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Can environmental flows moderate riparian invasions? The influence of seedling morphology and density on scour losses in experimental floods

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Abstract

1. Environmental flow releases are an effective tool to meet multiple management objectives, including maintaining river conveyance, restoring naturally functioning riparian plant communities, and controlling invasive species. In this context, predicting plant mortality during floods remains a key area of uncertainty for both river managers and ecologists, particularly with respect to how flood hydraulics and sediment dynamics interact with the plants' own traits to influence their vulnerability to scour and burial.
2. To understand these processes better, we conducted flume experiments to quantify different plant species' vulnerability to flooding across a range of plant sizes, patch densities, and sediment condition (equilibrium transport versus sediment deficit), using sand-bed rivers in the U.S. southwest as our reference system. We ran 10 experimental floods in a 0.6 m wide flume using live seedlings of cottonwood and tamarisk, which have contrasting morphologies.
3. Sediment supply, plant morphology, and patch composition all had significant impacts on plant vulnerability during floods. Floods under sediment deficit conditions, which typically occur downstream of dams, resulted in bed degradation and a 35% greater risk of plant loss compared to equilibrium sediment conditions. Plants in sparse patches dislodged five times more frequently than in dense patches. Tamarisk plants and patches had greater frontal area, larger basal diameter, longer roots, and lower crown position compared to cottonwood across all seedling heights. These traits were associated with a 75% reduction in tamarisk seedlings' vulnerability to scour compared to cottonwood.
4. *Synthesis and applications*. Tamarisk's greater survivability helps to explain its vigorous establishment and persistence on regulated rivers where flood magnitudes have been reduced. Furthermore, its documented influence on hydraulics, sediment deposition, and scour patterns in flumes is amplified at larger scales in strongly altered river channels where it has broadly invaded. Efforts to remove riparian vegetation using flow releases to maintain open floodways and/or control the spread of non-native species will need to consider the target plants' size, density, and species-specific traits, in addition to the balance of sediment transport capacity and supply in the river system.

KEYWORDS

biogeomorphic feedback, invasive species, plant uprooting, riparian seedlings, river point bar

1 | INTRODUCTION

Flooding is a master variable in riparian ecosystems because it drives many biophysical processes, including sediment dynamics, floodplain hydrology, and the establishment, community dynamics, and physical structure of floodplain vegetation (Bendix & Stella, 2013). How floods facilitate recruitment and establishment of disturbance-dependent riparian plants, especially woody pioneer species, has been well documented (Dixon, Turner, & Jin, 2002; Karrenberg, Edwards, & Kollmann, 2002; Rood, Braatne, & Hughes, 2003; Scott, Auble, & Friedman, 1997). Many field and experimental studies have quantified how floods and flow recession interact with plant life history processes, including seed release and dispersal (Merritt & Wohl, 2002; Stella, Battles, Orr, & Mcbride, 2006), seedling germination and growth (Shafroth, Auble, Stromberg, & Patten, 1998), desiccation mortality (Stella & Battles, 2010), and competition. Compared with recruitment and establishment processes, however, less is known about how riparian plants interact with the physical properties of floods—discharge rates, hydraulics, and sediment dynamics—to influence their own mortality and demography within river corridors (Cooper, Merritt, Andersen, & Chimner, 1999; Levine & Stromberg, 2001; Stromberg & Merritt, 2015). In particular, the influence of plants' own morphology on their vulnerability to scour and burial constitutes a critical knowledge gap in our understanding of how riparian communities co-develop with river floodplains (Cooper et al., 1999; Scott, Friedman, & Auble, 1996).

Plant losses to scour or burial can be highly variable within a river corridor (Wilcox & Shafroth, 2013). The balance of sediment transport capacity and sediment supply during floods influences the likelihood of erosion or deposition, and in turn of plant mortality via uprooting or burial, respectively (Friedman & Auble, 1999; Kui, Stella, Lightbody, & Wilcox, 2014). Plant roots provide cohesion that stabilises substrate and increases the resistance of plants to dislodgement, but where local shear stresses are high enough to scour sediment within the rooting zone of plants, plant mortality by uprooting may occur (Bendix, 1999; Bywater-Reyes, Wilcox, Stella, & Lightbody, 2015; Dixon et al., 2002; Edmaier, Burlando, & Perona, 2011). Plants can act as river engineers (Gurnell, 2014), and their traits, including size, density, stem flexibility, and root architecture, influence ecogeomorphic processes (Diehl, Merritt, Wilcox, & Scott, 2017). Flume experiments have studied interactions between herbaceous plants and hydrogeomorphic processes (Braudrick, Dietrich, Leverich, & Sklar, 2009; Crouzy & Perona, 2012; Edmaier et al., 2011; Nepf, 1999; Perona et al., 2012), yet studies that quantify the effects of plant architecture on their risk of loss during floods are rare, especially for woody plants, the dominant species in riparian zones (but see Burylo, Rey, Bochet, & Dutoit, 2012; Griffin, Perignon, Friedman, & Tucker, 2014; Manners et al., 2015).

Flow regulation from dams can profoundly influence riparian vegetation communities by modifying dispersal mechanisms, seedling establishment processes, resource availability, and mortality rates (Friedman, Osterkamp, Scott, & Auble, 1998; Kui, Stella, Shafroth, House, & Wilcox, 2017; Stromberg et al., 2007). Dams alter flow regimes and trap sediment, often inducing sediment deficit conditions during floods, which can enhance channel-bed degradation, bank erosion, and consequently loss of riparian plants to scour (Cooper et al., 1999; Kondolf, 1997; Pasquale, Perona, Francis, & Burlando, 2013). In the southwestern U.S., many riparian woodlands historically dominated by cottonwood (*Populus* spp.) and willow (*Salix* spp.) have been replaced by tamarisk (*Tamarix* spp.), a non-native, invasive shrub; this process has been common along regulated river systems following dam construction (Friedman et al., 2005; Nagler, Glenn, Jarnevich, & Shafroth, 2011). The patterns and processes of invasion vary by location, but include reduced flood magnitude that reduces floodplain disturbance and increases soil salinity, modified flood timing that affects seed dispersal and regeneration, altered fire regimes, and feedbacks between river morphodynamics and vegetation structure and density (Di Tomaso, 1998; Kui et al., 2017; Nagler et al., 2005; Stromberg et al., 2007). Consequently, a wide range of ecosystem functions and services provided by native riparian communities have been altered due to the expansion of tamarisk (Di Tomaso, 1998; Nagler et al., 2011; Stromberg, 1998). To date, restoring disturbance-dependent cottonwoods and willows has focused on designing environmental flow releases to maximise their establishment and early growth (Rood et al., 2003, 2005; Sprenger, Smith, & Taylor, 2001; Stella et al., 2006). However, questions remain as to how tamarisk and cottonwood may differ in their survival following floods and whether flow releases may also be used to favour removal of non-native species (Wilcox & Shafroth, 2013).

In this study, we investigated the effects of flood disturbance on live woody plants in an experimental flume setting, contrasting cottonwood and tamarisk seedlings, which differ in morphology and structural traits. The flume setup simulated conditions in sand-bed rivers in dryland regions where physical processes dominate the early stages of riparian community dynamics (Corenblit, Steiger, Gurnell, Tabacchi, & Roques, 2009). This research expands on the work of Manners et al. (2015) and Diehl, Wilcox, et al. (2017), who analysed within the same experiment the interactions of plants and sediment transport conditions on flow hydraulics, sediment transport, and bed morphology. This present study focuses on the fate of the plants themselves during floods, specifically how differences in root and crown architecture influence seedlings' vulnerability to flood scour. We investigated how these interactions scale across a range of plant densities, from isolated individuals to sparse and dense patches, and between fluvial systems with equilibrium sediment supply (i.e. where sediment supply and transport capacity are balanced) versus those that experience sediment deficit, as in regulated rivers downstream of dams.

2 | METHODS

2.1 | Experimental setup and plant propagation

The experiment took place at the University of California, Berkeley's Richmond Field Station (RFS) in a large, straight flume (28-m long by 0.60 m wide by 0.71 m deep) with a mobile, coarse-sand bed (D_{50} = 0.5 mm, D_{16} = 0.45 mm, and D_{84} = 0.75 mm) that we initially graded to a slope of 0.6% (Figure 1). The test section in the flume trials was 13–25 m downstream from the flume entrance (Figure 1b–d), where the sediment depth varied between 18 and 24 cm. The flume was equipped with a sediment recirculation and measurement system, and an automated cart that measured channel topography and water surface elevations. The flume facility and experimental setup is described further in Manners et al. (2015).

To acquire plants for our experiments, we collected live cottonwood and tamarisk seedlings (including *T. ramosissima* Ledebour, *T. chinensis* Loureiro, and *T. parviflora*) from the Bill Williams River (AZ), Virgin River (NV), and San Joaquin River (CA) basins in March 2013. Plants were greenhouse-healed for 2 months in vermiculite, and then shipped as bare-root plants to the RFS.

At the RFS, plants were transplanted into 30 cm diameter by 30 cm deep pots with sides that were removable during installation in the flume (Kui et al., 2014). The substrate of the planting medium was the same as that in the flume bed. We propagated plants in one of three configurations: *individual* (one plant per pot), *sparse* (two plants per pot), and *dense* (10 plants per pot), with the sparse group stratified between short (<40 cm) and tall (≥40 cm) plants. All plants were kept in full sun and watered every 2–3 days for 2 months.

2.2 | Plant morphological traits

We used a random subsample of 90 plants (47 cottonwood and 43 tamarisk) to quantify differences in morphological traits between species. At the end of the transplant and growth period, plants were carefully removed from their pots and rinsed of sand. We measured above-ground height, root length, basal stem diameter just above the root crown juncture, and plant dry biomass, with shoots and roots weighed separately. Bending force was measured by attaching a spring scale to the mid-point of the stem and recording the force (in N) required to pull the stem horizontally to an angle of 45°; higher values indicate a more rigid stem. We used a standard photographic method (sensu Kui et al., 2014) to measure the plant frontal area, which is the projected area perpendicular to the flow direction, for both roots and shoots. Aboveground frontal area is proportional to drag forces induced during floods (Manners et al., 2015; Rominger, Lightbody, & Nepf, 2010), whereas the below-ground frontal area correlates with plant roots' ability to stabilise substrate and counteract erosion during floods (Bywater-Reyes et al., 2015; Khuder, Stokes, Danjon, Gouskou, & Lagane, 2007). We further characterised the frontal area density (FAD) along the vertical dimension by calculating the frontal area per 1-cm stratum of the plant height (Kui et al., 2014; Lightbody & Nepf, 2006).

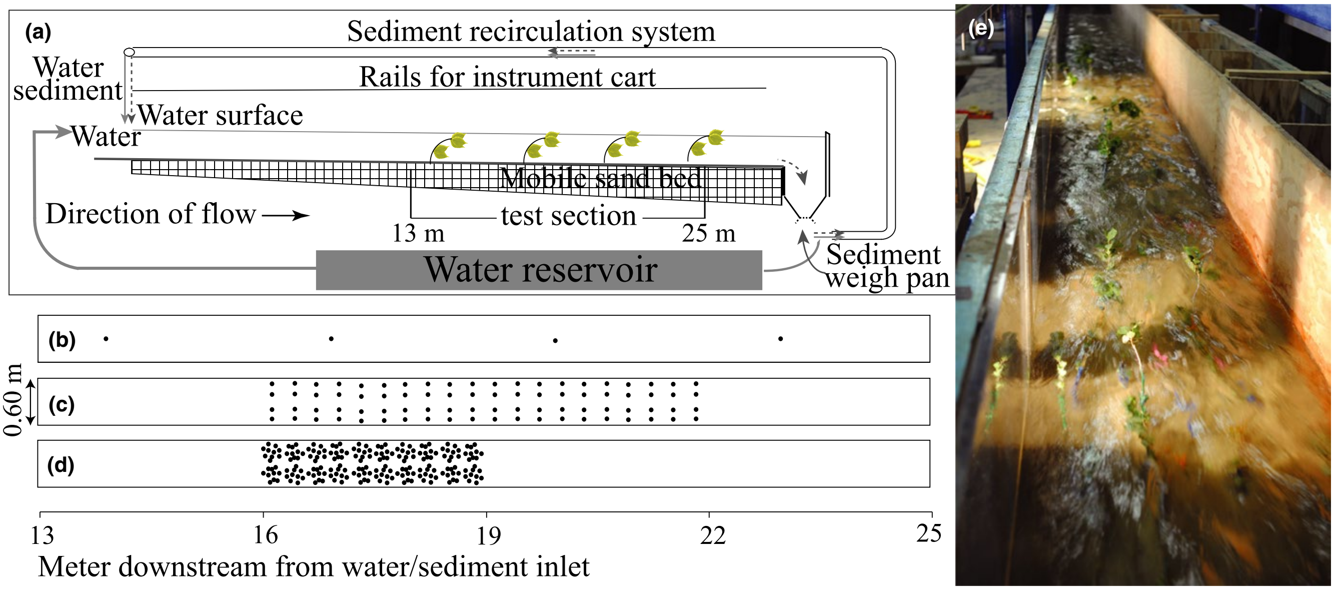

FIGURE 1 Flume setup at the Richmond Field Station. (a) Side view showing the mobile, coarse-sand bed initially graded to a 0.6% slope. (b–d) Plan view of plant configurations in the 12-m-long test section, where black dots represent individual plants. These plant configurations include (b) individual plants (runs 1–5); (c) sparse seedling patches (runs 6–9); and (d) a dense patch of cottonwood plants (run 10). (e) Photo of the flume during an experimental flood with sparse cottonwood seedlings. Adapted from Manners et al. (2015) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Configurations of plant treatment groups (species, height class and density) used in the 10 experimental trials. All trials proceeded consistently, with a recirculated sediment equilibrium phase (c. 4 hr) followed by a sediment deficit phase (2 hr). The number of dislodged plants includes those lost during both phases, though all but four plants (99% of all plants) were dislodged during the sediment deficit phase

Run	Species	Density (No. plants/m^2)	Plant height range (cm)	Diameter (mm)	Number of plants tested	Number of dislodged plants (%)[a]	Sediment flux (kg/s)[b] Equilibrium[c]	Sediment flux (kg/s)[b] Deficit[d]	Equilibrium phase final bed slope[e]
1	Both	Individual (0.6)	15–45	2.24–10.2	4	3 (75)	0.25–0.43	NA	0.004
2	Both	Individual (0.6)	17.5–91	4.5–10.8	4	3 (75)	0.17–0.32	NA	0.004
3	Both	Individual (0.6)	21–70	4.8–10.15	4	1 (25)	0.14–0.29	0.14 ± 0.07	0.004
4	Both	Individual (0.6)	21–71	2.2–10.9	5	4 (80)	0.15–0.30	0.14 ± 0.06	0.004
5	Both	Individual (0.6)	33–63	3.7–12.9	5	3 (60)	0.28–0.66	0.13 ± 0.07	0.004
6	Cottonwood	Sparse (18)	8–37 (*short*)	1–7.17	66	44 (67)	0.19–0.42	0.15 ± 0.20	0.006
7	Cottonwood	Sparse (22)	37–71 (*tall*)	3.2–11.95	80	30 (38)	0.12–0.25	0.12 ± 0.07	0.008
8	Tamarisk	Sparse (21)	7–44 (*short*)	1.76–12.8	76	36 (47)	0.12–0.28	0.11 ± 0.06	0.012
9	Tamarisk	Sparse (20)	9–93 (*tall*)	2.3–15.6	71	1 (<1)	0.05–0.16	0.02 ± 0.02	0.017
10	Cottonwood	Dense (93)	2.3–46	1.10–7.12	169	51 (30)	0.16–0.29	0.11 ± 0.06	0.015

[a] Percent of plants dislodged of the total plants present at the start of each run. [b] As measured at flume exit, where sediment was collected in a drum suspended from a load cell. For equilibrium runs, sediment was recirculated and fed to the upstream end of the flume. Deficit runs had zero sediment feed. Sediment flux data were not collected during deficit phase of runs 1 and 2. [c] Range of values measured between discharge of 0.17–0.36 m^3/s (Manners et al., 2015). [d] Average and one standard deviation of values measured during deficit phase. [e] Initial equilibrium phase bed slope was 0.06.

2.3 | Flood experiment design

We conducted 10 flume runs that differed with respect to species, plant size, and density (Table 1). Individual plants were tested in five of the trials, in which 4–5 plants were installed *c.* 3 m apart within a 12-m long test section (Figure 1b). Equal numbers of tamarisk and cottonwood were used, with planting locations randomly assigned. Four other trials tested a single sparse patch (21 plants/m^2) in different configurations of species and plant height (Table 1, Figure 1c), and a final trial tested a dense patch (93 plants/m^2) of cottonwood (Figure 1d), which reflected the upper density range reported in field studies (Scott, Shafroth, & Auble, 1999; Taylor, Wester, & Smith, 1999). We were not able to test a dense tamarisk patch due to a lower number of available plants. A total of 484 plants were used across all the flume trials, comprising 326 cottonwood and 158 tamarisk.

In all runs, plants were installed alive with intact root systems. This was achieved by burying the pots within the flume's substrate, detaching and removing the pot sides, and filling interstices with sand up to the flume's bed surface (Edmaier, Crouzy, & Perona, 2015; Kui et al., 2014; Manners et al., 2015). Plants were colour-coded using spray paint combinations and their planting locations noted to allow tracking their movement during and after the flume trials. During all runs, we recorded the time that each plant became entrained, and recovered it in a downstream net for follow-up measurements of stem height, root length, and dry weights of both above- and below-ground portions.

Each flooding trial consisted of two phases: sediment equilibrium was conducted first and lasted for *c.* 245 min, immediately followed by a sediment deficit phase that lasted for another 120 min (Figure 2). During the sediment equilibrium phase, we recirculated all the sand transported to the downstream end of the flume back to the flume entrance. Discharge was increased in step-wise fashion from 0.06 to 0.36 m^3/s to represent the rising limb of a flood (Figure 2).

During the sediment deficit phase, the recirculation system was stopped and all sediment transported past the downstream end of the flume was exported from the system. This phase simulated situations such as dam releases in which a river's transport capacity exceeds its sediment supply, which can produce downstream geomorphic effects such as bed degradation (Kondolf, 1997; Schmidt & Wilcock, 2008). We maintained a constant discharge of 0.19 m^3/s. The ranges of sediment flux during both phases of each run are shown in Table 1. As sediment was evacuated from the flume, the bed degraded, reducing the bed slope and changing the hydraulic and sediment transport conditions (Manners et al., 2015). The rate at which the bed slope changed during a run depended on the plant configuration (Diehl, Wilcox, et al., 2017).

2.4 | Data analyses

From the random subset of plants used to compare species morphological differences, we computed summary statistics for 10 metrics of shoot and root lengths, dry weights, stem bending force, and the distributions of frontal area (Table 2). We also standardised these measurements to their mean and standard deviations (i.e. *z*-scores) in order to compare relative differences among metrics. Because many of these parameters were collinear, we incorporated all of them within a multivariate linear discriminant analysis (LDA) to determine the traits that captured the strongest morphological differences between the species. This analysis used the *lda* function in R package *MASS* (Brenes-Arguedas, Roddy, & Kursar, 2013; R Core Team, 2018). Relationships between the linear discriminant scores and the individual traits were evaluated using Pearson correlations and single-factor regression.

To understand the effects of flooding on plant mortality for all experimental runs, we first computed and plotted Kaplan–Meier survival estimates of time of dislodgement (Machin, Cheung, & Parmar, 2006). The Kaplan–Meier survival analysis is a non-parametric method used to estimate the survival function for a population from empirical time-to-event data (e.g. death or dislodgement in this case). We tested differences in survival between groups using the Mantel–Haenszel log-rank test, which assumes that the hazard functions between the treatment groups are proportional (Machin et al., 2006). Second, we used generalised linear logistic models to predict the probability of an individual plant's dislodgement based on experimental factors and seedling morphological trait covariates. We constructed a candidate set of 27 alternative models, using combinations of species, density, shoot height and root length as measured on all plants retrieved and excavated following the flume runs. The strong relationships of stem height with frontal area density, diameter, bending force, and shoot dry mass all indicated that plant height was an appropriate representation of above-ground size (Supporting Information Appendix S1). As a plant size covariate, root length was included in the model but no model had both stem height and root length because they were substantially correlated ($R = 0.55$). Models were ranked based on lowest Akaike information criteria and highest Akaike weights (Burnham & Anderson, 2002).

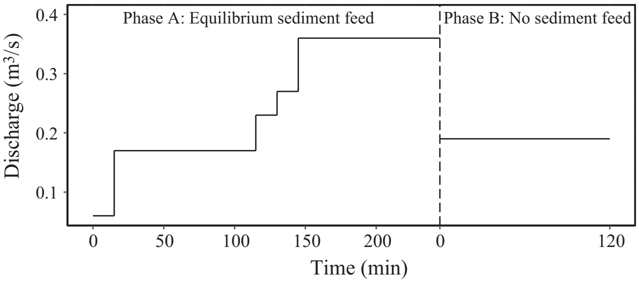

FIGURE 2 Flume hydrograph for Runs 1–10. Each run consisted of two phases with different relative sediment supply conditions. (1) Sediment equilibrium (Phase A), in which sediment supply was dynamically matched to transport capacity across five successive stages of increasing discharge. See Table 1 for ranges of sediment flux for each run. (2) Sediment deficit conditions (Phase B), in which sediment transport capacity exceeded sediment supply and discharge was constant. Almost all plant loss (99% of plants dislodged) occurred during the sediment deficit phase

To evaluate the relationship between plant dislodgement and local patterns of bed scour (Bywater-Reyes et al., 2015), we calculated each plant's *scour ratio*, which was the maximum scour depth at the plant's location derived from pre- and post-flood laser scans of the bed (Diehl, Wilcox, et al., 2017) divided by its root length. We used ANOVA tests to compare the scour ratio between species and between groups of plants that dislodged versus those that remained rooted in place. The scour ratio was log-transformed in this analysis to satisfy residual model assumptions.

All data presented in this study were archived and available on DataONE (https://www.dataone.org/) at: https://doi.org/10.6073/pasta/8981bd3ad378f6ecd55122b30fd7ec73 (Kui et al., 2018).

3 | RESULTS

3.1 | Plant structure

Average plant height was 45 cm (±20 cm *SD*) for cottonwood and 39 cm (±23 cm *SD*) for tamarisk within the representative sample used to measure multiple trait values, with no significant difference between the species ($t = 1.3185$; $df = 82.384$; $p > .05$). Despite statistical equivalency in height, the two taxa showed substantial difference in other morphological traits, which was evident for both raw measurements (Table 2) and standardised *z*-score values (Figure 3). This was particularly the case for the location of densest crown (FAD) on the plant, which best distinguished the two species (Figure 3b) and was most strongly correlated with the multivariate linear discriminant ($R = -0.91$; Table 2; Figure 3c). Cottonwood plants had the densest area of crown at 75% of their shoot height, whereas tamarisk's crown was densest at 28% of shoot height, indicating a shrubbier, squat profile (Figure 3b). Other traits that distinguished the two species were maximum FAD ($R = 0.59$; Figure 3d), basal diameter ($R = 0.55$; Figure 3e), shoot weight, root weight, and maximum root density, all of which were correlated with the LDA values and were higher for tamarisk of equivalent height (Table 2). These traits collectively described a strong morphological contrast between the tamarisk seedlings, which had multiple stems sprouting from the base and consequently a denser and lower crown, and cottonwood, which was typically single-stemmed with a distinct, high crown. In terms of the below-ground portion, tamarisk had a greater maximum root frontal area density, suggesting a greater degree of surface contact between soil and roots. However, the average maximum root lengths for the samples tested were not different between species (Table 2).

3.2 | Patterns of plant dislodgement

Under equilibrium sediment conditions, plant dislodgement rarely occurred; only 1% of plants (four individuals) dislodged, all of which were short cottonwood seedlings in the sparse configuration (run 6). Most of those dislodged plants had roots <10 cm long and stem heights <35 cm. Dislodgement was more prevalent, in contrast, during the sediment deficit phase, when 36% of all plants dislodged. In

TABLE 2 Comparison of plant morphological trait values between cottonwood and tamarisk ($N = 90$). Variable codes match those shown in Figure3

Response variable	Variable code	Cottonwood (mean ± 1 *SD*)	Tamarisk (mean ± 1 *SD*)	LDA coefficient	LDA correlation[c]
Above-ground variables					
Shoot height (cm)	H_{Shoot}	45 ± 20	39 ± 23	−0.017	−0.17
Basal diameter (mm)	D_{Shoot}	5.2 ± 2.6	8.3 ± 3.5	0.132	**0.55**
Shoot weight (g)	W_{Shoot}	3.7 ± 4.0	9.3 ± 12.4	−0.022	**0.36**
Bending force (N)	BF	0.71 ± 0.74	0.76 ± 1.25	0.003	0.03
Max shoot FAD[a] (cm^2/cm)	$MFAD_{Shoot}$	6.7 ± 4.2	13.6 ± 8.1	0.150	**0.59**
Relative location of max shoot FAD[b] (%)	$LMFAD_{Shoot}$	75 ± 24	28 ± 17	−3.482	**−0.91**
Below-ground variables					
Root length (cm)	L_{Root}	35 ± 10	38 ± 12	−0.015	0.17
Root weight (g)	W_{Root}	2.2 ± 2.5	4.6 ± 7.3	0.043	**0.27**
Max root FAD[a] (cm^2/cm)	$MFAD_{Root}$	15 ± 8	18 ± 10	−0.065	**0.21**
Relative location of max root FAD[b] (%)	$LMFAD_{Root}$	57 ± 25	58 ± 20	0.567	−0.04

[a] The maximum frontal area density (FAD) for both roots and shoots indicates the largest cross-sectional area per 1-cm stratum on the plant. [b] The location of the maximum frontal area as a percentage of the shoot height or root depth from the ground surface. [c] Pearson correlations between the linear discriminant analysis (LDA) axis score and the raw plant trait values. Bold text denotes significant correlations ($p < .05$) using *t*-tests.

the trials with individual plants (runs 1–5), 64% of plants (14 of 22 total individuals) dislodged, with equal numbers of each species. In the patch configurations, 35% of plants (162 of 462 total) dislodged.

Tamarisk seedlings were dislodged less frequently than cottonwoods of comparable height, and for both species, taller plants were less vulnerable (Figure 4). Among the runs with sparse, short plants, 67% of cottonwood plants were dislodged compared to 47% of tamarisk plants. For the runs with sparse, larger plants, 38% of cottonwood plants were dislodged versus <1% of the tamarisk plants (Table 1). Increased patch density also reduced the likelihood of dislodgement. In the dense cottonwood patch, 30% of plants dislodged, indicating a reduced vulnerability to floods compared to plants of comparable size in either the individual or sparse patch configurations, which experienced scour losses of 64% (Table 1). The Mantel–Haenszel log-rank test indicated that these differences were significant between groups ($\chi^2 = 88.2$; $df = 6$; $p < .001$).

The best logistic model predicting dislodgement included species, density, root length, and the interaction between species and density (Table 3; Figure 5). This model had the highest Akaike weight (0.44), indicating almost half the weight of evidence among the set of candidate models. The top four models, comprising 99% of the cumulative weight of evidence, all contained the variables species, density and root length, indicating overwhelming support for these three factors (Table 3). Root length was a much better predictor of dislodgement than stem height, which was not in any of the top models. The odds ratio of the root length effect indicated that for every additional centimetre of root length, the risk of dislodgement decreased by 5%. Increasing patch density also conferred greater protection, and this effect was stronger for tamarisk than for cottonwood (Table 3, Figure 5). Thus, tamarisk plants were at a lower risk of dislodgement than cottonwood and the risk attenuated at a greater rate with increases in density.

Plant dislodgement was more likely to occur after erosion of sediment at the base of the plant, particularly for the dense patch where a large number of plants dislodged after 100 min (Figure 4). We observed that the majority of plants that dislodged experienced scour down to ≥20% of their rooting zone's depth (Figure 6). For both species, plants that dislodged experienced greater scour than those that remained in place throughout the flume trial (ANOVA $F_{1,359} = 31.2$, $p < .001$). The ratio of rooting zone scoured (both for dislodged and intact plants) was greater for cottonwood, which tended to have shorter roots overall (ANOVA $F_{1,359} = 64.7$, $p < .001$).

4 | DISCUSSION

This study demonstrates that dislodgement of young woody plants during floods is influenced by both physical factors and the plants' own attributes, including their density and structural traits (Diehl, Merritt, et al., 2017). As a first control on plant losses, floods under sediment deficit conditions were much more effective at dislodging seedlings than under equilibrium sediment transport. This reinforces the *hungry water* model of Kondolf (1997) and extends its concepts to effects on biota. Secondly, denser plant configurations conferred a degree of protection—*safety in numbers*—across similar ranges of seedling sizes (Hamilton, 1971). Lastly, the plants' own

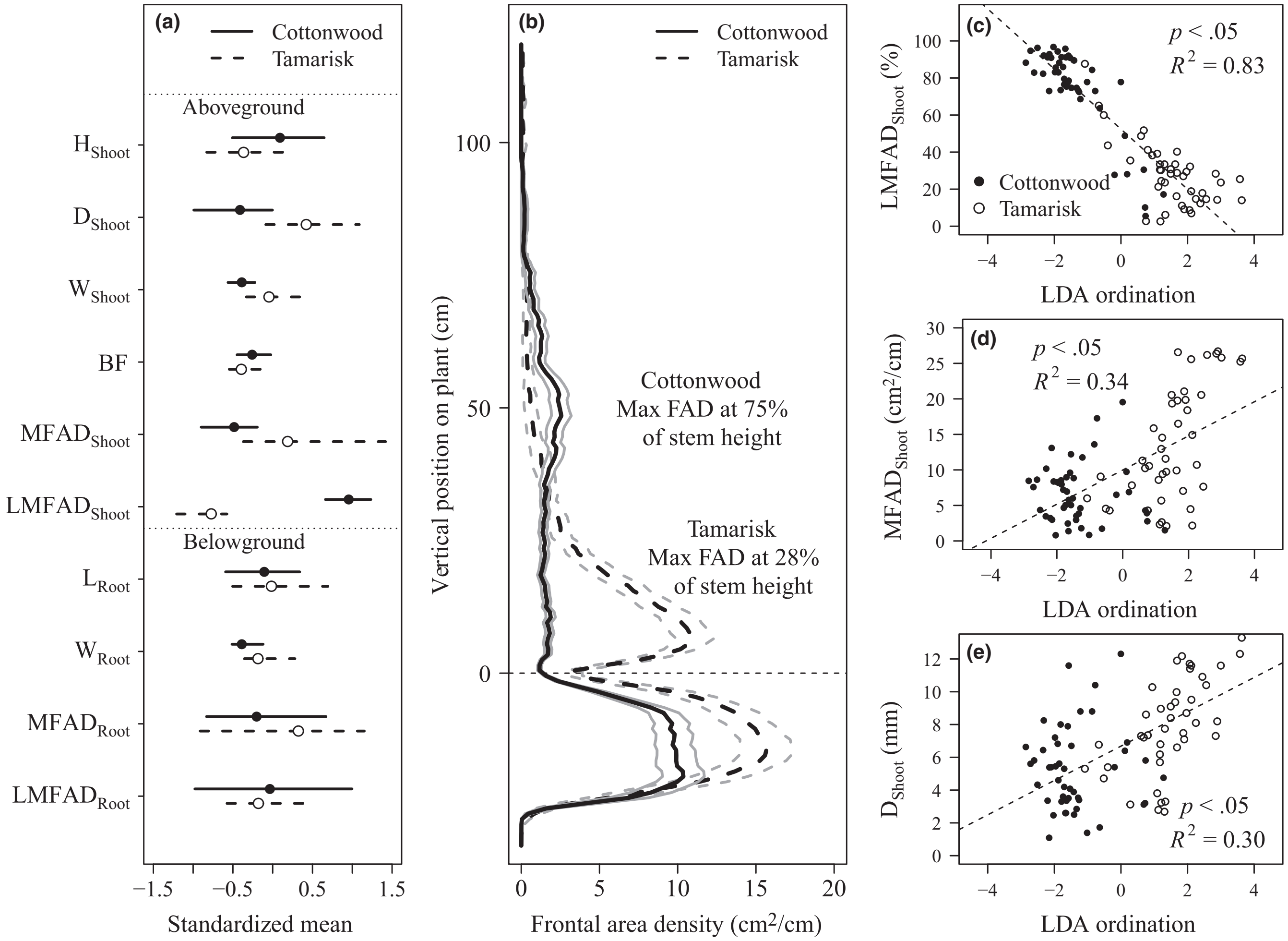

FIGURE 3 Species-level differences in plant morphology. (a) Median and interquartile range for standardised plant trait values (mean = 0, *SD* = 1) between cottonwood (solid symbols) and tamarisk (open symbols). (b) Comparison of frontal area density (FAD) distribution with species means (black lines) and 1*SE* (grey lines) indicated. The dashed horizontal line represents the soil surface. Panels (c–e) show relationships between linear discriminant analysis (LDA) values and the most strongly correlated traits (*R* > 0.5, Table 2) that describe differences between the two species, including (c) location of the maximum FAD (d) maximum shoot FAD, and (e) stem diameter. See Table 2 for explanations of abbreviations

traits, particularly root characteristics, were important in controlling the probability of dislodgement. Bed erosion deeper than 20% of the rooting depth resulted in a high probability of dislodgement. Tamarisk, which was significantly more resistant to scour loss, had longer roots and twice the root biomass as cottonwood.

4.1 | Species differences affecting the probabilities of plant dislodgement

Riparian woody species' architecture—primarily their shoot and root frontal area distribution—influences the probability of plant uprooting during floods. Partially or fully submerged plants are subject to a balance between the flow's drag force, which can scour sediment and uproot the plants, and the plants' resisting force, which depends on above- and below-ground traits (Bywater-Reyes et al., 2015). This force balance determines whether a plant will be dislodged or not (Edmaier et al., 2011; Pollen-Bankhead et al., 2011), and scour of sediments around the plant's stem can substantially lower resisting forces and predispose plants to dislodgement (Bywater-Reyes et al., 2015). Our results are consistent with Type II uprooting mechanisms of Edmaier et al. (2011), in which dislodgment occurs as from a combination of stem drag and erosion around roots. In a recent study, Perona and Crouzy (2018) formulated a physically based stochastic model to predict plant uprooting in floods. The empirical data in our present study, particularly the detailed plant morphological measurements and controlled flood conditions, may be suitable to test and validate that model in a follow-up study.

Compared with cottonwood seedlings of equivalent height, tamarisk has greater flood resistance, which could be due to higher root mass for better stabilising the soil substrate, and lower crown for reducing flow drag (Bywater-Reyes et al., 2015; Rhee, Woo, Kwon, & Ahn, 2008; Thompson, Wilson, & Hansen, 2004). All these plant traits were beneficial for improving tamarisk's ability to survive floods. The results of our study support Bywater-Reyes et al. (2015),

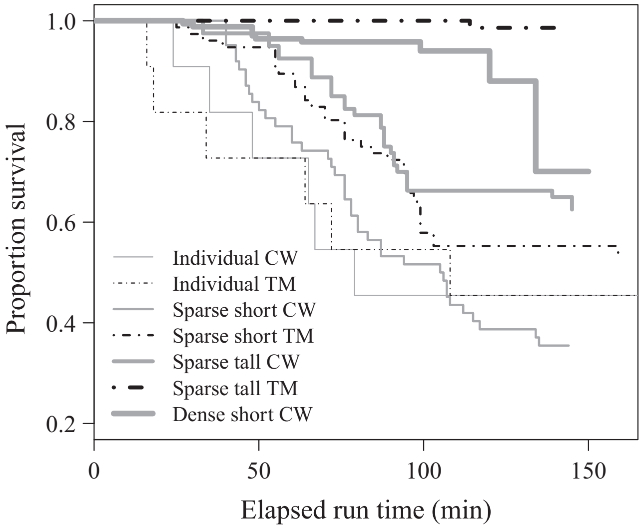

FIGURE 4 Kaplan–Meier survival curves for cottonwood (CW) and tamarisk (TM) for different density and size groups. Time zero represents the beginning of the sediment deficit phase

who found that pull-out force for in-situ tamarisk seedlings was greater than for conspecific cottonwoods, although their strengths varied with plant size and the accessibility to groundwater.

Our work demonstrates that root length is an important indicator of plant loss susceptibility. In natural settings, root growth varies by species and is also influenced by base flow conditions and accessibility to groundwater. For example, plants that establish in ephemeral streams have root networks that often extend to deeper depths than plants of similar age and size that establish in perennially wet areas with shallow groundwater (Stromberg & Merritt, 2015). Deep-rooted plants in ephemeral streams may therefore be adapted not only to survive drought conditions, but also to resist dislodgement via scour. Vertical root distribution, not measured in this study due to propagation limitations, may also be an important indicator of dislodgement vulnerability. Drought-adapted plants, and other plants growing in settings with shallow groundwater (e.g. river banks, sandbars, or secondary channels), may develop vigorous lateral root systems near the soil surface, resulting in a shallow rooting depth for most fine roots (Bywater-Reyes et al., 2015; Singer et al., 2012). In this case, dislodgement may occur when scour depth exceeds the dominant depth of the fine root network, rather than the maximum root length.

4.2 | Plant size and patch density

Our results also show that plants' flood resistance increases proportionally with their size. As young plants establish and grow, many attributes such as diameter, stem stiffness, mass and area of roots and crown increase proportionally with height (Supporting Information Appendix S1). All of these collinear traits increase plants' ability to stabilise the substrate and reduce water velocities and scour forces. Our experiments showcased this ability of plants to engineer their local environment (Diehl, Merritt, et al., 2017; Diehl, Wilcox, et al.,

TABLE 3 Model selection criteria used in ranking generalised linear logistic models predicting the probability of dislodgement for all plants. There were 27 candidate models compared, including a null (intercept-only) model and models containing main effects and/or two-way interactions between the experimental variables (species and density) and individual size covariates (root length and stem height). Candidate models did not include both stem height and root length as they were substantially correlated. Stem height coefficients are not shown in the table because none of the top models included height as a variable

Plant dislodgement model rankings						Coefficients for effects on plant dislodgement[a]					
Rank	*df*[b]	AIC	ΔAIC	Akaike weight	Cum weight	Species	Density[c]	Root length	Species: density[d]	Species: root length	Density: root length
1	5	579.1	0	0.44	0.44	1.091	−0.016	−0.053	−0.104		
2	6	579.9	0.9	0.28	0.72	2.011	−0.015	−0.046	−0.117	−0.021	
3	6	580.1	1.1	0.26	0.98	1.292	−0.024	−0.064	−0.114		0.0003
4	4	586.7	7.6	0.01	0.99	−0.952	−0.016	−0.048			
5	5	588.7	9.6	0.00	0.99	−0.824	−0.016	−0.047		−0.004	
27	1	637.6	58.5	0.00	1.00						

[a] Regression coefficients for the logistic models represent the log odds effect of each variable. [b] The term df indicates the number of parameters for each model, including the intercept. [c] Negative values for the density coefficient indicate that plants in the patch are less likely to be uprooted than ones in the individual runs. [d] Negative values for the species:density interaction indicate that tamarisk plants are less vulnerable than cottonwoods, and this difference is amplified at higher densities.AIC, Akaike information criteria

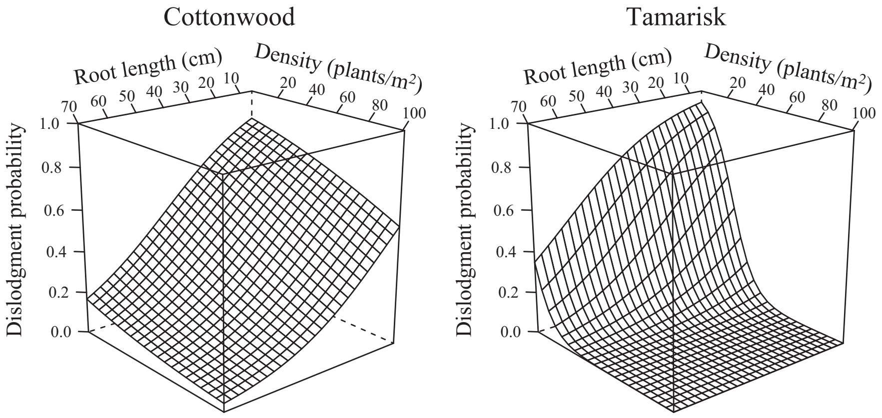

FIGURE 5 Response surface from the best generalised linear model predicting dislodgement as a function of plant density, root length, and species (Table 3). Longer roots confer greater resistance against dislodgement. The species × density interaction indicates that tamarisk plants are at a lower risk of dislodgement than cottonwood, and the risk attenuates at a greater rate with increases in density

2017), thereby controlling the rate of scour and eventual plant dislodgement. Given that only 1% of tamarisk that occurred in tall patches were lost, the lowest rate of any of the configurations, we would expect that bankfull and other moderate floods would not be likely to dislodge tamarisk seedlings larger than 40 cm in height (*tall* tamarisk in our experiment), particularly those occurring in high densities along river margins. When flood forces are sufficient in magnitude and duration to scour the substrate beyond a threshold depth, however, all or most plants in the patch will probably be entrained.

Plants' flood resistance also increases when in close proximity to neighbours (*safety in numbers*; Hamilton, 1971). With greater plant density, the increased shoot and root mass per unit area induces strong drag forces within the plant patch and increases substrate stability, in part due to the intertwining of fine roots between adjacent plants (Manners et al., 2015). The capacity of vegetation to stabilise substrates over decadal timeframes has also been inferred in many field settings. For example, a retrospective analysis of the Bill Williams River (AZ) corridor showed that dense vegetation patches had a stronger effect on stabilising islands and abandoned channels compared to sparse patches (Kui et al., 2017).

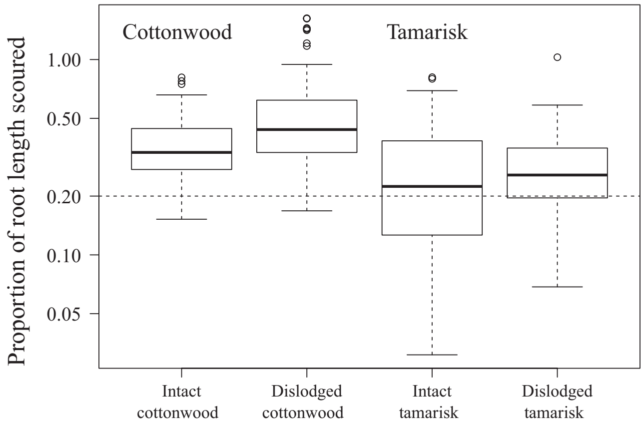

FIGURE 6 Ratio of maximum local scour to root length for intact and dislodged plants. Plants tended to dislodge after the depth of scour exceeded approximately 20% of the rooting zone profile. Cottonwood experienced greater scour than tamarisk overall

4.3 | Applications to riparian management

Using managed flood releases as the primary mechanism to remove invasive species may be impractical from a management perspective, at least under field conditions analogous to those in our experimental setting. Where cottonwood and tamarisk seedlings of equivalent size co-occur in similar densities, flooding may be likely to result in higher mortality of cottonwood than tamarisk. However, flood releases could be effective in specific cases, for example, when cottonwoods establish early in the year coincident with its earlier spring dispersal period (e.g. late March) and tamarisk germinate later in the summer (Stromberg et al., 2007). As cottonwood seedlings grow taller and develop longer roots and increased flood resistance, a controlled flow release may in theory reduce densities of shorter tamarisk plants (Wilcox & Shafroth, 2013). Therefore, under particular conditions, environmental flows may be effective in containing the spread of tamarisk (Shafroth et al., 2005). This window of opportunity would most probably be brief and imprecise, however, because tamarisk increases its flood resistance rapidly as it ages and grows, and hydraulic conditions and scour intensities vary greatly within river corridors. More generally, our work illustrates that the susceptibility of riparian plants to dislodgement during floods depends on not only the magnitude of a flood event, but also on the organisation and traits of the plants themselves and on the sediment balance, where a deficit of supply relative to transport capacity increases the likelihood of plant loss during floods.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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