15 yrs (R174)



C. 20 yrs (R221E)



D. 22 yrs (R178)

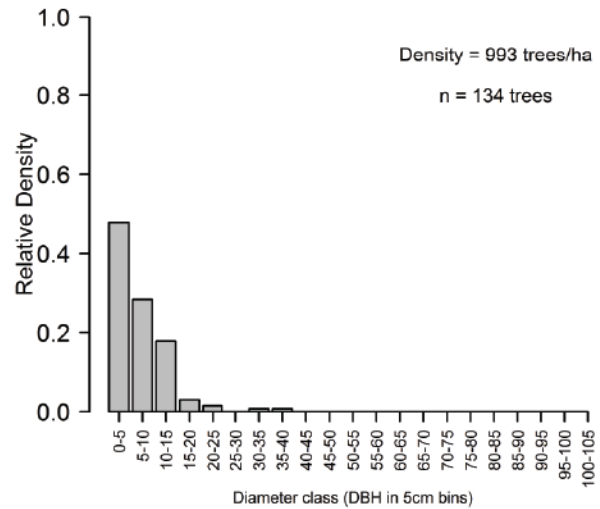
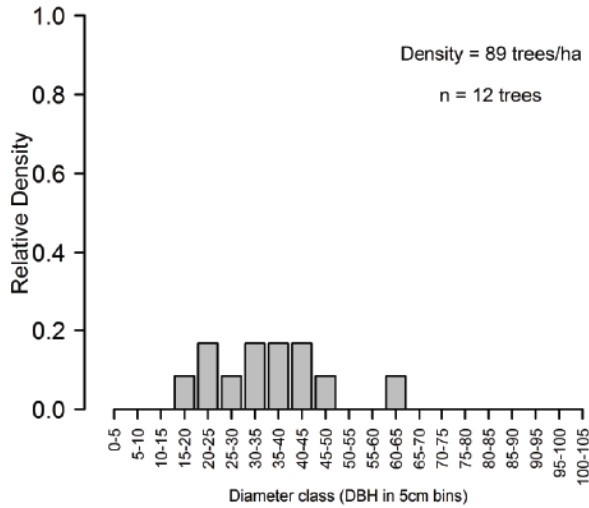
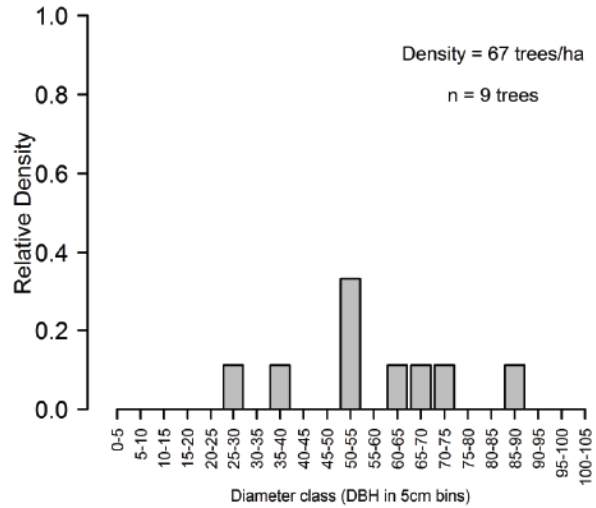


Figure 4. Relative density distributions by tree diameter class (5cm bins) that occurred along belt transects at each of the four oldest sites. Panels (A) and (C) are old backwater sites, and panels (B) and (D) are old active sites.

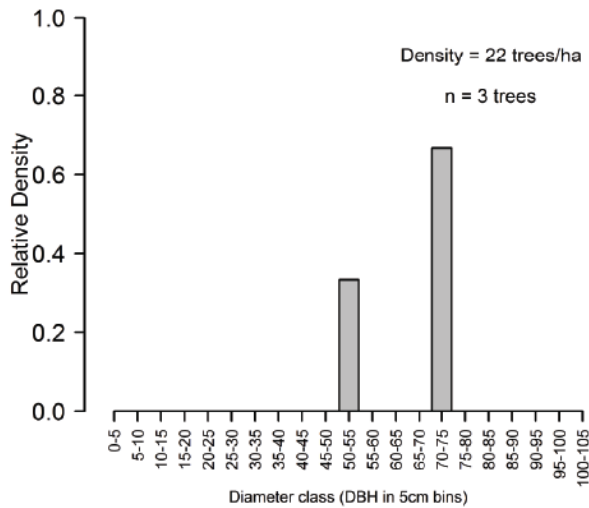
A. 28 yrs (R237)



B. 35 yrs (R168)



C. 40 yrs (R192)



D. 56 yrs (R189)

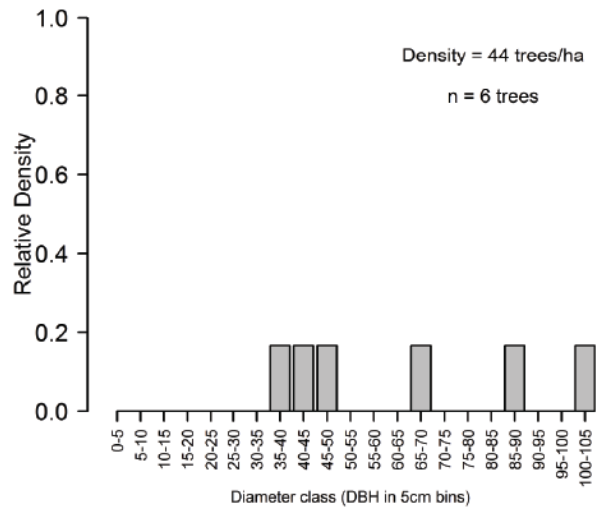


Figure 5. Estimated error in predicted number of years missing (mean \pm SE) due to (A) missing pith, and (B) coring height above root crown, based on Monte Carlo simulations. The missing pith sample size is 50 because 41 cores hit pith and did not need to be corrected. For visualization purposes, the regression line plotted for height to core assumes $\epsilon_{reg} = 0$, and tree-specific predictions were plotted against transect-averaged sediment depth + 1.3 m to account for coring at breast height. Mean variation around the regression line for tree-specific predictions (points) is due to error of regression and random selection of sediment depth (per transect) that occurred as part of Monte Carlo simulations.

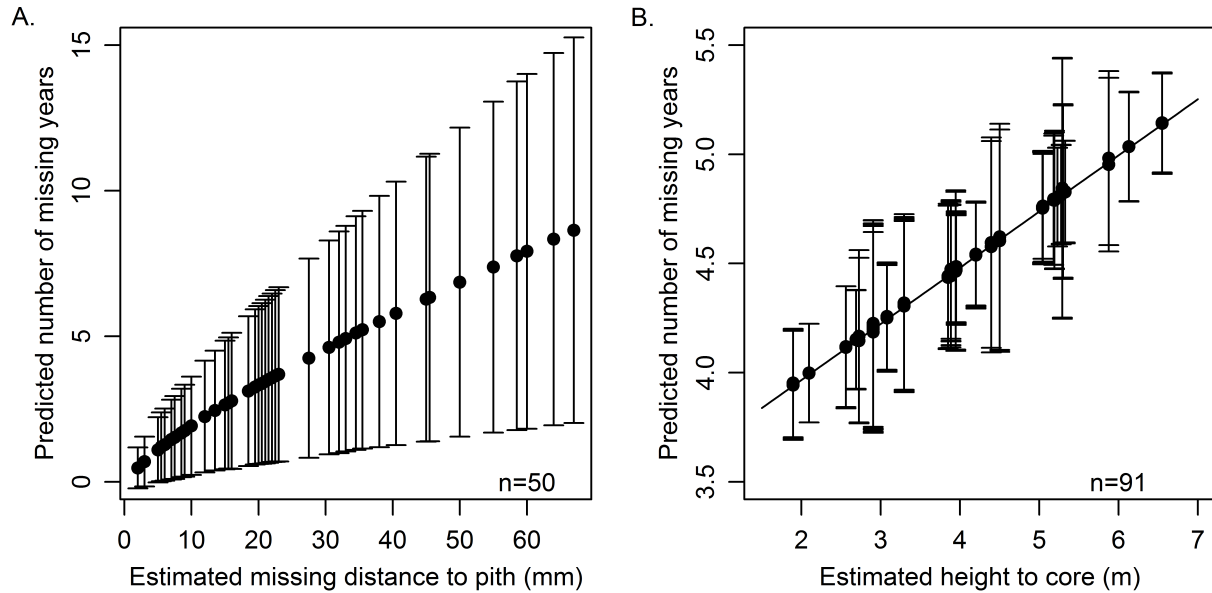


Figure 6. Tree core data by site. (A) Mean tree age for tree cores taken at each site, \pm SE that accounts for both measurement error (missing pith & height to core) and sampling error (number of trees sampled). (B) Median tree age \pm 95% confidence intervals (accounts for only measurement error). The 1:1 line indicates exact correspondence between aerial-photo-derived site age (years since abandonment) and tree age. Error in aerial-photo estimates (i.e., in x-direction) is not shown, but is approximately \pm 3 years.

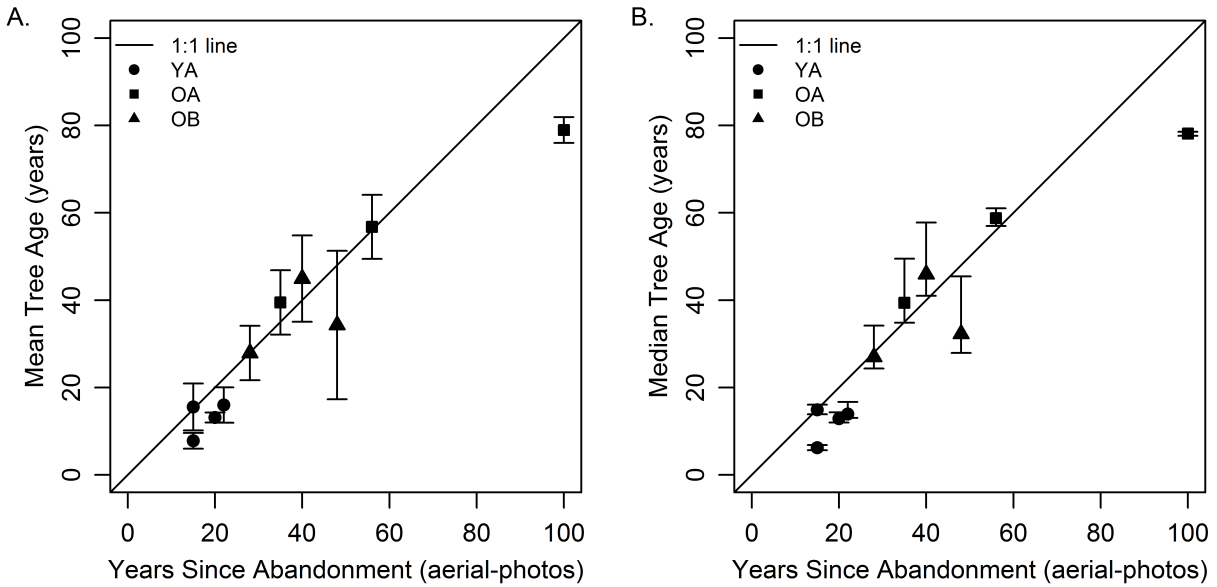


Figure 7. The number of years between (A) the oldest (97.5th percentile) and youngest (2.5th percentile) cottonwood trees sampled at each site was used to estimate (B) the “recruitment window” by site, and (C) the recruitment window by biogeomorphic stage (YA = young active; OA = old active; OB = old backwater). Tree age error bars are calculated as the standard deviation around the average quantile estimates resulting from Monte Carlo simulations. The grey dashed lines in panel (A) indicate the potential error in aerial-photo-derived site age (± 3 yrs). The 1:1 line in panels (B) and (C) indicates a recruitment window that would be the same length of time as the site age (i.e., trees have recruited throughout the entire lifespan of the abandoned channel). Recruitment windows that are below the line indicate sites that had a shorter period of time for cottonwood establishment.

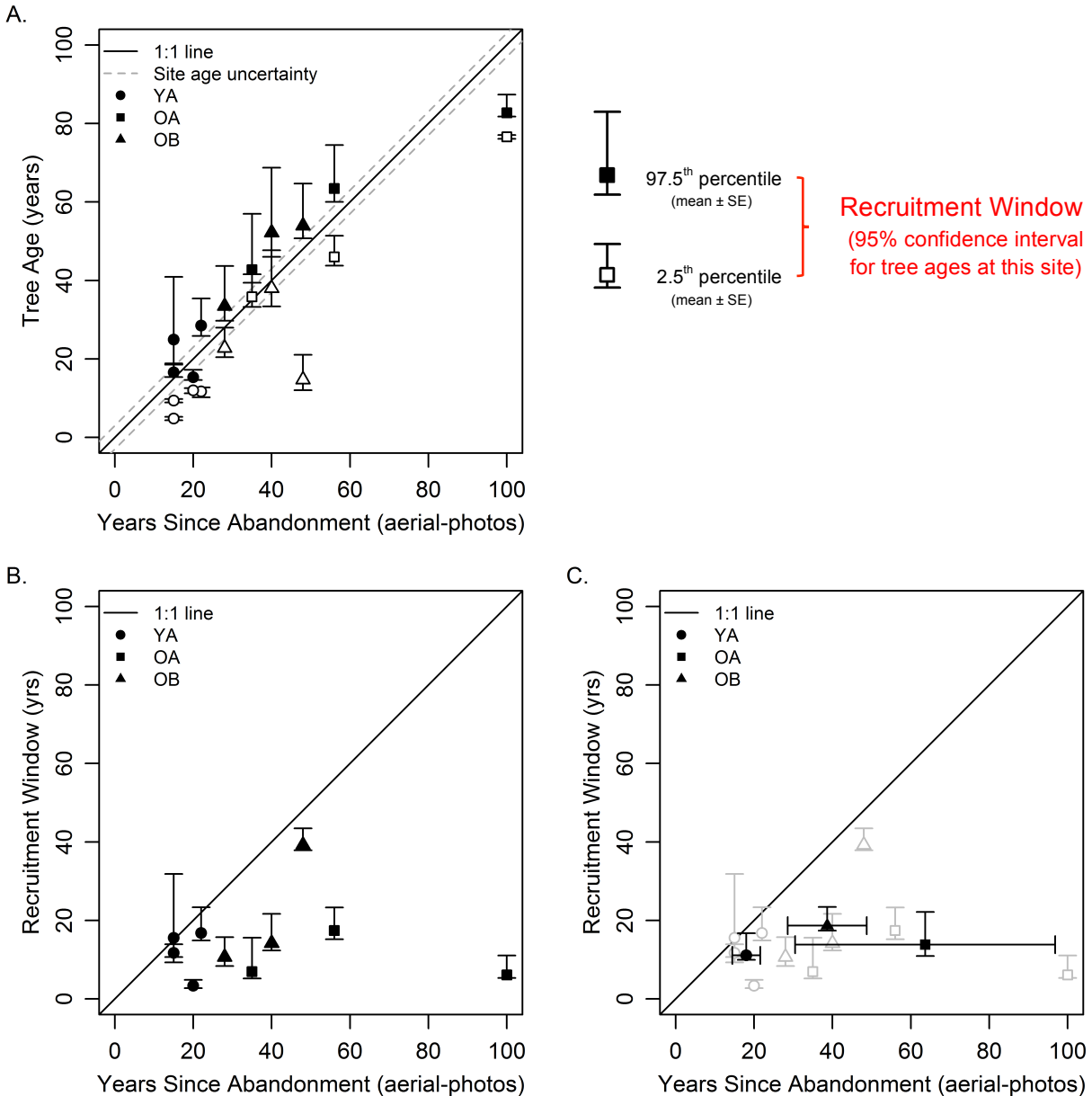


Figure 8. Correlation between diameter at breast height (DBH) and tree age corrected for missing pith (open circles). Raw age (grey points) is shown for reference. Linear fit line for $\ln(\text{pith corrected age})$ vs. $\ln(\text{DBH})$ is shown in black, along with 95% confidence band (grey band). Slope is significantly different from zero ($p < 0.0001$).

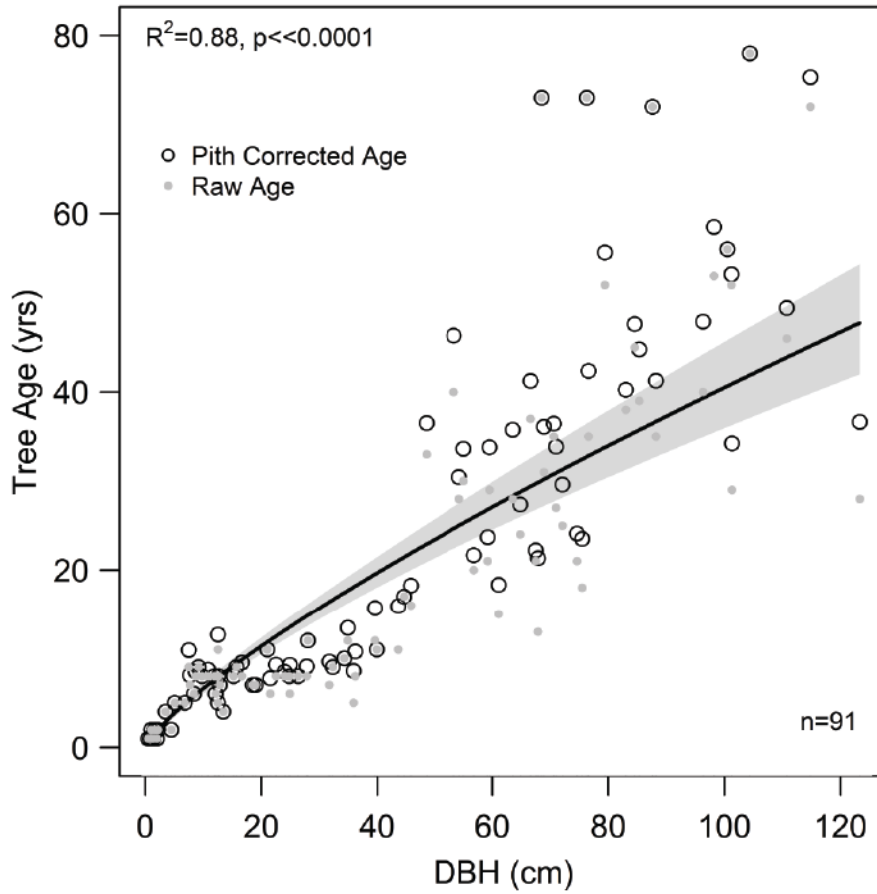
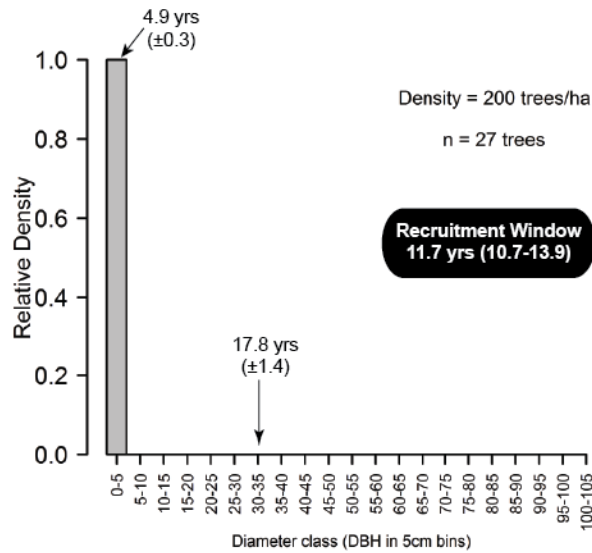
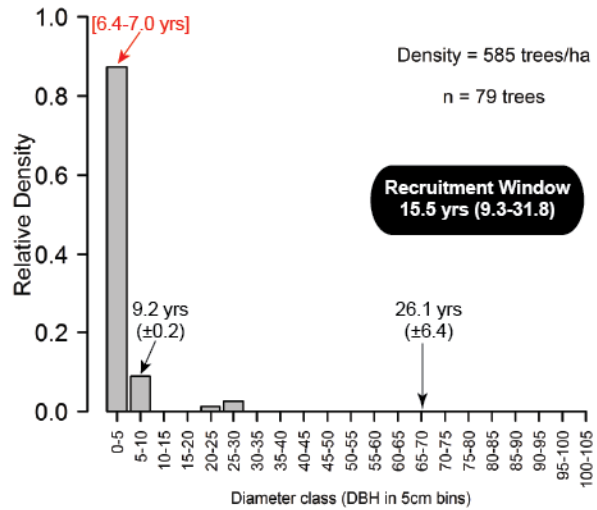


Figure 9. Cottonwood size class distributions with representative tree age data for young active sites. The recruitment window calculated from tree cores is provided in the black box for reference, and the youngest and oldest cored trees are noted in black text (mean age \pm SE from Monte Carlo error simulations). In cases where the youngest cored tree did not represent the smallest size class found within the transects, a predicted age (in red) is indicated for a tree of mid-point size class diameter. This prediction is based on the DBH-age relationship from Figure 6 + height to core correction for the smallest and largest sediment depths sampled at each site.

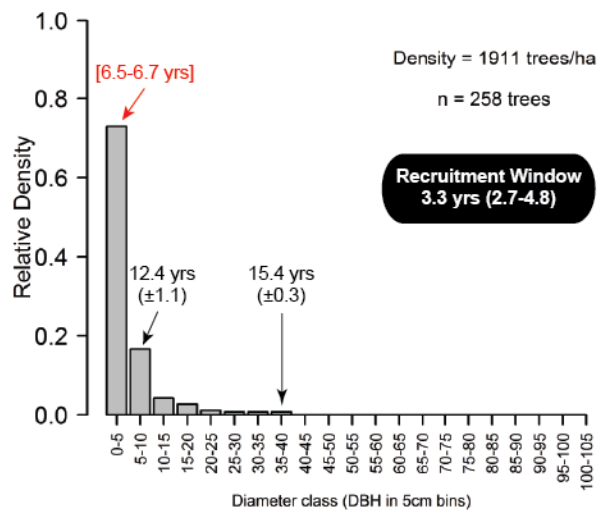
A. 15 yrs (L203)



B. 15 yrs (R174)



C. 20 yrs (R221E)



D. 22 yrs (R178)

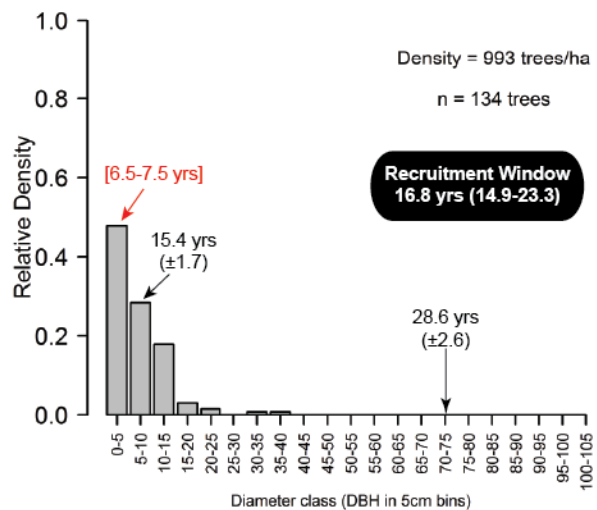
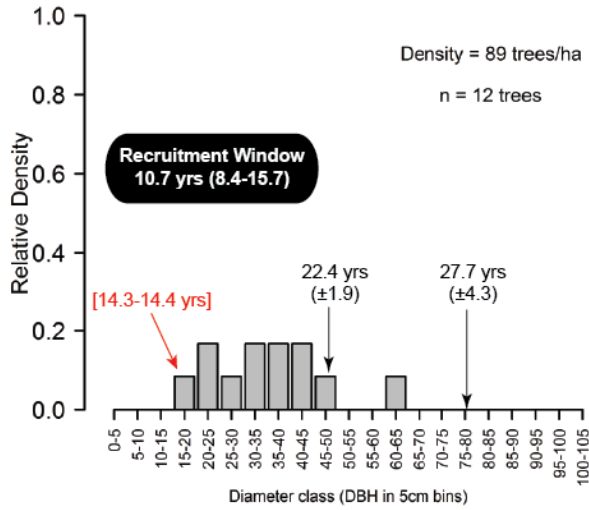
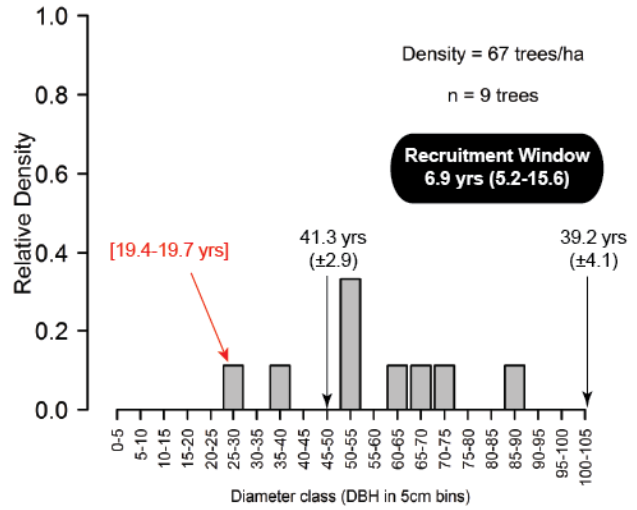


Figure 10. Cottonwood size class distributions with representative tree age data for older sites. All notation is the same as in Figure 9.

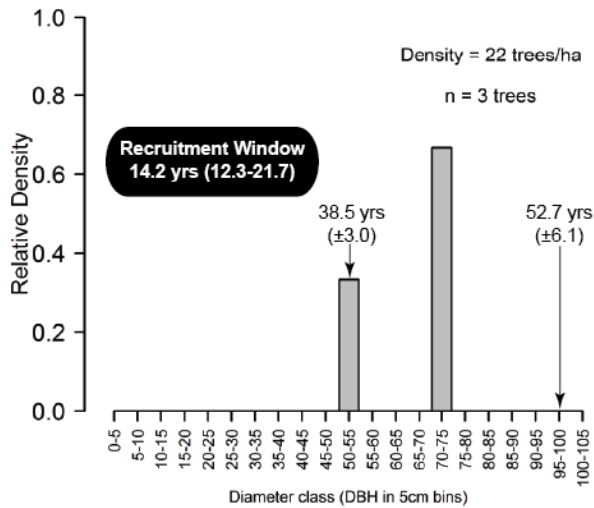
A. 28 yrs (R237)



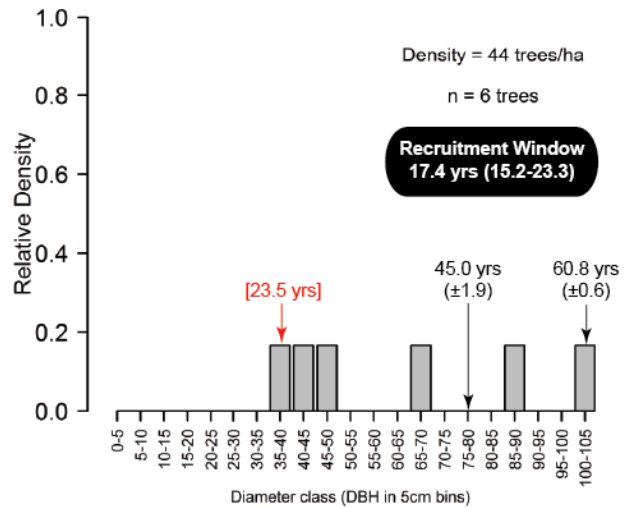
B. 35 yrs (R168)



C. 40 yrs (R192)



D. 56 yrs (R189)



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