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RESEARCH ARTICLE

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Key Points:

- Riparian plant structure and density influence local sedimentation pattern
- Flood-induced plant loss is mediated by hydraulic conditions and plant traits
- Ecogeomorphic feedbacks begin at an early stage of ecosystem development

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Ecogeomorphic feedbacks and flood loss of riparian tree seedlings in meandering channel experiments

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Abstract During floods, fluvial forces interact with riparian plants to influence evolution of river morphology and floodplain plant community development. Understanding of these interactions, however, is constrained by insufficient precision and control of drivers in field settings, and insufficient realism in laboratory studies. We completed a novel set of flume experiments using woody seedlings planted on a sandbar within an outdoor meandering stream channel. We quantified effects on local sedimentation and seedling loss to scour and burial across realistic ranges of woody plant morphologies (*Populus* versus *Tamarix* species), densities (240 plants m⁻² versus 24 m⁻²), and sediment supply (equilibrium versus deficit). Sedimentation was higher within *Tamarix* patches than *Populus* patches, reflecting *Tamarix*'s greater crown frontal area and lower maximum crown density. Plant dislodgement occurred rarely (1% of plants) and was induced in plants with shorter roots. Complete burial was most frequent for small *Tamarix* that occurred at high densities. Burial risk decreased 3% for *Populus* and 13% for *Tamarix* for every centimeter increment in stem height, and was very low for plants >50 cm tall. These results suggest that *Tamarix* are proportionally more vulnerable than *Populus* when small (<20 cm tall), but that larger plants of both species are resistant to both burial and scour. Thus, plant morphological traits and development windows must be considered in addition to physical drivers when designing process-based restoration efforts on regulated rivers such as flow releases to benefit native tree species.

1. Introduction

Abiotic and biotic forces combine to produce high diversity and physical complexity in riparian vegetation communities [Hupp and Osterkamp, 1996; Naiman et al., 2005]. Scour and deposition during high flows, water table dynamics, and other hydrogeomorphic properties interact with biological processes such as seed dispersal, germination, and seedling drought tolerance to directly or indirectly influence species establishment and successional trajectories of riparian vegetation communities [Naiman and Decamps, 1997; Mahoney and Rood, 1998; Karrenberg et al., 2002; Merritt and Shafroth, 2012; Bendix and Stella, 2013]. In turn, as riparian communities establish and develop following disturbance, they begin to exert feedbacks on the physical system, such as increasing sedimentation, stabilizing stream banks, and assisting soil formation, thus establishing a process of codevelopment of landforms and vegetation change [Stella et al., 2011; Gurnell, 2014].

Among the least-studied aspects of the codevelopment of riparian vegetation and geomorphic processes are the mechanisms governing the survival and feedbacks of plants at the individual and patch scales in response to physical disturbance [Steiger et al., 2005; Corenblit et al., 2011]. Seedling mortality from physical forces is a strong demographic bottleneck for riparian plant populations [Scott et al., 1997; Lytle and Merritt, 2004; Harper et al., 2011], yet a mechanistic understanding of cohort mortality is lacking [Mahoney and Rood, 1998]. Furthermore, the influence of plant morphology and density on topographic change (net scour and deposition) following floods is of critical importance in understanding initiation of vegetation feedbacks [Burylo et al., 2012a; van Dijk et al., 2013]. These processes have been studied in flume settings with plant proxies [Albayrak et al., 2012; Ortiz et al., 2013; Li et al., 2014], in flume studies with reduced-scale vegetation [Tal et al., 2004; Braudrick et al., 2009; Perona et al., 2012], and in observational field studies [Asaeda et al.,

2011; Dean and Schmidt, 2011; Manners et al., 2014]. Controlled studies with full-scale plants and realistic fluvial landforms are extremely rare (but see Freeman et al. [2000] and Rominger et al. [2010]), yet such studies are needed to further understand interactions between vegetation and physical forces.

Hydraulic forces during floods can cause high rates of plant damage and mortality. Plants may be uprooted directly by flow-induced drag forces or by drag combined with local substrate erosion around the plant roots [Edmaier et al., 2011]. Damage and mortality can also result from burial, which can occur when the stems and canopy are propped by floodwaters and then covered with sediment deposited as peak flows recede [Levine and Stromberg, 2001]. Some species are adapted to resprout from plant parts scoured and transported downstream [Bellingham and Sparrow, 2000; Pettit et al., 2006; Rodriguez-Gonzalez et al., 2010], or else re-emerge from buried sediment [Levine and Stromberg, 2001; Polzin and Rood, 2006; Burylo et al., 2012b]. Observational studies, however, suggest that plants that are scoured or completely buried experience substantially reduced rates of survival [Brewer et al., 1998; Polzin and Rood, 2006; Wilcox and Shafroth, 2013]. In a field experiment monitoring the survival of *Salix* cuttings over two flood seasons on the River Thur, Switzerland, mortality rates due to burial and/or dislodgement were 47% and 58% [Pasquale et al., 2013].

Plant loss and damage depend on physical factors such as stream power, shear stress, topography, substrate type, and sediment transport [Bendix, 1999; Dixon et al., 2002; Pasquale et al., 2013]. Additionally, a plant's own architecture (e.g., stem height, frontal area, root distribution, and stem flexibility) may influence the degree of scour and burial loss through its effects on flow hydraulics, sediment transport and deposition patterns, and substrate cohesion [Burylo et al., 2012a; Yager and Schmeckle, 2013].

Riparian vegetation and landforms codevelop in regions where flood regimes have a strong influence on plant establishment, subsequent mortality, and riparian community trajectories [Bendix and Stella, 2013]. For example, in many semiarid riverine systems, cottonwood (*Populus*) and willow (*Salix*) are flood-dependent ecosystem pioneers, establishing following disturbances and dominating riparian woody communities during the early stages of succession [Karrenberg et al., 2002; Stella et al., 2013]. Cottonwood in particular are high-biomass, foundational tree species, creating locally stable conditions within the riparian zone by defining the forest structure and driving key processes such as forest productivity, generation of woody debris, sedimentation, water balance, and microclimate [Ellison et al., 2005]. These trees provide a range of ecosystem services [Strange et al., 1999], yet are sensitive to altered flow regimes [Rood et al., 2003]. In riparian zones of the western U.S., native *Populus* and *Salix* trees have been extensively replaced by *Tamarix* (tamarisk, saltcedar) as a result of deliberate introductions, altered hydrology and land use, climate change, and differences in species' competitiveness under nonstationary conditions [Everitt, 1980; Merritt and Poff, 2010; Nagler et al., 2011]. This shift along many rivers to tamarisk-dominated communities has produced increases in vegetation density and changes in riparian canopy structure; whereas cottonwoods grow most often as single-stemmed trees, tamarisk is a large woody shrub with multiple branches emerging from the base of the plant. These changes have in turn altered river flood hydraulics, sediment transport and deposition rates, and sediment storage volumes [Perignon et al., 2013].

Several management strategies have been implemented to restore native riparian species [Shafroth et al., 2008], including flow releases that mimic natural floods along regulated rivers [Shafroth et al., 2010; Wilcox and Shafroth, 2013]. Timing and magnitude of floods are known to be critical for ensuring germination and early growth of some riparian species, such as *Populus fremontii*, *Salix gooddingii*, *Carex senta*, and *Polygonum spp* [Fenner et al., 1985; Stella et al., 2006; Stella et al., 2010; Kehr et al., 2014], but an outstanding question is whether flood releases can be used to selectively increase mortality rates for undesirable (e.g., invasive) species [Wilcox and Shafroth, 2013]. In the case of southwestern U.S. riparian communities, higher mortality rates in response to flooding, scour, and burial have been observed for tamarisk seedlings compared to native species in both experimental [Levine and Stromberg, 2001] and field conditions [Wilcox and Shafroth, 2013].

In the present study, we conducted a set of novel flume experiments to investigate ecogeomorphic feedbacks in a prototype study system of sand-bed rivers with young, woody pioneer vegetation colonizing newly created bars, and banks. Sand-bed rivers are live-bed [Henderson, 1963] or labile [Church, 2006] systems in which thresholds for bed mobility are easily exceeded, such that erosion and deposition occur frequently and produce dynamic channel morphology. In these systems, and in alluvial rivers in general,

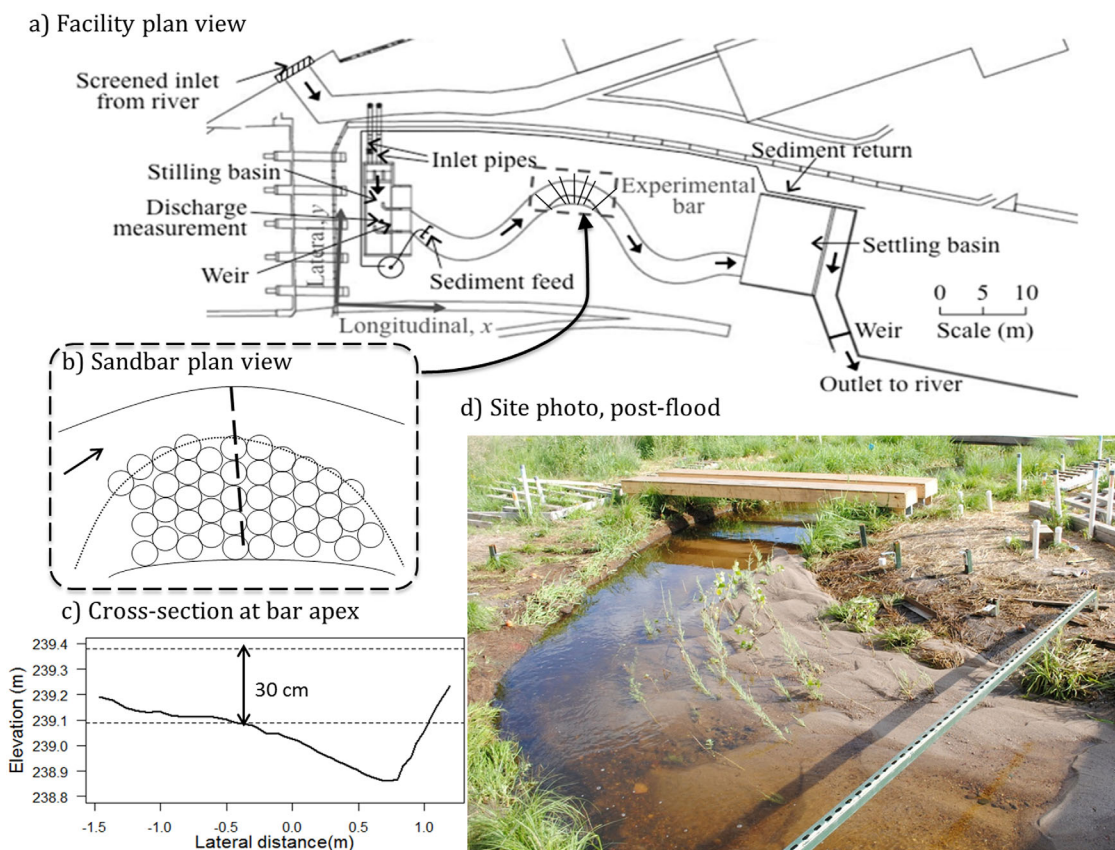


Figure 1. Experimental setup at the Outdoor Stream Laboratory, St. Anthony Falls Laboratory, University of Minnesota. (a) Plan view of OSL, with arrows showing flow direction. The experimental bar is located at the second meander band from upstream; (b) plan view of experimental pot locations on the naturally formed bar. The dotted line is the outer edge of the exposed bar after flood recession; (c) stream cross-section looking upstream at the apex (dark dash line in Figure 1b) of the vegetated bar; (d) photo of the OSL looking downstream after flood run #3, the low-density, mixed-species configuration.

floods that fill channels to their bankfull level and occur every 1–2 years can be channel-forming events [Wolman and Miller, 1960]. Such events may also be capable of producing substantial mortality of young woody seedlings, as a result of both scour and burial, in sand-bed rivers [Wilcox and Shafroth, 2013]. In dammed rivers where planned flood releases at the scale of the largest historic events are beyond the range of management feasibility, moderate-magnitude controlled flood releases are highly relevant to environmental flow management [e.g., Schmidt et al., 2001].

Motivated by these geomorphic, ecological, and management elements of our prototype study system, we sought to develop a mechanistic, quantitative understanding of ecogeomorphic processes associated with moderate (e.g., bankfull-level) floods. In particular, our goal was to understand the mechanisms of flood effects on riparian tree seedlings at the scale of individual plants and small patches (e.g., on alluvial bars and banks). We also aimed to investigate differential impacts on native (*Populus fremontii*) versus nonnative tamarisk species, a question that has widespread application throughout the semiarid U.S. west [Everitt, 1980; Nagler et al., 2011] and includes species with characteristic growth forms that span a range of physiognomies within woody riparian communities. Our flume experiments allowed for more detailed, controlled measurements and manipulation of study-system elements than is possible for field studies during floods, while addressing scaling challenges associated with laboratory experiments by using live, woody seedlings with essential root systems in a sinuous outdoor channel.

We hypothesized that (1) seedling loss, defined as plant dislodgement or complete burial, is influenced by a combination of abiotic and biotic factors, including local physical disturbance intensity, plant density, and individual plants' own morphological traits; and (2) the local effects of floods on net topographic change (scour or deposition) are influenced by plant density, species-specific traits (crown density and stem flexibility), and plant location in the active channel. We expected that denser patches offer greater protection

Table 1. Experimental Setup for the Six Flume Flood Runs With a Vegetated Sandbar^a

Run	Species	Density (#Plants m ⁻²)	Sediment Feed (kg min ⁻¹)
1	Cottonwood (mono)	High (240 m ⁻²)	7
2	Tamarisk (mono)	High (240 m ⁻²)	7
3	Mixed	Low (24 m ⁻²)	7
4	Mixed	High (240 m ⁻²)	7
5	Mixed	High (240 m ⁻²)	0
6	Mixed	Low (24 m ⁻²)	0

^aIn the "Species" column, "mono" stands for monospecific and mixed patches had approximately equal numbers of the two taxa interspersed regularly. Discharge was controlled at $283 \pm 4 \text{ L s}^{-1}$ in all flood runs.

against scour due to increased collective root strength and decreased flow drag experienced by individual plants, but also greater susceptibility to plant burial from deposition increased by greater overall canopy drag. Additionally, we expected that stem height, flexibility, and species-specific crown distribution have differential effects on local hydraulic conditions that would affect rates of plant loss. We tested these expectations using statistical models that quantified the physical response of local topographic change as a function of plant morphology, density, location, and sediment transport rate. The probability of burial or dislodgement was also quantified as a function of plant size, morphology, density, as well as local flood energy. Finally, we evaluated the relevance of our findings for designing flow-release strategies on regulated rivers to restore riparian ecosystems.

2. Methods

We conducted a series of controlled flume experiments with live tree seedlings at the University of Minnesota's St. Anthony Falls Laboratory Outdoor StreamLab (OSL) (Figure 1). The experiments were designed to test the effects of floods on both local topographic change and plant loss (burial and scour) under differing conditions of plant densities, target taxa, and sediment transport regime (Table 1). For each of six runs, cottonwood and tamarisk seedlings collected from southwestern U.S. rivers and then transplanted on a sandbar generated within the flume were subjected to 6–8 h of flooding at a constant flow and sediment discharge. Detailed measurements of plant attributes and topography after each run and associated statistical modeling were used to test hypotheses about ecogeomorphic feedbacks.

2.1. Outdoor Stream Laboratory Facility

The OSL is a unique experimental facility adjacent to the Mississippi River in downtown Minneapolis, MN, that provides the control and detailed observations characteristic of laboratory experiments in a field-scale setting, thus addressing scaling challenges associated with typical flume experiments [Wilcock *et al.*, 2008]. The OSL consists of a constructed sand-bed stream channel with three meander bends and floodplains on both banks (Figure 1a). The straight sections between meander bends were fabricated riffles with coarse-grained sediment to mimic the pool-riffle geometry of many natural streams [Rominger *et al.*, 2010]. The substrate used in the stream channel, sand bars, and plant propagation (see below) was coarse sand with a median grain size of 0.7 mm ($D_{16} = 0.35 \text{ mm}$, $D_{84} = 1.2 \text{ mm}$) that was representative of the plants' natural setting [Wilcox and Shafroth, 2013]. During flood runs, this sediment was introduced through a recirculating sediment feed at the upstream end of the reach, allowing us to control both the flow and sediment transport rate. Additional details regarding the OSL facility and its stream channel design are outlined in Rominger *et al.*, [2010]. We used a total station (Sokkia X30RK, Atsugi, Japan) installed on a permanent mount to precisely survey plant locations and channel dimensions before, during, and after each flume run. We also used a mobile high-resolution topographic scanning platform to provide detailed post flood bar topography at 1 cm spacing. All topographic data were referenced to a local x, y, z coordinate system with horizontal origin at upstream river right. The x and y coordinates from these surveys were later converted to a streamflow coordinate system with streamwise and lateral axes [Lightbody *et al.*, 2012].

2.2. Seedling Collection and Propagation

The test plants consisted of 1–2-year-old tamarisk and cottonwood seedlings that were excavated whole, with as minimal handling and damage to their roots as possible, from two sand-bed rivers in western Arizona: the Bill Williams and Santa Maria rivers. The tamarisk seedlings (~3–9 mos. old) were collected during

winter 2010. These plants were initially propagated for 5 months in a greenhouse at the State University of New York College of Environmental Science and Forestry in Syracuse, NY. To promote natural root growth analogous to a riverine floodplain environment, plants were irrigated from below within an indoor Missouri Gravel Bed system [Starbuck *et al.*, 2005], consisting of a 1 m deep pea gravel substrate with buried plumbing to control the water table level and moisture supply within the unsaturated rooting zone. In early May 2011, the tamarisk were removed from the gravel bed, packed in wet sphagnum and burlap to retain moisture, and shipped overnight to the OSL. At this time, cottonwood seedlings (~2–14 mos. old) were excavated directly from sandy alluvium along the Arizona rivers, packed using the same method as tamarisk, and shipped to the OSL. Therefore, though the plants had similar size ranges during the flume runs, the cottonwood seedlings spanned a greater range of ages (2010–2011 cohorts) than the tamarisk (2010 cohort only).

At the OSL, the seedlings of both species were transplanted into 30 cm diameter by 30 cm deep circular propagation pots with removable sides containing coarse sand extracted from OSL substrate materials ($D_{50}=0.7$), and spaced at either low density (two plants per pot, resulting in test density of 24 plants m^{-2}) or high density (17 plants per pot, resulting in test density of 240 plants m^{-2}). These densities span a range of documented field conditions for both species [Shafroth *et al.*, 2002; Sher *et al.*, 2002]. The plants were allowed to adjust to transplanting for 2 months, during which they were kept in full sun within a shallow pool in which the water level was controlled at 20 cm below the sediment surface to encourage root growth analogous to a riparian environment. A total of 2208 plants were used in our experimental flood runs.

2.3. Plant Architecture Measurements

To better understand how flooding effects on cottonwood and tamarisk are influenced by plant architecture, we quantified stem flexibility and aboveground frontal area (the area of plant stems and leaves perpendicular to the flow direction) for a subset of seedlings ($N = 92$ plants). Two to four days prior to experimental flooding, each plant's stem height was measured and its aboveground frontal area was photographed against a red background [Lightbody and Nepf, 2006]. A 5 cm checkerboard grid was also photographed at the same location to provide scale and to allow for digital correction of lens distortion. The corrected images were processed by extracting the area of plant pixels (nonred color) for every 1 cm increment of plant height, in $cm^2 cm^{-1}$. The resulting vertical distribution of frontal area, defined as frontal area density, was used to determine the vertical location of maximum crown density (that is, the elevation of the maximum frontal area), and the distribution was summed over height to calculate a total frontal area for each plant, in cm^2 . Stem flexibility was measured on the same plants using a spring scale (Amw-pen-100, American Weigh Scales, Norcross, GA). We fastened a nonstretchable string between the spring and the midpoint of the stem and measured the horizontal distance from the base of the stem to the attachment point (stem's midpoint) at zero force. Then, we applied 30 g force on the stem horizontally and measured its displacement distance again [Stone *et al.*, 2013]. The stem flexibility (in $cm cm^{-1}$) was calculated as the stem displacement with 30 g force relative to displacement with zero force, divided by the height of the attachment point on the stem. Before all plants went into the flume, we used spray paint to mark a unique color combination on plants in each pot. This coding system permanently recorded the initial locations of dislodged and buried plants.

2.4. Flume Flood Experiments

Over 5 weeks in July and August 2011, we conducted six flume runs with different experimental treatment combinations (Table 1), in addition to two runs using a bare (i.e., unvegetated) channel configuration as abiotic controls. Each run required a minimum of 3 days for vegetation installation and measurement, flood release, bar topography measurement, and vegetation removal and post flood measurement as specified below. During all baseflow (nonflood) periods, the streamflow rate in the OSL was maintained at 20 $L s^{-1}$. Floods were induced by increasing the streamflow over a period of 10–15 min to approximately 283 $L s^{-1}$, which was maintained for 6–8 h per run. This flood discharge rate represented the bankfull discharge in the OSL and resulted in an average flow depth of 0.3 m and a water surface slope over the length of the flume, averaged over all runs, of 0.0072 [Lightbody *et al.*, 2012] (Figure 1c). The bankfull floods during our runs resulted in reach-average shear stresses of 21 Pa ($\tau_o = \rho ghS$, where $\rho = 1000 kg m^{-3}$, the density of water; $g = 9.8 m s^{-2}$, gravitational acceleration; and h and S are the depth and slope values provided above). This

is well beyond the critical shear stress required to mobilize the sand-sized bed materials we added to flume of 0.5 Pa ($\tau_c = \tau_c^* (\rho_s - \rho) g D$), where τ_c^* is a dimensionless critical shear stress assumed equal to 0.045 [Church, 2006]; $\rho_s = 2700 \text{ kg m}^{-3}$, a sediment density assumed equal to the density of quartz; and $D = 0.7 \text{ mm}$, the median of the sand used in our experiment). Although reach-average shear stresses are not representative of those experienced at local scales by patches of bed material and individual plants, calculation of which is beyond the scope of this paper, comparison of the reach-average shear stresses to those required to mobilize sand in the flume illustrates that our floods produced forces far greater than those required for scouring bed materials.

Prior to the first run with plants, we released a flood run with a bare channel bed and constant sediment feed of 7 kg min^{-1} to build a stable point bar in the middle meander bend. The constant sediment feed rate of 7 kg min^{-1} was sustained during the first four runs with plants and resulted in an equilibrium sediment transport rate (i.e., neither net system erosion nor deposition). The last two plant runs and the final bare bed run were conducted with no sediment added to mimic nonequilibrium, sediment deficit conditions (e.g., as can occur on dammed rivers).

Before each run, we excavated the central exposed part of the sandbar and replaced it with plants and substrate from 43 propagation pots (Figures 1b and 1d). The density and composition of these vegetation patches were assigned as listed in Table 1, with the group of runs designed to contrast high and low densities, and single species versus dual taxon mixes. Mixed patches had approximately equal numbers of both taxa, with cottonwood pots alternating with tamarisk ones throughout the bar. To mimic seedling establishment on the sandbar, pots were installed with the sediment surface at the same elevation as that established after the initial bare bed run. Total station measurements confirmed that the center of each pot was within 1 cm of the target elevation. Following pot placement, spaces between pots were backfilled with sand and the pot sides were removed. This process kept plants and their rooting substrate intact to minimize the disturbance of transplanting. Scour during the floods was not deep enough to expose the pot bottoms buried in the channel bed, so keeping the bottoms in place did not affect flow or sediment transport during runs.

During the bankfull floods, the entire sandbar was submerged, and the plants dislodged from the sandbar were recovered downstream and marked. Following the return to base flow, post flood bar topography was obtained at 1 cm spacing [Lightbody *et al.*, 2012], providing a detailed snapshot of bar topography at one moment in time.

Two measurements of flood-induced topographic change were computed for each pot location. Flood-induced topographic change at the location of the plants (e.g., burial or scour) was calculated as the difference between the post run detailed scan of bar elevation averaged over the area of each pot and the initial soil surface elevation at the middle of the pot. To assess the plants' local impact on topographic change, we used the difference between the post flood scan elevation and the elevation of the bare-bed trial; the latter was time-averaged across five fixed cross sections during equilibrium transport conditions to eliminate bias due to transient bed forms.

Following bar topography measurement, all seedlings that emerged from the new bar surface were marked with spray paint and designated either dislodged (recovered downstream), completely buried, or viable (remaining in place with no or partial burial). Partially-buried plants were considered viable because empirical studies indicate that these species can readily recover if not completely buried, since they can continue photosynthesis and gas exchange through the exposed portions of their crowns [Burylo *et al.*, 2012b]. Each run concluded with all plants, substrate, and pot bottoms excavated from the sandbar. Soil was washed from around the roots, and plant height and length of the longest root were measured for each individual. There was no stem or root breakage observed in a subset of seedlings measured both before and after the flume runs, therefore these post run measurements represent plant dimensions during the floods.

2.5. Statistical Analysis

Plant morphological differences between the two species were compared for the subset ($N = 92$) of plants used for the plant architecture study. Analysis of covariance (ANCOVA) was used to quantify species-specific allometric relationships for plant frontal area and stem flexibility, with plant height and species as predictors. Frontal area was log-transformed in these linear models to satisfy residual assumptions. A two-sample

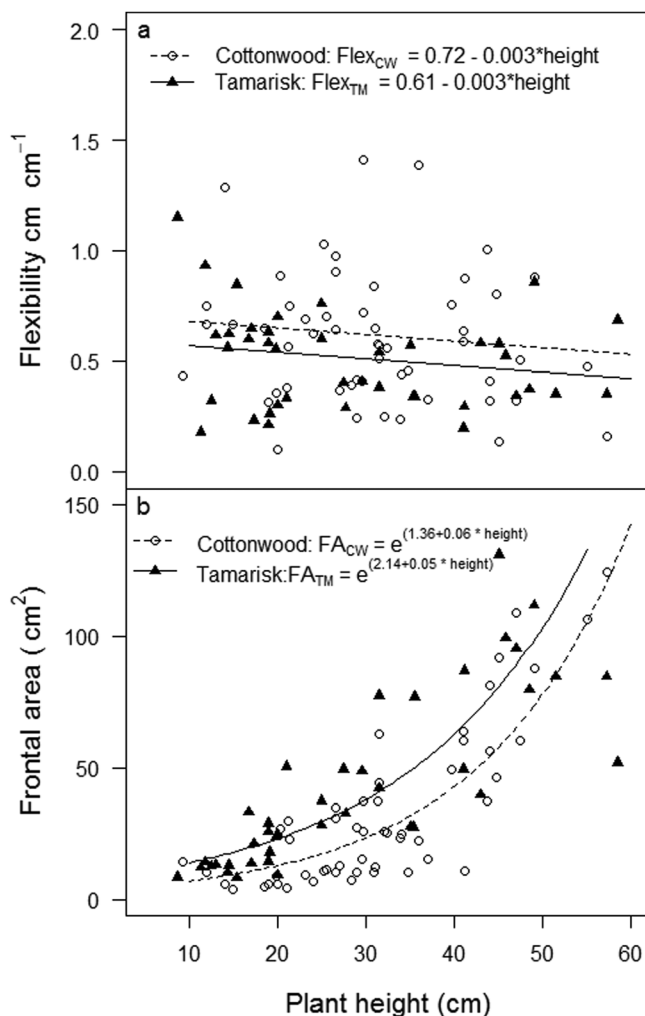


Figure 2. Plant architecture and growth-related characteristics for a random subset of 92 tamarisk (TM) and cottonwood (CW) seedlings: (a) stem flexibility versus plant height and (b) aboveground total frontal area (FA) versus plant height. Linear formulas in (b) reflect exponential functions fitted individually to each species.

and lateral dimensions. Models for probability of plant dislodgement had the same independent variables except that root length was substituted for shoot height, as other studies indicate that root size and morphology are important factors in resisting dislodgement [Crouzy *et al.*, 2013].

To understand how vegetation may affect fine-scale geomorphic change, particularly net scour and deposition around small plant patches, we used linear models to predict the local (pot-level) net elevation changes that were associated with plant species and density. We tested two models, one that compared the two runs with monospecific cottonwood and tamarisk (Runs 1 and 2; Table 1) at equivalent conditions of plant density (240 m^{-2}) and sediment transport (7 kg min^{-1}), and another model that included all the mixed runs with alternating patches of species (Runs 3–6), during which plant density and sediment supply also varied. The first model explicitly tested the species effect across the entire sandbar within a fixed physical configuration; the second model tested a more complicated set of parameters and included the possibility of distinguishing more fine-scale variation in topography (i.e., at the scale of small patches, or plant pots) due to the species effect. In both models, the pots' streamwise and lateral coordinates were included to account for differences in baseline flood energy across the sandbar [Perona *et al.*, 2012].

For each of the three response variables (probability of dislodgement, probability of burial, and net topographic change), we compared candidate model sets with different combinations of predictor variables using Akaike Information Criteria (AIC). The best model was the one with the lowest AIC value and highest

Kolmogorov-Smirnov test was used to compare the elevation of maximum frontal area density between the two species. This procedure tests the difference between two distributions, in this case the average distribution of frontal area along the height of the plant for each species.

In order to understand the overall effects of flooding on plant loss, we used generalized linear logistic models to predict the probability of plant dislodgement and burial for all individuals. Predictors for burial included continuous variables for plant height and categorical variables for species (tamarisk or cottonwood) and patch density (high or low). Two species-related interaction terms were also included (species \times plant height and species \times patch density) to account for possible differential effects of species architecture on the main experimental effects. We also included a continuous predictor, the local change in bar surface elevation, with negative and positive values indicating scour and deposition, respectively. This metric was used in these models to represent local variation in geomorphic change as a result of floods; this change varied across the bar in both the streamwise

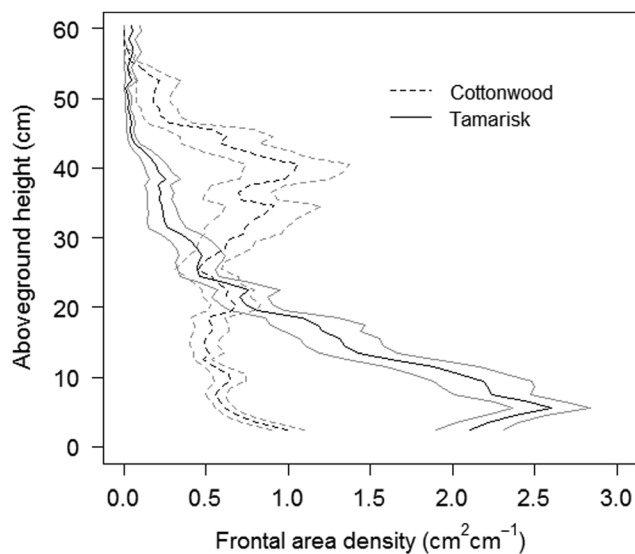


Figure 3. Frontal area density ($\text{cm}^2 \text{cm}^{-1}$) of cottonwood and tamarisk seedlings ($N = 92$) shown as means for 1 cm increments above the soil surface. Gray lines indicate the standard errors of the means. The bottom 1 cm for each seedling image was not analyzed because of interference from nonliving matter, dead plant materials, and soil clumps.

and root length was 19.5 ± 7.8 , whereas tamarisk seedling height averaged 27.4 ± 15.5 cm and its root length was 20.9 ± 9.7 cm. The morphologies of cottonwood and tamarisk were different in terms of stem flexibility and frontal area distribution. Though stem flexibility did not vary with plant height ($F_{1,90} = 1.9$; $p = 0.17$) for either species over the range of seedling sizes tested (10–60 cm height), cottonwood seedlings were more flexible overall than tamarisk (ANCOVA, $F_{1,90} = 4.0$; $p = 0.048$; Figure 2a). This suggests that tamarisk stems pronate less than cottonwood under equivalent flow conditions.

The frontal area of seedlings of both species was directly proportional to plant height (ANCOVA $F_{1,90} = 144.2$; $p < 0.001$), though this relationship varied significantly by species ($F_{1,90} = 22.3$; $p < 0.001$; Figure 2b). Tamarisk seedlings developed a larger frontal area with a greater increase in plant height than cottonwood, suggesting increased crown drag for tamarisk. In addition, tamarisk had a more bushy (i.e., multistemmed) structure with its highest density lower in the crown, whereas cottonwood seedlings typically had a single stem with a higher, sparser crown (Kolmogorov-Smirnov test, $D = 0.40$, $p = 0.001$). Tamarisk foliage was densest at 8.5 cm above the substrate surface, which represented 35% of the mean plant height above the ground (Figure 3). Cottonwood crowns were distributed high on the plant, in contrast, and the densest foliage was 18 cm above the substrate, or at 58% of the mean plant height (Figure 3). Given the systematic differences between tamarisk and cottonwood stem flexibility, frontal area and crown morphology, the “species” predictor terms in the plant-geomorphology linear models (see results below) can be interpreted to assimilate all of the species-level variation in plant architecture that was independent of plant height.

3.2. Plant Dislodgement and Burial

Of the 2208 plants used in our experimental runs, nearly all of them survived the experimental floods, despite the full submergence of nearly all seedlings in all runs and their pronation below the water surface within the first 5 min of each flood run. Only 19 plants (1% of the total) were dislodged. Of the 1066 plants that were located on the exposed bar, where the soil surfaces were above the water surfaces after the floodwaters receded, 144 plants (14%) were completely buried.

The probability of seedling dislodgement depended most strongly on the plant’s root length and local substrate elevation change, with plants preferentially lost in areas experiencing the greatest scour (Table 2 and Figure 4a). About half (55%) of the dislodged plants were located on the stream-ward edge of the sandbar. All of the top-ranked logistic models included a root length coefficient with a negative value, which when translated into odds ratios predicted that for every centimeter increase of root length, the probability of

AIC weight, which indicated the likelihood of that model being the best model among all given candidates [Burnham and Anderson, 2002]. We considered models with ΔAIC that were < 4 to be equally likely [Burnham and Anderson, 2002; Richards, 2005], and the top-ranked models were listed and their predictors and coefficients compared. We used conditional density plots to visualize the effects of plant species and size on displacement and burial risk [Hothorn and Everitt, 2009]. All data analyses were performed in R [R Core Team, 2013].

3. Results

3.1. Plant Structure

Across all the plants used in the study, cottonwood seedling height averaged 28.5 ± 9.7 cm (mean \pm 1SD)

Table 2. Model Selection Criteria Used in Ranking Logistic Regression Models Predicting the Probability of Plant Dislodgement^a

Plant Dislodgement Model Rankings						Coefficients for Effects on Plant Dislodgement ^b						
Rank	df	AIC	ΔAIC	Akaike Weight	Cumulative Weight	Root Length (cm)	Species ^c	Density	Sediment Feed	Net Elevation Change ^d (cm)	Root Length × Species	Species × Density
1	3	189.3	0	0.292	0.292	-0.18				-0.22		
2	4	191.2	1.9	0.114	0.406	-0.18	0.16			-0.23		
3	4	191.3	2.0	0.109	0.515	-0.18			-0.09	-0.22		
4	4	191.3	2.0	0.108	0.623	-0.18		0.12		-0.23		
5	5	191.7	2.4	0.088	0.711	-0.13	1.45			-0.23	-0.1	
6	5	193.2	3.9	0.043	0.754	-0.18	0.16		-0.08	-0.23		
7	5	193.2	3.9	0.042	0.796	-0.18	0.16	0.11		-0.23		
8	5	193.3	4.0	0.041	0.837	-0.18		0.13	-0.09	-0.22		
49	1	220.5	31.2	<0.001								

^aThe top-ranked models up to a ΔAIC threshold of ≤4 [Richards, 2005] are listed here, in addition to a null model.

^bRegression coefficients for the logistic models represent the log odds effect of each variable.

^cPositive values for the species coefficient indicate that tamarisk is more likely to dislodge than cottonwood with equivalent conditions.

^dPositive values for the net elevation change parameter indicate net deposition and negative values indicate net erosion.

dislodgement decreased by 16%. However, the small number of plants overall that dislodged indicated that, under the hydraulic conditions generated within the flume, the probability of plant dislodgement was only substantial for smaller plants with root lengths <10 cm (Figure 4a). Differences in dislodgement risk between species were not great; only four of the top-ranked eight models contained a species term, whose sign indicated that tamarisk had a marginally higher risk of dislodgement relative to cottonwood (Table 2).

Though all of the top-ranked models contained a parameter for net elevation change (Table 2) indicating a 20% greater risk of dislodgement with every additional centimeter of bed scour, the maximum scour depth achieved in the flume was 7.8 cm, which was shallower than the rooting depth of most of the plants. Thus, the given flood conditions did not scour the sandbar deeply enough to allow plant dislodgement on a large scale, although a few plants growing along the edge of the bar had the majority of their roots exposed and were pronated against the channel bed. During the last two runs with no sediment feed, we observed that the bar surface eroded sufficient quantities of coarse sand to expose the pea gravel sediment fraction, which acted to armor the bar surface in similar fashion to river conditions of sediment deficit [Dietrich et al., 1989].

The probability of plant burial depended strongly on plant density and height, as well as sediment supply (Table 3). All of the best burial models also included the interaction term of plant height and species, indicating that for shorter plants (<20 cm tall) tamarisk had higher burial risk than cottonwood. However, burial

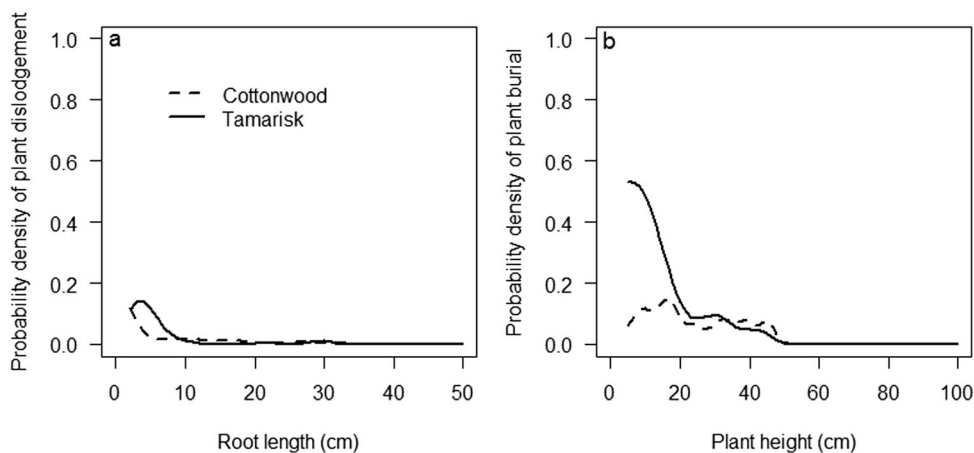


Figure 4. Conditional density plots isolating plant species (tamarisk and cottonwood) and size effects in the generalized linear models of (a) plant dislodgement probability as a function of root length and (b) plant burial probability as a function of plant height. These plots showed the computation of conditional density of x (root lengths or plant height) given the levels of y (plant dislodgement or burial), weighted by the marginal distribution of y [Hothorn and Everitt, 2009]. For smaller seedlings, risk of loss is greater for tamarisk than for cottonwood, but no species-level differences exist for plants with roots >10 cm in the case of dislodgement (a) and stems >20 cm in the case of burial (b).

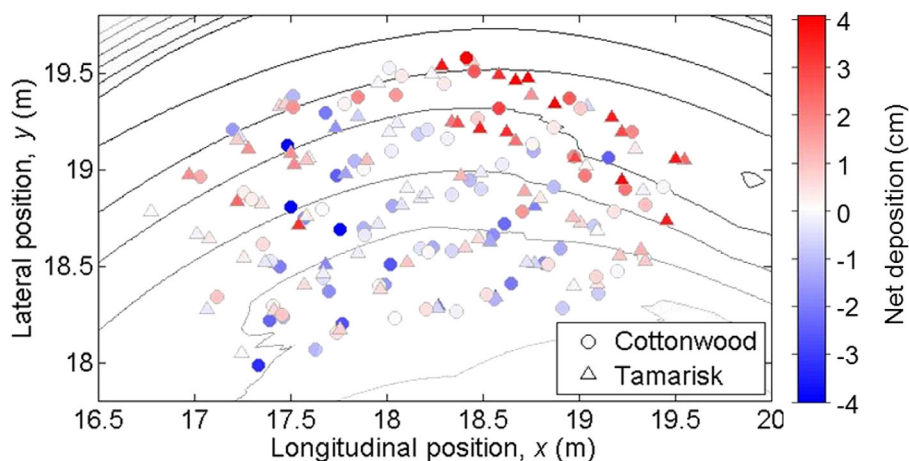


Figure 5. Average deposition within vegetated planters, calculated as the average difference between detailed scans of the post flood elevation and the bare-bed trial, which was time-averaged to remove bias from transient bedforms (see text). Symbols are displayed at the center of each pot, but averages are calculated over the full 30 cm diameter of each pot. Flow is from left to right.

risk declined dramatically with seedling size. For every centimeter increase in stem height, the probability of burial decreased by 3% for cottonwood and 13% for tamarisk until approximately 50 cm, at which height the risk of burial for both species was very low (Figure 4b).

In most of the top-ranked models, plants in high-density patches had four times greater risk of burial compared to ones in low-density patches. Approximately half of the top-ranked models contained a term for net elevation change, but indicated only a 4% greater risk of complete burial for each additional centimeter of sedimentation (Table 3).

3.3. Surface Elevation Change

The net surface elevation change on the study sandbar was strongly influenced by biotic and physical factors operating at scales ranging from the entire sandbar to fine scale individual patches within it (i.e., plant pots). Across all of the runs, scour occurred upstream across the lateral width of the sandbar, and sedimentation was greatest downstream from the bar apex and adjacent to the channel (Figure 5) [Lightbody et al., 2012]. This spatial pattern is reflected in the consistent, positive values for streamwise and lateral distance coefficients in both linear models of topographic change (Tables 4 and 5).

The presence of plants on the sandbar induced considerable net deposition compared to bare-bed conditions (range -5.62 to 10.96 cm; Figure 6), and post-flood sediment depth was influenced by plant density and species-specific architecture. When comparing the monospecific plant trials at high density and equilibrium sediment conditions (runs 1 and 2), tamarisk induced net deposition 2.4 cm deeper than cottonwood (Table 4 and Figure 6a). In the mixed-species experiments (runs 3–6), there were clear effects of plant density

Table 3. Model Selection Criteria Used in Ranking Logistic Regression Models Predicting the Probability of Plant Burial^a

Plant Burial Model Rankings						Coefficients for Effects on Plant Burial ^b						
Rank	df	AIC	Δ AIC	Akaike Weight	Cumulative Weight	Plant Height (cm)	Species ^c	Density	Sediment Feed	Net Elevation Change ^d (cm)	Plant Height \times Species	Species \times Density
1	6	678.5	0	0.277	0.277	-0.03	3.10	1.41	2.64		-0.11	
2	5	679.0	0.5	0.215	0.492	-0.04	3.07		2.62		-0.11	
3	7	679.7	1.1	0.158	0.650	-0.03	3.04	1.38	2.54	0.04	-0.11	
4	7	679.9	1.4	0.140	0.790	-0.03	16.02	13.95	2.64		-0.11	-12.92
5	6	680.1	1.6	0.127	0.917	-0.04	3.0		2.53	0.05	-0.11	
6	8	681.0	2.4	0.082	0.999	-0.03	16.08	14.01	2.54	0.04	-0.11	-13.04
7	5	692.0	13.5	<0.001	0.999	-0.10	0.72	1.38	2.58			
52	1	846.1	167.6	<0.001								

^aThe top-ranked models up to a Δ AIC threshold of ≤ 4 [Richards, 2005] are listed here, in addition to a null model.

^bRegression coefficients for the logistic models represent the log odds effect of each variable.

^cPositive values for the species coefficient indicate that tamarisk is more likely to be buried than cottonwood with equivalent conditions.

^dPositive values for the net elevation change parameter indicate net deposition and negative values indicate net erosion.

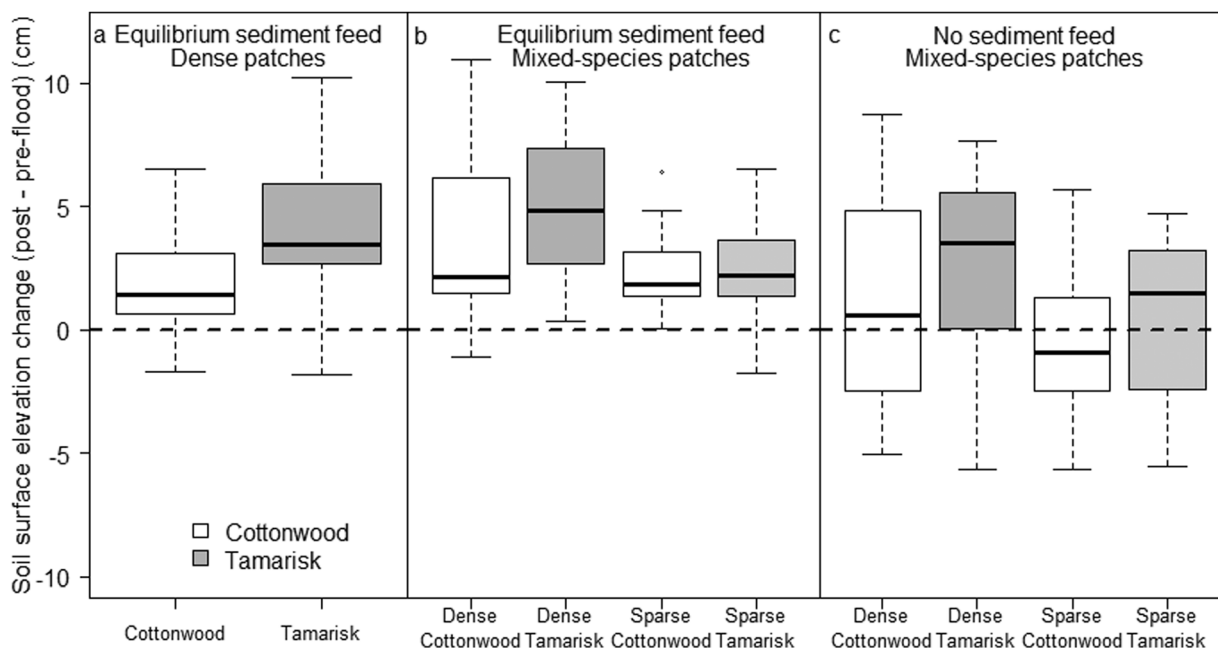


Figure 6. Boxplots of post flood soil surface elevation changes at the local (pot) scale compared to pre-flood conditions for cottonwood (blank boxes) and tamarisk (light gray boxes) across six experimental flood runs. Negative and positive values indicate net scour and deposition, respectively. Thick lines indicate medians and boxes encompass the second and third quartiles of the distributions. (a) In dense patches under equilibrium sediment transport conditions, tamarisk induced higher sedimentation than cottonwood. (b) Dense tamarisk induced more sedimentation than cottonwood and sparse ones in mixed-species patches under equilibrium sediment transport conditions. (c) Sediment deficit conditions induced minimal deposition in cottonwood patches. Net deposition still occurred in tamarisk patches.

and sediment supply on post flood topography. Coefficients for the top-ranked linear models indicated that sediment deposition was 1.5–1.8 cm greater within dense (240 m^{-2}) versus sparse (24 m^{-2}) runs, and 2.4 cm greater at equilibrium sediment supply compared to deficit conditions (Table 5; Figures 6b and 6c). In addition to these sandbar-wide effects, there were fine-scale (within-sandbar) differences in post flood topography associated with species-specific patches. Tamarisk patches in the mixed runs induced 0.62 cm on average greater deposition than adjacent cottonwood patches (Figures 6b and 6c), and this was evident in the positive species term in most of the top-ranked linear models for topographic change (Table 5). Under sediment deficit conditions, both sparse and dense tamarisk patches induced greater deposition and reduced scour compared to adjacent cottonwood patches, in which net topographic change was negligible (Figure 6c). High overall sedimentation in tamarisk only runs (Figure 6) corresponded to the greater vulnerability to burial by individual tamarisk seedlings, especially for densely-packed plants (Table 3 and Figure 4b).

4. Discussion

Our study used a novel experimental approach, with a field-scale flume and seedlings transplanted with essential root systems, to investigate the effects of bankfull floods on woody seedling loss and the

Table 4. Model Selection Criteria Used in Ranking Linear Regression Models Predicting the Net Elevation Change Corresponding to the Physical Conditions and Plant Traits, for Monospecific Runs (1 and 2)^a

Net Elevation Change Model Rankings						Variable Coefficients		
Rank	df	AIC	Δ AIC	Akaike Weight	Cumulative Weight	Species ^b	Streamwise Distance(m) ^c	Lateral Distance(m) ^c
1	4	373.9	0	0.616	0.616	2.42	0.85	
2	5	374.9	1.0	0.365	0.981	2.35	0.89	0.64
3	3	381.5	7.7	0.013	0.994	2.42		
7	1	399.4	25.5	<0.001				

^aThe top-ranked models up to a Δ AIC threshold of ≤ 4 [Richards, 2005] are listed here, in addition to a null model.
^bPositive values for the species coefficient indicate that tamarisk contributes more to sediment deposition than cottonwood with equivalent conditions.
^cStreamwise distance is measured from upstream to downstream, and lateral distance from the sandbar into the thalweg.

Table 5. Model Selection Criteria Used in Ranking Linear Regression Models Predicting the Net Elevation Change Corresponding to the Physical Conditions and Plant Traits, for Mixed Species Runs (3, 4, 5, and 6)^a

Rank	Net Elevation Change Model Rankings					Variable Coefficients					
	df	AIC	ΔAIC	Akaike Weight	Cumulative Weight	Species ^b	Density	Sediment Feed	Streamwise Distance(m) ^c	Lateral Distance(m) ^c	Species × Density
1	7	796.9	0	0.427	0.427	0.62	1.86	2.44	1.31	4.22	
2	6	797.6	0.7	0.306	0.733		1.85	2.44	1.36	4.27	
3	8	797.8	0.9	0.267	1.000	0.24	1.49	2.44	1.31	4.20	0.76
4	6	818.4	21.5	<0.001	1.000	0.57		2.41	1.29	4.27	
40	1	901.4	104.5	<0.001							

^aThe top-ranked models up to a ΔAIC threshold of ≤4 [Richards, 2005] are listed here, in addition to a null model.

^bPositive values for the species coefficient indicate that tamarisk contributes more to sediment deposition than cottonwood with equivalent conditions.

^cStreamwise distance is measured from upstream to downstream, and lateral distance from the sandbar into the thalweg.

mediating effects of plant characteristics and sediment supply. Both seedling dislodgement and burial occurred to a greater degree for tamarisk than cottonwood, and smaller plants were much more vulnerable to loss during floods. Higher plant densities induced both greater net sedimentation on the sandbar, and greater risk of burial. These results provide new insights into plant/geomorphic feedbacks, the initial stages of vegetation development and fluvial landform evolution, and strategies for using controlled flood releases on dammed rivers to restore downstream riparian ecosystems.

4.1. Controls on Plant Mortality

Our study illustrated the effects of both hydraulic forces and the plants' own morphological traits on flood-induced plant loss. Within the limitations of hydraulic and sediment transport conditions possible within the OSL facility, which we discuss further below, plant burial posed a much greater (~15-fold) risk to plant loss than complete dislodgement, against which plants were generally resistant. This suggests that under certain flow (e.g., moderate flood) and sediment supply conditions in rivers, burial may be the potentially stronger limitation on local populations than scour. However, the relative importance of these processes is unlikely to scale to larger and more powerful floods where greater erosion may result in bar-scale migration and higher rates of plant scour [Cooper *et al.*, 1999; Asaeda *et al.*, 2010]. For example, Cooper *et al.* [1999] suggested that substrate erosion during high flows caused 34%–47% mortality of seedlings in their second growing season across different reaches.

Plant dislodgement risk was highest in regions of the sandbar that experienced the greatest local scour. This vulnerability was mitigated, however, in plants with longer roots, which conferred protection against entrainment in the flow even when the majority of the root zone experienced scour [Bornette *et al.*, 2008; Crouzy *et al.*, 2013]. Given that our plants grew in pots with maximum root density near the pot bottom, the scour depth was only about one-third of the depth of maximum root density. Thus, the probability of dislodgement was very low. In a natural setting, root length can vary due to environmental conditions. For example, phreatophytic plants growing at higher elevations above the water table develop deeper roots to access perennial water sources (i.e., a hydrotropic response), whereas plants growing on lower surfaces with frequent inundation avoid anoxic conditions by extending their roots laterally within shallow, unsaturated substrate layers (i.e., an aerotropic response) [Imada *et al.*, 2008; Pasquale *et al.*, 2012]. Plants at higher elevations may thus experience less flood-induced mortality due both to lower frequency and magnitude of disturbance, and to the plants' own deeper rooting depth, which helps withstand erosion and dislodgement [Asaeda *et al.*, 2010; Pasquale *et al.*, 2012]. Longer roots also feed back to the physical system by increasing bank strength and resisting erosion [Langendoen *et al.*, 2009].

Secondary influences on dislodgement risk included the sediment transport rate, with greater plant removal under sediment-deficit conditions, and species, with tamarisk slightly more vulnerable than cottonwood. This latter condition may be related to the greater frontal area, stem stiffness, and lower crown density of tamarisk, all of which would induce greater drag resistance and thus greater pullout force [Albayrak *et al.*, 2012; Västilä and Järvelä, 2014]. Our results can be considered in the context of the two different mechanisms of plant uprooting proposed by Edmaier *et al.*, [2011]: Type I removal, in which flow-induced drag exceeds a threshold of root resistance and results in instantaneous dislodgement due to root breakage or pullout, and Type II, a more gradual process that combines flow drag with erosion around the stem and

progressive root exposure prior to dislodgement when scour exceeds the length of the root. In our logistic models of dislodgement risk, both root length and net elevation change (i.e., a proxy for scour forces) are in all of the top-ranked models, suggesting that substrate mobility and resistance to it by roots is a primary driver of plant vulnerability. This is supported by the fact that reach-average shear stresses generated during the bankfull floods (~ 21 Pa) were far greater than those required to mobilize the bed materials (~ 0.5 Pa), and that net elevation changes during sediment deficit conditions indicated substantial scour at the bed surface. In contrast, the species term, which encompasses all the aboveground morphological differences between the two plants, is present in half of the top eight models, suggesting that differences in aboveground drag forces played an intermediate role in influencing plant vulnerability. Our results thus suggest that the Type II dislodgement mechanism was more common in our experiment [Edmaier *et al.*, 2011], which is consistent with other recent flume and field studies [Bywater-Reyes *et al.*, 2013; Pasquale *et al.*, 2013] (R. Manners *et al.*, When do plants modify fluvial processes? Plant-hydraulic interactions under variable flow and sediment supply rates, submitted to *Journal of Geophysical Research Earth Surface*, 2014).

Plant burial was strongly influenced by plant height, density, and species, as well as sediment transport rate. Short tamarisk seedlings in dense patches were most likely to be buried, particularly under equilibrium transport conditions. Because tamarisk seedlings had more frontal area and less stem flexibility than cottonwoods of equivalent height, they would be expected to induce greater flow drag and deposition for a given stem density and canopy height [Burylo *et al.*, 2012a; Aberle and Järvelä, 2013], and therefore suffer greater rates of burial. As plants age and grow taller, all individuals of both species will be less prone to burial. A comparative study by Sher *et al.* [2000] showed that cottonwood seedlings increased their stem height much faster than tamarisk during the first growing season, although dense patches had slower growth overall and less of a difference in growth rate between species. In addition, cottonwood germination timing is typically earlier than tamarisk during a given growing season [Shafroth *et al.*, 1998]. Together these differences suggest that for a given annual cohort, cottonwood would be less vulnerable to scour and burial mortality due to differences in plant size. However, because these differences diminish over time as the plants grow, this implies that there is a threshold effect in which flooding produces the greatest differences in mortality rates between species when seedlings are small, likely within the first (or more rarely, second) growing seasons [Wilcox and Shafroth, 2013]. In addition, some types of disturbance may reduce the differences between the two species by modifying their aboveground morphology. For example, herbivory of otherwise single-stemmed plants (e.g., by beaver or elk) may trigger resprouting and development of shrubby growth forms [McGinley and Whitham, 1985]; this would presumably reduce hydraulic differences among riparian plant species. Though the risk of plant burial was highest in the trials that experienced the greatest deposition overall (i.e., dense tamarisk trials), it was surprising that the risk of plant burial was not strongly related to local sedimentation as measured at the level of individual plant pots. We had expected that plant burial would be highest on the downstream end of the bar, where post flood deposition was highest in almost all runs. However, flow velocity was slowest at the downstream edge of the bar [Lightbody *et al.*, 2012], therefore less stem pronation at the tail of the bar may have offset the higher net sedimentation as the main influence on plant burial. Regardless, the lack of local deposition as a strong predictor of burial suggests that hydraulic forces, sediment dynamics, and plant canopies interacting at scales larger than the plants themselves had more influence over individual plants' fates compared to local effects [Merritt, 2013].

4.2. Controls on Sedimentation and Scour

The interaction of plants with sediment transport influenced patterns of deposition and scour both at the sandbar scale and the pot scale. The clear species effect on sedimentation is consistent with differences in plant architecture. While there were no significant differences in height between the seedlings, the tamarisk seedlings had stiffer stems, greater frontal area at a given size, and the majority of its crown was distributed significantly lower on the plant, compared to cottonwood. Collectively, these characteristics may have served to increase hydraulic roughness and to promote sediment deposition [Burylo *et al.*, 2012a]. These effects were magnified with increased plant density, with potentially substantial ecological effects. Though the high-density patches induced only a minimal increase in sedimentation over sparse patches (average of 1.5–1.8 cm), they suffered 16 times greater plant loss, primarily due to burial. Another study using willow cuttings also found substantial mortality ($\sim 20\%$) associated with floods that induced only a modest degree of sedimentation (< 10 cm) [Pasquale *et al.*, 2013].

The least intuitive effect on net topographic change was that, at high densities, each species induced greater deposition when planted within mixed-species configurations compared to monospecific ones. This result suggests that the mixed species patch may have had greater influence on the local physical environment and induce greater deposition than monospecific configurations of either species alone. Although we have only six flood runs with one example for each treatment combination, the patterns of greater deposition within mixed patches were consistent. This may be caused by greater total hydraulic drag forces over the patch during the flood, possibly due to a more complex canopy created by a mixture of the two species with differing stem flexibility and complementary crown architectures resulting in a larger patch-scale blockage ratio [Luhar and Nepf, 2013]. These results support findings from numerous observational studies and manipulation experiments in which higher levels of biodiversity drive greater ecosystem function (e.g., primary productivity, or in this case, sediment deposition), primarily through complementarity of functional traits (e.g., soil rooting zones, or in this case, different canopy morphologies) [Loreau et al., 2001; Lecerf and Richardson, 2010]. Our findings highlight the need for additional research on the ecosystem effects of species richness, which is often high in riparian communities [Naiman et al., 1993; Décamps and Tabacchi, 1994], on river morphodynamics.

4.3. Plant/Geomorphic Feedbacks and Scaling Issues

Our results suggest that feedbacks between the physical regime and young tree seedlings start at a very early stage of riparian ecosystem development [Corenblit et al., 2007; Gurnell et al., 2012; Perona et al., 2012]. Some ecosystem feedbacks in riparian environments, such as the evolution of floodplain soils with plant community development, may be expressed only on the scale of decades to centuries [Luken and Fonda, 1983; van Cleve et al., 1993; Hoffmann et al., 2009]. However, the physical process/plant trait feedback that occurs early in fluvial ecosystem development, where plants modify the physical environment in a manner that then drives differences in plant demography (mortality and recruitment), is evident for small seedlings within the first year or two of establishment on new alluvial surfaces [Gurnell et al., 2012]. The volumes of sediment deposited within seedling plant canopies are likely to be much smaller than for mature trees [Asselman and Middelkoop, 1995; Cordes et al., 1997; Stella et al., 2011]. However, the sediment-trapping effects would be expected to accelerate nonlinearly with increases in stem height, diameter, rigidity, and especially crown area as plants grow [Burylo et al., 2012a; Manners et al., 2013]. Even under sediment-deficit conditions, the difference in plant density from low to high was sufficient to shift the sediment movement pattern from net scour or low deposition to strongly positive, suggesting a threshold effect. This was especially the case for tamarisk, whose presence within the mixed-species trials greatly accelerated these effects.

As plants grow larger and patches grow denser and more widespread in river corridors following disturbance, they will exert more influence on the physical system through increased flow drag, local and reach-scale scour and sedimentation patterns, floodplain accretion rates, and channel migration and morphology change [Micheli et al., 2004]. However, it is important to recognize the importance of scale on the strength of biotic feedbacks in river systems. In very low-energy systems such as estuarine salt marshes, even short herbaceous plants with high stem flexibility and shallow root systems can have a profound effect on sedimentation rates [Gleason et al., 1979; Li and Yang, 2009]. In contrast, a high-magnitude flood on a large river will remove mature trees and reset the physical template, even for mature or extensive forest ecosystems [Hawkins et al., 1997]. Between those extremes, where intermediate flood energy and deposition rates are matched by plants' resistive forces through their size, density and canopy architecture, feedbacks are expected to be strongest and most persistent [Corenblit et al., 2007; Perona et al., 2012]. Flume, field, and modeling studies support the concept that the proportional influence of vegetation varies with plant size and vegetation development time since disturbance, in proportion to the physical drivers of the system [Micheli et al., 2004; Tal et al., 2004; Perucca et al., 2006; Tal and Paola, 2010; Crouzy et al., 2013].

In using live plants with essential root systems and an experimental channel with meandering, bar-pool morphology and the capacity to vary flow and sediment supply, this study begins to bridge the gap between flume experiments and field settings, while also highlighting tradeoffs and scaling challenges associated with such an effort. In particular, the modest plant losses during flood runs illustrate difficulties in scaling the balance between plant resisting forces and flow driving forces. On the one hand, our effort to simulate field-like vegetation conditions, by allowing the plants in our study to grow natural root systems for several months prior to the experiment and to interweave roots with neighboring plants, resulted in a realistic representation of the above-ground and below-ground components of plant resistance to scour

and an advance relative to previous flume studies. On the other hand, the bankfull floods we tested, which corresponded to the maximum flow capacity and flood energy possible in the OSL, were limited compared to the range of natural flood conditions that produce plant losses. Our test floods exceeded the threshold for sediment mobilization and transport but were insufficient to scour substrates to a depth necessary to expose plant roots and thereby facilitate uprooting; average root length was 20.2 cm across all plants, but most plants on the bar edge experienced a maximum of ~ 7 cm scour. Field studies of naturally recruited seedling cohorts have shown much greater rates of plant losses during floods [Cooper *et al.*, 1999; Pasquale *et al.*, 2013; Wilcox and Shafroth, 2013], and replicating these conditions in flume settings with real plants has thus far proved infeasible. Another challenge in scaling between flume and field settings is the role of bar-scale versus plant-scale scour in removing plants. Whereas our observations suggest that bar-scale erosion and bed form migration may be required to induce plant mortality, flume experiments are more appropriate for simulating, measuring, and replicating plant-scale scour.

In order to develop a more robust and realistic understanding of factors driving scour mortality and geomorphic interactions with root strength across a greater range of flood intensity, experiments in larger flumes and/or field settings will be required [Bywater-Reyes *et al.*, 2013; Pasquale *et al.*, 2013] (R. Manners *et al.*, submitted manuscript, 2014). In addition, the results from experiments such as these need to be evaluated in relation to processes that operate at the scale of fluvial bar features (e.g., bed form movement, water table fluctuations, plant cohort recruitment, and stand dynamics), reaches (e.g., bar migration, sediment and plant propagule supply), and networks (e.g., changes in climate and flood frequency).

4.4. Tamarisk Control and Riparian Management Implications

Our findings of increased vulnerability of tamarisk to fluvial disturbance compared to cottonwood are supported by field observations and experiments (many with *Salix* tree species too), and suggest that flood releases may in some cases provide effective control on invasive species. Higher mortality of tamarisk compared to native tree seedlings has been observed in response to flooding and deposition [Horton *et al.*, 1960; Irvine and West, 1979; Wilcox and Shafroth, 2013], prolonged inundation [Gladwin and Roelle, 1998], and multiple abiotic stressors in combination with competition [Sher *et al.*, 2002]. Aboveground portions of young tamarisk tend to be smaller than co-occurring native cottonwood and willow seedlings either because of delayed dispersal and germination, or lower growth rates [Everitt, 1980; Gladwin and Roelle, 1998; Stromberg *et al.*, 2007; Wilcox and Shafroth, 2013], resulting in greater vulnerability at early growth stages. This suggests that floods occurring soon after the cohort germinates, especially within the same year, are most likely to control the spread of tamarisk and favor native species. Field observations of greater vulnerability to flood mortality among seedlings < 40 cm in height [Wilcox and Shafroth, 2013] suggest a threshold effect in seedling losses similar to our present study, and highlight the resiliency of rooted, larger plants to flooding under both flume and field conditions.

Floods released to control vegetation must be large and deep enough to fully submerge and pronate plants (to facilitate burial), and/or powerful enough to erode the substrate within seedling patches through the rooting zone (to facilitate dislodgement). Design of floods that are effective for seedling removal or other riparian restoration objectives requires site-specific information on, for example, stage-discharge relations, the distribution of maximum shear stress relative to seedling establishment elevations, and the balance of available sediment supply and transport rate, all of which are spatially variable. The potential influence of antecedent vegetation conditions on these physical processes highlights the importance of understanding ecogeomorphic feedbacks in planning flow management strategies.

Because of the high local variability and uncertainty of river flood hydraulics, it is unlikely that flooding alone will result in high differential species mortality everywhere within a channel network. In fact, some impacts of flooding may paradoxically increase plant density and resistance to future floods. Many riparian species have strong flood adaptation mechanisms such as flexible stems that reduce drag, self-pruning crowns, and vigorous sprouting ability that may increase the density of plant stems following a partially destructive flood [Lytle and Poff, 2004; Bornette *et al.*, 2008]. Tamarisk species in particular have a number of adaptations such as prodigious seed output, resprouting, and fast growth that make plants difficult to remove [Stevens and Siemion, 2012]. A flood thinning approach may therefore need to be combined with other management strategies, such as spring flow releases timed to promote recruitment of native species

[Stella et al., 2006; Stella et al., 2010; Stevens and Siemion, 2012], and/or other more active forms of restoration (e.g., biotic control [Shafroth et al., 2008]).

5. Conclusions

In our meandering flume study, we used statistical models to predict how plant characteristics and hydrogeomorphic variables affect seedling losses during bankfull floods. Our cottonwood and tamarisk seedlings were highly resilient to floods: only 1% of plants were dislodged and 14% buried, across six experimental runs. We attribute the lower-than-expected levels of plant loss to the inability of the bankfull floods in our experimental system to scour the sandbar to the rooting depth and to overcome the resisting forces achieved by the field-like plant and root conditions in our experiments.

In taking account of vegetation-specific characteristics such as plant size, density, and morphological characteristics, the predictive models we generated are meant to be a first step to guide future laboratory and field experiments aimed at understanding feedbacks between fluvial processes and vegetation, riparian vegetation succession models, and linkages among nested-scale research settings. Large-scale flume studies such as this, with more precise controls on discharge and sediment supply, allow us to measure biotic and physical responses at finer resolutions, from individual plants to point bars, than are often tractable in the field, especially during floods. Meandering channel experiments, particularly if integrated with field and numerical modeling investigations, hold promise for moving beyond unidirectional perspectives on relationships between physical processes and plants, to mechanistic, quantitative understanding of feedbacks. Continued observation and testing of plant/geomorphic interactions are needed to yield insights into the coevolution of channel morphology and vegetation communities, at varying scales from sandbars to river reaches and under different management scenarios.

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